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Theropod teeth from the upper Maastrichtian Hell Creek Formation "Sue" Quarry: New morphotypes and faunal comparisons

TERRY A. GATES, LINDSAY E. ZANNO, and PETER J. MAKOVICKY



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Isolated teeth from vertebrate microfossil localities often provide unique information on the biodiversity of ancient ecosystems that might otherwise remain unrecognized. Microfossil sampling is a particularly valuable tool for documenting taxa that are poorly represented in macrofossil surveys due to small body size, fragile skeletal structure, or relatively low ecosystem abundance. Because biodiversity patterns in the late Maastrichtian of North American are the primary data for a broad array of studies regarding non-avian dinosaur extinction in the terminal Cretaceous, intensive sampling on multiple scales is critical to understanding the nature of this event. We address theropod biodiversity in the Maastrichtian by examining teeth collected from the Hell Creek Formation locality that yielded FMNH PR 2081 (the *Tyrannosaurus rex* specimen "Sue"). Eight morphotypes (three previously undocumented) are identified in the sample, representing Tyrannosauridae, Dromaeosauridae, Troodontidae, and Avialae. Noticeably absent are teeth attributed to the morphotypes *Richardoestesia* and *Paronychodon*. Morphometric comparison to dromaeosaurid teeth from multiple Hell Creek and Lance formations microsites reveals two unique dromaeosaurid morphotypes bearing finer distal denticles than present on teeth of similar size, and also differences in crown shape in at least one of these. These findings suggest more dromaeosaurid taxa, and a higher Maastrichtian biodiversity, than previously appreciated.

Key words: Dinosauria, theropod, morphometrics, paleoecology, Cretaceous, North America.

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Introduction

The Maastrichtian Hell Creek and Lance formations provide critical information on the biodiversity and paleoenvironments of western North America leading up to the terminal Cretaceous extinction (Estes et al. 1969; Bryant 1989; White et al. 1998; Johnson et al. 2002; Fricke and Pearson 2008). These data have been interpreted as supporting either the cataclysmic or gradualistic views of dinosaur extinction at the K–T boundary. Although some studies utilize morphological disparity data (Brusatte et al. 2012) in the extinction debate, the vast majority invoke species-level biodiversity trends prior to and across the K–T boundary (e.g., Archibald 1992; Hurlbert and Archibald 1995; Fritsch and Hsu 1999; Sheehan et al. 2001; Fastovsky and Sheehan 2005). As such, shifts in latest Maastrichtian biodiversity in North America have profound implications for deciphering extinction rates prior to and during the K–T extinction.

Microfossil localities are the most utilized source of taxonomic data for biodiversity studies in the Hell Creek and Lance formations. Whereas skeletal remains of large dinosaur genera such as *Triceratops*, *Edmontosaurus*, and *Tyrannosaurus* are relatively abundant in these units (Horner et al. 2011), other dinosaur clades are rarer and most of their known diversity is recorded by isolated teeth. Maniraptoran theropods are an excellent example of a clade that suffers from a poor macrofossil record in North American Maastrichtian sediments. To date, only one species is known from substantial skeletal material (Lamanna et al. 2011), and nearly all knowledge of this group comes from isolated teeth.

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Although there is a wide literature on the morphology and systematics of theropod teeth (Currie et al. 1990; Fiorillo and Currie 1994; Baszio 1997b; Sankey et al. 2002; Smith et al. 2005; Sankey 2008; Longrich 2008; Larson and Currie 2013), much remains to be learned. Principally, few studies have compared variation in taxonomic and morphological makeup between localities of the same formation (Baszio 1997a). In this paper we describe isolated theropod teeth from the Hell Creek Formation locality that produced the *Tyrannosaurus rex* specimen FMNH PR 2081, known as "Sue". In addition to describing several new tooth morphotypes, we use morphometrics to evaluate variation between theropod teeth at several Maastrichtian localities.

Institutional abbreviations.— AMNH, American Museum of Natural History, New York, USA, FMNH, Field Museum of Natural History, Chicago, USA; MOR, Museum of the Rockies, Bozeman, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA.

Other abbreviations.—FABL, fore-aft basal length; PCA, principal components analysis.

Material and methods

Sediment from the "Sue" locality in Faith, South Dakota consists primarily of fine-grained sand and silt with interbedded plant layers and abundant microfossils. Approximately 5 m^3 of sediment (2 tons) from the field jackets of the *Tyrannosaurus rex* specimen FMNH PR 2081 was screen washed through 4 mesh, 20 mesh, and 30 mesh sieves. Ten individual theropod teeth were discovered in the 20-grade size matrix, referable to four taxonomic groups. Here we describe and classify isolated teeth to morphotype and restrict taxonomic referrals to the suprageneric level following Zanno et al. (2013), based on established characteristics identified from a variety of comprehensive microfaunal studies (Currie et al. 1990; Baszio 1997b; Sankey et al. 2002; Sankey 2008; Larson and Currie 2013) in combination with morphometric analyses.

Measurements on isolated teeth include fore-aft basal length (FABL), basal labiolingual width, height as measured from the base of the tooth crown to the apex perpendicular to the crown base, and denticle count/mm along the middle portion of the posterior carina. Principal components analysis (PCA), Discriminant analysis, plots, and statistical analyses were performed in PAST v. 2.16 (Hammer et al. 2001). Specimens were imaged on a Carl Zeiss NTS EVO60 XVP scanning electron microscope in both high and variable pressure vacuum modes, using VPSE detectors without extraneous coating.

The teeth described in this study were supplemented with specimens from databases of Smith et al. (2005) and Sankey (2008) to produce a total specimen count of 178. PCA was run with both mean substitution and pairwise deletion to accommodate missing data. Brown et al. (2012) cautioned that these two methods produce different results based on the amount of missing data. To test for the effect of missing data on our dataset we calculated the squared difference of each eigenvalue from a PCA run with each missing data estimator, producing an estimate for the absolute change in specimen placement within the PCA space. Average squared difference values for each variable within each sample were ranked, and tested for correlation with the percentage of missing data within that same specimen.

Description

Identification of theropod teeth is based on diagnostic characteristics of each taxonomic group and PCA groupings of all isolated theropod teeth from the Sue site, and specimens sampled by Sankey (2008) and Smith et al. (2005) (Fig. 1).

Tyrannosauridae.—FMNH PR 2902 (Fig. 2G) is a small premaxillary tooth sharing a suite of characters with *Tyrannosaurus rex*. The tooth morphotype is characterized by features outlined in Baszio (1997b) and Carr and Williamson (2004), such as D-shaped basal cross section, carinae on lingual side of tooth, and convergence of carinae toward tooth base. PR 2902 is a strongly D-shaped tooth in basal cross-section, with prominent mediolateral carina arching around the lingual side of the tooth, absence of denticles, and a distinct ridge extending along the lingual midline of the crown. A D-shaped premaxillary tooth cross section with a prominent lingual ridge is diagnostic of tyrannosaurids (Brusatte et al. 2010). A handful of other theropod taxa are known to exhibit a much more subtle manifestation of the D-shape, but lack the prominent lingual ridge and are not known to occur in uppermost Cretaceous strata of North America (e.g., *Ornitholestes hermanni*, AMNH 619, LEZ personal observation; allosauroids, Madsen 1976; dromaeosaurids, Currie and Varricchio 2004). Unserrated crowns of this shape were historically referred to the tooth taxon *Aublysodon*, which is widely now considered to represent juvenile teeth of *Tyrannosaurus* (Carr and Williamson 2004). In FMNH PR 2902, the apex angles to the left in labial view, indicating that it derives from the left premaxilla.

Dromaeosauridae.—FMNH PR 2893, 2895, and 2898 (Fig. 2A) show labiolingually wide tooth bases, oval in shape, and constricted slightly in the center of each lingual and labial crown face forming a weak hourglass-like basal cross-section. This constriction is widespread among dromaeosaurids, including unenlagiine dromaeosaurids (Gianechini et al. 2011), *Velociraptor mongoliensis*, *Bambiraptor* (Turner et al. 2012), but is not observed in the Hell Creek/ Lance morphotype designated as *Zapsalis* sp. (sensu Larson and Currie 2013), which possesses a convex lingual aspect and a flattened labial aspect (Sankey et al. 2002). Additionally, the mesial portion of the tooth base is slightly larger than the distal region, producing an egg-shaped cross section. Minute denticles bearing subtly rounded tips are present on the apical two-thirds of the mesial tooth crown, but terminate below the apex of the crown as

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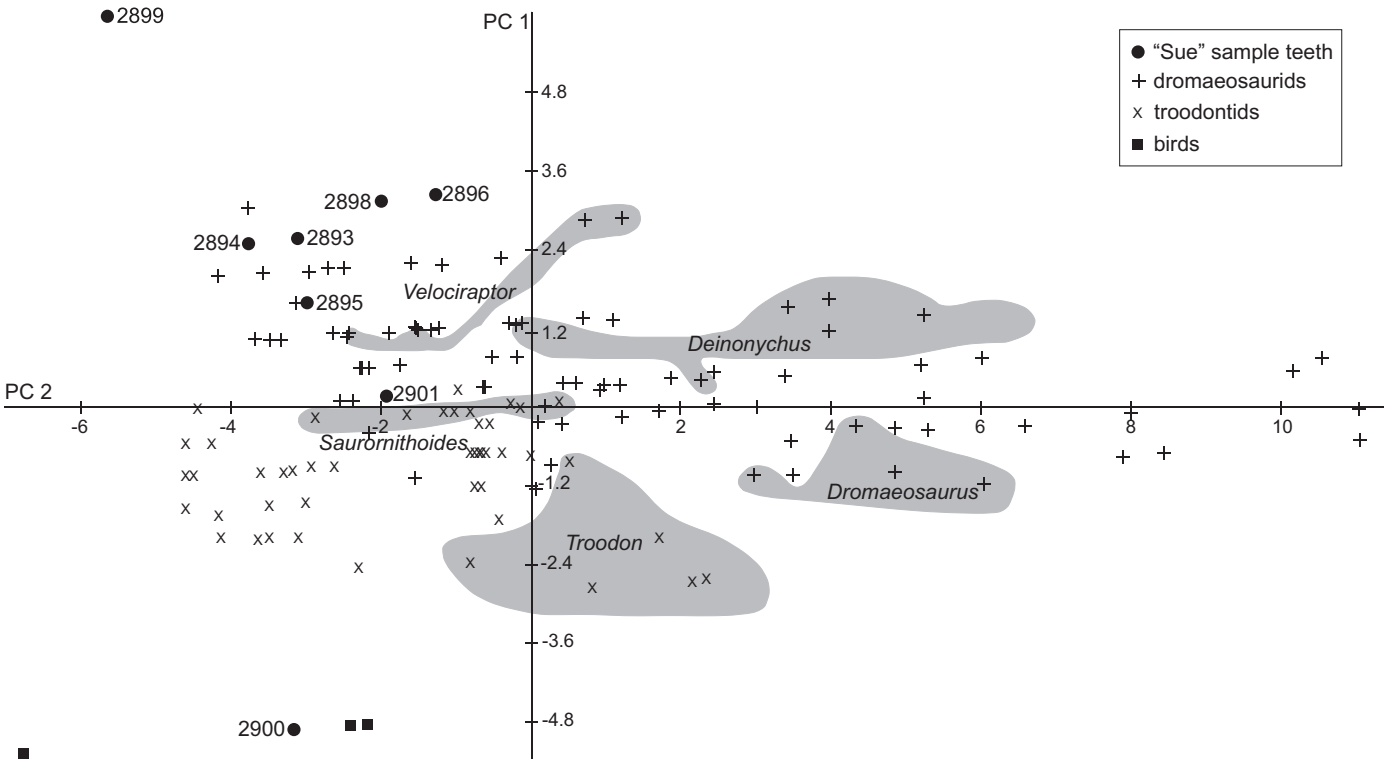


Fig. 1. Principal components analysis of all teeth from the "Sue" theropod sample, Sankey (2008) tooth database (except *Paronychodon* and *Richardoestesia*), and Smith et al. (2005; *Deinonychus*, *Dromaeosaurus*, and *Troodon*). Principal components: (1) ([0.41 FABL]+[0.1 basal width]+[0.90 height]-[0.07 denticles/mm]) explained 77.01% of variance; (2) ([-0.03 FABL]+[0.02 basal width]+[0.09 height]+[1 denticles/mm]) explained 16.58% variance; and (3) ([0.82 FABL]+[0.40 basal width]-[0.41 height]+[0.05 denticles/mm]) 5.00% variance.

in *Deinonychus* (Ostrom 1969). Significantly larger denticles with rounded tips and little to no interdenticle spacing are present along the entire distal tooth crown. A distal carina without denticles or with denticles significantly smaller than those on the mesial carina is a diagnostic trait of dromaeosaurids or a more inclusive clade within Dromaeosauridae (Currie et al. 1990; Turner et al. 2012). FMNH PR 2894 possesses one strong ridge near the middle of the tooth, with weaker ridges on either side delimiting two flat surfaces between them, which are not present on FMNH PR 2893, 2895, or 2898. This feature has been described as variable by Larson (2008), Longrich (2008), and Sankey (2008). The flattened areas preserve enamel; therefore, these are likely not wear facets on the lingual side of the tooth. A variable number of longitudinal ridges on the lingual and sometimes labial crown face were used to diagnose the tooth taxon *Paronychodon* (Larson 2008), but such ridges are observed in teeth that can be attributed to different theropod clades based on shape and denticle counts. *Zapsalis* (Larson and Currie 2013) and cf. *Saurornitholestes* (Sankey 2008) both possess ridges of varying number. This morphotype differs from *Zapsalis* sp. described by Sankey (2008) in the constriction of the tooth base. The same feature plus the smaller relative denticle size differentiates these "Sue" quarry teeth from cf. *Saurornitholestes* (Sankey 2008). FMNH PR 2893 has seven distal denticles/mm (height = 12.88 nm, width = 15.44 nm), FMNH PR 2894 has seven distal denticles/mm (height = 3.57 nm, width = 2.52 nm), FMNH PR 2895 has six distal denticles/mm, whereas FMNH PR 2898 has distal eight denticles/mm, although this count was taken toward the base of the crown instead of the middle as in the other samples, because mid-carina denticles are worn off on this specimen. The tooth morphotype is strongly recurved.

FMNH PR 2896 (Fig. 2B) overall is long and mesiodistally narrow, which differs from the more squared dromaeosaurid teeth described above, and represents a morphotype unique to the Hell Creek Formation based on published accounts and on comparison with other dromaeosaurid taxa (Fig. 1). The base is oval with no apparent constriction on labial or lingual surfaces, in contrast to all other dromaeosaurid tooth morphotypes from the "Sue" locality. Medial and lateral aspects of the crown are smooth and unornamented. Mesial denticles are slightly more prominent than those on other dromaeosaurid teeth by being approximately equal in height to distal denticles, although shorter in fore-aft width. Additionally, they extend from the apex to mid-crown. Tightly packed distal denticles are wider than long and bear rounded to pointed tips (height = 9.14 nm, width = 6.11 nm). This morphotype differs from others previously identified by having prominent denticles on the mesial carina. *Zapsalis*, cf. *Dromaeosaurus*, and cf. *Saurornitholestes* have minute to missing denticles on the mesial carina (Sankey 2008; Larson and Currie 2013).

FMNH PR 2897 (Fig. 2C) lacks the tooth base, but the preserved portion of the crown is nearly identical to *Zapsalis* sp. (Sankey et al. 2002; Larson 2008). The most diagnostic feature is the presence of at least seven prominent ridges with accompanying furrows on the rounded side of the tooth and

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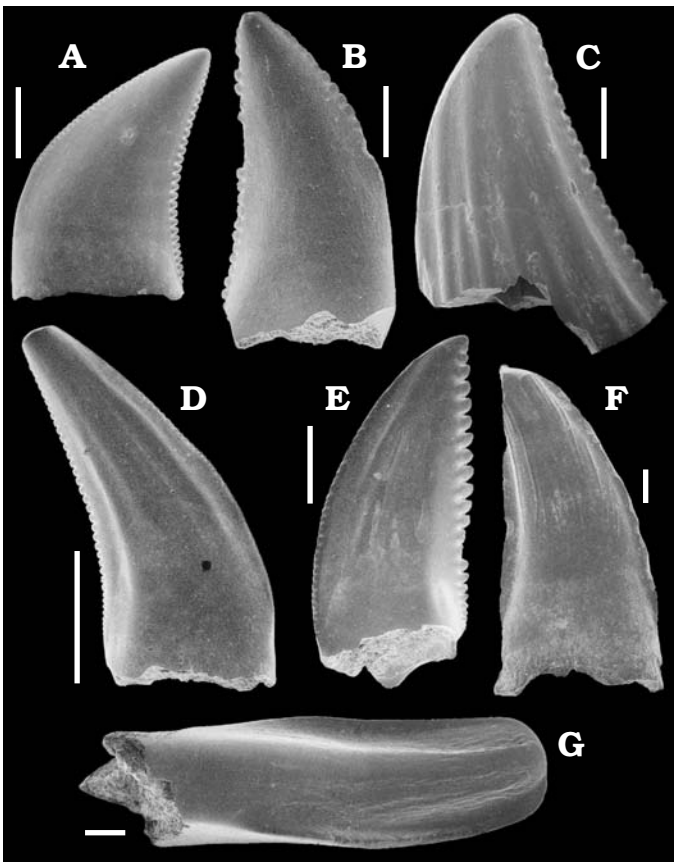


Fig. 2. Scanning electron image of select theropod teeth from the late Maastrichtian "Sue" locality, USA. **A**–**D**. Dromaeosauridae: FMNH PR 2893 (**A**), FMNH PR 2896 (**B**), FMNH PR 2897 (**C**), FMNH PR 2899 (**D**). **E**. Troodontidae: FMNH PR 2900. **F**. Avialae: FMNH PR 2901. **G**. Tyrannosauridae: FMNH PR 2902. Scale bars 1 mm (refer to Table 1 for measurements of each tooth).

a similar configuration on the opposite, flat side of the tooth. These ridges may originate from the base of the tooth and converge toward the tip, some terminating, while the remainder diminish gradually a short distance from the broadened worn apex. The distal denticles are short, straight along the proximal edge, and rounded at each corner with a well-defined gap between denticles. As such, their density of five denticles/mm is less than that in other dromaeosaurid teeth from the "Sue" quarry. Denticle height along the central carina is 19.77 nm and 8.73 nm wide. Denticles are absent on the mesial carina.

FMNH PR 2899 (Fig. 2D) represents a morphology not previously described in the literature to our knowledge. It is referable to Dromaeosauridae based on the synapomorphic presence of an oval-shaped base, mesial and distal denticulate carinae, morphology of the denticles, and recurvature of the crown. Yet, this specimen still falls well outside the cluster of other dromaeosaurid taxa in the PCA results seen in Figs. 1, 4, 5, and 6. In general aspect, the specimen is apically long and labiolingually narrow throughout the crown. The tooth base is oval with slight constriction on the medial and lateral sides as in the other dromaeosaurid teeth described above. Four rounded, low ridges rise from the base and extend to the apex of the crown. The basal half of the tooth is recurved, whereas the apical portion is straight, extending caudoapically. Denticles are present on the central portion of the mesial carina, although they are minute, with a count of 19/mm. Distal denticles are apically tall but diminutive, with well-rounded tips and little to no interdenticle spaces. They occur along the entire length of the tooth crown. Distal denticle height at the central carina is 16.68 nm and 6.67 nm wide. We compared FMNH PR 2899 to the *Richardoestesia* morphotype in a PCA (Fig. 3), and found it to be markedly different from *Richardoestesia* teeth.

Troodontidae.—FMNH PR 2901 (Fig. 2E) has an oval to subcircular base, and lacks a basal constriction. The lingual side of the tooth is flattened, whereas the labial side is convex. Faint longitudinal ridges sculpture the length of both sides. In general aspect the tooth is "fin"-shaped, bearing a relatively vertical distal keel and strongly recurved mesial margin. The mesial carina bears a well-offset keel and minute denticles. As is typical of derived troodontids including *Troodon*, *Saurornithoides*, and *Zanabazar* lateral teeth (Makovicky and Norell 2004), the distal denticles of FMNH PR 2901 are relatively large (height = 26.74 nm, width = 24.12 nm) and angled apically, with pointed to rounded tips. There is minimal interdenticle spacing.

Teeth approximating the morphology seen in FMNH PR 2901 are attributed to the tooth taxon *Pectinodon bakkeri* (Carpenter 1982; Longrich 2008) or *Troodon* sp. "flattened morphology" of Sankey (2008). Based on comparisons with troodontid teeth from the Lance Formation (Longrich 2008), it is possible that FMNH PR 2901 represents a premaxillary tooth. The one noticeable difference between this specimen and those of *Pectinodon* figured in Longrich (2008: figs. 9.5, 9.6) is the prominent keel on the mesial carina of FMNH PR 2901.

The troodontid tooth from the "Sue" quarry, FMNH PR 2901, differs considerably from those troodontid teeth from the Lance and Hell Creek formations (Fig. 4, based on Sankey (2008) database) as well as from *Troodon* (Fig. 1). When analyzed within the full taxonomic dataset, FMNH PR 2901 is most similar to *Saurornithoides*. However, given that the Smith et al. (2005) dataset does not contain denticle count for *Saurornithoides*, the similarity shown in Fig. 1 is based solely on dimensions. When compared to the teeth from the Sankey (2008) database, FMNH PR 2901 is unique in possessing a greater denticle/mm count relative to other troodontid teeth of similar size. Nonetheless, quantitative data is not yet available for comparison with *Pectinodon*; therefore it is unknown how FMNH PR 2901 compares to teeth of that morphotype in this regard.

Avialae.—FMNH PR 2900 (Fig. 2F) is in general aspect taller than wide with a graceful distal recurvature on the dorsal two-thirds of the crown. Mesial and distal carinae are present; however, denticles are noticeably absent. Instead, the carinae are prominently offset from the tooth crown forming a sharp keel. The distal keel is mesiodistally broader than its mesial counterpart. Both labial and lingual sides of the crown

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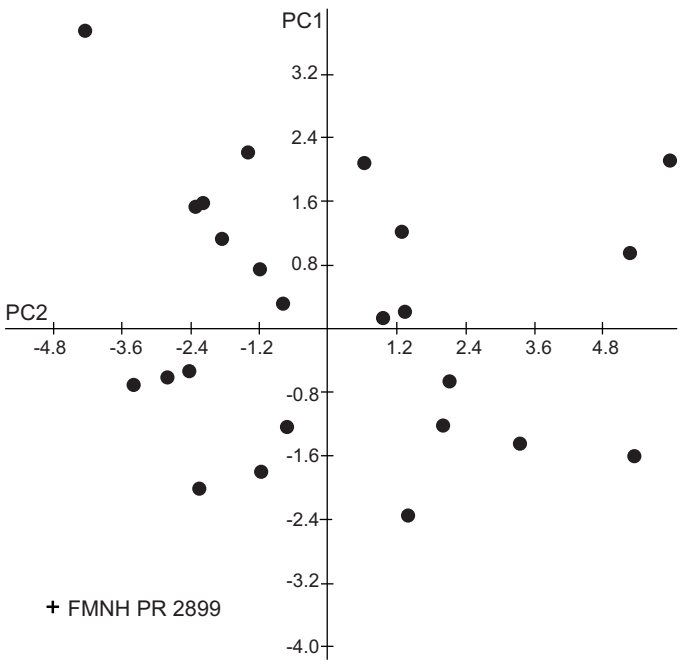


Fig. 3. Principal components analysis of *Richardoestesia* teeth from Hell Creek and Lance formations (circles) and dromaeosaurid tooth FMNH PR 2899 from the Sue quarry (cross). Analysis contained variables height, FABL, and denticles/mm. PC 1 ([0.28 FABL]+[0.94 height]-[0.19 denticles/mm]) explained 76.36% of the variance. PC 2 ([0.03 FABL]+[0.18 height]+[0.98 denticles/mm]) explained 22.51% of the variance. PC 3 ([0.96 FABL]-[0.28 height]+[0.02 denticles/mm]) explained 1.13% of the variance.

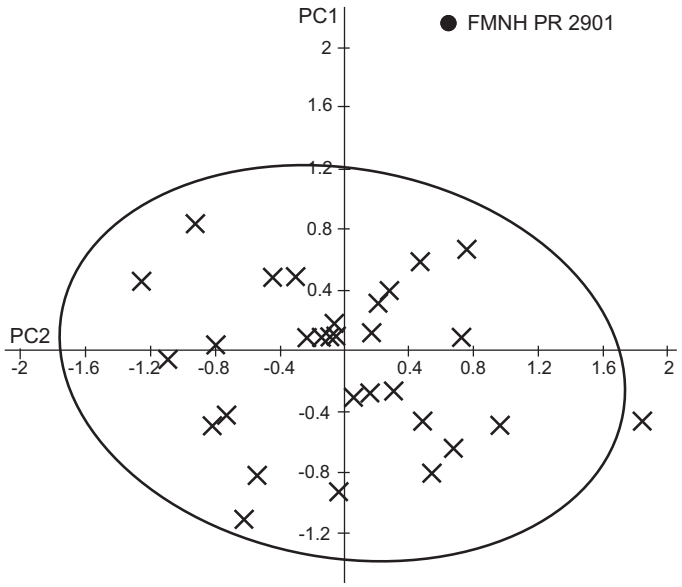


Fig. 4. Principal components analysis of troodontid teeth from Hell Creek and Lance formations (×) and alleged troodontid tooth FMNH PR 2901 from the "Sue" quarry (circle). Analysis contained variables height, FABL, and denticles/mm. PC 1 ([0.45 FABL]+[0.20 basal width]+[0.68 height]-[0.55 denticles/mm]) explained 48.04% of the variance. PC 2 ([0.01 FABL]+[0.03 basal width]+[0.62 height]+[0.78 denticles/mm]) explained 40.73% of the variance. PC 3 ([0.88 FABL]+[0.05 basal width]-[0.37 height]+[0.28 denticles/mm]) explained 9.46% of the variance.

are adorned with irregular longitudinal ridges and furrows that span the crown height. The base is oval.

This tooth is similar in morphology to *Paronychodon* and some teeth attributed to avialans, yet there are also differences of unknown taxonomic importance that render this morphotype unique among known theropod dinosaurs. The longitudinal ridges along the lateral sides of the teeth compare well to those of *Paronychodon* (Currie et al. 1990; Sankey 2008); however, they are not as prominent or numerous as is characteristic of this morphotype. The lack of denticles is a feature of most North American avialan teeth and *Paronychodon* teeth (Currie et al. 1990), yet is also widespread among other globally diverse Late Cretaceous taxa (e.g., Norell et al. 2000; Holtz et al. 2004; Gianechini et al. 2011). Some avialans also share the offset carina seen in FMNH PR 2900 (Sankey et al. 2002; Currie 2005; Currie and Coy 2008; Sankey 2008), as do teeth classified as Archosauria incertae sedis (Longrich 2008). An important distinction between the "Sue" specimen and avialan teeth is that the former does not possess a constricted tooth base as is nearly ubiquitous in the latter. Regarding *Paronychodon*, FMNH PR 2900 is convex on both medial and lateral sides in contrast to the former tooth type, which is convex on only one side (Currie et al. 1990; Sankey et al. 2002; Sankey 2008). The PCA plot (Fig. 1) shows that FMNH PR 2900 clusters with specimens referred to Avialae in the Sankey (2008) database; therefore, in combination with the morphological similarities mentioned above, it appears that this specimen represents a plausible avian morphotype, and provides additional documentation for toothed stem-birds at the end of the Cretaceous (Longrich et al. 2011).

Results and discussion

Morphometric analysis of theropod teeth allows a quantitative approach to defining tooth morphotypes and has been used in prior studies as a means of separating various teeth into distinct morphological groups (Sankey et al. 2002; Smith et al. 2005). We used standardized measurements derived from similar studies (Currie et al. 1990; Sankey et al. 2002; Longrich 2008; Sankey 2008) to investigate clade-level identifications of teeth from the "Sue" locality based on gross morphology in comparison to other Maastrichtian sites in western North America and to available data on Cretaceous paravians worldwide.

Sankey (2008) published a large comparative dataset of measurements taken from Lance and Hell Creek formations theropod teeth, which she tentatively identified as belonging to dromaeosaurid form-genera such as cf. *Saurornitholestes* and cf. *Dromaeosaurus* based on morphology. All teeth in the Sankey (2008) dataset were isolated prior to measurement, and were identified based on discreet traits such as constriction of tooth root, twisting carinae, etc., as well as more subjective characters such as size of denticles and overall appearance. This dataset, in combination with data from in situ dentitions of other theropod taxa from Smith et al. (2005), were used here to identify dromaeosaurid teeth from the

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"Sue" locality and to test for variation within dromaeosaurid teeth obtained from multiple Maastrichtian and Campanian sites. Note that the Sankey (2008) database combines all dromaeosaurid teeth together, including "*Saurornitholestes*" and the various "*Dromaeosaurus*"/*Zapsalis* morphotypes.

Results of missing data estimators show that there is no correlation between percentage of missing data per specimen and the amount of movement of that specimen in the PCA space (Spearman's D, Spearman's rho, and Kendall's tau, p [0.0001]; Supplementary Online Material: SOM available at http://app.pan.pl/SOM/app60-Gates_etal_SOM.pdf). Additionally, mean substitution was shown to result in the highest error rate among the PCA data estimators, yet it did not suffer from exponential error growth at high levels of missing data like all other estimation methods (Brown et al. 2012). Therefore, only the mean substitution method results are presented here, although we should note that there is only a relatively small change between missing data estimators in our dataset.

Troodontid and dromaeosaurid teeth overlap on the PCA plot in Fig. 1. A discriminant analysis was performed to determine if the groups truly represented different morphometric assemblages, and a significant difference in the means ($p = 8.14\times10^{-26}$) of the two a priori hypothesized taxonomic groups (dromaeosaurids and troodontids) was found, which included both confirmed and posited tooth identifications. Ninety percent of these teeth were classified correctly a priori, although almost all of the *Saurornithoides* teeth were placed by the discriminant analysis into the dromaeosaurid group, which probably is a result of not including denticle count for this taxon in the data matrix. Removal of *Saurornithoides* from the database meant that 96.21% of all teeth were properly partitioned a priori ($p = 7.05\times10^{-30}$). Only one *Troodon* tooth (first MOR 553 listed in SOM) was placed in the dromaeosaurid group, whereas four "dromaeosaurid" teeth (UCMP 187025, 187034, 187200, and 187139) were classified as troodontid. These teeth should be reexamined for characteristics more akin to troodontids than dromaeosaurids. The discriminant function produced ([1.37 FABL]+[1.76 basal width]+[0.31 height]+[3.45 denticles/mm]) with an offset constant of 25.58. Most importantly, among the results from this test is that all dromaeosaurid and troodontid teeth from the "Sue" site were correctly classified a priori based on morphology, and that even though FMNH PR 2901 lies close to the boundary of the two morphogroups, its troodontid affinity is robustly supported by statistical analysis.

Morphometric variation of isolated dromaeosaurid teeth.—Principal component analysis of "Sue" dromaeosaurid teeth yields two components that explain 97% of the variation within the sample (Fig. 5). The first component is overwhelmingly dominated by denticles/mm (0.395[FABL]+0.098[basal width]+0.540[height]-0.737[denticles/mm]), indicating that FMNH PR 2899 possesses a much higher density of denticles than all other Maastrichtian dromaeosaurid teeth sampled. There is little variation in denticles per mm amongst the remaining dromaeosaurid teeth. The second component from

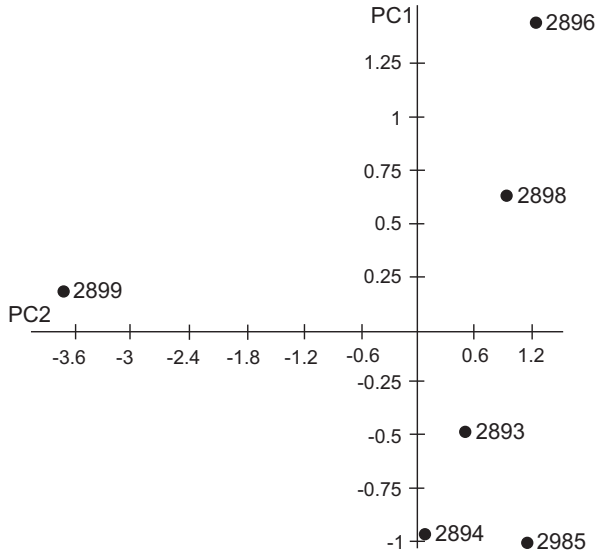


Fig. 5. Principal components analysis of "Sue" quarry dromaeosaurid teeth. Analysis contained variables height, FABL, basal width, and denticles/mm. PC 1 ([0.40 FABL]+[0.1 basal width]+[0.54 height]-[0.74 denticles/mm]) explained 77.53% of the variance. PC 2 ([0.06 FABL]+[0.03 basal width]+[0.79 height]+[0.61 denticles/mm]) explained 20.17% of the variance. PC 3 ([0.91 FABL]+[0.08 basal width]-[0.29 height]+[0.28 denticles/mm]) explained 2.30% of the variance.

the PCA shown in Fig. 5 is more complicated, constituting both denticles/mm and tooth height (0.060[FABL]+0.031[basal width]+0.787[height]+0.613[denticles/mm]). Crown height is expected to vary during ontogeny as well as along the tooth row in mature individuals, which complicates interpreting the importance of this variable within the eigenfunction; however, crown height may also confer a taxonomic signal that remains unaccounted for if, for instance, the "Sue" tooth sample includes small-bodied species. Given that denticles/mm is a strong factor determining PC1 and PC2, this seems to be the most taxonomically informative variable in explaining disparity between the "Sue" quarry dromaeosaurid teeth in our sample. Prior studies (Currie et al. 1990) have proposed ontogenetic variation in denticles/mm as well.

Indeed, based on the PCA (Fig. 1), there may be different theropod taxa in the Sankey (2008) database when one considers the clustered occurrences of *Deinonychus*, *Dromaeosaurus*, and *Velociraptor*. Given the great spread of the Sankey (2008) teeth in this plot, it is not unreasonable to assume at least two and upwards of four dromaeosaurid taxa are sampled, but more information is needed to substantiate this claim.

In order to further investigate variation in the "Sue" dromaeosaurid tooth sample, we used ratios, including crown height/FABL and (denticles/mm)/height (Table 1). The teeth FMNH PR 2899 and 2896 fell outside the t-test 95% confidence interval for the crown height/FABL ratio among all "Sue" site teeth (Table 1). Another t-test recovered FMNH PR 2899 outside the 95% confidence interval of the other "Sue" dromaeosaurid teeth for the ratio of (denticles/mm)/height. Removing FMNH PR 2899 from the sample and rerunning the t-test made FMNH PR 2896 an outlier, whereas the remainder of teeth fell within the 95% confidence interval. These analy-

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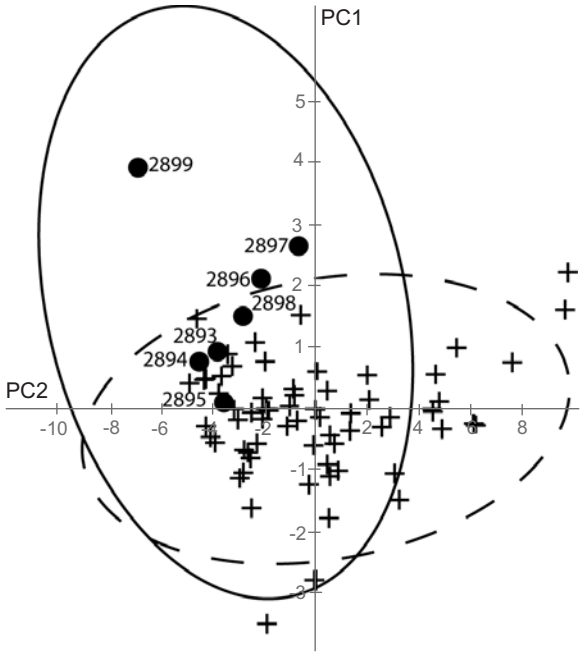


Fig. 6. Principal components analysis of "Sue" quarry dromaeosaurid teeth (dots) in addition to the dromaeosaurid teeth (crosses) included in Sankey (2008). Analysis contained variables height, FABL, and denticles/mm. Basal width was not included because this variable was not included in the Sankey (2008) dataset. PC 1 ([0.38 FABL]+[0 basal width]+[0.90 height]-[0.23 denticles/mm]) explained 89.91% of the variation. PC 2 ([-0.36 FABL]-[0.01 basal width]+[0.38 height]+[0.85 denticles/mm]) explained 6.91% of the variation. PC 3 ([0.85 FABL]-[0.01 basal width]-[0.24 height]+[0.47 denticles/mm]) explained 3.17% of the variation. Ovals are the 95% confidence ellipses for each dataset, "Sue" quarry solid oval and Sankey database in dashed oval. Sue specimens are designated by the specimen number that follows FMNH PR in each instance.

ses support the hypothesis that FMNH PR 2899 and perhaps FMNH PR 2896 are distinct morphotypes from the other dromaeosaurid teeth from the "Sue" locality. Of course, the low sample size (n = 6) means these t-tests are less statistically powerful than those for larger datasets, even with the broadened 95% confidence interval. An attempt to increase the sample size by including the entire Sankey (2008) dromaeosaurid database did not resolve this, because with the larger dataset came a smaller 95% confidence interval. Therefore, given the available data, the combination of diagnostic differences in both denticle counts and shape parameters makes a convincing case for taxonomic distinction of FMNH PR 2899.

When compared to the Sankey (2008) database, most of the "Sue" quarry dromaeosaurid teeth fall within the PCA 95% confidence ellipse (Fig. 6). However, the "Sue" teeth cluster together along PC1 (height; 90% of variation), whereas they show more dispersal along PC2 (denticles/mm; 6.9% of variation). Clustering along PC1 is explained by the fact that all dromaeosaurid teeth from the "Sue" quarry are small, ranging in height from 2.7 mm to 6.45 mm. This 3.75 mm height range contrasts with the range of variation in the Sankey (2008) dataset, a maximum of 13.5 mm. This suggests either a taxonomic signal in crown height and/or taphonomic filtering of the dromaeosaurid teeth from the "Sue" sample.

Denticle count is higher for teeth found in the "Sue" quarry relative to the sites reported by Sankey (2008). This difference is represented by PC2, where a wider range of variation can be observed in the "Sue" teeth than along PC1 (Fig. 6). FMNH PR 2899, 2896, and 2897 all fall outside the range of variation of the Sankey (2008) dromaeosaurid teeth, with higher than expected denticles/mm. We then added the Sankey (2008) dataset to the (denticle/mm)/height biplots dis-

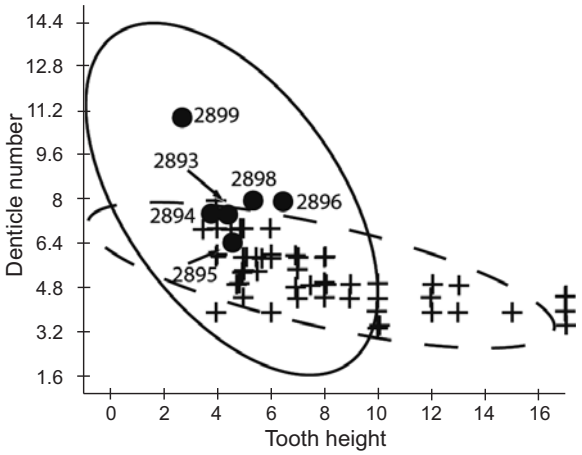


Fig. 7. Biplot of dromaeosaurid teeth from "Sue" quarry (dots) and Sankey (2008) database (crosses) measuring height versus denticles/mm. Ovals are the 95% confidence ellipses for each dataset, Sue quarry solid oval and Sankey database in dashed oval. Sue specimens are designated by the specimen number that follows FMNH PR in each instance.

Table 1. Measurements of theropod teeth collected from the "Sue" site; FABL, fore-aft basal length.

FMNH PR	Taxon	Fore-aft basal length (mm)	Medio-lateral basal width (mm)	Height (mm)	Anterior denitcles/mm	Posterior denticles/mm	Denticles/height	Height/FABL
2893	Dromaeosaurid	3.08	1.23	4.40	8.5	7	1.59	1.43
2894	Dromaeosaurid	2.81	1.05	3.80	?	7	1.84	1.35
2895	Dromaeosaurid	3.02	1.26	4.49	?	6	1.34	1.49
2896	Dromaeosaurid	3.11	1.31	6.45	4	6	0.93	2.07
2897	Dromaeosaurid	NA	NA	NA	NA	5	NA	NA
2898	Dromaeosaurid	3.73	1.31	5.37	?	8	1.50	1.44
2899	Dromaeosaurid	1.30	0.80	2.70	19	11	4.07	2.08
2900	Aviale	2.22	1.00	4.35	NA	0	NA	1.96
2901	Troodontid	2.75	1.29	5.85	8	4	0.68	2.13
2902	Tyrannosaurid	4.82	2.87	12.16	NA	0	NA	2.52

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cussed above (Fig. 7). These plots reveal that three dromaeosaurid teeth from the "Sue" quarry (FMNH PR 2899, 2898, and 2896) fall outside of the 95% confidence ellipse of the Sankey (2008) sample, in addition to several other dromaeosaurid teeth from the UCMP collections (note that FMNH PR 2897 was excluded from the biplot in Fig. 7 because an exact crown height could not be resolved). Further work is required to fully understand morphological variation of dromaeosaurid dental characters amongst and between microsite localities.

Taxonomic and biogeographic utility of isolated theropod teeth.—In this paper we elected to use upper level clade taxonomy in lieu of the more usual genus-species designations. This strategy places the specimens within a phylogenetic context, but without the risk of taxonomic instability should skeletal material reveal that named teeth are undiagnostic at the genus or species level. Additionally, this more conservative approach reduces biogeographic and stratigraphic Type I errors, that is, false presences of a specific taxon at a site, while allowing for a rigorous assessment of alpha diversity.

Biogeographic and stratigraphic studies have relied heavily on isolated theropod teeth for faunal data. In some cases, the attribution of isolated teeth to existing taxa has led to increases in stratigraphic and geographic distributions of theropod species when no other diagnostic skeletal material is available to validate the claim. There is evidence that at least some of these temporal and spatial range increases based solely on teeth erroneously skew genuine theropod diversity patterns (e.g., *Troodon*, Zanno et al. [2011]). The cladistic rules should evidently be the same whether one is considering skeletal fossils or teeth, a point of view presented by Zanno et al. (2013) for late Campanian teeth.

Most of the theropod tooth morphotypes observed in other North American Maastrichtian microsite localities are present in the "Sue" quarry. These include various dromaeosaurid tooth types, Troodontidae, Tyrannosauridae, and Avialae. Conspicuously absent are the taxa *Richardoestesia* spp. and unserrated *Paronychodon lacustris* (Currie et al. 1990). It is unclear why the "Sue" locality lacks these common Maastrichtian tooth morphotypes, although taphonomy and sampling bias are likely causes, with all of the teeth being relatively small and from a relatively small sediment sample. Further, it is not possible to obtain all 11 theropod tooth morphotypes known from the Hell Creek when this study concerned a total of 10 teeth. Brown et al. (2013) found evidence for preservational bias of small dinosaur species within the Dinosaur Park Formation; therefore, the same taphonomic processes may have limited preservation of a complete biocenosis. Based on the overall diversity of theropods and other vertebrates preserved in the "Sue" locality (Gates et al. 2010) a combination of ecological, taphonomic, and sampling factors may be needed to fully explain their absence.

Given the taxonomic considerations noted, it is difficult to assess the impact on Hell Creek dinosaur biodiversity of the new theropod tooth morphotypes from the "Sue" locality. Brusatte et al. (2012) used morphological evidence to suggest that carnivorous dinosaurs did not suffer from a diversity loss prior to the terminal Cretaceous unlike large herbivorous taxa such as *Triceratops* and *Edmontosaurus*. The data presented here begin to reconcile the perceived scarcity of theropod species in the Hell Creek Formation with the interpretations of Brusatte et al. (2012), provided that the recovered morphological diversity translates into taxonomic diversity. However, we note that individual, geographic, ontogenetic or even small stratigraphic variations could also explain the morphological discrepancy, although we are encouraged by the fact that our sample can be distinguished from the large sample of Sankey (2008), which is time averaged from a wide geographic area (Montana and Wyoming). Ontogenetic variation of theropod tooth morphology has been proposed by other authors to explain variation in tooth samples (Currie et al. 1990), but to date there has been no dedicated study to quantify these suggested differences. Given the small size of the teeth obtained from the "Sue" quarry matrix, we cannot discount the possibility that they are ontogenetically younger versions of theropods represented in other studies (Longrich 2008; Sankey 2008). Nevertheless, we suggest that the new morphotypes here represent additional diversity in the Hell Creek Formation until contrary evidence emerges. Future studies of biodiversity trends across the K–T boundary should consider the possibility that there are several additional theropod species in the Maastrichtian sediments of western North America.

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