# TAPHONOMIC APPROACHES TO TIME RESOLUTION IN FOSSIL ASSEMBLAGES

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# Systematic Patterns Of Time-Averaging In The Terrestrial Vertebrate Record: A Cretaceous Case Study

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## INTRODUCTION

What is the range of time-averaging in the terrestrial vertebrate record? How are time-averaged assemblages distributed within the terrestrial vertebrate record? What are the implications of time-averaging for vertebrate paleobiological analysis?

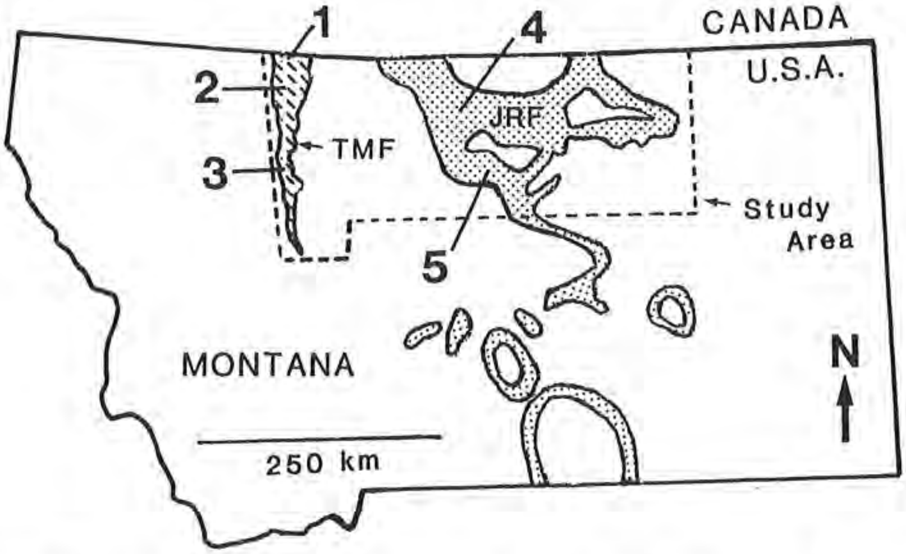
Foreland basins are ideal settings to search for answers to these questions. Foreland basins constitute the "major loci of preservable nonmarine sedimentation" (DeCelles, 1986, p. 912), and as such serve as major repositories of the nonmarine vertebrate record. Ancient foreland basins that preserve abundant vertebrate fossils include parts of the Karoo Basin of South Africa (Permo-Triassic reptiles: Haughton, 1919; Smith, 1993), the Western Interior Basin of North America (Cretaceous dinosaurs: Dodson, 1971; Béland and Russell, 1978), and the Himalayan Basin of northern Pakistan (Neogene mammals: Barry et al., 1982; Badgley, 1986). Because of their intrinsic differential subsidence (subsidence rates decrease exponentially from proximal to distal reaches: Beaumont, 1981; Jordan, 1981; Heller et al., 1988), foreland basins are also ideal settings to study how subsidence-related geologic variables (e.g., net sedimentation rates, durations of hiatus, fluvial styles) influence the nature of the fossil record (Efremov, 1940; Bown and Kraus, 1981; Behrensmeyer, 1987, 1988; Kidwell, 1988, 1993; Parsons et al., 1988; Eberth, 1990; Bartels et al., 1992).

In this chapter, I examine patterns of fossil preservation in a richly fossiliferous nonmarine foreland basin succession in Montana. The study interval includes proximal (Two Medicine Formation) and distal (Judith River Formation) deposits of an extensive Late Cretaceous (Campanian) alluvial/coastal plain. Since this is a short course devoted to time resolution in the fossil record, I will focus upon proximal-distal patterns in the time-averaging of vertebrate fossil concentrations.

## CASE STUDY: TWO MEDICINE-JUDITH RIVER INTERVAL

*Geologic Setting*--Upper Cretaceous Two Medicine and Judith River strata crop out in northwestern (Two Medicine Formation) and north-central (Judith River Formation)

Montana (Figure 1). The study interval comprises an eastward-thinning clastic tongue that accumulated in the Western Interior Foreland Basin during a major regressive-transgressive cycle of the Western Interior Seaway (R3 and T4 of Weimer, 1960; R8 and T9 of Kauffman, 1977). Post-Cretaceous uplift of the Sweetgrass Arch led to erosion of the middle part of this clastic tongue. Only proximal (Two Medicine Formation) and distal (Judith River Formation) deposits remain.



1. Milk River Area
TM-046 TM-061
TM-023 TM-052
TM-051 TM-041
TM-038 TM-019
TM-050 TM-020
TM-053 GM-1

2. TMF Type Area
TM-141 TM-066
TM-068 TM-068A
TM-067 TM-055
TM-140 TM-018

3. Choteau Area
TM-006A TM-006B
TM-006C TM-024A
TM-024B TM-008A
TM-008B TM-012
TM-003

4. Havre Area
JR-142 JR-120
JR122 UC-9210

5. JRF Type Area
UC-8302 UC-929
UC-8439 UC-915
UC-917 UC-919
UC-9110 UC-8322A
UC-92J UC-8315
UC-8303 UC-8322B
UC-8302A UC-8326
UC-913 CBH

FIGURE *1*--Generalized outcrop areas of the Two Medicine Formation (cross-hatched) and Judith River Formation (stippled) (modified from Eberth and Hamblin, 1993). General locations of vertebrate localities surveyed in this paper are also indicated (see Table 1 for additional site information).

Rocks of the Two Medicine-Judith River interval are primarily nonmarine alluvial and paralic deposits, although fossiliferous shallow marine shoreface and foreshore strata occur near the base and top of the Judith River Formation (Rogers, in press). The Two Medicine Formation is more proximal to the source area and is dominated by grey-green mudstone and siltstone, with lesser amounts of fine- to medium-grained grey sandstone (overall sandstone/mudstone ratio $\approx .30$). Mudstone and siltstone beds are generally thin ($< 1$ m) and tabular, and often show evidence of pedogenesis (root traces, caliche nodules, clay cutans, color banding/mottling, slickensides). Sandstone bodies are intercalated throughout the section, and range from roughly 1 m to 10 m in thickness. Most sandstone bodies are less than 4 meters thick, single story and lenticular, but thick multistory sandstone sheets occur low in the section. Sandstone bodies have erosional bases that are occasionally draped by thin (~ 10 cm) lag deposits of caliche and clay pebble rip-ups, wood fragments, unionid shell debris, and rare dinosaur bone. Trough cross-bedding is characteristic of lower and middle reaches of sandstone bodies, and the tops of sandstones are frequently ripple cross-stratified and/or planar laminated. Upper contacts of sandstones vary from sharp to gradational, and often show evidence of rooting or burrowing. The net accumulation rate (total subsidence) of the Two Medicine Formation is ~ 7.0 cm/1000 yrs (Rogers et al., in press).

The Judith River Formation is more distal to the source area and consists of grey, tan, and carbonaceous brown mudstone and siltstone, lignite, and grey and tan fine- to medium-grained sandstone (overall sandstone/mudstone ratio ≈ .56, excluding shallow marine deposits). Mudstone beds are thin (< 1 m) and tabular, and preserve abundant small root traces and carbonaceous plant debris. Lignite beds occur throughout the section, but are more common and thicker in the upper third. Nonmarine sandstone bodies of the Judith River Formation range from 1 m to 20+ m in thickness. Thick nonmarine sandstones near the base and top of the formation generally have sheet geometries and are often multi-story. Both lenticular and sheet sandstone bodies occur in the middle third of the formation. Basal contacts of sandstone bodies are erosional, and lag deposits of clay pebbles, ironstone pebbles, and wood fragments/logs are common. Bones and shells are frequent lag components (more so than in the TMF). Judith River sandstone bodies commonly display trough and tabular cross-bedding and ripple cross-lamination. Inclined heterolithic stratification (IHS) is developed locally in thick sandstone bodies in the upper third of the formation. Radioisotopic dating in northern Montana (Goodwin and Deino, 1989) and southern Alberta, Canada (Eberth and Deino, 1992), and preliminary $^{40}Ar/^{39}Ar$ analyses in the type area (Rogers and Swisher, in prep.) suggest that the net accumulation rate (total subsidence) of the Judith River Formation in the study interval is approximately 4.5 cm/1000 yrs.

*Paleoenvironmental Synthesis*--Streams draining the Cordilleran highlands flowed transversely across the Two Medicine-Judith River alluvial/coastal plain toward the sea. Proximal (upland TMF) reaches of this plain were characterized by low-sinuosity, shallow stream channels that have been interpreted as braided (Lorenz, 1981) and anastomosing (Lorenz and Gavin, 1984; Nadon, 1993). Calcic soils developed in interfluve areas, and shallow floodbasin ponds populated by small freshwater bivalves and gastropods were common. Sedimentologic (Lorenz, 1981; Gavin, 1986) and paleofloristic (Crabtree, 1987, Jerzykiewicz and Sweet, 1988) evidence suggest that the Two Medicine climate was seasonal and semi-arid.

Low-sinuosity stream channels also traversed distal (lowland JRF) parts of the basin, although channel belts seem to have been wider and streams somewhat deeper. Floodbasin ponds and swamps were more abundant, and soils were largely hydromorphic. The seemingly more persistent presence of water in the Judith River lowlands may have been due to a more humid climate and/or the proximity of the seaway (e.g., the water table may have been closer to the ground surface).

## VERTEBRATE SKELETAL CONCENTRATIONS

Fossil vertebrates have been collected from the Two Medicine-Judith River interval for well over one-hundred years (Leidy, 1856; Cope, 1876): the rich dinosaur-dominated assemblage has yielded numerous type specimens and a wealth of data bearing on dinosaurian evolution, paleoecology and behavior (Gilmore, 1914; Sahni, 1972; Case, 1978; Horner and Makela, 1979; Horner, 1982, 1984, 1988, 1992; Horner and Weishampel, 1988; Horner et al., 1992). From a taphonomic perspective, the interval is characterized by various kinds of vertebrate skeletal concentrations superimposed on a background of dispersed skeletal material (Eberth, 1990; Rogers, 1990; Fiorillo, 1991) (Table 1).

TABLE *1*--Vertebrate skeletal concentrations of the Two Medicine-Judith River interval. Locality data for TM and JR sites are on file at the Museum of the Rockies (MOR), Bozeman, Montana. Data pertaining to UC sites can be obtained from the author. GM-1 is the ?*Brachyceratops* bonebed of Gilmore (1917), CBH is the Clambank Hollow locality of Sahni (1972).

| CONCENTRATION TYPE | SEDIMENTARY CONTEXT | TAPHONOMIC ATTRIBUTES |
|---|---|---|
| CHANNEL-LAG CONCENTRATION (n=10): JR-142, UC-9210, 8302, 929, 8439, 915, 917, 919, 9110, 8322A | fluvial sandstone bodies, bases of single story channels, reactivation surfaces in multi-story channels, erosive bases of cross-bed sets | Taxonomically diverse vertebrate microfossil concentrations, aquatic and terrestrial taxa, variable states of fragmentation, abrasion, and weathering, elements dissociated |
| CHANNEL-FILL CONCENTRATION (n=2): TM-046, 023 | abandoned segments of channels, carbonaceous siltstone, freshwater invertebrates | Mono/paucispecific concentrations of dinosaurs, bones are disarticulated, weathering stages are low and uniform |
| NEST SITE CONCENTRATION (n=17): TM-006A, 006B, 006C, 024A, 024B, 008A, 008B, 038, 052, 018, 012, 068A, 061, 051, 066, JR-120, 122 | subaerial floodplain, silty mudstone/siltstone, associated with caliche and root traces | Clutches of hatched and unhatched eggs, occasional embryos, eggshell usually unweathered, microstructure usually intact, frequently associated with juvenile bones and bonebeds (nestling cohorts), bones are disarticulated, weathering stages are typically low and uniform |
| SUBAERIAL BONEBED CONCENTRATION (n=2): TM-041, 003 | subaerial floodplain, silty mudstone, associated with caliche and root traces | Mono/paucispecific concentrations of dinosaurs (various age classes), bones are disarticulated, weathering stages are low and uniform |
| SUBAQUEOUS BONEBED CONCENTRATION (n=7): TM-019, 068, 067, 055, 050, GM-1, UC-92J | floodbasin lakes/ponds, carbonaceous silty mudstone, freshwater invertebrates | Typically mono/paucispecific concentrations of dinosaurs, bones are disarticulated, weathering stages are low and uniform (TM-068 is multispecific) |
| SUBAQUEOUS MICROFOSSIL CONCENTRATION (n=11): TM-053, 020, 141, 140, UC-8315, 8303, 8322B, 8302A, 8326, 913, CBH | floodbasin lakes/ponds, carbonaceous silty mudstone, freshwater invertebrates | Taxonomically diverse vertebrate microfossil concentrations, aquatic and terrestrial taxa, minimal weathering (occasional elements show advanced weathering), elements dissociated |

*Channel-hosted Concentrations*--Vertebrate skeletal elements occur in stream channel deposits throughout the Two Medicine-Judith River study interval. Two general types of concentration are recognized: channel-lag and channel-fill (Behrensmeyer, 1988).

Channel-lag assemblages as defined by Behrensmeyer (1988) are concentrations of bones and/or teeth that occur at the bases of channel deposits: this includes the bases of single story channels, reactivation surfaces in multi-story channels, and the erosive bases of cross-bed sets within channels. Channel-lag assemblages are allochthonous (transported), and they often consist of dissociated bones and teeth (intact or fragmentary) that may or may not be abraded. Likewise, they may show evidence of hydrodynamic sorting due to differences in bone density, size and shape (cf. Voorhies, 1969; Dodson, 1973; Behrensmeyer, 1975), or they may not. Bone is contributed to channel-lag assemblages along three different "pathways" (Behrensmeyer, 1982a): death within the channel belt, transport into the active channel from death sites on contemporaneous ground surfaces, or re-working of older material exhumed during channel incision, lateral channel combing, or avulsion.

Channel-lag concentrations in the study interval are typically taxonomically diverse assemblages of physicochemically resistant elements such as teeth (various dinosaurs, crocodiles, champsosaurs, mammals), turtle shell, crocodile scutes, gar scales, and assorted small bones and bone fragments. Occasionally, large isolated dinosaur bones are found interspersed with smaller skeletal material. States of fragmentation, abrasion and weathering vary widely. Carbonaceous plant debris and silicified wood, unionid bivalves, and clay pebbles are frequently associated with the vertebrate material. Most lag concentrations occur at the bases of channels, although one site in the study interval (UC-8439) consists of recurrent local lag stringers at the erosive bases of trough cross-bed sets.

Channel-fill concentrations (Behrensmeyer, 1988) develop in abandoned segments of channels that form by neck cut-off in meandering systems or by other types of abandonment including avulsion. These types of concentrations typically include autochthonous or parautochthonous (locally derived) bone. Vertebrate material can be incorporated into channel-fill sites in two ways: *in situ* mortality or overland transport from nearby death sites.

Two channel-fill concentrations from the study interval have been described (Rogers, 1990). Both sites preserve dense concentrations of bones dominated by a single species of ceratopsian dinosaur. The concentrations occur in fine-grained carbonaceous sediments that preserve small freshwater bivalves and gastropods. The fine-grained bone-bearing lithosomes directly overlie, and in one case laterally abut, fluvial sandstones. Bones are disarticulated, and bone weathering stages are low and uniform (≤ stage 1 of Behrensmeyer, 1978). Ribs, vertebrae, and phalanges are under-represented in both assemblages, suggesting pre-burial winnowing of easily mobilized bones (Voorhies, 1969).

*Floodplain-hosted Concentrations*--Concentrations of vertebrate material also occur in fine-grained interchannel sediments of the Two Medicine-Judith River interval. Concentrations have been documented in both subaerial (floodplain) and subaqueous (floodbasin ponds/lakes) depositional settings.

Subaerial floodplain concentrations would include all fossil assemblages that show evidence of accumulation on a dry land surface, such as attritional paleosol concentrations (Bown and Kraus, 1981; Smith, 1993), "event" or "mass death" concentrations due to volcanism, drought, violent storms, or winter hardship (Voorhies, 1969, 1985; Weigelt, 1989; Borrero, 1990; Rogers, 1990), and predator concentrations (Mellet, 1974; Haynes, 1988). Subaqueous concentrations differ only in that they show evidence of accumulation in standing water; attritional, event, and predator-generated bone concentrations are all possible. I differentiated subaerial and subaqueous concentrations in the study interval using sedimentologic and paleontologic criteria. Basically, a fossil bone concentration was deemed to be of subaqueous origin if freshwater vertebrates, invertebrates, or varves were found in direct association with the bone assemblage. Freshwater deposits in the study interval frequently preserve invertebrate populations, and are often enriched in carbonaceous debris and amber.

The Two Medicine-Judith River interval is renowned for its preservation of dinosaur nests and nesting sites (Horner and Makela, 1979; Horner, 1982; Clouse and Horner, in press), which qualify as subaerial floodplain concentrations for obvious biological reasons (amniotes lay their eggs on dry land) as well as sedimentologic ones. Nests preserving clutches of both hatched eggs and unhatched eggs with intact embryos have been found (Horner and Weishampel, 1988; Clouse and Horner, in press). Clutches often appear to be largely undisturbed, preserving eggs as they were laid. Eggshell from most nest sites appears to be relatively unweathered, and eggshell microstructure is often preserved in fine detail (Hirsch and Quinn, 1990). Dense concentrations of bones apparently representing the remains of hatchling cohorts are frequently found within and around nest sites (Horner, 1982, pers. comm., 1993). Nesting horizons occasionally occur stratigraphically superposed in close succession (e.g., TM-006A,B,C, Horner, 1982).

Subaerial concentrations of dinosaur bones preserving various age classes (adult, subadult, juvenile) also occur in the study interval (Hooker, 1987; Rogers, 1990). These bonebed concentrations are typically monospecific assemblages of hadrosaurian taxa (*Maiasaura*, *Prosaurolophus*). Bones occur disarticulated within rooted host sediments. Weathering stages are generally low (stage 0 to 1) and show minimal within-site variation.

Two types of subaqueous floodplain skeletal concentrations occur in the Two Medicine-Judith River interval: dinosaur bonebed concentrations and vertebrate microfossil concentrations. The bonebeds are usually monospecific concentrations of hadrosaurs (*Maiasaura*, *Gryposaurus*, *Hypacrosaurus*), although at least one site (GM-1) preserves ceratopsians (?*Brachyceratops*, Gilmore, 1917), and one other

(TM-068) preserves skeletal remains of several dinosaurian taxa (Varricchio and Horner, in press). Bones are usually disarticulated and only mildly weathered (≤ stage 1). Vertebrae, ribs, and phalanges are typically under-represented. Isolated bones and teeth of aquatic vertebrates such as turtles, champsosaurs, and crocodiles are occasionally found scattered among the dinosaurian elements. The vertebrate microfossil concentrations are characterized by high diversity assemblages of small fossils representing both aquatic (fish, amphibians, reptiles) and terrestrial (dinosaurs, mammals) taxa (e.g., Sahni, 1972). As in the channel-lag concentrations, physicochemically resistant bioclasts such as teeth, scales and turtle shell predominate. Skeletal debris is abundant but typically disseminated throughout bone-producing horizons (as opposed to densely concentrated in pockets). Most skeletal elements show only minimal effects of weathering, although the occasional bone does show advanced stages of surface degradation (stage 4 - 5). Large dinosaur bones and bone fragments are periodically found in these microfossil-producing beds.

## ESTIMATES OF TIME-AVERAGING

Vertebrate skeletal concentrations in the Two Medicine-Judith River interval are the products of a variety of biologic, ecologic, and geologic phenomena. Some sites seem to record short term biologic events (mass death) that transpired on short-lived land surfaces (event concentrations), while others apparently record the attritional accumulation of skeletal debris within more persistent depositional settings (attritional concentrations). Still others presumably record the concentration of bone by geological processes (lag concentrations). What is the range of time-averaging represented by these three types of skeletal concentrations?

Various lines of reasoning can be used to estimate the time-averaging of Two Medicine-Judith River concentrations (see Behrensmeyer and Hook et al., 1992 for estimates of temporal resolution for several taphonomic modes) (Figure 2). The durations of mass death events in modern ecosystems provide a means of placing lower limits on the time-averaging of event concentrations. Mass mortality can be relatively instantaneous (Stager, 1987; Lockley, 1990) or drawn out over weeks, months, even years (Corfield, 1973; Borrero, 1990). Taphonomic criteria, such as weathering stages (Behrensmeyer, 1978) and articulation and association (Hill and Behrensmeyer, 1984), can help resolve the time of exposure since death. If mass death events are species-selective, and most certainly appear to be in the study interval, taxonomic diversity can also be used as a tool to assess scales of time-averaging (assuming pre- and post-event attritional input would contribute taxa unaffected by the "event"). The time-averaging of attritional concentrations, on the other hand, can be estimated using rates of attritional skeletal accretion in modern ecosystems (Behrensmeyer, 1982a). The durations of depositional environments hosting attritional concentrations provide upper limits on temporal resolution. Finally, the time-averaging of lag concentrations depends upon the "pathways" (Behrensmeyer, 1982a) bones followed to concentration. If bones were contributed from all possible sources (overland transport, death in channel, and bank erosion), then upper limits on temporal duration can be estimated from the depth of channel incision if net sedimentation rates are known. Lower limits of time-averaging can be estimated from taphonomic features of the lag concentrations themselves, such as weathering, sorting, and abrasion.

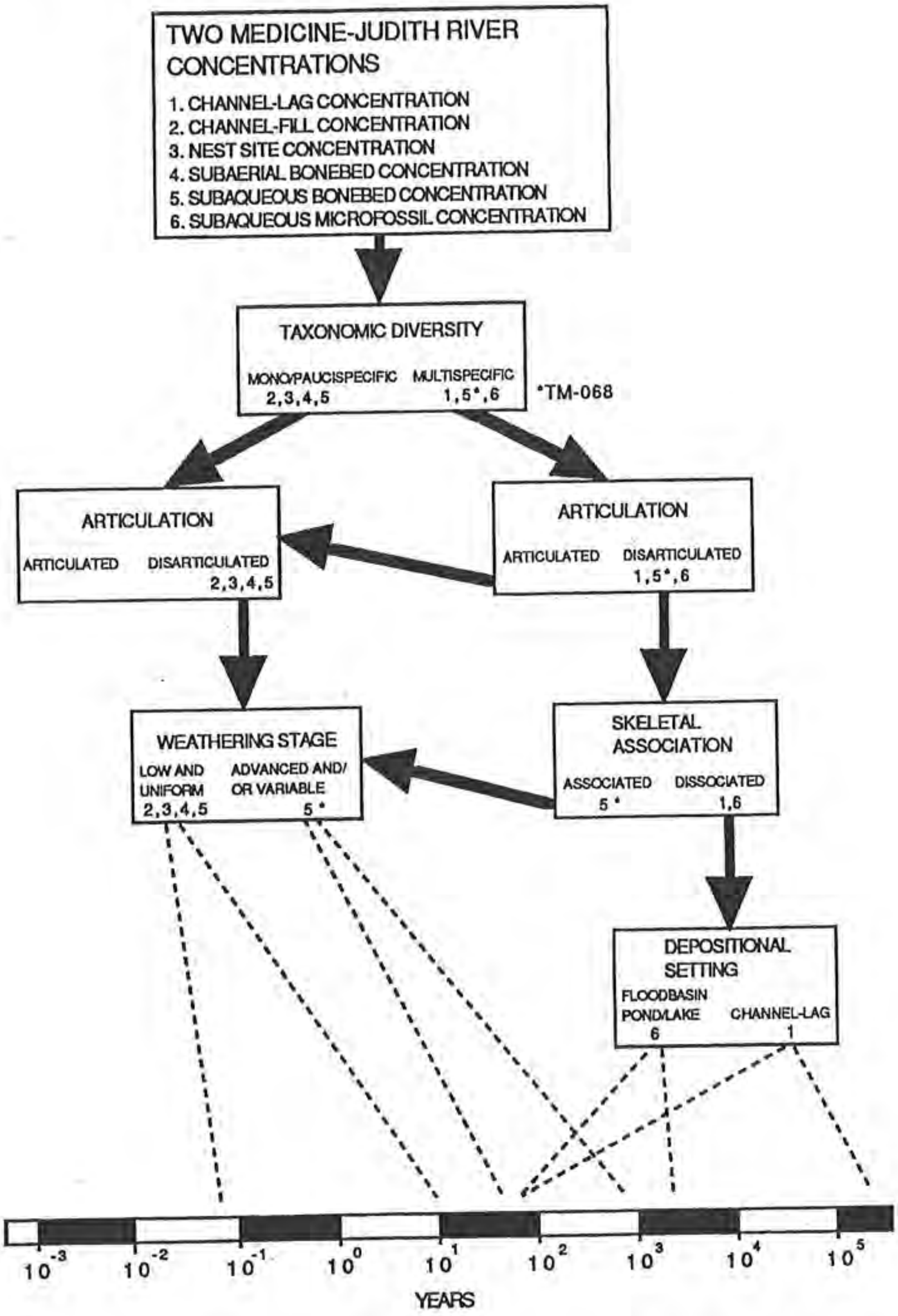


FIGURE 2--Flow chart used to estimate the time-averaging of Two Medicine and Judith River vertebrate concentrations. Refer to text for additional taphonomic and sedimentologic criteria used to estimate time-averaging of assemblages.

*Nest Site Concentrations*--Nest sites in the study interval are here considered examples of high temporal resolution assemblages (minimal time-averaging, $<10^0$ to $10^1$ yrs) because the flood sediments that entombed the nests often captured embryonic dinosaurs and periodically other small members of the local fauna (small mammals, land snails) *in situ* (Figure 3). Low diversity concentrations of juvenile skeletons that are frequently preserved in nesting grounds also suggest minimal time-averaging. Aggregates of juvenile carcasses remained exposed long enough to disarticulate (maybe a few months to at most a few years), but skeletal elements were seldom widely dispersed, and bones of other taxa were not added in abundance. Furthermore, the juvenile bones are typically not appreciably weathered (despite possible biases against juvenile bone, Behrensmeyer, 1978), and the associated eggshell debris does not show evidence of advanced dissolution (Hayward et al., 1991).

*Subaerial Bonebed Concentrations*--Taphonomic features of subaerial dinosaur bonebeds preserving mono/paucispecific concentrations of various age classes also suggest relatively short periods of accumulation. Bone weathering stages are characteristically low and uniform (Hooker, 1987; Rogers, 1990), and attritional input did not dilute low diversity signatures. Thus, they too probably represent some type of event concentration that was modified only briefly at the ground surface. Levels of time-averaging for subaerial bonebed concentrations are estimated to range from several months to a few years ($<10^0$ to $10^1$ yrs) (Figure 3).

*Subaqueous Bonebed and Microfossil Concentrations*--Floodbasin pond/lake concentrations of the study interval are characterized by a coarser degree of temporal resolution ($<10^0$ to $>10^3$ yrs) (Figure 3). These assemblages were concentrated in lacustrine or paludal settings that may have persisted for several thousands of years (Holland and Burk, 1982; Räsänen et al., 1991), or may have filled with sediment or desiccated to dry floodplain in but a few years. Rock accumulation rates averaged over the complete Two Medicine or Judith River sections offer little insight into these thin (typically $<1$ m) bone-bearing beds, for they do not take into account the highly episodic nature of sedimentation on an alluvial plain (Sadler, 1981). Taphonomic criteria, however, suggest two temporal end-members: event bonebeds ($<10^0$ to $10^1$ yrs) and attritional microfossil concentrations ($\leq 10^2$ to $>10^3$ yrs).

Subaqueous event bonebeds are very similar to their subaerial counterparts. They are typified by low-diversity skeletal assemblages (usually monospecific) with low, uniform weathering signatures. There appears to have been little time following death and disarticulation for taxonomic mixing or bone surface degradation. The rate of degradation may have been inhibited, however, due to the buffering effect of water (Behrensmeyer, 1978; but see Carpenter, 1987a).

Subaqueous vertebrate microfossil concentrations, on the other hand, are characterized by high taxonomic diversity. Bones and teeth are relatively unweathered (aside from the occasional stage 4 to 5 anomaly), but bones are thoroughly disarticulated and dissociated. In fact, it is virtually impossible to confidently conclude that any two skeletal elements are from the same individual. All of the skeletal material appears to have been thoroughly dissociated, possibly by "dinoturbation" (Lockley and Conrad, 1989) or other less dramatic types of sediment mixing. Much of the skeletal debris presumably accumulated through the attritional mortality of endemic aquatic taxa. Bones and teeth of terrestrial taxa may have been introduced by overland transport or bank erosion during flooding. Death due to senescence and predation along lake margins probably also played a role (Gifford-Gonzalez, 1984). The duration of the lake/pond setting places an upper limit on the temporal acuity of these sites (Holland and Burk, 1982; Räsänen et al., 1991). Subaqueous event bonebeds have not been found superimposed upon attritional microfossil concentrations within the study interval.

*Channel-fill Concentrations*--Channel-fill bonebeds of the study interval are virtually identical in taphonomic signature to subaqueous event bonebeds. Thus, they are assigned a temporal resolution of $<10^0$ to $10^1$ yrs (Figure 3).

*Channel-lag Concentrations*--Channel-lag concentrations occupy the upper end of the time-averaging spectrum in Figure 3 ($\leq 10^2$ to $>10^5$ yrs). Two lines of reasoning support this interpretation. First, the thickness of a channel deposit serves as a proxy for the depth of potential reworking. If rock accumulation rates are known, an upper limit on temporal resolution can be estimated. Channels in excess of 20 m thick preserve basal concentrates of bone in the Judith River Formation. Thus, with rock accumulation rates averaging 4.5 cm/1000 yrs, time averaging on the order of 4 x $10^5$ yrs is possible. Secondly, at least one "pathway" of bone input has been documented. A channel deposit in the study interval hosting a basal lag of bones and shells (UC-8302) intersects a subaqueous microvertebrate/invertebrate attritional concentration (UC-8302A) with an estimated temporal resolution of $\sim 10^2$ to $>10^3$ yrs. Two locally unfossiliferous channel sandstones also scour into underlying microfossil-bearing beds. Therefore, as suggested by Eberth (1990), stream channels of the Judith River Formation did at least occasionally rework pre-existing bone concentrations.

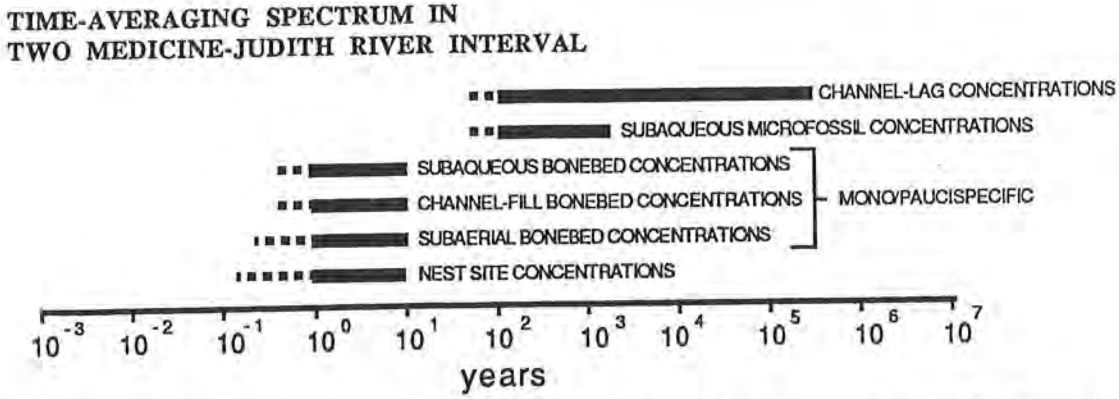


FIGURE *3*--Range of time-averaging of vertebrate skeletal concentrations in the Two Medicine-Judith River interval.

## PATTERNS IN TIME-AVERAGING

The next question is "are these different scales of time-averaging distributed randomly or systematically through the Two Medicine-Judith River record?". To address this question, the time-averaging of 49 known bone concentrations (Figure 1, Table 1) was estimated using the flow chart of Figure 2. Most of the 49 sites were surveyed in the field between 1987 and 1992. Curated samples at the Museum of the Rockies (MOR, Bozeman, Montana) were also examined. Data pertaining to nest sites and juvenile bonebeds were gathered largely through discussions with John R. Horner (MOR). Because the study interval has been the focus of paleontological research for well over 100 years (Leidy, 1856; Cope, 1876; United States National Museum expeditions in the early 1900s; intensive sampling by MOR since 1980), and because the emphasis is upon conspicuous bone concentrations rather than isolated fossils, the sample is considered a representative picture of the Two Medicine-Judith River vertebrate record.

Scales of time-averaging were grouped into three categories: $<1$ to 10 yrs, $\leq 100$ to $>1000$ yrs, and $\leq 100$ to $>100{,}000$ yrs. Overall, more than half (55%) of the concentrations fall into the "event" category, with time resolution ranging from less than one to 10 years (Figure 4). Time-averaged concentrations with estimated temporal resolution ranging from 100s to 1000s of years comprise 25% of the total sample. The top end of the Two Medicine-Judith River time-averaging spectrum ($\leq 100$ to $>100{,}000$ year temporal duration) is occupied by 20% of the surveyed concentrations.

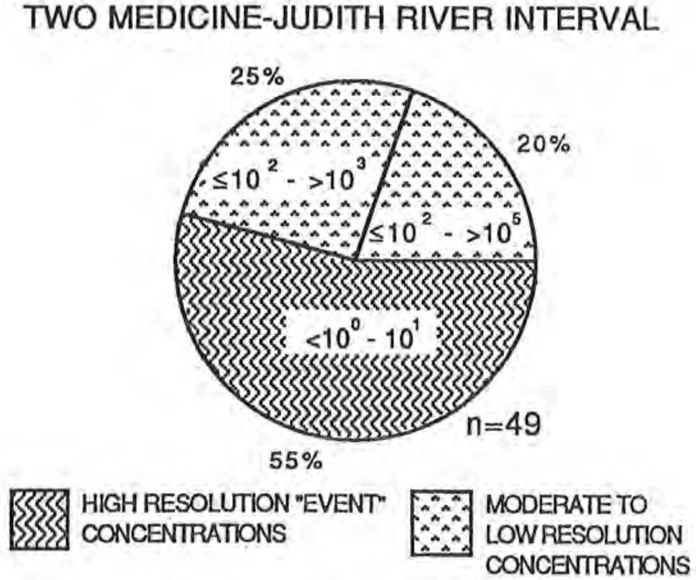


FIGURE *4*--Distributions of time-averaging categories in the entire Two Medicine-Judith River interval. Fifty-five percent of the surveyed concentrations fall within the high resolution "event" category. The remaining concentrations (45%) show evidence of time-averaging of roughly 100 years or more.

When the record is examined more closely, it is apparent that the proportions of categories vary across the foreland basin (Figure 5). Proximal and distal reaches of the Two Medicine-Judith River interval show striking disparity in levels of time-averaging. The proximal Two Medicine Formation is characterized by high temporal resolution assemblages (Figure 5): 83% of the concentrations surveyed (n=29) reflect time-averaging of 10 years or less, and none show evidence of time-averaging of more than several thousand years. In contrast, assemblages from the distal Judith River Formation (n=20) show moderate to high degrees of time-averaging (Figure 5). Eighty-five percent of Judith River concentrations may be time-averaged at levels greater than 100 years, and 50% may be time-averaged at the >100,000 year level. Only 15% of Judith River concentrations fall within the "event" (<1 - 10 yrs) category.

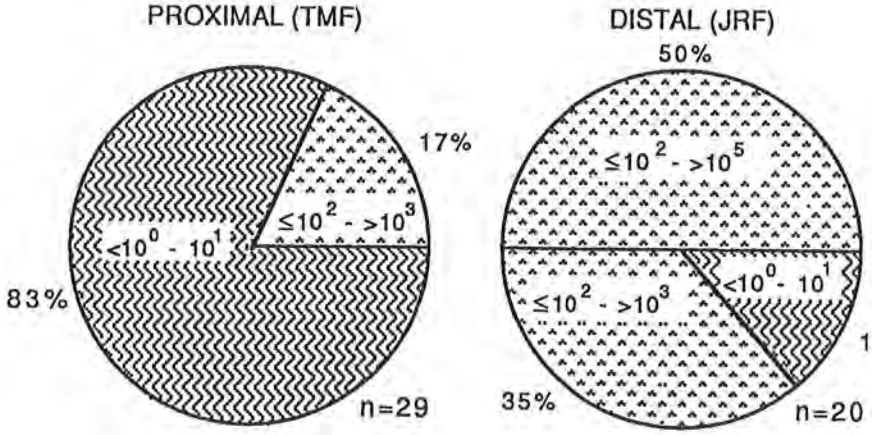


Figure 5--Distributions of time-averaging categories in proximal (Two Medicine Formation) and distal (Judith River Formation) reaches of the Two Medicine-Judith River interval. The proximal record is dominated by high resolution "event" concentrations (83%), whereas the distal record is dominated by vertebrate skeletal concentrations showing evidence of time-averaging of 100 years or more (85%).

## CONTROLS ON PROXIMAL-DISTAL TIME-AVERAGING

Several recent studies have linked subsidence-related geologic trends in alluvial depositional systems (e.g., varying sedimentation rates and fluvial regimens) with patterns in fossil preservation (Bown and Kraus, 1981; Behrensmeyer, 1987, 1988; Eberth, 1990; Bartels et al., 1992). For example, Behrensmeyer (1987) correlated a shift from a channel-fill to a channel-lag dominated vertebrate record in the Siwalik sequence (Miocene) with a change in fluvial regimen and an increase in sediment accumulation rates. Bartels and others (1992) correlated a shift from channel-lag concentrations in the Fort Union Formation (Paleocene) to paleosol concentrations in the overlying Willwood Formation (Eocene) with an increase in aggradation rates.

It is therefore not surprising that proximal and distal reaches of a foreland basin succession are characterized by dissimilar modes of fossil preservation. What is surprising is the disparity in levels of time-averaging that is revealed by a systematic investigation (Figure 5). Geology can explain only some of the disparity in the Two Medicine-Judith River interval (Figure 6); paleoecology and/or paleoclimate must also be involved.

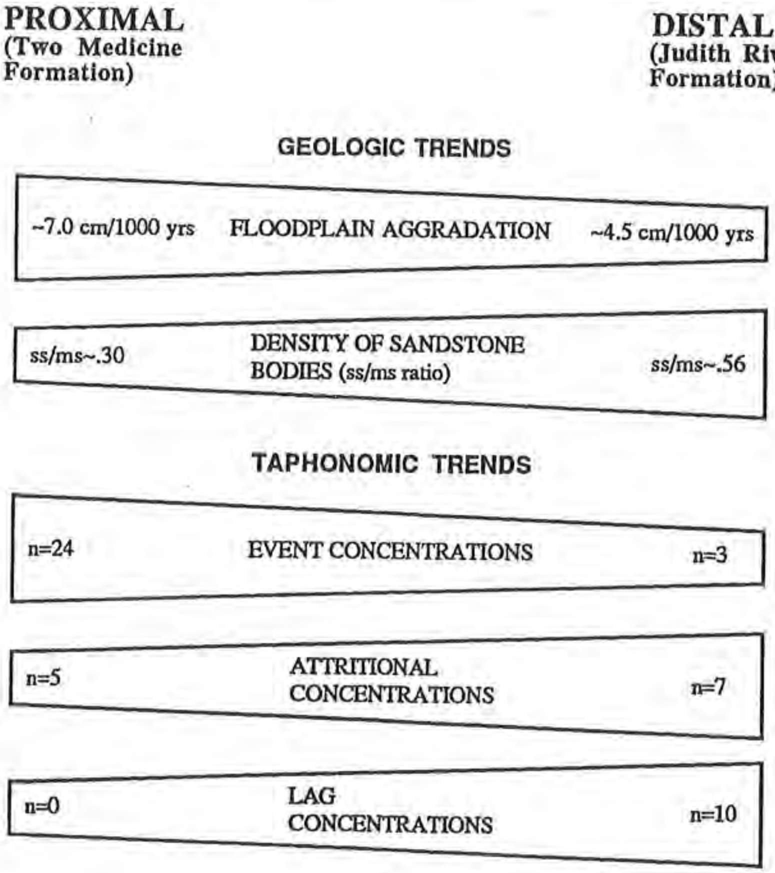


FIGURE *6*--Geologic and taphonomic trends in the Two Medicine-Judith River interval. Tapering of a wedge indicates lower absolute values for geologic trends and lesser frequencies for taphonomic trends.

*Geologic Controls*--The net accumulation rate of the Two Medicine Formation (~7.0 cm/1000 yrs) is roughly 1.5 times greater than that of the Judith River Formation (~4.5 cm/1000 yrs). In a setting characterized by relatively high rates of floodplain aggradation, overbank flood events would be expected to be more frequent and/or greater in magnitude. The preservation potential (= probability of permanent burial) of bone concentrations on the floodplain surface would therefore be enhanced relative to settings with lower rates of aggradation (assuming taphonomic variables such as rates of weathering and scavenging are comparable). The preservation of event concentrations would be favored in settings of relatively high net aggradation.

Relatively high rates of floodplain aggradation, however, could dilute the apparent density of bone incorporated into the rock record through attritional processes. Basically, time is needed for bone to accrue to "fossiliferous" levels before permanent burial (Behrensmeyer, 1982a; Behrensmeyer and Chapman, this volume). Hence, lower (or more sporadic) rates of floodplain aggradation may be required for the abundant preservation of attritional bone concentrations (Bown and Kraus, 1981; Smith, 1993).

Floodplain aggradation rates also exert strong controls on alluvial architecture. Allen (1978) modelled the effects of differential floodplain aggradation on fluvial sedimentation and concluded that the density and interconnectedness of sandstone bodies in alluvial suites should increase with decreasing rates of aggradation. The relative proportion of coarse-grained deposits (sandstone bodies) should therefore be greater in a setting characterized by lower rates of aggradation. Quantitative models and case studies in the rock record corroborate these general predictions (Leeder, 1978; Bridge and Leeder, 1979; Blakey and Gubitosa, 1984; Shuster and Steidtman, 1987). This suggests greater potential for the reworking of floodplain deposits in settings characterized by relatively low rates of floodplain aggradation. This in turn would increase the likelihood of recycling floodplain-hosted bone deposits into time-averaged channel-lag concentrations. Relatively low rates of floodplain aggradation may also favor the development of abandoned channels, which often serve as sites of accumulation for vertebrate skeletal debris (Behrensmeyer, 1988). Behrensmeyer (1987) found that the frequency of fine-grained channel fills (and channel-fill assemblages) was greater in parts of the Siwalik sequence characterized by relatively low net sedimentation rates. Parts of the same succession with higher net sedimentation rates were characterized by fewer fine-grained channel fills, and were dominated by channel-lag assemblages. This trend suggests that the overall time-averaging of a vertebrate-bearing interval may actually increase with increasing rates of aggradation.

*Non-geologic Controls*--The geological considerations outlined above offer insights into the distributions of attritional and lag concentrations in the Two Medicine-Judith River fossil record. However, very few of the copious "event" concentrations documented in the Two Medicine-Judith River interval can be attributed wholly to geologic events (trapping and immediate burial by flood sediments [obrution], burial by volcanic ash, etc.). Most event concentrations instead show evidence of brief exposure in subaerial or subaqueous settings prior to burial. The majority of event concentrations thus apparently record a biological event (mass mortality) not directly related to local geological processes or circumstances.

A variety of killing agents generate mass death assemblages in modern ecosystems. Volcanic events can rapidly kill virtually all members of a biota (plant and animal) through the rapid deposition of ash, tephra, or debris flows (Fritz and Harrison, 1985; Hayward et al., 1989; Lockley, 1990), or through the venting of poisonous gases (Stager, 1987). A classic example of an ancient volcanogenic mass death assemblage is the Poison Ivy Quarry (Miocene) of Nebraska (Voorhies, 1985). Vertebrates can also be killed in substantial numbers by flooding (McHugh, 1972; Schaller, 1973).

Severe climatic conditions also induce vertebrate mass death. Weigelt (1989) described a diverse carcass assemblage produced during a "norther" (a sudden cold wave) along the Texas Gulf Coast, and Borrero (1990) blamed successive years of winter stress for massed accumulations of Guanaco carcasses in Tierra del Fuego. Drought has been proposed as a recurrent killing-agent in the Two Medicine Formation (Carpenter, 1987b; Rogers, 1990). Drought selects for water-dependent taxa such as elephants, zebra, and wildebeest (Lamprey, 1963; Ayeni, 1975), thus low-diversity death assemblages are common (Hillman and Hillman, 1977; Conybeare and Haynes, 1984). Drought also recurs periodically or cyclically (Stockton and Meko, 1983; Currie, 1984; Kerr, 1984), and is therefore capable of generating successive mass death assemblages. Lastly, drought assemblages have a relatively high preservation potential because animals often congregate in the vicinity of persistent water sources (depositional loci), and because sediment-charged flooding is likely after an episode of drought (Shipman, 1975).

*Summary*--Proximal-distal trends in time-averaging within the Two Medicine-Judith River interval thus probably reflect both geologic and climatic controls (Figure 6). Geological conditions in proximal regions apparently favored the preservation of ecologically brief time-interval samples (mass death assemblages). Fortuitously, paleoclimatic conditions were apparently such that mass death assemblages were produced frequently enough to exploit this geologic trend. Geological conditions in proximal parts of the interval also inhibited the reworking of event assemblages into channel-lag concentrations. Geological conditions in distal reaches were apparently better suited for the preservation of attritional and lag concentrations. The rarity of mass death assemblages may be an artefact of preservation--mass death assemblages on the Judith River coastal plain may have been thoroughly degraded by taphonomic processes at the ground surface. Paleoenvironmental conditions may have also rendered mass mortality less likely in the distal Judith River ecosystem.

## PALEOBIOLOGICAL IMPLICATIONS

Finally, what do time-averaging trends in the Two Medicine-Judith River interval imply for paleobiological reconstructions?

The proximal Two Medicine Formation is dominated by high temporal resolution concentrations (brief time-averaging per assemblage), that in turn favor the collection of high resolution samples by paleontologists. Most of these samples are mass death assemblages that are presumably the products of selective killing agents. Thus, although high resolution, much of the record is probably biased towards vulnerable taxa, which suggests that we may have a rather limited sampling of the Two Medicine paleofauna. One very favorable aspect of the Two Medicine sampling regime is its high resolution record of ecologic-scale phenomena. Inferences concerning dinosaur nesting habits, herd structure, ontogenetic growth patterns, and mating behavior have all been drawn from the Two Medicine record.

In contrast, the Judith River Formation is dominated by relatively low temporal resolution samples (prolonged time-averaging per assemblage), making the collection of high resolution samples difficult. The numerous attritional and channel-lag concentrations that characterize the formation are likely drawn from time successive vertebrate communities. The Judith River Formation is thus better suited for evolutionary and long-term ecologic studies (Behrensmeyer, 1982 a, b; Dodson, 1987; Fiorillo, 1989; Brinkman, 1990), in which time-averaging is less of a disadvantage or perhaps even an advantage. The mixing of successive communities over hundreds to thousands of years, however, renders the Judith River record rather insensitive to short-term biologic or ecologic phenomena.

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