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).

Fig. 1. Microwear in *Edmontosaurus*. (*A*) Orientation of functional surfaces (wear facets) on teeth, in approximate life orientation; diagrams below show these same 4 functional surfaces oriented with tips upward and viewed perpendicular to the occlusal plane. (*B*) Right maxilla, specimen NHM R3638, anterior to left. Vector plots indicate mean scratch orientation and relative length for each of the 4 classes in 10 teeth, line weight proportional to number of scratches. (*C*) Mean orientations for each class of scratches in each of the 10 teeth; for each class, the mean of the mean orientations with 99% confidence interval is shown. Dashed lines lie outside the confidence interval. (*D*) Second tooth from posterior (box in *B*). Vector plots indicate mean scratch orientation and relative length for each of the 4 classes in 11 sites, line weight proportional to number of scratches. Gray boxes show sites sampled for transect data (Fig. S1): 1 toward tip, 6 toward base; site 7 more basal than field of view shown. (*E*) One of the sampled areas (black box in *D*); diagonal lower right shows feature markup from Microware 4.0.2. (*F*) Mean orientations for each class of scratches in each of the 11 sites; for each class, the mean of the mean orientations with 99% confidence interval is also shown. Dashed lines lie outside the confidence interval.

Microwear analysis is starting to be applied widely to dinosaurs (20–23), and recent research on living and fossil fish suggests that quantitative microwear analysis has broad applicability beyond mammals (24, 25), but to date there has been no quantitative analysis of tooth microwear in dinosaurs. However, there are significant differences between dinosaur and mammal feeding mechanisms that make microwear analysis and interpretation more complicated. Dinosaur jaws articulate differently and lack the highly differentiated heterodont dentition of mammals. This means that, unlike mammals, comparison of functionally equivalent wear facets developed on homologous tooth cusps between different individuals and taxa is not possible. Another significant difference concerns tooth retention. In mammals, which retain their permanent dentitions until death, informative tooth wear forms over a short period relative to the functional life of the tooth. By contrast, dinosaurs, like other reptiles, shed and replaced their teeth continually, so the functional life of a tooth could be as short as a few weeks or months (26). Is that long enough for informative microwear patterns to develop?

This is just one of several fundamental questions that must be addressed before quantitative microwear analysis can be applied to nonavian dinosaurs. By definition, microwear analysis requires relatively high magnification of tooth surfaces and, consequently, samples data from small areas, only a few hundred micrometers across. Can such small areas provide data that are representative of microwear over the large functional surface of a dinosaur tooth battery? Given the lack of homologous facets, how do we sample microwear in dinosaurs?

Here, we test the null hypotheses that microwear does not differ between sample sites within the occlusal surface of a tooth and that microwear does not differ between teeth along a tooth row within an individual. We show that hadrosaurid dinosaur teeth have well-developed microwear signatures that allow us to conduct robust statistical testing of these hypotheses, and we demonstrate that quantitative microwear analysis can constrain details of jaw motions and provide robust tests of hypotheses of feeding mechanics in dinosaurs.

Results and Discussion

Microwear Patterns. Microwear was sampled from 30 sites on the occlusal surface of 13 *Edmontosaurus* teeth (see *Materials and Methods*). Visual inspection of micrographs clearly demonstrated that hadrosaur teeth do preserve microwear, confirming Weishampel's qualitative observations (10), with scratched textures dominating (we use scratches throughout this paper to refer to all microwear features on a tooth; no pits were detected). Scratches are not random, appearing to fall into a small number of classes, within each of which scratches are straight and subparallel, but with an orientation that differs from that of other classes.

To test the hypothesis that discrete classes of scratch exist, raw microwear data (2,588 features from 20 sites on 10 teeth from the same maxilla) were partitioned into 4 subsets (classes 1–4) based on visual assessment of scratch orientation. Fig. 1 illustrates these findings for a central site from each of 10 teeth along the tooth row ("between-teeth" analysis) and for 11 sites within one of those teeth ("within-tooth" analysis). Discriminant function

Table 1. Summary statistics from pooled raw microwear data (20 sites on 10 teeth on maxilla NHM R3638) partitioned into 4 classes based on feature orientation

Subgroup	Class 1	Class 2	Class 3	Class 4
No. of observations	300	1581	424	283
Angular dispersion, R	0.95	0.93	0.89	0.95
Mean orientation (mean vector, μ)	15.91°	63.29°	117.30°	164.57°
95% confidence interval for μ	±1.02°	±0.55°	±1.31°	±1.08°
99% confidence interval for μ	±1.35°	±0.72°	±1.72°	±1.42°
Mean scratch length, μm	72.33	52.85	54.75	70.85
Mean log scratch length, μm	4.04	3.74	3.74	4.02
Mean scratch width (microns), μm	1.59	1.68	1.54	1.42

analysis (DFA) provides strong confirmation that the microwear data fall into 4 distinct classes—98.3% of scratches classified by visual inspection were correctly assigned by DFA. Rather than conduct subsequent statistical testing on these imperfectly classified data, the DFA results were used to reassign the few incorrectly assigned scratches to their correct class (leading to 100% correct discrimination; see Table 1 for summary). Analysis of this dataset revealed significant differences in scratch count, orientation, length, and width between classes (Table 2). A test based on the mean of means (see below) also rejects the null hypothesis that scratch orientation does not differ between classes (99% and 95% confidence intervals; Table 1). We were unable to reject the null hypothesis that angular dispersal (i.e., the degree of parallelism of scratches as measured by R, mean vector length) does not vary between classes.

Pairwise comparisons (Tukey–Kramer honestly significant difference for linear variables, Watson–Williams F for axial variables) indicate that for the within-tooth data, orientation differs significantly between all classes, and that for length, all classes except 2 and 3 differ significantly ($P < 0.05$). For the between-tooth data, orientation differs significantly between all classes; length differs significantly except between classes 1 and 4, and between classes 2 and 3 ($P < 0.05$). Variation within class for both within- and between- tooth datasets is illustrated in Fig. 1 C and F.

Analysis of Microwear Orientation. Despite the increasing use of microwear analysis, there has been little discussion of analysis of

feature orientations and statistical hypothesis testing. A few authors have acknowledged that, strictly speaking, standard tests based on properties of linear distributions are not applicable to directional data (16, 17), but we are unaware of any analysis that has applied directional statistical tests to microwear data. Rather, nonparametric linear statistical tests have been applied, either with or without explicit justification (16, 17, 27). To determine how best to test our null hypotheses, we applied 3 different tests (1 based on linear distributions; 2 specific to axial data) to a set of class 2 scratch orientation data sampled from 7 sites along a straight line transect from tip to base of tooth 2 (Fig. 1 and Fig. S1).

Scratches are straight, and the data exhibit a consistently high degree of parallelism (i.e., angular dispersion as measured by mean vector length, $R > 0.97$; ref. 28), and the Rayleigh uniformity test along with the V test show the pooled data for the 7 sites to be nonuniformly distributed, with a significant mean orientation ($V > 0.96$; $P < 0.001$). Two alternative interpretations of these data are possible: either the samples are drawn from a single population of scratches that are straight, strongly parallel, and occur over the whole length of the transect (i.e., orientation is the same across the surface of the tooth), or the samples are drawn from multiple populations of scratches that differ slightly in orientation, but within which scratches are straight and parallel. For the purposes of this study, with controlled sampling across the transect, it is quite clear that the first of these hypotheses is the correct one; yet, two of the tests reject it (type 1 error): a nonparametric Wilcoxon test shows significant differences between the 7 samples ($P < 0.05$), as does the Watson–Williams F test (29), with pairwise testing indicating significant differences ($P < 0.05$) in mean feature angle in 10 of the 21 comparisons. Even when sites 1 to 4, which are close together and clearly the most similar, are compared, the Wilcoxon test finds significant differences between all of the sites except 1 and 2, and the Watson–Williams F test finds that site 4 differs significantly from sites 1 and 2. The results of this analysis indicate that when testing for differences in microwear scratch orientation between sample sites, the Wilcoxon and Watson–Williams F tests are susceptible to type 1 errors. Taken at face value, the results of these tests would lead us to reject the hypothesis that scratch orientations for the 7 sites are drawn from the same population (i.e., the tests wrongly indicate that their means differ), when in fact they are drawn from the same population and, in the context of this analysis, the means are not

Table 2. Results of null hypothesis testing for differences in microwear collected from 11 sites on 1 tooth (within-tooth; 8 dentine, 3 enamel sites, tooth 2) and from single sites on each of 9 teeth (between-tooth; all dentine) on maxilla NHM R3638

	Within-tooth			Between-tooth			Within-tooth, enamel			Within-tooth, dentine		
Null hypothesis	df	F	P	df	F	P	df	F	P	df	F	P
Orientation does not differ between classes (Watson–Williams F; W, B, WE, WD)	3,1446	3794.49	0.0001	3,1380	3119.81	0.0001	3,209	937.85	0.0001	3,1233	2918.10	0.0001
Log length does not differ between classes (1-way ANOVA; W, B, WE, WD)	3,1446	30.49	0.001	3,1380	12.11	0.0001	3,209	30.89	0.0001	3,1233	15.02	0.0001
R does not differ between classes (1-way ANOVA)	3,39	1.644	0.194	3,34	0.83	0.485	3,8	0.39	0.76	3,27	1.56	0.22
N does not differ between classes (1-way ANOVA; W, B, WE, WD)	3,39	16.48	0.0001	3,34	6.69	0.0011	3,8	6.52	0.01	3,27	23.28	0.0001
		χ^2			χ^2			χ^2			χ^2	
Width does not differ between classes (Kruskal–Wallis 1-way; W, B, WD)	3,1446	19.27	0.0002	3,1380	19.54	0.0002	3,209	7.18	0.07	3,1233	17.93	0.0005

W, B, WE, WD in parentheses indicate for which dataset the null hypothesis is rejected ($P < 0.05$). W, within-tooth; B, between teeth; WE, within-tooth, enamel sites; and WD, within-tooth, dentine sites.

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 predentary) 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 ≈40° 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 ornithopods 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 ornithopod *Edmontosaurus* sp. that were collected from the Lance Formation (Upper Cretaceous, late Maastrichtian) of Niobrara County, Wyoming (right maxilla NHM R3638, complete, with ≈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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