

Taphonomy of Three Dinosaur Bone Beds in the Upper Cretaceous Two Medicine Formation of Northwestern Montana: Evidence for Drought-Related Mortality

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Taphonomic and sedimentologic attributes of three dinosaur bone beds discovered within the Campanian Two Medicine Formation of Montana suggest drought-related mortality. Two bone beds, Canyon Bone Bed and Dino Ridge Quarry, have yielded the near-exclusive remains of a new species of Styracosaurus (Family Ceratopsidae); the third bone bed, Westside Quarry, is dominated by a new species of Prosaurolophus (Family Hadrosauridae). All three assemblages are mono/paucispecific, parautochthonous concentrations of disarticulated and dissociated skeletal debris.

Evidence supporting a drought hypothesis includes: 1) a seasonal, semiarid paleoclimate, 2) associated caliche horizons, 3) aqueous depositional settings, 4) apparent age distributions characteristic of modern drought mortality (CBB and DRQ), and 5) the intraformational recurrence of low-diversity bone beds. Several alternative scenarios were considered, but drought proved most reasonable in light of the enhanced probability of preserving drought assemblages, and the species-selective and recurrent nature of modern drought mortality.

Styracosaurus sp. and Prosaurolophus sp. may have been gregarious, water-dependent taxa; during drought these particular taxa may have obligatorily congregated, either in herds, familial groups, or seasonal aggregates, in the vicinity of persistent water sources. The mono/paucispecific natures of the bone beds may reflect ecological segregation due to varying degrees of water-dependency, resource partitioning, or territorial/resource defense within

a Late Cretaceous dinosaur community. The preservational bias suggested by previous workers for drought assemblages is seemingly substantiated within the richly fossiliferous strata of the Two Medicine Formation.

INTRODUCTION

Mass mortality of terrestrial vertebrates during drought is a familiar and recurrent phenomenon in modern ecosystems (Tulloch, 1970; Corfield, 1973; Williamson, 1975; Hillman and Hillman, 1977; Coe, 1978; Barnes, 1982; Williamson and Mbanjo, 1988; Haynes, 1988). In light of this, and of the presumed high probability of preserving drought assemblages (Weigelt, 1989; Kurten, 1953; Shipman, 1975), the fossil record should be replete with drought-related concentrations of fossil vertebrates; however, vertebrate localities attributed to drought are infrequently described (Matthew, 1924; Huene, 1928; Brown, 1935; Case, 1935; Dalquest and Mamay, 1963; Saunders, 1977; Hulbert, 1982). One reason for such limited mention must be the difficulty of recognizing drought in the rock record. Indeed, although a number of paleobiologic/geologic features have been advanced to facilitate the recognition of fossil drought assemblages (Shipman, 1975), few, if any, geologic criteria are known to demonstrate paleo-drought unequivocally.

In this report, I present evidence for drought-related dinosaur mass mortality within the Upper Cretaceous Two Medicine Formation of northwestern Montana. I further speculate on the behavior and paleoecology of two ornithischian genera during episodes of water-stress. These interpretations are based on taphonomic and sedimentologic analyses of three bone beds—Canyon Bone Bed, Dino Ridge Quarry, and Westside Quarry—discovered by John R. Horner of the Museum of the Rockies in 1985 (Dino

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Ridge Quarry) and 1986 (Canyon Bone Bed, Westside Quarry).

The following abbreviations will be used in reference to the three quarries: CBB—Canyon Bone Bed; DRQ—Dino Ridge Quarry; WQ—Westside Quarry. All specimens referenced in this report are curated in the paleontological collections of the Museum of the Rockies (MOR), Bozeman, Montana.

Location and Methods

CBB, DRQ, and WQ are located in isolated badlands along the drainage of the Milk River, approximately 40 km northwest of Cut Bank, Montana. Badland exposures encompass approximately four km² in sections 15, 16, 21, 22, 27, and 28 of Township 37 North, Range 8 West of the Landslide Butte (1:24,000) quadrangle. The study area lies within Glacier County, on the Blackfeet Indian Reservation (Fig. 1).

MOR field crews excavated DRQ during the summer field seasons of 1985, 1986, 1987, and 1989, CBB was excavated during the summer field seasons of 1986, 1987, and 1989, and WQ was excavated in 1986 and 1987. Quarry matrices were worked with ice-picks and small brushes, and every effort was made to collect all bones and bone fragments encountered. Matrices were not systematically screened for microvertebrate remains, and thus a collecting bias against microvertebrates is possible. It is doubtful, however, that the CBB, DRQ, and WQ samples are significantly biased in regard to macrovertebrate skeletal debris (>1 cm³) considering the extent of excavations and the careful collecting procedures practiced in all three quarries.

I collected taphonomic and sedimentologic data from CBB, DRQ, and WQ as excavation and collection proceeded. Quarry maps were plotted from a meter grid system, and orientations of elongate skeletal elements were measured with a Brunton compass. Surface characteristics of bones were studied both in quarries and in the laboratory after preparation. Stratigraphic sections were measured through each site to place the bone beds in a local stratigraphic framework. Petrographic and micromorphologic paleopedologic features of bone bed matrices were analyzed from petrographic thin-sections, and clay mineralogies of bone bed matrices and associated paleosol horizons were resolved by X-ray diffraction analysis. The number of individuals within each assemblage was estimated using the MNI (minimum number of individuals) index (Badgley, 1986).

GEOLOGIC SETTING

Lithostratigraphy and Sedimentology

The Two Medicine Formation crops out to the east of the Rocky Mountain Overthrust Belt in northwestern Montana (Fig. 2). Two Medicine strata extend from the Montana Disturbed Belt (Mudge, 1970), where they are faulted and folded, eastward into the relatively unde-

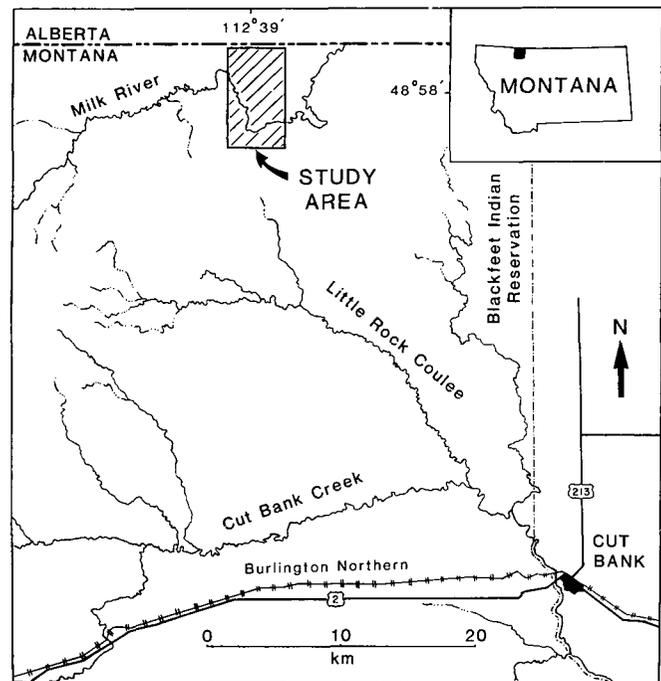


FIGURE 1—Location map of study area on Blackfeet Indian Reservation, Glacier County, Montana.

formed plains. The formation is approximately 600 m thick at its westernmost exposure along the Disturbed Belt, and gradually thins eastward, ultimately pinching out against the western limb of the Sweetgrass Arch. In the vicinity of the study area, the Two Medicine Formation conformably overlies the nearshore/strandline Virgelle Sandstone and is in turn conformably overlain by the marine Bearpaw Shale.

Two Medicine strata accumulated between and eastward advancing margin of the Cordilleran Overthrust Belt and the oscillating western shoreline of the Late Cretaceous Interior Seaway throughout most of the Campanian (Gill and Cobban, 1973). Terrigenous tectogenic sediments shed from the Cordilleran highlands to the west, and andesitic volcanoclastic debris derived from the Elkhorn Mountains Volcanics to the south, were deposited on the Two Medicine coastal plain by aggrading streams and river systems.

Lorenz (1981) described three lithofacies at the Two Medicine type section exposed along the Two Medicine River (Stebinger, 1914) (Table 1). He interpreted extensive sandstone sheets of the lower lithofacies as deposits of distributary channels located on a distal deltaic plain; the discontinuous, lenticular sand bodies of the middle and upper lithofacies were interpreted as deposits of shallow, braided streams of a mid to upper alluvial plain. Superposed sequences of fine-grained alluvial paleosols occur interstratified with channel sands throughout the formation.

Two Medicine Formation equivalents on the eastern

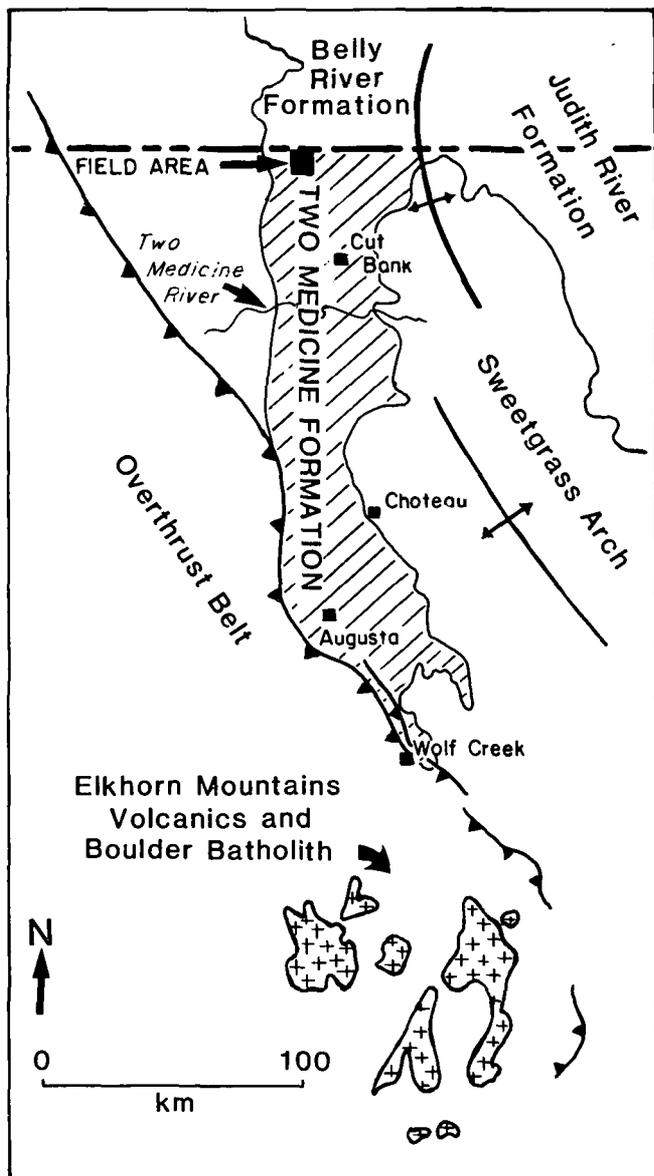


FIGURE 2—Generalized outcrop map of the Two Medicine Formation showing associated geologic and geographic features. Modified from Lorenz (1981).

flank of the Sweetgrass Arch in Montana include the Judith River Formation, Bearpaw Shale, Claggett Shale, and Eagle Sandstone. Correlative strata within Canada include the Belly River Formation and Bearpaw Formation, exposed in the southwestern foothills of Alberta, and the Milk River Formation, Pakowki Formation, and Judith River Formation, exposed further eastward in the plains of southern Alberta (Cobban, 1955; Russell, 1970; Balster et al., 1980; Thomas et al., 1990).

Paleogeography and Paleoclimate

The Two Medicine coastal plain was bounded to the west by the ascending mountain ranges of the North American Cordillera and sloped gently eastward to the Late Cretaceous Interior Seaway. Both of these mobile geographic features ultimately controlled the areal extent of habitat upon the coastal plain (Horner, 1984; Weishampel and Horner, 1987). The width of the Two Medicine coastal plain can be estimated by considering the strandline reconstructions of Gill and Cobban (1973) with palinspastic restorations of the overthrust belt during the Campanian (Sears, pers. comm., 1989). The latest Campanian Two Medicine coastal plain was at least 260 km wide, with the study area situated near the center of this plain at a paleolatitude of 48° N (Habicht, 1979).

Lorenz (1981) and Gavin (1986) concluded that the Two Medicine Formation was deposited under a seasonal, semi-arid climatic regime with a long dry season, warm temperatures, and predominant winds from the west. Evidence cited in support of their conclusions includes pedogenic caliche horizons, desiccated caliche nodules (septarian nodules), mud drapes in sand bodies, red oxidized paleosol horizons, abundant mud rip-ups in channel lags, unstable rock fragments and mineral grains in channel sands, an impoverished vertebrate and invertebrate aquatic fauna, and scarce lacustrine deposits. Fossil plants collected from the lower lithofacies of the formation by Crabtree (1987) corroborate much of the above interpretation. In addition, Jerzykiewicz and Sweet (1988) described an impoverished palynologic flora in the Belly River Formation of southwestern Alberta. Considering the proximity of their study area and their discovery of a southward trend toward aridity in the Campanian sediments in the foothills of the Canadian Rockies, it is likely that an impoverished palynological assemblage characterizes the Two Medicine Formation as well. Carpenter (1987), invoking the rainshadow effect of the Cordilleran highlands, suggested that occasional droughts may have affected the Two Medicine ecosystem.

Vertebrate Paleontology

Charles W. Gilmore (1914, 1917, 1922, 1929, 1930, 1937, 1939), collecting for the United States National Museum, and Barnum Brown of the American Museum of Natural History explored the dinosaur-bearing strata of the Two Medicine Formation during the early years of this century. Recent paleontologic inquiries have been directed by John R. Horner of the Museum of the Rockies (Horner, 1982, 1984, 1988; Horner and Makela, 1979; Horner and Weishampel, 1988). Dinosaurian genera documented within the formation include *Troödon*, *Albertosaurus*, *Corythosaurus*, *Leptoceratops*, *Monoclonius*, *Centrosaurus*, *Styracosaurus*, *Edmontonia*, *Dyoplosaurus*, *Maiasaura*, *Prosaurolophus*, *Orodromeus*, and *Stegoceras*, as well as an ornithomimid, a dromaeosaurid, and a lambeosaurine hadrosaur (Gilmore, 1930, 1939; Horner, 1984, pers. comm., 1990; Horner and Weishampel, 1988). A diverse non-di-

TABLE 1—Lithofacies described by Lorenz (1981) at the Two Medicine Formation type section.

Lithofacies	Thickness	Description	Depositional setting
Upper lithofacies	320–600 m	lenticular sand bodies, grey-green and red-brown mudstone, superposed paleosol horizons, abundant pedogenic carbonate (caliche), dinosaur bone beds and nesting sites	alluvial uplands, braided streams, small lakes, well-drained floodplain
Middle lithofacies	100–320 m	lenticular sand bodies, rare carbonaceous mudstone, grey-green mudstone, superposed paleosol horizons, pedogenic carbonate (caliche), abundant dinosaur bones, dinosaur bone beds	transitional zone between lower delta plain and alluvial uplands, low sinuosity streams, small lakes, swampy floodplain
Lower lithofacies	0–100 m	laterally extensive sand sheets interbedded with carbonaceous mudstone, rare vertebrate fossils	lower delta plain, distributary channels and marshes, poorly drained floodplain

nosaurian vertebrate assemblage including pterodactyloid pterosaurs (Padian, 1984), *Champsosaurus*, garpike, turtles, small lizards, and mammals (Montellano, 1988) has also been recovered from the formation.

TAPHONOMIC DATA

Taxonomic Composition

Approximately 300 bones and bone fragments representing a minimum of seven individuals (six subadults(?) and one juvenile) referable to the genus *Styracosaurus* were recovered from CBB (MOR locality 456). As yet, the animals have not been described to the species level, but it appears that the sample is monospecific and that the species is new (Horner, pers. comm., 1987). The only other vertebrate remains recovered from CBB are teeth shed from theropods.

More than 480 bones and bone fragments were recovered from DRQ (MOR locality 373). At least eight individuals referable to the genus *Styracosaurus*, two adults, five subadults, and one juvenile, comprise the sample. According to Horner (pers. comm., 1987), the same undescribed species of *Styracosaurus* is preserved in both DRQ and CBB. In addition to remains of *Styracosaurus* sp., bones of at least two hadrosaurids, teeth shed from theropods, a few small fragments of turtle carapace, and a few teeth and vertebrae of *Champsosaurus* were recovered from DRQ.

Of the ~220 identifiable bones in the DRQ sample, only ten are definitively hadrosaurid.

In this report, the bone bed designated "Westside Quarry" includes WQ proper (MOR locality 447) and stratigraphically equivalent Southside Quarry (MOR locality 454). Approximately 400 bones and bone fragments were collected from WQ representing at least five individuals, four adults and one juvenile, referable to a new species of *Prosaurolophus* (Horner, pers. comm., 1990). Numerous teeth shed from theropods, one lizard vertebra, and one nodosaur tooth were also collected.

Depositional Settings and Stratigraphic Relations

CBB, DRQ, and WQ occur within the upper lithofacies of the Two Medicine Formation, approximately 50 m below the contact with the superjacent Bearpaw Shale. Diagrammatic stratigraphic sections (Fig. 3) measured through the quarries demonstrate relative stratal positions; spatial relations between quarries are also illustrated in Figure 3. Lateral relationships of lithofacies and bone beds are schematically portrayed in Figure 4. Stratigraphic sections (Fig. 3) and bone bed maps (see Appendix) will be referenced as site specific taphonomic data.

CBB (Fig. 5) crops out 14.8 m above the bentonite datum in the study area, resting sharply but conformably above cross-bedded fluvial sandstone and beneath grey-green siltstone. To the east, west and south, the bone-bearing

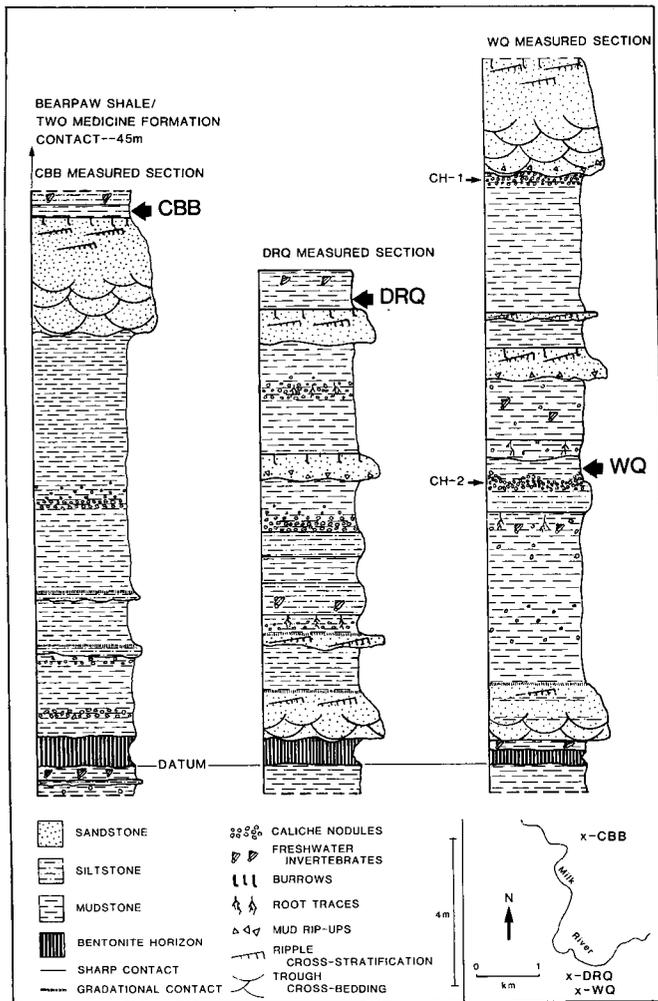


FIGURE 3—Diagrammatic stratigraphic sections measured through Canyon Bone Bed (CBB), Dino Ridge Quarry (DRQ), and Westside Quarry (WQ) showing relative stratal positions of quarries and associated caliche horizons (CH-1 and CH-2). An extensive bentonite horizon served as a datum. Spatial relations between quarries are also illustrated.

horizon abuts channel sandstone; to the north bone-bearing sediments have been eroded. The thickness of the bone bed varies, but is 20 cm on average; most bones were concentrated in the lowermost ten centimeters of the deposit. Essentially all of the bone-bearing strata comprising CBB, roughly 33 m², have been excavated.

DRQ crops out on top of a badland butte (Fig. 6), 12.3 m above the bentonite datum and 2.5 m beneath CBB (Fig. 3). The quarry conformably overlies a fine-grained, cross-bedded fluvial sandstone. The average thickness of the bone bed is one meter, although most bones were collected in the lower 10–15 cm. All of the outcrop on top of the butte, approximately 76 m², has been excavated.

The sedimentary matrices of both CBB and DRQ consist of massive, dark brown, organic-rich sandy siltstone. Clas-

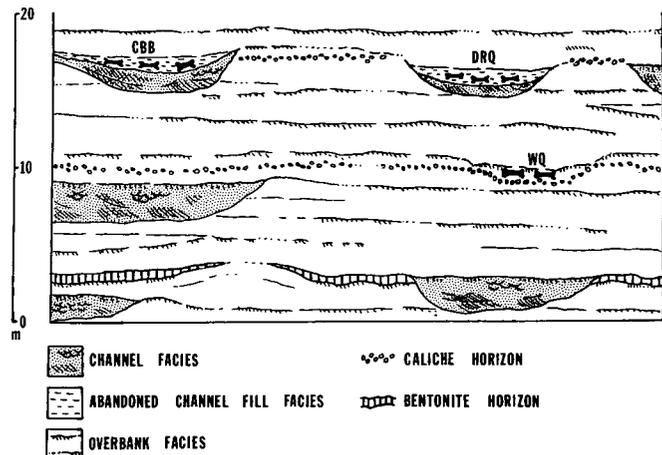


FIGURE 4—Schematic cross-section through the upper lithofacies of the Two Medicine Formation showing lateral relationships of lithofacies and bone beds. Horizontal axis is not to scale.

tic grains are poorly sorted and angular, grain size ranges from silt to fine sand. Clay minerals (predominantly smectite) intermixed with amorphous organic debris and microcrystalline calcium carbonate comprise approximately 20% of both matrices, and carbonized plant debris and fragmentary remains of small freshwater bivalves and gastropods are profuse within both quarries. The presence of freshwater invertebrates and facies relationships indicate that CBB and DRQ were deposited in small, shallow lakes. Both quarries directly overlie paleochannels, and CBB is laterally abutted by fluvial sandstones, suggesting that the lakes occupied abandoned stream channels or channel cut-offs. The abundance of carbonized plant debris implies that the lakes and/or lake margins were vegetated, and that lake sediments were probably in a reducing environment. Burial of skeletal material within CBB and DRQ resulted from trampling (see below) and/or clastic influx during flooding. CH-1 (Fig. 3), a laterally persistent pedogenic caliche horizon, is stratigraphically associated with both CBB and DRQ.

WQ (Fig. 7) is 7.6 m above the bentonite datum, 7.2 m and 4.7 m beneath CBB and DRQ, respectively (Fig. 3). The bone bed rests upon a 20–25 cm thick caliche horizon (CH-2, Fig. 3) and is unconformably overlain by unfossiliferous dark grey-green silty mudstone. Bones recovered from WQ were concentrated in a silty mudstone lens with a maximum thickness of 50 cm; additional lenses of bone-bearing sediment crop out along strike to the north and south of the main quarry (i.e., Southside Quarry—MOR locality 454; Fig. 7). The areal extent of WQ excavation is approximately 47 m²; excavation was halted when the extent of overburden became prohibitive. Bone-bearing sediments persist for an indeterminate distance into the eastern wall of the main quarry (MOR locality 447) and the northern wall of Southside Quarry (MOR locality 454).

The sedimentary matrix of WQ consists of grey-green, blocky, poorly indurated silty mudstone. More than 60%



FIGURE 5—Canyon Bone Bed (CBB) viewed from the east.

of the quarry matrix is composed of clay; X-ray diffraction analysis shows that the most abundant clay mineral is smectite, with only minor to trace amounts of mixed layer illite/smectite, illite, and kaolinite. Primary sedimentary structures were not observed in quarry sediments; however, relict pedogenic features were conspicuous. These features include small vertical root traces, pedotubules, pedogenic slickensides, incipient caliche nodules, and an underlying nodular caliche horizon (CH-2, Fig. 3). Relief on the underlying caliche horizon and geometry of the bone-bearing horizon suggest that WQ accumulated in a shallow depression on the ancient Two Medicine floodplain. Since pedogenic caliche horizons often impede the infiltration of meteoric water, it is quite possible that this depression periodically served as a waterhole. Bones scattered within and around the waterhole were buried in fine-grained sediments deposited during an overbank flood. Sediment deposited by flood waters did not completely fill the depression, thus the site may still have occasionally become saturated and ponded water.

Stratigraphic relations (Fig. 3) indicate that CBB and DRQ may be temporally correlative, as the slight difference in stratigraphic position between quarries can be attributed to topographic relief on the Two Medicine coastal plain. However, it is equally plausible that CBB and DRQ record temporally discrete fossil occurrences. Stratigraphic relationships and sedimentation rates (estimated with regard to stratal thickness and temporal duration of Two Medicine deposition) suggest that the WQ carcass assemblage accumulated on the order of 10^4 – 10^5 years prior to the CBB and DRQ carcass assemblages.

Skeletal Representation

Table 2 lists identifiable skeletal elements recovered from CBB, DRQ, and WQ. Bones most abundant in an intact vertebrate skeleton (i.e., vertebrae, ribs, phalanges) are notably uncommon in the CBB and DRQ samples. In con-



FIGURE 6—Dino Ridge Quarry (DRQ) viewed from the north.

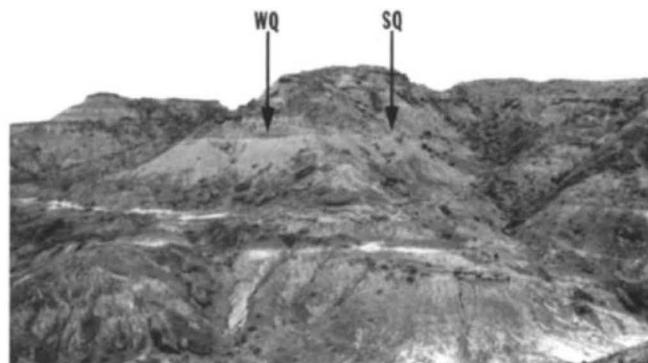


FIGURE 7—Westside Quarry (WQ) and Southside Quarry (SQ) viewed from the west.

trast, disarticulated cranial and limb elements are relatively abundant, representing almost 50% of the combined identifiable samples. As in CBB and DRQ, bones most plentiful in a vertebrate skeleton are under-represented

TABLE 2—Identifiable skeletal elements collected from Canyon Bone Bed, Dino Ridge Quarry, and Westside Quarry. Totals were compiled from the curated collections at the Museum of the Rockies, quarry maps, and field notes. Hadrosaurid bones in the Dino Ridge Quarry sample are indicated by parentheses.

Skeletal elements	Canyon Bone Bed			Dino Ridge Quarry			Westside Quarry		
	Complete	Partial	Total	Complete	Partial	Total	Complete	Partial	Total
Vertebrae	24	3	27	36	1	37	54	9	63
articulated	—	—	—	3	—	3	70	—	70
Vertebral processes	—	15	15	—	20	20	—	46	46
Phalanges	14	—	14	3	—	3	49	—	49
Ribs	6	57	63	9	29	38	3	26	29
Sternebra	—	—	—	1	—	1	1	2	3
Scapulae	3	4	7	2 (1)	2	5	2	1	3
Coracoids	1	—	1	1	—	1	2	—	2
Ulnae	—	2	2	—	—	—	—	1	1
Fibulae	1	1	2	1	1	2	2	1	3
Metapodia	8	3	11	2 (1)	1	4	12	2	14
Tibiae	2	4	6	1	2	3	1	2	3
Femora	4	1	5	1 (1)	1	3	3	—	3
Humeri	2	1	3	2	—	2	1	1	2
Radii	—	1	1	—	—	—	1	3	4
Sacrals	—	—	—	2	3	5	1	—	1
Crania	2*	72	74	—	83 (6)	89	—	73	73
Dentaries	8	2	10	6 (1)	—	7	5	4	9
			241			223			378

* Two nearly complete crania (SK-1, SK-2) were collected from Canyon Bone Bed (see Appendix).

in the WQ sample, although vertebrae and phalanges are considerably more abundant within WQ, both on a percentage basis and in absolute terms, than in either CBB or DRQ.

Skeletal Preservation

The mode of fossilization is analogous within CBB, DRQ, and WQ; bones are permineralized with calcium carbonate, and much of the original bone histology is preserved. Fossil bones collected from CBB and DRQ are medium to dark brown, whereas those from WQ are dark brown to black. Bones from all three quarries are slightly crushed and distorted as a result of lithostatic compaction.

All postcranial material within CBB was disarticulated and dissociated; several articulated cranial fragments were collected (see Appendix). A Montana National Guard helicopter was engaged to sky-lift two nearly complete crania (SK-1, SK-2) from the quarry. Skeletal material collected from DRQ and WQ was also disarticulated and dissociated with the exception of one articulated segment of cervical vertebrae (C1-C2-C3) within DRQ and several segments of articulated caudal vertebrae within WQ (see Appendix). Most bones comprising the CBB and DRQ samples are fragmentary: dentaries are invariably devoid of teeth, and limb bones often lack either one or both articular ends. Non-diagenetic bone breakage and fragmentation is less pervasive in the WQ sample: many fragile skeletal ele-

ments remain intact, limb bones are often complete, and most dentaries possess undamaged tooth batteries.

Fossil bones within CBB and DRQ were primarily flat-lying; interference between bones and irregularities on the underlying sandstone interface account for most bones that deviated from horizontal. Bones in WQ were crudely sorted; large limb bones and bone fragments occurred in the lower levels of the deposit, smaller skeletal elements and fragments were scattered throughout the bone-bearing lens. Most elongate skeletal elements within WQ were inclined at less than ten degrees, although some bones were oriented in unstable, almost vertical positions. Stereonet analyses of bone orientation data (Rogers, 1989) demonstrate that the azimuth of elongate skeletal elements in CBB, DRQ, and WQ was random.

Many bones in the CBB sample are differentially weathered (Fig. 8). Typically, one bone surface is rough with the inner cancellous bone exposed, whereas the opposite surface is unaltered and smooth, with intact surficial bone showing little indication of preburial cracking or exfoliation (~stage 1 weathering; Behrensmeier, 1978). This type of weathering is characteristic of, though not restricted to, flat cranial elements. Bones in the CBB sample that are not differentially weathered have smooth, relatively unweathered surfaces comparable to the unaltered surface of differentially weathered bone. Differential weathering was not observed on any bones in the DRQ sample, however, many DRQ bones are oxidized and disintegrating as



FIGURE 8—Differentially weathered cranial fragment (MOR 456/8-9-6-1) collected from Canyon Bone Bed. **A**) downward-facing surface showing preserved surficial bone. **B**) upward-facing, extensively weathered surface with exposed cancellous bone. Scale is in cm.

a result of recent weathering and pedogenesis. Bones in the DRQ sample that were not affected by recent weathering show similar surface weathering characteristics; bone surfaces are smooth with minimal indication of prefossilization cracking or exfoliation (~stage 1). Surfaces of bones comprising the WQ sample appear smooth and intact, approximating stage 0 weathering of Behrensmeier (1978).

Intersecting sets of fine parallel striations, presumed to be the result of trampling (see below), cover most unweathered bone surfaces in the CBB sample and, to a slightly lesser extent, the DRQ sample (Fig. 9). The minute surface scratch marks so prevalent in the CBB and DRQ samples are not conspicuous on any WQ bones. A few small, water-worn bone fragments were collected from CBB and DRQ; these water-worn fragments were probably transported into the quarries during flooding and thus exemplify “background” bones of Lehman (1982). There is no evidence of current abrasion in the WQ sample.

Sets of paired grooves, here interpreted as probable tooth

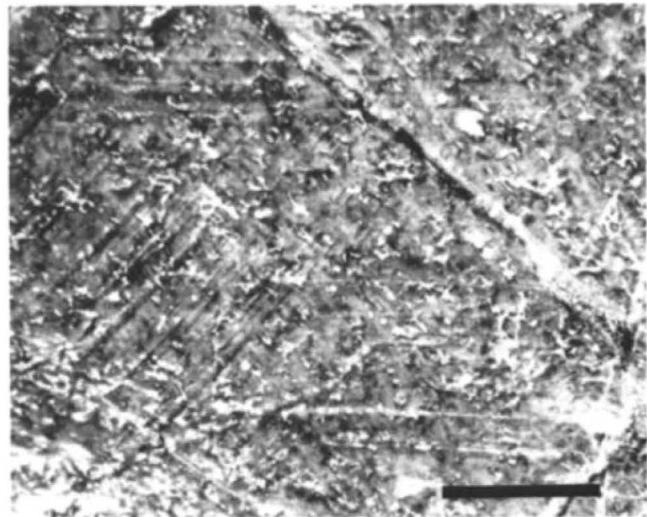


FIGURE 9—Intersecting sets of fine parallel striations interpreted as trample marks on a right maxilla (MOR 456/8-14-6-8) collected from Canyon Bone Bed. One set of striations is oriented parallel to the baseline of the photograph, the other set is oriented obliquely to the baseline. Scale bar = 250 microns.

marks, were observed on the medial surfaces of two jugals in the CBB sample (Fig. 10). Two additional bones in the CBB sample, both cranial fragments, and a dentary in the DRQ sample (Fig. 11) also bear what may very well be tooth marks. Tooth marks were not positively identified on any bones in the WQ sample.

Interpretations

Skeletal “lag” elements (*sensu* Voorhies, 1969; Behrensmeier, 1975; Lehman, 1982) predominate in the CBB, DRQ, and WQ samples, suggesting that post-mortem transport of discrete skeletal elements was minimal. This conclusion is supported by the lack of hydraulic equivalence between the fossil bones and their fine-grained encasing matrices (Behrensmeier, 1975) and shared low-energy depositional settings. Determining whether intact dinosaur carcasses were transported by currents to the burial sites or dinosaurs congregated under their own power and subsequently perished is more problematic. Flood-borne carcasses could plausibly accumulate in the abandoned channel settings of CBB and DRQ, although fluvial concentration of carcasses in the WQ waterhole seems unlikely (see Discussion). Alternatively, dinosaurs may have frequented the burial sites for ecological or behavioral reasons. Both scenarios should conceivably generate concentrations of locally-derived skeletal debris, at least with regard to the local channel belt (Behrensmeier, 1988). Local derivation coupled with conspicuous evidence of reworking (winnowing, trampling, scavenging—see below) indicate that CBB, DRQ and WQ are parautochthonous (Aigner et al., 1978; Kidwell et al., 1986) fossil concentrations.

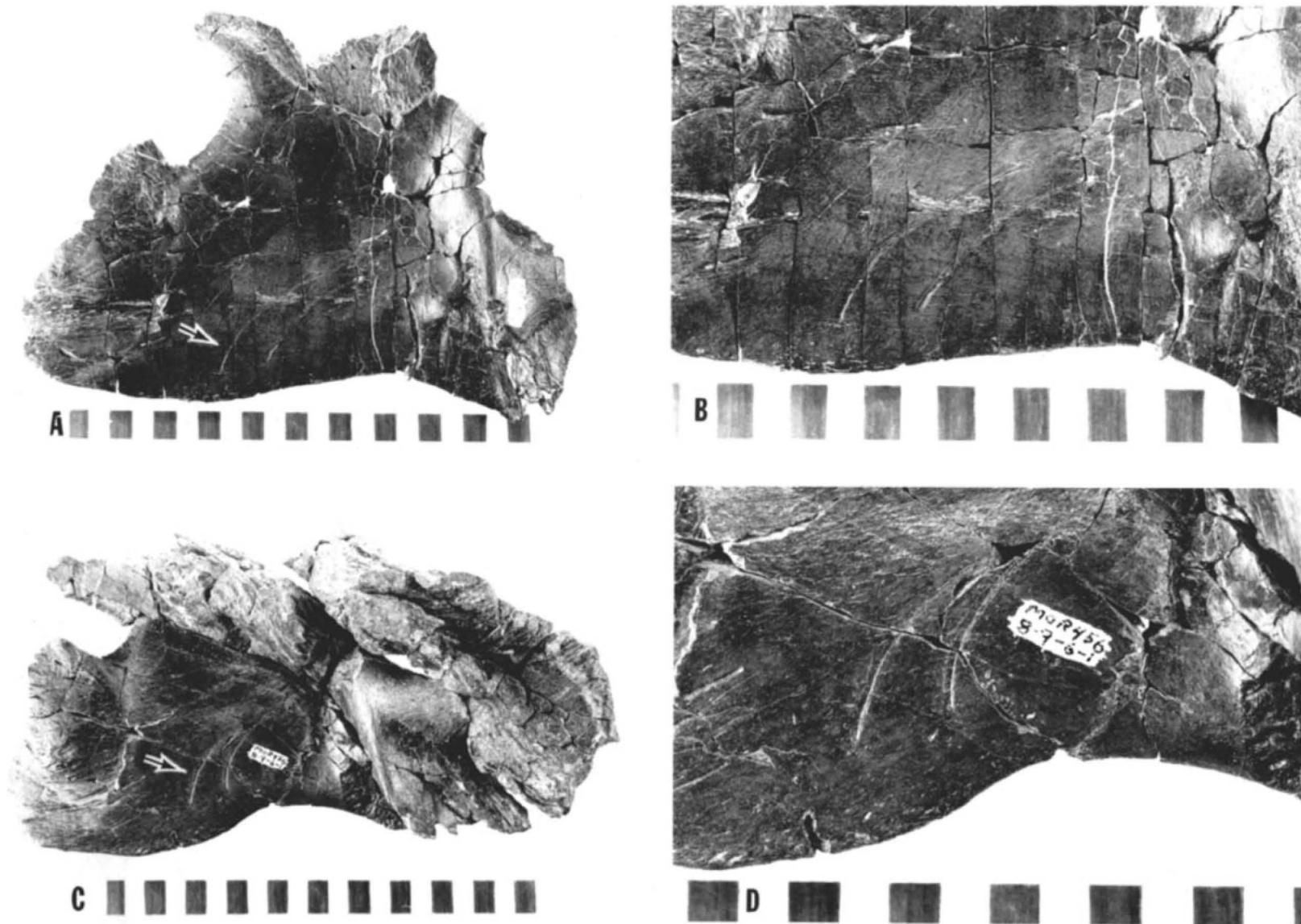


FIGURE 10—Probable tooth marks—**A**) left jugal (MOR 456/8-12-6-4) collected from Canyon Bone Bed (medial surface). **B**) close-up of MOR 456/8-12-6-4, scratch marks due to trampling are also visible. **C**) left jugal (MOR 456/8-9-6-1) attached to prefrontal-postorbital complex, collected from Canyon Bone Bed (medial surface). **D**) close-up of MOR 456/8-9-6-1. Scale is in cm.

The CBB, DRQ, and WQ assemblages are taxonomically depauperate (i.e., mono/paucispecific), and bones within all three quarries display similar surficial weathering characteristics (aside from differentially weathered bone in CBB and recently weathered bone in DRQ). These taphonomic attributes suggest relatively short-term mortality rather than time-averaged, attritional mortality (Voorhies, 1969; Behrensmeyer, 1978; Potts, 1986; Carpenter, 1989; but see Haynes, 1988). Unfortunately, exact durations of accumulation are impossible to ascertain; whether the CBB, DRQ, and WQ assemblages represent examples of Carpenter's (in press) "catastrophic mass mortality" (death measured in seconds or minutes) or "noncatastrophic mass mortality" (death measured in hours–months) is uncertain. However, geologic evidence suggestive of instantaneous mortality (i.e., an ash bed, Voorhies, 1981; fossil charcoal, Sander, 1987; flash-flood deposits, Case, 1932) is lacking at all three sites.

I attribute the under-representation of certain skeletal elements within CBB, DRQ, and WQ to winnowing of the death assemblages by currents (Voorhies, 1969; Dodson, 1973; Behrensmeyer, 1975; Lehman, 1982). Periodic floods may have temporarily reinitiated flow within the abandoned channels containing the CBB and DRQ assemblages (Hunt, 1978), and easily mobilized skeletal debris such as ribs, vertebrae, and phalanges may have been preferentially removed. Overbank flooding contemporaneous with burial may have winnowed easily mobilized skeletal debris from WQ. The slightly greater representation of vertebrae and phalanges within the WQ sample relative to the CBB and DRQ samples may reflect the state of articulation of the WQ carcass assemblage when exposed to current. Studies of disarticulation sequences in mammals indicate that vertebral columns and limb extremities are particularly resistant to disarticulation, especially under dry conditions (Toots, 1965; Hill, 1979). Articulated vertebral segments were obviously present within WQ when flooding and burial transpired, and it can be inferred that articulated limb extremities were as well. If conditions prior to burial were extremely dry, carcasses may have been partially mummified (Toots, 1965; Carpenter, 1987).

The meager hadrosaurid sample recovered from DRQ suggests that either 1) hadrosaurid carcasses were introduced into the quarry well in advance of the *Styracosaurus* sp. death assemblage and thus subjected to protracted/recurrent episodes of winnowing, 2) hadrosaurid carcasses were exposed to different or more intense taphonomic processes, or 3) discrete hadrosaurid bones were transported into the quarry. In any event, introduction of hadrosaurid material into DRQ was probably not coincident with the accumulation of the *Styracosaurus* sp. carcass assemblage.

Disarticulation, scattering, and fragmentation of bone in CBB, DRQ, and WQ is interpreted to be the result of bioturbation and trampling of the carcass assemblages by scavengers and herbivores frequenting the sites of mortality (Hill, 1979; Conybeare and Haynes, 1984; Gifford and Behrensmeyer, 1977; Behrensmeyer, 1981; Gifford, 1985). Surficial scratch marks (CBB and DRQ samples, Fig. 9) can also be attributed to trampling of the assem-

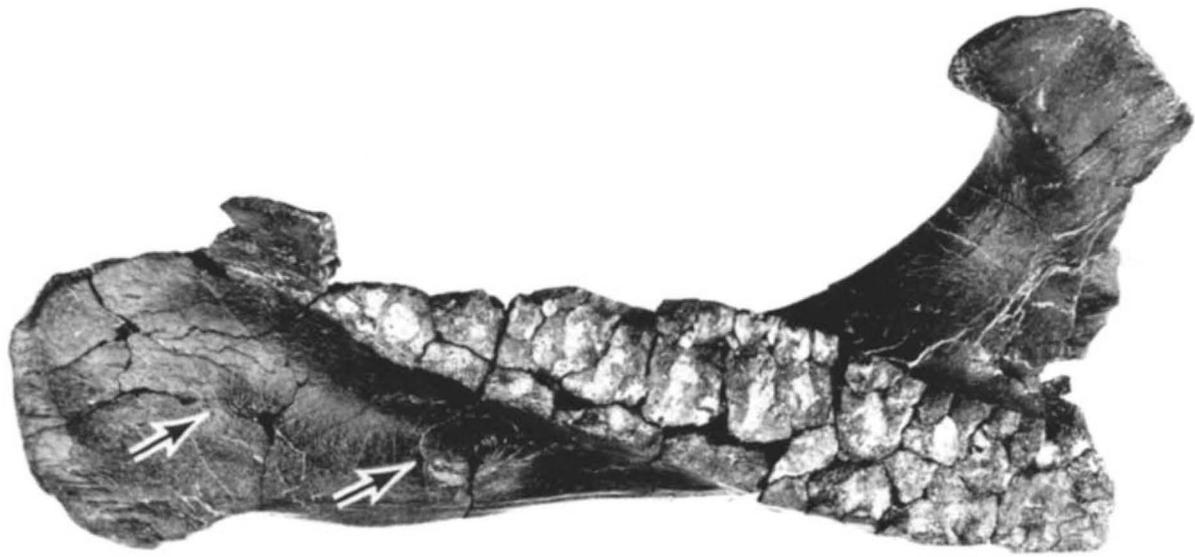
blages within abrasive silty sediment (Fiorillo, 1984; Behrensmeyer, Gordon, and Yanagi, 1986; Olsen and Shipman, 1988). I attribute the dearth of surface scratch marks in the WQ sample to the high clay content of the WQ matrix.

Burial of skeletal material within CBB and DRQ probably resulted from trampling (Gifford, 1985; Behrensmeyer, 1988), although clastic influx during flooding may have been a contributing factor. Trampling tends to promote the burial of dense bones with low surface area/volume ratios while breaking down bones with high surface area/volume ratios at the ground surface (Gifford, 1985). Perhaps trampling contributed to the differential representation of skeletal elements in all three assemblages. The paucity of articular ends of limb bones in CBB, DRQ, and to a lesser extent WQ may reflect the susceptibility of cancellous bone tissue to mechanical and/or chemical (Langston, 1976) destruction.

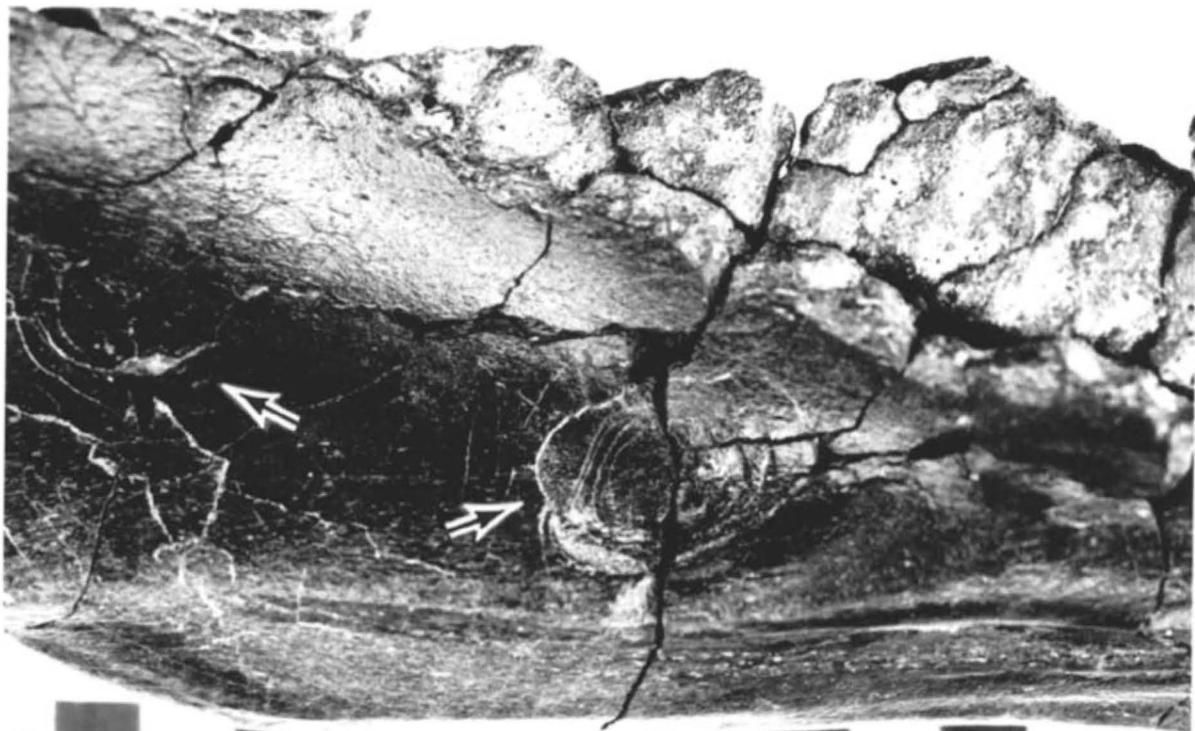
Bioturbation of bone within WQ evidently occurred both before and after burial, presumably after rewetting of the depression. Thus, the sedimentary matrix would have acted as a viscous cushion and considerably reduced mechanical breakage. Many of the isolated vertebrae and phalanges in WQ were probably disarticulated and dispersed by trampling following burial, and bones in unstable positions were apparently upended by trampling (Laporte and Behrensmeyer, 1980) and subsequently held in position as the matrix dried. Bones within CBB and DRQ originally upended by trampling may have been exhumed or undermined during floods and thus returned to stable orientations.

Tooth marks (Figs. 10, 11) in the CBB and DRQ samples probably resulted from scavenging since there is no indication of osteopathic healing, although it is plausible that they were inflicted by predators at the time of death. Judging by the size of the tooth marks, the most likely culprit is *Albertosaurus*, who was a contemporary of *Styracosaurus* and *Prosaurolophus* on the Two Medicine coastal plain, and whose teeth were recovered from all three bone beds. An interesting insight concerning the behavior of carnivorous dinosaurs may be afforded by these tooth marks. The concentration of tooth marks on jugals may reflect carnivores'/scavengers' substantial focus either on the adductor muscles themselves or on using the jugal as a lever to manipulate and/or dismember the skull. Two *Brachyceratops* specimens collected by C. W. Gilmore from the Two Medicine Formation evidently also possess jugals bearing tooth marks (Sampson, pers. comm., 1990), although Sampson now questions the validity of the "tooth mark" interpretation due to the seemingly anomalous abundance of ceratopsian jugals bearing paired grooves. Scavengers may have heightened the degree of differential preservation within CBB, DRQ, and WQ by carrying off or consuming small skeletal elements (Behrensmeyer, 1981).

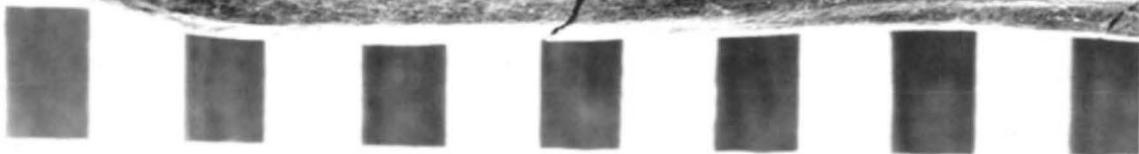
The originally unweathered condition of bone within CBB, DRQ, and WQ (with the exception of differentially weathered bone in CBB, see Fig. 8) indicates that either, 1) bones were rapidly interred subsequent to death and thus the period of surficial weathering was brief, or 2) weathering processes were inhibited. Thorough disartic-



A



B



ulation, scattering, and scavenging of bone in all three quarries argues against the first alternative, thus it seems likely that the CBB, DRQ, and WQ carcass assemblages accumulated in mildly weathering environments. It has been shown (Behrensmeyer, 1978) that swamps have fairly equable weathering climates due to only minor diurnal and seasonal fluctuations in temperature and humidity. The subaqueous depositional settings of CBB and DRQ probably buffered against extreme or rapid diurnal/seasonal fluctuations in both temperature and humidity and thus were conducive to the preservation of bone. Assuming the WQ bone sample accumulated on a desiccated land surface (see below), surficial weathering of bone may have been inhibited by the scarcity of water (i.e., negligible diurnal fluctuations in humidity) and possibly the mummification of carcasses.

Differential weathering of bone in CBB (see Fig. 8) may reflect desiccation of the paleo-lake preserving the death assemblage. Bone surfaces exposed during desiccation would have been subjected to subaerial weathering, thus bones displaying a differential weathering pattern may record a complex history of subaqueous and subaerial exposure (Shipman, pers. comm., 1990). The lack of differentially weathered bone in the DRQ sample could be explained if the paleo-lake preserving the DRQ assemblage did not desiccate prior to complete interment of the DRQ carcass assemblage.

Pedogenic features within the WQ matrix indicate that pedogenesis occurred subsequent to bone interment; the calcic paleosols that characterize the Two Medicine ecosystem were obviously conducive to bone preservation. The reducing, calcareous matrices of CBB and DRQ were also favorable for bone preservation. The proximity of DRQ to the modern ground surface resulted in present day weathering and fossil degradation.

Summary

Taphonomic attributes of CBB, DRQ, and WQ are summarized in Table 3. All three bone beds preserve mono/paucispecific, parautochthonous assemblages of dinosaurs. *Styracosaur* carcasses within CBB and DRQ accumulated in shallow, vegetated lakes which occupied abandoned stream channels. Carcasses presumably disarticulated subaqueously, although the CBB carcass assemblage may have experienced episodes of subaerial exposure. Disarticulation was expedited by trampling and scavenging. Easily mobilized skeletal elements were selectively winnowed from both sites during seasonal(?) floods. Bones which defied current transport were fragmented and scattered by bioturbators and were eventually interred, probably by trampling, into the soft bottom sediments of the lakes. Clastic influx during flooding may have contributed to burial.

Hadrosaurid carcasses within WQ accumulated in and around a floodplain waterhole. Disarticulation ensued under dry, subaerial conditions; some vertebral segments and limb extremities may have been held together in a partially mummified state. An overbank flood ultimately buried the assemblage, and this same flood apparently winnowed easily mobilized skeletal debris from the quarry area. Following burial, WQ may have been resaturated and trampled. Tooth marked bone in CBB and DRQ, and the shared presence of shed theropod teeth suggest that all three assemblages were scavenged prior to burial. Possible causes of mortality and a discussion of paleoecological and behavioral implications are presented below.

DISCUSSION

Cause of Death

Unfortunately, the cause(s) of mortality is not manifest within CBB, DRQ, or WQ, but it is possible to eliminate some unlikely hypotheses. Catastrophic volcanism and mass wasting can be dismissed as there is absolutely no supporting geologic or taphonomic evidence (i.e., ash horizons, debris flow deposits, articulated skeletons). Mass death related to fire is also improbable because fossil charcoal is not preserved in any of the quarries, and because a fire-induced mass death assemblage should seemingly preserve a diverse array of species that sought refuge in water (Sander, 1987). Mortality during a severe winter storm is unlikely since the Cretaceous was evidently a period of considerable warmth, and most Cretaceous plants evolved in an environment seldom affected by freezing temperatures (Frakes, 1979; Wolfe and Upchurch, 1987). Serial predation, the "regular and habitual killing of prey animals in the same loci" (Haynes, 1988, p. 219), is doubtful given the restricted taxonomic diversities and the similar bone weathering stages characteristic of all three bone beds. Fatal species-specific virus or plague unrelated to drought is possible, although I am unaware of any criteria capable of testing a disease-based hypothesis.

A frequently proposed death scenario is mass drowning in fluvial channels during floods (Koster, 1984; Koster and Currie, 1987; Turnbull and Martill, 1988; Wood, Thomas, and Visser, 1988). Mass drowning within a fluvial channel with subsequent concentration of carcasses outside of the active channel cannot be completely repudiated for CBB, DRQ, or WQ. However, especially in the case of WQ, I find the prospect of drowning several large dinosaurs in a stream channel, transporting their carcasses en masse downstream, conveying carcasses out of the channel, and ultimately depositing carcasses collectively within a floodplain waterhole extremely unlikely. It would require a major flood event to transport intact dinosaur carcasses across a

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FIGURE 11—A) Puncture marks (2) on the medial surface of a right dentary collected from Dino Ridge Quarry. The absence of teeth in the dentary is attributed to trampling. **B)** close-up of puncture marks. Scale is in cm.

TABLE 3—Summarized taphonomic attributes of Canyon Bone Bed, Dino Ridge Quarry, and Westside Quarry.

Taphonomic attributes	Canyon Bone Bed (MOR locality 456)	Dino Ridge Quarry (MOR locality 373)	Westside Quarry (MOR localities 447 and 454)
Taxonomic diversity	Dominated by <i>Styracosaurus</i> sp.	Dominated by <i>Styracosaurus</i> sp. (+2 hadrosaurids)	Dominated by <i>Prosaurolophus</i> sp.
Minimum number of individuals	7	8 + (2)*	5
Age spectrum	6 subadults (?)—1 juvenile	2 adults—5 subadults (?)—1 juvenile (excluding hadrosaurids)	4 adults—1 juvenile
Depositional setting	Shallow lake within an abandoned stream channel	Shallow lake within an abandoned stream channel	Floodplain waterhole
Quarry area	Approximately 33 m ²	Approximately 76 m ²	Approximately 47 m ²
Skeletal representation**	Dominated by groups 2 and 3	Dominated by groups 2 and 3	Dominated by groups 2 and 3, slightly greater representation of group 1 elements
Degree of articulation	Primarily disarticulated (a few partial crania)	Primarily disarticulated (articulated atlas-axis-C3)	Primarily disarticulated (several segments of articulated caudal vertebrae)
Spatial distribution	Randomly scattered in a sub-horizontal plane	Randomly scattered in a sub-horizontal plane	Randomly scattered in a sub-horizontal plane, some bones nearly vertical
Weathering stage***	-1-	-1-	-0-
Pre-fossilization bone modification	Some differentially weathered bone Tooth marks, surface scratch marks, fragmentation	Many bones degraded due to recent weathering Tooth marks, surface scratch marks, fragmentation	Fragmentation
Post-fossilization bone modification	Some distortion and fracturing due to lithostatic compaction	Some distortion and fracturing due to lithostatic compaction, fossil degradation due to recent weathering	Some distortion and fracturing due to lithostatic compaction

* Hadrosaurids.

** Based on transport groups 1, 2, and 3 of Voorhies (1969).

*** Based on bone weathering stages of Behrensmeyer (1978).

floodplain, and considering the high aggradation rates characteristic of the Two Medicine alluvial plain, partial burial of carcasses at the time of initial transport and deposition would be expected. Also, it seems likely that some type of crude size sorting should occur, with smaller carcasses transported farther downstream or farther out upon the floodplain. As for CBB and DRQ, evidence strongly supporting or refuting mass drowning and subsequent mass transport and concentration is lacking. I find it most reasonable to assume that fossil assemblages in low-energy depositional settings record in situ mortality unless conclusive evidence suggests otherwise.

A comparison of taphonomic and sedimentologic data from the three quarries with modern ecologic data suggests that CBB, DRQ, and WQ preserve fossil drought assemblages (*sensu* Shipman, 1975). Paleoclimatic data certainly support an environmental setting susceptible to drought, and the close association of the bone beds with caliche

horizons (CH-1 and CH-2, Fig. 3) and their shared occurrences within aqueous depositional settings (shallow lakes and a waterhole) are also suggestive of drought-related mortality (Shipman, 1975). Another feature consistent with drought is the preponderance of subadult animals in the CBB and DRQ samples. Age- and sex-specific mortality during drought, with a tendency for high rates of juvenile and female mortality in initial stages, has been noted in several recent studies (Corfield, 1973; Hillman and Hillman, 1977; Barnes, 1982; Conybeare and Haynes, 1984). The abundance of subadults (females?) and juveniles in CBB and DRQ may reflect heightened susceptibility of immature styracosaurus to water stress. A final consideration that may lend support to a drought-related scenario is the remarkable recurrence of mono/paucispecific bone beds within the middle and upper lithofacies of the Two Medicine Formation. At least six additional near-mono-specific dinosaur bone beds with taphonomic attributes

comparable to CBB, DRQ, and WQ have been documented within the Two Medicine Formation. Evidently, species-selective misfortune(s) with a high potential for preservation repeatedly befell the Two Medicine dinosaur fauna. Drought seems the most parsimonious explanation considering the species-selective nature of modern drought-induced mortality (Hillman and Hillman, 1977; Behrensmeyer, 1981; Conybeare and Haynes, 1984; Haynes, 1988), the probability of preserving drought assemblages owing to the concentration of animals around water sources during drought and the likelihood of flooding and burial subsequent to drought (Weigelt, 1989; Kurten, 1953; Shipman, 1975), and the documented recurrence of drought and drought-related mass mortality in modern ecosystems (Stockton and Meko, 1983; Currie, 1984; Kerr, 1984; Corfield, 1973; Hillman and Hillman, 1977; Coe, 1978; Barnes, 1982; Haynes, 1988).

I envision the following as a plausible scenario culminating in drought-related dinosaur mass mortality. Drought occurred on the Two Medicine coastal plain, instigating the depletion of food reserves and the desiccation of many floodplain water sources. *Styracosaurus* sp. congregated, either in herds, family groups, or seasonal aggregates, in the vicinity of persistent water sources in order to forage and drink. For similar reasons, although many thousands of years earlier, *Prosaurolophus* sp. congregated around a floodplain waterhole. As drought continued animals became increasingly undernourished, less mobile, and more dependent upon their limited, local supplies of food and water. Overgrazing and trampling eventually decimated food reserves, and many animals perished of disease and/or parasitization due to their malnourished condition. Weakened animals may have become mired in viscous sediments surrounding their terminal refuges or fallen victim to carnivores preying upon vulnerable, drought-weary animals. If water supplies were depleted prior to food resources, the regulation of body temperature and the excretion of soluble waste products may have been impaired (Runnells, 1954), and animals may have been susceptible to sunstroke (Carpenter, 1987). Following death, the CBB, DRQ, and WQ carcass assemblages underwent the previously described taphonomic processes.

Paleoecological and Behavioral Implications

Mono/paucispecific, biogenic mass death assemblages should preserve gregarious species, therefore *Styracosaurus* sp. and *Prosaurolophus* sp. were probably social, possibly herding taxa; whether they were gregarious year-round, or only during the dry season cannot be ascertained from the available data. Many herding animals in Africa today disperse during the rainy season and reconvene during the dry season when food and water are in short supply (Western, 1975). Provided death was drought induced, *Styracosaurus* sp. and *Prosaurolophus* sp. may have required access to free water during dry spells, and thus may have been water-dependent taxa. Elephants, zebra, buffalo, and wildebeest are examples of extant water-dependent species (Lamprey, 1963; Ayeni, 1975). Water-inde-

pendent taxa satisfy their water needs by selecting food with a high water content, such as flesh, blood, and certain types of browse (Ayeni, 1975).

A variety of paleoecological signals could be recorded by the mono/paucispecific natures of CBB, DRQ, and WQ. Water-independent dinosaur taxa of the Two Medicine coastal plain may have bypassed densely populated water sources during the dry season, thereby avoiding competition for limited food and water resources. Alternatively, water-dependent dinosaurs, like some extant mammals (Lamprey, 1963), may have utilized separate dry season refuges, and in this manner minimized competition. Partitioning of dry season resources by dinosaurs on the Two Medicine coastal plain could explain why the *Styracosaurus* sp. death assemblages occur in vegetated lacustrine paleoenvironments while the *Prosaurolophus* sp. death assemblage is associated with a floodplain waterhole. Interspecific aggression/avoidance and territorial behavior are also possible motives behind the taxonomically depauperate status of CBB, DRQ, and WQ. Ayeni (1975) observed that small species generally vacate a drinking site when larger species arrive, and Jarman (1972) reported that elephant and buffalo seemed to abstain from concomitant use of a watering site. Stress during the dry season may serve to intensify aggressive or territorial behavior (Henshaw, 1972). Considering the large size and gregarious nature of the dinosaur taxa in question, inter/intraspecific aggression and effective territorial defense during environmentally stressful periods are certainly feasible (Farlow and Dodson, 1975). One final paleoecological hypothesis is that highly selective mortality, as opposed to ecological segregation, aggression, or avoidance, resulted in the low-diversity assemblages. A diverse array of species may have frequented CBB, DRQ, and WQ, but only select species, those most susceptible to the adverse conditions, fell victim to drought.

CONCLUSION

Taphonomic and sedimentologic evidence suggest that the Two Medicine dinosaur fauna endured recurrent, perhaps periodic or cyclic episodes of drought. During drought, some dinosaur taxa apparently congregated, either in herds, familial groups, or seasonal aggregates, in the vicinity of persistent water sources. Subsequent mass die-offs of dinosaurs within and around aqueous refuges, presumably as a result of drought-related hardship (malnutrition, disease, starvation), are recorded by three parautochthonous bone beds in the upper lithofacies of the Two Medicine Formation—Canyon Bone Bed, Dino Ridge Quarry, and Westside Quarry. A minimum of seven animals referable to a new species of *Styracosaurus* were collected in Canyon Bone Bed, and at least eight individuals of the same undescribed species were recovered in Dino Ridge Quarry. At least five dinosaurs referable to a new species of *Prosaurolophus* were collected from Westside Quarry. The low taxonomic diversities of all three assemblages may reflect ecological segregation due to varying degrees of water-dependency, resource partitioning, or territorial/re-

source defense within a Late Cretaceous dinosaur community.

Criteria advanced by Shipman (1975) were utilized to identify Canyon Bone Bed, Dino Ridge Quarry, and Westside Quarry as fossil drought assemblages. These criteria include: 1) aqueous depositional settings, 2) associated caliche horizons, and 3) age distributions characteristic of drought-related mortality (CBB and DRQ). One additional drought criterion suggested by this study is the intraformational recurrence of mono/paucispecific bone beds. At least six additional mono/paucispecific dinosaur bone beds with taphonomic attributes comparable to Canyon Bone Bed, Dino Ridge Quarry, and Westside Quarry have been discovered in the Two Medicine Formation, and it seems reasonable to postulate that these bone beds may also represent fossil drought assemblages. I argue that drought should often prove to be the most parsimonious explanation for a repetitive record of low-diversity vertebrate mass death owing to the species-selective nature of drought-induced mortality (Hillman and Hillman, 1977; Behrensmeyer, 1981; Conybeare and Haynes, 1984; Haynes, 1988), the purported high probability of preserving drought assemblages (Weigelt, 1989; Kurten, 1953; Shipman, 1975), and the documented recurrence of drought and drought-related mortality in modern ecosystems (Stockton and Meko, 1983; Currie, 1984; Kerr, 1984; Corfield, 1973; Hillman and Hillman, 1977; Coe, 1978; Barnes, 1982; Haynes, 1988).

The preservational bias suggested for drought assemblages by Weigelt (1989), Kurten (1953), and Shipman (1975) appears to be substantiated within the fossiliferous strata of the Upper Cretaceous Two Medicine Formation of northwestern Montana. If this preservational bias holds for vertebrate-bearing strata of other regions and ages, and there is no *a priori* reason why it should not, fossil drought assemblages may prove to be much more abundant in the fossil record than currently appreciated.

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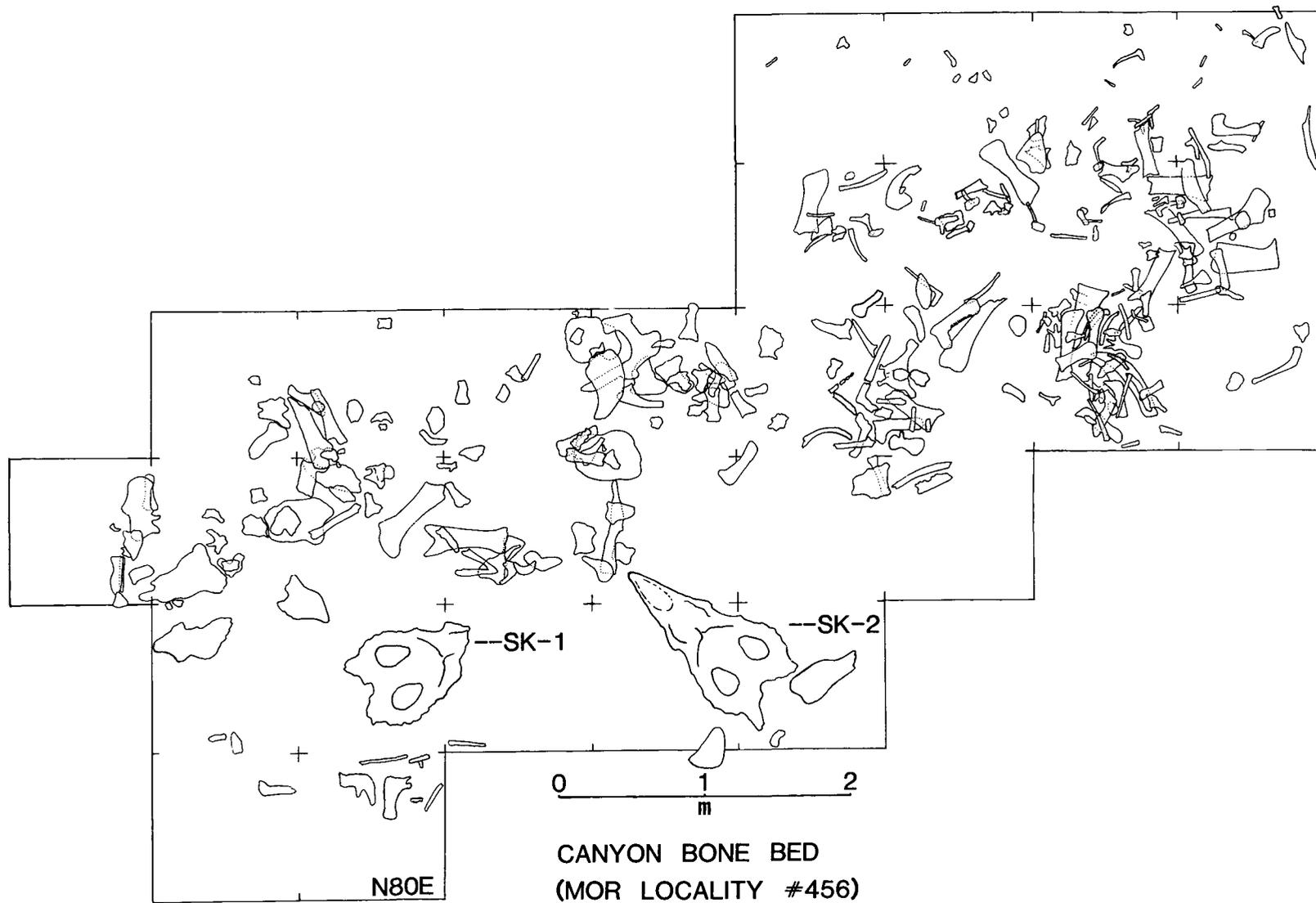
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APPENDIX—Canyon Bone Bed (MOR Locality #456), Dino Ridge Quarry (MOR Locality #373), and Westside Quarry (MOR Locality #447 & #454) site maps.

