



## Proboscidea from the Big Cypress Creek fauna, Deweyville Formation, Harris County, Texas



Ernest L. Lundelius Jr.<sup>a</sup>, Kenneth J. Thies<sup>b</sup>, Russell W. Graham<sup>c</sup>, Christopher J. Bell<sup>a,\*</sup>, Gregory James Smith<sup>d</sup>, Larisa R.G. DeSantis<sup>d,e</sup>

<sup>a</sup> Vertebrate Paleontology Laboratory, Jackson Museum of Earth History, The University of Texas at Austin, Austin, TX, 78712, USA

<sup>b</sup> Toxodon Exploration, LLC, L10618 Lynbrook Dr, Houston, TX, 77042, USA

<sup>c</sup> Earth and Mineral Sciences Museum & Art Gallery, The Pennsylvania State University, University Park, PA, 16802, USA

<sup>d</sup> Department of Earth and Environmental Science, Vanderbilt University, Nashville, TN, 37240, USA

<sup>e</sup> Department of Biological Sciences, Vanderbilt University, Nashville, TN, 37240, USA

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### ABSTRACT

In 2008 a rich accumulation of vertebrate bones and teeth was discovered in a small tributary drainage to Big Cypress Creek near the town of Hockley in Harris County, Texas. The fossils were recovered from sandy sediments of fluvial origin, interspersed with contemporaneous spring boil deposits, attributed to the Deweyville Formation and the recovered remains consist entirely of disarticulated and dissociated skeletal elements and teeth. Distinct stratigraphic horizons are limited in extent in the fossiliferous sections along the drainage, and the fossils are generally concentrated in close association with gravel lag deposits. Two radiocarbon dates on wood suggest that the fauna may have accumulated about 24,000 years ago but presence of spring deposits, association with lag deposits, and the aerial extent (approximately 125 m of exposed section along the length of the tributary) could indicate significant time averaging during the Rancholabrean (*Bison* occurs in the fauna).

The unique faunal character of the site is emphasized by a single tooth of *Mixtoxodon*, a notoungulate mammal, that provides the first evidence of this taxon from the United States. The fauna is dominantly composed of herbivorous megafauna with two proboscideans (*Mammuthus* and *Cuvieronioides*). *Mammut americanum* has not yet been found in the fauna. Isotopic analyses of the proboscideans and some of the other megafauna suggest that an open environment with scattered woodland habitat existed in southeastern Texas at the end of the last glacial period.

### 1. Introduction

The Gulf Coastal Plain extends from northern Mexico, along the Gulf coasts of Texas, Louisiana, Mississippi, Alabama, Georgia and the west coast of Florida. Today, it has low topographic relief. During glacial periods in the Pleistocene, the Gulf Coastal Plain was enlarged by hundreds of kilometers seaward as ocean levels were more than 100 m lower. In contrast, it was inundated to at least modern levels, and perhaps beyond, during the high-sea-level stands of the interglacials. The Gulf Coastal Plain was inhabited by a diverse mammal megafauna during the Pleistocene as evidenced by the abundant remains of fossils eroded from inundated sediments and deposited on beaches as ‘isolated finds.’ Unfortunately, these ‘isolated finds’ are of limited scientific value because, unless they can be radiocarbon dated, it is difficult, if not impossible, to determine their numeric ages. Likewise, it is difficult to

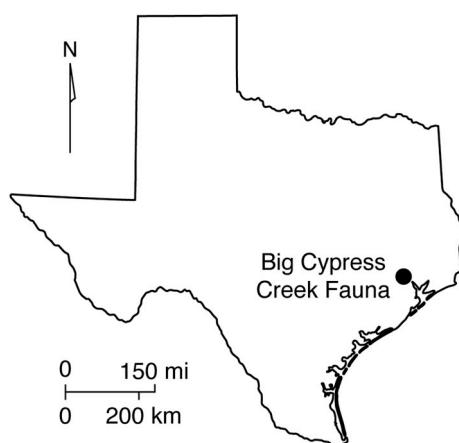
associate taxa that might have co-occurred at the same time in Pleistocene habitats along the coastal plain.

Because of the low relief of the Gulf Coastal Plain, natural outcroppings of sediments are rare except for some areas along downgrading rivers. Also, exposures are created by human developments along the coastal plain exposing sediments and fossils. Recently, a series of localities along Big Cypress Creek (BCC) near the town of Hockley in Harris County, Texas, yielded a diverse array of vertebrate fossils. The purpose of this paper is to document the Proboscidea from this site in order to facilitate a better understanding of the paleoecology of the site and the associated toxodont.

### 2. Location, geomorphology and stratigraphy

The Big Cypress Creek fauna occurs in a series of newly exposed

\* Corresponding author. Department of Geological Sciences, 1 University Station C1100, The University of Texas at Austin, Austin, TX, 78712, USA.  
E-mail address: [cjbell@jsg.utexas.edu](mailto:cjbell@jsg.utexas.edu) (C.J. Bell).



**Fig. 1.** Location map for the Big Cypress Creek fauna (adapted from Lundelius et al., 2013).

outcrops of complexly stratified deposits along the southeastern flank of the Hockley salt dome, near the town of Hockley, Texas (Fig. 1). The various localities represent different depositional aspects of the paleo-Big Cypress Creek fluvial system.

One of those localities (TxVP 45901) produced an isolated tooth of a toxodont (*Mixotroxodon*), a South American genus that emigrated into Central America ca. 1.5–1.3 Ma (Woodburne, 2010). The specimen from BCC is the first, and currently only known, occurrence of this animal from the United States (Lundelius et al., 2013). A small assemblage of additional taxa was collected from that locality and adjacent localities and includes two proboscideans that are the focus of this report. These specimens were collected from near the base of an approximately 2 m vertical section adjacent to a meander of the tributary. The majority of specimens were collected between approximately 0.25–0.5 m above an apparent basal clay. This clay is exposed at various locations along the modern creek bed. The paleo-Big Cypress Creek, as well as the modern creek, are strongly influenced, locally, by the Hockley Salt Dome.

The large diapiric salt body has a surface expression that is roughly oval with a long dimension trending north-northwest to south-southeast for about 3.2 km and a perpendicular short dimension of about 2.4 km. The ground gently rises as much as 5 m above the surrounding terrain and is seen as a southerly bulge on the southward or down-thrown side of the Hockley Escarpment. This rise is significant where the typical gradient is on the order of 0.2 m per km toward the coast on the coastal plain.

As a result of this passive diapirism the BCC is diverted southward around the dome from its predominant west-to-east flow direction before returning to the north on the eastern flank and returning to its easterly flow. During the time of deposition of the sediments at BCC, the creek moves near the dome and actually incises into the older sediments of the Lissie Formation (> 40 ka; Blum and Aslan, 2006) and the Miocene shale caprock of the dome. Today, BCC is shifted as much as 1.6 km away from the diapir to the south before returning back north as it flows east from the dome.

The limited Pleistocene shale caprock exposed only on the flanks of the dome and the undifferentiated Miocene shale covering most of the diapir attests to the long-running passive diapirism of the salt dome. Beneath the cap of Miocene-aged shale, the top of the underlying dome caprock comes within 30 m of the surface near the center of the dome. It declines to as deep as 300 m below the surface toward the edge of the dome where it is last encountered in a wellbore located ca. 150 m onto the dome from the fossiliferous outcrops. Two other wells located in the outcrop area of the modern ravine encountered no caprock but did penetrate directly into salt at about 910 and 1060 m below surface, respectively.

### 3. Chronology

The bone-bearing deposits at BCC are in sediments equivalent to the Deweyville Formation which is locally inset into the Lissie Formation. As noted by Blum and Aslan (2006) in their comprehensive study of the Deweyville Formation, larger streams of the Texas Gulf Coastal Plain exhibit at least three suites of landforms/deposits that represent streams that were graded to base level during lower sea-level stands. Regionally, the Deweyville Formation deposits are predominantly coarse grained and were aggraded during marine isotope stages (MIS) 4–2 (ca. 74,000–16,000 years B.P.; Blum and Aslan, 2006; Sylvia and Galloway, 2006).

Wood samples collected at depths of 1.0 and 3.5 m below the Deweyville surface at BCC yielded AMS radiocarbon ages of  $17,080 \pm 90$  (ISGS-A1513) and  $23,730 \pm 100$  (ISGS-A1183) yr B.P., respectively (Lundelius et al., 2013). Those dates are in accordance with the age of the Deweyville Formation (Blum and Aslan, 2006). However, because many of the fossils are fragmentary and some of them polished, re-deposition of fossil specimens is quite likely. Spring deposits in the outcrops further complicate the chronological assignment of fossils from BCC. In some cases, these deposits are sandy and have a vertical inclination which suggests that they probably represent spring vents that can recycle fossils from older and deeper deposits (Saunders, 1977, 1988), although geologically all specimens are probably from the Deweyville Formation.

Biostratigraphic dating can provide a minimum age for the fauna but the maximum age is not yet confined. Teeth of *Bison* were found, indicating the deposits preserve at least a Rancholabrean fauna (10–210 ka years BP; see Bell et al., 2004). Unfortunately, horn cores of *Bison* that can be useful in subdividing the Rancholabrean (Bell et al., 2004) have not been found. To date, the microfaunal remains from the site are sparse and none of the known taxa facilitate a biostratigraphic assignment. Bone samples that were submitted to Stafford Laboratories Inc, for radiocarbon dating did not have enough collagen in the bones to obtain reliable dates (Lundelius et al., 2013).

### 4. Systematic descriptions

#### 4.1. Class mammalia

Order Proboscidea  
Family Gomphotheriidae  
Subfamily Gomphotheriinae  
*Cuvieronioides* sp.

#### 4.2. Material

TxVP 45901–8, molar fragment; 45901–9, 2 M fragments; 45968–12, tooth (right M2 or left m2) with 10 associated fragments; 47200–169, tooth (M3 or m3?) partial cusp; 47200–170, terminal end of molar with apparent interdental facet on the end; 47200–171, distal portion of tooth crown with interdental facet (M1 or M2); 47200–172, well-worn M2 or m2; 47200–195, molar crown fragment; 47200–196, molar crown fragment; 47200–197, molar crown fragment; 47200–198, molar crown fragment; 47200–199, molar crown fragment; 47200–200, molar crown fragment; 47200–201, molar crown fragment; 47200–202, molar crown fragment; 47200–205, molar crown fragment; 47200–206, molar crown fragment; 47200–207, molar crown fragment; 47200–208, molar cusp; 47200–209, molar crown fragment; 47200–214, tusk fragment with enamel; 47200–216, 12 tooth fragments; 47200–228, tooth; 47200–229, 5 tooth fragments; 47200–230, tooth; 47200–231, tooth; 47200–232, tooth; 47200–233, tooth; 47200–234, tooth; 47200–243, molar crown fragment; 47200–244, molar crown fragment; 47200–245, molar crown fragment; 47200–250, molar crown fragment; 47200–252, molar crown fragment; 47200–253, molar crown fragment; 47200–254, molar crown fragment; 47200–255, molar crown fragment;

47200–256, molar crown fragment; 47200–257, molar crown fragment; 47200–259, I2 tusk fragment with enamel band; 47200–262, crown portion of right (?) tooth (?deciduous premolar); 45969–1, 19 tooth fragments; 45969–6, 13 dental root fragments.

#### 4.3. Description

*Cuvieronius* teeth are comprised of pairs of enamel-capped cusps united by crests with abundant accessory conules in the valleys between the main cusps. After a period of wear, the enamel pattern on the occlusal surface develops into a series of cloverleaf patterns called ‘trefoils.’ This differs from the relatively simple tooth morphology of mastodons (*Mammut*) whose teeth wear as simple transverse lophs without a trefoil pattern. *Cuvieronius* tusks are also quite diagnostic, with an enamel band that spirals along the upper tusk (Simpson and Paolo Couto, 1957 Mothé et al., 2016). The enamel band on the tusk separates *Cuvieronius* from *Stegomastodon*. A tusk fragment (35 × 48 mm) with an enamel band (TxVP 47200–259) was recovered from BCC (see below). The molar fragments clearly exhibit the dental pattern for *Cuvieronius*. Given the late Pleistocene age of BCC, taxonomic referral to the Plio-Pleistocene gomphothere, *Rhynchotherium*, is unlikely (see discussion in Lucas, 2008).

The vast majority of identifiable specimens of *Cuvieronius* are fragments of teeth. Specimens that are well enough preserved to show significant characters are listed and described below.

**47200–170**, The terminal end of a molar with the terminal loph and a cingular cusp. The loph shows the characteristic *Cuvieronius* pattern of a trefoil on one side and much simpler cusp on the other. The cingular area has one well-developed cusp on the side of the trefoil and some undifferentiated cusps on the other. There is apparently an interdental facet on the end, that by its size, indicates either the anterior end of a third molar or the posterior end of a second molar. Width 98 mm. (Fig. 2A).

**47200–259**, A fragment of a tusk (I2) with enamel. The width of the enamel band is 31.5 mm (Fig. 2B).

**45968–12**, A right M2 or left m2 with ten associated fragments. This tooth is unworn with well-developed trefoils on one side and rudimentary trefoils on the other side. Its measurements are length = 114 mm and width = 81 mm (Fig. 2C).

**47200–262**, A right DP2 (dp2?) This tooth matches the illustrated dp2 figured by Lucas (2008, Fig. 6A) in having trefoils on one side and single cones on the other. The posterior part of the tooth is missing. Although the tooth is incomplete its size appears to be similar to one figured by Lucas (2008), except for length, w = 37 mm (Fig. 2D).

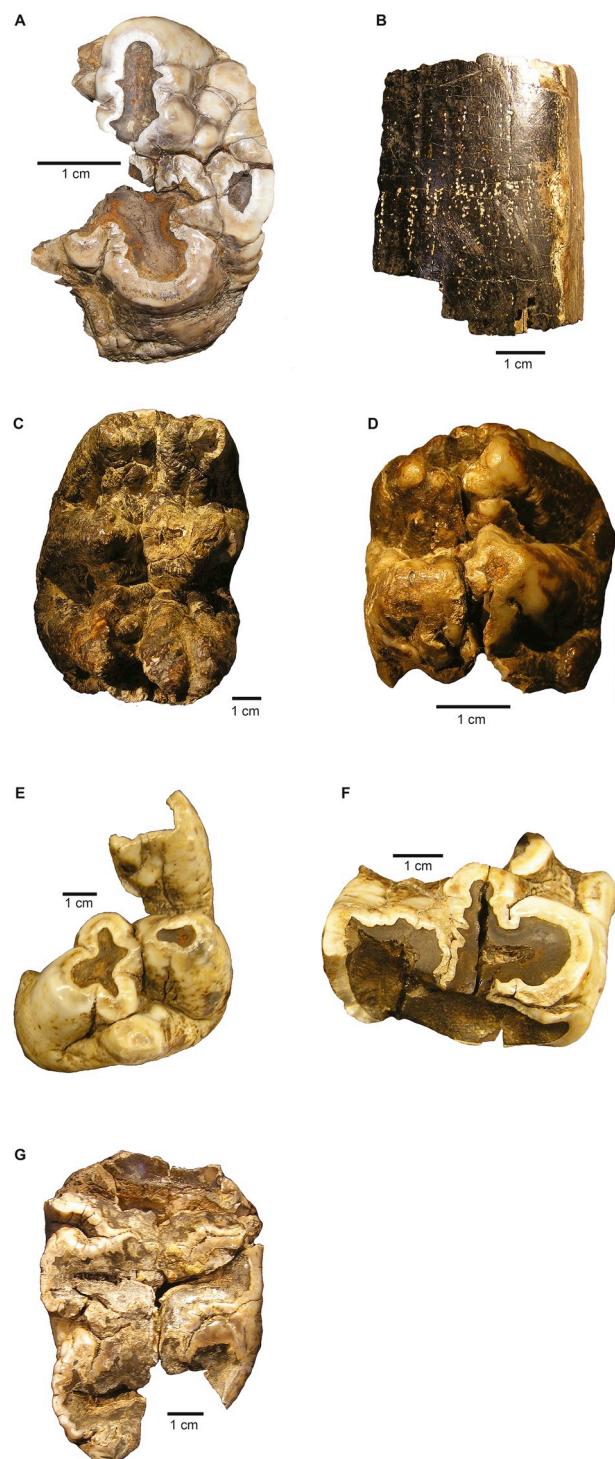
**47200–171**, The distal end of a molar with the terminal loph and part of the loph adjacent to it showing the trefoil on one side, a simple cusp on the other and a posterior cingular cusp. This tooth is either a first molar or a second molar because it has an interdental facet on the posterior end. Width = 65 mm (Fig. 2E).

**47200–195**, A well-worn molar loph with a trefoil on one side and cusp on the other. Width = 59 mm. (Fig. 2F).

**47200–172**, A well-worn M2 or m2. One end of the first loph is missing but shows the worn trefoil. The second and third lohs are deeply worn but show the trefoil on one side. The length is 89 mm; width of second loph is 54 mm, width of third loph is 63 mm (Fig. 2G).

#### 4.4. Discussion

*Cuvieronius* had a broad geographic distribution during the Pleistocene, ranging from Tarija, Bolivia, South America (Mothé et al., 2013) to the southern and southwestern parts of the United States. Its distribution in the United States encompassed South Carolina (Sanders, 2002), through Florida (Lucas, 2008), through Texas (Hibbard and Dalquest, 1966; Vanderhill, 1986; Lundelius, 1972; Vance, 2002; Baskin and Thomas, 2007) into New Mexico (Lucas et al., 1999) and Nevada (Lindsay et al., 2002). It survived to the end of the Pleistocene



**Fig. 2.** Teeth and tooth fragments of *Cuvieronius* sp. from Big Cypress Creek. A = TxVP 47200–170, end of a molar with the terminal loph and a cingular cusp; B = TxVP 47200–259, tusk fragment with enamel; C = TxVP 45968–12, right M2 or left m2; D = TxVP 47200–262, right DP2 or dp2; E = 47200–171, end of a molar with a terminal loph and part of the loph adjacent to it; F = 47200–195, well-worn molar loph with trefoil on one side and cusp on the other side; G = 47200–172, well-worn M2 or m2.

in Mexico (Montellano-Ballesteros, 2002; Sanchez et al., 2014; Gurrola-Riera et al., 2015).

Most of the occurrences in the United States are from Irvingtonian to early Rancholabrean faunas. The Ingleside fauna in Texas is Rancholabrean, probably late Rancholabrean with the presence of *Bison*

*antiquus* (Lundelius, 1972). The radiocarbon dates of  $17,080 \pm 90$  (ISGS-A1513) and  $23,730 \pm 100$  (ISGS-A1183) yr BP document a late Pleistocene age for BCC and are the youngest ages known for *Cuvierinus* in the United States.

#### Family Elephantidae

##### Subfamily Elephantinae

*Mammuthus* sp. (*Mammuthus columbi* morphotype).

#### 4.5. Material

TxVP 45901–19, 5 tooth fragments; 45901–36.1, distal portion of tooth (M1?); 45901–36.2, distal portion of tooth (M1?); 45970–1.1, left tooth (M2?); 45970–1.2, right tooth (M2?); 47200–3, tooth fragment; 47200–12, tooth (p4?) plus fragment; 47200–20, mid-section of molar; 47200–21, 1 M plate; 47200–22, tooth plate fragment; 47200–23, 1 M plate; 47200–49, one tooth plate; 47200–149, two-plate section of molar; 47200–150, two-plate section of molar; 47200–151, occlusal fragment of molar; 47200–152, midsection of upper molar with 3.5 plate section; 47200–153, occlusal fragment of molar; 47200–154, 1 M plate; 47200–155, 1 M plate; 47200–156, three-plate section of molar; 47200–157, distal plate of molar; 47200–158, distal plate of molar; 47200–159, distal end of tooth (M3?); 47200–160, distal three-plate section of molar; 47200–161, four-plate central section of tooth (m3?); 47200–162, four-plate central section of tooth (upper molar?); 47200–163, two-plate section of molar; 47200–164, unworn two-plate section of molar; 47200–165, 1 M plate; 47200–166, two-plate section of molar; 47200–167, 1 M plate; 47200–168, molar plate fragment; 47200–173, right lower molar; 47200–174, lower left cheek tooth (possibly m1); 47200–175, distal crown fragment of molar; 47200–176, six tooth plates with associated fragments; 47200–177, two root portions of molar; 47200–178, 16 tooth fragments; 47200–179, four plate fragments; 47200–189, four plate fragments; 47200–191, unworn tooth (cf. M2); 47200–192, unworn two-late section of molar; 47200–193, two-plate section of molar; 47200–194, distal two-plate section of molar; 47200–211, 70 tooth fragments; 47200–215, enamel plate fragment of tooth; 47200–217, enamel plate of tooth; 47200–218, enamel plate of tooth; 47200–219, enamel plate of tooth; 47200–220, enamel plate of tooth; 47200–221, enamel plate of tooth; 47200–222, enamel plate of tooth; 47200–223, enamel plate of tooth; 47200–224, enamel plate of tooth; 47200–225, enamel plate of tooth; 47200–226, enamel plate of tooth; 47200–227, enamel plate of tooth; 47200–239, two tooth fragments; 47200–242, 1 M plate; 47200–246, posterior half of broken tooth (upper?); 47200–247, distal portion of femur; 47200–248, 50 + cheek tooth fragments; 47200–249, distal five-plate section of molar; 47200–251, two-plate section of molar with six associated fragments; 47200–261, five-plate section of tooth in last stage of wear.

#### 4.6. Description

There are three incomplete teeth that can be used to determine lamellar frequency and enamel thickness. Specimen TxVP 47200–174 (Fig. 3A) is the posterior half of what appears to be a lower left cheek tooth, possibly m1. The occlusal surface of the tooth fragment is incompletely worn. The most anterior preserved loph is incomplete with two lophs that have not yet joined as a result of wear to form a single continuous loph across the tooth (Fig. 3A). The other lophs also are incomplete with lophs 5, 6 and 7 showing isolated ‘cones’ rather than elliptical lophs. TxVP 47200–173 appears to be a right lower tooth. Again, the posterior half of the tooth is preserved, although the lingual margin is broken (Fig. 3B). Portions of eight lophs are preserved on the fragment. The first, second, fourth, and fifth lophs are broken lingually. All of the first five lophs are completely worn. The sixth loph is worn but does not form a single loph across the width of the tooth. The seventh loph is worn but distinct ‘cones’ are still evident. The eighth loph is unworn. The third broken tooth (TxVP 47200–246) (Fig. 3C) is also

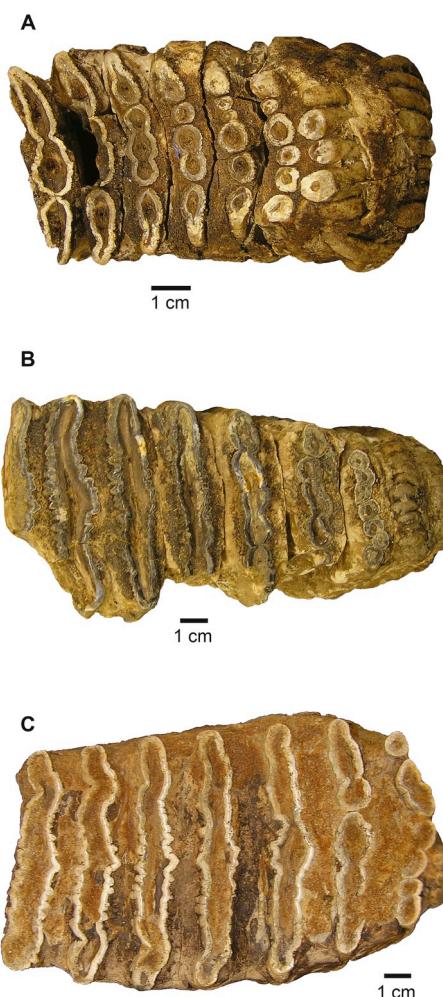


Fig. 3. Occlusal views of three partial mammoth teeth from Big Cypress Creek (A = TxVP 47200–174, B = TxVP 47200–173, C = TxVP 47200–246).

the posterior half of an incomplete tooth, possibly an upper as indicated by its width. The occlusal surface is completely worn and there are seven lophs preserved of which the first five are complete.

#### 4.7. Discussion

Mammoth taxonomy is complicated (Enk et al., 2011, 2016; Lister and Sher, 2015; Smith and Graham, 2017; Widga et al., 2017). The biometric parameters of the isolated teeth from BCC (Table 1) are consistent with *Mammuthus columbi* in the classical taxonomy of mammoths (Maglio, 1972; Lister and Sher, 2015). However, studies of North American mammoths suggest that there is considerable variation and overlap in systematic characters (lamellar frequency and enamel thickness) used in delineating species of mammoths (Widga et al., 2017). Thus, taxonomic assignment can be problematic. Furthermore,

Table 1

Measurements (mm) of teeth of *Mammuthus* sp. (*Mammuthus columbi* morphotype) from the Big Cypress Creek Fauna.

TxVP* Cat. Number	Length	Width	Enamel Thickness	Lamellar Frequency
47200–174	Inc.	58	1.85 (N = 4, 1.5–2.6)	6
47200–246	Inc.	93.	2.28 (N = 6, 2.0–3.1)	5
47200–173	Inc.	Broken	2.0 9 (N = 8, 1.0–2.7)	5

\*TxVP = Vertebrate Paleontology Collections, Jackson Museum of Earth History, Austin, Texas.

Smith and Graham (2017) have shown that these characters vary significantly with tooth wear within a single individual. Genetic studies of mammoths have also questioned the utility of taxonomic separation of North American mammoths and suggested introgression between *M. primigenius* and *M. columbi* occurred in the late Pleistocene (Enk et al., 2011, 2016).

Despite these challenges to traditional taxonomic analyses, Smith and Graham (2017) observed that in general the various taxonomic names for mammoth species (e.g., *M. primigenius* and *M. columbi*) do correspond to geographic patterns that suggest that the morphology of mammoth teeth may be more a function of environments, especially vegetation, rather than evolutionary history. The *M. primigenius* morphotype is characterized by a higher lamellar frequency and thinner enamel than *M. columbi* (Maglio, 1972; Lister and Sher, 2015). The *M. primigenius* morphotype occurs along the glacial ice front in the upper Midwest and northeastern part of the United States, as well as Canada and Alaska farther to the north (Faunmap Working Group, 1994; Neotoma Paleoecology Database, 2019). Environments for those areas were reconstructed as Pleistocene tundra, steppe tundra (Hibbert, 1982) or mammoth steppe (Guthrie, 1982) during the Full Glacial. *Mammuthus primigenius* had other morphological attributes (size of ears, fat deposits, fur, etc.) that were adaptations for cold environments (Kubiak, 1982; Wang et al., 2018).

Conversely, the *M. columbi* morphotype is restricted more to the western United States (e.g., generally west of the Mississippi River) and the Gulf Coastal Plain into Florida (Faunmap Working Group, 1994; Neotoma Paleoecology Database, 2019). Those areas had a wide diversity of environments but they are generally occupied by grassland and/or parkland-savanna types of environments (Williams et al., 2004). To this end, we applied the name *Mammuthus* sp. (*Mammuthus columbi* morphotype) to the materials from BCC rather than make a specific taxonomic assignment.

## 5. Taphonomy

The purpose of this study is not to focus on a detailed taphonomic analysis; however, general taphonomic pathways must be understood to understand the paleoecological implications. The absence of articulated skeletons or parts of skeletons in the assemblage discussed here, combined with isolated skeletal elements exhibiting significant breakage and abrasion, suggests relatively slow deposition with bones being exposed to a variety of processes (scavenging, trampling, weathering, etc.) on the surface. Mixing of vertebrate fauna is reflected in the vertical nature of some sand deposits that have been interpreted as spring-vents. As noted by others (Saunders, 1977, 1988; Haynes, 1985) spring vents move bones from lower levels to upper ones. Polish on some bones is also indicative of movement in sandy spring-vent deposits, although fluvial deposits can cause the same modification. Time averaging is also reflected by the concentration of bones in gravel lags that result from erosion and the concentration of heavier objects (rocks, bones, etc.) at the bottoms of stream deposits or the tops of deflated ones. This is further supported by the recovery of only one bone fragment and a few isolated teeth from an extensive excavation of 1m × 1.5m area that extended to a depth of ca. 2 m where the toxodont was found.

The bone accumulations at BCC probably result from a variety of factors. First, animals will congregate around water sources in dry environments, especially springs with salt-laden ground water. The large number of gypsum concretions found scattered throughout the ravine deposit at BCC attest to high mineral content in the ground water and strata during the time of fossil accumulation. Additionally, pollen indicative of nearby standing water (Lundelius et al., 2013) was found associated with fish remains in the fossiliferous sediments at BCC. In times of drought animals, especially younger and older individuals, can become ‘tethered’ to water bodies and eventually die near them (Haynes, 1991). Also, fluvial lag deposits like those at BCC will

commonly aggregate bones (Hanson, 1980). Because most of the animals in the fauna are large, the catchment area could be quite large for the mammals that accumulated at BCC.

## 6. Paleoecology

### 6.1. Stable isotope sampling

Bulk samples of the carbonate portion of enamel hydroxyapatite were removed from BCC samples held at the Vertebrate Paleontology Collections Jackson Museum of Earth History in Austin, TX. Sampling methods follow those of prior work (DeSantis et al., 2009). Enamel powder was collected from a 1 cm × 1 mm transect on all sampled teeth using a rotary drill with diameter carbide dental burrs. Transects were oriented parallel to the growth axis of the tooth (depth of sample was not controlled). The powder was pretreated with 30% H<sub>2</sub>O<sub>2</sub>, rinsed with distilled water, treated with 0.1N acetic acid for 18 h to remove secondary carbonates (similar to Koch et al., 1997 and DeSantis et al., 2009), and rinsed with distilled water again before being left to air dry. Samples were analyzed on a VG Prism stable isotope ratio mass spectrometer with an in-line ISOCARB automatic sampler at the University of Florida. The standard deviation (1σ) of the laboratory standard (NBS-19) included with these samples was < 0.05‰ for both carbon and oxygen. The analytical precision is ± 0.1‰, based on replicate analyses of samples and standards (NBS-19). Stable isotope data were normalized to NBS-19 and are reported in conventional delta notation.

Stable carbon isotopes in mammalian enamel are an average of the photosynthetic signature of foods consumed, referred to δ<sup>13</sup>C values. Carbon values from enamel (δ<sup>13</sup>C<sub>enamel</sub>) are reported relative to V-PDB (Coplen, 1994). In order to compare the stable isotope signature of BCC taxa with similar taxa from the Gulf Coastal Plain, we then carried out a series of conversions to reconstruct the stable isotopic signature of plants consumed. First, consumer δ<sup>13</sup>C<sub>enamel</sub> values were converted to the carbon isotope value of vegetation consumed (δ<sup>13</sup>C<sub>veg</sub>) using enrichment factors (ε\*) calculated using the regression equation for hindgut and foregut fermenters from Tejada-Lara et al. (2018) and body mass estimates from Smith et al. (2018) (Supplemental Table 1). δ<sup>13</sup>C<sub>veg</sub> values are sensitive to atmospheric carbon isotope values (δ<sup>13</sup>C<sub>atm</sub>), which fluctuate over geologic time (Kohn, 2010). Thus, we next converted δ<sup>13</sup>C<sub>veg</sub> values to their modern equivalent values (δ<sup>13</sup>C<sub>vmeq</sub>) using estimates of past δ<sup>13</sup>C<sub>atm</sub> values from benthic foraminifera (Tipple et al., 2010) following methods outlined in Kohn (2010). Specifically, we used estimates of minimum and maximum site age (Supplemental Table 1) to calculate average δ<sup>13</sup>C<sub>atm</sub> value over the age range of the sample. This value was inserted into Equation 3 from Kohn (2010) and used to calculate Δ. We then calculated δ<sup>13</sup>C<sub>vmeq</sub> using a linear regression equation obtained using the dataset in the supplemental material from Kohn (2010): δ<sup>13</sup>C<sub>vmeq</sub> = -0.9543\*Δ - 8.3617. The δ<sup>13</sup>C<sub>vmeq</sub> values reported here reflect isotopic values of C<sub>3</sub> shrubs and C<sub>4</sub> grasses, respectively, and are thus indicative of browsing, grazing, and mixed-feeding habits. We estimate that δ<sup>13</sup>C<sub>vmeq</sub> values less than -25.1‰ indicate diets of at least 85% C<sub>3</sub> vegetation while values greater than -16.0‰ indicate at least 85% C<sub>4</sub> vegetation; values in between suggest a mix of both C<sub>3</sub> and C<sub>4</sub> resources (Cerling et al., 1997; Kohn, 2010).

Oxygen isotopes in animal tissues reflect a physiological balance between oxygen inputs and outputs whose proportions may differ among species (Bryant and Froelich, 1995; Kohn and Cerling, 2002).

Geography impacts δ<sup>18</sup>O values of meteoric water (δ<sup>18</sup>O<sub>mw</sub>), such that values decline with increased altitude, increased distance from the coast, increased precipitation (especially in tropical or subtropical regions), and decreased surface air temperature (Dansgaard, 1964). δ<sup>18</sup>O<sub>mw</sub> values in the Gulf Coastal Plain fluctuate seasonally as a result of moisture source, with lower values in the fall and winter months reflecting precipitation sourced from subtropical bodies of water and higher values in the spring and summer months reflecting a significant

**Table 2**

Stable isotope summary statistics for all taxa analyzed from the BCC.

Taxon	n	$\delta^{13}\text{C}_{\text{vmeq}}$ V-PDB (‰)							$\delta^{18}\text{O}_{\text{enamel}}$ V-SMOW (‰)						
		mean	med	min	max	range	SD (1σ)	SE	mean	med	min	max	range	SD (1σ)	SE
<i>Bison</i>	1	-21.9	-	-	-	-	-	-	29.9	-	-	-	-	-	-
<i>Camelops</i>	3	-20.3	-18.5	-25.4	-17.0	8.4	4.5	2.6	30.7	30.8	29.7	31.7	2.0	1.0	0.6
<i>Cuvieroni</i>	12	-21.4	-20.6	-27.8	-19.7	8.1	2.3	0.7	30.4	30.3	28.6	32.6	4.0	1.1	0.3
<i>Equus</i>	11	-18.8	-18.9	-21.4	-15.5	5.9	1.9	0.6	30.7	30.9	28.6	32.7	4.1	1.3	0.4
<i>Mammuthus</i>	10	-20.2	-20.2	-21.2	-19.3	1.9	0.6	0.2	29.7	29.6	28.5	31.0	2.5	0.8	0.3

n, number of specimens; med, median; min, minimum; max, maximum; SD, one standard deviation ( $1\sigma$ ); SE, standard error of the mean ( $\sigma/\sqrt{n}$ ).  $\delta^{13}\text{C}_{\text{vmeq}}$ , modern equivalent vegetation stable carbon isotope signature of paleodiet;  $\delta^{18}\text{O}_{\text{enamel}}$ , stable oxygen isotope signature of enamel. All stable isotope values are listed in permil format relative to V-PDB (carbon) or V-SMOW (oxygen). Stable isotope data for *Mammuthus* are from Smith and DeSantis (2018).

component of moisture sourced from Pacific and Arctic air masses (Oster et al., 2019).

Because of the controlling effects of climate on meteoric water,  $\delta^{18}\text{O}_{\text{enamel}}$  preserved in fossil teeth can be useful for paleoenvironmental reconstructions (Higgins and MacFadden, 2004; Hoppe, 2004; Levin et al., 2006; Murphy et al., 2007; DeSantis et al., 2009; Yann et al., 2013). Proboscidean  $\delta^{18}\text{O}_{\text{enamel}}$  values can be used to separate glacial and interglacial periods (Ayliffe et al., 1992, 1994) and infer temporal changes in relative temperature and/or aridity (Levin et al., 2006; Yann et al., 2013), although the multiplicity of compounding effects (aridity, temperature, and altitude, for example; as shown in Iacumin et al., 2010) can make predicting accurate conditions difficult. An additional strength of oxygen isotopes is in identifying populations that have been spatially mixed (via migration, for example) or time-averaged; generally, when standard deviations in  $\delta^{18}\text{O}_{\text{enamel}}$  are large (e.g.,  $1\sigma \geq 2\text{‰}$  sensu Koch et al., 2004). Oxygen isotope values are reported here relative to V-SMOW. Previously published  $\delta^{18}\text{O}_{\text{enamel}}$  values reported relative to V-PDB were converted using the following equation:  $\delta^{18}\text{O}_{\text{V-SMOW}} = 1.03086 * \delta^{18}\text{O}_{\text{V-PDB}} + 30.86$  (Friedman and O'Neil, 1977).

## 6.2. Taxonomic composition

The BCC fauna is in many respects similar to other known late Pleistocene faunas on the Texas Gulf Coastal Plain. There are, however, some differences. The presence of a toxodont is unique. At present, BCC is the only known occurrence of a notoungulate from the United States (Lundelius et al., 2013). Toxodont remains are known from Michoacán and Veracruz, Mexico (Polaco et al., 2001). Stable carbon isotopes of *Toxodon* and *Mixotoxodon* from South and Central America suggest that both taxa were C<sub>3</sub>/C<sub>4</sub>-mixed feeding generalists adapted to feeding on local vegetation despite having hypsodont teeth (MacFadden, 2005). Isotopic analyses of late Pleistocene toxodonts from Brazil suggest that they were mixed feeders, although they plotted towards the end of the grazing spectrum (Dantas et al., 2013, 2017). In contrast, toxodonts from the early Pleistocene of Argentina consumed a diet consisting largely of C<sub>3</sub> vegetation (Domingo et al., 2012). *Mixotoxodon* likely inhabited a range of grassland and woodland environments.

Another key difference in the BCC fauna is the absence of the American mastodon, *Mammut americanum*. Mastodons were evolutionarily adapted to consume browse, with a molar dentition capable of crushing and milling twigs, bark, seeds, and fruit pits (Tobien, 1996; Newsom and Mihlbachler, 2006; Birks et al., 2019). However, mastodons tended to display considerable dietary niche plasticity, with food preferences shifting both seasonally and geographically with local resource diversity and abundance (e.g., Petersen et al., 1983; Lepper et al., 1991; Gobetz and Bozarth, 2001; Teale and Miller, 2012; Green et al., 2017). Mastodons on the Texas Gulf Coastal Plain preferred to inhabit woodland C<sub>3</sub> habitats with an abundance of woody browse (Yann et al., 2016; Smith and DeSantis, 2018). The absence of remains of *Mammut* at BCC is a stark contrast to the abundance of specimens of

*Mammut* recovered from the Ingleside deposits to the southwest (Lundelius, 1972), and suggests a relative rarity of closed forest stands or woodland environments at BCC during the time of deposition.

BCC is unique in having a prolific abundance of the Pleistocene gomphothere *Cuvieroni*. *Cuvieroni* was evolutionarily adapted to be a generalized mixed-feeder; this inference originally stemmed from the more complex molars of gomphotheres. The teeth have simple cones arranged in transverse pairs and interspersed with smaller accessory cusps that wear to form three-leaf clovers (a trefoil geometry; Lambert, 1996). Stable isotope studies of South American *Cuvieroni* confirm considerable dietary adaptability, with populations switching between browsing, grazing, and mixed-feeding habits commensurate with the range of resources available (MacFadden and Shockley, 1997; Prado et al., 2005; Sánchez et al., 2004; Nunez et al., 2010; Pérez-Crespo et al., 2016; Bravo-Cuevas et al., 2017). Stable carbon isotopes from *Cuvieroni* from BCC confirm a C<sub>3</sub>/C<sub>4</sub> mixed-feeding habit (Table 2), while dental microwear data indicate that BCC *Cuvieroni* consumed little grass and relatively hard foods including woody browse (Smith and DeSantis, in review). The relative abundance of *Cuvieroni* at BCC supports palynological data suggesting the East Texas Gulf Coastal Plain may have represented an ecotonal environment with both open grass and forest stands available (Bryant and Holloway, 1985).

In contrast to mastodons and gomphotheres, the mammoth (*Mammuthus* spp.) was evolutionarily adapted to be an efficient grazer, with hypsodont molars characterized by multiple horizontal lophs of enamel and dentine across a flat grinding surface that allowed grass to be clipped between occluding upper and lower molars (Maglio, 1972). However, like both the mastodons and gomphotheres, mammoth diets differed considerably with geography, environment, and climate, reflecting the cosmopolitan distribution of the genus. Although direct dietary evidence from dung and stomach contents confirm a preference for grasses in geographically widespread populations (e.g., Kubiaik, 1982; Mead et al., 1986; Gillette and Madsen, 1993; Karpinski et al., 2017), mammoths were apparently seasonal mixed-feeders with significantly different dietary habits during the winter and growing seasons (Metcalfe, 2017). In the Gulf Coastal Plain of Texas and Florida, mammoths held the large monogastric grazer niche, with evidence for a preference for C<sub>4</sub> grass (Koch et al., 1998, 2004; DeSantis et al., 2009; Yann and DeSantis, 2014; Yann et al., 2016; Smith and DeSantis, in review). The combined use of dental microwear and stable isotope analysis on a population of BCC mammoths confirms a mixed C<sub>3</sub>/C<sub>4</sub> diet with a preference for tough grasses (Smith and DeSantis, 2018, Table 2). BCC mammoths are significantly more depleted in <sup>13</sup>C as compared to mammoths from Ingleside (Table 3; Supplemental Table 2), suggesting less C<sub>4</sub> grass was present in the habitats of the BCC population. As mentioned previously, mammoths occupied a wide range of diverse environments; thus, their presence alone cannot define the specifics of the environment in which they lived. However, dietary information, in combination with the other large mammal fauna recovered from the BCC, suggest that mammoths likely exploited the open grasslands of this ecotonal environment.

**Table 3**

Comparisons of stable isotope values for disparate taxa in relation to the Big Cypress Creek taxa (bold indicates significant differences between populations, i.e.,  $p < 0.05$ ). Stable isotope data from Koch et al. (1998, 2004), Yann et al. (2016), and Smith and DeSantis (2018). Primary stable isotope data in Supplemental Table 1.

Site	$\delta^{13}\text{C}_{\text{vmeq}}$ V-PDB (‰) (mean $\pm$ 1 $\sigma$ )				$\delta^{18}\text{O}_{\text{enamel}}$ V-SMOW (‰) (mean $\pm$ 1 $\sigma$ )			
	<i>Camelops</i>	<i>Cuvieroni</i>	<i>Equus</i>	<i>Mammuthus</i>	<i>Camelops</i>	<i>Cuvieroni</i>	<i>Equus</i>	<i>Mammuthus</i>
Cypress Creek	$-20.3 \pm 4.5$	$-21.4 \pm 2.3$	$-18.8 \pm 1.9$	$-20.2 \pm 0.6$	$30.7 \pm 1.0$	$30.4 \pm 1.1$	$30.7 \pm 1.3$	$29.7 \pm 0.8$
Ben Franklin			$-19.9 \pm 1.7$	$-18.8 \pm 1.2$			$29.0 \pm 1.9$	$29.6 \pm 0.3$
Clear Creek			$-20.4 \pm 1.0$				$30.0 \pm 1.9$	
Cutler Hammock			$-15.1 \pm 0.4$	<b><math>-17.2 \pm 1.1</math></b>				$30.7 \pm 1.3$
Easley Ranch			$-17.7 \pm 1.4$				$28.7 \pm 0.5$	
Friesenhahn Cave			$-18.3 \pm 0.1$	<b><math>-17.6 \pm 1.4</math></b>			$28.4 \pm 0.1$	$29.7 \pm 0.7$
Howard Ranch			$-17.5 \pm 3.1$				$28.4 \pm 2.2$	
Ingleside	$-24.1 \pm 4.6$		<b><math>-16.5 \pm 1.1</math></b>	<b><math>-17.6 \pm 0.8</math></b>	$30.3 \pm 0.8$		$29.5 \pm 1.8$	$30.0 \pm 1.0$
Indian River		$-23.2 \pm 1.4$				$30.9 \pm 1.1$		
Leo Boatright Pit					$-20.1 \pm 2.2$			$28.6 \pm 1.5$
Moore Pit			$-20.5 \pm 1.4$		<b><math>-19.0 \pm 0.9</math></b>		$30.4 \pm 1.2$	<b><math>28.7 \pm 0.7</math></b>
Nobles Point					$-19.4 \pm 0.6$			$30.7 \pm 0.6$
Santa Fe River			$-18.2 \pm 1.1$		$-20.5 \pm 2.9$		$29.4 \pm 1.4$	$30.0 \pm 0.6$
Vero Beach Unit 2					$-17.9 \pm 0.3$			$30.1 \pm 1.0$
Waco					$-18.8 \pm 0.8$			$29.9 \pm 0.8$
Winter Beach (Luther Site)			<b><math>-26.3 \pm 0.2</math></b>				<b><math>28.6 \pm 0.8</math></b>	

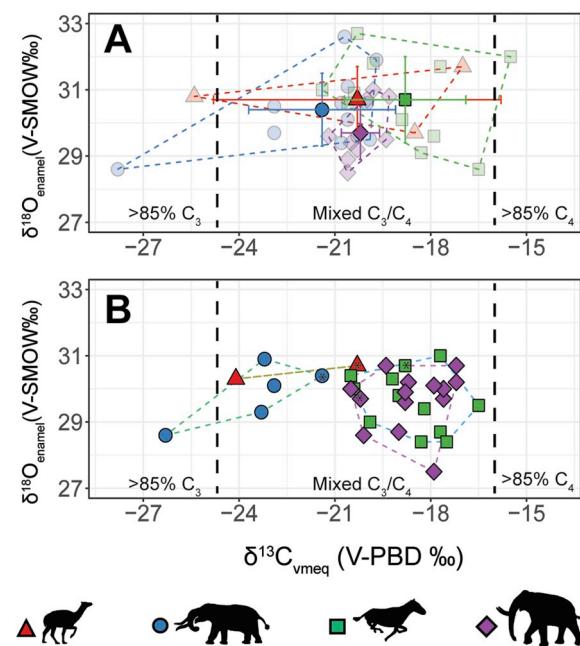
Additional data on the stable isotope ecology of taxa from BCC were collected and are presented herein. *Camelops* from BCC incorporated a mix of C<sub>3</sub> and C<sub>4</sub> vegetation into its diet (Table 2), with a range of  $\delta^{13}\text{C}_{\text{vmeq}}$  values ( $-25.4\text{‰}$  to  $-17.0\text{‰}$ ) that is similar to *Camelops* from Ingleside ( $-27.6\text{‰}$  to  $-14.7\text{‰}$ ) (Yann et al., 2016). Although the C<sub>3</sub> signature likely comes from the consumption of woody browse in closed forest stands, the enriched <sup>13</sup>C signature may reflect the consumption of C<sub>4</sub> shrubs such as chenopods (which were abundant in West Texas during the late Pleistocene; Bryant and Holloway, 1985) or CAM succulents (which likely co-evolved with North American megafauna including camels; Janzen, 1986). Populations of *Camelops* may have migrated to West Texas during the winters to feed on C<sub>4</sub> browse such as saltbush (*Atriplex*), the photosynthetic pathway of which is not limited by colder temperatures (Caldwell et al., 1977).

Members of the genus *Equus* have high-crowned (hypodont) teeth recognized as an adaptation for grazing on abrasive plants, particularly grasses. Stable isotope studies that incorporated late Pleistocene horses from the Gulf Coastal Plain of Florida and Texas confirm that those horses preferred C<sub>4</sub> grasses (MacFadden and Cerling, 1996; Koch et al., 1998, 2004; MacFadden et al., 1999a; Feranec and MacFadden, 2000). However, extinct horses displayed considerable adaptability and often altered their dietary habits when sympatric with potential competitors (e.g., bison, mammoths, and other horses; MacFadden et al., 1999b; Feranec, 2004; Feranec et al., 2009; Barrón-Ortiz et al., 2014; Jones and Desantis, 2017; Rivals and Semprebon, 2011; Rivals et al., 2007; Trayler et al., 2015). Horses at BCC had similar dietary tendencies as mammoths, as evidenced by similar mean stable carbon isotope signatures (Table 2). Interestingly, however, horses have a wider range in  $\delta^{13}\text{C}_{\text{vmeq}}$  values than mammoths ( $5.9\text{‰}$  as compared to  $1.9\text{‰}$ ). Additionally, *Equus* from BCC are significantly more depleted in  $\delta^{13}\text{C}_{\text{vmeq}}$  than *Equus* from Ingleside (Table 3), suggesting the incorporation of less C<sub>4</sub> grass than the Ingleside population.

Stable oxygen isotope data can help to distinguish the climatic setting of the BCC fauna. *Equus* from BCC are significantly more enriched in  $\delta^{18}\text{O}_{\text{enamel}}$  values than horses from Ingleside or Friesenhahn Cave (data from Koch et al., 2004, Table 3) suggesting that BCC horses inhabited an environment that was warmer and/or drier than Ingleside or Friesenhahn Cave. Because Ingleside is only about 366 km southwest of BCC, this difference is unlikely to represent a geographic difference and more likely to represent a difference in temporal and climatic setting.

Mammoths from BCC are indistinguishable in  $\delta^{18}\text{O}_{\text{enamel}}$  from their Ingleside counterparts (data from Koch et al., 2004, Table 3). However,

*Mammuthus*  $\delta^{18}\text{O}_{\text{enamel}}$  is also indistinguishable from  $\delta^{18}\text{O}_{\text{enamel}}$  of mammoths from Friesenhahn Cave suggesting that mammoths in East Texas were less sensitive to changes in climatic setting; this may reflect a greater reliance on drinking water (from surface- and/or ground-water sources) because mammoths are evaporation-insensitive taxa (Yann et al., 2013). It is also possible that *Mammuthus* had a larger home range and similarly averaged water sources across those broader ranges. Interestingly, *Camelops*  $\delta^{18}\text{O}_{\text{enamel}}$  values from BCC are not significantly different from  $\delta^{18}\text{O}_{\text{enamel}}$  values of *Camelops* from Ingleside (data from Yann et al., 2016, Table 3) despite being an evaporation-sensitive taxon (Yann et al., 2013). This may reflect the small sample size of *Camelops* at BCC which may not be equitably capturing seasonal changes in stable oxygen isotope values of precipitation. Mean  $\delta^{13}\text{C}_{\text{vmeq}}$  and  $\delta^{18}\text{O}_{\text{enamel}}$  values ( $\pm 1\sigma$ ) for genera from BCC are provided in



**Fig. 4.** Stable isotope data for studied taxa. Red triangles = *Camelops*; blue circles = *Cuvieroni*; green squares = *Equus*; purple diamonds = *Mammuthus*. (A) Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values ( $\pm 1\sigma$ ) for BCC genera. (B) Mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for each genus from all late Pleistocene sites in the Gulf Coastal Plain (asterisks denote BCC genera).

**Fig. 4**, in comparison with those for each genus from all late Pleistocene sites in the Gulf Coastal Plain.

Based on stable oxygen isotope data of *Equus* from BCC, we interpret that the large mammal fauna at BCC experienced warmer and/or drier conditions than the large mammal fauna from Friesenhahn Cave or Ingleside. Friesenhahn and Ingleside have been assumed to be Wisconsin full glacial faunal assemblages (Lundelius, 1972; Graham et al., 2013); we suggest that BCC mammals represent a warmer setting after the height of the LGM. This is consistent with radiocarbon dates on plant macrofossil remains from BCC (Lundelius et al., 2013) suggesting a mean calibrated age of 17–24 ka for the fauna. Assuming these dates are representative of the deposited bones, the BCC fauna was deposited during the end of the last glacial, just before the onset of the ‘Big Dry’ (Allen and Anderson, 2000; Broecker et al., 2009), the earlier dry phase of Heinrich Stadial 1.

Pollen associated with the BCC fauna is indicative of a shallow water environment (Lundelius et al., 2013). Palynological data are rare from East Texas, a phenomenon that Bryant and Holloway (1985) surmised may result from a variety of environmental factors, including soil conditions that make pollen preservation rare, rapid wet-dry cycles that cause the breakdown of otherwise resistant exterior layers of pollen, and high rates of microbial activity that may cause the degradation of certain pollen species. Pollen records from Tunica Hills in Louisiana (Delcourt and Delcourt, 1977) suggest that east Texas may have been covered by a deciduous woodland during the late Glacial period, with reduced abundance of spruce (*Picea*), hazel (*Corylus*), and alder (*Alnus*) but increased representation of oak (*Quercus* spp.), sweetgum (*Liquidambar* sp.), and pines (*Pinus* spp.). *Quercus* pollen was found abundantly in association with the BCC fauna (Lundelius et al., 2013), supporting that suggestion. Bryant and Holloway (1985) hypothesized that during the Wisconsinan glacial, East Texas represented 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. Based on the diversity and abundance of mixed-feeding and grazing taxa recovered from the BCC, we prefer the second hypothesis for a paleoenvironmental setting of the BCC, with the deciduous forest potentially dominated by oak. Additionally, the presence of cow lily (*Zantedeschia* sp.) and water milfoil (*Myriophyllum* sp.) in the BCC sediments suggests the presence of standing water. In dry grassland environments, water bodies are major attractants for animals, especially large mammals; this may, in part, explain the abundance and diversity of the accumulation of vertebrate taxa in this area.

In conclusion, the BCC fauna is a representative sample of the late Pleistocene mammal community on the Gulf Coastal Plain. Stable carbon isotopes suggest a generalized C<sub>3</sub>/C<sub>4</sub> mixed feeding habit for *Bison*, *Camelops*, *Cuvieronius*, *Equus*, and *Mammuthus* (Table 2) from BCC, which may indicate that dietary resource partitioning supported the existence of sympatric megaherbivores. Further, at least some of these mammals may have been seasonal migrants based on extremely variable stable carbon and oxygen isotopes. Comparing stable oxygen isotope data of BCC taxa with taxa from other well-studied sites from the Gulf Coastal Plain supports warmer or drier conditions experienced by the BCC fauna than by taxa living during the height of the Wisconsinan glacial. Along with previously-published radiocarbon dates (Lundelius et al., 2013), we suggest that the BCC fauna date to the end of the last glacial period and into the earlier dry phase of Heinrich Stadial 1, ca. 17–24 ka. Associated pollen and plant macrofossils support the interpretation of a shallow standing water body situated amidst an ecotonal open grassland with dispersed deciduous woodlands dominated by oak (*Quercus*).

#### Declaration of competing interest

On behalf of the authors of this submission, I declare we have no conflict of interest in presenting this research for publication.

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#### Appendix A. Supplementary data

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