Origins of microfossil bonebeds: insights from the Upper Cretaceous Judith River Formation of north-central Montana

Raymond R. Rogers and Mara E. Brady

Abstract.—Microfossil bonebeds are multi-individual accumulations of disarticulated and dissociated vertebrate hardparts dominated by elements in the millimeter to centimeter size range (≥75% of bioclasts ≤5 cm maximum dimension). Modes of accumulation are often difficult to decipher from reports in the literature, although predatory (scatological) and fluvial/hydraulic origins are typically proposed. We studied the sedimentology and taphonomy of 27 microfossil bonebeds in the Campanian Judith River Formation of Montana in order to reconstruct formative histories. Sixteen of the bonebeds examined are hosted by fine-grained facies that accumulated in low-energy aquatic settings (pond/lake microfossil bonebeds). Eleven of the bonebeds are embedded in sandstones that accumulated in ancient fluvial settings (channel-hosted microfossil bonebeds). In lieu of invoking separate pathways to accumulation based on facies distinctions, we present a model that links the accumulation of bioclasts in the two facies. We propose that vertebrate material initially accumulates to fossiliferous levels in ponds/lakes and is later reworked and redeposited as channel-hosted assemblages. This interpretation is grounded in reasonable expectations of lacustrine and fluvial depositional systems and supported by taphonomic data. Moreover, it is consistent with faunal data that indicate that channel-hosted assemblages and pond/lake assemblages are similar with regard to presence/absence and rank-order abundance of taxa.

This revised model of bonebed formation has significant implications for studies of vertebrate paleoecology that hinge on analyses of faunal data recovered from vertebrate microfossil assemblages. Pond/lake microfossil bonebeds in the Judith River record are preserved in situ at the scale of the local paleoenvironment, with no indication of postmortem transport into or out of the life habitat. Moreover, they are time-averaged samples of their source communities, which increases the likelihood of capturing both ecologically abundant species and more rare or transient members of the paleocommunity. These attributes make pond/lake microfossil bonebeds excellent targets for paleoecological studies that seek to reconstruct overall community membership and structure. In contrast, channel-hosted microfossil bonebeds in the Judith River record are out of place from a paleoenvironmental perspective because they are reworked from preexisting pond/lake assemblages and redeposited in younger channel facies. However, despite a history of exhumation and redeposition, channel-hosted microfossil bonebeds are preserved in relatively close spatial proximity to original source beds. This taphonomic reconstruction is counter to the commonly held view that microfossil bonebeds are biased samples that have experienced long-distance transport and significant hydrodynamic sorting.

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Introduction

Microfossil bonebeds (also known as microvertebrate assemblages, vertebrate microfossil assemblages, or microsites) play a central role in community-level reconstructions of terrestrial vertebrate paleofaunas and are commonly analyzed in order to derive estimates of relative abundance and species richness (e.g., McKenna 1960; Estes 1964, 1976; Estes and Berberian 1970; Sahni 1972; Archibald 1982; Dodson 1987; Bryant 1989; Brinkman 1990; Peng et al. 2001; Sankey 2001; Jamniczky et al. 2003; Carrano and Velez-Juarbe 2006; Demar and Breithaupt 2006;

Brinkman et al. 2004, 2007; Sankey and Baszio 2008; Wilson 2008). At the same time, most researchers readily acknowledge the potential for bias in the composition of microfossil bonebeds due to biotic (selective predation) and abiotic (hydrodynamic) sorting mechanisms that presumably act during the accumulation of biological material (e.g., Dodson 1971, 1973; Wolff 1973; Andrews and Nesbitt Evans 1983; Maas 1985; Koster 1987; Wood et al. 1988; Bryant 1989; Blob and Fiorillo 1996; Wilson 2008). With regard to the underlying cause(s) for the accumulation of vertebrate skeletal material in microfossil bonebeds, two

principal hypotheses prevail. Mellett (1974) championed a scatological mode of formation and argued that most vertebrate microfossil assemblages of Mesozoic and Cenozoic age are ''coprocoenoses'' that have been processed through the digestive tracts of carnivores. In contrast, Korth (1979: p. 281) concluded that the taphonomic properties of many microfossil bonebeds were incompatible with a scatological origin, and instead proposed that most sites represent accumulations due to ''selective sorting and deposition by alluvial processes.'' These two contrasting scenarios, which are not mutually exclusive (for example, see Badgley et al. 1998), have served to guide the taphonomic interpretation of vertebrate microfossil assemblages for decades.

In this report, we revisit the phenomenon of vertebrate microfossil concentration with a focus on the richly fossiliferous deposits of the Upper Cretaceous Judith River Formation of north-central Montana (Fig. 1). The Judith River Formation in its expansive type area along the Missouri River (Upper Missouri River Breaks National Monument) preserves abundant microfossil bonebeds in distinct facies that span marine and terrestrial depositional settings (Rogers 1995; Rogers and Kidwell 2000). Neither of the two scenarios presented above (Mellett 1974; Korth 1979) is compatible with the sedimentology and taphonomy of the Judith River microfossil bonebeds. Herein we describe several key sites from the terrestrial portion of the formation and present new views on their probable origins. Our findings provide insights into geological processes that play a role in the generation of vertebrate microfossil assemblages, and have significant implications for the interpretation of vertebrate paleoecology, both within the Judith River Formation and in other fossiliferous strata as well.

Microfossil Bonebeds Defined

Eberth et al. (2007) defined a microfossil bonebed as any multi-individual concentration of vertebrate skeletal material in which 75% or more of the elements (be they bone pebbles or articulated carcasses) are ≤5 cm in maximum dimension. According to this size-based classification, a multitaxic concentration of disarticulated and thoroughly dissociated skeletal elements would be classified as a microfossil bonebed, as would a monotaxic concentration of articulated small vertebrates (e.g., Estes et al. 1978; Henrici and Fiorillo 1993). In this report, we focus only on microfossil bonebeds that consist of predominantly disarticulated and dissociated skeletal material (bones, teeth, scales, scutes, spines, bone pebbles). This includes a variety of skeletal components and fragmentary remains from small animals (e.g., frogs, salamanders, snakes, fish, small mammals) and small skeletal components or skeletal fragments from larger animals (e.g., turtles, crocodiles, dinosaurs). Larger bones and bone fragments may be present, but they are rare in comparison to the dominant small (≤5 cm) bioclast fraction. In keeping with the general definition of Eberth et al. (2007), the microfossil bonebeds described in this study occur in a stratigraphically limited sedimentary unit (e.g., a single bed), include the remains of at least two (and in fact many orders of magnitude more) vertebrates, and preserve vertebrate fossils in considerably greater abundance than in surrounding strata. Fossil sites that satisfy the microfossil bonebed definition followed in this report have been collected and/or described by McKenna (1962), Estes (1964), Estes and Berberian (1970), Sahni (1972), Fisher (1981a,b), Dodson (1987), Wood et al. (1988), Bryant (1989), Brinkman (1990), Eberth (1990), Khajuria and Prasad (1998), Rogers and Kidwell (2000), Peng et al. (2001), Carrano and Velez-Juarbe (2006), Demar and Breithaupt (2006), Brinkman et al. (2007), and Wilson (2008), among others.

Microfossil Bonebeds of the Judith River Formation

The Judith River Formation of Montana has a long history of paleontological discovery and research. Some of the first skeletal remains of dinosaurs described from North America were collected from what was almost certainly a microfossil bonebed embedded in Judith River strata (Leidy 1856,
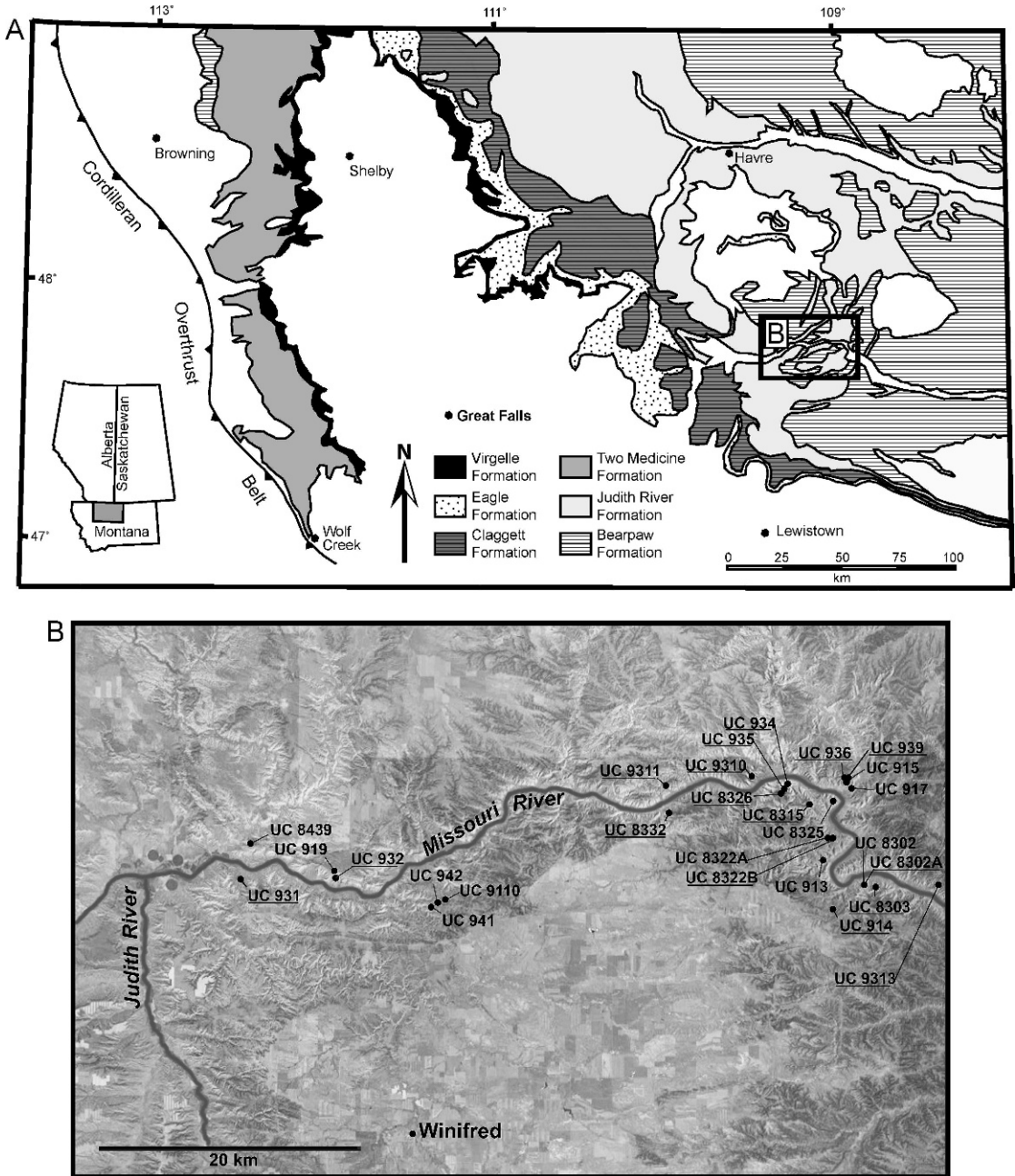
FIGURE 1. Judith River Formation study area. A, Generalized outcrop map of the Upper Cretaceous Judith River Formation (light gray) and associated units in northwestern and north-central Montana. The Judith River Formation type area on the Missouri River (inset B) preserves abundant microfossil bonebeds (modified from Rogers 1998). B, Location map of 27 microfossil bonebeds included in this study. Pond/lake microfossil bonebeds (Table 1) are underlined to distinguish them from channel-hosted microfossil bonebeds (Table 2). Image modified from Google Earth.

1860). Subsequent discoveries in the Judith River Formation and equivalent units in Canada (Eberth and Hamblin 1993; Eberth 2005) have continued to figure prominently in

dinosaur research (e.g., Currie and Koppel-hus 2005; Prieto-Marquez 2005; Fricke et al. 2008; Tweet et al. 2008). Non-dinosaurian vertebrates are also well represented in the

formation (e.g., Case 1978; Fiorillo 1989; Blob et al. 2001), including important Late Cretaceous (''Judithian'') mammal faunas (Sahni 1972; Clemens and Goodwin 1985; Montellano 1991).

The type area of the Judith River Formation lies in the Upper Missouri River Breaks National Monument, a vast region of badlands bordering the Missouri River and its tributaries in north-central Montana (Fig. 1). In the type area, the ~180-m-thick Judith River section is exposed in its entirety (Rogers 1995, 1998) and consists of strata that accumulated during regression of the Claggett Sea and subsequent transgression of the Bearpaw Sea. The formation consists of claystones, siltstones, and fine- to medium-grained sandstones of fluvial, lacustrine, tidal, and shallow marine origin. Beds of lignite and ironstone are common, and several bentonite beds are also intercalated in the section (Rogers 1995; Rogers and Swisher 1996). Radioisotopic data indicate that the formation accumulated during the Campanian, from approximately 79 Ma to 74.5 Ma (Goodwin and Deino 1989; Rogers 1995; Rogers and Swisher 1996; Foreman et al. 2008; R. Rogers and A. Deino unpublished data).

Several different taphonomic (preservational) modes characterize the Judith River Formation within the type area (Rogers 1993, 1995). (1) Single bones, bone fragments, and teeth that vary in taphonomic quality (states of weathering, abrasion, and breakage) are recovered from channel and floodplain facies throughout the formation. (2) Macro-element bonebeds that yield the remains of dinosaurs and other vertebrates also occur, but they are rare, especially in comparison to Judith River-equivalent exposures to the north in Canada (Dodson 1971; Ryan et al. 2001). In contrast, microfossil bonebeds are quite abundant, and to date 27 distinct localities that fit the definition provided above have been documented in the type area (Rogers 1995; Rogers and Kidwell 2000) (Fig. 1). (3) Sixteen of the known microfossil bonebeds are preserved in fine-grained facies that accumulated in low-energy aqueous settings, such as floodbasin ponds/lakes and fluvial backwaters. These localities are hereafter referred to as pond/

lake microfossil bonebeds (Table 1). (4) The remaining terrestrial sites ($n = 11$) consist of vertebrate microfossil concentrations closely associated with basal and internal scour surfaces in fluvial sandstone bodies, and these are hereafter designated channel-hosted microfossil bonebeds (Table 2). (5) The final type of vertebrate skeletal concentration characteristic of the Judith River Formation occurs in shallow-marine sandstones and is also best classified as a microfossil bonebed. These marine bonebeds, which yield shark teeth and teleost bones, along with marine reptile bones and rare dinosaurs bones (Case 1978; Tulu and Rogers 2004), are developed in localized scours (Figs. 2, 3) on a widespread ravinement surface (coincident with a fourth-order sequence boundary) that formed in shoreface sediments (surface D3 of Rogers and Kidwell 2000) (Fig. 2). They will not be discussed further in this report.

Pond/Lake Microfossil Bonebeds

Sedimentology.—Pond/lake microfossil bonebeds (Table 1, Fig. 1) are preserved in tabular to broadly lenticular beds of gray to brown silty claystone, siltstone, and very fine grained sandstone. Basal contacts of host lithosomes are typically sharp, whereas upper contacts vary from erosional, as in UC-8302A and UC-937, to gradational. The thickness of the bone-bearing facies varies within and among sites, ranging from 40 cm to 240 cm (Table 1). The lateral extent of pond/lake bonebeds is difficult to ascertain given the limits of exposure (bonebeds typically pass laterally to cover, or crop out on isolated buttes). However, UC-914 can be tracked for approximately 100 m along available outcrop (N–S), and UC-8303 can be traced approximately 250 m E–W and 100 m N–S (Fig. 4A).

The fine-grained facies of pond/lake bonebeds are characteristically massive to faintly horizontally laminated, and upon excavation tend to exhibit blocky to crude platy parting (Fig. 4B). Three of the bonebeds in our sample (UC-934, UC-935, UC-9312; see Fig. 4C) are distinctly heterolithic and exhibit contorted interbeds of siltstone comparable to those described by Eberth (1990, see his contorted siltstone/sandstone sites). Carbonaceous

TABLE 1. Sedimentologic and taphonomic characteristics of 16 pond/lake microfossil bonebeds in the Judith River Formation. Samples housed at Macalester College.

	Pond/Lake microfossil bonebeds	
Locality	Sedimentologic characteristics	Taphonomic and paleontologic characteristics
UC-8302A (Fig. 14)	Brownish-gray (2.5Y 6/2) clay-rich siltstone/very fine sandstone, massive, laminated carbonaceous debris, erosional upper contact (where truncated by overlying sandstone body [UC-8302, see below]), ~10 m lateral expanse, ~45 cm thick (base not exposed)	Vertebrate bioclasts, including angular to rounded bone pebbles, dispersed throughout bed, associated with abundant small invertebrates, intact and fragmentary, *Sphaerium*, *Viviparus*, *Campeloma*, ''*Unio*''
UC-8303 (Figs. 4, 5, 6, 12, 15)	Gray (5Y 6/1) silty claystone, massive, very carbonaceous and brown in upper few cm, carbonaceous debris tends to be laminated, sharp upper and lower contacts, tabular bed can be traced along continuous exposure for 250+ m, and presumably spans several thousand m², 85 cm thick	Bone debris abundant but dispersed, abundant bone pebbles, some scales and teeth devoid of ganoine/enamel, abundant shells and shell fragments of *Sphaerium*, *Viviparus*, and ''*Unio*''
UC-8315 (Fig. 5)	Light olive-gray (5Y 6/2) silty claystone, massive, scattered carbonaceous debris (laminated), small oxidized root traces, 10 cm thick bed of fine sandstone intercalated near top of unit, sharp basal contact, passes up to gray-green siltstone, tabular bed extends tens of meters to the limits of available exposure, passes laterally to cover, 60 cm thick	Vertebrate debris abundant but widely dispersed throughout bed, more abundant in upper half, abundant bone pebbles, associated with fossil wood and freshwater invertebrates, including *Sphaerium* and *Viviparus*, shells range from intact to fragmentary
UC-8322B	Brown silty claystone, massive, very carbonaceous, sharp basal and upper contacts, tabular bed extends ~10 m, passes laterally to cover, 90 cm thick	Vertebrate bioclasts dispersed throughout bed, associated with shells and shell debris of small freshwater invertebrates (*Sphaerium*), amber
UC-8326 (Fig. 6)	Gray-green silty claystone, massive, laminated carbonaceous debris, sharp basal contact, passes up to gray-green claystone, tabular bed can be traced for several tens of meters before passing to cover, 1.3 m thick	Vertebrate bioclasts dispersed throughout bed, associated with shell debris of small invertebrates including *Sphaerium* and *Viviparus*
UC-8332	Brown silty claystone, massive, carbonaceous (more so at top of unit), sharp basal contact, passes up into gray-green silty claystone, several tens of meters of lateral exposure, 70 cm thick	Vertebrate bioclasts dispersed throughout bed, associated with intact and fragmentary remains of *Sphaerium* and *Viviparus*
UC-914 (Figs. 4, 5, 6, 12, 15)	Gray brown (2.5Y 5/2) silty claystone, massive with crude platy parting, abundant laminated carbonaceous debris, small (<1 cm long axis) flattened green claystone pebbles scattered throughout, sharp basal contact, gradational upper contact, laterally persistent bed extends for at least 100 m along available exposures, 50–75 cm thick	Remains of a diverse array of vertebrate taxa (Table 3) dispersed throughout bed, quality ranges from pristine intact elements to rounded bone pebbles (Figs. 5, 6), vertebrate fossils interspersed with rare invertebrates, including *Sphaerium* and *Viviparus*
UC-931	Brown clay-rich siltstone, massive, abundant laminated plant debris, carbonaceous, sharp basal contact, erosional upper contact, ~45 m of lateral exposure, passes to cover, 2 m thick	Vertebrate bioclasts dispersed throughout bed, rare larger elements (e.g., ribs), associated with invertebrate shell debris, intact and fragmentary shells of *Sphaerium* and *Viviparus*
UC-932	Pale yellow (2.5Y 7/3) sandy siltstone, clay-rich, massive, abundant carbonaceous fragments, sharp basal and upper contacts, limited exposure, 2.4 m thick	Vertebrate bioclasts dispersed throughout bed, more abundant in lower half of unit, associated with shell debris, intact and fragmentary *Sphaerium* and *Viviparus*
UC-934 (Fig. 4)	Light gray (5Y 7/2) siltstone/very fine sandstone with brown mottles, massive to contorted bedding, carbonaceous, scattered green claystone pebbles, two internal scour surfaces, sharp basal and upper contacts, ~30 m lateral exposure, 1.4 m thick	Vertebrate bioclasts dispersed throughout bed, more densely concentrated above two silty interbeds, hadrosaur teeth notably abundant, abrasion common, vertebrate debris associated with *Sphaerium*, *Viviparus*, and fragmentary ''*Unio*''

TABLE 1. Continued.

	Pond/Lake microfossil bonebeds	
Locality	Sedimentologic characteristics	Taphonomic and paleontologic characteristics
UC-935	UC-935 crops out 7 m above UC-934, and is identical with regard to sedimentology and taphonomy, sharp basal and upper contacts, tabular bed can be traced ~35 m, 80 cm thick	See UC-934
UC-936	Gray clay-rich sandstone, very fine-grained, massive to crudely laminated, coaly stingers developed throughout unit (more common in lower 40 cm), sharp basal contact, passes up into gray-green silty claystone, laterally traceable for ~100 m, 90 cm thick	Small vertebrate bioclasts dispersed throughout bed, associated with intact shells and shell debris of *Sphaerium* and *Viviparus* and fragments of ''*Unio*,'' amber blebs
UC-939	Light brown-gray (10YR 6/2) clay-rich siltstone, massive, platy parting, laminated carbonaceous debris, sharp basal contact, erosional upper contact, tabular bed extends ~20 m to limits of exposure, 50 cm thick	Vertebrate bioclasts dispersed throughout bed, associated with rare shell debris of small invertebrates including *Sphaerium* and *Viviparus*
UC-9310	Light gray (5Y 7/1) very silty claystone, massive, carbonaceous, sharp basal and upper contacts, localized exposure on small ridge, 50 cm thick	Vertebrate bioclasts including angular to rounded bone pebbles dispersed throughout bed, rare invertebrate shell debris, *Sphaerium* and ''*Unio*''
UC-9311	Tan siltstone, massive, scattered carbonaceous debris, sharp basal contact, passes up to gray claystone, 40 cm thick	Vertebrate bioclasts dispersed throughout bed, associated with invertebrate shell debris, *Sphaerium* and *Viviparus*
UC-9313	Very dark gray (5Y 3/1) silty claystone, massive to locally fissile, carbonaceous, sharp basal and upper contacts, tabular bed, bound by laterally extensive lignite deposits, 80 cm thick	Vertebrate bioclasts dispersed throughout bed, rare aragonitic shell debris

plant debris is abundant in pond/lake microfossil bonebeds and is typically preserved in a laminated fashion (Fig. 4D). Carbonaceous debris is commonly found in association with scattered millimeter-scale blebs of amber, and in some localities (UC-914, UC-934, UC-935), small claystone pebbles.

Taphonomic Characteristics.—All pond/lake microfossil bonebeds in our sample preserve shell debris of freshwater invertebrates, including the bivalve *Sphaerium*, the gastropods *Viviparus*, *Campeloma*, *Lioplacodes*, and, more rarely, the aragonitic remains of the bivalve ''*Unio*'' (J. Hartman personal communication 2007). In some bonebeds, invertebrate shells and shell debris are extraordinarily abundant (e.g., UC-8302A, UC-8303, Fig. 5A), whereas in others (e.g., UC-914, UC-937) invertebrate skeletal debris is rare. The quality of preservation ranges from pristine intact shells to millimeter-scale fragmentary shell hash.

Vertebrate fossils preserved in pond/lake microfossil bonebeds include the disarticulated and dissociated hardparts (bones, teeth, scales) of a variety of aquatic, semiaquatic, and fully terrestrial animals (see Table 3), including fish, amphibians, turtles, crocodiles, champsosaurs, dinosaurs, and mammals. Skeletal debris is abundant but disseminated throughout bone-producing horizons as opposed to densely concentrated in pockets or along bed contacts. Pond/lake bonebeds are best classified as ''dispersed'' concentrations (sensu Kidwell and Holland 1991) characterized by sparsely distributed, matrix-supported vertebrate fossils.

With regard to the actual abundance of vertebrate hardparts in pond/lake microfossil bonebeds, small bulk samples (3–5 kg) of UC-8303 and UC-914 were disaggregated and washed through sieves, and each yielded less than 1% bone by volume. Despite very low volumetric abundance overall, several hundred millimeter-scale bones and bone fragments were recovered from each of the small test samples. The sheer abundance of millimeter-scale vertebrate bioclasts in Judith River pond/lake microfossil bonebeds is striking (Fig. 5B), and greatly exceeds the quantity of skeletal debris in the ≥1 cm size range. Much of the fine-grained bioclast fraction consists of unidentifiable bone frag-

TABLE 2. Sedimentologic and taphonomic characteristics of 11 channel-hosted microfossil bonebeds in the Judith River Formation. Samples housed at Macalester College.

| | Channel-hosted microfossil bonebeds | |
Locality	Sedimentologic characteristics	Taphonomic and paleontologic characteristics
UC-8302 (Figs. 7, 9, 10, 14)	Gray fine-grained sandstone characterized by low-angle inclined bedding, small- to medium-scale trough cross-bedding, ripple cross-lamination, climbing ripples near top, thin carbon/clay partings drape most set boundaries and some foresets, erosive basal contact with UC-8302A, passes up to siltstone, 7 m thick	Vertebrate microfossils occur in basal 30 cm of unit in association with ''Unio'' debris and fragmentary shells of *Sphaerium*, ironstone and claystone pebbles, and coaly stringers
UC-8322A (Figs. 7, 8)	Gray fine-to medium-grained sandstone, characterized by medium- to large-scale trough cross-bedding, carbon-/clay-draped foresets, sharp basal and upper contacts, 3.6 m thick	Vertebrate microfossils occur in basal 10 cm of unit in association with ''Unio'' debris (isolated and ''butterflied'' valves), claystone and flattened ironstone pebbles, carbonized wood, and rounded metamorphic pebbles (up to 6 cm long axis)
UC-8325 (Figs. 9, 10)	Gray to tan fine-grained sandstone, multistory, dominated by medium to large-scale trough cross-bedding, planar tabular cross bed sets locally developed, an internal scour surface mantled by a 10 cm thick lag of ''Unio'' shell debris and rounded green and orange claystone pebbles crops out 95 cm up-unit, a second through-going internal scour surface crops out 2.4 m up-unit, and this surface is mantled by a 10 cm thick lag of claystone and ironstone pebbles, shell debris, and vertebrate microfossils, erosional basal contact draped with small claystone and ironstone pebbles, passes up to claystone, 5 m thick	Vertebrate microfossils recovered from UC-8325 are relatively well sorted (most elements <5 mm long axis), and show evidence of rounding and polish, associated with fragmentary ''Unio'' debris
UC-8439 (Figs. 10, 13, 15)	Gray fine-grained sandstone, medium- to large-scale trough cross-bedding, planar bedded at top, erosive base, passes up to clayey siltstone, limited exposure, 3.2 m thick	At least three discrete set boundaries are mantled with vertebrate bioclasts, vertebrate microfossils are also preserved along basal contact, associated with gray-green claystone pebbles, fragmentary shell debris, and carbonized wood fragments
UC-9110	Gray fine-grained sandstone characterized by low-angle inclined bedding and medium- to large-scale trough cross-bedding, foresets and set boundaries commonly draped with carbonaceous debris, erosional basal contact, sharp upper contact to lignite, sheet geometry, 4.7 m thick	Vertebrate microfossil debris concentrated in basal 20 cm of unit, localized in ~10 m wide swath, bones, teeth, scales and scutes of terrestrial and aquatic taxa (including sharks) mantle surface, associated with carbonaceous debris, ironstone pebbles, claystone pebbles, and rare silicified wood
UC-913	Gray very fine- to fine-grained sandstone, faint 10–20 cm sets of trough cross-bedding, capped by ripple cross lamination, erosional basal contact, sharp upper contact, 2.45 m thick	Vertebrate microfossils occur in basal 30 cm of unit, associated with stringers of densely-packed shell debris, carbonaceous fragments, and scattered green claystone pebbles, bone-bearing facies can be traced for ~15 m at main site and correlated ~30 m to adjacent butte
UC-915	Tan fine-grained clay-rich sandstone, dominated by large-scale low-angle bedding delineated by carbon/clay drapes, faint ripple cross-lamination locally developed, numerous internal intraclast lags of pebbles and shell debris, upper few meters of unit characterized by trough cross-bedding with muddy interbeds, erosional basal contact, passes up to lignitic facies, 10.2 m thick	Vertebrate microfossil assemblage crops out 7.5 m above the base of unit in localized scour (~10 m lateral exposure), bones and teeth are preserved in association with small freshwater invertebrates and abundant carbonaceous debris
UC-917	Gray fine-grained multistory sandstone body, massive to faintly planar bedded, many bedding planes draped with thin veneers of clay and carbonaceous material, clay-content increases up-unit, through-going erosion surface 3.9 m above base, basal contact erosional, passes up to silty claystone, 7.9 m thick	Vertebrate microfossil assemblage associated with through-going internal scour 3.9 m above base, bones associated with intraclast claystone pebbles and carbonaceous debris

TABLE 2. Continued.

Locality	Channel-hosted microfossil bonebeds	
	Sedimentologic characteristics	Taphonomic and paleontologic characteristics
UC-919 (Fig. 10)	Gray to brown fine-grained sandstone, multistory, dominated by low-angle bedding delineated by clay/carbon drapes, ripple bedding locally developed, claystone pebbles, ''*Unio*'' debris, and rare fossil logs mantle basal contact, intraclast lags developed on numerous internal scours, erosional basal contact, passes up into siltstone, 11 m thick	Vertebrate fossils concentrated on through-going internal scour 2.8 m below top of unit, associated with carbonaceous debris and ironstone pebbles, some bones appear rounded and abraded, bone-bearing horizon traceable for ~20 m along available exposures
UC-941 (Figs. 7, 8, 12, 15)	Gray very fine- to fine-grained sandstone, inclined heterolithic stratification and medium- to large-scale (.3–1 m thick) trough cross bed sets, foresets commonly clay and carbon draped, thin intraclast lag stringers mantle some set boundaries, erosive basal contact with underlying lignite bed, sharp contact with overlying claystone bed, sheet geometry, 6.6 m thick	Vertebrate microfossils occur at base of unit along ~10 m wide swath, associated with ironstone and claystone pebbles, carbonaceous debris, rare silicified logs, and metamorphic pebbles
UC-942 (Figs. 7, 9, 12)	Gray very fine- to fine-grained sandstone, dominated by large-scale lateral accretion bedding dipping to south, beds at base of unit delineated by drapes of carbonaceous debris and clay, erosive basal contact with brown carbonaceous mudstone, sharp upper contact with brown carbonaceous claystone/lignite, 3.9 m thick	Vertebrate microfossils occur at base of unit along full extent of exposure, bioclasts are localized in the basal 10 cm, and are found in association with abundant cm-sale flat claystone pebbles, coaly stringers, and dispersed ironstone pebbles

ments, but intact millimeter-scale elements from small animals are also represented. The true size distribution of vertebrate hardparts preserved in pond/lake microfossil sites is not readily apparent in outcrop because the coarser-grained bioclastic fraction tends to accrue on weathered surfaces (Fig. 5C,D).

The quality of preservation of vertebrate hardparts in pond/lake microfossil bonebeds varies. Resilient skeletal elements in the millimeter to centimeter-plus size range, such as teeth, ganoid fish scales, and dense compact bones (caudal vertebrae, phalanges) are often recovered in good quality (e.g., dental serrations and cortical surfaces intact, see Fig. 6A). Interestingly, there does appear to be a greater proportion of well-preserved skeletal material in the millimeter-scale size fraction (Fig. 6B). Whether this general observation reflects a taphonomic bias favoring the preservation of intact elements in the sub-cm size range or simply tracks greater initial input from small animals remains to be resolved. The vast majority of skeletal material, however, exhibits evidence of breakage and surface degradation (abrasion/corrosion/rounding). With regard to assessing the extent of breakage, the unfortunate fact

is that much material is inadvertently broken during collection and processing (washing and sieving). However, many bones show evidence of breakage prior to fossilization (Fig. 6C–E), indicating that skeletal material in pond/lake bonebeds experienced mechanical stresses prior to final burial. With regard to surface degradation, ends of limb bones and phalanges often show cortical deterioration, as do processes and edges on many vertebrae. Rare teeth and gar scales show complete loss of enamel and ganoine (Fig. 6F).

Depositional Setting.—Pond/lake microfossil bonebeds are intercalated amidst facies that accumulated in a coastal setting characterized by hydromorphic floodplains and tidally influenced channels (Rogers 1995, 1998; Rogers and Kidwell 2000). The fine-grained nature of these deposits is consistent with a relatively low energy depositional setting. This interpretation is corroborated by the abundance of horizontally laminated plant debris (which presumably settled from suspension) and the presence of fragile, thin-shelled invertebrates (e.g., *Sphaerium*, *Viviparus*). These same invertebrates, in association with fish, frogs, salamanders, turtles, crocodiles, and champsosaurs, indicate that
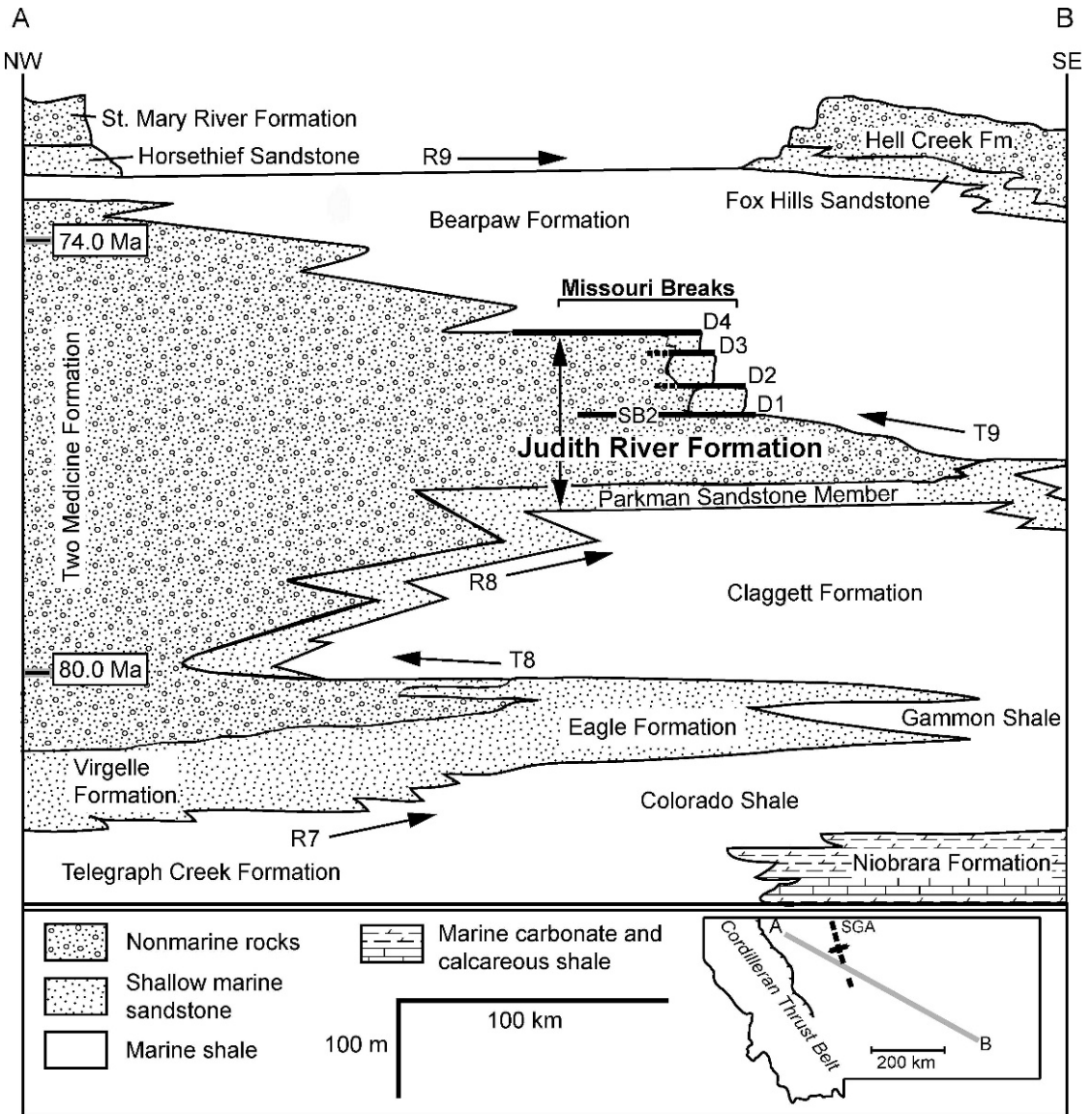
FIGURE 2. Schematic regional cross-section of Upper Cretaceous strata in Montana (modified from Gill and Cobban 1973). The Judith River Formation correlates to the west with terrestrial deposits of the middle and upper Two Medicine Formation, and is bounded above and below by marine shales of the Bearpaw and Claggett Formations. In the eastern part of the Judith River Formation type area, the SB2 discontinuity (see text, and Rogers and Kidwell 2000) correlates with the base of three back-stepping fourth-order sequences that accumulated during the Bearpaw transgression. Bounding surfaces of these marine sequences (D1–D4 in Rogers and Kidwell 2000) locally host microfossil bonebeds (see Fig. 3). R7, T8, R8, T9, R9 refer to the transgressive-regressive cycles of Kauffman (1977). Radioisotopic ages from Rogers et al. (1993). SGA, Sweetgrass arch.

the depositional setting was subaqueous. Many of these same taxa further suggest freshwater conditions.

Channel-Hosted Microfossil Bonebeds

Sedimentology.—Channel-hosted microfossil bonebeds of the Judith River Formation

(Table 2) are preserved in sandstone bodies intercalated within the terrestrial portion of the Judith River record. These sandstone bodies are fine- to medium-grained, and range in thickness from 2.45 m (UC-913) to 11.2 m (UC-919). The geometries of channel sandstone bodies in the Judith River Forma-
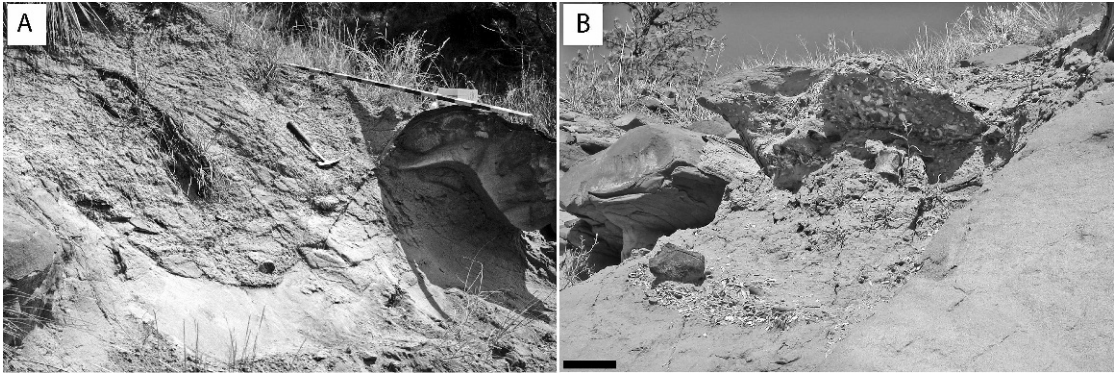
FIGURE 3. Localized microfossil bonebeds crop out in shallow marine sandstones of the Judith River Formation in the eastern sector of the type area. The two localities illustrated yield abundant shark teeth and teleost bones in association with ironstone pebble rip-ups (including cemented burrow casts) and invertebrate shell debris. Both sites are developed in meter-scale scours that formed in shoreface sediments during the early stages of the Bearpaw transgression (surface D3 of Fig. 2). Locality A is 2.9 km to the northwest of locality B. Scale bar in B, 10 cm.

tion are often difficult to ascertain given the limits of exposure, but most appear to have width-to-thickness ratios ranging from 15:1 to 100:1. Only rarely can bonebed-hosting sand-stone bodies be traced to their lateral margins (e.g., UC-8302, Fig. 7A).

Basal contacts of sandstone bodies hosting microfossil assemblages are invariably sharp,
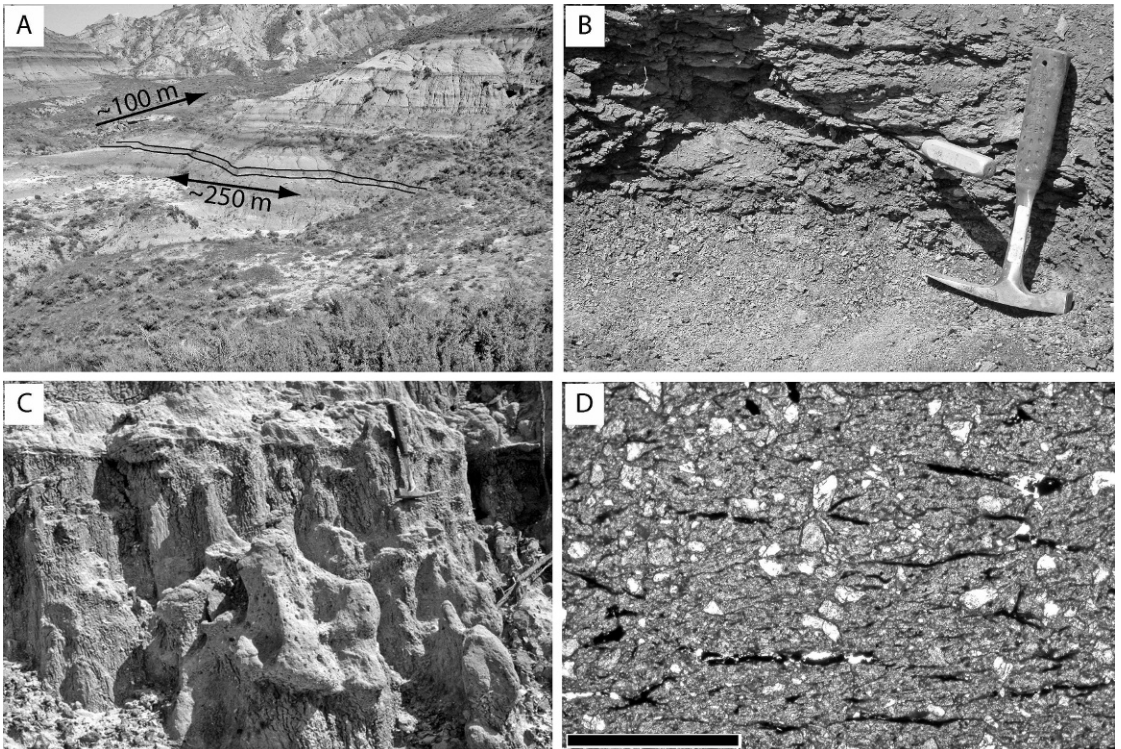

FIGURE 4. Sedimentary characteristics of pond/lake microfossil bonebeds. A, Outcrop view of locality UC-8303. This pond/lake bonebed is hosted by a tabular bed that spans at least 25,000 m². UC-8303 extends to the west (right) beyond the edge of the photograph. B, Platy parting developed in the carbonaceous matrix of bonebed UC-914. C, Contorted siltstone interbeds in the mudstone matrix of bonebed UC-934. D, Photomicrograph of bonebed UC-914 showing abundance of horizontally laminated carbonaceous debris in silty/sandy claystone matrix. Scale bar in D, 1 mm.
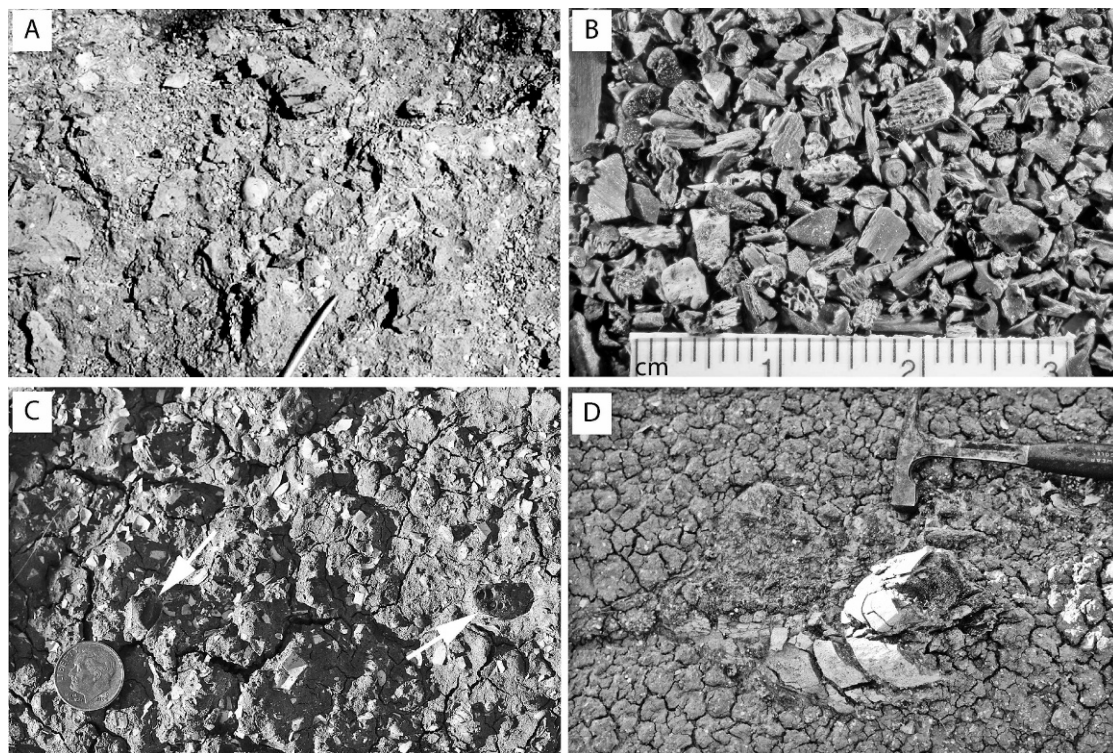
FIGURE 5. General taphonomic characteristics of pond/lake microfossil bonebeds. A, Bedding plane view of bonebed UC-8303 showing abundant invertebrate shell debris. Note intact gastropod to left of tip of ice pick and bivalve near center. See text for taxonomic details. B, View of abundant millimeter-scale bones and bone fragments in a screen-washed sample from bonebed UC-914. C, Outcrop exposure of bonebed UC-8315 showing abundant invertebrate shell debris and centimeter-scale vertebrate elements (left arrow gar scale, right arrow crocodile scute fragment) accumulating on weathered surface. D, Isolated dinosaur limb fragment weathering from bonebed UC-8303. Note abundance of invertebrate shell debris (white specks) on weathered surface.

TABLE 3. Faunal list of vertebrate taxa recovered from UC-914, a pond/lake microfossil bonebed in the Judith River Formation type area (from Rogers 1995). Teleost identifications based on Neuman and Brinkman (2005).

Order Ctenanacanthiformes	Order Choristodera
Hybodus	*Champsosaurus*
Order Batoidea	Order Saurischia
Myledaphus	Tyrannosauridae
Order Acispeneriformes	Troodontidae
Acispenser	theropoda indet.
Order Lepisosteiformes	Order Ornithischia
Lepisosteus	Hadrosauridae
Order Elopiformes	Ceratopsidae
Paralbula	Ankylosauridae
Teleosts IIIB-1, IIA-3,	Order Marsupialia
IIA-1, IIB-1, IA-	*Eodelphis*
1, IA-2, IC-1, IB-1, IIIA-2	*Alphadon*
Order Urodela	Order Multituberculata
Habrosaurus	*Cimolestes* (cf)
Opisthotriton	Order Insectivora
Prodesmodon	*Gypsonictops*
Scapherpeton	
Order Chelonia	
Aspideretes	
Basilemys	
Adocus	

and in most cases demonstrably erosional, as indicated by the truncation of surrounding beds and/or associated intraclast lag deposits. Small centimeter-scale claystone pebbles are the most common intraclasts (Fig. 7B) and are often admixed with ironstone pebbles (irregular/nodular morphologies; Fig. 7C), ironstone steinkerns and burrow casts, carbonaceous debris, silicified wood fragments, and invertebrate shell debris (Fig. 7D). Two sites (UC-8322A, UC-941) yielded extraformational metamorphic pebbles. The thickness of intraclast lag deposits also varies among sites, ranging from thin centimeter-scale pavements draping basal and internal scours (UC-8439) to beds tens of centimeters thick (UC-8302, UC-9110).

The single and multistory sandstone bodies that host microfossil bonebeds exhibit an array of sedimentary structures at a variety of scales
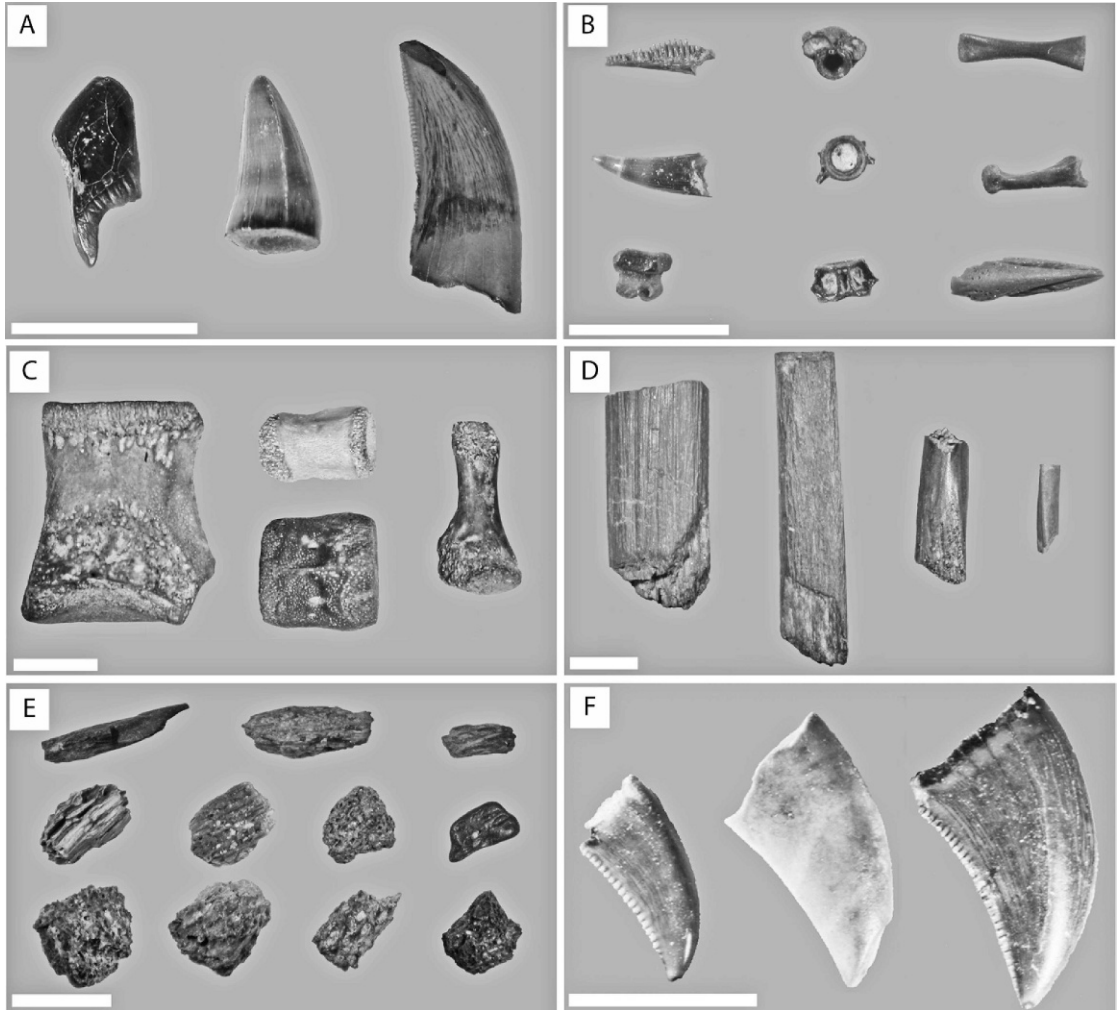
FIGURE 6. The taphonomic quality of vertebrate hardparts preserved in pond/lake bonebeds varies. A, Inherently resilient skeletal elements in the centimeter-scale size range, such as teeth and ganoid fish scales, are often recovered in good condition (UC-8303). Scale bar, 1 cm. B, Well-preserved millimeter-scale skeletal elements such as those figured from bonebed UC-914 are generally more abundant, and this may reflect a bias favoring the preservation of intact elements in the sub-cm size range or perhaps greater input of biological remains from small animals. Scale bar, 5 mm. C, Cortical bone surfaces in pond/lake assemblages frequently show evidence of corrosion. The ends of limb bones and the edges of vertebrae commonly show degradation. Elements figured are from UC-8303 (two vertebrae in center) and UC-914. Scale bar, 5 mm. D, Pre-fossilization breakage is common in pond/lake microfossil bonebeds, especially on more elongate elements. Specimens figured are from UC-8326 (specimen on left) and UC-914. Scale bar, 5 mm. E, The vast majority of skeletal debris preserved in pond/lake microfossil bonebeds consists of millimeter-scale bone pebbles and bone splinters that range from angular to rounded (all bones from site UC-914). Scale bar, 5 mm. F, A small fraction of the teeth and gar scales recovered from microfossil bonebeds show loss of enamel and ganoine (theropod teeth figured from site UC-8303). This potentially reflects passage through digestive systems of animals that decalcify ingested hardparts. Scale bar, 5 mm.

(see Table 2). Trough cross-stratification (TCS) is widely developed, with some sandstone bodies composed almost entirely of stacked sets of TCS. Several localities (UC-8302, UC-919, UC-941) also exhibit inclined heterolithic stratification (IHS of Thomas et al. 1987), with strata demarcated by interbeds of sandstone and carbonaceous sandy mudstone (Fig. 8).

Taphonomic Characteristics.—All channel-hosted microfossil bonebeds in our sample preserve invertebrate shell debris, most commonly ''*Unio.*'' Locally, shells and shell debris
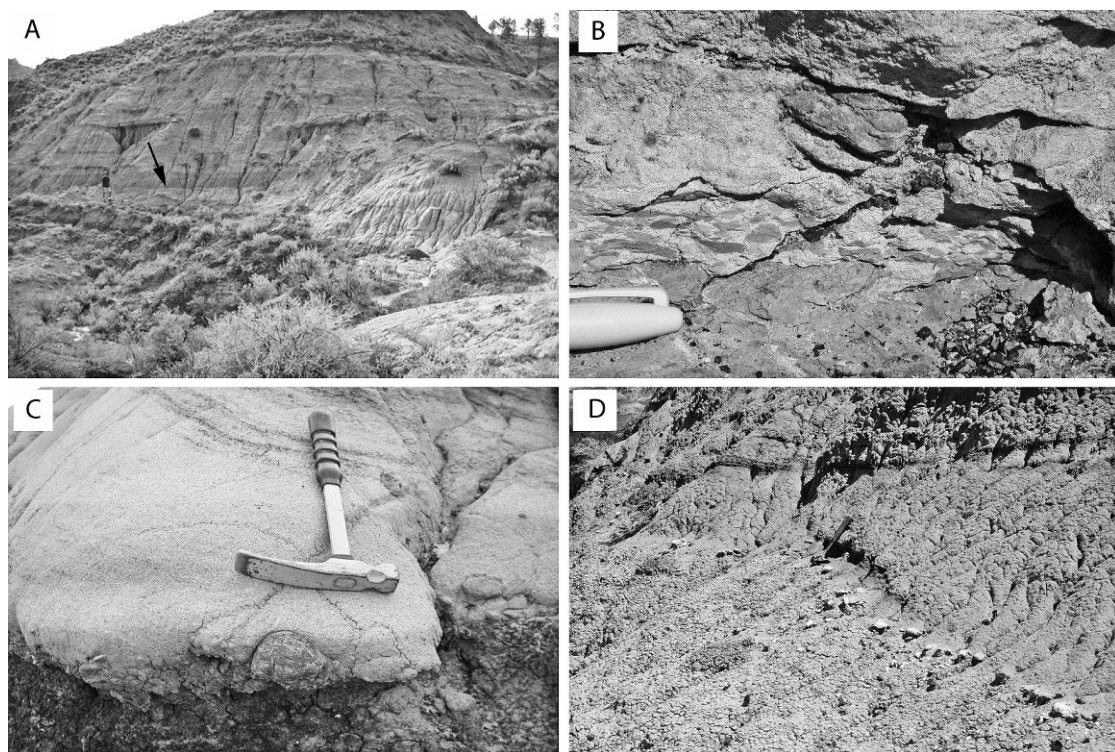
FIGURE 7. Sedimentary characteristics of channel-hosted microfossil bonebeds. A, Outcrop view of sandstone body hosting bonebed UC-8302 showing margin of channel facies (arrow) intercalated with floodplain facies. B, Claystone pebble intraclast lag associated with coaly stringers at the base of bonebed UC-942. Pen cap rests on underlying bed of carbonaceous claystone. C, Claystone pebbles associated with a large rounded ironstone pebble at the basal contact of bonebed UC-941. D, Intraclast lag of claystone pebbles and abundant intact valves of ''Unio'' at the base of bonebed UC-8322A. The basal lag of this channel deposit also yields rounded metamorphic pebbles.

can be abundant (e.g., UC-8302, UC-8322A), with the quality of preservation ranging from intact articulated valves (both closed and ''butterflied'') to shell hash. The remains of other mollusks, including *Sphaerium* and *Viviparus*, are also preserved in some localities (e.g., UC-8302), as are fine-grained steinkerns of small gastropods (e.g., UC-8325). Internal molds of bivalves have also been recovered.

Channel-hosted microfossil bonebeds yield disarticulated and dissociated hardparts of aquatic, semiaquatic, and fully terrestrial vertebrates. Fossils are generally more concentrated than they are in pond/lake bonebeds (Fig. 9A), although these bonebeds are still best characterized as comprising ''dispersed bioclastic fabrics'' (Kidwell and Holland 1991). Hardparts are localized along prominent basal and internal surfaces in sandstone bodies. For example, vertebrate fossils in UC-8302 are concentrated in the basal 30 cm of a 7-m-thick sandstone body (Fig. 9B). Fossils in UC-8325 are concentrated in a 10-cm-thick bed that overlies a through-going internal scour surface embedded in a 5-m-thick multistory sandstone body (Fig. 9C,D). Given that fossils are concentrated on surfaces or in thin intervals as opposed to dispersed more evenly throughout host lithosomes, as is the case in pond/lake bonebeds, it is difficult to derive meaningful estimates of their abundance relative to surrounding sediment. Even carefully collected bulk samples of channel-hosted bonebeds include sediment unassociated with the actual surface/interval of interest.

The preservational quality of vertebrate hardparts preserved in channel-hosted microfossil bonebeds generally parallels the condition of material recovered from pond/lake assemblages. Bioclasts range in size from sub-
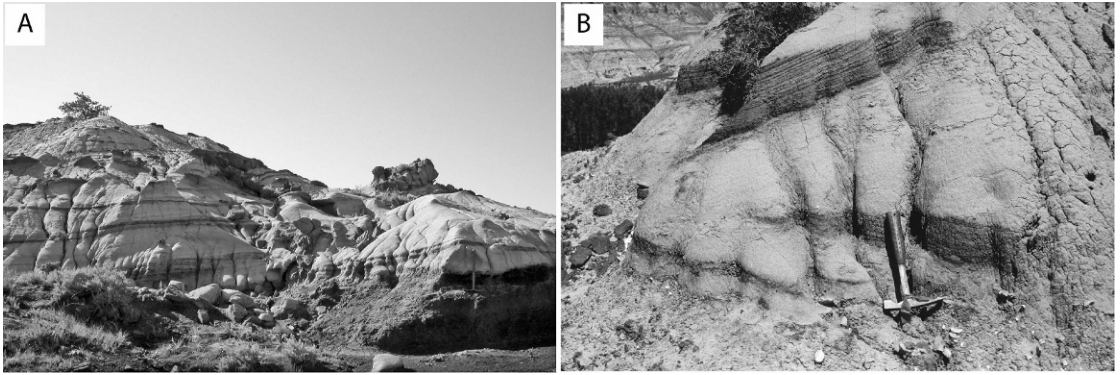
FIGURE 8. Carbon and clay drapes consistent with variable flow conditions characterize many of the sandstone bodies that preserve channel-hosted microfossil bonebeds. A, Inclined heterolithic stratification (IHS) developed in UC-941. In this view strata are dipping to the southeast. B, Carbon-draped foresets on large-scale trough cross-bed sets in UC-8322A.

millimeter to multi-centimeter, and the fine fraction is numerically predominant. Large elements such as partial dinosaur limb bones are occasionally encountered. Resilient skeletal elements (teeth, scales) are generally preserved in good quality, although they are preserved amidst plentiful skeletal material that exhibits extensive evidence of pre-fossilization breakage, abrasion, rounding, and corrosion (Fig. 10A,B). In contrast to pond/lake assemblages, many of the smaller bone pebbles recovered from channel deposits exhibit polish (e.g., UC-8302, UC-8325, UC-8439; Rogers and Kidwell 2000) (Fig. 10C,D).

Depositional Setting.—Channel-hosted microfossil bonebeds of the Judith River Formation are preserved in sandstone facies that accumulated in active channels. The abundant intraclast lags embedded in these deposits indicate that channels of the Judith River coastal plain regularly reworked underlying and laterally adjacent facies. The large-scale sets of IHS present in many deposits are interpreted as lateral accretion deposits that accumulated in channels that experienced variable flow conditions. Given the proximity of these ancient channels to the paleoshoreline, and their direct association with paralic facies (hydromorphic paleosols, lignite beds), this record of variable flow presumably reflects tidal influence in the lower coastal plain (Rogers 1998; Rogers and Kidwell 2000).

Stratigraphic Distribution of Microfossil Bonebeds

The stratigraphy of the 27 microfossil bonebeds examined in this report (Figs. 1, 2) was ascertained relative to formation contacts and a discontinuity that bisects the Judith River Formation in the type area (SB2 of Rogers and Kidwell 2000). Strata overlying the discontinuity, which were interpreted by Rogers (1995, 1998) to have accumulated during the Bearpaw transgression, preserve most of the microfossil bonebeds, with 24 of the 27 sites intercalated in transgressive-phase deposits (Fig. 11). Of the three sites positioned below the SB2 discontinuity, one is a pond/lake bonebed and two are channel-hosted bonebeds. Of the 24 bonebeds positioned above SB2, 15 are pond/lake bonebeds and nine are channel-hosted bonebeds. The stratigraphic overlap of pond/lake and channel-hosted microfossil bonebeds throughout the Judith River record has important implications for formative scenarios, and is revisited below.

Concentration of Vertebrate Microfossils

Previously Posited Modes of Accumulation

Mellett (1974) advocated a scatological origin for vertebrate microfossil assemblages and argued that most Mesozoic and Cenozoic localities are ''coprocoenoses'' that were processed through the digestive tracts of carnivores. This model was based on obser-
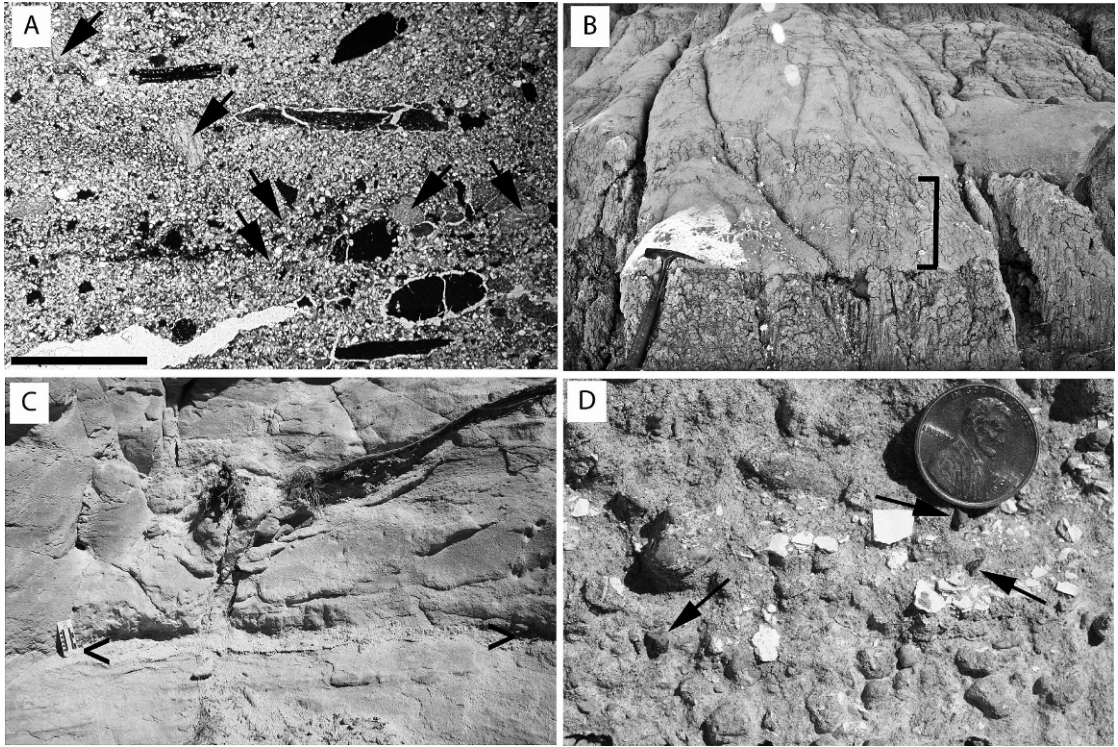
FIGURE 9.   Fossil-producing horizons in fluvial sandstone bodies are localized along prominent basal and internal scour surfaces. A, Photomicrograph of claystone pebbles, carbonaceous debris, and abundant vertebrate bioclasts (arrows) in the basal lag facies of UC-942. Scale bar, 5 mm. B, Fossil debris in bonebed UC-8302 is concentrated in the basal 30 cm of the sandstone body. C, Vertebrate fossils in bonebed UC-8325 are concentrated in a 10-cm-thick bed that overlies a through-going internal scour surface embedded within the host lithosome (brackets indicate thickness of bone-producing bed). D, Close-up view of vertebrate fossil debris (arrows), invertebrate shell debris, and claystone pebbles in UC-8325.

vations of modern small mammal bones and teeth recovered from carnivore scat, which were compared with fossil collections. Any microfossil bonebed ascribed to a predatory/ coprolitic origin should show a suite of diagnostic features consistent with this interpretation. First and foremost, animals represented in the assemblage should comprise a reasonable selection of prey species. Second, skeletal remains preserved in a carnivore-generated coprocoenosis should exhibit surface modifications consistent with mastication and gastric processing. Numerous studies have explored the end results of avian, mammalian, and crocodilian digestion in relation to the taphonomy of bones and teeth (e.g., Mayhew 1977; Dodson and Wexlar 1979; Fisher 1981a,b; Andrews and Nesbit-Evans 1983; Hoffman 1988; Andrews 1990; Kusmer 1990; Denys and Mahboubi 1992; Denys et al.

1992; Schmitt and Juell 1994; Terry 2004; Laudet and Selva 2005; among others), and these works provide criteria for differentiating the feces and regurgitate of various bone-ingesting species. Finally, a microfossil bonebed linked to a purely coprolitic origin should be preserved in a context (host facies) that would reasonably accommodate the carnivores suspected of generating the deposit and should be of a scale consistent with the localized accumulation of feces. Relatively few studies focused in ancient settings other than caves ascribe microfossil bonebeds to predatory/scatological origins (e.g., McGrew 1963; Maas 1985; Badgley et al. 1998; Vasileiadou et al. 2009).

Korth (1979) subsequently proposed that most microfossil bonebeds represent the hydrodynamic accumulation of vertebrate debris by fluvial processes based on observa-
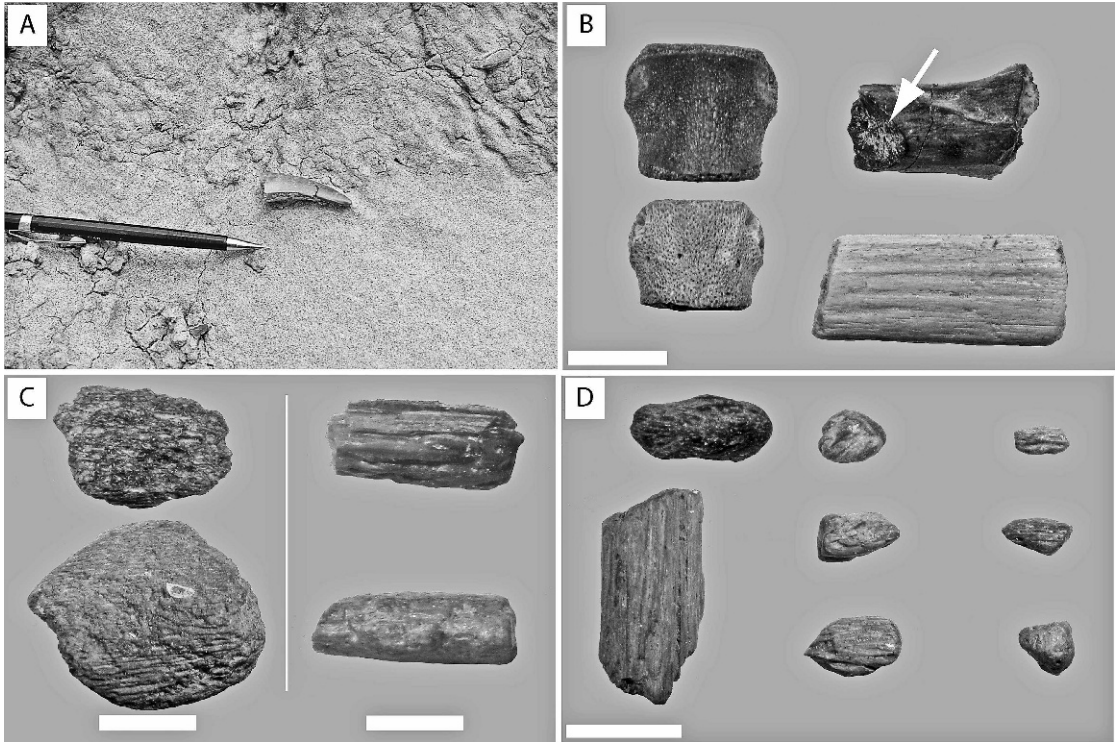
FIGURE 10. The preservational quality of vertebrate fossils in channel-hosted microfossil bonebeds generally parallels that in pond/lake assemblages. A, Theropod tooth and invertebrate shell fragment weathering from bonebed UC-919. Durable skeletal elements like this tooth are generally recovered in good quality (enamel surfaces and denticles intact), but are preserved amidst skeletal material that exhibits significant modification. B, Corrosion and breakage are common modification features in channel-hosted bonebeds. Here, centimeter-scale elements from bonebed UC-8439 exhibit loss of cortical bone, and smoothed prefossilization fractures. Arrow points to spiral fracture. Scale bar, 1 cm. C, Rounded bone pebbles from bonebed UC-8302. Larger elements on left (scale bar, 5 mm) are rounded. Smaller elements to right (scale bar, 1 mm) are rounded and polished. D, Rounded and polished bone pebbles recovered from bonebed UC-8325. Scale bar, 5 mm.

tions of modern carnivore scat, studies of bone settling rates and abrasion, and comparisons with fossil assemblages. Bonebeds of hydraulic origin should, like their coprocoenosis counterparts, be identified by diagnostic features. However, criteria used to identify such assemblages have been inferred on the basis of general expectations of fluvial systems. Actualistic studies in modern fluvial settings specifically focusing on the *accumulation* of small vertebrate elements are lacking. Nevertheless, from a taxonomic perspective, the accumulated skeletal debris should represent animals that would inhabit, or at least on occasion visit, the local environs of the river system. Bonebeds of hydraulic derivation should also presumably show physical evidence of fluvial transport. Size sorting,

abrasion, and rounding of bone material are commonly cited as features consistent with a hydraulic history (Wolff 1973; Korth 1979; Behrensmeyer 1988; Wood et al. 1988; Eberth 1990; Hunt 1991). Sedimentologic evidence consistent with the hydraulic formative scenario includes preservation in facies that exhibit indication of turbulent flow and bedload transport, and hydraulic equivalence between the bone assemblage and encasing matrix. Case studies that relegate ancient vertebrate microfossil assemblages to fluvial modes of accumulation are more common, and include Estes and Berberian (1970), Wolff (1973), Korth (1979), Wood et al. (1988), Bryant (1989), Hunt (1991), Srivastava and Kumar (1996), and Demar and Breithaupt (2006), among many others.
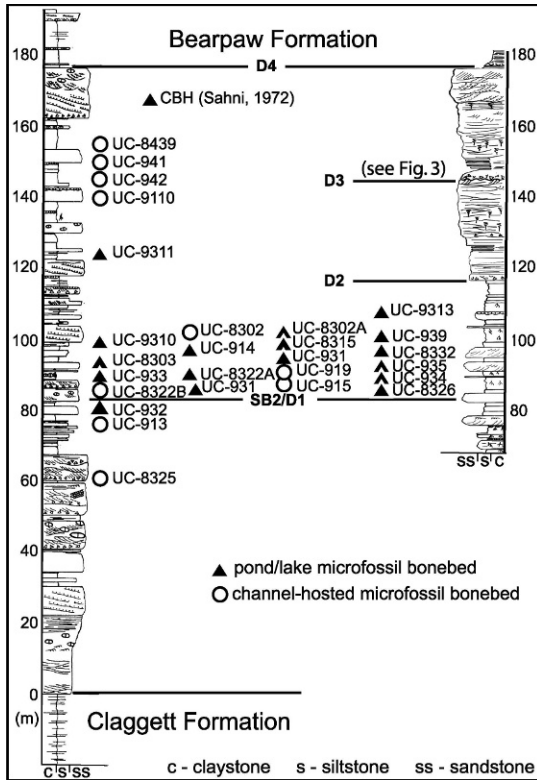
FIGURE 11. Stratigraphy of microfossil bonebeds in the Judith River Formation. Sites are positioned relative to the SB2 discontinuity, which subdivides the Judith River record into regressive and transgressive packages (Rogers 1998; Rogers and Kidwell 2000). The vast majority of sites (24/27) crop out above the SB2 discontinuity. The CBH locality, originally described by Sahni (1972) and revisited during the course of this study, is included as a pond/lake assemblage 12.5 m below the top of the formation. Of particular significance is the fact that both categories of microfossil bonebed are interstratified throughout the section. The measured section on the left is characteristic of exposures in the western portion of the type area, where nonmarine facies predominate. The section on the right is representative of exposures in the eastern half of the type area, where shallow marine strata (in this particular section D2 to D4 [see Figs. 2, 3]) constitute the upper part of the formation (Rogers 1998).

Some workers have taken a more diversified approach to the problem of vertebrate microfossil accumulations preserved in ancient channel deposits. For example, Badgley et al. (1998) proposed that localized concentrations of vertebrate microfossils in fluvial facies of the mid-Miocene Ghinji Formation of Pakistan are the product of initial biological accumulation (probably linked to predator activity) with subsequent reworking, transport, and redeposition in fluvial channels.

Eberth (1990) also proposed preconcentration of vertebrate microfossils in interchannel settings prior to reworking and entry into the active fluvial system, though no mode or specific locale of preconcentration was identified. In his study of vertebrate microfossil assemblages in the Judith River Formation of Alberta, Eberth (1990) proposed that preexisting concentrates were delivered to channels during bank collapse and erosive rip-up events. These concentrates were subsequently transported as bedload and hydrodynamically sorted. Transport of up to 10 km was deemed possible prior to final burial in fluvial facies.

Less attention has been paid to the accumulation of vertebrate microfossils in interchannel settings, with the notable exception of Bown and Kraus (1981), who examined the fossil record of the Eocene Willwood Formation and concluded that accumulations of vertebrate remains reflect a pedogenic origin (see also Schiebout et el. 2008). Bown and Kraus (1981) documented recurrent concentrations of fossils in A horizons of carbonaceous paleosols and argued that skeletal remains of large numbers of animals accumulated as attritional ''lag deposits'' on stable soil surfaces during periods of slowed sediment accumulation. Their study provided key insights into the sedimentology and taphonomy of fossil accumulations in pedogenically modified floodplain strata. Moreover, their taphonomic treatment of vertebrate fossils in the Willwood Formation provided a convincing alternative to the commonly invoked transport-based hydraulic origin for fossil deposits. However, Bown and Kraus' (1981) pedogenic model of bonebed formation did not fully address how skeletal remains from copious animals, including both terrestrial and aquatic forms, initially accumulated in close spatial proximity on alluvial soil surfaces and repeatedly survived the destructive taphonomic processes that accompany prolonged subaerial exposure.

A Critical Look at Accumulation Scenarios Based on the Judith River Record

The abundant microfossil bonebeds of the Judith River Formation afford an unparal-

leled opportunity to evaluate mechanisms of bone accumulation and bonebed formation. Here we take a critical look at microfossil bonebeds in the Judith River Formation in relation to predatory and fluvial/hydraulic mechanisms of concentration, and propose alternative scenarios that are more compatible with available data.

Evaluation of Existing Models of Bone Accumulation.—None of the bonebeds preserved in the Judith River record exhibit features compatible with a purely scatological origin. Perhaps most significantly, all sites yield assemblages of animals that cannot reasonably be interpreted as the remains of prey accumulated by any single predatory taxon. Vertebrates represented in Judith River microfossil bonebeds include fully terrestrial, semiaquatic, and aquatic forms that range from small-bodied fish, amphibians, lizards, and mammals to large-bodied crocodilians and dinosaurs (Table 3). In most sites, this diverse assemblage of vertebrates is found in direct association with the accumulated remains of invertebrates, including bivalves and gastropods.

In addition, bones and teeth preserved in Judith River microfossil bonebeds show scant evidence of carnivory (e.g., Mayhew 1977; Dodson and Wexlar 1979; Fisher 1981a,b; Andrews and Nesbit-Evans 1983; Fiorillo 1988; Hoffman 1988; Andrews 1990; Hunt 1991; Kusmer 1990; Denys and Mahboubi 1992; Denys et al. 1992; Schmitt and Juell 1994; Fiorillo et al. 2000; Ryan et al. 2001; Rogers et al. 2003). Tooth marks have been observed on a few bone fragments from UC-8303, and a few teeth and scales from UC-8303 and UC-8439 exhibit loss of enamel and ganoine (see Fig. 6F), which is consistent with passage through the digestive tracts of animals that decalcify vertebrate hardparts, such as crocodilians (Fisher 1981a). However, the vast majority of skeletal remains recovered from Judith River microfossil bonebeds show no indication of processing by carnivores.

Lastly, the spatial scales of most microfossil bonebeds documented in the Judith River record are far too great to represent the localized accumulation of feces or bone-infused regurgitate unless additional steps are invoked to disaggregate and widely disperse hardparts. Along these same lines, the bonebeds under investigation are also generally too expansive to accommodate serial predation in a spatially focused killing arena (Haynes 1988).

With regard to the fluvial/hydraulic model of bonebed formation, 16 of the 27 bonebeds examined in this study (Table 1) can be eliminated from consideration because they are not hosted in fluvial sandstones and are thus sedimentologically incompatible with this mode of accumulation. The remaining bonebeds fulfill the basic sedimentologic expectation in that they are embedded within the deposits of ancient fluvial channels. These same bonebeds also exhibit at least some of the proposed taphonomic attributes for fluvial/hydraulic accumulations (Korth 1979; Shipman 1981; Behrensmeyer 1982, 1987, 1988; Eberth 1990). For example, many bones, especially those in the bone sand/bone pebble category, show evidence of abrasion/corrosion, rounding, and the removal of cortical bone. However, many of the bones preserved in pond/lake bonebeds are also highly degraded and are preserved in a taphonomically comparable fashion (Fig. 6E). Given the abundance of abraded/corroded and sub-rounded to rounded bone pebbles in both pond/lake and channel-hosted assemblages, these modification features are equivocal indicators of transport and hydraulic accumulation.

In contrast, reflective polish does seem to be a distinctive characteristic of bone pebbles preserved in some channel-hosted microfossil bonebeds in the Judith River record (Fig. 10C,D). However, exactly how and when polish was imparted is unknown, and thus it seems presumptive to conclude that this modification feature reflects long-distance transport of bioclasts to the site of final burial. It is equally likely that polish was imparted to bone pebbles at the burial site, where small bioclasts may have taken on polish as they oscillated and jostled about with silt and sand in the boundary layer and in flow shadows (e.g., troughs of bedforms). Prefossilization of reworked elements may have enhanced the potential for elements to take on polish (Rogers and Kidwell 2000).
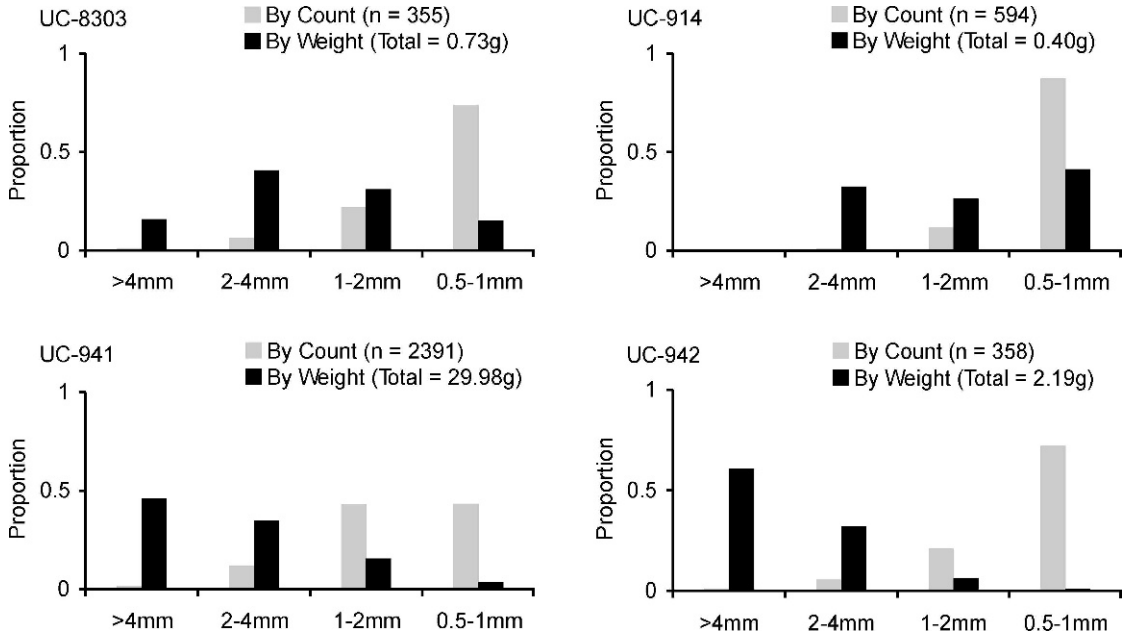
FIGURE 12. Size sorting of vertebrate hardparts (including unidentifiable bone fragments) in pond/lake (UC-8303 and UC-914) and channel-hosted (UC-941 and UC-942) microfossil bonebeds. Gray bars reflect counts of individual particles in each size class. Black bars reflect weight percent of vertebrate material in each size class. These two metrics yield very different views of size sorting in microfossil bonebeds. This is particularly evident in the channel-hosted assemblages where the size distribution is left-skewed when based on counts and right-skewed when based on weight percentages in each size class.

Evidence of sorting is another taphonomic attribute that has been linked to fluvial accumulations of vertebrate bioclasts, with the general assumption that hydraulic processes in surface flows act to sort vertebrate skeletal debris in relation to size, shape, and/or density as material is transported to the site of final burial. This premise has been explored in numerous studies that examine the transport and dispersal of bone in response to unidirectional flows (Voorhies 1969; Dodson 1973; Behrensmeyer 1975; Korth 1979; Hanson 1980; Frison and Todd 1986; Argast et al. 1987; Aslan and Behrensmeyer 1996; Blob 1997; Trapani 1998), and evidence of sorting has been used in studies of ancient bonebeds to infer transport-related accumulation scenarios. For example, Eberth (1990: p. 15) measured the maximum dimensions of 51 compact elements selected from a channel-hosted microfossil bonebed (BB 94) in the Dinosaur Park Formation and determined that the assemblage was moderately sorted. This in turn was used to argue that the assemblage experienced hydraulic transport prior to final burial.

We sieved small samples of bioclasts from known quantities of matrix in order to calculate sorting values for two channel-hosted bonebeds (UC-941 and UC-942) that had potential to be fluvially transported and/or winnowed. For purposes of comparison, we also sieved two pond/lake bonebeds (UC-914 and UC-8303), because these bonebeds were presumably not subject to fluvial currents (Fig. 12). For each site we determined the degree of sorting for all elements recovered by calculating the inclusive graphic standard deviation according to weight percent of bioclasts in different size classes (Folk 1980). Populations of bioclasts derived from the two channel-hosted bonebeds ranged from moderately well sorted (0.64 ϕ) in UC-941 to well sorted (0.44 ϕ) in UC-942. Populations of bioclasts derived from the pond/lake bonebeds were poorly sorted, with sorting values of 1.13 ϕ (UC-8303) and 1.09 ϕ (UC-914). Differences in sorting between the two types of bonebeds reflect a lower weight proportion of the finest fraction in the channel-hosted assemblages. However, all

four sieved samples still contain abundant bioclasts in the ≤2 mm size range, and when considered in terms of the numerical abundance of material in each size class (as opposed to weight proportion of each size class), the sorting is bimodal (sensu Kidwell and Holland 1991: p. 429) with ''a few large bioclasts loosely packed or dispersed among a multitude of significantly finer bioclasts.'' To further characterize the nature of channel-hosted sites, the hydraulic equivalence of bioclasts in bonebed UC-941 was assessed on the basis of particle volume, weight, and settling velocity (following methods outlined in Behrensmeyer 1975). Estimated quartz equivalents range from fine sand to small pebbles. Taken together, these various considerations are arguably consistent with the winnowing of preexisting accumulations of bioclastic material, rather than piecemeal accumulation and sorting due to long-distance fluvial transport.

Finally, most studies that link microfossil bonebeds to a fluvial/hydraulic mode of accumulation posit that vertebrate remains were (1) transported predominantly as bed-load (more rarely as suspended load [see Demar and Breithaupt 2006]) through a fluvial system (e.g., Wolff 1973; Wood et al. 1988), and (2) deposited in a localized area within this same fluvial environment. Unless a preexisting source of concentrated remains is explicitly proposed (e.g., Badgley et al. 1998; Eberth 1990), the bioclasts in question (be they carcasses, parts of carcasses, or single bones and bone fragments) are generally assumed to have entered the fluvial system from different places at different times (Korth 1979; Hanson 1980). From a practical standpoint, it is difficult to envision a river within which the millimeter-scale to multi-centimeter-scale bones and teeth of widely different types of animals introduced from widely separated point sources at different times would travel downstream through a complex channel belt and accumulate in localized pockets that yield thousands of elements. It is much more likely that bones, bone fragments, teeth, and scales, once entrained in a flow, would tend to disperse over time in relation to differences in size, shape, and

density. Any accumulation scenario that invokes significant transport of microfossil-scale vertebrate remains derived from disparate non-contemporaneous sources is highly improbable.

Revised Model for Microfossil Bonebeds

Given the considerations outlined above, microfossil bonebeds of the Judith River Formation cannot be attributed to either scatological or transport-based hydraulic origins (sensu Mellett 1974; Korth 1979). Instead, we envision a path to hardpart concentration that hinges upon the ecology and taphonomy of lacustrine ecosystems and the dynamics of aggrading, avulsion-prone fluvial systems.

Step 1: Attritional Accumulation in Freshwater Aquatic Basins.—First, with regard to pond/lake microfossil bonebeds, data are consistent with the in situ accumulation of skeletal debris via attritional mortality in long-lived aquatic ecosystems characterized by relatively low rates of net sedimentation. Ground truth for this attritional mode of accumulation comes from marine records, where hiatal concentrations of shell debris and vertebrate hardparts are documented (e.g., Sykes 1977; Kidwell 1993; Macquaker 1994; Brett 1995; Abbott 1998; Gillespie et al. 1998; Kondo et al. 1998; Conkin et al. 1999; Turner et al. 2001; Allulee and Holland 2005; Irmis et al. 2007; Pyenson et al. 2009). In marine settings, the supply of skeletal debris generated during hiatus apparently counteracts the negative aspects of delayed permanent burial. In theory, the same should hold true in terrestrial depositional systems, where conditions of low net sedimentation should also create conditions of low sedimentary dilution relative to the yield of skeletal material produced by contemporaneous animal populations (Behrensmeyer and Chapman 1993). However, well-substantiated examples of passive attritional assemblages from terrestrial settings are rarely described (Bown and Kraus 1981; Khajuria and Prasad 1998; Dyke and Malakhov 2004; Carrano and Velez-Juarbe 2006; Buscalioni et al. 2008), and this is not entirely unexpected, given the harsh conditions that can accompany bone exposure on

the land surface and pedogenesis during early burial (Behrensmeyer 1978; Behrensmeyer and Chapman 1993).

Despite potential factors that might inhibit the passive accumulation of skeletal debris in terrestrial systems, the pond/lake bonebeds of the Judith River record do apparently preserve hiatal concentrations of vertebrate and invertebrate hardparts in fully nonmarine facies. We propose that this reflects the alignment of multiple factors conducive to both the initial accumulation and the long-term preservation of biological materials in low-energy aquatic settings. Focusing first on the supply side of the equation, freshwater ecosystems today tend to be highly productive and can support large localized populations of aquatic and semiaquatic vertebrates and invertebrates (Froese and Burghardt 1975; Wetzel 2001; Gibbons et al. 2006; van der Valk 2006). They also tend to attract terrestrial animals to their shores and shallows for purposes of drinking, feeding, and wallowing. Over time, many generations of animals will inevitably contribute their skeletal hardparts to localized death assemblages. Mortality is generally assumed to be attritional, with animals perishing due to a variety of natural causes, including disease, predation, trauma, and senescence. It is also plausible that events of mass mortality could contribute to an otherwise attritional assemblage accruing in a pond or lake (e.g., Khajuria and Prasad 1998). However, there is no need to invoke mass mortality specifically, and given the taphonomic condition of microfossil bonebeds (see above), it would be difficult to distinguish mass death from other modes of mortality. Finally, it is important to note that the living can also contribute to the accumulating skeletal assemblage, specifically in the form of shed teeth, which are commonly recovered from pond/lake bonebeds of the Judith River Formation.

In our model, the attritional input of biological material outpaces the masking effects of sedimentation in lacustrine settings, and vertebrate remains accumulate to concentrated levels characteristic of a bonebed (Rogers et al. 2007; Buscalioni et al. 2008). Whether this in fact transpires would depend upon several additional factors, including the long-term balance of sediment yield versus biological input and the efficiency of taphonomic agents that degrade and destroy skeletal material (e.g., biological recycling, chemical dissolution). With regard to net sedimentation in the Judith River Formation, radioisotopic ages recently obtained from bentonite beds that bracket the upper ~100 m of the unit (R. Rogers and A. Deino unpublished data) suggest rock accumulation rates on the order of ~12.5 cm/1000 years. This average rate of sedimentation and thickness data derived from 16 pond/lake microfossil bonebeds (Table 1) suggest that the ancient wetlands of the Judith River coastal plain could have persisted for many hundreds to thousands of years. This estimate of lake longevity is consistent with reconstructions reported for modern floodplain lakes (Eckblad et al. 1977; Holland and Burk 1982; Räsänen et al. 1991; Citterio and Piégay 2009) and is arguably expansive enough to accommodate an attritional model of hardpart accumulation.

Even if organic hardparts do accumulate to appreciable quantities within the fill of a slowly aggrading pond or lake, taphonomic conditions must still be conducive to long-term preservation and eventual fossilization. Taphonomic processes heavily affected the bioclasts that accumulated in pond/lake microfossil bonebeds. Vertebrate skeletal debris is thoroughly disarticulated (with very rare exceptions) and dissociated, and the vast majority of well-preserved material can be categorized as durable and robust (small compact elements, teeth, scales). Biological activity in the form of bioturbation is viewed as a first-order taphonomic agent in these ancient lacustrine systems, with a wide variety of animals (e.g., annelids, arthropods, mollusks, vertebrates) churning and disrupting the lake sediments for various reasons (locomotion, nesting, aestivation). This in turn would cause breakage, fragmentation, disarticulation, and dispersal of skeletal debris. The ongoing effects of bioturbation would be enhanced by feeding activity (including scavenging), which would serve to further degrade and disperse biological remains. The

chemistry of lake and pore waters would also play a critical role, and although there is some indication of corrosion on bone surfaces, the abundance of carbonaceous debris and the occurrence of both calcitic and aragonitic shells indicate that pH and Eh conditions were generally favorable (Table 1).

Step 2: Preexisting Concentrations Reworked by Fluvial Channels.—With pond/lake microfossil bonebeds in place (accumulating in aquatic settings on contemporaneous land surfaces and embedded in near-surface strata), channel-hosted microfossil bonebeds would be an expected outcome of rivers reworking subjacent and laterally disposed fossil-rich facies on the Judith River coastal plain. The conceptual basis for this exhumational model of accumulation resides in the basic dynamics of fluvial systems. Modern channels erode and rework associated floodplain deposits, and materials originally embedded within the floodplain often accrue as localized conglomerates or ''lags'' within channel facies (Koster 1987; Behrensmeyer 1982, 1988; Lofgren et al. 1990). This model of bonebed formation generally parallels Eberth's (1990) proposal that preexisting concentrates of vertebrate hardparts were delivered to rivers during bank collapse and erosive rip-up events, thus forming the numerous ''in-channel intraclast bonebeds'' of the Dinosaur Park Formation (see p. 15 of Eberth's report for a list of criteria consistent with this reconstruction). Here we refine a key component of Eberth's (1990) model by identifying viable preexisting sources in the form of pond/lake bonebeds. These potential source beds are notably abundant and recurrently interstratified with fluvial facies that yield microfossil bonebeds (Figs. 1, 11). Moreover, because they formed in low-lying (inundated) regions of the Judith River floodplain, pond/lake assemblages accumulated where new flow paths were most likely to be established upon avulsion (Aslan and Blum 1999; Slingerland and Smith 2004; Jerolmack and Paola 2007). Thus, the pond/lake microfossil bonebeds of the Judith River Formation were not only abundant sources of concentrated skeletal material, they were also prime targets for fluvial incision in the avulsing alluvial system.

Our model diverges from most previous taphonomic reconstructions of channel-hosted microfossil bonebeds, however, in that we interpret the accumulations of vertebrate hardparts preserved in channel facies as essentially in place, at least in a purely spatial sense. Taphonomic data used to invoke transport, such as abrasion, rounding, and size sorting, are ambiguous in the Judith River bonebed record (see above). Without compelling evidence indicative of transport, it is more parsimonious to conclude that channel-hosted microfossil bonebeds accumulated in close proximity to source beds (meters to perhaps tens of meters downstream). Reworked bioclasts potentially moved short distances as bedload upon entering the channel, but were buried before traction currents could disperse them. It should be further noted that we recognize that channel-hosted assemblages may be somewhat winnowed in relation to their pond/lake source assemblages. This is consistent with data presented above (Fig. 12) that suggest that at least some channel-hosted microfossil bonebeds are better sorted than pond/lake counterparts. Moreover, despite close proximity to source beds, channel-hosted assemblages are by definition allochthonous (Kidwell et al. 1986), given that they are reworked out of life habitats and preserved in facies foreign to the original site of accumulation.

Reconciling the Model with the Judith River Record.—Several additional lines of evidence are consistent with the revised model of bonebed formation presented herein. A stratigraphic observation that lends credence to the model relates to the association of bonebeds and discontinuity surfaces (Rogers and Kidwell 2000). Channel-hosted microfossil bonebeds are not randomly distributed in channel facies of the Judith River Formation, but instead show a recurrent association with basal contacts and internal bounding surfaces in multistory deposits (Table 2). This association indicates that bonebeds developed shortly after channels reestablished themselves in new regions of the floodplain or in previously aban-
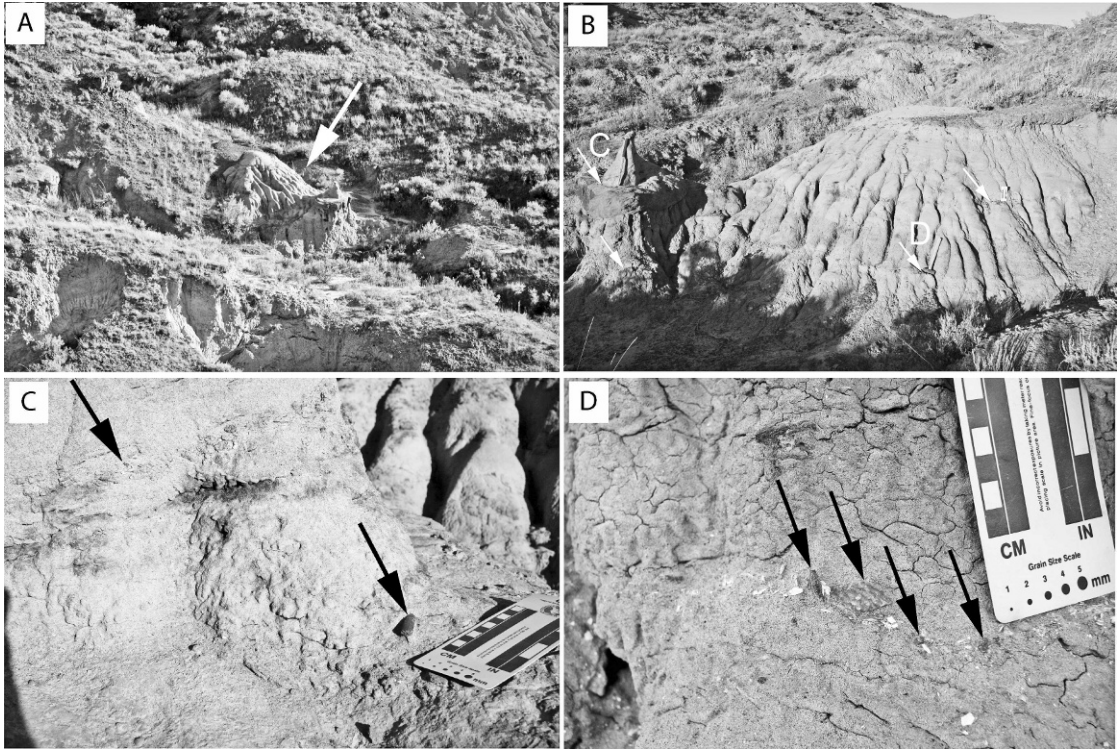
FIGURE 13. Field views of the channel-hosted bonebed UC-8439. A, The UC-8439 locality (arrow) is exposed only locally as a small rounded knob. B, Vertebrate fossils occur along the basal contact and mantle at at least three discrete set boundaries (arrows indicate local stringers of vertebrate bioclasts). The recurrence of vertebrate bioclasts, claystone pebbles, and plant debris on successive set boundaries is interpreted to reflect the reworking of a nearby source bed (pond/lake bonebed) that supplied the channel belt over time. C, Close-up of vertebrate fossils (arrows) in vicinity of arrow C in image B. D, Close-up of vertebrate fossils (arrows) in vicinity of arrow D in image B.

doned channel belts (in multistory sandstone bodies). This in turn is not only compatible with a reconstruction that hinges upon the reworking of preexisting deposits, but further indicates that channel-hosted microfossil bonebeds developed during episodes of significant erosion and geomorphic adjustment in the alluvial system. The alternative transport-based model of attritional bioclast accumulation in fluvial channels fails to explain the recurrent association of channel-hosted bonebeds and major fluvial bounding surfaces.

Shifting focus to individual localities, two channel-hosted bonebeds in particular provide significant support for this revised view of bonebed formation. The first, UC-8439 (Table 2), is a 3.2-m-thick fine-grained sandstone body characterized by medium- to large-scale trough cross-bedding. The UC-

8439 locality is limited in expanse and crops out locally as a small rounded exposure. Vertebrate fossils drape the basal contact and also mantle three discrete set boundaries intercalated within the host lithosome (Fig. 13). The recurrence of vertebrate bioclasts, claystone pebbles, and plant debris on successive set boundaries is interpreted to reflect the reworking of a nearby source bed (pond/lake bonebed) that supplied the channel belt over time. Bioclasts were presumably delivered to the active channel from an eroding source immediately upstream, and skeletal material accumulated in scour pits and was buried by advancing dunes as the channel filled. An alternative and much less plausible explanation would be that bones, teeth, and other assorted skeletal remains from multiple unrelated sources were common as bedload in the aggrading stream and
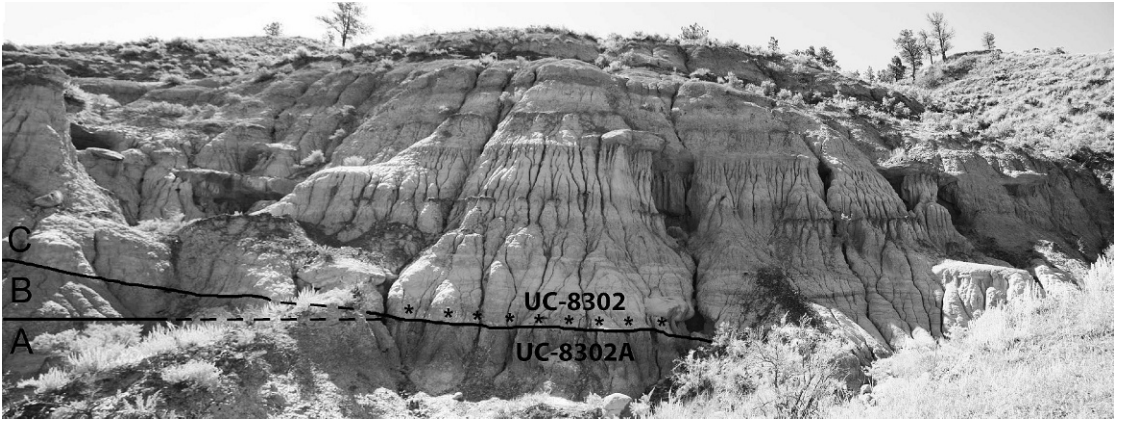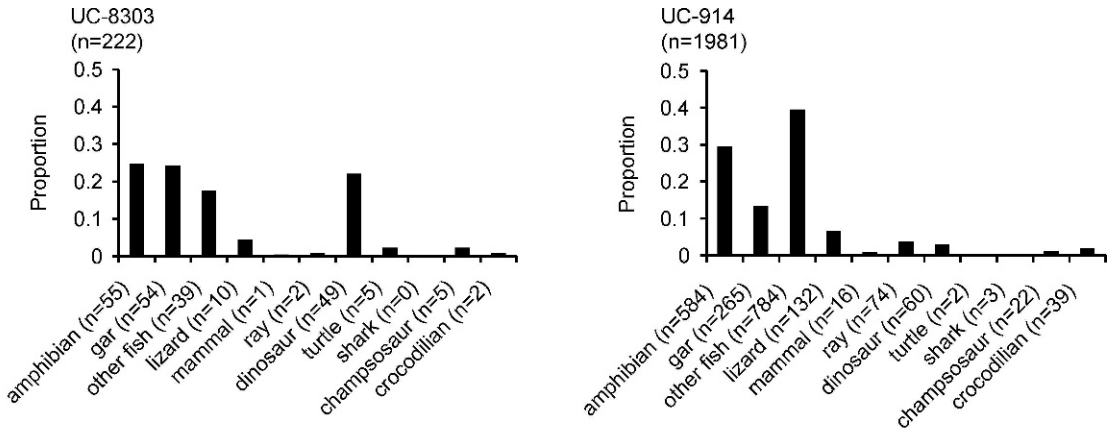
FIGURE 14. Field view of bonebeds UC-8302 and UC-8302A. The sandstone body hosting UC-8302 erodes down through several meters of fine-grained interchannel facies (including the full thickness of bed B), and in its most fossiliferous expanse (indicated by asterisks) intersects carbonaceous facies of pond/lake microfossil bonebed UC-8302A. This field relationship provides direct evidence for the erosional reworking of a preexisting pond/lake bonebed by a superjacent channel deposit. The UC-8302 lithosome continues downcutting to the right (contact obscured by vegetated slope in foreground).

accumulated as thin local pavements in the lee of advancing dunes in the same localized stretch of the channel. This scenario is unlikely given the general dearth of vertebrate fossils in background fluvial facies and the absence of apparent trapping mechanisms or other features that make these particular cross-bed sets unique.

A second channel-hosted microfossil bonebed, UC-8302 (Table 2), provides direct evidence for the erosional reworking of a preexisting bonebed. The UC-8302 bone assemblage is localized in the lower 30 cm of a 7-m-thick fine-grained sandstone body (see Fig. 9) characterized by low-angle inclined sets of massive to faintly cross-stratified sandstone. Vertebrate fossils are preserved in association with abundant ''Unio'' debris, fragmentary shells of smaller freshwater invertebrates (*Sphaerium* and *Viviparus*), ironstone and claystone pebbles, and coaly stringers. The sandstone body hosting UC-8302 erodes down through several meters of fine-grained interchannel facies, and in its most fossiliferous expanse intersects another microfossil bonebed, UC-8302A (Fig. 14). UC-8302A is a 45-cm-thick pond/lake bonebed (Table 1) that preserves dispersed vertebrate fossils in a massive clay-rich siltstone matrix that also yields abundant carbonaceous debris and the shells and shell fragments of *Sphaer-*

ium, *Viviparus*, and other small freshwater invertebrates. On-going research examining authigenic mineralization and the distribution and concentration of rare earth elements in fossils from numerous microfossil bonebeds in the Judith River Formation, including UC-8302 and UC-8302A, indicates that these two localities are indistinguishable from a diagenetic perspective (Dwyer et al. 2004; Harwood et al. 2005; Canavan et al. 2008). This in turn suggests that the vertebrate fossils in UC-8302A may have been fossilized prior to reworking and incorporation into UC-8302 (Trueman 2007).

Finally, significant taxonomic overlap would be expected if channel-hosted microfossil bonebeds were derived from preexisting pond/lake assemblages. Field observations and surface collection of material accruing on weathered surfaces indicate that the same broad taxonomic groups characterized by centimeter-scale elements (e.g., dinosaur, champsosaur, crocodilian, turtle, gar) are indeed represented in every microfossil bonebed investigated in this study. To determine relative proportions of all vertebrate taxa represented in these sites, including those with millimeter-scale elements, samples must be carefully screen washed and sorted under the microscope. Screen-washed samples from two channel-hosted sites (UC-8439,
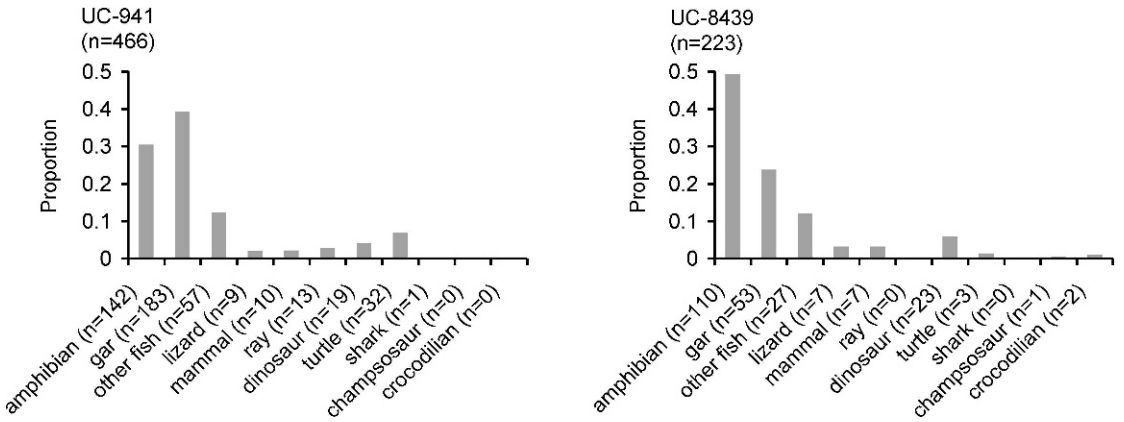
FIGURE 15. Proportional abundance and rank order correlation of major taxonomic groups in four microfossil bonebeds (pond/lake, UC-8303 and UC-914; channel-hosted, UC-941 and UC-8439). In each histogram the first six taxa (amphibian through ray) generally contribute sub-centimeter-scale elements, whereas the last five taxa (dinosaur through crocodilian) generally contribute centimeter-scale elements to the assemblage. Note significant overlap in taxonomic representation and rank-order abundances among the pond/lake localities and the channel-hosted localities and, in particular, the similar relative proportions of taxa that contribute small (sub-centimeter-scale) versus large (centimeter-scale) elements. The correlation table (middle) reports Spearman r-values for correlations among all possible pairwise comparisons. Note that correlations between rank order of sites from the same depositional setting (pond/lake or channel) are not higher than correlations between rank order of sites from different depositional settings (pond/lake versus channel). Within depositional setting comparisons: average Spearman r = 0.75. Between depositional setting comparisons: average Spearman r (of statistically significant correlations) = 0.73. (*Rank-order correlation $p < 0.05$; **Rank order correlation $p < 0.01$.)

UC-941) and two pond/lake localities (UC-8303 and UC-914) were compared with regard to the rank-order abundance of represented taxa. These four localities were previously collected and characterized by Blob et al. (1997) and Carrano et al. (1997), who assigned fossils to general taxonomic catego-

ries and estimated abundance from counts of identifiable specimens (NISP) (Fig. 15). This basic counting protocol is appropriate for disarticulated and thoroughly dissociated assemblages, such as those derived from Judith River microfossil bonebeds (Badgley 1986). However, this method of counting

individuals does not ensure that the reconstructed abundances precisely track the true relative abundance of taxonomic groups in the living populations. For example, upon fragmentation some taxa may be more likely to yield diagnostic specimens than others (Blob and Fiorillo 1996; Blob and Badgley 2007), and this can lead to erroneous inflation or underestimation of certain taxonomic groups.

However, this potential complication is not a problem for the purposes of this study because we are not attempting to reconstruct the actual nature of the living communities. Our goal is simply to test whether pond/lake assemblages are viable sources for the vertebrate fossils commonly preserved in channel-hosted assemblages. If the concentrations of skeletal material in the channel-hosted bonebeds were in fact reworked from preexisting pond-lake assemblages, we would expect significant correlation between the rank order of taxa in these two settings, and perhaps a potential deficit in the abundance of taxa with the smallest elements (due to winnowing in the channel environment). On the other hand, if the channel-hosted assemblages are in fact composed of hydraulically sorted skeletal material that was transported from multiple point sources prior to final accumulation, we would not expect significant correlation between the rank order of taxa in the channel-hosted deposits versus the pond/lake deposits.

Spearman Rank Correlation reveals that the rank-order abundances of taxa in the four microfossil bonebeds in question (UC-8439, UC-941, UC-8303, UC-914) cannot be distinguished from each other in relation to depositional setting (channel versus pond/lake). In fact, the two pond/lake bonebeds are no more similar to each other in terms of rank-order abundance than either is to the two channel-hosted bonebeds, and vice versa (Fig. 15). Moreover, there is no evidence of a proportional decrease in taxonomic groups whose elements are typically sub-cm scale (amphibians, fish, mammals) when the two pond/lake localities are compared with the channel-hosted localities, indicating that the two assemblage types are capturing both similar overall proportions of taxa and similar overall size distributions of animals. Finally, regardless of similarities in taxonomic rank order and proportions, all taxonomic groups represented in the channel-hosted bonebeds are also found in the pond/lake bonebeds. These results are consistent with a scenario in which the vertebrate material in channel-hosted localities has been drawn from preexisting pond/lake assemblages.

Discussion

Paleobiological Implications

The foregoing considerations have significant implications for the paleobiologist, particularly in relation to studies of vertebrate paleoecology. First, with regard to pond/lake microfossil bonebeds, the proposed model of accumulation yields assemblages of fossils derived from local communities of animals that inhabited ancient aquatic ecosystems and nearby terrestrial environs. The assemblages are parautochthonous (sensu Kidwell et al. 1986) because all included remains are native to the environment represented by the host facies (animals lived in, or regularly visited, the ancient aquatic locale). There is no indication of postmortem transport into or out of the local habitat, and any dispersal of remains presumably reflects small-scale disturbances related to bioturbation and similar local effects (e.g., scattering due to feeding).

Some degree of time-averaging is by definition developed in the attritional pond/lake microfossil bonebeds of the Judith River Formation. Skeletal material derived from the local community presumably accumulated during the time it took for the encasing bed to form. Skeletal hardparts accrued over time spans that potentially extended thousands of years, and multiple generations of animals are likely incorporated in the typical pond/lake assemblage. This temporal averaging of biological remains limits the degree to which researchers can address short-term ecological phenomena (e.g., age profiles of standing populations, feeding ecology). These limitations are balanced by the fact that the within-habitat time-averaging characteristic of these bonebeds increases the likelihood of recovering both ecologically abundant species and

more rare or transient members of the paleocommunity (Kidwell and Flessa 1996). Pond/lake microfossil bonebeds of the Judith River Formation yield diverse assemblages of fossils that provide insight into overall membership of Late Cretaceous communities developed around low-energy aquatic ecosystems. When sampled in a standardized fashion (Jamniczky et al. 2003), these same bonebeds should also yield robust collections suitable for estimating relative abundance, at least when considered in a broad ecosystem-scale sense (e.g., Carrano and Velez-Juarbe 2006). When placed in stratigraphic context, the abundant pond/lake microfossil bonebeds of the Judith River record also afford an excellent opportunity to track community composition and ecological associations through time in relation to environmental factors, such as climate and shifting proximity to paleo-shorelines.

The parauthochthonous nature of the pond/lake bonebeds in the Judith River record contrasts with the allochthonous condition of the channel-hosted bonebeds with which they are commonly intercalated. These in-channel assemblages are decidedly out of place from a paleoenvironmental perspective because they are reworked from preexisting pond/lake facies and redeposited in younger channel facies. However, despite a history of exhumation and redeposition, channel-hosted microfossil bonebeds are almost certainly preserved in relatively close spatial proximity to original source beds. Thus, instead of preserving hydraulically transported remains of animals that have traveled long distances and different paths to their eventual site of accumulation, channel-hosted microfossil bonebeds of the Judith River record preserve minimally transported assemblages of fossils that initially accumulated together in localized interchannel settings.

This view of channel-hosted microfossil bonebeds arguably necessitates a reevaluation of previous studies that interpret channel-hosted microfossil bonebeds as transported and hydrodynamically sorted deposits (e.g., Dodson 1971; Wolff 1973; Korth 1979; Wood et al. 1988; Bryant 1989). Moreover, it renders problematic an a priori assumption that fossils recovered from channel-hosted microfossil bonebeds necessarily represent a sample of animals that lived within or frequented active channel belts. That said, this model of fossil accumulation actually enhances our ability to accurately reconstruct aspects of ancient terrestrial ecosystems by clarifying the likelihood that channel-hosted microfossil bonebeds are, at least in some cases, subsamples of parautochthonous pond/lake assemblages. If this taphonomic reconstruction is correct (and it needs additional ground truth in both the ancient and modern), faunal data derived from channel-hosted assemblages can be used (albeit with some caution, given the effects of winnowing and potential addition of exotic bioclasts) to supplement and expand studies of interchannel pond/lake ecosystems. Preliminary data (Fig. 15) show that the relative ranking of major taxonomic groups is consistent across depositional environments, suggesting that channel-hosted assemblages do capture the relative abundance structure of the pond/lake assemblages from which they are apparently derived.

Taphonomic and
Sedimentologic Considerations

From a taphonomic standpoint, our findings provide a reasonable solution to the problem of how microfossil bonebeds develop in terrestrial depositional systems, and this is significant because existing literature, with a few notable exceptions, is often vague with regard to the critical question of how vertebrate microfossil concentrations initially accumulate. With the abundant microfossil bonebeds of the Judith River Formation contextualized in a sound taphonomic and sedimentologic framework, it is possible to delve deeper and explore more detailed aspects of their taphonomic history. For example, with the starting points of their taphonomic history clarified, we can now better explore the effects of fluvial processes on reworked vertebrate assemblages, and we can do so with many independent samples. We can also now potentially assess the timing of fossilization in alluvial successions by comparing diagenetic signatures of fossils preserved in pond/lake and channel-hosted

assemblages. Specifically, by focusing on rare earth elements and authigenic cements, we might be able to elucidate whether the bones and teeth that constitute these assemblages were reworked in a pre-fossilized condition, or whether they entered fluvial systems as unaltered bioclasts. Moreover, we can explore the uptake of the rare earth elements relative to the emplacement of authigenic cements in both depositional contexts, and thus better appreciate some of the intricacies of key diagenetic processes that encourage the long-term preservation of vertebrate hardparts.

With taphonomic histories clarified, we can further suggest basic guidelines for stable isotope-based inquiries into past climates and hydrological regimes that hinge on the paleoenvironmental context of the fossils from which geochemical data are drawn. For example, in the Judith River record, vertebrate microfossils recovered from fluvial sandstones would not necessarily be expected to hold isotopic records that reflect fractionation in rivers that drained distant mountainous terrain. The animals that yielded the biological remains in question potentially lived and died in interchannel settings where the isotopic signature of surface waters would differ from that expected in streams sourced in high-altitude locales (Fricke 2007). Work focusing on the taphonomy and geochemistry of microfossil bonebeds in the Judith River record is ongoing (Dwyer et al. 2004; Harwood et al. 2005; Rogers et al. 2005; Fricke et al. 2008; Koenig et al. 2009).

It is also possible to advance our understanding of sedimentation in terrestrial depositional systems through the analysis of microfossil bonebeds. For example, why are some vertebrate-bearing formations characterized by few, if any, microfossil bonebeds (e.g., Two Medicine Formation of Montana, Ischigualasto Formation of Argentina, Maevarano Formation of Madagascar) whereas others, such as the Judith River and Hell Creek Formations of Montana (and equivalent units in Canada), are notably enriched with this distinctive type of skeletal concentration? Presumably there are discernable patterns in sedimentation and facies distribu-

tions in alluvial records that track the overall abundance of microfossil bonebeds on the formation scale (e.g., Eberth 1990; Rogers 1993; Rogers and Kidwell 2000). Narrowing the focus to the Judith River record, why do some beds host vertebrate microfossil assemblages while others seemingly identical from a sedimentological perspective yield few, if any, vertebrate fossils? With regard to pond/lake microfossil bonebeds, the abundance of vertebrate skeletal debris could potentially be tracked as a means of comparing relative rates of sedimentation in aquatic depositional systems (other variables held equal), with the premise that lower net rates of sedimentation will foster richer concentrations of vertebrate debris. Analyses of channel-hosted microfossil assemblages could yield data that relate to stream competence, and at a grander scale, the abundance of channel-hosted assemblages relative to pond/lake assemblages could be assessed in relation to channel patterns, avulsion frequency, and subsidence history.

Conclusion

This study examined the question of how small vertebrate bioclasts accumulate to form microfossil bonebeds in alluvial records. Multiple lines of evidence, based on the analysis of microfossil bonebeds in the Judith River Formation of Montana, were brought to bear on this question. The model developed herein describing the origins of microfossil bonebeds is parsimonious (only one initial mode of accumulation is hypothesized) and grounded in reasonable taphonomic expectations of lacustrine and fluvial depositional systems. It arguably provides a solution to the problem of recurrently amassing vast quantities of taxonomically diverse biological remains in localized deposits. Moreover, it provides guidelines for framing paleoecological studies of microfossil bonebeds and suggests future lines of taphonomic inquiry that will enrich our understanding of how vertebrate remains in alluvial settings endure destructive postmortem processes and enter the fossil record.

Finally, this taphonomic study of microfossil bonebeds has elucidated general patterns

in the vertebrate fossil record that are clearly not unique to the Judith River Formation of Montana. We look forward to future studies that examine microfossil bonebeds from combined sedimentologic, stratigraphic, and taphonomic perspectives and predict that our reconstructions will translate to other fossiliferous strata. We also anticipate future actualistic investigations that test the conclusions reached in this report in modern settings. It is arguably through such a combined approach (record-based studies coupled with actualistic explorations of modern lacustrine and fluvial systems and experimental approaches [e.g., Behrensmeyer 1988; Eberth 1990; Aslan and Behrensmeyer 1996; Ralrick 2006]) that we stand to gain our richest understanding of these taphonomically complex and paleoecologically informative fossil deposits.

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