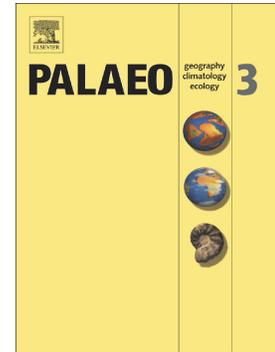


## Accepted Manuscript

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PII: S0031-0182(17)30561-8

DOI: doi:[10.1016/j.palaeo.2017.11.024](https://doi.org/10.1016/j.palaeo.2017.11.024)

Reference: PALAEO 8526

To appear in: *Palaeogeography, Palaeoclimatology, Palaeoecology*

Received date: 27 May 2017

Revised date: 31 October 2017

Accepted date: 8 November 2017

Please cite this article as: Gregory James Smith, Larisa R.G. Desantis , Dietary ecology of Pleistocene mammoths and mastodons as inferred from dental microwear textures. The address for the corresponding author was captured as affiliation for all authors. Please check if appropriate. *Palaeo*(2017), doi:[10.1016/j.palaeo.2017.11.024](https://doi.org/10.1016/j.palaeo.2017.11.024)

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**Dietary ecology of Pleistocene mammoths and mastodons as inferred from dental microwear textures**

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**Abstract**

The Columbian mammoth (*Mammuthus columbi*) and the American mastodon (*Mammut americanum*) have traditionally been considered to have been ecologically distinct, with mammoths often characterized as cosmopolitan grazers or mixed feeders and mastodons as forest-dwelling browsers. However, these large-bodied proboscideans occupying temperate, often resource-limiting environments in Pleistocene North America would have necessitated a much wider range of resources. For the isolated pygmy mammoth (*Mammuthus exilis*) of California's Channel Islands, the resource-limited nature of its insular home may have exacerbated the need for consumption of a wide range of less-preferred resources. The goal of this study is to better understand the degree to which each of these taxa consumed tough and/or hard food items, including grass, leaves, and woody browse in their respective environments. To this end, we examined the dental microwear of Pleistocene mammoths and mastodons to address the following questions: 1) do mammoths and mastodons with known differences in diet (via carbon isotopes) have similar dental microwear attributes?, 2) do juvenile and adult mammoth and mastodons consume foods with similar textural properties?, and 3) did the Channel Islands mammoths consume food with similar textural properties as the mainland Columbian mammoths? Our results demonstrate that the mammoths and mastodons here examined ate foods with similar textural properties, despite consuming plants with disparate stable isotope values. These data suggest that mammoths and mastodons were generalists (in regards to dietary textures) and did not eat softer or tougher foods as juveniles. Further, the Channel Islands mammoths ate food items with more variable textural properties (including a greater incidence of hard foods) than Columbian mammoths from Texas. While more work is needed to assess the

ubiquity of these results across time and space, collectively, these data suggest that extinct proboscideans are generalist feeders similar to extant elephants.

**KEYWORDS:** paleoecology, proboscidean, pygmy, ontogeny, Quaternary, megafauna

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## 1. Introduction

A wide diversity of large-bodied herbivorous taxa including bovids, camelids, and proboscideans occupied North America during the Pleistocene (Anderson, 1984). Proboscideans in particular experienced a three-pronged dispersal across the Bering Land Bridge from Eurasia, with subsequent colonization events introducing the mastodons, gomphotheres, and mammoths to North America (Shoshani, 1998). The earliest Mammutids (*Zygodon spp.*) arrived in North America sometime during the early Barstovian Land Mammal Age (Tedford et al., 2004), although *Mammut americanum* does not appear until the Blancan (Bell et al., 2004). Mammoths (*Mammuthus spp.*) were the final and most highly derived proboscideans to arrive, having tracked the expansion of grasslands out of Africa and into Eurasia *ca.* 3 Ma and arriving to North America as early as ~1.5 – 1.3 Ma (Agenbroad, 2005; Lister and Sher, 2015). The presence of *Mammuthus* south of 55° latitude defines the lower limit of the Irvingtonian Land Mammal Age (Bell et al., 2004).

Proboscideans in general are thought to have played a considerable role in shaping past ecosystems due to their classification as megaherbivores (i.e., > 1000 kg in body mass) (Owen-Smith, 1987) and current role as ecosystem engineers (Jones et al., 1994). Modern African elephants (*Loxodonta spp.*) and Asian elephants (*Elephas maximus*) are capable of large-scale turnover of vegetation and ecosystem transformations (Naiman, 1988). Elephants selectively consume a wide range of fruits and other species of plant, playing a large role in seed dispersal (Campos-Arceiz and Blake, 2011) while also selectively consuming specific plant parts over a wide diversity of species (Owen-Smith and Chafota, 2012). Additionally, they physically disturb and destroy trees and shrubs, leading to widespread vegetation changes and alteration of fire regimes (Laws, 1970), impacting food supply and population dynamics of other animals

(Pringle, 2008), altering soil formation and biogeochemical cycling, and ultimately changing the ecological regime of their habitats (Naiman, 1988).

Because of their close phylogenetic and morphologic affinities, extinct species of proboscideans are similarly likely to have acted as ecosystem engineers (Haynes, 2012). However, such behavioral and ecological inferences are difficult to interpret in the fossil record. Understanding the paleoecological roles played by fossil proboscideans has largely been based on tooth morphology (Maglio, 1972; Saunders, 1996; Tobien, 1996; Todd and Roth, 1996) and, more recently, stable isotopes (e.g., Baumann and Crowley, 2015; Bocherens et al., 1996; Connin et al., 1998; DeSantis et al., 2009; Fisher et al., 2014; Fox-Dobbs et al., 2008; Fox and Fisher, 2001, 2004; Koch et al., 1998, 2004; Metcalfe et al., 2013; Drucker et al., 2015; Pérez-Crespo et al., 2012; Trayler et al., 2015; Yann and DeSantis, 2014). For example, the zyglodont dentition of mastodons suggests adaptation for browsing (Tobien, 1996) while the hypsolodont dentition of mammoths is thought to have been an adaptation to more abrasive plants, such as grass (Maglio, 1972; Todd and Roth, 1996). Inferences into the stable isotope ecology of North American mammoths reveal a wide range of dietary preferences commiserate with the cosmopolitan nature of the genus. For example, stable carbon isotopes suggest the consumption of primarily  $C_4$  vegetation (likely grass) in Florida (Koch et al., 1998; DeSantis et al., 2009; Yann and DeSantis, 2014), predominately  $C_3$  vegetation in California (Trayler et al., 2015), and mixed  $C_3/C_4$  vegetation during the Last Glacial Maximum (LGM) in the Cincinnati region (Baumann and Crowley, 2015). Further, mammoths consumed primarily  $C_4$  vegetation from the Mojave Desert (in California and Nevada) through to the Southern High Plains (Arizona and New Mexico) and into Texas (Connin et al., 1998; Koch et al., 2004). Both  $C_3$  and  $C_4$  grasses have been hypothesized to have been a large component of the diet of

*Mammuthus* in these and other localities (including central Utah and the subarctic; e.g., Kubiak, 1982; Gillette and Madsen, 1993).

A third means of inferring the diet of extinct organisms is dental microwear. Dental microwear, the microscopic wear patterns formed during the processing of food, can be used to make inferences regarding foods consumed during the last days to weeks of an organism's life (e.g., Grine, 1986). Microwear can be examined quantitatively via counting the number of pits and scratches on a 2-dimensional surface using a scanning electron microscope (SEM) or by user recognition while looking directly through the lens of a stereomicroscope. Alternatively, one may use a white light scanning confocal microscope and scale-sensitive fractal analysis (SSFA) in a more automated and repeatable process known as dental microwear texture analysis (DMTA) (Scott et al., 2005, 2006; Ungar et al., 2003), which allows for more nuanced differences in diets to be detected and is less prone to issues of observer variability (DeSantis et al., 2013). DMTA has been used to reconstruct diets in a wide range of disparate extant and extinct taxa (see DeSantis, 2016 for a review of DMTA and studies utilizing this approach). Several studies have used dental microwear to analyze dietary tendencies in fossil proboscideans using the 2D analysis of SEM images (Capozza, 2001; Filippi et al., 2001; Palombo et al., 2005; Calandra et al., 2008), low-magnification user-based methods on a light microscope (Green et al., 2005; Todd et al., 2007; Rivals et al., 2010, 2012, 2015; Semprebon et al., 2016) and DMTA on a confocal microscope (Zhang et al., 2016; Green et al., 2017). These studies reveal a wealth of dietary preferences in mammoths ranging from predominately browsing to strictly grazing, while establishing evidence for more dietary flexibility in mastodons than had previously been inferred from dental morphology.

Here, we aim to test the following hypotheses: 1) mammoths and mastodons with known differences in diet (via stable carbon isotopes indicating C<sub>4</sub> grass or C<sub>3</sub> browse consumption - see Section 2.1) have disparate dental microwear attributes; 2) juvenile proboscidean microwear differs significantly from adult proboscideans, tested by examining a unique late Pleistocene site (Friesenhahn Cave in Texas) with exceptionally well preserved juvenile mammoth and mastodon teeth; and, 3) the pygmy mammoth (*Mammuthus exilis*) consumed texturally disparate foods from either of the larger mainland taxa examined here (*Mammuthus columbi* and *Mammuth americanum*). Collectively, DMTA data can help clarify the dietary preferences of Pleistocene mammoths and mastodons, including any size or age correlation with the textural properties of food consumed.

## 2. Background

### 2.1 Stable Isotopes in Mammalian Enamel

A wide variety of terrestrial plants (including trees, shrubs, herbaceous dicots, and high-latitude and high-elevation grasses) photosynthesize using solely the Calvin-Benson cycle (Ehleringer and Monson, 1993). Because this cycle fixes CO<sub>2</sub> using three-carbon acids, these plants are termed C<sub>3</sub> plants. In contrast, modern savanna/grassland biomes in temperate and tropical zones have a significant (i.e., 50 - 100 %) component of C<sub>4</sub> grasses that photosynthesize carbon using the Hatch-Slack cycle (which fixes CO<sub>2</sub> using four-carbon acids) followed by the Calvin-Benson cycle (Ehleringer et al., 1991). These two dominant photosynthetic pathways fractionate the stable isotopes of carbon (<sup>12</sup>C and <sup>13</sup>C) differently (Bender, 1971). As a result, the ratio of <sup>13</sup>C to <sup>12</sup>C (defined as  $\delta^{13}\text{C}_{\text{sample}} = [({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}}/({}^{13}\text{C}/{}^{12}\text{C})_{\text{PDB}} - 1] \times 1000$ , where PDB is the isotope reference standard – the Pee Dee Formation Belemnite, Coplen, 1994) yields average  $\delta^{13}\text{C}_{\text{veg}}$

values for modern C<sub>3</sub> plants of  $-27\text{‰}$  (Kohn, 2010) whereas modern C<sub>4</sub> plant  $\delta^{13}\text{C}_{\text{veg}}$  values average  $-13\text{‰}$  (Bender, 1971; Cerling et al., 1997). Plant  $\delta^{13}\text{C}_{\text{veg}}$  values are dependent upon  $\delta^{13}\text{C}_{\text{atm}}$  (the stable carbon signature of atmospheric CO<sub>2</sub>) (Marino et al., 1992; Leavitt, 1993; Schubert and Jahren, 2012), which fluctuates with  $p\text{CO}_2$  and was approximately  $+0.9\text{‰}$  higher during the Pre-LGM/LGM than today (Leuenberger et al., 1992). Thus, the  $\delta^{13}\text{C}_{\text{veg}}$  values of C<sub>3</sub> and C<sub>4</sub> plants from Pre-LGM/LGM Texas were probably closer to  $-26.6\text{‰}$  and  $-11.6\text{‰}$ , respectively (Koch et al., 2004).

Many species of succulents and euphorbias are characterized by crassulacean acid metabolism (CAM) and display  $\delta^{13}\text{C}$  values intermediate of C<sub>3</sub> and C<sub>4</sub> plants, depending on environmental conditions (Osmond et al., 1973). Although succulents have been hypothesized to have coevolved with megafauna (Janzen, 1986), their abundance during the LGM in Texas was likely limited due to longer, more intense cold winters (Yann et al., 2016). This conclusion stems from the observation that the growth of modern succulents in the southwestern US and northern Mexico is impacted by cold winters (Dimmit, 2000). Thus, it is reasonable to conclude that CAM plants are unlikely to have been a major contributor to the diets of the organisms in this study. Further, growing season temperature and soil moisture content apparently limit the abundance of C<sub>3</sub> grasses, C<sub>4</sub> shrubs, and CAM plants, suggesting that each of these are likely to have been rare in the study areas of Texas during the Late Pleistocene (Teeri and Stowe, 1976; Stowe and Teeri, 1978; Teeri et al., 1978).

Mammalian tooth enamel reflects the isotopic composition of ingested food with an enrichment factor of  $+14.1\text{‰}$  relative to an organism's diet for medium to large bodied mammals, including proboscideans (Cerling and Harris, 1999). Enamel records the chemical composition of diet as mineralization occurs; thus, stable carbon isotopes reflect the average

geochemical signature of diet as recorded during tooth mineralization (Koch, 2007). For animals such as elephants, in which the dentition completes mineralizing around 20 - 25 years of age (Asher and Lehmann, 2008), the  $\delta^{13}\text{C}_{\text{enamel}}$  in the third molar is a reliable estimate of the average diet through life. Furthermore, relying on the third molar minimizes any effect of incorporating the mother's milk or a weaning signal (e.g., Metcalfe et al., 2010). Analysis of  $\delta^{13}\text{C}_{\text{enamel}}$  values can provide an understanding of whether ancient herbivore diets consisted of predominantly  $\text{C}_3$  plants (mean  $\delta^{13}\text{C}_{\text{enamel}} \leq -9 \text{‰}$ ) or  $\text{C}_4$  plants (mean  $\delta^{13}\text{C}_{\text{enamel}} \geq -2 \text{‰}$ ; Kohn 2010). For mammals that lived in tropical and temperate zones during the late Neogene, this has been used to indicate whether they were likely browsers or grazers (e.g., MacFadden et al., 1994; MacFadden and Cerling, 1996; Cerling et al., 1997; DeSantis et al., 2009; França et al., 2014; Pérez-Crespo et al., 2016).

In addition to utilizing stable carbon isotopes to infer paleodiet, stable oxygen isotopes from tooth enamel can be used to infer external environmental factors including temperature, altitude, aridity, and seasonality (e.g., Koch et al., 2004; Levin et al., 2006; DeSantis et al., 2009; 2017). In herbivores, they consume surface water and/or obtain most of their water in or on plants (Kohn et al., 1996; Levin et al., 2006). Large mammals, including proboscideans, are obligate drinkers with low metabolisms and are thus heavily reliant on surface water (Sukumar, 2003); as a result, the  $\delta^{18}\text{O}$  of their tissues more accurately reflects  $\delta^{18}\text{O}$  of meteoric water as compared to small mammals (Bryant and Froelich, 1995). Although small deviations in  $\delta^{18}\text{O}_{\text{enamel}}$  could be due to different climates and/or physiological states (Kohn et al., 1996; 1998), larger deviations amongst a group of animals is more likely due to spatial mixing (e.g., migration) or time averaging (Koch et al., 2004). Koch et al. (2004) suggested a standard deviation ( $1\sigma$ ) of  $\geq 2 \text{‰}$  for a species at a locality might suggest time-averaged or spatially mixed

assemblages based on prior studies (Bocherens, 1996; Clementz and Koch, 2001); we use the same value to assess such mixing in our study (where  $\delta^{18}\text{O} = [({}^{18}\text{O}/{}^{16}\text{O})_{\text{sample}}/({}^{18}\text{O}/{}^{16}\text{O})_{\text{SMOW}} - 1] \times 1000$ , where SMOW is Standard Mean Ocean Water; Coplen, 1994).

## 2.2 Dental Microwear Texture Analysis

Dental microwear, the microscopic features on the wear facets of tooth surfaces, manifests as a pattern of scratches and pits on the surface of a tooth, the prominence and density of which can be interpreted to reflect the consumption of different food items (e.g., Walker et al., 1978; Grine, 1981, 1986; Solounias et al., 1988). In herbivores, scratches are interpreted to indicate the consumption of tougher or more pliant food items, such as phytolith-rich grasses, which require shear force to rupture tissues (Teaford and Walker, 1984). In contrast, a high incidence of pits indicates the consumption of harder or more brittle objects, such as woody bark, seeds or fruit pits, which are crushed and lead towards either small pits or larger, more obvious gauges, depending on the size and/or hardness of the food being consumed (e.g., Walker et al., 1978; Grine, 1981, 1986; Solounias and Semprebon, 2002; Semprebon et al., 2004). Because of the corroding effects of the acids in food and saliva in buccal cavities of organisms, microwear records food consumption during the last few days to weeks of an animal's life (Grine, 1986); therefore, the study of dental microwear provides a 'snapshot' of the diet of an organism.

Dental microwear texture analysis (DMTA) is the analysis of dental microwear in three dimensions using a scanning white light confocal microscope and scale-sensitive fractal analysis (Ungar et al., 2003; Scott et al., 2005, 2006). This method arose from a need to more accurately define and quantify dental microwear textures and reduce observer error from what might otherwise be considered a highly subjective process (e.g., Grine et al., 2002; Mihlbachler et al.,

2012; DeSantis et al., 2013). While traditional dental microwear analysis (i.e., counting pits and scratches and using their relative proportion and/or size to infer feeding preferences) has been carried out in proboscideans (e.g., Capozza, 2001; Filippi et al., 2001; Palombo et al., 2005; Todd et al., 2007; Calandra et al., 2008; Rivals et al., 2010, 2012, 2015; Semperebon et al., 2016), DMTA is just beginning to be studied in proboscideans (Zhang et al., 2016; Green et al., 2017).

DMTA can identify an herbivorous animal as consuming tougher (i.e., grasses or, to a lesser extent, leaves) or more brittle foods (i.e., woody browse, fruits and/or nuts) based on the relationship between anisotropy (exact-proportion length-scale anisotropy of relief – *epLsar*; the orientation of wear features) and complexity (area-scale fractal complexity – *Asfc*; surface roughness at varying scales) (Unger et al., 2003; Scott et al., 2005, 2006; Scott, 2012).

Specifically, complexity values increase from grazing to mixed feeding and from leaf-browsing to frugivory in bovids, marsupials, and primates (Unger et al., 2003, 2008, 2012; Scott et al., 2005, 2006; Prideaux et al., 2009; Scott, 2012; DeSantis et al., 2017). Increasing anisotropy is interpreted to result from an increasing proportion of grass or foliage (both structurally tough foods) in diet. Therefore, DMTA is useful for identifying organisms as frugivores, folivores, mixed feeders, and/or grazers (Table 1). Other DMTA variables include textural fill volume (*Tfv*; quantifies the total depth of microwear features) and heterogeneity (*HAsfc*) (Scott et al., 2006; DeSantis, 2016). Heterogeneity compares the microwear signatures between sub-surfaces of a scanned area and is most often used to compare 3x3 grids (*HAsfc<sub>3x3</sub>*, for a total of 9 sub-surfaces) and 9x9 grids (*HAsfc<sub>9x9</sub>*, for a total of 81 sub-surfaces) (DeSantis, 2016). DMTA is a powerful tool for distinguishing between browse and grasses when isotopes alone cannot do so – for example, prior to the expansion of C<sub>4</sub> grasses (Cerling et al., 1997) or in regions where grasses

are C<sub>3</sub> (typically cool-season grasses) or shrubs C<sub>4</sub> (typically dry-adapted shrubs; Ehleringer et al., 1997).

### 3. Materials and Methods

#### 3.1 Fossil Proboscidean Populations

A population recovered from Late Pleistocene deposits on the Gulf Coastal Plain near Ingleside, Texas (TMM Site 30967; Figure 1; Table 2) was examined to compare the microwear signatures of sympatric mammoths and mastodons. Previous work (Koch et al., 2004; Hoppe, 2004; Yann et al., 2016) has revealed a clear dietary disparity between mammoths and mastodons at this site, with mastodons displaying  $\delta^{13}\text{C}$  values of  $-12.6\text{‰}$  to  $-7.4\text{‰}$  and mammoths displaying  $\delta^{13}\text{C}$  values of between  $-2.6\text{‰}$  and  $+0.2\text{‰}$ . Further, there is little evidence for spatial or temporal mixing of these proboscideans based on low variation in  $\delta^{18}\text{O}_{\text{enamel}}$  values for mammoths ( $1\sigma = 0.8\text{‰}$ ; Koch et al., 2004) and mastodons ( $1\sigma = 0.9\text{‰}$ ; Yann et al., 2016). The age of Ingleside deposits is between 75 ka and 30 ka (uncalibrated radiocarbon years before present) based on faunal correlation (Lundelius, 1972), temporally prior to the Last Glacial Maximum (LGM). Koch et al. (2004) suggested that the Texas Gulf Coastal Plain was 70 - 90 % C<sub>4</sub> biomass during this time based on carbon isotope values in mammalian enamel ( $\delta^{13}\text{C}_{\text{enamel}}$ ) and climate-vegetation models. Bryant and Holloway (1985), on the basis of pollen records from elsewhere along the Gulf Coast, posited two hypotheses for the vegetation of east Texas *ca.* 30 ka: either, 1) a closed oak-hickory-pine forest, or 2) an ecotonal region between grasslands and scrubby vegetation to the west and deciduous forests to the east. Taken together, Ingleside is probably best considered to have been an ecotonal region consisting of predominately C<sub>4</sub> grasses interspersed by stands of C<sub>3</sub> forest (likely mixed coniferous). Thus, mammoths at Ingleside were

likely to have been predominately C<sub>4</sub> grazers, while mastodons at Ingleside were predominately C<sub>3</sub> browsers. This makes Ingleside an ideal location to discern whether dental microwear has the potential to discriminate between browse and grass in proboscideans or if the textural properties of food consumed were similar.

We also examined mammoths and mastodons from Friesenhahn Cave (TMM Site 933; Figure 1; Table 2), a site on the Edwards Plateau that acted as a den cave for the Pleistocene scimitar cat *Homotherium serum* (Evans, 1961; Meade, 1961). Friesenhahn is unique in that its mammoth and mastodon population is overwhelmingly comprised of juvenile individuals (Graham, 1976). Initial radiocarbon dates of mammoth material from Friesenhahn indicated multiple sedimentation events, with the two horizons bearing mammoth remains dated to 17,800 ± 880 ka and 19,600 ± 710 ka (excavation units 3B and 3A, respectively; Graham, 1976). Subsequent re-interpretations of these initial ages suggest that the reported dates are probably inaccurate since collagen is unpreserved and the material dated (bioapatite) is generally unreliable (Graham et al., 2013). However, Graham et al. (2013) still consider an age estimate of full glacial (15 – 20 ka) to be a reasonable estimate for the mammoth and mastodon remains from Friesenhahn. Pollen analyses of Friesenhahn LGM sediments are consistent with modern grassland assemblages, including 19 % Asteraceae, 18 % Poaceae, and 15 % *Ambrosia* (Hall and Valastro, 1995); although Graham et al. (2013) reasoned that riparian woodlands must also have been present near the edge of the plateau based upon the presence of woodland mammals such as *Mammut*, *Tapirus*, and *Mylohyus*. The presence of pollen from conifers such as *Pinus* (~16 %) and *Juniperus* (7 %) supports this reasoning (Hall and Valastro, 1995). Previously published stable carbon isotopes on mammoths from Friesenhahn suggest a predominantly C<sub>4</sub> (probably grazing) signature (−1.8 ± 1.4 ‰; Hoppe, 2004); however, no studies have as of yet compared

the juvenile dietary signature to that of the adults. The high sample size of juvenile *Mammuthus* and *Mammot*, published pollen record, and previously published  $\delta^{13}\text{C}$  values make Friesenhahn an ideal location to test for ontogenetic shifts in diet of proboscideans with well-resolved diets.

In addition to previously-published  $\delta^{13}\text{C}$  values from Ingleside and Friesenhahn Cave, we analyzed a sample of *Mammuthus columbi* recovered from a locality along Cypress Creek on the Gulf Coastal Plain near Hockley, Texas (TMM Site #47200; Figure 1; Table 2). The Cypress Creek deposits are equivalent to the Deweyville Formation, whose individual units are described by Blum and Aslan (2006) as representing former floodplain surfaces cut by channels and aggraded during the late Pleistocene falling stage to lowstand. Lundelius et al. (2013) reported the discovery of a toxodont, *Mixotoxodon sp.*, from one of the Cypress Creek outcroppings. Strata at this location were described as being horizontally-bedded but convoluted due to spring activity (Lundelius et al., 2013). Recovery efforts evidently were made from multiple locations, as the toxodont was found associated with other mammalian genera (including *Equus*, *Bison*, *Cuvieronius*, *Mammuthus*, *Eremotherium*, *Camelops*, and *Paleolama*) and wood samples that were collected upstream, with “little variation” in the stratigraphy between localities (Lundelius et al., 2013). These wood samples yielded AMS radiocarbon ages of  $17,080 \pm 90$  ka and  $23,730 \pm 100$  ka (Lundelius et al., 2013); along with the stratigraphic interpretation (Blum and Aslan, 2006), the fauna recovered from the Cypress Creek locality likely represent an LGM assemblage. Lundelius et al. (2013) interpreted the Cypress Creek environment to have been a mesic open grassland during the LGM based on the associated fauna and pollen, although they mention the possibility that large mammals from this locality could have been migrating inland when lower sea levels (~100 meters) pushed the coastline 80 – 160 km east of present. An interpretation of open grassland with scattered areas of riparian parklands or woodlands is in agreement with

pollen recovered from LGM sediment cores to the north and west of Cypress Creek (Bryant and Holloway, 1985).

*Mammuthus exilis*, the pygmy mammoth, was endemic to the California Channel Islands (CHIS) of Santa Rosa, San Miguel, and Santa Cruz, all of which once comprised the Late Pleistocene “super island” of Santarosae (Orr, 1968; Agenbroad, 2001). The pygmy mammoth is suggested to have been a descendent of the mainland *Mammuthus columbi* (Roth, 1982, 1996), which swam to Santarosae during periods of lower eustatic sea level when the distance between the island and the mainland was less (Johnson, 1978); likely either during the glacial periods of Marine Isotope Stage (MIS) 6 (~150 ka) or MIS 8 (~250 ka) (Muhs et al., 2015). The Columbian mammoths which made it to the island would then have left a line of descendants of decreasing size due to resource constraints regarding food availability and land area – the Island Rule (Foster, 1964; McNab, 2010) – leading eventually to the pygmy *Mammuthus exilis* (Agenbroad, 2012).

We collected dental microwear molds of 16 individuals of *Mammuthus* (15 *M. exilis*, including ‘intermediate’ forms, and 1 *M. columbi*) from Santa Rosa Island, CA (these 16 individuals had portions of their wear facets that were well preserved, in contrast to other available teeth which had a chalky texture and did not preserve dental microwear) and compared them to Pleistocene adult mammoth populations from the three Texas sites (Ingleside, Friesenhahn Cave, and Cypress Creek) as well as adult mastodons from Ingleside (Table 2). The dietary preferences of the CHIS mammoths have been examined elsewhere (Semperebon et al., 2016) via user-based light microscopy analysis, and results suggested that the CHIS mammoths’ microwear signature resembled that of browsing proboscideans such as Florida mastodon (*Mammut americanum*) and African forest elephants (*Loxodonta cyclotis*). We analyzed a sample

of the CHIS mammoth population and compared it with a large sample of mammoths and mastodons from Texas via 3D DMTA.

### 3.2 Assignment of Ontogenetic Stages

Mammoth cheek teeth are molariform, with deciduous premolars differing from permanent molars in maximum length, maximum width, and number of plates (Laws, 1966; Maglio, 1973; Graham, 1986). To determine the approximate age of a mammoth from isolated teeth, we measured these characters and compared them to previously published populations of extant African elephants (Laws, 1966; Lee et al., 2012) and Columbian mammoths (Graham, 1986; Smith and Graham, 2017) to assign tooth position and the mandibular vs. maxillary setting (e.g., dp4/DP4, m1/M1, m2/M2). An inherent uncertainty in this method is that elephantid teeth are sexually dimorphic and thus male teeth tend to be larger than female teeth (Maglio, 1973); however, differences are usually small and thus amount to little difference for the first four cheek teeth (Lee et al., 2012; Stansfield, 2015). We then used the morphology of the occlusal surface of each tooth to assign wear stages to each molar following Laws (1966), with updated approximate ages assigned to each tooth following Stansfield (2015; see Haynes, 2017 for discussion). These ages were then used to assign each tooth to an age category as originally presented by Saunders (1977a), which considers mammoth ages in African [elephant] Equivalent Years (AEY). Sukumar (2003) considered weaning to comprise a significant portion of modern African elephant diets until approximately 3 years of age (Laws Wear Stage I–V), and stable nitrogen work by Metcalfe et al. (2010) corroborates this for woolly mammoths (*Mammuthus primigenius*); to discern differences in weaning, we separate the juvenile age group used by Saunders (1977a) into two sub-categories. The five categories we delineate are: “Weaning

Juvenile” (0 –3 AEY), “Post-Weaning Juvenile” (4 –7 AEY), “Youth” (8 – 17 AEY), “Young Adult” (18 – 34 AEY), and “Mature” (>34 AEY).

Mastodon teeth differ in morphology along the tooth row as well as in their maximum length and maximum width (Green and Hulbert, 2005). The relative tooth position, as well as the amount of wear the tooth has experienced, can be used to separate molars into relative developmental age groupings (Saunders, 1977b; Green and Hulbert, 2005). We measured the length and width of each mastodon tooth included in our study and assigned a wear stage to each tooth following descriptions first proposed by Saunders (1977b) and later expanded upon by Green and Hulbert (2005). We then assigned each tooth to a developmental stage as outlined by Saunders (1977b) and Green and Hulbert (2005). Whereas Green and Hulbert (2005) subdivided their “Juvenile” stage into 5 subdivisions and their “Youth” into 2 subdivisions, we refrained from doing so because of sample size limitations at Friesenhahn Cave ( $n = 7$ ) and because we were largely interested in discerning between weaning juveniles and non-weaning adults. We used the same age categories as in mammoths (“Juveniles”, “Youth”, “Young Adult”, and “Mature”), but refrain from assigning African [elephant] Equivalent Years (AEY) to each grouping because of larger uncertainties in the life history differences between *Mammuthus* and elephantids.

### 3.3 Stable Isotope Analysis

While the majority of stable isotope data included here are from published sources (i.e., Hoppe, 2004; Koch et al., 2004; Yann et al., 2016), additional isotopic data were collected from 10 specimens of *Mammuthus columbi* at Cypress Creek for this study. All methods for enamel collection and treatment follow procedures described by DeSantis et al. (2009). Approximately 2

- 3 mg of enamel powder was drilled over a ~1 cm sampling transect oriented parallel to the tooth's growth axis using a variable speed rotary tool with a 1 mm diameter carbide bit. Samples were taken no less than 1 cm from the occlusal surface on the exposed exterior portion of the most well-preserved loph of each molar. The powder was collected and treated with 30 % hydrogen peroxide to remove organic material. Following hydrogen peroxide treatment, the samples were rinsed with distilled water and then treated with 0.1N acetic acid for exactly 18 hours to remove secondary carbonates, and subsequently rinsed with distilled water (similar to Koch et al., 1997 and DeSantis et al., 2009). After being left to air-dry, the treated samples were analyzed using a VG Prism stable isotope ratio mass spectrometer with an in-line ISOCARB automatic sampler in the Department of Geological Sciences at the University of Florida. The standard deviation ( $1\sigma$ ) of the laboratory standard (NBS-19) included with these samples was  $< 0.05\%$ . The analytical precision is  $\pm 0.1\%$ , based upon replicate analyses of samples and standards (NBS-19). Stable isotope data were normalized to the laboratory standard (NBS-19) and are reported in conventional delta ( $\delta$ ) notation against V-PDB for  $\delta^{13}\text{C}_{\text{enamel}}$  and V-SMOW for  $\delta^{18}\text{O}_{\text{enamel}}$ , as defined in Section 2.1. Isotope data are summarized in Table 3.

### 3.4 Dental Microwear Texture Analysis

Ante-mortem wear facets on the occlusal surface of proboscidean molars were sampled using polyvinylsiloxane dental impression material (Regular-Body President's Jet, Coltene-Whaledent Corporation, Alstatten, Switzerland). The resultant molds were reinforced with a polyvinylsiloxane dental putty to stabilize them and prevent leaking. The molds were then cast using a high-resolution epoxy (Epotek 301, Epoxy Technologies Corporation, Billerica, MA, USA), which were left to harden in a fume hood for 72 hours prior to scanning. Previous work

determined that a significant amount of variability is present in microwear features across extant elephantid teeth (Todd et al., 2007); to reduce this variability, maintain consistency with previous results by Semprebon et al. (2016), and allow for comparison with other proboscidean DMTA studies (e.g., Green et al., 2017), the center portions of the central enamel bands were preferentially sampled on each mammoth and mastodon molar.

The replica casts were scanned using a Sensofar *PLu neox* optical profiler at Vanderbilt University in the Department of Earth and Environmental Sciences (Solarius Development, Inc, Sunnyvale, CA). Only enamel wear facets were scanned, as the underlying dentine is not as robust and differs from enamel (Haupt et al., 2013). A total area of  $285.5 \times 381 \mu\text{m}^2$  was scanned on the surface of each cast; we then extracted a smaller area of  $204 \times 276 \mu\text{m}^2$  and split it into a  $2 \times 2$  grid so as to be comparable to prior work (e.g., Ungar et al., 2003; Scott, 2012). Further, scans from the Sensofar *PLu neox* optical profiler at Vanderbilt University (colloquially referred to as "Dolly") are not significantly different in dental microwear textural attributes as compared to scans acquired at the University of Arkansas on a white-light confocal microscope referred to as "Connie" (Arman et al., 2016). The scans underwent scale-sensitive fractal analysis (SSFA) using toothfrax and Sfrax software (<http://www.surfract.com/>), and were then analyzed for complexity ( $Asfc$ ), anisotropy ( $epLsar$ ), textural fill volume ( $Tfv$ ), and heterogeneity ( $HAsfc$ ) (Ungar et al., 2003; Scott et al., 2005, 2006; DeSantis, 2016). Like other studies (e.g., Scott et al., 2006), we report both  $HAsfc_{3 \times 3}$  and  $HAsfc_{9 \times 9}$  values (comparison among 9 and 81 sub-surfaces, respectively).

### 3.5 Statistical Analyses

Stable isotope values for all proboscidean populations were normally distributed (Shapiro-Wilks, all  $p \geq 0.05$ ; Table 3); thus, Student's t-tests were used to compare the stable isotope values of each population. Spearman Rank correlation tests were used to assess the correlation between DMTA values and stable isotope values. DMTA data are typically non-normally distributed. Therefore, we used non-parametric tests to compare DMTA attribute values (instead employing parametric tests when normally distributed, Shapiro-Wilk tests).

The Ingleside mammoth population was compared to other Texas mammoth localities (Friesenhahn, Cypress Creek) using a Kruskal-Wallis test with *post hoc* comparisons using Dunn's procedure (Dunn, 1964). Because *Asfc* and *epLsar* values were normally distributed for each of these populations (Table 4), we also compared the distributions of these attributes using an ANOVA with *post hoc* Tukey HSD tests. Mann-Whitney U tests were used to compare Ingleside mammoths and mastodons to test the null hypothesis that the distributions of DMTA variables for both taxa were equal. Ingleside mastodons were also compared to all Texas adult mammoths (i.e., non-weaning individuals) using a Mann-Whitney U test to see if mainland mammoths differed significantly from mastodons in the textural properties of their diet.

We compared "Weaning Juvenile" mammoths at Friesenhahn to Friesenhahn adults (collectively, the "Post-Weaning Juvenile", "Youth", "Young Adult", and "Mature" developmental age groups) using parametric or non-parametric Mann Whitney U tests to see if a diet partly supplemented by milk would impact the microwear signature of weaning individuals (based on inferences from Sukumar, 2003 and Metcalfe et al., 2010). We also compared the "Weaning Juvenile" Friesenhahn mammoths to Ingleside adult mammoths to test for environmental differences between the two groups. We then compared the "Juvenile" mastodons at Friesenhahn to adults at Ingleside using parametric t-tests or non-parametric Mann Whitney U

tests (depending on normality, see Table 5) to see if the two populations differed due to either environment or ontogeny. Further, all Texas adult *Mammuthus columbi* specimens were collectively compared to the Santa Rosa specimens using Mann-Whitney U tests (*epLsar* was normally distributed for these two populations; thus, a t-test was also used to compare between them). In addition, we implemented a Levene's Test on all comparisons to test whether the variances of the populations being compared were equal. For all tests, the Bonferroni correction factor was withheld as it can result in an increase in Type II errors (Cabin and Mitchell, 2000; Nakagawa, 2004). *P*-values of  $< 0.05$  were considered significant.

## 4. Results

### 4.1. Stable Isotopes

Stable isotope data for all taxa are summarized in Table 3; primary stable isotope data are included in Supplemental Table 1. Stable carbon isotope values of Cypress Creek mammoths ranged from  $-4.9\text{‰}$  to  $-2.9\text{‰}$  (total range of  $2\text{‰}$ ) with an average of  $-3.8\text{‰}$  (Figure 2, Table 3). Friesenhahn and Ingleside mammoths (as summarized in Table 3; Hoppe 2004; Koch et al., 2004; Yann et al. 2016) are statistically indistinguishable from one another in  $\delta^{13}\text{C}$  ( $p = 0.239$ ). Ingleside mastodons (total  $\delta^{13}\text{C}_{\text{enamel}}$  range of  $-12.6\text{‰}$  to  $-9.5\text{‰}$ ; Yann et al., 2016) have significantly lower  $\delta^{13}\text{C}$  values than Ingleside, Cypress Creek, and Friesenhahn mammoth populations (all  $p < 0.001$ ). Cypress Creek mammoths have significantly lower  $\delta^{13}\text{C}$  values than either Friesenhahn mammoths or Ingleside mammoths (all  $p < 0.001$ ). Stable oxygen isotopes of Cypress Creek mammoths ranged from  $28.6\text{‰}$  to  $31.5\text{‰}$  (total range of  $2.5\text{‰}$ ) with an average of  $29.8\text{‰}$  and were not significantly different from any of the other populations (Ingleside mammoths,  $p = 0.9033$ ; Friesenhahn mammoths,  $p = 0.7696$ ; Ingleside mastodons,  $p = 0.238$ ).

The standard deviations ( $1\sigma$ ) of  $\delta^{18}\text{O}_{\text{enamel}}$  for all proboscidean populations are  $\leq 1.0$  ‰ (Table 3).

#### 4.2. Dental Microwear

Dental microwear data for all proboscidean populations are summarized in Table 4; Table 5 breaks down dental microwear data for adult and juvenile proboscidean populations; primary DMTA data are included in Supplemental Table 2. Supplemental Table 3 lists molar dimensions, wear stage, and developmental age group for all Texas mammoth and mastodon molars used in this study. Supplemental Table 4 includes dental measurements for the CHIS mammoths and taxonomic classifications (all measurements were made by J. Hoffman at SBMNH). Examples of color 3D images for all proboscideans are shown in Figure 3 with biplots of complexity and anisotropy exhibited in Figure 4. Summaries of comparisons between mainland mammoth populations are in Supplemental Table 5; summary of comparisons between ontogenetic groups of mammoths and mastodons are in Supplemental Table 6.

Among all populations, the Channel Island mammoths (*Mammuthus exilis* and *Mammuthus columbi*) have the highest mean complexity value (5.698) followed by Friesenhahn *Mammuthus columbi* (2.885) and Ingleside *Mammut americanum* (2.684; Table 4). The lowest mean complexity value is for *Mammut americanum* from Friesenhahn (1.275; Table 4). Mean anisotropy values ranged between 0.0033 and 0.0048 for all populations (Table 4).

All Texas adult mammoth populations have indistinguishable mean complexity and anisotropy values (all  $p \geq 0.335$ ; Supplemental Table 5). Cypress Creek mammoths have significantly greater textural fill values than Ingleside mammoths ( $p = 0.008$ ). Friesenhahn mammoths have significantly greater heterogeneity values than both Cypress Creek mammoths

( $HA_{sfc_{3x3}}$ ,  $p = 0.036$ ) and Ingleside mammoths ( $HA_{sfc_{3x3}}$ ,  $p = 0.005$ ;  $HA_{sfc_{9x9}}$ ,  $p = 0.032$ ).

Further, with the exception of textural fill volume ( $Tfv$ ,  $p = 0.005$ ), variance of DMTA attribute values between these populations were similar to one another ( $Asfc$ ,  $p = 0.651$ ;  $eplsar$ ,  $p = 0.290$ ,  $HA_{sfc_{3x3}}$ ,  $p = 0.181$ ;  $HA_{sfc_{9x9}}$ ,  $p = 0.160$ ). All other comparisons between Texas adult populations were not significant (all  $p > 0.05$ ; Supplemental Table 5).

Ingleside mastodons are indistinguishable from mammoths for all DMTA attributes, whether compared to only Ingleside mammoths ( $Asfc$ ,  $p = 0.692$ ;  $eplsar$ ,  $p = 0.684$ ,  $Tfv$ ,  $p = 0.895$ ;  $HA_{sfc_{3x3}}$ ,  $p = 0.291$ ;  $HA_{sfc_{9x9}}$ ,  $p = 0.662$ ) or all Texas mammoths as a whole ( $Asfc$ ,  $p = 0.798$ ;  $eplsar$ ,  $p = 0.301$ ,  $Tfv$ ,  $p = 0.071$ ;  $HA_{sfc_{3x3}}$ ,  $p = 0.868$ ;  $HA_{sfc_{9x9}}$ ,  $p = 0.625$ ). There are no significant differences in variance between Ingleside mastodons and mammoths ( $Asfc$ ,  $p = 0.260$ ;  $eplsar$ ,  $p = 0.735$ ,  $Tfv$ ,  $p = 0.787$ ;  $HA_{sfc_{3x3}}$ ,  $p = 0.061$ ;  $HA_{sfc_{9x9}}$ ,  $p = 0.210$ ).

Friesenhahn “weaning juvenile” mammoths are indistinguishable from adult mammoths in all DMTA attributes (all  $p > 0.05$ ; Supplemental Table 6). Additionally, there are no significant differences in variance between the two ontogenetic age groups ( $Asfc$ ,  $p = 0.945$ ;  $eplsar$ ,  $p = 0.968$ ,  $Tfv$ ,  $p = 0.341$ ;  $HA_{sfc_{3x3}}$ ,  $p = 0.440$ ;  $HA_{sfc_{9x9}}$ ,  $p = 0.852$ ). Friesenhahn “weaning juvenile” mammoths have significantly greater  $epLsar$  values than Ingleside adults (Table 5; Supplemental Table 6). Friesenhahn juvenile mastodons have significantly lower  $Asfc$  values than Ingleside adult mastodons ( $p = 0.016$ ; Table 5), but are indistinguishable from one another in all other DMTA attributes ( $eplsar$ ,  $p = 0.993$ ,  $Tfv$ ,  $p = 0.359$ ;  $HA_{sfc_{3x3}}$ ,  $p = 0.199$ ;  $HA_{sfc_{9x9}}$ ,  $p = 0.647$ ).

CHIS mammoth DMTA attribute mean values are not significantly different from adult specimens of *Mammuthus columbi* from Texas ( $Asfc$ ,  $p = 0.881$ ;  $eplsar$ ,  $p = 0.663$ ,  $Tfv$ ,  $p = 0.629$ ;  $HA_{sfc_{3x3}}$ ,  $p = 0.729$ ;  $HA_{sfc_{9x9}}$ ,  $p = 0.915$ ) or adult *Mammut americanum* specimens from

Ingleside, Texas ( $Asfc$ ,  $p = 0.983$ ;  $eplsar$ ,  $p = 0.759$ ,  $Tfv$ ,  $p = 0.302$ ;  $HAsfc_{3x3}$ ,  $p = 0.686$ ;  $HAsfc_{9x9}$ ,  $p = 0.577$ ); however, complexity values are significantly more variable in CHIS mammoths than in either Texas proboscidean (*Mammuthus columbi* Levene's Test,  $p = 0.003$ ; *Mammut americanum* Levene's Test,  $p = 0.034$ ). The variance of all other DMTA attributes is indistinguishable between CHIS mammoths and adult specimens of either *Mammuthus columbi* from Texas ( $eplsar$ ,  $p = 0.649$ ,  $Tfv$ ,  $p = 0.154$ ;  $HAsfc_{3x3}$ ,  $p = 0.931$ ;  $HAsfc_{9x9}$ ,  $p = 0.113$ ) or *Mammut americanum* from Ingleside, Texas ( $eplsar$ ,  $p = 0.578$ ,  $Tfv$ ,  $p = 0.382$ ;  $HAsfc_{3x3}$ ,  $p = 0.546$ ;  $HAsfc_{9x9}$ ,  $p = 0.466$ ).

### 4.3 Relationships between DMTA and Stable Isotope Data

When examining all proboscideans, anisotropy values are positively correlated with  $\delta^{13}\text{C}$  values ( $epLsar$ ,  $\rho = 0.362$ ,  $p = 0.020$ ). All other relationships between  $\delta^{13}\text{C}$  values and DMTA attributes are not significant ( $Asfc$ ,  $p = 0.148$ ,  $Tfv$ ,  $p = 0.126$ ;  $HAsfc_{3x3}$ ,  $p = 0.385$ ;  $HAsfc_{9x9}$ ,  $p = 0.275$ ). Likewise, there are no significant relationships between  $\delta^{18}\text{O}$  values and DMTA attributes for all proboscideans ( $Asfc$ ,  $p = 0.575$ ;  $eplsar$ ,  $p = 0.960$ ,  $Tfv$ ,  $p = 0.517$ ;  $HAsfc_{3x3}$ ,  $p = 0.870$ ;  $HAsfc_{9x9}$ ,  $p = 0.719$ ). When these data are split taxonomically into genera, no significant relationships are observed between DMTA attribute values and  $\delta^{13}\text{C}$  values for either *Mammuthus* ( $Asfc$ ,  $p = 0.284$ ;  $eplsar$ ,  $p = 0.120$ ,  $Tfv$ ,  $p = 0.185$ ;  $HAsfc_{3x3}$ ,  $p = 0.506$ ;  $HAsfc_{9x9}$ ,  $p = 0.320$ ) or *Mammut* ( $Asfc$ ,  $p = 0.559$ ;  $eplsar$ ,  $p = 0.456$ ,  $Tfv$ ,  $p = 0.415$ ;  $HAsfc_{3x3}$ ,  $p = 0.178$ ;  $HAsfc_{9x9}$ ,  $p = 0.135$ ). Heterogeneity ( $HAsfc_{9x9}$ ) is negatively correlated with  $\delta^{18}\text{O}$  in *Mammut* ( $\rho = -0.524$ ,  $p = 0.031$ ); all other relationships between  $\delta^{18}\text{O}$  and DMTA attribute values are not significant for *Mammut* ( $Asfc$ ,  $p = 0.212$ ,  $epLsar$ ,  $p = 0.138$ ;  $Tfv$ ,  $p = 0.547$ ;  $HAsfc_{3x3}$ ,  $p = 0.087$ ) and *Mammuthus* ( $Asfc$ ,  $p = 0.260$ ;  $eplsar$ ,  $p = 0.067$ ,  $Tfv$ ,  $p = 0.615$ ;  $HAsfc_{3x3}$ ,  $p = 0.109$ ;  $HAsfc_{9x9}$ ,  $p = 0.247$ ).

## 5. Discussion

### 5.1 Ingleside *Mammuthus columbi* and *Mammut americanum*

The dental microwear signatures of mammoths and mastodons from Ingleside are remarkably similar, with similar mean values and ranges (Table 4, Figure 4). The high degree of overlap in DMTA attribute values is in stark contrast to the disparate geochemical signatures of tooth enamel (reflective of average diet; Koch et al., 2004; Yann et al., 2016). The  $\delta^{13}\text{C}$  signature of *Mammut americanum* at Ingleside is indicative of  $\text{C}_3$  vegetation while *Mammuthus columbi* consumed a significant portion of  $\text{C}_4$  vegetation and was likely a mixed  $\text{C}_3/\text{C}_4$  feeder (Koch et al., 2004; Yann et al., 2016). Specifically, in Texas during the late Pleistocene, carbon isotope signatures of mastodons most likely result from the consumption of dicotyledonous trees and shrubs; although it could also reflect water-dependent  $\text{C}_3$  grasses such as reeds, sedges, and rushes, the low mean anisotropy value of the Ingleside population (Table 4) suggests that grasses were unlikely to have made up a large portion of their diet. The  $\delta^{13}\text{C}$  signature of *Mammuthus columbi* from Ingleside is at the high end of  $\text{C}_3/\text{C}_4$  mixed feeding (Koch et al., 2004), and is in fact dominated by  $\text{C}_4$  vegetation (applying a mixing model of pure  $\text{C}_3$  and pure  $\text{C}_4$  vegetation, mammoths consumed approximately 74 %  $\text{C}_4$ ; Koch et al., 2004).  $\text{C}_4$  signatures are typically inferred to result from warm-adapted (mostly monocotyledonous) grasses due to the unlikely presence of CAM plants in Late Pleistocene Texas environments (Yann et al., 2016).

In past studies of DMTA in ungulates, grazers and browsers occupied distinct morphospaces on an *Asfc/epLsar* biplot, leading towards the dietary niche expectations summarized in Table 1. For example, Scott (2012) showed that among African bovids, the grazing common tsessebe (*Damaliscus lunatus*) had low *Asfc* values (< 2.0) and high *epLsar*

values (0.006 to 0.009), while the browsing common duiker (*Sylvicapra grimmia*) had moderate *Asfc* values (1.0 to 5.0) and low *epLsar* values (0.001 to 0.004). The range in complexity and anisotropy values for both Ingleside mastodons and mammoths completely encapsulates the ranges of all bovids with disparate diets from Scott (2012). The high anisotropy values for both proboscideans suggests a high proportion of tough foods likely dominated the diets of both organisms, although the disparity in  $\delta^{13}\text{C}$  values suggests that such food came from different plant sources and/or habitats (e.g., forests vs. grasslands; Figure 5). Tough food is expected for a partly  $\text{C}_4$  grazing *Mammuthus*, but higher complexity values than the grazing common tsessebe (Scott, 2012) suggest that mammoths at Ingleside were likely highly generalized in their diets. On the other hand, the predominately  $\text{C}_3$ -browsing *Mammut* might be expected to have had higher *Asfc* values if individuals were specialized on woody browse. Higher and more variable *Asfc* values than the browsing common duiker (Scott, 2012) suggests that Ingleside mastodons were also highly generalized and consumed a high proportion of brittle or hard components of vegetation such as bark, nuts, or fruits.

*Mammut americanum*, although displaying evolutionarily conservative tooth morphology as compared to *Mammuthus columbi*, has been shown to have a wide array of dietary preferences. Analysis of mastodon dung recovered from the late Pleistocene Page-Ladson site in Florida revealed a broad diversity of consumed vegetation, including the wood, bark, seeds, fruit, vines, stems, leaves, thorns, and fine woody debris of at least 57 different taxa including trees, shrubs, lianas, vines and aquatic and terrestrial herbs (Newsom and Mihlbachler, 2006). Critically, the dung samples from this site were overwhelmingly ( $\geq 98\%$  by volume) composed of distal growth twigs ( $\leq 2$  to 3 years of age). By comparison, the “Burning Tree” mastodon dung from Ohio largely consisted of non-coniferous leaves and twigs, mosses, and low

herbaceous growth (Lepper et al., 1991), suggesting a selective diet with both browsing and grazing habits. Another study on mastodon digesta from three boreal forest sites in New York State showed an overall reliance on *Picea* and *Pinus* with seasonal preferences for *Salix* and *Populus* (winter) and *Alnus* (spring; Teale and Miller, 2012). Further, a mastodon tooth from Washington was found with pollen primarily represented by *Pinus*, *Salix*, *Shepherdia canadensis*, *Rosaceae*, *Compositae*, *Cyperaceae*, and *Gramineae* (Petersen et al., 1983). Additional work examining opal phytoliths preserved in mastodon tooth calculus suggests that some mastodons were capable of a predominately grazing lifestyle, if the environment demanded it (Gobetz and Bozarth, 2001). Low magnification stereomicrowear work on *Mammut americanum* from the Pleistocene of Florida revealed that mastodon microwear most closely aligned with the folivorous browsing morphospace, followed by mixed grazers/folivores and then fruit browsers (Green et al., 2005). Recent work employing DMTA suggests that still subtler dietary differences exist when comparing *Mammut* populations from cypress swamps, boreal forests, and open-pine parklands (Green et al., 2017). *Mammut* is probably best considered as a proboscidean with significant adaptability in its browsing niche, capable of expanding its dietary choices outside of typical “browsing” specialist dietary niches (e.g., folivore, frugivore, mixed feeder) depending on environmental and/or climatic conditions.

Our results, in accordance with the findings of the aforementioned studies utilizing multiple proxies for paleodiet, suggest an overall reliance of *Mammut americanum* on tough and/or hard foods, likely dominated by leaves (tough) and bark/woody browse (brittle and hard). *Mammut* foraging strategy in Late Pleistocene Texas likely paralleled that of modern monogastric herbivores. In this sense, Ingleside and Friesenhahn mastodon diets were mostly comprised of low-quality but chemically undefended species (regionally local conifers)

supplemented by broadleaf and herbaceous species when toxin levels decreased on a seasonal basis (Teale and Miller, 2012). DMTA data support the prevailing view of mastodons as displaying considerable adaptability in their ecological resistance during changing climates and environments in the Late Pleistocene (e.g., Baumann and Crowley, 2015; Metcalfe et al., 2013; Newsom and Mithlacher, 2006; Green et al., 2017; Widga et al., 2017a). These data also support the reconstruction of mammoths as generalist mixed feeders in Late Pleistocene Texas, likely consuming a wide array of foods with varying textural and photosynthetic properties. While  $\delta^{13}\text{C}$  values suggest that  $\text{C}_4$  grasses were a dominant component of their diet, DMTA data demonstrate that they consumed food with a broader range of textures than just tough grasses. These findings corroborate past studies showing a trend toward mixed feeding for elephantids in the Late Pleistocene despite being evolutionarily adapted for efficient grazing (Cerling et al., 1999; Kingston and Harrison, 2007). Whether mastodons or mammoths were indiscriminate in their dietary choices, consuming the roots, tubers, stems, leaves, needles, bark, and seeds of every species of plant they relied upon or only some of these components distributed across hundreds of specific species (as modern elephants do (Owen-Smith and Chafota, 2012)) remains to be tested.

An additional aspect that could play a critical role in how dental microwear manifests on a wear facet is the masticatory apparatus of the organism – i.e., the manner in which the organism processed its food. In mammoths (as in modern elephants), the power stroke is concentrated in a fore-aft movement, wherein the lower molars contact the posterior portion of the upper molars and are brought forward (Maglio, 1972). The enamel cross-lophs of the molars contact one another at an oblique angle, shearing foods and wearing the tooth crowns to a flat surface crossed by low-relief enamel ridges (Maglio, 1972). Thus, wear features such as

scratches should be preferentially aligned antero-posteriorly if the rear-to-front movement of the jaw brings foods along the way. By contrast, American mastodon mastication was evolutionarily conservative and characterized by a bucco-lingual movement of the jaw during the power stroke (Laub, 1996). Laub (1996) suggested that the power stroke could only be fully executed when the teeth fully occluded, which would have only been possible at higher wear stages when the cones and conules were not as pronounced. The highly generalized microwear signature of *Mammuth* in our study might therefore have resulted from differing orientations of the power stroke at different stages of relative tooth wear.

A further complicating factor in dental microwear studies is the potential role of grit, which has previously been suggested to be the main controlling factor in forming dental microwear features (Lucas et al., 2013). Exogenous grit has been suggested to be capable of leaving microwear features on enamel surfaces, although such features might not necessarily be similar to those left from the phytoliths in plant opal (Grine, 1986; Solounias and Semprebon, 2002). Grit increases in abundance due to geographic (e.g., increased loess input) and/or climactic changes (e.g., increased aridity), which would be an important caveat to consider when looking at time-averaged assemblages. However, stable oxygen isotopes suggest that these Texas proboscidean populations were not significantly time-averaged (all  $\delta^{18}\text{O}$  standard deviations  $1\sigma \leq 1.0\text{‰}$ , Table 3) and that significantly different climatic conditions were not experienced by individuals in these assemblages. As a result, there is no evidence to suggest that grit load would have changed appreciably over time at either Friesenhahn, Ingleside, or Cypress Creek. Further, recent studies clearly show that not only can food items create microwear (Xia et al., 2015), but that variability of microwear features is positively associated with variation of dietary abrasiveness (Schultz et al., 2013). Additionally, controlled feeding studies in rabbits (Schultz et

al., 2013) and sheep (Ramdarshan et al., 2016; Merceron et al., 2016) demonstrate that dietary signals are not overwhelmed by the ingestion of grit. Even wild koalas, which are known to ingest dust and grit on leaves (and primarily consume eucalyptus which lacks phytoliths), exhibit DMTA that records textural properties of consumed foods (Hedberg and DeSantis, 2017). It is therefore unlikely that exogenous grit is solely responsible for the microwear signatures of the proboscideans in this study, and that the wide range of *Asfc* and *epLsar* values is instead a true reflection of the highly generalized textural properties of the diets of both *Mammut* and *Mammuthus* from the late Pleistocene of Texas.

## **5.2 Ontogenetic dietary shifts in *Mammuthus columbi* and *Mammut americanum***

Dietary partitioning between individuals at different stages of life prevents intraspecific competition, allowing an individual to avoid direct overlap in resource use with members of its own species (Werner and Gilliam, 1984). Additionally, size has a predominant influence on an animal's energetic requirements – large-bodied organisms require a high abundance of food, which can be of low quality, while smaller individuals require less food but of higher nutrient quality (Peters, 1983). It follows that the change in body size during ontogeny could change the resource intake rate (e.g., Peters, 1983) and composition (Werner and Gilliam, 1984) of an individual. Ontogenetic diet shifts are widespread in nature, although they are most often found in invertebrates and lower vertebrates living in freshwater communities (Werner and Gilliam, 1984). There is some evidence of ontogenetic dietary partitioning in mammals with precocial youth such as deer mice (Van Horne, 1982) and fur seals (de Albernaz et al., 2017). Some primates similarly show variations in feeding between juveniles and adults that is apparently related to food toughness (Chalk-Wilayto et al., 2016).

Our data do not support the hypothesis that juvenile mammoths consumed foods of different textural properties than their adult counterparts at Friesenhahn Cave (Figure 4). However, we do find evidence that Friesenhahn juvenile mammoths had significantly higher anisotropy than Ingleside adult mammoths (Table 5; Supplemental Table 6), suggesting two possible scenarios. The first possibility is that a higher proportion of tough foods comprised the diet of Friesenhahn juveniles as compared to Ingleside adults. The second possibility is that differing loads of exogenous grit were present in the environment at Friesenhahn during the LGM as were present at Ingleside pre-LGM, increasing the dietary *epLsar* signature of Friesenhahn mammoths. If the latter case were true, then we would expect grit to have caused an increase in *epLsar* values in both Friesenhahn adults and juveniles, as the grit would have been nonselective in being incorporated in the diets of all individuals at that site. Additionally, grit has been shown to play a minor (and non-significant) role in altering *epLsar* values of grazers in controlled feeding studies (Merceron et al., 2016). Because Ingleside and Friesenhahn adult mammoths are indistinguishable in all DMTA attributes (Supplemental Table 5), the first scenario of a dietary discrepancy is the more likely one. As Friesenhahn exhibited a very high percentage of grasses and sedges (64 %) compared to modern regional shortgrass prairies (47 %) and modern regional tallgrass prairies (38 %) (Hall and Valastro, 1995), it is very likely that Friesenhahn juvenile mammoths were consuming predominantly grasses. Ingleside mammoths, likely inhabiting an open C<sub>4</sub> grassland interspersed by stands of C<sub>3</sub> forest (Bryant and Holloway, 1985; Koch et al., 2004), would have encountered a variety of foods of varying textures, resulting in dampened *epLsar* values.

In addition, we find evidence that Friesenhahn juvenile mastodons had significantly lower complexity than Ingleside adult mastodons (Table 5; Supplemental Table 6). This suggests

that Friesenhahn mastodons were consuming less brittle and/or harder foods than Ingleside mastodons. However, as we lack an adult mastodon population at Friesenhahn, we cannot say for sure whether this phenomenon is due to a true ontogenetic difference between juveniles and adults or whether it is due to an environmental difference between the two sites. Juvenile mastodons could have been restricted to consuming less hard foods due to difficulties accessing and/or processing such foods; on the other hand, Ingleside may have had an abundance of harder foods – such as bark, seeds, fruit pits, or nuts – as compared to Friesenhahn due to either climatic differences (pre-LGM vs. LGM conditions) or geographic location (coastal vs. plateau setting). Because of the multiplicity of these compounding effects, we cannot explicitly state whether mastodons displayed an ontogenetic difference in diet. We encourage a future study focusing on dental microwear of juvenile and adult mastodons recovered from the same location, much as we were able to do with the Friesenhahn mammoth assemblage.

Juveniles and adults might not be expected to exhibit dietary partitioning for one of three reasons. First, elephant juveniles are highly precocial - newborns are capable of walking and feeding themselves almost immediately after birth, although juveniles rely at least partially on their mother's milk for the first 2 - 3 years of life (Sukumar, 2003). Second, individual elephant diets (regardless of age) within a population are not likely to vary significantly due to their herd's social structure. Newborns stay with their mothers and a herd of mostly female adults, roaming and foraging together as a unit (Sukumar, 2003). Thus, the vegetation spectra that individuals come into contact with are, on average, the same across a herd. This relationship might not hold true in closed forest-dwelling browsing mastodons because more resources might be available to full-sized individuals (for example, fruits hanging on high branches); however, it is equally likely that adults might knock these resources down and rupture fruit or seed hard skins for

juveniles, much as modern elephant mothers do for their young (Sukumar, 2003). Third, being a large-bodied forager with a cecal digestive system necessitates that elephants consume as much food as possible, as they are less limited by the amount of food consumed or rate of ingestion as compared to ruminants (Hanley, 1982). Elephants are therefore likely to consume whatever vegetation is available to them and would be expected to show little resource discrimination amongst the members of the herd.

Elephantids (including mammoths) might also be likely to show similar patterns in dental microwear from the juvenile through adult stage because of their molariform premolars and molars (Maglio, 1972). Deciduous premolars (i.e., dp2, dp3 and dp4) are composite organs of similar morphology and structure to permanent molars (i.e., m1, m2 and m3), with subsequent molars effectively being scaled-up versions of the previous cheek tooth. Thus, the masticatory process is likely unchanged with age as is the bulk morphology of the wear facet, limiting the potential for differential wear mechanisms between adults and juveniles. On the other hand, the molar morphology of mammutids does change from the juvenile through adult stage, with bilophodont DP2/dp2 and DP3/dp3, trilophodont DP4/dp4, M1/m1, and M2/m2, and tetralophodont (or greater) M3/3 tooth forms (Saunders, 1977b; Green and Hulbert, 2005). However, Laub (1996), who conducted the most in-depth consideration of mastodon chewing mechanics, did not mention any potential difference in the power strokes between juveniles and adults. It also seems unlikely that the mere addition of lophs from second deciduous premolars through permanent third molars would give cause for a significant alteration in the manner in which adult mastodons processed their foods as compared to juveniles. Laub (1996) considered prominent cusps preventing an efficient bucco-lingual shear stroke to be the most important aspect controlling microwear signatures in *Mammut*. Thus, any amount of variation in microwear

signature among different cheek teeth along the toothrow in proboscideans (e.g., deciduous premolars or permanent molars) is likely to be at least as much as would be seen when comparing among lophs (at potentially differing wear stages) on a singular molar. However, as Todd et al. (2007) did find significant variability among lophs of extant elephant molars, to yield the most comparable methods for researchers it is best to standardize the tooth position and/or loph that they choose to examine in dental microwear signatures – typically, the central enamel band in *Mammuthus* and the metaloph/id in *Mammot* (as is typically the practice in proboscidean microwear studies; e.g., Semprebon et al., 2016; Green et al., 2017).

### **5.3. Dietary comparison of Late Pleistocene *Mammuthus* and *Mammot* to Santa Rosa**

#### ***Mammuthus exilis***

Semprebon and colleagues (2016; their figure 4C) demonstrated via stereomicroscopic analysis that *Mammuthus exilis* had similar textural properties to *Loxodonta cyclotis* and *Mammot americanum*, the three of which fell within the extant ungulate browsing morphospace (Semprebon, 2002; Solounias and Semprebon, 2002). None of the 53 *Mammuthus exilis* or the singular *Mammuthus columbi* from Santa Rosa, Santa Cruz, and San Miguel fell within the smaller grazing morphospace defined by extant grazers (Semprebon et al., 2016; their figure 4B). Because of the pygmy mammoth's similarity in stereomicrowear to both mastodons and African forest elephants, Semprebon and colleagues suggested that Santa Rosa Island was more than likely a closed-forest environment during the Late Pleistocene and that mammoths there were likely consumers of tough vegetation such as spruce, cypress, and Douglas Fir (Semprebon et al., 2016). However, the authors noted that the stereomicrowear pattern of modern elephants (*Loxodonta cyclotis*, *L. africana*, *Elephas maximus*) and the pygmy mammoth (*Mammuthus*

*exilis*) were unique compared to other herbivorous mammals studied via stereomicroscopy to date (Sempere et al., 2016; p. 7).

Our data similarly show that the CHIS mammoths (*Mammuthus exilis* and *Mammuthus columbi*) are unique in having a wider range, higher variability, and higher mean values of complexity (*Asfc*) than either population of Texas *Mammuthus* or *Mammuthus* (Figure 4; Table 4). Further, the significantly higher variability in *Asfc* values for CHIS mammoths as compared to both populations of Texas proboscideans suggests a higher variability in diet for the island-restricted population of pygmy mammoths (and one Columbian mammoth).

There are some caveats to treating the Santa Rosa Island mammoths as a discrete population in space and time. Specimens of *Mammuthus exilis* are not well-constrained temporally, arriving on Santarosae at least 150 ka and perhaps as much as 250 ka (Muhs et al., 2015). The youngest dated mammoth specimen from Santa Rosa Island was reported as 11,030 ± 50 ka (Agenbroad, 2005); thus, this “population” is highly time-averaged, spanning multiple glacial-interglacial cycles and their associated transgressions and regressions. The microwear signature of mammoths from Santa Rosa therefore represents different environmental signatures – some likely during the warmer interstadials and others during cool interglacials. This may explain the higher variability in Santa Rosa complexity values because our sample likely represents a longer environmental and dietary history than any of the Texas mammoth or mastodon populations (Table 2).

Anderson et al. (2010) summarizes the LGM vegetation of southwestern California based on previous studies from multiple mainland sites (including Rancho La Brea and McKittrick) as being dominated by multiple coniferous species (*Pinus*, *Abies*, and *Juniperus* or *Cupressus*) and resembling mixed conifer forests of the higher elevation San Jacinto and San Bernardino

mountains today. During the LGM, the interpretation of Santa Rosa Island as a mixed coniferous forest with a lower abundance of grasses (Anderson et al., 2010) suggests that mammoths on the island were exposed to a greater abundance of hard foods including bark, twigs, and seeds than the Texas *Mammuthus columbi* and *Mammot americanum* populations examined in this study. Between 17 and 13 ka, Santarosae was characterized by Douglas fir (*Pseudotsuga menziesii*), Gowen cypress (*Cupressus governiana*), and bishop pine (*Pinus muricata*) with a diverse understory of forbs and shrubs (Chaney and Mason, 1930; Anderson et al., 2008). By the latest Pleistocene (*ca.* 11,800 cal. yrs BP), the mixed conifer forest was beginning to fragment into multiple plant communities, including pine stands, coastal sage scrub and grassland (Anderson et al., 2010), introducing a wide array of foods with highly variable structural properties and/or textures. The pygmy mammoths (*M. exilis*) occupying Santarosae during this period would have almost certainly been subsisting on a wide variety of resources, and our complexity values are reflective of this highly generalized diet.

Although our sample size of pygmy mammoths ( $n = 16$ ) was considerably smaller than the previous user-based light microscopy study ( $n = 51$ ), the overall environmental signature of Santa Rosa pygmies was similar between the two studies. One of the strengths of DMTA is its ability to discern dietary patterns with relatively small sample sizes (Scott, 2012; DeSantis et al., 2013). The hypothesis that *Mammuthus exilis* had a diet distinct in textural properties as compared to Texas *Mammuthus columbi* or *Mammot americanum* is supported via DMTA insofar as the variability in complexity values exceeds any other known artiodactyl, perissodactyl, or proboscidean previously studied (e.g., Scott, 2012; DeSantis and Schubert, 2015; Zhang et al., 2016; Jones and DeSantis, 2017; Green et al., 2017). As higher complexity values are expected from an organism feeding on bark, seeds, and woody material, our data

support previous interpretations of the feeding habits of pygmy mammoths (Semprebon et al., 2016).

Although the pygmy mammoth is the end-result of a long history of insular dwarfism and is considered to be a distinct species (*Mammuthus exilis*), the CHIS collections are time-averaged and record multiple colonization events (Muhs et al., 2015). Thus, dwarfism likely occurred several times on Santarosae. The CHIS mammoths are therefore comprised mostly of intermediate individuals represented by only a few 'pure' *M. columbi* and a few 'pure' *M. exilis* individuals. Indeed, not all mammoths we measured belong to *M. exilis* as evidenced by measurements of length, width, and other diagnostic dental characters outlined in Widga et al. (2017b). These measurements are part of an ongoing study on the character of the Channel Island mammoths (J. Hoffman, personal communication). This complication hints at the larger issue of identifying mammoth material to the species level, which has been previously suggested to have been a difficult task in the Late Pleistocene, when mammoths varied in size and morphology more due to phenetic conditions than genetic differences (Enk et al., 2011, 2016; Smith and Graham, 2017; Lister, 2017) – although there are promising methods in the works (Widga et al., 2017b). As result, it is possible that some specimens originally referred to *Mammuthus exilis* are in fact simply smaller or intermediate *Mammuthus columbi*. This complicating factor should not significantly impact our results because it is likely that *M. exilis* and *M. columbi* would have displayed similar feeding and foraging behavior on Santa Rosa Island due to similarities in feeding habits (Agenbroad, 2012).

## 6. Conclusions

We demonstrate that Ingleside mastodons were likely highly generalized in their consumption of  $C_3$  woody browse, while mammoths were  $C_3/C_4$  mixed feeders; however, both proboscideans consumed a wide variety of foods with varying textural properties. The overlap in DMTA signatures of the two organisms suggests that both mammoths and mastodons had generalized diets of tough and hard foods. There is no evidence for ontogenetic differences in the diet of *Mammuthus columbi*, despite large differences in size between juvenile and adult mammoths. There may be evidence that dietary choices between Friesenhahn juvenile mammoths and mastodons differed from their adult counterparts at Ingleside, although whether this difference is due to ontogenetic or environmental differences (or some combination of the two) is unclear. Finally, the pygmy mammoths on Santa Rosa Island had a more variable diet with extensive hard object feeding as compared to late Pleistocene *Mammuthus columbi* and *Mammut americanum* from Texas, consistent with previous reconstructions of the dietary behavior of *Mammuthus exilis* using user-based stereomicrowear methods. Our work suggests that microwear alone may not be sufficient to reconstruct “browsing” or “grazing” habits in proboscideans, as they were likely highly generalized in consuming a wide variety of plant parts while remaining somewhat specialized on the isotopic source of those plants. Thus, multiple dietary proxies may be needed to reconstruct the diets of proboscideans and potentially other large-bodied taxa, which consume a wide variety of foods to sustain themselves.

### **Acknowledgements**

We would like to thank the Vanderbilt Dietary Reconstructions and Ecological Assessments (DREAM) lab and others, including: E. Biedron, J. Bradham, J. Crites, C. Hedburg, B. Gibson, B. Jones, A. Reside, and J. Rubinstein for assistance in molding and/or feedback on this

manuscript. We would also like to thank E. Lundelius, C. Sagebiel, and M. Brown for access to and significant assistance with the collections of the Texas Memorial Museum. We would like to thank also E. Lundelius, J. Green, C. Widga, and an anonymous fourth reviewer for providing insightful reviews that significantly improved this manuscript. Further, we are grateful to J. Hoffman for providing measurement data of *Mammuthus* specimens from the Santa Barbara Museum of Natural History (Supplemental Table 4). Funding was provided by the Geological Society of America Student Research Grant (to Smith), Vanderbilt University, and NSF 1053839 (to DeSantis).

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## Figure Captions

**Figure 1.** Site map for all proboscidean populations examined in this study. A) The California Channel Islands as they appear today (all samples come from Santa Rosa Island); and, B) the late Pleistocene Texas sites of Ingleside, Friesenhahn Cave, and Cypress Creek.

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**Figure 2.** Stable carbon isotope values for Late Pleistocene mammoth populations from Texas. Horizontal dotted lines denote the boundary for predominately C<sub>3</sub> consumers, mixed C<sub>3</sub>/C<sub>4</sub> consumers, and predominately C<sub>4</sub> consumers. Open squares, *Mammut americanum* (Ingleside); filled circles, *Mammuthus columbi* (Ingleside); open circles, *Mammuthus columbi* (Friesenhahn); gray circles, *Mammuthus columbi* (Cypress Creek). Cypress Creek data is new data from this study. Other data sources: Hoppe, 2004 and Koch et al., 2004 (*Mammuthus* from Friesenhahn and Ingleside), Yann et al., 2016 (*Mammut* from Ingleside). *Mammut* and *Mammuthus* silhouettes from PhyloPic.org.

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**Figure 3.** 3D surface models showing examples of microwear for proboscidean populations used in this study. A) *Mammuthus columbi*, Ingleside); B) *Mammuthus columbi*, Cypress Creek; C) adult *Mammuthus columbi*, Friesenhahn; D) juvenile *Mammuthus columbi*, Friesenhahn; E) *Mammut americanum*, Ingleside; F) *Mammut americanum*, Friesenhahn; and, G) *Mammuthus exilis*, Santa Rosa Island.

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**Figure 4.** Bivariate plots of anisotropy and complexity for A) mammoths and mastodons from Ingleside; B) juvenile and adult mammoths from Friesenhahn; and, C) pygmy mammoths from Santa Rosa Island and all mainland adult mammoths in this study. Open squares, *Mammut americanum* (Ingleside); filled circles, *Mammuthus columbi* (Ingleside); open circles, adult *Mammuthus columbi* (Friesenhahn); black X's, juvenile *Mammuthus columbi* (Friesenhahn); gray circles, *Mammuthus columbi* (Cypress Creek); open triangles, *Mammuthus exilis* (Santa Rosa Island). [Formatted for 1 column width]

**Figure 5.** Bivariate plots of A) anisotropy, and B) complexity versus  $\delta^{13}\text{C}$  for all fossil proboscideans in this study. Open squares, *Mammut americanum* (Ingleside); filled circles, *Mammuthus columbi* (Ingleside); open circles, *Mammuthus columbi* (Friesenhahn); gray circles, *Mammuthus columbi* (Cypress Creek). See text for rank correlations and significances. [Formatted for 1 column width]

**Table Captions**

**Table 1.** Dietary categories and the expected DMTA or  $\delta^{13}\text{C}$  response variable for specialist populations in tropical or temperate locations where  $\text{C}_3$  grasses and  $\text{C}_4$  dicots are rare.

**Table 2.** Localities of mammoth and mastodon specimens analyzed for DMTA in this study.

**Table 3.** Stable isotope summary statistics for all proboscidean populations used in this study.

**Table 4.** Descriptive statistics of all DMTA attributes for all proboscidean populations used in this study, broken down by site.

**Table 5.** Descriptive statistics of all DMTA attributes for Texas proboscidean populations, broken down by site. Includes only those specimens with discernable age group designations.

**Supplemental Table Captions**

**Supplemental Table 1.** Stable isotope data for all specimens examined in this study.

**Supplemental Table 2.** DMTA data for all specimens examined in this study.

**Supplemental Table 3.** Molar dimensions, wear stage, and developmental age groupings for *Mammuthus columbi* and *Mammut americanum* specimens used in this study.

**Supplemental Table 4.** Dental measurements and taxonomic/subjective classification of *Mammuthus* specimens from Santa Rosa Island used in this study.

**Supplemental Table 5.** Summary of comparisons (p-values) for all DMTA attributes between Texas mammoth (*Mammuthus columbi*) populations.

**Supplemental Table 6.** Summary of comparisons (p-values) for all DMTA attributes between Texas mammoth (*Mammuthus columbi*) juveniles and adults.

**Supplemental Table 7.** Summary of comparisons (p-values) for all DMTA attributes between Texas mastodon (*Mammut americanum*) juveniles and adults.

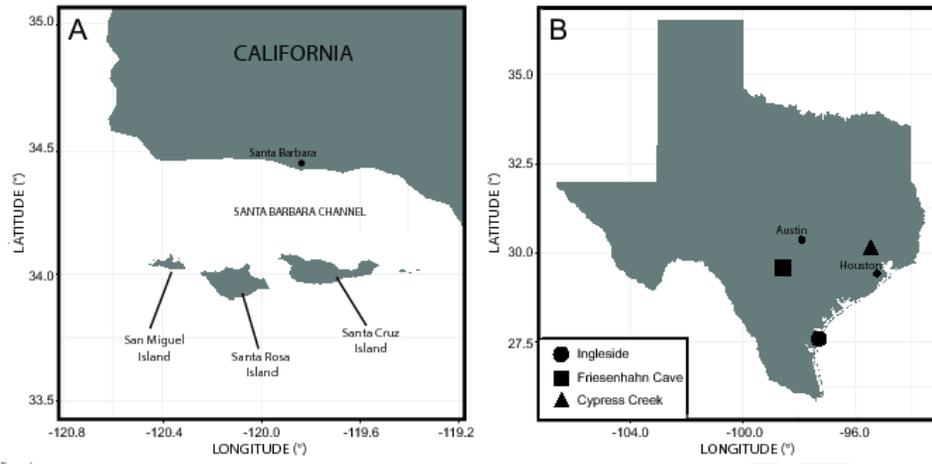


Figure 1



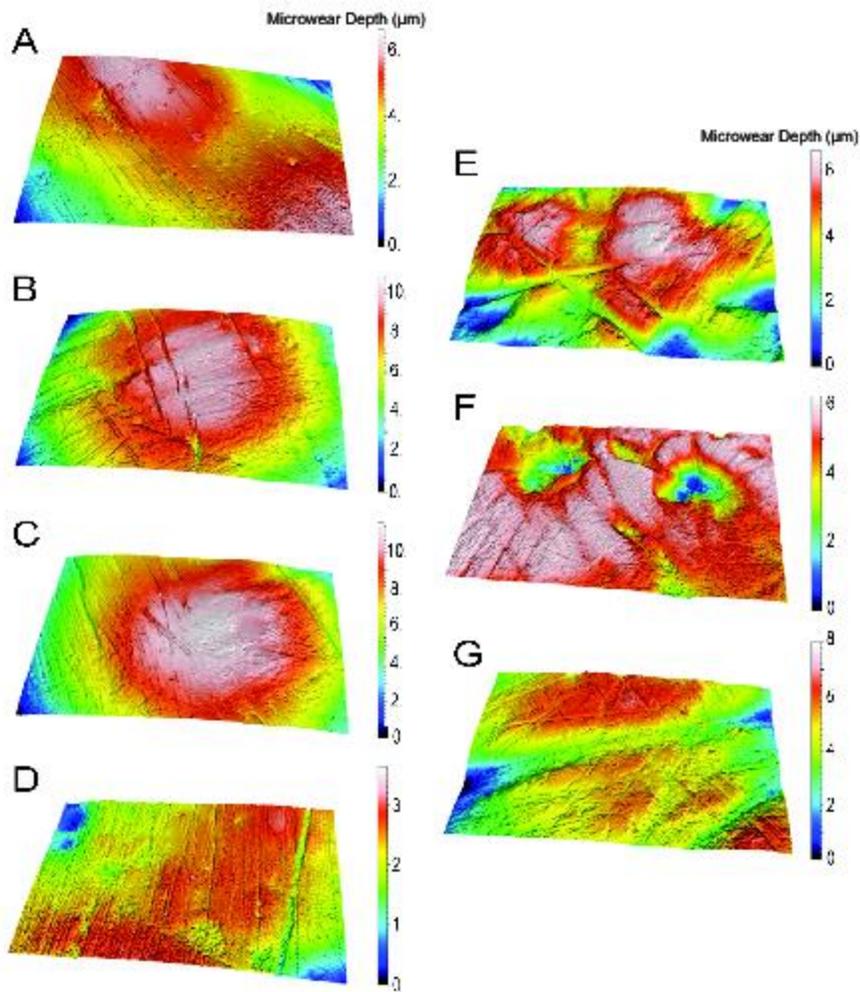


Figure 3

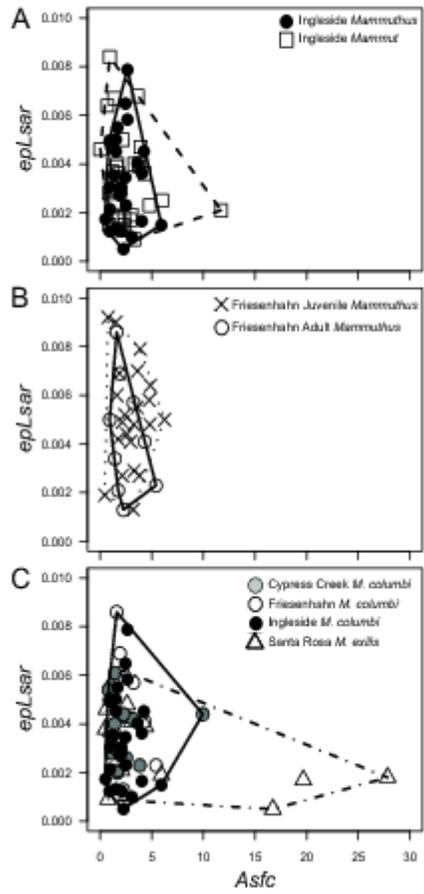


Figure 4

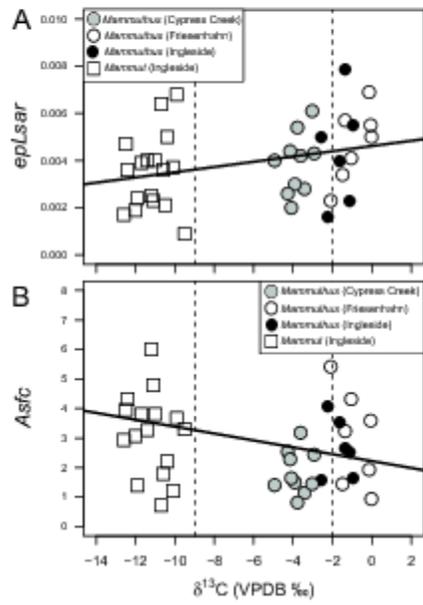


Figure 5

**Table 1.** Dietary categories and the expected DMTA or  $\delta^{13}\text{C}$  response variable for specialist populations in tropical or temperate locations where  $\text{C}_3$  grasses and  $\text{C}_4$  dicots are rare.

<b>Dietary Category</b>	<b>Expected <i>Asfc</i></b>	<b>Expected <i>epLsar</i></b>	<b>Expected <math>\delta^{13}\text{C}_{\text{enamel}}</math></b>
Grazer	Low	High	High
Woody Browser	Intermediate to High	Low	Low
Mixed Grazer/Woody Browser	Intermediate	Intermediate to Low	Intermediate
Fruit-Seed and Browse Consumer	Very High	Low	Low

*Asfc*, area-scale fractal complexity; *epLsar*, exact proportion length-scale anisotropy of relief. Dietary interpretations for DMTA follow those interpreted for bovids (Scott, 2012) while stable isotope expectations are based on data from O’Leary, 1988 and Koch et al., 1991.

**Table 2.** Localities of mammoth and mastodon specimens analyzed for DMTA for this study.

Site/Taxon	<i>n</i>	Age	Paleoenvironment	References
Cypress Creek, TX <i>Mammuthus columbi</i>	13	LGM 24 – 17 ka	Mesic open grassland with abundant sedges	Blum and Aslan, 2006; Lundelius et al., 2013
Ingleside, TX <i>Mammuth americanum</i> <i>Mammuthus columbi</i>	32 26	Pre-LGM 75 – 30 ka	Open C <sub>4</sub> grassland interspersed by areas of C <sub>3</sub> forest	Lundelius, 1972; Bryant and Holloway, 1985 Koch et al., 2004
Friesenhahn Cave, TX <i>Mammuth americanum</i> juvenile <i>Mammuthus columbi</i> adult juvenile	7 7 32 9 22	LGM 20 – 15 ka	Open C <sub>4</sub> grassland with some forests likely occupying canyons and riparian zones	Graham, 1976; Hoppe, 2004; Koch et al., 2004; Graham et al., 2013
Santa Rosa Island, CA <i>Mammuthus columbi</i> <i>Mammuthus exilis</i>	1 15	Pre-LGM to Post-LGM 150 – 11 ka	Cypress, pine, and Douglas Fir forest during the pre-LGM transitioning to a grassland, shrubland and parkland mosaic during the post-LGM	Anderson et al., 2008; Anderson et al., 2010; Agenbroad, 2012; Muhs et al., 2015

*n*, number of individuals sampled for dental microwear texture analysis. Age estimates and paleoenvironmental interpretations come from the references listed in the final column.

**Table 3.** Stable isotope summary statistics for all proboscidean populations used in this study.

Site	Taxon	N	$\delta^{13}\text{C}$ V-PDB (‰)							$\delta^{18}\text{O}$ V-SMOW (‰)						
			mean	min	max	range	SD (1 $\sigma$ )	SE	p-value	mean	min	max	range	SD (1 $\sigma$ )	SE	p-value
Cypress Creek	<i>Mammuthus columbi</i>	10	-3.8	-4.9	-2.9	2.0	0.6	0.2	0.930	29.8	28.6	31.1	2.5	0.8	0.3	0.395
Friesenhahn Cave	<i>Mammuthus columbi</i> <sup>A,B</sup>	16	-1.9	-5.1	0.0	5.1	1.4	0.4	0.118	29.7	28.1	31.1	3.0	0.7	0.2	0.592
Ingleside	<i>Mammuth americanum</i> <sup>C</sup>	19	-11.1	-12.6	-9.5	3.1	0.9	0.2	0.726	30.2	28.5	31.7	3.2	0.9	0.2	0.715
	<i>Mammuthus columbi</i> <sup>A,C</sup>	9	-1.3	-2.6	0.2	2.8	0.8	0.3	0.732	29.8	28.0	31.4	3.4	1.0	0.3	0.210

N, number of specimens; min, minimum; max, maximum; SD, one standard deviation (1 $\sigma$ ); SE, standard error of the mean ( $\sigma/\sqrt{n}$ ); p-value is that associated with a Shapiro-Wilks test to test for an underlying normal distribution (all p-values >0.05). All stable isotope values are listed in permil format relative to V-PDB (carbon) or V-SMOW (oxygen). <sup>A</sup> denotes stable isotope data from Koch et al., 2004. <sup>B</sup> denotes stable isotope data from Hoppe, 2004. <sup>C</sup> denotes stable isotope data from Yann et al., 2016.

**Table 4.** Descriptive statistics of all DMTA attributes for all proboscidean specimens used in this study, broken down by site.

<b>Taxon</b>	<b>Statistic</b>	<b>n</b>	<b>Asfc</b>	<b>epLsar</b>	<b>Tfv</b>	<b>HAsfc<sub>3x3</sub></b>	<b>HAsfc<sub>9x9</sub></b>
<b><i>Mammut americanum</i> Friesenhahn, TX</b>	Mean	7	1.275	0.0034	11299.5	0.331	0.712
	Median		1.047	0.0040	12658.1	0.214	0.566
	SD (1 $\sigma$ )		0.873	0.0016	3074.1	0.224	0.463
	Minimum		0.429	0.0011	4846.8	0.184	0.335
	Maximum		2.759	0.0049	13724.6	0.81	1.663
	Total Range		2.33	0.0038	8877.8	0.626	1.328
	<i>p</i> for Normality		0.120	0.144	<b>0.018</b>	<b>0.005</b>	0.057
<b><i>Mammut americanum</i> Ingleside, TX</b>	Mean	32	2.684	0.0034	10370.3	0.414	0.775
	Median		2.146	0.0032	11027.8	0.35	0.613
	SD (1 $\sigma$ )		2.11	0.0018	3580.6	0.227	0.541
	Minimum		0.715	0.0009	507.0	0.143	0.277
	Maximum		11.717	0.0084	16546.7	0.985	3.05
	Total Range		11.002	0.0075	16039.7	0.842	2.773
	<i>p</i> for Normality		<b>&lt; 0.001</b>	<b>0.019</b>	<b>0.017</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>
<b><i>Mammuthus columbi</i> Cypress Creek, TX</b>	Mean	12	1.989	0.0039	16507.0	0.42	0.725
	Median		1.8	0.0040	16361.6	0.352	0.642
	SD (1 $\sigma$ )		0.905	0.0014	7652.3	0.205	0.305
	Minimum		0.794	0.0020	3870.4	0.191	0.335
	Maximum		3.84	0.0072	32491.5	0.857	1.333
	Total Range		3.046	0.0052	28621.1	0.666	0.998
	<i>p</i> for Normality		0.614	0.355	0.913	0.130	0.641
<b><i>Mammuthus columbi</i> Friesenhahn, TX</b>	Mean	32	2.885	0.0048	12619.2	0.479	0.866
	Median		2.489	0.0048	12595.7	0.414	0.773
	SD (1 $\sigma$ )		1.52	0.0022	2653.6	0.271	0.388
	Minimum		0.457	0.0013	4431.6	0.195	0.375
	Maximum		6.471	0.0092	16973.2	1.664	2.095
	Total Range		6.014	0.0079	12541.6	1.469	1.72
	<i>p</i> for Normality		0.142	0.458	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	0.122
<b><i>Mammuthus columbi</i> Ingleside, TX</b>	Mean	26	2.285	0.0033	10455.8	0.33	0.644
	Median		2.062	0.0030	11304.1	0.333	0.587
	SD (1 $\sigma$ )		1.273	0.0019	3710.6	0.107	0.23
	Minimum		0.456	0.0005	739.3	0.157	0.372
	Maximum		5.937	0.0079	18019.5	0.545	1.402
	Total Range		5.481	0.0074	17280.2	0.388	1.03
	<i>p</i> for Normality		0.057	0.306	0.107	0.485	<b>0.002</b>
<b><i>Mammuthus exilis</i> / <i>Mammuthus columbi</i> Santa Rosa Island</b>	Mean	16	5.698	0.0034	11475.6	0.418	0.972
	Median		2.143	0.0038	12002.4	0.372	0.684
	SD (1 $\sigma$ )		8.197	0.0018	2654.4	0.203	0.932
	Minimum		0.537	0.0005	5345.4	0.175	0.347
	Maximum		27.829	0.0062	15270.7	0.976	3.497
	Total Range		27.292	0.0057	9925.3	0.801	3.15
	<i>p</i> for Normality		<b>&lt; 0.001</b>	0.433	0.603	<b>0.009</b>	<b>&lt; 0.001</b>

n, number of individuals sampled; SD, one standard deviation (1 $\sigma$ ); *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume, *HAsfc<sub>3x3</sub>*, *HAsfc<sub>9x9</sub>*, Heterogeneity of complexity in a 3x3 and

9x9 grid, respectively. Bold values indicate a non-normal distribution (Shapiro-Wilk;  $p < 0.05$  is significant).

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**Table 5.** Descriptive statistics of all DMTA attributes for Ingleside and Friesenhahn mammoths and mastodons, broken down by age group and site.

Taxon	Statistic	<i>n</i>	<i>Asfc</i>	<i>epLsar</i>	<i>Tfv</i>	<i>HAsfc</i> <sub>3x3</sub>	<i>HAsfc</i> <sub>9x9</sub>
<i>Mammut americanum</i> Friesenhahn, TX (Juveniles)	Mean	7	1.275	0.0034	11299.0	0.331	0.712
	Median		1.047	0.0040	12658.0	0.214	0.566
	SD		0.873	0.0016	3074.1	0.224	0.463
	Minimum		0.429	0.0011	4846.8	0.184	0.335
	Maximum		2.759	0.0049	13724.6	0.810	1.663
	Total Range		2.330	0.0038	8877.8	0.626	1.328
	<i>p</i> for Normality		0.120	0.144	<b>0.018</b>	<b>0.005</b>	0.057
<i>Mammut americanum</i> Ingleside, TX (Adults)	Mean	20	2.558	0.0036	9430.7	0.465	0.890
	Median		1.966	0.0038	10075.7	0.363	0.653
	SD		2.398	0.0017	4045.5	0.252	0.640
	Minimum		0.715	0.0013	507.0	0.185	0.384
	Maximum		11.717	0.0068	16546.7	0.985	3.050
	Total Range		11.002	0.0055	16039.7	0.800	2.666
	<i>p</i> for Normality		<b>&lt;0.001</b>	0.147	0.228	<b>0.002</b>	<b>&lt;0.001</b>
<i>Mammuthus columbi</i> Friesenhahn, TX (Adults)	Mean	13	2.871	0.0046	12349.4	0.473	0.883
	Median		2.254	0.0050	12462.4	0.407	0.734
	SD (1 $\sigma$ )		1.759	0.0021	2695.0	0.213	0.446
	Minimum		0.457	0.0013	6891.0	0.256	0.468
	Maximum		6.241	0.0086	16973.2	1.059	2.095
	Total Range		5.784	0.0073	10082.2	0.803	1.627
	<i>p</i> for Normality		0.535	0.954	0.964	0.011	0.012
<i>Mammuthus columbi</i> Friesenhahn, TX (Juveniles)	Mean	18	2.958	0.0052	12689.9	0.475	0.833
	Median		2.775	0.0048	12468.3	0.404	0.765
	SD (1 $\sigma$ )		1.395	0.0022	2712.7	0.317	0.353
	Minimum		0.774	0.0013	4431.6	0.195	0.375
	Maximum		6.471	0.0092	16966.2	1.664	1.981
	Total Range		5.697	0.0079	12534.6	1.469	1.606
	<i>p</i> for Normality		0.507	0.583	0.019	<b>&lt;0.001</b>	<b>0.002</b>
<i>Mammuthus columbi</i> Ingleside, TX (Adults)	Mean	21	2.436	0.0035	10973.0	0.347	0.673
	Median		2.191	0.0034	11527.6	0.340	0.663
	SD		1.348	0.0020	3522.8	0.103	0.236
	Minimum		0.456	0.0005	739.3	0.157	0.372
	Maximum		5.937	0.0079	18019.5	0.545	1.402
	Total Range		5.481	0.0074	17280.2	0.388	1.030
	<i>p</i> for Normality		0.252	0.725	0.085	0.836	0.015

*n*, number of individuals sampled; SD, one standard deviation (1 $\sigma$ ); *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume, *HAsfc*<sub>3x3</sub>, *HAsfc*<sub>9x9</sub>, Heterogeneity of complexity in a 3x3 and 9x9 grid, respectively. Bold values indicate a non-normal distribution (Shapiro-Wilk;  $p < 0.05$  is significant).

**Highlights**

- Mammoths and mastodons consumed foods with highly variable textures.
- Textural properties of mammoth diets are similar across ontogenetic stages.
- The pygmy mammoth consumed foods with variable textures, including hard foods.

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