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First application of dental microwear texture analysis to infer theropod feeding ecology

by DANIELA E. WINKLER[1,2,4,6,*], TAI KUBO[3,5], MUGINO O. KUBO[4], THOMAS M. KAISER[2] *and* THOMAS TÜTKEN[1]

[1]Institute of Geosciences, Johannes Gutenberg University Mainz, Johann-Joachim-Becher Weg 21, 55128 Mainz, Germany; daniela.eileen.winkler@k.u-tokyo.ac.jp
[2]LIB – Leibniz Institute for the Analysis of Biodiversity Change, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany
[3]The University Museum, The University of Tokyo, Hongo 7-3-1, Bunkyo-ku, Tokyo 113-0033, Japan
[4]Department of Natural Environmental Studies, Graduate School of Frontier Sciences, The University of Tokyo, Kashiwanoha 5-1-5, Kashiwa, Chiba 277-8563, Japan; daniela.eileen.winkler@k.u-tokyo.ac.jp
[5]Marine Macroevolution Unit, Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna-son, Okinawa 904-0495, Japan
[6]*Current address:* Department of Natural Environmental Studies, Graduate School of Frontier Sciences, The University of Tokyo, Kashiwanoha 5-1-5, Kashiwa, Chiba 277-8563, Japan
*Corresponding author

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Abstract: Theropods were the dominating apex predators in most Jurassic and Cretaceous terrestrial ecosystems. Their feeding ecology has always been of great interest, and new computational methods have yielded more detailed reconstructions of differences in theropod feeding behaviour. Many approaches, however, rely on well-preserved skulls. Dental microwear texture (DMT) analysis is potentially applicable to isolated teeth, and here employed for the first time to investigate dietary ecology of theropods. In particular, we test whether tyrannosaurids show DMT associated with more hard-object feeding than compared to *Allosaurus*; this would be a sign for higher levels of osteophagy, as has often been suggested. We find no significant difference in complexity and roughness of enamel surfaces between *Allosaurus* and tyrannosaurids, which conflicts with inferences of more frequent osteophagic behaviour in *Tyrannosaurus* as compared to other theropods. Orientation of wear features reveals a more pronounced bi-directional puncture-and-pull feeding mode in *Allosaurus* than in tyrannosaurids. Our results further indicate ontogenetic niche shift in theropods and crocodylians, based on significantly larger height parameters in juvenile theropods which might indicate frequent scavenging, resulting in more bone–tooth contact during feeding. Overall, DMT is found to be very similar between theropods and extant large, broad-snouted crocodylians and shows great similarity in feeding ecology of theropod apex predators throughout the Jurassic and Cretaceous.

Key words: dental wear, diet reconstruction, microwear, DMTA, theropod, dinosaur.

THEROPODA were among the largest carnivores of both Jurassic and Cretaceous terrestrial ecosystems in North America. During the Late Jurassic, allosauroid theropods were widespread and abundant, with new findings suggesting that they probably remained as apex predators until the mid-Cretaceous (Zanno & Makovicky 2013) in these food webs. From the mid–late Cretaceous onwards, allosauroids had disappeared, and tyrannosaurids became the dominant apex predators. The iconic genera *Allosaurus* and *Tyrannosaurus* are amongst the best-documented dinosaurs, represented by multiple complete and partial specimens, including a range of ontogenetic stages. An ever-growing body of literature has reconstructed their dietary ecology, including bite force, feeding mode and biomechanics (Chin *et al.* 1998; Rayfield *et al.* 2001; Rayfield 2004, 2005; Snively *et al.* 2013; Gignac & Gregory 2017), ontogenetic niche shift (Carbone *et al.* 2011; Woodward *et al.* 2020) and tooth replacement (Erickson 1996; D'Emic *et al.* 2019).

Advances in imaging techniques and computational methods have helped our understanding of theropod palaeobiology to grow immensely over the past two decades. Finite element analysis (FEA) modelling led to picturing *Allosaurus* as a high impact 'slash-and-tear' (Rayfield *et al.* 2001) predator with a relatively weak bite force, relying more on an avian-raptor-like retraction of the skull after striking (Snively *et al.* 2013). Its skull was very strongly built and could resist high tensional stress, seemingly 'overengineered' for the assumed bite forces that could withstand the impact of upper jaw smashing, augmented by vertical neck motion (Rayfield *et al.* 2001; Rayfield 2004; Snively *et al.* 2013). *Tyrannosaurus*, on the other hand, was well adapted for extreme osteophagy, generating bite forces of up to 34 500 N (Gignac & Gregory 2017) or even more (Meers 2002; Therrien *et al.* 2005; Bates & Falkingham 2012), with an extremely robust skull and semi-conical teeth to withstand high

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pressure during feeding (Gignac & Gregory 2017). Bite marks on bones of several species (DePalma *et al.* 2013; Drumheller *et al.* 2020), including other tyrannosaurids (Bell & Currie 2010), and finely comminuted bone fragments in tyrannosaur coprolites, well document their capability and habit to process and ingest bone (Chin *et al.* 1998; Brusatte *et al.* 2010). On the contrary, for *Allosaurus* such behaviour is sparsely documented and highly unlikely due to its weaker bite (Rayfield *et al.* 2001; Snively *et al.* 2013). Still, there is one singular piece of evidence in the form of a coprolite composed of about 50% bone fragments from the Morrison Formation, that might be attributed to *Allosaurus* (Stone *et al.* 2000). As coprolites from the Jurassic are rare, the actual frequency of bone consumption in *Allosaurus* might be underrated.

Ontogenetic dietary changes in large theropods are very likely, as both allosaurids (Therrien *et al.* 2005) and tyrannosaurids undergo morphological changes, besides obvious body size increase, during ontogeny. Moreover, the absence of mesocarnivores (100–1000 kg) from ecosystems with megatheropods such as *Tyrannosaurus rex* supports the hypothesis that the mesocarnivore niche was filled by juvenile megatheropods (Schroeder *et al.* 2021). Especially in Late Cretaceous tyrannosaurids, juveniles were built lighter, and their skulls and teeth were less robust (Brusatte *et al.* 2010). Such dietary shifts are also common in extant reptiles, and often accompanied by morphological changes in the dentition. For example, juvenile American alligator (*Alligator mississippiensis*) and Nile monitor (*Varanus niloticus*) possess sharp, needle-like teeth, and primarily feed on insects (Gignac & Erickson 2015; D'Amore 2015). In contrast, adult alligators have broader teeth, which in combination with a strong bite allow them to tackle large mammals and even bite through bone. The adult Nile monitor dentition is adapted towards durophagy, with round, blunt teeth for crushing the hard shells of molluscs (D'Amore 2015).

Besides skeletal morphology, direct evidence of feeding behaviour is reflected in macroscopic and microscopic tooth wear. A methodology to infer feeding preferences, and thus also ontogenetic dietary differences, is dental microwear texture analysis (DMTA), which uses microscopic wear traces on teeth that result from contacts with ingesta (e.g. Scott *et al.* 2005; Schulz *et al.* 2010, 2013). Recently, it was successfully employed to detect the feeding preferences of extant reptiles (Bestwick *et al.* 2019; 2021; Winkler *et al.* 2019*a*), to trace ontogenetic dietary shift (Winkler *et al.* 2019*a*), and led to further resolving dietary preferences, including ontogenetic shift and dietary niche occupation over time, in pterosaurs (Bestwick *et al.* 2020). Enamel chipping and formation of distinct, macroscopic wear facets has been reported in tyrannosaurids (Farlow & Brinkman 1994; Schubert & Ungar 2005). However, in theropods, microscopic wear has only been used for reconstruction of the puncture-and-pull feeding mechanism (Torices *et al.* 2018). We therefore suggest that DMTA might be a useful additional proxy to validate palaeoecological reconstructions of theropod feeding behaviour, and test for ontogenetic differences.

As it was initially developed for mammals, most comparative DMTA data have been obtained for primates and ungulates (Merceron *et al.* 2005; Ungar *et al.* 2007; Schulz *et al.* 2010, 2013; Calandra *et al.* 2012; Scott *et al.* 2012; Winkler *et al.* 2013; Schulz-Kornas *et al.* 2019). However, DMTA was also found to be indicative of durophagy (i.e. bone consumption) in mammalian carnivores (DeSantis *et al.* 2013), where high complexity (*Asfc*) was observed in *Crocuta crocuta*, which exhibits high levels of bone consumption (osteophagy). This is in congruence with the highest complexity and roughness of enamel surfaces being observed in durophagous lepidosaurs that fed on molluscs (Winkler *et al.* 2019*a*) as well as extant 'harder' invertebrate-feeding crocodylians (Bestwick *et al.* 2019). Furthermore, this indicates that basic relationships between the material properties of ingesta and tooth wear are comparable between taxa with sophisticated mastication through heterodont, occluding dentitions (mammals) and taxa with more homodont teeth and lower degrees of oral food processing (most extant reptiles). More frequent osteophagy in tyrannosaurids should therefore potentially be detectable by DMTA.

In this study, we test the following hypotheses derived from assumed theropod feeding behaviour by using DMTA:

1. *Bone consumption*: Morphological and other evidence suggests that the diet of Late Cretaceous tyrannosaurids contained higher proportions of bone than that of Jurassic *Allosaurus fragilis* (Rayfield *et al.* 2001; Rayfield 2004; Bates & Falkingham 2012; Snively *et al.* 2013; Gignac & Gregory 2017). Previous work indicates that hard-object feeding produces deeper wear features and higher surface complexity (e.g. DeSantis *et al.* 2013; Winkler *et al.* 2019*a*), so we expect to see this in the dental microwear texture (DMT) of tyrannosaurid teeth.
2. *Feeding behaviour*: Tyrannosaurids and crocodylians are assumed to be more similar in feeding behaviour, showing lateroflexive shake-feeding, while *Allosaurus fragilis* defleshed a carcass by retraction of the head. Therefore, we expect direction-related DMT parameters to be more similar between extant large crocodylians and tyrannosaurids, with *Allosaurus* showing two predominant directions (for the slash-and-tear motion), while shake-feeding should result in more random wear feature distribution.

3. *Ontogenetic diet change*: Ontogenetic niche shifts observed in extant crocodylians should be reflected in DMTA. We expect smaller individuals that fed on a larger proportion of invertebrates, fish and small vertebrates to show less abrasive wear (as expressed in lower surface height, shallower wear features, lower complexity) as compared to larger individuals which fed on larger vertebrate prey, and probably performed more prey size reduction. For both *Allosaurus* and tyrannosaurids a dietary change during ontogeny can be assumed. Juvenile *Allosaurus* and tyrannosaurids (represented by *Tarbosaurus baatar*) are likely to have occupied similar niches, and we therefore expect them to show similar DMT parameter values, while adults should differ.

We concentrate on *Allosaurus fragilis* (as a representative of Jurassic allosaurids) from the Morrison Formation, and tyrannosaurids represented by Late Cretaceous *Albertosaurus* from the Horseshoe Canyon Formation, *Bistahieversor sealeyi* (formerly '*Albertosaurus*') from the Kirtland Formation (Carr & Williamson 2010), *Tyrannosaurus rex* from the Hell Creek Formation, and unidentified tyrannosaurids from the Fruitland Formation, Kirtland Formation, Kaiparowits Formation and Horseshoe Canyon Formation (see Table S1, raw data). These latter isolated teeth were tentatively assigned to the following tyrannosaurid genera/species based on the geological formations they were recovered from (see Table S1, raw data): *Bistahieversor sealeyi* (Kirtland FM and Fruitland FM), *Albertosaurus* (Horseshoe Canyon FM) and *Teratophoneus curriei* (Kaiparowits FM). Additionally, one juvenile specimen from each of *Allosaurus fragilis* (UMNH VP 9201) and *Tarbosaurus bataar* (MPC-D 107/7), (Tsuihiji *et al.* 2011) was analysed to assess ontogenetic niche shift in allosaurids and tyrannosaurids. We note that as neither adult *Tarbosaurus* nor juvenile North American tyrannosaurids were available, we assume that the juvenile *Tarbosaurs bataar* did not differ in feeding ecology from its North American counterparts. Two specimens of Triassic *Herrerasaurus* (PVSJ-53, MACN-18060) were investigated to compare feeding behaviour in a smaller, comparatively basal theropod (though its exact phylogenetic position is still unresolved, see Langer *et al.* 2010), that was occupying the niche of a large-bodied generalist predator in its Late Triassic ecosystem (Garcia *et al.* 2021). We compare theropod DMT to that of extant Crocodylia, because they are the extant archosaurs with the largest recorded bite forces measured among vertebrates (Erickson *et al.* 2003), and adults of several species can prey on large vertebrates. Several large crocodylian species can bite through bones leaving characteristic bite marks (Njau & Blumenschine 2006). Prey-reduction through lateral shake-feeding has also been observed (Drumheller *et al.* 2019), and the so called 'death roll', a spinning movement of the body to tear a carcass apart, is commonly employed for prey-size reduction in crocodiles and alligators (Fish *et al.* 2007, and references therein). Thus, crocodylians are, by both bite force and feeding behaviour, likely to be the most appropriate extant comparative taxa to theropods.

Most crocodylians are highly opportunistic predators and undergo drastic changes in their diet spectrum (and bite force) during ontogeny (e.g. *Crocodylus niloticus*: Cott 1961; Hutton 1987; Wallace & Leslie 2008; *Alligator mississippiensis*: Delany & Abercrombie 1986; Wolfe *et al.* 1987). There is clear correlation between body sizes of broad-snouted crocodylian species and their prey size. In contrast, body size does not affect prey sizes as much in slender snouted taxa (Drumheller & Wilberg 2020). To address these ontogenetic dietary shift patterns, and general ecomorphological differences in broad-snouted vs slender-snouted taxa (Brochu 2001; Drumheller & Wilberg 2020), broad-snouted crocodylian species examined here (*A. mississippiensis*, *A. sinensis*, *C. niloticus*, *C. porosus*) were grouped into two size classes based on their skull length (<20 cm, >20 cm). For the slender-snouted category, two large individuals of the gharial (*Gavialis gangeticus*) and two large individuals of the African slender-snouted crocodile (*Mecistops cataphractus*) were analysed. The gharial is often assumed to be a specialized piscivore due to its extremely elongated snout, while *M. cataphractus* seems to prey on a wider range of prey items. Still, for both species, at least occasional ingestion of diverse invertebrate and vertebrate prey has been recorded (see Drumheller & Wilberg (2020) for a concise report of dietary surveys and case studies).

DMTA comprises up to 50 surface texture parameters of different dietary discriminatory power. We follow the method described in Winkler *et al.* (2019*a*, 2019*b*, 2020*a*, 2020*b*) employing parameters implemented in MountainsMap (https://www.digitalsurf.com) from ISO 25178 (roughness), scale-sensitive fractal analysis (*Asfc*, *epLsar*), motif, furrow and isotropy which results in a total of 42 parameters (Table S3). However, as several parameters provide redundant information on surface topography, and in order to focus on functional interpretation, we concentrate on suitable parameters for each hypothesis.

MATERIAL AND METHOD

Experimental design

The dataset comprises a total of 48 specimens (Table 1; Table S1, raw data): 14 extant crocodylians and 34 theropods (either represented by isolated teeth or teeth from a jaw). Among the crocodylian specimens, 10 were wild caught with known provenance. The other four specimens are of unknown provenance but were collected or bought at the end of the nineteenth or beginning of the twentieth century (see Table S1, raw data). These historic specimens were probably also wild caught.

Institutional abbreviations. NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, USA; UMNH, Natural History Museum of Utah, Salt Lake City, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; RGM, Naturalis Biodiversity Center, Leiden, The Netherlands; SMA Sauriermuseum Aathal, Switzerland; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, Argentina; MPC, Mongolian Paleontological Center, Ulaan-baatar, Mongolia; MACN, Museo Argentino de Ciencias Naturales 'B. Rivadavia', Buenos Aires, Argentina.

Dental microwear texture acquisition

Crocodylian DMT data were obtained from moulds using a low viscosity moulding silicone, Provil novo Light CD fast set EN ISO 4823, type 3, light (Heraeus Kulzer GmbH), because specimens were too large to fit under the confocal microscope. We preferably measured at the most prominent caniniform (prey-seizing) tooth of the upper jaw, from the buccal side and close to the apex. For examples of obtained surface textures, see Figure S1. Theropod teeth were treated similarly: most specimens were moulded using Provil novo Light, while the two *Herrerasaurus* and the juvenile *Tarbosaurus* were moulded using President jet light body. While Provil novo Light has not been formally compared to other moulding materials, it has been used in a large number of studies including Schulz *et al.* (2010, 2013), Calandra *et al.* (2012), Winkler *et al.* (2013, 2019*a*, 2019*b*, 2020*a*, 2020*b*). The latter impression material has been found to show highest precision among low viscosity media (Goodall *et al.* 2015). Generally, low viscosity media have been found to reproduce surfaces with higher fidelity than high viscosity media. DMTA was measured close to the apex and in upper jaws from the buccal side for attached teeth (Fig. 1). However, as the majority of specimens were single, isolated teeth, assessment of tooth position, identification of buccal and lingual side, or assignment to upper and lower jaw was not always possible (Table S1, raw data). Each specimen is represented by only one tooth, with the exception of the juvenile *Tarbosaurus bataar* for which both an upper and lower tooth were moulded and scanned from the buccal side. For one specimen of *Herrerasaurus* (PVSJ53) the mould was taken from the buccal side of a central tooth from the left dentary and for the other *Herrerasaurus* (MACN18060) of

TABLE 1. Number of individuals of extant crocodylians and fossil theropods analysed for DMTA.

Crocodylia	14	**Theropoda**	34
Broad-snouted (<20 cm)		*Herrerasaurus*	2
Alligator mississippiensis	1	*Allosaurus fragilis*	
Alligator sinensis	1	Adult	6
Crocodilus porosus	2	Juvenile	1
		Albertosaurus sp.	11
Broad-snouted (>20 cm)		*Bistahieversor sealeyi*	9
Alligator mississippiensis	1	*Teratophoneus curriei*	2
Crocodylus niloticus	4	*Tyrannosaurus rex*	2
Crocodilus porosus	1	*Tarbosaurus bataar**	
		Juvenile	1
Slender-snouted			
Gavialis gangeticus	2		
Mecistops cataphractus	2		

The total number of specimens is given per group and separated according to species. Isolated teeth of Tyrannosauridae, which are listed as 'Tyrannosauridae indet.' in their respective museum collections (see Table S1, raw data), are tentatively assigned to a species.

*The juvenile tyrannosaurid has been described as *Tarbosaurus bataar* (MPC-D 107/7). One tooth per specimen was analysed, except for *Tarbosaurus bataar*, for which one upper and one lower tooth were included. Details of each specimen are given in Table S1 (raw data).

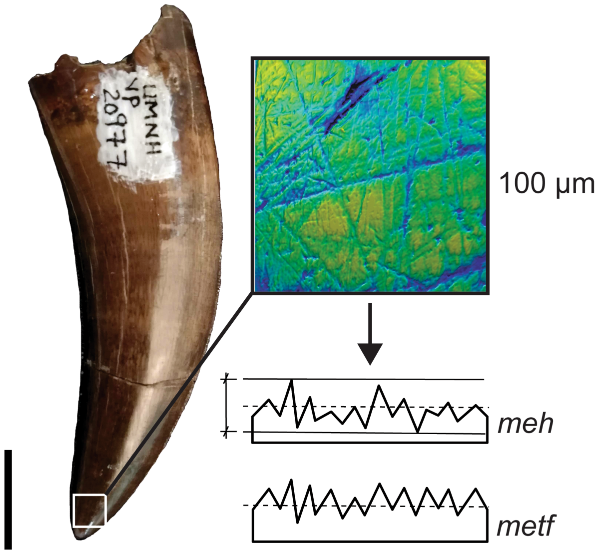

FIG. 1. Microwear texture data acquisition. Scans were taken close to the apex of the tooth. After applying a standard filtering procedure, 42 surface roughness parameters were generated in MountainsMap. The schematic drawings illustrate examples of wear parameters analysed: *meh* (mean height) and *metf* (mean depth of furrows). Tooth depicted is from an adult tyrannosaurid (cf. *Teratophoneus curriei*) UMNH VP 20977. Scale bar represents 10 mm. For a detailed parameter description, see Table S3.

the lingual side from the most prominent tooth of the right upper premaxilla.

Dental impressions, or original teeth if possible (for quality of each specimen, see Table S1, raw data), were scanned using the high-resolution confocal disc scanning measurement system µsurf Custom (NanoFocus AG, Oberhausen, Germany) with a blue LED (470 nm) and high-speed progressive-scan digital camera (984 × 984 pixel), set to a 100× long working-distance objective (resolution in x, y = 0.16 µm, step size in z = 0.06 µm). Areas of 100 × 100 µm were manually extracted from all original scans to reduce noise and excluded damaged surface parts. For each specimen, up to four single, non-overlapping scans were obtained (minimum number of scans: 3) and median values for parameters calculated. Example photosimulations of theropod enamel surfaces are shown in Figure 2. DMTA data for each scan is included in Table S1 (raw data); mean parameter values per species or category are given in Table S2.

We computed a set of 42 DMT parameters using MountainsMap Imaging Topography v9.0.9878. Data was processed employing the published filter routine for mammals (Schulz *et al.* 2013), using levelling, thresholding and de-noising median (5 × 5 filter size) and Gaussian filters (3 × 3 filter size). For other non-mammalian taxa (lepidosaurs), Winkler *et al.* (2019*a*) found the fourth order polynomial to provide better results than the default second order polynomial form removal. For theropods and crocodylians, however, the second order polynomial resulted in better discrimination between groups, thus we are here applying the more commonly used second order polynomial form removal. Templates of the filtering protocol are published in the Dryad Data Repository alongside the unfiltered 3D scan data of this study (Winkler *et al.* 2022). For further interpretation, we concentrate on evaluating selected parameters to answer the proposed hypotheses, detailed as follows.

Hypothesis 1. Parameters: *meh* (mean height), *metf* (mean depth of furrows), *Sq* (RMS surface roughness), *Sz* (maximum surface height) and *Asfc* (area-scale complexity). Parameters related to the overall height profile of the surface (including depth of furrows) are expected to be larger in species ingesting more bone and showing more prey processing behaviour. Large height parameter values were found in extant lepidosaurs to be related to hard-object feeding, but also in mammals feeding on abrasive diets (Schulz *et al.* 2010, 2013; Winkler *et al.* 2019*b*, 2020*b*). *Asfc* reflects the complexity of wear patterns and is known to be larger in species with frequent ingestion of harder objects, such as bone (DeSantis *et al.* 2013) or molluscs (Bestwick *et al.* 2019; Winkler *et al.* 2019*a*); it is also likely to reflect a more variable diet.

Hypothesis 2. Parameters: *Str* (texture aspect ratio) and *Tr1R* (first texture direction) to assess directionality of wear features. High directionality (indicated by $Str < 0.3$) would indicate a predominant movement during feeding (e.g. only lateral shaking) while low directionality ($Str > 0.5$) would indicate more random, or multi-phase mastication behaviour. *Tr1R* gives the most dominant direction of wear features in degree.

Hypothesis 3. Same parameters as for Hypothesis 1 but compared between ontogenetic stages of either crocodylians or theropods. For both Hypothesis 1 and 3, further height and volume parameters that are highly correlated are expected to show comparable trends (larger height and volume values when more bone or generally more abrasive diets are consumed). This would be in accordance with observations from mammals feeding on

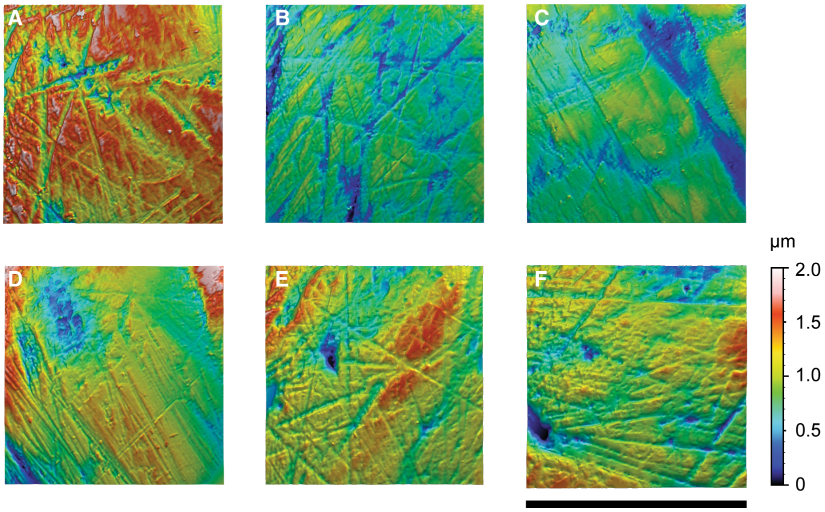

FIG. 2. Example 3D photosimulations of tooth enamel surfaces from representative individuals for each theropod group, including both juvenile specimens. A, *Allosaurus* (UMNH VP 5819). B, *Albertosaurus* (TMP1999.050.0098). C, cf. *Bistahieversor sealeyi* (NMMNH-P-27446). D, *Allosaurus* juvenile (UMNH VP 9201). E, *Tarbosaurus* juvenile (MPC-D 107/7). F, *Herrerasaurus* (MACN 18060). All images are to the same scale. Scale bar represents 100 µm; the size of each scan is 100 × 100 µm.

inherently abrasive (e.g. grass) and grit-loaded diets (Schulz *et al.* 2010, 2013; Winkler *et al.* 2019*b*, 2020*b*).

Statistics

Descriptive statistics were computed in JMP Pro v.16.0 and are given in Table S2. To facilitate interpretation, boxplots for all 42 DMTA parameters are included in Figure S2. A non-parametric, heteroscedastic pairwise comparison test (Wilcoxon test) was performed for all pairs in JMP Pro v.16.0 (this is comparable to the common procedure for DMT data described in Calandra *et al.* 2012; Schulz *et al.* 2013) (see Table S1, individual statistics for each parameter), as well as a principal component analysis (PCA) of 12 DMTA parameters (employing median parameter values per specimen) using correlations. This approach was applied because the dimensions of included parameters are on different scales, and covariances would be biased by parameters with larger dimensions. Factor varimax rotation was performed to facilitate interpretation of principal components. Appendix S1 includes an additional PCA (Fig. S3), which shows DMTA results for extant lepidosaurs from Winkler *et al.* (2019*a*) in comparison to the theropod and crocodylian data from this study. As lepidosaurs were found to show strikingly different DMTA results from both crocodylians and theropods, we do not discuss these data further, but would like to highlight that crocodylians are probably a more suitable extant comparison for theropod feeding ecology than lepidosaurs.

It has to be noted that the different number of comparisons conducted for testing each hypothesis will result in an increased type I error. Additionally, the small sample size does not allow for reliable statistical testing. Uncorrected *p*-values from the Wilcoxon test are nevertheless reported, to highlight potentially interesting dietary differences and hypotheses, but interpretation has to be undertaken with utmost care. Significances should be considered as tendencies expressed, rather than proof of statistically solid differences.

RESULTS

Principal component analysis

In addition to the six focal height and direction parameters *meh*, *metf*, *Sq*, *Sz*, *Asfc* and *Str* (texture aspect ratio), we included six more parameters of different functional categories (volume, slope, area) into a PCA (Fig. 3). Principal component 1 (PC1) describes increasing surface roughness and volume of surface features (Figs 3, 4F), while principal component 2 (PC2) describes distribution of wear features (complexity and uniformity of wear features, depth of furrows) with higher values indicating fine-scaled complex surfaces. PC1 and PC2 together account for 78.1% of the observed variance. Extant large broad-snouted crocodylians are separated from slender-snouted crocodylians along PC2, while small broad-snouted crocodylians overlap with both of the other crocodylian groups (Fig. 3; Fig. S3). The different adult tyrannosaurids and *Allosaurus* are not separated and overlap largely with extant large broad-snouted crocodylians (Fig. 3). *Allosaurus* is separated from large broad-snouted crocodylians along PC3, due to greater *Str* values. For depiction of PC2 vs PC3, see Figure S4. Generally, theropods show lower surface roughness (expressed in lower PC1) than the three crocodylian groups, but larger values than slender-snouted crocodylians along PC2. Juvenile theropods and *Herrerasaurus* are significantly different from several adult theropods in PC1 (Fig. 3) and fall within the overlapping space occupied by small and large broad-snouted crocodylians, and slender-snouted crocodylians, with *Herrerasaurus* being closer to small broad-snouted and slender-snouted crocodylians (Fig. 3; Fig. S3).

Bone consumption hypothesis

Parameter *meh* (mean height) was largest in broad-snouted crocodylians, and lowest in all adult tyrannosaurids (Table S2; Fig. 4C). This difference was significant for *Albertosaurus* (broad-snouted crocodylians (>20 cm): $p = 0.0312$; broad-snouted crocodylians (<20 cm): $p = 0.0182$) and *Bistahieversor* (broad-snouted crocodylians (<20 cm): $p = 0.0157$). All adult theropods, except *Herrerasaurus*, showed very similar mean height values. *Herrerasaurus* had overall larger *meh* values as compared to other theropods, but still lower than extant broad-snouted crocodylians. No significant difference was found between adult *Allosaurus* and adult tyrannosaurids. The distribution of maximum surface height (*Sz*) was the same as for *meh* (Fig. S3).

Crocodylians showed largest and highly variable *Sq* (RMS surface roughness) values (Table S2; Fig. 4B). The difference between small broad-snouted crocodylians and several theropods was significant (*Allosaurus*: $p = 0.0428$; *Albertosaurus*: $p = 0.0394$; *Bistahieversor*: $p = 0.0253$), and between large broad-snouted crocodylians and *Albertosaurus* ($p = 0.0312$).

Parameter *metf* (mean depth of furrows) was largest in large broad-snouted crocodylians (>20 cm), and significantly larger than in *Albertosaurus* ($p = 0.0307$) (Table S2; Figs 4, S2). For theropods, *Herrerasaurus*, *Allosaurus* and single individuals within *Bistahieversor* and *Albertosaurus* showed largest *metf*, but no significant differences between theropod groups were found.

Asfc (complexity) was smallest in slender-snouted crocodylians, *Herrerasaurus* and *Teratophoneus curriei*

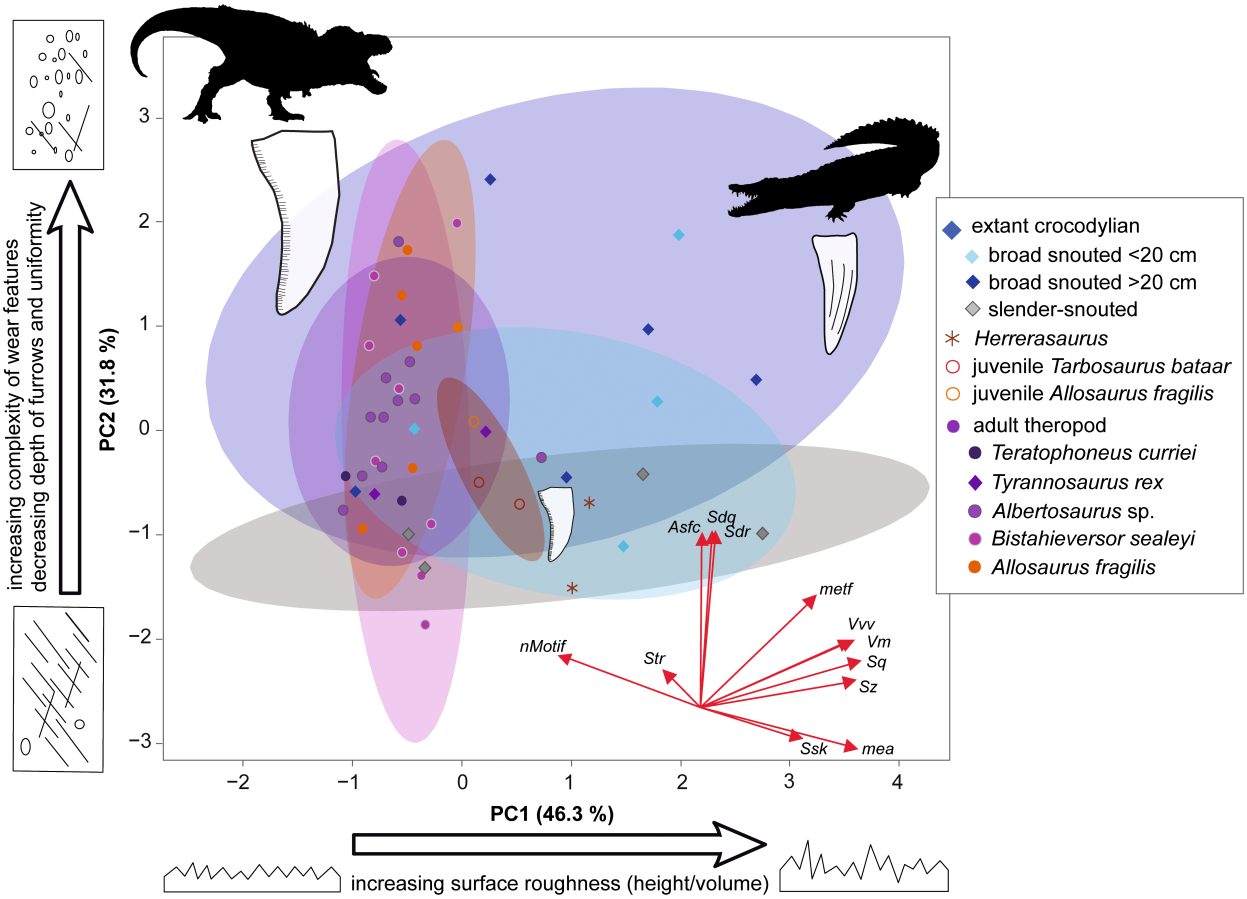

FIG. 3. PCA employing 12 DMTA parameters measured on enamel surfaces of extant crocodylians in comparison to those of fossil theropods. Coloured ellipses comprise 95% overlap with the DMTA parameter space occupied by adult tyrannosaurids (shades of purple), adult *Allosaurus fragilis* (orange), juvenile theropods (red), small broad-snouted crocodylians (light blue), large broad-snouted crocodylians (dark blue) and slender-snouted crocodylians (grey). PC1 indicates increasing surface roughness, PC2 distribution of surface wear features. Representative tooth morphologies of employed taxa are depicted roughly according to their sizes.

(Table S2; Fig. 4A). Large, broad-snouted crocodylians, *Allosaurus*, *Albertosaurus* and *Bistahieversor* showed high variability in *Asfc*. Significantly larger *Asfc* values were found for individual broad-snouted crocodylians of the larger size class ($p = 0.0252$), *Allosaurus* ($p = 0.0428$) and *Albertosaurus* ($p = 0.0157$) (all compared with slender-snouted crocodylians). Theropods displayed complexity values that fell within the range of extant Crocodylia.

Overall, height, volume, area, complexity and density parameters were comparable between *Allosaurus* and tyrannosaurids (Table S2; Fig. S2). Only for *S5p* (five-point peak height) and *Sku* (kurtosis of the height distribution) did *Allosaurus* show higher values than other adult theropods, but these differences were not significant. Extant crocodylians showed larger height and volume parameter values than theropods for most parameters. For *Sku*, small broad-snouted crocodylians and slender-snouted crocodylians had lower values than large broad-snouted crocodylians and theropods. *Herrerasaurus* had significantly larger height parameter values than adult theropods for *S10z* (ten-point height), *S5p* and *S5v* (five-point valley height). For closed dale volume (*Sdv*) and closed hill volume (*Shv*), *Herrerasaurus* displayed larger values than the other theropods, but also much larger variability for *Shv*. Area parameters were highest in crocodylians and *Herrerasaurus*, and similar between the other adult theropods. Density parameters showed the same range between crocodylians and theropods for *Sal* (autocorrelation length) and *medf* (mean density of furrows), while *Spd* (mean peak density) was generally higher in theropods than in crocodylians. *Herrerasaurus* showed significantly lower *Spd* and *medf* values as compared to other theropods (Fig. S2).

Feeding behaviour hypothesis

Str was very similar between broad-snouted crocodylians and adult theropods, except for *Allosaurus* (broad-snouted crocodylians (>20 cm): $p = 0.0202$; broad-snouted

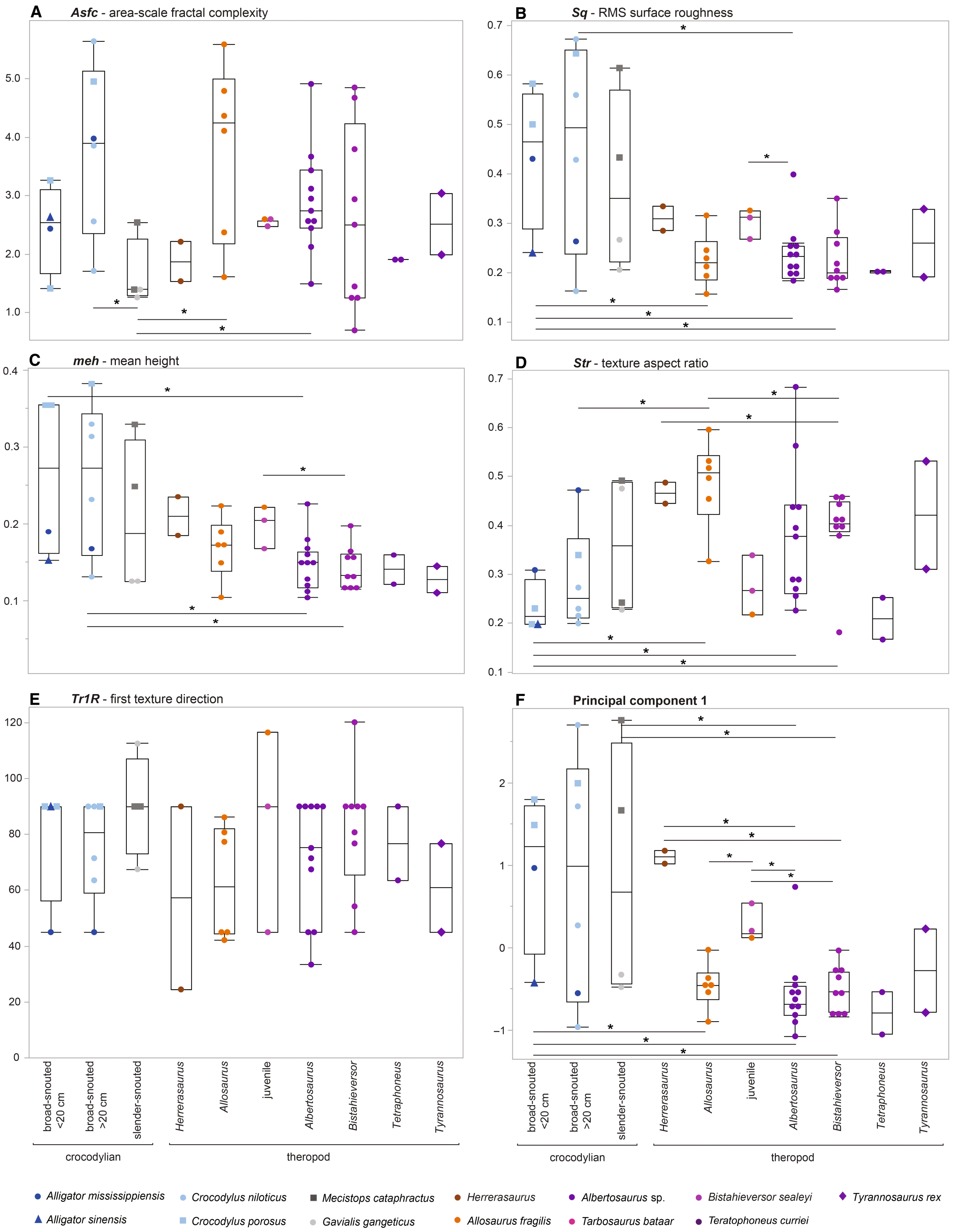

FIG. 4. Boxplots of selected DMTA parameters measured on modern reptilian teeth and fossil theropod teeth. A, *Asfc* = area-scale surface complexity. B, *Sq* = RMS surface roughness, vertical axis in μm. C, *meh* = mean height; vertical axis in μm. D, *Str* = texture aspect ratio. E, *Tr1R* = first texture direction, vertical axis in degrees. F, PC1. For detailed description of all DMTA parameters, see Table S3.

crocodylians (<20 cm): $p = 0.0142$; *Bistahieversor*: $p = 0.0392$), *Herrerasaurus*, and individual *Albertosaurus* specimens, which showed higher values (Table S2; Fig. 4D). *Teratophoneus curriei* had overall lower *Str* values, comparable to those of small broad-snouted crocodylians. For *Albertosaurus*, *Str* showed an almost bimodal distribution. The individuals with higher values more closely resembled *Allosaurus*, while the group with lower values more closely resembled small broad-snouted crocodylians.

The main texture direction (*Tr1R*) was similar between crocodylians and *Albertosaurus*, *Bistahieversor* and *Teratophoneus curriei*. *Herrerasaurus* and juvenile theropods showed extreme variability for *Tr1R*. *Allosaurus* (and the two individuals allocated to *Tyrannosaurus*) had lower mean *Tr1R*, but also a bimodal distribution of values *c.* 40° and *c.* 80° (Table S2; Fig. 4E). This bimodal distribution was also seen in *Std* (ISO-25178 texture direction) for *Allosaurus* but not for *Tyrannosaurus* (Fig. S2). Isotropy and anisotropy did not differ between *Allosaurus* and tyrannosaurids, but *Herrerasaurus* showed lower *epLsar* (anisotropy) values than other adult theropods (Table S2; Fig. S2).

Ontogenetic diet change hypothesis

For all three crocodylian groups, *meh* was more variable than in theropods. Therefore, no distinct trend of increasing values with body size could be seen. Juvenile theropods showed significantly larger *meh* values than *Bistahieversor* ($p = 0.0265$). Only *Herrerasaurus*, and single individuals of adult theropods reached *meh* values as high as juvenile theropods. *Sz* showed the same pattern, but large broad-snouted crocodylians had larger values than smaller broad-snouted crocodylians (Fig. S2).

A non-significant tendency of increasing for mean depth of furrows (*metf*) from smaller broad-snouted to larger broad-snouted crocodylians could be observed. For the related parameter maximum depth of furrows (*matf*), the increase from small to large broad-snouted crocodylians was significant ($p = 0.0252$). *Herrerasaurus* and juvenile theropods had slightly higher *metf* and *matf* values than most adult tyrannosaurids.

Asfc was lower in small broad-snouted Crocodylia (<20 cm) than in large broad-snouted Crocodylia. Slender-snouted crocodylians showed lowest complexity values, followed by *Herrerasaurus*. Juvenile theropods showed similar *Asfc* values as adult tyrannosaurids (Table S2; Fig. 4A).

Overall, juvenile theropods showed several significant differences to adult tyrannosaurids and *Allosaurus* in height, volume, area and density parameters (Appendix S1). Height, volume and area parameters were significantly higher than in tyrannosaurids and *Allosaurus*, while density (*Spd*, *medf*) parameters were lower, and thus more comparable to *Herrerasaurus* and extant crocodylians (compare Table S2; Fig. S2).

DISCUSSION

Theropod dietary ecology through the Mesozoic

DMTA of theropod dinosaurs and crocodylians reveals that feeding behaviour is more comparable between crocodylians and theropods than either are to lepidosaurs (Fig. S3). The two *Herrerasaurus* specimens (PVSJ-53, MACN-18060) show DMTs that are different from other adult theropods, and in the PCA they fall within the parameter space of small broad-snouted crocodylians and slender-snouted crocodylians (Fig. 3). Even though the basal theropod *Herrerasaurus* was the largest dinosaur of its Late Triassic fauna, and one of the specimens examined here is the largest *Herrerasaurus* specimen (PVSJ53, formerly known as *Frenguellisaurus*, now *Herrerasaurus ischigualastensis*), it was smaller than the other large bodied generalist predators of its ecosystem, the crocodylian-line archosaur *Saurosuchus* (Novas 1986). *Herrerasaurus* might therefore have filled a different ecological niche to the megacarnivores of the Jurassic and Cretaceous, and more frequently fed on smaller prey which was swallowed without much oral processing. That would be in line with the greater similarity to extant small broad-snouted and slender-snouted crocodylians. However, as these results are derived from only two *Herrerasaurus* specimens, this interpretation is very tentative and might need revision in the future.

Hypothesis 1: Bone consumption

Most adult tyrannosaurids as well as *Allosaurus* showed high variability in complexity of the enamel surface (*Sdr*, *nMotif*, *Asfc*). Large area-scale surface complexity (*Asfc*) is associated with high levels of bone consumption in mammalian carnivores (DeSantis *et al.* 2013) and was thus expected to also be indicative of bone consumption in theropods. Surprisingly, *Allosaurus* shows on average larger complexity values, with only some individuals of *Albertosaurus* sp. and *Bistahieversor sealeyi* reaching similarly high values (Fig. 4A). The two *T. rex* specimens are not characterized by particularly high complexity values; they fall within the mean for the other tyrannosaurids *Albertosaurus* and *Bistahieversor* (Fig. 3). The same high variability (and *Asfc* parameter range) is seen in extant broad-snouted Crocodylia of >20 cm skull length. Large crocodylians have the bite force to crush bone and leave bite marks on the skeletal remains of large vertebrates (Erickson *et al.* 2012, 2014). Smaller crocodylians probably ingested smaller vertebrate and invertebrate prey, that was swallowed whole without processing. Still, their opportunistic nature might result in them feeding on a variety of prey types, including more or less abrasive ones, and also result in some bone–tooth contact when feeding on small vertebrates. As bite force scales allometrically in crocodylians, and preferred prey size is dependent upon body size, smaller crocodylians may have bitten through (or into) the thinner bones of their smaller prey (Drumheller & Brochu 2014, 2016; Erickson *et al.* 2014; and references therein). Therefore, the range of complexity observed in this dataset may reflect infrequent bone crushing, and an opportunistic feeding behaviour in theropods similar to that seen in crocodylians.

Morphological and biomechanical evidence is unambiguous in assigning bone-crushing capacity to *Tyrannosaurus*, and not to *Allosaurus* (Rayfield *et al.* 2001; Rayfield 2004; Bates & Falkingham 2012; Snively *et al.* 2013; Gignac & Gregory 2017). Bite marks (Bell & Currie 2010; DePalma *et al.* 2013) and coprolites (Chin *et al.* 1998) further support this point. Still, this is only evidence that osteophagic behaviour occurred in *Tyrannosaurus*, but not that it was frequent. Only between 5% and 20% of carcasses are found to bear tooth marks (Jacobsen 1998). Such low frequencies suggest rare ingestion rather than deliberate bone consumption. In addition, it is known that coprolites with bone fragments have a much higher potential for preservation (Thulborn 1991; Barrios-de Pedro *et al.* 2018), which can result in a positive taphonomic bias for bone consumption. Studies of the diet of primates have shown that the biomechanical properties of teeth and skull were adapted to the hardest or toughest food, namely fallback food, in their diet and when softer and more nutritious food items are available, they feed on that (Marshall *et al.* 2009). This may also have been the case for tyrannosaurids. Bones were an occasional part of the tyrannosaurid diet, but this is not mutually exclusive with the hypothesis that they were opportunistic feeders, especially considering that they were often the only large terrestrial carnivore in their fauna. On the other hand, *Allosaurus* might not have been adapted towards bone-crushing, but may well also have scavenged if given the opportunity, or in a stressed palaeoecosystem where every available nutrient source would have been utilized, as inferred for the Upper Jurassic Mygatt–Moore Quarry (Drumheller *et al.* 2020). Singular evidence from one coprolite (Stone *et al.* 2000), as well as bite marks that may be attributed to *Allosaurus* (Fiorillo 1991; Hone & Chure 2018) further support this scenario. DMTA results do not allow us to extrapolate how often *Allosaurus* or other large theropods might have engaged in scavenging in other palaeoecosystems, however, infrequent bone-processing could be an explanation for the observed high complexity values in several *Allosaurus* specimens within our sample. Based on the results, we have to reject hypothesis 1 partially and rephrase it as follows:

> Morphological evidence (finite element analysis, tooth and skull morphology, bite marks) and coprolites show that Late Cretaceous tyrannosaurids possessed more specializations for osteophagy than the Jurassic *Allosaurus fragilis*. A larger proportion of hard-object feeding *could not* be inferred from DMTA through deeper wear features and larger surface complexity in tyrannosaurid teeth. Moreover, *Allosaurus* might have occasionally scavenged or bitten through bone, which might be reflected in higher surface complexity. We therefore assume that the analysed tooth specimens belonged to *Allosaurus* and tyrannosaurid individuals that engaged in similar, opportunistic feeding strategies before death, and similar levels of bone consumption.

We cannot predict how frequently tyrannosaurids actually processed bones, or in what situations: on every kill to salvage the whole carcass, or only when necessary, because the prey size was small, or while they were potentially occasionally scavenging (Hone & Rauhut 2009; Bell & Currie 2010; Carpenter 2013). Even though well capable of osteophagy, tyrannosaurids might not always have engaged in it (Hone & Rauhut 2009). Moreover, several tyrannosaurid tooth specimens with obvious mechanical damage are known (e.g. chipping, spalling, attritional wear facets Farlow & Brinkman 1994; Schubert & Ungar 2005). Such damaged specimens were excluded from the analysis because they were either missing a significant portion of the tooth, or because the enamel layer was completely abraded and only dentine left, making it highly unlikely that spots of enamel showing DMT would be found. However, exactly such conditions might be indicative of frequent osteophagy, thus potentially resulting in a sampling bias. Only well-preserved, mainly undamaged theropod teeth were analysed, thereby potentially excluding individuals with high levels of osteophagy.

Besides complexity, surface roughness is also expected to reflect dietary properties, especially abrasiveness, which would be expected to be larger in species consuming a larger amount of bones. When looking at parameters that can be informative on abrasiveness of the diet, such as RMS surface roughness (*Sq*), depth of furrows (*metf*), and maximum (*Sz*) and overall surface height (*meh*), no difference between tyrannosaurids and *Allosaurus* can be seen (Fig. 4, Fig. S3), which further supports the hypotheses above. Only *Herrerasaurus* was found to be significantly different from other theropods for several of these parameters, and in the combined PC1, which represents overall surface roughness (Fig. 3). Due to this similarity in parameter values, we would assume that all adult tyrannosaurids and *Allosaurus* analysed did not differ largely in their feeding behaviour, either because they resemble each other more than anticipated, or because the sample is already biased against individuals engaging in extreme osteophagy. In comparison to extant broad-snouted crocodylians of different size classes, theropods show relatively low surface roughness and furrow depth. This is unexpected, as the massive theropods are intuitively expected to show more dental wear than the smaller crocodylians due to the higher predicted bite forces of the former (Meers 2002; Therrien *et al.* 2005; Bates & Falkingham 2012). In addition, tooth replacement rates are faster in crocodylians than in theropods, which would result in crocodylian teeth experiencing less wear during their functional life span (Erickson 1996; D'Emic *et al.* 2019). Possibly, structural differences in enamel microstructure and thickness might also contribute to the observed differences in wear between theropods and crocodylians. However, Bestwick *et al.* (2020) showed that data obtained from species with very different enamel microstructure (bats, reptiles) both could provide a consistent framework using a multivariate approach for dietary inference in pterosaurs. Thus, the influence of enamel microstructure might be negligible.

It should also be noted that tooth position in crocodylians could be better controlled for than in theropods, where most specimens are represented by isolated teeth. Previous studies have shown that wear and usage of teeth is probably not homogenous along the tooth row in extant lepidosaurs and archosaurs, resulting in DMTA differences between tooth positions (Bestwick *et al.* 2021). Such a condition can also be expected for theropods and could influence variability of observed DMTA parameters in this study, thereby weakening discrimination of differences in their feeding ecology.

Hypothesis 2: Feeding behaviour

We expected to find indications for different feeding behaviour expressed by the parameter *Str* (texture aspect ratio). Smaller *Str* values indicate higher uniformity of surface texture (stronger alignment of wear features), while larger values indicate a more random distribution of features. Each phase of movement in feeding can produce a set of directional wear features, thus creating multiple directional sets, which may not be differentiable from a set of features with more random orientations. The inferences drawn from *Str* need to be considered cautiously, therefore we also evaluate the predominant direction of the observed wear marks *TR1R* (first texture direction).

Allosaurus is reconstructed as a puncture-and-pull feeder that defleshed a carcass by fast retraction of the head (Rayfield *et al.* 2001; Snively *et al.* 2013). The feeding motion therefore has two predominant directions: puncture and retraction. This bi-directional movement could lead to less overall parallel alignment of furrows as compared to crocodylians or tyrannosaurids, which are expected to engage more in lateral shake feeding (lateral shaking has been observed in alligators to detach small pieces from the prey; Fish *et al.* 2007). Large and small broad-snouted crocodylians showed lower *Str* values than *Allosaurus* and most tyrannosaurids, indicating stronger uniformity of wear features. Our data suggests that tyrannosaurids employed various methods to deflesh a carcass, indicated by the large parameter range seen for *Str*, especially for *Albertosaurus* sp. The point cloud even seems to separate into two parts for *Albertosaurus*, one exhibiting lower *Str*, the other higher *Str*.

Allosaurus, on the contrary, has overall higher *Str* values than tyrannosaurids. Wear features on *Allosaurus* teeth are thus less strictly aligned, which might indicate that both the initial puncture bite through flesh and the subsequent retraction of the head contribute to observed tooth wear, making it bi-directional. This is in accordance with observations from two dimensional microwear in several isolated theropod teeth, where scratches in two major orientations where observed (Torices *et al.* 2018), probably resulting from the puncture-and-pull-style feeding motion (Rayfield *et al.* 2001). When taking the first predominant direction of the surface texture (*Tr1R*) in *Allosaurus* into account, the analysed specimens seem to fall into two groups, one with a predominant direction of *c.* 40°, the other *c.* 80°. Tyrannosaurids show more individuals with higher values (*c.* 80°–90°), which is similar to extant crocodylians, but also several other predominant texture directions between 40° and 90° (Fig. 4E). Visualizations of surface scans for all *Allosaurus fragilis* and tyrannosaurid specimens analysed are included in the online repository, and confirm the impression of two predominant directions in *Allosaurus fragilis* (Winkler *et al.* 2022). For tyrannosaurids, both stronger aligned and more random wear feature distributions can be seen.

Even though individual manual alignment of teeth in DMTA hugely influences recorded texture direction, and therefore these parameters are seldom employed for further interpretation, it is striking how well these two predominant directions in *Allosaurus* match with those reported by (Torices *et al.* 2018). It is therefore plausible that in individual *Allosaurus* specimens, either the puncture or the pull motion left predominant furrows, while in tyrannosaurids their common feeding motions caused wear features aligned on various angles, but mainly higher angles.

Consequently, we partially accept hypothesis 2 and rephrase it to:

> Tyrannosaurids and extant crocodylians show more similarity in uniformity and orientation of wear features than *Allosaurids* and crocodylians. Overall, wear features show less directionality in *Allosaurus* than in tyrannosaurids and crocodylians. This might be due to lateroflexive shake-feeding being the predominant cranial movement in both tyrannosaurids and crocodylians, while *Allosaurus* engaged in two-directional puncture-and-pull feeding.

Hypothesis 3: Ontogenetic diet change

Several parameters indicate increasing dental wear in terms of increasing surface roughness (height and volume parameters) and depth of furrows between broad-snouted crocodylian size classes. This is in accordance with observed ontogenetic scaling of bite force (Erickson *et al.* 2012, 2014) and niche shifts in crocodylians (Cott 1961; Delany & Abercrombie 1986; Hutton 1987; Wolfe *et al.* 1987; Wallace & Leslie 2008), but other factors are also likely to influence microwear texture formation. Bestwick *et al.* (2021) found no simple relationship between bite force and DMT in crocodylians, but rather a complex interrelation between diet-related and non-dietary variables. We therefore accept part of hypothesis 3:

> Ontogenetic niche shifts observed in extant crocodylians are reflected in DMTA. We expect smaller individuals that fed on a larger proportion of invertebrates, fish, and small vertebrates to show less abrasive wear (as expressed in lower surface height, shallower wear features, lower complexity) as compared to larger individuals who fed on larger vertebrate prey, and probably performed more prey size reduction.

Slender-snouted crocodylians rely more on piscivory and showed lower height parameter values and significantly lower surface complexity (*Asfc*) as compared to large broad-snouted crocodylians (Fig. 4A). Overall lower surface roughness in piscivorous species was also observed by Bestwick *et al.* (2019) and seems to be a general characteristic of this diet. Still, for the broad-snouted <20 cm skull size group, parameter values were comparable in height and volume to the slender-snouted individuals. It is likely that this is due to the opportunistic feeding style of most Crocodylia, which brings diverse prey items into their diet, and indicates that smaller broad-snouted crocodylians might feed on overall less abrasive dietary items than larger broad-snouted crocodylians. Such a lower abrasive diet is more similar to the diet of slender-snouted (large) crocodylians analysed in this study. In agreement with previous observations (Njau & Blumenschine 2006), we would propose that a large proportion of small fish might make up the main diet for both smaller, broad-snouted crocodylians and the slender-snouted crocodylians. The PCA highlights the wide range of DMT observed in crocodylians (Fig. 3), as they occupy the broadest parameter space. If we consider the slender-snouted crocodylians in our sample as representative of a more piscivorous diet, then those individuals with similar DMT values can be interpreted as feeding primarily on fish before their death. Still this interpretation needs to be treated with caution, as the number of specimens in our sample is too small for statistical testing to be reliable.

Detection of ontogenetic dietary transition in extinct reptiles through DMTA was first shown by Bestwick *et al.* (2020) for pterosaurs. Similar to pterosaurs and extant crocodylians, theropods probably underwent distinct changes in bite force and prey spectrum during ontogeny (Therrien *et al.* 2021). Some young tyrannosaurids showed weaker skull morphology and lower bite force, and consequently had to pursue smaller prey than adults (Brusatte *et al.* 2010; Woodward *et al.* 2020; Rowe & Snively 2022). But why do younger individuals show relatively voluminous microwear features (Fig. S2, *Sdv*, *Shv*), larger surface height (Sz, *meh*), and generally higher surface roughness (*Sq*, PC1) that would intuitively be associated to harder, more abrasive diets, or maybe larger bite force? Large tyrannosaurids were single apex predators in their ecosystem and only faced competition from conspecifics of the same size. Even though they had the ability to crush bone (and did: Chin *et al.* 1998; Bell & Currie 2010; DePalma *et al.* 2013), it is not known if bone was a key component in their diet. Young tyrannosaurids and allosaurids might have had to ingest smaller prey, resulting in a higher frequency of bone ingestion, and feeding less selectively on the whole carcass. Moreover, juveniles might also have scavenged carcasses and scraped remaining meat off the bones, which they were not able to crush. It was predicted that the potential carcass search rates of smaller theropods are 14–60 times that of an adult *T. rex* (Carbone *et al.* 2011). Furthermore, modelling suggests that theropods between 27 and 1044 kg would have largely benefitted from scavenging (Kane *et al.* 2016). Scavenging on larger carcasses might thus have been frequent in younger theropods, and scraping off flesh from bones could be a major source of more voluminous wear features. However, based on the small sample size, these hypotheses remain rather speculative. We therefore tentatively accept and rephrase the remainder of hypothesis 3:

> For both *Allosaurus* and tyrannosaurids, dietary changes during ontogeny can be tentatively inferred. Juvenile *Allosaurus* and tyrannosaurids

(represented by *Tarbosaurus baatar*) are likely to have occupied similar niches, and show similar DMT parameter values that are significantly different from those of adult theropods.

Applicability and limitations of DMTA to infer theropod feeding ecology

Overall, microscopic dental wear traces were very similar between large Jurassic allosaurid and Cretaceous tyrannosaurid theropods, and both were comparable to those of extant crocodylians. The two basal Late Triassic *Herrerasaurus* fell within the small prey/piscivorous crocodylian parameter space. Under the assumption that the observed congruence in dietary signal as inferred from DMTA is not coincidental but reflects the conservation of dietary signals across significant temporal and phylogenetic distances, this indicates that diet-related DMTs on dinosaur (i.e. theropod) teeth can be preserved over millions of years (*c.* 230–66 Ma). If the mechanical wear induced by prey processing is similar between extant crocodylians and extinct theropods, we might infer analogies in feeding behaviour between these carnivorous archosaurs. In extant crocodylians, several DMTA parameters indicate ontogenetic niche differences by increasing surface wear along with increasing body size.

It has to be noted that the conclusions drawn from our data have to be treated with great care, as the sample size is very limited. Moreover, we cannot exclude the possibility that differences in enamel microstructure between groups (Crocodylia vs Theropoda) or species might affect formation of DMT. The composition of the dataset, which mainly comprises isolated theropod teeth but includes crocodylian teeth from complete jaws, adds more potential sources of variability to the data. While tooth position could be controlled for in crocodylians (by using the most prominent, caniniform tooth from the upper jaw), theropod samples are probably represented by different tooth positions, and upper as well as lower teeth. Even though both crocodylians and theropods, have overall homodont dentitions, some degree of heterodonty and tooth-position-specific functions exist in crocodylians: more anterior teeth are used for prey acquisition and dismemberment, while more posterior teeth are used for crushing (Cleuren & de Vree 1992, 2000; D'Amore & Blumenschine 2009). If we assume a similar feeding strategy and specialization of the dentition in theropods, tooth position may have an impact on DMTA, as has been shown for varanids and crocodylians (Bestwick *et al.* 2021). It would therefore be very important to test for dental wear gradients reflected in DMTA (Bestwick *et al.* 2021; Winkler *et al.* 2021) also in theropods. Still, for most parameters, we observed overall more variability in the crocodylian dataset, in which tooth position was controlled for, as compared to the theropods (Fig. 3). This is partly reassuring and suggests that a random tooth position sampling in theropods could be a viable option, as complete, articulated jaws are scarce.

CONCLUSION

Despite its limitations, our study provides preliminary mechanical wear evidence of younger theropods occupying different dietary niches to adult theropods, highlighting the potential of DMTA for assessing ontogenetic niche shift in theropods by application to more specimens. However, DMTA failed to detect different levels of osteophagy between *Allosaurus* and tyrannosaurids postulated by other studies. This could be due to a positive sampling bias, as only well-preserved tooth specimens were included in the analysis, or be attributed to some variation in tooth positions. However, these results might also indicate that bone consumption in tyrannosaurids was not frequent, and that *Allosaurus* was also capable of processing bone, which could explain the observed high wear pattern complexity. For future studies, it would be interesting to obtain DMTs from well-preserved enamel patches of tooth specimens with heavy wear marks. Despite this potential sampling bias, we can preliminarily infer a similar feeding strategy throughout the Jurassic and Cretaceous in apex predator theropods, where adaptations towards extreme osteophagy in *Tyrannosaurus* might be interpreted as adaptations towards 'fallback food', while they seem to feed more regularly on softer, more nutritious food than bone.

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Author contributions. **Conceptualization** T Tütken (TT), D E Winkler (DEW); **Methodology** DEW, M O Kubo (MOK), T M Kaiser (TMK); **Data Analysis** DEW, MOK, T Kubo (TK); **Sample Acquisition** DEW, MOK, TK, TMK; **Visualization** DEW; **Supervision** TT; **Writing – Original Draft** DEW; **Writing – Review & Editing** DEW, TK, MOK, TT.

DATA ARCHIVING STATEMENT

Data for this study, including 3D scan data and templates for data processing, are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.7d7wm37xk

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12632):

Table S1. DMTA parameter data and detailed test statistics.

Appendix S1. Supplementary results, Figures S1–S4, Tables S2, S3.

Table S2. Descriptive statistics for all DMTA parameters.

Table S3. DMTA parameter descriptions.

Figure S1. Exemplary 3D photosimulations of representative individuals for each crocodylian species.

Figure S2. Boxplots of all 42 DMTA parameters for extant crocodylians and theropods, and Principal component 1 and 2.

Figure S3. PCA employing 12 DMTA parameters measured on enamel surfaces of extant crocodylians and lepidosaurs in comparison to those of fossil theropods.

Figure S4. PCA of PC2 and PC3 employing 12 DMTA parameters measured on enamel surfaces of extant crocodylians in comparison to those of fossil theropods.

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