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BODY SIZE EVOLUTION OF THE LARGE PANTODONT MAMMAL CORYPHODON DURING PALEOGENE HYPERTHERMAL EVENTS

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INTRODUCTION

Climate change affects the resources available to animals, impacting factors such as their geographic ranges, growth rates, and reproductive behaviors. These effects can be measured in in the fossil record and used to predict ecosystem change in the future (Barnosky et al., 2017). One of the best-studied examples of past climate change and its effects is the Paleocene-Eocene Thermal Maximum (PETM) at about 56 Ma, which caused massive perturbations in floras (Wing et al., 2005), fluvial landscapes (Foreman et al., 2012), and mammalian evolution (Gingerich, 2003). The PETM was followed by a long-term warming trend during the early Eocene that culminated with the Early Eocene Climatic Optimum (Zachos et al., 2008). This long-term warming trend was punctuated by 'hyperthermal' events similar to the PETM during the early Eocene (Abels et al., 2015). In response to the PETM and other hyperthermals, rapid and extreme mammalian dwarfing occurred (Gingerich, 2003; Secord et al., 2012, d'Ambrosia et al., 2017). It is unclear how mammals evolved their smaller body size in terms of growth pattern and duration. During our Keck project, our team studied the evolution of body size, growth, and paleoenvironment of the first mammalian megaherbivore, Coryphodon.

Coryphodon is known from hundreds of localities in precisely dated paleosols of the Bighorn Basin, and its bones and teeth preserve annual growth rings that allow individual specimens to be aged (Figures 1, 2). Unprecedented for a mammal at the time, *Coryphodon* reached the size of a small rhinoceros during the mid-Paleocene (Uhen and Gingerich, 1995). Shortly

after the PETM, it underwent a dwarfing event to half its body mass, only to return to its original size later in the Eocene (Figure 2A; Uhen and Gingerich, 1995; unpublished data). Corvphodon is severely understudied-though thousands of specimens exist in museum collections, only a handful of biogeographic, isotopic, and taphonomic studies have been conducted (e.g., Simons, 1960; Fricke et al., 1998; McGee, 2001; McGee and Turnbull, 2010; Dawson, 2010). We have gathered bone and tooth measurements from over 1,000 individuals from museums. Many of these specimens were collected during the "fossil gold rush" of the 1880s-1910s and lack precise provenance data. Therefore, we have begun targeted fieldwork to fill in spatiotemporal gaps in the Coryphodon fossil record, which our Keck students assisted us with to great success.

PROJECT GOALS

The overall goal of our Keck project was to understand the evolution of body size, growth, and paleoecology in *Coryphodon* in relation to environmental change. We did this by making thin sections of bones and teeth from museums and newly collected field specimens. Bones and a tooth-anchoring tissue known as cementum record annual bands, akin to tree rings, that allow age and growth rates to be estimated in extinct mammals (Kolb et al., 2015; Figure 2). With the students in our Keck group, we undertook four objectives: (1) collect *Coryphodon* specimens via quarrying and prospecting, (2) place our finds in spatiotemporal, paleoenvironmental, and taphonomic contexts, and (3) assess the age of each *Coryphodon* specimen with incremental growth line counts in



Figure 1. Study area. (a) Map of western United States highlighting area shown in detail in (b), which shows the studied locations within the Bighorn Basin.

bones and tooth cementum. With our students, we began to densely sample *Coryphodon* to assess growth patterns before, during, and after dramatic climate change events (i.e., hyperthermals).

Fieldwork took place in the Fort Union and Willwood formations (Figure 3) of the northern Bighorn Basin, which are composed of a more than 2,000 m thick sequence of fluvial, floodplain, and minor palustrine deposits (Bown and Kraus, 1981). These extensive strata have been the target of over a century of detailed paleontological fieldwork, resulting in the recovery of tens of thousands of vertebrate fossil specimens (Gingerich, 2003). Fossil-hosting ancient soil horizons can be resolved temporally to ca. 100,000-year time intervals (Gingerich, 2003; Secord et al., 2012). Coryphodon has been reconstructed with a semiaquatic lifestyle, inferred from anatomy and oxygen isotope data (Simons, 1960; Fricke et al., 1998), yet is found in a variety of facies (Uhen and Gingerich, 1995). By collecting detailed paleoenvironmental and taphonomic data with our Keck students, we are addressing the habitat of Coryphodon in more detail, with an integrative approach.

RESEARCH PROJECTS

The five research projects conducted in this study integrated data from stratigraphy, taphonomy, paleohistology, and anatomy with intensive fieldwork aimed at understanding the evolution of body size in *Coryphodon*, the first mammalian megaherbivore, on fine spatial scales. In the field, we prospected for



Figure 2. Femur and canine of Coryphodon showing annual growth lines.

and excavated fossils and created high-resolution stratigraphic columns. In the lab, students were trained in photogrammetry, molding and casting, fossil preparation, and bone and tooth histology.

Emily Randall (Wooster College) recorded geologic data from several mammalian biozones across the northern Bighorn Basin in order to infer the paleoenvironments in which *Coryphodon* lived. She included data from paleosols and nodules to infer the moisture content of soils, capturing changes to the ecosystems that *Coryphodon* inhabited through the Paleogene.

Grant Bowers (University of Maryland) studied the bone histology of *Coryphodon* in order to determine its growth rates and longevity. Grant analyzed the microstructure of some of the bones the Keck team discovered and thin sectioned, after their morphology had been properly preserved through molding, casting, and photogrammetry. Grant compared his thin sections with those from extant animals to give us a better understanding of *Coryphodon* habitats and life



Figure 3. Keck Coryphodon field team at the site of a newly discovered specimen.

history.

Richard Gonzalez (University of Texas at San Antonio) analyzed scaling among *Coryphodon* bones in order to predict body mass from isolated elements, which are commonly recovered in the fossil record. Richard found that some isolated elements can be used to predict body mass more reliably than it had been predicted in the past, which will allow characterization of its body mass evolution through time.

Danika Mayback (Illinois State University) studied the histology of cementum, the tissue in *Coryphodon* that helps to anchor the teeth to the jaws (also found in our jaws). There has been a recent appreciation for how cementum can be used to estimate age in extinct animals; it has commonly been used as a technique in forensic anthropology and wildlife management. Danika found that some *Coryphodon* individuals lived long lives, upwards of 30 years. Her work forms a baseline for how to assess age and data quality from cementum in *Coryphodon*.

Isaac Sageman (Northwestern University) took nearly 100 samples from over a dozen *Coryphodon* sites in the basin and measured inorganic and organic carbon percentages and bulk carbon isotope values in order to better characterize the depositional environments of *Coryphodon* throughout its evolution and constrain our sampling temporally.

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