

A THREE-DIMENSIONAL ANIMATION MODEL OF *EDMONTOSAURUS* (HADROSAURIDAE) FOR TESTING CHEWING HYPOTHESES

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ABSTRACT

Here we describe a 3-D animated model of the craniodental system of a hadrosaur, developed for testing hypotheses of feeding kinematics. The model was created from scanned cranial elements of an *Edmontosaurus regalis* paratype (CMN 2289). Movements within the model were created in animation software using inverse kinematics and a wiring system composed of cranial elements. The model was used to reproduce the pleurokinetic hypothesis of hadrosaur chewing. The pleurokinetic hypothesis, formally developed in the 1980s, proposed that hadrosaurs employed transverse chewing movements via cranial kinesis. Specifically during the powerstroke the maxillae were abducted. This is the first model to allow investigation into secondary intracranial movements that must have occurred in order for the skull to accommodate the primary, pleurokinetic movements. This study found secondary movements to be extensive among the joints of the palate and face. Further refinement and development of the model, including the integration of soft-tissue structures, will allow for a more in-depth examination of the pleurokinetic hypothesis and comparison with alternative feeding hypotheses.

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INTRODUCTION

Reconstructing feeding behavior in extinct animals is fundamental to gaining insight into their ecology and evolution. Previous investigations into dinosaur feeding have utilized multiple approaches including, soft-tissue reconstruction (Ostrom 1961; Haas 1963; Galton 1984; Norman 1984; Molnar 1991) and study of toothwear patterns (e.g., Norman and Weishampel 1985; Weishampel and Norman 1989; Fiorillo 1998; Barrett 2000). Additionally, consideration of joint surfaces have served to help reconstruct kinematics of the feeding system, and more recently finite-element modeling has been used to investigate how the head skeleton may resist strains associated with feeding (e.g., Ostrom 1964; Weishampel 1984; Upchurch and Barrett 2000; Rayfield et al. 2001; Rayfield 2004; Therrien et al. 2006). A major challenge in reconstructing dinosaurian feeding behavior relates to our incomplete understanding of soft tissues (e.g., musculature, ligaments) (Witmer 1995). Even if the gross morphology of the soft tissues is properly reconstructed, it is still difficult to infer how the soft tissues would have interacted with the head skeleton to produce feeding movements (Lauder 1995). The challenge appears most acute for lineages where the head skeleton is highly derived, as seen in hadrosaur dinosaurs. Nonetheless, the architecture of the head skeleton does offer numerous data that can be used to identify constraints in mobility, an important first step in any kinematic reconstruction.

Within Dinosauria, feeding behavior of hadrosaurs has garnered particular attention. Hadrosaurs (Ornithopoda, Iguanodontia, Hadrosauridae) are a globally successful group of large-bodied, Late Cretaceous herbivores (Ostrom 1961; Norman and Weishampel 1985). A possible key to their success is a specialized feeding system that includes a transverse chewing stroke (Norman and Weishampel 1985). Transverse chewing in combination with other specializations such as a robust occluding dentition, may have allowed hadrosaurs to process tough foods more effectively than their less specialized herbivorous counterparts. Among tetrapods, transverse chewing appears to have arisen within only two lineages: mammals (Weijers 1994) and hadrosaurs. In mammals, transverse chewing is achieved through mandibular movements, whereas in hadrosaurs it has been hypothesized to involve a unique, complicated set of intracranial movements (i.e., pleurokinesis) (Weishampel 1984; Norman and Weishampel 1985). Despite many previous studies into the had-

rosaur feeding apparatus (Ostrom 1961; Heaton 1972; Norman 1984; Weishampel 1984) elucidating the mechanisms of cranial kinesis has been difficult in part because of conflicting interpretations of the soft tissues (Ostrom 1961; Weishampel 1984), but also because of the complex geometry associated with the proposed cranial kinesis. This study is the first to investigate hadrosaur feeding by combining three-dimensionally scanned, cranial elements with animation techniques. The advantage of this 3-D animation approach is that it allows us to take into account the geometry of each cranial element and investigate how the architecture of the skull and shapes of the intracranial joints constrains feeding movements.

Pleurokinesis and the evolution of the hadrosaur feeding apparatus

One of the most specialized components of the hadrosaur (cranial) feeding apparatus is the dental system. Primitively, the ornithopod dentition comprised separated, cusped teeth; however in the evolution of the lineage the teeth within the tooth rows became progressively more tightly packed together. In the most highly derived ornithopods (e.g., hadrosaurs) the teeth are interlocking and each tooth row forms a single occlusal surface. The resulting toothrow is referred to as a “dental battery.” The occlusal surfaces of the dental batteries tend to be heavily worn, suggesting that the animals employed a high degree of oral processing. Moreover, tooth wear evidence indicates that the powerstroke phase of the chewing cycle, when the upper and lower teeth are mechanically processing food, involved a large transverse component (Weishampel 1984). In early ornithopods, the transverse powerstroke was probably achieved by rotating the mandibles about their long axis, so that the dentaries pivoted against the prementary (Weishampel 1984; Crompton and Attridge 1986). In contrast, more derived ornithopods (i.e., Iguanodontia) were hypothesized to have abandoned mandibular rotation in favor of maxillary rotation (Weishampel 1984; Norman and Weishampel 1985; You et al. 2003). Maxillary rotation would have occurred about the pleurokinetic hinge, which is a complex set of articulations formed between multiple sets of elements. In hadrosaurids the pleurokinetic hinge is formed along the maxilla-premaxilla, lacrimal-jugal, postorbital-jugal, and quadrate-squamosal contacts (Weishampel 1984) (Figures 1, 2).

The pleurokinetic hypothesis of iguanodontid chewing assumes bilateral occlusion (i.e., isog-

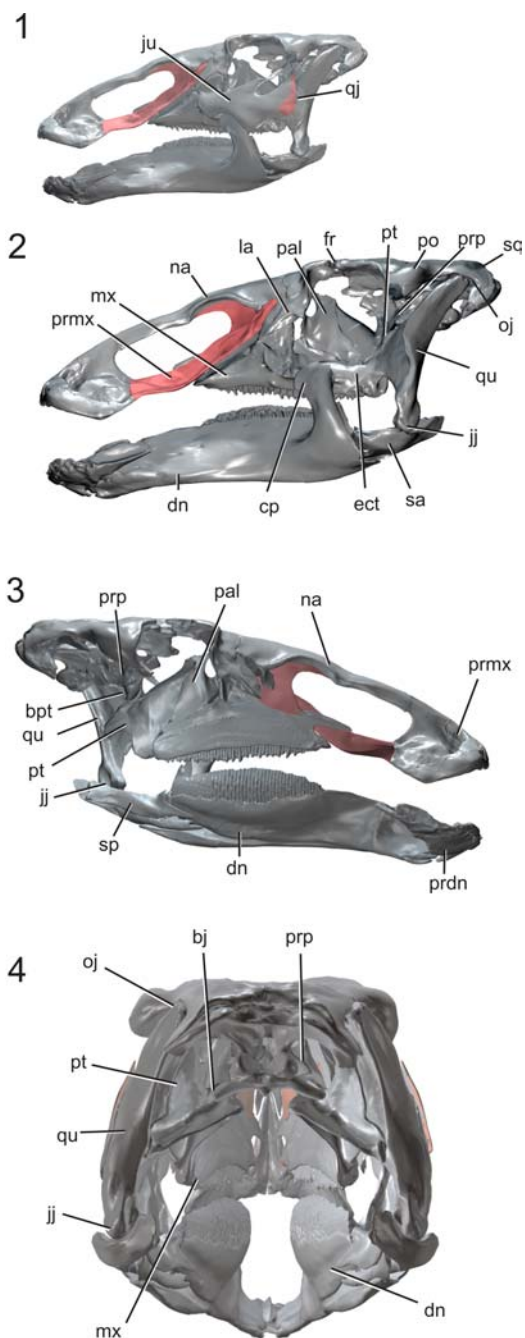


Figure 1. *Edmontosaurus* cranial anatomy. **1**, Left, lateral view; **2**, Left, lateral view with quadratojugal and jugal removed from relevant skeletal elements; **3**, Medial view of left half of skull with relevant skeletal elements labeled; **4**, Caudal view of skull with relevant skeletal elements. Abbreviations: bj, basal joint; bpt, basiptyergoid process; cp, coronoid process; dn, dentary; ect, ectopterygoid; fr, frontal; jj, jaw joint; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; o, otic joint; pal, palatine; po, postorbital; prdn, prementary; prm, premaxilla; prp, preotic pendant; pt, pterygoid; pt, pterygoid; qj, quadratojugal; qu, quadrate; sa, surangular; sp, splenial; sq, squamosal.

nathy) and a unique system of mobile intracranial joints (Norman and Weishampel 1985). To investigate how this complex system may have functioned during chewing Weishampel (1984) used an “Integrated Mechanisms Program.” This computer program allowed him to model the skull as a rigid-linked, closed-loop system with multiple degrees of freedom. Using an iterative approach, he resolved how a bilaterally occluding dentition, coupled with a pleurokinetic hinge system could produce a transverse powerstroke. The model captures the primary movements of the feeding mechanism. The movements involved in the powerstroke are: (1) mandibular adduction (2) abduction of the maxillae, and (3) abduction and retraction of the quadrates (Figure 3). Note that although abduction of the maxillae, and abduction and retraction of the quadrates are referred to as primary movements, they arise as a *consequence* of mandibular adduction, due to the geometry of the cranial linkage system.

Though sophisticated for its time, the original computer model could not easily account for the 3-D morphology of the joint surfaces (Figure 3) and so did not allow researchers to investigate secondary movements. Secondary movements are intracranial movements that occur beyond the pleurokinetic hinge (see above). They can also be thought of as movements that would be necessary in order for the primary movements (e.g., maxillary abduction) to occur. Regions of potential secondary movement include the pterygoid-palatine, pterygoid-ectopterygoid-maxilla, pterygoid-quadrate, pterygoid-basisphenoid, and jugal-quadratojugal contacts (see Weishampel 1984). Secondary movements are important as they may represent additional constraints within the linkage system. Additionally, some of the elements involved in the secondary movements (e.g., pterygoid) would have served as muscle attachment sites (e.g., *M. protractor pterygoideus*, *M. pterygoideus dorsalis*), and so are implicated in aspects of the feeding mechanism associated with force production.

This study represents the first step toward developing a new animation model that will be used to investigate and test chewing hypotheses in *Edmontosaurus*. Here we describe how the animation model was created from scanned fossil elements recovered from a single individual, and then mobilized using inverse kinematics and a wiring system. We finish with a discussion of the preliminary results and an outline of future directions. Notably, an additional objective of this study was to produce an animation, which could illustrate the pleurokinetic hypothesis of hadrosaur chewing for

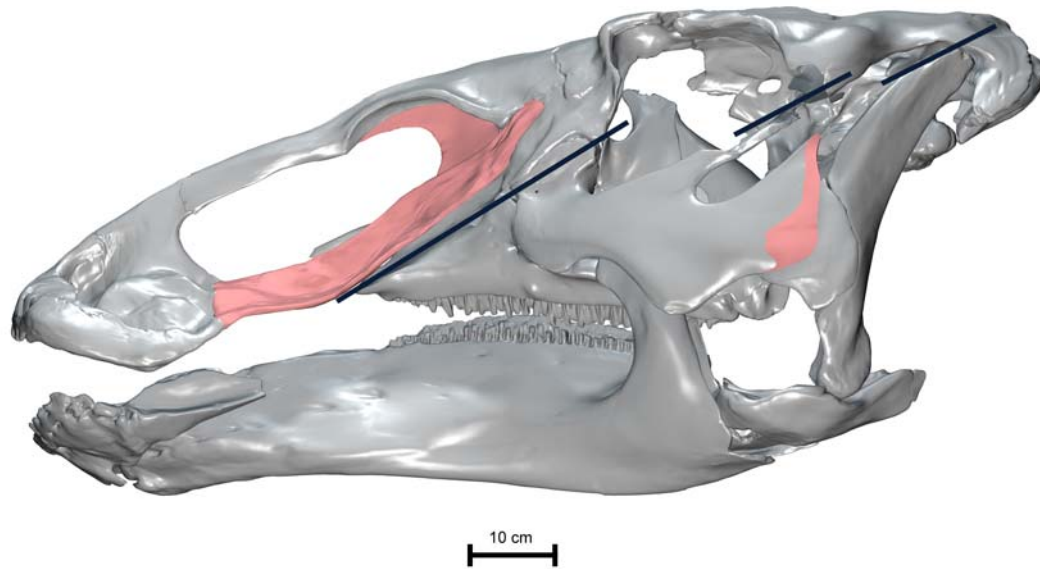


Figure 2. Location of the pleurokinetic hinge in *Edmontosaurus*.

museum visitors. The model described herein is currently on exhibit at the Canadian Museum of Nature, Talisman Fossil Gallery in Ottawa.

METHODS

Edmontosaurus material

The cranial material used for scanning is from Canadian Museum of Nature (CMN) specimen number 2289, a paratype of *Edmontosaurus regalis*. The specimen was recovered by C.H. Sternberg in 1916 from the Edmonton Formation along the Red Deer River, “seven miles west and north of Morrin” (Lambe 1920, p. 2). The head skeleton is mostly complete and exceptionally well-preserved. The skull is relatively undistorted and is only missing the predentary and premaxillae. The suspensorium (e.g., quadrates, palatal elements) were found disarticulated from the braincase. For this study, the braincase and available left-side elements were selected for scanning. The left-side elements were favored because they were more complete than those of the right side.

Arius 3-D laser scanner

The elements were scanned using an Arius 3-D laser scanner. The laser system characterizes each scanned point from the surfaces of the object according to its color and location in three-dimensional space. It does this by scanning the surface

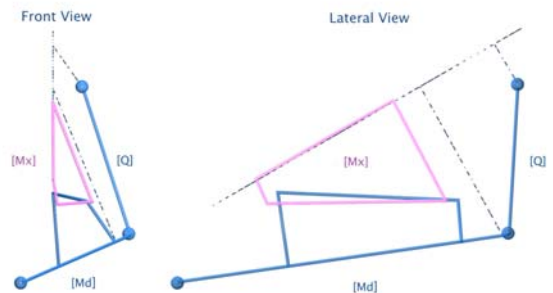


Figure 3. Animation showing pleurokinetic hypothesis, illustrated using *Corythosaurus casuarius* (CMN 8676). Animation is based on Weishampel (1984, figure 20). A limitation of this model is that it allows for investigation of the primary movements only (see text). Reproduced with permission of the Canadian Museum of Nature, Ottawa, Canada.

of an object using one focused laser beam comprising three wavelengths (red, green, and blue), and recording the reflected light using a charge couple device. Each point on the object is described by six numeric values; three positional values X, Y, and Z, and three surface color values R, G, and B. The X coordinate of each point on the object is calculated from an accurate measurement of the position of the scanning mirror in the camera. The Y coordinate is calculated from an accurate measurement of the camera motion system.



Figure 4. The Arios 3D laser scanner scanning dentary of *Edmontosaurus*, CMN 2289.

The Z coordinate is calculated through laser triangulation within the camera. At the same time color information at each point is gathered by measuring the intensity of the reflected laser beams. Color intensity measurements are accurate, being completely independent of ambient light. The total light exposure is about 3.5 milliwatts, roughly equivalent to shining a flashlight on the object. The laser light moves continuously at about 300 mm/sec across the surface of the object therefore the dosage of light on the specimen's surface is extremely small.

For each scan, the laser beam passes over the surface, one scan line at a time. The laser scans at a resolution as fine as 100 microns, recording 3-D shape and color simultaneously with high-resolution and perfect registration. In this study, each cranial component was scanned with

sequential overlapping scans until the entire surface was covered. The scanning resolution for each component ranged from 300 μm to 600 μm , depending on the size of the component being scanned. Larger components such as the brain-case were scanned at 600 μm . The dentary was scanned at 400 μm (see Figure 4), whereas smaller elements, such as the palatine, were scanned at 300 μm . Their's effective scanning area (i.e., field of view) is approximately 60 mm wide. Consequently larger objects require multiple scans (see Figure 5). An interactive 3-D model is available at: <http://www.arius3d.com/Edmontosaurus/>.

Each scan was processed using Pointstream 3DImageSuite (2007) to create a point-cloud form. Overlapping scans of the object were aligned in Pointstream. This process requires manually picking three to five points that are common between two scans. The alignment algorithm then uses these points to search for geometric commonality between scans and then shifts the selected scans into an aligned position.

Once the complete point-cloud model was created, it was converted into a triangulated polymesh comprising thousands of individual faces using surfacing software (Paraform v3.1, 2001). Compared to the number of points in the original point-cloud, the number of triangles in the original converted polymesh is roughly double. For example the dentary (scanned at 400 μm resolution) contained 2.2 million points and when converted to polymesh it yielded 4.4 million triangles. Models with such heavy computations require too much processing power and memory to be practically

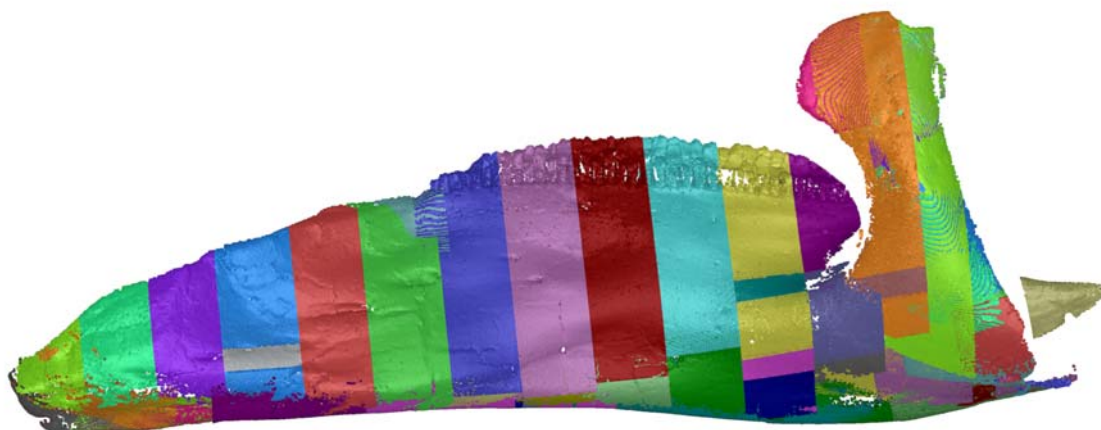


Figure 5. Random color display illustrating many scans aligned in Pointstream to make 3-D model. The dentary data includes a total of 1,246,121 xyzrgb points.

used in animation software. Therefore the face count in the polymesh models for all the scanned elements was reduced. For example the braincase was scanned at 500 μ m and yielded 1.1 million points and 2.2 million polymesh triangles that were then reduced to 100,000 triangles. The resulting element was much lighter to work with but still maintained its geometry. Other elements that were reduced substantially include the splenial, nasal, ectopterygoid, and palatine. Elements, or parts of elements, whose surfaces could be involved with cranial kinesis (e.g., upper and lower toothrows, pterygoid, jugal, quadratojugal) were not reduced as much. For example, in its reduced state, the maxillary tooth row comprised 100,000 polymesh triangles.

3-D animation

Assembling the model. The reduced-size polymesh skull-components were imported into the animation software 3-D Studio Max v. 8 (3ds Max; Autodesk 2006) as object files and digitally assembled to form the skull. Right-side elements that were not scanned (see above) were constructed in the animation software by creating a mirrored clone of the left-side elements. Most of the CMN 2289 skull components were fit together with little difficulty. One exception was the pterygoid, which initially did not fit well lengthwise within the skull. Given that the pterygoid is a very thin element, it was likely deformed post-mortem. For this model, the pterygoid was fit to the skull by slightly shortening the quadrate ramus of the pterygoid. For future versions of the model the question of how best to correct for deformation of the pterygoid will be explored more fully. There is also evidence of some deformation within the braincase. Examination of the braincase in anterior view (e.g., see Lambe 1920, figure 7) shows the bottom of the braincase is sheared slightly to the right. For this study the basiptyergoid processes were shifted slightly back toward the left so that they were more symmetrical.

Also uncertain in the model is the mediolateral position of the lower tooth rows relative to the uppers. For the current model the dentaries were positioned by aligning the upper and lower tooth rows so that the *Edmontosaurus* model is isognathous, as per the assumptions of the original pleurokinetic-hinge hypothesis (see above). The resulting configuration shows a small space between the anterior tips of the dentaries. Unfortunately, with the CMN 2289 predentary missing, it is difficult to ascertain whether this configuration of

the dentaries is reasonable. Future studies will examine the morphology of the predentary region in hadrosaurs in more detail in order to better constrain the positioning of the dentaries.

The predentary, premaxilla, and quadratojugal processes of the jugal were missing and were reconstructed either with computer modelling, or by scanning and modifying other specimens (Figures 6, 7). These reconstructions were for aesthetic purposes only. Importantly, these reconstructions do not influence the functioning of the model. The predentary model was created from a scan of an isolated CMN uncatalogued specimen that was modified to fit the dentaries of the model. The premaxilla was reconstructed in two parts. The anterior part was reconstructed based on a partial left premaxilla from the subadult specimen of *Edmontosaurus annectens*, BHI-6217. The posterior part of the premaxilla was reconstructed using 3-D surfacing tools in 3ds Max with reference to other *Edmontosaurus* (e.g., type specimen, CMN 2288). Despite the missing premaxilla, the maxilla could still be correctly positioned within the skull by considering its articulation with other elements (e.g., jugal). Also, although the back of the jugal is partially missing, part of its articulating surface for the quadratojugal is preserved, so the positional relationship between the quadratojugal and jugal is well understood.

Animation methods. The polymesh maxilla, mandible, and quadrate were attached to a 3-D framework. In animation terminology this framework is referred to as a "rig." Figure 8 shows a rig for the *Corythosaurus* and *Edmontosaurus* models. The *Corythosaurus* rig is derived from the model outlined in Weishampel (1984). The *Edmontosaurus* rig differs from the *Corythosaurus* rig in proportions of the elements, therefore the location of the articulations also differ. Both rigs include six enclosed shapes (i.e., "bones" in animation terminology), representing the paired mandibles, quadrates, and maxillae. Both rigs include a joint located at the mandibular symphysis, as well as at the mandible-quadrate, and the cranium-quadrate joints. In the rig the joints are represented by circles. There is also a hinge-line along the dorsal margin of the maxilla, which represents the maxillary portion of the pleurokinetic hinge.

Inverse kinematics. This is a tool often used in animation to recreate accurate limb movements. It is a method of determining how the linked elements of a system must move in order to produce a desired outcome movement. It is based on a bottom-up hierarchical approach where the child ele-

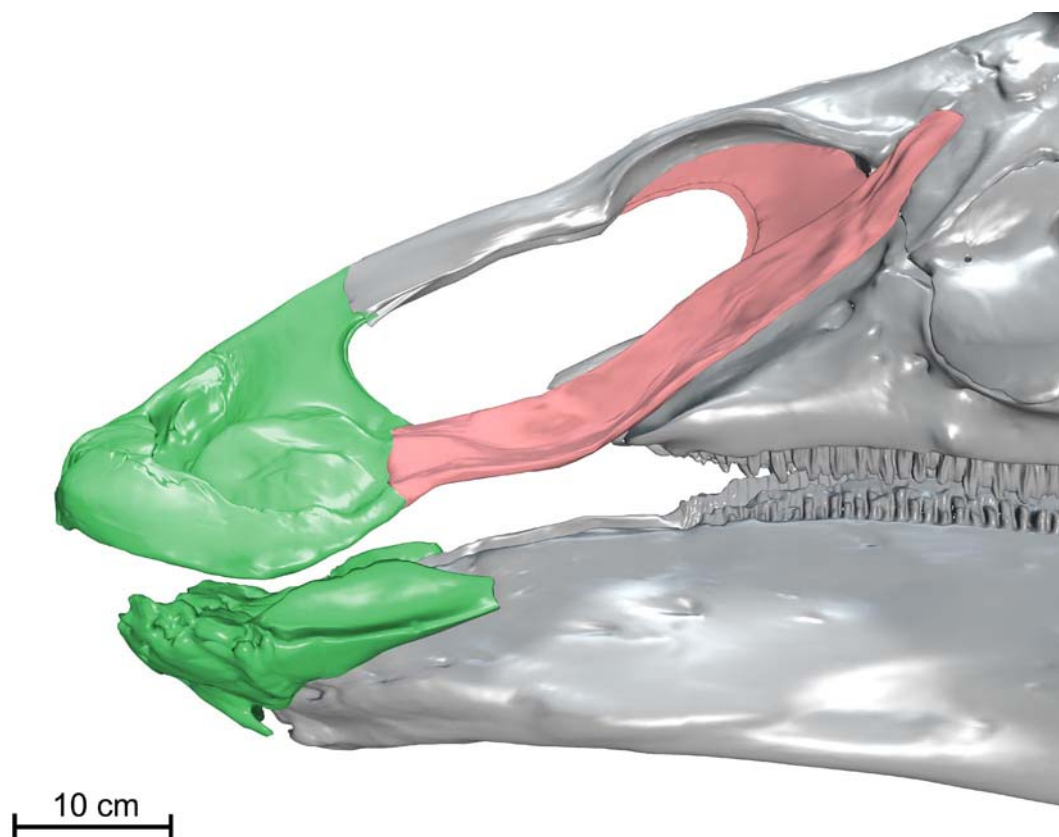


Figure 6. Lateral view of model showing premaxilla and predentary reconstruction. Pink regions indicate reconstruction using 3-D surfacing tools in 3dstudio max v. 8. Green portions are scanning from actual elements. Note that predentary scanning was deformed to fit model. Reconstructions are for aesthetic purposes (i.e., for museum exhibit).

ment controls the movement of the parent in the linked system. For example, the human arm is a hierarchal linked system that can be animated (without IK), by positioning the linked elements individually, starting from the parent of the system (e.g., upper arm) down to the last child of the hierarchal linked system (hand). In IK, the human arm is animated/moved by using the last child of the hierarchal linked system (hand) to determine the position of the upper elements of the arm (Autodesk Canada 2006). Figure 8 shows how the IK approach effectively recreates the adduction of the mandible and retraction of the quadrate observed in the pleurokinetic model presented in Weishampel (1984). In the *Edmontosaurus* 3-D model presented here, the mandible and quadrate were treated as a linked system because they shared a common pivot point (i.e., at the jaw joint). The child of the system is the mandible, and the parent is the quadrate. Given that the mandible and quadrate are linked as a hierarchal system, the quadrate was moved by manipulating the position of the mandible. The 3-D rig with the attached poly-

mesh skull components was mobilized using two types of animation methods: Inverse kinematics (IK) and a wiring system. These two approaches were used to ensure that the primary movements, including their rotational magnitudes presented in the original hypothesis (see *Corythosaurus* animation in Figure 3) were replicated in the *Edmontosaurus* model. The wiring system was used to link the maxilla and quadrate, whereas the mandible and quadrate were linked by inverse kinematics.

In the *Corythosaurus* model, the maxilla and quadrate are shown abducting simultaneously (Weishampel 1984, figure 20a). However, the degree of rotation of the quadrate and maxilla differ: In anterior view the rotation of the maxilla is greater than that of the quadrate (see Table 1). Weishampel (1984, p. 79) suggested that differences in rotation should be possible because the “palatine pterygoid articulation in hadrosaurids modifies the degree to which the quadrates are forced laterally and caudally by lateral rotation of the maxillae.” Yet, the maxilla and quadrate are also attached via the jugal and quadratojugal.

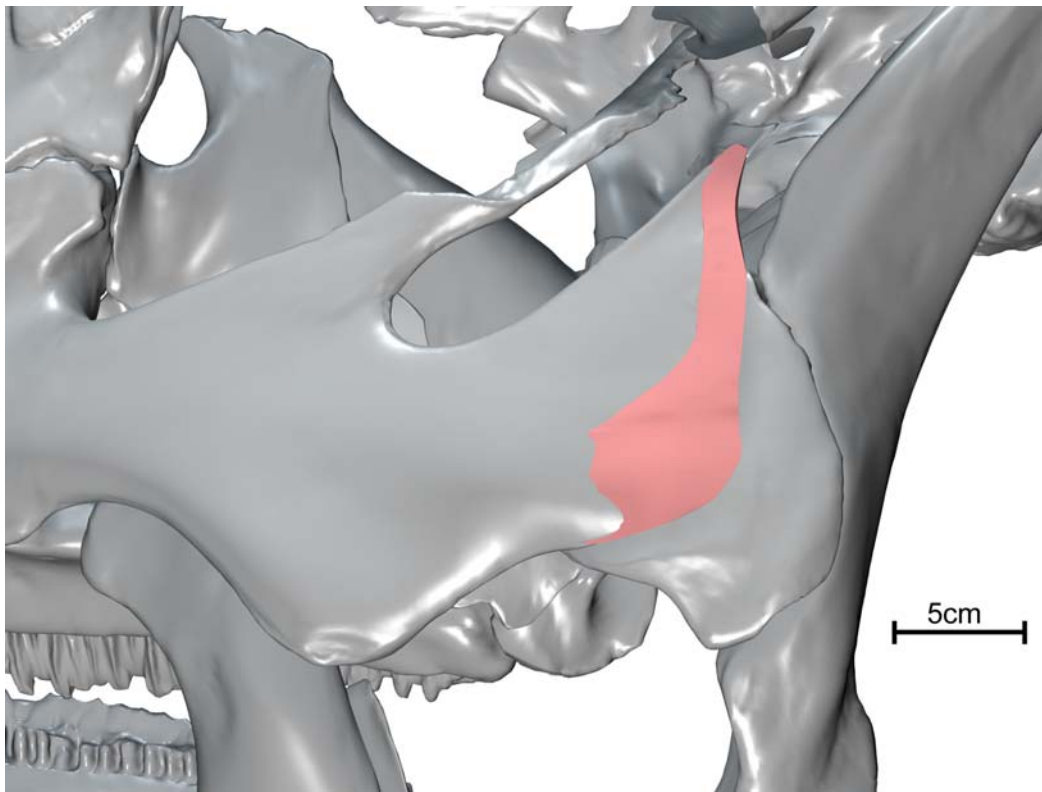


Figure 7. Lateral view of model showing jugal reconstruction. Reconstruction was created using 3-D surfacing tools in 3dstudio max v. 8 and was for aesthetic purposes (i.e., museum exhibit).

Thus, the movements of the maxilla and quadrate are linked medially by intervening palatal elements (i.e., palatine and pterygoid) and laterally by lateral facial elements (i.e., jugal, quadratojugal). For the

maxillary abduction to be greater than the quadrate there has to be movement through both the medial and lateral linkage systems. Lateral facial elements would have to disarticulate. For example the jugal

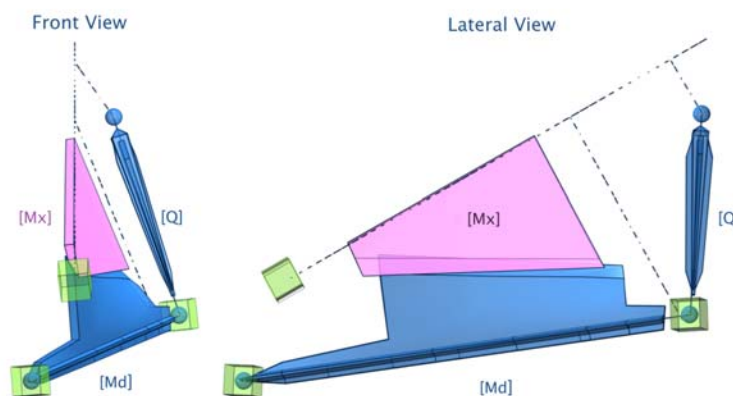


Figure 8. Animation of *Corythosaurus* and *Edmontosaurus* “rigs.” The animation starts by showing the rig, which corresponds to the *Corythosaurus* animation shown in Figure 3. The animation then transform from the *Corythosaurus* rig to the *Edmontosaurus* rig. Both rig animations use the same inverse kinematics and wiring system (see text). The *Edmontosaurus* rig forms the basis of the animation seen in Figure 8 and 9. Reproduced with permission of the Canadian Museum of Nature, Ottawa, Canada.

Table 1. Comparison of quadrate, maxillary, and mandibular rotational movements in *Corythosaurus* model (Weishampel 1984, figure 20) and *Edmontosaurus* model (this study). Rotational movements (in degrees) are described for lateral and anterior views of the skull and occurred at the powerstroke phase of the chewing cycle only. Quadrate movements occur at the squamosal articulation. Maxillary movements occur about the lacrimal joint. Rotational movements in anterior view are abduction.

Element	View			
	Lateral		Anterior	
	<i>Corythosaurus</i> model	<i>Edmontosaurus</i> model	<i>Corythosaurus</i> model	<i>Edmontosaurus</i> model
Quadrate	5	6	7	3
Maxilla	NA	NA	10	3
Mandible *	5	5	NA	NA

* Value presented in this table represents the change in angle between the mandible and quadrate from the beginning and to the end of the powerstroke.

would be pulled rostrally from the quadratojugal. Such a pattern of lateral disarticulation was not described as part of the original model (Weishampel 1984). We, therefore, incorporated the simplifying assumption that the lateral facial skeleton should function to ensure that the rotation of the maxilla and the quadrate would be matched in magnitude.

Wiring system. In the *Edmontosaurus* model, the maxilla and quadrate were linked using an animation technique referred to as a wiring system. A wiring system is an animation technique that creates a relationship between two or more elements so that any change in position or orientation made in the parent element (e.g., the maxilla) is translated to the child element(s), (e.g., the quadrate) (Autodesk Canada 2006). The wiring system linked a point near the posteroventral margin of the maxilla to a posteroventral point on the quadrate, so that when the maxilla was moved manually the quadrate moved in response. It is possible to move both the maxilla and quadrate manually; however the wiring system was used here to automate the model for the testing phase.

As mentioned above, only the mandible, maxilla, and quadrate polymesh components were attached to the rig. The braincase, nasals, and premaxilla were not attached to the rig, but were simply held stationary within the animation world space. The jugal and palatine were attached rigidly to the maxilla, so these three elements functioned as a single, solid object. The assumption that these elements would be a single functional unit is reasonable considering their shared attachment surface is large and complex. The various elements forming the mandible were also treated as a single rigid object.

In order to accommodate the quadrate retraction described in the original hypothesis (Figure 3) it was necessary to allow some mobility in the facial skeleton of the model. In particular, as the quadrate retracts, it should move away from the maxilla so that one or both of the intervening joints (i.e., the jugal-quadratojugal and/or quadratojugal-quadrate contacts) disarticulate. To simplify the model, we arbitrarily chose to fix the quadratojugal to the quadrate. The jugal and quadratojugal were left unconnected so that as the quadrate retracted separation could occur only between the quadratojugal and jugal. It is important to keep in mind that any observed separation between the quadratojugal and jugal should be taken to indicate that there is separation between elements somewhere along the chain of lateral facial elements.

The pterygoid contacts the basiptyergoid process, palatine and quadrate. In this model these attachments were not rigid. Rather, as the palatine and quadrate moved through the powerstroke, the position and orientation of the pterygoid was adjusted “manually” so that, first, connections were maintained between the pterygoid and its contacting elements, and second, there was no interference between the pterygoid and the surrounding elements.

Assumptions of the model. As in any model, animation models are necessarily simpler than their real-world counterparts. For research purposes, the simplifying assumptions used in the model should be matched to the research question. In this study, the model was developed to investigate the intracranial movements that may have occurred during chewing. Thus the focus of this model is on bony interactions among the cranial elements and occlusal surfaces of tooth rows.



Figure 9. Animation showing *Edmontosaurus*-model "chewing" according to Weishampel's (1984) pleurokinetic hypothesis, highlighting primary movements. Reproduced with permission of the Canadian Museum of Nature, Ottawa, Canada.

To investigate intracranial movements, we assumed that the braincase and parts of the facial skeleton were immobile, whereas particular joints in the palate and face were not. Mobile connections along the face were prevented from being displaced mediolaterally relative to one another, while being allowed some rostrocaudal separation. This constraint seems acceptable because most of these joints overlap mediolaterally. The remaining cranial elements were allowed to be mobile, allowing those movements resulting from mandibular adduction and maxillary abduction to occur.

Some of the assumed mobility, such as that seen at the otic and basal joints, is similar to that found in many birds and squamates (Zusi 1993; Herrel et al. 1999; Metzger 2002). The synovial morphology of these joints in hadrosaurs suggests that these may also have been mobile (Weishampel 1984). On the other hand, the model also assumes mobility within the facial and palatal skeleton (e.g., quadrate-quadratojugal, pterygoid-palatine). The occurrence of smooth joint-surfaces in the face of dinosaurs has led many researchers to infer sliding motion between them (e.g., Weishampel 1984; Bakker 1986; Rayfield 2004). Although facial mobility is present in some birds (e.g., some parrots developed synovial jugal-maxillary articulations) and snakes, the presence of mobility in the facial sutures of non-avian dinosaurs and most other diapsids remains uncertain (Holliday 2006), and the functional link between suture morphology and intracranial mobility is largely unexplored. It is beyond the goals of this study to analyze the morphological basis for cranial kinesis, and we allowed the potential for movement to occur at all of these joints during the experiment.

RESULTS

The preliminary model presented here attempted to replicate the primary movements (Figure 9) described in the original pleurokinetic model of chewing in hadrosaurid dinosaurs (Weishampel 1984) (see Figure 3). The original model, based on *Corythosaurus*, described intracranial movements during the powerstroke phase of the chewing cycle. A comparison of the primary movements (i.e. maxillary, quadrate, and mandibular movements) in the two models is shown in Table 1. In the presented animation model (Figure 8), the mandible protracted approximately 4.1 cm. The maxilla abducted 2.1 cm. The jaw joint retracted and abducted approximately 2.1 cm. In lateral view, the degree of rotation of the mandible (with respect to the quadrate) in both models is the same, and the rotation of the quadrate, leading to mandibular retraction, is also similar. The abduction of the quadrate and maxilla are the same in *Edmontosaurus* (3°) because they were linked (see Methods: Animation). The *Edmontosaurus* and *Corythosaurus* models differ dramatically in the degree to which the maxillae abduct. In *Corythosaurus* the maxillary rotation (abduction) is 10° and the quadrate is only 7° . In the *Edmontosaurus* model the maxillary and quadrate movements were linked, and 3° of movement sufficed to allow the upper and lower teeth to complete the powerstroke.

To accommodate the primary movements, secondary movements were required (Figure 10) at the pterygoid-palatine, pterygoid-ectopterygoid-maxilla, pterygoid-quadrate, pterygoid-basisphenoid, and jugal-quadratojugal contacts. In some cases these movements involved marked separation of the elements. For example, during the chewing cycle, the jugal and quadratojugal were separated 1.3 cm, and the separation between the ventral portion of the pterygoid and the quadrate was approximately 1.4 cm.

DISCUSSION AND FUTURE WORK

This model revealed that in order for the primary movements to occur, as described in the original pleurokinetic hypothesis (Weishampel 1984) (Figure 3), extensive secondary movements must also occur. Moreover, some of the secondary movements observed involved large (> 1 cm) separation of the elements, including movements between the jugal and quadratojugal, pterygoid and palatine, and pterygoid and quadrate (Figure 10). Importantly, these movements arose with only small amount of abduction of the maxillae and

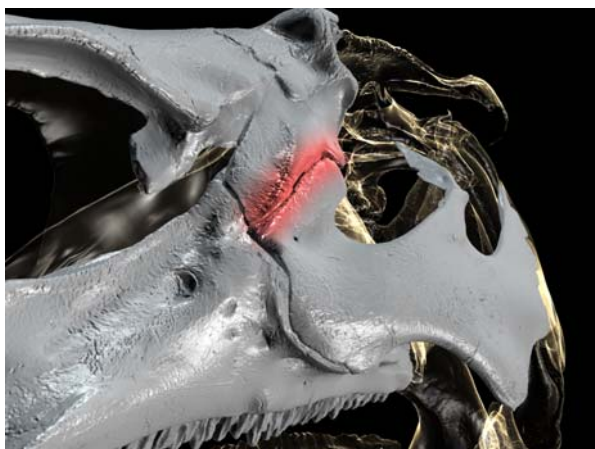


Figure 10. Animation showing *Edmontosaurus*-model "chewing" according to Weishampel's (1984) pleurokinetic hypothesis, highlighting secondary movements. Reproduced with permission of the Canadian Museum of Nature, Ottawa, Canada.

quadrate (e.g., 3°, Table 1), which were much less than those in the original *Corythosaurus* model. Presumably, the pleurokinetic model, as originally proposed by Weishampel (1984) would have yielded secondary movements much greater than those observed in the *Edmontosaurus* model presented here.

Both the original model and this one did not incorporate soft tissues such as ligaments, synovial capsules, and musculature though their inclusion would greatly enhance functional resolution and allow for more rigorous hypothesis testing. Ligaments, including those within sutures and larger ones, such as the quadrate-articular ligament if present, may have constrained some, if not much of the movement in the facial skeleton this model illustrated. In particular, it seems initially doubtful that such separation of cranial elements is likely to have taken place in the living animal considering that sutural ligaments are comprised of collagen, which yields at only 4 to 5% strains (measured in tendon, Wainwright et al. 1976). Additionally there is a significant amount of bony overlap between many of these articulations, suggesting that these contacts promoted stability rather than mobility. Similarly, synovial capsules were likely present, minimally at the otic (quadrate-squamosal), basal (pterygoid-basisphenoid), and jaw joints. These capsules would have potentially constrained movement expressed in the model. The significance of these factors would depend on the functional properties assigned to them at different time stages of the model, requiring multiple assumptions.

Consideration of jaw musculature may offer further insights into mobility and function of cranial elements during feeding. If maxillary and quadrate abduction existed, it would supposedly have been a passive movement because there are no muscles in a position that could implement it. Rather, abduction of the tooth rows would be driven by the adduction of the lower teeth against the upper. Resistance to maxillary abduction would have been provided by pterygoideus musculature. The attachments of *Mm. protractor pterygoideus*, *levator pterygoideus*, *pterygoideus ventralis*, and *pterygoideus dorsalis* suggest that this powerful complex of muscles could have restrained maxillary abduction (Figure 11). If the pleurokinetic hypothesis is viable, these antagonistic muscles would have played an important role modulating the cranial stiffness associated with maxillary abduction. The capacity to modulate stiffness, and therefore, bite force, would be critical for the system to be able to mechanically break down foods of different size and material properties (e.g., hardness, toughness).

In addition, many of the aforementioned jaw muscles attach across a number of the elements and joints that were implicated in secondary movements. The lateral surfaces of the palatine, pterygoid, and quadrate are a likely attachments for *M. pterygoideus dorsalis* and *M. adductor mandibulae posterior*, whereas the medial surfaces of these elements were probably attachment regions for *M. pterygoideus ventralis* and *M. protractor pterygoideus* (Figure 11). This pattern of muscle attachment suggests that the palatine, pterygoid, and quadrate formed a functional unit, providing a supposedly stable, immobile attachment for jaw musculature. Yet the model exhibited extensive sliding between the quadrate and pterygoid during chewing challenging functional hypotheses regarding how this part of the skull may have simultaneously served to produce and resist chewing forces. Therefore, jaw musculature, if modeled, would not only provide the power to the modeled feeding apparatus, enabling analyses of acceleration and bite force moments, but would also induce stresses across sutures and on the bones of attachment themselves, enabling analysis of deformation (e.g., via finite element modeling), and hypotheses of mobility (versus stability) to be tested.

Full consideration of the soft tissue systems may in the end reveal that maxillary abduction is not a viable mechanism for producing transverse chewing movements. With this in mind, additional insight into the potential mobility of the hadrosaurid

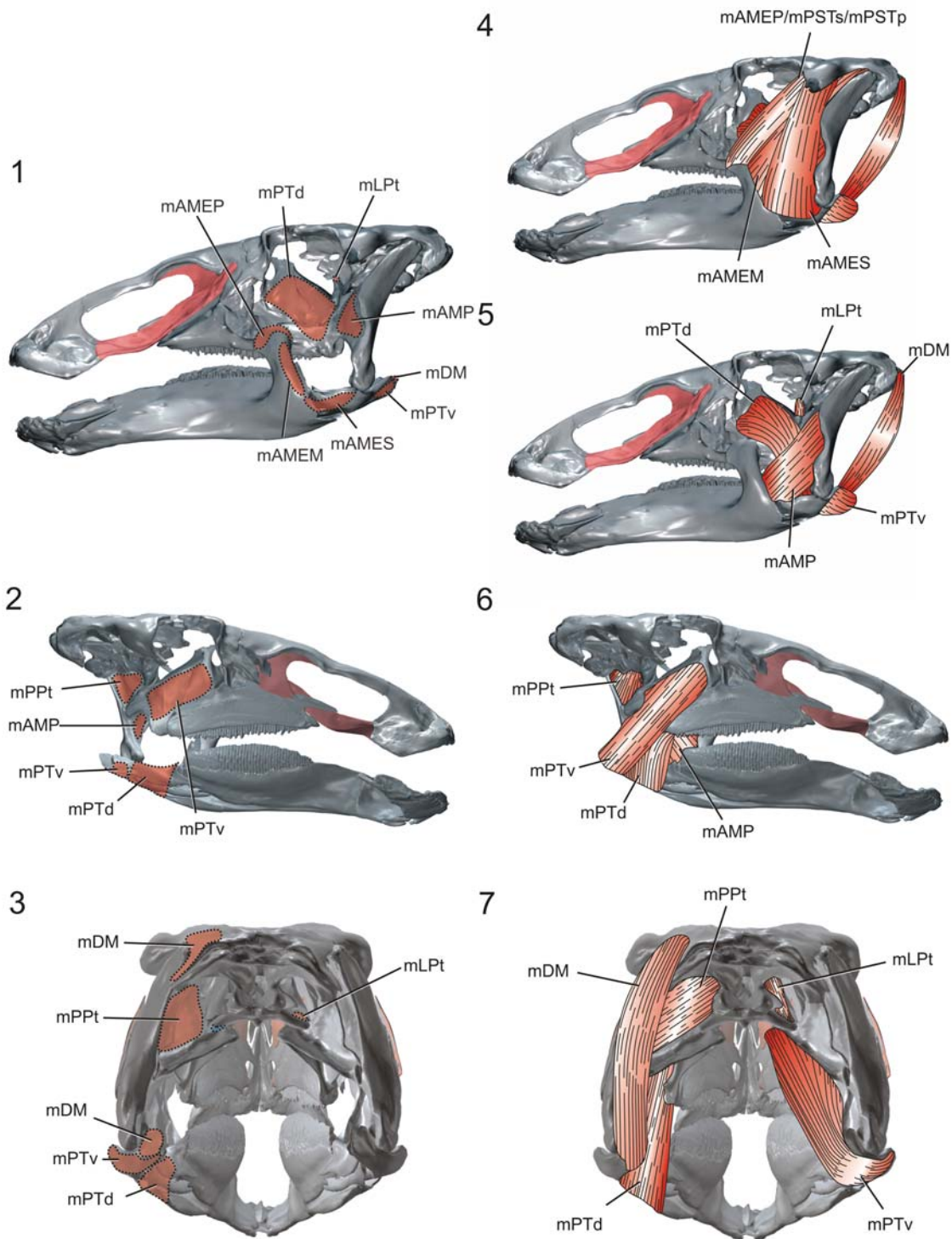


Figure 11. Reconstructed jaw muscle anatomy of *Edmontosaurus*. **1**, Left, lateral view of skull with muscle attachment surfaces; **2**, Medial view of left half of skull with muscle attachment surfaces; **3**, Caudal view of skull with muscle attachment surfaces; **4**, Left, lateral view of skull with reconstructed superficial jaw muscles; **5**, Left, lateral view of skull with reconstructed deep jaw muscles; **6**, Medial view of left half of skull with reconstructed jaw muscles; **7**, Caudal view of skull with reconstructed jaw muscles. Abbreviations: mAMEM, *Adductor mandibulae externus medialis*; mAMEP, *Adductor mandibulae externus profundus*; mAMES, *Adductor mandibulae externus superficialis*; mAMP, *Adductor mandibulae posterior*; mDM, *Depressor mandibulae*; mLpt, *Levator pterygoideus*; mPPt, *Protractor pterygoideus*; mPSTp, *Pseudotemporalis profundus*; mPSTs, *Pseudotemporalis superficialis*; mPTd, *Pterygoideus dorsalis*; mPTv, *Pterygoideus ventralis*.

quadrate may be derived from study of other hadrosaurid taxa. Indeed, a review of the cranial joints of *Brachylophosaurus*, another hadrosaurine dinosaur, found that the morphology of the pleurokinetic hinge regions (e.g., quadrate-squamosal joint) would have prohibited maxillary abduction (Cuthbertson 2006). Therefore cranial kinesis may be variable among hadrosaurs, or perhaps the hadrosaurid skull was less mobile than originally assumed. However, part of the difficulty in analyzing ornithopod chewing is that the proposed transverse abduction of the maxillae is rare, if not unique among amniotes, so identifying appropriate analogs is difficult.

In ongoing work we plan to further correct parts of the skull model, which may be still deformed, as suggested by the fact that during the powerstroke the teeth are not in precise occlusion (Figure 9). We will also investigate the role of soft tissues in constraining the model (Ostrom 1961, Holliday 2006). The system will be further constrained by incorporating dental wear data including the pattern of scratches (i.e., microwear striations) and orientation of the occlusal surface. If these wear features prove to be well-preserved they will provide an accurate map of the relative movements of the upper and lower tooth rows (e.g., Rybczynski and Reisz 2001). The inclusion of the additional functional parameters will allow future analyses to constrain the range of possible chewing movements (e.g., see Hutchinson and Gatesy 2006) to gauge how sensitive the model is to different variables. With these additional constraints in place, alternative hypotheses of feeding behavior can be more fully explored including simple quadrate streptostyly, akinesis, and mandibular propaliny or rotation.

In conclusion, preliminary results suggest that the integration of three-dimensional scanning technology with animation offers enormous promise for investigating the functional morphology of feeding behavior in *Edmontosaurus*. Although the goal of the methods described here is to resolve the feeding kinematics, the approach lays the groundwork for investigating questions related to biomaterials and chewing forces across all vertebrates. Ultimately, animation and biomechanical methods could be applied comparatively to yield insight into the evolution of feeding systems within lineages and ecosystems.

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