DINOSAUR DEATH PITS FROM THE JURASSIC OF CHINA

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ABSTRACT

Three newly discovered bonebeds from the Shishugou Formation of Xinjiang, China, are unusual in preserving vertically stacked and articulated to associated skeletons of at least 18 small, non-avian theropod dinosaurs in pits that are 1–2 m deep. The pits host a soft sediment-deformed mixture of alluvial and volcanic mudstone and sandstone. There is no evidence that the pits were discrete depressions in the topography that filled through time. Rather, they appear to have been highly localized areas of liquefaction caused by large-dinosaur (possibly sauropod) trampling of saturated sediments. Evidence indicates that the small theropods, and some other small vertebrates, became mired and died in these mud-filled pits. High quality skeletal preservation suggests that most individuals were buried within days to months after their deaths. Carcasses were buried successively, coming to rest above previously buried individuals. In some cases, skeletal body parts became separated or were removed, probably during scavenging. Given the large sizes of the pits relative to the small body sizes of the vertebrates contained within them, we conclude that small vertebrates (<3 m long and <1 m tall) were particularly susceptible to miring at these sites. Although the small, presumably herbivorous ceratosaur, *Limusaurus inextricabilis*, dominates the combined small theropod assemblage from these bonebeds (minimum number of individuals [MNI] = 15), there is no evidence that any biological features other than its small size and a large, and possibly, gregarious local population were responsible for its becoming mired in large numbers. A bias for small theropods in these bonebeds, compared to their relatively low abundance in the overall Shishugou Formation fauna, underscores that small theropods are underrepresented in Mesozoic fossil assemblages collected from other ancient alluvial and paludal settings.

INTRODUCTION

Studies of bonebeds provide opportunities to examine the interrelatedness of geologic processes and paleobiology and to integrate these data within a paleoecological framework (Behrensmeyer, 1991; Brinkman et al., 2007; Rogers and Kidwell, 2007; Varricchio et al., 2008). In particular, bonebeds dominated by one taxon or that exhibit unusual geological features may provide unique insights into the paleoecology and the physical nature of a depositional system not available otherwise (e.g., Currie, 2000; Eberth and Getty, 2005; Eberth et al., 2006; Qi et al., 2007; Varricchio et al., 2008).

The Middle to Upper Jurassic Shishugou Formation of Xinjiang, China, preserves a diverse continental vertebrate fauna (>35 taxa; Clark et al., 2006; Xu Xing and James M. Clark, personal observations, 2009), including at least 14 species of dinosaur. Our study of Shishugou Formation exposures and fossils in the Wucaiwan area (northeastern Junggar Basin, 2001–2006; Fig. 1) resulted in the collection of hundreds

of fossil vertebrates, including more than 100 dinosaur skeletons (Clark et al., 2006). Of particular interest was the discovery of three bonebeds (TBB2001, TBB2002, and TBB2005) dominated by the remains of small (≤3 m long; mass ≤100 kg), non-avian theropod dinosaurs—here referred to as small theropods. At least 18 individuals representing at least three genera of small theropods are present, and the combined assemblage is dominated by the remains of one taxon, *Limusaurus inextricabilis* (minimum number of individuals [MNI] = 15), a small herbivorous ceratosaur (Xu et al., 2009). In fossiliferous continental Mesozoic formations, well-preserved skeletons and other remains of small theropods are uncommon compared to those of ornithischians (cf. Currie and Russell, 2005), and bonebeds dominated by well-preserved skeletons of small theropods are rare (cf. Eberth et al., 2007).

The Wucaiwan bonebeds are also unusual in two other ways. First, partial to complete articulated skeletons of small theropods are positioned one above another, thus forming a vertical stack of interbedded skeletons and matrix. Secondly, the host matrix consists of a mixture of detrital and volcanic mudstone and minor sandstone that apparently experienced intense soft sediment deformation at about the time that the small theropods were interred.

Given these unusual compositional and preservational features, the Wucaiwan small theropod bonebeds represent a unique opportunity to (1) document an unusual preservational history of rarely preserved dinosaurs, and (2) assess aspects of the paleoecology and preservational biases for and against small theropods in the Shishugou Formation and other Mesozoic units.

Stacked skeletons that comprise TBB2001, TBB2002, and TBB2005 were removed from the field in columnar field blocks, jacketed by plaster and encased in wooden crates. The TBB2002 and TBB2005 blocks and all of the quarry sites were examined in the field. The TBB2002 and TBB2005 field blocks were further examined in the lab at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) facilities at Xiaotangshan near Beijing. Although the TBB2001 field block had been collected and its skeletons mostly prepared prior to the onset of this study, a silicone resin cast of that field block was available for study. Skeletons in the TBB2005 block were undergoing preparation during this study, and most were unavailable for taphonomic study.

Specimen numbers used here relate exclusively to vertebrate fossils in the collections of IVPP. Color values reported here were derived by use of the 1995 GSA Color Chart.

GEOLOGIC CONTEXT

Measured stratigraphic sections, sedimentological data, and previously published data (Eberth et al., 2001; Vincent and Allen, 2001) indicate that the Shishugou Formation was deposited along the northeastern edge of the internally drained, Mesozoic-age, Junggar foreland basin (Fig. 1). The formation is bounded above and below by unconformities and has been interpreted as a fining-coarsening upward
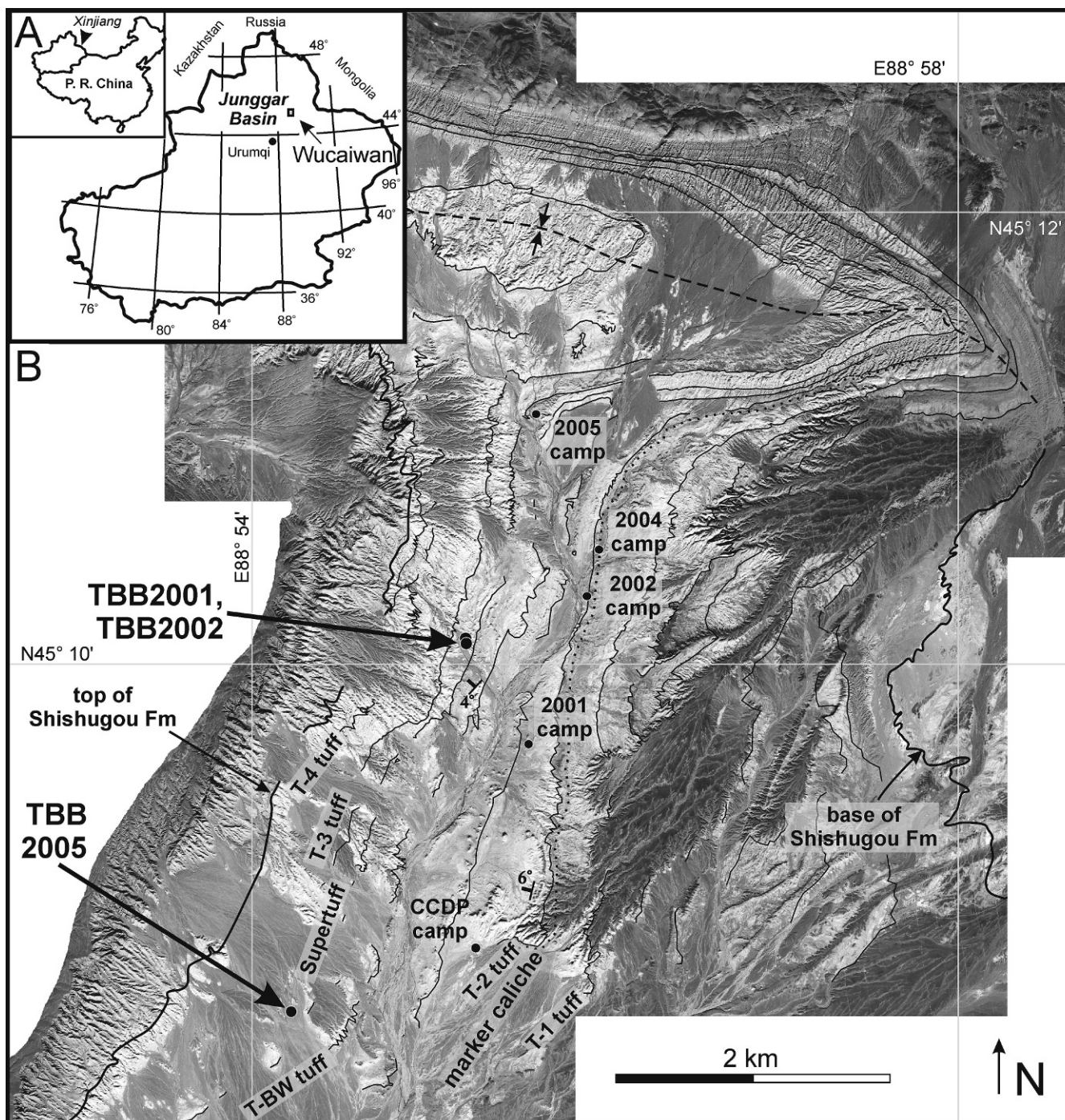
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FIGURE 1—Field area. A) Wucaiwan in the Junggar Basin, northwestern China. B) Quickbird satellite image of the Wucaiwan field area. Except in the northernmost part of the field area, beds dip west-northwest at <10°. Heavy lines = Shishugou Formation boundaries; light lines = marker tuffs (some labeled); dotted line = marker caliche; dashed line = axis of local syncline. Abbreviations: CCDP = China Canada Dinosaur Project; E = east; N = north.

megacycle, 350−400 m thick (Eberth et al., 2001; Fig. 2). The upper half of the Shishugou Formation, in which the bonebeds occur, is early Late Jurassic in age (Clark et al., 2006; Eberth et al., 2006), and was deposited under warm and seasonally dry climatic conditions (Fig. 2; Eberth et al., 2001, fig. 5).

Depositional environments of the upper Shishugou Formation include distal alluvial fans, straight to meandering stream channels, laterally extensive organic-rich wetlands and shallow lakes, and alluvial plains containing a variety of calcareous and noncalcareous paleosols (Fig. 2; Eberth et al., 2001, fig. 5, 2006; Vincent and Allen, 2001). Accommodation was generally high as indicated by a channel/overbank

facies ratio of approximately 0.5. Depositional gradients, alluvial flow volumes and rates, drainage conditions, and climate were variable due to tectonism (and volcanism) that occurred in response to accretionary tectonics throughout south-central Asia at this time and, possibly, retro-arc compressional deformation north of the southern continental margin (e.g., Vincent and Allen, 2001).

TBB2001 and TBB2002 are separated geographically from one another by 38 m and occur in the same mudstone bed, 283 m above the base of the 378-m-thick Shishugou Formation (Figs. 1−2). TBB2005 occurs 3 km south-southwest of TBB2001 and TBB2002 and ~6.5 m higher in section (Figs. 1−2).
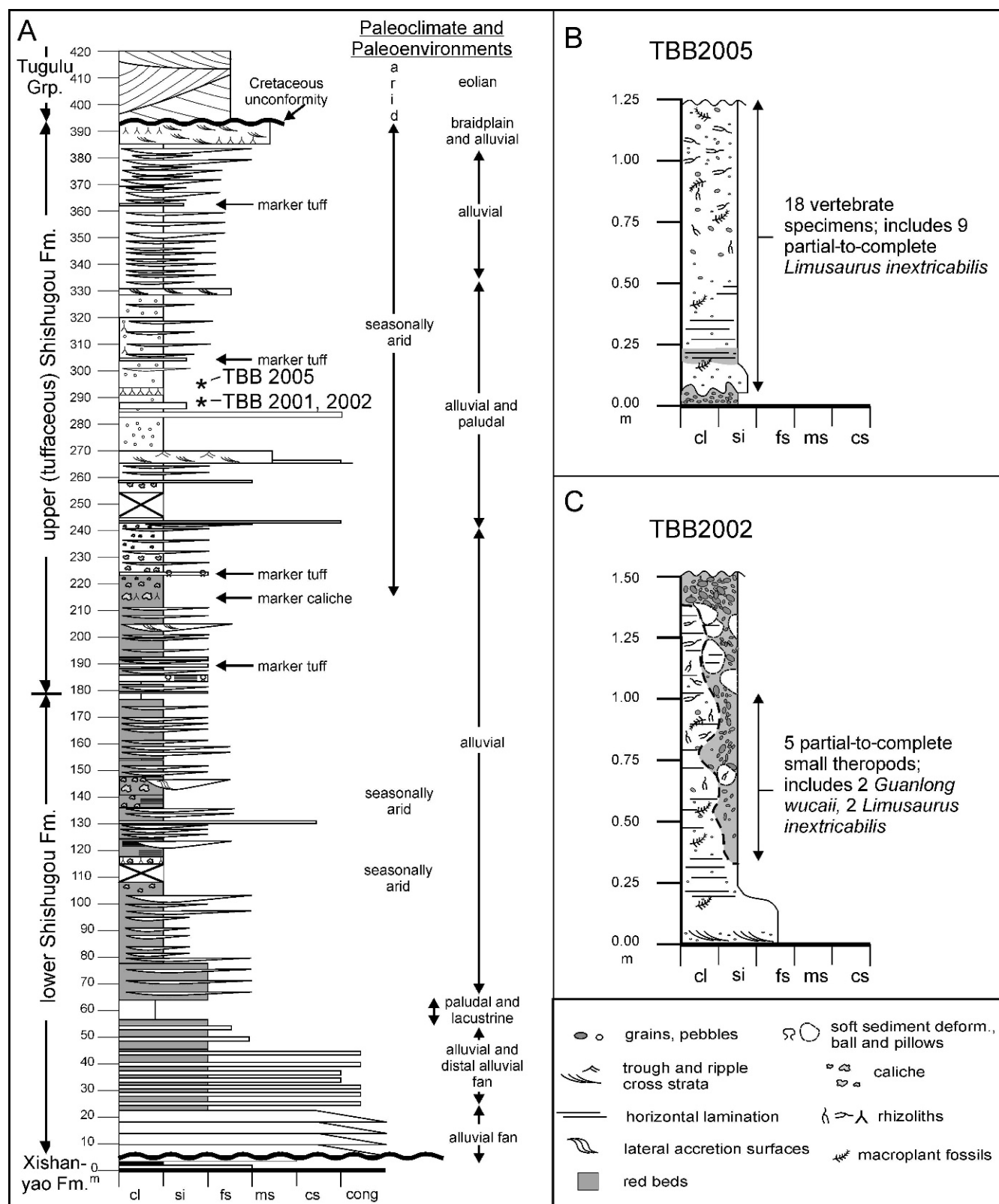
FIGURE 2—Stratigraphic data from Wucaiwan. A) Composite stratigraphic section of the Shishugou Formation. B) Measured section at TBB2005. C) Measured section at TBB2002. Abbreviations: cl = claystone; si = siltstone; fs = fine-grained sandstone; ms = medium-grained sandstone; cs = coarse-grained sandstone; cong = conglomerate.
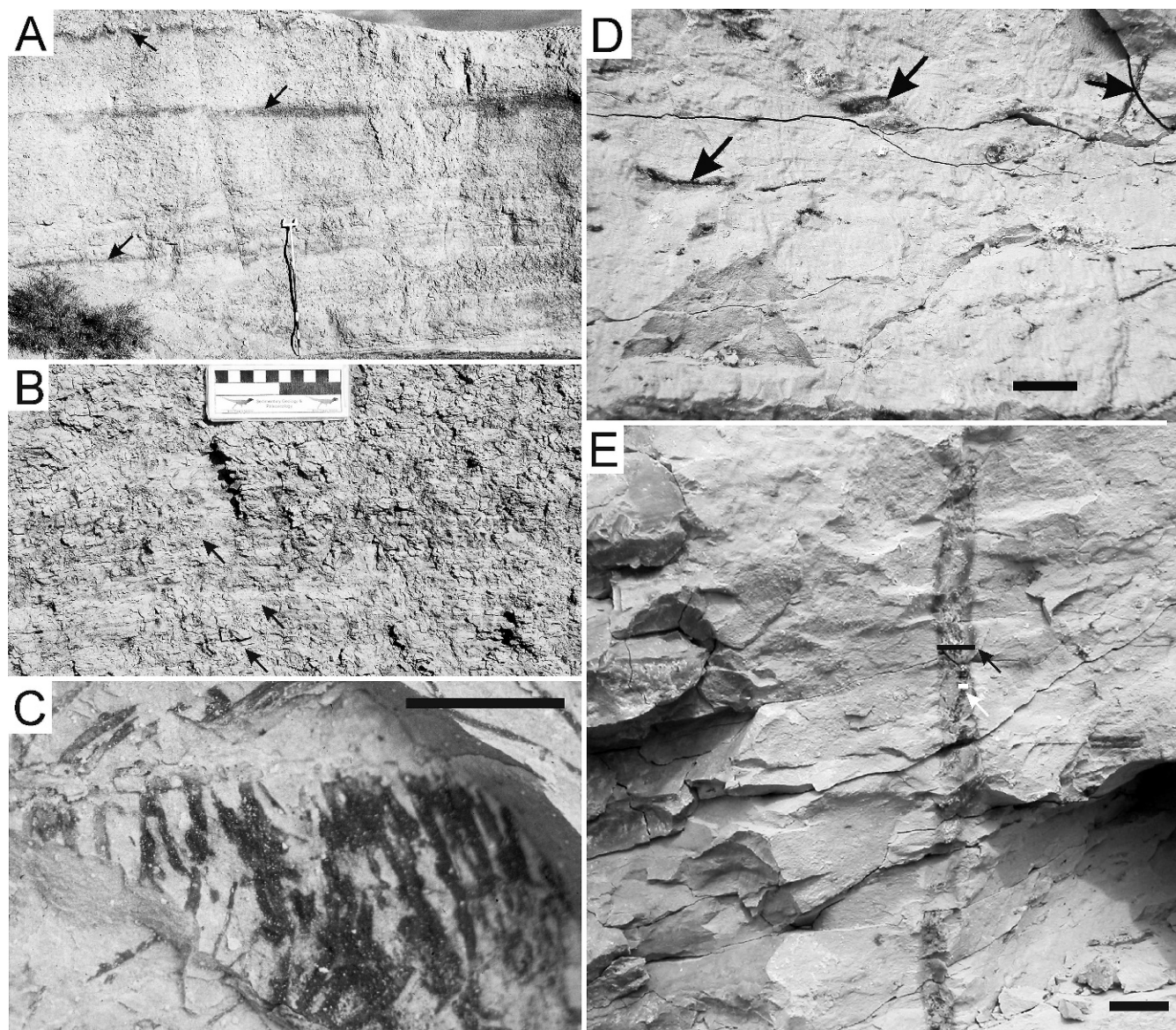
FIGURE 3—Geologic and paleontologic features of the tuffaceous mudstone facies that host the bonebeds. A) Stacked succession of four tuffaceous mudstones separated by red (pedogenic) mudstones (arrows). Jacobs Staff 1.5 m. B) Weakly expressed laminae (arrows) in a typical outcrop of tuffaceous mudstone. Scale bar = 10 cm. C) Coalified gymnosperm twig. Scale bar = 1 cm. D) Weakly laminated tuffaceous mudstone (adjacent to TBB2005) exhibiting vertically to horizontally oriented, simple rhizoliths (arrows) and dispersed plant fragments (black specks). Scale bar = 1 cm. E) Well-developed vertical rhizolith (white bar and arrow) with reaction halo (black bar and arrow). Scale bar = 1 cm.

SEDIMENTOLOGY

Host Beds

The beds that host the bonebeds can be traced for hundreds of meters to kilometers. Throughout the field area they exhibit flat-based, tabular geometries, rest sharply to gradationally on variegated red-grey to grey sandy siltstone and sandstone, and are typically overlain by massive, mottled red-tan-grey mudstones (Fig. 3A) that contain small rhizoliths and appear to be weakly developed paleosols (Retallack, 1990). With the notable exception of the bonebed sites themselves, the host beds consist mostly of laminated mudstone successions that are 0.5−2.0 m thick and pale colored (Fig. 3A; 5YR 7/2; 10YR 7/4). Laminations indicate subtle variations in sediment grain size, and range from silty claystone (darker color tones) to siltstone and very fine-grained sandstone (lighter color tones; Fig. 3B). Laminations are laterally continuous with even thicknesses, but thicknesses vary unpredictably between laminae. Fragments of chemically replaced (nonorganic)

gymnosperm leaves and twigs (Fig. 3C) and small (mm-scale) horizontal to vertical rhizoliths are present in varying abundance in different levels in the host beds (Fig. 3D−E), but generally increase in abundance upward through each deposit (Fig. 2B). Rhizoliths occur as tapering, nonorganic casts with dark-brown to black rims and red-brown chemical-reaction halos.

The mudstone bed that hosts both TBB2001 and TBB2002 passes laterally 140 m to the northeast and 2 km to the southwest into a prominent, white-tan colored, silty to sandy, volcanic ash that serves as one of the stratigraphic markers (Super Tuff; Fig. 1). Clinoptilolite is the dominant clay in this volcanic ash (>60% by weight; Table 1), and wave-ripple cross laminae are common in the sandier horizons of the deposit south of all of the bonebed localities.

Bonebeds

At TBB2001 and TBB2002, the host mudstone gradationally overlies a laterally extensive, 25-cm-thick, fine-grained, grey sandstone

TABLE 1—XRD analyses from Wucaiwan.

Clays (wt)	TBB2001	(%)	TBB2002	(%)	TBB2005	(%)	TBB2005; variegated seds at base	(%)	Supertuff marker tuff, south	(%)	Non-tuffaceous fossil locality (2004 theropod)	(%)
Kaolinite	0.02	0.0	0.03	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
Illite	0.73	0.8	0.70	0.7	0.70	0.7	0.39	0.4	0.17	0.2	0.27	0.3
Smectite	0.15	0.2	0.19	0.2	0.17	0.2	0.42	0.4	0.15	0.2	0.62	0.7
Clinoptilolite	0.06	0.1	0.03	0.0	0.08	0.1	0.15	0.2	0.59	0.6	0.00	0.0
Totals	0.96	1.0	0.95	1.0	0.95	1.0	0.96	1.0	0.91	1.0	0.89	1.0

(Fig. 2B−C). Adjacent to both sites, the host mudstone is overlain by a mottled red-pink (5R 7/4 and 5R 6/6) cm- to dm-thick mudstone bed. In contrast, the host mudstone at TBB2005 (Fig. 2B) sharply overlies a 25-cm-thick, variegated and gently deformed variegated succession of red-grey sandy mudstone and siltstone. Adjacent to TBB2005, the bed that overlies the host mudstone appears to be compositionally similar to the host mudstone but also exhibits a patchy, red iron-oxide stain.

At TBB2001 and TBB2005, the matrix that surrounds the specimens consists of tan-colored, massive silty and sandy claystone (5YR 7/2; 10YR 8/2, respectively) that is locally mottled with a light red stain. It contains numerous plant fragments and simple rhizoliths (Fig. 4) and exhibits soft-sediment deformed laminae, with rare, dispersed, small, red-to-pink and brown mudstone grains, especially in association with the skeletons.

Laminae are sharply truncated or soft-sediment deformed and disrupted decimeters lateral to the TBB2002 specimens (Fig. 5). The boundary between undeformed and truncated to deformed laminae ranges from vague to sharp, depending to a large extent on the juxtaposed colors of the sediment. Sediment deformation and sharp truncation at TBB2002 demarcate an irregularly shaped, 2.0 m wide and 1.5 m deep pitlike structure. In a few patches preserved along the back wall of the quarry site, horizontal laminae are sharply truncated, and the boundary of the pit in these limited areas is traceable as a convoluted surface rather than a smooth and regular slope (Fig. 5A−B). The pit hosts the skeletons, as well as a chaotic mixture of tan and red (5R 6/6 to 10R 6/6) mudstone (Fig. 5C−D). The red mudstone is continuous with and sourced from overlying red strata (Fig. 5C).

We infer the presence of similarly sized, but more poorly defined pits at TBB2001 and TBB2005 based on (1) the presence of highly localized soft-sediment deformation, and (2) the rare dispersed mudstone intraclasts surrounding the vertically stacked specimens. The spatial extent of each bonebed pit (1–2 m wide and 1–1.5 m deep) is, thus, ultimately defined by the extent of the skeletal assemblage, the horizontal and vertical limits of soft-sediment deformation and sharply disrupted laminae, and the vertical and horizontal distribution of dispersed mudstone intraclasts (Fig. 2C; Table 2).

Within the confines of the bonebed pit at TBB2002, the soft-sediment deformed, tan-colored host mudstone is preserved as irregularly shaped masses, discrete ball-and-pillow structures, and rounded to angular mudstone fragments (Fig. 5C). In contrast, the red mudstone is preserved as a vertically extensive, homogenous to diffuse mass that decreases in abundance down-section (rbr in Fig. 5C). This red mudstone also consists of a breccia of very poorly sorted, dark to light red (10R 8/2 to 10R 7/4; Fig. 5D) mudstone clasts (0.5 mm−3.0 cm in diameter) that are variously rounded and shaped (angular to well rounded; irregular to spherical). A few of these breccia clasts contain small rhizoliths.

Thin sections of hand samples and XRD analyses (Table 1) of clay smears from the bonebed matrix at all three bonebeds reveal fresh volcanic phenocrysts (quartz, sanidine, plagioclase, biotite) and altered volcanic glass (clinoptilolite [3%−16% by weight]), all mixed with nonvolcanic detritus (a variety of light minerals, rock fragments), as well as illite (40%−76% by weight) and smectite (16%−44% by weight).

Interpretation of the Host Beds, Excluding the Bonebeds

Laterally extensive, tabular mudstones consisting of horizontal laminae indicate that, in general, the host beds were deposited in settings where sediments aggraded vertically in standing water or on a saturated media. The predominance of drab sediments, dispersed organic fragments and the presence of small, horizontal to vertical rhizoliths at the top of the host successions also suggest consistent deposition in a saturated marshlike setting (Cohen, 1982). The presence of a decimeter-thick, mottled red to pink pedogenic mudstone on the top of the host bed in the vicinity of TBB2001 and TBB2002 suggests long term or episodic subaerial emergence of this upper portion of the mudstone succession after the host bed was deposited. We suggest that emergence was accompanied by development of a weakly rooted, playa-like crust and the precipitation of iron oxides (cf. Freytet and Plaziat, 1982; Mader, 1985; Platt, 1989; Retallack, 1990).

The presence of volcanic minerals and clays in these deposits indicates that this wetland setting was frequently blanketed by volcanic ash, but that the volcanics became mixed to varying degrees with other detrital sands and muds, probably due to dinosaur bioturbation and reworking. Thick deposits of volcanic ash elsewhere in the field area and the presence of small rhizoliths suggest that deposition, mixing, and rooting of the volcanic muds took place rapidly (e.g., months to a few years; Fisher and Schmincke, 1984). The lateral continuity of the host mudstones that merge to the south with volcanic ash deposits rich in clinoptilolite and wave ripples suggests that marshes passed laterally into saline, standing bodies of water (lakes and ponds; Collinson and Thompson, 1989; Stamatakis et al., 1996).

Interpretation of the Bonebed Host Sediment

Occurrences of soft-sediment deformation and disrupted laminae adjacent to and around the skeletons in each bonebed indicate that the host mud was fluid to plastic to brittle as the skeletons were interred (Lowe, 1975). The occurrence of red mudstone with intraclasts, some containing small rhizoliths, sourced from overlying strata is evidence that parts of a cohesive overlying redbed crust collapsed downward into underlying mud (especially at TBB2002). The pitlike areas of collapse and mixing were highly localized, but deep, suggesting that they resulted from highly focused downward loading. At TBB2002, some areas at the margin of the pit are sharply delineated from adjacent laminated sediments (Fig. 5A−B), indicating that, adjacent to the pit, strata may not have been homogeneously saturated and susceptible to soft-sediment deformation or did not experience the same type or degree of loading.

We reject an interpretation that these pits are load casts or sand volcanoes caused by differential-density loading of sediment layers (cf. Collinson and Thompson, 1989). The fills are not composed of sand or a sediment of appreciably different density from the host muds; some
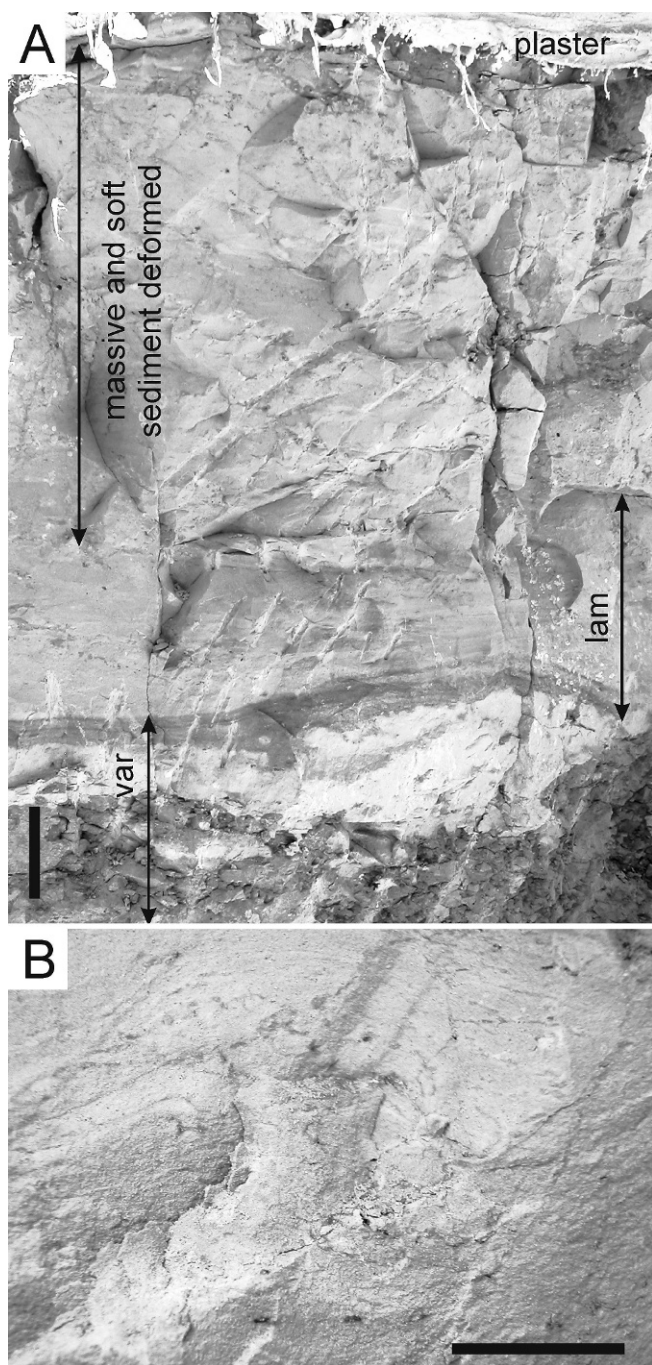
FIGURE 4—TBB2005 host rock. A) Field photograph of rock encasing the skeletons at TBB2005 (see Fig. 2B). Abbreviations: lam = weak laminations in lower portion of tuffaceous mudstone; var = variegated red and grey deposits. Note parts of the plaster field jacket at the top of the block. Scale bar = 10 cm. B) Close-up of soft-sediment-deformed laminae in the upper half of A.

laminations in the host mudstone exhibit sharp, vertical truncations uncharacteristic of differential density loading, and there is no evidence of the underlying mudstones being injected upward (cf. Reineck and Singh, 1980; Nadon, 1993, 2001; Platt and Hasiotis, 2006). Similarly, we reject an interpretation that these sites were sinkholes that formed due to some sort of natural collapse of the media or were at any time empty spaces or pits within the host mud (e.g., karstlike), because there is: (1) abundant evidence of soft-sediment deformation within the host sediments (e.g., ball and pillow structures); (2) no basal breccia; (3) matrix-supported clasts sourced from overlying strata at all sites; (4) an upward increase in breccia float at TBB2002; and (5) a regular

arrangement of articulated skeletons (see below). Sinkhole and karst accumulations of sediment and vertebrates are far more chaotic and are very often associated with disarticulated skeletal remains (e.g., Agenbroad, 1984; Pratt, 1989; Farlow et al., 2000).

We interpret the pits as large-scale but low fidelity tracks of large dinosaurs based on the following: (1) ubiquity of similar, well- to poorly defined load structures of varying size (but without fossils) in a variety of facies (alluvial sandstone and mudstone, and volcanic ash deposits) in the upper Shishugou Formation (Fig. 6); (2) consistent size of the pits (~2.0 m wide and 1.0−2.0 m deep); (3) presence of at least two locations in our field area where load structures appear as a linear trackway (Fig. 6B−C); and (4) abundant skeletal evidence for multi-ton dinosaurs in the Shishugou Formation that were large enough to trample saturated mud deeply without becoming mired.

Given the large size of these bonebed pits, it is highly unlikely that the theropods contained within them—the largest vertebrates preserved in the pits—were responsible for the full depth and extent of the loading events that created the pits. The largest individual (*Guanlong wucaii*, V14531; Xu et al., 2006) would have stood just 66 cm tall (hip height) with a foot size of 73 cm^2 and a mass of <40 kg (Donald M. Henderson, personal communication, 2006, based on Xu et al., 2006). Instead, we consider it more reasonable that larger dinosaurs were responsible for making these tracks. Although we cannot assign a tracemaker taxon to these features with any certainty, giant sauropods are reasonable candidates given that their fossil remains are present in the Shishugou Formation at Wucaiwan, and *Mamenchisaurus sinocanadorum* (Russell and Zheng, 1993; mass >20,000 kg; limb lengths >3 m), is known from the Shishugou Formation at Jiangjunmiao, 100 km to the southeast (and presumably at Wucaiwan). Sauropod tracks are common in continental Jurassic and Cretaceous strata, but most are shallower and better defined than those described here (Lockley et al., 2002; Platt and Hasiotis, 2006).

The variable expression of the boundaries of the bonebed pits and other nonfossiliferous sauropod tracks—some portions of the boundaries are sharp and easily demarcated, whereas others are vague and indefinite—suggest local variation in media rheology and response to loading (e.g., Platt and Hasiotis, 2006). Such variation, however, also raises the possibility that the history and complexity of subsequent media disturbances was highly variable from site to site (e.g., trampling by scavengers).

VERTEBRATE PRESERVATION

A detailed description of vertebrate composition and preservation in all three of the theropod bonebeds is presented in Supplementary Data[1]. Here we present only those compositional and preservational features that bear directly on our taphonomic interpretations.

At least three taxa of small theropod, represented by five skeletons, are present in TBB2002 (Fig. 7A−G). These include the toothed carnivore *Guanlong wucaii* (Xu et al., 2006; MNI = 2; V15302, V14531), an edentulous ceratosaur with gastroliths and nonraptorial forelimbs (*Limusaurus inextricabilis*; Xu and Clark, 2006; Xu et al., 2009; MNI = 2; V15303, V15304), and a third, unidentified taxon that is neither tyrannosauroid nor ceratosaur (MNI = 1; V15302). All the specimens in TBB2001 (Table 2; Fig. 7H) appear to be *Limusaurus inextricabilis* (MNI = 4; V15297, V15298, V15299, V15300, V15301). TBB2005 includes remains of at least nine *Limusaurus inextricabilis*, which is the only small theropod at that site (specimen numbers mostly unavailable at the time of writing; see Supplementary Data[1]). TBB2005 is unique among these three bonebeds, however, in also preserving the tail of a small ornithischian dinosaur and skeletons or skeletal parts of eight specimens of small nondinosaurians (two small crocodyliforms, two small mammals, a turtle, and three tritylodonts).
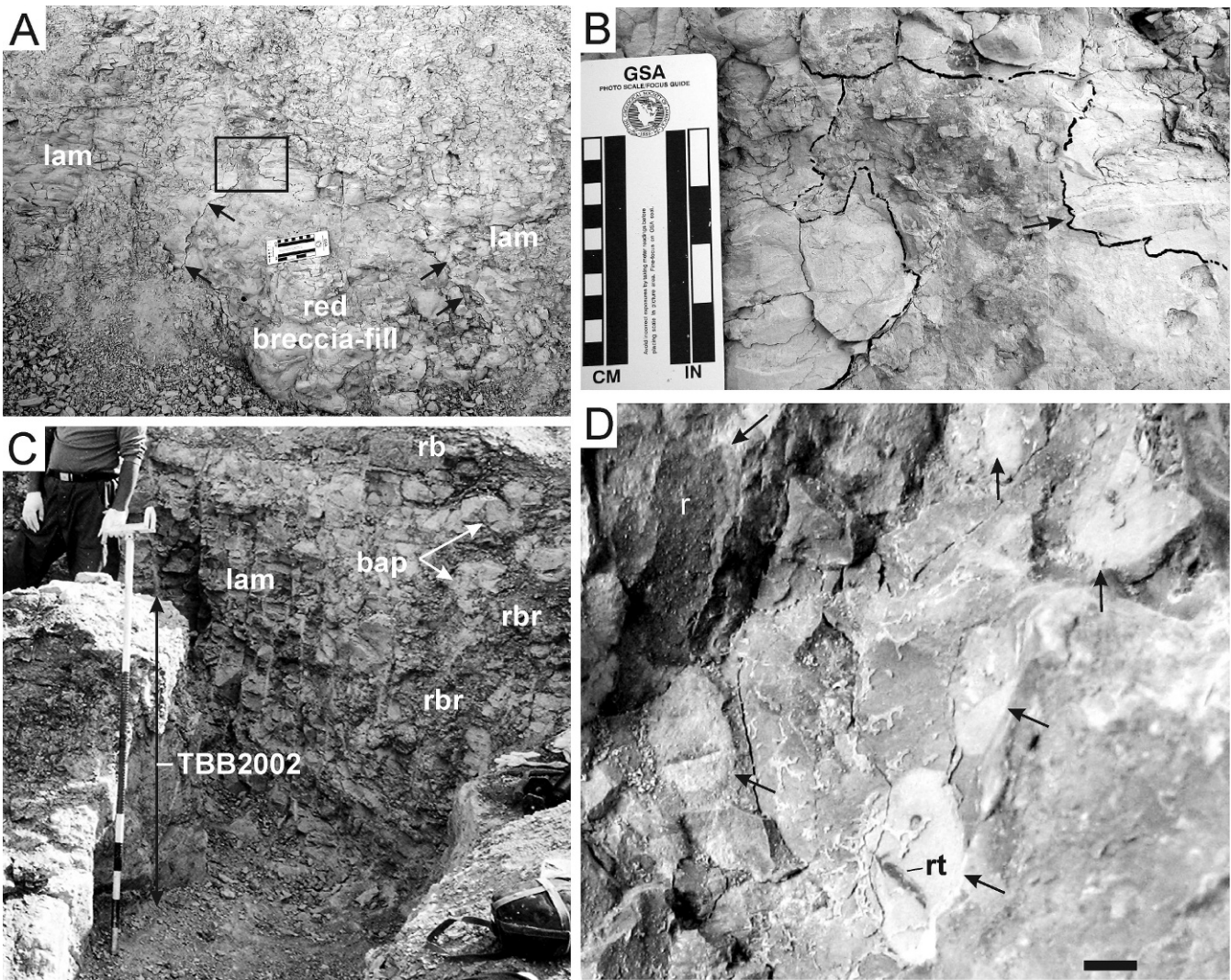
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[1] www.paleo.ku.edu/palaios

FIGURE 5—TBB2002 host rock and fossiliferous pit fill. A) Back wall of the quarry. Localized pit margins were drawn on the rock with a black marking pen (arrows). Pit fill is labeled red breccia fill; lam = adjacent laminated and tuffaceous host bed. Scale bar = 10 cm. B) Close-up of square in A; note well-defined pit margins and sharp truncation of adjacent laminae (arrow). C) TBB2002 field block (foreground left) and back wall of quarry showing: ball-and-pillow structures of tuffaceous host bed (bap); undisrupted portions of tuffaceous host bed (lam); red mudstone and breccia fill (rbr); and bounding red (pedogenic) mudstone (rb). Jacobs Staff = 1.5 m. D) Close-up of breccia clasts in the pit fill; note rounded, angular, and irregular shapes, variety of tones (dark and light), and rhizolith (rt). Scale bar = 1 cm.

Skeletal completeness is variable within and between each site (see Supplementary Data[1]). At least one half of the small theropod specimens are preserved as complete skeletons or appear to have been complete prior to erosion. The partial skeletons at both TBB2001 and TBB2002 are missing discrete body parts (skulls, limbs, tails) or are represented by a single body part. For example, V15302 (TBB 2002) is missing its skull, whereas V15298 (TBB2001) is represented by only an articulated pes. At both TBB2001 and TBB2002, there is better representation of hindquarters (dorsal vertebrae, hips, hind limbs, and tails) relative to skulls, necks, and forelimbs. Teeth are preserved in the jaws in the toothed forms (e.g., *Guanlong* and most of the nondinosaurs from TBB2005).

In both TBB2001 and TBB2002, skeletons are vertically stacked (Fig. 7F−H). Viewed in plan view, however, each site shows varying amounts of skeletal overlap. For example, at TBB2001, V15299 and V15297 face in opposite directions with only their tails overlapping

TABLE 2—Bonebed dimensions and taxonomic compositions.

Bonebed	Pit width (m)	Pit depth (m)	Fossil distribution (horizontal; m)	Fossil distribution (vertical; m)	Taxon and minimum number of individuals (MNI)
TBB2001	unknown*	unknown*	1.0	0.4	*Limusaurus inextricabilis* (4)
TBB2002	2.0	1.5	1.0	0.7	*Guanlong wucaii* (2); *Limusaurus inextricabilis* (2); undescribed small theropod (1)
TBB2005	unknown*	unknown*	1.5	0.9	*Limusaurus inextricabilis* (9); ornithischian dinosaur tail (1); crocodyliform (2); tritylodont (3); mammal (2); turtle (1)

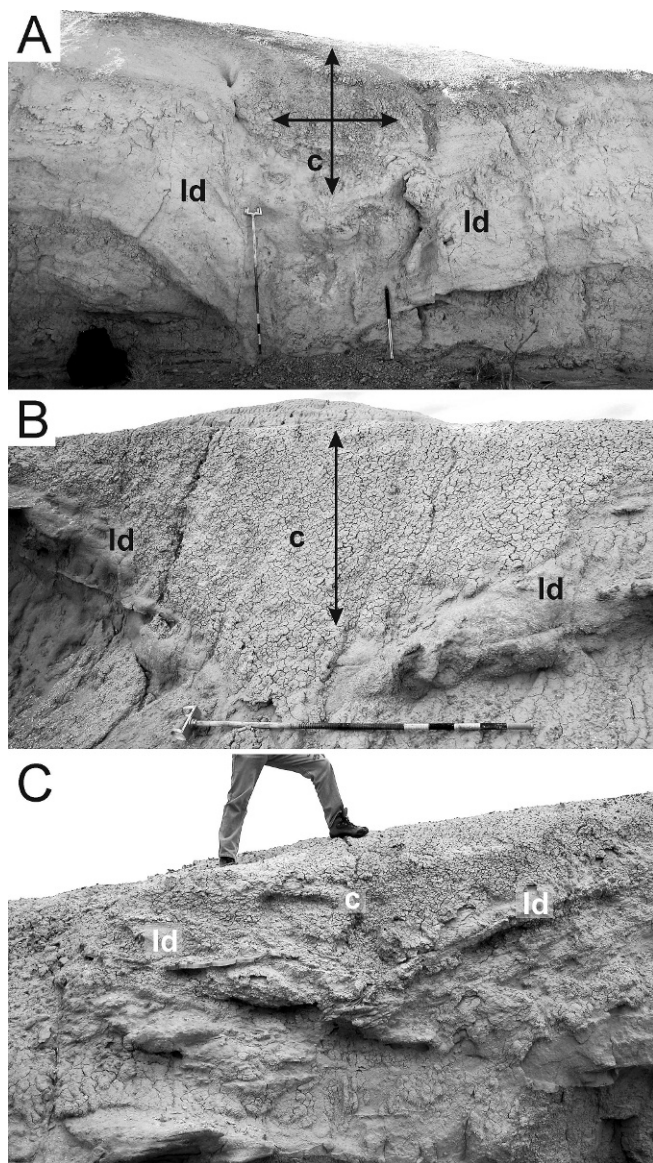* no observable features clearly demarcating the physical limits of the pit.

FIGURE 6—Three load structures interpreted as sauropod tracks and associated deformed strata in tuffaceous mudstone and sandstone in the upper Shishugou Formation at Wucaiwan. A) Load structure and associated sediments exhibiting: (1) a zone of load-deformed strata (ld; undertrack) that remained intact as it was pushed down into underlying muds; and (2) a central zone (c) of highly disrupted and contorted tuffaceous mudstone and sandstone that marks the relatively limited extent (arrows) of direct trampling. Jacobs Staff = 1.5 m. B−C) Two associated load structures (trackway) and associated deformed strata that occur in the same horizon, ~10 m apart (abbreviations in A). Note the extremely variable degree and extent of sediment disruption in each track. Depth of loading decreases from A to C.

(Fig. 7H), and V15301 was found to the side of the stacked skeletons (not shown here). In contrast, there is very little offset in the stacked assemblage of small theropods at TBB2002 (Fig. 7A−G).

Bone-on-bone contacts are common in overlapping skeletal parts within individuals. No bone-on-bone contacts were identified, however, between superposed skeletons, or the skeletal parts of different individuals. Where measurements could be made, superposed skeletons are separated from one another by 5−20 cm of matrix.

At all three sites, specimens lie mostly on their sides, but a few (e.g., V15303; Fig. 7D) lie on their backs or undersides relative to the horizontal. Although most specimens are preserved with their skeletal long axes parallel and subparallel to the horizontal, there are important exceptions: V15298 (an articulated pes) is preserved vertically (Fig. 7H), and V15302 (a skeleton in the middle of the TBB2002 stack)

is preserved with both its neck and tail extending vertically upward from its horizontally oriented trunk (Fig. 7C, F−G).

The degree of limb flexion is variable within and between specimens (Fig. 7). Some (e.g., V14532, V15297) exhibit highly flexed hind limbs folded close to the body. Others exhibit hind limbs flexed partially (V14531, V15304) or not at all (V15302, V15301). In a few specimens, articulated tails, necks, and limbs are sharply dislocated or flexed. For example, in V15302 the distal one half of the tail is twisted 90° from the horizontal, extends upward for 15 cm beside two overlying skeletons, and then is twisted 90° back into the horizontal adjacent to V14531, at the top of the block (Fig. 7A, F−G). A 90° dislocation in the horizontal plane is also present in the neck of V14532 (Fig. 7B), and V15301 exhibits a dorsally flexed tail and neck (not shown here).

Varying but minor degrees of skeletal element drift are present, especially in shoulder and pelvic girdles, and distal limb elements. Concentrated patches of gastroliths are present in the gut region anterior to the pubes in *Limusaurus* specimens V15304 and V15297 (Fig. 7E, H).

Skeletal preservation data from TBB2005 are more limited. The holotype of *Limusaurus inextricabilis* (V15923) is nearly complete and was preserved lying on its right side, subparallel to the horizontal. Like many specimens from TBB2001 and TBB2002, it exhibits highly flexed hind limbs and shows evidence of minor element drift in its hips, tail, and forelimbs. It, too, has a patch of small gastroliths preserved in its gut region. An almost complete skeleton of a small, crocodyliform reptile lying on its stomach is positioned adjacent and parallel to V15923.

In every specimen, bone surfaces are unmodified and show no direct evidence of erosion, weathering, etching, scratching, or biogenic alteration due to scavenging. There are no shed carnivorous dinosaur teeth at any of the sites.

Taphonomic Interpretations

The taxonomic diversity, vertical stacking of carcasses (and bones), and the presence of matrix-filled gaps between stacked skeletons at each site indicate that the fossil assemblages in these pits are time averaged, consisting of specimens that were added one at a time and not as a group during a short-term mass death event (cf. Schwartz and Gillette, 1994; Varricchio et al., 2008). Consistent stacking and skeletal overlap (in plan view) of the theropod carcasses indicates that the pits were of a consistent diameter and depth to concentrate sequentially interred skeletons into stacks. In each case, the pits had diameters (1−2 m) that were less than the length of the largest animals buried within them (adult *Guanlong wucaii*, 3 m long; Xu et al., 2006) and depths (1.0−1.5 m) that were at least twice the effective height of these same animals.

Complete skeleton preservation and the presence of articulated to closely associated skeletal elements indicate rapid perimortem to postmortem burial (Rogers and Kidwell, 2007). The presence of partial skeletons and body parts (e.g., limbs, tails), however, also indicates that some carcasses were exposed and rotted for a short time prior to final burial (no more than days to months; Meyer, 1991; Brand et al., 2003; Eberth and Currie, 2005).

The predominance of horizontally and subhorizontally oriented skeletons indicates that the mud in which they sank had little cohesion or shear strength. Carcasses settled out at the bottom of each deposit and shifted steadily upward as sediment and carcasses were added. The matrix-filled gaps between the skeletons indicate that sediment settling continued between burial events, thereby preventing the development of bone-on-bone contacts after soft tissues had rotted.

The vertical segments of neck and tail vertebrae in V15302 (Fig. 7F−G) occur at the margins of the TBB2002 pit, and these body parts were likely supported by a combination of natural skeletal stiffness (especially in the tail) and cohesive adjacent sediments. Sharp
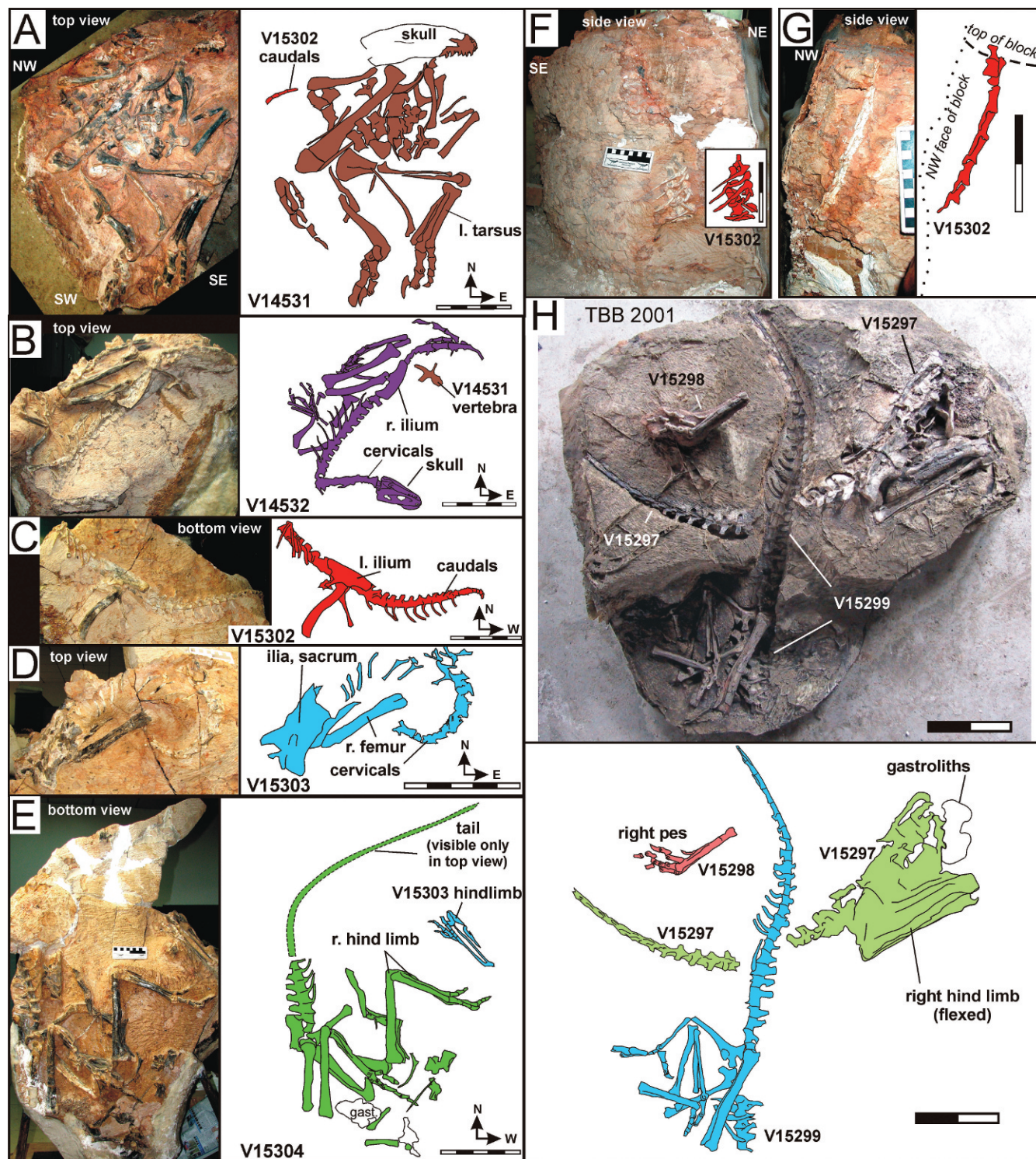
FIGURE 7—Fossil assemblages in TBB2002 and TBB2001. A−G) Photographs (plan view) and color-coded illustrations of 5 vertically stacked skeletons in TBB2002. During preparation, the field block (F−G) was divided horizontally into three subblocks (A; B−C; D−E), and specimens were prepared allowing top or bottom views of the skeletons (labeled). The holotype of *Guanlong wucaii* is in A; note the strong red color of the mudstone and the distal tail segment from V15302. Paratype of *Guanlong wucaii* (V14532) and an unidentified small theropod (V15302) are exposed on the upper and lower surfaces, respectively, of the middle subblock (B−C). Paratype skull is not present in specimen photo but is shown in the illustration. Two *Limusaurus inextricabilis* are exposed on the upper and lower surfaces of the lowest subblock (D−E). Note the presence in E of the left hind limb of the overlying specimen (V15303). Unprepared TBB2002 field block with vertically oriented cervical (F) and caudal (G) vertebral strings (same specimen also visible in C). H) Photograph and illustration of TBB2001, including two vertically stacked skeletons of *Limusaurus inextricabilis* (V15299 and V15297) and the right foot of a third individual (V15298) (bottom view); gast. = gastralia; l. = left; r. = right; E = east; N = north; W = west; NE = northeast; NW = northwest; SE = southeast; SW = southwest. Illustration scale bars are 25 cm in A−E; 10 cm in F−G; 20 cm in H.

dislocations where the neck and tail of V15302 turn upward suggest that this individual was trampled and pushed down into the mud (cf. Worthy and Holdaway, 1996), with its elongate body parts trailing behind.

Although the highly flexed hind limbs present in some of these specimens could be regarded as partial evidence for opisthotony (Faux and Padian, 2007), the consistent absence of other flexed skeletal parts (e.g., necks and tails) in these same specimens and the fact that some specimens exhibit both flexed and unflexed limbs, necks, and tails (e.g., V15301) argue against that interpretation. Flexed and folded hind limbs are a typical posture for resting modern avian theropods and their non-avian, small-theropod relatives (Norell et al., 1995; Xu and Norell, 2004). In this context, the co-occurrence of flexed hind limbs and complete skeletal preservation (V14532, V15297, V15299, and V15923) suggest that individuals likely died while they were at rest (trapped in the mud-filled pit) and subsequently were buried rather quickly. The overall better representation of ambulatory elements (hindquarters) compared to skulls, necks, and forelimbs at both TBB2001 and TBB2002 indicates that these portions of the skeletons were consistently better protected, probably due to preferential burial of these skeletal areas when individuals were trapped. High-quality bone-surface preservation and teeth preserved in jaws also support an interpretation of limited exposure times and rapid burial (Hill, 1980; Meyer, 1991; Brand et al., 2003).

Minor drift among elements indicates that some elements shifted their positions as connective tissues rotted but that the encasing mud prevented significant dispersal of the elements. The absence of scattered or isolated elements, tooth-marked bone, and shed theropod teeth is strong evidence that if vertebrate scavenging occurred at these sites, it was limited to the removal of body parts rather than onsite feasting (Spencer et al., 2003).

DISCUSSION

Size-Related Miring

The co-occurrence of soft-sediment-deformed sediments and redbed intraclasts in these pits (especially TBB2002) indicates that loading ruptured an upper layer of previously cohesive mudstone and induced liquefaction in deposits of saturated mud that were $1-2$ m thick. We propose that after the media failed, the surface of the churned mud filling the pits had a lower shear strength compared to the surrounding crust and media. We envisage a local landscape dotted with meter-scale, mud-filled pits generated by sauropod locomotion, in which small vertebrates could become mired and trapped (Fig. 8). The presence of vertically stacked skeletons, some vertically oriented body parts, a bias for ambulatory elements, the preservation of resting postures, and the absence of bone surface modification all support an interpretation of successive occurrences of miring, death, and burial in water-saturated mud (cf. Weigelt, 1980; Burrows, 1989; Sander, 1992; Hungerbühler, 1998, Spencer et al., 2003; Gates, 2005; Whistler and Webb, 2005; Varricchio et al., 2008).

In most studies of ancient mires, entrapment is thought to have occurred where negative pressures (stickiness) generated during attempted limb extraction from a viscous medium inhibited ambulation (Sander, 1992; Hungerbühler, 1998; Spencer et al., 2003; Khaldoun et al., 2005; Whistler and Webb, 2005; Varricchio et al., 2008). Furthermore, in cases where viscous sediment is inferred to have been shallow, the distal portions of ambulatory limb elements are often interpreted as being preserved at the exact location where individuals were mired and died (Burrows, 1989; Gallup, 1989; Sander, 1992; Hungerbühler, 1998; Whistler and Webb, 2005; Varricchio et al., 2008).

At Wucaiwan, however, the presence of horizontally oriented carcasses preserved in vertical stacks (Figs. 7−8) indicates that the host volcanic mud was neither very viscous nor shallow enough to

preserve specimens in their original death positions. Accordingly, we propose that miring of these small theropods (and other animals at TBB2005) was due more to their small sizes than high sediment viscosity and stickiness (cf. Alexander, 1985; Richmond and Morris, 1996). The largest animals in these pits, *Guanlong wucaii*, stood 66 cm tall at the hip. It would have been difficult for animals of this size or smaller to reach the firm medium at the bottom of the pit with their ambulatory hind limbs. This size-related explanation for miring at Wucaiwan is further supported (albeit weakly) by the absence in these pits of any skeletal material from large sauropods dinosaurs thought to be responsible for creating them.

After struggling to extricate themselves from the mud or becoming exhausted and weakened from exposure, starvation, or thirst, trapped theropods likely assumed a death or resting pose, floating partially submerged in the mud (Weigelt, 1980; Khaldoun et al., 2005). Individuals that entered the mire at a later time probably trampled the floating or previously buried carcasses, as evidenced by the sharply dislocated vertebral strings in V15302 and V14532. It is possible that during the later stages of bonebed development, some small animals were able to extricate themselves by stepping on carcasses of previously mired individuals.

It is reasonable to assume that each individual became trapped, died, and was buried over a span of days to, at most, months, based on these and other published taphonomic data (cf. Hill, 1980; Meyer, 1991; Brand et al., 2003). We conclude for the following reasons, however, that the amount of time represented by all the miring events at each site was relatively short, probably less than one year, and likely a single season. As interpreted by us, the formation of the pits and their functioning as mires most likely resulted from media trampling and liquefaction by large dinosaurs. Accordingly, it seems unlikely to us that in this seasonally dry setting, the sediment-water conditions suitable for miring could have remained unchanged in these pits year after year without more trampling by large dinosaurs to reestablish appropriate rheological conditions—a situation for which there is no evidence. Furthermore, the sediment composition and sediment thicknesses between the five skeletons in TBB2002 are consistent, indicating that identical kinds and amounts of sediment built up between specimens and replaced soft tissues as they rotted. Consistent sediment thicknesses between specimens indicate that skeletons were added at regular intervals, a pattern that is best explained by successive and rapid interment of skeletons in a setting with a high rate of sedimentation. It is simply unlikely that regular sediment thicknesses between skeletons would result if specimens were added less regularly and over long periods of time.

The Abundance of *Limusaurus* and Presence of *Guanlong*

The overwhelming presence of the small theropod, *Limusaurus inextricabilis*, in these pits suggests that (1) this form was particularly abundant among the small trappable vertebrates in the area, or (2) some individuals of this taxon were selectively drawn to or were selectively mired at these sites. Given the large variety of the small vertebrates present at these sites (especially TBB2005), it seems unlikely that vertebrates were selected for trapping at these sites on any basis other than size. Furthermore, it is difficult to explain why a presumed herbivore like *Limusaurus* (Xu et al., 2009) would have been preferentially attracted to sites where other vertebrates became mired. Accordingly, we consider it most likely that the large relative abundance of *Limusaurus inextricabilis* in these bonebeds (MNI = 15) indicates the presence of large numbers of these individuals in the vicinity during the time of miring (weeks to months). In this interpretation, their entry into the pits is regarded as accidental (cf. Hasiotis, 2007).

The inferred abundance of *Limusaurus* in the surrounding area and the evidence for rapid, successive burials of individuals in mud pits
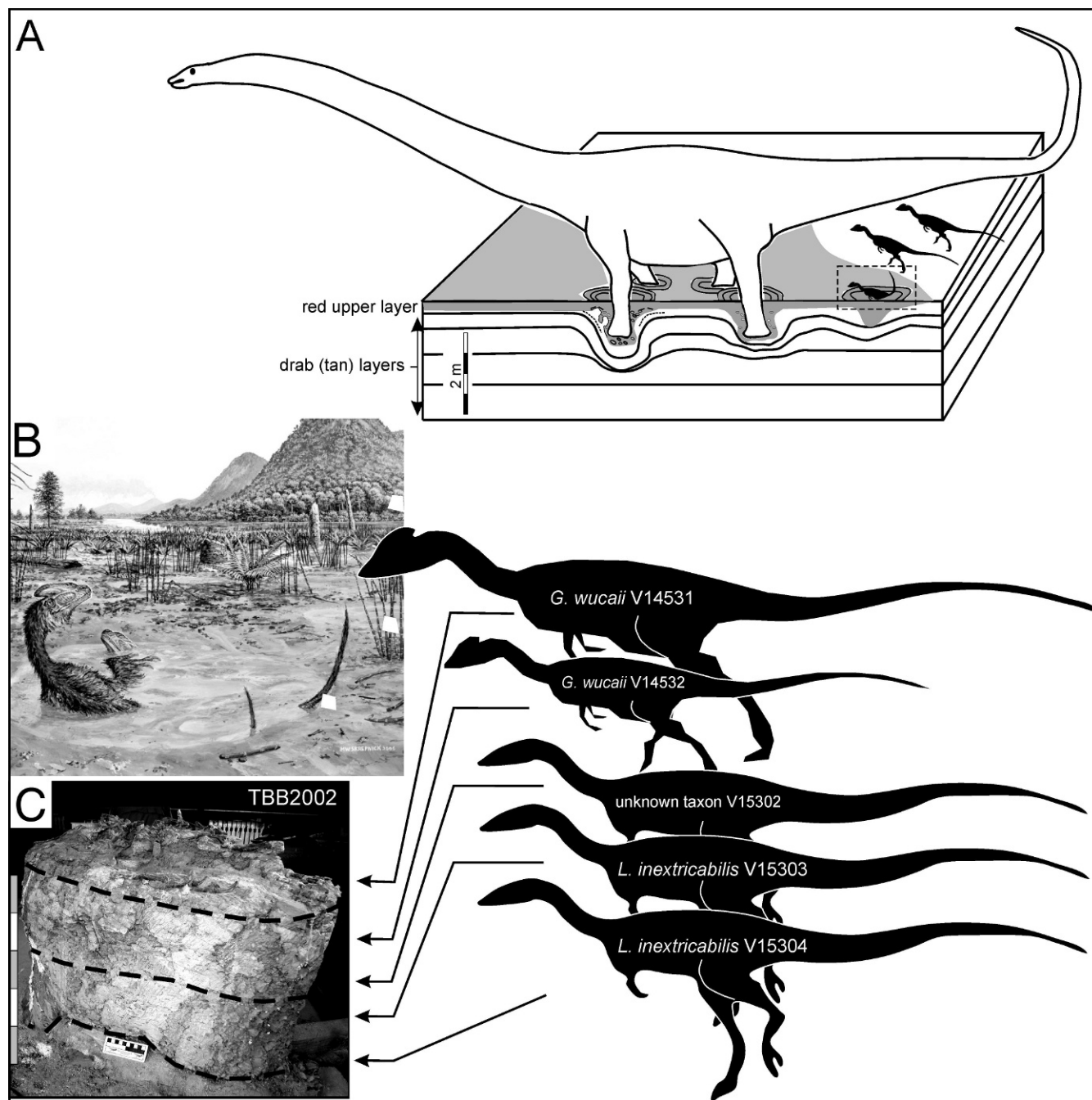
FIGURE 8—Inferred scenario for the origin and preservation of the theropod bonebeds at Wucaiwan. A) During trampling in a wetland setting, *Mamenchisaurus*—a 20 ton and 25 m long sauropod—breaks through and brecciates a cm–dm–thick surface crust (grey shading) and liquefies underlying saturated volcanic muds and sands; track and undertrack are ~2 m deep. No decompaction calculations have been made, thus, it is likely that the tracks were somewhat deeper than interpreted. Shortly after trampling, small theropods, including *Limusaurus inextricabilis* and *Guanlong wucaii*, and some other small vertebrates become mired in the breccia and liquefied volcanic sediment that fills some of the tracks. Susceptibility of the ground to liquefaction and disruption is highly variable across the landscape. Time between sauropod trampling and miring could be as long as months (but probably not years) depending upon local environmental conditions. Dashed line box is illustrated in B. B) Artist Michael Skrepnick's depiction of two mired and partially buried *Guanlong wucaii* at TBB2002. C) TBB2002 field block before preparation (summer 2004) and stratigraphic positions of five skeletons of small theropods within the block (cf. Fig. 7). Dashed lines indicate approximate boundaries between subblocks made during preparation. The field block represents a lithified track fill, which comprises dinoturbated mixtures of tuffaceous mudstone and sandstone, and brecciated red mudstone; note the mottled texture of the block in the photograph. It is likely that trapped individuals caused additional sediment mixing and liquefaction as well as brecciation of the surface crust. The fossiliferous block represents the deepest portion of the track fill (cf. Fig. 5C). Scale bar = 10 cm.

raises the possibility that this taxon was naturally gregarious. Evidence from trackways and other bonebed sites suggest that many kinds of small theropods were gregarious (Schwartz and Gillette, 1994; Kobayashi and Lü, 2003; Kirkland et al., 2005; Huh et al., 2006; but also see Roach and Brinkman, 2007 for a contrary opinion), and that some probably exhibited age-related social behaviors (Kobayashi and

Lü, 2003; Varricchio et al., 2008). Although the Wucaiwan bonebeds record sequential, one-at-a-time trapping and burial of small theropods, it is likely that the taphocoenoses in these bonebeds were derived, in part, from one or more large biocoenoses of gregarious *Limusaurus*. It is currently unknown, however, if the fossil assemblages preserve evidence of age-related sociality and segregation in this taxon.

Only two specimens at the top of TBB2002 represent the carnivorous small theropod, *Guanlong wucaii*. The presence of two individuals at this site is insufficient evidence upon which to base an interpretation of gregariousness. We consider it entirely reasonable, however, to speculate that these two individuals were attracted to the site to prey upon or scavenge mired small theropods. It is also reasonable to speculate that miring may have inhibited onsite feasting, because no direct evidence of predation or scavenging is preserved at these sites.

Small Theropod Preservational Biases

Of the total of 22 small theropod skeletons that we collected from the Shishugou Formation at Wucaiwan during six field seasons, 18 were collected from the bonebed pits described here. The four remaining individuals (unidentified, but not *Limusaurus*) were collected from a variety of other alluvial-paludal facies (these will be described elsewhere in the near future). Continental vertebrate fossil assemblages of Mesozoic age are most frequently associated with alluvial deposits that record sedimentological evidence for bone or carcass transport and reworking (cf. database in Eberth et al., 2007). In such deposits, small theropod skeletons are rarely encountered relative to those of most other dinosaurs, and it has been suggested that this rarity is an indication of greater susceptibility to disarticulation and bone scatter during the skeleton's taphonomic history rather than an original rarity of those forms in the fauna (e.g., Currie and Russell, 2005). Our observations from Wucaiwan support this idea by showing that, although dinosaur remains are abundant throughout the Shishugou Formation at Wucaiwan, a large part of our knowledge about the formation's small theropod taxonomy and diversity comes from three exceptional bonebeds formed under unusual circumstances. We conclude that small theropod diversity is underestimated in this and probably many other Mesozoic continental deposits.

The underrepresentation of small theropods in the Shishugou Formation—other than in the bonebeds described here—offers an explanation for the rarity of the dinosaur lineages most closely related to birds in the Middle–Late Jurassic and in spite of the presence of *Archaeopteryx* in the Tithonian. Several basal coelurosaurs are present in the Kimmeridgian (*Ornitholestes, Coelurus, Tanycolagreus*; Carpenter et al., 2005), and four recently described small theropods in the Middle to Upper Jurassic Daohugou Formation of northeastern China are all inferred to be members of the Paraves (Avialae and Deinonychosauria; Zhang et al., 2008). Coelurosaurian phylogeny (Turner et al., 2007; Zhang et al., 2008), however, indicates that members of the Compsognathidae, Ornithomimosauria, Therezinosauroidea, Oviraptorosauria, and Alvarezsauridae (or common ancestors to clades combining some of these taxa) should all be present in the Kimmeridgian, but, other than a disputed therezinosauroid dentary (Xu et al., 2001; Kirkland et al., 2005), none are yet reported earlier than the Early Cretaceous.

CONCLUSIONS

1. Well-preserved skeletons of three taxa of small theropods (*Guanlong wucaii*, *Limusaurus inextricabilis*, and one unidentified form) dominate three unusual bonebeds in the early Late Jurassic portion of the Shishugou Formation, Xinjiang, China. The skeletons are mostly preserved in vertical stacks and are interbedded with and surrounded by a mixture of alluvial-volcanic mudstone and mudstone intraclasts.

2. The depositional environment at each bonebed appears to have been a pit filled with fluid-plastic mud. Pits were formed during highly focused loading—likely caused by sauropod trampling—that disrupted a surface crust and liquefied underlying saturated mud.

3. Vertebrates with small body sizes (<3 m long; <1 m tall; <100 kg mass) were preferentially trapped via miring in these mud-filled pits.

4. The small herbivorous ceratosaur, *Limosaurus inextricabilis*, which dominates the combined assemblage, appears to have occurred in large and possibly gregarious populations in the bonebed area. Abundant trapping of this form was likely a function of its large numbers and accidental entries into the pits. The presence of two individuals of the predator *Guanlong wucaii* at the top of the stack of theropods in TBB2002 suggests that this form may have become mired during predation or scavenging.

5. A bias for small theropods in these unusual bonebeds, compared to their relatively low abundance elsewhere in the Shishugou fauna, underscores that small theropods are likely underrepresented in Mesozoic fossil assemblages collected from other alluvial and paludal settings.

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