

TAPHONOMY OF THE MOTHER'S DAY QUARRY, UPPER JURASSIC MORRISON FORMATION, SOUTH-CENTRAL MONTANA, USA

TIMOTHY S. MYERS^{1*} and GLENN W. STORRS²

¹Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221-0013, USA; ²Cincinnati Museum Center, 1301 Western Ave., Cincinnati, Ohio 45203, USA
e-mail: smyers@smu.edu

ABSTRACT

The Mother's Day Quarry, in the lower part of the Upper Jurassic Morrison Formation of south-central Montana, contains a low-diversity assemblage dominated by immature diplodocoid sauropods. The sauropod bones lie within a ~3-m-thick, massive, sandy siltstone containing scattered pebbles and carbonate nodules. Clay rip-up clasts indicate a high-energy depositional environment, and high-angle bone orientations are commensurate with a combination of the inferred high-energy burial event and postburial trampling of the assemblage. Since the Morrison Formation records deposition in an alluvial plain setting characterized by little topographic relief, heavy rainfall likely triggered the high-density flow event. Taphonomic analysis shows no indication that the Mother's Day assemblage was transported far by the entombing flow, though many elements may have been reworked. There is no statistically significant orientation of elongate elements and little apparent evidence of hydraulic sorting or transport damage. Remnants of soft tissue recovered from the quarry and the semiarticulated state of many of the bones demonstrate that the sauropod carcasses were buried a relatively short time after death. The cause of death of the sauropods is largely speculative; it is thought to have been related to drought based on the juvenile-dominated age profile of the assemblage and the inferred sequence of limb disarticulation. Comparison with other sauropod-dominated assemblages reveals that burial rates have little influence on the preservation of sauropod remains. Low-transport potential of sauropod bones implies that the sauropod component of dinosaurian assemblages should nearly always represent faunal elements derived from environments proximal to the site of deposition.

INTRODUCTION

This study examines the depositional setting of the Mother's Day Quarry (MDQ) in the Salt Wash Member of the Upper Jurassic Morrison Formation and compares site characteristics with those of other sauropod-dominated localities. Comparisons reveal some taphonomic patterns characteristic of most sauropod assemblages, as well as others expected to vary greatly between assemblages. Understanding better the processes affecting the accumulation and preservation of sauropod remains will aid in paleoecological reconstructions based on dinosaurian assemblages.

The MDQ sits on the northeastern rim of the Bighorn Basin, amid strata dipping shallowly to the southwest from the base of the Pryor Mountains (Fig. 1). Seven years of excavation confirm the presence of only two vertebrate taxa: a theropod identified possibly as *Allosaurus* sp. and numerous specimens of diplodocoid sauropods. Sauropod bones constitute over 99% of the 1489 identifiable elements recovered to date; only five specimens of the remaining total are attributable to theropods.

All sauropod material retrieved from the quarry belongs to juveniles or subadults. A fossil assemblage consisting almost entirely of immature

individuals of a single taxon is a relatively rare occurrence. Such a skewed age profile may result from taphonomic processes that bias against adults, it may imply a mortality event that was selective for certain age groups, or it may reflect a lack of adults in the original living assemblage. Abundant sauropod remains have also been reported from sites in India (Jain et al., 1975, 1979; Yadagiri et al., 1979; Jain, 1980; Yadagiri, 2001), China (Dong, 1990, 1992), Tanzania (Heinrich, 1999), Argentina (Coria, 1994), Germany (Sander et al., 2006), and Texas (Fiorillo, 1998; Winkler et al., 2000). Of these localities, only the Texas and Chinese assemblages lack adult material.

PREVIOUS WORK

The MDQ was discovered in 1994 by a volunteer for the Museum of the Rockies (MOR) in Bozeman, Montana (Horner and Dobb, 1997). Subsequently, the MOR began excavation during the summer of 1995 and concluded operations after a second season of collecting in 1996. Crews from the MOR removed and mapped a total of 502 identifiable elements. The Cincinnati Museum Center (CMC) assumed excavation responsibilities beginning with an abbreviated exploratory season in 1999, and work has continued for the past six summer field seasons. Over 987 identifiable elements have been removed to date, and approximately 30% have been prepared and curated in the CMC collections. This study is based on the CMC data and specimens collected between 2000 and 2003.

STRATIGRAPHY AND AGE

The Morrison Formation in Montana is divisible into the Salt Wash Member and the overlying Brushy Basin Member (Turner and Peterson, 1999). The Salt Wash Member is characterized by an abundance of sandstone beds and conglomerates, suggesting significant fluvial influence and a proximal location relative to regional clastic sources (Kowallis et al., 1998; Demko et al., 2004; Turner and Peterson, 2004), whereas the Brushy Basin Member is dominated by thick mudstone sequences indicative of more lacustrine conditions and increased fine-grained volcaniclastic input (Bilbey, 1998; Kowallis et al., 1998; Turner and Peterson, 2004). The MDQ falls within the Salt Wash Member of the Morrison based on regional lithologic correlations (F. Peterson, personal communication, 2004), suggesting a Kimmeridgian age for the quarry. The uppermost portion of the Brushy Basin Member appears to be missing near the site (F. Peterson, personal communication, 2004) and was presumably eroded before deposition of the Pryor Conglomerate (Fig. 2).

METHODS

Field Methods

The position and orientation of each bone in the quarry was mapped prior to its removal (Fig 3). Azimuth and distance from datum and depth below datum were recorded as well as the trend and plunge of all elongate elements (length-to-width ratio ≥ 2). Trend was always measured toward the distal end (anterior for vertebrae), and the plunge was recorded as

*Corresponding author. Current address: Department of Geological Sciences, Southern Methodist University, Dallas, Texas 75275-0395, USA.

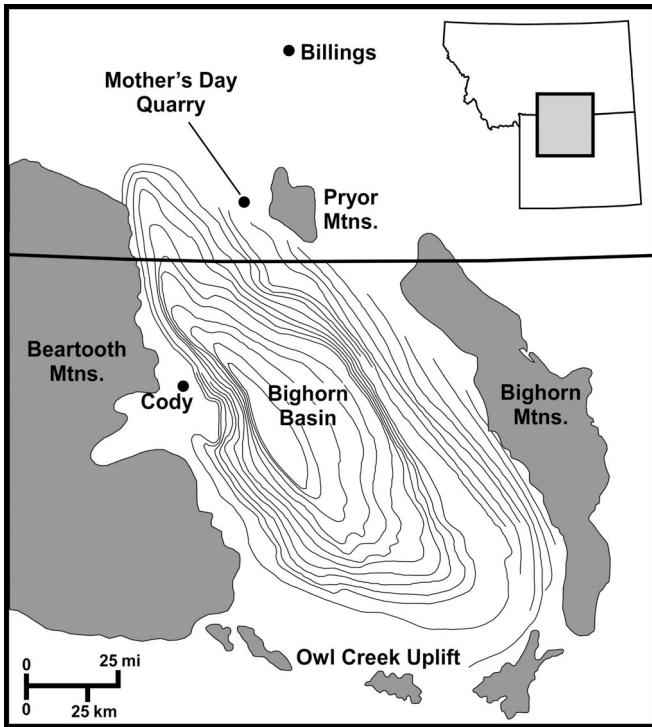


FIGURE 1—Map of Bighorn Basin (Montana and Wyoming) with the location of the Mother's Day Quarry. Modified from Baars et al. (1988).

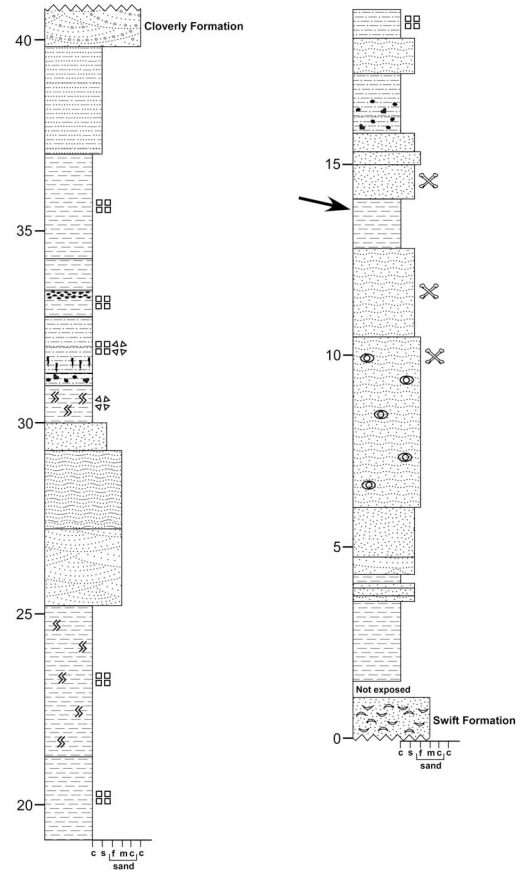
positive or negative for reconstruction of the general orientation of each element within the bone bed. All values were corrected for the south-westerly dip of the bone bed (average attitude: 165;19SW) by entering the raw data into Cauldron 2 (Stuart, 2001), a basic stereonet program, and rotating each orientation pole 19° around the strike of the bed. Though orientation measurements were recorded for all 6 years of CMC excavation, entries for the first 2 years (2000–2001) include only trend data; plunge was not recorded. MOR field notes from 1995, and notes from 1996 did not record orientation. When the dip-corrected 2002–2003 data were compared with the uncorrected data from those same seasons, the mean lineation orientation for the corrected data did not deviate from the 95% confidence interval for the uncorrected data set. Both corrected (2002–2003) and uncorrected (2000–2001) data, thus, were included in the analysis of two-dimensional orientation. The stereonet projection used for analysis of three-dimensional orientation included only the corrected 2002–2003 data.

The dip of the quarry beds affected depth calculations as well as orientation. All depth-below-datum measurements also required correction to determine actual depth below the upper contact of the bone-bed unit. The depth correction was done using a simple trigonometric equation:

$$\delta = (\cos q) \cdot (d - D[\tan q \cdot \cos(t - b)]),$$

where

- δ = corrected true depth;
- q = dip of quarry bed (19°);



	Massive sandstone		Angular blocky structure
	Sandstone with wavy bedding		Wedge-shaped structure
	Cross-bedded sandstone		Carbonate nodules
	Mudstone		Groundwater concretions
	Sandy-silty mudstone		Pedogenic slickensides
	Siltstone		Rhizoliths
	Cross-bedded sandy conglomerate		Vertebrate fossil material

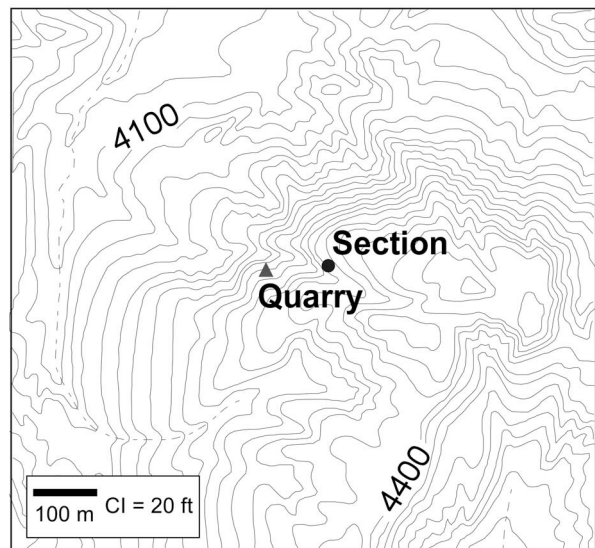


FIGURE 2—Composite lithologic section log of the Morrison Formation near the Mother's Day Quarry. Note Pryor Conglomerate (Cloverly Formation) at top of column. Stratigraphic position of Mother's Day Quarry indicated with arrow. Marked intervals are each 5 m thick. Poor outcrop exposure precluded description of a section running through the quarry itself. Position of section relative to the quarry is shown on the topographic map at bottom. Pedogenic symbols modified from Tabor and Montañez (2004).

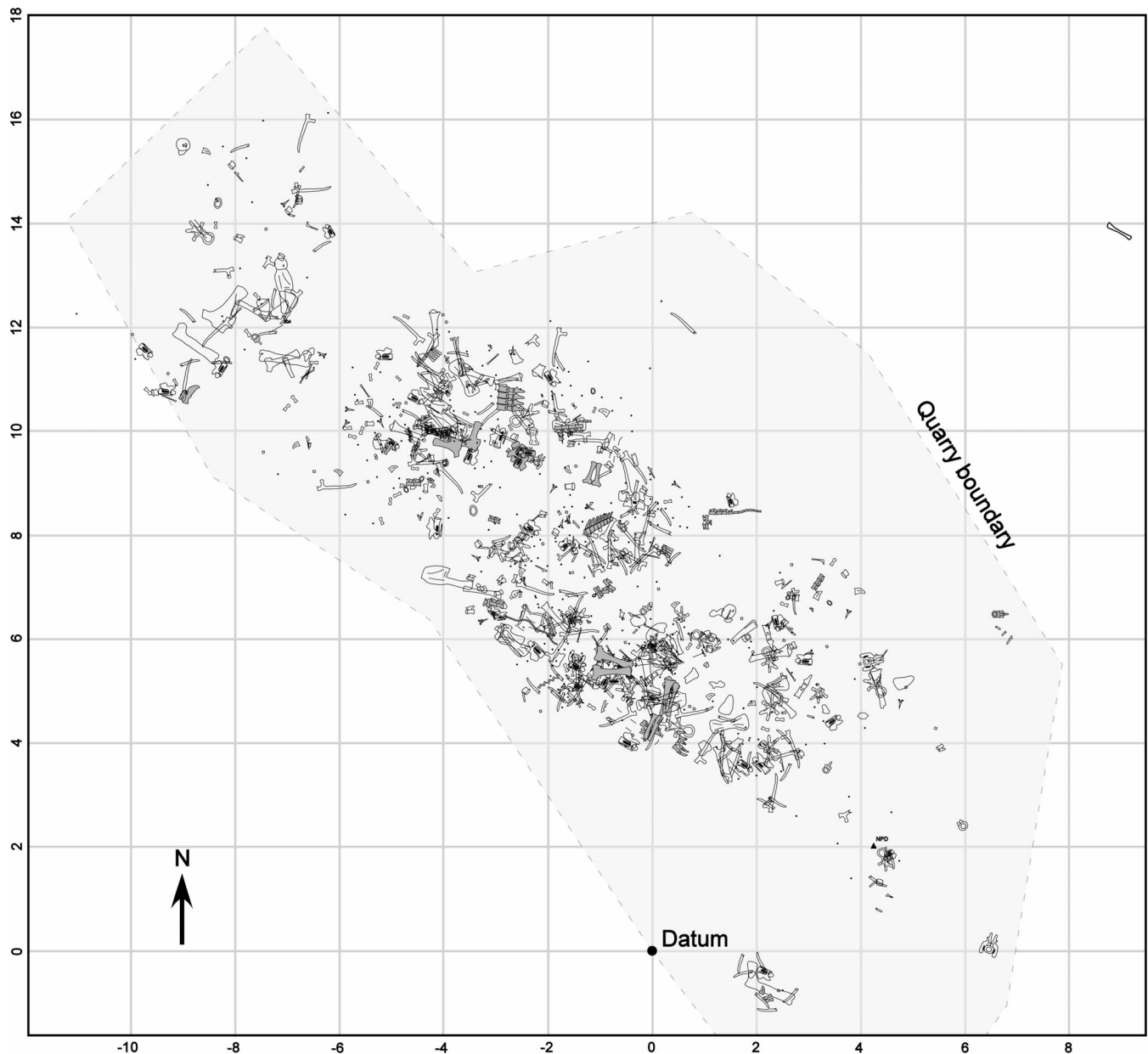


FIGURE 3—Quarry map showing position of bones excavated during the first four Cincinnati Museum Center field seasons (2000–2003). The bones are tightly packed, and adjacent specimens are often in contact with one another. Shading indicates bones that are either articulated or closely associated. Grid squares are each 2 m \times 2 m.

t = dip direction of quarry bed (255°);
 b = azimuth of element from datum;
 d = depth of element below datum;
 D = distance of element from datum.

Errors in corrected depth values arise as a result of variability in the average attitude of the quarry bed, creating inaccuracies in the absolute depths of elements below the upper contact of the bone bed. The corrected depth values, however, are internally consistent and accurately reflect the relative depth distribution of items. Given measurement errors in azimuth, distance, and depth relative to the quarry datum, corrected depth values reported here are reliable for only relatively low resolution analyses using depth intervals at least 25 cm thick.

A number of sediment samples from the quarry and the surrounding strata were collected for grain-size analysis to constrain spatial variation in grain size to aid in interpretation of the depositional environment at the site. The position of each sample within the quarry was recorded prior to removal.

Lab Methods

X-ray diffraction analysis was used to ascertain the mineralogical composition of the quarry sediments. Samples collected from the quarry and nearby vertical pits (Fig. 4C) were analyzed for horizontal or vertical transitions in grain size. Each sample was sonicated before analysis to break down any matrix not fully disaggregated by hydrochloric acid and peroxide treatments. Three analytical runs were performed on every sample using a Beckman Coulter particle-size analyzer, and the average of these analyses was used to produce grain-size curves.

Each skeletal element was examined for evidence of bone modification features such as bite marks (Chure et al., 1998), insect borings (Rogers, 1992), weathering cracks (Miller, 1975; Lyman and Fox, 1989), abrasion (Shipman and Rose, 1983), and breakage (Villa and Mahieu, 1991). Weathering damage was categorized using the stages developed by Behrensmeyer (1978) and modified with the understanding that grease content cannot be assessed for fossilized bone (Fiorillo, 1988). Some difficulty

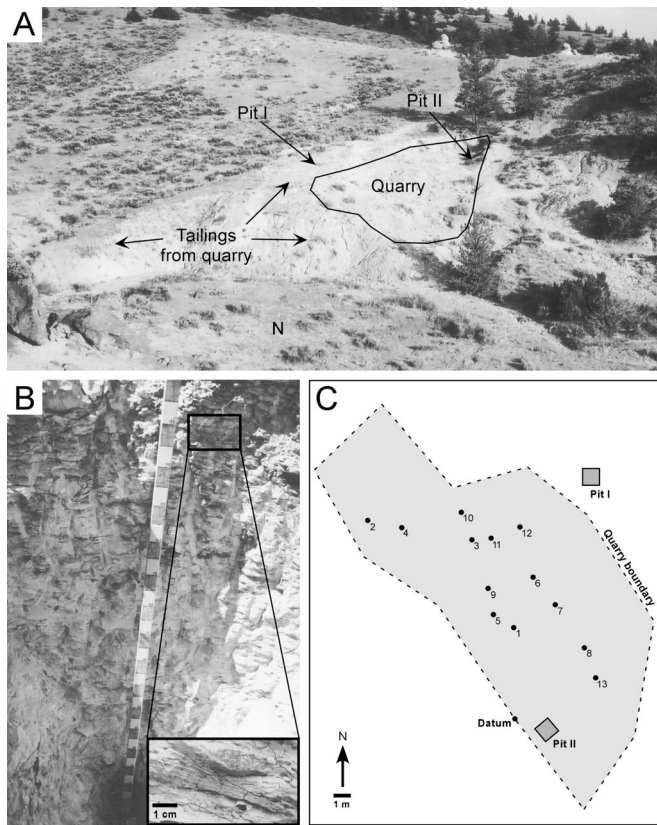


FIGURE 4—Photos and map of Mother's Day Quarry bone bed. A) Location of quarry on slope and positions of vertical pits dug within quarry. B) West wall of pit II showing the homogeneous bone-bed deposit and general lack of sedimentary structures. Inset shows small-scale, cross-bedded laminations near the top of the deposit. These are the only sedimentary structures noted within the quarry. C) Quarry map showing locations of grain-size samples and vertical pits dug to expose the bone bed in profile. The upper contact of the bone bed was visible in profile on the south wall of pit II, and the lower contact was exposed at the bottom of pit I.

arose, however, in assessing the weathering stage for elements with significant, external, postmineralization damage caused by recent erosion, excavation, preparation, or a combination thereof. Although great care was taken in both excavation and preparation of the bones, many specimens were extremely friable and susceptible to crumbling. Postmineralization damage not only obscured subtle surface modification features but also made it difficult to differentiate modified surfaces from areas damaged following fossilization. Assessment of breakage patterns involved less ambiguity. Breakage was classified as parallel, oblique, or transverse to the direction of bone fiber (Myers et al., 1980). Parallel or oblique breaks were attributed to damage that occurred prior to fossilization, and transverse breaks were attributed to damage that followed permineralization of the bone during diagenesis (Myers et al., 1980). Sedimentary matrix adhering to broken surfaces was interpreted as evidence that breakage occurred prior to final burial, whereas jagged but clean breaks were assumed to result from recent processes. Elements were examined for trample marks (Fiorillo, 1984, 1989; Behrensmeyer et al., 1986; Olsen and Shipman, 1988), but the generally poor preservation of the external surfaces of many specimens precluded accurate identification of such subtle features.

TAPHONOMY

Sedimentology

The local stratigraphy comprises a section of typical Morrison Formation fluvial sandstones with planar and trough cross-bedding and ripple marks, interspersed with thick mudstones representing interfluvial facies.

The quarry unit is a sandy siltstone bounded above and below by tabular sandstone beds, each approximately 0.5 m thick. These sandstones are characterized by unidirectional ripple marks and small-scale, trough cross-stratification, indicating a fluvial origin. Contacts between these beds and the MDQ unit are sharp and gently undulatory. No depositional features were observed within the small areas of the contact surfaces exposed at the bottom of pit I and in southern wall of pit II during excavation.

The bone bed matrix consists of light brown very fine-grained sand and silt-to-clay-sized particles. The matrix is composed primarily of quartz grains bound by calcareous cement but also includes trace amounts of feldspar. The deposit is 2.5–3.0 m thick with almost no visible primary sedimentary structures (Figs. 4A–B). Grain-size analysis reveals no significant horizontal or vertical textural variation within the quarry (Fig. 5), with the exception of scattered pockets of sandstone that contain a smaller silt- and clay-sized fraction than the surrounding sediments. Although the matrix itself is relatively homogeneous, clay rip-up clasts and sparsely distributed pebbles and carbonate nodules occur as minor components of the bone bed (Fig. 6). Though destruction of sedimentary structure often occurs as a consequence of pedogenesis and nearby strata show evidence of some minor paleosol development, the MDQ deposit lacks definitive indicators of paleopedogenesis, namely rooting, horizonation, and pedogenic structure (Retallack, 1988). The quarry facies does not appear to be laterally extensive. At the same stratigraphic level in nearby sections, deposits consist of finer-grained mudstones. Some bones have been recovered by surface collecting at a location several hundred meters from the quarry, but without intensive excavation of this area, lateral continuity with the MDQ cannot be established.

Carbonate in the bone bed occurs in two distinct forms: (1) nodular clasts distributed sparsely throughout the quarry deposit and (2) layers encrusting the skeletal material. The encrusting carbonate is presumably the result of soft-tissue replacement in an anoxic setting (Allison and Briggs, 1991) and is discussed later, along with other preservational characteristics. In contrast, the carbonate nodules show no signs of positive spatial association with the bones in the quarry, implying that they are not the product of microbial activity. Although the nodules do not appear to have formed by in situ paleopedogenesis, they may be reworked pedogenic products, inferred from their random distribution and orientation of their principal axes in the host facies.

Lithics recovered from the quarry all fall into the pebble size range (0.9–5 cm across the greatest diameter; 1.9 cm average). Pebbles are predominantly gray microcrystalline quartzite and chert scattered throughout the host facies, showing no indication of clustering or preferred skeletal associations. A plot of the vertical distribution for the Mother's Day pebbles shows that they are distributed through several meters (Fig. 7A) and are concentrated 150 cm and 224 cm below the upper contact of the bone bed. This vertical distribution pattern is the same for all objects in the quarry that are larger than sand size.

A single source is postulated for both the quartzite and chert as they co-occur in some of the clasts. These clasts may be gastroliths derived from sauropod carcasses within the quarry (e.g., Jennings and Hasiotis, 2006), though recent research suggests that gastric mills were restricted to relatively few sauropod taxa (Wings, 2004). The shape distribution of the pebbles was analyzed to determine if it differed greatly from those of reported gastrolith assemblages (Gillette, 1994; Sanders et al., 2001). The MDQ clast assemblage has a shape distribution similar to those of the probable gastrolith collections (Figs. 8A–B), but this similarity is equivocal because there is no current consensus on the validity of methods used to distinguish fluvial gravel from biologically processed clasts (Johnston et al., 1990; Chatelain, 1993; Manley, 1993; Lucas, 2000). Recent recognition that isolated pebbles in the Cloverly Formation, once purported to be gastroliths, are in fact related to debris-flow processes (Zaleha and Wiesemann, 2005) casts further doubt on a biogenic interpretation of the MDQ lithics.

In addition to the MDQ bones, small fragments of plant debris are scattered throughout the host facies. The debris consists primarily of un-

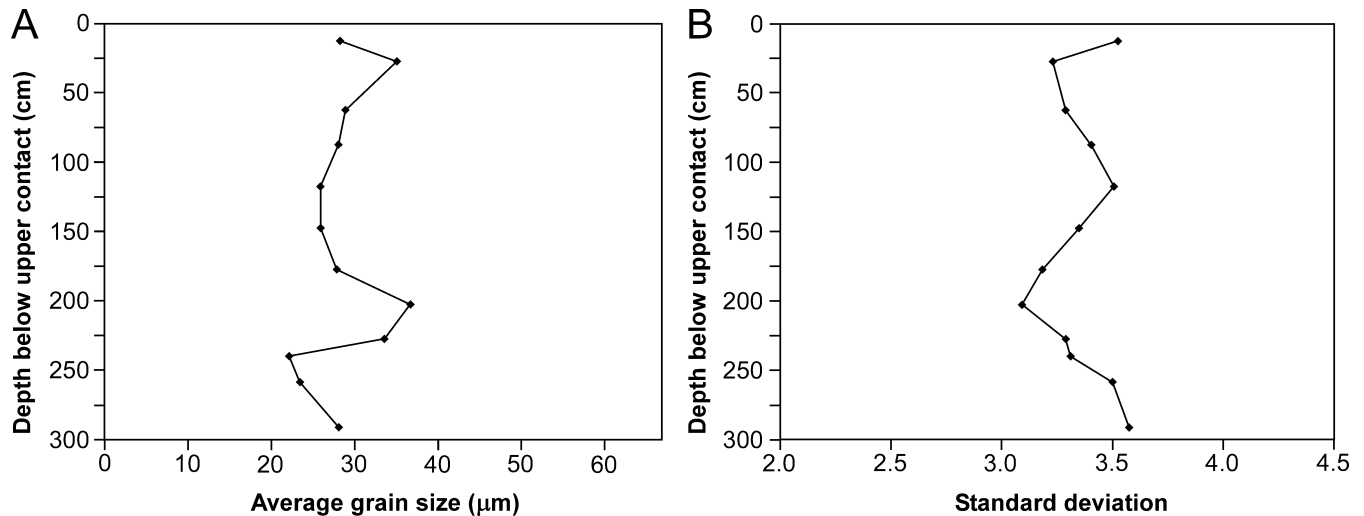


FIGURE 5—Graphs showing vertical textural variation through quarry bed. These are composite profiles generated by splicing together the data from pit I and pit II. The three uppermost samples from pit I were excluded from the analysis because of modern pedogenic alteration. A) Average grain size through vertical profile. B) Standard deviation through vertical profile. Slight increases in average grain size at 25 cm and 200 cm below the upper contact of the bone bed are accompanied by decreases in degree of sorting. Textural changes are minor ($<20 \mu\text{m}$), and there is no indication of increasing or decreasing overall trends in grain size.

identifiable, fragmented material, with occasional elongate stems and small leaf-like structures.

To determine if the MDQ assemblage was transported by the same event that deposited the host facies, the quartz equivalency of one of the larger MDQ bones (CMC VP7747, a left femur with a total length of 112 cm) was calculated for comparison with the sedimentary clasts in the bone bed. We used the equation developed by Behrensmeier (1975):

$$d_q = (\rho_b - 1)d_b/1.65,$$

where d_b = nominal diameter of the bone ($= \sqrt[3]{1.91 \times \text{bone volume}}$), and ρ_b = bone density.

Bone volume was determined by modeling the femur as a series of cylinders of various lengths and diameters, based on specimen measurements. Bone density was assumed to be $1.47 \text{ g}\cdot\text{cm}^{-3}$, using a 2:1 ratio of the densities of cancellous ($1.21 \text{ g}\cdot\text{cm}^{-3}$) and compact ($1.65 \text{ g}\cdot\text{cm}^{-3}$) bone as calculated by Richmond and Morris (1998) from the values given in Behrensmeier (1975). Applying this equation, the femur has a nominal diameter (d_b) of 29 cm, and the diameter of a spherical clast with equal density and an equivalent settling velocity (quartz-grain equivalent = d_q)

is 9 cm. The observed settling velocity of CMC VP7747 would be dependent on its orientation because femora are not spherical in shape. Consequently, the estimated d_q value will have an error range of $\pm 25\%$ (Behrensmeier, 1975). Incorporating this error, the quartz-grain equivalent of the femur is between 7 cm and 11 cm, notably larger than the largest pebbles in the host facies.

Taxonomic Diversity

The only nonsauropod skeletal elements recovered from the MDQ are five theropod teeth. One tooth clearly belongs to *Allosaurus* but is broken at its crown base. Each tooth lacks the root portion, but since there is no evidence of resorption, it cannot be verified that the teeth were shed rather than broken. All the MDQ sauropod material is attributable to gracile diplodocoids, based on slender limb proportions, distinctive cervical vertebral morphology, double-beam chevrons, biconvex distal caudal vertebrae, and bifurcate neural spines on posterior cervical and anterior dorsal vertebrae (McIntosh, 1990a; Wilson, 2002). The cervical vertebrae have elongate centra with cervical ribs extending to the posterior flange but not beyond, superficially similar to those of *Diplodocus* (Hatcher, 1901). The centra are not as elongate as those of *Barosaurus* (Lull, 1919; McIntosh, 2005). Given the observed suite of postcranial characters, the MDQ sauropods are assigned to Diplodocoidea. The genus *Diplodocus* is used here for purposes of comparison because of superficial similarities with the MDQ material, but these comparisons are not intended to suggest assignment of the MDQ sauropods to *Diplodocus*.

Number of Individuals

To calculate the minimum number of individuals present in the quarry, paired appendicular elements were counted. Positioning (e.g., right or left) and size comparison were used to further differentiate between individuals, thereby increasing counting accuracy. Metatarsal I was the most common element in the excavated fraction of the MDQ assemblage, with a total of 15 specimens. Five of the metatarsals are from the left side, five are from the right, and five unprepared specimens in MOR collections are currently indeterminate. The minimum number of individuals in the assemblage, thus, is eight, assuming 14 of the 15 specimens are matching pairs. Size comparison of the elements within each of these pairs does not alter the estimate for the minimum number of individuals, for none of the paired metatarsals differs by more than 10% in length.

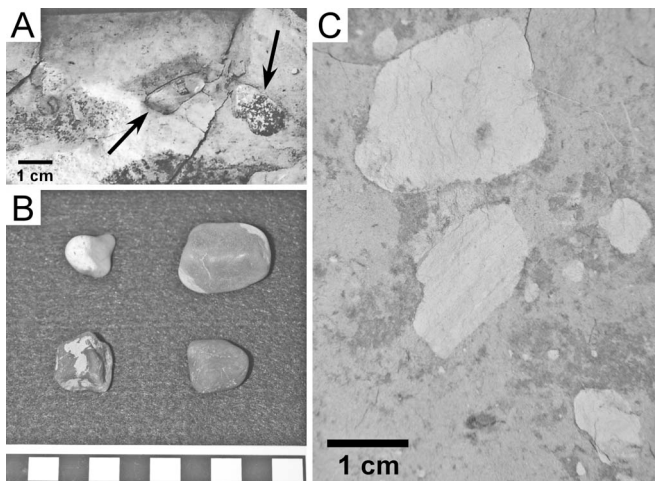


FIGURE 6—Sedimentary features in the Mother's Day Quarry. A) Carbonate nodules. B) Pebbles removed from the quarry and washed for analysis. C) Internally laminated clay rip-ups indicative of high flow velocity.

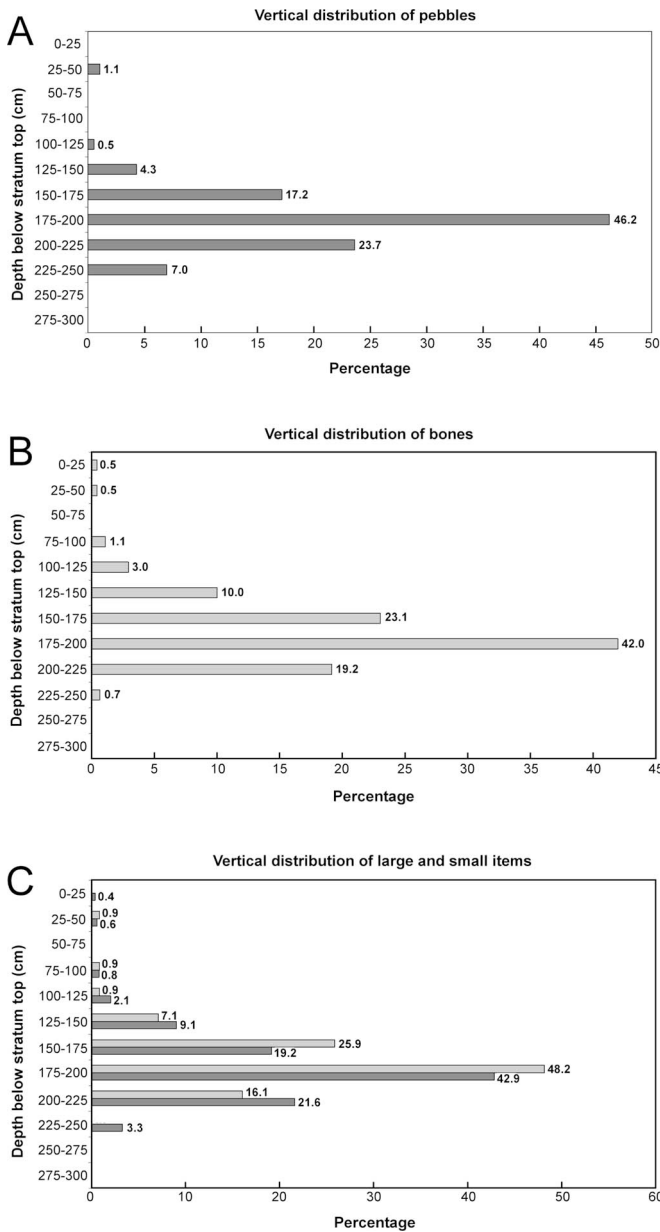


FIGURE 7—Plots of depth distributions for objects within quarry. A) Bar graph of depth distribution for pebbles showing concentration between 150 cm and 224 cm depth within the bone bed. B) Bar graph showing vertical distribution of bones by percent of total assemblage. Note that the greater concentration of bones exists between 150 cm and 224 cm. C) Bar graph showing vertical distribution of large and small items by percent of total assemblage. The concentration between 150 cm and 224 cm is similar to the distributions for the pebbles and bone. All categories are exclusive of upper bound.

Age Profile

Age determination in sauropod dinosaurs is difficult, as no ontogenetic studies based on linear proportions of skeletal elements are available at present. Currently, the only detailed work on sauropod ontogeny is a histological study of *Apatosaurus* (Curry, 1999). The most common MDQ element, metatarsal I, is not useful for age determination. The young age of individuals within the quarry was determined by the relatively small size of the skeletal elements and lack of fusion of neurocentral sutures on many of the vertebrae (Brochu, 1996). For verification, limb elements were measured and compared to adult *Diplodocus* in the Carnegie Museum (CM) and the Yale Peabody Museum (Hatcher 1901; McIntosh and Carpenter, 1998). Length percentage was then calculated

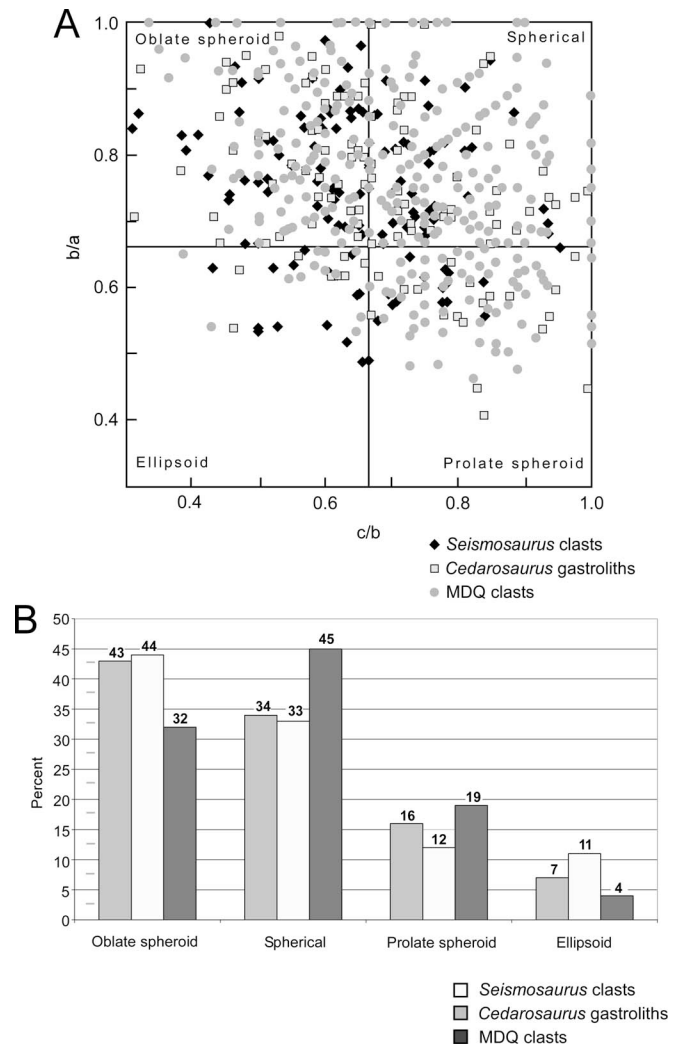


FIGURE 8—Shape distribution for pebbles removed from quarry. A) Quadrant plot. B) Summary graph comparing the shape distribution of the Mother's Day Quarry pebbles with those of purported gastrolith assemblages. Distributions of all assemblages appear similar, but the affinity of the Mother's Day Quarry clasts cannot be determined without knowledge of the population variance in shape for gastroliths. *Cedarosaurus* data tabulated from Sanders et al., (2001) and *Seismosaurus* data obtained from Lucas (2000). MDQ = Mother's Day Quarry.

and compared to the histologically based categories proposed by Curry (1999; see Table 1). According to Curry's (1999) age and body-size categories, juveniles range up to 73% of adult size, and subadults may be up to 91% of the size of a full grown adult. Elements selected for comparison were a femur (CMC VP7747), the largest element recovered from the quarry thus far, and a humerus (CMC VP7746). Compared with the smallest adult femur (CM-94), CMC VP7747 is 76% of the total length. The Carnegie Museum and Yale Peabody Museum *Diplodocus* specimens did not include humeri, so humeral lengths were estimated using the humerofemoral ratio provided in McIntosh (1990b). The CMC humerus is estimated to be 74% of the size of the smallest adult specimen (CM-94). Both the large femur (CMC VP7747) and the humerus (CMC VP7746) from the MDQ fall within the lower portion of the subadult-size range of Curry (1999) or the upper portion of the juvenile range. These findings verify that no adult material has been recovered from the MDQ thus far.

Vertical Distribution of Elements

All bones recovered from the bone bed were assigned to one of twelve 25-cm-thick stratigraphic intervals in order to assess their absolute and

TABLE 1—Calculation of percent adult size for largest forelimb and hindlimb elements recovered from quarry. Asterisks indicate humeral length values estimated from femoral lengths using the humerofemoral ratio for *Diplodocus* (0.65) given in McIntosh (1990b). Measurements taken from Hatcher (1901) and McIntosh and Carpenter (1998). Age-class size ranges from Curry (1999). CMC = Cincinnati Museum Center; CM = Carnegie Museum; YPM = Yale Peabody Museum.

Specimen	Taxon	Element	Length (cm)	Percent length	Age class size range
CMC VP7747	<i>Diplodocus</i> sp.	Left femur	1120	—	Subadult (73% < x < 91%)
YPM 1920	<i>Diplodocus longus</i>	Left femur	1620	69	—
CM 84	<i>Diplodocus carnegii</i>	Right femur	1542	73	—
CM 94	<i>Diplodocus carnegii</i>	Left femur	1470	76	—
CMC VP7746	<i>Diplodocus</i> sp.	Left humerus	710	—	Subadult (73% < x < 91%)
YPM 1920	<i>Diplodocus longus</i>	Left humerus	1053*	67	—
CM 84	<i>Diplodocus carnegii</i>	Right humerus	1002*	71	—
CM 94	<i>Diplodocus carnegii</i>	Left humerus	956*	74	—

relative vertical distribution within the host facies. Eighty-five percent of the bones fall into three superadjacent intervals, 150–225 cm below the top of the bed (Fig. 7B). Given that all of the stratigraphic intervals in the host facies were exposed and sampled extensively across the known geographic extent of the bone bed, we regard the concentration of elements between 150 cm and 225 cm as real and not an artifact of differential sampling.

All bones and lithic clasts were assigned to one of two roughly defined size categories (large items collected in plaster jackets versus small items collected in foil) to detect patterns related to vertical size sorting or grading. Large and small bones and clasts occur throughout the host facies, and there are no overall upward-coarsening or upward-fining trends (Fig. 7C).

Element Orientation

Bidirectional horizontal orientation or trend data were collected from 377 elongate elements and were plotted on a rose diagram (Fig. 9A). The sample was analyzed using Rao's spacing test (Rao, 1976) to determine existence of a preferred orientation. Rao's test was modified slightly to reflect the bidirectional nature of the orientation data. In the modified equation, given here, 180 is substituted for 360 in the calculation of λ :

$$U = \frac{1}{2} \sum_{i=1}^n |T_i - \lambda|$$

where

$$\begin{aligned} \lambda &= 180/n; \\ T_i &= \theta_{i+1} - \theta_i; \\ T_n &= (180 - \theta_n) + \theta_1; \text{ and} \\ U &= \text{Rao's test statistic.} \end{aligned}$$

Rao's test produced a U -statistic of 118.41 for the MDQ sample, and comparison of this value with the critical values provided in Russell and Levitin (1995) yields a p -value >0.90 . Accordingly, the null hypothesis of equal spacing of bones within the defined interval of 0° to 180° cannot be rejected, suggesting that these elements are oriented randomly. A subset of elongate elements—including only those that yielded trend and plunge data—was plotted on a lower hemisphere, equal area stereonet projection (Fig. 9B). Because a stereonet diagram of imbricated elements will show a cluster of points in the quadrant opposite that of the direction of flow, this method can be used to reveal the presence or absence of imbrication of elements within an assemblage (Fiorillo, 1991). The diagram shows no single cluster of points; instead, points are concentrated near the edges of the diagram, indicating that most bones have subhorizontal orientations. Eighteen percent of the identifiable elements for which plunge data exist have high-angle plunges of at least 30° to horizontal. The vertical distribution of high-angle elements within the bone bed follows the distribution patterns discussed above (Fig. 10).

Hydraulic Sorting of Elements

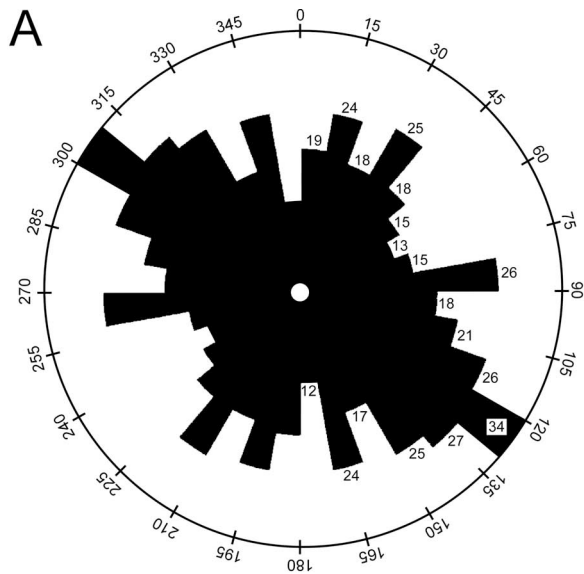
There are a number of different ways to assess hydraulic sorting in fossil assemblages. Elements may be divided into groups of differing transport potential based on size, shape, weight, or observed hydraulic behavior in flume experiments. Estimating the hydraulic behavior of sauropod bones presents a difficult challenge because many elements differ from available modern analogues in their size, shape, and density. For example, sauropod cervical vertebrae possess elaborate neural spines that would substantially alter their profile and interaction with a fluid current. Furthermore, extensive pneumatic cavities within the centra (Wedel, 2003) decrease dramatically the bulk density of both cervical and dorsal vertebrae, thereby reducing flow velocities necessary to mobilize those elements.

The specific hydrodynamic effects of element shape and density are difficult to quantify for the MDQ bones, but characterization of bones by size is somewhat less of a problem. The same crude classification used previously to assess vertical size sorting within the bone bed was used in an examination of potential hydraulic sorting. Small bones and bone fragments outnumber large bones in the quarry by almost threefold (302 to 113, respectively), suggesting that the assemblage was not heavily winnowed or did not undergo significant transport. Fragmentation, however, may have masked the removal of some small elements.

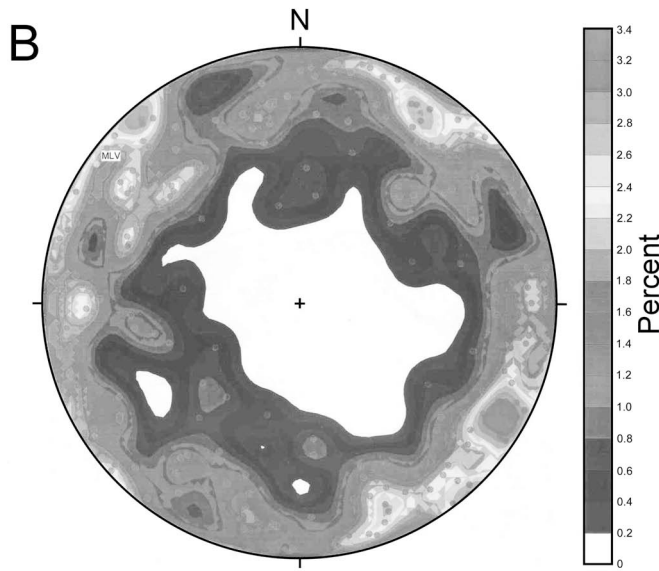
The traditional method for assessing hydraulic sorting in fossil assemblages is that developed by Voorhies (1969), where skeletal elements are assigned to one of three categories—Voorhies groups I, II, and III—based on their relative transport potentials. Voorhies groups, however, are not appropriate for determining hydraulic sorting in the MDQ because sauropod elements differ from the mammalian homologues in at least one of the three factors controlling hydrodynamic behavior—density, shape, and size (Behrensmeyer, 1975).

It is difficult to estimate accurately the transport potential of sauropod bones without conducting independent flume experiments using models of the elements in question. Using experimental data gathered from more appropriate modern analogues for sauropods, however, avoids many of the problems associated with use of Voorhies groups. Frison and Todd (1986) ran stream-transport experiments on bones of an Indian elephant (*Elephas maximus*) and calculated a fluvial transport index (FTI) to indicate average transport potential of each tested element. Elements were characterized as having high (>75), intermediate (74–50), or low (<50) FTIs, with those possessing a higher index being more susceptible to movement (Frison and Todd, 1986). The elephant provides more suitable skeletal analogues for sauropod bones because of convergently acquired morphological similarities, especially in the appendicular skeleton (Smuts and Bezuidenhout, 1993, 1994), related to graviportal locomotion and support of large body mass.

The only elements that differ significantly between elephant and sauropod are the cervical vertebrae. Elephant cervical vertebrae lack internal pneumaticity, are dramatically compressed anteroposteriorly, and have simple neural spines and vertebral arches (Bezuidenhout and Seegers,



N=377



N=189

FIGURE 9—Graphical analysis of bone orientation. A) Rose diagram showing two-dimensional orientation of elongate elements from 2000–2003 field seasons. Numbers on petals denote the observed frequency of elements in each 10° interval. There is no statistically significant orientation of elements as expected for an allochthonous assemblage. B) Stereonet projection showing three-dimensional orientations of elongate elements from 2002 and 2003 field seasons. Clustering around periphery of diagram indicates predominance of horizontal elements and lack of imbrication in assemblage. Note high-angle elements plotting nearer to the center of the diagram; these bones constitute 18% of the sample.

1996). In contrast, sauropod cervical vertebrae are generally elongate and possess elaborate neural spines and ramified pneumatic cavities within the centra (Hatcher, 1901; Wedel, 2003). The resulting discrepancy in estimates of transport potential, however, should not adversely affect analysis of hydraulic sorting because elephant cervical vertebrae have a high FTI (Frison and Todd, 1986) despite being denser than pneumatic sauropod vertebrae. To further ensure that inaccurate FTI estimates for cer-

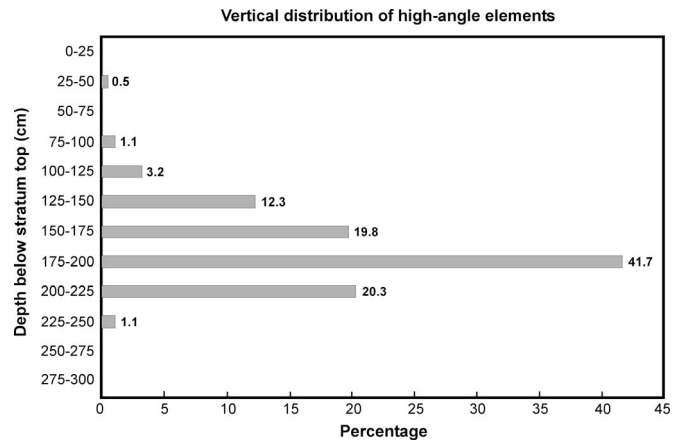


FIGURE 10—Graph of the vertical distribution of high-angle elongate elements. Depth profile mirrors that for all skeletal elements (shown in Fig. 7). High-angle bones are not concentrated in the upper portion of the bone bed, as would be expected if the majority of these orientations resulted from trampling.

vical vertebrae did not fatally bias the sorting analysis, element ratios were calculated both with and without cervical vertebrae included.

The robust elephant mandible was excluded from all analyses because delicate sauropod cranial elements are frequently disarticulated and dissociated from their postcrania due to weak articulation and high-transport potential (McIntosh and Berman, 1975; Dodson et al., 1980). Articulated elements were not included in the analysis, either, as they have a somewhat greater transport potential than their disarticulated component parts (Coard and Dennell, 1995). Similar to the method proposed by Fiorillo (1991) for adapting Voorhies groups for use with dinosaurian assemblages, ratios of different FTI groupings were calculated and compared to determine whether the MDQ assemblage is depleted in easily transported elements relative to those likely to compose the lag deposit. The ratios calculated from the MDQ assemblage can then be compared to the ratio of elements found in a standard sauropod skeleton (Fiorillo, 1991). All three of the FTI groups identified by Frison and Todd (1986) were retained for this analysis because each contains some postcranial elements; Fiorillo (1991) advocated discarding Voorhies group III, which consists entirely of cranial elements (Voorhies, 1969).

The ratios of FTI groups for the MDQ assemblage indicate that the accumulation is enriched in elements with intermediate transport potential relative to those with high FTI (Fig. 11A). Ratios were recalculated excluding all thoracic rib material since high fragmentation artificially inflated counts in the intermediate FTI category. Removal of ribs did not alter the trend toward intermediate FTI elements initially observed in the data (Fig. 11B). The general relationship of the ratios also remains static when both cervical vertebrae and thoracic ribs are removed (Fig. 11C).

Bone Modification

Such bone modification features as bite marks, insect borings, weathering cracks, breakage, and abrasion accumulate in an assemblage as exposure time increases. Conversely, carcasses buried shortly after death show little or no evidence of modification (e.g., Behrensmeyer, 1978). Of a sample of 262 bones from the MDQ assemblage, 71% show some evidence of modification; however, only a small fraction of these features occurred prior to fossilization.

Transverse breakage of elements due to postfossilization damage is the most common type of modification. Postfossilization breakage accounts for 84% of all broken elements (38% of total sample), whereas only 16% of observed breaks occurred prior to fossilization (7% of total sample). Many bones are also crushed and distorted, either by tectonism or lithostatic compaction of the fine-grained quarry matrix. A few specimens have been cut by small faults. Fresh breakage of elements, identified by

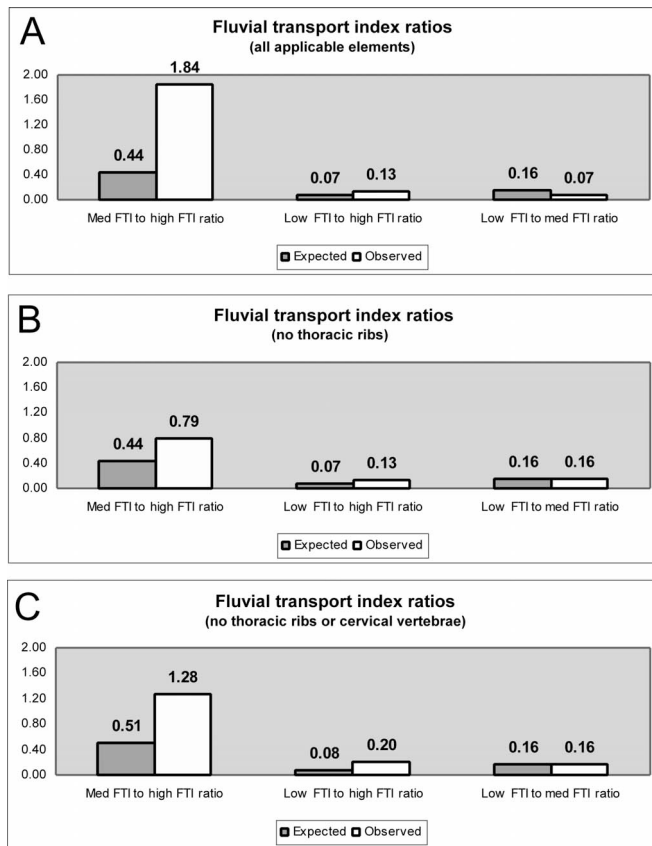


FIGURE 11—Graphs of fluvial transport index (FTI) ratios (Frison and Todd, 1986) showing the relatively high ratio of medium FTI to high FTI elements. The Mother's Day Quarry assemblage is enriched in elements with moderate-transport potential relative to those with high-transport potential. A slight enrichment of low-FTI elements relative to high-FTI elements is also detectable. A) Ratios calculated using all applicable elements. B) Ratios calculated with thoracic ribs excluded because of high fragmentation. C) Ratios calculated with both ribs and cervical vertebrae excluded.

obliquely oriented or infilled breakage surfaces, is observed infrequently. Signs of abrasion are noted on only 10% (24 elements) of the bones for which abrasion could be scored legitimately. Two elements have gouges identified as tooth marks. In one of the specimens, a femur (CMC VP7747), the marks are located on the proximal articular surface, indicating that they occurred postmortem and were probably the result of scavenging. Identification of weathering features in the prepared fraction of the assemblage, though tenuous given the degree of surficial damage to many specimens, reveals that the vast majority of the bones (97 specimens) show no indication of weathering. Only four specimens show more advanced weathering stages. No bones showed evidence of modification by insects.

Preservation

The MDQ assemblage consists of two primary taphonomic modes: fresh and highly altered bones. Most of the heavily altered bones are abraded and broken beyond recognition. A number have been reduced to small, rounded clasts. In contrast, the sauropod elements strewn throughout the quarry are well preserved with little evidence of external modification. Such relatively small, delicate skeletal elements as distal chevrons and vertebral processes are quite common. Additionally, the presence of soft-tissue remnants in the form of skin impressions (Fig. 12A) indicates that the sauropod carcasses were not completely decomposed at the time of burial. Other evidence for the presence of soft tissue at the time of deposition is the semiarticulated state of some of the skeletal remains

and the formation of calcareous rinds on the articular ends of many of the long bones. The precipitation of carbonate crusts around skeletal material indicates anoxic conditions created by the burial and subsequent decomposition of nonmineralized tissues (Bernier, 1968; Weigelt, 1989; Allison and Briggs, 1991). Series of articulated vertebrae are common, as are articulated pes units and pelvic elements (Figs. 12B–D). The vertical distribution of articulated elements within the bone bed differs slightly from the distribution of all MDQ elements. No articulated bones were recovered from the upper 125 cm or lower 50 cm of the bone bed (Fig. 13). The primary concentration of articulated elements is in the same 150–225 cm interval that contains the bulk of the MDQ bones.

DISCUSSION

Transport and Burial

The stratum containing the MDQ assemblage is similar in many respects to deposits created by fine-grained debris flows and hyperconcentrated flows (Martin and Turner, 1998; Benvenuti and Martini, 2002). Despite the high-energy burial mechanism inferred here, the skeletal assemblage shows no signs of significant transport. Debris flows are invoked as burial agents less commonly than floods (Andrews and Alpagut, 1990; Andrews and Ersoy, 1990; Fastovsky et al., 1995; Loope et al., 1998, 1999; Rogers, 2005; Eberth et al., 2006), but both mechanisms simply occupy different points along a continuous spectrum of flow types from fully plastic sediment flows to Newtonian fluid flows (Benvenuti and Martini, 2002). Fluvial flow is one of the most common abiotic mechanisms for transport and burial of terrestrial vertebrate remains (Behrensmeier, 1988). The MDQ deposit exposed in the quarry area, however, lacks definitive evidence of deposition by traditional fluvial processes, leading to the conclusion that the assemblage was buried by a high-density sediment flow.

The MDQ bed shares several features with deposits emplaced by hyperconcentrated flows. Hyperconcentrated flow deposits are typically massive, structureless beds that may be several meters thick, may contain mudclasts, or may show some evidence of lamination or grading (Vallance and Scott, 1997; Martin and Turner, 1998; Benvenuti and Martini, 2002; Zaleha and Wiesemann, 2005). Clasts within the flow show strong alignment with flow direction in areas with steep slopes but may show no preferred orientation on low gradients (Vallance and Scott, 1997). Clast breakage can be as high as 25% but is typically much less in matrix-supported deposits (Vallance and Scott, 1997). Sorting in hyperconcentrated flow deposits is poor compared to stream-flow deposits but better than in debris-flow deposits *sensu stricto* (Pierson and Scott, 1985).

Similarities between the MDQ deposit and deposits of hyperconcentrated flows include thick, massive bedding devoid of major sedimentary structures, poor sorting, and presence of mudclasts. The MDQ bone bed lacks the stratification, development of sedimentary structure, and systematic vertical variations in grain size commonly associated with stream-flow deposits (McKee et al., 1967; Miall, 1978; Stear, 1985). The presence of scattered pockets of sandstone is also difficult to explain as a consequence of flood deposition, for turbidity should fully homogenize sediments prior to settling and deposition. The sandy patches may be remnants of cohesive chunks of sediment incorporated by the flow that ultimately failed to homogenize with the surrounding matrix.

The orientation pattern of MDQ elongate elements appears to approximate the bimodal distribution observed in skeletal assemblages deposited or reoriented by unidirectional flow (Morris et al., 1996), but none of the concentrations of elements is statistically significant (Fig. 9). High-velocity fluvial currents typically generate a strong preferred orientation of elongate elements, even under turbulent flow conditions (Morris et al., 1996). Clast alignment in debris flows is primarily parallel to flow direction except at the flow margins where grains orient normal to flow (Major, 1998). The MDQ pattern, however, shows a large dispersion, suggesting little to no transport (Morris et al., 1996). The partially articulated condition of some of the MDQ material and the close proximity of the bones

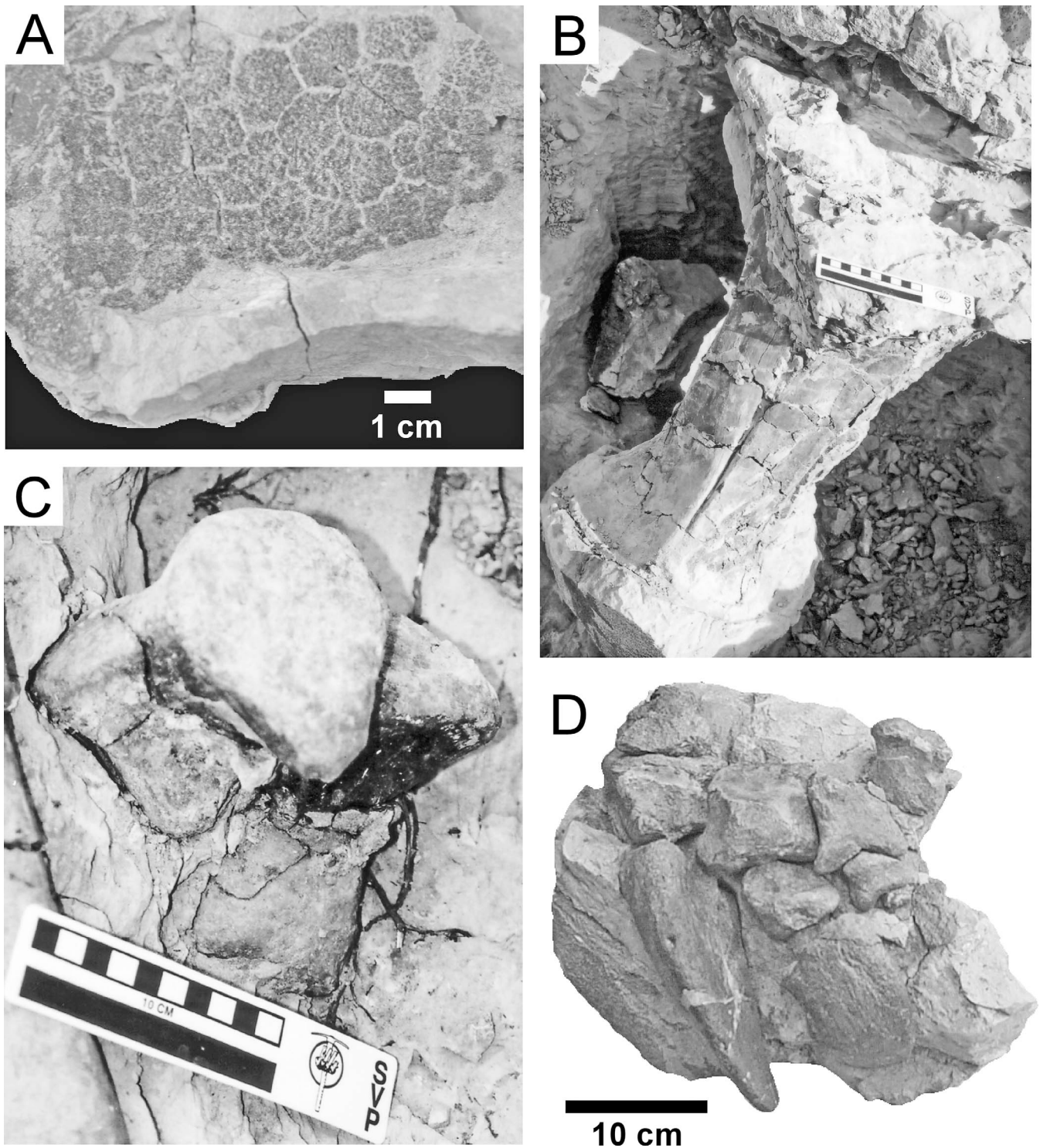


FIGURE 12—Examples of soft-tissue preservation from the Mother's Day Quarry. A) Skin impression (CMC VP8075). B) Articulated ischia associated with a sacrum. C) Articulated left metatarsals I and II. D) Semiarticulated left pes (CMC VP8080). Photo courtesy of M. Papp.

in the quarry may have worked to inhibit alignment of elongate elements with the flow direction. Increasing degree of articulation of skeletal elements has been shown experimentally to reduce their propensity to orient in a unidirectional flow (Coard and Dennell, 1995). Furthermore, unconfined flow regimes associated with flash floods and debris flows exhibit greater dispersion around the mean flow direction (Morris et al., 1996).

The high-angle elongate bone orientations may result from high-energy fluid flow (Voorhies, 1969; Fiorillo, 1989), trampling (Hill and Walker,

1972), or a high-density sediment flow. Fluid flow, however, can be dismissed as a potential cause of these orientations because there is no evidence of imbrication. Trampling cannot be excluded as the cause of the high-angle bone orientations, but it should be invoked with caution—only a small percentage of the MDQ bones shows fresh breakage, whereas modern, high-density bone accumulations affected by substantial trampling are characterized by large percentages of damaged elements (Haynes, 1988). Furthermore, trampling experiments demonstrate that

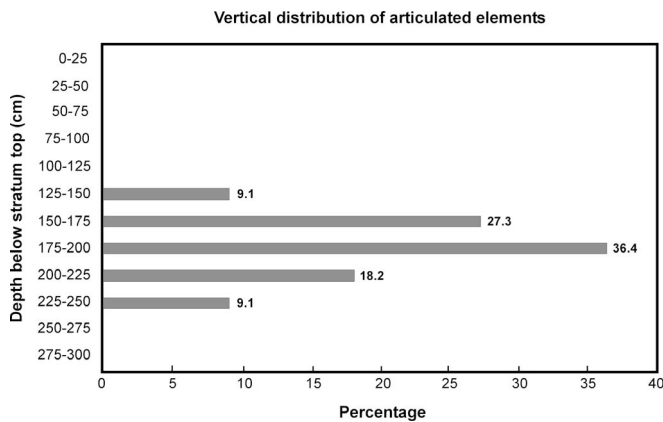


FIGURE 13—Graph of the vertical distribution of articulated elements. Articulated bones are absent in the uppermost 125 cm and lowermost portions 50 cm of the bone bed. Trampling may have disarticulated bones in the upper part of the upper part of the bed, but the observed intervals of absence may also be due to the small sample of articulated bones with associated depth data ($n = 11$).

vertical displacement is less likely to occur in such fine-grained sediments as the MDQ matrix (Gifford-Gonzalez et al., 1985).

Assemblages trampled while exposed on a surface generate a depth profile that approximates a normal distribution, whereas assemblages buried prior to trampling have profiles resembling a Poisson distribution (Gifford-Gonzalez et al., 1985). The MDQ profile is more similar to a normal distribution, so if the assemblage underwent bioturbation, trampling activity probably occurred prior to burial. Consequently, some size sorting of elements may be expected, with smaller elements showing higher vertical mobility than large elements (Villa and Courtin, 1983). The similar vertical distributions of large and small MDQ bones, however, precludes the possibility of sorting. Other methods of evaluating the effects of trampling include examination of the vertical distribution of high-angle and articulated elements. If heavy trampling created high-angle element orientations, these elements should occur more frequently in the upper portion of the bone bed. Similarly, trampling activity should hasten disarticulation, leaving the majority of articulated elements in the lower portion of the bone bed, beyond the direct effects of trampling. Though high-angle bones do not occur preferentially at shallow depths, articulated elements are noticeably absent from the uppermost and lowermost intervals. The lack of articulated elements in the upper 125 cm of the bone bed may be related to trampling but may also be due to the small sample size of articulated elements with associated depth measurements ($n = 11$).

It is probable that burial by the inferred high-energy flow at the MDQ played some role in the development of high-angle bone orientations. Debris-flow deposits are characterized often by well-developed imbricate clast fabrics (Major, 1998), but internal shear stress could conceivably rotate bones into high-angle positions without development of imbrication, and sudden cessation of flow could preserve unstable clast orientations. Rapid-flow termination is atypical of fluvial regimes, but sudden cessation of high-density sediment flows may happen by either cohesive or frictional freezing or abrupt deceleration (Benvenuti and Martini, 2002). Freezing occurs once internal shear stresses fall below a critical threshold and either cohesive or frictional forces become dominant, slowing and halting the flow before size sorting of sedimentary particles can take place (Major, 1998). Alternatively, rapid-flow deceleration may result in en masse deposition of poorly sorted sediments lacking primary sedimentary structure (Zaleha and Wiesemann, 2005). In contrast, high-energy fluid flows generate a fining-upward sequence typically as their current velocity wanes, their competency decreases, and suspended fines are deposited by receding waters (McKee et al., 1967).

The MDQ assemblage shows no evidence of hydraulic sorting, implying that the skeletal material was not transported a great distance. Some

small bones may have been winnowed from the assemblage, but this effect is difficult to assess accurately given the fragmentation of many of the MDQ elements. Calculation of hydraulic equivalence for the MDQ femur (CMC VP7747) further emphasizes the disjunction in fluvial transport potential between the bones and the sedimentary particles in the quarry matrix. If the largest bones were transported by hydraulic flow, their hydraulic equivalence would require that the flow be of exceptionally high energy, greater than that necessary to transport the lithic pebbles at the site. It is far more reasonable that most of the MDQ bones were not transported far from their initial accumulation site but, instead, were reworked and buried by inflowing sediment.

Preservation of delicate skeletal elements and soft-tissue remnants, as well as lack of substantial fresh bone breakage and abrasion, also suggests that the bone-bed assemblage is parautochthonous. In addition to preservation by rapid burial, skin may also be preserved through desiccation (e.g., Osborn, 1912). Heavily keratinized skin may prove resistant to disintegration, remaining in the vicinity of a carcass long after other soft tissues have been stripped away by decay (Coe, 1978; Hill, 1980). Relative resistance of keratinized tissues is not a viable explanation for the MDQ skin impressions because this method of preservation cannot account for retention of the nonkeratinized tissues ultimately preserved as calcareous encrustations on many of the bones. Though desiccation may have played a part in the preservation of the skin, the presence of calcified rinds indicates that exposure was minimal. Since these deposits likely formed by mineralization of soft tissues under anoxic conditions (Berner, 1968; Weigelt, 1989; Allison and Briggs, 1991), the MDQ carcasses were not subaerially exposed for a long period of time. Preservation of the skin impressions is best interpreted as the result of rapid burial of carcasses retaining extensive soft tissue following a brief period of desiccation.

The Morrison Formation is a rather unusual setting for mass movement of sediment given the low topographic relief of its fluvial channel, floodplain, and lacustrine paleoenvironments, but initiation of debris flows does not require steep gradients when sediments become fully saturated and runoff rates are especially high (Iverson et al., 1997). Hyperconcentrated flows may form because of sediment bulking resulting from overland sheet flow, rill erosion, or bank failure within a fluvial channel system (Benvenuti and Martini, 2002). Such a scenario is envisioned for the burial event that created the MDQ, similar to the proposed trigger events for debris flows identified in the Cretaceous of Madagascar (Rogers, 2005).

If the MDQ unit is a sediment-flow deposit, the occurrence of such flows in the area must have been a rare event, for massive, structureless beds of similar thickness are not present in nearby sections. The lack of multiple identifiable flow deposits in the vicinity of the MDQ stands in contrast to the apparently seasonal recurrence of other fossiliferous debris flows (Fastovsky et al., 1995; Rogers, 2005; Eberth et al., 2006). The disparity between the stratigraphic context of the MDQ bone bed and those sites with evidence of multiple flow events suggests that the MDQ deposit did not result from normal seasonal cycles of heavy precipitation and flooding. Instead, the MDQ may represent a unique confluence of anomalous conditions that favored debris-flow formation.

Mode of Mortality

The MDQ accumulation appears to be the result of a nonattritional mass mortality. This interpretation is supported by the incomplete skeletal disarticulation in the assemblage, remains of soft tissues, and the generally well preserved condition of the remains. Partial disarticulation of the MDQ skeletons indicates that the carcasses were exposed prior to their final burial. The paucity of bone-modification features and evidence of soft tissue at the time of deposition make it likely that exposure time was on the order of months (Coe, 1978). It is unlikely that modification of the highly abraded bone clasts in the quarry was contemporaneous with that of the sauropod material. Since no bones in intermediate stages of

modification have been recovered, these two taphonomic end members are inferred to be temporally distinct.

The age of individuals in a death assemblage also has the potential to yield information regarding mode of mortality, provided there is no ontogenetically based ecological partitioning of the population. In theory, attritional assemblages are enriched typically in both juveniles and individuals of advanced age because these two age groups have significantly higher mortality rates than other age classes in a stable population (Kurtén, 1953; Voorhies, 1969; Lyman, 1987). Such an attritional accumulation will be relatively depauperate in advanced subadult and young adult individuals, generating a bimodal mortality profile. In contrast, a catastrophic mortality should preserve a cross section of a population, creating a death assemblage with a unimodal, positively skewed distribution (Kurtén, 1953; Voorhies, 1969; Lyman, 1987). Since the MDQ contains both juveniles and subadults but no fully adult individuals, it does not conform to either the ideal attritional or catastrophic mortality scenarios. Given the lack of evidence for extensive postmortem modification or transport of the MDQ assemblage, it is unlikely that the observed age profile is the result of taphonomic or preservational bias. Either the mortality event connected with the MDQ selectively sampled a subset of a sauropod population, or the original living assemblage consisted entirely of juvenile animals.

Agent of Mortality

The agent of mortality associated with an accumulation is often difficult to discern, even for the most completely documented assemblages. Miring (Sander, 1992; Wells and Tedford, 1995; Hungerbühler, 1998), drowning (Turnbull and Martill, 1988; Wood et al., 1988; Ryan et al., 2001), and drought (Rogers, 1990; Varricchio, 1995; Fiorillo et al., 2000) have been suggested most commonly as causes of vertebrate mass mortality in the fossil record.

Miring is inferred often as the cause of death when articulated skeletal sections are found in life position within a fine-grained matrix (Brown, 1935; Haynes, 1988; Gallup, 1989; Sander, 1992; Wells and Tedford, 1995; Hungerbühler, 1998). Appendicular and posterior skeletal elements dominate miring assemblages because these portions of the body become submerged in the mire and are protected consequently from the effects of scavenging, bioturbation, and other agents of reworking and destruction (Abler, 1985; Haynes, 1988; Hungerbühler, 1998; Heinrich, 1999). Miring was proposed originally as the formative process for the MDQ, based largely on the presence of articulated pes units and a purported paucity of axial skeletal material in the deposit (Horner and Dobb, 1997). Subsequent excavation has revealed no significant bias toward either appendicular or posterior elements. In fact, the observed appendicular-to-axial ratio corresponds almost exactly to that expected for a standard *Diplodocus* skeleton (Fig. 14A), and the anterior-to-posterior skeletal ratio indicates a slight enrichment in anterior elements (Fig. 14B), opposite from the expected bias associated with mires (Hungerbühler, 1998). Articulated pes units in the MDQ assemblage cannot be considered diagnostic of miring because they are one example of a number of articulated series of elements. Articulated foot elements have also been reported from sauropod assemblages bearing no similarity to mires (Winkler et al., 2000).

Modern ungulates often perish in large numbers as herds cross swollen rivers along seasonal migration routes (McHugh, 1972; Schaller, 1972). As a result of swift currents or close packing within the herd, some individuals are trampled or swept away and ultimately drown. The carcasses of animals killed in such situations often collect in channel meanders (Aslan and Behrensmeyer, 1996) where high-carcass density mitigates the effects of scavengers (Haynes, 1986). This scenario is incompatible with the proximal-to-distal limb disarticulation sequence in the MDQ assemblage. Disarticulation sequences are somewhat taxon-specific, but certain observations appear to hold true for a wide range of higher taxonomic groups (Hill and Behrensmeyer, 1984). One of these is the

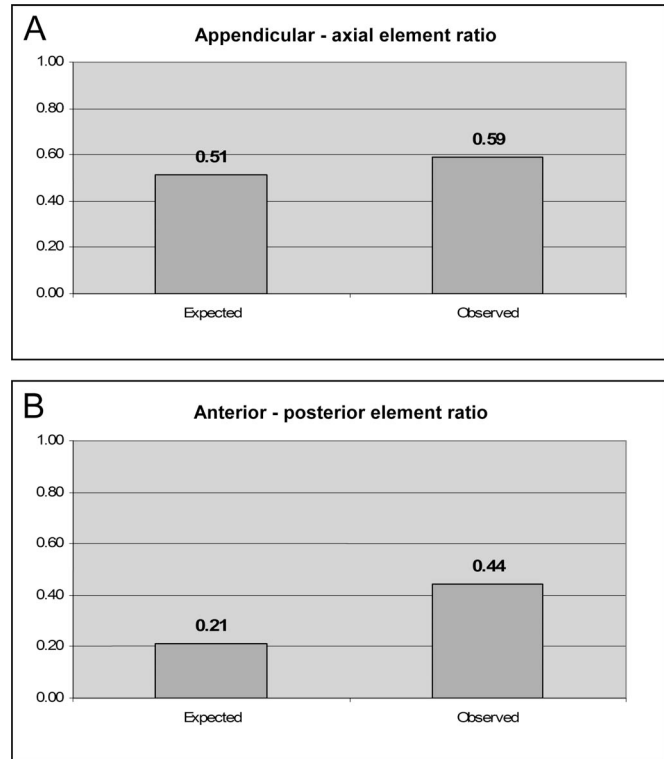


FIGURE 14—Analysis of element representation. A) Graph of ratios of appendicular-to-axial skeletal elements. Only a small bias toward appendicular elements is detectable, whereas miring should produce a strong bias toward appendicular elements. B) Graph of ratios of anterior-to-posterior skeletal elements. Bias toward anterior elements is opposite that expected for a miring site.

characteristic sequence of limb disarticulation in arid versus aqueous environments. In dry terrestrial conditions, limb disarticulation begins proximally and proceeds distally; the opposite trend occurs in aqueous environments, with disarticulation beginning distally and proceeding in a proximal direction (Hill, 1979; Brand et al., 2003). If decay and decomposition had occurred in an aqueous setting, limb disarticulation should have left few articulated pes units relative to articulated propodials and epipodials, which is inconsistent with observations at the MDQ.

The MDQ sauropods most likely died of malnutrition or starvation resulting from severe drought conditions. This inference is based on the age profile of the assemblage, the overall preservation state of the MDQ remains, and the aforementioned proximal-to-distal pattern of limb disarticulation. Observation of elephant mortality resulting from modern drought conditions in southern Africa reveals that subadult animals die in much higher frequencies than any other age class (Corfield, 1973; Conybeare and Haynes, 1984; Haynes, 1985, 1987, 1988), producing mortality profiles in which the proportion of subadults may be inflated by up to 100% relative to the live population (Haynes, 1985). Though the MDQ assemblage differs from both modern and fossil drought mortality profiles in that evidence of adults is completely lacking, the predominance of immature individuals implies that the MDQ animals succumbed to environmental stress arising from drought.

Disarticulation patterns are controlled by a number of factors, including scavenging, environmental conditions, and joint anatomy (Toots, 1965; Hill, 1979; Hill and Behrensmeyer, 1984). Many such articulated MDQ elements as cervical and caudal vertebrae were joined by significant amounts of fibrous connective tissue in life (Dodson, 1990; Rothschild and Berman, 1991). Drying of tendons and ligaments can prevent bones from fully disarticulating for some time after death (Hillman and Hillman, 1977; Hill 1980; Weigelt, 1989). Articulated MDQ elements suggest that in addition to rapid burial, arid conditions may also have been a factor

TABLE 2—Comparison of sauropod-dominated assemblages reported in the literature. Such assemblages are known from both high- and low-energy depositional environments. Of those sites with available depositional data, each is characterized by little to no transport.

Location	Geologic age	Taxon	Estimated # of individuals	Depositional environment	Depositional energy	Transport	References
India	Early Jurassic	<i>Barapasaurus</i>	≥6	fluvial (channel/floodplain)	high/low	minimal	Jain et al., 1975; Jain, 1980; Bandyopadhyay et al., 2002
India	Early Jurassic	<i>Kotasaurus</i>	≥12	fluvial (channel/floodplain)	high/low	minimal	Yadagiri et al., 1979; Yadagiri, 1988; Yadagiri, 2001
Argentina	Middle Jurassic	<i>Patagosaurus</i>	5	fluvial (floodplain)	low	none	Coria, 1994
China	Middle Jurassic	<i>Bellusaurus</i>	17	fluvial	high?	unknown	Dong, 1990, 1992
Tanzania	Late Jurassic	multiple	variable	marginal marine	variable	variable	Heinrich, 1999
Germany	Late Jurassic	<i>Europasaurus</i>	≥11	marine	low	minimal	Sander et al., 2006
Montana, USA	Late Jurassic	Diplodocoidea	≥8	fluvial (high-density flow)	high	none	this paper
Texas, USA	Early Cretaceous	unnamed	≥3	fluvial (channel)	high	minimal	Winkler et al., 2000
Texas, USA	Late Cretaceous	<i>Alamosaurus</i>	≥3	fluvial (floodplain)	low	none	Fiorillo, 1998

in their preservation. The predominance of articulated distal limb elements at the MDQ provides further evidence that initial disarticulation of the carcasses took place in a nonaqueous, arid environment (Hill, 1979; Brand et al., 2003). The inferred effect of arid conditions on the MDQ assemblage is compatible with the regional, seasonally dry climatic model for the Morrison Formation (Demko and Parrish, 1998; Parrish et al., 2004; Turner and Peterson, 2004).

Comparison with Other Sites

Sauropod-dominated assemblages have been reported from the Early Jurassic of India (Jain et al., 1975; Yadagiri et al., 1979; Jain, 1980), the Middle Jurassic of China (Dong, 1990, 1992) and Argentina (Coria, 1994), the Late Jurassic of Tanzania (Heinrich, 1999) and Germany (Sander et al., 2006), and the Early and Late Cretaceous of Texas (Fiorillo, 1998; Winkler et al., 2000) (Table 2). The Chinese locality, containing at least 17 *Bellusaurus* specimens, is located in fluvial deposits of the Wucaiwan Formation in the Junggar Basin (Dong, 1992). The animals are thought to have been killed in a flood event (Dong, 1992), though the basis for this claim cannot be evaluated because reported taphonomic or sedimentological data are lacking. Several sites with abundant sauropod bones are known from the fluvial deposits of the Kota Formation of India (Jain, 1980). The monospecific assemblages, composed of either *Kotasaurus* or *Barapasaurus* remains, are found typically within clay lenses near the top of a cross-bedded sandstone (Jain et al., 1975; Yadagiri, 1988; Yadagiri, 2001; Bandyopadhyay et al., 2002). Some assemblages have a preferred orientation coinciding with the general paleocurrent direction estimated for the Kota Formation, suggesting fluvial transport (Bandyopadhyay et al., 2002). The presence of large pieces of wood indicates initial transport and accumulation in high-energy channel systems, with bones and plant debris collecting in logjams (Jain, 1980; Bandyopadhyay et al., 2002). Final burial occurred in fine-grained, low-energy channel-fill or floodplain deposits (Bandyopadhyay et al., 2002). All the Kota sauropod skeletons are disarticulated but remain associated in some cases (Jain, 1980), suggesting minimal transport. A general dearth of such bone-modification features as breakage and weathering cracks indicates only brief subaerial exposure for some assemblages (Bandyopadhyay et al., 2002).

In contrast, several *Patagosaurus* specimens from southern Argentina were found in a calcareous tuff containing abundant plant remains, interpreted as a floodplain environment (Coria, 1994). Skeletal elements remained articulated in some cases and showed no signs of abrasion or breakage attributable to transport (Coria, 1994). The famous fossil-

bearing beds of Tendaguru, Tanzania, contain of a number of localities dominated by sauropod specimens. Those quarries that contain the remains of multiple individuals are all monospecific (Heinrich, 1999); examples of taxa found in these types of associations include *Brachiosaurus*, *Janenschia*, and *Dicraeosaurus* (Heinrich, 1999). Evidence for transport of the different Tendaguru assemblages is variable, with some bone accumulations showing signs of abrasion, disarticulation, and sorting, whereas other skeletons remained relatively articulated (Heinrich, 1999). Interpretations of transport distance based on abrasion, however, must be viewed with caution, for these two taphonomic factors do not necessarily correlate with each other (Behrensmeyer, 1982; Behrensmeyer et al., 1989). While it is clear that the Tendaguru sauropod material has undergone some amount of transport, the distances of movement involved remain unclear.

Recently, the marine deposits of northern Germany have yielded the remains of at least 11 individuals assigned to the new sauropod taxon *Europasaurus holgeri* (Sander et al., 2006). The sauropod material is found in a calcareous mudstone of variable thickness and ranges in completeness from isolated bones to partially articulated skeletons (Sander et al., 2006). Most specimens are disarticulated but remain associated. The associated remains, in conjunction with the presence of delicate elements and an abundance of skull material, imply brief transport. The bone bed also contains remains of fishes, crocodiles, pterosaurs, theropods, and a variety of invertebrates, but sauropods constitute the bulk of the assemblage (Sander et al., 2006). The relative paucity of marine fossils in the bone bed in comparison to surrounding strata suggests greater terrestrial influence and a shallow nearshore setting (Sander et al., 2006).

The Jones Ranch site, located in the Upper Cretaceous Twin Mountains Formation in Texas, contains a minimum of three individuals belonging to an as yet unnamed sauropod taxon. The Jones Ranch sauropods lay entombed in a channel sandstone characterized by cross-bedding and clay rip-ups, and the bones were associated with large logs, evidence of high-energy depositional processes (Winkler et al., 2000). The assemblage, however, shows no signs of long-distance transport (Winkler et al., 2000).

Also located in Texas is a site in the Upper Cretaceous Javelina Formation of Big Bend National Park that is associated with a low-energy depositional setting. Bones belonging to at least three *Alamosaurus* were removed from a 2 m vertical interval within a fine-grained floodplain deposit (Fiorillo, 1998). High-angle bone orientations and contorted bedding suggest that the assemblage underwent significant bioturbation, but no indications of transport are noted (Fiorillo, 1998).

Sauropod bones appear equally likely to be preserved in areas with

high- or low-accumulation rates, indicating that the large size and robust nature of most sauropod elements renders them highly resistant to destruction. Regardless of depositional setting, the sauropod-dominated assemblages reviewed here appear to have undergone little to no postmortem transport. From a paleoecological viewpoint, the low-transport potential of sauropod remains implies that the sauropod component of dinosaurian fossil assemblages will be derived locally and effectively autochthonous, except in exceptionally high-energy depositional settings.

CONCLUSIONS

The MDQ contains a fossil assemblage composed almost entirely of juvenile and subadult diplodocoid sauropod material. Lack of hydraulic sorting, substantial abrasion, or a preferred orientation of elongate elements strongly implies minimal transport of the assemblage. Partial disarticulation of the carcasses and rotation of elongate bones into high-angle orientations were achieved through some combination of high-energy flow and bioturbation. Skin impressions preserved throughout the quarry and calcareous encrustations on the articular ends of bones are consistent with rapid burial of partially desiccated carcasses.

The bone bed is similar in many respects to deposits created by hyperconcentrated flows. The quarry unit is poorly sorted, containing clay, silt, and sand-sized particles, as well as gravel-sized clasts and clay rip-ups. Lack of stratification or grading within the bed, in conjunction with the occurrence of discontinuous patches of clean, relatively well sorted sandstone, suggest that a massive, partially cohesive sediment flow buried the remains. The paucity of bone modification features in the MDQ assemblage and the preservation of soft-tissue structures suggest that exposure time prior to burial was relatively short, perhaps on the order of weeks to months. The sequence of limb disarticulation at the MDQ is consistent with arid subaerial conditions, indicating that the sauropods in the quarry may have succumbed to starvation or malnutrition related to severe drought conditions. Although drought mortalities cannot be classified as strictly catastrophic owing to the extended duration of their effects, drought assemblages should represent less than a year of carcass accumulation (Badgley, 1982).

Comparison of the MDQ with other sites containing abundant sauropod material indicates that sauropod-dominated assemblages are characterized by little to no transport. In rare cases where some transport may have occurred, it is usually the result of exceptionally high energy flow. Burial rates appear to have little effect on preservation potential of sauropod material. Sauropod-rich quarries are known from depositional settings with both high and low rates of accumulation. There is no indication that potentially longer exposure times in areas with relatively low sedimentation rates (e.g., floodplain environments) adversely affect the likelihood of preservation.

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