Life histories of female American mastodons (*Mammut americanum*): Evidence from tusk morphology, stable isotope records, and growth increments

by

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For Suguta.

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Abstract

Proboscidean tusks (hypertrophic incisors) are excellent sources of paleoecological data because they grow continuously by accretion. This allows for tracking of changes in morphology, stable isotope composition, and growth rate throughout an individual's life. Tusks can provide evidence of sex, age, and season and cause of death, as well as the timing of life events (e.g., maturation). Here, analyses of tusk morphology, stable isotope composition (oxygen, carbon, and nitrogen), and growth increments are used to characterize the lives and circumstances surrounding the deaths of female American mastodons (*Mammut americanum*) from the latest Pleistocene in North America. Female mastodons are less common in the fossil record than males, but the recent discovery of an assemblage of female mastodons at the Bothwell Site in Indiana substantially increased the number of female mastodons available for study. Tusks from this new site, and other localities, are used to investigate mastodon sexual dimorphism, social structure, and life history. Chapter 2 presents an improved method for identifying the sex of a mastodon using only tusk measurements. Chapter 3 documents similarities in the character of African elephant (*Loxodonta africana, Loxodonta cyclotis*) and mastodon tusk dimorphism that can be used to infer similar social structures and behavior in *Loxodonta* and *Mammut*. Chapter 4 presents evidence that indicates multiple, temporally discrete mortality events led to formation of the female mastodon assemblage at Bothwell. Evidence from tusks suggests that the site represents a Paleoindian meat cache. Chapter 5 presents long-term tusk growth records for two female mastodons. Periodic

variations in annual growth rate are proposed as evidence of pregnancy and lactation.

The analyses presented here have value for interpreting other mastodon sites as well as for understanding how mastodons responded to climate change and human hunting, factors commonly cited as causal hypotheses for extinction. The results of this study do not provide support for a specific hypothesis, but evidence from growth increment and stable isotope analyses indicates that these mastodons did not experience nutritional stress at death. This suggests that, although the late Pleistocene environment was changing, environmental change did not unduly stress these mastodons.

Chapter 1

Introduction

The American mastodon (*Mammut americanum*) was one of the most prominent members of the late Pleistocene North American fauna until its extinction at the end of the epoch. Mastodon extinction coincided with the extinction of nearly two-thirds of existing Pleistocene megafaunal genera worldwide (Barnosky et al. 2004). The cause of this extinction is unresolved, and questions pertaining to its driving mechanisms are hotly debated. Most investigations into the mechanisms of megafaunal extinction concentrate on over-hunting by humans, climate change, or a combination of these two factors.

Previous studies addressing megafaunal extinction have focused on the effects of increased seasonality on biotic communities (Guthrie 1984), associations between the timing of biogeographic expansion of humans and the onset of extinctions (Martin 1984), and simulations to investigate whether it was possible for humans to cause a mass extinction event (Mosimann and Martin 1973; Alroy 2001). Other approaches have sought to understand the cause of extinction by investigating the lives and deaths of individual victims (e.g., Fisher 2008; Fisher et al. 2008). These approaches include identifying evidence of mastodon butchery by humans (Fisher 1984), documenting seasonal patterns of mortality for butchered and non-butchered end-Pleistocene mastodons (Fisher 1987, 2009), and compiling individual mastodon life histories

(e.g., Fisher 2008; Fisher et al. 2008). Life history refers to the timing of life events as well as the allocation of energy to growth, maintenance, and reproduction (Smith 1992). Some life history parameters (e.g., age at maturation, length of inter-birth interval) are sensitive to environmental conditions, so changes in a mastodon's life history parameters can provide clues to its relationship with its environment. For example, female African elephants extend inter-birth intervals during periods of environmental stress (Lee and Moss 1986), so if the environment at the end of the Pleistocene was stressful, mastodon inter-birth intervals should increase toward the end of the epoch. Ultimately, life history studies can be used to evaluate whether climatic change at the end of the Pleistocene caused mastodons undue stress that limited their reproductive output and eventually led to their extinction.

The objective of this dissertation is to expand knowledge of American mastodon life histories – specifically, those of females – living in the latest Pleistocene of North America. This objective is addressed by studying mastodon tusks, the skeletal element that contains the most information about the life of an individual. Tusks – hypertrophic incisors – are excellent sources of paleoecological data because they grow continuously by accretion, recording changes in (1) morphology, (2) stable isotope composition, and (3) dentin growth rate over an animal's lifetime. Increments marking growth at annual, fortnightly, and daily scales are preserved in mastodon tusk dentin, so changes in the above three characteristics can be documented at different temporal scales and tied to specific times of the mastodon's life. Tusks have been used to assess age at weaning (Rountrey et al. 2007), season of death (Fisher and Fox 2003), sexual dimorphism (Smith and Fisher in revision), seasonal changes in diet (Fox and Fisher 2001), seasonality of the

environment in which mastodons lived (Koch et al. 1989), timing of maturation (Fisher 2008), and, potentially, inter-birth intervals (Fisher et al. 2008).

The content of this dissertation was shaped by the discovery of an unusual late Pleistocene mammalian site, the Bothwell Site. The Bothwell Site, located in the northwestern corner of Indiana (Hebron, Porter County), was discovered in 2005 during excavation for a pond on private property. The site yielded over 300 skeletal elements from a variety of late Pleistocene mammalian fauna, including *Castoroides* and artiodactyls, but most of the material belonged to mastodons. Notably, 13 mastodon tusks were recovered, indicating the presence of seven to 13 individuals. A site with multiple mastodons is rare, and its discovery raises a number of questions pertaining to the processes of site formation, including whether these mastodons were victims of a single, catastrophic event. If Bothwell mastodons died in a catastrophic event, then they would have been together when they died, which raises an additional question: were these individuals associated during life? If Bothwell mastodons did not die in a single, catastrophic event, then it is not likely that there were life associations among them, and other scenarios of site formation (e.g., natural trap, Paleoindian meat cache) need to be considered.

Mastodon social structure is unknown, but the behavior of modern elephants, their closest living relatives, can be used to formulate hypotheses about mastodon behavior. Furthermore, modern elephant life history can be used as a guide for interpreting patterns in mastodon tusk records that may be related to life events. Adult female African (*Loxodonta africana*, *Loxodonta cyclotis*) and Asian (*Elephas maximus*) elephants both live in matriarchal family units consisting of related females and their juvenile offspring

(Moss 1988; Vidya and Sukumar 2005). Females live in the family they are born into for their entire lives. Males live in matriarchal family units until their early teenage years, when they attain sexual maturity. At this point they leave their family unit, either willingly or by expulsion. After separation from their family units, their social affiliations depend on whether or not they are in musth, a period of sexual activity and heightened aggression that may last for months (Eisenberg et al. 1971; Poole 1994). Adult males and females are found in association with one another only when males are in musth. In a non-musth state, males live alone or in loose association with other non-musth males.

Elephants are polygynous, but non-territorial, allowing males to maximize opportunities for reproductive success. Female elephants come into estrous about every three to five years (Moss 1983), so a male that permanently lived with and defended a single family unit would have fewer opportunities for producing offspring than a non-territorial male. Furthermore, a non-territorial, polygynous male invests no energy in the rearing of his offspring (Poole 1994), whereas a male in a harem system invests energy into the defense of his family.

Males rely on large body and tusk size for reproductive success. Male elephants grow in stature throughout most of life (Lee and Moss 1995), and tusks are ever-growing, so older males have larger bodies and tusks than younger males. Bull elephants battle for access to oestrus females, and females seem to prefer larger bulls (Moss 1983), so older (larger) males have an advantage over younger (smaller) males for mate acquisition (Lee and Moss 1995). In this system, males generally do not successfully mate until they are 35 to 40 years of age, long after they first attain sexual maturity (Poole 1987).

For female elephants, reproductive success does not depend on tusk size. The primary function of tusks in females is food gathering, although they are also used for defense against predators and to intimidate other, smaller females, away displacing them from high-value food and water sources (Moss 1988; Haynes 1991). Females have two options for reproductive success (Lee and Moss 1995). In the first option, first pregnancy is delayed until their bodies are larger and better equipped for the demands of a long gestation (20-21 months in Asian elephants, Sukumar 2006; 22 months average for African elephants, Moss 1983) and protracted lactation (4 years, on average; Lee 1986). This option results in a shorter reproductive lifespan for a female, but increases the likelihood that her calves will survive to adulthood. In the second option, females calve earlier in life, around age 10, when they are still increasing in stature relatively rapidly. This results in a longer reproductive lifespan for a female, but the energetic costs of growth, added to those of reproduction and lactation, result in lower rates of calf survival (Lee and Moss 1986). Females have been known to give birth to their first calf at as young as 8.9 years, but most do not experience give birth until 3 to 6 years later (Moss 2001).

Raising a male calf is more stressful on an elephant mother than raising a female calf, because males nurse more frequently and have higher milk intake during the first three years of life in order to accommodate rapid early growth (Lee 1986; Lee and Moss 1986). The higher energetic investment in male calves is important for their future reproductive success, because males that do not begin growing quickly from birth will be smaller than their male competitors as adults and be at a disadvantage when they enter into battles for access to mates (Lee and Moss 1986). As a result of the greater

investment in male calves, the inter-birth interval is slightly longer for a mother when her first calf is male (Lee and Moss 1986). The greatest increase in inter-birth interval length, however, occurs due to environmental conditions. During wet periods, when vegetation is readily available, the mean inter-birth interval for a female is 3.5 years; during dry periods, when nutrients are scarcer, the mean interval increases to 5.6 years (Lee and Moss 1986).

Based on elephant social structure, if mastodons at the Bothwell Site were together when they died, they must have been members of a single family unit. To test this hypothesis, several questions are important to resolve. First, how can the sex of a mastodon be reliably determined from the tusk alone? Second, does the sex and age distribution of mastodons at Bothwell reflect that of an elephant family unit? Third, is there evidence that mastodons exhibited similar social structures similar to those of elephants? Finally, did the Bothwell mastodons die in a single, catastrophic event? This dissertation addresses these four questions by applying morphological, serial stable isotope, and growth increment analyses to tusks from the Bothwell site, tusks from additional Great Lakes-region mastodons, and tusks from African savannah and forest elephants. In addition, long-term stable isotope and growth increment records from female mastodon tusks were compiled to expand knowledge of female mastodon life history, with the specific goal of identifying patterns in these records that could be related to gestation and lactation. The results of these analyses are presented in four chapters, described as follows.

Chapter 2 focuses on development of a reliable method for identifying the sex of a mastodon through tusk measurements. Prior to this study, the most robust methods for

evaluating sex from tusk measurements required knowledge of age. Tusks exhibit indeterminate growth and change in size and shape throughout life, so although mastodons clearly exhibit tusk dimorphism, it is difficult to distinguish between the tusk of a young male and the tusk of an older female that exhibit similar morphologies. This issue is addressed through principal components analyses that incorporate two types of variables: (1) anatomical variables, that assess distinct aspects of tusk size and shape at the time of death, and (2) longitudinal variables, that reflect a sequence of ontogenetic change in a single tusk variable.

Chapter 3 addresses the question of whether it is reasonable to use elephants as behavioral models for mastodons. The two living proboscidean genera, *Loxodonta* and *Elephas,* diverged from a most recent common ancestor approximately five million years ago, and strong similarities in their life histories, social structures, and reproductive strategies are proposed to have emerged prior to the common ancestor of the two (Haynes 1991). Mastodons and elephants diverged from their most recent common ancestor over 20 million years ago (Gheerbrant and Tassy 2009), so it is possible that unique social and behavioral traits developed in each lineage since this divergence. Aspects of social structure, reproductive strategies, and parental investment can be inferred for mammalian species based on degree of sexual dimorphism, when males are larger than females. The goal of this chapter is assess morphological similarities in tusk dimorphism between *Loxodonta* and *Mammut*, which would provide a basis for inference of similar behavioral traits. Tusk dimorphism is characterized for each genus individually through discriminant function analysis of linear and curvilinear tusk variables, and dimorphisms are compared between genera through canonical variates analysis of the same tusk variables.

Chapter 4 explicitly addresses questions pertaining to formation of the Bothwell Site. Bothwell mastodon tusks are evaluated through a series of morphometric, stable isotope ($\delta^{18}O$, $\delta^{13}C$, $\delta^{15}N$), and growth increment analyses to determine: (1) number of individuals, (2) sex distribution, (3) age distribution, (4) season – or seasons – of death, and (5) simultaneity of death. Results of these analyses can be used to evaluate whether these mastodons were members of a single matriarchal family unit. Furthermore, tusk evidence is used to evaluate potential scenarios for causes of death, including a natural trap, death by nutritional stress, and death by human influence. Studies of single sites, like Bothwell, contribute to the larger goal of evaluating patterns of mortality and population dynamics for late Pleistocene mastodons.

Chapter 5 presents long-term growth and stable isotope ($\delta^{18}O$, $\delta^{13}C$) records from the tusk dentin of two female American mastodons, Bothwell 2-14 (northwestern Indiana) and New York State Museum V50 (southeastern New York State). Female mastodons have been less numerous in the fossil record than male mastodons, so more tusk studies have focused on males than on females. Prior to this dissertation, the complete growth record of only one female mastodon tusk had been compiled at the annual and fortnightly level (Fisher et al. 2008), and no stable isotope records were compiled for this individual. In the prior study, periodic oscillations in annual increment thickness were tentatively interpreted as resulting from the effects of gestation and lactation on the growth record. These periodic oscillations, or calving cycles, had also been noted in the annual-increment length growth records of other Great Lakes-region females (Fisher 1996). In this chapter, annual and fortnightly growth increment records, as well as stable isotope records, are investigated for evidence of reproductive events.

The results of this study substantially increase the number of detailed female mastodon tusk records and expand the geographic region of mastodons for which tusk records have been compiled.

This dissertation concludes with Chapter 6, which summarizes the contributions of this study to mastodon paleobiology and proposes directions of future research. This dissertation does not presume to determine the cause of late Pleistocene mastodon extinctions, but provides new insights into the study of female mastodon life history that can be used to explore the ecology, evolution, and extinction of the species. These insights are put in context with previous studies in order to explore broader patterns of life history and mortality for late Pleistocene mastodons.

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Chapter 2

Sexual dimorphism of structures showing indeterminate growth: tusks of American mastodons (*Mammut americanum*)[1]

Abstract

Documenting sexual dimorphism for structures that exhibit indeterminate growth can be more difficult than for structures exhibiting determinate growth. Most proboscidean tusks are ever-growing structures that change size and shape throughout life. Sexual dimorphism is pronounced in tusks of mature individuals, but the external form of tusks offers no clear evidence of maturation, and it is difficult to distinguish a young male's tusk from that of an older female. Thus, with previous approaches, knowledge of age was often required to assess sex from tusk measurements. This study examines sexual dimorphism of American mastodon (*Mammut americanum*) tusks through principal components analysis to determine which aspects of tusk form contribute most strongly to the variance among measurements and to explore the relationship between tusk form and individual age and sex. Twenty-one mastodon tusks from the Great Lakes region were evaluated in two analyses, the first focusing on geometrically distinct aspects of tusk form and the second adding measurements that reflect ontogenetic changes in a single aspect of morphology (circumference). Both analyses separated mastodons by sex (PC-I) and sorted them by age (PC-II). The

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distribution of tusks on the PC-II vs. PC-I plane provides better discrimination of sex than univariate or bivariate methods because tusks of similar size and opposite sex appear near opposite ends of an age spectrum. The second analysis enhances sorting by age, thereby clarifying assessment of sex. This work contributes to studies of mastodon paleobiology by presenting a reliable method for assessing the sex of an individual from tusk measurements without requiring independent knowledge of age.

Introduction

Most studies of sexual dimorphism deal with structures that exhibit determinate growth. These structures cease changing in size and shape at some point in life generally associated with maturation, so comparisons of morphology among individuals in strongly dimorphic species typically result in bimodal distributions of measurements. Examples of such studies include work on Eocene horse canines (Gingerich 1981), long bones of a Miocene rhinoceros (Mead 2000), and crania of polar bears (Derocher et al. 2005). Not all dimorphisms, however, yield to simple attempts to attribute two forms to two sexes. Proboscidean tusks (enlarged incisors, to put them in anatomical context) differ from most mammalian dental and skeletal structures in that they are ever-growing and subject to increase in size and change in shape throughout life. Tusks show pronounced differences in morphology attributable to sex, but because a series of tusks at successive stages in ontogeny exhibits a spectrum of sizes and shapes, tusk dimorphism is not revealed as a univariate or even bivariate bimodal distribution, but rather as partly discrete and partly overlapping ontogenetic trajectories. Additionally, indicators of maturity comparable to epiphysis fusion in mammalian skeletons are not evident

externally in tusks, so it is sometimes hard to distinguish tusks of mature and immature individuals as well as those of males and females. The goal of this study is to address the challenges of identifying the sex of proboscideans – specifically, American mastodons (*Mammut americanum*) – through measurements of tusk morphology, when age and degree of skeletal maturity are unknown.

Mastodons were prominent members of the North American Pleistocene fauna until their extinction at the end of the epoch. Studies of mastodon paleobiology have sought to recognize causes of this extinction through assessment of individual life histories (e.g., Fisher 1996, 2009). Life events, such as pregnancy for a female (Fisher et al. 2008a) and musth for a male (Fisher 2008), may be recognized by structural and compositional analysis of the growth record of tusk dentin, in which annual, fortnightly, and daily increments are preserved. A critical step in this analysis is identification of the sex of the mastodon, particularly when considering events unique to each sex, because misidentification of sex could result in misinterpretation of these events. Identification of life events in the tusk record could provide a basis for evaluating proposed mechanisms of mastodon extinction because changes in timing of these events can be interpreted as responses to external factors. For example, African savannah elephants respond to environmental stress by extending inter-birth intervals (Lee and Moss 1986), and to nutritional stress by delaying onset of musth (Poole 1987). Analyses of mastodon life history, with elephant behavior as a predictive model, can be used to evaluate the nature of the environment at the end of the Pleistocene and thus assess its potential for contributing to mastodon extinction.

An important aspect of sexual dimorphism in mastodons and elephants is sex-related differences in body size. Size dimorphism in modern elephants is a result of differing growth rates in males and females, with males growing faster and reaching determinate body size later in life than females (Lee and Moss 1995). The amount of energy dedicated to growth reflects the unique requirements of reproductive success for each sex. For males, reproductive success increases with body size (Poole 1994), whereas lower growth rates in females are associated with diversion of energy from growth to reproduction (Lee and Moss 1995). Sexual dimorphism in elephant tusks is partly a reflection of differences in body size – comparing males and females of similar age, males do generally have larger tusks – but the differences also include aspects of tusk form (Elder 1970). In American mastodons, size dimorphism is pronounced, with adult males 1.15 to 1.25 times larger (in linear dimensions) than adult females, and tusk dimorphism reflects these size differences, though again with differences in shape that are the subject of this study. The existence of tusk dimorphism in mastodons is not in question. It can be seen most easily in a bivariate context when even a single tusk variable such as circumference at the gingival margin is plotted against individual age, estimated from the number of annual increments in the tusk, if this is known, or expressed in terms of relative age classes based on the stage of eruption and wear of associated cheek teeth (Fisher 2008). However, for many tusk specimens, age data are not readily available, either because annual increments have not yet been analyzed, or because neither cheek teeth nor other indicators of age were found in association. Our goal in this study is to achieve a more comprehensive understanding of patterns of variability in tusk form, which might provide a method of identifying sex without prior

knowledge of age. If this works, it may also be applicable to other proboscideans, and perhaps to other structures exhibiting indeterminate growth.

Proboscidean Tusk Growth

Mastodon tusks are composed primarily of dentin, with lesser amounts of cementum and enamel. Cementum forms within the alveolus, on the exterior of dentin, and is subject to abrasion after eruption. Enamel is present only at the tusk tip and is abraded away early in life. Tusk dentin is added within the pulp cavity as a series of conical layers. Each subsequent layer lines the walls of the former pulp cavity, extends the tusk proximally, and defines a new pulp cavity offset in a proximal direction from the old. Dentin apposition is coupled with tusk eruption, resulting in exposure of additional tusk material at the alveolar margin. Dentin formed early in life is thus located near the tip, and dentin formed at the end of life lines the pulp cavity.

Tusks change their size and shape during ontogeny by a combination of additive and reductive processes. Although these processes seem simple, they sometimes interact in complex ways, generating variation in standard descriptors of tusk form. Deposition of dentin ordinarily increases tusk length as it adds to the local thickness of dentin, but the processes controlling these two components of growth are geometrically and physiologically distinct. The rate of increase in tusk length is determined by differentiation of new odontoblasts along the proximal margin of the tusk, whereas the rate of increase in dentin thickness is determined by the appositional output of active odontoblasts (Fisher 2001, 2008). The rate of increase in tusk length typically declines slowly throughout post-juvenile life, but the rate of dentin apposition is relatively

constant and usually does not decline appreciably until an animal reaches advanced age. The relatively constant rate of inward dentin apposition combined with the decline in annual increases of tusk length leads to a decrease in depth of the pulp cavity late in adult life. Documenting this pattern is complicated (see Fisher et al. 2008a for a detailed description) because rate of apposition varies proximodistally within the pulp cavity at any one time. Expressed in terms of the path of a single odontoblast moving from the cementum-dentin junction to the tusk axis, rate of apposition first increases, then maintains a relatively constant value (for roughly half its path length), then decreases again as it approaches the tusk axis. Focusing on the zone of relative constancy, and comparing annual increment thickness from year to year, rate of dentin apposition does not appreciably decrease until late in adult life.

There is also a decrease in tusk girth late in adult life. Tusk girth is determined by the number and dimensions of newly differentiated odontoblasts, as each cohort of odontoblasts forms at the proximal margin of the tusk. Once these odontoblasts begin depositing dentin, circumference at this point on the tusk is fixed, except for increases in cementum thickness. Cementum apposition does increase tusk circumference slightly, but cementum is only added between the proximal and alveolar margins of the tusk and (in mastodons) achieves a thickness of no more than about five millimeters.

Reductive processes include generalized abrasion of the external surface of the erupted part of a tusk and discrete episodes of tip breakage, in the wake of which abrasion near the tip may be accelerated. Abrasion clearly reduces tusk girth locally, especially near the tip, and could reduce tusk length, but this reduction tends to be gradual. In contrast, tip breakage is abrupt, and most directly affects tusk length.

However, tip breakage has an indirect effect that derives from the fact that some measurements include the tusk tip as one terminus. A single breakage event, by displacing this reference point in a proximal direction, tends – given the conical geometry of tusks – to shift tusk girths (measured at a certain distance from the tip) to larger values than would have been observed before the break. The increase is in a sense artificial because it is driven by no actual addition of dentin or cementum – only by a shift in the frame of reference with respect to which girth is measured. It is reasonable to ask whether this sensitivity to breakage events could be avoided by another choice of reference frame, but one option, the proximal margin of a tusk, changes its position continually, yielding an even less stable basis for comparison. On tusks of individuals that live into late adulthood, there is typically, as noted above, a zone of declining girth proximal to the point of maximal girth. Although the point of maximal girth might seem attractive as a landmark in the ontogeny of an individual, there is no guarantee that this point represents the same developmental stage in males and females, and it would limit analysis to tusks large enough to have grown beyond the stage of maximal girth. Choice of the tusk tip to define a reference frame, though imperfect, keeps the reference point in a relatively constant ontogenetic position. If substantial breakage occurs, it will tend to show up as abnormally large girths, unusually close to the tip.

Sexual Dimorphism in Proboscidea

Slight differences in growth rate between male and female African elephant calves are apparent even from birth, with body size dimorphism noticeable by ten years (Lee and Moss 1995). Body size dimorphism extends to tusk size (Elder 1970), and

measurements of tusk morphology have been successfully used to sex living elephants (Pilgram and Western 1986). In both elephants (Laws 1966; Elder 1970; Pilgram and Western 1986) and mastodons (Fisher 1996; Smith and Fisher 2007; Fisher 2008), tusks of males increase in circumference more rapidly with respect to length than do tusks of females. A number of tusk dimensions exhibit sexual dimorphism, but the relationship between alveolar circumference and age generally allows clear discrimination between males and females (with tusks of males more robust than those of comparably aged females), both in elephants (Elder 1970) and in mastodons (Fisher 2008). Other dimensions that exhibit sexual dimorphism include the axial depth of the pulp cavity (greater in males than in comparably aged females); the ratio of pulp cavity depth to alveolar depth (greater in males); maximum tusk circumference (greater in males); the angle at the distal end of the pulp cavity (greater in females, in part as a consequence of shorter pulp cavities); and the angle between the pulp cavity and the tusk exterior at the proximal end of the tusk (greater in females; Smith and Fisher 2007; Fisher 2008). When possible, assessment of sex based on tusk morphology has been corroborated with postcranial skeletal elements that also exhibit sexual dimorphism (Fisher 2008).

As implied above, the sex of a mastodon can often be determined by examining the relative positions of the distal end of the pulp cavity and the alveolar margin. In males the distal end of the pulp cavity often extends beyond the alveolar margin, whereas in females the distal end of the pulp cavity is usually proximal to the alveolar margin (Fisher 2008). This pattern is observed in African elephants, in which the "lip line," or gingival margin, has been used in place of the alveolar margin (Elder 1970). However, this criterion has limits too, as pulp cavities of young males do not extend beyond the

alveolar margin, and with shortening of pulp cavities in old age, old males may also have pulp cavities that do not reach the alveolar margin.

Evidence of age increases the certainty of sex discrimination for any method used. Because tusks show indeterminate growth, tusks of mature mastodons exhibit a wide range of sizes within each sex. Furthermore, individuals of different ages and sexes can exhibit similar morphologies, especially with respect to tusk length and girth. In particular, tusks of adult females outwardly resemble those of younger males (Fisher 1996, 2008). Therefore, it is useful to have at least a rough estimate of age to reduce the possibility of misidentifying a young male as an adult female. However, as noted above, evidence of age is not available for all tusks we would like to assign to sex, and our goal here is to develop a method that works without prior knowledge of age.

Materials and Methods

Materials

Twenty-one American mastodon tusks were evaluated in this study (Table 2.1). The sample was limited to post-Last Glacial Maximum (LGM) mastodons of the Great Lakes region in order to minimize variation in tusk morphology due to regional or temporal differences. Mastodons in this study for which direct radiocarbon dates (on collagen) are available show an age range of approximately 10,395 to 12,170 radiocarbon years before present (Table 2.1; Holman et al. 1986; Fisher 2009). Mastodons in this study without radiocarbon dates are interpreted as post-LGM based on stratigraphic context, location of recovery, and the tightly constrained range of radiocarbon age estimates for mastodons of this region. Each tusk is treated as representing a separate

individual, either because it is the only tusk recovered from a site, because it is one tusk of a known pair, or because it is morphologically distinct (beyond left-right symmetry) from other tusks at the site where it was recovered. The only difficult choice involved SMM 64-14-1 (L) and (R), identified in collection data as a tusk pair. However, since they differed in curvature, and there was no associated material to corroborate derivation from a single individual, both tusks were included.

To evaluate the consistency of results a posteriori, we examined univariate distributions of values of maximum tusk circumference and axial depth of the pulp cavity (Fig. 2.1), interpreted with respect to prior bivariate studies of tusk circumference and age and post-cranial evidence of sex. In retrospect, based on size and age comparisons with mastodons with documented life histories and age estimates, each tusk in Table 2.1 was likely from a sexually mature individual, but it was important not to assume this from the beginning. Age estimates were available for some but not all tusks, and were used only for a posteriori evaluation of patterns.

Tusks are fragile at their proximal margin because both dentin and cementum are just beginning to be deposited along this locus. Especially on a tusk that has come out of its alveolus, the proximal margin frequently exhibits some breakage, but the angular relationship between the pulp cavity surface and the external tusk surface permits the location of the proximal margin to be reasonably constrained. Length measurements that refer to this margin (alveolar depth, pulp cavity depth, tusk length) may require some estimation, but associated uncertainties are rarely greater than one centimeter.

Table 2.1. Mastodons used in this study. Sex-1 lists sex assignment based on prior work utilizing non-tusk dental evidence of age (^{D}), associated skeletal remains (^{S}), or position within the univariate distributions (^{U}) of Figure 2.1. Sex-2 lists sex assignments determined from tusk morphology alone, in this study. Radiocarbon age estimates as in Holman et al. (1986) and Fisher (2009). Age is the number of annual increments in tusk dentin on the tusk exterior (^{E}) or on a longitudinal section (^{L}). PRI = Paleontological Research Institution, Ithaca, NY; INSM = Indiana State Museum, Indianapolis, IN; UMMP = University of Michigan Museum of Paleontology, Ann Arbor, MI; MSUVP = Michigan State University Vertebrate Paleontology Division, East Lansing, MI; FMNH = Field Museum of Natural History, Chicago, IL; SMM = Science Museum of Minnesota, St. Paul, MN; BMS = Buffalo Museum of Science, Buffalo, NY.

Specimen	Abbreviation	Sex-1	Sex-2	State	Institution	C-14 Age	Age
Hyde Park	HP	$M^{D,S}$	M	New York	PRI	11,480	$32^{E,L}$
Buesching	Bues	$M^{D,S}$	M	Indiana	INSM	?	$32^{E,L}$
Pleasant Lake	PL	$M^{D,S}$	M	Michigan	UMMP	10,395	40^{E}
Heisler	Heis	M^{D}	M	Michigan	UMMP	11,380	$16^{E,L}$
North Java	NJ	F^{D}	F	New York	PRI	11,630	$34^{E,L}$
Powers	Pow	$F^{D,S}$	F	Michigan	UMMP	11,220	30^{L}
Laur	Laur	F^{D}	F	Michigan	UMMP	?	27^{L}
Miller	Mill	F^{D}	F	Michigan	UMMP	12,170	16^{L}
Sheathelm	Shea	F^{D}	F	Michigan	MSUVP	10,840	20^{E}
Bothwell 2-14	2-14	F^{U}	F	Indiana	INSM	?	22^{L}
Bothwell Pen-51	Pen-51	F^{U}	F	Indiana	INSM	?	31^{L}
FM 26631	FM	F^{U}	F	Illinois	FMNH	?	?
SMM 64-14-1 (L)	SMM (L)	F^{U}	F	Minnesota	SMM	?	?
SMM 64-14-1 (R)	SMM (R)	F^{U}	F	Minnesota	SMM	?	?
J3SW-186	186	F^{U}	F	New York	BMS	?	?
I3NW-117	117	M^{U}	M	New York	BMS	?	?
I2SE-113	113	M^{U}	M	New York	BMS	?	?
I2NE-170	170	M^{U}	M	New York	BMS	?	?
F10SW-71	71	F^{U}	F	New York	BMS	?	?
I3NW-110	110	F^{U}	F	New York	BMS	?	?
F9SW-106	106	F^{U}	F	New York	BMS	?	?

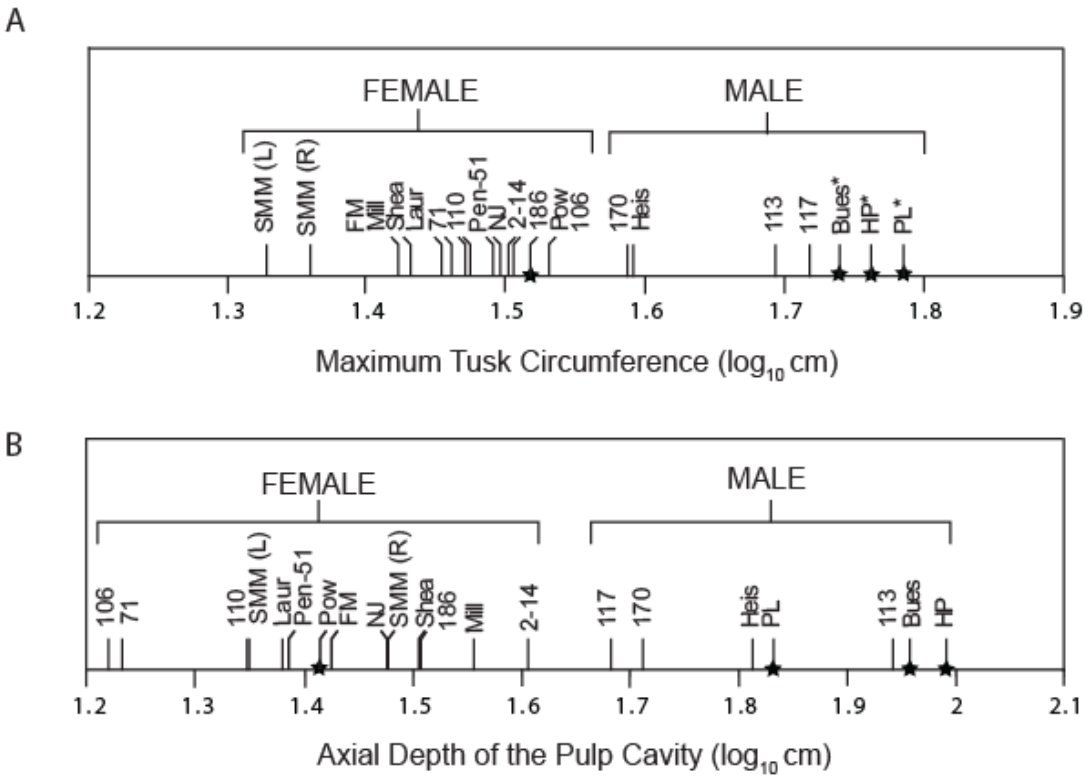

Figure 2.1. Plots of (A) maximum tusk circumference and (B) axial depth of pulp cavity for the twenty-one tusks listed in Table 2.1. Stars indicate mastodons for which sexual dimorphism has been identified in postcranial elements (Fisher 2008). Abbreviations as in Table 2.1.

Methods

The method used in this investigation is principal components analysis (PCA). PCA reduces the dimensions of variation among individuals, potentially illuminating relationships that might not have been apparent in the original, more highly dimensional, data (Zelditch et al. 2004). PCA constructs multiple, independent axes that are linear combinations of original variables (with the first axis describing the greatest proportion of variance) and calculates loadings that indicate the amount of variance contributed by each original variable to a given axis. Scores are computed for each specimen along each axis, and the plots of these scores yield patterns that can be explored to provide insight into biological questions (Zelditch et al. 2004). PCA of skeletal proportions has been used to interpret biological and functional aspects of modern and fossil organisms, including sexual dimorphism (Chapman et al. 1981; Mills 2008) and locomotion (Gingerich 2003; Bebej 2009). As discussed below, we had evidence for sex assignment for all tusks in this study (Fig. 2.1), but a multivariate analysis that explores differences among a priori groups (e.g., canonical variates analysis) was not undertaken here because our goal was to explore patterns of variation without assuming the validity of prior results.

Measurements used in this analysis are conventional morphometric variables as defined by Zelditch et al. (2004). Features that might be considered landmarks (e.g., the apex of the pulp cavity) are used to define the variables, but a landmark approach was not adopted here because few landmarks are available and some tusk dimensions cannot be captured by projection onto a plane. For example, one aspect of a tusk's size and shape is its extent in directions locally perpendicular to its structural axis. However, tusk cross sections may be circular, elliptical, or even less regular, and in the latter cases, the major

axis does not always have an identical orientation relative to a fixed plane in which measurement might occur. Circumference summarizes this variability in a single value but is not extractable as a two-dimensional distance between landmarks. In addition, the asymmetry sometimes observed for paired tusks suggests that configuration in three dimensions (projected into two) may be less important than variation along the length of a tusk's structural axis. Measurements in this study use distance from the tip along the outside curve of the tusk as a primary reference dimension – an operational proxy for position along the structural axis.

Anatomical Variables.–Five measurements that assess geometrically distinct aspects of tusk size and shape at the time of death (Fig. 2.2) were collected on each of the twenty-one tusks (Smith and Fisher 2007; Fisher 2008; this study) in Table 2.1. These measurements (axial depth of pulp cavity, alveolar depth, alveolar circumference, maximum tusk circumference, and tusk length) are here referred to as anatomical variables. See Appendix I for additional notes on these variables.

Longitudinal Variables.– Five additional variables were chosen to reflect ontogenetic change in a single aspect of tusk morphology – circumference. These are values of tusk circumference at 50, 60, 70, 80, and 90 cm from the tusk tip (Fig. 2.2). Because tusks increase in length throughout life, different positions along a tusk represent different times in life. These five variables show how tusk circumference changed from earlier (closer to the tip) to later (farther from the tip). They are referred to as longitudinal because they track tusk circumference (essentially, as measures of former values of alveolar circumference) at successive times in the life of the same mastodon, just as a longitudinal study tracks a single individual through successive times in its life. Due to

differences in growth rate or history of tip breakage, longitudinal variables do not generally represent the same points in ontogeny on each tusk, but they still offer access to an ontogenetic trajectory. Locations of longitudinal variables were chosen to meet the requirement of repeatability for a principal components analysis. The smallest tusk in the data set is just under 100 cm, so 90 cm is the maximum distance from the tip that can be included. Additionally, measurements close to the tip are more likely to be affected by tusk wear, so measurements closer to the tip than 50 cm were excluded to diminish the effect of wear on tusk size and shape.

Longitudinal variables were added to this study because they explicitly incorporate an aspect of ontogenetic change. Tusk growth profiles illustrating the change in circumference with respect to distance from the tusk tip have been shown to discriminate between adult male and adult female mastodons (Fisher 1996; Fisher 2008). Tusks of males increase in circumference more rapidly with respect to length than tusks of females, and although tusk circumference for both males and females reaches an approximately stable value at some point during ontogeny, tusks of females attain this stability at an earlier ontogenetic stage and at a smaller absolute size. The magnitude of change between circumference at 50 cm and at 90 cm can be used to evaluate sex, as the circumference of a male mastodon tusk shows a greater increase than the circumference of a female mastodon tusk over this range of distances from the tip.

Original measurements in cm were log-transformed because the normality of biological variation is geometric (Gingerich 2000); transformation thus tends to equalize variances among measurements spanning a wide range of values. Measurements were

log_{10}-transformed so that values were easier to relate to original measurements. A complete list of specimens and measurements is included in Appendix II.

Analysis.–Two PCAs were performed, the first incorporating the five anatomical variables, a collection of geometrically distinct aspects of tusk form with no inherently ontogenetic signal embedded within them. The second incorporated both anatomical and longitudinal variables. Rather than simply duplicating the result of the first PCA, the second analysis was intended to assess how the addition of longitudinal variables, individually reflecting a single aspect of tusk form (alveolar circumference) at a succession of times in life and collectively reflecting a sequence of ontogenetic change, might differ from the first analysis with its reliance on the more "ahistorical" anatomical variables. Tusk measurements were compared using principal components analyses of the covariance matrix of log_{10}-transformed measurements. Analyses were conducted using the "princomp" function in the statistical program *R* (RDCT 2006).

A posteriori comparisons.– As explained elsewhere, this study differs from prior treatments of sexual dimorphism in mastodon tusks by not relying on evidence of age or measurements of associated skeletal remains to infer sex. However, this study seeks to compare outcomes of earlier methods (Table 2.1, column "Sex-1") with outcomes from the methods presented here (Table 2.1, "Sex-2"). In one prior analysis (Fisher 2008, text-fig. 14), nine of the tusks included here were assigned a sex based on a bivariate plot of alveolar circumference relative to Laws' Age Group (a series of relative age categories based on cheek took eruption and wear; Laws 1966). In the same study, four of these nine tusks were also sexed based on comparative measurements of associated skeletal remains (Fisher 2008, text figures 11 and 12). The remaining twelve tusks, considered here for

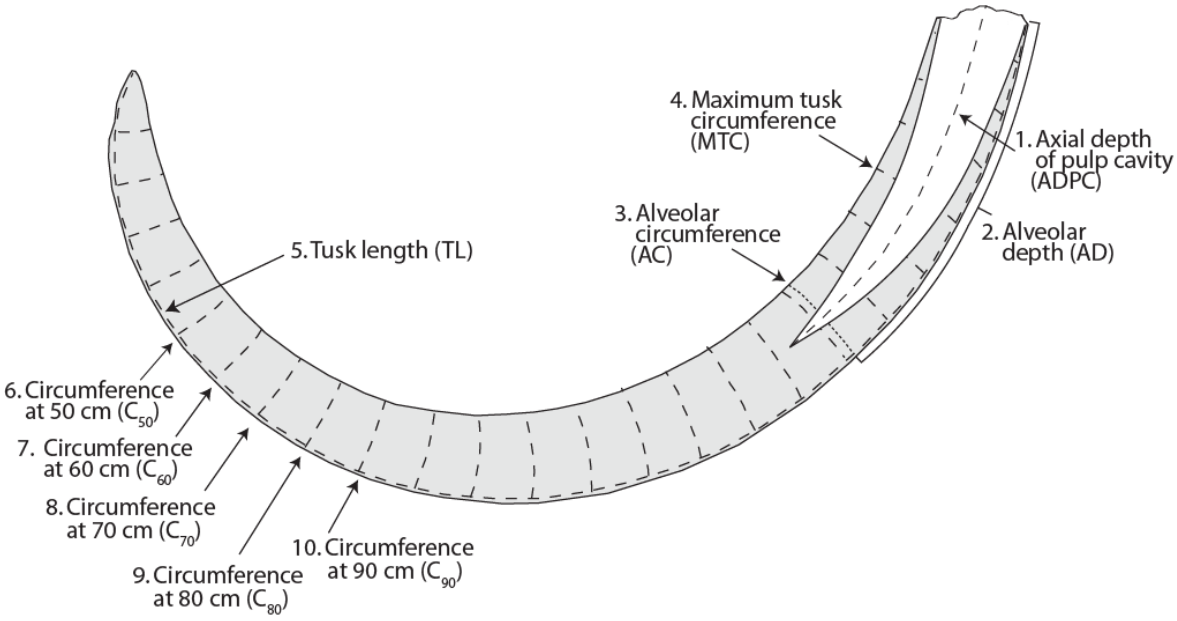

Figure 2.2. Measurements used in this study. Variables one through five are the anatomical variables used in the first analysis; variables six through ten are the longitudinal variables used in conjunction with the anatomical variables in the second analysis. The short, dashed lines that are approximately perpendicular to tangents to the outer curve of the tusk represent circumference measurements taken at 10-cm intervals along the outer curve.

the first time, have none of the associated dental or skeletal material on which prior sex determinations were based. In order to view them in the context of prior results, univariate distributions of maximum tusk circumference and axial depth of the pulp cavity for the new specimens were plotted along with data from specimens previously assessed for sex (Figs. 1A and 1B, respectively). There is no obvious gap between sexes on either univariate plot in Figure 2.1, exemplifying the difficulty of recognizing tusk dimorphism as bimodality. Indeed, we would not expect a gap in any suite of specimens covering the full range for both sexes (i.e., very young males would have values of MTC and ADPC overlapping those of females). Nonetheless, tusks in our sample that had prior sex assignments happen to fall into discrete regions of each plot. Tusks with cheek tooth and skeletal evidence of sex (Fisher 2008) that plot where overlap might occur include two females, Powers and Miller, and one male, Heisler. Bothwell 2-14 has a smaller tusk girth than Powers (Fig. 2.1A), and given her age estimate, is likely to be female; this suggests she might mark the upper end of the female bracket in Figure 2.1B. F9SW-106 appears well within the female bracket of Figure 2.1B and thus might be considered to mark the upper end of the female bracket in Figure 2.1A. Likewise, I3NW-117 has a larger tusk girth than Heisler, is probably male, and is thus taken as marking the lower end of the male bracket in Figure 2.1B. I2NE-170 has a deeper pulp cavity than I3NW-117, is probably male, and is thus taken as marking the lower end of the male bracket in Figure 2.1A. Following this pattern, tentative assignments for specimens analyzed for the first time here are indicated by a superscript “U” in Table 2.1, column Sex-1.

Structures that grow by apposition retain ontogenetic changes in form within their structure, so age information, even if only in a relative sense, may emerge from this

study. As with prior sex assignments discussed above, previously determined age estimates (for eleven mastodons; Table 2.1) were used only for a posteriori evaluation of patterns. The age of a mastodon can be assessed by counting the number of annual increments in tusk dentin, though age determined in this way is a minimum, because years may be lost by tip fracture or abrasion.

Results

PCA of Anatomical Variables

The first PCA, which included the five anatomical variables and 21 tusks, resulted in two interpretable axes. Table 2.2 summarizes the variance associated with each principal axis that accounts for more than 1% of the variance among measurements. Scores for the first principal component (PC-I) and second principal component (PC-II) are plotted in Figure 2.3A. Loadings for each variable along each axis that accounts for more than 1% of the total variance are listed in Table 2.3, and those for PC-I and PC-II are plotted in Figure 2.3B-C.

PC-I, which accounts for 86.5% of the total variance among the measurements, sorts tusks by size and separates them into two groups that include respectively males (positive scores) and females (negative scores; Fig. 2.3A) according to prior determinations (Table 2.1). Because all loadings have the same sign (positive), it is likely that PC-I is a measure of overall size (Fig. 2.3B). To test this, an estimate of tusk volume was regressed on PC-I scores (mass would have been affected by preservational artifacts such as weathering). Tusk volume was estimated as the volume enclosed by four bounding surfaces: a distal cone from the tip to 50 cm back from the tip, a cylinder from

50 to 90 cm from the tip, a cylinder from 90 cm from the tip to the proximal margin, and a cone representing the pulp cavity. Volumes enclosed by the distal cone and the two cylinders were summed, and the pulp cavity volume was subtracted from this sum to obtain total volume. For the distal cone ($V = 1/3\pi r^2 h$), height (h) was 50 cm and radius (r) was the circumference at 50 cm divided by 2π. For the middle cylindrical segment ($V = \pi r^2 h$), height was 40 cm and radius was calculated from the circumference at 90 cm. For the proximal cylindrical segment, height was total tusk length minus 90 cm and the radius was calculated from maximum tusk circumference. For the pulp cavity segment, height was the axial depth of the pulp cavity and radius was calculated from maximum tusk circumference. Regression of $\log_{10}$-transformed tusk volumes on PC-I scores yielded an R^2 value of 0.840. The relationship between tusk volume and PC-I is significant ($p < 10^{-8}$), supporting the interpretation that PC-I is a good indicator of size.

Larger tusks may come from older mastodons, but this relationship, even if significant, might not be linear. The relationship between age and PC scores cannot be fully explored in this analysis because only eleven mastodons in the data set have age estimates. Nonetheless, these ages were compared with PC-I scores through a Kendall rank correlation test (conducted in R; McLeod 2005) in order to explore the possibility of an association between age and PC-I. There was not a significant relationship between PC-I scores and age for these eleven specimens, either as a group or for inferred males and females separately.

PC-II, which accounts for 8.6% of the total variance (Table 2.2), describes a shape contrast between both circumference (alveolar and maximum) and tusk length versus axial depth of the pulp cavity (Fig. 2.3C). Along this axis, tusks are sorted

Table 2.2. Summary of components that account for >1% of the variance in the analysis of anatomical variables (numbers one through five).

	PC-I	PC-II	PC-III	PC-IV
Proportion of variance	0.865	0.086	0.027	0.021
Cumulative proportion	0.865	0.951	0.978	0.999
Eigenvalue	0.102	0.010	0.003	0.002
Standard deviation	0.312	0.099	0.055	0.049

Table 2.3. Eigenvector coefficients (loadings) for principal axes that account for >1% of the variance in the analysis of anatomical variables (numbers one through five). Loadings for PC-I and PC-II are plotted in Figures 2.3B-C.

Loadings:

	PC-I	PC-II	PC-III	PC-IV
Axial depth of pulp cavity	0.701	0.684	0.002	-0.203
Alveolar depth	0.194	0.064	-0.400	0.888
Alveolar circumference	0.379	-0.483	-0.355	-0.279
Maximum tusk circumference	0.383	-0.411	-0.319	-0.115
Tusk length	0.425	-0.356	0.782	0.281

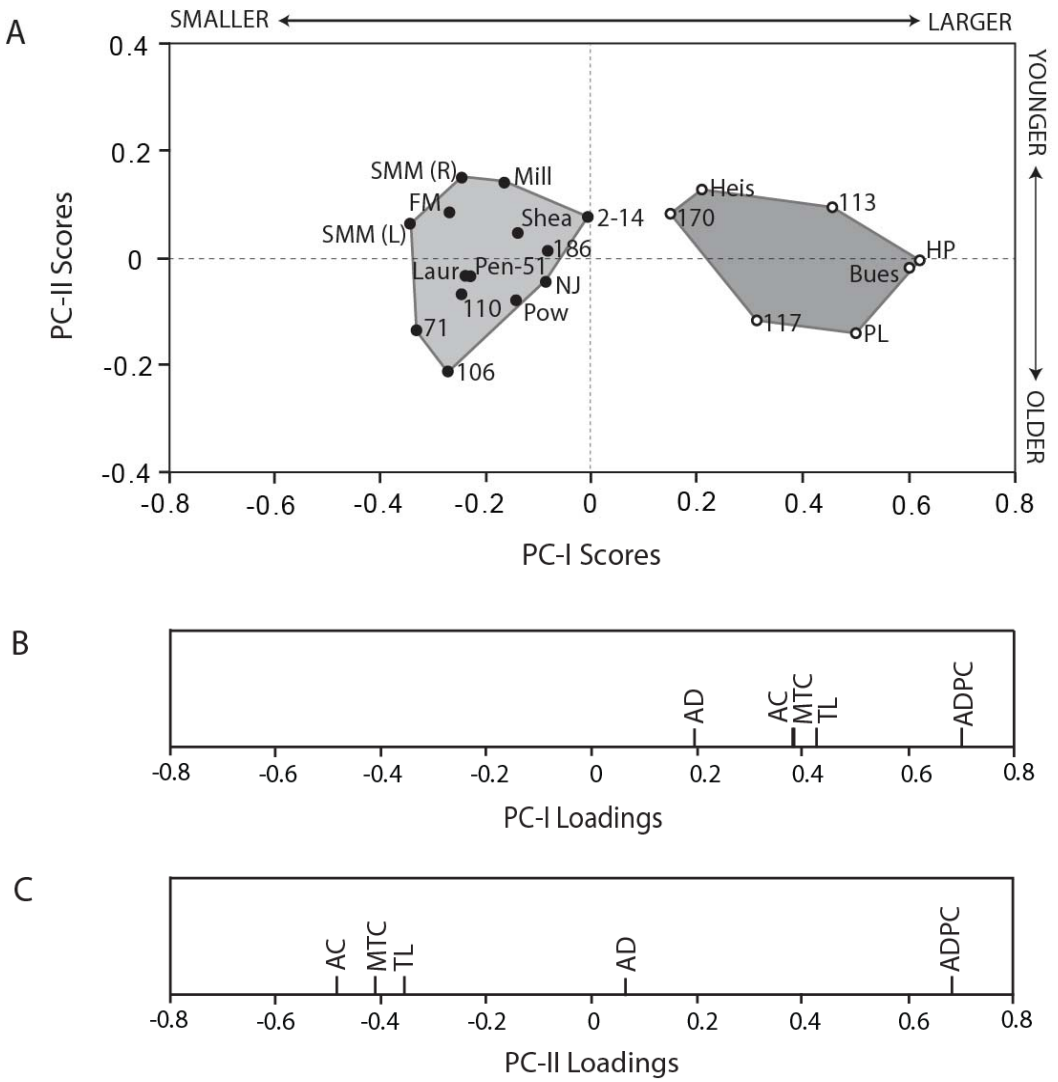

Figure 2.3. A) PC-II (8.6% of total variance) scores plotted against PC-I (86.5% of total variance) scores. Males are represented by open circles and females by closed circles. Abbreviations as in Table 2.1. B) Loadings for PC-I. C) Loadings for PC-II. Abbreviations as in Figure 2.2.

approximately by age, with older mastodons (more negative scores) that have longer tusks and larger girths relative to pulp cavity depth distinguished from younger ones (more positive scores) with shorter tusks and smaller girths relative to pulp cavity depth (Fig. 2.3A). Regression of $\log_{10}$-transformed tusk volumes on PC-II scores indicates no statistically significant relationship between volume and PC-II ($R^2 = 0.141$; $p = 0.093$). However, the Kendall test shows a significant association between PC-II scores and age ($\tau = -0.648$; two-sided $p = 0.008$) for the eleven specimens with age estimates.

PC-III and the remaining principal axes, both individually and cumulatively, account for less than 5% of the total variance. No reasonable interpretation could be applied to the sorting of tusks along these axes, so they are considered uninformative.

PCA of Anatomical and Longitudinal Variables

The second PCA, which included ten variables (five anatomical plus five longitudinal) and 21 mastodon tusks, produced two interpretable axes. Table 2.4 summarizes the variance associated with each principal axis accounting for more than 1% of the variance among measurements. Scores for PC-I and PC-II are plotted in Figure 2.4A. Loadings for each variable along each axis that accounts for more than 1% of the total variance are listed in Table 2.5, and those for PC-I and PC-II are plotted in Figure 2.4B-C.

PC-I, which accounts for 80.3% of total variance (Table 2.4), sorts tusks by size and separates them into two groups that include respectively males (positive scores) and females (negative scores; Fig. 2.4A) according to prior determinations (Table 2.1). Loadings for PC-I are all positive, and axial depth of the pulp cavity again makes the

greatest contribution to the variance accounted for by PC-I (Fig. 2.4B; Table 2.5). The contribution made by the longitudinal variables to variance along this axis depends on their distance from the tip of the tusk; the closer they are to the tip, the less they contribute to this axis. Regression of $\log_{10}$-transformed tusk volumes on PC-I scores indicates a significant relationship between volume and PC-I ($R^2 = 0.907$, $p < 10^{-10}$), but Kendall's coefficient of rank correlation does not indicate a statistically significant association between PC-I scores and age for the eleven specimens with age estimates.

PC-II, which accounts for 14.2% of total variance (Table 2.4), describes a contrast between axial depth of the pulp cavity and all measurements of tusk circumference (all five longitudinal variables, alveolar circumference, and maximum tusk circumference). This contrast, involving different variables from those that contrast to sort tusks along PC-II in the first analysis, still supports the interpretation that PC-II sorts tusks by approximate age. Older mastodons (more negative scores) have larger tusk circumferences relative to pulp cavity depth, and younger ones (more positive scores) have smaller tusk circumferences relative to pulp cavity depth. Longitudinal variables contribute less to variance along this axis the farther from the tusk tip they are located.

Regression of $\log_{10}$-transformed tusk volumes on PC-II scores indicates that there is not a significant relationship between volume and PC-II ($R^2 = 0.030$, $p = 0.456$), but there is a significant association between PC-II scores and age ($\tau = -0.500$; two-sided $p = 0.042$) for the eleven specimens with age estimates.

PC-III and the remaining principal components each account for less than 5% of total variance, and cumulatively account for just over 5% of total variance. No reasonable interpretation could be applied to these axes, so they are considered uninformative.

Table 2.4. Summary of components that account for >1% of total variance for the analysis of anatomical (numbers one through five) and longitudinal (numbers six through ten) variables.

	PC-I	PC-II	PC-III	PC-IV
Proportion of variance	0.803	0.142	0.028	0.017
Cumulative proportion	0.802	0.945	0.973	0.990
Eigenvalue	0.124	0.022	0.004	0.003
Standard Deviation	0.343	0.145	0.064	0.050

Table 2.5. Eigenvector coefficients (loadings) for principal axes that account for >1% of the variance among the measurements in the analysis of anatomical (numbers one through five) and longitudinal (numbers six through ten) variables. Loadings for PC-I and PC-II are plotted in Figure 2.4B-C.

Loadings:

Variables	PC-I	PC-II	PC-III	PC-IV
Axial depth of pulp cavity	0.601	0.667	-0.314	-0.239
Alveolar depth	0.173	0.096	-0.170	0.945
Alveolar circumference	0.364	-0.217	-0.020	-0.129
Maximum tusk circumference	0.364	-0.164	-0.007	0.021
Tusk length	0.387	0.021	0.882	0.064
Circumference at 50 cm	0.159	-0.364	-0.201	-0.100
Circumference at 60 cm	0.170	-0.358	-0.140	-0.103
Circumference at 70 cm	0.193	-0.297	-0.150	0.015
Circumference at 80 cm	0.212	-0.271	-0.104	0.027
Circumference at 90 cm	0.241	-0.221	-0.028	0.083

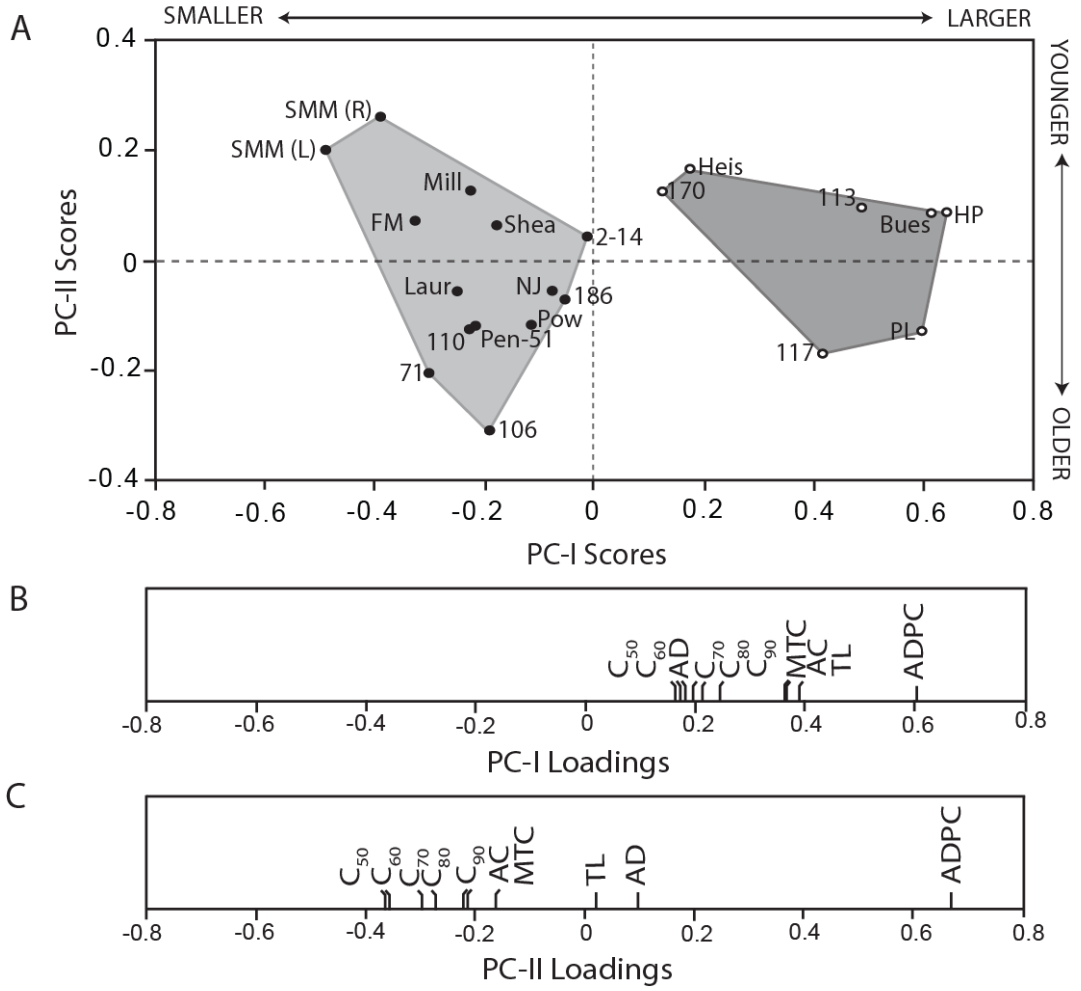

Figure 2.4. A) PC-II (14.2% of total variance) scores plotted against PC-I (80.2% of total variance) scores in the second analysis, which includes anatomical and longitudinal variables. Males are represented by open circles and females by closed circles. Abbreviations as in Table 2.1. B) Loadings for PC-I. C) Loadings for PC-II. Abbreviations as in Figure 2.2.

Discussion

In both the first and second analyses (Figs. 2.3A, 2.4A), hereafter referred to as PCA-1 and PCA-2, respectively, PC-I sorts tusks by size and discriminates between inferred males (positive scores) and inferred females (negative scores). The variable with the strongest contribution to variance along PC-I in both analyses is axial depth of the pulp cavity. This measurement does tend to segregate males and females, but as noted in the discussion of Figure 2.1B above, it would have been difficult to identify the bounds applicable for each sex based on the distribution of values for this variable alone. In both PCA-1 and PCA-2, but most notably in PCA-2, there is a gap between the two inferred males with lowest PC-I scores (I2NE-170 and Heisler) and the remaining males. I2NE-170, which has the lowest score among inferred males, is approximately the same distance from the next closest male (I3NW-117) along PC-I of PCA-1 (Fig. 2.3A) as he is from the closest female (Bothwell 2-14). In PCA-2, the projected positions of Heisler and I2NE-170 on PC-I are actually closer to the nearest females than they are to the closest males (Fig. 2.4A). For a young male, tusk circumference can be similar in magnitude to the tusk circumferences of older females, but circumference values near the tip differ by five to ten centimeters between older males and females. The addition of longitudinal variables has the effect that older males, with the largest circumferences, are positioned even farther from females along what is essentially a size axis, and younger males are positioned closer to females. Using PC-I scores in either PCA-1 or PCA-2, without the independent information on sex provided by Figure 2.1, it would have been unclear whether to group I2NE-170 and Heisler with males or with females. In this way, PC-I

alone is no better at discriminating mastodons by sex than univariate treatments of tusk morphology.

The addition of longitudinal variables resulted in some re-ordering of female tusks along PC-I from PCA-1 to PCA-2. FM 26631, one of the smaller inferred females, is clustered with SMM 64-14-1(R), Laur, Bothwell Pen-51, I3NW-110, and F9SW-106 on PC-I of PCA-1 (Fig. 2.3A). The addition of longitudinal variables separates FM 26631 from this cluster and places her closer to F10SW-71 (Fig. 2.4A). SMM 64-14-1(R) and SMM 64-14-1(L) are clustered with other female tusks in PCA-1, but are distinctly separate from them in PCA-2. In both analyses, SMM 64-14-1(L) occupies the small end of the size spectrum. In PCA-1, SMM 64-14-1(R) is positioned within a cluster of other females (Fig. 2.3A). In PCA-2, SMM 64-14-1(R) moves away from this cluster and is positioned as the second-smallest tusk along PC-I, adjacent to SMM 64-14-1(L) (Fig. 2.4A). With increased representation of circumference measures, it is not surprising that projections of the most slender of the inferred female tusks move in the opposite direction to those of greater girth.

All variables in this study are linear or curvilinear measurements, and because older individuals tend to have larger tusks than younger individuals within each sex, age is a factor in the variance among measurements on all axes. PC-II, however, is the axis in both analyses where sorting of tusks best matches the ordering expected based on qualitative assessments of how tusk form changes with age. In PCA-1, circumference (maximum and alveolar) and tusk length strongly contrast with axial depth of the pulp cavity (Fig. 2.3C). Because tusks grow throughout life, older individuals tend to have longer tusks and larger circumferences than younger members of the same sex. The tusk

pulp cavity, however, increases in depth in early ontogeny, maintains a maximum depth for some time, and then decreases in depth in older adults. Thus, a tusk with a large circumference relative to pulp cavity depth is indicative of an older mastodon (more negative scores; Fig. 2.3A), and a tusk with a small circumference relative to pulp cavity depth is indicative of a younger individual (more positive scores, Fig. 2.3A). Likewise, a shallow pulp cavity relative to tusk length indicates an older mastodon, and a deep pulp cavity relative to tusk length indicates a younger mastodon.

The loadings that strongly contrast along PC-II change with the addition of longitudinal variables (Fig. 2.4C), but the interpretation of PC-II as an age axis remains the same. In PCA-2, all circumference variables contrast with axial depth of the pulp cavity to sort tusks along PC-II (Fig. 2.4C). This axis separates younger mastodons (more positive scores; Fig. 2.4A), whose tusk pulp cavities are deep relative to tusk circumference, from older mastodons (more negative scores; Fig. 2.4A), whose tusk pulp cavities are shallow relative to tusk circumference. Addition of longitudinal variables virtually eliminated the contribution of tusk length to the variance along PC-II (Fig. 2.4C).

The comparison of PC-II scores and age (for the eleven tusks with age estimates) for PCA-1 using Kendall's rank correlation test supports the interpretation that PC-II represents variance due to age. Notably, the Miller (female) and Heisler (male) mastodons, the youngest mastodons with age estimates, have the highest PC-II scores for their respective sexes. The Pleasant Lake mastodon, the oldest male with an age estimate, has the lowest PC-II score among males. For females, there is a cluster of low-scoring mastodons with age estimates. North Java is the oldest (34 years), but Powers (30 years)

has the lowest score within this cluster. This suggests that PC-II does not strictly order mastodons by age, but positions mastodons of similar age in close proximity to one another. Kendall's rank correlation test also yields a significant value for PC-II scores and estimated ages in PCA-2, but the significance of this result was lower. This is likely because PC-II scores sort tusks by age within each sex, but not for the entire group. To check this interpretation, each inferred sex was treated separately. Males show no violations of expected order (Fig. 2.5) and no change in order between analyses. Kendall's rank correlation suggests that there is not a significant relationship between age and PC-II scores for males, but this is a consequence of small sample size (with only four age estimates). Females do change their order along PC-II between analyses but in a compensatory fashion such that their correlation coefficient with age remains the same. At face value, this implies that PC-II scores are no more closely related to age in the second analysis than in the first. However, the switch in rank order between Sheathelm and Bothwell 2-14 involves a greater change in PC-II scores than the switch between Laur and North Java. Thus, PC-II in PCA-2 likely provides an improved reflection of age for members of each sex, even though it results in the same mismatch of age- order among all tusks with age estimates.

J3SW-186 offers another hint that PC-II in PCA-2 is a better indicator of age than it was in PCA-1. J3SW-186 is a relatively straight tusk similar to the North Java tusk (34 tusk-years) in every dimension except for tusk length (in which JS3W-186 is shorter), but heavy wear near its tip suggests that this difference is a consequence of breakage. Because this tusk shows a proximal decrease in girth characteristic of older females ($C_{80} > C_{90}$), it was surprising when it plotted between Sheathelm (20 years) and Laur (27

years) in PCA-1 (Fig. 2.3A). In PCA-2, J3SW-186 moves to a position between Laur (27 years) and Powers (30 years), and close to North Java (Fig. 2.4A), a position more in keeping with our qualitative age estimate. Bothwell Pen-51 is another tusk that exhibits heavy wear due to breakage as well as circumference decrease at the proximal margin ($C_{50} > C_{60} > C_{70} > C_{80} > C_{90}$). In PCA-1, Bothwell Pen-51 (31 years) was positioned most closely to Laur (27 years). Although the number of years in the tusk might place these two in the same age bracket, morphological comparison suggests that Bothwell Pen-51 is older. In PCA-2, Bothwell Pen-51 moves away from Laur to a position on PC-II that is more in keeping with this qualitative age assessment.

Two intriguing patterns in our results are the gradients of loadings of longitudinal variables on PC-I and PC-II in PCA-2. On PC-I, longitudinal variables with the greatest magnitudes (generally C_{90}) contribute most to the variance along this axis (considering just these five variables), followed by the remaining longitudinal variables, in order of decreasing distance from the tip. This is because most tusks are slender near their tips, and the differences between small tusks and large tusks thus become more pronounced with distance from the tip. On PC-II, the longitudinal variable with the lowest value (generally C_{50}) contributes the most to variance along this axis (considering just these five variables), followed by the remaining longitudinal variables, in order of increasing distance from the tip. This is because tip fracture is cumulative. Tusks from young animals have lost little from their tips and thus tend to have relatively small C_{50} values; in contrast, tusks from older mastodons have usually lost more from their tips, giving them larger C_{50} values. This contrast between young and old is usually greatest at 50 cm.

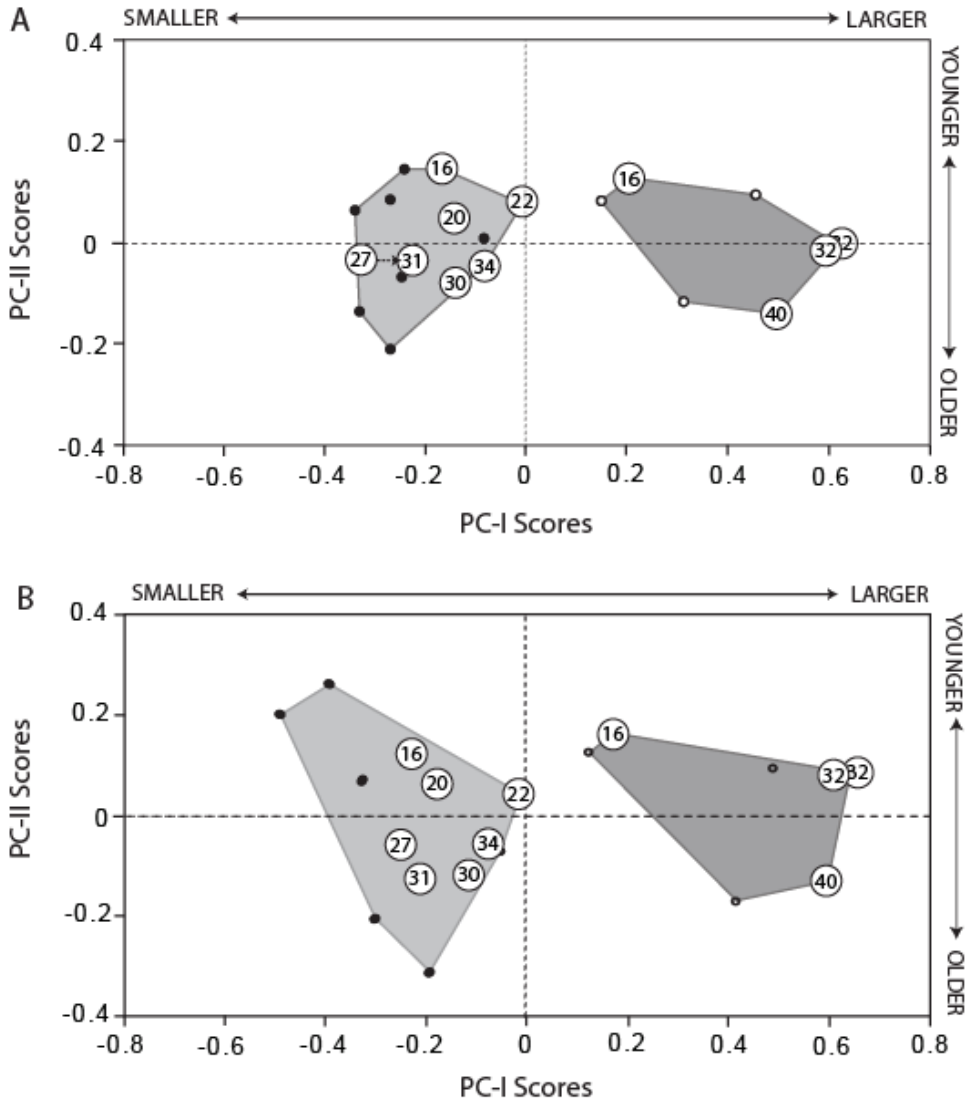

Figure 2.5. PC-II vs. PC-I scores for PCA-1 (A; as in Fig. 2.3A) and PCA-2 (B; as in Fig. 2.4A). Specimen labels are removed and replaced with known ages for the seven females (in lighter polygons on left) and four males (in darker polygons on right) for which they are available, to display the pattern assessed by Kendall's coefficient of rank correlation. The arrow in (A) indicates the position of Laur, whose age (27) would have been obscured by Bothwell Pen-51's age (31) if it had been plotted in its actual position.

Imperfections in the age-ordering of tusks along PC-II of both analyses could result from differences in tusk growth rate and wear. Mastodons of comparable age (within each sex) have similar tusk dimensions, but a tusk of a slightly older mastodon is not necessarily larger. Each tusk likely grew at a different rate depending on nutritional status (Fisher 1996), geographic location, and reproductive status (Fisher et al. 2008a; Smith and Fisher 2008). If one tusk grew at a higher rate than another that was just a few years older, the faster-growing tusk may appear slightly older (i.e., have a lower PC-II score). In addition, mastodons abraded tusk material during normal use, and each tusk experienced a unique wear history. This is evident even on a pair of tusks from one individual. Tusk dimensions unaffected by wear (axial depth of pulp cavity, alveolar circumference, and alveolar depth) should be more or less consistent for a given age and sex, but tusk length, highly susceptible to wear, could distort covariance of tusk measurements. If two tusks belong to different mastodons of the same age and sex (and thus have similar tusk dimensions), but one is shorter because more material was abraded from its tip, then the shorter tusk would have a deeper pulp cavity relative to tusk length and thus is expected to appear younger (i.e., have a higher score on PC-II). Two tusks of similar age that exhibit different degrees of wear are North Java and Powers (Fisher et al. 2008a). These tusks are similar in every dimension except for tusk length (Appendix II), but North Java scores higher than Powers on PC-II in both analyses. Fisher et al. (2008a) determined, based on comparison of tusk girths, cross sections, and radii, that North Java had considerably more material worn off her tusk tip (equivalent to as much as six years of growth and 50 cm of length) than Powers, whose tip was acute and nearly symmetrical about the longitudinal axis, indicating it experienced little wear. Increasing the North

Java tusk length by 50 cm and re-running PCA-1 resulted in a lower PC-II score for North Java, displacing her below Powers, but re-running PCA-2 with this greater tusk length did not change her projection on PC-II (relative to Powers). This suggests that abrasion and breakage have only minor effects on the relative positions of mastodons along PC-II, especially in PCA-2, in which the contribution of tusk length to the variance along the axis is substantially diminished.

PC-III was evaluated to determine if it independently captured variance due to wear. However, highly-, moderately-, and minimally-worn tusks project onto the axis in no consistent order, indicating that PC-III does not sort mastodons by degree of tusk wear in either PCA-1 or PCA-2. In light of these results, and for lack of alternate interpretations, we have no reason to consider PC-III informative.

Most discussion thus far has treated variation along PC-I and PC-II separately, as if they were independent, and the plot of PC-II vs. PC-I scores in the first analysis (Fig. 2.3A) gives little hint that the statistical model of orthonormal variation underlying PCA might be violated in this study. However, addition of the longitudinal variables increases the proportion of total variance explained by PC-II (relative to PC-I) and markedly changes the "shape" of the point-clouds associated with the two sexes. That is, whereas the two convex polygons of Figure 2.3A show little commonality in shape or orientation, their counterparts in Figure 2.4A are conspicuously drawn out obliquely in a "northwest-southeast" direction. The oblique orientation of point clouds in Figure 2.4A clearly shows that, within each sex, tusks of younger mastodons are small and tusks of older mastodons are large; this association, though intuitive, is not clear in Figure 2.3A. This evident covariation between PC-I and PC-II scores means that PC-II is not just capturing

variation independent of that captured by PC-I. Although this complicates interpretation of the PCA, the analysis has succeeded in revealing a relationship that was anticipated from the beginning. That is, in a structure like a tusk, growing by accretion, with the mass-flux occurring predominantly at one end (exclusively at one end, except for tip breakage and abrasion), there is bound to be a correlation between size and age. A larger sample and broader age-range of tusks might better illustrate these patterns, in which a younger mastodon is expected to plot "northwest" of, and an older mastodon "southeast" of, any "middle-age" tusk of the same sex. Once this oblique array for each sex is recognized, it becomes easier to distinguish tusks of males and females, even if their distributions were to overlap on PC-I. In this sense, Figure 2.4A is the first plot of results from this analysis on which sex assignments for all individuals included in this study are clear, independent of cheek tooth and skeletal evidence. These assignments (Table 2.1, column Sex-2) are compatible with all prior analyses. Thus, although use of longitudinal variables increases the non-independence of PC-I and PC-II (for the sexes taken separately), their inclusion in PCA improves the clarity of sex assignments.

In elephants, sexual dimorphism in the tusk, a prominent secondary sexual character, is indicative of different reproductive strategies for males and females. Male elephants with large tusks represent a commitment to somatic growth as a means of enhancing reproductive success, whether as an outcome of female choice or through dominance in male-male interactions; female elephants with relatively small tusks employ a mixed strategy of committing resources toward both growth and reproduction (i.e., growth of offspring; Poole 1992; Lee and Moss 1995). This study joins others in demonstrating pronounced sexual dimorphism in mastodon tusks, similar to that observed

in African elephant tusks. The observation of similar patterns of sexual dimorphism suggests that mastodons had strategies for reproductive success similar to those of modern elephants. These strategies are associated with characteristic social structure and behavior, so the results of this study support the use of elephants as behavioral models for mastodons in studies of life history.

Conclusions

Sex and age are the two biological traits that emerge from this study as accounting for most of the variance in measurements of mastodon tusk morphology, and of these two traits, sex accounts for most of the variance. In previous studies of tusk dimorphism, workers have recognized the difficulty of sexing tusks without knowledge of age. However, PCA succeeds in separating tusks by sex and sorting them by relative age. Sorting of tusks by age, which is enhanced by the addition of longitudinal variables, clarifies interpretations of sex by segregating young males from older females that are morphologically similar. In this way, PCA can be used to reliably discriminate between sexes without prior knowledge of age.

Indeterminate growth of structures is a characteristic that can prevent a sample from showing a clear-cut bimodal distribution in univariate and bivariate analyses. In this study, tusk measurements reflecting ontogeny, which are retained in tusk structure because tusks grow by apposition, enhanced discrimination between male and female tusks. Male and female tusks exhibit unique ontogenetic trajectories of growth, so measurements that reflect ontogenetic changes in tusk morphology also reflect differences between the sexes.

An important basis of life history studies is identifying the sex of an individual, because misidentifying sex could lead to misinterpretation of life history events. Characterizing changes in life history parameters (e.g., maturation age, length of inter-birth intervals) for mastodons at the end of the Pleistocene has the potential to clarify the nature of the environment at the end of the epoch because these events, as in living elephants, are functions of environmental conditions. Ultimately, life history data could be used to clarify the cause(s) of mastodon extinction in North America by providing evidence for environmental stress, or lack thereof, at the end of the Pleistocene. The results of this study contribute to studies of mastodon paleobiology by presenting a more reliable method for sexing a mastodon using tusk measurements alone.

Beyond identifying the sex of an individual, the analyses presented here have the potential to address other paleontological questions. For example, PCA could characterize age and sex for mastodons in assemblages when tusks are dissociated from other skeletal elements. This would help to assess processes of site formation. For example, an assemblage exhibiting the age and sex distribution expected for a family unit may indicate a single mortality event affecting multiple individuals. Additionally, this study has implications for studying populations of island mammoths. For island mammoths, sex can be difficult to ascertain from tusk measurements because male tusks may exhibit sizes and morphologies more similar to those of mainland females than mainland males (Fisher et al. 2008b). A PCA using island mammoth tusks could clarify to what degree tusk dimorphism is retained in island mammoths. We do not yet know enough about dimorphism in island mammoths to anticipate the outcome of such a study,

but whatever pattern is observed would be significant for understanding the mechanism and context of changes that occurred between mainland and island populations.

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Appendix I. Descriptions of variables used in this study.

Variable 1. Axial Depth of Pulp Cavity (ADPC): Pulp cavity depth is specified as "axial" to clarify that it is measured along the pulp cavity axis (with a stiff wire probe, gently flexed to follow the course of the axis). Measuring pulp cavity depth in this way is more precise than projecting it to the exterior curve of the tusk.

Variable 2. Alveolar Depth (AD): Alveolar depth is the length along the outer curve of the tusk from the proximal end to the alveolar margin, where the latter feature was usually approximated based on staining at the gingival margin (Elder 1970). The gingival margin can also be identified by a change in texture. Tusk material within the alveolus is not subject to abrasion, whereas erupted tusk material is, so the transition between worn and unworn cementum surfaces, if detectable on the tusk exterior, can be used to locate this position.

Variable 3. Alveolar Circumference (AC): Alveolar circumference is measured at the alveolar margin. Uncertainty in locating the alveolar margin (or error from using the alveolar margin and gingival margin interchangeably) has little effect on the value of alveolar circumference. Near the proximal end of the tusk, where this margin is located, circumference generally does not vary by more than 1 cm over a distance of 10 cm along the outer curve.

Variable 4. Maximum Tusk Circumference (MTC): Maximum tusk circumference was determined by measuring circumference every 10 cm along the outer curve of the tusk, beginning at 10 cm from the tip. For three tusks (Miller, I3NW-117, I2SE-113) it was only possible to obtain measurements of diameter; these were converted to estimated circumference values using the equation for a circle. When the value of alveolar circumference was greater than any measurement of circumference taken at 10-cm intervals (the case for Buesching, Heisler, Miller, and Bothwell Pen-51; implying that the 10-cm interval simply missed "finding" the maximum), the AC value was also used as the MTC value.

Variable 5. Tusk Length (TL): Tusk length was measured from the distal to the proximal end using a flexible tape measure positioned to follow the locally recognizable outer curve of the tusk along its entire spiral form. In principle, the amount of material lost from the tusk tip could be estimated by examining the outcrop pattern of dentin cones on the outer surface of the tusk (Fisher et al. 2008a), but this is not attempted here.

Appendix II. Measurements (cm) used in this study.

Specimen	ADPC	AD	AC	MTC	TL	50 cm	60 cm	70 cm	80 cm	90 cm
Hyde Park	98.0	59.0	55.0	57.9	279.0	31.0	33.5	35.8	38.3	40.5
Buesching	91.0	64.0	55.0	55.0	290.5	31.6	32.8	34.6	36.9	39.0
Pleasant Lake	68.0	44.0	58.0	61.0	278.8	35.0	38.8	41.0	43.5	46.0
Heisler	65.0	47.0	39.0	39.0	133.0	24.1	26.5	28.8	30.7	31.7
North Java	30.0	39.0	31.2	31.4	152.9	27.2	28.3	28.9	30.2	31.3
Powers	26.0	38.0	32.0	33.0	132.4	27.1	28.7	29.7	31.2	32.5
Laur	24.0	37.0	27.5	28.9	119.0	25.9	26.4	26.8	27.5	28.2
Miller	36.0	40.0	27.0	27.0	95.4	23.6	24.8	24.8	25.1	25.1
Sheathelm	32.0	40.0	28.0	28.4	124.0	22.2	24.9	27.0	28.2	27.3
Bothwell 2-14	40.5	46.5	30.0	31.7	136.0	26.5	28.1	29.2	30.4	31.2
Bothwell Pen-51	24.3	42.2	31.0	31.0	98.4	30.9	30.4	29.0	28.2	25.6
FM 26631	26.7	42.1	22.8	26.5	99.6	22.6	23.1	24.2	25.6	26.5
SMM 64-14-1 (L)	22.4	42.0	20.5	21.3	120.5	17.0	18.4	19.7	20.5	21.3
SMM 64-14-1 (R)	30.1	45.4	20.4	22.9	116.0	18.3	19.0	20.3	20.8	21.6
J3SW-186	32.2	48.5	31.7	32.0	120.5	29.2	30.5	31.6	32.0	31.1
I3NW-117	48.1	66.0	48.7	52.2	201.0	34.6	37.7	39.6	42.1	44.6
I2SE-113	87.6	65.0	46.8	49.3	179.0	30.2	30.5	36.1	38.0	42.1
I2NE-170	51.6	57.0	32.9	38.6	146.8	23.4	26.0	29.4	31.5	32.9
F10SW-71	17.1	42.6	29.3	29.5	109.6	27.8	28.6	29.3	29.5	29.1
I3NW-110	22.3	39.5	29.8	29.8	112.5	26.8	28.0	29.3	29.8	29.4
F9SW-106	16.6	44.8	33.7	34.0	120.5	29.7	32.6	33.4	34.0	33.2

Chapter 3

Sexual dimorphism in tusks of American mastodons (*Mammut americanum*) and African elephants (*Loxodonta africana, Loxodonta cyclotis*): A multivariate comparison

Abstract

Aspects of social structure, mating strategies, and parental investment can be inferred for mammalian species based on degree of sexual dimorphism, especially when males are substantially larger than females. African elephants (*Loxodonta africana*, *Loxodonta cyclotis*) exhibit marked dimorphism in tusk size and show behaviors typical of strongly dimorphic species. American mastodons (*Mammut americanum*) also exhibit pronounced tusk dimorphism, but mastodons and elephants diverged from a most recent common ancestor in or before the early Miocene, so it is possible that unique behavioral and life-history traits evolved in each lineage since then. Similar behavioral traits in mastodons and elephants could be supported if details of tusk dimorphism are consistent across the two genera. Separate discriminant function analyses (DFA) of 21 mastodon tusks of inferred sex (assessed in independent analyses) and 45 elephant tusks of known sex, using the same ten tusk variables, illustrate that similar patterns of ontogenetic change in tusk circumference, regardless of genus, effectively discriminate between sexes. Slight differences in patterns of ontogenetic change between genera suggest that mastodons exhibited pronounced tusk dimorphism earlier in ontogeny than elephants.

Canonical variates analysis (CVA) of tusks from male and female mastodons and male and female elephants, using the same tusks and measurements as in DFA, shows that male tusks are larger than female tusks across all measurements, especially in maximum tusk circumference and pulp cavity depth, for both genera. CVA also emphasizes differences in tusk morphology between genera that imply mastodon tusks are, in general, more robust than elephant tusks, although this difference does not affect the nature of tusk dimorphism. Overall, this study illustrates that there is a characteristic male and a characteristic female tusk form shared by elephants and mastodons. Thus, mastodons, like modern elephants, likely exhibited behaviors associated with strongly dimorphic species, and aspects of modern elephant behavior may have emerged prior to the divergence of elephants and mastodons.

Introduction

Sexual dimorphism can be defined as all of the differences in form between males and females of the same species (excluding primary sexual features). In fossil species, sexual dimorphism can be observed in skeletal proportions, and in the presence or enlargement of a skeletal structure in one sex only. Sexual dimorphism is important to the study of fossil species because (1) its recognition prevents the identification of two species where there is only one, (2) much about the behavior of fossil species can be interpreted through the presence of pronounced, male-dominated dimorphism, and (3) the character of dimorphism provides a method for evaluating which modern species is best suited to serve as an analog for a fossil species with multiple modern descendants. The nature of sexual dimorphism in modern taxa is commonly used to interpret the behavior

of closely related extinct species. For example, sexual dimorphism in fossil taxa has been used to infer the social structure of early Eocene horses (Gingerich 1981), Miocene rhinoceroses (Mihlbachler 2003), ungulates (Berger et al. 2001) and proboscideans (Haynes 1991), and the reproductive strategies of carnivores (Gittleman and Van Valkenburgh 1997) and proboscideans (Haynes 1991).

American mastodon (*Mammut americanum*) behavior is often interpreted as comparable to modern elephant behavior (e.g., Fisher 1996, 2008). Elephant behavior is the most likely indicator of American mastodon behavior because (1) elephants and mastodons have similar skeletal structures and sizes, (2) they have similar diets (Koch et al. 1997; Cerling et al. 1999; Fisher and Fox 2003), (3) they exhibit sexual dimorphism in skeletal proportions and tusks (Haynes 1991; Lister 1996; Fisher 2008; Smith and Fisher in review; Chapter 2, this dissertation), and (4) elephants are the living group most closely related to mastodons. However, mastodons and elephants diverged from a most recent common ancestor over 20 million years ago (Fig. 3.1), so it is possible that unique or convergent behaviors evolved in either lineage since then. It may be that another modern animal, or perhaps no modern animal, could serve as a behavioral analog for mastodons. Haynes (1991) considered that either moose (*Alces alces*) or giraffe (*Giraffa camelopardalis*) behavior would be a good model for mastodon behavior, because moose, giraffes, and mastodons are all large-bodied mammals with similar dietary strategies (selective feeders that eat dicotyledonous plants). Moose and giraffes, however, exhibit differences in life history and behavior, and moose, giraffes, and African elephants all exhibit unique behavioral traits. Although Haynes ultimately concluded that mastodons were most likely to behave like modern African elephants, his considerations

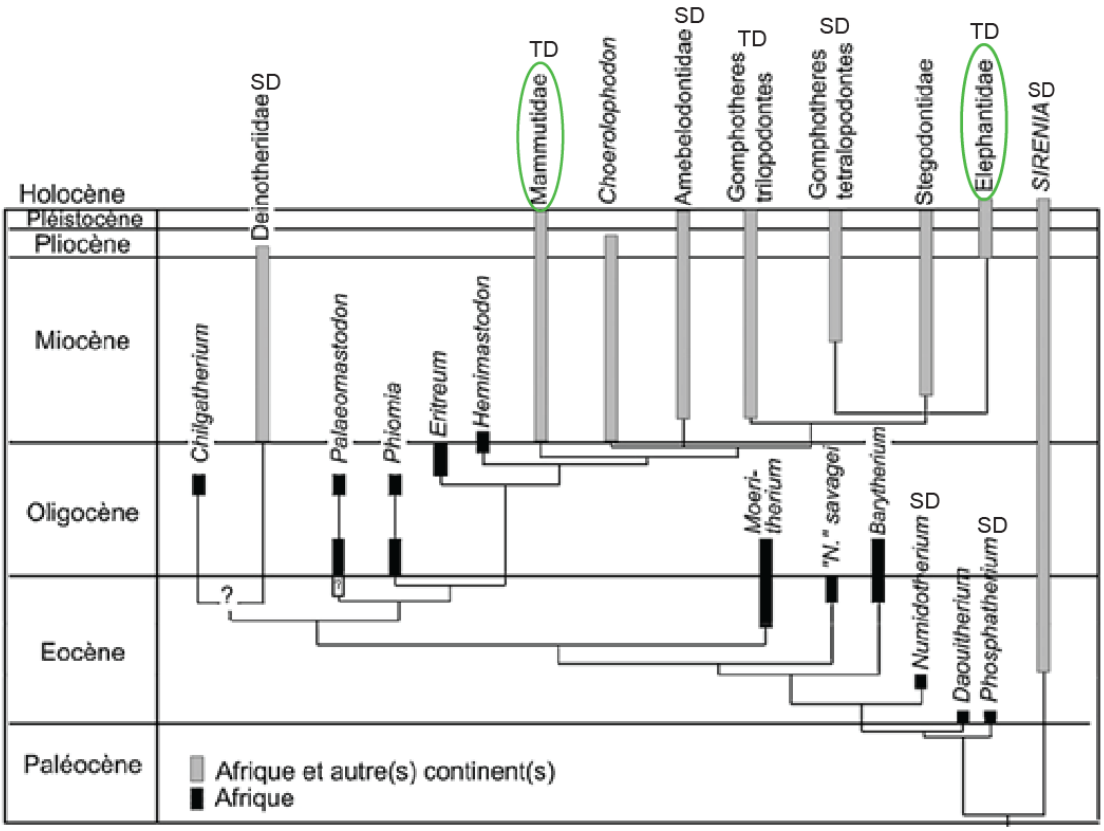


Figure 3.1. Phylogeny of Order Proboscidea (Gheerbrant and Tassy 2009), with the family that includes mastodons (Mammutidae) and the family that includes African elephants (Elephantidae) circled. Note that mastodons and elephants diverged from a most recent common ancestor in or before the early Miocene. The Order Sirenia, which includes dugongs and manatees, serves as the outgroup. Taxa in which sexual dimorphism has been reported (see Appendix I for details) are indicated with "TD" (if there is evidence of tusk dimorphism) or "SD" (if dimorphism is of other skeletal elements). Citations of tusk dimorphism for Elephantidae include Elder (1970), Averianov (1996), and this study. Trilophodont Gomphothere tusk dimorphism was reported in Tassy (1996). Citations for Mammutid tusk dimorphism include Fisher (2008) and this dissertation (Chapters 2 and 3). Sexual dimorphism in tetralophodont Gomphotheres was reported by Madden (1986), in Elephantidae by Lister (1996), in Amebelodontidae and trilophodont Gomphotheres by Tassy (1996), in Deinotheriidae by Huttunen and Gohlich (2002), in *Phosphatherium* by Gheerbrant et al. (2005)*;* in *Numidotherium* by Noubhani et al. (2008), and in Sirenia by Spain et al. (1976) and Zalmout and Gingerich (2008).

(and the possibility that there are no living animals that could serve as behavioral analogs for mastodons) illustrate that, to fully understand mastodon behavior, additional quantitative evidence of mastodon behavior is required. Aspects of mastodon behavior could be inferred as similar to elephant behavior if the character and degree of tusk dimorphism between them are similar. This issue is addressed here through quantitative comparisons of African elephant and mastodon tusk dimorphism, with the goal of evaluating the use of elephant behavior as a model for mastodon behavior.

Proboscidean Tusk Growth

Tusk growth is described in detail in Fisher (1996) and Smith and Fisher (in revision; Chapter 2, this dissertation) and reviewed briefly here. Proboscidean tusks are enlarged second upper incisors (Luckett 1996) that are composed primarily of dentin. Proboscidean tusks grow by accretion, and most exhibit indeterminate growth. Thus, ontogenetic changes in size and shape over much of the life span are preserved in tusk structure. A hierarchy of structural increments (on annual, approximately fortnightly, and daily scales) preserved in tusk dentin allow changes in growth rate, stable isotope composition, and morphology to be tied to specific times in an individual's life.

A tusk grows as odontoblasts lining the surface of the existing pulp cavity deposit a new layer of dentin inward, displacing the pulp cavity apex proximally. Tusk length increase is achieved by the deposition of new dentin at the proximal margin of the pulp cavity. Tusk length increase is coupled with tusk eruption, exposing new tusk material along the alveolar margin and freeing space within the alveolus for continued tusk growth. Tusk circumference increases at successive positions along much of the tusk's

length because each annually deposited cone exhibits an overall increase in circumference at its proximal margin relative to the previous year's cone. However, as an individual reaches advanced age, the proximal circumference of each new annual dentin cone exhibits an overall decrease relative to the proximal circumference of the previous cone.

The pulp cavity exhibits a different pattern of growth, in which depth increases in early ontogeny, reaches a maximum at some midpoint in life, and decreases in later ontogeny. Thus, tusks of older adults are longer, have larger maximum girths and relatively shallow pulp cavities. Conversely, tusks of younger adults are shorter, and have smaller maximum girths and relatively deep pulp cavities. Abrasion and breakage to the tip, however, can lead to subsequent decreases in tusk length, so the oldest individuals may have tusks that are shorter than those of middle-aged adults.

Sexual Dimorphism in Mammals

Sexual dimorphism refers to all the differences in size, shape, and even behavior between males and females of the same species, although differences that are directly related to reproduction (e.g., differences in sex organs) are generally excluded from this definition. One type of sexual dimorphism, sexual size dimorphism, occurs when one sex grows at a faster rate than the other, when one sex grows for a longer period of time than the other, or when one sex grows at a faster rate for a longer period of time than the other (Badyaev 2002 and references therein). Male-dominated sexual size dimorphism is thought to arise as a consequence of sexual selection (Darwin 1871; Ralls 1977). Differences between sexes can result from (1) mate choice, in which members of one sex

preferentially choose mates based on coloring, ornamentation, patterns, or body size, or (2) intra-sex competition, in which large body size and pronounced secondary sexual characteristics result in more opportunities for mating (Reynolds and Harvey 1992). Only a strong opposing selective pressure should prevent a continuing increase in body size for males of species that rely on large body size for reproductive success (Clutton-Brock 1994).

Strongly dimorphic mammalian species in which males are larger than females typically group by sex and have polygynous mating systems (Gittleman and Van Valkenburgh 1997; Weckerly 1998; Berger et al. 2001). The males of such species generally invest little in the care of offspring (Ralls 1977), and as a whole exhibit more variation in reproductive success than females (Clutton-Brock 1994). Sexual size dimorphism is most pronounced in species in which males enter into intra-sex competitions for access to females. Larger males are more likely to win these battles and have more opportunities for mating, so body size is directly related to male reproductive success (Ralls 1977; Clutton-Brock 1994; Lee and Moss 1995). For mammalian species in which females are larger than males, social structure and degree of parental investment varies from species to species (Ralls 1976). The males of mammalian species with no or weakly developed dimorphism are typically monogamous or near-monogamous (Ralls 1997; Vanpe et al. 2008), and they invest in rearing their offspring (Ralls 1977). In these species, sexes are equally variable in terms of reproductive success (Clutton-Brock 1994). Monomorphic species exhibit a variety of social structures, in which they may live in permanent mixed-sex groups, temporary mixed-sex groups, or no groups at all (Berger et al. 2001).

Proboscidean Dimorphism and Behavior

There are two species of modern African elephants, the savannah or bush elephant (*Loxodonta africana*) and the forest elephant (*Loxodonta cyclotis*; Grubb et al. 2000; Groves and Grubb 2000; Roca et al. 2001). Both species exhibit sexual-size dimorphism in which males are larger-bodied and have larger tusks than females of comparable age. This dimorphism occurs because males grow faster and for longer portions of their ontogeny than females (Lee and Moss 1995; Sukumar et al. 1988). Male African elephants can grow to be 1.3 times taller (Lee and Moss 1995) and twice as heavy (Hanks 1972) as female elephants. Size dimorphism is not pronounced in immature elephants, but male calves grow at slightly higher rates than female calves from birth, and sex differences in height become marked by 10 years of age, around the time of maturation (Lee and Moss 1995). Both male and female elephants continue to grow long after the onset of sexual maturity because epiphysis fusion of long bones is delayed (Poole 1994). Fusion occurs later in life for males than for females. Female height stabilizes between 15 and 25 years, but male height does not stabilize until up to 45 years (Poole 1994).

Modern Asian elephants (*Elephas maximus*) also exhibit tusk dimorphism, but because Asian elephant females have very small, often unerupted tusks, or lack tusks altogether, reports of Asian elephant tusk morphology have inevitably focused on males. Thus, when tusk dimorphism is discussed it is generally referred to as an absence of tusks in females and a presence in males (Sukumar 1989). With respect to stature, males grow faster than females beginning as early as two years of age. As adults, males can grow up to 1.25 times taller than and nearly twice as heavy as females (Sukumar et al. 1988; Sukumar 2006).

A number of linear and curvilinear tusk measurements (e.g., circumference, length, pulp cavity depth, tusk length) have been shown to discriminate between male and female elephants (Laws 1966; Elder 1970; Pilgram and Western 1986) and male and female mastodons (Smith and Fisher 2007; Fisher 2008), with varying degrees of certainty. The inclusion of age in any analysis increases the reliability of sex assessment because two tusks of similar size and shape, but vastly different ages, are unlikely to be members of the same sex (Fisher et al. 2008). Pilgram and Western (1986) proposed that sex and age could be more accurately predicted from tusks using multivariate models than from the bivariate models they presented that used different combinations of tusk length, exposed tusk length, tusk weight, alveolar circumference, and age, but they were unable to conduct such an analysis using the measurements available to them. Principal components analysis (PCA) of mastodon tusk measurements (axial depth of the pulp cavity, alveolar depth, alveolar circumference, maximum tusk circumference, tusk length, and tusk circumference at 50, 60, 70, 80, and 90 cm from the tip) did improve discrimination by sex, relative to univariate and bivariate methods, by distinguishing between male and female tusks of similar form but dissimilar age (Smith and Fisher in review; this dissertation, Chapter 2).

Female elephants live in matriarchal family units consisting of related adults and their juvenile offspring (Moss 1988). Young males leave or are evicted from their family units upon attaining sexual maturity in their early teenage years (Poole 1994), after which point they either live alone or, when they are not in a state of heightened aggression and sexual activity known as musth, in loose association with other males (Eisenberg 1971; Poole 1987; Poole 1994). In addition, elephants exhibit a non-territorial polygynous

mating system, in which males invest no energy into the care of their offspring and engage in intra-sex battles for access to oestrus females (Moss 1988; Poole 1994; Lee and Moss 1995). Reproductive success for males is directly related to size; larger males with prominent tusks are more likely than smaller males to prevail in intra-sex battles (Lee and Moss 1995). Male calves nurse more frequently and have higher milk intake than female calves during the first three years of life. Because of this, males grow more rapidly than females from birth. Males that do not grow rapidly from birth will be smaller than their male competitors as adults and be at a disadvantage when they enter into intra-sex battles for access to mates (Lee and Moss 1986).

Skeletal evidence in mastodons suggests that elephants and mastodons shared some behaviors. Death for several male mastodons has been attributed to puncture wounds to the skull caused by tusks. These wounds were interpreted as injuries incurred during intra-sex battles (Fisher and Fox 2007; Fisher 2008, 2009). A sharp decline in annual tusk growth rate for males in their early teenage years has been connected to the eviction of the male from its family unit (Fisher 1990, 2008), as low growth rate reflects nutritional stress (Fisher 1996) and a young male elephant experiences considerable stress the year following eviction (Lee and Moss 1999). For female mastodons, three- to four-year cycles of variation in annual tusk growth rate may reflect the effect of gestation and lactation on tusk growth, suggesting a similarity in inter-birth interval for mastodons and elephants (Fisher et al. 2008; Smith and Fisher 2008).

This study addresses mastodon tusk dimorphism and behavior by performing a series of multivariate analyses on African elephant and American mastodon tusks in order to (1) characterize tusk dimorphism for each genus; (2) compare and contrast the

character and degree of tusk dimorphism in these genera; and (3) compare and contrast the character of tusk morphology in these genera. In addition, an exploratory analysis of tusk dimorphism in juvenile elephants is performed to evaluate the efficacy of sexing juveniles using tusk measurements. Ultimately, the goal of this study is to investigate whether elephant behavior can be used to infer mastodon behavior, with implications for the evolution of modern elephant behavior within Proboscidea.

Materials and Methods

Materials

Twenty-one mastodon tusks were included in this study (Appendix II). All tusks belong to post-Last Glacial Maximum (LGM) mastodons of the Great Lakes region, USA. Mastodon tusks with direct radiocarbon dates (on tusk collagen) show an age range of 10,395 to 12,170 BP (Chapter 2, this dissertation). These same tusks were included in the PCA of mastodon tusk morphology (Smith and Fisher in revision; this dissertation, Chapter 2); interpretations of sex for these mastodons are based on PCA. All tusks exhibit lengths greater than or equal to 90 cm.

Eighty-seven African elephant tusks from United States museum collections were included in this study (Table 3.1). African elephant tusk measurements were collected on specimens of known and unknown sex belonging to adult and juvenile elephants. There are relatively few tusks held in U.S. collections, so restriction of tusks to a tightly constrained geographic region, though it would have been ideal, would have severely limited sample size. Consequently, tusks belonging to elephants from sub-Saharan African countries (n=59), from zoo elephants (n=3), and from unknown localities (n=25)

were included in this study (Table 3.1). Although inclusion of elephants from such a broad area adds variation in tusk morphology that may be attributable to differences in habitat and species (Grubb et al. 2000), these variations are not likely to be great enough to obscure overall differences in morphology due to sex. For example, Elder (1970) evaluated tusk morphology for elephants of Uganda (east-central Africa) and Congo (west-central Africa) as a group. A clear pattern of tusk dimorphism emerged from Elder's study for tusks belonging to sexually mature individuals.

Most tusks in this study were referred to *L. africana*, but, because the division of modern elephants into two species is a relatively new distinction, and many of the tusks were collected in the early twentieth century, it is possible that specimens identified as *L. africana* at the time of collection would be referred to *L. cyclotis* today. Additionally, there were many tusks with no information on country of origin. Because included tusks were not restricted to a specific geographic region, there seemed little reason to exclude a tusk because its country of origin was unknown. Tusks are extremely fragile at their true proximal margins, so they are often broken proximally. Thus, measurements of length (tusk length, pulp cavity depth, and alveolar depth) may require estimation. Tusks in this study that exhibit proximal breakage are usually missing less than 3 cm of length, and uncertainties associated with estimation are likely less than 1 cm.

Methods

Multivariate analyses were conducted on measurements of American mastodon and African elephant tusks. Ten of these measurements have been shown to sort mastodons by inferred sex and by relative age in PCA (Smith and Fisher in revision; this

dissertation, Chapter 2). Measurements (Fig. 3.2) are divided into two categories: anatomical variables and longitudinal variables. Anatomical variables depict geometrically distinct aspects of tusk size and shape at the time of death; these variables are axial depth of the pulp cavity, alveolar depth, alveolar circumference, maximum tusk circumference, and tusk length (see Chapter 2, Appendix I, for detailed descriptions of variables). Longitudinal variables reflect ontogenetic change in a single aspect of tusk morphology (circumferences); these variables are measures of tusk circumference at 30, 40, 50, 60, 70, 80, and 90 cm from the tusk tip. Because tusks increase in length throughout life, different positions along a tusk represent different times in ontogeny, so longitudinal variables show how circumference changed from earlier (closer to the tip) to later (farther from the tip) in life. All measurements in cm were log-transformed prior to inclusion in the analysis because the normality of biological variation is geometric Gingerich 2000). Log_{10}-transformation was used so that values could be easily related to the original measurements.

Comparison of tusk measurements was undertaken using canonical variates analysis (CVA) and discriminant function analysis (DFA), a two-group case of CVA. CVA describes differences among a priori group means by maximizing between-group variation relative to within-group variation (Campbell and Atchley 1981; Zelditch et al. 2004); thus, it is a useful analysis for characterizing morphological differences among groups. CVA produces multiple, independent axes that are linear combinations of original data. Scores are computed for each individual along each axis, and eigenvalue coefficients (loadings), which indicate the contribution of each variable to the variance along each axis, are also computed for each axis (Zelditch et al. 2004).

Table 3.1. List of all African elephants included in this study. "R & L" indicates the inclusion of both the right and left tusk for an individual. Species name is as indicated in the respective museum's database or as *[L. africana]* is there is limited information on the tusk's origin. Some tusks are labeled *L. a. oxyotis*, which is a synonym for the savannah or bush elephant (Wilson and Reeder 2005). Continued on page 71.

Institute	Specimen	Species	Sex	Stage	Country of Origin	DFA Classification
FMNH	No.3 R341/2 R & L	*[L. africana]*	M[a]	adult	Unknown	M
FMNH	101836	*L. africana*	U	juvenile?	South Africa	M
FMNH	K40HB R & L	*[L. africana]*	M[a]	adult	Unknown	M
FMNH	no catalog #	*[L. africana]*	U	juvenile?	Unknown	F
FMNH	53749 R & L	*L.africana*	U	juvenile?	Unknown - Zoo	F
USNM	165176 R & L	*L. africana*	M	adult	Kenya	M
USNM	165499 R & L	*L. africana*	M	adult	Kenya	M
USNM	49759	*L. africana*	M[a]	adult	Unknown	M
USNM	22147 R & L	*L. africana*	M[a]	adult	Unknown	M
USNM	163318 R & L	*L. africana*	M	adult	Kenya	M
USNM	304615 R & L	*L. africana*	M	adult	Angola	M
USNM	163319 R & L	*L. africana*	F	adult	Kenya	F
USNM	165501 R & L	*L. africana*	F	adult	Kenya	F
USNM	49489	*L. africana*	M[a]	adult	South Africa	M
USNM	270993 R & L	*L. africana*	F	adult	Unknown	F
USNM	KEB78 R & L	*[L. africana]*	M[a]	adult	Unknown	M
USNM	KEB385 R & L	*[L. africana]*	M[a]	adult	Unknown	M
USNM	Mum/38/73/5 R & L	*[L. africana]*	M[a]	adult	Unknown	M
USNM	LKA/74/1006	*[L. africana]*	M[a]	adult	Unknown	M
USNM	LKA/64/1	*[L. africana]*	M[a]	adult	Unknown	M
USNM	220146 R & L	*L. cyclotis*	M	juvenile?	Gabon	M
USNM	49553	*L. africana*	U	juvenile?	Unknown	M
USNM	61706 R & L	*L. africana*	U	juvenile?	Congo	M
AMNH	52093 R & L	*L. africana africana*	M	juvenile	Congo	M
AMNH	51944 R & L	*L. africana oxyotis*	M	adult	Congo	M

FMNH = Field Museum of Natural History, Chicago, IL; USNM = National Museum of Natural History, Washington, D.C.; AMNH = American Museum of Natural History, New York, NY.

[a]Not catalogued as male, but identified as such if pulp cavity depth for at least one tusk in a pair exceeds 60 cm (Elder 1970).

[b]Individuals classified as male and female had one tusk classified as male and the other classified as female in DFA.

Institute	Specimen	Species	Sex	Stage	Country of Origin	DFA Classification
AMNH	51937 R & L	*L. africana oxyotis*	M	adult	Congo	M
AMNH	80598 R & L	*L. africana africana*	M	adult	Angola	M
AMNH	217684 R & L	*L. africana*	M	adult	Unknown	M
AMNH	51939 R & L	*L. africana oxyotis*	M	adult	Congo	M
AMNH	39083 R & L	*L. africana oxyotis*	M	adult	Kenya	M
AMNH	88403 R & L	*L. africana oxyotis*	F	adult	Kenya	F
AMNH	51936	*L. africana oxyotis*	F	adult	Congo	F
AMNH	120444 R & L	*L. africana*	M[a]	adult	Unknown	M
AMNH	no catalog # R & L	*L. africana*	U	adult	Unknown	F
AMNH	51869 R & L	*L. africana*	M	juvenile?	Congo	M
AMNH	52094 R & L	*L. africana oxyotis*	M	juvenile?	Congo	M
AMNH	51949 R & L	*L. africana oxyotis*	F	juvenile?	Congo	F
AMNH	89453 R & L	*L. africana cyclotis*	F	juvenile	Liberia	F
AMNH	146606 R	*L. africana*	U	juvenile?	Unknown - Zoo	F
AMNH	51943 R & L	*L. africana*	U	juvenile?	Congo	M
AMNH	51950	*L. africana*	U	juvenile?	Congo	F
AMNH	51947 R & L	*L. africana*	U	juvenile	Congo	F
AMNH	51934 R & L	*L. africana oxyotis*	U	juvenile?	Congo	F
AMNH	54082 R & L	*L. africana africana*	U	juvenile?	South Africa	M & F[b]
AMNH	119510 R & L	*L. africana cyclotis*	U	juvenile	Congo	M
AMNH	69399 R & L	*L. africana*	U	juvenile	Unknown	M & F[b]
AMNH	81897	*L. africana cyclotis*	U	juvenile?	Liberia	M
AMNH	54082 R & L	*L. africana africana*	U	juvenile?	South Africa	F
AMNH	51938 R & L	*L. africana*	U	juvenile?	Congo	F

FMNH = Field Museum of Natural History, Chicago, IL; USNM = National Museum of Natural History, Washington, D.C.; AMNH = American Museum of Natural History, New York, NY.

[a]Not catalogued as male, but identified as such if pulp cavity depth for at least one tusk in a pair exceeds 60 cm (Elder 1970).

[b]Individuals classified as male and female had one tusk classified as male and the other classified as female in DFA.

The first canonical variate of a CVA, the most effective discriminator between groups, is the sole discriminant function in a DFA. DFA can be used to predict group membership for an individual of unknown affiliation by calculating a discriminant score for this unknown. This score is calculated by summing the products of the unstandardized discriminant function coefficients and the corresponding log-transformed measurements for the unknown, and adding a constant to this summation (Campbell and Atchley 1981).

Four separate multivariate analyses were performed on different combinations of mastodon and elephant tusks. All DFAs were conducted using SPSS 17.0 (SPSS Inc.), and CVA was conducted using PAST (Hammer et al. 2001). In the first analysis, DFA was conducted on 21 mastodon tusks and 10 tusk variables (Fig. 3.2, variables 1-5 and 8-12), to characterize differences between male and female mastodon tusks.

In the second analysis, DFA was performed on a set of elephant tusks belonging to elephants of known sex (n=45), using the same 10 measurements used in the mastodon DFA, to characterize differences between male and female elephant tusks. Tusks included in this analysis were restricted to those 90 cm or longer to allow for direct comparison with the mastodon DFA, which includes measurements that require tusks to be 90 cm or longer. Discriminant scores were calculated for elephant tusks of unknown sex (n=6) to assign them to a group.

In the third analysis, DFA was performed on 37 juvenile elephant tusks of known (n=12) and unknown (n=25) sex to investigate the efficacy of sexing juveniles, which exhibit weak dimorphism (Lee and Moss 1995). Tusks not classified as “juvenile” were included in this analysis if they were shorter than 90 cm. Tusk length is not an indicator of sexual maturity, but a function of age, so these tusks do not necessarily belong to

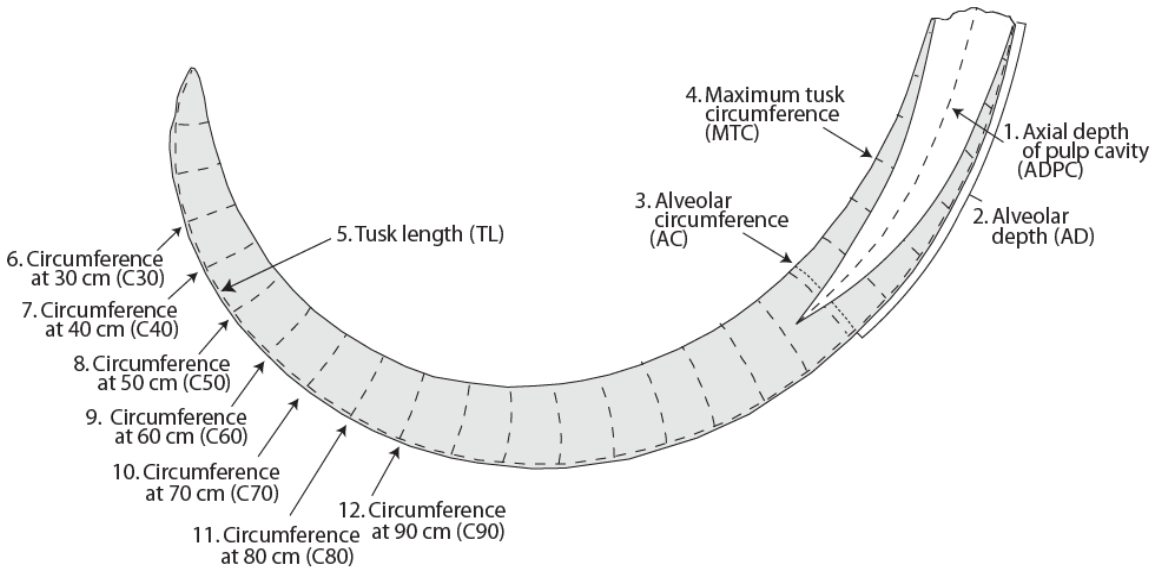


Figure 3.2. Schematic of a tusk illustrating morphometric tusk variables (modified from Smith and Fisher in review; this dissertation, Chapter 2). Variables 1-5 are anatomical variables, and 6-12 are longitudinal variables.

elephants that did not reach sexual maturity prior to death, but restricting this analysis to shorter tusks at least ensures that young males are being compared to young females. In addition, tusks shorter than 90 cm with extreme abrasion at the tip were excluded from this analysis because tusks with such morphology typically belong to older individuals. All five anatomical variables were used in this analysis, but some longitudinal variables differed from those in the previous two DFAs to accommodate tusks shorter than 90 cm (Fig. 3.2, variables 1-7).

An exploratory analysis of all 87 elephant tusks, showed that extreme size differences between adult and juvenile tusks, regardless of sex, damped dimorphic differences between male and female juvenile tusks. Thus, juvenile tusks were analyzed in a separate DFA to ensure that differences between sexes would be highlighted. The decision of whether to include both modern elephant species was also made through exploratory analysis. The juvenile DFA was run twice, once with and once without *L. cyclotis* tusks, to evaluate the effect of including two species in a single analysis. There was no substantial difference between the results of these two analyses, so the juvenile DFA reported here includes *L. africana* and *L. cylcotis*. This was not an issue for the adult elephant DFA because no tusks longer than 90 cm were referred *to L. cyclotis*.

In the fourth analysis, CVA was performed on four a priori groups: female mastodon tusks, male mastodon tusks, female elephant tusks, and male elephant tusks. This analysis was conducted to investigate morphological differences attributable to sex, regardless of genus, as well as those attributable to genus, regardless of sex. Tusks of known sex in CVA included elephant tusks assigned to a sex through DFA. This analysis did not include tusks of juveniles, as there were known juvenile elephants in the sample

Figure 3.3. Results of a DFA of 10 measurements on 21 mastodon tusks.

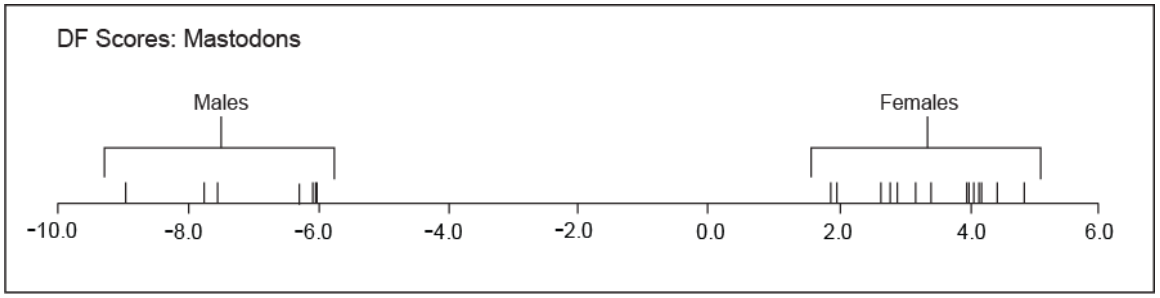


Table 3.2. Discriminant function coefficients for each variable in the DFA of mastodon tusks. Abbreviations as in Figure 3.2. Standardized coefficients are calculated from the original measurements that are standardized to have equal variance, and show the relative importance of each coefficient to the variance between groups. Unstandardized coefficients are calculated from unstandardized original measurements, and show the absolute importance of each coefficient to the variance between groups.

Variable	DF Coefficient	
	Standardized	Unstandardized
ADPC	0.418	3.629
AD	-0.552	-11.343
AC	-1.302	-16.891
MTC	-4.895	-73.270
TL	1.809	19.729
C50	3.199	42.789
C60	-0.079	-1.100
C70	2.120	32.913
C80	0.603	9.601
C90	-0.875	-14.258
(Constant)		8.627

set, but no known juvenile mastodons. Ten variables (Fig. 3.2, variables 1-5 and 8-12), the same used in the DFAs of elephant and mastodon tusks longer than 90 cm, were included in this analysis.

Results

Discriminant Function Analysis

DFA of 10 measurements on 21 mastodon tusks (Figure 3.3) shows that male and female tusks can be distinguished based on relative differences between maximum tusk circumference and circumference at 50 cm, the discriminant function (DF) coefficients that contribute the most to the variance between the groups (Table 3.2). The Wilks' Lambda test indicates there is a significant difference between male and female mastodon tusk morphology (Wilks' Lambda = 0.036; df = 10; $p < 10^{-5}$).

DFA of 10 measurements on 51 African elephant tusks (Fig. 3.4) shows that male and female tusks can be discriminated primarily based on relative differences in maximum tusk circumference and alveolar circumference (with a strong contribution from circumference at 90 cm; Table 3.3). Of the six ungrouped tusks, DFA classified one pair as female, one pair as male, and two isolated tusks as male. The Wilks' Lambda test indicates there is a significant difference between male and female elephant tusk morphology (Wilks' Lambda = 0.118; df = 10; $p < 10^{-12}$).

DFA of seven tusk measurements on 37 juvenile elephant tusks (Fig. 3.5) shows that male and female juvenile tusks can be distinguished primarily based on relative differences between the circumference at 30 cm and the circumference at 40 cm (with contributions from alveolar circumference; Table 3.4). Of the 25 ungrouped tusks, 12

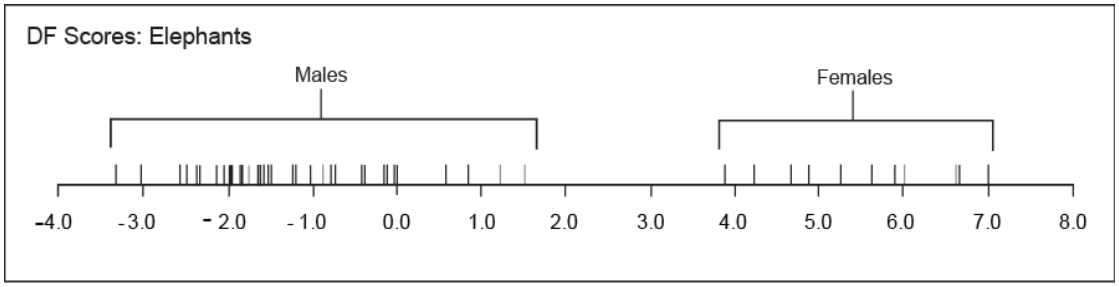


Figure 3.4. Results of a DFA of ten measurements on 51 elephant tusks. Gray lines indicate the tusks assigned to a sex by DFA (n = 6).

Table 3.3. Discriminant function coefficients for each variable in the DFA of elephant tusks greater than 90 cm in length. Abbreviations as in Figure 3.2. Differences between standardized and unstandardized coefficients are described in the caption of Table 3.2.

Variable	DF Coefficient	
	Standardized	Unstandardized
ADPC	-0.407	-5.043
AD	-0.279	-3.509
AC	4.026	59.295
MTC	-4.325	-73.622
TL	-0.065	-0.662
C50	-0.165	-2.260
C60	0.184	2.565
C70	-0.714	-10.907
C80	-1.306	-20.737
C90	1.886	31.345
(Constant)		39.135

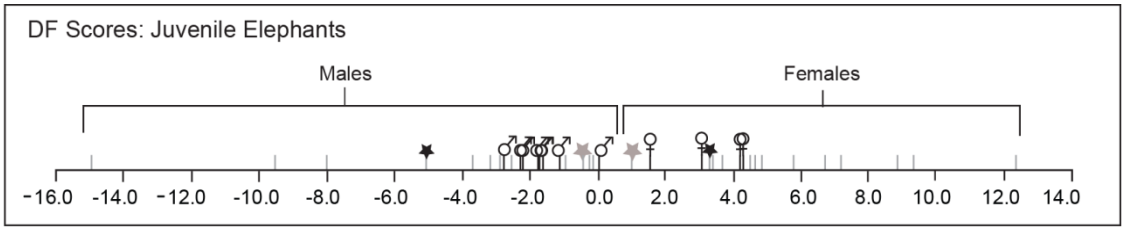


Figure 3.5. Results of a DFA of six measurements on 37 juvenile elephant tusks. Male and female symbols indicate scores of tusks from juveniles of known sex. Gray lines indicate tusks that were assigned to a group through DFA. Stars indicate two tusks from the same individual that were classified as different sexes.

Table 3.4. Discriminant function coefficients for each tusk variable in the DFA of juvenile elephant tusks. Abbreviations as in Figure 3.2. Differences between standardized and unstandardized coefficients are described in the caption of Table 3.2.

Variable	DF Coefficient	
	Standardized	Unstandardized
ADPC	-2.661	-20.108
AD	-1.774	-16.288
AC	8.894	97.954
MTC	0.578	6.647
TL	-2.395	-20.819
C30	-16.505	-252.619
C40	11.807	171.261
(Constant)		54.403

were classified as male and 13 were classified as female. For two elephants of unknown sex (AMNH 54082 and AMNH 69399), one tusk from each pair was classified as male, and the other as female. The Wilks' lambda test shows that there is a difference between group means, but the difference is not significant (Wilks' Lambda = 0.132; df = 7; p = 0.068), which is illustrated by the indistinct division between males and females on the plot of DF scores (Fig. 3.5).

Canonical Variates Analysis

CVA on tusks pre-sorted into four groups – female mastodons (n=14), male mastodons (n=7), female elephants (n=11), and male elephants (n=40) – resulted in two interpretable axes (Fig. 3.6). The first canonical variate (CV-I), which accounts for 76.1% of the between-group variance, illustrates the difference between sexes, in which males generally exhibit higher scores than females. Most eigenvector coefficients (loadings) for this variate are positive (with the exception of tusk length, which is just below zero, and thus has a negligible contribution to the variance accounted for by CV-I). Axial depth of the pulp cavity (ADPC) and maximum tusk circumference (MTC) contribute the most to the variance between sexes (Fig. 3.6B). High scores on this axis are individuals with large MTCs and ADPCs (males), and low scores are individuals with small MTCs and ADPCs (females). Thus, most of the variance between the groups is attributable to size, in which males are larger than females across all measurements, especially in maximum tusk circumference and axial depth of the pulp cavity. The Wilks' lambda test indicates that all groups are significantly different (Wilks' lambda = 0.030; df = 30; $p < 10^{-30}$).

To test the relationship between CV-I score and size, tusk volumes (used as a proxy for tusk size) were regressed on CV-I scores, following methods described in Smith and Fisher (in revision) and Chapter 2 of this dissertation. Regression of $\log_{10}$-transformed volumes on CV-I scores indicated a statistically significant relationship between CV-I and size ($p<10^{-15}$; $R^2 = 0.7825$).

The second canonical variate (CV-II), which accounts for 19.3% of the between-group variance, sorts tusks by genus, in which male and female mastodons generally exhibit higher scores than male and female elephants. The loadings that strongly contrast to sort groups along this axis are axial depth of the pulp cavity and maximum tusk circumference (Fig. 3.6C). High scores on this axis (mastodons) are associated with larger maximum tusk circumferences and relatively shallow pulp cavities, and low scores (elephants) are associated with smaller tusk circumferences and relatively deep pulp cavities. Regression of CV-II scores on tusk volume indicates no significant relationship between CV-II and size ($p = 0.1753$; $R^2 = 0.2608$).

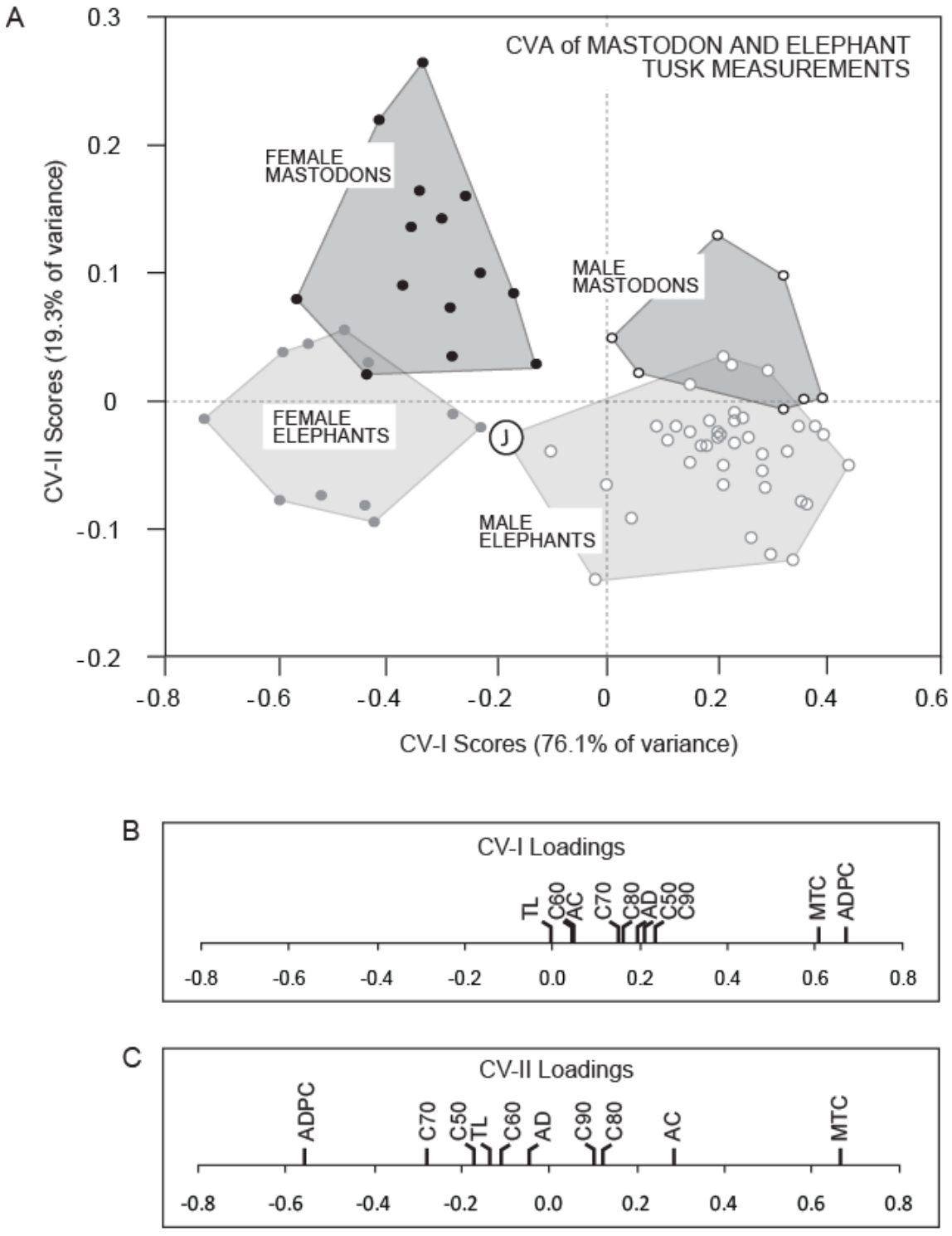
The third canonical variate accounts for less than 5% of the between-group variance. No reasonable interpretation could be made from the scores and loadings, so CV-III is here considered uninformative.

Discussion

Discriminant Function Analysis

The DF coefficients that strongly contrast to differentiate mastodon tusks by sex are maximum tusk circumference (MTC) and circumference at 50 cm (C50; Table 3.2). The contrast of these variables reflects different patterns of ontogenetic change in tusk

Figure 3.6. Graphical representation of CVA scores (A) and loadings (CV-I, B; CV-II, C) from a CVA of mastodon and elephant tusk variables. In (A), closed black circles represent female mastodons, open black circles represent male mastodons, closed gray circles represent female elephants, and open gray circles represent male elephants. “J” in A indicates the position of a juvenile male elephant tusk. Variable abbreviations as in Figure 3.2.


A
CVA of MASTODON AND ELEPHANT TUSK MEASUREMENTS
FEMALE MASTODONS
MALE MASTODONS
FEMALE ELEPHANTS
MALE ELEPHANTS
J
CV-II Scores (19.3% of variance)
CV-I Scores (76.1% of variance)
0.3
0.2
0.1
0
-0.1
-0.2
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
B
CV-I Loadings
TL
C60
AC
C70
C80
AD
C50
C90
MTC
ADPC
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
C
CV-II Loadings
ADPC
C70
C50
TL
C60
AD
C90
C80
AC
MTC
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8

circumference for each sex. In all tusks, regardless of sex, circumference increases with distance from the tip, attains relative stability at some distance from the tip, and, in older adults, gradually declines to the proximal margin. However, female tusks exhibit relatively stable circumferences earlier in life (that is, closer to the tip) than males (Fisher 1996), so C50 (usually located closer to the tip than to the proximal margin) and MTC (usually located closer to the proximal margin than to the tip) differ more in magnitude for male tusks than for female tusks. Tusks of adult males grow longer than tusks of adult females, though, so the distance between 50 cm from the tip and the location of MTC is also usually greater for males than for females. This might indicate that the loadings do not reflect ontogenetic differences in tusk circumference change between sexes, but indirectly reflect the distance between measurements. A greater difference in circumference would be expected with a greater difference between measurements. A comparison between two tusks of opposite sex but similar length, however, indicates that the young male mastodon Heisler exhibits a greater difference in magnitude between C50 and MTC values (14.9 cm) than does the older female mastodon Powers (3.9 cm), illustrating that rate of circumference change does, in fact, differ between the sexes, when standardized for tusk length.

Comparison of males and females of comparable age shows that there is less difference between sexes for C50 values than for MTC values, indicating that male and female mastodon tusks are more similar in size early in ontogeny (at 50 cm, closer to the tip) than later in ontogeny (where MTC was measured, closer to the proximal margin). This suggests that mastodon tusk dimorphism became more pronounced throughout ontogeny, and that DFA is best able to discriminate between sexes by contrasting

measurements reflecting tusk dimensions early in life to those reflecting dimensions later in life.

The DF coefficients that strongly contrast to discriminate between male and female elephants (Table 3.3) are maximum tusk circumference (MTC) and alveolar circumference (AC), with contributions from the circumference at 90 cm (C90). Values of MTC and AC are highly correlated for this data set ($R^2 = 0.9907$), and the values themselves are frequently identical, so a contrast between these variables is suspect. Likely, substantial differences between these measurements exhibited by a few males (Appendix II) erroneously inflate the importance of this contrast to the variance between sexes. Thus, morphological differences between male and female elephant tusks are interpreted based on the contrast between MTC and C90, a variable that also substantially contributes to the variance between the sexes. As in the mastodon DFA, a contrast between MTC and C90 illustrates unique ontogenetic changes in tusk circumference for each sex, in which MTC and C90 values differ more for males than for females. This is, again, related to rates of circumference change, in which male elephants increase in circumference more rapidly with distance from the tip than females (Elder 1970), and attain relative stability in circumference later in life than females. In addition, a comparison of MTC and C90 values shows that male and female elephants are more different in MTC than in C90, indicating that dimorphic differences in elephant tusks, as in mastodon tusks, become more pronounced with age.

Two solo tusks that were originally ungrouped and subsequently classified as males, USNM 49489B and FMNH 101836, are both less than 100 cm long and have no associated age information. At first glance, they bear a strong resemblance to tusks of

females. That DFA classified them as male speaks to the importance of looking at proportional tusk dimensions rather than just size, as well as the use of a multivariate approach for sexing tusks (Pilgram and Western 1986; Smith and Fisher in revision).

One of the objectives of this study was to quantify tusk dimorphism in elephants and mastodons to explore whether the character of tusk dimorphism is similar across genera. This is done here by comparing the loadings that discriminate between male and female mastodons and male and female elephants on their respective DFAs. The two DFAs (1) use identical variables, (2) present no ambiguity in the separation between sexes for either genus, and (3) show that male and female tusks, regardless of genus, have significantly different morphologies (with the exception of juveniles). Both the elephant and mastodon DFAs discriminate between sexes based on ontogenetic differences in tusk circumference, but dimorphism in mastodons is characterized by the difference between MTC and C50, and dimorphism in elephants is characterized by the difference between MTC and C90. The difference in loadings may reflect differences in the timing of the onset of pronounced tusk dimorphism in elephants and mastodons. Because the longitudinal tusk axis is essentially an axis of time, in which time moves from the tip to the pulp cavity surface (i.e., death), C50 reflects the circumference at a younger age than C90 does. In this way, sexual dimorphism in tusk form may be apparent earlier in life for mastodons than for elephants. In African elephants, pronounced sexual dimorphism is approximately commensurate with timing of maturation (as inferred by timing of first conception). Thus, mastodons may have matured at a younger age than modern elephants do.

If DFA is providing evidence for the difference in timing of maturation between elephants and mastodons, as proposed, then DFA could also be used to investigate trends in this life history parameter for mastodons throughout the Pleistocene. The introduction of extrinsic mortality factors alters life history parameters (Reznick et al. 1990; Jones et al. 2008; Fisher 2009); delayed maturation may occur as a result of reduced resources (Eberhardt 2002), and earlier maturation occurs with reduced adult survival or decrease in population densities (Charnov and Schaffer 1973; Fisher 2009). So, if there are changes in the timing of the onset of maturation in mastodons throughout the Pleistocene, the nature of these changes could be used to evaluate proposed causes of mastodon extinction (Fisher 2009). For example, if the onset of maturation occurred earlier in ontogeny toward the end of the Pleistocene, then reduction of resources was not a major factor in mastodon extinction. Instead, mastodons may have been driven to mature earlier by increased adult mortality rates potentially caused by the preferential hunting of older (thus larger) mastodons. If older mastodons were preferentially hunted, then mastodon life span would decrease; earlier maturation could counteract the reduction in reproductive success caused by a reduced life span. In addition, a preferential decrease in the male population would result in reduced male-to-male competition for mates. This scenario could drive younger (thus smaller) males to mature at a younger age to fill the role typically held by older males (Fisher 2009).

All juvenile elephant tusks of known sex were correctly classified by DFA (Fig. 3.5). In this analysis, there was a difference between group means, but this difference was not statistically significant. These results suggest that juvenile male and female tusks may be morphologically distinct, but morphological differences are subtle and difficult to

characterize. This difficulty is illustrated by DFA twice classifying one tusk in a pair from a single individual (of unknown sex) as female and the other tusk as male. Thus, the use of tusk morphology to assess the sex of a juvenile is dubious, although this conclusion is tentative due to the small number of juveniles of known sex (n = 12) included in this analysis.

Canonical Variates Analysis

CVA of mastodon and elephant tusks indicates that the two genera exhibit strong similarities in tusk dimorphism (Fig. 3.6A), in which male tusks (more positive scores) are generally larger across all variables than female tusks (more negative scores), especially in MTC and ADPC (Fig. 3.6B). This difference likely reflects differences in tusk growth and use between sexes, regardless of genus. As observed in African elephants, males use their robust tusks primarily as weapons in intra-sex combats for access to mates (Lee and Moss 1995), and females use their more gracile tusks for food gathering and to ward off predators or intimidate unfamiliar family units from desirable food and water sources (Moss 1988; Haynes 1991).

Although male and female point clouds do not overlap for either genus along CV-I, there is a greater distance between male and female mastodons than there is between male and female elephants. This suggests that there is a greater difference between male and female mastodon tusks than between male and female elephant tusks. However, this observation is specific to the tusks in this analysis, which includes one known juvenile elephant (AMNH 52093 L). This tusk (which is greater than 90 cm in length, required by this CVA) plots closer to female elephant tusks than to all other males (Fig. 3.6).

Juveniles are less dimorphic than adults in body size (Lee and Moss 1995) and tusk size (this study; Fig. 3.4), so a juvenile male is expected to appear "more female." Thus, the inclusion of AMNH 52093 L, not the difference in degree of dimorphism between genera, resulted in a less distinct separation between male and female elephants on CV-I.

There is considerable overlap between female mastodons and elephants and male mastodons and elephants on CV-I. The male mastodon point cloud is completely enclosed within the male elephant point cloud on this axis; their shared space on CV-I indicates that male mastodon and male elephant tusks are similar in form across all tusk variables. There is also considerable overlap between the female mastodon and the female elephant point clouds along CV-I. However, the female mastodon point cloud is shifted slightly to the right of the female elephant point cloud on CV-I, with most of the mastodons scoring greater than -0.4, and most of the elephant scores less than -0.4. This suggests that female mastodon tusks are slightly larger across all tusk measurements than female elephant tusks. Overall, the considerable overlap between tusks of mastodons and elephants of the same sex illustrates that there is a characteristic tusk form for males and a characteristic tusk form for females that is shared across these genera.

CV-II sorts groups by taxon by contrasting MTC with ADPC (Fig. 3.5C). Higher-scoring individuals (mastodons) have larger MTCs and smaller ADPCs, and lower-scoring individuals (elephants) have smaller MTCs and larger ADPCs. This could indicate that tusks of elephants are more slender than tusks of mastodons, an observation consistent with other differences between elephant and mastodon skeletons. For example, midshaft femoral circumference is greater in mastodons than in elephants (Haynes 1991), and mastodon metapodials are more robust than elephant metapodials (Smith, pers. obs.).

The difference between elephant and mastodon tusk morphology illustrated by CV-II suggests that elephants evolved more gracile skeletons since mastodons and elephants diverged from a most recent common ancestor, that mastodons evolved more robust skeletons since this divergence, or that both processes occurred. Future studies involving morphometric analyses on additional skeletal elements from both genera could more fully evaluate proposed differences in robustness attributable to genus.

CV-II accounts for much less of the between-group variance than CV-I (19.3% versus 76.1%). The difference in proportion of variance between axes shows that tusks of different genera of the same sex are more similar to each other than they are to tusks of the opposite sex of the same genus, and that more of the differences in tusk morphology can be attributed to sex rather than to generic differences. The sorting of tusks by sex along CV-I shows that female elephants and mastodons exhibit strong similarities in tusk form, and that male elephants and mastodons exhibit strong similarities in tusk form. The offset between genera on CV-II indicates that elephants and mastodons exhibit differences in tusk morphology, but this difference does not override the fundamentally similar character of their tusk dimorphism.

Conclusions

Overall, this study shows that mastodons and African elephants exhibit strong similarities in the character of tusk dimorphism, in which similar ontogenetic changes in tusk circumference across the genera can be used to discriminate between sexes (Figs. 3.2 and 3.3). Furthermore, males of both species are larger in tusk dimensions than females, especially in maximum tusk circumference and axial depth of the pulp cavity (Fig. 3.6).

If this pattern of tusk dimorphism was inherited from a most recent common ancestor, then there have been limited evolutionary changes in tusk dimorphism since mastodons and elephants diverged from a most recent common ancestor approximately 20 million years ago, and selection pressures favoring these patterns of dimorphism remained relatively constant since this divergence. If selection pressures favored this pattern of dimorphism in mastodons, as it does in elephants, then it must have contributed to the reproductive success of mastodons, as it does for elephants. Thus, it is probable that male mastodons, like male elephants, relied on large tusk size for reproductive success. Comparably, it is probable that female mastodons, like female elephants, invested more energy into male calves than female calves in order to promote rapid early growth in males that prepared them for future reproductive success.

Much about the behavior of a taxon can be inferred from the degree of sexual dimorphism when males are larger than females. Modern elephants, strongly dimorphic in body and tusk size, exhibit behaviors typical of dimorphic species. Because elephants and mastodons exhibit quantitative similarities in tusk dimorphism, mastodons likely exhibited these behaviors as well. However, as the separate DFAs of mastodons and elephants illustrate, the character of tusk dimorphism across genera is similar, but not identical. This difference may be attributable to differences in the timing of the onset of dimorphism, and thus the onset of sexual maturity, rather than the character of dimorphism itself. If mastodons matured earlier than elephants, as the DFAs suggest, then other life history parameters, such as lifespan or inter-birth interval, could differ as well. Because of the strong similarities in the character of tusk dimorphism, however, it is unlikely that there were many differences in behavior or social structure between the two.

Haynes (1991) suggested that strong similarities in behavior among modern African and Asian elephants, which diverged from a most recent common ancestor over five million years ago (Maglio 1973) and have since come to occupy non-overlapping geographic ranges and a wide variety of habitats, may be the result of inheriting these traits from their common ancestor. Because African elephants and mastodons exhibit similar tusk dimorphism, there is a strong possibility that many behavioral traits shared by modern elephant species emerged deeper within Proboscidea, coincident with the emergence of modern patterns of dimorphism. In this way, modern proboscidean behavior may have emerged in Proboscidea at least as early as the Miocene, prior to the most recent common ancestor of mastodons and African elephants (Fig. 3.1; Gheerbrant and Tassy 2009). However, this proposition is based on only two proboscidean lineages, so future studies on the evolution of tusk dimorphism in Proboscidea need to be conducted in order to evaluate more fully when modern tusk dimorphism, and modern elephant behavior, emerged.

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Appendix I. Sexual Dimorphism in Proboscidea.

Reports of sexual dimorphism in proboscidean tusks, crania, and post-crania (for taxa other than mastodons and modern elephants) are as follows. Dimorphism has been identified in the crania of *Phosphatherium* (Gheerbrant et al. 2005) and *Numidotherium* (Noubhani et al. 2008); the mandible of the Deinotherid *Prodeinotherium* (Huttunen and Gohlich 2002); the crania and mandibles of the Amebelodontid *Archaeobelodon fiholi* (Tassy 1996) and the trilophodont gomphothere *Gophotherium augustidens* (Tassy 1996); the molars of the tetralophodont gomphothere *Stegomastodon* (Madden 1986); and the pelvis of the Elephantid *Mammuthus* (mammoths; Lister 1996). Tusk dimorphism has been identified in several *Mammuthus* species (Averianov 1996) and the trilophodont gomphothere *Gophotherium augustidens* (Tassy 1996), in which males exhibit larger tusk dimensions than females of similar age. The phylogenetic position of each taxon can be seen in Figure 3.1. Other proboscidean taxa than listed here likely exhibit sexual dimorphism, but reports of dimorphism in these taxa were not found.

Appendix II. Measurements (cm) used in this study. Mastodons (*Mammut americanum*) are designated by "*M.a.*" and African elephants (*Loxodonta africana*, *Loxodonta cyclotis*) are designated by "*L.a.*" or "*L.c.*"

Measurements (cm)

Name	Sex	Species	ADPC	AD	AC	MTC	TL	C30	C40	C50	C60	C70	C80	C90
Hyde Park	M	*M.a.*	98.0	59.0	55.0	57.9	279.0	-	-	31.0	33.5	35.8	38.3	40.5
Buesching	M	*M.a.*	91.0	64.0	55.0	55.0	290.5	-	-	31.6	32.8	34.6	36.9	39.0
Pleasant Lake	M	*M.a.*	68.0	44.0	58.0	61.0	278.8	-	-	35.0	38.8	41.0	43.5	46.0
Heisler	M	*M.a.*	65.0	47.0	39.0	39.0	133.0	-	-	24.1	26.5	28.8	30.7	31.7
I3NW-117	M	*M.a.*	48.1	66.0	48.7	52.2	201.0	-	-	34.6	37.7	39.6	42.1	44.6
I2SE-113	M	*M.a.*	87.6	65.0	46.8	49.3	179.0	-	-	30.2	30.5	36.1	38.0	42.1
I2NE-170	M	*M.a.*	51.6	57.0	32.9	38.6	146.8	-	-	23.4	26.0	29.4	31.5	32.9
North Java	F	*M.a.*	30.0	39.0	31.2	31.4	152.9	-	-	27.2	28.3	28.9	30.2	31.3
Powers	F	*M.a.*	26.0	38.0	32.0	33.0	132.4	-	-	27.1	28.7	29.7	31.2	32.5
Laur	F	*M.a.*	24.0	37.0	27.5	28.9	119.0	-	-	25.9	26.4	26.8	27.5	28.2
Miller	F	*M.a.*	36.0	40.0	27.0	27.0	95.4	-	-	23.6	24.8	24.8	25.1	25.1
Sheathelm	F	*M.a.*	32.0	40.0	28.0	28.4	124.0	-	-	22.2	24.9	27.0	28.2	27.3
Bothwell 2-14	F	*M.a.*	40.5	46.5	30.0	31.7	136.0	-	-	26.5	28.1	29.2	30.4	31.2
Bothwell Pen-51	F	*M.a.*	24.3	42.2	31.0	31.0	98.4	-	-	30.9	30.4	29.0	28.2	25.6
FM 26631	F	*M.a.*	26.7	42.1	22.8	26.5	99.6	-	-	22.6	23.1	24.2	25.6	26.5
SMM 64-14-1 L	F	*M.a.*	22.4	42.0	20.5	21.3	120.5	-	-	17.0	18.4	19.7	20.5	21.3
SMM 64-14-1 R	F	*M.a.*	30.1	45.4	20.4	22.9	116.0	-	-	18.3	19.0	20.3	20.8	21.6
J3SW-186	F	*M.a.*	32.2	48.5	31.7	32.0	120.5	-	-	29.2	30.5	31.6	32.0	31.1
F10SW-71	F	*M.a.*	17.1	42.6	29.3	29.5	109.6	-	-	27.8	28.6	29.3	29.5	29.1
I3NW-110	F	*M.a.*	22.3	39.5	29.8	29.8	112.5	-	-	26.8	28.0	29.3	29.8	29.4
F9SW-106	F	*M.a.*	16.6	44.8	33.7	34.0	120.5	-	-	29.7	32.6	33.4	34.0	33.2
FMNH No.3 R341/2 R	M	*L.a.*	108.4	60.9	42.8	50.8	217.4	-	-	31.6	33.7	35.2	36.5	38.0
FMNH No.3 R341/2 L	M	*L.a.*	105.4	64.3	41.2	50.8	222.3	-	-	28.6	30.6	32.2	34.1	35.5
FMNH K40HB R	M	*L.a.*	67.5	56.1	39.1	50.8	275.9	-	-	23.7	25.6	28.1	29.4	31.2
FMNH K40HB L	M	*L.a.*	70.0	56.7	39.5	50.8	275.5	-	-	24.6	26.4	28.6	29.9	31.6
FMNH 101836	U	*L.a.*	49.5	31.3	27.7	29.9	99.3	-	-	25.8	27.0	28.5	28.7	29.9
FMNH no catalog #	U	*L.a.*	24.3	30.1	13.2	14.4	68.1	12.6	13.3	-	-	-	-	-
FMNH 53749 L	U	*L.a.*	31.4	22.8	12.0	12.3	40.2	12.3	11.9	-	-	-	-	-
FMNH 53749 R	U	*L.a.*	29.1	22.1	12.6	12.8	43.7	12.8	12.6	-	-	-	-	-
USNM 165176 L	M	*L.a.*	71.5	102.0	38.8	38.8	156.0	-	-	26.3	28.0	29.7	31.0	32.0
USNM 165499 L	M	*L.a.*	72.3	48.0	38.0	40.2	138.0	-	-	31.6	33.2	35.6	36.9	38.4
USNM 165499 R	M	*L.a.*	69.5	51.8	36.0	39.6	155.8	-	-	27.0	29.6	30.8	32.9	34.4

Measurements (cm)

Name	Sex	Species	ADPC	AD	AC	MTC	TL	C30	C40	C50	C60	C70	C80	C90
USNM 165176 R	M	*L.a*	79.5	55.5	40.1	40.6	187.0	-	-	31.0	32.9	34.2	34.2	36.8
USNM 49759 R	M	*L.a.*	85.0	64.0	46.0	47.2	195.0	-	-	34.5	36.5	38.7	40.5	41.9
USNM 22147 R	M	*L.a.*	74.5	57.0	39.2	39.3	228.0	-	-	26.3	28.5	30.7	32.6	34.0
USNM 22147 L	M	*L.a.*	59.5	55.0	32.5	33.1	220.0	-	-	31.6	31.4	31.7	31.9	32.5
USNM 163318 L	M	*L.a.*	83.5	55.0	39.2	39.9	164.0	-	-	38.5	38.7	38.4	38.6	38.6
USNM 163318 R	M	*L.a.*	59.5	56.0	39.2	39.3	183.0	-	-	35.5	36.4	37.8	38.8	39.0
USNM 304615 R	M	*L.a.*	89.5	78.0	50.8	51.0	199.0	-	-	42.0	43.9	45.6	47.0	47.8
USNM 304615 L	M	*L.a.*	83.5	73.0	50.3	50.7	212.0	-	-	39.1	41.0	43.2	45.1	46.6
USNM KEB78 L	M	*L.a.*	75.0	61.0	38.2	40.3	153.0	-	-	31.3	33.3	35.1	36.4	38.2
USNM KEB78 R	M	*L.a.*	72.5	59.0	38.8	40.2	139.0	-	-	33.2	24.8	36.3	37.3	38.3
USNM KEB385 L	M	*L.a.*	66.2	68.0	42.0	43.2	193.0	-	-	33.7	36.4	38.4	40.3	41.3
USNM KEB385 R	M	*L.a*	68.5	61.5	41.6	42.4	187.0	-	-	35.3	37.2	38.7	39.9	41.3
USNM Mum/38/73/5 L	M	*L.a.*	76.5	68.5	49.1	49.1	162.5	-	-	43.6	45.3	46.9	48.1	48.1
USNM Mum/38/73/4 R	M	*L.a.*	73.5	65.0	47.5	47.5	157.0	-	-	43.0	44.8	46.2	46.9	47.4
USNM LKA/74/1006 R	M	*L.a.*	63.5	45.5	29.1	32.2	119.5	-	-	26.4	27.7	28.4	29.3	30.2
USNM LKA/64/1 L	M	*L.a.*	75.5	70.0	41.4	41.8	146.0	-	-	40.1	40.7	41.4	41.6	41.7
USNM 49489B R	M	*L.a.*	71.5	44.0	27.0	27.7	98.0	-	-	27.0	27.1	27.3	27.5	27.7
USNM 220146 R	M	*L.c.*	25.2	23.2	21.0	21.0	73.8	19.5	20.2	-	-	-	-	-
USNM 220146 L	M	*L.c.*	24.2	24.3	20.7	20.7	77.5	19.0	19.9	-	-	-	-	-
USNM 49553	U	*L.a.*	38.1	21.5	19.2	21.0	72.5	16.6	17.4	-	-	-	-	-
USNM 61706 R	U	*L.a.*	26.4	20.5	14.8	14.9	62.0	13.6	14.7	-	-	-	-	-
USNM 61706 L	U	*L.a.*	21.2	20.0	14.6	14.8	57.8	13.9	14.7	-	-	-	-	-
AMNH 52093 L	M	*L.a*	47.6	34.5	24.6	27.5	92.0	20.3	22.6	23.9	25.2	26.0	27.4	27.5
AMNH 52093 R	M	*L.a.*	48.3	32.5	24.9	27.9	88.0	20.7	22.7	-	-	-	-	-
AMNH 51944 R	M	*L.a.*	72.9	66.0	44.0	44.8	199.0	-	-	31.8	34.3	36.3	38.2	39.2
AMNH 51944 L	M	*L.a.*	77.5	44.0	44.0	45.1	175.0	-	-	30.9	33.6	36.1	38.0	39.3
AMNH 51937 R	M	*L.a.*	87.4	61.0	41.7	45.0	189.0	-	-	30.8	32.7	34.6	36.2	37.5
AMNH 51937 L	M	*L.a.*	77.4	52.0	41.0	43.4	194.0	-	-	28.7	30.4	32.5	34.6	36.0
AMNH 80598 L	M	*L.a.*	54.2	72.0	39.1	40.7	164.0	-	-	33.3	36.1	38.3	39.0	38.8
AMNH 80598 R	M	*L.a.*	59.0	68.0	39.4	40.0	141.0	-	-	38.4	39.4	38.7	39.7	39.8
AMNH 217684 R	M	*L.a.*	67.1	50.0	41.2	41.4	156.0	-	-	36.2	38.2	39.9	40.5	41.2
AMNH 217684 L	M	*L.a.*	60.2	59.0	44.7	44.7	155.0	-	-	37.4	39.3	40.6	41.9	44.4
AMNH 51939 R	M	*L.a.*	81.5	49.5	42.9	44.9	174.5			30.8	33.7	36.9	38.2	39.3
AMNH 51939 L	M	*L.a.*	80.4	64.5	44.1	44.8	200.0	-	-	32.6	35.3	36.9	38.4	40.0

Measurements (cm)

Name	Sex	Species	ADPC	AD	AC	MTC	TL	C30	C40	C50	C60	C70	C80	C90
AMNH 39083 R	M	*L.a.*	100.5	60.0	47.5	47.7	265.0	-	-	33.5	35.0	36.3	38.4	40.4
AMNH 39083 L	M	*L.a.*	96.5	56.0	46.5	47.4	255.0	-	-	34.9	35.8	38.3	40.3	41.4
AMNH 120444 L	M	*L.a.*	58.7	62.0	45.9	46.1	220.0	-	-	35.2	36.7	38.3	39.8	41.2
AMNH 120444 R	M	*L.a.*	72.1	57.0	49.9	50.6	238.0	-	-	34.5	36.5	38.9	41.0	43.1
USNM 270993 L	F	*L.a.*	41.0	34.8	19.6	19.8	116.0	-	-	17.2	17.4	18.2	19.6	19.8
USNM 270993 R	F	*L.a.*	42.1	36.0	19.4	19.9	116.0	-	-	17.1	17.7	19.0	19.4	19.8
USNM 165501 L	F	*L.a.*	41.0	38.7	27.2	27.2	153.7	-	-	24.0	24.9	25.7	26.0	26.7
USNM 165501 R	F	*L.a.*	38.5	40.2	25.9	26.1	157.2	-	-	21.5	22.9	23.9	24.7	25.5
USNM 163319 R	F	*L.a.*	27.9	34.5	22.9	23.3	123.5	-	-	22.3	22.8	23.1	23.3	22.9
USNM 163319 L	F	*L.a.*	24.7	38.0	22.8	22.8	122.5	-	-	21.3	22.4	22.5	22.6	22.3
AMNH 88403 L	F	*L.a.*	37.3	33.0	16.5	18.8	99.0	-	-	15.2	16.6	16.5	16.8	18.8
AMNH 88403 R	F	*L.a.*	33.6	29.0	16.6	17.0	91.0	-	-	15.7	16.5	16.6	16.9	17.0
AMNH 51936 R	F	*L.a.*	25.5	23.0	15.0	16.4	94.0	-	-	13.7	14.7	15.8	16.1	16.4
AMNH 51949	F	*L.a.*	44.8	35.5	20.2	21.2	89.0	17.9	19.6	-	-	-	-	-
AMNH 89453	F	*L.c.*	25.2	19.5	15.1	15.5	50.5	15	15.2	-	-	-	-	-
AMNH no catalog # R	U	*L.a.*	23.7	40.5	20.6	20.7	94.5	-	-	20.0	20.7	20.7	19.9	19.7
AMNH no catalog # L	U	*L.a.*	23.0	37.0	19.8	19.8	99.0	-	-	19.3	19.7	19.8	19.2	19.0
AMNH 51950 L	U	*L.a.*	32.8	32.0	15.6	16.0	62.0	15.5	15.7	-	-	-	-	-
AMNH 51947 L	U	*L.a.*	36.6	32.0	16.4	17.1	78.0	14.8	15.7	-	-	-	-	-
AMNH 51947 R	U	*L.a.*	35.2	31.5	16.9	17.6	77.5	15.4	16.2	-	-	-	-	-
AMNH 51934 R	U	*L.a.*	7.4	30.0	23.6	24.0	84.0	21.2	23.1	-	-	-	-	-
AMNH 51934 L	U	*L.a.*	12.4	29.5	21.9	22.8	87.0	19.6	19.7	-	-	-	-	-
AMNH 54082 L	U	*L.a.*	34.6	21.0	16.3	18.0	56.0	15.4	17.4	-	-	-	-	-
AMNH 54082 R	U	*L.a.*	33.1	24.6	15.4	17.8	55.6	15.8	16.8	-	-	-	-	-
AMNH 119510 L	U	*L.c.*	30.5	20.5	16.8	17.8	67.5	13.9	15.7	-	-	-	-	-
AMNH 119510 R	U	*L.c.*	31.9	18.0	16.7	18.0	69.0	13.8	15.2	-	-	-	-	-
AMNH 69399 L	U	*L.a.*	42.6	27.0	18.8	18.7	70.0	17.0	18.7	-	-	-	-	-
AMNH 69399 R	U	*L.a.*	42.3	25.0	18.8	18.8	69.5	17.1	18.4	-	-	-	-	-
AMNH 81897 L	U	*L.c.*	48.4	31.5	23.2	26.1	82.0	19.3	21.4	-	-	-	-	-
AMNH 54082 R	U	*L.a.*	32.0	37.0	19.0	20.0	73.0	19.5	19.2	-	-	-	-	-
AMNH 54082 L	U	*L.a.*	42.8	33.5	19.1	20.6	75.0	18.1	19.0	-	-	-	-	-
AMNH 51938 R	U	*L.a.*	46.6	41.0	22.9	26.3	84.0	21.1	22.5	-	-	-	-	-
AMNH 51938 L	U	*L.a.*	46.0	41.5	22.7	26.7	86.5	20.5	22.0	-	-	-	-	-

Measurements (cm)

Name	Sex	Species	ADPC	AD	AC	MTC	TL	C30	C40	C50	C60	C70	C80	C90
AMNH 39083 R	M	*L.a.*	100.5	60.0	47.5	47.7	265.0	-	-	33.5	35.0	36.3	38.4	40.4
AMNH 39083 L	M	*L.a.*	96.5	56.0	46.5	47.4	255.0	-	-	34.9	35.8	38.3	40.3	41.4
AMNH 120444 L	M	*L.a.*	58.7	62.0	45.9	46.1	220.0	-	-	35.2	36.7	38.3	39.8	41.2
AMNH 120444 R	M	*L.a.*	72.1	57.0	49.9	50.6	238.0	-	-	34.5	36.5	38.9	41.0	43.1
USNM 270993 L	F	*L.a.*	41.0	34.8	19.6	19.8	116.0	-	-	17.2	17.4	18.2	19.6	19.8
USNM 270993 R	F	*L.a.*	42.1	36.0	19.4	19.9	116.0	-	-	17.1	17.7	19.0	19.4	19.8
USNM 165501 L	F	*L.a.*	41.0	38.7	27.2	27.2	153.7	-	-	24.0	24.9	25.7	26.0	26.7
USNM 165501 R	F	*L.a.*	38.5	40.2	25.9	26.1	157.2	-	-	21.5	22.9	23.9	24.7	25.5
USNM 163319 R	F	*L.a.*	27.9	34.5	22.9	23.3	123.5	-	-	22.3	22.8	23.1	23.3	22.9
USNM 163319 L	F	*L.a.*	24.7	38.0	22.8	22.8	122.5	-	-	21.3	22.4	22.5	22.6	22.3
AMNH 88403 L	F	*L.a.*	37.3	33.0	16.5	18.8	99.0	-	-	15.2	16.6	16.5	16.8	18.8
AMNH 88403 R	F	*L.a.*	33.6	29.0	16.6	17.0	91.0	-	-	15.7	16.5	16.6	16.9	17.0
AMNH 51936 R	F	*L.a.*	25.5	23.0	15.0	16.4	94.0	-	-	13.7	14.7	15.8	16.1	16.4
AMNH 51949	F	*L.a.*	44.8	35.5	20.2	21.2	89.0	17.9	19.6	-	-	-	-	-
AMNH 89453	F	*L.c.*	25.2	19.5	15.1	15.5	50.5	15	15.2	-	-	-	-	-
AMNH no catalog # R	U	*L.a.*	23.7	40.5	20.6	20.7	94.5	-	-	20.0	20.7	20.7	19.9	19.7
AMNH no catalog # L	U	*L.a.*	23.0	37.0	19.8	19.8	99.0	-	-	19.3	19.7	19.8	19.2	19.0
AMNH 51950 L	U	*L.a.*	32.8	32.0	15.6	16.0	62.0	15.5	15.7	-	-	-	-	-
AMNH 51947 L	U	*L.a.*	36.6	32.0	16.4	17.1	78.0	14.8	15.7	-	-	-	-	-
AMNH 51947 R	U	*L.a.*	35.2	31.5	16.9	17.6	77.5	15.4	16.2	-	-	-	-	-
AMNH 51934 R	U	*L.a.*	7.4	30.0	23.6	24.0	84.0	21.2	23.1	-	-	-	-	-
AMNH 51934 L	U	*L.a.*	12.4	29.5	21.9	22.8	87.0	19.6	19.7	-	-	-	-	-
AMNH 54082 L	U	*L.a.*	34.6	21.0	16.3	18.0	56.0	15.4	17.4	-	-	-	-	-
AMNH 54082 R	U	*L.a.*	33.1	24.6	15.4	17.8	55.6	15.8	16.8	-	-	-	-	-
AMNH 119510 L	U	*L.c.*	30.5	20.5	16.8	17.8	67.5	13.9	15.7	-	-	-	-	-
AMNH 119510 R	U	*L.c.*	31.9	18.0	16.7	18.0	69.0	13.8	15.2	-	-	-	-	-
AMNH 69399 L	U	*L.a.*	42.6	27.0	18.8	18.7	70.0	17.0	18.7	-	-	-	-	-
AMNH 69399 R	U	*L.a.*	42.3	25.0	18.8	18.8	69.5	17.1	18.4	-	-	-	-	-
AMNH 81897 L	U	*L.c.*	48.4	31.5	23.2	26.1	82.0	19.3	21.4	-	-	-	-	-
AMNH 54082 R	U	*L.a.*	32.0	37.0	19.0	20.0	73.0	19.5	19.2	-	-	-	-	-
AMNH 54082 L	U	*L.a.*	42.8	33.5	19.1	20.6	75.0	18.1	19.0	-	-	-	-	-
AMNH 51938 R	U	*L.a.*	46.6	41.0	22.9	26.3	84.0	21.1	22.5	-	-	-	-	-
AMNH 51938 L	U	*L.a.*	46.0	41.5	22.7	26.7	86.5	20.5	22.0	-	-	-	-	-

Chapter 4

Age, sex, and seasons of death for individual American mastodons (*Mammut americanum*) from the Bothwell Site, northwestern Indiana, USA

Abstract

The Bothwell Site in northwestern Indiana (Great Lakes region, USA) produced an assemblage of late Pleistocene (11,440 ± 60 BP) faunal remains, including thirteen American mastodon (*Mammut americanum*) tusks. Analyses of tusk dimensions and growth increments in dentin indicate that at least eight, and possibly all tusks belong to reproductive-age females. Sites with remains of multiple female mastodons are extremely rare, and the tusks are analyzed here to determine what might have led to formation of such an assemblage. Age and sex demographics of the mastodons are similar to those expected for a matriarchal family unit, raising the possibility of a single catastrophic mortality event. However, seasonal variation in the oxygen isotope composition of carbonate in tusk dentin allowed determination of season of death for four individuals, and these analyses indicate that there were two or more distinct mastodon mortality events at the Bothwell site. Patterns in sub-annual variation in the carbon isotope composition of carbonate in tusk dentin suggest that the mastodons experienced similar seasonal changes in diet for the years just prior to their deaths. Carbon isotope analyses of dentin collagen indicate that the mastodons consumed a diet of mainly C_3 plants. Causes of death are unresolved, but the evidence for sustained growth rates prior to death

suggests that nutritional stress was not a factor. Entrapment is also judged to have been unlikely. Evidence from tusk data suggests that the site could represent a Paleoindian meat cache. Further studies on bone modification and duration of fossil accumulation will aid in evaluation of these hypotheses.

Introduction

The Bothwell site was discovered in 2005, in Hebron, Porter County, Indiana, during excavation for a pond on private property (Fig. 4.1). The site yielded an assemblage of over 300 skeletal elements from late Pleistocene mammals, including material from American mastodons (*Mammut americanum*), *Castoroides* sp., and currently unidentified artiodactyls. Most material, although damaged by a bulldozer during excavation of the pond, appears to be associated with mastodons. Thirteen mastodon tusks were recovered, indicating the presence of seven to thirteen mastodons (Table 4.1). This assemblage is unusual because all tusks are relatively slender for their length, suggesting that they belonged to females (Fisher 1996). Female mastodons are less abundant than male mastodons in the late Pleistocene fossil record of the Great Lakes-region, and a site with multiple females is especially rare. In addition, mastodons most frequently occur in isolation, with only a few sites producing multiple-mastodon assemblages (Haynes and Klimowicz 2003). For example, out of 211 mastodon sites in Michigan (Abraczinskas 1993), only three sites yielded more than one individual (Fisher 2009).

There are three species of living elephants, the African savannah elephant (*Loxodonta africana*), the African forest elephant (*Loxodonta cyclotis*), and the Asian

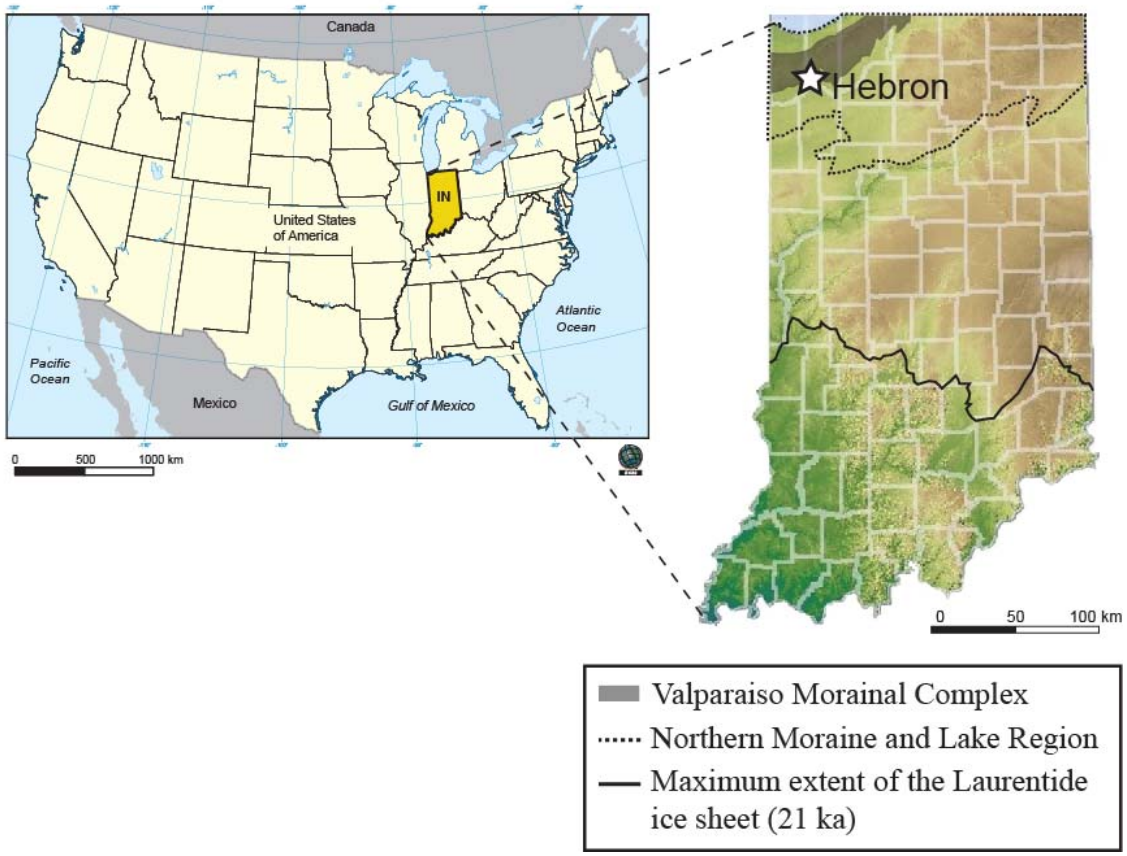


Figure 4.1. Location of the Bothwell Site (Hebron, IN). The Indiana map is from the Indiana Geological Survey (http://igs.indiana.gov). Boundaries of the Valparaiso Morainal Complex, the Northern Moraine and Lake Region, and the maximum extend of the Laurentide ice sheet were applied using Gray (2000).

Table 4.1. Summary of Bothwell Site mastodon tusks. Tusks are arranged in order of completeness. Ages are the number of annual increments in the tusk, unless otherwise noted. An "e" indicates an estimated measurement. The two tusks with italicized field numbers are a hypothesized pair.

	Field Number	Condition	Age	Tusk Side	Maximum Tusk Circumference (cm)	Total Length (cm)	Pulp Cavity Depth (cm)
1.	2-14[a]	complete tusk	22	Left	31.7	136.0	40.5
2.	*2-36*[a,b]	complete tusk	25	Left	29.8	109.1	33.9
3.	*Pen-62*[a,b]	complete tusk	29	Right	32.3	114.3	32.0
4.	Pen-50[a]	complete tusk	19	Left	29.2	95.3	38.8
5.	Pen-51[a]	complete tusk	31	Left?	30.9	98.4	24.3
6.	M-1[a,b]	proximal and distal portion	30	Right?	33.5 (e)	124.2 (e)	19.4
7.	Pen-2[a,b]	proximal portion with tip fragments	24	Right?	29.1 (e)	n/a	26.9
8.	2-22[a,b]	proximal portion	29	Unknown	33.0	n/a	29.5
9.	Pen-52	distal portion	Unknown	Left?	n/a	n/a	n/a
10.	Pen-54	distal portion	Unknown	Left?	n/a	n/a	n/a
11.	Pen-60	distal portion	Unknown	Unknown	n/a	n/a	n/a
12.	Pen-61	distal portion	Unknown	Unknown	n/a	n/a	n/a
13.	Pen-63	distal portion	Unknown	Unknown	n/a	n/a	n/a
14.	Pen-73	cementum fragments only	Unknown	Unknown	n/a	n/a	n/a

[a] included in the morphologic analysis of sex (Fig. 4.6)

[b] aged by morphologic comparison (Fig. 4.7)

elephant (*Elephas maximus*). All modern elephants exhibit matriarchal family units consisting of related females and their juvenile offspring (Moss 1988; Vidya and Sukumar 2005). African elephants (both *L.africana* and *L.cyclotis*) and mastodons exhibit similar patterns of tusk dimorphism, in which males and females, of either genus, exhibit a characteristic tusk form unique to their sex (Chapter 3, this dissertation). Asian elephants also exhibit tusk dimorphism, in which males exhibit larger tusks than females of the same age. However, female tusks often do not erupt or are not developed (Sukumar 1989). Thus, a detailed comparison of mastodon and Asian elephant tusk dimorphism has not been performed.

Characteristics of social structure and behavior can be inferred for mammalian species based on the degree of dimorphism, when males are larger than females (e.g., Berger et al. 2001). Males are larger than females in both African elephants and mastodons, and the two groups share patterns of tusk dimorphism (Chapter 3, this dissertation). Because tusk dimorphism is linked to social structure in elephants, female mastodons, like female elephants, most likely lived in matriarch family units. Thus, the recovery of multiple female mastodons from a single site raises the question: were the Bothwell mastodons members of a single matriarchal family unit?

This study investigates the processes that led to formation of the Bothwell mastodon assemblage using data collected from tusks. Tusks are excellent sources of paleoecological data because they grow continuously by accretion, recording changes in morphology, incremental growth rate and stable isotope composition throughout the life of an individual. Tusk morphology can be used to infer the sex and age of an individual (Fisher 2008; Smith and Fisher in revision; Chapter 2, this dissertation), and analyses of

tusk growth rate and compositional change can be used to identify life history events such as weaning (Rountrey et al. 2007) and, potentially, pregnancy (e.g., Fisher and Fox 2003; Fisher et al. 2008; Chapter 5, this dissertation).

Recent studies (Fisher and Fox 2003, 2007) have used seasonal variation in the oxygen isotope composition of tusk and tooth dentin to infer season and simultaneity of death for multiple proboscideans from a single fossil assemblage. Evidence of season of death for multiple individuals at a single site can be used to investigate processes of site formation. For example, if individuals died in different seasons, then there must have been more than one mortality event at the site, and there may have been as many causes of death as there were number of mortality events. If individuals died in the same season, however, multiple deaths may have been caused by a single, catastrophic event. This study applies morphological, growth rate, and serial stable isotope analyses to Bothwell mastodon tusks in order to determine the sex, age, number of individuals and season and simultaneity of mortality events. This information is used to evaluate whether Bothwell mastodons were members of a single matriarchal family unit. A matriarchal family unit is expected to consist of adult females and juvenile offspring that travel together, eat the same food, and drink from the same water sources. Thus, if Bothwell mastodons were members of a single family unit, the assemblage should consist of (1) females or juvenile males, (2) mastodons from a wide range of ages, (3) mastodons that died in the same mortality event; and (4) mastodons that exhibit similar seasonal changes in dietary and water input. Death in the same mortality event would support that there were social relationships among individuals because individuals that died together would have been in the same place at the same time, the expectation for members of a family unit. In

addition to evaluating the hypothesis that this assemblage represents a matriarchal family unit, tusk data are used to discuss scenarios for the circumstances surrounding the deaths of the Bothwell mastodons.

Geographic and Geologic Context

Hebron, Indiana, is located within the Northern Lake and Moraine Region, near the southern margin of the Valparaiso Morainal Complex (Fig. 4.1). The site is latest Pleistocene in age, evidenced by the formation time of the Valparaiso Morainal Complex (after 15.5 ka; Gray 2000; Larson and Schaetzl 2001), and an AMS ^{14}C age estimate of 11,440 ± 60 years BP (Beta Analytic Inc., Beta-262766) for Bothwell tusk 2-14 (see methods for details on radiocarbon dating). The fossils at the Bothwell site were preserved in a sediment-filled basin, approximately one half-acre in expanse. Three main stratigraphic units were identified at the site: (1) Late Wisconsin till formed the underlying depositional unit in which the basin was developed; (2) greenish lake clay was the lowest unit within the basin; and (3) organic-rich silt overlay the clay, grading up into additional organic layers. Fossils were restricted to the silt layer, which, in addition to mammalian bones, contained woody plant macrofossils (S. Brown field notes and R. Richards, pers. comm.).

Tusks as Recording Structures

Mastodon tusks are primarily composed of dentin, which is approximately 50% hydroxyapatite [$Ca_{10}(PO_4)_6(OH)_2$], 30% organic material (primarily collagen), and 20% water (by volume; Linde 1992). A tusk grows as odontoblasts lining the pulp cavity

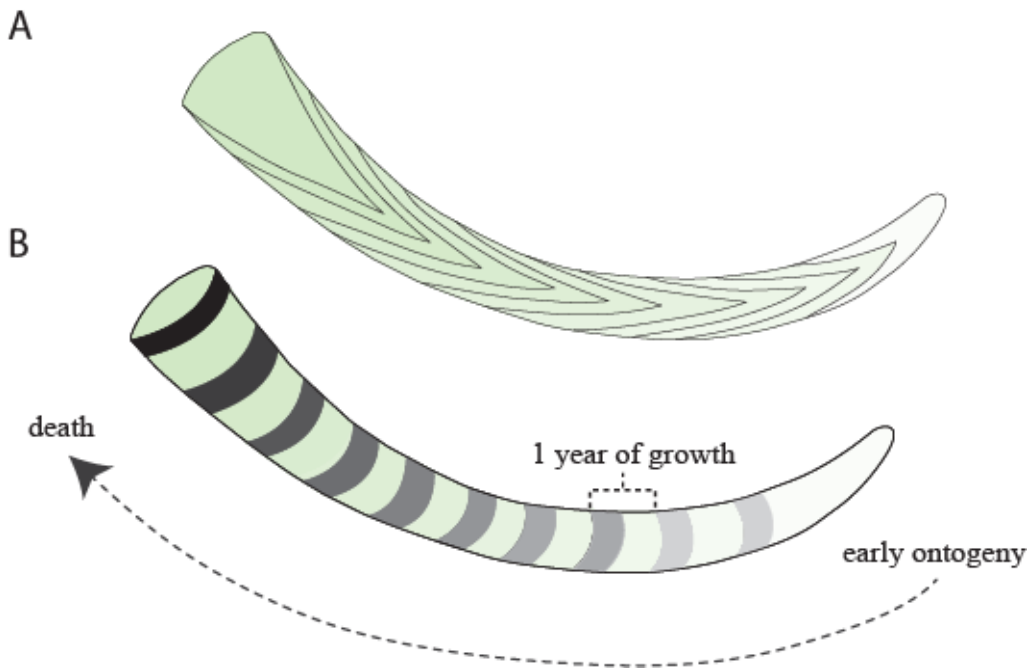


Figure 4.2. Schematic longitudinal cross-section of a tusk (A) and exposed dentin on the tusk exterior (with cementum removed; B). A illustrates the tusk's cone-in-cone structure, in which each cone reflects the amount of dentin deposited in a year. In B, dark bands indicate winter growth, and light-dark couplets reflect a year of growth (Koch et al. 1989). The arrow indicates the direction of time for the longitudinal axis in A and B. A and B both exhibit ten tusk years.

surface deposit a layer of new dentin. Deposition occurs inwardly as well as proximally, resulting in the formation of a new pulp cavity surface that is displaced inwardly and proximally from the existing pulp cavity surface (Fisher 1996). Growth in the proximal direction is coupled with eruption distally, resulting in an overall increase in the length of the exposed tusk and providing room within the alveolus for continued tusk growth. The process of tusk growth results in a cone-in-cone structure (Fig. 4.2A), in which dentin formed earliest in life is at the tip, dentin formed just prior to death lines the pulp cavity, and the longitudinal axis of the tusk is essentially an axis of time.

A series of nested, periodic structural increments is preserved in tusk dentin. First-order increments mark approximately annual periods of growth and may be identified as light-dark couplets, in which dark dentin reflects winter growth (Fig. 4.2B; Koch et al. 1989). There are approximately 365 third-order, or daily, increments within each annual increment. In mastodon tusks, approximately every fourteenth third-order increment is accentuated as a dark band. These bands are referred to as second-order increments, which mark approximately two weeks of growth.

Growth increments can be counted, and increment thickness can be measured, to explore seasonal patterns of variation in tusk growth rate. Increment thickness is associated with nutritional status (Fisher 1996), so, within the tusk record of a single individual, periods of high growth rate are associated with favorable environmental conditions, and periods of comparatively low growth rate are associated with harsh environmental conditions. For temperate-latitude mammals, periods of high growth rate are typically associated with summer, and periods of low growth rate are typically associated with winter (Koch et al. 1989).

Dentin is not remodeled after accretion (Hillson 1986), so the isotopic composition of a layer of dentin reflects the isotopic inputs at the time in life when the dentin was deposited (Koch et al. 1989; Stuart-Williams and Schwartz 1997; Fisher and Fox 2003; Rountrey et al. 2007). Thus, when serial isotope samples parallel dentin growth lines, specific isotope compositions from these samples can be associated with specific times in an individual's life. In this way, serial isotope analyses of tusk dentin provide data that can be used to (1) infer season of death (Koch et al. 1989; Fisher and Fox 2003), (2) evaluate changes in nutritional status and diet within an individual's lifetime (Fisher and Fox 2003; Fisher 2008), and (3) identify life history events in the tusk record such as weaning (Rountrey et al. 2007) and, potentially, pregnancy (Fisher and Fox 2003; Chapter 5, this dissertation).

Sexual dimorphism has been documented in mastodon tusks. Male tusks are larger than female tusks in all linear and curvilinear tusk measurements, particularly in maximum girth and pulp cavity depth (Fisher 2008; Chapter 3, this dissertation). Measurements of length, maximum girth, pulp cavity depth, and other tusk dimensions can be used to discriminate between male and female mastodons, with varying degrees of certainty, but principal components analysis (of axial depth of the pulp cavity, maximum tusk circumference, alveolar circumference, alveolar depth, tusk length, and tusk circumference at 50, 60,70, 80, and 90 cm from the tip) is the most robust way to assess sex using tusk measurements alone (Smith and Fisher in review; Chapter 2, this dissertation).

The inclusion of age increases the certainty of sex assessment for any method used. Tusks grow continuously, but tusks of males grow faster than tusks of females,

most notably after a male attains maturity. Due to sex-specific differences in growth rates, young male tusks and older female tusks exhibit similar morphologies, and it can be difficult to discriminate between the two in the absence of age. Knowledge of age can be used to discriminate between tusks of young males and older females because tusks of similar morphology but vastly different ages are unlikely to belong to the same sex. Among methods that use age data, the relationship between alveolar circumference (tusk circumference at the alveolar margin) and age has been shown to discriminate clearly between sexes (Fisher 2008).

Materials and Methods

Materials

Thirteen tusks or tusk fragments were recovered from the Bothwell site (Table 4.1; Fig. 4.3). Bothwell 2-14 is the most complete tusk because it did not incur damage from the bulldozer. Pen-73 consists of cementum fragments only; these fragments may be associated with one of the other tusks, so their presence does not increase the total tusk count. The remaining tusks were damaged to different degrees by the bulldozer. Five are complete or nearly complete, two are represented by substantial proximal portions with intact pulp cavities, and five are represented by distal portions only. Most tusks, with the exception of Bothwell 2-14, required extensive reconstruction, and all tusks benefitted from consolidation. Tusks were reconstructed using quick-set epoxy and consolidated using low-viscosity epoxy, neither of which interferes with analysis of tusk growth

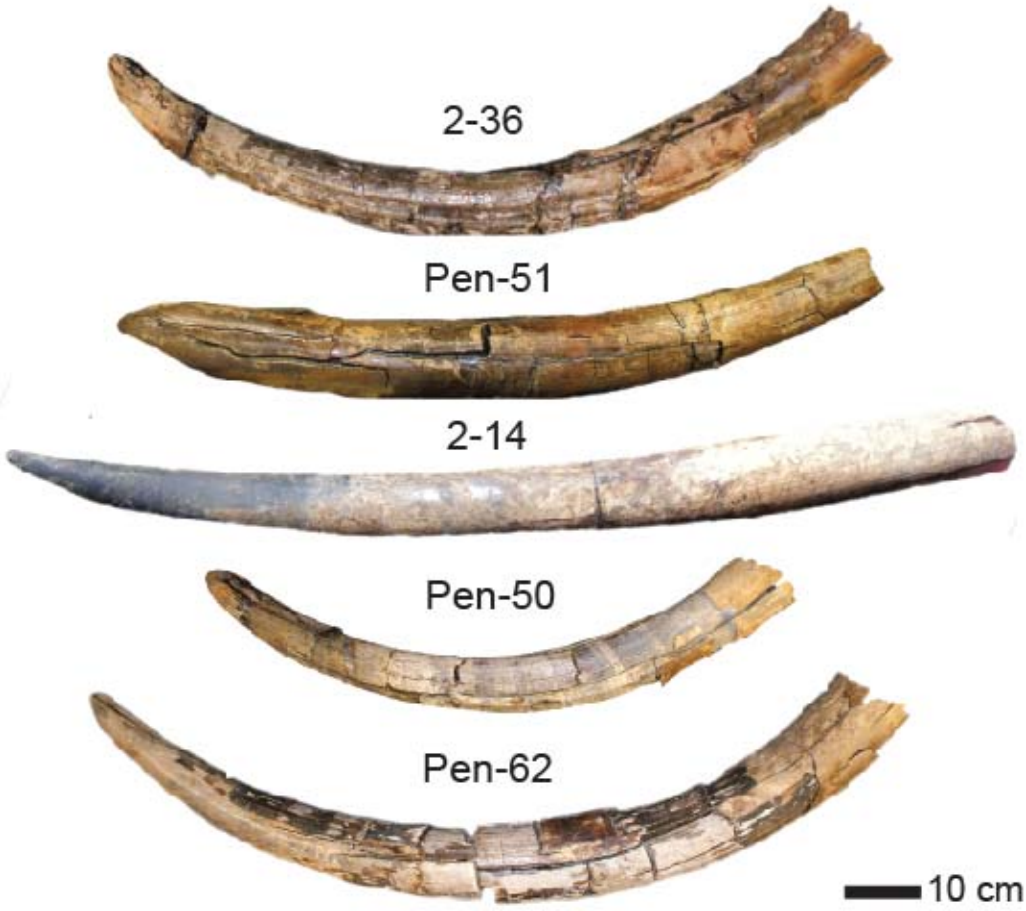


Figure 4.3. The five most complete Bothwell tusks. The photograph of 2-14 is from the collections of the Indiana State Museum and Historic Sites.

increments or isotopic composition (Fisher and Fox 2003).

Methods

Radiocarbon Age Estimate. – A 2.8 g sample of tusk dentin from 2-14 was sent to Beta Analytic Inc. for ^{14}C dating of tusk collagen. This is a standard procedure done commercially, and its reliability is continually being tested and refined.

Number of Individuals.– The number of mastodons at the Bothwell site was determined by assessing tusk side (left or right) as well by investigating morphological similarities among tusks. Tusk side was determined by identifying the direction of the tusk curve, in which a left tusk curves dextrally and a right tusk curves sinistrally. In addition, a tusk may exhibit more abrasion on the lateral than the medial side, so investigating patterns of tusk wear can aid in evaluation of tusk side. Measurements for two tusks in a pair should be similar, but some variation is expected and has been observed on tusk pairs from mastodons and living elephants (Fisher 2008; Chapter 3, this dissertation).

Sex and Age Assessment.– Eight tusks exhibited the preservation necessary for morphologic assessment of sex and age (Table 4.1). The sex distribution of mastodons at Bothwell was assessed based on the relationship between axial pulp cavity depth and maximum tusk circumference, as compared to the same measurements on tusks of other male and female Great Lakes-region mastodons (Smith and Fisher 2007; Fisher 2008; Smith and Fisher in revision). The PCA presented in Smith and Fisher (in review) cannot be used for to assess sex for most Bothwell tusks – with the exception of 2-14 and Pen-51 (see Chapter 2, this dissertation) – because many are incomplete, so the number and types of measurements that could be obtained from them were limited. In this study, pulp

cavity depth and maximum tusk circumference were used to evaluate sex because these values can be obtained from tusks that exhibit only a proximal portion, and because both pulp cavity depth and maximum tusk circumference strongly contribute to the discrimination between sexes in multivariate analyses (Chapter 3, this dissertation).

Age can often be evaluated based on the number of annual increments visible in tusk dentin. Because material is lost from the tusk tip due to wear, age determined in this way is a minimum. However, most Bothwell tusks are incomplete, and annual increments are only clearly visible on three of the four complete tusks. Thus, it was necessary to use other methods to better understand the age distribution for mastodons at Bothwell. As discussed earlier, the relationship between alveolar circumference and age provides clear discrimination between sexes (Fisher 2008). This method, with some modification, was used to predict age for the Bothwell tusks. Alveolar margins cannot be located on many of the Bothwell tusks, so maximum tusk circumference, which closely approximates the value of alveolar circumference (Smith and Fisher in revision; Chapter 2, this dissertation), was used instead.

Age, interpreted from the number of annual increments in the tusk for three Bothwell mastodons, six female Great Lakes-region mastodons, and seven male Great Lakes-region mastodons (Smith and Fisher 2007; Fisher 2008; Smith and Fisher in review) was plotted against $\log_{10}$-transformed measurements of maximum tusk circumference. A least-squares regression of age on maximum tusk circumference was performed on each sex individually. Each sex was treated separately because tusks of males and tusks of females exhibit different growth rates, so regression of age on maximum tusk circumference for a group including both sexes would not have yielded

reliable age estimates. Ages of unknowns were predicted using the equation of the regression line. Because each sex was treated separately, it was necessary to hypothesize sex for each unknown prior to its inclusion in this analysis.

Growth Increment Analysis.– Growth increment analysis was conducted on four Bothwell tusks (2-14, Pen-2, Pen-62, and M-1) that were interpreted, based on morphologic differences, to represent four different individuals. Methods were modeled after Fisher and Fox (2003) and Rountrey (2009). Sample removal for 2-14, the best preserved tusk in the assemblage, was conducted in a manner that allowed for analysis of the entire tusk record (Chapter 5, this dissertation). Sample removal for the remaining tusks focused on the pulp cavity only. Tusk 2-14 was bisected along its longitudinal axis using a band saw with a ½-inch blade. A band saw or coping saw was then used to remove transverse dentin blocks (approximately 2 cm in thickness and 1.5 to 2 cm in depth) from one longitudinal half. Blocks, including one at the pulp cavity, were removed at 10-cm intervals along the entire tusk length. For Pen-2, Pen-62, and M-1, one dentin block, approximately 3 cm in thickness, was removed from the pulp cavity of each tusk using a Dremel tool with a ⅛-inch tile-cutting bit.

For all four pulp cavity blocks, two transverse slabs, each approximately 1 cm in thickness, were cut from either the proximal or distal side of each block using an Isomet saw with a diamond wafering blade. A thin section was made from one block, and the adjacent block was reserved for collecting samples for isotope analysis. For all four tusks, second-order (bi-weekly) and annual increments were counted and measured on photographs of thin sections using ImageJ and a custom plug-in (Rountrey 2009).

Stable Isotope Analysis.– Structural carbonate is carbonate that substitutes at the

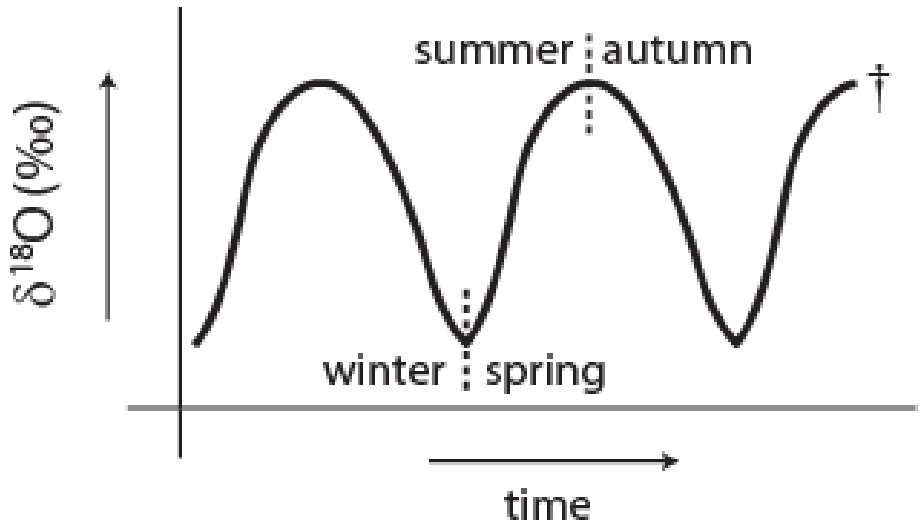


Figure 4.4. Hypothetical profile of seasonal variation in $\delta^{18}O$ composition of tusk dentin for temperate-latitude mastodons. This profile indicates that death occurred in late summer or early autumn.

phosphate and hydroxyl group lattice sites of hydroxyapatite (Koch et al. 1997). Analysis of the oxygen and carbon isotope composition of structural carbonate in tusk dentin was conducted on 2-14, Pen-2, Pen-62, and M-1, the same tusks analyzed for dentin growth rate. The oxygen isotope composition ($\delta^{18}O$) in the structural carbonate of mammalian teeth and bones is determined by the $\delta^{18}O$ of body water (Longinelli 1984; Luz et al. 1984; Bryant et al. 1996). The isotopic composition of mammalian body water primarily reflects the isotopic composition of drinking water, which, in turn, reflects the isotopic composition of meteoric water (Koch et al. 1989; Bryant and Froelich 1995). In middle and high latitudes the $\delta^{18}O$ of meteoric water is correlated with air temperature; when temperatures are low, $\delta^{18}O$ values are low, and when temperatures are high, $\delta^{18}O$ values are high (Dansgaard 1964). For large-bodied, temperate-latitude mammals, the $\delta^{18}O$ of teeth lags behind the $\delta^{18}O$ of meteoric water (Stuart-Williams and Schwarcz 1997). In serial isotope analyses, the lowest oxygen values are at winter-spring boundaries, and the highest values are in late summer or early autumn (Koch et al. 1989; Stuart-Williams and Schwarcz 1997; Sharp and Cerling 1998). Studying sub-annual patterns of oxygen isotope variation in a tusk for the final years of life permits inference of season of death for an individual (Fig. 4.4; Koch et al. 1989; Fisher and Fox 2003, 2007). Although dentin is prone to diagenetic alteration, any effect on $\delta^{18}O$ values derived from proboscidean tusk dentin is minor (Koch et al. 1997). Even if the values themselves are shifted as group by diagenetic alteration, seasonal variation is typically preserved (Koch et al. 1989; Sharp and Cerling 1998; Fisher 2008).

The carbon isotope composition ($\delta^{13}C_{carb}$) in the structural carbonate of mammalian teeth and bones reflects the proportion of C_3 and C_4 plants in an animal's diet (DeNiro and Epstein 1978). C_3 plants use the Calvin Cycle to fix CO_2, and exhibit average $\delta^{13}C$ values of -27‰ (O'Leary 1988). C_4 plants use the Hatch-Slack Cycle to fix CO_2, and exhibit average $\delta^{13}C$ values of -13‰ (O'Leary 1988). These values are offset by +14.1‰ in tusk dentin as a result of metabolism and biomineralization (Cerling and Harris 1999).

Great Lakes-region mastodons primarily consume C_3 plants (e.g., Jackson et al. 1986; Lepper et al. 1991), so $\delta^{13}C_{carb}$ values should be about -12.9‰ or less. The carbonate carbon composition in the tusk dentin of Pleistocene proboscideans, however, is typically shifted to higher values as a result of diagenetic processes (Koch et al. 1997), rendering $\delta^{13}C_{carb}$ values virtually useless for evaluating the proportion of C_3 and C_4 plants in the diet. However, seasonal variation in $\delta^{13}C$ values may be retained, allowing for the interpretation of seasonal changes in diet without identifying specific dietary inputs.

Analysis of the carbon and nitrogen isotope composition of tusk collagen was conducted on Pen-2. The carbon composition of tusk collagen ($\delta^{13}C_{coll}$) reflects the source of dietary protein that produces collagen, and is offset by 4.7‰ to 6.1‰ relative to the $\delta^{13}C$ of dietary protein in large herbivorous mammals such as mastodons (Ambrose and Norr 1993). Collagen is more resistant to diagenetic processes than structural carbonate, and allows for interpretation of dietary inputs even when $\delta^{13}C_{carb}$ is altered.

The nitrogen isotope composition of tusk collagen ($\delta^{15}N$) depends on the $\delta^{15}N$ of the animal's diet, in which body tissues are enriched in $\delta^{15}N$ relative to the $\delta^{15}N$ of the

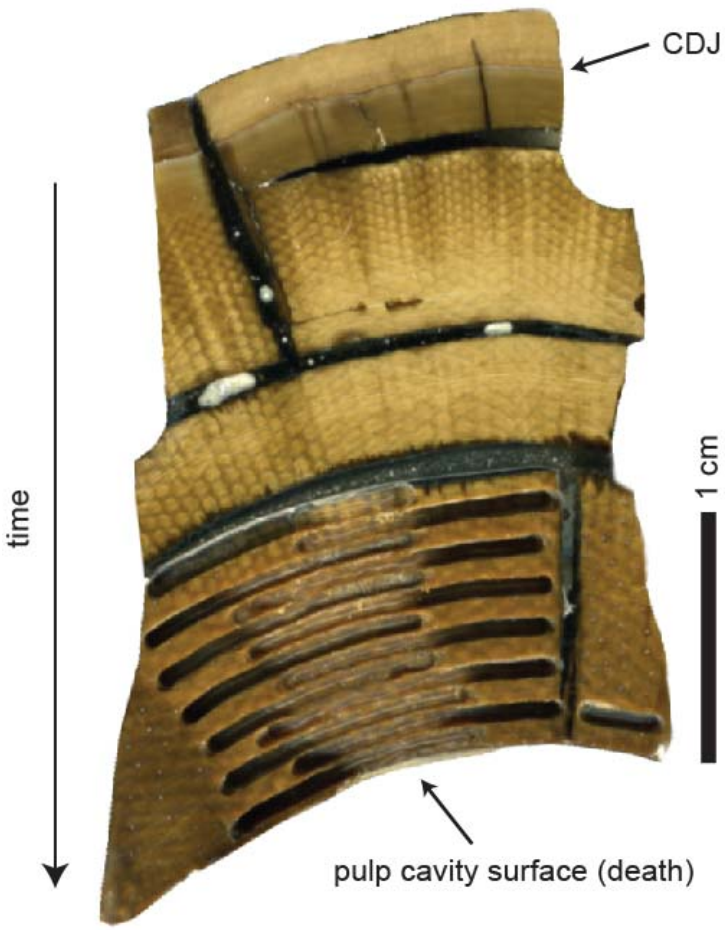


Figure 4.5. Transverse slab of M-1, with samples for isotope analysis removed. Drill paths parallel growth increments. “CDJ” is the cementum-dentin junction; cementum is above the arrow and dentin is below the arrow.

animal's diet (DeNiro and Epstein 1981). Increases in $\delta^{15}N$ occur when an animal is under nutritional stress (Hobson et al. 1993). This enrichment is most likely caused by the increased proportion of nitrogenous compounds derived from catabolism (a source enriched in $\delta^{15}N$ relative to diet) for protein synthesis that occurs when an animal is fasting or under nutritional stress (Hobson et al. 1993).

Sample Preparation and Stable Isotope Analysis.– Prior to sample extraction, a sampling plan targeted discrete bands of dentin for removal, using methods in Rountrey (2009). Growth increments were used as a guide for removing samples for isotope analysis; samples parallel growth lines and reflect a time-series of compositional change (Fig. 4.5). A dental drill with a 0.7 mm carbide-tipped bit was used to collect dentin samples, which were powdered upon removal. A bit width of 0.7 mm resulted in each sample including approximately six second-order increments, with a temporal resolution of approximately six samples per year. Each band was milled for two-thirds of its length, leaving a solid block of dentin, reflecting the same amount of time as the powder sample, in place. Adjacent powder samples were drilled from alternating sides of the slab to facilitate block removal. Powder samples were collected for analysis of structural carbonate in tusk dentin, while blocks were reserved for analysis of tusk collagen. Isotope analysis was conducted on dentin that formed during approximately the final three to four years of life. Ideally, the number of years sampled for isotope composition would be known in advance of sampling. For these tusks, however, features indicative of winter-spring boundaries were not easily identifiable, so a portion of the tusk inferred to represent between three and four years, based on thickness, was sampled instead of a known number of years.

Powdered dentin samples were pretreated for analysis of structural carbonate using methods from Koch et al. (1997), Stephan (2000), and Rountrey (2009). In brief, 30% H_20_2 was added to each 10 mg sample to oxidize organic matter. Samples were agitated and left to soak for 24 hours, after which point they were centrifuged to facilitate removal of H_20_2. Each sample was then rinsed with 10 mL of distilled/deionized water and centrifuged to facilitate removal of the supernatant. This rinsing procedure was repeated five times. After rinsing, 1 M acetic acid-calcium acetate buffer was added to each sample to remove diagenetic carbonate minerals; samples were agitated and left to soak for 24 hours. Next, samples were again centrifuged to facilitate removal of the supernatant, and then rinsed five times. After rinsing, samples were frozen and then freeze-dried overnight. One milligram was weighed from each dried, pretreated dentin sample. Samples were sent to the Stable Isotope Lab at the University of Michigan, where they were roasted at 200°C for one hour, loaded into glass vessels, and analyzed for C and O isotopic composition on a Finnegan Kiel IV coupled to a ThermoMAT 253 isotope ratio mass spectrometer.

Dentin block samples were pretreated for collagen analysis using methods from Fisher and Fox (2003). All pretreatment was performed in glassware capped with aluminum foil, and all glassware, foil, and tools were baked for eight hours at 500°C to combust organic compounds that might contaminate the samples. Blocks were placed into individual vials, and 10 mL of 0.5 N HCl was added to each sample for decalcification. Blocks were then refrigerated for three days. After three days, acid was decanted, and each sample was rinsed five times with 20 mL of distilled/deionized water. Next, blocks were defatted by adding 20 mL of 2:1 chloroform:methanol to each sample

vial. Vials were sonicated for 30 minutes, and then the solution was decanted. Samples were rinsed five times using distilled/deionized water, and then freeze-dried over night. 0.8 mg was weighed from each pretreated and dried block. Samples were sent to the Stable Isotope Laboratory at the University of Michigan, where they were analyzed for C and N isotopic composition on a Costech ECS 4010 combustion elemental analyzer coupled to the inlet of a Thermo Fisher Delta V Plus isotope ratio mass spectrometer.

Isotope composition is expressed in conventional δ notation, in which $\delta = [(R_{sample} / R_{standard}) - 1)*1000]$, R is the ratio of the heavy to the light isotope, and standards are VSMOW (oxygen), VPDB (carbon), and AIR (nitrogen).

Results

Radiocarbon Age Estimate

Tusk collagen extracted from Bothwell tusk 2-14 yielded an AMS ^{14}C date of 11,440 ±60 BP. The bulk carbon isotope composition value obtained from the collagen of this sample was -20.0‰. There was minimal evidence of post-mortem contamination in the dentin sample submitted for analysis, and the carbon isotope composition of the collagen in this sample is well within the range of values for unaltered mastodon tusk collagen (Fisher and Fox 2003). Thus, the ^{14}C date obtained from 2-14 is likely a good estimate of the age of this mastodon.

Number of Individuals

Tusk side was identified for nine tusks, although assessment was tentative for four of these tusks is due to state of preservation and/or degree of tusk wear. Nonetheless,

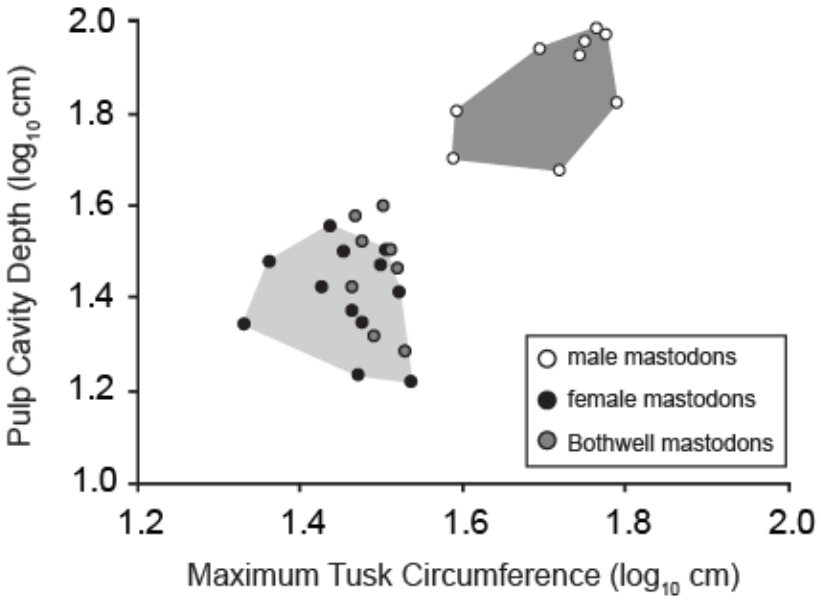


Figure 4.6. Sex assessment for eight Bothwell tusks, by comparison with tusks of Great lakes-region mastodons of known sex (Fisher 2008; Smith and Fisher in review; Chapter 2, this dissertation). Table 4.1 indicates which Bothwell mastodons are included in this figure. Bothwell tusks are more similar in form to female than to male tusks.

three are assessed as right tusks and six as left tusks (Table 4.1). Morphological similarities between two complete tusks, Pen-62 (a right tusk) and 2-36 (a left tusk), suggest they are a pair. From a qualitative perspective, Pen-62 and 2-36 both exhibit a spiral curve different in character from that exhibited by other Bothwell tusks. Quantitatively, lengths of these two tusks are comparable (114.3 and 109.1 cm, respectively), and comparison of pulp cavity depth and maximum tusk circumference shows differences of a few centimeters only (Table 4.1). Although the morphological comparisons presented here do not unequivocally show that Pen-62 and 2-36 belonged to the same mastodon, the evidence provides support for this possibility. Assuming that these two tusks are from one mastodon, the maximum number of mastodons found at the Bothwell site decreases from 13 to 12, and the minimum remains at seven.

Sex

Plotting pulp cavity depth against maximum tusk circumference yielded two distinct point clouds, one of female mastodons, and one of male mastodons (Fig. 4.6). Eight Bothwell mastodon tusks fell in and around the female mastodon point cloud, indicating that all belong to female mastodons. The remaining five Bothwell tusks are distal portions only, so sex for these tusks could not be assessed using this method. Of these five, Pen-52, Pen-54, Pen-60, Pen-61 are relatively slender with slight wear at the tips, a morphology suggestive of either adult females or juvenile males. In contrast, Pen-63 has a relatively robust, highly worn tip. The degree of wear suggests Pen-63 belongs to an older individual, and its girth, though large compared to the aforementioned four, is slender compared to that of any adult male. Thus, Pen-63 most likely belongs to an older

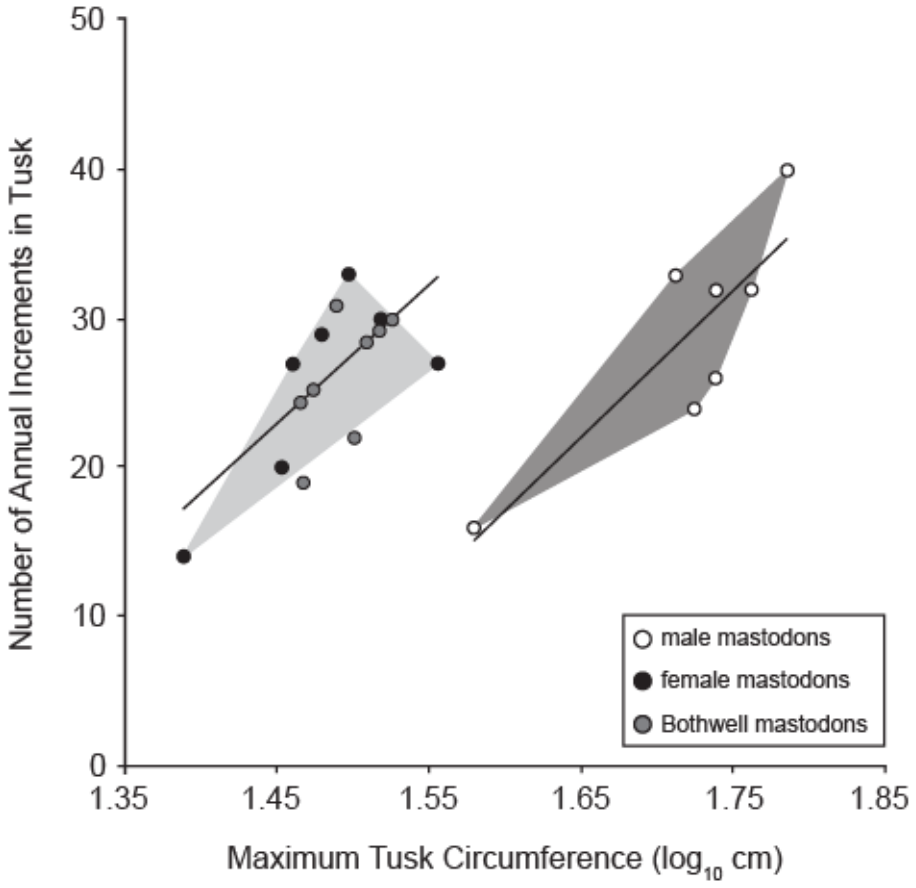


Figure 4.7. Age assessment for eight Bothwell tusks, by comparison with tusks from Great Lakes-region mastodons of known sex and age (Fisher 2008; Smith and Fisher in review). Table 4.1 indicates which Bothwell tusks were included in this figure. Bothwell tusks that do not fall on the least-squares regression line have age estimates based on the number of annual increments visible in tusk dentin. Bothwell tusks belong to mastodons that were between the ages of about 19 and 31 at death.

female. Overall, Bothwell tusks exhibit morphologies that are characteristic of female tusks, but it is possible that as many as four tusks belong to juvenile males.

Age

Age was estimated for three Bothwell tusks– Pen-50, Pen-51, and 2-14 – by counts of the number of annual increments visible in tusk dentin. Approximately 19 increments were visible on the exterior of Pen-50, approximately 31 annual increments were visible on the surface of a longitudinal section of Pen-51, and 22 annual increments were counted in a comprehensive analysis of the entire tusk record of 2-14 (Chapter 5, this dissertation). For five tusks in which age was estimated through morphologic comparison (Fig. 4.7), 2-22 died at approximately 29 years of age, 2-36 at approximately 25 years, M-1 at approximately 30 years, Pen-2 at approximately 24 years, and Pen-62 at approximately 28 years. Thus, Bothwell mastodons range in age from 19 to 31 years. The presence of juvenile tooth crowns at the site indicates that there is at least one mastodon in the Bothwell assemblage that falls below the age range established here, though it is unclear whether the tooth crowns are associated with any tusk.

Tusk 2-36 and Pen-62, the proposed pair, exhibit a four-year difference in estimated age. This age difference does not rule out the possibility that they are a pair because the method used here – which is sensitive to factors such as tusk breakage, abrasion, and preservation – is expected to provide only a rough approximation of age for an individual. Furthermore, because each tusk is subject to unique amounts of wear, even a comparison of annual increment number between two tusks in a known pair would not necessarily yield the same age estimate.

Growth Increment Profiles

Results of growth increment analyses are presented graphically, with increment thickness plotted against increment number. The increment number is essentially time, such that the first increment represents the earliest time of life in each sample, and the last increment reflects the time just prior to death (Fig. 4.3). None of the Bothwell tusk second-order increment profiles exhibit clear seasonal patterns of variation (Fig. 4.8), so winter-spring boundaries could not be located by identifying local minima in growth rate. Additionally, none of the dentin slabs exhibit dark-light couplets, in which the boundary between the dark and light portion of each couplet marks the winter-spring boundary (Koch et al. 1989). Winter-spring boundaries for these tusks were initially located based on the presence of increments that were darker relative to adjacent increments, or on the presence of longitudinal cracks, which parallel growth lines and form as dentin cones separate due to desiccation. Both types of features (hereafter referred to as enhanced increments) were initially taken to represent winter-spring boundaries because they repeated on what appeared to be an annual scale, based on expected annual increment thicknesses for females (Fisher et al. 2008). However, after the growth increment profiles were compared to $\delta^{18}O$ profiles, it was found that for Pen-62, M-1, and 2-14 enhanced increments were not in the dentin samples that yielded local minima in the $\delta^{18}O$ profiles.

For Pen-2, winter-spring boundaries and enhanced increments represented nearly the same time period, but this tusk slab was unusual because there were ten or more enhanced increments visible in a single isotope year. Ultimately, winter-spring boundaries for all four tusks were identified by association with local minima in the $\delta^{18}O$ profiles (Fig. 4.9). Each sample for isotope analysis included approximately six second-

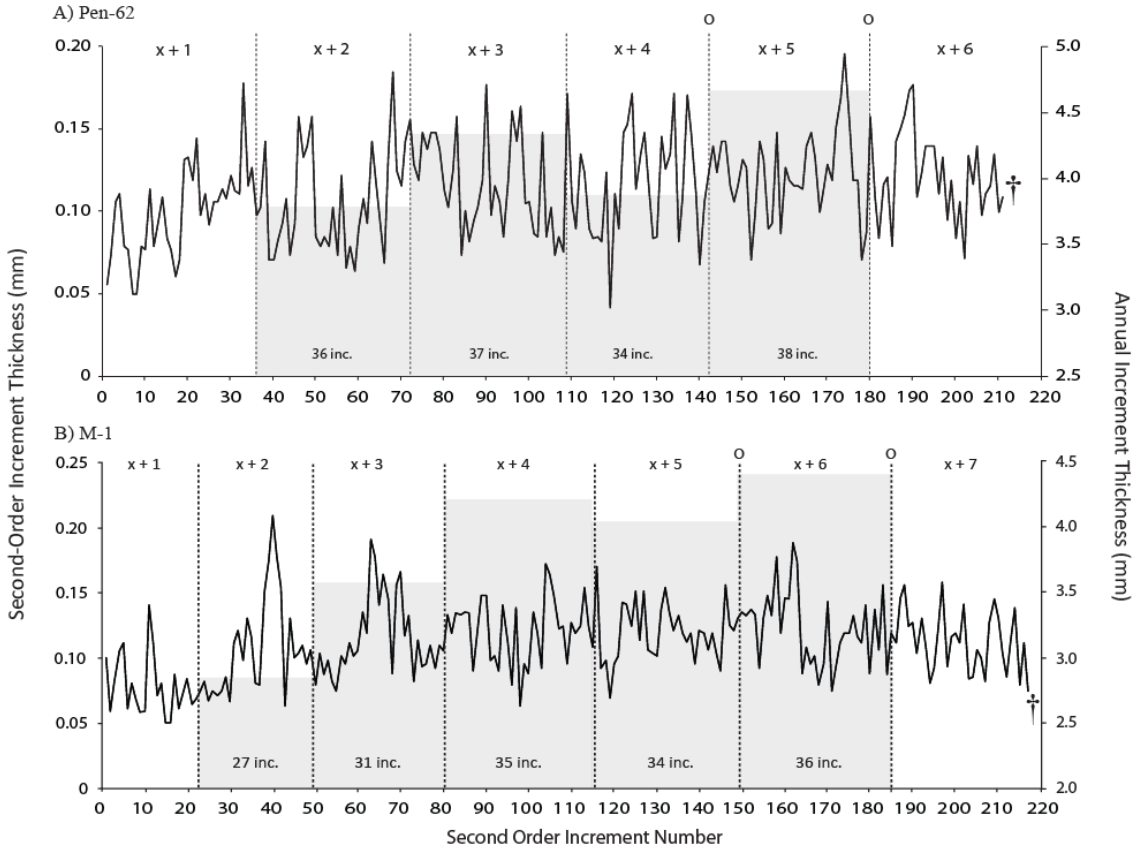


Figure 4.8. Growth increment profiles for Pen-62 (A), M-1 (B), 2-14 (C), and Pen-2 (D). Solid lines track changes in second-order increment thickness (primary y-axis) and shaded bars indicate annual increment thickness (secondary y-axis). Numbers above the data indicate the tusk year, which is preceded by an "x +" when the number of years in the tusk record prior to those presented here is unknown. Numbers below the data indicate the number of second-order increments per year. Vertical dashed lines mark winter-spring boundaries. "O" denotes a boundary that was marked based on local minima in the $\delta^{18}O$ profile (Fig. 4.8). Daggers mark the last dentin deposited prior to death. Figure 4.8 is continued on page 130. Note the general lack of seasonal variation in second-order increment thickness, which suggests these individuals lived in an area with low seasonality.

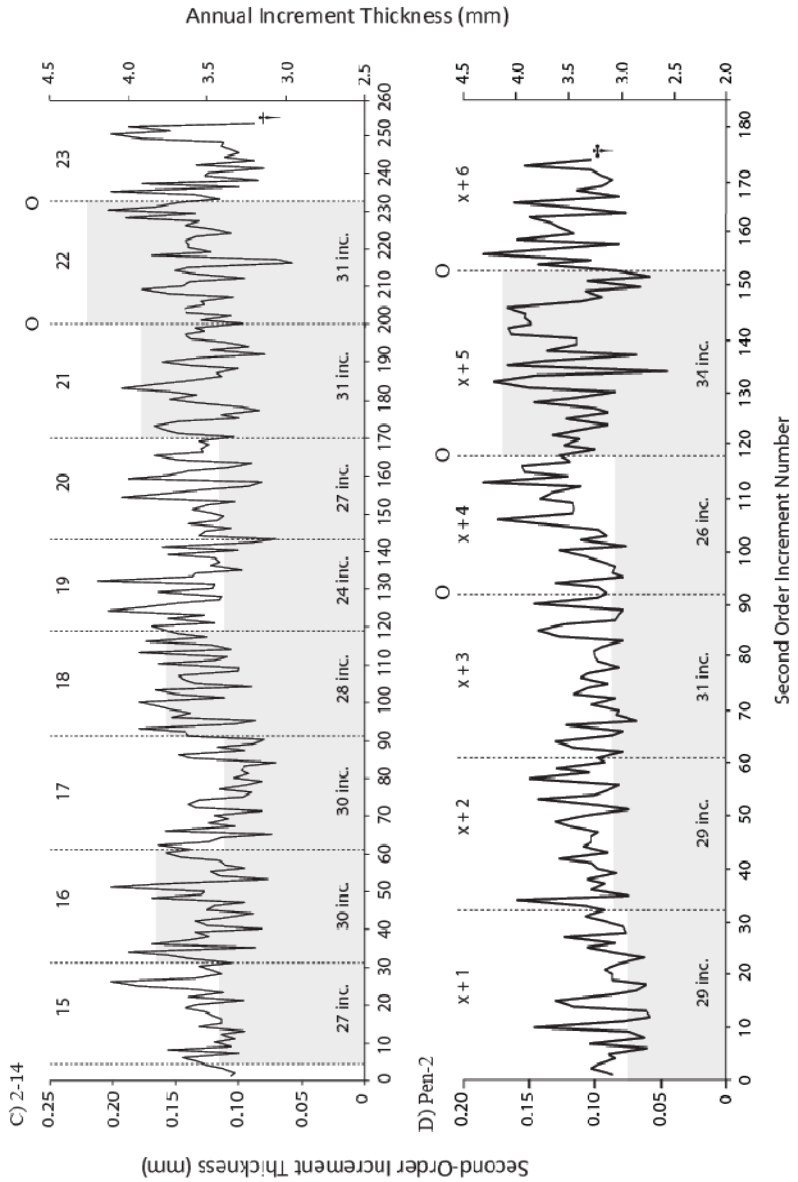
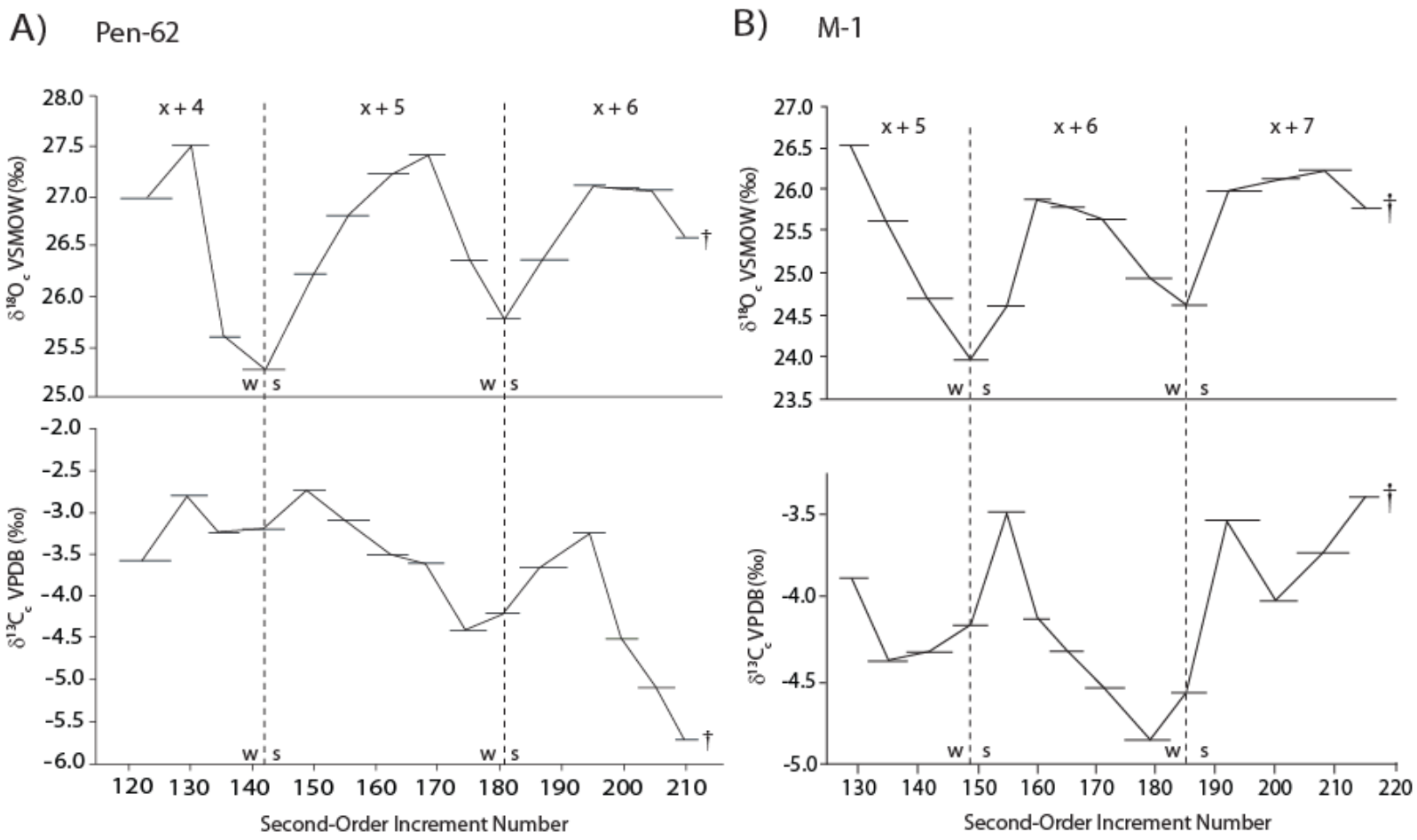


Figure 4.8 (continued).

Figure 4.9. Results from the serial isotope analyses (carbon and oxygen) of structural carbonate in tusk dentin. Horizontal lines indicate the second-order increments sampled to obtain each isotope value. Note that winter-spring boundaries ("w s"),marked by vertical dashed lines, are located on local minima in each $\delta^{18}O$ profile. Daggers indicate the dentin formed just prior to death. $\delta^{18}O$ profiles for Pen-62 (A) and M-1 (B) both terminate during a decreasing phase of seasonal variation, indicating both died in winter. $\delta^{18}O$ profiles for 2-14 (C) and Pen-2 (D) both terminate during an increasing phase, and possible peak, of seasonal variation, indicating both died in late summer or early autumn. For at least two years in each tusk, $\delta^{13}C$ values increase after the winter-spring boundary and decrease to just before the next winter-spring boundary. This pattern may be related to fat metabolism (high values indicate fat storage and low values indicate fat utilization) or differences in the proportion of C_3 and C_4 plants in the diet (high values indicate a greater C_4 input) Figure 4.9 is continued on page 133.


A)
Pen-62
B)
M-1
x + 4
x + 5
x + 6
x + 7
w
s
†
$\delta^{18}O_c$ VSMOW (‰)
$\delta^{13}C_c$ VPDB (‰)
Second-Order Increment Number

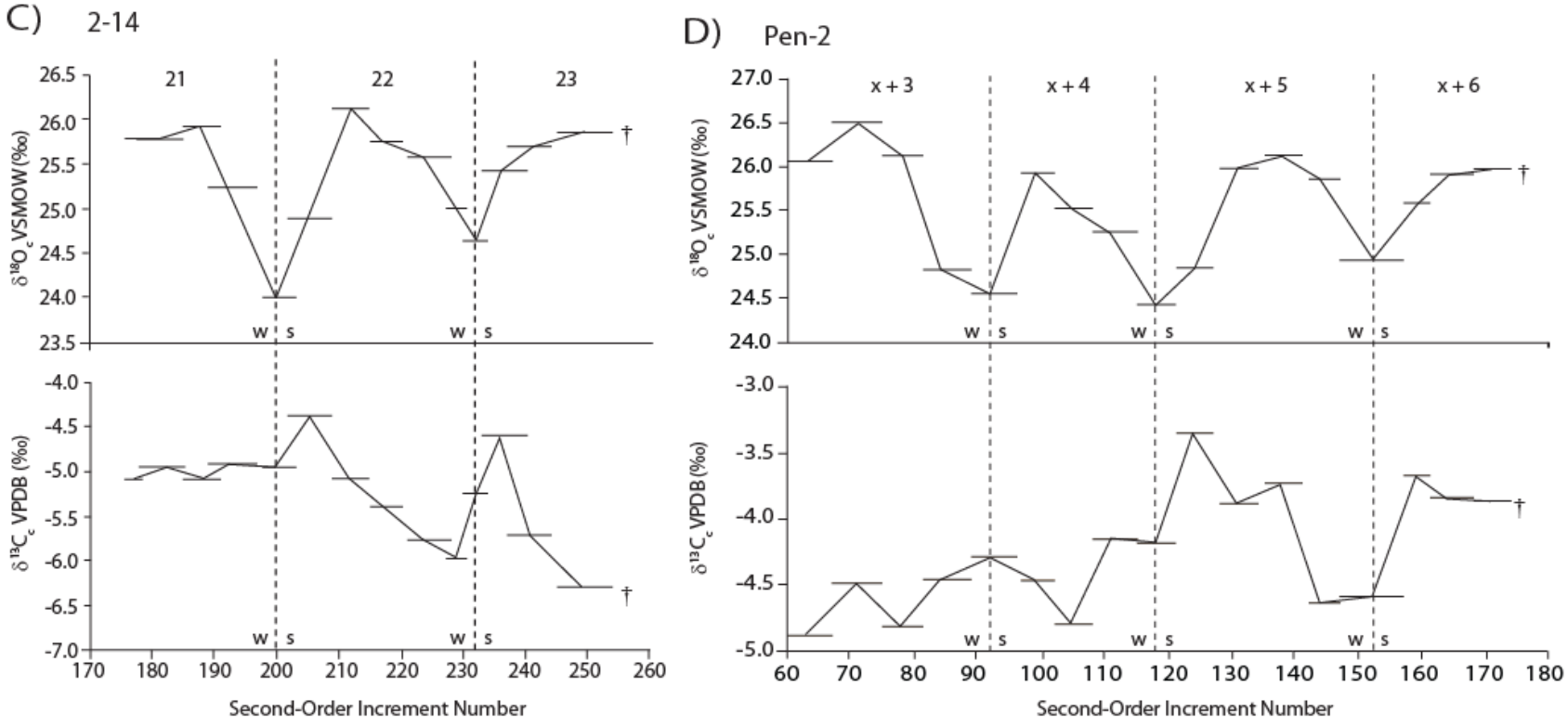


Figure 4.9 (continued).

order increments, so, in lieu of other evidence for the location of these boundaries, the winter-spring boundary was marked as the increment in the center of the isotope sample that exhibited a local minimum in the $\delta^{18}O$ profile. Although not necessarily the true winter-spring boundary, this method of locating the boundary is at least consistent from one year to the next, and does not interfere with assessment of season of death. Additionally, the inference that the winter-spring boundary is in the middle of the sampling path means that the true winter-spring boundary would not be more than three increments, on average, from the inferred winter-spring boundary.

To locate winter-spring boundaries on portions of slabs not analyzed for isotopic composition, the temporal relationship between winter-spring boundaries (based on local minima in the $\delta^{18}O$ profile) and enhanced increments was established for each slab (Appendix I). If, for example, a winter-spring boundary was located eight second-order increments after an enhanced increment, then for an un-sampled section, a winter-spring boundary was placed eight second-order increments after an enhanced increment. In practice, every local minimum in the $\delta^{18}O$ profile on a single slab was not located the same number of second-order increments from an enhanced second-order increment . Winter-spring boundaries in un-sampled portions were located the average number of second-order increments between enhanced increments and local minima in $\delta^{18}O$ composition (for a single slab) after an enhanced increment.

With locations of winter-spring boundaries in place, terminal growth histories could be evaluated at the annual scale, and the number of second-order increments per year could be discerned (Fig. 4.8). Because of the uncertainty involved in locating winter-spring boundaries, the number of second-order increments per year could vary by up to

three increments, and annual increment thicknesses could vary by up to 0.35 mm (the average thickness of three second-order increments). Nonetheless, annual increment thicknesses for the Bothwell tusks are comparable to those of other Great Lakes-region female mastodons. Table 4.2 shows a comparison of annual growth rates between Bothwell tusks and tusks of female mastodons from Hiscock (Fisher and Fox 2003). The Hiscock Site, located in western New York, yielded at least 21 mastodon tusks from both male and female mastodons. Hiscock females were noted to have slightly lower growth rates than other Great Lakes-region females (Fisher and Fox 2003). The annual increment thicknesses for Bothwell mastodons fall within the thickness range for Hiscock tusks, so if Hiscock tusks exhibit relatively low growth rates, then Bothwell tusks did as well. The number of second-order increments per year is greater for the Bothwell tusks than for the Hiscock tusks. For Pen-62, 2-14, and M-1, the difference is substantial. Each of these Bothwell tusks exhibited 32 second-order increments or more per tusk year, and three of four Hiscock tusks exhibited fewer than 27 second-order increments per tusk year.

$\delta^{18}O$ of Structural Carbonate

Results of serial isotope analysis are presented graphically, in which isotope value is plotted against increment number (i.e., time). All four tusks in this study exhibit seasonal variation in carbonate oxygen ($\delta^{18}O$) composition expected for mammals living in temperate-latitude climates (Fig. 4.9; Koch et al. 1989; Stuart-Williams and Schwarcz 1997), so local minima in $\delta^{18}O$ values were used to identify winter-spring boundaries, as discussed above, and to infer season of death. Oxygen isotope values obtained from the four Bothwell tusks are similar to values derived from tusks of other Great Lakes-region

Table 4.2. Dentin growth rates for the Bothwell tusks (this study) and tusks of female mastodons from the Hiscock site (Fisher and Fox 2003). Bothwell and Hiscock mastodons presented here are both female, but Bothwell mastodons have higher numbers of annual increments per year and greater average annual increment thicknesses than Hiscock mastodons.

Tusk	Average no. of 2nd-order increments per year	Average annual increment thickness (mm)
Bothwell Site		
Pen-62	36.1	4.02
M-1	32.6	3.80
2-14	28.5	3.68
Pen-2	29.5	3.30
Hiscock Site		
BMS H7NW-181	26.0	3.18
BMS F10SW-71	26.7	3.67
BMS F9SW-106	25.8	4.34
BMS F8SE-79	25.5	3.23

BMS = Buffalo Museum of Science, Buffalo New York. BMS tusks are from the Hiscock site in southwestern New York State.

proboscideans, but the amplitude of seasonal variation for these tusks (~2‰) is less than that exhibited by other Great Lakes-region proboscideans (~3 to 6 ‰;Koch et al. 1989; Fisher and Fox 2003; Fisher 2008).

Pen-62 exhibited two local minima in its $\delta^{18}O$ profile, and the dentin sampled reflects nearly three years of tusk growth; the profile terminated during the declining phase of the seasonal cycle, indicating a winter death (Fig. 4.9A). M-1 exhibited two local minima in its $\delta^{18}O$ profile, and the dentin sampled reflects nearly three years of growth; the profile terminated during the declining phase of the seasonal cycle, indicating another winter death (Fig. 4.9B). Tusk 2-14 exhibited two local minima in its $\delta^{18}O$ profile, and the dentin sampled reflects nearly three years of growth; the profile terminated during the increasing phase, and possible peak, of the seasonal cycle, indicating a late summer or early autumn death (Fig. 4.9C). Pen-2 exhibited three local minima in its $\delta^{18}O$ profile, and the dentin sampled reflects nearly four years of growth; the profile terminated during the increasing phase, and possible peak, of the seasonal cycle, indicating another late summer or early autumn death (Fig. 4.9D).

$\delta^{13}C$ of Structural Carbonate

The $\delta^{13}C$ values for all four tusks are higher than expected for animals that primarily consumed C_3 plants (Fig. 4.9). Carbonate $\delta^{13}C$ values are typically higher than expected for Great Lakes-region mastodon tusks, but tusk collagen usually yields $\delta^{13}C$ values indicative of C_3 diets (e.g., Koch et al. 1997; Fisher and Fox 2003). Thus, carbonate $\delta^{13}C$ values derived from Bothwell mastodon tusk dentin – that suggest these mastodons consumed primarily C_4 plants – are suspect, and diagenesis likely altered the values.

Nonetheless, some seasonal variation in $\delta^{13}C$ is evident in each of the four tusk profiles. For Pen-62, $\delta^{13}C$ values track the pattern exhibited by $\delta^{18}O$ for the first year analyzed (Fig. 4.9A). For the last two years of life, $\delta^{13}C$ values exhibit an abrupt increase just after the winter-spring boundary, then decline to just before the next winter-spring boundary. For M-1, there is an abrupt increase in $\delta^{13}C$ values just after the winter-spring boundary for the last two years of life (Fig. 4.9B). For the first and last year analyzed, there are local lows in $\delta^{13}C$ values mid-year. This low is followed by a steady increase in $\delta^{13}C$ values to spring of the following year. For 2-14, the first year in the $\delta^{13}C$ profile exhibits low amplitude of variation (Fig. 4.9C). The $\delta^{13}C$ values for the last two years in 2-14 exhibit variation similar to that for the last two years of Pen-62, in which $\delta^{13}C$ values abruptly increase just after the winter-spring boundary, and then decrease to just prior to the winter-spring boundary. Pen-2 showed little variation in $\delta^{13}C$ for the first two years analyzed (Fig. 4.9D). For the final two years of life, the $\delta^{13}C$ profile is similar to that of the last two years of Pen-62 and 2-14 and the penultimate year of M-1, in which $\delta^{13}C$ values abruptly increase just after the winter-spring boundary, and exhibit an overall decrease in $\delta^{13}C$ values to just prior to the winter-spring boundary

$\delta^{13}C$ and $\delta^{15}N$ of Tusk Collagen

The collagen in dentin from Pen-2 was poorly preserved, so although serial analyses were performed, most values derived from this dentin were altered. The average C:N ratio for this tusk was 5.2 (Appendix II), well above the acceptable limit for unaltered collagen (2.9 to 3.6, DeNiro 1985). However, five of the 17 samples exhibited C:N ratios that suggest the collagen was unaltered. The average $\delta^{13}C_{coll}$ value for these

samples was 21.5 ‰., which is within the range expected for an animal that consumed primarily C_3 plants (approximately -17 to -30‰; Fisher and Fox 2003), and the average $\delta^{15}N_{coll}$ value for unaltered samples was 3.7 ‰. Because collagen was poorly preserved in Pen-2, time was not invested in the serial analysis of tusk collagen for additional Bothwell mastodons.

Discussion

Paleoenvironment

The stratigraphic sequence at the Bothwell Site is indicative of a pond that was gradually infilled. The abundance of woody plant macrofossils within the fossil-bearing layer suggests that the area was forested. Analyses of plant macrofossils and pollen from mastodon sites associate mastodons with coniferous trees, such as spruce, fir, and pine (Moeller 1984; Jackson et al. 1986; Bearss and Kapp 1987; Kapp et al. 1990; Harrington et al. 1993; Gobetz and Bozarth 2001; Griggs and Kromer 2008; Miller 2008). Thus, it is generally accepted that mastodons inhabited boreal forests, although mastodons may have lived in deciduous woodlands with open grassy areas as well (Graham et al. 1981; Lepper et al. 1999). Palynological and macrofossil analyses at the Kolarik mastodon site, a late Pleistocene site located about 75 km southeast of the Bothwell Site, indicate the environment there was a patchy boreal forest, dominated by spruce (Jackson et al. 1986). The environment at the Bothwell Site was likely similar to that at the Kolarik Site, a typical post-glacial landscape of small ponds scattered through patchy boreal forests. A detailed report on site geology, currently being compiled by the Indiana State Museum (S. Brown in prep.), will provide additional insight into questions pertaining to the

paleoenvironment at the Bothwell site, as will future studies on pollen and plant macrofossils recovered there.

The Matriarchal Family Unit Hypothesis

A mastodon family unit should consist of adult females spanning a wide range of ages as well as juveniles of either sex. The Bothwell mastodons exhibit the appropriate age and sex demographics for a single family unit. Sex evidence shows that Bothwell mastodons are either (1) all mature females or (2) mature females and juvenile males. The presence of juvenile molar crowns indicates that at least one immature mastodon is present in the assemblage. Age evidence shows that the adult females range from 19 to 31 years in age, and the tusk with 31 annual increments present (Pen-51) exhibits a high degree of wear at the tip, indicating she is much older than the number of increments suggests and that the age range at the site is wider than indicated by the methods of age assessment used here.

Isotope values are plotted against increment number (i.e., time), so all profiles are expressed in a common frame of reference. Analyses of season of death, based on $\delta^{18}O$ profiles, show that two Bothwell mastodons died in winter and two died in late summer or early autumn (Fig. 4.8). This indicates that at least two separate mortality events occurred at the site, and that these mastodons were not victims of a single, catastrophic mortality event. $\delta^{18}O$ profiles for mastodons that died in winter (Pen-62 and M-1) differ in character for the years leading up to their deaths. For example, the profile for Pen-62 exhibits a peak in $\delta^{18}O$ values late in the year preceding her death, and the profile for M-1

exhibits a peak in $\delta^{18}O$ values substantially earlier in the year preceding her death (Fig. 4.9A and B).

Individuals that travel together, drink from the same sources, and eat the same food (i.e., members of the same family unit) should have similar isotope profiles (Fisher and Fox 2003; Hoppe 2004). Because Pen-62 and M-1 experienced different seasonal changes in environment and accessed different water sources during the final years of their lives, they were not likely members of the same family unit. The two mastodons that died in late summer or early autumn (2-14 and Pen-2) also do not exhibit similar patterns of $\delta^{18}O$ variation in the year prior to death. In this year, 2-14 exhibits a peak early on and Pen-2 exhibits a peak later in the year (Fig. 4.9C and D). Thus, these two mastodons were not likely members of the same family unit either.

If mastodons that died in the same season were not members of the same family unit, then the number of mastodon mortality events at Bothwell increases from at least two to at least four. Because four season-of-death evaluations yielded four temporally discrete mortality events, it is unlikely that only four mortality events were responsible for the deaths of all seven to 12 mastodons. Tests of season of death on additional Bothwell mastodons have the potential to reveal as many as twelve mortality events at the Bothwell site.

The non-simultaneous nature of Bothwell mortality events dispels the notion that the Bothwell mastodons were members of a single social unit. Had the deaths been simultaneous, then there would be evidence that the Bothwell mastodons were in the same place at the same time, which would be the expectation if they were members of the same family unit. However, the non-simultaneous nature of the death events cannot

completely falsify the hypothesis that there was a life association among individuals, because different members of a family unit could have died at the same location at different times.

Differences among profiles, as discussed above, indicate that Bothwell mastodons that died in the same season did not die together, but similarities among profiles suggest some of the mastodons may have been contemporaries. For example, year "x + 6" in M-1 (Fig. 4.10B) and year 22 in 2-14 (Fig. 4.10C) exhibit strong similarities in patterns of $\delta^{18}O$ and $\delta^{13}C$ variation, so these two mastodons could have died in different seasons of the same calendar year. Growth increment profiles for M-1 and 2-14, however, exhibit numerous qualitative differences that suggest that they were not contemporaries (Fig. 4.9B-C). Additional information, such as radiocarbon ages obtained from the collagen of other tusks, might clarify whether Bothwell mastodons were contemporaneous. Such information cannot clarify whether they were members of the same social unit, but, if the life spans of these mastodons did not overlap, then the hypothesis that they were members of the same social unit could be definitively rejected.

Growth Increments, Diet, and Seasonality

Patterns of tusk growth rate were not informative for inferring season of death. Increment thickness, however, provided additional evidence for assessment of sex because increments are thinner in tusks of adult females than in tusks of comparably-aged males (Fisher 2008), and annual increment thicknesses of Bothwell tusks are within the range of those of female mastodons at the Hiscock site (Table 4.2). There is, however, a high number of second-order increments per year in the Bothwell tusks, as compared to

the Hiscock tusks. Differences in the number of second-order increments per year among Bothwell and Hiscock tusks may be an example of variation among individuals, akin to the variation among individuals in the number of striae of retzius in tooth enamel (Fitzgerald 1998).

The lack of seasonal variation in the second-order growth increment profiles (Fig. 4.8), in contrast to the seasonal variation evident in other Great Lakes-region mastodons, could be due to geographic location. If temperatures south of Lake Michigan were milder than they were east of Lake Michigan, then the Bothwell mastodons may not have been as nutritionally stressed during the winter months, and tusk growth during winter might not noticeably decline. In addition, the amplitude of seasonal variation in $\delta^{18}O$ is low relative to other Great Lakes-region mastodons, which raises the possibility that Bothwell mastodons lived in an area with lower seasonality. However, the amplitude of seasonal variation in $\delta^{18}O$ values in tusks and teeth is typically damped with respect to the amplitude of seasonal variation in meteoric $\delta^{18}O$, so these values are not ideal as paleoclimate indicators (Stuart-Williams and Schwarz 1997). Nonetheless, the growth increment and stable isotope data are at least consistent with the hypothesis that the climate south of Lake Michigan was slightly milder than in other parts of the Great Lakes-region.

Diagenesis rendered $\delta^{13}C_{carb}$ values ineffective for directly assessing diet for the Bothwell mastodons. However, the increase in $\delta^{13}C_{carb}$ values after the winter-spring boundary and the subsequent decrease to just before the winter-spring boundary for at least one year in the tusk record of each (Fig. 4.9) suggests that Bothwell mastodons experienced similar seasonal changes in diet. The increase across the boundary is

relatively minor (~2‰) and could reflect an increase in the proportion of C_4 plants in the diet in spring. This difference could also be related to fat metabolism. Lipids are isotopically light, so fat production should leave an animal's body plasma (and tusk dentin) enriched in $\delta^{13}C$ (Fisher and Fox 2003). Fisher and Fox (2003) suggested that $\delta^{13}C$ (collagen and carbonate) values decrease in winter and early spring due to utilization of fat reserves (to compensate for short-term nutritional deficits). Conversely, $\delta^{13}C$ values should increase during summer, when an animal is unlikely to utilize fat reserves and is typically storing fat. $\delta^{13}C$ values for Bothwell mastodons peak in spring, and are lowest before and at the winter-spring boundary. Thus, like the Hiscock mastodons, Bothwell mastodons likely utilized fat reserves during winter. Summer is the least likely time of year to use fat reserves, but Bothwell mastodon $\delta^{13}C$ values are highest in spring. Thus, it is possible that (1) spring in Pleistocene northwestern Indiana was a time of high nutrient availability, so Bothwell mastodons did not need to utilize fat then, (2) Bothwell mastodons experienced relatively mild winters, and seasonal variation in $\delta^{13}C$ values was dominated by changes in diet, or (3) both are true.

Pen-2's average $\delta^{13}C_{coll}$ value for unaltered tusk collagen (-21.3%) and 2-14's bulk $\delta^{13}C_{coll}$ value (-20.0‰) are indicative of diets consisting primarily of C_3 plants. These values are within the range of $\delta^{13}C_{coll}$ values reported for other Great Lakes-region mastodons (Fisher and Fox 2003), signifying that mastodons in northwestern Indiana had diets similar to mastodons in other parts of the region. The average unaltered $\delta^{15}N_{coll}$ value (4.07 ‰) is also within the range of values reported for other Great Lakes-region mastodons (Fisher and Fox 2003). This pattern suggests that mastodons in northwestern

Indiana did not experience undue nutritional stress compared to other mastodons in their region.

Cause of Death Scenarios

The taphonomic processes that led to formation of the Bothwell site cannot be resolved by the analyses presented here, but data obtained from the tusk records of four mastodons allow for evaluation of potential causes of death, thus providing evidence for processes that could and could not have been involved in site formation. Tusk evidence indicates that death was not caused by a single, catastrophic event, such as a flood or an ambush by human hunters, and a different mechanism could be responsible for the death of each Bothwell mastodon. Here, tusk evidence for the following causes of death for Bothwell mastodon is considered: (1) nutritional stress, (2) natural trap, and (3) human influence.

Nutritional Stress.– Death by nutritional stress is more likely for mastodons that died in winter (Pen-62 and M-1), when the environment is harsh and nutrients are not as abundant, but is unlikely for mastodons that died in summer/autumn (Pen-2 and 2-14), when nutrients are likely to be readily available. However, annual and bi-weekly growth increment profiles indicate that none of the mastodons experienced nutritional stress at the end of life, as increments deposited just prior to death – at either scale – did not exhibit a substantial decline in growth rate compared to increments deposited earlier in life (Fig. 4.8). Analysis of the $\delta^{15}N$ composition of tusk collagen (Appendix II), in which elevated nitrogen values are indicative of nutritional stress (Hobson et al. 1993), also indicates that Pen-2 – a summer/autumn death – was not stressed at death. Death by

injury or illness, which may have acted too rapidly to be reflected in the tusk record, remains a possibility.

Natural Trap.– Because mastodons are frequently found in bogs or ponds, it has been proposed that mastodons died after becoming trapped in these ponds (Jackson et al. 1986). Frison (1998) asserts, however, that large mammals – e.g., bison and elephants – have the ability to free themselves from bogs unless they are injured, sick, or otherwise weakened. Thus, if the site was a trap, the assemblage should consist of the oldest and youngest mastodons, those which might have trouble extricating themselves from the trap, not non-stressed mastodons of prime reproductive age like the Bothwell mastodons.

The winter season of death for two of the Bothwell mastodons creates another complication for the natural trap hypothesis. Winter should be cold in post-LGM Indiana., so a small body of water would have been frozen in the winter, and a frozen lake cannot act as a trap. However, if winters were mild – as the lack of seasonality in growth increments and low amplitude of variation in $\delta^{18}O$ implies – or death occurred in early winter, ice cover on the pond could have been thin. If thin ice was covered by snow or brush, a mastodon may have been caught by surprise, fell into the pond, and sustained an injury that made it difficult for the mastodon to escape.

Natural traps typically accumulate animals slowly (e.g., Agenbroad and Mead 1986), so determining rate of accumulation for Bothwell mastodons by obtaining ^{14}C dates on additional specimens, could be used to evaluate the natural-trap hypothesis. Evidence of injury on post-cranial elements could also provide support for the natural-trap scenario, as would an assessment of association among skeletal elements, because a natural trap should include complete skeletons.

Human Influence.– Clovis weapons have been found in association with North American mammoths and mastodons (e.g., Graham et al. 1981; Frison and Todd 1986), and multiple Great Lakes-region mastodons have exhibited patterns of bone modification indicative of butchery by humans (e.g., Fisher 1984). Butchered mastodons exhibit autumn or winter deaths, and mastodons that died in other seasons do not exhibit evidence of butchery (Fisher 1987, 2009). Thus, mastodons butchered by humans were likely also victims of human hunting (Fisher 1987). Season of death for Pen-62 and M-1 (early winter) is comparable to those of butchered mastodons, and season of death for 2-14 and Pen-2 (late summer/early autumn) is comparable to butchered mastodons if they died in autumn rather than summer.

Butchered mastodons are often preserved in wetland depositional environments. These sites have been interpreted as underwater Paleoindian meat caches (Fisher 2009). Above-ground meat caches are traditionally thought to include animals killed during cold-weather seasons because it is difficult to prevent meat spoilage in warm-weather seasons (Frison 1987). Caching meat underwater prolongs edibility and allows for storage through much of summer (Fisher 1995), so a subaqueous meat cache could include animals killed in seasons other than late autumn or winter. Tusks, though not sources of meat, may be included in a meat cache because tusk ivory may be used to make tools for processing the mastodon carcass itself (Frison 1998; Pearson 1999; Yesner 2001).

The depositional environment of the Bothwell site – a pond - is plausible for an underwater meat cache. Additionally, the 11,440 BP date obtained from Bothwell 2-14 indicates that these mastodons were contemporary with Clovis people. Overall, tusk

evidence supports the possibility the Bothwell mastodons were hunted by humans, and the site potentially represents a subaqueous Paleoindian meat cache.

Natural Trap vs. Human Influence.– A study of Bothwell mastodon post-crania could provide evidence to distinguish between death by natural trap and death by human influence. Some megafaunal death traps, such as the Mammoth Site of Hot Springs, South Dakota (Agenbroad and Mead 1986), include remains of opportunistic carnivores that were trapped themselves while feeding on trapped animals. Others, such as the Rancho La Brea tar seeps, exhibit patterns of bone modification suggestive of action by carnivores (Spencer et al. 2003). Presumably, when early humans cached meat, they would store it in locations inaccessible to predators. If Bothwell mastodons were cached, an investigation of their post-crania may reveal evidence of bone modification and the absence of certain elements suggestive of processing by humans. If Bothwell mastodons were trapped, post-cranial elements may exhibit evidence suggestive of scavenging, or remains of predators themselves may be identified within the assemblage. Future studies on patterns of bone modification will aid in evaluation of the natural trap and human influence hypotheses.

Conclusions

Serial stable isotope analyses of tusk dentin indicate that mastodons at the Bothwell site were most likely not members of a single matriarchal family unit. Age and sex demographics for Bothwell mastodons resemble those of a modern elephant family unit, but because mortality events were not simultaneous, there is no conclusive evidence that individuals were associated in life. Collagen from additional tusks will be radiocarbon dated to determine if Bothwell mastodons could have lived at the same time;

if radiocarbon age estimates for Bothwell mastodons differ by more than a few decades, then the hypothesis that Bothwell mastodons were members of a single family unit could be definitively rejected. The cause or causes of death for Bothwell mastodons remain unresolved, but tusk evidence eliminates the possibility of a catastrophic event and provides evidence against the nutritional stress hypothesis. The most likely scenario for the origin of the Bothwell mastodon assemblage, based on tusk evidence alone, is that they were brought to the site by humans to be stored in an underwater meat cache.

The Bothwell site provided a unique opportunity for studying the paleoecology of late Pleistocene Great Lakes-region mastodons because it offers a sample of the female mastodon population. Female mastodons are uncommon in the Great Lakes-region fossil record, compared to males, so analyses of Bothwell mastodon tusks provide a rare glimpse into the life histories of late Pleistocene females. Studying the lives and deaths of mastodons is one approach to investigating what caused the end-Pleistocene mastodon extinction, as changes to life history parameters (see Chapter 5, this dissertation) and causes of mortality are responses to changes in the mastodons' environment. Mastodons living at the end of the Pleistocene experienced substantial environmental change, both through the introduction of a new predator – humans – and through climatic changes that altered the seasonality and plant composition of their habitat, among other factors. The question of mastodon extinction is still open, but comprehensive analyses of mastodon sites like Bothwell serve to further the understanding of this intriguing question.

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Appendix I. The relationship between second-order increments associated with local lows in the $\delta^{18}O$ profile (inferred winter-spring boundaries) and enhanced increments. This relationship is used to hypothesize (h) the location of winter-spring boundaries on portions of tusk dentin not analyzed for isotope composition.

Tusk	Winter-Spring Boundary	Enhanced Increment	Increments/ year	Increments between enhanced increments
Pen-62	—	6	—	—
	36 (h)	45 (e)	—	39
	72 (h)	81	36	36
	109 (h)	118	37	37
	142	151	33	33
	180	190	38	39
M-1	22 (h)	33	—	—
	49 (h)	60	27	27
	80 (h)	91	31	31
	115 (h)	126	35	35
	149	162	34	36
	185	195	36	33
2-14	4 (h)	8	—	—
	31 (h)	35	27	27
	61 (h)	65	30	30
	91 (h)	95	30	30
	119 (h)	123	28	28
	143 (h)	147	24	24
	170 (h)	174	27	27
	200	205	30	31
	232	236	32	31
Pen-2	32 (h)	33	—	—
	61 (h)	62	29	29
	92	96	31	34
	118	118	26	22
	152	150	34	32

The location of winter-spring boundaries for portions of dentin not analyzed for isotopic composition are hypothesized (h) using the equation: h = (enhanced increment number - [Average (enhanced increment - increment associated with $\delta^{18}O$ low)] ; Because there are no "half" increments, h is rounded to the nearest whole number; e = estimate, made on a section of dentin where increments are unclear.

Appendix II. Weight percent yields and C:N ratios from the analysis of tusk collagen. A C:N ratio between 2.9 and 3.6 (in bold) indicates collagen is unaltered. Samples are ordered temporally, with number 17 representing the earliest time in this slab, and number 1 representing the last dentin deposited before death occurred.

Sample no.	Wt. % Yield	C:N Ratio
Pen-2 #17	6.9 %	4.0
Pen-2 #16	10.0 %	9.1
Pen-2 #15	0.0 %	n/a
Pen-2 #14	18.4 %	3.9
Pen-2 #13	4.6 %	9.4
Pen-2 #12	16.5 %	3.8
Pen-2 #11	0.0 %	n/a
Pen-2 #10	15.4 %	**3.5**
Pen-2 #9	0.8 %	6.0
Pen-2 #8	20.4 %	5.3
Pen-2 #7	7.4 %	9.6
Pen-2 #6	31.7 %	5.4
Pen-2 #5	18.3 %	4.0
Pen-2 #4	22.8 %	**3.6**
Pen-2 #3	15.0 %	**3.4**
Pen-2 #2	23.1 %	**3.5**
Pen-2 #1	19.5 %	**3.4**

Chapter 5

Stable isotope and growth rate analysis of structural increments in the tusk dentin of two female American mastodons (*Mammut americanum*)

Abstract

This chapter documents variation in the stable isotope composition and growth rate of two tusks from female American mastodons (*Mammut americanum*), New York State Museum (NYSM) V50 and Bothwell 2-14. The primary goal of this study is to document the life histories of these mastodons, with specific focus on identifying one life-history parameter, the inter-birth interval, in the tusk record. NYSM V50 is an isolated tusk recovered in southeastern New York State; the number of annual dentin increments in the tusk indicates a minimum age of 35 years at death. Bothwell 2-14 is part of an assemblage of female mastodon tusks recovered in northwestern Indiana; the number of annual dentin increments in the tusk indicates a minimum age of 22 years at death. The annual increment profile of NYSM V50 exhibits a conspicuous period of growth rate increase, decrease, and recovery that is tentatively interpreted as a five-year inter-birth interval. The annual increment profile of Bothwell 2-14 exhibits three such intervals, all four years in length. Neither tusk exhibits a substantial decrease in growth rate (at the annual or sub-annual level) at the end of life as would be expected if nutritional stress were a major factor in their deaths. Sub-annual variation in the oxygen isotope composition of tusk dentin indicates that NYSM V50 died in autumn and

Bothwell 2-14 died in late summer or early autumn. Evidence from tusk records, in these instances, cannot resolve cause of death for either mastodon, but the season of death suggests that death by human influence is a possibility.

Introduction

Age of weaning and maturation, inter-birth interval, duration of gestation, reproductive life span, and age at death are all parameters of mammalian life history (e.g., Stearns 1977; Smith 1992). Life history parameters differ among species, but the events themselves are common to all mammals (Smith 1992). Certain life history events result in physiological changes that are reflected in the skeleton of an organism. Any layered structure that changes its growth rate and morphology as a response to changes in an organism's physiological condition can be thought of as a recording structure (Klevezal 1996). The specialized, elongate upper incisors of proboscideans – tusks – are ideal recording structures because they grow continuously by apposition and preserve periodic dentin increments in their structure (Fisher 1996). Thus, a single tusk exhibits a near-complete record of growth rate, stable isotope composition, and morphology for an individual.

This chapter documents long-term variation in the stable isotope composition and annual and fortnightly growth rate of the tusks of two female American mastodons (*Mammut americanum*). The goal of this study is to increase the body of knowledge on female mastodon life history, with a focus on identifying evidence of a specific life history parameter – the inter-birth interval – in the tusk record. Animals respond to external factors by altering life history parameters, such that certain factors can be

associated with specific responses (Reznick et al. 1990; Jones et al. 2008); so, if an animal exhibits changes in life history parameters over time, the nature of the changes themselves can provide evidence for what caused them. Inter-birth intervals increase when an animal is under nutritional stress (Lee and Moss 1986), so if criteria for identifying inter-birth intervals in tusk records can be established, then trends in the magnitude of mastodon inter-birth intervals throughout the Pleistocene can be used to evaluate the contribution of environmental stress, or lack thereof, to the extinction of the species at the end of the Pleistocene.

This chapter begins with a brief overview of tusk structure and growth, followed by a discussion of the life history of the mastodon's closest living relatives, modern elephants; life history traits shared by mastodons and modern elephants are also discussed. Next, a hypothesis for the effects of pregnancy and lactation on the tusk growth and stable isotope record is presented. The tusks and the methods used to analyze them are then described. Growth increment and stable isotope records of each tusk are presented, and the hypothesized criteria for recognizing pregnancy and lactation in the tusk record are applied to these data. This chapter concludes with a summary and a discussion of the results in the broader contexts of mastodon paleobiology.

Tusk Structure and Growth

Tusk growth is described in detail elsewhere (e.g., Fisher 1996, 2009; Smith and Fisher in revision), and reviewed briefly here. Tusks, like other teeth, are composed of dentin, cementum, and enamel. The bulk of a tusk is composed of dentin. A tusk grows as dentin both lines and extends the pulp cavity. Odontoblasts lining the pulp cavity deposit

a layer of dentin that displaces the pulp-cavity apex proximally. Odontoblasts deposit dentin at the tusk's proximal margin, increasing the overall length of the tusk. The increase in tusk length proximally is coupled with eruption distally, providing space for the addition of new material in the proximal direction.

Tusks are cone-in cone structures, in which dentin at the tip was formed earliest in life and dentin that lines the pulp cavity was formed just prior to death; thus, the longitudinal axis of the tusk is essentially an axis of time. Periodic dentin increments, at different temporal scales, are preserved in tusk dentin, allowing changes in dentin growth rate, stable isotope composition, and morphology to be tied to specific times in an animal's life. Annual, or first-order, increments may be identified as light-dark couplets, in which dark dentin reflects winter growth (Koch et al. 1989). Within each annual increment are 365 bands. Each band reflects one day of growth, and these daily bands are referred to as third-order increments. In mastodons, approximately every fourteenth daily band is accentuated. These bands reflect growth on the order of about two weeks, and are referred to as second-order increments. The thickness of structural increments varies seasonally (Koch et al. 1989) and with the nutritional status of the animal (Fisher 1996); the thinnest increments typically reflect those that formed during winter, when an animal is expected to be under nutritional stress, and the thickest increments typically reflect those that formed during summer, when nutrients are expected to be plentiful.

The rate of deposition, both inwardly (reflected by the thickness of each increment, which is typically measured in millimeters) and proximally (reflected by the length of each increment, which is typically measured in centimeters), is not constant. The inward rate of deposition varies based on relative position within the pulp cavity

(Fisher 1996). This variation in thickness is not substantial, but it is quantifiable. When tracing a single increment from the cementum dentin junction to the longitudinal axis, the rate of apposition first increases, then maintains a relatively constant value (for roughly half its path length), then decreases again as it approaches the tusk axis. Because of the gradient of dentin apposition, any study of patterns of variation in the thickness of dentin increments must account for variation in thickness attributable to the location where the increment was measured. This study focuses on changes in rate of inward deposition (i.e., patterns of variation in increment thickness).

Proboscidean Life History

Life-history traits differ between males and females of the same species, and life history parameters may differ between individuals in a species as well as between sexes (Stearns 1977; Smith 1992). Male and female mastodons, like male and female African elephants, are strongly dimorphic in body and tusk size (e.g., Elder 1970; Lee and Moss 1995; Smith and Fisher in revision; Chapter 2, this dissertation). Strongly dimorphic species, with males larger than females, typically group by sex and engage in sex-specific strategies for reproductive success (Gittleman and Van Valkenburgh 1997; Weckerly 1998; Berger et al. 2001). African elephants and mastodons exhibit tusk dimorphism that is similar in character; male tusks are significantly larger than female tusks, especially in pulp cavity depth and maximum tusk circumference; males and females, regardless of genus, can be discriminated based on sex-specific patterns of tusk ontogeny (Chapter 3, this dissertation). In addition, elephants and mastodons have similar skeletal structures, and elephants are the closest living relative to mastodons. Thus, African elephant

(*Loxodonta africana*, *Loxodonta cyclotis*) life history is likely the best analog, of any living species, for mastodon life history. This paper investigates life histories of female mastodons using the well-documented life histories of female African elephants (*L. africana*; e.g., Moss 1988) to interpret life events that may be preserved in the female mastodon tusk record.

Female elephants live in matriarchal family units consisting of related females and their juvenile offspring. Male elephants are evicted from or willingly leave their family units upon attaining maturation in their early teenage years, after which time they live alone or in loose association with other males (Moss 1988). Males typically do not successfully mate until well into their thirties. Tusks are ever-growing, and elephants increase in stature for most of life, so older males (i.e., those with the largest bodies and tusks) are more likely to win intra-sex battles for access to mates (Lee and Moss 1995). Female elephants do not rely on large body or tusk size for reproductive success, although a larger-bodied female is better equipped for the demands of raising a calf (Lee and Moss 1995). Females that reproduce before they have ceased rapid growth must sacrifice energy devoted to growth for energy devoted to calf-rearing. These females have longer reproductive life spans than females who delay reproduction until their growth has largely stabilized, but the calves of females who delay reproduction are more likely to survive to adulthood.

The youngest female elephant observed to have birthed a calf was 8.9 years old, but most elephants do not experience parturition until 3 to 6 years later (Moss 2001). As in females of most polygynous mammals, female elephants have a much greater parental investment in offspring than do male elephants (Ralls 1977; Lee and Moss 1995).

Reproduction is particularly stressful on female elephants, compared to other mammals, because of the long gestation period (22 months) and duration of lactation (4 years, on average; Lee 1986), and because females reach sexual maturity and may reproduce before statural growth rate slows significantly (Lee and Moss 1995). The life span of an elephant is around 60 years, and a female is capable of birthing calves until her death. However, African elephants frequently enter a post-reproductive period around age 50, when calf production ceases or slows substantially (Moss 1988).

Raising a male calf is more stressful on a female elephant than raising a female calf because males nurse more frequently and have higher milk intake during the first three years of life in order to accommodate rapid early growth (Lee 1986; Lee and Moss 1986). If males do not begin growing quickly from birth, they will be smaller their male competitors as adults, and be at a disadvantage when they enter into intra-sex battles for access to mates. As a result of the greater investment in male calves, the inter-birth interval is slightly greater for a female when her first calf is male (Lee and Moss 1986). However, the greatest increase in inter-birth interval occurs due to environmental conditions. During multi-year wet periods, when nutrients are readily available, the mean inter-birth interval for a female is 3.5 years; during multi-year dry periods, when nutrients may be scarce, the mean interval increases to 5.6 years (Lee and Moss 1986). Thus, the length of an inter-birth interval is a life history trait than can be used to understand the nature of an animal's environment.

Previous Work on Mastodon Life History

The majority of tusk records that have been compiled are of Great Lakes-region mastodons (e.g., Fisher 2009). Aspects of mastodon life history have been identified in the tusk record from specific changes in growth rate and stable isotope composition. For males, eviction from the matriarchal family unit has been identified as a period of low growth rate that occurs in early teenage years (Fisher 1990, 2008). Male elephants are typically stressed during the year following eviction (Moss 1988; Lee and Moss 1999), and low growth rate indicates nutritional stress (Fisher 1996), as decreased nutrient intake reduces the amount of energy that can be allocated to growth. Musth, a period of heightened aggression and sexual activity, has also been identified in the tusk record (Fisher 2008). Male elephants tend to fast during musth; this fasting is reflected in the tusk record as a rapid decline in growth rate (i.e., nutritional stress) in early spring.

Aspects of female mastodon life history, the focus of this study, have been tentatively identified in the tusk record. As discussed above, mastodon life history is expected to bear strong similarities to elephant life history. So, mastodons, like elephants, should exhibit gestation lengths that exceed one year and lactation periods that span multiple years. Associating variation in annual growth rate with calving cycles was first proposed by Fisher (1996), in which periodic undulations in annual increment length in the female tusk record were distinct from those exhibited in the male tusk record. This idea was further explored in the tusk record of a female mastodon from the North Java site (southwestern New York state; Fisher et al. 2008), in which there was a steady increase in annual increment thickness and length during the early years of life, followed by a sharp decrease at year ten. This decrease was followed by three- to four-year cycles of variation in tusk growth rate. North Java exhibited six to seven of these cycles over an

approximately 34-year tusk record. The sharp decrease in growth rate is interpreted as first pregnancy, and the three- to four-year cycles are interpreted as inter-birth intervals, reflecting changes in growth rate caused by different energetic requirements of gestation and lactation. In addition, Fisher and Fox (2003) proposed that an increase in the carbon isotope composition ($\delta^{13}C$) of structural carbonate in the tusk dentin of four female mastodons might be evidence of lactation, in which a mother's plasma would be enriched in $\delta^{13}C$ due to the diversion of lighter isotopes to the formation of lipid-rich milk.

"What to Expect when Mastodons are Expecting" (and lactating)[1]

Documenting evidence of female mastodon reproductive biology in the tusk record is a relatively new endeavor. As discussed above, identifications of birthing and calving in the tusk growth records are promising, but tentative. Here, evidence of reproductive biology documented in the body plasma, collagen, and dentin growth increments of other mammals is considered in order to develop expectations, independent of other studies of mastodon inter-birth intervals, for the effects of lactation and pregnancy on the growth rate and stable isotope composition of tusk dentin.

Both gestation and lactation are costly for a female, but the costs of lactation far exceed the costs of gestation (Clutton-Brock et al. 1989; Lee 1996). In humans, for example, energy devoted to gestation amounts to about 250 to 300 calories a day (Lee 1996), but lactation requires most mammalian mothers to increase energy intake by two to five times their normal levels (Sikes 1995). Specifically, healthy human mothers devote approximately 0.375, 1.20, and 1.950 megajoules/day to fetal development during the first, second, and third of gestation, respectively, and approximately 2.62

[1]Thank you to Heidi Murkoff and Sharon Mazel, authors of What to Expect When You're Expecting, for inspiring the title of this section.

megajoules/day to lactation (Butte and King 2007). Thus, if the energetic costs of reproduction are reflected in the tusk growth record, lactation should have the greatest impact on tusk growth rate.

In the continuously-growing incisors of rats, there was a significant increase in the rate of dentin apposition during gestation, and a significant decline in dentin apposition for the period between parturition and weaning (Miller et al. 1985). After the pups were weaned, rates of dentin apposition recovered to that of nulliparous rats. Other evidence of parturition in dentin includes the occurrence of accentuated, darkly-stained layers within annual growth layers in the teeth of mature female dolphins, in which the darkly-stained layers have been temporally associated with parturition (Klevezal and Myrick 1984).

Polar bears exhibit enrichment in $\delta^{13}C$ of blood plasma during lactation (Polischuk et al. 2001). The stable isotope composition of body plasma is reflected in the stable isotope composition in tusk dentin, so enrichment in $\delta^{13}C$ of tusk dentin could be used to identify lactation in mastodons. In human females, there is a significant decrease in nitrogen ($\delta^{15}N$, measured in hair collagen) from conception to parturition (Fuller et al. 2004), which may be related to the utilization of nitrogen in fetal development (Fuller et al. 2006). The nitrogen composition of body plasma is related to nutrition, in which a decrease in $\delta^{15}N$ indicates growth, and an increase in $\delta^{15}N$ indicates nutritional stress (Hobson et al. 1993; Fuller et al. 2004). Growth increment thickness has also been associated with nutritional status, in that relatively thin increments are associated with periods of nutritional stress (Fisher 1996). In this way, gestation may be identifiable in the tusk record as an increase in growth rate, as observed in rats (Miller et al. 1985).

Prior to this study, the long-term, annual and fortnightly growth records of only one female mastodon had been compiled (Fisher et al. 2008), and growth records of four additional females had been compiled at annual scales (Fisher 1996). In both studies, inter-birth intervals were tentatively identified as periodic oscillations in annual growth rate. In this chapter, two female mastodon tusks are analyzed for annual and sub-annual growth rate as well as for stable isotope composition. These analyses are conducted to increase the body of data on female mastodon life history and to propose criteria for identifying the effects of gestation and lactation in the tusk record.

Materials and Methods

Materials

NYSM V50 – NYSM V50 was recovered in southeastern New York State (Orange County; Fig. 5.1); the left tusk is the only skeletal element associated with the individual. This tusk, estimated at 152 cm in length, consists of a relatively well-preserved distal portion, a highly fragmented middle portion, and a proximal portion with a nearly complete pulp cavity (Fig. 5.2A). Portions of NYSM V50 were reconstructed using quick-set epoxy, and the tusk was consolidated using low-viscosity epoxy.

The tip is acute and slightly asymmetrical about the longitudinal axis (Fig. 5.2A), suggesting that only a few years are missing from the beginning of the growth record. A comparison of tusk widths between NYSM V50 and North Java, a female mastodon with a blunt tip inferred to have abraded as much as 50 cm of length and at least five annual

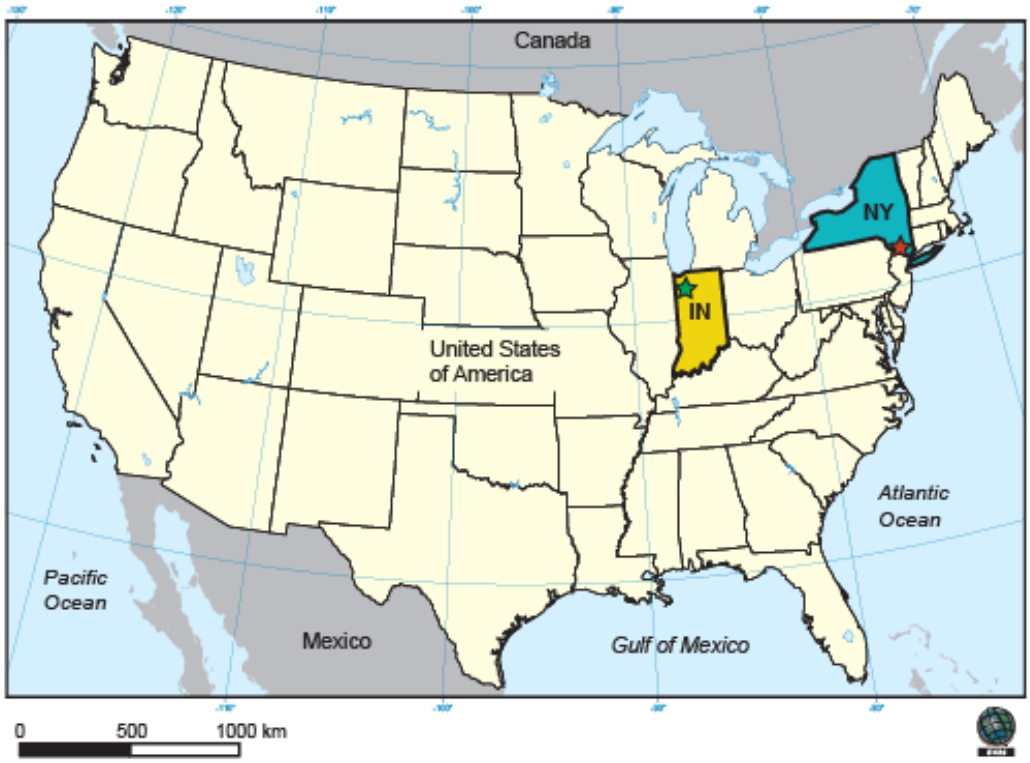


Figure 5.1. Localities of recovery for NYSM V50 (red star; Orange County, New York) and Bothwell 2-14 (green star, Porter County, Indiana).

increments from her tip (Fisher et al. 2008), shows that the width at North Java's tip is equivalent to the width at 30 cm from the tip for NYSM V50. This suggests that NYSM V50 lost no more than 20 cm of length from her tusk. The average annual increment length for the first three years in North Java's profile is just over 7 cm (Fisher et al. 2008). Thus, if NYSM V50 lost 20 cm of length from her tip, she likely lost between two and three annual increments from her tusk record.

Preservation of tusk dentin varies throughout the tusk, from darkly stained (yet un-deteriorated) to chalky (some deterioration). NYSM V50 is identified as female based on its small circumference and short pulp cavity, as compared to a set of inferred male and female mastodon tusks (Fig. 5.2). Due to fragmentation and poor preservation in the tusk mid-section, only the distal and pulp cavity portions were analyzed here. No tusk records of mastodons from coastal New York State had been compiled previous to this study, so analysis of this tusk allows for a comparison of Great Lakes-region and southeastern New York State mastodon growth and stable isotope records.

Bothwell 2-14. – Bothwell 2-14 was recovered from the Bothwell Site in Hebron, Porter County, Indiana (Fig. 5.1). This tusk is part of a larger assemblage of late Pleistocene mammalian fauna that consists of over 300 skeletal elements, including twelve additional mastodon tusks (Chapter 4, this dissertation). Fossils were recovered from a layer of silty, organic sediment that partially filled a small depression (likely, a pond within a forested wetland). The left tusk is the only skeletal element associated with Bothwell 2-14. The tusk, which is complete but broken into distal and proximal halves, is approximately 136 cm long (Fig. 5.2B). Bothwell 2-14 was consolidated using low-viscosity epoxy, and no additional reconstruction was required.

Figure 5.2. Images of (A) NYSM V50, New York State Museum, Albany, New York, and (B) Bothwell 2-14, Indiana State Museum, Indianapolis, IN. Photograph (B) is from the collection of the Indiana State Museum and Historic Sites.

The tip of Bothwell 2-14 is acute and asymmetrical about the longitudinal axis, and appears to have experienced more wear than NYSM V50 (Fig. 5.2B), so is likely missing a few additional annual increments from the beginning of the tusk growth record. Comparison of tusk widths between Bothwell 2-14 and North Java, as was done for NYSM V50, indicated that North Java's tusk width at the tip is equivalent to Bothwell 2-14's tusk width at 20 cm from the tip. Thus, it is inferred that Bothwell 2-14 abraded as much as 30 cm of length, corresponding to approximately four annual increments, from her tip.

Preservation of tusk dentin in Bothwell 2-14 ranges from darkly stained (yet un-deteriorated) in the distal portion, to a mixture of relatively un-deteriorated, darkly stained, lightly stained, and unstained dentin, and small patches of chalky, slightly deteriorated dentin in the proximal portion. AMS ^{14}C dating of tusk collagen yielded a radiocarbon age estimate of 11,440 ± 60 BP (Beta 262766; Chapter 4, this dissertation). Bothwell 2-14 was identified as belonging to a female based on a principal components analysis of linear and curvilinear tusk measurements (Smith and Fisher in revision; Chapter 2, this dissertation), as well as by its relatively small circumference and shallow pulp cavity, as compared to a set of inferred male and female mastodon tusks (Fig. 5.3). Here, the entire tusk record of Bothwell 2-14 was analyzed.

Methods

Growth Increment Analysis.– Methods of growth increment analysis used in this study are modeled after those in Fisher and Fox (2003) and Rountrey (2009). The distal portion of NYSM V50 and the whole tusk of Bothwell 2-14 were longitudinally

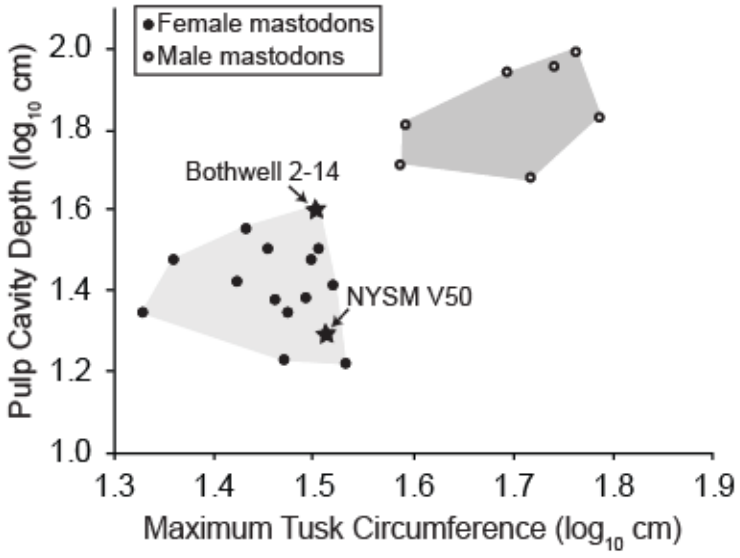


Figure 5.3. Pulp cavity depth versus maximum tusk circumference for a sample of male and female American mastodons (Chapter 4, this dissertation). NYSM V50 and Bothwell 2-14 are more similar to female than to male mastodon tusks.

sectioned using a metal-cutting band saw with a ½-inch bi-metal blade. Transverse blocks, approximately 2.0 cm in width and 1.5 to 2.0 cm in depth, were removed from a longitudinal half of each tusk at 10-cm intervals along the tusk's outer curve. Two transverse slabs, each approximately 1 cm wide, were cut from each block using an Isomet saw with a diamond wafering blade. One slab was reserved for isotope sampling, and a thin section was made from the adjacent slab for increment analysis. The pulp cavity portion of NYSM V50 was too fragile to be longitudinally sectioned with a band saw; instead, one block of dentin (that included the pulp cavity surface) was removed using a Dremel tool with a ⅛-inch tile cutting bit.

Second-order and annual increments from the distal portion of NYSM V50, which was analyzed early in the study, were counted and measured from thin sections using OPTIMAS 5.2 image analysis software. Second-order and annual increment data from the pulp cavity of NYSM V50 and the entire tusk of Bothwell 2-14 were collected with new methods developed by Rountrey (2009). In these methods, increments were counted and measured from photographs of thin sections using Image J and a custom plug-in. Second-order increments were measured on each slab, and increments were correlated between slabs (Fig. 5.4). Second-order increment profiles are time series of increment thickness measured at selected locations on the tusk (i.e., not close to the pulp cavity apex or proximal margin) and on the slab (i.e., not close to the CDJ or the longitudinal axis). It was not always possible to measure in ideal locations, however, because increment visibility was sometimes obscured by Schreger bands (that mark retreating paths of odontoblasts and exhibit a "checkerboard" pattern) or fractures. In addition, growth increments reflecting the earliest portion of the tusk record are only located near the CDJ,

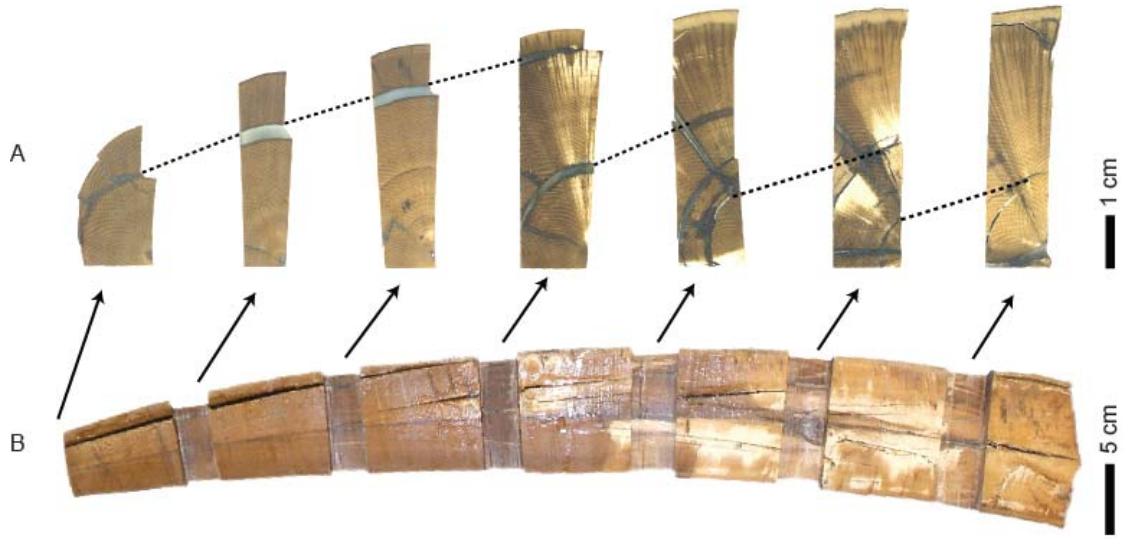


Figure 5.4. Bothwell 2-14 dentin slabs (A), and the longitudinal section from which these slabs were removed (B). Slabs in A are rotated 90° from their transverse orientation in the tusk to show the surface used for isotope sampling and thin section construction. Dashed lines illustrate the same increment at different locations along tusk length.

and growth increments deposited just prior to death are only located at the pulp cavity surface.

Empirical mode decomposition (EMD), an analytical method that identifies and extracts oscillatory patterns in non-stationary data (Huang et al. 1998, Huang 2005, Huang and Wu 2008), was applied to each series of second-order increments (both of which are non-stationary data sets) to identify patterns within increment data that might be related to seasonality or reproductive events. Extracted oscillatory patterns, or intrinsic mode functions (IMF), contrast with harmonic functions in their ability to vary in amplitude and frequency with time. This method is ideal for studies of tusk growth increments, in which there is often variation in the number of second-order increments per year, and changes to an animal's environment and nutritional status from year to year are expected to result in unique increment thickness profiles for each year. Statistical significance of each IMF is determined by testing whether the power of the IMF (i.e., the sum of squared amplitudes scaled by the number of increment measurements) falls above or below confidence intervals based on Gaussian white noise (Wu and Huang 2004). The analysis was performed in R (RDCT 2006) using a script written by A. Wood.

Locations of winter-spring boundaries were identified in order to evaluate the number of years in a tusk, document changes in annual increment thickness, and associate sub-annual changes in tusk growth rate and stable isotope composition to specific times during a year. Winter-spring boundaries were located based on (1) local minima in oxygen isotope composition ($\delta^{18}O$; Koch et al. 1989), as described below, (2) the relationship between lows in $\delta^{18}O$ and macroscopically visible enhanced increments,

and (3) patterns of variation in the appearance of microscopically visible second-order increments. In addition, the application of EMD to second-order increment thickness profiles could yield IMFs at the scale of one year, and thus may aid in locating winter-spring boundaries.

The locations of winter-spring boundaries are typically identified based on patterns of variation in increment thickness, in which low growth rates are associated with winter, and by the identification of dark-light couplets, in which dark dentin is indicative of winter growth, and the boundary between dark-light couplets is the winter-spring boundary (Koch et al. 1989). These methods were not applicable here because there was no seasonal variation in the second-order increment profile for either tusk, and dark stains in tusk dentin prevented reliable identification of true dark-light couplets. Annual increment thickness was measured on select portions of this tusk, such that annual increment thickness is the sum of thicknesses of second-order increments that comprise one year. Average annual increment thickness was also calculated for each year. by measuring each annual increment on every slab where it was present and averaging all the thicknesses obtained for a single year. An annual increment was present on as few as one and as many as five slabs, but on average the same annual increment was present on three slabs.

Ages for mastodons in this study are estimated by counting the number of annual increments in tusk dentin. Age determined with this method is a minimum, as dentin is abraded from the tip due to tusk use.

Stable Isotope Analysis.– Samples for stable isotope analysis of carbonate carbon and oxygen were removed parallel to growth lines so that variation in stable isotope

composition could be tied to specific times in the mastodons' lives (Fig. 5.5). Studying sub-annual patterns of oxygen isotope variation in a tusk allows for the identification of increments associated with winter-spring boundaries as well as the inference of an individual's season of death (Koch et al. 1989; Fisher and Fox 2003, 2007; Chapter 4, this dissertation).

The oxygen isotope composition ($\delta^{18}O$) in the structural carbonate of mammalian teeth and bones is determined by the $\delta^{18}O$ of body water (Longinelli 1984; Luz et al. 1984; Bryant et al. 1996). Body water composition in mammals primarily reflects the isotopic composition of drinking water, which in turn reflects the isotopic composition of meteoric water (Koch et al. 1989; Bryant and Froelich 1995). The $\delta^{18}O$ of meteoric water is correlated with air temperature in middle and high latitudes, such that $\delta^{18}O$ is low when temperatures are low and high when temperatures are high (Dansgaard 1964). For large-bodied, temperate-latitude mammals, the $\delta^{18}O$ of teeth lags behind the $\delta^{18}O$ of meteoric water (Stuart-Williams and Schwarcz 1997). For these reasons, in serial isotope analyses of temperate-latitude mammals, the lowest oxygen values are at winter-spring boundaries, and the highest values are in late summer or early autumn (Koch et al. 1989; Stuart-Williams and Schwarcz 1997; Sharp and Cerling 1998).

The carbon isotope composition ($\delta^{13}C$) in the structural carbonate of mammalian teeth and bones reflects the proportion of C_3 and C_4 plants consumed by the animal (DeNiro and Epstein 1978). C_3 plants, those that use the Calvin Cycle to fix CO_2, exhibit an average $\delta^{13}C$ value of -27‰ (O'Leary 1988). C_4 plants, those that use the Hatch-Slack Cycle to fix CO_2, exhibit an average $\delta^{13}C$ value of -13‰ (O'Leary 1988). In the structural carbonate of tusk dentin, these values are offset by +14.1‰ as a result of

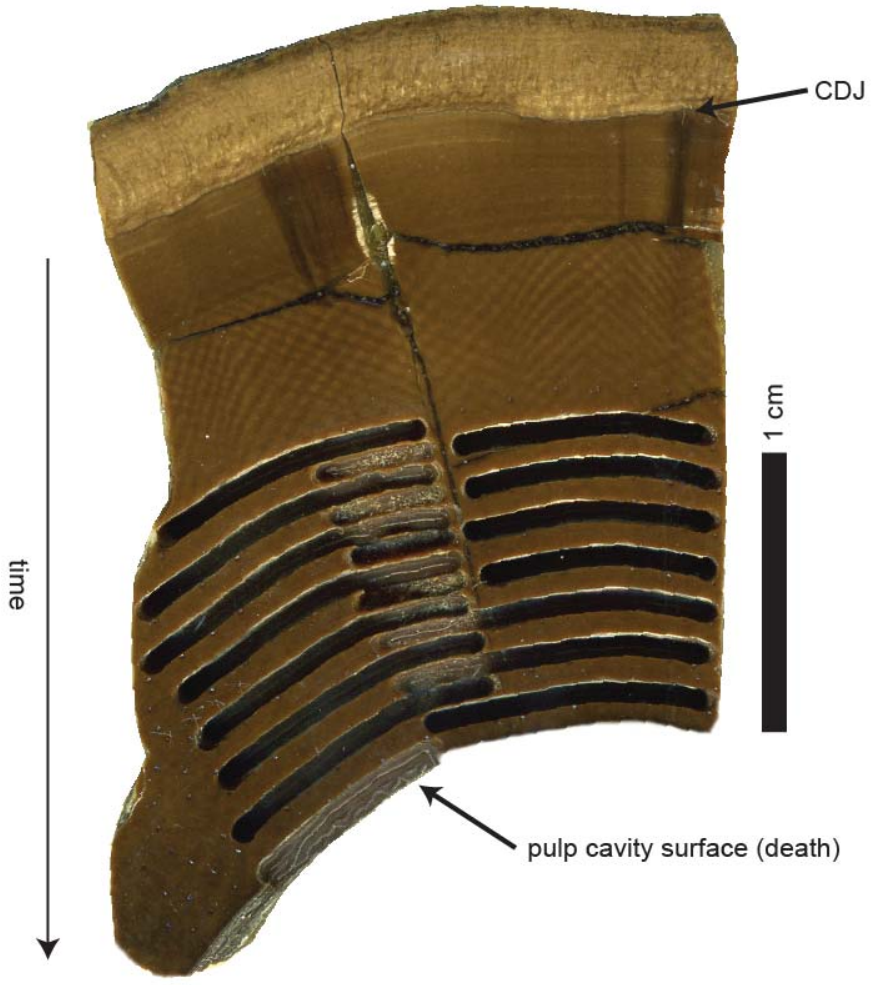


Figure 5.5. Transverse dentin slab from the pulp cavity of NYSM V50. Drill paths, which parallel growth increments, illustrate where isotope samples were removed. The "CDJ" is the cementum-dentin junction. In this orientation, material above the line is cementum, which is present as a thin layer on the tusk exterior; material below the line is dentin, which comprises the bulk of the tusk.

metabolism and biomineralization (Cerling and Harris 1999). Great Lakes-region mastodons primarily consumed C_3 plants (e.g., Jackson et al. 1986; Lepper et al. 1991), so $\delta^{13}C$ values in mastodon tusk dentin should be about -13.0‰ (Koch et al. 1997).

Dentin is prone to diagenetic alteration, but diagenesis could affect $\delta^{18}O$ and $\delta^{13}C$ differently. The effect of diagenesis on $\delta^{18}O$ values derived from structural carbonate in tusk dentin of Pleistocene proboscideans is minor (~0.5 ‰; Koch et al. 1997), and, even if the values themselves are shifted, seasonal variation is typically preserved (Koch et al. 1989; Sharp and Cerling 1998). The $\delta^{13}C$ values derived from structural carbonate in tusk dentin of Pleistocene proboscideans may, unlike $\delta^{18}O$, be substantially shifted due to diagenesis, so the data are not useful for identifying specific inputs of C_3 and C_4 plants in the diet. However, seasonal variations may be preserved.

Three slabs from NYSM V50 (one removed at 30 cm from the tusk tip, one removed at 50 cm from the tusk tip, and one removed from the pulp cavity portion) and two slabs from Bothwell 2-14 (one removed at 29 cm from the tip and one removed at 99 cm from the tip, which included the pulp cavity surface) were sampled for isotope analysis. The two distal NYSM V50 slabs were analyzed early in this study and were treated slightly differently from the remaining slabs, as sampling methods were adjusted to refine temporal constraints and pretreatment methods were altered in light of work by Rountrey (2009). Pre-treatment methods are modeled after Koch et al. (1997), Stephen (2000), and Rountrey (2009). For the two distal slabs, samples were collected by powdering dentin using a dental drill with a 1-mm diamond bit. Each sample included, on average, eight second-order increments. Fifteen-milligram samples were weighed into micro-centrifuge tubes, and 1.2 mL of NaOCl was added to each sample to oxidize

organic matter. Samples were agitated and then soaked for 24 hours, after which they were centrifuged to facilitate removal of liquid. Samples were then rinsed five times with deionized/distilled water. After rinsing, 1.2 mL of 1 M acetic acid-Ca acetate buffer was added to each sample to remove diagenetic carbonates. Samples were left to soak for 24 hours, after which they were centrifuged, fluid was removed, and samples were again rinsed five times. Samples were frozen and then freeze-dried over night. One-milligram samples were measured from the dried, pre-treated dentin, and were then sent to the Stable Isotope Laboratory at the University of Michigan for analysis. There, samples were roasted for one hour at 200°C, loaded into glass vessels, and analyzed on a Finnegan Kiel IV coupled to a Thermo MAT 252 Isotope Ratio Mass Spectrometer. Isotope composition is expressed by conventional δ notation, in which $\delta = [(R_{sample} /R_{standard}) - 1)*1000]$, R is the ratio of the heavy to the light isotope, and standards are VSMOW (oxygen) and VPDB (carbon).

Four changes were made to the procedure for pre-treating dentin samples for the pulp cavity slab of NYSM V50 and the two slabs from Bothwell 2-14. First, samples were powdered using a dental drill with a 0.7-mm carbide bit, which allowed for better control when drilling and higher temporal resolution. For the pulp cavity slab of NYSM V50, each sample included, on average, five second-order increments. For Bothwell 2-14, each sample included, on average, six second-order increments. Second, 10 mg of powdered dentin, instead of 15 mg, were weighed out into centrifuge tubes for pre-treatment. Third, during pre-treatment, 30 % H_2O_2 was used in lieu of NaOCl to oxidize organic matter (Koch et al. 1997; Rountrey 2009). Fourth, only 0.8 mL of NaOCl and acetic acid-calcium acetate buffer were added to each sample, to compensate for smaller

sample size. Other than these four changes, the procedures used to pre-treat this dentin were the same as for the earlier procedure.

Results

The tusk records of NYSM V50 and Bothwell 2-14 are presented here graphically, with dentin growth rate and stable isotope composition plotted against increment number. When increment number is plotted on the x-axis, this axis becomes essentially an axis of time; the first increment represents the earliest time of life preserved in the tusk, and the last increment reflects the time just prior to death. Annual increment profiles are represented in two ways: as average annual increment thickness and selected annual increment thickness. In addition, the number of second-order increments per year, though not strictly a measure of growth rate, is also plotted against time. All three data sets are plotted on the same graph to permit direct comparison among the three.

Second-order thickness profiles are of second-order increments measured at selected locations. No average second-order increment profiles are presented because in some tusk sections second-order increments were less clear than in others, on account of fractures or the presence of prominent Schreger bands, so averages are not likely to be an accurate portrayal of second-order increment thicknesses.

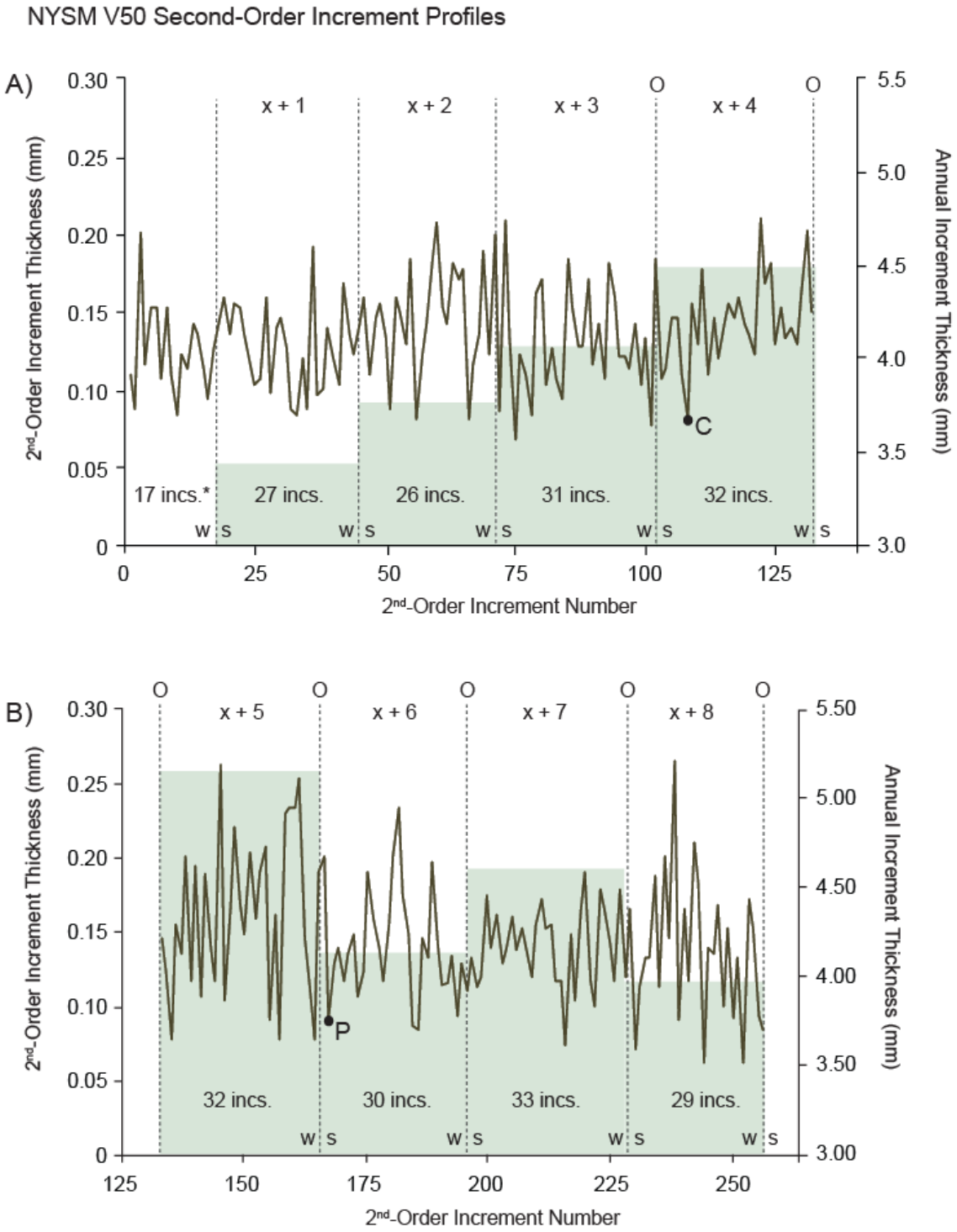
NYSM V50

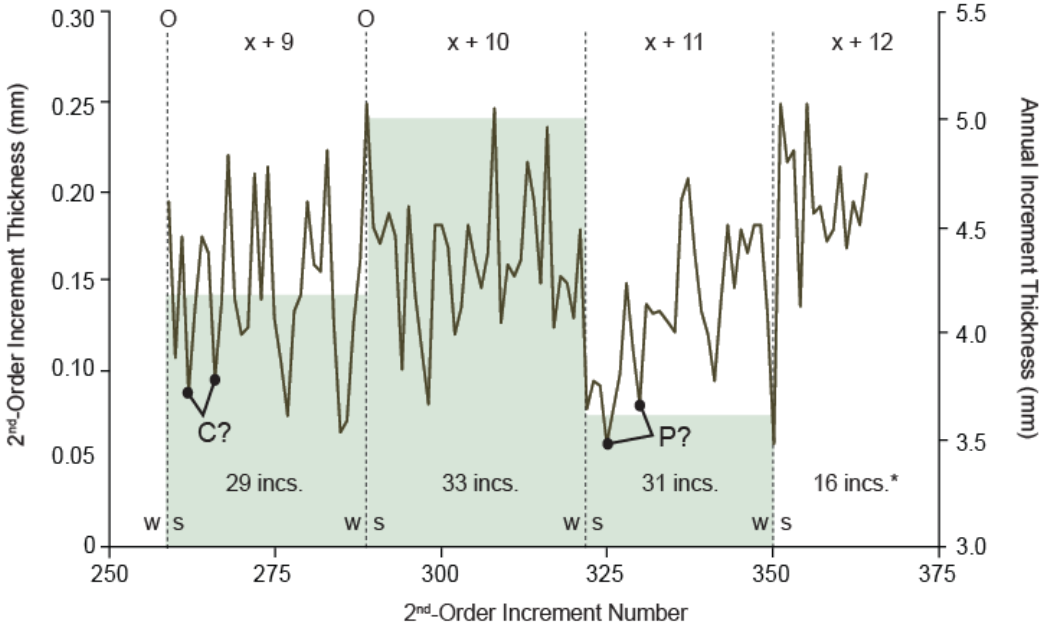
Tusk Growth Record.– The complete tusk record of NYSM V50 could not be compiled because of the tusk's fragmentary state, but it was possible to compile growth profiles from the distal portion and the pulp cavity section. The second-order growth profile of

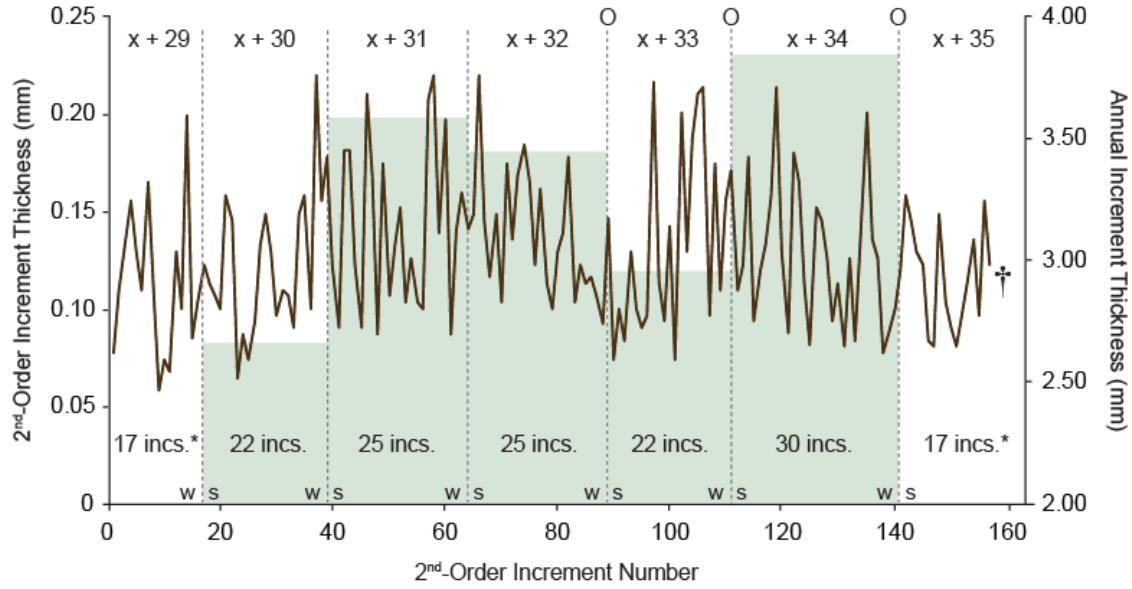
the distal tusk portion reflects eleven full years of growth as well as one partial year at each end of this sequence (Fig. 5.6A-C). The second-order growth profile for the pulp cavity slab reflects five full years of growth as well as one partial year at either end of the portion (Fig. 5.6D). The partial years at the proximal end of the distal portion and the distal end of the pulp cavity portion can be considered parts of full years because they border the fragmented middle portion of the tusk. The partial years at the tip and at the proximal end of the pulp cavity (the end of life) need not be considered full years because they represent the beginning and the end of the growth record. Thus, the tusk profile indicates that NYSM V50 was at least 18 years of age at death. Neither second- order increment profile exhibited strong seasonal patterns of variation, but seasonal variation is not completely absent from the profile, as growth rate is low near and at some winter-spring boundaries, as expected (Fig. 5.5C). Because a substantial amount of fragmented, chalky dentin in the middle could not be analyzed, a more reliable age estimate was established by counting the number of increments visible in exposed dentin on the tusk exterior. This method indicated that NYSM V50 was at least 35 years old at death, an age appropriate for her pulp cavity depth and maximum tusk circumference, in comparison to other known-age female mastodons (Fig. 5.2).

In NYSM V50, winter-spring boundaries were identified based on local minima in the oxygen isotope profile, in which $\delta^{18}O$ values exhibited seasonal variation typical of temperate-latitude mammals (Fig.5.5). Prior to isotope analysis, the locations of winter-

Figure 5.6. Second-order (lines, primary y-axis) and annual (bars, secondary y-axis) increment thicknesses for NYSM V50. Increment thicknesses collected from the distal tusk portion are presented in A-C, and thicknesses collected from the pulp cavity portion are presented in D. Note that seasonal variation in second-order increment thickness is not clear in these profiles, suggesting NYSM V50 lived in a region of low seasonality. The year in the tusk, located above the data, is indicated as "x + #" to indicate that the number of years lost due to wear is unresolved. The number of second-order increments per year is located below the data. An asterisk after this number indicates an incomplete year. Second-order increment thickness is plotted against second-order number, making the x-axis essentially an axis of time, moving from left (earlier in life) to right (later in life). Vertical dashed lines mark the locations of winter-spring ("w s") boundaries. An "O" indicates a winter-spring boundary supported by evidence of local minima in the $\delta^{18}O$ profile. "C" and "P" denote the inferred timing of conception and parturition, respectively, as explained in the text. The dagger in D indicates the death of the mastodon. Note the gap in time between C and D, an interruption of the continuous series of growth-increment data that was the result of the tusk having a poorly preserved middle section. This gap required a restart of second-order increment numbering on the x-axis in D. Figure 5.5 is continued on page 185.


NYSM V50 Second-Order Increment Profiles
A)
x + 1
x + 2
x + 3
x + 4
O
O
C
17 incs.*
27 incs.
26 incs.
31 incs.
32 incs.
w s
2nd-Order Increment Thickness (mm)
Annual Increment Thickness (mm)
2nd-Order Increment Number
B)
x + 5
x + 6
x + 7
x + 8
P
32 incs.
30 incs.
33 incs.
29 incs.


O
O
x + 9
x + 10
x + 11
x + 12
C?
P?
29 incs.
33 incs.
31 incs.
16 incs.*
w s
w s
w s
w s
0.30
0.25
0.20
0.15
0.10
0.05
0
5.5
5.0
4.5
4.0
3.5
3.0
250
275
300
325
350
375
2nd-Order Increment Thickness (mm)
Annual Increment Thickness (mm)
2nd-Order Increment Number


x + 29
x + 30
x + 31
x + 32
x + 33
x + 34
x + 35
O
O
O
17 incs.*
22 incs.
25 incs.
25 incs.
22 incs.
30 incs.
17 incs.*
w s
0.25
0.20
0.15
0.10
0.05
0
4.00
3.50
3.00
2.50
2.00
0
20
40
60
80
100
120
140
160
2nd-Order Increment Thickness (mm)
Annual Increment Thickness (mm)
2nd-Order Increment Number

spring boundaries were hypothesized based on the location of macroscopically visible second-order increments that were enhanced in comparison to adjacent second- order increments and appeared to repeat on an annual scale. However, isotope samples with the lowest $\delta^{18}O$ values were associated with winter-spring boundaries, and most enhanced increments were not part of the dentin sample that yielded the lowest $\delta^{18}O$ values. Thus, although these enhanced increments originally looked promising as winter-spring boundaries, the isotope data provided evidence to the contrary. For this tusk, one specific increment could not be identified with certainty as a winter-spring boundary. Rather, a series of increments in the sample that yielded the lowest $\delta^{18}O$ values was inferred to include the increment that represented the true winter-spring boundary. So, winter-spring boundaries were chosen as the central increment of each isotope sample that exhibited a local minimum in $\delta^{18}O$ values. Although not necessarily the true winter-spring boundary, this method at least provides consistency from one boundary to the next. Errors associated with this choice for the distal tusk portion should not be greater, on average, than four second-order increments and 0.57 mm (the average thickness of four second-order increments) of thickness per year. Errors associated with this choice are reduced for the pulp cavity section because it was sampled at a higher temporal resolution than the distal slabs, so errors should not be greater, on average, than three second-order increments and a thickness of 0.39 mm (the average thickness of three second-order increments) per year. These errors do not interfere with season-of-death analysis, but their possible effects on patterns of variation in the annual increment profiles are considered in the discussion of the profiles.

In locations not sampled for stable isotope composition, winter-spring boundaries were identified based on the relationship between the second-order increments associated with local lows in the $\delta^{18}O$ profile and the appearance of second-order increments, which can appear darker than adjacent increments in thin section, thick section, or both. In addition, local minima in increment thickness occur at winter-spring boundaries for temperate latitude mammals (Koch et al. 1989), so, although seasonal variation in increment thickness is not apparent in most of NYSM V50's years, this criterion was still considered. EMD identified five IMFs in the second-order increment profiles of both the distal and the pulp cavity section. None of these IMFs were significantly different from noise, however, so they could not be used to aid in identification of winter-spring boundaries. Thus, for un-sampled areas of NYSM V50's pulp cavity section, winter-spring boundaries were interpreted as slightly enhanced increments that were located between two strongly enhanced, macroscopically visible increments (in thick section). For the distal portion, winter-spring boundaries were interpreted through visual assessment of recurring patterns in the appearance of second-order increments (in thin section), and by identifying local lows in increment thickness that might be related to winter tusk growth (Fig. 5.6C).

With winter-spring boundaries in place, annual and sub-annual variations in growth rate could be analyzed, and the number of second-order increments per year could be determined. NYSM V50 exhibits an average annual increment thickness of 4.0 mm, with approximately 29 second-order increments per year. In mastodons, second-order increments typically reflect approximately fourteen-day periods, so it is expected that each year would consist of 26 bi-weekly, second-order increments (e.g., Koch et al. 1989;

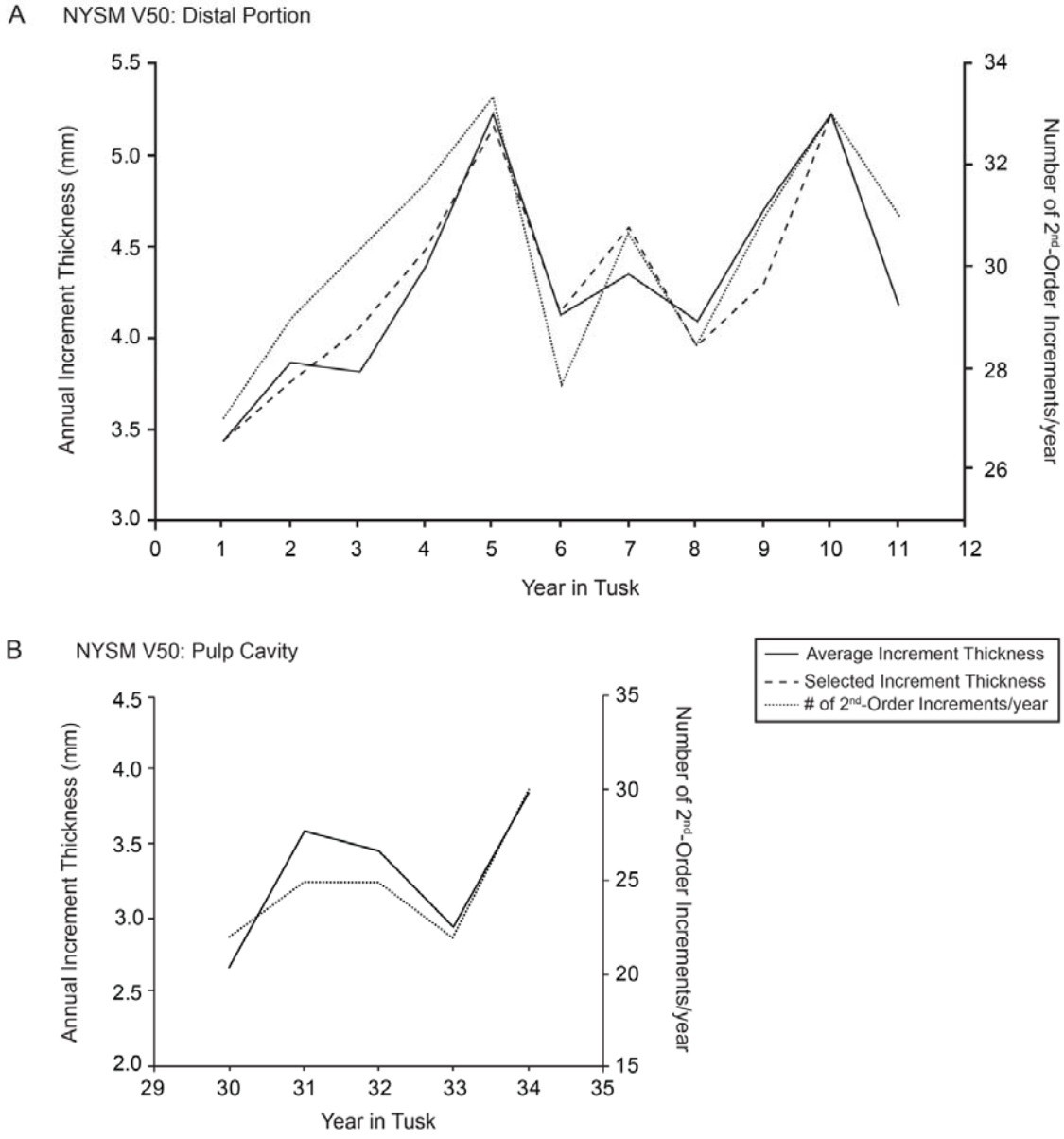


Figure 5.7. Annual increment profiles for (A) the distal portion and (B) the pulp cavity section of NYSM V50. There is no selected increment thickness line for (B) because all increments were measured on a single slab. Note the steady increase in annual growth rate early in life (years 1-5) followed by periodic oscillations in growth rate that occur until the end of life. This pattern of growth has been observed in profiles of annual increment length and thickness in other female mastodons (Fisher 1996; Fisher et al. 2008).

Fisher 1996, 2008). Because NYSM V50 averages 29 second-order increments per year, each second-order increment in her tusk is inferred to reflect approximately thirteen instead of fourteen days of growth. However, because third-order increments were difficult to discern in thin section, this number cannot be reliably validated by counting the number of daily increments between second-order increments, only inferred.

In the annual increment thickness profiles (Fig. 5.7), growth rate begins low at tusk-year one, then sharply increases to year five. This increase is followed by a period of low growth rate from years six to eight. There is a slight increase in rate for year seven in the average annual increment profile; this increase is enhanced in the selected annual increment thickness profile, but differences between the average and selected increment profiles are insignificant (paired t-test; $p = 0.8738$). Resuming at year 30, growth rate is again low; this rate increases sharply to year 31, steadily declines until year 33, and then increases to year 34, the last complete annual increment recorded in the tusk.

Two multi-year cycles can be qualitatively identified in the annual increment profiles. Each cycle begins with a peak in growth rate followed by a multi-year period of low growth rate; the cycle ends with a peak in growth rate. The first cycle includes years five through ten (with an additional cycle from years seven through ten pronounced in the selected annual increment and number of second-order increments per year profiles), and the second cycle includes years 31 to 34 (Fig. 5.7).

Because the second-order increment profile does not exhibit clear seasonal variation, and EMD did not identify any IMFs that were significantly different from noise in these data, deviations from seasonal patterns that might indicate a life event, such as parturition, or external perturbation are not immediately apparent. Throughout the year,

growth rates for temperate-latitude mastodons are expected to be the highest when vegetation is abundant (summer) and the lowest when vegetation is less readily available (winter; Koch et al. 1989; Fisher 1996). Deviations from this seasonal pattern of growth reflect the interruption of a mastodon's regular feeding schedule. For example, adult males exhibit drastic decreases in growth rate during spring or early summer that reflect fasting during musth (Fisher 2008). Deviations from seasonal variation could also be attributed to limitations in food availability caused by drought or other environmental factors.

The low seasonal variation in the tusk record of NYSM V50 suggests that there was little seasonal change in food availability in the latest Pleistocene of southeastern New York State. However, low seasonal variation does not explain why drastic decreases in growth rate occur throughout the profile. For example, tusk years six and seven exhibit conspicuously low growth rates for brief periods (2-3 increments) in late summer or early autumn, and tusk year 29 exhibits conspicuously low growth rates in summer (Fig. 5.5). These decreases in growth rate may be relatable to life events.

Stable Isotope Record.– The $\delta^{18}O$ values for NYSM V50 range fluctuate between 24.0‰ and 28.0‰. As mentioned above, serial analysis of $\delta^{18}O$ composition revealed seasonal patterns of variation in the tusk dentin (Figs. 5.8 and 5.9). Evaluating $\delta^{18}O$ variation in the pulp cavity slab, which includes isotope values obtained from dentin formed just prior to death, made it possible to infer season of death for NYSM V50. This individual died at the beginning of a declining phase in the $\delta^{18}O$ profile, indicating an autumn or early winter death (Fig.5.9).

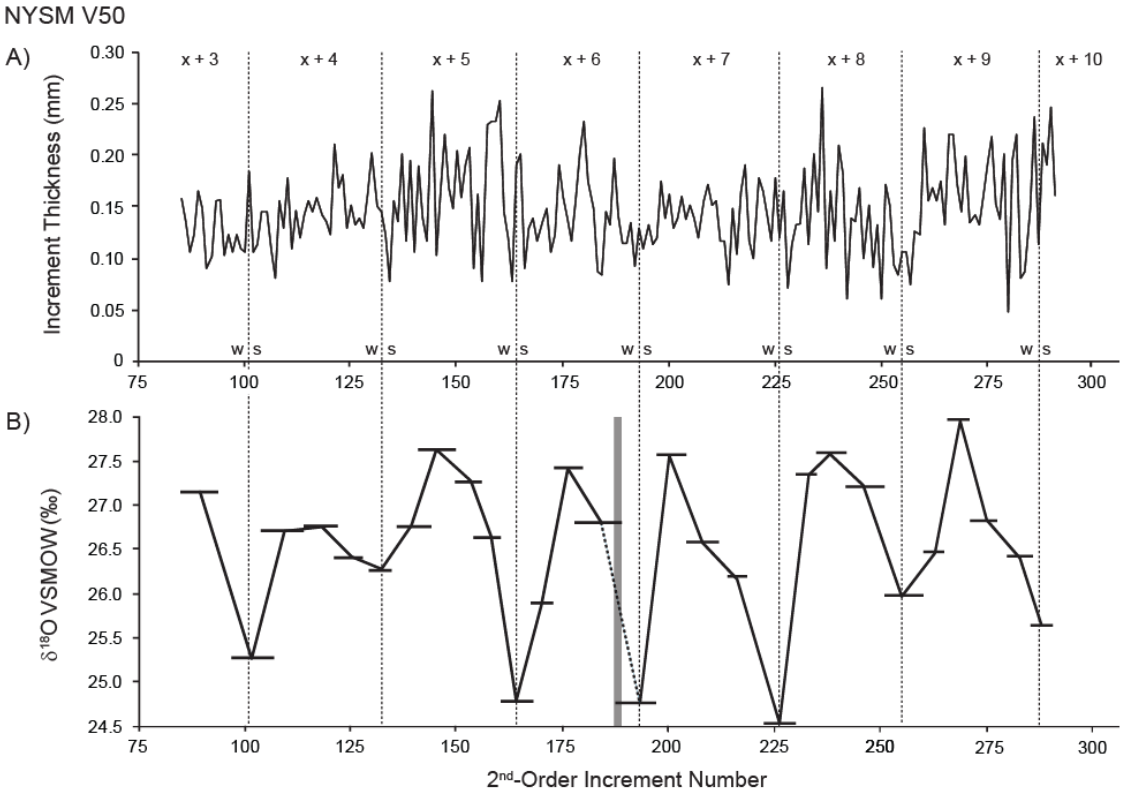


Figure 5.8. Second-order increment thicknesses (A) and $\delta^{18}O$ values (B) for the distal portion of NYSM V50. Horizontal bars indicate which second-order increments were sampled to obtain a specific $\delta^{18}O$ value. This profile contains data from two slabs; the dark gray vertical bar indicates a temporal overlap between slabs, and the dotted line that passes through the bar connects the values obtained from the slab 30 cm from the tip (left of the solid vertical line) and from the slab 50 cm from the tip (right of the solid vertical line). Winter-spring boundaries were located by associating local minima in the $\delta^{18}O$ profile (B) with the increments sampled to yield these minima (A). All other labels are as in Figure 5.6.

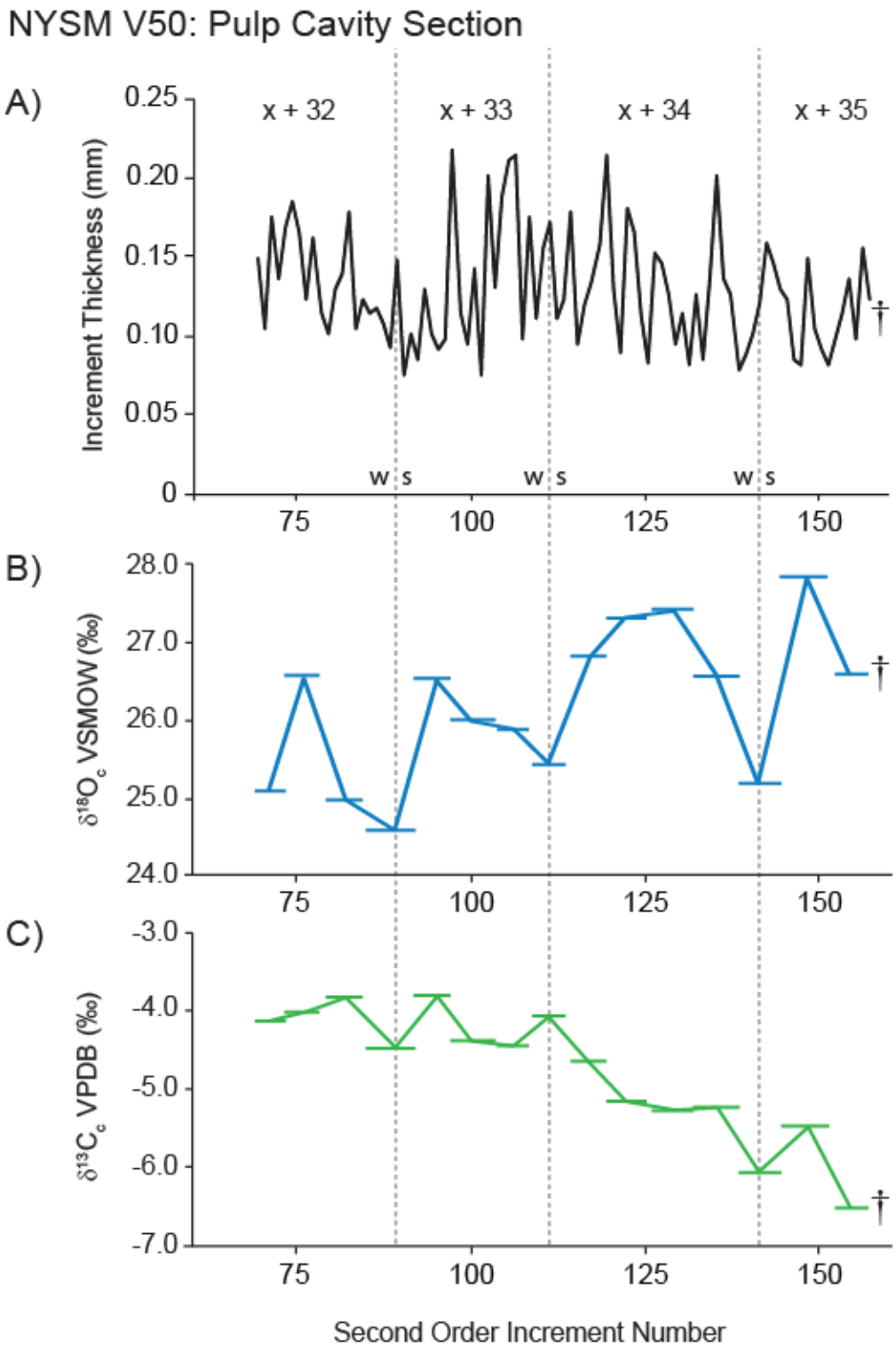


Figure 5.9. Second-order increment thickness (A), $\delta^{18}O$ values (B), and $\delta^{13}C$ values (C) for the pulp cavity section of NYSM V50. All labels are as in Figures 5.6 and 5.8. Note the lack of seasonal variation in the $\delta^{13}C$ profile (C) as compared to seasonal variation in the $\delta^{18}O$ profile (B).

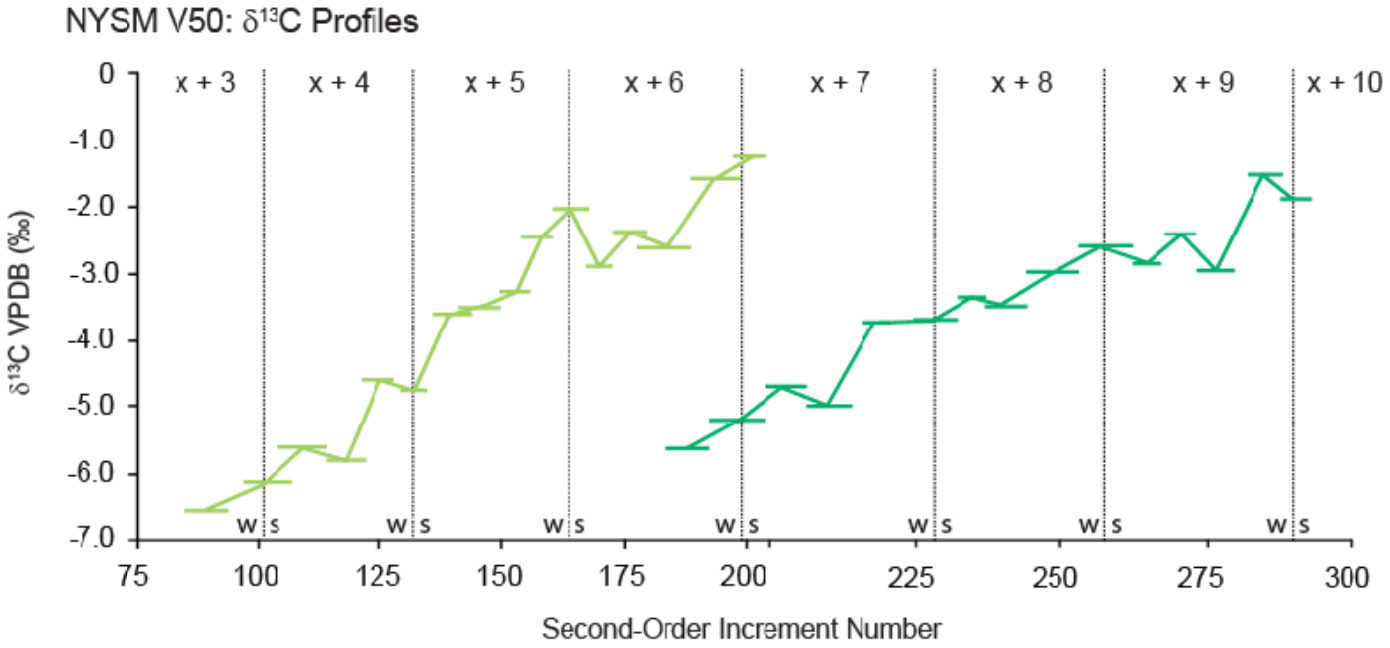


Figure 5.10. $\delta^{13}C$ profiles for the distal portion of NYSM V50. The line on the left shows values obtained from the tusk slab 30 cm from the tip, and the line on the right shows values obtained from the tusk slab 50 cm from the tip. Note that $\delta^{13}C$ values increase from the cementum-dentin junction (lower increment numbers) to the tusk's longitudinal axis (higher increment numbers) on each slab. In addition, the same increments analyzed on different slabs yielded substantially different $\delta^{13}C$ values.

The distal and proximal sections of NYSM V50 exhibit different preservation, but the values and amplitude of variation in $\delta^{18}O$ values are similar between sections, suggesting that neither section was disproportionately affected by diagenesis. The $\delta^{13}C$ profiles for both tusk sections, however, exhibit little to no seasonal variation (Figs. 5.9 and 5.10), and the $\delta^{13}C$ values themselves (ranging from -7.0 to -1.0 ‰) suggest that NYSM V50 was eating an exclusively C_4 diet, which is unlikely given that mastodons primarily consumed C_3 plants (~13‰; Koch et al. 1997). In addition, $\delta^{13}C$ values are consistently lower for increments sampled near the cementum-dentin junction and show an overall increase towards the tusk's longitudinal axis (Fig. 5.10). Furthermore, the dentin sampled from the 30 cm block has a much higher value (approximately +6.0 ‰) than the same increments sampled from the 50 cm block (Fig. 5.10). In light of these results, it is likely that the $\delta^{13}C$ composition of NYSM V50 has been substantially altered by diagenesis, so the $\delta^{13}C$ composition of NYSM V50 will not be considered further here.

Bothwell 2-14

Growth Increment Record.– There are 21 complete years and two near-complete years (one at each end of the profile) in Bothwell 2-14's tusk record, indicating that she was at least 22 years of age at death (Fig. 5.11). This age is consistent with the age expected based on her tusk morphology, as compared to other female mastodons (Smith and Fisher in revision; Chapter 2, this dissertation). As in NYSM V50, there was little seasonal variation in Bothwell 2-14's second-order increment thickness profile, so it was difficult

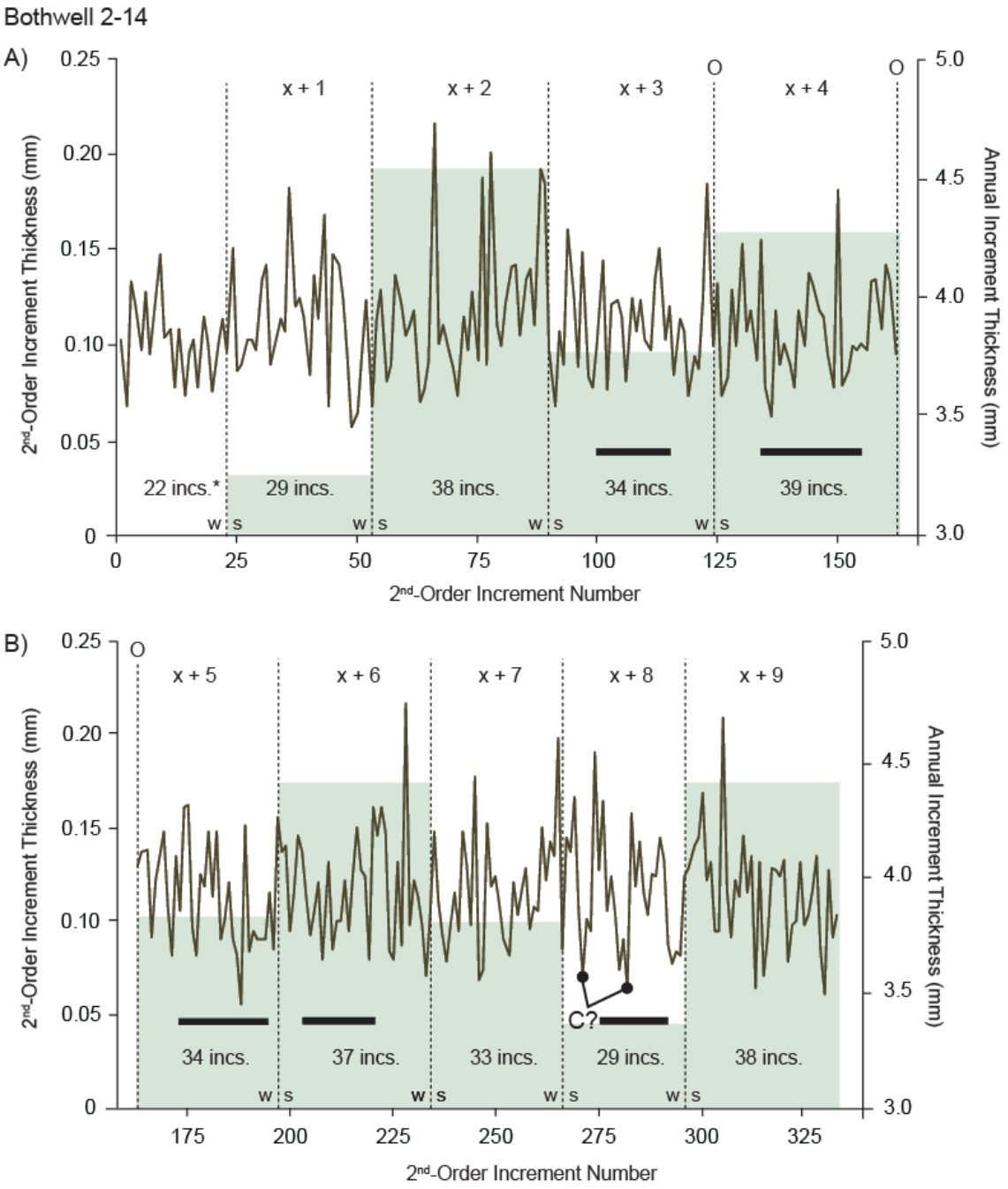


Figure 5.11. Annual and second-order increment thicknesses for Bothwell 2-14. All labels as in Figure 5.6. Horizontal black bars indicate the increments associated with dark bands of dentin. Figure continued on pages 196 and 197. Note the general lack of seasonal variation in second-order increment thickness, and the conspicuous dips in growth rate that may be attributable to reproductive events (C = conception, P = parturition).

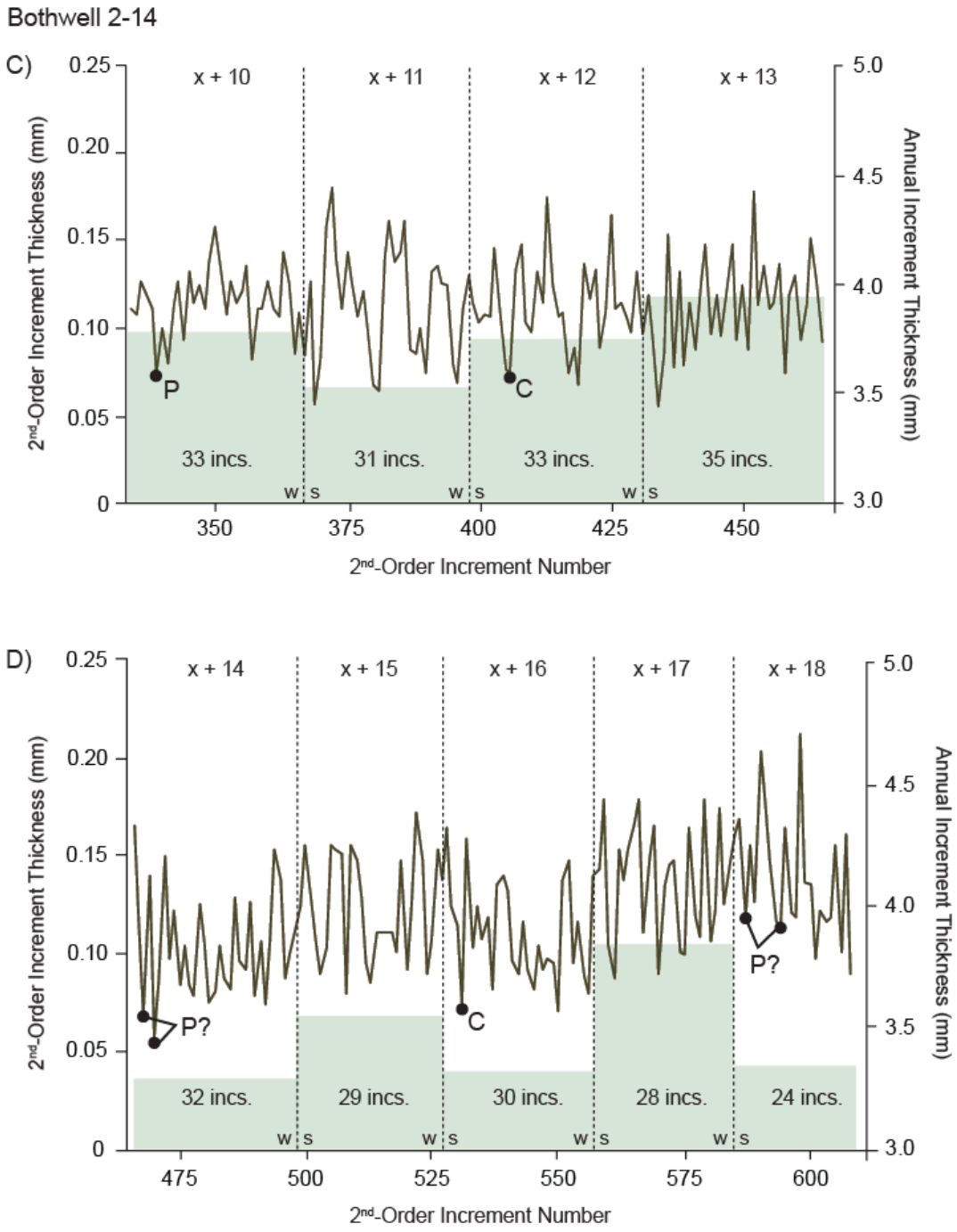


Figure 5.11 (continued).

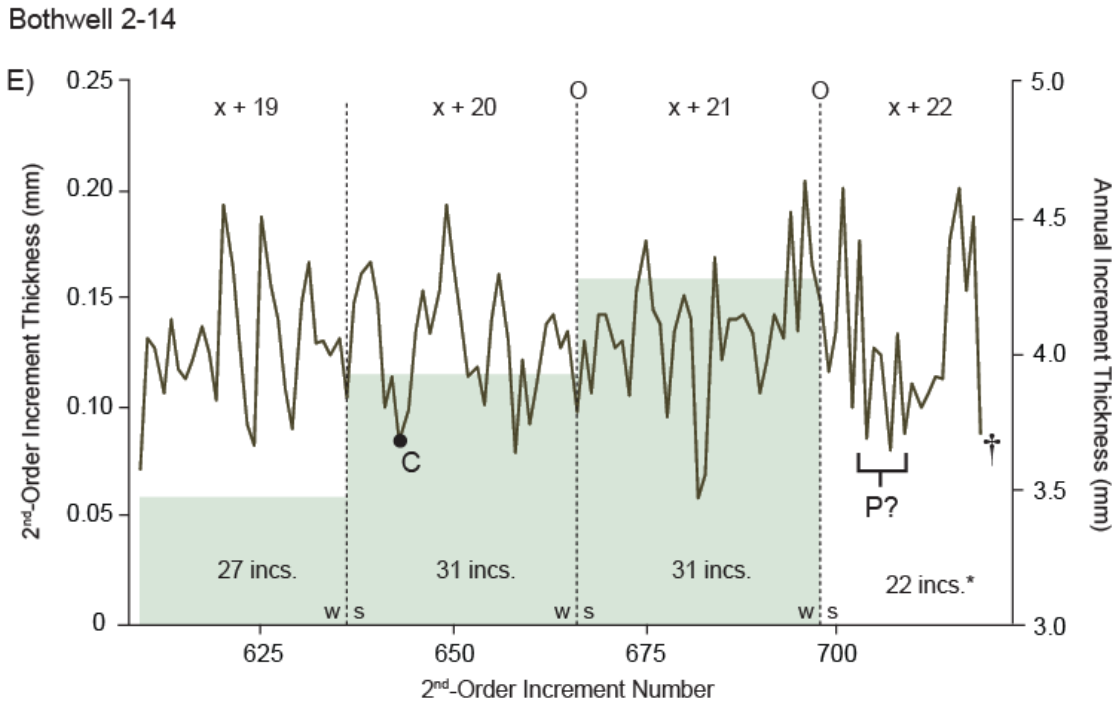


Figure 5.11 (continued).

to mark winter-spring boundaries by locating zones of low growth rate (Koch et al. 1989). In addition, although there were portions of the tusk that exhibited dark-light couplets, the increments in the light-dark couplets were not associated with local minima in the $\delta^{18}O$ profile. Thus, light-dark couplets could not be used to locate winter-spring boundaries, either, and, like NYSM V50, winter-spring boundaries were identified as the central increment in the isotope sample with the lowest $\delta^{18}O$ value. Errors associated with this choice should not be greater than three second-order increments and a thickness of 0.37 mm per year.

Locations of winter-spring boundaries for increments not analyzed for stable isotope composition were again inferred based on the relationship between local lows in the $\delta^{18}O$ profile and enhanced second-order increments. EMD identified six IMFs in the second-order increment profile, but none of these IMFs were significantly different than noise, so IMFs could not be used to aid in identification of winter-spring boundaries. For this tusk, the central increment in a sample with the lowest $\delta^{18}O$ value were typically located, on average, five second-order increments before an enhanced, macroscopically visible second-order increment. The number of increments between enhanced second-order increments was similar to (within two increments) or the same as the number of increments between isotope years, so the thickness between enhanced increments likely reflects one year of growth. Thus, winter-spring boundaries in un-sampled areas were inferred to be located five increments before an enhanced increment.

The average annual increment thickness for Bothwell 2-14 is 3.80 mm, and each year includes approximately 32 second-order increments. Bothwell 2-14, like NYSM V50, has a greater number of second-order increments per year than expected. Each

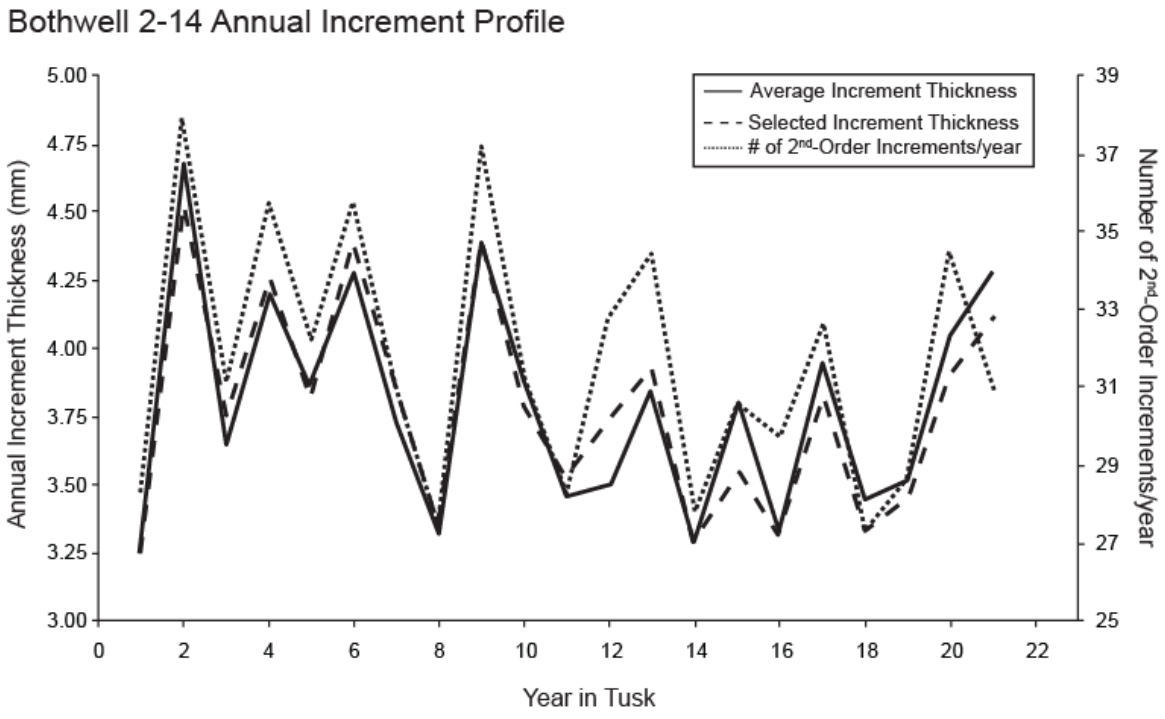


Figure 5.12. Annual increment thicknesses from the complete tusk record of Bothwell 2-14. Note that, as in NYSM V50, annual growth rate generally increases early in life (years 1-6), and then exhibits periodic oscillations in growth rate until the end of life.

second-order increment in Bothwell 2-14, then, is inferred to reflect approximately 11 instead of 14 days of growth. The number of days between second-order increments, however, cannot easily be validated by counting daily increments, as these increments were difficult to discern in thin section.

Bothwell 2-14's average and selected annual increment thickness profiles exhibit strong similarities in patterns of variation (Fig. 5.12). A notable difference among the profiles occurs at year 21, when the selected increment profile exhibits a decrease and the other profiles exhibit an increase. In addition, the selected annual increment profile has consistently higher peaks than the other profiles. There is not, however, a significant difference (paired t-test; $p = 0.6932$) between the profiles. Annual dentin growth rate begins low in tusk year one, and rapidly increases to year two. After year two, there is considerable fluctuation in annual growth rate of Bothwell 2-14. Qualitative analysis of the annual growth rate profile yielded four multi-year cycles of growth rate, as identified in the annual growth rate profile for NYSM V50. The first cycle includes years six through nine, the second includes years nine through thirteen, the third includes years thirteen through seventeen, and the fourth includes years seventeen through twenty (Fig. 5.12).

Like NYSM V50, the lack of seasonal variation in second-order increment thickness data, and the absence of IMFs that are significantly different from noise, makes it difficult to identify unusual patterns in the growth record. Nonetheless, qualitative assessment of the profiles allowed for identification of brief periods of unexpected low growth rate (two to three increments) in late spring or early summer of tusk years two,

four, seven, eight, 11, 12, 19, and 21, and brief periods of unexpected low growth rate in spring of tusk years 17 and 20 (Fig. 5.11).

Stable Isotope Record.– The $\delta^{18}O$ values for Bothwell 2-14 exhibit seasonal patterns of variation expected for a temperate latitude mastodon, and fluctuate between 23.5‰ and 27.0 ‰ (Figs. 5.13 and 5.14). The $\delta^{18}O$ profile from the pulp cavity section terminates at a potential peak in the profile, indicating that she died during late summer or early autumn (Fig. 5.14B).

Seasonal variation are also evident in the $\delta^{13}C$ profile for Bothwell 2-14 (Figs. 5.13C and 5.14C), but the values themselves suggest an unlikely mastodon diet of C_4 plants. The bulk $\delta^{13}C$ value from the tusk collagen of Bothwell 2-14 (-20.0‰) indicates that her diet was dominated by C_3 plants, a diet generally exhibited by mastodons (e.g., Lepper et al. 1991; Fisher and Fox 2003). Thus, the different $\delta^{13}C$ values obtained from analysis of tusk collagen and analysis of the structural carbonate in tusk dentin suggests that the latter analysis was on diagenetically altered material.

The amplitude of variation in $\delta^{13}C$ values is approximately 2‰ (Figs. 5.13C and 5.14C). There is an increase in $\delta^{13}C$ values in early spring for each tusk year except for 20 (which shows little sub-annual variation in $\delta^{13}C$ values overall). From this time, values decrease until reaching a local minimum in late autumn or early winter, after which they exhibit a steady increase until early spring of the following year. Similar sub-annual variation was exhibited in three additional tusks from the Bothwell Site (this dissertation, Chapter 4). This variation was interpreted as seasonal differences in proportion of C_3 and C_4 plants in the diet in addition to the utilization of fat stores during winter (associated with decrease in $\delta^{13}C$).

Figure 5.13. Second-order increment thickness (A), $\delta^{18}O$ composition (B), and $\delta^{13}C$ composition (C) for tusk years four to six in Bothwell 2-14. All labels are as in Figures 5.5 and 5.7. Local minima in the $\delta^{18}O$ profile (B) were used to locate winter-spring boundaries. Note the seasonal variation in the $\delta^{13}C$ profile (C), in which an increase in $\delta^{13}C$ composition occurs just after every winter-spring boundary.

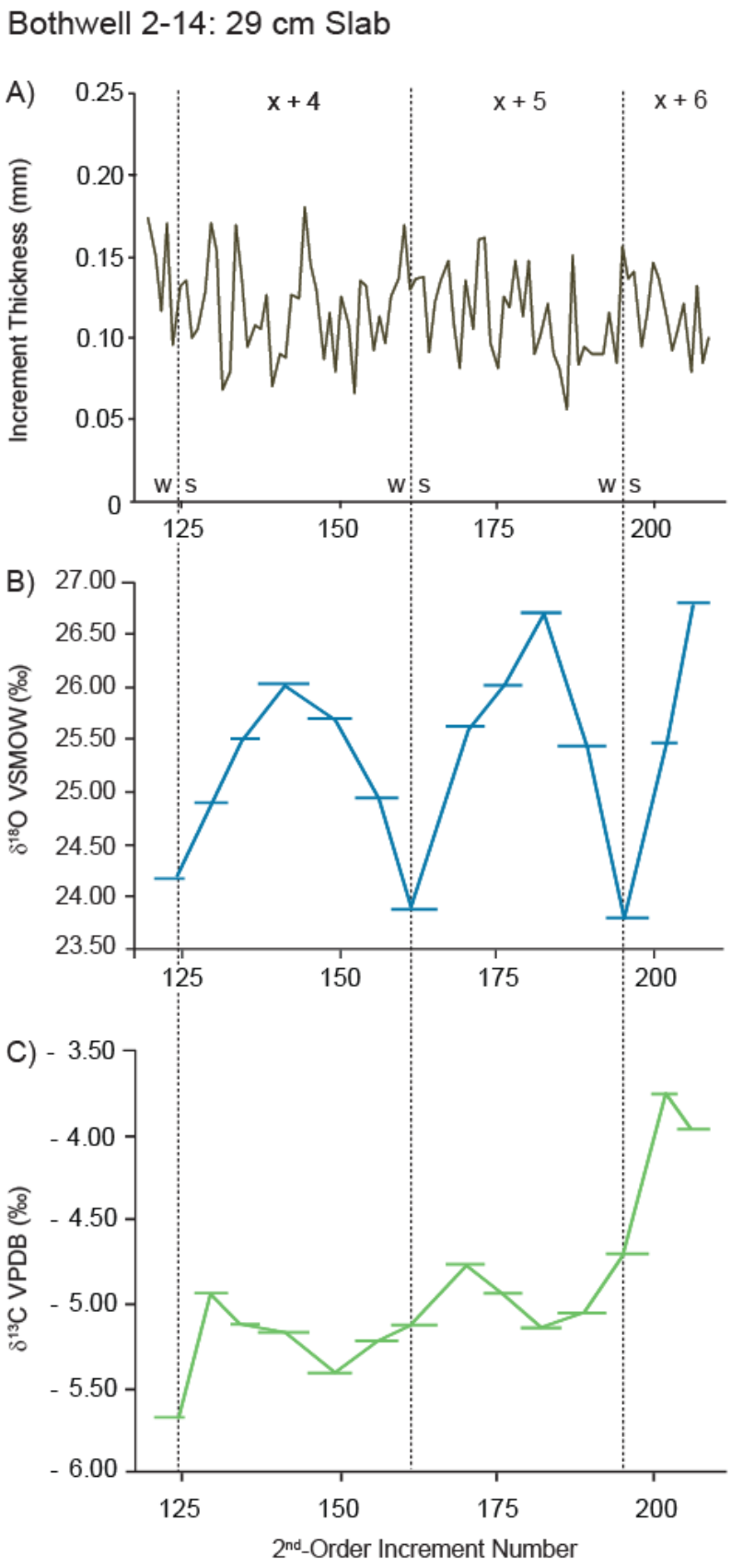
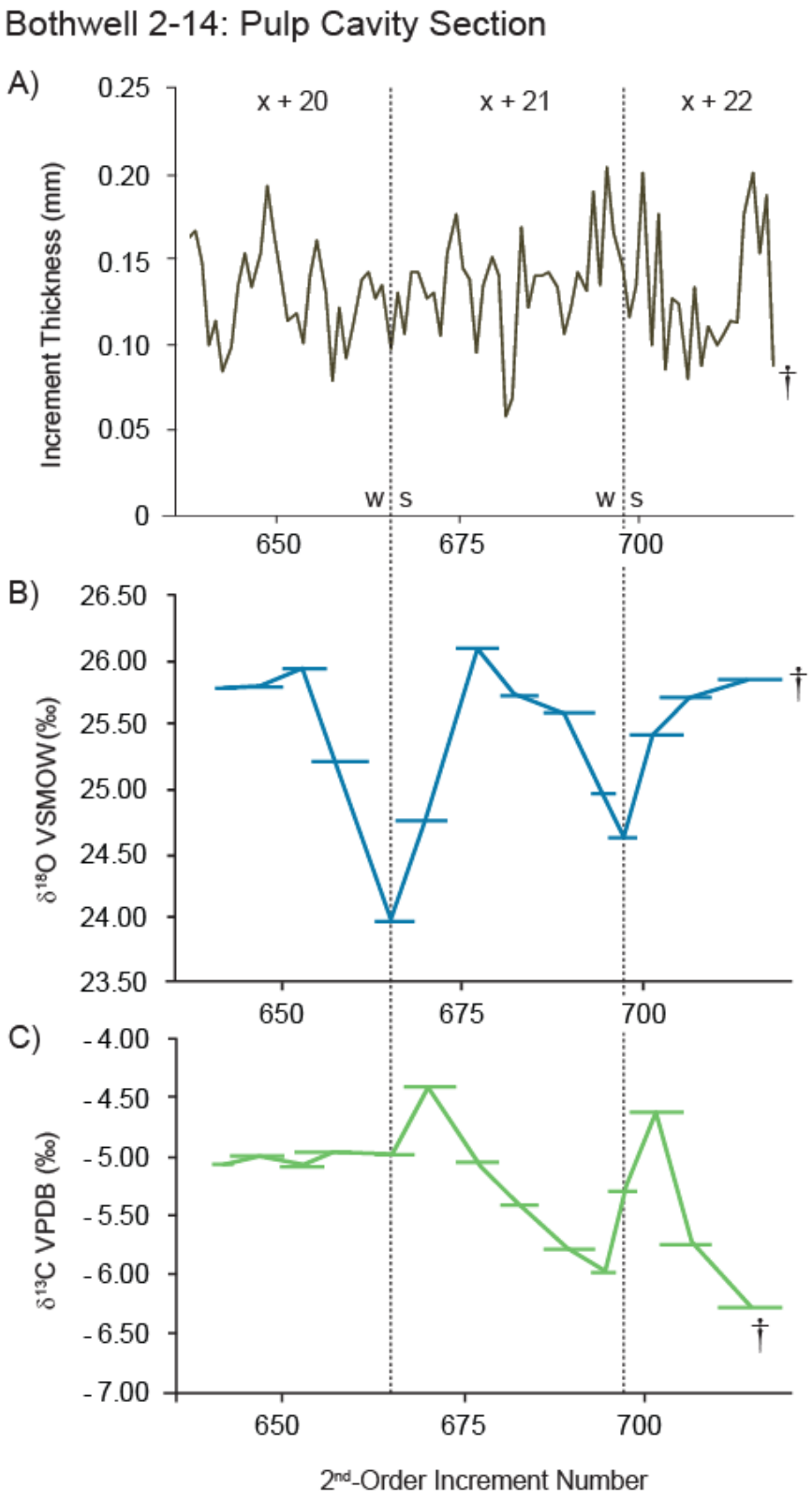

Bothwell 2-14: 29 cm Slab
A)
Increment Thickness (mm)
0.25
0.20
0.15
0.10
0.05
0
x + 4
x + 5
x + 6
w s
w s
w s
125
150
175
200
B)
δ18O VSMOW (‰)
27.00
26.50
26.00
25.50
25.00
24.50
24.00
23.50
125
150
175
200
C)
δ13C VPDB (‰)
- 3.50
- 4.00
- 4.50
- 5.00
- 5.50
- 6.00
125
150
175
200
2nd-Order Increment Number

Figure 5.14. Second-order increment thickness (A), $\delta^{18}O$ composition (B), and $\delta^{13}C$ composition (C) for tusk years twenty to twenty-two in Bothwell 2-14. All labels are as in Figures 5.5 and 5.7. Local minima in the $\delta^{18}O$ profile (B) were used to locate winter-spring boundaries. Note that the $\delta^{13}C$ profile (C) exhibits the same seasonal variation exhibited in Fig. 5.12C, in which there is an increase in $\delta^{13}C$ composition just after every winter-spring boundary.


Bothwell 2-14: Pulp Cavity Section
A)
x + 20
x + 21
x + 22
Increment Thickness (mm)
0.25
0.20
0.15
0.10
0.05
0
w s
w s
650
675
700
B)
26.50
26.00
25.50
25.00
24.50
24.00
23.50
δ18O VSMOW (‰)
650
675
700
C)
-4.00
-4.50
-5.00
-5.50
-6.00
-6.50
-7.00
δ13C VPDB (‰)
650
675
700
2nd-Order Increment Number

Discussion

Growth Increment Record

Comparison to previous studies.–The average annual increment thickness of NYSM V50 (~4.0 mm) is similar to annual increment thicknesses in the North Java mastodon tusk (a female from southwestern New York State; Fisher et al. 2008), generally greater than those in tusks of female mastodons from the Hiscock site (southwestern New York State; Fisher and Fox 2003), and generally greater than those in tusks of female mastodons from the Bothwell Site (northwestern Indiana; this dissertation, Chapter 4), including Bothwell 2-14 of this study. Average annual increment thickness for Bothwell 2-14 (~3.80 mm) is consistent with those of other Great Lakes-region females (North Java, Hiscock, and other Bothwell mastodons). NYSM V50 lived near the southeastern coast of New York State, and the mastodons she is compared to are from the Great Lakes region. Although the sample size is too small to test for significant differences in annual growth rate, it is possible that female mastodons living near the Atlantic coast exhibited higher tusk growth rates than mastodon in the Great Lakes region.

The expected number of second-order increments per year is 26, as each second-order increment reflects approximately two-weeks of growth. Both NYSM V50 and Bothwell 2-14 exhibit higher-than-expected numbers of second-order increments per year (29 and 32, respectively). These numbers are greater than the number of second-order increments per year observed in the tusk of North Java and the Hiscock females (Fisher and Fox 2003; Fisher et al. 2008). The average number of second-order increments per year for NYSM V50 is slightly lower than those observed for the Bothwell females (including Bothwell 2-14; Chapter 4, this dissertation), and Bothwell 2-14 falls in the

middle of the range of those observed for Bothwell females. The origin of second-order increments is not fully understood (see Fisher and Fox [2003] for a detailed hypothesis), so it is difficult to ascertain a reason for differences in the average number of second-order increments per year. The average annual increment thickness for Bothwell 2-14 is less than that of NYSM V50, but the number of second-order increments per year for Bothwell 2-14 is greater than that of NYSM V50, so second-order increment number, at least from tusk to tusk, does not increase with annual increment thickness.

The simplest explanation for the higher than expected number of second-order increments per year in NYSM V50 and Bothwell 2-14 is that third-order (daily) increments in these tusks were occasionally enhanced relative to adjacent third-order increments, making them appear as prominent second-order increments. In this way, the number of second-order increments per year might be artificially inflated. If the numbers are not inflated, though, a higher number of second-order increments per year indicates a lower formation time per second-order increment, which could be due to differences in region or to intra-species variation. One way to evaluate these scenarios would be to count the number of daily increments between second-order increments. In thin sections from these slabs, however, it was difficult to obtain an accurate count of daily increments.

Annual increment record, – Annual dentin growth was presented in two different ways (average and selected annual increment thickness; Fig. 5.10) in order to identify discrepancies in each profile that might be related to the location on the tusk where the increments were measured. There were no significant differences between average and

selected annual increment thicknesses for either tusk, so discussion of variation in annual growth rate will focus on the average annual increment profile.

Second-order increment record. – EMD did not identify any IMFs that significantly differed from noise in NYSM V50 or Bothwell 2-14 second-order increment profiles, so EMD could not assist in identifying patterns within the second-order increment data that might relate to reproductive events. In light of this, and because neither tusk record produced second-order increment profiles that exhibited clear seasonal variation in growth rate, life events could not be interpreted from these profiles alone. However, discrepancies noted in the second-order increment profiles can be related to larger-scale changes in the annual increment profile to determine if low growth rate for a year was the result of particularly low growth rate over a certain time of the year. An overall decrease in annual dentin growth rate coupled with knowledge of the time of year when growth rate was at its lowest (if this is not during winter, when low growth rate is the expectation) may aid in interpretation of life events.

Stable Isotope Record

Comparison to previous studies. – The amplitude of variation in $\delta^{18}O$ and $\delta^{13}C$ profiles could be used to infer differences in seasonality for different regions. For example, a mastodon living in a highly seasonal environment could exhibit larger amplitudes of $\delta^{18}O$ variation than a mastodon living in a region with low seasonality. In addition, vegetation available for consumption in regions of low seasonality may not change drastically throughout the year. The tusk dentin of a mastodon in a region of low seasonality might exhibit smaller amplitudes of $\delta^{13}C$ variation than a mastodon living in a more seasonal

region because if vegetation varied little throughout the year, than the composition of the mastodon's diet would not vary much, either. However, the $\delta^{13}C$ composition of tusk dentin is also complicated by processes of fat metabolism and storage, and possibly lactation (Fisher and Fox 2003), so patterns in $\delta^{13}C$ variation are less likely than patterns in $\delta^{18}O$ variation to provide evidence of seasonality.

The $\delta^{18}O$ values and amplitude of seasonal variation for NYSM V50 (~24.0 ‰ to ~28.0 ‰) are similar to those reported for male mastodons Taylor and Van Sickle (southeastern Michigan; Koch et al. 1989) and male mastodon Hyde Park (southwestern New York State; Fisher 2008). The $\delta^{18}O$ values of NYSM V50 are also similar to those of the Bothwell and Hiscock females, but the amplitude of seasonal variation is greater for NYSM V50 than for the Bothwell females. Profiles of Hiscock female tusks lack seasonal variation exhibited by other temperate-latitude mastodons, so no amplitude comparisons could be done. The $\delta^{18}O$ values and amplitude of variation for Bothwell 2-14 (~23.5 to ~27.0 ‰) are similar to those reported for the Taylor and Van Sickle mastodons, the Hyde Park mastodon, and the remaining Bothwell females. The $\delta^{18}O$ values for Bothwell 2-14 are similar to those reported for the Hiscock females. Based on these comparisons, Bothwell 2-14 may have lived in a region with lower seasonality than northern Great Lakes-region mastodons as well as NYSM V50 (southeastern New York State).

The amplitude of variation in $\delta^{13}C$ for Bothwell 2-14 (~2 ‰) is similar to the magnitude of variation exhibited by other Bothwell females, by the Hyde Park mastodon, and by the Hiscock females. The pattern of variation is similar to that exhibited by other Bothwell females, in which an increase in $\delta^{13}C$ occurs just after the winter-spring

boundary, but dissimilar to that exhibited by the Hyde Park mastodon, in which $\delta^{13}C$ values generally track the seasonal variation exhibited in the $\delta^{18}O$ profile. Bothwell 2-14 exhibits a stronger signal of periodic, sub-annual variation than the Hiscock females, who exhibited little periodic variation overall. Based on these comparisons, Bothwell 2-14 and northern Great Lakes-region mastodons likely exhibited similar changes in diet throughout the year.

Possible diagenetic alteration. – The $\delta^{13}C$ of tusk dentin for both NYSM V50 and Bothwell 2-14 yielded values that were substantially higher than expected, suggesting that the structural carbonate of dentin was diagenetically altered. A periodic, sub-annual pattern of $\delta^{13}C$ variation was retained in Bothwell 2-14, but such a pattern is absent from the tusk record of NYSM V50. A comparison of taphonomic histories between the two tusks might have revealed why patterns of $\delta^{13}C$ variation were retained in Bothwell 2-14 but not in NYSM V50, but the lack of information about the depositional environment of NYSM V50 prevents such a comparison. Examining the tusks alone, some differences in dentin preservation between the two tusks were observed (Fig. 5.2). First, there was a difference in the density of dentin. Dentin block and powder samples were easier to remove from NYSM V50 than from Bothwell 2-14, indicating the dentin was less dense (thus, more deteriorated) in NYSM V50. Next, there was a difference in dentin staining, such that NYSM V50 dentin was generally darker than Bothwell 2-14 dentin. Finally, there were differences in dentin texture. Bothwell 2-14exhibited some patches of lightly-colored, chalky (thus, deteriorated) dentin in the tusk interior, but this type of dentin could generally be excluded from samples for isotope analysis. NYSM V50 exhibited more patches of white, chalky dentin than Bothwell 2-14; and this dentin was necessarily

included in samples for isotope analysis.. Because Bothwell 2-14 was denser, exhibited less staining, and had fewer patches of chalky dentin, the dentin in Bothwell 2-14 exhibited better preservation than the dentin in NYSM V50, which likely led to Bothwell 2-14's retention of sub-annual $\delta^{13}C$ variation in her tusk record.

Tusk Evidence for Cause of Death

Human influence? – NYSM V50 died at the beginning of a declining phase in her oxygen isotope profile, indicating a late autumn or early winter death (Fig. 5.9). Either season of death is commensurate with seasons of death for mastodons with evidence of human butchery (Fisher 2001). Because mastodons that died during other seasons do not exhibit evidence of butchery, mastodons that were butchered by humans were also likely killed by humans (Fisher 1987). Thus, NYSM V50's season of death makes her a reasonable candidate for death by human influence.

The season and possible cause of death for Bothwell 2-14 were fully discussed in Chapter 4. The $\delta^{18}O$ profile of Bothwell 2-14 terminated at a peak (Fig. 5.12), which suggests she died in late summer or early autumn. If autumn, and not late summer, was her season of death, then Bothwell 2-14, like NYSM V50, is also a reasonable candidate for death by human influence.

Nutritional Stress? – Sub-annual growth rates for the last four years in NYSM V50's life are low, compared to the record of sub-annual growth in her first twelve years. This could suggest that she lived in a high-stress environment for several years prior to death. However, sub-annual growth rate is similarly low for several years leading up to her death. If environmental stress led to her death, her sub-annual growth profile should

exhibit drastic declines in growth rate at the end of life, which it does not. So, if low growth rates for the last four years in her life indicate that the environment was stressful during that period, the stress was unlikely to have caused her death.. An injury or illness that may have acted too quickly to be recorded in the tusk record remains a possibility.

Alternatively, differences in growth rate between the beginning and end of life could be attributed to ontogeny, in which annual increment thickness and second-order increment thickness gradually decline with age (Fisher et al. 2008). If increment thicknesses from the middle portion of the tusk could be obtained, the growth-rate decline exhibited in NYSM V50's profile might appear more gradual.

Bothwell 2-14 exhibited no change in dentin growth rate at the end of life, at the annual or sub-annual level, that would suggest nutritional stress as a cause of death. However, as for NYSM V50, a quickly-acting injury or illness remains a possible cause of death.

Reproductive Events in the Tusk Record

Expectations for life history parameters in female mastodons related to reproductive biology include (1) parturition of first calf between life-years eight and twenty (Moss 2001), (2) gestation length between 1.5 and 2.0 years (Lee and Moss 1986), (3) duration of lactation of four or more years, with the highest milk output in the first two years (Lee and Moss 1986), (4) inter-birth intervals of 3.5 to 5.6 years (Lee and Moss 1986), and (5) parturition in late spring or early summer. Expectations for the effects of gestation and lactation on the tusk record used here include (1) high growth rate during gestation, as compared to growth rate during lactation (Miller et al. 1985; Fuller et al.

2004, as inferred from a decrease in $\delta^{15}N$), (2) decrease in growth rate during lactation (Miller et al. 1985), and (3) enrichment in $\delta^{13}C$ during lactation (Polischuk et al. 2001; Fisher and Fox 2003). The tusk records of NYSM V50 and Bothwell 2-14 are analyzed here with respect to these three sets of expectations.

Reproductive Events in NYSM V50.

Annual Increment Profile. – The first eleven annual growth increments in the distal portion of NYSM V50 (Fig. 5.7A) do not reflect the first eleven years in her life because material representing the earliest years of life was abraded from the tip. Abraded material is equivalent to two to three years of growth (see "Materials and Methods," this chapter), so it is inferred that her tusk record begins at life-year four and ends at life-year 38. For consistency, and because it is unknown exactly how many years of growth are actually missing from her tip, years referred to in this discussion are tusk years, not life years. In the earliest part of the annual increment thickness profile, NYSM V50 exhibited low growth rates that steadily increased from year one to five (Fig. 5.15A). The earliest year in a tusk record is expected to be thin, because the only place it can be measured is near the CDJ, where a single increment is generally thinner than at other locations on the tusk. The second year in the tusk record is also probably thinner than it would be at its maximum, because it is also measured in close proximity to the CDJ. Regardless, nearly 0.5 mm – a considerable difference in increment thickness attributable to location (Fisher et al. 2008) – would need to be added to the thicknesses of the first and second years to disrupt the steady increase in growth rate exhibited here. Even if the pattern in the early years were to change, growth rate at the beginning of the tusk record would still be

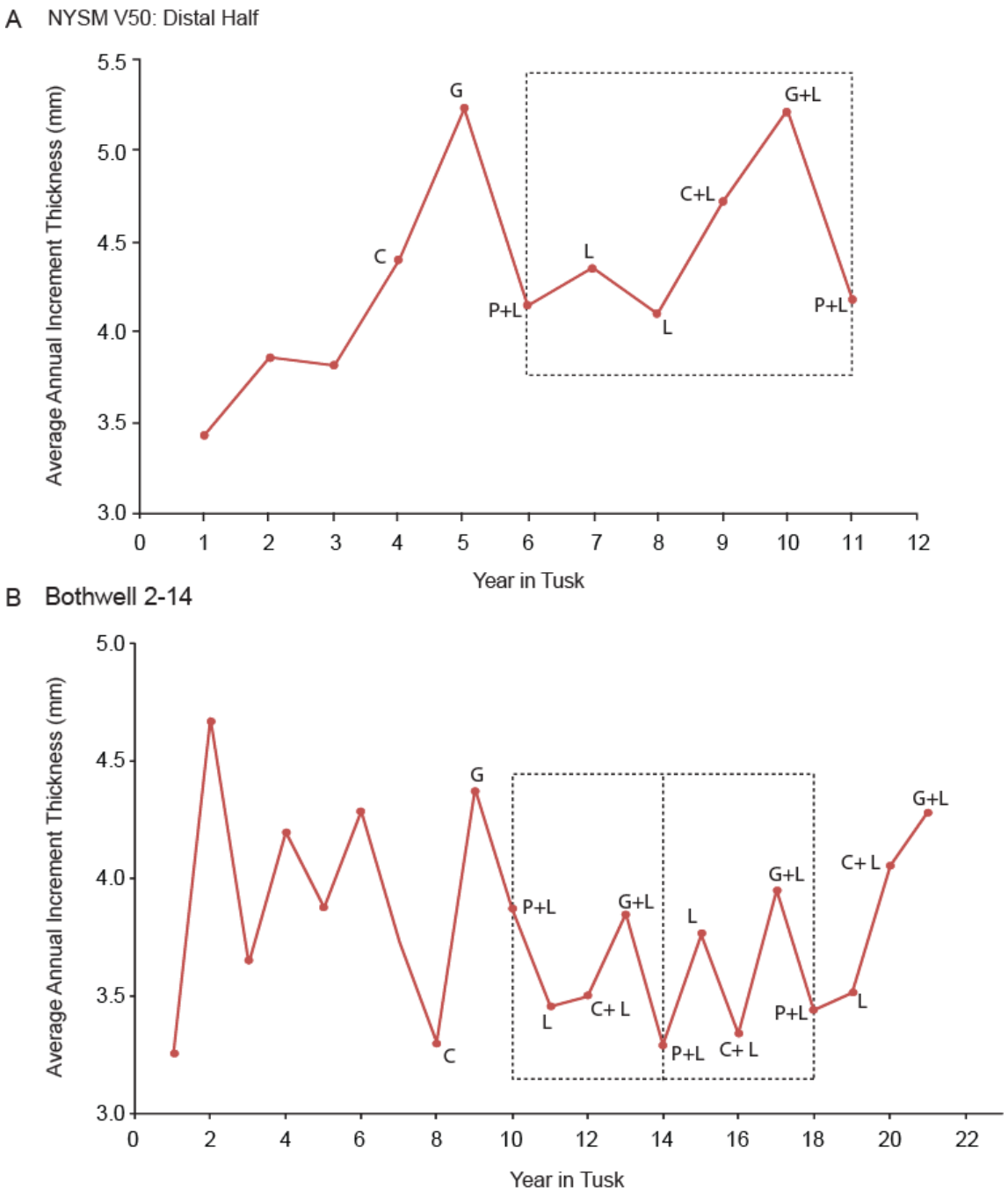


Figure 5.15. Reproductive events interpreted in the annual increment profiles of (A) NYSM V50 and (B) Bothwell 2-14. C = conception, P = parturition, G = gestation, and L = lactation. Dashed squares indicate inferred inter-birth intervals. Note the peaks in growth rate associated with the one full year of gestation, the most recognizable feature of inter-birth intervals in the tusk record.

relatively low.

A similar rapid increase in growth rate in the early years of life has been observed in the tusk record of North Java (Fisher et al. 2008). After this increase, North Java exhibited periodic oscillations in tusk growth rate (interpreted as calving cycles), superimposed on an overall decline in annual increment thickness. Because fragmentation of the middle portion presented difficulties for analyzing growth rate for a portion of NYSM V50's life, it could not be determined if there was an overall decline in annual increment thickness over her entire life. However, annual growth rates at the end of life were significantly lower (Welch two sample t-test; $p = 0.005$) than the annual growth rates in the distal tusk portion, so there was, at least, a decline in growth rates from earlier to later in life.

NYSM V50's peak in growth rate at year five is followed by a multi-year period of low growth rate from years six through nine. A recovery to pre-six growth rate occurred in year 10. Because low growth rate is associated with lactation, years six through nine might have represented a time in NYSM V50's life when she was nursing a calf. Lactation must be preceded by gestation, which is associated with higher growth rates. With these criteria, the increase in growth rate at tusk-year four (life-year seven) suggests conception, likely in late spring or early summer, when male mastodons entered musth (Fisher 2008). That growth rate does not peak at conception was not surprising, as the first mating season for a young female is particularly stressful, and the increase in growth rate related to gestation may be damped by the interruption of normal feeding activities during courtship.

Gestation proceeded through year five, evidenced by an increase in growth rate. The most substantial increase in growth rate related to gestation was expected to occur at year five, because NYSM V50's fetus was gestating for the entire calendar year. In addition, growth rate could also have increased because she was able to resume normal feeding activities in this year. Parturition occurred in year six, evidenced by low growth rate attributable to lactation as well as the stress associated with birth. There was a slight increase in growth rate to year seven, although rate remained low through year eight. At the beginning of year eight, the calf would have been nursing for two years. After two years, elephant calves decrease their milk intake but still nurse regularly (Lee and Moss 1986). There was an increase in growth rate at year nine, which was interpreted as a second conception, again in late spring or early summer. This year was also associated with lactation, as a female elephant will nurse her current calf through most of her subsequent pregnancy, with the first calf ideally being weaned by the time the second calf is born (Lee 1986).

By spring of year ten, the first calf would have been nursing for four years. After four years, the calf would have substantially decreased its milk intake, thus relieving the energetic burden of lactation on NYSM V50 and allowing her dentin growth rate to recover to pre-lactation levels. The increase in year ten was also attributed to a full year of gestation. The subsequent decrease in growth rate at year eleven was attributed to the birth of the second calf in early spring as well as the energetic costs of nursing the second calf while possibly occasionally nursing the first calf as well.

Based on these patterns, NYSM V50 is interpreted to have matured at life-year seven (conception), given birth to her first calf in life-year nine, and to have had an inter-

birth interval of five years. Conception at life-year seven is within the range of first conception for African elephants (Moss 2001) – though at the lowest end – and earlier than the timing of first conception inferred for North Java (life year nine or ten, Fisher et al. 2008). An inter-birth interval length of five years is similar to lengths for African elephants experiencing environmental stress, within the range of inter-birth intervals – though at the high end – interpreted in the North Java mastodon tusk record, and higher than intervals reported in annual increment length records for four additional female mastodons (Fisher 1996).

The most conspicuous features of inter-birth intervals proposed here are the peaks in growth rate associated with full years of gestation. The approximately two-year gestation period spans three calendar years: a partial year beginning at conception, a full year in the middle, and a partial year ending in birth. The second year of gestation is the only year in which a female is pregnant from beginning to end, so if gestation is associated with an increase in growth rate, the highest increase should occur during this year. The number of annual increments between these peaks, though not specifically marking the distance from one birth to the next, reflects the number of years between births, so the number of years between these peaks in growth rate could be used to mark inter-birth intervals in the tusk record.

The annual increment record from the pulp cavity section of NYSM V50 (Fig. 5.7B) does not yield clear interpretations of gestation or lactation. The low growth rate at year 30 could reflect conception, and the increase at year 31 could reflect a full year of gestation. The slight decrease in growth rate at year 32 could reflect parturition and lactation, and the decrease at year 33 could indicate lactation. However, the sharp

increase at year 34 cannot be interpreted with respect to expected patterns of gestation or lactation. If NYSM V50 conceived again in year 34, then this year, which would then be a year of conception and lactation, is not expected to exhibit a higher growth rate than all previous years in the profile. If there was no conception in year 34, this year would reflect the third year of lactation. Growth rate in this year may not be affected as much as in the first two years of lactation, and could show some recovery, but this rate, again, is not expected to exceed growth rates exhibited by all other years in the profile. If this tusk exhibited a 35th year, and year 35 exhibited an increase in growth rate relative to year 34, then it could be interpreted that years 30 to 35 exhibit a growth sequence like that of years four to ten in the distal half, which begins at conception and ends with the second year of gestation combined with the last year of lactation for one calf (Fig. 5.15A). Since there is no year 35, however, other scenarios are considered. It is possible that NYSM V50 did not give birth to a calf during the last five years of her life. This is not unusual for African elephants, in which inter-birth interval lengths typically increase with senescence, and females of advanced age often enter into a post-reproductive period (Moss 1988).

Alternatively, the interruption of expected patterns of variation in growth rate could reflect the death of a calf in year thirty-three or early in year thirty-four. Fisher (1996) observed similar "truncated" calving cycles in the tusk records of the Owosso and Sheathelm mastodons; these truncated cycles were identified as possible calf deaths.

Second-order increment record. – In an exploratory study of NYSM V50's tusk record (Smith and Fisher 2008), it was proposed that sharp dips in the second-order increment profile that occurred during seasons when low growth rate is not expected (i.e., late

spring and early summer) might reflect aspects of reproductive biology. These dips were attributed to either the interruption of normal feeding activity during mating season or the stress of parturition. This hypothesis is reconsidered here, in light of the additional stable isotope and growth increment analyses that have been conducted since the first study. These interpretations remain, as in the initial study, tentative because NYSM V50's sub-annual growth profile does not exhibit a seasonal pattern of growth. However, an aseasonal pattern of growth rate does not render sharp decreases and increases in growth rate meaningless. Here, the tusk record is investigated for conspicuous changes in second-order growth rate that may be associated with reproductive events (as identified in the annual increment profile), rather than defining reproductive events based on variation in the second-order increment profile itself.

First conception is inferred, in the annual increment profile, to have occurred during late spring or early summer of year four. There is a sharp dip in the seventh second-order increment of year four corresponding to late spring or early summer (Fig. 5.6A). The next event, parturition, is expected to occur in early spring of year six (Fig. 5.6B). Year six exhibits two periods of low growth rate, one at second-order increment number three and one at second-order increment numbers 20 and 21. The former period of low growth rate occurs in mid-spring; parturition here indicates a gestation length of just over 22 months (1.85 years). This birth date would occur in a time of high nutrient availability, which would slightly relieve the energetic burden imposed on NYSM V50 by lactation. This period of gestation is similar to periods of gestation exhibited by modern African elephants (Lee and Moss 1986). The latter period of low growth rate occurs at the end of fall; parturition here indicates a gestation length of about 30 months

(2.5 years). Birthing a calf just prior to winter would increase the energetic burdens of lactation on the mother, as nutrients would become increasingly scarce during winter. In addition, growth rate is expected to decrease in winter, so low growth rate at day 260 is expected. Furthermore, a gestation of 30 months is approximately eight months longer than gestation in the African elephant, which has the longest gestation period of any living terrestrial mammal (Gaeth et al. 1999). Thus, the low growth rates in second-order increments twenty and twenty-one likely do not correspond to parturition.

The next life event, the conception of NYSM V50's second calf, is expected to occur in late spring or early summer of year nine (Fig. 5.6C). There are several declines in growth rate during year nine, but of those that occur during spring and summer, one occurs at second-order increment number four (mid-spring), and one occurs at second-order increment number seven (late spring/early summer). NYSM V50 could have conceived at either second-order increment number seven or nine, but two low periods of growth rate during the inferred mating season could also suggest that she experienced two different mating events during year nine, and only the second mating event resulted in conception. Because it is not expected that a female would continue mating after conceiving, the second mating event (increment number seven) is interpreted as the time of conception. However, either event could have resulted in conception.

The final reproductive event in the distal tusk record of NYSM V50 is the birth of NYSM V50's second calf, which is inferred to occur in early spring of year eleven (Fig. 5.6C). There are two declines in second-order increment thickness in the early part of year eleven. The first is at second-order increment number four (mid-spring); parturition here would indicate a gestation of about 23 months (1.9 years). The second is at second-

order increment number seven (late spring/early summer); parturition here would indicate a gestation of 24 months (2.0 years). Either birth date is possible, but a two-year gestation seems less likely. In addition, it would be more advantageous for the mother and calf for birth to occur in early spring (when NYSM V50's first calf was interpreted to be born), so the calf has more time to grow before it enters its first winter. Thus, the second birth is interpreted to occur in early spring. There is, however, anecdotal evidence that male calves gestate longer than female calves (Lee and Moss 1986), so if the second birth occurred on seventh rather than the fourth second-order increment, it is possible that NYSM V50's second calf was a male.

Interpretations of reproductive events in the second-order increment profile initially looked promising, but, because there are sharp declines in growth rate in spring and summer of years not expected to be associated with reproductive events, the correspondence between brief periods of low growth rate and hypothesized timing of reproductive events, from the annual increment profile, may be coincidental and should be treated tentatively.

Stable isotope record. – The stable isotope record for NYSM V50 does not clarify interpretations of reproductive events in the tusk record because $\delta^{13}C$ was diagenetically altered, preventing evaluation of an association between $\delta^{13}C$ increase and proposed growth-rate evidence of lactation.

Reproductive Events in Bothwell 2-14

Annual Increment Record –The amount of material abraded from the tip of Bothwell 2-14 is equivalent to four years of growth (see "Materials and Methods," this chapter).

Thus, the first year of growth in her annual increment thickness profile could reflect life-year five, and Bothwell 2-14 was at least 25 years of age at death.

The earliest part of Bothwell 2-14's annual increment record exhibits a sharp increase in growth rate (Fig. 5.14), as exhibited by NYSM V50 and North Java. The most substantial increase for Bothwell 2-14 occurs between years one and two instead of occurring gradually over the first few years, but there is also a general trend of annual increment increase up to and including year six. Year one should be thinner than other increments because of its proximity to the CDJ, but in this case nearly 1.5 mm would have to be added to the first increment to disrupt the abrupt increase in growth rate exhibited here, an unprecedented difference in thickness attributable to location of measurement (Fisher et al. 2008). Like NYSM V50 and North Java, there is an overall decline in annual dentin growth rate to the end of life that follows the initial increase, but there is not a significant difference (Welch two sample t-test; $p = 0.27$) between thicknesses in early years (one through six) and thicknesses in later years (six through twenty-one), as there was in NYSM V50.

Year six is followed by oscillations in tusk growth rate that persist to the end of the profile. The first substantial decline occurs at year eight, which is followed by an abrupt increase in year nine. After year nine there is a series of overall decreases and increases in growth rate. As in the tusk record of NYSM V50, each peak in these undulations is interpreted as an increase in growth rate associated with a full year of gestation, and each trough is interpreted as a period of lactation (Fig.5.14). Thus, first conception for Bothwell 2-14 is interpreted to have occurred during year eight (life-year 12, likely in late spring or early summer), and first parturition occurred in year 10.

Relatively high growth rates at years 13, 17, and 21 are also suggestive of a full year of gestation. These growth rates likely do not recover to the growth rate of the second year of gestation in the first pregnancy because every subsequent gestation period after the first gestation period also involves lactation of the current calf, which is expected to cause a decrease in growth rate. In NYSM V50 there was a recovery to pre-first parturition levels between her first and second calves, but her longer inter-birth interval allowed for more recovery time.

Years 10 to 12, 14 to 16, and 18 to 21 each reflect a possible birth-lactation-conception sequence. The final inferred inter-birth interval in the annual increment profile is incomplete, as it ends with the inferred second year of gestation instead of the birth of a calf. Bothwell 2-14 died about two-thirds of the way through the 22nd year of her tusk record, so she would have had time to give birth to her fourth calf before she died. Given this interpretation, Bothwell 2-14 is inferred to have birthed four calves within her lifetime, and her tusk record includes two complete inter-birth intervals, each four years in length. If Bothwell 2-14 had lived through year 22, a third inter-birth interval, also four years long, would likely be present in the profile. A length of four years is similar to lengths exhibited by African elephants during times of high nutrient availability, and is within the range of interval lengths exhibited in the annual increment thickness profile of the North Java mastodon as well as in the annual increment length profiles for four additional females. Bothwell 2-14 is inferred to have matured, based on age at first conception, during tusk year ten (life year twelve), which is older than the age of maturation in North Java and NYSM V50, but within the range of maturation times for African elephants.

Year 21 exhibits an increase in growth rate higher than exhibited for a year of both gestation and lactation, given the growth rates associated with such a year earlier in the tusk record. However, female African elephants stabilize in stature around year 20 (Lee and Moss 1995), so it is possible that the greater increase in growth rate exhibited at year 21, relative to years 13 and 17, reflects Bothwell 2-14 attaining her maximum stature, and the freeing of additional energy resources for calf development and tusk growth.

Second-order increment record. – Patterns of variation in Bothwell 2-14's second-order increment profile are compared to life events inferred from her annual increment profile, as was done for NYSM V50. The second-order increment profile of Bothwell 2-14 does not, like that of NYSM V50, exhibit seasonal patterns of growth expected for a temperate-latitude mammal. So, identification of reproductive events in the second-order increment profile should be treated tentatively.

There are sharp dips in growth rate in the fifth and fifteenth second order increment of year eight, the inferred year of first conception (Fig. 5.11B). The fifth second-order increment reflects mid-spring, and the fifteenth second-order increment reflects late spring. There is no reason to choose one date over the other for timing of first conception, so both are considered here. In year ten, the year of parturition, there is a sharp dip in growth rate in the fifth second-order increment, again in mid-spring (Fig. 5.11C). Conception in mid-spring indicates a gestation of 24 months, while conception in late spring indicates a gestation of 20 $^{2}/_{3}$ months. A 24-month gestation is longer than that exhibited by African elephants (~22 months), and a 20 $^{2}/_{3}$-month gestation is shorter than that exhibited by both NYSM V50 and African elephants. However, it is within the range

of gestation periods exhibited by Asian elephants (20-21 months; Sukumar 2006), and, given that mastodons are no more closely related to African elephants than to Asian elephants, there is no reason to discount the possibility that mastodon inter-birth interval lengths resemble those of Asian elephants. A shorter gestation in Bothwell 2-14 could also be due to regional differences, in which northeastern mastodons (NYSM V50) may have had longer gestation lengths than Great Lakes-region mastodons. Alternatively, the difference could be related to the calf's sex, in which a longer gestation (NYSM V50) could suggest a male calf, and a shorter gestation (Bothwell 2-14) could suggest a female calf (Lee and Moss 1986). However, there is no definitive reason to discount either gestation length from the evidence here, so both are considered feasible.

The first noticeable decrease in growth rate in year 12, interpreted as Bothwell 2-14's second conception (Fig. 5.11C), occurs at the sixth second-order increment (late spring). Birth is expected to occur in year 14, in which there are two sharp declines in growth rate at the beginning, in the second (early spring) and fourth (mid-spring) second-order increment. Birth in early spring indicates a gestation of just less than 23 months, and birth in mid-spring indicates a gestation of 23 $^{2}/_{3}$ months. Based on the two possible gestation lengths for her first pregnancy, either birth date is feasible.

The third conception event is interpreted to have occurred in year 16 (Fig. 5.11D). Most second-order increments in year 16 are similarly low, but the first noticeable decline occurs in the sixth second-order increment (mid- to late spring). The next birth is interpreted to have occurred in year 18 (Fig. 5.11D), in which a noticeable decline in growth rate does not occur until the ninth second-order increment (early summer). If mid-summer is the time of birth, then gestation would have been just under 25.5 months,

which seems unlikely based on other periods of gestation for 2-14. It is possible that by the time Bothwell 2-14 birthed her third calf, parturition did not cause sufficient stress to be recorded in the tusk record. With this reasoning, birth may have occurred at the third second-order increment (early spring), which exhibits a slight decline in growth rate, reflecting a relatively low-stress birth. Parturition in early spring indicates a gestation of just over 23 months, which seems more likely based on gestation periods associated with earlier pregnancies.

Bothwell 2-14's final conception is interpreted to have occurred in year 20. The lowest growth rate in spring or summer of this year occurs at the fifth second-order increment, so conception is inferred to have occurred in mid-spring (Fig. 5.11E). The birth of Bothwell 2-14's final calf is interpreted to have occurred in year 22. There is a zone of relatively low growth rate between second-order increments seven (late spring) and twelve (early summer), so, if parturition occurred during deposition of one of these increments, gestation was between 25 and 27 months, both of which seem too long to be likely. As in year 18, it is possible that birth of the calf in year 22 was not overly stressful, thus not identifiable in the tusk growth record.

Stable isotope record. – Bothwell 2-14's stable isotope record was not useful for identifying reproductive events in the tusk record. Years four to six exhibit no deviations from the sub-annual pattern of $\delta^{13}C$ variation, in which the value increases in early spring, decreases to a mid point in the year, and increases to the winter-spring boundary (Fig. 5.13C). These years are interpreted as pre-maturation, based on the annual increment profile (Fig. 5.12), so none are expected to be associated with reproductive events. Years 21 and 22, both of which occur at a time when Bothwell 2-14 should have

been nursing, show this same pattern of $\delta^{13}C$ variation as in years four to six. Year 20, which is also associated with lactation, shows little to no variation in $\delta^{13}C$ values throughout the year.

The $\delta^{13}C$ values associated with years 20 to 22, when Bothwell 2-14 was interpreted to be lactating, are significantly different (Welch two sample t-test; $p = 0.043$) – and lower, on average – than the values associated with years four to six. This evidence leads to three interpretations: (1) an increase in $\delta^{13}C$ is not associated with lactation in mastodons, (2) an increase in $\delta^{13}C$ is associated with lactation in mastodons, but factors such as diet, fat utilization, and fat storage (all of which contribute to the $\delta^{13}C$ composition of tusk dentin; Fisher and Fox 2003) damp the lactation signal, or (3) Bothwell 2-14 was not lactating during years 20 to 22. If the first possibility is correct, then the tusk record should be analyzed in light of other compositional signals that could be associated with lactation. If growth interpretations of reproductive events are correct, then the second possibility is the most likely scenario. If the third possibility is correct, then interpretations of the timing of lactation in the tusk growth record are incorrect.

Conclusions

The ultimate goal of this study was to increase knowledge of female mastodon life history. This study succeeded in enlarging the sample size of female mastodon tusk records analyzed at the annual and sub-annual scales from one to three. In addition, the records compiled from these females allowed for the development of interpretations of the effects of pregnancy and lactation on the tusk record. The females in this study are interpreted to have matured at ages seven (NYSM V50) and 12 (Bothwell 2-14), and

exhibited inter-birth intervals of four (Bothwell 2-14) and five (NYSM V50) years. Inter-birth intervals are proposed to be recognized as a sequence of variation in annual dentin growth rate defined by one year of low growth rate (conception and gestation), one year of high growth rate (gestation only), and two to three years of low growth rate (parturition and multiple years of nursing). This sequence of growth is complicated by a number of intrinsic and extrinsic factors, such as nutritional status, nursing one calf while pregnant with another, and age, but this general sequence of variation is observed in annual increment profiles of both tusk records.

A lack of seasonal growth patterns distinguishes NYSM V50 and Bothwell 2-14 from Michigan proboscideans, which typically exhibit sub-annual patterns of growth that correspond to expected seasonal changes in growth rate (e.g., Koch et al. 1989). This could indicate that NYSM V50 and Bothwell 2-14 lived in environments of lower seasonality than their contemporaries in Michigan. Reduced amplitude of variation in $\delta^{18}O$ variation for Bothwell 2-14, as compared to northern Great Lakes-region mastodons, supports the hypothesis that at least Bothwell 2-14 lived in a region of lower seasonality. However, sub-annual increment profiles for temperate-latitude male proboscideans generally conform to seasonal patterns of variation better than female proboscideans of the same region. Thus, aspects of female reproductive biology, which are multi-year events, may perturb dentin growth rate more than aspects of male reproductive biology, which, post-maturation, are essentially restricted to short-term events such as musth battles and mating.

Inter-birth interval lengths posited here are similar to those proposed in earlier studies (Fisher 1996; Fisher et al. 2008), but an association between criteria for

identifying these intervals and inter-birth intervals themselves has not yet been confirmed. Serial analysis of major and trace element concentrations (e.g., Se, Zn, Cu; Wasowicz et al. 1993; Rountrey 2009), using tusk records compiled here as a template, could be essential to identifying reproductive events in the tusk record. It has been proposed that documenting trends in the timing and spacing of mastodon reproductive events throughout the Pleistocene could be used to evaluate the contribution of environmental stress to the cause of late Pleistocene mastodon extinction (e.g., Fisher et al. 2008). Thus, the results presented here could ultimately be used to interpret the underlying causes of mastodon extinction, thereby providing evidence for the causes of megafaunal extinctions in general.

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Chapter 6

Conclusions

Tusks are excellent sources of paleoecological data because they grow continuously by accretion, providing a near-complete record of changes in morphology, stable isotope composition, and growth rate for the life of an individual. Tusks often occur in isolation or without associated skeletal elements. Yet, a single tusk can reveal much about a mastodon's life, including its sex, minimum life span, timing of maturation, and season of death. Furthermore, tusk data can be used to infer cause of death, and data from an assemblage of co-occurring tusks can be used to assess processes of site formation. The studies in this dissertation were developed around the Bothwell Site, which yielded a rare assemblage of female mastodon tusks. These and other post-LGM mastodon tusks were analyzed in order to expand knowledge of American mastodon life history, with particular emphasis on the lives and deaths of females. The contributions of this dissertation to mastodon paleobiology follow.

(1) Presenting a reliable method for identifying the sex of a mastodon from tusk measurements. An important basis of life history studies is identifying the sex of an individual, because misidentification of sex could lead to misinterpretation of life

events. Prior to this study, assessment of sex from tusk measurements relied on various univariate and bivariate methods, which, without independent knowledge of age, were tentative. The tusk's continuously growing nature presented a problem for reliable identification of sex without knowledge of age because measurements from a random sampling of tusks show a continuous spectrum of size and shape change rather than a clear bimodal distribution.

Principal components analysis of linear and curvilinear tusk measurements sorted tusks by sex (PC-I) and age (PC-II). The PC-II vs. PC-I plane provided an improved method of sex assessment, relative to earlier methods, because tusks of young males and older females that exhibited similar morphologies were separated on this plane. Sex discrimination in PCA was enhanced by the addition of longitudinal variables, a new category of variables that exhibit an ontogenetic sequence of change in a single measurement. Adding an aspect of ontogeny to the analysis refined assessment of relative age and increased the gap between tusks of young males and older females that exhibit similar morphologies. Thus, PCA is shown to be a robust method for sexing tusks, without a priori knowledge of age, and is recommended as a method for assessing sex from other structures that exhibit indeterminate growth.

(2) Quantifying details of tusk dimorphism in mastodons and modern African elephants. Modern African elephant behavior has been well-documented through long-term studies of wild elephant populations (e.g., Moss 1988). Modern elephant behavior has often been used as a model for mastodon behavior because elephants are the closest living relative to mastodons, and elephants and mastodons share similar body plans and exhibit similar dimorphisms. Much can be inferred about the behavior of an

animal based on degree of dimorphism, when males are larger than females, so this study sought to perform a quantitative comparison of tusk dimorphism between the two genera that would help to evaluate the likelihood of similarities in behavior .

Comparison of tusk dimorphism by canonical variates analysis indicated that (1) the discriminating factor between sexes for elephant and mastodons is similar, and primarily involves unique ontogenetic changes in tusk circumference for each sex, regardless of genus, (2) slight differences between genera in the discriminating factor between sexes suggest that mastodons may have matured at an earlier age than modern elephants do, (3) male tusks are larger than female tusks across all variables, regardless of genus, especially in pulp cavity depth and tusk circumference, and (4) there are differences in tusk morphology between genera that indicate mastodon tusks are, in general, more robust than elephant tusks.

CVA of linear and curvilinear tusk measurements showed that there is a characteristic male and a characteristic female tusk form shared by elephants and mastodons. Because tusk dimorphism and behavior in modern elephants are closely linked, the evidence presented here supports the inference that mastodons exhibited behaviors similar to those of modern elephants. If aspects of modern elephant behavior emerged coincident with the emergence of modern tusk dimorphism, then these aspects may have emerged prior to the divergence of elephants and mastodons, over 20 million years ago.

(3) Evaluating processes of formation for an all-female mastodon assemblage. Documenting the circumstances surrounding death for late Pleistocene mastodons can be used to establish patterns of mastodon mortality as the species neared its

extinction. The Bothwell Site produced an assemblage of female mastodons, a rarity among Great Lakes-region mastodon sites. Sex and age distribution for Bothwell mastodons suggests that they could have been members of a single matriarchal family unit, but this hypothesis is invalidated because of the non-simultaneous nature of Bothwell mastodon mortality events.

Season of death analyses indicate that Bothwell mastodons exhibit seasons of death commensurate with those of butchered mastodons (autumn or early winter). No evidence of morbidity was found in the tusk growth record, and healthy animals are rarely trapped in ponds, so death by nutritional stress and by entrapment are both unlikely. The most likely scenario for site formation, based on tusk evidence, is that the Bothwell Site was a Paleoindian meat cache revisited year after year. The investigation of Bothwell mastodon post-crania for evidence of bone modification suggestive of butchery (e.g., Fisher 1987) will aid in evaluation of this hypothesis.

(4) Proposing evidence of reproductive events in the tusk record. This dissertation substantially increased the body of knowledge on female mastodon life history by documenting long-term patterns of tusk growth rate and stable isotope composition for two female mastodons, NYSM V50 and Bothwell 2-14. Previous to this study, only one other female mastodon tusk record had been compiled at both the annual and sub-annual level. Periodic oscillations in annual increment thickness were identified as possible evidence of inter-birth intervals. These intervals – characterized by increases in growth rate associated with gestation and decreases in growth rate associated with lactation – ranged from four to five years. Intervals here are consistent with those identified in prior studies. No definitive criteria for identifying

gestation or lactation in the tusk record could be established, but tusk records produced could be used as templates for applying different analyses, such as serial analyses of major and trace element concentrations (e.g., Se, Zn, Cu; Wasowicz et al. 1993; Rountrey 2009), that might provide evidence of reproductive events.

American mastodons were remarkable creatures that were abundant across North America until their extinction at the end of the Pleistocene. The results of this dissertation cannot be used to implicate a specific cause for this extinction, but the two most frequently proposed mechanisms, environmental stress and over-hunting by humans, can be considered in light of knowledge of the lives and deaths of female mastodons presented in this dissertation. There is no evidence to suggest that any of these mastodons died as a result of environmental stress. First, none exhibited substantial decreases in either annual or sub-annual growth rate at the end of life that would indicate nutritional stress. Second, mastodon tusk dentin from the Bothwell site exhibited a range of nitrogen isotope values similar to those exhibited by other Great Lakes-region mastodons whose deaths were not caused by nutritional stress. Third, the age and sex distribution of mastodons at the Bothwell Site is not reflective of a death assemblage formed by climatic stresses. Death assemblages formed by drought for example, are expected to contain a high proportion of sub-adults (Haynes 1984), not the prime-age females like the Bothwell mastodons. Finally, Bothwell 2-14's tusk record was interpreted to contain evidence of four birth events that occurred approximately every four years. This uninterrupted series of births suggests that Bothwell 2-14's environment was favorable during her reproductive lifespan, providing her with adequate nutrients to birth and raise calves on a regular schedule.

There is some evidence that implicates humans in the deaths of mastodons studied here. Bothwell mastodons and NYSM V50 were all interpreted to have died in autumn or early winter, seasons of death commensurate with mastodons that have been butchered by humans. Mastodons that died in other seasons have not exhibited evidence of butchery, so mastodons with autumn or early winter deaths were also likely killed by humans (Fisher 1987, 2009). Thus, evidence collected from tusks provides support for human hunting as a cause of death for these mastodons.

The goal of this dissertation was to contribute to the body of knowledge on female mastodon life history. Investigating evidence of reproductive biology in the tusk record was of particular interest because aspects of reproductive biology, including inter-birth intervals, are sensitive to environmental conditions. Inter-birth intervals are extended during periods of environmental stress, so knowledge of inter-birth interval length can be used to explore the relationship between a mastodon and its environment. Currently, all female mastodon tusk records with proposed evidence of inter-birth intervals are younger than 12,000 BP. Once criteria for identifying inter-birth intervals are established, inter-birth interval lengths for mastodons living at different times during the Pleistocene can be documented, and trends in inter-birth interval length throughout the Pleistocene can be used to evaluate the contribution of environmental stress to mastodon extinction at the end of the epoch.

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