



Mammoth Graveyard

2011 FIELD REPORT

Background Information

Lead PI: Larry Agenbroad, Ph. D.

Project scientists: Larry Agenbroad, Ph.D.; Don Morris; Justin Wilkins; Wanda Agenbroad; Willow Nguy

Report completed by: Larry Agenbroad

Period Covered by this report: 2011

Date report completed: 2011-11-16 11:21:51

Research site: Agenbroad, South Dakota, United States

Research site latitude / longitude: 43° 25' 45" N; 103° 28' 27" W

Protected area status: Paleontological museum. The world's largest Columbian mammoth exhibit and a world-renown research centre for Pleistocene studies. Sinkhole and the in-situ exhibit enclosed and protected by a climate controlled building.



The Mammoth Site®

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]Dear Earthwatch Participants 2011: I want to thank you for your efforts and individual contributions to a successful 2011 field season. I suppose the most impressive accomplishment was the discovery of the 118th tusk, on the first day of the excavation, completing the 59th mammoth (by tusk count). You also produced the recovery and mapping of 54 new mammoth (*Mammuthus columbi*) bones, plus more than 500 fragments. In addition, a new immature rib (non-mammoth) was located and prepared for removal. Possibly the most spectacular events were the final preparing, casting plaster field jackets, and removal of two tusks from previous seasons (76-391 and 89-005). My best estimates are that you removed 13.5 tons of fill dirt putting at least 10 tons through the screen wash. The concentrates from that process will be sorted and identified during this fall and winter. In addition to all the efforts during the excavations, you enhanced the experience, appreciation, and interest of thousands of individuals of the visiting public. You added to the experiences of visiting scholars, guides, and staff. Thank you for your participation in an excellent, productive, field season. Best wishes, Larry D. Agenbroad, Ph. D. Director/Principal Investigator, Mammoth Site.

Larry D. Agenbroad

SECTION ONE: Scientific research achievements

Top highlight from the past season

The top highlight of the 2011 season was the discovery of the 118th tusk, which completed the 59th mammoth from the site, to date (by tusk count).

Reporting against research objectives

Objective 1: Excavation and exhibit of lateral and vertical areas of the site. This objective was well met. A total of 13.5 tons of sediment was removed via hand tools; 10 tons were screen washed. A total of 54 new bones were discovered plus more than 500 small fragments. Several specimens were cast in plaster jackets and removed to the laboratory.

Objective 2: Taphonomic analyses of the bone bed maps and selected skeletal elements via the computer mapping program. This objective is on-going and enhanced with each season's results. Two new areas of special interest: a) the 2010 discovery of a worn premolar of *Arctodus simus*, in the south-central portion of the excavation; b) continued discovery of juvenile ribs in the south west portion of the bone bed. Tentative interpretations suggest an immature bear, further comparisons are necessary.

Objective 3: Continued mapping using the Trimble Robotic EDM transit. New batteries were purchased allowing use of the EDM and the on-board computer module. This allows transfer to the PC mapping software. All specimens have been mapped.

Objective 4: Continued numbering and recording of in situ bones and those in storage. The numbering sequence includes year of discovery and sequential numbers for that year. Bones in storage have also had laboratory numbers applied. Both paper and electronic records are kept.

Objective 5: Water screen 100% of the dirt near bone; 10% otherwise. At least 10 tons of the 13.5 on total, removed in the 2011 season, was water screened.

Objective 6: Continued metric analyses: All portions of the skeleton have been measured and are being combined with drawings, photos, and text to create an Atlas of the Columbian mammoth skeleton.

Objective 7: Collaborative research with other professionals. Collaboration with Dr. Carlos Cordova (University of Oklahoma) on opal phytoliths in the sediments is underway. Dr. Evgeny Maschenko (Institute of Paleontology; Moscow, Russia) was hosted by the Mammoth Site, in September, 2011, to do metric analyses comparisons with woolly mammoths.

Objective 8: Continued research on associated fauna: Several non-mammoth elements have been recovered. We are certain we have antelope cranial remains. Small ribs have been tentatively identified as a possible juvenile short-faced bear. CATSCAN tomography of the adult short-face bear cranium has provided insights as to cranial capacity, and other cranial information.

SECTION TWO: Impacts

Partnerships

The Mammoth Site of Hot Springs, SD Inc. has been the primary partner, insuring success of the project. They supply lecture facilities, meeting rooms, kitchen and dining facilities, and staff salaries. In addition, they provide office support Xerox, computers, mapping equipment, and other services.

Contributions to conventions, agendas, policies, management plans

- **International**

I am on the organizing committee of the International Mammoth Conference (IMC). These conferences allow interaction with other professional (world-wide) who are also researching mammoths and their ancient environments, throughout the northern hemisphere. The 2010 conference was held in Le Puy en Velay, France 8/30-11/4/2010. The next conference is scheduled for 2013 in Anchorage, Alaska.

- **National or regional**

The American Quaternary Association (AMQUA); the International Quaternary Association (INQUA); the Tertiary-Quaternary Association (TERQUA); the Society for Vertebrate Paleontology (SVP) and the Plains Anthropological Conference (PA).

- **Local**

Island in the Plains Conference (IIP) which covers the Black Hills and northern Plains. Mammoth Site hosted the 2011 Conference (October 7-9, 2011)

Impacting Local Livelihoods

The local economy is positively influenced by the number of visitors who stay in local area lodging and camp facilities, dine at local restaurants, service their transportation needs such as tour companies, fuel and similar services. The site is one of the regional tourist destinations within the Black Hills of South Dakota. It has become one of the locations for tour bus companies for foreign travelers, school groups, field trips, etc. National and international conferences have been hosted on-site. Educational materials are distributed nation-wide via 'Mammoth in a Trunk' activities in age/grade levels from K-12. It is a focal point for television and film documentaries.

Local community activities

The local community benefits in many ways. Local individuals serve on the Board of Directors, serve as staff, interpreters, etc. We hire up to 20 individuals for the period May-August, plus 10 full-time staff, In addition we host 6 college/university interns. Local cooks are hired, a local motel houses the EW teams. The community gives a 'Welcome Pot Luck' for each EW team. Two area residents are selected as 'Dig-for-a-Day' prizes. Free access for locals on Mother's Day weekend, with canned food contributions headed for the annual food pantry drive.

Dissemination of research results

Scientific peer-reviewed publications

Dirks, W., T. Bromage, and L. Agenbroad. 2011. 'The timing and rate of molar lamella formation in *Paleoloxodon cypristes* and *Mammuthus columbi*, from dental histology.' *Quaternary International*. (accepted, in press).

Spilde, M., A. Lanzirotti, C. Qualls, G. Phillips, A. Ali, L. Agenbroad, and O. Appenzeller 'Biological rhythms derived from Siberian mammoth hairs.' *PLoS One* (on-line journal 6/30/2011) p. 1-12.

Grey literature and other dissemination

- **Lecture**

Agenbroad, L. 'Mammoth meanders: adventures of a Pleistocene bone hunter' Lecture to the Tampa Bay Fossil Club, Tampa, FL. 2/11.

- **Meetings**

Wilkins, J., D. Esker, L. Agenbroad, and J. Schwabauer. 'An examination of the internal structure of a giant short faced bear skull at the Mammoth Site, Hot Springs, SD' TERQUA annual meeting, Casper, WY. 6/2-4/2011.

Esker, D., J. Wilkins, and L. Agenbroad. 'A multivariate analysis of the ecology of North American Pleistocene bears, with a focus on *Arctodus simus*. TERQUA annual meeting, Casper, WY. 6/2-4/2011.

SECTION THREE: Anything else

Project funding

Funding for the Mammoth Site is generated through ticket sales from visitors to the site. We also apply for Museum grants to upgrade collections, laboratory facilities, exhibits, curation, etc. Two groups, Elderhostel, and Project Exploration provide funds for permission to hold short duration (4 days) visits to the site. We have initiated a capital campaign drive to provide a theater, and visitor education.

Acknowledgements

Earthwatch Institute for supplying teams of excavators each season. Mammoth Site for continued support and facilities throughout the year.



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The duration and rate of molar plate formation in *Palaeoloxodon cypristes* and *Mammuthus columbi* from dental histology

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Fossil elephantids are often assigned chronological ages based on tooth eruption and wear in extant elephants. Differences in body mass are likely to be accompanied by shifts in life history strategies, however, and hypotheses about these shifts cannot be tested using relative age. A better understanding of interspecific differences in the duration of tooth formation would help test hypotheses about life history variation. In this study, periodic incremental features visible in the enamel of histological thin sections of molar plates were used to estimate the rate and duration of plate formation in an insular dwarf, *Palaeoloxodon cypristes*, which is smaller than extant elephants, and *Mammuthus columbi*, which is larger. Polarized light microscopy and image analysis software were used to determine the daily secretion rate of enamel and plate extension rate, the rate at which the plate increases in height each day, utilizing the daily incremental features, the cross striations, and accentuated lines representing the forming front of enamel at a particular time during plate formation. Estimates were made of total plate formation time from crown height and extension rate. Histological sections were prepared from molar fragments from each species. Five sections were prepared in the same plane from the large *M. columbi* plate. The daily secretion rate, 2–5 μm , is similar in both elephants, but the extension rate is higher in the larger *M. columbi*. The initial extension rate is estimated to be 62.5 μm per day, but drops to around 32.3 toward cervical portion of the plate. In *P. cypristes*, the initial extension rate is estimated to be 34.4 μm per day, dropping to 12 μm per day and then rising to 23.3 μm per day in the cervical region. Estimated plate formation time is around 10.6 years for 180.9 mm of height in *M. columbi* and 5.9 years for 51.1 mm of height in *P. cypristes*. *M. columbi* thus forms a taller plate by increasing both extension rate and the duration of formation. These differences could be allometric, with higher crowned teeth forming more rapidly than low crowned teeth, or they could be related to differences in life history strategies between taxa.

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1. Introduction

Knowledge of the age at death of fossil proboscideans is important for understanding their paleobiology in general and their life history specifically. Ages at death for fossil specimens are currently assigned using criteria from extant elephants using a combination of ages at tooth eruption and wear (e.g., Laws, 1966; Roth and Shoshani, 1988; Froehlich and Kalb, 1995) and are frequently used to calculate the age structure of fossil populations (e.g., Saunders, 1992; Agenbrood, 1994, 2003; Germonpré, 2003;

Haynes and Klimowicz, 2003; Mothé et al., 2010). An important aspect of the paleobiology of a fossil species is its life history strategy, the scheduling of its life stages and the timing of variables such as gestation length, age at weaning, age at first reproduction and life expectancy, all of which impact on lifetime reproductive success (Stearns, 1992). Life history variables are correlated with body mass (Western, 1979; Boyce, 1988; Promislow and Harvey, 1990; Stearns, 1992; Charnov, 1993), with larger taxa taking longer to grow and reproducing later than smaller species. Many fossil proboscideans differ in body mass from extant elephants. African elephants are highly sexually dimorphic, females weighing around 2800 kg and males around 5000 kg (Kingdon, 1979). At an estimated 7673 kg (Shipman, 1992) the Columbian mammoth, *Mammuthus columbi*, was significantly larger than an African elephant, and at an estimated 200 kg (Davies and Lister, 2001),

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Palaeoloxodon cypristes, the pygmy elephant of Cyprus, was significantly smaller. Age estimates using African elephants are likely to underestimate age in *M. columbi* and overestimate age in *P. cypristes*. Knowing the precise chronological ages of individual specimens, however, is critical to understanding differences in life history strategies between taxa. Because teeth are the most common elements in the fossil record and develop in a predictable chronology during ontogeny, dental development is frequently used to determine life history strategies in extinct taxa, based on the relationship of tooth development to life history variables in extant taxa (e.g., Kelley and Smith, 2003; Schwartz et al., 2005; Jordana and Köhler, 2011). This paper, as a first step in the process of understanding how dental development might differ between proboscideans, describes the duration of molar plate formation in *M. columbi* and *P. cypristes*.

Studies of incremental features in dentine have led to advances in the understanding of proboscidean life history and paleobiology (Fisher, 1988, 1990, 1996; Koch et al., 1989; Fox, 2000; Fisher et al., 2003; Rountrey et al., 2007, 2011). These features are described as first order or annual increments, second order increments, which in proboscideans are approximately weekly, biweekly, or monthly, and third order increments, which are daily (Koch et al., 1989; Fisher, 1996; Fox, 2000). The third order increments correspond to the incremental features in dentine described as von Ebner lines in primate teeth, and the second order increments to longer period incremental features called Andresen lines (Dean, 1995). Enamel also exhibits daily and long period lines which correspond to the incremental features in dentine. The daily lines, visible along enamel prisms, are cross striations, and the longer period lines are striae of Retzius (Dean, 2000). There are a fixed number of daily lines between long period lines in every tooth in an individual, referred to as the periodicity or repeat interval (Bromage, 1991; FitzGerald, 1998; Smith, 2006; Antoine et al., 2009). Bromage et al. (2009) have demonstrated that striae periodicity is equivalent to the number of days for the formation of one bone plate in a selection of mammals. Small mammals have lower periodicities than larger mammals and form bone at a relatively faster rate, taking fewer days to form a single plate than in larger mammals. In proboscideans, for example, the small *P. cypristes* has a periodicity of 6, while the large *Palaeoloxodon antiquus* has a periodicity of 12 (Bromage et al., 2009). In addition to the normal incremental features, accentuated lines visible in ground sections record the forming front of enamel at the time of a physiological stressor. These hypomineralized lines can occur from illness, parasite load or during life history events such as weaning and menarche (reviewed in Dirks et al., 2002, 2010).

The Elephantidae have a highly derived dentition, comprised of a deciduous and permanent upper incisor, the tusk, and six molariform cheek teeth, sometimes numbered M1eM6 (Laws, 1966). Embryological studies (Kozawa et al., 1995, 2001) have resolved the homologies of elephantid molariform teeth. The six comprise three deciduous premolars and three permanent molars, and that nomenclature is preferred. Although elephantids have an unusual form of horizontal tooth replacement rather than the vertical replacement of most mammals (Laws, 1966; Roth and Shoshani, 1988), enamel formation within the plate is similar to enamel formation in cusps of other mammalian teeth. The inner dental epithelium forms a series of deep folds, outlining the future shape of the tooth plates (Roth and Shoshani, 1988; Kozawa et al., 2001). The enamel forming cells, the ameloblasts, differentiate along the inner dental epithelium. The rate at which they differentiate determines the speed at which the plate increases in height, the extension rate, and the angle at which the striae of Retzius meet the enamel dentine junction (EDJ), is a reflection of this rate (Shellis, 1984). The measured distance between the daily lines in enamel,

the cross striations, is called the daily secretion rate (DSR), and represents the amount of enamel secreted daily by the ameloblast (reviewed in Dean, 2000; Smith, 2008). The formation of plates is sequential, beginning with the anterior of the tooth and continuing posteriorly (Roth and Shoshani, 1988; Kozawa et al., 2001). Cementum formation between the plates and root formation apically complete the process. A complete description of the duration of tooth formation would include the length of time to form an individual plate, or plate formation time, taking both height and thickness into account, the number of plates in the individual tooth, the degree of overlap in the formation of adjacent plates, and the time to form the roots. Lamellar frequency, the number of plates in a standard crown length of 10 cm, differs between species and between teeth within a species, as does the hypsodonty index, a measure of relative crown height (Maglio, 1973; Lister and Joysey, 1992). Tooth formation can take years and the anterior part of the tooth may be in occlusion before the posterior part of the tooth is complete (reviewed in Metcalfe et al., 2010).

Previous studies of proboscidean enamel have mainly focused on microstructural details and schmelzmuster, the characteristic patterning of enamel types within the plate (e.g., Kozawa, 1978; Sahni, 1982; Koenigswald et al., 1993; Kozawa and Suzuki, 1995; Ferretti, 2003a, 2003b, 2008; Tabuce et al., 2007), rather than growth processes. Ferretti (2003b) describes the striae of Retzius in mammoth molars, and Bromage et al. (2002) describe the daily enamel secretion rates in *Elephas recki* and *P. cypristes*, but neither describes the overall plate formation time. A better understanding of differences in plate formation time is the first step in understanding the differences in the duration of formation of the complete tooth. This could help devise a more precise method for aging individuals and understanding life history differences between taxa. For example, using Laws (1966) criteria for aging, Metcalfe et al. (2010) recently suggested that woolly mammoths from Old Crow, Yukon had a prolonged period of nursing without supplemental non-milk foods. They noted, however, that Maschenko's (2002) ages for dental development in woolly mammoths are slightly younger than those in African elephants, and suggested that the use of incremental features in dental tissues to acquire more precise aging could help clarify the differences. Recently, Rountrey et al. (2011) have used growth increments in dentine to derive age at death in two woolly mammoth calves and also suggest accelerated dental development in a male calf relative to extant elephants. In addition to clarifying differences in the chronology of tooth development between species, a better knowledge of plate formation time could also refine studies of diet and seasonality using stable isotopes in molar enamel (e.g., Hoppe, 2004; Pérez-Crespo et al., 2009), although the complete maturation of the enamel occurs after the height and thickness of the plate are complete (e.g., Tafforeau et al., 2007).

This study describes plate formation time, extension rate, and daily secretion rate in molars of *M. columbi* and *P. cypristes*. The choice of species for this initial report on plate formation in the Elephantidae is based on differences in body size rather than phylogeny, but Shoshani and Tassy (2005), whose taxonomy is followed here, included three genera in the Elephantini, *Mammuthus*, *Elephas*, and *Palaeoloxodon*, excluding *Loxodonta*. The existence of a clade consisting of *Mammuthus* and *Elephas* to the exclusion of *Loxodonta* is strongly supported by the Rohland et al. (2007) study of the mitochondrial genomes of mammoths and extant elephants using the mastodon, *Mammuth americanum*, as an outgroup. Although the separation of *Palaeoloxodon* and *Elephas* raises taxonomic questions beyond the scope of this report (Shoshani and Tassy, 2005), future reports will focus on phylogenetic issues using molar plates from *E. recki*, *Elephas maximus*, *P. antiquus* and *Mammuthus primigenius* (Dirks and Bromage, in prep).

2. Material and methods

There is variation in the height of individual plates within a tooth, and molar fragments, such as those in this study, are challenging to identify. The sample comprised 1 molar fragment from *M. columbi* and 1 molar fragment from *P. cypristes*. The *M. columbi* fragment, MSL 1083, is from the Mammoth Site of Hot Springs, South Dakota, dated to the Late Pleistocene, approximately 26,000 years ago (Agenbroad, 1994, 2005). It is made up of two unworn plates and half of an adjacent plate, which is broken at about one half of its height (Fig. 1). The plates were incomplete and still forming at the time of death. The height of the middle plate measured before sectioning was 193.3 mm, suggesting that this tooth may be an M² or an upper or lower third molar (Agenbroad, 1994; McDaniel and Jefferson, 2006: Appendix A. Supplementary material). If this is a third molar, the complete tooth would have comprised more than 20 plates (Kurtén and Anderson, 1980; McDaniel and Jefferson, 2006: Appendix A. Supplementary material).

The *P. cypristes* molar fragment is from a locality near the village of Tatlisu (URM 4945 14 N, 39 117 13 E), also known by its Greek place name as Akanthou Arkangelos Mikhail, in the Turkish Republic of Northern Cyprus (Bromage et al., 2002). Cypriot fossil sites are also Late Pleistocene, but the island may have been colonised by elephants and hippos earlier, perhaps in the Middle Pleistocene (van der Geer et al., 2010). The fragment was not photographed prior to sectioning. The fragment consists of one half of one unworn, incomplete plate and the enamel of part of an adjacent plate. The more complete of the two plates measured 60.5 mm, suggesting that the fragment is an M² or M³, based on measurements of *P. cypristes* plate height taken by the first author on specimens from the Bate collection at the Natural History Museum, London, and are consistent with those reported by Bate (1904). If it is an M², it would have comprised 8e9 plates originally, and 11e12, if it is an M³. Attribution of both fragments is tentative, however, as it is impossible to know precisely from which tooth they originate.

The size differences between the 2 molar fragments meant that slightly different techniques were required to prepare the histological sections. The *P. cypristes* molar fragment was embedded in polymethylmethacrylate and a thick section of 300 microns was cut on a Buehler (Lake Bluff, IL, USA) Isomet low-speed saw. The section was hand ground through graded carbide papers to 1200 grit on a Buehler Handimet II, mounted on a glass slide and then ground from the other side to a thickness of 100 µm. The section was then polished on a Buehler Ecomet III with a 1-µm diamond suspension and mounted with a cover slip (Fig. 2).

Due to its height, the *M. columbi* molar fragment had to be mounted on five separate microscope slides and care had to be taken during the preparation to ensure that the same plane of section was maintained between the separate sections. After investing in polyester resin, the molar fragment was cut to a 1 mm thick section on a high-speed saw. The thick section was cut into



Fig. 1. *Mammuthus columbi* MSL1083 molar fragment before sectioning.

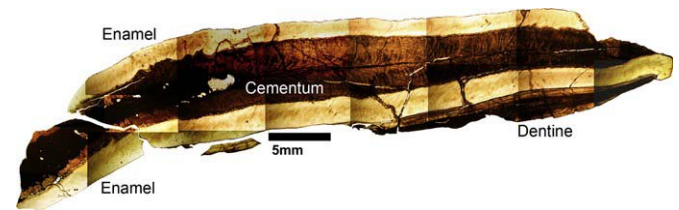


Fig. 2. Montage of ground histological section of adjacent molar plates from *Palaeoioxodon cypristes*. The dentine and enamel of the more complete plate in the lower part of the picture are separated from the adjacent partial plate by cementum. All measurements reported in the text were made in the more complete plate.

five pieces and each was fixed to a microscope slide with dental sticky wax. The sections were lapped on a Logitech (Glasgow, Scotland, UK) PM2 lapping machine with 3 mm alumina suspension, taking care to ensure that the same thickness was removed from each section. The lapped surfaces were bonded to microscope slides and lapped to a thickness of 100 µm from the other side, polished with 1-µm diamond suspension and mounted with cover slips. After mounting, accentuated lines could be identified from one section to another, confirming that the plane of section was equivalent between the five sections (Fig. 3).

The daily enamel secretion rate (DSR), the extension rate, and the total plate formation time were calculated from the histological sections using an Olympus BX51 microscope mounted with a Q-Imaging Micropublisher 3.3 RTV camera and Improvision Openlab 5.0.2 image analysis software, adapting the method described by Dirks et al. (2009). Fig. 4 illustrates the process in the occlusal enamel of the *P. cypristes* plate. In the *P. cypristes* section, an accentuated line was identified in the occlusal enamel above the dentine horn that could be followed back to its intersection with the enamel dentine junction (EDJ). The distance from the dentine horn to the accentuated line was measured along an enamel prism. Care was taken to follow the prism as it decussated rather than measuring along straight lines. Measurements were made between daily cross striations along the enamel prism and the mean DSR was calculated. Although a single prism was apparently followed on the image, prism decussation may have resulted in measurement along the local trend of prism direction rather than a single prism. The distance from the dentine horn to the accentuated line was divided by the mean DSR to obtain the number of days that it took for the tooth to grow to the size represented by the area beneath the accentuated line and its intersection with the EDJ. Because each accentuated line is a reflection of the surface of the forming plate at a particular moment in time, this method measures both the increase in the thickness of the plate and its height simultaneously and permits an estimate of total plate formation time. The distance along the EDJ from the dentine horn to the intersection of the accentuated line was measured. This distance was divided by the number of days of enamel formation to obtain the extension rate, the rate at which the plate grew in height each day. The process was repeated at the point where the accentuated line intersected the

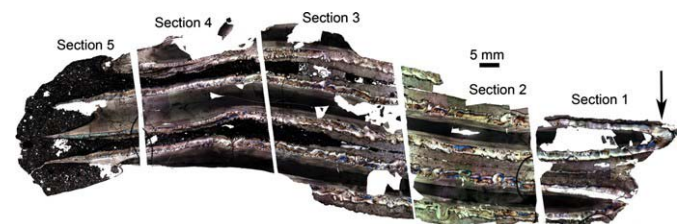


Fig. 3. Montage of five ground histological sections of adjacent molar plates from *Mammuthus columbi*. The arrow points to the central plate in which the measurements reported in the text were made.

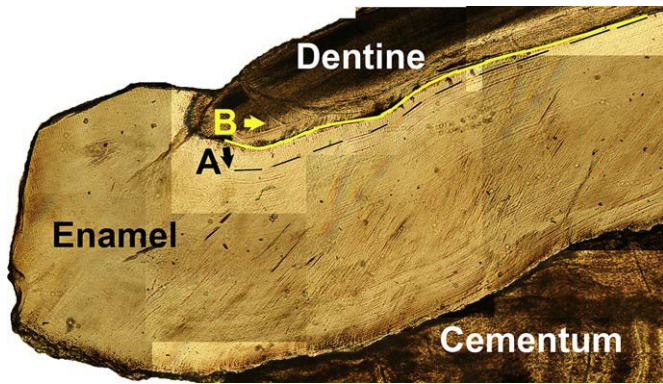


Fig. 4. Montage of occlusal molar plate from *Palaeoloxodon cypristes* at 16x magnification, illustrating the method for determining extension rate. 'A' represents the measurement made along the prism from the enamel dentine junction (edj) to the marked accentuated line. The mean daily secretion rate (DSR) is determined along the prism by measuring the distance between daily cross striations. 'A' is divided by mean DSR to determine the number of days of plate formation (C) when the forming front of enamel was at the accentuated line. 'B' represents the measurement along the edj from the measured prism to its intersection the accentuated line with the edj. B/C yields the daily extension rate.

EDJ, measuring along a prism to another accentuated line visible in the lateral enamel of the plate that could be followed back to its intersection with the EDJ. The entire process was repeated until the time it took to form the entire plate was determined, as well as the extension rate at which it grew. The maximum errors in plate formation time and extension rate were calculated from the standard error of cross striation measurements.

A similar procedure was carried out on the *M. columbi* sections, only beginning at the bottom of the plate and working upwards to the occlusal enamel. Because striae of Retzius passed over more than one section in the *M. columbi* plate, local extension rates for each section were determined by following the point of intersection of an accentuated line toward the occlusal surface as far as possible within each section. The mean DSR was calculated from the edj to a point on the accentuated line within the same section and the extension rate calculated from the point where the DSR was calculated back to the intersection of the accentuated line with the edj. The duration of the time for formation of each section was calculated separately by dividing the height of the plate along the EDJ in each one by the local extension rate for that section. The total plate formation time was calculated by summing the values for each of the five sections. It was not possible to determine an extension rate for section 2 because no accentuated lines were visible intersecting the edj in that section, so the mean value between section 1 and 3 was used.

3. Results

Daily enamel secretion rate was similar in both *M. columbi* and *P. cypristes* (see Table 1). In both taxa, ameloblasts appear to secrete enamel between 2 and 5 μm daily.

Table 1
Daily enamel secretion rate (microns per day) in *Mammuthus columbi* and *Palaeoloxodon cypristes* measured as distance between cross striations.

	<i>Mammuthus columbi</i> (n = 92)	<i>Palaeoloxodon cypristes</i> (n = 89)
Mean	3.5	3.2
Standard Deviation	0.5	0.6
Standard Error	0.1	0.1
Minimum	2.3	1.9
Maximum	4.7	4.7
Confidence Interval (95%)	0.1	0.1

Table 2
Cumulative plate formation time, cumulative height and daily extension rate in *Palaeoloxodon cypristes*.

Cumulative formation duration (days)	Cumulative formation duration (years)	Cumulative plate height (mm)	Extension rate (mm day)
135	0.37	4.65	34.4
371	1.02	11.85	30.7
761	2.08	23.10	28.7
1188	3.25	34.45	26.6
1696	4.65	40.57	12.0
2141	5.87	50.96	23.3

Although the height of the *P. cypristes* plate before sectioning was 60.5 mm, along the EDJ on the section itself, it measured 53.56 mm. The difference arises because it is a measure of the internal surface of the enamel, rather than the external surface measured before sectioning. Table 2 gives the extension rate along the plate as it increased in height during its formation and the plate formation time at each measured height. The measured heights are a reflection of the points of intersection of clearly visible accentuated lines in the enamel rather than equally spaced intervals along the EDJ. Plate formation initiated at 34.4 mm per day and gradually dropped to 12.0 mm per day when the plate had reached 40.57 mm in height, then speeding up to 23.3 mm per day toward the end of plate formation at 50.96 mm. If the final 2.6 mm grew the rate of 23.3 mm per day, the plate formation time of the incomplete plate would be around 6.2 years. The maximum error in plate formation time along each measured segment was 15 days and 1.1 mm per day in extension rate. It is unknown how much of the broken plate was lost, but the height suggests that the fragment is almost complete.

The height of the *M. columbi* plate was 180.89 mm along the EDJ, slightly more than three times the height of the *P. cypristes* plate. Similarly, this is less than the height of the plate on the external surface before sectioning of 193.3 mm. Table 3 gives the height and average extension rate for each of the five sections, as well as the cumulative height of the plate and its plate formation time as it reached each value of cumulative height. The maximum error in plate formation time along the five sections was 20 days and 1.9 mm per day in extension rate. The extension rates in *M. columbi* are around twice as fast as in *P. cypristes*, ranging from 62.5 mm per day in the most occlusal section down to 32.3 mm per day in the most cervical section. Thus, the *M. columbi* plate grows to three times the height of the *P. cypristes* plate at twice the daily rate of increase. The incomplete *M. columbi* plate is estimated to have taken 10.6 years to form. As in *P. cypristes*, it is unknown how much of the *M. columbi* plate was left to form at the time of death, but the height of the plate suggests that it was almost complete. Fig. 5 illustrates growth in height against age in both taxa.

4. Discussion

Certain aspects of plate growth are similar in *M. columbi* and *P. cypristes*. The amount of enamel secreted daily by individual

Table 3
Cumulative plate formation time, cumulative height and section extension rate in *Mammuthus columbi*.

	Cumulative formation duration (days)	Cumulative formation duration (years)	Cumulative plate height (mm)	Section extension rate (mm day)
Section 1	518	1.42	32.41	62.5
Section 2	1100	3.01	60.40	48.1
Section 3	2053	5.62	120.79	37.9
Section 4	3002	8.22	153.49	34.4
Section 5	3851	10.55	180.89	32.3

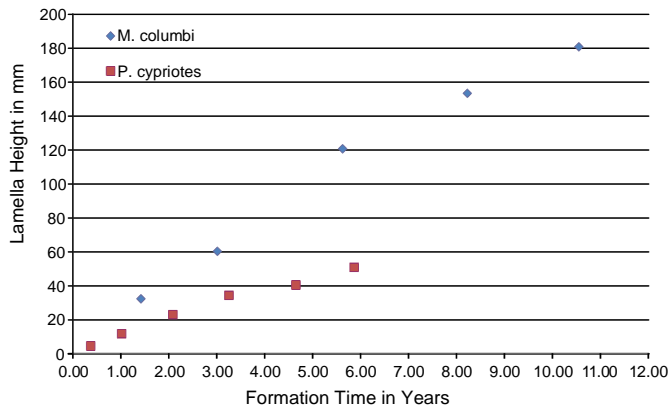


Fig. 5. Growth in plate height plotted against formation time in years for *Mammuthus columbi* and *Palaeoloxodon cypristes*. Both height and rate of growth are higher in *M. columbi*.

ameloblasts is similar in both taxa, ranging from just over two to just under five microns. This suggests that the differences in the plate formation time between the elephantid taxa are more likely to be related to differences in the extension rate rather than the secretion rate. Similar enamel secretion rates are reported for the Pliocene taxon, *E. recki* (Bromage et al., 2002). Daily secretion rate is reported to be higher in some artiodactyls and perissodactyls than in the elephantids. For example, Tafforeau et al. (2007) reported daily secretion rates of around 10 mm in the cuspal enamel of two fossil rhinoceros species, *Brachypotherium stehlini* and *Diaceratherium aurelianense*, although in extant horses, mean DSR is reported to be around 5 mm (Hoppe et al., 2004). In the extant sika deer, mean DSR is 10.6 mm (Iinuma et al., 2004) while in the extant sheep, it is 11.6 mm (Jordana and Köhler, 2011). In the fossil bovid, *Myotragus balearicus*, an island dwarf like *P. cypristes*, mean DSR is 9.3 mm (Jordana and Köhler, 2011). Daily enamel secretion rates in two species of Paleocene phenacodontids, a family of “archaic ungulates” or “condylarths,” are between 2 and 5 mm (Dirks et al., 2009), as in the proboscideans. Interestingly, phenacodontids have been hypothesized to be members of the afrotherian clade, along with elephants, while artiodactyls and perissodactyls are members of the laurasiatherian clade (Asher, 2007). The daily secretion rate of enamel is likely to be dependent on a complex interaction of tooth size, morphology and life history, however, with phylogeny influencing those factors rather than DSR directly.

In both elephantid taxa, the extension rate decreases steadily from the initiation of plate formation at the occlusal surface of the tooth to the cervical region, as has been reported for several taxa, such as fossil rhinos (Tafforeau et al., 2007), *M. balearicus*, extant sheep (Jordana and Köhler, 2011), chimpanzees, and humans (Dean, 2009, 2010). In *P. cypristes*, however, there is an increase in extension rate close to the end of plate formation. The *M. columbi* plate was still forming, and extension rates may also increase at the end of plate formation in that taxon as well. The differences in methods necessitated by the height of the *M. columbi* plate, with local extension rates for each section, may also mask any small changes in extension rate. There are significant differences, however, in the rate at which the plates increase in height between the two elephantid taxa, suggesting differences in the relative rate of tooth formation. The molar plate from *M. columbi* was almost three times the height of the plate from *P. cypristes*, yet it grew to that height in only twice the time it took for the *P. cypristes* plate to form. The plate extension rate in *M. columbi* started at almost twice that in *P. cypristes* and remained at almost twice the rate of *P. cypristes* at the end of plate formation.

What do these differences in extension rate mean? These data are not enough to determine whether the differences are related to the size of the elephant, the size of the teeth, or whether they are taxon specific. Without more data from other taxa, it cannot be determined if mammoths grow their teeth relatively quickly compared to other proboscideans or if dwarf elephants grow their teeth relatively slowly. Do the molar plates of *P. antiquus*, the large ancestor of the Cyprus dwarf, have extension rates similar to that of *P. cypristes*? Do dwarfed mammoths, such as the Channel Island dwarf *Mammuthus exilis*, have high extension rates? The data presented in this study are not enough to answer these questions, but other lines of evidence suggest possible answers to the questions and potential avenues for further research.

Does the relatively slow extension rate of *P. cypristes* reflect a slow rate of tooth formation, and if so, is this indicative of a relatively slow life history or long life span? Palkovacs (2003) presents an explanation for island dwarfing in which lack of predation pressure reduces extrinsic mortality and reduced resource availability reduces growth rate. Under these conditions, the reaction norm for size and age at maturity shifts, resulting in a smaller body size with a relatively late age at first reproduction. In a study utilizing bone histology, Köhler and Moyà-Solà (2009) suggest that the insular dwarf bovid *Myotragus* made a shift to an unusually slow life history strategy, with a prolonged juvenile period and lifespan, as part of an adaptation to an energy-poor island environment. They also suggest that this may have been true of insular dwarf elephants.

Dwarfing in elephants, however, has been suggested to be an outcome of a shift to a faster life history strategy than in their large mainland ancestors (Bromage et al., 2002; Raia et al., 2003; Raia and Meiri, 2006). Bromage et al. (2002) draw on Charnov's (1993) theoretical perspective on life history, in which extrinsic mortality determines when production should switch from growth to reproduction and juvenile mortality is density dependent. Bromage et al. (2002) suggest that extrinsic mortality in small founder populations would have a profound effect and favour an earlier age at first reproduction at smaller body sizes in large mammals on islands, such as elephants and hippopotamuses. Individuals who grow more slowly are more likely to die before reproducing while lack of predation would mean lack of selection for maintaining large body size. Once size reduction occurred, density dependent juvenile mortality would maintain viable population sizes. Raia et al. (2003) examined the age structure of *Elephas falconeri* remains from Spinagallo Cave in Sicily, a dwarfed elephant of 100 kg, a body mass half that of *P. cypristes*. They suggest a shift toward the faster end of the fast-slow life history continuum in this island dwarf due to an increase in reproductive effort in conditions of seasonal food abundance rather than resource deprivation. This led to reproduction at smaller body sizes, with first reproduction occurring at three to four years of age and a life span of 26 years. Raia and Meiri (2006) carried this further by suggesting that there is selection for small body size in insular ungulates because resources normally used for growth in the presence of predation and competition can be allocated to reproduction when these are reduced.

Current work on plate formation in *P. antiquus*, the mainland ancestor of *P. cypristes*, may help to resolve whether these hypotheses of slowed versus accelerated life histories are conflicting or whether more than one strategy has evolved to result in island dwarfing.

Based on its body mass, *M. columbi* would be expected to have a slower life history than extant elephants. In an allometric study, Shipman (1992) calculated age at first reproduction in *M. columbi* as 12.9 years, gestation as 2.5 years and a lifespan of 90.1 years. Does the relatively fast rate extension rate of plate formation in

M. columbi reflect rapid tooth growth and a relatively fast rate of overall growth in this extremely large elephantid, or in *Mammuthus* generally? Plate extension rate is unknown at this time in other species of mammoths. An allometric explanation, however, may apply to the relatively fast extension rates in this large elephant. Elephantid evolution has been characterized by an evolutionary trend toward increased hypsodonty (Maglio, 1973). In *E. recki* from the Pliocene of Africa, life history variables, including lifespan, are reconstructed to be similar to those in *M. columbi* (Shipman, 1992), yet crown height is lower (Maglio, 1973). If lifespan and dental eruption were similar in elephants of the same body mass, then increases in hypsodonty could require higher extension rates to form a plate in the same length of time as in a lower crowned tooth. It may be that there is an allometric relationship between crown height and extension rate, with higher crowned teeth having relatively faster rates, both intraspecifically within the tooth series, as height increases from dp2 to M3, and between species with different degrees of hypsodonty. Mandibular teeth are lower crowned than maxillary teeth and may also have lower extension rates. Further investigation of plate extension rates will help to resolve this (Dirks and Bromage, in prep).

5. Conclusions

This study raises more questions than it answers but is a first step toward a more precise understanding of differences in dental development between proboscidean taxa. This paper has introduced a new method for determining the timing of plate formation. Because DSR is similar in both *M. columbi* and *P. cyriotes*, it appears that extension rates are the primary mechanism in creating teeth with different crown heights in elephantids. Further research is required to understand more about intraspecific differences between teeth in the molar series and interspecific differences. The ultimate goal is a method that will allow for precise aging of individual specimens and thus a better understanding of the evolution of life history in these large mammals.

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