1998

Taphonomy and suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota

Paul D. White
University of Rhode Island

David E. Fastovsky
University of Rhode Island

Peter M. Sheehan

Citation/Publisher Attribution

White, P. D., Fastovsky, D. E., & Sheehan, P. M. (1998). Taphonomy and suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota. *PALAIOS, 13*(1), 41-51. doi: 10.2307/3515280
Available at: https://doi.org/10.2307/3515280

Taphonomy and suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota

Taphonomy and Suggested Structure of the Dinosaurian Assemblage of the Hell Creek Formation (Maastrichtian), Eastern Montana and Western North Dakota

PAUL D. WHITE, DAVID E. FASTOVSKY[1]
Department of Geology, University of Rhode Island, Kingston, RI 02881

PETER M. SHEEHAN
Department of Geology, Milwaukee Public Museum, 800 West Wells St., Milwaukee, WI 53223

PALAIOS, 1998, V. 13, p. 41–51

This study quantifies the taphonomic context of fossil dinosaur elements in the Late Cretaceous Hell Creek Formation of Montana and North Dakota, USA. A previously published data base consisting of 649 individuals (counted at the family level) was used to establish statistically fundamental associations between the vertebrate faunal elements and the fluvial architectural elements in which they were found.

In the Hell Creek, preservation is not equally distributed among the various fluvial architectural elements. Floodplain and channel deposits preserve the preponderance of the Hell Creek dinosaur fauna. Articulated fossils most commonly occur within floodplain and point-bar deposits. Floodplain and related deposits, however, preserve the highest dinosaur faunal diversities.

The dinosaur sample inferred to be most representative of the original dinosaurian assemblage structure, therefore, is obtained from floodplain and genetically related deposits. These yield eight families of dinosaurs represented in the following proportions: Ceratopsidae, 61%; Hadrosauridae, 23%; Ornithomimidae, 5%; Tyrannosauridae, 4%; Hypsilophodontidae, 3%; Dromaeosauridae, 2%; Pachycephalosauridae, 1%; and Troodontidae, 1%. Among these groups, dromaeosaurs and troodontids are represented only by teeth, a circumstance attributed at least in part to thin-walled bones whose potential for preservation in an active fluvial system is jeopardized.

Ornithomimids constitute 5% of the total assemblage, which makes them the third most common dinosaur in this study. Their relatively high abundance may suggest a herbivorous dietary preference.

INTRODUCTION

Studies in Recent fluvial environments have made important strides towards quantitatively characterizing the taphonomic processes that lead to fossil accumulations (Behrensmeyer, 1978, 1982; Behrensmeyer et al., 1979). Comparable studies in ancient sedimentary rocks, however, have been more difficult to carry out. Nonetheless, Bown and Kraus (1981b), Behrensmeyer (1982, 1988, 1991), Retallack (1984, 1988), Badgley (1986), Koster (1987), and Smith (1993) have all concluded that the nature of the taphonomic accumulation can be a function of the depositional environment.

This study establishes quantitatively the fundamental associations between dinosaur elements and fluvial architectural elements (AE's; Miall, 1985) in an ancient fluvial system. Using dinosaur material preserved in the latest Cretaceous Hell Creek Formation of eastern Montana and western North Dakota, it statistically examines the relationships that exist between vertebrate faunal elements and the AE's in which they are found. Here, the following questions are addressed:

(1) Do stream channels effectively sample the floodplain biota?
(2) Is the incidence of taxa dependent upon whether bone or teeth are preserved?
(3) Are fossil elements AE-dependent?
(4) Is fossil quality facies dependent?

The answers to these questions establish the occurrence pattern of dinosaur fossils found in the Hell Creek Formation and test current taphonomic hypotheses.

Depositional Setting

The Hell Creek Formation was deposited during the last 2.2 million years of Cretaceous time (Johnson and Hickey, 1990) and is among the most fossiliferous and carefully studied Late Cretaceous terrestrial units in the world (Van Valen and Sloan, 1977; Archibald et al., 1982; Sloan et al., 1986; Sheehan et al., 1991).

The Hell Creek formed as part of a prograding clastic wedge of sediment associated with the retreat of the Western Interior Seaway (Frye, 1969; Butler, 1980; Belt et al., 1984; Cherven and Jacob, 1985). Fastovsky (1987, 1990) reconstructed the Hell Creek Formation as an aggrading meandering fluvial system with a high, fluctuating water table. Fastovsky and McSweeney (1987) concluded that an unstable landscape resulted from channel migration and periodic flooding which, in turn, led to weakly developed soils.

Fastovsky (1987) recognized five lithofacies representing Hell Creek fluvial architectural elements. These were later expanded by Sheehan et al. (1991) to the nine (Table 1) that are used in this investigation to establish relationships between fossils and subenvironments of the river systems in which they are found.

[1] Author to whom correspondence should be sent.

0883-1351/98/0013-0041/$3.00

TABLE 1—Facies identified in the Hell Creek formation and interpreted fluvial architectural elements (Fastovsky, 1987; Sheehan et al., 1991).

Facies description	Architectural element	Pooled architectural elements
Medium-grained, cross-stratified sandstone	Thalweg	Channel
Inclined, heterolithic strata in medium- to fine-grained sandstone	Point bar	Channel
Inclined, heterolithic strata in medium-grained, cross-stratified sandstones	Toe-of-point bar	Channel
Fine-grained, cross-stratified sandstones interbedded with mudstones	Distal levee	Distal levee
Fine-grained, cross-stratified sandstones	Crevasse splay	Crevasse splay
Purple- and green-banded rooted mudstones	Floodplain paleosol	Floodplain
Planar-laminated siltstones and mudstones	Floodplain pond	Floodplain
Non-coalified organic accumulations	Floodplain swamp	Floodplain swamp
Coalified organic accumulations	Peat swamp	Peat swamp

Fossil Occurrences in the Hell Creek Formation

Vertebrate fossil elements were found in seven of the nine lithofacies identified in the Hell Creek Formation. They were not found in floodplain peat deposits or swamp deposits. The taphonomic modes of vertebrate fossil occurrence are similar to those described by Wood et al. (1988) for the Upper Cretaceous "Judith River Formation" (Dinosaur Park Formation of Eberth and Hamblin, 1993), Alberta, and are outlined in Table 2. In thalweg deposits, fossils represent material reworked from the floodplain via bank erosion or possibly via the disarticulation of a carcass in or close to the channel. Articulated elements were rare in channel deposits but did occur in point-bar deposits and represent carcasses that became stranded on and buried in the point bar during falling flood stages (Wood et al., 1988). Fossils found in floodplain deposits, whether articulated or disarticulated, have been interpreted to represent the death site, or at least something proximal to it, because the energy to remove elements from the channel and deposit them on the floodplain rarely exists (Winkler, 1983; Retallack, 1988). They could also represent accumulations from scavenging or predation (Behrensmeyer, 1991).

DATA COLLECTION AND ANALYSIS

Database

The database used in this study comes from the Dig-a-Dinosaur project that took place between 1987 and 1990 (Sheehan et al., 1991). The goal of that project was to study the diversity and abundance of dinosaurs in the Hell Creek Formation. Over 3000 specimens, representing 15,000 person/hours of surveying by field crews from the Milwaukee Public Museum, form the database. Six collecting areas (Fig. 1) were systematically combed for fossils in a "search-party fashion" (Sheehan et al., 1991). If a fossil was determined to be "in place" (i.e., not eroded from a stratigraphically higher position) it was included in the database. Taxonomic identity, element type, fossil quality, stratigraphic level, and facies type were recorded and entered into a computerized database at the base camp. The result was a multi-dimensional, cross-classifiable data matrix that can be examined in a statistically rigorous manner to establish fundamental associations between fossil elements and the facies in which they occur.

This database uniquely quantifies the relationship between fossils found and the area (m^2) of outcrop surface. During fossil collection, over 200 columnar sections throughout the relevant collection sites were measured. This geologic information was incorporated into digitized topographic maps to generate three-dimensional surface maps of facies distributions (Fig. 2). The combination of geologic and topographic data was used to calculate the total area searched for each facies (Table 3). Calculating the total area of a facies searched allowed meaningful comparisons of the density of elements (or other dimensions in the database) found per given area of a particular facies.

In addition to its size and structure, this database differs significantly from others (e.g., those of Dodson et al.,

TABLE 2—Taphonomic mode of vertebrate fossil elements in the Hell Creek Formation (modified from Wood et al., 1988).

Taphonomic mode of vertebrate fossil occurrences	Architectural element	Taphonomic interpretation
1) Isolated, articulated carcasses (in variable degrees of completeness)	Stream thalweg, point bar, and toe-of-point bar	Floating carcasses that either became stranded on point bars during waning floods or sank to channel bottom.
	Floodplain paleosol and floodplain pond	Site represents the death site or something proximal to it; carcasses disarticulated by scavengers.
2) Isolated single bones	Stream thalweg, point bar, and toe-of-point bar	Bones transported as traction load.
	Floodplain paleosol and floodplain pond	Carcass disarticulated by action of scavengers on the floodplain or near ponds.
3) Accumulation of many bones of different taxa	Stream thalweg, point bar, and toe-of-point bar	Channel thalweg or point bar lag deposits with multiple bone sources.

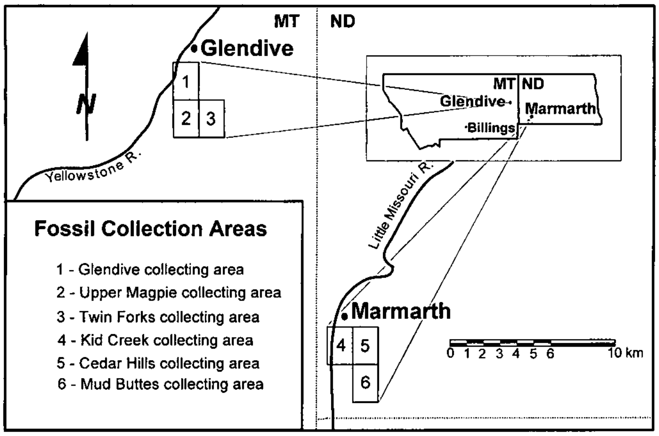

FIGURE 1—Location of study area showing individual collection sites. Precise locations are available in White (1996, Appendix 3) and are on file at the Departments of Geology, University of Rhode Island, and Milwaukee Public Museum.

1980; Wood et al., 1988) in that it incorporates the occurrence of vertebrate fossils from numerous isolated sites throughout an ancient fluvial system and not from productive quarries. It should be noted, however, that although the Sheehan et al. (1991) database is possibly the most comprehensive, single field-based collection of dinosaurian fossil elements to date, it is biased toward large individuals. During collection, only elements exposed at the surface were counted; the matrix was not screen-washed.

Statistical Tests

Four statistical tests, the chi-square test of independence, the one-way analysis of variance (ANOVA), the Fisher Least Significant Difference test (LSD), and the t-test, were used to establish fundamental associations between terrestrial vertebrate elements and the AE's in which they were found. The chi-square test of independence was applied to examine independence or dependence between dimensions within the database. A one-way ANOVA was utilized to test if familial densities varied among AE's. If the ANOVA resulted in the rejection of the null hypothesis (H_o), the LSD test was used to make pairwise comparisons between AE means to identify significantly different means. The t-test was used to make inferences about means when only two means were being compared. Hypotheses were evaluated at $\alpha = 0.05$.

All tests are valid when the populations under consideration are normally distributed. This is a reasonable expectation given the sample sizes, methods, and the parameters used in this study, and the applicability of the Central Limit Theorum to them (see Ott, 1993). Nevertheless, the data were shown to be normally distributed by graphic means, and a Hartley's test (Ott, 1993) was applied to confirm the assumption of equal variance.

Family-level identification (Table 4) was chosen for the analyses because it is the lowest taxonomic level that provides meaningful statistical results. Because the groups used are generally considered to be monophyletic (see Weishampel et al., 1990), they provide a suitable framework to analyze the structure of the dinosaurian assemblage.

In this study, estimates of maximum and minimum number of individuals were used. The maximum number of individuals estimator is the sum of all dinosaurs identified at the familial level at all sites (Fig. 3). The minimum number of individuals (MNI) estimator as used here is the least number of individuals identified at the family level that could have been present at a given site (Fig. 4).

Gilinsky and Bennington (1994) have demonstrated that when the sampling domain is assumed to be finite and sampling is exhaustive, the MNI estimator is best-suited for assessing assemblage structure. The sampling strategy used during the Dig-a-Dinosaur project meets the two criteria outlined by Gilinsky and Bennington (1994); a finite sampling area was designated before the collecting started, and sampling was exhaustive as a result of the collecting methods.

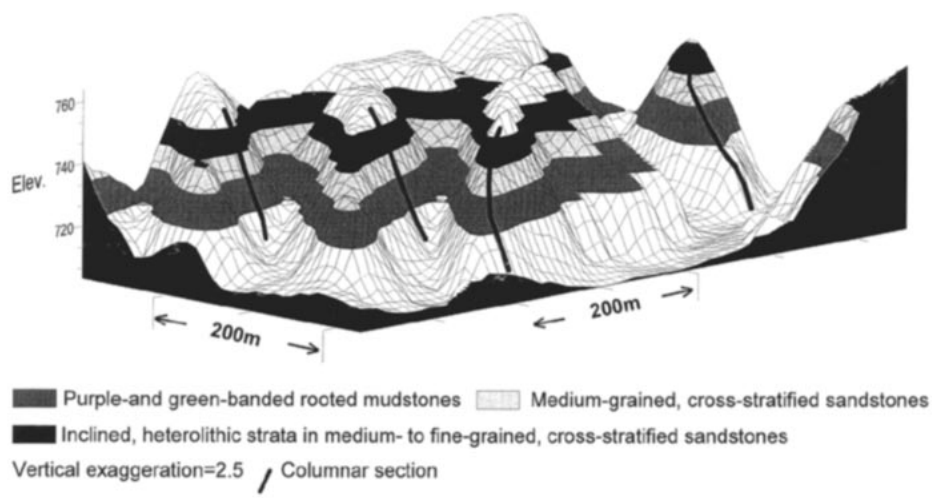

FIGURE 2—Diagrammatic representation of the method used for obtaining facies surface areas. The exposed area of a particular facies (represented by banded areas) was calculated once its distribution within a triangulated-irregular network (TIN) was established over a search area. Thus, element abundance and density could be obtained as a function of the exposed area of each facies. The distribution of over 1000 fossil elements was examined within several collecting sites (Fig. 1) whose total area is approximately 11.5×106 m² (Table 3).

TABLE 3—Areas (m^2) searched within each fluvial architectural element at each fossil collection area.

	Fluvial architectural element									
Map area	Thalweg	Point bar	Paleosol	Flood-plain swamp	Pond	Distal levee	Toe-of-point bar	Crevasse splay	Peat swamp	TOTAL
Cedar Hill	618,172	634,934	1,484,862	60,537	80,439	0	0	170,611	1,512	3,050,527
Glendive 1	404,294	96,990	120,700	12,796	0	4,109	9,257	63,023	2,451	713,620
Glendive 2	133,396	8,556	239,304	10,524	3,593	9,236	0	367,000	0	771,608
Glendive 3	197,615	52,429	409,221	21,170	17,814	12,289	0	69,223	622	780,384
Kid Creek	447,435	745,554	505,713	20,832	702	0	0	24,646	0	1,744,882
Mud Buttes	524,303	576,224	1,197,501	28,337	116,673	19,790	0	45,395	5,133	2,516,355
Twin Forks Reservoir	130,450	34,655	603,896	5,763	7,037	79,344	0	95,710	4,179	961,033
Upper Magpie Reservoir	146,547	47,617	577,112	3,244	97,852	17,535	0	50,205	2,579	942,689
TOTAL	2,602,211	2,199,419	5,138,308	163,203	324,110	142,303	9,257	885,814	16,476	11,481,100

Tamm et al. (1991) were unable to detect systematic changes in the Hell Creek fluvial system through time. Therefore, we infer that the dinosaurian biota was subjected to a spatially and temporally constant "taphonomic filter" (see Williams, 1994). This allowed the pooling of all elements throughout the thickness of the Hell Creek when testing taphonomic hypotheses.

TAPHONOMIC QUESTIONS

Do Stream Channels Effectively Sample the Floodplain Biota?

Two different views have been expressed with regard to obtaining the best overall sample of the paleocommunity within an ancient fluvial system. Bown and Kraus (1981a, b), Retallack (1988), and Winkler (1983) suggested that fossils found in floodplain paleosols best represent the overall paleocommunity. By contrast, Behrensmeyer (1988) suggested that channel-lag assemblages provide the most homogeneous sample of the overall paleocommunity. Bown and Kraus (1981b) and Retallack (1988) noted that paleosols by definition are *in situ* and that the bones in them are a relatively instantaneous sample (i.e., not time-averaged). Therefore, they argued, paleosols provide the best sample of the paleocommunity. Behrensmeyer (1988), on the other hand, noted that rivers sample the floodplain along their lengths and that elements can be concentrated in channel deposits.

This study provides a unique opportunity to attempt a resolution of these divergent viewpoints in the Hell Creek fluvial system, at least. If indeed channels do concentrate material from the floodplains, then the mean density of elements in channel deposits should be equal to, if not greater than, the elemental density of the floodplain deposits. To test the hypothesis that channel deposits concentrate fossil elements, a t-test was used to compare the mean element density of the pooled channel AE[2] (condensing thalweg, point bar, and toe-of-point bar) with that of the pooled floodplain AE (condensing floodplain paleosols and floodplain pond deposits). For this analysis, the data required transformation due to a high frequency of zero counts and samples of different sizes (Ott, 1993). The transformation used was log linear:

$$\log((1 + \text{element count})/\text{area}).$$

The results of the test indicate that there is insufficient evidence to conclude that the mean element density is greater in the pooled channel depositional environment ($t'=0.048$, $df=68$).

The question of whether channels concentrate elements can also be addressed by examining the relationships that may exist between AE's and families. Four AE's were used: pooled channel deposits, pooled floodplain deposits, crevasse-splay deposits, and distal levee deposits. The relationship between families and AE's was tested using two statistical methods. The first was a one-way ANOVA to compare mean familial densities among AE's (Ho: there is no significant difference between mean pooled channel and floodplain familial densities; see Fig. 5) and the second was a chi-square test of independence to see if familial counts are AE-dependent (Ho: familial counts are independent of AE; see Table 5).

The results of the one-way ANOVA indicate that at least one mean familial density differs ($F=4.23$, $df1=3$, $df2=28$, $p=0.0138$). To identify this AE, the Fisher least significant difference (LSD) test was used to make pair-wise comparisons between AE means (Fig. 5). The LSD test demonstrates that the mean familial densities of the distal levee

TABLE 4—Dinosaurian families.

Ceratopsidae
Hadrosauridae
Hypsilophodontidae
Pachycephalosauridae
Dromaeosauridae
Ornithomimidae
Troodontidae
Tyrannosauridae

[2] In the Sheehan et al (1991) study, the data were collected by individual facies. By "pooled" AE's. we mean data from facies grouped together to constitute a single broad architectural element (see Table 1).

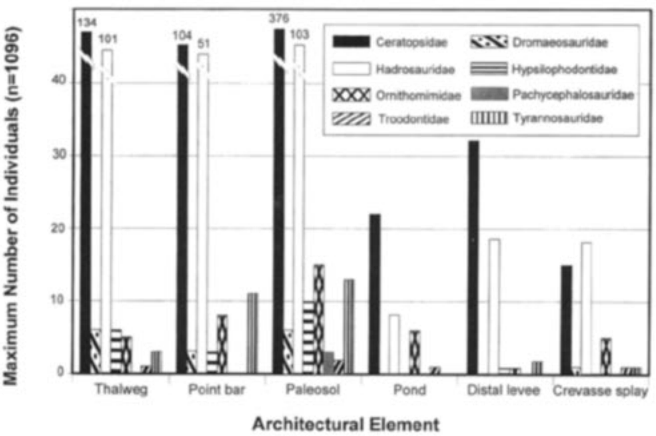

FIGURE 3—Distribution of the maximum number of individuals within AE's. See Table 1 for explanation of facies and corresponding architectural elements.

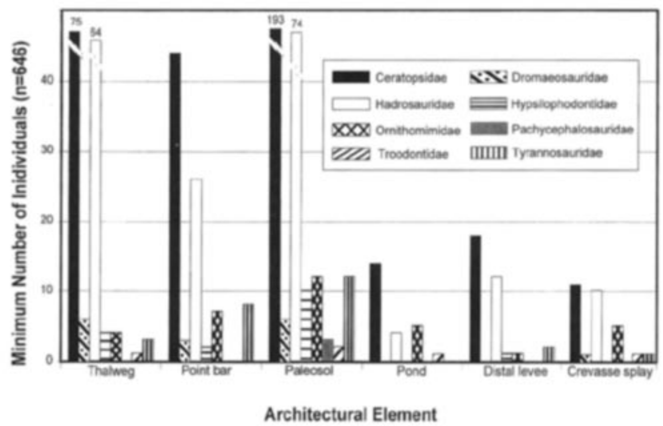

FIGURE 4—Distribution of the minimum number of individuals within AE's. See Table 1 for explanation of facies and corresponding AE's and text for the definition of the minimum number of individuals.

deposits are significantly different from all other AE's tested.

The data for the chi-square test are shown in Table 5. The results indicate the two variables, AE's and families, are dependent (χ^2=35, df=21). This means that the proportion of a particular family varies depending on the facies in which it occurs.

Interpretation

The results of the ANOVA and t-test indicate that the mean density of elements in channel and floodplain deposits do not differ and that, in the Hell Creek, channel deposits do not have a higher concentration of elements (*contra* Fastovsky, 1987; 1990).

Fastovsky (1987) speculated that channel avulsion was an important part of Hell Creek aggradation. Because our results do not show an increased amount of dinosaur fossil material in channels relative to floodplains, it appears that bank erosion did not concentrate fossil elements in channels of the Hell Creek system. This indicates that avulsion must have been an important mode of channel migration.

In summary, these results indicate:

(1) significant aggradation by avulsion decreases the amount of material concentrated from the floodplain relative to the amount that might be expected as a result of bank erosion;
(2) it is only in the floodplain deposits that all eight dinosaurian families are accounted for; and
(3) familial counts are AE-dependent;

The data indicate that, *contra* the predictions of Behrensmeyer (1988), floodplain deposits are the best source of paleoecological data on large, terrestrial vertebrates, at least in the Hell Creek Formation.

The results of the chi-square test of independence and t-test also affect the way one may assess the number of individuals represented in a fluvial setting. We have seen that familial counts are facies-dependent and that a stream channel in an avulsing system need not concentrate elements. In their study of bone dispersal in the East Fork River, Wyoming, Aslan and Behrensmeyer (1996) found that the average greatest distance a bone traveled over a thirteen-year period was only 900 m. It can be inferred that meandering rivers do not concentrate elements from sources far upstream. All of the above, in turn, indicate that the fossils found in channel deposits may duplicate (i.e., bones eroded from the bank and being deposited in the same general area) what is found in channel-proximal floodplain deposits. Indeed, channels may be a replicate, albeit a poor one, of the floodplain.

The inclusion of individuals from channel deposits in an analysis of assemblage structure may result in duplicate counts, which, in turn, may lead to specious proportions of the assemblage represented by a taxon. In the Hell Creek Formation, the occurrence of all families is consistently lower in channel deposits except for hadrosaurs and dromaeosaurs. Figure 6 demonstrates the affects of pooling channel counts with floodplain counts on taxa proportions; three families experience an increase and five a decrease when compared to floodplain AE's only.

When taxa are ranked by their proportion in the assemblage (Table 6), the differences between floodplain and channel preservation are highlighted. For example, the rank of pachycephalosaurs changes from seventh—when channel and floodplain deposits are combined—to eighth when only floodplain deposits are considered. In combined channel and floodplain deposits, dromaeosaurs rank sixth; however, their rank changes to fourth when channel AE's are considered alone. Dromaeosaurs rank sixth in floodplain deposits, but fourth in channel AE's. Troodontids follow the same pattern, changing from sixth to a rank of seventh in channel deposits.

Is the Incidence of Taxa Dependent Upon Whether Bone or Teeth are Preserved?

A chi-squared test of independence was used to test the hypothesis that the preservation of taxa is dependent

Architectural Element			
Pooled channel	Pooled floodplain	Crevasse splay	Distal levee
-5.6394	-5.5280	-5.4721	-4.7192

FIGURE 5—Summary of the Fisher LSD test used to make pair-wise comparisons of familial densities between fluvial AE's. Means joined by a common line are interpreted to be statistically equal.

TABLE 5—Contingency table for the chi-square test of independence testing the null hypothesis that the two variables, architectural element and family, are independent. Expected values have been rounded.

Architectural element	Ceratopsidae actual/expected	Dromaeosauridae actual/expected	Hadrosauridae actual/expected	Hypsilophodontidae actual/expected	Ornithomimidae actual/expected	Pachycephalosauridae actual/expected	Troödontidae actual/expected	Tyrannosauridae actual/expected	TOTAL
Thalweg, point bar and toe-of-point bar	119/136	9/6	90/73	6/7	11/13	0/1	1/2	11/10	247
Floodplain paleosol and floodplain pond	207/185	6/8	78/99	10/9	17/18	3/2	3/3	12/14	336
Distal levee	18/19	0/1	12/10	1/1	1/2	0/0	0/0	2/1	34
Crevasse splay	11/16	1/1	10/9	0/1	5/2	0/0	1/0	1/1	29
TOTAL	355	16	190	17	34	3	5	26	646

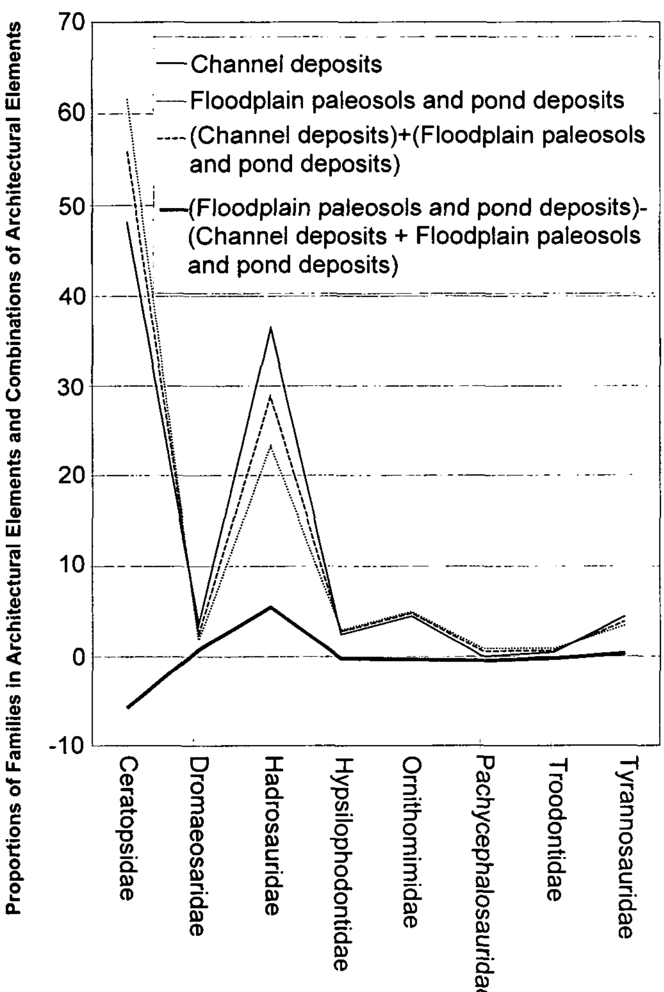

FIGURE 6—Familial proportions within AE groupings. The low, solid, heavy line results from the subtraction of the total pooled AE's from the pooled floodplain AE's.

upon whether bone or teeth are preserved (Ho: taxa and element type are independent). For this analysis MNI data were pooled into two element types, bones and teeth. Pachycephalosaurs and troodontids were not included in the analysis because the sample sizes (n=3 and n=5, respectively) did not lend themselves to meaningful statistical analysis.

Table 7 shows that the preservation of small theropods (Troodontidae and Dromaeosauridae) depends on the preservation of their teeth. It also shows that pachycephalosaurs and hypsilophodontids are preserved by bone only. The chi-square test supports the hypothesis that the occurrence of some taxa is element-dependent ($\chi^2=50{,}000$, df=4).

Interpretation

It is not surprising that the lightly built and hollow-boned dromaeosaurs are represented by teeth only. Exposed on the floodplain, they could easily be broken and/or fragmented by trampling (Behrensmeyer, 1991). If they were buried, they may be destroyed more readily than larger bones by acids in the soil because of the higher surface-to-volume ratios of the light bones (Retallack, 1988). Dromaeosaurid bones probably did not survive long enough to be eroded into channels and, if they did, they

TABLE 6—Ranks of families in the Hell Creek dinosaurian assemblage.

Family	Rank in channel deposits	Rank in *flood-plain* deposits	Rank in combined channel and *flood-plain* deposits
Ceratopsidae	1	1	1
Hadrosauridae	2	2	2
Ornithomimidae	3	3	3
Tyrannosauridae	3	4	4
Hypsilophodontidae	5	5	5
Dromaeosauridae	4	6	6
Troodontidae	6	7	7
Pachycephalosauridae	not present	7	8

TABLE 7—Contingency table for the chi-square test of independence testing the null hypothesis that preservation of bones and teeth is independent of family. Expected values have been rounded.

Family	Bone actual/ expected	Tooth actual/ expected
Ceratopsidae	290/278	65/77
Dromaeosauridae	0/16	16/3
Hadrosauridae	159/149	31/41
Hypsilophodontidae	17/13	0/4
*Ornithomimidae	34	0
*Pachycephalosauridae	3	0
*Troodontidae	0	5
Tyrannosauridae	10/20	16/6

* Not used in analysis.

were probably quickly destroyed or at least rendered unrecognizable. Although troodontid remains could not be analyzed statistically, they are nonetheless rare in all Cretaceous sedimentary rocks, a fact that has also been attributed to thin-walled bones (Osmólska and Barsbold, 1990).

Among ornithischians, hypsilophodontids are common in the Hell Creek Formation, and their occurrence as bone material only may be attributable to the fact that the tiny (5 mm) teeth of these animals may have been overlooked during the data collection. Ceratopsian and hadrosaurid remains are the most abundant fossils found in the Hell Creek Formation and are most often represented by bone material, although the occurrence of teeth is not uncommon. Both animals had large dental batteries with numerous teeth; hence, it is not surprising that a significant number of individuals are represented by tooth material.

The results of this analysis provide support for studies such as that of Fiorillo and Currie (1994), who examined the distribution and relative abundance of theropods using teeth only. The data presented here show that the paleoecology of lightly built theropods requires the use of tooth material due to the rare occurrence of bone.

Are Faunal Elements AE-Dependent?

It has been shown by Aslan and Behrensmeyer (1996) that bone elements do not become sorted by size or shape within AE's in modern fluvial systems. To test this idea in an ancient fluvial system a chi-square test was used to determine if faunal elements are AE-dependent (Ho: elements are AE-dependent). Elements that have left and right-hand equivalents were combined (i.e., left- and right-hand jaws). The outcome of the chi-square test of independence indicates that elements and AE's are independent (χ^2=200, df=170).

Interpretation

Given the observation that all fluvial sediments may be considered reworked and that dinosaurs were not riparian animals, it is not surprising that fossil elements are not preferentially preserved in particular AE's. This result parallels that of Dodson et al. (1980) who could not obtain AE-dependent relationships in the distribution of the bones of Late Jurassic (Morrison) dinosaurs.

TABLE 8—Ranks used to describe fossil quality and abrasion for bone and teeth.

Rank	Description	Degree of abrasion
1	Articulated, Whole	Unabraded
2	Articulated, Broken	Little abraded
3	Articulated, Fragmented	Abraded
5	Isolated, Whole	Very abraded
6	Isolated, Broken	
7	Isolated, Fragmented	
8	Fragmented	

Is Fossil Quality AE-Dependent?

If fossil quality is an indication of reworking and contact time with moving sediment, fossils found in channel deposits (thalweg, point bar, and toe-of-point bar) should show more evidence of disarticulation and abrasion than fossils found in floodplain deposits (paleosols and pond deposits). Assuming that most fossils found in floodplain paleosols and pond deposits are autochthonous (Behrensmeyer, 1975, 1982; Bown and Kraus 1981a, b; Retallack, 1988), fossil quality should be facies-dependent.

The conditions of the fossils were qualitatively ranked from 1 to 8, with 1 being fully articulated (i.e., two or more elements oriented in life position), 5 being isolated but unfragmented, and eight being splintered (Table 8). A two-by-two contingency table (Table 9) was constructed to test the null hypothesis that AE's and fossil quality are independent. The chi-square test of independence results in the rejection of Ho, indicating that the two variables are dependent (χ^2=72.72, df=30). In other words, fossil preservation quality is dependent on the AE in which it is found. From Table 9 it is clear that the best-preserved fossils occur in point-bar deposits and paleosols.

Another measure of fossil quality is degree of abrasion (Table 8). Due to low counts, fossils that were found in pond, distal levee, and crevasse-splay deposits were removed from the analysis. Likewise, bones and teeth ranked as unabraded were excluded from the analysis due to low counts.

A two-by-two contingency table (Table 10) was constructed to test the null hypothesis that AE's and bone abrasion are independent. The two variables are independent (χ^2=6.70, df=4); therefore, in this database, bone abrasion is not AE-dependent. Likewise, the results of the chi-squared test of independence for the variables AE and tooth abrasion are similar to those for bone (Table 11; χ^2=9.5, df=4). It appears that very abraded teeth occur just as often in floodplain sediments as they do in channel deposits.

Interpretation

In the case of articulation, 35 of the 37 articulated fossils are found in paleosols or point bar deposits. This accounts for the dependence of the two variables. It is not surprising that the majority of articulated fossils are found in the low-energy floodplain environment where partial disarticulation results from predation or scavenging (Behrensmeyer, 1991). Nor is it surprising that a large proportion of articulated fossils are found in point-bar deposits where carcasses can be quickly buried (Behrensmeyer, 1991).

TABLE 9—Contingency table for the chi-square test of independence testing the null hypothesis that the two variables, architectural element and fossil preservational quality, are independent. Expected values have been rounded.

Quality rank Architectural element	1 actual/ expected	2 actual/ expected	3 actual/ expected	5 actual/ expected	6 actual/ expected	7 actual/ expected	8 actual/ expected	TOTAL
Thalweg and toe-of-point bar	0/1	1/4	0/4	33/21	138/141	83/83	1/1	256
Point bar	3/1	7/3	3/3	22/15	104/99	40/59	1/1	180
Floodplain paleosol	2/2	7/8	13/1	27/44	283/291	193/172	3/3	528
Floodplain pond	0/0	0/1	0/1	2/3	17/20	18/12	0/0	37
Distal levee	0/0	1/1	0/1	7/4	30/30	16/18	0/0	54
Crevasse splay	0/0	0/1	0/1	0/3	33/23	7/13	1/0	41
TOTAL	5	16	16	91	605	357	6	1096

With one significant exception, the results reported here are similar to those of Wood et al. (1988), who examined the vertebrate taphonomy of the Upper Cretaceous "Judith River Formation" (i.e., Dinosaur Park Formation) in Alberta. Wood et al. (1988) found large numbers of articulated skeletons associated with channel-bottom or lower point-bar deposits. In the Hell Creek, however, only one of the 37 articulated fossils was found in a thalweg deposit. Wood et al. (1988) concluded that articulated fossils found in trough cross-bedded facies were caused by the rapid burial of a carcass by aggrading sinuous-crested dunes during falling flood stages. The absence of articulated specimens in Hell Creek thalweg deposits may reflect greater in-channel reworking in the Hell Creek than in channels represented by the Dinosaur Park Formation.

Attritional assemblages in channel deposits result from the accumulation over time of allochthonous elements whose sources are from reworked floodplain deposits and /or from animals that have died in or beside the channel. When elements are introduced into the channel, they are subjected to further abrasion, disarticulation, and transport if they are not quickly buried (Behrensmeyer, 1982, 1991). The result is an attritional assemblage of disarticulated elements showing varying amounts of abrasion. Given this, it has been claimed that amount and variability of abrasion, and disarticulation within the assemblage may be used to assess the amount of time represented (Behrensmeyer, 1978, 1982, 1991). Fossil articulation may not be a good indication of the amount of time represented in attritional assemblages, such as those in the Hell Creek. Fossil abrasion, however, may reflect residence time in an active fluvial system, particularly when applied to attritional assemblages.

Fossil abrasion, as noted above, is not facies-dependent. Highly-abraded fossil elements found in Hell Creek stream deposits could have had long residence times within the stream before their final burial. However, it is equally possible that abraded bones did not have long residence times in Hell Creek streams, because abrasion is not correlated with AE. It has been shown that the abrasion and disarticulation of elements occurs readily on the surface of the floodplain via trampling, scavenging, and predation and, once the elements are incorporated into the soil, they are subjected to further alteration by acids and biological action (Behrensmeyer, 1978, 1991; Retallack, 1984; Smith, 1993). Multiple pathways can produce abraded fossils (Behrensmeyer, 1991) and, therefore, the amount of time represented by an attritional fossil assemblage, if only abrasion is considered, can be misleading.

STRUCTURE OF THE HELL CREEK DINOSAURIAN ASSEMBLAGE

The statistical relationships described herein indicate that the best sample of the Hell Creek dinosaurian assemblage is obtained from the pooled floodplain paleosol and floodplain pond deposits. These relationships also indicate that the abundance of troodontids, dromaeosaurids, and possibly ornithomimids may have been greater than this study suggests. A ceratopsian-dominated fauna emerges, with the other seven families comprising the remaining 39% of the total assemblage. Of that 39%, over half are hadrosaurs, leaving six families to account for the remaining 16%.

In his analysis of late Maastrichtian dinosaurian biogeography, Lehman (1987) recognized three distinct faunal

TABLE 10—Contingeny table for the chi-square test of independence testing the null hypothesis that the two variables, architectural element and bone abrasion, are independent. Expected values have been rounded.

Abrasion rank Architectural element	Little abraded actual/ expected	Abraded actual/ expected	Very abraded actual/ expected	TOTAL
Thalweg and toe-of-point bar	32/23	65/68	100/106	197
Point bar	18/17	49/50	78/78	145
Floodplain paleosol	41/51	159/154	244/238	444
TOTAL	91	273	422	786

TABLE 11—Contingeny table for the chi-square test of independence testing the null hypothesis that the two variables, architectural element and tooth abrasion, are independent. Expected values have been rounded.

Abrasion rank Architectural element	Little abraded actual/ expected	Abraded actual/ expected	Very abraded actual/ expected	TOTAL
Thalweg and toe-of-point bar	12/15	24/23	14/12	50
Point bar	9/10	18/16	8/8	35
Floodplain paleosol	23/19	27/29	12/14	62
TOTAL	44	69	34	147

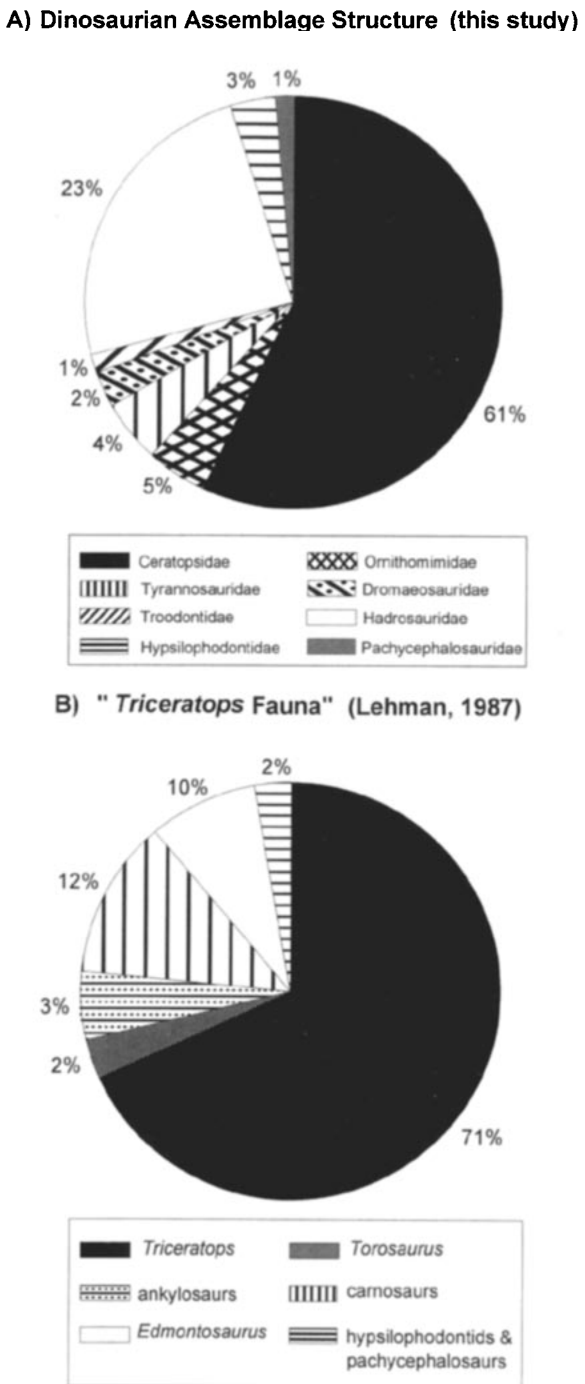

FIGURE 7—(A) Structure of the Hell Creek dinosaurian assemblage that results from using only the minimum number of individuals found in pooled floodplain deposits. (B) Structure of Lehman's (1987) *Triceratops* fauna from the Hell Creek lithosome. Proportions are estimated because numerical values were not published.

assemblages. His "*Triceratops* fauna" dominated coastal lowland environments from southern Saskatchewan to eastern Colorado. The proportions of families obtained in our study (Fig. 7) are similar to, although not precisely identical to, those of Lehman's (1987) "*Triceratops* fauna."

The proportion of ornithomimids in the total assemblage may be related to their ambiguous trophic status. Russell (1972) and Barsbold and Osmólska (1990) have claimed that these theropods were carnivorous. However, Nicholls and Russell (1985) suggested that ornithomimids were herbivorous. Ornithomimids are the third most abundant dinosaur in the assemblage. Within modern terrestrial vertebrate communities (Houston, 1979; Sinclair, 1975; see also Bakker, 1980 and references therein), it is hard to find a carnivore or even an omnivore that ranks as high within its community. By analogy, the abundance of ornithomimids may be a reflection of herbivorous dietary preferences, if the assemblage was behaving like a Recent endothermic community.

SUMMARY AND CONCLUSIONS

The modes of vertebrate fossil occurrences in the Hell Creek Formation are similar to those found in other dinosaur-bearing strata such as the Jurassic Morrison Formation (Dodson et al., 1980) and the Upper Cretaceous Judith River Formation (Koster, 1987; Wood et al., 1988). Fossils most commonly occur in floodplain and channel deposits, and less frequently in crevasse-splay and distal levee deposits. They are not found in swamp or peat deposits. Fossils found in pooled floodplain deposits are, in the Hell Creek at least, best-suited to the reconstruction of the dinosaurian assemblage; pooling of all AE's may result in misinterpretation of the rank of rare taxa within the assemblage.

Fossil articulation in the Hell Creek is AE-dependent. Articulated fossils most commonly occur in floodplain paleosols and point-bar deposits. Their occurrence in floodplain deposits can be attributed to the fact that the energy required to disarticulate elements rarely exists there and supports the claim that most disarticulation results from scavenging and/or predation (Retallack, 1988; Behrensmeyer, 1991). Articulated fossils are also found in point-bar deposits. Their presence there results from the rapid burial of carcasses that have become stranded on the point-bar during falling flood stages (Wood et al., 1988; Behrensmeyer, 1991).

ACKNOWLEDGMENTS

We particularly thank T. and M. Kohler and the Windway Foundation, Inc., for their support. Likewise we thank the many Dig-a-Dinosaur volunteers without whom this project would not have been possible. C. B. Barreto and the late D. L. Gabriel contributed to the establishment of the database, as did the staffs who were involved in the three years of data collection. Earlier versions of this manuscript were read by S. Twombly, J. C. Boothroyd, R. F. Costantino, A. K. Behrensmeyer, and three anonymous reviewers as well as the Editors of PALAIOS, and were vastly improved for their efforts. R. C. Hanumara provided unstinting statistical expertise. The computerized aspects of this study were facilitated by J. P. Klinger, T. Marinelli, and M. Szanto. This work is part of an unpublished M.S. thesis in the Department of Geology, University of Rhode Island, and was funded in part by National Science Foundation grant EAR 9304513 and, in part, by the Department of Geology, University of Rhode Island.

REFERENCES

ARCHIBALD, D., BUTLER, R.F., CLEMENS, W.A., DINGUS, L., and LINDSAY, E.H., 1982, Upper Cretaceous-Paleocene biostratigraphy and magnetostratigraphy, Hell Creek and Tullock Formations, northeastern Montana: Geology, v. 10, p. 153–159.

ASLAN, A., and BEHRENSMEYER, A.K., 1996, Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: PALAIOS, v. 11, p. 411–421.

BADGLEY, C., 1986, Counting individuals in mammalian fossil assemblages from fluvial environments: PALAIOS, v. 1, p. 328–338.

BAKKER, R.T., 1980, Dinosaur heresy—dinosaur renaissance: Why we need endothermic archosaurs for a comprehensive theory of bioenergetic evolution: *in* THOMAS, R.D.K., and OLSEN, E.C., eds., A cold look at the warm-blooded dinosaurs: American Association for the Advancement of Science Selected Symposium, 28, p. 351–462.

BARSBOLD, R., and OSMÓLSKA, H., 1990, Ornithomimosauria: *in* DODSON, P., OSMÓLSKA, H., and WEISHAMPEL, D.B., eds., The Dinosauria: University of California Press, p. 225–258.

BEHRENSMEYER, A.K., 1975, The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya: Bulletin of the Museum of Comparative Zoology, v. 146, p. 475–574.

BEHRENSMEYER, A.K., 1978, Taphonomic and ecological information from bone weathering: Paleobiology, v. 4, p. 150–162.

BEHRENSMEYER, A.K., 1982, Time resolution in fluvial vertebrate assemblages: Paleobiology, v. 8, p. 211–227.

BEHRENSMEYER, A.K., 1988, Vertebrate preservation in fluvial channels: Paleogeography, Paleoclimatology, Paleoecology, v. 63, p. 183–199.

BEHRENSMEYER, A.K., 1991, Terrestrial vertebrate accumulations: *in* ALLISON, P.A., and BRIGGS, D.E.G., eds., Taphonomy: Plenum Press, New York, p. 291–335.

BEHRENSMEYER, A.K., WESTERN, D., and DECHANT BOAZ, D.E., 1979, New perspectives in vertebrate paleoecolgy from a recent bone assemblage: Paleobiology, v. 5, p. 12–21.

BELT, E.S., CONWAY, K.M., FLORES, R.M., JOHNSON, K.R., WARWICK, P.D., and WASKOWITZ, R.S., 1984, Relationships of fluvio-deltaic facies to coal deposition in the lower Fort Union Formation (Paleocene), southwestern North Dakota: *in* RAHMANI, R., and FLORES, R.M., eds., Sedimentology of Coal Deposits: International Association of Sedimentologists, Special Publication No. 7, p. 317–335.

BOWN, T.M., and KRAUS, M.J., 1981a, Lower Eocene alluvial paleosols (Willwood Formation, northwest Wyoming, U.S.A.) and their significance for paleoecology, paleoclimatology, and basin analysis: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 34, p. 1–30.

BOWN, T.M., and KRAUS, M.J., 1981b, Vertebrate fossil-bearing paleosol units (Willwood Formation, Lower Eocene, northwest Wyoming, U.S.A.): Implications for taphonomy, biostratigraphy, and assemblage analysis: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 34, p. 31–56.

BUTLER, R.D., 1980, Stratigraphy, sedimentology, and depositional environments of the Hell Creek Formation (Late Cretaceous) and adjacent strata, Glendive area: Unpublished Ph.D. Dissertation, University of North Dakota, Grand Forks, 398 p.

CHERVEN, V.B., and JACOB, A.F., 1985, Evolution of Paleogene depositional systems, Williston Basin, in response to global sea level changes: *in* FLORES, R.M., and KAPLAN, S.S., eds., Cenozoic Paleogeography of the West Central United States: Rocky Mountain Symposium No. 3: Society of Economic Paleontologists and Mineralogists, Rocky Mountain Section, Denver, p. 127–170.

DODSON, P., BEHRENSMEYER, A.K., BAKKER, R.T., and MCINTOSH, J.S., 1980, Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation: Paleobiology, v. 6, p. 208–232.

EBERTH, D.A., and HAMBLIN, A.P., 1993, Tectonic, stratigraphic, and sedimentologic significance of a regional discontinuity in the upper Judith River Group (Belly River Wedge) of southern Alberta, Saskatchewan, and northern Montana: Canadian Journal of Earth Sciences, v. 30, p. 174–200.

FASTOVSKY, D.E., 1987, Paleoenvironments of vertebrate-bearing strata during the Cretaceous-Paleogene transition, eastern Montana and western North Dakota: PALAIOS, v. 2, p. 282–295.

FASTOVSKY, D.E., 1990, Rocks, resolution, and the record; A review of depositional constraints on fossil vertebrate assemblages at the terrestrial Cretaceous/Paleogene boundary, eastern Montana and western North Dakota: *in* SHARPTON, V.L., and WARD, P.D., eds., Global catastrophes in Earth history: Geological Society of America Special Paper 247, p. 541–547.

FASTOVSKY, D.E., and MCSWEENEY, K., 1987, Paleosols spanning the Cretaceous-Paleogene transition, eastern Montana and western North Dakota: Geological Society of America Bulletin, v. 99, p. 66–77.

FIORILLO, A.R., and CURRIE, P.J., 1994, Theropod teeth from the Judith River Formation (Upper Cretaceous) of south-central Montana: Journal of Vertebrate Paleontology, v. 14, p. 74–80.

FRYE, C.I., 1969, Stratigraphy of the Hell Creek Formation in North Dakota: North Dakota Geological Survey Bulletin No. 54, 65 p.

GILINSKY, N.L., and BENNINGTON, J.B., 1994, Estimating numbers of whole individuals from collections of body parts: A taphonomic limitation of the paleontological record: Paleobiology, v. 20, p. 245–258.

HOUSTON, D.C., 1979, The adaptations of scavengers: *in* SINCLAIR, A.R.E., and NORTON-GRIFFITHS, M. eds., Serengeti, Dynamics of an Ecosystem: The University of Chicago Press, p. 263–286.

JOHNSON, K.R., and HICKEY, L.J., 1990, Megafloral change across the Cretaceous/Tertiary boundary in the northern Great Plains and Rocky Mountains, U.S.A.: *in* SHARPTON, V.L., and WARD, P.D., eds., Global catastrophes in Earth history: Geological Society of America Special Paper 247, p. 433–444.

KOSTER, E.H., 1987, Vertebrate taphonomy applied to the analysis of ancient fluvial systems: *in* ETHRIDGE, F.G., FLORES, R.M., and HARVEY, M.D., eds., Recent developments in fluvial sedimentology: Society of Economic Paleontologists and Mineralogists, Special Publication No. 39, p. 159–168.

LEHMAN, T.M., 1987, Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western Interior of North America: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 189–217.

MIALL, A.D., 1985, Architectural-element analysis: a new method of facies analysis applied to fluvial deposits: Earth Science Reviews, v. 22, p. 261–308.

NICHOLLS, E.L., and RUSSELL, A.P., 1985, Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae): Palaeontology, v. 28, p. 638–667.

OSMÓLSKA, H., and BARSBOLD, R., 1990, Troodontidae: *in* Dodson, P., Osmólska, H., and Weishampel, D.B., eds., The Dinosauria: University of California Press, p. 259–268.

OTT, L.R., 1993, An introduction to statistical methods and data analysis: Duxbury Press, Wadsworth Publishing Company, Belmont, 1051 p.

RETALLACK, G.J., 1984, Completeness of the rock and fossil record: Some estimates using fossil soils: Paleobiology, v. 10, p. 59–78.

RETALLACK, G.J., 1988, Down-to-Earth approaches to vertebrate paleontology: PALAIOS, v. 3, p. 335–344.

RUSSELL, D.A., 1972, Ostrich dinosaurs from the Late Cretaceous of Western Canada: Canadian Journal of Earth Sciences, v. 9, p. 375–402.

SHEEHAN, P.M., FASTOVSKY, D.E., HOFFMANN, R.G., BERGHAUS, C.B., and GABRIEL, D.L., 1991, Sudden extinction of the dinosaurs: Latest Cretaceous, Upper Great Plains, U.S.A.: Science, v. 254, p. 835–839.

SINCLAIR, A.R.E., 1975, The resource limitation of trophic levels in tropical grassland ecosystems: Journal of Animal Ecology, v. 44, p. 497–520.

SLOAN, R.E., RIGBY, J.K., VAN VALEN, L., and GABRIEL, D.L., 1986, Gradual dinosaur extinction and simultaneous ungulate radiation in the Hell Creek Formation: Science, v. 232, p. 629–633.

SMITH, R.M.H., 1993, Vertebrate taphonomy of the Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa: PALAIOS, v. 8, p. 45–67.

TAMM, V., FASTOVSKY, D.E., and HOGLER, J.A., 1991, Depositional environments of the lower Hell Creek Formation (Maastrichtian),

Upper Great Plains, U.S.A.: Geological Association of Canada, Program with Abstracts, v.16, p. A122.
VAN VALEN, L., and SLOAN, R.E., 1977, Ecology and extinction of the dinosaurs: Evolutionary Theory, v. 2, p. 37–64.
WEISHAMPEL, D.B., DODSON, P., and OSMÓLSKA, H., eds., 1990, The Dinosauria: University of California Press, Berkeley, 720 p.
WHITE, P.D., 1996, The taphonomy and a suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota: Unpublished M.S. Thesis: University of Rhode Island, 75 p.
WILLIAMS, M.E., 1994, Catastrophic versus noncatastrophic extinction of the dinosaurs: Testing, falsifiability, and the burden of proof: Journal of Paleontology, v. 68, p. 183–190.
WINKLER, D.A., 1983, Paleoecology of an early Eocene mammalian fauna from paleosols in the Clarks Fork Basin, northeastern Wyoming (U.S.A.): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 43, p. 261–298.
WOOD, J.M., THOMAS, R.G., and VISSER, J., 1988, Fluvial processes and vertebrate taphonomy: The Upper Cretaceous Judith River Formation, south-central Dinosaur Provincial Park, Alberta, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 66, p. 127–143.

ACCEPTED JUNE 13, 1997