

PALEOECOLOGY OF EXTINCT XENARTHANS AND THE GREAT AMERICAN BIOTIC INTERCHANGE

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The Xenarthra were the most successful South American mammals to participate in the Great American Biotic Interchange (GABI) and representatives of each family dispersed to at least the middle latitudes in North America. The ability of xenarthrans to insinuate themselves into the North American fauna suggests their ecology was sufficiently different from endemic North American taxa to avoid direct competition and sufficiently different amongst themselves to avoid competition with each other. Despite the diversity of xenarthrans in South America at the time of the interchange only one member of each major xenarthran group (roughly equivalent to a family) reached temperate North America. The morphological diversity displayed by ground sloths, glyptodonts, pampatheres, armadillos and anteaters, indicates that no single ecological explanation can account for their successful dispersal into North America as each represents a distinct ecological adaptation, including a variety of feeding strategies such as omnivore/insectivore, specialized myrmecophage, and herbivory including low browser, high browser, aquatic grazer, intermediate feeder on coarse vegetation/grazer, and large grazer/intermediate feeder. Despite this ecological diversity there do seem to be some trends common to the group. Ecologically the dispersing member was more of a generalist than other members of the family and dispersing members tended to be small with a subsequent increase in size following their entry into North America.

Key Words: Great American Biotic Interchange; Xenarthra; paleoecology; biogeography

INTRODUCTION

In recent years there has been a renewed interest in the Great American Biotic Interchange (GABI) (Stehli & Webb 1985 and papers within). The dispersal of some North American mammals into South America and the reciprocal dispersal of some South American forms northward has been looked at from a variety of angles, particularly the resulting impact of the appearance of these “exotic” species on the respective native fauna of each continent (Webb 1991). Usually the emphasis has been on the greater impact of the northern forms on the South American native fauna than vice versa. There is no question that in terms of number of taxa, there was disequilibrium with regard to the dispersers, with the number of taxa of North American origin going south exceeding that of the southern invaders going north. However, of all the groups of South American origin with members dispersing northward, none were as successful as the xenarthrans. Not only did more members of

the Xenarthra reach temperate North America than any other South American disperser, but once present, most became an integral part of the North American fauna and were common enough to be present in numerous individual local faunas. The xenarthrans were able not only to compete ecologically with the native North American forms, in terms of food resources, but were able to survive the native predators, the group whose North American members have been identified as having had the greatest impact on the native fauna after entering South America (Marshall 1981). Their success continued until the end of the Pleistocene when along with the natives they also became extinct. This seems to be a rather unexpected history given our generally biased view of this metabolically challenged group.

As noted by Marshall and Hecht (1978), the trophic role assumed by an animal in a community is best understood when the structure of the community is viewed within a historical perspective. A critical component of this historical perspective for the entrance of xenarthrans into North America includes understanding what facilitated the dispersal of certain taxa through the Panama-

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nian land bridge. Was it their physical or behavioral attributes or merely the opportunity to exploit available adaptive zones or niches present in both the tropical and temperate parts of North America? In order to understand the success of xenarthrans in establishing themselves within the North American fauna it is equally important to understand what permitted them to successfully disperse.

GENERALIZATIONS ABOUT XENARTHROAN GENERALISTS

In addition to a distinctive suite of skeletal features that unite the xenarthrans, a physiological trait common to all members is a low basal metabolism. This low basal metabolism is an important factor that determines many of their ecological attributes, such as long gestation periods, low growth rates, extended periods of parental care, and small litter size (McNab 1985). The result is that xenarthrans are K-selected with an overall low rate of reproduction. The one possible exception is *Dasypus*, which may be relatively more r-selected than other xenarthrans given its unusual approach to reproduction, especially in the subgenus *Dasypus*. Any consideration of the ecology of xenarthrans, the ability of some not only to disperse into North America but also their long-term success until the Pleistocene extinction event must include a careful consideration of their metabolism, whether considered as a detriment or an advantage.

Traditionally the low basal metabolism of xenarthrans has been considered as indicative of their primitive status as the earliest offshoot from other eutherians (Englemann 1985). However, McNab (1978) has argued that for many of the living xenarthrans a low basal metabolism is directly linked to the nutritive levels of their food sources – sloths as arboreal folivores, and anteaters as termite and ant specialists. Currently there is only one study that indicates that a fossil xenarthran, the sloth *Nothrotheriops shastensis*, had like its extant relatives, a low basal metabolism and consequently a lower core body temperature than expected for its body size (Ho 1967). An estimated core body temperature of $35.3 \pm 0.5^\circ \text{C}$, based on the hydroxyproline content of bone collagen, was calculated for *Nothrotheriops shastensis*. This lower metabolism in herbivorous xenarthrans such as sloths and glyptodonts may have permitted them to eat either nutritionally poorer plants than could be used by mammals with a higher metabolism or to consume plants containing higher levels of secondary metabolites.

There are two broad categories of herbivores based on digestive strategy and the part of the gut that is enlarged in order to facilitate microbial fermentation of vegetation. Extant mammals with an enlarged foregut to provide the main site of microbial activity include ruminants, camelids, suiforms, leaf-eating monkeys, sloths, and macropod marsupials. Those mammals with an enlarged hindgut and in which gastric and intestinal digestion occurs before microbial fermentation include perissodactyls, lagomorphs, capybaras, hyrax and proboscideans. In all of these latter herbivores there is an enlarged caecum and colon (Parra 1978). The significance of differences between fore- and hindgut fermenters in ungulates and their relative evolutionary success with regard to the utilization of available vegetation has been discussed by Janis (1976).

Previously the digestive physiology of the extinct ground sloths has been considered to be similar to that of monogastric hindgut fermenters or caecalids such as proboscideans and perissodactyls (Guthrie 1984), so it has been with these animals that they were considered to have competed as megaherbivores. However, the stomach in the living tree sloths is large and complex; being composed of four chambers (Goffart 1971; Bauchop 1978) and composes 20 to 30% of the body weight of living sloths (Britton 1941). Its overall similarity to a rumen has been noted (Grassé 1955). Bauchop (1978) considered its general development in modern sloths to be broadly similar to that of a camel and the presence of numerous pillars also gives it a more ruminant-like structure. Despite the overall general similarities, the construction of the sloth stomach is not as complex as in ruminants and lacks the equivalent of the ruminant omasum. While there is no direct evidence for the structure of the stomach in any of the extinct xenarthrans, since both of the living genera, *Bradypus* and *Choloepus*, which are placed in separate families, have similar stomach morphology, it is not unreasonable to extrapolate that the stomach in the extinct ground sloths was also chambered. Modern armadillos have a simple sac-like stomach, simpler in construction than sloth's, reflecting food habits that tend to be insectivorous. Their extinct herbivorous relatives, pampatheres and glyptodonts, probably also had simple stomachs, which may account for the greater complexity of their teeth and associated masticatory apparatus for the mechanical processing of vegetation, particularly in the glyptodonts.

It should also be noted that all living xenarthrans, including both extant tree sloths, lack a caecum (Goffart

1971) and this is most likely also true for their extinct relatives. In living sloths the large intestine is short (Bauchop 1978) and therefore also departs from the digestive anatomy of proboscideans and perissodactyls and other hindgut fermenters.

The feeding strategy of large caecalid grazers (hindgut digesters) is to consume the entire grass plant, resulting in a dilution of the leaf nutrients. This feeding strategy results in the consumption of large volumes of plant material of low to modest nutrient value and also allows these animals to utilize plant parts not available to other herbivores including those parts high in silica and fiber. Based on the plant parts preserved in the dung of *Nothrotheriops*, a browser, and *Mylodon*, a grazer (Moore 1978), sloths were more selective in their feeding habits than caecalids.

Given the large body size of *Eremotherium* it has been assumed that it would have been in competition with the other megaherbivores present in North America. This would have been initially with both gomphotheres such as *Cuvieronius* and the mastodon *Mammuthus* during the Blancan, with the addition of mammoths (*Mammuthus*) during the Irvingtonian and Rancholabrean. In South America, *Eremotherium* and the gomphothere *Haplomastodon* are closely associated in their distribution and the presence of one in a fauna is often indicative of the presence of the other. The ability of these large bodied herbivores to coexist and share habitat has a more reasonable explanation if we consider that *Eremotherium* did not have a digestive physiology similar to that of proboscideans, but instead was more similar to non-ruminant artiodactyls. This would have permitted these animals to better partition the habitat they shared with regard to either the types of plants they consumed or at least the plant parts. Janzen and Martin (1982) have postulated that frugivory by extinct horses, gomphotheres, and ground sloths may explain the reproductive traits of some plants in the Central American lowland forests and that these animals may have been important dispersal agents that influenced the distribution of these plant species. Recent stable isotope studies by MacFadden et al. (1994) for the gomphothere *Cuvieronius* resulted in a wide range of values for ^{13}C (-8.5 to -0.1‰) suggesting that it fed on a wide range of plant parts and was not restricted to fruits. Pending the discovery of more direct evidence on the diet of these animals, I suggest that if both gomphotheres and *Eremotherium* were in competition foraging in trees, then their respective roles may have been analogous to

modern African elephants and giraffes with *Eremotherium* filling the “giraffe niche” and feeding on selected leaves and twigs, thus functioning as a high browser, in the New World ecosystems.

In examining the success of herbivorous xenarthrans in North America, it is more likely that the best possible candidates for direct competition were non-ruminant artiodactyls such as peccaries and camelids. As will be discussed below there are functional similarities in the premaxillae between sloths and those artiodactyls that lack upper incisors.

Besides *Eremotherium*, the smaller browsing sloths *Megalonyx* and *Nothrotheriops* may have been selective feeders and were capable of utilizing the more nutrient rich parts of plants along with some ingestion of twigs and branches of mature parts of the plant.

Lacking direct evidence of diet, such as dung, in most fossil species we often have to rely on distinctive anatomical features to serve as proxies that permit some reasonable inferences as to the animal's feeding strategies. Often this is accomplished by looking for a correlation between a specific anatomical structure and the diet in extant forms and then looking for similar structures in extinct forms. One approach has been to examine the relationship of the shape of the premaxillae and the proportions of the anterior part of the skull to infer the general feeding strategies of ruminant artiodactyls and their sister group the Tylopoda (Solounias et al. 1988; Janis & Ehrhardt 1988; Dompierre & Churcher 1996). Given the general similarities in the edentulous premaxillae of artiodactyls and sloths, the relationship between its shape and diet seen in this one set of herbivores seems applicable to the other and most likely performed similar functions with regard to feeding. Using this ungulate model it is possible to make some generalizations with regard to the feeding strategies of those sloths that dispersed northward in comparison to those taxa restricted to South America.

It appears that the dispersing sloth taxa all had more primitive or generalized premaxillae in comparison to other members of their family present at the time of the dispersal event. The premaxillae of *Eremotherium* are triangular and more primitive in comparison to those of *Megatherium* (Fig. 1), which are highly modified, and suggest a more specialized feeding function, perhaps limiting it to a smaller selection of plants or plant parts upon which it fed. Likewise, the premaxillae of *Glossotherium/Paramylodon* are intermediate in structure between scelidotheres or even the more closely related genus

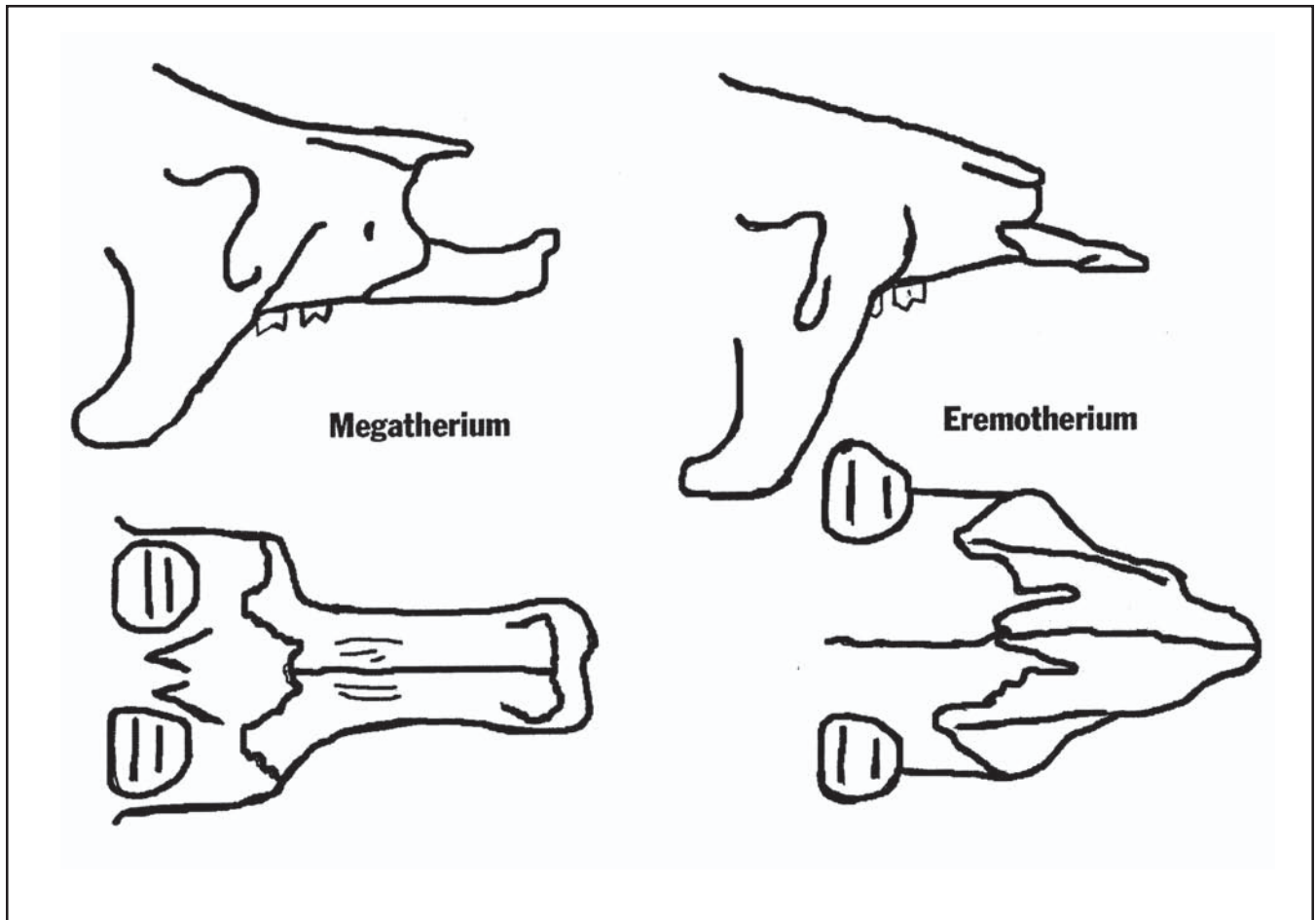


Figure 1. Comparison of the shape of the premaxillae of *Eremotherium* and *Megatherium*.

Myiodon in which the premaxillae and facial region are long and narrow, and that of either *Oreomyiodon* or *Lestodon* in which the anterior part of the muzzle is expanded along with a related widening of the premaxillae (Fig. 2). While we do not have specific details on the relationship of premaxillae and muzzle shape or proportions and feeding habits in either scelidotheres or lestodonts, they do represent extremes in skull morphology within the family Mylodontidae and presumably, like *Megatherium*, reflect some type of feeding specialization. The shape of the premaxillae and muzzle in the *Glossotherium/Paramyiodon* lineage represents an intermediate and relatively unspecialized morphology and most likely more generalized and less specialized feeding habits.

Of all the North American xenarthrans, the one taxon that we have the most dietary information for is *Nothrotheriops shastense*, thanks to the preservation

of its dung in numerous dry caves in the southwestern United States. Numerous workers have analyzed the dung of *Nothrotheriops* (Hansen 1978; Laudermilk & Munz 1934, 1938; Martin et al. 1961; Thompson et al. 1980) and these studies have provided detailed information on the variety of vegetation in the diet of this extinct species. Hansen (1978) identified 72 species of plants in the dung of *Nothrotheriops* from Rampart Cave, the vast majority of which are low growing bushes and shrubs. While most of the species consumed are xerically adapted desert vegetation, indicating that *Nothrotheriops* was capable of surviving in relatively dry environments, other taxa such as the reed *Phragmites* indicates the animal fed in a variety of habitats.

Mylodont sloths have generally been thought of as grazers although Naples (1989) suggested that based on her analysis of the skull morphology of *Paramyiodon harlani* from Rancho La Brea, this species may have

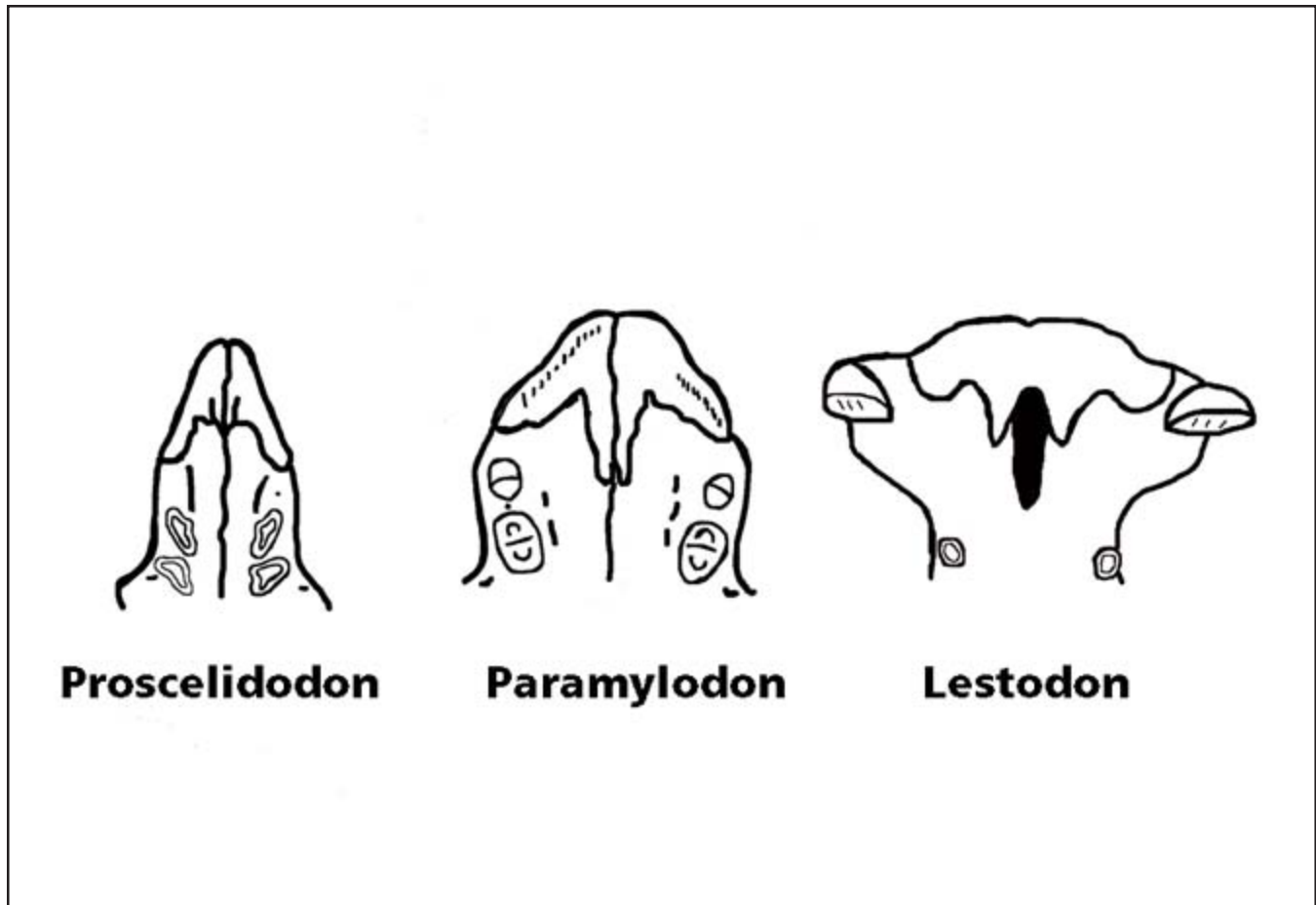


Figure 2. Comparison of the shape of the premaxillae of *Paramylodon* with a scelidotherid, *Proscelidodon* and a lestodont, *Lestodon*, showing its intermediate morphology.

been an intermediate in its habits and included browse as well as graze. Coltrain et al. (2004) analyzed the ^{13}C and ^{15}N in *Paramylodon* from Rancholabrean and obtained mean values of -20.99‰ for carbon and 7.93‰ for nitrogen based on 10 specimens. The value for nitrogen was more positive than for equids or true ruminants from Rancho La Brea and placed the sloth between nonruminants and ruminants isotopically. McDonald (1995) examined the relationship between jaw depth and alveolar length of the tooth row in *Paramylodon* and noted a relatively greater increase in jaw depth suggesting a greater degree of hypsodonty in later forms. Despite the presence of ever-growing teeth, the lack of enamel on the teeth in xenarthrans can result in a rapid rate of wear if they consume highly abrasive food such as grasses. An increased depth of the jaw permitted an overall increase in the height of the tooth and thus compensated for the more rapid rate of wear.

This suggests that later members of the lineage were more adapted to grazing or at least consuming more abrasive vegetation than their predecessors. If this was the case, then the ancestors of this lineage participating in the faunal interchange may have been more generalists in their feeding and less dependent on grasses, thus facilitating their dispersal.

Dasypus novemcinctus is morphologically derived compared to other armadillos and shows specializations for myrmecophagy, although behaviorally it is one of the most generalized of the armadillos with regard to its food habits (Smith & Redford 1990) and amongst all the armadillos is one of the most omnivorous (Redford 1985). Since we have no direct evidence for the diet of *D. bellus* it may be unreasonable to only consider the diet of *D. novemcinctus* to interpret the food habits of *D. bellus* and an examination of the diet in other species of *Dasypus* can provide a somewhat broader perspective.

In examining the diet of *Dasypus* Redford (1986) found that in the tropics the diet of *D. novemcinctus* is similar to that of *D. sabanicola* consisting predominately of ants and termites. In contrast, the stomach contents of *Dasypus kappleri* had only 29% ants and termites and in *Dasypus hybridus* it was 58%. The overall impression is that all species of *Dasypus* are somewhat labile in their diet and what is consumed is dependent on the local environment and what food is available. Smith and Redford (1990) interpreted the food habits of *D. novemcinctus* as a dietary generalist that along with its unique reproductive habits of monozygotic polyembryony permitted its success in expanding into new habitats and environments. Consequently it has the widest distribution of all armadillos ranging from South to North America.

While we have no direct evidence of the food habits of *Dasypus bellus*, there is direct evidence that like the other species of the genus, *D. bellus* produced multiple young. Usually four young are produced in *D. novemcinctus* and *D. sabanicola* and 4 to as many as 12 young have been documented in *D. hybridus* (Wetzel & Mondolfi 1979). The remains of multiple young were found associated with the skeleton of an adult *D. bellus* preserved in a cave in Florida (Auffenberg 1957).

Based on a functional analysis of the skull of *Holmesina* and comparisons with some extant species of armadillo, Vizcaino et al. (1998) concluded that it fed on a variety of vegetable matter and although not necessarily strict grazers, *Holmesina* probably fed on coarse vegetation. In their analysis they compared feeding strategies in armadillos and African antelopes and noted a relationship between size and feeding strategies. Small armadillos, like small antelopes, tend to be browsers and that with an increase in size there is a shift in the degree of grazing, with glyptodonts being primarily grazers and pampatheres occupying an intermediate feeding strategy. With the size increase in the North American lineage of *Holmesina* (see below) it is possible that *H. floridanus* was more of a browser while the larger *H. septentrionalis* included a larger proportion of graze in its diet.

While Webb (1978) included the glyptodonts as one of nine genera of savanna grazers, Gillette and Ray (1981) suggested that they were likely "aquatic grazers" along with the capybaras. Recently Fariña (1995) questioned Gillette and Ray's interpretation of *Glyptotherium* having a preference for marshy, lowland habitats based on a biomechanical analysis of dif-

ferent South American genera of glyptodonts. His analysis was based on the size relationship between glyptodont feet and estimates of body weight. He concluded that the feet were too small in proportion to the body size to support the animal in this type of terrain. He also noted the absence of glyptodont tracks at Bahia Blanca in Argentina, which had a soft substrate at the time the tracks were formed. However, Aramayo and Manera de Bianco (1996) later reported a single track of a glyptodont from the locality. While not as well represented as other ichnotaxa reported from the fauna, it does indicate that at least one individual of glyptodont did wander onto this soft substrate. The jaw and dentition of *Glyptotherium* as in other glyptodonts is well adapted for processing grasses. These features include a deep jaw with extremely hypsodont, ever-growing teeth, the complexity of the teeth with an arrangement of osteodentine to compensate for the lack of enamel, and the structure of the zygomatic arch to orient the masseter muscles to grind abrasive vegetation such as grasses (Ferigolo 1985; Fariña 1985, 1988)

At first glance it would seem that *Myrmecophaga* is a major contradiction to the argument that those xenarthrans that dispersed northward were generalists. The giant anteater is an obligate myrmecophage with a diet consisting almost entirely of ants and termites. Redford (1985) noted that it is not specialized on either ants or termites per se but rather small arthropods found in dense aggregations. It can however, in terms of diet, be considered the most highly specialized xenarthran to participate in the faunal interchange. In this regard it provides an interesting contrast to *Dasypus novemcinctus* and by extrapolation *Dasypus bellus* which although morphologically could be considered a myrmecophage probably had a diet consisting of a broad range of invertebrates, vertebrates, and plant material. While its diet is specialized, *Myrmecophaga* inhabits a large variety of habitats from tropical rainforest to the xeric scrub of the Chaco (Eisenberg & Redford 1999). Since all of the living xenarthran anteaters are highly specialized for feeding on ants and termites, within this context, the giant anteater, *Myrmecophaga*, can be considered the most generalized in terms of inhabiting a greater variety of habitats. The smallest form, *Cyclopes*, the most highly adapted, is strictly arboreal in habits, while the intermediate sized *Tamandua* is semi-arboreal with a distribution restricted to forest with closed canopy, so both are restricted to forests with a closed canopy. Since *Myrmecophaga* favors open country

savanna, it is not surprising that it was at least a minor participant in the GABI, since this type of habitat is considered to have provided the major access between North and South America (Webb 1978). Its dispersal northward was probably not limited by available habitat as much as by an available food source in the form of colonial ants and termites. With its distribution controlled primarily by the distribution of its food source and ant and termite diversity is greatest in the tropics and decreases rapidly with increasing latitude (Redford 1986), it is not surprising that the northern limit of *Myrmecophaga* in North America at El Golfo, Mexico at about 30 degrees, is similar to its southernmost latitude of 28 degrees in Argentina. The record of the anteater in northern Mexico is not only limited geographically but also chronologically, as it is based on a single record from the Irvingtonian El Golfo fauna (Shaw & McDonald 1987). Further study of Irvingtonian faunas in Mexico should provide additional records and enhance our understanding of the environmental and climatic conditions that permitted its short foray northward.

THE FEW, THE PROUD, THE CHOSEN

The corridor through the Panamanian isthmus connecting North and South America acted as a filter and prevented a wholesale exchange of taxa between the two continents (Webb 1978). At each stage of the interchange, with the first xenarthrans dispersing northward in the Huayquerian to the last in the Lujanian there was a diverse xenarthran fauna in South America from which to derive the dispersers. Yet despite the large number of potential candidates, whether pilosans (Fig. 3) or cingulates (Fig. 4), at each phase of the interchange only one taxon from each major group passed through the filter and reached temperate North America. Rather than thinking of the Panamanian corridor as a filter, perhaps a more accurate model with regard to the xenarthrans is that of a nested sieve. The different size holes in each layer of the sieve represent different ecological parameters that allowed different taxa to disperse varying distances northward but at the same time held back other taxa. This sieving essentially resulted in only one member of each xenarthran family at any one time during the interchange to disperse as far northward as temperate North America while others were restricted to the tropics (see discussion below). As previously discussed, each xenarthran participating in the interchange seems to have been a generalist, at least in comparison to other members of its family. As such, each xenarthran

that participated in the interchange was capable of not only avoiding potential ecological competition with the endemic North American mammals but with the more specialized members of their own respective family and with other members of its order. Each represents a distinct morphological and presumably ecological type within the broader categories of omnivory, insectivory, and herbivory (both browsers and grazers). This is reflected not only in each animal's anatomy but in size as well. The earliest representatives of each group in North America fall into well separated size classes and this distinction tends to be maintained even as each lineage increases in size (Fig. 5). The only exception seems to be in *Megalonyx*, a browser, which from the Blancan to the end of the Pleistocene has members comparable in size to *Paramylodon*, a grazer or at least a mixed intermediate feeder.

While the premaxillae of *Nothrotheriops* and *Eremotherium* are somewhat similar in morphology (Fig. 6) and both have been interpreted as browsers, the difference in size between the two genera would certainly indicate different feeding strategies. *Nothrotheriops* can be considered a low browser while *Eremotherium* would have been a high browser. The distribution of both genera overlapped in the eastern United States during the Irvingtonian but by the Rancholabrean there was no overlap in their distribution suggesting even more pronounced differences in their preferred habitat reflecting significant differences in their ecology and presumably diet.

Much closer in size and presumably with greater potential for ecological competition would have been *Nothrotheriops* and *Megalonyx*, both interpreted as browsers. Each has its own distinctive skull and dental morphology, which reflect different feeding strategies. Both genera co-occur in faunas in North America during the Rancholabrean but in inverse proportions so when one is common the other is rare. McDonald (1996) examined the distribution and association of ground sloths in parts of the western United States where the distribution of the two genera overlapped and found that it was more likely that either of the two genera would be found with the grazer *Paramylodon* in a fauna than with each other.

Within the cingulates, there is an omnivore/insectivore specialist for ants and termites in the form of *Dasypus*, the larger herbivorous pampathere *Holmesina*, and the even larger grazing glyptodont *Glyptotherium*. To this suite of cingulates in the Irvingtonian we can add

North American Land Mammal Age	North American Ground Sloths				South American Ground Sloths				South American Land Mammal Age
	Megalonychids	Nothrotheres	Megatheres	Mylodonts	Megalonychids	Nothrotheres	Megatheres	Mylodonts	
Rancholabrean	<i>Megalonyx jeffersonii</i>	<i>Nothrotheriops shastensis</i>	<i>Eremotherium laurillardii</i>	<i>Paramylodon harlani</i>	<i>Valgipes Xenocnus</i>	<i>Nothrotherium Nothropus Ocnopus</i>	<i>Megatherium Eremotherium</i>	<i>Scelidotherium Catonyx Mylodon Mylodontopsis Glossotherium Oreomylodon Lestodon</i>	Lujanian
					<i>Megalonychops</i>	<i>Nothropus Nothrotherium</i>	<i>Megatherium Eremotherium</i>	<i>Scelidotherium Catonyx Glossotherium Lestodon</i>	Ensenadan
Irvingtonian	<i>Megalonyx wheatleyi</i>	<i>Nothrotheriops texanum</i>	<i>Eremotherium laurillardii</i>	<i>Paramylodon harlani</i>	<i>Synhapalops</i>		<i>Megatherium</i>	<i>Scelidotherium Glossotherium</i>	Uquian
Blancan	<i>Megalonyx leptostomus</i>		<i>Eremotherium eomigrans</i>	<i>"Glossotherium" chapadmalense</i> <i>Glossotherium garbanii</i>	<i>Diheterocnus</i>	<i>Pronothrotherium Thalassocnus</i>		<i>Scelidotherium Proscelidodon Glossotherium</i>	Chapadmalan
						<i>Pronothrotherium Thalassocnus</i>	<i>Plesiomegatherium</i>	<i>Proscelidodon</i>	Montehermosan
Hemphillian	<i>Megalonyx curvidens</i> <i>Megalonyx mathisi</i> <i>Pliometanastes protistus</i>			<i>Thinobadistes wetzelli</i> <i>Thinobadistes segnis</i>	<i>Amphiocnus</i> <i>Megalonychops</i> <i>Neohapalops</i> <i>Paranabradys</i> <i>Pliomorphus</i>	<i>Pronothrotherium</i>	<i>Plesiomegatherium</i>	<i>Proscelidodon</i> <i>Megabradys</i> <i>Sphenotherus</i> <i>Acremylodon</i>	Huayquerian

Figure 3. Chronologic distribution of sloths in North and South America during the Great American Biotic Interchange.

North American Land Mammal Age	North American Cingulates			South American Cingulates			South American Land Mammal Age
	Dasypodids	Pampatheres	Glyptodonts	Dasypodids	Pampatheres	Glyptodonts	
Rancholabrean	<i>Dasypus bellus</i>	<i>Holmesina septentrionalis</i>	<i>Glyptotherium floridanus</i>	<i>Propraopus</i>	<i>Pampatherium Holmesina</i>	<i>Glyptodon Doedicurus Hoplophorus Lomaphorus Panochthus Sclerocalyptus</i>	Lujanian
				<i>Dasypus</i> <i>Eutatus</i>			<i>Propraopus</i>
Irvingtonian	<i>Dasypus bellus</i>	<i>Holmesina septentrionalis</i> <i>Holmesina floridanus</i>	<i>Glyptotherium arizonae</i> <i>Pachyarmatherium leiseyi</i>	<i>Pampatherium</i> <i>Glyptodon</i>			Uquian
Blancan	<i>Dasypus bellus</i>	<i>Holmesina floridanus</i>	<i>Glyptotherium texanum</i>			<i>Paraglyptodon Plohophoroides Trachycalyptus Urotherium</i>	Chapadmalalan
							Montehermosan

Figure 4. Chronologic distribution of cingulates in North and South America during the Great American Biotic Interchange.

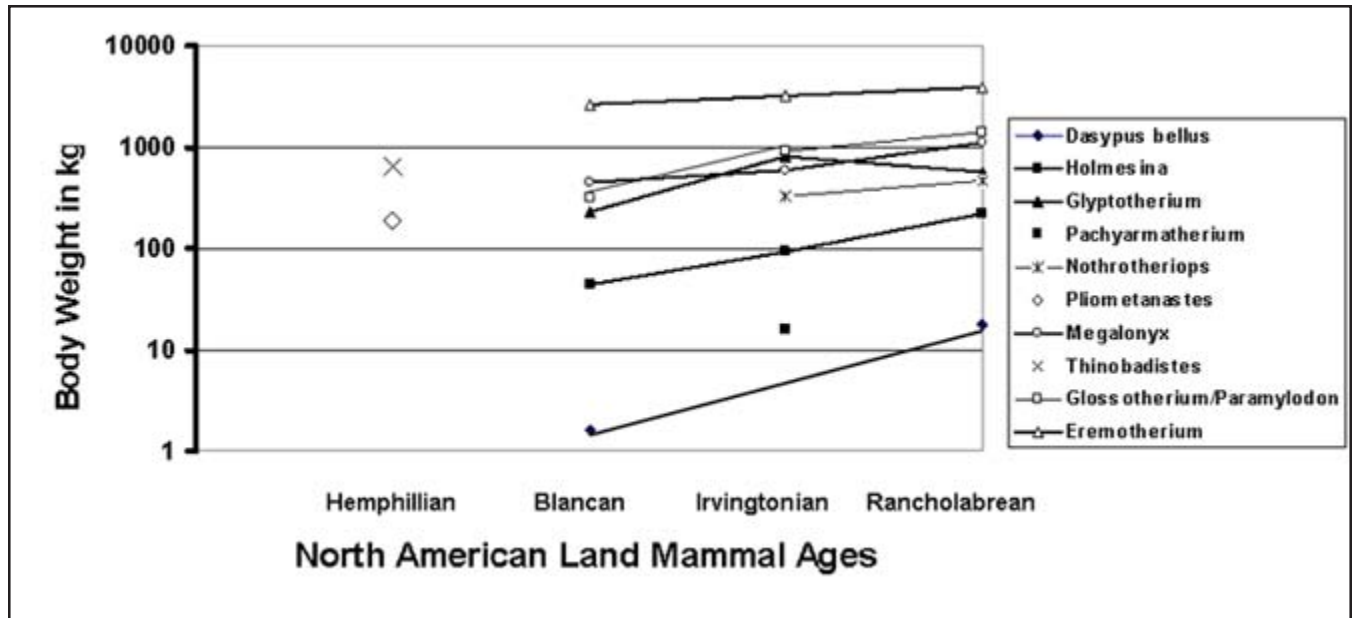


Figure 5. Change in body weight through time for North American xenarthrans.

the strange form, *Pachyarmatherium*, which unfortunately is not well represented in the fossil record thus preventing any real inferences about its paleoecology. For the other better known cingulates there does not seem to be any overlap in their ecology and as armored mammals, definitely nothing comparable existed in the North American fauna.

Webb (1976) identified a number of features of the interchange that need to be considered with regard to trying to determine the ecological attributes of the xenarthrans involved. One consideration is topographic. South American vertebrates dispersing northward may have utilized the mountain corridor connecting the Colombian Andes with the Central Highlands of Panama (Webb's high road) or alternatively followed a lowland coastal route as they moved northward (Webb's low road). Secondly, the types of habitat present in each corridor might aid in identifying more specifically what animals could or could not move northward through the region. Webb (1976) suggested that at the time of the interchange there was a broad spectrum of habitats represented in the crucial tropical regions, including mesic forests, an array of low gradient streams, and major throughways of scrub and savanna. Recent studies of pollen from the Panamanian isthmus by Graham (1992) indicates that by the middle Pliocene grass goes from virtually absent to a maximum of 7.5% indicating the

first appearance of some version of an open tropical dry forest. Prior to this time what is now the Panamanian isthmus consisted of low-lying islands with maximum elevations of 1200 to 1400 meters and habitat type was limited to those of the lowland tropics. These are the conditions that would have existed at the time of the dispersal of the two sloths *Pliometanastes* and *Thinobadistes*, but prevented the other xenarthrans as well as other South American mammals from dispersing northward. The presence of moderate habitat diversity with temperate environments at higher elevations, tropical dry forests with a significant grass component, and sufficient topographic relief to produce different rainfall regimes on the Atlantic and Pacific sides of the isthmus all developed after the middle Pliocene and it was at this time that the greatest variety of xenarthrans moved northward. This diverse set of habitats was eventually replaced by closed tropical forest resulting in the last wave of xenarthran dispersers adapted to this closed forest habitat but also unable to disperse any farther north than its northernmost extent. To quote Graham (1992:126) "The earlier stepping stones were highly selective in terms of habitat requirements for potential migrants, and the present bridge is a very recent pathway for dispersal ..." While his discussion centered on plants, the description is equally applicable to xenarthran dispersal via the isthmus. During the time of the interchange, the

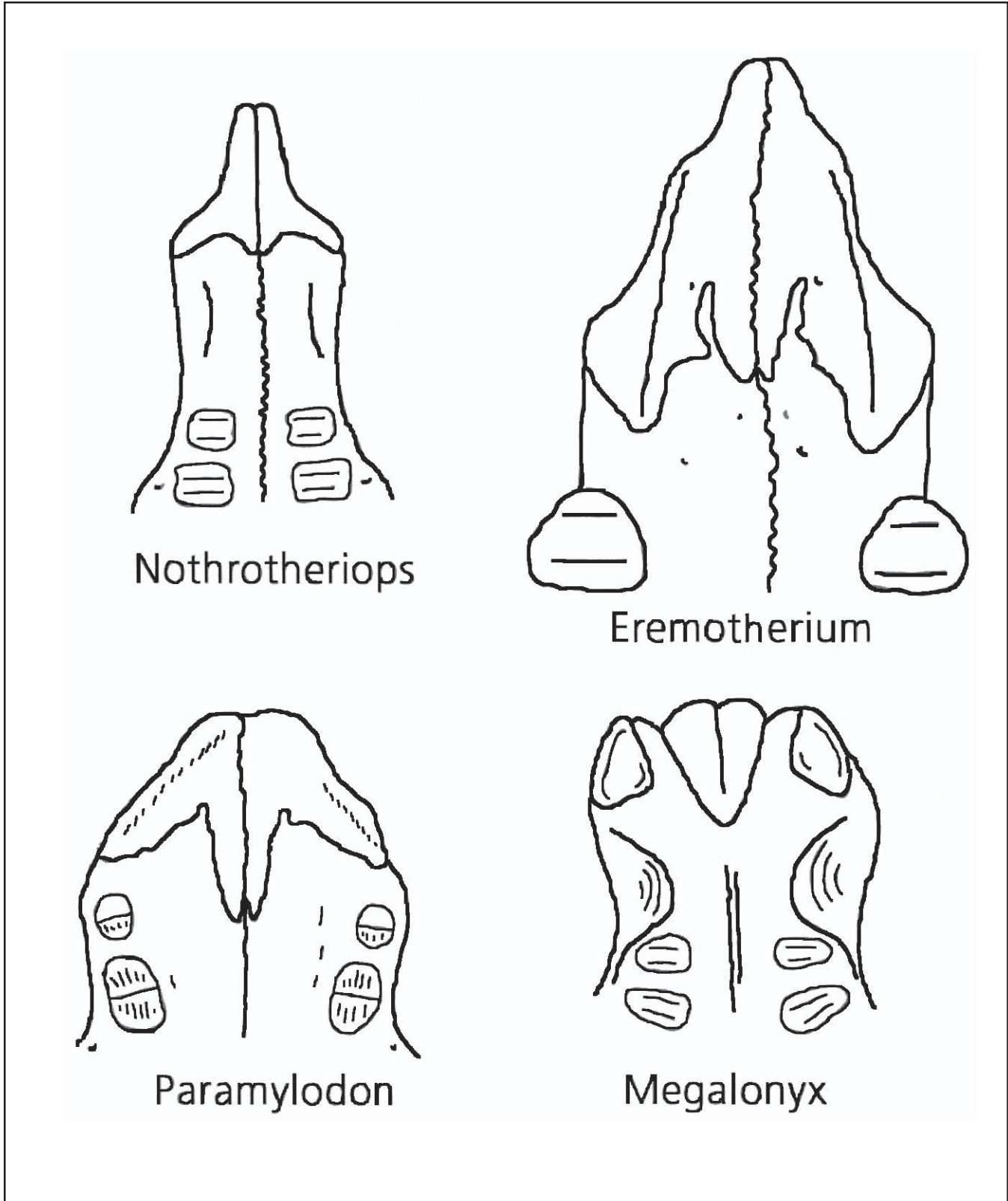


Figure 6. Shape of the premaxillae in four North American ground sloths. *Nothrotheriops*, *Eremotherium* and *Megalonyx* are interpreted as browsers, *Paramylodon* as a grazer or intermediate mixed feeder.

creation of a diversity of habitats provided the opportunities for a member of each of the different xenarthran groups to disperse northward. Given the wide range of feeding strategies and habitat preference represented by the xenarthrans that participated in the interchange, the xenarthran diversity in each habitat was probably low with different habitat preferences for each species. For example, Williams (1960) described the Tertiary topography of the interchange corridor in Guatemala as consisting of meandering rivers on broad floodplains and locally shallow lakes, a description that matches closely the interpretation of Gillette and Ray (1981) that *Glyptotherium* lived in lake and stream communities near permanent bodies of water. However, this type of habitat may not have been equally suitable for the sloth *Nothrotheriops*, which seems to have utilized drier habitats. It is very likely that many of the habitat preferences of xenarthrans eventually seen in faunas in North America may not have existed at the time of the interchange and are secondary adaptations. The entrance of different xenarthrans into North America at different times, *Glyptotherium* with its preference for wetter habitat in the Blancan and the more arid adapted *Nothrotheriops* in the Irvingtonian reflects the dynamics of changing habitat in the Panamanian isthmus over time which contributed to it acting as a sieve.

STARTING SMALL, GROWING LARGE

Except for *Dasybus bellus* all of the late Pleistocene xenarthrans in North America are considered part of the megafauna, i.e. > 100 kg body mass and our view of these animals is generally one of large size. However as shown in Figure 5, the founding representative of each lineage in North America was smaller than later members. Previous discussions of trends for an increase in size includes *Dasybus bellus* (Klippel & Parmalee 1984), *Holmesina floridanus* to *H. septentrionalis* (Edmund 1987; Hulbert & Morgan 1993), the *Megalonyx* series of chronospecies (McDonald 1977), *Nothrotheriops texanum* to *N. shastensis* (McDonald 1995), "*Glossotherium*" *chapadmalense* to *Paramylodon harlani* (McDonald 1995) and *Thinobadistes segnis* to *T. wetzelli* (Webb 1989).

In order to calculate an estimate of the body mass for each species of North American xenarthran the length of the femur was used. The femur was selected since it is preserved for all taxa. Fariña and Vizcaino (1997) have shown that relationship of the femur length to body mass in the armadillos scales closely to that of general-

ized mammals, while other bones such as the humerus scale differently because of its functional tie to digging. Choice of a single element reduces the error that might be generated by utilizing different skeletal elements in different taxa and at least makes the data more useful for comparison and identifying trends in size changes in the various lineages through time. Choice of this formula, (Formula F1 of Fariña et al. 1998 and Scott 1990) using the length of the femur between proximal and distal articular surfaces to calculate body weight, also has the added advantage as it generates a body weight estimate that can be compared with those calculated by these workers for various South American late Pleistocene xenarthran taxa. The formula utilized is: $\log_{10} \text{mass} = 3.485 \times \log_{10} (\text{femur length in cm}) - 2.9112$. The femora lengths used in calculating body weights are derived from personal measurements of specimens and from the literature. Whenever possible averages of specimens were used but in some cases only a single specimen is available for some taxa for a particular land mammal age.

The calculated weights of the various taxa listed in Table 1 provide a reasonable approximation for each species at different points in time. There have been few calculations of body weight for any of the North American xenarthrans although Jerison (1973) reported an estimated weight for *Paramylodon harlani* of 1100 kg, which is close to the value of 1392 kg derived from the formula used here.

All of the xenarthrans show a roughly similar increase in size: *Dasybus bellus* 1.8, *Holmesina* 4.9, *Pliometanastes* to *Megalonyx* 5.9, *Nothrotheriops* 3, and *Glossotherium-Paramylodon* 4.5. The smallest increase is in *Eremotherium* with 1.5, a not unexpected value given the already large size of *E. eomigrans*.

The only exception to this trend is *Glyptotherium*. While there is a 3.4 increase in size from the Blancan to Irvingtonian, the Rancholabrean species is smaller, just 0.71 times the size of its Irvingtonian predecessor. A decrease in size has been documented in other Pleistocene lineages of both herbivores such as *Bison* (Wilson 1992) and carnivores such as jaguars (Seymour 1993) and it appears that perhaps *Glyptotherium* in a similar way was responding to the dramatic environmental changes taking place in North America during the Rancholabrean.

Hulbert and Morgan (1993) in their study of the evolution of *Holmesina* in Florida noted that the rate of change in this lineage was variable, with rates being more

rapid, by a factor of 3 to 10 times, during some intervals than others. They observed that over a 2.3 million year interval the evolutionary rate of this lineage was two to three times greater than the “normal” evolutionary rate of 0.06 to 0.07 d calculated by Gingerich (1983). While similar studies have not been performed on any other North American xenarthrans and would be instructive, the study by Hulbert and Morgan does indicate that following its appearance in North America *Holmesina* underwent a rapid evolutionary response, as indicated by the increase in body size. As they noted, what was unusual about the evolution of *Holmesina* was not the rate of size increase, but rather that it was sustained almost continuously for such a long interval. This rapid evolutionary rate suggests that there were few ecological constraints on this lineage after entering North America and there existed only limited competition, if

any, with any of the endemic mammals. That the lineage was able to evolve rapidly in size suggests the absence of competition that previously existed with related species in South America. Marshall and Hecht (1978) described the North American ungulates as insinuating themselves into the South American biota, but this term seems equally applicable to all of the xenarthrans that entered North America and became successfully integrated into the fauna.

As a result of this increase in body size over time the various species of endemic mammals with which each xenarthran lineage would have ecologically competed would have changed. This would have been particularly true of the herbivorous sloths, pampatheres, and glyptodonts. One consequence resulting from a change in body size of the herbivorous xenarthrans would have been their feeding strategies. Smaller herbivores tend

Table 1. North American xenarthrans from each North American Land Mammal Age and their calculated body weights.

Taxon	North American Land Mammal Age	Length of Femur in cm	Calculated Body Weight in kg
<i>Dasypus bellus</i>	Blancan	13.72	10.07
<i>Dasypus bellus</i>	Rancholabrean	15.6	17.68
<i>Holmesina floridanus</i>	Blancan	20.3	44.27
<i>Holmesina septentrionalis</i>	Irvingtonian	25	91.48
<i>Holmesina septentrionalis</i>	Rancholabrean	33.2	216.27
<i>Glyptotherium texanum</i>	Blancan	32.6	230.74
<i>Glyptotherium arizonae</i>	Irvingtonian	46.4	789.68
<i>Glyptotherium floridanum</i>	Rancholabrean	42.1	562.65
<i>Pachyarmatherium leiseyi</i>	Irvingtonian	15.0	15.42
<i>Pliometanastes protistus</i>	Hemphillian	30.6	185.05
<i>Megalonyx curvidens</i>	Hemphillian	30.6	185.05
<i>Megalonyx leptostomus</i>	Blancan	39.3	442.64
<i>Megalonyx wheatleyi</i>	Irvingtonian	42.8	595.93
<i>Megalonyx jeffersonii</i>	Rancholabrean	50.9	1090.35
<i>Nothrotheriops texanum</i>	Irvingtonian	35.9	322.91
<i>Nothrotheriops shastensis</i>	Rancholabrean	39.8	462.59
<i>Eremotherium eomigrans</i>	Blancan	65.2	2584.40
<i>Eremotherium laurillardi</i>	Irvingtonian	69	3148.54
<i>Eremotherium laurillardi</i>	Rancholabrean	73.7	3961.48
<i>Thinobadistes segnis</i>	Hemphillian	43.8	645.89
“ <i>Glossotherium</i> ” <i>chapadmalense</i>	Blancan	35.5	310.54
<i>Paramylodon harlani</i>	Irvingtonian	48.4	914.81
<i>Paramylodon harlani</i>	Rancholabrean	54.6	1392.47

to be more selective in their feeding especially with regard to consuming those parts of the plant with higher nutritive value and least defended, while large herbivores tend to consume a wider selection of plant parts with varying nutritive value (Guthrie 1984). The ability of these relatively small herbivorous xenarthrans to disperse may have been facilitated by their ability to utilize the parts of plants with the highest nutritional value present in the more tropical parts of the corridor. As they increased in size, their ability to compete with the native herbivores and success in becoming integrated into the North American fauna may have been facilitated by being able to utilize a wider variety of plant parts with relatively lower nutritional value which would have been facilitated by their low basal metabolism. Their success in temperate North America with increased seasonality and a restricted seasonal flush of nutrients during a more limited growing season may have been a result of the combination of their inherent digestive capability resulting from an extended digestive period and better absorption of nutrients which would have increased along with their increase in body size which would have increased the transit time in the intestines.

INTEGRATION BUT NOT RADIATION

As noted above, generally only one representative of each major xenarthran group (essentially equivalent to the family) dispersed into North America. While most of the xenarthrans that dispersed into North America can be considered "successful" in the sense that many survived until the Pleistocene extinctions, this is not true for all. There are some taxa that following their dispersal northward did not become established and are present in North America for a very limited time. The first mylodont to enter North America in the Hemphillian, *Thinobadistes*, appears to have become extinct by the end of that land mammal age (Webb 1989). The strange cingulate *Pachyarmatherium* is known from the late Blancan through the middle Irvingtonian (Downing & White 1995) and the only record of the giant anteater, *Myrmecophaga tridactyla*, is known from a single Irvingtonian locality (Shaw & McDonald 1987). While those xenarthrans that did survive filled a niche that permitted them to become integrated into the North American mammal fauna and survive until the Pleistocene extinction event, in none of these groups is there any type of radiation or diversification similar to what occurred in South America with many of the northern invaders.

While there are evolutionary changes in each of the lineages after their appearance in North America

there are few that show any major modifications of the basic bauplan. Each lineage consists of a series of chronospecies distinguished by various morphological characters or a difference in size but none greatly depart from the ancestral morphology. The modification of the caniniform teeth from *Pliometanastes* to *Megalonyx* reflects one of the more radical morphological changes in any of the North American xenarthrans. The occlusal surfaces of the caniniforms in *Pliometanastes* form at an oblique angle to the axis of the tooth so that occlusion produced a shearing of vegetation. This pattern of occlusion is present in the earliest megalonychids and is retained to some degree in most of the later members of the family. *Megalonyx* departs from this pattern in that the occlusal surface of the caniniforms is perpendicular to the axis of the tooth so that they functioned to crush or hold rather than shear. As the caniniforms in *Megalonyx* become greatly enlarged there is a concurrent reduction in the size of the mandibular spout (Fig. 7). While this morphology in *Megalonyx* is specialized relative to other megalonychids, it did not develop until after the lineage was present in North America. The morphology of the caniniform in *Pliometanastes*, the ancestor of *Megalonyx*, is more similar to that of the basic morphology seen in other megalonychids and presumably more generalized ecological specializations compared to *Megalonyx*.

In the *Glossotherium-Paramylodon* lineage one striking evolutionary change is the reduction in the size of the anteriormost upper teeth or caniniforms (McDonald 1995). There are two morphologies to the occlusal surface of the tooth in all members of the lineage from the Blancan to the Rancholabrean and in the earlier members there is also a distinct size difference between the two morphs. In Rancholabrean *P. harlani* the two morphs are still present but there is no longer any distinction in size and in many individuals the caniniforms were never present. The two tooth morphs are associated with two skull morphs and the inference is that this represents sexual dimorphism in the species. It would appear that there is a decrease in sexual dimorphism through time in this mylodont lineage. Like the other North American xenarthrans, the mylodonts displayed evolutionary changes within the lineage but no morphological innovation that allowed them to diversify.

Within the *Holmesina* lineage numerous skeletal and dental modifications have been described that permit the earliest and latest species to be readily distinguished (Edmund 1987; Hulbert & Morgan 1993), yet

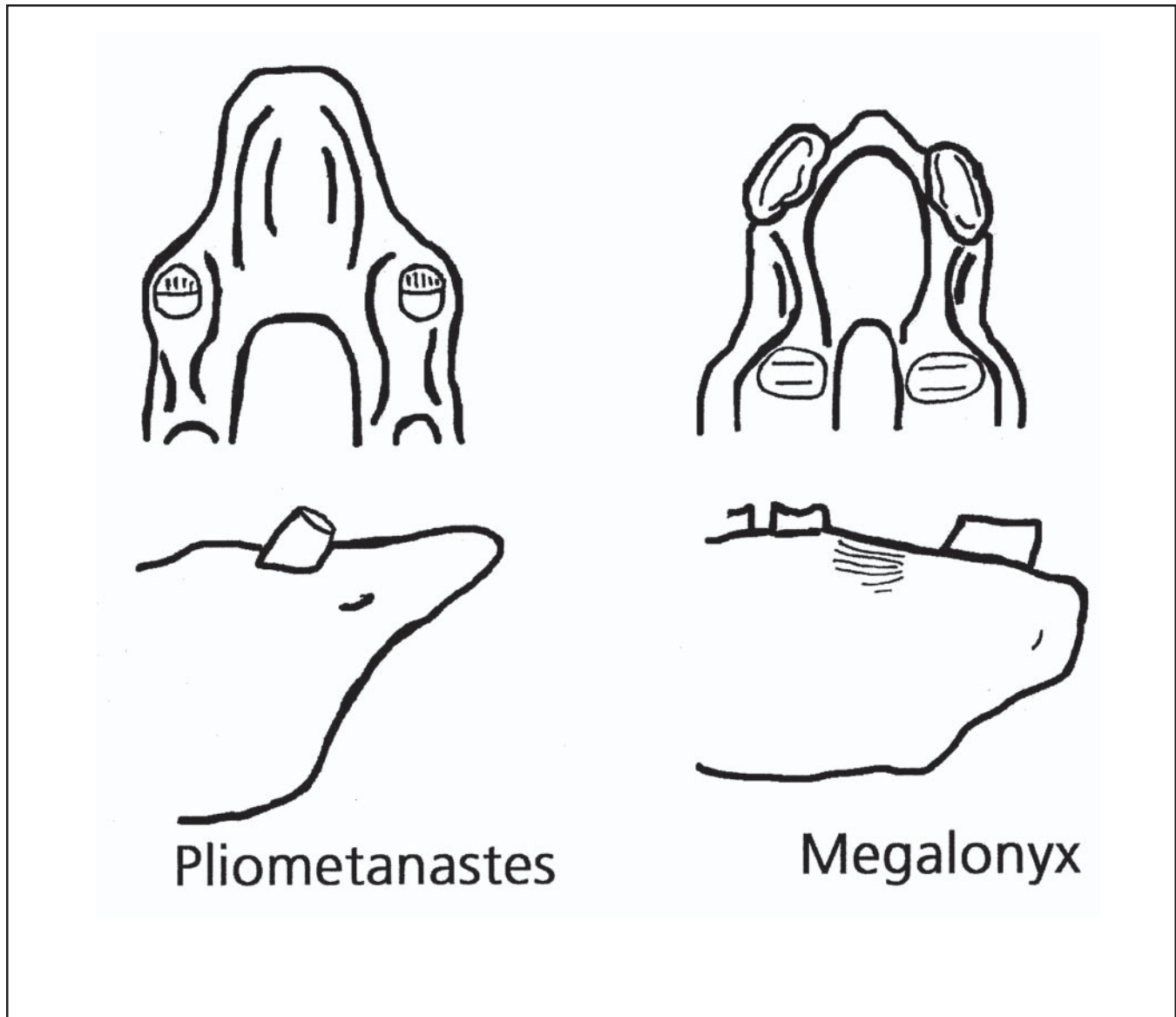


Figure 7. Comparison of the caniniform and shape of the mandibular spout in *Pliometanastes* and *Megalonyx*.

as in other xenarthrans there are no new modifications or real taxonomic diversity, merely a series of chronospecies.

All in all each lineage of North American xenarthrans remains rather conservative in its morphology. As discussed above the one trait they all have in common is a general increase in body size.

DISTRIBUTION – OPPORTUNITIES AND LIMITS

The only extant xenarthran in temperate North America is the armadillo, *Dasypus novemcinctus*, whose pres-

ence is essentially a Holocene event. While this species is the most widespread of all living armadillos, extending as far south as southern Brazil, the northern edge of its range in the United States is limited and essentially confined to the Gulf Coast and southeastern United States, although on the Great Plains the species has dispersed as far north as Nebraska. There is a strong similarity in its distribution and that of two of its extinct cingulate relatives in North America, *Dasypus bellus* and *Holmesina* spp., and the sloth, *Eremotherium*. This list can be somewhat expanded if *Glyptotherium* is included. While the Blancan records of *Glyptotherium* extend

westward to southern Arizona, there is a progressive contraction of the range of the genus to the Gulf Coast and southeastern United States and by the Rancholabrean its distribution roughly coincides with that of *Dasyus novemcinctus* today. These patterns of distribution generally correspond to North American patterns of precipitation in which seasonally the greatest amount of rainfall in the United States is in the southeastern part of the continent (World Meteorological Organization [F. Steinhauser, Tech. Super] 1979). Gillette and Ray (1981) described the habitat requirements of *Glyptotherium* as restrictive, requiring proximity to standing water in a region with extensive lowland terrain, lush tropical or subtropical vegetation, a warm climate without excessive extremes of temperature, and relatively high constant moisture. The last factor, which is dependent on the annual precipitation, was needed to maintain the permanent bodies of water and abundant vegetation. While these factors may have limited the northward expansion of *Glyptotherium* in temperate North America, none of these would have necessarily been a limiting factor to the northward dispersal through the tropics of the earliest members of this lineage. A long-term drying trend from the Blancan to Rancholabrean resulting in increasing aridity in the southwest (Thompson 1991) may account for the contraction of the range of *Glyptotherium* eastward and the concurrent westward contraction of the range of *Nothrotheriops*.

In contrast to *Glyptotherium*, the ground sloth *Nothrotheriops*, contracts its range in the opposite direction. Initially widespread in the Irvingtonian from coast to coast by the Rancholabrean the genus is restricted to the western United States with the largest number of occurrences in the southwest (Akersten & McDonald 1991).

The single record of giant anteater from El Golfo, Mexico also indicates a maximum northward expansion of the range of this species in the Irvingtonian (Shaw & McDonald 1987) followed by a retraction to its present northern limit in southern Guatemala. As with the changes in distribution of *Glyptotherium* and *Nothrotheriops* this probably reflects the environmental change in North America that took place from the Irvingtonian to the Rancholabrean. The impact on the distribution of *Myrmecophaga* due to climatic change may not have been direct, but rather was a secondary effect, the primary impact being on the animal's food source, colonial termites and ants.

Not all of the North America xenarthrans were as restricted in their distribution. By the Rancholabrean, the oldest lineage of sloths in North America, *Megalonyx*,

is also the most widespread and ranged above the Arctic Circle (McDonald et al. 2000) to both coasts and into southern Mexico (McDonald 2002). While not quite as widespread as *Megalonyx*, the mylodont *Paramylodon* is known from as far north as Washington and Montana, from coast to coast and south into Mexico. The earliest records of both lineages, presumably recording their appearance shortly after dispersal into North America are limited to the southern United States and Mexico but seem to be followed by a fairly constant expansion of their respective ranges across the continent during the Irvingtonian and Rancholabrean.

THE FORGOTTEN DISPERSERS – XENARTHTRANS IN CENTRAL AMERICA

Webb (1985) identified two principle phases in the GABI. The first phase includes those animals that entered either continent prior to the establishment of the land bridge. The earliest arrivals from South America, two sloths in the Hemphillian of North America were termed “heralds of the south”; this was followed by a large set of bridge-crossers, which he called “legions”. Both of these groups dispersed northward at a time when the Panamanian land bridge contained a mosaic of habitats that preceded the establishment of the tropical lowland forest that exists today. There is however a third set of dispersers including a number of xenarthrans present in Central America today that probably entered the region after the establishment of the tropical lowland forest, a habitat to which they are restricted. This stage is identified in Webb (1985:fig. 1) as the final tropical mingling. In keeping with Webb's terminology of “heralds” and “legions” I propose that this last group be called “camp followers”. Unlike the earlier xenarthran dispersers, which utilized a variety of habitats in the interchange corridor, most members of this last suite are closely associated with a specific habitat, tropical rainforest.

While the focus tends to be on those xenarthrans (and other dispersers of South American origin) that were able to disperse to temperate latitudes in North America, there is a subset of dispersing xenarthrans and other South American mammals restricted to the tropical portions of North and Central America. Some are extinct, such as the toxodont, *Mixotoxodon*. However, with regard to the xenarthrans, unlike their temperate counterparts that became extinct, many are still present in Central America and comprise a significant part of the fauna. These include the anteaters, *Myrmecophaga tridactyla*, *Tamandua mexicana*, and *Cyclopes didactylus*, the tree sloths *Bradypus variegatus* and

Choloepus hoffmanni and the armadillos, *Cabassous centralis* and *Dasyurus novemcinctus*. Except for *D. novemcinctus*, which as a generalist has the widest distribution of any living xenarthran, these xenarthrans are restricted to a warmer tropical habitat, which has limited their northward expansion. Unfortunately the fossil record of Central America is poorly documented and none of these taxa including *D. novemcinctus* is known from fossils, so we have no idea how long any of them have been in the region. While it is assumed that they are relatively new arrivals and most likely did not move northward until after the formation of the tropical forests, it is possible they may have a long established history in the northern Neotropics. However, what their modern presence does indicate is that the dispersal of xenarthrans out of South America is richer than the traditional view of only looking at those forms that made it into the North American temperate zones.

Just as there are modern xenarthrans unable to disperse farther north than the tropics so the northern part of their range is restricted to Central America, such seems to have also been the case for some extinct taxa as well. The fossil record of xenarthrans in Central America is limited and most records are from the widespread *Eremotherium laurillardi* (Cartelle & DeIuliis 1995). One good example of the potential richness of the diversity of the xenarthran dispersal limited to tropical North and Central America is the endemic megalonychid sloth genus, *Meizonyx* from El Salvador (Webb & Perrigo 1985). This large species is known from a single specimen but clearly indicates that along with those taxa that were able to disperse farther north, there are taxa that participated in the interchange that are restricted to the tropics. It is very likely that continued fieldwork in Central America will result in the discovery of other extinct xenarthra that were part of the GABI but because of their ecology did not disperse north of the tropics.

SUMMARY

While topography and ecology have been two major factors that have been discussed with regard to the GABI, another factor that needs to be examined in more detail is climate at the time of the interchange. Thompson (1991) reviewed evidence that indicates that during the early and middle Pliocene (prior to ~2.4 Ma, the time of appearance of Webb's legion from the south) the climate in the western United States was less seasonable (more equable) and generally more humid and the terrestrial record parallels that seen in oxygen isotope

records in the North Pacific. While these factors may not have been quite as critical to other mammals, this may be a much more critical factor to xenarthrans with their overall lower basal metabolism (McNab 1985).

Climate during the interchange was more equable (Thompson 1991) and upon their initial appearance in temperate North America many xenarthran taxa became widely distributed. The increase in seasonality during the Pleistocene resulted in major shifts in the range, often a reduction for some taxa such as *Nothrotheriops* and *Glyptotherium*. Their sensitivity to temperature reflects their low basal rates of metabolism and a high conductance resulting in a low body temperatures and a high lower limit of thermoneutrality at given body mass (McNab 1985). This thermal sensitivity may also be an important factor with regard to the trend of increase in overall body size in all of the North American xenarthrans. An increase in overall size would have provided greater thermal inertia. This was probably an important factor particularly for the cingulates with their general lack of hair as insulation. It would seem that this group would be most susceptible to climate, particularly seasonal temperature extremes and this is reflected in their more limited distribution in North America compared to sloths. Temperature (and possibly humidity) also seems to be a primary factor regarding the distribution of two sloths, *Nothrotheriops* and *Eremotherium*, and the anteater, *Myrmecophaga*. As the largest of the sloths, it would seem that *Eremotherium* would possess the greatest amount of thermal inertia and thus have a greater tolerance to colder temperatures. Two other sloths, *Megalonyx* and *Paramylodon*, do not seem to have been affected by this environmental change and seemed to have been widespread until the time of their extinction. The range of both genera extended farther north than any of the other xenarthrans, with *Megalonyx* crossing the Arctic Circle (McDonald et al. 2000). This may have been a consequence of their larger size and subsequently better thermal inertia and by the end of the Pleistocene both genera are exceeded only by *Eremotherium* in size. It is possible both may have developed better insulation or even had higher basal metabolisms but we have no direct evidence for either of these adaptations. If temperature was not a limiting factor in the continued northward dispersal in *Eremotherium* then the availability of food may have been the limiting factor. While *Eremotherium laurillardi* is widely distributed (Cartelle & DeIuliis 1995), its distribution is centered in tropical South America and only extends to the subtropics in South America and as a

general rule to the subtropics of North America. The distribution of *Eremotherium* may have therefore been limited secondarily by preferred vegetation found in tropical to semi-tropical rainforests and not by temperature.

While this paper attempts to review what is known of the paleoecology of fossil xenarthrans as a means to better understand their success as members of the GABI, much more data is needed. The data currently available ranges from very comprehensive such as for the sloth *Nothrotheriops*, for which we have dung and detailed knowledge of its diet to the small cingulate, *Pachyarmatherium*, which consists of a few meager specimens in the fossil record. Despite this spotty database there do seem to be a few common features shared by those xenarthrans that participated in the GABI and established themselves as members of the North American mammalian fauna.

1. Despite the potential variety of xenarthrans in South America only one member of each major xenarthran group (roughly equivalent to a family) participated in the faunal interchange and dispersed northward into temperate North America at any particular phase of the GABI.
2. Each of these dispersers represent an ecological adaptation distinct from all other xenarthran dispersers so there does not appear to have been any ecological competition between any members of a particular xenarthran cohort participating at any phase of the interchange. This includes a variety of feeding strategies including omnivore/insectivore – *Dasyopus bellus*; specialized myrmecophage – *Myrmecophaga tridactyla*; a variety of herbivores including two low browsers – *Nothrotheriops* and the *Pliometanastes/Megalonyx* lineage, each with different skull morphologies indicating different feeding strategies; a high browser – *Eremotherium*; an aquatic grazer – *Glyptotherium*; an intermediate feeder on coarse vegetation/ grazer – *Holmesina* and a large grazer/ intermediate feeder – *Glossotherium/Paramylodon* lineage. There is insufficient data on the small cingulate, *Pachyarmatherium*, to make any inferences as to its feeding strategy or ecology. Given the variety of habitats present in the corridor used by these dispersers, each was utilizing different habitats with probably limited overlap. Another aspect of the xenarthrans participating in the GABI is distinct body sizes with very little overlap unless they have different feeding strategies i.e. by the late Pleistocene, *Megalonyx*, a browser is similar in body size to *Paramylodon*, a grazer or intermediate mixed feeder.
3. Ecologically the dispersing member was more of a generalist than other members of the family. This may include morphological features that lack some of the extreme specializations seen in other members of the family or by having a more generalized ecology or habitat preference. Any specialization seems to have evolved after the lineage entered North America.
4. Dispersing members tended to be small with a subsequent increase in size following their entry into North America. This size increase may indicate they lacked any ecological competitors among the native North American mammals and thus filled an empty niche or alternatively may merely indicate a response to cooling temperatures and greater seasonality in a temperate environment and provided thermal inertial to compensate for a low basal metabolism and high thermal conductance.
5. While evolutionary change did take place in the North American xenarthrans after they became integrated into the North American mammalian fauna, they did not diversify or undergo any adaptive radiation. They seem to have avoided ecological competition with endemic members of the North American fauna but the ecological niche they filled did not permit any diversification.

ACKNOWLEDGEMENTS

At the time I went to Florida to study with Dave Webb for my masters thesis, my interest was confined to ground sloths. Thanks to both his mentoring and through discussions and his publications, my horizons were broadened to consider the broader implications of the role of xenarthrans within the scope of the Great American Biotic Interchange. The development of the ideas presented here has not been one of punctuated equilibrium but rather gradualistic and have evolved over many years. An initial version of this paper was first presented in a talk entitled “Gallivanting Gravigrades and Sedentary Sloths: Ecological Adaptations of Xenarthrans and the Great American Faunal Interchange” presented at the

Fifth International Theriological Congress in Rome, Italy in August, 1989 at a symposium organized by Dave Webb and Rosendo Pascual entitled Late Cenozoic Mammals: Dispersal Between Americas. During the intervening years many of the initial ideas have been refined and it is with great pleasure that I contribute this paper on a topic that has been of major interest to my professor, Dave Webb. For better or for worse, the ideas developed here are a result of his influence. I would like to extend my appreciation to the two anonymous reviewers for their insightful comments.

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