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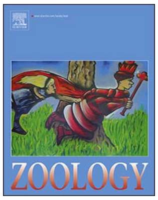

# Editorial: Determinants of mammalian feeding system design

## 1. Introduction

Few aspects of mammalian biology are as important as the feeding system, which enables the high metabolic rates of this class of vertebrates. Using a combination of experimental and modelling approaches, workers have strived to discover the mechanisms that drive intra- and interspecific variation in the form-function relationships (design) of the feeding system. Throughout the evolutionary history of mammals substantial morphological changes to the masticatory apparatus have occurred, typically associated with diversification and changes in diet. However, the relative importance of different selective forces and constraints in shaping the present diversity in morphology, physiology, and behavior is not clear.

The current special issue of *Zoology* comprises papers presented at the 11th International Congress of Vertebrate Morphology (ICVM) held in 2016 in Washington DC as part of the symposium entitled "*Determinants of mammalian feeding system design*" funded by the Society of Experimental Biology, Animal Section. By showcasing different methodological approaches and bringing together experts from different disciplines but with a similar research focus, this issue expands on our current understanding of mammalian feeding system design and delineates future research directions.

## 2. Overview of the articles in the current issue

### 2.1. The form-function relationships of the mandible and temporomandibular joint

**Dechow et al.,** in their study "*Biomechanical implications of cortical elastic properties of the macaque mandible*", measure the elastic properties of the cortical bone from rhesus macaque mandibles using ultrasound velocity measurements and compared them against data from baboons and humans. The results reveal substantial regional variation in elastic properties (cortical thickness, density, elastic moduli, shear moduli and anisotropy) across the macaque mandible. In a companion article by **Panagiotopoulou et al.,** entitled "*In vivo bone strain and finite element modeling of a rhesus mandible during mastication*", the authors are the first to combine *in vivo* experimental data on jaw kinematics, muscle activity and bone strain with the *ex vivo* data on cortical bone material properties measured by **Dechow et al.,** to create a subject-specific finite element simulation of a rhesus macaque during feeding. The authors performed a series of sensitivity analyses to test the effects of bone and teeth material properties, joint and bite constraints, and muscle forces on the mechanical performance of the model. They found that variation in bite point and joint constraints elicit substantial variation in bone strain regimes.

**Terhune,** in her study "*Revisiting size and scaling in the anthropoid temporomandibular joint*", thoroughly covers the relationship between size and shape of the primate temporomandibular joint (TMJ) and its effect on the joint biomechanical performance, an important topic in craniofacial design and evolution of the primate feeding system. Through analysis of a large dataset of 3D TMJ measurements, this study provides a comprehensive exploration of the scaling of joint morphology with mandible length and body size and of the patterns of shape variation across primate clades using geometric morphometrics techniques. Results reveal that several aspects of TMJ shape scale either with isometry or positive allometry with body mass but with substantial variation among clades, suggesting different, and potentially competing, selective pressures.

**Iriarte-Diaz et al.'s** study "*Functional correlates of the position of the axis of rotation of the mandible during chewing in non-human primates*" assesses mandible movement during chewing using instantaneous axes of rotation (a.k.a., helical axes), in three species of non-human primates. Using a mix of experimentally collected 3D jaw kinematic data with computational 3D modeling, they explore the effect of normal mandibular movement on muscle dynamics and nerve strain, and evaluated three long-standing hypotheses explaining the location of the mandibular axis of rotation. This study also provides data on the effect of intra- and interspecific morphological variation on mandible mechanics, and highlights the potential of using 3D modeling techniques to generate and test biomechanical hypotheses in complex morphological systems.

**Stover et al.,** in their manuscript entitled "*An ontogenetic perspective on symphyseal fusion, occlusion and mandibular loading in alpacas (*Vicugna pacos*)*", investigate the process of symphyseal fusion during ontogeny in alpacas in the context of the dynamics of mastication and the stresses exerted on the mandible. This study provides important longitudinal data on the timing and process of symphyseal fusion, in addition to *in vivo* bone strain data from the mandible of animals of different ages. The data show that symphyseal fusion occurs before the development of adult-like strain magnitudes at the symphysis, suggesting that the joint is protected from adult strains until it is structurally ready to resist masticatory loads.

### 2.2. Developmental plasticity, craniomandibular development and phenotypic variation

**Franks and colleagues** make a novel contribution to the ongoing debate about the role of plasticity and phenotypic variation in the developing skull via their study "*Intracranial and hierarchical perspective on dietary plasticity in mammals*". Using a developmental sequence of rabbits obtained at

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weaning and raised until adulthood, the authors assess the long-term diet-induced plasticity of the cranium (at macro- and micro-levels of bone organization) to altered loading levels. The results show variations in cortical bone formation and biomineralization in sites that are highly strained during mastication; however, minimal adaptive changes were recorded in non-masticatory sites. The authors also show that the functional signal is influenced by cortical bone quantity and quality, highlighting the importance of incorporating multiple architectural parameters when making form–function interpretations of anatomical tissues. In a complementary study, **Ravosa and Kane** examined developmental plasticity in articular cartilage of the temporomandibular joint (TMJ) in rabbits. In their article "*Dietary variation and mechanical properties of articular cartilage in the temporomandibular joint: implications for the role of plasticity in mechanobiology and pathobiology*" the authors evaluate the effect of increased loading conditions on the histology and biomechanical properties of the articular cartilage of the TMJ. They show that increases in masticatory stresses due to greater cyclical loading result in an increase in proteoglycan expression and a corresponding decrease in the stiffness of the TMJ articular cartilage. These results illustrate how a mechanically challenging diet can produce a potentially mal-adaptive phenotype in mandibular cartilage, an important contribution to the growing literature on the mechanisms of developmental plasticity and their role in functional and evolutionary interpretations of morphology.

**Thompson and colleagues,** in their study "*Bone up: craniomandibular development and hard-tissue biomineralization in neonate mice*", provide novel insights into the links between hard tissue biomineralization and cranial bone formation. After measuring tissue mineral density in multiple sites across the mouse cranium, the authors recorded an increase in biomineralization levels during perinatal ontogeny in the calvaria and the mandible. They also found variable mineral density across the skull, with the mandible and the calvaria showing the highest and lowest levels, respectively. The results suggest that variations in the biomineralization levels are influenced by the functional role of each of the examined bone sites.

**Menegaz and Ravosa**'s paper *"Ontogenetic and functional modularity in the rodent mandible"* explores the role of seasonal and ontogenetic changes in diet on growth and plasticity of the mandible. Using weaning rats as a model, they compared jaw morphology across cohorts differing in their exposure to dietary mechanical properties throughout ontogeny to understand how and where variation in mandibular morphology arises. Results reveal that the impact of diet differently affects different regions of the mandible, and that the timing of exposure to different diets is also important. Thus, this study has implications for understanding how the mandible responds to altered loads over an important period of growth and maturation, and for understanding potential sources of epigenetic influences.

## 3. Conclusion and outlook

The papers presented in the symposium and published here demonstrate the complexity of the mammalian feeding apparatus, the study of which requires the integration of observational, experimental and modelling studies. Contributions to this symposium emphasize the importance of developmental plasticity at multiple morphological levels for understanding not only the adult morphology but also how the system is maintained through ontogeny. For the design of the mammalian feeding system, developmental plasticity might be particularly important considering the changes in the feeding mechanical environment during weaning. For example, variation in onset of mastication and exposure to routine chewing loads will have considerable effect on the growth of the developing alveolar bone. In the same vein, the effect of variability in food availability in seasonally fluctuating environments on adult morphology is still not fully understood. This symposium emphasized that the skull responds variably to mechanical stimuli during feeding, highlighting the need for more *in vivo* data on patterns of strain, muscle activation and kinematics during ontogeny. In addition, modelling studies are needed to relate the patterns of plasticity to observed stress and strain regimes during development.

Adult *in vivo* data, however, have been more readily available. Work presented in this symposium shows the importance of recording bone strain, muscle activation and kinematics simultaneously to enhance our understanding of the function of the adult masticatory system during feeding and when engaging in non-feeding behaviors, including gape-related social behaviors. The variation in *in vivo* data can be associated with differences in muscle and joint morphology between species as well as individual differences when dealing with different foods. This highlights the modulatory capacity of the feeding system and the different mechanical regimes that the masticatory apparatus is exposed to during experimental, and more importantly, during natural conditions. This is especially important when evaluating masticatory system design. The relationship between form and function has usually been studied from a perspective of specific optimality criteria. In the feeding system, these criteria are diverse (e.g., ability to produce or resist bite force at a range of gapes) and deciding which of these is more important is not trivial. In addition, the feeding apparatus is not only used for feeding but also for other functions such as vocalizations and social displays, which might produce trade-offs between parts of the system. To address this complexity, it is necessary to evaluate the form–function relationship of the feeding apparatus within a functional, ecological, and historical framework. This requires an integration of laboratory studies with field observations of natural behaviors to understand the relative importance of different uses of the feeding system. Additionally, studying evolutionary changes in morphology is essential for understanding how performance has changed in association with ecological shifts in diet. However, obtaining experimental *in vivo* data from a wide range of mammals is unfeasible so modelling techniques that allow us to study how changes in feeding behaviors might affect overall feeding performance are imperative. As shown in this issue, validated mechanical models can be used to explore how variability in different morphological and physiological features (e.g., muscle force or bite position) can produce different complex stress regimes across the cranium and mandible. The use of these experimentally informed models has the potential to greatly increase our understanding of the form–function relationship of the feeding system in conditions not easily accessible through experimental recordings. Thus, the combination of observational, theoretical, experimental and modelling approaches can provide an effective and productive framework to study the development, functional morphology, and evolution of the mammalian feeding system.

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