COMPARATIVE TAPHONOMY AND PALEOECOLOGICAL RECONSTRUCTION OF TWO MICROVERTEBRATE ACCUMULATIONS FROM THE LATE CRETACEOUS HELL CREEK FORMATION (MAASTRICHTIAN), EASTERN MONTANA

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ABSTRACT

Although microvertebrate accumulations are commonly used for paleoecological reconstructions, taphonomic processes affecting the final taxonomic composition of an accumulation are often ignored. This research explores the effects of abiotic taphonomic processes on the taxonomic composition of terrestrial microvertebrate accumulations by comparing a floodplain and a channel lag deposit from the Maastrichtian Hell Creek Formation in eastern Montana. Distribution of skeletal elements with specific physical attributes and relative abundance of taxa correlate with the hydraulic indicators (i.e., grain size, sedimentary structures) of the depositional facies. Transport distances, hydraulic equivalencies of dominant skeletal elements, amount of hydraulic sorting and reworking, and degree of time averaging vary between deposits and significantly affect taxonomic distributions. Relative abundance data, in conjunction with chi-square test results and rank-order analysis, show that size, shape, abrasion, and taxonomic compositions vary significantly between assemblages. The fine-grained assemblage is dominated by tabular, low-density elements, such as cycloid scales and fish vertebrae. Dense, equidimensional elements, such as teeth and ganoid fish scales, dominate the sandstone assemblage. Rank-order analysis results demonstrate that relative abundance of hydraulically equivalent skeletal elements from morphologically similar organisms can be compared regardless of accumulation in nonisotaphonomic deposits. Statistical comparisons were made among osteichthyans using ganoid scales, caudates using vertebrae, ornithischians using teeth, and testudinates using shell fragments. Results show that portions of the assemblage analyzed using hydrodynamically equivalent elements are not significantly different, despite different depositional environments.

INTRODUCTION

Microvertebrate fossil accumulations (also termed microsites) provide a wealth of data derived from the regional faunal and floral communities as well as local transport processes. This research focuses on the quantification of taphonomic effects on paleoecological reconstructions from microsites. Because of the abundance of vertebrate taxa, and sometimes abundant taxa of invertebrates and plants, much information can be gained concerning the local paleoecology. Marine invertebrate accumulations (e.g., Martin et al., 1996; Meldahl et al., 1997; Best and Kidwell, 2000a, 2000b) and bone beds of large terrestrial vertebrates (e.g., Fiorillo, 1991; Varricchio and Horner, 1993; Varricchio, 1995; Fiorillo et al., 2000; Ryan et al., 2001) have routinely been subject to extensive paleoecological and taphonomic analysis. Given their wider taxonomic sampling and larger sample sizes, microsites provide a unique opportunity for taphonomic and paleoecological analysis. Consequently, understanding taphonomic processes affecting a fossil accumulation is fundamental before taxonomic composition can be compared between assemblages.

Taphonomic research since Efremov (1940) has focused primarily on how taphonomic biases affect the deposition and preservation of organisms in the fossil record (e.g., Behrensmeyer and Kidwell, 1985; Kowalewski, 1996; Cutler et al., 1999; Hedges, 2002). Transport and preservation of microvertebrate remains have been analyzed experimentally and theoretically (Dodson, 1973; Korth, 1979; Blob and Fiorillo, 1996), but the application of these concepts is still underutilized in microsite paleoecology. Although early paleoecological studies of microsites attempted to relate relative abundances of organisms to specific environments distal and proximal to the site of deposition (e.g., Shotwell, 1955, 1958; Estes and Berberian, 1970), no analysis of transport and time averaging was completed. More recent microsite analyses in the Judith River Group of Alberta, Canada (e.g., Brinkman, 1990; Eberth, 1990; Eberth and Brinkman, 1997; Brinkman et al., 2004) are exploring broad paleoecological questions by combining large sample sizes, detailed stratigraphic frameworks, and statistical analysis.

The purpose of this study is to compare the taphonomic processes affecting faunal content in microsites from two distinctly different sedimentary facies. Collection biases often associated with microsites include unequal sampling among sedimentary facies, but a comprehensive study of the sediments, fossils, and depositional regime provides invaluable insights for the paleoecological analysis of multiple localities across different facies. Collecting from different facies is important for recovering taxa that may not be preserved in a given facies owing to the hydrodynamic characteristics of skeletal remains or habitat preference of an organism. The following questions guide this investigation: (1) How do microsite assemblages deposited in different sedimentary facies vary taphonomically? (2) How do taphonomic processes bias the diversity and relative abundance of taxa in a deposit? (3) Can paleocommunity structure be determined from microvertebrate assemblages in different facies?

GEOLOGIC SETTING

The study area is located along Fort Peck Reservoir in Garfield County, eastern Montana (Fig. 1). Late Cretaceous strata exposed in the area include (from oldest to youngest) the Bearpaw, Fox Hills, and Hell Creek Formations. This sequence is overlain by the Paleocene Tullock Member of the Fort Union Formation, but these strata have been eroded from the immediate study area. The Late Cretaceous rocks of eastern Montana and the western Dakotas were deposited during the final regression of the Western Interior Seaway (Gill and Cobban, 1973; Hartman and Kirkland, 2002).

Interbedded sandstones, mudstones, and siltstones define the Hell Creek Formation. Sedimentology reflects fluvial, overbank, and lacustrine deposition. Sediment provenance of the Late Cretaceous strata in this area is considered to be the Sevier uplifts to the west and northwest (Gill and Cobban, 1973; Dickinson and Suczek, 1979; Dickinson et al., 1983; Zaleha, 1988; Hartman and Kirkland, 2002), with the Hell Creek sediments deposited as a prograding clastic wedge (Hartman and Kirkland, 2002). Sediment deposition persisted for 2.5 myr in central North Dakota and easternmost Montana (Lund et al., 2002).
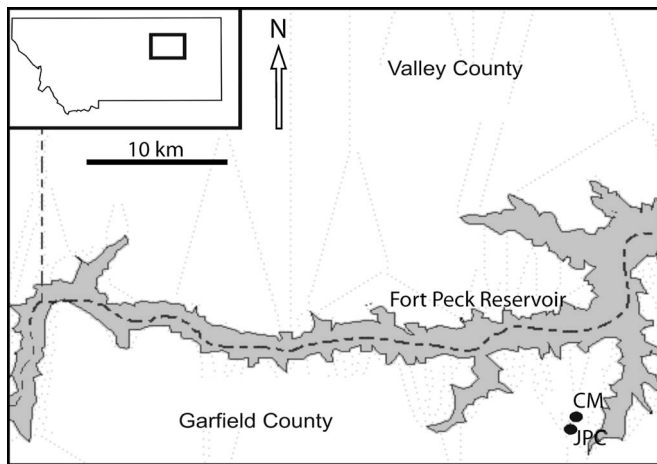
FIGURE 1—Microsite quarry localities along Fort Peck Reservoir in Garfield County, eastern Montana. CM = Conor's Microsite (fine grained); JPC = Just Past Celeste Microsite (sandstone); dotted lines = county borders.

METHODS

The two microsites in this study were selected based on geographic and sedimentologic criteria. They represent different facies of the lower half of the Hell Creek Formation exposed in Garfield County, Montana, and are within 0.5 km of each other. Both microsites also had identifiable horizons with dense fossil distribution, permitting the efficient collection of horizontal and vertical distribution data for each specimen by quarrying. One stratigraphic section was measured through each quarry; stratigraphic descriptions include lithology, grain size, sediment color, unit thickness, and sedimentary and biogenic structures. Detailed, decimeter-scale stratigraphic measurements and notes were taken through the fossiliferous horizons, with attention given to lithologic changes and sedimentary and biogenic structures.

Taphonomic Data Collection

Field Data.—Only quarried vertebrate specimens were used in the study, although tailings were also bagged and wet sieved. There are several advantages to using quarried specimens: (1) Fossils collected by quarrying reduce the likelihood that a broken fossil would be counted multiple times. (2) Surface-collected assemblages can be biased against small-bodied taxa (Wolff, 1975). (3) Spatial distribution data relating to the original depositional context can be accurately collected only for quarried specimens..

Horizontal distribution data were collected by the floating-grid method, which is similar to that described by Organ et al. (2003). Each quarry was divided into 0.5 m × 0.5 m quadrats labeled with an alphanumeric system (Fig. 2), using rebar rods and heavy wire. A 0.50 m × 0.50 m grid of 0.25″ PVC pipe was then suspended over each quadrat, and each

specimen location was plotted. Vertical distribution data were taken using a transit and meter stick, with the transit erected and leveled atop a tripod at the edge of the quarry. A datum spike was used to ensure consistency in daily measurements.

Laboratory Data.—All vertebrate specimens were returned to the laboratory for further research and data collection regardless of taxonomic resolution. The majority of specimens were <2 cm long, and none required plaster jackets. Each fossil was assigned to the lowest taxonomic level possible. Additional data collected from each fossil included size, shape, degree of abrasion, and degree of weathering. Size was measured with an electronic digital caliper to 0.01 mm, and each fossil was placed into one of four shape classes following the categories of Blob and Fiorillo (1996): tabular (class 1), elongate (class 2), equidimensional (class 3), and conical (class 4). Degree of abrasion was measured on a 0–3 scale, with 0 being no abrasion and 3 representing well-rounded fossils that were no longer anatomically identifiable. Weathering was also noted on a scale of 0–3 (Fiorillo, 1988), where 0 corresponds to no cracking or breaking, 1 to minor (shallow) cracking, 2 to flaking and deeper cracking, and 3 to loss of external bone.

Statistical Analysis

Data were analyzed and comparisons made between the two assemblages using a variety of measures. Chi-square tests were used to determine whether distribution of taxa and physical attributes between the two assemblages were statistically significant. Assumptions of the chi-square test included sample sizes greater than four. Where this assumption was not met, taxa were aggregated, or results relied on rank order analysis. Power tests were run to determine the potential of a data set for determining differences between two statistical samples given the sample size. They were run at three levels, where w = 0.5 indicates the ability of the sample to determine large differences, w = 0.3 indicates potential for determining medium-sized differences, and w = 0.1 represents small differences. Lastly, Spearman rank-order analyses were used to determine the level of correlation between assemblages based on rank orders. Rank-order analysis does not make any assumptions about sample sizes, but because it compares rank order (i.e., relative abundance) and not the total numbers of specimens, the power of the test to determine differences among samples is reduced.

RESULTS

Sedimentology and Stratigraphy

Fine-Grained Microsite.—Conor's Microsite (CM) comprises a sequence of interbedded mudstone, siltstone, and sandstone (Fig. 3). Vertebrate, invertebrate (bivalves and gastropods), and plant remains (leaf impressions and seeds) are common, as well as gypsum, amber nodules, rounded clay clasts, and slickensides. The fossiliferous unit was deposited atop mottled clay with abundant *in situ* traces of stems and roots. A minor erosional surface is indicated by local scouring between the fossil-bearing sediments and the underlying clay. The quarried horizon is capped by a
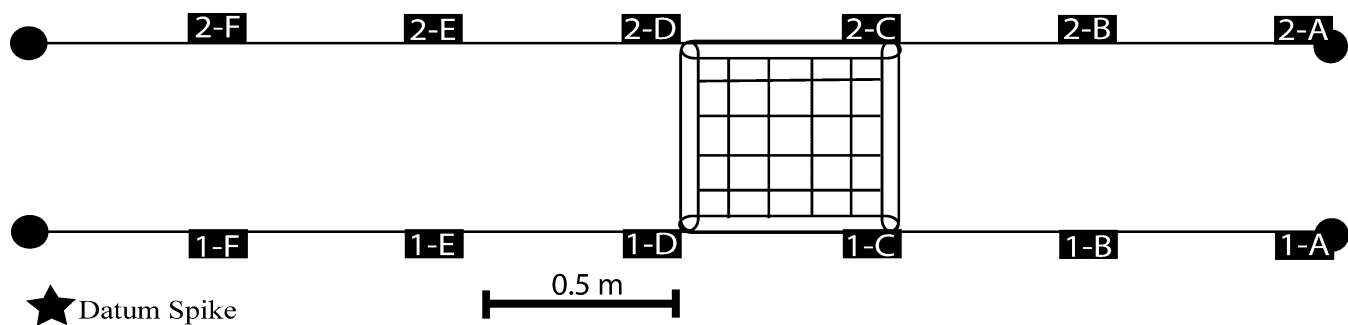

FIGURE 2—Diagram of the 0.5 m floating-grid system used for microvertebrate data collection. See text for further details.
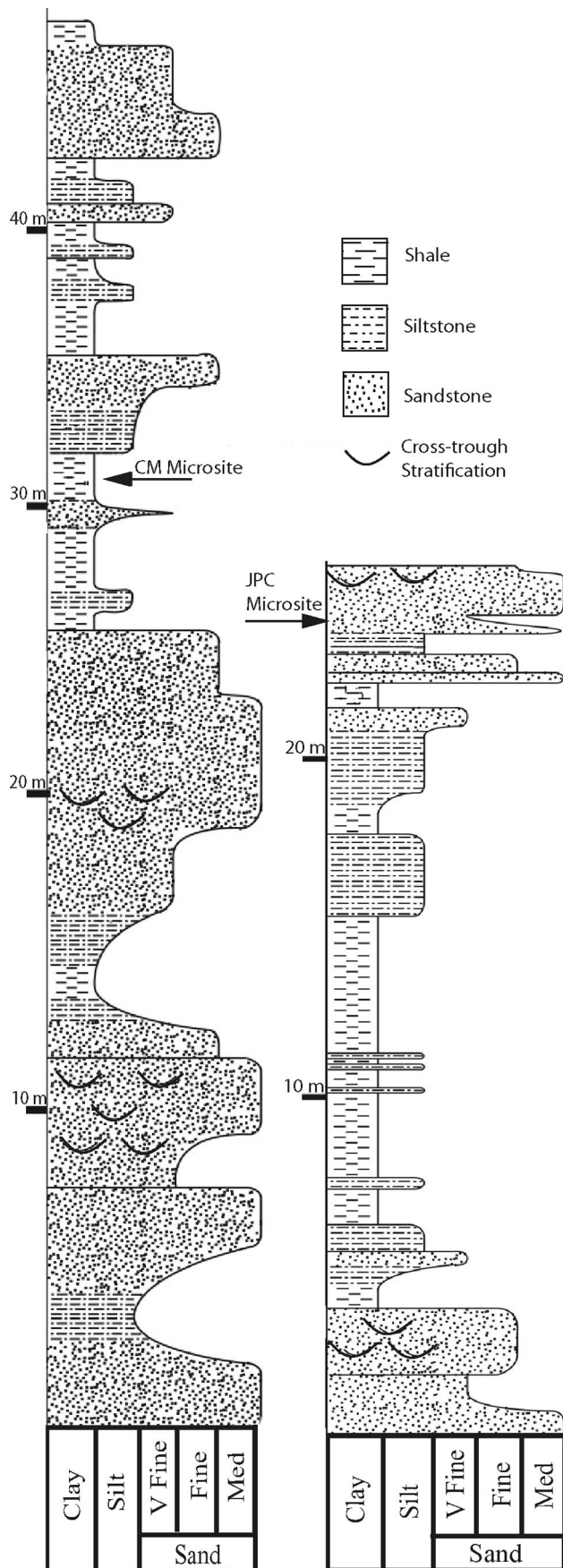
thin layer of carbonized wood fragments and a coarsening-upward, mud-rich siltstone containing traces of plant stems.

The fossiliferous unit falls within a laminated, fine-grained facies signifying deposition under lower current velocities or by suspension settling (Wilson, 2006). Rip-up clasts and millimeter-scale lenses of coarser sediments indicate fluid movement during the onset of fossil deposition, with waning velocities toward the top of the deposit as grain size becomes more homogenous. The abundance of *in situ* stem and root traces combined with slickensides, small-scale fractures, and gypsum nodules directly below the fossil horizon indicate paleosol development with possible wet-dry cycles (Fastovsky, 1987; Fastovsky and McSweeney, 1987; McSweeney and Fastovsky, 1987; Retallack, 1994). Paleosol development overlying and directly underlying the fossiliferous unit suggests that the fossils represent a single event horizon. The influx of mud, silt, and sand, as well as rip-up clasts and bioclasts, on a paleosol could indicate a crevasse splay deposit.

Sandstone Microsite.—The Just Past Celeste Microsite (JPC) includes a medium-grained sandstone that fines upward (Fig. 3). The fossil horizon is underlain by a clay-dominated mudstone and is capped by a medium-grained sandstone unit. Mudstone clasts, iron concretions, vertebrate fossils, and well-rounded, pebble-sized bone fragments are interbedded within the 40-cm-thick fossil-bearing sandstone. Shell hash is found throughout the unit.

The fossiliferous horizon occurs in a massive sandstone facies, indicating that the sandstone was either primarily structureless owing to rapid deposition or that structures were obliterated by later currents and bioturbation (Wilson, 2006). The JPC quarry is interpreted to represent bioclast accumulation in a basal channel lag, since channel lag deposits are found in association with coarse clastic material in channel thalwegs and are often deposited upon fine-grained facies or stacked sandstones (Behrensmeyer, 1988). Sorting and abrasion are common taphonomic signals (Behrensmeyer, 1982).
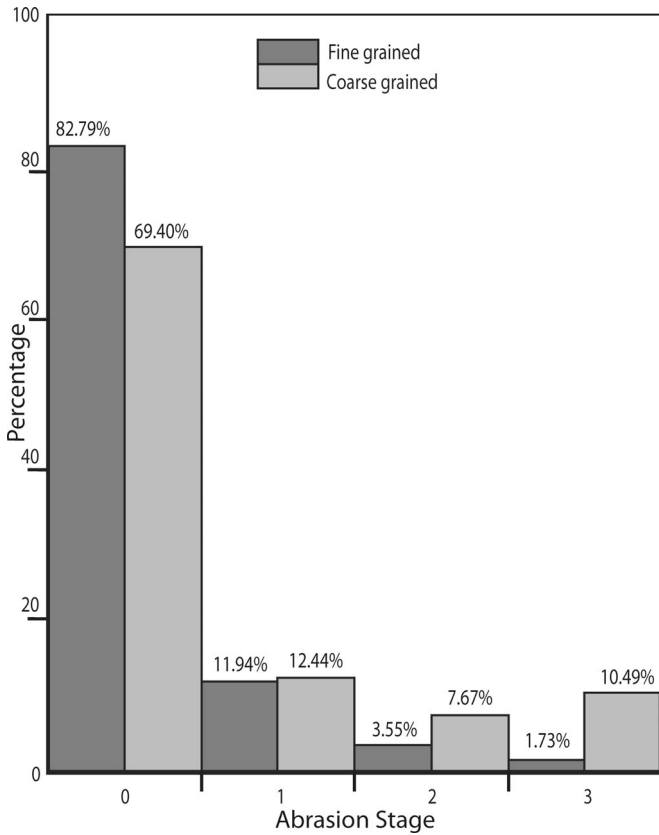
Taphonomy

The fine-grained (CM) and sandstone (JPC) assemblages are characterized by distinct distributions of physical attributes of microvertebrate specimens. Distribution of elements in specific abrasion categories (Fig. 4) and shape classes (Fig. 5) varies greatly between assemblages. The sandstone assemblage has higher overall abrasion, with 18.2% of specimens showing stages 2 and 3 abrasion (Fig. 4). The majority of fossils from the fine-grained accumulation are tabular in shape (shape class 1) and of low density, while the majority of specimens from the sandstone unit are equidimensional (shape class 3) and of higher density. Hydraulically significant characteristics of common fossils are shown in Table 1. Specimens in the sandstone assemblage also have a more limited average size range than those from the fine-grained deposit (Fig. 6) and a higher proportion of weathering (3.4% in the sandstone versus 0.4% in the fine-grained assemblage; see Supplementary Data 1[1]).

Element type also differs between the two microsites. Cycloid scales, ganoid scales, vertebrae (especially flatter amiid vertebrae), and smaller jaws are more common in the fine-grained assemblage (CM), while teeth, shells and scutes, ganoid scales, larger jaws (especially those with teeth), and round amiid vertebrae are more common in the JPC assemblage. Despite the shape classification, the abundance of palatal teeth in the JPC assemblage most likely reflects their small size, higher relative density, and high number per individual. The higher density and tabular shape of ganoid scales accounts for their high preservation potential in both assemblages.
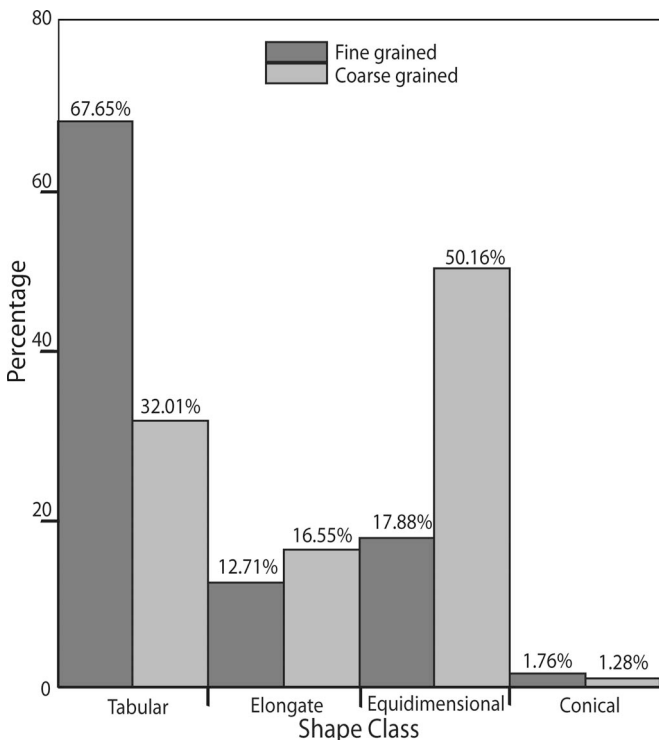
Taxonomic Assemblage

Faunal assemblages from the two microsites also differ taxonomically (Fig. 7), and a chi-square analysis of taxa identified to class or order

FIGURE 3—Stratigraphy of the Hell Creek Formation at Conor's (CM, fine grained) and Just Past Celeste (JPC, sandstone) microsites.

FIGURE 4—Percent specimens in abrasion stages 0–3 in the fine-grained (CM = Conor's Microsite) and coarse-grained (JPC = Just Past Celeste Microsite) assemblages; N_{CM} = 2312, N_{JPC} = 2451.

TABLE 1—Physical attributes relating to the hydraulic characteristics of common skeletal elements in the Conor's and Just Past Celeste microsite assemblages.

Element	Relative Density	Shape	Relative Size
Ganoid scale	high	tabular	small-medium
Amiid vertebra	low	tabular-round	large
Amiid palatal tooth	high	round	small
Cycloid scale	low	tabular	small-medium
Teleost vertebra	low	round	small
Turtle shell	high	tabular-round	large
Jaw	high	tabular	small-medium
Dinosaur tooth	high	round	medium-large

shows the difference to be significant (Tables 2A, 3A). The CM assemblage is dominated by osteichthyan remains, predominantly teleostean scales and Amiidae vertebrate and teeth (Table 2A; Supplementary Data 2[1]); *Lepisosteus occidentalis* scales are also common. The JPC sandstone assemblage consists of considerably fewer teleost remains (55 scales vs. 695 at CM), as well as a larger proportion of nonosteichthyan taxa (Table 2A; Supplementary Data 2[1]). Amiidae and *L. occidentalis* are common, but ornithischian teeth, *Myledaphus bipartitus* teeth, and turtle shell fragments are found in significantly higher abundances.

Significant differences were evident in the relative abundance of tabular-shaped taxa from CM as compared to JPC (χ^2_4 = 296.88, p ≪ 0.001). The large number of teleosts with thin, light scales at CM and the concentration of dense, turtle shell fragments at JPC contributed most significantly to taxonomic differences in tabular-shaped elements. Taxonomic comparisons of equidimensional elements between the two sites are also significantly different (χ^2_4 = 102.40, p ≪ 0.001). The high

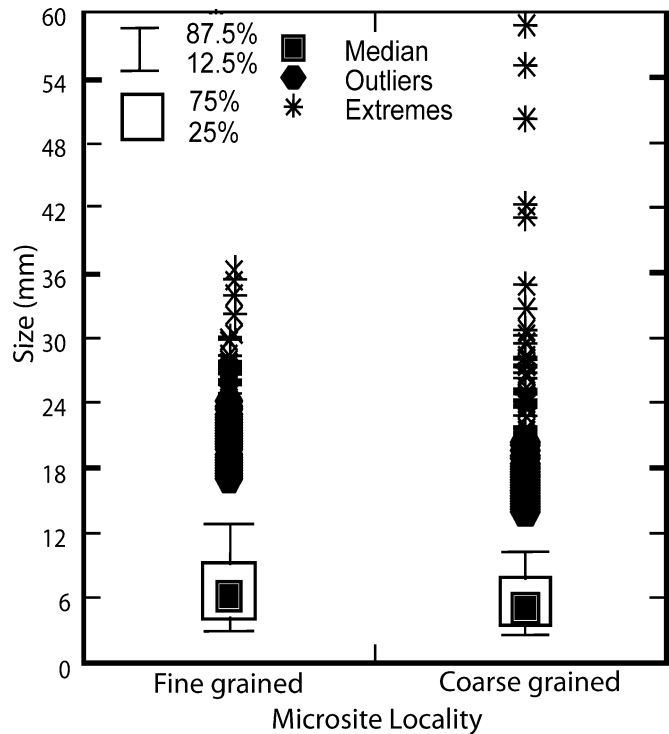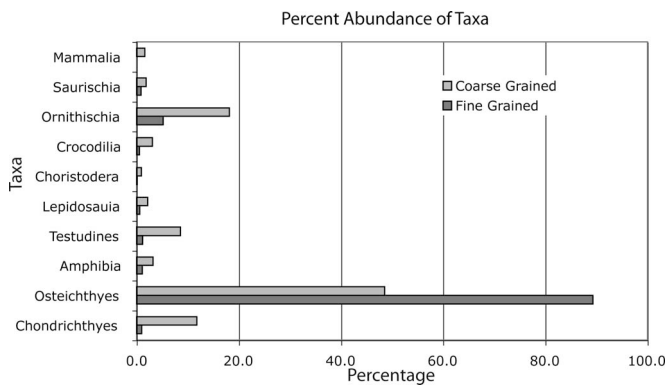FIGURE 5—Percent specimens in four shape classes in the fine-grained (CM = Conor's Microsite) and coarse-grained (JPC = Just Past Celeste Microsite) assemblages; N_{CM} = 2439, N_{JPC} = 2451.

FIGURE 6—Box and whisker plot comparing average specimen size from the fine-grained (CM = Conor's Microsite) and coarse-grained (JPC = Just Past Celeste Microsite) assemblages; N_{CM} = 1723, N_{JPC} = 2455. The limits of the box represent the median 50% of specimens (distance between is the interquartile range). The whisker limits represent the nonoutlier minimum and maximum (the median 75% of specimens). Outliers are specimens with sizes >1.5 × interquartile range, and the extremes have size values 3 × interquartile range.

FIGURE 7—Relative abundances of specimens from major taxonomic groups within the fine-grained (CM = Conor's Microsite) and coarse-grained (JPC = Just Past Celeste Microsite) assemblages; N_{CM} = 1360, N_{JPC} = 744.

number of porous amiid vertebrae in the CM assemblage and the number of dense ornithischian and chondrichthyan teeth in the JPC assemblage are responsible for these distinctions.

Relative abundance of the caudates *Opisthotriton kayi* (most abundant), *Scapherpeton tectum*, *Habrosaurus dilatus*, and *Prodesmodon copei* (least abundant) is similar in both assemblages, and rank order is preserved (Tables 3D, 4); *Lepisosteus occidentalis* and Holostean A are the first- and second-most abundant primitive fish, respectively (Table 4), in both assemblages. Specimens of Holostean morphotype B and sturgeons (*Acipenser*) are less common and vary in abundance between localities, but low sample size makes conclusions regarding relative abundance of these two taxa tenuous. Ornithischian teeth (Ceratopsidae, Hadrosauridae; cf. *Thescelosaurus*, Ankylosauridae, and Pachycephalosauridae) hold the same rank order at both localities (Table 4). It should be noted that the theropod data set is the smallest one used in these analyses, and results are therefore the least reliable as a potential reflection of a time-averaged paleocommunity. Theropod rank order is poorly correlated between the fine-grained and sandstone assemblages (Table 4). Turtles are also poorly correlated between assemblages. Baenids and *Basilemys* show the most significant divergence between the two assemblages, and *Basilemys* is the only turtle taxon present at just one locality, the CM fine-grained site (Tables 3D, 4). Statistical analysis excluding *Basilemys* sp. specimens results in higher rank-order correlation between assemblages (Table 3D), and sample size is still sufficient for indicating large changes between data sets.

DISCUSSION

Taphonomic Differences between Assemblages

Variance in abrasion, shape, size, and relative density distributions of specimens between the two assemblages indicates nonisotaphonomic deposits (*sensu* Brinkman et al., 2004). Grain-size differences between the two deposits reflect a difference in hydraulic equivalence of bioclasts and provide insight into transport histories. The higher degree of abrasion exhibited by the specimens in the sandstone assemblage is consistent with the suggested higher transport energy of the depositional system. The slightly higher proportion of weathered fossils in the sandstone assemblage (Supplementary Data 1[1]) suggests some specimens underwent reworking cycles before final deposition and burial. The concentration of teeth, reduced number of vertebrae, and more constrained average size range of specimens indicates a preburial history of winnowing and sorting of the sandstone assemblage.

Hydraulic analyses of skeletal elements in a deposit is useful in unraveling transport histories and ideally can indicate the likelihood of bones and sediments being transported together to the site of final deposition (Behrensmeyer, 1975). Based on Behrensmeyer's (1975) hydrodynamic equivalency measurements, most bones and teeth from the

TABLE 2—Taxa and sample sizes of skeletal elements from the two assemblages used for chi-square tests. (A) Taxonomic abundances. (B) Distribution of tabular taxa. (C) Distribution of equidimensional taxa. Chi-square results presented in Table 3. (D) Distribution and number of skeletal elements per shape class for specific taxa; statistical results not presented because of small sample sizes. CM = Conor's Microsite; JPC = Just Past Celeste Microsite.

	Number of specimens	
Taxon	CM (fine grained)	JPC (sandstone)
A. Taxonomic Composition		
Chondrichthyes	14	88
Osteichthyes	1204	361
Amphibia	16	24
Testudines	17	64
Lepidosauria	9	16
Crocodilia	8	23
Ornithischia	76	135
Saurischia	13	14
Total (N)	1357	725
B. Tabular Taxa		
Acipenser	9	7
Holostean	94	60
Lepisosteus	128	70
Telesostei	705	59
Reptilia	30	77
Total (N)	966	273
C. Equidimensional Taxa		
Chondrichthyes	14	88
Amiidae	221	137
Telesostei	19	8
Caudata	8	19
Reptilia	85	165
Total (N)	347	417
D. Distribution of shape classes in specific taxa Osteichthyes		
Class 1	1414	311
Class 2	12	6
Class 3	221	158
Class 4	25	8
Total (N)	1672	483
Teleostei		
Class 1	705	60
Class 2	9	3
Class 3	12	6
Class 4	0	0
Total (N)	726	69
Non-Teleostei		
Class 1	256	139
Class 2	1	0
Class 3	200	152
Class 4	21	2
Total (N)	478	293
Lepidosauria		
Class 1	4	2
Class 2	3	6
Class 3	0	3
Class 4	2	5
Total (N)	9	16
Caudata		
Class 1	0	0
Class 2	8	2
Class 3	8	20
Class 4	0	0
Total (N)	16	22

TABLE 3—Statistical results analyzing taxonomic and hydrodynamic differences between assemblages. (A–C) Chi-square and power test results for data sets listed in Table 2. All three show significant differences between the assemblages. (D) Spearman rank-order analysis and power test results for hydrodynamically equivalent elements in specific taxa between assemblages. See Table 4 for data sets and rank orders.

	X^2	p	Power w = 0.5	w = 0.3	w = 0.1
A. Taxonomic composition					
	408.16	≪0.001	1	1	0.939
B. Tabular taxa					
	296.88	≪0.001	1	1	0.817
C. Equidimensional taxa					
	102.40	≪0.001	1	1	0.582
	r^2	p	w = 0.5	w = 0.3	w = 0.1
D. Hydrodynamically equivalent skeletal elements					
Ganoid fishes	0.800	0.200	1.000	0.997	0.284
Caudata	1.000	0.000	0.654	0.265	0.070
Testudines	0.410	0.368	0.954	0.504	0.089
Testudines*	0.632	0.367	0.951	0.534	0.094
Ornithischia	1.000	0.000	0.968	0.565	0.095
Theropoda	−0.636	0.174	0.398	0.158	0.060
Dinosauria	0.430	0.187	0.961	0.504	0.083

* Does not include *Basilemys* sp.

TABLE 4—Sample sizes and rank orders of hydrodynamically equivalent skeletal elements of specific taxa used in statistical analysis. Spearman rank-order analysis results presented in Table 3. CM = Conor's Microsite; JPC = Just Past Celeste Microsite.

Taxon	Fine-Grained Microsite (CM) Number of Specimens	Rank Order	Sandstone Microsite (JPC) Number of Specimens	Rank Order
Ganoid fishes				
Acipenser	5	4	3	3
Holostean A	75	2	30	2
Holostean B	7	3	2	4
Lepisosteus	124	1	65	1
Total	211		100	
Caudata				
Opisthotriton kayi	5	1	8	1
Scapherpeton tectum	4	2	5	2
Habrosaurus dilatus	3	3	4	3
Prodesmodon copei	2	4	1	4
Total	14		18	
Testudines				
Baenidae	1	4.5	19	2
Chelydridae	4	2	11	3
Adocus sp.	1	4.5	2	4
Basilemys sp.	3	3	0	5
Trionychoidae	7	1	24	1
Total	16		56	
Ornithischia				
Ceratopsidae	20	1	22	1
Hadrosauridae	8	2	18	2
cf. *Thescelosaurus*	0	5	1	5
Ankylosauridae	1	4	2	4
Pachycephalosauridae	5	3	5	3
Total	34		48	
Theropoda				
Richardoestesia gilmorei	3	1	0	5.5
Saurornitholestes langstoni	2	2.5	0	5.5
Paronychodon lacustris	2	2.5	2	2.5
R. isosceles	1	4.5	1	4
Tyrannosauridae	1	4.5	8	1
Dromaeosaurus albertensis	0	6	2	2.5
Total	9		13	
Dinosauria				
Ceratopsidae	20	1	22	1
Hadrosauridae	8	2	18	2
cf. *Thescelosaurus*	0	10.5	1	8.5
Ankylosauridae	1	8	2	6
Pachycephalosauridae	5	3	5	4
S. langstoni	2	5.5	0	10.5
D. albertensis	0	10.5	2	6
Tyrannosauridae	1	8	8	3
Paronychodon lacustris	2	5.5	2	6
R. isosceles	1	8	1	8.5
R. gilmorei	3	4	0	10.5
Total	43		61	

sandstone assemblage fall within the size range dictated by the average grain size of the deposit. Flat elements have the most variation in quartz equivalencies and are consistent with the medium-sized sand of the deposit. The larger ornithischian and theropod teeth are potentially equivalent to medium-sized sand grains. Bones and teeth with equivalencies higher than a medium-sized sand grain could have been deposited by disarticulation of a floating carcass or reworking of immediately adjacent bank or floodplain deposits. In the fine-grained deposit, the larger teeth, turtle scutes, and bone fragments are outside the mud and silt equivalency. This suggests that the floodplain deposit is a mix of allochthonous and more locally derived autochthonous assemblages. If fluid density increased because of suspended load (which is common during flood stage), then larger and denser elements could have been transported along with the sediment. Disarticulation of floating carcasses could also lead to deposition of elements with larger hydrodynamic equivalencies.

Transport and depositional processes also help to determine the amount of time represented in an assemblage. Because of the pathways by which fossils are introduced into channel assemblages (reworking of floodplain deposits, overland transport, or death within the channel; see Behrensmeyer, 1982), channel deposits are allochthonous over wide spans of time and space, and channel lag concentrations can represent from ≤10^2 to >10^5 years of time averaging (Rogers, 1993). Floodplain deposits are considered to be either autochthonous (Behrensmeyer, 1982) or at least contain a less time averaged assemblage (Rogers, 1993). Because the floodplain deposit used in this study was probably deposited in a single flood event, however, skeletal elements were derived from the channel, eroded levee, and floodplain surface, mixing autochthonous and allochthonous assemblages. As a result, the amount of time averaging within the fine-grained assemblage occupies the upper limits (>10^3 years) of Rogers's (1993) time-averaging model but perhaps does not represent as much time as the sandstone lag deposit. The long interval of time potentially represented in these deposits is better suited to evaluating long-term evolutionary and paleoecology trends (Behrensmeyer, 1982; Rogers, 1993) and must be considered when using attritional microfossil accumulations for paleoecological research.

Taxonomic Differences between Assemblages

Taphonomic processes specific to the fine-grained and sandstone accumulations strongly influenced the relative abundance of taxa found in the assemblages. Clasts in the sandstone assemblage were in a higher-energy environment with increased likelihood of exhumation and redeposition cycles before final burial. As a result, there is a lower abundance of the thin, fragile specimens in the sandstone assemblage. The higher energy of the channel environment allowed for hydrodynamic sorting of clasts with distinctive size, shape, and density characteristics, as well as winnowing of lighter elements. The high tooth-to-vertebrae ratio (in addition to the lack of cycloid scales) also suggests winnowing of the final deposits (Behrensmeyer, 1975). The sandstone assemblage not only contains fewer osteichthyan scales and skull fragments, but contains more

nonosteichthyan teeth and scutes, that is, equidimensional elements and bones with higher densities.

Hydrodynamic influences were explored by comparing taxonomic distribution within specific shape classes (Tables 2B–C) and shape-class distribution within specific taxa (Table 2D) between assemblages. Significant differences in the number of specimens in each shape class for a given taxon also highlight the effects of abiotic taphonomic factors on an assemblage (Tables 3B–C). Only lepidosaurian samples are not significantly different between assemblages, but this data set does not meet the assumption of the chi-square test and contains only jaw elements (with similar hydraulic equivalences). Large taxonomic groups like Osteichthyes, which contain a wide variety of skeletal elements of various sizes, shapes, and densities, are significantly different between accumulations.

Although the relative abundance of taxa is significantly different between the two assemblages, taxonomic diversity is similar within each deposit. When taxonomic lists are combined, there is a total of 47 taxa, and the majority of these are found at both sites (Supplementary Data 2[1]), suggesting that similar original paleocommunities were sampled. Taxa appearing in markedly low abundance or in only one assemblage can be attributed to (1) taphonomic biases selecting against preservation at one site, (2) membership in a distal community, or (3) status as a rare member of the proximal community. Whether organisms are rare within the final time-averaged paleocommunity, hydrodynamic explanations can explain most of the taxa found in only one assemblage. The most prominent example is the abundance of mammal teeth in the sandstone deposit (JPC) compared to only one mammal from the fine-grained deposit (CM). Mammals are most commonly represented by teeth but are relatively rare in Cretaceous deposits. Equidimensional and relatively dense, mammal teeth fall into the same general shape, size, and density classifications. They have a higher concentration at JPC, which, as this study shows, favors the concentration and preservation of equidimensional and dense skeletal elements. Thus, it is important to sample different facies (with the understanding of the time represented in the assemblage) in order to determine the extent of taxonomic diversity in a time-averaged paleocommunity, especially when a taxon can be identified by numerous skeletal elements with different hydrodynamic equivalence.

Determining Paleocommunity Structure

Assemblages with different depositional histories and time averaging emphasize the difficulty of correlating abundance data with original ecological population trends. Problems arise when attempting to interpret relative abundance of taxa between nonisotaphonomic deposits (Blob and Fiorillo, 1996; this study). Taxonomic discrepancies resulting from selective preservation of element size, shape, and density may inhibit reliable results, and attritional and reworked deposits representing varying degrees of time averaging permit taxonomic analysis only within the time represented by the deposit. The amount of time averaging represented in the CM and JPC deposits is on the order of 10^2–10^5 years (Rogers, 1993) and undoubtedly varies between the two assemblages owing to differences in attritional and reworking processes. Deposits with coarse time resolution are still useful, however, for recognizing long-term ecological shifts (Rogers, 1993). Thus, only reconstructions of a time-averaged paleocommunity can be determined. Faunal analyses, when considered in the light of taphonomy, can aid in drawing conclusions even among nonisotaphonomic assemblages.

Broad taxonomic comparisons are problematic given the differences in size, shape, and density of skeletal elements in these two assemblages. Because of differences in physical attributes, comparisons of hydrodynamically equivalent elements within specific categories (e.g., caudate vertebrate, osteichthyans with ganoid scales, ornithischian teeth) provide a more accurate reflection of paleoecological relationships. Comparison of similar skeletal elements minimizes the biases of biotic and abiotic taphonomic processes. Several groups of organisms are represented by

hydrodynamically similar elements in the two Hell Creek Formation microsites. Caudates are represented predominantly by vertebrae and jaws (none of which contain teeth), which vary in size by only a few millimeters; ganoid fish scales (of nonteleost fish) fall into the same shape, density, and size categories. Ornithischian teeth are equidimensional and similar in size and density, and turtle shell fragments are also similar in size, shape, and density.

Because of the similar morphologies and equivalent preservation potential of caudate vertebrae, rank order is interpreted as the actual relative abundance of caudates in the time-averaged paleocommunity (Table 4); the same is true for ganoid scale-bearing fish and ornithischian dinosaurs. Within ornithischians, ceratopsians are the most abundant, followed by hadrosaurs, pachycephalosaurs, and ankylosaurs. Although the number of tooth families per jaw correlates with skull size in both hadrosaurs and ceratopsians owing to changes through ontogeny (Dodson et al., 2004; Horner et al., 2004), hadrosaurs consistently have more teeth per individual than ceratopsians. Thus, the higher abundance in both assemblages of ceratopsian teeth indicates that members of this group, such as *Triceratops* and *Torosaurus*, were the most abundant ornithischians in the time-averaged paleocommunity.

In the Theropoda, small, laterally compressed *Saurornitholestes*, *Paronychodon*, and *Richardoestesia* teeth were analyzed alongside the more robust *Dromaeosaurus* teeth and tyrannosaurid fragments, mixing different shape and size categories (Table 4). Given the different physical characteristics of theropod taxa, it is not surprising that the two assemblages are poorly correlated; the fine-grained assemblage contains mostly small, laterally compressed teeth, and the sandstone assemblage contains larger, equidimensional teeth. It is unknown at this time whether a larger sample size would provide more certainty on theropod abundances.

As noted above, turtle remains consist of elements of similar size and density and thus present another ideal assemblage for abundance analysis. Turtle rank orders do not correlate well, however, when *Basilemys* is included in the analysis (Tables 3D, 4). *Basilemys* is the only terrestrial turtle in the faunas, based on jaw morphology, limb robustness, and toe length (Brinkman, 1998). Although the sandstone (JPC) assemblage has a higher overall concentration of turtles owing to hydrodynamic sorting and possibly to the aquatic ecology of the taxa, it does not include *Basilemys*, which is found only in the overbank deposit (CM), a site that would be more likely to sample organisms inhabiting the floodplain. This raises the question of whether preservation, life habitat, and depositional environment are correlated.

Turtles are the only group included in this study with representatives from different habitats—terrestrial, semiaquatic, and aquatic environments. The four caudate species identified in this Hell Creek fauna are all considered aquatic to semiaquatic based on postcranial adaptations favoring undulatory movement and phylogenetic relationships with extant taxa (Estes, 1964). *Scapherpeton tectum* has an uncertain phylogenetic relationship with modern taxa but has been considered aquatic based on its abundance in fluvial deposits (Estes, 1964). Though caudate remains are more common in the channel deposit, the relative abundances are not shown to be significantly different between assemblages. Being semiaquatic, it is likely that caudates would inhabit both terrestrial and fluvial environments alternately throughout life.

Taphonomic processes and other depositional factors (including sedimentation rate) associated with fluvial deposition produce variation in the geographic range sampled (Behrensmeyer, 1988), in the amount of time averaging (Behrensmeyer, 1982; Rogers, 1993), and in length and hydrodynamics of transport (e.g., Voorhies, 1969; Behrensmeyer, 1975; Hanson, 1980). These processes also confuse trends in preferential preservation of taxa in specific depositional environments (i.e., channel vs. floodplain). Within any attritional assemblage, more than one community will be sampled (Behrensmeyer, 1982; Shotwell, 1958), as members of more distal environments are introduced by predators or scavengers, stream action, or random occurrences of an organism outside its home range.

CONCLUSIONS

Relative abundance of skeletal elements with specific physical attributes in conjunction with sedimentological data and statistical results indicate that the two faunal assemblages in this study have been strongly affected by taphonomic processes, including transport, sorting, winnowing, reworking, and time averaging. While the taphofacies concept is not new to paleontological studies (see, e.g., Brett and Speyer, 1990; Rogers, 1993), results presented in this study provide a quantification of the variability, accentuated by hydrodynamic forces, between assemblages. Statistical tests support significant differences in the distribution of elements based on physical attributes correlated with transport, sorting, winnowing, and reworking processes. Analysis of the hydrodynamic equivalences of skeletal elements reveals that the fine-grained deposit is dominated by flat, low-density elements (e.g., cycloid scales, fish skull, fish vertebrae), and the sandstone deposit by equidimensional, higher-density elements (e.g., teeth).

Given the taphonomic differences between assemblages and variations in hydrodynamic equivalence of skeletal elements within taxonomic groups, the analysis of physically similar elements presents a reliable way of comparing taxonomic abundances between nonisotaphonomic deposits. Although sample sizes become problematic when the assemblages are divided into hydraulic and taxonomic groups, relative abundance data and statistical results indicate similar trends among the groups analyzed. Despite low sample sizes, similar taxonomic trends from analyses of hydraulically similar elements are interpreted as significant. Results indicate that within the time-averaged Hell Creek paleocommunity (1) *Ophisthotriton kayi* is the most abundant caudate (based on vertebrae), followed by *Scapherpeton tectum*, (2) the gar *Lepisosteus occidentalis* is the most abundant ganoid scale-bearing fish, followed by the Holostean A morphotype, (3) ceratopsians are the most abundant ornithischian dinosaur based on teeth, followed by hadrosaurs, and (4) trionychids are the most abundant turtle based on analysis of shells. Results from taxonomic groups with significant differences between assemblages can be explained by hydrodynamic analysis. Theropod data sets combine small, flat teeth and larger, equidimensional teeth; thus they are not limited to hydrodynamically equivalent elements. The turtle assemblage also suggests that some taxa may be preferentially preserved in certain depositional environments based on habitat preferences. Because of the effects of transport and deposition, paleoecological conclusions from microsite analysis should take into account facies, depositional environment, and the taphonomic signature of the assemblage.

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REFERENCES

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. 473–578.

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: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 63, p. 183–199.

BEHRENSMEYER, A.K., and KIDWELL, S.M., 1985, Taphonomy's contributions to paleobiology: Paleobiology, v. 11, p. 105–119.

BEST, M.M.R., and KIDWELL, S.M., 2000a, Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings, pt. 2: Effect of bivalve life habitats and shell types: Paleobiology, v. 26, p. 103–115.

BEST, M.M.R., and KIDWELL, S.M., 2000b, Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings, pt. 1: Environmental variation in shell condition: Paleobiology, v. 26, p. 80–102.

BLOB, R.W., and FIORILLO, A.R., 1996, The significance of vertebrate microfossil size and shape distributions from faunal abundance reconstructions: A Late Cretaceous example: Paleobiology, v. 22, p. 422–435.

BRETT, C.E., and SPEYER, S.E., 1990, Taphofacies, *in* Briggs, D.E.K., and Crowther, P.R., eds., Palaeobiology: A Synthesis: Blackwell Publishing, Oxford, UK, p. 258–263.

BRINKMAN, D.B., 1990, Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: Evidence from the vertebrate microfossil localities: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 78, p. 37–54.

BRINKMAN, D.B., 1998, The skull and neck of the Cretaceous turtle *Basilemys* (Trionychidae, Nanhsiungchelyidae), and the interrelationships of the genus: Paludicola, v. 1, p. 150–157.

BRINKMAN, D.B., RUSSELL, A.P., EBERTH, D.A., and PENG, J., 2004, Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 213, p. 295–313.

CUTLER, A.H., BEHRENSMEYER, A.K., and CHAPMAN, R.E., 1999, Environmental information in a recent bone assemblage: Roles of taphonomic processes and ecological change: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 359–372.

DICKINSON, W.R., BEARD, S.L., BRAKENRIDGE, G.R., ERJAVEC, J.L., FERGUSON, R.C., INMAN, K.F., KNEPP, R.A., LINDBERG, A.F., and RYBERG, P.T., 1983, Provenance of North American Phanerozoic sandstones in relation to tectonic setting: Geological Society of America Bulletin, v. 94, p. 222–235.

DICKINSON, W.R., and SUCZEK, C.A., 1979, Plate tectonics and sandstone composition: AAPG (American Association of Petroleum Geologists) Bulletin, v. 63, p. 2164–2182.

DODSON, P., 1973, The significance of small bones in paleoecological interpretation: University of Wyoming Contributions to Geology, v. 12, p. 15–19.

DODSON, P., FORESTER, C.A., and SAMPSON, S.D., 2004, Ceratopsidae, *in* Weishampel, D.B., Dodson, P., and Osmolska, H., eds., The Dinosauria, University of California Press, Berkeley, p. 494–513.

EBERTH, D.A., 1990, Stratigraphy and sedimentology of vertebrate microfossil sites in the uppermost Judith River Formation (Campanian), Dinosaur Provincial Park, Alberta, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 78, p. 1–36.

EBERTH, D.A., and BRINKMAN, D.B., 1997, Paleoecology of an esuarine, incised-valley fill in the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) of Southern Alberta, Canada: PALAIOS, v. 12, p. 43–58.

EFREMOV, J.A., 1940, Taphonomy: A new branch of paleontology: Pan-American Geologist, v. 74, p. 81–93.

ESTES, R., 1964, Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming: University of California Publications in Geological Sciences, v. 49, p. 1–180.

ESTES, R., and BERBERIAN, P., 1970, Paleoecological of a Late Cretaceous vertebrate community from Montana: Breviora, v. 343, p. 1–35.

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

FIORILLO, A.R., 1988, Aspects of bone modification applied to time resolution in the fossil record: An example from the Miocene of western Nebraska: Current Research in the Pleistocene, v. 5, p. 103–109.

FIORILLO, A.R., 1991, Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland County, Montana, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 81, p. 281–311.

FIORILLO, A.R., PADIAN, K., and MUSIKASINTHORN, C., 2000, Taphonomy and depositional setting of the *Placerias* Quarry (Chinle Formation: Late Triassic, Arizona): PALAIOS, v. 15, p. 373–386.

GILL, J.R., and COBBAN, W.A., 1973, Stratigraphy and geologic history of the Montana Group and equivalent rocks, Montana, Wyoming and North and South Dakota: U.S. Geological Survey Professional Paper, v. 776, p. 1–37.

HANSON, B.C., 1980, Fluvial taphonomic processes: Models and experiments, *in* Behrensmeyer, A.K., and Hill, A.P., eds., Fossils in the Making: Vertebrate Taphonomy and Paleoecology: University of Chicago Press, Chicago, Illinois, p. 156–181.

HARTMAN, J.H., and KIRKLAND, J.I., 2002, Brackish and marine mollusks of the Hell Creek Formation of North Dakota: Evidence for a persisting Cretaceous seaway, *in* Hartman, J.H., Johnson, K.R., and Nichols, D.J., eds., The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous, Geological Society of America Special Papers, v. 361, p. 271–296.

HEDGES, R.E.M., 2002, Bone diagenesis: An overview of processes: Archaeometry, v. 44, p. 319–328.

HORNER, J.R., WEISHAMPEL, D.B., and FORESTER, C.A., 2004, Hadrosauridae, *in* Weishampel, D.B., Dodson, P., and Osmolska, H., eds., The Dinosauria, University of California Press, Berkeley, p. 438–463.

KORTH, W.W., 1979, Taphonomy of microvertebrate fossil assemblages: Annals of the Carnegie Museum, v. 48, p. 235–285.

KOWALEWSKI, M., 1996, Time-averaging, overcompleteness, and the geological record: Journal of Geology, v. 104, p. 317–326.

LUND, S.P., HARTMAN, J.H., and BANERJEE, S.K., 2002, Magnetostratigraphy of interfingering Upper Cretaceous–Paleocene marine and continental strata of the Williston Basin, North Dakota and Montana, *in* Hartman, J.H., Johnson, K.R., and Nichols, D.J., eds., The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous, Geological Society of America Special Papers, v. 361, p. 57–74.

MARTIN, R.E., WEHMILLER, J.F., HARRIS, M.S., and LIDDELL, W.D., 1996, Comparative taphonomy of bivalves and foraminifera from Holocene tidal flat sediments, Bahia la Choya, Sonora, Mexico (Northern Gulf of California): Taphonomic grades and temporal resolution: Paleobiology, v. 22, p. 80–90.

MCSWEENEY, K., and FASTOVSKY, D.E., 1987, Micromorphological and SEM analysis of Cretaceous–Paleogene petrosols from eastern Montana and western North Dakota: Geoderma, v. 40, p. 49–63.

MELDAHL, K.H., FLESSA, K.W., and CUTLER, A.H., 1997, Time-averaging and postmortem skeletal survival in benthic fossil assemblages: Quantitative comparisons among Holocene environments: Paleobiology, v. 23, p. 207–229.

ORGAN, C.L., COOLEY, J.B., and HIERONYMUS, T.L., 2003, A non-invasive quarry mapping system: PALAIOS, v. 18, p. 74–77.

RETALLACK, G.J., 1994, A pedotype approach to latest Cretaceous and earliest Tertiary paleosols in eastern Montana: Geological Society of America Bulletin, v. 106, p. 1377–1397.

ROGERS, R.R., 1993, Systematic patterns of time-averaging in the terrestrial vertebrate record: A Cretaceous case study, *in* Kidwell, S.M., and Behrensmeyer, A.K., eds., Taphonomic Approaches to Time Resolution in Fossil Assemblages, Paleontological Society, Knoxville, Tennessee, p. 228–249.

RYAN, M.J., RUSSELL, A.P., EBERTH, D.A., and CURRIE, P.J., 2001, The taphonomy of a *Centrosaurus* (Ornithischia: Ceratopsidae) bone bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny: PALAIOS, v. 16, p. 482–506.

SHOTWELL, J.A., 1955, An approach to the paleoecology of mammals: Ecology, v. 36, p. 327–337.

SHOTWELL, J.A., 1958, Inter-community relationships in Hemphillian (Mid-Pliocene) mammals: Ecology, v. 39, p. 271–282.

VARRICCHIO, D.J., 1995, Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 114, p. 297–323.

VARRICCHIO, D.J., and HORNER, J.R., 1993, Hadrosaurid and lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of Montana: Taphonomic and biologic implications: Canadian Journal of Earth Sciences, v. 30, p. 997–1006.

VOORHIES, M., 1969, Taphonomic and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska: University of Wyoming Contributions to Geology, v. 1, p. 1–69.

WILSON, L.E., 2006, Comparative taphonomy and paleoecological reconstruction of two microvertebrate accumulations from the Late Cretaceous (Maastrichtian) Hell Creek Formation, Eastern Montana: Unpublished Master's thesis, Montana State University, Bozeman, 116 p.

WOLFF, R.G., 1975, Sampling and sample size in ecological analysis of fossil mammals: Paleobiology, v. 1, p. 195–204.

ZALEHA, M.J., 1988, The Hell Creek Formation (Maastrichtian), Glendive area, Montana: Sedimentology, paleoenvironments, and provenance of their stratigraphic and taphonomic implications: Unpublished Master's thesis, Ohio University, Athens, 138 p.