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Paleoenvironmental implications of size, carapace position, and incidence of non-shell elements in White River turtles

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Abstract

In this study, 314 fossil turtles of Nebraska's White River Group were used to gain insights into the regional paleoecology of the late Eocene and Oligocene. We collected taphonomic information about the size, the associated fossils, carapace position (up vs down), the presence of non-shell elements, and the presence of pre-burial weathering. A plot of turtle size vs strata reveals that turtle size decreased dramatically in the Whitney (ca. 31 Ma), and then increased again by the time the Arikaree was deposited. These size fluctuations appear to reflect the major cooling and warming trends at the beginning and end, respectively, of the Oligocene. Analyses of carapace position (up vs down), pre-burial weathering, and non-shell elements indicate several modes of death and preservation among the different turtle populations, including scavenging, burial by flood, and prolonged cold or drought. One 10 m interval in the Whitney Member, near the 31 Ma Lower Whitney Ash, contains a large number of small, completely articulated turtles preserved in mostly upright position. This indicates an expiration and subsequent preservation environment free of scavenging or high energy disturbances that might overturn a turtle.
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1. Introduction

The ecosystems of the late Eocene and Oligocene appear to have evolved in a major global cooling trend that occurred across the Eocene–Oligocene transition. This cooler climate carried through the Oligocene and was followed by a global warming spell marking the Oligocene–Miocene transition. The fossil record of the White River Group of northwestern Nebraska shows the presence of a complex and evolving ecosystem throughout the late Eocene and Oligocene; one teem-

ing at various times with snails, turtles, oreodonts, leptictids, rabbits, rodents, deer, entelodonts, camilids, horses, lizards, birds, and brontotheres, whose various populations evolved, fluctuated, and disappeared in response to environmental changes. In this study we have collected taphonomic data from the turtle fossils of the White River to enrich our view of the complex and changing Eocene–Oligocene ecosystem of this region.

Exposures in northwestern Nebraska consist of Late Eocene–Oligocene sediments, and Nebraska's White River Group has historically provided many vertebrate fossils from the Eocene and Oligocene epochs (Shultz, 1968; Emry et al., 1987; LaGarry and Hunt, 1994; LaGarry, 1997; Prothero and Whittlesey, 1998), includ-

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ing fish (Evans and Walzenbach, 1998). There have also been reports describing invertebrate fossils, plant fossils, and trace fossils of vertebrates (footprints), invertebrates (burrows), and plants (root casts) (LaGarry et al., 1998; Evans and Walzenbach, 1998). Among the fauna that occur in the White River are also the Testudines, or turtles, which occur in such numbers as to be the most common vertebrate fossil found in White River deposits.

Our study area is in the Toadstool Park badlands of the Oglala National Grasslands. It is thought to have the richest deposits of Chadronian through Whitneyan turtles in North America (Hutchison, 1996, 1992). Although there are large fossil collections from the White River, its biostratigraphy remains ill defined because most of the collectors retained only vague records of the stratigraphic and geographic location of the specimens (Prothero and Whittlesey, 1998). In addition, while White River turtles have been repeatedly sampled and are present in many North American collections, published stratigraphic information about these specimens and their relationship to other fauna and the paleoenvironment of the late Eocene and Oligocene is scarce. As such, we have conducted a systematic study aimed at rigorously collecting stratigraphic and taphonomic information from these turtles and their associated fossils; this in turn has allowed us to relate these turtles to many aspects of their paleoenvironment. With a mind toward a broad survey of the strata, several hundred turtles were located throughout the White River formations and members. From these turtles we present data showing turtle density trends, turtle sizes trends, carapace orientation trends, nonshell element trends, existence of pre-burial weathering, and association of fossil turtles with the fossilized remains of other organisms. The presence of literally thousands of well-preserved turtles widely distributed in all locally exposed members of the White River Group has also provided a unique opportunity to obtain statistical security for a variety of observations, allowing us to address a number of paleoenvironmental hypotheses.

2. Methods

2.1. Study area

Fig. 1A shows the geographic distribution of the fossil turtles in the study area. The study area ranged from the bluffs and ravines near Roundtop Mountain northwesterly to the erosional flats just south of the Orella road. A number of specimens were located in deep ravines intersecting the grassland prairie of this region, but most were in the badlands terrain that breaks into the east-facing escarpment visible from the Toadstool Park road. Fig. 2A shows typical Toadstool terrain and Fig. 2B shows our measured composite section. The strata dip to the south at an angle of 6°, and are often displaced by small faults. Two major faults, shown in Terry and LaGarry (1998), each with a greater than 15 m displacement, occur in the study area.

2.2. Geographic locality by global positioning

The latitude and longitude of each turtle was recorded as a waypoint in a Garmin 12 global positioning system (GPS). This data was converted into Arcview feature classes for generation of maps showing spatial distributions of specimens in the study area. An example is shown in Fig. 1. The precision of this method is ±5 to 10 m. In addition, each specimen was field marked with a 12 in. galvanized spike. Typical terrain of the region is shown in Fig. 2A, which shows the east-facing escarpment near the Toadstool Park campground.

2.3. Stratigraphy

The White River Group consist of the Chadron and Brule Formations. The Chadron Formation contains the Peanut peak and Big Cottonwood Creek members, and the Brule Formation the Orella, Whitney, and Sharp's Members. Much of the stratigraphy of this region has been recently revised (Terry and LaGarry, 1998; Terry, 1998; LaGarry, 1998), and herein we follow the conventions proposed in those revisions. In addition, the upper Brule has been called the Brown Siltstone in the literature, but more recently it has been recognized as correlative with the Sharps Member of the Brule in the South Dakota Big badlands (LaGarry et al., 2002). Herein we refer to it as the Sharps Member. Using a Brunton compass to perform eye height measurements of stratigraphic thickness, each turtle was stratigraphically related to either a published marker bed, such as the 'upper purplish white layer' (UPWL) of the upper Chadron Formation (Shultz and Stout, 1955) or the lower ash of the Whitney Member (Swinehart et al., 1985; Terry and LaGarry, 1998), or to a contact between formations or members. Our composite section is shown in Fig. 2B. We located turtles from 36 m below the Orella/Whitney contact to 32 m above the Whitney/Sharps contact. These measurements were used to generate the composite section shown in Fig. 1B. Since we were unable to find a location with exposures that
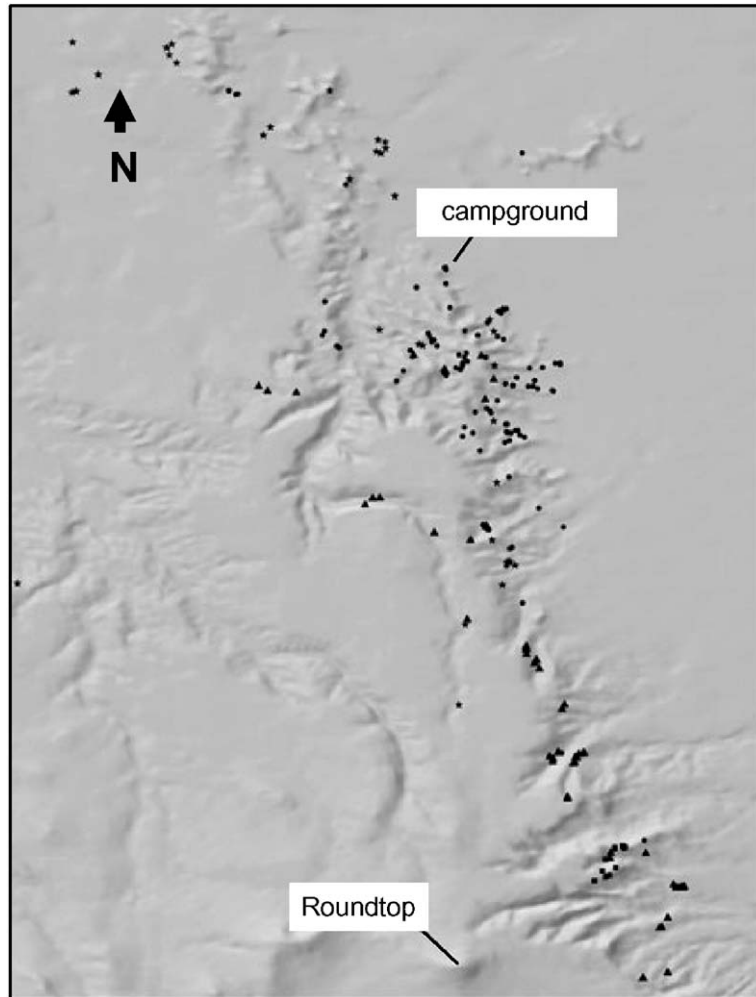
Fig. 1. Distribution of fossil turtles in the Toadstool Park study area. It is located 20 miles north of Crawford, Nebraska, in the northwest corner of the state (Latitude=42.8562820, Longitude=−103.5855658 (NAD83=North American Datum of 1983) Rev 2–5. Squares represent turtles in the Brown Siltstone, diamonds those in the Whitney, closed those in the Orella, and stars those in the Chadron. This image was generated with ArcGIS.

allowed measuring from the base of the Chamberlain Pass Formation to the Chadron/Orella contact, the 0–40 m region from the base of White River is based upon measurements by Terry and LaGarry (1998) at nearby Pete Smith Hill. We also did not locate the Sharps/ Arikaree contact, so the thickness of the Sharps Member is taken from LaGarry (1998).

Our composite section proposes a minor revision of the Terry and LaGarry section. Near the Toadstool Park campground we have repeatedly measured directly from the base of the Upper Purplish White Layer through the precipitous cliff band to a distinct bed in the upper Orella Member. We traced this bed south through channel sands cutting through the upper Orella, to a point where the Orella/Whitney contact was vertically continuous with this bed. The measured sections were not interrupted by faults. Repeated measurements of these extremely steep cliff bands yielded a span of 52 m from the base of the UPWL to the Orella–Whitney contact. We have also repeatedly measured the base of the UPWL to the Chadron/Orella contact to be 9 m, as reported by Terry and LaGarry (1998); thus the thickness of the Orella Member is 42 m (51 m−9 m=42 m). This contrasts to the Terry and LaGarry (1998) studies, which determined the thickness of the Orella Member to be 25–30 m, and our numbers are in close agreement with those originally put forth by Shultz and Stout (1955). We also note that the distance between the Upper and Lower Whitney Ash increases by 10 m as one proceeds north from the exposures east of Round-top to the point at which the Upper Whitney Ash disappears at the top of the escarpment. Thus, if the
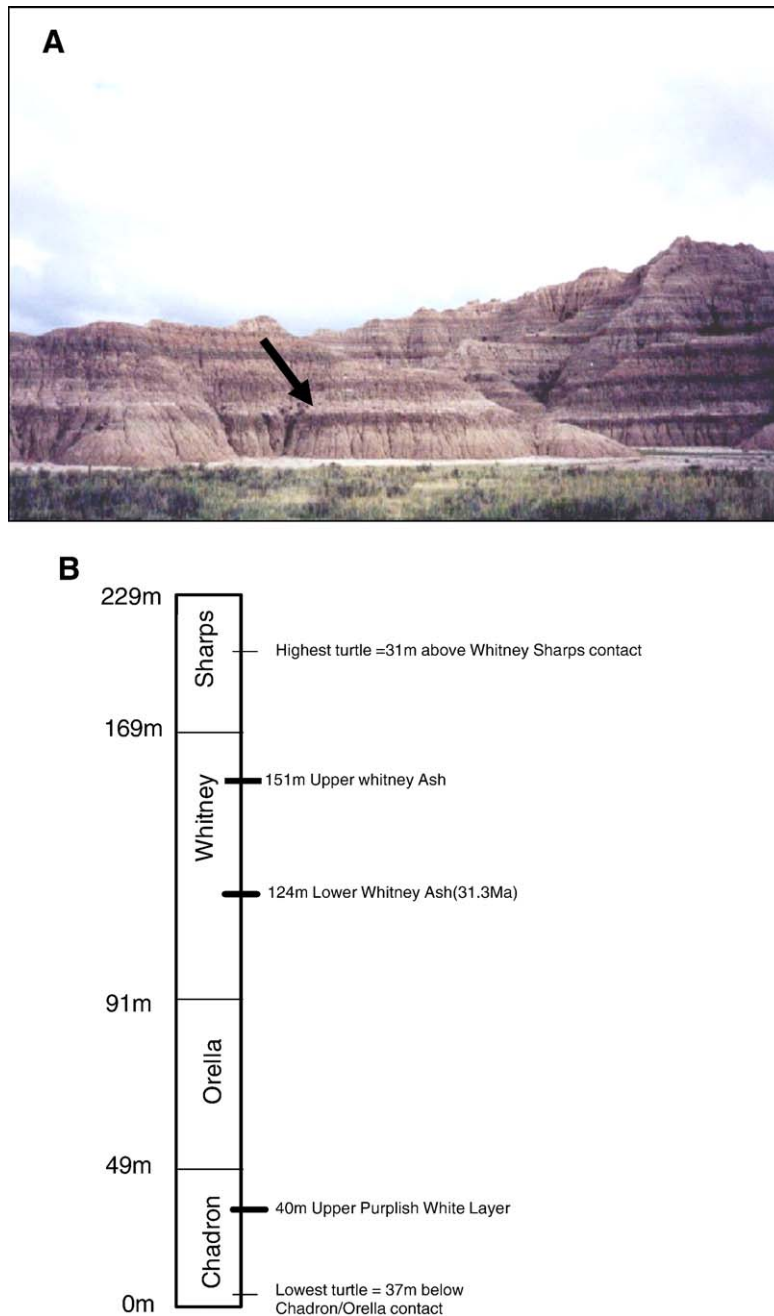
Fig. 2. (A) Typical White River terrain—the prominent white band marked by the black arrow is the Upper Purplish White Layer of Shultz and Stout (1955). Tortoises in the Chadron and Orella reached sizes of up to 90 cm in diameter. (B) Measured composite section of the White River Group. Nomenclature taken from Terry and LaGarry, 1998.

entire section were exposed directly east of Roundtop, one would measure 64 m between the Orella/Whitney contact and the Whitney/Sharps contact, and if the entire section were exposed 1 mile north, one would measure 74 m between those same contacts (See Fig. 2B). Parts of the contacts between the various members of the White River group are also inter-tonguing, but we were always able to correlate to an obvious (non-intertongued) contact for our measurements.

2.4. Prospecting

Most of the specimens were located during forays initiated at random spots in the study area (see Fig. 3).
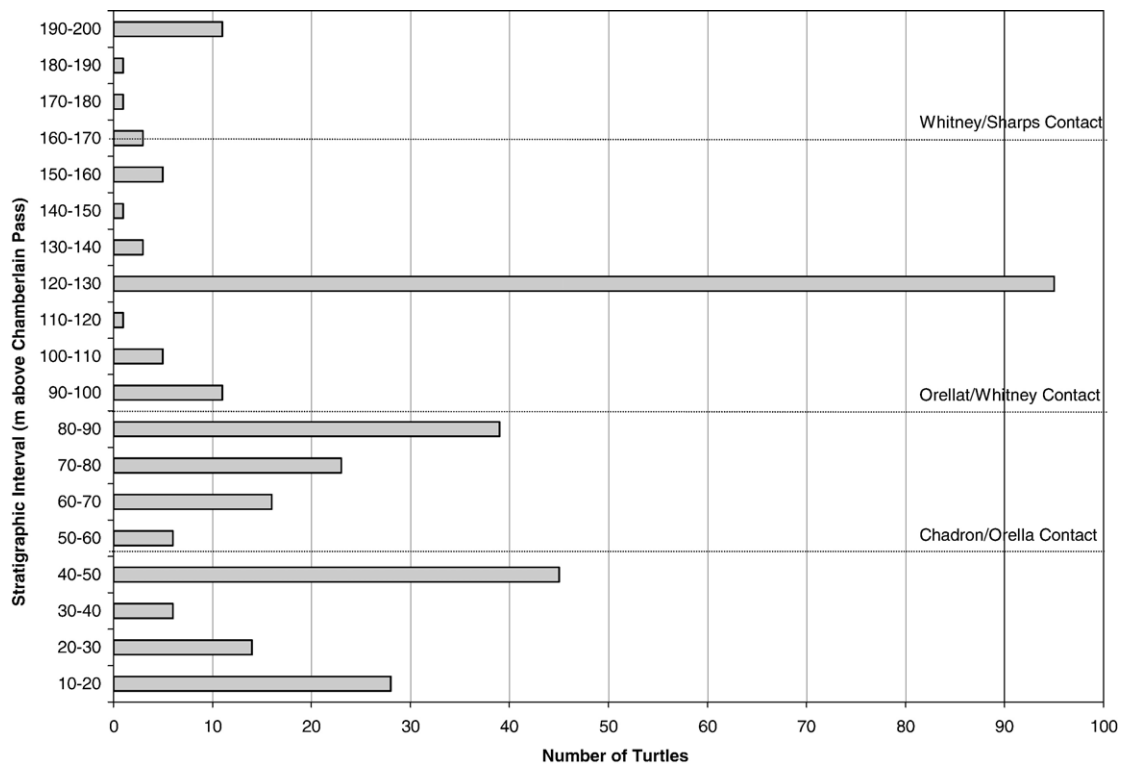
Fig. 3. The stratigraphic distribution of the randomly sampled turtles. The data set was sorted into 10 m stratigraphic intervals using Visual Basic algorithms. Stratigraphic designations are taken from Terry and LaGarry (1998). Locations of contacts are indicated.

Since the terrain is rugged and sometimes impassable, these forays were dictated to a certain extent by the topography. A small number of the specimens were located as a result of systematic, GPS-based transects designed to sample turtle density changes through the Orella/Whitney contact and through the Lower Whitney Ash (manuscript in preparation).

2.5. Taphonomic data collection

The field protocol involved the following six steps: 1). The length, width, and depth of the exposed portion of each turtle were measured. We primarily collected in situ data and often could not determine the complete set of dimensions without significant excavation; hence, some of the measurements we report are smaller than the actual dimensions that we will obtain upon eventual excavation. In general, however, the turtles were sufficiently exposed to allow accurate measurement. 2). A 2-m radius around each turtle was inspected for the presence of other fossils. In this report we make no distinction between associated fossils found in situ and those found in the float (surface occurrence). 3). Each turtle was inspected to determine whether it had been preserved with its carapace up or down. 4). The turtles

were inspected for presence of non-shell elements. 5) When possible, the compass orientation of the antero-posterior axis was determined with a Brunton compass. 6) Indications of pre- and post-burial weathering (splintering, rounding, cracking, crack re-mineralization) were recorded.

2.6. Data sorting and statistical analyses

We first entered each turtle and its associated data, as listed above, into an Excel spreadsheet. The data entries are either binary or percentages. The sorting of the turtles with respect to the various parameters was then accomplished using Visual Basic algorithms, which are available upon request. Many of the observations of interest are of a binomial nature (carapace orientation either up or down, non-shell elements either present or missing), which can be confidently approximated by a standard normal distribution of the binomial observations (a normal distribution normalized by z if the population is large enough). Then the analyses of the data are based on population proportion outcomes.

In order to assess the confidence in a measured proportion, say carapace up to carapace down, we

utilized the formulas for standard statistical estimators, such as sample mean, $n*p$, (an estimator of the population mean) and the sample error, $s(p)$, (an estimator of the variance) which allowed us to specify a relationship between sample size, n, and the uncertainty of estimation for the various proportions. The sample proportion is given as p. The equations can be solved for the sample size required to obtain an estimate with a desired level of precision. The uncertainty in estimating the mean proportion is limited to a tolerable error, e, given by $z_{\alpha/2}*s(p)$; $z_{\alpha/2}$ is the quantile from a normal distribution necessary for the desired confidence probability. The resulting equation, assuming that the overall population, N, is large, is given as:

$$n = (Z_{\alpha/2})^2 * p * (1-p)/e^2.$$

Allowing for a tolerable error, e, of 10%, the required sample size can be determined for various confidence intervals. Table 1 shows the number of turtles required to obtain 65%, 75%, 85%, 90%, and 95% confidence intervals. Note that the population proportion is given as 50%, this results in the most conservative estimate of required sample size (largest sample size, which in this case is the largest number of turtles required to attain a given level of confidence), since the actual proportion of each parameter (for example, carapace up to down) is unknown.

Table 1

A) Chart displaying confidence in the observed binomial distributions for the given number of specimens; assuming that the overall population, N, is large the number of specimens (n) required for a given confidence interval is given as: $n = (z_{\alpha/2})^2 * p * (1-p)/e^2$

Confidence interval (%)	Number of turtles required
65	22
75	33
85	52
90	67
95	96

B) Numbers of turtles used in the carapace up vs down and presence or absence of non-shell element determinations

Formation/member	Number of turtles available for:	
	Carapace determination	Non-shell element determination
Chadron	50	93
Orella	75	84
Whitney	88	121
Whitney 110–120 m	68	95
Sharps	14	16

3. Results

3.1. Study area

Fig. 1A shows the geographic distribution of the fossil turtles in the study area. The study area ranged from the bluffs and ravines near Roundtop Mountain northwesterly to the erosional flats just south of the Orella road. A number of specimens were located in deep ravines intersecting the grassland prairie of this region, but most were in the badlands terrain that breaks into the east-facing escarpment visible from the Toadstool Park road. Fig. 2A shows typical Toadstool terrain and Fig. 2B shows our measured composite section. The strata dip to the south at an angle of 6°, and are often displaced by small faults. Two major faults, shown in Terry and LaGarry (1998), each with greater than 15 m displacement, occur in the study area.

3.2. Stratigraphic locations of randomly sampled specimens

We located turtles in the Chadron Formation, the Whitney Member, and the Sharps Member (Fig. 3). The turtles shown in Fig. 3 were randomly sampled in strata that ranged from 34 m below the Chadron/Orella contact to 30 m above the Whitney/Sharps contact, and excluded those identified during the systematic transecting. While not strictly quantitative, we spent roughly equal amounts of time inspecting similar surface areas as we prospected in the various members. Furthermore, we have conducted systematic, statistically oriented investigations of the changes in turtle density/m^2 of outcrop, across the Orella/Whitney contact and through the Lower Whitney Ash (manuscript in preparation). These studies clearly show that turtle density drops dramatically during the transition into the Whitney, and then rises again during deposition of sediments near the Lower Whitney Ash. Thus, our random sample of the White River outcrops provides a general reflection of the changes in turtle density throughout the deposition of the White River sediments. Turtle density, whether a reflection of actual concentration in the ecosystem or of preservation biases, appears to have cycled, with maxima occurring in the Chadron Formation, and the Whitney Member. Note that several of the intervals show a paucity of turtles. Two of the intervals, 110–120 and 120–130 m above the White River base, have been repeatedly sampled, at times with systematic transects that confirm the turtle density change observed in the random sampling (manuscript in prepara-

tion); thus these data appear to portray real reductions in turtle numbers during these depositional periods. The occurrence of other fossils is also reduced in these two intervals. The interval from 160–170 m above the White River base occurs in the Sharps cliffs exposed near Roundtop Mountain, so was not well represented (in terms of total surface area prospected) in the random sample.

3.3. Turtle size reaches a minimum in the Middle Whitney

Fig. 4 shows that turtle size changed throughout the time of White River deposition. There were four large specimens found: one in the Big Cottonwood Creek Member (74 cm), one in the Orella Member (89 cm), one in the upper Whitney (72 cm), and one in the Sharps Member (75 cm). Several very small specimens, presumably juveniles, were also discovered. Fig. 3A shows the longest dimension of each turtle plotted against its stratigraphic position. There are two minor nadirs in turtle size: one in the upper Chadron Formation and one in the middle of the Orella Member. One major nadir occurs in the middle Whitney, in the interval 110–130 m; there are no turtles greater

than 30 cm in this interval, despite the fact that we observed many specimens above 40 cm in the Chadron, Orell, and Upper Whitney. Because we measured only the exposed parts of a given turtle, it is theoretically possible that we simply did not encounter a large turtle that was sufficiently exposed to allow us an accurate estimate of its size. Statistical hypothesis testing using estimators of proportions indicate, however, that we sampled a sufficient number (50) of turtles to allow us to accept with 95% confidence the hypothesis that the proportion of turtles in that interval exceeding 50 cm is zero (our observed proportion). In addition, we compared the Whitney 120–130 m interval to the Orella 80–90 m interval using a z test for proportions. The results show that the percentages of turtles above 50 cm are significantly different (28% in the Orella bin and 0% in the Whitney bin.

In addition, the stratigraphic interval between 90 and 130 m above the White River base spans the Orella/Whitney boundary and has been repeatedly sampled, both with systematic transects (manuscript in preparation) and during less systematic forays, confirming that turtles really do dramatically decrease in size across the Orella/Whitney boundary.
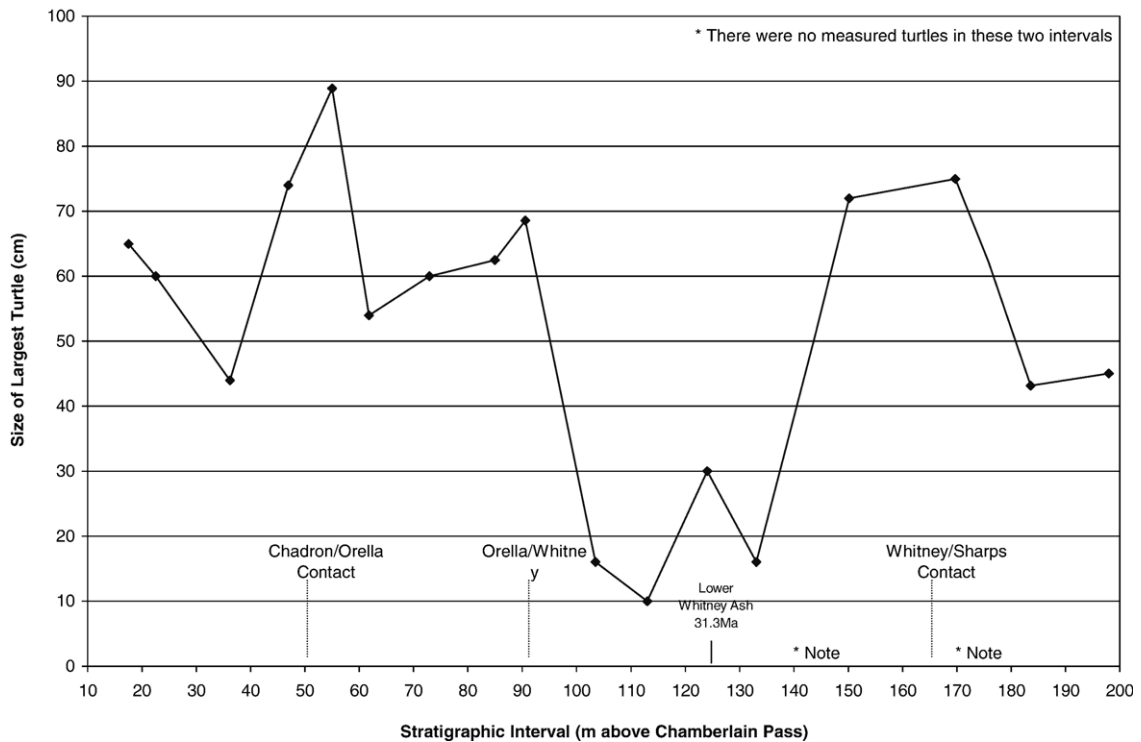

Fig. 4. Size distributions of the sampled turtles. Scatter plot displaying the stratigraphic position and longest measured dimension of each turtle. See Fig. 2 for description of contacts. The lower Whitney Ash occurs in the interval 120–130 m and has been dated at 31.26 Ma.

3.4. A bias toward the carapace up position

Many of the White River turtles are well articulated, making it convenient to gather information about orientation of the carapace. A summary of carapace up compared to carapace down turtles, in 10 m bins (intervals), is shown in Fig. 5. With the exception of one 10 interval at the lower Whitney ash, secure statistical analyses were possible only at the level of the lithologic member (Fig. 6). Out of the 295 turtles sufficiently articulated to allow determination, 250 were in the carapace up position (85%). All intervals except those in the Sharps Member show a clear bias toward preservation in the upright position (see Table 1 for confidence limits based upon the number of turtles available for the analysis). The lowest percentage of carapace up turtles occurred in the Sharps Member (50%=7/14), and the highest percentage, (91%=80/88), occurred in the Whitney. One 10 m interval, 120–130 m, in the Whitney Member had highly significant numbers of turtles, and it was observed to have 93% (63/68) turtles in the upright position. The large number of turtles located in the Whitney Member and particularly in the Whitney 120–130 m interval

allowed us to place 90% confidence limits on these ratios.

3.5. Presence of non-shell elements

Many of the turtles retained non-shell elements (NSE's), limb bones, bone fragments with condyles and pelvic or shoulder girdle bones. Fig. 5 shows a summary of all turtles in the study group, distributed into 10 m bins. Again, with the exception of the Whitney 120–130 m bin, a high degree of statistical security was possible only at the level of the lithologic member. In the Chadron Formation and the Orella, Whitney, and Sharps Members at least 52% (48 out of 93), 63% (53/84), 46% (56/121), or 38% (6/16) of the turtles, respectively, retained at least one non-shell element (Fig. 7). Many of the turtles observed in the field were not sufficiently exposed to accurately determine the presence or absence of non-shell elements, so our data represent the minimum number of turtles that retained NS elements. See Table 1 for confidence limits placed upon above percentages based upon the number of turtles available for the analysis.
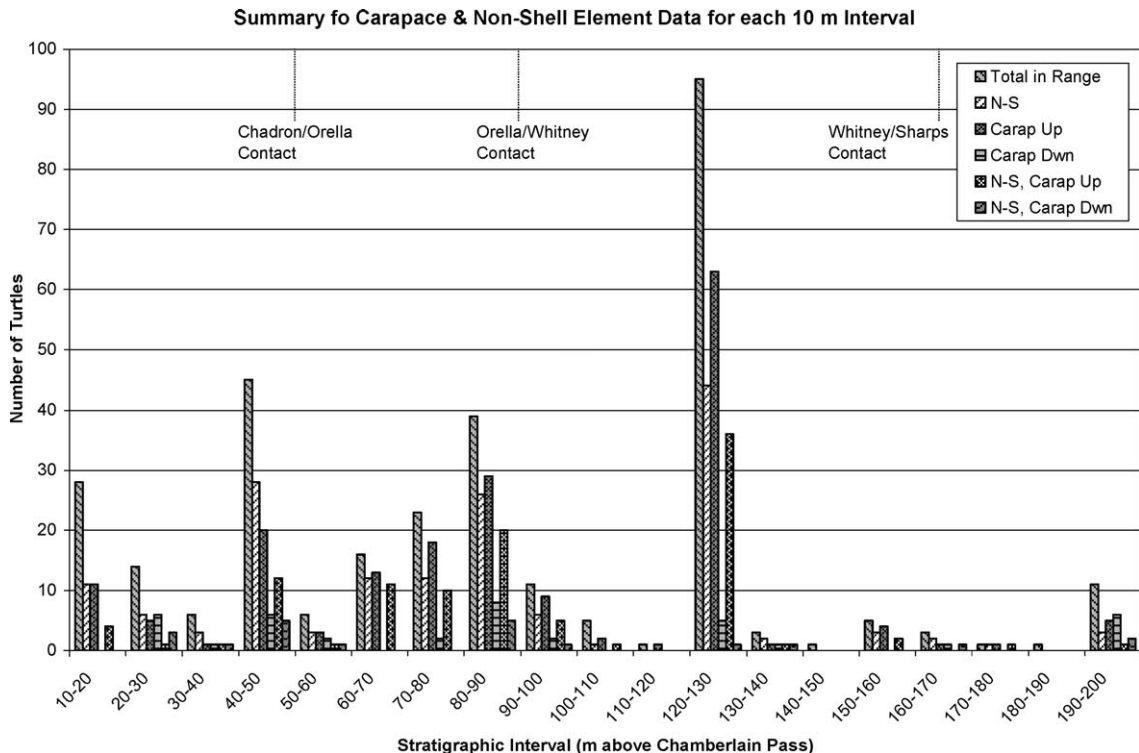

Fig. 5. Summary of all turtles in the study group. N-S refers to turtles that retained their non-shell elements. Carap Up refers to those turtles that were carapace up, Carap Dwn to those that were carapace down. N-S, Carap Up refers to those that retained their non-shell elements and were in the carapace up position. N-S, Carap Dwn refers to those turtles retaining their non-shell elements and in the carapace down position.
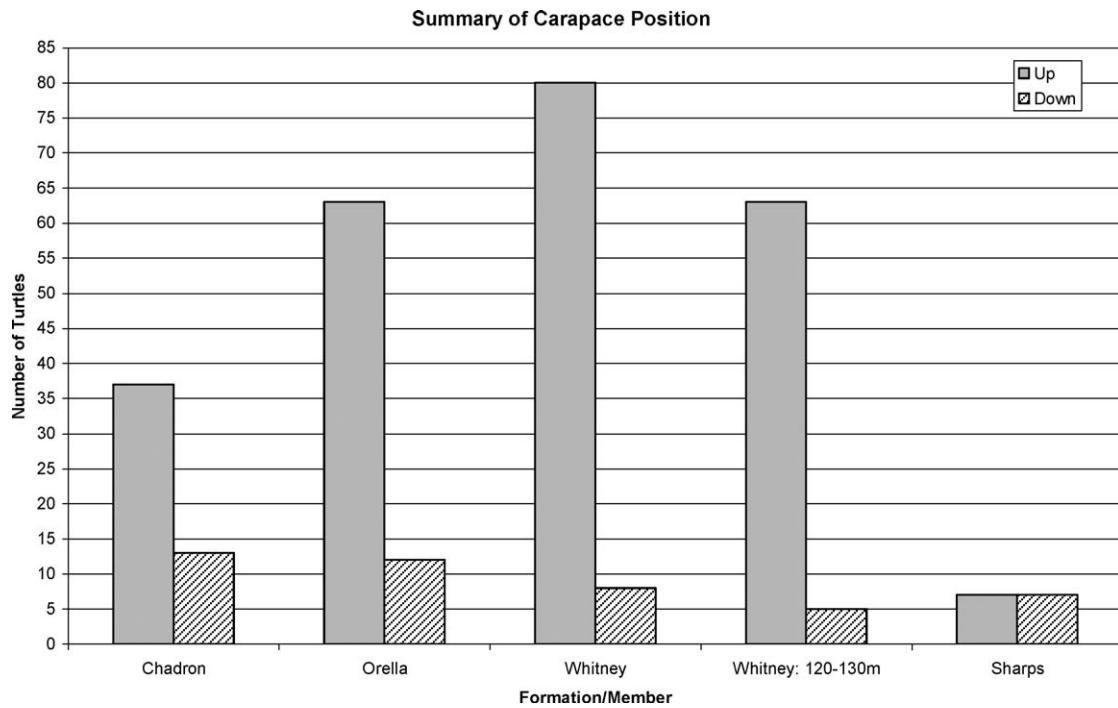
Summary of Carapace Position

Fig. 6. Carapace position of turtles in Chadron, Orella, and Whitney, and Sharps. Those turtles with indeterminate carapace position were eliminated from the data set.

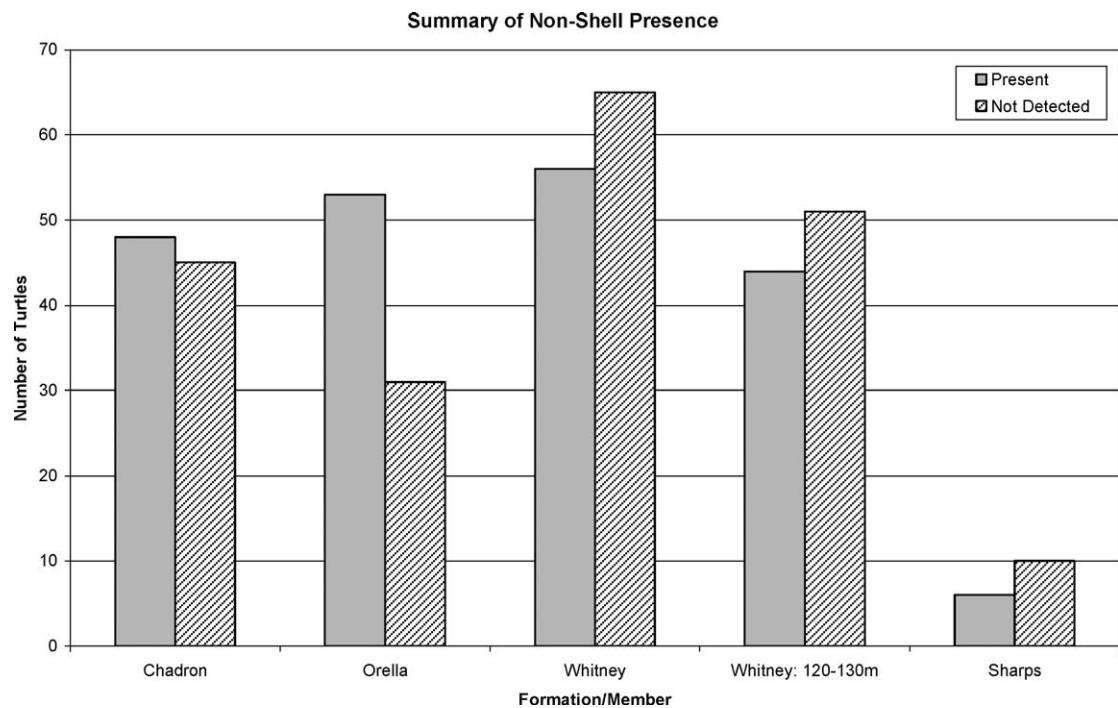**Summary of Non-Shell Presence**

Fig. 7. Summary of the turtles retaining non-shell elements compared to those with no detected non-shell elements. The presence of just one NSE was sufficient to a positive score for NSE.

We also determined the fraction of turtles retaining NSE's and in the carapace up or down position (Fig. 8). In the Chadron Formation, 67% (18 out of 27) of the turtles both retained their NSE's and were in the carapace up position. In the Orella Member, the ratio was 88% (42/48 turtles), in the Whitney Member the ratio was 94% (45/48), in the Lower Whitney Ash interval the ratio was 97% (36/37 turtles), and in the Sharps Member 40% (2/5 turtles). See Table 1 for statistical confidence limits based upon the number of turtles available for the analysis.

3.6. Turtle associated fossils

Many non-turtle fossils were discovered and collected near turtles. These included mammal, invertebrate (snail or traces), and plant (root casts) fossils. Many turtles also displayed gnaw marks on both shell and non-shell elements (data not shown). A brief summary of the turtle-associated fossils is shown in Table 2. These fossils were found within ± 2 vertical m and 30 lateral m of a turtle. Many of the mammals have been identified and include: *Leptomeryx*, *Mericoidodon*, *Palaeolagus*, *Miohippus*, camelid, and rhinocerotids including at least one *Subhyracodon*. We also identified body and trace fossil evidence of invertebrates. The first of these was snails (*Helix*). The Whit-

Table 2
A summary of turtle-associated fossils in the Chadron and Brule Formations

	Snail	Plant	Mammal	Turtle	Coprolite
Chadron	2/93	5/93	18/93	37/93	3/93
Orella	1/84	2/84	31/84	33/84	7/84
Whitney	16/121	1/121	29/121	66/121	0/121
Sharps	0/16	0/16	3/16	5/16	0/16

The number of associated fossils is shown with respect to the total number of turtles in formation (or member). Fossils occurring within 30 lateral m and 2 vertical m of a turtle were considered to be associated.

ney Member contains a much higher density of snails than any other member (Table 2). The second was thousands of shallow, irregular impressions, which may be invertebrate traces, found in fine-grained units that appear to constitute a paleopond or backwater near the Orella–Whitney contact—no turtles were found in these sediments. Numerous siliceous, roughly cylindrical features were located near turtles; we have interpreted these as root casts. The Chadron contained a higher proportion of these features than the other members, and many of these were found on turtle shells. Numerous coprolites were observed during prospecting, mostly in the Orella beds and never in the Whitney beds. Those that were observed near a turtle are also presented in Table 2.
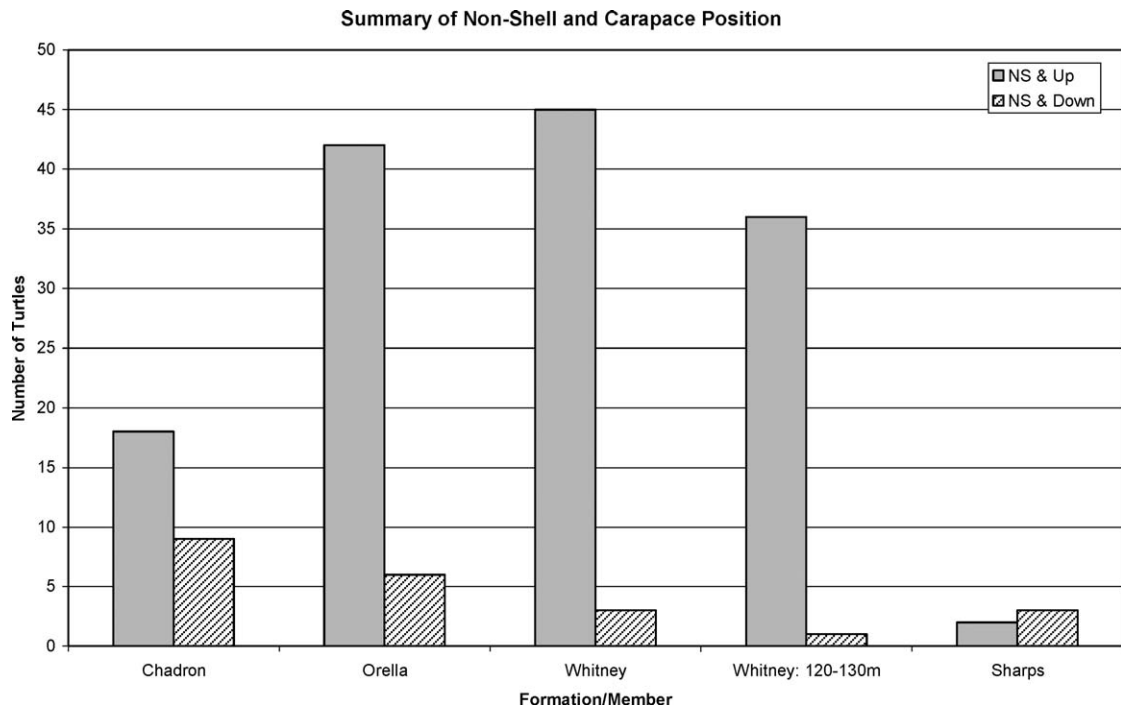

Fig. 8. Turtles retaining NSE's and in either the carapace up or the carapace down position. Those turtles with indeterminate carapace position or indeterminate NSE's status were eliminated from the data set.

Turtles were often observed near at least one other turtle. The highest frequency of this association occurred in the Whitney Member, with 54% of the turtles occurring within 30 m (± 2 vertical m) of another turtle. In the other units the association frequencies were: 40% of the turtles in the Chadron Formation, 39% in the Orella Member, and 31% in the Sharps Member. We also observed many instances of 'twins', or pairs of turtles within several meters of each other and at the same stratigraphic horizon (Table 3). These 'twins' were observed in all lithologic units.

3.7. Weathering of the turtles

We recorded information concerning rounding of elements, presence of cracks, re-mineralization of those cracks, splintering, and presence of bone flakes in the stone matrix within the specimen. None of the specimens showed any significant rounding, indicating that they were not transported by water prior to or after lithification. Most specimens showed cracking and, often, many of those cracks had re-mineralized with silica or calcite. Many specimens displayed bone splinters, chips, and fragments embedded in either the internal concretion or the rock surrounding the specimen. We have interpreted this splintering or fragmenting to be a consequence of pre-burial deterioration of the turtle bones, probably due to UV radiation and oxidation. The fraction of turtles exhibiting pre-burial weathering varied as shown in Fig. 9. The 'not determined' turtles were not included in the analysis. The highest percentage of pre-burial weathering occurred in the Whitney Member, 70% (58/83) and the lowest in the Chadron Formation, 60% (15/25). The determination in the Sharps Member involved only five turtles, so the ratio is not significant—see Table 1 for confidence limits.

4. Discussion

In a number of instances, taphonomic studies of turtles have proved useful in understanding local depo-

Table 3
The number of turtle pairs found in each of the study units

Strata	Number of turtle twins
Chadron	6
Orella	7
Whitney	15
Sharps	6

A pair was considered 'twinned' if they occurred within 6 horizontal m and 0.2 vertical m of each other.

sitional environments and the way they relate to regional paleoclimate and paleoecology. Brand et al. (2000) carried out an extensive survey of turtles in the Bridger Formation in southwestern Wyoming, and Hutchison (1980) reported results from a stratigraphic study of turtles in the Bighorn Basin of north central Wyoming. Becker and Chamberlain (2001) have presented preliminary studies detailing the environment that led to reworking of fossil turtles from the Maastrichtian of New Jersey. In addition, comparisons of forelimb ratios (hand-humerous–ulna) in extant and extinct turtles have allowed investigators to better assess degree of aquatic adaptation of turtles to their environment, thus aiding in reconstruction of local paleoenvironments (Joyce and Gauthier, 2004).

Many of the White River turtles appear to be land tortoises, and we have tentatively identified members of the genera *Gopherus*, *Stylemys*, and *Hesperotestudo*. We have also located a number of what appear to be Emydid (pond) turtles in the lower Whitney. The large number of well preserved, articulated specimens in the Toadstool Park region has allowed us to make accurate determinations of size, carapace position, presence of non-shell elements, and pre-burial weathering, which can be related to the paleoenvironment. Below we discuss a number of hypotheses that relate these turtles to their paleoenvironment.

4.1. Size fluctuations in the white river turtles

Our first hypothesis was that the size of White River turtles would decrease coincident with the reported cooling trends from Eocene through early Oligocene. This hypothesis appears to have been borne out by our observation of the turtle size nadir in the Whitney Member near the Lower Whitney Ash (Fig. 4). The Whitney dates show that the lower Whitney Ash was deposited some 31.26 (± 0.06) million years ago (average of four dates presented in LaGarry, 1998), and the Upper Whitney Ash at 31.85 (± 0.02) million years ago. The cause of these conflicting dates has not been resolved, but they indicate that the Whitney rocks were probably deposited over a 1–2 million year time span at about 30–32 million years ago. Fluctuation in reptilian size is an accepted indicator of flux in paleoclimates (Hibbard, 1960; Hutchison, 1980, 1982; Cassiliano, 1997). While there is recent evidence raising the possibility that the cooling trend across the Eocene–Oligocene was not as pronounced as once thought and perhaps was not even a global event (Kohn et al., 2004), our data support the idea that the central U.S. experienced a cooling trend culminating around 31
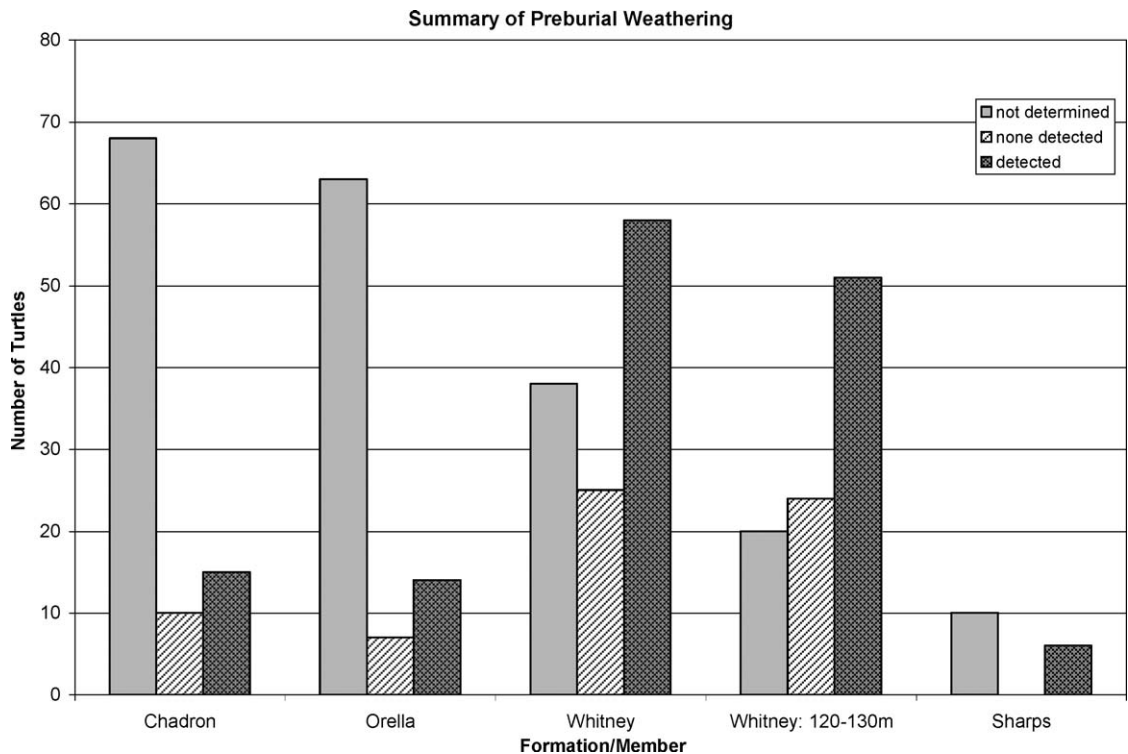
Fig. 9. Pre-burial weathering of turtles. Weathering was indicated by presence of bone chips and/or splinters embedded in the stone matrix inside or surrounding the shell.

million years ago that led to a reduction in turtle size. The subsequent increase in turtle size appears to reflect the warming trend thought to have occurred at the Oligocene–Miocene transition (Barnosky and Carrasco, 2002; Zachos et al., 2001). We note that our data would place the cooling event, hence the Oligocene–Eocene boundary, at the end of the Orellan land mammal age, while most representations place the Eocene–Oligocene transition at the Chadron–Orella boundary (see LaGarry, 1998; Hoganson et. al., 1998; Terry, 1998). In addition, the Oligocene–Eocene boundary is generally placed well into the Arikaree, while our turtle size data would indicate that the warming trend marking the Oligocene Eocene boundary occurred well before the Arikaree rocks were laid down. Perhaps the regional cooling and subsequent warming trends were milder and of shorter duration than that experienced in other parts of the prehistoric world.

Auffenberg (1974) has identified the giant tortoise *Geochelone* from Orellan beds of South Dakota, and Holman (1987) has identified a specimen of *Geochelone* from the late Orellan beds of northeastern Colorado (Chimney canyon), again indicating mild Oligocene climates in the region able to support these large turtles. We have detected two turtles greater than 70 cm

in the upper Orella Member, observations consistent with the earlier reports and their interpretations. Our turtle size graph (Fig. 3A) is also in good agreement with paleobotanical (leaf margin indices) and reptile diversity trends in this time period (Hutchison, 1982), which place a minimum at ca. 30 million years ago. The size of turtles preserved in the White River Group appears to have varied throughout the late Eocene and Oligocene, with the general trend toward small turtles reaching a nadir around the time that the Lower Whitney Ash was deposited. By the time of Upper Whitney Ash deposition, turtles had increased in size again to dimensions of at least 72 cm, as evidenced by discovery of a turtle of this size located 2 m above the base of the Upper Whitney Ash.

The nadir in turtle size that occurs in the middle Whitney has also been identified at the regional level by Hutchison (1996). His report shows a decline in the maximum carapace length of Trionychidae, Testudinidae, and Emydidae beginning in the Uintan and Duchenian and reaching a nadir in the middle Whitney. His data indicate a state that the largest turtle discovered in the Orella is ca. 50 cm long; we are able to revise this, having located one turtle 90 cm in length, two over 70 cm, and several over 60 cm in length. Maximum cool-

ing, as demonstrated by the nadir in the smooth-margined plant species, probably occurred about 30 million years ago, after which the percentage of entire-margined plants began to increase (Hutchison, 1982, 1996). Reptile diversity also reached a low point 31–32 million years ago, but, unlike turtle size and leaf margin changes of plants, there was apparently a 10 million year lag before it began to increase again (Hutchison, 1992, 1996). More evidence for at least a regional general cooling and drying trend from late Eocene through the Oligocene comes from paleosol, floral, and faunal studies in the Big Badlands (Retallack, 1983), as well as from O^{16}/O^{18} isotope studies (Zachos et al., 2001; Kohn et al., 2004). As mentioned above, our data are generally consistent with the notion of a general cooling trend beginning at about 34 million years ago, reaching a low point at about 30 Ma, and then slowly reversing after that to carry on into the Oligocene–Miocene warming trend at about 25 Ma. Again, however, our data would place the Eocen/Oligocene boundary at the Orella/Whitney contact rather than the Chadron/Orella contact.

Interestingly, although the size of the White River turtles appears to have decreased by the time of the Lower Whitney Ash deposition, our random walk through the White River Group (Fig. 3) suggests that the turtle density had apparently increased by that time. It is also possible that this reflects preservation biases rather than directly reflecting the number of turtles in the Whitneyan paleoecosystem.

4.2. Carapace position of the white river turtles

The second hypothesis addressed was that all turtles would be in their living, or carapace up, position. Any deviation from this carapace up position implies a disturbance of some sort, and induces the development of corollary hypotheses to identify the nature of the disturbance. During preliminary forays into the study area, we had observed that in certain sediments a large number of turtles were present in the carapace down position. We have established that, in general, turtles in the White River deposits were preserved in the carapace up position. This bias for carapace up was especially evident in the interval that crosses the Orella/Whitney boundary (70–80) and in the interval that contains the Lower Whitney Ash (110–120). A heavy bias towards the carapace up indicates a lack of disturbance after death, because unless disturbed, when a turtle dies the preferred position for preservation is carapace up. An exception to this might be an aquatic turtle that dies on the surface of water, which, as

detailed by Brand et al. (2000), would tend to flip carapace down prior to arriving at the floor of water body. Excepting the turtles near the Lower Whitney Ash, which we have tentatively assigned to the family Emydidae, most of the White River turtles appear to be large land tortoises. We have thus invoked other modes of conversion to the carapace down position. Such a conversion requires a disturbance sufficient to overturn the turtle, which in many cases is quite large, and there are several hypothetical mechanisms for overturning upright turtles. First, a turtle might be overcome by fluvial action, overturned and then buried in mud. Second, a turtle may be overturned during either predation or scavenging. Third, a turtle may tumble from a cliff or ledge. Fourth, strong winds, such as those that occur in a tornado, could conceivably overturn a large turtle, which might die in the overturned position. In all of these situations, we would expect to observe that lower energy situations (smaller scavengers, low water or wind velocity) would overturn smaller turtles but not larger ones, and that, at higher energies, larger turtles would begin to overturn.

The Chadron Formation had a fairly high fraction of overturned turtles, 39% (14/36). We have found some large gouge and puncture marks on Chadron turtles, so some of them were probably overturned by large predators or scavengers. At Toadstool Park there is also a paleochannel in the Peanut Peak member of the Chadron Formation, and periodic flooding could account for some of the overturning that occurs in the vicinity of that channel. There were numerous large Orellan turtles (>40 cm) found in an overturned state; these turtles also must have been exposed to higher energy environments, such as large scavengers, high-energy floods, or perhaps a tornado. Since extensive channel sandstones occur throughout Toadstool Park's Orella Member, we favor a scenario that invokes periodic spring flooding that tumbled and killed these large turtles, perhaps partially or completely burying them in the process. Many of the large Orellan turtles have sustained gnawing by small creatures (data not shown), presumably mammals, so their carcasses must have been accessible, either on or near the surface of the presumed flood sediments.

4.3. Retention of non-shell elements

We also hypothesized that in the undisturbed turtle, non-shell elements would be preserved and present in or near the shell. An absence of non-shell elements would indicate significant disturbance of the turtles by either scavenging or tumbling after decomposition of

flesh. We point out here that we use the presence, but not the absence, of non-shell elements as taphonomic evidence. This is because while we observed many turtles with no apparent non-shell elements, most of these were not sufficiently exposed to confidently determine whether or not NSE's were present, so excavation may reveal a higher percentage of NSE retention. Thus, we don't know how many of the turtles with no visible non-shell elements might actually turn out to have them upon excavation. We do, however, know that the ones that do have visible NS really have them.

A modern day comparison with fossil turtle data is possible from a study of a modern painted turtle (*Chrysemys*) kill site at a pond 20 miles from Toadstool Park. Seven out of seven recovered turtles retained a pelvic girdle, 2 of these seven retained all of their non-shell elements with flesh in a state of partial decay and desiccation, and 2 more of these seven had incomplete internal skeletons but retained a substantial number of non-shell elements. In addition we have also observed the pelvic girdle in two dead *Gopherus* turtles discovered in the Mojave desert of southern California. Based upon these modern examples, it appears that most fossilized turtles whose shells are still intact will likely have at least an associated pelvic girdle.

4.4. Non-shell retention and carapace position

Our fourth hypothesis was that those turtles retaining NSE's would be predominantly in the carapace up position. Interestingly, in the Chadron Formation, Orella Member, and Whitney Member, those retaining NSE's were predominantly in the carapace up position (with the Sharps Member not having sufficient numbers of turtles to make the determination with any statistical security). Note that those turtles in the upright position and in which no NSE's were observed could end up revealing NSE's upon excavation. Because of this, we used only the presence of non-shell elements as information when drawing taphonomic conclusions.

The Chadron turtles had the highest rate of overturned turtles retaining NSE's, with 33% (9/26) of the specimens with NSE's occurring in the carapace down position. Many of these turtles were greater than 40 cm, so they required a relatively high energy situation for overturning. We have found some large gouge and puncture marks on some Chadron turtles retaining NSE's, so some of them were probably overturned by large predators or scavengers who were unable to efficiently dismember the turtle. Because of the paleochannel in the Peanut Peak member of the Chadron, periodic flooding could account for some of the overturning we observed in those strata. Of the large turtles in the Orella Member, 84% of those in upright position retained some NSE's. This indicates that most of the Orellan turtles which remained upright after death were not significantly scavenged.

The Whitney Member and the Lower Whitney ash interval yielded ratios of 93% and 99%, respectively, of turtles retaining NSE's remained in the upright position. Death by predation would be likely to disperse NSE's and overturn many of these small turtles, as would tumbling of a decomposed carcass in water or wind. Thus, it appears that these Whitneyan turtles died and remained undisturbed throughout the preservation process.

4.5. Preburial weathering of the White River turtles

Another hypothesis asserts that the bones of turtles that die and are preserved in an undisturbed environment on the surface will decompose slowly as they are buried. Indications of pre-burial weathering of intact fossil turtles are primarily in the form of bone chips and splinters that are embedded in the internal concretion of the surrounding rock. Many turtles in all strata displayed chips and splinters in the internal matrix and in the rock surrounding the turtle. This phenomenon was most striking in the population of turtles in the Whitney Member, where most of the turtles, and all of the rhinocerotids in the Whitney Member, displayed extensive bone decomposition, which could have arisen in two hypothetical ways. First, a turtle might die and rest on the surface, slowly deteriorating and filling with dirt or mud over the period of time. Alternatively, a turtle could have been buried quickly, say during a flood or filling-in of a hibernation burrow. Slow rotting of the fleshy body inside the shell could be accompanied by deterioration of the shell bones to form chips and splinters as dirt and mud are slowly (over the period of years) forced into the space formerly occupied by flesh of the body. There has been little work on the taphonomy of modern turtles, with one exception being studies on the decomposition of freshwater turtles (Brand et al. (2003) and L. Brand personal communication). This work indicates that shells stored underwater for up to 3 years did not show any visible cracking or splintering. After 2 years, shells stored outside in the California sun and rain showed some cracking, but no visible chipping or splintering. This suggests that the turtles displaying the splintering and chipping were exposed to the elements for greater than 3 years and probably for at least 10–15 years.

4.6. The fauna of Toadstool Park

The range of fauna in the White River Group of Toadstool Park has in the past been well characterized (Emry et al., 1987; LaGarry, 1997; Prothero and Whittlesey, 1998). The Chadron sediments of Toadstool Park contain numerous turtles, oreodonts, and titanotheres/brontotheres, as well as the occasional lizard, entelodont, snail, and rhinoceros. The titanotheres disappeared by the time of Orella sediment deposition, and the Orella Member is marked by rhinocerotids (*Hyracodon* and *Subhyracodon*), deer (*Leptomeryx*) camelids (*Poebrotherium*), horses (*Mesohippus*), and entelodonts, as well as numerous turtles (*Stylemys* and *Gopherus*), squirrels (*Ishcyromys*), mice (*Eumys*), rabbits (*Paleolagus*), and leptictids. Toadstool Park's Whitney Member is marked by abundant turtle, snail, rhinoceros, oreodont (with the first occurrence of *Leptauchenia major*), as well as deer and horse fossils.

However, as has been noted, the precise stratigraphy of many, if not most, of the White River specimens is questionable (Prothero and Whittlesey, 1998). The exception to this is the works by LaGarry (1997) and LaGarry and Hunt (1994) who have conducted an extensive survey of the paleontological resource at Toadstool Park. Because fossil associations are important to understanding paleoecosystems, our study has begun to construct a precise stratigraphic picture of the fossil assemblage of Nebraska's White River as it relates to fossil turtles. Below we provide a brief summary of the associations we have observed and recorded (Table 3). In the Chadron Formation we have located snails, lizards, titanotheres, birds, and oreodonts in close proximity to a turtle. In the Orella Member we have observed rabbit (*Paleolagus*), leptictid, oreodont, and horse fossils very near a turtle. In the Whitney Member we have located oreodonts, rhinoceroses (*Subhyracodon*) and many snails (*Helix*) in the same fossil horizon within several meters of a turtle. Several interesting stratigraphic associations were observed. In the Sharps Member at 104.5 m above the Orella Whitney contact an upside down turtle was found 0.3 m away, at the same stratigraphic level, from an oreodont skull. In the upper Whitney, a rhinocerotid was found 0.75 m from a turtle, at the same stratigraphic level (7 m above the base of the lower Whitney Ash). In the upper Chadron Formation we collected a limb bone from a passerine bird (identified by Barb Beasley) while excavating a large turtle. Another turtle in the Orella Member (7 m below the Orella/Whitney contact) was 20 cm above and 5 horizontal m away from a nearly intact oreodont skeleton.

Since we found only two snails in the Chadron Formation and one in the Orella Member, there also appears to have been a substantial increase in the number of *Helix* snails during deposition of the Whitney sediments; in fact, snails contend with turtles for the title of the most abundant macro-fossil of the Whitney Member and perhaps of the White River Group. This increase in snail numbers might be explained by a reduction in snail predators, or by acquisition of a trait that allowed expansion into an unoccupied niche. Finally, we note that the abundant small mammals of the Orella were greatly reduced in number by the time of the Whitney, for throughout the course of our studies we found many small mammals in the Orella Member, but found virtually none in the Whitney Member.

Assuming that the turtle–turtle associations (Table 3) provide a rough indicator of turtle density during deposition of the matrix sediments, it appears that, at least locally, the turtle density was highest during the formation of Sharps Member and lowest during the genesis of the Chadron Formation. This is probably a reasonable reflection of the turtle density changes in the White River Group, though we point out that the total number of turtles identified in the Sharps Member is small compared to other members because we have been restricted in our sampling of Sharps Member by its local topography, which consists mostly of a precipitous cliff band. This cliff band is capped by lower profile exposures that yielded most of the specimens. In general the turtle density appears to fluctuate through time, as do the mammal to turtle ratios. This suggests that the fluctuations in turtle density are closely paralleled in mammal populations. This indicates that stresses affecting turtle density also affected the entire ecosystem. Alternatively, the fossil density changes could indicate changes in the preservation rate (fossilization) rather than changes in faunal density.

4.7. The Lower Whitney Ash turtles

As expected, preservation of the turtles of the White River appears to have been preserved in numerous environments and via numerous taphonomic mechanisms. Most of the 10 m intervals do not have sufficient numbers of turtles for secure statistical analyses, one exception being the group of turtles in and near the Lower Whitney Ash. This group appears to be comprised entirely of the small turtles (tentatively assigned to the family *Emydidae*) that are mostly in the carapace up position and that mostly retain NSE's. We also see

many small bone chips in the internal and external matrices of most of these turtles, indicating significant pre-burial weathering. Extensive scavenging or reworking would be expected to both overturn and dismember these relatively small turtles (less than 30 cm); instead most of them (93%) are in the carapace up position, and 63% retain at least one non-shell element. Thus, they appear to have been buried slowly after death, as the observed weathering would not be expected to develop in situations of rapid burial. We have also found a rhinoceros skull in this interval, 2 m away from and at the same stratigraphic level as a turtle. This skull, while reasonably well articulated, also had bone splinters and chips in the stone matrix surrounding and inside of it. Two more well articulated rhinoceros skulls showing the same type of pre-burial weathering were also recovered higher in the strata, 19 and 21 m above the Upper Whitney Ash. As with the turtles, these observations suggest partial deterioration of the bone concomitant with burial. Together, these data suggest that turtles preserved in the stratigraphic vicinity of the Lower Whitney Ash died in an environment that was relatively free of large scavengers/predators— perhaps a fairly rapid drying and/or cooling trend, that also killed or drove off birds and mammals. Indeed, evidence for an Eocene–Oigocene cooling and/or drying trend has been noted (Retallack, 1983; Janis, 1993; Zachos et al., 2001; Barnosky and Carrasco, 2002), and our turtle size data appear to support the notion of a cooling trend. So, in light of this, how is it that so many of these Whitneyan turtles retain their NSE's (63%) and remained in the upright position (93%)? Either there were no large scavengers or these turtles and their associated fossils lived in an environment so replete with more palatable prey and carrion that the turtles were considered 3rd rate fare. Alternatively, it could be that the lower Whitney turtle kills resulted from several cycles of cooling or drying that in short periods of time (a single season) caused mass killings of the turtles, perhaps in a dried out lake, and drove off the scavengers and predators before they could disturb the turtles. Support for yet another possibility comes from our observation that very few Whitney turtle skeletons have revealed small mammal gnaw marks, in contrast to the very many Orellan turtles with rodent gnaw marks (data not shown). A substantially buried turtle would not be expected to sustain extensive gnawing, so it is possible that the turtles were simply frozen into hibernation burrows by an unusually cold season, never to emerge again. A variation of this would be turtles driven into estivation and subsequent death by prolonged drought.

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