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Physical properties, geochemistry, and diagenesis of xenarthran teeth: Prospects for interpreting the paleoecology of extinct species

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ABSTRACT

Xenarthrans (also called edentates) include modern armadillos, sloths, and numerous extinct clades (e.g., glyptodonts and ground sloths) that lack enamel on their teeth. In contrast to mammals with tooth enamel, which oftentimes preserves geochemical proxy data, paleoecological interpretations of xenarthrans based on geochemical analyses (e.g. stable isotopes) have been limited. Xenarthrans have evolved a distinctive outer dentine layer that seems to be the functional analog of enamel. Here we evaluate the physical and chemical properties of xenarthran outer dentine to understand its potential use for investigating geochemical proxies. The mean hardness (*H*) of xenarthran outer dentine (3.8) is significantly less than that of enamel (5.7) and there is no difference in *H* between the two main groups, i.e., armadillos (cingulates) and pilosans (sloths). Although the mean *H* does not change significantly during diagenesis, its range increases, indicating the replacement of secondary minerals (e.g., carbonate representing the lower range) within the original hydroxylapatite mineral lattice. Results of FT-IR analyses indicate that xenarthran outer dentine has a high degree of organics and H_2O, similar to normal dentine, and its crystallinity index and carbonate content are affected in varying degrees during diagenesis. Thus, although xenarthran outer dentine functions like enamel, it retains compositional similarities to dentine.

The uptake of rare earth elements (REE) was analyzed from three late Neogene localities in Florida as a proxy for understanding diagenesis in xenarthrans as compared to other mammals. Relative to modern specimens, the fossils have about two orders of magnitude higher concentrations of REE. Uptake rates vary significantly among different dental tissues, i.e., bone>dentine (both inner and outer)>enamel. REE concentrations of fossil vertebrate specimens vary significantly between different localities. The REE Index (ratio of outer dentine/bone or enamel/bone for a given specimen) is proposed here to evaluate relative diagenesis in xenarthrans and other mammals, respectively. Other (non-xenarthran) mammals tend to have a lower REE Index, interpreted to represent less diagenesis. Nevertheless, many xenarthrans likewise have a low REE Index relative to other mammals at the same locality, indicating a similar degree of diagenesis. While the REE Index will likely be a reliable indicator of relative diagenesis in xenarthrans, the outer dentine provides challenges to the ultimate goal of interpreting proxy geochemical (e.g., stable isotope) data from these extinct mammals.

1. Introduction

1.1. Background, statement of problem, purpose, and goals

Bone is characteristically porous and thus is particularly prone to diagenesis in the fossil record. Because of this specter of diagenesis, some early studies (e.g., Schoeninger and DeNiro, 1982) asserted that fossil bones could not be used to reconstruct original stable isotope signatures (although see opposing point of view in Sullivan and Kreuger, 1981). Thus, investigators turned their attention to other vertebrate skeletal hard tissues (i.e., tooth enamel) characteristically preserved in the fossil record. Because of the mostly mineral (>95% hydroxylapatite) composition of enamel and dense crystal structure, it was proposed that tooth enamel is relatively resistant to diagenesis and thus provides a more acceptable method for interpreting stable isotope signatures preserved in fossils (e.g., Lee-Thorp and van der Merwe, 1989). This proposal was confirmed by both theoretical models and empirical data (e.g. Wang and Cerling, 1994). Once tooth enamel became accepted as preserving relatively unaltered stable isotope data, the potential applications greatly increased and these

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geochemical proxies are widely used for interpretations of vertebrate paleoecology.

Despite a rich fossil record during the Cenozoic, the xenarthrans, including the armadillos (Order Cingulata) and sloths (Order Pilosa, *sensu* McKenna and Bell, 1997) in the New World, are conspicuously absent in stable isotope studies of extinct species. The reason for this absence is understandable because xenarthrans characteristically lack enamel on their teeth (e.g., Vizcaíno, 2009). Thus it is not clear if and where one should be able to find relatively unaltered stable isotope signatures. As xenarthrans represent a significant component of terrestrial faunas in the ancient New World over the past 35 million - yrs, their absence in stable isotope studies impedes a more comprehensive understanding of vertebrate paleoecology, particularly at the community level.

The purpose of this paper is two-fold, i.e., to better understand the: (1) physical properties and geochemistry of modern and extinct xenarthran teeth, particularly the outer dentine; and (2) diagenesis of fossil xenarthran teeth as compared to other mammals that have enamel. Several different analytical methods and techniques are used, including hardness tests, Fourier transform infrared spectroscopy, and rare earth elemental analyses. With regard to diagenesis, the fundamental question to be answered is, as follows: is the functional analog of enamel, i.e., the outer dentine of xenarthrans, a good source for proxy paleoecological data archived in teeth? This will be answered primarily through analysis of the uptake of rare earth elements (REE) in vertebrate skeletons during early diagenesis. Although relatively new to vertebrate paleoecology, the application of REE analyses is rapidly gaining acceptance as a tool to assess temporally mixed assemblages, diagenesis, and thus meaningful interpretations of biologically relevant data preserved in the fossil record.

1.2. Histology and geochemistry of xenarthran teeth: what we know so far

> "Edentates owe their rather inappropriate name to the occasional absence and constant degeneracy of their teeth." (Simpson, 1932, p. 1)

The Magnorder Xenarthra (Cope, 1889; used interchangeably with Edentata, *sensu* McKenna and Bell, 1997) consists of a complex array of taxa that today include two principal clades, i.e., the Order Cingulata, including armadillos, and the Order Pilosa, including the anteaters and tree sloths. To this adaptive diversity can be added a vast array of extinct xenarthrans ranging from the late Paleocene (McKenna and Bell, 1997), including such curious creatures as the armored glyptodonts and giant ground sloths, both of which flourished along with several other extinct clades before their eventual extinction at the end of the Pleistocene. In addition to a unique morphology of the vertebral articulations (giving rise to "Xenarthra," meaning foreign [or strange] articulation), and with the exception of the Eocene armadillo *Utaetus buccatus* from Argentina (Simpson, 1932) and some primitive ground sloths from South America (Flower and Lydekker, 1891), other xenarthrans that have teeth lack enamel. These traits are defining characteristics of the Xenarthra, i.e., by either lacking teeth (anteaters) or enamel (all other taxa). For the remainder of this discussion, we will be dealing with both the cingulates and pilosans, although with regard to the latter, we will no longer be concerned with the toothless anteaters (Family Myrmecophagidae).

As noted by Simpson (1932) in the quote at the beginning of this section, xenarthrans have highly derived dentitions in which the anterior incisors and canines are either lost or so highly modified, that along with the cheek teeth, dental positional homologies are uncertain. Xenarthran teeth are characteristically ever-growing (hypselodont), which is widely asserted to be an adaptation that compensates for the loss of enamel (e.g., Bargo et al., 2006; Vizcaíno, 2009). Ever since the classic studies of Owen (1840–1845), it has been recognized that along with hypsodonty, xenarthrans modify their tooth histology and evolve an outer layer of hard dentine that appears to be the functional analog of enamel in other mammals. A principal function of outer dentine, therefore, is to provide a relatively harder dental tissue that is more resistant to wear and, in some clades, also forms a vertical (or differential) shearing surface alongside softer inner dentine that facilitates trituration (Janis and Fortelius, 1988). The nomenclature, actual histology, and phylogenetic distribution of the dentines in xenarthrans are exceedingly complex (Vizcaíno, 2009). Dentine is a hard dental tissue characteristically with about 70 to 75% mineral hydroxyapatite, 18–21% organics (mostly collagen), and 4 to 12% water (Carlson, 1990). Unlike bone, dentine has a more dense, compact matrix that lacks the characteristic porosity observed in a trabecular, or spongy, bone. Unaltered biogenic hydroxylapatite, also referred to as bioapatite, is part of the apatite mineral group (each with slightly different minor elements) with a basic chemical formula of $Ca_5(PO4)_6OH_2$ and is referred to as the specific mineral dahlite. The apatite group has a relative hardness of 5 on the Mohs scale (Mason and Berry, 1968). The crystallites in dentine are small like in bone, average 100–200 Å in length, and are considerably smaller than in enamel, which average 1600–10,000 Å in length (Carlson, 1990). Original bioapatite characteristically undergoes chemical loss, replacement, and recrystallization during diagenesis, as will be discussed below.

The various kinds of dentine present in xenarthrans are both complex and there is little consensus about how various histological names have been used in the literature. The inner dentine in xenarthrans, similar in location to other mammals, characteristically contains tubules that radiate from the center of the tooth adjacent to the pulp to the outer dentine. This inner dentine has been either reported to have the same general composition and density as "normal" dentine, or it can be hypermineralized, i. e, contains a greater percentage of hydroxylapatite (Carlson, 1990). This inner dentine is most characteristically called orthodentine, in reference to the parallel and radial alignment of tubules and has been reported in a wide array of xenarthrans. Numerous authors also describe a type of inner dentine that is vascularized, called vasodentine (e.g., Owen, 1840–1845; Bödecker, 1926; Hoffstetter, 1958; Boyde, 1971), which occurs in modern xenarthrans such as the tree sloth *Bradypus*, armadillo *Dasypus*, and in extinct forms including the giant ground sloth *Megatherium* (Boyde, 1971). In one of the most comprehensive syntheses of xenarthran dental histology, Ferigolo (1985) considers vasodentine as a special type of orthodentine. The outer dentine in most edentates is widely considered a special, hypermineralized case of regular dentine that has been variously referred to as hard, or outer dentine, or sometimes durodentine, e.g., the latter in the extant armadillo *Euphractes* (Smith and Redford, 1990) and the Pliocene aquatic sloth from Peru (de Muizon et al., 2004).

In terms of dental histology and nomenclature, glyptodonts (Family Glyptodontidae) represent a special case within xenarthrans (Gillette and Ray, 1981; Ferigolo, 1985). The dentines in glyptodont teeth are usually referred to as osteodentine consisting of softer and harder varieties, and like other xenarthrans, located respectively on the inside and outside of the individual tooth. However, unlike other xenarthrans, glyptodonts also have harder osteodentine located within the inner softer dentine. This network of hard and soft osteodentines therefore functions to decrease tooth wear, particularly when feeding on abrasive foods. This observation along with their ever-growing teeth has led to interpretations that glyptodonts are either being savanna (Webb, 1978), or perhaps aquatic, grazers (Gillette and Ray, 1981).

With the exception of glyptodonts, the standard xenarthran pattern of dental histology consists of softer inner dentine and harder outer dentine. Likewise it should be noted that Vizcaíno et al. (1998) reported the presence of a central island of resistant dentine that acts

as a functional analog of the ectoloph in the giant pampatheriid armadillo *Vassallia*. Cement (or cementum) characteristically surrounds the outer dentine in xenarthrans (although it is thinner in glyptodonts; Ferigolo, 1985) as it also does in many other herbivorous mammals (Bödecker, 1926). Although a primary function of cement is as a connective tissue to seat the tooth in the alveolus, it likewise further provides resistance to abrasion, and this dental tissue is particularly well-developed in most grazers, e.g., bison, horses, notoungulates, and mammoths (Janis and Fortelius, 1988; MacFadden, 1997).

In the discussion that follows, we will mostly restrict our terminology of xenarthran dental histology to inner (or "regular" or "normal") dentine and outer dentine, as compared in other mammals to inner dentine and enamel. In so doing, we simply use the location of the particular tissue within xenarthrans and therefore circumvent the confused nomenclature that has developed in the literature.

1.3. Previous geochemical studies of fossil xenarthran teeth

Realizing their importance within mammalian herbivore guilds, several recent studies have started to use teeth from xenarthrans to analyze their paleodiets using dental microwear (Green, 2009a,b), and of relevance to the goals of this paper, a few papers dealing with stable isotopes. Kohn et al. (2005) analyzed the orthodentine of the giant Pleistocene ground sloth *Megalonyx jeffersoni* from the Camelot local fauna (l.f.), Pleistocene of South Carolina. *Megalonyx jeffersoni* has carbon isotope ($\delta^{13}C$) values of ~−14‰, similar to those of some of the other sympatric herbivores interpreted to inhabit woodlands or forests, including the deer *Odocoileus virginianus* and tapir *Tapirus veronsis*. The $\delta^{13}C$ values for *M. jeffersoni* were interpreted to indicate a browser, similar to previous suggestions for the diet of this extinct species consisting of leaves, twigs, and nuts (Kurtén and Anderson, 1980). With regard to the oxygen isotopes, Kohn et al. (2005) noted that the variation in $\delta^{18}O$ taken from 5 samples was considerably lower than for the other species analyzed in the Camelot l.f. and this modulation in the former could represent diagenesis specific to the orthodentine of *M. jeffersoni*. Given these isotope results, Kohn et al. (2005) understandably expressed caution with interpreting isotopic data from *M. jeffersoni*.

In another study, Ruez (2005) analyzed both the inner dentine and functional analog of enamel, outer dentine, in the xenarthran *Paramylodon harlani* from the Pleistocene of Texas. He found that this giant ground sloth had $\delta^{13}C$ values of ~−4‰ and these were similar in both kinds of dentine. In comparison with what is known of the expected $\delta^{13}C$ values for tooth enamel of browsing versus grazing herbivores, Ruez (2005) asserted that *P. harlani* was a mixed feeder, albeit on the C_4 grazing end of the spectrum. He subsequently concluded (p. 329) that: "Although this study does suggest the validity of geochemical analyses of sloth teeth in dietary determinations, caution must be used. Extent of diagenesis must be evaluated at least in part by also considering sample from animals of known diet, taken from the same locality." This latter sentence brings up another fundamental challenge with comparing xenarthrans to other mammals within a given fauna: while we understand that the plant to tooth enrichment factor (e^*) for medium to large ungulates is about 14‰ (Koch et al., 1992; Cerling and Harris, 1999), we know nothing about this corresponding value in xenarthrans. Furthermore, with the significantly different (lower) metabolism of xenarthrans relative to other placental mammals (McNab, 1985), inferring a similar e^* is, depending upon how you look at it, either an unsupportable or tenuous proposition.

1.4. Diagenesis of vertebrate fossils and rare earth elements (REE)

In the context of Vertebrate Paleontology, diagenesis is any and all of the physical and chemical changes that occur during the process of fossilization. Diagenesis begins soon after death and potentially continues for as long as the fossil is part of the lithosphere. As paleontologists seek to reconstruct the past, frequently using chemical data such as stable isotopes, we must be concerned with how diagenesis affects the original biological signals preserved in the fossils. Of relevance to paleontology and archaeology, an excellent series of articles based on the Fifth International Bone Diagenesis Workshop, held in Capetown, South Africa in 2005, was presented in a recently published volume (Lee-Thorp and Sealy, 2008). Because of its relevance to the goals of this paper, our discussions of REEs will focus on how to understand diagenesis of fossil vertebrates.

REEs occur naturally in very low concentrations in living tissues, i.e., in the ppb to low ppm range. Soon after death, however, vertebrate bones and teeth can take up REEs rapidly by adsorption and substitution as they begin diagenesis (Henderson et al., 1983; Reynard et al., 1999). Trueman et al. (2004) found that in as little as 15 yr, vertebrate skeletons at the soil interface at Amboseli National Park in Kenya can increase their REE concentrations by 100 to 1000%. Although few studies have calibrated this process, the uptake of REEs can occur during early diagenesis for 10,000 to 30,000 yr (Patrick et al., 1991). Thereafter during the process of fossilization and diagenesis, this uptake decreases significantly and, so far as is known, this system is closed to further significant uptake in REE. Tütken et al. (2008) recently found that the uptake of REEs is inversely proportional to the loss of organics in vertebrate skeletal tissues, particularly bone. Many workers have used the patterns and relative concentrations of REE incorporated into vertebrate skeletal tissues as an indicator for diagenesis, including in marine (Reynard et al., 1999; Trueman et al., 2003; Lécuyer et al., 2004; Labs-Hochstein and MacFadden, 2006; Tütken et al., 2008) and terrestrial fossils (Trueman et al., 2004; Metzger et al., 2004; MacFadden and Hulbert, 2009), and from archaeological sites (Wright and Schwarcz, 1996; Nielsen-Marsh and Hedges, 2000; Turner-Walker and Jans, 2008). In a recent study, Koenig et al. (2009); also see Brady et al., 2008) used laser ablation-inductively coupled plasma mass spectrometry to map the microscopic gradients of REE uptake in Cretaceous bones, thus confirming intrabone trends in REE uptake reported previously (Trueman et al., 2006).

2. Materials and methods

Specimens analyzed during this study are mostly housed within the Vertebrate Paleontology (UF), Mammalogy (UF-M), or Zooarchaeology (UF-ZA) collection at the Florida Museum of Natural History (http://www.flmnh.ufl.edu). Specific locality and age data associated with these specimens are contained in the supplementary tables. Statistics were done with XLSTAT-Pro 7.5® (www.xlstat.com) using both parametric (*T*-test, ANOVA) and non-parametric (Mann Whitney U, Kruskal Wallis) equivalent tests for significance. In the text if the probability levels of the comparable statistical tests on the same sample are the same, they are reported as a single value (e.g., $p<0.0001$); if different, then the p values are reported separately.

2.1. Comparative hardness of xenarthran outer dentine and mammalian enamel

Hardness (H) is defined as the resistance of a mineral to scratching (Mason and Berry, 1968). In the current context of tooth hydroxylapatite, the relative hardness using the widely accepted Mohs' scale is considered a proxy for understanding relative durability, i.e., the resistance to wear during mastication. One of our goals in this paper is to determine if the outer hard dentine is harder or softer than the enamel in most mammals and if the process of fossilization affects relative hardness. We do this by determining the relative hardness using Mohs' scale (1–10) for 80 teeth from different specimens, with a sampling design as follows: xenarthran (40) and other mammals (40); with these teeth further representing modern specimens (40)

and fossils (40), the latter including Miocene (12), Pliocene (14), and Pleistocene (14; Supplementary Table 1). *H* was simply determined by using either a basic physical geology mineral hardness scratch test kit or a set of commercially available hardness picks. Because of possible anisotrophy, scratch tests were made in multiple directions along the specimen and then averaged to produce the final reported values. Fractional values (e.g., 4.8) between integers (e.g., 4 and 5) were estimated qualitatively by the relative ease of scratching a specimen between hardness values, or represent the mean values calculated from multiple determinations on a single specimen.

2.2. Fourier transform infrared spectroscopy (FT-IR), crystallinity, and carbonate content

In order to analyze FT-IR, ~1 mg samples were drilled with a low-speed Foredom drill from either the inner or outer dentine of six representative extinct (*Holmesina*, *Glyptotherium*, and *Megalonyx* from the Plio-Pleistocene of Florida, and *Thalassocnus* from the Mio-Pliocene of Peru), modern (*Bradypus* from Panama) xenarthran teeth, and proboscidean enamel (internal UF lab standard MEme). Standard KBr pellets were prepared using the method discussed in MacFadden et al. (2004). Infrared spectra were obtained between 4000 and 400 cm^{-1} on a FT-IR Nicolet 20 SXB Bench in the Major Analytical Instrument Center in the University of Florida Material Science and Engineering Department (http://maic.msc.ufl.edu/facilities.htm). Interferences from KBr were cancelled by subtracting a standard KBr spectrum from the sample spectra. The crystalline structure of our samples was determined by calculating the crystallinity index (CI) from the extent of phosphate peak splitting at 565–605 cm^{-1} in an FT-IR spectrum. Apatites with larger, more ordered crystals show greater separation of these peaks and a higher CI (Shemesh, 1990; Wright and Schwarcz, 1996). An estimate of the carbonate content is given by the absorption ratio of the height of the carbonate peak at 1428 cm^{-1} to the height of the phosphate peak at 1042 cm^{-1} of the FT-IR spectrum (Featherstone et al., 1984; Lee-Thorp and van der Merwe, 1991; Stuart-Williams et al., 1996; Wright and Schwarcz, 1996).

2.3. Rare earth elements (REE)

In order to understand the diagenesis of xenarthrans and other mammals, 25 modern and 125 fossil specimens were analyzed for their REE signatures, i.e., concentrations. These specimens were taken from either the outer dentine, inner dentine, enamel, or bone from xenarthrans (including cingulates and pilosans) or non-xenarthran mammals (Supplemetary Table 2). The fossil xenarthrans were compared to non-xenarthran taxa from three Neogene fossil localities in Florida, including the late Pliocene Inglis 1A and Haile 7G, and early Pleistocene Leisey 1A localities (Morgan, 2005). About 5–10 mg of cortical bone, dentine, or enamel were removed from each fossil specimen using a Dremel™ rotary drill. In order to remove organic matter and other potential contaminants and insoluable residues, these specimen powders were weighted, placed in clean Savillex™ vials, and dissolved with 2 ml of 8 M HNO_3 overnight on a hot plate. Samples were then opened and dried on the hotplate. 0.8N HNO_3 spiked with 8 ppb Re was added to the samples by weight to re-dissolve the dry residue and bring the final dilution to about 2000×. The final dilution for trace element analyses was determined by weight for each sample. REE analyses were performed on a Thermo Finnigan ELEMENT2 Inductively Coupled Plasma Mass Spectrometer (ICPMS) in the University of Florida Department of Geological Sciences (http://www.geology.ufl.edu/icpmslab.html). All measurements were performed in medium resolution with Re used as internal standards. Quantification of results was done by external calibration using a set of gravimetrically prepared REE standards and SRM 1400 (bone ash) standard. The analytical error on the reported REE concentrations is better than 5% based on long-term analyses of USGS standards. Fourteen of the 15 REE (excluding Pm [Promethium], $Z=61$) are analyzed during this procedure. In order to compensate for the Oddo–Harkins even–odd abundance effect, the REE concentrations reported here are normalized to PAAS (Post-Archean Australian Shale; McLennan, 1989), and indicated by REE_N. In this study the elements La ($Z=57$) to Nd ($Z=60$) are considered light REE (LREE), Sm ($Z=62$) to Tb ($Z=65$) middle REE, and Dy ($Z=66$) to Lu ($Z=71$) heavy REE (HREE; Trueman, 1999, although Dy and Tb are reversed here).

3. Results, interpretations, and discussion

3.1. Comparative hardness of xenarthran outer dentine and mammalian enamel

We analyzed the hardness (*H*) of xenarthran outer dentine relative to the enamel of other mammals in both extant and fossil taxa as a proxy for understanding the potential for tooth diagenesis in these two subsets. The mineralization of hydroxylapatite is highly conservative (Janis and Fortelius, 1988; Carlson, 1990), although the relative proportions of mineral and organic phases likely affect hardness. Nevertheless, little quantitative data are available that assess the relative hardness resulting from the different compositions of outer hard dentine versus enamel. Our results (Table 1, Fig. 1) indicate several interesting comparisons: (1) as might be predicted because xenarthran outer dentine has less (~70 to 75%) of the mineral phase hydroxylapatite than enamel (>95%), the outer dentine is, in general, significantly softer (mean $H=3.8$) than enamel (mean $H=5.7$). This may be related to the fact that many clades of edentates have evolved ever-growing (hypselodont) dentitions in which teeth continuously mineralize at the root during ontogeny (Janis and Fortelius, 1988; Bargo et al., 2006). In doing so, the hypselodont teeth thereby compensating for the more rapid wear likely in these mammals relative to other placentals. (2) Modern teeth (pooled sample of xenarthrans and other mammals) are significantly harder (mean $H=5.7$) than the fossil sample (mean $H=4.7$). This probably indicates the introduction of common groundwater ions forming minerals such as calcium carbonate ($H=3$; Mason and Berry, 1968) during diagenesis. (3) Within the two main clades of xenarthrans (pooled sample of modern and fossil), there is no significant difference between the hardness of cingulates (i.e., armadillos in our sample) relative to

Table 1
Comparison of hardness (*H*, using Mohs' scale) for modern and fossil xenarthrans and other (non-xenarthran placental) mammals. Abbreviations: sd, standard deviation; max, maximum; min, minimum. Results for parametric (*T*-test) and non-parametric (Mann Whitney U) pair-wise comparisons are expressed as probabilities (*p*) for these respective tests for the groups (subsets) indicated.

Group (subset)	*N*	mean *H*	sd *H*	min *H*	max *H*	*T*-test	Mann Whitney
1. All xenarthrans, modern and fossil	40	3.8	0.80	2.5	6.0		
2. All other mammals, modern and fossil	40	5.7	0.99	3.0	7.0	$p<0.0001$	$p<0.0001$
3. All modern, xenarthrans and other mammals	40	5.7	0.99	3.0	7.0		
4. All fossil, xenarthrans and other mammals	40	4.7	1.31	3.0	7.0	$p<0.001$	$p<0.0001$
5. All cingulates (armadillos)	16	4.0	0.80	3.0	6.0		
6. All pilosans (sloths)	24	3.6	0.78	2.5	5.5	$p=0.120$	$p=0.087$

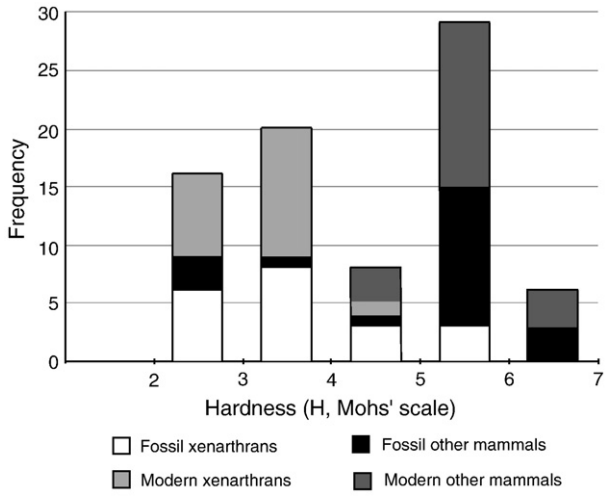

Fig. 1. Histogram of dental hardness measurements (using Moh's scale) for modern and fossil xenarthrans and other (non-xenarthran) mammals (total $N = 80$; Table 1; specimen data are presented in Supplementary Table 1).

pilosans (i.e., sloths in our sample). In summary, as has also been shown in other studies comparing dentine, bone, and enamel (e.g., Wang and Cerling, 1994), our results predict that the softer outer dentine of xenarthrans will be more prone to diagenesis than corresponding enamel of other non-xenarthran mammals.

3.2. General composition, organics, crystallinity, and carbonate content

FT-IR spectral analyses were used to understand differences in the composition of modern and fossil xenarthran inner and outer dentine of selected cingulate and pilosan teeth, as compared to a modern enamel specimen (MEme internal lab standard). Relative to the modern enamel and fossil samples (Fig. 2), both of the dentine types represented by the extant sloth *Bradypus* specimen from Panama have a high degree of organics (mostly consisting of collagen), particularly as represented by the amide I (1660 cm^{-1}) and amide II (1550 cm^{-1}) absorbance bands and to a lesser extent, the amide III (1236 cm^{-1}) band that flanks the CO_3^{2-} band at 1415 cm^{-1}. The increased absorbance between 3000 and 4000 cm^{-1} in *Bradypus* indicates the presence of H_2O, which oftentimes masks, i.e. in modern specimens is superimposed on, the OH^- bands at 3567 cm^{-1} (Shemesh, 1990; Pasteris et al., 2004). Relative to extant *Bradypus*, several fundamental changes in the composition of fossil xenarthran inner and outer dentine are seen in all of the FT-IR spectra of fossil cingulates (*Glyptotherium* and *Holmesina* from Florida) and pilosans (*Thalassocnus* and *Megalonyx*, from respectively Peru and Florida), including the absence of the H_2O and multiple amide bands.

It is already known that dentine has a higher degree of organics (as much as 20%) and water (can range from 4 to 12%) relative to enamel (e.g., Carlson, 1990), but little was known before about how the outer dentine might differ from, or be similar to, these other dental hard tissues. Based on our study the outer dentine of the *Bradypus* specimen is similar in organic composition to that of corresponding inner dentine, and both of these are different from enamel. So, although the hard dentine is a functional analog of enamel, it retains the composition similar to normal dentine. Furthermore, based on the FT-IR spectra for the four fossil xenarthrans, we conclude that during early diagenesis the organics and H_2O are characteristically lost in the fossils, a general observation that is known for other vertebrates (Carlson, 1990), but not reported previously for xenarthrans.

Other chemical and physical properties have been used to assess diagenesis of sedimentary and bioapatites (Shemesh, 1990), in particular carbonate content and crystallinity index (CI), both of which can be calculated from the FT-IR spectra (see Section 2.2) and

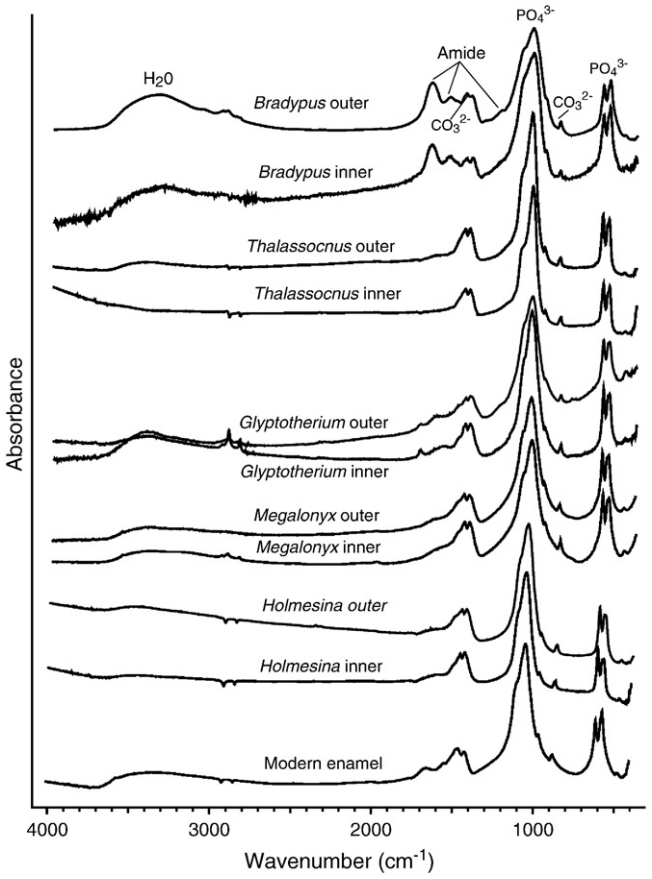

Fig. 2. FT-IR spectra for modern and fossil xenarthran teeth (inner and outer dentine) as compared to an enamel sample. The modern sloth *Bradypus* is from Panama and the enamel was taken from a modern elephant, *Elephas* (MEme; UF internal laboratory standard). The fossil xenarthrans *Glyptotherium*, *Megalonyx*, and *Holmesina* are from the Plio-Pleistocene of Florida, and the aquatic sloth specimen of *Thalassocnus* is from Peru.

have been reported to covary (e.g., Wright and Schwarcz, 1996). Fig. 3 shows our results of these data for the same samples plotted in Fig. 2. With regard to CI, unaltered modern bone samples from other studies have previously been reported to range from 2.8 for mineralized shark centra (MacFadden et al., 2004), to 2.9 to 3.25 (Wright and Schwarcz,

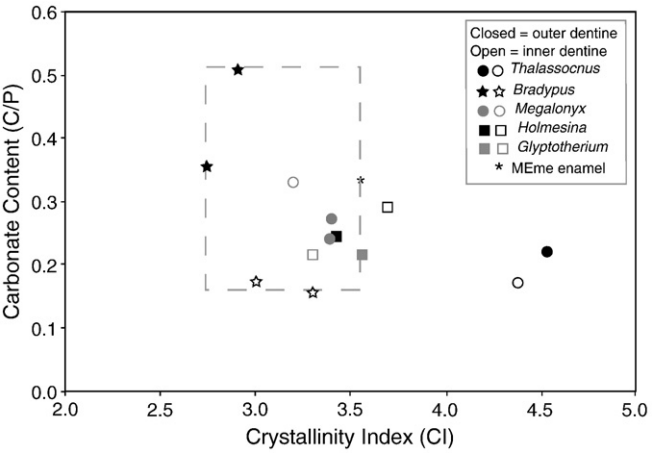

Fig. 3. Plot of crystallinity index (CI) versus carbonate content for modern and fossil xenarthrans, and a modern enamel sample (MEme). The fossil specimens are the same as listed in Fig. 2. The rectangular box with dashed lines near the center of the plot indicates the zone predicted values of unaltered vertebrate skeletal tissues based on previous studies (Shemesh, 1990; Wright and Schwarcz, 1996; MacFadden et al., 2004) and empirical data from modern samples (*Bradypus* and *Elephas* [MEme UF internal laboratory standard]).

1996) for modern bone, to 3.0 for fish debris (bone fragments and scales; Shemesh, 1990). Greater CI values are interpreted to have resulted from recrystallization during diagenesis (Shemesh, 1990; Wright and Schwarcz, 1996; although see caution by Trueman et al., 2008). Although the modern enamel (MEme) is slightly greater (3.5), the CIs of the modern sloth inner and outer dentine range from about 2.8 to 3.2 (Fig. 3), similar to the previous reports of unaltered modern bone. Some fossil samples in Fig. 3, however, fall outside the range of variation of CIs expected for relatively unaltered CIs, i.e., those similar to modern values. One of these, i.e., the fossil armadillo *Holmesina* inner dentine has a CI of 3.7 (although the outer dentine at 3.4 falls within the expected), and the other, the Neogene aquatic sloth, *Thalassocnus* has CIs of ~4.5. These latter values are similar to, for example, highly altered shark vertebrae from the Eocene of Morocco with CIs of 4.5 (MacFadden et al., 2004; Labs-Hochstein and MacFadden, 2006).

At about 4.5 weight%, carbonate (CO_3^{2-}) is the third most abundant inorganic constituent in bioapatites after Ca and phosphate (Francillon-Vieillot et al., 1990). Carbonate content, expressed as C/P ratios in the FT-IR spectra (see Section 2.2), has also been used as a proxy for understanding diagenesis (e.g., Shemesh, 1990) in apatites, and it has been observed that carbonate content is inversely proportional to CI (Wright and Schwarcz, 1996; Labs-Hochstein and MacFadden, 2006). Carbonate content has been reported to range from as high as 0.43 in modern calcified shark centra (Labs-Hochstein and MacFadden, 2006) to as low as 0.24 in unaltered modern bone (Wright and Schwarcz, 1996), thus demonstrating a large range of values. Our data do not show the high degree of inverse correlation between these two variables that has been reported previously in the literature, but several observations are relevant here: (1) the carbonate content of most of our dentine (and enamel) specimens analyzed in Fig. 3 fall within the range reported for modern bone; and (2) outliers include low values for modern *Bradypus* and the Pliocene sloth *Thalassocnus*. While the low values for the extant sloth *Bradypus* are currently difficult to explain, those from *Thalassocnus* are probably related to increased crystallinity, as has been reported previously (e.g., Wright and Schwarcz, 1996).

While the interpretation of CIs as proxies for understanding diagenesis in fossilized bone is open to debate (e.g., Trueman et al., 2008), the results of our analyses provide some insight about CIs and carbonate content in modern and fossil xenarthran dentines: (1) Most specimens fall within the range of expected values previously reported for unaltered modern bone. (2) The aquatic sloth from Peru is highly altered; any consequent interpretations about, for example, stable isotope signatures in specimens such as these should therefore be carefully scrutinized, if not rejected altogether.

3.3. REE uptake rates as a diagenetic proxy

Unlike many trace elements (e.g., Ba, Sr, and Mg) that occur naturally in vertebrate skeletons during life (e.g., Price, 1989; Carlson, 1990), REEs are reported to occur in very low concentrations in these systems (ppb, or less; e.g., Denys et al., 1996; Grandjean and Albarède, 1989; Trueman and Tuross, 2002). Soon after death, however, REEs are rapidly taken up in bones and teeth (e.g., Henderson et al., 1983; Elderfield and Pagett, 1986). Trueman et al. (2004) showed that concentrations of some REEs (such as La) in post mortem bone accumulations in surficial soils in Amboseli National Park, Kenya, can increase by 100 to 1000% within 15 yr.

Given this background we wanted to determine a living baseline control for comparison with our fossil bones and teeth analyzed during this study. As demonstrated in Fig. 4, the 25 modern bone and teeth samples (Supplementary Table 2) have very low concentrations, on the order of ppb, as predicted from previous studies. In contrast, taken as a group ($N=125$) the fossil bone and tooth samples from the three Plio-Pleistocene localities of Florida (Fig. 5) have significantly

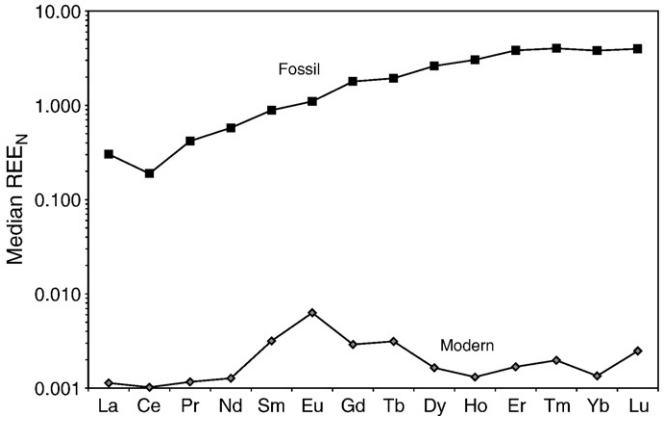

Fig. 4. Plot of median REE_N concentrations for modern mammal specimens ($N=25$) as compared to fossil bone and tooth samples ($N=128$) from the Plio-Pleistocene of Florida. Data from Supplemental Table 2.

greater ($p<0.0001$) concentrations in the parts per thousand range and at least three orders of magnitude greater than seen in the modern specimens. The relatively flat slope of the median REE_N data for the fossil specimens (Fig. 4), and the lack of a significant Ce anomaly (i.e., lower concentration than La and Pr) indicate a primarily continental signal consisting of carbonate-rich pore waters (Trueman, 2007). This pattern is not surprising given the vertebrate faunas and geological content of the three localities studied here. We conclude that relative to modern specimens, there is a significant uptake of REEs during diagenesis of fossils. We assert that this occurs during the early phase of this process, probably within 10 to 30 thousand yr after death (Patrick et al., 1991) and thus the Florida specimens retain a primitive REE signature from the Plio-Pleistocene.

One of our assumptions is that relative rates of REE uptake represent a proxy for understanding the relative degree of diagenesis (e.g., recent study by Koenig et al., 2009). Thus, within a similar sedimentary environment or system the relative REE_N concentrations can represent a proxy for relative diagenesis. Given previous studies of bone versus enamel diagenesis (Dauphin and Williams, 2004) as these relate to stable isotope signatures (e.g., Wang and Cerling, 1994), our prediction was that the former would have significantly higher REE_N concentrations than the latter. With regard to xenarthran

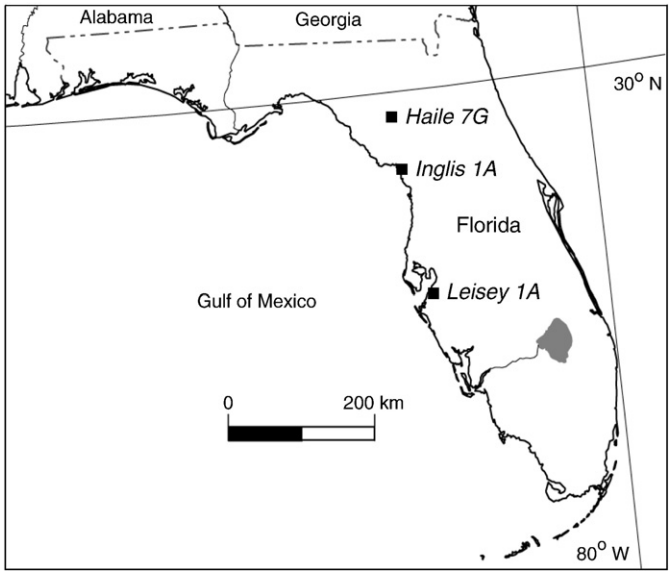

Fig. 5. Map of Plio-Pleistocene fossil localities of Florida from which specimens were analyzed for REEs, i.e., Haile 7G (late Blancan, ca. 2.2 Ma), Inglis 1A (late Blancan, ca. 2.0 Ma), and Leisey 1A (early Irvingtonian, ca. 1.4 Ma; also see Supplemental Table 2).

outer dentine, little has been reported previously concerning the uptake of REEs. Regular dentine was considered similar in its diagenetic uptake to that of bone for Plio-Pleistocene mammals from Florida (MacFadden and Hulbert, 2009), although that conclusion differs from our results presented below. As shown in Fig. 6, a comparison of all available fossil specimens analyzed during this study elucidates relative uptake rates in fossil specimens from the three Plio-Pleistocene fossil sites from Florida. As predicted from previous studies, bone ($n=56$) has significantly higher concentrations ($p<0.0001$) than outer dentine ($n=23$), regular dentine ($n=28$), and enamel ($n=20$) specimens, and conversely, enamel has significantly lower concentrations ($p<0.0001$ [*T*-test]; $p<0.0002$ [Mann Whitney]) than bone, outer dentine, or regular dentine. These two kinds of dentine analyzed here have indistinguishable REE_N concentrations ($p=0.308$ [*T*-test]; $p=0.088$ [Mann Whitney]). As a group the dentines ($n=51$), are significantly lower ($p<0.0001$) in REE_N concentrations than bone and, given that the corresponding data sets are non-normally distributed (Shapiro–Wilk test, $p<0.0001$), they are not significantly different ($p=0.421$ [Mann Whitney]) from enamel ($n=20$).

Another way to look at the REE_N results is for all taxa by locality, i.e., a comparison of the pooled samples of bone, outer dentine, inner dentine, and enamel from Haile 7G, Inglis 1A, and Leisey 1A. As is clear from Fig. 7, The median REE_N concentrations from Inglis are significantly greater ($p<0.0001$) for medians of individual elements by at least an order of magnitude relative to those from either Leisey 1A or Haile 7G. The explanation for the greater REE_N concentrations from Inglis 1A is currently unclear, but may relate to local ancient porewater geochemical conditions at this site relative to the other two localities which have lower REE_N concentrations. Another conclusion of the geographic and/or possible temporal differences in REE uptake at these three localities is that taxonomic and/or paleoecological comparisons are best done within specific sites, thereby removing the additional component of variation seen among Inglis 1A, Haile 7G, and Leisey 1A.

3.4. REE Index

In this paper we propose a "REE Index" as a proxy for understanding relative diagenesis for enamel or bone as normalized to bone for a given specimen. Simply put, the REE Index of a particular fossil specimen equals either REE_N enamel/REE_N bone for non xenarthrans or REE_N outer dentine/REE_N bone for xenarthrans. The rationale is that bone will provide an indication of the maximum diagenesis relative to enamel or outer dentine. We already have seen (Fig. 6) that for our pooled sample from the three Plio-Pleistocene localities in Florida, bone has significantly greater REE_N values relative to either enamel,

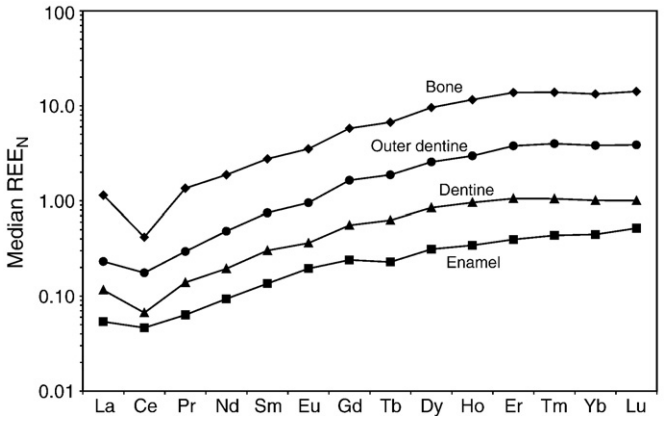

Fig. 6. Plots of median REE_N concentrations for enamel, dentine, outer dentine, and bone for the samples of xenarthrans and other mammals from the Plio-Pleistocene of Florida. Compiled from data presented in Supplemental Table 2.

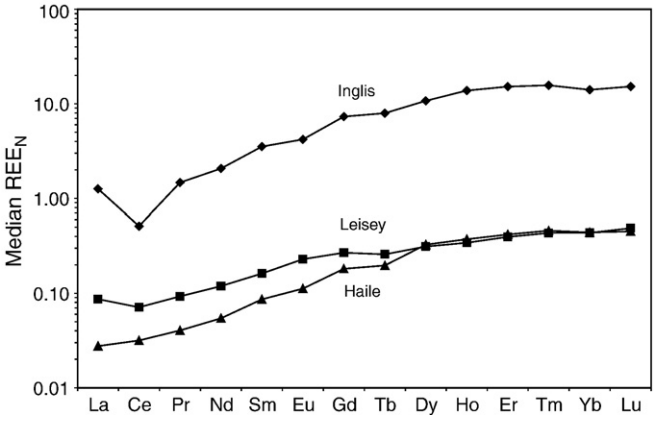

Fig. 7. Plots of median REE_N concentrations for all samples from three localities from the Plio-Pleistocene of Florida (see map in Fig. 4; compiled from data presented in Supplemental Table 2).

inner dentine, or outer dentine. A hypothetical fossil *Equus* specimen with a low REE Index of, e.g., 0.1, indicates that the bone is altered 10× relative to enamel. Conversely, a hypothetical fossil sloth specimen with a REE Index of 0.9 indicates that its outer dentine is almost as altered as the bone. Intuitively, the former case should have relatively less altered associated geochemical proxy data (e.g., stable isotopes), whereas the latter might be considered with more caution. REE Index values greater than 1.0 indicate that either the enamel or outer dentine is more highly altered than the bone of the same specimen. In this case, the associated geochemical proxy data should be carefully scrutinized before these are interpreted for paleobiological or paleoecological purposes, or even rejected altogether.

The REE Index was calculated for 40 enamel/bone and outer dentine/bone pairs from the three Plio-Pleistocene localities analyzed in this study (Fig. 8, Table 2). The mean REE Index of enamel (0.17) is significantly ($p<0.0001$) less than that of outer dentine (0.41), indicating that in general, enamel is less altered via diagenesis. Nevertheless, if one takes into account 1 standard deviation (0.18) greater than the enamel mean (i.e., 0.17 [mean] + 0.18 [standard deviation] = REE Index of 0.35), then with the exception of an extreme outlier (3.76 for an enamel/bone specimen of *Cuvieronius* from Haile 7G), 17 of the 20 enamel/bone pairs fall below this value. We assert that assuming fossil enamel is a good recorder of geochemical proxy (e.g., stable isotope) data, then a corresponding outer dentine/bone sample with a similarly low REE Index will also preserve

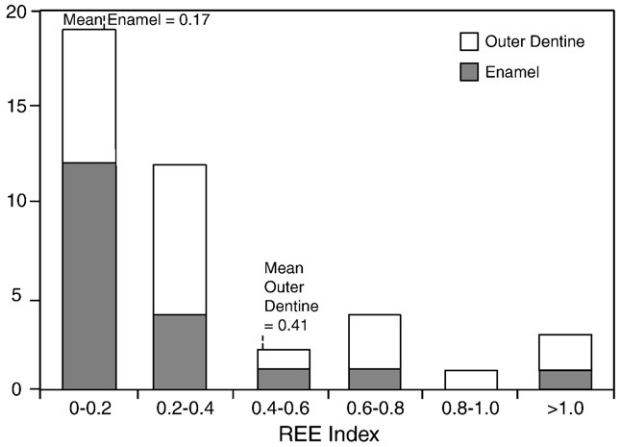

Fig. 8. Histogram showing the distribution of REE Index values for 40 bone/outer dentine or bone/enamel pairs from the three localities from the Plio-Pleistocene of Florida. Note that one specimen of the proboscidean *Cuvieronius* from Haile 7G with a REE Index of 3.76, which is considered an outlier, is included in the >1.0 bin. Data from Supplemental Table 3.

Table 2
Comparison of REE Index for fossil xenarthrans and other (non-xenarthran placental) mammals. Abbreviations: sd, standard deviation; max, maximum REE Index; min, minimum REE Index. Results for parametric (*T*-test, ANOVA) and non-parametric (Mann Whitney, Kruskal Wallis) comparisons are expressed as probabilities (*p*) for these respective tests for the groups (subsets) indicated.

Group (subset)	*N*	mean	sd	min	max	Parametric	Non-parametric
1. All xenarthrans outer dentine	22	0.41	0.36	0.03	1.41		
2. All other mammals enamel	18	0.17	0.18	0.01	0.60[a]	$p<0.0001$	$p<0.0001$
3. All mammals from Haile 7G	8	0.23	0.21	0.01	0.72		
4. All mammals from Inglis 1A	22	0.36	0.32	0.06	1.42		
5. All mammals from Leisey 1A	10	0.22	0.32	0.01	1.00	$p=0.406$	$p=0.068$
6. All cingulates (armadillos) outer dentine	7	0.41	0.25	0.07	0.72		
7. All pilosans (sloths) outer dentine	15	0.41	0.41	0.04	1.42	$p=0.98$	$p=0.70$

[a] One specimen of *Cuvieronius* enamel from Haile 7G, with a REE Index of 3.76, is rejected as an outlier.

biologically meaningful data. Conversely, whether it be enamel or outer dentine samples, those with a high REE Index should be interpreted with caution, if not rejected altogether. For example, two enamel/bone specimens, the peccary *Platygonus* (0.56) and llama *Hemiachenia* (0.60) from Inglis each have a relatively high REE Index (another of the proboscidean *Cuvieronius* from Haile 7G with a REE Index of 3.76 is rejected as an outlier). Likewise, seven outer dentine specimens of the sloths *Eremotherium* (1.42, 0.91), *Paramylodon* (0.73), and armadillos *Holmesina* (0.53) from Inglis, and the sloth *Nothrotheriops* (1.00) and *Holmesina* (0.69) from Leisey 1A, and *Holmesina* (0.72) from Haile 7G have high REE Index values (Supplementary Table 3).

We also considered how diagenetic environments at different localities may have affected the REE Index (see, e.g., Nielsen-Marsh and Hedges, 2000; Trueman, 2007). Using pooled enamel/bone and outer dentine/bone ratios for Haile 7G ($n=8$), Inglis 1A ($n=22$), and Leisey 1A ($n=10$), there are no statistically significant differences ($p=0.406$ ANOVA; $p=0.068$, Kruskal Wallis) among these samples. Likewise we also explored whether cingulate and pilosan outer dentines have different uptake rates that might be reflected in the REE Index. The pooled sample from the three localities indicates no difference (*T*-test $p=0.98$; $p=0.70$ Mann Whitney) between cingulate and pilosan outer dentines. This is perhaps not surprising because our results presented above indicate that hardness is similar in these two orders of xenarthrans.

4. Conclusions, caveats, and recommendations

Xenarthran outer dentine is softer than enamel. It is therefore not surprizing that many xenarthran clades have evolved ever-growing (hypselodont) teeth as a feeding strategy (Vizcaíno, 2009) particularly in extinct clades like glyptodonts (Gillette and Ray, 1981) and some pampatheriid cingulates (Vizcaíno et al., 1998) purported to be on the grazing end of the dietary spectrum. Despite being a functional analog of enamel, outer dentine has a mineralogy and composition similar to regular dentine. The uptake of REEs is an effective means of assessing relative diagenesis in fossil vertebrate skeletal tissues, including bone, enamel, regular dentine, or outer dentine. In general, enamel is less prone to diagenetic uptake of REEs than are dentines, and bone is clearly the most vulnerable to this process. The uptake of REEs during early diagenesis reflects the local pore water geochemistry and REE concentrations can therefore vary greatly by location and age. The REE Index proposed here has the potential to evaluate relative diagenesis rates in fossil mammals with different dental hard tissues. Enamel generally has lower REE Index values than outer dentine, the former indicating less diagenesis. Nevertheless, many specimens of outer dentine have a REE Index value that falls within acceptable limits (<0.35), similar to corresponding enamel samples. Regardless of dental tissue type, geochemical proxy data derived from specimens with high REE Index values (between 0.5 and 1.0, or greater) must be carefully scrutinized before meaningful interpretations about the paleobiology and paleoecology of extinct taxa can be made, if at all.

In addition to characterizing the physical properties and mineralogy of outer dentine, another principal goal of this study was to quantify diagenesis in xenarthrans as compared to enamel, the latter of which is routinely considered to be relatively unaffected by diagenesis. While the results of this study, and the development of the REE Index, represent steps toward resolution to this problem in xenarthrans, we have not yet found a panacea in which we can accept proxy data, e.g., the widespread use of stable isotopes, without further consideration of the timing of this geochemical signal and how it relates to biologically meaningful information. As with all such studies, the use of the REE Index and similar studies of diagenesis will further benefit from other corroborative evidence, e.g., comparisons of $\delta^{18}O$ from the more stable phosphate, as compared to the carbonates phase of hydroxylapatite within the same fossil (e.g., Bryant et al., 1994, 1996; Iacumin et al., 1996), although even this method continues to have its challenges (e.g., Martin et al., 2008; Tütken et al., 2008). Other paleoecological data, such as microwear studies of xenarthran dentine (e.g., Green, 2009a,b), and how stable isotope data for xenarthrans compare with the browser–grazer $\delta^{13}C$ spectrum of other extinct herbivores within the same fauna can elucidate the robustness of proxy geochemical signals interpreted from outer dentine. To our knowledge, this is the first study that evaluates diagenesis in xenarthran teeth, and it is based on data from three late Neogene localities in Florida. How these data and results are generalizable to other localities and the specific xenarthran taxa found there, remains to be demonstrated.

Xenarthrans have undergone a fascinating evolutionary history and paleoecological diversification over most of the Cenozoic and are in many cases dominant representatives in terms of abundance, diversity, and biomass within faunas. It therefore behooves us to endeavor to understand geochemical proxy data archived in their teeth.

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Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2010.02.021.

References

Bargo, S.M., De Iuliis, G., Vizcaíno, S.F., 2006. Hypsodonty in Pleistocene ground sloths. Acta Paleontologica Polonica 51, 53–61.

Bödecker, C.F., 1926. Fundamentals of Dental Histology and Embryology. The MacMillian Company, New York.

Boyde, A., 1971. Comparative histology of mammalian teeth. In: Dahlberg, A.A. (Ed.), Dental Morphology and Evolution. University of Chicago Press, Chicago, pp. 81–94.

Brady, A.L., White, C.D., Longstaffe, F.J., Southam, G., 2008. Investigating intra-bone isotopic variations in bioapatite using IR-laser ablation and micromilling: implications for identifying diagenesis? Palaeogeography, Palaeoclimatology, Palaeoecology 266, 190–199.

Bryant, J.D., Luz, B., Froelich, P.N., 1994. Oxygen isotopic composition of fossil horse tooth phosphate as a recorder of continental paleoclimate. Palaeogeography, Palaeoclimatology, Palaeoecology 107, 303–316.

Bryant, J.D., Koch, P.L., Froelich, P.N., Showers, W.J., Genna, B.J., 1996. Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. Geochimica et Cosmochimica Acta 60, 5145–5148.

Carlson, S.J., 1990. Chapter 21. Vertebrate dental structures. In: Carter, J.G. (Ed.), Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, Volume I. New York, Van Nostrand Reinhold, pp. 531–566.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363.

Cope, E.D., 1889. The Edentata of North America. American Naturalist 23, 657–664.

Dauphin, Y., Williams, C.T., 2004. Diagenetic trends of dental tissues. Comptes Rendus Palevolution 3, 583–590.

de Muizon, C., McDonald, H.G., Salas, R., Urbina, M., 2004. The evolution of feeding adaptations of the aquatic sloth *Thalassocnus*. Journal of Vertebrate Paleontology 24, 398–410.

Denys, C., Williams, C.T., Dauphin, Y., Andrews, P., Fernandez-Jalvo, Y., 1996. Diagenetical changes in Pleistocene small mammals bones from Olduvai Bed I. Palaeogeography, Palaeoclimatology, Palaeoecology 126, 121–134.

Elderfield, H., Pagett, R., 1986. Rare earth elements in ichthyoliths: variations with redox conditions and depositional environment. In: Riley, J.P. (Ed.), Sciences of the Total Environment, pp. 175–197.

Featherstone, J.D., Pearson, B.S., LeGeros, R.Z., 1984. An infrared method for quantification of carbonate in carbonate apatites. Caries Research 18, 63–66.

Ferigolo, J., 1985. Evolutionary trends of the histological pattern in the teeth of Edentata (Xenarthra). Archives Oral Biology 30, 71–85.

Flower, W.H., Lydekker, R., 1891. An Introduction to the Study of Mammals Living and Extinct. Adam and Charles Black, London.

Francillon-Vieillot, H., de Buffrénil, V., Castanet, J., Géraudie, J., Meunier, F.J., Sire, J.Y., Zylberberg, L., de Ricqlès, 1990. Chapter 20. Microstructure and mineralization of vertebrate skeletal tissues. In: Carter, J.G. (Ed.), Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Volume I. Van Nostrand Reinhold, New York, pp. 471–530.

Gillette, D.D., Ray, C.E., 1981. Glyptodonts of North America. Smithsonian Contributions to Paleobiology 40, 1–255.

Grandjean, P., Albarède, F., 1989. Ion probe measurements of rare earth elements in biogenic apatites. Geochimica et Cosmochimica Acta 53, 3179–3183.

Green, J.L., 2009a. Dental microwear in the orthodentine of the Xenarthra (Mammalian) and its use in reconstructing the palaeodiet of extinct taxa: the case study of *Nothrotheriops shastensis* (Xenarthra, Tardigrada, Nothrotheriidae). Zoological Journal of the Linnean Society 156, 201–222.

Green, J.L., 2009b. Intertooth variation of orthodentine microwear in armadillos (Cingulata) and tree sloths (Pilosa). Journal of Mammalogy 90, 768–778.

Henderson, P., Marlow, C.A., Molleson, T.I., Williams, C.T., 1983. Patterns of chemical change during bone fossilization and their significance. Nature 306, 358–360.

Hoffstetter, R., 1958. Xenarthra. In: Piveteau, J. (Ed.), Traité de Paléontologie. Masson, Paris, pp. 535–636. 6.

Iacumin, P., Bocherens, H., Mariotti, A., Longinelli, A., 1996. Oxygen isotope analyses of co-existing carbonate and phosphate in biogenic apatite: a way to monitor diagenetic alteration of bone phosphate? Earth and Planetary Science Letters 142, 1–6.

Janis, C.M., Fortelius, M., 1988. On the means whereby mammals have increased functional durability of their dentitions, with special reference to limiting factors. Biological Reviews 63, 197–230.

Koch, P.L., Zachos, J.C., Gingerich, P.D., 1992. Correlation between isotope records in marine and continental carbon reservoirs near the Palaeocene/Eocene boundary. Nature 359, 319–322.

Koenig, A.E., Rogers, R.R., Trueman, C.N., 2009. Visualizing fossilization using laser ablation — inductively coupled plasma-mass spectrometry maps of trace elements in late Cretaceous bones. Geology 37, 511–514.

Kohn, M.J., McKay, M.P., Knight, J.L., 2005. Dining in the Pleistocene — who's on the menu? Geology 33, 649–652.

Kurtén, B., Anderson, E., 1980. Pleistocene Mammals of North America. Columbia University Press, New York, NY.

Labs-Hochstein, J., MacFadden, B.J., 2006. Quantification of diagenesis in Cenozoic sharks: elemental and mineralogical changes. Geochimica et Cosmochimica Acta 70, 4921–4932.

Lécuyer, C., Reynard, B., Grandjean, P., 2004. Rare earth element evolution of Phanerozoic seawater recorded in biogenic apatites. Chemical Geology 204, 63–102.

Lee-Thorp, J.A., Sealy, J. (Eds.), 2008. Beyond Documenting Diagenesis: The fifth International Bone Diagenesis Workshop: Palaeogeography, Palaeoclimatology, Palaeoecology, 266, pp. 129–265. includes Preface and 15 articles.

Lee-Thorp, J.A., van der Merwe, N.J., 1989. Carbon isotope analysis of fossil bone apatite. South African Journal of Science 83, 712–715.

Lee-Thorp, J.A., van der Merwe, N.J., 1991. Aspects of the chemistry of modern and fossil biological apatites. Journal of Archaeological Science 18, 343–354.

MacFadden, B.J., 1997. Origin and evolution of the grazing guild in New World terrestrial mammals. Trends in Ecology & Evolution 12, 182–187.

MacFadden, B.J., Hulbert, R.C., 2009. Calibration of mammoth (*Mammuthus*) dispersal into North America using rare earth elements of Plio-Pleistocene mammals from Florida. Quaternary Research 71, 41–48.

MacFadden, B.J., Labs-Hochstein, J., Quitmyer, I., Jones, D.S., 2004. Incremental growth and diagenesis of skeletal parts of the lamnoid shark *Otodus obliquus* from the early Eocene (Ypresian) of Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology 206, 179–192.

Martin, C., Bentaleb, I., Kaandorp, R., Iacumin, P., Chatri, K., 2008. Intra-tooth study of modern rhinoceros enamel $\delta^{18}O$: is the difference between phosphate and carbonate $\delta^{18}O$ a sound diagenetic test? Palaeogeography, Palaeoclimatology, Palaeoecology 266, 183–189.

Mason, B., Berry, L.G., 1968. Elements of Mineralogy. W. H Freeman and Company, San Francisco.

McKenna, M.C., Bell, S.K., 1997. Classification of Mammals Above the Species Level. Columbia University Press, New York, NY.

McLennan, S.M., 1989. Rare earth elements in sedimentary rocks: influence of provenience and sedimentary processes. In: Lipin, B.R., McKay, G.A. (Eds.), Geochemistry and Mineralogy of Rare Earth Elements. : Reviews in Mineralogy, 21. Mineralogical Society of America, Washington, D.C, pp. 169–200.

McNab, B.K., 1985. Energetics, population biology, and distribution of xenarthrans, living and extinct. In: Montgomery, G.G. (Ed.), Evolution and Ecology of Armadillos, Sloths, and Vermilinguas. Smithsonian Institution Press, Washington, D.C., pp. 219–232.

Metzger, C.A., Terry Jr., D.O., Grandstaff, D.E., 2004. Effect of paleosol format on rare earth element signatures in fossil bone. Geology 32, 497–500.

Morgan, G.S., 2005. The great American biotic interchange in Florida. Bulletin of the Florida Museum of Natural History 45, 271–311.

Nielsen-Marsh, C.M., Hedges, R.E.M., 2000. Patterns of diagenesis in bone I: the effects of site environments. Journal of Archaeological Science 27, 1139–1150.

Owen, R., 1840–1845. Odontography. Baillière, London.

Pasteris, J.D., Wopenka, B., Freeman, J.J., Rogers, K., Valsami-Jones, E., van der Houwen, J.A.M., Silva, M.J., 2004. Lack of OH in nanocrystalline apatite as a function of degree of atomic order: implications for bone and biomaterials. Biomaterials 25, 229–238.

Patrick, D., Terry Jr., D.O., Gradstaff, D.E., 1991. Rare earth element (REE) variation in fossil and modern bones: the influence of osteological materials and time. Geological Society of America Abstracts with Programs v. 33 (1), 1.

Price, T.D., 1989. Multi-element studies of diagenesis in prehistoric bone. In: Price, T.D. (Ed.), The Chemistry of Prehistoric Human Bone. Cambridge University Press, Cambridge, pp. 211–229.

Reynard, B., Lécuyer, C., Grandjean, P., 1999. Crystal-chemistry controls on rare-earth element concentrations in fossil biogenic apatites and implications for paleoenvironmental reconstructions. Chemical Geology 155, 233–241.

Ruez, D., 2005. Diet of Pleistocene *Paramylodon harlani* (Xenarthra: Mylodontidae): review of methods and preliminary use of carbon isotopes. Texas Journal of Science 57, 329–344.

Schoeninger, M.J., DeNiro, M.J., 1982. Carbon isotope ratios of apatite from fossil bone cannot be used to reconstruct diets of animals. Nature 297, 577–578.

Shemesh, A., 1990. Crystallinity and diagenesis of sedimentary apatites. Geochimica Cosmochimica Acta 54, 2433–2438.

Simpson, G.G., 1932. Enamel on the teeth on an Eocene edentate. American Museum Novitates 567, 1–4.

Smith, K.K., Redford, K.H., 1990. The anatomy and function of the feeding apparatus in two armadillos (Dasypoda): anatomy is not destiny. Journal of Zoology 222, 27–47.

Stuart-Williams, H.Q., Schwarcz, H.P., White, C.D., Spence, M.W., 1996. The isotopic composition and diagenesis of human bone from Teotiuacan and Oaxaca, Mexico. Palaeogeography, Palaeoclimatology, Palaeoecology 126, 1–14.

Sullivan, C.H., Kreuger, H.W., 1981. Carbon isotope analyses of separate chemical phases in modern and fossil bone. Nature 292, 333–335.

Trueman, C., 2007. Chapter 7: Trace element geochemistry of bonebeds. In: Rogers, R.R., Eberth, D.A., Fiorillo, A.R. (Eds.), Bonebeds: Genesis, analysis, and paleobiological significance. University of Chicago Press, Chicago, pp. 397–435.

Trueman, C.N., 1999. Rare earth element geochemistry and taphonomy of terrestrial vertebrate assemblages. Palaios 14, 555–558.

Trueman, C.N., Tuross, N., 2002. Trace elements in Recent and fossil bone apatite. In: Kohn, M.J., Rakovan, J., Hughes, J.M. (Eds.), Phosphates: Geochemical, Geobiological, and Materials Importance: Reviews of Mineralogy and Geochemistry, 48, pp. 489–521.

Trueman, C.N., Benton, M.J., Palmer, M.R., 2003. Geochemical taphonomy of shallow marine vertebrate assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology 197, 151–169.

Trueman, C.N.G., Behrensmeyer, A.K., Tuross, N., Weiner, S., 2004. Mineralogical and compositional changes in bones exposed on soil surfaces in Amboseli National Park, Kenya: diagenetic mechanisms and the role of sediment pore fluids. Journal of Archaeological Science 31, 721–739.

Trueman, C.N., Behrensmeyer, A.K., Potts, R., Tuross, N., 2006. High-resolution records of location and stratigraphic provenance from the rare earth element composition of fossil bones. Geochimica et Cosmochimica Acta 70, 4343–4355.

Trueman, C.N., Privat, K., Field, J., 2008. Why do crystallinity values fail to predict the extent of diagenetic alteration of bone material? Palaeogeography, Palaeoclimatology, Palaeoecology 266, 160–167.

Turner-Walker, G., Jans, M., 2008. Reconstructing taphonomic histories using histological analyses. Palaeogeography, Palaeoclimatology, Palaeoecology 266, 227–235.
Tütken, T., Vennemann, T.W., Pfretzschner, H.-U., 2008. Early diagenesis of bone and tooth apatite in fluvial and marine settings: constraints from combined oxygen isotope, nitrogen and REE analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 266, 254–268.
Vizcaíno, S.F., 2009. The teeth of the "toothless": novelties and key innovations in the evolution of xenarthrans (Mammalia, Xenarthra). Paleobiology 35, 343–366.
Vizcaíno, S.F., Iuliis, De., Bargo, M.S., 1998. Skull shape, masticatory apparatus, and diet of *Vassallia* and *Holmesina* (Mammalia: Xenarthra: Pampatheriidae): when anatomy constrains destiny. Journal of Mammalian Evolution 5, 291–322.
Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology 107, 281–289.
Webb, S.D., 1978. A history of savanna vertebrates in the New World. Part II. South America and the Great American Interchange. Annual Review of Ecology and Systematics 9, 393–426.
Wright, L.E., Schwarcz, H.P., 1996. Infrared and isotopic evidence for diagenesis of bone apatite at Dos Pilas, Guatemala: paleodietary implications. Journal of Archaeological Science 23, 933–944.