



FINITE ELEMENT ANALYSIS OF UNGULATE JAWS: CAN MODE OF DIGESTIVE PHYSIOLOGY BE DETERMINED?

Thomas M. Fletcher, Christine M. Janis, and Emily J. Rayfield

ABSTRACT

In order to efficiently deal with cellulose-rich vegetation, different ungulate (hoofed) mammals utilize either foregut (e.g., ruminant artiodactyls) or hindgut fermentation (e.g., perissodactyls, proboscideans and hyraxes). Hindgut fermenters are known to have a greater food intake than ruminants (of similar size and diet), and horses may chew their food more thoroughly on initial ingestion. These facts have led to the prediction that jaws of hindgut fermenters should be more 'robust' than those of ruminants, and on this basis extinct hindgut or foregut fermenters may be identified in the fossil record. This hypothesis was tested by creating 2D finite element (FE) models of the mandible of six pairings of extant foregut and hindgut fermenters matched for body mass. All models were scaled to the same size, constrained at the jaw condyle and first molar, and loaded with 100 N of muscle force, divided between the temporalis and masseter muscles in proportion to the size of their relative insertion areas. Mean Von Mises stress through the mandible at a mid-point transect of the tooth row was recorded and the two groups compared with a paired t-test. The mandibles of extant hindgut and foregut fermenters differed significantly in robustness ($p = 0.023$) with very little overlap in mean stress values.

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INTRODUCTION

A challenge common to all herbivores is the processing of tough plant tissues, notably high in

lignin and cellulose. Cellulose (a polysaccharide) is the major structural component of the plant cell wall, and it cannot be hydrolysed by the endogenous enzymes of vertebrates (Stevens and Hume

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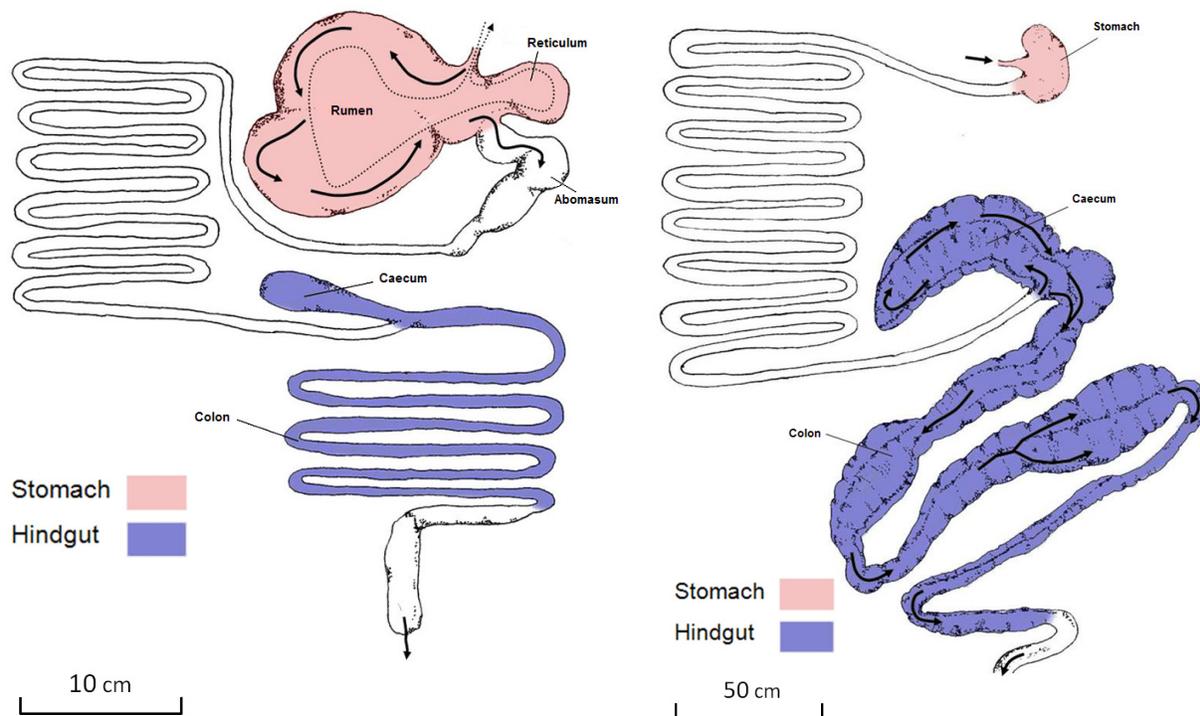


Figure 1.1. Details of the digestive physiology of a typical ruminant (a cow) (modified from Stevens and Hume 1995). **1.2.** Details of the digestive physiology of a typical hindgut fermenting species (a horse) (modified from Stevens and Hume 1995).

1995). It is only after symbiosis with cellulase-producing micro-organisms that sufficient nutritional content can be gained from this food source. Herbivorous mammals all utilise fermentation chambers in some portion of the gastrointestinal tract to maximise exposure of fibrous foods to these digestive bacterial agents. The fermentation chamber may be situated in the foregut area of the stomach (e.g., ruminating artiodactyls, hippos, colobine monkeys, sloths, muroid rodents, kangaroos, koalas) or in the hindgut area of the caecum and/or colon (e.g., perissodactyls, hyraxes, proboscideans, ateline monkeys, caviomorph rodents, rabbits, wombats). This study is concerned primarily with the differences between ruminating artiodactyls (antelope, cattle, deer, giraffe, camels, etc.), which are the only foregut fermenters to regurgitate their food (i.e., “chew the cud”), and perissodactyls (horses, rhinos, and tapirs) (Figure 1).

Note: the opportunity for a confusion of terminology: the term “ruminant” can either refer to physiology, that of foregut fermentation combined with cud-chewing, or to a phylogenetic grouping of artiodactyls [subfamily Ruminantia] that excludes camelids (camels and lamas, in the artiodactyl sub-

family Tylopoda). We will use the term “ruminant” in the physiological sense here, to include camelids.

Ruminating artiodactyls possess three non-absorptive chambers of the stomach (two in camelids) where food is stored and processed, followed by a digestive chamber called the abomasum, the equivalent of the true stomach in other mammals (Figure 1.1). The first (and largest) chamber is the rumen, which serves as the main fermentation “vat”, where the huge numbers of bacteria and protozoans that break down cellulose are cultured. The products of fermentation (volatile fatty acids) account for the majority of the animal’s nutritional requirement (up to 70% in cattle) (Schmidt-Nielson 1997). The acids are buffered by large volumes of saliva, containing dilute sodium bicarbonate (100-190 litres a day in cattle), and this also aids in maintaining an appropriate growing medium for the digestive microorganisms (Schmidt-Nielson 1997). This system is extremely efficient as the cellulose is fermented prior to the site of absorption in the small intestine, and additionally this breakdown of the plant cell wall means that the cell contents are released prior to the site of absorption. Ruminants also engage in a process termed “nitrogen cycling” whereby the ammonia

produced by protein fermentation in the rumen is transported via the blood system to the liver, returned to the rumen as urea and then used for further bacterial growth. The overspill of bacteria into the abomasum then provides the animal with microbial protein as its protein source. As a result, ruminants can afford to be specialist feeders, given that all essential amino acids and many vitamins are synthesised by the bacteria (Schmidt-Nielson 1997). The process of thorough fermentation in the rumen, although allowing for a high degree of cellulose digestion, entails a long retention time of the digesta, and as a result food intake may be more limited than in nonruminants (Clauss et al. 2003).

Hindgut fermentation takes place mainly in the colon in perissodactyls and additionally in the enlarged caecum (Figure 1.2), which act like fermentation chambers in much the same way as the rumen does in ruminants. This arrangement presents the problem that the cellulose is not fermented until this point, and the volatile fatty acids must be absorbed in the colon, rather than in the small intestine. Hindgut fermenters have a shorter passage time than ruminants, and hence are less efficient in cellulose digestion, for which they compensate with a higher intake of food (Clauss et al. 2003, 2007, 2009b). Note that an additional problem for hindgut fermenters is that they must access the cell contents of the herbage prior to the fermentation of the cellulose in the hindgut. Although the products of cellulose fermentation can be absorbed in the colon, the enzyme-producing glands for the digestion of the sugars, fats and proteins of the cell contents are located in the small intestine. Some non-ungulate hindgut fermenters, such as rabbits and certain rodents, circumvent this problem by refection (eating the initially-produced faeces): however, refection is not practiced by any ungulate (nor by hyraxes and elephants). Thus it must be the case, for hindgut fermenting ungulates, that the initial mastication of the food is sufficient to fracture the plant cell walls to release the cell contents prior to the site of cellulose fermentation (Janis et al. 2010).

Thus, hindgut fermenters face two functional problems with food comminution in which they differ from ruminants. Not only must they consume more food per day than a ruminant of similar size and diet, but they must also ensure that the cell walls are ruptured on initial food ingestion (while a ruminant can rely on fermentation to break down the cell walls). One would therefore predict that initial food mastication would be more prolonged and intensive in hindgut fermenters than in ruminants.

Even though ruminants later regurgitate their food and chew it as cud, at this point the food has been softened by fermentation processes and may present a reduced load on the masticatory system (Fortelius 1985). Morphological studies do appear to show that hindgut fermenters have deeper jaws, larger areas for the insertion of masticatory muscles and greater cheek tooth occlusal area than ruminants (e.g., Turnbull 1970; Janis 1990a; Mendoza et al. 2002), which would accord with the hypothesis that hindgut fermenters experience a greater load on the masticatory system than ruminants. However, these observations have not been subjected to rigorous biomechanical analysis.

With regards to food ingestion, and digestive physiology in general, the usual comparison between hindgut fermenters and ruminants is between horses and cattle both medium to large-sized ungulates (~300 kg) with a similar diet of grass. Both animals have been the subject of many agricultural studies, and while other ruminants have also been studied in this fashion (sheep, deer, llamas, etc.) studies of other extant hindgut fermenting ungulates (rhinos, tapirs, hyraxes, elephants) are few in number. Direct comparisons of food intake behaviour between horses and cows are rare, although horses do seem to show longer grazing times and/or higher food intake than cattle (Arnold 1984; Duncan et al. 1990; Menard et al. 2002). In addition, it has been shown that while ruminants initially swallow large particles, which are later reduced in size via rumination (Clauss et al. 2009a), the faecal particle size in horses is relatively small, despite the fact that they only chew their food once (Fritz et al. 2009). One pilot study has directly compared the ingestion behaviour of horses and cows (Janis et al. 2010). This study suggests, although it cannot statistically be demonstrated (because of small sample sizes), that horses chew their food longer than cows on initial ingestion, and that this difference is more pronounced with forage of increasing fibre content.

Here we test the hypothesis that, as hindgut fermenters most likely chew their food more on initial ingestion than ruminants, and also must process more food per day, then hindgut fermenters should possess features that increase mandibular robustness relative to ruminants to deal with prolonged, cyclical stress and strain produced during mastication. As mentioned above, morphological observations and measurements suggest that this case holds true, but has not been tested within a biomechanical framework. For this study it is assumed that a robust jaw would exhibit less defor-

Table 1. Study species pairings based on body mass and feeding strategy. Emboldened pairs used in extant ruminant and hindgut paired t-test comparison.

Approximate Mass*	Feeding Strategy	Foregut Fermenters	Hindgut Fermenters
~3kg	Browser	<i>Tragulus javanicus</i> (lesser mouse deer)	<i>Dendrohyrax dorsalis</i> (tree hyrax)
~6kg	Browser	<i>Cephalophus monticolor</i> (blue duiker)	<i>Eurohippus parvalus</i> † <i>Hyracotherium</i> sp. †
~25kg	Browser	<i>Cephalophus ogilbly</i> (Ogilbly's duiker)	<i>Mesohippus</i> sp. † <i>Mesohippus</i> sp. †
~60kg	Mixed Feeder	<i>Dama dama</i> (fallow deer)	<i>Merychippus</i> sp. † <i>Merychippus insignis</i> †
~75kg	Browser	<i>Odocoileus virginianus</i> (white-tailed deer)	<i>Kalobatippus</i> sp. †
~120kg	Grazer	<i>Damaliscus lunatus</i> (tsessabe)	<i>Calippus martini</i> †
~250kg	Grazer	<i>Tragelaphus strepsiceros</i> (greater kudu) <i>Okapia johnstoni</i> (okapi)	<i>Tapiris bairdii</i> (Baird's tapir) <i>Tapiris terrestris</i> (lowland tapir)
~250kg	Browser	<i>Connochaetes taurinus</i> (blue wildebeest)	<i>Equus burchelli</i> (common zebra)
~450kg	Grazer	<i>Bos taurus</i> (domestic cow)	<i>Equus caballus</i> (domestic horse)
~800kg	Browser	<i>Giraffa camelopardalis</i> (giraffe)	<i>Dicerorhinus sumatrensis</i> (Sumatran rhino)

mation under a set load than a more gracile one, and thus robustness is defined here by the stress observed in the jaw when experiencing quasi-feeding loads. More robust jaws would be expected to experience lower stresses. In this study we estimate Von Mises stress, which is a function of the three principle stress directions formed under loading conditions that distort a material.

MATERIALS AND METHODS

Study specimens - 25 specimens of 23 species were included (of which 8 species were extinct) (Table 1) from the University Museum of Zoology Cambridge (UMZC), the American Museum of Natural History, New York (AMNH), the collections of the University of Bristol School of Biological Sciences (UBBS), and from the Digimorph collection of the University of Texas at Austin (<http://digimorph.org>) (see Appendix for details). Lateral aspect photographs comprised the majority of raw data, with the exception of a CT scan of a skull of *Tapiris terrestris* (lowland tapir), from which a lateral aspect image was created. This specimen was originally obtained from collections of the Texas Memorial Museum, University of Texas, United States of America (TMM).

In general, grazers tend to have jaws that appear to be more robustly built than those of browsers (Janis 1990a, 1990b, 1995; Clauss et al.

2007). To reduce the likely influence of diet, on craniodental morphological features, and also possibly confounding effects of body size (allometric scaling, etc.), ruminant and hindgut-fermenting species were paired according to feeding strategy (i.e., browser, mixed feeder or grazer) and body mass (Table 1). Comparisons were made between each matched pair, and then compared overall.

There are substantially fewer extant hindgut fermenters than ruminants in all dietary types and size groups. This imbalance is problematic as it means we do not have a full representative range of feeding strategies and body masses for the two groups. To partially redress this balance and explore the hypothesis in a broader range of taxa (i.e., removing the influence of phylogenetic affiliation), we included a species of hyrax (*Dendrohyrax dorsalis*), and we also examined some extinct equids to increase the range of size and dietary comparisons. (Other hyraxes [such as species of the mixed-feeding *Heterohyrax* or the grazing species of *Procavia*] were not included because there are no extant [or extinct] ruminants of this small of a body size [< 5 kg] that have this type of more fibrous diet [all are browsers or frugivores].) The extinct equids were assumed to be hindgut fermenters, like all other perissodactyls, and their diets were estimated from their dental morphology, from the degree of hypsodonty (see Janis 1995) and also from microwear studies (see Solounias

and Semprebon 2002). Ontogenetic variation in all taxa was accounted for by using only specimens of adult animals (as determined by a fully erupted third molar).

Modelling Teeth

To test the effect of tooth row inclusion, 2D jaw FE-models of 16 species were created with and without the tooth row (simplified to a quadrilateral block consisting of all premolars and molars). Scaling was 1:1 with 10 mm model surfaces used for all species below ~100 kg and 20 mm for those above. Constraints were added at the dentary condyle above the mandibular notch and the back edge of the coronoid process and downward force of 100 N applied to a distal node of the tooth row and results recorded at five point intervals along a vertical transect originating from the mid-point of the tooth row. Although mean Von Mises stress across the transect differed, similar patterns of stress distribution were recovered.

It was clear from this study, that the unique dental morphology of individual taxa would heavily influence perceived robustness. It appeared also that the treatment of the tooth row as an immobile strip was wholly inaccurate, and each tooth unit would require individual modelling if they were to be included. Besides time constraints, this creates a problem generally in that it would also require the inclusion of periodontal ligament (a fibrous soft tissue attached to the cementum) around the base of each tooth. Unlike bone and dentine (where stress and strain increase in proportion under normal loading conditions) soft tissue in general is known to act with nonlinear elasticity with some studies suggesting transmission of load from teeth to the mandible is affected as a result (Kober et al 2008). Finally, it is important to consider that the direction of force transmitted through the tooth acts principally in the vertical plane; having little impact on resulting mandibular stress patterns. These additional intrinsic variables and the time involved in modelling realistic tooth units was therefore not justified for the remit of this study.

2D FE-Models

To create 2D FE models, basic line outlines of the jaw were generated from lateral aspect photographs of all 25 mandibles. Finite element analysis (FEA) is an engineering analysis tool that calculates stress and strain in a digital structure after the application of user-defined loads. It is used increasingly to determine functional mechanical behaviour of zoological and palaeontological speci-

mens (see Rayfield 2007; Richmond et al. 2005 for reviews). The digital structure of interest is divided into a finite number of element blocks of regular geometry, linked at apices by nodal points. The stress-strain behaviour of each discrete region is computed, dependent upon user-defined loads and material properties, to provide a composite picture of the mechanical behaviour of the structure. Two-dimensional FE models have a standard thickness (20 mm), and so the models used in this study capture the outline geometry of the mandible but do not account for any differences in mandibular thickness. Jaw images were digitised using a polyhedral line tool of the java-based imaging software ImageJ (<http://rsb.info.nih.gov/ij/>).

Planar (x,y) co-ordinates of the image outline were then plotted in the Geostar component of CosmosM Finite Element Analysis (FEA) package (v. 2.8, SRAC, Ca. USA and Cenit Ltd, UK). Spline curves were generated to connect imported co-ordinates to recreate 2D FE model geometry with appropriately scaled surfaces (Pierce et al. 2008, 2009; Rayfield 2005).

A user error study was conducted by digitising the outline of the jaw of a plains zebra (*Equus burchelli*) 20 times. Error involved while capturing geometry was negligible with 0.98% difference in area between attempts, with areas of complex curvature appearing to produce the greatest variation. It is worth noting that these and more subtle deviations from true geometry are largely negated by recreation of object margins with the spline curve tool of the FE processing software.

The model was meshed using triangular 3-noded finite elements, which were then attributed the material properties of bovine Haversian bone (Young's modulus = 10 GPa; Poisson ratio = 0.4: Reilly and Burstein 1975).

The 2D FE models were linearly transformed to the scale of *Equus burchelli*, a mid-sized species (~250 kg) from the study set (Table 1). The scaling allowed analysis of pure geometric properties, reducing the influence that skull size may have had on the results. Average element size and model thickness was 20 mm, with number of elements ranging from 807 to 1561 depending largely on shape.

Loading and Constraint. Areas of attachment for both the temporalis and masseter muscles were standardized (Figure 2, Figure 3) and the ratio for force allocation calculated. The masseter attachment was limited to an area below the mandibular notch between the condyle and coronoid process, and behind a vertical line drawn at the posterior

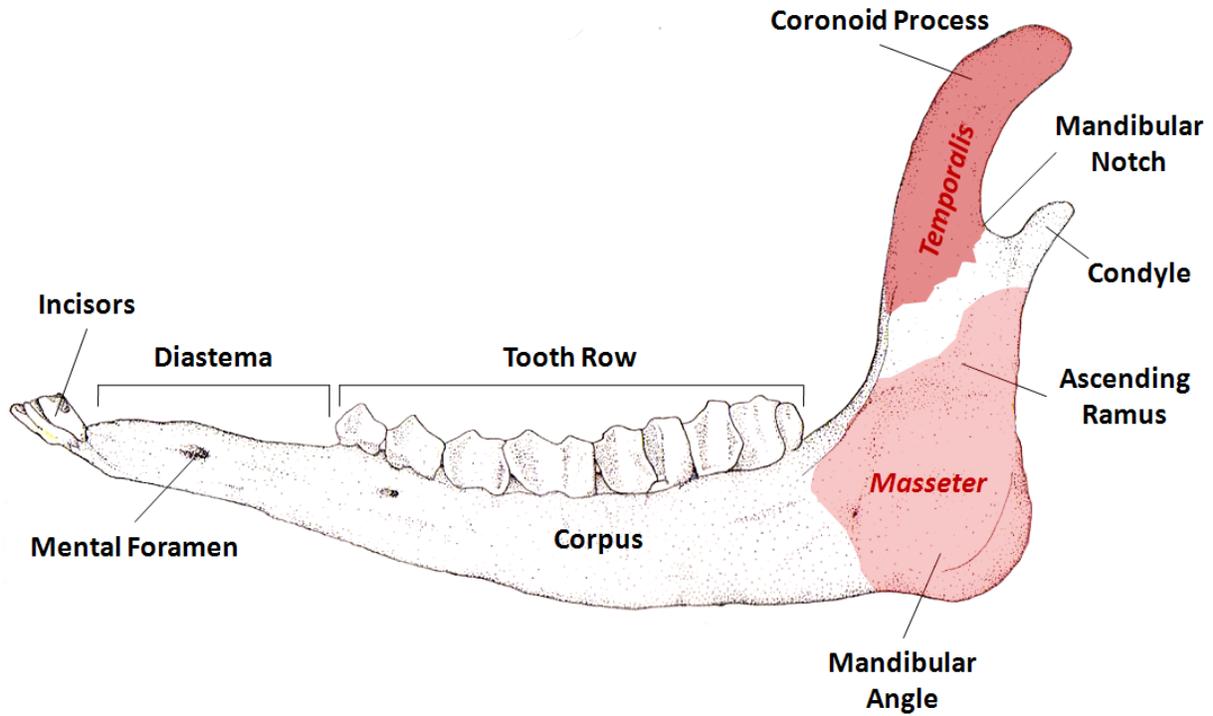


Figure 2. Generalised diagram of typical ungulate mandible (fallow deer: *Dama dama*) showing major muscle attachment areas.

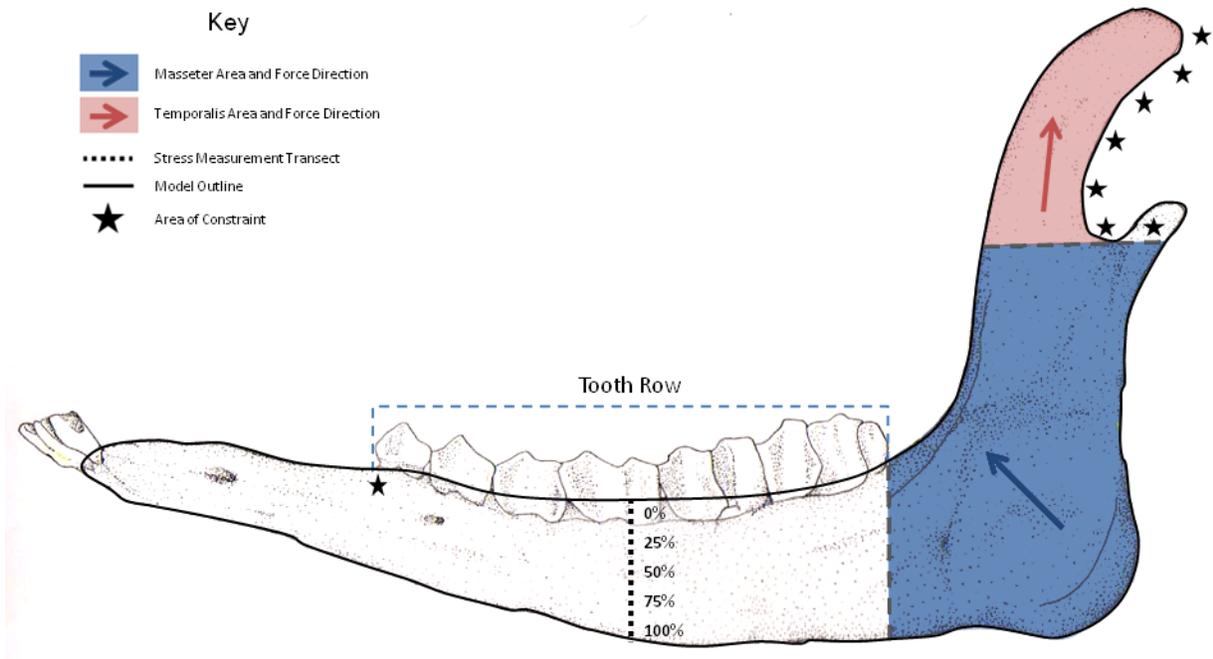


Figure 3. Lateral view of standardized model of ungulate mandible (*Dama dama*) indicating finite element boundary conditions and region of stress measurement.

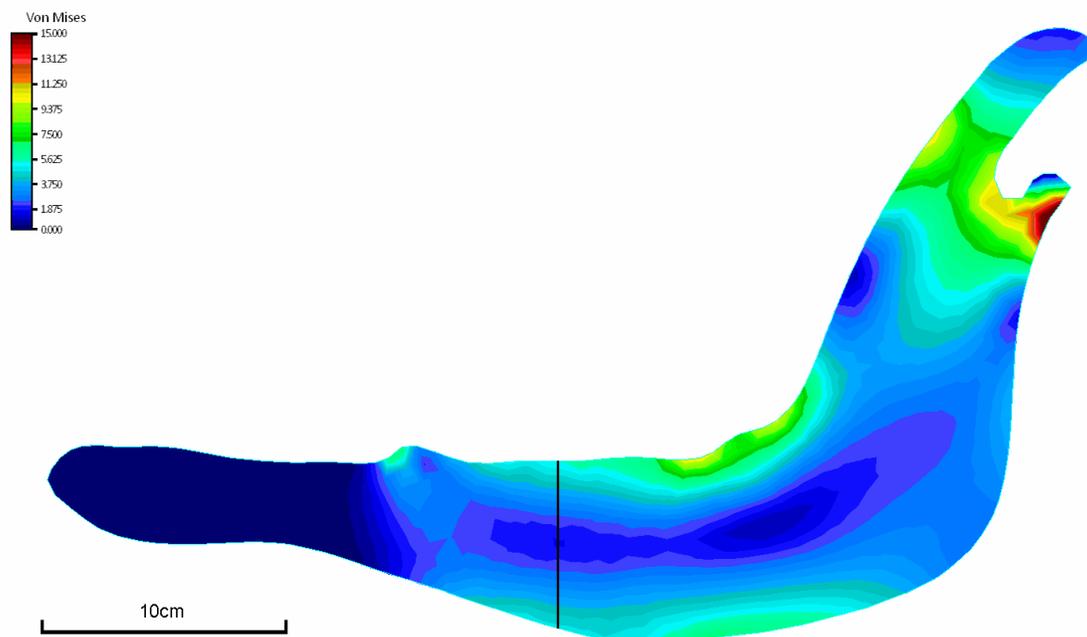


Figure 4. Typical jaw FE-models of *Connochaetes* (wildebeest, ruminant) with colour plot of Von Mises stress distribution and position of mid-toothrow transect (black line).

border of the lower molar row (i.e., behind the third molar). The temporalis attachment consisted of the coronoid process area immediately above the mandibular notch. The models were constrained at both the distal anterior tooth of the tooth row in the Y direction to simulate a bite at this point, and an area extending from the posterior edge of the coronoid process and the condyle above the level of the mandibular notch: in all comprising six degrees of freedom to represent immobilisation of the mandible at the temporomandibular joint. An arbitrary muscle force value of 100 N was used for comparative purposes, but was distributed in proportion to surface area across the finite element nodes of the masseter and temporalis in directions appropriate for the relative direction of force during mastication (Figure 3).

Measurement. Stress measurements were taken from five evenly distributed nodes along a vertical transect of the model at the mid-line of the tooth row (Figure 3). These nodes were measured at 0%, 25%, 50%, 75% and 100% from the uppermost to lowermost point, respectively. Von Mises stress values were recorded for each of these points, and whole jaw colour plots were created to visualize the distribution of stress. Differences in stress patterns and magnitudes between ruminants and hindgut fermenters were analysed for all jaw models pooled together; pairs of extant ruminants

and hindgut fermenters matched for dietary habit (grazer, browser, mixed feeder) and body size; pairs of extant ruminants and extinct hindgut fermenters also matched for dietary habit and body size.

RESULTS

Stress Distribution

Figure 4 documents that large stresses appear in the jaws when subject to a quasi-functional feeding load. Warm colours (red, orange and yellow) indicate regions of high stress; blue indicates little or no stress. All models are shown to the same stress scale. Areas of unusually high stress were always observed at the condyle where the model was constrained from movement, an issue familiar to engineers as Saint-Venant's Principle (Cook 1995).

These stresses are artificially inflated by the constraints, but occur at a reasonable distance from our region of interest (mid-point of the tooth row) to not significantly influence the outcome of our analysis. Similarly high stresses were commonly observed around the base of the coronoid process (Figure 4). This area is the attachment point of two muscle groups with differently oriented force vectors, which may be at least partly

Table 2. Stress measurements across vertical transect of mid-toothrow, and mean values for extant and extinct species.

Species (Collection)	Von Mises Stress (MPa)					Mean
	0%	25%	50%	75%	100%	
Foregut Fermenters						
<i>Tragulus javanicus</i> (UMZC)	3.41	1.72	0.49	1.34	3.29	2.05
<i>Cephalophus monticolor</i> (UMZC)	4.01	1.57	0.59	1.99	3.55	2.34
<i>Cephalophus ogilbyi</i> (UMZC)	4.25	6.46	0.75	2.01	3.50	3.39
<i>Dama dama</i> (UMZC)	4.62	3.41	0.67	1.90	4.49	3.02
<i>Odocoileus virginianus</i> (UMZC)	6.67	2.70	0.49	2.67	5.22	3.55
<i>Damaliscus lunatus</i> (AMNH)	4.00	1.45	0.89	1.74	2.94	2.20
<i>Tragelaphus strepsiceros</i> (UMZC)	3.79	1.91	0.98	2.01	3.94	2.53
<i>Okapia johnstoni</i> (UMZC)	4.36	2.17	1.43	2.39	3.99	2.87
<i>Connochaetes taurinus</i> (UMZC)	5.16	2.78	1.42	2.82	4.62	3.36
<i>Bos taurus</i> (UBBS)	4.80	1.76	0.81	1.92	3.25	2.51
<i>Giraffa camelopardalis</i> (UMZC)	8.53	2.65	1.26	3.46	6.32	4.44
Hindgut Fermenters						
<i>Dendrohyrax dorsalis</i> (UMZC)	1.84	0.79	0.42	0.88	1.78	1.14
<i>Tapiris bairdii</i> (UMZC)	1.55	1.19	0.76	0.82	1.67	1.20
<i>Tapiris terrestris</i> (TMM)	1.08	0.68	0.60	0.77	1.43	0.91
<i>Equus burchelli</i> (UMZC)	4.24	2.62	1.57	1.82	4.32	2.92
<i>Equus caballus</i> (UBBS)	4.36	1.62	0.90	1.70	3.73	2.46
<i>Dicerorhinus sumatrensis</i> (UMZC)	3.38	1.42	0.65	1.62	3.22	2.06

responsible for this observed pattern. Again, however, the region of interest appeared unaffected.

Within the ramus of the jaw, a typical bending pattern was observed in which the highest stress values were recorded from the dorsal and ventral edges of the jaws, whilst the central jaw experienced little stress (akin to the neutral axis of a beam). As the load is applied, material of the upper margin undergoes tension, and the lowermost margin is compressed. As the model is two dimensional, this represents purely parasagittal bending. On average the dorsal and ventral jaw margins exhibited 2.84 MPa greater Von Mises stress than the centre.

The distal portions of the mandible, including most of the diastema, tended to exhibit very little if any stress. Such low stresses were also observed in the mandibular angle, where two patterns of stress could be differentiated. In species where this area was discordantly bulbous in relation to the thickness of the mandible corpus, stress tended to concentrate in exterior borders immediately surrounding it. In mandibular angles with wider curves and less protuberance, stress was generally distributed further from this area (Figure 4).

Comparative Stress Magnitudes

Collective data. For all jaws scaled to the same linear dimensions, mean Von Mises stress was greater at all transect points in the extant ruminants than hindgut fermenters (only marginally so at the centre of the jaw, where the neutral axis of bending occurs, as would be expected [Table 2]).

Mean stress across the mid-tooth row transect for all extant hindgut fermenters was 1.78 MPa ($n = 6$), while ruminants showed generally higher values with a mean stress of 2.93 MPa ($n=11$) (Table 2, Figure 5). This collective difference in stress values is seen regardless of size or dietary habits (e.g., grazer versus browser). Extant hindgut fermenters showed a smaller range of mean stress values (0.91 MPa for *Tapiris terrestris* to 2.92 MPa for *Equus burchellii*, $SD = 0.82$) than ruminants (2.05 MPa for *Tragulus javanicus* to 4.44 MPa for *Giraffa camelopardalis*, $SD = 0.71$). Mean Von Mises stress values for all extinct equid species was 2.18 MPa ($n = 8$), ranging from 0.93 MPa (*Hyracotherium*) to 2.47 MPa (*Meshippus* sp.). The stress values in all hindgut fermenters (extant and extinct) were lower than the mean stress values for rumi-

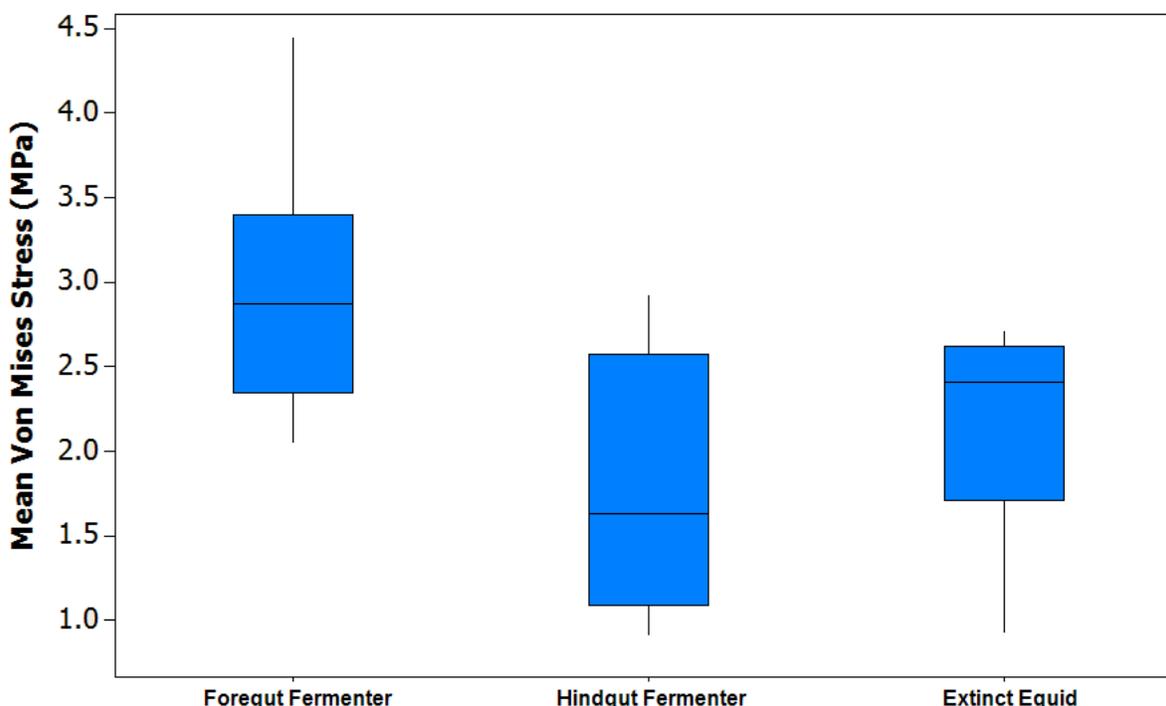


Figure 5. Box plot showing mean Von Mises stresses for all ruminants, hindgut fermenters and extinct equid species.

nants. Our results show that there is little overlap between mean stress for ruminants and hindgut fermenters (Figure 5), but this observation may be influenced by sample size.

Paired data. Data were paired according to similar body size and feeding behaviour (grazer, mixed feeder or browser; see Table 1) to remove dietary habit and allometric effects from consideration. Paired t-tests comparing six extant pairings of ruminants and hindgut fermenters (Table 1) revealed a statistically significant difference in mean transect values ($p = 0.023$).

The extinct species of hindgut fermenters (all equids) were paired with extant ruminants of similar body size and likely similar diet (Table 1). The reason for including these forms was to “fill in the gaps” that no extant hindgut fermenting ungulate occupies today (i.e., small to medium-sized browsers and mixed feeders) to see if the pattern held over the entire range of diets and body sizes. As diet was obviously conjectural in these extinct species, estimated from dental features (hypsodonty index and microwear, as previously discussed), statistical differences in stress between these pairs was analysed separately from the pairings that contained only extant taxa.

Pairings of extant ruminants and extinct equids (Table 1) were compared on an individual basis (Figure 6.2) and showed that the jaws of most extinct equids were more robust than those of the extant ruminants. The exception here was the pairing of *Damaliscus lunatus* (tseesabe) with the equid *Calippus martini*: here the equid showed a mean stress of 2.67, greater than that of the ruminant, with a mean stress of 2.20. Without further sampling it is impossible to know if this figure is significant.

The jaws of the extinct equids showed an average of 24.68% less stress across the transect than their paired extant ruminant, with values ranging from 18.11% less stress (*Merychippus* sp.) to 60.39% less stress (*Hyracotherium* sp.). With the exclusion of *Damaliscus* and *Calippus*, the average for all pairs increased to 31.23% ($n = 7$) lower stress in extinct equids than their extant ruminant pairing. Kruskal-Wallis nonparametric analysis showed borderline insignificance between mean Von Mises stress values between ruminants and extinct hindgut fermenters ($p = 0.058$). If *Damaliscus* and *Calippus* are excluded, the groups are significantly different ($p = 0.019$).

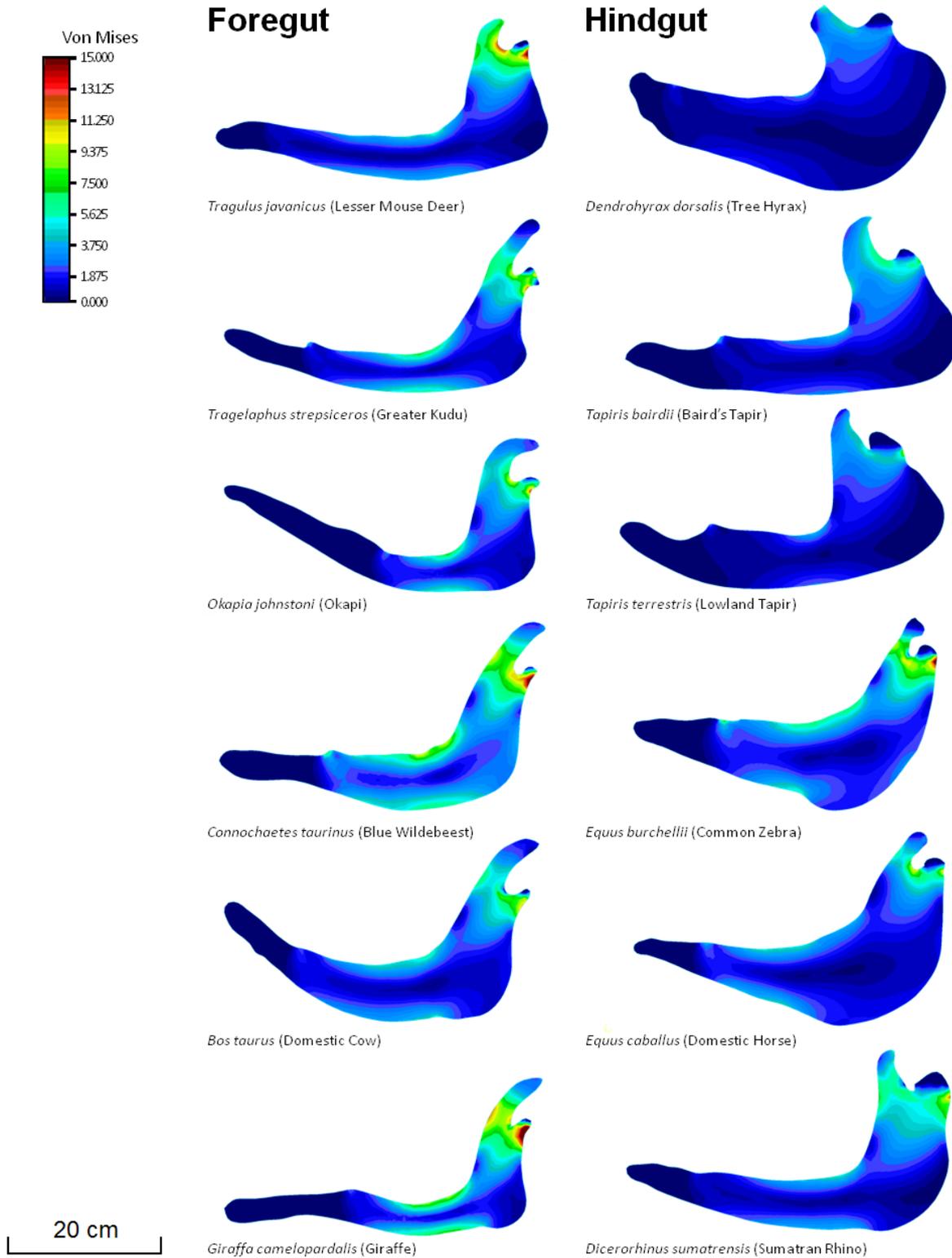


Figure 6.1. Jaw FE-models of extant pairs (ruminant and hindgut fermenting ungulates) with colour plot of Von Mises stress distribution.

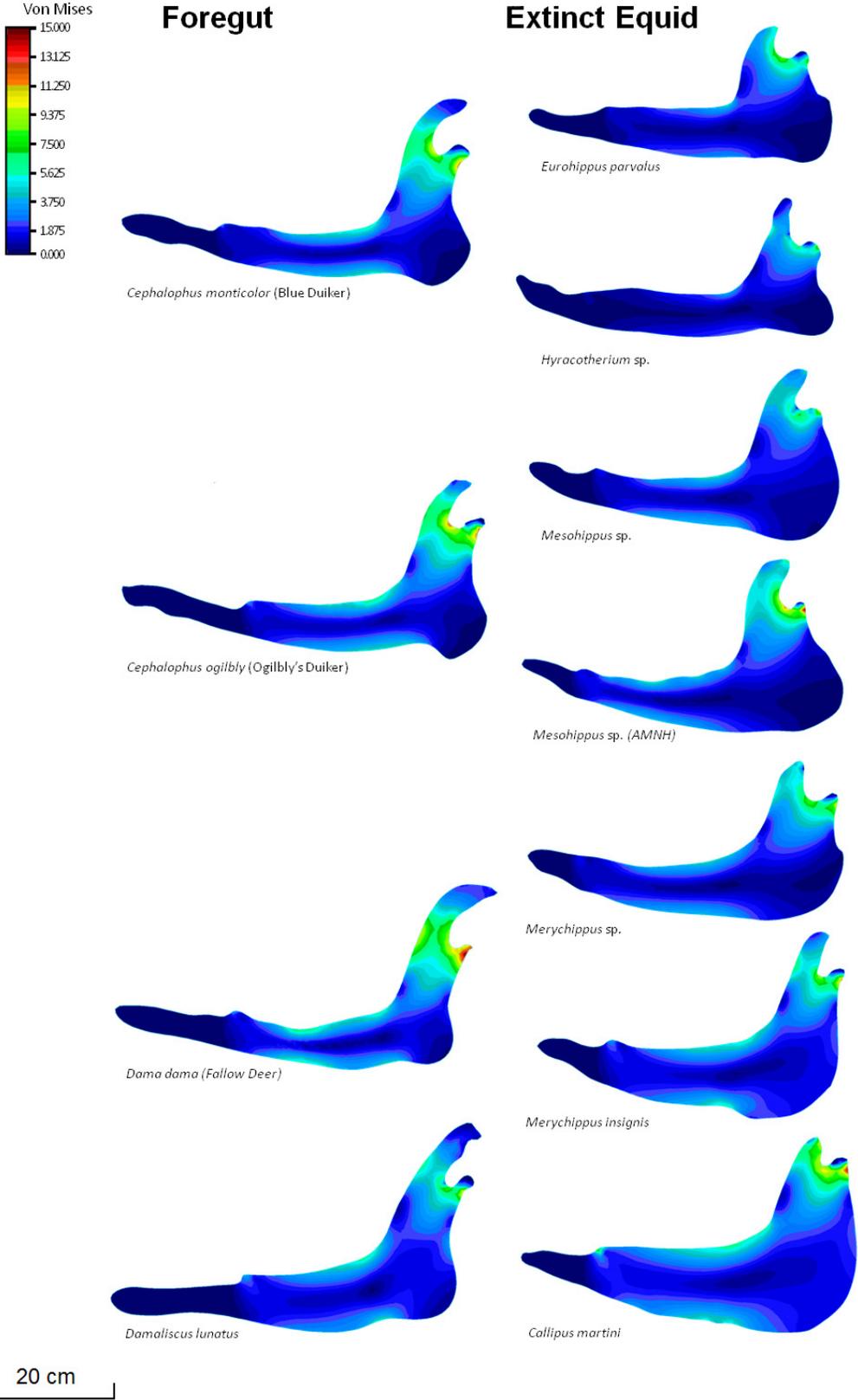


Figure 6.2. Jaw FE-models of mixed extant (ruminants) and extinct (equids) pairs with colour plot of Von Mises stress.

DISCUSSION

Extant hindgut fermenters have more robust jaws than ruminants, when size is removed from comparison, and regardless of whether dietary habit (grazer versus browser) is considered. “Robustness” is defined by our criteria of a jaw possessing lower mandibular stress than other jaws subject to the same loading regime. A similar trend is seen in the pairings that include extinct equids, which can be assumed on phylogenetic grounds to be hindgut fermenters, with extant ruminants. A prediction from this result is that this methodology could be used to identify the probable digestive physiology of extinct ungulates with no extant relatives, such as the endemic South American litopterns and notoungulates.

Feeding Strategy and Body Size

As previously discussed, feeding strategy has a significant effect on jaw morphology. For example, grazers have larger masseter muscles than browsers (Clauss et al. 2009b), which will produce larger forces during mastication, and the jaws of grazers appear to be more robustly built in terms of general morphology. However, no clear pattern of differences between stresses in browsers and grazers within digestive physiology groups emerges from this study. Perhaps surprisingly, some of the lowest stress levels (and hence higher robustness) were recorded in the smaller browsing forms, in the tree hyrax (*Dendrohyrax*) among the hindgut fermenters, and the mouse deer (*Tragulid*) among the ruminants and also in the larger browsing tapirs (hindgut fermenters). It appears that depth of the jaw at the point in front of the mandibular angle generally has the most effect on robustness here, but further work would be required to elucidate the true nature of the biomechanics involved. It might be the case that smaller animals can “afford” to have jaws that are more robust than larger ones, but that with increasing body size the absolute weight of the jaw becomes an increasing consideration in craniodental design, given that it is manipulated with muscles placed only at the posterior end, with a relatively weak mechanical advantage. Of course, this remains to be tested.

These observations on extant browsers can also be seen in some extinct ones. *Hyracotherium* is the earliest known (early Eocene) and most primitive fossil equid, usually considered to have a folivorous/frugivorous type of diet (like that of a modern mouse deer), due to its brachydont and bunolophodont cheek teeth (MacFadden 2005). However, despite the apparent gracile nature of the

jaw morphology (see Figure 6.1), the FEA analysis revealed the jaw of this species shows low levels of stress (0.93 MPa), and thus possess a high level of robusticity, much more so than in other, slightly younger brachydont equids (*Mesohippus*), or even the more closely related, contemporaneous *Eurohippus*. One morphological feature that may be related to this is the unusual (for an equid) deepening of the mandibular corpus beneath the premolars. This morphology could suggest feeding adaptations such as cracking seeds or nuts, a notion possibly supported by dental microwear (Solounias and Semperebon 2002 p. 30). Alternatively, at least one species of *Hyracotherium* (*H. tapirinum*) has been shown to be sexually dimorphic in canine size, with (presumed) males having larger canines (Gingerich 1981). If this mandibular robusticity was sexually dimorphic it might relate to male fighting behaviour. Further study would be needed to elucidate this idea.

Model Limitations

The finite element models presented here are two-dimensional and can only measure in-plane stress and strain generated by behaviour such as parasagittal bending. In vivo strain gauge, data and kinematic analysis of feeding in two ruminating artiodactyls (goat and alpaca) (Lieberman and Crompton, 2000; Williams et al. 2007, 2009) demonstrate that the working side mandible also undergoes torsion about its longitudinal axis, and transverse and/or parasagittal bending in the balancing side mandible. Feeding loads are therefore experienced in three dimensions in these artiodactyls, and probably also in other ungulates, due to the laterally directed adductor muscle resultant seen in these taxa. Our 2D FE models restrict the extent to which the full effect of ungulate feeding loads on jaw morphology can be assessed. Further work using three dimensional FE-models is desirable, but there are practical and time-constraint issues to this process. Computed tomography (CT) scanning would be required to capture the internal and external 3D geometry of specimens, and for some taxa that are poorly preserved or of a large size, scanning would be required to capture the internal and external 3D geometry of specimens, which would be difficult for taxa that are poorly preserved or of a large size. This paper offers a first step towards these future research directions.

CONCLUSION

The mandibular robustness of ungulate jaws appears to be reliably correlated with digestive

physiology in a range of extant species and potentially also in extinct species. In general hindgut feeders have jaws which show lower levels of stress when equal muscle forces are applied in FEA analysis (i.e., are more “robust”), and these jaws can be significantly differentiated from the relatively more gracile jaws of ruminants, especially when the species are matched for body mass and dietary type. This observation accords with the greater amount of stress predicted for hindgut fermenters due to their relatively greater levels of food ingestion and mastication.

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APPENDIX – MUSEUM SPECIMEN CATALOGUE NUMBERS

Specimen	Reference Code	Collection
<i>Cephalophus monticolor</i>	H21621	University Museum of Zoology, Cambridge, UK
<i>Cephalophus ogilbly</i>	H21461	
<i>Connochaetes taurinus</i>	H21242	
<i>Dama dama</i>	H17179	
<i>Dendrohyrax dorsalis</i>	H5281	
<i>Dicerorhinus sumatrensis</i>	H6387	
<i>Equus burchelli</i>	H9357	
<i>Giraffa camelopardalis</i>	H23090	
<i>Odocoileus virginianus</i>	H189902	
<i>Okapia johnstoni</i>	H20302	
<i>Tapirus bairdii</i>	H7451	
<i>Tragulus javanicus</i>	H15013	
<i>Tragelaphus strepsicerus</i>	H25161	
<i>Eurohippus parvulus</i>	Uncatalogued Cast of Skull	Natural History Museum, UK (original in Senkenberg Musuem, Germany)
<i>Kalobatippus</i>	Uncatalogued Cast of Skull	Natural History Museum, UK (original in AMNH, New York)
<i>Merychippus sp.</i>	Uncatalogued Cast of Skull	Natural History Museum, UK
<i>Mesohippus sp.</i>	MT00033	
<i>Calippus martini</i>	FAM114159	American Museum of Natural History, New York, USA
<i>Damaliscus lunatus</i>	AMNH150150	
<i>Hyracotherium sp.</i>	AMNH55986	
<i>Merychippus insignis</i>	FAM87003	
<i>Mesohippus sp.</i>	AMNH 39001	
<i>Tapiris bairdii</i>	AMNH 80076	
<i>Bos taurus</i>	S2J3.6	School of Biological Sciences, University of Bristol, Bristol, UK
<i>Equus caballus</i>	R8a.3	
<i>Tapiris terrestris</i>	TMM M-16	Texas Memorial Museum, University of Texas, Austin, Texas, USA