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THE DECIDUOUS PREMOLARS OF *MAMMUT AMERICANUM* (MAMMALIA, PROBOSCIDEA)

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ABSTRACT—Deciduous premolars of *Mammut americanum* have received relatively little study, and previous work was based on small sample sizes. We present morphologic descriptions and quantitative data for a sample of over 135 deciduous premolars of *M. americanum* from Florida. Most second and third deciduous premolars are bilophodont, although a few anomalous teeth deviate from this pattern to a varying degree. Although the premolars are morphologically similar to the adult molars in many respects, differences in development of cingula, orientation of lophs and lophids, and relative strengths of enamel crests are observed. Distal cingula and stylar cusps are the most variable portions of the crown. Crown length increases distally along the tooth row, with no observed overlap in length between adjacent teeth.

INTRODUCTION

The American mastodon (*Mammut americanum*) is a very common member of the extinct Pleistocene megafauna of North America. Mounted skeletons are found in many museums across the United States, and some in Europe. *Mammut americanum* has received much attention in the popular and scientific literature since its discovery in 1705, and general aspects of its dentition have been well known since the mid-1800s (e.g., Warren, 1852; Leidy, 1869; Hay, 1914). The dentition of *M. americanum* consists of upper, and frequently small lower tusks (which have very small, deciduous precursors; Luckett, 1996), and six cheek teeth per jaw quadrant. The latter erupt using the well-known 'horizontal displacement' pattern found in all elephantoids (Tassy, 1996b). The first three cheek teeth are regarded as homologous to the standard second through fourth deciduous premolars of typical eutherian mammals, while the latter three are homologous with the first through third molars. Although some elephantoids, including the early mammutid *Zygolophodon*, have 'vertical replacement' of some of their deciduous premolars, this does not occur in *Mammut* (Schlesinger, 1922; Tassy, 1996b).

Molars of *M. americanum* are very common and many aspects of them are especially well studied, including tooth size and morphology (Hay, 1914; Osborn, 1936; Skeels, 1962; Saunders, 1977; King and Saunders, 1984; Laub, 1992; Abraczinskas, 1993), functional morphology (Laub, 1996), and paleodiet (Koch et al., 1998; Hoppe et al., 1999; Gobetz and Bozarth, 2001; Green et al., 2003). Such studies tend not to examine the deciduous premolars in much detail, if at all, primarily for lack of sufficient sample sizes. Published descriptions and quantitative data on the smaller, first two deciduous premolars are limited and based on five or, more typically, fewer teeth per sample (Leidy, 1869; Hay, 1914; Peterson, 1926; Hatt, 1965; Mead et al., 1979; Ray and Sanders, 1984; Laub, 1992; Daeschler, 1996). The larger, more common fourth deciduous premolars have received slightly more attention. Notably, Saunders (1977) published descriptive statistics for a sample of eleven dp4s, more than any previous author, but he did not describe these teeth in detail. No thorough morphologic description has been published on *M. americanum* deciduous premolars based on samples of significant size.

Deciduous teeth of *M. americanum*, especially the dp2/DP2 and dp3/DP3, are generally rare, even in large samples from Missouri (Saunders, 1977; King and Saunders, 1984) and Michigan (Skeels, 1962; Abraczinskas, 1993). The situation for the Eurasian *Mammut borsoni* is similar to that of its North American relative; published descriptions of deciduous premolars are based on very small sample sizes (e.g., Schlesinger, 1922; Hopwood, 1935; Tobien, 1975; Tobien et al., 1988). In the course of accumulating large samples of *M. americanum* teeth from Florida for analysis of evolutionary trends (Green, 2002) and paleodiet using microwear (Green et al., 2003), we noted that relatively large samples of all six deciduous premolars were available, much larger than in any published study. These samples allow the first comprehensive, quantitative analysis of the deciduous teeth of *M. americanum* (or any other mammutid), and the first detailed description of their morphology with samples large enough to account for individual variation. Our descriptions will allow other workers to more accurately identify isolated mammutid teeth, in turn allowing better understanding of the demographics of this common taxon.

MATERIALS AND METHODS

For this study, we examined 139 deciduous premolars of *Mammut americanum* from Florida, both isolated teeth and those in jaws (see Supplementary Data, www.vertpaleo.org/jvp/JVPcontents.html). In addition to specimens from museums, our sample includes 77 specimens borrowed from private collections. Molds and casts were made of the latter teeth and deposited in the Florida Museum of Natural History vertebrate paleontology collection. By limiting our study sample to specimens from Florida, we minimize the effects of geographic variation on our quantitative analyses. These specimens range in age from late Blancan to latest Rancholabrean, although geologic age is uncertain for many isolated teeth recovered from riverbeds (see Supplementary Data). To maintain large sample sizes, we did not attempt to subdivide the teeth chronologically in this study. If sample sizes for Irvingtonian and Blancan specimens substantially increase in the future, comparative analyses would be worthwhile. Green (2002) found a slight trend for increased tooth size over time in adult molars of *M. americanum* from Florida, but no significant change in morphology.

Each tooth in our sample was assigned to one of six tooth categories, either of the lower dentition (i.e., dp2, dp3, or dp4) or the upper dentition (i.e., DP2, DP3, or DP4). Deciduous premolars still in situ in maxillae and dentaries are relatively easy to

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identify accurately, based on their positions relative to each other and, if present, the molars. Isolated teeth account for a large portion of our sample and were identified to their original position in the mouth by comparison with teeth still in jaws, published descriptions (e.g., Hay, 1914; Saunders, 1977; Laub, 1992), and distribution of crown length and width (see below).

The wear stage of each tooth is recorded in Supplementary Data. Table 1 lists the criteria for determining tooth wear stages, modified from Simpson and Paula Couto (1957) and Saunders (1977). Their criteria were based on lower teeth, but we find that the same pattern also holds for uppers, so we applied this terminology to both categories. We also add one new wear stage, symbolized by 0/+, for unworn, isolated teeth. The 0 and 0+ wear stages of Simpson and Paula Couto (1957) and Saunders (1977) were defined on the eruption state of the tooth, which is clearly evident only for teeth that are still in mandibles and maxillae. While the absence of roots on an isolated tooth likely means that it was unerupted, this is not conclusive. Erupting teeth typically have formed roots, but they are thin and fragile, and easily broken off. Rather than assume the eruption state, we created the new category to minimize error. Most teeth in wear stage 4 exhibit extreme interstitial wear and the original length has decreased significantly. Tooth length was not measured for specimens of wear stage 4, but width was recorded, as it is not affected by wear.

The wear stages on premolars and molars still in mandibles and maxillae were used to define nine developmental stages for young mastodons (Table 2). Once developmental stages were established based on tooth wear, measurements of mandible depth were taken to help define these stages further. To compare juveniles with older adults and completely describe growth of the mandible, we also measured the depth of 16 'adult' (defined here as individuals that have lost the m1) mandibles. Horizontal tooth displacement does not allow for a standardized method of measuring mandible depth based on tooth position. Therefore, mandibular depth was measured at the position of the posterior mental foramen to standardize our measurements. The data were compiled in a graph of mean mandible depth for each developmental stage.

Tooth dimensions were measured to the nearest 0.1 mm with calipers. Maximum length along the transverse axis of the tooth and maximum width of each loph/lophid, using the methods of Simpson and Paula Couto (1957), were recorded for each tooth, except where modified by wear or breakage (Supplementary Data). The greatest of the width measurements determined the maximum width for each tooth. We measured enamel thickness on worn teeth (stages 2–4) at the protocone or protoconid to the nearest 0.01 mm. If both left and right teeth were present in a specimen, we only took measurements on one side. Standard

descriptive statistics were calculated for each of the six tooth categories. Following Haldane (1955), the coefficient of variation was adjusted for sample size using the equation $V^* = V(1 + 1/(4n))$. Significant differences among V^* were tested using the method of Sokal and Braumann (1980).

We use Smith and Dodson's (2003) standardized terminology of anatomical notation and orientation for mammalian dentitions. Tassy (1996a) is used for dental terminology of proboscidean teeth, and Tobien (1975; 1996) for features specific to teeth of mammutids.

Anatomical Abbreviations—**a.cr.**, anterior crescentoid (Tobien, 1975); **LTH**, tooth length; **p.cr.**, posterior crescentoid (Tobien, 1975); **TRW**, transverse width. If anatomical terms or abbreviations are followed by a numeral from 1 to 3, this specifies a particular loph/id: 1, protoloph/id; 2, metaloph or hypolophid; 3, tritoloph/id.

Institutional Abbreviations—**CPI**, Coastal Plains Institute and Land Conservancy, Tallahassee, Florida; **MCZ**, Museum of Comparative Zoology, Harvard University; **MOSI**, Museum of Science and Industry, Tampa, Florida; **SFSM**, South Florida Science Museum, West Palm Beach, Florida; **UF**, Florida Museum of Natural History, Gainesville; **UF/FGS**, Florida Geological Survey collection, now housed at UF.

Statistical Abbreviations—**Max**, maximum value in a sample; **Min**, minimum value in a sample; **n**, sample size; **sd**, standard deviation; **V**, coefficient of variation; **V***, adjusted V, after Haldane (1955).

DESCRIPTION OF TOOTH MORPHOLOGY

The deciduous premolars of *M. americanum* are zygolophodont, with bilophodont DP2/dp2 and DP3/dp3, and trilophodont DP4/dp4 (Figs. 1, 8), with rare exceptions noted below. Compared to the molars, the deciduous premolars are smaller and more brachydont, and have thinner and more crenulated enamel. In both upper and lower dentitions, crown length and width increases sequentially with no overlap among the three deciduous premolars (Table 3; Fig. 2; Supplementary Data). Enamel thickness also increases, on average, from the DP2/dp2 to the DP4/dp4, but with overlap.

The DP2/dp2 and DP3/dp3 have labial and lingual roots at the mesial and distal ends of each tooth. The two mesial roots are fused for most of their entire length, separating only near their apices, as are the distal pair. The location and orientation of the fused pairs of roots generally correspond to those of the loph(id)s of the crown. The roots of the trilophodont DP4 and dp4 are more complicated. Roots are preserved in five of our DP4s (UF/FGS 5372, UF 918, 991, 1862, and 205747). The fused lingual and labial distal roots are also fused with the labial root of the metaloph; the latter is separate from the lingual root of the metaloph, which is instead fused with the lingual root of the protoloph. The labial root of the protoloph is elongated transversely, mesodistally narrow, and not fused with the more distally located lingual root of the protoloph. A DP4 from Oklahoma described by Hay (1914:fig. 109) has similar root development. On the dp4, each of the three lophids is supported by lingual and labial roots. As shown by UF 137929, the lingual and labial pair of the protolophid are fused together transversely, as are those of the tritolophid. The lingual and labial roots of the hypolophid are not fused with each other, but with the corresponding root of the tritolophid.

Upper Second Deciduous Premolar

The TRW2 of the DP2 is always greater than the TRW1 (Table 3; on average, 16 percent greater, n = 29) and is approximately equal to the LTH (mean ratio of TRW2/LTH is 0.978, n = 26). Thus, the outline of the crown in occlusal view is approxi-

TABLE 1. Wear stage symbols with descriptions for premolars and molars of *Mammut americanum* (modified after Simpson and de Paula Couto, 1957, and Saunders, 1977).

Symbol	Description
0	Crown formed but not fully erupted (teeth in mandibles and maxillae only).
0+	Crown fully erupted but unworn (teeth in mandibles and maxillae only).
0/+	Crown unworn, eruption state unclear (isolated teeth only).
1	Wear on protoloph/id only.
2	Light wear on all lophs/ids; protoloph/id may show adjacent enamel figures.
2+	Protoloph/id and metaloph/id showing adjacent enamel figures.
3	Extensive wear but pattern still clear; all lophs/ids with adjacent enamel figures.
4	Severe wear, pattern partly or wholly obliterated; enamel figures contiguous.

TABLE 2.   Developmental stages for young mandibles and maxillae of *Mammut americanum* based on tooth eruption and wear stage (see Table 1).

Developmental stage	DP2/dp2	DP3/dp3	DP4/dp4	M1/m1	M2/m2	M3/m3
Fetus	0 (erupting)	0 (erupting)				
Juvenile 1	0+–1	0+	Forming			
Juvenile 2	2	1	0			
Juvenile 3	2–2+	2	0–0+	Forming		
Juvenile 4	3–4	2+–3	1–2	0		
Juvenile 5	4/Absent	4	2–2+	0–0+	Forming	
Youth 1	Absent	Absent	3–4	1–2	0–0+	Forming
Youth 2	Absent	Absent	4/Absent	2–2+	1	Forming
Young adult	Absent	Absent	Absent	3–4	2–2+	0–0+

mately trapezoidal, narrowing mesially (Fig. 1A). The entire lingual side of the crown is convex, while the labial margins of the paracone and metacone are also convex, but the labial margin is sharply indented or notched across from the interloph (Fig. 1A).

Unlike the molars, the lophs of the DP2 are not parallel, but diverge to a minor degree labially. The distance between the paracone and metacone is slightly greater than that between the protocone and hypocone. The protoloph is oriented perpendicular to the long axis of the tooth, while the metaloph slants mesiolingual-distolabially (Fig. 1A). However, in situ DP2s in maxillae are not oriented parallel to the midline of the skull, but instead the long axis of the tooth slants mesiolingual-distolabially (Fig. 3A). Thus the true orientation of the protoloph (relative to the skull) is mesiolabial-distolingual, while the metaloph runs approximately transversely.

The posttrite portion of the DP2 (the area labial to the median sulcus) is broader than the pretrite portion. In unworn and slightly worn specimens (n = 14), the notch in the protoloph created by the median sulcus is usually deeper or about equal in depth to the notch in the metaloph. However, in three of the teeth with distinctly different notch depths, that of the metaloph is deeper (UF 80286, 212593, 212649). The posttrite of each loph consists of two conelets, of which the more labial is slightly taller in unworn teeth (Fig. 4A, B). The pretrites of the protoloph and metaloph each consist of a single main cusp, the protocone and hypocone, respectively. The unworn cusps on the pre- and posttrite of the metaloph are about equally tall. The unworn paracone is taller, to a varying degree, than the protocone. For example, in UF 135747, 137930, 160000, and 212595, the difference in height is about 1 mm or less, while in UF 212593, 212606, and 212649, the difference is greater than 1.5 mm. Variable numbers of very small, secondary conelets are often present on the crest of the lophs in unworn DP2s, most commonly on posttrite 2, but quickly disappear with only slight wear.

The unworn mesial and distal surfaces of both lophs are covered with a series of fine wrinkles and crenulations (Figs. 1A, 4). The zygodont crests are poorly developed; if present they are best developed on the distal side of the posttrite cusp (e.g., UF 137930, 212629, 212649). In most DP2s (15 of 20 unworn and slightly worn specimens), a strong a.cr.1 extends vertically down the mesial side of the protocone, and then abruptly turns labially to form a weak mesial cingulum with a serrated crest (Fig. 4A). A second, weaker, more external cingulum that begins in the mesiolingual corner of the crown is sometimes also present. If so, it ends about halfway across the mesial border of the crown, while the cingulum that starts from the a.cr.1 continues across the entire mesial side, ending near the base of the crown at its mesiolabial corner. The distal cingulum is stronger than the mesial cingulum with one exception (UF 212619). It originates on the lingual side, either from a strong p.cr.2 (e.g., UF 80286, 212595, 212628) or, more rarely (n = 2), from a distolingual stylar cusp that is separate from pretrite 2 (Fig. 4B, C; UF 135747, 137930).

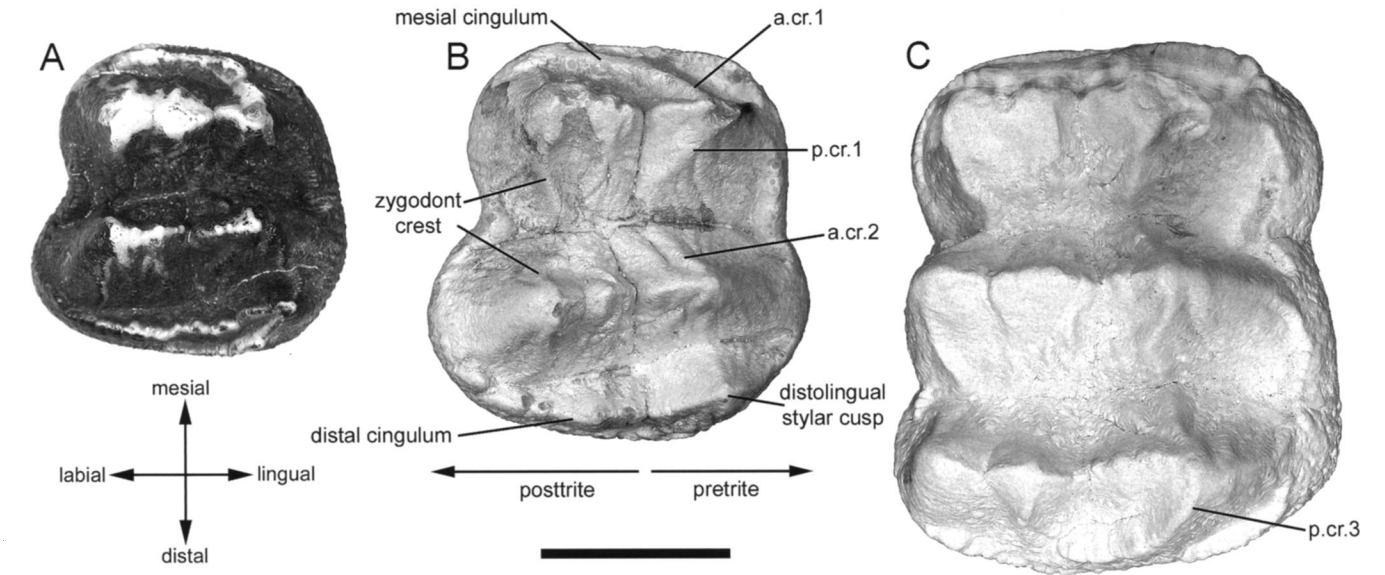As is typically the case, the pretrite cusps show more wear than

FIGURE 1.   Occlusal views of upper deciduous premolars of *Mammut americanum* from Florida. **A**, UF 137930, left DP2 (reversed). **B**, UF 212640, right DP3 (cast). **C**, UF 212609, right DP4 (cast). Scale bar equals 2.5 cm for A,B, 2 cm for C. Locality information for these and other figured teeth in Supplementary Data.

TABLE 3. Descriptive statistics for deciduous premolars of *Mammut americanum* from Florida. Abbreviations defined in text.

	LTH	TRW 1	TRW 2	TRW 3	max TRW	Enamel thickness
DP2						
Mean	32.8	27.8	32.3	—	32.3	1.3
Sd	1.81	2.57	2.25	—	2.25	0.16
V*	5.55	9.33	7.03	—	7.03	12.12
n	34	29	29	—	29	11
Max	36.4	34.3	36.5	—	36.5	1.60
Min	27.6	22.0	28.3	—	28.3	1.05
DP3						
Mean	42.8	35.2	41.7	—	41.7	1.5
Sd	2.26	2.86	2.84	—	2.84	0.17
V*	5.35	8.24	6.90	—	6.90	11.80
n	17	19	18	—	18	6
Max	46.5	41.3	47.0	—	47.0	1.72
Min	39.3	30.1	35.7	—	35.7	1.28
DP4						
Mean	71.9	53.9	59.2	60.5	60.6	2.0
Sd	3.12	2.30	3.10	2.33	2.45	0.26
V*	4.44	4.36	5.36	3.96	4.14	13.34
n	11	11	11	10	10	5
Max	76.5	58.8	64.5	64.1	64.5	2.40
Min	65.4	51.4	53.9	57.0	57.0	1.73
dp2						
Mean	31.6	22.1	25.8	—	25.8	1.3
Sd	2.08	1.84	2.68	—	2.68	0.14
V*	6.65	8.42	10.51	—	10.51	10.58
n	22	27	24	—	24	8
Max	34.6	24.5	30.1	—	30.1	1.55
Min	27.5	17.3	20.1	—	20.1	1.10
dp3						
Mean	43.8	30.0	36.5	—	36.5	1.3
Sd	2.68	2.58	2.41	—	2.41	0.12
V*	6.19	8.70	6.68	—	6.68	9.39
n	19	22	21	—	21	5
Max	51.9	34.3	41.8	—	41.8	1.54
Min	40.8	23.8	31.2	—	31.2	1.23
dp4						
Mean	71.1	42.6	51.4	50.6	52.0	2.0
Sd	5.16	1.86	3.39	4.48	3.14	0.13
V*	7.40	4.48	6.70	9.01	6.17	6.46
n	13	11	16	14	12	6
Max	79.0	46.1	56.2	56.8	56.8	2.16
Min	62.4	40.5	44.2	40.0	48.0	1.80

the posttrite cusps, and are the first to expose dentine on the occlusal surface (e.g., UF 212312). After moderate wear, dentine is exposed on all four pre- and posttrite cusps; the median sulcus initially prevents the dentine exposed on the lingual and labial sides of a loph from merging (e.g., UF 212307, 217410). After about half of the original height of the cusps is worn away, the dentine surfaces of the pre- and posttrite begin to merge, first on the metaloph and then on the protoloph. The dentine surfaces of the two lophs do not merge until the tooth is extremely worn (wear stage 4).

Two specimens in our sample of DP2s exhibit unusual morphology. UF 212619 has well-developed zygodont crests on both the mesial and distal sides of the posttrite and a very strong mesial cingulum (stronger than the distal cingulum) that terminates in the mesiolabial corner with a stylar cuspule. UF 212638 (Fig. 5) has normally formed posttrite cusps, but has only a single, large, centrally located lingual cusp. This lingual cusp, presumably the protocone, is widely separated from the paraconule and paracone, but has a strong crest that extends to near the base of the metaconule. A low, rounded cusp whose original height was less than half that of the protocone is located in the distolingual corner of the crown and is isolated from both the protocone and the metaconule. The distal cingulum originates from this cusp, making it similar to the distal cusp on UF 135747 and 137930. As even the earliest proboscideans had fully lophodont cheek teeth (Tassy, 1996a), it is interesting to see this quasi-
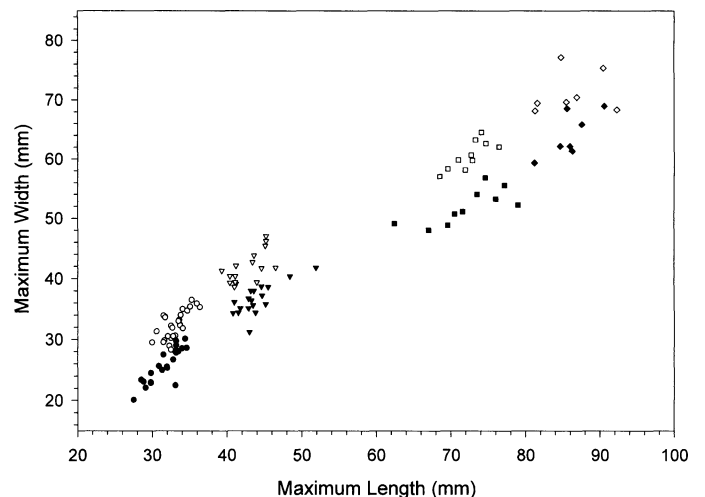

FIGURE 2. Distribution of maximum tooth length versus maximum width of deciduous premolars and first molars of *Mammut americanum* from Florida. Filled symbols represent lower teeth; open symbols, upper teeth. Circles, second deciduous premolars; triangles, third deciduous premolars; squares, fourth deciduous premolars; diamonds, first molars.
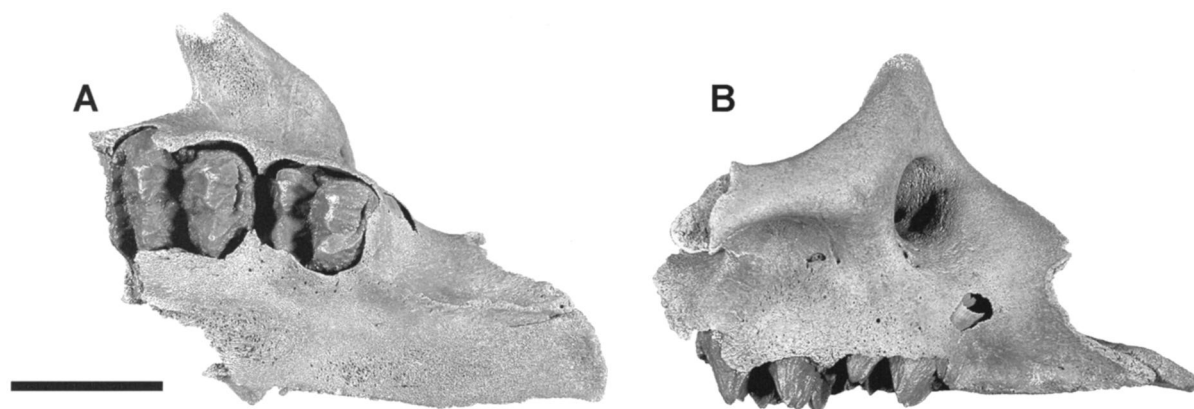
FIGURE 3. Fetal maxilla of *Mammut americanum* from the Oklawaha River, Marion County, Florida. **A**, occlusal, and **B**, lateral views of CPI OCK-D131, with erupting right DP2-DP3. Scale bar equals 4 cm.

tritubercular tooth in a member of a derived elephantoid clade, even as an anomaly.

Upper Third Deciduous Premolar

The DP3 is proportionally similar to the DP2, but on average about 23 percent larger (Table 3; Fig. 2). The mean ratio of TRW2/LTH is 0.981 (n = 15). In occlusal view, both lingual and labial margins of the crown are convex opposite the two lophs, but are strongly indented or concave opposite the interloph valley (Fig. 1B). The protoloph and metaloph lie approximately parallel to each other and perpendicular to the long axis of the tooth. The pre- and posttrite sides of the crown are approximately equal in area, unlike the DP2. The notches in the protoloph and metaloph along the medial sulcus in unworn or slightly worn specimens (n = 14) are subequal in depth and shallow, about a quarter or less of the total height of the loph.

As in the DP2, the posttrite of each loph consists of two conelets and the pretrite usually one cusp. However, adaxial conelets on both the pre- and posttrite are more abundant and stronger than on the DP2. Unworn pretrite cusps are slightly taller than the corresponding posttrite conelets.

A distinctive difference between the DP2 and DP3 is that the zygodont crests, crescentoids, and other wrinkles on the unworn enamel surface are stronger on the DP3 (Fig. 1). Zygodont crests are almost always present on the distal side of the paracone and mesial side of the metacone; 11 of 14 specimens also have a zygodont crest on the distal side of the metacone (e.g., UF 80286, 212643); and 7 of 14 have a weak zygodont crest on the mesial side of the paracone (e.g., UF 212608). The a.cr.1 extends down the mesial side of the protocone and curves labially. It merges with the strong mesial cingulum that extends between the mesiolabial and mesiolingual corners of the crown. Partial lingual and labial cingula are variably present, and are strongest opposite the interloph region. The distal side of the hypocone has two to four ridges of variable strength. With the exception of UF 212641 (described below), all DP3s have a moderately tall, mesiodistally compressed stylar cusp in the distolingual corner of the crown (Figs. 1B, 6), like that of some DP2s (Fig. 4B, C). The unworn height of this stylar cusp varies between one-third and two-thirds of the unworn height of the hypocone. In distal view, the stylar cusp has a sharp apex and several wrinkles on its distal side. In three of 14 specimens (UF 212608, 212618, and 212623), the stylar cusp even has a distinct p.cr., which leads labially to the weak, secondary cingulum. The stronger, more internal of the two distal cingula extends from the labial side of the distolingual stylar cusp, generally in the form of a serrated ridge whose height gradually decreases labially and ends in the distolabial corner of the crown. In UF 212608 and 212640, a second, smaller, low stylar cusp is formed along the cingulum on the posttrite side of the crown. Whether or not the distolingual stylar cusp has a p.cr., a weaker, lower, secondary cingulum is found on the central part of the distal crown in DP3. Tooth wear patterns on the DP3 resemble those of the DP2.

The only highly unusual DP3 in our sample of 21 specimens is UF 212641 (Fig. 7). It has the typical outline and size of a DP3 (Supplementary Data), and the morphology of its protoloph is normal. But in the metaloph, the median sulcus is located much more lingually than usual, and the hypocone is located more distally and is lower in height than is normal. Perhaps because of the more distal location of the hypocone, the size of the distolingual stylar cusp is much smaller and more closely appressed to the hypocone than in other DP3s. The distal cingulum proceeds from the cusp, as is usual, but when it nears the distolabial corner, instead of decreasing in height, it rises into a tall stylar cusp. In size, height, and shape, this distolabial cusp is identical to the distolingual cusp found in the other DP3s. Arguably, we may have incorrectly determined that this tooth is from the right side, and it is in fact a left, in which case the stylar cusp on the distal cingulum is on the normal side of the tooth. However, all other features used to determine the side of the tooth (e.g., two posttrite conelets and a single pretrite cusp) argue against such an interpretation.

Upper Fourth Deciduous Premolar

The fully trilophodont DP4 (Fig. 1C) has the same general morphology as the well-known M1 (e.g., Osborn, 1936), but is smaller (Fig. 2). The observed ranges of LTH, TRW1, and TRW2 do not overlap those of the DP3 (Table 3). TRW1 of DP4 is less than TRW2 or TRW3 (Table 3; Supplementary Data); TRW2 is greater than TRW3 in 33% of our sample (n = 12), while TRW3 is greater in the remainder. The a.cr. and p.cr. are strong, especially those on the protocone and postentoconule. The a.cr.1 and p.cr.3 curve labially to merge with the mesial and distal cingula, respectively. The lingual cingulum is stronger and more complete than the intermittent labial cingulum. Strong stylar cusps are not present on the distal cingulum (Fig. 1C).

Although our measured samples of DP4s and M1s show some overlap in width (Fig. 2), the DP4 of any particular individual is substantially smaller than its M1 (e.g., UF 210410). Enamel thickness of Florida M1s ranges between 3.2 and 4.6 mm (n = 7), while in DP4s it is always less than 2.5 mm (Table 3). Thus, a combination of length and enamel thickness should be sufficient to distinguish isolated DP4s and M1s from the same geographic region.
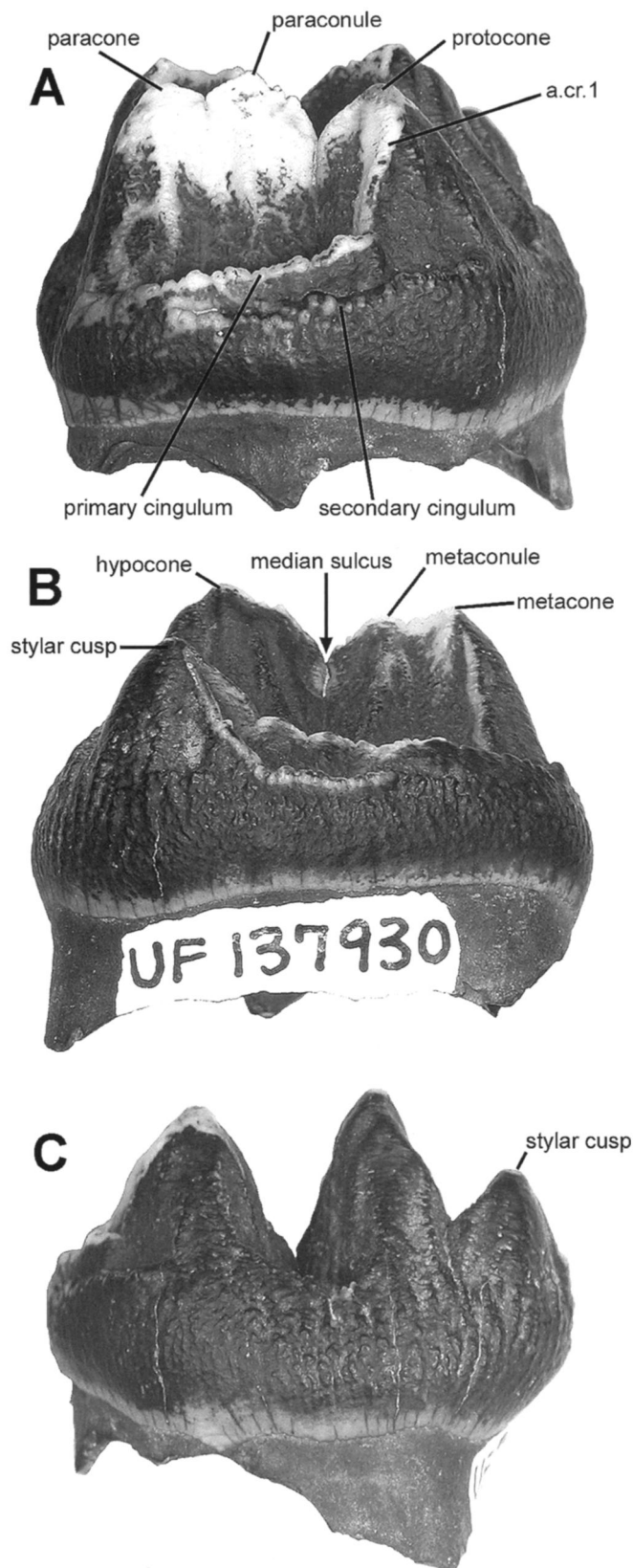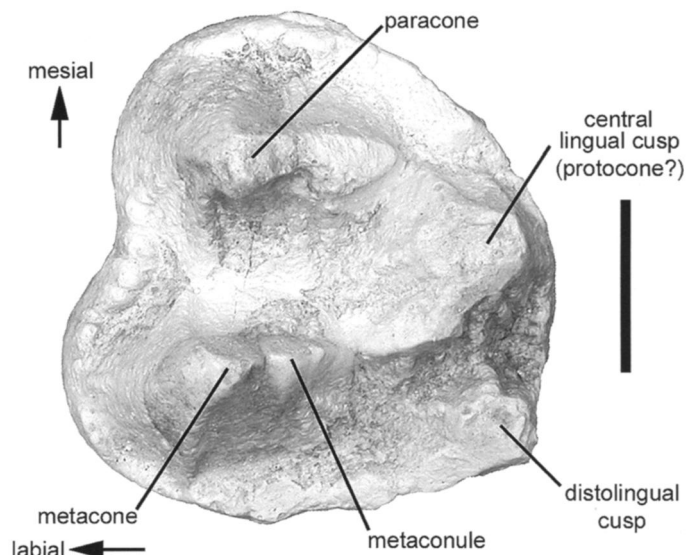
FIGURE 5. Occlusal view of UF 212638 (cast), right DP2 of *Mammut americanum* with anomalous cusp formation. Scale bar equals 1 cm.

Lower Second Deciduous Premolar

The TRW2 of the dp2 is always greater than TRW1 (Table 3; on average, 14.7% greater, n = 24) and not equal to LTH (mean ratio of TRW2/LTH is 1.22, n = 22). The crown in occlusal view is 'bullet'-shaped (Fig. 8A). Both the lingual and labial margins of the tooth are notched across from the interlophid, with convex lingual and labial margins of both the protolophid and hypolophid. The labial notch is always more pronounced than the lingual notch.

The lophids of dp2 are neither parallel to each other nor uniformly slanted distolabially, unlike those of the lower molars. The protolophid is usually either slanted mesiolabially (observed
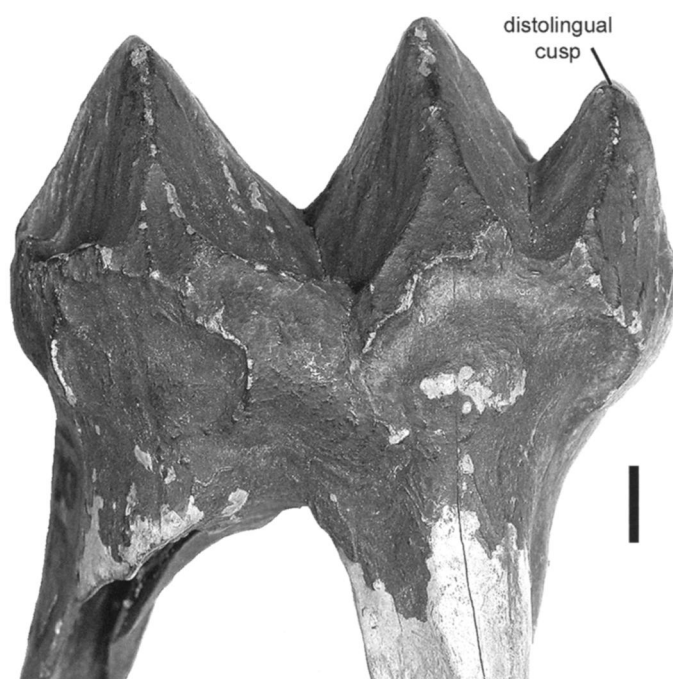

FIGURE 4. **A**, mesial, **B**, distal, and **C**, lingual views of UF 137930, left DP2 of *Mammut americanum*. Scale bar equals 1 cm.

FIGURE 6. Lingual view of UF 1863, right DP3 of *Mammut americanum* showing development of distolingual stylar cusp. Scale bar equals 1 cm.
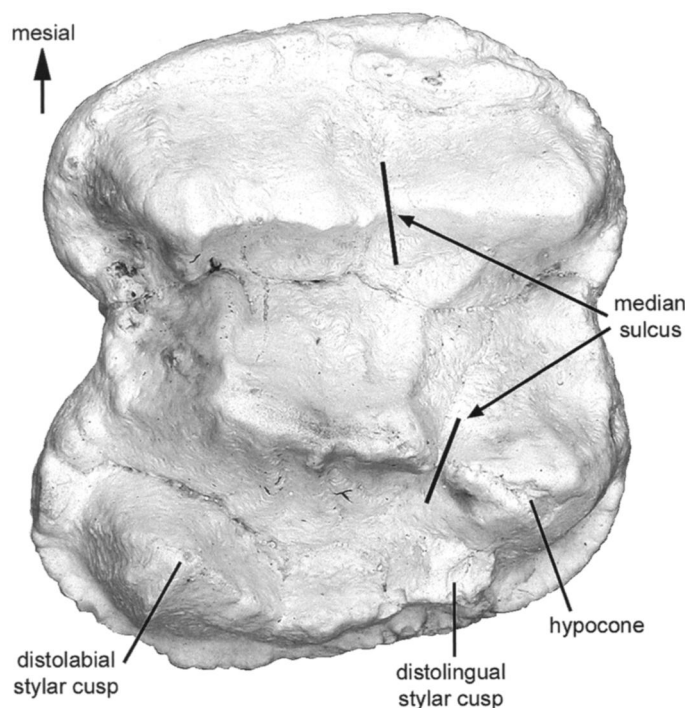
FIGURE 7.   Occlusal view of UF 212641, right DP3 of *Mammut americanum* with anomalous development of the hypocone and distolabial stylar cusp. Scale bar equals 2 cm.

in 12 out of 19 unworn or slightly worn teeth; e.g., UF 80286, 212589), or not slanted at all (observed in the remaining sample; e.g., UF 212624, 212645). The hypolophid is always slanted distolabially, with the hypoconid slanted to a greater degree than the entoconid. Specimens with the mesiolabial slant of the protolophid have a wide divergence of the lophids at the labial interlophid, with a wide valley between the protoconid and metaconid (Fig. 8A).

The posttrite portion of the dp2 (the area lingual to the median sulcus) is broader than the pretrite portion, with the notch created by the median sulcus always being deeper in the hypolophid than the protolophid and about a quarter or less the height of the lophid. The posttrite and pretrite portions of both lophids consist of two conelets. In the posttrite, the lingual conelet (metaconid or entoconid) is always taller. In the pretrite, the labial conelet (protoconid or hypoconid) is always taller. Evidence of two conelets is eliminated in early wear as the lophid crests are worn away, so only the least worn teeth display this feature. The maximum height of the pretrite and posttrite cusps is about equal in both lophids, with one exception (UF 212587) where the entoconid is ca. 1 mm taller than the hypoconid. Secondary conelets are often present on the unworn lophid crests of dp2s and most common on the hypolophid, but disappear after slight wear.

The mesial and distal surfaces of unworn dp2 lophids are covered with very fine wrinkles and crenulations. Zygodont crests are poorly developed and, if present, occur on the distal side of the posttrite cusps (e.g., UF 212587, 212590, 212622). In all unworn dp2s, the a.cr.1 is poorly developed and always separate from the mesial cingulid, which is usually a small ridge with a finely serrated crest. Sixteen of 19 unworn or slightly worn teeth have a triangular mesial cingulid (in mesial view), with the maximum height occurring centrally, where the lophids are notched. The exceptions (UF 212581, 212587, 212601) have the mesial cingulid as a simple transverse ridge with no change in height.

All dp2s have strongly developed p.cr.1 and a.cr.2, which project from the abaxial conelet on the mesial and distal side of the protoconid and hypoconid, respectively, and meet in the interlophid valley (Fig. 8A). The p.cr.2 is poorly developed and does not connect to the distal cingulid. The distal cingulid originates at the distolingual margin of the tooth, sometimes as a stylar cusp (11 of 19 unworn or slightly worn dp2s; e.g., UF 212590, 212587). It extends along the distal margin of the tooth and continues as a finely serrated ridge that continues around the base of the entoconid and terminates at the notch of the interlophid (Fig. 8A). Sometimes the cingulid ends at the interlophid notch as a stylar cuspule (five of 19 dp2s; e.g., UF 212647, 212624).

Enamel wear of the dp2 proceeds in the same manner as that of DP2, with one difference. The strongly developed p.cr.1 and a.cr.2 are subject to wear and, due to thin enamel, are obliterated quickly. Because they meet in the interlophid, they provide a bridge between the protoconid and hypoconid, allowing their enamel figures to become contiguous at about wear stage 2 or 2+ (e.g., UF 137932, 212620), an earlier wear stage than the enamel figures of the DP2 or molars.

Seven of 19 unworn or slightly worn dp2s have a small conulid at the base of the distal side of the metaconid, along the lingual margin (where the zygodont crest should run). The mandible MOSI 30601(Fig. 9A) has this conulid on its right and left dp2s and dp3s.

Only one specimen in our sample of dp2s shows unusual morphology. UF 210411 (Fig. 10) is a left dentary with in situ dp2, dp3, and dp4. The dp2 of UF 210411 consists of only the protolophid (determined from comparisons with width measurements; Supplementary Data); the hypolophid is absent. The distal cingulid of this dp2 is present directly behind the protolophid (Fig. 10B), indicating the second lophid failed to develop. The length and maximum width of this dp2 fall well outside the range of other dp2s (Table 3; Supplementary Data) and, if included in the sample, dramatically increases the V*. Therefore, it was not included in the statistical sample. Detailed analysis of enamel morphology is impossible because the tooth is in wear stage 4. If the corresponding left DP2 and right dp2 of this animal had also been found, comparative study might have yielded more conclusions about this anomaly. The left dp3 and dp4 of UF 210411 formed normally. Had the dp2 been found as an isolated tooth, identification as belonging to *M. americanum* would have been difficult, especially considering its advanced wear stage.

Lower Third Deciduous Premolar

The dp3 is proportionally similar to dp2, just as DP3 is to DP2, but is on average about 29% larger (Table 3; Figs. 8B, 9). In occlusal view, the shape is similar to that of dp2, with two notches occurring about the level of the interlophid on the lingual and labial margins and both lingual and labial margins of the lophids convex. The approximate shape is trapezoidal (Fig. 8B). Tooth wear patterns on the dp3 are similar to those of dp2 (Fig. 10B).

The lophids are not parallel to each other, somewhat similar to the pattern on the dp2. One major difference from dp2 is that, of the 14 unworn or slightly worn specimens, 10 have the protolophid slanted mesiolabially and the hypolophid slanted distolabially (e.g., UF 137931, 212600, 212611, 212636). In the remaining four specimens, the protolophid is not slanted, but is perpendicular to the long axis of the tooth (e.g., UF 212599, 212635; Fig. 8B). The posttrite portion of the tooth is broader than the pretrite, but to a lesser degree than in the dp2. The hypolophid notch along the median sulcus is always deeper than the protolophid notch, although the difference is less than in the dp2. The notch in unworn or slightly worn specimens (n = 14) is shallow, about a quarter or less of the total height of the lophid.

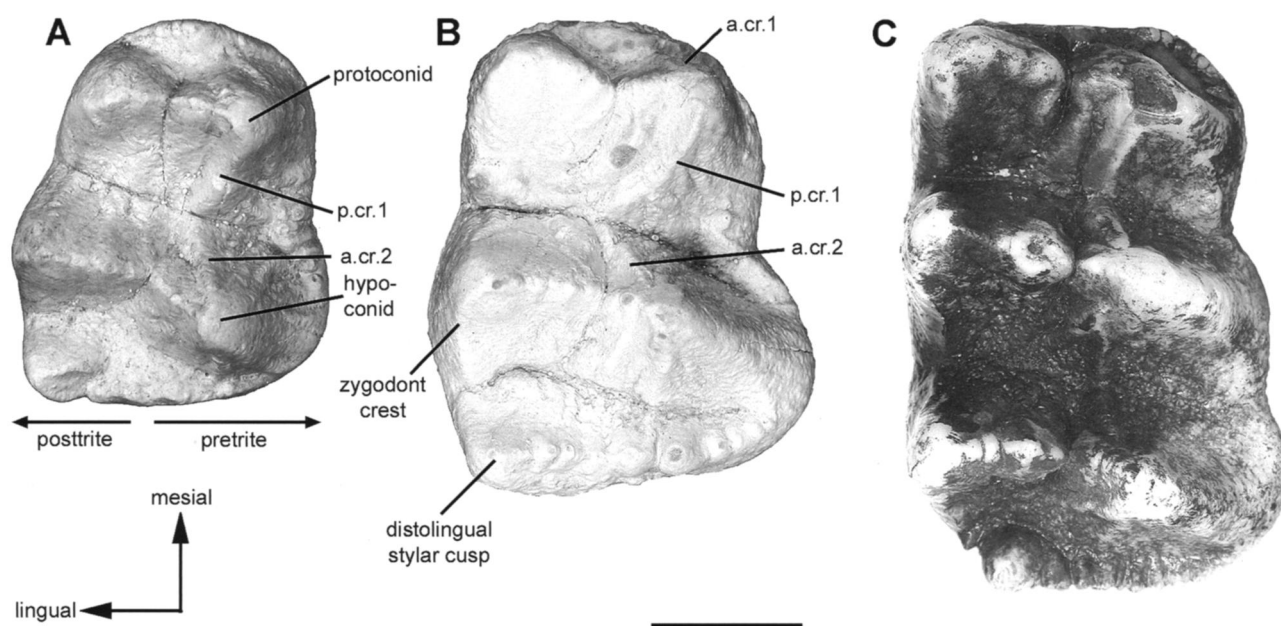Like the dp2, both posttrite and pretrite cusps are composed of

FIGURE 8. Occlusal views of lower deciduous premolars of *Mammut americanum* from Florida. **A**, UF 212590, right dp2 (cast). **B**, UF 212635, right dp3 (cast). **C**, UF 137929, right dp4. Scale bar equals 3 cm for A-B, 2 cm for C.

two conelets (Fig. 11B). Adaxial conelets are more abundant and stronger on both pretrite and posttrite cusps than on the dp2, the protoconid or hypoconid is always taller on the pretrite cusps, and the metaconid or entoconid is taller on the posttrite cusps. However, unlike dp2, the unworn posttrite cusp is always taller (usually by 1 to 2 mm) than the unworn pretrite in both lophids (Fig. 11B).

The zygodont and crescentoid crests, along with wrinkles and crenulations, are much stronger on dp3 than dp2 in unworn specimens. Zygodont crests are always present on the distal surface of the metaconid and the mesial and distal surfaces of the entoconid (e.g., UF 212611, 212635). Eleven of 14 unworn or slightly worn teeth have a zygodont crest on the mesial surface of the metaconid (e.g., UF 212591, 212636). The a.cr.1 is stronger than in dp2 and always present, yet always separate from the mesial cingulid. The mesial cingulid is similar to that of dp2, yet more developed and always triangular (Fig. 11A). The crenulations and wrinkles on the enamel surface are strongest on the distal side of the protolophid and the mesial side of the hypolophid, extending into the interlophid. Like those of the dp2, the p.cr.1 and a.cr.2 are strongly developed and join at the base of the interlophid between the protoconid and the hypoconid (Fig. 8B). Also, strongly developed ridges originate from adaxial conelets 1 and 2 of the pretrite and extend lingual to p.cr.1 and p.cr.2, respectively. Of 14 unworn to slightly worn dp3s, 13 have ridges parallel to p.cr.1 and p.cr.2 (e.g., UF 212599, 212611), while UF 212600 has only one ridge parallel to p.cr.2. In all dp3s, p.cr.2 is strongly developed and separate from the distal cingulum, which is also strongly developed. Like some dp2s, the distal cingulum of dp3 originates at the distolingual corner of the crown, with a stylar cusp present in 10 of 14 unworn to slightly worn dp3s (e.g., UF 137931, 212599, 212591). This cusp is usually about a third to half the height of the hypolophid (Figs. 8B, 11B). The other four teeth just possess a strongly developed ridge with a serrated crest (e.g., UF 27901, 80286, 82373, 212600). Whether a cusp is present or not, the distal cingulid always decreases in height from the lingual to the labial margin of the crown with a serrated crest (Fig. 11B). No specimens show the distal cingulid extending around the hypoconid and terminating at the interlophid, as in dp2. However, a separate labial cingulid is present in

all unworn to slightly worn dp3s. Large stylar cusps on the labial cingulid are observed in eight of 14 unworn dp3s. The dp3 lacks a lingual cingulid.

A median sulcus in the distal cingulid is observed in six of 14 unworn to slightly worn specimens (e.g., UF 137931, 212591, 212599, 212600). Nine of 14 specimens show a poorly developed p.cr, which runs from the apex of the distolingual stylar cusp (if present), or from the extreme lingual margin of the distal cingulid, down to a distinct ridge with a finely serrated crest along the central distal margin of the crown behind the distal cingulid (e.g., UF 137931, 212591, 212599, 212611; Fig. 11B). This marks the presence of a secondary, weaker distal cingulid.

As in dp2, six of 14 dp3s have a small cusp or conulid where the zygodont crest terminates at the distal base of the metaconid. It usually looks like a small point extruding from the enamel (UF 212635). One exception (UF 212611; Fig. 12) has a 2 to 3 mm tall conulid, with a crenulated surface and two smaller accessory cusps mesial to it. In UF 137931, the conulid is not only at the base of the metaconid, but a second similar cusp is at the base of the entoconid, between the distal cingulum and the entoconid. UF 212636 is unique in lacking a conulid at the metaconid, but having one at the base of the entoconid.

Lower Fourth Deciduous Premolar

The dp4 is fully trilophodont with a morphology that is very similar to that of the m1 and m2 (Figs. 8C, 10), but has smaller size, development of a distal stylar cusp (described below), and thinner enamel. TRW1 is always less than TRW2 or TRW3 (Table 3; Supplementary Data); TRW2 is greater than TRW3 in 50% of complete teeth in our sample (n = 10), with the rest having TRW3 greater than TRW2. The a.cr. and p.cr. are strong, especially in the interlophids between the protoconid and hypoconid and between the hypoconid and hypoconulid (Fig. 8C). The a.cr.1 curves to merge with the crest of the mesial cingulid, which is triangular like that of most dp2s and all dp3s. The zygodont crests are stronger than on dp2 and dp3, yet still relatively weak. They are strongest on the distal surfaces of the lophids, where they may be present as a finely serrated ridge. On the
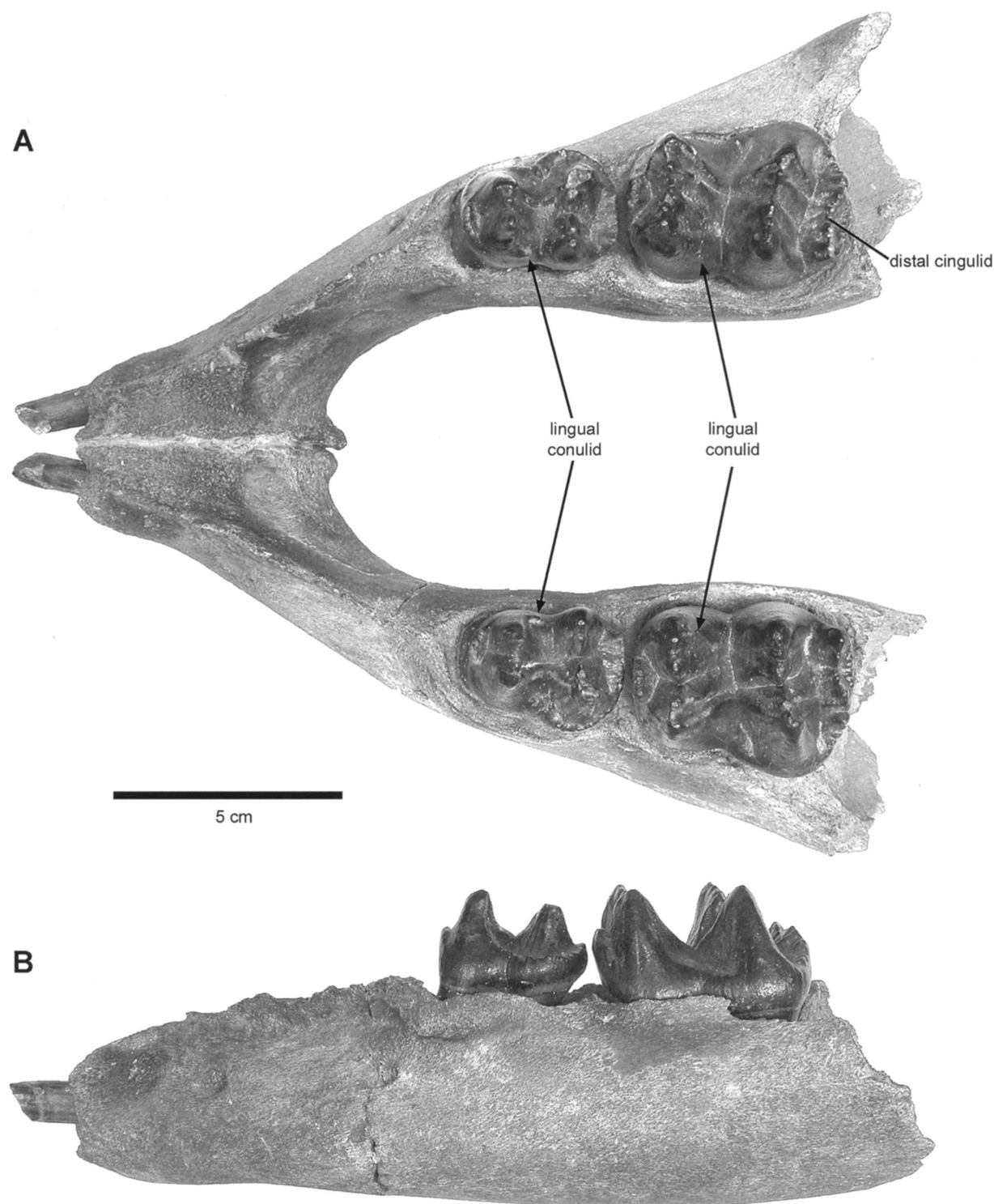
FIGURE 9.   **A**, occlusal, and **B**, left lateral views of MOSI 30601, mandible of *Mammut americanum* with right and left dp2-dp3 (and deciduous tusks).

entoconid II, the zygodont crest curves down to meet the distal cingulid (e.g., UF 81453, 131987, 212626). The lingual cingulid is absent and the labial cingulid weak, represented either by a single stylar cusp (three of nine unworn or slightly worn specimens; e.g., UF 131987, 212610), a short ridge with several cusps on the crest at the interlophids (four of nine specimens; e.g., UF 212626, 135706), or not present at all (two of nine specimens; UF 201288, 210411). The distal cingulid is similar in variation to that of dp2s and dp3s, with either a stylar cusp at or near the disto-lingual corner of the crown (four of nine specimens; e.g., UF 201288, 212626; Fig. 8C) or as a ridge with a serrated crest or series of cusps (five of nine specimens; e.g., UF 210411, 212610). In UF 81453, the distal zygodont crest of the entoconid II curves down and continues as a strong ridge with a serrated crest along
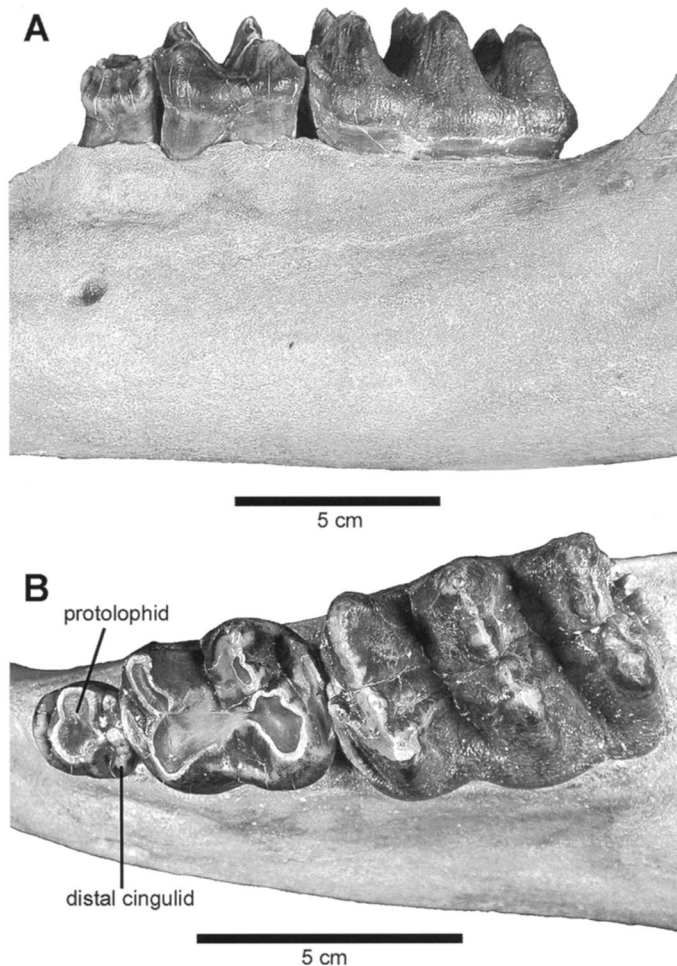
FIGURE 10. **A**, lateral, and **B**, occlusal views of UF 210411, left dentary of *Mammut americanum* with dp2-dp4. The dp2 is anomalous, with only a single lophid.

the distal margin and connects to p.cr.3; the actual cingulid is located distal to that crest.

Our measured samples of dp4s and m1s show minimal overlap in length and width (Fig. 2), and the dp4 of a particular individual is substantially smaller than its corresponding m1 (e.g., UF 81453, 210411). Enamel thickness of m1s from Florida ranges between 2.6 and 3.9 (n = 4), compared to 1.8 to 2.2 mm for dp4s (Table 3). Thus, a combination of length, width, and enamel thickness should easily distinguish dp4s and m1s.

DISCUSSION

Previous descriptions and measurements of the deciduous premolars of *Mammut americanum* (e.g., Leidy, 1869; Hay, 1914; Peterson, 1926; Hatt, 1965; Mead et al., 1979; Ray and Sanders, 1984; Laub, 1992; Daeschler, 1996) are generally confirmed in this study. But our larger samples allow a better sense of intraspecific variation, provide several anomalous or pathologic specimens, and permit quantitative analyses.

The juvenile dentition of mammutids other than *M. americanum*, such as those of *Mammut borsoni* or *Zygolophodon* sp., are also poorly represented in the published scientific literature, with few illustrations and only brief descriptions (Schlesinger, 1922; Hopwood, 1935:plate VI, fig. 5; Bergounioux et al., 1953:figs. 515, 519, 532; Tobien et al., 1988:figs. 57–60). While morphologic differences exist between these teeth and those of *M. america-*

num (i.e., enamel structure, strength of choerodonty, and lingual and labial cingula), analysis of available material shows basic similarities between juvenile dentitions of different mastodons. The DP2/dp2 and DP3/dp3 of *M. borsoni* and *Zygolophodon* are bilophodont with strong mesial and distal cingula, and the DP4/dp4 are trilophodont. The a.cr.s and p.cr.s are strongly developed and meet in the interloph(-id) valley. Of particular interest, Bergounioux et al. (1953:fig. 532) figured a maxilla of *Zygolophodon* with DP2-DP4. The DP2 is poorly preserved and the orientation of the protoloph and metaloph relative to the long axis is not clear. However, the long axis of the DP2 is not parallel to the midline of the skull, but slanted mesiolingual-distolabially, as in *M. americanum*. Thus, it is likely that *Zygolophodon*, as well as other mammutids, had the labial divergence of the protoloph and metaloph of the DP2 that is characteristic of *M. americanum*.

Deciduous teeth of *M. americanum* from the midwestern and northeastern United States are poorly represented in museum collections (Skeels, 1962; Hatt, 1965; Saunders, 1977; Abraczinskas, 1993). In Florida, far more deciduous premolars were collected at Leisey Shell Pit 1A than adult molars (Webb and Dudley, 1995). While this is not true for other localities in Florida producing a number of *M. americanum* individuals, neither are deciduous premolars exceptionally rare. For example, the number of deciduous premolars relative to total number of collected cheek teeth is 80% for Leisey Shell Pit 1A (n = 20), 53% for Hornsby Springs (n = 17), and 31% for the Tri-Britton site (n = 13). It is unclear whether this is primarily the result of taphonomic factors, or greater juvenile mortality rates of *M. americanum* in Florida than other regions (or both). As our specimens come from many different types of localities, the latter hypothesis seems more likely. The year-round warm climate in Pleistocene Florida would have allowed a relatively constant supply of vegetation for large populations of resident ungulate mammals. This in turn would have supported relatively high population densities of large carnivorans capable of preying on juvenile mastodons, such as large saber-toothed cats (*Smilodon*, *Xenosmilus*, *Homotherium*), lion (*Panthera atrox*), ursids (*Arctodus*), and packs of dire wolves (*Canis dirus*). Fossils of the above taxa have been discovered at Florida localities spanning the chronologic range of *M. americanum* (Berta, 1987, 1995; Emslie, 1995; Emslie and Morgan, 1995; Hulbert, 2001). Evidence of predation on juvenile proboscideans by *Homotherium* has been recorded from Friesenhahn Cave, Texas (Evans, 1961; Rawn-Schatzinger, 1992), and from the Guadix-Baza Basin, Spain (Palmqvist et al., 2003). More specifically, evidence of predation on juvenile mastodons by *Arctodus*, *Canis*, and *Panthera* has been reported from Pennsylvania (Holland, 1908; Daeschler, 1996). Although direct evidence for predation on juvenile mastodons in Florida is lacking, it is likely that the predatory behavior of these large carnivores was the same in Florida as elsewhere.

Specimens with unworn enamel were examined for the 'rugged' or 'smooth' morphology of mastodon teeth first noted by Leidy (1869). King and Saunders (1984) suggested that individuals with 'rugged' teeth lived in pine-dominated environments, while those with 'smooth' teeth lived in spruce-dominated environments. All unworn deciduous premolars from Florida (wear stages 0, 0+, or 0/+; n = 34) have the 'rugged' morphology, with strong choerodonty, plicated enamel, and interloph(-id) valleys obstructed by well-developed crests (Figs. 1, 8). This is consistent with reconstructions of late Pleistocene environments in Florida (Watts and Hansen, 1988). Pine forests were dominant in northern Florida and pine and scrub alternated in southern Florida during the glacial maximum. As the ice sheets retreated, pine forests became dominant across the state (Watts and Hansen, 1988). However, only deciduous teeth from Florida have been analyzed for this feature, and there is a need to examine molars to further clarify this trend.

Saunders (1977) analyzed a large sample of mandibles in order

A
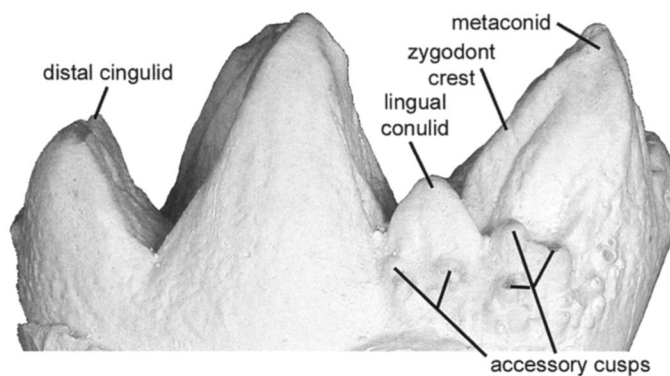
FIGURE 12. Lingual view of UF 212611, left dp3 of *Mammut americanum* with unusual development of multiple cuspules distal to metaconid in the interlophid valley. Scale bar equals 2 cm.

to reconstruct the developmental stages of *M. americanum*. However, his sample of juvenile to youth mandibles was very limited and did not provide an accurate representation of young mastodon developmental stages. We expand on Saunders' work here and further define the stages of young mastodons (from fetus to young adult). Using Savage's (1955) definitions of elephant age groups, we defined one fetal stage, five juvenile stages, and two youth stages (Table 2). Our results can be combined with Saunders' (1977) to form a detailed correlation of enamel wear to developmental stage for the entire potential life span of *M. americanum*. However, Green (2002) showed that Florida mastodon molars tend to be smaller, sometimes significantly, than those from Missouri (Saunders, 1977), although body size (inferred from postcranial dimensions) was not different. This, along with differences in diet, may affect the rate at which the teeth wear, and adversely affect the correlation of developmental stages between the two regions.

The developmental stages, or dental ages, for modern elephants are well known (e.g., Laws, 1966; Sikes, 1971; Hanks, 1972; Roth and Shoshani, 1988; Haynes, 1991), and often applied to mammoths. However, this procedure has rarely been done with non-elephantid proboscideans. Two exceptions are the work of Saunders (1977) on *M. americanum* and Tassy (1996c) on *Gomphotherium angustidens*. In contrast to Saunders (1977) and Daeschler (1996), we do not assign ages in years to the developmental stages of mastodons. Haynes (1991) assumed that mastodons had a similar life span to mammoths and modern elephants because body size, ontogenetic processes, and dental development are similar. We refrain from assigning ages in years to mastodon developmental stages because of the great differences in dental and jaw morphology between *Mammut* and elephantids.

Saunders (1977) speculated that the dp2 formed and erupted prior to the dp3 in *M. americanum*. If the dp2 erupted and was in use while the dp3 was forming, then the dp2 should be in an early to middle stage of wear when the dp3 erupts. In UF 160000 (mandible and maxilla of same individual) and CPI OCK-D131 (maxilla only; Fig. 3), the DP2/dp2 and DP3/dp3 have both formed and are beginning to erupt through the bone, but are not fully erupted. Thus, the first two premolars form and erupt at approximately the same time, and the animal is probably born with both in the process of erupting. In MOSI 30601 (Fig. 9), both dp2 and dp3 are at the same early wear stage (0+). These three specimens suggest that both teeth formed and erupted simultaneously, contrary to Saunders (1977). In older juveniles, the dp2 is at a later wear stage than the dp3 (Table 2), but this must result from a greater wear rate rather than a difference in time of eruption.

B

FIGURE 11. Deciduous lower third premolars of *Mammut americanum* showing development of cingulids. **A**, mesial view of UF 82373, left dp3. **B**, distal view of UF 212611 (cast), left dp3. Scale bar equals 2 cm.

Mammut americanum is born with paired deciduous incisors (di2 sensu Luckett, 1996) in the mandibular symphysis. These are replaced by permanent incisors (i2 sensu Luckett, 1996) early in life. Co-occurrence of di2 and i2 in a juvenile mastodon mandible from Frankstown Cave, Pennsylvania, was first described by Peterson (1926:plates 22–23) and discussed by Tassy (1987) and Luckett (1996). This individual is either in our Juvenile Stage 2 or 3 (exact determination of developmental stage from Peterson's illustration is difficult). We examined incisors and symphyseal alveoli in all mandibles used in this study, and found two specimens (UF 131987 and 27901; both in Juvenile Stage 3; Supplementary Data) that had evidence for two sets of incisors. We propose that juvenile mastodons had only di2 in Juvenile Stages 1 and 2 (Fig. 9), with the i2 forming in Stage 2, and beginning to erupt in Stage 3. Deciduous incisors were shed by Juvenile Stage 4. Thus, individuals could have visible deciduous and permanent lower tusks in Juvenile Stage 3. UF 47217 is a Juvenile Stage 2 mandible (Supplementary Data) that lacks any evidence for deciduous tusks in its symphysis. Increased sample size of juvenile mandibles with symphyses are needed to further document presence/absence patterns of the deciduous lower tusks of *M. americanum*.

Figure 13 depicts the relationship between mandibular depth and developmental stage. We have no representatives for Juvenile Stage 5. Growth is continuous for Florida mastodons throughout their juvenile life, until the youth stage is passed and the molars erupt and come into wear. Although females apparently completed growth earlier than males (Haynes, 1991), all mastodons would have stopped growth completely by the Young Adult Stage.

Some overlap occurs in maximum TRW between adjacent deciduous premolar categories, but no overlap in LTH (Fig. 2; Table 3), as noted by Saunders (1977) and Laub (1992), but with much smaller samples. In each category, upper and lower coun-

FIGURE 13. Mean mandibular depth at posterior mental foramen for developmental stages (Table 2) for *Mammut americanum*. Abbreviations: **A**, adult developmental stage; **F**, fetus developmental stage; **J**, juvenile developmental stage; **Y**, youth developmental stage. Sample sizes are: F, 1; J1, 1; J2, 3; J3, 2; J4, 5; J5, 0; Y1, 2; Y2, 2; A, 16. The adult sample is comprised of Rancholabrean individuals from Florida (Green, pers. obs.). The Y2 sample includes the uncatalogued mounted skeleton at the SFSM from the West Palm Beach Site. It has a well worn M1 and m1 (late stage 3 or early 4), a slightly worn M2 and m2 (stage 2) and an erupting but unworn M3 and m3, and thus falls close to the boundary between the Y2 and young adult development stages. Our adult sample includes only full adults, lacking the m1 and with m3 fully erupted and in wear (stage 2 or greater). Individual values for mandibular depth are listed in Supplementary Data for all individuals except full adults; data for adults available upon request from the senior author.

terparts (e.g., DP3 and dp3) have great overlap in LTH and some overlap in TRW. In identifying isolated teeth, LTH is most diagnostic of the tooth category to the level of dp2/DP2, dp3/DP3, or dp4/DP4, although a combination of enamel thickness, TRW2, and details of morphology are useful, especially if breakage prevents measurement of crown length. Upper teeth are best distinguished from their lower counterparts on the basis of morphology, although relative width is often useful (upper premolars are on average wider than their lower counterparts; Fig. 2). Obviously, bilophodont teeth are normally either second or third deciduous premolars, while fully trilophodont teeth are either fourth deciduous premolars or first or second molars. If the posterior part of the tooth is missing, TRW 1 is sufficient alone to separate fourth deciduous premolars from second or third deciduous premolars (and DP4s from dp4s). Deciduous fourth premolars are best distinguished from relatively small first molars by a combination of LTH, TRW2, and enamel thickness. Given the relatively large number of anomalous teeth in our samples and the observed range of variation in formation of lophs and cusps, the existence of very rare deciduous fourth premolars with two and a half or even two loph/ids is probable, although our sample did not include such a tooth. Likewise, with increased samples, it is likely that a fully trilophodont DP3 or dp3 will eventually be found.

In terms of tooth morphology, *M. americanum* deciduous premolars are unique in several characters compared to the molars. While the lower molars have lophids that are uniformly parallel to each other and possess a slight distolabial slant, the dp2 and dp3 do not (Fig. 8A–B). Their protolophid has a slight mesiolabial slant, while the hypolophid has the typical distolabial slant. In addition, the DP2 and DP3 protolophs have a slight mesiolabial slant (Fig. 1A–B; first noted on the DP2 by Laub, 1992), a character not found in upper molars. The dp2, dp3, and sometimes dp4 have distal cingulids with increasing height and development from the labial to the lingual margin of the tooth, with possible formation of stylar cusps (Figs. 8A–C, 11B). DP2 and DP3 have distal cingula that follow the same trend, with the labial side of the tooth usually expressing little development, while the lingual side usually has a well-developed cingulum often with a large stylar cusp (Figs. 1A, B, 4B). These characters of the distal cingula are not found on trilophodont mastodon teeth, with the exception of the dp4.

Some deciduous premolars with well-developed distal cingula have a median sulcus separating two well-defined cusps (corresponding to the pretrite and posttrite). This condition is most common in the dp3. Previous authors have referred to this strongly developed cingulid as a 'rudimentary' third lophid (e.g., Leidy, 1869; Hatt, 1965; Laub, 1992). The secondary cingulid distal to the proposed 'rudimentary' lophid on some dp3s lends support to this idea. Indeed, it is generally agreed that loph/ids are added to proboscidean teeth by transformation of distal cingula (Tobien, 1996). The development of the distal cingulid on the dp3 and, to a slightly lesser extent, on the DP3, are suggestive that the species was beginning to evolve trilophodont deciduous third premolars. Late Pleistocene samples tend to have more developed distal cingula than early Pleistocene samples. This observation could be related to increased mean tooth size in late Pleistocene individuals or selection pressure towards development of a third lophid. One trilophodont dp4 (UF 212626) had a well-developed distal cingulid with a median sulcus and secondary external cingulid. As mammutids show no evolutionary tendency to evolve tetralophodont intermediate molars (unlike some gomphotheriid lineages), it is also possible that this variation in the distal cingula is a result of developmental noise rather than evolutionary pressure for 'more loph/ids.'

The accessory labial conulid variably present at the distal base of the posttrite is not limited to deciduous teeth. UF 135701 (Aucilla River, Taylor County) is a right adult dentary with worn
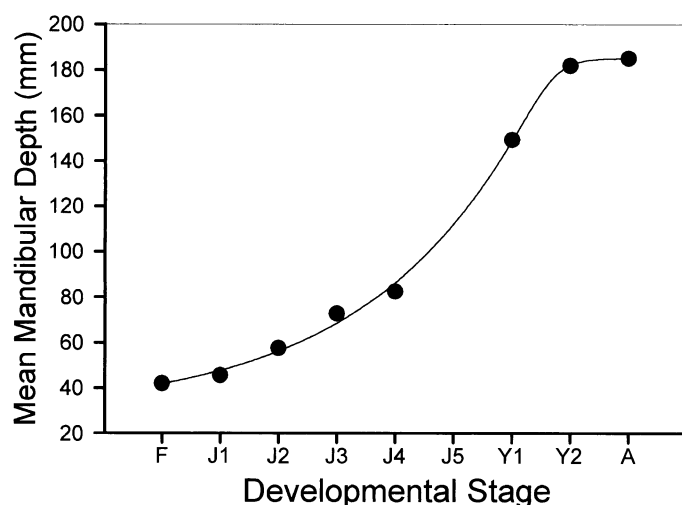
m2 and m3 (Mature age group of Saunders, 1977). A strongly developed accessory conulid is present at the distal base of each posttrite cusp on the labial margin of both teeth. The corresponding left dentary was not available, but it is very likely that its teeth would show the same structure, as in MOSI 30601. Skeels (1962) noted similar conulids in *M. americanum* molars from Michigan. The observed pattern for this conulid in teeth from adult and juvenile mandibles is that it is either present or absent on all of the teeth in the jaw, suggesting an underlying genetic cause. No similar feature was observed in the upper dentition.

Several dental anomalies are reported in this study. Anomalous teeth are present in the dentitions of other proboscideans (Roth, 1989). However, Roth described mostly adult molars in her study and suggested the cause of such anomalies was 'fabricational noise' (external forces, such as mastication, eruption, and progression, that affect the morphology of teeth as they are forming in the jaw). However, our anomalies were in samples of the dp2, DP2, and DP3, which have already formed at birth. Therefore, the cause of our anomalies was not fabricational noise, but rather stemmed from pathologies and complications that occurred in utero. Without examples from the right and left sides of the same individual, it is unknown if their cause is genetic.

We analyzed V* values for differences in variation in crown length and width along the tooth row. With one exception, we found no V*s to be extremely high or low (falling below four or above ten; Table 3), which indicates a representative sample of sufficient size from a single species (Simpson et al., 1960). The exception is dp2 TRW2 or maximum TRW (V* = 10.51). Our sample size for dp2 width is large (n = 24), so this is apparently representative of the true natural variation present in dp2s of *M. americanum*. Enamel thickness is frequently more variable than LTH or TRW1, with V* greater than 10 for four of the six deciduous premolars (Table 3). As sample size for enamel thickness is one-half to one-fourth of that for the crown dimensions, some of this may be an artifact of sampling. Only 12 of 153 total two-tailed t-tests for differences in V* of length, maximum width, and enamel thickness of upper and lower deciduous premolars produced significant levels of difference. Of these, the V*s of dp2 TRW2 and DP2 enamel thickness were both significantly greater than five other V*s (out of 17 possible combinations). The remaining two cases of significant differences involved the enamel thickness of the DP3. The overall variation in any single tooth analyzed was not greater than any of the other teeth.

CONCLUSIONS

This is the first comprehensive, quantitative description of a large sample of the deciduous premolars of *Mammut americanum*. While examination of only a few teeth would have revealed their general morphology (as in previous studies, such as Laub, 1992), the large sample allowed us to observe some anomalous teeth and analyze and quantify variation in the morphology of crown and roots. Quantitative comparisons need large sample sizes to provide accurate estimates of the mean and standard deviation. Differences in length, width, and enamel thickness are sufficient to identify almost all isolated deciduous mastodon teeth to tooth category, with the exception being those severely affected by pathology or extreme wear.

Morphologic features of mastodon deciduous teeth include a divergence of the lophids on dp2 and dp3 at the pretrite cusps, a mesiolabial slant of the protoloph in DP2 and DP3, and an increase in height and development of the distal cingula from the labial to the lingual margin of the tooth for all deciduous premolars except DP4. Some dp3s have distal cingulids with a median sulcus and the presence of two cusps, which previous au-

thors have called a 'rudimentary lophid.' This was also observed to a lesser extent in the other deciduous premolars (except DP4). The dp4 is a transitional form between the bilophodont dp2-dp3 and trilophodont m1-m2 by retaining the strong distal cingulid while adding the tritolophid to the crown. All unworn deciduous teeth in our samples have the 'rugged' crown morphology described by Leidy (1869). Many of the observations made here probably apply to other members of *Mammut*, such as *M. borsoni* (Plio-Pleistocene, Eurasia) and *M. matthewi* (Hemphillian, North America), although large samples of their deciduous premolars are needed to confirm this.

ACKNOWLEDGMENTS

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