Comparative finite element analysis of the cranial performance of four herbivorous marsupials

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**Abstract**

Marsupial herbivores exhibit a wide variety of skull shapes and sizes to exploit different ecological niches. Several studies on teeth, dentaries and jaw adductor muscles indicate that marsupial herbivores exhibit different specializations for grazing and browsing. No studies, however, have examined the skulls of marsupial herbivores to determine the relationship between stress and strain, and the evolution of skull shape. The relationship between skull morphology, biomechanical performance and diet was tested by applying the finite element method to the skulls of four marsupial herbivores: the common wombat (*Vombatus ursinus*), koala (*Phascolarctos cinereus*)*,* swamp wallaby (*Wallabia bicolor*) and red kangaroo (*Macropus rufus*). It was hypothesized that grazers, requiring stronger skulls to process tougher food, would have higher biomechanical performance than browsers. This was true when comparing the koala and wallaby (browsers) to the wombat (a grazer). The cranial model of the wombat resulted in low stress and high mechanical efficiency in relation to a robust skull capable of generating high bite forces. However, the kangaroo, also a grazer, has evolved a very different strategy to process tough food. The cranium is much more gracile and has higher stress and lower mechanical efficiency, but they adopt a different method of processing food by having a curved tooth row to concentrate force in a smaller area and molar progression to remove worn teeth from the tooth row. Therefore, the position of the bite is crucial for the structural performance of the kangaroo skull, while it is not for the wombat which process food along the entire tooth row. In accordance with previous studies, the results from this study show the mammalian skull is optimized to resist forces generated during feeding. However, other factors, including the lifestyle of the animal and its environment, also affect selection for skull morphology to meet multiple functional demands.

**Introduction**

Among the four orders within Marsupialia, the Diprotodontia is the most diverse group and includes many iconic Australian species, such as kangaroos, koalas and wombats. Almost all of the living diprotodonts are herbivorous, although some incorporate a more insectivorous or omnivorous diet where available. The order also exhibits a variety of sizes and morphologies from the tiny 10 g feather-tail glider (*Acrobates pygmaeus*) to the largest kangaroo, the red kangaroo (*Macropus rufus*) which can weigh up to 90 kg ([Dawson, 1995](#_ENREF_16)). This diversity allows species to exploit many different ecological niches.

Within the suborder Vombatiformes, wombats and koalas display different morphology adapted for either grazing (eating primarily the leaves of grasses) or browsing (feeding primarily on the leaves and stems of woody plants and herbs). Wombats are unique among marsupials in having hypsodont molars for processing a diet composed of tough vegetation, including tussock grasses ([Triggs, 2009](#_ENREF_61); [Tyndale-Biscoe, 2005](#_ENREF_65)). The jaw adductor musculature is large and well suited to generate a very high bite force. The zygomatic arch is set well away from the midline and the temporalis muscle is confined to the lateral surface of the cranium giving the wombat’s skull a broad, flat appearance. The laterally displaced zygomatic arch relative to the ascending ramus of the mandible allows the masseter muscles to exert a very strong lateral force to the jaw, as well as the usual compressive force ([Murray, 1998](#_ENREF_40); [Tyndale-Biscoe, 2005](#_ENREF_65)). Mastication is characterized by short powerful chewing strokes using only the muscles of the working-side ([Crompton et al., 2008](#_ENREF_13)).

In contrast, koalas are browsers and almost exclusively consume leaves from the genus *Eucalyptus* ([Moore and Foley, 2000](#_ENREF_39)). As a consequence, the skull and tooth morphology of koalas reflects a diet of relatively soft vegetation. Koala molars are characterized as having four tightly interlocking cusps with curved blades well suited for shearing eucalyptus leaves ([Lanyon and Sanson, 1986](#_ENREF_32)). The close interlocking pattern is essential for the efficient scissor-like action of the cutting edge. Unlike in wombats and macropods, koalas do not possess an inflected angle of the mandible and hence, exhibit a masticatory motor pattern more similar to an alpaca than a wombat ([Crompton et al., 2010](#_ENREF_14)). The incisors and premolars do not restrict transverse jaw movement in the koala as they do in macropods ([Crompton, 2011](#_ENREF_12)).

The teeth of wallabies and kangaroos (macropods) reflect a range of diets from facultative insectivore and granivore through to strictly browsers or grazers with intermediates between the latter two ([Sanson, 1989](#_ENREF_52)). Grazing macropods, such as those from the genus *Macropus,* have modified their molars to crop and break down tough grasses which compose 90% of their diet ([Sanson, 1980](#_ENREF_51); [1989](#_ENREF_52)). They have evolved high-crowned transverse lophs adapted to shear food as the jaw moves vertically, and to crush food between the lophs and the well-developed links as the jaw moves transversely ([Crompton, 2011](#_ENREF_12); [Sanson, 1980](#_ENREF_51)). All grazing kangaroos also exhibit some degree of molar progression, a reduced premolar and a dorsally convex curve of the lower tooth row so that the whole tooth row is never in contact at one time. Molar progression allows worn teeth to be removed from the occlusal plane and gradually replaced by unworn teeth that move anteriorly in the mandible and dorsally into the occlusal plane. As a tooth becomes so worn that it is useless, it moves anteriorly and ventrally out of the occlusal plane. These features correlate with a predominant diet of tough grass ([Bensley, 1903](#_ENREF_5); [Ride, 1959](#_ENREF_49); [Sanson, 1980](#_ENREF_51); [1989](#_ENREF_52)).

In contrast, browsing wallabies, such as the swamp wallaby (*Wallabia bicolor*), have more simple molars without strong links between the lophs, a well-developed premolar, a flat tooth row and no molar progression ([Sanson, 1980](#_ENREF_51); [1989](#_ENREF_52)). These features combined, the swamp wallaby has a cheek tooth row crushing action for processing softer plant material. Worn molars therefore retain some useful function and are not replaced over the life of the individual. The lower tooth row remains flat, so that all teeth occlude simultaneously in the adults.

In the present study, the finite element method is applied to examine the differences in biomechanical performance between the skulls of four herbivorous marsupials: the common wombat (*Vombatus ursinus*), the koala (*Phascolarctos cinereus*), the swamp wallaby (*Wallabia bicolor*) and the red kangaroo (*Macropus rufus*). These species have different dietary preferences and show differences in skull morphology (Figure 1). The objective is to gain a better understanding of how cranial morphology reflects diet and feeding ecology of marsupial herbivores by comparing biomechanical metrics, such as stress and strain.

Finite element analysis (FEA) is an engineering technique that reconstructs stress, strain and deformation in response to applied loads, taking into account the material properties and geometry of the structure ([Bright, 2014](#_ENREF_6); [Rayfield, 2007](#_ENREF_47); [Richmond et al., 2005](#_ENREF_48)). The finite element (FE) method centres on representing complex geometry by a finite number of elements with simple geometries, readily analyzed using mathematics. This allows the mechanical function of complex structures, such as the skull and the masticatory apparatus, to be studied in a non-invasive way. The FE method has been used to investigate cranial morphology and feeding biomechanics in many taxa, including mammals, reptiles, birds and dinosaurs ([Attard et al., 2011](#_ENREF_1); [Cox et al., 2012](#_ENREF_11); [Dumont et al., 2011](#_ENREF_17); [Dumont et al., 2005](#_ENREF_19); [Figueirido et al., 2014](#_ENREF_22); [Gill et al., 2014](#_ENREF_26); [Jasinoski et al., 2009](#_ENREF_30); [McHenry et al., 2006](#_ENREF_35); [Oldfield et al., 2012](#_ENREF_41); [Piras et al., 2013](#_ENREF_42); [Rayfield, 2004](#_ENREF_45); [2005](#_ENREF_46); [Soons et al., 2012](#_ENREF_54); [Tseng and Wang, 2010](#_ENREF_64); [Young et al., 2012; among many others](#_ENREF_72)).

It is hypothesized that the differences in skull shape have arisen to better accommodate the stresses produced by the given processing requirements of the animals dietary preference. Different skull morphologies will display different patterns of stress and strain during biting and these differences may relate to the diets, bite location and bite force between the four species. Therefore, the skull morphology of each species will be optimally adapted for their diet and mode of feeding. Specifically, it is hypothesized that grazers will be more specialized for processing tough vegetation, and this will correlate with higher performance in one or more performance metrics - lower stress and higher bite forces. In contrast, browsers have a greater variance in dietary habits and hence will be well adapted to multiple feeding modes, but may experience higher stress under similar biting conditions to grazers.

**Material and Methods**

*Data Acquisition*

The crania and mandibles of a swamp wallaby (*Wallabia bicolor*; NMV C10226) and a red kangaroo (*Macropus rufus*; NMV C23045) were scanned by computed tomography (CT) using a Siemens Sensation 64 scanner (Siemens Medical Solutions) at St Vincent's Public Hospital in Melbourne, Australia (Table 1). CT scans and magnetic resonance imaging (MRI) of wet specimens of a common wombat (*Vombatus ursinus*) and koala (*Phascolarctos cinereus*) were generated by the University of Melbourne Veterinary Hospital in Werribee (Table 1). These specimens were also used for dissection, along with two additional wombats, two koalas and one eastern grey kangaroo (*Macropus giganteus*). Wet specimens were collected under the Victorian Department of Sustainability and Environment permit to receive and retain specimens of wildlife found dead from natural or accidental causes (Flora and Fauna Permit number 10005574); no animals were euthanized for this study. CT scans of a dry skull of a koala (*P. cinereus*) were also generated at the University of Texas (Austin) CT facility and obtained from the Digital Morphology Library (http://www.digimorph.com) with permission from Dr. Timothy Rowe, Project Director of Digimorph.

*Model Construction*

The CT data were imported into the image visualization and processing software program Avizo (Visage Imaging, Inc.), in which a combination of automated thresholding, the process of selecting and isolating areas of interest based on their grey values, or density, and manual editing were used to separate the cranium from the mandible and generate 3D surface models. The 3D surface models were constructed from a mesh of triangular elements, which were smoothed and edited to improve the quality of the mesh, including testing the aspect ratio and the dihedral angles of the surface triangles. The aspect ratios of the triangles were adjusted to below 10 and the dihedral angles were set at above 10 degrees to ensure a good quality mesh. The surface meshes were then converted to solid 3D FE meshes composed of 4-node tetrahedral elements (tet4) (Table 2). The element size was chosen so that thin bones in the skull were composed of at least two elements thick to simulate bending in the models The element type and mesh density where considered sufficient for this type of comparative analysis ([Bright and Rayfield, 2011a](#_ENREF_8); [Tseng and Flynn, 2015](#_ENREF_62)). Finally, each model was exported as an Abaqus input file (\*.inp) for easy importation to the FEA software package Abaqus CAE v6.12 (Simulia). The cranium and mandible were imported separately for each species, so that the mandible could be used for muscle force alignment.

*Material Properties*

Due to a lack of data on the material properties for the bone in marsupial herbivores, all models were assigned as homogeneous and isotropic. Average values of Young’s modulus (E = 20 GPa) and Poisson’s ratio (ν = 0.3) for mammalian bone were assigned to all models in Abaqus CAE ([Dumont et al., 2005](#_ENREF_19); [Erickson et al., 2002](#_ENREF_21); [Figueirido et al., 2014](#_ENREF_22); [Tseng et al., 2011](#_ENREF_63); [Tseng and Wang, 2010](#_ENREF_64)). This methodology is suitable for the present study, which compares relative stress and strain values, and is not concerned with absolute values. It has also been demonstrated that varying material properties within the model has less of an impact on large-scale patterns of stress and strain than variation in model shape ([Strait et al., 2005](#_ENREF_57); [Tanner et al., 2008](#_ENREF_58); [Walmsley et al., 2013](#_ENREF_67)). Therefore, by applying the same material properties to each model, and modeling the bone as homogenous and isotropic, it will enable direct comparison between models and is not likely to affect confidence in the results obtained.

*Constraints*

To prevent rigid body motion, each model was constrained by a single node at both temporomandibular joints (TMJ). The left TMJ was fully constrained against displacement in the x- (lateral), y- (vertical), and z-direction (anterior-posterior), and the node on the right TMJ was constrained in the y- and z- axis to allow lateral displacement of the skull. A single node was also constrained at the bite point(s) in the axis perpendicular to the occlusal plane.

A number of biting scenarios were modeled to simulate bilateral and unilateral molar biting and incisor biting. It has been observed that wombats, koalas and macropods all display different modes of feeding ([Crompton, 2011](#_ENREF_12); [Crompton et al., 2008](#_ENREF_13); [Crompton et al., 2010](#_ENREF_14); [Lentle et al., 2003](#_ENREF_33); [Sanson, 1989](#_ENREF_52)), so all possible molar biting scenarios were modeled for each species: unilateral biting on each molar, bilateral biting on each pair of molars and on the entire tooth row for both unilateral and bilateral biting. When the incisors were constrained, the models were loaded bilaterally.

*Modeling Muscle Forces*

The jaw adductor musculature was modeled as three main components; the temporalis, masseter and pterygoid muscles. Each muscle group was modeled with two to four subdivisions based on other published studies ([Crompton et al., 2008](#_ENREF_13); [Davison and Young, 1990](#_ENREF_15); [Murray, 1998](#_ENREF_40); [Tomo et al., 2007](#_ENREF_60); [Warburton, 2009](#_ENREF_68)) and dissections carried out for this study following the methods outlined in [Sharp and Trusler (2015)](#_ENREF_53). The muscles included are *masseter superficialis, masseter profundus, zygomaticomandibularis*, *temporalis superficialis, temporalis posterior, temporalis profundus, pterygoideus medialis* and *pterygoideus lateralis.*

The maximum force produced by a muscle is proportional to the total cross-sectional area of all muscle fibers perpendicular to their longitudinal axes, or the physiological cross-sectional area (PCSA). Muscle force magnitudes are then calculated by multiplying muscle cross-sectional area by a constant value of muscle stress, 0.3 N mm-2 ([Cox et al., 2012](#_ENREF_11); [McHenry et al., 2007](#_ENREF_36); [Rayfield, 2007](#_ENREF_47); [Strait et al., 2005](#_ENREF_57); [Thomason, 1991](#_ENREF_59); [van Spronsen et al., 1989](#_ENREF_66); [Weijs and Hillen, 1985](#_ENREF_69); [Wroe et al., 2005](#_ENREF_71)). Morphological cross-sectional area (MCSA), the cross-sectional area perpendicular to the longitudinal axis at the thickest part for each muscle, can be substituted for PCSA in muscles where the fibers run parallel to the longitudinal axis. All muscles for all species were modeled with parallel fibers as was observed in dissections of fresh wombat, koala and kangaroo specimens.

All muscle forces applied to the models were calculated from the MSCA of 3D digitally reconstructed muscles for each species. Each muscle was reconstructed by manually segmenting the muscles in Avizo from CT and MRI data. Each muscle was selected first in the frontal plane and then edited in the sagittal and horizontal planes for biological accuracy. Muscle attachment sites and orientation were also identified for each muscle from gross dissections, and this information was used to validate the digital reconstructions. The MCSA for each muscle was then measured from the 3D muscle reconstructions in Rhinoceros 5.0 ("Rhino") following a similar method to [Quayle (2011)](#_ENREF_44). In summary, a line representing the fiber direction of each muscle was drawn along the surface of the reconstructed muscle in the 3D model from the midpoint of the origin to the midpoint of the insertion. This line was then used to produce perpendicular cross-sections through the muscle, and the area at the thickest point was calculated (Figure 2). The estimated muscle force for each muscle for each species is presented in Table 3.

Muscle forces were applied to the skulls by distributing the load for each muscle over the entire surface of the muscle origin. Muscle orientations were determined by creating a vector between the origin and the corresponding insertion on the mandible. In order to simulate unilateral biting and differential activation of the working- and balancing-side muscles, a percentage of maximum activation (muscle force) was applied to the opposite site to the bite point (balancing-side), while maximum force was applied to the working-side. Activation of balancing- and working-side muscles differ for each species, so a range of values were applied to each model based on data derived from muscle activation patterns in marsupials ([Crompton, 2011](#_ENREF_12); [Crompton et al., 2008](#_ENREF_13); [Crompton et al., 2010](#_ENREF_14)). Seven different simulations were run for each species: one with all balancing-side muscles at 0%, one with all balancing-side muscles at 10%, and so on up to 60% of the maximum muscle force applied to the working-side.

*Analyzing Model Performance*

The type of stress reported in this study is von Mises (VM) stress, which is a good predictor of stress in ductile materials. The failure of ductile materials, such as bone and many other biological materials, most often occurs due to deformation. Ductile failure is predicted when the VM stress reaches the yield strength of the material, so VM stress is a good indicator of the strength of a structure. When comparing the maximum VM stress between models, the structure with the lower value is less likely to fail under a given load. Median VM stress was also compared for each model. This removes the influence of modeling artifacts and outliers due to constraints on single nodes, and gives an idea of the spread of stress over the entire model. Stress distributions plotted as contour maps were extracted from Abaqus. The distribution of stress was also analyzed by sampling stress values in different areas of the cranium. For analysis of variation over the dorsal cranium, ten equidistant landmarks were sampled along the mid-sagittal axis from the tip of the nasals to the occipital crest. The maximum stress was also calculated for the working-side and balancing-side zygomatic arch for each species.

Strain energy (U) is a performance metric that quantifies energy efficiency, or work efficiency. Analyses of stresses or deformations alone provide limited insight into the trade-offs between stiffness and internal load distributions. Strain energy is the energy stored in the structure due to the work done by the externally applied loads. The strain energy of a structure equals the area under the stress-strain curve and relates to the stiffness of a structure. A stiff structure will more easily transfer energy from the muscle force to the bite, whereas a flexible, compliant structure will store more energy and work will be expended to deform the structure ([Dumont et al., 2009](#_ENREF_18)). Assuming that the function of the jaw system is to transmit forces more efficiently, without causing failure, this implies that the system should minimize deformation. Thus, stiffer models will be more efficient than compliant models.

Finally, the mechanical efficiency of each model during biting was compared by calculating the ratio of the bite reaction force to the applied muscle force ([Dumont et al., 2009](#_ENREF_18)). This measure provides a scale independent estimate of the efficiency of the jaw lever system that is defined by the fulcrum (TMJ), the effort (muscle force) and the resistance (bite point) as a third-class lever. It tells us the efficiency at which the muscle force is translated to bite force.

*Scaling*

When comparing performance metrics such as stress and strain, the size of the structure must be taken into account. Results such as strain energy and maximum VM stress will depend on the size of the structure. For example, a smaller structure will be stiffer than a larger one, whereas a larger structure will be stronger. To remove the effects of size and compare the performance of the models based on their shape alone, the models were scaled to the same surface area or volume. All surface area and volume data was calculated from the models in Avizo.

To compare the strength (VM stress) between models, the models were scaled to the same ratio of muscle force to surface area. We can compare the stress results of model *A* and *B* by scaling the results for model *B* to match the force (F):surface area (SA) ratio of model *A* following equation 1 ([Dumont et al., 2009](#_ENREF_18)):

(1)

When comparing strain energy, which is the amount of energy stored per unit volume, the models were scaled to the same force:volume ratio. Therefore, to compare strain energy (U) of models of different volume (V), the results from model *B* can be scaled to the same force:volume ratio to model *A* according to equation 2 ([Dumont et al., 2009](#_ENREF_18); [Strait et al., 2010](#_ENREF_56)):

(2)

*Validation*

The only way to validate FE models is to compare the results to *in vivo* or *in vitro* data of bone strain ([Bright, 2014](#_ENREF_6); [Rayfield, 2007](#_ENREF_47)). Studies of *in vivo* forces and strains generated during biting are often logistically challenging to accomplish, as they require specialty equipment. To date, there are no data on bone strain in the crania of the marsupial herbivores modeled in this study. However, the general approaches applied here have been validated against experimental data from other taxa ([Bright and Gröning, 2011](#_ENREF_7); [Bright and Rayfield, 2011b](#_ENREF_9); [Kupczik et al., 2007](#_ENREF_31); [Metzger et al., 2005](#_ENREF_37); [Porro et al., 2013](#_ENREF_43)).

In the absence of validated data for material properties and forces, a sensitivity analysis was carried out to determine the effects of modeling different bite positions and muscle activation patterns. Previous sensitivity studies have shown that variations in muscle force and bite position has the greatest effect on FEA results. In these studies, the number of muscles, and total force generated by muscles, is more important than muscle activation patterns, or using multiple material properties when comparing broad patterns of deformation and stress ([Fitton et al., 2012](#_ENREF_23); [Metzger et al., 2005](#_ENREF_37); [Ross et al., 2005](#_ENREF_50); [Strait et al., 2005](#_ENREF_57); [Walmsley et al., 2013](#_ENREF_67)). Hence, muscle forces were modeled as accurately as possible by including multiple muscle groups and 3D muscle vectors directed from the origin to the insertion for each muscle. For the present study a comparative approach has been applied, which compares relative stress and strain values, and is not intended to predict absolute values ([Attard et al., 2011](#_ENREF_1); [Dumont et al., 2005](#_ENREF_19); [McHenry et al., 2006](#_ENREF_35); [Rayfield, 2007](#_ENREF_47); [Wroe, 2008](#_ENREF_70)). Therefore, modeling complex material properties of trabecular bone, cortical bone and tooth enamel, cranial sutures, or the periodontal ligament was not considered necessary for the current study, and would likely introduce more complexity and assumptions that cannot be validated with *in vivo* or *ex vivo* data at this time.

**Results**

*Bilateral biting*

The predicted distribution of VM stress is different for all species for each biting location (Figure 3). In all models the rostrum is most highly stressed during incisor biting, and the zygomatic arch is the most highly stressed region in molar biting. However, in the common wombat and koala, which have shorter rostrums compared to macropods, the rostrum is also slightly stressed during biting at the premolar. For all bite locations, the koala also has four clear hot spots of stress on the zygomatic arch: on the dorsal and ventral surface mid-way along its length; on the masseteric process at the attachment for the superficial masseter; and, at the zygomatic root of the squamosal, superior to the TMJ. In contrast, the red kangaroo, swamp wallaby and common wombat models only experience two hot spots: kangaroo and wallaby both at the zygomatic suture and the masseteric process; and, wombat at the anterosuperior site of the zygomatic suture and the excavated maxillojugal region located under the orbit. The koala, wallaby and kangaroo models also experience higher stress at the anterior ventral boarder of the orbit, which is not present in the wombat.

Figure 4 presents quantitative performance metrics that complement the stress contour plots for bilateral biting at different bite points. The kangaroo model registered the highest maximum VM stress for all cheek tooth locations, indicating that the cranial structure is more susceptible to fracture under high forces. The wallaby model only exceeded the kangaroo for maximum VM stress when biting at the incisors. The kangaroo also registered a distinct increase in maximum stress when biting at the fourth molar; which biting at M1 maximum stress was lowest and biting at M4 was considerably higher. This increase is slightly less distinct in the wallaby and is not evident in the wombat or koala models that maintain a relatively flat distribution of stress along the entire tooth row. The koala model experiences the lowest stress at the incisors, premolar and first molar, indicating that for these bite locations the koala model is more resistant to fracture. The wombat model also experiences relatively low maximum VM stress, especially at the second, third and fourth molars.

When comparing median VM stress, which eliminates the outliers created by single node constrains and offers an estimate of the distribution of stress over the entire skull, the wombat model performs better than all other models; it is least stressed and therefore more resistant to fracture overall (Figure 4). Low median VM stress may also indicate that the distribution of stress over the skull is more even in the wombat model. The highest median VM stress was recorded in the kangaroo model, and intermediate stress was recorded for the wallaby and koala models.

The red kangaroo also performed poorly in terms of the mechanical efficiency with which muscle force was transmitted to bite force, or the efficiency of the jaw as a third-class lever (Figure 4). For all models, the mechanical efficiency increased along the tooth row as the bite point (the resistance) approached the TMJ (the fulcrum). The wombat model is the most mechanically efficient when biting at the molars (except M4 where the wallaby is most efficient) and the koala is the most mechanically efficient when biting at the incisors. The kangaroo model is the least mechanically efficient for all bite locations.

When comparing the energy efficiency of the models, the koala model has the lowest internal strain energy and is therefore stiffer, spending less energy on deformation (Figure 4). The common wombat has higher strain energy for all bite locations except M4, indicating it is less stiff and the least energy efficient.

*Unilateral biting*

Figure 5 displays dorsal view plots of stress distribution for each model while biting at the left second molar and the balancing-side muscle force is half that of the working-side. The pattern of stress when viewed in lateral view on the working-side is similar to that for bilateral biting in Figure 3. The balancing-side zygomatic arch, however, experiences less stress during unilateral biting for all models (Table 4). The quantitative results for stress distribution along the dorsal surface are also presented in Figure 5. The stress distribution changes considerably for each species but is generally highest in the middle of the cranium where it is narrowest. Overall, the kangaroo model experiences higher stress at most locations along the dorsal surface of the skull.

Table 4 presents quantitative performance metrics for unilateral biting at the left second molar when the balancing-side muscle force is 50 percent of the working side. For this biting scenario, the wombat performed best in terms of mechanical efficiency and has the lowest VM stress between the models. This would indicate that the cranial structure is very efficient at transmitting muscle force to bite force and is more resistant to failure under high loads. In terms of energy efficiency, however, the wombat has the highest strain energy and therefore spends more energy in deformation. The red kangaroo model has the lowest mechanical efficiency and experiences the highest stresses over the skull, meaning it is more likely to fail under high loads. However, it has low internal strain energy so it is maximising energy efficiency by being stiffer. The koala model has the lowest strain energy, indicating it is the stiffest model, and has intermediate values for the other performance metrics.

As a part of the sensitivity study, the balancing-side muscle activation was varied during unilateral biting to identify how this affects the mechanical response in each model. Since each species studied here exhibits different muscle activation while chewing ([Crompton, 2011](#_ENREF_12)), the balancing-side muscle force was adjusted to test a range of scenarios (from zero to 60% activation) to allow comparisons between species. The level of muscle activation on the balancing-side did not have a great effect on the overall trends seen in stress, strain or mechanical efficiency (Figure 6). When the balancing-side muscle activation was increased from 0 to 60%, median VM stress, maximum VM stress and strain energy increased in each model. The only exception was the wombat model, in which maximum VM stress decreased until an activation of 40% and then increased. Mechanical efficiency remained relatively constant for each model. In most cases, this means that varying the activation of the balancing-side muscles does not change the trends or conclusions drawn from this comparative study. The only exception is maximum VM stress in which the wombat model decreased, while the other models increased. At lower values of balancing-side muscle activation, the wombat model has slightly higher VM stress compared to the koala model. If we were interested in absolute values for validation with *in vivo* data, the activation would need to be considered to provide specific conditions for each species. As each species displays different masticatory motor patterns while chewing, it might be important to simulate the activation of each species to obtain absolute values that match those seen in reality.

**Discussion**

The results indicate that all four models behave differently under biomechanical loads, reflecting variation in skull morphology which is potentially correlated with diet. When simulating unilateral biting, the common wombat (*V. ursinus*) model experienced relatively low maximum and median von Mises (VM) stress compared to the other species modeled (Table 4). The wombat model also had the highest mechanical efficiency meaning the cranium is not only strong, but also very efficient at transmitting muscle force to bite force. This indicates that the wombat skull is optimized to resist failure from high bite forces, and, efficiently transmits the force from its large masticatory muscles to the teeth. A wombat’s diet is composed of tough vegetation, including tussock grasses, and many adaptations have evolved to process such abrasive food. The broad flat skull, short rostrum, and large masseter muscles all provide a powerful compressive bite along the cheek tooth row. Hypsodont molars are a unique case in marsupials and require constant abrasion to maintain a functional tooth and cutting edge, and hence, this requires a powerful grinding system. Together, these morphological features provide strong, robust skulls able to resist the high biomechanical demands imposed by feeding on tough vegetation.

Red kangaroos (*M. rufus*) also eat tough, abrasive vegetation but have evolved a very different method of processing this food. In contrast to wombats, grazing kangaroos have long rostra, narrow skulls and have a curved tooth row with molar progression where new molars erupt from the back of the tooth row and move forward to replace worn teeth at the front. These morphological differences also manifest as biomechanical differences: high stress and low mechanical efficiency in the kangaroo compared to the wombat. During unilateral biting, the kangaroo model experienced the highest maximum and median VM stress and the lowest mechanical efficiency, indicating that the cranium is relatively weak and inefficient at transmitting muscle force to bite force. A curved tooth row and molar progression have evolved to enhance the ability of kangaroos to effectively process the tough, abrasive vegetation without over stressing the skull. The curved tooth row allows pressure, or force, to be concentrated between the first and second molar to grind vegetation ([Sanson, 1980](#_ENREF_51); [1989](#_ENREF_52)), and worn teeth are removed from the tooth row when they are no longer functional. The position of the bite is crucial for the structural performance of the skull: maximum stress, and hence the likelihood of failure is lowest when biting at M1.

Different tooth row morphologies observed between the wombat and kangaroo (flat versus curved respectively) also result in different patterns of stress with changes in bite position. The maximum VM stress recorded for the wombat remains relatively consistent as the bite point moves from the premolar to the fourth molar; the lowest stress being recorded at M2 and M3. In contrast, the maximum stress for the kangaroo peaks at the premolar and fourth molar and is lowest at the incisors and first molar. Premolar and fourth molar contact is not a major or consistent part of chewing in adult kangaroos, and therefore greater stresses are experienced when forces act at these points. When biting at M1, as they do in reality, the kangaroo skull experiences less stress and is therefore less likely to fail. This is likely connected to the condition in which they chew, and as such the skull is optimized for chewing at this position. Conversely, all molars have a significant role for wombats which process food along the entire tooth row, exerting an effect on skull performance and shape by applying forces at these points.

The difference between the wombat and kangaroo reflects their independent lines of evolution and multiple factors that drive selection of skull morphology. Many studies have used stress is a predictor of diet in extinct and extant animals, concluding that low stress indicates an adaptation for stronger skulls, given that lower stress means it is less likely to fail, and therefore a diet high in hard foods is likely ([Attard et al., 2011](#_ENREF_1); [Attard et al., 2014](#_ENREF_2); [Dumont et al., 2005](#_ENREF_19); [Tanner et al., 2008](#_ENREF_58); [Wroe, 2008](#_ENREF_70); [Young et al., 2012](#_ENREF_72)). It is assumed that selection for high structural strength is optimal and a driver for evolution within species that consume hard foods. Similarly, increasing mechanical efficiency is viewed as optimal to transmit muscle force to bite force. However, the kangaroo model had both higher stress and lower mechanical efficiency, despite the high biomechanical demands of consuming tough food. In accordance with previous studies, these results show the mammalian skull may not be optimized solely to resist forces generated during feeding ([Dumont et al., 2011](#_ENREF_17); [Dumont et al., 2005](#_ENREF_19); [Hylander and Johnson, 1997](#_ENREF_29)). Non-biomechanical factors or ecological factors, including the lifestyle of the animal and its environment (e.g. latitude) have a role in selection for skull morphology to meet multiple functional demands ([Hadley et al., 2009](#_ENREF_27); [Milne and O'Higgins, 2002](#_ENREF_38)). Phylogenetic, ecological, locomotor and sensory constraints on the evolution of the kangaroo skull may restrict its size and morphology. Analyzing the lower jaws may have a stronger link to diet as they are not as affected by other constraints or functional influences such as housing neural and sensory organs.

Another factor that may influence skull shape in marsupials is digestive tract morphology; wombats and koalas have hindgut fermentation, while macropods have foregut fermentation ([Hume, 1984](#_ENREF_28); [Stevens and Hume, 1998](#_ENREF_55)). In ungulates, [Fletcher et al. (2010)](#_ENREF_24) observed that hindgut feeders have jaws that show significantly lower levels of stress than foregut feeders (e.g. they are more “robust”) and this may be due to their relatively greater levels of food ingestion and mastication. The hindgut digestive system in wombats enables them to utilize a diet high in fiber while having small home ranges, low food intake and longer retention times ([Barboza, 1993](#_ENREF_3); [Barboza and Hume, 1992](#_ENREF_4)). However, the breakdown of food by the teeth is particularly important to release cell contents and maximise the energy available because once the food has passed into the digestive tract, it cannot return for further mechanical processing by the teeth. Therefore, wombats need to chew their food considerably more before it is swallowed. This may explain why the skull of wombats exhibits less stress (e.g. higher performance) than grazing kangaroos. Grazing kangaroos like the red kangaroo can also utilize a diet high in fiber due to their complex stomach morphology and foregut fermentation. As a consequence of this foregut fermentation system, kangaroos, like ruminants, can regurgitate and chew their food multiple times with the food becoming softer with each cycle, allowing kangaroos to process tough vegetation without high bite forces.

In contrast to wombats and kangaroos, the swamp wallaby (*W. bicolor*) and koala (*P.* *cinereus*) are both browsers consuming softer vegetation. The wallaby has a varied diet including leaves from shrubs and bushes, fungi and some grass ([Edwards and Ealey, 1975](#_ENREF_20); [Sanson, 1980](#_ENREF_51)). This broad diet has manifested morphologically as simple bilophodont molars, a flat tooth row and no molar progression. During unilateral biting, the stress and mechanical efficiency of the wallaby model are intermediate to the wombat and kangaroo models. With a generalist diet, they have maintained generalist skull morphology, because high biomechanical performance, high bite force and strong skulls are not required for processing softer food.

The higher performance of the wallaby skull compared to the kangaroo (e.g. lower stress and higher mechanical efficiency) could be explained by the length of the rostrum. In a recent study using geometric morphometric of cranial shape, it was shown that macropods follow the ‘rule’ that among closely related species, larger mammals tend to have a longer face and a proportionally smaller braincase ([Cardini et al., 2015](#_ENREF_10)). Rostrum length and shape has also been linked to latitude in various species of macropods ([Hadley et al., 2009](#_ENREF_27); [Milne and O'Higgins, 2002](#_ENREF_38)). The relatively longer rostrum in the red kangaroo explains both the higher stress and lower mechanical efficiency compared to the swamp wallaby. In addition, the swamp wallaby can handle stress at different bite positions, whereas the red kangaroo, being a more specialized species with a narrower diet is adapted to function best at speciﬁc bite positions.

Koalas almost exclusively consume leaves from the genus *Eucalyptus* ([Moore and Foley, 2000](#_ENREF_39)), a poor-quality food source high in toxins. Numerous adaptations allow the koala to cope with such a diet, including low energy requirements, a complex hindgut and the ability to regurgitate and remasticate preingested leaf material ([Logan, 2003](#_ENREF_34); [Moore and Foley, 2000](#_ENREF_39)). Being a browser also means they do not consume abrasive silicates or grit. The koala model experiences intermediate median VM stress during bilateral and unilateral biting, indicating that the skull is relatively weak compared to the wombat model, and strong compared to the kangaroo model. During bilateral biting, maximum VM stress was lowest at the incisors, premolars and first molar. This may indicate that koalas have a relatively strong skull when biting at these teeth and these teeth may be the proffered location for chewing in reality.

The koala model has the lowest strain energy, indicating that the skull is relatively stiff compared to the other skull models examined here. This increases work efficiency during mastication by spending less energy on deformation. Since the models have been scaled to remove the effect of size, deformation is due to skull shape alone. The skull shape of the koala is very high compared to macropods and narrow compared to the wombat and this may explain the lower strain energy. It was expected that the wombat model would have the lowest strain energy to increase functional efficiency. Surprisingly, the wombat model had the highest strain energy for almost all biting scenarios, indicating the skull is more compliant than the other skull models. Despite undergoing more deformation, the skull is the strongest (low VM stress) and is therefore least likely to fail under high bite forces. Therefore, the energy spent on deformation may be inconsequential. The temporalis fascia and postorbital ligament were not modeling in this study and may prevent some deformation of the zygomatic arch as it is pulled down by the masseter. Therefore, in future studies it might be interesting to model the effect of these ligamentous structures.

There are some limitations to be addressed in this study. This study provides useful, quantitative comparisons between four species of herbivorous marsupial during simulated biting, but the models used here, like any model, are constrained by the simplifications, assumptions and data used to construct them. Perhaps most critically, the approach used here does not incorporate realistic material properties for bone, enamel, sutures or fascia and ligaments that can affect deformation. This simplification, however, was considered necessary because of the lack of material properties data for marsupials. The assumption was made that this would not affect the conclusions, as the goal of the study was to make broad comparisons of cranial biomechanics, and it was not considered necessary to model the material properties in more detail. It has also been shown in previous work that using homogeneous or inhomogeneous material properties has little effect on stress patterns ([Gil et al., 2015](#_ENREF_25); [Strait et al., 2005](#_ENREF_57); [Walmsley et al., 2013](#_ENREF_67)).

Future work might improve upon this study by increasing the sample size of species, in particular including more species of macropods to compare a broader range of diets and ecological niches. Similarly, the other surviving genera of wombat, *Lasiorhinus*, could be included to examine the role of habitat type and morphology between wombat species. It is also a limitation of this study that the jaw was not modeled, as this structure may correspond more closely to diet as is it not limited by other constraints or functional influences such as housing neural and sensory organs. However, the main aim of this study was to examine the respond of the cranium to biomechanical demands to elucidate the connection between forces during feeding and other factors that might influence skull morphology. In agreement with previous studies, the results of this study show the mammalian skull is optimized to resist forces generated during feeding, but other factors, including phylogeny and ecology, have a role in selection for skull morphology to meet multiple functional demands.

In summary, the results derived from this study offer preliminary evidence to suggest that the biomechanical performance of marsupial herbivore skulls is reflective of their morphology and has links to masticatory demands, including bite location and diet. The results highlight the relative importance of biomechanical and non-biomechanical factors in constraining skull morphology to meet multiple functional demands. Despite the fact that common wombats and red kangaroos have a similar diet of tough, abrasive grasses, their skull morphology is considerably different due to different biomechanical, phylogenetic and ecological factors that drive selection. Tooth and jaw morphology in the kangaroo has adapted to concentrate force in a smaller area, and remove worn molars from the tooth row, instead of having strong skulls with large muscles and high bite forces as seen in wombats. This variation in skull morphology to meet the demands of the same diet suggests a complex interplay of multiple selective pressures in controlling skull shape.

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Figure Captions

**Figure 1.** Three-dimensional finite element models of the skull of *Vombatus ursinus* (row 1), *Phascolarctos cinereus* (row 2), *Macropus rufus* (row 3) and *Wallabia bicolor* (row 4) all scaled to the same skull length. Skulls are shown in lateral (A), dorsal (B) and anterior (C) views. Scale bars represent 5 cm.

**Figure 2**. Muscle force was estimated by calculating the maximum cross-sectional area of each muscle from 3D reconstructed muscles of each species. This process is shown on the internal superficial masseter of the common wombat (*Vombatus ursinus*) where a line representing the vector of muscle force was drawn through the centre of the muscle and the maximum cross-sectional area perpendicular to this line was determined. The maximum cross-sectional area was then multiplied by an estimate of muscle tension (0.3 N mm-2) to give muscle force. This process was repeated for each muscle for all species.

Figure 3. Predicted distribution of von Mises (VM) stresses across the cranial models of the common wombat (*Vombatus ursinus*), koala (*Phascolarctos cinereus*), red kangaroo (*Macropus rufus*) and swamp wallaby (*Wallabia bicolor*) during bilateral biting. Arrows indicate the bite location for each row and the bottom row shows bilateral biting on all molars simultaneously. Warm colors indicate areas of high VM stress and cool colors indicate low stress. Grey areas indicate VM stress that exceeds the specified maximum of 10 MPa.

Figure 4. Biting performance during bilateral biting at each tooth in the red kangaroo (*Macropus rufus*), swamp wallaby (*Wallabia bicolor*), common wombat (*Vombatus ursinus*) and koala (*Phascolarctos cinereus*) cranial models. Abbreviations: I, incisor; PM, premolar; M1, first molar; M2, second molar; M3, third molar.

Figure 5. Predicted distribution of von Mises (VM) stresses across the cranial models of the (A) common wombat (*Vombatus ursinus*), (B) koala (*Phascolarctos cinereus*), (C) red kangaroo (*Macropus rufus*), (D) and swamp wallaby (*Wallabia bicolor*) in dorsal view during unilateral biting at the second molar, balancing-side at 50% activation. Warm colors indicate areas of high VM stress and cool colors indicate low stress. Grey areas indicate VM stress that exceeds the specified maximum of 10 MPa. The graph (E) shows VM stress along the mid-sagittal plane for each species. The positions of the landmarks are shown on the wombat skull on the right.

**Figure 6.** Von Mises (VM) stress, strain energy and mechanical efficiency during unilateral biting at the second molar with varying levels of activation (0 – 60%) of the balancing-side muscles for each species studied.