

Quantitative analysis of dental microwear in hadrosaurid dinosaurs, and the implications for hypotheses of jaw mechanics and feeding

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Understanding the feeding mechanisms and diet of nonavian dinosaurs is fundamental to understanding the paleobiology of these taxa and their role in Mesozoic terrestrial ecosystems. Various methods, including biomechanical analysis and 3D computer modeling, have been used to generate detailed functional hypotheses, but in the absence of either direct observations of dinosaur feeding behavior, or close living functional analogues, testing these hypotheses is problematic. Microscopic scratches that form on teeth *in vivo* during feeding are known to record the relative motion of the tooth rows to each other during feeding and to capture evidence of tooth–food interactions. Analysis of this dental microwear provides a powerful tool for testing hypotheses of jaw mechanics, diet, and trophic niche; yet, quantitative analysis of microwear in dinosaurs has not been attempted. Here, we show that analysis of tooth microwear orientation provides direct evidence for the relative motions of jaws during feeding in hadrosaurid ornithopods, the dominant terrestrial herbivores of the Late Cretaceous. Statistical testing demonstrates that *Edmontosaurus* teeth preserve 4 distinct sets of scratches in different orientations. In terms of jaw mechanics, these data indicate an isognathic, near-vertical posterodorsal power stroke during feeding; near-vertical jaw opening; and propalinal movements in near anterior and near posterior directions. Our analysis supports the presence of a pleurokinetic hinge, and the straightness and parallelism of scratches indicate a tightly controlled occlusion. The dominance of scratched microwear fabrics suggests that *Edmontosaurus* was a grazer rather than a browser.

Cretaceous | Ornithopoda | tooth | trophic ecology | Vertebrata

Reconstructing the feeding mechanisms and details of trophic ecology of extinct animals based on functional morphology is fraught with difficulty (1). In vertebrates, tooth form provides only a general guide to diet: the same tooth form can serve more than one function, and that function can vary with specific feeding behavior. Further complications arise because functional optimization of tooth form can be constrained by the need to process fallback foods during times of resource scarcity (2), and animals with an apparently specialized feeding apparatus can have generalist diets (3). These problems are especially acute in groups like herbivorous, nonavian dinosaurs, where most species have generalized homodont dentitions and lack close living analogues.

Among herbivorous dinosaurs, feeding of hadrosaurids has attracted particular attention. They were the dominant herbivorous vertebrates in many Late Cretaceous ecosystems, in terms of both species richness and abundance, and they achieved a near-global distribution (4, 5). This success is frequently attributed to the complex jaw mechanisms possessed by these taxa, which would have given them a level of masticatory prowess equal to that of many extant mammals (6). Current models of feeding mechanisms in hadrosaurid dinosaurs are based on analyses of functional morphology and rely on interpretations of musculature rather than direct evidence. No extant species has a sufficiently similar skull morphology to act as a convincing

functional analogue, and no fossil evidence exists to show the size and shape of the interarticular fibrocartilages and the limitations these would have placed on jaw motions. Here, we present the results of quantitative tooth microwear analysis of a hadrosaurian dinosaur, and we demonstrate how these provide a robust test of functional hypotheses.

Previous research into hadrosaurid feeding mechanisms reached contradictory conclusions. The extensive early work of Ostrom (7) suggested propalinal translation of the mandibles (an anteroposterior movement of the lower jaw during the power stroke). This was later questioned (8), and tooth wear was used to infer side-to-side (transverse) movements of the mandibles relative to the maxilla. Norman and Weishampel (6, 9–11) conducted kinematic and detailed functional anatomical analyses of all available hypotheses of hadrosaurid jaw mechanics and postulated a novel jaw mechanism, termed pleurokinesis. In this model, isognathic vertical adduction of the lower jaws generated a transverse power stroke. This was brought about by lateral rotation of the maxillae and suspensorium relative to the skull roof and driven by contact between the dentary and maxillary teeth during occlusion. Lateral rotation of the maxillae was accommodated by a pleurokinetic hinge (between the maxilla/jugal/quadrate and the akinetic skull) and was associated with slight propalinal movements caused by abduction and retraction of the quadrate (streptostylism). However, recent work involving 3D modeling of feeding kinematics in *Edmontosaurus* has suggested that pleurokinesis would generate extensive secondary (intracranial) movements beyond the pleurokinetic hinge (12). Testing of these functional models has been difficult because of the absence of direct evidence for the mastication process in hadrosaurids.

Quantitative analysis of tooth microwear offers a hitherto unexplored route to testing feeding mechanisms in nonavian dinosaurs. Microwear refers to the microscopic polished, scratched, or pitted textures produced *in vivo* by the actions of abrasives in food and by the compressive and shearing forces that act on teeth during feeding (13, 14). Quantitative analysis of tooth microwear is an extremely powerful tool and has been applied extensively to fossil primates and hominins to evaluate the role of dietary changes in human evolution (15, 16). Applied to extinct nonprimate mammals, quantitative tooth microwear analysis has also provided direct evidence of tooth use, diet, and feeding (13, 17, 18) and has revealed how feeding in ungulates has tracked past environmental change (19).

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Table 3. Data for transect across tooth 2 (class 2; 7 sites): means (μ) by site, mean of means, and 99% confidence interval

Site	1	2	3	4	5	6	7
Angular dispersal, R	0.995	0.995	0.975	0.996	0.998	0.977	0.970
Mean vector, μ	62.235	62.598	62.548	64.423	61.704	59.375	66.056

Mean of means, 62.702; 99% confidence interval, 58.28–67.16.

significantly different. The third test, using confidence intervals (CIs) calculated for the mean of mean angles (30, 31), yields correct results (i.e., the means of the 7 sites all fall within the 99% CI for the mean of means; see Table 3). This provides a less error-prone yet appropriately stringent statistical test, and we therefore used it for all subsequent testing of class mean orientations. Our analysis does not support the view advocated in previous analyses of microwear orientation data (16, 17, 27) that axial data (i.e., distributed through 0–180°) can be treated as linear data and subjected to linear statistical tests. This approach would have led us to wrongly reject the hypothesis that mean orientation does not differ between sites, and previous analyses of this type may have made similar errors.

Analysis of the within-tooth and between-tooth datasets (Table S1 and Table S2) reveals that overall, we can reject the hypothesis that data within classes for each site are uniformly distributed (i.e., they show a preferred orientation; Rayleigh uniformity test and Rao spacing test, $P < 0.05$). Of the 77 samples tested (4 classes, 20 sites, 3 sites with $n = 0$), there are only 3 exceptions to this result—a class 1 and a class 4 sample on tooth 2, and a class 3 sample on tooth 5—but in all 3 cases, the number of scratches assigned to the class that failed the test was 3 or fewer. Mean orientation for each class for each site does not differ significantly from the overall class mean (pooled data, all sites, all teeth; V test, $P < 0.05$).

For the within-tooth dataset (testing class 1 data from 11 sites, class 2 data from 11 sites, and so on for each of the 4 classes), only 2 between-site differences in mean orientation are significant [99% CI test; Fig. 1 and Table S1; we note, however, that like the analysis of the transect data, application of linear statistical tests, such as t tests or nonparametric Mann–Whitney/Wilcoxon tests, wrongly indicates highly significant differences ($P < 0.01$ for a large number of sites)].

In the between-tooth analysis, tooth-to-tooth variation in class mean orientation is significant in only 4 of the 38 samples (99% CI test; Fig. 1 and Table S2). Orientation does not vary significantly with distance from the posterior of the jaw, except for class 4, which exhibits a strong correlation (circular–linear correlation: $r = 0.72$; $P = 0.02$) (29, 32). For class 4 scratches, R exhibits a strong positive correlation with distance from the posterior of the jaw ($r = 0.9$; $P < 0.01$); for class 2 scratches, the correlation is also significant, but weaker and negative ($r = -0.65$; $P = 0.04$).

To assess variation between individuals, we analyzed teeth selected from an additional right maxilla, a left maxilla and a right dentary (with data from the left maxilla and right dentary suitably transformed; Fig. 1). This yielded comparable results to our previous analyses: scratches within classes have preferred orientations, and the mean orientation for each class from each site falls within the 99% confidence limits of the means of means calculated from both the between-tooth and the within-tooth datasets (Table S2).

Functional Interpretation and Discussion. Microwear on occlusal tooth surfaces is created by tooth-to-tooth and tooth-food-tooth contact during biting and chewing (14). Thus, by comparing our actual scratch data with the patterns predicted from the published models of jaw mechanics in hadrosaurids, we can provide a robust

test of the various functional hypotheses. Predicted microwear patterns are as follows: (i) Propalinal action (7) would have produced dominant scratch orientations near the horizontal (anteroposterior). (ii) Vertical adduction followed by a transverse (labiolingual) power stroke and slight propalinal action (11) would have produced dominant scratch orientations near 90° to the tooth row long axis (inclined in 3D at the same angle as the occlusal surface), coupled with less dominant, near-horizontal scratches. (iii) Secondary movements (disarticulation of the facial bones during the power stroke) and rotation of the mandibles about their long axes during occlusion (12) would cause scratch curvature and systematic variation in microwear scratch orientation: mandibular rotation (labiolingual, pivoting around the prementary) would lead to an increase in lateral movement (and, hence, systematic change in scratch orientation) distally along the length of the tooth row. Disarticulation of the facial bones would cause multiple changes in the relative attitude of the maxillae, leading to variations in scratch orientation across the surface of a tooth and between adjacent teeth.

How does the pattern of microwear in *Edmontosaurus* fit these predictions? That scratches occur as 4 distinct classes with significantly different orientations suggests a more complex jaw action than was initially anticipated or has been suggested by previous authors. The 4 classes reflect 4 distinct jaw motions: 2 around 20° from the long axis of the tooth row (classes 1 and 4), 1 at 110° (class 3), and the dominant pattern 60° from the axis (class 2). On the inclined plane of the functional surface of the tooth battery (50° slope, 7.5° rake relative to sagittal plane; refs. 5 and 7), these orientations equate to the following 3D axes (relative to anterior direction in horizontal plane): class 1 trends 11° and plunges 21°; class 2 trends 50° and plunges 45°; class 3 trends 121° and plunges 43°; and class 4 trends 164° and plunges 9° (see Fig. S2 for stereographic projection).

We interpret class 2 scratches as being formed during the power stroke, and that most food-processing jaw motions were in this direction; scratches in this class outnumber all other scratches [both combined (Table 1) and in all sites except 4 of the 23 sampled (Table S1 and Table S2)] and cut across microwear fabrics in other orientations because they are more deeply incised into the tooth surface (up to 3 μm deep). This indicates more frequent movements and higher forces. The orientation of this dominant microwear indicates that jaw closure was not brought about by pure vertical adduction (which equates to a trend of 82.5° and plunge of 50° on the occlusal surface). This steeply oblique motion with a posterior component was, however, much closer to the vertical adduction and/or lateral translation predicted by the pleurokinetic model than to propalinal movements (trending 30° off pure vertical adduction; Fig. S2). Other points of note are the straightness of class 2 scratches, their high degree of parallelism (high R values, increasing toward the jaw hinge), the lack of variation in mean orientation within a tooth, and the lack of significant variation in orientation along the length of the jaw (Fig. 1, Table S1, and Table S2). These data provide direct evidence that the leading edges of the maxillary and dentary tooth batteries were parallel during jaw closure (i.e., motion was not scissor-like) (33–35), and that jaw articulation was very tightly constrained.

Class 3 scratches, in contrast, vary more in mean orientation, both within and between teeth (Fig. 1, Table S1, and Table S2), and have lower overall *R* values (Table 1), indicating that this second steeply oriented oblique motion (trending $\approx 40^\circ$ off pure vertical adduction/lateral translation) was under looser mechanical constraint. This suggests that these scratches were formed during jaw opening. This is consistent with models of jaw opening in herbivorous reptiles (36).

Class 1 and 4 scratches are less frequent and were formed by propalinal action, but we are unable to determine whether scratches assigned to class 1 were formed during anteroposterior (palinal) or posteroanterior (proal) movement, and the same is true of class 4 scratches. That the orientation of class 1 and 4 scratches does not differ significantly between maxillary and dentary teeth indicates that they formed while the teeth were in occlusion. This evidence of propalinal movement, albeit weaker and less frequent, is somewhat surprising, given that enamel thickness (greater on the lingual margin of dentary teeth and on the labial margin of maxillary teeth) seems to be strongly adapted to the transverse power stroke, with thicker enamel on the leading edge of the teeth (11). The change in the orientation of class 4 scratches and the increase in parallelism along the length of the jaw indicate slight rotation of the tooth row and a greater freedom of movement at the back of the jaw during formation of these scratches.

Except for class 4, the lack of significant systematic variation in scratch orientation along the tooth row indicates that there was no marked long-axis rotation of the jaw element in the horizontal plane during feeding. However, the strong parallelism and straightness of the scratches, especially those in classes 1, 2, and 4, and the lack of variation, both within and between teeth, are not consistent with disarticulation of facial bones during jaw closure (12).

All but 3 of our sample sites were from dentine surfaces. It has been suggested that dentine microwear may be unsuited to quantitative analysis (37), but our results do not support this. Quantitative analysis of scratch orientations provides direct evidence of both steeply inclined and anteroposterior relative motion of the jaws during feeding. This confirms that the predictions of both Ostrom (7) and Norman and Weishampel (11) were correct in part, but our data provide direct evidence of high-angle oblique adduction and an isognathous oblique transverse power stroke, which is consistent with and supports the hypothesis of flexure along a pleurokinetic hinge. If class 3 scratches were formed in the way we suggest above, this lends additional support to the hypothesis, because it implies tooth-on-tooth contact during at least part of the jaw-opening phase of feeding.

In terms of our initial hypotheses, our results clearly demonstrate that in *Edmontosaurus*, teeth exhibit microwear that within classes does not differ between sample sites within the occlusal surface of a tooth, and differs little between teeth along a tooth row. We also found no significant differences between individuals. Perhaps surprisingly, our results indicate that the microwear in an area of 0.1 mm² provides a reasonably representative sample of the whole tooth as well as the whole jaw, and thus provides reliable information about the diet and jaw mechanics of an individual animal. One important implication of this result is that microwear-based analysis of jaw mechanics in hadrosaurs could be carried out by using isolated teeth. Obviously, these are much more common as fossils than complete skulls or substantial parts of dentary and maxilla elements. Although relatively complete jaw elements provide a frame of reference for tooth orientation within the jaw and allow more detailed testing of mechanical hypotheses, being able to conduct microwear analysis based on isolated teeth hugely increases the potential database for such work.

In addition to providing robust tests of models of jaw mechanics, microwear is also informative with regard to diet. In herbivorous mammals, microwear textures in grazers (grass eaters) differ from

those of browsers (which eat less abrasive vegetation, such as leaves, as well as twigs) (38). If the same microwear–diet relationship holds true for herbivorous dinosaurs, the dominance of scratches and lack of pits on both the dentine and enamel of the teeth of *Edmontosaurus* indicate that they were grazers rather than browsers. Early grasses certainly existed in the Cretaceous (39), but it is unlikely that they were common enough to have formed a major part of herbivore diets, and it is tempting to conclude that if they grazed, *Edmontosaurus* fed on plant material with mechanical and abrasive properties similar to those of grass. There has been much speculation about the diet of herbivorous dinosaurs. Direct evidence from gut contents and coprolites (40–43) is rare and often tenuous but indicates a range of plant food materials, including hornworts, liverworts, lycopsids, ferns, horsetails, twigs, branches, needles, leaves, bark, fruit, and seeds. Of these, only the horsetails would appear to be sufficiently abrasive to generate the microwear patterns of a grazer (silica concentration in horsetails >25% dry mass; ref. 44). However, we cannot assume that silica phytoliths alone are responsible for tooth microwear, because there is evidence that heavily striated enamel surfaces in grazing mammals can be caused by high levels of soil ingestion (45). If they grazed on low-stature vegetation, this could also be case with *Edmontosaurus*.

Our results demonstrate that with appropriate statistical testing, microwear analysis of dinosaur teeth can provide robust tests of hypotheses of jaw mechanics and feeding mechanisms. More hadrosaurid specimens and specimens of other ornithomorphs need to be analyzed to determine how microwear varies within and between species, but morphological analysis suggests that hadrosaurs were ecologically comparable to modern ungulates (46). In mammals, microwear patterns can be associated with specific food plants and trophic niches (47–49): microwear has great potential for unraveling the mystery of dinosaur feeding mechanisms, diet, and trophic niche partitioning.

Materials and Methods

The teeth studied are from left and right maxillae and dentaries of the hadrosaurid ornithomorph *Edmontosaurus* sp. that were collected from the Lance Formation (Upper Cretaceous, late Maastrichtian) of Niobrara County, Wyoming (right maxilla NHM R3638, complete, with $\approx 70\%$ of full tooth row preserved; right maxilla NHM R3653, complete with full but damaged tooth row; left maxilla NHM R3654, preservation as R3653; right dentary NHM R3658, fragment). For details of specimen preparation and microwear data acquisition, see *SI Text*. All microwear features within each sampling area were recorded. All microwear was scored by the same operator (V.S.W.) to minimize operator error (25, 50). The software used to score microwear (51) produces overlay files of *x/y* coordinates. It also calculates summary statistics for feature length, width, and orientation, but these were not used in this study. Our analysis was based on raw microwear data extracted from Microware 4.02 (51) output as *x/y* coordinates and processed by using simple trigonometric functions in a database to derive the length, width, and long-axis orientation for every feature in a sample site. Length data were not normally distributed, and were therefore log-transformed before statistical analysis. Previous microwear analyses that have used mean scratch length have not taken this into account.

Statistical testing and analyses of microwear data were conducted by using JMP IN 5.1 (SAS Institute) and Oriana 2.02e software (52). DFA was performed to test the robustness of the allocation of data to orientation classes. DFA was first performed by using scratch length, count, angular dispersion, and orientation combined, and then by using orientation alone (the latter reported here). Within-tooth and between-tooth variation were also tested by using ANOVA and a variety of other statistical techniques. Orientation data are directional, and such data have statistical properties that differ from those upon which standard statistical tests are based. Consequently, our hypothesis testing used a number of tests specifically formulated for data of this kind.

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