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ABSTRACT

PALEOENVIRONMENTAL IMPLICATIONS OF SMALL-ANIMAL FOSSILS FROM
THE BLACK MOUNTIAN TURTLE LAYER AND ASSOCIATED LAYERS,
EOCENE OF WYOMING

By

JEREMY MCLARTY

Chair: H. Thomas Goodwin, Ph.D.

ABSTRACT OF GRADUATE STUDENT RESEARCH

Thesis

Andrews University

College of Arts and Sciences

Title: PALEOENVIRONMENTAL IMPLICATIONS OF SMALL-ANIMAL FOSSILS FROM THE BLACK MOUNTAIN TURTLE LAYER AND ASSOCIATED LAYERS, EOCENE OF WYOMING

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The Bridger Formation is an Early Middle Eocene deposit in southwestern Wyoming that preserves a rich record of life from North America. Some horizons within the Bridger Formation contain abundant fossil turtle shells, but turtle skulls are rarely found. Previous research focused on one of these fossil-rich horizons, the Black Mountain turtle layer, to develop a model for the abundance and taphonomic condition of the fossil turtles. The proposed model begins with a limestone layer deposited in a lake. Then, an influx of fine-grained volcanic ash (forming the Black Mountain turtle layer) was rapidly deposited into this lake likely causing the mass death of turtles in the lake and rapid (but not instantaneous) burial of the turtles. Subsequent units of the lithofacies

association were deposited as the lake was filled with sediment, eventually transforming into a floodplain environment.

Although the depositional model developed to explain the concentration of fossil turtles in the Black Mountain turtle layer envisions accumulation within a broad, shallow lake, subsequent investigation of the taxonomic makeup and taphonomic condition of small-animal fossils associated with the fossil turtles showed that terrestrial animals, especially lizards, were the most common taxa present and that these fossils were probably not transported into the system. These findings seemed puzzling in light of the lacustrine model because large numbers of terrestrial fossils would be unexpected in a lake deposit unless transported into the lake.

In the current study, I analyzed small-animal fossils from nine sites along exposures of the Black Mountain turtle layer to test the proposed model that the limestone and overlying mudstone were deposited in a broad, shallow lake. Small-animal fossils were identified as specifically as possible and assigned to ecological groups that were identified as either aquatic or terrestrial. The geographic and stratigraphic patterns of the fossils were compared to the predictions of the proposed lake environment. My findings confirmed that the presence of terrestrial fossils, especially lizards, was much higher than would be expected for a lacustrine deposition of the limestone layer and Black Mountain turtle layer. Sites towards the west had the highest proportion of terrestrial fossils, while sites to the east had the highest proportion of aquatic fossils. However, there was no clear gradient in the geographically intermediate sites. The majority of sites had a high proportion of terrestrial fossils in the basal limestone layer with little change in this proportion over time.

These findings contradict the proposed model of a lacustrine deposition for the limestone layer and Black Mountain turtle layer. An alternative depositional environment of a fluctuating paludal/lacustrine environment does account for several patterns observed in the small-animal fossils, but does not appear to account well for the fossil turtles. These findings highlight the need for further work in reconstructing the paleoenvironment of the Black Mountain turtle layer. This study also emphasizes the need for inclusion of small-animal fossil data in paleoenvironmental reconstructions.

Andrews University
College of Arts and Sciences

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THE BLACK MOUNTAIN TURTLE LAYER AND ASSOCIATED LAYERS,
EOCENE OF WYOMING

A Thesis
Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Jeremy A. McLarty
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CHAPTER 1

INTRODUCTION

The Bridger Formation is an Early Middle Eocene deposit in southwestern Wyoming. It contains a rich record of Eocene life from North America, including mollusks, fish, reptiles, birds, and a large diversity of mammals. The abundance and diversity of fossils found in the Bridger Formation has made it the focus of many studies for over 100 years (for example, Matthew, 1909; Murphey et al., 2018; Sinclair, 1906).

One of the first major studies of the Bridger Formation was by Matthew (1909), who sought to place its rich mammal fauna in stratigraphic and paleoenvironmental context. Matthew (1909) divided the Bridger into five horizons, A-E, with Horizon A as the oldest and Horizon E the youngest, and these stratigraphic divisions are still used today (Fig. 1). Matthew (1909) also hypothesized that the Bridger Formation represented a heavily forested flood plain that was subject to repeated flooding that formed large, shallow lakes.

Gunnell and Bartels (1994) further investigated the paleoenvironments of the Bridger Formation, drawing paleoenvironmental inferences from mammal and reptile groups found in the Bridger; and they concluded that the environment was warm and moist with dense forests. Moreover, they interpreted the lower and upper Bridger [Bridger A and C–E, respectively, of Matthew (1909)] as representing wetter, more poorly drained environments than the middle Bridger (Bridger B), which they interpreted to be drier.

Although Gunnell and Bartels (1994) interpreted Bridger B as drier than Bridger A and C-E, Bridger B includes multiple bench-forming limestones that have been

interpreted as forming in shallow, basin-wide lakes (Brand, 2007). Many of the limey white layers in the Bridger Formation have been interpreted as forming in lakes (Bradley, 1964; Murphey, 2001; Murphey, 2007; Sinclair, 1906; West and Hutchison, 1981). One of the bench-forming limestones within Bridger B underlies a fossil-rich mudstone with abundant fossil turtles, the Black Mountain turtle layer (Brand et al., 2000). This layer forms part of a lithofacies association described by Buchheim et al. (2000), consisting of a bench-forming limestone followed by mudstone and then sandstone (Fig. 1). The sediments overlaying these limestones have been identified as volcanic in origin (Sinclair, 1906).

Brand et al. (2000) investigated the taphonomy of fossil turtles across multiple sites within the Black Mountain turtle layer and associated layers. The turtle fossils at these locations represented shells or portions of shells; limb elements were occasionally preserved but heads were never found. Few turtle bones showed abrasion and weathering, and evidence of scavenging or predation was rare (Brand et al., 2000).

Buchheim et al. (2000) developed a model using fossil and sedimentological evidence to explain the distribution and taphonomy of fossil turtles, as well as the lithofacies association that includes the Black Mountain turtle layer. In their proposed model, a shallow, basin-wide lake was present in the Bridger basin, within which the limestone layer formed at the base of the lithofacies. At some point, a volcanic event produced abundant ash, which came into the lake via ashfall and/or overbank deposits from finger-like deltas that extended into the lake. This resulted in the deposition of a fine-grained mudstone layer, the Black Mountain turtle layer, in a short period of time. At many localities, this layer is claystone, thus Buchheim et al. (2000) designated this layer

as a claystone facies. The deposition of ash at this time may have caused the mass death of turtles and other animals within the lake, explaining the high numbers of fossils found. Burial of fossils was not instantaneous; sufficient time elapsed to allow the limbs and heads of turtles to disarticulate from the shell, but not so long that the shells disarticulated, since most of the fossil turtle shells were still intact when found (Brand et al., 2000). Based on experimental taphonomic work by Brand et al. (2003), the burial timeframe in this model for the Black Mountain turtle layer would be weeks to months.

Buchheim et al. (2000) concluded that the Black Mountain turtle layer (the claystone facies in their lithofacies association) was deposited in a lacustrine environment based on several factors including associated fossils (gastropods, gar, and crocodylians), the presence of this layer over a wide area, and the presence of the clay mineral clinoptilolite indicating alkaline lakes. Buchheim et al. (2000) also suggested that the sharp contact between the basal limestone and the mudstone layer indicated an abrupt paleoenvironmental change may have occurred with the deposition of this layer.

After deposition of the claystone facies, according to the model by Buchheim et al. (2000), a thin-bedded sandstone and siltstone facies was deposited in a fluvial environment with floodplain ponding. The deposition of this layer filled in the shallow lake, as a delta prograded into and eventually replaced the lake. The final layer in the lithofacies association was a cross-bedded sandstone facies. This was interpreted as being deposited in a high-energy fluvial floodplain environment (Buchheim et al., 2000). The lithofacies association extended up to the Meadow Springs white layer, which represented an ash-rich layer above the cross-bedded sandstone facies.

As subsidence rates of the local basin grew greater than depositional rates, a new, shallow lake formed, starting the cycle over again. This cycle appears to have happened multiple times within Bridger B (Buchheim et al., 2000).

The model proposed by Brand et al. (2000) and Buchheim et al. (2000) accounted for the abundance of and taphonomic condition of fossil turtles, as well as the sedimentological features described above. However, their model did not consider the distribution, diversity, and taphonomic condition of the small-animal fossils present at collection sites across the basin. To address these questions, Schafer (2008) studied microfossils across five locations from the Black Mountain turtle layer used in the original studies (Fig. 2).

Schafer (2008) reported that small-animal fossils from her study sites were highly fragmented, with no articulated skeletons. A mammal tooth to vertebrae ratio of 21.2:1 pointed strongly away from the possibility of rapid burial of small-mammal carcasses, which should yield a ratio of ~1:1 in most mammals (Behrensmeyer, 1975). Thus, it appears vertebrae were either transported out of the system or were destroyed, while teeth remained. However, transportation of bones and bone fragments as single units was unlikely because their equivalent grain sizes were larger than the sediment grain size and fragments had jagged breaks with little to no rounding, indicating little transportation of isolated elements. Finally, Schafer (2008) reported that both aquatic and terrestrial small-animal taxa were present across her study sites, but with terrestrial forms numerically dominant.

Schafer (2008) offered two alternative scenarios for the composition and taphonomic condition of microfossil assemblages. These assemblages might have

resulted from the transportation of carcasses before fragmentation, with subsequent fragmentation. Alternatively, given the high abundance of terrestrial forms, if there was a mostly terrestrial habitat present at these sites, then an attritional accumulation of microfossils with bones accumulating *in situ* was possible. In both scenarios, the evidence seems to imply some time for disarticulation of skeletons and subsequent degradation of less robust elements, such as vertebrae.

While many of the limey white layers of the Bridger Formation have been interpreted as forming in lakes, some, including the Lonetree white layer, have been interpreted as forming in lakes with paludal (marshy) borders or lakes that were replaced by paludal environments (Bradley, 1964; Garrett, 2007). Sedimentary characteristics interpreted as indicating a paludal environment include carbonaceous shale and lignite beds and lenses associated with limey white layers and associated plant fossils such as reed stems and algal-covered logs (Murphey, 2007).

The findings of Schafer (2008) raise several questions about the model developed by Buchheim et al. (2000). If the microfossils were brought into the Black Mountain turtle layer system as carcasses, as proposed for the turtle fossils, why were larger portions of their skeletons not found with the turtles? Why was there an abnormal mammal tooth to vertebrae ratio, if the carcasses were buried fairly rapidly and there was little transport of individual bony elements? And of particular interest, if the bench-forming limestones represent shallow, basin-wide lakes, why were the microfossil assemblages analyzed by Schafer (2008) dominated numerically by terrestrial forms?

In this study I build on the previous work done by Schafer (2008) by performing a more comprehensive analysis of small-animal fossils from sites across the Black

Mountain turtle layer. First, I examined fossils across a greater number of sites, across a greater geographic range, and with increased sampling density (Fig. 2). Also, I identified fossils more precisely, with many fossils identified to genus, allowing for a more refined ecological analysis. Finally, I performed a more comprehensive stratigraphic analysis of small-animal fossil distribution at two new sampling sites where this was possible.

These analyses allow for a more thorough test of the existing models for the depositional environment of the Black Mountain turtle layer and associated layers. I explicitly attempt to offer such a test by comparing the ecological characteristics of small-animal fossils across sample sites and stratigraphic intervals with the predictions of existing models.

CHAPTER 2

MATERIALS AND METHODS

Selection of Sites

During the 2001 collection season, sediment samples were collected from 16 sites along exposures of the Black Mountain turtle layer and associated lithofacies (field notes provided by Goodwin, pers. comm.). Schafer (2008) previously studied microfossils from five of these sites (AK-9, RR-7, WB-25, NR-29, and BSR-1; Fig. 2). Here, I examined fossils from four additional sites (BKD-9, NR-46, DP-11, and DP-14) (Fig. 2). All of these sites yielded microfossils. BKD-9 and NR-46 filled in a geographic gap from Schafer's (2008) study. DP-11 and DP-14 were chosen because sediment samples were collected from more stratigraphic levels than was the case at the other sites, allowing for a more comprehensive stratigraphic analysis of the fossil assemblages at these sites. Site labels referred to specific collection localities (numbers) within a specific USGS topographic map (AK, Antelope Knoll; BKD, Butcher Knife Draw; BSR, Black Spring Reservoir; DP, Devil's Playground; NR, Needle Reservoir; RR, Reed Reservoir; WB, Wildcat Butte).

Collection and Screen Washing of Sediment Samples at Each Study Site

At most of the sites along the Black Mountain turtle layer, a ~ 5-gallon (one bucket) sediment sample was collected, where appropriate exposures were available, from each of four stratigraphic intervals from within the Black Mountain turtle layer lithofacies: the limestone (LS) just below the Black Mountain turtle layer, the mudstone of the Black Mountain turtle layer (sample 1, S1), and from finer-grained units (mudstone

to fine sandstones) within the thin bedded sandstone and siltstone facies ~1.8m (sample 2, S2) and ~4.5m (sample 3, S3) above the limestone (Fig. 1).

Sediment samples from the LS and S1 intervals are likely time-equivalent across sites, because the LS interval at most sites was easily identified and the S1 interval was always collected from just above the LS. However, the S2 and S3 intervals may not be precisely time-equivalent across sites, lacking prominent sedimentary structures that could be used to identify the S2 or S3 intervals in the field across sites. These samples represented the two lowest, fine-grained deposits within the thin-bedded sandstone and siltstone facies of Buchheim et al. (2000). Despite the S2 and S3 samples not necessarily being time-equivalent across sites, these samples still represent sequential intervals at each site after the LS and S1 intervals and are therefore used in this study to track local changes over time at each site. At DP11A and DP14, equivalent intervals to the S2 and S3 of other sites were determined by using the distance above the LS interval as a measurement to align layers (Fig. 3).

At DP11A and DP14, ~5-gallon sediment samples were collected at additional levels within and above the Black Mountain turtle layer, including layers substantially higher in the lithofacies association (Fig. 3). The underlying limestone at these sites was not collected because it was very hard and could not be readily broken down to release fossils. Above the limestone, the sample designation (S1, S2, etc.) did not align with sample designations at other sites. For example, both the S1 and S2 samples were obtained from within the Black Mountain turtle layer (the claystone facies above the limestone). Thus, in subsequent analyses, these two samples were combined to be equivalent to the S1 samples of other sites. The detailed sampling regime at one of these

sites (DP-14), and the estimated equivalence with the S2 and S3 samples at other sites (based on distance above the limestone layer), are illustrated in Fig. 3.

All sediment samples were processed via screen washing. Water was run through a set of nested boxes with increasingly finer screen bottoms (mesh sizes were ~ 3 mm, ~ 2 mm, and ~ 0.5 mm). The samples from each mesh size were allowed to dry and then carefully searched for fossil elements. In some cases, after screen washing, chunks of sediment remained. These were soaked in a weak hydrogen peroxide solution to aid in the breakdown of these chunks in order to expose possible fossil elements within them. In some cases, samples with a large volume of washed sediment had a subsample removed which was then searched for fossil elements. Thus, I did not attempt to draw conclusions from the absolute number of fossils from a sample, given that in some cases not all of the sediment was processed for fossils. Rather, I analyzed the relative proportions of taxa present within each sample.

Identification and Characterization of Fossils

All fossils from each sediment sample were removed for inspection; a total count of fossils was obtained. After initial inspection, fossils that I judged to be potentially identifiable were separated from the bulk of material for further work. All fossils were stored in vials and the vials were placed in gridded boxes with labeled columns and rows. In some cases, vials contained a single fossil, but vials often contained batches of fossils.

Identification was done based on comparative material at Andrews University, figures and descriptions in the literature, and the collections at the Denver Museum of Nature and Science and the University of Colorado Museum. Representative specimens

of most identified taxa, and especially mammal teeth, were photographed. In most cases, these specimens were coated with ammonium chloride prior to photographing to increase contrast when photographed. This was accomplished by passing the specimen through a vapor cloud of ammonium chloride, generated by heating a test tube containing ammonium chloride with a propane torch in a fume hood. The coated element was then photographed at multiple focal planes and imported into Adobe Photoshop CC 2019 for focus stacking and editing.

Photographed fossils were assigned temporary specimen numbers to facilitate future investigations by other researchers. For example, specimen G-D3 represents a fossil located in box G, and within that box, in the grid location at the intersection of column D and row 3.

Fossils from sites studied by Schafer (2008) had already been sorted and identified. The fossils that were identified by Schafer (2008) were reexamined and identifications were confirmed or revised to insure that the same taxonomic framework was applied to all sites used in my analysis.

For ecological characterization, fossils were placed into one of two broad categories: aquatic or terrestrial, both with three subcategories. The subcategories for aquatic taxa were aquatic mollusk, fish, and aquatic tetrapod (frogs, salamanders, turtles, and crocodiles). The subcategories for terrestrial taxa were land snail, squamate (lizards and snakes), and mammal. These broad categories were used to designate whether a given interval at a site was more aquatic or more terrestrial in taxonomic signature.

Analytical Methods

The ecological signature of sample sites with at least 10 identifiable fossils was determined. Relative proportions of aquatic and terrestrial taxa were assessed using the categories noted above. The spatial and stratigraphic patterns in the aquatic:terrestrial proportions of the fossil assemblages were analyzed graphically. Statistical tests were not performed because it could not be assumed that individual fossil fragments were independent of one another.

CHAPTER 3

RESULTS

Identification and Characterization of Taxa

Over 16,500 fossils were recovered from the sample sites that I studied (BKD-9, NR-46, DP-11A and DP-14). Most of these fossils represented fragments of vertebrate bones that were not identified more specifically. However, 1,513 fossils from these sites were identified more specifically. These identified fossils, together with the 1,732 fossils that I inspected and identified from sites previously reported by Schafer (2008), form the basis of the taxonomic and ecological characterization that follows. Actual counts of fossils per site per interval are given in Appendix 1. The order of taxa follows the order given in the taxonomic list provided in Appendix 2.

Mollusca— A very small, unidentified bivalve was present at AK-9 in the S2 and S3 intervals (Fig. 4A). When compared to published photographs of *Unio*, which has been reported from the Bridger (Paleobiology Database downloaded 01/24/2020¹), the beak of these small bivalves is located more centrally along the dorsal margin of the valves, suggesting that they belong to a different genus. Bivalves clearly indicate local presence of aquatic habitat.

Five taxa of gastropods were present across study sites (Fig. 4 B–G). Four of these were referred to modern genera that have previously been identified in Bridger deposits (Murphey, 2001). Fossils assigned to *Stagnicola* have shells that are wider at the aperture and then gradually narrow to the shell apex (Fig. 4B). *Stagnicola* was present at

¹ http://paleobiodb.org/data1.2/occs/taxa.tsv?datainfo&rowcount&base_name=animalia&rank=genus&taxon_status=accepted&interval=bridgerian,bridgerian&time_rule=contain&cc=NOA,US&state=wyoming&strat=bridger%20fm&show=class&order=hierarchy

four sites and multiple sampling intervals. *Stagnicola* never account for more than 7% of identified fossils. Modern *Stagnicola* are freshwater pulmonates (Murphey and Evanoff, 2011).

Fossils assigned to *Biomphalaria* exhibit a tight spiral with planispiral morphology (Fig. 4C). Fossils of *Biomphalaria* were present at six sites and from multiple intervals. When present in a sample, *Biomphalaria* varied dramatically in relative abundance, from <1% of identified fossils (LS of BSR-1) to ~ 74% of identified fossils (LS of NR-29). Extant species of *Biomphalaria* occupy warm–water habitats in South America, the Caribbean and Africa (Morgan et al., 2001; Pierce and Constenius, 2014).

Fossils assigned to *Physa* exhibit a large body whorl compared to the spire (Fig. 4D) and were identified by comparison with modern examples and fossils figured in Yen (1946). Fossils of *Physa* were present at two sites in low numbers (S3 of AK-9, n=2; S1 of DP-14, n=1). Modern species of *Physa* are all aquatic but are found in a variety of environmental settings (La Rocque, 1960).

Fossils assigned to *Gastrocopta* have shells that retain relatively the same width along most of their length before narrowing to the apex (Fig. 4E), and that display complex teeth extending into the aperture (Fig. 4F). Fossils of *Gastrocopta* were present at six sites and from multiple intervals. When present in a sample, *Gastrocopta* varied dramatically in relative abundance, from < 2% of identified fossils (LS of NR-29) to ~ 50% or more of identified fossils (S3 of AK-9, S3 of DP-11A). Extant species of *Gastrocopta* are terrestrial snails that inhabit wooded areas and grasslands (Anderson, 2005; Archer, 1939; Lee and Schroeder, 2012; Roth, 1986).

Multiple gastropod fossils appear to represent another taxon, but they have not yet been identified to genus. These fossils displayed a wide shell that narrowed towards the apex (Fig. 4G). However, relative to the width at the base of the shell, the spire is not as tall as it is in other genera from the Bridger Formation (compare Fig. 4G with Figs. 4B, D, E-F). These fossils were present at six sites and from multiple intervals. Because these fossils were not assigned to genus, I was unable to determine if they represent terrestrial or aquatic forms. Thus, these fossils were not included when determining relative frequencies of aquatic and terrestrial taxa.

Osteichthyes— Many fossils were assigned to bony fish but not to a more specific taxon. The majority of these were vertebrae (Fig. 5B), identified by their biconcave morphology and the ridge and valley structures on their surface; and teeth (Fig. 5C), identified by comparison to fossils at the Denver Museum of Nature and Science [DMNH EPV. 57552, Locality: DMNH 869]. Fossils assigned to bony fish were present in 21 of 23 samples with > 10 identified fossils, with relative abundance of identified fossils ranging from ~ 1% – 63%. Fish clearly indicate local presence of aquatic habitat.

In addition to fossils identified no more specifically than bony fish, some fossils were identified as *Lepisosteus* (gar) and *Amia* (bowfin). The most common fossils identified as *Lepisosteus* were rhomboidal ganoid scales (Fig. 5D). Other fossils included fragments of dermal bone, teeth, and ray parts. Teeth and ray part identifications were based on comparisons with fossils at the Denver Museum of Nature and Science [DMNH EPV. 58805, Locality: DMNH 870]. Fossils of *Lepisosteus* were present at six sites and from multiple intervals. In most samples, fossils of *Lepisosteus* occur in relatively low abundance, but in some cases, they were abundant; for example, gar represented ~ 35%

of identified fossils in the S1/S2 sample at DP-11A. Today, *Lepisosteus* is associated with shallow freshwater habitats (Ferber and Wells, 1995).

Fossils identified as *Amia* were fragments of tooth patches containing multiple tooth sockets (Fig. 5A), consistent with morphology of both modern and fossil *Amia* (Grande and Bemis, 1998). Fossils of *Amia* were present at eight sites and from multiple intervals; and in all samples where present, *Amia* account for <15% of identified fossils. Today, *Amia* is associated with shallow, vegetated freshwater habitats (Koch et al., 2009; Midwood et al., 2018).

Amphibia— One fossil from the S1/S2 sample of DP-14 was identified as a urodelan (salamander) atlas vertebra (Fig. 6D-G). This identification was supported by the presence of two anterior condyles, a concave posterior cotyle and subcentral foramen and comparison with images from Demar (2013).

Two fossils from the LS sample of BKD-9 and S1 sample of BSR-1 were identified as anuran (frog) vertebrae (Fig. 6A-C). These identifications were based on the double condyles present in both elements and by comparisons with images of anuran vertebrae from Folie et al. (2012).

Reptilia— Shell fragments belonging to Testudinata (turtles) were present at five sites, and from the LS and S1 or S1/S2 intervals. These fragments were identified based on the texture of their bony surfaces as well as their porous internal structure. Where present, turtle fossils usually represent a low percentage ($\leq 3\%$) of identified fossils, with two exceptions: turtles account for 14% of identified fossils from the S1/S2 sample of DP-11A and 27% of identified fossils from the S1/S2 sample of DP-14.

Lizard fossils were very abundant in multiple samples with osteoderms being the most common element (Fig. 5G). These compared favorably to images from Klembara and Green (2010), Cicimurri et al. (2016), and Bolet (2017). Although these previous studies of Eocene and Paleocene lizards are from a range of locations, two outside of North America, the close morphological resemblance to my material gives me confidence that these identifications are correct. Other elements identified as lizard included vertebrae (Fig. 5F), recognized by their distinct ball-shaped condyle on the vertebral centrum; jaws (Fig. 5E), identified by their pleurodont dentition; and teeth identified by comparison with fossils at the Denver Museum of Nature and Science [DMNH EPV. 19936, Locality: DMNH 878]. Fossils identified as lizard were present from all 23 samples with ≥ 10 identified fossils and were often proportionately dominant ($\sim 50\%$ or more of identified fossils in 14 of 23 samples). I interpret these fossil lizards as indicating local presence of terrestrial habitats.

Three fossil vertebrae were identified as snake (Fig. 6H-J). This identification was based largely on the distinctive shape of the neural canal, roughly like an inverted heart-shape. These fossils were identified from the S3 sample of NR-29 (n=1) and the S1/S2 sample of DP-14 (n=2).

Fossils of Crocodylia (crocodiles and alligators) were identified from all but two sites, with most of these fossils from the LS, S1 or S1/S2 intervals. Most crocodylian fossils were teeth with a bulbous crown, and with grooves that extend from the base toward the apex of the crown (Fig. 5H). This morphology compares favorably to teeth of the small alligator, *Procaimanoidea*, as figured in Gilmore (1946) and Cidade et al. (2019). Crocodylian osteoderms were also identified from three samples (S1 of NR-29,

S2 of BSR-1, and S3 of DP-14). Given that all teeth identified as crocodylian were assigned to *Procaimanoidea*, the osteoderms were tentatively assigned to this genus as well. Given modern habitat of crocodylians, these fossils were interpreted to represent aquatic habitat.

Mammalia— Many fossil elements were identified as mammal. These included long bones, vertebrae (Fig. 5J), and teeth. Some teeth were identified to more specific taxonomic groups (see below). Other teeth were only identified as mammal, either because they were highly fragmented or because a search of the literature yielded no comparable images (e.g., teeth displayed in Fig. 7 H-I). Mammals were present in 22 of 23 samples with > 10 identified fossils, with relative abundance of identified fossils ranging from ~ 1–47%. I interpret the presence of mammals as probably indicating local presence of terrestrial habitats.

Six teeth were assigned to the small metatherian *Herpetotherium*. These teeth were identified from three sites (BKD-9, BSR-1, and DP-11A) and from the LS, S1, and S2 intervals. One tooth was identified as a lower left molar (Fig. 8K). The entoconid is large and there is a shelf posterior to the talonid basin. This tooth morphology was congruent with lower left molars of *Herpetotherium* from Murphey et al. (2018). Five teeth were identified as upper molars (two illustrated in Fig. 8I-J). These teeth have multiple styler cusps and the metacone and paracone are elevated above the protocone. These teeth compared favorably with images from McGrew et al. (1959) and Guthrie (1971). Sánchez-Villagra et al. (2007) suggested that the skeleton of *Herpetotherium* indicates a terrestrial rather than an arboreal lifestyle. *Herpetotherium* has a temporal range from the early Eocene to the early Miocene (Korth, 2008).

Two teeth from BKD-9 (from LS and S3) were tentatively assigned to the extinct family Leptictidae (Fig. 8E-F). The metaconule and paraconule are present and the hypocone forms a prominent posterior shelf at the base of the protocone. These teeth compared favorably with images of teeth assigned to species within Leptictidae from Clemens (2015) and Velazco and Novacek (2016); however, both of the teeth from BKD-9 differed in morphologic detail from those presented in these papers. Therefore, I did not assign them to a genus. Leptictids were insectivorous, terrestrial mammals with a temporal range from the late Cretaceous through the late Oligocene (Gunnell, 2008; Rose, 1999).

One tooth from the S1 of BKD-9 was identified as an incisor fragment of *Nyctitherium* (identified in private correspondence with P. Murphey; Fig. 8L). This fragment contains the root of the incisor and two cusps; the rest of the tooth had broken off. Individuals of *Nyctitherium* were small, insectivorous mammals that are currently only known from the Eocene (Gunnell et al., 2008).

Seven teeth were identified as the condylarth *Hyopsodus* (Fig. 8A-D). Fossils assigned to *Hyopsodus* were present at three sites (NR-29, BSR-1, and DP-11A) and from the S1, S1/S2, and S3 intervals. Of the mammal teeth that were identifiable to a genus, more belonged to *Hyopsodus* than any other genera. All teeth identified as *Hyopsodus* were lower molars or premolars. These teeth were identified by comparison with previously identified material [University of Colorado Museum 70017]. *Hyopsodus* is well known and abundant in the Bridger formation (Matthew, 1909). *Hyopsodus* has been interpreted as a fast-moving mammal capable of digging, with individuals likely

occupying burrows (Orliac et al., 2012). *Hyopsodus* has a temporal range from the late Paleocene to the late Eocene (Archibald, 1998).

Numerous fossils (n = 61) were identified as rodent. In a number of cases, rodent fossils were too fragmented to support generic identification, or a search of the literature found no comparable images. Several rodent teeth not identified to family or genus are figured (Fig. 7C-G).

Three fossils were assigned to the extinct rodent family Ischyromyidae, a rodent family consisting of 21 genera known from the late Paleocene to the early Oligocene (Anderson, 2008). One small ischyromyid tooth from the LS sample of NR-46 was identified as *Microparamys* (Fig. 7B) based on comparisons with fossils figured by Kelly and Murphey (2016). *Microparamys* has a temporal range from the late Paleocene to the mid late Eocene (Anderson, 2008).

Two teeth from the LS sample of BKD-9 were assigned to a second extinct rodent family, Sciuravidae (Fig. 7A) based on comparisons with teeth figured by Dawson (1962) and Kelly and Murphey (2016). Sciuravids were small, mouse to hamster sized rodents only known from the early and middle Eocene; their diets and ecological roles are unknown (Walton and Porter, 2008).

Two fossil teeth from BKD-9 were assigned to Microsyopidae, a family within the extinct plesiadapiformes, which Silcox and Gunnell (2008) placed within the order Primates. One tooth from the LS sample was only identified to this family (Fig. 7J), whereas one jaw fragment with three teeth still in place from the S1 sample was identified as *Uintasorex* (Fig. 8H). This jaw fragment compares favorably with images of *Uintasorex* from McGrew et al. (1959) and Kelly and Murphey (2016). Microsyopids

were probably omnivorous (Silcox and Gunnell, 2008). The temporal range of Microsycopidae extends from the late Paleocene to the middle Eocene; *Uintasorex* is found from the early and middle Eocene (Silcox and Gunnell, 2008).

Plants—The focus of my study was small-animal fossils. However, four fossil seeds were identified from the LS of NR-46 (Fig. 5K). These seeds were identified as *Celtis* (hackberry), based on comparison with modern examples. Modern hackberries are usually found in more high ground sites rather than lowlands (Winkler, 1983b). Hackberry has previously been reported from the Eocene of Wyoming (Gingerich, 1987; Winkler, 1983a).

Patterns in the Aquatic:Terrestrial Proportions of Fossil Samples

The diversity of taxa present in fossil samples varied from site to site and across intervals. In 23 fossil samples with ≥ 10 identifiable fossils from the LS, S1, S2 and S3 intervals, all included both aquatic and terrestrial forms (Fig. 9). In 21 of these samples, remains of fish were identified and in 22 of these samples, mammal remains were identified. Squamate material was recovered from all of the 23 samples and accounted for $>50\%$ of terrestrial fossils at 19 of them. Other taxa were present in fewer samples.

There was no consistent stratigraphic pattern in the aquatic:terrestrial proportions across fossil samples. The pattern of the proportions varied from site to site from apparently stochastic fluctuation (e.g., BKD-9), to a substantial increase in the terrestrial signal (e.g., NR-29), to a substantial increase in the aquatic signal (e.g., BSR-1). Sites with a dominate terrestrial signature in the LS interval retained this through all intervals

with the exception of BSR-1, which shifted to a dominate aquatic signature in the S2 interval.

The detailed stratigraphic analysis at DP-11A and DP-14 from the LS interval to the base of the Meadow Springs white layer (Fig. 3) showed that A) within the Black Mountain turtle layer small-animal fossils were concentrated in the lower ~0.5 m of sediment; and B) that identifiable fossils were either absent or few in number at higher stratigraphic levels, with the exception of one interval from DP-11A with abundant land snails and a few mammal and squamate fossils.

Within the Black Mountain turtle layer, the two most “terrestrial” fossil samples were from the two westernmost sites (S1 of RR-7 and WB-25) and the two most “aquatic” fossil samples were from the two easternmost sites (S1/S2 of DP-11A and DP-14; Figs. 2, 9). However, the geographically intermediate sites did not display a clear gradient in terrestrial:aquatic proportions (Figs. 2, 9). The highly “terrestrial” sites to the west were dominated by squamates; the highly “aquatic” sites to the east were dominated by fish and aquatic tetrapods (Fig. 9).

CHAPTER 4
DISCUSSION

Small-animal Fossils from the Black Mountain Turtle Layer Lithofacies Association

Small-animal fossils from the Black Mountain turtle layer and associated layers were taxonomically and ecologically diverse across samples. The composite fossil assemblage across samples represented five major groups and at least five species of mollusks; two species of fish; one each of salamander, anuran, turtle and alligator; two squamates (a snake and lizard); and seven species of mammals. The taxonomic composition of mammals aligns well with the published list of Bridger B mammals from Gunnell et al. (2009), with the exception of Leptictida which was not reported in their study.

Individual fossil samples with meaningful numbers of fossils likewise were characteristically diverse (Fig. 9). For example, 21 of 23 samples with at least 10 fossils included fish, mammals and squamates; and 19 of 23 samples incorporated at least four of the six taxonomic-ecological categories displayed in Fig. 9.

Both aquatic and terrestrial taxa were present in all samples with samples sizes >10, but terrestrial taxa were proportionally dominate in 17 of 23 of these samples. There was no consistent stratigraphic pattern in aquatic to terrestrial proportions from site to site. Geographically, the S1 interval was most terrestrial to the west and most aquatic to east, but there was no clear gradient from terrestrial to aquatic among the geographically intermediate sites (Fig. 2).

Taken together, these findings indicate that environmental conditions necessary for preserving small-animal fossils were generally persistent across space and time during

deposition of the basal limestone, the Black Mountain turtle layer (S1), and subsequent episodes of mudstone deposition (S2 and S3 intervals). Furthermore, these environmental conditions always sampled both aquatic and terrestrial small animals with terrestrial forms normally dominant proportionally. These findings have bearing on the proposed model for deposition for these fossil-rich layers.

Evaluation of a Lacustrine Depositional Environment

Buchheim et al. (2000) interpreted the limestone layer that forms the base of the Black Mountain turtle layer lithofacies association as forming in a shallow, basin-wide lake. This interpretation was based on the basin-wide occurrence of the limestone layer, the calcitic composition of the layer, and the associated fossils (aquatic gastropods and fish).

Furthermore, Buchheim et al. (2000) interpreted the fossil-rich, ash-derived mudstone lying just above the limestone as likewise forming in this shallow, basin-wide lake, with rapid accumulation of fine-grained, ash-rich sediments (in weeks to months) from ashfall and/or deposition from finger-like deltas extending out into the lake. In this model, the influx of ash likely contributed to the death of many turtles living in the lake, and then buried turtles rapidly enough to maintain intact shells. However, deposition was not instantaneous; sufficient time elapsed to allow taphonomic removal of skulls and limbs of most turtles prior to burial, likely on the scale of weeks to a few months (Brand et al., 2003).

The depositional model proposed by Buchheim et al. (2000) would predict that during deposition of the LS and S1 intervals, sediments accumulating within the lake

would have preserved primarily aquatic fossils and few terrestrial fossils. This prediction is based on two factors. First, if these deposits were formed in a shallow, basin-wide lake, most locations within the lake would have been distant from the shoreline. The occasional terrestrial animal (or bony element of a terrestrial animal) preserved in the lake would have been transported a substantial distance before burial. Second, if the deposits were accumulated rapidly (in weeks to months), there would have been little time for terrestrial animals to populate the finger-like deltaic extensions in sufficient numbers to form a dominant component of fossil assemblages.

However, in 11 of 14 samples from the LS and S1 intervals with >10 identified fossils, fossils of terrestrial taxa were more abundant than fossils of aquatic taxa, usually dominantly so (> 75% of fossils from 10 of 14 samples). Fossils of mammals and squamates were identified from all 14 of these samples and in the majority of samples, squamates (almost entirely lizards) account for >50% of identified fossils (Fig. 9). In summary, terrestrial organisms were present in all samples from the LS and S1 intervals, and were proportionally dominant in most samples. These findings are inconsistent with the lacustrine depositional model.

The depositional model of Buchheim et al. (2000) also predicts a shift from dominantly aquatic fossils in the basal lacustrine deposits (LS and S1 intervals), to a mix with more terrestrial fossils in the overlying thin bedded sandstone and siltstone facies (including S2 and S3 intervals). The thin bedded sandstone and siltstone facies was interpreted as being formed by fluvial deposition with floodplain ponding. A meaningful aquatic-to-terrestrial stratigraphic shift was observed at NR-29 and DP-11A (Fig. 9). However, at most sites, the aquatic:terrestrial proportions either varied non-directionally

(e.g., BKD-9) or showed, if anything, increase in aquatic proportions in the S2 and/or S3 intervals (e.g., RR-7, AK-9, NR-46, BSR-1).

Given the preceding predictions, any terrestrial fossils found at sites within the LS and S1 intervals should show evidence of being transported; the nearest shoreline of the basin-wide lake would have been 100s of m to a few km away from most sampling sites, based on the geographic extent of the LS and S1 intervals. However, Schafer (2008) found that microfossils from the S1 layer and associated layers showed little abrasion and that the quartz-grain equivalent sizes of fossil fragments were larger than for the sediment grains. These findings indicate that fossil fragments were not transported as individual fragments with sediment into the lake. Schafer (2008) also reported no clumping of fossils and no articulated skeletons, indicating that transport of whole carcasses was unlikely to have occurred.

Taken as a whole, the composition and taphonomic condition of small-animal fossils from the LS and S1 intervals of the Black Mountain turtle layer contradict the hypothesis that these sediments accumulated in a shallow, basin-wide lake. However, these interpretations depend on appropriate identification of fossils and correct assignment of these taxa to aquatic or terrestrial environments. For example, mammals were interpreted as representing local terrestrial habitats. However, the ecology of all mammal genera identified in this study is not yet fully known and some genera may represent a much wetter environment than is assumed in this study.

In addition, two factors could bias the proportions of aquatic:terrestrial taxa in sediment samples. The first is preservation bias. Smith et al. (1988) found that there was a preservation bias against small fish in Cenozoic floodplain environments. Bones of

small fish are delicate and easily destroyed during digestion or taphonomic processes and small fish are usually heavily preyed upon. In contrast, fossil elements such as gar scales, mammal teeth, and lizard osteoderms are more robust and would be more likely to fossilize.

The second possible bias is identification bias. Bones of small fish that are fossilized are not as distinct as those of larger fish such as gar and bowfins (Smith et al., 1988). Likewise, mammal teeth and lizard osteoderms are very characteristic and easy to identify even from fragments. This could lead to an apparent overabundance of terrestrial forms. However, given the high abundance of lizard material, even if lizards are over-represented because of these biases, there is still clearly an unexpectedly high terrestrial signature in the LS and S1 intervals given the predictions of the model proposed by Buchheim et al. (2000). Therefore, even if there are biases present that may inflate the proportion of terrestrial fossils in studied samples, the results of this study still indicate consistent presence of terrestrial animals in all samples, and thus contradict the proposed lacustrine environment for the LS and S1 intervals.

One aspect of the small-animal record seems to be consistent with the predictions of the model by Buchheim et al. (2000): the greater abundance of fossils in the lower ~ 0.5 m of sediment above the limestone layer (Fig. 3). This is congruent with their model, which proposed that the rapid deposition of ash-derived sediment in the lake killed and buried much of the life in the lake. Also, it is consistent with the abundance of fossil turtles in the basal mudstone from DP-11 reported by Brand et al. (2000), where 83% of turtles were found in the first 1.31 m above the limestone layer.

Evaluation of a Fluctuating Paludal/Lacustrine Depositional Environment

Small-animal fossils may be congruent with a paludal/lacustrine interpretation of the limey white layer below the Black Mountain turtle layer. A paludal or marshy environment has been proposed for some layers in the Bridger Formation including some of the limey white layers, such as the Lonetree white layer of Bridger D (Bradley, 1964; Garrett, 2007; Murphey, 2007; West and Hutchison, 1981). Sedimentary characteristics interpreted as indicating a paludal environment include carbonaceous shale and lignite beds and lenses associated with limey white layers and associated plant fossils such as reed stems and algal-covered logs (Murphey, 2007). Such an environment might explain the consistent mix of aquatic and terrestrial taxa across samples, since an environment fluctuating between paludal and lacustrine systems would sample both habitat types over time.

A paludal/lacustrine environment would suggest an attritional accumulation of material. Some amount of time would have elapsed for fluctuations between the two environments to have occurred and enough time for animal material to collect and carcasses to disarticulate must have elapsed before burial. Therefore, this type of environment would predict a diversity of taphonomic conditions among fossils across all taxa. However, Brand et al. (2000) found that the majority of turtle shells appeared to represent complete shells, which would indicate a similar taphonomic stage for the majority of turtle fossils. In addition to the turtle fossils, the amount of bioturbation found in the claystone facies was lower than expected for a lacustrine or paludal environment accumulating sediment over an extended period of time (Brand et al., 2000). Thus, the

turtle shells and sedimentary characteristics do not appear to fit the predictions of a paludal/lacustrine environment where fossils and sediments were accumulated over time.

Conclusion

The results of my study highlight the need for further work on the paleoenvironments and taphonomy of fossil-rich units in the Bridger Formation, including the Black Mountain turtle layer. The model proposed by Buchheim et al. (2000) accounts for the geologic evidence and the fossil turtles, but it does not explain the patterns observed in the small-animal fossils. Further work needs to be done accounting for the geologic evidence as well as the fossils of small and large animals to evaluate A) how an environment during the LS and S1 can account for both the geological evidence and small-animal fossil evidence, or B) how terrestrial fossils could be transported into a lake system with no evidence of transport and how these fossils could be present in such high abundance when compared to aquatic fossils.

In summary, my study provides a test of the model proposed by Buchheim et al. (2000) by analyzing small-animal fossils from multiple sites across the Black Mountain turtle layer. The small-animal fossils in the LS and S1 intervals are dominated by terrestrial forms, especially squamates, which contradicts the proposed environment of a shallow, basin-wide lake. With this detailed taxonomic analysis of the small-animal fossils from the Black Mountain turtle layer and associated layers, further studies can take a more holistic approach, accounting for multiple lines of evidence, including the small-animal fossils.

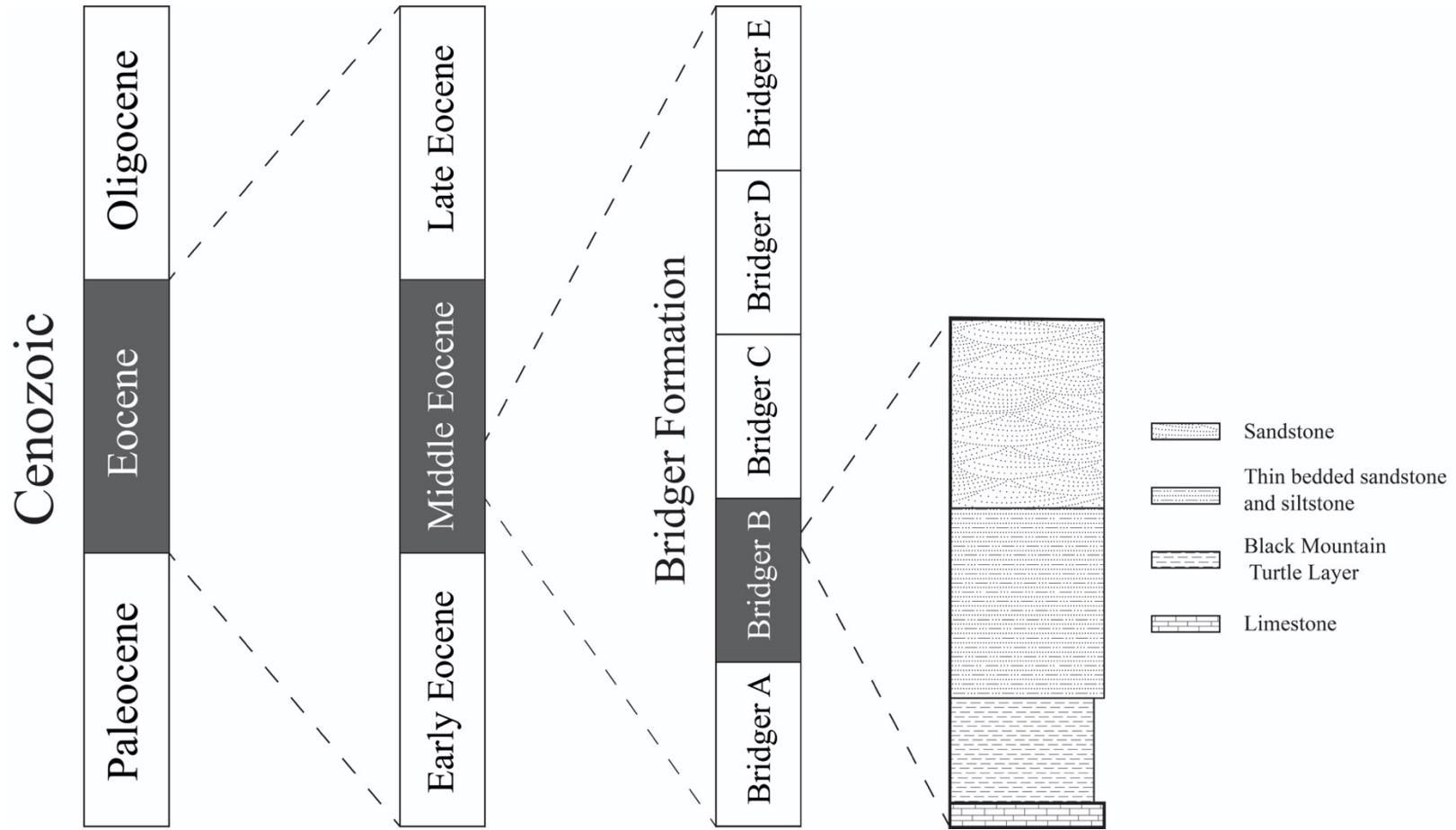


Figure 1. The Black Mountain turtle layer and its associated layers that form the lithofacies association described by Buchheim et al. (2000), placed within the Bridger Formation and the geologic column. The relative width of units within the columns are not to scale.

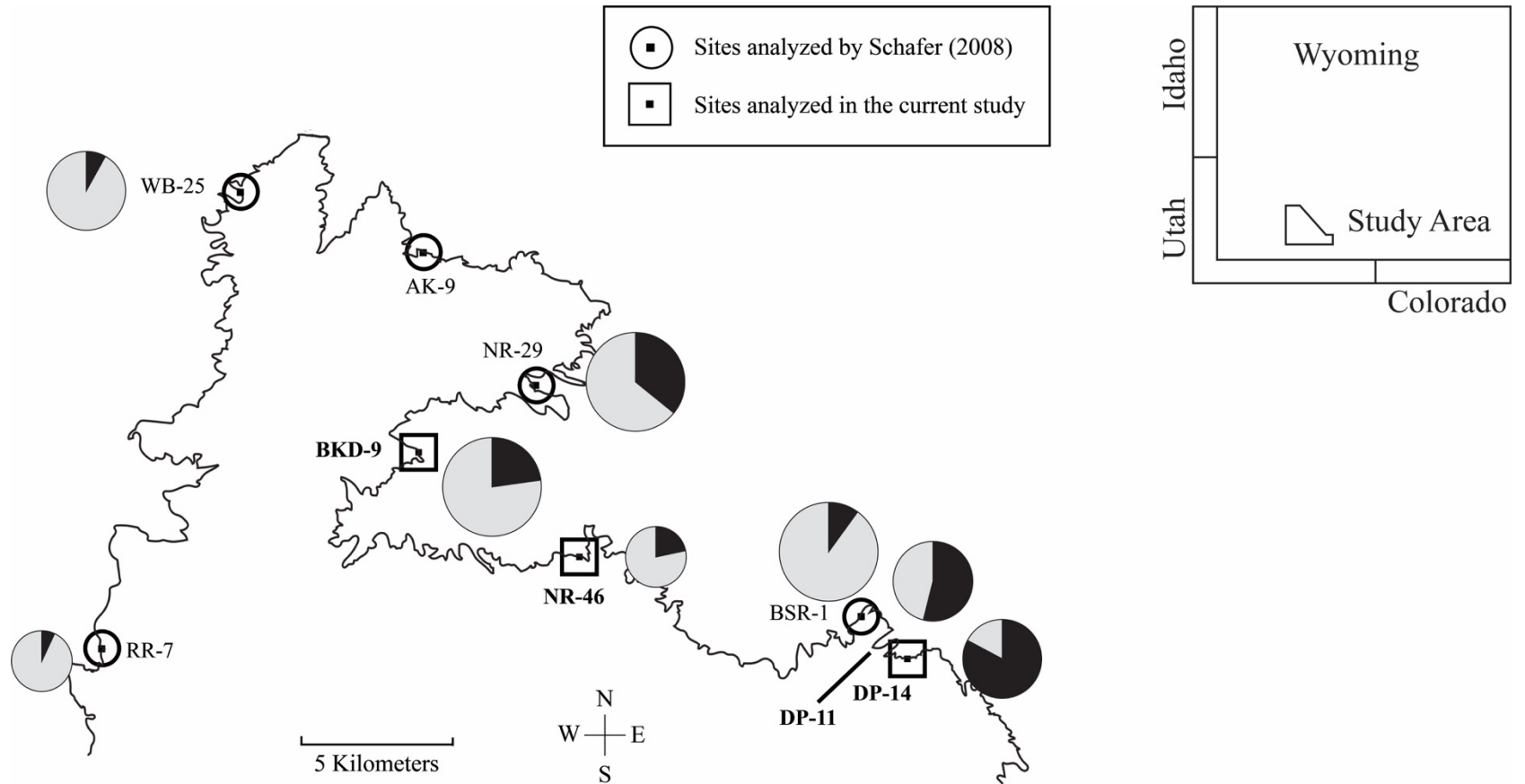


Figure 2. Map of the Black Mountain turtle layer depicting the fossil sites analyzed by Schafer (2008) and the additional sites analyzed in the current study. Exposures of Black Mountain turtle layer redrawn from Brand et al. (2000). The panel shows the Black Mountain turtle layer in wider geographic context. Pie charts represent the proportion of fossils representing aquatic and terrestrial taxa for the S1 samples (see methods) across fossil sites.

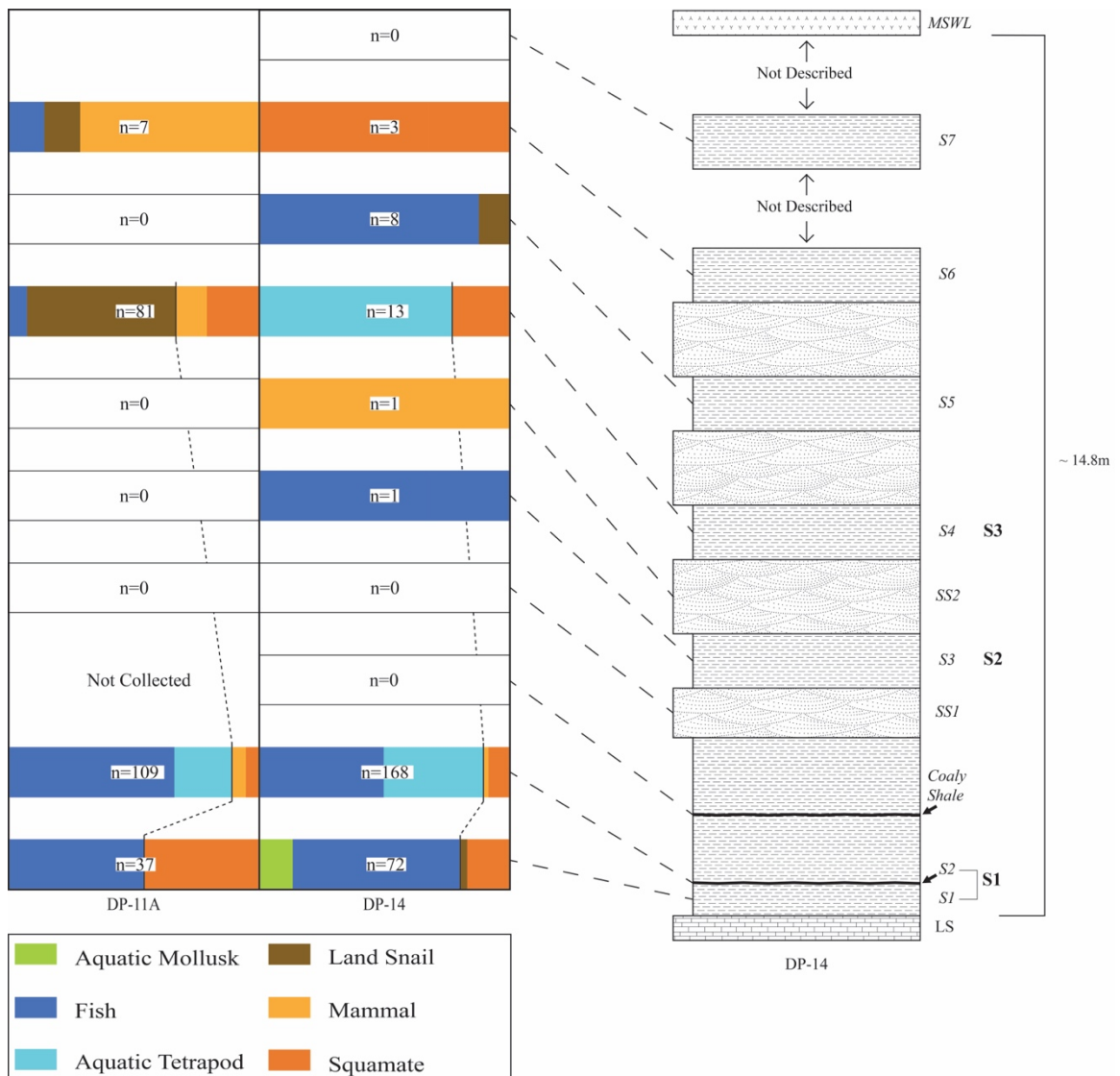


Figure 3. Proportions of fossils assigned to taxonomic ecological categories at DP-11 and DP-14 where collecting was done at multiple stratigraphic intervals from the limestone at the base to the top of the lithofacies association, the Meadow Springs white layer. Numbers represent the total number of identifiable fossil elements from each interval. Vertical black bars separate proportions of aquatic and terrestrial fossils and dotted lines track the change in this proportion through stratigraphic intervals (sites with less than ten identifiable elements were not included when creating the dotted lines). The stratigraphic column is representative of the Black Mountain turtle layer and its associated layers from the limestone bench to the Meadow Springs white layer. Labels in italics represent identifications for the samples taken at DP-11A and DP-14 only. Bold labels show estimated equivalence of the specific samples from DP-14 with the intervals, in addition to the LS, that were sampled across sites.

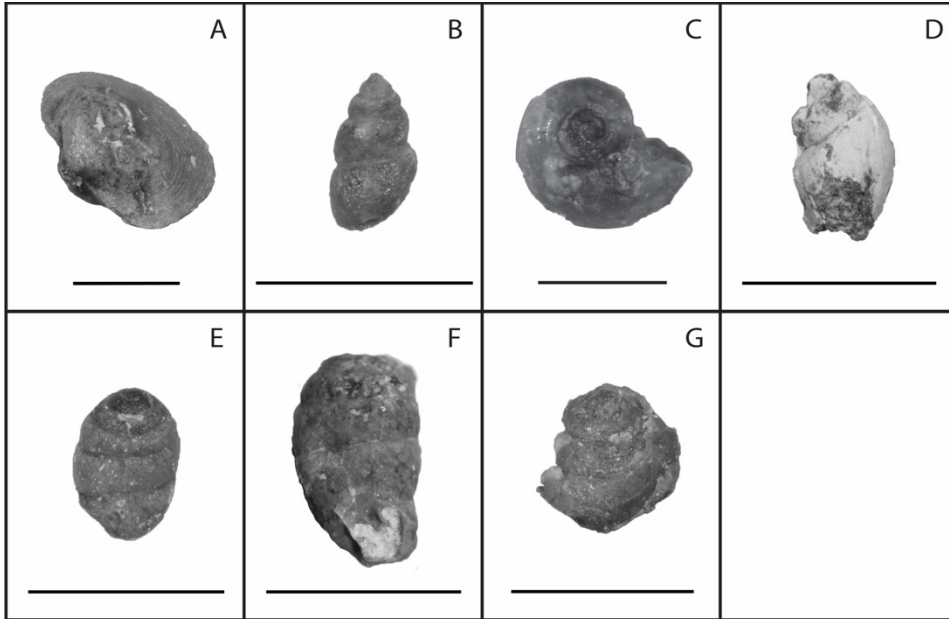


Figure 4. Fossil mollusks identified in this study. A, Bivalve. B, *Stagnicola*. C, *Biomphalaria*. D, *Physa*. E, *Gastrocopta*. F, *Gastrocopta* showing the aperture. G, Unidentified snail.

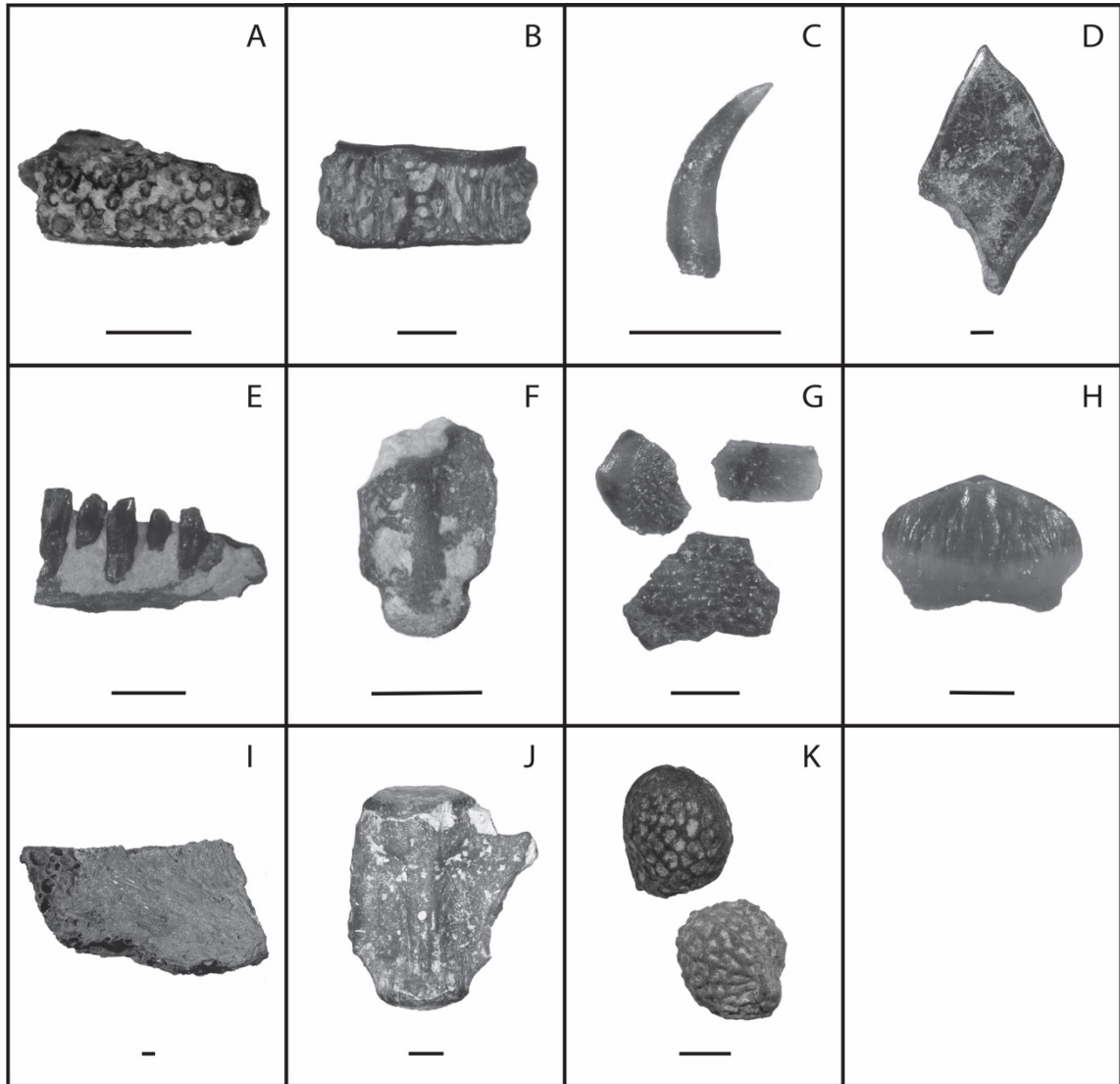


Figure 5. A, *Amia* fragment (S1 of NR-46, specimen A-H1). B, Unidentified fish vertebra (S1 of BKD-9, specimen B-K2). C, Unidentified fish tooth (S3 of BKD-9, specimen A-B7). D, Gar scale. E, Unidentified lizard jaw fragment (LS of BKD-9, specimen B-F2). F, Unidentified lizard vertebra. G, Unidentified lizard scutes. H, Crocodile tooth (S1 of NR-46, specimen G-I6). I, Turtle bone fragment. J, unidentified mammal vertebrae (LS of BKD-9, specimen B-G3). K, Hackberry seeds (LS of NR-46, specimen A-F1). Scale bars equal 1 mm.

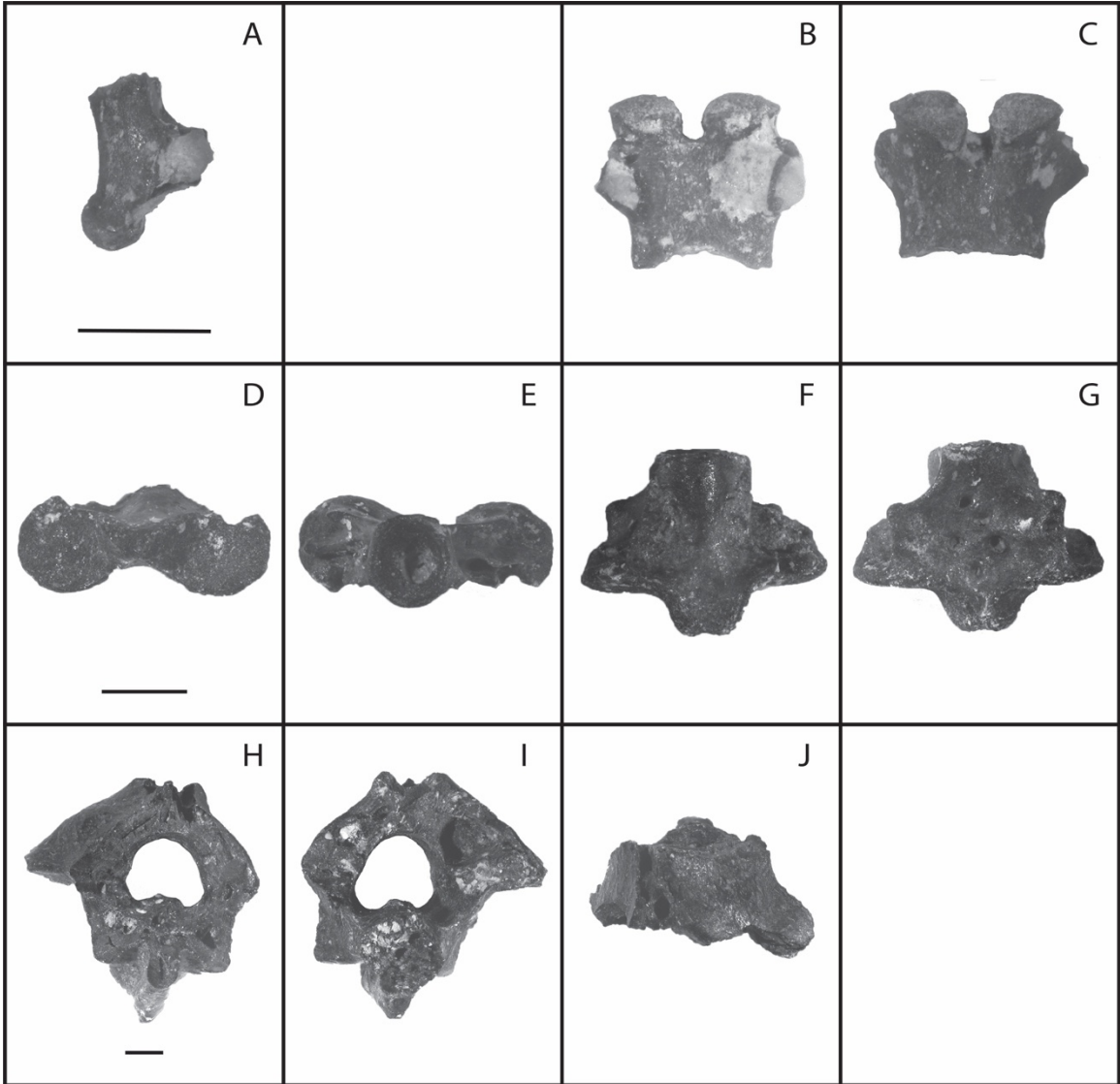


Figure 6. Examples of three fossil vertebrae uncommon in this study. A, Anuran lateral view. B, Anuran dorsal view. C, Anuran ventral view (A-C: LS of BKD-9, specimen B-A2). D, Urodelan anterior view. E, Urodelan posterior view. F, Urodelan dorsal view. G, Urodelan ventral view (D-G: S2 of DP-14, specimen D-D1). H, Snake anterior view. I, Snake posterior view. J, Snake dorsal view (H-J: S2 of DP-14, specimen D-C2). Scale bars equal 1 mm.

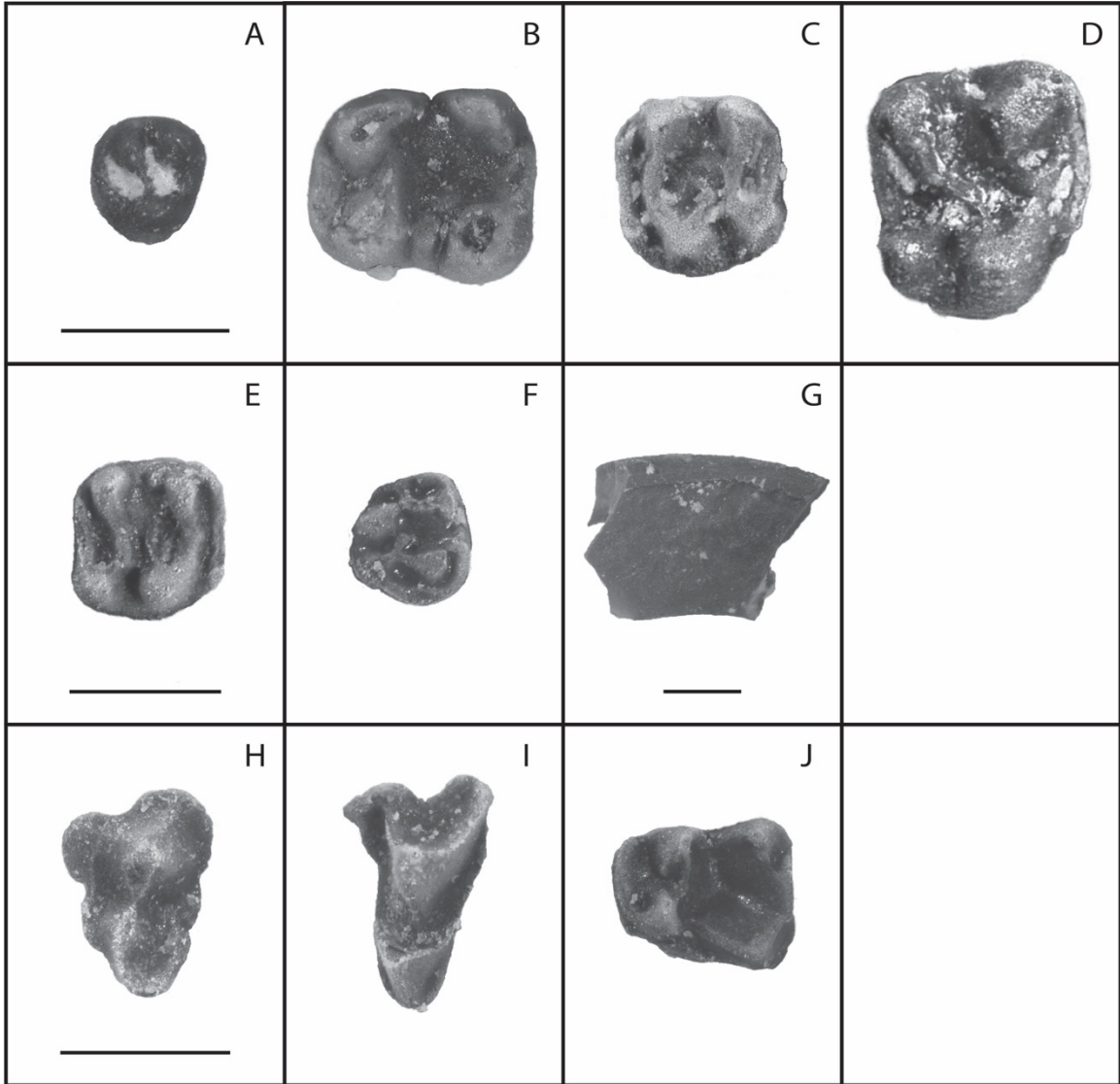


Figure 7. A, Sciuravidae p^3 (LS of BKD-9, specimen B-C2). B, *Microparamys* lower m^1 or m^2 (LS of NR-46, specimen G-H3). C-F, Unidentified rodent tooth (C, LS of BKD-9, specimen G-B2; D, LS of BKD-9, specimen G-A2; E, S1 of NR-46, specimen G-I4; F, S1 of NR-46, specimen G-I4). G, Unidentified rodent incisor (LS of BKD-9, specimen B-D2). H-I, Unidentified mammal tooth (H, S3 of BKD-9, specimen G-F4; I, S1 of NR-46, specimen G-I8). J, *Microsyopidae* lower left molar (LS of BKD-9, specimen B-A8). Scale bars equal 1 mm. Where scale bars are absent, the scale bar in the left column applies to the rest of the row.

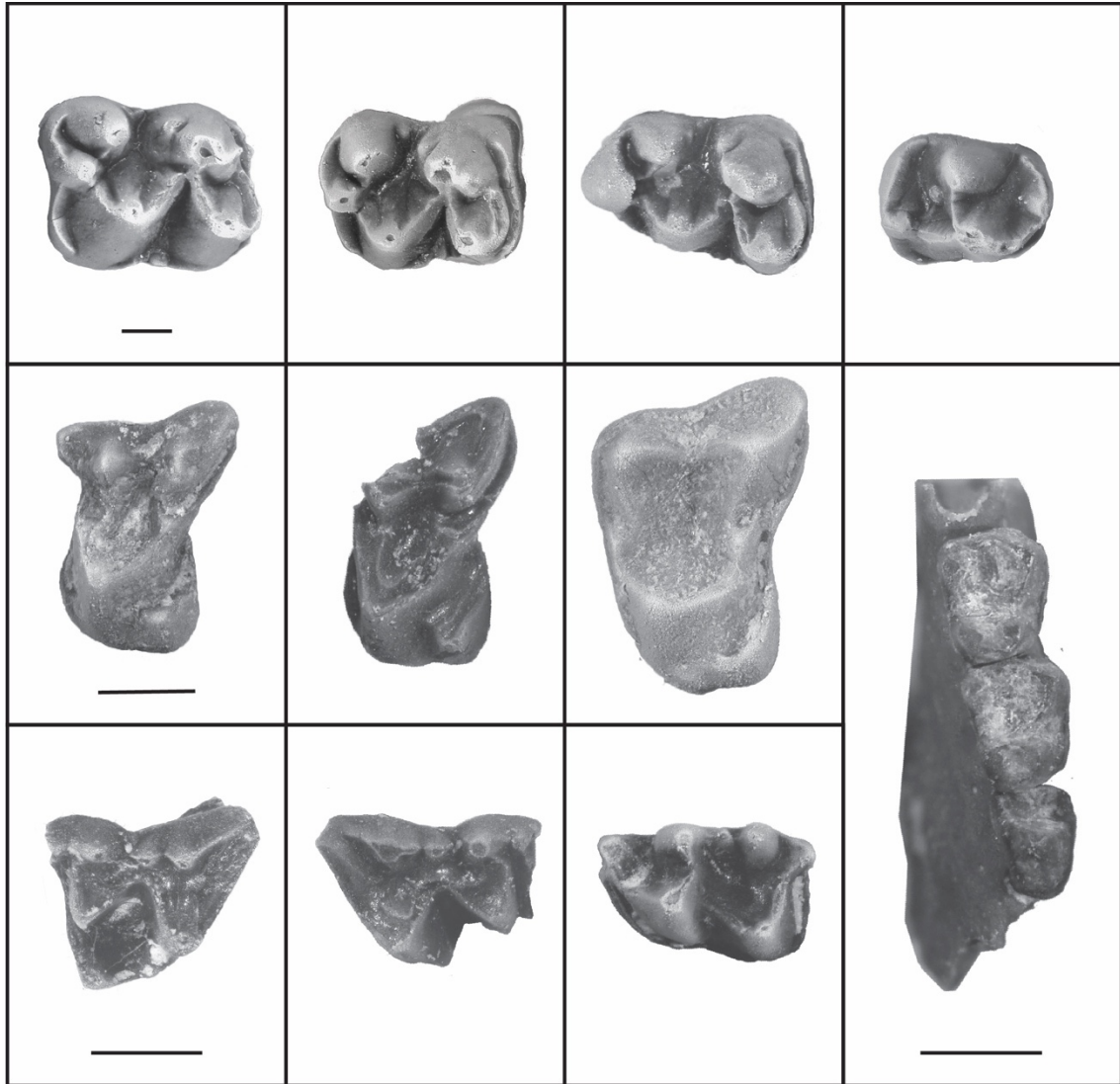


Figure 8. A, *Hyopsodus* Rm² (S2 of DP-11A, specimen G-K3). B, *Hyopsodus* Rm² (S2 of DP-11A, specimen G-K5). C, *Hyopsodus* Rm³ (S2 of DP-11A, specimen G-K3). D, *Hyopsodus* Rp⁴ (S2 of DP-11A, specimen G-K5). E-F, *Leptictidae* (E, LS of BKD-9, specimen G-B4; F, S3 of BKD-9, specimen G-F2). G, Unidentified mammal molar (LS of NR-46, specimen G-H5). H, *Uintasorex* lower right jaw fragment (S1 of BKD-9, specimen G-C6). I-J, *Herpetotherium* upper molars (I, LS of BKD-9, specimen G-B3; J, S1 of BKD-9, specimen B-H2). K, *Herpetotherium* lower left molar (LS of BKD-9, specimen G-A5). L, *Nyctitherium incisor* (S1 of BKD-9, specimen B-H1). Scale bars equal 1 mm.

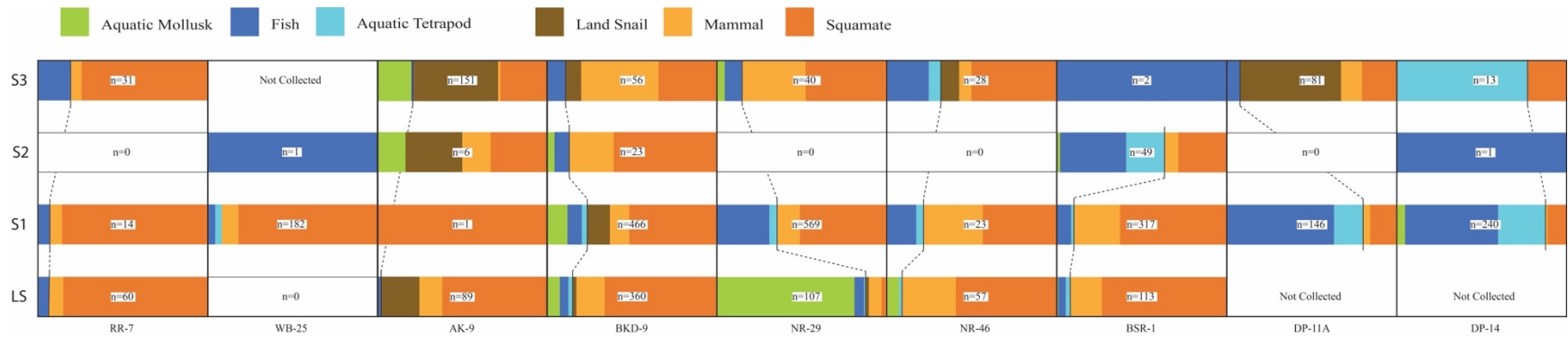


Figure 9. Proportions of fossils assigned to taxonomic ecological categories across sites and stratigraphic intervals. Numbers represent the total number of identifiable fossil elements from each interval. In some sediment samples, no identifiable fossils were recovered (indicated as open bar); at some sites a sediment sample was not collected at each interval (indicated on figure). Vertical black bars separate proportions of aquatic and terrestrial fossils and dotted lines track the change in this proportion through stratigraphic intervals (sites with less than ten identifiable elements were not included when creating the dotted lines). Sites are ordered geographically from west to east (see Fig. 2).

APPENDIX 1

Appendix 1. Counts of identified taxa specified by collection interval for each site. Fossils from sites with an asterisk were first examined by Schafer (2008) and reexamined in this study.

Class	Order	Genus	RR-7*	WB-25*	AK-9*	BKD-9	NR-29*	NR-46	BSR-1*	DP-11	DP-14
Bivalvia		Unknown			1 (S2) 17 (S3)						
Gastropoda		<i>Stagnicola</i>			1 (S3)	6 (LS) 3 (S1)	7 (LS)				2 (S1)
Gastropoda		<i>Biomphalaria</i>			10 (S3)	21 (LS) 53 (S1) 1 (S2)	80 (LS) 2 (S3)	4 (LS)	1 (LS) 1 (S2)		9 (S1)
Gastropoda		<i>Physa</i>			2 (S3)						1 (S1)
Gastropoda		<i>Gastrocopta</i>			20 (LS) 2 (S2) 75 (S3)	8 (LS) 62 (S1) 5 (S3)	2 (LS)	3 (S3)		48 (S7) 1 (S9)	1 (S5)
Osteichthyes	Lepisosteiformes	<i>Lepisosteus</i>	4 (S3)			3 (LS) 4 (S1) 1 (S3)	3 (LS) 148 (S1)		1 (LS) 2 (S1) 14 (S2)	5 (S1) 46 (S2) 2 (S7)	6 (S1) 19 (S2)
Osteichthyes	Amiiformes	<i>Amia</i>	3 (LS)	1 (S1)		2 (LS) 14 (S1) 2 (S2) 2 (S3)	11 (S1)	1 (S1) 4 (S3)	4 (LS) 6 (S1)	1 (S1) 2 (S2)	7 (S1) 8 (S2)
Osteichthyes		Unidentified fish	1 (LS) 1 (S1) 2 (S3)	6 (S1) 1 (S2)	2 (LS) 2 (S3)	13 (LS) 21 (S1) 3 (S3)	3 (LS) 19 (S1) 4 (S3)	3 (S1) 3 (S3)	19 (S1) 5 (S2) 2 (S3)	14 (S1) 24 (S2) 3 (S7) 1 (S8) 1 (S9)	35 (S1) 56 (S2) 1 (S3) 7 (S5)
Amphibia	Urodela	Unknown									1 (S2)
Amphibia	Anura	Unknown				1 (LS)			1 (S1)		

Class	Order	Genus	RR-7*	WB-25*	AK-9*	BKD-9	NR-29*	NR-46	BSR-1*	DP-11	DP-14
Amphibia		Unidentified amphibian						2 (S3)	4 (S2)		
Reptilia	Testudinata	Unknown				1 (LS) 12 (S1)	1 (LS) 10 (S1)		1 (LS)	21 (S2)	65 (S2)
Reptilia	Squamata	Unidentified lizard	51 (LS) 12 (S1) 23 (S3)	150 (S1)	55 (LS) 1 (S1) 2 (S2) 42 (S3)	238 (LS) 241 (S1) 14 (S2) 18 (S3)	3 (LS) 289 (S1) 18 (S3)	34 (LS) 10 (S1) 13 (S3)	83 (LS) 199 (S1) 14 (S2)	12 (S1) 6 (S2) 3 (S7) 14 (S8)	12 (S1) 13 (S2) 3 (S4) 3 (S6)
Reptilia	Squamata	Unidentified snake					1 (S3)				2 (S2)
Reptilia	Squamata	Unidentified squamate				2 (LS) 1 (S3)		1 (S3)		5 (S1)	
Reptilia	Crocodylia	Unknown		7 (S1)		8 (LS) 3 (S1)	16 (S1)	1 (LS) 1 (S1)	2 (LS) 4 (S1) 7 (S2)	4 (S2)	1 (S2) 10 (S4)
Mammalia		<i>Herpetotherium</i>				1 (LS)					
Mammalia		<i>Peratherium</i>				1 (LS) 1 (S1)			1 (S1)	2 (S2)	
Mammalia	Leptictida	Unknown				1 (LS) 1 (S3)					
Mammalia	Lipotyphla	<i>Nyctitherium</i>				1 (S1)					
Mammalia	Condylarthra	<i>Hyopsodus</i>					1 (S1) 1 (S3)		1 (S1)	4 (S2)	
Mammalia	Rodentia	<i>Microparamys</i>						1 (LS)			
Mammalia	Rodentia	Unidentified Ischyromyid			1 (S2) 2 (S3)						
Mammalia	Rodentia	Unidentified Sciuravid				2 (LS)					
Mammalia	Rodentia	Unidentified rodent		1 (S1)	2 (LS)	4 (LS) 2 (S1) 1 (S3)	2 (LS) 12 (S1) 4 (S3)	2 (S1)	2 (LS) 17 (S1) 1 (S2)	5 (S7)	
Mammalia	Plesiadapiformes	Microsyopidae (Family)				1 (LS)					

Class	Order	Genus	RR-7*	WB-25*	AK-9*	BKD-9	NR-29*	NR-46	BSR-1*	DP-11	DP-14
Mammalia	Plesiadapiformes	<i>Uintasorex</i>				1 (S1)					
Mammalia		Unidentified mammal	5 (LS) 1 (S1) 2 (S3)	17 (S1)	10 (LS)	47 (LS) 48 (S1) 6 (S2) 24 (S3)	6 (LS) 63 (S1) 10 (S3)	17 (LS) 6 (S1) 2 (S3)	19 (LS) 67 (S1) 3 (S2)	1 (S7) 4 (S8) 5 (S9)	3 (S2) 1 (SS2)

APPENDIX 2

Appendix 2. Taxonomic list of identified taxa.

Phylum Mollusca

Class Bivalvia

Class Gastropoda

Family Lymnaeidae

Genus *Stagnicola*

Family Planorbidae

Genus *Biomphalaria*

Family Physidae

Genus *Physa*

Family Gastrocoptidae

Genus *Gastrocopta*

Phylum Chordata

Subphylum Vertebrata

Class Osteichthyes

Order Lepisosteiformes

Family Lepisosteidae

Genus *Lepisosteus*

Order Amiiiformes

Family Amiidae

Genus *Amia*

Class Amphibia

Order Urodela

Order Anura

Class Reptilia

Order Testudinata

Order Squamata

Order Crocodylia

Class Mammalia

Infraclass Metatheria

Family Herpotheriidae

Genus *Herpotherium*

Genus *Peratherium*

Order Leptictida

Order Lipotyphla

Family Nyctitheriidae

Genus *Nyctitherium*

Order Condylarthra

Family Hyopsodontidae

Genus *Hyopsodus*

Order Rodentia

Family Ischyromyidae

Genus *Microparamys*

Family Sciuravidae

Order Plesiadapiformes

Family Microsyopidae

Genus *Uintasorex*

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