Hypsodonty in Pleistocene ground sloths

M. SUSANA BARGO, GERARDO DE IULIIS, and SERGIO F. VIZCAÍNO

Although living sloths (Xenarthra, Tardigrada) are represented by only two genera, their fossil relatives form a large and diverse group. The evolution of hypsodonty, the crown height of a tooth, has traditionally been viewed as a response to dietary shifts toward abrasive vegetation. But recent work indicates that hypsodonty is also due to the higher prevalence of grit and dust in more open environments. The teeth of sloths are both high-crowned and open-rooted, or hypselodont, but distinctions between the selective factors acting to produce differing degrees of hypsodonty have not been rigorously considered. A comparative analysis of hypsodonty was performed in eleven species of Pleistocene sloths. It suggests that differences in hypsodonty may be explained by dietary preferences, habitat and habits. Among mylodontids, morphologic and biomechanical analyses indicate that hypsodonty was unlikely to be due solely to feeding behavior, such as grazing. Some mylodontids (e.g., *Scelidotherium leptocephalum*, *Lestodon armatus*, *Glossotherium robustum*, *Mylodon darwini*) were capable diggers that likely dug for food, and ingestion of abrasive soil particles probably played a considerable role in shaping their dental characteristics. Increased hypsodonty over time in *Paramylodon harlani*, however, is apparently due to a change in habitat from closed to more open environments. Geographical distributions of the megatheriids *Eremotherium* and *Megatherium* indicate differing habitats as possible factors in hypsodonty differences. In summary, among Tardigrada hypsodonty is apparently affected by diet, habitat and habit. The absence of enamel must be responsible for much of the hypsodonty observed in xenarthrans, which obscures the interpretation of contribution of each of the mentioned factors.

Key words: Pleistocene, Xenarthra, Tardigrada, hypsodonty, diet, habits, habitat.

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Introduction

Hypsodonty has traditionally been linked to dietary preferences, particularly to grazing habits (Simpson 1951, 1953; McNaughton et al. 1985; MacFadden 1997). These authors considered the increase in tooth crown height as an adaptation for an abrasive herbivorous diet, consisting primarily of grasses. Fortelius (1985), Janis (1988; 1995), and Janis and Fortelius (1988), in their analyses of extinct and extant ungulates, noted that another important factor in determining hypsodonty is the accumulated grit or dust on plants consumed in more open habitats. Ungulates feeding at ground level in open habitats, even with diets containing little grass, are more hypsodont than those living and foraging in closed habitats. In other words, both habitat preference (and therefore abrasive particles such as dust and grit) and dietary preference are highly important determinants of degree of hypsodonty. Williams and Kay (2001) examined the evolution of increased molar crown height in extant African ungulates and South American rodents in relation to ecological and behavioral variables. They found that both diet and exogenous dust and grit play a role in shaping the evolution of hypsodonty.

Xenarthra comprises armadillos and glyptodonts (Cingulata), anteaters (Vermilingua), and sloths (Tardigrada), and are considered by some authors as one of the four major clades of placental mammals (the other three being Afrotheria, Euarchontoglires and Laurasiatheria; see Murphy et al. 2001; Madsen et al. 2001; Delsuc et al. 2003). Other authors, following McKenna (1975), consider the Xenarthra as the sister group to all other placentals, the Epitheria. While debate continues on the relationships among these groups of mammals, it does not change the fact that xenarthran dental morphology is extremely different from that of the other placental mammals. For convenience, we refer to non-xenarthran placental mammals as "epitherians". The homodont teeth, which lack enamel, are reduced in number and are hypsodont and ever growing (i.e., hypselodont). As the homology of xenarthran teeth with those of other mammals has not been established, xenarthran teeth have traditionally been referred to as molariforms. Some sloths also have a canine-like tooth, termed a caniniform, anteriorly in the oral cavity.

Although hypsodonty is well developed in all Tardigrada, the giant Pleistocene ground sloths apparently achieved the greatest development of this feature (Figs. 1, 2). A great

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number and diversity of small and medium sized tardigrades, probably arboreal in habits and folivorous in diet have been recorded from the Santacrucian and Friasian South American ages (early and middle Miocene) (Scillato-Yané 1986; White 1997). Based on their narrow muzzles and teeth bearing cutting, transverse lophs, McDonald (1997) suggested that these early forms might have been browsers. Thus, it might be expected that they were less hypsodont than the Pleistocene forms, especially if they inhabited more closed and forested environments. Scillato-Yané et al. (1987) indicated that increased hypsodonty was among the evolutionary trends of the Nothrotheriinae *sensu* Hoffstetter 1958 (late Oligocene to Pleistocene), but this trend has not been quantified. Nothrotheres are excluded from this analysis. As the dental formula of Pleistocene nothrotheres is reduced, compared to mylodontids and megatheriids, due to loss of the most anterior tooth, equivalent comparisons cannot be made with the taxa studied here. Megalonychids are also excluded due to inaccessibility of material.

The hypsodonty indices for ungulates calculated by Janis (1988, 1995) and Janis and Fortelius (1988) are determined as unworn m3 height divided by m3 width, as the third lower molar is usually the tooth with the greatest crown height in ungulates. However, as the cheek teeth of xenarthrans cannot be homologized with those of "epitherians", this hypsodonty index is unsuitable for sloths. A further consideration is that the hypselodont teeth of xenarthrans have very delicate basal portions that are almost never preserved. For these reasons, xenarthran specialists have recognized that the relative increase in depth of the jaw in sloths reflects increased hypsodonty. Kraglievich (1930) noted that depth of the mandible is important in determining evolutionary relationships among megatheriines. Later, Zetti (1964) made the first attempt to quantify the degree of hypsodonty in megatheres and developed a Hypsodonty Index where a higher HI reflects increased hypsodonty. De Iuliis (1996), De Iuliis and Cartelle (1999), and Saint-André and De Iuliis (2001) applied this index to various megatheriine species. Similarly, McDonald (1995) compared hypsodonty in North American mylodontine ground sloths using the same index.

The goal of this work is to quantify the degree of hypsodonty in different species of Pleistocene megatheriid and mylodontid ground sloths in order to determine whether hypsodonty is correlated with dietary behavior, habits, and habitat. Bargo and De Iuliis (1999) made a first approach on this theme, analyzing hypsodonty of the two giant Pleistocene megatheres, *Megatherium americanum* Cuvier, 1796, and *Eremotherium laurillardi* (Lund, 1842). Saint-André and De Iuliis (2001) compared hypsodonty among several *Megatherium* species (*Megatherium altiplanicum* Saint-André and De Iuliis, 2001, *M. medinae* Philippi, 1893, *M. tarijense* Gervais and Ameghino, 1880); and De Iuliis and Cartelle (1999) between *Eremotherium laurillardi* and *Eremotherium eomigrans* De Iuliis and Cartelle, 1999. Neither study, however, noted possible correlations of hypsodonty with diet, habits or habitat.
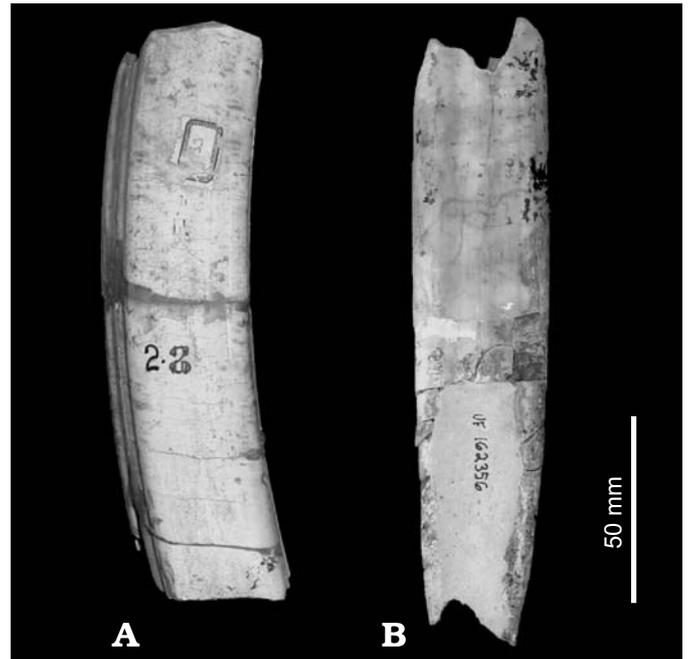

Fig. 1. **A**. MLP 2-3, molariform of *Megatherium americanum* Cuvier, 1796, Pleistocene, Buenos Aires province, Argentina. **B**. UF 162356, molariform of *Eremotherium eomigrans* De Iuliis and Cartelle, 1999, Pleistocene, Alachua, Florida, USA. Because of the homodonty of the upper and lower megatheriine molariforms, determining the position of the isolated teeth is not reliable (except for M1, M5, and m5, but these do not have the ridges and grooves so prominent as in the illustrated material); thus, we have not attempted to identify the exact position of these teeth, but only figure them to show their occlusal features and the development of the tooth crown height.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BM(NH), Natural History Museum, London, England; F:AM, Frick Collection, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; ILSB, Instituto de La Salle, Bogotá, Colombia; LACMHC, Los Angeles County Museum, Hancock Collection, Los Angeles, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCL, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MHM, Museo Histórico Municipal, General Belgrano, Provincia de Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMCIPAS, Museo Municipal y Centro de Investigaciones Paleontológicas de Salto, Buenos Aires Province, Argentina; MMP, Museo Municipal de Ciencias Naturales, Mar del Plata, Argentina; MNHN, Museo Nacional de Historia Natural de Montevideo, Uruguay; MNHNM, Museo Nacional de Historia Natural, Madrid, Spain; MNHNP, Muséum National d'Histoire Naturelle, Paris, France; MNP, Museo Nacional de Panamá, Panamá; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MPBC, Museo de Paleontología Rodrigo Botet (= Museu de Ciències Naturals de València), Valencia, Spain; NRM, Swedish Museum of Natural History, Stockholm, Sweden; ROM, Royal Ontario Museum, Toronto, Ca-

nada; UF, University of Florida, Vertebrate Paleontology Collection, Gainesville, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, USA; ZMUC, Zoologisk Museum Universitat Copenhagen, Copenhagen, Denmark.

Other abbreviations.—DM, depth of the mandible; HI, Hypsodonty Index (HI = mandibular height/tooth row length × 100); LTR, length of the molariform tooth row; OSA, occlusal surface area.

Material and methods

The taxa analyzed included the mylodontids *Glossotherium robustum* (Owen, 1842), *Lestodon armatus* Gervais, 1855, *Mylodon darwini* Owen, 1839, and *Scelidotherium leptocephalum* Owen, 1840 from southern South America; *Paramylodon harlani* (Owen, 1840) from North America; and the megatheriids *Megatherium americanum* from southern South America, *M. altiplanicum*, *M. tarijense*, *M. medinae* from north central and northwestern South America, *Eremotherium laurillardi* from northern South America and North America, and *E. eomigrans* from Florida, USA (Figs. 1, 2). The specimens studied are listed in Table 1.

As the morphologies of the mandible and dentition differ between the megatheriines and mylodontids analyzed in this study, HI was standardized as follows: depth of the mandible (DM), measured at the level of the third molariform tooth, divided by length of the molariform tooth row (LTR). Although the indices obtained cannot be compared with those of ungu-
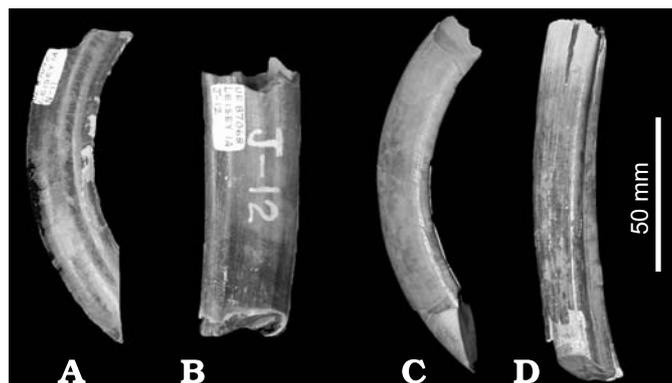
Fig. 2. **A**, **B**. *Paramylodon harlani* (Owen, 1840), early Pleistocene, Hillsborough, Florida, USA. **A**. Left upper caniniform, UF 87042. B. Left M2, UF 87068. **C**, **D**. *Glossotherium robustum* (Owen, 1842), Pleistocene, General Belgrano, Buenos Aires province, Argentina. **C**. Left upper caniniform, MHM no catalogue number. **D**. Left M3, MHM no catalogue number.

lates, they represent a useful reference for comparing the degree of hypsodonty among ground sloths.

Results

Table 1 provides the list of studied specimens. Table 2 provides specimen measurements and calculated HI. Table 3 includes the means and standard deviations, where applicable, for each species. In mylodontids mean HI ranges between 0.62 (*Lestodon armatus*) and 0.91 (*Scelidotherium leptocephalum*). HI of *Glossotherium robustum* and *Para-*

Table 1. List of specimens.

Mylodontidae
Glossotherium robustum
    MLP 3-136
    MLP 3-138
    MLP 3-140
Lestodon armatus
    MLP 3-3
    MLP 3-28
    MLP 3-29
    MLP 3-30
Mylodon darwini
    MACN 991
    MLP 3-125
    MLP 3-126
Paramylodon harlani
    LACMHC 1718-LR-20
    LACMHC 1718-LR-21
    LACMHC 1718-LR-24
    LACMHC 1718-LR-25
    LACMHC 1718-LR-26
    LACMHC 1718- LR-27
    LACMHC 1718-LR-28
    LACMHC 1718-LR-29
    LACMHC 1718-L6-R8
    LACMHC 1718-L-16

    LACMHC 1718-R-16
    LACMHC 1718-L-9
    LACMHC 1718-R-15
    LACMHC 1718-L-36
    LACMHC 1718-LR-30
    LACMHC 22000
    LACMHC 1718-LR-19
    LACMHC 1717-32
Scelidotherium leptocephalum
    MLP 3-401
    MLP 3-420
    MLP 3-456
    MLP 3-671
    MMP 157-S
    MMP 549-S
    MMP 1155-M

Megatheriidae
Megatherium americanum
    MLP 2-37
    MLP 2-50
    MLP 2-52
    MLP 2-54
    MLP 2-56
    MLP 2-58
    MLP 2-59

    MLP 2-60
    MLP 2-207
    MLP 27-VII-1-1
    MLP 28-III-16-2
    MLP 44-XII-28-1
    MACN 1000
    MACN 2831
    MACN 2832
    MACN 5002
    MACN 15154
    MNHNM 6
    MNHNP R247
    MPBC 1
    BMNH 19953
    BMNH 19953f
    FMNH P14293
    ZMUC 212
M. tarijense
    FMNH P14216
    NRM M4890
M. medinae
    SGO PV236
    SGO PV252
    SGO PV288
    SGO PV5000

M. altiplanicum
    MNHN AYO 101
Eremotherium laurillardi
    MCL 1700/02
    MCL 1701/02
    MCL 1702/02
    MCL 7225
    MCL 7229
    MCL 7231
    MCL 7233
    MNRJ 2225
    MNRJ 3858
    MNP 44
    MNP 46
    USNM 18498
    USNM 20867
    ILSB s/n
    AMNH 95742
    F:AM s/n
    ROM 40324
E. eomigrans
    UF 121737

Table 2. Hypsodonty index of the ground sloths. LTR, length of the tooth row; DM, depth of the mandible; HI, Hypsodonty Index.

Taxa		LTR	DM	HI
G. robustum	MLP 3-136	130	90	0.69
	MLP 3-138	128	95	0.74
	MLP 3-140	130	93	0.71
L. armatus	MLP 3-3	190	124	0.65
	MLP 3-28	175	101	0.58
	MLP 3-29	170	99	0.58
	MLP 3-30	160	103	0.64
	MMP 47-S	165	105	0.63
M. darwini	MACN 991	126	110	0.87
	MLP 3-125	137	105	0.76
	MLP 3-126	131	94	0.71
P. harlani	LACMHC1718-LR-21	136.3	95.2	0.69
	LACMHC1718-LR-24	142.9	103.5	0.72
	LACMHC1718-LR-25	142.4	94.5	0.66
	LACMHC1718-LR-26	137.4	93.2	0.68
	LACMHC1718-LR-27	141.2	96.0	0.68
	LACMHC1718-LR-28	142.3	97.6	0.68
	LACMHC1718-LR-29	140.0	104.6	0.75
	LACMHC1718-L6-R8	130.6	100.6	0.77
	LACMHC1718-L-16	142.2	89.2	0.63
	LACMHC1718-L-9	134.6	98.2	0.73
	LACMHC1718-R-15	139.0	96.7	0.7
	LACMHC1718-L-36	123.7	96.8	0.78
	LACMHC1718-LR-30	150.0	95.1	0.63
	LACMHC22000	145.6	95.8	0.66
	LACMHC1718-LR-19	136.0	94.3	0.69
	LACMHC1717-32	144.0	105.2	0.73
	LACMHC1718-LR-20	127.7	102.0	0.8
S. leptocephalum	MLP s/n	101	103	1.01
	MLP 3-420	113	95	0.84
	MLP s/n	108	94	0.87
	MLP 3-456	107	93	0.87
	MMP 157-S	101	90	0.89
	MMP 549-S	98	101	1.03
	MMP 1155-M	116	100	0.86
M. americanum	MLP 2-37	239	242	1.01
	MLP 2-50	192	182	0.95
	MLP 2-52	220	222	1.00
	MLP 2-54	192	215	1.12
	MLP 2-56	200	207	1.04
	MLP 2-58	201	214	1.06
	MLP 2-59	206	191	0.93
	MLP 2-60	186	180	0.97
	MLP 2-207	202	201	1.00
	MLP 28-III-16-2	213	215	1.01
	MLP 44-XII-28-1	223	235	1.05
	MACN 1000	212	227	1.07
	MACN 2831	237	210	0.89
	MACN 2832	231	216	0.94
	MACN 5002	228	205	0.90
	MNHNM 6	209	206	0.99
	MNHNP R247	211	227	1.08
	MPBC 1	215	235	1.09
	BMNH 19953	259	254	0.98
	BMNH 19953f	201	227	1.13
	FMNH P14293	216	213	0.99
	ZMUC 212	193	220	1.14

M. tarijense	FMNH P14216	152	140	0.92
	NRM M4890	204	169	0.82
M. medinae	SGO PV236	172	161	0.93
	SGO PV252	151	142	0.94
	SGO PV288	142	116	0.81
	SGO PV5000	130	118	0.90
M. altiplanicum	MNHN AYO 101	143.6	145.0	1.01
E. laurillardi	MCL 1700/02	196	152	0.77
	MCL 1701/02	186	136	0.73
	MCL 1702/02	174	127	0.73
	MCL 7225	190	146	0.77
	MCL 7229	182	141	0.77
	MCL 7231	188	143	0.76
	MCL 7233	194	152	0.78
	MNRJ 2225	198	153	0.77
	MNRJ 3858	192	142	0.74
	MNP 44	193	152	0.79
	MNP 46	186	143	0.77
	USNM 18498	185	143	0.77
	USNM 20867	185	136	0.73
	ILSB s/n	196	152	0.78
	AMNH 95742	182	151	0.83
	F:AM s/n	200	151	0.76
	ROM 40324	193	156	0.81
E. eomigrans	UF 121737	215	169	0.78

mylodon harlani are equal (0.71), and that of *Mylodon darwini* slightly higher (0.78). In megatheriines HI ranges between 0.77 (*Eremotherium laurillardi*) and 1.02 (*Megatherium americanum*). HI in *E. eomigrans* (0.78) and *M. altiplanicum* (1.01) are nearly identical to these extremes, whereas it is intermediate in *M. medinae* and *M. tarijense*.

Discussion and conclusions

Hypsodonty, dietary behavior, habits, and habitat.—As mentioned above, Janis (1988, 1995) and Janis and Fortelius (1988) pointed out that habitat preference (closed or open) would be as important as dietary preference in the development of hypsodonty in ungulates. In other words, the abrasive materials (dust and grit) accumulated on ground level plants or dry environments should have influenced the evolution of hypsodont teeth as much as the silica of the grasses. Recent work (Williams and Kay 2001) has made it clear that both factors must figure strongly in discussions concerning the development of hypsodonty in several "epitherian" groups.

The two groups under consideration (Megatheriidae and Mylodontidae) are morphofunctionally distinct from each other, but taxa within each group are markedly similar to each other. De Iuliis (1996) noted that the masticatory apparatus of Megatheriinae taxa (for which the skull is adequately known) varies mainly in degree of hypsodonty and in features related to hypsodonty. For example, the maxilla and dentary are deeper in *Megatherium americanum* than in *Eremotherium laurillardi*, in order to accommodate their higher molariforms. Biomechanically, however, the appara-

Table 3. Mean values of Hypsodonty Index (HI). n, sample size; SD, standard deviation.

Species	n	HI	
		mean	SD
Glossotherium robustum	3	0.71	0.03
Lestodon armatus	5	0.62	0.03
Mylodon darwini	3	0.78	0.08
Paramylodon harlani	17	0.70	0.05
Scelidotherium leptocephalum	7	0.91	0.08
Megatherium americanum	22	1.02	0.07
Megatherium tarijense	2	0.87	0.07
Megatherium medinae	4	0.90	0.06
Eremotherium laurillardi	17	0.77	0.03

tuses of these species are essentially identical, suggesting similar food processing capabilities. Bargo (2001a) indicated that *M. americanum* had a strong bite force relative to mylodontids. Its masticatory movements were predominantly vertical, with mediolateral movement restricted.

The analysis of occlusal surface area (OSA) by Vizcaíno et al. (in press) indicates that *Megatherium americanum* has an expected, or even higher, OSA value for a mammal of its size, suggesting that *M. americanum* (and almost certainly also *E. laurillardi*) was well suited for food processing in the oral cavity, while the opposite is the case in mylodontids. However, this feature is probably related to the digestive efficiency of sloths rather than with the type of food taken (Vizcaíno et al. in press). Further, the teeth of both megatheriines are bilophodont, forming a battery of high-crested lophs. The sagittal section of each loph is triangular with a sharp blade of hard dentine at the apex. This morphology indicates that tough fibrous food, which requires grinding, did not constitute the most appropriate dietary item. Instead, *M. americanum* and *E. laurillardi* were apparently better suited for consuming a variety of turgid or moderate to soft tough food items. As this dental morphology precludes grazing, this dietary mode was not an important factor influencing hypsodonty in megatheriines.

Bargo and De Iuliis (1999) and De Iuliis et al. (2000) noted that the distribution of the contemporaneous megatheriines *Megatherium americanum* and *Eremotherium laurillardi* broadly coincided with temperate and tropical New World regions, with *M. americanum* present mainly in southern South America and *E. laurillardi* ranging from Brazil to the southeastern United States. These authors suggested that the difference in hypsodonty between these megatheriines might be explained as adaptations to these different environments as reflected by their geographical distributions. *E. laurillardi* inhabited more tropical to subtropical, closed or forested environments, and is considerably less hypsodont than *M. americanum*, which inhabited a more temperate, arid to semiarid environment.

Relevant paleoecological information for the other *Megatherium* species is not available in the published literature.

Megatherium altiplanicum is from the Altiplano of Bolivia and has an HI nearly equivalent to that of *M. americanum*. The other two species considered here, *M. medinae* and *M. tarijense*, are known primarily from elevations approximately intermediate between those of *M. americanum* and *M. altiplanicum* (see Saint-André and De Iuliis 2001), and their HI is intermediate between that of *M. americanum* and *M. altiplanicum*, on the one hand, and *E. laurillardi*, on the other. While it is tempting to postulate that this altitudinal cline in HI might be explained by environmental factors (i.e., the high elevation for *M. altiplanicum* being equivalent in terms of vegetation coarseness or grit as in the temperate lowland for *M. americanum*), this hypothesis must remain speculative pending further investigations of the paleoecology of the areas concerned.

Based on morphological and biomechanical analyses, Bargo (2001b) demonstrated that the masticatory apparatus of mylodontids was not particularly suited for producing strong bite forces during mastication, and that the main masticatory movement was anteromedial. This evidence suggests that mylodonts were not well suited for extensive oral food processing. Moreover, Vizcaíno et al. (in press) found that mylodontids have extremely low OSA values in comparison with living herbivorous mammals of equivalent body size, which also suggests that mylodonts had poor food oral processing. Bargo (2001b) also analyzed the relationship between dietary habits and shape and width of the muzzle in sloths, which has been studied in ungulates by various authors (Janis and Ehrhardt 1988 and references therein; Solounias and Moelleken 1993). The results of Bargo's (2001b) analysis suggest that *Lestodon* and *Glossotherium* were bulk feeders (i.e., mainly grazers) while *Mylodon* and *Scelidotherium* were more selective, that is, browsers. These dietary regimes do not correlate well with the pattern of HI for mylodonts: *Scelidotherium* has the highest hypsodonty index, followed by *Mylodon*, while *Lestodon* and *Glossotherium* have the lowest indices, which is the reverse of the traditionally expected pattern of grazers having more hypsodont teeth than browsers. As noted above, however, the nature of food items is not necessarily the most important or only factor influencing hypsodonty, and factors other than typical grazing habits must be considered in explaining the pattern of hypsodonty in mylodontids. Recent ecomorphological studies in living ungulates (Mendoza et al. 2002) have indicated that a combination of (rather than any single) variables must be considered for prediction of dietary habits. One obvious factor is an increased presence of grit caused by environmental differences resulting from geographic distribution (as noted above for megatheriines) or environmental change over time, or particular habits (see below).

Evidence for distributional or temporal environmental differences is lacking for South America, but the following record of the North American mylodontid *Paramylodon* is particularly relevant. Stock (1925) suggested that *Paramylodon harlani* was a grazer, a hypothesis followed by many subsequent workers. But McDonald (1995) argued that the

powerful forelimbs, with the expanded distal end of the humerus, short radius, ulna with an enlarged olecranon process, and dorsoventrally flattened unguals, permitted *Paramylodon* to dig up roots and tubers and he viewed *Paramylodon* as an inhabitant of scrub or open country habitat. Independent of the possible diets of *Paramylodon harlani*, McDonald (1995) suggested that the greater hypsodonty observed in Irvingtonian (early Pleistocene) individuals of this species as compared to the more recent Rancholabrean (late Pleistocene) individuals might reflect a change over time from closed to more open habitats. This is an example of morphological change in a single species apparently in response to a temporal, rather than geographic, environmental change.

Habit or behavior is also a factor to consider in hypsodonty. Various authors (Owen 1842, 1856; Winge 1941; Cuenca Anaya 1995; McDonald 1995) have postulated that mylodontids obtained food by excavating the subterranean portions of plant matter with their powerful forelimbs. The biomechanical study by Bargo et al. (2000) supported the hypothesis of digging behavior in mylodontids, which suggests the ingestion of large quantities of abrasive soil elements. A study based on ichnological and geological evidence in the Pampean region of South America (Vizcaíno et al. 2001) demonstrated that *Glossotherium robustum* and *Scelidotherium leptocephalum* were capable diggers and excavated extensive burrows. This study not only indirectly reinforces the hypothesis that these mylodontids might have searched for food by digging, but further indicates that abrasive soil particles were a major component of these sloths' environment, and thus that grit probably played a role in the development of hypsodonty. The greater hypsodonty in *Scelidotherium* may be an indirect indication that digging behavior was more prevalent than in the other mylodontids.

Mendoza et al. (2002) demonstrated that, at least in ungulates, adaptation to a given trophic niche involves complex patterns of covariation between many morphological characters of the skull and mandible. The lack of living analogues to the ground sloths precludes performing appropriate ecomorphological analyses to establish unequivocal correlations between feeding behavior and morphological variables. Thus we cannot determine the degree to which higher hypsodonty values in megatheriids and mylodontids correspond to feeding on abrasive grasses rather than on browse, as has been done for living ungulates (Janis 1988; Solounias and Dawson-Saunders 1988), simply because we cannot know the proportion of grass in their diet. However, the available evidence allows us to state that habitat and burrowing habit are evident factors in explaining differences in hypsodonty in Pleistocene ground sloths. Differences in habitat, such as between closed and open environments, were apparently important in mylodontids, as well as in megatheriines. In addition, morphologic and biomechanical analyses in mylodontids indicate that digging behavior, including but not limited to searching for food, played a considerable role in shaping the dental characteristics of these

sloths. In each case, the important agent was the relative abundance of abrasive soil particles. Other morphological variables may influence the degree of hypsodonty. Such variables include OSA, crown features such as presence of lobes or lophs, hardness of dentine, and perimeter length. It is the interplay among these variables, often phylogenetically constrained, as well as abrasive particles in the food and environment, that determine hypsodonty. Covariance between skull and jaw variables has been proposed for other xenarthrans. For instance, Vizcaíno et al. (in press) noted that among pampatheres, a reduction in tooth lobation is compensated by a considerable increase in OSA.

Phylogenetic constraint to hypsodonty.—Among Tardigrada, and indeed Xenarthra in general, hypsodonty is apparently affected by diet, habitat and habit, but the individual contributions of these factors cannot be as clearly partitioned as in "epitherians" because the role of another factor, the absence of enamel, must be considered. Enamel is absent in the teeth of all xenarthrans (when teeth, of course, are present), except probably in the Eocene armadillo *Utaetus* (Simpson 1931). As discussed by Vizcaíno and De Iuliis (2003), this absence of enamel has been a strong developmental constraint that has influenced the morphology of xenarthran dentitions in such a way as to narrow the range of possible morphological responses compared with those occurring in "epitherians". These authors demonstrated that xenarthrans nonetheless possess morphological adaptations that allow interpretations of their feeding behaviors, but that these features are usually much more subtle than those evolved among "epitherians" (see also Vizcaíno 1994a; Vizcaíno and Fariña 1997; Vizcaíno and Bargo 1998; Vizcaíno et al. 1998; De Iuliis et al. 2000; Fariña and Vizcaíno 2001; Bargo 2001a, b, 2003; Vizcaíno et al. 2004, in press).

Certainly all xenarthrans (except the anteaters, the only true "edentates") have teeth that are relatively hypsodont (i.e., they are tall with respect to their occlusal area), regardless of their particular dietary and feeding modes, in contrast to "epitherians". This is true despite the generally myrmecophagous to broadly omnivorous behaviors of armadillos, the grazing behaviors of glyptodonts and pampatheres, and the browsing, omnivorous and grazing behaviors of sloths. "Epitherians" are much more variable in this regard; omnivory is never associated with hypsodonty, for example. In this respect, variation in hypsodonty among "epitherians" may be appropriately explained almost entirely in terms of exclusively adaptational scenarios related to environmental factors affecting wear.

It is, however, highly probable that the absence of enamel, which would make the teeth less durable and wear down faster, is responsible for much of the hypsodonty observed in xenarthrans. In other words, the presence of high crowned teeth is not an adaptational response to particular selection pressures affecting wear, as seems likely in "epitherians", but a general requirement of xenarthrans. In this context the term hypsodonty does not necessarily reflect convergent de-

velopments in xenarthrans and "epitherians". The requirement of high crowned teeth results in similar indices among different sloths, which tends to obscure the possible reasons for the comparatively small differences in relative tooth height. While the presence of hypsodonty itself cannot be explained mainly by the reasons typically given for "epitherians" (e.g., grazing *versus* browsing; open *versus* closed habitats), differences in hypsodonty among sloths apparently do correlate with dietary behavior, habits and habitat, suggesting that they are appropriate for explaining the variation in sloths as well.

Further considerations on the evolution of hypsodonty in South America.—Increased tooth height in xenarthrans appears to be part of a common adaptive strategy among South American mammal lineages. Clearly, hypsodonty was acquired independently in xenathrans and "epitherians" but hypsodonty also seems to have occurred among multiple, diverse South American mammalian taxa. For example, South American gondwanatherians acquired hypsodonty earlier than and independently of therians. The trait had arisen by the Late Cretaceous (Koenigswald et al. 1999) and persisted until the Paleocene. In xenarthrans hypsodonty had already arisen by the late Paleocene, based on the first record of the group. The earliest teeth of this group are known from armadillos whose mandibles and teeth are very similar to those of the living *Dasypus novemcinctus* (Vizcaíno 1994b), a species that is clearly not a "grazer," but essentially animalivorous (Redford 1985; Vizcaíno et al. 2004). By the Paleocene hypsodonty had not clearly developed in the already diverse South American ungulates (Notoungulata, Litopterna, Astrapotheria, Pyrotheria). Bond (1986) stated that brachydont cheek teeth were characteristic of most ungulate lineages, with only some groups of notoungulates showing a tendency to increase tooth crown height, a tendency accentuated by the early Eocene. Later changes in degree of hypsodonty among essentially plant feeding xenarthrans such as glyptodonts and sloths apparently reflect adaptation to different diets, feeding behaviors, or environmental conditions. Pascual and Ortiz Jaureguizar (1990) stated that, during the latest part of the Cenozoic, many xenarthrans (in addition to ungulates), as well as varied gigantic native rodents, followed a similar dental modification pattern, from a low-crowned to high-crowned morphology, in response to general environmental and climatic trends from predominantly closed-forested, warm and wet habitats to open temperate grasslands, to hot deserts, or to cold habitats. These authors further noted that this general pattern was also detectable in smaller native rodents (Kraglievich 1940), and some peculiar marsupials convergent on the rodent adaptive zone (Pascual et al. 1988), and primates (Kay et al. 2002). The evolution of hypsodonty in diverse mammalian lineages during the Cenozoic is also recorded in other continents; i.e., North America (Stirton 1947; Janis 1988, 1995), Africa (Bobe et al. 2004), Europe (Jernvall and Fortelius 2002) and Eurasia (Fortelius et al. 2002). However, differences in the quality of databases hinder comparison of this process among different continents. For instance, while hypsodonty degree is recorded in extensive databases of Neogene fossil mammals from Eurasia (NOW: http://www.helsinki.fi/science/now/) and Africa (see Bobe et al. 2004, ETE Program), a comparable tool is as yet unavailable for South America.

The repeated occurrence of hypsodonty in so many diverse and even unrelated lineages leads one to wonder whether there is some peculiarity of the South American continent that has led so many lineages along the path to hypsodonty. Although this may appear far fetched, similar thoughts have been expressed with respect to folivory (van Schaik et al. 1993). Unfortunately, current knowledge of the paleobiology and ecomorphology of South American mammals is far too incomplete to provide a definitive answer; and much work remains to be done on the various lineages, especially those with a long history in the continent (in this respect, the Xenarthra has clearly received the most attention in the past decade). We suggest that one possible factor is the long geographic isolation of the continent. This imposed ecological relationships that are not readily understood using the parameters that apply to the Old World (and the connected North America) and require different explanatory models (e.g., Fariña 1996; Croft 2001).

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