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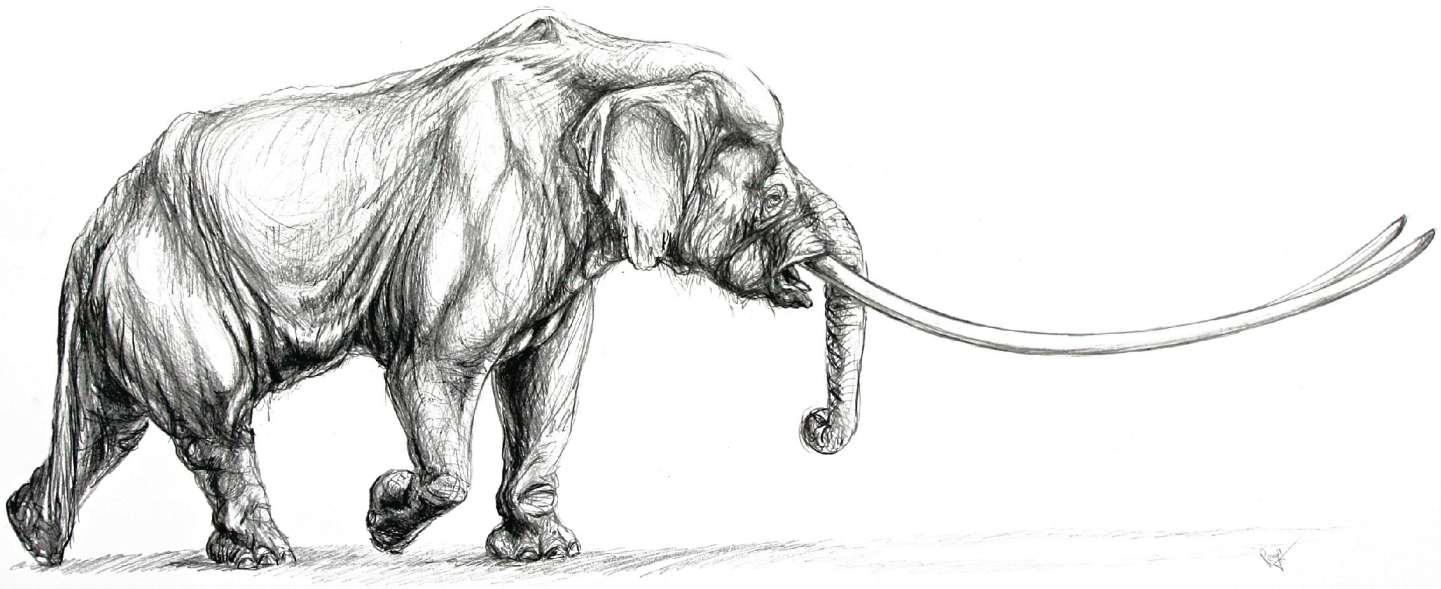

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ABSTRACT BOOK

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MicroCT analysis of mandibular tusks from the Ziegler Reservoir mastodons

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Ever-growing proboscidean tusks provide remarkable opportunities to investigate life histories of fossil individuals. X-ray computed tomography (CT) of tusks shows seasonal variability in dentin density and expands our ability to characterize tusk growth at annual and subannual scales. Complete microCT scans of twenty mastodon mandibular tusks from male and female adults as well as adolescents and juveniles from the Ziegler Reservoir fossil site (ZR; ranging from 130,000 to 80,000 yrBP) show distinct, regularly repeating radiodensity cycles over extended growth intervals (Fig. 1A). We interpret these as annual growth increments based on correspondence to patterns of structural and compositional variation that they share with annual increments documented in premaxillary tusks (e.g. Fisher, 1987, 2001; Koch et al., 1989), and we use them to compare dentin growth rates through life and between individuals.

In some ZR tusks density features are clear enough to enable direct volume measurement of annual increments in dentin growth (Fig. 1B). To streamline the process and incorporate specimens for which increment volumes are more difficult to measure directly, we used increment

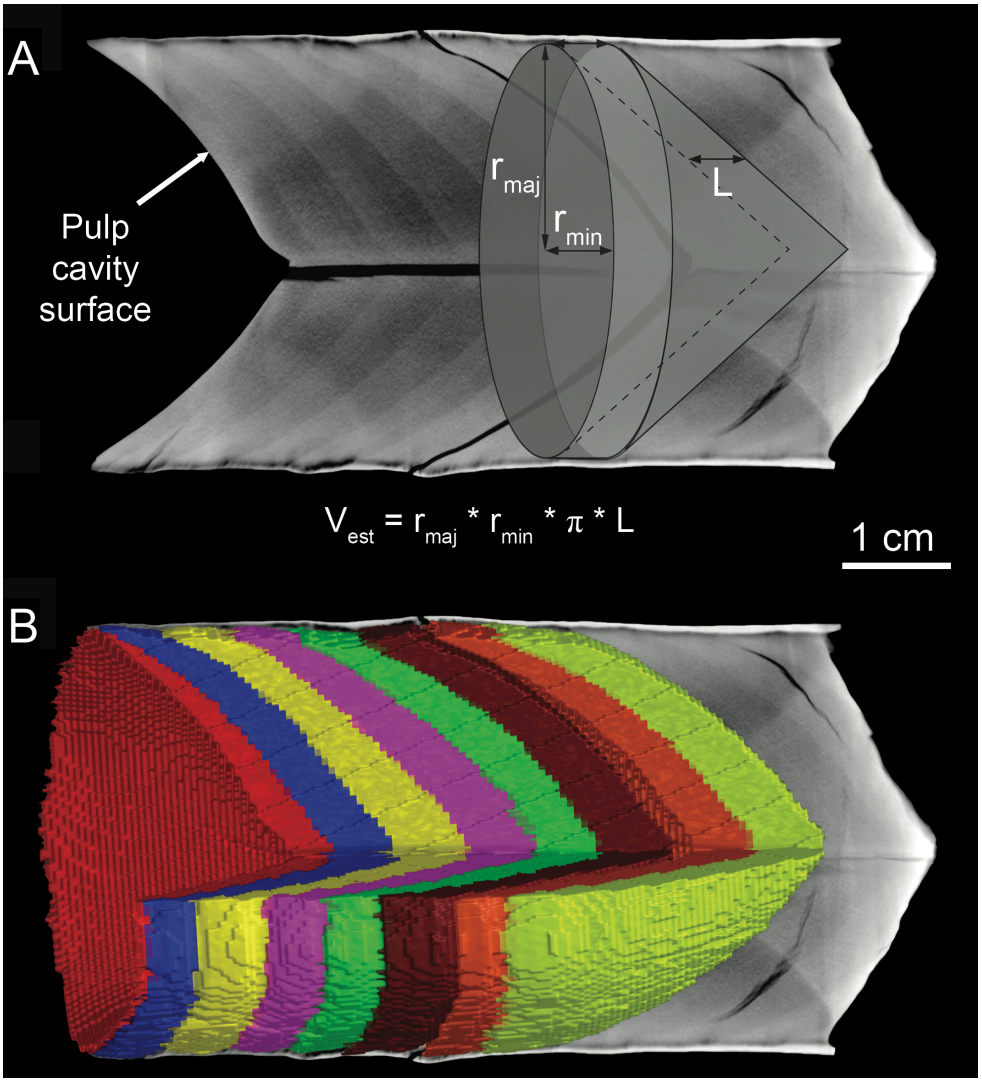

Fig. 1. *Mammut americanum* mandibular tusk from Ziegler Reservoir site in Colorado, USA; field no. 60.057 (Denver Museum of Nature & Science). **A**, virtual 2D longitudinal slice through the tusk axis projected from 3D microCT data showing radiodensity variation. Each gradual transition from dark (low radiodensity) to light (high radiodensity) defines a zone that parallels the pulp cavity surface and represents a year of growth. Linear measurements taken from 2D projections of CT data provide a close approximation of increment volumes. **B**, segmentation of microCT data enables direct volumetric measurement of annual growth increments (years distinguished by color).

V_{est}, estimated increment volume; **L**, increment length measured along a line half-way between axis and CDJ; r_{maj}, half the major diameter (usually dorsoventral) of the tusk at location of increment length measurement; r_{min}, half the minor diameter (usually mediolateral) of the tusk at location of increment length measurement.

volume estimates to compare growth series between individuals. Estimates were calculated using linear measurements from two-dimensional virtual slices of CT data and closely approximated measured volumes when comparisons were possible (Fig. 1A). The relatively simple curvature and regular cone-in-cone geometry of mastodon mandibular tusks contribute to the precision of volume estimates in our study, but we see potential for this metric as an alternative to linear increment measurements in large tusks and others for which we do not have complete three-dimensional CT data.

Comparisons between CT scans and thin-sections demonstrate that first-order (annual) CT increments and first-order thin-section increments are roughly equivalent for ZR mandibular tusks. Scans of premaxillary tusks and molars of proboscideans from various other sites also show density features that parallel other first-order features in the tusks. In addition to first-order features, some CT scans of ZR and other tusks display distinct changes in density within annual increments. In some cases, year-to-year consistency in these subannual variations likely reflects variation related to seasonal climatic and/or migratory patterns. In other cases, intra-annual variation is less consistent and is more likely a result of climatic perturbations, life history events (such as pregnancy in females and musth in males), or pathological conditions that could alter parameters of tusk growth.

Extended series of estimated first-order CT increment volumes in ZR mandibular tusks, which in some cases cover more than twenty years of growth, show sexual differences, ontogenetic patterns, year-to-year variability, and intra-annual timing of death. These series also present an opportunity to quantify growth variability using mean sensitivity (MS), a metric that has been employed in dendrochronology to assess environmental stress in tree populations (Fritts, 1976; Laxson, 2011). Further research is needed to determine if MS thresholds for recognizing stress in trees provide useful guidelines for interpreting variation in proboscidean tusks, but differences in MS between ZR individuals at least indicate relative levels of environmental stress within the sample population.

Recent advances in CT technology have made it more accessible, leading to increased use by paleontologists, but we are just beginning to realize its potential contributions to studies of fossils. Further work is necessary to establish mechanistic models detailing the causes of common patterns of radiodensity variation in tusks, but our extensive CT work on ZR mastodon mandibular tusks demonstrates that analysis of variation in dentin X-ray attenuation is a useful addition to existing modes of tusk analysis.

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