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Mammuthus meridionalis (Proboscidea: Elephantidae) from the Borrego Badlands of Anza-Borrego Desert State Park®, California: phylogenetic and biochronologic implications

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A nearly complete skeleton of a mature female southern mammoth was recovered from the Borrego Badlands in Anza-Borrego Desert State Park®, California, USA. The remains represent a late evolutionary stage of the *Mammuthus meridionalis* (NESTI, 1825) chronocline, and constitute the most complete skeleton of this taxon in North America. Magnetostratigraphy and tephrochronology date the specimen at approximately 1.1 Ma BP. The osteology and osteometrics are presented herein. This late stage of *Mammuthus meridionalis* co-existed with an early evolutionary stage of *M. columbi* (= *M. imperator* of some authors). Significant morphological differences between the two taxa from the Borrego Badlands suggest that *M. armeniacus* rather than *M. meridionalis* was immediately ancestral to *M.columbi*. A dispersal of *M. armeniacus* to North America approximately 1.2 Ma BP is implied. At least two mammoth lineages (excluding *Mammuthus primigenius*) are seen in North America. An early *M. meridionalis* lineage and a later *M. armeniacus* - *M. columbi* lineage. *M. meridionalis* is recognized as the earliest species of mammoth in North America.

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INTRODUCTION

In December of 1986, the skull, mandible and about 70% of the skeleton of an adult female southern mammoth, *Mammuthus meridionalis* (NESTI, 1825) was discovered in the Borrego Badlands of northern Anza-Borrego Desert State Park® (ABDSP), California, USA by G. Miller of Imperial Valley College Museum (El Centro, California) (Miller *et al*. 1988; Miller 1989; Parks *et al*. 1989; Miller *et al*. 1991; McDaniel & Jefferson 1997). The specimen, ABDSP(IVCM) V5126, represents the most complete skeleton of this taxon from North America.

The site, ABDSP(IVCM) 1277, lies east of Borrego Springs and south of San Diego County road S22 (Fig. 1). Here, the fluvial-floodplain deposits of the Ocotillo Conglomerate (Dibblee 1954, Remeika & Pettinga 1991, Remeika 1992) have yielded a diverse Irvingtonian North American Land Mammal Age terrestrial vertebrate assemblage, described as the Borrego local fauna by Remeika & Jefferson (1993), and Remeika *et al*. (1995).

Table 1 Dental measurements of ABDSP(IVCM) V5126. Explanation: **TP** = tooth position; **L** = length in mm; **W** = width in mm; **CH** = crown height in mm; **PN** = number of plates, + indicates minimum number, ( ) estimated number based on stage of wear; **LF** = lamellar frequency, number of plates / 10 cm, ( ) number of averaged measurements; **ET** = enamel thickness in mm, ( ) number of averaged measurements; **M3/L** = upper M3, left; **M3/R** = upper M3, right; **M/3L** = lower M3, left; **M/3R** = lower M3, right.

TP	L	W	CH	PN	LF	ET
M3/L	253	110	47.9	12+(15)	5.1(6)	2.84(6)
M3/R	234	99	46.9	12+(15)	4.9(6)	2.82(6)
M/3L	238	92	59.5	10+(12)	4.3(6)	2.86(6)
M/3R	246	91	36.0	10+(12)	4.2(6)	2.84(6)

A thorough taphonomic study reveals that carnivores and scavengers prior to burial had heavily damaged the carcass. Magnetostratigraphic and tephrochronologic methods date the specimen at approximately 1.1 Ma BP (Remeika & Beske-Diehl 1996).

ABDSP(IVCM) V5126 represents a very late evolutionary stage of *Mammuthus meridionalis*. The molar dental parameters fall well within the reported range of *M. meridionalis* (see Maglio 1973) (Table 1). The skull and mandible are shorter antero-posteriorly and wider than that in the imperial mammoth, *M. imperator* (LEIDY, 1858). The incisor in ABDSP(IVCM) V5126 is thin, relatively long and gently curving with an Index of Curvature significantly less than in *M. imperator* and *M. columbi* (Fig. 2). These characters distinguish *M. meridionalis* from the later species (Agenbroad, pers. comm. 1996). The corpus of the mandible in ABDSP(IVCM) V5126 is gracile rather than robust, and has a forward projecting mandibular symphyseal process plus chin that is not turned down as in *M. imperator*. The ascending ramus of ABDSP(IVCM) V5126 is low and inclined slightly posteriorly. In contrast, the ascending ramus of *M. imperator* has rotated anteriorly. Significant morphologic differences between ABDSP(IVCM) V5126 and *Mammuthus*

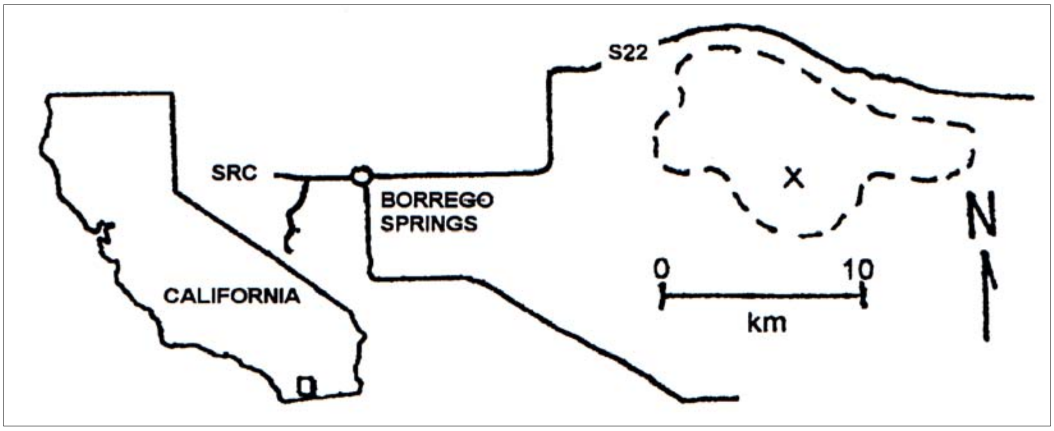


Figure 1 Northern Anza-Borrego Desert State Park®, and the Borrego Badlands of eastern San Diego County, California. Explanation: **SRC** = Colorado Desert District Stout Research Center; **S22** = county road 22; **X** = locality ABDSP(IVCM) 1277; dashed outlined area = Borrego Badlands.

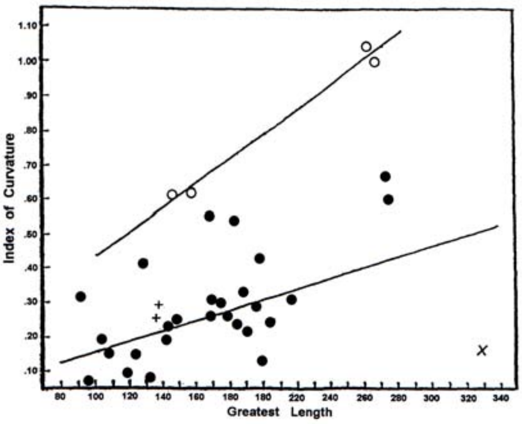


Figure 2 Scattergram of greatest length of incisor in cm / Index of Curvature. Explanation: **X** = *Mammuthus meridionalis* ABDSP(IVCM) V5126; **+** = *M. imperator* ABDSP(IVCM) V4056; black dots = *M. columbi* (Agenbroad 1994); open circles = *M. primigenius* (Haynes 1991; Kunz 1916).

imperator, as represented by ABDSP(IVCM) V4214 and V4260, recovered from the same stratigraphic horizon in the Ocotillo Conglomerate, make an ancestor-descendant relationship (Maglio 1973; Madden 1981) between these species highly unlikely. This implies that the steppe mammoth, *M. armeniacus* (Falconer, 1857), rather than *M. meridionalis*, was immediately ancestral to *M. imperator*. *Mammuthus meridionalis* is recognized as the earliest species of mammoth in North America. As first suggested by Harington (1984), it follows that *M. meridionalis* represents the end of one lineage, and *M. imperator* the beginning of a second lineage that arrived in North America approximately 1.2 Ma BP.

GEOLOGIC SETTING AND STRATIGRAPHY

ABDSP(IVCM) V5126 was collected in a geologically complex area south of the east end of the seismically active San Jacinto Fault zone. This setting has made stratigraphic correlations with dated horizons within the Ocotillo Conglomerate difficult (Remeika & Beske-Diehl 1996). The general location (N $^{1}/_{2}$ of section 36, T10S R7E, Fonts Point 7.5 minute USGS topographic quadrangle) is transected on the southern side from southwest to northeast by the Valle Escondido anticline (Remeika, pers. comm. 1996). This structure plunges gently to the northeast, exhibits axial faulting, and has a very steeply dipping north limb which approaches vertical. The south limb steepens to over 30^{0} near the axis of the anticline. Locality ABDSP(IVCM) 1277 lies south of the axis, where the strata strike approximately N26^{0} E and dip gently 5^{0} to 6^{0} to the southeast.

Stratigraphically, ABDSP(IVCM) V5126 was recovered from a predominately fluvial horizon that complexly interfingers with the lacustrine Brawley Formation (Dibblee 1954). Individual beds pinch out to the east within the Brawley Formation (Remeika, pers. comm. 1996). The paleozoic metamorphic and mesozoic crystalline rocks in the Santa Rosa Mountains to the north and northwest provide a source for the sandy fossiliferous sediments that crop out on both limbs of the Valle Escondido anticline.

DEPOSITIONAL ENVIRONMENT AND TAPHONOMY

Apparently, the skeleton was deposited within a 1m deep, ephemoral, braided stream channel system. The texture, sedimentary structures and bedding of these deposits are typical

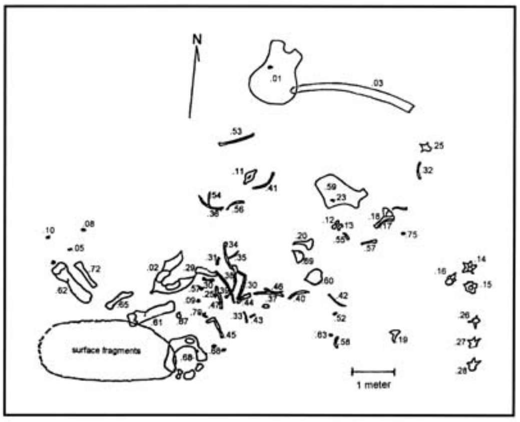


Figure 3 Bone bed plan view, ABDSP(IVCM) 1277/V5126 (after Miller *et al.* 1991) (see element numbers, Table 2).

Table 2 Represented skeletal elements of ABDSP(IVCM) V5126. Materials are listed by skeletal element number (see Fig. 3).

Skull	
.01	skull: M3/, right; M3/, left; I2/, prox.
.02	mandible; M/3, right; M/3, left
.03	I2/, right
.05	M/3 fragment
.06	stylohyoid, left
.07	stylohyoid, right
.08	thyrohyoid, right
.09	basihyoid
.10	?(hyoid fragment)
Vertebrae	
.11	cervical, atlas
.12	cervical, axis
.13	cervical, third
.14	cervical, fifth
.15	cervical, sixth
.16	cervical, seventh
.17	thoracic, first
.18	thoracic, second
.19	thoracic, third
.20	thoracic, sixth
.21	thoracic, spinous process
.22	thoracic, spinous process
.85	thoracic, spinous process
.23	thoracic, centrum
.79	thoracic, centrum
.25	lumbar, first
.26	lumbar, second
.27	lumbar, third
.28	lumbar, fourth
Ribs	
.29	rib, first, left
.30	rib, second, left
.31	rib, third, left
.32	rib, fifth, left
.33	rib, sixth, left
.34	rib, eighth, left
.35	rib, tenth, left
.36	rib, twelfth, left
.37	rib, thirteenth, left
.38	rib, fourteenth, left
39	rib, fifteenth, left
40	rib, sixteenth, left
41	rib, seventeenth, left
.42	rib, eighteenth, left
.43	rib, nineteenth, left
.44	rib, first, right
.45	rib, sixth, right
.46	rib, eighth, right
.47	rib, fifteenth, right
.48	rib, sixteenth, right
.49	rib, seventeenth, right
.50	rib, eighteenth, right
.51	rib, nineteenth, right
.52	rib, right, fragment
.53	rib, fragment
.54	rib, fragment
.55	rib, fragment
.56	?rib, fragment
.57	?rib, fragment
.58	?rib, fragment
Thoracic Limb	
.59	scapula, left
.60	scapula, right
.61	humerus, left
.62	humerus, right
.64	radius, fragment
.65	ulna, left
.66	pisiform, right
.67	cuneiform, right
Pelvic Limb	
.68	innominate, left, fragments
.69	innominate, right, fragments
.71	femur, right, distal
.72	tibia, right
.74	astragalus, left
Podials	
.75	podial, fragment

of distal bajada, fluvial floodplain depositional environments. Local crossbedding and channel direction at the excavation site suggests a north/northeast to south/southwest current. Oxidization of iron-bearing minerals directly below most of the skeletal elements suggests that the fluvial channel may have been dry for an extended period before deposition of the fossil-bearing layer. Also, some scouring or erosion occurred on the surface at the time ABDSP(IVCM) V5126, was deposited. Overlying the specimen are distal fan sheet flood deposits.

There is no readily identifiable cause of death. Based on the extensive wear on the anterior plates of the last molars (third molars), ABDSP(IVCM) V5126 was approximately 55 to 60 AEY (African elephant years) old (Haynes 1991) at the time of death. If AEY are applicable to *Mammuthus meridionalis*, the animal could have lived another 5 to 10 years. No skeletal evidence of trauma and no spiral fractures indicating green-bone breakage are present. The shallow fluvial depositional environment rules out sediment entrapment or drowning.

Osteopathologic evidence of long-term, progressively debilitating arthroses is present in the degenerative state of the tempero-mandibular articulations (see 'Comparative Osteology and Osteometrics' below). This condition would have made chewing increasingly difficult and painful. The inability to feed adequately probably resulted in a weakened condition during life and may have contributed to starvation. Furthermore, predation is a distinct possibility with an infirm adult elephantid. Potential large predators in the Borrego local fauna include *Borophagus diversidens* (COPE 1893) (bone-eating dog), *Arctodus simus* (COPE 1879) (short-faced bear), and *Homotherium* sp. cf. *H. serum* (COPE 1893) (dirk-toothed cat) (Remeika and Jefferson 1993, Remeika *et al*. 1995). Undetectable short term, acute disease also remains a possible cause of, or contribution to death.

The positions of the various skeletal elements (Fig. 3, Table 2) indicate that the carcass had largely decomposed and the remains had been moved prior to burial. The scatter of skeletal elements, separation of once associated elements, the lack of many distal foot bones, and inferred depositional conditions, suggests a short duration transport within the fluvial system after carcass decomposition. ABDSP(IVCM) 1277 was buried in fine-grained siltstones, indicating low energy transport conditions that are consistent with Behrensmeyer's (1988) small scale, braided stream channel-fill deposits. The lack of evidence of sediment abrasion (Olsen & Shipman 1988) on bone surfaces (Miller *et al*. 1991) is consistent with minimal fluvial transport. The long axis orientation of the various skeletal elements within the main ABDSP(IVCM) V5126 bone cluster (Fig. 4) indicates a northeast to southwest flow direction. This direction is consistent with that determined from sedimentary structures.

The skull rested in a nearly upright position with the left side slightly elevated out of the depositional plane. The orientation of the skull (anterior directed N15°E) and the main bone concentration, with the long limb bones located on the west side of the bone cluster

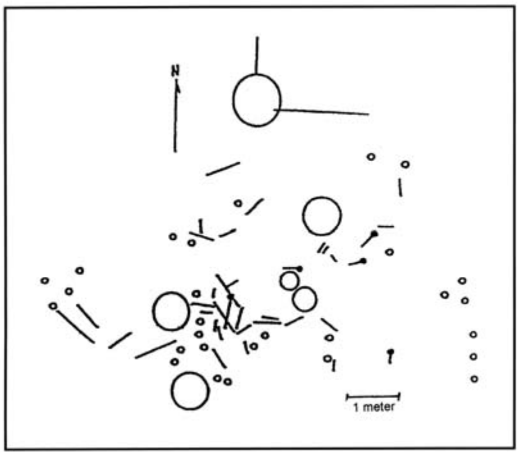


Figure 4 Orientation of skeletal elements of ABDSP(IVCM) V5126. Explanation: large and small open circles = round or nearly round large and small bones; line segments = long bones, ends equal in size; line segments with dot = long bones with one heavy end (dot).

(Fig. 3), suggests that the animal died with its right side down and head directed upstream. Given the inferred transport direction, the skull was transported less than the other skeletal elements, and probably was moved very little. The right incisor had become detached, and rotated 65^0 counter-clockwise (or less likely, clockwise 245^0) relative to the axis of the right alveolus. The tip of the incisor, which would have been more readily transported relative to the larger/heavier proximal end, came to rest under the right zygomatic arch of the skull with the dorsal surface up. The left tusk remained rooted and accounts for the skull being tipped to the right. The fact that the right incisor fell out and the left incisor did not, may indicate that the peridontal tissue of the right alveolus was damaged when the animal presumably collapsed on its right side, allowing the incisor to become more easily dislodged.

The mandible was transported approximately 5.8 m in the inferred flow direction away from the skull. The symphysis pointed downstream as expected. The position of the long limb bones and the mandible indicate that these elements were among the first to become disarticulated (Fig. 3). The mandible had to have been disarticulated prior to, or at about the same time that the right incisor became detached and moved.

Not all of the vertebrae of ABDSP(IVCM) V5126 were recovered. Those remaining indicate that a great deal of postmortem predepositional carnivore and/or scavenger activity had occurred. Although only a few marks typical of damage by carnivore canine teeth are evident, most vertebrae are missing part or all of most of the zygapophyses and processes as well as parts of the centra. These are prime areas for gnawing by carnivores (Shipman 1981). The axis and third cervical vertebra as well as the first and second thoracic vertebrae remained articulated. The anterior surface of the first thoracic vertebra was oriented downward. These elements are positioned with the dorsal spinous process pointing downstream. The fourth cervical vertebra and the majority of the thoracic vertebrae are missing. The anterior surfaces of the fifth and sixth cervical vertebrae were directed up, while that of the seventh was down. Two clusters of vertebrae, the fifth, sixth and seventh cervical vertebrae, and the third thoracic, second, third and fourth lumbar vertebrae lie to the east of, and are separated from the main concentration of skeletal elements (Fig. 3). Carnivores or scavengers moving sections of articulated vertebral elements and individual bones away from the skeleton most easily explain this distribution.

There is much evidence of gnawing on the third lumbar vertebra. The position of the fourth lumbar vertebra and the two groups of vertebrae discussed above (Fig. 3), close to the southern slope of the exposed fossiliferous horizon, suggests that some of the missing vertebral elements may have been lost through erosion.

Some ribs are complete, but many are missing one or both extremities. Many ribs show remnants of tooth marks and gnawing. A number of ribs have tooth puncture marks on the lateral edge, and pieces of the shaft of the rib have been broken away. The ribs generally are aligned at right angles to the direction of flow. The few rib that is aligned parallel to the flow direction retain a large/heavy proximal end. The distal ends of these ribs point downstream. A series of five grooves is present on the lateral and antero-lateral surfaces of the shaft of the left fourteenth rib in an area 87.2 mm long and 48.7 mm wide. Detailed studies, including SEM imagery, reveal that they are "U"-shaped in cross-section with no evidence of parallel striations. The deepest parts of four of these grooves are on the postero-lateral aspect of the rib, and become shallower anteriorly. Very small fragments of bone have been lost from the edges of the groove. The fifth mark is similar but the direction is reversed. These features are typical of carnivore canine bite-and-glide tooth marks.

The left humerus and left ulna are aligned with long axes parallel to the inferred flow.

However, the long axis of the right humerus and that of the right tibia are oriented at nearly 900 to the inferred transport direction (Fig. 3). These large elements should align parallel to the flow direction. This suggests that more than one braid channel may have been involved in fluvial transport of the skeleton, or that the activities of scavengers affected their orientation during the transport and burial processes. The innominates became separated from the sacrum and separated at the pubic symphysis. The left innominate was transported about 3 m. The right, which is represented only by fragments, appears to have been moved very little relative to the presumed position of the front of the body (Fig. 3). The sacrum was not found.

While some of the smaller skeletal elements may have been lost through predation, differential transport of many of the smaller, more equi-dimensional podials and foot bones down stream and away from the main bone concentration, best explains their absence in ABDSP(IVCM) V5126. Sorting of such elements from the larger/longer bones is consistent with low energy, fluvial transport conditions (Behrensmeyer 1988). Some flaking of bone surfaces evidences stage two weathering (Shipman 1981). Most elements exhibit some stage one weathering, indicating less

Table 3 Selected measurements, in cm, of the skull of ABDSP(IVCM) V5126. Measurement numbers correspond to those used by Agenbroad (1994). Explanation: **L** = left; **M** = midline or transverse; **R** = right.

Measurement	L	M	R
2. length of premaxilla	51.6		51.4
4. width of distal extremity of maxilla		52.2	
9. width of anterior end of premaxilla		42.3	
11. length of braincase	64.7		61.8
12. dorso-ventral outside diameter, distal end, premaxilla		21.4	
13. height of braincase		68.3	
14. length, frontal end supraorbital process to distal end of premaxilla	86.7		83.8
16. length of zygoma	45.3		45.4
17. width between center of M3/'s, anterior		12.7	
18. width across zygomatic arches		83.6	
19. width between center of M3/'s, posterior		18.9	
20. distance, center of posterior nares to anterior end of premaxilla		81.8	
21. greatest breadth of occipital condyles		26.8	
22. distance, anterior surface of occipital condyles to anterior extremity of M3/ alveolus	52.4		49.3

Table 4 Asymmetry of the skull, ABDSP(IVCM) V5126. All measurements are in mm. * = The left malar bone is fractured and is displaced posteriorly.

Character	Left	Right
orbit, diameter	137.8	122.8
zygomatic arch - maxilla	256.4	224.7
malar - temporal condyle	224.5*	237.9
occipital condyles, width	118.8	112.9
occipital condyles, length antero-posteriorly	112.3	109.1
temporal condyles, width antero-posteriorly	23.7	12.4
temporal condyles, length, latero-medially	105.5	103.2
temporal condyles, height dorso-ventrally	37.8	26.6

than one-year exposure. Postburial damage to the specimen resulted primarily from sediment loading and compaction. Seasonal (average annual precipitation 16.5 cm) swelling and shrinking of clays within the matrix, has fractured many elements. The skull exhibits minor vertical, top to bottom, crushing. Most larger bones are fractured extensively both parallel and perpendicular to the long axes (see Haynes 1983), and the ulna and tibia exhibit depressed crushing on the upside of the diaphyses. Most of the recovered, smaller elements are preserved intact.

Postburial groundwater leaching has altered extensively the bone chemistry but not the morphology. Soil formation and plant growth have had little effect on the specimen. Recent surface weathering and erosion at ABDSP (IVCM) 1277, prior to discovery of ABDSP (IVCM) V5126, has resulted in considerable damage to those elements exposed, including most of the large limb bones. Total loss of some elements to surface weathering and erosion is highly probable.

COMPARATIVE OSTEOLOGY AND OSTEOMETRICS

Wherever possible, the osteometrics proposed by Agenbroad (1994), Olsen (1972), or Sisson and Grossman (1953), and the dental terminology of Froelich & Kalb (1995) are used. A thorough osteometric study of all skeletal elements has been completed (McDaniel & Jefferson 1999). However, only those elements that show marked differences between *Mammuthus meridionalis* and *M. imperator*, the skull, mandible and scapula are discussed herein.

Skull

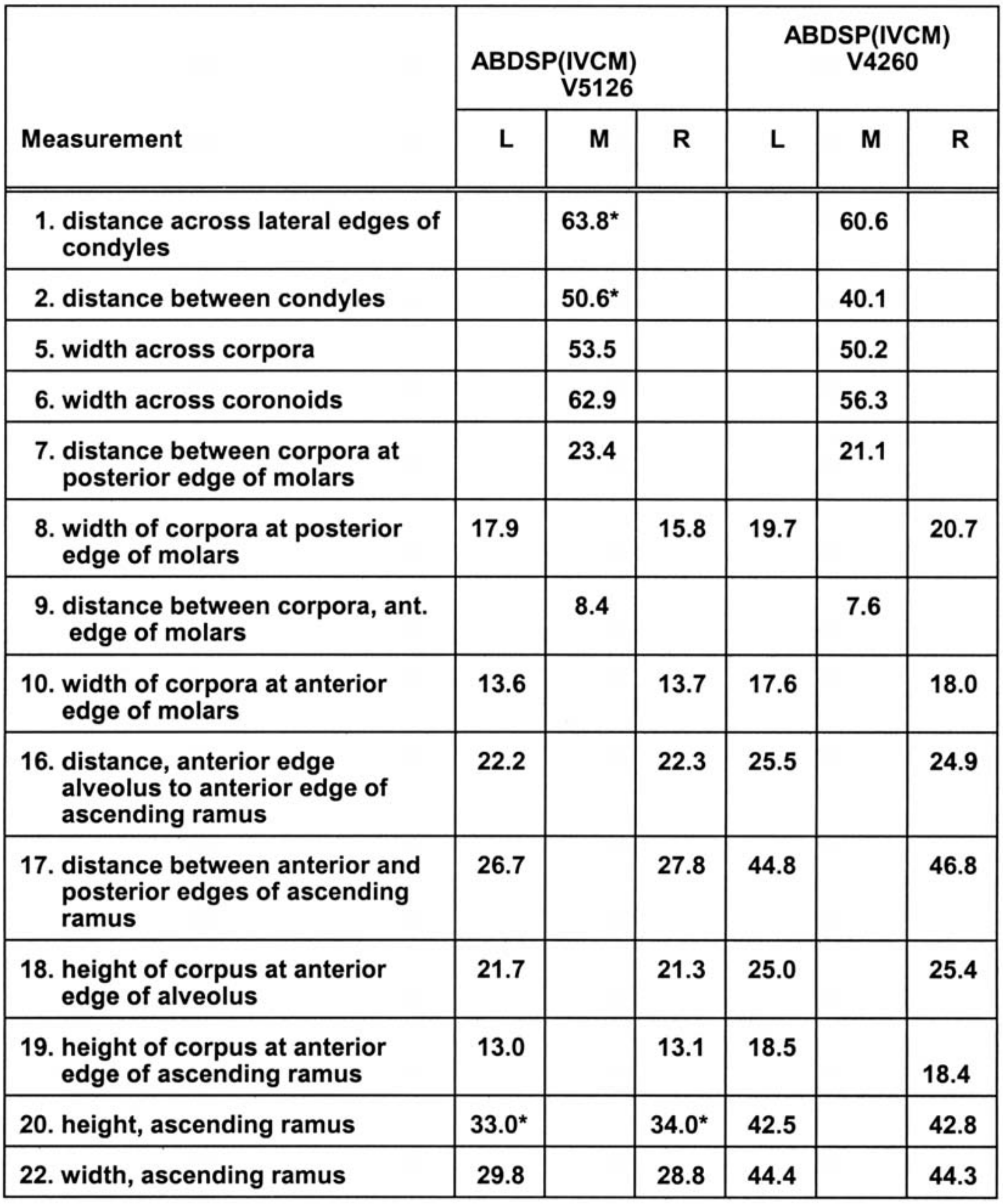
Only the dorsal portion of the cranium is missing. Although the remainder of the skull exhibits some post-depositional crushing, it is essentially complete and intact. The right incisor is complete but separate. The root and base of the left incisor are preserved in the alveolus. Both upper last molars (third molars) are present and well preserved. Measurements of the skull are presented in Table 3. The skull, as a whole, is asymmetric, and exhibits congenital abnormalities. The ventral aspect of the mid-sagittal plane displays a slight "S"-shaped curve. The left upper molar and maxilla, and left basicranium are offset anteriorly 11 mm in the palatal plane relative to the right side. This appears to be largely developmental, although some displacement on post-depositional fractures may contribute to this condition. The lateral parts of the occipital bone are roughened for muscle attachments. Depressions for attachment of the complexus tendons on the posterior surface of the occipital bone are 142.2 mm wide, 193.0 mm long, and 115.4 mm deep. The foramen magnum is circular, and measures 62 mm in diameter.

Both occipital condyles are intact, and show no fractures or erosion of the articular surfaces. The two condyles are slightly skewed in the palatal plane. The left condyle is placed about 2 cm anterior to the right. Post-depositional distortion of the skull does not account for this asymmetry. The left condyle is larger than the right (Table 4). A matching asymmetry is present in the prezygapophyses of the atlas, but not on the posterior articular surfaces. The articular surfaces of the temporal condyles show considerable erosion, and osteopathology indicative of inflammation and bone resorption. The surface of the left temporal condyle exhibits substantial pitting. Pits average 5.4 mm in diameter and 0.8 mm in depth. The right temporal condyle displays much invivo deterioration. The articular surface is rough and irregular, and erosion of the surface is extensive. A smooth, relatively flat, secondary or false articular surface, measuring 7.9 cm medio-laterally by 5.6 cm dorso-ventrally has developed on the anterior surface of the right postglenoid process. Furthermore, the temporal condyles are unequal in size, the left being larger in all dimensions (Table 4).

In the evolution of the skull of mammoths (Maglio 1973), the premaxillae rotate downward to an angle of 50-60°. In ABDSP(IVCM) V5126, the frontal-premaxilla plane is flat, while in *Mammuthus imperator* as represented by ABDSP(IVCM) V4260, the premaxillae have rotated ventrally. The premaxillae of ABDSP(IVCM) V5126 are slightly divergent, but not nearly as much as in *M. imperator* and *M. columbi* (FALCONER, 1857) (see Gillette and Madsen 1993; Agenbroad 1994). The divergent angle at the base of the two incisors is 13°. The right medial alveolar margin diverges a few degrees to the right of the mid-sagittal plane, while the left veers nearly 10° to the left of the mid-sagittal plane. The posterior nares are partially divided by the vomer bone, and together are slightly wider than long, measuring 106.6 mm by 94.8 mm respectively. A supporting specimen cradle, prohibiting measurement covers the anterior nares. The orbit is incomplete in the Elephantidae, lacking the posterior part of the orbital rim, and the supraorbital process of the frontal bone is shortened. The left orbital diameter (Table 4) in ABDSP(IVCM) V5126 is greater than the right. Post-depositional distortion of the skull does not account for the difference between these dimensions. The zygomatic arches are asymmetric, largely a result of post-depositional compressive fracturing. The greatest distance between the internal margin of the left arch and the lateral surface of the left maxilla is greater than that on the right side (Table 3). The distance from the malar bone to the temporal condyle is greater on the right side than on the left (Table 3). However, the left arch is fractured immediately anterior to the orbit, and the zygomatic process of the left maxilla also has been fractured at the base of the premaxilla, and has been crushed inward about 18 mm.

Important dimentional differences are present between the skull measurements of ABDSP(IVCM) V5126 (Table 3) and the sample (twenty three male individuals) of *Mammuthus columbi* from the Mammoth Site, Hot Springs, South Dakota (Agenbroad 1994). The premaxillae of ABDSP(IVCM) V5126 are longer, less divergent, and have a greater diameter than in *M. columbi*. The upper molars (third molars) are farther apart. The skull of ABDSP(IVCM) V5126 is wider transversely but not as long antero-posteriorly as the Hot Springs specimens.

Table 5 Selected measurements, in cm, of mandibles of *Mammuthus meridionalis* ABDSP(IVCM) V5126 and of *M. imperator* ABDSP(IVCM) V4260. Measurement numbers correspond to those used by Agenbroad (1994). * = condyles missing.



Measurement	ABDSP(IVCM) V5126			ABDSP(IVCM) V4260		
	L	M	R	L	M	R
1. distance across lateral edges of condyles		63.8*			60.6	
2. distance between condyles		50.6*			40.1	
5. width across corpora		53.5			50.2	
6. width across coronoids		62.9			56.3	
7. distance between corpora at posterior edge of molars		23.4			21.1	
8. width of corpora at posterior edge of molars	17.9		15.8	19.7		20.7
9. distance between corpora, ant. edge of molars		8.4			7.6	
10. width of corpora at anterior edge of molars	13.6		13.7	17.6		18.0
16. distance, anterior edge alveolus to anterior edge of ascending ramus	22.2		22.3	25.5		24.9
17. distance between anterior and posterior edges of ascending ramus	26.7		27.8	44.8		46.8
18. height of corpus at anterior edge of alveolus	21.7		21.3	25.0		25.4
19. height of corpus at anterior edge of ascending ramus	13.0		13.1	18.5		18.4
20. height, ascending ramus	33.0*		34.0*	42.5		42.8
22. width, ascending ramus	29.8		28.8	44.4		44.3

Table 6 Comparison of the characteristics of *Mammuthus meridionalis* (ABDSP [IVCM] V5126), *M. armeniacus*, and *M. imperator*, ABDSP(IVCM) V4260.

Character	*M. meridionalis* Maglio (1973)	ABDSP(IVCM) V5126	*M. armeniacus* Maglio (1973)	ABDSP(IVCM) V4260
premaxilla rotated down*ward*	no	no	yes	yes
curvature of tusk	gentle	gentle	great	great
corpus of mandible	gracile	gracile	gracile	robust
projection of chin and symphyseal process	forward	forward	downward	downward
position of coronoid to alveolus M/3	posterior	posterior	anterior	anterior
plate number (M3)	11 - 14	12	15 - 21	20
lamellar frequency (M3)	3.5 - 7.7	4.2	5 - 8	6.1
enamel thickness (M3)	2 - 4 mm	2.8 mm	1.5 - 3. mm	2.2 mm

ABDSP(IVCM) V5126 exhibits the same differences with respect to specimen USHS 88.18.52 from Huntington, Utah, identified as a large male *M. columbi* (Gillette & Madsen 1993). The Huntington specimen is geologically older and larger in size than those from Hot Springs.

Mandible

With the exception of both condyles, the mandible in ABDSP(IVCM) V5126 is complete and symmetric. The corpus of the dentary is relatively gracile compared to the robust dentary in ABDSP(IVCM) V4260 (Table 5). The anterior symphyseal process of the mandible of ABDSP(IVCM) V5126 is longer, and extends forward rather than downward as in latter specimen. The mandibles of *Mammuthus imperator* and *M. columbi* are morphologically more similar to each other than to this element in *M. meridionalis*. As with the skull, the mandible of ABDSP(IVCM) V5126 is shorter antero-posteriorly and wider than that in ABDSP(IVCM) V4260 (Table 5) and the Hot Springs Mammoth Site sample (Agenbroad 1994). The corpora of both ABDSP (IVCM) V4260 and in the Hot Springs sample are much higher dorso-ventrally and wider transversely (more robust) than that of ABDSP(IVCM) V5126. The ascending rami of ABDSP(IVCM) V5126 are much more inclined posteriorly than in *Mammuthus imperator* and *M. columbi*, in which the rami have rotated anteriorly and are vertical to the corpus. The coronoid processes in later species are anterior to the posterior margin of the lower molars. Consequently, the height of the ascending ramus is greater in both ABDSP (IVCM) 4260 (Table 5) and Hot Springs sample (Agenbroad 1994) than in ABDSP (IVCM) V5126.

Dentition

Both the upper and lower last molars (third molars of Saunders 1970, Madden 1981, and Froelich & Kalb 1995; the sixth molars of Laws 1966) of ABDSP(IVCM) V5126 are preserved intact. The teeth are in full wear, with the first two or possibly three plates worn away. The dental parameters (Maglio 1973) of ABDSP(IVCM) V5126 fall within the range of *Mammuthus meridionalis* (Table 1). The asymmetry of the skull is seen in the maxillary placement of the upper molars. Both the upper and lower molars on the right side are worn considerably more than those on the left. This indicates that the animal chewed much more frequently or heavily on the right side. Such behavioral asymmetry may be habitual in healthy individuals. However, it is likely that asymmetric chewing in ABDSP(IVCM) V5126 was due to pain

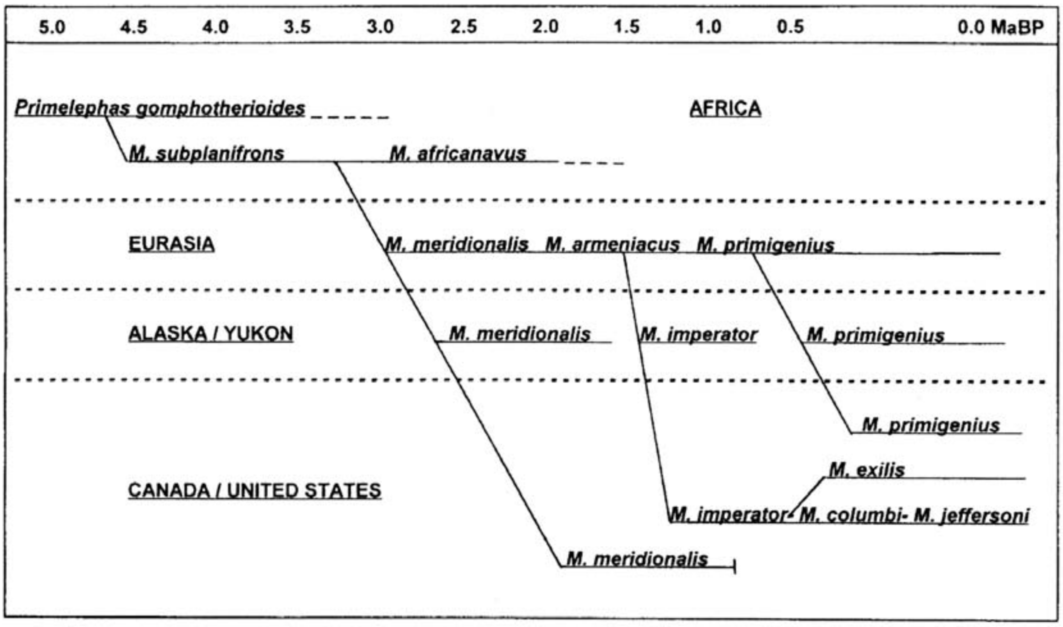


Figure 5 Suggested phylogeny and chronology of *Mammuthus* in North America.

associated with the pathologic tempero-mandibular joint. The right incisor of ABDS (IVCM) V5126 is fully intact. From the alveolus, it extends downward, gently curving laterally, then upward, and finally curving medially. This long sweeping, gentle "S"-shaped compound curve has a low 'Index of Curvature' (Table 6) in contrast to the sharply curved incisors of *Mammuthus imperator* and *M. columbi* (Fig. 2) (Agenbroad, pers. comm. 1996). The incisor of ABDSP (IVCM) V5126 is thinner, longer, and much less curved than those in the Hot Springs sample (Agenbroad 1994). All of these are much shorter than ABDSP(IVCM) V5126, the longest being 277 cm maximum length, and 177 cm cord length. Only four Hot Springs specimens have an Index of Curvature less than ABDSP(IVCM) V5126, and these are less than 150 cm maximum length (Fig. 2). Of the twenty two specimens measured by Agenbroad (1994), only six have a basal diameter less than that of ABDSP(IVCM) V5126 (17.2 cm). There is a small wear facet on the distal 66.2 mm of the medial surface of the tip of the incisor of ABDSP(IVCM) V5126, and a larger wear facet on the distal 150.8 mm of the lateral surface. Thus, the tip of the tooth is not conical, but flattened on both the lateral and medial surfaces. The incisor pulp cavity in female elephantids fills in after maturity, while that in males remains open (Haynes 1991). A very shallow pulp cavity is present in the right incisor of ABDSP(IVCM) V5126. This character and the basal diameter of the incisor indicate the specimen is female.

CONCLUSIONS

Major differences in the morphology of the skull, mandible, incisor, and cheek teeth of specimens of *Mammuthus meridionalis* and *M. imperator* (Table 6), recovered from the same stratigraphic horizon, argue against an ancestor-descendant relationship between these species as previously thought (Maglio 1973; Madden 1981). *Mammuthus meridionalis* is recognized as the earliest species of mammoth in North America. The taxon represents the end of a lineage that persisted here

from about 1.8 to 1 Ma BP. *M. imperator* represents the beginning of a second, *M. imperator - M. columbi* lineage that co-existed with the former in North America from approximately 1.2 to 1 Ma BP (Fig. 5).
At least three separate dispersals of *Mammuthus* from Eurasia to North America have occured, the earliest at approximately 1.8 Ma BP with appearance of *M. meridionalis*, the second at 1.2 Ma BP with the appearance of *M. armeniacus*/*M. imperator* (Harington 1984), and the third in the late Pleistocene with the arrival of the wooly mammoth, *M. primigenius* (BLUMENBACH, 1803) (Fig. 5).

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