PROBOSCIDEA FROM THE LEISEY SHELL PITS, HILLSBOROUGH COUNTY, FLORIDA

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ABSTRACT

Leisey Shell Pits are remarkable for producing three species of Proboscidea representing three genera and indeed three separate families. Gomphotheres of the genus *Cuvieronius* are relatively rare at north temperate latitudes, and that is also true at Leisey 1A. At Leisey 3B, however, *Cuvieronius tropicus* is relatively common. Molars of *Mammut americanum*, a presumed browser, are represented by about 12% as many molars as *Mammuthus hayi*, a presumed grazer, thus suggesting a predominance of grassland and savanna near the site of the bone bed accumulation.

The Leisey sample of *Mammuthus hayi* provides the richest population sample of this early Pleistocene (Irvingtonian) mammoth species. It is one of the earliest North American samples of mammoths. The wide variation of molar characters in mammoths are discussed, and the names *M. haroldcooki* and *M. sonoriensis* are synonymized with *M. hayi*.

RESUMEN

El depósito de conchuelas de Leisey es sobresaliente por el hecho de haber producido tres especies de proboscídeos los cuales además de representar tres géneros distintos, también pertenecen a tres familias diferentes. Gomfoterios pertenecientes al género *Cuvieronius* son relativamente raros en Leisey 1A y por lo general en latitudes temperadas del Hemisferio Norte. Sin embargo, *Cuvieronius tropicus* es relativamente común en Leisey 3B. Molares pertenecientes a la especie presumiblemente ramoneadora *Mammuthus americanum* representan un 12% con respecto a los molares de *Mammuthus hayi*, especie que presumiblemente consumía hierbas lo que hace pensar en un predominio de pastizales y savana cerca del sitio de acumulación de huesos.

La muestra de *Mammuthus hayi* proveniente de los depósitos de conchuelas de Leisey otorga la más rica muestra de esta especie perteneciente al Pleistoceno temprano (Irvingtoniano). Esta es una de las más tempranas muestras de mamuts en America del Norte. Se discute la amplia variación en características de los molares, sinonimizándose los nombres *M. haroldcooki* y *M. sonoriensis* con *M. hayi*.

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INTRODUCTION

One of the remarkable features of the Leisey mammalian fauna is the abundance and diversity of its Proboscidea. Both Leisey 1A and 3B produce three species, representing three distinct families. The mammoths represent by far the largest early Pleistocene sample of mammoths in North America. The abundant mammoth remains are accompanied by somewhat rarer mastodons and gomphotheres. The Leisey fauna thus has the rare distinction (in the New World) of producing three apparently sympatric families of Proboscidea.

The primary purpose of this chapter is to place on record these proboscidean occurrences, with relevant discussions of their systematics, biogeography, and paleoecology. A secondary purpose, with respect to the early mammoth record at Leisey, is to compare its geochronologic age with that of other Irvingtonian mammoth records in North America. For convenience, the following systematic account begins with the families Mammutidae and Gomphotheriidae. The systematic account of Elephantidae thus precedes the discussion of its geochronology. And finally there is a brief ecological discussion indicating the distinct adaptive zones that may have allowed the Leisey representatives of these three families to coexist in ecological compatability.

ACKNOWLEDGEMENTS

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SYSTEMATIC PALEONTOLOGY

Order PROBOSCIDEA Illiger 1811
Family MAMMUTIDAE Cabrera 1929

The mammutids are distinguished from other Late Cenozoic proboscidean families by simple cross crests on their cheek teeth and by their vestigial lower tusks. In North America the transition between Pliocene mammutids, usually referred to the genus *Pliomastodon*, and their presumed Pleistocene descendants of the genus *Mammut* is not well-defined; nonetheless, there is general agreement that Irvingtonian samples can be referred to *Mammut*.

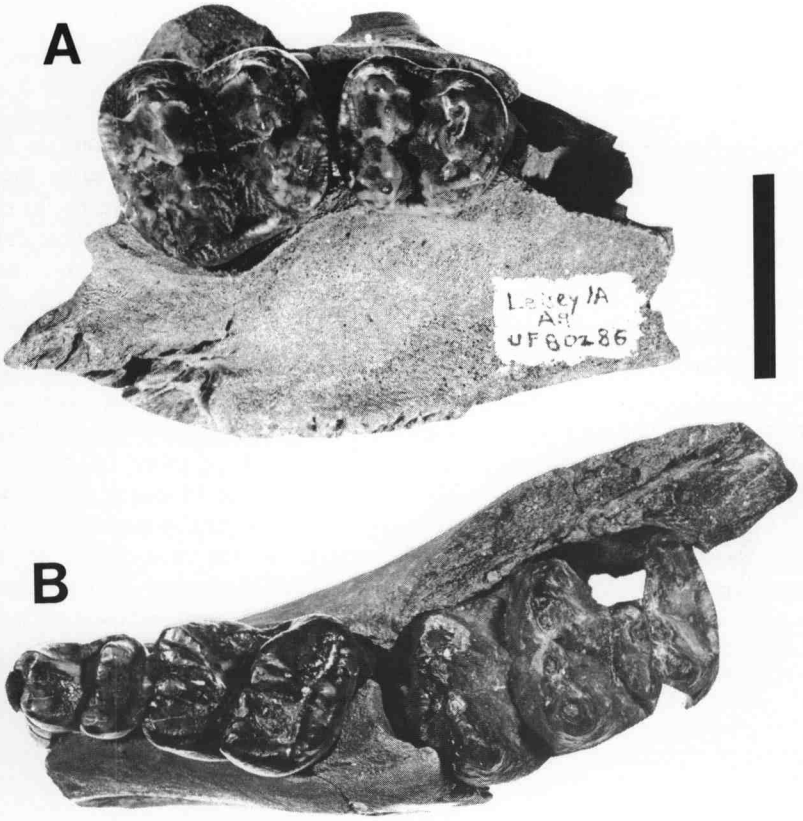

Figure 1. *Mammut americanum* juvenile dentitions from Leisey Shell Pit 1A. (A) UF 80286, left maxillary with DP2 and DP3; (B) UF 80286, right mandible with dp2-4. Scale bar = 40 mm.

Genus *Mammut* Blumenbach 1799
Mammut americanum Kerr 1791

Referred Specimens.--Leisey Shell Pit 1A: UF 80286, DP2-3 and mandible with dp2-4 (Fig. 1); UF 82255, M1; UF 86826, M1; UF 81453, mandible with dp4-m1; UF 84751, mandible with broken tooth; UF 84443, broken dp4; UF 84444, broken dp4; UF 80691, broken m1; UF 81936, dp4; UF 82373, dp3; UF 85138, broken m2; UF 80004, fragmentary cheektooth. Unlisted are a number of other fragmentary mandibles, as well as skull fragments, tusk fragments and limb bones.

Discussion.--The Leisey sample of American mastodon in the UF collection consists primarily of 11 fairly complete cheek teeth. As indicated by dental

morphology and in some localities by stomach contents, *Mammut* represents a browsing habitus, whereas *Mammuthus* presumably preferred grazing in open environments. This suggests that Leisey consisted predominantly of grassland and coastal savanna.

Mammut cheek teeth occur 12 percent as abundantly as *Mammuthus* cheek teeth in the Leisey sample. A striking feature of the mastodont sample is the large number of juvenile teeth and heavily waterworn tusks and tusk fragments.

Family GOMPHOTHERIIDAE Cabrera 1929

The gomphotheriids are distinguished by complex cusps (wearing to a trefoil pattern) on their cheek teeth and, in most genera, elaborate lower as well as upper tusks. The loss of lower tusks, however, came to characterize the progressive Pleistocene gomphotheriids, including *Cuvieronius*, which radiated in the American tropics and spread throughout South America (Webb 1985).

Genus *Cuvieronius* Osborn 1923

Cuvieronius tropicus (Cope 1884)
(=Cordillerion oligobunis in Osborn 1936)

Referred Specimens.--Leisey Shell Pit 1A: five fragmentary cheek teeth: UF 40073, 40074, 65061, 88005, and 88006; and an upper tusk fragment, UF 88008. **Leisey 3B**: well-preserved left M3, UF 129033 (Fig. 2).

Discussion.--The rarest proboscidean taxon at Leisey, *Cuvieronius tropicus*, nonetheless occurs at both Leisey 1A and 3B. The Leisey material is similar in all respects to the much richer sample (as yet undescribed) from the approximately contemporaneous site at Punta Gorda (Webb 1974).

Cuvieronius evidently had its origin in North America in the Pliocene and ranges through both American continents until about the end of the Pleistocene. An early plesiomorphous (or transitional) form of *Cuvieronius* occurs in the late Blancan of Florida, e.g. at Macasphalt Pit in Sarasota Co, Florida (Jones et al. 1991). Webb and Perrigo (1984) provided evidence from the late Miocene of Honduras in support of the hypothesis that *Rhynchotherium* is the primitive sister group of *Cuvieronius* (Tobien 1973; May and Repenning 1982; Webb and Perrigo 1984; Miller 1990), as suggested by the presence of spiral enamel bands on the upper tusks and by the downturned and progressively abbreviated mandibles in *Rhynchotherium*. A practical definition of *Cuvieronius*, distinguishing it from *Rhynchotherium*, can be based on the loss of its lower tusks. Improved samples of *Cuvieronius* and/or *Rhynchotherium* from Blancan faunas are needed to clarify the transition.

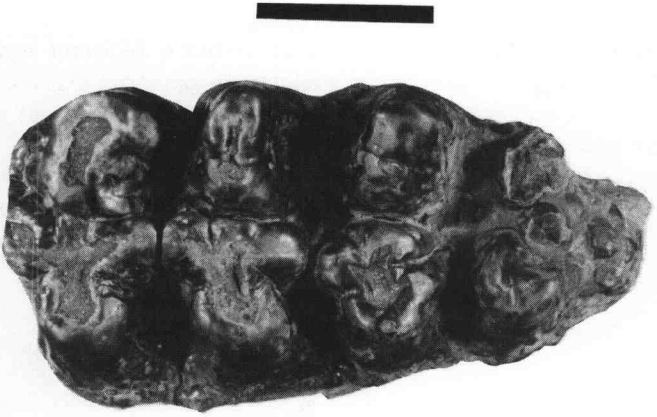

Figure 2. *Cuvieronius tropicus.* UF 129033, M3 from Leisey 3B. Scale bar = 50 mm.

During the Pleistocene *Cuvieronius tropicus* ranged from Florida (e.g. at Punta Gorda and in the early Rancholabrean at the Daytona Beach site), around the Gulf Coastal Plain and southward through Mesoamerica. The species was named by Cope from Mexico; it is also known in Honduras, El Salvador, and Costa Rica (Freudenberg 1922; Webb and Perrigo 1984; Laurito 1988). *Cuvieronius* is also the earliest known proboscidean to enter South America, appearing in the Uquian at a time roughly equivalent to the early Irvingtonian (Webb 1985). It is best known in the middle and late Pleistocene from the Andes. Its South America sister genera are *Haplomastodon* and *Notiomastodon* (Simpson and Paula Couto 1957; Webb 1992).

Family ELEPHANTIDAE Gray 1821
Genus *Mammuthus* Brookes 1828
***Mammuthus hayi* Barbour 1915**
(=*M. scotti* Barbour 1925)
(=*M. haroldcooki* Hay 1928)
(=*M. sonoriensis* Osborn 1929)

Referred Specimens.--Leisey 1A: UF 80664, right m3 with associated jaw fragments (Fig. 3C); UF 81748, mandible with right and left p4 and m1; UF 81749, M2; UF 82211, partial M2; UF 87201, partial M2; UF 85326, partial maxilla with right and left M2, and M1 fragments;UF 87451, m3; UF 85325, juvenile mandible with right and left dp3, d4, and part of m1 (Fig. 4); UF 86974,

m3; UF 86975, partial m3; UF 65395, m3; UF 81750, m2; UF 86825, dp4; UF 81707, m3; UF 84185, M1; UF 84476, m1; UF 85326, DP4; UF 83549, partial maxilla with DP3; UF 64686, 81708, 81570, 83550, 86748, 80064, 86748, 81347, 88017, deciduous premolars; UF 86978, left and right M3's in maxilla (Fig. 3A); UF 67200, mandible with m3; UF 85324, left and right M3's in maxilla; UF 86976, partial mandible with m3 (Fig. 3B); and about 60 limb elements not cited.

Description.– As the richest collection of early Pleistocene mammoths in North America, the Leisey sample of *Mammuthus hayi* warrants thorough characterization. Fortunately the sample of cheek teeth spans the entire ontogenetic range of the mammoth population, and has especially strong representation of deciduous teeth.

Tables 1 and 2 present measurements of 16 upper and 10 lower molars from Leisey. The most diagnostic features traditionally used to separate mammoth species are the number of lamellae (LN) in the last upper and lower molars and also the lamellar frequency (LF) (i.e. the average number of lamellae in 100 mm of occlusal length). For the Leisey sample of 10 lower third molars, the mean for lamellar frequency is 5.1. In upper third molars, based on four complete specimens, this figure is 5.6. These lamellar frequencies, among the lowest observed in North American mammoths, result partly from the large spacing between lamellae and partly from the very thick, crenulated enamel making up the grinding battery of each molar. Although the full lamellar number, ranging up to 17 in m3 and 19 in M3, is given for each molar, it should be noted that typically there are only about 10 plates in wear at any given stage, leaving the equivalent of 30% of an ultimate molar in reserve. Figure 3C illustrates a left m3 in early wear with each anterior plate partly integrated by wear, but with many cuspids still distinct, with the next seven plates unworn, and with an estimated four posterior plates absent.

Another very important feature of each molar is its height or degree of hypsodonty. The maximum unworn height of m3 in the mandible, UF 86976, is 185 mm (Fig. 3B).

A fourth commonly used measure in comparing elephantid taxa is the enamel thickness (ET). Mean enamel thickness in ultimate molars from the entire Leisey sample is 2.5 mm for both upper and lower third molars. In addition to very thick enamel, the cheek teeth of the Leisey mammoth are characterized by the strongly crenulated or corrugated surface of the enamel crests, presumably an adaptation for cutting and tearing fibrous vegetation. It is not uncommon, especially in early wear stages, for the cheek teeth to develop a "loxodont sinus," i.e. a separate median loop of enamel in the lamella. In three dimensions a loxodont sinus may be viewed as an enamel cusp that broadens beyond the normal anteroposterior width of the lamella during a particular wear stage. This

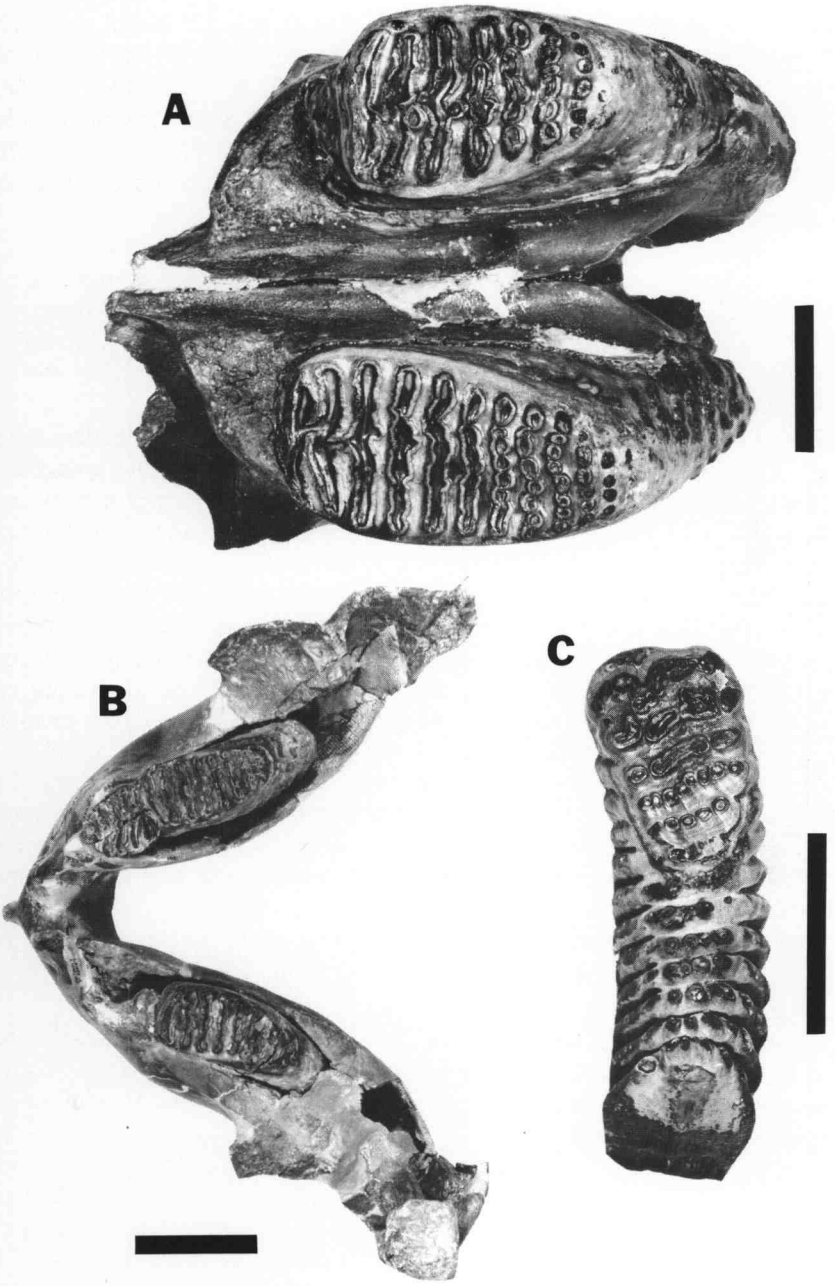

Figure 3. *Mammuthus hayi* from Leisey 1A. (A) UF 86978, palate with left and right M3 in early wear stage; (B) UF 86976, mandible with left m3 and right m2-3; (C) UF 80664, left m3 in early wear stage, showing six weakly worn anterior plates, seven unworn plates, and missing an estimated four posterior plates. Scale bars = 100 mm in length.

Table 1. Measurements of *Mammuthus hayi* upper molars from Leisey 1A.

Catalog #	Tooth	LN	L	W*	H*	LF	ET
UF 85324	RM3	19+	242+	95^{4}	-	6.50	3.10
Pendergraft a	LM3	-	-	92^{4}	-	6.00	2.89
UF 86978	RM3	12+	265(e)	96^{4}	-	5.00	2.21
Pendergraft b	LM3	12+	265(e)	97^{4}	-	5.00	2.30
UF 87201	LM2	12+	184+	99^{2}	158^{9}	5.75	2.28
UF 86137	RM2	x15	246+	92^{3}	148^{7}	6.00	2.50
UF 81749	RM2	13+	248+	83^{6}	108^{10}	4.75	2.90
UF 81750	LM2	x13	286	86^{6}	128^{10}	5.00	2.69
UF 85326	RM1	14	187	79^{3}	181^{7}	7.50	2.33
Pendergraft c	LM1	13	179	78^{4}	178^{7}	7.50	2.35
UF 86979	RM1	11+	215+	72^{7}	$118+^{10}$	5.75	2.18
UF 84185	RM1	8+	182+	68^{3}	$51+^{3}$	5.60	2.70
UF 85309	RM1	10+	186+	78^{4}	78^{4}	6.00	1.87
UF 81748	RM1	13	185	72^{5}	-	7.00	2.55
Pendergraft d	LM1	12(e)	-	70^{4}	-	7.00	2.73
UF 84476	LM1	11+	175+	80^{7}	80^{3}	6.75	2.62

*Superscript refers to loph number on which W and H measurements were taken.

phenomenon is especially common in primitive elephantids with very thick enamel, as in living African elephants of the genus *Loxodonta*. Other teeth form irregular lamellar patterns based on unusual temporary unions between individual enamel cusps.

Similar statistics for the penultimate molars are also valuable for comparisons, although they are based on smaller samples. In the Leisey mammoth sample the following means are found: M2 has a lamellar number of 12, a frequency of 5.8, and enamel thickness of 2.4; while m2 has equivalent data of 12, 4.9, and 2.4.

A number of complete mammoth tusks were collected at Leisey 1A. They vary considerably in length and diameter, but all are nearly straight, with only slight spiral curvature noticeable in the longest specimens. When viewed from above the tusks would have converged somewhat anteriorly, giving a subtly lyrate pattern.

Table 2. Measurements of *Mammuthus hayi* lower third molars from Leisey 1A.

Catalog #	Tooth	LN	L	W*	H*	LF	ET
UF 65395	rm3	4++	102+	$77+^{4}$	$102+^{4}$	4.00	2.66
UF 67200	rm3	9++	205+	88^{5}	-	4.00	2.56
UF 80664	lm3	15+	284+	75^{4}	143^{6}	6.25	2.58
UF 81707	rm3	10+	185+	78^{3}	$141+^{6}$	6.25	2.00
UF 86974	rm3	12+	254+	90^{7}	$135+^{3}$	4.50	3.29
UF 86975	lm3	8+	171+	96^{5}	$132+^{8}$	4.50	2.80
UF 86976	lm3	8+	197+	87^{4}	-	4.75	2.18
ESTEVEZ a	lm3	8+	158+	98^{4}	$95+^{3}$	5.25	2.13
ESTEVEZ b	rm3	15+	218+	96^{3}	163^{9}	5.75	2.28
UF 67451	lm3	17+	322+	108^{4}	189^{9}	5.50	2.21

*Superscript refers to loph number on which W and H measurements were taken.

Elephantidae have six cheek teeth in each jaw half, three deciduous premolars and three molars. Uppers and lowers for all these positions are represented in the Leisey sample.

A series of three relatively complete mandibles represents three distinct growth stages. This series extends from UF 85325, with both left and right dp3 and dp4(Fig. 4), through UF 81748, with left dp4 and right and left m1, to UF 86976, a mature individual with left and right m3 in full wear (Fig. 3B). Another mandible, UF 67200, is somewhat more worn and somewhat less complete than UF 86976. The length of the symphysis evidently grew from more than 53 mm in the juvenile to about 115 mm in the adolescent, of which nearly 30 mm formed a prominent "chin" which was not downturned (Fig. 3B). With just three symphyses at hand, the significance of this variation in symphyseal prominence length cannot be determined.

The depth in these mandibles progressed from 69 mm below dp3, to 148 below m1, to 185 below m3. The width between opposite cheek teeth increased from 57 between dp2's, to about 65 between dp4's, to 75 at the anterior end of m2, to 120 at the anterior end of m3. The coronoid process reached only slightly above the alveolar border in the adult. In UF 81748, with m1 in wear, the coronoid reaches about 250 mm above the jaw base and the articular process

about 430 mm above. In UF 67200, these features are 240 mm and 420 mm respectively.

About 60 postcranial elements of the Leisey mammoth were preserved. These limb bones show the characteristically long-limbed proportions of elephantids, but were somewhat smaller than typical Rancholabrean skeletons of *Mammuthus columbi* from Florida. For example, an adult ulna (albeit with weakly fused epiphyses) from Leisey has an overall length of 995 mm and an articular length of 825 mm, as compared with a younger (unfused) stage in *M. columbi* from the Aucilla River (UF 14779) which measures 1055 mm and 940 mm respectively.

Discussion.--The wide range of molar variation documented in the Leisey mammoth sample (Tables 1 and 2) suggests that early Pleistocene mammoths in North America may all represent a single relatively primitive species. Observed plate counts in third lower molars from Leisey ranged from 8 to 17 plates. It is inappropriate to develop any statistical profile other than observed range under these circumstances. On the other hand, the enormous variability to be found in a population of elephantid teeth was recently stressed in a detailed meristic study of *Elephas maximus*. In that study Roth and Shoshani (1989, p. 26) noted that "recognition of this variability will demand a re-evaluation of the status of many fossil species named within the Elephantidae." More recently, Roth (1992) showed that many samples of fossil elephantid teeth express even greater sample variability than in other mammals. When applied to the early mammoths in North America this warning clearly places an immense burden of proof on anyone splitting species on the basis of minor meristic differences.

The extraordinary variation seen in the Leisey sample, briefly described above, fully encompasses the quantitative and qualitative variation seen in much more limited samples of early Pleistocene *Mammuthus* elsewhere in North America. These include the types of four nominal species, as discussed below.

The oldest available name for a primitive mammoth in North America is *Mammuthus hayi* Barbour 1915. The type specimen (UNSM 1301) is a fully mature mandible with very shallow depth (241 mm below coronoid process), and only 11 lamellae on each of its last molars (Barbour 1915; Osborn 1942). The last molars are 229 mm long by 76 mm maximum width with a plate frequency just over 4. Unfortunately the type was discovered as an isolated specimen at Crete, Nebraska, with no associated fauna nor any clear basis for dating the surrounding sediments, although they were said to be "Aftonian" gravels. Its morphology alone must serve as the evidence for its probable early Pleistocene age. We accept this type as the appropriate name-bearer for the early North American mammoth species that is more fully sampled and dated at Leisey. Madden (1981) has referred several specimens from other western sites to this species.

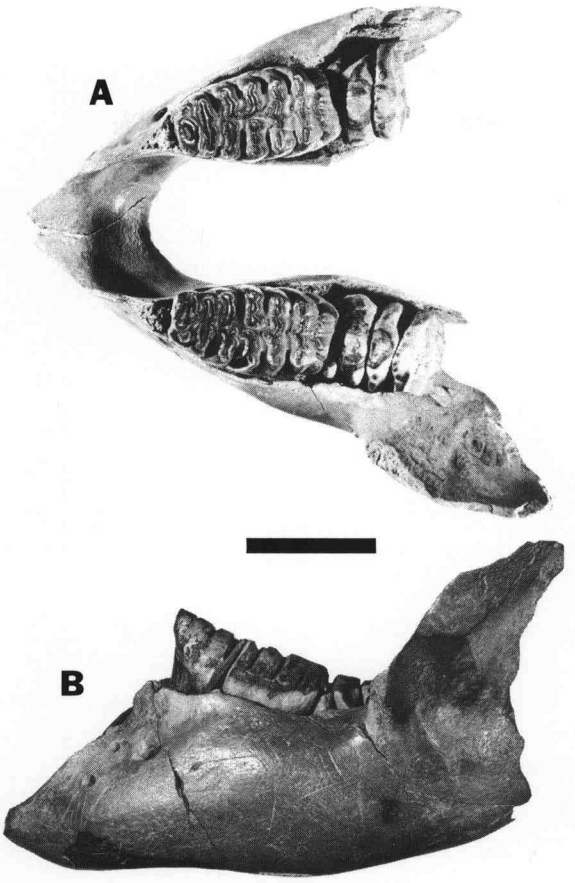

Figure 4. *Mammuthus hayi* from Leisey 1A. UF 85325, juvenile mandible with left and right dp3 and first few plates of left and right dp4. Scale bar = 50 mm.

The Leisey sample includes one specimen quite similar to the type: UF 67200 is the right mandible of an old individual with 10 plates; its articular process is 420 mm tall, its coronoid about 230 mm tall, and it has a very similar long flat jaw profile. Its last molar measures 205 mm by 88 mm maximum width and has a lamellar frequency of 4 plates per decimeter (see Table 2). This is a remarkably close match for the type of *M. hayi*, in view of the wide range of age and wear variation in the whole Leisey mammoth sample.

Another Nebraska specimen with a similar but larger lower third molar was named *M. scotti* by Barbour, but it is clearly a synonym of *M. hayi*. A second probable synonym is *M. sonoriensis* (Osborn 1942), an excellent middle Pleistocene mammoth record from northern Mexico that closely resembles some

of the larger Leisey specimens. A third early Pleistocene synonym, well known from the Irvingtonian fauna at Holloman Gravel Pit in Oklahoma, is *M. haroldcooki*, use of which was advocated by Hibbard and Dalquest (1966).

The precise relationship of *Mammuthus hayi* to various Old World species lies beyond the scope of this study. Presumably it is derived from an early Pleistocene species in Asia, such as *M. armeniacus* or *M. gromovi*. Application of a European name, such as *M. meridionalis*, to North America samples has been advocated by Maglio (1973) and Kurtén and Anderson (1980), but the type of *M. meridionalis* belongs to a much less progressive species from the Plio-Pleistocene of southern Europe. Other modern discussions of North American mammoth species nomenclature generally agree with the usage of Kurtén and Anderson (1980), Agenbroad (1984), and Graham (1986).

Osborn (1942) had supposed that there was a separate immigration of a middle Pleistocene mammoth species from the Old World, and this break was represented by his distinction between the genera *Archidiskodon* (including *M. hayi*) and *Parelephas*. This concept is no longer tenable, as there is ample evidence of continuity between Irvingtonian and Rancholabrean samples of mammoths. Indeed it could be argued that only one species of North American mammoth should be recognized prior to the arrival of the woolly mammoth (*M. primigenius*). On the other hand we prefer to follow the tradition to the extent of recognizing a break between the early and late Pleistocene mammoth species in North America. Thus, *M. hayi* gave way to a more progressive stage of late Irvingtonian and Rancholabrean mammoths known as *Mammuthus columbi*. One of the earliest samples assigned to *M. columbi* occurs in the Irvington gravels in California (Savage 1951). Late Rancholabrean samples of this species typically have third molars with 18 to 24 plates, lamellar frequency from 6 to 8, enamel thickness from 2.0 to 2.4 mm, and unworn crown heights ranging from 180 to 280 mm. The tusks were large and curved. The mandible wholly lacked a chin, and the coronoid process extended well above the alveolar border. These features adequately distinguish *M. columbi*, even in its late Irvingtonian stage, from *M. hayi*.

Within *Mammuthus columbi*, thus broadly used, several distinctive populations are known. The most distinctive is surely the population of dwarf mammoths from the northern Channel Islands off the California coast, often called *M. exilis*. Another frequently distinguished variety is the large, very-progressive mammoth population that ranged from the Great Lakes region southward into Florida during the late Pleistocene. Osborn (1942) called the northern populations *M. jeffersoni* and the southern ones *M. floridanus*, but his concepts were essentially typological. Among these populations some ultimate molars attain plate counts that rival those of *M. primigenius*, and they are sometimes difficult to distinguish from that species (Maglio 1973; Kurtén and Anderson 1980). Unless one or both of these nominal species can be distinguished from *M. columbi* in a reliable statistical study of adequate

population samples, it is better to leave them as subjective synonyms. The type sample of *M. floridanus* in the Bradenton fauna of early Rancholabrean (pre-Sangamonian) age is not statistically distinguished from earlier or later Rancholabrean samples in Florida and can be comfortably incorporated into *M. columbi*. Even if Osborn's species concepts could be substantiated, there are several older names, such as *M. roosevelti* and *M. jacksoni*, that probably would be senior synonyms of *M. jeffersoni*. In this respect we support Graham's (1986) position that *M. columbi* encompasses all the late Pleistocene populations except *M. primigenius*. It is worth remembering that the type of *M. columbi* itself derives from a late Pleistocene population from southeastern Georgia.

GEOCHRONOLOGY OF IRVINGTONIAN *MAMMUTHUS* IN NORTH AMERICA

Several records of relatively primitive North American mammoths fall within the early to middle Irvingtonian. At Rock Creek, Texas *Mammuthus hayi* and a late-surviving *Stegomastodon* are overlain by the Cerro Toledo ash, which correlates the occurrence directly with a radiometric date of 1.2 to 1.4 million years ago (Izett 1981; Schultz 1986). A mammoth mandible with both last molars was recovered from the Santa Fe Formation near Albuquerque, New Mexico, in sediments overlying the 1.4 million year old Guaje Pumice (Tedford 1981; Sobus and Logan 1984). The molars retained only 11 widely spaced plates, but they are so heavily worn that these data may be abnormal statistically. *Mammuthus hayi* material from Idaho overlies the Bruneau Basalt, which has an age of 1.36 million years (Malde and Powers 1962). A mammoth specimen from Thornton Beach near San Francisco might be the oldest record in North America; it occurs 10 meters below a tuff dated by the potassium/argon method at 1.5 million years ago, but the standard error of 0.8 million years associated with this date indicates that it must be treated with caution (Madden 1981). An Alaskan specimen from Old Crow 47, consisting of upper and lower posteriormost molars, represents *Mammuthus hayi* on the basis of its 12 well-spaced plates. It occurred below a tephra lying in normally magnetized sediments thought to represent the Olduvai magnetochron. Unfortunately, however, the sediments may in fact be considerably younger (W.E. Morlan, pers. comm.). Thus we find that the earliest mammoth records in well-dated sections in North America range back to about 1.2 to 1.4 million years ago.

Some recent authors have inferred from dental patterns that *Mammuthus* entered North America in the Pliocene. Churcher (1986) found isolated teeth with primitive measurements in the Old Crow Basin, and Madden (1985) studied a molar taken from a creek bank in North Carolina. Each author gauged the primitive appearance as indicative of a pre-Pleistocene age. The looseness of

such arguments, unsupported by any independent stratigraphic evidence such as faunal associations or dated sediments, must be resisted.

In summary, the first North American mammoths appeared during the early Irvingtonian and spread widely throughout North America, leaving records in Alaska, Alberta, Idaho, California, Arizona, Texas, Nebraska, Florida, Mexico, and as far south as Honduras, Nicaragua, and Costa Rica (Webb and Perrigo 1984; Laurito 1988). At present all early to middle Irvingtonian samples appear referable to *M. hayi*. Latest Irvingtonian mammoth samples, notably the Irvington Gravels, are more closely comparable to Rancholabrean samples and are thus referable to *M. columbi*.

AN ECOLOGICAL PERSPECTIVE

It is reasonable to ask how three proboscidean species, at least one of which probably formed large herds, could coexist in a region as small and topographically flat as central Florida. Of course, Leisey 1A may have accumulated over a considerable time interval, a century or more perhaps, and thus may have sampled a diversity of habitats. Leisey 3A, on the other hand, was a catastrophic assemblage. A relatively simple indication of ecological separation among these Proboscidea may be sought in the adaptive differences in their masticatory and locomotor systems. Fortunately such evidence is readily available to paleobiologists interested in such problems.

The dentitions of elephantids are so highly adapted to grazing, that it would be quite odd if they did not ordinarily eat coarse fodder and range through essentially open country habitats. In later Pleistocene faunas, from the arctic to the arid west, the reliance of mammoths on grasses and sedges is well documented. Mammutids, on the other hand, are dentally adapted to browse on softer vegetation and would be expected to range in or near woodland habitats. At Leisey this more distal distribution (transported) that is expected of *Mammut* is suggested by relatively abundant remains of its water-worn tusks and teeth. Recent studies of late Pleistocene mastodont digesta from a Florida underwater site indicate that they fed on a great variety of conifer needles, riparian leaves such as willow and buttonbush, and fruits of grapes and gourds (Webb et al. 1992). The gomphotheriids are broadly intermediate in these respects; *Cuvieronius*, with its progressive dentition, is best considered to be a mixed feeder inhabiting lowland subtropical savanna (Webb and Perrigo 1984; Laurito 1988).

The relative numbers of the three taxa indicate that mammoth herds predominated near the site of deposition, possibly along grassy tidal flats or in coastal savannas developed from former dune systems. On the other hand, mastodons, which were only 12% as numerous as mammoths, ranged at some

distance from the sites of deposition, probably in patches of riparian woodland. *Cuvieronius* was rare at Leisey 1A and may have been generally remote from that area. This genus is relatively common at Leisey 3, however. Similarly, at the Punta Gorda site and in the Bermont Beds overlying the Caloosahatchee Formation at Alva on the Caloosahatchee River, *Mammuthus hayi* and *Cuvieronius tropicus* occur together in roughly equal numbers. Possibly they formed mixed herds in coastal savannas.

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