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## Taphonomy of turtles in the Middle Eocene Bridger Formation, SW Wyoming

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### Abstract

This study seeks to document and account for the distribution, abundance, and taphonomic condition of fossil turtles in a fossiliferous section of the Bridger Formation, Unit B (Early Middle Eocene of Wyoming). The following patterns were documented: (1) Fossils were non-randomly distributed stratigraphically and sedimentologically with most specimens concentrated in mudstones within a few meters above two of three widespread limestone beds. These concentrations were not artifacts of accumulations of eroded fossils on low angle slopes. (2) Fossil concentrations above limestones were widespread in the study area—tens of kilometers in at least one case. The well-exposed Black Mountain turtle layer shows a gradient in fossil density, highest to the south and lowest to the north. (3) Most specimens from fossil accumulations exhibited a similar taphonomic condition, with many shells mostly intact and unweathered, and with no skulls and few limb elements. Few elements bore predator tooth marks. Some bones in channel deposits were abraded, but most bones in fine-grained sediment were not. The largest concentrations of turtles were associated with specific layers of fine-grained sediment. These features suggest mass mortalities of turtles, and burial before many shells disarticulated. A model is presented to account for these data. In this model, a limestone forms in a shallow, basin-wide lacustrine environment. Then, a series of fluvial/lacustrine sedimentary units resulting from a large-scale episode of volcanism accumulated in the lake and buried the turtles. The volcanic event may have been the cause of death, from breathing ash-choked air, for large turtle populations in the lake/marsh environment, which were then buried early in the volcanic episode. Turtle populations evidently did not recover significantly until another shallow lake filled the basin. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Bridger Formation; Eocene; paleoenvironment; Reptilia; taphonomy

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## 1. Introduction

The Early Middle Eocene Bridger Formation of SW Wyoming has been divided into units A–E (Matthew, 1909), with units A and B in the Twin Buttes Member, and units C and D forming the Blacks Fork Member (Wood, 1934). Units A–D have been further subdivided into lower, middle, and upper subdivisions, separated by mapped marker beds (Evanoff et al., 1998). Limestone beds or white layers serve as stratigraphic markers (Bradley, 1964; West, 1976). Gunnell and Bartels (1994) recognized three biochronologic zones for the Bridgerian of the Green River Basin, and Bridger B constitutes zone Br2, or middle Bridgerian.

The Bridger Formation is a fluvial and lacustrine deposit exposed in the southern portion of the Green River Basin (Bradley, 1964). Deposition of Bridger sediments began in the floodplain adjacent to Lake Gosiute, and progressively filled the basin until Lake Gosiute was replaced by a broad floodplain of low relief, represented by the Bridger Formation, unit B. The last remnants of the relatively permanent Lake Gosiute were apparently in the southern part of the basin, at the base of the Uinta Mountains (Gustav, 1974). However, fluctuating water levels continued producing widespread, temporary lakes in which prominent widespread limestone beds were formed (Bradley, 1964; West, 1976). Sediments of the Bridger Formation are primarily of volcanic origin (Sinclair, 1906; Bradley, 1964; Gustav, 1974), apparently derived from the Absaroka volcanic field in the Yellowstone region of northwestern Wyoming (Bradley, 1964; Evanoff and Rossetti, 1992), punctuated periodically by these limestones.

The Bridger Formation has been well-known for its rich fossil vertebrate fauna since the 1870s (West, 1976; Evanoff and Ivy, 1992). In some stratigraphic units in the Bridger, the most abundant fossils are turtles, which were quite diverse during Bridgerian time (Hutchison, 1980, 1982). Bridger B fauna and flora suggest that the climate was warm temperate to tropical (Dickinson et al., 1988; Gunnell, 1990) and may have supported moist, closed forest (Gunnell and Bartels, 1994).

Previous paleontological studies in the Bridger Formation have often emphasized mammals (e.g.

Matthew, 1909; McGrew and Sullivan, 1971; Gazin, 1976; Stucky, 1984; Gunnell, 1996), with less study of the abundant turtles. Taxonomic work has documented the identity and diversity of the turtles (e.g. Hay, 1908; Gaffney, 1972; Hutchison, 1984), but there has been little documentation of their distribution within the formation. The fossil turtles could serve as an important tool for analyzing the processes responsible for the rich fossil content of the Bridger Formation. They are useful because they are abundant, widespread, and have not been collected intensively, and thus, surface samples are likely to be more complete than for mammals.

Some attention has been given to general taphonomic comparison of the Bridger Formation with associated formations (Bartels, 1994; Zonneveld, 1994; Murphey, 1996). Zonneveld (1994) indicated that the Bridger turtles consist of complete shells, and Gilmore (1945) examined a concentration of articulated turtle shells. He concluded that they were transported to their burial site after death, because of the absence of skulls, cervical and caudal vertebrae, and articulated limbs. Murphey (1996, 1998) interpreted a concentration of bones in Bridger C as a complex assemblage representing bird bones and eggshell near a nesting site, bones from owl pellets, combined with an overprint of attritional accumulation.

Our goals in the present study are (1) to characterize in a semi-quantitative manner the lateral, stratigraphic, and sedimentological distribution of fossil turtles within and across specific stratigraphic units in the Bridger Formation, unit B; (2) to characterize the taphonomic condition of fossils recovered from selected sites within one of these stratigraphic units; and (3) to develop, in connection with a complementary sedimentological study, a model to account for the distribution and condition of turtle fossils in the selected study interval (Brand et al., 1993). This report concentrates on the taphonomy of the turtles, with more detailed sedimentologic analysis reported elsewhere (Buchheim et al. 2000).

## 2. Methods

### 2.1. Selection and mapping of study units

The study was centered in the Devil's Playground area (Fig. 1, inset), in the SE part of

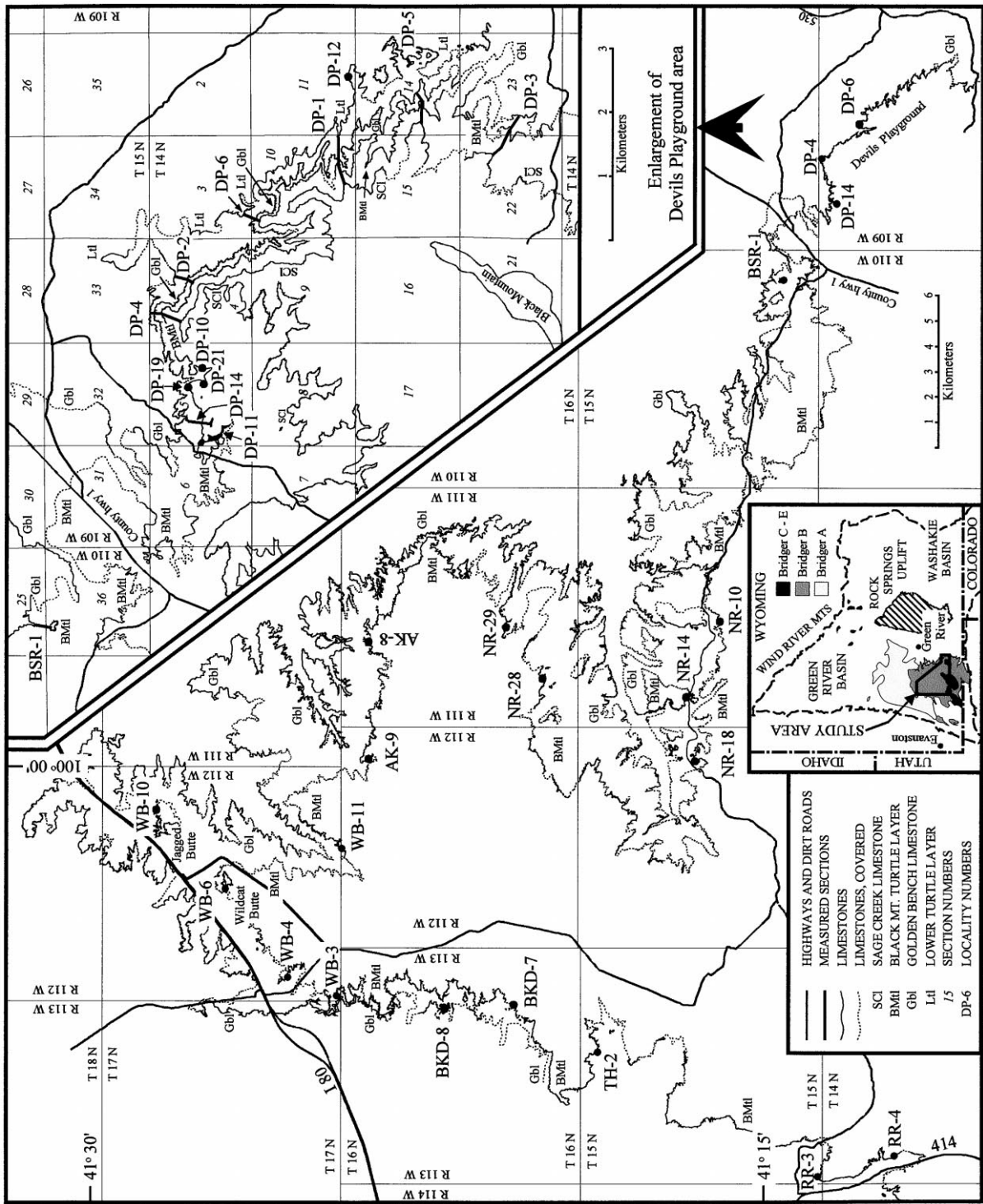


Fig. 1. Map showing outcrops of the Black Mountain turtle layer, the Golden bench limestone, and study localities. The main map shows only the 21 study sites of the basin-wide study. Mapping on the west side of the basin was done, in part, by Emmett Evanoff.

the basin, and extended to the NW and W, over much of Bridger B exposure (Fig. 1). In the Devil's Playground area, three stratigraphic units were selected and mapped. They were selected because all three were fossil-bearing mudstones lying on prominent, bench-forming limestones. Fossil turtles were common in two of these units and much less common in the third, providing a context for comparative study of factors favorable to burial and/or preservation of turtles. All three units were traceable and well exposed for several kilometers. The upper unit was termed the Black Mountain turtle layer (BMtl), the next was called the Golden bench limestone (Gbl), and the lowest layer was called the Lower turtle layer (Ltl).

The three study units were mapped in the field on aerial photos and on 7.5 minute topographic maps. Stratigraphic relationships between these and other reference units were established by measuring sections at eight sites in the Devil's Playground area, using a Jacobs staff and Abney level (Brand, 1995). Two of these units were mapped more extensively to the W and NW. The Golden bench limestone is a prominent bench-former mapped around the entire study area (Fig. 1). The BMtl was also mapped around the study area. It was identified by its sedimentological characteristics and stratigraphic relationship to the Golden bench limestone. Correlations and mapping were verified by walking out the units throughout the basin. The Meadow Springs white layer (MSwl), apparently a reworked tuff, was identifiable at almost all sites 12–18 m above the BMtl, and provided additional verification of the stratigraphic position of the BMtl. Additional Bridger B marker beds were also mapped in the same way, providing additional confirmation in correlating our study units (Brand, 1997; Evanoff et al., 1998).

## 2.2. Detailed taphonomic site study of the BMtl

Our investigation involved three complementary studies beginning with a detailed site study and extending to a broader, basin-wide comparative study of fossil distribution. A 4.5 ha exposure of the BMtl with abundant turtles (locality DP-11) was studied in detail. This area was at the base of

a steep slope eroded to form a nearly flat bench, with lobes of mudstone providing extensive fossil-bearing surface (Ambrose, 1993) (Fig. 2).

Other sites were examined for comparison with the DP-11 site. Immediately to the east of the main study area, a concentration of turtles (locality DP-10) in the same mudstone unit, and an adjacent concentration of bones in a sandstone channel at the same stratigraphic level were observed, and a sample of bones from each was collected. Other sites in the same horizon, DP-19 and DP-21, were sources of specific data, mentioned later.

The distribution of turtles was documented in a 13–15 m thick complex of mudstones and sandstones associated with the BMtl at DP-11, delimited by the limestone bench-forming unit at the base and the MSwl at the top. The entire area was carefully searched for fossil turtles, and each was marked with a flag. A complete turtle, a distinct cluster of at least 15 bones (almost always many more) of the same type and size range, or a string of turtle bones of a similar type and size range coming downslope from one point was counted as one turtle. These piles of bones appeared to be turtles that disarticulated into distinct clusters after they were uncovered by erosion. Two of us (L.B. and P.A.) marked and recorded all bone concentrations. This provides an index of turtle abundance but not an absolute number of turtles. Some bone clusters could represent only a portion of a shell. However, attempts to assemble a few of the bone clusters indicated that some consist of at least two turtles, so on average, we believe that the number of bone clusters is a reasonable estimate of number of turtles present. Scattered bones were also abundant in places but were not documented in this study.

A grid of flags at 10 m intervals was laid out over the approximately level part of the area, below the steep slope, using a compass and a 30 m measuring tape. A map of the area was then made, and the position of all fossil turtles exposed at the surface ( $n=340$ ) was plotted on the map (Fig. 2). The vertical position of each turtle was measured in reference to the nearest exposures of two marker units: the basal limestone unit, and a thin, persistent coaly shale layer 0.8–2.3 m above the limestone. These measurements were made with two

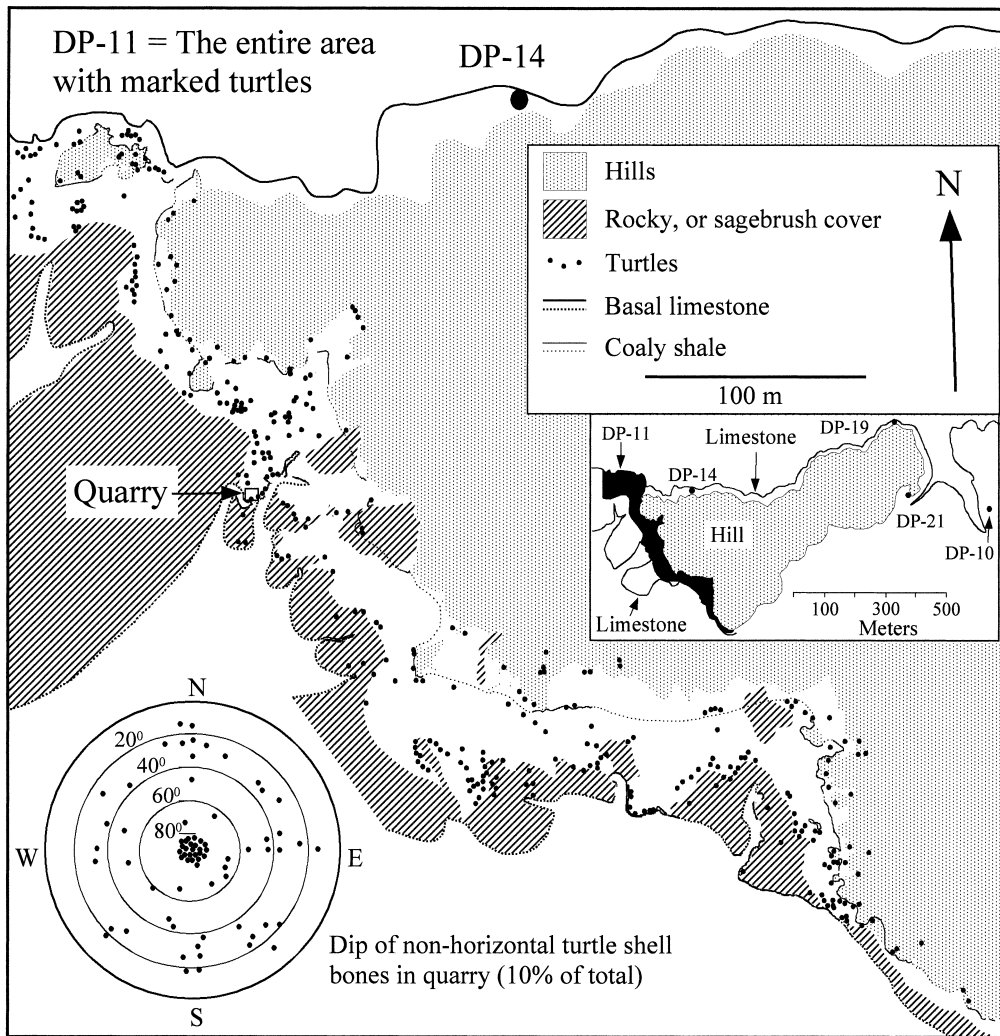


Fig. 2. Map of locality DP-11. Each dot is the location of one turtle ( $n=340$ ), as described in the text. Dotted lines are approximate location of rock units where covered (coaly shale) or not mapped in detail (limestone). The inset shows the entire hill involved in this study. The lower left diagram shows the direction and magnitude of dip for turtle bones dipping more than  $10^\circ$  from the horizontal. Horizontal bones would appear at the perimeter of this graph, but since they do not have a directional component, they could not be included.

Jacob's staffs marked at 1 cm intervals, one with a  $5\times$  magnifying Abney level (Brand, 1995) used as a surveying transit and the other as a stadia rod. The same method was used to measure changes in elevation of the two marker beds across the study area. From these measurements, the dip of the basal limestone was determined, and the vertical position of the turtles was adjusted to correct for regional dip. The position of turtles on

the steep hillside, within the 13–15 m vertical section, was estimated. A sample of 50 clusters of turtle bones, randomly selected from across the study area, was collected for further study (the DP-11 surface sample).

An  $11\text{ m}^2$  quarry (the DP-11 quarry) was excavated within this area (Fig. 2), just above the basal limestone, to better characterize distribution of bones within the sediment before erosion. All

bones were numbered, collected and their position plotted on a quarry map, in relation to a grid. The grid was laid out over the quarry with string at 1 m intervals, and a 1 m<sup>2</sup> wood frame with strings at 20 cm intervals was used for determining the position of fossils. The dip of non-horizontal bones (dip greater than  $\sim 10^\circ$ ) was measured with a compass. Sediment samples were collected, representing the section exposed in the quarry from 10 cm below to 10 cm above the fossil-bearing layer.

At DP-11, most fossils occurred on the extensive, almost flat surface, flanked by a steep slope with few turtles. To determine the effect of these different slopes on turtle abundance, the fossil distribution was studied at DP-21. This site has a uniform, gentle slope through most of our studied section. The concentrations of turtle bones were flagged, and the vertical position of each was determined in relation to the limestone and coaly shale. This analysis utilized the same methods as those used at DP-11.

### 2.3. Taphonomic condition

The completeness of the turtle skeletons was evaluated in the turtles in the DP-11 quarry and was estimated in the surface turtle specimens at DP-11 (especially the random sample of 50 turtles).

Articulation of turtle bones in the DP-11 quarry was also noted.

Turtle shell bones from several samples (Table 1) were analyzed for taphonomic features such as weathering, abrasion, and bite marks. These included the DP-11 quarry, 10 randomly selected turtles from the surface sample in the main study area, a sandstone channel at DP-10 and an adjacent mudstone with abundant turtles, a sandstone channel near the main study area (DP-19), and five study localities in the center and northern part of the Bridger B exposures. In each sample, bones were selected before being closely examined, to prevent bias based on taphonomic features. If a selected bone was too small or too broken to provide the needed taphonomic information, another bone was chosen to make up the desired sample size. Upon examination in the lab, a few bones in these samples were not considered adequate to provide reliable data.

Abrasion of turtle shell bones was determined by comparison to a set of standards, with abrasion levels between 0 and 4. Abrasion of turtle shell bones could be most consistently measured on the articulation surfaces of the bones. The scale of abrasion used in this study is specific to turtle bones, and is adapted from the scale used by Shipman (1981) (p. 114). The rounding of the points on the articulation surfaces could be readily

Table 1  
Samples and sample sizes (number of turtle shell bones) used in the study of abrasion and weathering<sup>a</sup>

Site	Description	Weathering	Abrasion
		n	n
WB-6	Surface bones in mudstone	50	50
AK-8	Surface bones in mudstone	50	50
AK-9	Surface bones in mudstone	50	50
NR-28	Surface bones in mudstone	50	50
NR-29	Surface bones in mudstone	50	44
DP-11	Associated bones of two <i>Echmatemys</i> turtles in quarry	55	55
DP-11	Associated bones of a partial trionychid turtle in quarry	37	
DP-11	Scattered bones in quarry	133	100
DP-11	Surface sample—10 bone clusters assumed to represent intact turtles, with other bones mixed in		100
DP-10	Random selection from turtles in mudstone		100
DP-10	Disarticulated bones in sandstone channel		100
DP-19	Disarticulated bones in sandstone channel		61

<sup>a</sup> At each site, bones were selected at random for this study. See text for more details.

differentiated from broken points that sometimes resulted from uncovering the bones in a quarry. We tested for differences in frequency of abrasion levels across samples using the Chi-square test.

Potential tooth punctures were evaluated by comparison with published examples (Shipman, 1981). Weathering stage was assigned according to the stages (0–5) described by Behrensmeyer (1978). In some cases, the surface of the fossil turtle shell bone began to disintegrate as it was uncovered. This could generally be distinguished from weathering, but it is possible that some cases of true advanced weathering were not identifiable because of post-exposure bone surface damage. Weathering of modern turtle bones was studied for comparison with the fossil bones (Brand, to be published elsewhere). The modern turtle shells were observed for up to 3 years in aquatic and terrestrial situations, and weathering was assigned to stages 0–5 by the same methods.

#### 2.4. Comparison of three mudstone units in the Devil's Playground area

The study of turtle distribution in the BMtl was extended to the rest of the Devil's Playground area, and compared with distribution in the Gbl and Ltl. Seven study sites were selected at approximately equally spaced intervals along Devil's Playground E and SE from DP-11 (DP-1-6, 14) (Fig. 1). These sites were chosen on a topographic map, without reference to fossil content, to provide an unbiased assessment of turtle abundance. An additional site NW of DP-11 was found with suitable exposure of the BMtl, and it was also included (BSR-1). Fossil abundance on each of the three study units was surveyed at each site. At two sites (DP-3, 14) one or two of the units were not exposed. One additional site was selected to provide data for the Lower turtle layer (DP-12).

At each study site, we documented the occurrence and distribution of all observed fossils in sediments above each bench-forming limestone (BMtl, Gbl, Ltl) and determined surface area prospected to allow calculation of density. Turtle fossils were recorded as single elements or clusters of bone of estimated number, and the fossil distribution within the sediments was recorded as fol-

lows: A = bench above limestone; B–D = subsequently higher, arbitrary units each representing one eye height (~1.7 m). To minimize any investigator bias, all transects were done by two of us (L.B., T.G.) with each transect split and data pooled. All documentation was done in transects 10–30 m long; multiple transects were done at each site and limestone. To allow the calculation of surface area prospected, we estimated the width of the bench in each transect by pacing (always involving an average of at least two estimates) and estimated or measured the slope of levels B–D. In all cases, the total surface area prospected per limestone per site was  $\geq 2100 \text{ m}^2$ . Densities of turtles were estimated by using the number of complete turtles or clusters of  $\geq 40$  elements as an index of turtle density. The number of turtles as a function of surface area prospected (expressed as hectares;  $1 \text{ ha} = 10\,000 \text{ m}^2$ ) was calculated. Differences in frequencies of turtles were tested using the Chi-square test. Statistical tests were confined to the BMtl and Ltl samples because low frequencies on the Gbl compromised statistical comparison. Separate tests were done on level A, B, and C+D. For the Chi-square test, expected frequencies were estimated based on the area of exposure that was prospected.

One of us (T.G.) walked approximately 4 km of BMtl and 3 km of Ltl exposure, noting the precise position in the sediments of in-situ turtles, and making a field determination of the grain size of the sediment entombing each turtle. If the turtle was located in or within  $\pm 10 \text{ cm}$  of a thin organic-rich unit often containing abundant turtles (the organic turtle bed), this was also noted.

The overall distribution of turtles in the Bridger B section, from the Ltl up to the Sage Creek limestone (formerly the Sage Creek white layer; Evanoff et al., 1998) (top of Bridger B) was quantified in a 30 m wide vertical transect of the hillside at locality DP-6. The surface exposure of each rock unit, in square meters, was estimated (using thickness and slope, as noted above), and all vertebrate fossils were counted in each unit. The number of bones per hectare in each rock unit was then calculated. The results of this quantitative analysis of one site were compared with qualitative observations at many other locations to evalu-

ate whether the stratigraphic distribution of turtles was consistent across the basin.

### 2.5. Broad distribution of fossil turtles in the Black Mountain turtle layer

To better characterize broad patterns in the density and distribution of turtles in the BMtl across the basin, the fossil content and sediments were studied at 21 sites (Fig. 1, main map). Study sites were selected from available outcrops with adequate exposed surface to achieve an approximately evenly spaced geographical distribution of sites.

A stratigraphic section was measured at each site, and rock samples were collected for analysis. The survey method for determining density of turtle bone was similar to that used at Devil's Playground, but with some differences. One transect of 30 m width was laid out at each site, extending vertically from the basal limestone up through the fossiliferous units (approximately 10 m above the limestone). The area of exposure was estimated at each transect, using the method described above. All fossils exposed at the surface were marked with a colored flag, and were counted by one of us (L.B.). Because this method differed somewhat from that used in the study at Devil's Playground, we also used it at three sites within the latter area to tie it in with previous methods of estimation. The number of turtle bones per hectare of exposure was calculated for each transect.

### 3. Extent and relationships of study units, and fossil plant content

The three limestones are continuous through most of the Devil's Playground area (Fig. 1) and were readily mapped. The Lower turtle layer goes underground before reaching the S and the NW extent of Devil's Playground, and outcrops of this unit were not reliably identified in other parts of the basin at the time this study was done. However, the other two study units are widespread. The Golden bench limestone is a prominent and almost continuously exposed marker around the entire

basin (Fig. 1) and could be followed and mapped with a high level of confidence. The Meadow Springs white layer (MSwl) is present at most study localities, and was a valuable aid in identifying the BMtl. The BMtl interval was not continuously exposed. However, at every location where we have examined the appropriate stratigraphic interval, 20–30 m above the Gbl, the BMtl is conspicuous and continuous. In some areas, these exposures extend  $\geq 2$ –4 km. The basal limestone below the BMtl in the Devil's Playground area and at locality RR-4 was usually represented farther north as a calcareous claystone unit.

Occasional horizontal fossil logs were found associated with the Ltl and Gbl (Fig. 3), but identifiable plant material was not found to be associated with the BMtl. There was commonly a thin unit associated with the Gbl that contained abundant fragments of woody plant material, some leaves, and other plant fossils. Identifiable taxa were *Sequoia sp.*, *Sabalites sp.* (Palm), *Acrostichum sp.* (Fern), and possible algal mat material. Just below the Gbl at some locations was a deposit of laminated, organic-rich, fine sand to siltstone with abundant plant fragments. No logs or other identifiable plant material were found to be associated with the Bmtl, but the organic turtle bed, present throughout the Devil's Playground area, contained many small (< mm size) and several larger carbonized pieces of plant material.

### 4. Distribution and condition of fossil turtles in study areas

#### 4.1. Distribution of turtles in the Bmtl at DP-11 and vicinity

The turtle density was high at DP-11, with 76 turtles per hectare (340 turtles in 4.5 ha). Most turtles were exposed in the outer half of the broad bench flanking a small butte (Fig. 2). The vertical distribution of the turtles was skewed; 83% occurred in mudstones between the limestone and a thin, persistent, coaly shale unit, which averaged 1.31 m above the limestone; 89% were in the lower 2 m above the limestone (Fig. 3). This concentration in the lower few meters of section was not



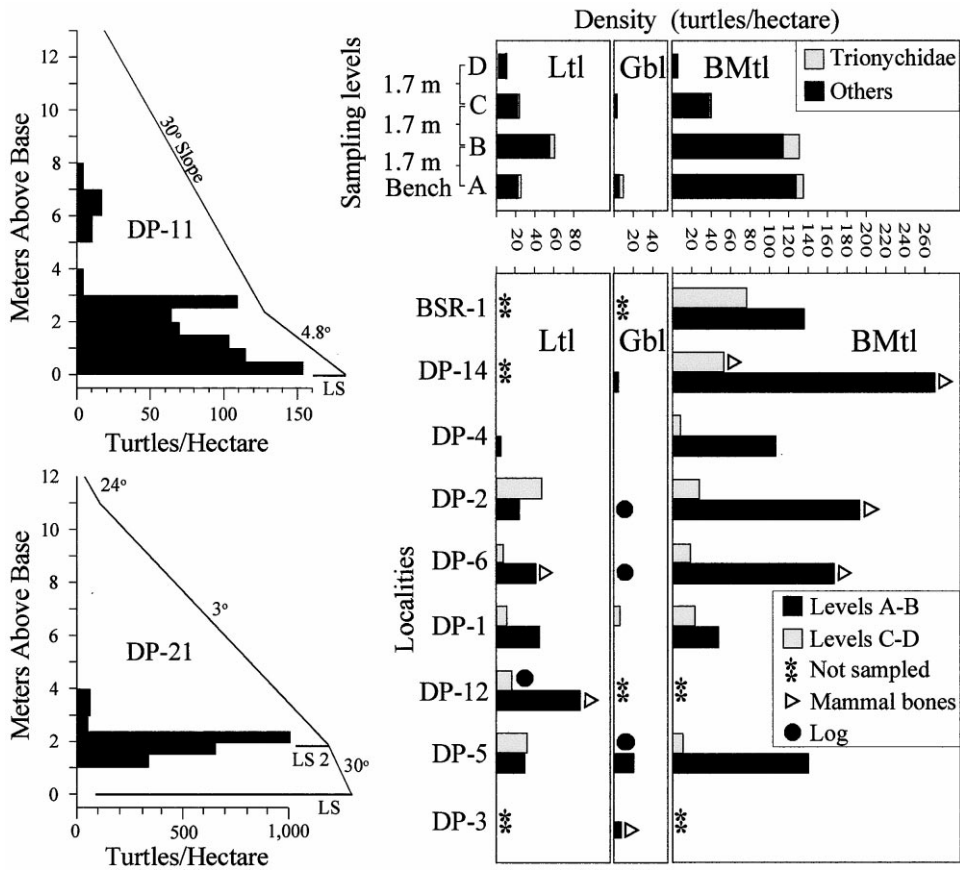


Fig. 3. Left: stratigraphic distribution of turtles between the basal limestone of the Black Mountain turtle layer, and the overlying Meadow Springs white layer, at two locations. LS—basal limestone; LS 2—a local limestone layer at location DP-21. To the right of each diagram is shown the mean slope of the surface, in two or three segments. Right: density of turtles on three benches at Devil’s Playground. Top: mean density of turtles in each sampling level, with all localities combined. Bottom: density at each locality. Ltl= lower turtle layer; Gbl=Golden bench limestone; BMtl=Black Mountain turtle layer. A hectare is 10 000 m<sup>2</sup>.

an artifact of exhumed bones collecting preferentially on the flat bench. A similar pattern was observed 850 m east at DP-21 (Fig. 2) with a bench that sloped gradually and uniformly upward through most of the section (Fig. 3). Also, on a nearby steep hillside (BSR-1), there was no bench, but turtle bones were still concentrated within the lower few meters of the BMtl study unit.

Many fossils were recovered from the DP-11 quarry (1246 turtle bones and 175 elements representing other vertebrates), mostly from the organic turtle layer. The turtles were represented primarily by shell bones, with some limb bones, but no skulls or skull elements were observed. Two clus-

ters of bones represented turtles that had disarticulated but were still associated. The bones of each cluster were scattered over ~1 m<sup>2</sup>. In each case, there was a main cluster of bones arranged in three dimensions, rather than in one plane, as was the other material. One contained about one-third of a trionychid turtle, and the other cluster contained significant portions of two *Echmatemys*. Orientation of recovered bones indicated that the *Echmatemys* were originally upside down. Many of these bones were in non-horizontal positions, but were not turned over. These turtles may have been buried when still articulated, with bones subsequently separated by soft-sediment deforma-

tion, for which there was abundant evidence in the sediment (Buchheim et al., 2000). Most (90%) of the turtle bones were approximately horizontal (0–10°), with the remaining elements dipping 10–90°, with random strike directions (Fig. 2).

The remaining bones in the quarry seemed to be a random scatter of disarticulated turtle elements, gar scales, and a small number of other small vertebrate specimens [mammal teeth and jaws included specimens of *Hyopsodus* ( $n=2$ ), *Orohippus* ( $n=3$ ), *Notharctus* ( $n=2$ ), *Omomyss* ( $n=1$ ), *Microsypops* ( $n=1$ ), and an unidentified insectivore].

#### 4.2. Taphonomic condition of turtles in the DP-11 area

Most associated clusters of turtle bones on the sediment surface apparently represented shells or partial shells buried intact. Most are now disarticulated, but the disarticulation appears to have occurred after the turtles were exposed by erosion, because the bones are in such distinct clusters. Some turtles are still partly buried, with the buried portion of shell articulated, and the exposed portion disarticulated as in the other bone clusters. This observation supports the interpretation of the turtle bone clusters as turtles disarticulating where they eroded out of the sediment. Turtles in the quarry were disarticulated, but three were still associated. No turtle skulls or identifiable skull bones were found, and there were only a few turtle limb bones (Table 2).

A randomly selected sample of 30 turtles in the surface sample at DP-11 contained 32 turtle limb bone fragments and eight girdle bone fragments, but no identifiable skull bones. It is unlikely that these bones were selectively removed after exposure of the turtles, since there were many small turtle shell fragments that should have been as easily transported as skull or limb bones. It is not known whether any bones were transported from the site before burial.

The percentage of bones showing evidence of abrasion was low, except in channels (Table 1, Fig. 4). Because it was not clear to us that abrasion level 1 on these fossil bones is sufficient to indicate

Table 2

Turtle limb bones recovered in the quarry at DP-11

Two turtles in quadrant B-2	Other
R humerus	R humerus
R femur	R femur—2
L femur	R ilium—2
R ulna	L ilium
L scapula—2	Scapula
Phalanges—4	Pelvic
Pelvic fragment	R humerus
Unidentified girdle fragment	Radius
	Fibula
	Tibia
	Phalanges—8
	Unidentified limb bone fragments—4

transport, it was combined with level 0 in this study.

In the DP-11 quarry 31% of the disarticulated bones or bone fragments showed abrasion above level one. Smaller bone fragments were more abraded than larger ones. Mean length times width of these bones was 602 mm for those in abrasion levels 0–1.5, and 324 mm for those in abrasion levels 3–4 ( $n=271$ ). The two *Echmatemys* in the quarry experienced little or no abrasion (the 10% of bones that were abraded may not have been from those turtles). The surface sample of 10 turtles buried intact were mostly unabraded (Fig. 4). It is likely that some disarticulated bones were mixed into these samples and may be the source of the abraded bones.

All samples from sandstone channels exhibited significantly higher levels of abrasion than bones in mudstone (chi-square = 174.8,  $df=4$ ,  $P<0.001$ ). The percentage of bones showing abrasion differed among the mudstone samples, but the differences were small and not related to bone size. At locality DP-10, the mudstone surface sample collected adjacent to a sandstone channel contained a higher percentage of abraded bones than was found in other mudstone samples.

In all samples, most bones had not been weathered. Ten per cent of disarticulated bones in the mudstone sample of quarry DP-11 were at weathering stage 1, and 3% were at stages 2 or 3. This was by far the highest amount of weathering seen

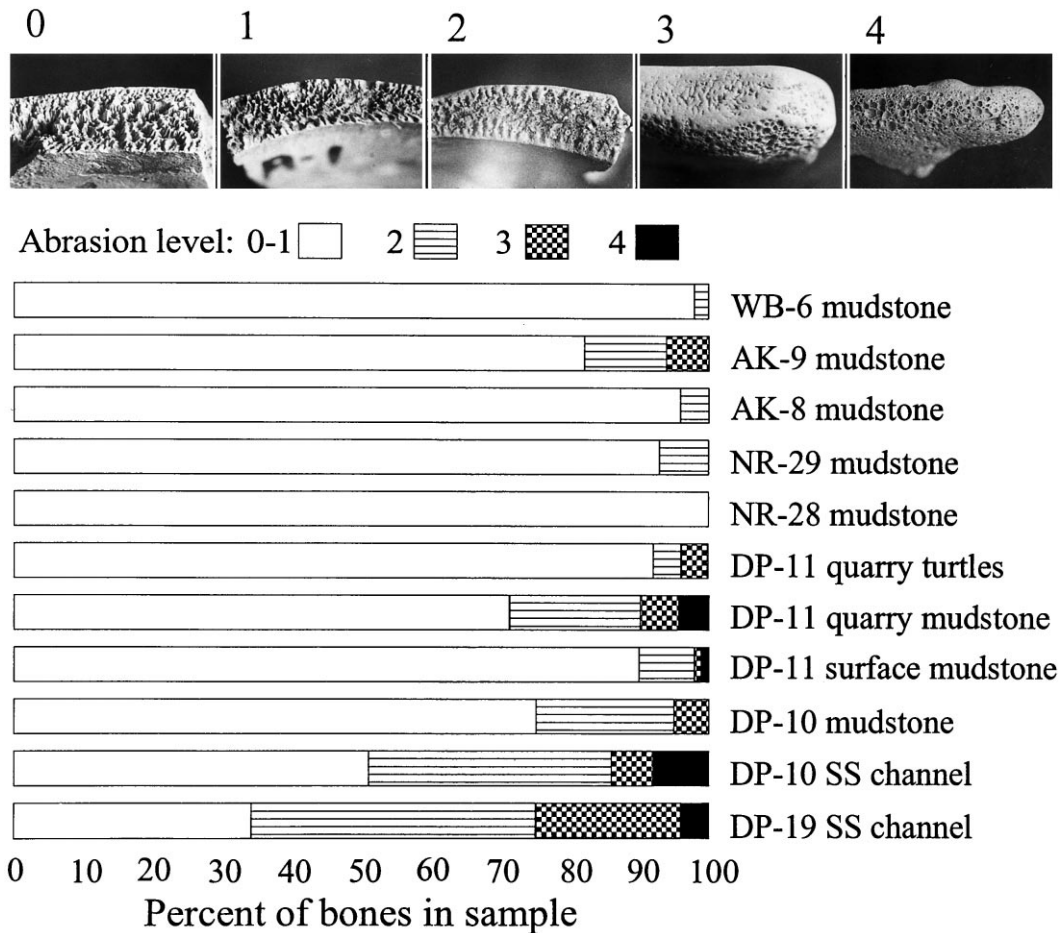


Fig. 4. Upper: standards for evaluating abrasion of turtle bone, representing abrasion levels 0 to 4. Level 0—no abrasion; 1—slight abrasion of the edges; 2—about half of the articulation surfaces eroded away; 3—articulation surfaces almost entirely missing, but still detectable; 4—bone edge smooth and rounded, with no articulation surfaces evident. Lower: percentage of bones in each abrasion level, at several localities. See Fig. 1 for locality information.

in any of the samples (Fig. 5). The *Echmatemys* in this quarry were at stage zero, and the partial *Trionychid* was at stage 1. In all other samples, stage 1 was the highest level of weathering seen, and very few bones were clearly at stage 1.

In an experimental taphonomy study (Brand, unpublished), turtle shell bones showed no evidence of weathering after 3 years in fresh water. In a terrestrial situation, with the bones lying on the ground in warm, dry southern California, after 1 year, 16% were at stage 1, and the rest were at stage 0. After 3 years, 37% had reached stage 1,

and 14% were at stage 2. A turtle shell is composed of many bones that separate during the disarticulation process. In these experiments, turtle shells in fresh water were 25% disarticulated within 14–21 weeks (depending on the temperature), and 75% disarticulated by 18–43 weeks. Turtle shells in the terrestrial setting were 25% disarticulated in 69 weeks, and almost 75% disarticulated in 3 years.

Evidence of predator or scavenger activity was rare on the fossil turtle bones. Out of 400 specimens from the DP-11 quarry and five additional study sites, there was one rodent gnaw mark, and

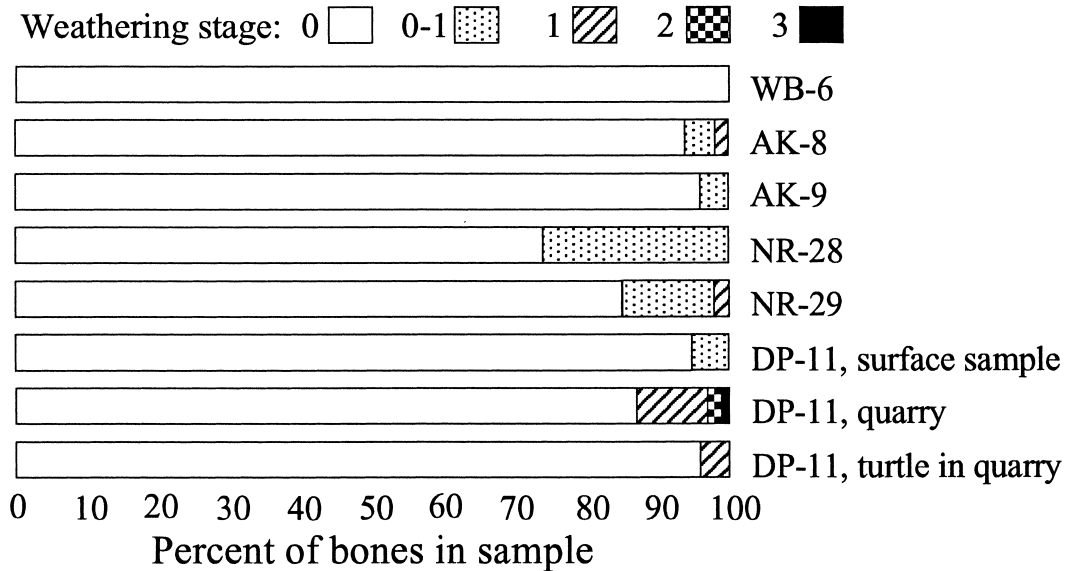


Fig. 5. Weathering stages (stages 0–5, as described by Behrensmeier, 1978) in samples of turtle shell bones from the BMtl.

10 cases of possible tooth punctures or scratches. Most were of somewhat questionable origin, but they may be tooth marks.

#### 4.3. Patterns within and between study units, across the Devil's Playground area

In the 30 m wide transect at DP-6, most turtles were concentrated at a few levels (Fig. 6). This pattern was found at all study localities. In the Devil's Playground area, turtle-rich units include the Lower turtle layer, the Black Mountain turtle layer, and a stratigraphically higher turtle-rich unit not included in this study. Each of these is a mudstone immediately above a resistant, bench-forming, limestone.

Of the three levels studied in the Devil's Playground area, fossil turtles were most abundant in the BMtl, with most fossils in levels A and B (Fig. 3); the pattern of basal concentration of turtles, observed at DP-11 (see above), is thus a general one. The turtle density remained high throughout the documented exposures of BMtl at Devil's Playground, over an area 11.1 km across.

Although the fossil turtles were always concentrated in levels A and B of the BMtl, the densities varied significantly across BMtl sample localities,

ranging from 46 to 268 turtles per hectare (combined A and B: chi-square = 35.0,  $df=6$ ,  $P<0.001$ ). The highest concentration among the randomly sampled sites was at DP-14. A more spectacular concentration was observed at DP-10, where the density was 386 turtles per hectare; however, this site was not part of our random sample.

A comparison across the BMtl, Gbl, and Ltl documented substantial inter-unit differences. The turtle density was much lower in the Golden bench sediments than in the other two units. Although isolated elements were found at most sites on the Golden bench, this unit yielded few associations of elements that could be interpreted as representing intact turtles (Fig. 3). In contrast, Ltl yielded numerous turtles, but with overall densities substantially lower than for BMtl. Ltl had significantly lower frequencies of fossil turtles than the BMtl in level A (chi-square = 34.9,  $df=1$ ,  $P<0.001$ ) and B (chi-square = 13.5,  $df=1$ ,  $P<0.001$ ), but not in levels C+D (chi-square = 0.49,  $df=1$ ,  $P<0.05$ ). Many Ltl turtles were associated with a widespread claystone/siltstone unit, located in sample level B and often containing abundant small tufa-covered logs at its top. The pattern of turtle abundance in the Lower turtle layer continued for at least 5.3 km of the 6.2 km of exposure of the unit.

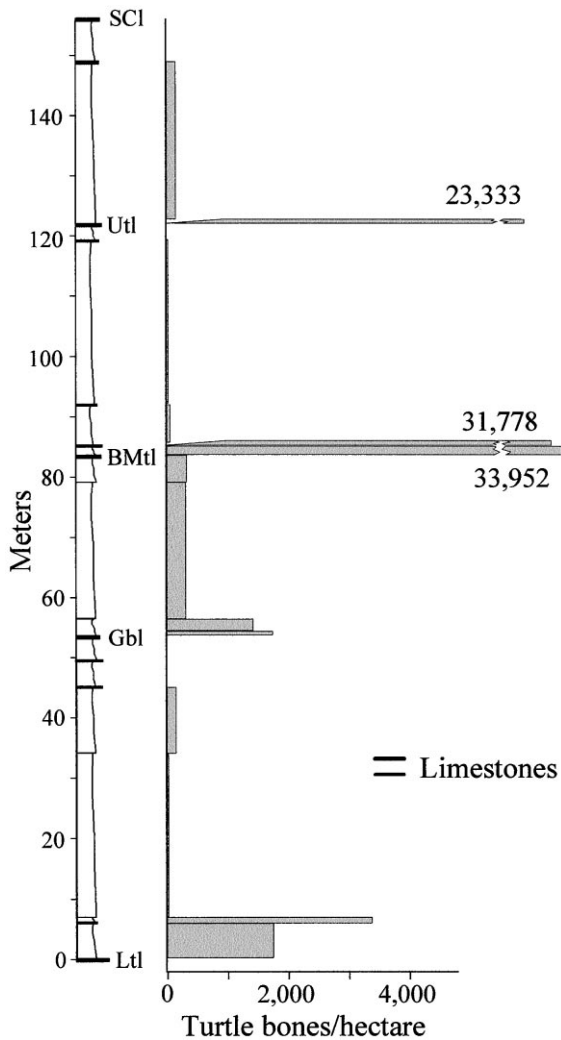


Fig. 6. Turtle density along a 30 m wide vertical transect of Bridger B exposures at DP-6. The upper turtle layer (~120 m above Ltl) was not included in this study. Ltl=Lower turtle layer; Gbl=Golden bench limestone; BMTl=Black Mountain turtle layer; SCI=Sage Creek limestone; Utl=Upper turtle layer. A hectare is 10 000 m<sup>2</sup>.

Sedimentological associations with fossils were striking. In both the BMTl and Ltl, 80% of in-situ turtles examined specifically for sedimentary context were in fine-grained sediments (siltstone, claystone), with 15% in sandstones. There was no difference observed in sedimentary context between BMTl and Ltl. In the BMTl, 53% of in-situ turtles examined were associated with a persistent,

organic-rich layer (organic turtle bed). This concentration may be responsible for greater densities in the BMTl than Ltl. When 53% of the turtles were removed from the BMTl sample, the differences between BMTl and Ltl were not significant (pooled sample of A and B; chi-square=3.2, df=1,  $0.1 > P > 0.05$ ). The organic turtle bed was not observed farther north and west in the basin.

#### 4.4. Basin-wide patterns in distribution of fossil turtles in Black Mountain turtle layer

The turtle bones in the BMTl were most abundant in the southern part of the basin, and the abundance dropped off toward the north (Fig. 7). The levels of abrasion and weathering were very low throughout this extended area (Figs. 4 and 5).

## 5. Discussion

The available data warrant discussion of more than one interpretation regarding the processes responsible for accumulating fossil turtles in middle Bridger B. Issues that will be addressed include (1) the paleoenvironment, (2) the source of the turtles, and (3) the process responsible for the massive accumulations of turtles. These processes operated at a large geographic scale, with fossil concentrations at particular horizons over kilometers to tens of kilometers of exposure. In the BMTl, this process seemed to be operating across the entire basin. These widespread, continuous accumulations of turtles do not seem to be compatible with the occurrence in local ponds and small marshes. A large-scale turtle-rich habitat is needed, such as a very extensive marsh or a large lake with a suitable turtle habitat scattered throughout. This habitat was not necessarily uniform, since, within the most widespread and well-studied turtle-rich layer, the Black Mountain turtle layer, there was a clear N–S density gradient, with the highest density of turtles in the south.

The density of turtles in these concentrations is not unusual compared to modern turtle densities in suitable pond or marsh habitats (Iverson, 1982, and literature reported therein). However, in modern environments, the turtles are common



only in ponds or marshes (where modern turtle densities were measured), whereas in the Bridger Formation, these high densities continued for many kilometers across Bridger exposures, as indicated by our random samples. Modern turtle densities based on random sampling across modern landscapes would be much lower than densities of fossil turtles measured in the Bridger Formation.

Most of the fossil turtles fit a common taphonomic condition—relatively intact shells, with few limbs and almost no heads (we found no skulls; other collectors have found a few). These generally lack abrasion and evidence of predation or scavenging, and are relatively unweathered. This implies a highly stereotypic taphonomic history. The turtles died in large numbers and remained unburied for a short time to allow removal of heads and many limbs but left shells intact and relatively unweathered at the time of burial. Experimental work cited above indicates that the time frame for this process is most likely weeks to months. It seems very unlikely that this common taphonomic pattern could be produced by turtles dying attritionally and then exposed for significantly varying lengths of time. Gustav (1974) applied a similar interpretation to a fossil-rich locality near our NR-10. He concluded that the large number of remarkably preserved turtles indicates a rapid entrapment. They must have died in the lake, perhaps smothered by vast amounts of ash, and then quickly settled to the bottom, where they were covered by the settling ash.

There are several mechanisms that offer possible explanations for the rarity of skulls and limb bones. Laboratory observation of turtle disarticulation indicates that turtle heads and limbs separate from the body early in the process, while the shell is the last to disarticulate (Brand, 1994; and unpublished data). Turtle skulls disperse in a water current more readily than other turtle bones (Blob, 1995), and this factor may also have been involved in sorting the skulls from the turtle shells. There also are unpublished reports that some birds will remove the heads of dead turtles. More data are needed on the effect of predators or scavengers on dead turtles.

These widespread mass die-offs occurred repeatedly in a specific stratigraphic and sedimentological

context. The concentrations are in the first few meters of mudstone overlying a limestone. This suggests that a specific paleoenvironmental context is occurring repeatedly. The limestones represent widespread, shallow lakes, and the fossil accumulations occurred soon after the limestone depositional regime was replaced by a mudstone depositional regime. This happened several times, but not after every limestone-depositing lacustrine system, as documented by the relative rarity of turtle bones in Gbl sediments. What were the conditions operative during deposition of these mudstones? A paleoenvironmental model (model 2) may allow integration of the above interpretations. An alternate model (model 1) will be discussed first, because it may seem intuitively attractive. However, we will present reasons why it does not adequately explain the data.

#### *5.1. Model 1: Basin-wide lake with only attritional turtle death*

A model based on attritional death of turtles, may seem intuitively adequate to account for accumulations of fossil turtles. It can be considered the default until another model demonstrates a more adequate explanation. In this attritional model, the turtles living in the shallow, basin-wide lake die at varying times of normal causes and sink to the soft, bioturbated muddy lake bottom. Scavengers remove their heads and limbs, and the turtle shells accumulate on the lake bottom over tens to hundreds of years as sediment gradually buries them in a time-averaged fossil assemblage, consistent with the time-averaging concepts of Behrensmeyer (1982). However, several lines of evidence indicate that this model does not explain the turtle concentrations reported in this paper.

The assemblage of turtle bones in our study does include a portion of isolated, disarticulated elements that likely originated with attritional death. However, turtle shells that were complete or almost complete account for the majority of turtle bones in our sample. It is well recognized that articulated vertebrate skeletons indicate fairly rapid burial or other special conditions, and the rate of disarticulation is influenced by the environment and type of animal (Behrensmeyer, 1991).

In experimental research in the laboratory, turtle shells in water were 75% disarticulated within 18–43 weeks after death (Brand, unpublished). The numerous articulated fossil turtles in the Bridger Formation were at approximately the same stage in the taphonomic process, and the experimental evidence indicates that they must have been buried at least within 6 months to a year after death. The possibility that such a large proportion of a turtle population could be preserved with articulated shells by gradual burial over tens to hundreds of years seems very remote. In a time-averaged assemblage of turtles, we would expect a much greater proportion of disarticulated bones.

Over 50% of the turtles in the BMtl were in, or immediately adjacent to, the organic turtle layer, a discrete, organic-rich clay layer, a few centimeters thick, that continued undisturbed for at least 11 km. This further supports the interpretation of a mass death of many turtles and fairly rapid burial associated with a widespread sedimentary event.

The mudstone of the BMtl shows only scattered, limited evidence of bioturbation, not the extensive bioturbation expected in a lake or marsh sediment accumulating over tens to hundreds of years. Our cut and polished samples show abundant fine details that do not indicate the mixing expected in bioturbated sediment. Also, the organic turtle layer and coaly shale units are continuous and unbroken for kilometers, often with sharp boundaries, and do not show the mixing expected to result from bioturbation. The only disturbance in these layers consists of small pieces of sediment, distinguishable by color and texture, that show soft sediment deformation and movement in relation to each other. We do see evidence of bioturbation in a few samples, and this evidence is clearly distinguishable from the non-bioturbated samples.

An additional problem with an attritional, time-averaged model is the near absence of turtles higher than a few meters above the base of the turtle concentrations. The sedimentary changes present higher in each sedimentary cycle (Buchheim et al., 2000) may indicate environmental conditions consistent with a reduction in turtle abundance, but would not preclude the presence of significant turtle populations.

For the BMtl, the concentration of dying turtles in ponds that were drying up or were in time-averaged attritional accumulations does not provide an adequate explanation for most of the bones because of the similar taphonomic state of most of these turtles, combined with the existence of large numbers associated with specific, widespread sedimentary units. Model 2 provides a more consistent explanation for these observations.

### 5.2. *Model 2: Basin-wide lake, with episodic death and burial of turtles*

This model proposes that the sediment above limestones was deposited in a basin-wide lake, with sandstone channels forming long finger-like deltas into the lake, as seen in Lake Turkana and elsewhere today (Buchheim et al., 2000). Bridger sediments are often interpreted as floodplain deposits, including ponds and marshes. However, Bridger B also contains several limestone units that are essentially basin-wide, indicating periodic formation of extensive lakes (Buchheim et al., 2000). Several lines of evidence indicate that the center of at least some of these lakes was in the southern part of the basin (Buchheim et al., 2000), and there were probably systematic environmental changes from the lake center to the basin margin. Thus, Bridger B paleoenvironments may have varied spatially and may have been dynamic temporally, with repeated cycles of depositional environments including lacustrine, followed by fluvial–lacustrine, wet fluvial floodplain, and dry fluvial floodplain.

Large numbers of turtles living in and around the lake were killed by some basin-wide episodic event, perhaps coincident with a series of volcanic eruptions, which began a rapid process of volcanoclastic sedimentation into the lake. The cause of death of the turtles is not clear, but one hypothesis is suffocation from breathing air choked with volcanic ash. Within months after death, the turtles in the lake sank to the lake bottom, and perhaps others were carried through channels and into quieter water in the open lake, where they also sank to the bottom and were buried by fine sediments and organic matter. In the BMtl in the southern part of the basin, the thin ‘organic turtle



bed' apparently was deposited by the transport of much fragmentary plant matter and other organic debris mixed with sediment, along with abundant turtles. The turtles were not buried immediately, but must have been buried within months to about a year.

In the episodic death model, the limestone represents a stable phase in the lake's history, and the mudstone above the limestone was deposited fairly rapidly during an extensive volcanic episode. If the same volcanic episode killed most of the turtle population that had developed in and around the lake, this would explain the large numbers of turtles in the first few meters of mudstone above the limestone and their paucity in the mudstone above that. If this process occurred more than once in the lake's history, it could also explain the repeating pattern of turtle concentrations just above some limestones.

In the channels, high flow velocities may have kept articulated turtles, with their large surface area and greater buoyancy, in suspension, while disarticulated bones were more likely to sink and be buried. There may have been enough flesh on the turtles to facilitate floating. Modern turtles float for a mean of 28 days after death (Brand, unpublished). After the floating turtles were carried out of the channels and into quiet water, they sank, along with turtles already in the lake, and were buried. A large percentage of the disarticulated turtle bones in the DP-11 quarry showed little or no abrasion. This could have resulted from bones falling off floating turtles in the quiet lake water. More difficult to explain are the turtle bones in fine sediments with level 3 or 4 abrasion. Pockets of disarticulated shell bones, many well-rounded by abrasion, occurred in sandstone channels, as expected. It is not as clear how some of these abraded bones were carried out into quiet water, away from any known channels. Analysis of disarticulated bones in the mudstone of quarry DP-11 indicated that the abraded bones were smaller than non-abraded bones. The small size of these bones could facilitate transport, but it is not clear whether this is adequate to explain how they got into the fine sediment.

The episodic death model offers an explanation for the basin-wide rapid death and burial of large

concentrations of turtles and for their concentrations above some limestones. The cline of turtle abundance in the BMtl (Fig. 7) could have resulted from a more favorable turtle habitat in the southern part of the basin (turtles mostly buried in-situ), or from the transport of floating turtles to the south in an open lake. The in-situ model seems better able to account for the higher concentration of turtles in the southern part of the basin.

The relationship of this model to the mammals needs further study. It seems that the factors that killed large numbers of turtles would have a similar effect on the mammals. No quantitative studies of numbers of mammals have been performed through this section, for comparison with the data on turtles.

The sediments above the Gbl limestone contained much more sandstone than the other two study units. This higher energy environment may partly explain the small number of turtles in Gbl sediments. However, at one study site on the Gbl (DP-5), the sediments were as fine-grained as the BMtl, and yet there were very few turtles. This may indicate that during deposition of the Gbl sediments, the source of turtles was reduced, or this sedimentary interval was not accompanied by the same process that killed so many turtles at other intervals in the history of the basin.

## 6. Conclusions

Fossil turtles were especially abundant in mudstones above two of three bench-forming limestones studied in the middle of Bridger B. They were most abundant in the upper unit (BMtl), intermediate in abundance in the lower unit (Ltl), and rare in the middle unit (Gbl).

Most turtles in these concentrations were in a similar taphonomic condition, with many shells mostly intact and unweathered, but with no skulls and few limb elements. The largest concentrations of turtles were associated with specific layers of fine-grained sediment. A scatter of disarticulated turtle bones was also found at some localities in the mudstones. The majority of these isolated bones were not abraded and had little evidence of weathering or predator tooth marks. Turtles on

the floodplain may have floated there while bloated, with some bones dropping from the floating turtles. Some individual abraded bones were also being carried out into the quiet water by some means.

The scattered, disarticulated and somewhat weathered bones seem to represent a background component resulting from attritional death. Overprinted on this, in some mudstones, is a concentration of turtles at approximately the same stage in the disarticulation process, mostly associated with a specific, thin sedimentary layer, which seems to represent large-scale mortality events over a wide area.

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