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Distribution and Paleobiology of Hibernation in Fossil Ground-Dwelling Squirrels from the Great Plains, USA

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HONS 497
Honors Thesis

Distribution and paleobiology of hibernation in fossil ground-dwelling squirrels from the Great Plains, USA

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March 30, 2016

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Primary Advisor Signature: [Signature]
Department: Biology
Abstract

Hibernation is a widespread phenomenon present across mammalian taxa, including in many ground-dwelling squirrels (family Sciuridae). Prior work has shown that a hibernation mark can be identified in the ever-growing incisors of these ground squirrels through surface inspection. In this study, we inspected fossil incisors, originating from the Great Plains, from the C.W. Hibbard collection at the University of Michigan for features associated with hibernation marks in modern species. We noted hibernation mark-like features in several fossil ground squirrel incisors from the genera *Otospermophilus*, “*Spermophilus*”, and *Urocitellus*, ranging stratigraphically from the early Pliocene to the late Pleistocene and providing the oldest known record of hibernation for ground squirrels.
Introduction

Hibernation is a phenomenon consisting of a decrease in metabolic activity along with a drop in body temperature and heart rate, characterized by a prolonged state of dormancy (Williams et al. 2014). Although hibernation is present across a wide range of mammalian taxa, it has been most extensively studied in the rodent family Sciuridae, which includes the ground squirrels and their relatives. Most genera of ground squirrels are capable of hibernation, but the ones relevant to our study include Otospermophilus (Oaks et al. 1987) and Urocitellus (Michener 1984). The geographic range of Otospermophilus has varied since the Pliocene, but today encompasses much of Mexico northward through much of the western United States (Oaks et al. 1987). Urocitellus can usually be found in central and western North America and also northeastern and central Asia (Helgen et al. 2009).

Studies with ground squirrels have shown that hibernation affects the growth of their ever-growing incisors. Incisors are made up of enamel and dentin deposits, and in rodents these deposits are laid down on a daily basis throughout the animal’s lifetime. The position on the incisor where the enamel meets with the dentin is known as the enamel-dentin junction (EDJ). This junction is characterized by a pair of reflective lines that run parallel to the EDJ in ground squirrels (Goodwin et al. 2005). Due to severe metabolic reductions during hibernation, the deposition of enamel and dentin is interrupted, creating physical abnormalities on the surface of the incisor that are visible under a stereo light microscope. These abnormalities attributed to hibernation (a hibernation mark) usually include a diagonal disruption to the pair of reflective bands on the medial surface of the incisor adjacent to the EDJ, irregularities in the medial enamel, depression in the dentin, and/or often fine and indistinct dentin increments (Goodwin et al 2005). The hibernation mark was first identified in marmots, genus Marmota (Rinaldi 1999) and subsequently confirmed in Urocitellus (Goodwin et al. 2005), Cynomys (Goodwin and Ryckman 2006), Ictidomys (Kisser 2009) and Spermophilus
This indicates the broad distribution of the hibernation mark across taxa of hibernating ground squirrels. Prior study of fossil ground squirrels has recorded hibernation as far back as the Pleistocene in Porcupine Cave, Colorado (Goodwin et al. 2005).

Data from stable isotope studies from the Great Plains characterized the Pliocene time period as being different in climate when compared to the modern-day environment. During the Pliocene-Pleistocene time period, there was a shift in climate and in plant ecology of the region, with isotope data showing a step-wise shift from warmer climate and C3-dominated habitat in the Pliocene to that of cooler climate and C4-dominated grasslands in the early Pleistocene (Fox et al. 2012a; 2012b). This shift in vegetation/climate is not well understood, but provides a broad framework for interpreting the paleobiology of fossil ground squirrels from the sequence.

Our study investigated fossil ground-squirrel incisors from the Claude W. Hibbard Pliocene-Pleistocene Mammalian collection from the University of Michigan Museum of Paleontology. This collection was chosen because it provided a rich source of fossils that was readily available to our study. Hibbard’s collection focused on the central United States, the Great Plains, and covered the Pleistocene-Pliocene time period, which ranges from 11,700 thousand to 5.3 million years ago based on the standard radiometric chronometry. Most of the fossils collected by Hibbard were concentrated in the Meade Basin of southwestern Kansas, but other fossils from Oklahoma, Nebraska, and Idaho were also included. The incisors were inspected for hibernation marks in order to elucidate the history of hibernation among ground squirrels of the region, set in context of changes in paleoenvironments.

**Methods**

The Claude W. Hibbard Collection was accessed at the University of Michigan Museum of Paleontology. The collection consisted of thousands of vertebrate fossils, including a diverse set of
rodent incisors, which included those of squirrels. We initially attempted to pull out isolated squirrel incisors from a large batch of rodent incisors, but found this to be unreliable. We then focused on specimens whose incisor was in or associated with a known squirrel jaw. Based on a refined search image, we were also able to identify a few additional isolated squirrel incisors for inspection.

All squirrel incisors were then analyzed under a light microscope for any physical abnormalities on the surface of the incisor that resembled a hibernation mark. A modern squirrel incisor with a known hibernation mark, and images of hibernation marks from prior work (Goodwin et al. 2005), were used as a comparison when identifying hibernation mark-like features on these incisors. These incisors originated from the Buis Ranch fauna in Oklahoma; Fox Canyon, Jones, and Rexroad 3 faunas in Kansas; the Sand Draw fauna in Nebraska; and the Hagerman fauna in Idaho.

The generic taxonomy proposed by Helgen and colleagues was applied when possible to fossil species; this taxonomy raised previous subgenera to genera, resulting in the elimination of *Spermophilus* from North America (Helgen et al. 2009). However, we refer to the genus “*Spermophilus*” in quotation marks for “*S.* meltoni due to the uncertainty of which genus it belongs to. This holotype was collected by Hibbard in 1965 from the upper part of the Keim Formation in Brown County, Nebraska and described by Skinner and Hibbard (Skinner et al. 1972).

For each specimen examined, the catalog number and locality were recorded along with a brief description of the incisor and its characteristics. A photograph was taken under the microscope if the specimen had a probable hibernation mark and when available, the dimensions of the incisors were obtained. After these incisors were analyzed, those with a possible hibernation mark were plotted geographically and stratigraphically to show physical locations and most importantly their location in time in relationship to each other.
Results

Incisors examined – We inspected 19 incisors from 6 localities ranging from Oklahoma in the South, to the Nebraska and Idaho in the north and northwest (Table 1). Of these specimen, four of them showed features similar to those caused by hibernation.

Descriptions of fossil incisors with a possible hibernation marks – The holotype for “Spermophilus” meltoni (UMMP 52167) from the late Pliocene Sand Draw fauna, NE had an abrupt disruption in the pair of reflective bands that run parallel to the EDJ on the medial side (Figure 1A). The disruption creates a diagonal feature in the upper reflective band. Fine dentin increments were also observed just basal to the diagonal (Figure 1B). An incisor of Urocitellus richardsonii (UMMP 56482) from the late Pleistocene Jones fauna, KS exhibited a slight depression in the dentin on its medial side, and irregularities in enamel adjacent to the EDJ associated with and just basal to the depression (Figure 2). The incisor of Otospermophilus rexroadensis (UMMP 60813) from the mid-Pliocene Rexroad 3 locality, KS exhibited a depression in the dentin on the medial side of the incisor with narrow increments that looked similar to features seen on incisors with hibernation marks. A short diagonal disruption in the pair of reflective lines of the EDJ was also evident just apical to the zone of depression (Figure 3). An incisor of Otospermophilus sp. (V56578) from the Pliocene Buis Ranch fauna, OK displayed some abnormalities of the reflective bands of the EDJ but did not display other physical features usually associated with hibernation (this incisor is not pictured). Fossils with a probable hibernation mark ranged from northern Oklahoma to northern Nebraska and from the early Pliocene to the late Pleistocene (Figure 5).

Discussion

While some of the incisors we examined showed a very probable hibernation marks – S. meltoni, U. richardsonii, and O. rexroadensis – the specimen of Otospermophilus sp from Buis Ranch, OK was
not as convincing because it lacked other abnormalities normally found in a hibernation mark (Goodwin et al. 2005). For the other incisors, there was a greater confidence level due to more than one feature usually observed in modern day marks, including the diagonal disruption in the medial surface of incisors’ enamel (Goodwin et al. 2005). Prior work has shown this feature in fossil *Urocitellus elegans* from the mid-to late Pleistocene (Goodwin et al. 2005). Our study documented hibernation in the middle Pliocene and thus provides the oldest record of hibernation in fossil ground squirrels.

We also provide the first record of hibernation in a pre-modern environment of the Great Plains. Currently, the ecosystem dominating the Great Plains is a moderate temperate grassland with a C-4 dominated plant ecosystem (Fox and Koch 2003). Although the paleoclimate of the Great Plains during the Pliocene is not well characterized, some studies have suggested that there was a warmer, more arid ecosystem in the central United States in contrast to today’s environment (Martin et al. 2008). Whatever the environment, we can assume it supported squirrels that employed hibernation during their life history even if warmer than the modern day environment. Of particular interest, the extinct species “*Spermophilus*” *meltoni* was a hibernator.

The Pleistocene brought about changes in the ecosystem and the climate that was present during the Pliocene. Climate cooled and a transition in the vegetation from a C3-dominated environment to a C4-dominated environment occurred (Fox et al. 2012a; 2012b). Therefore, it is no surprise that the incisor of *Urocitellus richardsonii* from the Pleistocene had a hibernation mark given the cooling climate of the later Pleistocene and the fact that the species is an obligate hibernator at present.

Our study could be pushed further by expanding coverage geographically. The stratigraphic time period can also be expanded earlier than the Pliocene to the Miocene or even earlier. Data from ancient environment studies can also be correlated with the newfound data with the intent to piece
together information and make a well-formed hypothesis about the climate during the Pliocene and what occurred during the Pliocene-Pleistocene ecological shift.

**Literature Cited**


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**Table 1 Data of incisors analyzed.** The table below provides a summary of information about the incisors that were analyzed, listed from earliest in the record to latest. The table displays the age and locality of the fauna analyzed, the genus of the ground squirrels whose incisors were analyzed in that fauna, the number of incisors analyzed (n), and some remarks (if necessary) about what was found for each location.

<table>
<thead>
<tr>
<th>Age</th>
<th>Locality</th>
<th>Genus</th>
<th>n</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early Pliocene</td>
<td>Buis Ranch, OK</td>
<td><em>Otospermophilus</em></td>
<td>4</td>
<td>UMMP V56578 with possible HM.</td>
</tr>
<tr>
<td>Early Pliocene</td>
<td>Fox Canyon, KS</td>
<td><em>Ictidomys</em></td>
<td>2</td>
<td>No incisors a had visible signs of a HM.</td>
</tr>
<tr>
<td>Mid Pliocene</td>
<td>Rexroad 3, KS</td>
<td><em>Otospermophilus</em></td>
<td>1</td>
<td>UMMP 60813 was wiggle free from jaw, had a clear HM.</td>
</tr>
<tr>
<td>Late Pliocene</td>
<td>Hagerman, ID</td>
<td>N/A</td>
<td>6</td>
<td>No incisors had visible signs of a HM.</td>
</tr>
<tr>
<td>Late Pliocene</td>
<td>Sand Draw, NE</td>
<td><em>Spermophilus</em></td>
<td>2</td>
<td>UMMP 52167 with HM.</td>
</tr>
<tr>
<td>Late Pleistocene</td>
<td>Jones, KS</td>
<td><em>Urocitellus</em></td>
<td>4</td>
<td>UMMP 56482 with HM.</td>
</tr>
</tbody>
</table>
Figure 1 "Spermophilus" meltoni holotype (UMMP 52167) from Sand Draw, NE. (A) Lower right incisor of "Spermophilus" meltoni holotype, in medial view. Apical to the right. Two slightly different orientations display (A) diagonal disruption of enamel adjacent to the EDJ (in box), and (B) fine increments towards the base of the incisor (surrounded by the dashed rectangle). Scale increments = mm.
Figure 2 Right lower incisor of *Urocitellus richardsonii* from Jones fauna, Kansas (UMMP 56482), in medial view, displaying the zone of depressed dentin (dashed polygon) and irregular enamel (arrow). Apical to the right. Scale increments = mm.
Figure 3 Lower right incisor of *Otospermophilus rexroadensis* from Rexroad 3 fauna, Kansas (UMMP 60813), in medial view. The dashed polygon outlines a depression in the dentin on the medial side of the incisor. Above the depression (seen in the panel on the top), there is an overlap of a new enamel sleeve over a pre-existing sleeve. Scale increments = mm.

Figure 4 Stratigraphic distribution of incisors with possible hibernation marks. The incisor specimen that had probable signs of hibernation were plotted stratigraphically below. The orange dot represents *U. richardsonii*, the purple dot represents the "*S." meltoni* holotype, the red dot represents *O. rexroadensis*, and the blue dot represents *Otospermophilus* sp.

<table>
<thead>
<tr>
<th>Period</th>
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</thead>
<tbody>
<tr>
<td>Quaternary</td>
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</tr>
<tr>
<td></td>
<td>Pleistocene</td>
</tr>
<tr>
<td>Tertiary</td>
<td>Pliocene</td>
</tr>
<tr>
<td></td>
<td>Miocene</td>
</tr>
</tbody>
</table>

*U. richardsonii*

"*S." meltoni"

*O. rexroadensis*

*Otospermophilus* sp.