

The Late Jurassic Cleveland-Lloyd Dinosaur Quarry as a Drought-Induced Assemblage

TERRY A. GATES

Department of Geology and Geophysics, University of Utah, Utah Museum of Natural History, 1390 E Presidents Circle, Salt Lake City, UT 84112; E-mail: tgates@umnh.utah.edu

PALAIOS, 2005, V. 20, p. 363–375 DOI 10.2110/palo.2003.p03-22

A comprehensive taphonomic analysis has yielded a novel interpretation for one of the most famous dinosaur quarries in the world. The Cleveland-Lloyd Dinosaur Quarry (CLDQ) traditionally has been interpreted as an attritional predator trap. This scenario is based largely on a remarkable 3:1 predator:prey ratio, dominated by the remains of the theropod *Allosaurus fragilis*. This study addresses the taphonomy of CLDQ by combining analyses of fossils and entombing sediments along with putative modern analogues.

Thousands of bones have been excavated from CLDQ, representing at least 70 individual dinosaurs from a minimum of nine genera. The fossils occur in a 1-m-thick fine-grained calcareous mudstone interpreted as a floodplain ephemeral-pond deposit. The bones show minimal carnivore modification and surface weathering, whereas approximately 1/3 of the elements studied possess pre-depositional fractures and evidence of abrasion. The vast majority of elements are found horizontal to subhorizontal, without a preferred long-axis orientation. The demographic profile of the CLDQ dinosaur assemblage appears to be highly skewed toward subadult individuals.

Numerous lines of evidence question the traditional predator-trap hypothesis. Of the alternatives, catastrophic drought appears to be most consistent with available data. Evidence includes a large assemblage of animals in a low-energy ephemeral-pond depositional setting and geologic and biologic evidence of desiccation. Additional support comes from modern drought analogues that frequently result in mass-death assemblages of large vertebrates. Climatic interpretations during Late Jurassic times are consistent with a semiarid environment characterized by periodic drought conditions.

INTRODUCTION

The Morrison Formation is famous for its abundant multi-generic dinosaurian bone beds, including Dinosaur National Monument, Dry Mesa, and Como Bluff. The taphonomy of these Morrison sites has been described in several studies (Lawton, 1977; Dodson et al., 1980; Richmond and Morris, 1998), but few Morrison bone beds have received as much attention as the Cleveland-Lloyd Dinosaur Quarry (CLDQ). CLDQ is one of the most productive dinosaur quarries in the world, having yielded over 10,000 dinosaur bones representing at least nine genera and at least 70 individuals since its first excavation in 1927 (Miller et al., 1996).

Remarkably, CLDQ preserves the remains of at least 46 individuals of the theropod dinosaur *Allosaurus fragilis*, as well as elements from four other theropod genera and at least four genera of herbivorous dinosaurs (Madsen, 1974, 1976a, 1976b; Stokes, 1985). Despite the nearly equal generic diversity of carnivores and herbivores, the overwhelming abundance of individual allosaurs results in a predator-prey ratio of 3:1 (Madsen, 1976b), otherwise unknown from any other Morrison site.

Since few comparable examples exist with such a high predator:prey ratio (e.g., La Brea Tar Pits, Los Angeles, California; Harris, 2001; *Albertosaurus* bone bed, Alberta, Canada; Currie, 1998; Ghost Ranch *Cœlophysis* bone bed, Abiqui, New Mexico; Schwartz and Gillette, 1994), the taphonomic history of CLDQ has been a topic of great interest to paleontologists.

Several hypotheses have been proposed to account for the taphonomic origin of this assemblage. Initially, Stokes (1945) hypothesized that the deposits formed in a lakebed desiccated by a volcanic ash fall. Alternatively, Dodson et al. (1980) cited the high proportion of theropods as evidence that the deposit was a predator trap in an oxbow lake. The predator-trap hypothesis has remained the prevalent interpretation since 1980. Although the hypothesis gained support from several additional authors, each differed in their interpretation of the depositional environment (Stokes, 1985; Richmond and Morris, 1996; Bilbey, 1999). The predator-trap model posits that an herbivore would become mired in viscous mud within a floodplain pond. Several carnivores, attracted to the dead or dying herbivore, would then become stuck themselves. The assemblage eventually was buried, resulting in the elevated predator:prey ratio present in the quarry. Hunt (1986) hypothesized a catastrophic flood as the possible culprit, which is the only recent alternative to the predator-trap scenario. However, Hunt did not rule out the predator-trap hypothesis, and instead, cited lines of evidence supporting each of the two hypotheses.

The bulk of these previous taphonomic studies focused on two major issues—the depositional environment and the large number of allosaurs—while largely ignoring the breadth of biological evidence. The current study reexamines the accumulation of the CLDQ fossil remains, addressing a range of biological and geological data collected from the site, as well as regional taphonomic characteristics of the Morrison Formation. This broad-scale approach attempts to identify the range of taphonomic forces that may have resulted in such a diverse, extensive, and unique assemblage.

GEOLOGY AND AGE OF THE MORRISON

As a result of over a century of geologic study by a number of researchers (Gilluly and Reeside, 1928; Gregory, 1938; Peterson and Turner-Peterson, 1987), the Morrison Formation has been subdivided into eight members. Of these, the Tidwell, Salt Wash, and Brushy Basin members are the most laterally extensive, and comprise the entire thickness of the Morrison in the immediate area of the Cleveland-Lloyd Dinosaur Quarry (Peterson and Turner-Peterson, 1987; Bilbey, 1992).

The basal member of the Morrison Formation, the Tidwell Member, is dominated by playa/sabka limestone and evaporite deposits in the lower section and slope-forming mudstones deposited on a large-scale mudflat higher up (Peterson and Turner-Peterson, 1987). The Salt Wash Member represents an alluvial-fan complex that contains a number of localized sediment packages, including fluvial sheet gravels and sands, fluvial ribbon sands, lake and floodplain mudstones, and rare eolian sands (Peterson and Tyler, 1985). Sediments in the abundant coarse siliciclastic sandstones possibly were derived from the Sevier highlands to the west and southwest in California and Nevada (Peterson and Turner-Peterson, 1987).

The Brushy Basin Member, in which CLDQ is located, is the most extensive unit in the Morrison Formation. This member contains relatively little sandstone, yet the sediments were derived from the same source rocks as those in the Salt Wash Member (Peterson and Turner-Peterson, 1987). The majority of this member is composed of variegated mudstone, drab-gray mudstone, and limestone/marl lithofacies. Interpreted paleoenvironments range from well-drained floodplain deposits, to poorly drained floodplain sediments in ponds and swamps, to freshwater lakes (Dodson et al., 1980). Interbedded within these rock units are numerous layers of bentonite derived from a magmatic arc to the west (Dodson et al., 1980; Peterson and Turner-Peterson, 1987; Bilbey, 1992). Dodson et al. (1980) pictured the overall depositional environment of the Brushy Basin Member as dominated by a meandering river-system floodplain peppered with lakes.

Climatic reconstructions of the Morrison Formation in Utah depict a seasonally arid environment (Stokes, 1945; Dodson et al., 1980; Parrish et al., 1982; Peterson and Turner-Peterson, 1987; Turner and Fishman, 1991; Demko and Parrish, 1998; Demko et al., 2004; Parrish et al., 2004) that received half to one-quarter the rainfall as that of surrounding areas on the continent (Demko and Parrish, 1998). Geological support for this paleoenvironmental interpretation comes from a paucity of coals and plant remains (Dodson et al., 1980), as well as the possible presence of a basin-wide, bulls-eye pattern of various authigenic clay minerals known to occur only in arid environments (Turner and Fishman, 1991).

The age of the Morrison Formation has been debated in the literature for decades (Lee and Brookins, 1978; Kennedy and Odin, 1982; Bralower et al., 1990; Kowallis et al., 1991; Steiner et al., 1994). Recently, Kowallis et al. (1998) dated samples from across the entire Morrison Formation of Utah, obtaining ages ranging from 148.1 ± 0.5 Ma at the top of the Brushy Basin Member to 154.8 ± 1.4 Ma in the middle of the Tidwell Member. Earlier studies attempted to bracket the age of CLDQ using two local ash

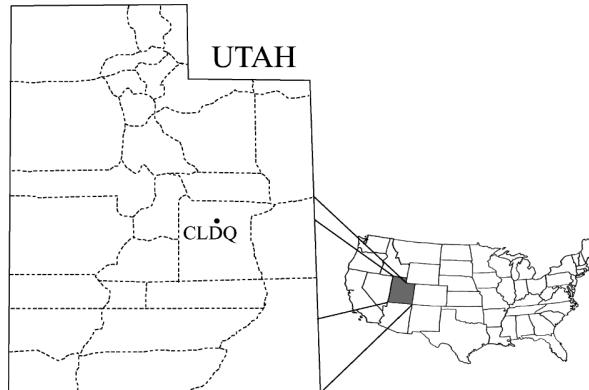


FIGURE 1—The location of the Cleveland-Lloyd Dinosaur Quarry in Utah. Adapted from Miller et al. (1996).

beds (Bilbey-Bowman et al., 1986; Kowallis et al., 1986). The age of the lower ash layer, 3 m below the quarry level, has been dated at 152 Ma (Kowallis et al., 1986), whereas the upper layer, only 1 m above the deposit, produced a date of 146.8 ± 1 Ma (Bilbey-Bowman et al., 1986). Averaging the two estimates yields an approximate deposition date of 149 Ma, well within the Tithonian/Portlandian stage of the late Jurassic (Gradstein et al., 1994).

LOCATION AND METHODS

CLDQ occurs in the Morrison Formation of Emery County, Utah and is situated on the northwestern flank of the San Rafael Swell, about eight miles east of the town of Cleveland on the Cow Flats quad (Fig. 1). An area of over 21 m^2 was excavated during the summers of 2001 and 2002 by Utah Museum of Natural History (UMNH) field crews, resulting in the collection of over 400 specimens, of which 360 were used in this analysis. Bones were mapped *in-situ* with the use of a grid square and plumb bob. A depth measurement was taken in millimeters using a datum and tape measure. Orientation ($0\text{--}180^\circ$) and dip of bones were determined using a Brunton compass along the long axis of a bone if it had a length:width ratio of at least 2:1; otherwise, the specimen was considered to lack a definite long axis, and orientation data were not recorded. Other taphonomic observations, such as relationships to neighboring elements, were made during excavations and after preparation of the fossils at the UMNH. Sediment samples, including mudstone, limestone, and limestone nodules, were collected from the quarry in varying locations and depths, and processed into thin sections at the University of Utah. All specimens collected during this study are housed in the UMNH paleontology collection.

The incorporation of previously collected datasets was restricted to published results (Bilbey, 1992; Richmond and Morris, 1996; Morris et al., 1996; Bilbey, 1999), with the exception of data collected from the composite quarry map from Miller et al. (1996). Orientations of the bones on this published map (Miller et al., 1996) were collected by the author in order to compare them to the orientation data collected from the 2001 and 2002 excavations.

TABLE 1—List of vertebrate taxa recovered from CLDQ. The number to the right of each taxon represents the minimum number of individuals of that taxon. Original counts from Madsen (1976b), with additions to the *Allosaurus* count based on recently excavated material at the UMNH.

Reptilia	
Dinosauria	
Saurischia	
Theropoda	
<i>Allosaurus fragilis</i> —46	
<i>Ceratosaurus dentisulcatus</i> —1	
<i>Stokesosaurus clevelandi</i> —2	
<i>Marshosaurus bicentesisimus</i> —2	
<i>Torvosaurus cf. tanneri</i> —1	
Sauropoda	
<i>Camarasaurus lentus</i> —5	
<i>Barosaurus</i> sp?—1	
Ornithischia	
Thyreophora	
<i>Stegosaurus cf. stenops</i> —5	
Ornithopoda	
<i>Camptosaurus</i> —5	

CLDQ GEOLOGY

A localized stratigraphic section was compiled using lithologic information obtained from cores taken at CLDQ by Bureau of Land Management geologists, supplemented with material from Bilbey (1992). The lowest unit in the section is a silty mudstone that has a sharp contact with an overlying, fossiliferous calcareous mudstone. Resting above the bone layer is a capping limestone, which, in turn, is overlain by a volcanic ash bed (Bilbey, 1992). The two bone-bearing units, the focus of this study, are the calcareous mudstone and the overlying limestone.

Mudstone Unit

The main bone-bearing unit is a one-meter-thick calcareous mudstone, although this thickness varies due to an undulating contact with the overlying limestone. The mudstone is composed primarily of the smectitic clay montmorillonite, but also contains high amounts of quartz, feldspar, and biotite, along with clasts of volcanic and sedimentary rocks, all of medium-silt to medium-sand size (Bilbey, 1992). The mudstone contains virtually no bedding and has intraformational clay clasts, observed both in this study and by Bilbey (1992). Less-common constituents of the sediment include gastropods, charophytes, ostracodes, and carbonized plant material.

Aside from fossil bone, the most common components of the bone-bearing layer are diagenetic limestone nodules. Their mineralogy closely resembles that of the surrounding mudstone, with the primary difference being a significant increase in the percentage of calcite and a corresponding decrease in the amount of clay and detrital grains within the nodules (Bilbey, 1992). A wet depositional environment inferred from the charophytes and ostracodes, along with a lack of rhizoliths and evidence of soil oxidation, helps preclude these nodules as pedogenic. Approximately 90% of the examined nodules nucleated around fossil bone, whereas the boneless examples seemed to lack any evidence of a nucleus. There does not

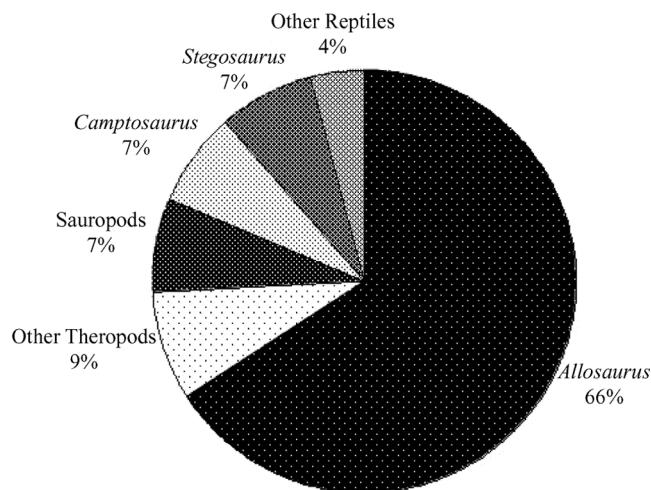


FIGURE 2—Relative abundance of dinosaur taxa at CLDQ. Data used in chart is based on Madsen (1976b), with a revision of the allosaur census based on specimens from 2001–2002 excavations.

appear to have been preferential precipitation around specific types of bones.

The geometry of the mudstone unit was indeterminate due to a large talus pile resulting from construction of protective buildings. However, based on the limited exposure, it appears the unit begins to pinch-out laterally 50–75 m to the south, giving the impression of a confined basin.

Limestone Unit

The overlying limestone ranges in thickness from 0.3–1.0 m, due to the aforementioned undulating contact with the underlying mudstone. Bilbey (1992, p. 133) described the limestone as a “slightly fossiliferous, muddy micrite,” comprised, on average, of 50% calcite. The limestone also contains significant amounts of quartz, feldspar, and clay—mostly montmorillonite (Bilbey, 1992). Compared to the mudstone, the limestone contains a larger percentage of fossil gastropods, charophytes, and ostracodes.

TAXONOMIC DATA

Taxonomy and Ontogeny of Dinosaurs

Table 1 lists the vertebrate taxa identified from the Cleveland-Lloyd Dinosaur Quarry. Of these, *Allosaurus* is by far the most abundant genus, with a minimum of 46 individuals (MNI) identified on a count of left femora (original count by Madsen, 1976b, plus two additional femora from 2001–2002 excavations). Remarkably, theropods constitute 75% of all individuals present (Fig. 2), creating an unusually high predator:prey ratio of 3:1. The herbivorous dinosaur genera include *Camarasaurus*, *Camptosaurus*, and *Stegosaurus*, each represented by at least five individuals (Table 1). With the exception of *Allosaurus*, which includes multiple size classes, remains of all genera appear to represent adult individuals, based on the large size of elements present and no evidence of unfused vertebrae. *Allosaurus* femoral length, ranging from 25 to 76 cm, was utilized to estimate the relative age at death of

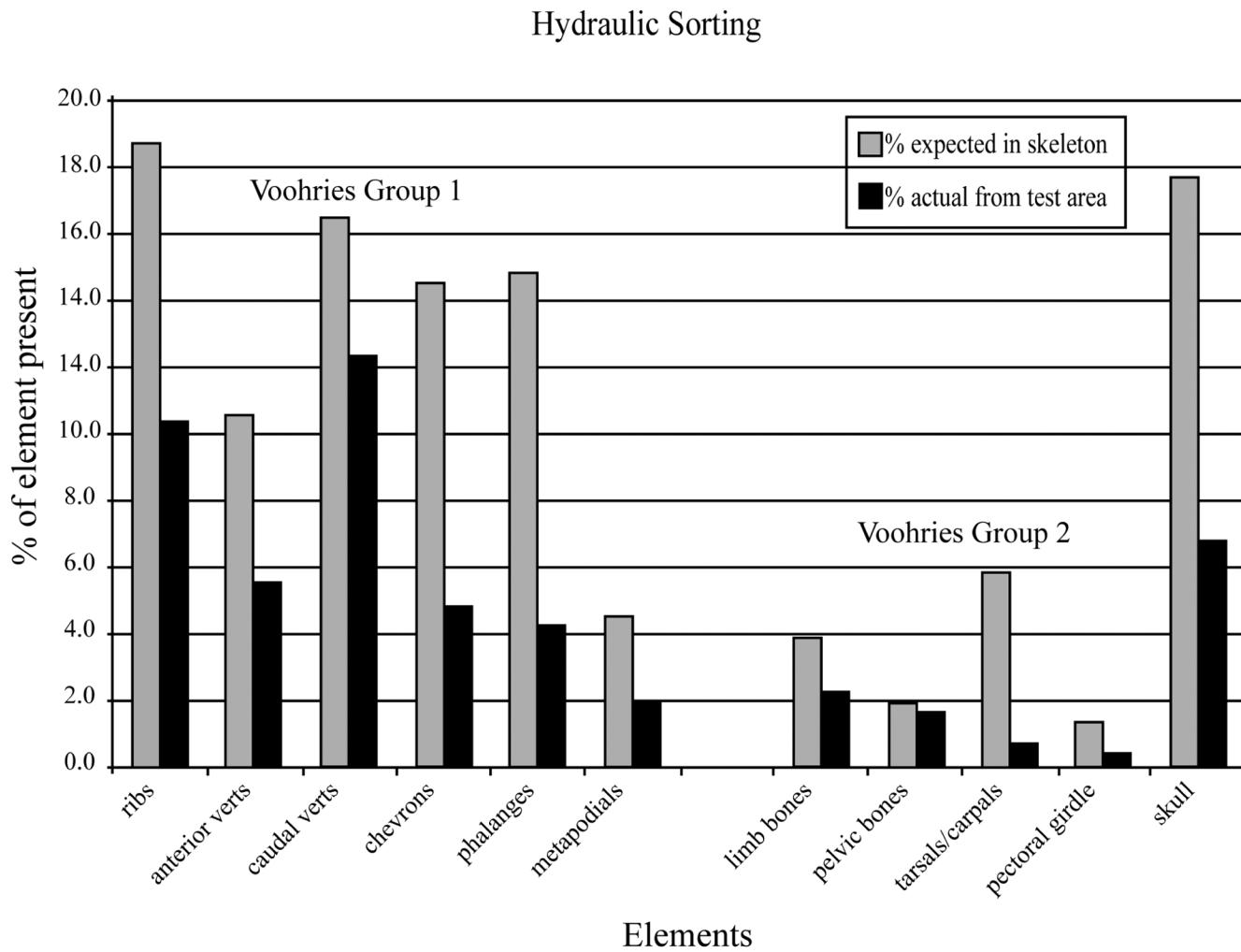


FIGURE 3—Relative frequencies of allosaur bones from excavated sample. The gray column shows the relative frequencies of bones from an ideal allosaur skeleton, whereas the black column shows the frequencies from the excavated sample. The bones are divided into two sorting groups based on Voohries (1969).

those preserved at CLDQ. A length of 56 cm was used to represent the upper boundary for a subadult allosaur (Madsen, pers. comm., 2002), with an estimated 82% of the specimens falling within the juvenile/subadult range.

Skeletal Data

Bones occur throughout the entire thickness of the mudstone unit. There is a higher concentration of larger elements at the top and the bottom of the bone layer, with smaller bones occurring predominantly between these zones. Numerous bones co-occur in both the mudstone and the limestone unit.

Bone density per unit area varied considerably, with maximum densities exceeding 60 bones/m². Variations in local bone density appear to correspond with fluctuations in the thickness of the capping limestone. Specifically, areas with the densest bone accumulations seem to be situated beneath the thickest limestone undulations.

Most specimens collected from CLDQ were found disarticulated, with the exception of several articulated sauropod and allosaur vertebral segments. Despite this high de-

gree of disarticulation, many specimens show evidence of association. For example, the remains of the taxa *Camarasaurus*, *Barosaurus*, and *Ceratosaurus* are all found in isolated pockets around the quarry.

The *Allosaurus* skeletal material, on the other hand, is densely packed throughout the entire quarry, which makes discerning individual skeletons difficult. However, close-lying allosaur elements have been recovered that appear to reflect specimen association, including a partial pelvic assemblage (UMNHVP 12194, 12042, and 12193) and two associated skulls (UMNHVP 5470, UMNHVP 12226), which are reposed at the Utah Museum of Natural History. Richmond and Morris (1996) also provide evidence for skeletal association by illustrating clusters of toothed elements around the quarry. Although the associated elements mentioned above do not provide definitive evidence for allosaur skeletal association, when combined with the known association of other taxa, the occurrence of at least partial *Allosaurus* carcasses at the time of burial is likely.

Figure 3 compares the relative frequencies of bones expected to occur within a complete allosaur skeleton to

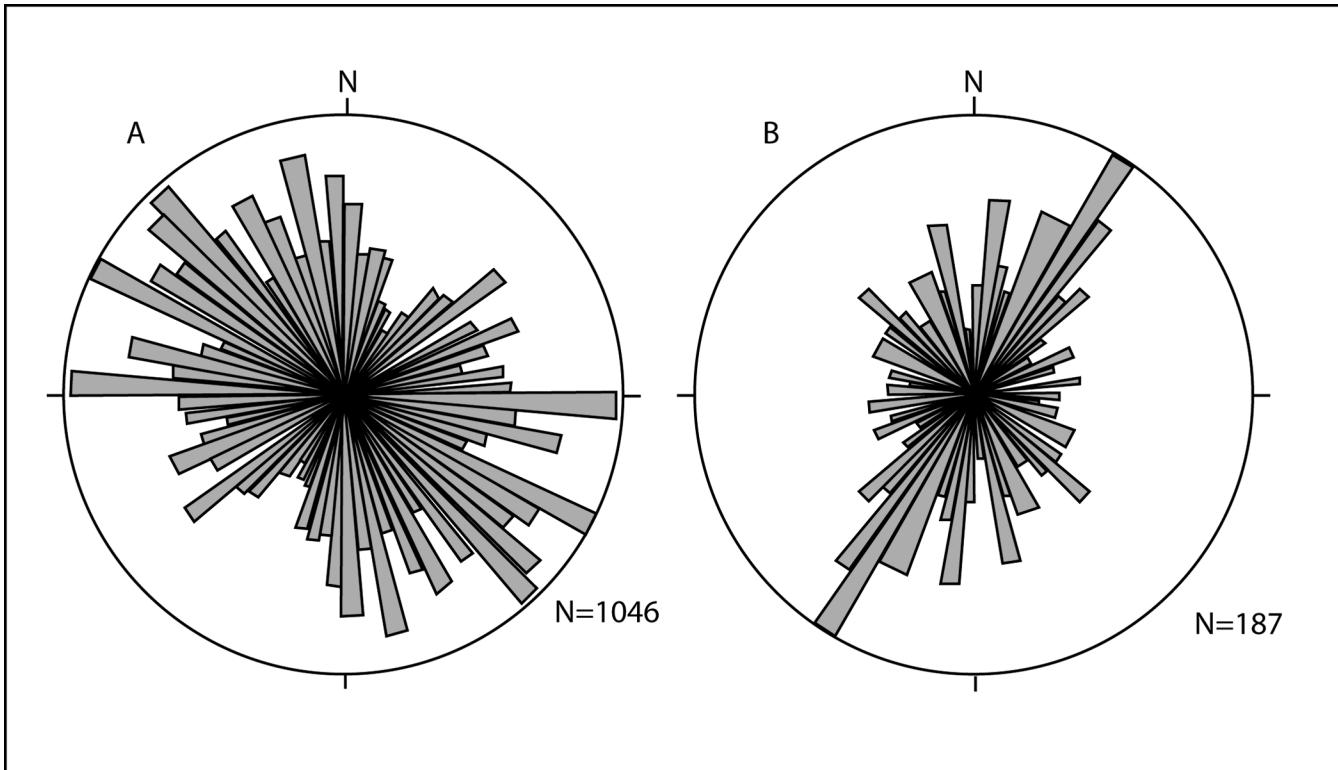


FIGURE 4—Mirror rose diagrams constructed for CLDQ with 5° petals. (A) Rose diagram produced from the large composite map. The sample from the map spans the entire depth of the bone-bearing layer and covers an area of over 450 m². Value of outer circle is 4% of total. (B) Rose diagram produced from data collected during 2001–2002 excavations throughout the fossiliferous layer over 21-m² area. The mean vector is 15.2° and the length of the mean vector (r) is 0.19. Statistical analysis of these data show that the null hypothesis of a uniformly distributed dataset is rejected; Rayleigh Test ($Z = 6.69, p = 0.001$); Rao's Spacing Test ($U = 180.96, p = <0.01$).

those recovered from the recent excavations at the CLDQ. These skeletal elements are separated into two hydraulic sorting groups (*sensu* Voohries, 1969). It should be noted that all skull elements have been placed into sorting group two because Voohries' original study (1969), based on modern mammalian remains, characterized a third sorting group consisting largely of fused skulls. In contrast to mammals, dinosaur skulls typically do not exhibit fusion outside the braincase, and, due to an absence of flume studies simulating disarticulation and sorting of dinosaur skull elements, the disarticulated skull elements were placed conservatively into sorting group two based largely on the flat and/or rod-like shape of most skull bones (Frostick and Reid, 1983). Elements from both sorting groups are present in consistent percentages, indicating there was minimal winnowing of elements. Based on this evidence, CLDQ appears to represent an autochthonous, or at least a paraautochthonous, assemblage. The lack of hydraulic equivalence (Behrensmeyer, 1975) between the bones and the entombing fine-grained matrix further corroborates site autochthony. The great majority of bones from the recent sampling were flat-lying in the strata, with less than 10% showing any significant dip.

A rose diagram was constructed for data collected from the composite CLDQ map in Miller et al. (1996) and from data collected during the 2001 and 2002 excavations (Fig. 4A, B). The rose diagram from the composite map (Fig. 4A) shows an orientation distribution similar to the one gen-

erated by Morris et al. (1996). They argue, and this author agrees, that the data did not indicate any preferred bone mode because the diagram lacked data points perpendicular to the main mode (Voohries, 1969) and, more specifically, because no significant primary mode was found within their dataset (Morris et al., 1996). However, the rose diagram constructed from data derived from recent excavations (Fig. 4B) yields a statistically significant mode of 15° NE/SW (see figure caption for statistical values). No significant perpendicular mode was found.

The two datasets produced different results, which may be linked to three factors. The first is that the composite quarry map from Miller et al. (1996) was assembled from smaller map sections documenting the last 40 years of excavation. The resultant composite map has been recognized as containing errors because of mapping inconsistencies over the course of this time (Madsen, pers. comm., 2002). The orientation dataset taken from this map likely suffers from these issues. The second possibility is that both of the datasets are reliable, and the variation results from size differences in the elements sampled. The vast majority of bones measured from the composite map are over 0.3 m in length, while the majority of bones from the recent excavations are shorter and more gracile (i.e., small ribs and phalanges). Therefore, if a weak current ran through the bone assemblage, it may have been strong enough to align only the smallest bones, leaving the larger bones virtually unmoved. Lastly, the overriding pattern of

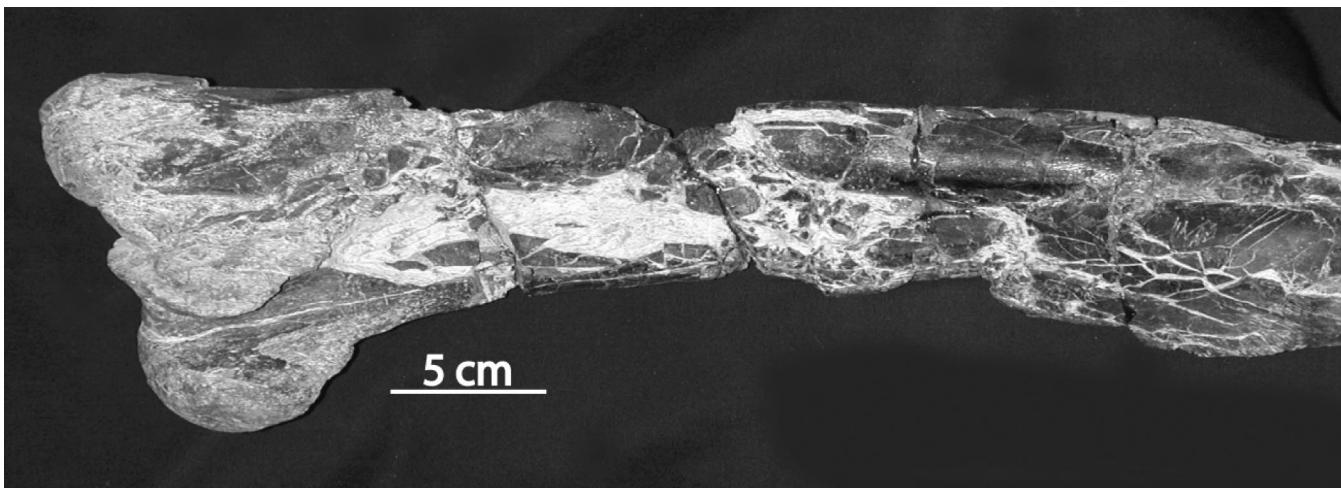


FIGURE 5—*Allosaurus fragilis* femur (UMNHVP 12196) showing evidence of crushing. The crushing plausibly reflects trampling by another dinosaur.

bone orientation within the quarry may be random. However, evidence from the smaller dataset may indicate that at least some areas within the deposit were subject to minor current-related alignment.

Bone Modification

Pre-depositional bone modification by various agents was surveyed across the CLDQ sample, with specific reference to weathering, abrasion, fracturing, and surface traces.

Weathering: Bone weathering was estimated using the 0–5 scale of bone modification established by Behrensmeyer (1978; see Fiorillo, 1988 for a comparable weathering scale). The majority of bones at CLDQ display weathering stage 0. Only four percent of the observed specimens ($n = 360$) exhibit any signs of weathering. The highest stage encountered was a modest stage 2, noted only for a single bone fragment (UMNHVP 11578). The remainder of weathered specimens exhibit minimal alteration and are considered stage 1.

Abrasion: The 0–3 scale created by Fiorillo (1988) was used to assess abrasion from the CLDQ bone samples. Of the specimens sampled, 37% show signs of abrasion, and of those, 92% were level one. Vertebrae and ribs display the most signs of abrasion. Fractured edges of bone also consistently show rounding that varies between level one and level two, while rare specimens possessed rounding level three.

Fracturing: Fracturing simply was noted as being present or absent on specimens examined. No distinction was made between various types of postmortem fractures. If a specimen was not 100% complete, and did not contain post-fossilization breaks, it was considered fractured. Based on these criteria, 30% of the bones displayed fracturing. Some elements, such as specimens UMNHVP 12196 (allosaur femur) and UMNHVP 12197 (allosaur tibia), not only are fractured, but are crushed through the shaft as well (Fig. 5).

Surface Traces: Surface traces are defined here as any mark on a bone made by an organism, including tooth marks, trample marks, and borings. In this study, the

presence or absence of traces was noted, and the type of trace identified. Only 4% of specimens exhibit traces of any kind, and of these, all but one represent tooth marks. The exception is a probable boring that exhibits similarities with dermestid-beetle borings (Rogers, 1992; Martin and West, 1995; Hasiotis et al., 1999; Roberts et al., 2003), but is not a conclusive match. Bones of herbivorous dinosaurs contain the most tooth traces (Fig. 6), in spite of the high number of allosaur elements present. In addition, multiple examples were found of tooth-marked bone on distal-limb elements (two metapodials and an astragalus; UMNHVP 5937, 9887, and 9414, respectively). Finally, a few specimens collected display evidence of multiple types of modification including abrasion, fracturing, and rotting, suggesting a longer land-surface residence time (Fig. 7).

Interpretations

Depositional Environment: The depositional environment for the CLDQ assemblage is interpreted to be an ephemeral pond, based largely on the vertebrate and invertebrate fossils. A persistent water body would have been necessary to support the invertebrate fauna mentioned above, yet the conspicuous absence of fish and amphibians seems to preclude the idea that CLDQ was a permanent waterhole. The remains of crocodiles (one tooth) and turtles (pieces of shell) also are scarce (Madsen, 1976b) implying that the waterhole may not have been filled every season. This interpretation is based on observations that modern crocodiles in Australia tend to frequent the same permanent waterholes every year (Webb and Manolis, 1988). Additional evidence for desiccation includes intraformational clay rip-up clasts that may represent slightly transported fragments of mud-cracked sediments. Recurring desiccation and inundation cycles are consistent with an ephemeral-pond interpretation. After periods of dryness, the basin feasibly refilled from storm run off or seasonally flooding rivers. Parallel interpretations have been invoked for Lower Miocene rocks in the Arikaree Formation, founded on similar evidence (Hunt, 1990).

Bioturbation of the mudstone almost certainly occurred

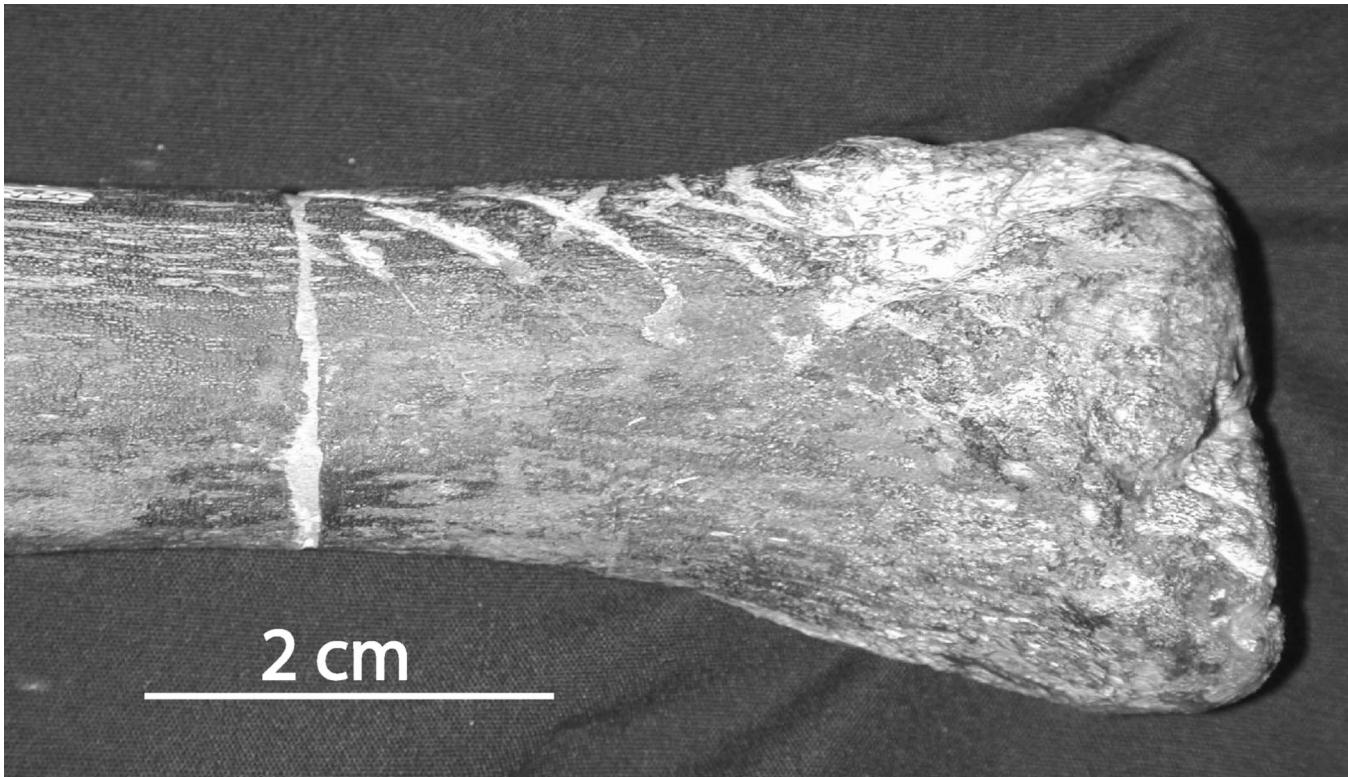


FIGURE 6—*Camarasaurus* metapodial (UMNHVP 5937) displaying tooth marks. Such extreme examples are rare among the quarry remains.

as numerous dinosaurs trampled the sediment, destroying any bedding present and possibly creating the topography of ridges and valleys now preserved as the undulating mudstone/limestone contact. Richmond and Morris (1996) described the undulose contact as the result of compaction by a rapidly deposited limestone on top of a water-filled mud. An alternative explanation is that the fossils tended to concentrate in the natural depressions created by bio-

turbation. As mentioned above, the greatest bone density is found beneath the thickest areas of limestone (i.e., depressions in the pond bottom). Perhaps the most important implications of the mudstone/limestone contact is that it marks the end of the ephemeral pond environment, the point at which the basin became permanently flooded, as well as the last occurrence of large dinosaur bones in the quarry.

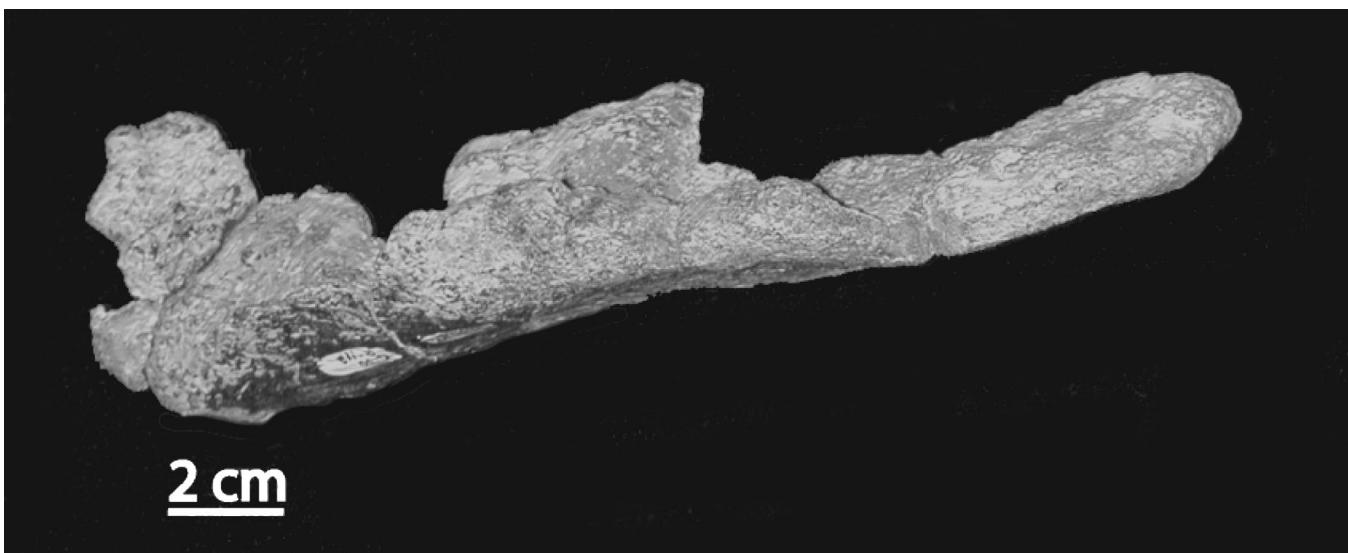


FIGURE 7—Unidentified element (UMNHVP 12010) displaying evidence of abrasion, fracturing, and possible rotting.

Bilbey (1992) explained the presence of nodules as the result of bacteria creating a calcic soap around the bones during the decay of organic material (Berner, 1968; Canfield and Raiswell, 1991). Due to the abundance of bacteria in both the bones and flesh of carcasses, calcic soap likely did form around some of the specimens. However, this scenario can account for only the initial precipitation of calcite, leaving the remaining, and much larger, portion of the nodule unexplained. Calcium-rich pore waters, derived from either ground water or dissolved from volcanic ash, likely played a more important role by providing the abundant Ca⁺ ions necessary for continued calcite precipitation around the nucleation points of the calcic soaps. Similar preservation is described by Briggs et al. (1996), Downing and Park (1998), and Rogers et al. (2001).

Dinosaur Occurrences: Based on studies of modern skeletal dispersal (e.g., Hill, 1979), the carcasses likely were disarticulated due to a combination of scavenger activities and trampling. Carcass parts that did not disarticulate fully during initial scavenging may have done so following disintegration of remaining muscles and connective tissues (Coe, 1978). Articulated remains are rare at the quarry, suggesting that the bones were not buried rapidly.

Direct evidence of scavenging at the site is minimal, consisting only of a few tooth traces (Madsen, 1976b; present study), biased toward the remains of herbivorous dinosaurs. This paucity of tooth traces at CLDQ may not be unusual in light of the rarity of tooth traces in other Jurassic sites (Fiorillo, 1991). The occurrence of scavenged lower-limb elements is interesting because, in order for such carcass utilization to occur, the legs of these dinosaurs must have been exposed completely to scavengers, rather than buried in mud.

Most of the bones were lying horizontal prior to burial. The few exceptions are bones that may have been perched on the sides of depressions in the pond bottom, or were trampled during burial (Behrensmeyer, 1988). The percentages of fractured (30%) and abraded (34%) bone testify to the impact of trampling on the bone assemblage (Haynes, 1991; Brain, 1967; White, 1992). However, no scratch-marks indicative of trampling were found in the CLDQ bone assemblage—a finding that may be attributable to a lack of coarse-grained siliciclastics (Fiorillo, 1984, 1987; Behrensmeyer et al., 1986; Olsen and Shipman, 1988). Fracturing also could have resulted from bone crushing by feeding carnivores (Hill, 1989), but the lack of tooth traces on bone, as well as the suggestion that carnivorous dinosaurs did not engage actively in bone crushing (Fiorillo, 1991), brings to question the importance of carnivore mastication.

The majority of bones at CLDQ had an approximate subaerial exposure time of two years or less (*sensu* Behrensmeyer, 1978), with rapid burial or submersion in water halting the progression of weathering (Gifford, 1985). Numerous small bone fragments (<5 mm) found within the matrix may be the remains of highly weathered and fractured bones that were left on the surface for many years.

DISCUSSION

The results described above provide compelling evidence that the Cleveland-Lloyd Dinosaur Quarry repre-

sents a non-transported assemblage. This conclusion eliminates a number of taphonomic hypotheses, including flood and carnivore concentration, which require specimen transport. Of the remaining autochthonous alternatives, possible contenders include fire, disease, volcanism, the classic predator trap, and drought.

Fire is an unlikely taphonomic scenario because the site contains no evidence of charcoaled wood or bone (Sanders, 1987). Disease, such as botulism, has been invoked to account for part of a Late Cretaceous bone bed in Montana (Varricchio, 1995), but there is no justification for regarding it as the primary killing agent in this study. Typically, botulism does not kill herbivores unless they consume the carcasses of infected animals (Sugiyama, 1986); but more importantly, no criteria currently exist that can be used to distinguish disease deposits in the dinosaurian fossil record (see Henrici and Fiorillo, 1993 for a disease-induced bone bed of frogs).

Even though the CLDQ mudstone contains sediments of volcanic origin, a postulated mass death of dinosaurs due to volcanic activity is questionable for a number of reasons. First, the nearest known volcanic center during the Late Jurassic is located in Nevada (Peterson and Turner-Peterson, 1987), which is hundreds of miles from the quarry. Second, bone beds generated by volcanism usually display spectacular preservation and widespread articulation (Voohries, 1981; Rogers et al., 2001). Third, there is no definitive volcanic ash or bentonite bed that can be associated directly with the quarry horizon. Finally, a volcanism hypothesis necessitates the dense gathering of over 70 individual dinosaurs, at least 46 of which are *Allosaurus fragilis*, at exactly the same time—a highly improbable scenario.

Predator Trap

The classic predator-trap scenario frequently has been invoked to explain the disproportionately high number of carnivores found at CLDQ. As mentioned above, this hypothesis predicts that multiple carnivores would become trapped in mud near the center of a pond while pursuing a concomitantly mired herbivore. Certainly this explanation accounts for the skewed predator:prey ratio, yet there is minimal additional evidence in support of this hypothesis. First, there is no known modern analog of a miring predator trap (however, see White et al., 1984 for a discussion of recent predator traps in caves). Although there are reports of cattle becoming mired in mud or quicksand and consequently dying (Weigelt, 1989), the lack of contemporaneously mired predators at these sites prevents their use as direct analogs.

Based on studies of the swelling properties of the quarry mudstone, Richmond and Morris (1996) calculated that the maximum thickness of the trapping mud was 6.75 m, later compacting to its present thickness of about 1 meter. However, the maximum thickness potential is only an estimate of possible mudstone thickness at maximum water capacity, and may not correlate directly to its depositional thickness (Richmond and Morris, 1996).

Given that the mud was thick enough to mire dinosaurs, some predictions can be made as to the preservation of the victims. First, articulated remains should be common, particularly with regard to the locomotor limbs. Second,

these limb bones, particularly the distal portions, should be oriented vertically or nearly vertically. These predictions are met at an analogous site in New Zealand called the Pyramid Valley Moa Swamp. The swamp contains hundreds of moas that apparently were trapped by walking into a soft miring mud, in a similar fashion to that inferred for CLDQ (Duff, 1949; Holdaway and Worthy, 1997). The remains of some of the moas are articulated and oriented vertically, as if they sank straight down (Duff, 1949). In stark contrast to Pyramid Valley, none of the collected limb segments from CLDQ remains articulated, and the vast majority of bones lie nearly horizontal. Numerous other fossil localities exist that illustrate the correlation between miring and vertically oriented, articulated locomotor- and posterior-skeletal elements (Sander, 1992; Wells and Tedford, 1995; Fowler et al., 2003; Storrs and Garcia, 2001).

Previous speculations on the cause of the disarticulation and scattering of bones centered around bioturbation by floundering dinosaurs (Bilbey, 1999; see Richmond and Morris, 1996, for smectitic clay disarticulation). The basic premise of the predator trap implies that the dinosaurs were ensnared in a viscous mud so confining that they could not struggle free. If, once trapped, the dinosaurs were unable to move significantly, it seems unlikely that their death throes would have resulted in the skeletal disarticulation of previous victims. Finally, the occurrence of scavenged distal-limb elements is contradictory to this hypothesis. Following the predator-trap model, there seems little chance that predators would have been able to scavenge distal-limb segments of their prey, since the latter should have been fully immersed in mud.

Drought

Of all the possible taphonomic hypotheses considered, drought is regarded here as the preferred hypothesis. Drought is a worldwide phenomenon, known to occur in almost every climatic regime (Wilhite, 2000) and has been postulated for Late Jurassic climates of the Western Interior (Demko and Parrish, 1998). Interpretation of the CLDQ paleoenvironmental setting as an ephemeral pond provides geologic support for the occasional desiccation of local waterholes. The sustained need for water certainly would account for the presence of such large numbers and diversity of dinosaurs in one location during approximately the same time interval. In addition, a stressed environment produced from a lack of water, coupled with a high population density, would have weakened the local animals, making them more susceptible to death. Evidence for this stress was found at the site in 1987. A dinosaur egg was recovered from the quarry containing an extra layer of eggshell, which commonly precipitates during stressful conditions in modern animals (Hirsch et al., 1989). The egg further testifies to a long-term stressful environment that plagued these animals.

In modern assemblages, juveniles are especially prone to drought-induced mortality because they lack the ability to tolerate the stress of depleted environments (Hanks, 1979; Conybeare and Haynes, 1984; Haynes, 1991). This observation is fully consistent with the high percentage of juveniles preserved in the CLDQ.

Although drought is a major killing mechanism known to

be associated with the formation of bone beds (Haynes, 1991), such mass deaths rarely are the result of dehydration. Instead, water-dependent animals tend to gather around water holes during periods of extended drought, consuming all available forage in the area (Hanks, 1979). The resultant physiological weakening of the animals tends to make them more susceptible to a variety of lethal agents, including intraspecific aggression, predation, malnutrition, and disease (Carpenter, 1987; Haynes, 1991). The occurrence of rotting carcasses and abundant feces in and around remnant pools of water can provide a vehicle for the spread of diseases such as botulism (Sugiyama, 1986). Once initiated, botulism can run through a population of carnivores and rapidly decimate their numbers, yet leaving no tangible evidence in the fossil record. One last drought-induced killing agent that occurs in modern assemblages is miring of weakened juveniles in soft sediment around waterholes. This phenomenon occurs relatively rarely in modern deposits (Haynes, 1991; Behrensmeyer, pers. comm.) and, as mentioned above, is not expected to have occurred at CLDQ, but should be included in any thorough list of causes of drought-induced mortality.

As already mentioned, herbivores are the most common victims of drought (Haynes, 1991), making the overabundance of carnivores at CLDQ seemingly contradictory. However, an analogous drought-induced mass death has been postulated for the Late Triassic *Coelophysis* Quarry, where perhaps thousands of *Coelophysis* individuals accumulated (Schwartz and Gillette, 1994). It seems feasible that *Allosaurus*, as the most commonly occurring large-bodied carnivore, would have been able to dominate waterholes during extended periods of drought in the Late Jurassic if their numbers reached a critical level. Herbivores, likely intimidated by the abundant carnivores, may have left the waterhole in search of safer areas and consequently biased the deposit toward predators. Initially, however, the allosaurs may have been attracted to the site by large numbers of easy-to-obtain, weakened prey. This scenario is supported by a concentration of large herbivorous dinosaur bones in the base of the deposit and increasing domination of allosaur remains toward the middle of the bonebed.

The concentration of relatively large bones at the top and bottom of the deposit suggests that CLDQ represents multiple events rather than a single catastrophic episode. The thinness of the bone layer, as well as modern evidence on the duration of waterholes and associated times of bone-bed accumulations, suggests that the site formed over a relatively brief period—on the order of decades rather than millennia or even centuries. This brief duration for site formation is supported by estimates of accumulation rate for drought-induced deposits in the Late Cretaceous (Rogers, 1993).

Paleoecological Speculations

The Morrison Formation is famous for its large-scale multi-generic bone beds (Dodson et al., 1980). In light of the semi-arid climate of the Late Jurassic across much of western North America, as well as similarities among many of the Morrison bonebeds, drought may have been a factor in a number of these assemblages (Richmond and Morris, 1998; Hubert and Panish, 2000). Rogers (1990)

proposed that a large number of monospecific bone beds within a formation might be an indicator of drought. Rogers (1990) further speculated that mono-/paucispecific bone beds may suggest territorial resource partitioning by herding dinosaurs (e.g., ceratopsians and hadrosaurs), citing evidence from modern African elephants and buffalo herds (Jarman, 1972). Large herds of ceratopsians and hadrosaurs likely had the ability to exclude other species from a waterhole by sheer numbers, thereby facilitating the formation of low-diversity bone beds.

In contrast, Morrison Formation bone beds usually do not preserve large numbers of a single species. One possible explanation is that the Late Jurassic dinosaurs did not congregate into large aggregations, or herds, like their Late Cretaceous counterparts. Even though trackways preserve the movement of possible sauropod aggregations (Lockley, 1991; Barnes and Lockley, 1994), group size may not have been nearly as large as has been postulated for Late Cretaceous hadrosaurs and ceratopsids. Therefore, the scarcity of monospecific bonebeds in the Morrison may reflect the absence of such gregarious behavior among Late Jurassic dinosaurs in North America.

Low population densities and group sizes among Late Jurassic herbivorous dinosaurs also seem reasonable on climatic grounds, given that the semi-arid environments may have been responsible for limited plant productivity (Dodson et al., 1980; Engelmann et al., 2004). The Morrison Formation multi-generic bone beds also may reflect a lower supply of viable watering holes compared to the Late Cretaceous Two Medicine Formation of Montana. Although there is no cited geologic evidence for fewer waterholes during the Late Jurassic, it seems reasonable that a paucity of water sources would result in dense accumulations of multiple species, as is seen in Morrison deposits.

If drought were a factor in the formation of the Cleveland-Lloyd Dinosaur Quarry, as argued here, it also may have impacted the lives of Morrison Formation dinosaurs generally. Certainly drought has a profound impact on modern ecosystems in which it occurs. For example, in sub-Saharan Africa, the onset of the dry season causes many grazing animals that normally are solitary or found in small groups to gather into large aggregations around remaining bodies of water (Western, 1975). The reproductive cycles of these animals also are regulated environmentally, with most species giving birth concurrently at the onset of the wet season (Hanks, 1979). Late Jurassic dinosaurs may have displayed similar behavioral patterns, perhaps timing egg hatching during the most productive part of the year, and then congregating around persistent sources of water during the dry season.

CONCLUSIONS

The Cleveland-Lloyd Dinosaur Quarry is a truly remarkable fossil assemblage that includes thousands of bones representing at least 70 individual dinosaurs from at least nine genera (Madsen, 1976b). Most abundant by far is the large-bodied theropod *Allosaurus fragilis*, which comprises at least 46 individuals and approximately two-thirds of the assemblage. The autochthonous assemblage occurs in a fine-grained mudstone, representing an ephemeral-pond setting. The quarry layer is capped by a thick limestone unit, which probably represents a lake

that filled the basin subsequent to deposition of the extensive bone bed. In recent decades, CLDQ has been regarded almost exclusively as a predator trap by several authors (Dodson et al., 1980; Richmond and Morris, 1996; Bilbey, 1999). Several lines of evidence seriously destabilize this scenario. Of the remaining scenarios, drought-induced mass death currently is the most parsimonious. The drought hypothesis is strengthened by modern taphonomic studies demonstrating that drought is a widespread phenomenon commonly implicated in the formation of large vertebrate mass-death assemblages. Taphonomic clues present at CLDQ consistent with the drought hypothesis include a large concentration of animals in an aqueous depositional setting, geologic evidence of desiccation (e.g., mud rip-up clasts), and age-class data suggesting a subadult-dominated assemblage.

A drought-induced mass death at CLDQ is further supported by studies that suggest a semi-arid climatic regime with periodic drought conditions for the Morrison Formation (Demko and Parrish, 1998; Parrish et al., 2004). Indeed, the preponderance of large-scale dinosaur bone beds throughout much of the upper Morrison Formation suggests a regionally and temporally consistent killing mechanism, with drought being a likely culprit (Rogers, 1990). Ultimately, this concentration of carnivores is considered a rarity in the Late Jurassic ecosystem.

ACKNOWLEDGEMENTS

I would like to thank Scott Sampson, Ray Rogers, and Dave Eberth for continuous revisions and insightful comments of this manuscript, and Mike Getty, Eric Lund, the graduate students, and volunteers at the Utah Museum of Natural History for their help excavating and preparing the hundreds of specimens collected for this study. I am indebted to Mike Leschin, his SCA's, and Laurie Bryant of the Utah BLM for allowing full access to the quarry and its treasures. Jim Madsen and Sue Ann Bilbey always freely gave their extensive experience and knowledge of CLDQ. Jason Lillegraven, Tom Morris, George Engelmann, and Anthony Fiorillo provided useful reviews of this paper. I had many great taphonomy conversations with Eric Roberts and Kay Behrensmeyer. Finally, I am very grateful to my wife Lindsay Zanno for editing this paper and, more importantly, for inspiring me. Funding was provided by the Jurassic Foundation and the University of Utah Department of Geology and Geophysics.

REFERENCES

- BARNES, F.A., and LOCKLEY, M.G., 1994, Trackway evidence for social sauropods from the Morrison Formation, eastern Utah (USA): Gaia, v. 10, p. 37–42.
- BEHRENSMEYER, A.K., 1975, The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolph, Kenya: Bulletin of the Museum of Comparative Zoology, v. 146, p. 473–578.
- BEHRENSMEYER, A.K., 1978, Taphonomic and ecologic information from bone weathering: Paleobiology, v. 4, p. 150–162.
- BEHRENSMEYER, A.K., 1980, Patterns of natural bone distribution on recent land surfaces: implications for archaeological site formation: in Behrensmeyer, A.K., and Hill, A.P., eds., Fossils in the Making: University of Chicago Press, Chicago, p. 93–106.
- BEHRENSMEYER, A.K., 1988, Vertebrate preservation in fluvial chan-

- nels: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 63, p. 183–199.
- BEHRENSMEYER, A.K., 1999, Bonebeds through geologic time: Journal of Vertebrate Paleontology, v. 19, p. 31A.
- BEHRENSMEYER, A.K., GORDON, K.D., and YANAGI, G.T., 1986, Trampling as a cause of bone surface damage and pseudo-cutmarks: Nature, v. 319, p. 768–771.
- BERNER, R.A., 1968, Calcium carbonate concretions formed by the decomposition of organic matter: Science, v. 159, p. 195–197.
- BILBEY, S.A., 1992, Stratigraphy and sedimentary petrology of the Upper Jurassic–Lower Cretaceous rocks at Cleveland-Lloyd Dinosaur Quarry with a comparison to the Dinosaur National Monument Quarry, Utah: unpublished Ph.D. dissertation, University of Utah, Salt Lake City, 295 p.
- BILBEY, S.A., 1999, Taphonomy of the Cleveland-Lloyd Dinosaur Quarry in the Morrison Formation, central Utah—a lethal spring-fed pond: in Gillette, D.D., ed., Vertebrate Paleontology in Utah: Utah Geologic Survey, Miscellaneous Publication 99-1, p. 121–133.
- BILBEY-BOWMAN, S.A., BOWMAN, J.T., and DRAKE, R.E., 1986, Interpretation of the Morrison Formation as a time-transgressive unit: Fourth North American Paleontological Congress, Boulder, Colorado, Abstracts and Program, p. A5.
- BRAIN, C.K., 1967, Bone weathering and the problem of bone pseudo-tools: South African Journal of Science, v. 63, p. 97–99.
- BRALOWER, T.J., LUDWIG, K.R., OBRADOVICH, J.D., and JONES, D.L., 1990, Berriasian (Early Cretaceous) radiometric ages from the Grindstone Creek section, Sacramento Valley, California: Earth Planetary Science Letters, v. 98, p. 62–73.
- BRIGGS, D.E.G., SIVETER, D.J., and SIVETER, D.J., 1996, Soft-bodied fossils from a Silurian volcaniclastic deposit: Nature, v. 382, p. 248–250.
- BROWN, B., 1935, Sinclair dinosaur expedition, 1934: Natural History, v. 36, p. 3–15.
- CANFIELD, D.E., and RAISWELL, R., 1991, Carbonate precipitation and dissolution: its relevance to fossil preservation: in Allison, P.A., and Briggs, D.E.G., eds., Taphonomy: Releasing the Data Locked in the Fossil Record: Plenum Press, New York, p. 411–453.
- CARPENTER, K., 1987, Paleoenvironmental significance of droughts during the Late Cretaceous of the western interior: in Currie, P.J., and Koster, E.H., eds., Fourth Symposium on Mesozoic Terrestrial Ecosystems: Occasional Papers of the Tyrell Museum of Paleontology No. 3, p. 42–47.
- CHIN, K., and KIRKLAND, J.I., 1998, Probable herbivore coprolites from the Upper Jurassic Mygatt-Moore Quarry, western Colorado: Modern Geology, v. 22, p. 249–275.
- COE, M., 1978, The decomposition of elephant carcasses in the Tsavo (East) National Park, Kenya: Journal of Arid Environments, v. 1, p. 71–86.
- CONYBEARE, A., and HAYNES, G., 1984, Observations on elephant mortality and bone in watering holes: Quaternary Research, v. 22, p. 189–200.
- CURRIE, P.J., 1998, Possible evidence of gregarious behavior in tyrannosaurids: Gaia, v. 15, p. 123–133.
- DEMKO, T.M., CURRIE B.S., and NICOLL, K.A., 2004, Regional paleoclimatic and stratigraphic implications of paleosols and fluvial/overbank architecture in the Morrison Formation (Upper Jurassic), Western Interior, USA: Sedimentary Geology, v. 167, p. 115–135.
- DEMKO, T.M., and PARRISH, J.T., 1998, Paleoclimatic setting of the Upper Jurassic Morrison Formation: Modern Geology, v. 22, p. 283–296.
- DODSON, P., 1973, The significance of small bones in paleoecological interpretation: University of Wyoming Contributions to Geology, v. 12, p. 15–19.
- DODSON, P., BEHRENSMEYER, A.K., BAKKER, R.T., and MCINTOSH, J.S., 1980, Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation: Paleobiology, v. 6, p. 208–232.
- DOWNING, K.F., and PARK, L.E., 1998, Geochemistry and early diagenesis of mammal-bearing concretions from the Sucker Creek Formation (Miocene) of southeastern Oregon: PALAIOS, v. 13, p. 14–27.
- DUFF, R., 1949, Pyramid Valley: Pegasus Press for the Association of Friends of the Canterbury Museum, New Zealand, Christchurch, 48 p.
- ENGELMANN, G.F., CHURE, D.J., and FIORILLO, A.R., 2004, The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation: Sedimentary Geology, v. 167, p. 297–308.
- EVANS, S.E., and MILNER, A.R., 1993, Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America: Journal of Vertebrate Paleontology, v. 13, p. 24–30.
- FIORILLO, A.R., 1984, An introduction to the identification of trample marks: Current Research, University of Maine, Orono, v. 1, p. 47–48.
- FIORILLO, A.R., 1987, Trample marks: caution from the Cretaceous: Current Research in the Pleistocene, v. 4, p. 73–75.
- FIORILLO, A.R., 1988, Taphonomy of the Hazard Homestead Quarry (Ogallala Group), Hitchcock County, Nebraska: University of Wyoming Contributions to Geology, v. 26, p. 57–97.
- FIORILLO, A.R., 1991, Prey bone utilization by predatory dinosaurs: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 88, p. 157–166.
- FOWLER, D., SIMMONDS, K., GREEN, M., and STEVENS, K.A., 2003, The taphonomic setting of two mired sauropods (Wessex Fm, Isle of Wight, UK), palaeoecological implications and taxon preservation bias in a Lower Cretaceous wetland: Journal of Vertebrate Paleontology, v. 23, Supplement, p. 51A.
- FROSTICK, L., and REID, I., 1983, Taphonomic significance of sub-aerial transport of vertebrate fossils on steep semi-arid slopes: Leharia, v. 16, p. 157–164.
- GIFFORD, D.P., 1985, Taphonomic specimens, Lake Turkana: Research Reports, National Geographic Society, v. 17, p. 419–428.
- GILLULY, J., and REESIDE, J.B., JR., 1928, Sedimentary rocks of the San Rafael Swell and some adjacent areas in eastern Utah: United States Geological Survey Professional Paper 150, p. 61–84.
- GRADSTEIN, F.M., AGTERBERG, F.P., OGG, J.G., HARDENBOL, J., VAN VEEN, P., THIERRY, J., and HUANG, Z., 1994, A Mesozoic time scale: Journal of Geophysical Research, v. 99, p. 24,051–24,074.
- GREGORY, H.E., 1938, The San Juan Country: United States Geological Survey Professional Paper 188, 123 p.
- HANKS, J., 1979, The Struggle for Survival: Mayflower Books, New York, 176 p.
- HARRIS, J.M., 2001, Reconstructing a late Pleistocene environment: Terra, v. 38, p. 12–21.
- HASIOTIS, S.T., FIORILLO, A.R., and HANNA, R.R., 1999, Preliminary report on borings in Jurassic dinosaur bones: evidence for invertebrate–vertebrate interactions: in Gillette, D.D., ed., Vertebrate Paleontology in Utah: Utah Geologic Survey Miscellaneous Publications, 99-1, p. 191–200.
- HAYNES, G., 1988, Mass death and serial predation: comparative taphonomic studies of modern large mammal death sites: Journal of Archaeological Science, v. 15, p. 219–235.
- HAYNES, G., 1991, Mastodons, Mastodons, and Elephants: Biology, Behavior, and the Fossil Record: Cambridge University Press, Cambridge, 413 p.
- HENRICI, A.C., and FIORILLO, A.R., 1993, Catastrophic death assemblage of *Chelomophryne bayi* (Anura, Rhyinophrynidae) from the middle Eocene Wagon Bed Formation of central Wyoming: Journal of Paleontology, v. 67, p. 1016–1026.
- HILL, A., 1979, Disarticulation and scattering of mammal skeletons: Paleobiology, v. 5, p. 261–274.
- HILL, A., 1989, Bone modification by modern spotted hyenas: in Bonichsen, R., and Sorg, M.H., eds., Bone Modification: University of Maine, Orono, p. 169–178.
- HILLMAN, J.C., and HILLMAN, A.K.K., 1977, Mortality of wildlife in Nairobi National Park, during the drought of 1973–1974: East African Wildlife Journal, v. 15, p. 1–18.
- HIRSCH, K.F., STADTMAN, K.L., MILLER, W.E., MADSEN, J.H. JR., 1989, Upper Jurassic dinosaur egg from Utah: Science, v. 243, p. 1711–1713.
- HOLDWAY, R.N., and WORTHY, T.H., 1997, A reappraisal of the late Quaternary fossil vertebrates of Pyramid Valley Swamp, North Canterbury, New Zealand: New Zealand Journal of Zoology, v. 24, p. 69–121.

- HUBERT, J.F., and PANISH, P.T., 2000, Sedimentology and diagenesis of the dinosaur bones exposed at the Dinosaur Ridge along Alameda Parkway in the Morrison Formation (Upper Jurassic), Morrison, Colorado: *The Mountain Geologist*, v. 37, p. 73–90.
- HUNT, A.P., 1986, Taphonomy of the Cleveland-Lloyd Dinosaur Quarry, Morrison Formation (Late Jurassic), Emery County, Utah—a preliminary report: *Fourth North American Paleontological Convention*, Boulder, Colorado, Abstracts and Program, p. A21.
- HUNT, R.M., JR., 1990, Taphonomy and sedimentology of Arikaree (lower Miocene) fluvial, eolian, and lacustrine paleoenvironments, Nebraska and Wyoming: a paleobiota entombed in fine-grained volcaniclastic rocks: *in* Lockley, M.G., and Rice, A., eds., *Volcanism and Fossil Biotas*: Geological Society of America Special Paper 244, p. 69–111.
- JARMAN, P.J., 1972, The use of drinking sites, wallows and salt licks by herbivores in the flooded Middle Zambezi Valley: *East African Wildlife Journal*, v. 10, p. 193–209.
- KENNEDY, W.J., and ODIN, G.S., 1982, The Jurassic and Cretaceous time scale in 1981: *in* Odin, G.S., ed., *Numerical Dating in Stratigraphy, Part II*: John Wiley & Sons, Ltd., Chichester, p. 557–592.
- KIRKLAND, J.I., and ARMSTRONG, H.J., 1992, Taphonomy of the Mygatt-Moore (M&M) Quarry, Middle Brushy Basin Member, Morrison Formation (Upper Jurassic) western Colorado: *Journal of Vertebrate Paleontology*, v. 12, Supplement, p. 37A.
- KOWALLIS, B.J., CHRISTIANSEN, E.H., and DEINO, A.L., 1991, Age of the Brushy Basin Member of the Morrison Formation, Colorado Plateau, western USA: *Cretaceous Research*, v. 12, p. 483–493.
- KOWALLIS, B.J., CHRISTIANSEN, E.H., DEINO, A.L., PETERSON, F., TURNER, C.E., KUNK, M.J., and OBRADOVICH, J.D., 1998, The age of the Morrison Formation: *Modern Geology*, v. 22, p. 235–260.
- KOWALLIS, B.J., HEATON, J.S., and BRINGHURST, K., 1986, Fission-track dating of volcanically derived sedimentary rocks: *Geology*, v. 14, p. 19–22.
- LAWTON, R., 1977, Taphonomy of the dinosaur quarry, Dinosaur National Monument: *University of Wyoming Contributions to Geology*, v. 15, p. 119–126.
- LEE, M.J., and BROOKINS, D.G., 1978, Rubidium-strontium minimum ages of sedimentation, uranium mineralization, and provenance, Morrison Formation (Upper Jurassic), Grants Mineral Belt, New Mexico: *American Association of Petroleum Geologists Bulletin*, v. 62, p. 1673–1683.
- LOCKLEY, M., 1991, *Tracking Dinosaurs: A New Look at an Ancient World*: Cambridge University Press, New York, 238 p.
- MADSEN, J.H., JR., 1974, A new theropod dinosaur from the Upper Jurassic of Utah: *Journal of Paleontology*, v. 48, p. 27–31.
- MADSEN, J.H., JR., 1976a, A second new theropod dinosaur from the Late Jurassic of Eastern Utah: *Utah Geology*, v. 3, p. 51–60.
- MADSEN, J.H., JR., 1976b, *Allosaurus fragilis*—a revised osteology: *Utah Geologic Survey, Bulletin* 109, 163 p.
- MADSEN, J.H., JR., 1987, The dinosaur department store: *in* Averett, W.R., ed., *Paleontology and Geology of the Dinosaur Triangle: Guidebook for 1987 Grand Junction Geological Society Field Trip*, September 18–20, 1987: Museum of Western Colorado, Grand Junction, p. 65–74.
- MADSEN, J.H., JR., and STOKES, W.L., 1972, University of Utah Cooperative Dinosaur Project, a progress report: *Proceedings of the Utah Academy of Science, Art, and Letters*, v. 49, p. 48–50.
- MADSEN, J.H., JR., and STOKES, W.L., 1977, University of Utah Cooperative Dinosaur Project: a final report: *Encyclia*, v. 54, p. 68–70.
- MARTIN, L.D., and WEST, D.L., 1995, The recognition and use of dermestid (Insecta, Coleoptera) pupation chambers in paleoecology: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 113, p. 303–310.
- MILLER, W.E., HORROCKS, R.D., and MADSEN, J.H., JR., 1996, The Cleveland-Lloyd Dinosaur Quarry, Emery County, Utah—a U.S. National Landmark (including history and quarry map): *Brigham Young University Geology Studies*, v. 41, p. 3–24.
- MORRIS, T.H., RICHMOND, D.R., and GRIMSHAW, S.D., 1996, Orientation of dinosaur bones in riverine environments: insights into sedimentary dynamics and taphonomy: *in* Morales, M., ed., *The Continental Jurassic: Museum of Northern Arizona, Flagstaff*, p. 521–530.
- NORTHROP, H.R., 1982, Origin of the tabular-type vanadium-uranium deposits in the Henry Basin, Utah: Unpublished Ph.D. dissertation, Colorado School of Mines, Golden, No. T-2614, 340 p.
- OLSEN, S.L. and SHIPMAN, P., 1988, Surface modification on bone: trampling versus butchery: *Journal of Archaeological Science*, v. 15, p. 535–553.
- PARRISH, J.T., PETERSON, F., and TURNER, C.E., 2004, Jurassic “savannah”—plant taphonomy and climate of the Morrison Formation (Upper Jurassic, western USA): *Sedimentary Geology*, v. 167, p. 137–162.
- PARRISH, J.T., ZIEGLER, A.M., and SCOTESE, C.R., 1982, Rainfall patterns and the distribution of coals and evaporites in the Mesozoic and Cenozoic: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 40, p. 67–101.
- PETERSON, F., and TURNER-PETERSON, C., 1987, The Morrison Formation of the Colorado Plateau: recent advances in sedimentology, stratigraphy, and paleotectonics: *Hunteria*, v. 2, 18 p.
- PETERSON, F., and TYLER, N., 1985, Field guide to the upper Salt Wash alluvial complex: *in* Flores, R.M., and Harvey, M.D., eds., *Field Guidebook to Modern and Ancient Fluvial Systems in the United States: Proceedings of the Third International Fluvial Sedimentology Conference*, Colorado State University, Fort Collins, Colorado, p. 45–64.
- RICHMOND, D.R., and MORRIS, T.H., 1996, The dinosaur death-trap of the Cleveland-Lloyd Dinosaur Quarry, Emery County, Utah: *in* Morales, M., ed., *The Continental Jurassic: Museum of Northern Arizona, Flagstaff*, p. 535–545.
- RICHMOND, D.R., and MORRIS, T.H., 1998, Stratigraphy and catastrophic deposition of the Dry Mesa Dinosaur Quarry, Mesa County, Colorado: *Modern Geology*, v. 22, p. 121–143.
- ROBERTS, E., ROGERS, R.R., and FOREMAN, B.Z., 2003, An experimental approach to identifying and interpreting dermestid (Insecta, Coleoptera) bone modification: *Journal of Vertebrate Paleontology*, v. 23, Supplement, p. 89A.
- ROGERS, R.R., 1990, Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: evidence for drought-related mortality: *PALAIOS*, v. 5, p. 394–413.
- ROGERS, R.R., 1992, Non-marine borings in dinosaur bones from the Upper Cretaceous Two Medicine Formation, northwestern Montana: *Journal of Vertebrate Paleontology*, v. 12, p. 528–531.
- ROGERS, R.R., 1993, Systematic patterns of time-averaging in the terrestrial vertebrate record: a Cretaceous case study: *in* Kidwell, S.M., and Behrensmeyer, A.K., eds., *Taphonomic Approaches to Time Resolution in Fossil Assemblages: The Paleontological Society, Knoxville*, p. 228–249.
- ROGERS, R.R., ARCUCCI, A.B., ABDALA, F., SERENO, P.C., FORSTER, C.A., and MAY, C.L., 2001, Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), northwestern Argentina: spectacular preservation in volcanogenic concretions: *PALAIOS*, v. 16, p. 461–481.
- SANDER, P.M., 1987, Taphonomy of the Lower Permian Geraldine Bonebed in Archer County, Texas: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 61, p. 221–236.
- SANDER, P.M., 1992, The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 93, p. 255–299.
- SCHWARTZ, H.L., and GILLETTE, D.D., 1994, Geology and taphonomy of the *Coelophysis* quarry, Upper Triassic Chinle Formation, Ghost Ranch, New Mexico: *Journal of Paleontology*, v. 68, p. 1118–1130.
- SHIPMAN, P., 1975, Implications of drought for vertebrate fossil assemblages: *Nature*, v. 257, p. 667–668.
- SHIPMAN, P., and ROSE, J., 1983, Early hominid hunting, butchering, and carcass-processing behaviors: approaches to the fossil record: *Journal of Anthropological Archaeology*, v. 2, p. 57–98.
- STEINER, M.B., LUCAS, S.G., and SHOEMAKER, E.M., 1994, Correlation and age of the Upper Jurassic Morrison Formation from magnetostratigraphic analysis: *in* Caputo, M.V., Peterson, J.A., and Franczyk, K.J., eds., *Mesozoic Systems of the Rocky Mountain Region, USA: SEPM Rocky Mountain Section, Denver*, p. 315–330.
- STOKES, W.L., 1945, A new quarry for Jurassic dinosaurs: *Science*, v. 101, p. 115–117.

- STOKES, W.L., 1985, The Cleveland-Lloyd Dinosaur Quarry: United States Government Printing Office, 27 p.
- STORRS, G.W., and GARCIA, W.J., 2001, Preliminary analysis of a monospecific sauropod locality from Carbon County, Montana: *Journal of Vertebrate Paleontology*, v. 21, Supplement, p. 105A.
- SUGIYAMA, H., 1986, *Clostridium botulinum*: in Gyles, C.L., and Thoen, C.O., eds., *Pathogenesis of Bacterial Infections in Animals*: Iowa State University Press, Ames, p. 60–68.
- TURNER, C.E., and FISHMAN, N.S., 1991, Jurassic Lake T'oo'dichi'—a large alkaline, saline lake, Morrison Formation, eastern Colorado Plateau: *Geological Society of America Bulletin*, v. 103, p. 538–558.
- TURNER, C.E., and PETERSON, F., 1999, Biostratigraphy of dinosaurs in the upper Jurassic Morrison Formation of the Western Interior, USA: in Gillette, D.D., ed., *Vertebrate Paleontology in Utah: Utah Geologic Survey Miscellaneous Publication 99-1*, p. 77–114.
- VARRICCHIO, D.J., 1995, Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 114, p. 297–323.
- VOOHRIES, M.R., 1969, Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska: University of Wyoming Contributions to Geology, Special Paper 1, 69 p.
- VOOHRIES, M.R., 1981, Ancient skyfall creates Pompeii of prehistoric animals: *National Geographic*, v. 159, p. 66–75.
- WEBB, G., and MANOLIS, C., 1988, *Australian Freshwater Crocodiles*: G. Webb Pty. Limited, Winnellie, 32 p.
- WEIGELT, J., 1989, *Recent Vertebrate Carcasses and Their Paleobiological Implications* [translated by J. Schaefer]: University of Chicago Press, Chicago, 188 p.
- WELLS, R. T., and TEDFORD, R. H., 1995, *Sthenurus* (Macropodidae: Marsupialia) from the Pleistocene of Lake Callabonna, South Australia: *Bulletin of the American Museum of Natural History*, v. 225, 112 p.
- WESTERN, D., 1975, Water availability and its influence on the structure and dynamics of a savannah large mammal community: *East African Wildlife Journal*, v. 13, p. 265–286.
- WHITE, J.A., McDONALD, H.G., ANDERSON, E., and SOISET, J.M., 1984, Lava blisters as carnivore traps: *Special Publication of the Carnegie Museum of Natural History*, v. 8, p. 241–256.
- WILHITE, D.A., 2000, Drought as a natural hazard: concepts and definitions: in Wilhite, D.A., ed., *Drought, Volume 1: a Global Assessment*: Routledge, New York, p. 3–18.
- WHITE, T.D., 1992, *Prehistoric Cannibalism at Mancos 5MTUMR-2346*: Princeton University Press, Princeton, 462 p.

ACCEPTED DECEMBER 3, 2004

