

# Dietary change across the Paleocene-Eocene Thermal Maximum in the mesonychid *Dissacus praenuntius*

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## ABSTRACT

The effect of climate change and ecological disruption on species diets is critical for understanding the evolution of mammalian adaptations and potential risks from the current climate crisis. Here, we use dental microwear texture analysis (DMTA), a likely correlate of the mechanical properties of masticated food, to infer changes in diet within the mesonychid *Dissacus praenuntius* across the Paleocene-Eocene Thermal Maximum (PETM), a period of geological rapid warming and aridification ~56 million years ago. Our results clarify previous reconstructions of this species as a small vertebrate mesocarnivore by emphasizing a durophagous dietary component. By comparing dental microwear across the PETM, we conclude that *Dissacus praenuntius* consumed less flesh and more bone during and after the PETM in comparison to before the event. Coupled with body mass reduction, dietary change during the PETM supports reduced primary and secondary productivity, rather than increased temperatures directly as a major probable cause of body mass reduction. We show that climate and ecological changes during the PETM caused dietary shifts in a species of flesh-eating mesonychid. These results reveal the ecology of the first large mammal predators as well as how mammalian diet may respond to modern climatic and habitat disruption.

## 1. Introduction

The impact of climate change on the biology and ecology of mammals has been well-documented in both the modern and fossil records (Grimm et al., 2013; Kiessling et al., 2025; Schmidt, 2018). Modifications to body mass, range, and ecology as well as extinction are all possible effects on mammals in response to rapid anthropogenic climate change (Barnosky et al., 2003; Hetem et al., 2014; Levinsky et al., 2007). As modern temperature trends exceed even the highest predictions of The Intergovernmental Panel on Climate Change, understanding how mammals adapt to rapid climate change is crucial to predict future trends of evolution and extinction (IPCC, 2021).

The Paleocene Eocene Thermal Maximum (PETM) serves as a good model for the effects of rapid global warming on the biology and ecology of mammals over a geologically fine time scale. About 56 million years ago, a massive release of isotopically light carbon dioxide caused average global surface temperatures to rise 5.4–5.9 degrees Celsius over a period of as little as a few thousand years, with these conditions

persisting roughly 270,000 years (Li et al., 2022; Piedrahita et al., 2025; Tierney et al., 2022; Zeebe and Lourens, 2019). Precipitation plummeted with evidence of progressive aridification through the PETM, peaking during the latter half of the event (Kraus et al., 2013; Kraus and Riggins, 2007). There is also evidence of increased frequency of extreme seasonal precipitation events across the PETM (Carmichael et al., 2018; Schmitz and Pujalte, 2007). Thus, the PETM can serve as a relevant case applicable to understanding the effects of current rapid global warming on mammals.

Places like the Bighorn Basin of Wyoming in western North America provide a near-unparalleled look into late Paleocene—early Eocene ecosystems due to a remarkably complete depositional record and over a century of systematic fossil collecting (Gingerich, 1980 and references therein, Gingerich, 1989; Rose, 1981). Fossils here suggest high floral turnover with humid subtropical forests replaced by open, dry tropical forests and savannas rich in dry-tolerant and thermophilic taxa (Korassidis and Wing, 2023; Wing and Currano, 2013; Wing et al., 2005). The PETM also includes the first appearance of ‘APP’ taxa (Artiodactyla,

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Perissodactyla, and Primates) near simultaneously across the Holarctic (Bowen, 2002 and references therein; Smith et al., 2006). For this reason, fossil assemblages from the PETM are often referred to as Wasatchian “Zero” (Wa-0), demarcating the start of the Wasatchian North American Land Mammal Age (NALMA).

Many native and immigrant taxa exhibit significant reduction in body mass during the PETM including the phenacodontids *Ectocion* and *Copecion*, the perissodactyl *Sifrhippus*, the carnivoraform *Uintacyon*, and the oxyaenid *Palaeonictis* (Chester et al., 2010; Gingerich, 2006; Secord et al., 2012). While the ultimate cause of dwarfing remains controversial, one hypothesis suggests adaptation to increased temperatures of the PETM: an application of Bergmann’s rule. This rule posits that populations living in warm environments near the tropics tend to be less massive than their relatives that reside in colder climates at higher latitudes (Bergmann, 1847). While traditionally used to explain spatial variation in body mass within a species, this pattern has been documented in paleontological, historical, and modern mammal samples in relation to changing temperatures over time (Ashton et al., 2000 and references therein; Meiri et al., 2004 and references therein; Smith et al., 1995).

Conversely, primary productivity in the Bighorn Basin may have decreased due to increased aridity during the PETM. The resource availability hypothesis posits that body size is closely correlated with primary productivity because resource availability sets a limit to the maximum attainable body size that an animal can reach (Rosenzweig, 1968). A more general “resource rule” suggests that body size is largely driven by the size, abundance, and availability of food resources (McNab, 2010). This pattern has been widely recovered in modern ecosystems and helps to explain discrepancies in Bergmann’s rule such as the lack of latitudinal patterns within the tropics (Huston and Wolvert, 2011; Kelly et al., 2018). Under a scenario where food becomes less abundant, the ability of an animal to alter its typical diet may be predictive of changes in body mass. Animals that adhere to a strict diet may face extinction or selection pressure for smaller mature body sizes while generalists that are able to exploit a greater variety of resources may be partially shielded from the effects of resource limitation (DeSantis et al., 2019; Smith et al., 2022).

Responses to climate change in faunivorous mammals may differ in that body size is heavily dependent on available prey biomass. As prey body mass shrunk, carnivore body mass may be expected to follow suit as an adaptation to decreased resource availability (Gittleman, 1985; Raia and Meiri, 2006; Tucker and Rogers, 2014). The validity of this hypothesis for faunivores is tenuous due to the relative paucity of specimens of “dwarf” *Uintacyon* and *Palaeonictis* during the PETM (Chester et al., 2010).

A clade of faunivores better represented than *Uintacyon* and *Palaeonictis* across the Paleocene-Eocene transition in western North America are Mesonychia. *Dissacus* was one of the earliest and most widespread genera, with species known across the Holarctic from the early Paleocene to the end of the Ypresian age of the early Eocene, persisting through the PETM (O’Leary and Rose, 1995). Ranging from 12 to 20 kg, *Dissacus praenuntius* Matthew and Granger, 1915 was a small, generalized mesocarnivore that was fairly common in early Cenozoic forests (Solé et al., 2021; Thewissen, 1991). Features of the humerus and elbow suggest limited lateral mobility and enhanced flexion/extension, while the position and extension of the astragalar trochlear facet suggest that *Dissacus* was likely digitigrade and a cursorial pursuit predator (Jenkins, 1973; Thewissen, 1991).

Although superficially resembling the modern carnivoran Bauplan, mesonychids were more closely related to modern ungulates (Spaulding et al., 2009). Compared to modern Carnivora, mesonychid dental morphology differs in the following ways: 1) lack of modified upper/lower posterior tooth blade (carnassial), 2) incipient talonid basin development, and 3) loss of hypocones (Szalay, 1969). Nevertheless, various dental adaptations exist within mesonychids for effective flesh tearing and bone consumption. Mandibular molars are premolarized

and laterally compressed, with tall protoconids and trenchant talonids. A tight, U- or V-shaped notch between the enlarged protoconid and elevated, sharpened cristid obliqua is likely analogous to the carnassial between the protoconid and paraconid of carnivores, serving to anchor meat as it is chewed and sliced (Szalay, 1969).

*Dissacus* is dentally basal within Mesonychidae, maintaining a complete set of third molars typically lost in latter mesonychids (Matthew, 1915). Maxillary molars lack a paraconule and metaconule, possess a well-developed parastyle and metastyle, and the preprotocrista as well as the post-protocrista form prominent transverse ridges on the protocone (Szalay, 1969). Posterior mandibular teeth maintain well-developed metaconids, entoconids and hypoconulids (albeit in a reduced form) and reduced paraconids (Szalay, 1969). Among species of *Dissacus*, *D. praenuntius* is dentally derived in exhibiting slightly retroflexed protoconids on the lower third and fourth premolars, as well as remolarization of the lower molar talonids through lingual broadening and development of a rudimentary entoconid, though this feature seems subject to individual variation over time (O’Leary and Rose, 1995; Solé et al., 2021). While basal mesonychids like *Dissacus* possessed an unfused mandibular symphysis, fusion occurred in later, larger forms potentially as adaptations for strengthening the mandible against high compression forces associated with powerful biting (O’Leary and Rose, 1995; Szalay, 1969).

Mesonychids have been assigned to various levels of carnivory, omnivory, and hard-object specialization (Gould and Szalay, 1966). Gould and Szalay (1966) described *Dissacus* as a “carnivore” (i.e., mesocarnivore) based on the ratio of length to width of the posterior mandibular dentition, though they differentiate it from “advanced carnivore” (i.e., hypercarnivore) mesonychids based on lacking elongate, cutting lower teeth. The presence of “acute-angled” Hunter-Schreger-Bands in the posterior dentition suggests hard-object adaptations in *Dissacus* and fellow mesonychid *Pachyaena* (Stefen, 1997). Furthermore, dental microwear in the latter genus is suggestive of large, hard object feeding (O’Leary and Teaford, 1992). Chester et al. (2010) also found greatest similarity to carnivores for *D. praenuntius* based on orientation patch count. Compared to contemporaneous Paleocene mammals, the lower molars of *Dissacus* from the Torrejonian inhabit an extreme position in morphospace, argued to represent carnivory (Grossnickle and Newham, 2016).

Although earlier studies suggested body mass stasis through the PETM in *D. praenuntius*, further collecting from the PETM in the Bighorn Basin shows modest body mass reduction of ~20 %, with the smallest individual (UF 253359) occurring after the hottest PETM temperatures, thus not supporting abiotically-driven dwarfing in this taxon (Chester et al., 2010; Secord et al., 2012; Solé et al., 2021). Though dentition is relatively unchanged (other than size) across the PETM, Solé et al. (2021) suggest that they generally differ from Clarkforkian *D. praenuntius* by exhibiting lesser development of the entoconid and postcristid, and transversally narrower, less basined talonids on lower p4 – m2. In a similar vein, a large specimen from the early Wasatchian appears morphologically similar to previous samples from the Clarkforkian and PETM (Solé et al., 2021). *D. praenuntius* therefore serves as an important species towards understanding faunivorous mammal responses to rapid climatic warming.

To investigate dietary ecology and change in response to the PETM, we conducted dental microwear texture analysis (DMTA) on specimens of *D. praenuntius* ranging from the Clarkforkian to the early Wasatchian NALMA. DMTA has been used to investigate diet and ecology from both the paleontological and modern record and is effective in tracing dietary changes over time (DeSantis et al., 2019; Schubert et al., 2010; Scott et al., 2005). Dental microwear records perimortem feeding events, potentially being overwritten every few weeks or so (Winkler et al., 2020). In short, dental microwear should reflect diet shortly prior to death rather than a compilation of lifelong dietary patterns.

We expect dental microwear in *D. praenuntius* to most closely resemble that of generalist carnivores that neither avoid nor

preferentially target bone. Based on previous conclusions drawn from cranial and post cranial morphology, Hunter-Schreger band morphology, and orientation patch count comparisons, *D. praenuntius* was not specially adapted for crushing bones or other hard objects and should therefore exhibit dental microwear that reflects only modest tough flesh and hard bone consumption (Chester et al., 2010; Stefen, 1997; Szalay, 1969).

We also predict that *D. praenuntius* will show no change in dental microwear across the PETM despite documented body mass reduction. If this were to be the case, the effects of the PETM on primary productivity (such as prey body mass reduction) would seem suitable selection pressure for reduced body mass in *D. praenuntius* and no change in diet would be expected. On the other hand, if *D. praenuntius* exhibits different dental microwear during the PETM, then reduced size alone may have been insufficient to cope with the reduced primary productivity of the PETM. This would suggest that *D. praenuntius* incorporated additional or alternative resources such as insects, fruits, or bones to supplement its diet in response to environmental stresses.

2. Materials and methods

2.1. Materials

2.1.1. Fossil materials

This study targeted North American specimens of *D. praenuntius* that exhibited well-defined wear facets. Specimens are housed in the vertebrate paleontology collections of the University of Florida, University of Michigan Museum of Paleontology, and the Yale Peabody Museum of Natural History (Table 1). To assess dietary variation across the Paleocene-Eocene Thermal Maximum, we sampled 24 specimens of *D. praenuntius* molars deriving from the late Paleocene Clarkforkian through the early Eocene Wasatchian NALMA for dental microwear texture analysis. All specimens were recovered from northwestern Wyoming within the Bighorn and smaller Clarks Fork basins. Localities are geographically close to each other, with the maximum distance being less than 150 km (see Supplementary Material S1 for locality details). Clarkforkian specimens were recovered from the late Paleocene Fort Union and Polecat Bench formations while specimens from the PETM and early Wasatchian derive from the overlying Willwood Formation. Late Paleocene sediments tend to be gray to grayish-yellow mudstones and carbonaceous shales that were deposited in low-lying floodplains, while PETM and early Wasatchian sediments tend to be deeply colored red, orange, and purple mudstones representing fluvial mudstones and mature paleosols formed by abandoned river channels and well-drained floodplain deposits (Gingerich, 1989; Wing, 1998). Fauna shared between localities suggests similar depositional environments and ecosystems in the Bighorn and Clarks Fork basins during each NALMA (Gingerich and Clyde, 2001; Gingerich, 1989; Rose et al., 2012).

Only *D. praenuntius* specimens from the Cabin Fork (PETM) locality have detailed resolution within the stratigraphy of the Willwood Formation. Other specimens are assigned to the Clarkforkian, PETM, or early Wasatchian based on biostratigraphy and position relative to the Carbon Isotope Excursion accompanying the PETM. Assigning specimens to specific biozones is more dubious as these rely on biostratigraphy that has more recently come under scrutiny (Anemone et al., 2024). As a result, we group all specimens by NALMA regardless of historically assigned biozone (Clarkforkian = Cf-1, Cf-2, Cf-3; PETM = Wa-0; early Wasatchian = Wa-1, Wa-2) while also acknowledging that each biozone reflects hundreds of thousands of years and may mask ecological change (see Supplementary Data S1 for assigned biozone of individual specimens).

Teeth sampled included upper and lower first or second molars (Table 1, Fig. 1A). Lower third molars were excluded due to late eruption possibly delaying the formation of dental microwear in comparison to earlier erupting dentition. Shearing facets were identified on the lingual protocone on the upper molars and the buccal protoconid and

**Table 1**  
Description of *Dissacus praenuntius* sample provenance and tooth position. The synonymy of the Polecat Bench and Fort Union formations is debated, with many opting to continue usage of the traditional “Fort Union” for Paleocene strata in the Wyoming (Hartman, 1986).

| Species               | Specimen         | Tooth | Basin       | Formation            | NALMA        |
|-----------------------|------------------|-------|-------------|----------------------|--------------|
| <i>D. praenuntius</i> | UM65067          | lm1   | Clarks Fork | Polecat Bench        | Clarkforkian |
| <i>D. praenuntius</i> | UM65555          | lmx   | Clarks Fork | Polecat Bench        | Clarkforkian |
| <i>D. praenuntius</i> | UM67360          | lm2   | Clarks Fork | Lower Willwood (Sic) | Clarkforkian |
| <i>D. praenuntius</i> | UM71590          | lm1   | Clarks Fork | ?Polecat Bench       | Clarkforkian |
| <i>D. praenuntius</i> | YPM. VPPU.013295 | rm2   | Clarks Fork | Fort Union           | Clarkforkian |
| <i>D. praenuntius</i> | YPM. VPPU.013309 | RMX   | Clarks Fork | Upper Polecat Bench  | Clarkforkian |
| <i>D. praenuntius</i> | YPM. VPPU.018711 | lm2   | Clarks Fork | Lower Willwood (Sic) | Clarkforkian |
| <i>D. praenuntius</i> | YPM. VPPU.019597 | rm2   | Clarks Fork | Upper Fort Union     | Clarkforkian |
| <i>D. praenuntius</i> | YPM. VPPU.022314 | RM1   | Bighorn     | Upper Fort Union     | Clarkforkian |
| <i>D. praenuntius</i> | UF324098         | lmx   | Bighorn     | Willwood             | PETM         |
| <i>D. praenuntius</i> | UF328056         | lm2   | Bighorn     | Willwood             | PETM         |
| <i>D. praenuntius</i> | UF328800         | lmx   | Bighorn     | Willwood             | PETM         |
| <i>D. praenuntius</i> | UF329903         | lm2   | Bighorn     | Willwood             | PETM         |
| <i>D. praenuntius</i> | UF252475         | lm2   | Bighorn     | Willwood             | PETM         |
| <i>D. praenuntius</i> | UF253493         | lmx   | Bighorn     | Willwood             | PETM         |
| <i>D. praenuntius</i> | UF311432         | lm2   | Bighorn     | Willwood             | PETM         |
| <i>D. praenuntius</i> | UM83631          | rm2   | Bighorn     | Willwood             | PETM         |
| <i>D. praenuntius</i> | UM111835         | lmx   | Clarks Fork | Willwood             | Wasatchian   |
| <i>D. praenuntius</i> | UM73732          | rmx   | Clarks Fork | Willwood             | Wasatchian   |
| <i>D. praenuntius</i> | UM79635          | lm2   | Clarks Fork | Willwood             | Wasatchian   |
| <i>D. praenuntius</i> | UM85385          | rmx   | Bighorn     | Willwood             | Wasatchian   |
| <i>D. praenuntius</i> | UM98135          | rmx   | Clarks Fork | Willwood             | Wasatchian   |
| <i>D. praenuntius</i> | YPM. VPPU.023127 | rm2   | Bighorn     | Willwood             | Wasatchian   |
| <i>D. praenuntius</i> | YPM. VPPU.023129 | LMX   | Bighorn     | Willwood             | Wasatchian   |

talonid area buccal to the cristid obliqua (Fig. 1B) through comparison to the schema found in Szalay and Gould (1966). Wear facets on the mesiobuccal and distobuccal protoconid were preferentially targeted with mesiobuccal wear facets on the talonid utilized as a secondary option. Elderly individuals with molar crowns obliterated by wear (leaving only exposed dentin) were excluded.

While there are some differences between the first and second lower molars in *D. praenuntius*, these are often minute and easily obscured due to wear, postmortem breakage, or individual variation (O’Leary and Rose, 1995). As a result, some specimens within our sample are assigned “mx” to indicate ambiguity as to their identity as a lower first or second molar. Previous work has shown that dental microwear accumulates in a similar fashion across homologous facets regardless of molar position or placement in the maxilla or mandible (Kelly et al., 2021; Tanis et al., 2018). Therefore, including both lower first and second as well as upper molars into our analysis does not jeopardize our methodology and serves to greatly increase our sample size.

The impacts that taphonomic processes potentially have on dental microwear were considered when selecting samples to analyze for dental microwear. Previous work has shown that taphonomic processes such as exposure to acid, trampling, sediment abrasion, and fossil laboratory preparation are capable of alteration or even obliteration of

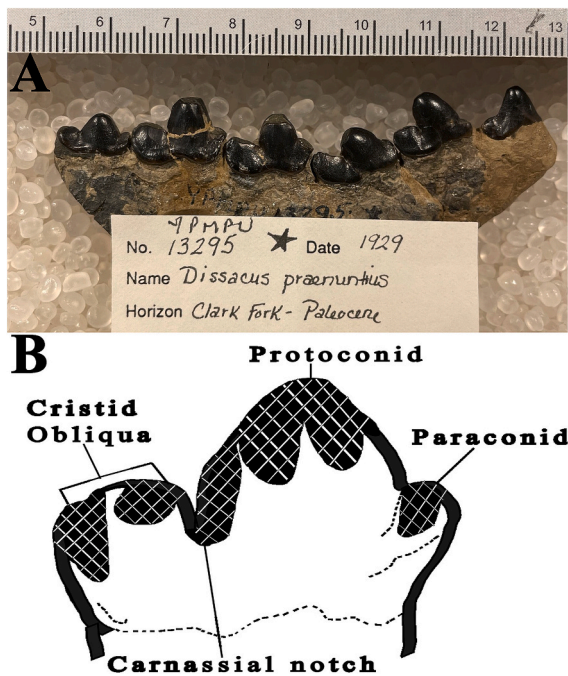


**Fig. 1.** Dentition of *Dissacus praenuntius* exhibiting areas targeted for analysis. A: Right hemimandible including p<sub>2</sub> - m<sub>3</sub> in buccal view (right is mesial). B: Labeled schema of a right lower molar in buccal view (right is mesial). Shearing facets are indicated by hatch-marked areas on the paraconid, protoconid, and distal to the carnassial notch, adapted from (Gould and Szalay, 1966).

dental microwear features through polishing, attrition, breakage, and etching (King et al., 1999; Weber et al., 2021, 2022). However, many of these taphonomic processes are easily identifiable through diagnostic features created (cracks, varnish residue, drill marks, irregular striations) and by the fact that alteration will not be limited to the occlusal surface of the tooth (Micó et al., 2023; Teaford, 1988; Weber et al., 2021). Specimens in which considerable taphonomic alteration occurred on the wear facets were identified and removed from our sample.

#### 2.1.2. Modern comparative sample

To approximate dietary ecology, we compared dental microwear of *D. praenuntius* to five extant feliform carnivores published by DeSantis and Patterson (2017): *Acinonyx jubatus* Schreber, 1775, *Panthera leo* Linnaeus, 1758, *Crocota crocota* Erxleben, 1777, *Hyaena hyaena* Linnaeus, 1758, and *Parahyaena brunnea* Thunberg, 1820. Feliform carnivores were chosen (as opposed to canids or ursids) as our comparison for *D. praenuntius* due to general similarities in dental morphology. Unlike canids and ursids, mesonychids lacked bunodont molars with basined talonids adapted for grinding. Rather, mesonychids possessed three premolariform mandibular molars with trenchant talonids (O'Leary and Rose, 1995). Combined with observable differences between canid shearing and grinding dental microwear, this precludes the use of caniforms as modern proxies for mesonychid dietary ecology (Ungar et al., 2010). In contrast, feliforms share greater dental similarity to *Dissacus* in lacking adaptations for grinding through reduction of the talonid basin (Van Valkenburgh, 1991). For these reasons, feliform carnassial shearing facets are more appropriate for comparison to the shearing facets of mesonychid carnassial notches.

#### 2.2. Sample preparation

Samples were prepared using the protocol outlined by DeSantis et al. (2012). Specimens were cleaned using 70 % isopropyl alcohol applied with a toothbrush and cotton swabs to remove detritus and oils, with

acetone additionally applied to specimens treated with preservatives or glues such as Paraloid B-72. Surface molds were prepared using President's Jet regular body polyvinylsiloxane dental impression material (Coltène-Whaledent Corp., Cuyahoga Falls, OH, USA). High-resolution translucent casts were then poured using Epotek 301 epoxy resin and hardener (Epoxy Technologies Corp., Billerica, MA, USA).

#### 2.3. Dental microwear texture analysis (DMTA)

Wear facets on the casts were scanned using the Sensofar P Lu neox confocal profiler (Solarius Inc., Sunnyvale, CA, USA) at Vanderbilt University. To eliminate the effects of inter-microscope variability and software-specific differences, data collection and analysis were performed on the same microscope and software used to collect our comparative sample of feliforms described in DeSantis et al. (2017). Specimens were scanned in three dimensions in nine areas and stitched together, leveled, and subdivided into four adjacent areas of equal size ( $102 \times 138 \mu\text{m}^2$ ) for a total sampled area of  $204 \times 276 \mu\text{m}^2$  in accordance with protocol from previous studies (Scott et al., 2006). These scans output four files (.sur) available for DMTA using Sfrax and Toothfrax software. By combining three-dimensional scans of wear facet surfaces with scale-sensitive fractal analysis, DMTA is able to analyze the surface texture of these high resolution three-dimensional models (Scott et al., 2005; Ungar et al., 2003).

We included the following DMTA variables in our analysis: Anisotropy (*epLsar*), complexity (*Asfc*), and textural fill volume (*Tfv*). Anisotropy measures the directionality of the textures and implies tough food consumption, exemplified by a surface presenting a high degree of parallel scratches (Fig. 2A; Scott et al., 2006). High anisotropy is correlated with increased feeding on tough foods, while complexity measures the maximum change in surface roughness as the scale of observation increases and is used as a proxy for brittle food consumption (DeSantis et al., 2017). A surface with a large number and variety of features (pits and scratches) will have high complexity values (Fig. 2B, Scott et al., 2006). In carnivores, high complexity is correlated with increased carcass utilization (DeSantis et al., 2017, 2019; Schubert et al., 2010). Textural fill volume is a measure of microwear feature size, recording the volume required to fill the features on the enamel surface with small ( $2 \mu\text{m}$ ) and large ( $10 \mu\text{m}$ ) diameter cuboids. A surface with considerably large or deep features would possess high textural fill volume and generally parallels complexity in reflecting hard-object feeding (DeSantis et al., 2017). For more detailed description of these variables, see Scott et al. (2006).

#### 2.4. Data analysis

A Spearman's Rank Correlation showed a moderate, positive correlation with complexity and textural fill volume ( $R_s(22) = 0.593$ ,  $p = 0.005$ ) as well as a moderate, negative correlation with complexity and anisotropy ( $R_s(22) = -0.639$ ,  $p = 0.002$ ). Specimens were divided into NALMA intervals (*D. praenuntius*<sub>CF</sub> = Clarkforkian; *D. praenuntius*<sub>PETM</sub> = Paleocene-Eocene Thermal Maximum; *D. praenuntius*<sub>Wa</sub> = Wasatchian). DMTA data collected in this study were not normally distributed (Shapiro-Wilk tests, Table 2). Thus, nonparametric tests (e.g., Kruskal-Wallis) were used to compare differences between *D. praenuntius* and the comparative sample of modern feliform carnivores, as well as between specimens ranging across the Clarkforkian – Wasatchian NALMAs. When significant differences were recovered, Dunn's procedure (Dunn, 1964) was used to conduct multiple comparisons of complexity, anisotropy, and textural fill volume between taxa or NALMA. While previous studies of DMTA have utilized the Bonferroni correction to reduce the likelihood of type I errors when multiple comparisons were being made, this method also increases the probability of type II errors when a large number of comparisons are being made (DeSantis et al., 2017; Nakagawa, 2004). Therefore, we employed a Benjamini-Hochberg procedure (with false discovery rate set at 0.05) to address increased

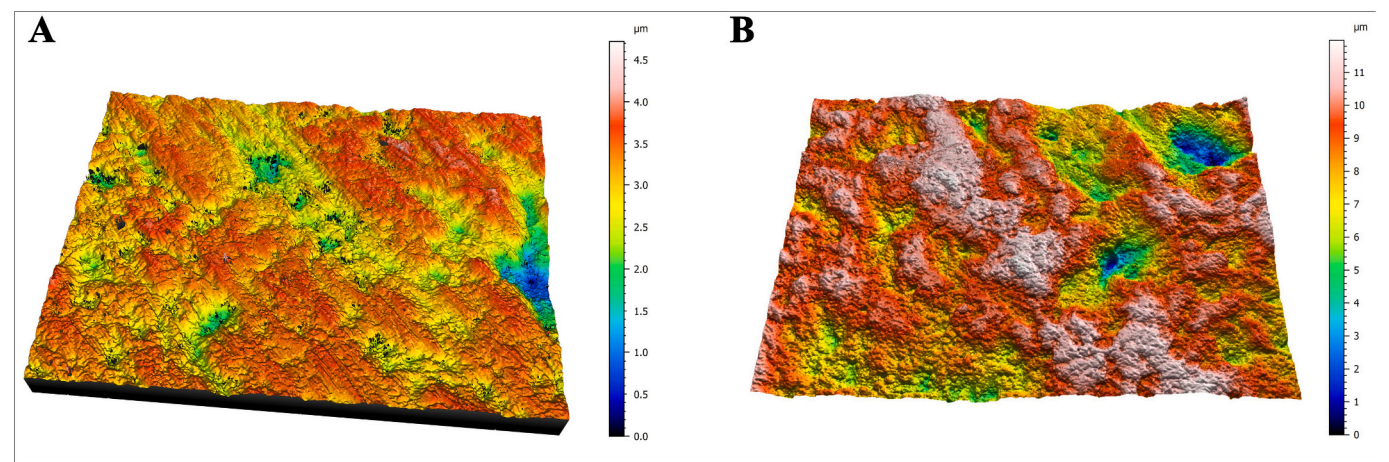


**Fig. 2.** 3D digital elevation dental microwear surface models of *Dissacus praeununtius* exhibiting high (A) anisotropy and (B) complexity. Both models represent 204 × 274 μm in area with depth scales noted to the right of each image.

**Table 2**  
Descriptive statistics of each DMTA variable for *Dissacus praeununtius* specimens deriving from each North American Land Mammal Age (NALMA). *n*, number of individuals sampled; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume.

| Taxon                  | NALMA        | Statistic                             | <i>n</i> | <i>Asfc</i>   | <i>epLsar</i>  | <i>Tfv</i>    |
|------------------------|--------------|---------------------------------------|----------|---------------|----------------|---------------|
| <i>D. praeununtius</i> | Clarkforkian | Median                                | 9        | 3.122         | 0.0031         | 9352          |
|                        |              | Mean                                  |          | 3.672         | 0.0032         | 8683          |
|                        |              | SD                                    |          | 1.297         | 0.0007         | 4788          |
|                        |              | Skewness (Fisher)                     |          | 1.164         | 1.7045         | −0.283        |
|                        |              | <i>p</i> for normality (Shapiro-Wilk) |          | 0.053         | <b>0.0274*</b> | 0.8709        |
|                        | PETM (Wa-0)  | Median                                | 8        | 7.513         | 0.0017         | 12,444        |
|                        |              | Mean                                  |          | 7.046         | 0.0017         | 10,834        |
|                        |              | SD                                    |          | 3.024         | 0.0010         | 4545          |
|                        |              | Skewness (Fisher)                     |          | −0.364        | 0.147          | −1.932        |
|                        |              | <i>p</i> for normality (Shapiro-Wilk) |          | 0.893         | 0.076          | <b>0.001*</b> |
|                        | Wasatchian   | Median                                | 7        | 5.195         | 0.0016         | 7237          |
|                        |              | Mean                                  |          | 6.047         | 0.0016         | 9051          |
|                        |              | SD                                    |          | 2.106         | 0.0004         | 5816          |
|                        |              | Skewness (Fisher)                     |          | 1.600         | 0.2849         | 0.361         |
|                        |              | <i>p</i> for normality (Shapiro-Wilk) |          | <b>0.031*</b> | 0.7690         | 0.808         |

\* Significant *p*-values (*p* < 0.05).

type I errors (Benjamini and Hochberg, 1995). This procedure is preferable to approaches that seek to control the family-wise error rate due to being less conservative and producing fewer type II errors (Williams et al., 1999). The Benjamini-Hochberg procedure has been increasingly used in DMTA studies as opposed to the Bonferroni correction (Adams et al., 2020; Purnell et al., 2017; Winkler et al., 2022). All analyses were conducted using RStudio 2023.06.2. (R Core Team, 2022; RStudio Team, 2023). See Supplementary Data S2 for source code.

3. Results

3.1. Comparison of *Dissacus* microwear with modern feliform microwear

3.1.1. Comparison to modern felids

Dental microwear of our sample of *D. praeununtius* molars ranging from the Clarkforkian to the Wasatchian NALMA differed compared to that of modern feliforms from previous work, documented in Table 3 and Figs. 3 and 4 (DeSantis et al., 2017; Schubert et al., 2010). *D. praeununtius* specimens from the PETM (*Z* = 3.906, *p* < 0.001) and Wasatchian (*Z* = 3.367, *p* = 0.002) had significantly higher complexity

**Table 3**  
Statistical results (Dunn’s Test) for taxonomic comparisons of complexity values (*Asfc*), anisotropy values (*epLsar*), and textural fill volume (*Tfv*) values for *Dissacus praeununtius* separated by NALMA compared to extant feliforms. Benjamini-Hochberg procedure used to reduce the likelihood of type I errors.

| Variable      |                                          | <i>A. jubatus</i> | <i>Pan. leo</i> | <i>C. crocuta</i> | <i>H. hyaena</i> | <i>Par. brunnea</i> |
|---------------|------------------------------------------|-------------------|-----------------|-------------------|------------------|---------------------|
| <i>Asfc</i>   | <i>D. praeununtius</i> <sub>(Cf)</sub>   | 0.128             | 0.512           | <b>0.029*</b>     | 0.056            | 0.100               |
|               | <i>D. praeununtius</i> <sub>(PETM)</sub> | < <b>0.001*</b>   | 0.255           | 0.931             | 0.896            | 1.000               |
|               | <i>D. praeununtius</i> <sub>(Wa)</sub>   | <b>0.002*</b>     | 0.504           | 0.668             | 0.969            | 0.949               |
|               | <i>D. praeununtius</i> <sub>(Cf)</sub>   | 0.096             | <b>0.050*</b>   | <b>0.037*</b>     | 0.054            | 0.079               |
| <i>epLsar</i> | <i>D. praeununtius</i> <sub>(PETM)</sub> | 1.000             | 1.000           | 0.878             | 1.000            | 0.943               |
|               | <i>D. praeununtius</i> <sub>(Wa)</sub>   | 1.000             | 0.886           | 0.381             | 1.000            | 1.000               |
|               | <i>D. praeununtius</i> <sub>(Cf)</sub>   | 0.456             | 0.492           | <b>0.033*</b>     | <b>0.008*</b>    | 0.273               |
| <i>Tfv</i>    | <i>D. praeununtius</i> <sub>(PETM)</sub> | 0.089             | 0.713           | 0.346             | 0.123            | 0.739               |
|               | <i>D. praeununtius</i> <sub>(Wa)</sub>   | 0.377             | 0.732           | 0.117             | <b>0.039*</b>    | 0.433               |

\* Significant *p*-values (*p* ≤ 0.05).

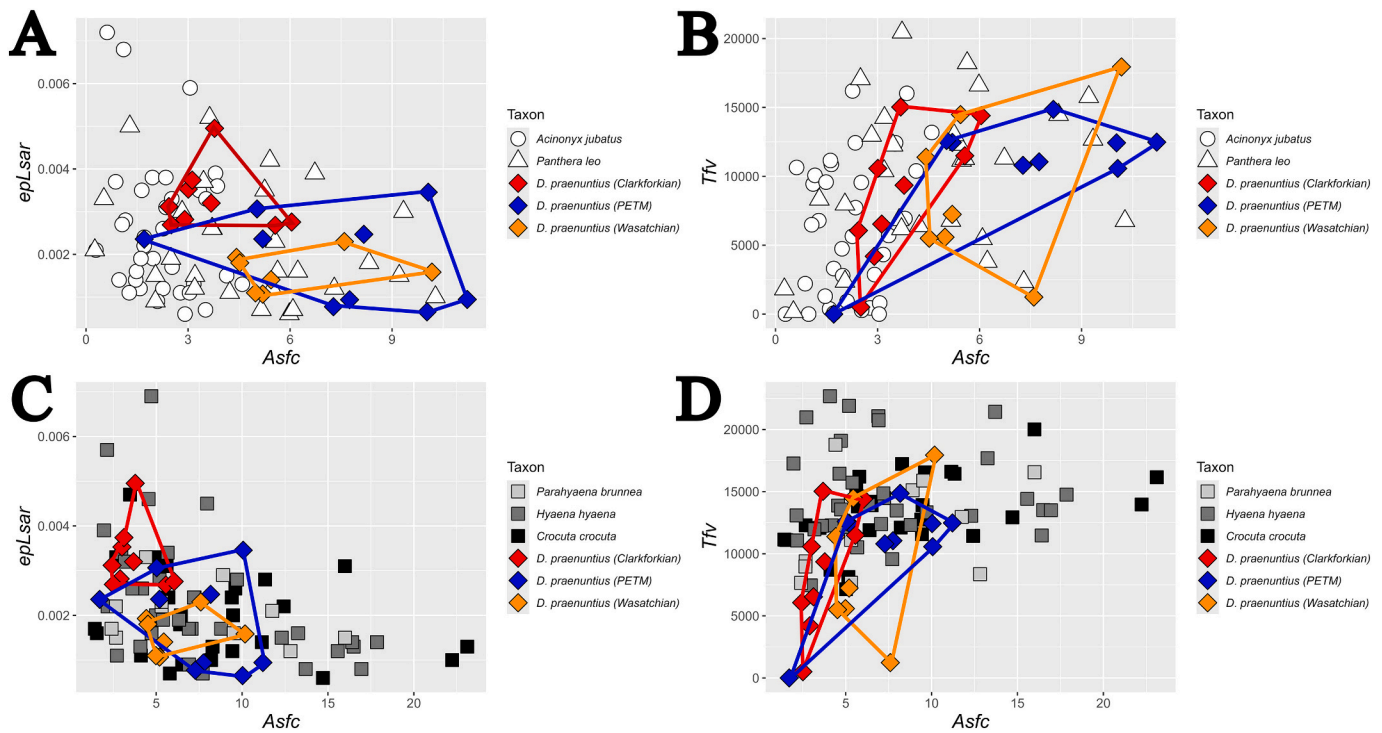


**Fig. 3.** Scatterplot of dental microwear from *Dissacus praenuntius* (this study) and extant feliforms reported by DeSantis et al. (2017). Dental microwear comparison of *D. praenuntius* and extant felids (*Acinonyx jubatus* and *Panthera leo*) using (A) complexity (Asfc) and anisotropy (eplSar); (B) complexity (Asfc) and textural fill volume (Tfv,  $\mu\text{m}^3$ ). Dental microwear comparison of *D. praenuntius* and extant hyaenids (*Crocuta crocuta*, *Hyaena hyaena*, and *Parahyaena brunnea*) using (C) complexity (Asfc) and anisotropy (eplSar); (D) complexity (Asfc) and textural fill volume (Tfv,  $\mu\text{m}^3$ ).

than the cheetah *Acinonyx jubatus* (Table 3, Fig. 4A). In comparison to the lion *Pan. leo*, only *D. praenuntius*<sub>(CF)</sub> exhibited significantly higher anisotropy ( $Z = 2.712$ ,  $p = 0.050$ ). Complexity and textural fill volume were not significantly different between *Pan. leo* and *D. praenuntius* from the Clarkforkian, PETM, or Wasatchian (Table 3, Fig. 4A, B).

### 3.1.2. Comparison to modern hyaenids

*D. praenuntius* showed significant differences in dental microwear from the extant sample of hyaenids (Table 3, Fig. 4A, B). Post-hoc Dunn's tests showed that *D. praenuntius*<sub>(CF)</sub> exhibited significantly lower complexity ( $Z = -2.586$ ,  $p = 0.029$ ), higher anisotropy ( $Z = 3.023$ ,  $p = 0.037$ ), and lower textural fill volume ( $Z = -2.376$ ,  $p = 0.033$ ) than the spotted hyaena *Crocuta crocuta*, as well as lower textural fill volume ( $Z = -3.078$ ,  $p = 0.008$ ) than the striped hyaena *Hyaena hyaena*. No significant differences in anisotropy, complexity, or textural fill volume were recovered between *D. praenuntius* from the PETM and Wasatchian and the hyaenas *C. crocuta* and *H. hyaena*. However, textural fill volume was significantly lower ( $Z = -2.483$ ,  $p = 0.039$ ) in *D. praenuntius*<sub>(Wa)</sub> compared to *Par. brunnea*.

### 3.2. Differences in dental microwear between Clarkforkian, PETM, and early Wasatchian *Dissacus praenuntius*

Dental microwear in *D. praenuntius* showed significant differences across the Clarkforkian – early Wasatchian in complexity ( $\chi^2_{\text{Kruskal-Wallis}}(2) = 7.407$ ,  $p = 0.025$ ; Table 4, Fig. 5A) and anisotropy ( $\chi^2_{\text{Kruskal-Wallis}}(2) = 14.356$ ,  $p = 0.001$ ; Table 4, Fig. 5B). Post-hoc Dunn's tests showed lower complexity ( $Z = -2.603$ ,  $p = 0.028$ ; Table 4, Fig. 5A) and higher anisotropy ( $Z = 3.218$ ,  $p = 0.002$ ; Table 4, Fig. 5B) in Clarkforkian samples compared to those from the PETM. Additionally, Clarkforkian samples exhibited higher anisotropy ( $Z = 3.243$ ,  $p = 0.004$ ) than those from the Wasatchian. Dental microwear between the PETM and Wasatchian did not show significant differences in complexity ( $Z = 0.605$ ,  $p = 0.545$ ) or anisotropy ( $Z = 0.137$ ,  $p = 0.891$ ). No significant

differences in textural fill volume ( $\chi^2_{\text{Kruskal-Wallis}}(2) = 1.244$ ,  $p = 0.537$ ) were recovered between any groups

## 4. Discussion

### 4.1. Comparison to extant feliforms and general dietary interpretation

Collectively, the *D. praenuntius* fossil sample exhibits microwear textures intermediate between felids and hyaenids. While *D. praenuntius*<sub>(CF)</sub> shows similarities to *A. jubatus* and *Par. brunnea*, *D. praenuntius* from the PETM and early Wasatchian most closely match dental microwear from *Pan. leo* and extant bone-crushing hyaenids (Table 3, Figs. 3–4).

Notably, *D. praenuntius*<sub>(PETM)</sub> and *D. praenuntius*<sub>(Wa)</sub> show significantly greater complexity compared to the cheetah *A. jubatus* (Table 3, Figs. 3A, B, 4A). Observations of *A. jubatus* in the wild suggest general feeding behavior consisting of bone avoidance, or limited ingestion of small-sized bones (Van Valkenburgh, 1996). Low complexity and high anisotropy supports this interpretation (Schubert et al., 2010). Exhibiting greater complexity, *D. praenuntius* from the PETM and early Wasatchian can be reconstructed as more frequent consumers of bone than *A. jubatus*. While *A. jubatus* tend to avoid larger bones such as those of the limbs and skull, both captive and free-ranging animals have been observed nearly completely consuming the bodies of prey <10 kg as well as much of the axial skeleton of larger prey (Phillips, 1993). This behavior may be indicative of reliance on early access/incomplete carcass utilization. In their normal range, cheetahs often develop avoidance behavior to predators and kleptoparasites such as lions and spotted hyenas, including more rapid consumption, carcass hiding, and spatial/temporal foraging modification (Durant, 2000; Hilborn et al., 2018; Hunter et al., 2007). These behaviors are compatible with preference for flesh and organs and discrimination against bones.

Near-complete carcass consumption of prey <10 kg by *A. jubatus* draws an interesting parallel to predation behavior reconstructed for

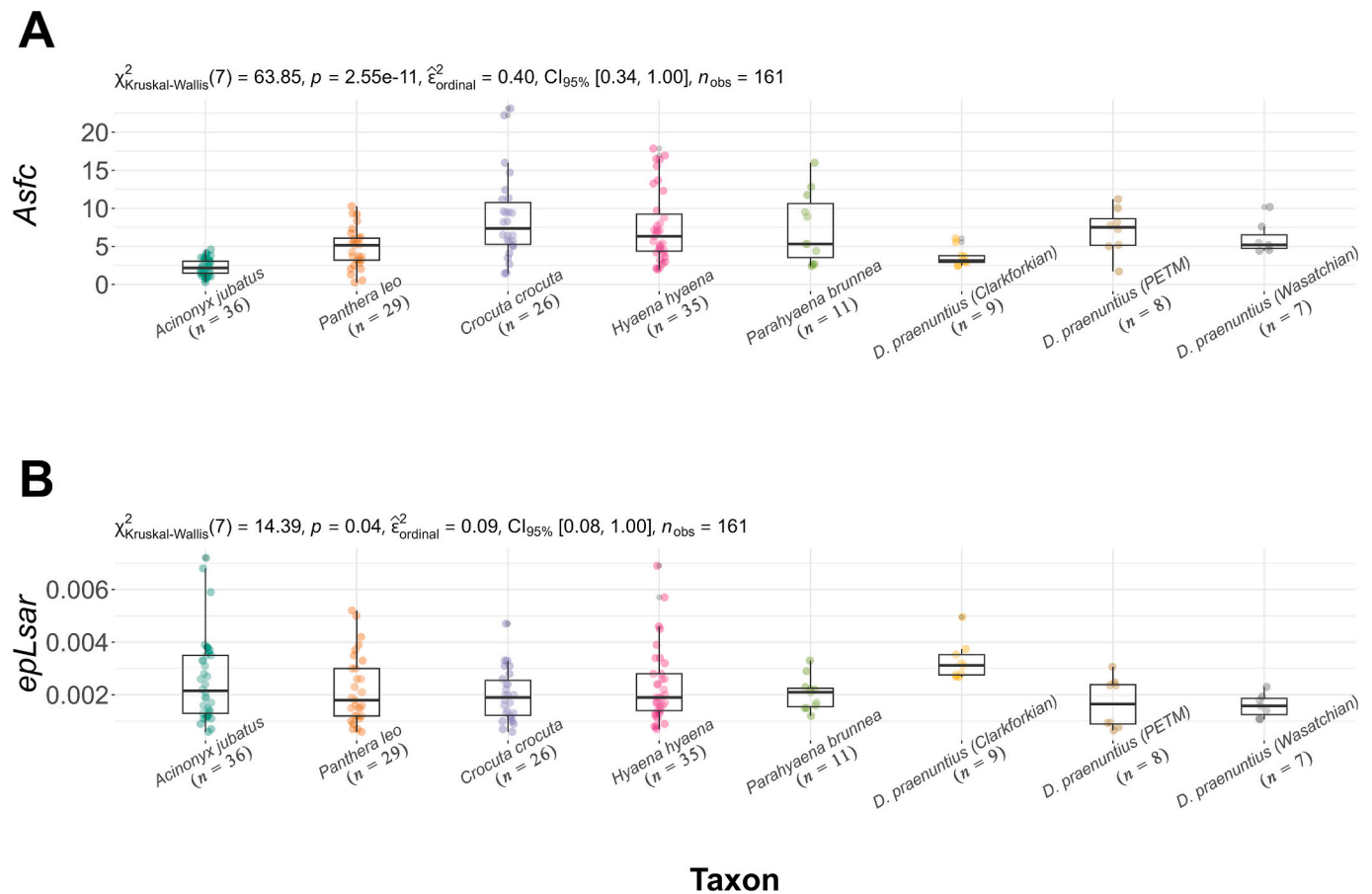


**Fig. 4.** Results of dental microwear texture analysis for *Dissacus praenuntius* compared to extant feliforms (*Acinonyx jubatus*, *Panthera leo*, *Crocuta crocuta*, *Hyaena hyaena*, and *Parahyaena brunnea*) reported by DeSantis et al. (2017).

**Table 4**  
Statistical results of pair-wise Dunn's Test for NALMA comparisons of complexity values (*Asfc*), anisotropy values (*epLsar*) and textural fill volume (*Tfv*) values for *Dissacus praenuntius*. Benjamini-Hochberg procedure used to reduce the likelihood of type I errors.

| Variable      |                                         | <i>D. praenuntius</i> <sub>(PETM)</sub> | <i>D. praenuntius</i> <sub>(Wa)</sub> |
|---------------|-----------------------------------------|-----------------------------------------|---------------------------------------|
| <i>Asfc</i>   | <i>D. praenuntius</i> <sub>(CF)</sub>   | 0.0277*                                 | 0.0884                                |
|               | <i>D. praenuntius</i> <sub>(PETM)</sub> |                                         | 0.5451                                |
| <i>epLsar</i> | <i>D. praenuntius</i> <sub>(CF)</sub>   | 0.0019*                                 | 0.0036*                               |
|               | <i>D. praenuntius</i> <sub>(PETM)</sub> |                                         | 0.8913                                |
| <i>Tfv</i>    | <i>D. praenuntius</i> <sub>(CF)</sub>   | 0.8687                                  | 0.8656                                |
|               | <i>D. praenuntius</i> <sub>(PETM)</sub> |                                         | 0.6102                                |

\* Significant *p*-values (*p* < 0.05).

*D. praenuntius*. Observations from modern predator-prey interactions suggest that carnivores weighing <21.5 kg feed mostly on prey that are 45 % or less of their own body mass (Carbone et al., 1999). The largest specimens of *D. praenuntius* from the Clarkforkian are estimated to weigh 21 kg, falling just shy of this carnivore threshold (Solé et al., 2021). Additionally, using equations to calculate mean prey size in modern carnivores supports *D. praenuntius* primarily as a predator of animals weighing less than 10 kg such as early ungulates like *Ectocion* and *Sifrhippus* (Gingerich, 2006; Peters, 1983; Secord et al., 2012).

More regular large bone consumption may account for higher complexity in *D. praenuntius*<sub>(PETM)</sub> and *D. praenuntius*<sub>(Wa)</sub> than *A. jubatus*. Differences in predator body mass may account for some of this difference as even the largest *D. praenuntius* individual is roughly half the size of the average adult *A. jubatus* (Boast et al., 2013). Once again using equations from Peters (1983), maximum prey body mass for a 21 kg

*D. praenuntius* would have been nearly 35 kg. Even if prey of similar size were consumed by both taxa, bones would be relatively larger to the comparatively smaller *D. praenuntius* and may leave more complex dental microwear. To better resolve this, more work is needed to better understand the role bone size plays in the creation of dental microwear features.

Alternatively, differences in the thickness of bones consumed may contribute to differences in dental microwear complexity. As previously mentioned, *A. jubatus* tend to avoid the larger bones of the appendicular skeleton when feeding upon large prey (Phillips, 1993). Limb bones tend to be some of the thickest on a carcass while also containing large amounts of nutrition via fatty yellow bone marrow (Gurevitch et al., 2007). If larger diameter bones create more complex dental microwear, *D. praenuntius* from the PETM and early Wasatchian may have targeted thicker bones such as those of the pelvis and limb that are often avoided by *A. jubatus*. We further emphasize the need to determine the role of bone thickness on the formation of dental microwear.

Dental microwear in *D. praenuntius* from the PETM and early Wasatchian more closely approximates that of *Pan. leo* than *A. jubatus* in possessing greater complexity (Table 3, Figs. 3A, B, 4A). Despite general similarities in post-canine dentition, significantly different dental microwear between these two felids suggests differential prey or carcass exploitation (Schubert et al., 2010; Van Valkenburgh, 1996). *Pan. leo* tends to prefer prey an order of magnitude larger than those preferred by *A. jubatus*, while also scavenging considerably more often (Hayward and Kerley, 2008; Pereira et al., 2014; Ritwika et al., 2024). Additionally, *Pan. leo* often consumes between 40 and 60 % of medium (10–100 kg) and large (>100 kg) carcasses (Amorós et al., 2020). These ecological differences are in general agreement with previously reported dental microwear that suggest greater durophagy in *Pan. leo* (Schubert et al.,

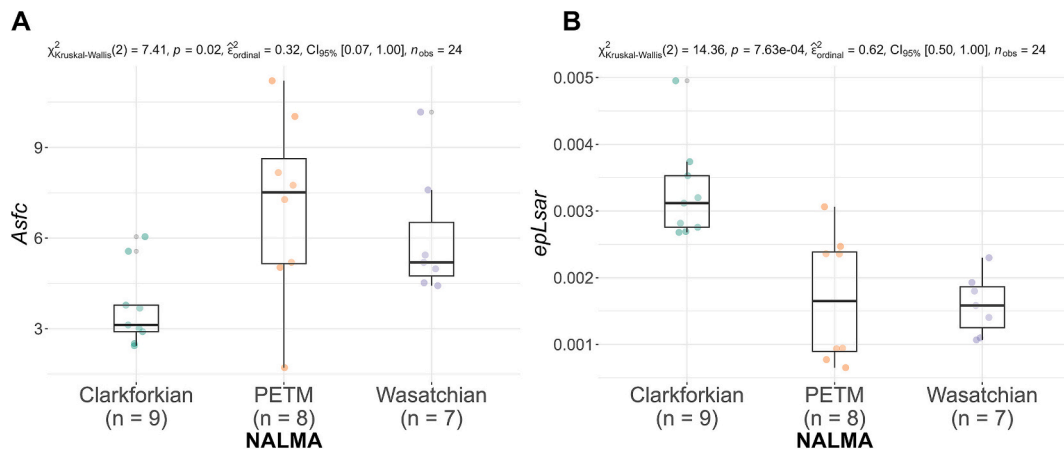


**Fig. 5.** Results of dental microwear texture analysis for *Dissacus praenuntius* across the Clarkforkian, Paleocene-Eocene Thermal Maximum (PETM), and Wasatchian North American Land Mammal Ages (NALMA). Significant differences between (A) complexity (*Asfc*) and (B) anisotropy (*epLsar*) adjusted using Benjamini-Hochberg procedure.

2010; DeSantis et al., 2017). In contrast, anisotropy in *D. praenuntius*<sub>(CF)</sub> is significantly greater than in *Par. leo* and is congruent with greater tough flesh consumption (Table 3, Fig. 4B). Whether this suggests preference for tougher flesh or general dietary habits to *A. jubatus* is unclear.

Dental microwear in *D. praenuntius* showed variable similarities to that of extant hyaenids respective to NALMA. *D. praenuntius*<sub>(CF)</sub> showed significantly lower complexity and textural fill volume, as well as higher anisotropy compared to *C. crocuta* (Table 3, Fig. 4). Textural fill volume was also lower than in *H. hyaena*, with differences in complexity and anisotropy falling just shy of significance at  $p < 0.05$  (Table 3, Fig. 4). These results suggests greater tough flesh and lesser bone consumption in *D. praenuntius*<sub>(CF)</sub> compared to some modern bone-crushing hyaenids. In contrast, no significant differences in complexity or anisotropy were found between these hyaenids and *D. praenuntius* from the PETM and early Wasatchian (Table 3, Figs. 3C, D, 4). *D. praenuntius*<sub>(Wa)</sub> also exhibited significantly lower textural fill volume than *H. hyaena*. No significant differences in complexity, anisotropy, or textural volume were recovered between *D. praenuntius* and *Par. brunnea* (Table 3).

Public perception often erroneously depicts hyaenas as dedicated scavengers. While *Par. brunnea* predominantly scavenge large vertebrates, *C. crocuta* are prolific predators and derive 50–98 % of their diet from successful prey capture (Gasaway et al., 1991; Kingdon and Hoffmann, 2013). *H. hyaena* tend to fall between these two extremes, relying on a mix of large vertebrate carrion, small vertebrate/invertebrate prey, and some plant material (Kruuk, 1976). However, all three taxa possess adaptations for and habitually consume large bones (Fourvel et al., 2015; Therrien, 2005). Based on taphonomic studies of hyaena dens, reduction and fragmentation of long bones is more intensive in *H. hyaena* and *Par. brunnea* than it is for *C. crocuta* (Fourvel et al., 2015). Habitual consumption of large bones in *D. praenuntius*<sub>(PETM)</sub> and *D. praenuntius*<sub>(Wa)</sub> therefore has some support through dental microwear similarity to these hyaenids.

The dietary implications of textural fill volume are more unclear. Previous studies (as well as those presented here) have found some positive correlations between complexity and textural fill volume (DeSantis et al., 2017). However, it remains a relatively poor metric for differentiating species with different diets (Scott et al., 2006, 2012). Scott et al. (2012) postulated that greater textural fill volume is indicative of larger amounts of dental microwear, particularly in response to mastication of higher quantities of large abrasives. DeSantis and Haupt (2014) suggest differences in textural fill volume may be related to the coarseness of objects consumed. Ergo, textural fill volume should be used in concert with complexity to refine more minute differences between taxa with overall similar complexity. Significantly greater

textural fill volume in *H. hyaena* compared to *D. praenuntius* is therefore interesting. *H. hyaena* seems to have a more diverse diet than the other species of hyaena, including small, medium, and large vertebrates, invertebrates, plant material, and even human trash into their diet (Kingdon and Hoffmann, 2013 and references therein). It is therefore possible that a greater diversity of hard objects drives textural fill volume while having only minor impacts on complexity. From this, it can be inferred that *D. praenuntius* would have consumed brittle objects of lower diversity than those eaten by *H. hyaena*.

Alternatively, insects and hard fruits may have been regular components in the diet of *D. praenuntius*. The exoskeletons of insects and hard fruits have been shown to cause complex and deep dental microwear (Winkler et al., 2022). Previous work has classified *Dissacus* as a “carnivore” as opposed to an “advanced carnivore” (hypercarnivore) based on dental morphology and orientation patch counts, suggesting occasional consumption of non-flesh resources (Chester et al., 2010; Gould and Szalay, 1966). However, distinguishing whether hard/tough plants or animal tissues are responsible for dental microwear without behavioral observation is challenging. Indeed, dental microwear complexity and anisotropy are not significantly different between bone-crushing hyenas despite differences in the quantity of insects and fruits incorporated into their diets (DeSantis et al., 2017). Textural fill volume is significantly higher in *H. hyaena* than in *C. crocuta*, which may reflect observations that the former consumes the widest range of insects, fruits, and vegetation (Kingdon and Hoffmann, 2013 and references therein). *D. praenuntius* from all NALMA show the greatest similarity in textural fill volume to *Par. brunnea* (Table 3, Fig. 4), a taxon that merely supplements its diet with insects, fruits, and vegetation (Kingdon and Hoffmann, 2013 and references therein). Therefore, insects and plant matter may have only made up a small proportion of the diet of *D. praenuntius*.

We recognize that our comparative group of feliforms is not a perfect proxy for the mesonychid *D. praenuntius* due to differences in morphology and considerably larger body sizes of the former. It can be argued that early Cenozoic environments inhabited by archaic mammalian groups like mesonychids are so different from modern ecosystems that there are no perfect analogues with observable diets to compare to (Rose, 2006). However, smaller modern feliforms within the size range of *D. praenuntius* such as *Caracal caracal* Schreber, 1776, *Cryptoprocta ferox* Bennett, 1833, and *Lynx lynx* Linnaeus, 1758 may be more appropriate ecological proxies and should be targeted for dental microwear in the future.

#### 4.2. Differences in dental microwear through the Paleocene-Eocene Thermal Maximum

While admittedly our sample size is small, dental microwear of *D. praenuntius* across the late Paleocene Clarkforkian through the early Eocene Wasatchian NALMA reflects a probable shift in diet that took place during the PETM. Specifically, *Asfc* increases and *epLsar* decreases (Table 4, Fig. 5) which is typically interpreted as lesser flesh and greater bone consumption in faunivores (DeSantis and Patterson, 2017; Schubert et al., 2010). This coincided with a fall in body mass during the PETM documented in Solé et al. (2021).

Significant microwear differences in *D. praenuntius* over time are quite informative when attempting to connect biological and ecological responses to the climatic impact of the PETM. Compared to other PETM taxa such as the herbivorous *Ectocion parvus* Granger, 1915 and *Sifrhippus sandrae* Froehlich, 2002, the omnivorous *Palaeonictis wingi* Chester, 2010, and the early carnivoraform *Uintacyon gingerichi* Heinrich, 2008, *D. praenuntius* only exhibits minor body mass reduction (~20 %; Fig. 6), occurring towards the end of the PETM (Chester et al., 2010; see Table 4 in Solé et al., 2021). Because the smallest individual (UF 253359) was recovered after the hottest PETM temperatures, it seems more likely that *D. praenuntius* body mass was affected directly by biotic and ecological factors during the PETM (such as changing prey size or community) than by changes in mean annual temperature or precipitation (Lavergne et al., 2010).

Our modern feliform proxies (see Section 4.1) suggest that *D. praenuntius*<sub>(CF)</sub> was a cheetah-like generalist faunivore that consumed relatively few bones while *D. praenuntius*<sub>(PETM)</sub> and *D. praenuntius*<sub>(Wa)</sub> more closely resemble lions and bone-crunching hyaenids (Table 3, Fig. 4). The implications of these apparent ecological shifts are a bit nuanced and unclear, especially in terms of cause versus effect. If body mass reduction was an ecological response to limited prey (and therefore decreased net primary productivity), these dental microwear patterns may reflect a change in prey species preference, greater carcass utilization, or increased scavenging of meat-depleted carrion.

Increasing complexity and decreasing anisotropy across the late Paleocene – early Eocene may represent more complete consumption of small prey as well as greater incorporation of larger diameter bones

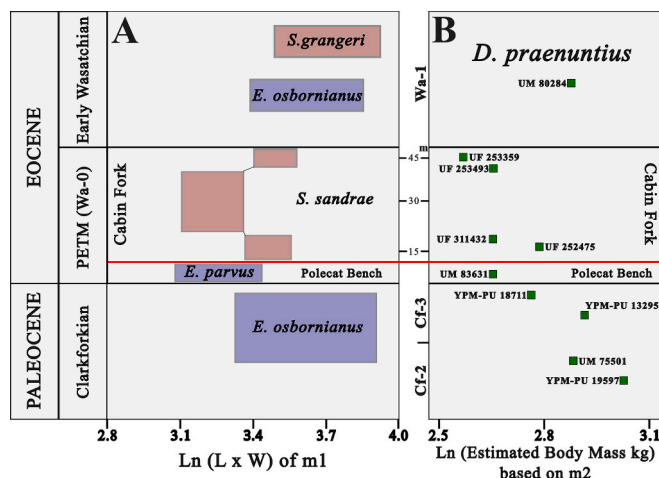


Fig. 6. Chart showing body mass changes in three lineages across the PETM in the Bighorn Basin. (A) Lower 1st molar area in the phenacodontid *Ectocion* and early equid *Sifrhippus*. Note that *Ectocion parvus* specimens derived from Polecat Bench and have unresolved stratigraphy within the PETM. *Sifrhippus sandrae* body mass is plotted through the PETM from the Cabin Fork locality; (B) Estimated body mass of *Dissacus praenuntius* during the Clarkforkian, PETM, and early Wasatchian originally presented by Solé et al. (2021). Note that UM83631 was recovered from Polecat Bench and is not accurately positioned within the stratigraphy of the Cabin Fork locality.

(Fig. 5). Body mass reduction in nearly 40 % of PETM taxa suggests prey size, but not available biomass affected *D. praenuntius* ecology (Gingerich, 1989, 2006; Secord et al., 2012). At 18 kg, an average specimen of *D. praenuntius* during the Clarkforkian would have been a terrestrial predator of small vertebrates such as archaic “condylarth” ungulates, rodents, tillodonts, and possibly plesiadapiforms (Gingerich, 1989). As body mass within some of these taxa decreased during the PETM (see Fig. 1 in Secord et al., 2012), *D. praenuntius* prey choice may have become broader or shifted towards animals that were more abundant, possibly including some of the many immigrant taxa (Artiodactyla and Perissodactyla) that first appeared in the Bighorn Basin early during the PETM (Smith et al., 2006).

A shift towards less fleshy, bonier prey as symptomatic of ecological stress agrees with dental microwear patterns observed elsewhere in the fossil record. Coyotes (*Canis latrans* Say, 1823) from the La Brea Tar Pits in California shifted towards greater durophagy in the wake of megafaunal extinctions during the Pleistocene-Holocene transition (DeSantis et al., 2019). In East Africa, black-backed jackals (*Lupulella mesomelas* Schreber, 1775) shifted towards greater durophagy over the past century, possibly as a response to anthropogenic environmental impact (Schwartz et al., 2025). Most telling is that a substantial number of large carnivores in Africa have shifted towards small prey consumption in response to declining populations of large prey species over the past half-century (Creel et al., 2018). It seems plausible then that as larger preferred prey became less abundant during the PETM, *D. praenuntius* adapted by shifting towards smaller, more common prey that provided relatively less flesh with more bone (Rouse et al., 1970).

Based on similarity to the dental microwear of extant hyaenids, more complete carcass utilization or scavenging is an alternative explanation for *D. praenuntius* dental microwear across the PETM. Food unavailability or stress often drives carnivores towards exploitation of lesser-consumed or suboptimal resources. In modern scavengers such as *Par. brunnea*, food stress results in more intensive bone breakage and consumption (Fourvel et al., 2015). The consumption of bones and desiccated hide has also been observed in dingoes (*Canis lupus dingo* Meyer, 1793) during periods of chronic food shortage (Allen, 2010). Late-stage carcass consumption often results in the utilization of less-desirable or otherwise inaccessible portions passed over by earlier consumers, including nutrient rich marrow-containing bones (Kane et al., 2017). Under this scenario, greater complexity in *D. praenuntius*<sub>(PETM)</sub> reflects exploitation of less-favorable resources such as defleshed bones and carcasses during the PETM.

An alternative driver of dental microwear is exogenous grit. There remains fierce debate about the role of grit in the formation of dental microwear, with research coming to opposing conclusions (Ackermans et al., 2020; Merceron et al., 2016; Winkler et al., 2020). Sedimentology and precipitation proxies suggest increasing aridity and accompanying small-particle grit during the PETM, implying the possibility of higher grit consumption by animals during this time (Kraus et al., 2015; Wing et al., 2005). In-vitro studies testing the role of grit on dental microwear formation found that accompanying food mechanical properties have an effect on the impact of grit (Hua et al., 2020). To summarize, differences in complexity and anisotropy were minimal when grit was applied to meat. We therefore consider it unlikely that increased intake of exogenous grit is a plausible explanation for dental microwear patterns recovered for *D. praenuntius* during the PETM. However, the relationship between grit and dental microwear needs to be fully resolved before conclusions can be drawn about grit during the PETM.

One of the main limitations towards implicating a cause for body mass reduction in *D. praenuntius* is a relative dearth of fossils from the middle body (20–40 m level, Cabin Fork locality, Fig. 6) of the PETM (Solé et al., 2021). This hiatus conceals the true nature of body mass change in *D. praenuntius* across the main “body” of the PETM. The recovery of more fossils from the crucial time will help pinpoint the timing of body mass reduction and indicate whether temperature or ecological change may be implicated in the observed patterns in *D. praenuntius*.

The general similarities of dental microwear between *D. praenuntius* during the PETM and early Wasatchian merits discussion (Table 4, Fig. 5). Despite a return to pre-PETM body mass, dental microwear of *D. praenuntius*<sub>(Wa)</sub> more closely resembles that of *D. praenuntius*<sub>(PETM)</sub> than of the similar-sized *D. praenuntius*<sub>(CF)</sub>. This suggests that ecological changes that took place during the PETM persisted even after environmental conditions improved and *D. praenuntius* body mass increased (Fig. 6). The PETM coincides with the beginning of the Wasatchian NALMA (Wa-0) as diagnostic taxa first immigrate into Wyoming during this time (Gingerich, 1989). Even after climatic conditions improved to pre-PETM levels, Wasatchian ecosystems were composed of taxa that were far different than those of the Clarkforkian including multiple species of potential prey such as perissodactyls, artiodactyls, and primates, as well as potential faunivorous competitors including hyaenodonts, oxyaenids, carnivoramorphs, and the large mesonychid *Pachyaena* (Gingerich, 1989; Rose et al., 2012). Therefore, it is not unexpected that dental microwear from the early Wasatchian would closely resemble that from the PETM.

Sudden ecological shifts among faunivores are not permanent and can be “reversed” upon restoration of previously disturbed habitats or food-webs. *Pan. leo* in Zakouma National Park, Chad were documented shifting from small prey to more-typical large prey in response to significant recovery of wildlife populations (Fratlicelli et al., 2024). That *D. praenuntius*<sub>(Wa)</sub> did not completely return to prey typical of the Clarkforkian despite the reemergence of pre-PETM conditions suggests that new immigrant fauna in the Bighorn Basin during the PETM had notable impacts on its ecology. It is noteworthy that immigration during the PETM did not drive considerable extinction of native fauna in the Bighorn Basin, likely due to unsaturated niche space and elevated primary productivity towards the end of the PETM “body” (Fraser and Lyons, 2020; Whittingham et al., 2024). This makes it unlikely that *D. praenuntius* was forced to shift to the only prey available in its habitat. Rather, both immigrant and native taxa were potential prey in the early Wasatchian Bighorn and Clarks Fork basins. Non-significant differences in complexity between *D. praenuntius*<sub>(CF)</sub> and *D. praenuntius*<sub>(Wa)</sub> (Table 4, Fig. 5) may then reflect relaxed bone consumption due to alleviation of previous food stress. We caution this interpretation though as our sample size of *D. praenuntius*<sub>(Wa)</sub> is admittedly small ( $n = 7$ ) and differences in complexity approach significance ( $p = 0.0884$ ). Our study would benefit from more samples following the PETM recovery to better understand how *D. praenuntius* responded to the alleviation of PETM climatic conditions.

Additionally, the impact of new competitors on the dietary ecology of *D. praenuntius* during the Wasatchian should be considered. The diversification of similarly sized faunivores with dentition better adapted than mesonychids for the processing of flesh may have driven *D. praenuntius* towards utilization of harder resources like bones or fruits in order to avoid competition. However, the much larger mesonychid *Pachyaena* also first appears in Wyoming during the PETM (Gingerich, 1989). Examinations of the cranial, dental, and postcranial morphology of *Pachyaena* suggest that it was a cursorial bone-crushing scavenger that traversed long distances in search of carcasses (Zhou et al., 1992). In northwestern Europe, the disappearance of *Dissacus* in the early Eocene coincides with the first appearances of *Pachyaena* and the oxyaenid *Palaeonictis* in the region (Solé et al., 2018). Notably, *D. praenuntius* apparently became extinct in the Bighorn Basin during the middle Wasatchian (Clyde, 1997; Solé et al., 2021). This coincides with the diversification of *Pachyaena* and the immigration of the smaller mesonychid *Hyaenodictis willwoodensis* O’Leary and Rose, 1995 into the Bighorn Basin, hinting at potential competitive replacement (Solé et al., 2018, 2023). To evaluate the role of competition in the dietary ecology and eventual extinction of *D. praenuntius*, dental microwear from these Wasatchian faunivores needs to be collected.

## 5. Conclusions

Dental microwear from 24 specimens of *Dissacus praenuntius* spanning the late Paleocene – early Eocene exhibited significantly different dental microwear than that of extant feliforms. *D. praenuntius* from the Clarkforkian was found to be most similar to cheetahs (*A. jubatus*), while specimens from the PETM and early Wasatchian showed greatest similarities to lions (*Pan. leo*) and bone-crushing hyaenids. There were significant differences in anisotropy and complexity in *D. praenuntius* across the PETM, with complexity increasing and anisotropy decreasing over time.

These results compliment earlier research that recovered *D. praenuntius* as a mesocarnivore with the ability to occasionally process bones. Most crucially, our results suggest that along with modest body mass reduction, this species exhibited a dietary shift towards greater durophagy during the PETM which persisted into the early Wasatchian. We have shown that ecological changes accompanied body mass reduction in response to rapid climatic warming and drying. Our results suggests that changes in faunal body size, abundance, and diversity will have direct impacts on modern carnivore body mass over time. Carnivores that possess sufficient dietary flexibility are likely to be less affected by changes in prey biology and ecology that result from climate change and habitat destruction. Thus, the very ancient record of rapid warming and drying emphasizes the need for modern ecological studies on shifts related to diet.

## Author contribution

A.F.S. conceived of this study, prepared samples, conducted laboratory work, collected data, performed statistical analyses, wrote all drafts of the manuscript, and created the figures. R.S.S. advised this study, contributed to manuscript revisions, and gave final approval for publication. L.R.G.D. provided access to equipment, processed data, and contributed to manuscript revisions.

## CRediT authorship contribution statement

**Andrew Schwartz:** Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Larisa R.G. DeSantis:** Writing – review & editing, Software. **Rob S. Scott:** Writing – review & editing, Validation, Project administration.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2025.113089>.

## Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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