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New absolute dates and comparisons for California's *Mammuthus exilis*

A nearly complete (+90%) skeleton of the pygmy mammoth (*Mammuthus exilis*) was recovered from Santa Rosa Island, California, in August 1994. An intensive, GPS controlled, pedestrian survey of the northern Channel Islands was initiated January 1996. That survey, collection of specimens subject to loss by erosion, and submission of samples for absolute dates has yielded more than 140 locations of mammoth remains and six new radiocarbon dates for *M. exilis*. Using existing museum collections and newly collected osteological and dental remains, comparisons were made with the common mainland mammoth (*M. columbi*) from the Mammoth Site of Hot Springs, South Dakota.

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INTRODUCTION

Mammoth remains have been known on the northern Channel Islands of California (Fig. 1) since 1856. They were first reported in scientific literature in 1873 (Stearns 1873). Paleontological studies of the animal began with Stock and Furlong (1928). These authors and later parties made collections from the Los Angeles County Museum. Phil Orr collected mammoth remains in the later 1940's and 1950's, to support his claim that early people (Chumash) on the islands ate the last mammoths (Orr 1968). Boris Woolley, a member of the ranching family operating on the island of Santa Rosa, collected, avocationally in the 1970's. Louise Roth completed a doctoral dissertation on *M. exilis* remains (Roth 1982). In the latter half of the 1980's the National Park Service acquired Santa Rosa Island and created Channel Islands

National Park. Minor, salvage collecting continued until the 1994 discovery. Concurrent with the discovery of the 1994 skeleton (the only nearly complete individual) the antiquity of human occupation on the islands has been extended (Erlandson *et al.* 1996; Johnson *et al.* 1999) to circa 11,500 yr B.P. (radiocarbon date). Dating of mammoth remains, or associated material, prior to 1994 had yielded eleven published radiocarbon dates.

POST-1994 RESULTS

Radiocarbon chronology

Wenner and others (Wenner *et al.* 1991) have labeled all previous radiocarbon dates as 'equivocal' and should be stated as 'unknown'. In part, their conclusion was based on several assumptions: (1) that all mammoth remains were in secondary context; therefore asso-
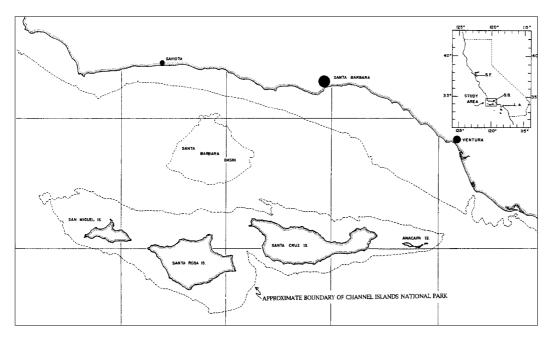
Figure 1   Location map of Northern Channel Islands, California.

ciated material did not date the mammoth; (2) there was no charcoal originating from natural fires on the island; that the 'charcoal' was due to ground water carbonization (Cushing *et al*. 1986; Cushing 1993; (3) there were no dates on the mammoth remains themselves.

In reviewing the literature regarding *M. exilis* from the Channel Islands, I find that Orr (1956, 1960) and Liu & Coleman (1981) provide at least two radiocarbon dates, directly from mammoth bones. Six new dates have been generated on island mammoths since 1994. One of those dates is from bone collagen, extracted from the right femur of the 1994 skeleton. That date, of 12,840 + 410 (CAMS 24429) was produced by Dr. Tom Stafford, using AMS techniques on collagen he extracted. The additional dates are from associated charcoal (fire-produced charcoal), with one from a snail shell within a mammoth cranium. Erlandson *et al*. (1996) have demonstrated an excellent correlation of dates obtained from mollusc shell and charcoal on their excavations of Daisy Cave, San Miguel Island. Absolute chronology (Table 1) of the island mammoths is the weakest element of the research, to date. Attempts at obtaining additional radiocarbon dates are currently underway. These dates are essential to understanding the rate of change taking place on the islands. The dates suggest the presence of *M. exilis* on the island prior to 40,000 yr B.P. Those determinations will require alternate absolute dating methods. Dental characteristics suggest *M. columbi*, the late Pleistocene mainland mammoth, was the ancestral form (Madden 1981; Agenbroad 1998, 2000). Current models suggest *M. columbi* appeared ca 125,000-100,000 years ago, in North America. Current taxonomic models are discussed later in this article.

Mammuthus exilis DENTITION
One of the initial conclusions with respect to dentition of the pygmy mammoths is that the teeth must also reduce in size. Maglio (1973) published tables of dental measurements for *Mammuthus meridionalis* and *Mammuthus primigenius*, but did not do a similar table for *Mammuthus imperator* (under which he

Table 1   Radiocarbon dates for Channel Island mammoths.

Lab. #	^{14}C Date	Technique	Mtl.
B 76532	700 ± -60	AMS	charcoal *
B 85274	+ 47,990	std	charcoal
CAMS 24429	12,840 ± -410	AMS	collagen
B 96610	13,770 ± -60	AMS	charcoal
B 92053	18,130 ± -70	AMS	charcoal
B 85077	18,880 ± -190	std	charcoal
B 94256	+ 47,100	AMS	charcoal
B 94609	41,360 ± -660	AMS	snail **

Note: AMS = accelerator-mass spectrometer method; std = standard (gas) method; due to small sample sizes of material in association with *M. exilis* remains, AMS method was required. CAMS 24429 required chemical extraction and pre-treatment of bone collagen; * = cultural charcoal recycled from a Chumash hearth; ** = San Miguel Island; all other dates are from Santa Rosa Island.

placed *Mammuthus exilis*), or *Mammuthus columbi*. Table 2 (listed at the end of this paper) provides summary dental measurements following Maglio's (1973) format, for *Mammuthus columbi* and *Mammuthus exilis*. To my knowledge, this is the first summary of dental attributes (both mandibular and maxillary) published for these species.

The dental attributes of the Columbian mammoth were derived from the population of The Mammoth Site of Hot Springs, South Dakota; a large, local population in primary context (non-transported accumulation). It should be noted that this population is somewhat anomalous, having been derived primarily from male animals in the 11-30 year (AEY) age range, as Hot Springs was a young male, mammoth: selective, natural trap (Lister & Agenbroad 1994). The Channel Islands population represents both sexes, of all ages (individual age and absolute age) for

Mammuthus exilis, plus several teeth that must be assigned to the ancestral *Mammuthus columbi*, based on overall size as well as other dental attributes (Fig. 2). Two island mandibles (245 a, b) collected by Phil Orr, represent neonates, or stillborn calves (Fig. 3). The M1's (dp2's) are intact, and exhibit no wear. The second teeth, M2 (dp3) had not yet erupted through the gums. From these age-zero individuals, there is a continuum of dental progression to >50 year old individuals. An age-structure plot (Fig. 4) for the Channel Island mammoths provide a slightly skewed attritional death assemblage pattern. It can be quickly noted that the first three decades of island mammoth life appear to have been hazardous. The first three 10-year age sets are nearly equal in death frequency (25%, 22.6%, 25%=72.4%). The 30-39 year age interval is relatively low (5.4%), with a higher mortality (16.7%) in the 40-49 year interval, and an even lower percentage
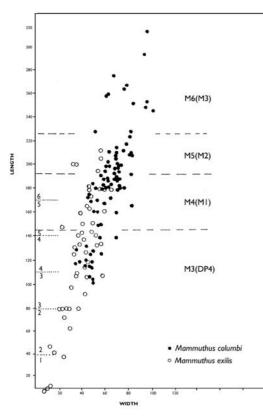
Figure 2 Dental plot (L vs W) of *M. columbi* and *M. exilis* (modified from Agenbroad 1999).

(4.8%) in the >50 year old category. Compared with other mammoth assemblages, it appears the island mammoths had a shorter, more hazardous life span than their mainland counterparts. As unique as the neonate mandibles is the fact that several mandibles reflect old-age individuals; animals that have lost all their mandibular teeth, yet display evidence of continued mastication, against the bone, devoid of mandibular teeth (Fig. 5). Intuition suggests that sufficient, high quality forage must have been present to support aged, toothless individuals.

A plot of the number of plates per M6 (M3) of North American mammoths (Fig. 6) illustrates an increase in the number of plates, and corresponding lamellar frequency; it also indicates a decrease in enamel thickness with geologically younger, more progressive forms. This plot is also indicative of a possi-

ble resolution to some of the problematic nomenclature with North American mammoths. One problematic species is *Mammuthus imperator* (Leidy 1858). Osborn's (1922) specimen as well as Leidy's specimen, were 'fragmentary' and 'incomplete' (Maglio 1973). In his discussion, Maglio (1973) discusses 'primitive' and 'advanced' forms of *M. imperator*. He states that the 'primitive' form of this species is indistinguishable from *M. meridionalis* and the more advanced form grade (morphologically) into the late Pleistocene mammoth *M. columbi* (Falconer 1857). Using Figure 6 it appears *M. imperator* ('primitive' form) and *M. meridionalis* are essentially the same, whereas the 'advanced' form is represented within the range of *M. columbi*. It is my suggestion, that *M. imperator* is probably not a valid species, based solely on dental criteria. Having measured the mammoth teeth from Rancho la Brea, California, I find them to overlap and extend the length vs. width dental plot of *M. columbi*; the 'advanced' *M. imperator* fall easily within the *M. columbi* data. Another note is that *M. imperator* is generally considered to be a late Irvingtonian species, whereas *M. columbi* is considered to represent the Rancholabrean land mammal age; the radiocarbon dates from Rancho la Brea are of the late Pleistocene, further evidence that the Rancho la Brea mammoths are not *M. imperator*. Osborn (1922) suggests the two holotypes were probably conspecific, a conclusion I also favor, at least for the 'advanced' form of what has been called *M. imperator*.

Similarly, North American late Pleistocene mammoths are often classified as *M. jeffersonii* (Maglio 1973). This species is described as the 'typical' mammoth of the Sangamon interglacial and the Wisconsin glacial stage of the late Pleistocene. Maglio (1973) goes on to state that there is a 'southern' form and a 'northern' form of *M. jeffersonii*. He also states that *M. jeffersonii* and *M. primigenius* cannot be distinguished by dental characteristics alone, and that this progressive stage cannot be distinguished from earlier forms,

Figure 3 Neonate *M. exilis* mandible containing M1 and M2 (SBMNH 245a) collected by Phil Orr. [Photo: Monica Weisblott]

which grade into it. He (Maglio 1973) chose to list *M. jeffersonii* as a synonym of *M. columbi*; the information of Figure 6 suggests that *M. jeffersonii* and *M. primigenius* are probably conspecific. The distribution pattern reported for *M. jeffersonii* (Agenbroad & Barton 1991) overlaps that for reported *M. primigenius* in the Great Lakes region of North America.

From the discussion above and the data presented in Figure 6, I consider there are four species of mammoths in North America: *M. meridionalis*; *M. columbi*; *M. exilis* (a pygmy island species derived from *M. columbi*); and *M. primigenius*. In this format, New World mammoths parallel (with the exception of *M. exilis*) the Old World forms: *M. meridionalis*; *M. trogontherii*, and *M. primigenius*. Additional studies will be needed to support, or refute, this suggestion.

TUSK COMPARISONS: *M. columbi* and *M. exilis*

Table 3 summarizes the tusk data for the mainland and island mammoth species. The index of curvature values signifies that in both species the tusks are relatively straight, as contrasted to the curvature of tusks in *M. primigenius*. Tusk length and maximum diameters for *M. exilis* are approximately 50% those of *M. columbi*.

POST-CRANIAL COMPARISONS

A plot of limb bone lengths of *M. columbi* vs. *M. exilis* (Agenbroad 2000) supports conclusions formed by Paul Sondaar (1976), i.e. that the lower limb bones are dramatically shortened in his 'elephant-deer-hippopotamus' oceanic island colonizing triad. This modification provides "low speed locomotion" (Sondaar 1976) and is a response to selective pressures of the island, providing a smaller mammoth (*M. exilis*) that can negotiate steep uplands, gaining pasturage unavailable to the larger, mainland forms. A further test of this idea was attempted, by the calculation of the center-of-gravity for both the mainland, and the island mammoths, using scale models derived from bone measurements. Once the center-of-gravity was determined, it was possible to approximate the steepness of slope that could be negotiated by the different sized animals. Figure 7 provides a graphic representation of the results of this determination. From the diagram, it is apparent that the smaller, island mammoth could negotiate slopes ca. 8^0 steeper than the mainland mammoths. *M. columbi* was restricted to slopes less than 25^0, which equates to the northern half of the island of Santa Rosa, plus coastal marine terraces. Slope measurements of the southern uplands indicates most slopes exceed 30^0, with some exceeding 40^0.
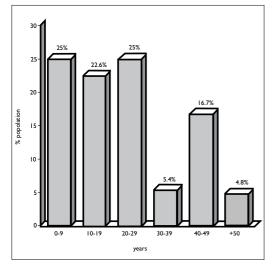
In addition to lower limb shortening, modifications of the humeri and femora were also noted. Figure 8 depicts the proximal humerus, with three of the angles measured. In steep slope negotiation, the humerus takes on a new function, as a braking mechanism for down-slope movement. Figure 8 demonstrates a change in the angle of the supracondylar tuberosity. This can be used to infer a different muscle function and attachment, reflecting new functions of the forelimb. The femora of the island mammoths lack the robust lateral tuberosity characteristic of the large mainland mammoths. In addition, the cross-section of *M. exilis* femora is nearly round, as contrasted to the elongate, elliptical cross section for *M. columbi* femora (Fig. 9). The interpretation of lower limb shortening, plus the physical characteristics described in the preceding paragraphs suggests a smaller, more gracile, island mammoth, shaped by, and selected for, the island environment. *M. exilis* was capable of obtaining upland resources which were denied the ancestral, mainland form. In addition, the diminished size would also require less forage and result in less range requirements per animal, providing the island mammoth with a greater survivability in times of environmental stress such as drought, overcrowding, or a combination of these and other factors.

SEXUAL DIMORPHISM

Plots of selected bone metrics allow differentiation of the fossil population into sexual groups. From these graphs it was possible to estimate the range of sexual dimorphism of the island mammoths. Perhaps the most revealing bone is the calcaneum. Figure 10 shows the range in size of the calcanea from Santa Rosa Island. There is a size gradation from those approaching the mainland mammoths, to those approximately the size of a baseball. Bone fusion of the articular surfaces provides clues as to the maturity, or immaturity, of the individuals. Two calcanea in the series are mid-sized, reflecting the probability

Figure 4 Channel Island mammoth age-structure analysis plot.

Figure 5 An old-age individual of mandible *M. exilis* with evidence of longevity after the loss of the last tooth (M6). [Photo: Monica Weisblott]

of immature males (the smaller one is larger than the largest, fused, female specimen). Using these data, the sexual dimorphism based solely on the calcanea, ranges from 18-38% reduction for females, as contrasted to male *M. exilis*. Long bones range from 13-22% reduction for females vs. males. This equates well with shoulder height calculations (circa 25%) and long bone dimorphism (16-25%).

DISCUSSION

M. exilis from the northern California Channel Islands represent an island form derived from *M. columbi*, the mainland mammoth. A comparison of the island animals and the mainland mammoths from the Hot Springs Mammoth Site of South Dakota indicates a smaller, more gracile form, whose lowered center of gravity and decreased length of the lower limb bone allowed access to pasturage on steep uplands, which was denied their larger ancestral forms. Sexual dimorphism ranges from about 13 to 25% as determined by shoulder height and the comparisons of several limb bones. Tusks resemble those of the Columbian mammoth, being relatively straight, but about half the size. Additional absolute chronology is needed to ascertain rates of dwarfing, environmental stress, extinction, and the possibility of contemporeneity with the earliest human inhabitants of the islands. Inventory and dating are currently on going, for the islands.

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NUMBER OF PLATES, LAMELLAR FREQUENCY, AND ENAMEL THICKNESS: NORTH AMERICAN MAMMOTH SPECIES
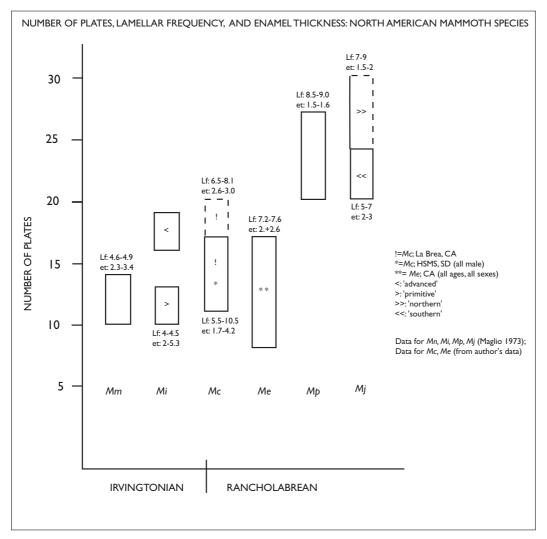

Figure 6 A plot of the number of enamel plates per 6th molar, for North American mammoth species.
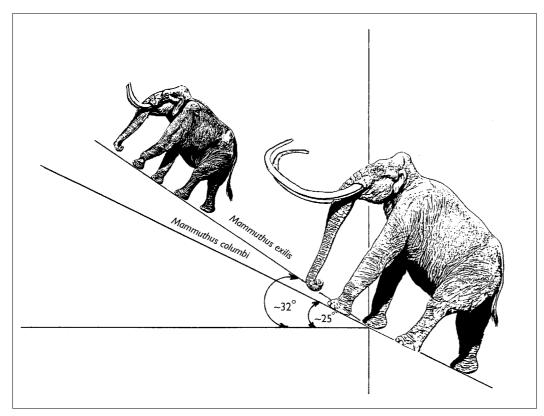
Figure 7 A diagram of estimated slope negotiability based on center of gravity determinations for *M. columbi* and *M. exilis*.
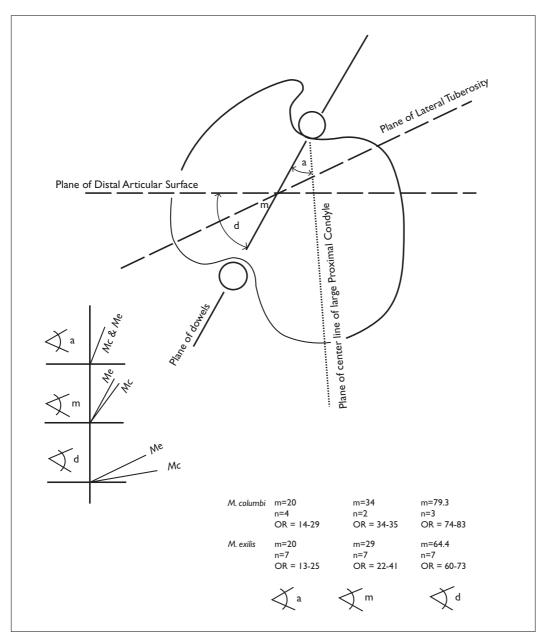
Figure 8 A plot of the change of orientation portions of the humeri of *M. exilis* compared to *M. columbi*.
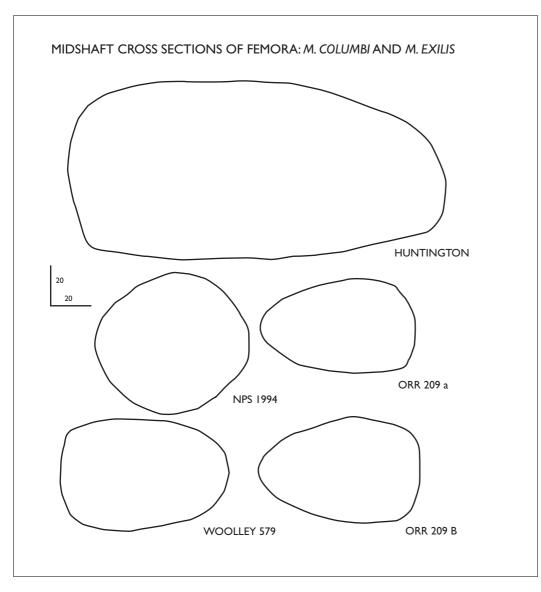
Figure 9 Cross section diagrams at the minimum mid-shaft location for femora of *M. columbi* and *M. exilis.*
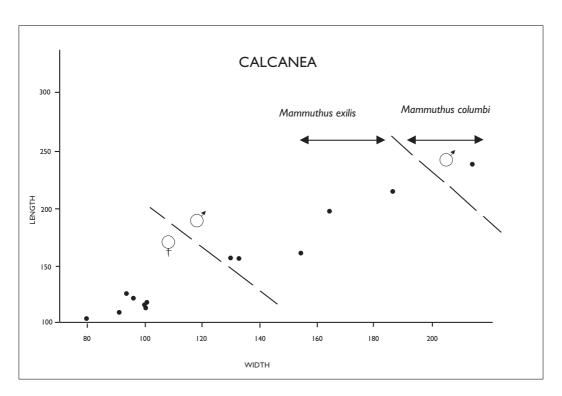
Figure 10 A plot of size difference due to sexual dimorphism of the calcanea of *M. exilis*.

Table 2 Dental measurements (in mm) of *M. primigenius* (Maglio 1973); *M. columbi* (Agenbroad 1994); and *M. exilis* (Agenbroad, this publication).

mandibular teeth

Mammuthus primigenius (Maglio 1973)

		PL	L	W	H	Lf	et	IH
$M_6(M_3)$	OR	20-25	207-320.2	65-100	123-184.1	6.8-10.2	1.3-2.0	137.8-189.2
	m	21.8	267.4	87.6	137.8	8.5	1.5	159.7
	n	5	5	8	8	8	8	8
$M_5/(M_2)$	OR	15-16	147-185	43-85	100-136	7.6-11.4	1-2	159.8-232.6
	m	15.3	174.3	67	121.9	9.2	1.3	197
	n	7	5	10	7	9	8	6
$M_4/(M_1)$	OR	12-15	124-146	41-76.9	69-104	7.7-11	1-1.7	168.3-192.5
	m	13.3	135	56.2	91.7	9.9	1.2	180.4
	n	3	2	4	3	4	4	2
$M_3/(dp_4)$	OR	10-11	98-105	37	65-70	11.4-11.5	1.0	189.2
	m	10.5	101.5	37	67.5	11.4	1.0	189.2
	n	2	2	1	2	2	1	1

Mammuthus columbi (Agenbroad 1994)

		PL	L	W	H	Lf	et	IH
$M_6/(M_3)$	OR	12-17	208-294	88-100	122	5.5-7	1.9-4.2	–
	m	14	243.7	92.3	122	6.5	2.6	–
	n	3	3	3	1	3	4	–
$M_5/(M_2)$	OR	9-15	177.5-255	68-106	150-202	5.5-8	1.9-4.4	158.5-209.8
	m	12.4	204.4	84	184	6.9	2.9	176.3
	n	11	11	11	3	11	10	3
$M_4/M_1)$	OR	9-12	139-189	72-91	70-139	5.5-8	2.8-4.2	150-164
	m	11	176.6	80.4	104.4	6.6	3.5	157
	n	8	8	8	5	8	7	2

Mammuthus exilis (Agenbroad, this paper)

		PL	L	W	H	Lf	et	IH
$M_6/(M_3)$	OR	8-14	160-211	30-65	91-126	5.5-9	2.0-3.3	145.6-215.6
	m	10.7	178.9	48.8	103.9	7.2	2.58	174.2
	n	10	12	15	7	14	22	14
$M_5/M_2)$	OR	8-12	113-150	22-57	74-95	5-13.5	1.4-3.2	128-216
	m	9.9	125.8	41.6	86.4	5.9	2.32	173.1
	n	15	15	17	9	15	15	14
$M_4/(M_1)$	OR	7-9	91-109	30-57	47-106	5-11	1.3-2.8	86.2-188.4
	m	8.4	101.8	40.1	77.5	8.3	2.16	164
	n	5	5	8	4	5	8	4
$M_3/(dp_4)$	OR	8-11	62-80	20-37	36-87	10-14	1.0-2.4	97.3-208
	m	9	75.1	27	58.4	13	1.5	163
	n	7	7	7	8	7	6	4
$M_2/(dp_3)$	OR	7-10	41-49	12-15	28-45	16.5-22	1.5-1.8	110-126
	m	9	45.8	13.5	22.7	20	1.65	116
	n	3	3	2	2	3	2	4
$M_1/(dp_2)$	OR	3	10-12	10-12	–	–	–	–
	m	3	11	11	–	–	–	–
	n	2	2	2	–	–	–	–

Table 2 (continued)

maxillary teeth

Mammuthus primigenius (Maglio 1973)

		PL	L	W	H	Lf	et	IH
$M^6/(M^3)$	OR	20-27	226-285	68-113	135-188.5	6.5-11.1	1.3-2.0	164.6-211.8
	m	23.2	263.8	92.5	168.1	9.0	1.6	184.4
	n	12	7	17	15	17	17	15
$M^5/(M^2)$	OR	15-16	154-172	64-80	127-151	9.4-11.5	1-1.3	198.4-228.8
	m	15.5	163.5	70.7	141.2	10.3	1.3	214.7
	n	8	6	7	4	8	7	4
$M^4/(M^1)$	OR	12-14	122-154.5	48-76	99-123.5	10.3.11	1-1.4	206.3-208.3
	m	12.7	138.2	57.3	107.5	10.7	1.1	207.3
	n	3	2	3	3	3	3	2
$M^3/(dp^4)$	OR	10-13	102-121	37-57.9	60-84	8.2-16	1-1.5	141.3-189.2
	m	10.4	109	46.6	69.7	11.7	1.1	189.2
	n	7	6	6	4	7	7	3

Mammuthus columbi (Agenbroad 1994)

		PL	L	W	H	Lf	et	IH
$M^6/(M^3)$	OR	12-16	165-242	84.8-105	177-225	6-10.5	1.7-3.6	182.5-225
	m	13.5	200.2	98.8	209	8.1	3.0	203.8
	n	4	5	5	3	4	4	4
$M^5/(M^2)$	OR	10-15	176-212	71-112	169-259	5.5-9.6	1.9-3.5	111.6-266.7
	m	11.9	195.9	88.6	212	7.5	2.7	175.1
	n	12	14	15	6	14	14	8
	OR	–	–	84	126-188	7.5	2.3	134.7
	m	–	–	84	157	7.5	2.3	134.7
	n	–	–	1	2	1	1	1

Mammuthus exilis (Agenbroad, this paper)

		PL	L	W	H	Lf	et	IH
$M^6/(M^3)$	OR	12.5-16	166-214	63-88	120-171	6-8.5	2.0-3.0	201.3-230.2
	m	13.8	183.3	73.3	143.4	7.6	2.44	217.5
	n	8	7	8	7	7	9	3
$M^5/(M^2)$	OR	10-15	130-146	48-69	120-177	6-10	2.0-2.5	200-221.1
	m	12	137.3	64.2	150.5	9.0	2.2	215.2
	n	10	10	10	4	8	3	3
$M^4/(M^1)$	OR	10-12	102-115	49-53	–	10-14	1.7	–
	m	11	106.3	50.7	–	12	1.7	–
	n	3	3	3	–	2	1	–

Table 3 Tusk metric comparisons: *M. columbi* and *M. exilis* (measurements in cm)

measurement 4 = base of alveoli   I = (5/1)

	1	2	3	4	5	6	7	I
Hot Springs Mammoth Site (*M. columbi*)								
OR	97-277	93-170	10.4-22.7	13.8-20.6	95-177	71-161	-	0.60-0.98
m	186.91	129.55	18.25	16.65	147.83	110.86	-	0.78
n	22	11	22	10	18	14	-	16
Channel Islands (*M. exilis*)								
OR	9-143	21-121	3.1-7.8	4.8-10.5	7.5-72	17.5-97	4.4-10.7	0.5-0.87
m	51.5	65.1	5.4	7.4	38.1	60.6	8.4	0.74
n	5	5	5	8	6	7	4	5