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TAPHONOMIC ANALYSIS OF A DINOSAUR FEEDING SITE USING GEOGRAPHIC INFORMATION SYSTEMS (GIS), MORRISON FORMATION, SOUTHERN BIGHORN BASIN, WYOMING, USA

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ABSTRACT

Geospatial data collected with a Nikon Total Station from a dinosaur quarry in the upper part of the Morrison Formation in north-central Wyoming were plotted on ArcGIS ArcScene software. The resulting three-dimensional maps indicate two distinct sauropod bone assemblages with closely associated shed theropod teeth separated by a weakly developed paleosol. Consequently, previous hypotheses that all bone elements and theropod teeth in the quarry were chronologically connected are amended. Synthesis of geological and paleontological data provides evidence that a juvenile *Camarasaurus* was the center of feeding activity in a shallow-water, palustrine-lacustrine setting in the lower assemblage. The high ratio of juvenile to adult allosaurid teeth suggests one or two adults in the company of several juveniles during a scavenging event. A high incidence of theropod teeth in the upper assemblage suggests that another feeding event may have occurred, but data loss from initial traditional excavation techniques precludes a more detailed interpretation. Although the Upper Jurassic Morrison Formation in the western United States yields abundant sauropod and theropod remains, few sites documenting theropod-prey interactions have been reported. Evidence of theropod feeding activities has been difficult to establish in seemingly homogeneous continental deposits with traditional excavation techniques alone. Geographic Information Systems (GIS) is a valuable tool that allows paleontologists to establish chronostratigraphic constraints in complex continental assemblages, assess the degree of time averaging, and evaluate important geospatial patterns.

INTRODUCTION

The purpose of this paper is to document an *Allosaurus* feeding site in the Upper Jurassic Morrison Formation near Thermopolis, Wyoming, United States, and to illustrate the usefulness of Geographic Information Systems (GIS) for taphonomic reconstructions. Although the Morrison Formation has yielded abundant sauropod and theropod remains, few theropod-prey interactions have been documented. Tooth-damaged sauropod bones led to hypotheses of theropod feeding activities (Hunt et al., 1994; Chure et al., 1998; Jacobsen, 1998) and speculations about theropod parental behavior (Bakker, 1997). Allosaurid feeding events associated with sauropod remains have been interpreted from the Howe Quarry in northern Wyoming (Lockley et al., 1998), Como Bluff, Wyoming (Bakker, 1997), and one Upper Jurassic quarry in Thailand (Buffetaut and Suteethorn, 1989), based on the occurrence of shed theropod teeth, sauropod remains, and dinosaur tracks within the same quarry. High incidence of theropod teeth is a characteristic connected with theropod feeding (Molnar and Farlow, 1990; Farlow and Holtz, 2002), but bones and teeth can accumulate over a significant amount of time in continental deposits (Martin, 1999). Without data to constrain timing of burial, chronological relationships between bones and associated teeth can be considered ambiguous.

Whether tracks, skeletal remains, and shed teeth can be related directly to a short-lived feeding event relies on high-resolution taphonomic data that delimit the degree of time averaging and distinguish subtle changes in environmental conditions. Traditional excavation and mapping techniques do not document critical, vertical relationships between fossils, particularly in homogeneous continental lithologies.

While excavating a new quarry on the Warm Springs Ranch near Thermopolis, Wyoming, in 1995, workers at the Wyoming Dinosaur Center discovered dozens of shed theropod teeth and scattered sauropod bones above a heavily trampled carbonate mudstone. Naus and Stein (1997) interpreted the site as either a predator ambush site or an *Allosaurus* den. These hypotheses were based on large numbers of shed theropod teeth, small and large tridactyl tracks, and damaged bones at the site (Naus and Stein, 1997). Excavation was suspended temporarily until spatial data could be collected and a detailed taphonomic and sedimentary analysis could be conducted to assess the time averaging of the assemblage and test the hypotheses.

GEOLOGIC SETTING

During the Late Jurassic–Early Cretaceous, north-central Wyoming was situated on a long, broad, floodplain (Lawton, 1994). The Nevadan orogeny allowed substantial accumulation of lacustrine and floodplain sediments in the broad, shallow sedimentary basin to the east (Lawton, 1994; Dunagan, 1998). Subsequent thrust faulting and folding resulted in lacustrine development in semi-isolated to isolated basins throughout the Western Interior (Carson, 1998; Dunagan, 1998) as island-arc terranes were accreted to the northwestern continental margin between the Middle Jurassic and the Middle Cretaceous (DeCelles, 2004). Volcanism and uplift along the collision belt increased sedimentation rates during the Kimmeridgian and Tithonian (Brenner and Peterson, 1994) as significant amounts of volcanic debris and ash were generated from the Transcontinental Arc to the west and deposited eastward and northeastward across the Western Interior (Suttner, 1969; Peterson, 1972; Santos and Peterson, 1986; Johnson, 1991; Dunagan, 1998; DeCelles, 2004).

The subject of this study, the Something Interesting (SI) quarry, is located approximately 2.5 km southeast of Thermopolis, in north-central Wyoming, at the southernmost extent of the Bighorn Basin (Fig. 1, upper right). A semitemporary shelter covers the current excavation surface of 4 m × 15 m. A metal walkway was built across the quarry to protect a trampled surface from any unnecessary traffic and to allow access for Wyoming Dinosaur Center museum tours.

Outcrops in the study area trend east-northeast, dipping 6° N. The Morrison Formation is approximately 60 m thick in most local stratigraphic sections and is bounded by disconformable contacts with the Upper Jurassic Sundance Formation at the base and the Lower Cretaceous

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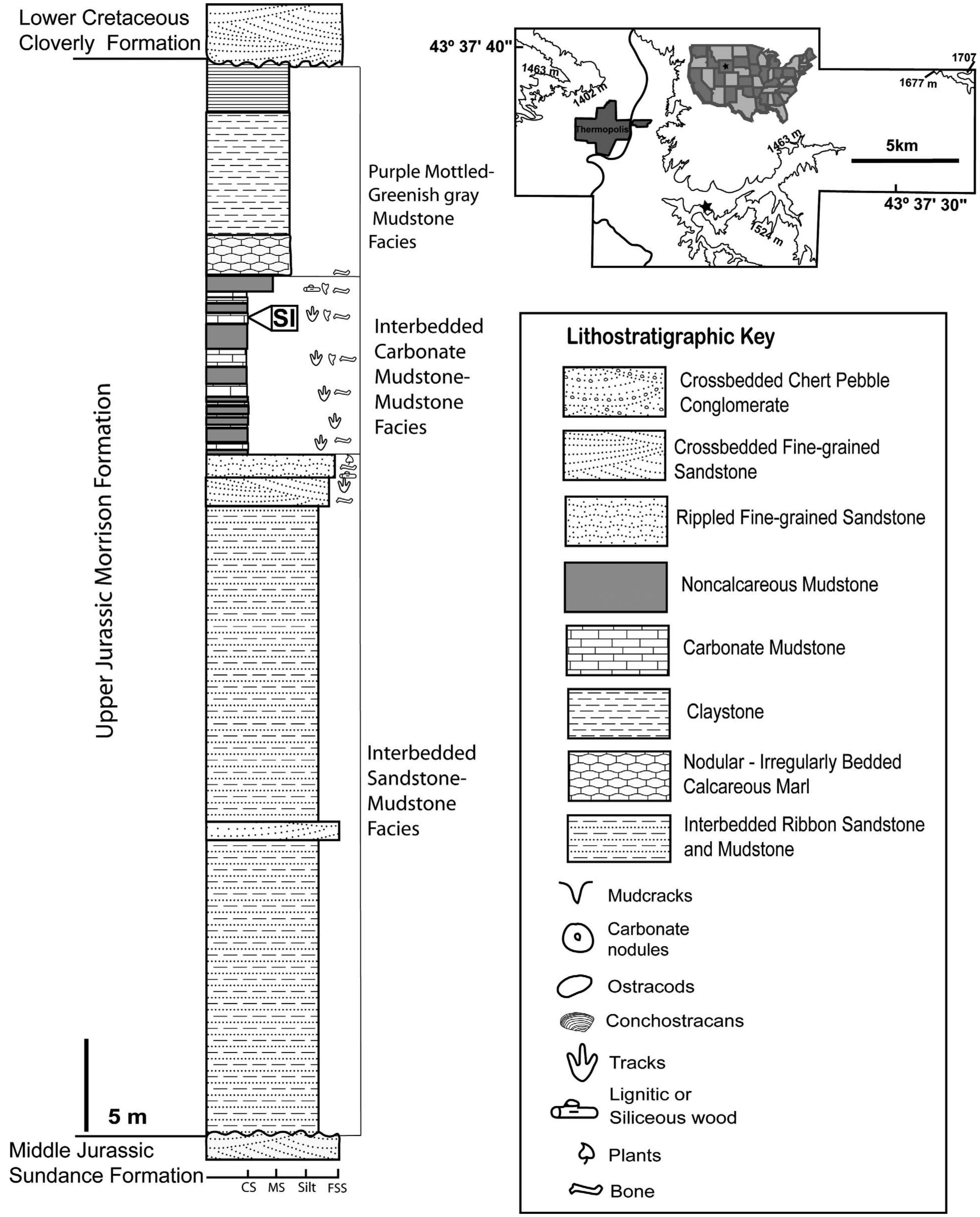

FIGURE 1—Location of study area (upper right) and generalized stratigraphy of the Morrison Formation in the quarry vicinity.

Cloverly Formation at the top. The contact between the Morrison and the Sundance Formation is identified as the contact between a quartz-rich, trough-crossbedded sandstone unit lying directly above a green, glauconitic, bioclast-rich sandstone unit. The Morrison-Cloverly contact is highly erosional with large, trough-crossbedded, chert-pebble conglomerate of the Cloverly overlying greenish gray or black, organic-rich claystone of the Morrison (Fig. 1).

METHODS

Stratigraphic sections of the entire Morrison Formation in the area were measured with a precision Jacob's staff and described to put the quarry in stratigraphic context. A cross section was generated from three high-resolution stratigraphic sections measured along the length of the quarry.

Awls, oyster knives, and dental picks were used to pry apart rocks, working from the top of the deposits down to the basal carbonate mudstone. Each rock was examined carefully with a hand lens as it was disaggregated to ensure that spatial data for all teeth, gastroliths, invertebrate fossils, and skeletal elements were documented as accurately as possible. The use of rock hammers was limited to splitting indurated rocks into pieces small enough to ensure that no small constituents were overlooked and to preserve the integrity of the location data. All elements were documented *in situ* before they were transported to the museum for final laboratory preparation.

All specimens in the quarry were initially mapped on grid paper using traditional methods. A meter grid was established, and each element was measured with a Brunton compass and tape measure and then drawn on a master map. Plan-view maps of the quarry were generated from a one-meter grid system marked off with string and compass. Digital photographs taken perpendicular to each grid were used to correct preliminary quarry maps and confirm the exact location of each element. The strike and dip of each specimen was measured with a Brunton compass.

A Nikon Total Station was used to collect *x-y-z* data on each element from reference points in the quarry. Precision for the Nikon Total Station is 5 mm to within 100 m of the datum. Location data for multiple reference points were calculated from one known datum to limit the introduction of systematic error. Two measurements were taken along the long axis of bones longer than 6 cm. Teeth and small fragments were documented as point data. All *x-y-z* data were entered into a database file and imported into ArcGIS ArcScene as vector data to create a three-dimensional map. A corrected map of the lower bone assemblage was generated using data from the three-dimensional map.

Thin sections of carbonate mudstone and mudstone units, bone material–matrix interface, and concretions found in the quarry were examined for pedogenic microfabric, microfossils, and other mineralogical characteristics. Samples of mudstones, carbonates, and nodules systematically collected every 5 cm throughout the sequence were analyzed with X-ray diffraction (XRD) to identify the composition of environmentally specific authigenic minerals and changes in clay composition that may indicate a change in environmental conditions. The less than 0.5 μm size fraction of the clay minerals was separated from samples by standard centrifugation methods. Clay samples were then saturated with 10% KCl and MgCl (Moore and Reynolds, 1997), mounted on glass slides using Drever's Millipore method (1973), and glycolated for two days. Randomly oriented powdered samples of nodules associated with bone material and clay samples were analyzed by powder XRD on a SCINTAG XDS 2000 with Cu Kα radiation. Scans were evaluated with methods described in Moore and Reynolds (1997).

All fossils for this study were accessioned into collections at the Wyoming Dinosaur Center (WDC), Thermopolis, Wyoming. Specimen numbers are given in figure captions.

STRATIGRAPHY AND SEDIMENTOLOGY

Outcrop Stratigraphy

Although deposits are laterally variable, stratigraphic sections exhibit three basic lithofacies associations (Fig. 1). Terminology used to describe sandstone bedding is from McKee and Weir (1953) and Boggs (1995). The lower 45 m are composed of interbedded quartz-rich, fine-grained sandstone and mudstone. The sandstone units are trough cross-stratified with few ripple cross laminations. Three meter-scale, white sandstone units at the top of this sequence show small-scale cross beds topped by ripple cross laminations separated by thin centimeter-scale shale layers.

The interbedded sandstone-mudstone facies is overlain by 12 m of interbedded carbonate mudstone and mudstone. Carbonate units thin and thicken, and in some places appear nodular, similar to palustrine-lacustrine strata described by Freytet and Plaziat (1982) and Wright and Platt (1995). Micritic concretions from 1 to 30 mm in diameter are well distributed throughout the mudstone. Up section, carbonate mudstone units thicken and mudstone units thin until reaching a 1-m-thick nodular unit. The interbedded carbonate mudstone–mudstone succession has a lenticular geometry, thinning to the north and south along the outcrop.

Eight nearly complete dinosaur skeletons have been discovered in the carbonate mudstone-mudstone facies. Most quarries yield well-preserved, articulated camarasaurid, apatosaurid, or diplodocid sauropod material. SI quarry is located approximately 12 m below the Morrison-Cloverly contact.

The top 3 m of the Morrison are composed of purple (5P4/2), clay-rich mudstone with greenish gray (5GY6/1–5GY4/1) mottles, overlain by approximately 1 m of organic-rich claystone. Dense globular concretions in the purple mudstone range in size from 2 to 24 cm in diameter. These concretions appear to be nucleated around organic material or are associated with large conical-shaped steinkerns. Topping the sequence is a structureless, black, organic-rich claystone.

High-Resolution Quarry Stratigraphy

Bone-bearing units vary in thickness from 30 to 80 cm vertically, with the thickest deposits near the middle of the quarry (Fig. 2). Although only two units are readily apparent, synthesis of geological, geochemical, and paleontological data revealed two additional layers.

Unit one is composed of a 40-cm-thick, heavily trampled, light gray (N6) carbonate mudstone (Fig. 2). Some tracks observed in cross section at the north end of the quarry extend to 20 to 40 cm into the carbonate mudstone. The matrix is dominantly Ca-Mg smectite with a minor component of bioclasts and volcanic airfall ash material including zircons, plagioclase, and minor amounts of olivine. Darker gray, clay-rich (5GY4/1) mudstone infills the lowest levels of undulations in the trampled surface.

Barite nodules are closely packed around bone material in unit one (Fig. 3A). No barite nodules have been found in any other units in the quarry or more than 1 cm away from bone elements. Overlying mudstone is compacted preferentially around the barite nodules, suggesting they formed in the sediments prior to significant burial. The nodules have a granular texture with sparry calcite in dilational fractures (Fig. 3B). Bone material in this unit is permineralized with calcite and shows no signs of stress from compaction (Fig. 3C).

Unit two is composed of a 20–50 cm greenish gray (5GY5/1) silty mudstone that is noncalcareous except for sparse micritic calcite nodules with poorly defined boundaries and micritic coatings on unidentifiable bone fragments (Fig. 2). Bone fragments 0.5–6 cm in size are larger at the base of the unit, becoming smaller and less well preserved toward the top of the unit. Poorly preserved bone fragments appear brecciated with sparry calcite infilling remnant cells. The micritic matrix fills pores between brecciated bone and collapsed cells (Fig. 3D). Minor dark gray clay intraclasts are found in the lower 6 cm of the unit. Vermiculite-illite mixed-layer clays dominate the mudstone. Desiccation cracks with associated slickensides extend to 5–10 cm above unit 1 (Fig. 3E). Vertical to subvertical burrows extend from the top of unit two near the southern end of the quarry (Fig. 3F).

Unit three is a trampled, light gray (N6) carbonate mudstone 10–20 cm in thickness (Fig. 2). Clay composition in this unit is dominantly Fe-rich smectite. One tridactyl track was found directly underneath an undulation in this unit at the top of unit two (Figs. 4A–4D). Darker greenish gray claystone (5GY4/1) occurs in carbonate mudstone that together infill the track (Fig. 4B). Loading was restricted to approximately 4 cm directly underneath the track, and disruption was limited to 6 cm laterally adjacent to the track (Fig. 4B). Pull-ups in this track (Fig. 4D) and morphology of the trampled carbonate mudstone (Figs. 4A and 4B) suggest that it was made when the carbonate mud and overlying clay sediments were saturated to the top of unit two. This track delineates a disconformable surface between unit two and unit three that would otherwise appear conformable. Black claystone (N2) 10-cm-thick infills unit three (unit 4; Fig. 2). Near undulations in unit three there is convoluted bedding. Some small stringers of siltstone occur across the quarry.

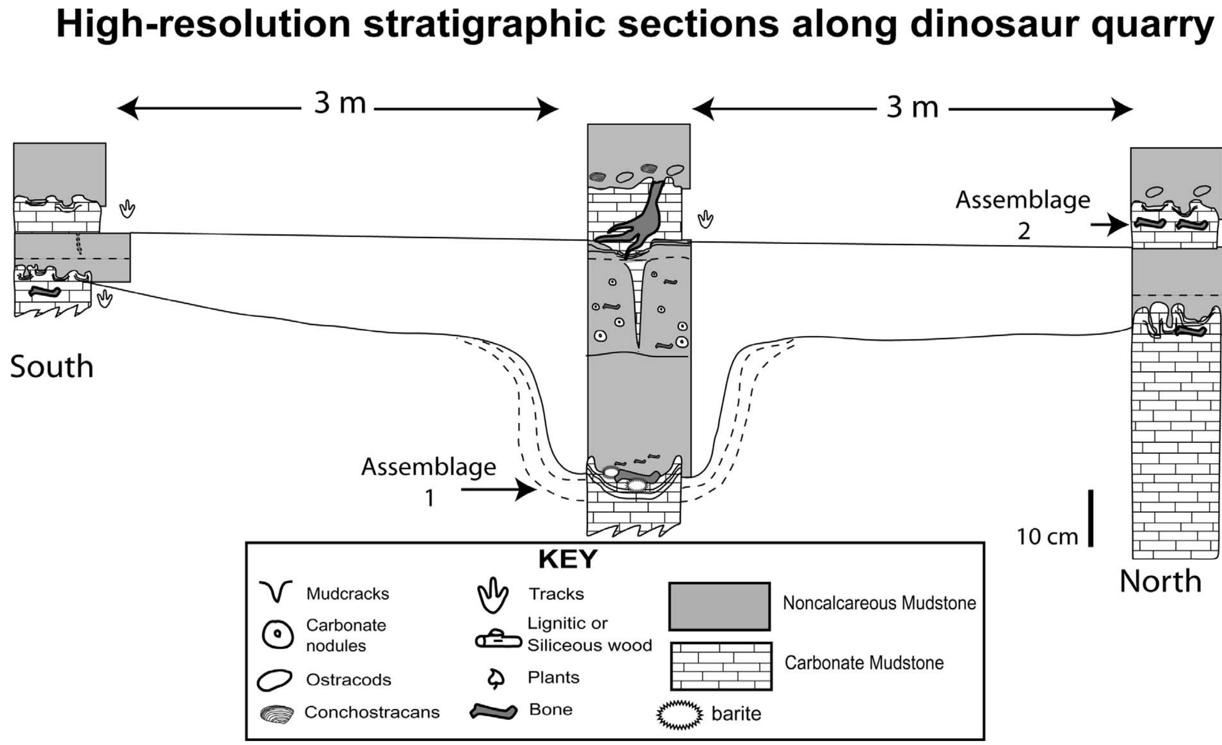

FIGURE 2—High-resolution stratigraphic sections along dinosaur quarry; units are numbered on the right; sections are vertically exaggerated.

PALEONTOLOGY

Invertebrate and Vertebrate Fossils

Thin sections of the basal carbonate mudstone show bioclasts of ostracodes, bivalves, and gastropods (Fig. 5A). Pockets of ostracodes and conchostracans were also found associated with convolute bedding in the upper claystone of unit four (Figs. 5B and 5C). No invertebrates have been documented in unit two, but occasional vertical to subvertical calcite-lined burrows are present in the upper 10 cm (Fig. 3F).

A total of 101 theropod teeth from 2 to 50 mm in length (Fig. 5D) was discovered in the quarry; 53 were removed during initial excavations and 48 were collected with associated spatial data. Vertebrae of three genera of sauropods were field identified as *Camarasaurus*, *Apatosaurus*, and *Diplodocus* during initial excavations. Sauropod material includes pes claws from 3 to 10 cm in length, rib fragments, one whole rib, caudal, sacral, and cervical vertebrae, pubic bones, scapulae, limb elements, and teeth complete with roots. Most of the sauropod material is disarticulated, but there are three distinct groups of articulated remains associated with theropod teeth. Specimens have been permineralized with calcite and show some variability in preservation. Bones found in carbonate mudstone show no indication of alteration from subaerial exposure in spite of trampling and tooth damage. Bone material excavated from unit two is fragmented, worn, and weathered.

The largest group of bones is located at the southwest end of the quarry in a depression in unit one (Fig. 6A). The morphology of closely associated caudal vertebrae and chevrons indicate that the specimen is a juvenile *Camarasaurus*. Although the bones are not articulated, there is a predictable anterior to posterior distribution of material with ilium, ischium, and caudal bones to the north, and rib fragments and skull material to the south. Twenty-three caudal vertebrae are distributed at the north end of this assemblage. No evidence of alteration from subaerial exposure of the bone material has been documented.

Two scapulae, a pubis, and half a humerus in the basal carbonate mudstone have V-shaped grooves along damaged edges where large pieces of bone are missing (Fig. 6B). The pubis is approximately 1 m to the south of the ilium and ischium bones. The scapulae were separated by 1.5 m. Sacral vertebrae were displaced nearly 2 m to the east of the ilium and ischium, and limb bones were scattered away from the main bone assemblage by 0.5–2 m. Also associated with the sacral vertebrae are several large fragments of a radius.

Most theropod teeth are within 3 cm of rib fragments and large bones, with the heaviest concentration between the pectoral and pelvic elements. Theropod tooth morphology and serration counts of 12 to 18 per 5 mm are consistent with allosaurid teeth (Farlow et al., 1991). The ratio of juvenile to adult theropod teeth is approximately 2:1. Thirteen juvenile *Camarasaurus* teeth were scattered among bones found in unit one. Most were lying directly on the carbonate mudstone surface.

Five caudal vertebrae were vertically impressed into the carbonate mudstone (Fig. 6C). Trampling in unit one ends abruptly in the middle of the assemblage around a definite depression where most of the rib material was found (Fig. 6A). Also associated with caudal vertebrae and broken ischium and ilium bones were 14 polished quartz clasts from 1 to 13 cm in diameter (Fig. 6D). All but three of these stones were suspended in the clay-rich mudstone immediately above unit one and were restricted to 0.025 m^3 of rock between caudal vertebrae and broken pelvic bones. These are interpreted as gastroliths.

Vertebrate Traces

Dinosaur tracks occur at three levels in unit one. Most tracks extend to 30–40 cm below the trampled surface (Fig. 7A), obliterating any discernible track morphology. The morphology of most shallow tracks is consistent with juvenile sauropod tracks (Lockley and Hunt, 1995). Bordering the caudal vertebrae at the northwest end of the quarry are at least five well-preserved pentadactyl tracks that crosscut the deeper tracks and extend only 13–15 cm into the carbonate mudstone. The best-preserved track is 35 cm wide $\times$ 41 cm long $\times$ 9 cm deep and is complete with five digits and a heel-pad impression (Fig. 7B). The carbonate mudstone is pushed up around the front of each of these tracks, indicating an east-west sense of movement. No clear trackway is apparent. In the middle of the quarry two sauropod tracks over 40 cm in diameter also crosscut the deeper tracks but extend only 5 centimeters into the carbonate mud-

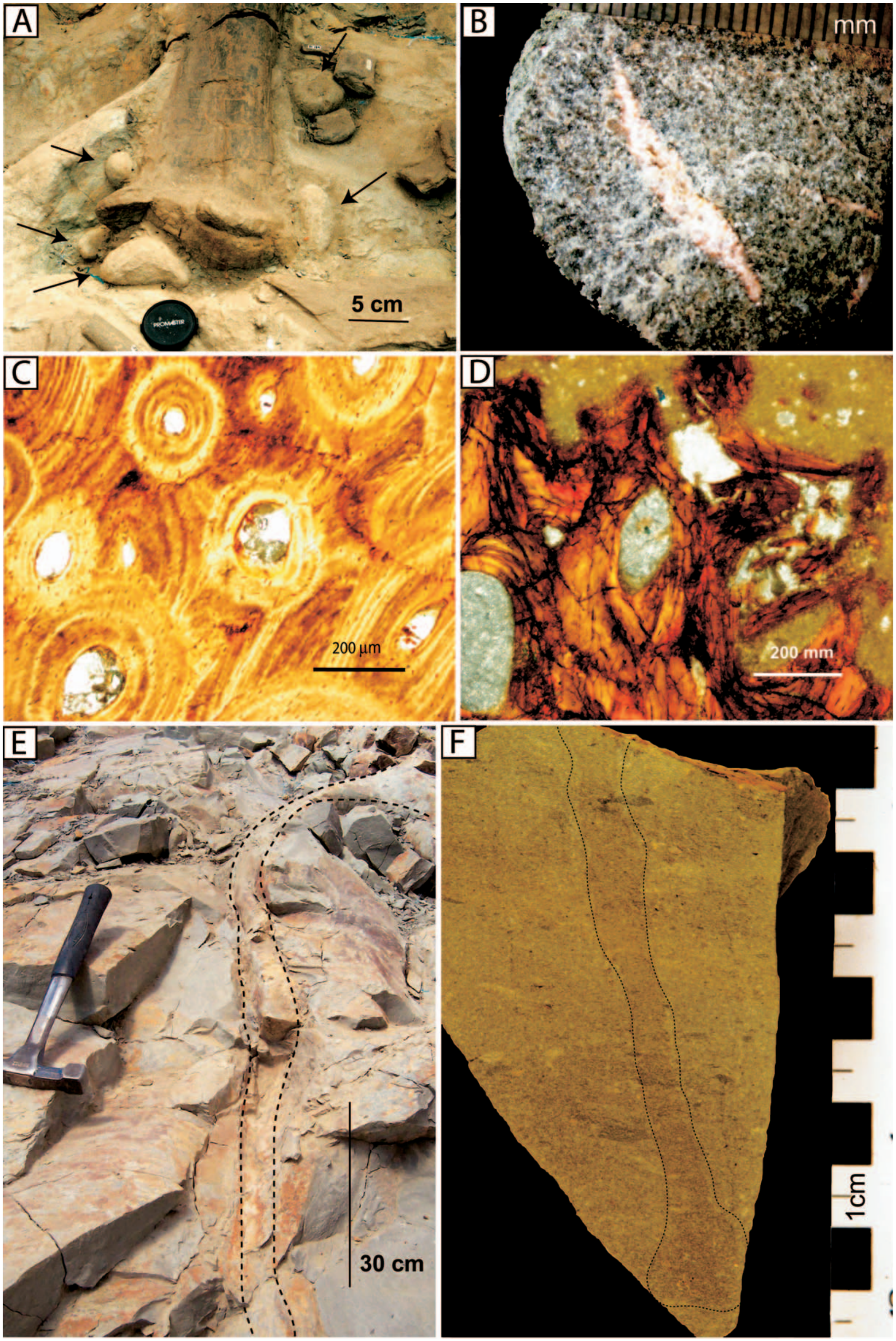

FIGURE 3—Features in two apparently homogeneous units. (A) Barite nodules formed around limb bones in unit 1. (B) Granular textured barite nodule with sparry calcite in center. (C) Permineralized bone from unit 1 showing no compaction features; cross-polarized light (XPL). (D) Weathered bone fragment in micritic carbonate from unit 2, XPL. (E) Desiccation crack (dashed lines) in unit 2. (F) Vertical burrow (dotted line) from unit 2.

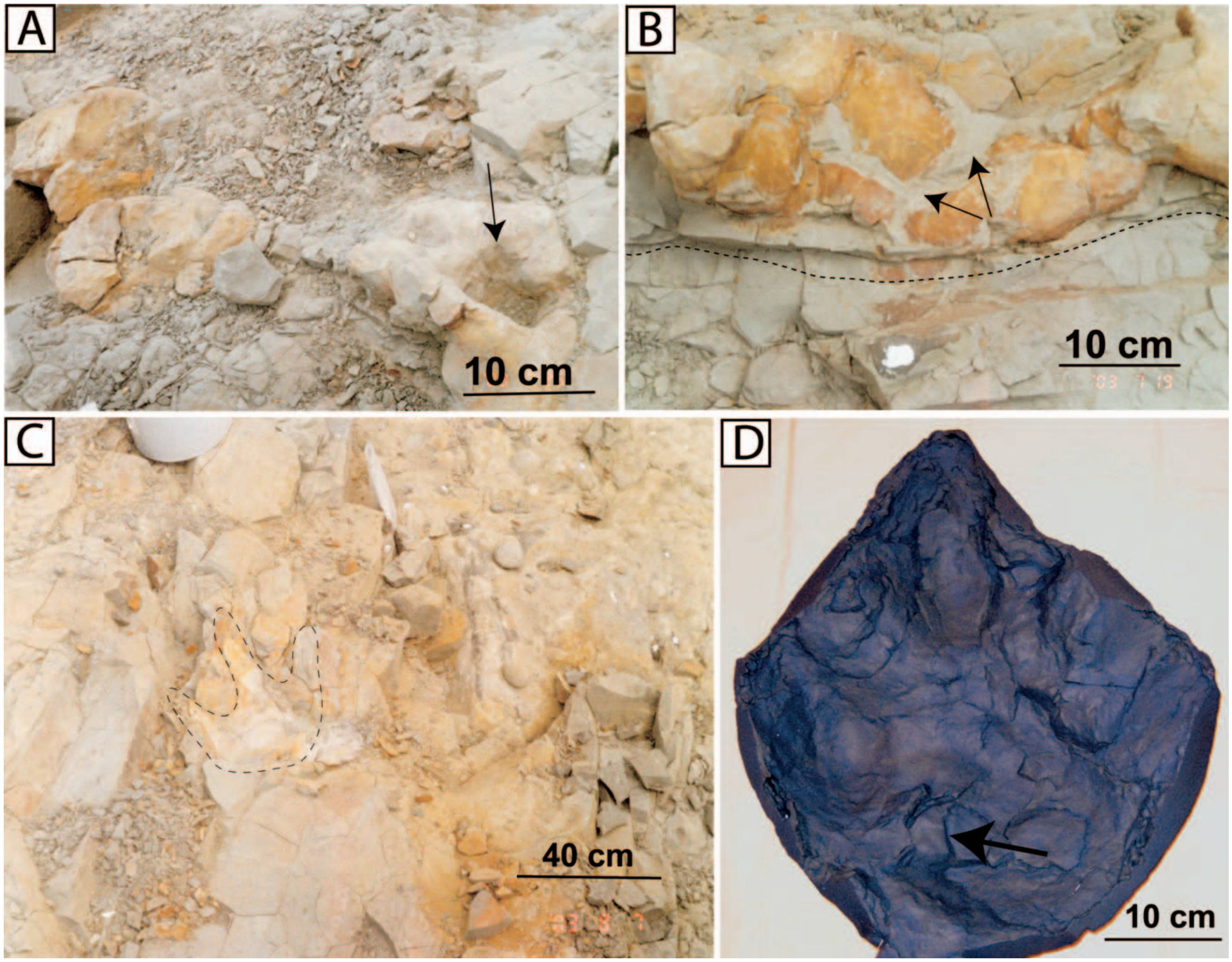

FIGURE 4—Identification of tracks in unit 3 sediments. (A) Unit 3 carbonate mudstone immediately above track. Note the collapse feature indicated by arrow. (B) Loading under carbonate mudstone. Claystone inside carbonate mudstone is shown by arrows. (C) Tridactyl track on unit 2 (dashed line) before casting. (D) Cast of tridactyl track from top of unit 2. Arrow indicates pullup; specimen WDC-SI-696.

stone (Fig. 7A). Two small, flattened, caudal vertebrae were found in the base of the tracks (Fig. 7A).

Isolated theropod tracks are found around the depression in the carbonate mudstone of unit one. At the south end of the depression in unit one, there is one distinct tridactyl track 62 cm long and 42 cm wide associated with fragments of skull material. Immediately adjacent to this track are three V-shaped grooves with claw impressions at one end (Figs. 7C and 7D). The grooves are approximately 5 cm wide and are infilled with dark gray claystone, becoming deeper toward the claw impressions. The total spread is 43 cm at midpoint, and there are about 20 cm between each groove at the widest end (Figs. 7C and 7D). Similar grooves flank the *Camarasaurus* remains on the east side of the depression. Claystone is impressed into these grooves and is much finer grained than in the overlying unit. One large groove correlates with a tooth-damaged humerus bone located at the south end of the quarry.

Spatial Distribution of Vertebrate Fossils

Three-dimensional maps generated with ArcGIS ArcScene show two distinct genetic assemblages of sauropod bones and associated theropod teeth (Fig. 8A). The lower assemblage is the most extensive, in which 25 theropod teeth are grouped in a depression with associated rib fragments and pectoral elements in unit one and the lower part of unit two. The assemblage thickens in the region of the depression and spans approximately 13 m laterally. Twelve theropod teeth are associated with the scapula and caudal vertebrae at either end. The relationship of bones, teeth, and gastroliths can be examined by rotating the three-dimensional map. A view of the highest concentration of bones and teeth indicates that the bone fragments, gastroliths, and theropod teeth are distributed within an area of less than 4.5 m^3 (Fig. 8B). Figure 9A is the map generated using traditional methods. Figure 9B shows the corrected map of only the lower bone assemblage produced from the three-dimensional data.

The second and smallest assemblage is in unit three, at the north end of the quarry. Fragmentary bones and theropod teeth are clustered along a 3 m line, trending in a general north-south direction (Fig. 8A). No large bones or vertebrae are associated with this assemblage.

DISCUSSION

Paleoenvironmental Interpretations

Ostracodes and conchostracans in the fine-grained mudstone and claystone of units one, three, and four indicate a shallow, neutral to alkaline lacustrine setting for the SI quarry (Lucas and Kirkland, 1998; Schudack et al., 1998; Stankiewicz et al., 1998). Modern ostracodes tolerate a wide range of water chemistry and fluctuating environments, but modern conchostracans prefer small, shallow, ephemeral water bodies that range in

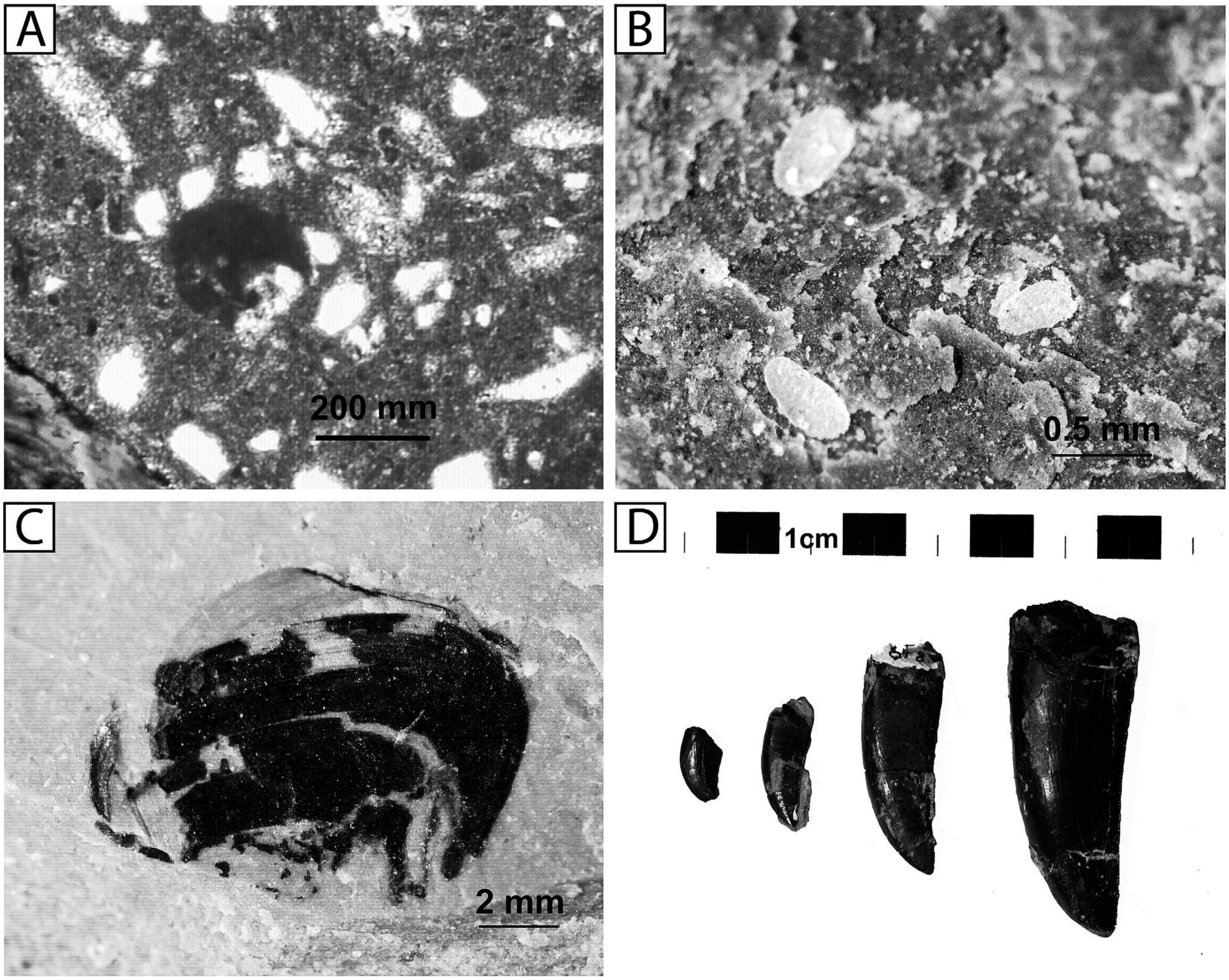

FIGURE 5—Fossils from units 1 and 4. (A) Bioclasts in unit 1; XPL. (B) Ostracodes in unit 4; specimen WDC-SI-837. (C) Conchostracan from unit 4, specimen WDC-SI-838. (D) Range of sizes of theropod teeth from SI quarry; left to right: WDC-SI-659, WDC-SI-698, WDC-SI-748, WDC-SI-754.

temperature from 4 to 30° C with a pH range of 7 to 9.7 (Frank, 1988). Based on comparison to modern analogues it is reasonable to expect that Morrison ostracodes and conchostracans likely indicate fluctuating water chemistry and alternating wet and dry conditions in transitional areas surrounding shallow-water environments. Although chitinous organisms such as conchostracans were once thought to be very delicate with a low preservation potential, Smith (2000) documented a larger preservation potential of chitin-producing organisms in palustrine-lacustrine deposits near ephemeral lakes.

Burrows and micritic calcite-coated bone fragments in unit two show that during regressive phases poorly developed paleosols formed in transitional areas as plants and animals moved into previously submerged areas (Freytet and Plaziat, 1982). Sporadic influx of surface water and slight fluctuations in groundwater resulted in shrink-swell features such as slickensides and deep desiccation cracks in sediments dominated by swelling clays (Freytet and Plaziat, 1982). Ca-Mg smectite in the palustrine carbonate mudstones suggests a higher alkalinity (Chamley, 1989; Hillier, 1995). Vermiculite-illite mixed-layer clays, often found in better-drained, poorly developed soils, indicate that smectite-rich sediments resulting from alteration of fine-grained volcanic ash continued to be modified in a marginal, alkaline, aqueous environment (Velde, 1995; Moore and Reynolds, 1997). Pedogenic processes, resulting in weathered and fragmented bones, modified bones previously buried in submerged sediments. Continued wetting and drying caused micritic calcite coatings of grains and larger clasts in unit two in a process similar to that described by Nahon (1991). Remnant cells of poorly preserved and weathered bone material infilled with sparry calcite in unit two suggest the bone fragments were permineralized and pedogenically reworked.

Barite concretions are not well documented in continental deposits, but similar concretions have been reported from modern deep-water marine sediments, and barite precipitation has been documented in a few alkaline-saline lakes (Lyons et al., 1994; Breheret and Brumsack, 2000; Smith et al., 2004). Barite precipitation is a process that almost always occurs in environments where separate barium-rich and sulfate-rich fluids converge (Hanor, 2000). Granular texture is associated with low-temperature precipitation of barite (Hanor, 2000). Brumsack (1986) suggested that low-temperature barite precipitation is closely associated with decaying organic matter. High concentrations of barium have been documented in clay-rich sediments of volcanically influenced wetland systems (Ashley and Driese, 2000). In this setting, the oxidation of thiol from residual decaying flesh of the juvenile *Camarasaurus* would have provided the necessary sulfate for barite precipitation around bones buried in shallow water.

Synthesis of geologic data indicates that the interlayered carbonate mudstone-mudstone units at SI quarry were deposited during alternating wet and dry conditions. Interlayered carbonate mudstone-mudstone units were deposited rapidly in marginal, shallow-water environments with shorelines fluctuating in response to alternating wet-dry episodes (Platt,

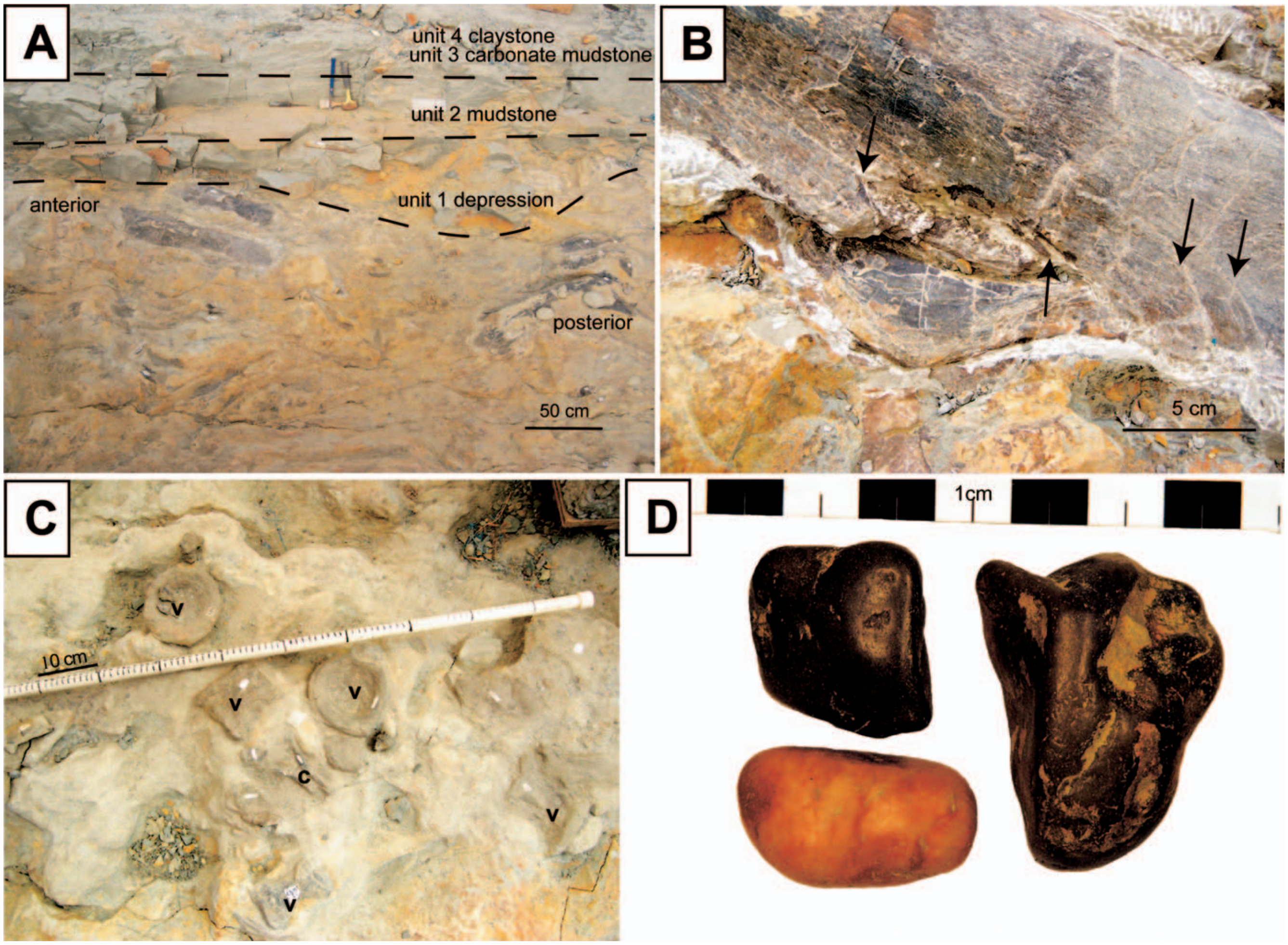

FIGURE 6—Tooth-damaged and trampled bones in unit 1. (A) Depression in unit 1 with scapulae and pubic bone. Unit contacts are indicated by dashed lines. (B) Tooth damage in the form of V-shaped grooves on scapula indicated by arrows. (C) Caudal vertebrae (v) vertically impressed into unit 1 with adjacent chevron (c) and other horizontal vertebrae. (D) Three presumed gastroliths found near pelvic girdle elements.

1989; Wright and Platt, 1995; Dunagan and Turner, 2004). During wet periods, submersion of low-lying areas allowed accumulation of carbonate mud and recolonization of freshwater invertebrates.

Taphonomy

Two distinct assemblages of sauropod bone material associated with high numbers of shed theropod teeth indicate that two feeding events occurred at distinctly different times. The upper assemblage is fragmentary and incomplete, but the close association of shed theropod teeth and bone material suggests that it was part of another feeding event. Unfortunately, it is likely that many elements from the upper assemblage were removed without corresponding spatial data during initial quarry work, making it impossible to document a scatter pattern from this level.

The lower assemblage reveals a high juvenile-adult ratio of allosaurid teeth associated with tooth-damaged juvenile *Camarasaurus* remains. Presuming a slow rate of theropod tooth replacement suggested by Farlow et al. (1991), this ratio likely corresponds to the number of individuals present at the time of the feeding event. Consequently, barring ontogenetic differences in tooth loss, the number of juvenile allosaurids appears to have been at least twice that of the number of adults.

Distribution of allosaurid teeth in unit one indicates that most of the feeding activity was centered in the anal and gastrointestinal regions of the sauropod, an area that would offer the easiest access to visceral elements (Weigelt, 1989). Scavengers and predators often begin feeding by rupturing the body cavity near the pelvic girdle (Weigelt, 1989; Wings, 2004). Associated large polished stones found suspended in clay-rich mudstone near the body cavity are difficult to explain in a sedimentary context. The velocity of flowing water necessary to move quartz clasts up to 3 cm in diameter is 200 cm/s in a low-gradient system, a velocity that would also move large sauropod bones and clay-size sediments (Reinck and Singh, 1980). Gastroliths are also scattered when a decaying carcass drifts in water currents (Wings, 2004). The preservation of gastroliths is highest in autochthonous skeletons buried in quiet, shallow-water settings (Wings, 2004). The most parsimonious explanation of such large clasts suspended in clay-rich mudstone in close association with pectoral and pelvic girdle elements is that these stones are gastroliths (Sanders et al., 2001; Wings, 2004).

The occurrence of 14 gastroliths clustered near pelvic elements suggests that the body cavity was protected from normal surficial degradational processes (Wings, 2004). The juvenile *Camarasaurus* carcass was partially submerged in less than a 1 m of water, preventing the gastroliths from being separated more than a few centimeters from the gastric area (Wings, 2004). Remains were subsequently buried in this shallow-water setting with no subaerial exposure.

Grooves around the body, interpreted as claw marks, suggest that overlying clay-rich sediments were pushed into the underlying cohesive substrate under saturated conditions. Orientation of claw marks along the edges of the pubic bone and scapula indicates that these elements were

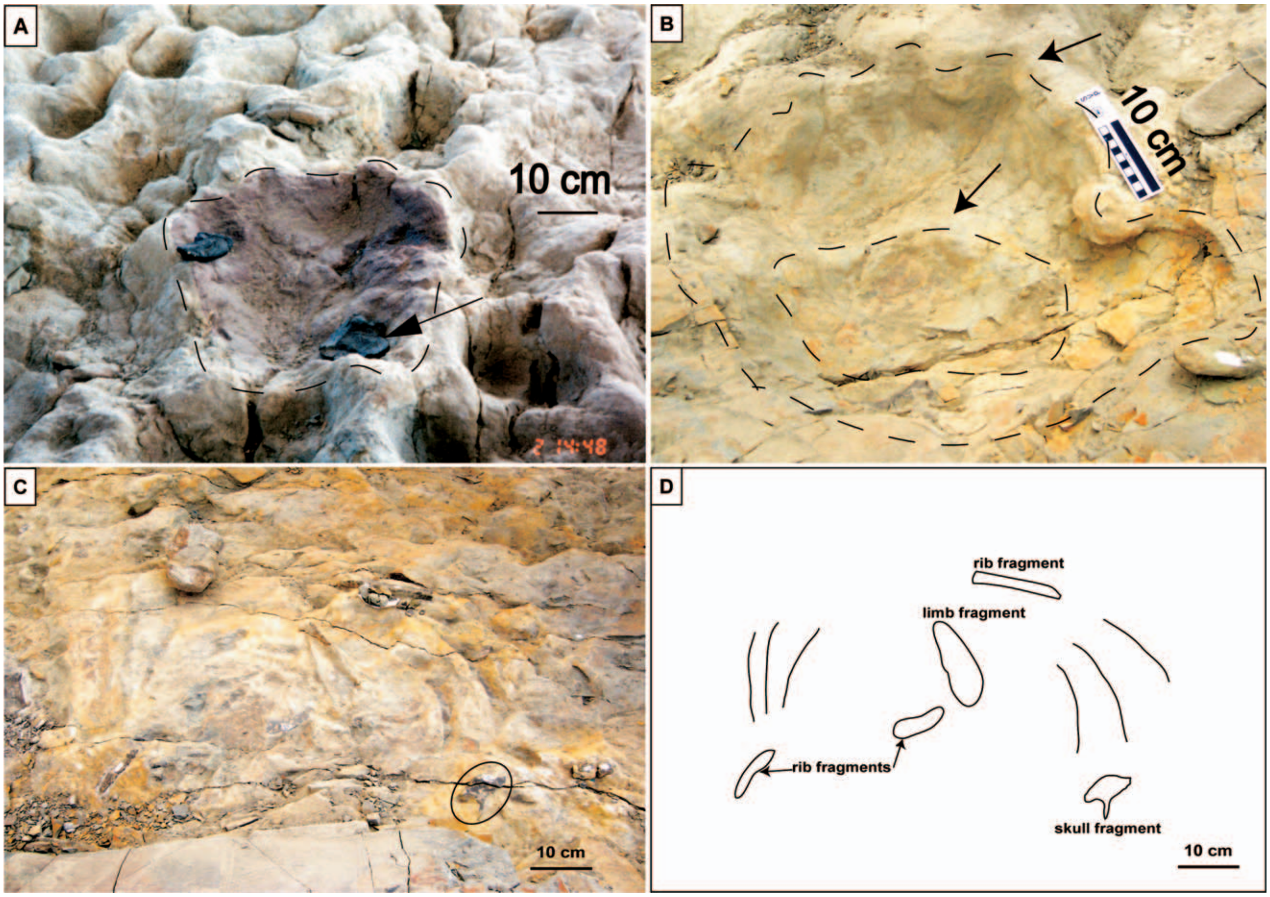

FIGURE 7—Bioturbation in unit 1. (A) Oblique view of a large track cutting across tracks that extend deeper into the trampled surface. Cast of small flattened caudal vertebrae in approximate original position in the track is indicated by arrow. (B) Juvenile sauropod track with heel-pad impression indicated by dashed lines. Arrows show pushups in direction of movement (east). (C) Tridactyl, clay-filled V-shaped grooves at south end of the depression in unit 1. Skull fragment is circled. (D) Diagram of V-shaped grooves and associated bones.

dislocated past one another during the feeding activity. Because large portions of the juvenile *Camarasaurus* were dislodged and removed from the central body elements, and caudal vertebrae were vertically trampled into the carbonate mud, the body may already have been in a state of decay when the allosaurids began feeding. The body of the juvenile sauropod lying in shallow water prevented trampling of the mud under the body but did not preclude trampling around the periphery. After the feeding event, remaining bones in shallow water were protected from weathering and were quickly buried and subsequently permineralized.

Tracks in the basal carbonate mudstone infilled with greenish gray mudstone are strikingly similar to tracks documented in palustrine-lacustrine deposits adjacent to alkaline lakes in Tanzania (Ashley and Liutkus, 2002). Multiple levels of tracks indicate a high-traffic nearshore area during a period of drying, followed by flooding that subsequently buried and preserved the tracks.

Synthesized data indicate that a juvenile *Camarasaurus* was scavenged in a nearshore, shallow, aqueous setting (Figs. 10A and 10B). Feeding activity was centered in the anal area and body cavity. Limb material was highly tooth-damaged and scattered away from the body, indicating a normal scatter pattern for feeding activity (Weigelt, 1989). There are not sufficient data to document how the juvenile *Camarasaurus* died, but because at least 40 percent of the individual is present and associated with gastroliths it is likely that it was not transported by the allosaurids that fed on it. The occurrence of gastroliths in clay-rich sediments and in close association with rib fragments suggests a relatively quiet-water system. Moderately alkaline water contributed to barite precipitation within a few centimeters of the sediment-water interface during microbial decay of residual flesh (Fig. 10C).

The feeding events were separated by enough time for a weak paleosol to develop (Fig. 10D). How much time is represented by this unit is indeterminable, but it is reasonable to suggest that it was enough to separate the feeding events by as much as a decade or more, judging from rates of weathering in modern soils (Birkeland, 1999). Subsequently, subaqueous conditions returned, allowing a second accumulation of trampled carbonate mud and bone assemblage (Fig. 10E).

CONCLUSIONS

As a result of this study previous hypotheses of recurrent allosaurid feeding events in a den or ambush activity are rejected. Geological and spatial data that restrict chronological association between the two assemblages indicate that although there were two feeding events at this location, recurrent feeding events by one group of individuals is not supported. Shallow-water conditions interpreted from the paleoenvironmental reconstruction of the quarry rule out the possibility that the area was the site of an allosaurid den. Indications that the *Camarasaurus* was already in later stages of decay before the allosaurids began feeding suggest that a scavenging event is more likely, rather than ambush predatory activity.

The abundance of well-preserved sauropod and theropod dinosaurs in the Morrison Formation contrasts with the paucity of documented feeding sites. This is likely a function of collection bias, inasmuch as most excavation foci have been on harvesting the fossils and not on collecting independent geologic and three-dimensional spatial data. Apparently homogeneous continental deposits also make it difficult to assess accurately the time averaging of such complex assemblages as feeding sites. Archaeologists have long recognized that collecting spatial data with the

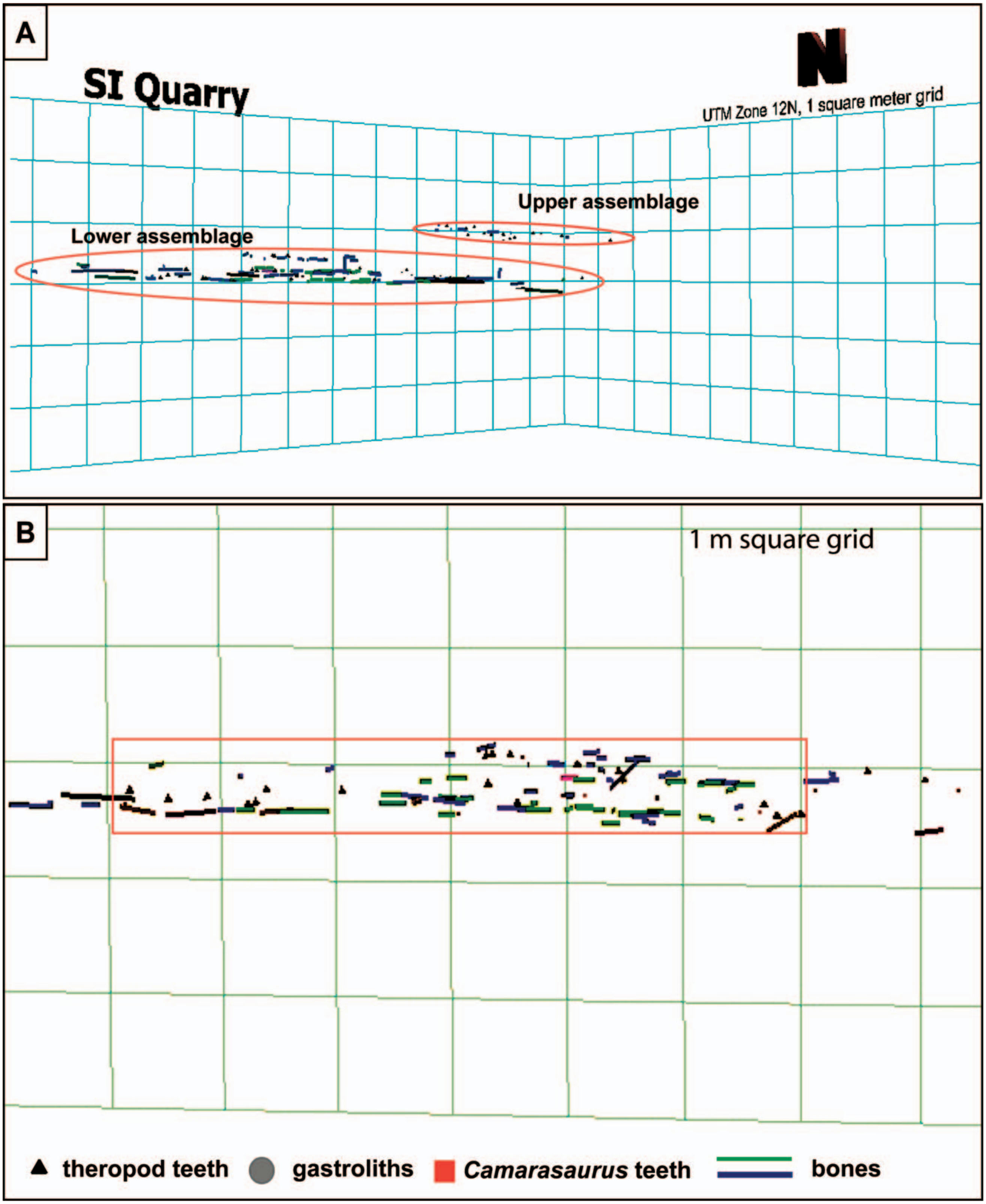

FIGURE 8—Three-dimensional maps of SI quarry. (A) Quarry map generated with ArcGIS ArcScene showing two distinct assemblages of sauropod bones and theropod teeth separated by 20–30 cm of sediments. (B) Distribution of bones and teeth in the lower assemblage. Note the close association of theropod teeth with bone material.

help of a Total Station provides increased precision of element-location data and have used this method to establish higher-resolution chronological constraints in excavations since the 1980s (Lock, 2003). The use of GIS allows paleontologists to do more accurate quantitative and semi-quantitative analyses of spatial relationships pertinent to taphonomic interpretations. Although the GIS analyses exemplified in this paper were a simple application that helped evaluate the distribution of bones and teeth in this quarry, more quantitative analyses can be conducted in the

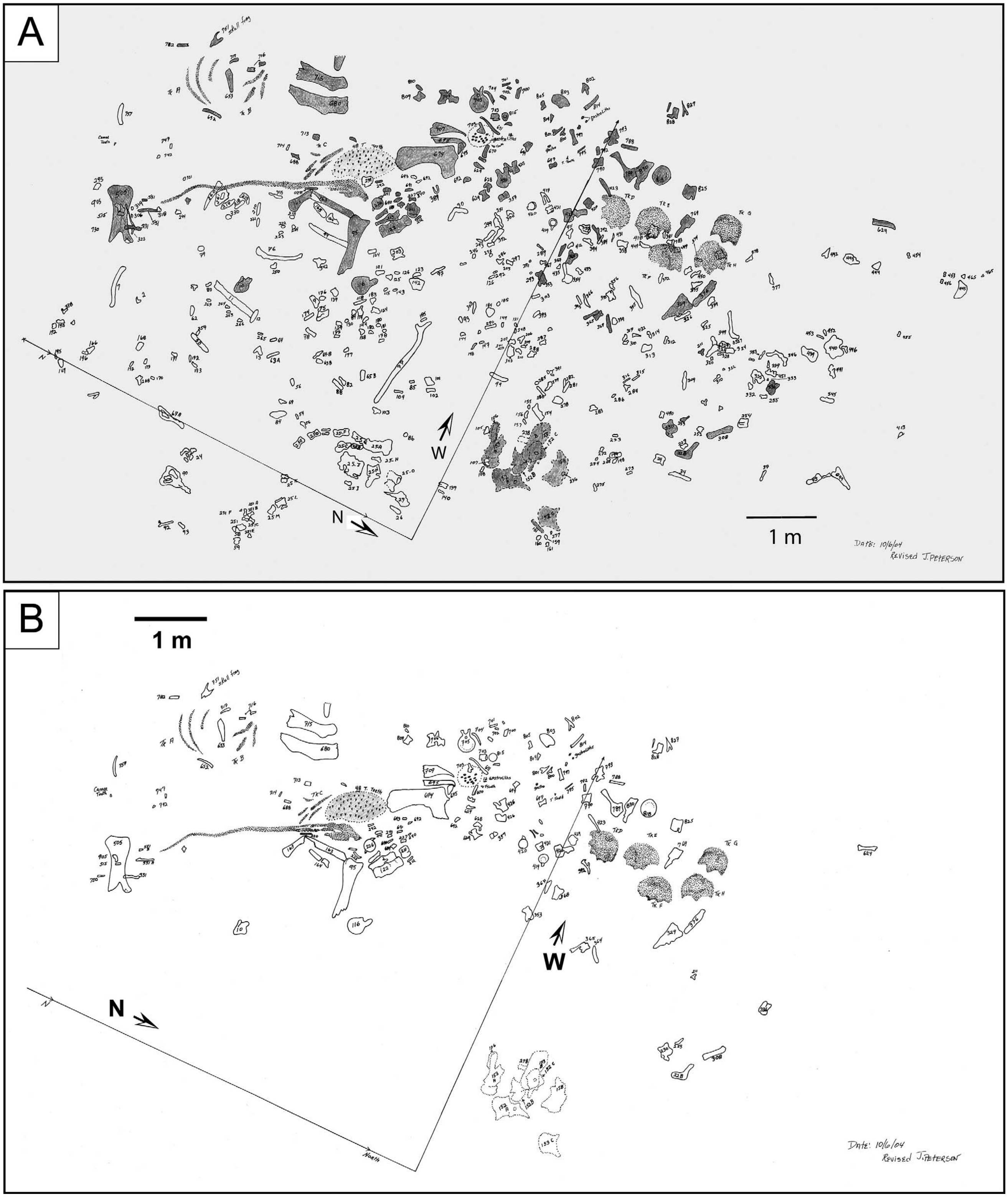

FIGURE 9—Plan-view quarry maps. (A) Original plan-view map. Elements left *in situ* are shaded. Tracks and V-shaped grooves are stippled (after Bighorn Basin Foundation map by Judy Peterson). (B) Corrected plan-view map of the lower juvenile *Camarasaurus* assemblage. Tracks and claw marks are stippled (modified from Bighorn Basin Foundation map by Judy Peterson).

future (e.g., comparative analyses of scatter patterns with those of modern predation sites). Results presented here show that GIS is a useful tool that permits paleontologists to assess time averaging of vertebrate assemblages, particularly those preserved in complex continental deposits.

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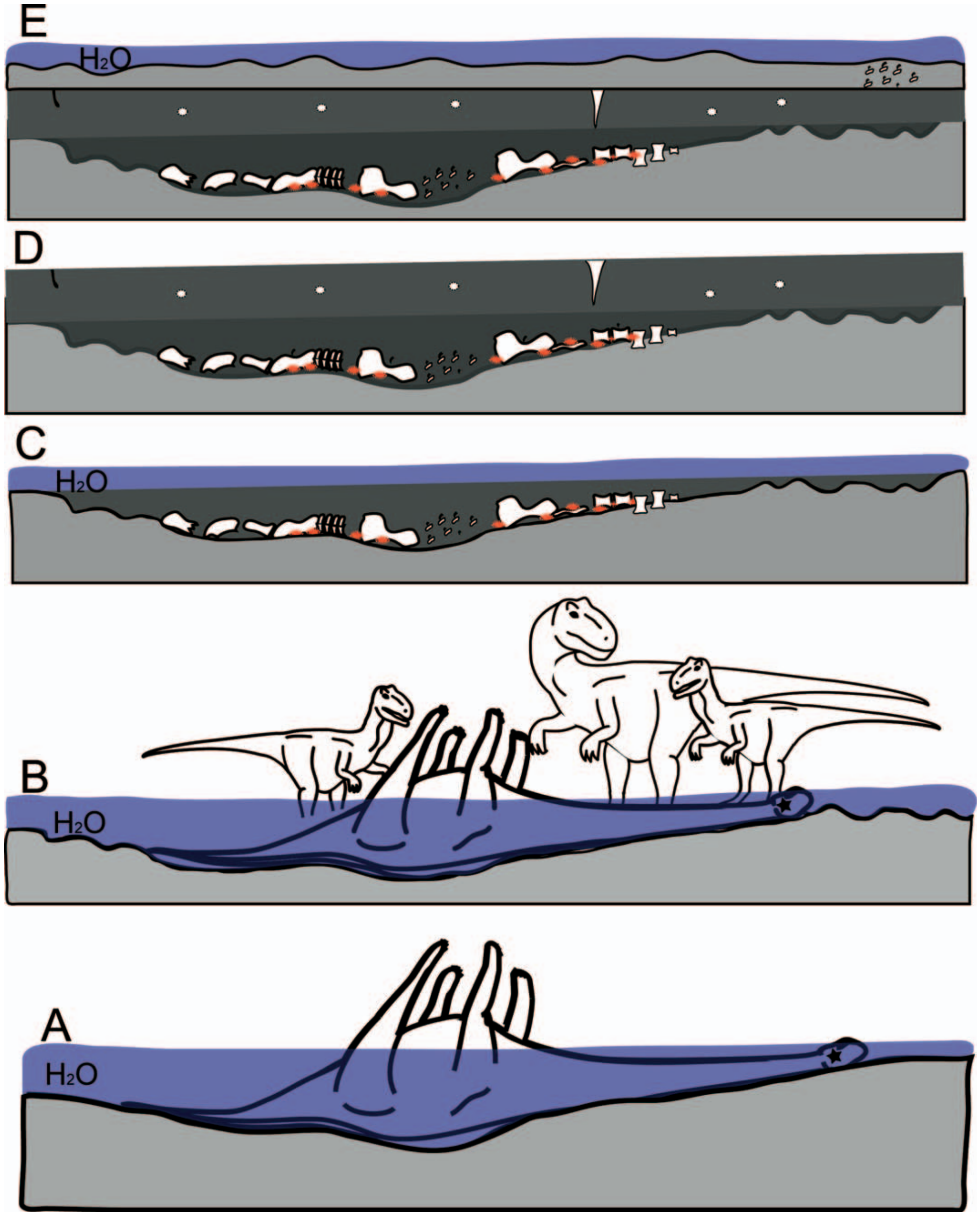

FIGURE 10—Sequence of events at SI quarry. (A) Dead juvenile *Camarasaurus* in shallow water. (B) Allosaurids scavenging the decaying carcass. (C) Burial after scavenging and subsequent barite precipitation (D) Weak paleosol development after regression of water. (E) Return of subaqueous conditions followed by the development of trampled carbonate mud and second theropod tooth-bone assemblage.

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