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DIET OF PLEISTOCENE *PARAMYLODON HARLANI* (XENARTHRA: MYLODONTIDAE): REVIEW OF METHODS AND PRELIMINARY USE OF CARBON ISOTOPES

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Abstract.–The use of carbon isotopic evidence for determination of dietary preference was previously restricted to the use of enamel (with the exception of some archaeological work), because other materials are more susceptible to diagenesis. For this reason, ground sloths were not included in prior studies. However, the abundance of these animals in deposits of North and South America necessitate a better understanding of their ecology. While sloths lack enamel, their teeth do consist of two layers of dentine: a harder outer layer surrounding a softer inner core. This study sampled both layers of dentine from a lower molariform tooth of *Paramylodon harlani* and from dentine and enamel of animals of known dietary preference. All samples were taken from fossils from the Ingleside fauna, San Patricio County, Texas. The carbon isotopic signatures from the enamel of the grazer *Bison antiquus* and the browser *Palaeolama mirifica* very closely follow expected values, at -0.4‰ and -12.2‰ respectively. Their dentine values lie intermediate to those extremes. Both the outer and inner layers of dentine from the ground sloth, *Paramylodon harlani*, show $\delta^{13}C$ values of near -4‰, in the range expected of mixed feeders, but close to the carbon isotopic composition of modern and fossil grazers. Although this study does suggest the validity of geochemical analysis of sloth teeth in dietary determinations, caution must be used. Extent of diagenesis must be evaluated at least in part by also considering samples from animals of known diet, taken from the same locality.

Ground sloths (Mammalia: Xenarthra) belong to a group of extinct, large herbivores originating on and confined to South America through most of the Cenozoic. They reached North America in at least two pulses of immigration, the first in the early Hemphillian (late Miocene), and subsequently in the late Blancan (late Pliocene). The latter event was part of the Great American faunal interchange corresponding with the emergence of the Panamanian land bridge (Hirschfeld & Webb 1968; Marshall et al. 1982; Hirschfeld 1985). When present in a fauna, ground sloths often are abundant. Unfortunately, their unique morphology has hampered previous attempts to evaluate their ecological position, especially in diet. Traditional methods of dietary analysis use modern analogs, tooth and skull morphology, and dung contents to determine if an herbivore was primarily a grazer, browser, or mixed feeder. A more recently developed technique utilizes the carbon isotopic signature incorporated during the ingestion of plants (e.g., DeNiro & Epstein 1978). This analytical method has helped clarify ecosystem partitioning in some paleontological faunas (e.g., MacFadden 1998; MacFadden et al. 1999). Sloths and other xenathrans are not included in most geochemical studies, even when abundant in the fauna (e.g., MacFadden & Shockey 1997) because they lack the requisite material usually examined isotopic analysis, tooth enamel.

Sloth teeth are composed of two types of dentine, a hard outer layer encapsulating a softer inner layer (Fig. 1). This current study begins to evaluate the possibility of using the isotopic composition of the harder layer as a proxy for enamel in diet determination. In order to assess any diagenetic alteration, samples were also taken from both a known grazer and browser. All samples come from the late Rancholabrean (late Pleistocene) age Ingleside fauna (Lundelius 1972).

The isotopic value of teeth is incorporated during development and therefore only represents the diet during that time. Because juveniles may differ from the adults in diet, it is important to only use teeth from a mature individual. Most mammals have a deciduous set of dentition followed by an adult series, but sloths only have a permanent generation of teeth (Grassé 1955; Naples 1982). The teeth in juvenile sloths are conical, while adult teeth are parallel-sided; therefore adult dentition is easily recognized for sloths. Generally, the most posterior teeth in the skull are the last to erupt; therefore identification of tooth position is helpful to obtain the tooth formed during the oldest age. Most sloths show little differentiation of molariform teeth, but *Paramylodon harlani* teeth, especially the lower third molar, can be precisely identified (Figure 1).

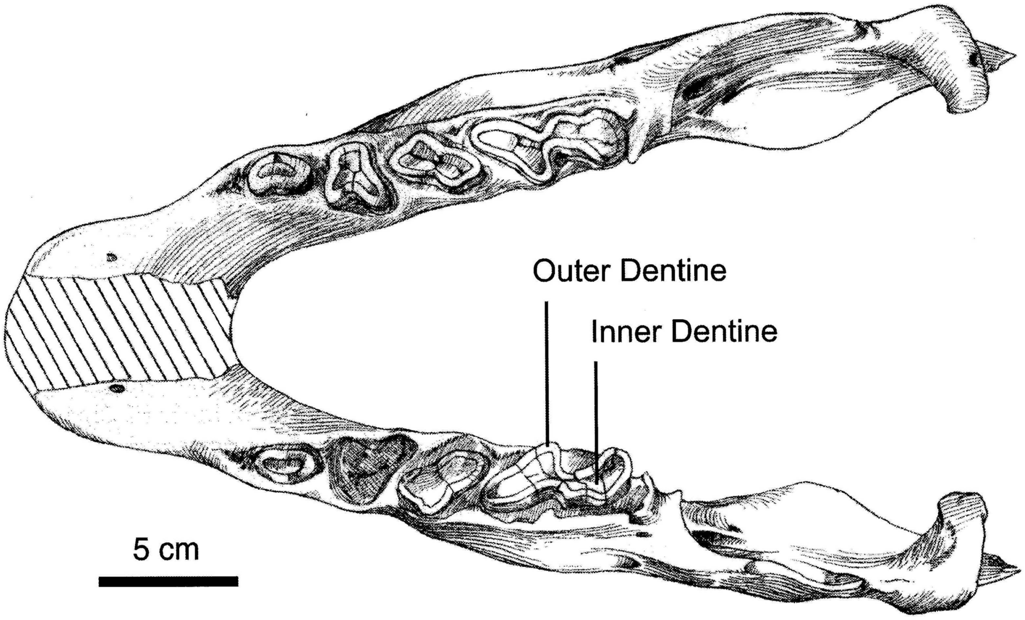

Figure 1. Mandible of *Paramylodon harlani* from Ingleside, with tooth parts labeled. Sloth teeth lack enamel, but have a harder outer layer of dentine surrounding a softer inner layer. Modified from Lundelius (1972).

Paleontologists have debated the diet of *Paramylodon harlani* since the early 1900s, reaching no consensus (Table 1). Considering the problematic standing, any additional evidence is justified.

BACKGROUND AND PREVIOUS STUDIES

Methods of Dietary Analysis

Recreating biology from fossils has often included much guesswork. Even rigorous studies can sometimes misjudge diet due to phylogenetic constraints in the morphology (MacFadden et al. 1999). In spite of the difficulties, diet aids in interpretation of the habitat and ecological interactions, thus imploring its continued study. The indirect evidence from herbivores is sometimes the only indication of plant types in the area, because the fluctuation of herbivore abundance yields insight to the climatic transitions of an area (Wang et al. 1994; Cerling et al. 1997; 1998).

Table 1. Proposed diet of *Paramylodon harlani*.

Browser	Grazer	Mixed
Lull (1915)	Parker (1885)	Stock (1920)
Dalquest & Schultz (1992)	Brown (1903)	Stock (1925)
	Allen (1913)	Naples (1989)
	Webb (1978)	

Modern analogs.–Comparison to taxonomically similar mammals in modern faunas is the primary method of deducing the paleoecology of an animal. This can only be accomplished with confidence for species for which there are close modern analogs, effectively eliminating many extinct groups from consideration. At some level all life is related, and therefore it is possible to find a living, though not necessarily close, relative. The arbitrary rank of genus was suggested as the level at which such analogs are useful (Shotwell 1955). Unfortunately the genera of modern tree sloths have no known fossil representatives and it is unclear how closely related *Paramylodon* is to extant taxa.

Two genera of tree sloths live today in Central and South America, the two-toed sloth, *Choloepus*, and the three-toed sloth, *Bradypus*. Extant sloths live entirely in trees, and their diet consists almost exclusively of leaves, buds, and fruits, much of which comes from the cecropia tree (e.g., Britton 1941; Lundy 1952). Fossil tree sloths are not known, but paleontological records of ground sloths extend to the Deseadan (early Oligocene) of South America (Hirschfeld 1985; Marshall & Cifelli 1990). Further, the phylogenetic relationship between these groups is unclear (Gaudin 1995), although the hypothesis of Gaudin (2004) has a very distant relationship between mylodont sloths, including *Paramylodon*, and the living *Bradypus* and *Choloepus*. The validity of this comparison is also quickly questioned considering the immense size difference of these animals; the body mass of ground sloths is as much as four orders of magnitude greater than that of tree sloths (Fariña et al. 1998; Adam 1999).

Morphology.–Morphological features independent of taxonomic affiliation can sometimes give clues to the diet. This is advantageous when there is no modern analog, or when the group being studied has changed its ecological behavior. Three features in particular are the most utilized in this way: teeth, muzzle shape, and musculature attachments.

Grasses contain abrasive silica structures called phytoliths that quickly erode teeth during grazing. Consumption of grass may also be responsible for increased amounts of abrasive sediment ingested as compared to a diet of browse. Compensation for this additional wear is achieved by increasing the height and complexity of these teeth (Fortelius 1982; 1985; Janis 1986; 1990). Shorter, simpler teeth are sufficient for a diet of leaves. The most familiar character representing a grazing diet is the presence of high-crowned, or hypsodont teeth. This connection between tooth size and diet is well documented in the study of horse evolution and the overall trend from browsing to grazing (e.g., Kowalevsky 1873; Matthew 1926; Simpson 1953; MacFadden 1992). The teeth of ground sloths are hypselenodont, the extreme case of hypsodonty, and grow throughout life with an open pulp cavity. However, their teeth are very simple in pattern, often consisting of only a simple peg. This combination of characters is difficult to interpret because hypselenodonty typically indicates a grazing diet, but simple occlusal patterns suggest a browsing diet. An additional line of morphological evidence, tooth microwear of herbivores (e.g., Walker & Teaford 1989; Solounias & Moelleken 1992a; 1992b; Solounias & Hayek 1993, Rivals & Deniaux 2003), may prove useful when applied to sloths. This method reveals the most recent diet of the animal before death, which may not be typical of the entire life of the animal (Solounias et al. 1988).

Another adaptation for eating grass is the complex folding of the enamel in the teeth of herbivores. Although relatively complex for a xenarthran tooth, the molariform dentition of *Paramylodon* consists only of simple lobes that show much variation in development, even within the same population (Stock 1925). Development of cementum in mylodont sloths, which includes *Paramylodon*, was presented as evidence for a grazing habit (Parker 1885), but this character also occurs in the living tree sloths (Ferigolo 1985), which are browsers.

A narrow snout allows an animal to selectively pick the part of the plant to eat, obtaining the most nutritious portions, while a wide muzzle allows more food to be cropped from a flat surface (Solounias & Moelleken 1993; Dompierre & Churcher 1996). While the shape of the muzzle and incisors are useful for dietary interpretations in many extant and fossil animals, it does not apply to ground sloths. They lack incisors, probably using their upper lips or tongue against the large, spatulate mandibular symphysis (predental spout) to crop food (Naples 1989). It is not known if the shape of the premaxilla can be correlated to diet. Grazers process larger volumes of more abrasive food and therefore have larger masticatory muscles than browsers, as inferred by attachment scars on both the skull and jaw (Bramble 1978; Solounias et al. 1995). Analysis of facial musculature suggests that *Paramylodon harlani* was a mixed feeder, though better adapted for grazing than browsing (Naples 1989).

Dung contents.–In the rare localities where fossil vertebrates and plants co-occur, the integration of flora and fauna allows for insights that may be applied to other localities and situations. Identification of plant fragments in dung balls associated with the extinct North American megatheriid sloth *Nothrotheriops shastensis* determined the browsing diet of that taxon in northern Arizona (Hansen 1978). While it may be reasonable to assume most other populations of that species had a similar diet, it may not extend to other sloth taxa. Remains of a species more closely related to *Paramylodon*, *Mylodon darwinii*, was found in a South American cave with dung that suggested a grassland environment (Salmi 1955; Moore 1978), but this interpretation was subsequently challenged (Heusser et al. 1992). Also, an overestimate of grasses in the diet of herbivores limits the applicability of fecal analyses (Holechek & Valdez 1985).

Carbon Isotopes and Diet

The use of carbon isotopic ratios from fossil tooth enamel of mammalian herbivores in order to determine diet has quickly gained popularity and avoids some problems encountered with the traditional methods of dietary determinations discussed above (e.g., MacFadden & Shockey 1997; MacFadden 1998; MacFadden et al. 1999; Feranec 2003). Differentiation between carbon isotopic ratios in grazers and browsers can be used because plants incorporate carbon isotopes differently. Initial $\delta^{13}C$ (see Materials and Methods for definition of $\delta^{13}C$) measurements of plants returned values of averaging -28‰ (Craig 1953; 1954), while subsequent research discovered that some plants gave more enriched values of -14‰ (Bender 1968; 1971). The difference came from sampling plants that follow different photosynthetic methods (O'Leary 1981; 1988). More recent measurements have refined these values and the currently accepted average values are -27‰ and -13‰ respecttively (Farquhar et al. 1989; Boutton 1991). The more depleted measurements were taken from plants that use the C_3 (Calvin) pathway, including trees, shrubs, and high elevation/latitude grasses. The relatively enriched values were from corn and other temperate and tropical grasses, which utilize the C_4 (Hatch-Slack) pathway. A third photosynthetic pathway, crassulacean acid metabolism (CAM), is found in desert plants and other succulents which are assumed to not comprise a significant component of the flora at Ingleside in the late Pleistocene. The apatite in the enamel of teeth from modern mammalian herbivores shows an additional fractionation in the form of an enrichment of about +14‰ from that of the plant materials consumed (Cerling & Harris, 1999). Therefore the $\delta^{13}C$ of grazers should average about 1‰, and that of browsers should near -13‰.

MATERIALS AND METHODS

All fossils come from the Ingleside fauna (Texas Memorial Museum locality 30967), San Patricio County, Texas, which was referred to the Rancholabrean (late Pleistocene) North American Land Mammal Age (Lundelius 1972). Precise age determination is problematic as there is a lack of radiometric, and little superpositional, data, but Lundelius (1972) suggested a time range of 122,000 to 19,000 years.

Analytical methods generally follow those outlined by Koch et al. (1997) for collecting and preparing biological apatite from tooth enamel. The teeth were cleaned to remove any loose surficial contaminants, and then samples were drilled. The edges were removed to obtain a pristine sample, as far from any potential surficial alteration as possible. Care was also taken to ensure the separation of enamel and dentine. After pulverizing, 50 mg of each sample was soaked in 2 mL of 3% NaOCl. The mixture was continuously agitated with the lids loose (so CO_2 from oxidation could escape) for one and three days for the enamel and dentine respectively. The samples were centrifuged and the fluid removed by aspiration through a pipette. Distilled water was added to each sample, which was again mixed and centrifuged with the resultant fluid being removed. This was repeated five times. The samples were then soaked in a 2 mL solution of 1N acetic acid-calcium acetate buffer for two days to remove any carbonate minerals. The rinsing procedure described above was repeated to clean the samples, which were then allowed to air dry.

On-line purification and extraction followed standard techniques detailed by MacFadden & Cerling (1996) and MacFadden et al. (1996). The samples were analyzed for their carbon isotopic composition using a VG Prism mass spectrometer in the Department of Geological Sciences at The University of Texas at Austin. All results are given in the standard delta notation (δ) as the deviation in parts per mil (‰) of the sample from that of the V-PDB standard for carbon (Coplen 1994), where:

$$\delta^{13}C = [(^{13}C_{sample}/^{12}C_{sample}/^{13}C_{standard}/^{12}C_{standard}) - 1] \text{ x } 1000.$$

Samples were taken from a presumed grazer, *Bison antiquus*, a presumed browser, *Palaeolama mirifica*, and the ground sloth, *Paramylodon harlani*, all from the Ingleside fauna. Enamel and dentine from *Bison* and *Palaeolama* and both layers of dentine from the sloth were sampled. Previous examination of enamel from fossil *Bison* from Florida produced average $\delta^{13}C$ values of -3.4‰ for middle Rancholabrean faunas and -1.1‰ for late Rancholabrean faunas (Feranec & MacFadden 2000). Those values are consistent with the diet of a grazer. The average $\delta^{13}C$ value for enamel from *Palaeolama* from Tarija, Bolivia, was -11.4‰ (MacFadden & Shockey 1997), consistent with the diet of a browser. Enamel samples from the *Bison* and *Palaeolama* from Ingleside were analyzed to verify that isotopic signatures of both grazers and browsers were recorded in the fossil locality and to confirm that values from the enamel were consistent with that from other localities examined in previous studies. Dentine from *Bison* and *Palaeolama* was also sampled; if the dentine from *Paramylodon* at Ingleside was diagenetically altered, the dentine from *Bison* and *Palaeolama* should be similarly changed.

ANALYTICAL RESULTS AND DISCUSSION

The enamel values of *Bison* and *Palaeolama* (Fig. 2) represent the extreme ends of the grazing-browsing spectrum. The *Bison* $\delta^{13}C$ value of -0.4‰ and the *Palaeolama* value of -12.2‰ (Fig. 2) fall within the expected range of grazers and browsers respectively, as well as within previously observed ranges of fossil *Bison* (MacFadden & Feranec 2000) and *Palaeolama* (MacFadden & Shockey 1997). In each of these animals the dentine values differ by slightly more than 4‰ from that of the enamel, but in opposite directions. The Ingleside *Bison* and *Palaeolama* had $\delta^{13}C$ values of -4.6‰ and -8.1‰ respectively. Both layers of dentine in *Paramylodon* produced values of about -4‰ (-3.5‰ and -4.1‰).

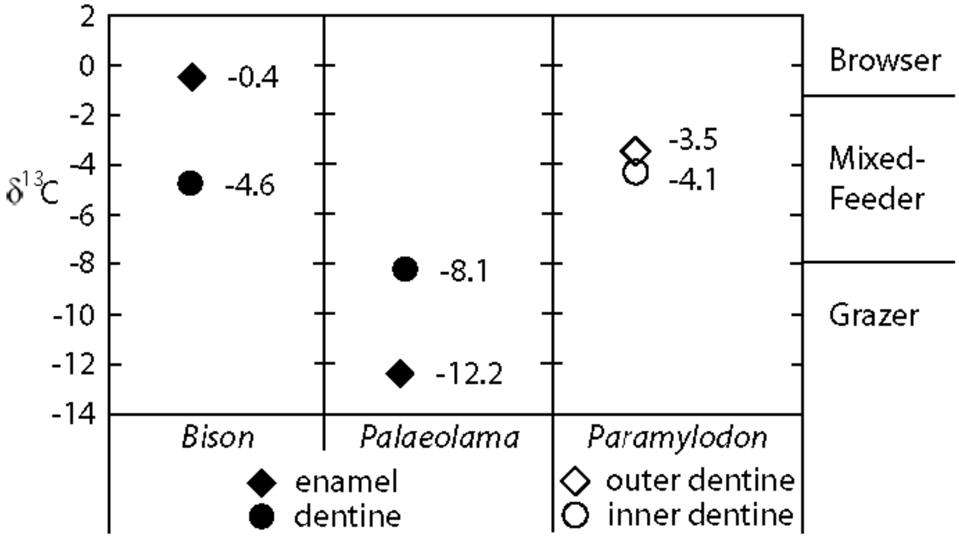

Figure 2. Carbon isotopic results from Ingleside, Texas. The vertical axis shows the $\delta^{13}C$ of the sample. The enamel value for *Paramylodon* is that of the outer layer of dentine. Texas Memorial Museum (TMM) specimens sampled were Bison, left upper first or second molar, TMM 30967-1097; *Palaeolama*, right upper first or second molar, TMM 30967-2573; and *Paramylodon*, right lower fourth molariform, TMM 30967-2430. The divisions shown between grazers and mixed-feeders (-1.3‰) and between mixed-feeders and browsers (-7.9‰) are from Feranec (2003).

Before an interpretation of the *Paramylodon* results can be interpreted, the dentine values of the other taxa must be examined first. There are two possible scenarios for the discrepancy between the dentine and enamel $\delta^{13}C$ values for the Ingleside *Bison* and *Palaeolama*: the dentine is diagenetically altered or the dentine values are a biological product.

In the first scenario, the carbon isotopic composition of both dentine and enamel were the same (or similarly offset), but was subsequently altered. Because the *Bison* dentine sample was depleted relative to the enamel by about 4‰ and the *Palaeolama* sample was enriched by the same amount, the altering fluid must then have had an intermediate $\delta^{13}C$ value of about -6‰. The *Paramylodon* $\delta^{13}C$ values are similar to the dentine of *Bison* and if subject to similar diagenesis would alter in the same manner, meaning the original value must have been near 0‰, close to the value of the *Bison* enamel. The author is unaware of a potential altering fluid near Ingleside with a δ^{13}C of -6‰. Because the Ingleside fauna is on the coast, both marine and surface waters could be in contact with the fossils, but the δ^{13}C values of these waters are 0‰ and 2-4‰ respectively (Anderson & Arthur 1983).

Alternately, the dentine values may represent a biological effect and were not altered. Dentine values may be offset from enamel during tooth formation due to different constraints during tooth formation. Grazers build a more hypsodont, more complex tooth that usually contains cementum surrounding the enamel. This different construction may be reflected in the isotopic signature of the dentine. In the case of *Bison* and *Palaeolama*, the dentine δ^{13}C values may change during the life of the individual, because it is a vascular tissue. In *Paramylodon*, however, the outer layer of dentine lack vascular canals (Ferigolo, 1985). The difference in hardness of the inner and outer dentine layers is extreme and causes the complex wear facets seen in many xenarthrans (Naples 1982, 1995). If the teeth had undergone diagenesis it would be expressed differently in the two distinct types of dentine in *Paramylodon*. Since the carbon isotopic ratios of both types of dentine in *Paramylodon* are very similar, there were probably not any significant diagenetic effects. In this scenario *Paramylodon* was a mixed feeder.

The first scenario requires an altering fluid more depleted in δ^{13}C than expected for either marine or surface water, but allows for diagenesis of the *Paramylodon* dentine. The second scenario implies a different biological effect on dentine of different animals. Neither situation can be excluded as a possibility, although the presence of an altering fluid at Ingleside having such a depleted δ^{13}C value is here regarded as less likely. There is very little difference in δ^{13}C of the inner and outer layers of dentine in *Paramylodon*.

CONCLUSION

This study is the first to utilize carbon isotopes in an investigation of the diet of a sloth. The similarity between the different dentine layers suggests the isotopic signature of *Paramylodon* is unaltered at this locality; diagenesis would likely have impacted the inner and outer layers differently. These carbon isotopic data indicate that *Paramylodon harlani* from Ingleside, Texas, probably had a mixed diet dominated by grass. The other possible scenario, here considered less likely, is that the *Paramylodon* dentine was altered by the same fluid that altered the *Bison* and *Palaeolama* dentine. In this scenario, *Paramylodon* originally had an isotopic signature suggesting the diet of a grazer. There is no evidence in either scenario for *Paramylodon* being a browser.

As this study contained only two samples from each of three teeth, much room is left for further refinement. Diagenesis in the sloth dentine may be addressed through analysis of more teeth and from multiple samples along a vertical gradient on a single tooth. Altered specimens will widely vary in $\delta^{13}C$, while pristine samples show much less fluctuation (Koch et al. 1997). Additionally, Ingleside and many other fossil localities contain multiple species of sloths. If they partition the ecosystem in a manner seen in other large herbivores, they will show different isotopic signals, reflective of different diets. While extant sloths are dramatically different from their extinct relatives, future inclusion of samples from modern teeth will help elucidate the variation between the two dentine types.

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