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## Morphometrical analyses of *Mammuthus columbi* from the Dent Site, Weld County, Colorado

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Excavations at the Dent site, northeastern Colorado (USA), in 1932 and 1933 recovered well-preserved partial remains of 14 individual mammoths (*Mammuthus columbi*) and projectile points in fine colluvial sand on a terrace of the South Platte River. This paper presents morphometrical analyses of the Dent mammoth sample based on dentitions and postcranial elements stored in the Denver Museum of Natural History, Denver, Colorado. Although individual ages vary (2-43 African Elephant-Equivalent Years) and the majority of individuals in the sample (n = 8) are reproductively immature, the latest Pleistocene Dent mammoths (<sup>14</sup>C age = 10,800 yBP) were relatively small individuals, congruent with the sizes of penecontemporary *M. columbi* from the Lehner site, Arizona. Morphometrical comparisons of Dent with an earlier, interstadial sample from Hot Springs, South Dakota (<sup>14</sup>C age = c. 26,000 yBP), is constrained, however, by the special taphonomic pathways at Hot Springs that accumulated almost exclusively the remains of male mammoths. In addition, Hot Springs includes the remains of two different mammoth species, *M. columbi* and *M. primigenius*. Thus differences between Hot Springs and other localities including Dent and Lehner (Arizona) are explained primarily by considerations of taphonomy, taxonomy, age, and sex, and only in part by evolutionary processes on the North American Plains. Comparisons of samples such as Dent with Hot Springs nevertheless support the hypothesis that late Pleistocene populations of mammoths were organized - like those of modern elephantids - into matriarchal family units (as at Dent) representing a kin group of sexually immature males and females of all ages, as well as into units composed exclusively of reproductively mature males (as at Hot Springs).

*Morphometrische analyse van Mammuthus columbi uit de vindplaats Dent, Weld County, Colorado – Ogravingen in 1932 en 1933 in de vindplaats Dent, noordoostelijk Colorado (USA), brachten goed geconserveerde overblijfselen van 14 mammoeten (Mammuthus columbi) en pijlpunten aan het licht, uit fijne rivierzanden op een terras van de South Platte River. In dit artikel wordt een morphometrische analyse gepresenteerd, gebaseerd op kiezen en postcraniale skeletelementen uit de collectie van het Denver Museum of Natural History, Denver, Colorado. Ondanks de variërende leeftijd van de mammoeten (2-43 Afrikaanse olifant-equivalente jaren) en ondanks het feit dat de meeste dieren (8 van de 14) nog geen reproductieve leeftijd hadden bereikt, waren de laat-Pleistocene mammoeten van Dent (<sup>14</sup>C leeftijd = 10,800 jaar BP) relatief kleine dieren. Dit komt overeen met de maten van ongeveer even oude Mammuthus columbi van de vindplaats Lehner (Arizona). Vergelijking van het Dent materiaal met een ouder, interstadiaal, monster uit Hot Springs, South Dakota (<sup>14</sup>C leeftijd = ca. 26.000 jaar BP), wordt gehinderd door de bijzondere taphonomie van Hot Springs, waar alleen mannelijke mammoeten zijn aangetroffen. Bovendien bevat Hot Springs twee mammoet-soorten: M. columbi en M. primigenius. De verschillen tussen Hot Springs en andere vindplaatsen zoals Dent en Lehner zijn grotendeels te verklaren vanuit de taphonomie, de taxonomie, leeftijd en geslacht, en zijn slechts gedeeltelijk een gevolg van evolutionaire processen op de Noord-Amerikaanse vlakten. De vergelijking van een monster zoals Dent met Hot Springs ondersteunt desondanks de hypothese dat laat-Pleistocene mammoet-populaties – net als bij moderne olifanten – waren opgebouwd uit matriarchale familiegroepen met onvolwassen mannetjes en vrouwtjes van alle leeftijden (Dent) of uit groepen die uitsluitend uit reproducerende mannetjes bestonden (Hot Springs).*

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## INTRODUCTION

Excavations at the Dent site in northeastern Colorado, USA (Fig. 1), in 1932 and 1933 were conducted in terrace deposits of the South Platte River. The Dent site is situated beside the Union Pacific Railway, on the west side of the river, approximately midway between La Salle and Gowanda, Colorado. The site is located 29 feet (9 m) above the low-water stage of the river, which occurs today 0.5 mile from the locality. Dent's elevation is 1440 m above mean sea level. The discovery of Dent and the recovery of mammoth remains there in 1932-1933 are well documented (Figgins 1933, Bilgery n.d. ?1933, Sellards 1952, Wormington 1957, Spikard 1972). Following a flood in the fall of 1932,

large bones were found outcropping in the bank of a small gully about 500 feet south of the Union Pacific railroad station at Dent, Colorado. This finding was reported to Father Conrad Bilgery of Regis College in Denver. Bilgery investigated the discovery in 1932. He determined the bones were those of mammoths and began excavations assisted by Regis College students. During these excavations Bilgery found a large fluted projectile point beneath a mammoth pelvis (Wormington 1957: 43-44).

The Colorado Museum of Natural History (now the Denver Museum of Natural History, DMNH) continued excavations at

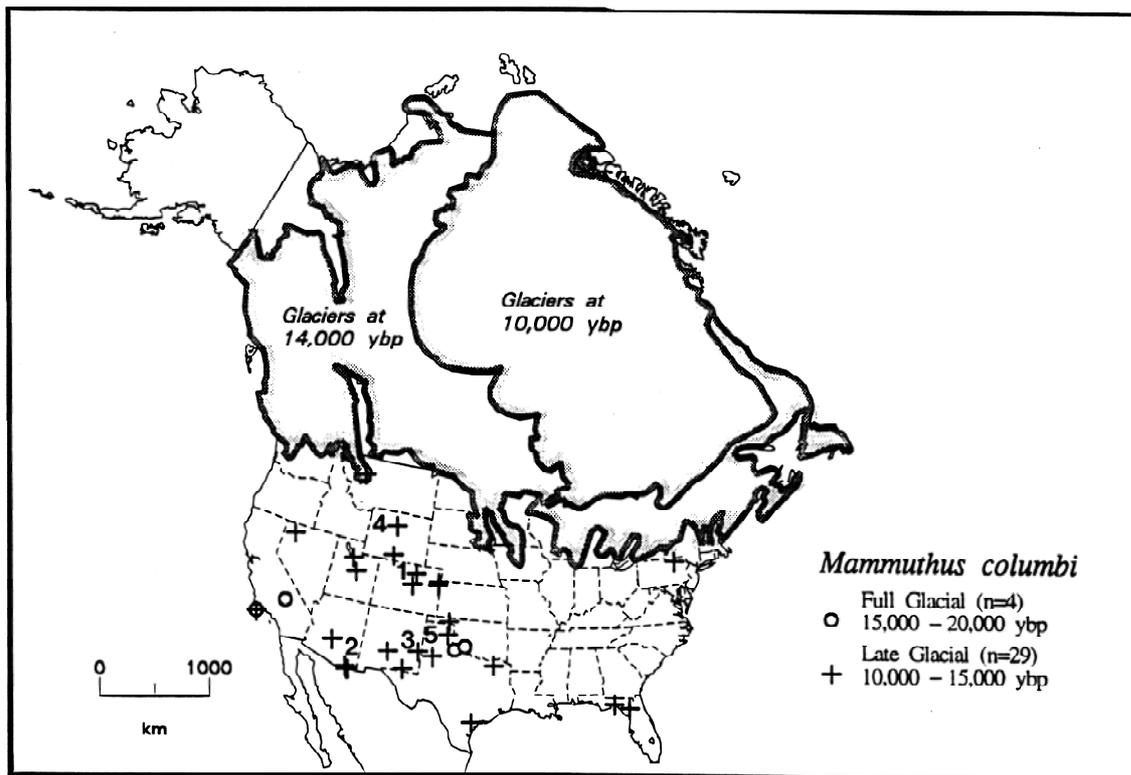


Figure 1 The full (open circles) and late (crosses) glacial distribution of *Mammuthus columbi* (from FAUNMAP Working Group 1994: 418). Crosses in northcentral Colorado (1), southeastern Arizona (2), east central New Mexico (3), northern Wyoming (4), and northern Texas (5) represent the Dent, Lehner, Clovis (= Blackwater Draw Locality No. 1), Colby, and Miami sites, respectively. Physiographically (1) and (4) are in the Northwestern High Plains (Frison 1991), (3) and (5) are in the Southern High Plains (Wendorf 1975), and (2) is in the Basin and Range (Haury et al. 1959).

Dent in 1933. A second projectile point associated with articulated mammoth bones was recorded *in situ* (Figgins 1933: plate II). A third Dent artifact, the tip of a projectile point similar in size and shape to the first point found, was given to the Denver Museum of Natural History in 1955. This artifact was found in 1932 lying about 1 ft (30.5 cm) from the teeth of one of the mammoths. For these recoveries the Dent site was recognized as providing 'the first generally accepted discovery of a fluted point unmistakably associated with articulated mammoth remains' in North America (Wormington 1957: 43). The projectile points, the culture, and the humans associated with these mammoths are named Clovis after stratified discoveries of similar fluted points and mammoth remains in Blackwater Draw near the town of Clovis, New Mexico.

The mammoth bone stratum at Dent is 4.5 feet (1.5 m) in thickness. The uppermost bone occurs about 4 feet (1.25 m) beneath the present day ground surface. Figgins (1933) noted the bone-enclosing matrix at Dent includes prominently fine yellow coluvial sand originating from the erosion of Cretaceous sediments. In addition to this sand, quartz and granitic pebbles and small boulders form a portion of the matrix in the lower third of the bone deposit. It was noted by Figgins (1933) that numerous large boulders also were found with the mammoth remains, although boulders of comparable size are rare elsewhere in the vicinity. I have noted (Saunders, unpublished data) that butchery damage to at least one Dent mammoth scapula (EPV.3931) is consistent with snap-breakage of the distal spine. Snap-breakage suggests the possible use of these larger boulders as expedient hammerstones. In Sellards' (1952:31) view Dent presented unusual circumstances in that the partial skeletons were found within a confined area. He noted for the mammoth remains that one individual was a large adult and the others were young animals or

small adults. He stated the species is 'probably *Parelephas columbi*' (= *Mammuthus* (*Parelephas*) *columbi* = *Mammuthus columbi*; genera/subgenera given by Simpson 1945:134).

A photograph of the Dent excavations in 1932 reproduced by C. V. Haynes, Jr. (1966) shows exposed remains, in part articulated and in part jumbled, notably a tibia/fibula in a plaster jacket, an ulna and possibly a radius, a lower jaw, and a pelvis. The excavation was conducted quarry-style. Weakly cemented, friable sandy matrixes in this area of the excavation can be discerned in the photograph, as it can in two photographs presented by Figgins (1933: plate II). The Dent remains were taken to the Colorado (= Denver) Museum of Natural History where parts of the collection were dispersed. Skeletons were sent to the Cleveland Museum of Natural History in Ohio (a 10-year-old female; Saunders 1980: table 1) and to the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania (a 23-year-old female; Saunders 1980: table 1). The skeletons in Cleveland and Pittsburgh are mounted and individual bones cannot be fully examined or measured.

Morphometrical results given here for the Dent sample are therefore limited to the unmounted material stored in Denver.

Stafford *et al.* (1991) determined a  $^{14}\text{C}$  age for Dent mammoth remains based on an average of dates from isolated individual amino acids in bone collagen. This average is  $10,810 \pm 40$  yBP and is one of the youngest dates obtained for *Mammuthus* in North America, for which a terminal date of  $10,550 \pm 350$  yBP has been reported, also from the Northwestern Plains (Rawhide Butte, Wyoming; *vide* Meltzer & Mead 1983). In Eurasia during this latest Pleistocene interval *Mammuthus* was restricted to polar regions, primarily in the Taimyr Peninsula and East Siberia (Sulerzhitskii 1995:166).

## THE DENT MAMMOTHS

### Previous work

In 1978 I examined skulls, mandibles, and teeth of the Dent mammoth sample in storage in the DMNH's Fossil Vertebrates Collection and in mounted skeletons in museums in Cleveland and Pittsburgh. Isolated teeth in the DMNH were assembled into dentitions

with skulls and mandibles. Including the skeletons in Cleveland and Pittsburgh, 13 individuals were identified as composing the Dent sample. Age at death was assigned to each individual on the bases of cheek tooth eruption, tooth progression in the jaw, and occlusal wear using criteria for *Loxodonta africana* (African elephant) given by Laws (1966).

Table 1 Age criteria, age groups, and age at death of *Mammuthus columbi* from the Dent Site (including Saunders 1980; AEY= African elephant-equivalent age, in years)

Spec. No.	Individual	Age criteria	Laws' age group	AEY
EPV.1897	1	dp3 in wear, dp4 beginning wear	IV	2
EPV.1893	2	dp4 with 50% ridge plates worn	V	3
EPV.1898	3	left dP3, left & right dP4: comparison with 1893, for which associated upper teeth are available, shows 1898 to be slightly older	Ve	3e
EPV.1637	4	dp4s in wear, m1s in germ cavity	VII	6
EPV.1895	5	dp4s with 100% ridge plates worn, m1: 27% worn	VIII/IX	9
EPV.1899	6	left & right m1 in early middle wear	IX	10
CMNH <sup>2</sup>	7	dp4s with 100% ridge plates worn, m1: 50% worn	IX	10
EPV.1896	8	dp4s eliminated, m1s 86% worn, m2s unerupted	X/XI	14
EPV.1901	9	dp4 alveoli closed, m1s 100% worn, m2 germ cavity persists	XI/XII	16
EPV.1636	10	m1s with 100% ridge plates worn, m2s 40% worn	XIV	22
CaMNH <sup>3</sup>	11	m1s nubbin-like, m2s with 50% ridge plates worn	XIV/XV	23
EPV.1894	12	m1s nubbin-like, m2s with 67% ridge plates worn	XVI	26
DMNH 1450 <sup>4</sup>	13	m1s nubbin-like, m2s with 72% ridge plates worn	XVII	28
EPV.1635	14	m3s with 75% ridge plates worn	XXIII	43±2

e estimate; contra Laws 1966, based on wear of upper teeth

<sup>1</sup> In 1978 paleontological specimens from Dent in the Denver Museum of Natural History bore the prefix DMNH followed by a 4-digit number (e.g., Saunders, 1980:Table 2). In 1994 and 1995, after collections' renovation, these specimens bear the prefix EPV., followed by the same 4-digit number as previously.

<sup>2</sup> Cleveland Museum of Natural History

<sup>3</sup> Carnegie Museum of Natural History, Pittsburgh; specimen number CM 12066

<sup>4</sup> DMNH 1450 is as labeled when recorded in 1978

Ages of Dent mammoths were thus reported in African elephant-equivalent years or AEY (Saunders 1980).

Following the 1978 study in the DMNH (Saunders 1980) another mandible came to light in the Denver collection (EPV.1901) that on the bases of preservation and other likenesses is viewed as part of the Dent sample. I recorded this jaw's attributes from photographs given me by K. D. Lindsay. EPV.1901 brings to 14 the number of mammoth individuals currently in the Dent collection (Table 1, Appendix 1). EPV.1901 is 9th in age series and was 16 AEY at death. The oldest individual has an inferred age at death of  $43 \pm 2$  AEY (Saunders 1980, Appendix 1). The sample mean age is 15 AEY, much above the modal age class of 2-4 AEY. Recruitment (= calves, i.e., elephants between 0 and 18 months of age that can stand between their mother's front legs; *vide* Laws 1966: 36) is 0%, but sexually immature individuals (= 14 years of age and younger) are numerous (8 of 14 individuals = 57%). In these demographical indices, the Dent mammoth sample agrees with *Loxodonta africana* samples from, e.g., Murchison Falls, Uganda that are matriarchal family units (Laws & Parker 1968).

Comparison of the ages of the Dent mammoths with individual ages of mammoths in other Clovis-associated samples (Saunders 1980, localities shown in Fig. 1) suggested that sample compositions from Dent and the Lehner (Arizona) site, and probably from the Miami (Texas) and Colby (Wyoming) sites as well, were consistent with natural matriarchal family groups as observed in modern elephantids. In conjunction with gender-determination studies of the Hot Springs (South Dakota) mammoth sample, Lister & Agenbroad (1994) examined two incomplete adult pelvises from Dent in the DMNH. They reported on the bases of oblique aperture height and ilium shaft width that these pelvises are female. In their view this finding corroborated

the conclusion previously drawn on the basis of individual ages that the Dent mammoths represent one (or more?) matriarchal family group(s) (Saunders 1980).

In 1978 it was suggested that 'natural' samples like Dent represented catastrophic mass kills of matriarchal groups by Clovis hunters (Saunders 1980), similar to modern culls of matriarchal groups of *Loxodonta africana* in, for example, Zimbabwe (G. Haynes 1991). Preliminary results of studies of dentinal banding in tusks and cheek teeth from Dent reported by Fisher (1995) suggested that the individuals died during the autumn season. In Fisher's opinion this inference independently supports the view from artifact associations that the Dent individuals had been hunted.

### Systematic discussion

The 1978 study showed the Dent mammoths are assigned to the Columbian mammoth, *Mammuthus columbi* (FALCONER, 1857). This is based on standard variates of the m3, including ridge plate number (20), width (89 mm), enamel thickness (2.1 mm), and lamellar frequency (6.3); standard variate values for *M. columbi* are reported in, e.g., Saunders 1970, and Madden 1981. *Mammuthus columbi*, believed to have evolved from *M. imperator* (LEIDY, 1858) by 700,000 yBP (e.g., Webb *et al.* 1989), was the most successful endemic North American mammoth. *M. columbi* occurred in the western, southern, and northern United States, Mexico, and western Canada. A descendant variety, *M. c. orri*, has been recognized from the Channel Islands, California (Madden 1981). During the late-glacial period from 10,000 to 15,000 yBP the species (following Madden 1981, the nominal subspecies) ranged from Florida westward to Texas, New Mexico, and Arizona and northward to Colorado, Utah, Wyoming, and Nevada (Fig. 1; FAUNMAP Working Group 1994). Characteristically *M. columbi* bore up to 21 plates on m3, 14 plates on m2, and 12 plates on m1 (Saunders 1970, Madden 1981).

Analyses of possible food residues obtained from Dent mammoth molars provide direct evidence of a mixed diet including grass, conifer bark, and prickly pear cactus (*Opuntia* sp.) for latest Pleistocene *M. columbi* on the Northwestern Plains (Cummings & Albert 1995). These limited data are consistent with the mixed diet (grasses, conifer twigs) previously determined from *Mammuthus* (?*M. columbi*) coprolites in the American Southwest (Mead *et al.* 1986).

As noted by Lister & Bahn (1994), *M. columbi* attained a stage of evolution approximating that of Eurasian *M. trogontherii*, the steppe mammoth, i.e., possessing approximately 20 plates on the third molars. (Compare, e.g., *M. columbi* as noted here and by Madden 1981, with *M. chosaricus* [= *M. trogontherii*] as noted by Guseva & Nikitin 1995: ridge plate

number = 20 vs 22, length = 259-382 vs 277, width = 88.8 vs 90, enamel thickness = 2-2.2 vs 1.8-2.2, and lamellar frequency = 6.5 vs 7). Although smaller than *M. trogontherii*, latest Pleistocene *M. columbi* was generally larger than *M. primigenius* from Siberian deposits of broadly contemporary geological age, such as Berelekh (Figs. 2, 3). Large individuals of *M. columbi* were noted (as *Parelephas?* cf. *columbi*) from early excavations in deposits in Blackwater Draw, New Mexico (Stock & Bode 1936: 235) dating to 11,170 yBP (C.V. Haynes 1991, 1995). Mammoth 1 (male) and Mammoth 2 (?female), for example, excavated at the Clovis site in Blackwater Draw in 1936 (Cotter 1937) measured (based on calculations) 3.96 m (13 feet) and 3.75 m (12.4 feet) in height, 'in the flesh', respectively (Saunders & Daeschler 1994). Results of a zooarchaeological study

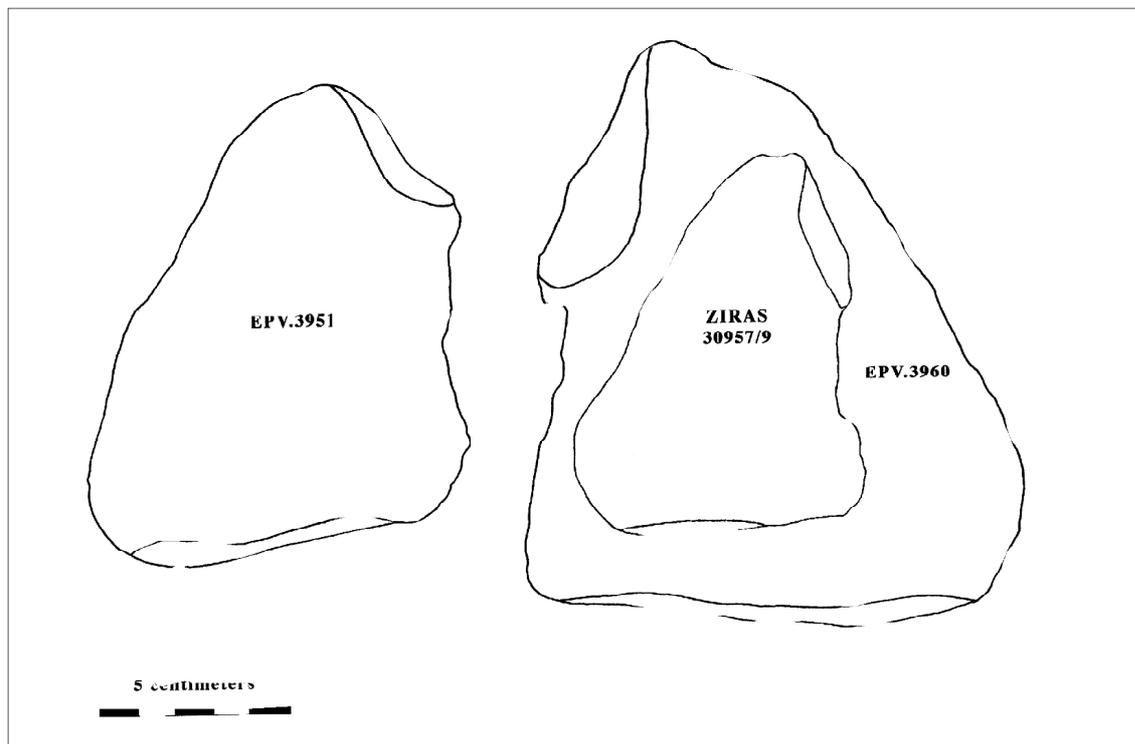


Figure 2. Lateral silhouette sketches of adult Dent (*Mammuthus columbi*, EPV.3951, EPV.3960) and characteristic adult Berelekh female (*Mammuthus primigenius*, ZIRAS 30957/9) scaphoids. Measurements for the Dent scaphoids are given in Appendix 2; measurements (in mm) of ZIRAS 30957/9 are GL = 99.4, GB = 76.1, and GD = 42.6 (Saunders and Baryshnikov unpublished data). EPV.3951 and ZIRAS 30957/9 are of the left side; EPV.3960 is of the right side.

of the Dent mammoth remains have been submitted for publication elsewhere. Here morphometrical analyses of Dent mammoth remains, in part orally presented previously (Saunders 1995), are emphasized.

## MORPHOMETRICAL RESULTS

### Methods

Measurements and calculations of mammoth teeth and bones given here (in millimeters) are for standard variates. For teeth these variates are primarily from Osborn (1942). Variates for mammoth bones are also standardized (e.g., Saunders 1970, Dutrow 1980, Madden 1981, Agenbroad 1994, Saunders & Baryshnikov unpublished data). These include the osteological measurement points given by von den Driesch (1976) for ungulates.

Variates reported here are thus in standard and general usage. Measurements and calculations of teeth and limb bones in the Dent sample are compared (1) with measurements and calculations of the sample of *Mammuthus columbi* (*M. c. columbi*) reported by Madden (1981) in his doctoral dissertation, and (2) with measurements of the sample of *Mammuthus* from Hot Springs, South Dakota studied and reported by Dutrow (1980) in her Master's thesis. Madden's study at the time of its completion was exhaustive and hence his reported sample of *M. columbi* is here treated as a 'population'. The first two comparisons provide insight into the relative position of the Dent sample in the morphometrical framework of the taxon. In addition, measurements and calculations for teeth in the Dent sample

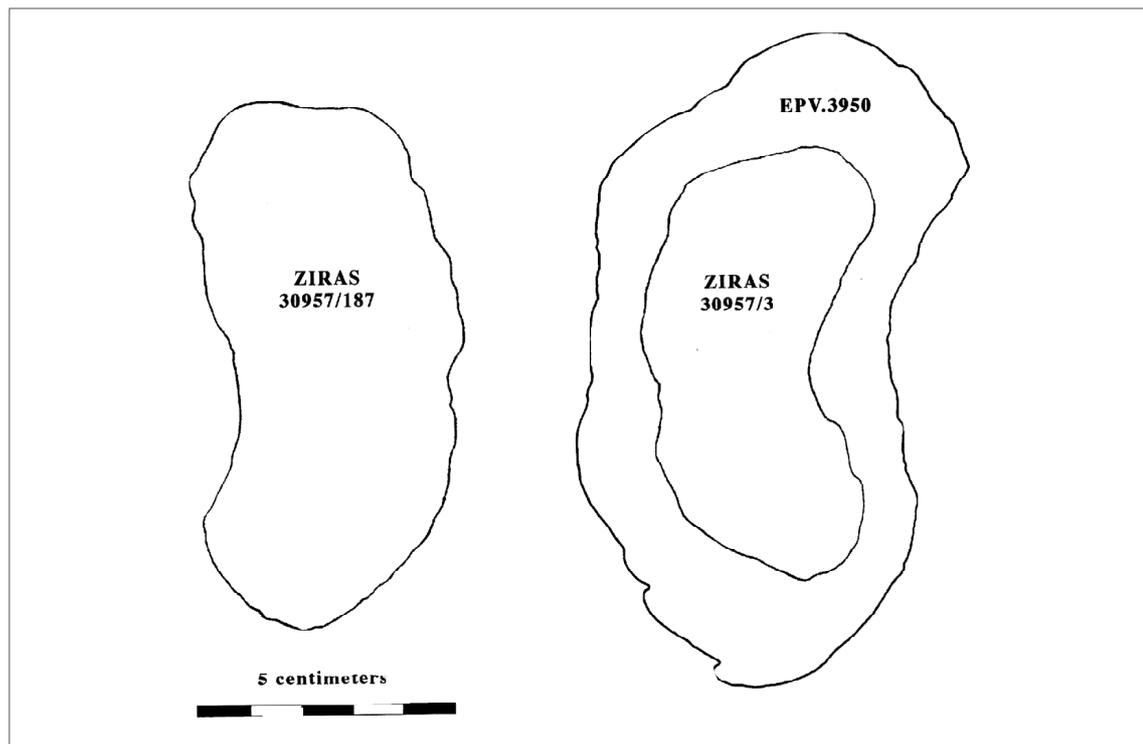


Figure 3 Lateral silhouette sketches of adult Dent (*Mammuthus columbi*, EPV.3950) and characteristic adult Berelekh female (*Mammuthus primigenius*, ZIRAS 30957/3) and male (*Mammuthus primigenius*, ZIRAS 30957/187) pisiforms. Measurements for the Dent pisiform are given in Appendix 2; measurements (in mm) of ZIRAS 30957/3 and ZIRAS 30957/187 are, respectively: GL = 106.65, 129.9; GB = 35.6, 53.0; GD = 62.9, 60.5; and CD = 118.0, 160.0 (Saunders and Baryshnikov unpublished data). EPV.3950 and ZIRAS 30957/3 are of the left side; ZIRAS 30957/187 is of the right side. The latter is the largest pisiform in the ZIRAS Berelekh assemblage.

are compared (3) with measurements and calculations of a penecontemporaneous sample from the Lehner site, Arizona. The third comparison provides a spatial contrast. These broadly (1) and narrowly (2, 3) focused comparisons enhance conclusions concerning the Dent sample and draw attention to local evolutionary process.

#### **Dentitions: Dent dp4-m3 (Madden 1981)**

Data on Dent dentitions and teeth are given in Appendix 1. Table 2 gives sample statistics for dp4-m3 from Dent. Two m3s in a mandible are available in the Dent sample. Each is composed of 20 ridge plates. Length and height of Dent m3 are not determinable.

Values for other variates of the two m3s are width: 87.3 and 90.2, enamel thickness: 2 and 2.2, and lamellar frequency: 6 and 6.5.

Comparisons of these values with statistics for Madden's (1981: 88) sample ('population') of *M. columbi* shows for Dent that (1) m3 ridge plate number is characteristic of *M. columbi* (mean = 21, n = 16, OR = 18-23), (2) m3 widths are less than the mean of Madden's sample but are well within his sample's range (mean = 93, n = 48, OR = 73-111), and (3) both m3 enamel thicknesses (mean = 2.1, n = 40, OR = 1.2-3.2) and m3 lamellar frequencies (mean = 6.2, n = 48, OR = 3.7-8.5) are characteristic. On the bases of these variates the Dent m3s are 'characteristic' to 'possibly narrow'.

Eight m2s are available in the Dent sample (here and below, the number of specimens varies with the attribute recorded). Ridge plate number for Dent m2s is consistent at 15. This Dent value is above the mean for this variate (14, n = 18) in Madden's sample but occurs within this sample's range (OR = 12-16). The mean length of Dent m2s (190, n = 4) is less than the mean length reported by Madden (204, n = 19) but like ridge plate number, is within his sample's range (OR = 178-204). The mean width of Dent m2s (58.3, n = 6), however, is much less than the mean

reported by Madden (76, n = 28) and outside (below) the range (OR = 65-102) reported for m2 width in his sample. Mean enamel thickness for Dent m2s (2, n = 6) is characteristic of *M. columbi* based on agreement with Madden's sample (mean = 1.8, n = 24, OR = 1.1-2.3). Mean lamellar frequency of Dent m2s (8.3, n = 6) is above the mean value in Madden's sample (7.4, n = 39) but is within the range (OR = 5.5-9.5) for this variate in the latter sample. Height of Dent m2s could not be determined as specimens were in alveoli, were incomplete, or have their tallest ridge plate shortened through occlusal wear. Compared with Madden's sample, the Dent m2s are 'narrow' and 'platy'.

Eight m1s are also available from Dent. The mean m1 ridge plate number for Dent mammoths (13.5, n = 4) is both above the mean ridge plate number reported by Madden (12, n = 14) and outside (above) his sample's range (OR = 11-13). The mean length of Dent m1s (167.4, n = 3) is greater than the mean length in Madden's sample (159, n = 21) but is within his sample's range (OR = 134-178). The mean width of Dent m1s (58.3, n = 8), on the other hand, is less than the mean m1 width reported by Madden (64, n = 33) but is within his sample's range (OR = 49-76). Mean height (109.3, n = 2) and mean enamel thickness (1.5, n = 8) of Dent m1s are above the means reported for these variates by Madden (102, n = 21 and 1.3, n = 29, respectively) but both are within his sample's ranges (OR = 80-121 and OR = 0.7-2.2, respectively). The mean lamellar frequency of Dent m1s (9, n = 5) is characteristic for the species (mean = 9, n = 30, OR = 7-10.7). From these comparisons, the Dent m1s depart from the characteristic form in being 'quite platy' and 'probably narrow'.

Five dp4s are available in the Dent sample. The mean ridge plate number for Dent dp4s (11.3, n = 4) is both above the mean ridge plate number reported for the broader sample

Table 2. Sample statistics for characters of lower teeth in *Mammuthus columbi* from the Dent Site (data from Appendix 1).

Tooth	Statistic	Pl.	Lg.	W.	Ht.	En.	Lf.
m3	$\bar{x}$	20±0		84.8±1.45		2.1±0.1	5.3±0.25
	s	0		2.05		0.14	0.35
	V	0		2.31		6.67	5.56
	n	2	-	2	-	2	2
	OR	20		87.3 - 90.2		2 - 2.2	5 - 6.14
m2	$\bar{x}$	15±0	190±4.9	54.3±1.5		2±0.05	8.3±0.2
	s	0	9.9	3.0		0.1	0.2
	V	0	5.2	5.2	-	6.16	5.02
	n	8	4	5		6	5
	OR	15	181.5 - 200	55.6 - 60.3		1.7 - 2.1	8 - 9
m1	$\bar{x}$	13.5±0.3	167.4±5.5	54.3±1.2	109.3±0.7	1.5±0.1	9±0
	s	0.58	9.54	1.33	0.99	0.21	0
	V	4.9	5.7	5.7	0.9	13.8	0
	n	4	3	5	2	8	5
	OR	13 - 14	157 - 175.8	50 - 61	108.6 - 110	1.3 - 1.9	9
dp4	$\bar{x}$	1.3±0.5	124.6±4.7	51.7±2.6	84.9	1.3±0.1	9.7±0.3
	s	0.96	8.08	5.81	-	0.23	0.58
	V	8.5	6.5	11.2		7.7	6.0
	n	4	3	5	1	5	3
	OR	10 - 12	15.3 - 129.4	44.9 - 57	84.9	1-1.6	9 - 10

(Madden 1981: 89, mean = 10, n = 10; where dp5 = dp4 of this paper) and outside (above) this sample's range (OR = 9-11). The mean length of Dent dp4s (124.6, n = 3) is characteristic for the population (mean = 124, n = 11, OR = 116-133). The mean width of Dent dp4s (51.7, n = 5), however, is below the

mean width reported by Madden (58, n = 18) but is within (although low in) his sample's range (OR = 47-68). For Dent dp4s, height (84.9, based on one measurement), mean enamel thickness (1.3, n = 5), and mean lamellar frequency (9.7, n = 3) are all above the means (80, n = 7; 1.1, n = 17; and 9, n = 17,

respectively) but within the ranges reported by Madden (OR = 62-89; OR = 0.6-2.2; and OR = 7.7-10.1, respectively). On these bases the Dent dp4s, like the Dent m1s, depart from the characteristic form by being 'quite platy' and 'probably narrow'.

#### Dentitions: Dent dp4-m2; Lehner dp4-m2

The Lehner site is a Clovis mammoth-kill near Hereford, in the San Pedro Valley, south-eastern Arizona (Fig. 1). The site occurs at an

elevation of 4,190 ft (1,270 m) on the right bank of a modern arroyo tributary to the south-flowing San Pedro River. In 1955-1956 and 1974-1975 the Arizona State Museum conducted large-scale systematic excavations at Lehner. During these excavations the culturally associated remains of 13 mammoths (*Mammuthus columbi*, Saunders 1970) were recovered from sand and clayey sand. Twelve radiocarbon dates for the Clovis occupation at the Lehner site average  $10,930 \pm 40$  yBP

Table 3 Range of variation in upper and lower cheek teeth of *Mammuthus columbi* from the Dent and Lehner Sites (measurements in mm; Lehner data from Saunders, submitted).

Site	n	Pos.	PL(A.)	Lg.	Ht.	W.	En.	M.	c.
Dent	3	dp3	5+7+	512e-63.5		31.8-43.6	0.9-1.1	5+	<0.8
	4	dp4	12(12)-14(5)	119.5-141.3	87.8-91.0	37.0e-53.6	1.2-1.5	8%-10	<1.2
	3	M1	9(9)-14(11)	110e-158.6	121.6-123.8	58.3-62.5	1.5-1.6	8-8½	<0.9
	1	M2	16(9)	183.6	148	68	1.9	7	thin
Lehner	1	dp3	10	96	62	56	1	10e	1e
	1	dp4	13	131	105	65	1	11-12	<1
	4	M1	11-13	145-174	110-132	74-75	2	7-9	2-4
	3	M2	17	216	140-148	70e-85	2-2.5	8-10	1->5
Dent	1	dp3	8+(8+)	68.1		35.7e	1.0	8+	thin
	6	dp4	10(10)-12+(1)	107+-129.4	84.9	31.4-57	1.0-1.6	9+-10+	<1.9
	15	m1	1+(1+)-14(13)	38+-175.8	108.6-110	39-61	1.3-1.9	7-9	<0.8
	8	m2	15(6)-15(11)	181.5-200		53.6-63	1.7-2.1	8-9	thin
	2	m3	20(15)-20(16)			87.3-90.2	2.0-2.2	6-6½	thin
Lehner	2	dp3	14	124		41-42	1	11½	<1.5
	6	dp4	10-12	119-140	70-74	50-59	1-1.5	8%-9%	2-5
	13	m1	12-15	150-168	130-140	59-69	1.5-2	6-11	<1-6
	4	m2	13-15	164-215		79	2.5	6-8½	2.5

Symbols— as in APPENDIX 1

(C.V. Haynes 1991). Clovis occupations in the San Pedro Valley ended with deposition of a black organic clay dated to  $10,880 \pm 90$  yBP at the Lehner site. These dates show that the Lehner and Dent sites are penecontemporaneous in the latest Pleistocene.

Teeth from Dent and the Lehner site can now be compared to address the question: do 'platy' and 'narrow' dental patterns also emerge from comparison of Dent with its nearest temporal neighbor (10,810 yBP vs. 10,930 yBP)? Measurements and calculations for dentitions and teeth of *M. columbi* from Lehner have been reported elsewhere (Saunders 1970, unpublished data). Tables 3 and 4 give range of variation and sample statistics (for ridge plate number, length, width, and enamel thickness), respectively, for cheek teeth of *M. columbi* from the Dent and Lehner sites. From Tables 3 and 4 it is noted that:

- (1) Dent m2s are on average 'more platy' (15 vs. 14 ridge plates) and 'shorter/smaller' (length = 190 vs. 193) than m2s from the Lehner site (m2 width cannot be compared);
- (2) Dent m1s are on average 'narrower' (58.3 vs 63.3) and 'shorter/smaller' (167.4 vs. 171.8) than Lehner m1s; and
- (3) Dent dp4s are on average 'more platy' (11.3 vs. 10.5 ridge plates) and 'narrower'

(51.7 vs. 53.5) than dp4s from the Lehner site; Dent dp4s are on average also 'shorter/smaller' (124.6 vs. 131.5) than Lehner dp4s.

**Postcranial skeleton: Dent (Madden 1981, Dutrow 1980)**

Standard measurements of postcranial elements of *Mammuthus columbi* in the DMNH are given in Appendix 2. Madden (1981: 93) presented broader sample data only for selected adult limb bones of *M. columbi* and comparison of his data therefore cannot be made with the entire osteological assemblage reported in Appendix 2. Comparison is also made with measurements of limb bones reported by Dutrow (1980) for a sample of *Mammuthus* from Hot Springs, South Dakota. For convenience, comparison with Dutrow's data is also based on selected elements reported by Madden. Comparison with Hot Springs is made in awareness of the taxonomical (*M. columbi* and *M. primigenius*) and taphonomical (primarily males) caveats previously noted. Comparison with the Lehner site, which was useful for the teeth, is precluded because a suitable sample of adult limb bones is not available from that Arizona locality. Comparisons that follow are therefore between portions of the Dent and Hot Springs sample that correspond with material presented in Madden's (1981) summary of *M.*

Table 4 Measurements of lower teeth of *Mammuthus columbi* from the Dent and Lehner Sites (measurements in mm; Lehner Site data from Saunders, submitted).

		Pl.				L.g.				W.				En.	
		n	x	s	v	s	v	r	s	v	r	s	v		
dp4	Dent	5(4)(3)	(11.3±0.5)	(.0)	(8.5)	[104.6±4.7	[8.1]	[6.5]	51.7±2.6	3.8	11.2	1.3±0.1	(.2)	17.7	
	Lehner	6(4)	(10.5±0.5)	(1.0)	(9.5)	(131.5±4.5)	(9.0)	(6.8)	53.5±1.6	3.8	7.1	(1.4±0.1)	(0.1)	(7.1)	
m1	Dent	8(4)(3)	(13.5±0.3)	(0.6)	(4.3)	[167.4±3.3]	[9.2]	[3.7]	38.3±1.2	3.3	3.7	1.3±0.1	(.2)	13.8	
	Lehner	13( 1)(10)	(13.5±0.2)	(0.8)	(5.9)	(171.8±4.0)	(13.2)	(7.7)	63.3±0.9	3.1	4.9	[1.8±0.1]	[0.2]	[11.1]	
m2	Dent	8(6)(4)	15±0	0	0	[190.0±4.9]	[9.9]	[5.2]	(53.3±1.5)	(3.6)	(6.2)	(2.0±0.05)	(0.1)	(6.16)	
	Lehner	4	14.0±0.6	1.2	8.6	193.0±12.2	24.3	12.6							

*columbi*. Measurements of this material are given in Table 5.

In the forelimb, morphometrical data for adult individuals from Dent and in Madden's and Dutrow's samples can be compared for the humeri, ulnae, and radii. For the humeri, the greatest breadth of the proximal end (Bp in von den Driesch 1976, PW in Madden 1981) of EPV.2775 is 262.5. Although below the mean value for greatest breadth of the proximal end reported by Madden (307) and by Dutrow (295.3), the Dent value falls within the range of this variate in Madden's sample (OR = 225-390) but outside (below) the range of Dutrow's sample (OR = 280e-

325). Measurements of greatest breadth of the distal end (Bd, DW) are available for two Dent humeri. For EPV.3934 this value is 247.5 and for EPV.3933 it is 246.5. Although within the range of greatest breadth of the distal end reported by Madden (OR = 244-366), both Dent values are well below the mean (302, n = 14) and quite near the lower limit of variation reported for this broader sample. Both Dent values for this variate are outside (below) the range of the Hot Springs sample reported by Dutrow (mean = 304.25, OR = 278-335, n = 8). Measurements of greatest breadth of the proximal end of two Dent radii, EPV.2778 and EPV.3941 (131.3e and 115e respectively), are smaller than this

Table 5 Comparison of forelimb and hindlimb elements of *Mammuthus columbi* from Dent with the *M. columbi columbi* population reported by Madden (1981) and the Hot Springs, South Dakota, *Mammuthus* sample reported by Dutrow (1980) (measurements in mm).

	Dent (EPV.)				Madden's Population		Dutrow's Sample <sup>1</sup>	
Humeri	2775	3934	3933	x	OR (n)	x	OR (n)	
Bp	262.5			307	225-390 (10)	295.3	280e-325 (3)	
Bd		247.5	246.5	302	244-366 (14)	304.25	278-335 (8)	
Radii	2778	3941						
Rp	131.3e	115e			142	136.8	116e-157 (5)	
Ulnae	3945	3944						
Ua	173	170		214	201-227 (3)	204		
Femora	3991	3992	3997	3996				
Dp	227.5			374	327-417 (8)			
Bd	115.5	244.5	268	248	260	225-300 (9)		
Fibulae	2200	4068						
Bd	64.5	77		66	62-70 (2)			

<sup>1</sup>exclusive of partial measurements

variate reported by Madden (142) based on only one radius. Measurements of greatest breadth of the proximal end of the Dent radii are also small in comparison with the Hot Springs mean (136.8,  $n = 5$ ). Although EPV.2778 is within the range of this variate in Dutrow's sample (116e-157), EPV.3941 is outside (below) her sample's range.

Two Dent ulnae, EPV.3945 and EPV.3944, can be compared based on greatest breadth of the distal end (173 and 170, respectively) with three ulnae reported by Madden and with one ulna reported by Dutrow. In these comparisons both Dent ulnae are below the mean value reported by Madden (214) and outside (below) his reported range for this variate (OR = 201-227). The Dent ulnae are also both smaller than the Hot Springs ulna reported by Dutrow, based on greatest breadth of the distal end (204).

In the hindlimb, morphometrical data for adult individuals from Dent and in Madden's sample can be compared for the femur and fibula. For the femur, the greatest breadth of the proximal end of EPV.3991, 327.5, is well below the mean (374,  $n = 8$ ) and near the lower limit of variation (OR = 327-447) reported by Madden. Small size persists in comparison of the greatest breadth of the distal end. For Dent, values for this variate are 215.5, 244.5, 268, and 248 mm. In Madden's sample ( $n = 9$ ), the mean value for greatest breadth of the distal end is 260, with an observed range of 225-300. Based on this comparison, the greatest breadths of the distal end of three Dent femora are below the mean value reported by Madden and the greatest distal breadth of one Dent femur is outside (below) the variation he reported for his broad sample. Measurements of the greatest breadth of the distal end of two Dent fibulae can be compared with two fibulae reported by Madden. This value for one Dent fibula, EPV.2200, 64.5, is within the range reported by Madden ( $n = 2$ , 62-70) but for the other Dent fibula, EPV.4068, the greatest breadth

of the distal end, 77, is outside (above) the variation Madden reported.

## DISCUSSION AND CONCLUSIONS

While the m3s ( $n = 2$ ) from Dent are characteristic of *M. columbi*, dp4-m2 in the Dent sample are 'platy' (on the calculation of the ridge plate number only, Lister [1995] provided the rationale for excluding lamellar frequency as an indication of 'platy') and 'narrow'. In most other variates they are 'above average'. In Dent dp4-m2, these are advanced departures from the characteristic form (ancestral *M. imperator* had wider teeth with fewer plates). Note from Appendix 1, #8 - #9 that it is the dp4-M2/dp4-m2 that are present when the individual reaches breeding condition (by age 14 in *Loxodonta africana*, Moss 1988); by the time of eruption of the third molars the reproductive 'potential' of the individual will have been determined. The evolved condition of the Dent sample in both dimensional (width) and configurational (ridge plate number) attributes vis-a-vis the total range of variation in the *M. columbi* sample reported by Madden (1981) is presumably consistent with its young geological age.

There is also suggestion that Dent dp4-m2, c.10,800 yBP, are 'narrow', 'short', and 'platy' in comparison with Lehner teeth dating to c.10,900 yBP, i.e., the former are more advanced. This is consistent with a trend toward smaller size (based on dentitions) and more advanced cheek teeth during the latest Pleistocene in the western United States (Colorado, Arizona) in response to climatic amelioration (e.g., C.V. Haynes 1991) and floristic changes. As shown elsewhere, mammoth populations were evolutionarily dynamic on islands before their extinction (e.g., Wrangel, Russia: Vartanyan *et al.* 1993, Santa Rosa, USA: Agenbroad *et al.* 1995). Evolutionary dynamics were presumably not limited to island situations but happened on the mainland as well, e.g., at Dent, Lehner, and perhaps also in northeast Siberia (Berelekh: Saunders & Baryshnikov unpublished data).

A Dent humerus (EPV.2775) is narrow proximally. Although it is within the range reported by Madden (1981) for *Mammuthus columbi*, it is outside and below the range reported by Dutrow (1980) for a *Mammuthus* sample from Hot Springs. Two Dent humeri (EPV.3934, EPV.3933) are also narrow distally and near the lower limit reported by Madden (1981) for his broad sample. Both Dent humeri are outside and below the range reported by Dutrow for Hot Springs. Two Dent femora are shorter than average but are within Madden's sample. One femur is narrow proximally, at the lower limit of Madden's sample. Three of four Dent femora are narrow distally, in one case outside (below) the range of Madden's sample. Two distal fibulae are available. The width of one is below Madden's average and near the lower limit of his range; the other is huge, with a distal width exceeding the limits of Madden's reported range. In summary, in two instances measured limb bone variates exceed Madden's mean values but in 14 instances the Dent measurements are below the mean values reported by Madden in his broad study. This provides skeletal support for the conclusion, attained based on the lower dentitions, that the Dent mammoths were smaller than average individuals of *Mammuthus columbi*. This conclusion that small individual specimens can belong to fully adult, sexually mature individuals was earlier suggested by study of teeth from the Lehner site (Saunders 1977), but could not be verified based on Lehner postcranial skeletal material, which was unavailable. It had been suggested earlier (e.g., Haury *et al.* 1959) that because the Lehner mammoths were apparently small, they must also be individually young. It is now known that small size is only partially explained by individual age differences or by relative youth.

Regarding stature, information on latest Pleistocene *M. columbi* from the Clovis site, New Mexico, has been noted above.

Dutrow (1980: 46) reports information on estimated shoulder height of Hot Springs *Mammuthus* and of selected museum specimens. Specific information is also available for Dent. The Dent skeleton mounted for display in the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania, measures 296 cm in height. This Dent individual was 23 AEY at death (Table 1, Appendix 1) and inferred to be female based on adulthood in a presumed matriarchal family group such as characterizes modern elephantids (Laws 1966, Moss 1988). From Laws' (1966: 21) study, a female *Loxodonta africana* 23 years in age has attained 89% of her growth in shoulder height. On this basis the Carnegie individual, had she lived to a maximum longevity, may have attained a height of 335 cm.

Latest Pleistocene Dent mammoths were smaller individuals than those comprising well-studied interstadial samples, such as from the Mammoth Site of Hot Springs (26,000 yBP; Dutrow 1980, Agenbroad 1994). Comparison of Dent with Hot Springs, however, is constrained by taphonomic pathways at Hot Springs that preferentially accumulated the remains of sexually mature male individuals (Lister & Agenbroad 1994). Furthermore, Hot Springs includes the remains of both *M. columbi* and *M. primigenius* (Agenbroad *et al.* 1994). Thus differences between Dent, Lehner, and other sites versus Hot Springs are explained primarily by taphonomic, taxonomic, individual age, and sex considerations and only partially by local evolution. The point of interest here is that comparison of Dent with Hot Springs supports the view that late Pleistocene mammoths were organized like those of modern elephantids (Moss 1988) into matriarchal family units (Dent) representing a kin group of sexually immature males and females of all ages and into units composed exclusively of reproductively mature males (Hot Springs).

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APPENDIX I

Individual/ Locus/ Group AET	Spec. No.	Sex	HL (A)	Lg.	HS	W.	hls	LI	L	Remarks
17775										
	EPV.1857	sig?	8+ (14)	68.1		317(21)	1.1	8+	thin	
	EPV.1857	sig?	14+ (1)	118.20	919	89.24		18	thin	
2605										
	EPV.1859	sig?	10+ (9)			31.4	1.3	18+	thin	Four teeth in the position of a juvenile; L&I EPV.1859 in wear; also has associated L&I?
	EPV.1859	sig?	7+	69.5		43.1	1.1		thin	
	EPV.1859	sig?	8+	61.0		31.6	0.5		thin	
	EPV.1859	sig?	14 (5)	174	916	974(7)	2	20	thin	
	EPV.1859	sig?	14 (5)	141.3	97.0	40.2	1.4		thin	
267-1412										
	EPV.1858	sig?	5 (5)	51.74		41 (14)		5+	thin	Associated with EPV.1858 associated with juvenile wear level; EPV.1857, associated with EPV.1859, EPV.1858 in older
	EPV.1858	sig?	8+ (5)			31.3 (14)	1.3	8+	thin	
	EPV.1858	sig?	10+ (7)			36.7 (14)	1.1	18+	thin	
2748A										
	EPV.1871	sig?	12 (1)	129.4		46.2 (1)	1.5	9	1.0	Midline associated with L&I 140-1411 & 1409
	EPV.1877	sig?	12 (1)	129.2		44.9 (1)	1.3	11	1.9	
	EPV.1877	sig?	12 (1)	119.0		42.4	1.8	11	1.2	
	EPV.1877	sig?	12 (1)	134.3		33.6	1.5	10	0.9	
3740-1859										
	EPV.1852	sig?	10 (1)	107.6		37.0 (6)	1.1	9+	thin	Five wear teeth and two associated fragments
	EPV.1852	sig?	11 (1)	117.1		37.0 (6)	1.2	9+	thin	
	EPV.1852	sig?	12+ (2)	141.2+	1.9	46.0 (6)	1.9	9	thin	
	EPV.1897	sig?	8+ (2)		100.7	15.0 (4)		9	thin	
5751B										
	EPV.1855	sig?	36 (1)						thin	Two middle ridge plates of a full, seven anterior middle ridge plates of a rim.
	EPV.1855	sig?	7 (1)			31.8	1.5	7+	thin	
7751B										
	Same	sig?	70 (1)	32.0						System with EPV.1855, EPV.1856 & EPV.1857 is a shell with varying 7 ridge plates from 1825
	Same	sig?	140 (1)							
	Same	sig?	140 (1)							
130-1814										
	EPV.1898	sig?	14 (1)	173		34.4 (4)	1.7	5	1.7	Left partial mandible with six and a half teeth & right partial mandible with six, eight to ten teeth, with indications of a complete left mandible associated
	EPV.1898	sig?	14 (1)	168.5		33.3 (4)	1.9	5+		
	EPV.1898	sig?	14 (1)	166.5	153.5	35.1 (4)	1.5	5+	thin	
	EPV.1898	sig?	15 (1)	166.6	153.5	35.2 (4)	1.6	5+	thin	



**APPENDIX 2**

Species	1870	1881	1885									
<b>B</b>	225		267									
<b>CG</b>	222											
CG (length of 1885)	117.0	88	120									
BBV	281.0	158										
BBV1	284.0	204.0	148									
<b>Asa</b>	1839	2014	1820	1821								
<b>B</b>	250	214	271									
<b>LCBa</b>		115	188									
<b>BP1a</b>	1752	1711		1261								
<b>BP1b</b>	1152	1171										
<b>BP1c</b>	1248	1244	811	1261								
<b>LCBa</b>		811	87	1261								
Asa (length of 1885)	51	66.5	82									
Asa (Asa/1000)		13.02	16.4	20.04								
<b>Central Provinces (1878)</b>	1840	1878										
<b>CLB</b>	71.0	85.0										
<b>EP1</b>	80.1											
<b>EP2</b>	151.1	111.6										
<b>EP3</b>	42.4	-										
<b>EP4</b>	11.8	8.1										
<b>EP5</b>	11.0	11.0										
<b>Western Provinces</b>	1870	1882										
<b>BP1</b>		281.0										
<b>BP2</b>	186.0											
<b>BP3</b>	111.0											
<b>BP4</b>	181.0											
<b>Eastern Provinces</b>	1870	1877	1880	1880	1881	1882	1883	1884	1885	1886	1887	1888
<b>CLB</b>			18.1	18.0		118.0	18	51.6	127	54.0	104	
<b>BP1</b>	180									1117		
<b>BP2</b>				1.04				1.02		1112		
<b>BP3</b>	184.0								126.0			
<b>BP4</b>		182.0	124.4		89.1			122.0		110.0		
<b>BP5</b>	111.0	116						81.7	125			

**APPENDIX 2 (continued)**

<b>SNOUTS</b>	1890							
CL	279.2							
No. of segments	4							
Position	1-4th							
<b>4 Dental Vertebrae</b>	1890							
SLV	129.7							
EPV	81							
EPVd	47							
<b>Stapes/hamuli</b>	1890	1890	1890	1890				
ES (cp. of length)	208.5		208.5	211				
ESM				439.5				
LA				206				
SLC	189.1	82	221.8	200				
CLD	267	266	266	271.6				
LD			300.3	166.3				
BT			118.4					
<b>Hamuli</b>	1890	1890	1890	1890				
SLD		169						
EP			162.8					
SL	81	81.0						
LD	247.0	246.0						
BT		125.5		126				
<b>Utricle</b>	1890	1890	1890	1890	1890	1890	1890	1890
LD	174.1							
SLC	181.1			48	51	56.4	64.4	78
CLD	277			164.0	162	178	186	200
SL	81			53	52.2	60	62.5	67
CLD	164			178	177	201	177	166
EP		175	171					
SLC		112.1						
Length of transverse muscle (LDMV) (mm)	126.1							140
<b>Radius/O</b>	1770	1810	1810	1810	1810			
RO	121.3	120						
ROp		180.5	-					
SL		12.5	47.5		30.5			
EP		110	61		50			
EPd				180.1				

**APPENDIX 2 (continued)**

<i>Staphylinidae</i>	19103	59628		
GL	116	1111		
GB	541	7516		
GD	300	114		
<i>Lasius</i>	19120	25610	20220	19120
GL	82	83	99	
GB	11	1132		1656
GD	112	11	145	1472
<i>Cladornis</i>	19121	20200	20200	
GL	526	1152	124	
GB	1142	144	131	
GD	-	517		
<i>Phthorinidae</i>	19122			
GL	124			
GB	46			
GD	1112			
GP	172			
<i>Tripanitidae</i>	20000			
GL	216			
<i>Megastomatidae</i>	20001	20001		
GL	952	1212		
GB	222	1122		
GD	112	122		
<i>Neotomidae</i>	20002			
GL	1222			
GB	112			
<i>Meloidae</i>	20003	20003		
GL	214			
B	82	212		
GP	42	42		
GD	222	222		
DD	42	42		
DJ	212			
<i>Meloidae</i>	20004			
B	72			
D	21			
GP	212			

**APPENDIX 2 (continued)**

<i>Phidolomys</i>	27146r	27146s	27154r	27154s	27155r	27155s	27156r	27156s	27157r	27157s	27158r	27158s
<i>Testis</i> (µg)	Meu/TV											
<i>Phidolomys</i> 1, 2, or 3		1	1		1	1	1	1	1	2	2	3
UL	15	69	54.9							87.1	91.1	99.6
U <sub>p</sub>	64.9	54.1	55.6			47.3	48.1	54.7				11.1
U <sub>b</sub>	58.8	51.1	55.1					54.3	54.8			52.1
GD	41.5	49.2	45.8	49.4	55	45.1	57	44.6		47.3		12.7
SD	38.8	51.4	51.2	51.3	60.2					48.8		15.1
<i>Spermoids</i>	2401	2684	2503	2621	2622	2403	2585	2769				
UL	255	51.1	11.2	57.2		41.1		51.2				
U <sub>p</sub>	26.1	51	27.4	35.2	41.3	25.0	34.9	25.1				
U <sub>b</sub>	13.2	21.0	25.8	30.1	28.2	25.7	24.2	31.1				
<i>Immature/total</i>	291.57	369.01	299.11									
LA	165											
SC		51.2	75.5									
SL		131.2	189									
ST		51.5	48.9									
LS	121.1											
<i>Fluorescible</i>	29204	36937	29273	36924	21424	21425	29221	29221	36921	36921	36921	36921
UL	2921	1121										
U <sub>p</sub>	221.1											
U <sub>b</sub>	181	171		121.2	159	78.2						
GD	121.2	151					181	121	131	131		85.2
SD	111	249					147	171	149	149		149
SL	211.2	241.2	251							249		
<i>Tubules</i>	21947	23951	21851	21851	21907	23907						
UL			491.2									
U <sub>p</sub>			52.1									
U <sub>b</sub>	61.2	81.2	89.1	10.1	11.2	149						
GD	171	211	21.8	21.1	371	51.2						
SD			271									
SL		115.1	151									
<i>Fluorescible</i>	22021	42781										
SD	89.6											
UL	55											
U <sub>p</sub>	61.2	79										
U <sub>b</sub>	121.1	129.7										

**APPENDIX 2 (continued)**

Geographical Area	1992/93	1993/94	1994/95
<b>GL</b>		95	87
<b>GR</b>	133	168	
<b>GD</b>		138	139
<b>Calculus Value</b>	25100		
<b>GR</b>	12722		
<b>GR (excl. fossil fuel)</b>	71		
<b>Measured Value</b>	79420	14785	
<b>GL</b>	26	27	
<b>GR</b>	12717	134	
<b>GD</b>	13.9		
<b>Estimated Value</b>	13617		
<b>GL</b>	75.9		
<b>GR</b>	16.4		
<b>GD</b>	32.2		
<b>Calculus Value</b>	95597	19785	
<b>GL</b>	99	23	
<b>GR</b>		1.3	
<b>GD</b>	112	146	
<b>Measured Value</b>	79720		
<b>GR</b>	30.4		
<b>GD</b>	41.3		
<b>GD</b>	1.9		
<b>GR</b>	34.2		
<b>Measured Value</b>	30790		
<b>GR</b>	21.2		
<b>GD</b>	34		
<b>GD</b>	21.9		
<b>GR</b>	37		
<b>Measured Value</b>	27950	23815	
<b>GL</b>		87.9	
<b>GR</b>		77	
<b>GR</b>	76	12.9	
<b>GR</b>		74	
<b>GR</b>		72	
<b>GR</b>		92	
<b>GR</b>		187.5	

\* continued