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Inter- and intraspecific variation in theropod dinosaur dental microwear and its palaeoecological implications

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Abstract

Differences in skull and tooth morphology, stomach contents, and estimated bite force between medium-to-large sized (≥100 kg) predatory theropod dinosaurs have long been suspected to correlate with differences in their diets and dietary guilds (e.g., hypercarnivory, piscivory). However, excluding exceptionally rare specimens with associated stomach contents or coprolites, the diets and dietary guilds of these taxa can be difficult to infer in detail. To enable comparisons across a wider array of taxa, especially those lacking stomach contents, an accurate, reliable proxy for diet needs to be employed. Dental microwear texture analysis (DMTA) has been used to investigate the diets of extant and extinct diapsids through examination of micron-scale surface textures. Here, we present a pilot study to determine the utility of DMTA for assessing diet in theropod dinosaurs and whether single teeth can act as a proxy for microwear across the entire dentition. To accomplish this, we examined texture variation along the tooth row in four medium-to-large-bodied theropods: *Allosaurus*, *Ceratosaurus*, *Irritator*, and *Tyrannosaurus*. Our results suggest that tooth position does affect DMTA and therefore DMT samples should be constrained using the following three guidelines: teeth should be sampled from within a single cranial element (premaxilla, maxilla or dentary); if comparing across elements, samples should be constrained to a single side of the teeth (labial or lingual); and comparisons across the labial surfaces of the dentary and maxillary teeth should be avoided. Our findings imply that taxonomically distinct isolated theropod teeth can be used to infer the dietary ecology of theropod faunal assemblages if constrained sampling occurs.

KEYWORDS

dental microwear, palaeoecology, theropod dinosaurs, *Tyrannosaurus*

1 | INTRODUCTION

Theropod dinosaurs exhibit substantial interspecific variation in tooth and jaw shape (Hendrickx et al., 2015), skull morphology (D'Amore et al., 2024; Foth & Rauhut, 2013; Henderson, 2003; Sakamoto, 2010), and estimated bite force (Monfroy, 2017; Rayfield, 2011; Sakamoto, 2022). This morphological and functional diversity is thought to be associated with, but not the exclusive cause of, dietary variation, enabling ecological niche partitioning between taxa within ecosystems (Amiot et al., 2010; Bakker & Bir, 2004; Hassler et al., 2018; Rauhut et al., 2016). Sympatry of multiple medium-(100–1000 kg) to-large-sized (>1000 kg) faunivorous theropods has been documented in many Mesozoic terrestrial ecosystems (Benson et al., 2018; Holtz, 2021; Schroeder et al., 2021). Notable examples include the Upper Jurassic Morrison Formation of North America (six medium-to large-sized theropod species [Whitlock et al., 2018]), the Upper Cretaceous Bahariya Formation of Egypt (>4 large species [Salem et al., 2022]), and the Upper Cretaceous Candeleros Formation of South America (at least six medium-to-large-sized theropod species [Canale et al., 2016]). These diverse theropod faunas raise questions about how these sympatric species partitioned food resources.

Observations of modern African mammalian predators demonstrate the effectiveness of resource partitioning, including the use of different hunting techniques. For example, lions preferentially hunt wildebeest and zebra, but also hunt smaller, agile herbivores, like gazelles, and opportunistically hunt larger herbivores, such as buffaloes or giraffes (Owen-Smith, 2021; Sinclair et al., 2003; Vogel et al., 2019). Leopards, by contrast, generally prefer small antelope (e.g., gazelle, impala) and primates (Owen-Smith, 2021; Sinclair et al., 2003; Vogel et al., 2019). Such dietary separations reduce direct interspecific competition (Marshall et al., 2009; Owen-Smith, 2021; Sinclair et al., 2003; Vogel et al., 2019) and enable co-occurrence of these predators. Similar dietary considerations have not been evaluated for Mesozoic carnivore guilds outside of Cretaceous formations where spinosaurids are present such as the Elrhaz and Wessex formations, which indicated that spinosaurids utilize more aquatic prey compared to co-occurring non-spinosaurid theropods (Amiot et al., 2010; Hassler et al., 2018).

Various quantitative analyses have been employed to constrain the diets of non-avian dinosaurs. Dietary partitioning has been demonstrated among sympatric hadrosaurids, ceratopsids, and ankylosaurids through a combination of vertical feeding range and two-dimensional dental microwear (Mallon & Anderson, 2014). Further, isotopic analysis of carbon, oxygen, and strontium has been used to support partial niche partitioning in ornithischians (Cullen et al., 2022), and stomach contents and coprolites have provided direct evidence of the diet in predatory theropods such as *Baryonyx* (Charig & Milner, 1997), *Tyrannosaurus* (Chin et al., 1998), and *Gorgosaurus* (Therrien et al., 2023).

Although useful, the above-mentioned techniques cannot be broadly applied. Isotopic analyses are destructive and require large numbers of teeth to acquire statistically robust results and are therefore limited to highly fossiliferous sites. Furthermore, isotopic analysis provides robust information only on broad trophic levels and foraging habitats of taxa (e.g., freshwater versus brackish environments) rather than the utilization of specific foods (Cullen et al., 2020; Hassler et al., 2018). Stomach contents and coprolites provide direct evidence of diet, but such finds are rare, subject to taphonomic biases, and based on digestibility (Henry, 2012; Rawlence et al., 2016).

Vertebrate teeth usually contact food during feeding, causing chipping, scratching, and deformation of the enamel, which provides dietary information over timeframes intermediate between those recorded by stomach contents and stable isotope analyses (Bestwick et al., 2019; Bestwick et al., 2020; Kubo et al., 2023; Winkler, Iijima, et al., 2022; Winkler, Kubo, et al., 2022). Numerous studies have used two-dimensional dental microwear to determine dinosaur feeding behaviors (Fiorillo, 1998; Mallon & Anderson, 2014; Schubert & Ungar, 2005; Torices et al., 2018; Whitlock, 2011; Williams et al., 2009) but are subject to inter-observer variation, including but not limited to determining the qualitative differences between scratches and pits, alongside determining the relative orientation of features.

Dental microwear textural analysis (DMTA) is a non-destructive, potentially widely applicable quantitative method for determining diet in vertebrates (Bestwick et al., 2019; DeSantis, 2016; Winkler et al., 2019). DMTA of extant archosaur and lepidosaur teeth has shown that dental microwear textures (DMTs) are dependent on the material properties of consumed food items. At least six different dietary guilds have been correlated to DMTs based on extant archosaur and lepidosaur teeth: terrestrial vertivory; piscivory; herbivory; omnivory; soft invertebrate; and hard invertebrate-dominated diets (Bestwick et al., 2019; Winkler et al., 2019). Five sub-divisions of the aforementioned guilds have been described: algivorous; frugivorous; ovivorous (egg consumers); insectivorous; and molluscivorous (Winkler et al., 2019). The microwear textures of these extant reptilian taxa have been used subsequently to provide a comparative framework to constrain the diets of multiple groups of unrelated extinct reptiles, including pterosaurs, phytosaurs and mosasaurs (Bestwick et al., 2020; Bestwick, Jones, et al., 2021; Holwerda et al., 2023).

Theropod skulls are often fragmentary and incomplete: however, isolated teeth are relatively common. While this represents a powerful, previously untapped resource for collecting dinosaur dietary data, variation in DMTs due to both the location of the teeth within the jaw and sampling location must first be constrained. DMTA has been applied to both isolated and in situ teeth from non-avian theropods, where it was inferred that *Allosaurus* and tyrannosaurids consumed food items of similar material properties, with little evidence for osteophagy by tyrannosaurs contrary to previous hypotheses (Winkler, Kubo, et al., 2022). Indeed, while isolated theropod teeth have been used to infer diet (Winkler, Kubo, et al., 2022), this analysis was criticized for failing to account for tooth position. The impact of tooth position on DMTs has been demonstrated in extant taxa as well as extinct large-bodied phytosaurs and small-bodied pterosaurs (Bestwick et al., 2020; Bestwick, Unwin, et al., 2021), and DMTs have been used to assess interspecific variation in theropod teeth (Winkler, Kubo, et al., 2022). However, the impact of tooth position combined with tooth sampling location has never been fully constrained.

To utilize isolated teeth for DMTA it is imperative that isolated theropod teeth be taxonomically identifiable. The position of isolated theropod teeth can sometimes be identified (Hendrickx et al., 2023; Smith et al., 2005), and some theropod teeth can be identified to specific clades, if not a higher taxonomic level, using phylogenetic character state distributions, geometric morphometrics (Hendrickx et al., 2015) and machine learning approaches (Barker et al., 2024; Wills et al., 2021, 2023). These approaches, in combination with DMTA, could potentially allow dietary ecological comparisons within and between faunal assemblages, even when crania and other body fossil remains are rare or absent.

Here we assess the potential for using isolated theropod teeth based on tooth position and sampling location. We evaluate DMT variation between four medium-to-large-bodied theropod dinosaur species to determine which teeth can be used to reliably compare intra- and interspecific microwear variation in theropods. This work aims to provide a framework for future studies on dietary partitioning among sympatric theropods, as well as testing for intraspecific dietary variation (including spatial and temporal variation) and has the potential to be applied to other dinosaurian and non-dinosaurian clades, especially those known from only fragmentary or partial remains.

Institutional abbreviations:

BYU—Brigham Young University Museum of Paleontology, Provo, Utah, USA;
CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA;
SMNS—State Museum of Natural History Stuttgart, Stuttgart, Germany;
UMNHVP—Natural History Museum of Utah, Salt Lake City, Utah, USA.

2 | METHODS AND MATERIALS

2.1 | Study species and material sampled

A total of 91 microwear samples were taken from teeth that were in situ within the premaxilla, maxilla and dentary of specimens of four theropod species: *Ceratosaurus dentisulcatus* (UMNHVP 5278; premaxilla, maxilla and dentary [38 samples]); *Allosaurus fragilis* (BYU 6718901; premaxilla, maxilla and dentary [23 samples]); *Irritator challengeri* (SMNS 58022; maxilla [seven samples]); and *Tyrannosaurus rex* (CM 9380; maxilla and dentary [23 samples], NB, premaxillary teeth are not preserved in this specimen). These specimens were selected due to their accessibility, the relative completeness of their tooth rows, and the fact that they represent medium-to-large-bodied species of four distinct theropod clades (Ceratosauria, Allosauroidea, Megalosauroidea, Tyrannosauroidea). Where possible, microwear data were collected from every tooth with suitably preserved enamel. Microwear was only sampled from enamel as it is more physically and chemically resistant to post-mortem alteration than dentin, which has different material properties; thus, the microwear textures between the two would not necessarily be comparable even if the same foods were consumed (Haupt et al., 2013; DeSantis, 2016; Belmaker, 2018).

2.2 | Sampling strategy

Samples were acquired on both the lingual and labial sides of each tooth, where possible, from non-occlusal tooth surfaces, avoiding elliptical wear facets (as described by Schubert & Ungar, 2005), and from as close to the crown apex as possible. The following information was also recorded: tooth position as counted from the anterior tip of the skull (for *Irritator* this was from the first preserved maxillary tooth, as the premaxilla is not preserved), from which bone the tooth originated (i.e., premaxilla, maxilla or dentary), and the tooth surface from which the sample was taken (i.e., lingual or labial).

Teeth were cleaned using 98% ethanol-soaked cotton swabs (but if the specimen was covered in D72 consolidant, 99% acetone was used instead) to remove dirt and consolidants. High fidelity molds were made using President Jet Regular Body polyvinylsiloxane (Coltène/Whaledent Ltd., Burgess Hill, West Sussex, UK), which produces molds whose surface textures are statistically indistinguishable from those recorded on the original tooth surfaces (Goodall et al., 2015; Bestwick et al., 2019). Initial molds were discarded to remove any dirt not removed by cleaning, with all analyses taking place using the second mold, following prior work (e.g., Bestwick et al., 2019; Winkler, Kubo, et al., 2022; Kubo et al., 2023).

Although multiple specimens of each species would have strengthened the robustness of statistical analyses, it was not possible to gain access to suitable material due to specimen availability and logistical constraints. Although the *Allosaurus* specimen has teeth preserved in its dentary, these were inaccessible due to the close apposition of the upper and lower jaws, and it was only possible to collect one suitable dentary sample from this species.

2.3 | Surface data acquisition

Surface texture data acquisition from the dental molds followed standard laboratory protocols (Goodall et al., 2015; Bestwick et al., 2019). Data were captured using an Alicona Infinite Focus microscope G5 using a x20 objective lens, capturing a field of view of between 2 and 3 mm depending on the specimen size. Lateral and vertical resolutions were set at 880 and 300 nm, respectively. The scans were imported into MountainsMap premium 10.3.10908, first being mirrored on the Z axis, followed by selecting a 2 × 2 mm area to generate the International Organization for Standardization (ISO) surface parameters, avoiding non-dental microwear surface textures such as excessive dirt or mechanical preparation (Schulz-Kornas et al., 2020; Weber et al., 2021). A Gaussian filter was then applied to remove the surface form associated with the tooth shape (filter LSP 3), followed by anomalies above and below the 99.95% and 0.05% percentiles, respectively. This was followed by removing outliers and applying a filter to compensate for missing data. The surface textures were then extracted from this dataset, using a 0.8 mm Gaussian filter (see Figure 1). Twenty-eight International Organization for Standardization 3D texture parameters were calculated in this study (see Table S1).

All surface parameter data were log-transformed to reduce skewness and approximate normally distributed data. This resulted in the Ssk parameter (see Table S1) being excluded as it contained negative values that could not be log-transformed. For some samples, MountainsMap was unable to generate all parameters (see Table S1 for details) due to computational limitations. The remaining parameters were dimensionality reduced, combining them into principal components (PC) to enable a principal component analysis (PCA), using R v.4.4.1 (Wickham, 2016; R Core Team, 2020). To test if the microwear textures had surface parameters that are statistically significantly different, a Manova type II test was performed, as two or more variables (ISO parameters) may be dependent. Different combinations of teeth, varying by the tooth side sampled and cranial elements they belonged to, were tested (see Table 1) to determine the significance between the DMTs, and whether it would be possible to compare different combinations of teeth for diet and dietary guild comparisons. The Benjamini–Hochberg procedure was applied to account for false discovery rate (Benjamini & Hochberg, 1995).

3 | RESULTS

3.1 | Microwear descriptions

The microwear of *Ceratosaurus* includes limited scratches (<10% of the surface) on the majority of teeth: these scratches are fine and oriented mainly parallel to one another. On most teeth there is limited relief and few depressions are present, resulting in homogenous wear, with a few circular pits on some teeth. *Irritator* has the highest, on average, Sk, Smrk2, Spk, Vmc and Vvc parameters in the study (see Supporting Information for definitions of each parameter), suggesting that in some

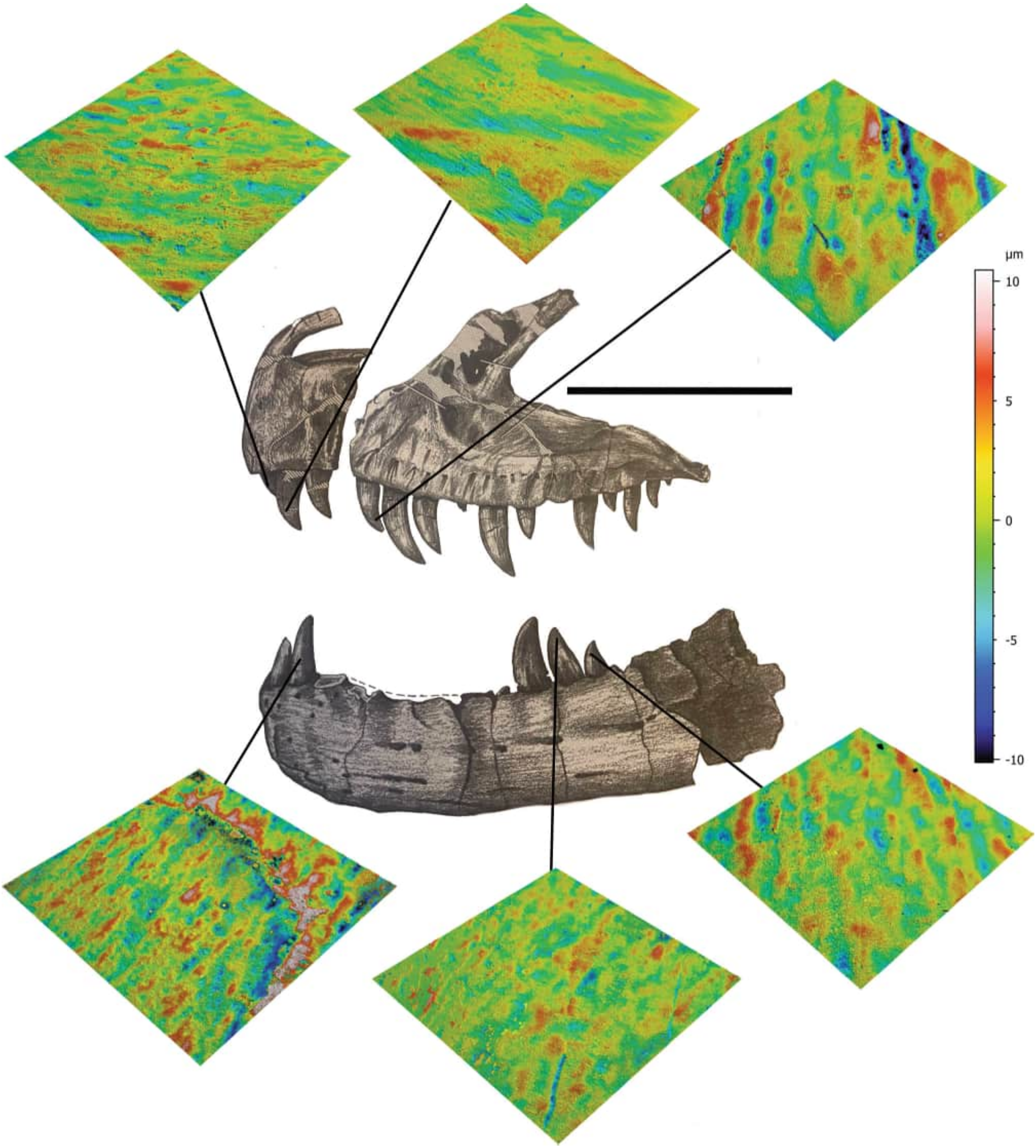

FIGURE 1 Tooth-bearing bones of *Ceratosaurus dentisulcatus* (UMNHVP 5278) with respective dental microwear textures for the labial surface of the premaxilla, maxilla and dentary teeth obtained using MountainsMap. Vertical scale bar is the topographical scale of the DMTs. The DMTs are 2 mm by 2 mm on the x and y axes. Horizontal scale bar equals 100 mm. *Ceratosaurus* images modified from Madsen and Welles (2000).

respects it has the most uniform microwear. *Irritator* has very fine scratches that are hard to distinguish and that cover <10% of the surface. These are mainly parallel to each other, with a few perpendicular scratches (<3% of the total number of scratches) to these. The textures for *Irritator* are primarily of low relief with shallow depressions, resulting in smooth and homogenous wear on most teeth. *Tyrannosaurus*, on average, has the highest

TABLE 1 Results summary of the PCA of ISO surface parameters and the Manova Type II tests to determine if there is significant variation in the DMTs of different teeth within the same specimen.

Test	Taxa	Cranial element where teeth were sampled	Tooth side sampled	*p*-values (overall)	PC 1, *p*-value	PC 2, *p*-value	PC 3, *p*-value	PC 4, *p*-value
1	*Ceratosaurus*	Premaxilla, maxilla and dentary	Both	**0.0004**	0.0846	**0.0001**	0.5823	0.5658
2	*Ceratosaurus*	Premaxilla, maxilla and dentary	Labial	0.0106	0.0773	0.0057	0.4904	0.4668
3	*Ceratosaurus*	Premaxilla, maxilla and dentary	Lingual	0.0060	0.6738	**0.0011**	0.2421	0.9704
4	*Ceratosaurus*	Premaxilla, dentary	Both	0.0071	0.0920	**0.0048**	0.9025	0.2392
5	*Ceratosaurus*	Maxilla, dentary	Both	**<0.0001**	0.2285	**<0.0001**	0.2426	0.1837
6	*Ceratosaurus*	Premaxilla, maxilla	Both	0.0108	0.1668	**0.0014**	0.6034	0.8586
7	*Ceratosaurus*	Premaxilla, maxilla	Labial	0.2726	0.0726	0.1862	0.7493	0.7128
8	*Ceratosaurus*	Premaxilla, dentary	Labial	0.0117	0.0710	0.0965	0.1140	0.3397
9	*Ceratosaurus*	Maxilla, dentary	Labial	**0.0004**	0.3315	**<0.0001**	0.6939	0.9749
10	*Ceratosaurus*	Premaxilla, maxilla	Lingual	0.0572	0.7830	0.0055	0.4765	0.5382
11	*Ceratosaurus*	Premaxilla	Both	0.2993	0.1217	0.2952	0.2752	0.9186
12	*Ceratosaurus*	Maxilla	Both	0.0190	0.7416	**0.0031**	0.3523	0.3392
13	*Ceratosaurus*	Dentary	Both	0.3165	0.4013	0.1657	0.3470	0.2935
14	*Ceratosaurus*	Premaxilla	Labial	N/A—Too few samples	n/a	n/a	n/a	n/a
15	*Ceratosaurus*	Maxilla	Labial	0.0261	0.9958	**0.0017**	0.8075	0.3671
16	*Ceratosaurus*	Premaxilla	Lingual	N/A—Too few samples	n/a	n/a	n/a	n/a
17	*Ceratosaurus*	Maxilla	Lingual	N/A—Too few samples	n/a	n/a	n/a	n/a
18	*Ceratosaurus*	Premaxilla, dentary	Lingual	0.0117	0.0710	0.0965	0.1140	0.3397
19	*Ceratosaurus*	Maxilla, dentary	Lingual	0.1198	0.4180	0.0071	0.8329	0.9733
20	*Ceratosaurus*	Dentary	Labial	0.6304	0.2264	0.4846	0.9425	0.3382
21	*Ceratosaurus*	Dentary	Lingual	N/A—Too few samples	n/a	n/a	n/a	n/a
22	*Irritator*	Maxilla	Labial	0.6062	0.7759	0.4713	0.6465	0.0959
23	*Allosaurus*	Premaxilla, maxilla and dentary (single tooth)	Labial	0.7880	0.7657	0.2130	0.8196	0.7090
24	*Allosaurus*	Premaxilla and maxilla	Labial	0.5389	0.7398	0.1114	0.5979	0.5559
25	*Allosaurus*	Premaxilla, dentary	Labial	0.6857	0.1348	0.8656	0.7777	0.6857
26	*Allosaurus*	Maxilla, dentary	Labial	0.6575	0.9536	0.3223	0.5873	0.6575
27	*Allosaurus*	Premaxilla	Labial	0.8326	0.3679	0.6156	0.409	0.4707
28	*Allosaurus*	Maxilla	Labial	0.5721	0.9647	0.5631	0.3841	0.1573

TABLE 1 (Continued)

Test	Taxa	Cranial element where teeth were sampled	Tooth side sampled	*p*-values (overall)	PC 1, *p*-value	PC 2, *p*-value	PC 3, *p*-value	PC 4, *p*-value
29	*Tyrannosaurus*	Maxilla	Labial	0.9038	0.6867	0.7375	0.3020	0.6628
30	*Tyrannosaurus*	Dentary	Labial	0.0512	0.0870	0.3825	0.0291	0.911
31	*Tyrannosaurus*	Maxilla, dentary	Labial	**<0.0001**	**0.0002**	0.0425	0.7984	0.2603

Note: Different samples with known locations were used to determine if a significant *p*-value was obtained or not. Values in bold are significant values after the Benjamini–Hochberg correction. See S3 for values after the Benjamini–Hochberg correction.

Smr, Spc and Spd parameters, which may contribute to the variation in the peaks and valleys present. The scratches on *Tyrannosaurus* are subparallel to each other, with a few forming an acute angle between these scratches and the subparallel scratches present. There is heterogeneity in the relief and variation in the depths of the depressions, resulting in heterogenous wear. Pits are present, but uncommon, and are circular to elliptical in outline. *Allosaurus* has the highest Sdq and Sdr parameters, on average. The scratches of *Allosaurus* are parallel to one another and some pits are present. There is a moderate difference in the relief, with some depressions, producing a heterogeneous microwear surface. There is a greater disparity in the relief and depressions between teeth of *Allosaurus* compared to specimens of the other three taxa.

3.2 | Statistical analysis and impact of tooth position sampling

In the results presented herein, if there is a significant *p*-value between different sampling locations in the same animal, indicating there are significant differences in microwear and such sampling locations cannot be used (or must be used with caution) as representative when comparing to other specimens or species for inferring diet because they vary within the individual. In cases where *p*-values are not significant, this indicates that there are sufficient similarities in the sampled microwear that dietary comparisons between individuals and taxa can be made in a meaningful way.

We found DMTs vary significantly within individuals based on cranial element, although inconsistently. For example, we found samples taken from either side of the jaw (labial or lingual) did not have a significant *p*-value within a single cranial element (premaxilla, maxilla, or dentary), independent of sampling location in any of the four taxa (see Table 1, tests: 10–15, 18–21, 22, 26–29), enabling dietary comparisons using the same cranial element. The lingual surfaces on the premaxillary, maxillary, and dentary teeth are similar enough to make comparisons as there is no statistically significant *p*-value between sampling locations of the different jaw elements when the lingual sides are sampled consistently, but not both (Table 1, tests: 10, 18, 19). Comparisons of the DMTs show that those in the premaxilla and maxilla are generally similar to each other (see Table 1, tests: 6, 7, 18, 24). The is no statistically significant result between the premaxilla and dentary when sampling irrespective of using the lingual and/or labial surfaces (Table 1, tests: 8, 18, 25). However, dentary and maxillary samples cannot be compared using their labial surfaces, as there was a significant *p*-value. DMTs show statistically significant *p*-values between maxillary and dentary teeth only when samples were collected from labial or both the labial and lingual surfaces, but not the lingual surface (see Table 1, tests 5, 9 and 31). Additionally, there are also visible differences between the four taxa when comparing the DMTs of their maxillary labial tooth surfaces.

The majority of the variation in DMTs is explained by the first four principal components (PCs), with the first PC accounting for the greatest proportion (between 46% and 63%) of the variation in the different analyses (see Figures 2 and 3). Parameters (see the Supporting Information for definitions of each parameter) most strongly correlated with PC1 are: Smr, Spd, Sal, Smr1, Sp, Sv, Sz, Vmc, Vmp, Vvc and Vvv (see Table 2 for full details). Among the different PCs, our results show that PC2 has significant separation in the variables driving it, although PC2 contains less variation (Table 1). The following ISO parameters show their greatest correlation with PC2 out of any PC (Table 2) across all four taxa when their labial premaxillary and maxillary DMTs are compared: Ssw is strongly negatively correlated; Smc, Spk, Sq and Svk are strongly positively correlated; and Sa, Sdc and Sk are very strongly positively correlated. Std has only a very weak positive correlation with PC2.

PC1 and PC2 explain over 70% of the surface texture variation for the sampled theropods. *Tyrannosaurus* occupies a distinctly different dietary texture space compared to the other three taxa, suggesting it has the most dissimilar food sources. PC2 has the most variation between individual teeth (Table 2), suggesting that PC1 vs. PC3 might be most useful in determining dietary texture-space intra- and interspecifically.

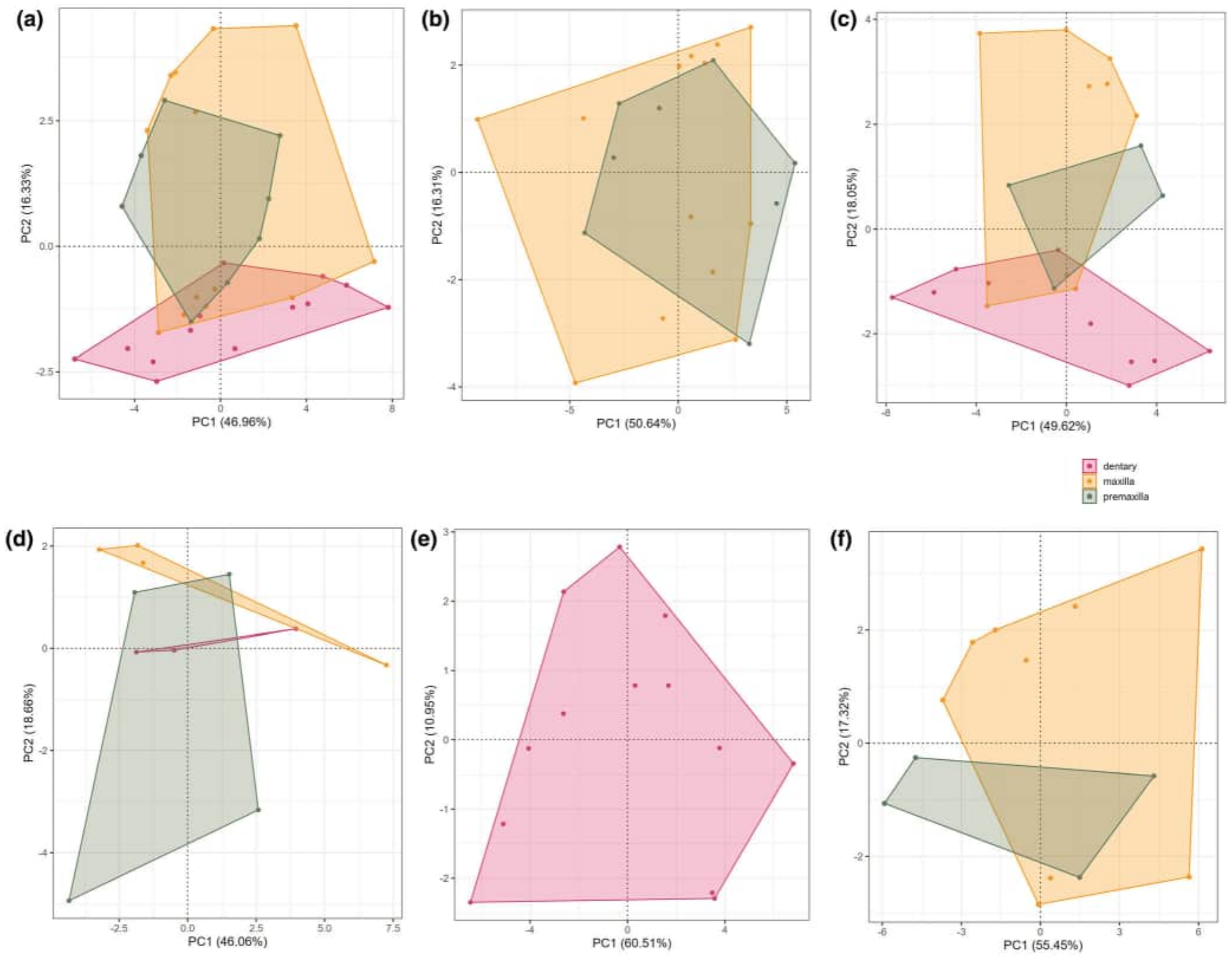

FIGURE 2 The principal component analysis of different samples from *Ceratosaurus* to evaluate if there is significant variation depending on sampling position. PC1 and PC2 are plotted as they compromise the majority of the data. Key, (a) All tooth samples, (b) All premaxilla and maxilla samples, (c) All labial samples, (d) All lingual samples, (e) All dentary samples, and (f) All labial premaxilla and maxilla samples.

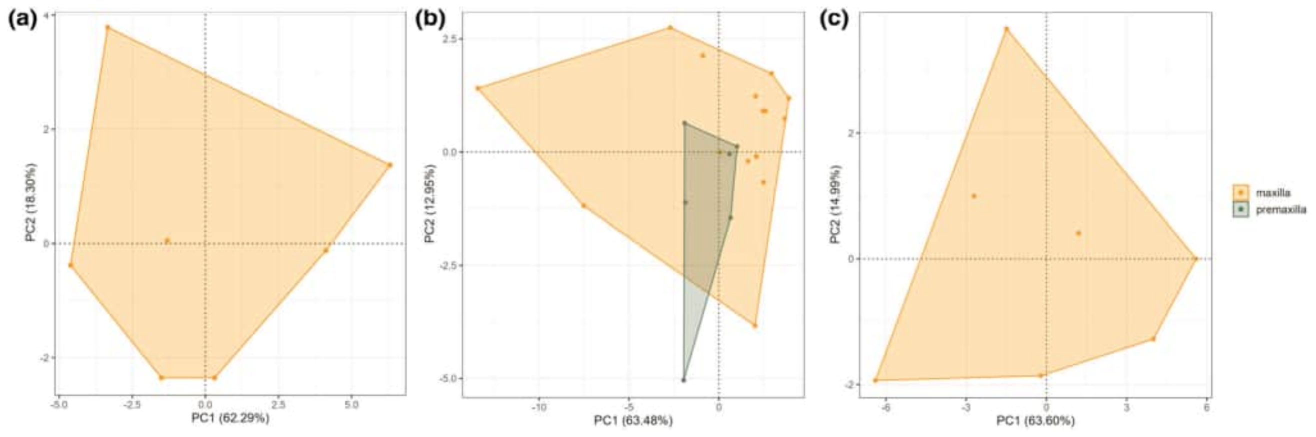

FIGURE 3 The principal component analysis for the maxilla of (a) *Irritator*, (b) *Allosaurus* (and premaxilla samples), and (c) *Tyrannosaurus* to evaluate if there is significant variation in the DMTs depending on sampling position. PC 1 and PC 2 are plotted as they comprised the majority of the data.

TABLE 2 The ISO surface texture parameters and their strongest correlation with different principal components and the strength of that correlation based on labial sides of the four theropod premaxilla and maxilla DMTs.

Parameter	Positive or negative correlation	Strength of correlation	PC2	*p*-value	PHO value
Sa	Positive	Very strongly correlated	2	>0.0001	0.8140
Sal	Positive	Moderate	1	0.0003	0.5656
Sdc	Positive	Very strongly correlated	2	>0.0001	0.8041
Sdq	Negative	Moderate	3	0.0004	−0.5503
Sdr	Negative	Moderate	3	0.0011	−0.5150
Sk	Positive	Very strongly correlated	2	>0.0001	0.8162
Sku	Negative	Moderate	3	0.0012	−0.5111
Smc	Positive	Strong	2	>0.0001	0.7956
Smr	Negative	Moderate	1	0.0013	−0.5067
Smrk1	Positive	Moderate	1	0.0001	0.5895
Smrk2	Positive	Strong	3	>0.0001	0.7170
Sp	Positive	Strong	1	>0.0002	0.6420
Spc	Negative	Strong	3	0.0001	−0.6081
Spd	Negative	Very strongly correlated	1	>0.0001	−0.7923
Spk	Positive	Strong	2	>0.0000	0.6772
Sq	Positive	Strong	2	>0.0001	0.7954
Ssw	Negative	Strong	2	0.0001	−0.6073
Std	Positive	Very weak	2	0.3219	0.1647
Sv	Positive	Strong	1	>0.0000	0.6284
Svk	Positive	Strong	2	>0.0001	0.6956
Sz	Positive	Strong	1	>0.0001	0.6960
Vmc	Positive	Very strongly correlated	1	>0.0001	0.9547
Vmp	Positive	Very strongly correlated	1	>0.0001	0.9150
Vvc	Positive	Very strongly correlated	1	>0.0001	0.9663
Vvv	Positive	Very strongly correlated	1	>0.0001	0.9796

Note: See Supporting Information for full details of the parameters and *p*-value after the Benjamini–Hochberg correction.

4 | DISCUSSION

4.1 | Implications for using isolated teeth to determine dietary category

Our results demonstrate that the DMT patterns between jaw elements rely heavily on the sampling location, indicating that teeth can only be compared following these three guidelines: (1) teeth from within a single cranial element (premaxilla, maxilla or dentary) can be compared; or (2) if comparing across elements, samples must be constrained to a single surface of the teeth (labial or lingual); and (3) comparisons between the labial surfaces of the dentary and maxillary teeth must be avoided. This is in addition to the standard protocol for sampling extinct reptile microwear (see Methods and materials: Sampling strategies for details). We encourage sampling as close to the apex of the tooth as possible, following previous work (Bestwick et al., 2019; Winkler et al., 2019). Our findings demonstrate that DMTA comparisons can be made both inter-and intraspecifically for the purpose of dietary guild and diet comparisons using the three guidelines.

Another consideration when sampling microwear that may not be as prominent in reptiles that are smaller than the medium-to-large-sized theropods sampled here, or where there are specimens with multiple teeth to choose from, is to avoid comparing newly erupted teeth where possible, as these teeth are less likely to have had the time and/or contact with food items to acquire the same microwear textures as fully erupted teeth. However, for determining dietary guilds rather than specific foods, the impact of such comparisons would be limited as dietary guilds are constructed from numerous food items within that guild as per Bestwick et al. (2019) and Winkler et al. (2019).

The difference between the maxillary and dentary teeth may be due to the processing of food or its acquisition, as there is variation in the DMTs of crocodilians (Bestwick, Jones, et al., 2021) due to different cranial elements processing the food substrate differently. It has been suggested that *Allosaurus* used its head like a hatchet (Rayfield, 2011), supporting different mechanical uses of the maxilla and dentary that would likely result in differences in microwear textures between these two cranial elements. This could potentially leave more abrasive microwear, such as greater peaks and valleys, in the maxillary teeth compared to the dentary teeth. Differences in the DMTs of the maxillary and dentary teeth of *Tyrannosaurus rex* could potentially support the puncture and pull mechanism proposed for feeding in tyrannosaurids (Snively & Russell, 2007a, 2007b). This implies that such mechanical use of the jaws for processing of food may result in the food substrate leaving different DMT signals between the maxilla and dentary.

Determination of the food items that produced the microwear could be accomplished by comparing the dental textures with specimens of these species that have stomach contents; however, this might provide a misleading interpretation if the stomach contents are substantially different from the food items normally consumed. This is because microwear captures diets over the timescale of months (Winkler et al., 2025), whereas stomach contents represent a single meal (or a small number of meals). A potentially better way to identify the food items producing the microwear in theropods would be a combination of work on modern analogues (sensu Bestwick et al., 2019, Winkler et al., 2019), preserved stomach contents, coprolites (if the maker can be positively identified), and isotopic analysis (Cullen et al., 2020; Norris et al., 2025) to assess the range, generality, and stability of the diet (Davis & Pineda-Munoz, 2016; Norris et al., 2025). In addition, differences between maxillary and dentary DMTs in theropods could be tested by biomechanical observations and comparisons with DMTs in modern crocodylians and varanids (Bestwick, Unwin, et al., 2021; Winkler, Iijima, et al., 2022), as the most suitable modern analogues to help infer how theropods might have used their jaws in the oral processing of food during consumption, and if there was any disparity between the upper or lower jaws.

4.2 | Taxon-specific implications

The four theropod taxa plot in different areas of dietary texture space (Figure 4), providing the potential to determine their diets by comparison with extant reptile taxa. In all three plots, *Tyrannosaurus* and *Irritator* show minimal overlap with other taxa, suggesting that their food sources are the most different. *Irritator* has been inferred as a facultative to obligate piscivore based on its cranial morphology and neuroanatomy (Schade et al., 2020; Schade et al., 2023), yet this behavior might not have been widespread among spinosaurids as there is evidence that they consumed a wide range of prey, including terrestrial prey such as dinosaurs and pterosaurs (Charig & Milner, 1997; Buffetaut et al., 2004; D'Amore et al., 2024). By contrast, adult *Tyrannosaurus* likely hunted large ornithischian dinosaurs based on coprolites and biomechanical modeling (Chin et al., 1998; Rowe & Snively, 2022). It has been suggested that *Allosaurus* preferentially predated juvenile sauropods (Hone & Chure, 2018) while *Ceratosaurus* may have had a broad, generalist diet including aquatic tetrapods, fish and dinosaurs (Bakker & Bir, 2004; Foster & Chure, 2006;

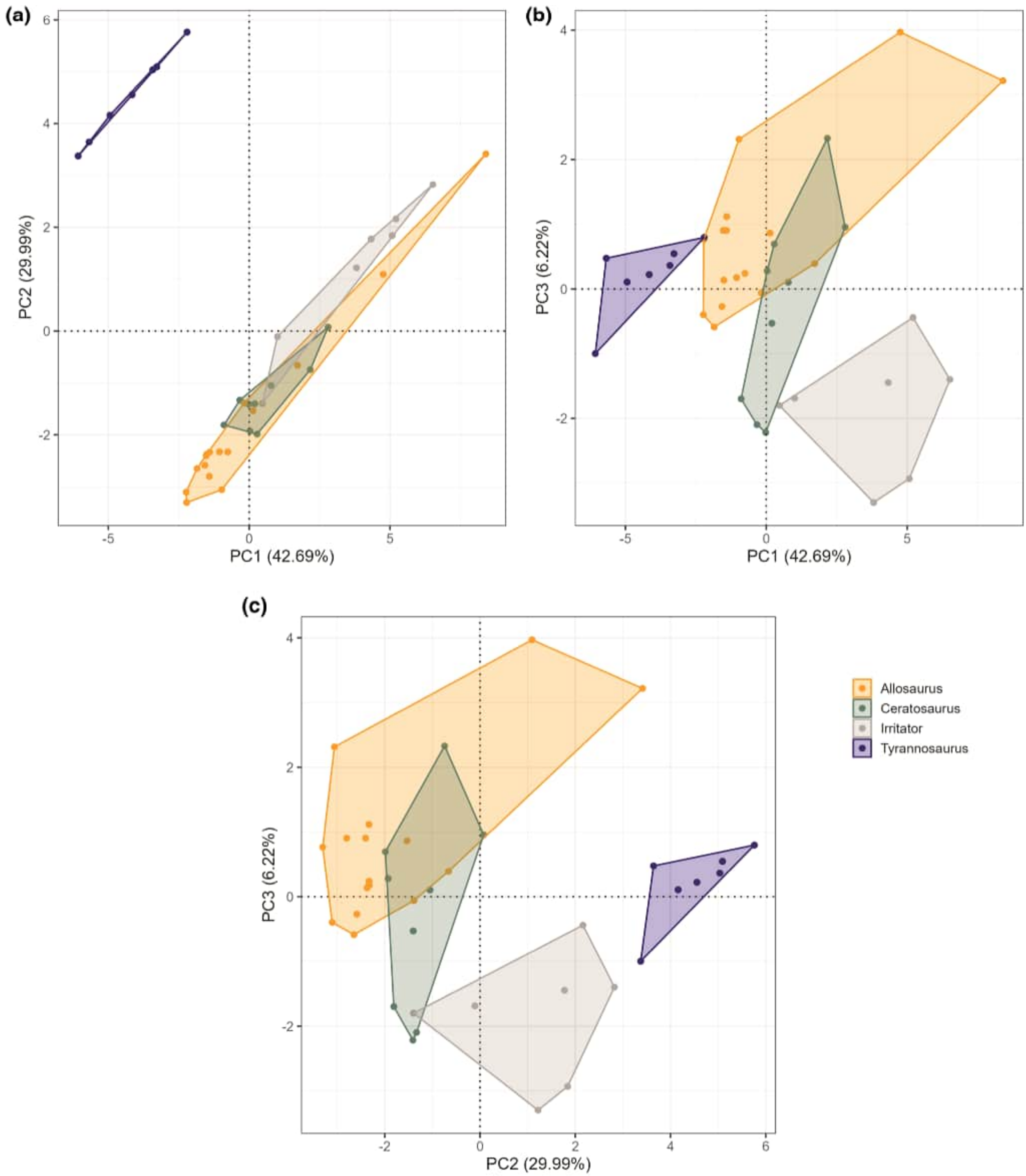

FIGURE 4 The PCs 1, 2, and 3 plotted for the four different theropod taxa using the labial sides of the premaxilla and maxilla.

Yun, 2019; Drumheller et al., 2020). Our results support such dietary differences due to disparity in dietary texture space (Figure 5), but robustly testing these disparities would require comparisons with extant archosaurs with known diets. The disparity in dietary-texture space may be due to prey utilization that could have varied inter- and intraspecifically, as different predators potentially consume different parts of the carcass, with those that consume the harder parts (e.g., bone) resulting in different microwear textures even though they may be feeding on the same types of animal(s) (Bestwick et al., 2019; Winkler, Kubo, et al., 2022). Additionally, as disparity in foods consumed among modern predatory taxa can vary due to seasonal food changes and differences between or

FIGURE 5 The four theropods featured in this study are included in this palaeoart reconstruction: *Tyrannosaurus*, *Irritator*, *Ceratosaurus*, and *Allosaurus*. Dental microwear texture analysis in conjunction with other proxies such as coprolites and isotopes, has the potential to determine the food items consumed by theropods that are only known from fragmentary remains or lacking exceptionally preserved stomach contents. From right to left, *Tyrannosaurus* hunting a *Triceratops*, with *Edmontosaurus* in the background representing the Hell Creek Formation. In the center, the spinosaurid *Irritator* is about to consume a fish, surrounded by pterosaurs and a crocodilian, illustrating some of the fauna of the Romualdo Formation. On the left, *Ceratosaurus* hunts a turtle, whereas *Allosaurus* captures a small *Apatosaurus*, where an adult Apatosaurus wanders in the background, representing various quarries of the Morrison Formation including Dry Mesa Quarry (Morrison et al., 2026). Artwork by Sergey Krasovskiy and Pedro Salas.

within populations (such as individual preferences or environmental pressures resulting in rarer foods being consumed), among other factors (Sinclair et al., 2003; Vogel et al., 2019; Owen-Smith, 2021), this has the potential to impact the microwear textures. The length of time a tooth has been erupted should also be considered, as this may impact the microwear signal; this could be mitigated by choosing teeth that have been erupted for similar lengths of time when making diet and dietary guild comparisons. However, this could be difficult to determine beyond identifying newly erupted teeth as, among theropods, tooth replacement rates vary between 56 days (e.g., *Majungasaurus*) to around 100 days (e.g., *Ceratosaurus* and *Allosaurus*) (D'Emic et al., 2019). Whereas the aforementioned factors may affect the microwear textures when trying to determine the specific foods consumed, exploring the broader dietary guilds of specimens should not be affected, as carnivory, piscivory, and insectivory, among other guilds, could be detected based on a range diets within each guild as per Bestwick et al. (2019) and Winkler et al. (2019), even if it is more difficult to elucidate the specific foods consumed by extinct taxa.

4.3 | Implications for palaeoecological reconstructions

Our findings imply that it is now possible to use DMTA to compare sympatric theropod diets from isolated teeth and fragmentary cranial remains, but only if sampling locations are constrained. If samples cannot be constrained to the lingual sides of isolated teeth, the isolated tooth must be confidently identified to a specific jaw element. This would allow for sympatric theropod diets to be compared in dinosaurian faunal assemblages such as the Kem Kem Group, and formations where articulated or semi-articulated remains are rare but fossilized teeth are preserved and common (Meso et al., 2024). Due to theropods producing a multitude of continuously replaced teeth, the ability to find their teeth is greater than the chance of finding more complete body fossils, as exemplified by the Tendaguru Formation that has yielded a plethora of theropod teeth from different stratigraphical horizons but very limited skeletal material (Rauhut, 2011).

5 | CONCLUSION

Our findings suggest that DMT sampling between teeth is possible with the three caveats: (1) sample teeth from a single cranial element (premaxilla, maxilla, or dentary); (2) constrain samples to a single side of the teeth (labial or lingual); and (3) avoid comparisons between the labial surfaces of dentary and maxillary teeth. These guidelines would enable dietary inferences to be made intra- and interspecifically using both isolated theropod teeth and teeth associated with cranial remains. The potential ability to make comparisons to infer diet or dietary guilds for theropod dinosaurs from isolated teeth, as also shown by Bestwick et al. (2019) for other extinct reptile taxa, enables theropod dietary guilds to be reconstructed and compared from sites that have limited articulated or semi-articulated remains, as well as for those clades that are poorly preserved and have a fragmentary fossil record such as Megaraptora and Noasauridae (Aranciaga Rolando et al., 2022; Mohabey et al., 2023).

AUTHOR CONTRIBUTIONS

Cassius Morrison: Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; project administration; formal analysis; data curation; validation; methodology; software. **James Gregory:** Methodology; software. **Christopher Jackson:** Methodology; software. **Jordan Bestwick:** Methodology; supervision. **Katlin Schroeder:** Methodology; supervision. **Samuel J. L. Gascoigne:** Methodology. **Paul Bills:** Methodology; software; supervision. **Laura B. Porro:** Supervision; writing – review and editing. **Philip D. Mannion:** Writing – review and editing; supervision. **Paul M. Barrett:** Writing – review and editing; supervision; methodology.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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