Terrestrial evidence for the Lilliput effect across the Cretaceous-Paleogene (K-Pg) boundary

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Highlights:

- Changes in the diet of subterranean insects may have caused body size reductions.
- Several edaphic factors are statistically correlated with burrow size in paleosols.
- The K-Pg Lilliput effect occurred in both marine and terrestrial ecosystems.

RRH: K-Pg continental ichnology

LRH: Wiest et al.

Keywords: *Naktodemasis bowni*; mass extinction; dwarfism; Big Bend National Park; subterranean insects

23 Abstract

24 Recent research has demonstrated that the Lilliput effect (reduction of body size in biota
25 associated with the aftermath of mass extinctions) affected all trophic levels in the marine realm
26 following the Cretaceous-Paleogene (K-Pg) event. However, it is unclear if this size change was
27 strictly a marine signal, or a global phenomenon that also affected continental ecosystems.
28 Herein we present the results of an ichnological proxy for body size of soil-dwelling insects
29 across the K-Pg boundary in Big Bend National Park, Texas, U.S.A. Quantitative efforts focused
30 on *Naktodemasis bowni*, which are characterized as unbranching burrows composed of
31 ellipsoidal packets of backfill menisci. These traces were likely produced by beetle larvae or
32 cicada nymphs based on previous comparison with structures generated in modern soils and
33 laboratory experiments. As an approximation for the body size of the subterranean insects, this
34 dataset indicates that a smaller *N. bowni* diameter (D_N) is statistically correlated ($\alpha < 0.05$) with
35 several edaphic factors including poor soil drainage and weak soil development (Entisols).
36 Additionally, the D_N in strata immediately superjacent to the highest Cretaceous-specific taxa is
37 smaller by 23% (5.6 ± 1.8 mm) in comparison to D_N within the subjacent Cretaceous interval (7.3
38 ± 2.7 mm). This abrupt shift occurs in a well-drained Inceptisol, and cannot be attributed to
39 facies changes, drainage, or paleosol maturity. Furthermore, a reduced D_N (6.6 ± 2.3 mm)
40 persists above this anomalous shift for at least 20 stratigraphic meters within chron 29r. The
41 cause for this negative response in body size within soil-dwelling biota may be attributed to
42 plant-community shifts in taxonomic composition and ecological strategies, which would have
43 caused fundamental alterations to the diet of the herbivorous, subterranean insects. This study
44 provides empirical evidence that the Lilliput effect was not restricted to marine environments
45 during the aftermath of the K-Pg event.

1. Introduction

Recent studies have demonstrated that planktic foraminifera (Keller and Abramovich 2009), coccolithophores (Gardin and Monechi 1998), marine mollusks and vermiform organisms (Gallagher 1990; Aberhan et al. 2007; Łaska et al. 2017), decapod crustaceans (Wiest et al. 2015, 2016; Martínez-Díaz et al. 2016, 2017; Łaska et al. 2017), and lamniform sharks (Belben et al. 2017) experienced a reduction in body size during the aftermath of the Cretaceous-Paleogene (K-Pg) extinction event. Importantly, this reveals that the Lilliput effect (c.f. Twitchett 2007; Harries and Knorr 2009) occurred at all trophic levels in the marine realm. In this study, the term “Lilliput effect” refers to extinction selectivity for small sizes (phyletic dwarfism), and also small-sized organisms preferentially surviving the extinction event and replacing the larger-sized clades. Changes in body size provide insight into the response of organisms to large-scale environmental perturbations operating in ancient ecosystems, and understanding the magnitude and extent of this phenomenon from past events may help constrain predictions for current biodiversity loss (Bottjer and Droser 1994; Morrow and Hasiotis 2007; Sheridan and Bickford 2011; Cheung et al. 2013).

It remains uncertain if the Lilliput effect following the K-Pg event was strictly a marine signal, or a broader phenomenon that also affected continental ecosystems. This study focuses on terrestrial ichnotaxa preserved in paleosols. These traces formed *in situ*, are well-preserved, and are sensitive metrics of subterranean-organism biology and behavior, and environmental conditions (Bown and Kraus 1983; Hasiotis and Bown 1992; Hasiotis 2002; Rodríguez-Tovar 2007; Smith et al. 2009; Wiest and Buynevich 2015; Hembree and Blair 2016; Genise 2017). Furthermore, soils have been hypothesized as refugia for terrestrial organisms during the widespread environmental disturbance associated with the K-Pg event (Harries et al. 1996;

Robertson et al. 2004; Bardeen et al. 2017). The response of soil-dwelling invertebrates to environmental disturbance may serve as a proxy for overall ecosystem health across the K-Pg interval because these organisms inhabit low trophic levels.

Herein we report the results of a quantitative ichnological study that reveals an abrupt and persistent reduction in body size within the soil-dwelling community across the K-Pg boundary from Big Bend National Park, Texas, U.S.A. This dataset provides empirical evidence that the Lilliput effect also occurred in terrestrial settings during the aftermath of the K-Pg mass extinction, and implies that burrowing insects were also substantially affected by the event.

2. Geological setting

The Upper Cretaceous (Maastrichtian) and Paleocene (Danian) strata within the Dawson Creek section of Big Bend National Park, Brewster County, Texas, U.S.A., consist of southwestward-dipping channel sandstone bodies, fine-grained fluvial overbank deposits, and associated paleosols (Fig. 1; Lehman 1985, 1990, 1991; Atchley et al. 2004). The Dawson Creek exposure within the Tornillo Basin is an extensively studied continental K-Pg section in the southwestern United States. The framework of this particular set of outcrops includes biostratigraphy (Wilson 1970; Schiebout 1974; Standhardt 1986; Schiebout et al. 1987; Lehman 1991), magnetostratigraphy (Rapp et al. 1983; Leslie et al. 2015, accepted), terrestrial sequence stratigraphy (Atchley et al. 2004), paleopedology (Nordt et al. 2003, 2011), and paleoenvironmental reconstruction (Lehman 1990). Previous studies of the paleosols occurring throughout the stratigraphic succession suggested that paleoclimate conditions were subhumid to semiarid, vegetation was predominantly dry woodland, and the paleosols resemble modern Entisols, Inceptisols, and Vertisols (Atchley et al. 2004; Nordt et al. 2011). Of particular note

was the documentation of two greenhouse events preceding the K-Pg impact, based on analysis of stable isotopes of pedogenic carbonates from the Dawson Creek section (Nordt et al. 2003).

Our analysis focused on the stratigraphic interval that includes the Upper Cretaceous Javelina Formation, as well as the lowermost Paleocene Black Peaks Formation (Fig. 2). The formational contact between the Javelina and Black Peaks is conformable (Lehman, 1990), occurs within chron 29r (Leslie et al. accepted), and has been interpreted to represent the K-Pg boundary (e.g., Lehman 1990; Nordt et al. 2003, 2011), although there remains an apparent absence of diagnostic impact indicators such as shocked minerals, impact-derived spherules, or geochemical anomalies (e.g., iridium), nor have there been recovered identifiable palynomorphs. The highest Cretaceous-specific remains recovered from this section are disarticulated *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from a fluvial body between paleosol 21 (P21) and P22 within the Javelina Formation (Fig. 2; Lawson 1972, 1975; Lehman 1990). Paleocene mammals occur within the Black Peaks Formation at 20 m above the last occurrence of Cretaceous fossils in a channel complex (superjacent to P28) that is interpreted to be unconformable at its base (Atchley et al. 2004; Lehman and Busby 2007; Leslie et al. 2015; Cobb 2016). Reanalysis of the Black Peaks mammalian faunas, coupled with revised magnetostratigraphy for the section, indicate that the mammals occur within the Torrejonian North American Land Mammal Age and were deposited in chron 27r (Leslie et al. accepted).

3. Methods

A series of field excursions were conducted within Big Bend National Park during the spring and fall of 2015. All field activities complied with U.S. National Park Service regulations. Individual stratigraphic units and paleosols documented in Nordt et al. (2003, 2011) and in

Atchley et al. (2004) were located via GPS coordinates in conjunction with photomosaics labeled with stratal surfaces and paleosols tops, which were generated in the field with a laptop during 2002 (S. Atchley, pers. comm. 2015). Assignment of stratigraphic position in meters, paleosol nomenclature, facies associations, and drainage parameters were adapted from Atchley et al. (2004; cf. their Fig. 3). Paleosol drainage was characterized by Atchley et al. (2004) based on matrix color, where poorly drained paleosols were gray to blue-gray, moderately drained paleosols were yellow or brown, and well-drained paleosols were red to purple. Accordingly, these drainage indices were easily confirmed in the field. Interpretations of paleosol taxonomic order assigned by Atchley et al. (2004) followed USDA-NRCS soil taxonomy and were cross-checked in the field based on paleosol morphology and horizonation. Entisols were typically stacked A-C horizons without subsurface B horizon development, Inceptisols had weakly developed B horizons (typically Bw), and Vertisols contained pedogenic slickensides in Bss horizons.

Multiple, laterally distributed, fresh excavation surfaces within each sedimentary unit were examined in the field for biogenic structures (plant and animal). Trace fossils were described based on surficial and architectural morphology, dimensions, and burrow fill. The depth of maximum bioturbation was determined with a measuring tape for each paleosol. The minimum inner diameters of shafts and tunnels of each trace observed were measured with a digital caliper to the nearest 0.1 mm, except for root traces, which were distinguished by their characteristic tapering and bifurcation (Retallack 1988; Driese et al. 1997; Elick et al. 1998). A semiquantitative ichnofabric index was used to characterize the degree of bioturbation where 1 = no bioturbation; 2 = discrete, isolated burrows; 3 = 10-40% of bedding is disturbed; 4 = nearly complete bioturbation; and 5 = complete bioturbation (Droser and Bottjer 1986; Genise et al.

2004). Burrow diameters were evaluated using the nonparametric Wilcoxon/Kruskal-Wallis Test for mean ranks, with post-hoc analyses using Tukey's honest significant difference (HSD) to test for directionality in mean sizes using JMP (v.13) statistical software.

4. Results

Celliforma isp. (capsule-shaped, smooth cells) and *Skolithos* isp. (vertical cylindrical tubes) occur in Cretaceous portions of the study interval, but quantitative analysis, instead, focused on *Naktodemasis bowni*, also referred to as adhesive meniscate burrows (Smith and Hasiotis 2008; Smith et al. 2008; Counts and Hasiotis 2009), due to the pervasiveness of this structure throughout the section and occurrence in both Cretaceous and Paleocene strata (Fig. 3).

4.1 *Naktodemasis morphology*

The *N. bowni* observed from the Dawson Creek section are characterized as unlined, unbranching burrows composed of packets of densely spaced meniscate backfill. The traces do not differentially weather from the outcrop or exhibit any relief, but are otherwise apparent on freshly broken ped surfaces because of differences in menisci color in comparison to host matrix (Fig. 3). Traces are readily visible in areas of the paleosols that do not have a homogenous color. Burrows are generally straight, and are highly variable in orientation, ranging from vertical to horizontal. True branching was not observed; however, burrows commonly overlap each other in intensely bioturbated intervals and seldom generate what appears to be false branching. *N. bowni* were only observed in fine-grained mudrocks, and were not found in lithologies composed of only clay or well-sorted sand (Fig. 2).

4.2 *Naktodemasis bowni* size and edaphic controls

In total, 808 inner diameters of *N. bowni* (D_N) were measured from 15 paleosols distributed over approximately 85 m of stratigraphic section (Fig. 4). Summary statistics for D_N are presented in Table 1; all measured D_N and associated paleosol characteristics are reported in Supplemental Data Table A1. Where possible, a minimum of 35 measurements of D_N was acquired for each paleosol.

The abundance of D_N in each paleosol was characterized using ichnofabric index (Droser and Bottjer 1986). Whereas differences were observed between ichnofabric index (ii) categories, D_N decreases in a non-sequential order of ii = 4, 2, 5, and 3. Ichnofabric index values are not homogeneous across categories of stratigraphic age (K vs. Pg), drainage, soil order, or paleosol number (chi-square, $p < 0.001$ for each). Drainage conditions are a significant predictor of ichnofabric index, with more well-drained paleosols tending to have a higher ichnofabric index value (Fig. 2). The distribution of ichnofabric index values varies across the measured section - the base of the section generally has lower ichnofabric index values, on average, and a series of high ii values (5) were observed only in P23 and P24 (Fig. 2). Regardless of this, the number of measured D_N per paleosol is not correlated with mean (F-test, $p = 0.56$) or median ($p = 0.63$) D_N .

Poorly-drained paleosols contain D_N significantly different than both moderately drained and well-drained paleosols ($p < 0.01$ for both); whereas there is no significant difference in D_N between moderately and well-drained paleosols ($p = 0.8$). Tukey's HSD run post-hoc demonstrates that D_N within poorly drained paleosols is smaller than those occurring in moderately and well-drained paleosols ($p < 0.05$ for both).

Finally, D_N is significantly different in Entisols compared to both Inceptisols ($p < 0.001$) and Vertisols ($p < 0.01$). Tukey's HSD indicates that D_N is smaller in Entisols than in Inceptisols ($p < 0.001$) and Vertisols ($p < 0.05$).

The population of *N. bowni* from the interval below P22, which is known to be of Cretaceous in age, contains D_N significantly different than those above the highest known Cretaceous vertebrate fossil (P22 and above; $p < 0.001$), regardless of paleosol type or drainage. Tukey's HSD run post-hoc indicates that the population above the Cretaceous taxa have smaller D_N than those within the Cretaceous interval ($p < 0.001$).

5. Discussion

5.1 Ethology of the tracemakers

The *N. bowni* are most similar to traces produced by such extant soil-dwelling insects as burrower bugs (Hemiptera: Cydnidae), cicada nymphs (Hemiptera: Cicadidae), and beetle larvae (Coleoptera: Scarabaeidae) in modern soils and laboratory experiments (Marlatt 1907; Smith and Hasiotis 2008; Smith et al. 2008; Counts and Hasiotis 2009). Beetles (Coleoptera) occur occasionally during the Permian, and cicadas (Cicadoidea) and have been recovered from as early as the Triassic, but it remains a possibility that other burrowing insects with similar body plans and behaviors were capable of producing these traces (Lefebvre et al. 1998; Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005; Feng et al. 2017). Subterranean nymphs and larvae of certain extant species of cicadas and beetles, respectively, burrow through the soil to feed on the xylem sap of plant roots, living plant roots, and disseminated soil organic matter (White and Strehl 1978; Tashiro 1987). Smith and Hasiotis (2008) and Counts and Hasiotis (2009) demonstrated through laboratory experiments that *N. bowni* were generated as an open, elongate

or ovoid cell that was continuously moved forward as the tracemaker repeatedly removed material from the front of the cell, rotated to transport the sediment, and packed the material in the back of the cell.

5.2 Mechanisms for reduced body size of soil-dwelling fauna

Trends in D_N , similar to the results reported herein, have been previously documented across the Paleocene-Eocene Thermal Maximum (PETM) in paleosols similar to those within the Dawson Creek section from Big Bend National Park. The reduction in trace-fossil size generated by soil-dwelling insects was attributed to 1) drier floodplain conditions (lower soil moisture), 2) higher surface temperatures, or 3) vegetation (food source) with diminished nutritional value due to elevated atmospheric CO_2 (see Smith et al. 2009 and references therein).

Whereas drier soil conditions have been correlated with smaller D_N across the PETM interval and in some species of extant dung beetles (Vessby 2001), a reduction in soil moisture is an improbable forcing mechanism for the K-Pg trend observed in Big Bend for multiple reasons. First, as mentioned previously, larger D_N were observed in well-drained paleosols compared to poorly drained conditions (Table 1). Second, soil drainage does not appear to change systematically from the Upper Cretaceous through the lower Paleocene (Atchley et al. 2004). Finally, paleosols in the Dawson Creek section generally have deeper carbonate horizons and less weatherable base oxides up-section, suggesting that the climate gradually became wetter during the early Paleocene, but not coincident with the proposed extinction interval between P21 and P22 (Lehman 1990; Nordt et al. 2011). These observations indicate that edaphic and climatic variables are not dominant factors in the dramatic and persistent decrease in D_N that begins in P22.

The Late Maastrichtian Event (LME), which is a transient episode of increased atmospheric CO₂ and surface temperature just below the K-Pg boundary, has been previously identified at this same outcrop succession based on paleosol proxies (Nordt et al. 2003). The CO₂ and warming spike was observed in P19 (Fig. 2; Nordt et al. 2003). P19 also contains abundant *N. boweni* and therefore presents an opportunity to assess the correlation between *p*CO₂, increased surface temperatures, and D_N (Fajer et al. 1989; Atkinson 1994; Sibly and Atkinson 1994; Parmesan 2006). Surprisingly, we found no evidence of a change in D_N over the interval of elevated *p*CO₂ and temperature reported in Nordt et al. (2003). Given the assumption that active pedogenesis of P19 occurred during a time of intensified greenhouse conditions, and that P23-P28 were developed during a relatively cooler period (Nordt et al. 2003, their Fig. 3), it is improbable that increased temperature is a driving mechanism for the negative response in D_N for this dataset.

The biogeochemistry of paleosols throughout the Dawson Creek section was reconstructed by Nordt et al. (2011), which provided results pertinent to our study. First, there is no observed change in overall soil quality or biogeochemical function in the paleosols across our study interval. The paleosols were generally nutrient-rich, had relatively high-water holding capacity, and ranged from circumneutral to alkaline pH. Accordingly, no evidence exists for aluminum or sodium toxicity, which can occur at extreme low and high pH, respectively, and limit nutrient availability in soils (Delhaize and Ryan 1995; Beyrouthy et al. 2000; Qadir and Schubert 2002). Taken together, there were no systematic changes in possible edaphic controls for the habitability of the paleosols in the section, therefore, forcing mechanisms external to the substrate must account for the observed overall up-section reduction in D_N.

Plant tissue forms the base of the soil food web, and alterations in diet quality and/or plant type affects physiological determinants of herbivorous-insect body size (Frajer et al. 1989; Young et al. 1998; Davidowitz et al. 2004; Smith et al. 2009). Thus, a shift in plant taxa, plant ecological strategies and/or reduction of detrital-plant nutritional value between the Cretaceous and Paleocene could have been a primary driving mechanism for the Lilliput effect in soil-dwelling organisms. There was a major, abrupt extinction of Cretaceous plant taxa across the K-Pg boundary, which caused significant changes in plant communities globally (e.g., Vajda and Bercovici 2012; Nichols and Johnson 2008). In the Big Bend area, there is a well-documented, diverse record of late Cretaceous – early Paleocene wood fossils that demonstrates a change from araucariacean conifer dominated fossil wood assemblage in the Javelina Formation to a wood assemblage made up of primarily angiosperm taxa in the Black Peaks Formation, indicating a change in plant communities across the K-Pg boundary (Wheeler et al. 1994; Wheeler and Lehman 2000, 2005, 2009; Lehman and Wheeler 2001; Manchester et al. 2010). However, the fossil wood occurrences in the upper Javelina and Black Peaks Formations are restricted to a few stratigraphic intervals that are separated by a significant amount of time (Wheeler and Lehman 2005; 2009), and the fossil wood record is only representative of a portion of the total plant community. This limits our ability to assess the full extent of plant extinction and floral turnover at the K-Pg boundary in Big Bend.

Whereas there is no high-resolution plant record for the K-Pg boundary from the Big Bend area, records from across North America, including from the geographically proximate Raton Basin, document a 30 to >50% extinction of plant taxa at the K-Pg boundary followed by a short-lived interval dominated by fern taxa (the “fern spike”) and then a prolonged recovery dominated by angiosperms (Vajda and Bercovici 2014, and references therein). When compared

to their Cretaceous counterparts, Paleocene floras were lower in diversity and were dominated by a few species that were geographically widespread (e.g., Wing et al. 1995; Wilf and Johnson 2004; Peppe 2010). Given that this pattern has been observed across North America, it is very likely that the Big Bend region experienced a similar extinction of plants and plant community response across the K-Pg boundary. Therefore, we interpret the observed reduction in D_N at Dawson Creek to have occurred contemporaneously with the plant extinction at the K-Pg boundary.

In addition to a significant extinction of Cretaceous taxa, there is evidence for a shift in plant ecological strategies across the boundary. A study of fossil leaves from the Williston Basin in North Dakota documents the selective extinction of slow-growing evergreen plant species across the K-Pg boundary, which suggests a fundamental shift in plant ecological strategies towards taxa that favored fast growth strategies with minimized high carbon assimilation rates and low carbon investment (Blonder et al. 2014). Generally, leaves of plants with fast growth strategies are associated with high amounts of insect damage because they are thinner and have higher nutrient content making them more palatable to insect herbivores (e.g., Coley and Barone, 1996; Royer et al. 2007; Currano et al. 2008; Wilf 2008). Studies of fossil wood from the Big Bend area indicate Paleocene taxa have notable anatomical changes from Cretaceous taxa, such as an increase in growth rings and a decrease in exclusively scalariform perforation plates (Wheeler and Lehman, 2009). This suggests changes in the ecological strategies of at least some tree species between the Cretaceous and Paleocene.

The combination of a major plant extinction and a shift in plant ecological strategies across the K-Pg boundary would have caused fundamental alterations in the diet of the *N. bowni* tracemakers. Thus, we hypothesize that the dramatic plant-community shifts in taxonomic

composition and ecological strategies that occurred at the K-Pg boundary were an important forcing mechanism for the observed Lilliput effect in subterranean insects.

The Lilliput effect in D_N documented across the K-Pg boundary could reflect either a reduction in organism body size (phyletic dwarfism) or the replacement of larger-bodied clades with smaller-bodied forms or species that generate morphologically identical structures. Though the insect fossil record is relatively limited, insect damage on fossil leaves is a proxy for insect herbivory, and in turn insect diversity; and therefore, can be used to assess changes in insect diversity and compositional heterogeneity (Carvalho et al. 2014). Analyses of insect damage on Cretaceous and Paleocene floras from the Western Interior of the United States have documented a significant change in insect herbivory, and by extension in insect communities across the K-Pg boundary (e.g., Labandeira et al. 2016 and references therein). Detailed studies of insect damage across the K-Pg boundary in the Williston Basin in North Dakota document a substantial decrease in insect herbivory, a significant decline in intermediate and specialized leaf mines, and a major extinction of leaf-mining insect species at the K-Pg boundary, as well as a significantly unbalanced plant-insect food web in the early Paleocene (Labandeira et al. 2002a, b; Wilf et al. 2006; Donovan et al. 2014). This major insect extinction and community-level change has been hypothesized as a cascading response to the extinctions of Cretaceous host plant species (Labandeira et al. 2002a). Based on these records from North America, it seems reasonable that there was also a significant extinction of insects across the K-Pg boundary in the Big Bend region. Therefore, it is possible that the reduction in body size we document in our trace fossil analyses could reflect an extinction of larger-bodied tracemakers and/or a change in the insect community structure and composition.

5.3 Stratigraphic position of the K-Pg boundary within the Dawson Creek section

There is currently no definitive age control on P22-P28, except that this conformable succession of stacked paleosols occurs between Maastrichtian fauna (~172 m; Fig. 2) and early Paleocene fauna (~195 m; Lawson 1972, 1975; Lehman 1985, 1990; Standhardt 1986; Schiebout et al. 1987). It is possible that the K-Pg boundary occurs at the unconformity surface immediately superjacent to P28. If this is the case, this entire dataset and interpreted environmental disturbance would have occurred prior to the K-Pg event sometime within chron 29r. However, this interpretation is very unlikely based on the reversed polarity of the sequence, the occurrence of the Late Maastrichtian Event (LME) in P19, and sedimentation-rate calculations based on magnetostratigraphy and pedogenesis (Nordt et al. 2003; Leslie et al. accepted). Therefore, we agree with the existing interpretations that the chronostratigraphic K-Pg boundary is at or near P23 (Fig. 2; e.g., Lehman 1990; Nordt et al. 2003; Atchley et al. 2004; Lehman and Busby 2007; Cobb 2016; Leslie et al. accepted).

Trace-fossil analysis has been demonstrated previously as an effective tool for refining the sedimentological history and stratigraphic relationships at other K-Pg exposures (Ekdale and Bromley 1984; Savrda 1993; Ekdale and Stinnesbeck 1998; Twitchett and Barras 2004; Rodríguez-Tovar et al. 2004, 2010, 2016; Rodríguez-Tovar 2005; Chin et al. 2013; Sosa-Montes de Oca et al. 2013, 2016; Horner et al. 2016). Thus, in the absence of diagnostic K-Pg boundary indicators, we propose that the trace fossil dataset herein can be used to refine the stratigraphic position of the K-Pg event in the Dawson Creek section. Our ichnological proxy indicates a significant reduction in tracemaker body size in P22, which is like patterns seen across other K-Pg boundary sections in North America and Europe (e.g., Wiest et al. 2015, 2016; Łaska et al. 2017). Based on these results, we interpret the trace fossils within P22 to represent a post-event

recovery community, stratigraphically above the K-Pg transition. This implies that the chronostratigraphic boundary is associated with the channel-sand body containing reworked pterosaur remains just below P22 (~172 m; Fig. 2; Lehman 1990). Thus, we posit that the apparent absence of extraterrestrial-impact indicators at this site (e.g., Lehman, 1990) is potentially attributed to widespread erosion that occurred contemporaneous with, or shortly after, the K-Pg event. Current and ongoing advancements in absolute dating of sandstones may permit further testing of this hypothesized placement of the stratigraphic K-Pg boundary in the future.

5.4 Is there a common forcing mechanism?

Each of the studies that have documented the Lilliput effect across the K-Pg boundary thus far have provided rationale for marine-environmental mechanisms that could have potentially driven the phenomenon for that particular type of taxon. It has been demonstrated that planktic foraminifera can experience the Lilliput effect from a diverse range of stressors including greenhouse warming, anoxia/dysoxia, restricted basins, and volcanism (Keller 2003; Keller and Abramovich 2009). The dwarfism of some coccolithophore species during the earliest Paleocene is attributed to unfavorable environmental conditions such as anomalous fluctuations in primary productivity and poor stratification of surface waters (Gardin and Monechi 1998). Aberhan et al. (2007) found that the most likely explanation for a reduction in body size within mollusk-dominated benthic shelf ecosystems is a reduction in nutrient availability associated with the decline in primary production. Likewise, dwarfism of marine vermiform organisms has also been attributed to limited food supply associated with a collapse of the food web in the latter stages of the extinction event (Hsü and McKenzie 1985; Hansen et al. 1993; Łaska et al. 2017). The reduction of body size of infaunal crustaceans from diverse, widespread shallow-marine

environments is most likely attributed to either a decrease in oxygen availability following the extinction event (Savrda et al. 1984; Ekdale 1985; Savrda and Bottjer 1987a, 1987b; Wiest et al. 2015), a restricted nutrient supply, or a combination of these factors (Wiest et al. 2016; Łaska et al. 2017; Rodríguez-Tovar et al. 2017). In addition to bony fish, lamniform sharks, which were apex marine predators across the K-Pg transition, also experienced the Lilliput effect (Belben et al. 2017). This phenomenon, as evidenced by quantitative shark-tooth morphometrics, is attributed to taxonomic turnover, as well as major shifts in ecological function, such as changes in the available prey and/or dietary preference of the sharks (Belben et al. 2017).

There does not appear to be an unambiguous, all-encompassing explanation to account for this widespread phenomenon, but it does seem to be a universal response to different components of a complex, interrelated disruption of the food web. Likewise, the driving mechanism for the reported body-size decrease in terrestrial *N. bowni* tracemakers is seemingly a combination of the Cretaceous plant extinctions and a shift in plant ecological strategies across the K-Pg boundary, which would have caused fundamental alterations in the diet of the herbivorous, subterranean insects.

6. Conclusions

The addition of terrestrial evidence for the Lilliput effect in response to the K-Pg event indicates that this phenomenon affected diverse biota across highly disparate ecosystems. Future studies should focus on extending such datasets across different taxa and depositional environments, particularly from the continental realm, to better understand the spatial, temporal, and ecological context of the Lilliput effect as it relates to the response and recovery of the end-Cretaceous mass extinction. Trace fossils have great potential to yield such an archive because

they are commonly preserved in a variety of settings, are generated by a wide range of organisms, and often occur in numbers sufficient for statistical analysis.

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Fig. 1. (COLOR USE REQUESTED) Location of Dawson Creek K-Pg section (yellow star) within Big Bend National Park. The red box in the inset indicates the position of the map relative to Texas, U.S.A.

Fig. 2. (COLOR USE REQUESTED) Dawson Creek stratigraphic section modified from Nordt et al. (2003) and Atchley et al. (2004). Paleosol type E = Entisol; I = Inceptisol; V = Vertisol. See section 3 (Methods) for explanation of ichnofabric index values. Geomagnetic Polarity Time Scale (GPTS) data is from Leslie et al. (accepted).

Fig. 3. (COLOR USE REQUESTED) *Naktodemasis* in pedogenically modified overbank deposits from the Dawson Creek K-Pg section; A) horizontal burrow in P-26. Note the packets of densely spaced meniscate backfill; B) two burrows with differing contrast to P-25 host matrix; C) multiple backfilled traces in P-23; D) single tunnel from P-22; E) several traces ranging in diameter in an unoriented ped from P-20; F) multiple traces displaying various contrast to P-15.

Fig. 4. Notched-box plots of *Naktodemasis* diameter (D_N) from the Dawson Creek K-Pg section. Notches on the boxes represent the 95% confidence interval for the mean. See section 5.3 for discussion on K-Pg boundary position.

Table 1: Summary statistics for D_N .

	Min	Mean	Max	SD	n
<i>Age interval</i>					
K	2.8	7.3	15.0	2.7	425
Pg	2.4	6.6	13.8	2.3	383
<i>Drainage category</i>					
Poor	2.8	6.4	13.8	2.4	177
Moderate	2.9	7.1	15.0	2.5	218
Well	2.4	7.1	14.6	2.6	413
<i>Paleosol type</i>					
Entisol	2.4	6.5	13.8	2.4	277
Inceptisol	2.9	7.2	15.0	2.7	361
Vertisol	2.8	7.1	14.0	2.4	170

Note: Dimension values are in mm.