

A model for the bite mechanics in the herbivorous dinosaur *Stegosaurus* (Ornithischia, Stegosauridae)

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Abstract Although the herbivorous dinosaur *Stegosaurus* (Ornithischia, Stegosauridae) is a well-described Late Jurassic taxon, little is known about the feeding habits and biomechanics of its homodont dentition. The presence of a rhamphotheca has been suggested, but it is still unknown how much such structure would have participated in the foraging behaviour of *Stegosaurus*. To better understand the feeding mechanism of this taxon, three-dimensional models of a *Stegosaurus* tooth were created, using the software ZBrush[®]. One model was simple and lacked serrations, whereas the other model included serrations. Those models were then transferred to the software Strand7[®], where finite element analyses took place. The models were given material properties of enamel, based on studies done with crocodylian and mammalian teeth. In addition to that, bite forces were calculated for *Stegosaurus*, based on skull proportions. The results show little difference between the force distributions on the serrated and non-serrated models, indicating an efficient mechanism of stress dissipation that avoids high stresses being transferred to the jaw bones during biting. Digital plant models were also created to test the calculated bite forces in *Stegosaurus*, which suggests this animal was capable of biting through smaller branches. Computer modelling and analyses provide additional information about feeding habits and plant preferences for *Stegosaurus*, and can be adapted for studying other comparable herbivorous taxa.

Keywords *Stegosaurus* · Tooth · Biomechanics · Morrison Formation · Finite element (FE) · Digital plant model

Institutional abbreviations

SMA Sauriermuseum Aathal, Switzerland
USNM National Museum of Natural History, Smithsonian Institution (formerly United States National Museum), Washington DC, USA

Introduction

The clade Stegosauria was erected by Marsh in 1877 and in the same year he described the genus *Stegosaurus*. In spite of over 130 years of studies, little has been described about the detailed tooth morphology for this taxon. Generally, each *Stegosaurus* tooth is subtriangular in mesiodistal view, has a prominent cingulum, and has a variable number of rounded denticles, ranging from seven to fifteen (Barrett 2001; Galton and Upchurch 2004). A *Stegosaurus* tooth also has a complex network of secondary longitudinal ridges (Galton and Upchurch 2004). The descriptions of *Stegosaurus* teeth are not detailed enough to group them into separate species, nor do they include interpretations about the functions of the structures observed.

Aspects of feeding in stegosaurs have been addressed, however. It has been suggested that this taxon may have had cheeks, supported by a pronounced dorsolateral ridge on the maxilla (Galton and Upchurch 2004), and may have had a horny beak or rhamphotheca (Czerkas 1998, 1999; Papp and Witmer 1998). Tooth wear has been described as being the result of tooth-food contact (Galton and Upchurch 2004). The wear facets occur on the occlusal

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surface of the crown, are generally horizontal, and are sometimes angled slightly posteriorly. The jaw action is described as strictly orthal (Barrett 2001).

These inferences about the bite and chewing behaviour in *Stegosaurus* have yet to be tested biomechanically. In this paper, the bite force of *Stegosaurus* is estimated based on cranial proportions, and its ability to bite through plant materials of different thicknesses is tested. Additionally, complex enamel structures, such as denticles and longitudinal ridges, are tested for their influence on overall tooth performance under normal stresses related to bite forces. The main method used in this study is finite element (FE) analysis, which reveals the structural performance of a realistically modelled object subdivided into a mesh of small elements.

Materials and methods

The FE analyses are based on three-dimensional (3D) models made with the software ZBrush[®]. The 3D models are based on measurements and the general morphology of tooth crowns from cf. *Stegosaurus armatus* (SMA 0173-DS-RCR2003-02, 'Sarah'), (Fig. 1), and *Stegosaurus stenops* (USNM 4934), both from the Late Jurassic (Kimmeridgian–Tithonian) Morrison Formation of Wyoming, USA. CT scans were not used in this analysis. Even though CT scans provide finer details, the emphasis of this study is in the proportions observed in the specimens, which are reflected in the simplified 3D models, and how objects with such proportions respond to stresses similar to those in stegosaur jaws. CT scans will be a good tool for



Fig. 1 Photograph of the cf. *Stegosaurus armatus* specimen SMA 0173-DS-RCR2003-02 ['Sarah'; from the Late Jurassic (Kimmeridgian–Tithonian) Morrison Formation, Wyoming, USA], isolated tooth (number 269) in lingual or labial view. Photograph is a courtesy of Jean-Paul Billon-Bruyat. Scale bar 2 mm

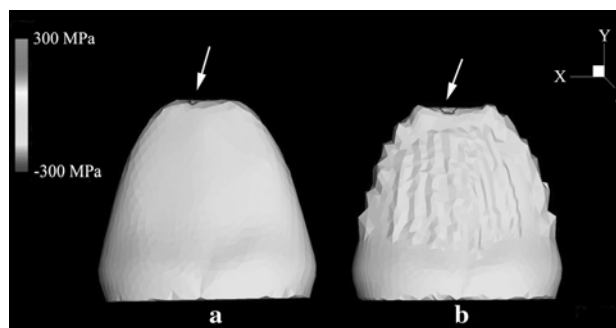


Fig. 2 Three-dimensional models of a *Stegosaurus* tooth. **a** without the external features. **b** with some external features: denticles and ridges. White arrows indicate the direction and area where loads were applied. Note the dark area of higher compression surrounding a small white area (indicating enamel failure) where the load was applied. Scale in Megapascals (MPa)

comparisons in the future, especially for studies focusing on morphological differences within or between stegosaur species.

Two digital models were made for a generalized *Stegosaurus* tooth. Because the dentition of *Stegosaurus* is essentially homodont, it is irrelevant to make different models for different tooth positions. One model is plain (Fig. 2a), without the denticles or vertical ridges, and the other model (Fig. 2b) has the external features that are observed in the original specimens, such as vertical ridges and denticles. The models were not given a cingulum at this stage, and the significance of this structure is not addressed in this paper. The models are 5.0 mm tall (from the base to the tip of the crown), 3.2 mm labiolingually wide (at the base of the crown), and 5.0 mm anteroposteriorly wide (at the base of the crown).

After building the 3D models, they were converted to NASTRAN format through the software Mimics[®], and imported into Strand7[®] for FE meshing and analysis. The models were given material properties of enamel, because the thickness of the enamel layer in ornithischian dinosaurs is significantly high, reaching about 50 μm in Ankylosauria (Hwang 2005), although the thickness of enamel in Stegosauria is not currently known. The forces were applied to the occlusal surfaces of the crowns and the models were constrained along the X, Y, and Z axes at their bases. The constraint was both translational and rotational, so that the condition observed in the jaws (in which teeth have virtually no movement) was simulated.

Four material and structural performance properties dictate how a 3D object will react to the forces applied to it. There are not many studies on comparative values for those enamel properties among vertebrates, but reptiles and mammals share some developmental characteristics for the enamel, such as its ectodermal origin (Edmund 1969). The values used in this analysis were based on reptile studies

whenever possible, but the rarity of such studies on reptile enamel forced some of the data to be based on mammalian research. The elastic or Young's Modulus is a ratio of stress to strain and is thus a measure of stiffness (Boresi and Schmidt 2003). The Young's Modulus value used in the analyses is 6.04×10^{10} Pascals (Pa), and is based on the value measured in fresh crocodilian teeth (Creech 2004). Poisson's ratio (transverse versus axial strain) describes how a structure deforms perpendicularly to the direction of force, by bulging transversely under compression and thinning under tension (Boresi and Schmidt 2003). The Poisson's ratio used in the analyses was 0.30, which is the same as in human teeth (Rees and Hammadeh 2004). The density—2800 kilograms per cubic meter (kg/m^3)—assigned to the models is that of human enamel (Manly et al. 1939). Finally, the model's yielding point (or failure stress) indicates the breaking point of the material, and sets an upper level for the structure's performance. The failure stress of enamel (for compressive stress) was estimated at values that average 300 megapascals (MPa) by Currey (2002) and Waters (1980). Waters (1980) also estimated the yielding point for enamel as an average of 35 MPa (for tensile stress), and 80 MPa (for shear stress). The scale on the models was therefore set as a maximum of 300 MPa to reflect the maximum compressive stress that can be yielded by tooth enamel.

An additional 3D model was made to simulate a tree branch (Fig. 3), in order to test how efficient the estimated *Stegosaurus* bite forces were at breaking plant materials. This model consists of a hollow cylinder (the hollow core represents the air and water content in the branch). The material properties given to that model were those of green timber (default settings by Strand7[®] for white cypress). The Young's Modulus for the model is 9.1×10^9 Pa, and the density is 8.5×10^{-7} kg/mm^3 . The failure stress (compressive strength) has been measured in juvenile wood of *Taiwania cryptomerioides* (a species of modern timber) by Lin et al. (2006), and is 25.3 MPa, parallel to grain. This value was used to set the upper limit for the material failure stress in all models. The same model geometry was tested in four different diameters of 4, 8, 12, and 24 mm. The length of the cylinders increased proportionately to the increase in diameter, starting with 20 mm for the smallest model.

The forces were applied transversely to the cylinder on the midsection of the model. All models were restrained along the X, Y and Z axes (translational and rotational constraint) on one end of the cylinder to simulate the site of attachment of the branch to the plant. The results were viewed with the von Mises yield criterion, which is appropriate for wood because it is ductile under moderate, gradually applied loads. The von Mises criterion evaluates relative proximity to yield within the structure, as a

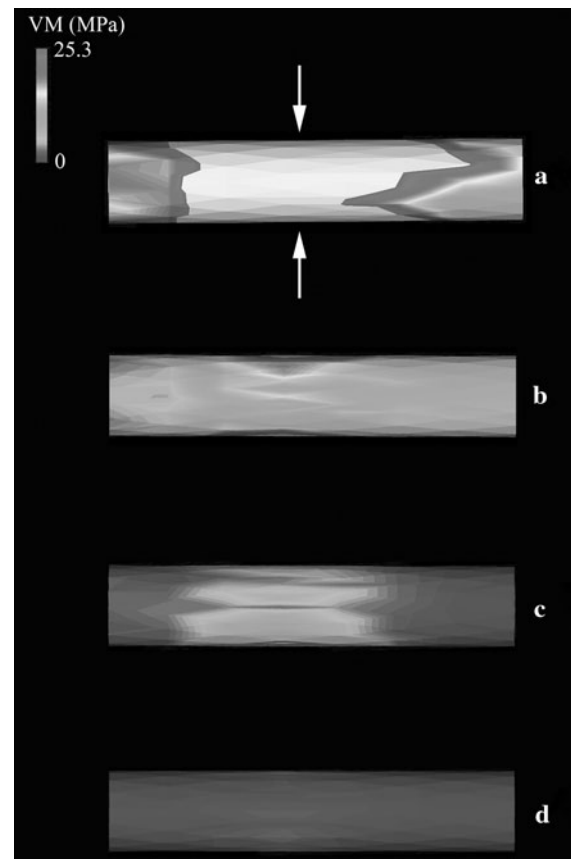


Fig. 3 Three-dimensional models of cylinders with plant material properties. The forces applied in all models are as represented by the white arrows in (a). Constraint in all models was applied to the right end. Models have diameters of (a) 4 mm; (b) 8 mm; (c) 12 mm; (d) 24 mm. Models are not to scale. The white area in (a) indicates failure of the material. Dark areas in (c) and (d) indicate low von Mises (VM) stresses. Scale in Megapascals (MPa)

reflection of strain energy density (Farke 2008). The results are shown as a summation of principal components of stress, and not a characterizable force/area, and they are therefore not informative for determining types of stress (Bell et al. 2009).

The bite forces for *Stegosaurus* imposed on its teeth and food were estimated following the method used by McHenry (2009) for the pliosaur *Kronosaurus queenslandicus*. The cross-sectional area of bite muscles through the subtemporal fenestra was calculated as 19.7 cm^2 , based on ventral images of USNM 4934 (*Stegosaurus stenops*) from Ostrom and McIntosh (1966). The skull of the specimen 'Sarah' (SMA 0173-DS-RCR2003-02) is disarticulated and therefore not appropriate for the measurements needed in this analysis. The jaw proportions necessary for calculating forces at the teeth were also measured from *Stegosaurus stenops* (USNM 4934). The "in lever" (from the jaw articulation to the centre of the jaw muscle insertions) measures 7.42 cm. The "out lever" is the distance

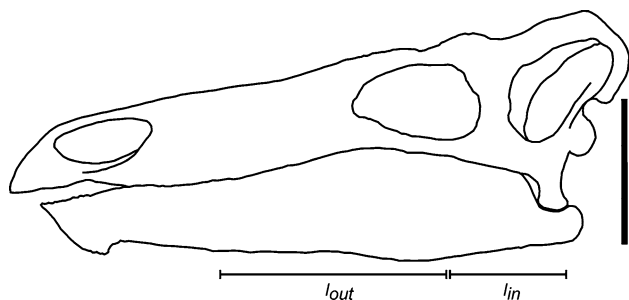


Fig. 4 Schematic of the skull of *Stegosaurus stenops* (USNM 4934) with lines indicating the measurements for the “in lever” (l_{in}) and “out lever” (l_{out}). Scale bar 100 mm

from the centre of the jaw muscle insertions to specific positions along the tooth row (Fig. 4). In *Stegosaurus stenops*, respective out levers for the anterior, middle, and posterior teeth are 29.5, 22.5, and 15.0 cm. The angle between the muscle insertion and the dentary bone was estimated to be approximately 45° . Based on these measurements, the bite force calculations were done as follows. The concentric specific tension (as a muscle shortens) is generally equivalent to 20 N per square centimetre (Bamman et al. 2000; Snively and Russell 2007). This multiplied by the cross sectional area gives the muscle force (F_y). The total vertical force (F_{in}) applied by the temporal muscles to its point of attachment (in this case, to the jaw) is given by the following formula:

$$F_{in} = \sin \alpha \times F_y \text{ (in which } \alpha = 45^\circ, \text{ the muscle's angle of pull relative to the vertical).}$$

The overall line of pull for each the temporal muscles is in the same sagittal plane as its insertion on the mandible, so medial or lateral components of the force were judged to be insignificant for calculating the F_{in} .

After F_{in} is known, it is possible to calculate the bite forces for each part of the jaw using the following formula:

$l_{in} \times F_{in} = l_{out} \times F_{out}$ [in which l_{in} and l_{out} are, respectively, the “in lever” and the “out lever” (measured previously in centimetres), and F_{in} and F_{out} are, respectively, the concentric force applied by the muscle to its point of attachment and the bite force at the measured point of the jaw].

There were three sets of FE analyses. In the first set, the calculated bite forces for anterior, middle and posterior teeth were applied directly to the tooth model. In the second set, smaller forces were applied to the model, taking into consideration the number of teeth in each of the anterior-, mid- and posterior-sections, and dividing the calculated bite force for each area by the number of teeth in the same area. In the third set of analyses, the bite force (the highest one) calculated for the posterior portion of the

jaw was applied to plant 3D models with varying diameters.

Results

The calculated bite force for *Stegosaurus stenops* is 140.1 N on the anterior teeth, 183.7 N on the middle teeth, and 275 N on the posterior teeth. Any of these forces, when applied straight to both 3D models of the tooth, caused failure of the enamel around the area where the force was applied (considering the 300 MPa yielding point for compressive stress in enamel). The load was applied to a small area of the model and therefore this localized enamel failure may be an artefact. The highest stress levels are found around the tip, and significantly lower stress levels are found near the base. The main stresses are compressive. In all models, values lower than 1% of the stress observed at the tip were found at the base, indicating an efficient dissipation of compressive stresses associated with the load on the tooth. The presence of denticles and ridges did not seem to offer an advantage or disadvantage to the overall stress handling of the models.

The maximum bite force (275 N) was applied to the plant models. The force was applied transversely to the cylinder. In the model with a 4 mm diameter, the stresses caused by the bite force were high enough to cause the plant material to fail throughout the diameter of the cylinder. In the 8 mm diameter model, the force was enough to cause the plant model to fail near the nodes where the load was applied, but the stresses were significantly lower and the failure did not follow throughout the whole diameter, as in the first case. In the 12 mm diameter model, there was a significantly smaller area in which the plant model failed, immediately around the nodes where the load was applied. In the 24 mm diameter model, the plant model did not fail.

Discussion

The bite forces calculated for *Stegosaurus* (140.1 N, 183.7 N, and 275 N for anterior, middle and posterior teeth, respectively) are relatively low when compared to those estimated by Erickson et al. (1996) for the posterior portion of the jaws of Labrador dogs (550 N), humans (749 N), or wolves (1,412 N). However, the calculated bite forces of *Stegosaurus* suggest that this taxon had the ability to bite through smaller branches and leaves. The plant models show that *Stegosaurus* had the potential to break smaller branches, but did not have enough force in its jaws to crush a thick (more than 12 mm in diameter) object with the material properties of green timber, even when using its

highest biting forces, measured at the position of the last tooth in the maxilla. Any larger plant parts could be incorporated into the diet only if *Stegosaurus* was capable of biting more efficiently than predicted in this analysis. Parrish et al. (2004) describe the Morrison Formation flora as dominated by herbaceous, short-lived plants, characteristic of a seasonal environment. *Stegosaurus* probably took advantage of the abundance of smaller, fast growing plants. More tests with different material properties from other plants, such as modern ferns, would further inform about dietary preferences in *Stegosaurus*.

The tooth wear observed by Galton and Upchurch (2004) is mainly attributed to tooth-food contact, and indicates some ability to chew. But it is also true that the wear facets are neither common nor extensive, which suggests that this may have been an occasional, rather than a repetitive behaviour in *Stegosaurus*. The models did not show potential for enamel failure near the denticles at any of the forces applied. It seems therefore that the overall morphology of the tooth is structurally sound enough to carry denticulate edges, which increase the efficiency of teeth in cutting food materials (Abler 1992).

The fact that small failure areas appeared in all tooth models around the area where the force was applied suggests a few points:

1. *Stegosaurus* was not using its full potential bite force most of the time.
2. *Stegosaurus* had a high tooth replacement rate, and therefore the teeth could be subjected to high stresses, because each tooth would not have stayed in use for long.
3. The tooth models with material properties of enamel are more brittle than what is observed in reality.

The second option seems unlikely due to the rarity of isolated shed crowns in the fossil record, but that could be due to preservational bias. Also, some *Stegosaurus* teeth have a significant amount of wear (J.-P. Billon-Bruyat, personal communication 2010), suggesting that they could have stayed in use for an extended amount of time. Additional studies in stegosaur tooth replacement rates would reinforce this conclusion. The first possibility is more likely, and can be combined with the fact that *Stegosaurus* could be using a beak (Galton and Upchurch 2004) during most of its foraging behaviour. In that case, the teeth would receive less stress attributed to bite. However, the anterior part of the jaws is capable of inflicting the least amount of force. If *Stegosaurus* was indeed making use of its beak most of the time, the plants it fed on would have even thinner branches than predicted in this analysis, or different material properties.

The third point is also to be taken into consideration. Future analyses should test the same tooth models with layers of dentine and enamel in order to verify if the failure areas are due to the brittle nature of enamel.

Another point not addressed in this paper is the presence of a cingulum in stegosaur teeth. This structure has been reported as an important feature for reducing strains near the base of mammalian teeth (Anderson et al. 2009). However, even without the addition of a cingulum to the stegosaur tooth models, only small stresses are concentrated at the base. It would still be interesting to study the function or systematic distribution of this structure within Stegosauria in the future.

Conclusions

In conclusion, this analysis shows that *Stegosaurus* had bite forces lower than those (550 N) measured on posterior tooth positions of Labrador dogs (Erickson et al. 1996) and that the tooth morphology is efficient in dissipating the compressive stresses generated during bite, so that a minimal amount of stress is transferred to the jaw bones.

This study also shows that the morphology and biomechanics of *Stegosaurus* teeth can give clues about the feeding habits of this taxon and some indication about plant preferences. More data on stegosaur tooth morphology and variations along the tooth row are needed, as well as more data on tooth wear and jaw and tooth replacement rates. Microwear studies, which have a great potential for plant preference studies, also would improve this analysis. Additionally, using those methods on models with material properties equivalent to the plants described for the Morrison Formation would help to pin down the taxa that could likely be part of the diet of *Stegosaurus*.

This paper's methods have potential for studies with other herbivorous taxa and could provide tools to quantify morphological differences between closely related taxa. This particular study demonstrated that the relatively small teeth of *Stegosaurus* could participate in the food processing of plants, but the small amount of wear observed in most specimens suggests that a significant percentage of the bite stresses could have been concentrated on the beak.

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References

- Abler, W. L. (1992). The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. *Paleobiology*, 18, 161–183.
- Anderson, P., Gill, P., & Rayfield, E. (2009). How the cingula of basal mammal teeth may alleviate strain in the enamel caused by a soft food diet. *Journal of Vertebrate Paleontology*, 29(Suppl. 3), 54A.
- Bamman, M. W., Newcomer, B. R., Larson-Meyer, D., Weisner, R. L., & Hunter, G. R. (2000). Evaluation of the strength-size relation in vivo using various muscle size indices. *Medicine and Science in Sports and Exercise*, 32, 1307–1313.
- Barrett, P. M. (2001). Tooth wear and possible jaw action of *Scelidosaurus harrisonii* Owen and a review of feeding mechanisms in other thyreophoran dinosaurs. In K. Carpenter (Ed.), *The armored dinosaurs* (pp. 25–52). Bloomington, IN: Indiana University Press.
- Bell, P. B., Snively, E., & Shychoosky, L. A. (2009). Comparison of the jaw mechanics in hadrosaurid and ceratopsid dinosaurs using finite element analysis. *The Anatomical Record*, 292, 1338–1351.
- Boresi, A. P., & Schmidt, R. J. (2003). *Advanced mechanics of materials*. New York: Wiley, 681 pp.
- Creech, J. E. (2004). *Phylogenetic character analysis of crocodylian enamel microstructure and its relevance to biomechanical performance*. Unpublished Masters thesis, Florida State University, Tallahassee, 59 pp.
- Currey, J. D. (2002). *Bones: structure and mechanics* (436 pp). New Jersey: Princeton University Press.
- Czerkas, S. (1998). The lips, beaks, and cheeks of ornithischians. *Journal of Vertebrate Paleontology*, 18(Suppl. 3), 37A.
- Czerkas, S. (1999). The beaked jaw of stegosaurs and their implications for other ornithischians. In D. D. Gillette (Ed.), *Vertebrate paleontology in Utah* (Vol. 99, pp. 143–150). Miscellaneous Publications of Utah Geological Survey.
- Edmund, A. G. (1969). Dentition. In C. Gans, et al.: *Biology of the reptilia—morphology A* (Vol. 1, pp. 117–200). London, UK: Academic Press.
- Erickson, G. M., Van Kirk, S. D., Su, J., Levenston, M. E., Caler, W. E., & Carter, D. R. (1996). Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature*, 382, 706–707.
- Farke, A. A. (2008). Frontal sinuses and head-butting in goats: a finite element analysis. *Journal of Experimental Biology*, 211, 3085–3094.
- Galton, P. M., & Upchurch, P. (2004). Stegosauria. In D. B. Weishampel et al. (Eds.), *The Dinosauria* (2nd ed., pp. 343–362). Berkeley: University of California Press.
- Hwang, S. H. (2005). Phylogenetic patterns of enamel microstructure in dinosaur teeth. *Journal of Morphology*, 266, 208–240.
- Lin, C.-J., Wang, S.-Y., Yang, T.-H., & Tsai, M.-J. (2006). Compressive strength of young Taiwan (*Taiwania cryptomerioides*) trees grown with different thinning and pruning treatments. *Journal of Wood Sciences*, 52, 337–341.
- Manly, R. S., Hodge, H. C., & Ange, L. E. (1939). Density and refractive index studies of dental hard tissues: II. Density distribution curves 1, 2. *Journal of Dental Research*, 18, 203–211.
- Marsh, O. C. (1877). New order of extinct Reptilia (Stegosauria) from the Jurassic of the Rocky Mountains. *American Journal of Science*, 14, 513–514.
- McHenry, C. R. (2009). *Devourer of gods: the paleoecology of the Cretaceous pliosaur Kronosaurus queenslandicus*. Unpublished Ph.D. dissertation, University of Newcastle, 635 pp.
- Ostrom, J. H., & McIntosh, J. S. (1966). *Marsh's dinosaurs—the Collections from Como Bluff* (2nd ed., 388 pp). New Haven: Yale University Press.
- Papp, M. J., & Witmer, L. (1998). Cheeks, beaks or freaks: A critical appraisal of buccal soft-tissue anatomy in ornithischian dinosaurs. *Journal of Vertebrate Paleontology*, 18(Suppl. 3), 69A.
- Parrish, J. T., Peterson, F., & Turner, C. E. (2004). Jurassic “savannah”—plant taphonomy and climate of the Morrison Formation (Jurassic western USA). *Sedimentary Geology*, 167, 139–164.
- Rees, J. S., & Hammadeh, M. (2004). Undermining of enamel as a mechanism of abfraction lesion formation: a finite element study. *European Journal of Oral Sciences*, 112, 347–352.
- Snively, E., & Russell, A. P. (2007). Cranio-cervical feeding dynamics of *Tyrannosaurus rex*. *Paleobiology*, 33, 610–638.
- Waters, N. E. (1980). Some mechanical and physical properties of teeth. In J. F. V. Vincent & J. D. Currey (Eds.), *The mechanical properties of biological materials. Society of Experimental Biology, 34th Symposium. The mechanical properties of biological materials* (pp. 99–135). Cambridge: Cambridge University Press.