Hypsodonty in the Pleistocene ground sloth *Megalonyx*: Closing the "diastema" of data

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Hypsodonty in Pleistocene ground sloths was reported by Bargo et al. (2006), but no data was provided for megalonychids. Herein, hypsodonty indices (HI) are presented for 22 *Megalonyx* specimens (mean = 1.06, SD = 0.10), and statistical analysis suggests that there were no significant changes in HI during the ontogeny or phylogeny of the genus during the Pleistocene.

Introduction

In their recent paper Bargo et al. (2006) calculated hypsodonty indices (HI) for eleven taxa of Pleistocene ground sloths (Xenarthra: Tardigrada). Hypsodonty, or tooth crown height, has been explored for a number of mammal groups (see Bargo et al. 2006 for a list of references), but sloth teeth, like all xenarthran teeth, have no enamel, and hypsodonty is likely affected by a number of factors. Bargo et al. (2006) reviewed several such factors, including diet, habit, and habitat preference. However, while the taxa analyzed included mylodontids and megatheriids from North America and South America, Bargo et al. (2006) did not include megalonychids, citing inaccessibility to material.

Within the Xenarthra, there are several families of ground sloths, including Mylodontidae, Megatheriidae, and Megalonychidae (McKenna and Bell 1997). Within the Megalonychidae, the genus *Megalonyx* comprises a chronospecies from the late Hemphillian through late Rancholabrean North American Land Mammal Ages (NALMA) of the Pliocene and Pleistocene Epochs (McDonald 1977). During the Pleistocene the chronospecies was represented by *Megalonyx leptostomus* Cope, 1893 during the late Blancan, *Megalonyx wheatleyi* Cope, 1871 during the Irvingtonian, and *Megalonyx jeffersonii* (Desmarest, 1822) during the Rancholabrean (Bell et al. 2004). An overall increase in size and a few qualitative character changes (see McDonald 1977) appear to account for the differences among the three species of Pleistocene *Megalonyx* known from over 152 sites in North America (McDonald 2003) from Florida (Hulbert 2001) to Alaska (Stock 1942).

It is the purpose of this paper to present hypsodonty indices for three species of *Megalonyx* (Xenarthra: Megalonychidae) to compliment the work of Bargo et al. (2006) and add to the known database of hypsodonty indices for Pleistocene ground sloths. Additionally, HI values in *Megalonyx* are compared across space and time to assess any changes in hypsodonty.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; ANSP, Academy of Natural Sciences at Philadelphia, USA; SCSM, South Carolina State Museum, Columbia, USA; UF, University of Florida Museum of Natural History, Gainesville, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, USA.

Other abbreviations.—df, degrees of freedom; DM, depth of the mandible; e, early; HI, Hypsodonty Index; l, late; lm, late–middle; LTR, length of the molariform tooth row; NALMA, North American Land Mammal Age; SD, standard deviation.

Materials and methods

Mandibular elements (see Table 1) were measured with Mitutoyo MyCAL 0–8"/0200 mm digital calipers to the nearest 0.1 mm. Hypsodonty index (HI) was calculated as in Bargo et al. (2006) using depth of the mandible (below the third molariform tooth) divided by the length of the molariform tooth row (Fig. 1) and multiplied by 100. In specimens for which both sides of the mandible are intact, HI was calculated for each side, and HI for the individual was then determined by adding HI of both sides and dividing by two.

To determine if hypsodonty values changed during the ontogeny or phylogeny of *Megalonyx*, mean HI was compared for three subsets of data as follows:

(1) Ontogeny: HI for juveniles from the Blancan of Florida was compared to HI for adults from the Blancan of Florida. Juveniles and adults were compared from the same time and region to minimize the effects of temporal and geographic variation, respectively. Results were statistically analyzed using a Kruskal-Wallis one-way analysis of variance.

(2) Temporal: HI for specimens from the Blancan, Irvingtonian, and Rancholabrean were all compared using a Kruskal-Wallis one-way analysis of variance.

(3) Geographic: HI for specimens from the Irvingtonian NALMA: the early Irvingtonian Port Kennedy Cave, Montgomery County, Pennsylvania; the late–middle Irvingtonian McLeod Mine, Levy County, Florida, and the late Irvingtonian Camelot local fauna, Dorchester County, South Carolina were all compared using a Kruskal-Wallis one-way analysis of variance.

Results

Table 1 provides the list of *Megalonyx* specimens studied, measurements and HI obtained. Table 2 provides means and standard deviations for three sets of *Megalonyx* samples. HI values ranged from 0.95 to 1.17, mean = 1.05, SD = 0.06, n = 22. The

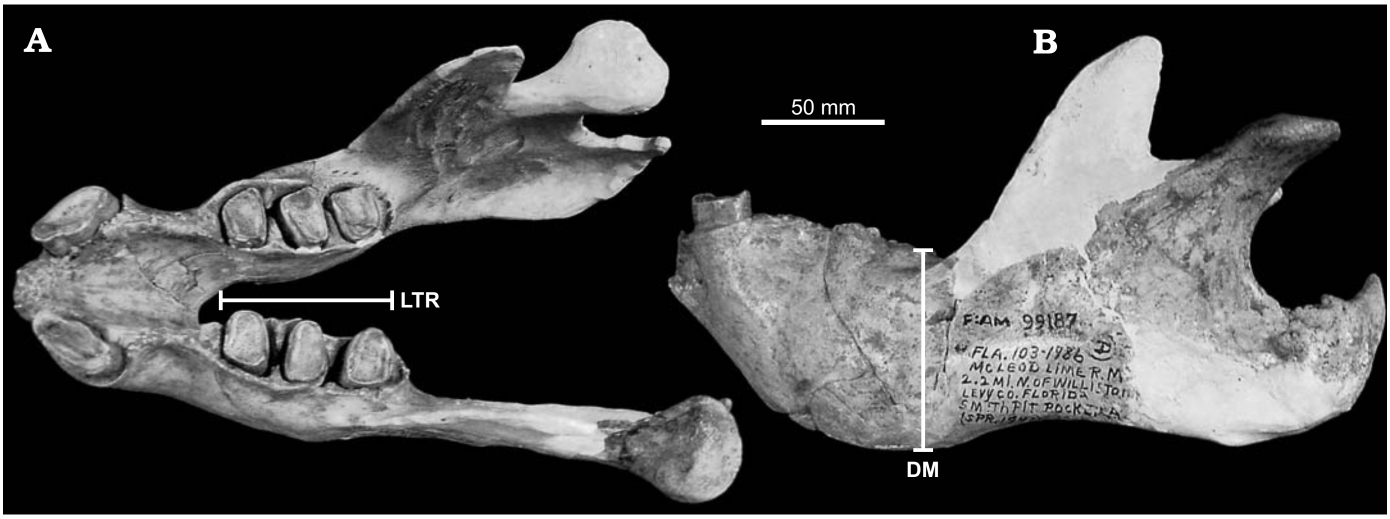

Fig. 1. Measurements used to calculate hypsodonty index (HI) in *Megalonyx*. HI is calculated as the depth of the mandible (DM), usually measured below the third molariform tooth (see B), divided by the length of the tooth row (LTR; see A), and multiplied by 100. Specimen displayed is AMNH F:AM 99187—mandible of *Megalonyx wheatleyi* from the middle Irvingtonian McLeod Mine, Florida, in occlusal (**A**) and lateral (**B**) views.

mean HI value of *Megalonyx* is closest to that of *Megatherium americanum* (mean HI = 1.02) reported by Bargo et al. (2006). Statistical analyses revealed no differences in HI for *Megalonyx* across ontogeny, time, or space (see Table 2):

(1) Ontogeny: juveniles from the Blancan of Florida: mean HI = 1.06, SD = 0.10, n = 3; adults from the Blancan of Florida: mean HI = 1.10, SD = 0.04, n = 2; results of comparison of both samples using Kruskal-Wallis test: H = 0.3333; df = 1; p = 0.5637.

(2) Temporal: specimens from Blancan: mean HI = 1.08, SD = 0.07, n = 5; specimens from Irvingtonian: mean HI = 1.05, SD = 0.06, n = 11; specimens from Rancholabrean: mean HI = 1.00, SD = 0.05, n = 2; results of comparison of all three samples using Kruskal-Wallis test: H = 3.5528; df = 2; p = 0.1692.

(3) Geographic: specimens from Port Kennedy: mean HI = 1.06, SD = 0.10, n = 3; specimens from Camelot: mean HI = 1.04, SD = 0.05, n = 4; specimens from McLeod: mean HI = 1.05, SD = 0.05, n = 4; results of comparison of all three samples using Kruskal-Wallis test: H = 0.0530; df = 2; p = 0.9738.

Table 1. Hypsodonty indices of *Megalonyx*. HI = mandibular height/tooth row length × 100. All measurements are in millimeters (mm). See note in Discussion regarding *Megalonyx wheatleyi/jeffersonii*. Abbreviations: BLA, Blancan; DM, depth of the mandible; HI, Hypsodonty Index; IRV, Irvingtonian; LTR, length of the molariform tooth row; NALMA, North American Land Mammal Age; RLB, Rancholabrean.

Catalog number	Specimen	Locality	NALMA	DM	LTR	HI
UF 20949	*Megalonyx leptostomus*	Inglis IA, Florida	BLA-l	48.5	45.2	1.07
UF 223806	*Megalonyx leptostomus* (right side)	Haile 7G, Florida	BLA-l	60.6	53.4	1.13
UF 223806	*Megalonyx leptostomus* (left side)	Haile 7G, Florida	BLA-l	60.6	54.7	1.11
UF (no number)	*Megalonyx leptostomus*, juvenile	Florida	BLA-l	42.5	44.8	0.95
UF 206571	*Megalonyx leptostomus*, juvenile	Haile 7C, Florida	BLA-l	28.1	24.9	1.13
UF ML-12	*Megalonyx leptostomus*, juvenile	Florida	BLA-l	48.4	43.7	1.11
ANSP 180	*Megalonyx wheatleyi*	Port Kennedy Cave, Pennsylvania	IRV-e	70.0	59.7	1.17
ANSP 188	*Megalonyx wheatleyi*	Port Kennedy Cave, Pennsylvania	IRV-e	65.8	63.4	1.04
USNM 11633	*Megalonyx wheatleyi*	Port Kennedy Cave, Pennsylvania	IRV-e	65.9	68.1	0.97
AMNH F:AM 99190	*Megalonyx wheatleyi*	McLeod Limerock Mine, Florida	IRV-lm	63.5	59.9	1.06
AMNH F:AM 99191	*Megalonyx wheatleyi*	McLeod Limerock Mine, Florida	IRV-lm	50.1	50.6	0.99
AMNH F:AM 99193	*Megalonyx wheatleyi*	McLeod Limerock Mine, Florida	IRV-lm	53.3	50.9	1.05
AMNH F:AM 99187	*Megalonyx wheatleyi* (left side)	McLeod Limerock Mine, Florida	IRV-lm	69.4	63.2	1.10
AMNH F:AM 99187	*Megalonyx wheatleyi* (right side)	McLeod Limerock Mine, Florida	IRV-lm	68.2	61.0	1.12
SCSM 2004.1.3	*Megalonyx wheatleyi/jeffersonii* (right)	Camelot, South Carolina	IRV-l	68.5	63.9	1.07
SCSM 2004.1.3	*Megalonyx wheatleyi/jeffersonii* (left)	Camelot, South Carolina	IRV-l	63.7	62.9	1.01
SCSM 2004.1.26.1	*Megalonyx wheatleyi/jeffersonii* (right)	Camelot, South Carolina	IRV-l	64.2	64.1	1.00
SCSM 2004.1.26.1	*Megalonyx wheatleyi/jeffersonii* (left)	Camelot, South Carolina	IRV-l	62.4	65.6	0.95
SCSM 2003.75.330	*Megalonyx wheatleyi/jeffersonii*	Camelot, South Carolina	IRV-l	68.9	69.7	0.99
SCSM 2003.75.424.1	*Megalonyx wheatleyi/jeffersonii*	Camelot, South Carolina	IRV-l	71.3	64.6	1.11
ANSP 12536	*Megalonyx jeffersonii*	Georgia	RLB	72.7	70.5	1.03
UF 3920	*Megalonyx jeffersonii*	Ichetucknee River, Florida	RLB-l	72.6	75.8	0.96

Table 2. Mean values of Hypsodonty index (HI) for *Megalonyx* from various Pleistocene sites. Data subsets represent ontogenetic, temporal, and geographic variation. Abbreviations: n, sample size; SD, standard deviation.

Subset		n	Hypsodonty	
			mean	SD
Ontogeny	juveniles, Blancan, Florida	3	1.06	0.10
	adults, Blancan, Florida	2	1.10	0.04
Temporal	Blancan	5	1.08	0.07
	Irvingtonian	11	1.05	0.06
	Rancholabrean	2	1.00	0.05
Geographic	Port Kennedy, Pennsylvania	3	1.06	0.10
	Camelot, South Carolina	4	1.04	0.05
	McLeod, Florida	4	1.05	0.05
Total	all specimens	22	1.05	0.06

Discussion

Specimens from the late Irvingtonian Camelot local fauna from Dorchester County, South Carolina deserve a special note here. In this paper I refer to the sample as *Megalonyx wheatleyi/jeffersonii* because specimens show characters of both *M. wheatleyi* and *M. jeffersonii* as described by McDonald (1977). The Camelot population was apparently in a state of transition within the chronospecies. The detailed morphometrics of this sample is beyond the scope of this paper, but a detailed description of the *Megalonyx* elements from Camelot forms the basis of the author's Ph.D. dissertation and will, therefore, be presented in another paper.

Mean HI for *Megalonyx* was 1.05, close to HI (1.02) for *Megatherium americanum* reported by Bargo et al. (2006). These represent the highest mean HI values for all of the ground sloths studied. However, as Bargo et al. (2006) indicated, determining the reasons for increased hypsodonty in these taxa is problematic as there are likely several contributing factors. In fact, the comparability of HI in different ground sloths is questionable because dental formulas vary among taxa. For example, LTR is different for *Megatherium* (with four lower molariforms) and *Megalonyx* (with three lower molariforms and a longer diastema); furthermore, tooth morphology differs among various ground sloth taxa (Gerardo De Iuliis, personal communication 2008). See also Fig. 2 for an illustration of the skull and upper tooth morphology of *Megalonyx*. Accordingly, similar HI values for *Megatherium* and *Megalonyx* do not necessarily indicate similar diets. Still, *Megatherium* was not a grazer, but "… better suited for consuming a variety of turgid or moderate to soft tough food items." (Bargo et al. 2006: 57). Furthermore, *Megalonyx* is generally considered to be a browser (Kurtén and Anderson 1980; Schubert et al. 2004). A recent isotope study by Kohn et al. (2005) supported a forest-dwelling, browsing niche for *Megalonyx*.

The analysis of HI over space and time revealed no significant change in hypsodonty in *Megalonyx*. Admittedly, sample sizes were small for some subsets of data (e.g., n = 2 for Rancholabrean specimens and for adults from the Blancan of Florida). However, sample sizes reported in Bargo et al. (2006) were also relatively small (five samples where n = 5). Still, the

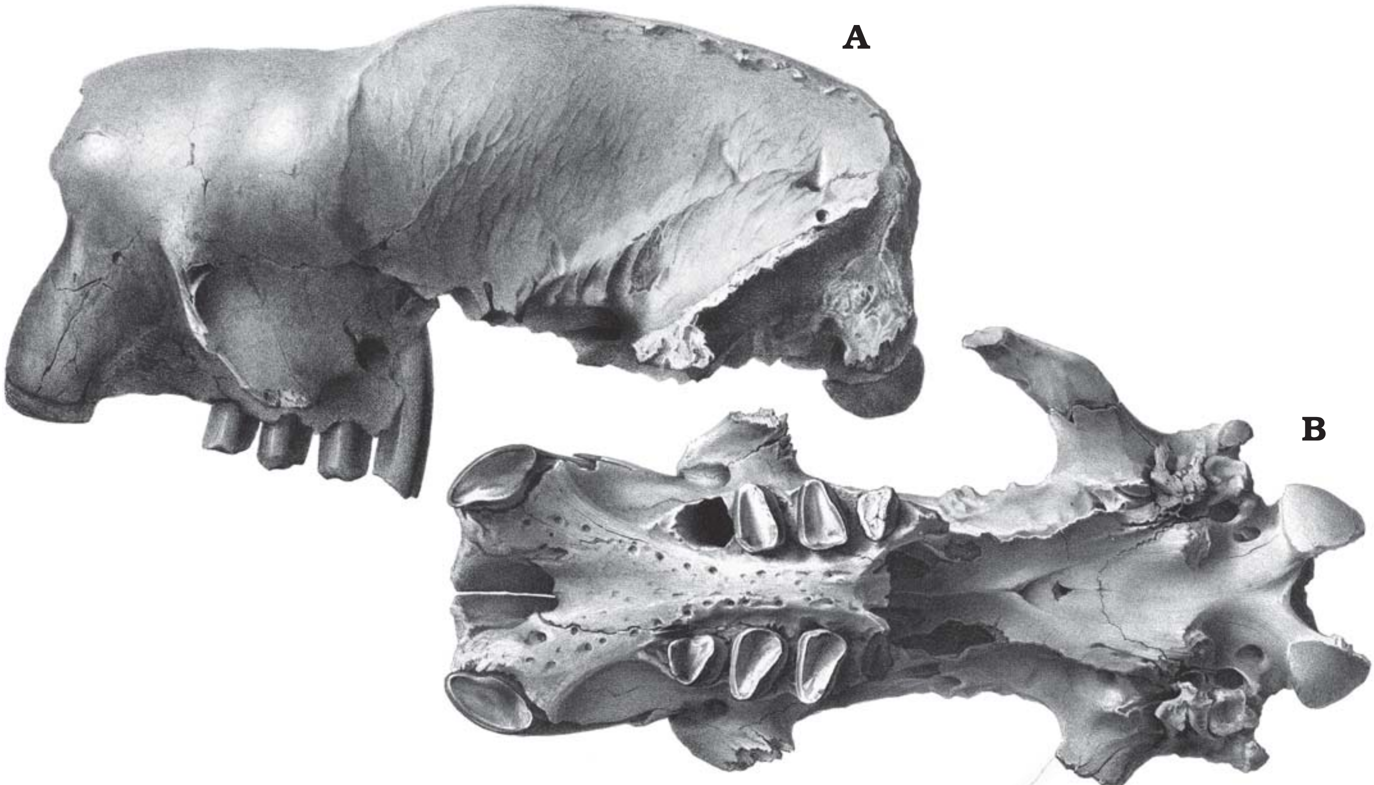

Fig. 2. Drawing of *Megalonyx* skull, based on Leidy (1855: pls. 1 and 3) showing upper dentition in left lateral (**A**) and occlusal (**B**) views. Positions of caniniforms and molariforms are indicated. Not to scale.

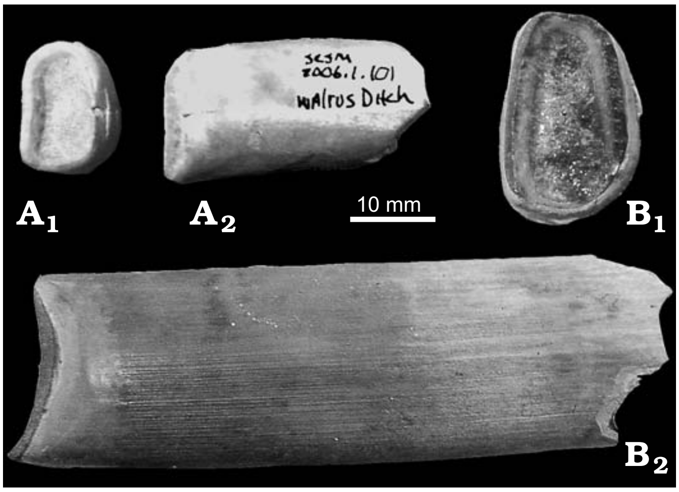

Fig. 3. Comparison of molariforms of two taxa of *Megalonyx* from South Carolina. **A**. SCSM 2006.1.101, *Megalonyx leptostomus* from the late Blancan Walrus Ditch Local Fauna near Summerville, in Dorchester County, South Carolina, in occlusal (A_1) and lateral (A_2) views. **B**. SCSM 2004.1.26.2, *Megalonyx wheatleyi/jeffersonii* from the late Irvingtonian Camelot Local Fauna near Harleyville, in Dorchester County, South Carolina, in occlusal (B_1) and lateral (B_2) views. While *M. jeffersonii* is larger than both *M. leptostomus* and *M. wheatleyi*, hypsodonty indices were statistically the same in all species.

prevailing trend appears to be that there was no change in hypsodonty during the ontogeny or phylogeny of *Megalonyx*.

Mean HI values for juveniles (1.06) and adults (1.10) of *Megalonyx* from the Blancan of Florida were not significantly different. The morphology of juvenile *Megalonyx* molariforms is different than that of adults in that juvenile molariforms are broader at the base than the occlusal surface. However, HI was measured using the length of the molariform tooth row, which is correctly assessed at the level of the alveoli (i.e., the base of the tooth). It appears that whatever the factors contributing to hypsodonty, there was little or no change during the ontogeny of *Megalonyx*.

Mean HI values for *Megalonyx* from the Blancan (1.08), Irvingtonian (1.05), and Rancholabrean (1.00) were also not significantly different. As stated before, the primary change in the chronospecies over time was an increase in size (McDonald 1977). Apparently, changes in the mandible and teeth remained proportional (see Fig. 3). The fact that mean HI values remained statistically the same from the Blancan through the Rancholabrean can be added to other morphological similarities in the chronospecies of *Megalonyx* that suggest a revision of taxonomy may be in order. The number of species and rates of evolution are currently under study for this genus and will be reported in a future paper.

Finally, mean HI values for *Megalonyx* from the different Irvingtonian sites were not statistically different (1.06 for Port Kennedy, PA; 1.04 for Camelot, SC; 1.05 for McLeod, FL). It appears, then, that geographic variation was also not a factor affecting hypsodonty. *Megalonyx* had the largest geographic distribution of any North American ground sloth, ranging from Mexico to Alaska and coast to coast (McDonald 1977; McDonald et. al 2000; Woodburne 2004). More data is needed to assess HI for other specimens at the periphery of the range to see if differences do indeed exist. Hopefully, further research will shed light on the reasons for apparent fixed degree of hypsodonty in *Megalonyx*, and if similar patterns exist in other ground sloths.

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