Biomechanics of juvenile tyrannosaurid mandibles and their implications for bite force: Evolutionary biology

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Abstract
The tyrannosaurs are among the most well-studied dinosaurs described by science, and analysis of their feeding biomechanics allows for comparison between established tyrannosaurid genera and across ontogeny. 3D finite element analysis (FEA) was used to model and quantify the mechanical properties of the mandibles (lower jaws) of three tyrannosauroid tyrannosaurids of different sizes. To increase evolutionary scope and context for 3D tyrannosaurine results, a broader sample of validated 2D mandible FEA enabled comparisons between ontogenetic stages of *Tyrannosaurus rex* and other large theropods. It was found that mandibles of small juvenile and large subadult tyrannosaurs experienced lower stress overall because muscle forces were relatively lower, but experienced greater simulated stresses at decreasing sizes when specimen muscle force is normalized. The strain on post-dentary ligaments decreases stress and strain in the posterior region of the dentary and where teeth impacted food. Tension from the lateral insertion of the looping m. ventral pterygoid muscle increases compressive stress on the angular but may decrease anterior bending stress on the mandible. Low mid-mandible bending stresses are congruent with ultra-robust teeth and high anterior bite force in adult *T. rex*. Mandible strength increases with size through ontogeny in *T. rex* and phylogenetically among other tyrannosaurs, in addition to that tyrannosaurid mandibles exceed the mandible strength of other theropods at equivalent ramus length. These results may indicate separate predatory strategies used by juvenile and mature tyrannosaurs; juvenile tyrannosaurs lacked the bone-crunching bite of adult specimens and hunted smaller prey, while adult tyrannosaurs fed on larger prey.

KEYWORDS
biomechanics, evolution, functional morphology, ontogeny, paleontology
1 | INTRODUCTION

Predatory theropod dinosaurs of the clade Tyrannosauridae comprise some of the largest terrestrial animals to have ever lived, including the famous North American predator *Tyrannosaurus rex* (Osborn, 1905), its Mongolian counterpart *Tarbosaurus bataar* (Maleev, 1955), and the Chinese *Zhuchengtyrannus magnus* (Hone et al., 2011). They are characterized by their large heads, fused nasal bones (Snively, Henderson, & Phillips, 2006), spring-loaded feet (Coombs Jr., 1978; Holtz Jr., 1994; Holtz Jr., 1995; Snively & Russell, 2002, 2003; Snively, Russell, & Powell, 2004), and robust teeth (Farlow, Brinkman, Abler, & Currie, 1991; Molnar, 1991; Osborn, 1906). Tyrannosaurs are nested within the Tyrannosauroidea, a relatively derived group of theropods being more closely related to birds than to other large carnivores such as allosauroids and spinosaurids (Brusatte et al., 2010; Rauhut and Pol, 2019). Tyrannosaurid specimens and infer how bite capabilities changed with ontogenetic and phyletic scaling. Biomechanics is the study of the structure and function of the mechanical aspects of biological systems, including locomotion and feeding. In extinct animals, active phenomena such as bite force or body movements can be inferred, starting with fossilized bones. Finite element analysis (FEA) is a nondestructive modeling technique that allows for calculations of stresses exerted and experienced by living and extinct animals. FEA is commonly used in engineering to test for weaknesses in the design of bridges, buildings, and machines, as it can analyze any solid structures. In recent decades, FEA has been used in zoology and paleontology mostly to study the crania (upper part of the skull of both living and extinct animals).

Rayfield (2005a), Mazzetta, Cisilino, and Blanco (2005), Lautenschlager et al. (2016a), and Cost et al. (2019) used FEA to study sutures and bite performance in theropod dinosaurs. FEA has concentrated on mandibles (lower jaws) of other animals, such as in analyses of mammal chewing biomechanics (Zhou, Winkler, Fortuny, Kaiser, & Marcé-Nogué, 2019) and crocodilian strain response to biting and twisting loads (Porro et al., 2011; Walmsley et al., 2013). Mandibles of horned and duckbilled dinosaurs analyzed in FEA revealed their chewing mechanics (Bell, Snively, & Shychocki, 2009), and Lautenschlager et al. (2016b) examined diversity of mandible stresses in therizinosaurid specimens. Besides these examples, there have not been many 3D analyses for dinosaur mandibles, especially in blade-toothed theropods. This study is among the first to analyze 3D carnivorous dinosaur mandibles with FEA and to test for changes in biting capability as dinosaurs mature. Discoveries of several nearly complete tyrannosaurid skeletons in recent decades make the group of macropredators ideal candidates for 3D computerized reconstruction and finite element analysis, as tyrannosaur ontogeny is relatively well-understood and skull material is readily available for analysis.

Three tyrannosaur specimens across different ontogenetic stages were tested: a small juvenile tyrannosaurine originally named *Raptorex kriegsteini*, a larger subadult *T. rex*, and a large adult *T. rex* (Figure 1; Carr, 2020 for ontogenetic assessment of *Tyrannosaurus* specimens). *Raptorex* served as a proxy for a small juvenile *T. rex* given its young age (based on limb histology: Fowler, Woodward, Freedman, Larson, & Horner, 2011), juvenile character states (Carr, 2020), and completeness. Differences in age allow us to better understand changes in stresses the animals experienced as they matured and how they were able to cope with higher bite forces at maturity. Stress is a physical quantity that expresses the internal forces that neighboring particles of a material exert on each other, while a strain is the measure of the deformation of the material.

The primary purpose of this study was to compare the mandibular biomechanical capabilities of several tyrannosaurid specimens and infer how bite capabilities changed with ontogenetic and phyletic scaling. Biomechanics is the study of the structure and function of the mechanical aspects of biological systems, including locomotion and feeding. In extinct animals, active phenomena such as bite force or body movements can be inferred, starting with fossilized bones. Finite element analysis (FEA) is a nondestructive modeling technique that allows for calculations of stresses exerted and experienced by living and extinct animals. FEA is commonly used in engineering to test for weaknesses in the design of bridges, buildings, and machines, as it can analyze any solid structures. In recent decades, FEA has been used in zoology and paleontology mostly to study the crania (upper part of the skull of both living and extinct animals).

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The scope of this investigation of mandible stress was increased by producing 2D, sagittal view profile models, similar to those of Rayfield (2005b) for theropods, Fletcher, Janis, and Rayfield (2010) for ungulates, Snively, Anderson, and Ryan (2010) for arthrodires, and Morales-García, Burgess, Hill, Gill, and Rayfield (2019) for early mammals (the latter two explicitly testing extruded 2D sections). 3D FEA results are emphasized because they are more realistic. However, 2D models increase the size of the comparative sample, and 2D and 3D models for two taxa were compared to test how closely 2D results approximate 3D stresses.

1.1 | Primary hypotheses and rationale

Two main hypotheses were tested with results from simulated stress and strain in the 3D mandibles.

Hypothesis (1). Larger tyrannosaurid mandibles experienced absolutely lower peak stress, because they became more robust (deeper and wider relative to length) as the animals grew (Currie, 2003). This hypothesis would be falsified (greater peak stresses in the adult) if muscle and food reaction forces are sufficiently great in the adult.

Hypothesis (2). At equalized mandible lengths, younger tyrannosaurids experienced greater stress and strain relative to the adults, suggesting relatively lower bite forces consistent with proportionally slender jaws. Setting mandible lengths to be equal in length enables comparisons of
adaptations for bite performance: at the same body size, a deeper mandible with lower stress would indicate the ability to deliver a more forceful bite.

1.2 Criteria for testing hypotheses and interpreting relative stresses

These hypotheses relate to the stress and strain of skeletal structures. Comparing the mandibles requires a biologically appropriate criterion to assess strength (how close structures are to becoming damaged) during experienced stresses (Gilbert, Snively, & Cotton, 2016). Mandible strengths were primarily compared with von Mises stress (von Mises, 1913), a value which accurately predicts how close ductile (slightly deformable/non-brittle) materials like a bone (Keyak & Rossi, 2000; Lotz, Chea, & Hayes, 1991) are to breaking (absolute strength) or permanent deformation (yield strength) when the larger of compressive (in the case of bone) or tensile strengths is less than 1.5 times that of the other (Kayak et al. 2000). Mandibles with lower von Mises stress were judged to be stronger under the imposed bite simulations, as lower stresses indicate less susceptibility to breakage or deformation under the imposed load.

A question rarely addressed in such comparisons is whether there is the informative adaptive significance if two structures experience stress far below failure levels (T. Greiner, personal communication 2019). For example, neither 40 MPa (about 40% of shear failure stress) in a slender mandible nor 5 MPa in a robust mandible will break either structure, although the slender mandible is closer to the threshold. Comparing these stress results is still informative. Excessively repeated moderate stress
can lead to fatigue, weakening a structure over time. Yet bone remodels even under normal loading regimes, and relative experienced stresses, therefore, are reflecting active bone adaptation to loading from actual behavior. Bone responds directly to muscular and reaction loading throughout ontogeny, influencing morphology, functional capability, and adaptive scope. Furthermore, lower relative stress can reflect momentarily excessive construction (Gans, 1979), the overhead capability for rare life-or-death situations where loading is exceptionally great.

As with most such biomechanical studies in vertebrate paleontology, the small sample sizes of rare fossil specimens limit statistical testing, and unknowns about fossil preservation constrain confidence in specific point stresses and especially strain values, because tissue stiffnesses (stress/strain) are not precisely known (Rayfield, 2007). Fortunately, overall stress distribution and magnitude depend on mandible shape, size, and force loading, that are well-constrained in this study’s specimens on their jaw hinges and teeth that impacted food. Therefore, visual, color-indexed comparison of stress magnitudes (Rayfield, 2007) and strain magnitudes were primarily used, which revealed overall magnitudes and distribution of stress and strain on specific points in the mandibles tested. Evaluation of these hypotheses is predictive for future statistical comparisons including phylogenetic and developmental influences, possible with sample sizes of at least 10 per compared group (Snively et al., 2019).

In addition to testing these hypotheses, further implications for feeding at different growth stages in tyrannosaurs and the evolution of their jaw muscles were considered. Specific muscles may have been particularly important for facilitating unique feeding strategies used by tyrannosaurs, by applying opposite forces and distributing stress favorably for safety factors of bones, teeth, ligaments, and tendons (Cost et al., 2019). Adult tyrannosaurids are noted for their “puncture-pull” biting technique in which they splintered bone (Erickson et al. 1996; Carr & Williamson, 2004); muscles that impart high bite force without over-stressing bones and ligaments of the mandible would enable such a feeding strategy.

1.3 Specimens for 3D analyses and tests for secondary hypotheses

Three specimens of tyrannosaurine tyrannosaurid were selected to represent different ontogenetic stages: a small juvenile, a large juvenile or subadult, and a large adult. Their ages and ontogenetic status were based on limb bone histology (Erickson et al., 2004; Fowler et al., 2011; Sereno et al., 2009; Woodward et al., 2020) and other ontogenetically consistent postcranial features (Carr, 2020). Criteria for assessing the ontogenetic stage were therefore independent of mandible morphology, which might invite circularity in this study’s list of specimens (Table 1).

The recently described tyrannosaur Raptorex kriegsteini from Asia is important as a representative small juvenile tyrannosaurid. Raptorex was less than 2 m long yet exhibits all major tyrannosaurid functional specializations in the skull and skeleton, including a small forelimb. Little is known its biting performance and hunting behavior. Raptorex was initially described as a small adult ~5–6-year-old from the lower Cretaceous Yixian Formation of China (Peixian, Deying, Yougui, & Jingxian, 1994; Sereno et al., 2009). However, the specimen is now considered a 3–6-year-old juvenile of much later, extensively studied tyrannosaurs (Fowler et al., 2011), such as Tarbosaurus bataar from the upper Cretaceous Nemegt Formation of Mongolia (Hurum & Currie, 2000; Hurum & Sabath, 2003; Maleev, 1965, 1974; Saveliev & Alifanov, 2007; Tsuihiji et al., 2011).

A large juvenile T. rex (BMRP 2002.4.1) represents a later ontogenetic stage (Carr, 2020) near the inflection of the taxon’s logistic growth curve (Erickson et al., 2004; Woodward et al., 2020), at its period of the fastest absolute growth. This specimen lacks a preserved angular bone, which was reconstructed by BMRP through comparison with other tyrannosaurid specimens. A cast of the reconstructed mandible was scanned and digitized courtesy Heather Rockhold (O’Byness Memorial Hospital, Athens, OH), Lawrence Witmer, and Ryan Ridgeley (Ohio University). In addition to examining mandible stress distribution at this growth stage, the function of post-dentary ligaments was tested, behind the mandible’s tooth-bearing bone. Comparative analyses with and without these ligaments can reveal their effect on stress and strain the animals experienced when biting.

| Specimen name                  | Specimen number | Mandible length (cm) |
|--------------------------------|-----------------|----------------------|
| Adult *Tyrannosaurus rex*      | FMNH PR 2081    | 127.5                |
| Juvenile *Tyrannosaurus rex*   | BMRP 2002.4.1   | 70.3                 |
| *Raptorex kriegsteini*         | LH PV18         | 29                   |

Note: Genera, museum catalog numbers, and mandible lengths are listed. Museum abbreviations: FNMH, Field Museum of Natural History, Chicago, IL; BMRP, Burpee Museum Rockford Paleontology, Rockford, IL; LH, Long Hao Institute of Geology and Paleontology, Hohhot, Inner Mongolia, China.
The final specimen (FMNH PR 2081; “Sue”) is a large senescent adult of *T. rex* (Carr, 2020), at least 28 years old at mortality (Erickson et al., 2004). With this specimen the effects of two phenomena were examined. First, peak tooth stresses with an absolute fixed constraint (common in engineering) were compared with biting down on an object with food material properties, which is in turn immobilized (Moazen et al. 2008). Second, the effects of two inferred insertions of the ventral pterygoid muscle were assessed, which loops around the mandible in reptiles. This insertion can be reconstructed as restricted to the posterolateral surface of the angular (Cost et al., 2019; Gignac & Erickson, 2017). However, all adult *T. rex* specimens possess a lateral fossa impressed upon the surangular, angular, and posterior end of the dentary (Carr, 2020), which suggests a larger insertion for this muscle. Different extents of this attachment potentially have substantial consequences for mandible stress in life.

### 2 METHODS

#### 2.1 3D finite element modeling

To study the mechanical behavior of tyrannosaurid lower jaws, finite element analysis (FEA) was applied, which makes use of a virtual model of a structure that is divided into many smaller shapes called elements. FEA is a standard mathematical tool in biomechanics to quantify the strain and stress state within a solid, given its material properties, and under the actions of appropriate loads and constraints that represent a particular functional or behavioral scenario (Maiorino, Farke, Kotsakis, Teresi, & Piras, 2015). FEA produces a reconstruction of stress and strain within the skeleton and allows assessment of how the skeleton functioned and how evolution shaped it in a particular manner (Rayfield, 2007). Its noninvasiveness and applicability to extinct taxa have resulted in a surge of FEA applications to research on extinct animals (Rayfield, 2007).

#### 2.2 Construction of 3D finite element models

CT data were imported into Avizo and smoothed to reduce pixilation for a more realistic model. Smoothing often facilitates the construction of a more biologically realistic, less blocky, or jagged final surface from lower-resolution original scans, and fewer stress and strain artifacts that occur at unrealistically sharp boundaries. To capture the 3D shape from 2D orthogonal slices, a range of densities were entered in the CT scan to capture the bones and teeth of the object and make a surface from the selected data. The resulting surface may have computationally prohibitive resolution, so the triangle count was reduced and the model was remeshed to make surface triangles as equilateral as possible for realistic results in Strand7: 15 times taller than wide was adequate. The surface editor tested the model surface for intersecting triangles, closeness, and aspect ratio of triangles. Another surface editor function (“prepare generate tetra grid”) was used to fix remaining high aspect ratio surface triangles and generate a “solid” tetrahedral volume mesh from the surface for FEA. Surface and volume meshes of multiple sizes were made—larger models are more accurate, but take longer to solve. The largest mesh was kept for convergence analyses of the smaller meshes; the most accurate results for the minimal solving time were found by comparing results from smaller meshes with those from the largest mesh.

Reconstructions of dinosaur jaw muscles were derived from Holliday (2009) and Gignac and Erickson (2017; Figure 2). Muscle force is proportional to cross-sectional area multiplied by a force/area that muscles produce (31.5 N/cm²: Gignac & Erickson, 2017) and is scalable linearly to cross-sectional area of muscles between tyrannosaur species. A muscle’s physiological cross-sectional area (PCSA) incorporates its volume, pennation angle, and fiber length. If all fibers in the muscle were arranged in parallel, the PCSA would equal their anatomical cross-sectional area (Zatsiorsky & Prilutsky, 2012). To estimate a maximum force that would stringently test each mandible’s

**FIGURE 2** Muscle insertions where nodes were mapped for *Raptorex kriegsteini* model in Strand7 based on Holliday, 2009 and Gignac & Erickson, 2017. Nodes were mapped in identical areas for all tyrannosaurid models tested while accounting for mandible size and shape variation. Full muscle names in Table 2
structural capability, fiber lengths of 0.35 times that of each muscle's length were incorporated based on data from Bates and Falkingham (2012, 2018). Estimated forces from Gignac and Erickson (2017) were multiplied by 1/0.35 to obtain forces corrected for this adjustment to PSCA.

Gignac and Erickson (2017) scaled muscle forces of adult *T. rex* specimen FMNH PR 2081, used in the present study, from forces estimated for a reconstruction of another adult, BHI 3033. Muscle forces of the large juvenile *T. rex* were scaled relative to the force values from FMNH PR 2081, and muscle cross-sectional areas and forces of LH PV18 (*Raptorex*) were scaled via the sub-temporal fenestra method (Sakamoto, 2006); the sub-temporal fenestra is where the jaw muscles extend in a typical reptile mandible. Because the method uses an area, forces were scaled from the large juvenile *T. rex* to *Raptorex* (*Raptorex* length/juvenile *T. rex* length)$^2$.

Muscle force components were trigonometrically calculated (Table 2-5) by measuring distances and angles from origin to insertion in these models and after Gignac and Erickson (2017). To transfer these components into the coordinate system of Strand7 and with the jaws slightly open, coordinate frame rotation methods from Gilbert et al. (2016) were used. Frame rotation reoriented each muscle vector from the specimen’s original coordinate system into the Strand7 coordinate system. Muscle lines of pull and force components were determined from musculoskeletal reconstructions and the vectors were reoriented the model. Rotations are often necessary because models vary from the original CT scanned orientation which may be lying on their side, upside down, slightly tilted up, or sideways.

For most analyses, properties of *Alligator* mandible bone (Porro et al., 2011) were applied to all the specimens, to ensure comparable results. In one model and set of analyses for the large juvenile *Tyrannosaurus* BMRP 2002.4.1, separate properties for bone, dentine (which makes up most of the teeth of reptiles), and ligaments (Porro et al., 2011) were applied. This analysis assessed the effects of ligaments, which accommodate more strain than bone, on bone stresses and tooth reaction forces. Mesh models were imported into Strand7 and appropriate material properties were assigned to the tetrahedral model in brick or solid object properties: elastic modulus and Poisson’s ratio. An elastic modulus is a quantity that measures an object’s resistance to being deformed elastically when a stress is applied to it. The elastic modulus of an object is defined as the slope of its stress–strain curve (stress/strain) in the elastic deformation region (Askeland & Phulé, 2006), when it can spring back to its original shape. Poisson’s ratio describes the resistance of a material to distort under mechanical load rather than to alter in volume (Greaves, Greer, Lakes, & Rouxel, 2011) and is the quotient of transverse strain (bulging under compression or thinning under tension) and longitudinal strain from applied loads. Bone, tooth, and ligament material properties of alligators were applied as a proxy for those of the tyrannosaurids, given the close evolutionary relationship between dinosaurs and crocodilians (Porro et al., 2011; Table 5).

To apply forces, nodes were selected in the areas where forces were being tested and divided by the total respective estimated muscle force by the total number of nodes selected. Constraints were assigned to restrict free body motion, at the hinges of the jaw and two mesial teeth for both constraints to obtain bite reaction forces. Models with just one ramus (FMNH PR 2081 and BMRP 2002.4.1) were constrained against mediolateral translation, which has the effect of simulating the structural response of one side of a perfectly symmetrical structure. For several analyses of FMNH PR 2081, a food object was simulated by assigning the properties of bone in contact with the teeth. This arrangement was more realistic for stress at points of constraint, which is a necessary artifice of FEA. Beam elements were extruded from nodes of contact (the originally constrained nodes) and the beams were constrained at their other ends. The beams were assigned stiffness of compact bone (Table 5).

Once satisfied with constraint placement based on tooth positions, beam placement, and node placement based on Holliday (2009) and Gignac and Erickson (2017) muscle reconstructions, FE analyses were done under

| TABLE 2  | Muscle force components in Newtons for the adult *Tyrannosaurus rex* FMNH PR 2081 model |
|----------|-----------------------------------------------------------------------------------------|
| mames    | mamep | mamp | mps | mint | mptd | mptv |
| x        | 12,963.79 | 4,871.56 | 12,212.41 | 10,211.07 | 10,152.18 | 6,491.49 | 2,640.76 | 40,916.35 |
| y        | −603.86   | −127.53  | 481.84   | 696.25   | 3,030.57  | −1,500.35 | 374.41   | 14,928.06  |
| z        | 4,145.24  | 1,284.74 | 86.61    | 2,578.99 | 3,139.31  | 3,533.01  | 2,735.86 | −15,531.11 |

Note: The left side of the jaw was tested, with a rotation of −6° at the jaw joint to angle the ramus toward the life position of the mandibular symphysis. Abbreviations: mamem, *Musculus adductor mandibulae externus medialis*; mamep, *M. adductor mandibulae externus profundus*; mames, *M. adductor mandibulae externus superficialis*; mamp, *M. adductor mandibulae posterior*; mint, *M. intramandibularis*; mps, *M. pseudotemporalis* complex; mptd, *M. pterygoideus dorsalis*; mptv, *M. pterygoideus ventralis*.
linear static assumptions, with unchanging loads and material properties. Stresses were compared with von Mises stress, which is a good predictor of failure under ductile fracture, or fracture characterized initially by plastic deformation, commonly occurring in the bone. It is a function of principal stresses in $\sigma_1$, $\sigma_2$, and $\sigma_3$, that measures how stress distorts a material. Failure of ductile material is estimated when von Mises stress equals the yield strength of the material in uniaxial tension (Rayfield, 2007). These were drawn as contours with a user-specified range of colors on the model to indicate where stresses experienced are least and most significant (Figures 3 and 4).

### 2.3 2D finite element comparisons of theropod mandibles

2D finite element models of theropods were constructed as listed in Table 6. Most of the 2D mandible models were based on complete specimens. Three *Tyrannosaurus* mandibles were incomplete and were partially reconstructed:

#### TABLE 3  
Muscle force components for the juvenile *Tyrannosaurus rex* BMRP 2002.4.1 model

|        | mames | mamem | mamep | mamp | mps  | mint  | mptd | mptv  |
|--------|-------|-------|-------|------|------|-------|------|-------|
| x      | −1,101.66 | −411.63 | −1,025.92 | −861.81 | −1,042.63 | −564.23 | −240.76 | −3,229.78 |
| y      | 31.82  | 5.52  | −67.78 | −67.09 | −263.13 | 105.27 | −46.71 | −1,102.39 |
| z      | 231.99 | 64.16 | 86.61 | 118.91 | 150.19 | 243.39 | 199.07 | −1,722.26 |

*Note:* The left side of the jaw was tested, with rotation of 7.81° at the jaw joint to angle the ramus toward the life position of the mandibular symphysis. Abbreviations: mamem, *Musculus adductor mandibulae externus medialis*; mamep, *M. adductor mandibulae externus profundus*; mames, *M. adductor mandibulae externus superficialis*; mamp, *M. adductor mandibulae posterior*; mint, *M. intramandibularis*; mps, *M. pseudotemporalis* complex; mptd, *M. pterygoideus dorsalis*; mptv, *M. pterygoideus ventralis*.

#### TABLE 4  
Muscle force components for *Raptorex kriegsteini* (LH PV18) model

|        | mames | mamem | mamep | mamp | mps  | mint  | mptd | mptv  |
|--------|-------|-------|-------|------|------|-------|------|-------|
| Right ramus |       |       |       |      |      |       |      |       |
| x      | −29.41 | −8.13 | −10.75 | −14.83 | −18.23 | −31.06 | −25.02 | −220.81 |
| y      | 139.26 | 52.04 | 129.69 | 108.94 | 131.79 | 71.33  | 30.43 | 408.26 |
| z      | −3.36  | −0.51 | 8.81   | 8.82  | 33.68  | −12.60 | 6.47  | 134.37 |

|        | mames | mamem | mamep | mamp | mps  | mint  | mptd | mptv  |
|--------|-------|-------|-------|------|------|-------|------|-------|
| Left ramus |       |       |       |      |      |       |      |       |
| x      | 29.41  | 8.12  | 10.75 | 14.83 | 18.23 | 31.06  | 25.02 | 220.81 |
| y      | 139.26 | 52.03 | 129.68 | 108.94 | 131.79 | 71.32  | 30.43 | 408.26 |
| z      | −3.36  | −0.51 | 8.81   | 8.82  | 33.68  | −12.60 | 6.48  | 134.38 |

*Note:* Both sides of the jaw were tested. Angles of muscle vector rotation (left = −6.51°/C14, right = +6.51°/C14) ensured anatomically accurate lines of pull. Abbreviations: mamem, *Musculus adductor mandibulae externus medialis*; mamep, *M. adductor mandibulae externus profundus*; mames, *M. adductor mandibulae externus superficialis*; mamp, *M. adductor mandibulae posterior*; mint, *M. intramandibularis*; mps, *M. pseudotemporalis* complex; mptd, *M. pterygoideus dorsalis*; mptv, *M. pterygoideus ventralis*.

#### TABLE 5  
Properties applied to dinosaur jaw models based on alligator data (Porro et al., 2011)

| Material | Orientation | Elastic modulus (GPa) | Shear modulus (GPa) | Poisson’s ratio |
|----------|-------------|-----------------------|---------------------|----------------|
| Bone     | x           | 8.1                   |                     | 0.38           |
|          | y           | 9.26                  |                     | 0.38           |
|          | z           | 19.71                 |                     | 0.38           |
|          | xy          | 3.17                  |                     | 0.38           |
|          | xy          | 4.45                  |                     | 0.38           |
|          | yz          | 5.51                  |                     | 0.38           |
| Teeth    | All         | 21                    | N/A                 | 0.31           |
| Ligaments | All        | 0.1                   | N/A                 | 0.3            |
an angular added to BMRP 2002.4.1, post-dentary elements of LACM 28471 after Carr and Williamson (2004), and the teeth of LACM 23845 as reconstructed by Bruñén (2019). For photographed specimens, perspective and lens distortion were corrected for in Adobe Photoshop (Filter>Distort>Lens correction), using orthogonal straight lines in the photographs as a guide.

Perimeters of mandibles, teeth, and mandibular fenestrae, scaled to their actual dimensions, were traced using the pen tool in Adobe Illustrator® and exported as dxf files into COMSOL Multiphysics®. Fenestrae were subtracted from the mandible perimeter using the “Difference” tool in Multiphysics®. The profile models were meshed to between 80,000 and 90,000 triangular elements each. Meshes were extruded a thickness to 5% of mandible length and given the same material properties as the 3D models with appropriate axes transposed.

2.4 Validation of profile models

Although semi-2D models simplify model creation and accelerate comparative analyses (Fletcher et al., 2010; Morales-García et al., 2019; Rayfield, 2005b, 2011; Shychoski, 2006; Snively et al., 2010), they do not capture anatomical details such as the mandibular fossa, curvature in coronal planes (in dorsal or ventral views) (Therrien et al., 2005) and variations in mandible thickness. This necessitated the validation of 2D models through comparisons with 3D FEA results.

The validity of profile models was tested by comparing stress distributions for two, 2D representations with respective three-dimensional counterparts, matched for profile dimensions, material properties, constraints, and forces. For these validation analyses, all models were constrained at the jaw joint and a force applied to the mesialmost tooth. A profile model of T. rex FMNH PR 2081 was compared with a 3D representation after methods of Wroe et al. (2008) and Moreno et al. (2008). Results for a 2D mandible model of Carnosaurus sastrei (MACN CH 894) were compared with those for the 3D model by Mazzetta et al. (2005), using their data for material properties and forces of an anterior bite.

2.5 Forces and constraints for 2D models

Two methods were used to estimate adductor muscle forces for the expanded sample of 2D mandible models.
As a baseline of relative adductor force, estimates from the subtemporal fenestra method (Shychoski, 2006) were used for *T. rex* (AMNH FARB 5027) and *Gorgosaurus libratus* (TMP 91.36.500). By this procedure, the area of the subtemporal fenestra serves as a proxy for anatomical cross-sectional area, which is then multiplied by muscle’s isometric specific tension (31.5 N/cm²) to obtain a force for the temporal adductors (Shychoski, 2006).

When subtemporal estimates were unavailable, section moduli of dentaries (Therrien et al., 2005) were calculated as an index of comparative bite force and related these estimates to subtemporal estimates of closely related taxa. Therrien et al. (2005) calculated section moduli for resistance to vertical bending (Zx) for several *T. rex* dentaries used in the present study. Zx estimates were averaged at two tooth positions for *T. rex* specimens AMNH FARB 5027 and FMNH PR 2081, respectively, and used these as an index of bite force relative to Therrien et al.’s (2005) mean estimate for adult *T. rex* (in units of “times stronger than *Alligator*”). Ratios of Zx for these specimens were remarkably close to the squared ratios of their minimum dentary depths. For other specimens, ratios were squared between their depths and that of AMNH 5027. These quotients were multiplied by subtemporal estimates for AMNH 5027 to obtain muscular forces.

Similarly to 3D analyses, forces for *T. rex* were scaled to obtain forces for other tyrannosaurids. The crania of *T. rex* are relatively broad, and the subtemporal fenestrae elongate. Force estimates were therefore modified from narrower-skulled tyrannosauroids (Shychoski, 2006) by multiplying them by the ratio of areas measured in ImageJ (0.57) between *Daspletosaurus torosus* (CMN 8506) and *T. rex* (AMNH 5027), normalized for skull length.

Equal percentages of total force were applied for muscles influencing specific regions of the mandible. Forces of the pseudotemporalis muscle, adductor mandibulae externus profundus muscle, and pterygoideus dorsalis muscle were consolidated into an insertion within the adductor fossa, and those for the adductor mandibulae externus superficialis muscle and adductor mandibulae posterior muscle along the posterodorsal surface of the

### TABLE 6  Specimens for 2D FEA, for including mandibular rami lengths, and for the theropods section modulus Zx relative to the *Alligator* specimen in Therrien, Henderson, and Ruff (2005), and calculated muscle force

| Taxon                  | Specimen   | Length (cm) | Zx (x *Alligator*) | F<sub>muscle</sub> (N) |
|------------------------|------------|-------------|---------------------|------------------------|
| **Tyrannosaurids:**    |            |             |                     |                        |
| *Tyrannosaurus rex*    | LACM 28471 | 25.4        | 0.252               | 1,173.6                |
| *Tyrannosaurus rex*    | BMRP 2002.4.1 | 72.0     | 3.02               | 14,065.1               |
| *Tyrannosaurus rex*    | LACM 23845 | 88          | 7.0                | 32,625.8               |
| *Tyrannosaurus rex*    | AMNH FARB 5027 | 116.0  | 13.21              | **61,523.0**           |
| *Tyrannosaurus rex*    | FMNH PR 2081 | 140.0   | 20.34              | 94,729.6               |
| *Albertosaurus sarcophagus* | TMP 81.10.1 | 92.2      | 6.31               | 29,387.6               |
| *Daspletosaurus torosus* | NMC 8506   | 96.6       | 7.221              | 33,630.4               |
| *Dilong paradoxus*     | IVPP V11579 | 18.1      |                    | 468.1                  |
| *Gorgosaurus libratus* | TMP 91.36.500 | 70.6   |                    | 4,711.8                |
| *Tarbosaurus bataar*   | ZPAL MgD 1/4 | 106.3    | 8.25               | 38,422.8               |
| **Non-tyrannosaurids:**|            |             |                     |                        |
| *Acrocanthosaurus atokensis* | NCSM 14345 | 119.6     | 3.79               | 17,651.2               |
| *Allosaurus fragilis*  | UUVP 6000   | 88.3       | 1.787              | 8,322.6                |
| *Suchomimus tenerensis* | MNH GDF500 | 102       | 0.867              | 4,037.9                |
| *Carnotaurus sastrei*  | MCAN-CH 894 | 50.3     | 2.305              | 10,735.1               |
| *Ceratosaurus nasicornis* | USNM 4735 | 59.6      | 1.362              | 6,343.2                |
| *Dilophosaurus wetherelli* | UCMP 37302 | 59.7     | 0.71               | 3,306.7                |
| *Giganotosaurus carolinii* | MUCP-CH 1 | 178.2     | 5.363              | 24,977.1               |
| *Sinraptor dongi*      | IVPP 10600  | 86.7       | 1.723              | 8,024.5                |
| *Yangchuanosaurus shangyouensis* | CV 00215 | 81.0       | 1.504              | 7,004.6                |

Note: For simulation of stress relative to mandible length, all specimens were equalized for the length and estimated muscle force of *Tyrannosaurus rex* AMNH FARB 5027.
surangular. M. pterygoideus ventralis loops around the mandible, and its force was applied as compression on the posteroventral surface. Modeling this muscle’s pull on the lateral surface of the mandible was simulated in a 3D analysis. Constraints were similar to those of the 3D analyses. Each model was constrained to zero displacement at the jaw joint (along the dorsal surface of the articular), and at two anterior teeth.

To compare the effects of mandible morphology on stress magnitude and distribution, each model was scaled to the length and forces applied to the mandibular ramus of adult *T. rex* specimen AMNH FARB 5027. Scaling to mandible length and force of one specimen enables comparisons of stress if the theropods were at hypothetical, ecologically equivalent sizes, rather than estimating absolute stresses. Lower stress will suggest a mandible’s ability to accommodate greater bite force, and vice versa.

3 RESULTS

3.1 3D stress distributions and magnitudes

Small juvenile and larger subadult tyrannosaurs experienced greater mandible stresses when mandible lengths are equalized by adjusting their sizes in Avizo and Strand7. At equal mandible lengths, the larger juvenile tyrannosaur BMRP 2002.4.1 experienced 3.29 times the compressive and tensile bending stresses relative to the adult tyrannosaur FMNH PR2081 (Figure 5). The small juvenile *Raptorex* experienced 6.05 times the bending stresses relative to FMNH PR2081, and 1.84 times the stresses of BMRP 2002.4.1. However, at the actual size, the juveniles experienced lower absolute stresses when compared to the adult, contradicting Hypothesis 1. With calculated muscle forces and simulation at actual size, *Raptorex* experienced the overall lowest peak von Mises stresses of all the tyrannosaurs (Figures 5, 6). When post-dentary ligaments are incorporated into the juvenile *T. rex* mandible, the strain on post-dentary ligaments decreases stress and strain in the posterior portion of the dentary, and where teeth impacted their food (Figure 7). Incorporating ligaments reduce overall stresses at the teeth and on the mandible by roughly 10 MPa, creating a more realistic scenario when the animal was biting down (Figure 8).

Despite greater stress than in juveniles, the adult mandible maintains safety factors, or expressions of how much stronger the system is than it needs to be for an intended load, of 3–4 relative to ultimate stress in the bone. The adult *T. rex* with the simulated food object experienced tooth tip stresses of 300 MPa, and with greater values of over 1,000 MPa when the contact points served as constraints (Figure 9). These values are consistent with high pressures calculated by Gignac and Erickson (2017), with the point constraint similar to initial contact with the very tip of the tooth.

Tension from the lateral insertion of the looping ventral pterygoid muscle is linked to increasing compressive...
Stresses on the angular, a large bone near the posterior end of the mandible, but it serves to decrease anterior bending stresses on the mandible (Figure 10). Lowered mid-mandible bending stresses would be advantageous with the highly robust and conical teeth on the anterior end of the tyrannosaur jaw, where, usually, they may have applied their highest impact bite forces. Crocodilians experience the reverse situation: they possess robust teeth near the posterior end of their mandible where they apply their highest bite forces (Erickson et al., 2012). Stresses are also notable on the pseudotemporalis profundus muscle (mamep) located near the posterior teeth, achieving between 25 and 30 MPa in adult T. rex (Figures 5, 9 and 10).
3.2 3D comparisons validate 2D stress results

For both the *T. rex* and *Carnotaurus* comparisons, the pattern of stress distribution in the profile models was nearly identical between the 3D models in lateral view (Figure 11). Stress magnitudes were similar in most regions of the respective models but were lower in the 2D models at the dorsal dentary-surangular articulation in *Carnotaurus*, and lateral to the position of the mandibular fossa in *T. rex*. The highest stresses on the *T. rex* dentary are farther forward in the 2D model (Figure 11b) than in the 3D simulation (Figure 11a).

3.3 2D stress distributions and magnitudes

Distributions of mandible stress are similar between juvenile tyrannosaurids and adults of other species (Figure 12). Stress patterns in juvenile tyrannosaurids most closely resemble those of the allosauroid *Sinraptor dongi*. Magnitudes of von Mises stress are lower in adult tyrannosaurids than in juveniles, whose magnitudes are closer to those of adults of other taxa. (Figure 12). Scaled mandibular rami of *Ceratosaurus nasicornis* and *Suchomimus tenerensis* experience notably high magnitudes of von Mises stresses, which is consistent with shallow post-dentary regions.

4 DISCUSSION

The results show how changes in ontogeny result in different mandible stresses and strains, indicating that predatory lifestyles of juvenile and adult tyrannosaurids may have differed significantly. Using the *Raptorex* mandible as a proxy for that of a small juvenile *Tyrananosaurus* was not ideal but enabled us to include the best-preserved example of a young juvenile tyrannosaurid specimen. Similar results with a juvenile *T. rex* the size of the *Raptorex* specimen would be predicted, although its skull would be posteriorly broader (Carr, 1999, 2020), and bite force perhaps concomitantly greater (Erickson et al., 2012; Gignac & Erickson, 2017) than in a juvenile *Tarbosaurus* skull of the same length. The stress results may correlate with proposed ontogenetic growth series that have been constructed (Carr, 1999, 2020; Carr & Williamson, 2004; Currie, 2003): elongate and gracile skulls of juveniles become deeper, more robust, and more heavily ornamented. These adult features are integral to the novel tyrannosaurid “bone-crunching” puncture-pull feeding, suggesting it was only used by larger, older individuals; this hypothesis may be further supported by the adults experiencing lower stresses compared to juvenile forms at equalized mandible lengths. While the adult tyrannosaurs experienced higher absolute stresses near the mid-mandible relative to the smaller tyrannosaurs, safety factors were sufficient and they were able to accommodate such high forces because the mandible

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**FIGURE 11** 3D FEA results largely validate von Mises stress distribution in 2D models. A and B. Respective 3D (modified from Mazzetta et al. (2005), with Photoshop® Cartoonize function) and 2D results for *Carnotaurus sastrei*. C and D. Respective 3D and 2D results for *Tyrananosaurus rex*. Distributions of von Mises stress are similar in 3D and 2D simulations for each specimen, evident despite different color scales (insets) for the 3D results.
Stresses on the mid-mandible are lessened but increased near the mandible hinge by the ventral pterygoid muscle insertion in the late-stage juvenile tyrannosaur BMRP 2002.4.1. This presents a trade-off for the animal. While a risk to the jaw hinge is costly and teeth can be replaced, teeth are still immediately necessary for prey capture, feeding, and combat. Tyrannosaur remains with broken or fractured jaw hinges are rare, suggesting that this stress distribution along the mandible was more beneficial to the animal in the long term. However, BMRP 2002.4.1 displays a distinct lesion on the right quadrate condyle and a mottled surface of the ipsilateral surangular (T.D. Carr, personal communication 2021), consistent with high forces and stresses at and near the joint.

In addition, analysis with simulated bone biting reduces artificially high stress at the originally constrained nodes. However, the resulting stress (300 MPa) is far beyond the shear strength of the afflicted bone (about 100 MPa), while overall remaining lower distally (180–200 MPa) than the compressive strength of dentine that makes up most of the teeth (197 MPa: Chun, Choi, & Lee, 2014). This high stress is consistent with enormous tooth-tip pressures calculated for adult *T. rex*, splintering of prey bone under catastrophic failure (seen in fossils and simulated experimentally: Erickson et al., 1996; Gignac & Erickson, 2017), and even with occasional breakage seen in tyrannosaurid teeth still within the jaw.

For 2D stresses relative to mandible length and at equalized forces, *T. rex* shows an ontogenetic gradient of diminishing stress consistent with hypothesized shifts in diet. These results have additional implications for theropod diets. *T. rex* mandible stresses in response to feeding loads recapitulate those of adults of other tyrannosauroids, in that as *T. rex* grew its mandible robustness and relative stress resembled those of adults of similar body size. The results for adult Asian *Tarbosaurus* are similar to those of younger adult *T. rex*. This similarity gives confidence in using the Asian *Raptorex* as representative of overall small juvenile morphology for tyrannosaurines, including *T. rex*. 2D stress results for *T. rex* itself are also congruent with the dramatic shift in skull robustness that Carr (1999, 2020) identified between juvenile and subadult ontogenetic stages.

In addition to their increasing robustness, tyrannosaurid mandibles vary ontogenetically in several discrete

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**Figure 12** von Mises stress (mega pascals) in planar models of theropod mandibles, scaled to length and muscle force of adult *Tyrannosaurus rex* AMNH FARB 5027. Stress is predictably greater (hotter colors) at smaller sizes ontogenetically in *T. rex* and with ontogeny and phylogeny in other tyrannosauroids. Mandible stress is greater in the other theropods than in tyrannosaurs of similar size, especially in the spinosaur *Suchomimus tenerensis* and surprisingly in *Ceratosaurus nasicornis*. 
traits (Carr, 2020). These features include a diagnostic posterior surangular fenestra near the jaw joint (Figures 3 and 12; notably large in *Daspletosaurus*), the laterally projecting surangular shelf above this opening, and the external mandibular fenestra at the junction of the dentary, angular, and surangular. The surangular fenestra of the large juvenile BMRP 2002.4.1 was surrounded by the lowest bone stresses and was largest in this specimen, suggesting that fenestra size varies inversely with experienced relative loading (less bone is “needed” for resisting lower local forces). Both the small juvenile and large adult have smaller surangular fenestræ and greater surrounding stresses (Figure 5).

Proportionally greater loadings in the adult *Tyannosaurus* are further consistent with discrete mandibular traits. The ventrolateral slope of the surangular shelf (Carr, 2020) would resist bending moments imposed by inserting muscles and may reflect a ventral pull by the posterior pterygoid if this muscle is inserted ventrally onto the shelf. The adult’s external mandibular fenestra has an anterior, dorsal notch (Carr, 2020), and a more posterior, ventral intrusion by the surangular. The notch would distribute stresses around the opening (Farlow et al., 1991) better than the flat dorsal margin of the fenestra in other theropods. The projection from the surangular may reflect loading on attaching ligamentous tissue that traversed the fenestra, resisting relatively high loads (although the projection is less evident in other adult specimens: Carr (2020)).

The ability of the tyrannosaurid mandible to resist high forces (especially in adults) is consistent with cranial adaptations. Tyrannosaurs are notable for their possession of fused nasals (Snively et al., 2006) and substantial ossification of the secondary palate that most other large-bodied theropods lacked (Holtz Jr., 1998; Holtz Jr., 2000; Holtz Jr., 2003; Holtz Jr., 2004). (“Secondary palate” is used by its definition as an embryologically posterior palatal structure formed by outgrowths of the maxillary processes (Abramyan & Richman, 2015), the patent in most reptiles but fused and largely ossified in crocodylians and mammals.) A typical large theropod skull would be relatively strong in vertical compressive loads but lack solid support to resist torsional or twisting loads (Snively et al., 2006). An extensive bony portion of the secondary palate of tyrannosaurs, formed by medial extensions of the maxillae and reinforced by the diamond-shaped anterior end of the vomer, would allow for greater resistance to torsional loads (Gignac & Erickson, 2017; Holtz Jr., 2008). These FEA findings for the mandible further validate the animal’s powerful bite and demonstrate the potential to inflict tissue damage that few other large theropods could achieve (Cost et al., 2019). Spinosaurids, such as *Suchomimus tenerensis* (Figure 13) also possessed a

**FIGURE 13** Skeletons of five herbivorous dinosaur genera that coexisted with *Tyrannosaurus rex* in Maastrichtian North America based on fossil material recovered. Clockwise from above left: bird-like caenagnathid *Anzu* (Carnegie Museum of Natural History, Pittsburgh, PA; photo by E. Snively), adult hadrosaurid *Edmontosaurus* (Dinosaur Resource Center, CO; photo by A. Rowe), adult ceratopsian *Triceratops* (Burpee Museum of Natural History, Rockford, IL; photo by A. Rowe), an armored *Ankylosaurus* (American Museum of Natural History, New York City, NY; photo by Wikimedia Commons user Ghedoghedo), and long-necked sauropod *Alamosaurus* (Perot Museum of Nature and Science, Dallas, TX; photo by E. Snively)
bony secondary palate (Sereno et al., 1998; Taquet & Russell, 1998), which likely compensated for torsional weakness in a hydrodynamically efficient low, narrow cranium, as in some crocodylians and pliosaurus (Rayfield, Milner, Xuan, & Young, 2007; McHenry 2009; Cuff & Rayfield, 2013; Foffa et al., 2014). The secondary palate of tyrannosaurids was an enhancement of high structural strength, rather than compensation for a gracile or dorsoventrally compressed rostrum as seen in spinosaurids and some crocodylians.

4.1 Paleoeological implications

Subadult tyrannosaurids mandibles experienced relatively low von Mises stresses in contrast to the mature individuals; this suggests that subadult or smaller tyrannosaurid genera fed on smaller, potentially more agile prey, while the bone-crunching bite used by mature individuals was reserved for large, less mobile prey, such as hadrosaurids. Hadrosaurids were large, herbivorous duck-billed dinosaurs such as Edmontosaurus (Figure 14) which possess ample evidence for active predation from tyrannosaurs (Carpenter, 1997; Hone & Watabe, 2010; Rothschild & DePalma, 2013).

FEA data indicate that younger individuals were active predators, somewhat akin to dromaeosaurs such as Deinonychus (Ostrom, 1970). Dromaeosaurs were a group of theropod dinosaurs distinguished from tyrannosaurs by their well-developed slashing talon on their second pedal digit, a stiffened tail which possibly functioned as a dynamic stabilizer, and large grasping hands. Tyrannosaurids are noted for their surprising agility, including the Raptorex and juvenile T. rex specimens (Snively et al., 2019). This agility may be ideal for out-maneuvering prey after fast and energetically-efficient tracking (Dececchi, Mloszewska, Holtz Jr., Habib, & Larsson, 2020) of presumably slower prey (Currie, 1983; Persons & Currie, 2014).

Late-stage juvenile tyrannosaurids at a near-identical age to the larger juvenile T. rex in this study were likely feeding on large prey despite lacking the bone-crunching adult bite (Peterson & Daus, 2019). While biomechanically capable of puncturing bone during feeding, and doing so without the large, blunt dental crowns of the adult, feeding traces on adult prey animals are likely postmortem. Ventral bite traces on the hadrosaurid vertebrae suggest that the tyrannosaur was eating after the haemal complexes or blood vessels and most of the superficial hypaxial muscles (“core” muscles on the tail) and m. caudofemoralis longus (tail muscle) had been removed. Hadrosaurs grew exceptionally fast, perhaps minimizing predation pressure from younger tyrannosaurs (Cooper, Lee, Taper, & Horner, 2008). The crushing bite of adult and perhaps late-

FIGURE 14  Skeletons of five herbivorous dinosaur genera that coexisted with Tarbosaurus bataar in Maastrichtian Mongolia based on fossil material recovered. Clockwise from above left: horned ceratopsian Protoceratops (Field Museum, Chicago, IL; photo by E. Snively), hadrosaurid Saurolophus (Gifu, Japan; photo by Y. Tamai), long-clawed theropod therizinosaur Nothronychus (Utah Museum of Natural History, Salt Lake City, UT; photo by E. Snively), long-necked sauropod Opisthocoelicaudia (Museum of Evolution of Polish Academy of Sciences; photo by A. Grycuk) and a small, agile oviraptorid (Field Museum, Chicago, IL; photo by E. Snively). Note that Nothronychus did not originate in Mongolia but therizinosaur material has been recovered there
stage juvenile tyrannosaurids was likely useful for dispatching adult hadrosaurs and other large herbivores (Figures 13 and 14).

Prey of adult tyrannosaurids likely included the large, herbivorous ceratopsians. The ceratopsians were a group of dinosaurs renowned for their imposing facial horns and large frills. Tyrannosaurus and Triceratops coexisted in Maastrichtian North America and are popularly depicted engaged in combat. Various frill pathologies and cranial lesions have been attributed to predation from T. rex (Hopp, 2008); these pathologies may be as extreme as horns being bitten off (Hopp, 2008; Hone & Rauhut, 2010).

The potential diet of large Asian tyrannosaurids like Tarbosaurus and Zuchengtyrannus represented here by the small juvenile Raptorex specimen, consisted of large sauropods and hadrosaurids (Owocci, Kremer, Cotte, & Boherens, 2019, Hone et al., 2011; Figure 14). The Nemegt Basin of Southern Mongolia offers a wealth of fossil material for the isotopic study of paleoenvironments. Stable isotopes of oxygen and carbon are notable in paleontological work as they can aid in diet reconstructions and paleoecology. Tooth enamel carbonate along the growth axes of five Tarbosaurus bataar teeth have aided in the identification of seasonal climatic variations and imply the presence of a woodland ecosystem dominated by large herbivores. Tooth drag and puncture marks attributed to Tarbosaurus have been reported from bones of the hadrosaurine Saurolophus (Hone & Watabe, 2010; Figure 14) and the sauropod Opisthocoelicaudia (Borsuk-Bialynicka, 1977; Figure 14). These data combined with carbon isotope signatures and FEA data imply that Tarbosaurus was an apex predator in the Late Cretaceous of the Gobi region.

In Maastrichtian (72.1–66 million years old) North America, T. rex was considered the apex tyrannosaurid; skin pathologies (Rothschild & DePalma, 2013), healed prey vertebrae containing teeth (DePalma, Burnham, Martin, Rothschild, & Larson, 2013), and coprolite or fossil feces analyses (Chin, Tokaryk, Erickson, & Calk, 1998) indicate an active predatory lifestyle. The extent of active predation in Tyrannosaurus has remained a contentious topic for decades (Holtz Jr., 2008; Horner, 1994, 1997). Bone healing seen in herbivorous dinosaurs (Carpen ter, 1997) seems to verify the active predatory hypothesis; herbivorous dinosaurs may have escaped the attacking predator and later died elsewhere. This FEA data along with the deep-set jaws of adult T. rex indicates a powerful, locking or catastrophically damaging bite (Cost et al., 2019; Erickson et al., 1996; Gignac & Erickson, 2017; Happ, 2008) however, there remains the possibility of potential prey escaping from non-fatal wounds that afflicted the tail or other appendages.

4.2 Conclusions and predictions

In conclusion, tyrannosaurids possessed a rigid, bone-crunching bite that other predatory dinosaurs of the Mesozoic era lacked, despite similarities of some in the secondary palate. Their wide-set jaws and stress-resistant biting allowed them to easily subdue prey and swallow chunks of flesh and bone. Their biting capabilities, massive size, and surprising agility likely made them the apex predators in their ecosystems.

This study centered on the mandibles of tyrannosaurids at varying ontogenetic stages. It is predicted that 3D comparison of a broader phylogenetic sample will elucidate divergent feeding styles within ecosystems. FEA comparisons will be informative about skull function in adult tyrannosaurids with differing morphology. Slender mandibles of adult low-snouted tyrannosaurids such as Alioramus altai (Brusatte, Carr, Erickson, Bever, & Norell, 2009) are predicted to constrain bite force compared with that of subadults of contemporaneous large tyrannosaurines. Further analyses of Morrison Formation theropods, including Ceratosaurus and Allosaurus (Figure 12), will inform hypotheses of niche fulfillment within their own diverse predatory guild (Van Valkenburgh & Molnar, 2002).

Given that absolute numbers in FEA studies are not often examined, for future comparisons homologous points in the dinosaur mandibles can be sampled (Gilbert et al., 2016) and numerical methods can compare stresses and strains (Snively et al., 2010).

Within jaws of given tyrannosaurs, stress and strain can be investigated as they bit at different points in their jaws. Constraints simulate the contact points for teeth as they bit down on prey and faced resistance from flesh and bone. FE analyses on the tyrannosaurid mandibles presented here are focused on the anterior teeth, which likely first made contact with flesh. Assigning these constraints only to the posterior teeth could yield entirely different stress and strain results; given the significance of anterior teeth in tyrannosaur feeding, the hypothesis that the smaller and less robust posterior teeth would break and deform under similar loads placed on the anterior teeth can be tested, validating the necessity of large, robust anterior teeth in the clade for purposes of efficient feeding.

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**AUTHOR CONTRIBUTIONS**

**Andre Rowe:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; validation; visualization; writing-original draft; writing-review & editing. **Eric Snively:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing-original draft; writing-review & editing.

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