Puncture-and-Pull Biomechanics in the Teeth of Predatory Coelurosaurian Dinosaurs

Highlights

- Theropods used puncture-and-pull feeding movements, based on microwear analyses
- Troodontid teeth were most likely to fail at non-optimal bite angles
- Troodontids may have favored prey requiring lower bite forces than dromaeosaurs

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In Brief

Torices et al. use tooth microwear to show that theropod dinosaurs with differing bauplans used similar feeding movements for dismembering prey. Finite element analyses further reveal that troodontid teeth were more likely to fail at non-optimal bite angles and may have had a markedly different diet than their close dromaeosaurid relatives.
Puncture-and-Pull Biomechanics in the Teeth of Predatory Coelurosaurian Dinosaurs

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SUMMARY
The teeth of putatively carnivorous dinosaurs are often blade-shaped with well-defined serrated cutting edges (Figure 1). These ziphodont teeth are often easily differentiated based on the morphology and density of the denticles [1, 2]. A tearing function has been proposed for theropod denticles in general [3], but the functional significance of denticle phenotypic variation has received less attention. In particular, the unusual hooked denticles found in troodontids suggest a different feeding strategy or diet compared to other small theropods. We used a two-pronged approach to investigate the function of dentine shape variation across theropods with both congruent body shapes and sizes (e.g., dromaeosaurids versus troodontids) and highly disparate body shapes and sizes (e.g., troodontids versus tyrannosaurids), using microwear and finite element analyses (Figure 1). We found that many toothed coelurosaurian theropods employed a puncture-and-pull feeding movement, in which parallel scratches form while biting down into prey and oblique scratches form as the head is pulled backward with the jaws closed. In finite element simulations, theropod teeth had the lowest stresses when bite forces were aligned with the oblique family of microwear scratches. Different denticle morphologies performed differently under a variety of simulated biting angles: *Dromaeosaurus* and *Saurornitholestes* were well-adapted for handling struggling prey, whereas troodontid teeth were more likely to fail at non-optimal bite angles. Troodontids may have favored softer, smaller, or immobile prey.

RESULTS

Microwear Analyses
Scratches were observed covering the denticles and carinae of all teeth in our sample except for one somewhat eroded tooth (Figures 2 and S1; Data S1). In most of the specimens, scratches are more abundant on the posterior border than on the anterior one, except for two indeterminate coelurosaur teeth (DPM-MON-T6, DPM-VIR4-T5), which have the same amount of scratches on both borders. All denticle morphologies show the same microwear patterns despite differences in denticle shape, tooth size, body size, and phylogenetic relatedness. Two families of microwear can be distinguished based on their orientation (Figures 2 and S1):

1. Parallel to subparallel scratches. These scratches are oriented parallel to the borders of the tooth following its curvature on the posterior and anterior borders and are sometimes found in clusters. They are most common near the carinae and on the posterior edge of the tooth. The majority of these scratches are short (10–50 microns) and only a little larger than the width of the denticles, although a few scratches up to 100 microns in length were observed. In cross section, most of the scratches are U-shaped. Small parallel scratches follow the curvature of the denticle.

2. Oblique scratches. These form angles of 30°–40° with the border of the tooth, with each angle oriented toward the tip on the anterior border and the base on the posterior one. Oblique scratches are less common than parallel scratches and are larger, with lengths of at least 200 microns. They are more commonly observed on the flat labial and lingual sides of the teeth rather than toward the carinae. They are present on the denticles but are less abundant than the parallel scratches. Although parallel scratches can cross oblique scratches, oblique scratches more frequently overlaid parallel scratches.

Finite Element Analyses
All three tooth models experienced approximately equal amounts of stress at their optimum bite angle (Figures 3, S2, and S3; see Data and Software Availability). At almost all other cutting angles, the troodontid tooth experienced the greatest mean and maximum stresses. The troodontid experienced its lowest average and maximum stress at 30° and increasing stress at angles further from this optimal angle. The *Saurornitholestes* model behaved in a similar pattern, with the least stress...
experienced at 30°. The stress at the non-optimal bite angles for Saurornitholestes was less than that observed in the troodontid. Dromaeosaurus experienced similar mean stress across all bite angles. Human dentine has a compressive strength of 275–300 MPa (megapascals) [4]. At the optimal cutting angle of 30°, all theropod teeth had similar proportions of elements exceeding 300 MPa (Figure 3). At cutting angles further from the optimal angle, the proportion of elements experiencing stress greater than 300 MPa increased in all teeth. Overall, Troodon had the greatest proportion of elements with stress greater than 300 MPa, and Dromaeosaurus experienced the smallest proportion. In all teeth at their optimal cutting angle, the greatest stresses were restricted to the denticles, and the tooth bodies did not experience high internal stresses (Figure 3). Saurornitholestes and the troodontid showed high degrees of variation in the stress distributions between the optimal and non-optimal cutting angles, while Dromaeosaurus showed little variation. The troodontid tooth had the largest regions experiencing more than 300 MPa of stress at the non-optimal bite angles compared to Dromaeosaurus and Saurornitholestes. At these angles, stress propagated further into the tooth. The Saurornitholestes tooth also had large regions of high stress, but they made up proportionately less of the tooth than the troodontid. Saurornitholestes also performed well on a wider range of cutting angles than the troodontid. Dromaeosaurus showed little variation in the stress distribution between cutting angles. Stress greater than 300 MPa is restricted to the denticles at all cutting angles and was present in a relatively small proportion of the overall tooth. Higher levels of stress tended to accumulate toward the tip of the tooth, although these values remained relatively low.

DISCUSSION

Puncture-and-Pull Feeding in Theropod Dinosaurs

Tooth microwear patterns provide indirect evidence of diets and chewing mechanisms, independent of tooth morphologies. Microwear analyses are particularly useful when applied to problematic fossil species with unusual teeth that cannot be compared directly with known species. Most analyses of microwear patterns in dinosaurs have focused on herbivorous taxa [5–8], and although there have been some studies focusing on theropod wear facets [9–11], the microwear patterns present on theropod teeth have been mentioned [9, 12] but never studied in depth.

Two families of scratch orientations are present on all of the theropod teeth we studied, independent of tooth size, body size, or clade. All theropod teeth had a group of scratches oriented parallel to the long axis of the tooth and a group oriented 30°–40° to the carina. There are no differences in the microwear patterns on large and small theropods, and therefore, biting movements must have been similar across the taxa we studied.

The observed orientations of the oblique scratches in our sample of theropod teeth matched the orientations predicted by the formula proposed by Frazzetta [13] for a serrated blade used in a
Figure 2. SEM Images Showing Microwear Patterns on Three Theropod Teeth

cf. *Pyroraptor* (MCNA-14607), a dromaeosaurid from Lahn, Spain; *Gorgosaurus libratus* (UALVP 53586), a tyranosaurid from Dinosaur Provincial Park, Canada; and *Troodon inexactis* (UALVP 55303), a troodontid from Dinosaur Provincial Park, Canada. Two scratch orientations were present on all studied teeth: one oriented parallel to the border of the tooth, and one oriented $30^\circ$–$40^\circ$ to the tooth border. See also Figure S1.
puncture-and-pull-style motion [14] (Table S1). In this model, the tip of the tooth is the first zone in contact with the prey (Figure 4), and because the teeth are curved, the anterior border meets the most resistance [10]. The tooth continues its descent into the flesh of the animal to puncture it, forming the family of parallel scratches (Figure 4). Finally, as the theropod closed its mouth and pulled its head away from the prey, the tooth made an oblique movement through the flesh, which formed the oblique scratches (Figure 4). The results of our microwear analyses show that different theropod denticle morphotypes had a puncture-and-pull function that resulted in similar microwear patterns.

Although scratches were common on the theropod teeth in this study, pits were extremely rare. Pitting has been correlated with ingestion of abiotic grit, as well as jaw movements in domestic sheep [15], and with a greater frequency of bone ingestion in several extant carnivores [16], primates, and bats [17]. The scarcity of pits on theropod teeth suggests that they were not regularly biting bone or other hard materials and that they were selectively removing flesh from bone, ingesting their prey whole, or eating softer prey such as invertebrates. This is consistent with behavioral observations of *Varanus komodoensis*, which has similar ziphodont teeth and either defleshes carcasses or swallows pieces whole and does not intentionally gnaw or fracture bone [18].

The results of our finite element analyses demonstrate that theropod teeth perform best when forces are directed in the same orientation as the oblique scratches observed in our microwear data (Figure S2; Table S2). In particular, less stress was observed on the mesial carina, consistent with biomechanical models proposed by D’Amore [19] to explain the presence or absence of denticulation on theropod teeth (Figure S3). In all teeth, a greater percentage of finite elements exceeded the failure level of dentine when the forces were directed at angles greater or less than 30°. The highest stresses were restricted to the posterior denticles and carina, and they experienced comparable mean and maximum values of stress. This suggests that theropod denticles are adapted for the cutting angle employed during the puncture-and-pull process. However, *Troodon* denticles had higher overall stresses compared to *Dromaeosaurus* and *Saurornitholestes*, even at the optimal force angle, and differences in performance become more apparent at non-optimal cutting angles.

**Comments on the Diet of Troodon, Dromaeosaurus, and Saurornitholestes**

Troodontids are enigmatic deinonychosaurians from the Campanian-Maastrichtian of North America. Although troodontids co-occur and share similar bauplans with dromaeosaurids—each has a raptorial pedal digit; small or medium body sizes; and long, feathered forearms, for example—their teeth differ significantly from dromaeosaurids and other predatory theropods. The large, hooked denticles in *Troodon* have led several authors to propose that this taxon may have been omnivorous or feeding on markedly different prey items than other predatory theropods [20–22].

Holtz et al. [21] were the first to suggest that *Troodon* may have incorporated plants into its diet, citing the size of the denticles relative to the overall tooth, large brain, grasping hands, and stereoscopic vision. However, they argued against *Troodon* having been strictly herbivorous: the jaws have loose mandibular symphyses and intramandibular joints, the manual unguals are curved and there is a raptorial pedal digit, and the pubes are not opisthopubic. D’Amore [19] noted differences in theropod denticulation patterns that suggested troodontids had diverged from the flesh-based diet of most toothed theropods. Zanno and Makovicky [23] used phylogenetic comparative methods to investigate traits correlated with extrinsic evidence of herbivory (such as gut contents or gastroliths) in coelurosaurians and found clear evidence for herbivory in at least one troodontid, the basal taxon *Jinfengopteryx*, and evidence for carnivory in the derived troodontids *Byronosaurus*, *Sinornithoides*, *Sinovenator*, and *Zanabazar*. Basal troodontids (besides *Jinfengopteryx*) had a lower number of traits correlated with extrinsic evidence of herbivory and thus could be interpreted as omnivorous or insectivorous. Tooth microstructure has also revealed additional information regarding the potential diet of *Troodon*. Dentine tubule density in *Troodon* is more similar to carnivorous theropods than to herbivorous sauropods and ornithischians, and overall dentine ultrastructure indicates that *Troodon* was not well suited to processing tough plant material [24]. Most non-avian theropod dinosaurs have a unique tooth microstructure in which deep interdental folds with globular mantle dentine are present between denticles [25], which may have facilitated hypercarnivory and the ability to feed on large prey and/or bone. *Troodon* secondarily lost these deep interdental folds, suggesting a shift away from hypercarnivory. In contrast, Currie et al. [1] interpreted the denticles of *Troodon* as efficient processors of both meat and bone, and Jacobsen [26] noted the presence of *Troodon* bite marks on a ceratopsian bone from Dinosaur Provincial Park, which suggests that this taxon at least occasionally fed on large vertebrates. Shed teeth have also been found in close association with isolated skeletal remains and eggs of ornithopods in the Horseshoe Canyon [27] and Two Medicine formations [28]. Taken together, these lines of evidence suggest that *Troodon* was probably neither strictly herbivorous nor hypercarnivorous.

The results of our finite element analyses suggest that troodontids were not as well adapted to acquiring struggling prey compared to dromaeosaurids. Our troodontid tooth showed the highest levels of stress at non-optimal cutting angles and is therefore especially vulnerable to breakage at these angles. The asymmetric shape of troodontid denticles distributes stress the most optimally when the force is directed in line with the long axis of the denticle. When the force is directed away from this axis, it acts on the denticle like a lever, generating greater overall stress, and this may have prevented breakage of the tooth, enabling the predator to acquire struggling prey more efficiently.

**Figure 3. Results of the Finite Element Analyses**

(A) *Dromaeosaurus*, *Saurornitholestes*, and Troodontidae indet. stress distributions under 90 N (Newtons) of force applied at 15°, 30°, and 45° to the crown tip. (B) Proportion of elements in each tooth model experiencing stress greater than 300 MPa. (C) Average von Mises stress (MPa) experienced throughout the entire tooth. All teeth show the least stress at the optimal bite angle of 30°. *Dromaeosaurus* shows the least variation in performance at different angles, and *Troodon* shows the greatest variation. See also Figures S2 and S3 and Table S2.
stress that propagates throughout the tooth body. Although the values of some of the stresses within the troodontid tooth body are below the yielding point for dentine, the higher levels of stress may cause the tooth to weaken over its lifetime, possibly accumulating damage and making the denticles or tooth more likely to fail. This susceptibility to breakage at non-optimal cutting angles may provide a functional limitation to the size of the prey that troodontids could process, restricting them to softer food items, only processing smaller, thinner bones, or limiting tooth-bone contact during feeding [29].

In contrast, the rounded shape of *Dromaeosaurus* denticles means bite forces act on the denticles similarly regardless of bite angle, and so the *Dromaeosaurus* tooth performed similarly under different simulated bite angles. *Dromaeosaurus* teeth were less likely to fail during biting even at non-optimal bite angles, which is especially important during the acquisition of struggling prey or during thrashing or jerking movements of the head during feeding, as observed in Komodo dragons [18, 29]. *Dromaeosaurus* and *Saurornitholestes* were able to exert more powerful bite forces without risking tooth failure compared to *Troodon*. *Troodon* was probably a predator of smaller and/or softer prey compared to the dromaeosaurids.

**Conclusion**
Predatory theropod dinosaur teeth from the Upper Cretaceous of Spain and Canada have two families of scratches that formed during feeding: a set of parallel scratches and a set of oblique scratches. The consistency of this pattern across clades and tooth morphologies indicates that most coelurosaurian theropods employed a puncture-and-pull feeding movement, in which parallel scratches form while biting down into prey and oblique scratches form as the head is pulled backward with the jaws.

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*Figure 4. Puncture-and-Pull Feeding in Predatory Theropod Dinosaurs, Based on the Results of Our Microwear Analysis and Finite Element Analyses*

(A) Parallel tooth scratches formed as the theropod bit downward into prey (1 and 2), and oblique scratches formed as the head was pulled back to rip flesh (3). (B) Life restoration of *Saurornitholestes* employing puncture-and-pull feeding to dismember prey. Theropod teeth performed best in our FEA simulations when bite-force angles matched the orientation of the oblique scratches observed on fossil teeth. Illustration in (A) by Javier Ruiz, modified by Victoria Arbour. Illustration in (B) by Sydney Mohr.
Closed. In finite element simulations, theropod teeth had the lowest stresses when bite forces were aligned with the oblique family of microwear scratches. Together, our microwear and finite element analysis results show that most predatory theropods employed similar feeding movements but that different denticle morphologies performed differently under a variety of simulated biting angles. *Dromaeosaurus* and *Saurornitholestes* were well adapted for handling struggling prey or for processing some bone as part of their diet. In contrast, *Troodon* teeth were more likely to fail at non-optimal bite angles, and as such, troodontids may have favored softer prey such as invertebrates, smaller prey that required lower bite forces or could be swallowed whole, or immobile prey such as carrion.

**STAR★METHODS**

Detailed methods are provided in the online version of this paper and include the following:

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**SUPPLEMENTAL INFORMATION**

Supplemental Information includes three figures, two tables, and one data file and can be found with this article online at https://doi.org/10.1016/j.cub.2018.03.042.

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**AUTHOR CONTRIBUTIONS**

A.T. conceived the project. A.T. prepared the dental material, SEM analyses, and microwear analyses. R.W. performed the finite element analyses. A.T., R.W., and V.M.A. prepared the figures. A.T., R.W., V.M.A. J.I.R.-O., and P.J.C. wrote the manuscript.

**DECLARATION OF INTERESTS**

The authors declare no competing interests.

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**REFERENCES**

STAR METHODS

KEY RESOURCES TABLE

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Other

| Tooth fossils | This paper | Data S1: permanently accessioned at the University of Alberta (Edmonton, Alberta, Canada), Departamento de Paleontología de Madrid, Complutense University of Madrid, (Madrid, Spain), and Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz (Madrid, Spain) |

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Angelica Torices (angelica.torices@unirioja.es).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Taxon sampling and tooth terminology

Our microwear sample includes 57 teeth in total from two geographic locations: the South Pyrenees Basin of Spain, and southern Alberta, Canada (Data S1). Thirty-two teeth from Campanian-Maastrichtian sites in the South Pyrenees Basin include cf. Richardoestesia, two distinct dromaeosaurs (cf. Pyroraptor olympus and Dromaeosauridae indet.), coelurosaurians of uncertain affinity with unserrated teeth, and an indeterminate large theropod [30]. Our Albertan samples represent the Dinosaur Park and Oldman formations, which are Campanian in age [31]. These include 25 teeth representing the dromaeosaurs Dromaeosaurus albertensis and Saurornitholestes langstoni, the troodontid Troodon inequalis, and the tyrannosaurid Gorgosaurus libratus. We use one troodontid tooth from the younger Horseshoe Canyon Formation of Alberta for our finite element analysis; this tooth is morphologically indistinguishable from the Dinosaur Park and Oldman Formation teeth observed in the microwear dataset. Although the taxonomy of troodontids from the Campanian-Maastrichtian of Alberta is currently in flux [32, 33], we follow the taxonomic opinions of Evans et al. [33] and refer isolated troodontid teeth in the Dinosaur Park Formation to Troodon inequalis, and isolated troodontid teeth from the Horseshoe Canyon Formation to Troodontidae indet. Tooth anatomical terminology follows Currie et al. [1] and all terminology is congruent with recent revisions by Hendrickx et al. [2].

METHOD DETAILS

Microwear Analysis

Fifty-seven theropod teeth were analyzed to determine the orientation and abundance of wear scratches, which were used to interpret movements of the teeth and jaws during feeding (Data S1, Figure S1, Table S1). We measured the number, length, and orientation of microwear features on theropod teeth using a Zeiss Sigma Field Emission SEM at the University of Alberta (Canada) and a JEOL JSM-820 SEM at Universidad Complutense (Spain). We measured the orientations relative to the carina of the tooth of one hundred scratches for each taxon and calculated the mean value orientation for each specimen and its standard deviation (Table S1). Scratches were measured along the length of the carina to a distance of about 130 μm from the base of the denticle. Taphonomic scratches are more likely to occur on the flank of the tooth during transport, so we limited our observations to the carina.

Finite Element Analysis

We analyzed the performance of different denticle morphologies under puncture-and-pull feeding using finite element analysis. Shed teeth (lacking roots) belonging to Dromaeosaurus albertensis (UALVP 55333), Saurornitholestes langstoni (UALVP 55410), and Troodontidae indet. (UALVP 48639) were scanned using a SkyScan 1174 micro-CT scanner set to 50 kV and 800 μA with a pixel size of 10.60 μm. The resulting DICOM files were imported into Mimics x64 14.01 [34] to generate three-dimensional models, and were exported as stereolithography (.stl) files for additional refinement in Geomagic Studio 12 (64 bit) [35], where they were scaled.
to the same crown height (SI 3). The models were converted into volume meshes in Strand7 [36] and assigned the material properties of dentine (Young’s modulus = \(2.5 \times 10^4\) MPa, Poisson’s ratio = 0.31, density = 0.0021 g/mm\(^3\)) [37]. The enamel layer in theropods is thin [38], and similar in thickness in all of the teeth modeled here. Since our study investigates the response of the overall denticle shape to bite forces, and not the influence of tooth microstructures in stress dissipation, we gave the teeth uniform material properties of dentine and did not model the external enamel layer.

In Strand7, the models were restrained by the nodes at the tips of the denticles, and a force of 90 N was distributed equally across the nodes at the base of the tooth, simulating a bite. This is the unilateral bite force of the Komodo dragon, *Varanus komodoensis* [29], and the maximum bite force of velociraptorines has been estimated to be comparable to that of *V. komodoensis* [39]; we are interested in testing how denticle morphology affects stress distribution within the tooth at different bite angles, and as such the applied force does not need to represent the exact bite force of these animals to permit comparison of their stress response [40]. The force was applied to the tooth at six different cutting angles to provide a coarse-scale evaluation of the performance of the tooth at different cutting angles: 0°, representing a plunging bite vertically through the substrate; and 15°, 30°, 45°, 60°, and 75°, each representing an increasingly horizontal cutting angle. Dentine has a maximum compressive strength of 300 MPa [4, 37], and so this value was used as the maximum on the scales for the contour diagrams. The proportion of the model under the maximum stress was calculated as the ratio of bricks over 300 MPa divided by the total number of bricks.

**QUANTIFICATION AND STATISTICAL ANALYSIS**

For microwear analyses we measured, using a Zeiss Sigma Field Emission SEM at the University of Alberta (Canada) and a JEOL JSM-820 SEM at Universidad Complutense (Spain), the number, length, and orientation of microwear for the canadian and spanish tooth sample. We introduced the data, one hundred measurements for each taxon, on EXCEL where media and standard deviation were calculated for each taxon (Table S1).

Regarding finite element analyses, we used Strand 7, where the models were converted into volume meshes, assigned dentine properties and restrained by the nodes at the tips of the denticles. The mean and maximum von Mises stress was recorded for each tooth at each cutting angle after a force of 90 N was distributed equally across the nodes at the base of the tooth, simulating a bite (Table S2). Stresses exceeding 300 MPa, the yielding point of dentine, were classified as extreme stresses [37]. 300 MPa was used as the maximum value on the scales for the contour diagrams. The proportion of the model under the maximum stress was calculated as the ratio of bricks over 300 MPa divided by the total number of bricks.

**DATA AND SOFTWARE AVAILABILITY**

Tooth microwear measurements are provided as supplemental information in .csv format as Data S1. Digital models (.stl) of the *Dromaeosaurus* tooth, *Saurornitholestes* tooth, and troodontid tooth (doi: P440), used for the finite element analyses, are available for download at MorphoSource (http://www.morphosource.org/Detail/ProjectDetail/Show/project_id/440).