JAW MECHANICS AND EVOLUTIONARY PALEOECOLOGY
OF MEGAHerbIVOROUS DINOSAURS FROM THE DINOSAUR PARK FORMATION
(UPPER CAMPANIAN) OF ALBERTA, CANADA

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ABSTRACT—The question of what role differential jaw mechanics may have played in facilitating dietary niche partitioning among Late Cretaceous megaherbivorous dinosaurs from Laramidia is examined, using the fossil assemblage of the Dinosaur Park Formation as a test case. We use phylogenetic inference to reconstruct the mandibular adductor musculature of these animals, which we then apply to the construction of biomechanical lever models of the mandible to estimate relative bite forces. Our findings reveal predictably weak bite forces in ankylosaurs, and comparatively high bite forces in ceratopsids and hadrosaurs, both of which possessed a mechanical advantage that produced bite forces 2–3 times higher than those forces exerted by the adductor musculature. The impressive jaw mechanism shared by the last two taxa evolved in a stepwise fashion, independently in each lineage. There is tentative evidence to suggest that nodosaurids had more powerful bites than ankylosaurs, but the overall mechanical diversity among megaherbivores from the Dinosaur Park Formation is low, suggesting that differential jaw mechanics could have played only a subsidiary role in niche partitioning. Such mechanical conservatism may have may have been selected for, or it may simply reflect the limits imposed by evolutionary constraints. Regardless, mechanical disparity patterns remained stable throughout the ~1.5 Ma evolution of the Dinosaur Park Formation megaherbivore chronofauna.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

ARTICLE

INTRODUCTION

Megaherbivorous Dinosaurs of Laramidia

The fossil assemblage of what was the Late Cretaceous island continent of Laramidia preserves the remnants of some of the most diverse megaherbivore (herbivores >1000 kg) faunas ever to have existed (Lehman, 1987, 1997, 2001). How so many of these dinosaurs cohabited a relatively small landmass has long puzzled researchers and has generated a number of mechanistic hypotheses (reviewed in Mallon et al., 2013). Recent work has focused on the hypothesis of dietary niche partitioning, as revealed by feeding height stratification (Mallon et al., 2013), skull (Mallon and Anderson, 2013) and beak (Mallon and Anderson, 2014a) morphology, and tooth wear (Mallon and Anderson, 2014b). The present study seeks to build on this previous work by examining the role that differential jaw mechanics may have played in the coexistence of these dinosaurs. We refer specifically to the fossil assemblage of the upper Campanian Dinosaur Park Formation (DPF) of Alberta, which we have used elsewhere to model megaherbivore paleoecology on Laramidia (Mallon et al., 2012, 2013; Mallon and Anderson, 2013, 2014a,b).

Plant Properties and Jaw Mechanics

The interaction between plants and their herbivorous predators on an evolutionary timescale has been compared to an arms race (e.g., Labandeira, 2002; Schoonhoven et al., 2005; Becklin, 2008), where each clade adapts continuously to overcome the innovations of the other. Plants have evolved a variety of defenses in response to predation, including toxins, thigmomastaxy, phytoliths, resins, spines, and a variety of organic polymers that reduce palatability by increasing the plant’s mechanical resistance. Chief among the last are cellulose, hemicellulose, and lignin (Lucas, 2004). Because not all plants or plant parts contain the same polymers arranged in the same way, they often differ in their intrinsic stiffness (resistance to bending) and toughness (resistance to crack propagation). For example, leaves are exceptionally tough and resistant to mastication, whereas fruits are not (Lucas, 2004:fig. 7.1).

Vertebrate herbivores may overcome these mechanical defenses by modifying their jaw systems in various ways. The vertebrate mandible can generally be modeled as a third-class lever (Hildebrand, 1995), where the force exerted by the adductor muscles is applied between the jaw joint and the bite point. In addition to increasing the bite force exerted by the jaws by increasing the cross-sectional area of the adductor muscles, the effective bite force can also be increased by modifying this system to increase its leverage. In short, this can be done by either reducing the length of the jaw or by increasing the distance between the adductor musculature and the jaw joint (or both). Psittaciforms, for example, have shorter jaws and more rostrally placed adductor muscles than most other birds (Thompson, 1899; Hofer, 1950; Witmer and Rose, 1991; Zusi, 1993; Sereno et al., 2009), allowing them to specialize on a diet of hard seeds and nuts. These mechanical principles are elaborated in the next section.

Given that different jaw mechanisms are required to process different plants or plant parts, it might be expected that
sympatric herbivore species facilitate coexistence by evolving disparate jaw arrangements, thereby reducing competition for food resources. Perhaps the best-documented example of this involves Darwin’s finches from the Galápagos Islands, which, although not all strictly herbivorous, exhibit an array of jaw configurations even among primarily granivorous species. Bowman (1961) described the mandibular musculature and cranial architecture of 12 species of Darwin’s finches. He showed that granivorous species differ in the size and orientation of their adductor musculature, whereby those species that feed on the largest and most resistant seeds have both shorter beaks and larger adductor muscles situated further rostrally along the jaws (similar to the psittaciforms described above), resulting in a more powerful bite. More recently, Herrel et al. (2005a, 2005b) and van der Meij and Bout (2008) documented a close relationship between the morphology of the jaws and absolute bite force in a sample of Darwin’s finches, corroborating the findings of Bowman (1961). Similar adaptations are seen among contemporary artiodactyls; grazers, which feed primarily on tough grasses, possess enlarged areas for the insertion of m. masseter that extends further rostrally on the face relative to their browsing counterparts (Turnbull, 1970; Axmacher and Hoffman, 1988; Janis, 1995; Solounias et al., 1995; Clauss et al., 2008). These patterns recur within a variety of artiodactyl families, including Bovidae and Cervidae (Axmacher and Hoffman, 1988; Solounias et al., 1995), and also among platyrrhine primates (Anapol and Lee, 1994).

It follows from the aforementioned principles of ecomorphology that the sympatric megaherbivorous dinosaurs from the DPF may also have achieved dietary niche partitioning by differing in their jaw mechanics. Ostrom (1966) used lever mechanics to propose differences in mandibular leverage between the contemporary ceratopsid genera Monoclonius ( = Centrosaurus) and Chasmosaurus, both of which are known from the DPF. However, this hypothesis was not subjected to statistical testing because only two specimens of each genus were considered. Similar comments were echoed by Henderson (2010), who posited that centrosaurine and chasmosaurine ceratopsids differed in their bite forces, as reflected by their relative skull dimensions, but he did not comment on how this was achieved. It might also be argued that the same mechanical principles operated between and within members of Ankylosauria and Hadrosauridae to minimize competitive interactions. The study of jaw mechanics has previously been used to examine niche partitioning among Late Jurassic sauropods (Calvo, 1994; Fiorillo, 1998), but this study is the first to examine whether the coexistence of megaherbivorous dinosaurs from the DPF was achieved in part due to differential jaw mechanics, using a statistically rigorous approach.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; ACM, Beneski Museum of Natural History, Amherst, Massachusetts, U.S.A.; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; MCSNM, Museo Civico di Storia Naturale di Milano, Milan, Italy; NHMUK, Natural History Museum, London, U.K.; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMM, Texas Memorial Museum, Austin, Texas, U.S.A.; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; USNM, United States National Museum, Washington, D.C., U.S.A.; YPM, Yale Peabody Museum, New Haven, Connecticut, U.S.A.

Anatomical Abbreviations—m.AME, m. adductor mandibulae externus; m.AMEM, m. adductor mandibulae externus medialis; m.AMPE, m. adductor mandibulae externus profundus; mAMES, m. adductor mandibulae externus superficialis; mAMP, m. adductor mandibulae posterior; mLAO, m. levator anguli oris; mPST, m. pseudotemporalis; mPSTp, m. pseudotemporalis profundus; mPSTS, m. pseudotemporalis superficialis; mPT, m. pterygoideus; mPTd, m. pterygoideus dorsalis; mPTv, m. pterygoideus ventralis.

Other Abbreviations—DPF, Dinosaur Park Formation; MAZ, megaherbivore assemblage zone; RF, relative bite force.

MATERIALS AND METHODS

The data set used here (Supplementary Data 1) comprises 77 specimens spanning 12 megaherbivorous dinosaur genera, representing the clades Ankylosauria, Ceratopsidae, and Hadrosauridae, all from the DPF. We did not include the ankylosaurids Dyoplosaurus acutosquameus (Parks, 1924; Arbour et al., 2009) or Scolosaurus cutleri (Nopcsa, 1928; Penkalski and Blows, 2013), or the ceratopsid Spinops sternbergorum (Farke et al., 2011), because sufficient material is lacking. There is also some question as to whether all these specimens originated from the DPF. We disregarded specimens suffering from severe taphonomic deformation. Otherwise, this distortion was minimized by considering only the best-preserved side of the skull.

Mandibular Adductor Musculature

The mechanical model of the mandible presented in this study requires knowledge of the adductor musculature that acts upon it, particularly relating to the main line of pull (vector resultant) exerted by those muscles. It is therefore necessary to reconstruct the mandibular myology of the megaherbivores considered here. This was done using the extant phylogenetic bracketing approach of Bryant and Russell (1992) and Witmer (1995). Briefly, the method works by optimizing unpreserved character states in a fossil taxon of interest, with reference to two successive, living outgroups. This results in varying degrees of inferential certitude, depending on whether the character state being inferred is present in one, both, or none of the outgroups. In the case of the mandibular adductor muscles considered here, their origin and insertion points are all Level I (Witmer, 1995; or Category 1 of Bryant and Russell, 1992) inferences (Holliday, 2009), which is the strongest kind possible. The inferred muscle attachment sites are listed in Table 1, with further details given in Supplementary Data 2. Vectors for the various muscle complexes are depicted in Figure 1. Our interpretations largely agree with previous ones, but we briefly document certain points of contention with respect to the mAMES complex below because it forms the basis for our lever models. Our treatment of the mandibular adductor musculature adheres to the trigeminal topological paradigm of Ludwig (1914).

Ankylosauria—In Euoplocephalus, Haas (1969:fig. 5) illustrates the mAMES as originating from an apparent muscle scar lateral to the caudal end of the maxillary tooth row. However, the mAMES never originates outside the temporal fossa in extant archosaurs (Holliday, 2009), and it is therefore unlikely that this was the case for ankylosaurs. It seems more probable that the scar noted by Haas was for the attachment of the rictal plate (a fold of skin in the corner of the mouth), or it may have been left by the jugal blood vessels making their way to the buccal margins of the tooth row (C. Holliday, pers. comm. to J.C.M., 2010). Instead of originating on the maxilla, the mAMES more likely attached to the medial surface of the supratemporal bar, caudal to the postocular shelf, as it does in extant sauropods (Holliday, 2009). The point of insertion for this muscle is poorly delineated, but it probably inserted on the caudal coronoid eminence of the mandible.

Haas (1969) reconstructed the mAMEM and mAMEP as originating within the adductor chamber, attaching to the temporal roof and postocular shelf. These muscles were said to insert in and around the mandibular fossa. As indicated by Holliday (2009), the points of attachment for the mAMEM are particularly difficult to infer in non-avian dinosaurs because the muscle
is often indistinguishable from the mAMEP both anatomically and topologically even in extant sauropsids. mAMEM almost certainly originated along the supratemporal fossa and may have inserted either along or immediately caudal to the coronoid process, but likely not within the mandibular fossa as suggested by Haas (1969). The sites of attachment for the mAMEP are slightly easier to infer: this muscle probably originated along most of the caudomedial portion of the supratemporal fossa; it inserted on the coronoid process.

**Ceratopsidae**—Many authors (Lull, 1908; Russell, 1935; Haas, 1955; Ostrom, 1961, 1964a, 1966) have illustrated the ceratopsid mAME (= m. temporalis of Lull, 1908, and Russell, 1935) as originating on the dorsocaudal parietosquamosal frill. However, as Dodson (1996) pointed out, this arrangement is unlikely for three reasons: (1) The force exerted by a muscle is proportional to that muscle’s cross-sectional area rather than to ventrolateral surface of surangular muscle mass, separated by the median parietal bar, that lead up to the supratemporal fossa; it inserted on the coronoid process. (2) Except for that proximal part of the frill adjacent to the supratemporal fenestrae, the dorsal and ventral surfaces of the frill tend to be heavily vascularised, suggestive of a tightly adhering dermis. If the jaw adductors originated along the distal part of the frill, one would expect the dorsal surface of the frill to be smooth. (3) Assuming the frill to be involved somehow with defense from either predation or ritualistic combat, it would be maladaptive to place the jaw adductors in an area where they might be regularly prone to injury. For these reasons, it seems much more likely that the jaw adductors originated near the base of the frill. The mAMES originated on the medial surface of the upper temporal bar, but beyond this, osteological correlates are lacking. It inserted on the smooth surface of the surangular along the caudal margin of the coronoid fossa (Dodson, 1996). The mAMES and mAMEP probably both originated at the base of the frill, attaching to the proximal margin of the parietal fenestrae (Dodson, 1996). The dorsal surface of the frill here is smooth and excavated by paired channels, separated by the median parietal bar, that lead up to the parietal fenestrae. Haas (1955) illustrated these muscles, together with the mAMES, inserting in the mandibular fossa, but Ostrom (1964a) noted that a more mechanically efficient arrangement would have the mAMES and mAMEP inserting on the apex of the coronoid process. Holliday (2009) posits an insertion for these muscles along the dorsal surface of the coronoid process, although he notes that the mAMEP might just as likely have inserted on the apex of the process. Ostrom (1964a: fig. 7) illustrates the resultant force of the mAME complex as extending straight from the apex of the coronoid process to the distal part of the frill, which yields a vector directed strongly dorsocaudally. However, in life, the mAMES and mAMEP must have first passed through the adductor chamber and emerged at the base of the frill via the supratemporal fenestrae, after which they would have angled caudally to attach to the proximal margins of the parietal fenestrae. Although the combined resultant of these muscles would be the same as described

| Taxon     | Muscle complex | Muscle belly | Origin                                      | Insertion                                      |
|-----------|----------------|-------------|---------------------------------------------|-----------------------------------------------|
| Ankylosauria | mPST | mPSTs | Lateral surface of epipterygoid | Medial rim of mandibular fossa |
|           | mPT  | mPTp | Laterosphenoid                    | Medial rim of mandibular fossa |
|           |      | mPTd | Dorsum of rostral pterygoid and palate | Ventral face of articular |
|           |      | mPTv | Caudodorsal surface of pterygoid | Medial surface of mandible beneath jaw joint, ventrolateral surface of surangular |
|           | mAME | mAMES | Medial surface of supratemporal bar, caudal to postocular shelf | Caudal coronoid eminence of mandible |
|           | mAMEM | | Supratemporal fossa | Along or immediately caudal to coronoid eminence |
|           | mAMEP | | Caudomedial portion of supratemporal fossa | Coronoid eminence |
| Ceratopsidae | mAMP | mAMRP | Rostral face of quadrate | Meckel’s cartilage within mandibular fossa |
|           | mPST | mPSTs | Lateral surface of laterosphenoid | Medial or rostralateral surface of coronoid process |
|           | mPT  | mPTp | Muscle absent | Muscle absent |
|           |      | mPTd | Dorsum of pterygoid and palate | Medial surface of the mandible, ventral to adductor fossa |
|           |      | mPTv | Ventral edge of palate | Ventrolateral surface of retroarticular process, may have continued onto lateral surface of mandible |
|           | mAME | mAMES | Medial surface of the upper temporal bar | Surangular along caudal margin of coronoid process |
|           | mAMEM | | Proximal margin of the parietal fenestrae | Dorsal surface of coronoid process |
|           | mAMEP | | Proximal margin of the parietal fenestrae | Dorsal surface or apex of coronoid process |
| Hadrosauridae | mAMP | mAMRP | Rostral face of quadrate | Meckel’s cartilage within mandibular fossa |
|           | mPST | mPSTs | Rostromedial surface of the supratemporal fossa | Medial surface of the coronoid process |
|           |      | mPTp | Small fossa immediately ventral to origin of mPSTs | Medial surface of coronoid process or surangular |
|           | mPT  | mPTd | Dorsum of pterygoid and palate | Excavation along medial surface of retroarticular process |
|           |      | mPTv | Ventral surface of palate | Fossa on lateral aspect of retroarticular process |
|           | mAME | mAMES | Upper temporal bar | Caudodorsal surface of surangular |
|           | mAMEM | | Caudomedial portion of supratemporal fossa | Fossa on dorsal surface of mandible between coronoid process and jaw joint, or coronoid process alongside mAMEP |
|           | mAMEP | | Caudomedial portion of supratemporal fossa | Coronoid process |
|           | mAMP | mAMRP | Rostral surface of quadrate | Medial mandibular fossa |

Sources: Lull (1908), Russell (1935), Lull and Wright (1942), Haas (1955, 1969), Ostrom (1961, 1964a, 1966), Dodson (1996), Holliday (2009), Tanoue et al. (2009).
The vertebrate mandible has traditionally been modeled in two dimensions as a third-class lever in static equilibrium (e.g., Ostrom, 1961, 1964a, 1966; Crompton and Hotton, 1967; Killie, 1982; Smith, 1993; Weishampel, 1993; Hildebrand, 1995; Tanoue et al., 2009; Sakamoto, 2010), where the applied force exerted by the adductor muscles is enacted between the fulcrum (jaw joint) and the resistance force (bite point) (Fig. 2). This type of model depicts the mandible in lateral view and assumes only arclinear (rotational) movements about the jaw joint in the absence of friction. The arrangement of the mandible as a third-class lever favors the maximal depression of the mandible (gape) and speed of adduction over improved leverage because, by definition, the distance from the fulcrum to the point of resistance is always greater than the distance from the fulcrum to the point of the applied force. Therefore, the force exerted at the bite point will always be less than the force exerted by the mandibular adductor muscles.

As implied above, the bite force exerted at any point along the mandible is a function not only of muscle size (cross-sectional area) but also of leverage. Given two third-class levers acting upon by the same applied force, it is possible to increase the effective bite force in one by increasing its leverage. This can be done by increasing the length of the moment arm, which is the perpendicular distance between the direction of force (adductor muscle resultant) and the fulcrum (jaw joint). The product of a force and the length of its moment arm is known as the moment of that force.

In a third-class lever (Fig. 2A), the moment arm of the applied force is distance b, and the moment arm of the resistance force is distance a + b. The moment arms are perpendicular to their respective force resultants, which themselves act perpendicular to the lever axis. This is the simplest possible arrangement of a third-class lever. However, if the resultant of the applied force acts at some other angle to the lever axis, the new moment arm will be shorter and will result in reduced leverage (Fig. 2B).

By applying these same principles to the vertebrate mandible, it follows that the optimal arrangement would locate the adductor muscles as far rostrally as possible and have them act perpendicular to the long axis of the mandible. However, this arrangement is disadvantageous because it reduces gape and requires that the adductor muscles originate rostral to the orbit by Ostrom (1964a), the effective force exerted by these muscles on the mandible would have been more nearly vertical because the base of the frill acts as a pulley about which the muscles work. An analogous system is observed in derived turtles, where the adductors bend about the enlarged otic chamber by means of a pulley-like trochlear process (Gaffney, 1975). Therefore, the effective resultant force of the mAME complex illustrated here is oriented dorsocaudally (Fig. 1B), but more dorsally inclined than depicted by Ostrom (1964a).

**Lever Mechanics**

The vertebrate mandible has traditionally been modeled in two dimensions as a third-class lever in static equilibrium (e.g., Ostrom, 1961, 1964a, 1966; Crompton and Hotton, 1967; Killie, 1982; Smith, 1993; Weishampel, 1993; Hildebrand, 1995; Tanoue et al., 2009; Sakamoto, 2010), where the applied force exerted by the adductor muscles is enacted between the fulcrum (jaw joint) and the resistance force (bite point) (Fig. 2). This type of model depicts the mandible in lateral view and assumes only arclinear (rotational) movements about the jaw joint in the absence of friction. The arrangement of the mandible as a third-class lever favors the maximal depression of the mandible (gape) and speed of adduction over improved leverage because, by definition, the distance from the fulcrum to the point of resistance is always greater than the distance from the fulcrum to the point of the applied force. Therefore, the force exerted at the bite point will always be less than the force exerted by the mandibular adductor muscles.

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where there is less room available for muscle attachment. Given these restrictions, it is possible to increase the leverage of the mandible by either elevating the point of applied force application above the lever axis (via the development of a coronoid process) or by depressing the fulcrum below the lever axis (via depression of the jaw joint), or both. The last optimized arrangement is shared by ankylosaurs, ceratopsids, and hadrosaurids, although it is taken to an extreme in the last two taxa, which have both greatly elevated coronoid processes and depressed jaw joints (Ostrom, 1961, 1964a).

The ceratopsid mandible is modeled as a third-class lever in Figure 3. In this figure, the combined lengths of segments e', e'', and b represent the length of the mandibular lever rostral to the jaw joint. Line segments e' and e'' together represent the length of the tooth row (depicted by a thick black line). Line segment h represents the dorsoventral height of the apex of the coronoid process above the level of the jaw joint, which occurs at a rostro-caudal distance a from the jaw joint. The resistance force (S), depicted at the mesial end of the tooth row, is assumed to act perpendicular to the tooth row. The applied force (F), exerted by the mandibular adductor musculature, is interpreted as acting on the apex of the coronoid process at an angle θ from the tooth row. The location and orientation of the muscle resultant is a simplification, but not without justification; among sauropsids, the largest adductor muscles capable of exerting the most force typically pertain to the mAME complex (Ostrom, 1964a). These muscles insert at the apex of the coronoid process and along its caudal margin (see above). The resultant produced by these muscles may not have stemmed from the coronoid apex, but this landmark is easy to observe and is a reasonable approximation of the position of the muscle resultant because it provides the most leverage to the mandible (Ostrom, 1964a; Tanoue et al., 2009). Moreover, although the m. adductor mandibulae internus complex (mPST + mPT) is also integral to mandibular adduction, its constituent muscles are unlikely to have generated substantial bite forces for a couple of reasons. First, the mPST was probably diminutive, as inferred from the small space available for it within the rostral part of the temporal region (Ostrom, 1964a; Throckmorton, 1980), and its moment arm, along with that of the mAMP, was likely quite short (Ostrom, 1964a). For these reasons, the actions of the m. adductor mandibulae internus and mAMP complexes were ignored in this study.

In ankylosaurs, ceratopsids, and hadrosaurids, the resultant of the mAME complex was assumed to point toward the caudal margin of the supratemporal fenestra, which is where the bulk of this complex originated (see above). These simplifying assumptions allow for models that produce tractable results (sensu Greaves, 1995) and for meaningful comparisons to be made between the taxa considered here.
When a lever model is in static equilibrium—that is, when there is no rotation of the lever about the fulcrum—the moment of the resistance force is equal to the moment of the applied force. In Figure 3, the resistance moment is \( S(e' + a) \), where \( S \) equals the resistance force and \( e' + a \) equals the moment arm of that force. The applied moment is \( F(m) \), where \( F \) equals the applied force and \( m \) equals the moment arm of that force. Because \( m \) cannot be measured directly, it must be calculated as \( m = \frac{\sin(\theta + \delta)}{d} \), where \( d \) equals the diagonal distance between the jaw joint and the point of insertion of the adductor musculature at the apex of the coronoid process, \( \theta \) is the angle made by the adductor resultant relative to the tooth row, and \( \delta \) is the angle between \( d \) and the tooth row.

The vertebrate mandible in its occluded (static) state can therefore be described as follows:

\[
S(e' + a) = F[\sin(\theta + \delta)d]
\]

where \( e' \) represents any desired distance rostral to the coronoid process (if the bite point is caudal to the coronoid process, this distance is subtracted from \( a \)), and \( F \) is assumed to be unity. From this, it is possible to solve for \( S \). Because \( S \) is calculated relative to unit applied force, it is herein referred to as the relative bite force (RBF).

We took the appropriate linear measurements from specimens with dial callipers and a tailor's measuring tape to the nearest millimeter at bite points coinciding with the apex of the premaxillary and, with the mesial and distal teeth. We ignored the keratinous rhamphotheca when calculating RBF at the premaxillary apex because it rarely fossilizes and otherwise has a negligible effect on the calculation (Farke et al., 2013). We measured angles from photographs using ImageJ 1.43s (Abramoff et al., 2004), with the skulls oriented so that the tooth row was horizontal.

In some instances, it was necessary to estimate the location of certain landmarks because they were obscured by bone or matrix. For example, among ceratopsids and hadrosaurids, the distal end of the tooth row is not always observable because of inadequate preparation of the matrix between the coronoid process and the jaw joint. However, the tooth row typically terminates at the caudal margin of the coronoid process and was therefore assumed to end at this point in specimens where the distal tooth row could not be seen. Also, in many hadrosaurid skulls where the mandible is fully occluded, the apex of the coronoid process is often hidden from view behind the jugal. If the temporal fossa was not fully prepared, it was sometimes necessary to estimate the apex of the coronoid process based on the curvature of its distal end as it disappeared behind the jugal.

Some specimens used in this study could not be measured directly because they were inaccessible (e.g., displayed behind glass). It was therefore necessary to estimate their dimensions from photographs, using measurements given in the literature to provide scale. If these measurements were not available, we calculated relative dimensions instead. This is possible because absolute dimensions are inconsequential; RBF is a unitless quantity. We made measurements from photographs using ImageJ 1.43s (Abramoff et al., 2004).

**Sensitivity Analysis**

To determine the effect that variations in the above variables would have on our results, we conducted a sensitivity analysis whereby we varied the values by \( \pm 10\% \) of the original ‘best guess’ estimates. The resulting RBFs were compared with the original estimates to gauge the percentage difference between them.

**Jaw Mechanics and Body Size Correlation**

Many of the available lambeosaurine (Corythosaurus and Lambeosaurus) specimens represent immature growth stages (e.g., AMNH 5340, 5382, CMN 8633, 34825, ROM 758, 869, 1947), as evidenced by their relatively small size and undeveloped cranial ornamentation (Dodson, 1975; Evans, 2007). To determine whether their inclusion in the data set would overprint the ecomorphological signal of interest with an ontogenetic one, we regressed RBF against the length of the mandible \((a + e' + b)\); a proxy for body size) using reduced major axis (RMA) regression. RMA is preferable to ordinary least squares regression because it does not assume that the independent variable is measured without error. We computed the coefficient of determination \((R^2)\) and the probability \((P)\) that size and RBF are not correlated to determine the strength of this relationship.

**Statistical Comparisons**

We compared RBF values at coarse (family/suborder), medium (subfamily/family), and fine (genus) taxonomic scales. We did not consider the species level because sample size was consistently too low at this resolution to permit meaningful statistical comparisons (even so, many of the genera considered here are monospecific). We employed nonparametric statistics because of issues with both non-normality and low sample size \((n < 30)\). These tests lack the power of parametric statistics but are more robust against committing Type I errors (reporting differences where none exist). Typically, arcsine transformation is recommended to normalize percentages and proportions (Sokal and Rohlf, 1995); however, it is inapplicable in this instance because the value of RBF may be greater than 1. We tested systematic differences in bite performance along the mandible using nonparametric multivariate analysis of variation (NPMA-NOVA), which tests for differences between two or more groups of multivariate data using a specified distance measure (Andersen, 2001). In the case of the Euclidean distance measure used here, NPMANOVA is analogous to the more familiar multivariate analysis of variance (MANOVA), both of which return an F statistic. In NPMANOVA, significance is estimated by permutation across groups, which we performed using 10,000 replicates.

We likewise conducted post hoc pairwise comparisons using NPMANOVA with Bonferroni correction. Bonferroni correction was designed to counteract the problem of multiple comparisons, whereby the probability of committing a type I error increases with the number of simultaneous comparisons being made (Sokal and Rohlf, 1995). This problem is rectified by multiplying the P value by the number of pairwise comparisons, effectively lowering the significance level. However, because Bonferroni correction provides little power and is probably too conservative (Sokal and Rohlf, 1995; Nakagawa, 2004), we also report uncorrected probabilities here for comparison.

Where appropriate, we made comparisons of two univariate samples at selected bite points along the mandible using a two-tailed (Wilcoxon) Mann-Whitney U test, which tests for differences in sample medians. We set statistical significance for all tests at \( \alpha = 0.05 \). We performed all statistical tests using PAST 2.12 (Hammer et al., 2001).

Because the DPF does not represent a single assemblage of contemporaneous organisms, time-averaging is an issue. This has the effect of masking paleoecological patterns that are otherwise distinguishable only at fine temporal resolutions (Behrensmeyer and Hock, 1992). For this reason, we minimized the effects of time-averaging by making the above comparisons within each of the two most inclusive Megaherbivore Assemblage Zones (MAZs) identified by Mallon et al. (2012). To summarize, MAZ-1 encompasses the lower 28 m of the DPF, whereas MAZ-2 encompasses intervals from 29 to 52 m. Although this time-constrained approach theoretically increases the
probability of recovering differences that would otherwise be masked by the effects of time-averaging, there is a trade-off in that sample size (and hence statistical power) is reduced considerably. Also, this approach does not completely remove the effects of time-averaging because the above-mentioned MAZs are themselves time-averaged over a period of approximately 600 Kyr (Mallon et al., 2012).

RESULTS

Sensitivity Analysis

The sensitivity analysis reveals that ±10% deviations in the measurements used here result in RBF estimates that vary from 0% to 11% of the original ‘best guess’ hypothesis (Table 2). Importantly, the most significant RBF deviations are related to measurements of the mandibular ramus and coronoid process, which can be determined with relative confidence. Conversely, variations in θ or δ, which are the most difficult variables to estimate, produce minor differences in RBF (1–2%). This suggests that any errors associated with the estimation of these variables are unlikely to be particularly misleading.

Relative Bite Force and Body Size

RBF decreases with increasing mandible length at the rostral-most bite points and decreases with increasing mandible length at the distal tooth (Fig. 4). The R² value at the predentary apex is moderate, but the relationship between RBF and mandible length is significant (Fig. 4A). Elsewhere along the mandible, these values are low and insignificant (Fig. 4B, C). Because there does not appear to be a particularly strong correlation between RBF and mandible length at all points along the jaw, we retained the immature lambeosaurine specimens in all subsequent analyses.

Time-Averaged Approach

The results of the lever analysis (Fig. 5A) demonstrate that RBF increases distally along the mandible for all taxa. In ankylosaurs, the increase in RBF is gradual along the entire length of the mandible, varying from ~0.25 at the predentary apex to ~0.75 at the distal tooth. Panoplosaurus generally possesses higher RBFs than Euoplocephalus at each point along the mandible; however, their confidence intervals overlap considerably. The confidence interval of Ceratopsidae is likewise large, which appears to reflect the fact that CMN 2245 (Chasmosaurus) possesses an especially powerful bite (Table S1). Ceratopsids and hadrosaursids have higher RBFs than ankylosaurs, particularly at the distal tooth, where the mean RBF varies between ~2.0 and ~2.5. Ceratopsids and hadrosaursids do not appear to differ systematically in their RBFs at any point along the mandible.

Highly significant differences are recovered among the higher-level taxa (N = 77, F = 56.4, P < 0.0001). Post hoc pairwise comparisons (Table 3) reveal that ankylosaurs differ from both ceratopsids and hadrosaursids, but the last two taxa do not differ significantly from one another, even despite their larger sample sizes. Ceratopsids have significantly higher RBFs than ankylosaurs at the mesial (N = 25, U = 14, P < 0.01) and distal (N = 23, U = 0, P < 0.001) ends of the tooth row. Hadrosaursids have significantly higher RBFs than ankylosaurs at the predentary apex (N = 32, U = 6, P < 0.05), and at the mesial (N = 57, U = 5, P < 0.0001) and distal (N = 60, U = 0, P < 0.0001) ends of the tooth row. The lambeosaurines Corythosaurus and Lambeosaurus reportedly differ in their jaw mechanics when the uncorrected P values are considered (Table 5), but the follow-up Mann-Whitney U tests along the mandible do not corroborate this. The difference detected by NPMANOVA might therefore be attributed to the effects of missing data, because both genera are missing approximately half the data for the predentary apex. There are otherwise no further differences recovered at either the family/subfamily (Table 4) or genus (Table 5) level.

Time-Constrained Approach

MAZ-1—The results of the MAZ-1 lever analysis closely mirror those of the time-averaged analysis (Fig. 5B). Although Euoplocephalus is known from MAZ-1 (Mallon et al., 2012), it is not present in this analysis because of a lack of adequate data. Ceratopsids and hadrosaursids once again possess particularly high RBFs at the distal tooth, but their confidence intervals overlap considerably.

Highly significant differences are recovered among the higher-level taxa (N = 40, F = 32.22, P < 0.0001). Again, ankylosaurs differ from both ceratopsids and hadrosaursids, but the last two taxa do not differ significantly from one another (Table 6). Ceratopsids possess significantly higher RBFs than ankylosaurs at the distal tooth (N = 11, U = 0, P < 0.05). Hadrosaursids possess higher RBFs than ankylosaurs at the mesial (N = 50, U = 2, P < 0.01) and distal (N = 31, U = 0, P < 0.01) ends of the tooth row. No further differences are recovered with increasing taxonomic

TABLE 2. Sensitivity analysis of the mechanical mandibular model used here, exemplified by ROM 767 (Centrosaurus apertus).

| Iteration | Variable | a + e' + b | a + e' | a - e' | d | θ | δ | RBF | % difference in RBF |
|-----------|----------|------------|--------|--------|---|---|---|-----|---------------------|
| Original  | a + e' + b | 612 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| +10% a    | a + e' + b | 612 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| -10% a    | a + e' + b | 612 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| +10% δ    | a + e' + b | 612 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| -10% δ    | a + e' + b | 612 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| +10% J to beak tip | a + e' + b | 673.20 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| -10% J to beak tip | a + e' + b | 550.80 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| +10% J to ant tooth | a + e' + b | 612 | 379.50 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| -10% J to ant tooth | a + e' + b | 612 | 379.50 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| +10% J to post tooth | a + e' + b | 612 | 379.50 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| -10% J to post tooth | a + e' + b | 612 | 379.50 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| +10% d    | a + e' + b | 612 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |
| -10% d    | a + e' + b | 612 | 345 | 61 | 182 | 53.81 | 47.93 | 0.29 | 0.52 | 2.92 |

Symbols (after Ostrom, 1964b): a, horizontal distance between coronoid process and jaw joint; b, horizontal distance between predentary tip and mesial end of tooth row; d, diagonal distance between jaw joint and point of insertion of adductor musculature at apex of coronoid process; e', horizontal distance between apex of coronoid process and mesial end of tooth row; e", horizontal distance between apex of coronoid process and distal end of tooth row; θ, angle made by adductor muscle resultant relative to tooth row; δ, angle between d and tooth row. See Materials and Methods and Figure 5 for further details.
resolution, at either the family/subfamily (Table 7) or genus (Table 8) level.

MAZ-2—The results of the MAZ-2 lever analysis closely resemble those of the time-averaged analysis (Fig. 5C). Ankylosaurs could not be included in the statistical analyses due to insufficient sample size (Mallon et al., 2012). No significant differences were recovered either between the ceratopsids and hadrosaurids \( (N = 19, F = 1.103, P > 0.05) \) or between subfamilies within each of these taxa \( (N = 19, F = 2.066, P > 0.05) \).

**DISCUSSION**

**Relative Bite Force and Body Size**

Some comments bear mentioning regarding the correlation between \( R^2 \) and the position of the bite point along the lambeosaurine mandible. It is likely that the higher \( R^2 \) and significant \( P \) value calculated at the predentary apex reflects some degree of autocorrelation because the length of the mandible, used as the independent variable in the RBF regressions, is also used in the calculation of RBF at the predentary apex. On the other hand, the lowest \( R^2 \) and highest \( P \) value calculated at the distal tooth position might result from variation associated with the occasional estimation of the distal tooth position (see Materials and Methods). For this reason, the results produced at the mesial tooth position are likely more representative of the true relationship between body size and RBF.

These findings are of added interest in light of recent work concerning ontogenetic scaling of bite force in vertebrates more generally. Owing to their smaller body size, young animals are at a competitive disadvantage compared with their adult conspecifics, both in terms of attaining resources and avoiding predators. Juveniles are therefore under strong selection pressure to compensate for their absolute size disadvantage. Several studies have demonstrated that locomotor performance scales negatively allometrically in mammals (Carrier, 1983, 1995; Carrier and Leon, 1990; Trillmich et al., 2003), and less commonly in terrestrial ectotherms (Garland, 1985; Marsh, 1988; Toro et al., 2003), suggestive of just such compensation. However, the same is not generally true of bite performance in vertebrates (Hernandez and Motta, 1997; Herrel et al., 1999, 2005a; Binder and Van Valkenburg, 2000; Erickson et al., 2003; Herrel and O’Reilly, 2006).

Our results largely agree with these previous studies in finding no negatively allometric relationship between relative bite force and body size in lambeosaurines; that is to say, juveniles typically do not have relatively more powerful bites than adults. Whether the same is true for the other dinosaurian taxa considered here is difficult to say, in light of the paucity of appropriate material. However, the near universality of bite performance scaling implies that juvenile ankylosaurs and ceratopsids were no more capable of compensating for their size disadvantage with enhanced RBFs.

It should be noted that bite performance usually scales positively allometrically in vertebrates (Herrel and Gibb, 2006), but our findings reveal no significant relationship between RBF and body size in lambeosaurines. This may simply be a sampling issue, in which case, more data are necessary.

Although it is clear why juveniles should be under selection pressure for enhanced locomotory performance, there is also a priori reason to think that feeding performance should not be similarly compensated in juveniles. Effectively, the disparity in bite performance facilitates interspecific niche partitioning and

![FIGURE 4. Regression plots depicting the relationship between basal skull length and relative bite force at various points along the mandible. A, predentary apex; B, mesial tooth; C, distal tooth.](image-url)
increases the niche breadth of the species. It is therefore likely that lambeosaurines (and other megaherbivores considered here) exhibited some form of ontogenetic niche partitioning, whereby immature individuals subsisted on a softer, more nutritious diet than older ones (Werner and Gilliam, 1984).

Mandibular Lever Mechanics

The increased RBF produced moving caudally along the mandible in all taxa (Fig. 5) is in accordance with the predicted behaviour of a third-class lever. Moving the bite point caudally effectively shortens the moment arm of the applied force relative to that of the resistance force, resulting in higher RBFs.

The fact that ceratopsids and hadrosaurids possess statistically higher RBFs than ankylosaurs can be attributed primarily to the relatively taller coronoid processes and depressed jaw joints of the first two taxa, and also to their more dorsally inclined adductor muscle resultants (Fig. 1, Table S1). This has the effect of increasing the length of the moment arm of the applied force relative to that of the resistance force, thereby improving the leverage of the system. Similar adaptations are seen among ungulates (Greaves, 1995, 1998; Janis, 1995), although the arrangement of the jaw system is opposite that seen in megaherbivorous dinosaurs. In dinosaurs—as in all saurischians—the mAME complex exerts the most force when the mandible is fully adducted. The resultant of this muscular complex is oriented dorsocaudally. Therefore, increasing the length of the moment arm of the applied force requires that the jaw joint be depressed, that the coronoid be elevated, or both. In ungulates, the main adductor is the m. masseter, which originates along the zygomatic arch and inserts on the angle of the mandible, yielding a dorsorostrally inclined resultant. Therefore, the only way to increase the length of the moment arm of the applied force in ungulates is to depress the point of insertion of the masseter or to elevate the jaw joint relative to the tooth row, or both. Cerapods (ceratopsids + hadrosaurids) and ungulates have thus evolved similar adaptive responses to herbivory, albeit in very different ways, each constrained by a different phylogenetic legacy.

This mechanism does not, however, account for the convergence of RBF values at the predentary apex across all taxa (Fig. 5). This likely reflects the fact that ankylosaurs possess relatively shorter diastemae than both ceratopsids and hadrosaurids. Therefore, although ankylosaurs have a relatively shorter moment arm of the applied force compared with ceratopsids and hadrosaurids, they also have a relatively shorter moment arm of the resistance force at the predentary tip, resulting in comparable RBFs across taxa at this particular bite point.

The sudden increase in RBF at the distal tooth in both ceratopsids and hadrosaurids (Fig. 5) also cannot be attributed to the morphology of their jaw joints and muscle attachments. Rather, it is a consequence of the fact that the tooth row in these two taxa extends caudal to the coronoid process, where the bulk of the adductor musculature inserts, and upon which the applied force acts. Thus, caudal to the coronoid process, the ceratopsid and hadrosaurid mandible behaves as a second-class lever, with the resistance force acting between the fulcrum and the applied force. This system is mechanically advantageous and is able to generate higher forces than are applied to the system (i.e., RBF > 1).

If the apparent disparity in jaw mechanics between the ankylosaurs Euoplocephalus and Panoplosaurus (Fig. 5A) is real, rather than an artefact of small sample size, it would appear to be due to the fact that the jaws of the latter have coronoid eminences and jaw joints that are more displaced relative to one another than in the former (Table S1), resulting in a longer moment arm of the applied force. The angle of the adductor resultant is similar between the two taxa and does not appear to contribute to their differential jaw mechanics.

FIGURE 5. Results of the mandibular lever analyses. A, time-averaged analysis; B, MAZ-1 analysis; C, MAZ-2 analysis. Note that the same mechanical patterns are maintained between MAZ-1 and -2, despite genus-level differences in taxonomic composition between the two assemblage zones.
TABLE 3. NPMANOVA results for the time-averaged family/subfamily-level pairwise comparisons.

|               | Ankylosauria (n = 8) | Ceratopsidae (n = 17) | Hadrosauridae (n = 52) |
|---------------|----------------------|-----------------------|-----------------------|
| Ankylosauria  | 0.000***             | 0.000***              | 0.000***              |
| Ceratopsidae  | 0.000***             | 0.255                 |                       |
| Hadrosauridae | 0.000***             |                       | 0.765                 |

Bonferroni-corrected P values shown below diagonal; uncorrected P values shown above diagonal. Significant results indicated by asterisks at P < 0.001 (**). Total analysis: N = 77, F = 56.4, P = 0.000***.

Ostrom (1966) argued that the coexisting ceratopsids *Chasmosaurus* and *Monoclonius (= Centrosaurus)* differed in their jaw mechanics, a result of their different frill orientations. He reasoned that, because the frill of *Centrosaurus* is more erect than that of *Chasmosaurus*, the former taxon possessed more vertical external mandibular adductor musculature than the latter (Ostrom believed that these muscles originated along the dorsocaudal margins of the parietal fenestrae). As a consequence, *Centrosaurus* must have exerted a more powerful bite than the similar-sized *Chasmosaurus*.

The results of the present study do not agree with those of Ostrom (1966) for two reasons. First, the total sample size used here is much larger than that of Ostrom, who examined just two specimens per taxon. This increased sample size produces increased taxonomic overlap and, consequently, decreased statistical significance. Second, and more importantly, Ostrom’s contention that the external mandibular adductor musculature originated along the dorsocaudal margins of the parietal fenestrae is unrealistic. If the musculature originated instead at the base of the frill, as argued here, and if the pulley-like arrangement of these muscles is recognized (see Materials and Methods), then the differences in the orientation of the frill between *Centrosaurus* and *Chasmosaurus* are negated, and their jaw mechanics become indistinguishable.

Henderson (2010) also argued that centrosaurines exerted stronger bite forces than chasmosaurines. His argument stemmed from his demonstration that the former taxon exhibits dorsoventrally deeper skulls than the latter. According to beam theory, this would allow the skull to resist elevated bite forces. The results of the present study do not support the findings of Henderson (2010). It is possible that centrosaurines had more powerful bites than chasmosaurines if a difference in mandibular adductor muscle size could be established, but this has not been done and is, in fact, quite difficult to demonstrate (Bryant and Seymour, 1990; Bryant and Russell, 1992).

**Phylogenetic Considerations**

The efficient jaw mechanism of ceratopsids and hadrosaurids is impressive, and its evolution bears further consideration. For example, did the character states that constitute the system evolve in tandem or in a stepwise fashion? If the latter, in which order did they appear? The present data set was not designed to answer these questions, but a preliminary attempt can be made to address them with reference to recent phylogenetic work.

Of the three mechanically important osteological components of the ceratopsid/hadrosaurid jaw system (development of coronoid process, elongation of tooth row behind coronoid process, depression of jaw joint), the first was primary. A well-developed, distinctly elevated coronoid process is derived for Ornithischia and is, in fact, reduced secondarily in ankylosaurs and their closest kin (Butler et al., 2008). The height of the process becomes increasingly more exaggerated independently among ornithopods (Butler et al., 2008) and ceratopsians (Tanoue et al., 2009).

A jaw joint depressed slightly below the level of the tooth row likewise appears in the earliest ornithischians. However, it only becomes strongly depressed in heterodontosaurids, various ‘hypsilophodontids,’ ankylopollexians (*Camptosaurus* + Hadrosauridae), and ceratopsids (Butler et al., 2008; Tanoue et al., 2009).

The last feature to evolve is the caudally elongate tooth row that extends beyond the coronoid process. This requires that the coronoid process first be displaced lateral to the dentition, which occurred independently in the clades (*Anabisetia* + Ankylopollexia) and Ceratopsia (Butler et al., 2008; Tanoue et al., 2009). The progressive caudal elongation of the tooth row continued in both these lineages, culminating with the Hadrosauridae and Ceratopsidae.

Thus, the mechanically advantageous jaw mechanism shared by ceratopsids and hadrosaurids evolved in a piecemeal fashion, of which the various components evolved independently in each lineage. Such remarkable convergence suggests adaptation within a similar selection regime. Perhaps these two clades evolved to consume foods with comparable mechanical properties. This interpretation must nevertheless be tempered in light of differences in tooth function (Dodson, 1993; Mallon et al., 2014b).

**Paleodiетary Implications**

**Ankylosauria**—Given their small, phylliform teeth (Coombs, 1990), ankylosaurs are traditionally thought to have fed on soft,
TABLE 5: NPMANOVA results for the time-averaged genus-level pairwise comparisons.

|                | Euoplocephalus (n = 4) | Panoplosaurus (n = 4) | Centrosaurus (n = 9) | Styracosaurus (n = 2) | Chasmosaurus (n = 4) | Gryposaurus (n = 6) | Prosaurolophus (n = 9) | Corythosaurus (n = 16) | Lambeosaurus (n = 20) |
|----------------|------------------------|-----------------------|----------------------|-----------------------|----------------------|--------------------|-------------------------|------------------------|-----------------------|
| Euoplocephalus (n = 4) | 0.144 | 0.002** | 0.063 | 0.029* | 0.005** | 0.002** | 0.000*** | 0.000*** |                      |
| Panoplosaurus (n = 4) | 1 | 0.002** | 0.068 | 0.033* | 0.004** | 0.002** | 0.000*** | 0.000*** |                      |
| Centrosaurus (n = 9) | 0.068 | 0.083 | 0.493 | 0.396 | 0.739 | 0.576 | 0.113 | 0.296 |                      |
| Styracosaurus (n = 2) | 1 | 1 | 1 | 0.542 | 0.823 | 0.856 | 0.880 | 0.392 |                      |
| Chasmosaurus (n = 4) | 1 | 1 | 1 | 1 | 0.513 | 0.268 | 0.073 | 0.399 |                      |
| Gryposaurus (n = 6) | 0.169 | 0.148 | 1 | 1 | 1 | 0.698 | 0.379 | 0.646 |                      |
| Prosaurolophus (n = 9) | 0.054 | 0.061 | 1 | 1 | 1 | 1 | 0.575 | 0.232 |                      |
| Corythosaurus (n = 16) | 0.007** | 0.014* | 1 | 1 | 1 | 1 | 1 | 0.037* |                      |
| Lambeosaurus (n = 20) | 0.007** | 0.007** | 1 | 1 | 1 | 1 | 1 | 1 |                      |

Bonferroni-corrected P values shown in lower left triangle; uncorrected P values shown in upper right triangle. Significant results indicated by asterisks at P < 0.05 (*), P < 0.01 (**), and P < 0.001 (***).

Total analysis: N = 77, F = 14.66, P = 0.000***.
lush vegetation, requiring minimal oral processing (Russell, 1940; Haas, 1969; Russell, 1977; Bakker, 1978; Dodson, 1983; Weishampel, 1984; Galton, 1986; Mustoe, 2007). However, after studying the tooth wear and jaw joint morphology of *Euoplocephalus tutus*, Rybczynski and Vickaryous (2001) inferred the existence of a previously unrecognized propalinal jaw mechanism in at least one species. They therefore suggested that *E. tutus* was capable of processing tough foodstuffs and that the ankylosaur diet was perhaps more varied than traditionally assumed. Additional evidence fostered in support of this interpretation includes the transversely wide skull, deep mandible fossa, and distally dilated process (Carpenter, 1990; Vickaryous, 2006). It therefore seems possible that the ankylosaur jaw mechanism may have been more efficient than traditionally assumed, the present study confirms that the mechanism was not particularly efficient—certainly not to the same degree as in the contemporaneous ceratopsids and hadrosaurids. It is therefore unlikely that ankylosaurs consumed as much woody plant material as the other two taxa (see Ceratopsidae and Hadrosauridae, below), which were better able to generate the higher bite forces required to fracture mechanically resistant foodstuffs. This interpretation is corroborated by circumstantial evidence in the form of a cololite associated with a Lower Cretaceous ankylosaurid from Australia (Molnar and Clifford, 2001). The fossil contains vascular tissue (probably leaves), angiosperm fruits or endocarps, small seeds, and possible fern sporangia, but there is no evidence for woody twigs or stems.

The suggestion that *Panoplosaurus* may have had a more efficient jaw mechanism than *Euoplocephalus*, although statistically unsupported, finds some corroborati

fracturing of hard objects, such as seeds (Lucas, 2004), it is likely that the more efficient jaw mechanism of *Panoplosaurus* was instead an adaptation to coping with tough plant material, including leaves and perhaps some woody vegetation.

In spite of the foregoing discussion, it is prudent to call attention to the fact that the limited degree to which ankylosaurs were capable of oral processing may have been offset by the alleged possession of a muscular gizzard. This was suggested after the finding of gastrooliths associated with a specimen of *Panoplosaurus mirus* (ROM 1215; Carpenter, 1990). However, there is some doubt about whether the gastrooliths truly pertain to the specimen in question, because neither the field notes nor the original description (Russell, 1940) mention the existence of gizzard stones (K. Seymour, pers. comm. to J.C.M., 2011).

**Ceratopsidae and Hadrosauridae**—The complex, independently derived tooth batteries of ceratopsids and hadrosaurids have led many to believe that these animals fed on a variety of resistant plant materials (Hatcher et al., 1907; Tait and Brown, 1928; Lull, 1933; Russell, 1935; Lull and Wright, 1942; Ostrom, 1961, 1964a, 1964b, 1966; Russell, 1977; Bakker, 1978; Béland and Russell, 1978; Farlow, 1987; Dodson, 1993, 1996; Dodson et al., 2004; Horner et al., 2004; Hwang, 2005; Williams et al., 2009; Varriale, 2011), a position corroborated by the present study. The ungulate-like adaptations of the jaws, developed in an equal-but-opposite way, suggest that these mechanical systems evolved in response to similar selection pressures. The ungulate masticatory system is thought to have evolved in response to a shift from omnivory or low-herbivory to folivory, with leaves becoming a more readily available food source in the early Eocene (Janis, 2008). It is therefore conceivable that both ceratopsids and hadrosaurids used their highly derived jaws to comminute woody browse as well. This interpretation is supported in the case of the hadrosaurids by evidence from enterolithes (Kräusel, 1922; Currie et al., 1995; Tweet et al., 2008) and coprolites (Chin and Gill, 1996; Chin, 2007), which indicate that these animals fed on conifer and angiosperm browse, including abundant woody materials (unfortunately, circumstantial evidence for ceratopsid diet is lacking). However, there is some question about whether all of the gut contents are truly autochthonous (Abel, 1922; Currie et al., 1995), and the attribution of isolated coprolites to any one taxon is similarly problematic (Chin, 1997). These data must therefore be regarded with due caution.

Although their mandibular leverage is effectively identical, ceratopsids, with their larger skulls, probably achieved a more powerful bite than hadrosaurids. This is a consequence of the fact that muscle mass typically scales positively with skull size (Kiltie, 1982; Herrel et al., 2001, 2002; Meers, 2002; Verwaijen et al., 2004; Horner et al., 2004; Hwang, 2005; Williams et al., 2012). Nonetheless, such an inference should not be taken to mean that ceratopsids necessarily possessed greater dietary breadths than hadrosaurids. Rather, their pointed beaks (Mallon and Anderson, 2014a) suggest that ceratopsids were selective, and their specialized, shearing dentition (Ostrom, 1964a, 1966) likewise attests to the fact that they were adapted to eating mostly tough

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**TABLE 7. NPMANOVA results for the MAZ-1 family/subfamily-level pairwise comparisons.**

|          | Nodosauridae (n = 4) | Centrosaurinae (n = 8) | Hadrosauridae (n = 5) | Lambeosaurinae (n = 22) |
|----------|----------------------|------------------------|----------------------|------------------------|
| Nodosauridae (n = 4) | 0.002** | 0.008** | 0.000*** |
| Centrosaurinae (n = 8) | 0.013* | 0.310 | 0.592 |
| Hadrosaurinae (n = 5) | 0.049* | 1 | 1 |
| Lambeosaurinae (n = 22) | 0.001*** | 1 | 1 |

Bonferroni-corrected P values shown in lower left triangle; uncorrected P values shown in upper right triangle. Significant results indicated by asterisks at P < 0.05 (*), P < 0.01 (**), and P < 0.001 (**). Total analysis: N = 39, F = 20.84, P = 0.000***.

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**TABLE 6. NPMANOVA results for the MAZ-1 suborder/family-level pairwise comparisons.**

|          | Ankylosauria (n = 4) | Ceratopsidae (n = 9) | Hadrosauridae (n = 27) |
|----------|----------------------|----------------------|------------------------|
| Ankylosauria (n = 4) | 0.002** | 0.000*** | |
| Ceratopsidae (n = 9) | 0.005** | 0.266 | |
| Hadrosauridae (n = 27) | 0.001*** | 0.796 | |

Bonferroni-corrected P values shown in lower left triangle; uncorrected P values shown in upper right triangle. Significant results indicated by asterisks at P < 0.01 (**), and P < 0.001 (**). Total analysis: N = 40, F = 32.22, P = 0.000***.
Table 8. NPMANOVA results for the MAZ-1 genus-level pairwise comparisons.

|                | Panoplosaurus | Centrosaurus | Gryposaurus | Corythosaurus | Lambeosaurus |
|----------------|---------------|--------------|-------------|---------------|--------------|
| Panoplosaurus  | 0.002**       |              | 0.007**     | 0.001***      | 0.004**      |
| (n = 4)        | (n = 8)       | (n = 5)      | (n = 15)    | (n = 6)       |              |
| Centrosaurus   | 0.017*        | 0.303        | 0.200       | 0.393         | 0.197        |
| (n = 8)        |              | (n = 5)      |            |               |              |
| Gryposaurus    | 0.069         | 1            | 0.200       | 0.200         | 0.100        |
| (n = 5)        |              |              | (n = 15)    |               |              |
| Corythosaurus  | 0.007**       | 0.200        | 0.293       | 1             | 0.996        |
| (n = 15)       |              |              | (n = 6)     |               |              |
| Lambeosaurus   | 0.036*        | 0.200        | 0.293       | 1             |              |
| (n = 6)        |              |              | (n = 6)     |               |              |

Bonferroni-corrected P values shown in lower left triangle; uncorrected P values shown in upper right triangle. Significant results indicated by asterisks at P < 0.05 (*), P < 0.01 (**), and P < 0.001 (**). Total analysis: N = 38, F = 17.37, P = 0.000***.

Evolutionary Paleoeconomy

Of the 12 genera examined here—six of which typically coexisted at any one time (Mallon and Anderson, 2014a)—only two or three distinct jaw mechanisms are distinguishable. Ankylosaurs can be discerned from ceratopsids and hadrosaurs on the basis of their mandibular mechanics, and among ankylosaurs, there is tentative evidence to suggest that Panoplosaurus and Euoplocephalus differed. This mechanical conservatism may have resulted from stabilizing selection; however, some form of geometric, functional, phylogenetic, or developmental constraint (sensu McGhee, 2007) cannot be discounted. For instance, Greaves (1995) has shown that caudal displacement of the tooth row may eventually cause dislocation of the jaw joint. Such functional constraint, in tension with directional selection for enhanced leverage, could conceivably result in the low mechanical disparity observed here, wholly apart from stabilizing selection.

If megaherbivore coexistence in the DPF was facilitated by dietary niche partitioning, it must therefore have occurred as a result of multiple facets of morphology acting in concert to produce distinct feeding ecologies and is not solely attributable to differential jaw mechanics. Previous studies have shown that symphatic ankylosaurs and nodosaurs differ in the morphology of their teeth (Coombs, 1990; Mallon and Anderson, 2014b) and beaks (Carpenter, 1982, 1997a, 1997b, 2004; Mallon and Anderson, 2014a), which may have alleviated competition between these two taxa. Ceratopsids and hadrosaurs likely differed according to their browse heights (Mallon et al., 2013), overall skull proportions (Mallon and Anderson, 2013), snout shape (Mallon and Anderson, 2014a), and tooth wear (Mallon and Anderson, 2014b). Henderson (2010) posited that the dorsoventrally deeper skulls of centrosaurines may have enabled them to macerate more resistant plant tissues than chasmosauroines—a finding that recently garnered only weak statistical support (Mallon et al., 2013). Sympatic hadrosaurs and lambeosaurines from the DPF appear quite similar in most aspects of inferred ecomorphology, save for possible size differences that might have allowed the larger hadrosaurs to subsist on a lower quality diet (Mallon and Anderson, 2013).

The temporal longevity of the patterns identified here, spanning ~1.5 Ma, suggests, first, that time-averaging does not obscure the paleoecological relationships of the DPF megaherbivores, other than to artificially increase taxonomic diversity. Second, it lends additional support to the contention that the DPF fossil assemblage constitutes a chronofauna (Brinkman et al., 2004; Mallon et al., 2012). This term was coined by Olson (1952:181) to refer to “a geographically restricted, natural assemblage of interacting animal populations that has maintained its basic structure over a geologically significant period of time.” This structural stability is traditionally attributed to environmental stasis (Olson, 1952; Brinkman et al., 2004); however, the DPF records a continuous transgression of the Western Interior Seaway, shifting from alluvial depositional environments low in section to coastal/estuarine settings higher in section (Eberth, 2005). Paleopalynological data also indicate a shift to more abundant hydrophytic plant taxa (Braman and Koppelhus, 2005; Braman, pers. comm. to J.C.M., 2010). The stability of the DPF megaherbivore chronofauna might instead be attributable to evolved mutualisms, historical contingency, or the ‘law of large numbers’ (DiMichele et al., 2004).

CONCLUSIONS

Brusatte (2012:233) noted that “[o]ne of the most salient, yet puzzling, features of many dinosaur assemblages is the coexistence of numerous species that seem to share a similar feeding ecology.” This is certainly true of the Late Cretaceous megaherbivore assemblage of Laramidia, which supported a rich diversity of ankylosaurs, ceratopsids, and hadrosaurs (Lehman, 1987, 1997, 2001). There is mounting evidence to suggest that, within the upper Campanian DPF of Alberta, megaherbivorous dinosaur diversity was facilitated by dietary niche partitioning (Mallon et al., 2012, 2013; Mallon and Anderson, 2013, 2014a,b). However, this study reveals that RBF diversity is not correspondingly high, which suggests that differential jaw mechanics played only a subsidiary role in niche partitioning, according to the model used here. Ankylosaurs probably fed primarily on less resistant, non-woody herbage, whereas ceratopsids and hadrosaurs used their mechanically advantageous jaws to consume tougher, woodier browse. The impressive jaw mechanism shared by last two taxa evolved in a stepwise fashion, independently in each lineage. There is tentative evidence among ankylosaurs that Panoplosaurus had a more powerful bite than Euoplocephalus, and probably ate more fibrous vegetation as a result, but systematic differences in bite mechanics are not observed among either ceratopsids or hadrosaurs. The temporal stability of the patterns identified here supports the contention that the megaherbivorous dinosaur assemblage of the DPF constitutes a chronofauna.

Our data further indicate that jaw proportions are conserved both ontogenetically and phylogenetically at the family level. The lack of mechanical compensation in juveniles may have facilitated interspecific niche partitioning. The low shape disparity among confamilials might likewise have resulted from natural selection, but evolutionary constraints on variation cannot be discounted.

Although the biomechanical models used in this study are practical, they nevertheless provide only a first-order understanding of the jaw mechanics of the megaherbivorous dinosaurs.
An ideal next step would be a consideration of actual bite forces, which would provide further insight into what types of plant tissues these animals were capable of processing. Currently, it is possible to approximate absolute bite forces from three-dimensional, computer-aided muscle reconstructions (e.g., Young et al., 2012), but the uncertainty associated with such an approach can lead to serious underdetermination (Bryant and Seymour, 1990; Bryant and Russell, 1992; Curtis et al., 2010). The role of the predentary in ornithischian jaw mechanics also requires elucidation, particularly in answer to the question of whether it transmitted bite forces across the mandibular symphysis (Nabavizadeh, 2011, 2014; Ohashi, 2011). Likewise, the function of cranial kinesis in food comminution is hotly debated (e.g., Holliayd and Witmer, 2008; Rybczynski et al., 2008; Cuthbertson et al., 2012) and requires further attention. Finally, it must be said that more sophisticated modeling techniques require better, three-dimensionally preserved fossil material, which can pose a serious problem for comparative paleoecological studies such as this, where sample size is an issue. To be sure, there remains much work to do, but continual advances in biomechanical modeling and fossil recovery provide warrant for optimism.

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