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Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana

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Abstract

Jack's Birthday Site is a diverse vertebrate assemblage from the Upper Two Medicine Formation of western Montana. Age is roughly 74 Ma. The site covers roughly 3000 m^2, and excavations over 140 m^2. A large bone sample (> 1600 skeletal elements) allowed statistical evaluation of the preservational and compositional variation within the site. Evidence, including sedimentary facies, plant and invertebrate fossils, and bone orientation and condition, indicates Jack's Birthday Site represents part of a small, shallow floodplain lake. Lithologies and fossil preservation vary from northwest to southeast over a distance of 50 m. This variation represents a transition from lake through shoreline to marginal shoreline/floodplain environments.

Containing ten dinosaur taxa and a variety of non-dinosaurs, Jack's Birthday Site provides one of the best single faunal samples of the region. The vertebrate assemblage includes two taphonomic fractions. The first, consisting of attritional, predominantly isolated and allochthonous elements, represents a time-averaged assemblage. The other consists of associated, parautochthonous remains restricted to a single horizon. Taxa represented by associated remains include three iguanodontoids, *Hypacrosaurus*, *Prosaurolophus*, and *Gryposaurus*, and the theropod *Troodon*. Associated individuals of these taxa have non-random distributions within the site (Fisher's Exact Test, $p < 0.01$) and observed taxonomic clustering may reflect group behavior and/or event mortality. The four or more *Troodon* represent the first described multi-individual troodontid occurrence.

The diversity and spatial complexity of the parautochthonous fraction of the Birthday Site assemblage is difficult to explain. Discussion of possible event mortality mechanisms focuses on three: drought, botulism and cyanobacterial toxicosis. These share an ability to act over an ecologically significant period of time, affect a variety of species and concentrate mortality along water sources, aspects that may have been important in generating the Birthday Site assemblage. Evidence at the site favors drought or perhaps a drought/botulism hypothesis. However, taxonomic clusters could represent completely separate events with a variety of causes.

1. Introduction

Preservation in fossil vertebrate assemblages can range from nearly complete, the burying of a Miocene rhinoceros herd including stomach contents in a volcanic ash (Voorhies and Thomasson, 1979; Voorhies, 1985), to mere fragments, a microfossil accumulation of isolated bones and teeth in a channel lag (Brinkman, 1990). Both yield paleobiological information. The former records information on posture and herd demographics in an almost photographic fashion. The latter, when compared to similar localities, reveals the spatial and temporal pattern of species distributions. Many bonebeds show a range of preservation, a mix of articulated skeletons to isolated bones or both parautochthonous and allochthonous elements. The precise paleobiological meaning of such bonebeds often remains unclear.

Mono- to paucispecific bonebeds preserve a wide

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variety of dinosaurs representing most of the major groups. Among theropods, such assemblages typically include the ceratosaurs, *Coelophysis bauri* and *Syntarsus rhodesiensis* (Colbert, 1964, 1989; Raath, 1990; Rowe and Gauthier, 1990) and Ostrom (1969, 1990) reported at least four *Deinonychus antirrhopus* with a single *Tenontosaurus tilletti*. Monospecific mass accumulations are characteristic of prosauropods, for example the Trossingen, Germany *Plateosaurus* assemblage (Weishampel, 1984; Weishampel and Westphal, 1986; Galton, 1990).

Ornithischian known by associations of a few individuals include: *Tenontosaurus tilletti*, *Iguanodon bernissartensis*, *Leptoceratops gracilis* and *Protoceratops andrewsi* (Brown and Schlaikjer, 1940; Sternberg, 1951; Norman, 1986; Forster, 1990). However, the Late Cretaceous hadrosaurid, lambeosaurid and ceratopsian bonebeds are unsurpassed in both size and abundance (Gilmore, 1929; Currie and Dodson, 1984; Hooker, 1987; Wood et al., 1988; Nelms, 1989; Lehman, 1990; Rogers, 1990; Christians, 1991; Varricchio and Horner, 1993). (Note: Hadrosauridae and Lambeosauridae are used in this text sensu Horner, 1990.)

These low-diversity assemblages, commonly interpreted as the products of mass mortality events, may represent biological aggregations. Based on these accumulations, workers envision "herds" for many species: *C. bauri* (Colbert, 1990); *S. rhodesiensis* (Raath, 1990); *Iguanodon* (Norman and Weishampel, 1990); the hadrosaurids, *Maiasaura peeblesorum* (Hooker, 1987) and *Edmontosaurus annectens* (Christians, 1991); and numerous ceratopsians (Currie and Dodson, 1984; Wood et al., 1988). Juvenile *T. tilletti* may have formed groups as an important survival strategy (Forster, 1990). Ostrom (1969) suggested pack-hunting for the dromaeosaurid *D. antirrhopus*, while Von Huene (1928) viewed *Plateosaurus* as a gregarious migrator. Recently, mass assemblages have been critical for the interpretation of morphology, allowing for the recognition of dimorphism and the explanation of various cranial structures as social or sexual display features (Colbert, 1989; Lehman, 1989, 1990; Raath, 1990; Rowe and Gauthier, 1990; Sampson, 1993).

The criteria generally used to recognize mass mortality are relatively simple: a predominance of one species and concentration of bones on a single horizon. Uniformity of preservation and the demographics of the assemblage can assert this interpretation. Nevertheless, attritional mortality from local settings where one taxon far outnumbers all others or with size- or taxonomically-selective mortality, may result in near monospecific assemblages. Rogers (1990) noted that three monospecific parautochthonous assemblages from the Two Medicine Formation may have resulted from the aggregation and death of individuals, not herds, attracted to a specific locale, here, waterholes in times of drought. Similarly, conditions at the Hot Springs Mammoth Site (Agenbroad, 1984) may have trapped over time only subadult to mature mammoths. The abundance and physical attributes of *Plateosaurus*, rather than mass mortality, may account for the predominance of this species on some horizons at Trossingen (Weishampel, 1984; Weishampel and Westphal, 1986; Sander, 1992). Therefore, the interpretation of monospecific assemblages warrants some caution.

Multispecific dinosaur bonebeds, common to both the Jurassic (Dodson et al., 1980) and Cretaceous (Currie and Dodson, 1984; Wood et al., 1988), usually represent attritional allochthonous accumulations within channel sands (Lawton, 1977; Wood et al., 1988; Britt, 1991; Fiorillo, 1991). Notable exceptions include the Cleveland–Lloyd Quarry, a presumed predator trap (Madsen, 1976), and Scabby Butte, a catastrophic mix of hadrosaurid and ceratopsian material (Langston, 1976).

Recent discovery of a rich dinosaur bonebed, Jack's Birthday Site, in the Two Medicine Formation of Montana, allowed the opportunity to consider the taphonomic and biologic meaning of a multispecific but primarily parautochthonous assemblage.

2. Location and methods

Jack's Birthday Site is located in badlands along Badger Creek in Glacier County, Montana within the Blackfeet Indian Reservation (Fig. 1A).

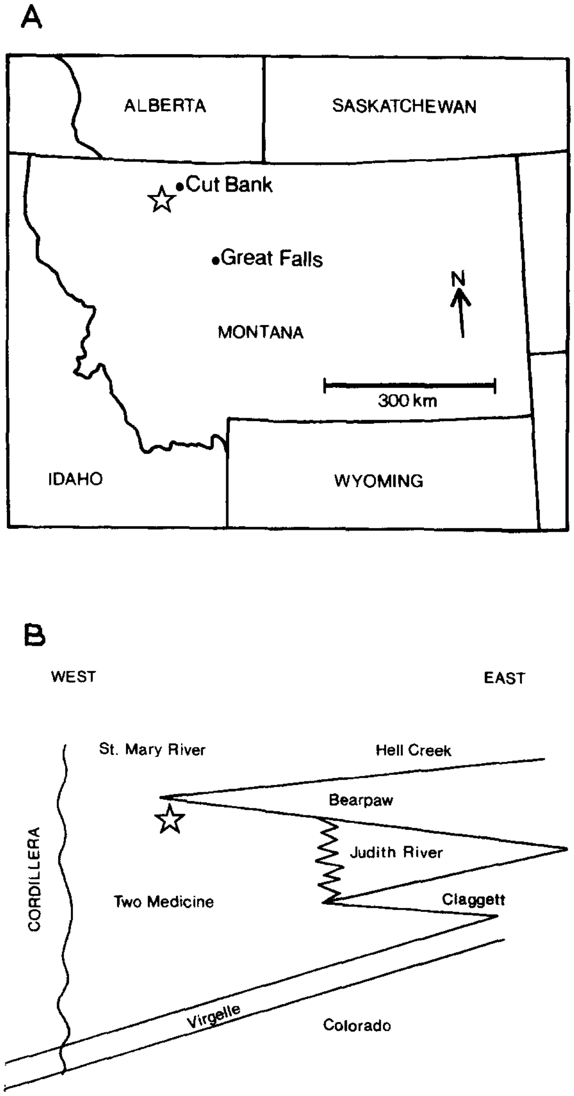

Fig. 1. Location of Jack's Birthday Site, Museum of the Rockies locality TM-068, section 11, T31N, R8W, Glacier Co., Montana (A). (B) is a stylized cross section of the Upper Cretaceous strata of north central Montana, modified from Horner et al. (1992). Star represents approximate position.

Fig. 2. Aerial photo from hydrogen balloon of Jack's Birthday Site showing the quarries: *B*=Brad; *L*=Lower; *M*=Middle; *S*=South; and *E*=East. To the northwest, Brad, Middle and Lower, represent part of a lake basin and the dotted line marks the southeast limit of sedimentary bedding and plant preservation. The greatest density of bone and wood occur along this line in Brad and Middle and may represent a strand line. Bone weathering and breakage increase significantly from northwest to southeast, where South and East represent shoreline and marginal shoreline/floodplain environments. Hadrosaurid remains are concentrated in Brad, Lower and Middle, *Hypacrosaurus* in South and East, and *Troodon* in South. Vertical line at bottom center is the tether for the balloon and the white dot at end of tether is Dr. Johnson.

Excavation commenced in late June, 1988. The bonebed crops out on three sides of a N–S trending ridge and initial excavations consisted of two west-side quarries, Lower and Middle (Fig. 2). Three additional quarries, South, Brad, and East, opened in 1989, extended work to all three sides of the ridge. Small crews continued to dig on both east and west sides from 1990 to 1992. Excavation of

140 m^2 of bonebed represents roughly 200 work days. All excavations and exposures suggest lateral continuity for the bonebed. Based on visible bonebed exposure on each side of the ridge, and assuming lateral continuity, total preserved area of the site is over 3000 m^2.

Full taphonomic investigation began in 1989. Excavation was carried out with hand tools, and an effort was made to collect all potentially identifiable bones and a sample of unidentifiable fragments. Washing and screening of matrix was minimal (<100 kg of matrix); therefore, a bias against microvertebrates may exist in the overall sample. Microfossils include some small limb bones and gastropods, but the washing process rendered most unidentifiable. The large sample size (>1600 skeletal elements), large area excavated, and distinctiveness in color and hardness between bone and matrix likely minimized any bias in the macrovertebrate (elements >1 cm^3) fraction.

As each element was uncovered in the field, excavators noted bone condition: degree of completeness, wear and weathering, and the presence of fractures, tooth marks, etc. After preparation in the lab, specimens were re-examined for these same features.

Specimens were mapped using a meter-square grid system. Orientation (i.e trend and plunge) of linear bones, ossified tendons and plant fragments were measured using a Brunton compass. Additionally, in 1989, workers plotted specimens in 3-D space using a dumpy level, with large or steeply inclined elements measured at two or more points. Also in 1989, Dr. Jerry Johnson conducted a trial experiment of two documentation techniques used in archaeology. This involved low-level photography using both a 5 m bi-pod and an unmanned hydrogen balloon (Fig. 2).

All specimens are curated in the Museum of the Rockies (MOR) paleontological collections in Bozeman, Montana.

3. Regional setting

Rogers et al. (1993) provide a recent review and dating of the Two Medicine Formation. Age of the formation, based on $^{40}Ar/^{39}Ar$ values from bentonites, falls between 86 and 74 Ma. Correlatives of the formation include: eastward in Montana, the Eagle, Claggett, Judith River and Bearpaw Formations; and in southwestern Alberta, the Belly River and Bearpaw Formations (Russell, 1970; Koster and Currie, 1987; Shurr et al., 1989; Fig. 1B).

Montana Late Cretaceous geography consisted of western mountains shedding sediments eastward onto a low coastal plain bordering the Western Interior Seaway (McGookey, 1972; Gill and Cobban, 1973). Floras indicate that the Two Medicine region was within a transition zone between warm or sub-humid tropical and temperate climates (Dodson, 1971; Wolfe and Upchurch, 1986; Crabtree, 1987). This boundary marks a switch from southern evergreen to northern deciduous forests (Krassilov, 1981). The following evidence supports a seasonally semi-arid climate with a long dry season for the Late Cretaceous of Montana: tree rings, unexpected in a thermally equable region (Dodson, 1971; Crabtree, 1987); a substantial number of evergreens with leathery leaves without drip tips (Crabtree, 1987); impoverished palynological assemblages (Jerzykiewicz and Sweet, 1987); fusain or charcoal, evidence of fires (Carpenter, 1987); caliche paleosols (Lorenz, 1981; Jerzykiewicz and Sweet, 1987); desiccated (septarian) carbonate nodules; sandstone bodies of episodic (ephemeral) rivers; abundant clay-flake rip-up clasts; and fresh, unstable volcanic rock fragments (Lorenz, 1981).

The rich dinosaur fauna from the Two Medicine Formation includes massive ceratopsian, hadrosaurid and lambeosaurid bonebeds (Gilmore, 1917; Rogers, 1990, 1993; Varricchio and Horner, 1993), hypsilophodont and hadrosaurid nesting grounds (Horner and Makela, 1979; Horner, 1982; Horner and Weishampel, 1988), and numerous isolated specimens (Gilmore, 1917, 1930, 1939; Horner, 1983).

4. Jack's Birthday Site

The Two Medicine Formation along Badger Creek consists primarily of mudstones with occasional sandstones (Fig. 3). Relatively common caliche horizons contrast with rare lacustrine platy shales and siltstones. Mudstones typically are massive and represent floodplain deposition. Their unusual thickness and abundance reflect the proximal basin subsidence experienced by this area in the Campanian (Lorenz, 1981). Sandstones are generally either thin (<2 m thick), fine-grained and well sorted with pervasive climbing ripples or thick (2–8 m), medium-grained, fairly well-sorted

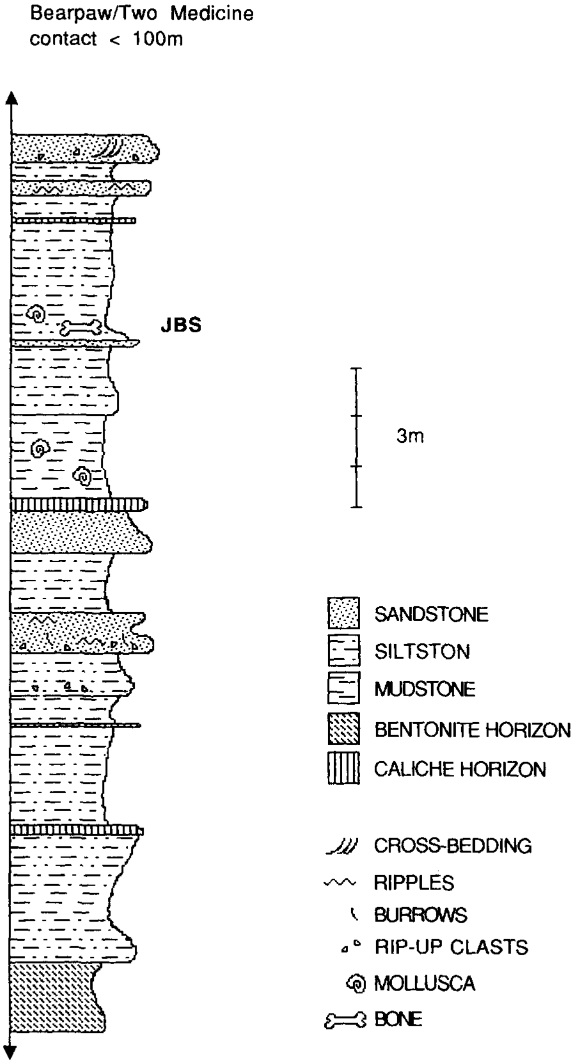

Fig. 3. Stratigraphic column through Jack's Birthday Site (JBS). Prominent volcanic ash at base may correlate to a horizon, TM-4, dated at 74.1 Ma (Rogers et al., 1993).

and lenticular (width/height ratios between 5:1 and 30:1) with trough and planar–tabular crossbeds (Lorenz, 1981).

Bone, though found at various levels throughout Jack's Birthday Site, is concentrated within a green–gray, calcic, massive, and poorly-sorted mudstone (Fig. 4). The horizon lies roughly 100 m below the Two Medicine Formation–Bearpaw Shale contact (Horner et al., 1992) and 14 m above a prominent ash horizon (Fig. 3). This may correlate with TM-4, an ash recently dated at 74.1 Ma (Rogers et al., 1993).

A poorly sorted, fine-grained sandstone underlies the main bone horizon in the northwest quarries, Brad, Lower, and Middle (Figs. 2 and 4). This thin, <20 cm thick, sandstone coarsens upwards so that the upper 5 cm contains an abundance of small (1–10 cm), well-abraded bone fragments, isolated caliche nodules and rip-up clasts. The sharp, flat upper contact with the overlying mudstone may represent an omission or winnowed surface. This unit both pinches and grades laterally to the southeast into a mudstone continuous with the main bone-bearing mudstone (Figs. 2 and 4).

In the northwest quarries (Figs. 2 and 4), the main bone-bearing mudstone is about 0.5 m thick. Concentrated in the basal 30 cm of the unit, most bones lie in contact with the underlying sandstone. In contrast, in the southeast, the bone-bearing mudstone is roughly 5 m thick. This results from the units in the northwest that under- or overlie the bone-bearing mudstone (for example, the basal sandstone) pinching out and/or grading laterally to the southeast into the massive mudstone (Fig. 4). This lithologic change occurs rapidly within the Middle and Brad quarries (Fig. 2). Despite this lateral variation, a bone layer 30 cm thick persists as a continuous horizon from 25 m north of the Lower quarry south to the limits of the South and East quarries (Fig. 2). The mudstone unit extends in visible exposures some 100 m beyond the limit of the excavations and the bonebed. At least two unexcavated bone horizons of unknown extent sit within 3 m beneath the main bonebed.

The bone-bearing mudstone is poorly-sorted. Grain-size analysis reveals that silt- and sand-sized grains, mostly highly-angular quartz, make up

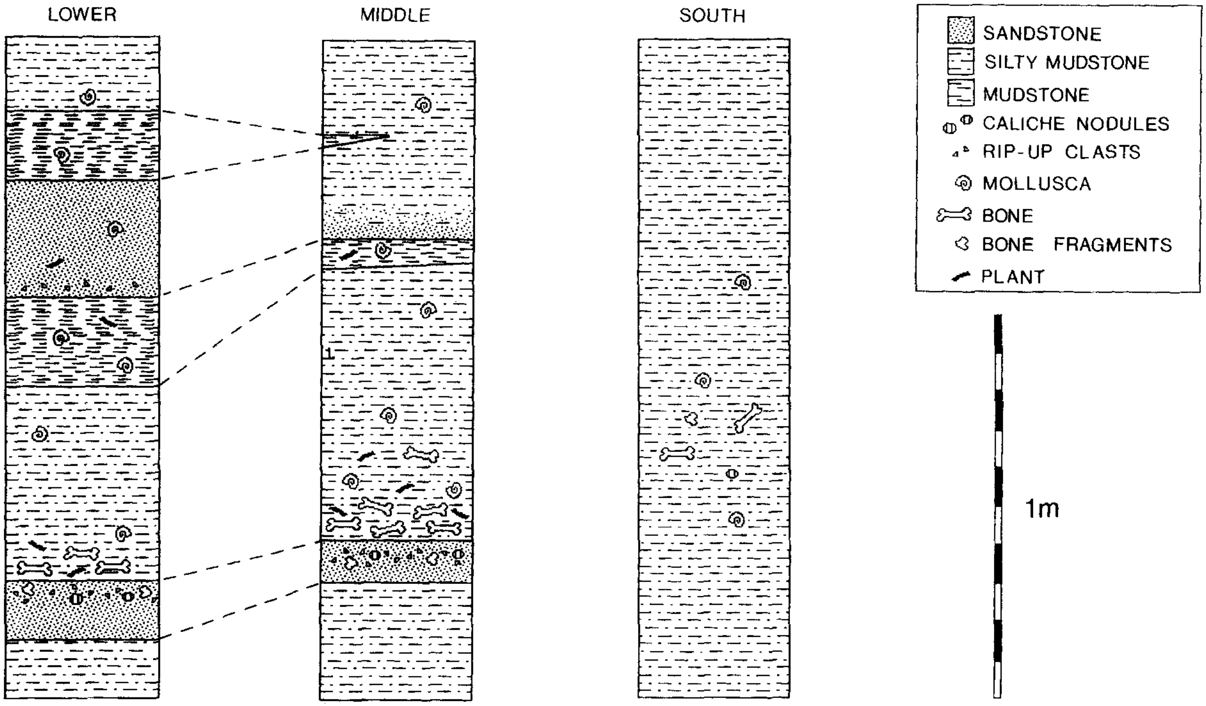

Fig. 4. Sedimentary profiles for the three west side quarries, Lower, Middle, and South (see Fig. 2). Columns are roughly 10m apart along a N20°W trend. Bones mark main bone concentration only.

over 10% by weight of the unit. The northwest quarries contain compressed, coalified wood, showing conchoidal fractures and a vitreous luster. Pieces range in size up to 0.1–0.2 m by 1.5 m. Plant remains are absent from the southeast quarries.

The bone-bearing unit contains abundant gastropods. Shells are complete, unabraded, but distorted by lithostatic compaction. Opercula occur separately. An aquatic pulmonate, *Physa*, and terrestrial snails dominate the gastropod assemblage (Table 1). A complete range of ontogenetic sizes, suggesting the presence of viable populations, exists for both *Physa* and the most common terrestrial snail. The few *Viviparus* are all large, while the remaining gastropod species show some size variation. In the main bone-bearing unit, rare unionids and other bivalves occur as isolated, primarily fragmentary valves and are likely allochthonous (Brett, 1990). Also present are charaphyte (green algae) nucules and ostracods.

Two finely-laminated units, with maximum thicknesses of 30 and 40 cm, overlie the bone-bearing unit in the northwest (Fig. 4). A poorly-sorted, fine-grained sandstone separates these two units. The finely-laminated units consist of interbeds of dark organic-rich muds and veneers

Table 1
Jack's Birthday Site gastropod assemblage

Count	Percentage	
31	16%	Pleuroceridae, three species, including cf. *Lioplacodes williamsi* and *Lioplacodes* cf. *L. judithensis*
6	3%	Viviparidae, probably *Campeloma*
71	38%	Physidae, *Physa* cf. *P. copei*
16	9%	unidentified aquatic forms, two species
64	34%	unidentified terrestrial forms, two species
188	100%	Total

Gastropod assemblage collected during excavation of the main bone-bearing horizon. Pleuroceridae, Viviparidae and Physidae are aquatic forms.

of silt or sand (Fig. 5). Thicknesses of these layers range from 0.2 to 7 mm. Though somewhat irregular in thickness, their discrete alternations are reminiscent of non-glacial varves (Anderson et al., 1985). Preserved within both finely-laminated units is a minimum of 200 alternations between dark fines and coarser material. Some portions show soft-sediment deformation. Compressed plant debris, common on some horizons, includes needles and stems of Taxodiaceae and reed-like monocots. Invertebrates include gastropods and bivalves of the genus *Sphaerium*, which typically occurs as small aggregations of open but articulated valves. Vertebrate remains consist of articulated fish, fish scales, and rare isolated dinosaur bones. Two types of coprolites, both irregularly–ellipsoidal in shape, are recognized: one is dark, massive and possibly phosphatic, and the other consists of loosely-bound molluscan shell debris. Both finely-laminated units thin to the southeast and terminate in Brad and Middle as dark stains in the normally green–gray mudstone (Fig. 4). The intervening sandstone contains mud rip-ups along its base, fairly large (> 10 cm) plant material, and occasional to common invertebrates, mostly gastropods. This unit also pinches and grades laterally into the massive mudstone to the southeast (Fig. 4).

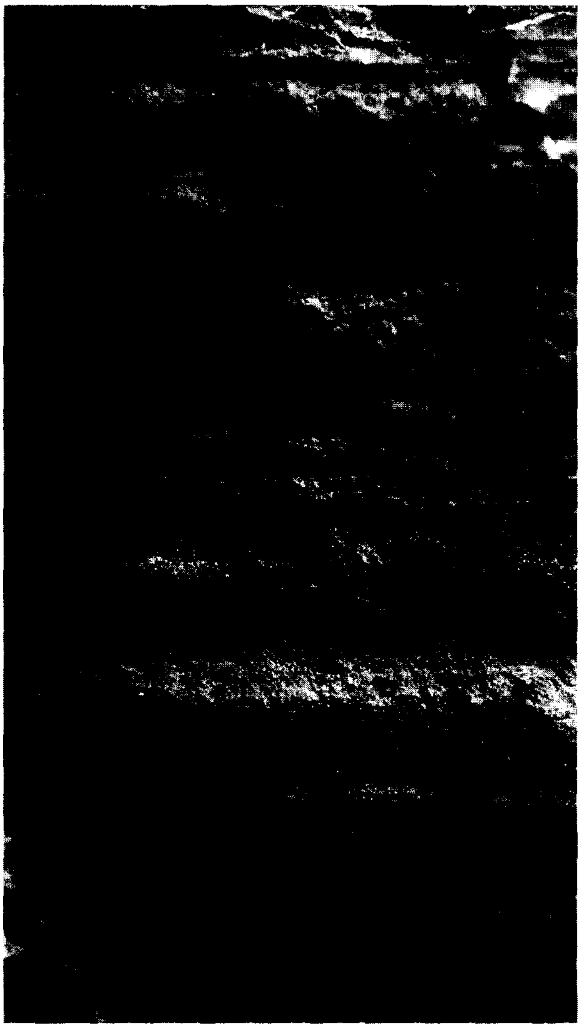

Fig. 5. One of the finely-laminated units lying just above the main bone-bearing unit at Jack's Birthday Site and showing dark organic-rich mudstones (*m*) separated by veneers of silt- and sandstone (*s*). Scale bar equals 1 cm. Photo courtesy of Frankie Jackson.

5. Bone sample

Over 1600 identifiable vertebrate elements have been collected and prepared. Bone composition as determined by heavy-ion-induced X-ray satellite emission (HIXSE) and X-ray diffraction (XRD) at the Oak Ridge National Laboratory, Tennessee, consists of hydroxyapatite, calcite, iron, and manganese (Jack Young, pers. commun.) Petrographic thin sections show preservation of the bone's original mineral structure and calcite permineralization (Varricchio, 1993).

Ten dinosaur taxa make up over 90% of the assemblage (Table 2). Three iguanodontoids, *Hypacrosaurus* sp., *Prosaurolophus blackfeetensis* (Horner, 1992), and *Gryposaurus* sp., together account for over 65% of the elements and roughly 40% of the individuals preserved. The similarity of lambeosaurid and hadrosaurid postcrania prevents taxonomic assignment of this fraction even at the family level. *Hypacrosaurus* elements represent juveniles through adults; those of *P. blackfeetensis* and *Gryposaurus* primarily subadults and adults (Varricchio and Horner, 1993). *Troodon formosus* and tyrannosaurids are the next most common dinosaurs. Other dinosaur taxa are rare. Theropods as a group are relatively abundant and account for over 20% of the elemental and over

Table 2
Jack's Birthday Site species list

NISP	MNI	
42		UID
2	1	Osteichthyes
17	1	Lepisosteidae
1	1	Amphibia
6		Chelonia
11	1	Chelydridae
9	1	*Basilemys* sp.
1	1	Mammalia
9	1	Squamata
4	1	Champsosauridae (1)
10	1	Crocodilia (8)
21		Pterosauria
4	1	Azadarchidae
61		Theropoda
113	2	Tyrannosauridae (48)
5	1	Ornithomimidae
8	1	Dromaeosauridae (6)
15	2	Saurornitholestes sp. (13)
195	4	*Troodon formosus* (17)
1	1	*Richardoestesia* sp. (1)
1	1	*Avisaurus* sp.
933	1	Iguanodontoidea (68)
84	8	*Hypacrosaurus* sp.
24		Hadrosauridae
35	4	*Prosaurolophus blackfeetensis*
15	3	*Gryposaurus* sp.
4	1	Ceratopsia (2)
29	1	Ankylosauria (8)
1660	40	Totals (172)

Number of identifiable specimens (NISP), minimum number of individuals (MNI), and species list for the vertebrate assemblage at Jack's Birthday Site. Number of NISP represented by isolated teeth in parentheses. MNI's for nested taxonomic categories are not redundant.

25% of the individual counts. Aquatic vertebrates, crocodiles, champsosaurs, turtles and fish represent less than 4% of the bone sample.

In most instances, particularly in theropods, functional teeth were lost from jaws and all unfused elements were disarticulated. Disarticulation occurred even in elements representing very large individuals, for example centrums and neural arches of "mature" (i.e. crested) *Hypacrosaurus*. Nevertheless, many examples of clearly associated remains exist throughout the locality. Tyrannosaurid elements, representing a single large individual in the East quarry, provides the most explicit example. These parts, easily separated from other taxa and individuals, consist of dorsal through caudal vertebrae, pelvic elements, and portions of both fore- and hindlimbs scattered over 20 m^2. The randomness of the distribution of tyrannosaurid elements within the site (Table 3), was evaluated using a χ^2-test and expected values calculated from the total number of identifiable tyrannosaurid specimens and total and individual quarry areas. The non-random distribution of the tyrannosaurid elements ($p < 0.001$) demonstrates their associated nature. Other examples of similarly well-dispersed but associated individuals include: *P. blackfeetensis* remains in Lower and Middle; juvenile *Hypacrosaurus* in the East quarry; and turtle, pterosaur, *Troodon formosus* and adult *Hypacrosaurus* in South quarry. This last example is notable for preserving one individual with several caudal vertebrae with pathologic neural spines. The randomness of the distributions of identifiable specimens within the site for *Hypacrosaurus*, unidentified hadrosauridae, *P. blackfeetensis*, *Gryposaurus*, unidentified theropoda, and *Troodon formosus* (Table 3), were also independently tested using a χ^2-test. Bone counts for each of the taxa have non-random distributions across the three quarries ($p < 0.001$).

Within Jack's Birthday Site, bone preservation varies from northwest to southeast over a distance of 50 m. In the three northwestern quarries, Brad, Lower and Middle, nearly all the elongate elements lie flat, a result of the underlying sandstone (Appendix 1). The few steeply inclined elements typically involve bones braced by other bones. Brad and Middle (Fig. 2) have, relative to the other quarries, a higher density of both bone and wood, with bones stacked upon each other up to five or even seven elements thick (Figs. 6 and 7).

Few elements in South and East contact other bones (Fig. 8). In contrast to the northwest quarries, numerous elongate elements are steeply inclined (Appendix 1, Fig. 9A) and several broad, flat bones, e.g. a lambeosaurid pubis, stand on edge (Fig. 9B). Throughout the site, elongate elements align to the SE–NW and to a lesser degree to the SW–NE (Appendix 1).

Bone breakage and weathering increase significantly from the northwest to the southeast

Table 3
Distribution of dinosaur taxa, NISP, and individual counts, within Jack's Birthday Site

	Hypacrosaurus		Hadrosauridae	*Prosaurolophus*		*Gryposaurus*		Theropoda	*Troodon*		Tyrannosauridae	
	NISP	ind.	NISP	NISP	ind.	NISP	ind.	NISP	NISP	ind.	NISP	ind.
BLM	16	1	22	33	4	8	2	3	11	0	7	0
South	30	2	2	2	0	7	1	50	165	4	13	0
East	38	5	0	0	0	0	0	8	2	0	49	1
Totals	84	8	24	35	4	15	3	61	178	4	65	1

NISP exclusive of teeth and numbers of associated individuals (ind.) broken down by quarry for the five dinosaur taxa represented by associated material. The table includes unidentified hadrosaurid and theropod element counts, because the former likely includes additional *Prosaurolophus blackfeetensis* and *Gryposaurus* material and the latter additional *Troodon formosus* material. Areal extent of the three northwest quarries, Brad, Lower, and Middle (BLM) = 50 m^2; South = 60 m^2; and East = 32 m^2.

(Table 4). Modified bones occur in the East quarry at a rate two to six times higher than in the three northwestern quarries. Coincident with this is an increase in unidentifiable angular bone fragments within the bone-bearing unit. These fragments, common in the East quarry, are rare in Brad, Lower and Middle. Also of note in the South and East quarries, are many broken bones with their constituent pieces closely associated. The sizable displacement between pieces rules out lithostatic compaction (Fig. 9C). Tooth-marked elements are uncommon (12 of 1300). Abrasion, distinguishable from weathering (see discussions on bone modification in Behrensmeyer, 1991) is rare, and less than 8% of complete to half-complete bones show wear. Frequencies of class 2 and 3 abrasion (Shipman, 1981), compare with those of weathering: 3% in the northwest quarries; 7% in South; and 16% in East.

Counts of the various dinosaur skeletal elements from the site (Table 5) were compared to predicted values based on data in Weishampel et al. (1990). For some bone categories, observed values of near complete to complete bones differ significantly from predicted values. The assemblage shows an abundance of stockier elements, primarily limb bones, metapodials, vertebrae and to a lesser extent phalanges. In contrast, gracile or elongate bones, transverse processes, chevrons, ribs and to a lesser degree cranial elements are underrepresented. After conducting experiments with disarticulated mammal skeletons in hydraulic flumes, Voorhies (1969) listed both ribs and vertebrae as some of the most easily transported elements (Group I). If true for dinosaur elements, the over-representation of vertebrae and under-representation of ribs at Jack's Birthday Site precludes the assemblage from being a primarily hydraulically-winnowed sample. Additionally, the overall closeness of observed and expected values for all elements suggests that the assemblage does not represent an allochthonous collection of hydraulically-gathered isolated elements. Instead, given the excess of more robust elements and deficiency of gracile or elongate ones, bone loss and breakage was likely primarily through trampling and weathering (Behrensmeyer and Dechant Boaz, 1980). Element counts and the abundance of associated material indicate that the bulk of the assemblage represents a parautochthonous collection of animals that gathered at, or were transported as carcasses to this locality with subsequent removal or destruction of selected elements.

Conspecific individuals cluster together within the assemblage (Table 3). *Hypacrosaurus* remains are most abundant in the South and East quarries, and represent two adults and an adult and four juveniles respectively. Numerous, appropriately-sized postcranial elements from these two quarries (not included in Table 3) are likely assignable to these individuals. The northwest quarries contain subadult and adult *Prosaurolophus blackfeetensis* remains, as well as the bulk of all hadrosaurid elements, including those of *Gryposaurus*. Total bone count for *Troodon formosus* within the South quarry approaches 170 elements and represents at

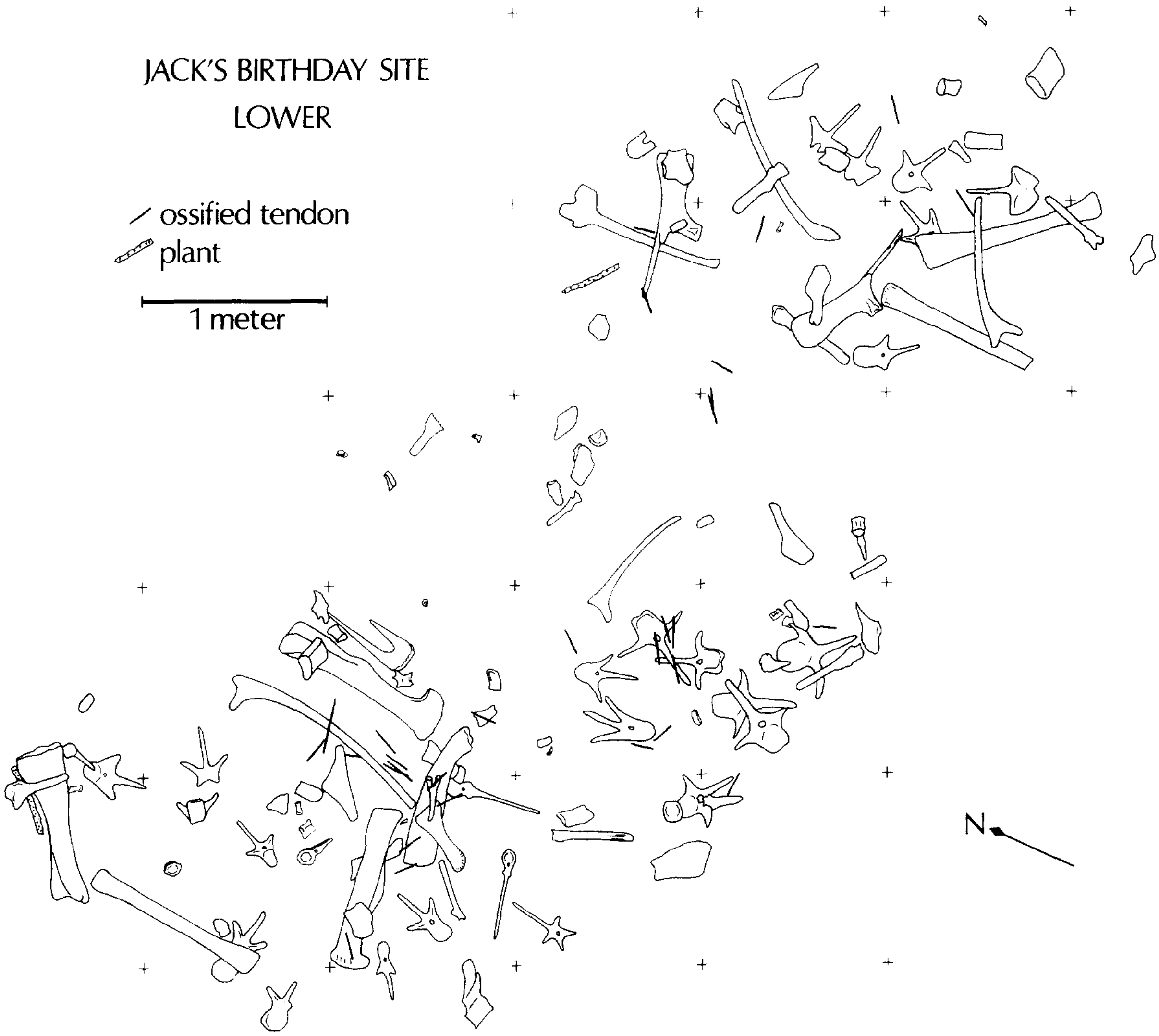

Fig. 6. Quarry map for Lower.

least four individuals. The mix of large and small individuals in South and East rules out the possibility of size-related sorting such as size-specific miring (e.g. Sander, 1992).

Fisher's Exact Test provided a measure of the randomness of quarry compositions and taxa distributions based on counts of associated individuals for *Hypacrosaurus*, *P. blackfeetensis*, *Gryposaurus*, and *T. formosus* (Table 3). This test calculates a probability for the observed distribution and all more extreme cases. Both the quarry compositions across the four taxa and the taxa distribution across the three quarry areas are highly unlikely ($p < 0.01$).

6. Depositional environment

Discrete sedimentary units, including finely-laminated horizons suggestive of quiet water deposition, extend through Brad, Lower and Middle to the northwest. These units pinch out or grade laterally into a single mudstone to the southeast. This transition reflects a shift from intermit-

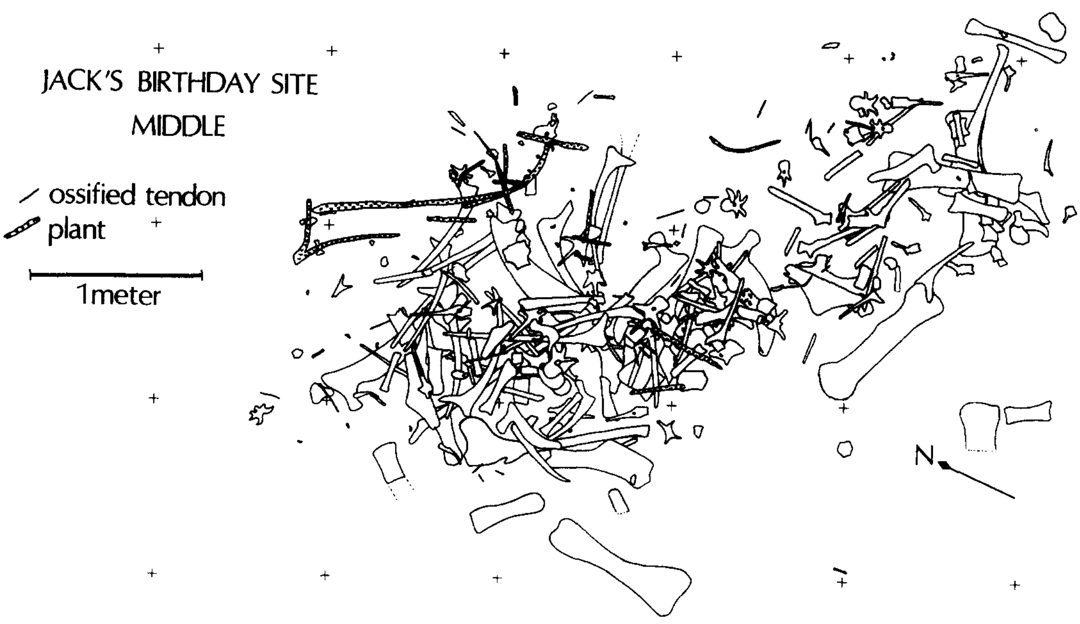

Fig. 7. Quarry map for Middle. Middle is about 3 m to the southeast of Lower (see Fig. 2). Only the central portion of Middle was fully excavated; unmapped bones remained in the incompletely excavated areas. Note the abundance of bone and plant material in Middle relative to the other quarries (Figs. 6 and 8.

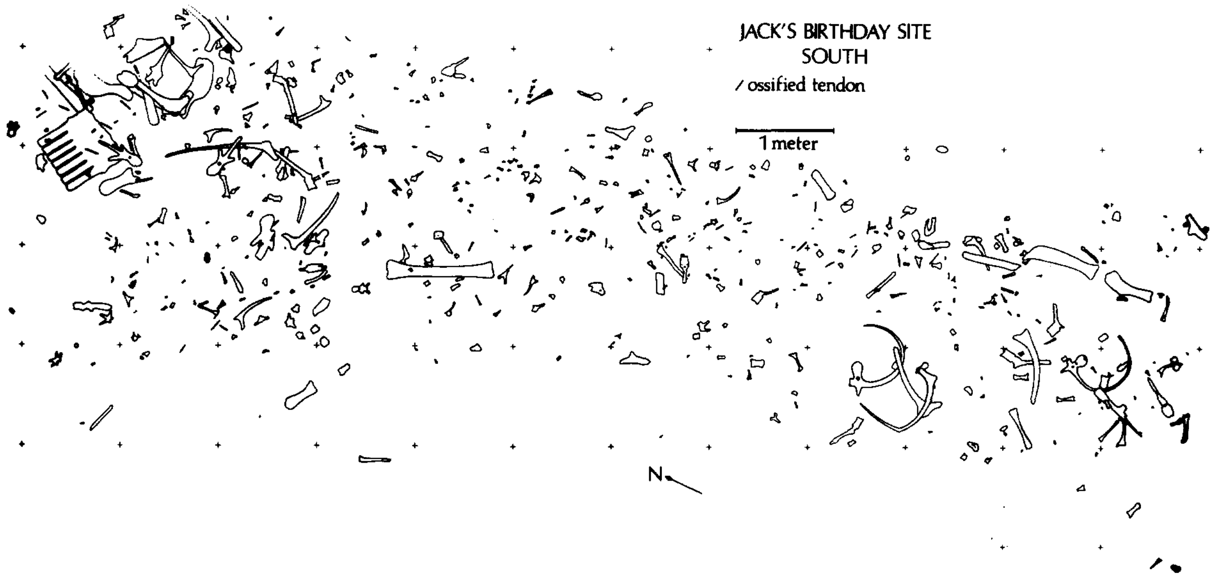

Fig. 8. Quarry map for South. South is about 3 m south of Middle (see Fig. 2).

tent to more persistent bioturbation (Rhoads, 1975) and/or increased pedogenesis. Preservation of small scale bedding in the finely-laminated units (Fig. 5) could occur only in the absence of bioturbation and presumably oligoxic or anoxic bottom conditions. Additional evidence of anoxia in the northwest include: abundant plant remains, absent in the southeast quarries; articulated fish, undis-

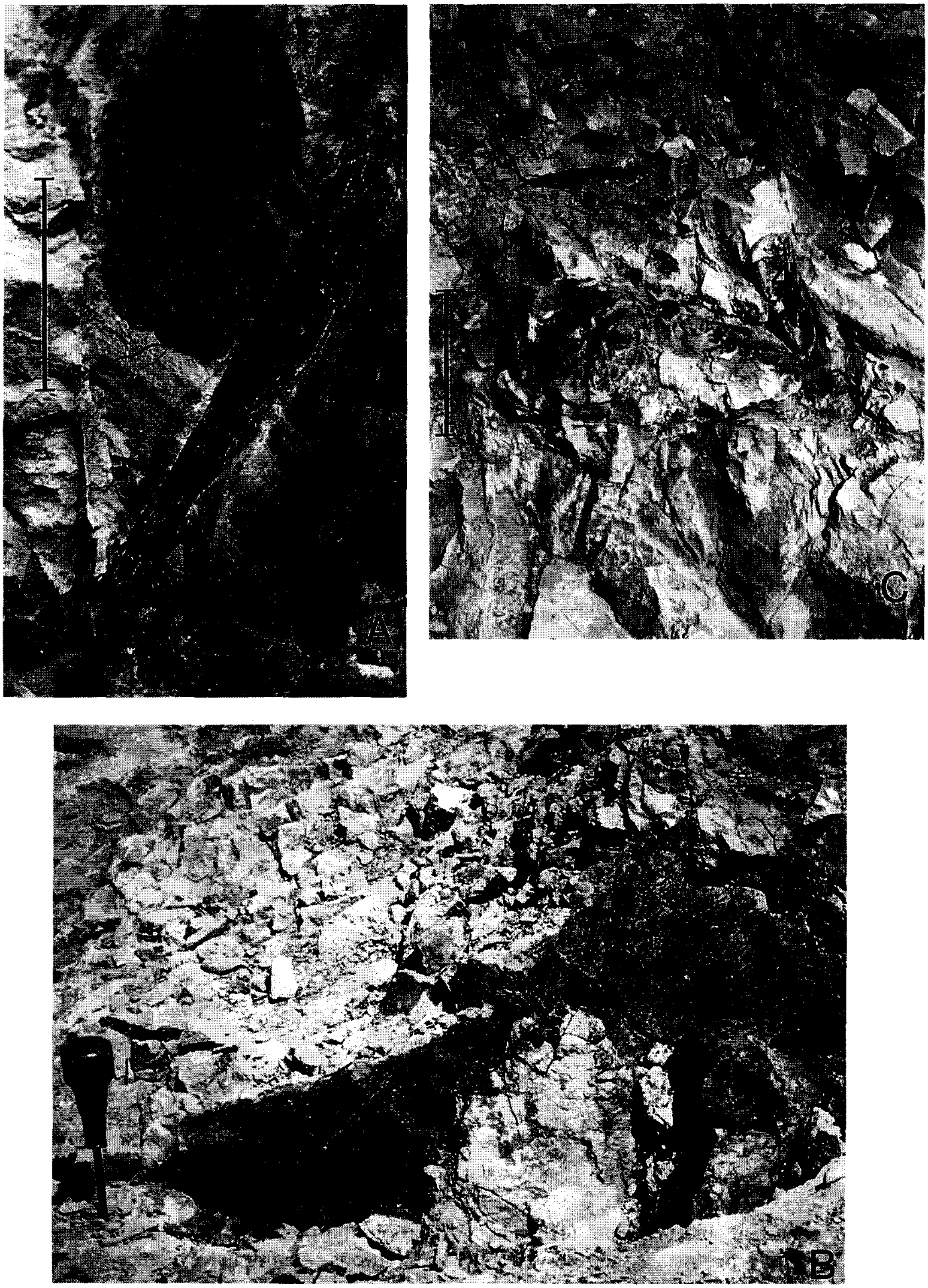

Fig. 9. Bones with unusual orientations or breaks from South. (A) Horizontal view of steeply-inclined iguanodontoid metacarpal. (B) Horizontal view of iguanodontoid adult pubis (*1*) and juvenile metatarsal (*2*), both oriented nearly vertically. (C) Oblique view of iguanodontoid caudal vertebrae (*3*) with its broken neural spine (*4*) lying alongside and steeply inclined. Scale bars in (A) and (C), and visible portion of awl in (B) equal 10 cm. Note absence of sedimentary structures.

Table 4
Bone modification

	BLM		South		East		Totals	
Breakage								
A	325	0.92	477	0.83	229	0.71	1031	0.82
B	21	0.06	48	0.08	52	0.16	121	0.10
C	7	0.02	48	0.08	43	0.13	98	0.08
Totals	353		573		324		1250	
Weathering								
0	378	0.97	537	0.91	263	0.76	1178	0.89
1	6	0.02	29	0.05	46	0.13	81	0.06
2	3	0.01	17	0.03	19	0.06	39	0.03
3	1	0.00	9	0.02	16	0.05	26	0.02
Totals	388		592		344		1324	
Tooth marks	1		2		9		12	0.01
"Nicks"	8		26		22		56	0.04

Frequency of bone modification for a sample of identifiable elements, exclusive of teeth, from the main bonebed. Breakage categories are: A, <10% of bone missing; B, 10–50% missing; and C, >50% missing. Weathering stages as in Fiorillo (1988b, table 6) and assessed using criteria of Behrensmeyer (1978) where applicable. Breakage and weathering vary significantly (χ^2-test, $p<0.001$) between the northwest quarries, Brad, Lower and Middle (BLM), South, and East. "Nicks" are apparent impact damage to bone that is likely due to either biting or trampling. Percentiles for tooth marks and nicks based on a total bone sample of 1300 elements.

turbed by scavengers (Wilson, 1988); and the organic-rich interbeds of the finely-laminated units. The variation from northwest to southeast within Jack's Birthday Site represents a change from a restricted, lacustrine environment to a well-aerated, pervasively-bioturbated floodplain. Further evidence of a lacustrine environment to the northwest are small aggregations of articulated bivalves, *Sphaerium*. These occur within fine-grained sediments and must represent parautochthonous assemblages.

Freshwater invertebrate fossils provide additional environmental clues. Modern sphaeriid bivalves are adapted for easy dispersal and colonization, and are capable of estivating during habitat desiccation (McMahon, 1991). *Physa* represents 57% of the aquatic gastropod fauna (Table 1), and, like most modern pulmonates, is semelparous and adapted to seasonally varying conditions (Brown, 1991). The gastropod assemblage, the bivalve *Sphaerium*, plus charaphyte nucules suggest quiet, shallow, restricted and possibly ephemeral waters (La Rocque, 1960; Hanley, 1976; Brown, 1991; McMahon, 1991).

Molluscan species-area studies on medium-latitude freshwater lakes (Lassen, 1975; Browne, 1981; Brönmark, 1985), predict a lake area

Table 5
Element counts are from the '89, '90, and '91 field seasons at Jack's Birthday Site. Expected percentages are based on values in Weishampel et al. (1990). Increases (+ +, major; +, minor) and decreases (–, major; -, minor) are for Jack's Birthday Site counts relative to the expected values. Similarity between observed and expected values were tested independently for each element class using a χ^2-test. Shoulder elements include: scapulae, coracoids and sternums; pelvic elements: ischia, illia and pubi; and limb elements: humeri, radii, ulnae, femora, tibias and fibulae

	Observed		Expected	Net change	Significance
	Count	%	%		p
Cranial elements	127	12	14	-	<0.05
Vertebrae	372	35	24	+ +	<0.01
Cervical + dorsal ribs	139	13	19	–	<0.01
Transverse processes	34	3	8	–	<0.01
Chevrons	56	5	11	–	<0.01
Shoulder elements	24	2	2	none	
Pelvic elements	24	2	2	none	
Limb elements	63	6	3	+ +	<0.01
Metapodials	58	6	4	+ +	<0.01
Tarsals and carpals	20	2	2	none	
Phalanges	135	13	11	+	<0.05
Total	1052				

between 0.001 and 10 km^2 for the molluscan diversity at Jack's Birthday Site. The rarity of large aquatic vertebrates suggests a small or ephemeral body of water, probably smaller than 1 km^2.

Bone preservation is consistent with a NW–SE, lacustrine to floodplain interpretation. Bone modification, primarily breakage and weathering, increases significantly away from the lake through the South and East quarries, indicating more prolonged subaerial exposure (Behrensmeyer, 1978; Fiorillo, 1988a). The very low frequency of weathering in the northwest quarries (Table 4) suggests minimal subaerial exposure (Behrensmeyer, 1978). Elongate elements align NW–SE and NE–SW (Appendix 1), consistent with a NW–SE trending shoreline (Fig. 2).

While bones in Lower are flat-lying and dispersed, those just southeast in Brad and Middle are concentrated several elements thick with large woody fragments (Figs. 6 and 7). Coincident with these concentrations are lateral lithologic changes (Fig. 4) and the southeastern limit of plant preservation, features which suggest the limits of the lacustrine basin (Fig. 2). Given this association, the massing of bone and wood may represent a strand line (cf. Weigelt, 1989, plates 25–27). In South and East, many bones show unstable near vertical orientations, "nicks" and in situ breaks (Table 4; Fig. 9). Trampling can produce such features (Hill, 1979; Behrensmeyer and Dechant Boaz, 1980; Lockley et al., 1986; Fiorillo, 1988b, 1989, fig. 5; Behrensmeyer et al., 1986). Further, track-making activity is typically most abundant along shorelines (Laporte and Behrensmeyer, 1980; Lockley, 1991) and can lead to a complete reworking of substrates (Lockley and Conrad, 1989).

Fine-scale laminae within modern meromictic lakes can be confidently interpreted as the result of seasonal climatic forcing and as varves, i.e. annual in nature (Anderson et al., 1985; Anderson and Dean, 1988). The mud and silt laminae observed here have irregular thicknesses and alternations (Fig. 5). Whether annual or not, they indicate a persistence of this lacustrine environment for some time.

Evidence suggests that Jack's Birthday Site represents a small, shallow floodplain lake. Two taxa, *Physa* and *Sphaerium*, adapted to variable environments, dominate the molluscan assemblage. This, together with the alternating sequence of coarse and organic-rich fine sediments within the finely-laminated unit, suggests that the Birthday Site lake may have been subjected to recurrent fluctuations in environmental conditions such as water influx and oxygen levels.

7. Taphonomic interpretation

The assemblage consists of two main fractions that represent different taphonomic histories. The first and much smaller consists of predominantly isolated elements representing a diversity of taxa, dispersed widely both horizontally and vertically. This fraction shows a variety of bone conditions ranging from relatively pristine to extensively weathered or abraded, stages 0 to 3 (Fiorillo, 1988b) and classes 1 to 3 (Shipman, 1981), respectively. Vertical dispersion and variable preservation suggests these represent an attritional collection of elements, both locally-derived and transported into the lake basin. Serial predation, observed to produce low bone density assemblages associated with small water bodies (Haynes, 1988), offers a probable source for some of this fraction.

The second fraction consists of completely disarticulated, well dispersed but associated elements, and represents the bulk of the bonebed. The effects of trampling and weathering, rather than transport, likely account for the deviations in element counts from expected values (cf. Table 5; Behrensmeyer and Dechant Boaz, 1980, fig. 5.6). The observed lateral variation in bone condition reflects the shift from lake basin through shore to floodplain (Behrensmeyer, 1978; Hill, 1980). Consequently, the bonebed fraction of the assemblage represents either parautochthonous animals that gathered at, or allochthonous carcasses transported to, the Birthday Site lake. Attritional mortality during periods of non- or low sedimentation could result in a bonebed (Kidwell, 1986). However, high bone density, associated skeletons, and a non-random distribution of taxa (Table 3) including clusters of several individuals each of *Hypacrosaurus*, *Prosaurolophus blackfeetensis*, and

Troodon formosus, suggest that the bonebed resulted from a series of mortality events (cf. Haynes, 1988). The close juxtapositioning of these taxonomic clusters, suggests a single underlying cause.

A variety of causes, both observed or inferred, produce mass vertebrate mortality: volcanism (Voorhies, 1985; Stager, 1987), mass-wasting (Weishampel and Westphal, 1986), fire (Sander, 1987), winter storms (Berger, 1986, p. 86; Lemke, 1989; Grayson, 1990), entrapment in muddy substrates (Berger, 1986, p. 84; Weigelt, 1989; Sander, 1992), drowning (Talbot and Talbot, 1963; Sullivan, 1984; Haynes, 1988; Turnbill and Martill, 1988; Wood et al., 1988), serial predation (Haynes, 1988), drought (Shipman, 1975; Sinclair, 1977, plate 41; Behrensmeyer and Dechant Boaz, 1980; Rogers, 1990) and disease (Ingram and Prescott, 1954; Sinclair, 1977, p. 253; Locke and Friend, 1987). Several of these mechanisms seem inappropriate for the assemblage at Jack's Birthday Site. The site lacks volcanic ash, slumped sediments or fusain (fossil charcoal). Entrapment in soft substrates should preserve at least partial articulation or close association of elements (Sander, 1992). Further, taxonomic clustering would be unexpected with most of these mechanisms. For example, winter storms, drowning or poisonous volcanic gas can kill a variety of taxa, but it would require fortuitous circumstances to produce the assemblage found here. Mortality would have to either coincide with the gathering of a variety of taxa at Jack's Birthday Site or occur repeatedly as each group gathered at the lake. These mechanisms remain unlikely possibilities. Interpreting the taxonomic clusters at Jack's Birthday Site as resulting from a single or related events, favors mechanisms capable of both affecting a variety of species and concentrating mortality at a floodplain lake. Three such examples, drought and two types of disease, botulism and cyanobacterial toxicosis, are examined.

7.1. Drought

Paleontologists have noted the potential of drought to generate fossil assemblages (Romer, 1961; Shipman, 1975; Behrensmeyer and Dechant Boaz, 1980; Carpenter, 1987; Rogers, 1993), and Rogers (1990) suggested it as the most likely cause of three Two Medicine dinosaur bonebeds. Biologists have documented drought's effect on modern ecosystems. Modern ungulates, particularly water-dependent grazers, congregate at available water holes during both the dry season and droughts (Western, 1975; Corfield, 1973; Conybeare and Haynes, 1984). As dry spells persist, animals deplete suitable forage nearby and, by necessity, consume poorer and poorer quality fodder. Eventually, animals die due to malnutrition and starvation. This often occurs well before water sources have completely dried (Corfield, 1973; Hillman and Hillman, 1977; Conybeare and Haynes, 1984; Carpenter, 1987). Mortality occurs primarily around water sources (Corfield, 1973; Behrensmeyer and Dechant Boaz, 1980; Conybeare and Haynes, 1984; Haynes, 1988; Williamson and Mbano, 1988) and may result in large and diverse bone assemblages (Haynes, 1988, table 1).

For elephants, drought strikes the young and to a lesser extent the old (Corfield, 1973, fig. 5; Conybeare and Haynes, 1984). For artiodactyls and perissodactyls, drought primarily affects the young and adult females first, but in time mortality reflects the age and sex ratios of a normal, living population (Hillman and Hillman, 1977). In four drought-generated bone assemblages from modern Africa, carnivores accounted for less than 4% of the total MNI (Haynes, 1988, table 1). Drought may not affect predators as severely as it does herbivores (Carpenter, 1987) or the paucity of predators within these drought death assemblages may simply reflect their low abundances within extant mammalian faunas.

Drought-related mortality is a plausible explanation for the bonebed at Jack's Birthday Site for several reasons. The seasonally wet/dry Two Medicine climate would have been susceptible to droughts (Dodson, 1971; Lorenz, 1981; Gavin, 1986; Crabtree, 1987; Jerzykiewicz and Sweet, 1987), and drought has been invoked as a taphonomic explanation for a variety of Late Cretaceous fossils from the region (Carpenter, 1987; Rogers, 1990). The concentration of primarily herbivore remains, namely three species of iguanodontoids,

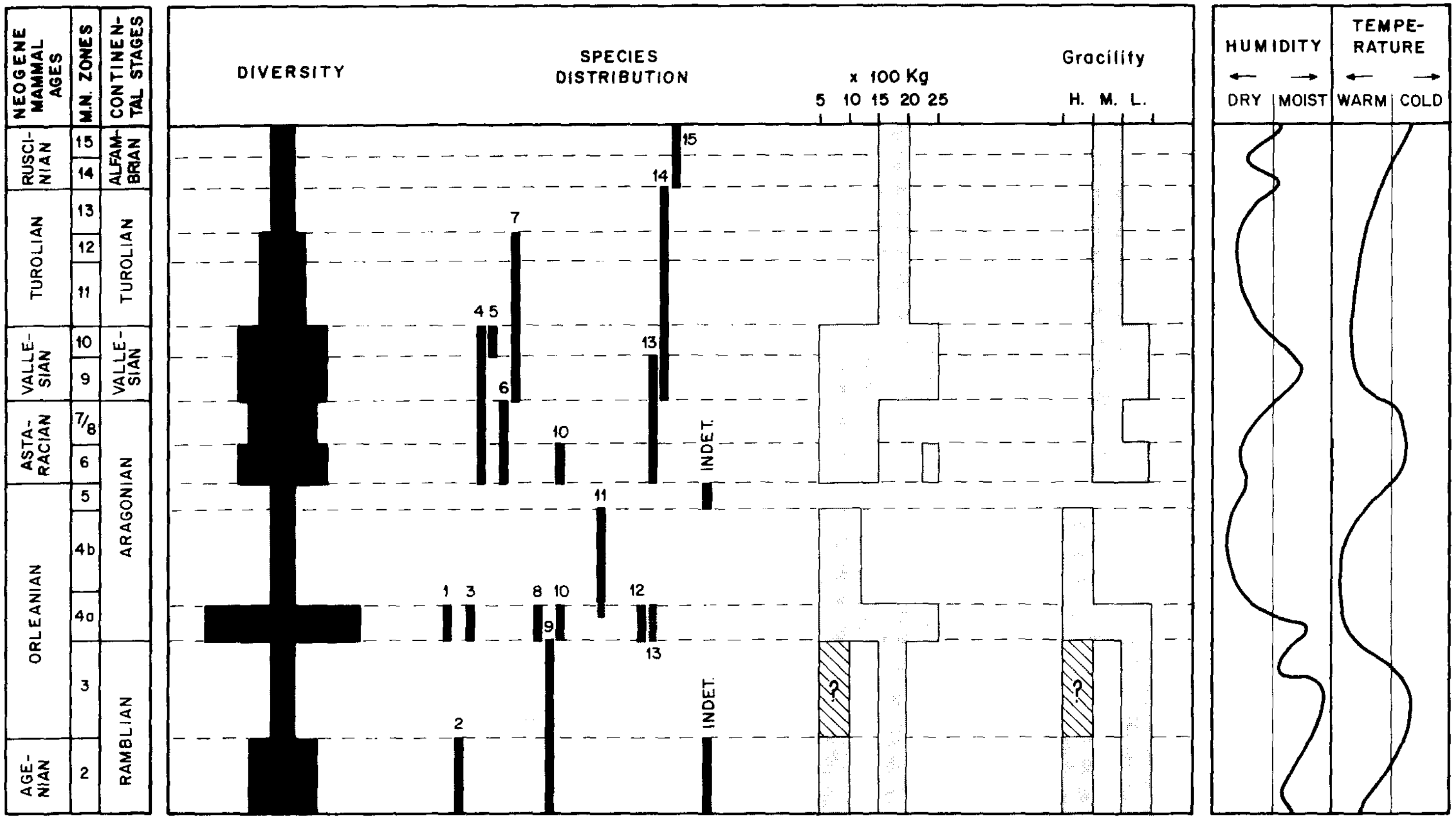

Fig. 7. Chronostratigraphic correlation between Spanish rhinocerotid distribution, diversity and morphological features and the paleoclimatic curves (Calvo et al., in press). The continuity between *P. minutum* and *P. platyodon* during MN 3 is supposed. Weights and gracility indexes not available in certain stages are estimated from the same species of other periods.

Fig. 10. Typical scene of avian botulism resulting in the mass mortality of waterfowl along the shore of a small, shallow lake. Note the exposed mud bank and lines of carcasses paralleling the shore, both due to a drop in water level, and the transition from lake to shore to floodplain. Photograph courtesy of Dr. Jim Runnigan and the National Wildlife Health Research Center, Madison, Wisconsin.

outbreaks killing thousands of birds (Fay et al., 1965; Locke and Friend, 1987; Gophen et al., 1991). Like other clostridia, *C. botulinum* is a strict anaerobe that persists as heat and drought resistant endospores. These spores occur unevenly throughout the world in soils and wetland sediments (Locke and Friend, 1987; Rocke, 1993). Botulism outbreaks happen under a variety of conditions, but nearly always in association with rotting carcasses. In lacustrine settings, *C. botulinum* initially grows and produces toxins in carcasses of terrestrial invertebrates killed by flooding or in aquatic invertebrates killed by receding water (Rocke, 1993). Environmental factors commonly but not universally associated with these settings include: high ambient temperatures; shallow anoxic water; fluctuating water levels, particularly sharp draw downs; rotting vegetation and an abundance of vertebrate or invertebrate carcasses (Smith, 1976; Locke and Friend, 1987). Lines of carcasses coinciding with receding water lines typify outbreaks of avian botulism in lacustrine settings, and several freshly dead birds may be found within a few feet of a maggot-laden carcass (Locke and Friend, 1987; Fig. 10). Botulism affects a wide variety of mammals and birds, including various carnivores and raptors (Halliwell and Graham, 1986; Locke and Friend, 1987, fig. 7.2; Rocke, 1993). Several carrion-eating species, coyote (*Canis latrans*), crows (*Corvus brachy-*

rhynchos) and turkey vultures (*Cathartes aura*), have antibodies to the botulism neurotoxins (Rocke, 1993).

Three species of *Clostridium*, *C. barati*, *C. butyricum*, and *C. botulinum*, produce botulism toxins (Rocke, 1993) and *C. botulinum*, though referred to as a single species, is really a conglomerate of culturally distinct groups (Smith and Williams, 1984). *Clostridium* belongs to the low gram-positive bacteria, a phylogenetically deep and presumably ancient cluster, sharing a close relationship to cyanobacteria (Woese, 1987, 1991) Evolutionary distances among species of clostridia are often far greater than those between the two enteric bacteria, *Escherichia* and *Salmonella*, a distance estimated to represent several hundred million years. Thus, a Cretaceous botulism-producing *Clostridium* is possible (C.C. Woese, pers. commun.).

The depositional environment at Jack's Birthday Site is similar to lake settings where botulism commonly occurs today. The climate was warm (Dodson, 1971; Wolfe and Upchurch, 1986; Crabtree, 1987) and the invertebrate fauna indicates shallow water. Evidence supporting anoxic conditions, includes: coalified plant material and the finely-laminated units with millimeter-scale bedding, organic-rich horizons, and undisturbed fish remains. As discussed above (see p. 312), bone preservation as a possible strand line in Brad and Middle, and as disarticulated, well-dispersed trampled bones in mud in South and East, likely reflects fluctuating water levels. Plant material occurs as horizontally-oriented fragments, clearly not in life position. This plant material and the abundant invertebrates would provide decaying organic matter. All of the above features could occur in association with drought.

The abundance and distribution of theropods may differentiate between drought and botulism mortality.

Where determined, the source of botulism toxin is always attributable to decaying carcasses. Consequently free-ranging animals that are most likely to encounter botulism are those that feed on invertebrates or vertebrates. Though habitual scavengers do show some resistance, occasional carnivores and predaceous species remian susceptible (Rocke, 1993). Theropods, considered to be the most predaceous of the dinosaurs, are unusually abundant Jack's Birthday Site. No other Two Medicine bonebed has any associated theropod remains (Rogers, 1990; Varricchio and Horner, 1993). This includes three localities considered a result of drought mortality (Rogers, 1990). The theropods, particularly the *Troodon*, rest on the lake margin, and the first field sign listed by Locke and Friend (1987) for the recognition of avian botulism is an association of bird carcasses and shore line (Fig. 10). Theropod mortality could result from consumption of toxic-laden carcasses, invertebrate or vertebrate, possibly involving a bird–maggot-like cycle. Finally, the ancestry (Gauthier, 1986) and near universal susceptibility of birds to botulism, make theropods good candidates for botulism mortality.

Mass mortality of generally herbivorous animals due to botulism happens rarely, and only if the herbivores consume carcasses, either inadvertently or purposefully (Smith, 1976; Locke and Friend, 1987; Rocke, 1993). Thus, botulism is an unlikely cause of the iguanodontoid mortality at Jack's Birthday Site. Drought produces conditions in lacustrine settings favorable for botulism outbreaks. So, both drought and botulism mortality could occur together. Iguanodontoids dying of starvation and malnutrition within the lake basin would provide a suitable substrate for *Clostridium botulinum* growth and toxin production. A drought/botulism hypothesis might better account for the peculiar composition and distribution of taxa at the site than a single mechanism. Whether it is more parsimonious to infer drought and/or botulism mortality depend on future understanding of dinosaur physiology and ecology. For example, might iguanodontoids, like some waterfowl, have consumed invertebrates when feeding on aquatic vegetation? or would *Troodon* have been as drought susceptible as *Prosaurolophus*?

Recognition of *Clostridium* bacilli and spores within fossil sediments remains unlikely. Both are very small (e.g. bacillus size is 4.6 μm by 0.9 μm) and species are morphologically indistinguishable (Smith and Williams, 1984; Smith 1976). Proper identification requires bacilli or spores to be preserved with their specific chemistry intact.

Clostridia toxins, as degradable proteins, are equally unlikely to be detected (Smith and Holderman, 1968). Bones from Jack's Birthday Site have not been specifically tested for the presence of proteins. Because the botulism toxins act by blocking the release of neurotransmitters (Rocke, 1993), toxin would be unexpected in bones in significant amounts.

7.3. Cyanobacterial toxicosis

Several varieties of blue–green algae, cyanobacteria, have potent toxins within their cell walls. Death and decay of cells releases these toxins into the water (Beasley et al., 1989). Favorable environmental conditions lead to algal blooms where released toxins reach concentrations potent enough to kill animals drinking from the algal-infested water (Stephens, 1945; Rose, 1953; Juday et al., 1981; Beasley et al., 1989). Favorable conditions for growth include: warm, sunny weather; quiet to stagnant water with a *p*H between 6 and 9 or higher and a temperature between 15° and 30°C; and sufficient nutrients such as nitrogen and phosphorus (Beasley et al., 1989; Wicks and Thiel, 1990). Steady winds precipitate vertebrate mortality by driving the toxic algae to shores where animals drink (Rose, 1953; Beasley et al., 1989). Some of the 12 genera known to produce toxins resulting in animal deaths include *Anabaena*, *Aphanizomenon*, *Microcystis*, *Nodularia*, and *Oscillatoria* (Carmichael, 1994). Algae produce either hepato- or neurotoxins. Death may result from within a few minutes to 48 hours after exposure, depending upon the toxin type and amount ingested (Gorham, 1964; Beasley et al., 1989). Rapid death leads to an accumulation of animals in or near water sources (Stephens, 1945; Beasley et al., 1989; Fig. 11). Algal blooms may occur repeatedly over a season and result in the mass mortality of both birds and mammals (Stephens, 1945; Rose, 1953; Ingram and Prescott, 1954; Juday et al., 1981).

Cyanobacteria have a long fossil record (Rickards, 1990) and the diversity of toxin-producing algae, increases the likelihood of a

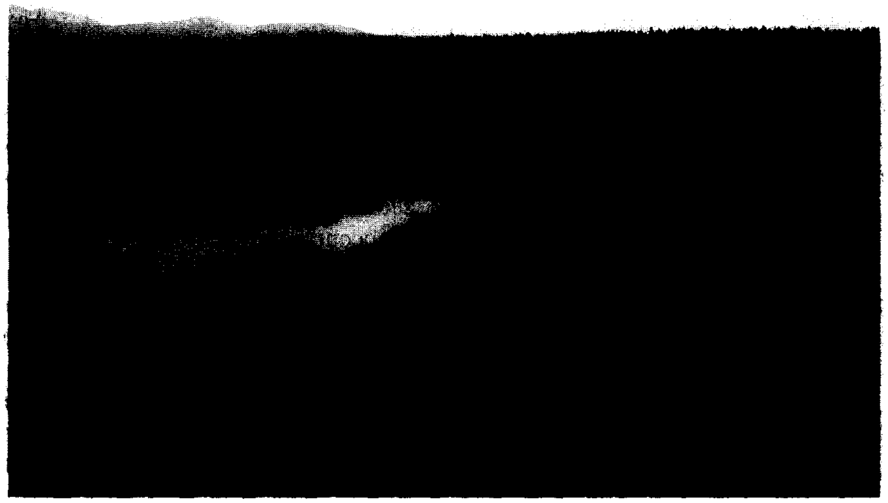

Fig. 11. A small arm of Hebgen Lake, Montana, where two cows have perished from cyanobacterial toxicosis, a result of drinking from adjacent water. Photo courtesy of Dr. Larry Stackhouse, Veterinary Diagnostic Laboratory, Montana State University.

similar form in the Cretaceous. Currently, little evidence exists for cyanobacterial toxicosis mortality at Jack's Birthday Site. The dinosaur/lake association, alkaline sediments, and climate fit cyanobacterial toxicosis outbreaks. The preservation of toxins, consisting of degradable alkaloids and peptides (Beasley et al., 1989), remains unlikely, but no chemical search was attempted. Scums or paints at or under the water's surface characterize blue–green algae growths, with major blooms result in thick "porridge-like" scums (Rose, 1953; Beasley et al., 1989; Carmichael, 1994). Despite their small cellular size, aggregates of blue–green algae could potentially fossilize. The mostly fragmentary plant material at Jack's Birthday Site contained nothing reminiscent of cyanobacteria. Finally, it is unclear how the environmental factors leading to algal toxicosis could account for observed sedimentologic features, for example, the concentration of bones at the base of the mudstone in the northwest quarries.

8. Discussion

Jack's Birthday Site, a multispecific, primarily parautochthonous assemblage associated with a small floodplain lake, differs from most other Late Cretaceous bonebeds. Generally, multispecific vertebrate assemblages of the Two Medicine–Judith River interval consist of either channel lag or microvertebrate concentrations (Wood et al., 1988; Eberth, 1990; Rogers, 1993), while bonebeds from Birthday Site-like depositional environments preserve only mono- to paucispecific faunas dominated by a single iguanodontoid or ceratopsian species (Rogers, 1990, 1993; Varricchio and Horner, 1993). Several diverse Jurassic Formation assemblages associated with floodplain deposits resemble Jack's Birthday Site: Como Ridge, Morrison Quarry, and the M and M Quarry (Dodson et al., 1980; Kirkland and Armstrong, 1992).

The assemblage at Jack's Birthday Site has two components. The first and less abundant consists of unassociated material with variable preservation. This fraction, despite the numerous macrovertebrate remains, corresponds to the "subaqueous microfossil concentration" type of Rogers (1993). Local attritional mortality and transport of isolated elements over some 100 to 1000 years produce these bone accumulations.

The second and larger component at the site comprises most of the bonebed. It consists primarily of taxonomically-segregated associated individuals. Simple statistical tests demonstrate the nonrandom distribution within the site of taxa by both element and individual counts (Table 3). Except for being multispecific, this second component fits the "subaqueous bonebed concentration" type of Rogers (1993), event bonebeds representing less than one to ten years of accumulation. This portion of the bonebed evades a simple explanation, for it is unclear if the taxonomic clustering represents a single event, a series of related events or unrelated events. A variety of mortality mechanisms could be invoked, but alone most seem unlikely to produce the diversity and spatial arrangement of taxa found here. If the assemblage at Jack's Birthday Site represents a single event or related events, then the most probable mechanisms are those that act over an ecologically significant period of time, e.g. a season; affect a variety of taxa; and concentrate mortality around persistent water sources. Examples include drought and some diseases, namely botulism and cyanobacterial toxicosis. The seasonally wet/dry climate, concentration of herbivorous dinosaurs, similarity of the bonebed to type III or IV shell beds of Kidwell (1986) and possible indication of a drop in lake water level favor drought. These features do not rule out the possibility of botulism, and it may best account for the abundance of theropods. Currently a connection between cyanobacterial toxicosis and the sedimentologic aspects of the site is lacking and its occurrence seem doubtful. Though drought or drought/botulism mortality are favored, the assemblage may have resulted from an unknown series of events from a variety of mechanisms.

Diseases, such as botulism and cyanobacterial toxicosis, may have generated fossil assemblages. Both result from bacteria of possibly ancient lineages and both concentrate mortality around persistent water sources, depositional settings where vertebrates have a higher preservational potential. Botulism assemblages should consist predominantly of insectivorous and carnivorous species, excluding habitual scavengers. Age- and sex-selective mortality should not be apparent in the death assemblage. In lacustrine settings, sedimentologic and paleontologic features should reflect environmental factors favoring outbreaks (see p. 313, 315) with a possible association of vertebrate remains and shoreline indicators. Wherever botulism occurs, potentially there should be remnants of both the consumed, vertebrate or invertebrate carcasses, and the consumer. Botulism mortality is a reasonable hypothesis for several Mesozoic bonebeds dominated by presumably carnivorous dinosaurs, for example, the occurrence of several *Deinonychus* and the remains of a single *Tenontosaurus* (Ostrom, 1990) or the *Coelophysis* beds where at least two large individuals apparently consumed smaller ones (Colbert, 1989). Botulism may be totally inappropriate for both, but proper evaluation here and elsewhere requires detailed investigation and description.

Environmental factors leading to algal blooms (see p. 315) may not affect sedimentation significantly, thus precluding the recognition of cyanobacterial toxicosis in the fossil record. Preservation of algal scums may require special circumstances. Algal toxicosis should affect a variety of taxa, but water-dependent species, such as grazers (Western, 1975) should dominate resulting death assemblages. Whereas a drought assemblage would likely be associated with a sedimentologic change, one resulting from algal toxicosis may not.

Jack's Birthday Site represents a significant record of the Two Medicine fauna and contains most of the dinosaur families of the time. Exceptions include rare caenagnathid and elmisaurid theropods, hypsilophodontids, protoceratopsids and pachycephalosaurids. Interspecific differences in physiology (e.g. water-dependence), behavior, habitat, and preservational potential have likely skewed diversity both in abundance and presence/absence (Behrensmeyer and Dechant Boaz, 1980).

The taxonomic clustering of individuals suggest at least a tendency among these dinosaurs to aggregate. Hadrosaurids and lambeosaurids are known from a number of paucispecific bonebeds (Gilmore, 1929; Nelms, 1989; Rogers, 1990; Christians, 1991; Fiorillo, 1991; Varricchio and Horner, 1993). Given the variety of depositional settings in which these bonebeds occur, they most likely reflect herding or group behavior. Tracksites (Carpenter, 1992) and the cranial ornamentation observed in both groups is consistent with gregariousness (Geist, 1966; Jarman, 1974; Hopson, 1975; Weishampel and Horner, 1990).

Troodontids are rare (Béland and Russell, 1978, table 4; Osmólska and Barsbold, 1990). The unusual finding of four or more *Troodon formosus*, within the South quarry, represents the first co-occurrence of troodontid individuals. The lack of comparable localities, hinders the interpretation of this *T. formosus* assemblage. It could reflect habitual use of a choice feeding or drinking spot; site-specific mortality, e.g. botulism; a tendency to aggregate; or the remnants of a social group. Histologic work indicates that at least two juveniles, a subadult and adult were present (Varricchio, 1993). Nearly all group behavior of modern carnivores, particularly those including juveniles and adults, involve related individuals (Kleiman and Eisenberg, 1973; MacDonald, 1983; Bekoff et al., 1984; Frank, 1986; Rogers, 1987). If the *T. formosus* assemblage represents the remnants of a group, it was possibly some type of family unit.

9. Conclusions

Jack's Birthday Site represents deposition within a small floodplain lake, with a discernible transition from lake through shoreline to marginal shoreline/floodplain environments (cf. Figs. 2 and 10, and Haynes, 1985, fig. 13). Within the lake basin, oligoxic or anoxic bottom conditions prevented extensive bioturbation and contributed to the preservation of sedimentary bedding and plant material. At the periphery of the lake basin, bedding and plant preservation are lost due to an increase in bioturbation and pedogenesis. Here, massed bone and wood represent a strand line. Moving to the southeast and toward the marginal shoreline and floodplain environments, bones show signs of being trampled and significant increases in both breakage and weathering.

Jack's Birthday Site differs from most other Late Cretaceous assemblages in being a multispecific but primarily parautochthonous bonebed. Five species of dinosaurs, represented by associated individuals, include three iguanodontoids, *Hypacrosaurus*, *Gryposaurus*, and *Prosaurolophus blackfeetensis*, a tyrannosaurid, and the first multi-individual troodontid occurrence. Individuals represented by associated material show segregation by species. Although attritional mortality and transport of isolated elements may account for much of the diversity of the assemblage, multi-individual species clusters suggests event mortality. Mechanisms such as drought, botulism, and cyanobacterial toxicosis, could account for this mortality, for they act over an ecologically significant period of time, affect a variety of taxa, and concentrate death along water sources. Evidence supports drought or a combination of drought and botulism but the diversity and spatial complexity of the site evades a definitive explanation. Taxonomic clustering may represent a series of events and a variety of suggested or unknown mechanisms may be responsible for the assemblage.

Diseases, such as botulism and algal toxicosis can propagate within water bodies and cause rapid death of terrestrial vertebrates. Both could have generated mass mortality in the past and they should be considered when generating hypotheses for the interpretation of fossil assemblages.

Statistical tests can be formulated to evaluate complex fossil localities. These may help in the recognition or demonstration of pattern, for example: skeletal association or completeness, taxonomic clustering, rates of bone modification, etc., and may provide important clues for interpreting bonebed origins.

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Appendix: Bone orientation

Trends and plunges of elongate bones and plant fragments were plotted on a stereonet and contoured through Spheristat-S (Fontenac Wordsmiths, 1990), an orientation analysis and plotting program based in part on Robin and Jowett (1986). Northwest (Brad, Middle and Lower) and southeast (South and East) quarries were plotted and analyzed separately. The small formational dip, roughly 1° or 2° to the west, was ignored. Relevant statistics shown are: N = number of data points; k = number of counting stations used in contouring; E = expected number of points per station; σ = standard deviation; *Peak* = trend and plunge of the peak distribution; *Peak Height* = significance of the peak measured in σ; the three eigenvector trends and plunges; K = an eigenvector-based measure of the distributions shape; and C = a measure of the significance of K (Woodcock, 1977). The lowest contour level (lightest stippling) plotted has a value of E. Subsequent contour levels increase by a value of 2σ, so that the highest (solid black) has a value of $E+8\sigma$. Values greater than $E+4\sigma$ are considered significant at the 95% level (Jowett and Robin, 1988).

The contour for the northwest quarries approaches a nonpreferred distribution in an approximately horizontal plane (Fiorillo, 1988c). This distribution is characterized by the low K and relatively large C-values (Woodcock, 1977). Significant clusters occur in the northwest and southeast directions. The peak value occurs in the latter.

Southeast quarries show a more uniform distribution, a product of the increased numbers of moderately to steeply inclined bones. The lower σ and C-values reflect this. Significant orientation and the peak value occur to the northwest, what is interpreted as the lakeward (downslope) direction. Contour plot of the entire data set, both northwest and southeast quarries, is very similar to that of the northwest quarries.

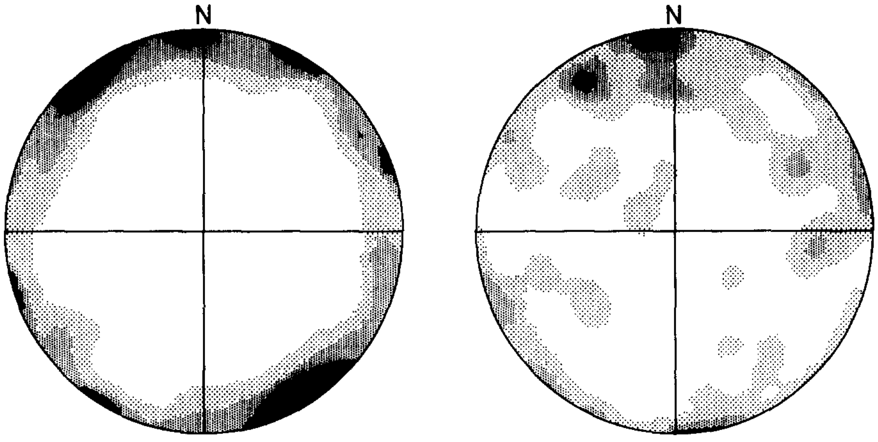

Fig. A1. Plots for the northwest and southeast quarries showing trends and plunges of elongate bones and plant fragments.

	Northwest quarries	Southeast quarries
N	215	181
k	100	100
E	2.15	1.81
σ	1.03	0.94
Peak	144°, 2°	353°, 4°
Peak height	8.9	5.9
eigenvector 1	2°, 88°	188°, 75°
eigenvector 2	245°, 1°	96°, 1°
eigenvector 3	155°, 2°	6°, 15°
K	0.18	0.39
C	1.58	0.67

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