

Learning Science Through Research Published by the Keck Geology Consortium

LONG BONE HISTOLOGY OF THE LARGE PALEOGENE MAMMAL CORYPHODON

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INTRODUCTION

Fifty-six million years ago, at the boundary between the Paleocene and Eocene epochs, the Earth's climate increased by around five to eight degrees Celsius for over a hundred thousand years (McInerney & Wing, 2011). This event, known as the Paleocene-Eocene Thermal Maximum (PETM), had a major impact on the biota, and understanding these impacts is of considerable interest due to the parallels between this event and modern anthropogenic climate change. One of these impacts is a dwarfing event that can be seen in several genera that existed during this event (Gingerich, 2003). One animal that dwarfed (albeit after the PETM) is Coryphodon, a genus thought to be the earliest mammal to evolve a large body size, at over 500 kg (Uhen and Gingerich, 2003). Its large baseline size and extreme abundance in the fossil record make it a promising case study to examine many body-size-related questions. Previous work on Coryphodon body size has been based on estimates of tooth size, and appears to indicate a dwarfing event in the Wasatchian-3 biochron, several hundred meters above the PETM rocks (Fig. 1; Uhen & Gingerich 1995). Before using bone histology to gain a deeper insight into the evolution of body size in Coryphodon, the microanatomy of their bones needs to be investigated and described.

There are many aspects of bone histology that are useful in learning more about an animal. Bones are often filled with canals that house nerves and blood vessels. These canals are oriented in different ways in different bones, and the organization of these canals can give insight into the rate of bone growth. Another indicator of bone growth rates is the appearance of



Figure 1. Body mass of Coryphodon (as estimated by molar size) versus the stratigraphic height for specimens in the northern Bighorn Basin (based on data given in Uhen and Gingerich, 1995). Red line is a smoothed average of the values. The PETM occurs around 1500 m.

the bone tissue itself. Bone tissue ranges from slowgrowing parallel fibered bone, to lamellar bone, to fast-growing woven bone. Another feature that many vertebrates exhibit is an inborn tendency to briefly slow the addition of new bone to the outer surface once a year, creating a thin dark ring of dense bone for each year that the animal has been alive, called a line of arrested growth (LAG). Alternatively, growth continues without halting as drastically, creating an annulus. Often times, bone is remodeled (usually starting from the center of the bone), absorbing and redepositing bone tissue. If and when an animal reaches its full size, bone growth will slow, but LAGs will still be laid down, creating an outer ring of tightly packed LAGs called an external fundamental system (EFS) (Padian & Lamm 2013). In addition to its usefulness in analysis of an animal's lifestyle, bone histology

can be used in determining the minimum ages of specimens, the relative rate at which they grew, and whether or not they had reached adulthood prior to death. The purpose of this publication is to explore all of these potential applications of *Coryphodon* bone histology.

METHODS

Here I investigate the bone histology of three Corvphodon specimens from the University of Michigan (UM), Yale Peabody Museum (YPM) and one collected during the Keck Wyoming field 2019 field season (CORY). These specimens consist of a femur (UM 110898) and two tibiae (CORY 19-22; YPM 35317). The morphology of these bones was preserved through molds, casts, and photogrammetry, prior to preparing thin sections. 3D models of the bone were created through photogrammetry. Thin sections were made on a low-speed diamond saw by making two closely spaced cuts across the bone at a position as close to the midshaft as possible. This wafer was sanded briefly at 600 grit, affixed to a plexiglass slide with cyanoacrylate, and ground to a thickness of about 100 microns. Thin sections were photographed using a Zeiss Axioimager microscope using Zen2 software, producing high-resolution montaged images.

The bone histology is described using terminology established by Padian and Lamm (2013). Patterns of vascularization (reticular, plexiform, laminar, radial, and longitudinal), when not obscured by decomposition or diagenesis, were identified by the directions of the neurovascular canals, which appeared as dark grooves crisscrossing the section (or as holes in the bone in the case of longitudinal canals). LAGs were identified as dark lines that represent a break in tissue around osteons. An EFS, if present, appears as many LAGs packed together near the outer surface of the bone. Annuli were identified as regions of slow growth that stretched around the entire bone.

RESULTS

UM 110898 (femur)

This specimen's histology is well preserved, with

decomposition limited to the areas surrounding neurovascular canals (Fig. 2A). The transition from porous inner bone to dense cortical bone is somewhat abrupt, with the cortex occupying the outer third of the bone thickness. The middle of the bone was not microscopically photographed due to file size restrictions of the microscope. The outer cortex of bone contains varying degrees of neurovascular canal infiltration, with some regions having low porosity and others displaying extensive plexiform or reticular vascularization patterns, suggesting somewhat variable rates of bone growth depending on the region of the bone. The overall bone vascularization pattern is reticular in organization, except for the outermost cortex, which is more laminar in nature. A thin layer of many tightly packed dark rings is present around most of the bone's outer edge, likely representing an incipient EFS. However, some neurovascular canals occasionally pierce the outer bone surface all the way around the bone, suggesting that growth had not fully stopped.

CORY 19-22 (tibia)

This specimen's histology is also well preserved, save for a few major cracks and missing parts of the cortex (Figs. 2B, 3). The bone has been crushed taphonomically such that the cortex has been partially pushed into the medullary cavity, and some of the cortex has been lost (Figure 2). The cortex of the bone is relatively thick and dense. The larger cavities in the center are relatively small, and they quickly



Figure 2. Thin sections examined in this publication: (A) UM 110898 femur (B) CORY19-22 tibia, and (C) YPM 35317 tibia.



Figure 3. A closeup of the microanatomy of the CORY19-22 tibia section.

transition into small, circular osteons. Most of the osteon edges are obscured by decomposition, making it unclear whether they are primary or secondary. However, sparse remodeling can be observed through the inner half of the cortex. A minimum of four LAGs and/or annuli can be seen, with a possible fifth LAG intersecting the bone surface. This suggests an animal of at least four to five years old, although decomposition and Haversian remodeling have likely obscured more LAGs from earlier in development. The gap between the third and fourth LAG from the center is much larger and filled with much more reticular bone, suggesting a period of rapid growth relative to the slower growth in other stages in life, when LAGs are more closely appressed. No clear EFS can be seen.

YPM 35317 (tibia)

This bone is uncrushed, although most of the inner bone structure has been decomposed, save for the margin near where the periosteum would be in life (Fig. 2C). The bone is overall dense, with the porous inner region being composed of small canals all the way through. At around halfway to the bone surface, there is an abrupt transition from porous bone to dense cortical bone with few canals. The overall vascularization pattern is longitudinal with some circumferential and radial anastomoses. Within the outermost millimeter or so of the cortex, a single inner LAG is present, followed externally by a series of at least eight dark lines packed against the outer surface, representing an EFS.

DISCUSSION

Even with the varying quality of preservation, most major elements of bone histology were identified in the sections, including the presence of LAGs, external fundamental systems, secondary remodeling, variable vascular patterns, and porous medullary cavities. Beyond comparison with other genera, it is clear that *Coryphodon* bones contain the necessary histological data needed to compare bone growth between *Coryphodon* specimens of different sizes, time periods, and localities.

This study demonstrates that secondary remodeling obscures about the first half of the growth record in *Coryphodon* thin sections. This makes it difficult to determine the absolute age of an individual, but a minimum age can be obtained. However, there are many techniques that can calculate the number of LAGs lost during ontogeny, ranging from simple estimations to complex modeling approaches (e.g., Lee & O'Connor 2013).

In sum, there are many future applications of the study of *Coryphodon*'s bone histology, from learning more about the animal's life to answering broader questions about how body size changed over time, and what developmental mechanisms caused this change.

ACKNOWLEDGMENTS

This research is supported by the Keck Geology Consortium and the National Science Foundation under Grant No.1659322. Thanks to D. Brinkman and M. Fox (YPM) and P.D. Gingerich, J. A. Wilson, and A. Rountrey (UM) for collections access and to my research advisors (Michael D'Emic, Simone Hoffmann, John Merck) and fellow Keck researchers: Emily Randall, Danika Mayback, Richard Gonzalez, Isaac Sageman, and Michael Ford.

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