Investigating equid mobility in Miocene Florida, USA using strontium isotope ratios

Wallace Jenelle P.[a,*], Crowley Brooke E.[a,b,**], Miller Joshua H.[a]

[a] University of Cincinnati, Department of Geology, 500 Geology-Physics Building, Cincinnati, OH 45221, USA
[b] University of Cincinnati, Department of Anthropology, 481 Braunstein Hall, Cincinnati, OH 45221, USA

ABSTRACT

Despite extensive research on the evolutionary history and ecology of horses, surprisingly little is known about the daily and seasonal movements (i.e. mobility) of extinct species. We used strontium isotope ratios (^{87}Sr/^{86}Sr) in tooth enamel to estimate mobility patterns of equids from two Miocene fossil sites in northern Florida, USA: Thomas Farm (ca. 18 Ma) and Love Bone Bed (ca. 9.5–9 Ma). The species included in our sample have a range of body sizes (45–252 kg) and reconstructed diets. Gomphotheres and tapirs from Love Bone Bed were also included to represent browsers. Based on modern species' behavior, we predicted small-bodied and browsing taxa living in closed habitats had limited mobility and ^{87}Sr/^{86}Sr similar to local northern Florida limestone. We anticipated larger-bodied and grazing taxa living in open environments had increased mobility, with higher and more variable ^{87}Sr/^{86}Sr reflecting larger movements across differing geologies. Contrary to expectations, the majority of taxa at both sites have higher ^{87}Sr/^{86}Sr than expected for local Eocene bedrock and instead are similar to contemporary Late Oligocene to mid-Miocene seawater. The most plausible explanation for these findings is that most individuals foraged close to the paleo-coastline, where vegetation would have been influenced by marine-derived strontium via sea spray or precipitation. Tapirs have considerably higher and more variable ^{87}Sr/^{86}Sr than horses or gomphotheres at Love Bone Bed, which may reflect foraging on aquatic vegetation in the river channel that is preserved at the site. Our results suggest that horses were relatively sedentary in Florida, even during their peak radiation.

1. Introduction

The evolution of horses (Equidae) is one of the most widely studied radiations in the history of mammals (MacFadden, 1992). During the Miocene Epoch, ca. 23–5 million years ago (Ma), closed forests shifted into open grasslands (Latorre et al., 1997; Passey et al., 2002; Retallack, 1997) and ungulate diversity exploded into novel grazing habitats. Between 23 and 8 Ma, the number of equid genera more than quadrupled (MacFadden, 1992; Maguire and Stigall, 2008; O'Sullivan, 2008; Strömberg, 2004). Concurrent morphological changes, including higher crowned teeth, increased limb length and body mass, and a reduction in toe number, all suggest that horses adapted to fill the new grazer niche in more open environments (Alberdi et al., 1995; Damuth and MacFadden, 1990; MacFadden, 2005). These morphological changes, combined with an increasingly open habitat, imply that, over time, equids increased the spatial extent of their landscape use (e.g., mobility). However, this has not been comprehensively explored.

Here, we use strontium isotope ratios (^{87}Sr/^{86}Sr) in tooth enamel to investigate mobility of co-occurring equids with differing body masses and reconstructed diets. We include taxa from two sites in northern Florida, USA dating to the early (ca. 18 Ma) and late Miocene (ca. 9.5–9 Ma; Fig. 1). We predict that species foraging within limited geographic areas (i.e. smaller bodied or browsing taxa from closed habitats) will have similar ^{87}Sr/^{86}Sr to local limestones. Taxa that moved seasonally, or had broader home ranges (i.e. larger bodied or grazing taxa from open habitats), should have higher and more variable ^{87}Sr/^{86}Sr, reflecting foraging across more geologically complex areas, potentially from regions beyond the largely homogenous Florida carbonate platform (Fig. 2).

1.1. Strontium isotope background

Strontium has four naturally occurring isotopes: ^{84}Sr, ^{86}Sr, ^{87}Sr, and ^{88}Sr. Three of these are stable; however, ^{87}Sr is produced through the
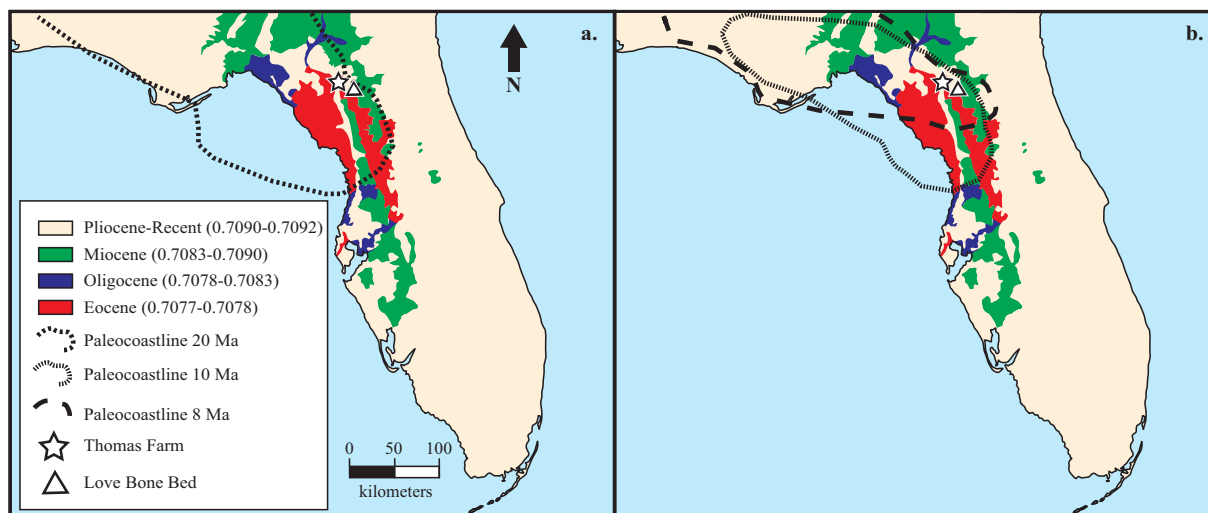

Fig. 1. Map of Florida showing bedrock geology and reconstructed paleo-coastlines for (a) 20 Ma and (b) 10 and 8 Ma (Markwick, 2007; Scott et al., 2001). Estimated bioavailable ^{87}Sr/^{86}Sr for different-aged carbonates is based on expected ^{87}Sr/^{86}Sr for contemporary seawater (McArthur et al., 2001).

radioactive decay of rubidium (^{87}Rb; reviewed in Capo et al., 1998). Both chemical composition and age influence ^{87}Sr/^{86}Sr in rocks (Banner, 2004; Capo et al., 1998). For example, potassium-bearing minerals have more more naturally occurring ^{87}Rb. Consequently, silica-rich igneous, metamorphic, and clastic sedimentary rocks have higher strontium isotope ratios than mafic volcanics (Bataille and Bowen, 2012). Carbonates contain an abundance of strontium and have ^{87}Sr/^{86}Sr comparable to seawater (~0.707 to 0.709; Capo et al., 1998; Bentley, 2006; McArthur et al., 2001). Age also impacts ^{87}Sr/^{86}Sr; older rocks have higher ^{87}Sr/^{86}Sr than younger rocks due to the accumulation of ^{87}Sr from radioactive decay. Nevertheless, due to the long half-life of ^{87}Rb (48.8 billion years), the ratio of ^{87}Sr to ^{86}Sr is relatively stable over ecologically meaningful timescales.

Within most terrestrial settings, the main source of biologically available (bioavailable) strontium is surface geology (reviewed in Åberg, 1995; Banner, 2004; Bentley, 2006; Capo et al., 1998). Weathered bedrock leaches strontium into ground and surface water systems. This bioavailable strontium is then taken up by plants and subsequently incorporated into animal tissues through diet and drinking water (Capo et al., 1998). Due to strontium's large mass, there is negligible isotopic fractionation during physical and chemical reactions (Banner, 2004). Thus, the ^{87}Sr/^{86}Sr in an animal's tissues closely reflects the ^{87}Sr/^{86}Sr of the underlying bedrock and therefore can be used to track faunal movement across regions of varying geology.

In some settings, atmospheric deposition of dust and marine-derived strontium via wind or precipitation can also contribute to the bioavailable strontium pool (Fig. 3; Åberg, 1995; Capo et al., 1998; Raiber et al., 2009). Exogenous dust is the primary source of bioavailable strontium for plants growing on rocks with low strontium concentrations or weathering rates; both dry and wet deposition of dust in these settings can greatly influence bioavailable strontium and even conceal the signal of weathering bedrock (English et al., 2001; Graustein and Armstrong, 1983; Hartman and Richards, 2014; Miller et al., 2014; Raiber et al., 2009; Reynolds et al., 2012). However, the influence of dust on ^{87}Sr/^{86}Sr in regions dominated by carbonate bedrock appears to be relatively insignificant (Reynolds et al., 2012; Schulting et al., 2018). This is most likely because high strontium concentrations in carbonates, combined with their potential to rapidly weather, can overwhelm the local bioavailable strontium pool (Bern et al., 2005).

Marine-derived strontium can be deposited in terrestrial settings via sea spray or precipitation. The extent to which marine-derived

strontium influences the terrestrial bioavailable strontium pool, and the distance that it can be detected inland, are not well-constrained and likely vary as a function of regional climate patterns. The influence of marine strontium is detectable up to ca. 70–100 and 160 km inland from the windward coast in Australia and Scandinavia, respectively (Andersson et al., 1990; Quade et al., 1995; Raiber et al., 2009). Marine-derived strontium may dominate the bioavailable strontium pool in regions with high annual precipitation, such as Hawaii and Great Britain (Chadwick et al., 2009; Evans et al., 2010; Stewart et al., 2001). Even fewer studies have specifically investigated the influence of sea spray because it is often isotopically indistinguishable from precipitation. Sea spray-derived strontium appears to be limited to within 1 km from the ocean on both windward and leeward coasts in Ireland (Snoeck, 2014) and the Caribbean (Schulting et al., 2018). To the best of our knowledge, these are the only studies that have explicitly attempted to quantify the distance inland from the coast that marine-derived strontium is detectable.

1.2. Background on equids

Equids first appeared in North America during the Eocene and persisted on the continent for over 55 million years (MacFadden, 2005; Mihlbachler et al., 2011). Over time, they evolved from *Hyracotherium* sp., a small (ca. 24–35 kg), unspecialized hooved herbivore, into a family adapted for speed and open country (MacFadden, 1992, 1986). By the early Miocene, there were 4–5 horse genera, all of which had three toes, elongated metapodials, and an increased body mass relative to their ancestral groups (ca. 50–150 kg). Tooth enamel complexity increased and tooth crown height shifted from brachydont (low-crowned teeth) to hypsodont (high-crowned teeth) in response to grassland expansion and increased consumption of abrasive grass and grit (MacFadden, 1992). By the end of the Miocene, equid species diversity had increased to over 15 genera (Mihlbachler et al., 2011). The majority of these taxa were larger than 240 kg and had hypsodont teeth, suggesting heavy reliance on grasses (MacFadden, 1986). However, some species stayed relatively small and had mesodont (intermediate-crowned) teeth, suggesting dietary niche partitioning among genera.

1.3. Patterns of mobility in ungulates

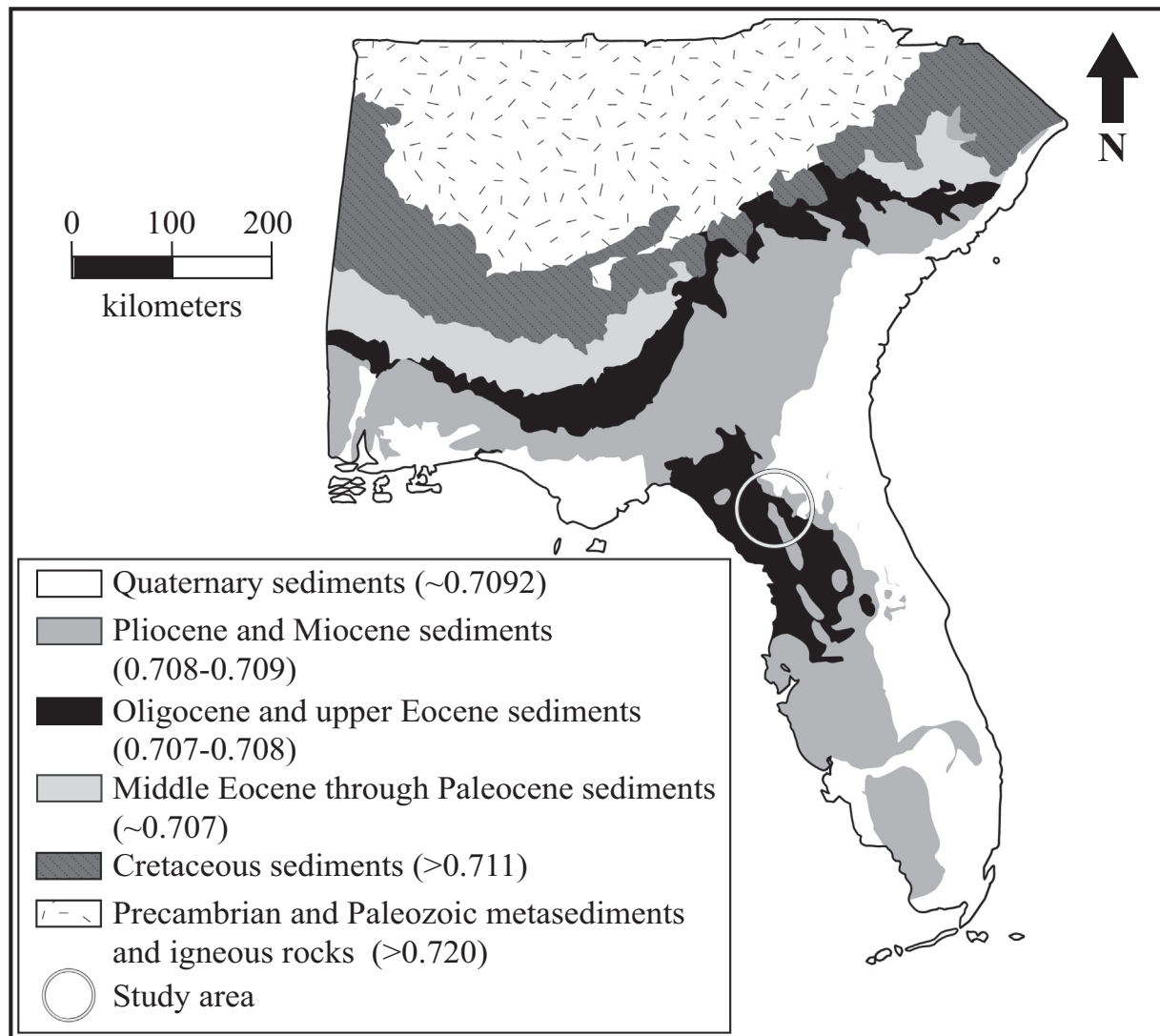In this paper, mobility is defined as the daily and seasonal

Fig. 2. Map of the southeastern U.S.A. illustrating the regional bedrock geology (adapted from United States Geological Survey, 2016) and estimated regional bioavailable [87]Sr/[86]Sr (Bataille and Bowen, 2012; Hoppe and Koch, 2007; McArthur et al., 2001).

movements of an individual related to foraging, mating, caring for young, and other social dynamics. Two important drivers of ungulate mobility are preferred habitat type (open versus closed) and body size (Ofstad et al., 2016). Ungulates inhabiting open environments are generally more mobile than those from closed habitats due to an abundance of lower quality forage and increased distance between areas used for predator avoidance. For example, in eastern South Dakota, USA, pronghorn antelope (*Antilocapra americana*) inhabiting grasslands have home ranges between 19.7 and 127 km² (Jacques et al., 2009) while forest-dwelling white-tailed deer (*Odocoileus virginianus*) have considerably smaller home ranges of 1.1–4.3 km² (Sparrowe and Springer, 1970).

Ungulate home ranges also increase allometrically with body size (Ofstad et al., 2016). For example, large grazing elk (*Cervus elaphus*) in the western USA have home ranges between 71 and 129 km² (Anderson et al., 2005), whereas smaller-bodied grazing bighorn sheep (*Ovis canadensis*) occupy smaller home ranges between 6.1 and 35.3 km² in the same region (Singer et al., 2001). Similarly, large browsers, such as moose (*Alces alces*) in central Sweden, have larger home ranges (13–26 km²) than co-occurring smaller-bodied browsing roe deer (*Capreolus capreolus*), which have very small home-ranges (0.01–1.2 km²; Cederlund, 1983; Cederlund and Sand, 1994).

1.3.1. Equid mobility

The mobility of modern equid species reflects dispersal from natal bands and daily and seasonal foraging patterns. All contemporary equids have similar social structures in that one dominant male controls a group of multiple females. Offspring emigrate from their natal herds between the ages of one and three years, often in conjunction with the birth of their mothers' next foal (Feh, 2005; Kaseda et al., 1997). Female dispersal to a new group usually coincides with estrous, which naturally prevents inbreeding. Subadult males are often chased away from their natal groups and form small bands, or bachelor groups, until they are strong enough to obtain and defend their own herds (reviewed in Ransom and Kaczensky, 2016).

Daily and seasonal mobility patterns for equids vary depending on resource availability. Similar to other ungulates, equids that occupy areas with abundant resources are more likely to be relatively sedentary. For example, Canadian feral horses (*Equus ferus*) that inhabit the forests and grasslands of the Rocky Mountain foothills have a home range of roughly 15 km² and reintroduced Eurasian herds of Przewalski horses (*E. ferus przewalskii*) in Mongolian mesic steppe grasslands inhabit areas of 3–78 km² (reviewed in Ransom and Kaczensky, 2016). Populations living in highly seasonal environments, or regions with widely dispersed resources, have greater mobility. African zebra (e.g. *E. quagga burchellii* and *E. grevi*) seasonally travel up to 100 km in one
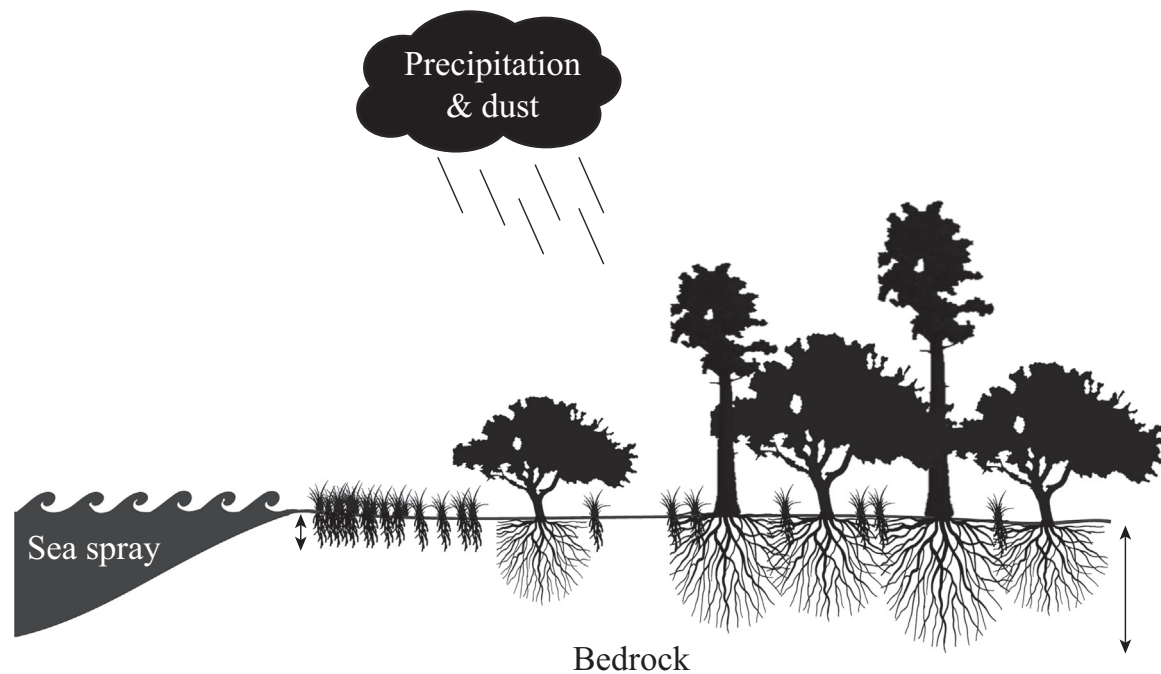
Fig. 3. Schematic showing anticipated sources of bioavailable strontium in Miocene Florida. The influence of marine-derived strontium should be highest closest to the coast. Vegetation rooting depth (arrows) may also influence ^{87}Sr/^{86}Sr; whereas weathering bedrock should be the dominant source for deep-rooted trees, grasses with shallow root systems may be more susceptible to atmospherically deposited strontium.

direction and the Asiatic wild ass (*E. hemionus*) in the southwest Gobi Desert has a home range between 18,186 and 69,988 km² (reviewed in Ransom and Kaczensky, 2016).

Few studies have explored the mobility of Miocene equids. It has been postulated that a small early Miocene equid, *Parahippus* sp., was relatively sedentary based on modern forest-dwelling artiodactyls with similar body masses and diets (Hulbert, 1984). Conversely, the mid-Miocene equid, *Neohipparion* cf. *leptode*, is thought to have migrated seasonally, like modern zebras, based on distinct age classes and the absence of foals within an attritional fossil assemblage (Hulbert, 1982). Lastly, Tütken and Vennemann (2009) analyzed ^{87}Sr/^{86}Sr for a single *Anchitherium aurelianense* from the Middle Miocene in Southern Germany and determined this individual was relatively sedentary, although it may have traveled up to 50 km to the northeast.

1.3.2. Using strontium isotopes to track mobility

Strontium isotope ratios in an animal's bones or teeth can be used to distinguish relatively sedentary from highly mobile individuals, or trace an individual's movement across regions with variable geology (Britton et al., 2009; Hoppe et al., 1999; Hoppe and Koch, 2007; Price et al., 1985). Dispersal from a natal herd, seasonal migration, and daily movement within a home territory or range can be tracked using strontium isotopes. Foraging on different types of vegetation may also influence ^{87}Sr/^{86}Sr in herbivores (Crowley et al., 2018; Hedman et al., 2009; Maurer et al., 2012; Radloff et al., 2010). Whereas deeper rooting plants gain the majority of their strontium from bedrock, shallow rooting plants are more likely to be influenced by atmospheric deposition (Fig. 3; Graustein and Armstrong, 1983; Reynolds et al., 2012).

This geochemical tool has been used to examine foraging territories and migration patterns for modern herbivores, including African antelope, zebra, and elephants (Koch et al., 1995; Radloff et al., 2010; Vogel et al., 1990), as well as North American and European caribou (Britton et al., 2011, 2009; Gigleux et al., 2017). Strontium isotopes have also been used to reconstruct the mobility of various Quaternary herbivores in Europe and North America, including bison, caribou, horse, deer, mammoth, and mastodon (Baumann and Crowley, 2015; Britton et al., 2011; Hoppe, 2004; Hoppe and Koch, 2007; Pellegrini et al., 2008;

Widga et al., 2010). Studies on older taxa are more rare and have focused on Miocene hominids (e.g. Copeland et al., 2011).

We are only aware of three studies that have used strontium isotopes to investigate the mobility of extinct horses. As mentioned above, ^{87}Sr/^{86}Sr suggest *Anchitherium aurelianense* had a small home range in southern Germany (Tütken and Vennemann, 2009). Pellegrini et al. (2008) measured ^{87}Sr/^{86}Sr for four Pleistocene *Equus hydruntinus* in western and central Italy. Low variability in ^{87}Sr/^{86}Sr among individuals suggests they were also relatively sedentary. Lastly, Hoppe and Koch (2007) analyzed ^{87}Sr/^{86}Sr for a diversity of Pleistocene herbivores, including three *Equus* sp. from Northern Florida. The authors concluded that one individual likely stayed in Florida while the other two individuals traveled ca. 150 km north into Georgia.

2. Methods

2.1. Regional setting

The geographic focus of this study is Northern Florida, USA, which has relatively homogeneous bedrock and is known for its abundant Miocene fossil deposits. The region is underlain by the Florida Platform, which is composed of a thick sequence of Paleocene to Oligocene carbonates (Fig. 1; Scott, 1992). The strontium isotope ratios leached from these rocks should be relatively low and comparable to contemporaneous seawater: ca. 0.7077–0.7078 for the Eocene and 0.7078–0.7083 for the Oligocene (Fig. 1; McArthur et al., 2001). Several hundred kilometres to the north, bedrock is composed of older sediments as well as metamorphic and igneous rocks that date back to the formation and uplift of the Appalachian Mountain range during the early Paleozoic (Fig. 2). These rocks should have considerably higher (≥0.7110) and more variable ^{87}Sr/^{86}Sr than limestone (Capo et al., 1998; Hoppe et al., 1999; McArthur et al., 2001). Published ^{87}Sr/^{86}Sr for modern surface water, plants, and rodents from the region reflect underlying geology. Samples from northern and central Florida have strontium isotope ratios that are broadly consistent with those expected for carbonates (0.7075–0.7092; Hoppe et al., 1999; McArthur et al., 2001). In contrast, samples from Georgia have higher and more variable

ratios, ranging from 0.7103 to 0.7633 (Hoppe et al., 1999; Samson et al., 1995; van Breemen and Dallmeyer, 1984).

Throughout the Miocene, global sea levels were higher than they are today. Oxygen isotope data, supported by seismic stratigraphy, indicate the global sea level was ~130 metres above modern sea levels (mamsl) during a high stand ca. 19 Ma (Abreu and Anderson, 1998; Haq et al., 1987). In Florida, the maximum sea level at 19 Ma was ca. 100 mamsl (Mallinson et al., 1994; Missimer, 2002), which resulted in the continental landmass barely extending into northern Florida (Fig. 1a). Global sea level continued to fluctuate, but the general trend was a gradual decline, paralleling a decrease in temperature (Haq et al., 1987; Lewis et al., 2007; Scott, 1997). In the later Miocene, sea levels were roughly 50 mamsl. However, a transgression ca. 9.5 Ma in Florida raised sea level from modern levels to 20 mamsl (Haq et al., 1987; Missimer, 2002), which may have created a strait that separated Florida from the North American continent (Fig. 1b).

Minor eustatic sea level fluctuations and longshore drift allowed for the progressive influx of North American clastic sediment onto the Florida Platform from the Oligocene to the Late Miocene (Missimer, 2001; Missimer, 2002; Missimer and Maliva, 2017; Scott, 1988). At least seven major pulses of sediment derived from the Appalachians reached Florida throughout the Cenozoic, including one in the Middle Miocene (Boettcher and Milliken, 1994; Gallen et al., 2013; Missimer and Maliva, 2017; Scott, 1992). Although much of the Miocene stratigraphic record in northern Florida is represented by unconformities (Scott, 1997), increased clastic input may have created localized geologic and isotopic variability within an otherwise essentially homogenous region.

2.2. Site descriptions

Specimens were selected from two Miocene fossil sites in northern Florida that are known for their abundant and diverse fossil horses: Thomas Farm and Love Bone Bed (Fig. 1). Thomas Farm is a Hemingfordian (ca. 18 Ma) sinkhole in Gilchrist County (29.9° N, 82.8° W). Fossils have been recovered from unconsolidated Miocene fluvial and cave sediments that cut into Eocene Crystal River limestone (Pratt, 1990). Lower cyclic layers of clay and sandy clay contain the majority of larger faunal remains; upper layers of limestone sand contain abundant microfauna. The dominant large-bodied species (comprising roughly 70% of identifiable macrofaunal remains) is the equid *Parahippus leonensis* (Hulbert, 1984). Remains from two other equids, *Archaeohippus blackbergi* and *Anchitherium clarencei*, have also been recovered. Other fauna include camels, deer, canids, alligators, turtles, rodents, and bats (Pratt, 1990, 1989). The abundance of browsing ungulates and short-limbed carnivores suggest the surrounding environment was wooded or relatively closed (Pratt, 1990). Furthermore, the presence of aquatic fauna and plants indicate the sinkhole may have acted as a perennial water source (Pratt, 1990).

Love Bone Bed is a well-studied Clarendonian (ca. 9.5–9.0 Ma) fossil deposit located ca. 47.5 km southeast of Thomas Farm in Alachua County (29.5° N, 82.5° W). Fossils were buried in fluvial sands and clays of the Miocene Alachua Formation (Webb et al., 1981), which filled a meandering river channel cutting into Late Eocene Crystal River limestone. Over 84 aquatic and terrestrial species have been identified at Love Bone Bed, nine of which are horses (Feranec and MacFadden, 2006; Hulbert, 1993). Other taxa include canids, rhinoceros, camels, gomphotheres, tapirs, rodents, alligators, turtles, and euryhaline bull sharks (Webb et al., 1981). Based on the stratigraphy and species recovered, Webb et al. (1981) proposed three depositional terrestrial environments for this locality: marine-influenced streambank, forest, and open savannah. Carbon and oxygen isotope data for terrestrial fauna (Table 1; Feranec and MacFadden, 2006) support Webb's reconstructed environments.

2.3. Species descriptions

We sampled two equids from Thomas Farm: *Archaeohippus blackbergi* and *Parahippus leonensis* (Table 1). *Archaeohippus blackbergi* is the smallest equid found at Thomas Farm, with a mean body mass of roughly 45 kg (MacFadden, 1986). Brachydont teeth and dental microwear patterns indicate it was a browser, or possibly a frugivore (Mihlbachler et al., 2011; O'Sullivan, 2005; Semprebon et al., 2016). These dietary inferences, combined with paleoenvironmental reconstructions, suggest *A. blackbergi* was a forest dweller (O'Sullivan, 2005). *Parahippus leonensis* was a relatively small horse (mean body size ca. 85 kg) characterized by mesodont teeth (MacFadden, 1986). Its tooth wear patterns and carbon isotope data indicate a diet consisting of mixed leaves and grass in a woodland habitat (Hulbert, 1984; Mihlbachler et al., 2011; Moran, 2014; Semprebon et al., 2016).

We sampled five equid species from Love Bone Bed: *Nannippus westoni*, *Neohipparion trampasense*, *Cormohipparion ingenuum*, *C. plicatile*, and *Protohippus gidleyi* (Table 1). While larger than *Archaeohippus* and *Parahippus*, *N. westoni* was a relatively small (ca. 101 kg) horse that had hypsodont teeth (Damuth and MacFadden, 1990; MacFadden, 1986; Mihlbachler et al., 2011). On the basis of tooth-crown height and enamel complexity, this species was likely a grazer (MacFadden, 1992). Carbon and oxygen isotope data are consistent with this species regularly foraging in a relatively open habitat at Love Bone Bed (Feranec and MacFadden, 2006).

Neohipparion trampasense is the ancestral species of the genus *Neohipparion*, which proliferated in the late Miocene (Hulbert, 1987). Florida individuals weighed ca. 180 kg, which was 5–10% smaller than populations in the Great Plains (Hulbert, 1987). *Neohipparion trampasense* had hypsodont cheek teeth, indicating a diet dominated by grasses (MacFadden et al., 1999). Carbon and oxygen isotope values also suggest that *N. trampasense* inhabited an open environment at Love Bone Bed (Feranec and MacFadden, 2006).

Cormohipparion ingenuum and *C. plicatile* weighed ca. 153 kg and ca. 223 kg, respectively (Damuth and MacFadden, 1990). These species had hypsodont cheek teeth, suggesting a diet dominated by grasses (Damuth and MacFadden, 1990; MacFadden et al., 1999). Carbon and oxygen isotopic data indicate that both species frequented relatively open habitats at Love Bone Bed (Feranec and MacFadden, 2006), although *C. ingenuum* might have spent more time in a slightly more closed habitat than *C. plicatile* (Table 1).

Protohippus gidleyi was a relatively large (ca. 252 kg) horse (Alberdi et al., 1995; MacFadden and Dobie, 1998; Mihlbachler et al., 2011). Tooth wear patterns and hypsodont teeth indicate it was adapted for grazing (Fraser and Theodor, 2013). Carbon and oxygen isotope data for *P. gidleyi* at Love Bone Bed are similar to those for *C. ingenuum* and suggest this species lived in a moderately open habitat, possibly an ecotone between riparian forest and open savanna (Table 1; Damuth and MacFadden, 1990; Feranec and MacFadden, 2006).

To generate comparative data on obligate browsing taxa at Love Bone Bed, we also sampled tapirs (*Tapirus webbi*) and gomphotheres (*Gomphotherium* sp.). Tapirs (Tapiridae) have changed very little since their first appearance in the early Eocene, ca. 56–48 Ma (DeSantis and MacFadden, 2007). They have brachydont teeth and relatively large body masses ranging from 150 to 375 kg (Clauss et al., 2003; García et al., 2012; Medici, 2010). Extant tapirs inhabit dense, closed-canopy forests often associated with riparian environments and have average home ranges of ca. 2.5 km² (Foerster and Vaughan, 2002; Medici, 2010). Their diet consists of leaves, fruits, and aquatic plants (Medici, 2010). Miocene tapirs likely behaved similarly. Carbon and oxygen isotope data are not available for *T. webbi* at Love Bone Bed; however, data for its congener, *T. simpsoni*, support a closed forest habitat (Feranec and MacFadden, 2006; Fraser and Theodor, 2013; Hulbert, 2005; MacFadden and Cerling, 1996).

Gomphotherium (Gomphotheriidae) was a genus of proboscidean that radiated throughout the Miocene. Species identity has not been

Table 1
Summary of morphological features and reconstructed ecology of analyzed taxa.

Species	Tooth crown height	Body mass mean and range (kg)	Subsistence[e]	Habitat[f]	Mean $\delta^{18}O_{VPDB}$ (‰)[g]	Mean $\delta^{13}C_{VPDB}$ (‰)[g]
Thomas Farm						
Archaeohippus blackbergi	Brachydont	44.7[a]	Browser/frugivore	Woodland with open patches	–	–
Parahippus leonensis	Mesodont	85.2[a]	Mixed feeder	Woodland with open patches	1.4	−11.2
Love Bone Bed						
Cormohipparion ingenuum	Hypsodont	153.3, 120–226[b]	Mixed feeder	Ecotone between forest and open habitat	−1.7	−10.8
Cormohipparion plicatile	Hypsodont	222.5, 156–315[b]	Mixed feeder	Open	−1.5	−11.4
Nannippus westoni	Hypsodont	100.7, 76–118[b]	Grazer	Open	−1.1	−11.2
Neohipparion trampasense	Hypsodont	179.5, 130–268[b]	Grazer	Open	−0.5	−10.8
Protohippus gidleyi	Hypsodont	252.3, 189–320[b]	Grazer	Ecotone between forest and open habitat	−2.1	−11.2
Gomphotherium sp.	Brachydont	–, 4173–6078[c]	Browser	Closed forest	−1.2	−12.6
Tapirus webbi	Brachydont	343.3, 248–455[d]	Browser	Closed forest	−1.8	−13.2

[a] Body mass estimates for Thomas Farm equids are based on upper first molar anteroposterior lengths (MacFadden, 1986). Ranges of body size not indicated.
[b] Body masses for Love Bone Bed equids are based on the first molar anteroposterior lengths using the equation: $\log W = (3.263 * \log(\text{upper M1 length})) + 1.337$ (Damuth and MacFadden, 1990).
[c] Mass estimates for *Gomphotherium* sp. are calculated by the Graphic Double Integration volumetric method (Larramendi, 2016).
[d] Mass estimates for *Tapirus webbi* are based on humeri and femoral measurements from closely related *Tapirus simpsoni* (Damuth and MacFadden, 1990).
[e] Subsistence is inferred on the basis of tooth crown height, microwear patterns, and enamel complexity (Fraser and Theodor, 2013; Hulbert, 1984; MacFadden, 1992; Semprebon et al., 2016).
[f] Reconstructed habitats are based on a tooth crown height and comparison with modern forest-dwelling artiodactyls for Thomas Farm (Hulbert, 1984), and carbon and oxygen isotope data for Love Bone Bed (Feranec and MacFadden, 2006).
[g] Data for Thomas Farm (*P. leonensis*) are from Moran (2014) and data from Love Bone Bed are from Feranec and MacFadden (2006).

determined for the individuals found at Love Bone Bed. Estimated body masses for the genus range from 4173 to 6078 kg (Larramendi, 2016). Brachydont teeth and tooth wear patterns indicate gomphotheres were primarily browsers (Fox and Fisher, 2004; Fraser and Theodor, 2013). Both carbon and oxygen isotope data suggest that the *Gomphotherium* sp. at Love Bone Bed inhabited a closed or riparian habitat (Feranec and MacFadden, 2006).

2.4. Sample selection, preparation, and analysis

We analyzed 89 teeth from nine taxa (Table S1). All specimens were loaned from the Florida Museum of Natural History. For each equid species, we selected 8–11 third molars to avoid capturing a nursing signal (Bryant et al., 1996; Hoppe et al., 2004). We selected 10 second or third molars for gomphotheres and eight molars for tapirs (molar position was unavailable).

We chose to analyze tooth enamel rather than bone for a number of reasons. First, enamel is more likely to retain its original strontium signature. Unlike bone, enamel is naturally resistant to diagenetic processes due to its non-porous, crystalline structure (Stack, 1955). Second, minor diagenetic alteration can almost be completely removed through sample pretreatment (Hoppe et al., 2003). Third, biogenic $^{87}Sr/^{86}Sr$ has previously been reported in tooth enamel for Miocene whales, hominins, proboscideans, and an equid (Copeland et al., 2011; Hoppe et al., 2003; Tütken and Vennemann, 2009). Fourth, teeth are much more abundant and readily identifiable for equid species at our fossil localities. Lastly, specimens from both Thomas Farm and Love Bone Bed have previously been analyzed for carbon and oxygen isotopes, and the resulting data have been considered biogenic (Feranec and MacFadden, 2006; Moran, 2014).

A handheld Dremel tool equipped with a dental drill bit was used to extract ~20 mg of enamel powder from each specimen. To incorporate temporal variability within each tooth, enamel was removed along a ca. 2 mm wide band from the tooth crown to neck. Powdered enamel was then chemically pretreated following Baumann and Crowley (2015). Samples were soaked in 30% hydrogen peroxide at room temperature

for 24 h and then rinsed five times with ultrapure water. Powders were then reacted with 1 M acetic acid buffered with calcium acetate at 4 °C for 24 h, rinsed five times with ultrapure water, and freeze dried. Roughly 3–4 mg of pretreated sample was weighed for analysis.

Strontium was extracted and analyzed in the Department of Geology's Multicollector ICPMS Laboratory at the University of Illinois, Urbana-Champaign. Samples were first dissolved in 0.5 mL of 3 M nitric acid and then filtered through Teflon mini-columns containing Eichrom Sr-specific resin. They were then sequentially rinsed with 0.05, 3, and 8 M nitric acid to selectively remove cations from the resin to isolate strontium. Strontium was eluted from the resin with 3 mL of ultrapure water and 1 mL of 0.05 M nitric acid into 4 mL autosampler vials.

Samples were analyzed on a Nu Plasma high resolution multi-collector inductively-coupled plasma mass spectrometer. Data were corrected for drift using the international standard NBS 987. Two internal laboratory references ('Coral' and 'E&A') were used to monitor accuracy and precision.

3. Results

Strontium isotope ratios for all samples are between 0.70813 and 0.70934. Individuals from Thomas Farm have lower (Wilcoxon $\chi^2 = 45.65$, DF = 1, p < 0.0001) and considerably less variable $^{87}Sr/^{86}Sr$ than Love Bone Bed (0.70832–0.70859 versus 0.70813–0.70934; Bartlett p < 0.0001; Table 2; Fig. 4). Data for all individuals are provided in Table S1.

At Thomas Farm, there are marginally significant differences in median $^{87}Sr/^{86}Sr$ between *Archaeohippus blackbergi* and *Parahippus leonensis* (Wilcoxon $\chi^2 = 3.29$, DF = 1, p = 0.070), but no significant differences in variance (Bartlett p = 0.52).

Among the Love Bone Bed fauna, there are significant differences in $^{87}Sr/^{86}Sr$ (Kruskal-Wallis $\chi^2 = 26.04$, DF = 6, p = 0.0002) and variance (Bartlett p = 0.046), which are driven by tapirs and gomphotheres. Tapirs have higher $^{87}Sr/^{86}Sr$ than all other taxa. More subtle differences between gomphotheres and horses are not significant when tapirs are excluded (Table 2; Fig. 4).
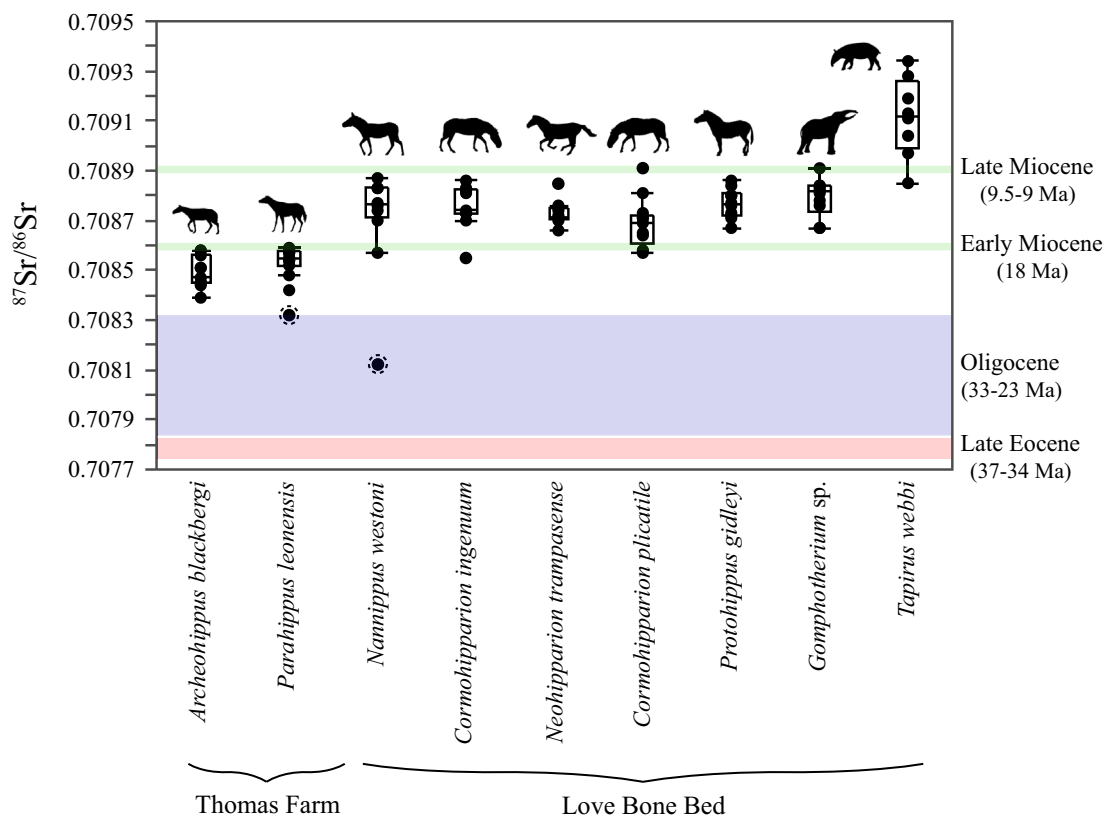
Fig. 4. Box plots of ^{87}Sr/^{86}Sr for all taxa at Thomas Farm and Love Bone Bed. Dashed circles encompass statistical outliers that were excluded from analyses. Shaded boxes represent the range of ^{87}Sr/^{86}Sr expected for seawater during different time bins (McArthur et al., 2001).

Further investigation of taxa at Love Bone Bed indicates no relationships between log body mass and median ^{87}Sr/^{86}Sr or isotopic variance (p > 0.05). However, significant differences are observed among taxa with differing diets and reconstructed habitats (Table 3). Steel-Dwass post hoc tests indicate that browsers (*Gomphotherium* sp. and *Tapirus webbi*) have significantly higher ^{87}Sr/^{86}Sr than grazers (*Nannippus westoni*, *Neohipparion trampasense*, and *Protohippus gidleyi*) or mixed feeders (*Cormohipparion ingenuum* and *Cormohipparion plicatile*). Variance also differs among groups (Bartlett p < 0.0001); browsers have the largest variance while grazers have the smallest. Closed environment species (*Gomphotherium* sp. and *Tapirus webbi*) have higher and more variable ^{87}Sr/^{86}Sr than taxa that likely inhabited moderately open or open habitats (Table 3). Species from moderately open habitats (*Cormohipparion ingenuum* and *Protohippus gidleyi*) have qualitatively smaller variance and slightly higher ^{87}Sr/^{86}Sr than those from open habitats (*Nannippus westoni*, *Neohipparion trampasense*, and *Cormohipparion plicatile*; Table 3), but these comparisons are not significant. Tapirs are the clear driver of these results and excluding them removes

any significance from diet or habitat comparisons (p > 0.05 for all analyses; Table 3).

Because equids at Thomas Farm and Love Bone Bed differ isotopically (Wilcoxon χ^2 = 40.45, DF = 1, p < 0.0001), we did not directly compare median ^{87}Sr/^{86}Sr among all equids. We did, however, examine the relationship between log body mass and isotopic variance across equid taxa from both sites as well as compare variance among equid groups with differing reconstructed diets and habitats. Looking across all equids, there is no relationship between log body mass and ^{87}Sr/^{86}Sr variance (r^2 = 0.058; p = 0.60). However, variance differs among taxa with differing diets (Bartlett p = 0.0032). Mixed feeders (*C. ingenuum* and *C. plicatile*) have larger variance (0.00012) than either grazers (*N. westoni*, *N. trampasense*, and *P. gidleyi*) or browsers (*A. blackbergi*; 0.000063). Species preferring open or moderately open habitats have qualitatively, but not significantly, larger variance (0.000087 and 0.000074, respectively) than those from closed forests (0.000062; Bartlett p = 0.25).

Table 2
Summary strontium isotope data for each taxon at each site both including and excluding outliers.

Site	Species	N	^{87}Sr/^{86}Sr (mean ± 1 SD)	N[a]	^{87}Sr/^{86}Sr (mean ± 1 SD)[a]
Thomas Farm	*Archaeohippus blackbergi*	11	0.70849 ± 0.000063		
	Parahippus leonensis	12	0.70852 ± 0.000080	11	0.70854 ± 0.000051
Love Bone Bed	*Cormohipparion ingenuum*	10	0.70875 ± 0.000090		
	Cormohipparion plicatile	10	0.70870 ± 0.00011		
	Gomphotherium sp.	10	0.70879 ± 0.000076		
	Nannippus westoni	9	0.70869 ± 0.00023	8	0.70876 ± 0.000094
	Neohipparion trampasense	9	0.70873 ± 0.000053		
	Protohippus gidleyi	10	0.70877 ± 0.000060		
	Tapirus webbi	8	0.70911 ± 0.00016		

[a] Statistical outlier for taxon excluded.

Table 3
Comparison of taxa with differing diets and habitats at Love Bone Bed. Tapirs drive significant differences among groups.

Type of comparison	Category	Taxa included	N[a]	Median and mean $^{87}Sr/^{86}Sr \pm 1\,SD^a$	N[b]	Median and mean $^{87}Sr/^{86}Sr \pm 1\,SD^b$
Diet	Browser	*Gomphotherium, T. webbi*	18	0.70885, 0.70894 ± 0.00020	10	0.70882, 0.70879 ± 0.000076
	Mixed feeder	*C. ingenuum, C. plicatile*	20	0.70873, 0.70873 ± 0.000098	20	0.70873, 0.70873 ± 0.000098
	Grazer	*Nannippus westoni, Neohipparion trampasense, P. gidleyi*	27	0.70875, 0.70875 ± 0.000069	27	0.70875, 0.70875 ± 0.000069
				$\chi^2 = 16.37$, df = 2, p = 0.0003		$\chi^2 = 4.33$, df = 2, p = 0.11
Habitat	Closed forest	*Gomphotherium, T. webbi*	18	0.70885, 0.70894 ± 0.00020	10	0.70882, 0.70879 ± 0.000076
	Relatively open	*C. ingenuum, P. gidleyi*	20	0.70875, 0.70876 ± 0.000074	20	0.70875, 0.70876 ± 0.000074
	Open	*C. plicatile, Nannippus westoni, Neohipparion trampasense*	27	0.70872, 0.70873 ± 0.000087	27	0.70872, 0.70873 ± 0.000087
				$\chi^2 = 16.78$, df = 2, p = 0.0002		$\chi^2 = 4.86$, df = 2, p = 0.088

[a] Including tapirs.
[b] Excluding tapirs.

4. Discussion

We anticipated that grazers and larger-bodied species would have higher and more variable $^{87}Sr/^{86}Sr$, reflecting a higher degree of mobility across a larger array of geologies, than browsers and smaller-bodied taxa. Unexpectedly, we did not find any differences in $^{87}Sr/^{86}Sr$ among co-occurring equids nor did we detect relationships between $^{87}Sr/^{86}Sr$ and habitat type or body mass. However, variance differs significantly among equids with differing diets. Additionally, *Tapirus webbi*, a presumed dedicated browser, has elevated $^{87}Sr/^{86}Sr$ compared to all other taxa at Love Bone Bed. Excepting tapirs, all analyzed specimens have strontium isotope ratios that are generally consistent with limestone (ca. 0.707–0.709; McArthur et al., 2001). Yet, with the exception of the two outliers (one from Thomas Farm and one from Love Bone Bed), none of the sampled individuals have $^{87}Sr/^{86}Sr$ compatible with that expected for Eocene limestone (the bedrock at both sites) and the two sites differ isotopically despite being on the same bedrock (Fig. 4). Measured strontium isotope ratios are likely too low to reflect foraging on Appalachian sediments (ca. 0.7103–0.7633; Fig. 2; Hoppe et al., 1999; Samson et al., 1995; van Breemen and Dallmeyer, 1984). Instead, most individuals have $^{87}Sr/^{86}Sr$ that resemble Miocene seawater (Fig. 4).

There are several potential explanations for our results. First, the isotopic composition of enamel may have been influenced by diagenesis. Second, taxa may have foraged on relatively young sediments deposited during the Late Oligocene/Early Miocene (at Thomas Farm) or mid-Miocene (at Love Bone Bed). Lastly, $^{87}Sr/^{86}Sr$ of vegetation consumed by equids may have been impacted by marine-derived strontium via precipitation, groundwater, or sea spray.

Diagenesis is unlikely due to the naturally resistant characteristics of enamel to post-depositional alteration (Stack, 1955). Additionally, biogenic carbon and oxygen isotopes have been found in specimens at both sites (Feranec and MacFadden, 2006; Moran, 2014). Furthermore, diagenesis would presumably have had a relatively uniform influence on all specimens within each site. The occurrence of isotopic variability within and among co-occurring taxa (particularly for Love Bone Bed specimens) suggests specimens have not been systematically altered.

It is possible that elevated $^{87}Sr/^{86}Sr$ reflects foraging on younger sediment. Florida is relatively flat; its current elevation ranges from 0 to 105 m above sea level. Paleogeographic reconstructions suggest that higher elevations in Northern Florida remained above sea level from the earliest Miocene to recent (Markwick, 2007; Missimer and Ginsburg, 1998), while lower areas were likely inundated with seawater. Although fossils at both localities are preserved in Eocene limestone, the sites may have once been covered by thin layers of younger sediments that were deposited during sea level highs. Major sea level fluctuations occurred throughout the Miocene. Most notably, a high stand around 19 Ma that was ca. 100 m above modern sea level (Haq et al., 1987; Missimer, 2002) would have flooded both Thomas Farm (ca. 18 mamsl) and Love Bone Bed (48 mamsl; Missimer, 2002).

Although subsequent transgressions were much smaller, on the order of 50 mamsl ca. 13.5 Ma and ~20 mamsl ca. 9 Ma, the region surrounding Love Bone Bed was likely periodically inundated (Fig. 1b; Haq et al., 1987; Missimer, 2002). Reworked Miocene clays and sands are found throughout northern Florida and often fill sinkholes or stream channels, such as those at Thomas Farm and Love Bone Bed. These sediments provide additional evidence that currently exposed bedrock was once covered by younger material (Scott, 1988). Additionally, Miocene sediments are exposed just to the east of both fossil sites (Fig. 1). Variable exposure of different-aged sediments could help explain why Thomas Farm and Love Bone Bed are isotopically distinct. Under this scenario, most individuals would have foraged predominantly on a thin layer of young sediments blanketing the fossil localities, or exposed to the east, while the two site outliers would have foraged on older exposed bedrock (Fig. 5a).

However, this scenario is based on several assumptions that weaken its plausibility. First, the relative isotopic consistency among specimens at each fossil site would either require that Miocene sediment was isotopically homogenous or that its coverage was relatively uniform when sampled taxa were alive. The influx of Miocene siliciclastic sediment derived from the Appalachians was not compositionally homogenous (Missimer and Maliva, 2017). Progressive amounts of quartz and clay were transported into Florida from the mid-Miocene to the Pliocene. Moreover, the minimal presence of reworked Miocene clays and sands at Thomas Farm (Scott, 1988; Pratt, 1990) along with a relatively shallow river at Love Bone Bed (Webb et al., 1981) suggest any Miocene sediment cover was thin and likely discontinuous. Second, this scenario would require that individuals selectively foraged on young sediment. Eocene-aged sediments are currently exposed at higher elevations to the south and west of our fossil sites (Fig. 1). Based on our knowledge of Cenozoic sea-level fluctuations, local Eocene sediment would have also been exposed at the time when Thomas Farm and Love Bone Bed fauna were alive. It seems improbable that both browsing and grazing species foraged exclusively on Miocene sediment amidst a region of exposed Eocene bedrock.

Finally, it is possible that vegetation consumed by herbivores was influenced by marine-derived strontium (Fig. 5b). Both Thomas Farm and Love Bone Bed were located on the windward coast of Florida during site deposition (Fig. 1) and, therefore, were presumably exposed to marine-derived strontium either through precipitation, sea spray, or potentially marine-influenced groundwater. Precipitation seems unlikely for several reasons. Although marine-derived strontium has previously been observed in precipitation ca. 70–160 km inland from the ocean (Andersson et al., 1990; Raiber et al., 2009), strontium concentrations in rainfall tend to be quite low (Capo et al., 1998). Considering northern Florida is underlain by readily weatherable, and strontium-rich, carbonate bedrock, any influence of precipitation on bioavailable strontium would likely be negligible (Bern et al., 2005). Saline groundwater is also unlikely. Ocean water can infiltrate groundwater systems, forming a brackish lens within shallow aquifers;
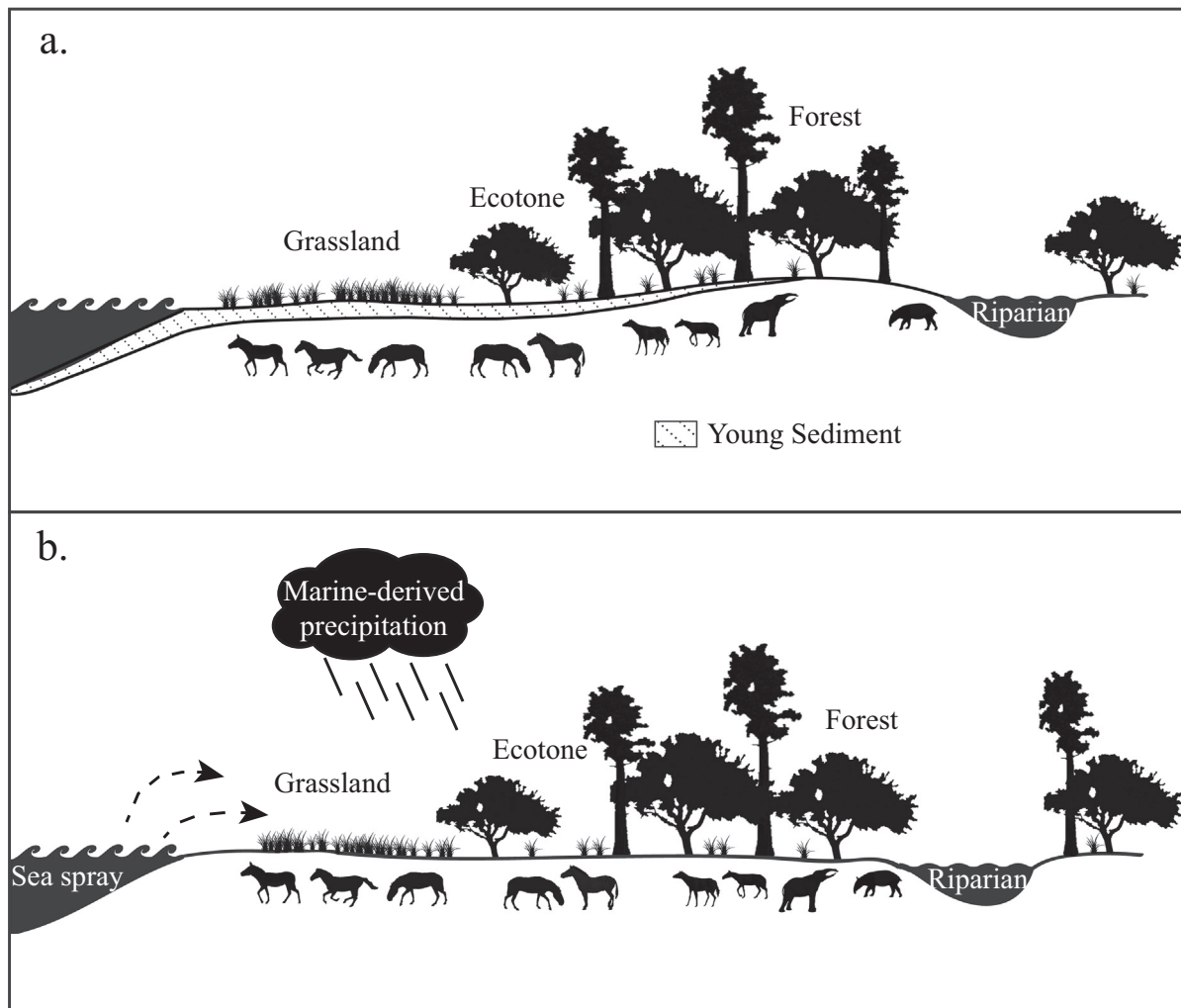
Fig. 5. Possible scenarios that could explain elevated ^{87}Sr/^{86}Sr (0.7083–0.7090) at Love Bone Bed: (a) foraging on Miocene-aged sediments; (b) influence of marine-derived strontium via precipitation or sea spray.

however, saline lenses in modern northcentral Florida generally occur ca. 255–407 m below sea level (Williams and Kuniansky, 2016), which is considerably deeper than the rooting depth for most vegetation in the region (~5 m; Canadell et al., 1996). Conditions were likely similar during the Miocene.

Foraging closer to the coast on vegetation regularly exposed to sea spray may be more plausible. During the Miocene, the Floridian coastline was much further inland than its present-day position (Fig. 1; Markwick, 2007). Although coastline reconstructions are approximate, they suggest that both Thomas Farm and Love Bone Bed were close to the shoreline when fossils accumulated. The aquatic faunal assemblage at Love Bone Bed is dominated by freshwater taxa, but remains from marine and estuarine vertebrates, including several species of bony fish, sharks, and a sea cow, are also present (Webb et al., 1981). If, indeed, both sites were near the coast, then it may be reasonable to attribute the observed ^{87}Sr/^{86}Sr to sea spray (Fig. 5b). Under this scenario, the two statistical outliers with lower ^{87}Sr/^{86}Sr presumably would have foraged further inland, where there was less of an influence of marine-derived strontium.

In summary, there are several possible scenarios that could explain elevated strontium isotope ratios for herbivores in Miocene Florida. Individuals may have foraged on young marine sediments that were deposited during sea level high stands or they may have foraged close to the coast and consumed vegetation that was influenced by marine-derived strontium. Additional studies that explore strontium isoscapes

in modern coastal settings across a diversity of geologies and climatic regimes are needed to further disentangle these scenarios. Regardless, neither of these scenarios supports our original predictions that equid species with larger bodies or grazing adaptations moved more than those with smaller bodies or browsing adaptations. Comparable and relatively homogenous isotope data among taxa are inconsistent with horses foraging across a diversity of sediments or geologies. Instead, our results suggest that all equid taxa, regardless of diet, habitat, or body size, foraged relatively close to the shoreline and, with the exception of two individuals, did not forage on older bedrock further inland.

A lack of evidence for large scale movement may reflect locally abundant resources or movement predominately along the Floridian coast, perhaps as a result of a small geographic home range restricted by rising sea levels. Modern feral horses that inhabit islands and beaches along the east coast of North America or southern France may be reasonable analogues (Duncan, 1992; Rubenstein, 1981; Seliskar, 2003; Zervanos and Keiper, 1998).

Our strontium isotope data do not support a previous suggestion that *Neohipparion* migrated seasonally (Hulbert, 1982). They more closely align with predictions of localized movement for *Parahippus* (Hulbert, 1984) and an early Miocene equid from Germany (Tütken and Vennemann, 2009). Although additional work is warranted, our results do not support the idea that grazing adaptations and increased body size were accompanied by increased mobility, even during the peak radiation of equids.

4.1. Why are tapirs isotopically distinct?

Strontium isotope data for *Tapirus webbi* are considerably higher than other taxa at Love Bone Bed (Fig. 4). Based on what we know about the foraging behavior and evolutionary history of tapirs, it is improbable that individuals moved seasonally or traveled long distances to forage. Instead, tapirs may have had access to a unique strontium source, most likely due to their semi-aquatic (fluvial) habit and consumption of aquatic plants. Distinct ^{87}Sr/^{86}Sr has been observed for terrestrial versus aquatic or semi-aquatic taxa in other settings (Hamilton, 2018; Hedman et al., 2009; Maurer et al., 2012; Sillen et al., 1998). The river channel at Love Bone Bed is filled with Miocene siliciclastics (Webb et al., 1981), which presumably have higher and more variable ^{87}Sr/^{86}Sr than local limestone. Therefore, river water, as well as aquatic and riparian plants growing in and adjacent to the river channel at Love Bone Bed, may have been isotopically distinct from other available vegetation (Curtis Jr and Stueber, 1973; Hamilton, 2018). Although all fauna at Love Bone Bed likely had access to the river, drinking water contributes nominally to ^{87}Sr/^{86}Sr in animal tissues (Lewis et al., 2017). Tapirs are the only taxon expected to have regularly consumed aquatic vegetation. Thus, the river at Love Bone Bed should have impacted tapirs more than other co-occurring taxa that primarily foraged on terrestrial vegetation (Fig. 5). Slightly elevated ^{87}Sr/^{86}Sr for gomphotheres (the only other browser sampled at Love Bone Bed), as well as larger variance for mixed feeders, may reflect drinking water, infrequent feeding on aquatic plants, or a small contribution of river water to vegetation growing in a riparian forest corridor (Hamilton, 2018; Sillen et al., 1998; Lewis et al., 2017).

5. Conclusions

Here, we provide the first test of the hypothesis that morphological and dietary adaptations for grazing in open habitats resulted in increased mobility. We had anticipated that strontium isotope ratios in tooth enamel would elucidate differences in mobility among co-occurring equids and other large-bodied herbivores in Miocene Florida with varying body masses and morphological adaptations. Surprisingly, the majority of individuals have higher ^{87}Sr/^{86}Sr than expected for local Eocene bedrock and co-occurring taxa are statistically indistinguishable. Tapirs are an exception. Elevated ^{87}Sr/^{86}Sr for this group most likely reflects consumption of aquatic vegetation growing in the river bed at Love Bone Bed.

Our data suggest that Miocene equids in Florida were relatively sedentary. While these results are broadly consistent with what researchers have previously suggested for Miocene taxa (Hulbert, 1982; Tütken and Vennemann, 2009) they are in stark contrast to Pleistocene equids from the same region (Hoppe and Koch, 2007). Analysis of Late Miocene and Pliocene equids from Florida could prove useful for establishing when horses became more mobile in the region. Additional studies in modern settings will also greatly enhance our ability to use strontium isotopes as a paleoecological tool.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.11.036.

Acknowledgements

References

Åberg, G., 1995. The use of natural strontium isotopes as tracers in envitonental studies. Water Air Soil Pollut. 79, 309–322. https://doi.org/10.1007/BF01100444.

Abreu, V.S., Anderson, J.B., 1998. Glacial eustasy during the Cenozoic: sequence stratigraphic implications. Am. Assoc. Pet. Geol. Bull. 82, 1385–1400. https://doi.org/10.1306/1D9BCA89-172D-11D7-8645000102C1865D.

Alberdi, M.T., Prado, J.L., Ortiz-Jaureguizar, E., 1995. Patterns of body size changes in fossil and living Equini (Perissodactyla). Biol. J. Linn. Soc. 54, 349–370. https://doi.org/10.1111/j.1095-8312.1995.tb01042.x.

Anderson, D.P., Forester, J.D., Turner, M.G., Frair, J.L., Merrill, E.H., Fortin, D., Mao, J.S., Boyce, M.S., 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. Landsc. Ecol. 20, 257–271. https://doi.org/10.1007/s10980-005-0062-8.

Andersson, P., Löfvendahl, R., Åberg, G., 1990. Major element chemistry, δ²H, δ¹⁸O and ^{87}Sr/^{86}Sr in a snow profile across central Scandinavia. Atmos. Environ. Part A 24, 2601–2608. https://doi.org/10.1016/0960-1686(90)90138-D.

Banner, J.L., 2004. Radiogenic isotopes: systematics and applications to earth surface processes and chemical stratigraphy. Earth Sci. Rev. 65, 141–194. https://doi.org/10.1016/S0012-8252(03)00086-2.

Bataille, C.P., Bowen, G.J., 2012. Mapping ^{87}Sr/^{86}Sr variations in bedrock and water for large scale provenance studies. Chem. Geol. 304–305, 39–52. https://doi.org/10.1016/j.chemgeo.2012.01.028.

Baumann, E.J., Crowley, B.E., 2015. Stable isotopes reveal ecological differences amongst now-extinct proboscideans from the Cincinnati region, USA. Boreas 44, 240–254. https://doi.org/10.1111/bor.12091.

Bentley, R.A., 2006. Strontium isotopes from the Earth to the archeological skeleton: a review. J. Archaeol. Method Theory 13, 135–187. https://doi.org/10.1007/s10816-006-9009-x.

Bern, C.R., Townsend, A.R., Farmer, G.L., 2005. Unexpected dominance of parent-material strontium in a tropical forest on highly weathered soils. Ecology 86, 626–632. https://doi.org/10.1890/03-0766.

Boettcher, S.S., Milliken, K.L., 1994. Mesozoic-Cenozoic unroofing of the Southern Appalachian Basin: apatite fission track evidence from Middle Pennsylvanian sandstones. J. Geol. 102, 655–668. https://doi.org/10.1086/629702.

Britton, K., Grimes, V., Dau, J., Richards, M.P., 2009. Reconstructing faunal migrations using intra-tooth sampling and strontium and oxygen isotope analyses: a case study of modern caribou (*Rangifer tarandus granti*). J. Archaeol. Sci. 36, 1163–1172. https://doi.org/10.1016/j.jas.2009.01.003.

Britton, K., Grimes, V., Niven, L., Steele, T.E., McPherron, S., Soressi, M., Kelly, T.E., Jaubert, J., Hublin, J.J., Richards, M.P., 2011. Strontium isotope evidence for migration in late Pleistocene *Rangifer*: implications for Neanderthal hunting strategies at the Middle Palaeolithic site of Jonzac, France. J. Hum. Evol. 61, 176–185. https://doi.org/10.1016/j.jhevol.2011.03.004.

Bryant, D.J., Froelich, P.N., Showers, W.J., Genna, B.J., 1996. Biologic and climatic signals in the oxygen isotopic composition of Eocene-Oligocene equid enamel phosphate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 126, 75–89. https://doi.org/10.1016/S0031-0182(96)00071-5.

Canadell, A.J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E., 1996. Maximum roothing depth of vegetation types at the global scale. Oecologia 108, 583–595. https://doi.org/10.1007/BF00329030.

Capo, R.C., Stewart, B.W., Chadwick, O.A., 1998. Strontium isotopes as tracers of ecosystem processes: theory and methods. Geoderma 82, 197–225. https://doi.org/10.1016/S0016-7061(97)00102-X.

Cederlund, G., 1983. Home range dynamics and habitat selection by roe deer in a boreal area in Central Sweden. Acta Theriol. (Warsz.) 28, 443–460.

Cederlund, G., Sand, H., 1994. Home-range size in relation to age and sex in moose. J. Mammal. 75, 1005–1012. https://doi.org/10.2307/1382483.

Chadwick, O.A., Derry, L.A., Bern, C.R., Vitousek, P.M., 2009. Changing sources of strontium to soils and ecosystems across the Hawaiian Islands. Chem. Geol. 267, 64–76. https://doi.org/10.1016/j.chemgeo.2009.01.009.

Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G.E., Streich, W.J., 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. Oecologia 136, 14–27. https://doi.org/10.1007/s00442-003-1254-z.

Copeland, S.R., Sponheimer, M., de Ruiter, D.J., Lee-Thorp, J.A., Codron, D., le Roux, P.J., Grimes, V., Richards, M.P., 2011. Strontium isotope evidence for landscape use by early hominins. Nature 474, 76–78. https://doi.org/10.1038/nature10269.

Crowley, B.E., Castro, I., Goodman, S.M., Soarimalala, V., 2018. Isotopic evidence for niche partitioning and the influence of anthropogenic forest loss and disturbance on the diet and mobility of endemic and introduced rodents in the Central Highlands of Madagascar. Sci. Nat. 105, 44.

Curtis Jr., J.B., Stueber, A.M., 1973. ^{87}Sr/^{86}Sr ratios and total strontium concentrations in surface waters of the Scioto river drainage basin, Ohio. Ohio J. Sci. 73, 166–175.

Damuth, J., MacFadden, B.J., 1990. Body Size in Mammalian Paleobiology: Estimation and Biological Impacts. Cambridge University Press.

DeSantis, L.R.G., MacFadden, B., 2007. Identifying forested environments in deep time using fossil tapirs: evidence from evolutionary morphology and stable isotopes. Cour. Forschungsinst. Senck. 147–157.

Duncan, P., 1992. Horses and Grasses: The Nutritional Ecology of Equids and Their

Impact on the Camargue, first ed. Springer Publishing Company, New York, USA.

English, N.B., Betancourt, J.L., Dean, J.S., Quade, J., 2001. Strontium isotopes reveal distant sources of architectural timber in Chaco Canyon, New Mexico. Proc. Natl. Acad. Sci. U. S. A. 98, 11891–11896. https://doi.org/10.1073/pnas.211305498.

Evans, J., Montgomery, J., Wildman, G., Boulton, N., 2010. Spatial variations in biosphere $^{87}Sr/^{86}Sr$ in Britain. J. Geol. Soc. Lond. 167, 1–4. https://doi.org/10.1144/0016-76492009-090.SPECIAL.

Feh, C., 2005. Relationships and communication in socially natural horse herds. In: Mills, D.S., McDonnell, S.M. (Eds.), The Domestic Horse: The Origins, Development and Management of Its Behaviour. Cambridge University Press, pp. 83–93.

Feranec, R.S., MacFadden, B.J., 2006. Isotopic discrimination of resource partitioning among ungulates in C_3-dominated communities from the Miocene of Florida and California. Paleobiology 32, 191–205. https://doi.org/10.1666/05006.1.

Foerster, C.R., Vaughan, C., 2002. Home range, habitat use, and activity of Baird's tapir in Costa Rica. Biotropica 34, 423–437. https://doi.org/10.1111/j.1744-7429.2002.tb00556.x.

Fox, D.L., Fisher, D.C., 2004. Dietary reconstruction of Miocene *Gomphotherium* (Mammalia, Proboscidea) from the Great Plains region, USA, based on the carbon isotope composition of tusk and molar enamel. Palaeogeogr. Palaeoclimatol. Palaeoecol. 206, 311–335. https://doi.org/10.1016/j.palaeo.2004.01.010.

Fraser, D., Theodor, J.M., 2013. Ungulate diets reveal patterns of grassland evolution in North America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 369, 409–421. https://doi.org/10.1016/j.palaeo.2012.11.006.

Gallen, S.F., Wegmann, K.W., Delwayne, R., 2013. Miocene rejuvenation of topographic relief in the southern Appalachians. GSA Today 23, 4–10. https://doi.org/10.1130/GSATG163A.1.

García, M.J., Medici, E.P., Naranjo, E.J., Novarino, W., Leonardo, R.S., 2012. Distribution, habitat and adaptability of the genus *Tapirus*. Integr. Zool. 7, 346–355. https://doi.org/10.1111/j.1749-4877.2012.00317.x.

Gigleux, C., Grimes, V., Tütken, T., Knecht, R., Britton, K., 2017. Reconstructing caribou seasonal biogeography in Little Ice Age (late Holocene) Western Alaska using intra-tooth strontium and oxygen isotope analysis. J. Archaeol. Sci. Rep. 0–1. https://doi.org/10.1016/j.jasrep.2017.10.043.

Graustein, W.C., Armstrong, R.L., 1983. The use of Strontium-87/Strontium-86 ratios to measure atmospheric transport into forested watersheds. Science 219, 289–292. https://doi.org/10.1126/science.219.4582.289.

Hamilton, M.I., 2018. Reconstructing landscape use patterns using strontium isotope ratios. https://digitalrepository.unm.edu/anth_etds/144/.

Haq, B.U., Hardenbol, J.A.N., Vail, P.R., 1987. Chronology of fluctuating sea levels since the Triassic. Science 235, 1156–1167. https://doi.org/10.1126/science.235.4793.1156.

Hartman, G., Richards, M., 2014. Mapping and defining sources of variability in bioavailable strontium isotope ratios in the Eastern Mediterranean. Geochim. Cosmochim. Acta 126, 250–264. https://doi.org/10.1016/j.gca.2013.11.015.

Hedman, K.M., Curry, B.B., Johnson, T.M., Fullagar, P.D., Emerson, T.E., 2009. Variation in strontium isotope ratios of archaeological fauna in the Midwestern United States: a preliminary study. J. Archaeol. Sci. 36, 64–73. https://doi.org/10.1016/j.jas.2008.07.009.

Hoppe, K.A., 2004. Late Pleistocene mammoth herd structure, migration patterns, and Clovis hunting strategies inferred from isotopic analyses of multiple death assemblages. Paleobiology 30, 129–145. https://doi.org/10.1666/0094-8373(2004)030<0129:LPMHSM>2.0.CO;2.

Hoppe, K.A., Koch, P.L., 2007. Reconstructing the migration patterns of late Pleistocene mammals from northern Florida, USA. Quat. Res. 68, 347–352. https://doi.org/10.1016/j.yqres.2007.08.001.

Hoppe, K.A., Koch, P.L., Carlson, R.W., Webb, S.D., 1999. Using strontium isotope ratios tracking mammoths and mastodons: reconstruction of migratory behavior using strontium isotope ratios. Geology 27, 439–442. https://doi.org/10.1130/0091-7613(1999)027<0439.

Hoppe, K.A., Koch, P.L., Furutani, T.T., 2003. Assessing the preservation of biogenic strontium in fossil bones and tooth enamel. Int. J. Osteoarchaeol. 13, 20–28. https://doi.org/10.1002/oa.663.

Hoppe, K.A., Stover, S.M., Pascoe, J.R., Amundson, R., 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 206, 355–365. https://doi.org/10.1016/j.palaeo.2004.01.012.

Hulbert, R.C., 1982. Population dynamics of the three-toed horse *Neohipparion* from the Late Miocene of Florida. Paleobiology 8, 159–167. https://doi.org/10.1017/S0094837300004504.

Hulbert, R.C., 1984. Paleoecology and population dynamics of the Early Miocene (Hemingfordian) horse *Parahippus leonensis* from the Thomas Farm Site, Florida. J. Vertebr. 4, 547–558. https://doi.org/10.1080/02724634.1984.10012030.

Hulbert, R.C., 1987. Late Neogene *Neohipparion* (Mammalia, Equidae) from the Gulf Coastal Plain of Florida and Texas. J. Paleontol. 61, 809–830. https://doi.org/10.1017/S0022336000029152.

Hulbert, R.C., 1993. Late Miocene *Nannippus* (Mammalia: Perissodactyla) from Florida, with a description of the smallest hipparionine horse. J. Vertebr. Paleontol. 13, 350–366. https://doi.org/10.1080/02724634.1993.10011515.

Hulbert, R.C., 2005. Late Miocene *Tapirus* (Mammalia, Perissodactyla) from Florida, with description of a new species, Tapirus webbi. Bull. Fla. Mus. Nat. Hist. 45, 465–494.

Jacques, C.N., Jenks, J.A., Klaver, R.W., 2009. Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of Western South Dakota. J. Mammal. 90, 433–441. https://doi.org/10.1644/07-MAMM-A-395.1.

Kaseda, Y., Ogawa, H., Khalil, A.M., 1997. Causes of natal dispersal and emigration and their effects on harem formation in Misaki feral horses. Equine Vet. J. 29, 262–266. https://doi.org/10.1111/j.2042-3306.1997.tb03121.x.

Koch, P.L., Heisinger, J., Moss, C., Carlson, R.W., Fogel, M.L., Behrensmeyer, A.K., 1995. Isotopic tracking of change in diet and habitat use in African elephants. Science 267, 1340–1343.

Larramendi, A., 2016. Shoulder height, body mass and shape of proboscideans. Acta Palaeontol. Pol. 61, 537–574. https://doi.org/10.4202/app.00136.2014.

Latorre, C., Quade, J., McIntosh, W.C., 1997. The expansion of C_4 grasses and global change in the late Miocene: stable isotope evidence from the Americas. Earth Planet. Sci. Lett. 146, 83–96. https://doi.org/10.1016/S0012-821X(96)00231-2.

Lewis, A.R., Marchant, D.R., Ashworth, A.C., Hemming, S.R., Machlus, M.L., 2007. Major middle Miocene global climate change: evidence from East Antarctica and the Transantarctic Mountains. Geol. Soc. Am. Bull. 119, 1449. https://doi.org/10.1130/B26134.

Lewis, J., Pike, A.W.G., Coath, C.D., Evershed, R.P., 2017. Strontium concentration, radiogenic ($^{87}Sr/^{86}Sr$) and stable ($\delta^{88}Sr$) strontium isotope systematics in a controlled feeding study. STAR Sci. Technol. Archaeol. Res. 3, 53–65. https://doi.org/10.1080/20548923.2017.1303124.

MacFadden, B.J., 1986. Fossil horses from "Eohippus" (*Hyracotherium*) to Equus: scaling, Cope's Law, and the evolution of body size. Paleobiology 12, 355–369.

MacFadden, B.J., 1992. Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equidae. Cambridge University Press, Cambridge.

MacFadden, B.J., 2005. Fossil horses—evidence for evolution. Science 307, 1728–1730. https://doi.org/10.1126/science.1105458.

MacFadden, B.J., Cerling, T.E., 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10 million-year sequence from the Neogene of Florida. J. Vertebr. Paleontol. 16, 103–115.

MacFadden, B.J., Dobie, J.L., 1998. Late Miocene three-toed horse *Protohippus* (Mammalia, Equidae) from Southern Alabama. J. Paleontol. 72, 149–152. https://doi.org/10.1017/S0022336000024082.

MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. Science 283, 824–827. https://doi.org/10.1126/science.283.5403.824.

Maguire, K.C., Stigall, A.L., 2008. Paleobiogeography of Miocene Equinae of North America: a phylogenetic biogeographic analysis of the relative roles of climate, vicariance, and dispersal. Palaeogeogr. Palaeoclimatol. Palaeoecol. 267, 175–184. https://doi.org/10.1016/j.palaeo.2008.06.014.

Mallinson, D.J., Compton, J.S., Snyder, S.W., Hodell, D.A., 1994. Strontium isotopes and Miocene sequence stratigraphy across the northeast Florida Platform. J. Sediment. Res. B Stratigr. Glob. Stud. 3. https://doi.org/10.1306/D4267FD2-2B26-11D7-8648000102C1865D.

Markwick, P.J., 2007. The Paleogeographic and paleoclimatic significance of climate proxies for data-model comparisons. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.), Deep-time Perspectives on Climate Change: Marrying the Signal From Computer Models and Biological Proxies. The Micropalaeontological Society Special Publications The Geological Society, London, pp. 251–312.

Maurer, A.F., Galer, S.J.G., Knipper, C., Beierlein, L., Nunn, E.V., Peters, D., Tütken, T., Alt, K.W., Schöne, B.R., 2012. Bioavailable $^{87}Sr/^{86}Sr$ in different environmental samples - effects of anthropogenic contamination and implications for isoscapes in past migration studies. Sci. Total Environ. 433, 216–229. https://doi.org/10.1016/j.scitotenv.2012.06.046.

McArthur, J.M., Howarth, R.J., Bailey, T.R., 2001. Strontium isotope stratigraphy: LOWESS Version 3: best fit to the marine Sr-isotope curve for 0–509 Ma and accompanying look-up table for deriving numerical age. J. Geol. 109, 155–170. https://doi.org/10.1086/319243.

Medici, E.P., 2010. Assessing the Viability of Lowland Tapir Populations in a Fragmented Landscape. https://doi.org/10.1111/j.1749-4877.2012.00318.x. (Ph.D. Diss.).

Mihlbachler, M.C., Rivals, F., Solounias, N., Semprebon, G.M., 2011. Dietary change and evolution of horses in North America. Science 331, 1178–1181. https://doi.org/10.1126/science.1196166.

Miller, O.L., Kip, D., Fernandez, D.P., Cerling, T.E., Bowling, D.R., 2014. Evaluating the use of strontium isotopes in tree rings to record the isotopic signal of dust deposited on the Wasatch Mountains. Appl. Geochem. 50, 53–65. https://doi.org/10.1016/j.apgeochem.2014.08.004.

Missimer, T.M., 2001. Siliciclastic facies belt formation and the Late Oligocene to Middle Miocene partial drowning of the southern Florida Platform. Am. Assoc. Pet. Geol. Bull. 85, 229–238. https://doi.org/10.1306/8626CF55-173B-11D7-8645000102C1865D.

Missimer, T.M., 2002. Late Oligocene to Pliocene Evolution of the Central Portion of the South Florida Platform: Mixing of Siliciclastic and Carbonate Sediments. Florida Geological Survey, Tallahassee, FL.

Missimer, T.M., Ginsburg, R.N., 1998. Homogenized carbonates and siliciclastics in the Tertiary of Southwest Florida. Gulf Coast Assoc. Geol. Soc. Trans. 48, 263–274.

Missimer, T.M., Maliva, R.G., 2017. Late Miocene fluvial sediment transport from the southern Appalachian Mountains to southern Florida: an example of an old mountain belt sediment production surge. Sedimentology 64, 1846–1870. https://doi.org/10.1111/sed.12377.

Moran, S., 2014. Stable isotope paleoecology on of Early Miocene equid (*Parahippus leonensis*) from the Thomas Farm site, Gilchrist County, Florida. http://ufdcimages.uflib.ufl.edu/UF/E0/04/68/85/00001/MORAN_S.pdf.

Ofstad, E.G., Herfindal, I., Solberg, E.J., Sæther, B.-E., 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. Proc. R. Soc. B Biol. Sci. 283, 20161234. https://doi.org/10.1098/rspb.2016.1234.

O'Sullivan, J., 2005. Population dynamics of *Archaeohippus blackbergi* (Mammalia; Equidae) from the Miocene Thomas Farm fossil site of Florida. Bull. Fla. Mus. Nat. Hist. 45, 449–463.

O'Sullivan, J., 2008. Evolution of the proximal third phalanx in Oligocene-Miocene equids, and the utility of phalangeal indices in phylogeny reconstruction. Mamm.

Evol. Morphol. 159–165. https://doi.org/10.1007/978-1-4020-6997-0_8.

Passey, B.H., Cerling, T.E., Perkins, M.E., Voorhies, M.R., Harris, J.M., Tucker, S.T., 2002. Environmental change in the Great Plains: an isotopic record from fossil horses. J. Geol. 110, 123–140. https://doi.org/10.1086/338280.

Pellegrini, M., Donahue, R.E., Carolyn, C., Evans, J., Lee-Thorp, J., Montgomery, J., Mussi, M., 2008. Faunal migration in late-glacial central Italy: implications for human resource exploitation. Rapid Commun. Mass Spectrom. 22, 1714–1726. https://doi.org/10.1002/rcm.3521.

Pratt, A.E., 1989. Taphonomy of the microvertebrate fauna from the early Miocene Thomas Farm locality, Florida (U.S.A.). Palaeogeogr. Palaeoclimatol. Palaeoecol. 76, 125–151. https://doi.org/10.1016/0031-0182(89)90107-7.

Pratt, A.E., 1990. Taphonomy of the large vertebrate fauna from the Thomas Farm locality (Miocene, Hemingfordian), Gilchrist County, Florida. Biol. Sci. 35, 35–130.

Price, D.T., Connor, M., Parsen, J.D., 1985. Bone chemistry and the reconstruction of diet: strontium discrimination in white-tailed deer. J. Archaeol. Sci. 12, 419–442. https://doi.org/10.1016/0305-4403(85)90003-2.

Quade, J., Chivas, A.R., McCulloch, M.T., 1995. Strontium and carbon isotope tracers and the origins of soil carbonate in South Australia and Victoria. Palaeogeogr. Palaeoclimatol. Palaeoecol. 113, 103–117. https://doi.org/10.1016/0031-0182(95)00065-T.

Radloff, F.G.T., Mucina, L., Bond, W.J., Le Roux, P.J., 2010. Strontium isotope analyses of large herbivore habitat use in the Cape Fynbos region of South Africa. Oecologia 164, 567–578. https://doi.org/10.1007/s00442-010-1731-0.

Raiber, M., Webb, J.A., Bennetts, D.A., 2009. Strontium isotopes as tracers to delineate aquifer interactions and the influence of rainfall in the basalt plains of southeastern Australia. J. Hydrol. 367, 188–199. https://doi.org/10.1016/j.jhydrol.2008.12.020.

Ransom, J.I., Kaczensky, P., 2016. Wild Equids: Ecology, Management, and Conservation. Johns Hopkins University Press, Baltimore.

Retallack, G.J., 1997. Neogene expansion of the North American Prairie. SEMP Soc. Sediment. Geol. 12, 380–390. https://doi.org/10.2307/3515337.

Reynolds, A.C., Quade, J., Betancourt, J.L., 2012. Strontium isotopes and nutrient sourcing in a semi-arid woodland. Geoderma 189–190, 574–584. https://doi.org/10.1016/j.geoderma.2012.06.029.

Rubenstein, D.I., 1981. Behavioral ecology of island feral horses. Equine Vet. J. 13, 27–34.

Samson, S.D., Coler, D.G., Speer, J.A., 1995. Geochemical and Nd-Sr-Pb isotopic composition of Alleghanian granites of the southern Appalachians: origin, tectonic setting, and source characterization. Earth Planet. Sci. Lett. 134, 359–376. https://doi.org/10.1016/0012-821X(95)00124-U.

Schulting, R., Richards, M.P., Pouncett, J., Naqqi Manco, B., Freid, E., Ostapkowicz, J., 2018. Absence of Saharan dust influence on the strontium isotope ratios on modern trees from the Bahamas and Turks and Caicos Islands. Quat. Res. 89, 394–412.

Scott, T.M., 1988. The Lithostratigraphy of the Hawthorn Group (Miocene) of Florida. Florida Geol. Surv.

Scott, T.M., 1992. A Geological Overview of Florida. Florida Geol. Surv., pp. 99–178.

Scott, T.M., 1997. The geology of Florida. In: Randazzo, A.F., Jones, D.S. (Eds.), The Geology of Florida. University Press of Florida, Gainsville, FL, pp. 57–68.

Scott, T.M., Campbell, K.M., Rupert, F.R., Arthur, J.D., Missimer, T.M., Lloyd, J.M., Yon, J.W., Duncan, J.G., 2001. Geologic Map of the State of Florida. Florida Geol. Surv.

Seliskar, D.M., 2003. The response of *Ammophila breviligulata* and *Spartina patens* (Poaceae) to grazing by feral horses on a dynamic mid-Atlantic barrier island. Am. J.

Bot. 90, 1038–1044.

Semprebon, G.M., Rivals, F., Solounias, N., Hulbert, R.C., 2016. Paleodietary reconstruction of fossil horses from the Eocene through Pleistocene of North America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 442, 110–127. https://doi.org/10.1016/j.palaeo.2015.11.004.

Sillen, A., Hall, G., Richardson, S., Armstrong, R., 1998. $^{87}Sr/^{86}Sr$ ratios in modern and fossil food-webs of the Sterkfontian Valley: implications for early hominid habitat preference. Geochim. Cosmochim. Acta 62, 2463–2478.

Singer, F.J., Zeigenfuss, L.C., Spicer, L., 2001. Patch extinction disease, size, and movement in rapid extinction of Bighorn Sheep. Conserv. Biol. 15, 1347–1354. https://doi.org/10.1046/j.1523-1739.2001.99488.x.

Snoeck, C., 2014. Impact of strontium sea spray effect on the isotopic ratio ($^{87}Sr/^{86}Sr$) of plants in coastal Ireland. Q. Newsl. 37–39.

Sparrowe, R.D., Springer, P.F., 1970. Seasonal activity patterns of white-tailed deer in eastern South Dakota. J. Wildl. Manag. 34, 420–431.

Stack, M.V., 1955. The chemical nature of the organic matrix of bone, dentin, and enamel. Ann. N. Y. Acad. Sci. 60, 585–595. https://doi.org/10.1111/j.1749-6632.1955.tb40053.x.

Stewart, B.W., Capo, R.C., Chadwick, O.A., 2001. Effects of rainfall on weathering rate, base cation provenance, and Sr isotope composition of Hawaiian soils. Geochim. Cosmochim. Acta 65, 1087–1099.

Strömberg, C.A.E., 2004. Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 239–275. https://doi.org/10.1016/j.palaeo.2003.09.028.

Tütken, T., Vennemann, T., 2009. Stable isotope ecology of Miocene large mammals from Sandelzhausen, southern Germany. Paläontol. Z. 83, 207–226. https://doi.org/10.1007/s12542-009-0011-y.

United States Geological Survey, 2016. Ground water Atlas of the United States: Alabama, Florida, Georgia, South Carolina: HA730-G. https://pubs.usgs.gov/ha/ha730/ch_g/G-text1, Accessed date: 23 March 2018.

van Breemen, O., Dallmeyer, R.D., 1984. The scale of Sr isotopic diffusion during postmetamorphic cooling of gneisses in the Inner Piedmont of Georgia, southern Appalachians. Earth Planet. Sci. Lett. 68, 141–150. https://doi.org/10.1016/0012-821X(84)90146-8.

Vogel, J.C., Englington, B., Auret, J.M., 1990. Isotope fingerprints in elephat bone and ivory. J. Colloid Interface Sci. 374, 685–689. https://doi.org/10.1016/0021-9797(80)90501-9.

Webb, S.D., MacFadden, B.J., Baskin, J.A., 1981. Geology and paleontology of the Love Bone Bed from the late Miocene of Florida. Am. J. Sci. https://doi.org/10.2475/ajs.281.5.513.

Widga, C., Walker, J.D., Stockli, L.D., 2010. Middle Holocene bison diet and mobility in the eastern Great Plains (USA) based on $\delta^{13}C$, $\delta^{18}O$, and $^{87}Sr/^{86}Sr$ analyses of tooth enamel carbonate. Quat. Res. 73, 449–463. https://doi.org/10.1016/j.yqres.2009.12.001.

Williams, L.J., Kuniansky, E.L., 2016. Revised hydrogeologic framework of the Floridan aquifer system in Florida and parts of Georgia, Alabama, and South Carolina. In: U.S. Geological Survey Professional Paper 1807, https://doi.org/10.3133/pp1807.

Zervanos, S., Keiper, R., 1998. Forage utilization and resource partitioning by Assateague Island feral ponies. J. Pennsylvania Acad. Sci. 72, 11–16.