Mandibular biomechanics as a key factor to understand diet in mammals

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Introduction

The mammalian mandible plays a fundamental role in food processing, as it transmits the forces generated by masticatory muscles to the food through the teeth (Maynard-Smith & Savage 1959). Generally speaking, the greater the forces required to fracture ingesta, and the more often such forces are needed, the stronger the mandible has to be to maintain its structural integrity (Hogue 2008). In that line, it has been suggested that among primates, those that include hard-food in their diets have stiffer mandibles when compared to soft-food eaters (Marcé-Nogué et al. 2017b). However, other attempts to establish relationships between mandibular morphology and dietary categories have not been particularly successful (Ross et al. 2012).

If the latter is true and biomechanics cannot be used to establish relationships between morphology and function, it has been argued that it is probably because these biomechanical analyses are flawed or incomplete, or that non-mechanical factors such as phylogeny are more important determinants of morphology (Ross & Iriarte-Diaz 2014). Nevertheless, there is a general consensus that trying to understand the interaction between the mammalian feeding mechanism and the processed ingesta represents a unique opportunity for the study of ecomorphological adaptations in extant species, as well as having the potential to acquire valuable tools for the reconstruction of oral behaviors in extinct taxa. Hence the importance of this particular topic.

The association between dietary preferences and biomechanical performance has traditionally been studied as the relationship between dental and mandibular morphology (Fig. 4.1). For example, carnivorous mammals have carnassials that act as blades allowing enlarged and often self-sharpening edges to pass by each other in a shearing manner. Herbivorous ungulates have developed reduced canine teeth and specialized molars to grind fibrous food by lateral movements. Among other examples, primates have teeth that exhibit an elaborated cusp pattern of the molars that crush the food (Kardong 2014). The way teeth work (e.g. blading, grinding, or crushing) is adapted to the diet as well as the morphology of the mandibles, thus enabling the generation of different models of distribution and position of the muscular forces and bite positions based on different geometries (Vizcaíno et al. 2016). The influence of muscular forces on the design of the shape of the mandible (e.g., Sella-Tunis et al. 2018 in humans), as well as the influence of the position of the condyle allowing different mandible movements (Maynard-Smith & Savage 1959) are evidence that reinforces the idea that food is processed differently depending on mandibular morphology.

For these reasons, feeding biomechanics represents the set of analyses performed to “[...] relate variation in feeding system morphology (size and shape of muscles, bones, teeth, tongues or joints) to variation in how animals feed (feeding behavior) and what they feed on (diet).” (Ross & Iriarte-Diaz 2014: 105). This relationship between muscular and bite forces, mandibular size and shape, and the consumed ingesta have previously been studied in the mandibles of different mammalian clades such as terrestrial Cetartiodactyla (Christiansen & Wroe 2007, Hogue & Ravosa 2001, Spencer 1995, Varela & Fariña 2015), Chirottera (Freeman 1979, 1981, 1984, 1988, 2000), Primates (Bouvier 1986a,b, Taylor 2006) and Carnivora (Biknevicius & Ruff 1992, Radinsky 1981a,b). These works used classical biomechanics based on the laws of static mechanics and beam theory, hence not requiring the application of computer simulation techniques to model complex biological geometries, thus avoiding a high computational cost.

The eruption of computational methods opened a whole array of new possibilities to investigate feeding biomechanics. Specifically, computational biomechanics represents the application of engineering computational tools, such as the finite element analysis (FEA) (Zienkiewicz & Taylor 1981) to study the mechanics of biological systems. Computational models and simulations are particularly useful to predict the relationship between parameters that are otherwise challenging to test using experimental approaches and are also quite helpful when designing more relevant experiments, hence reducing the time and costs of such tests. The underlying premise of the method is that a complex geometry can be subdivided into a mesh consisting of a number of finite elements in which the respective mechanical equations are approximately solved. Although FEA (see Rayfield 2007 for a review) or multibody dynamic analysis (see Curtis 2011 for a review of MDA) have been common approaches in engineering and biomedicine for more than thirty years, they have also been applied to biological research in order to address questions related to biomechanics and the evolution of living and extinct vertebrates (using both 2D or high-resolution 3D models). Vertebrate paleontologists have also applied complementary non-invasive techniques, such as computed tomography (CT), which is a useful tool to generate accurate 3D images of living structures in a reverse engineering process, thus facilitating the application of computational biomechanics. The reliability and bio-fidelity of the biomechanical models has increasingly improved by capturing the real geometries of the specimens under analysis. Previous approaches...
relied on simplified lever or beam models, which although still useful, possess many known limitations that can be overcome by modern computational biomechanics.

To date, FEA has been conducted in a wide spectrum of vertebrates providing new insights into biomechanical function, particularly regarding the constraints and adaptive values of certain morphologies and bone structures. These bony structures are generally considered to be a force transmission system that can be studied by means of mechanics laws. For instance, the biomechanics of the mandible in different mammalian families has been studied using FEA to obtain the state of stresses during mastication in 3D models (Gill et al. 2014, Gröning et al. 2011b, Lautenschlager et al. 2018, Püschel et al. 2018, Tseng & Binder 2010, Zhou et al. 2019), as well as using simplified planar models (Fletcher et al. 2010, Marcé-Nogué et al. 2017b, Neenan et al. 2014, Piras et al. 2013, Serrano-Fochs et al. 2015). Other studies have approached this problem including the study of both the skull and the mandible (Dumont et al. 2011, Strait et al. 2013, Tseng 2013, Veitschegger et al. 2018). Nonetheless, it is important to keep in mind that if a study aims to detect dietary preferences, it would be preferred to analyze mandibles as part of the antagonistic system, since the lower jaw may be more susceptible to failure than the cranium (Wroe et al. 2010), and also because cranium morphology is influenced by several other non-feeding variables (Tseng & Flynn 2018). In fact, it has been noted that cranial shape reflects a compromise between several diverse functions (e.g., phonation, cognition, respiration), which could mask a strong dietary signal (Püschel et al. 2018). By contrast, the mandible is primarily involved in food acquisition and consumption, and consequently it is to be expected that its morphology better reflects ingesta-related adaptations (Gröning et al. 2011b).

It is logical to wonder how paleontologists and paleoanthropologists have applied these biomechanical tools in fossil taxa, taking into account that many variables are unknown and impossible to obtain from skeletal morphology alone. The answer is relatively simple. If it is possible to study extant species that are phylogenetically related and/or share the same or similar diet to the fossil taxa of interest, and if it is possible to find correlations, associations or differences to their dietary preferences or their ingesta characteristics, then it would be possible to study the biomechanics of the fossil taxa and find the appropriate relationships with the biomechanical data. Nonetheless, there are two important questions that need to be addressed before carrying out analyses on fossil specimens. These questions are related to the intrinsic nature of biological data and make the study of biological structures completely different to the more common mechanical problems solved by engineers in other fields. The first one is variation, which focuses on how different models are properly compared when considering both intra and inter species variability. This means that it is necessary to create an appropriate comparative

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**Fig. 4.1.** Morphology and bite forces in mammalian crania and mandibles. **A,** cranium and mandible; **B,** details showing different tooth morphologies; **C,** free-body diagram of the biomechanical problem of the mandible during chewing; **D,** von Mises stress results after a finite element analysis of three different taxa: Canis lupus (carnivore), Macaca fascicularis (primate) and Connochaetes taurinus (ungulate). Not to scale.
A framework where a large number of different models and data can be analyzed and compared. The second one is how to post-process the extremely large amount of data derived from FEA results or classical biomechanics in a quantitative way that allows the obtained data to be used and combined with statistics, geometric morphometrics, phylogenetic models or even machine-learning algorithms to try to find affinities between the feeding behavior and the diet of the taxa.

Consequently, the aim of this chapter is to discuss classical and computational biomechanics of the mandible in the study of dietary adaptations in mammals. Firstly, a brief theoretical background in mechanics will be provided to facilitate understanding of the concepts used in this chapter. Afterwards, these concepts will be used in examples of biomechanics of the mandible. Secondly, the use of FEA in mammalian mandibles will be discussed, along with the concept of a comparative framework that enables the comparison of different models, as well as reviewing the latest methods to quantify and compare a large number of FEA models. Finally, an example using different mandibles of armadillos will be provided and discussed to further develop the understanding of the topics under discussion. This will provide insights about the connection between mandibular biomechanical performance and dietary preferences.

### Brief introduction to biomechanics

#### Theoretical background

Biomechanics is the study of the structure and function of the mechanical aspects of biological systems, at any biologically relevant organization level, from whole organisms to small cells, using the methods of mechanics (Alexander 2005). By contrast, mechanics is a more general field of science concerned with the behavior of any physical body subjected to forces or displacements.

Biomechanics comprises several sub-areas, such as for example aerodynamics to study the flight of birds and insects, hydrodynamics to study how fish swim, locomotor mechanics to study how animals move, as well as the study of chewing mechanisms using static theory, among other sub-fields. Statics is the branch of mechanics that is concerned with the analysis of loads acting on physical systems that are in static equilibrium with their environment. It means that a body is in static equilibrium when it fulfills the first condition for equilibrium, which requires that the net force applied to the system must equal zero, as well as the second condition for equilibrium, meaning that the net torque applied to the system must also be zero. This is the application of Newton's second law when the body has a null acceleration.

Newton's three laws of motion are physical laws that, taken together, constitute the basis of classical mechanics.

- **First law:** An object in uniform motion remains in that state of motion unless an external force is applied to it.
- **Second law:** The vector sum of the external forces \( \mathbf{F} \) on an object is equal to the mass of that object multiplied by the acceleration vector of the object.
- **Third law:** When one body exerts a force on a second body, the second body simultaneously exerts a force equal in magnitude and opposite in direction against the first body. They are called action force and reaction force.

Newton’s laws describe the relationship between a body and the forces acting upon it. Therefore, they are the base of any biomechanical model, both classical as well as the computational ones.

**Free-body diagram.** A free-body diagram (FBD) is a graphical illustration which is used to visualize the applied forces, movements, and resulting reactions on a body in a given condition or mechanical scenario. They depict a body or connected bodies with all the applied forces and moments, as well as reactions that act on that/those bodies. An FBD is an important step in understanding statics, dynamics and other forms of classical mechanics, because it is not meant to be a scaled drawing. It is a diagram that is modified as the problem is solved.

A free body diagram explicitly excludes some things:

1. Bodies other than the free body
2. Constraints; the body is not free from constraints; constraints have just been replaced by the forces and moments that they exert on the body (Newton’s third law)
3. Forces exerted by the body (supported by Newton’s third law)
4. Internal forces and
5. In the case to solve a dynamic problem, the velocity or acceleration vectors.

**Lever mechanics.** Lever mechanics are based on Newton’s laws and the condition for static equilibrium of statics. A lever is a body connected to a fixed point by a hinge or pivot called fulcrum and obeys the following physical law: the ratio of output to input force is given by the ratio of the distances from the fulcrum to the points of application of these forces.

Lever mechanics is useful in the context of chewing biomechanics, when studying the effect of muscles of the mandible on the bite force. There is a parameter called mechanical advantage (MA, equation 1) that is a measure of the force amplification achieved by using a mechanical system and is defined as the ratio of the force produced by the mechanical system \( F_{\text{output}} \) to the force applied to it \( F_{\text{input}} \)

\[
MA = \frac{F_{\text{output}}}{F_{\text{input}}} \quad \text{(equation 1)}
\]

This parameter is useful because it is a dimensionless proportion (or ratio) of forces and, consequently, is not related to the size of the system. It allows to compare models without the influence of size on the results.

**Elasticity: Stress and strain.** Up to this point we have presented the concepts of biomechanics without considering what is happening inside the analyzed bodies, and without taking into consideration the effect of the forces on the deformation of a body. All the bodies in our surroundings experience deformations. For instance, there could be small
deformations that we cannot see in concrete buildings, or there might be larger deformations in rubbers, such as in the case of a chewing gum.

In physics, elasticity is the ability of a body to resist reversible deformations when it is under the action of external forces, and to return to its original size and shape when that force is removed. Although solid objects will deform when adequate forces are applied to them, it is important to bear in mind that perfect elasticity is only an approximation of the real world because few materials remain purely elastic, even after very small deformations.

When we want to study what is happening inside a body, and how this body deforms under the application of a load, we need to study the laws of elasticity using the methods of continuum mechanics (Mase & Mase 1999). Continuum mechanics is a branch of mechanics that studies the mechanical behavior of materials when they are modelled not as discrete particles but as a continuous mass.

In biomechanics, bony structures can be considered bodies modelled as a continuous mass with small deformations, which means that one can apply to them all the equations derived from continuum mechanics and the linear theory of elasticity. Other biological structures such as soft tissues, are beyond the scope of this chapter and should be analyzed using non-linear theories.

When studying continuum mechanics, two concepts of great interest need to be mentioned, namely stress and strain. Stress is a quantity that corresponds to the internal forces that adjacent particles of a continuous material apply on each other. Stress is computed in a specific plane of the body and it is equivalent to the force divided by the surface of this plane. Strain is the ratio of the deformation of the material. It is computed as the proportion of displacement when a body is deformed with the original dimension of the body. Both are commonly used in biomechanics to study what is happening inside a body subjected to external loads.

\[
\sigma = \frac{F_x}{S} \left[ \frac{N}{mm^2} \right] \quad \text{(equation 2)}
\]

\[
\varepsilon = \frac{x}{l} \quad \text{(equation 3)}
\]

Where \( \sigma \) is the stress, \( F \) is the force, \( S \) the surface, \( \varepsilon \) the strain, \( x \) the distance of the elongation and \( l \) the original length of the bar (Fig. 4.2A). Compression or traction are obtained depending on how the balanced forces are applied (i.e. inwardly or outwardly) (Fig. 4.2B).

In general, stress and strain are computed in a specific point of the body in relation to a perpendicular plane and may be regarded as the sum of two components: the normal stress (compression or tension) perpendicular to this plane (Fig. 4.3A), and the shear stress that is parallel to this plane surface (Fig. 4.3B). Note that, for one point it is possible to define infinite normal and shear stress as function of the perpendicular plane in which they are computed (see tensorial notation below for further explanation).

\[
\sigma = \frac{F_x}{S} \left[ \frac{N}{mm^2} \right] \quad \text{(equation 4)}
\]

\[
\tau = \frac{F_y}{S} \left[ \frac{N}{mm^2} \right] \quad \text{(equation 5)}
\]

In linear elasticity, stress and strain are related via the Hooke’s law that links both variables by means of the Young’s modulus. \( E \) is the Young’s modulus, a mechanical property of linear elastic solid materials. Constitutive equations are used to relate two physical quantities that are specific to a material and that describe the response of that material to external inputs such as applied fields or forces. They are combined with other equations governing physical laws to solve physical problems; the relationship between applied stresses to strains is a linear constitutive equation because the relationship between them is linear and proportional to the Young’s modulus. Other materials such as soft tissues use other constitutive equations because they do not follow linear elasticity. For bones, the use of Hooke’s law is quite common (Doblare et al. 2004).

\[
\sigma = E \cdot \varepsilon 
\]

The Poisson coefficient is the ratio of transverse contraction strain to longitudinal extension strain in the direction of stretching force. It measures the Poisson effect, which is the phenomenon that happens when a material tends
to expand in directions perpendicular to the direction of compression or conversely, tends to contract if the material is stretched. This value is also necessary when defining the constitutive equation of the Hooke’s law in two or three dimensions.

**Beam mechanics.** Classical beam theory is a simplification of the linear theory of elasticity that provides a way of calculating the loads and deflection of beams when they are subjected to outer forces. The main difference between lever mechanics and beam theory is that levers are not deformable whilst beam theory assumes the deformation of the body under study. Another important difference is that in lever mechanics only Newton’s laws are used to solve the input and output forces whereas in beam theory, the use of the Newton’s laws is needed to get the input and output forces and then the stresses and strains inside the beam. For this reason, a beam is a mechanical prism: a line with an associated cross-section where we calculate the output forces and then the stresses and strains inside the beam. For this reason, a beam is a mechanical prism: a line with an associated cross-section where we calculate the output forces and then the stresses and strains inside the beam. For this reason, a beam is a mechanical prism: a line with an associated cross-section where we calculate the output forces and then the stresses and strains inside the beam. For this reason, a beam is a mechanical prism: a line with an associated cross-section where we calculate the output forces and then the stresses and strains inside the beam. For this reason, a beam is a mechanical prism: a line with an associated cross-section where we calculate the output forces and then the stresses and strains inside the beam.

In the above-mentioned examples, stress was measured for bending moments. Torsion, compression, or shear can also be studied using beam models. In this case, other diagrams must be obtained instead of the bending diagrams, and other equations (instead of Navier’s) are needed to relate the diagram to stress values. All these equations to transform the results from beam theory to stress require the definition of the geometric properties of the section of the beam. In this case the beam is the mandible. A good example to understand the implications of these simplifications in the mammal jaw can be found in van Eijden (2000).

**Classical biomechanical methods applied to mammalian mandibles**

Three examples are presented here in which the authors have used classical biomechanics. The two first examples by Maynard-Smith & Savage (1959) and Crompton & Parkyn (2009) are based on lever mechanics to study mechanical advantage, whereas Thomason (1991) used beam theory.

Firstly, Maynard-Smith & Savage (1959) studied the biomechanics of the mandible of one carnivore (*Martes*) and one artiodactyl (*Strepsiceros*). They analyzed the efficiency during chewing via the mechanical advantage of these two taxa which feed in different ways and have different mandibular shapes. The models included the temporalis and the masseter muscular forces, as well as the bite force of the canines. A reaction force appeared on the articulation point in the glenoid fossa. They found big differences between the mechanical advantage of the temporal and masseter muscles in the carnivore and the herbivore. These differences were associated with the different geometries of the lower mandible to perform a high mechanical advantage, whereas Thomason (1991) used beam theory.

By using lever models, Crompton & Parkyn (2009) studied the lower mandible of Triassic mammals in which both the reptilian and mammalian mandible articulations were defined. The models included the resultant forces of jaw closing muscles (temporalis, masseter, and pterygoid) and the bite force and the reaction force in the articulation thrust. They demonstrated how the component parts of the mandible musculature gradually changed their orientation (due to the changes in their geometry), in such a way that the reaction force to which the jaw joint was subjected in the articular thrust (the fulcrum of the lever) was progressively decreased whereas there was an increase in the bite force across the post-canine teeth.
Finally, Thomason (1991) modeled the skull of Canidae and Felidae as tubular beams formed by the facial and neurocranial regions, with the attached ‘jug handles’ of the zygomatic arches. In that case, the model included the reaction force at the articulation thrust and the muscular forces from the masseter and the temporalis. The bite force was studied in two cases: on the canine and on the molar positions. The authors wanted to test the hypothesis that the bending strength of the skull in some mammals correlates with the maximal loads imposed through the masticatory apparatus. The application of the beam theory allowed to assess the cranial strength during bending and, for instance, the Navier-Bernouilli equation was used to relate muscle and bite forces with the stresses inside the skull. In that case, the author used between 20 and 30 transverse CT scan sections through each skull to calculate the cross-sectional properties for the equation. This is one of the first works to show that bending stresses might be of importance in the cranial design of mammals and also has set the stage for more detailed future modelling.

**Practical example A.** Two different armadillos are studied: *Dasypus kappleri* and *Chaetophractus villosus*, each one presenting different dietary preferences. *D. kappleri* is a generalist insectivore, whereas *C. villosus* has an omnivore diet. The free-body diagram of the mandible, including masseter and temporalis muscle forces, is shown in Figure 4.4. Fixed positions are located on the bite position and on the jaw joint, thus constraining both directions on the jaw-joint and the vertical displacement on the bite point.

Muscle forces are calculated using muscle areas, and a value of 0.3 MPa (force per unit area) is assumed as muscular contraction. This value, estimated by Alexander (1992), has been considered in several works as a valid estimate for the isometric contraction of each adductor muscle (Thomason 1991). In this example, we assumed that the insertion area of the muscle is a good proxy of the 3D muscle cross-section, thus enabling the computation of muscular forces.

Equilibrium of forces in the free-body diagram: According to the equations of equilibrium of forces and the condition for static equilibrium of the statics, the bite force – applying the equilibrium of moments in the jaw joint – can be solved using equation 7. Results can be found in Table 4.1. $F_M$ and $F_T$ are the forces of the masseter and temporalis, $l_M$ and $l_T$ the lever arms of the masseter and the temporalis and $l_{Total}$ the length between the bite point and the jaw joint.

$$BF = \frac{F_M \cdot l_M + F_T \cdot l_T}{l_{Total}} = \frac{0.3A_M \cdot l_M + 0.3A_T \cdot l_T}{l_{Total}}$$

(equation 7)

The results from classical biomechanics using the free-body diagram show that *Chaetophractus villosus* generates a higher bite force and possesses a more efficient mechanical advantage. This higher biomechanical performance allows *Chaetophractus villosus* to eat a more demanding diet.
omnivore diet, whereas *Dasypus kappleri* probably does not need to perform a high bite force in order to crush insects before processing them.

Beam theory in a linear model: The use of the beam theory enables to find the maximum bending moment in the mandible by assuming that mandibular morphology can be represented as a straight line (Fig. 4.4). Curiously, both *Dasypus kappleri* and *Chaetophractus villosus* present similar values of maximum bending moment (1010 and 946 N·mm respectively) but this does not mean that there is a lack in functional differences, because the capacity to withstand this bending moment exclusively depends on the design of the mandible. According to Serrano-Fochs et al. (2015), the mandible of *Chaetophractus villosus* is thicker (5 mm vs. 3.5 mm) and the body of the mandible is broader than that of *Dasypus kappleri*. The corpus of the mandible of *Dasypus kappleri* is narrow in height and limiting its capacity to sustain the stresses derived from the bending moment. These results from beam models clearly suggest that *Chaetophractus villosus* is capable to withstand higher bending moments than *Dasypus kappleri* when chewing, therefore also is capable to process more demanding diets such as an omnivore one.

There is a difference between using the free-body diagram and the beam-model which explains the different bite force values (see Tab. 4.1 and 4.2 for the two approaches). The geometry assumed in both cases is different. In the free-body-diagram, the distances used from the muscles to the bite point and the condyle are based on the actual geometry, whereas in a beam model the position of the forces is in the line defined by the beam. This changes the values of the distances, and consequently, the value of the bite force. The free-body diagram is better suited to study muscle and bite forces, whereas the beam model allows the study of stresses in the cross-sections.

From the values of the maximum bending moment and from geometrical properties of the section of the mandible, normal stress values in the mandible can be found using the Navier equation (equation 8). In this example, we will assume a hollow ellipse as a constant cross-section of the mandible, and the second moment of inertia is obtained via equation 9.

\[
\sigma_{xx} = \frac{M_z}{I_z} \cdot \frac{y}{b} = \frac{M_z}{\pi (ab^3 - a_1b_1^3)} \cdot \frac{b}{2} \quad \text{(equation 8)}
\]

\[
I_z = \frac{\pi (ab^3 - a_1b_1^3)}{64} \quad \text{(equation 9)}
\]

Where \(M_z\) is the bending moment computed in the beam, \(I_z\) the second moment of inertia in the axis of the bending and \(y\) the distance from the centroid of the section to the point of the section under study.

High stresses are in the farthest point from the center of the cross-section during bending. Geometrical parameters of the section are described in Table 4.3 assuming, for this example, a constant cortical bone thickness of 1 mm in both models. The geometric parameters \(a\), \(a_1\), \(b\), and \(b_1\) are defined in Table 4.3 and are real measurements from the models (Serrano-Fochs et al. 2015). The normal stress obtained using equations 8 and 9 for both mandibles assuming a beam model (Tab. 4.3) also supports that the mandible of *Chaetophractus villosus* is stronger than the one of *Dasypus kappleri* during chewing.

### Table 4.1. Results from equilibrium of forces.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Masseter area (mm²)</th>
<th>Temporalis area (mm²)</th>
<th>Masseter force (N)</th>
<th>Temporalis force (N)</th>
<th>Bite force (N)</th>
<th>Mechanical advantage (MA)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dasypus kappleri</em></td>
<td>105.37</td>
<td>153.18</td>
<td>31.6</td>
<td>45.9</td>
<td>15.66</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Chaetophractus villosus</em></td>
<td>300.58</td>
<td>156.08</td>
<td>90.2</td>
<td>46.8</td>
<td>34.97</td>
<td>0.25</td>
</tr>
</tbody>
</table>

### Table 4.2. Results from beam theory.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Masseter area (mm²)</th>
<th>Temporalis area (mm²)</th>
<th>Masseter force (N)</th>
<th>Temporalis force (N)</th>
<th>Bite force (N)</th>
<th>Mechanical advantage (MA)</th>
<th>Mz max (N·mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dasypus kappleri</em></td>
<td>105.37</td>
<td>153.18</td>
<td>31.6</td>
<td>45.9</td>
<td>12.87</td>
<td>0.16</td>
<td>-1010</td>
</tr>
<tr>
<td><em>Chaetophractus villosus</em></td>
<td>300.58</td>
<td>156.08</td>
<td>90.2</td>
<td>46.8</td>
<td>17.63</td>
<td>0.13</td>
<td>946</td>
</tr>
</tbody>
</table>

### Table 4.3. Reometrical parameters for the mandibles of *Dasypus kappleri* and *Chaetophractus villosus* when assuming a beam with a hollow elliptic cross-section.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>(a) (mm)</th>
<th>(a_1) (mm)</th>
<th>(b) (mm)</th>
<th>(b_1) (mm)</th>
<th>(I_z) (mm⁴)</th>
<th>(M_z) (N·mm)</th>
<th>(\sigma_{xx}) (N·mm⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dasypus kappleri</em></td>
<td>3.51</td>
<td>0.51</td>
<td>8</td>
<td>6</td>
<td>82.81</td>
<td>1010</td>
<td>48.8</td>
</tr>
<tr>
<td><em>Chaetophractus villosus</em></td>
<td>4.94</td>
<td>2.94</td>
<td>12</td>
<td>10</td>
<td>274.71</td>
<td>946</td>
<td>20.7</td>
</tr>
</tbody>
</table>
Finite element analysis in mammalian mandibles

Brief introduction to finite element analysis

The finite element analysis (FEA) is a non-invasive computer simulation technique used in engineering. It uses the numerical technique of the finite element method (FEM) to solve the equations of continuum mechanics by dividing a geometry into a finite number of discrete elements known as a mesh (Kupczik 2008) to which the equations are applied. Mechanical properties of these elements are defined in order to give the structure a realistic behavior. The model is constrained to anchor it in space and includes the external forces applied to it. FEA is used to solve the equations of the elasticity in a deformable body under the effect of external forces.

FEA and beam theory are two different approaches to solve the same mechanical problem, yet with the limitation that beam theory can be exclusively used when assuming linear geometries with cross-section, whereas FEA can be applied to any geometry. The equations of lever mechanics based on Newton’s Laws are included when solving a mechanical problem in both FEA and beam theory. They are also solved when these methods are used. Therefore, beam theory and FEA can also solve reaction forces but it makes no sense to use these approaches to exclusively calculate these external forces, since they can be solved by hand using Newton’s laws (Sellers et al. 2017, Snively 2010).

In mammalian mandibles, FEA enables the observation of stress distribution patterns of the specimens by simulating loadings and forces involved in the masticatory function. Under equivalent loads, these stress patterns can be interpreted as a sign of the relative strength, with higher stress indicating a weaker mandible. Assuming that differences in the stress distribution pattern may give a clue regarding different aspects of the feeding ecology of the analyzed species.

There are several types of FEA depending on the nature of the geometry imported. A three-dimensional geometry e.g., from a CT-scan implies the use of three-dimensional solid models; a two-dimensional geometry requires the solution of a planar model using the equations of plane elasticity. Surface geometries in a 3D space require the use of shell models, whilst geometries based on lines need the use of linear elements. The latter is the exact computational translation of beam theory.

It is usual to model mammal mandibles as three-dimensional solid models (Gill et al. 2014, Gröning et al. 2011b, Püschel et al. 2018, Tseng & Binder 2010) or to represent them as simpler planar models (Fletcher et al. 2010, Marcé-Nogué et al. 2017b, Piras et al. 2013, Serrano-Fochs et al. 2015). In continuum mechanics, plane elasticity makes reference to the study of particular solutions of the general elastic problem in bodies that are geometrically mechanical prisms (that is, an area with a constant thickness) (Mase & Mase 1999). In particular, a plane stress solution occurs in structural elements where one dimension (the thickness) is very small compared to the other two, and the stresses are negligible with respect to the smaller dimension.

Steps to perform a finite element analysis

Geometry of the model. Models of mammalian mandibles can be obtained from the digitalization of real specimens by using CT-scans, photogrammetry or similar digitalization techniques that can register morphologies in three-dimensions and in full detail (see review in Cunningham et al. 2014). Another option is to generate them from scratch based on photos or other templates in CAD software (see Rahman & Lautenschlager 2016 for the box modelling approach).

The advances in computational tools to perform virtual reconstruction and restoration techniques of the original morphology of fossils, enable the creation of accurate and realistic three-dimensional models (Lautenschlager 2016). In all cases, during the reconstruction process, irregularities in the surface due to the generation of the model from the CT scanner need to be repaired using refinement and smoothing tools (Marcé-Nogué et al. 2011).

Planar models can be created from published photographs or built from scratch. In order to take the photographs in the most consistent way, some procedures need to be carried out in order to standardize images (de Esteban-Trivigno 2011), and then the use of CAD software allows the creation of models based on splines which are traced on the picture (see Fortuny et al. 2010 and Serrano-Fochs et al. 2015 for the full methodology).

Material properties. Bone is a rigid organ that forms part of the vertebrate skeleton. The hard and dense outer layer is composed of cortical bone tissue. Trabecular bone tissue corresponds to the internal tissue of the skeletal bone, being an open cell porous network. The mechanical properties of a particular bone depend on both composition and structure, which are fundamental parameters to be considered when simulating the behavior and response of a model when loads are applied. Although composition is not constant in living tissues, it is normally assumed (for simplicity and computational costs) that the mechanical properties of cortical and trabecular bone depend on apparent density and mineral content (see Doblaré et al. 2004 for a review).

The difficulties in modeling bone material properties in FEA models have driven researchers to assume isotropic behavior and to consider that bone, like most biological materials, is elastic and fails under a ductile model of fracture (Nalla et al. 2003). Isotropy means that the properties are taken to be the same in all directions, whereas anisotropy means having different properties in different directions. Orthotropy is present when the material
properties differ along the three orthogonal axes. Another common assumption of most FE analyses in the literature is to consider the mechanical behavior of bone (trabecular and cortical) as being linear, which is usually an accurate enough assumption (Doblár et al. 2004). This means that the relationship between stress and strain is proportional and the constitutive equation of linear elasticity based on Hooke’s law can be assumed. This also implies that using Young’s modulus and Poisson coefficient is enough to characterize bone. Cortical bone is stiffer and, therefore, has a higher Young’s modulus than trabecular bone.

One of the main problems when working with animal bones – and especially with fossil taxa – is the absence of material data to define Hooke’s law (Young’s modulus and coefficient of Poisson). This problem is normally tackled by using data available from closely related species, or from species with similar bone structure. The use of appropriate material properties depends on the available information from phylogenetically or ecologically related taxa. It is important to bear in mind that modelling other materials such as soft tissues, implies the application of non-linear constitutive equations, which in turn results in more computation time, (i.e., solutions mostly based on the equations of hyperelasticity). A hyperelastic material is a type of constitutive model of an ideally elastic material for which the stress-strain relationship derives from a strain energy density function that does not follow a linear relationship. It is common to use these constitutive models in FEA for ligaments (Qian et al. 2009), cartilage (Gislason et al. 2017), or arteries (Early et al. 2009) but not when analyzing osteological structures, such as mandibles.

**Biting scenarios.** Different biting scenarios have been used to study the chewing mechanism of mammals. According to Preuschoft & Witzel (2002), the skull of mammals can be loaded in three different ways: (1) assuming the weight of the head and prey or food acting downward on the mandible, (2) applying arbitrary forces or movements in the plane of the tooth row that create movements of the prey in relation to the head (defined as extrinsic loads by McHenry et al. 2007), and (3) applying the adduction of the mandible via the muscle forces which leads to reaction bite forces in the teeth (defined as intrinsic loads by McHenry et al. 2007). The cases with intrinsic loads can be modelled at the different tooth positions as bilateral (Püschel et al. 2018), or unilateral bites (Ledogar et al. 2016), whereas the group with extrinsic loads can be used to model axial twist, lateral shake, pullback, and dorsoventral movements (Attard et al. 2014).

The values of the forces in the different scenarios can be obtained from different information sources (e.g., literature, experiments, other modeling approaches such as MDA, etc.) or can be arbitrarily selected. When comparing different extrinsic models, arbitrary values can be a good choice (Attard et al. 2014), whereas for the intrinsic cases the values of the muscular forces can be calculated as a muscular contraction (see muscular forces in the intrinsic cases).

Several authors have used multibody dynamic analysis (MDA) to previously predict bite forces or muscular forces as a source of information for the forces applied at the FEA models (Lautenschlager et al. 2018). A multibody dynamic system consists of solid bodies that are connected to each other by joints that restrict their relative motion. This kind of studies analyzes how mechanical systems move under the influence of forces and can also be used to identify which forces are produced during the dynamic behavior of the system under analysis. This topic is, however, out of the scope of this chapter and further exposition can be found in Curtis (2011) where the application of MDA in vertebrates is reviewed.

**Muscular forces in the intrinsic cases.** The external loads that are acting on a body are applied as force or pressure on a surface. In a dynamic analysis, muscles are acting in combination to create a succession of individual static cases with several component contributions through time. In a static analysis (which is the one we are mostly referring to here) the muscle can be simplified as a force vector with an associated value for a specific case study. It is usual to analyze the so-called “theoretical maximum” which is when all muscles are acting together in a maximal tetanic contraction.

Muscle forces are calculated using muscular cross-sectional areas and a value for the specific muscular tension of 0.3 MPa (force per unit area), which is assumed as muscular contraction. This value, estimated by Alexander (1992), is considered as an isometric contraction of each adductor muscle. The physiological cross-sectional area (PCSA) is the area of the cross-section of a muscle perpendicular to its fibers, generally at its widest point.

\[
F = P \cdot A_{PCSA} \quad \text{(equation 10)}
\]

Where F is the muscle force, P is the specific muscular tension and \( A_{PCSA} \) is the physiological cross-sectional area.

Usually, when solving models of mammalian mandibles, the muscle forces (pterygoid, masseter, and temporalis) correspond to input values that have previously been calculated, whilst bite force is the output value solved by the static equations.

Muscular forces can be applied homogeneously on the insertion areas (Püschel et al. 2018) or can be distributed tangentially over the attachment areas wrapped around the bone surface (Tseng et al. 2017). To define the direction of the muscular forces, there are several accurate methods that create frames of linear elements all over the muscle attachments that linked the upper and lower jaws, with forces applied at the center of the frame (Attard et al. 2014). The simplest approach to determine the directions of the forces is defining the lines joining the centroid of the insertion area on the skull with the centroid of the insertion areas on the mandible (Panagiotopoulou et al. 2017, Püschel et al. 2018). In fact, if we assume homogeneous muscle force all over the muscle insertion, a single equivalent load applied at the centroid of the surface can replace a homogeneously distributed load applied on a surface. However, it should be mentioned that this single equivalent force generates little difference in the output values of stress and strain in the regions immediately outside of the applied force. This is because the specific force may create an artificially high stress (for more details see the problem of the maximum peak value addressed below).
Boundary conditions. Boundary conditions are defined to represent the unknown loads (for Newton’s third law), displacements, and constraining anchors that the structure experiences during the action of the forces. In general, it is recommended to avoid over-constrained models and redundant supports. Redundant supports are those in excess when the equilibrium is already guaranteed. It means that the number of unknown loads is higher than the number of degrees of freedom of the body. In a FEA planar model, the degrees of freedom of the body are three (the displacements in both directions and the rotation on the plane). For example, in Marcé-Nogué et al. (2017b) the boundary conditions are fixing both directions in the jaw-joint and only the vertical displacement at the bite point. This is a total of three constraints which is exactly the number of degrees of freedom for a planar model. The degrees of freedom of the body are six when analyzing 3D models using solid elements: three displacements in each direction, and three rotations in each axis. Excessive constraints tend to add stiffness to the model, thus making it stiffer than it should be.

In addition, it is fundamental to avoid under-constrained models which could produce rigid-body motions of the model. This means that the number of unknowns is lower than the number of degrees of freedom and that we need to be sure that the model is fixed to avoid any possibility of translation or rotation.

In the case of mandibular models, boundary conditions are often defined so they represent the fixed displacements that mandibles experience during biting scenarios. The first boundary condition restrains the condyle at the level of the contact points with the mandibular fossa of the cranium, in order to represent the immobilization of the mandible, thereby constraining the translation of the jaw in all the directions.

In intrinsic cases, a second boundary condition is applied to individual dental positions by fixing the displacement in the vertical axis. They are usually applied at different dental positions in order to simulate different biting scenarios (e.g., molar or incisive bite). According to Newton’s third law, the corresponding reaction force represents the unknown bite force.

When a unilateral bite is modelled, then the phenomenon of torsion has great importance because only one bite point is being considered on one side of the mandible (namely the working side), which means that there is a balancing side that is not directly acting in the biting action. In the balancing side, muscle forces can be reduced in order to remove a distractive tensile reaction force at the working side jaw to avoid being pulled apart (Greaves 1978, Spencer 1999).

In extrinsic cases, the fixed condition of the teeth is not used because instead of defining muscular forces to the posterior part of the mandible, a force is applied at the dental position. For cases in which the weight of the head and prey/food are simulated, this fixed condition of the teeth is also not considered because the weight of the prey/food is also applied to the teeth as a force.
Mesh generation. The mesh of a FEA model is a collection of interconnected elements joined at nodes, which defines the shape of the model where the physical problem will be solved using the mathematical equations of the FEM. Elements usually consist of triangles, quadrilaterals, tetrahedrals, hexahedrals or other simple convex polygons which simplify and discretize the geometry of the original model.

A problem can be solved as a two-dimensional model or as a three-dimensional model. However, different finite elements are required (see Marcé-Nogué et al. 2015 for further details about FEA meshes). When the geometry that is required to be meshed consists of surfaces or lines, it is necessary to use shell or beam elements projected in a three-dimensional space. These elements require different formulation compared to the standard solid elements used in three-dimensional models but, usually, FEM packages allow their easy implementation. Two-dimensional problems are solved using the equations of plane elasticity and the model can be meshed with planar elements, which means that it is required to consider their thickness.

Currently, the main commercial FEA packages include several methods to automatically generate the mesh of the desired geometry without human intervention. This improves the analysis, but the mathematical complexity of the FEM still means that mesh generation has to be treated with care. It is important to find a reasonable balance between the best mesh to be built and analyzed, and computational limitations. Depending on the specific package, software or the file format of the imported geometry, there are differences in the order of steps required to carry out a FEA. In some cases the mesh is generated in the first steps and then, the creation of the boundary conditions and the application of the forces are performed on the mesh (Figueirido et al. 2018) or, inversely, in other cases the inclusion of the forces and boundary conditions are performed on the geometry to then finally mesh the model (Püschel et al. 2018).

The different types of elements and the different types of mesh (structured, non-structured, uniform, non-uniform) and their pros and cons in the context of biological problems are discussed in detail in Marcé-Nogué et al. (2015). The quality assessment and the reliability of the mesh to solve FEA models is also discussed in Marcé-Nogué et al. (2015), and some examples of convergence results when the size of the elements is reduced can be found in Bright & Rayfield (2011b) and Tseng & Flynn (2015), where vertebrate species were analyzed.

Understanding the outputs of FEA

Scalar results. The solution of a FEA model generates several different outputs. A scalar is a quantity represented by a numerical value or magnitude that is independent of specific classes of coordinate systems, or one that is usually said to be described by a single real number. Strain energy or mechanical advantage are examples of scalar values. For example, they were used by Tseng et al. (2017) in FEA mandibular models to study the feeding capability in fossil and living Ursidae. Based on their results, it was hypothesized that the extinct species of giant otter Siamogale melilutra exhibited feeding ecomorphological adaptations that have no living analog.

Vectorial results. FEA vectorial results are the ones represented by a vector. A vector is a quantity that has magnitude and direction and that is commonly represented by a directed line segment whose length represents the magnitude and whose orientation in space represents the direction. This can be also represented by separating the vector into two or three components depending on the dimensionality of the problem (i.e., 2D or 3D).

The force reactions derived by Newton’s laws are vectorial results. In cranial mechanics, the bite force is computed as an output result when muscle forces are applied as input variables. Bite force strongly depends on the size (Wroe et al. 2005) of the models and needs to be carefully used when comparing models of dissimilar sizes. However, if analyzed properly, it can be used in a comparative setting to evaluate bite performances given different tooth positions (Figueirido et al. 2014).

Displacements are also a vectorial result providing the information from the original position of a node of the model with respect to the new position of the same node after being loaded by the input forces. These results have been used to compare the deformation between the unloaded and the loaded model (Gröning et al. 2011a).

Tensorial results. Tensors are important in physics because they provide a concise mathematical framework to formulate and solve problems of physics in areas such as stress, elasticity, fluid mechanics, and general relativity.

Stresses and strains are tensorial which means that they are represented by a tensor. Tensors are geometric objects that describe linear relations between geometric vectors, scalars, and other tensors and are represented by an organized multidimensional array of numerical values. The order (also known as degree or rank) of a tensor is the dimensionality of the array needed to represent it, or in other words, the number of indices needed to label a component of that array. For example, stresses and strains in three-dimensional models are represented by a matrix (a three-dimensional array) in a basis, and consequently correspond to a 3rd-order tensor.

In plane elasticity, tensors are kept as a third order tensor but with zero values in all the stresses related to the third direction in plane stress, and with zero values in all the strains related to the third direction in plane strain. Plane stress stays different from zero in $\sigma_{x}$ and plane strain $\varepsilon_{x}$ but these values are negligible with respect to the other values, and, therefore, we can assume plane elasticity as a two-dimensional solution and solve only the x-y components.
This means that, in order to define the stress state or the strain state of a FEA model, it is necessary to know all the values of the components of the respective tensors in each point of the model under analysis. FEA simplifies this statement by solving the stress and strain tensor in points inside each element of the mesh. It is important not to confuse the FEA elements with the sides of the square in Figure 4.6. The square in Figure 4.6 is not a FEA element but just the graphical representation of the Cartesian planes that are required to be known in a point when we want to know all the values of the stress/strain tensor.

Depending on the orientation of the plane under consideration, each component of the tensor represents a value of stress/strain: the component normal to the plane, called normal stress, and another component parallel to this plane, called the shearing stress. The symmetry of the stress/strain tensor simplifies the question to know only six values for defining all the tensor.

**Principal and equivalent values.** Principal stresses/strains are the maximum normal stress a body can have at a point of its body. It represents only normal stress and it does not have any shear stress component. Mathematically speaking, principal values are the ones in the tensor when the shear components are null. They are useful to summarize all the stress states of a FEA model for the two maximum and minimum values instead of using all the different values of the stress tensor.

\[
\sigma = \begin{bmatrix}
\sigma_x & \sigma_y & \sigma_z \\
\sigma_y & \sigma_y & 0 \\
\sigma_z & 0 & \sigma_z
\end{bmatrix} \quad \varepsilon = \begin{bmatrix}
\varepsilon_x & \varepsilon_y & \varepsilon_z \\
\varepsilon_y & \varepsilon_y & 0 \\
\varepsilon_z & 0 & \varepsilon_z
\end{bmatrix}
\]

(equation 11 and 12, for three-dimension problems)

\[
\sigma = \begin{bmatrix}
\sigma_x & 0 & 0 \\
0 & \sigma_y & 0 \\
0 & 0 & \sigma_z
\end{bmatrix} \quad \varepsilon = \begin{bmatrix}
\varepsilon_x & 0 & 0 \\
0 & \varepsilon_y & 0 \\
0 & 0 & \varepsilon_z
\end{bmatrix}
\]

(equation 13 and 14, for plane stress problems)

\[
\sigma = \begin{bmatrix}
\sigma_x & 0 & 0 \\
0 & \sigma_y & 0 \\
0 & 0 & \sigma_z
\end{bmatrix} \quad \varepsilon = \begin{bmatrix}
\varepsilon_x & 0 & 0 \\
0 & \varepsilon_y & 0 \\
0 & 0 & \varepsilon_z
\end{bmatrix}
\]

(equation 15 and 16, for plane strain problems)

Equivalent values are scalar values of stress that can be computed from the stress/strain tensor in order to summarize the stress state defined by all the components of the tensor to a unique value. In other words, an equivalent stress is the value of stress that creates a uniaxial stress state in the point to study, equivalent to the previous multiaxial stress state. The von Mises stress criterion, the Tresca criterion or the Rankine theory are different ways to reduce the multiaxial stress state to an equivalent stress. Von Mises and Tresca criteria are applicable for ductile materials whereas Rankine’s theory is preferred for brittle materials (Chen & Saleeb 1994).

The von Mises criterion is the most popular criterion for predicting the yield of ductile materials. Bone can be assumed to be either brittle (Doblár et al. 2004) or ductile (Dumont et al. 2009). However, according to Doblár et al. (2004), when isotropic material properties are used in cortical bone, von Mises is the most accurate criterion for predicting fracture location. This probably explains why it is in fact the most common criterion used in mandibular mechanics (Panagiotopoulou et al. 2017, Piras et al. 2013, Püschel et al. 2018, Tseng et al. 2017).

**Uses of stress and strain.** There are several different approaches that have been applied to analyze the results derived from mandibular mechanics. While some works analyze stress (Attard et al. 2014, Lautenschlager et al. 2016, Püschel & Sellers 2016, Tseng et al. 2017), other focus on strain (Gröning et al. 2013, Oldfield et al. 2012, Püschel et al. 2018, Tseng et al. 2017).
Panagiotopoulou et al. 2017). When using linear and elastic properties, it has been shown that both values are proportional and that the results of the distributions along the mandible are the same. This is due to the application of Hooke's law, which establishes a proportional relation between stress and strain.

Both stress and strain are accepted when comparing models below the fracture point, but, when we want to extrapolate these models to study fracture mechanics, a new debate is triggered: Is it stress or strain that causes failure? Probably the longest standing issue regarding failure criteria is whether they should be expressed in terms of stresses or in strains. This transformation can be easily done using a simple mathematical procedure, but this does not mean that all criteria can be switched from stress to strain (and vice versa). This is not always possible, especially when considering anisotropic material properties, but equally so for some isotropic cases. As an example, the maximum normal stress criterion and the maximum normal strain criterion take different forms when interconverted.

In this text, stress is taken as the fundamental form to be used when focusing on failure criteria. This is the direct consequence of the following conditions. Stress must be used if one wishes to have compatibility with fracture mechanics in the brittle range and with dislocation dynamics in the ductile range. Both of these classical theories require formulations in terms of stress.

On the other hand, strain has been shown valuable when comparing simulation results with experimental data (Bright & Rayfield 2011a, Gröning et al. 2012a), since strain gauges are commonly used in experimental settings. These electrical components experience changes in length as changes in resistance, and this property can be used to measure strain on a surface (e.g. bone) and compare it with FEA models.

### Comparative framework

One of the most important decisions when comparing different specimens is the selection of taxa, provided that it allows to create an appropriate biological comparative framework. In addition, it is also important to build the models considering that they will be compared under equivalent loads in order to interpret the stress pattern differences of the models as a sign of relative strength. Comparing the strength allows to discern that more robust or stronger mandibles are needed to be able to process more demanding diets such as, for example, nuts, shells, or bones. A comparative framework can be defined as all the decisions we need to take into account in the post-processing of FEA models. Post-processing involves all the steps carried out after solving the FEA models. All these considerations are not necessary, if the purpose is to simply analyze the distribution of stress or strain of just one mandible, e.g. to compare it against real data or to study mandibular fracture.
Orientation of the models. All models must be oriented in the same way. Several options exist for mammalian mandibles, such as positioning them in an anatomical orientation, central occlusion or according to anatomical planes, such as the Frankfurt horizontal plane (Marcé-Nogué et al. 2017b, Osborn 1987). Another option is to apply algorithms such as a best-fit alignment to orient all the models with respect to a common plane (e.g., Püschel et al. 2018 applied to talar morphology). It is important to orient all models consistently because different orientations can result in different muscle force orientations, which can potentially have a significant effect in the variation of the results (Gröning et al. 2012b).

Scaling the models. When the analyzed specimens exhibit significant size differences, it is necessary to adjust the models to a comparable size. There are two main ways of answering the question of how performance can be compared so that the effects of size and shape are disentangled, in order to exclusively focus on how shape affects mechanical performance for a given loading condition (Dumont et al. 2009).

1. Change the size of all the models to the same size and apply the same force.
2. Keep the differences in size in the models and apply an appropriate force that generates the same effect as carrying out the procedure described in 1.

In vertebrate models, it is more common to follow the second approach, thus keeping the original size of the model. However, even though both approaches are correct, they display the results in a different context. Some recent works have discussed which equations should be used to scale the models to the same size in order to study the stress patterns or the strain energy (Dumont et al. 2009, Marcé-Nogué et al. 2013), thus proposing that size could be removed either by modifying the dimensions of the model, or the values of the muscular forces or muscular pressures applied. It is important to note that when comparing stress/strain the forces should be scaled in a different way than when comparing other values, such as displacements.

For FEA planar models, the forces applied should be scaled using – for example – the quasi-homothetic transformation proposed by Marcé-Nogué et al. (2013) to allow meaningful comparison between planar models. In this case, it is important to bear in mind if our planar models are following the equations of plane stress or plain strain. For FEA models in three-dimensions, the volume ratio should be considered for calculating the different forces. The equations that must be fulfilled between two models that are to be compared without the effect of size are shown in Table 4.4 depending on the elasticity problem used.

Some criticisms and improvements have been made in recent papers (Parr et al. 2012) regarding the widely used scaling methodology proposed by Dumont et al. (2009). In particular, the analysis of 3D complex biological structures

**Table 4.4.** Force equations in a scaled model B with reference to model A. $A_A$ is the area of the reference model, $A_B$ the area of the scaled model, $t_A$ the thickness of the reference model, $t_B$ the thickness of the scaled model, $V_A$ the volume of the reference model and $V_B$ the volume of the scaled model.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Comparing strain/stress</th>
<th>Comparing displacements</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plane stress</td>
<td>$F_B = \frac{A_B}{A_A} \left( \frac{t_B}{t_A} \right) F_A$</td>
<td>$F_B = \frac{t_B}{t_A} F_A$</td>
</tr>
<tr>
<td>Plane strain</td>
<td>$F_B = \frac{A_B}{A_A} F_A$</td>
<td>$F_B = F_A$</td>
</tr>
<tr>
<td>3D models</td>
<td>$F_B = \left( \frac{V_B}{V_A} \right) F_A$</td>
<td>$F_B = \left( \frac{V_B}{V_A} \right) F_A$</td>
</tr>
</tbody>
</table>
has been improved, by considering complex inner cavities such as those present in skulls. In the latest literature it is possible to find several works focused on mammalian mandibles which followed the suggestions of Dumont et al. (2009) to scale their models in order to be able to compare von Mises stress via the surface ratio (e.g., Lautenschlager et al. 2016). Many other works have scaled their models using the volume ratio to then compare stress based on the allometric proportions between muscular forces and body mass (e.g., Attard et al. 2014, Tseng et al. 2017). The main controversy regarding the scaling procedures is whether the scaling should be carried out by means of a surface ratio or via a volume ratio. Interestingly, authors such as Dumont et al. (2009) which propose the use of surface ratios, do not deny the usefulness of volume ratios when scaling models to compare von Mises stress. In fact, they define an “area proportion” which can be calculated from the areas but can also be deduced from volumes \([\text{volume}]^{2/3}\) or length \([\text{length}]^2\) which can be substituted for an area ratio. This means that both the surface ratio and the volume ratio are equivalent when the latter is raised to the \(2/3\) power. However, exchanging ratios in the equations cannot be done when comparing models that differ in shape, because models with different shapes do not necessarily have the same surface area to volume ratios.

To clarify some of the issues in this debate (i.e., how the scaling should be done when comparing von Mises stress), Marcé-Nogué et al. (2013) published a methodological paper that was later followed by a practical application for 3D models by Fortuny et al. (2015), where it was shown that the relationship using the equations of continuum mechanics should be made by means of the volume ratios and not using surface ratios. These results agree with the fact that muscular forces and body mass/volume are related with the \(2/3\) power (Meers 2003, Wroe et al. 2005).

**Material properties.** The difficulty of obtaining information on the material properties (namely Young’s modulus and Poisson’s coefficient) of bony structures due to the absence of data for the species under study or any close relatives, makes it very difficult to create a comparative framework with different material properties for each model. It is common to consider bone as an isotropic material for simulations, as real data for bone materials are unavailable for most species. Moreover, if the comparison is made between the same bony structures in close relatives, it makes sense to use the same material properties for all the specimens compared. This is the usual procedure when comparing mammalian mandibles (e.g., Serrano-Fochs et al. 2015, Tseng & Binder 2010), even though some authors have obtained heterogenic and orthotropic properties by carrying out experiments (Panagiotopoulou et al. 2017).

When linear and elastic material properties are assumed in a comparative analysis, the effect of the elastic modulus of the material is irrelevant for stress patterns. In the case of the strains and displacements, there is an inverse proportionality that is kept constant, between the values of the metrics and the changes in the elastic modulus. These properties allow comparative studies without considering the real elastic materials properties (Gil et al. 2015).

This evidence suggests that the use of the values that define a linear material (namely Young’s modulus and coefficient of Poisson) is not crucial for the development of the analyses proposed here, because these values do not affect the results when a relative comparison of stress results between models is performed. In that sense, material properties should not be an issue when comparing bony structures.

**Simplifications.** Apart from the material properties discussed above, models are, by definition, a simplification of reality which means that one has to be aware of which assumptions are required, so as to keep them in mind when interpreting the results. There are at least two issues of great importance that should be considered in relation to model simplifications (when required):

1. Knowing whether the model simplifications are not extremely affecting the sensitivity of the results.
2. Carrying out the same simplifications in all the models under comparison in order to avoid non-comparable scenarios/results.

In that context, a sensitivity analysis will test the influence of the different parameters of the FEA models. For example, Gröning et al. (2012b) tested the sensitivity of FEA models of a human mandible with different trabecular bone defined as a solid inner material with a lower Young’s modulus. For instance, this kind of analysis can give us information of how we can simplify trabecular bone without excessively changing the results of our models. Simplified modelling assumptions of material properties and muscle activation patterns may introduce analytical errors in analyses where quantitative accuracy is critical for obtaining rigorous results (Panagiotopoulou et al. 2017). For example, when comparing mammalian mandibles it is common to segment the models as solid models without including trabecular bone properties, since it has been shown that the exclusion of trabecular bone does not affect the general results of a comparative FEA (Fitton et al. 2015) and because it has been argued that simplified models can reproduce the overall stress distribution patterns in ex vivo validation experiments (Bright & Rayfield 2011a). Additionally, it is common not to segment the periodontal ligament (PDL) despite some debate in the literature regarding the importance (or lack of it) of modelling this...
tissue in models of the mandible in FEA (Bright 2014). Some modelling studies of the primate mandible have suggested that the presence or absence of the PDL might affect the obtained results substantially throughout the whole structure (Gröning et al. 2011a, Marinescu et al. 2005).

Another discussed simplification in mammalian mandibles is the accuracy of results when analyzing planar models instead of 3D models. Planar models can be useful to get insights of the main patterns of variation of stress from both a morphological and a biomechanical perspective, as it has been exemplified by Fletcher et al. (2010), Marcé-Nogué et al. (2017b), Neenan et al. (2014), Piras et al. (2013), and Serrano-Fuchs et al. (2015). Planar models can be consistent with the results obtained from more complex scenarios, even though the level of detail is not the same. Probably the most important reason is that planar models study a specific biological scenario that can be simplified, and the validity of the models will be accepted if they can achieve the objective for which they were created. For example, planar models of primate mandibles can be good FEA models when distinguishing hard and soft-food eaters because the use of this simpler models allows to distinguish these categories in terms of stress values (Marcé-Nogué et al. 2017b).

Planar models are easier and faster to build than 3D models and can also be a better option in some cases, as they allow the creation of models that would not be easy to carry out in 3D when the original data are impossible to reconstruct. On one side, in the field of paleontology it is usual to rely on morphotaxa defined from scarce and fragmentary elements of few individuals, which means that it could be potentially difficult to carry out reconstructions in three dimensions, but not equally so in two dimensions. On the other side, 3D reconstructions of the fossils can be difficult to produce if no access is granted to digitize the original materials.

**Using FEA of mandibles to understand diet**

The use of FEA to study the mechanics of mandibles and relating it to diet has been widely used in the last years (Fletcher et al. 2010, Gill et al. 2014, Gröning et al. 2011b, Lautenschlager et al. 2018, Marcé-Nogué et al. 2017b, Neenan et al. 2014, Piras et al. 2013, Püschel et al. 2018, Serrano-Fuchs et al. 2015, Tseng & Binder 2010, Zhou et al. 2019). The underlying hypothesis is that under equivalent loads, the stress patterns observed in the different FEA models can be interpreted as a sign of the relative strength, with specimens with higher stress being weaker. Therefore, the hypothesis assumes that more robust or stronger mandibles would be needed to process more demanding diets. The study of extant species has been fundamental to this approach, because the information of the dietary preferences of extant species is readily available hence facilitating the correlation of this information with the results obtained using FEA models. Some examples are presented here, showing how authors have used FEA to infer or study the dietary preferences of different mammals.

Figueirido et al. (2014) exclusively analyzed extant species when comparing the results obtained in both cranial and mandibular FEA models of red and giant pandas, with the dietary differences of each one of these species reflecting their distinct bamboo feeding preferences. Püschel et al. (2018) studied the sclerocarp adaptations in the mandible of pitheciid primates. This was done using FEA models which demonstrated that there is indeed a relative robusticity continuum for some aspects of shape, but this gradient could be related to other factors rather than sclerocarpic specialization. Finally, Marcé-Nogué et al. (2017b) studied a large number of planar models of different primate mandibles under different loading scenarios. They found that there are significant differences in mandibular biomechanical performance depending on food categories and/or food hardness in Primates.

The understanding of dietary preferences in extant species enables a comparative framework with fossil taxa to infer dietary preferences in extinct species. This is, probably, one of the most widely applied aspects of FEA for mandible biomechanics, both using three-dimensional and planar models.

In that sense, using planar models Fletcher et al. (2010) tested, if mandibles of hindgut-fermenter ungulates are more robust than those of ruminants. They addressed the question, if extinct hindgut or foregut fermenters can be identified in the fossil record. Similarly, Serrano-Fuchs et al. (2015) studied FEA mandible models of armadillos. The results of this FEA showed that omnivorous species have stronger mandibles than insectivorous species, and also that the studied fossil herbivore taxa possess very strong mandibles due to a great amount of oral processing.

Three-dimensional models of extant taxa have been used in several carnivores to study fossil species. For example, Tseng & Binder (2010) compared strain distributions during a biting scenario between two bone-cracking ecomorphologies that evolved convergently, *Crocuta crocuta* and *Canis lupus*, and the fossil *Dinocrocuta gigantea*. *Kolponomos* has been interpreted as an otter-like shell-crusher based on a similar dentition. Tseng et al. (2016) studied different feeding strategies of extant carnivores in different FEA models. They tested whether there was a convergent morphology in the Miocene *Kolponomos* and the Pleistocene sabre-tooth feline *Smilodon* by using their anterior mandibles as anchors. The same authors studied the feeding capability of the Mio-/Pliocene giant otter *Siamagomia melilitia* using FEA models of the mandible of different living Lutrinae to infer that the mandibular strength in *S. melilitia* strikingly surpasses molluscivores such as the sea otter and the Cape clawless otter (Tseng et al. 2017).

In fact, the combination of both FEA models of the mandible and skull has been common in the study of fossil carnivores. Others such as Wroe et al. (2007) studied the extinct marsupial wolf *Thylacinus cynocephalus* and the placental grey wolf, which are commonly presented as an iconic example of convergence. In spite of this convergence, comparisons of stress distributions in the FEA models not only revealed considerable similarity, but also provided informative differences suggesting ecological overlap yet different prey strategies. They suggest that the grey wolf is better adapted to withstand the high extrinsic loads likely to accompany social hunting of relatively large prey. Other authors (Attard et al. 2011) studied the biomechanical performance of the skull and mandible of *T. cynocephalus* in relation to those of two extant marsupial carnivores with
known diets that occurred sympatrically – the Tasmanian devil, *Sarcophilus harrisii*, and the spotted-tailed quoll, *Dasyurus maculatus* – suggesting that *T. cynocephalus* is likely to have consumed smaller prey compared to its size. Oldfield et al. (2012) created several FEA models of ursids to predict the feeding behavior of the extinct *Agriotherium africanum*. According to these authors, the findings did not resolve whether the fossil was more likely a predator or a scavenger of large terrestrial vertebrates but showed that it was well adapted to resist the forces generated by either activity. Sabre-tooths have been examined by Wroe et al. (2013) using FEA models to suggest that, in many respects, the placental *Smilodon fatalis* was more similar to the marsupial *Thylacosmilus atrox* than to a conical-toothed cat. Similarly, Attard et al. (2014) used FEA models of marsupial carnivores to test whether the fossil species *Nimbacinus dicksoni* was more similar to its recently extinct relative *Thylacinus* or to several large living marsupials.

This comparison in a key aspect such as feeding ecology suggested that it was a large-prey specialist.

The difficulties of comparing fossil taxa with extant species has driven a handful of works using FEA models of the mandible to study dietary preferences in extinct species only comparing them to their extinct close relatives. However, the advances in computational tools to perform virtual reconstruction and restoration techniques of the original morphology of fossils (Lautenschlager 2016) allow the creation of accurate and realistic three-dimensional models. In that line, Gill et al. (2014) studied the dietary specializations and diversity in feeding ecology of the earliest stem mammals using FEA. Three-dimensional models of the mandible of the early mammaliaforms *Morganucodon* and *Kuehneotherium* were analyzed suggesting that the lineage split during the earliest stages of mammalian evolution due to ecomorphological specialization and niche partitioning.

![Fig. 4.10. Free-body and von Mises stress diagrams of armadillo mandibles with real muscular force values. A, free-body diagram of a mandibular bilateral bite using a plane stress approach and; B, von Mises stress from a finite element analysis of Chaetophractus villosus and Dasypus kappleri from Serrano-Fochs et al. (2015). Results using real muscular forces values.](image)

### Table 4.5. Real muscular force values and obtained results: Bite force, mechanical advantage and strain energy of *Chaetophractus villosus* and *Dasypus kappleri* mandibles using a plane stress approach.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Masseter force (N)</th>
<th>Temporalis force (N)</th>
<th>Bite force (N)</th>
<th>Mechanical advantage (MA)</th>
<th>Strain energy (mJ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dasypus kappleri</td>
<td>31.6</td>
<td>45.9</td>
<td>15.29</td>
<td>0.197</td>
<td>6.8667</td>
</tr>
<tr>
<td>Chaetophractus villosus</td>
<td>90.2</td>
<td>46.8</td>
<td>34.69</td>
<td>0.253</td>
<td>4.9075</td>
</tr>
</tbody>
</table>

### Table 4.6. Scaled muscular force values and obtained results: Bite force, mechanical advantage and strain energy of *Chaetophractus villosus* and *Dasypus kappleri* mandibles using a plane stress approach.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Thickness (mm)</th>
<th>Model area (mm²)</th>
<th>Masseter force (N)</th>
<th>Temporalis force (N)</th>
<th>Bite force 1 (N)</th>
<th>Mechanical advantage (MA)</th>
<th>Strain energy (mJ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dasypus kappleri</td>
<td>3.51</td>
<td>971.37</td>
<td>62.0</td>
<td>33.2</td>
<td>23.22</td>
<td>0.244</td>
<td>15.54</td>
</tr>
<tr>
<td>Chaetophractus villosus</td>
<td>4.94</td>
<td>1038.90</td>
<td>90.2</td>
<td>46.8</td>
<td>34.69</td>
<td>0.253</td>
<td>4.9075</td>
</tr>
</tbody>
</table>
New developments in the comparison of mammalian mandibles: the example of the armadillo mandible

Quantification of FEA results

In recent years, FEA models and the respective results have been compared in a predominantly qualitative way, by comparing the stress or strain distributions. Visual comparison using only the stress or strain distribution of contour plots can be a good option when the number of models to compare is small and the results are distinctive enough between the analyzed models. For example, in Tseng & Binder (2010), comparison of stress distributions during a biting scenario in Crocuta crocuta, Canis lupus and the fossil Dinocrocuta gigantea was feasible, because the differences in the graphical representation of the von Mises stress are clearly visible and distinct from one another. However, when the number of models to be compared increases, such comparison becomes difficult (Neenan et al. 2014) and more rigorous quantification of the FEA results is useful.

Quantifying stress data at specific points of a model has been useful in ecomorphological analyses (Attard et al. 2014, Fortuny et al. 2011, 2016, Piras et al. 2015, Serrano-Fochs et al. 2015), but to take into account the biomechanical behavior of the complete model, single mean values of stress were adopted as quantitative measurement to provide a metric of the relative strength of vertebrate structures. This approach involves computation of the von Mises stress averages in finite element models. In spite of this approach having been used in several paleobiological studies (Aquilina et al. 2013, Farke 2008, Figueirido et al. 2014, Fish & Stayton 2014, Neenan et al. 2014, Parr et al. 2012, Tseng 2009), we employed the recently proposed “weight-meshed values” and the “quasi-ideal meshes” to compute these values as adapted by Marcé-Nogué et al. (2016, 2017a). The latter is more robust, because it takes into account the effects caused by the different size of the individual mesh elements in a FEA model.

Similarly, the quantification and post-processing of the results of FEA models has also evolved to be combined with other morpho-functional methodologies such as geometric morphometrics (GM). FEA and GM outputs have been used in mandible models to explore questions in functional morphology, ecomorphology, macroevolution, among others, by applying standard statistical methods. These methods involve multivariate regressions, ANOVAs or PLSs (Maiorino et al. 2015, Piras et al. 2013) or, even, GM as a tool to analyze the deformations resulting from FEA analyses (Gröning et al. 2011a).

Finally, it is worth mentioning that the influence of the size of the individual elements of the FEA mesh in the results must be always taken into account by performing sensitivity analysis (Tseng & Flynn 2015). To avoid the influence of the size of the elements in the results, an ‘intervals’ method was proposed by Marcé-Nogué et al. (2017a), which incorporates element volumes to provide an additional way of quantifying and comparing FEA results, thus avoiding the problems with the mesh. This method could allow for considerably more effective comparisons of finite element models, and maybe more precise distinction between dietary traits.
The problem of the maximum peak value

Maximum values of stress or strain (or peak stress/strain) could be potentially useful as a value to consider when comparing the biomechanical performance of different FEA models. However, peak stress and strain should not be taken into account because the value could be a numerical singularity, which is a well-known problem in FEA (Morris 2008).

This singularity could be a consequence of a boundary condition or a perfect square within the geometry. A simply supported condition is an idealistic assumption. This condition has been applied specially in planar models, as in the examples provided by this chapter, where fixed displacements were imposed at the bite position and at the jaw joint in a simple point of the model. This condition creates a numerical effect that leads to the stress increasing without limit when the mesh is refined for both 2D and 3D elements. In 3D models of mandibles, simply supported conditions are usually applied in the bite position or in the jaw joint where the displacements are restrained in a specific area of the model. In a similar way, the perfect square condition is also an idealistic assumption where a corner with zero radius in the original geometry creates a stress concentration that also leads the value to increase without limit when the mesh is refined. To avoid artificially high stress magnitudes, it is not recommended to record the maximum stress or strain values in the whole model, because maximum values could be the result of singular high yet unrealistic magnitudes. As some authors have warned (e.g., Rayfield 2007), it may be difficult to assess the peak stresses of the model in the whole model. Some approaches regarding how to handle this problem are described in Marcé-Nogué et al. (2015). For example, this can be achieved by just studying the results obtained from an area of the model that is far enough from the artificially high magnitudes, or by adapting the mesh to avoid the visualization of this high value. Coarse meshes can avoid these extremely high stress values whereas very fine meshes can concentrate these high values in a very small region of the model. Finally, other authors have suggested to exclude elements displaying the stress or strain values within the top 5% (Tseng & Flynn 2018).

Use of specific points to quantify data

Quantifying stress or strain data at specific points has been useful in ecomorphological analyses of mammalian mandibles. An example of this can be found in Attard et al. (2014) who selected equidistant points along the mandible to measure the distribution of von Mises stress for each loading case and then compared them with other models. This approach allows us to plot these values of stress in a graph where one of the axes is the value of stress and the other one is the position from anterior to posterior along the mandible.

This approach has also been used in combination with the values of von Mises stress in specific points with data from morphometric analysis in other vertebrate groups (Fortuny et al. 2011). Or in a different way, using the values of stress from the specific points to plot in a dispersion plot of a principal component analysis (PCA) (Fortuny et al. 2016, Marcé-Nogué et al. 2015). Quantifying data from FEA models allows the use of such data to test the significance using statistics or other methods, opening the door to new methodologies to be used in combination of FEA.

Case example: armadillos

Biomechanical problem and FEA data. Finite element analyses were applied to assess the lower jaw biomechanics of cingulate xenarthrans in Serrano-Fochs et al. (2015). The main goal of this work was to make a comparative assessment of the biomechanical capabilities of the mandible based on FEA, and to relate the obtained stress patterns with dietary preferences. To do this, a comparative framework was created following the indications of the previous section of this chapter, so to solve the biomechanical problem described in the free-body diagram of Figure 4.11. The mandible was constrained at the most posterior part and at the condyle level of the mandibular notch following the procedures described in Serrano-Fochs et al. (2015) and Marcé-Nogué et al. (2016, 2017a).

Planar models of 11 armadillo mandibles (Tab. 4.1), each one corresponding to a different species, were created. Two main masticatory muscles (i.e., temporals and masseter) were included in the model as a vector between the centroid of the muscular attachment on the mandible and the centroid of the equivalent muscle attachment on the skull. To compare the models, a scaling of the values of the forces was applied using the equations defined in Table 4.4 in order to compare stresses in planar models, by using Chaetophractus villosus as reference model (Tab. 4.7).

Isotropic and linear elastic properties were assumed for the bone. In the absence of data for Cingulata or any other closer relative, and due to the absence of data for any mammalian clade with a similarly shaped mandible, the authors decided to apply the mandibular material properties of *Macaca rhesus*: E (elasticity modulus) = 21000 MPa and v (Poisson coefficient) = 0.45 (Decho & Hylander 2000). The available properties of *Macaca rhesus* were chosen, provided that it has a wide range of habitats and diet which resembles omnivorous or generalist insectivorous diets, as observed in the analyzed armadillos (Richard et al. 1989).

The stress distribution obtained in each armadillo is shown in Figure 4.12A. These stress patterns can be interpreted as a sign of relative strength. Assuming that more robust or stronger mandibles would be needed both for processing harder food items, insect-feeding armadillos (which have none or little processing in the mouth) should be expected to have weaker mandibles (i.e. with higher stress levels) than those feeding on other items, such as herbivorous or omnivorous species.

On the other hand, differences in stress distribution patterns may provide a clue regarding different aspects of the feeding ecology of the analyzed species. The aim of the methods presented below is to show that using a comparative framework and post-processing the results (e.g., with specific points, mesh-weighted values, quasi-ideal meshes or the intervals’ method) the interpretation of the results can be greatly improved.
Specific points. In Serrano-Fochs et al. (2015) the strength of the mandibles was studied using the values of stress in eight specific points. The values of stress in each specific point were plotted according to the different dietary traits of the studied armadillos. They are classified as omnivores or insectivorous specialists and generalists (Fig. 4.12A) and a Kruskal-Wallis test was applied to check if there were significant differences in the results. However, despite the lack of significant results, some patterns appear in the boxplots for some specific points (Fig. 4.12B). Moreover, a principal component analysis (PCA) of the stress values for all specific points recorded was carried out using the variance-covariance matrix (Fig. 4.12C). The aim of these analyses was to evaluate the stress values in a multivariate manner and to look for diet-related patterns.

The most obvious result is that in general, insectivorous species showed a larger variance than omnivorous species, and also that omnivorous species have some coincident stress patterns. However, the absence of significant results could be due to a lack of statistical power, or possibly because the selected points represent local non-significant regions, or the specific points were hindered by the lack of information about the whole FEA model.

Mesh-weighted average values and quasi-ideal mesh. A quantitative single measurement of the relative strength of the studied structure could be preferred to summarize the strength of the whole model. The most common approach has been the computation of the average von Mises stresses of the various models considered. Even though...
this approach has been used previously in paleobiological studies of mammalian mandibles (Figueirido et al. 2014, Neenan et al. 2014, Wroe et al. 2013), it represents a common error that should be avoided. When obtaining descriptive statistics from FE models, such as mean or median values, the problem of having non-uniform meshes is crucial and could lead to skewed results. For example, if by chance high stress values are obtained in larger elements, these high stress values will be under-represented because they are present in fewer elements despite the area with high values being large.

To solve this issue, Marcé-Nogué et al. (2016) proposed the creation of quasi-ideal meshes (QIM), which are meshes where all the elements have practically the same size. The use of QIM avoids the use of weight-meshed corrections in the mesh, thus allowing the use of average values without correcting them. Moreover, with the use of QIM it is also proposed to use percentile values (e.g., 25th, 50th, 75th or 95th) as quantitative values, which allows to visualize the distribution of stress in each FEA model as a boxplot, facilitating the comparison between models. Moreover, and following the idea proposed by Walmsley et al. (2013), the use of the 95th percentile can be assumed as the maximum peak value to avoid the necessity to consider numerical singularities.

The arithmetic mean is calculated by summing all individual observations or items of a sample and dividing this sum by the number of items in the sample. In FEA results of stress, the arithmetic mean (AM) would be the sum of individual observations or items of the sample and dividing this sum by the number of items in the sample. In FEA results of stress, the arithmetic mean (AM) would be the sum of individual observations or items of the sample and dividing this sum by the number of items in the sample.

The box plots of Fig. 4.12 (A) illustrate the distribution of von Mises stress in the 11 armadillos' mandibles separated by diet: omnivore/carnivore and specialist or generalist insectivore. The box plots show the five-number summary statistics, namely the minimum, first quartile, median, third quartile, and maximum values of the von Mises stress. The box plot also shows the outliers, which are defined as observations that lie outside the interquartile range (IQR) of the data. The IQR is the difference between the third quartile (Q3) and the first quartile (Q1). Outliers are defined as observations that lie more than 1.5 times the IQR below Q1 or above Q3. The box plots also show the mean value of the von Mises stress, represented by a horizontal line within the box.

The box plots of Fig. 4.12 (B) illustrate the distribution of von Mises stress in the 11 armadillos' mandibles separated by diet: omnivore/carnivore and specialist or generalist insectivore. The box plots show the five-number summary statistics, namely the minimum, first quartile, median, third quartile, and maximum values of the von Mises stress. The box plot also shows the outliers, which are defined as observations that lie outside the interquartile range (IQR) of the data. The IQR is the difference between the third quartile (Q3) and the first quartile (Q1). Outliers are defined as observations that lie more than 1.5 times the IQR below Q1 or above Q3. The box plots also show the mean value of the von Mises stress, represented by a horizontal line within the box.

The box plots of Fig. 4.12 (C) illustrate the distribution of von Mises stress in the 11 armadillos' mandibles separated by diet: omnivore/carnivore and specialist or generalist insectivore. The box plots show the five-number summary statistics, namely the minimum, first quartile, median, third quartile, and maximum values of the von Mises stress. The box plot also shows the outliers, which are defined as observations that lie outside the interquartile range (IQR) of the data. The IQR is the difference between the third quartile (Q3) and the first quartile (Q1). Outliers are defined as observations that lie more than 1.5 times the IQR below Q1 or above Q3. The box plots also show the mean value of the von Mises stress, represented by a horizontal line within the box.
Chapter 4. Mandibular biomechanics

Two indicators were proposed to evaluate whether a mesh is uniform enough to use the raw stress data for statistical analysis: the percentage error of the arithmetic mean (PEofAM) and the percentage error of the median (PEofM). These two indicators evaluate the difference between the non-weighted value and the weighted value of mean and median (PEofAM in equation 22 and PEofM in equation 23),

$$PEofAM = \left( \frac{MWAM - AM}{MWAM} \right) \times 100$$  
(equation 22)

$$PEofM = \left( \frac{MWAM - M}{MWAM} \right) \times 100$$  
(equation 23)

If the mesh of the model is close to an ideal fine uniform mesh, the non-weighted and the weighted indicators should be equal. If the error is lower than a certain threshold, the mesh can be considered a QIM, and quantitative and statistical analysis of the FEA data can be computed without any corrections and e.

When this approach was used to analyze the armadillo mandibles, the significant differences among different diets found in the statistical analyses were more conclusive than the results obtained when analyzing stress values at a few specific points (Serrano-Fochs et al. 2015). This supports the analysis of the stress values of the whole specimen rather than focusing on just a few isolated points. An alternative would be to use both sources of information as isolated points, which could give an alternative view of some specific areas.

Statistics showed significant results when comparing omnivore and insectivore species (Tab. 4.8). However, this significance should be interpreted as illustrative more
than fully conclusive. This is because when a Bonferroni correction was applied, the mean values between specialized insectivores and omnivores are non-significant (most probably due to the small sample size of the specialist insectivores).

**Intervals’ method.** In Marcé-Nogué et al. (2017a), a new method was proposed, named the intervals’ method, that can be used to analyze data from finite element models in a comparative multivariate framework. As a case study, several armadillo mandibles were analyzed with success, showing that the proposed method was useful to distinguish and characterize biomechanical differences related to diet/ecomorphology.

This so-called intervals’ method consists of generating a set of variables, each one defined by an interval of stress values. Each variable is expressed as a percentage of the area (in planar models) or the volume (in 3D models) of the mandible occupied by those stress values. Once all the stress values of a single specimen are obtained, they can be subdivided into different intervals, each one of them representing the amount of area in percent values of the original model having a specific range of stress values.

Afterwards these newly generated variables can be analyzed using multivariate methods. The use of this new method in the FEA models of cingulate mandibles allowed us to positively discriminate between specialist and generalist species of insectivores, which was not possible with the approaches defined above. The method described in Marcé-Nogué et al. (2017a) requires the definition of certain parameters such as a fixed upper threshold \( FT_{\text{upper}} \) and a specific number of intervals \( N \). For example, in this work, \( FT_{\text{upper}}=0.1 \text{ MPa} \) and \( N=50 \). This value is assumed based on the convergence procedure defined in Marcé-Nogué et al. (2017a), when the results of the regressions of the PCs indicate that the scores are almost completely correlated.

We carried out a PCA using the variance-covariance matrix (Fig. 4.13). The PCA of the correlation matrix successfully distinguishes the main three diets, with omnivore-carnivore species on lower-left area of the plot. PC2 separates specialist insectivores from the rest of species, while *Chlamyphorus truncatus* (i.e., a generalist insectivorous species exhibiting a very particular diet due to its completely fossorial lifestyle) is located near the omnivore/carnivore species in the negative part of the PC1 and PC2. Within this PCA, omnivore/carnivore species were characterized by very low stress values (lower-left quadrant of the plot), whilst generalist insectivores showed a proportionally larger area of intermediate stress values than the rest of the species. Specialist insectivores have proportionally larger areas of high stress.

**Further usage of quantification of stress**

Once we have quantified our models using specific points, average values or percentiles from a QIM or applying the intervals’ method, we can use different ideas and methods to organize our data. On one hand, values of specific points, scalar values from the models (such as strain energy) and the mesh-weighted proposed averages values can be used for the comparison of models and their behavior. On the other hand, the intervals’ method or the use of the stress quartiles are a good approach to check similarities between models.

Scalar values from the FEA models such as the strain energy were used to compare with other scalar values such as the mechanical advantage (Tseng et al. 2016) or used in regression with other values such as the volume of the model to check for allometry (Tseng et al. 2017).

Average values were used to compare different dietary traits and hardness of ingesta in planar FEA models of extant primates (Marcé-Nogué et al. 2017b), showing that there is a strong association between mandibular biomechanical performance, mandibular form, food hardness, and diet categories. The same work (Marcé-Nogué et al. 2017b) used average values to estimate the ancestral states for internal nodes using maximum likelihood and then by interpolating the states along the branches of the phylogeny. This approach was applied to get insights about the possible evolution of mandibular stiffness.

Finally, it is worth mentioning that the use of the different percentile values as a unique set of multivariate data, the average values or the powerful intervals’ method, are all opening a window of opportunity for post-processing FEA-derived data. Using these kinds of data allows the application of multivariate analysis, and they can even be used to run machine learning algorithms in order to infer dietary preferences of fossil taxa from the data of living species. Both supervised (Marcé-Nogué et al. 2020) and unsupervised (Zhou et al. 2019) algorithms can be used to study mandibular biomechanics and its relationship with diet.

<table>
<thead>
<tr>
<th></th>
<th>Specialist insectivore vs. generalist insectivore</th>
<th>Specialist insectivore vs. omnivore</th>
<th>Generalist insectivore vs. omnivore</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kruskall-Wallis p-value</td>
<td>0.0089</td>
<td>0.0369/0.1107</td>
<td>0.0058/0.0173</td>
</tr>
<tr>
<td>MWAM</td>
<td>0.0081</td>
<td>0.0358/0.1073</td>
<td>0.0057/0.0170</td>
</tr>
<tr>
<td>MWM</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 4.8.** Statistics for the Kruskal-Wallis test: mesh-weighted arithmetic mean (MWAM), and mesh-weighted median (MWM).
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References

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