Jacks birthday sit, a diverse dinosaur bonebed from the cretaceous two medicine formation of Montana
by David Joseph Varricchio

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
Jack's Birthday Site, a diverse vertebrate assemblage from the Upper Cretaceous Two Medidne Formation of western Montana, was taphonomically investigated and compared with other predominantly iguanodontoid bonebeds from the area. The large bone sample at Jack's Birthday Site allowed statistical evaluation of the preservational and compositional variation within the site. Evidence, including sedimentary fades, 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, representing a transition from lake through shoreline to marginal shoreline/floodplain environments.

The vertebrate assemblage contains ten dinosaur taxa and a variety of non-dinosaurs and indudes two taphonomic fractions. The first, consisting of attritional, predominantly isolated and allochthonous elements, represents a time-averaged assemblage. The other consists of assodated, parautochthonous remains restricted to a single horizon. Taxa represented by associated remains indude three iguanodontoids, Hypacrosaurus, Prosaurolophus, and Gryposaurus, and the theropod Troodon. Associated individuals of these taxa have non-random distributions within the site and observed taxonomic dustering may reflect group behavior and/or event mortality. The four or more Troodon represent the first described multiindividual troodontid occurrence.

Other predominantly iguanodontoid assemblages, like Jack's Birthday Site, are single highly concentrated bone horizons occurring in silty mudstones. Most are primarily parautochthonous with some degree of skeletal assodation and likely represent mass-mortality. The size-frequency profile of the Camposaur bonebed supports a catastrophic origin. Jack's Birthday Site differs in its diversity, the other localities being nearly monospecific, and its size-frequency profile for iguanodontoids which suggests strongly selective mortality and/or preservation. These plus the site's variable preservation indicate that Jack's Birthday Site is a much more time-averaged assemblage.

Both hadrosaurids and lambeosaurids appear to have been gregarious. Lack of association between small (total length <3 m) and larger individuals suggests that juvenile growth rates may have been as rapid as large ungulates. Size-frequency profiles for Maiasaura peeblesorum suggest seasonally synchronous reproduction and high juvenile mortality.

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David Joseph Varricchio

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Jack's Birthday Site, a diverse vertebrate assemblage from the Upper Cretaceous Two Medicine Formation of western Montana, was taphonomically investigated and compared with other predominantly iguanodontoid bonebeds from the area. The large bone sample at Jack's Birthday Site 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, representing a transition from lake through shoreline to marginal shoreline/floodplain environments.

The vertebrate assemblage contains ten dinosaur taxa and a variety of non-dinosaurs and 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 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.

Other predominantly iguanodontoid assemblages, like Jack's Birthday Site, are single highly concentrated bone horizons occurring in silty mudstones. Most are primarily parautochthonous with some degree of skeletal association and likely represent mass-mortality. The size-frequency profile of the Camposaur bonebed supports a catastrophic origin. Jack's Birthday Site differs in its diversity, the other localities being nearly monospecific, and its size-frequency profile for iguanodontoids which suggests strongly selective mortality and/or preservation. These plus the site's variable preservation indicate that Jack's Birthday Site is a much more time-averaged assemblage.

Both hadrosaurids and lambeosaurids appear to have been gregarious. Lack of association between small (total length <3 m) and larger individuals suggests that juvenile growth rates may have been as rapid as large ungulates. Size-frequency profiles for *Maiasaura peeblesorum* suggest seasonally synchronous reproduction and high juvenile mortality.

CHAPTER 1

INTRODUCTION

Dinosaur bonebeds such as the Late Jurassic Cleveland-Lloyd and Dry Mesa quarries provide hundreds of specimens and a wealth of information on morphology and taxonomy. These rich assemblages also stimulate much speculation about their origin. At the Cleveland-Lloyd Quarry near Cleveland, Utah more than 40 individuals of the large and presumably carnivorous *Allosaurus* are found mixed with a variety of far less numerous dinosaurs (Madsen, 1976). Do these *Allosaurus* represent a group killed in a catastrophic event, animals trapped through cycles of miring and predation, or simply attritional mortality at a favored locale? At the Dry Mesa Quarry south of Grand Junction, Colorado, the disarticulated remains of seventeen species of dinosaurs are preserved within a channel sandstone (Britt, 1991). Do the relative abundances of these dinosaurs accurately reflect the once living dinosaur community or simply hydraulic transport and sorting?

Taphonomy is the study of fossil preservation, of how material moves from the biosphere to the lithosphere (Efremov, 1940). Much of taphonomy concerns the loss of data due to destructive processes such as weathering, trampling, and lithostatic crushing and the resulting discrepancies between a living community and a death assemblage. Nevertheless, by documenting information loss, taphonomy exposes processes. Bone damage represents both a loss of morphological data and a record of the modifying agents. Tooth-marked bone reflects carnivore behavior. Thus, taphonomy can provide information not only concerning the history of specimens, but also about past environments and their physical, chemical and biologic attributes (see Wilson, 1988).

At the most basic level, bonebeds reflect the interplay between the rates of sedimentation and bone accumulation (Kidwell, 1986). For example, when sedimentation is minimal or absent, background attritional mortality can eventually produce a fossil concentration which may then have the look of a single event horizon. In contrast, high sedimentation rates may swamp even higher than normal mortality, leaving fossils spread out vertically through a stratigraphic sequence. Where animals die within or adjacent to depositional environments, bone accumulation rates reflect mortality rates to the extent that post-mortem modification allows. An even greater discrepancy likely occurs between the two rates where transportation to a depositional environment is required. Sorting, mixing and reworking by hydraulic transport and selective behavior by biotic collecting agents such as scavengers may potentially obscure the relationship between mortality and bone accumulation. Fundamental to the interpretation of bonebeds is an assessment of the amount of time and transport they represent.

Taphonomic interpretations depend on both geologic and paleobiologic data. Geologic data comprise relevant stratigraphy and sedimentology, including the shape, thicknesses, lateral relationships and contacts of units; grain size, sorting and mineralogy; and sedimentary structures. Paleobiologic data consist of taxa represented; their abundance both by individual and element counts and size/age composition; degree of articulation through association of skeletons; site geometry; bone density and orientation; type, abundance and size of skeletal parts; and abundance and stage of bone modification such as abrasions, weathering damage, breaks, borings, etchings, and trample, tooth and gnaw marks. Invertebrate, plant and trace fossils and their preservation also provide significant information.

Rogers (1993) and Behrensmeyer and Cutler (1994) suggest that bonebed abundance and attributes vary non-randomly through space and time. Tectonic setting, climate and the evolution of traits imparting a susceptibility to mass mortality (e.g. body size, herding behavior), apparently influence bonebed occurrences.

In the summer of 1988 a rich dinosaur bonebed was discovered in the Upper Cretaceous Campanian Two Medicine Formation of Glacier County, Montana. Found by John "Jack" Horner on June 15th, his birthday, the locality, Museum of the Rockies (MOR) TM-068, became known as Jack's Birthday Site (JBS).

The occurrence of a bonebed in the Two Medicine Formation was not unusual. Previous excavations by the Museum of the Rockies included several paucispecific ceratopsian and iguanodontoid bonebeds (see Rogers, 1990). From the initial surface collections however, Jack's Birthday Site appeared both unusually extensive and diverse. Theropods, those dinosaurs generally considered carnivorous and rare at all other Two Medicine sites, appeared exceptionally abundant.

Excavation began shortly after the site's discovery. To evaluate the site's geologic and biologic significance, full taphonomic investigation commenced in the field in 1989 and continued through 1992. Taphonomy of Jack's Birthday Site is decribed (Chapter 2) and then compared with other Two Medicine bonebeds (Chapter 3).

CHAPTER 2

TAPHONOMY OF JACK'S BIRTHDAY SITE

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 fragmentary, 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 hydraulically 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 variety of dinosaurs representing most of the major groups. Among theropods, such assemblages include the ceratosaurs, *Coelophysis bauri* and *Syntarsus rhodesiensis* (Colbert, 1964, 1989; Raath, 1990; Rowe and Gauthier, 1990), and *Deinonychus antirrhopus* (Ostrom 1969, 1990). Monospecific mass accumulations such as the Trossingen, Germany *Plateosaurus* assemblage are characteristic of prosauropods (Weishampel, 1984; Weishampel and Westphal, 1986; Galton, 1990).

Ornithischians 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). Numerous Late Cretaceous hadrosaurid, lambeosaurid and ceratopsian bonebeds have each produced hundreds of bones representing tens of individuals (Gilmore, 1929; Currie and Dodson, 1984; Hooker, 1987; Wood et al., 1988; Nelms, 1989; Lehman, 1990; Rogers, 1990; Christians, 1991). (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 explanation of various cranial structures as social or sexual display features (Colbert, 1989; Lehman, 1989, 1990; Raath, 1990; Rowe and Gauthier, 1990; Sampson, 1993).

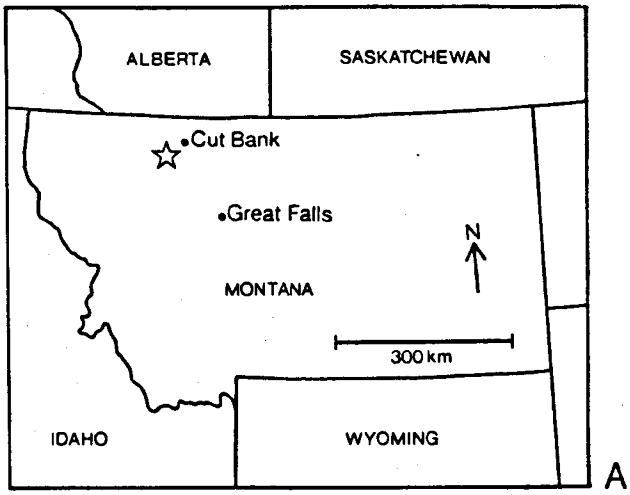
The criteria generally used to recognize mass mortality are relatively simple: a predominance of one species and concentration of bones on a single horizon. Uniformity of preservation and the demographics of the assemblage may support this interpretation. Nevertheless, attritional mortality in environments with one predominant taxon 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 waterholes in times of drought. Conditions at the Hot Springs Mammoth Site (Agenbroad, 1984) preferentially trapped only the largest animals, resulting in an attritional assemblage dominated by 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, 1991a). 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.

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). Excavation commenced in late June, 1988. The bonebed crops out on three sides of a north-south 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



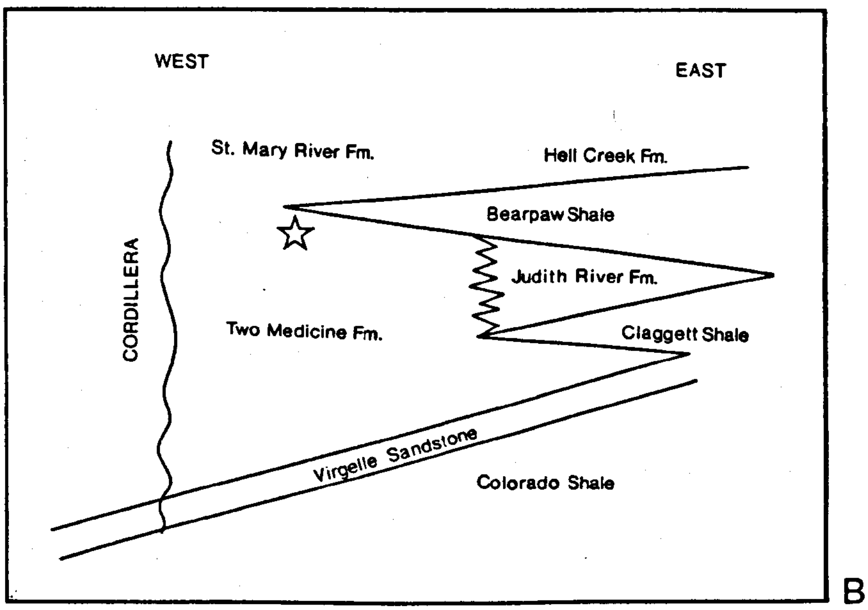


FIGURE 1. Location of Jack's Birthday Site (star), Museum of the Rockies locality TM-068, sec. 11, T31N, R8W, in Glacier Co., Montana (A) and in a stylized cross section of the Upper Cretaceous strata of north central Montana (B), modified from Horner et al. (1992).

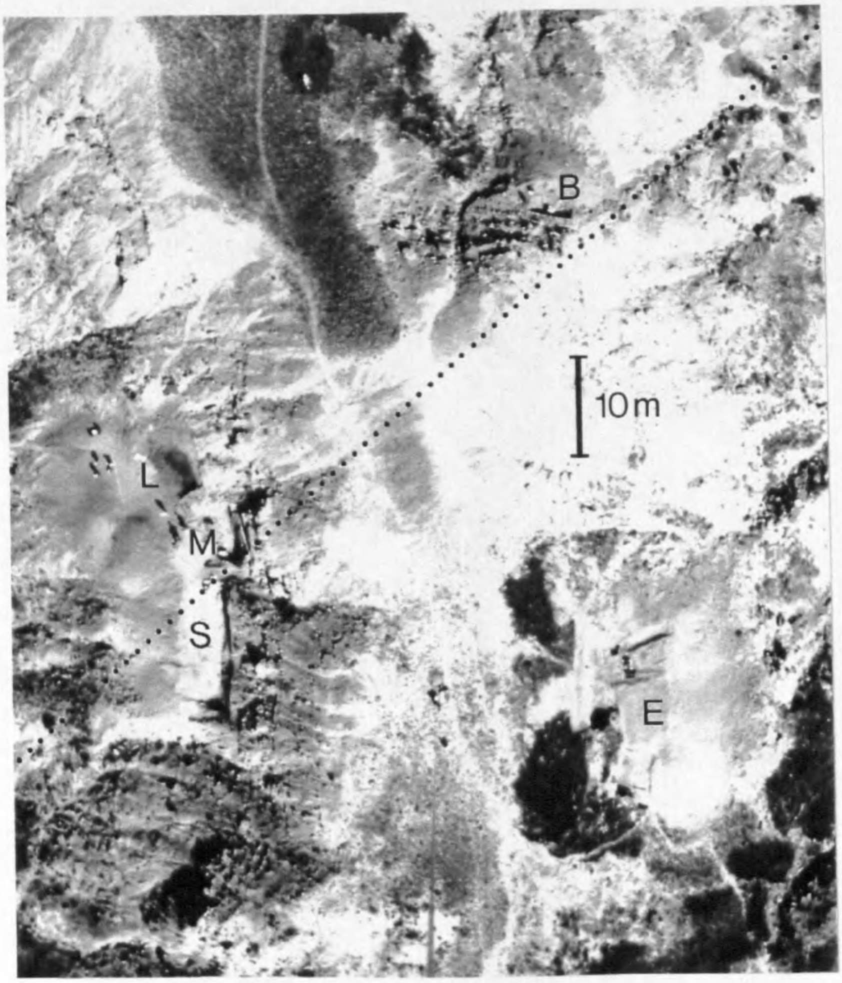


FIGURE 2. Aerial photo from hydrogen balloon of Jack's Birthday Site showing the quarries: **B**, Brad; **L**, Lower; **M**, Middle; **S**, South; and **E**, East. To the northwest, Brad, Middle and Lower, represent part of a lake basin and the dotted line marks the southeast limit of all small through medium-scale 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. 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.

excavated, and contrast 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 and tooth marks. 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 three-dimensional 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.

Regional Setting

Rogers et al. (1993) provide a recent review and dating of the Campanian 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 paleogeography 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), 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).

Jack's Birthday Site

The Two Medicine Formation along Badger Creek consists primarily of mudstone and some sandstone. Relatively common caliche horizons contrast with rare lacustrine platy shale and siltstone. Mudstones typically are massive and represent floodplain deposition. The abundance of mudstone relative to sandstone reflects the proximal basin subsidence experienced by this area during 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, moderately-sorted 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. The fossiliferous horizon lies roughly 100 m below the Two Medicine Formation-Bearpaw Shale contact (Horner et al., 1992) and 14 m above a prominent bentonite (Fig. 3) which may correlate with TM-4, a volcanic 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, 4). This thin, <20 cm thick, sandstone coarsens upwards so that the upper 5 cm contain 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 a crevasse splay, an omission or

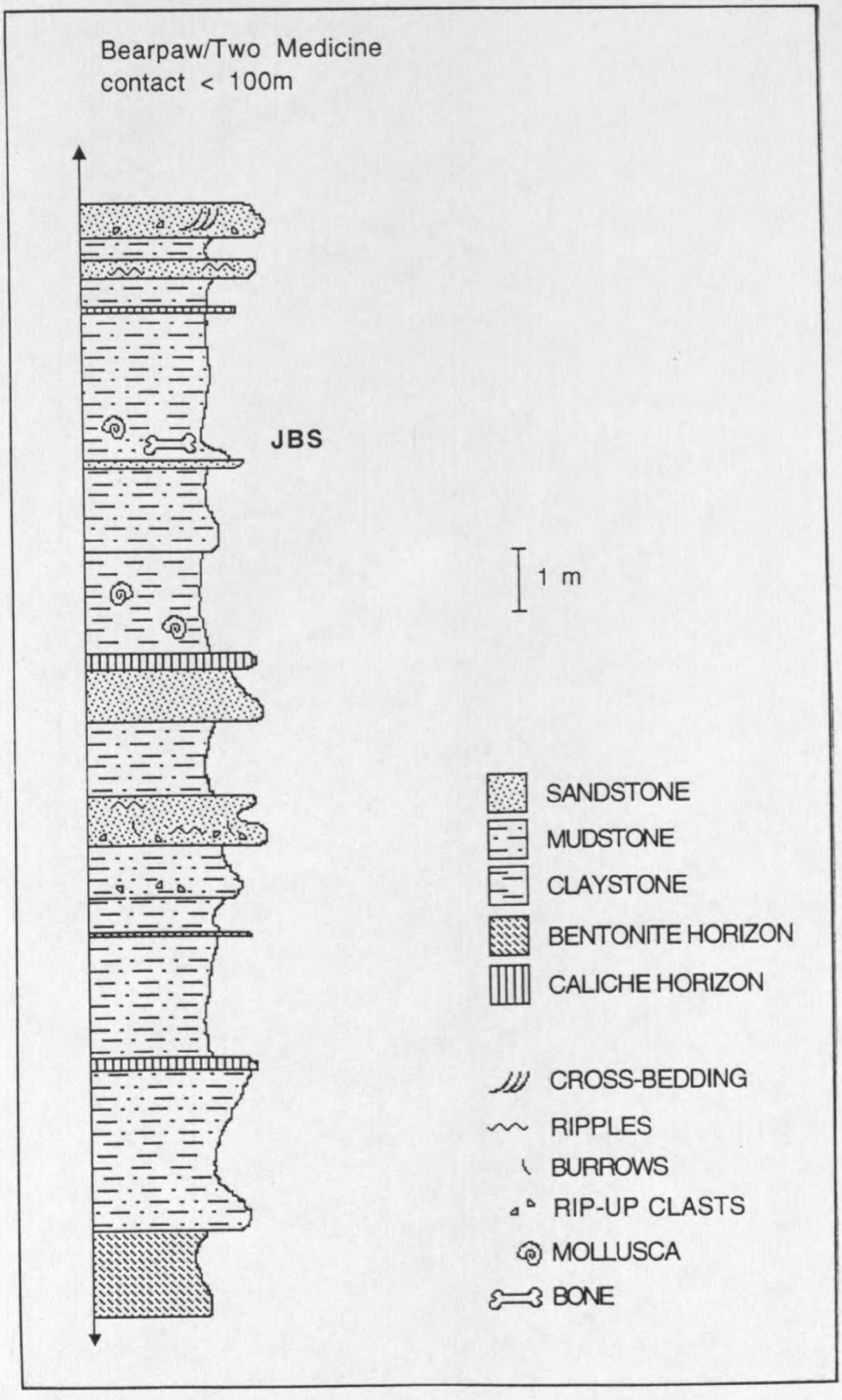


FIGURE 3. Stratigraphic column through Jack's Birthday Site (JBS). Prominent bentonite at base may correlate to an ash horizon, TM-4, dated at 74.1 Ma (Rogers, et al., 1993).

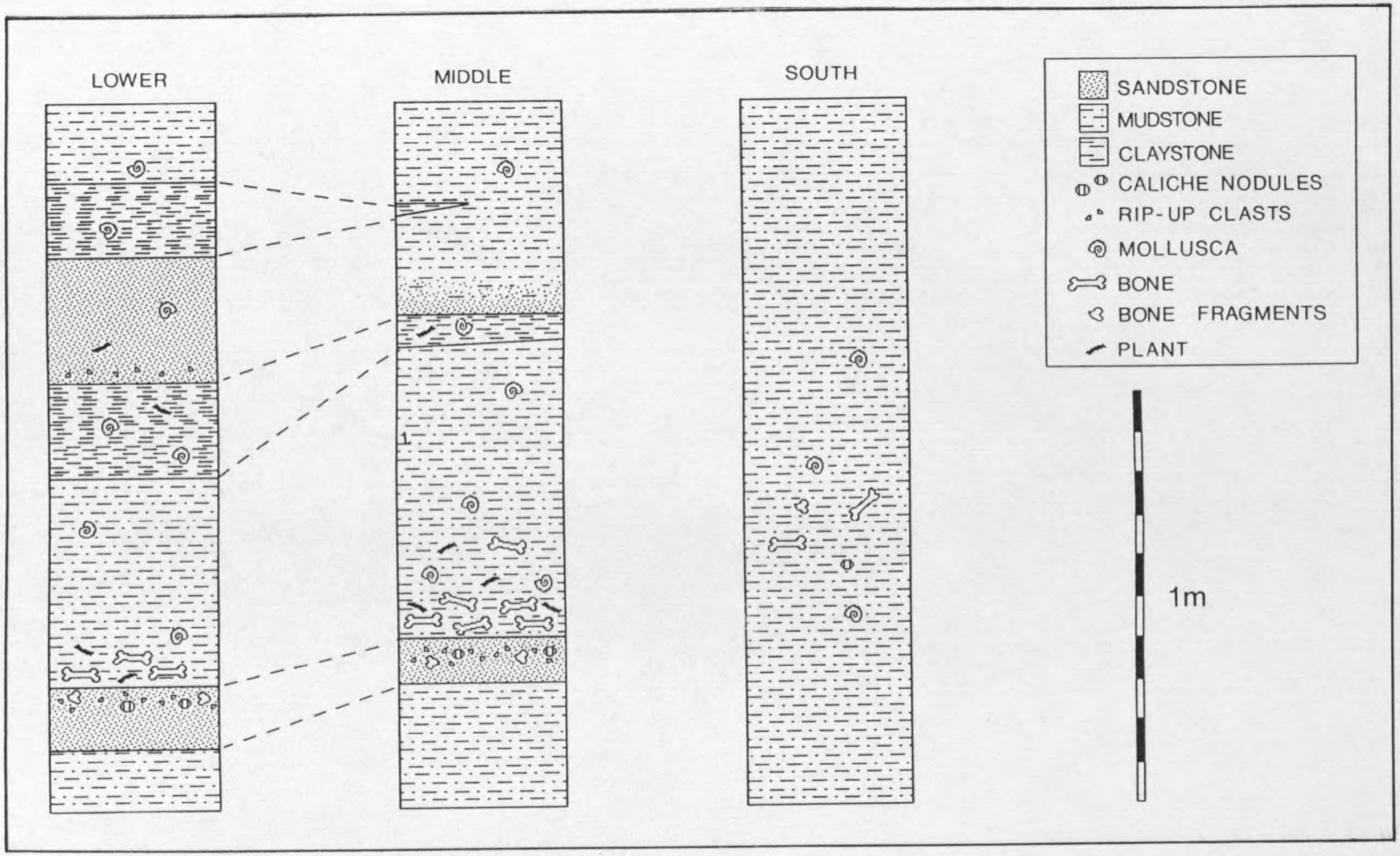


FIGURE 4. Stratigraphic profiles for the three west side quarries, Lower, Middle, and South (see Fig. 2). Columns are roughly 10 m apart along a N20°W trend. Bones mark main bone concentration only.

winnowed surface. This unit both pinches and grades laterally to the southeast into a mudstone continuous with the main bone-bearing mudstone.

In the northwest quarries (Fig. 2, 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 the 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 over 10% by weight of the unit. This unit in 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 and includes both aquatic forms such as physids, pleurocerids and viviparids, and terrestrial ones (Table 1). Shells are complete, unabraded, but distorted by lithostatic compaction. Opercula occur separately. An aquatic pulmonate,

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

Physa, and terrestrial snails dominate the gastropod assemblage. 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 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, R. 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

FIGURE 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 clay (c) separated by veneers of silt and sand (s). Scale bar equals 1 cm. Photo courtesy of Frankie Jackson.

intervening sandstone contains mud rip-ups clasts along its base, large (>10 cm) pieces of plant material, and scattered to common invertebrates, mostly gastropods. This unit also pinches and grades laterally into the massive mudstone to the southeast (Fig. 4).

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, and unidentified iron and manganese minerals (Jack Young, pers. comm.) Petrographic thin sections show preservation of the bone's original mineral structure and calcite permineralization (Varricchio, 1993).

Table 2 lists the number of identifiable specimens (NISP) and minimum number of individuals (MNI) for the vertebrate assemblage. NISP represented by isolated teeth are given in parentheses. Elements less than 50% complete make up only 8% of the NISP and problems of redundant counting of elements (See discussion in Lyman, 1994) are likely minimal. MNI's for nested taxonomic categories are not redundant. Ten dinosaur taxa account for over 90% of the assemblage's NISP and 75% of its MNI. 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

TABLE 2. Jack's Birthday Site Species List.

NISP	MNI	
42		Unidentified
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)

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 (See Chapter 3). *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 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 (Figs. 6, 7, 8). 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. Table 3 lists the NISP, exclusive of teeth, and numbers of associated individuals (ind.) for the five dinosaur taxa represented by associated material. Data are presented for each taxa by quarry. 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. Tyrannosaurid elements, representing a single large individual in the East quarry, provides the most explicit example of an associated individual. 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

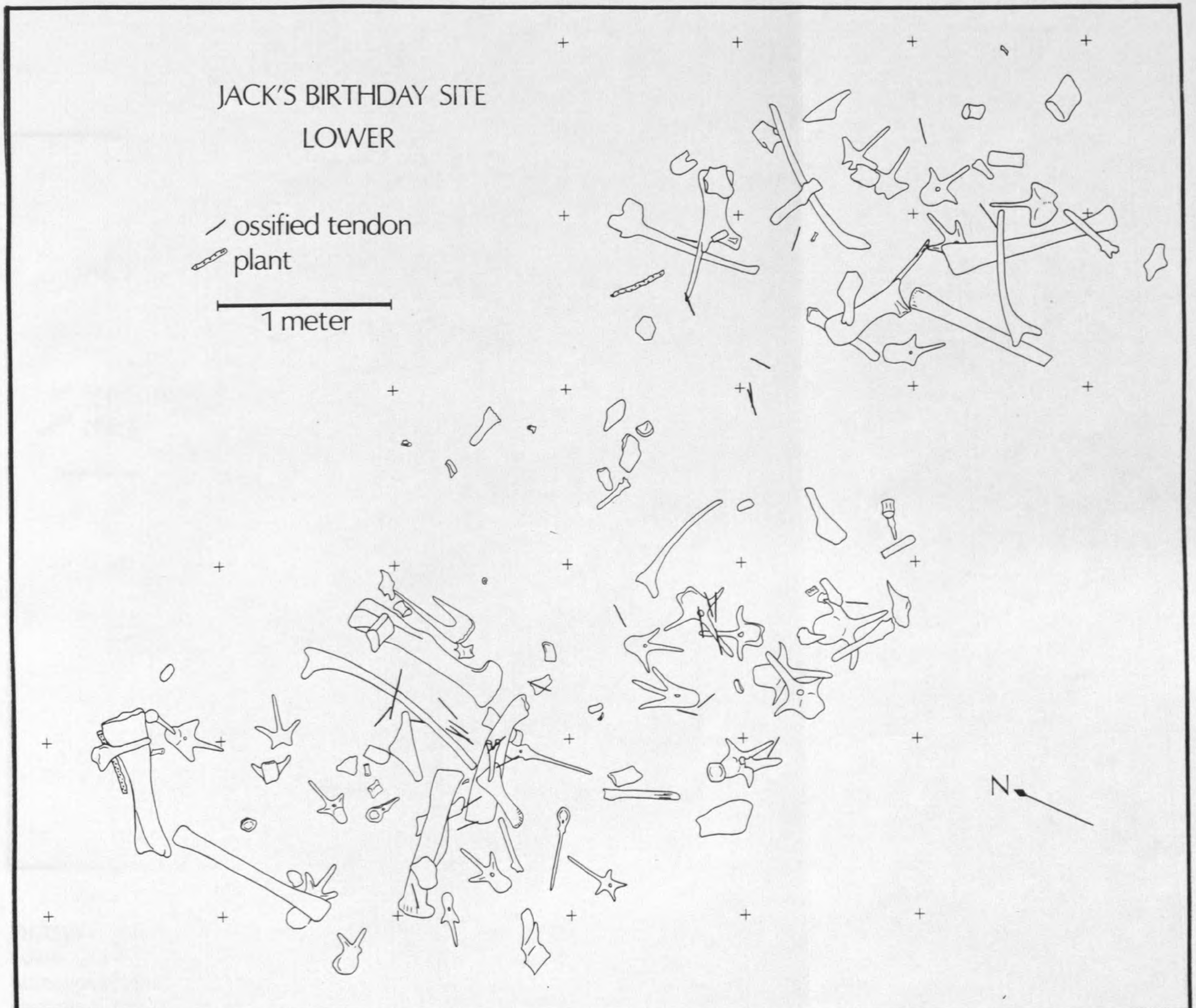


FIGURE 6. Map of Lower Quarry. Bones dispersed vertically through 50 cm.

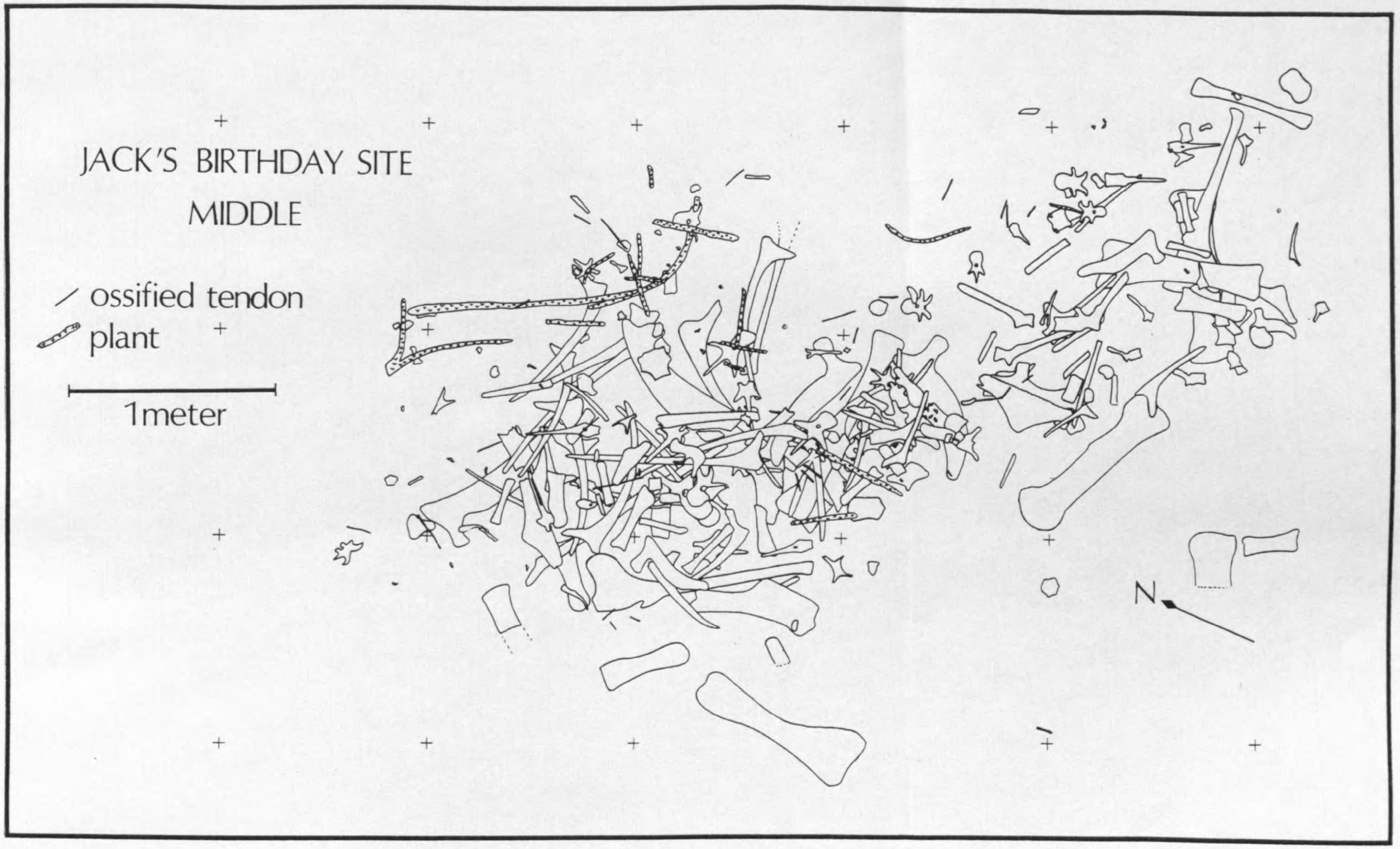


FIGURE 7. Map of Middle Quarry. Middle is about 3 m to the southeast of Lower (see Fig. 2). Only the central portion of Middle was fully excavated; unmapped bones remained in the incompletely excavated areas. Note the abundance of bone and plant material in Middle relative to the other quarries (Figs. 6, 8). Bones dispersed vertically through 50 cm. Reproduced at roughly same scale as Figures 6 and 8.

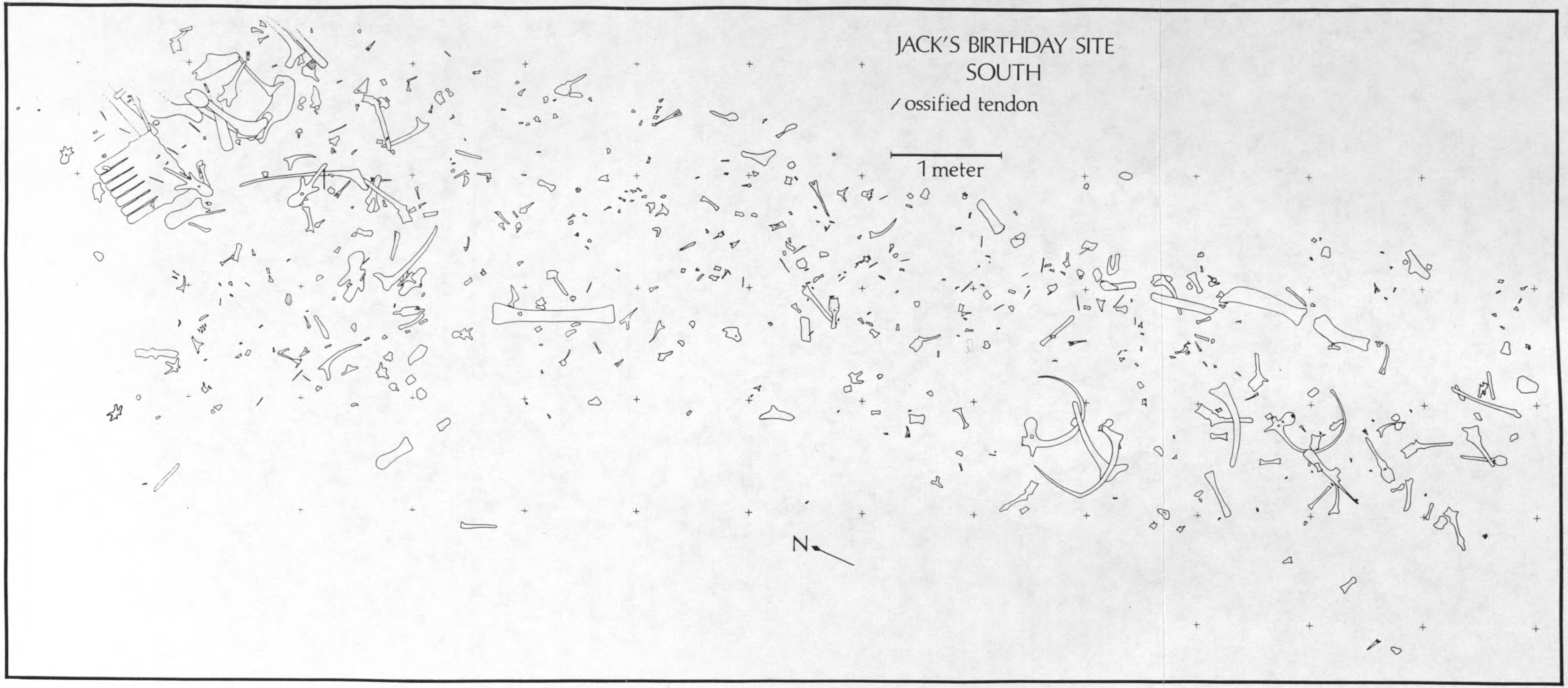


FIGURE 8. Map of South Quarry. South is about 3 m south of Middle (see Fig. 2). Bones dispersed vertically through 50 cm. Reproduced at roughly same scale as Figures 6 and 7.

TABLE 3. Distribution of dinosaur taxa by 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

calculated from the total number of identifiable tyrannosaurid specimens and total and individual quarry areas. The three sedimentologically-similar northwest quarries, Brad, Lower, and Middle (BLM) were treated as one unit. Total areas quarried for BLM, South and East are respectively, 50, 60, and 32 m^2. 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 the 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 changes from northwest to southeast over a distance of 50 m. Bone orientation, abundance, weathering, breakage, and abrasion, all vary.

Trends and plunges of elongate bones and plant fragments were plotted on a stereonet and contoured through Spheristat-S (Frontenac 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 (Fig. 9). The low formational dip, roughly one or two degrees to the west, was

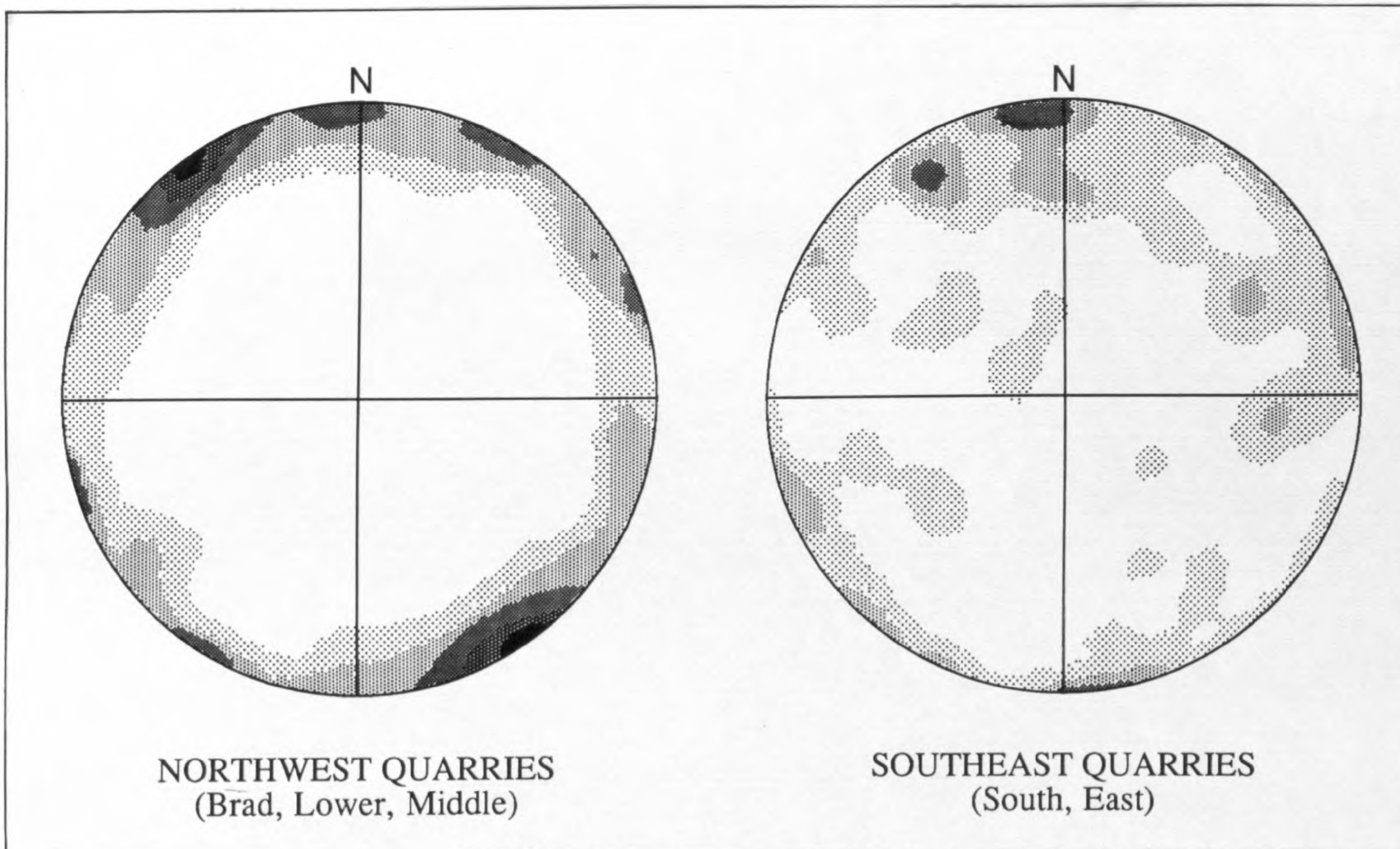


FIGURE 9. Stereonet plots for the northwest and southeast quarries showing trends and plunges of elongate bones and plant fragments. The lowest contour level (lightest stippling) plotted has a value of E (See Table 4 and text). Subsequent contour levels increase by a value of 2σ, so that the highest (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).

ignored. Table 4 shows the relevant statistics, including: 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).

Nearly all the elongate elements in Brad, Lower and Middle, lie flat, a result of the underlying sandstone (Table 4; Fig. 9). The few steeply inclined elements typically involve bones braced by other bones. Thus, the contour for the northwest quarries approaches a non-preferred distribution in an approximately horizontal plane (Fiorillo, 1988a). This distribution is characterized by the low K and relatively large C-values (Woodcock, 1977). Significant clusters occur in the northwest and southeast directions, with the peak value in the latter.

In contrast to the northwest quarries, numerous elongate elements in South and East are steeply inclined (Table 4; Figs. 9, 10) and several broad, flat bones, e.g. a lambeosaurid pubis, stand on edge (Fig. 11). The increased numbers of moderately to steeply inclined bones give the southeast quarries a more uniform stereonet distribution. The lower σ and C-values reflect this. Significant orientation and the peak value occur to the northwest. A contour plot of the entire data set, both northwest and southeast quarries, is very similar to that of the northwest quarries and shows an alignment of elongate elements to the southeast /northwest and to a lesser degree to the southwest/northeast.

TABLE 4. Stereonet Statistics

	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

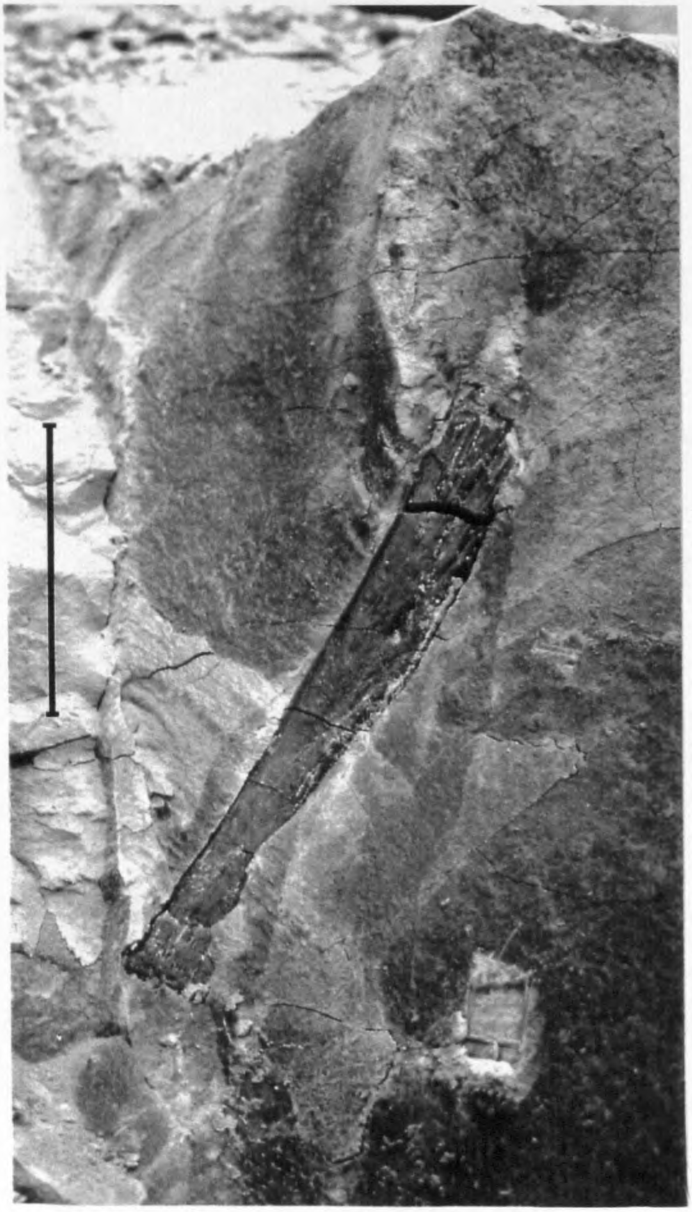


FIGURE 10. Horizontal view of a steeply-inclined iguanodontoid metacarpal from South. Note absence of sedimentary structures. Scale bars equals 10 cm.

FIGURE 11. Horizontal view of an iguanodontoid pubis (1) and a metatarsal (2) from South. Blade of pubis and long-axis of metatarsal oriented nearly vertically. Note absence of sedimentary structures. Visible portion of awl equals 10 cm.

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 (Fig. 7). Few elements in Lower, South, and East contact other bones (Figs. 6, 8).

Table 5 lists the amount of bone modification in the northwest quarries, Brad, Lower and Middle (BLM), South, and East. Three breakage categories were recognized: A, <10% of bone missing; B, 10-50% missing; and C, >50% missing. Weathering was assessed using the stages of Fiorillo (1988b, table 6) and the criteria of Behrensmeyer (1978) where applicable. "Nicks" represent apparent impact damage to bone that is likely due to either biting or trampling. Percentages for tooth marks and nicks are based on a total bone sample of aproximately 1300 elements.

Bone breakage and weathering increase significantly from the northwest to the southeast (χ^2-test, $p<0.001$). 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. 12). 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

TABLE 5. Frequency of bone modification for a sample of identifiable elements, exclusive of teeth, from the main bonebed.

		BLM		SOUTH		EAST		TOTALS	
		n	%	n	%	n	%	n	%
	A	325	92	477	83	229	71	1031	82
BREAKAGE	B	21	6	48	8	52	16	121	10
	C	7	2	48	8	43	13	98	8
	TOTALS	353		573		324		1250	
	0	378	97	537	91	263	76	1178	89
	1	6	2	29	5	46	13	81	6
WEATHERING	2	3	1	17	3	19	6	39	3
	3	1	0	9	2	16	5	26	2
	TOTALS	388		592		344		1324	
	TOOTH MARKS	1		2		9		12	1
	"NICKS"	8		26		22		56	4

FIGURE 12. Oblique view of iguanodontoid caudal vertebrae (1) from South with its broken neural spine (2) lying alongside and steeply inclined. Note absence of sedimentary structures. Scale bars equals 10 cm.

(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 6) were compared to predicted values based on data in Weishampel et al. (1990). Similarity between observed and expected values was tested independently for each element class using a χ^2-test. Some observed values of near complete to complete bones differ significantly from predicted values. Table 6 displays increases (++, major; +, minor) and decreases (--, major; -, minor) for Jack's Birthday Site counts relative to the expected values. The assemblage shows an abundance of stockier elements, primarily limb bones (humeri, radii, ulnae, femora, tibiae and fibulae), 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

TABLE 6. Element counts from the '89, '90, and '91 field seasons at Jack's Birthday Site.

	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				

assemblage represents a parautochthonous collection of animals that gathered at or carcasses transported 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 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 (Siegel, 1956) 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* and total area quarried (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 ($p<0.01$).

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 intermittent 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, undisturbed 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 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 and periodically anoxic body of water, probably smaller than 1 km^2.

Bone preservation is consistent with a northwest/southeast, 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, 1988c). The very low frequency of weathering in the northwest quarries (Table 5) suggests minimal subaerial exposure (Behrensmeyer, 1978). Elongate elements align northwest/southeast and northeast/southwest (Table 4, Fig. 9), consistent with a northeast/southwest 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, 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, 5; Figs. 10, 11, 12). 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, R. 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.

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 6; 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.

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, within and around a small lake fits with observed modern drought mortality. *P. blackfeetensis* and *Gryposaurus* make particularly good candidates for water-dependent species. Their dental battery and wide, square muzzle suggest a grazing diet (cf. Solounias et al., 1988, fig 1c; Horner, 1992: plate 38b; Carrano and Janis, 1991). Isotope data for another broad-beaked hadrosaurid supports this interpretation (Bocherens, et al., 1988). Modern ungulate species generally show spatial or temporal separation in their use of water holes that reflects in part their herding behavior (Henshaw, 1972; Jarman, 1972; Ayeni, 1975). This may explain the segregation of the *Hypacrosaurus* and *P. blackfeetensis* assemblages. Alternatively, they may reflect separate events or different stages of the same drought (See Shipman,1975).

Two sedimentologic features are consistent with and perhaps suggestive of drought. First, the bonebed in the northwest rests sharply on a possible winnowed or omission surface and shows a decreasing bone-packing density upwards from its base. Similar shell beds, type III and IV of Kidwell (1986), reflect a shift in net sedimentation from erosion or omission to deposition. Drought and its termination could produce such a shift in sedimentation rate (Shipman, 1975). Secondly, trampling in a soft muddy substrate explains the near-vertical orientations of bones in the South and East quarries (Figs. 10, 11)(Behrensmeyer and Dechant Boaz, 1980; Haynes, 1985). Some elongate bones extend through a vertical distance of over 30 cm, suggesting a minimum thickness of mud at the time of their emplacement. Elements from these two quarries represent associated pterosaur, tyrannosaurid, *Gryposaurus*, *Hypacrosaurus*, and *Troodon* individuals. The latter two include juveniles. No articulated elements are present, and skeletons are well-dispersed over at 20 m^2. Post burial bioturbation might disrupt articulated elements, but it is unlikely to disperse bones to the extent found here. Consequently, the non-preservation of articulated elements implies an absence of trampling activity or a consolidated substrate during the period of complete disarticulation. Trampling on a muddy substrate occurred only subsequent to disarticulation. High lake water levels could prohibit trampling activity, but it is unclear how animals or carcasses would segregate under such conditions. More likely, the substrate changed from consolidated to muddy. This implies a shift from dry to wet conditions, perhaps the result of new rains and/or a small rise in lake level. The laterally adjacent bone and wood concentrations in Brad and Middle (Figs. 2, 7), if correctly interpreted as a strand line, would support a rise in water level subsequent to the disarticulation of the dinosaurs, consistent with a drought scenario.

None of the above features provides definitive evidence of drought at Jack's Birthday Site, and some proposed drought indicators (Shipman, 1975) are missing, for example: mud-cracks, evaporites, or articulated specimens representing desiccated carcasses. Age-profiles of iguanodontoids, though indicative of strong selective mortality (See Chapter 3), are equivocal for drought mortality. Juveniles are under-represented in the hadrosaurids and to a lesser extent in *Hypacrosaurus*. The preserved assemblage could reflect physiological differences between these dinosaurs, between dinosaurian and mammalian herbivores, or simply late stage drought mortality (Shipman, 1975; Hillman and Hillman, 1977). The latter poses the problem of why early-stage mortality, primarily juveniles, is not preserved. Finally, among individuals represented by associated material, there are five theropods versus 15 iguanodontoids (Table 3). This represents a disproportionally high number of presumed carnivores compared with values for other Two Medicine bonebeds (Rogers, 1990; and Chapter 3), surveys of articulated dinosaur specimens (Béland and Russell, 1978), and mammalian drought assemblages (Haynes, 1988).

Botulism

Botulism is caused by the inadvertent ingestion of a neurotoxin produced by the bacterium, *Clostridium botulinum*. Death results from paralysis of voluntary muscles and so, animals may die near the place where they first ingested the toxin (Smith, 1976; Locke and Friend, 1987; Gophen et al., 1991; Rocke, 1993) . Mass mortality perpetuates through a bird-maggot cycle, with single 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. 13). 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 brachyrhynchos*) 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

FIGURE 13. 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.

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 (Woese, pers. comm.).

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 mm-scale bedding, organic-rich horizons, and undisturbed fish remains. 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 remain susceptible (Rocke, 1993). Theropods, considered to be the most predaceous of the dinosaurs, are unusually abundant at Jack's Birthday Site. No other Two Medicine bonebed has any associated theropod remains (Rogers, 1990). 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. 13). 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 depends 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 micrometers by 0.9 micrometers) 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.

<u>Cyanobacterial Toxicosis</u>

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 pH between 6 and 9 or higher and a temperature between 15°-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. 14). 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 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 resulting 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

FIGURE 14. 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.

features, for example, the concentration of bones at the base of the mudstone in the northwest quarries.

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). Several diverse Jurassic assemblages associated with floodplain deposits resemble Jack's Birthday Site: Como Ridge, Morrison Quarry, and the M&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 non-random 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 seems 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 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 may be 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).

Environmental factors leading to algal blooms 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, 1991a). 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 are 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.

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 (c.f. Figs. 2, 13 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.

CHAPTER 3

COMPARISON OF HADROSAURID AND LAMBEOSAURID BONEBEDS FROM THE TWO MEDICINE FORMATION

Introduction

Age-frequency distributions or age-profiles have proved useful in the interpretation of fossil and historical vertebrate assemblages, particularly those dominated by ungulates. For a variety of extant and extinct vertebrates, use of age-profiles has determined life-history parameters (Van Valen, 1964; Voorhies, 1969; Hulbert, 1982), number of offspring/female (Klein, 1982a), catastrophic versus attritional mortality (Hulbert, 1982; Weishampel and Westhphal, 1986; Turnbull and Martill, 1988), and cause and/or season of death (Nimmo, 1971; Frison, 1978; Klein, 1982b; Klein and Cruz-Uribe, 1984; Grayson, 1990). Proper interpretation of a species' age-frequency distribution from a fossil assemblage requires an understanding of either: 1) that species' population dynamics or 2) the origin of the assemblage under study. Where the former is known or inferred, for example with extinct ungulates, age-profiles from a particular locality can yield information about the origin of the assemblage. Generally, the age-profile is compared with two hypothetical endpoints representing either a "catastrophic" or "attritional" distribution

(Voorhies, 1969; Klein, 1982a; Klein and Cruz-Uribe, 1984). In a catastrophic profile (Fig. 15), age-class abundances match those typical of a living population with the difference between one age class and the next being equivalent to the attritional mortality at each age class. Thus fossil assemblages with such an age-profile would in theory represent catastrophic (i.e. non-selective) mass-mortality (see terms in Carpenter, 1988). In an ideal attritional profile (Fig. 15), age-class abundances reflect the numbers of animals dying from one age class to the next (Voorhies, 1969; Klein, 1982a), showing peaks corresponding to ages where normal or background mortality rates are the highest, among the very young and to a lesser extent the very old. Intermediate profiles would reflect selective mortality or preservational bias. Where the origin of an assemblage is understood, age-profiles may yield biological information such as population structure and age-class mortality rates.

Several dinosaur clades are characterized by mass accumulations: among saurischians, Ceratosauria (Colbert, 1989; Welles, 1984; Raath, 1990; Rowe and Gauthier, 1990) and Prosauropoda (Weishampel and Westphal, 1986; Galton, 1990), and among ornithischians, the Iguanodontoidea sensu Sereno, 1986 (Gilmore, 1929; Dodson, 1971; Norman, 1986; Nelms, 1989; Forster, 1990; Rogers, 1990; Christians, 1991) and Neoceratopsia (Brown and Schlaikjer, 1940; Sternberg, 1951; Currie and Dodson, 1984; Lehman, 1990; Rogers, 1990). Nevertheless, opportunities to use age-frequency distributions in the interpretation of dinosaur assemblages have been rare. An age-profile from an assemblage interpreted to be catastrophic in origin was used to assess age in individuals of the ceratopsian *Centrosaurus* (Currie and Dodson, 1984).

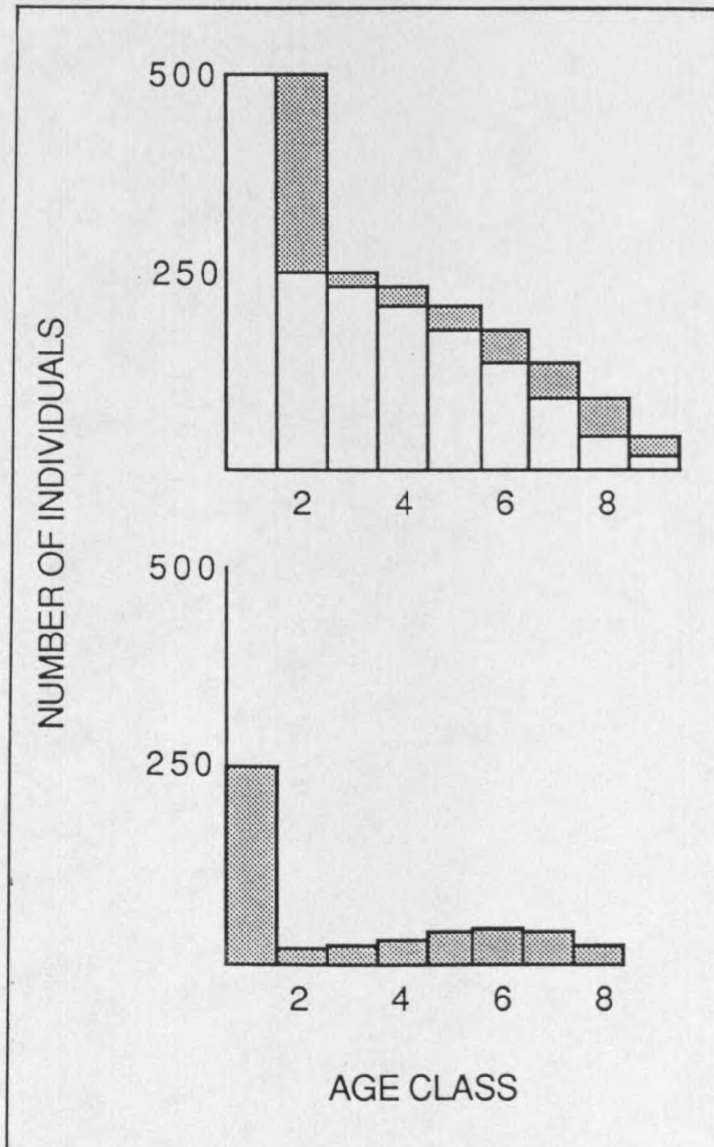


FIGURE 15. Blank bars represent the age structure of a hypothetical population of large terrestrial vertebrates in which females give birth to one offspring each year and consequently a "catastrophic" age-profile. Shaded bars represent the number dying per year in each age class in order to maintain this population's age structure. As arranged below these shaded bars thus show a model "attritional" age-profile for this population. Figure is adapted from Klein (1982a).

At Trossingen, Germany, catastrophic mortality was inferred for one assemblage of the prosauropod *Plateosaurus* in part on the shape of its age-profile (Weishampel and Westphal, 1986).

Hadrosauridae and Lambeosauridae are two lineages of Upper Cretaceous Iguanodontoidea (Horner, 1990, 1992). These large (7-10 m long, wt ≈ 3000 kg) facultative bipeds with broad edentulous beaks and complex dental batteries were the dominant terrestrial herbivore of the Late Cretaceous (Weishampel and Horner, 1990). Over the last ten years, crews from the Museum of the Rockies have collected and prepared six predominantly hadrosaurid and/or lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of western Montana. These Two Medicine bone beds provide the opportunity to taphonomically compare and contrast assemblages of closely related species from the same environmental setting. Age-profiles based on these assemblages are here discussed in regard to their taphonomic and biologic implications.

Age-profiles and Dinosaur Paleobiology

Establishing age-frequency distributions relies on adequate aging criteria; for ungulates these are typically epiphyseal fusion and dental eruption and wear (Klein and Cruz-Uribe, 1984). Limb-bone growth from a single ossification center and polyphyodont, homodont dentition of dinosaurs prohibits the use of any of these aging-criteria. Nevertheless, past (Nopsca, 1933) and recent (Horner and Weishampel, 1988; Chinsamy, 1991; Varricchio,

1993) histologic and morphologic (Dodson, 1975,1976) work on dinosaurs indicates that growth of "mature" bone microstructures and secondary sexual features correspond to increases in overall body size. Thus size-frequency distributions should approximate age-profiles. Two factors may complicate sized-based aging, individual variation and sexual dimorphism. Changing growth rates with ontogeny (Varricchio, 1993) may further muddle interpretations. Nevertheless these are the only available aging-criteria at present.

Properly interpreting age-profiles requires a clear understanding of an animal's biology and ecology. For fossil ungulates there are often closely-related extant forms on which to base inferences. Dinosaurs lack clear modern analogues. Birds and crocodilians share historical morphologic and physiologic constraints with dinosaurs but are ecologically divergent. Some large-bodied herbivorous dinosaurs, such as hadrosaurids and lambeosaurids, may be more analogous to mammalian ungulates; Table 7 compares relevant aspects of these groups' biology and morphology. Ungulate data are taken from Eisenberg (1981) and dinosaur data from Nopsca (1933), Lull and Wright (1942), Ostrom (1961), Dodson (1975), Horner and Makela (1979), Horner (1982, 1984), and Currie and Horner (1988).

Several aspects of hadrosaurid, lambeosaurid, and likely of general dinosaurian biology should affect the shape of both the ideal catastrophic and attritional age-profiles. Dinosaurian oviparity with large broods of very small young versus typical ungulate viviparity with one or two large young creates a population with a larger proportion of juveniles and is likely associated with higher juvenile mortality. Consequently, ideal living age-frequency

TABLE 7. Comparison of extant ungulate and hadrosaurid and lambeosaurid iguanodontoid morphology and biology.

	EXTANT UNGULATES	IGUANODONTOIDS
BONE GROWTH	determinant, three ossification centers/limb element	indeterminant, single ossification center/limb element
DENTITION	majority hypsilophodont, heterodont, diphyodont	dental batteries, homodont, polyphyodont
ADULT SIZE	most between 10 and 1000 kg	> 2000 kg
DISPLAY FEATURES	cranial ornamentation, typically dimorphic	cranial ornamentation, possibly dimorphic
METABOLISM	endothermic and high	unknown, but possibly endothermic and high
REPRODUCTION	viviparous	oviparous
LITTER SIZE	small, typically 1 or 2	large, > 15
NEONATES	small relative to adults, > 2% adult body weight	very small relative to adult, < 0.1% adult weight
PARENTAL CARE	nursing	care of nest-bound young

distributions of dinosaurs should be much more positively-skewed than those of ungulates. Further, given the larger adult size and indeterminant growth of most dinosaurs, age-profiles should trail out farther toward older size classes. Size-frequency distributions with such a shape are found in modern populations of crocodilians, a group more reproductively similar to dinosaurs (Brandt, 1991, fig. 1; Taylor et al., 1991). The greater size difference between dinosaur neonates and adults may increase the potential for preservational bias in mixed age-class assemblages (Behrensmeyer, 1975).

Localities

All the assemblages, Camposaur (Museum of the Rockies locality number TM-003), West Hadrosaur Bonebed (TM-067), Westside Quarry (TM-041), Blacktail Creek North (TM-066), Lambeosite (TM-019), and Jack's Birthday Site (TM-068), are from the mid to upper portions of the Two Medicine Formation (Fig. 16). This formation runs north-south along the eastern flank of the Rockies in western Montana (Stebinger, 1914; Gavin, 1986; Rogers, 1990). In this region during the Late Cretaceous a coastal plain stretched between the proto-Rockies to the west and the inland seaway to the east. The Two Medicine Formation represents a clastic terrestrial wedge located between regressive and transgressive phases of the inland sea (Gill and Cobban, 1973). Lithofacies consist of prograding coastal plain and alluvial apron deposits. Age of the formation ranges between 82.6 and 74 Ma (Rogers et al., 1993). A seasonal and semi-arid climate with a long dry season

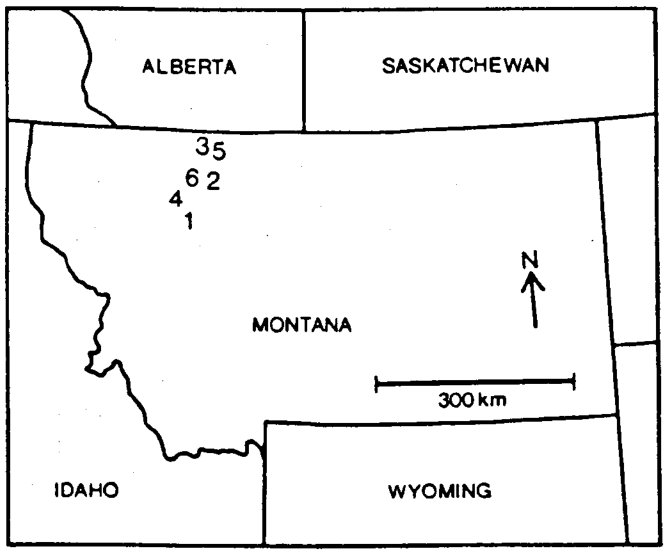


FIGURE 16. Location map of the six hadrosaurid and/or lambeosaurid assemblages from the Two Medicine Formation: 1, Camposaur; 2, West Hadrosaur Bonebed; 3, Westside Quarry; 4, Blacktail Creek North; 5, Lambeosite; and 6, Jack's Birthday Site. 1 from Teton County; 2 from Pondera County; and 3, 4, 5, and 6 from Glacier County, Montana.

and warm temperatures is postulated for the Two Medicine region from a variety of paleontologic and sedimentologic data (Dodson, 1971; Lorenz, 1981; Gavin, 1986; Carpenter, 1987; Crabtree, 1987; Jerzykiewcz and Sweet, 1987; Rogers, 1990).

Relevant taphonomic data including hadrosaurid and lambeosaurid Minimum Number of Individuals (MNI) and the number of identified specimens (NISP) for each locality are given in Table 8. Total samples at Camposaur, Blacktail Creek North, and Jack's Birthday Site, are much larger; numbers reflect only available prepared material. MNI's are based upon the most common element using matching (Bökönyi, 1970). Lefts and rights had to differ by >10% of the total length to be considered as representing separate individuals. At West Hadrosaur in addition to eight left juvenile femurs there is one adult represented by several non-duplicated elements. All adult elements are well weathered in comparison to the juvenile bones, implying a separate origin for them. Nevertheless, the MNI is given as nine. NISP's represent counts of near-complete to complete bones. Skeletal representation based on transport groups I, II and III of Voorhies (1969). Data for Camposaur, Westside Quarry, and Blacktail Creek North taken in part from Lorenz (1981), Rogers (1990), and Horner (1994), respectively.

All six bonebeds are predominantly composed of disarticulated hadrosaurid and/or lambeosaurid remains and each is located on a single horizon within a silty mudstone (Fig. 17; see also Rogers, 1990, appendix). Except for Jack's Birthday Site, they also have very nearly (>95%) monospecific bone counts. *Maiasaura peeblesorum* predominates in Camposaur and West Hadrosaur Bonebed, *Prosaurolophus blackfeetensis* (Horner, 1992) in

TABLE 8. Taphonomic data for the six Two Medicine assemblages.

LOCALITY	Camposaur	West Hadrosaur Bonebed	Westside Quarry	Blacktail Creek North	Lambeosite	Jack's Birthday Site
MOR #	TM-003	TM-067	TM-041	TM-066	TM-019	TM-068
SEDIMENTS	silty mudstone	silty mudstone	silty mudstone	silty mudstone	silty mudstone	silty mudstone
DEPOSITIONAL ENVIRONMENT	possible slurry flow	oxbow lake	floodplain waterhole	crevasse splay deposit	small lake	small lake
DIVERSITY	nearly monspecific	nearly monspecific	nearly monspecific	nearly monspecific	nearly monspecific	multispecific
IGUANODONTOIDS PRESENT	*Maiasaura peeblesorum*	*Maiasaura peeblesorum*	*Prosaurolophus blacfeetensis*	*Hypacrosaurus* sp.	*Hypacrosaurus* sp.	*Prosaurolophus blackfeetensis*, *Gryposaurus* sp. and *Hypacrosaurus* sp.
OTHER VERTEBRATES	articulated hypsilophodont, a few shed theropod teeth and misc. elements	shed theropod teeth and a few misc. turtle, champsosaur and crocodilian elements	a few shed theropod and nodosaur teeth, one lizard element	a few shed theropod teeth	a few turtle elements	several associated *Troodon* and a tyrannosaurid plus misc other dinosaur, pterosaur, cocodilian, lizard, and fish elements
NISP	450	194	330	1450	85	1091
MNI	20	9	5	18	4	17
NISP/MNI	23	22	66	81	21	61
BONE DENSITY	>10/m^2	aprox. 5/m^2	7/m^2	aprox. 100/m^2	5/m^2	9/m^2
SKELETAL REPRESENTATION	group I underepresented	group I underepresented	roughly all groups proportionally represented	roughly all groups proportionally represented	group I underepresented	roughly all groups proportionally represented
SKELETAL ASSOCIATION	disarticulated and dissassociated	disarticulated w/ some association	ranges from disarticulated to partial articulation	ranges from disarticulated to partial articulation	ranges from disarticulated to partial articulation	disarticulated but commonly associated
ORIENTATION	flat-lying, varies from random to alligned	flat-lying, allignment unkown	mostly flat-lying with no allignment	flat-lying with weak allignment	flat-lying with strong allignment	flat-lying to vertical with weak alignment
PRE-FOSSILIZATION MODIFICATION	most elements with broken or weathered ends	little to no breakage or weathering	little to no breakage or weathering	little to no breakage or weathering	little to no breakage or weathering	breakage or weathering varies from none to severe
POST-FOSSILIZATION MODIFICATION	some distortion and fracture due to lithostatic compaction, calcite permineralization	some distortion and fracture due to lithostatic compaction, calcite permineralization	some distortion and fracture due to lithostatic compaction, calcite permineralization	some distortion and fracture due to lithostatic compaction, calcite permineralization	some distortion and fracture due to lithostatic compaction, calcite permineralization	some distortion and fracture due to lithostatic compaction, calcite permineralization

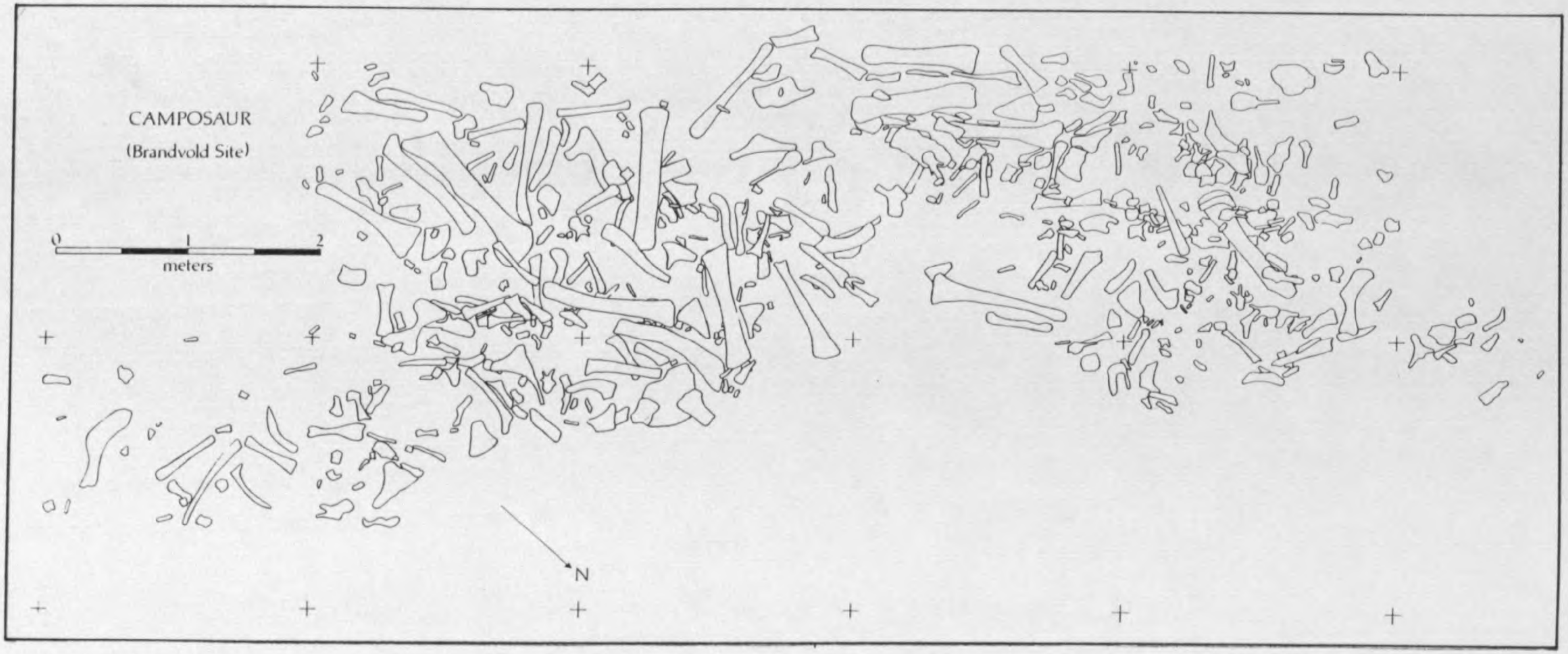


FIGURE 17. Map of the Brandvold Site quarry (Princeton University locality #23255), a portion of the Camposaur assemblage, sec. 30, T24N, R6W, Teton County, Montana. Modified from an unpublished map by W. Crancro.

Westside Quarry and *Hypacrosaurus* sp. in Blacktail Creek North and Lambeosite. Jack's Birthday Site has both hadrosaurids, *P. blackfeetensis* and *Gryposaurus*, and the lambeosaurid, *Hypacrosaurus*. In five localities bones are well preserved with some degree of association. These assemblages are likely parautochthonous. Camposaur is the sole locality with strictly unassociated, worn, and broken bone and thus probably represents an allochthonous assemblage (Lorenz, 1981, p. 116-117). Blacktail Creek North consists of skeletal elements derived from a nesting horizon concentrated in a crevasse splay deposit (Horner, 1994).

Westside Quarry rests directly on a caliche horizon, suggesting ponded water (Haynes, 1988; Rogers, 1990). Small lacustrine settings are inferred for this as well as three other localities, West Hadrosaur Bonebed, Lambeosite, and Jack's Birthday Site, based on sedimentologic and paleontologic evidence, including: massive mudstones, associated varve-like lamina, bone horizon geometry, abundant freshwater invertebrates, and associated fish and carbonized plant remains. West Hadrosaur Bonebed appears to represent an oxbow lake. Further, the disarticulated but associated, and relatively cleanly preserved nature of the skeletal debris in all but Camposaur is more consistent with subaqueous exposure in quiet water and minimum subaerial exposure.

Bones from Jack's Birthday Site exhibit variability in orientation and pre-fossilization modification which vary in a regular way along an offshore to shoreline trend. Further the bonebed shows distinct taxonomic segregation, where several individuals of either the hadrosaurids, *Hypacrosaurus*, or *Troodon* are separately concentrated. Associated skeletal material within a fine-grained matrix suggests that the assemblage is primarily parautochthonous. High taxonomic diversity including isolated elements would be more typical of an attritional assemblage. Concentration of bone on a single horizon and discrete taxonomic groupings suggests that mortality may be related or at least episodic in nature with the monospecific groups perishing in separate events.

Uniformity of preservation, single horizon, high bone density, and monospecifity within the other sites strongly suggests that they too are the result of mass mortality (cf. Haynes, 1988). Rogers (1990) proposed drought-related mortality for Westside Quarry and Hooker (1987) suggested volcanic-related mortality for Camposaur, but the latter has not been documented.

Winnowing is observed in three localities and could bias these samples (Table 8). Tooth marks are uncommon in all, but this may or may not reflect actual bone loss to scavengry (Fiorillo, 1991b).

Two Medicine Formation Profiles

Size-frequency distributions (Fig. 18) represent the lengths of the most common side and unmatched opposites of a given paired element. Additionally, tooth row distributions are based on the matching of dental battery lengths from both dentaries and maxillas.

Although hadrosaurid and lambeosaurid humeri can often be distinguished on the basis of the size and shape of the deltopectoral crest (Horner, 1990; Weishampel and Horner, 1990), too many Birthday Site elements remain indistinguishable, in part due to diagenetic deformation and

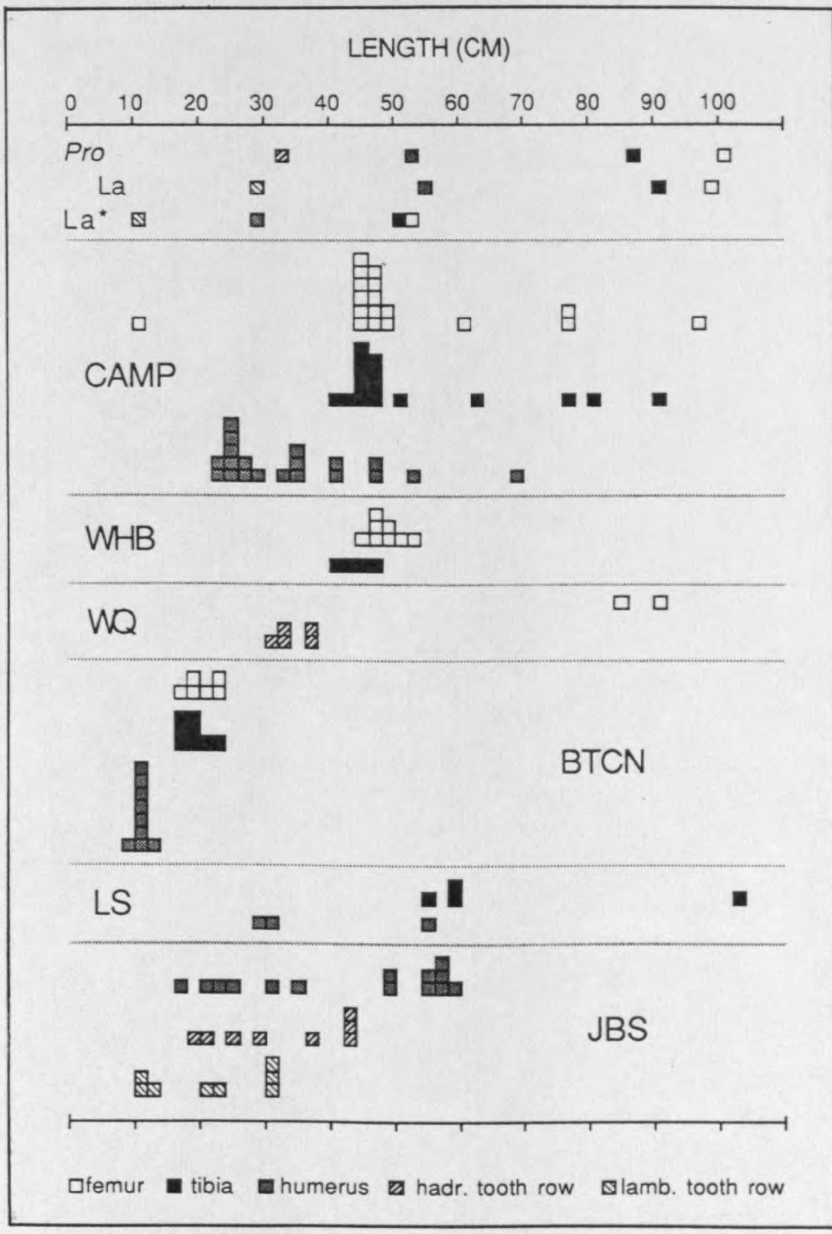


FIGURE 18. Representative length measurements for three articulated specimens and size-frequency distributions for the most common elements from the six Two Medicine assemblages. Abbreviations: **BTCN**, Blacktail Creek North; **CAMP**, Camposaur; **JBS**, Jack's Birthday Site; **La**, adult lambeosaurid, American Museum of Natural History (AMNH) 5338; **La***, juvenile lambeosaurid, AMNH 5461; **LS**, Lambeosite; ***Pro***, *Prosaurolophus maximus*, Royal Ontario Museum 4971; **WHB**, West Hadrosaur Bonebed; **WQ**, Westside Quarry. CAMP, WHB, and WQ data are for hadrosaurids, BTCN and LS for lambeosaurids and JBS for both. Length of tooth row refers to the anterior-posterior length of either dentary or maxilla tooth batteries. Each square represents a single individual.

ontogenetic variation. Thus the size-profile for humeri from Jack's Birthday Site combine *Prosaurolophus, Gryposaurus,* and *Hypacrosaurus* elements. Combination of data in this manner is not preferred but here at least both taxa hatch from similarly sized eggs (Currie and Horner, 1988; Hirsch and Quinn, 1990) and obtain similar adult sizes (Lull and Wright, 1942). Cranial elements (here maxillae and dentaries) are more easily differentiated, so separate hadrosaurid and lambeosaurid profiles for tooth rows are presented.

As a guide for comparison of the various plots, lengths for the various elements used are presented for three articulated specimens, an adult hadrosaurid, *P. maximus* and a juvenile and adult lambeosaurids (Fig. 18).

Discussion

At least within the four largest assemblages, size-frequency distributions for each of the most common elements have similar shapes (Fig. 18). The repeatability of the data suggests the samples, despite their small size are representative of the quarry areas excavated. Further, it indicates that size-sorting has not been significant over the size-range present. It does not rule out the possibility of winnowing outside the preserved range but the sediment size would rule out the loss of at least the large-end spectrum.

A minimum of 18 individuals are preserved in the Blacktail Creek North assemblage. These are all quite small with a total head to tail length (TL) of roughly 1.5 m. The narrow size range and minimal variance of the distributions suggests the assemblage is composed of a single age class.

Horner (1994) interpreted this assemblage as consisting of juveniles still restricted to the nesting ground.

West Hadrosaur Bonebed contains at least eight juvenile and a single adult *M. peeblesorum*. Average length of the juveniles based on data in Lull and Wright (1942) is between 3 and 3.5 m. Variation in these plots ($sigma_{ave}$ = 2.4 cm) is similar to those from Blacktail Creek North ($sigma_{ave}$=2.8 cm) and again suggests normal variation within a single age class.

The small samples from Westside Quarry and Lambeosite consist of subadults (TL > 7 m) and adults, and large juveniles (TL > 4 m) and adults, respectively. Isolated small elements (e.g. unguals and distal caudals) are preserved at Westside Quarry and it is unlikely that the absence of smaller individuals is strictly taphonomic. Fewer small elements are present at Lambeosite but one could minimally expect individuals with femur lengths of roughly 30 cm (TL ≈ 2 m) to be present.

The two largest samples, Camposaur and Jack's Birthday Site, have very distinctive size-frequency profiles. Camposaur profiles each show a distinct peak corresponding to a juvenile total length of 3 m. Larger individuals of varying sizes are present, but smaller size classes are represented by a single femur 12 cm long.

As with the other monospecific localities, the uniform preservation within a single horizon at Camposaur strongly suggests a mass mortality. Whether Camposaur is a result of catastrophic (i.e. non-selective) or non-catastrophic (selective) mass mortality (Carpenter, 1988) is difficult to determine. Environmental perturbations such as drought or severe winters are often hardest on the young (Corfield, 1973; Conybeare and Haynes, 1984;

Haynes, 1988; Lemke, 1989). Nevertheless, the oviparity and large clutch-size of hadrosaurids and lambeosaurids should produce a size-frequency distribution for a living population that is strongly positively skewed. Similarity then between the size frequency distributions of Camposaur and those for extant crocodilian populations (Brandt, 1991) would suggest a catastrophic origin for Camposaur.

Camposaur size-frequency distributions are notable for their near total absence of very small individuals. The sole small femur corresponds to a size that is still considered nest bound (Horner and Makela, 1979), so given the close proximity (< 100 m) of *M. peeblesorum* nesting grounds to Camposaur, the femur was likely transported in. Humeri with lengths down to 22 cm are present and thus one would expect that given their nearly equivalent densities, similarly sized tibias or femora representing smaller individuals would be preserved. The absence of *M. peeblesorum* individuals with femur lengths between 22 and 44 cm long is biologically real and not a result of hydraulic winnowing. Juveniles associated with nesting horizons have femur lengths up to 19 cm (Horner, 1994). So it is only individuals with femur lengths between 20 and 22 cm that could have been transported out of the Camposaur assemblage. No single element as yet records this class as part of the assemblage. Curiously the size-frequency distribution for one Trossingen *Plateosaurus* assemblage (Weishampel and Westphal, 1986, fig.11), interpreted to represent catastrophic mass mortality, is similarly shaped with a notable absence of individuals with femur lengths less than 52 cm.

Corresponding peaks occur in the Camposaur femur, tibia, and humerus profiles indicative of an abundance of juveniles roughly 3 - 3.5 m in length. The variation occurring immediately around these peaks is consistent with that observed within Blacktail Creek North and West Hadrosaur Bonebed. Further, the juveniles at West Hadrosaur Bonebed appear to be of the same size class. Including the sole adult, West Hadrosaur Bonebed may simply represent a smaller sample of a Camposaur-like assemblage. Interpreting the juvenile peak at Camposaur as an age class leads to several conclusions. Since the sample is drawn from a very large assemblage and excavated from quarries located tens of meters apart, it is unlikely that these juveniles represent a single clutch. Presence of this age class then suggests that reproduction was both synchronous among *M. peeblesorum* and seasonal. This concurs with the existence of *M. peeblesorum* nesting grounds (Horner and Makela, 1979; Horner, 1982, 1984) and with the seasonal Two Medicine climate. This peak is further evidence of a mass-mortality.

If the juvenile peak in the Camposaur profile is a distinct age class, then two hypotheses may explain the absence of smaller individuals from Camposaur: 1) 3 to 3.5 m long juveniles may represent near one-year olds and no younger age classes may have existed at the time of the Camposaur mortality or 2) the Camposaur juveniles may represent an older age class and missing age classes may not have participated in the group represented. For these juveniles to have been one-year olds would require a rapid rate of growth. Using the equation of Anderson, J. et al. (1985, eq. 9) for estimating the weight of a bipedal dinosaur, a weight of 180 kg is predicted. Large ungulates gain similar weights in their first year (Peterson, 1974; Sinclair, 1977) and ostriches reach weights of 100 kg a year after hatching (Degen et al., 1991); so it is feasible that a 3.5 m long hadrosaurid is a yearling. This hypothesis may be testable through histology (see Ricqles et al., 1991).

If very young individuals (2 m < TL < 3 m) did not participate in Camposaur-type group, perhaps they remained alone, in juvenile groups or perhaps in juvenile groups with a few protective adults. To date no isolated or assemblages of predominantly small animals have been found for *M. peeblesorum*. Blacktail Creek North with only small individuals (TL < 1.5 m) is apparently an example of a strict juvenile group from a nesting area (Horner, 1994). Recently it has been proposed on the basis of several juvenile dominated assemblages (Forster, 1990) that ornithischians may have participated in juvenile groups as a general strategy. The existence of such a group could also explain the Trossingen size-frequency profile of *Plateosaurus*. The smallest size class in this assemblage has an average femur length of 60 cm, a size that would be difficult to explain by one year's rapid growth.

Finally, if Camposaur represents a non-selective mass mortality, then the rapid fall off in numbers of individuals after a body size of 3.5 m (femur length = 47 cm) as well as the reported large clutch size for *M. peeblesorum* (Horner and Makela, 1979; Horner, 1984) suggests a high background mortality among young with a much lower rate among individuals beyond 3.5 m in size. Predation likely had a significant role in this (see Kruuk, 1972, fig. 23) and suggests theropods preferentially selected young and small individuals.

The humerus size-frequency distributions for Jack's Birthday Site contrast sharply with that of Camposaur (Fig. 18). Both are unimodal but the former is negatively skewed with a peak at 55 cm while the latter is positively skewed with a peak at 25 cm. Notably at Jack's Birthday Site smaller individuals are separated from larger ones by a gap between humeral lengths of 35 and 48 cm. Tooth-row profiles for both the hadrosaurids and lambeosaurids from the site show similar trends, the rightward shift of the hadrosaurid plot being accounted for by their attainment of relatively longer dental batteries with age (Lull and Wright, 1942). None of the three profiles fit either a hypothetical attritional or catastrophic mortality model. Thus strongly selective mortality is indicated with both hadrosaurid and lambeosaurid adults being hardest hit with some selection for juveniles. Gaps in the profiles may reflect non-selection of the most fit groups such as prime adults. However this may be an artifact of the small sample size. Nevertheless, taphonomic evidence such as a single bone horizon, discrete taxonomic grouping and the size-frequency profiles, suggests the bulk of the assemblage to be accounted for by a single or repeated selective mass mortalities which apparently affected hadrosaurids and lambeosaurids alike.

Both the hadrosaurid and lambeosaurid fractions at Jack's Birthday Site lack individuals smaller than 2.3 m in total length. Only two individuals appear to be smaller than 3 m. The large sample size (Table 8) and the abundance of Voorhies I type elements rules out significant loss by winnowing. Whether this deficiency is a similar phenomenon as that observed at Camposaur or simply a product of selective mortality is not determinable. If it is the former then the discussion for Camposaur small juveniles might be applicable to both hadrosaurids and lambeosaurids in general.

A hydraulic origin for these bonebeds is unlikely. Each site is either nearly monospecific and/or has associated material implying an autochthonous origin or where transport may have been involved, a derivation from a monospecific origin. Consequently the localities likely have an underlying biologic cause.

Lorenz (1981) suggested that Camposaur may represent a slurry flow from a catastrophically drained lake. Blacktail Creek North occurs adjacent to a small stream channel and may represent a crevasse splay deposit. West Hadrosaur Bonebed consists of abandoned-channel fill.

Three sites, Westside Quarry, Lambeosite and Jack's Birthday Site, represent small floodplain lacustrine or waterhole environments. The occurrence of these parautochthonous assemblages within lacustrine/waterhole settings is probably best explained by drought (see arguments in Shipman, 1975 and Rogers, 1990). The seasonally wet/dry Two Medicine climate would be susceptible to droughts (Dodson, 1971; Lorenz, 1981; Gavin, 1986; Carpenter, 1987; Crabtree, 1987; Jerzykiewcz and Sweet, 1987). Further modern ungulates are known to congregate at available water holes during both the dry season and droughts, frequently perishing there (Jarman, 1972; Corfield, 1973; Ayeni, 1975; Western, 1975; Hillman and Hillman, 1977; Conybeare and Haynes, 1984; Haynes, 1988; Williamson and Mbano, 1988). Monospecific ceratopsian bonebeds interpreted as drought-generated are also known from the Two Medicine Formation (Rogers, 1990).

Age-profiles of these three assemblages are dominated by large individuals, Westside Quarry with hadrosaurids, Lambeosite with lambeosaurids and Jack's Birthday Site with both. Environmental crises typically preferentially select against one age class or sex (Corfield, 1973; Conybeare and Haynes, 1984; Grayson, 1990; Lemke, 1989). Early stage drought typically affects young individuals (Shipman, 1975). Consequently, the age-profiles could reflect any number of factors such as late stage drought (i.e. predominantly adult mortality), sex differences, group composition, preservational bias, or simply small sample sizes.

An alternative explanation for these three assemblages is mass drowning in fluvial channels during floods (Sullivan, 1984; Haynes, 1988; Turnbull and Martill, 1988) but this would require a major flood event to transport dinosaur carcasses out of the channel and across a floodplain to a waterhole(Rogers, 1990). Segregation of taxa as in Jack's Birthday Site also seems an unlikely result. Floods may be expected to produce high juvenile mortality. West Hadrosaur Bonebed with a predominance of juveniles and channel-fill sediments might be a good candidate for a flood scenario.

Though arguably these Two Medicine assemblages could be a result of the aggregation of individuals at a particular place or resource, such as animals congregating at a waterhole in times of drought, it is more likely that they represent the products of gregariousness or herding. Among modern ungulates individuals of different species may mix at a waterhole but the monospecific congregation of individuals at the exclusion of other species is not observed. Where one taxa predominates it is the result of a herd occupying the site and generally there is species separation in space and time of drinking sites and wallows (Henshaw, 1972; Jarman, 1972; Ayeni, 1975). Interestingly the sole multispecific bone bed has discrete areas of taxonomic separation.

The cranial ornamentation present in hadrosaurids and lambeosaurids (Ostrom, 1961; Hopson, 1975; Weishampel and Horner, 1990), features associated with social behavior in extant terrestrial herbivores (Geist, 1966; Jarman, 1974) and the occurrence of multiple iguanodontoid trackways showing consistent spacing and parallel movements (Currie, 1983) supports the interpretation of these assemblages as the by-product of herding. How close these assemblages fit the life-composition of herds would be skewed by any selective mortality and preservational bias.

Conclusions

Observations based on the analysis of these Two Medicine assemblages are:

1) All six localities are single highly-concentrated bone horizons within fine-grained sediments. Most are monospecific and parautochthonous with some degree of skeletal association. Consequently they are likely the result of mass mortality.

2) At least four assemblages occur in small lacustrine environments ranging from floodplain waterholes to small lakes and three are interpreted as drought-generated bone beds. Hadrosaurids, lambeosaurids, and ceratopsians of the Two Medicine Formation may have been water-dependent and affected by droughts (Rogers, 1990). The fourth assemblage may represent the remnants of a mass drowning.

3) These assemblages together with trackways, cranial ornamentation and the occurrence of nesting grounds, are evidence of gregarious herding behavior in both hadrosaurids and lambeosaurids.

4) Hadrosaurids and lambeosaurids likely <u>either</u> had very rapid juvenile growth rates, in the case of *M. peeblesorum* reaching a length of 3.5 m in a year, <u>or</u> as juveniles delayed association with mixed-age herds, possibly living in strictly juvenile groups as has been suggested for other ornithischians (Forster 1990).

5) As evidenced by the age class peak at Camposaur, *M. peeblesorum* had intraspecifically synchronous and seasonal (iteroparous) reproduction as well as high, possibly predation-related, juvenile mortality. Whether this holds for hadrosaurids and lambeosaurids in general remains to be determined.

CHAPTER 4

CONCLUSIONS

1) Jack's Birthday Site consists of both parautochthonous (locally-derived) associated and allochthonous (distally-derived) isolated elements. The bone assemblage likely represents both attritional and event mortality.

2) Jack's Birthday Site differs from most contemporary bonebeds in being both diverse and primarily parautochthonous. Other unique features include the abundance of theropods, the presence of three iguanodontoid species, and the association of varve-like sediments. In the region, diverse assemblages generally consist of isolated elements concentrated within channel lags or floodplain lakes while parautochthonous bonebeds exhibit low diversity, with a single species of iguanodontoid or ceratopsian predominant (Rogers, 1990, 1993). Persistence in time of the depositional environment at Jack's Birthday Site likely accounts for the differences between it and these latter assemblage.

3) As a primarily parautochthonous assemblage, Jack's Birthday Site represents a good sample of the local Two Medicine community. Though interspecific differences in ecology and preservational potential probably bias the assemblage in species presence and abundance, time-averaging was likely not great enough to invalidate its ecologic significance.

4) Taxonomic clustering of individuals, particularly of *Prosaurolophus* and *Hypacrosaurus*, at Jack's Birthday Site and other bonebeds dominated by a single species of hadrosaurid or lambeosaurid, strongly suggests that these animals formed herds. Tracksites, cranial display features and nesting grounds support this interpretation (Geist, 1966; Jarman, 1974; Hopson, 1975; Horner, 1982; Carpenter, 1992).

5) The *Troodon* material from the South Quarry at Jack's Birthday Site is the first multi-individual troodontid occurrence. With at least 4 individuals and 180 elements, this assemblage represents a significant proportion of all *Troodon* material from North America. Unfortunately, the paleoecological significance of this material remains unclear. Some possible explanations include: attritional mortality at a favored watering or feeding site; serial mortality, like miring or botulism, that affected individuals drawn to this spot by some aspect of their ecology (e.g. scavengry or insectivory); or event mortality of a *Troodon* group.

6) Recognition of significant lateral variation in bone preservation and taxonomic clustering supported the interpretation of Jack's Birthday Site. Statistical evaluation of within-site geometry should prove useful in the study of bonebeds, especially where large and diverse. Further study could include multivariate cluster analysis applied to 1 x 1 m or 2 x 2 m portions of a bonebed. This could reveal trends in preservation or composition.

7) With proper documentation, particularly of their internal geometry, bonebeds provide significant paleontologic information:

In primarily disarticulated assemblages, taphonomic investigation can recognize whether particular fractions represent one or several individuals or taxa. This information allows ambiguous collections to be evaluated for their taxonomic worth. At Jack's Birthday Site, taphonomy permits some isolated elements, previously unknown in any troodontid, to be assigned with some certainty to *Troodon*. These will be significant for future phylogenetic analysis.

Modern event mortality, like drought, botulism, or cyanobacteria toxicosis, provide analogs for the investigation of bonebed origins. Taphonomy allows these hypotheses to be evaluated. Though currently the assessment of mortality in fossil assemblages remains somewhat problematic, these investigations may eventually yield important physiological and behavioral data.

Understanding the evolution of behavior depends on essential taphonomic data. Behavior is often based upon form and consequently, patterns of behavioral evolution may coincide with those of morphology. Taphonomy provides behavioral data wholly independent of morphology. For example, Nopsca (1929) interpreted the crests of lambeosaurids as important display structures. Lambeosaurid bonebeds confirm the social nature of these animals.

8) Finally, it should be emphasized that taphonomic data, such as the spatial relationships between bones and skeletons, must be recorded at the time of excavation. Otherwise, this data and the potential paleobiologic information it yields, may be forever lost.

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