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Taphonomy of the Lamy Amphibian Quarry: A Late Triassic bonebed in New Mexico, U.S.A.

By: **Andrew B. Heckert,** Spencer G. Lucas, Larry F. Rinehart, Karl Krainer & Justin A. Spielmann

Abstract

Located in Santa Fe County, New Mexico, USA, the Lamy amphibian quarry is a Late Triassic (Adamanian) bonebed stratigraphically low in the Garita Creek Formation of the Chinle Group. Well known for its mass accumulation of metoposaurid amphibians, it was initially interpreted as a drought-induced death assemblage. Based on microstratigraphic and sedimentological studies, additional and extensive collecting at the quarry and a revised understanding of the bonebed, we provide a detailed taphonomic analysis of the Lamy amphibian quarry that identifies it as a low diversity multitaxic and monodominant bonebed in pedogenically modified floodplain mudstone. The Lamy bonebed shows no evidence of drought and is characterized by a high density of completely dissociated bones that show clear alignment by current and sorting (enrichment of Voorhies Group II and III elements). The bones show no significant abrasion or weathering (stage 0), preserve virtually no evidence of scavenging and show no evidence of trampling. Based on skull lengths, the metoposaurid assemblage has a type I survivorship curve and lacks juveniles. We thus posit that the following sequence of events formed the Lamy amphibian bonebed: (1) aggregation (cause unknown) of a large number of metoposaurid amphibians at a site different from the location of the bonebed, though not distant; (2) catastrophic mass mortality; (3) complete disarticulation and disassociation of the skeletons; and (4) rapid transport of the disarticulated bones onto a floodplain surface that was undergoing pedogenesis. The Lamy amphibian bonebed is representative of the Late Triassic metoposaurid bonebeds from Morocco and the western USA, which are monodominant and nearly monotaxic. They indicate that aggregation (probably of breeding populations) and mass death of metoposaurids were relatively common across the riverine floodplains of Late Triassic Pangea.

1. Introduction

Located just south of Lamy, New Mexico, USA (Fig. 1), the Lamy amphibian quarry was discovered in 1936, excavated by the Harvard University Museum of Comparative Zoology in 1938 and excavated further by the National Museum of Natural History (Smithsonian Institution) in 1947. The Lamy amphibian quarry is well known for its mass accumulation of metoposaurid amphibians identified as *Buettneria perfecta* (Fig. 2), and Romer's (1939) initial interpretation of it as a drought-induced death assemblage (the drying up of a pond in which the amphibians lived) is classic. Colbert and Imbrie (1956) provided a biometric analysis of the metoposaurid amphibian material from the quarry, and more recently Rinehart et al. (2001, 2006) reported on microvertebrates and tooth marks on an amphibian bone from the quarry. Hunt and Lucas (1989, 1995) questioned Romer's (1939) interpretation of the genesis of the Lamy amphibian quarry, suggesting that it was hydraulically accumulated. The only attempt at a taphonomic analysis of the Lamy amphibian quarry, by Zeigler et al. (2002), also questioned Romer's conclusions; they interpreted the amphibian quarry as a hydraulically sorted and transported, semi-attritional death assemblage.

Zeigler et al. (2002) used field notes and published data in Colbert and Imbrie (1956) to reach this conclusion, without being able to examine the quarry itself due to restricted land access. Beginning in 2007, the New Mexico Museum of Natural History gained access to the Lamy amphibian quarry and excavated the amphibian bonebed, the first institution to do so in 60 years. Based on microstratigraphic and sedimentological studies, additional and extensive collecting at the quarry and a revised understanding of the bonebed, we provide a detailed taphonomic analysis of the Lamy amphibian quarry.

2. Institutional abbreviations

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; NMMNH, New Mexico Museum of Natural History, Albuquerque;
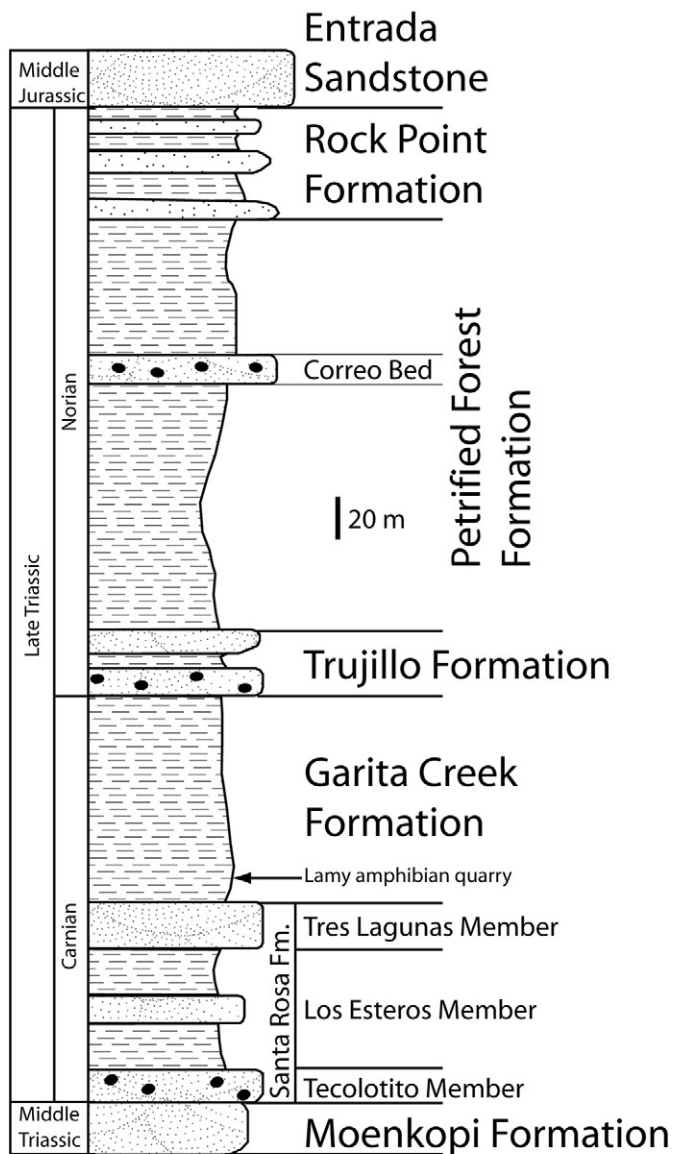
Fig. 1. Generalized, regional stratigraphic section of Triassic strata south of Lamy, New Mexico, USA. Inset, Map of New Mexico with Triassic outcrops highlighted in black. Star locates the Lamy amphibian quarry.

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

2.1. Regional stratigraphy

The Lamy amphibian quarry is located in an extensive and very fossiliferous outcrop area of Triassic strata south and southeast of Lamy, Santa Fe County, New Mexico (Fig. 1) (Hunt and Lucas, 1989,

Fig. 2. Photograph of Harvard (MCZ) slab collected from the Lamy amphibian quarry in 1938. Fossils include skulls, mandibles and various postcrania of the metoposaurid amphibian *Buettneria perfecta*.

1995; Hunt et al., 2005; Johnson, 1973; Lucas, 1991, 1993; Read et al., 1944; Stearns, 1953). Recent fieldwork has established a detailed Triassic lithostratigraphy for the area around Lamy, including the Lamy amphibian quarry (Spielmann and Lucas, 2008). Thus, the Triassic strata south of Lamy encompass the Middle Triassic Moenkopi Formation and an Upper Triassic Chinle Group section that consists of (in ascending order) the Santa Rosa Formation (divided into the Tecolotito, Los Esteros and Tres Lagunas members), Garita Creek, Trujillo, Petrified Forest (including the Correo Bed) and Rock Point formations (Fig. 1). The Upper Triassic strata are bracketed by unconformities, with the Chinle section unconformably overlying the Middle Triassic Moenkopi Formation and unconformably overlain by the Middle Jurassic Entrada Sandstone (Spielmann and Lucas, 2008).

As reported previously (Hunt and Lucas, 1989, 1995; Lucas, 1991), the Lamy amphibian quarry is stratigraphically low in the Garita Creek Formation (Fig. 1). Locally, the Garita Creek Formation is ~40 m thick, and the quarry is ~4 m above the contact with the underlying Tres Lagunas Member of the Santa Rosa Formation (Figs. 1, 3). The tetrapod assemblage of Garita Creek strata elsewhere in east-central New Mexico indicates an Adamanian (late Carnian) age for the Garita Creek Formation generally and the Lamy amphibian quarry in particular (Hunt et al., 2005; Lucas et al., 2001).

3. Sedimentology of the Lamy amphibian quarry

3.1. Microstratigraphy

The Lamy bonebed is in a several-meter-thick succession of mudstone that is overlain by a ledge-forming interval of crossbedded sandstone and conglomerate (Figs. 1, 3, 4). The entire stratigraphic succession and the bonebed itself dip 15° west. The lowermost part of this succession (Fig. 3, units 1–4) is red mudstone with intercalated fine-grained sandstone and a 15-cm-thick, lenticular, polymict conglomerate. The conglomerate is grain-supported, poorly sorted and composed of different types of (mostly subrounded) sedimentary rock fragments, with carbonate and siltstone clasts most common. The conglomerate contains abundant bone fragments (up to 7 cm long) and oxidized plant stem impressions (up to 20 cm long) and pinches out laterally. It is overlain by 2 m of poorly exposed, red mudstone to siltstone (Fig. 3, unit 5). Near the top of this bed, we collected the lower jaw and some associated postcrania of a very large phytosaur as well as additional phytosaur teeth and pelvic elements. The overlying bed is massive, red and green mottled mudstone,
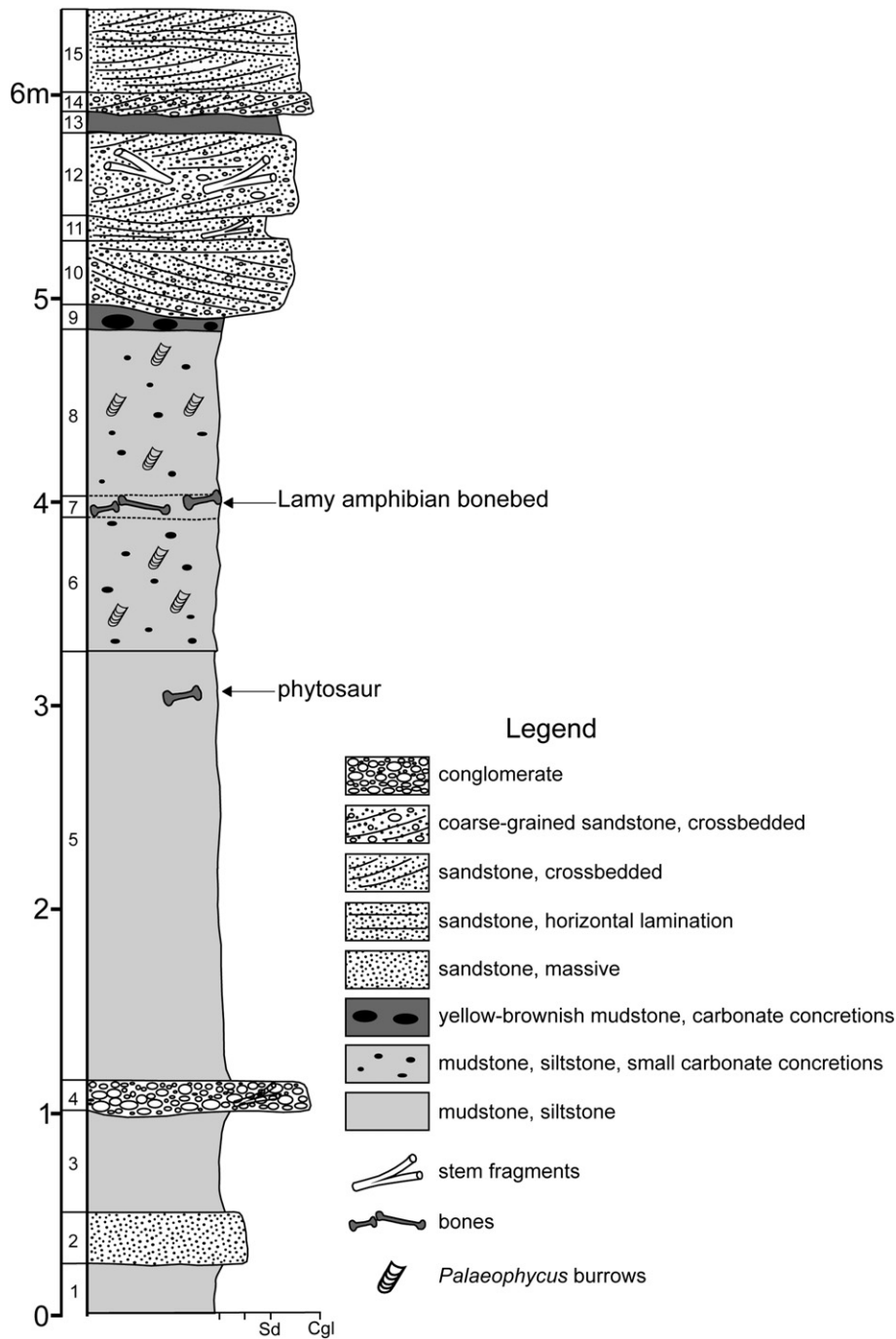
Fig. 3. Detailed stratigraphic section through the Lamy amphibian quarry (bonebed). Base of section = local base of Garita Creek Formation.

containing scattered brownish carbonate concretions up to ~1 cm in diameter and numerous burrows of *Palaeophycus* (Fig. 3, unit 6).

The amphibian quarry bonebed (Fig. 3, unit 7, Fig. 4C–D), which overlies this mudstone interval, is approximately 10 cm thick, extends more than 8 m on strike, consists of red sandy mudstone with some green and purple mottles and is densely packed with tetrapod bones, virtually all of which pertain to the large metoposaurid amphibian *Buettneria perfecta* (Figs. 2, 4C–D, 5). The bones are coated by a thin (~1 mm) carbonate crust and some rhizoliths are present. The azimuths of bones that were at least four times longer than their widths were measured; they show a preferred orientation (Fig. 6A). The main bone-bed is overlain by green and purple color-mottled mudstone containing scattered carbonate concretions and *Palaeophycus* burrows (Fig. 3, unit 8; Fig. 4A–B), similar to unit 6. A yellowish–

brownish mudstone horizon contains numerous brownish carbonate concretions up to ~8 cm in diameter and forms the top of the mudstone succession (Fig. 3, unit 9; Fig. 4A–B).

At the amphibian quarry, the mudstone succession is overlain by a 1.4-m-thick complex of crossbedded sandstone (Fig. 3, units 10–15; Fig. 4A–B). Sandstone in this interval is medium-grained (dominant grain size 0.2–0.5 mm), moderately to well sorted and grain supported. The grains are subrounded to rounded, and the dominant grain type is monocrystalline quartz, comprising 50–61% of the sandstone, and less common grains are polycrystalline quartz, chert, granitic rock fragments, metamorphic rock fragments and rare detrital feldspar. The basal sandstone bed (Fig. 3, unit 10) is 30 cm thick and thins out laterally; it is coarse-grained, displays trough crossbedding (lithofacies St of Miall, 1996) and has a basal erosional
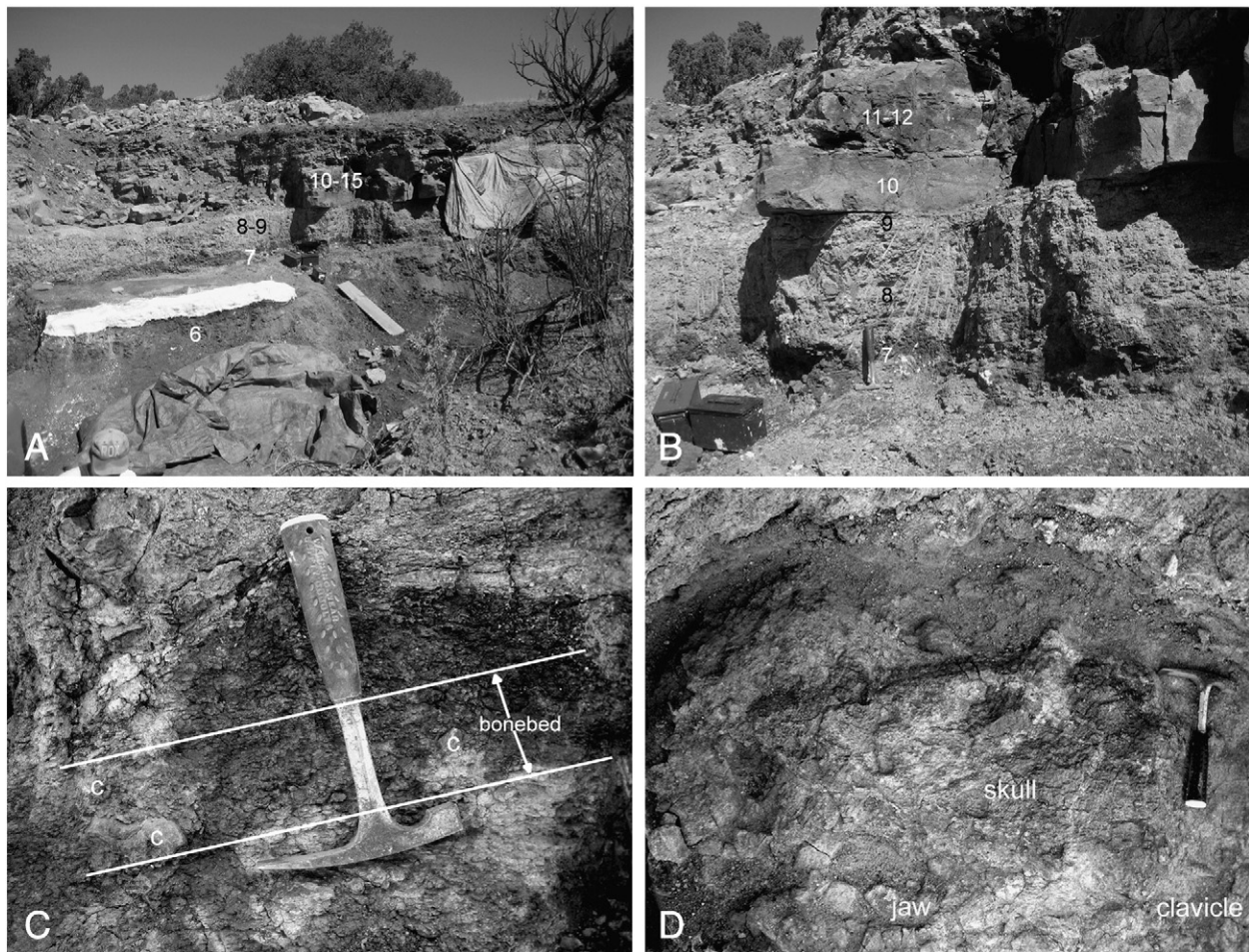
Fig. 4. Selected photographs of the Lamy amphibian quarry. View from the south, apparent dip in the photo is approximately the actual dip (15° west). A, Overview of the quarry. B, Close-up of base of sandstone complex that overlies the quarry. C–D, Views of bonebed in cross section (C) and on bedding plane (D). Numbers refer to units in measured section in Fig. 3; c = vertebral centrum.

contact. Above unit 10 lies a 10-cm-thick, fine-grained sandstone containing small plant stem fragments (lithofacies Sh of Miall, 1996) (Fig. 3, unit 11), overlain by another coarse-grained, trough-cross-bedded sandstone (lithofacies St) (Fig. 3, unit 12), which is 40 cm thick and contains sedimentary rock clasts (up to 3 cm long) and stem fragments (up to half a meter long) near the base (lag). A thin (10 cm) greenish-gray mudstone layer (Fig. 3, unit 13) rests on the sandstone bed. The mudstone layer contains a few quartz grains up to 5 mm in diameter and plant debris (lithofacies Fm of Miall, 1996).

The uppermost 50 cm of the sandstone complex consist of coarse-grained, arkosic, trough-crossbedded sandstone, overlain by a trough-crossbedded sandstone. This crossbedded sandstone (lithofacies St) (Fig. 3, units 14–15) thins laterally and fills scours in the underlying greenish mudstone. The facies of the crossbedded sandstone complex changes laterally. To the east this complex contains conglomerate layers with sedimentary rock clasts (up to 7 cm long), but lacks reworked calcrete, in a sandy matrix. The conglomerate is mainly matrix supported and contains some tetrapod bone and plant stem fragments (lithofacies Gmm of Miall, 1996). The conglomerate layers alternate with crossbedded sandstone layers. Towards the west the crossbedded sandstone complex grades into a 1.8-m-thick horizon of crossbedded sandstone lacking conglomerate or mudstone–siltstone intercalations.

About 50 m east of the amphibian quarry, two siltstone to fine-grained sandstone layers, each 15–20 cm thick, are intercalated in red mudstone about 1.7 to 2 m below the crossbedded sandstone complex. These layers are micaceous, display horizontal lamination, current ripples and are locally bioturbated. They are laterally equivalent to units 5 (upper part) and 6 at the quarry (Fig. 3).

3.2. Sedimentological interpretation

We interpret the mudstone complex at the Lamy amphibian quarry (Fig. 3, units 1–9) as floodplain deposits, consistent with interpretation of similar Chinle Group mudstone intervals elsewhere (e.g., Blakey and Gubitosa, 1983, 1984; Dubiel, 1989; Newell, 1993; Tanner and Lucas, 2006). The mudstone facies, lithofacies Fm of Miall (1996), forms a thick succession composed of sheet-like beds extending laterally over hundreds of meters. This facies is typical of a distal floodplain, and the vertical changes in lithology may reflect minor changes on the nearly flat depositional surface of the floodplain. In the lower part of the amphibian quarry succession (Fig. 3, units 1–5), intercalated siltstone to fine-grained sandstone layers within the mudstone may represent sheetflood deposits formed during individual flood events, whereas the conglomerate layer (unit 4), which laterally thins and pinches out, is interpreted as a fluvial channel-fill deposit. Laminated, ripple-laminated and burrowed sandstone laterally equivalent to some of these mudstone strata (units 5–6) represent unchannelized flow (sheetflood) deposits on the floodplain surface.

We further interpret the mudstone beds that encompass the amphibian quarry as pedogenically modified floodplain mudstones. Units 6–9 (Fig. 3) show color mottling, dispersed carbonate nodules, gleyed textures, pedogenic slickensides, calcareous rhizoliths and
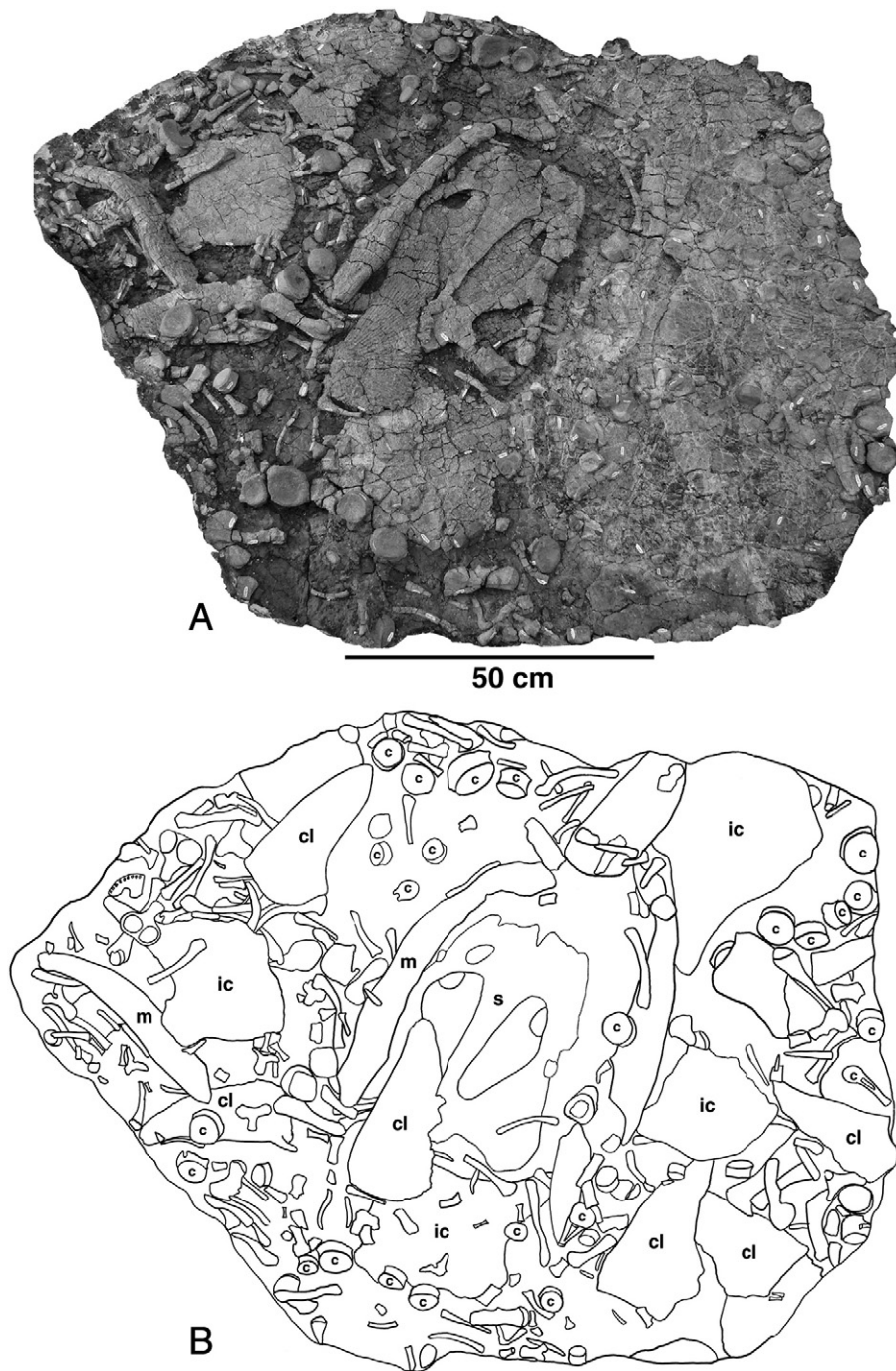
Fig. 5. Photo and bone map of a 2 m² block from the Lamy amphibian quarry in the NMMNH collection. The bone surface is exposed upside-down from its original position in the quarry. A, Photograph of block excavated by the NMMNH during the summer of 2008. B, Line drawing of block with elements labeled. Abbreviations are: c = centrum, cl = clavicle, ic = interclavicle, m = mandible and s = skull. Unlabelled bones are ribs and appendicular elements.

arthropod burrowing, all suggestive of pedogenesis (e.g., Mack et al., 1993). Thus, we identify these strata (units 6–9) as calcic alfisols that begin with a relatively thick B (Bk) horizon (unit 6) overlain by the sandy bonebed, which truncates the underlying paleosol. The bonebed forms a relatively thin, dark-colored and sandy A horizon (unit 7) overlain by another Bk horizon (unit 8) similar to unit 6, topped by a Bk horizon (unit 9) truncated by the overlying paleochannel (unit 10) (cf. Tanner and Lucas, 2006). This alfisol profile hosts stage II to stage III calcrete pedogenesis in the form of scattered, cm-size carbonate nodules, which in unit 9 are indicative of incipient stage III pedogenesis (Gile et al., 1966). Thus, in unit 9, the nodules are concentrated in a discrete horizon in clay that displays pedogenic slickensides. The

nodules are up to 9 cm in diameter, have distinct boundaries and are subspherical to irregularly shaped. Calcic alfisols are a common kind of paleosol in lower Chinle Group strata (e.g., Kraus and Middleton, 1987; Tanner and Lucas, 2006; Therrien and Fastovsky, 2000), so the pedogenically-modified interval at the Lamy amphibian quarry is not unusual for lower Chinle Group strata. Significantly, the bonebed is in strata that show no evidence of lacustrine deposition, such as laminated clays or lacustrine microfossils (conchostracans, ostracods, etc.), nor is there any evidence of severe drought, such as mudcracks, preserved in the sediments (cf. Shipman, 1975).

The crossbedded sandstone interval stratigraphically above the amphibian quarry (Fig. 3, units 10–15) extends laterally over at least
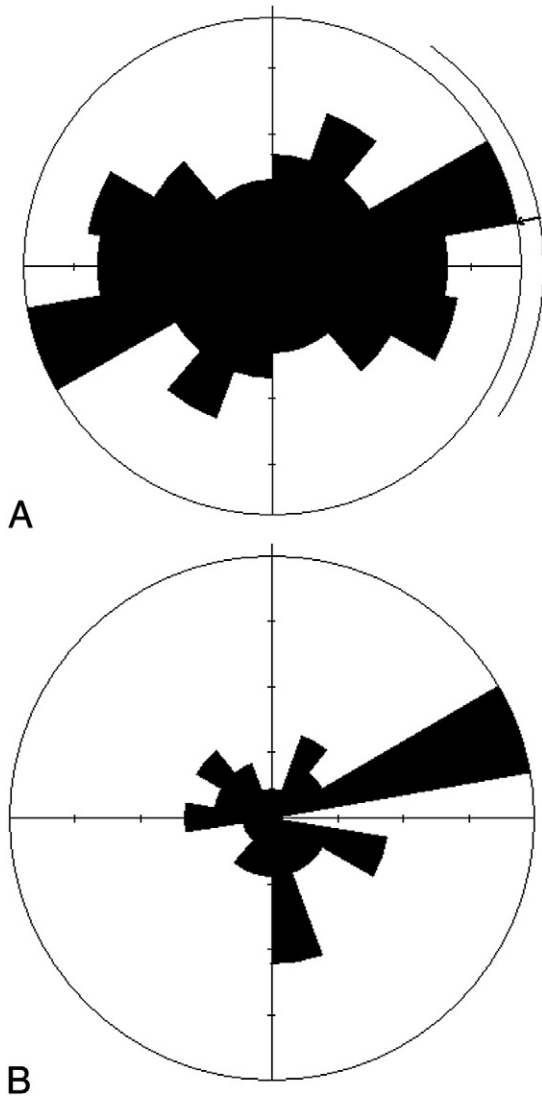
Fig. 6. A, Rose diagram, top north. Azimuth measurements of mandibles, limb bones, ribs and other elongate elements with 95% confidence arc (N = 106). B, Flow vector plot, top north. Pointing directions are of elongate elements with one end distinctly heavier (N = 42).

a mudstone interval that represents two phases of development of calcic alfisols that host stage II carbonate pedogenesis. The bonebed is a thin bed within the paleosol succession, and rhizoliths in the bonebed (Fig. 5) as well as mottling and carbonate deposition on the bones suggest that the bonebed underwent some pedogenic modification after it was formed. Thus, the bonebed is a sandy mudstone with transported clasts (the bones) that truncated the underlying B horizon of paleosol and formed the basis for the next phase of pedogenesis. There is no evidence that the bonebed was in a pond deposit (no laminated mudstone, lacustrine microfossils, etc.) or that it experienced a severe drought.

4.1.2. Bone abrasion

Bones from the Lamy amphibian quarry show no signs of abrasion, although nearly all of the teeth are missing from both skulls and mandibles. The teeth were probably lost shortly after death, during decomposition or during brief transport, which otherwise had little effect on the bone surfaces. Thus, all of the bones are in an excellent state of preservation and often preserve small, thin and delicate portions of the bones essentially undamaged. All breakage of the bones appears to be compression fracturing due primarily to sediment loading and unloading, and shrinkage/swelling of the clays that encase the bones (see below). No indication of trampling is present, further supporting identification of the bonebed as a hydraulically-sorted, attritional deposit (Hunt and Lucas, 1989, 1995; Zeigler et al., 2002), not a shrinking pond as originally interpreted by Romer (1939). The bones in the amphibian quarry were not abraded by sediment or other objects in flowing water.

4.1.3. Bone deposition

At the Lamy quarry, bones are concentrated in a single depositional layer only 10 cm thick (Figs. 3, 4C). The bonebed matrix is clay that lacks any gravel-size objects (notably, no mudstone rip-ups) and contains some sand. Bone density is high, averaging 112 bones/m^2 over the 2 m^2 surface shown in Fig. 5; bone densities for the blocks in Fig. 2 were not calculated as the matrix is obscured and it is clear that some elements were removed during preparation. In some areas of the bonebed, skulls and shoulder girdle elements form a solid pavement with essentially no matrix exposed between them (Fig. 2). The base of the bonebed shows no evident topography, though a few bones are underneath others in the bed (Fig. 5). These features suggest that bones accumulated during a single and very rapid depositional event.

4.1.4. Bone alignment

All of the metoposaurid amphibian bones, which comprise most (~98%) of the elements in the quarry, are disarticulated and mixed in a single layer (Figs. 2, 5). Skulls, mandibles, clavicular and limb elements and vertebral centra dominate the assemblage, with manual, pedal, rib and pelvic girdle elements being proportionally less common. Elongate bones (criterion: four times longer than wide) exposed on a large (2 m^2) prepared slab show a preferred east–northeast––west–southwest orientation (Fig. 6A, 106 bone trends). If we limit the analysis to bones with one end distinctly heavier than the other (42 bones) and assume that the heavier end lags in the current, then these flow indicators resolve to show east–northeast flow (Fig. 6B). The elements within the MCZ slab (Fig. 2) demonstrate a strong preferred orientation, whereas the elements within the USNM slab (Colbert and Imbrie, 1956, pl. 28, Fig. 2) have a weak preferred orientation (Zeigler et al., 2002, Fig. 4). This could be due to sample size, as the MCZ block is much larger than the USNM block. Bone alignment and the ability to be transported are not related to bone size, but rather to shape and density. The bones in all of the examined slabs show slight imbrication, especially of flat (mediolaterally compressed) elements (e.g., skulls, mandibles, clavicles, interclavicles).

tens of meters and encompasses sheet sandstone forming a prominent ledge. This fluvial sheet sandstone is composed of multistory channel fill sandstones of lithofacies St (Miall, 1996) associated with thin beds of lithofacies Gmm and overbank fines of lithofacies Fm. Laterally, the sandstone complex grades into a sandstone-conglomerate complex, which fills scours in the underlying mudstones. The vertical stacking of different bedforms reflects fluctuations in the flow depth and discharge.

4. Taphonomy

4.1. Sedimentological evidence

Here, we address the following topics: lithologic context, bone abrasion, bone deposition, bone alignment and hydrodynamics as sedimentological evidence bearing on the taphonomic interpretation of the Lamy amphibian quarry.

4.1.1. Lithologic context

The lithologic context of the Lamy amphibian bonebed was described in detail above, and the bonebed was interpreted to be in

The complete disarticulation of bones at the quarry and their alignment strongly suggest some sort of hydraulic transport of the bones, and indicate a strong current to align the bones (e.g., Behrensmeyer, 1988; Fiorillo, 1991; Sander, 1987; Voorhies, 1969). However, the lack of abrasion of the bones and their completeness suggest that this was probably not transport over a long distance, though the degree of abrasion of bones does not always correlate with transport distance (Aslan and Behrensmeyer, 1996).

4.1.5. Hydrodynamics

All bones of a metoposaurid skeleton are present in the quarry, from skulls (~60 cm long) to phalanges (≤3 cm long). Voorhies (1969) defined three groups of modern mammalian bones distinguished by surface-area-to-volume-ratios (SA:V). Group I bones have high SA:V ratios, and include vertebrae, ribs and foot bones, whereas group II bones have intermediate SA:V values and include the femur, tibia, ulna, radius and metatarsals. Group III bones have low SA:V ratios and include skulls and mandibles. The Voorhies groups reflect the hydrodynamic properties of the bones, so each group is moved by different current velocities – low velocity currents move group I bones and high velocity currents move group III bones. The Voorhies groups were based on mammal bones, so they don't necessarily apply equally to the bones of lower vertebrates (Blob, 1997). However, we apply them to the metoposaurid bones from the Lamy quarry, with the modification that we place metoposaurid clavicles and interclavicles (which are long, flat bones) into group III, not group II, where mammal clavicles and "interclavicles" (sternebrae) are placed. We based this on the idea that the metoposaur clavicles and interclavicles would be more difficult to transport because the flowing water would have less traction on the bone (i.e., lower SA:V than the corresponding mammal bones).

If we assign all the elements of a complete metoposaur skeleton (Dutuit, 1976; Sawin, 1945; Sulej, 2007) to Voorhies groups, the expectation is domination of Voorhies group II – 64%, 34% group I and only 3% group III (Fig. 7). However, the observed values based on metoposaurid bones collected at the Lamy quarry are substantially different – 75% group II, 13% group I and 12% group III (Fig. 7). This enrichment of group II and group III elements suggests a low to medium velocity current that winnowed away group I elements, which are under-represented.

4.2. Biological evidence

Here, we address the associated microvertebrate assemblage, association of skeletal elements, bone weathering, scavenging, bone fracture, MNI (minimum number of individuals) and age profiles as biological evidence bearing on the taphonomic interpretation of the Lamy bonebed.

4.2.1. Microvertebrate fossils

As noted above, virtually all of the bones from the Lamy bonebed are of the metoposaurid amphibian *Buettneria*. Otherwise, among vertebrate macrofossils, we have only noted isolated phytosaur teeth and an archosaur sacrum in the material we have collected. Thus, following Behrensmeyer (2007); also see Rogers, 1990) this is a monotaxic assemblage. Rinehart et al. (2001) reported microvertebrate fossils recovered by disaggregating and screenwashing sediment from beneath a partial interclavicle during preparation of a small (~7 kg) MCZ block collected at the Lamy amphibian quarry. This yielded fossils of a small archosaur (procoelous caudal vertebra), fish scales and skull elements of semionotids and redfieldiids and cm-size skull elements of a temnospondyl, probably young metoposaurids. The presence of these small elements, disarticulated in the quarry assemblage and associated with much larger bones, is consistent with hydraulic transport and sorting of the fossils (Rinehart et al., 2001). However, such microfossils are not ubiquitous in the quarry matrix. So, it is possible that the microvertebrate fossils from the MCZ block represent gut contents of one of the amphibians in the quarry.

Indeed, based on the experience with the small MCZ block it was anticipated that screenwashing matrix from the numerous NMMNH blocks would produce many more microvertebrate fossils. This has not been the case. With the exception of a few small teeth, mostly temnospondyl, screenwashing approximately 0.5 m³ of sediment has produced no significant finds.

4.2.2. Association of skeletal elements

As already stated, metoposaurid bones at the Lamy quarry are totally disarticulated and closely packed in the bonebed, but in no way associated. Even short strings of vertebral centra are not present, which underscores the total disarticulation evident in the bonebed (Figs. 2, 5). Furthermore, bones in proximity to each other are not obviously part of a single skeleton. The bonebed thus must have come
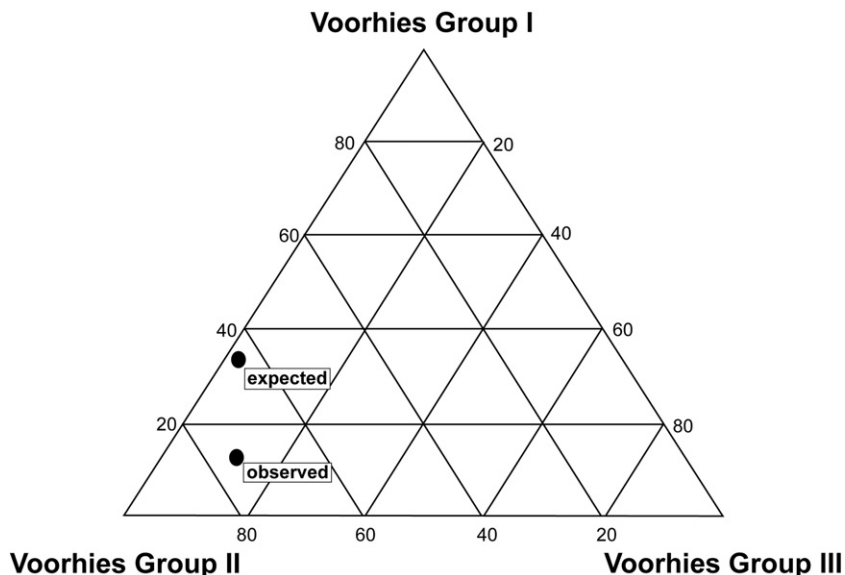

Fig. 7. Ternary plot showing the expected (based on complete metoposaurid skeleton) and observed (based on bones in Lamy amphibian quarry) Voorhies Group percentages.

from fully decayed carcasses that lacked any tissues to bind bones together (cf. Hill, 1979; Holz and Barberena, 1994).

4.2.3. Bone weathering

None of the bones in the Lamy quarry shows any evidence of a significant degree of subaerial weathering. They thus correspond to stage 0 of Behrensmeyer (1978), in which bone surfaces are smooth and lack cracks other than those associated with post-depositional and post-fossilization stresses. Zeigler et al. (2002, p. 281) considered some limb bones to represent stage 1–2 weathering based on minor splintering revealing "inner bone tissue" in some limb bones, but we suspect that this is more of a reflection of the relatively cartilaginous metoposaurid skeleton and, using the much larger sample of bones available to us now, we only identify stage 0 weathering of skeletal elements in the quarry.

Based on modern bones, this limits the duration of bone exposure to a maximum of ~3 years (Behrensmeyer, 1978). However, bone does not survive for long in subaerial environments and must be buried quickly to appear unweathered when fossilized (Behrensmeyer, 1975). Thus, it seems likely that the Lamy metoposaurid bones were only exposed for weeks or months. This low degree of bone weathering is consistent with mass death and rapid burial whereby all of the metoposaurid bones were exposed to chemical and physical degradation at the same time (Fiorillo et al., 2000).

4.2.4. Scavenging

To date, among all the bones in the quarry, we have found only one bone, a metoposaurid clavicle fragment, that has tooth marks on it. These are the holotype of the ichnospecies *Heterodontichnites hunti*, and were interpreted as bite marks made by a phytosaur during scavenging or a fatal predation event (Rinehart et al., 2006). They are the only prima facie evidence of scavenging of the Lamy metoposaurids. However, predators and scavengers are the greatest agents of dissociation of a carcass (Behrensmeyer, 1975), so it could be argued that scavengers played a large role in disarticulating the Lamy metoposaurid bones. It has also been argued that the rarity of tooth marks on dinosaur bone relative to mammal bone may indicate differences in carcass utilization by Mesozoic scavengers (Fiorillo, 1991; Hunt, 1987), though taphonomic biases could also be a factor (Erickson and Olson, 1996). Thus, extensive scavenging in which little damage was done to bone may in part explain the dissociation of the Lamy metoposaurid bones, though this can only be advocated as reasonable speculation.

4.2.5. Bone fractures/trampling

As noted above, metoposaurid bones at the Lamy quarry are very well preserved, but generally are fractured, usually in multiple places. These fractures are perpendicular to bone long axes, and the break surfaces are straight and smooth. This indicates post-burial and post-fossilization damage, in part due to sediment loading and subsequent unloading as evidenced by slickensides in the clay, but largely due to swelling and shrinking of the clays that contain the bonebed (e.g., Behrensmeyer, 1975; Dodson, 1971). No fractures due to trampling (cf. Fiorillo, 1984, 1987) are evident.

4.2.6. MNI and survivorship

The minimum number of individuals (MNI) of the metoposaurids collected from the Lamy amphibian quarry (based on counting prepared skulls) stands at >30. This sets an absolute minimum size on the sample of animals preserved at the quarry. Based on field notes regarding collected, but unprepared skulls, and skulls exposed but not yet collected in the quarry, the actual MNI is >60.

We calculated a survivorship curve of the Lamy metoposaurids based on midline skull length, and the LOG_{10} number of survivors, which shows the rate of mortality (Fig. 8). The plot is essentially a concave-down or type I curve where animals are born with a high
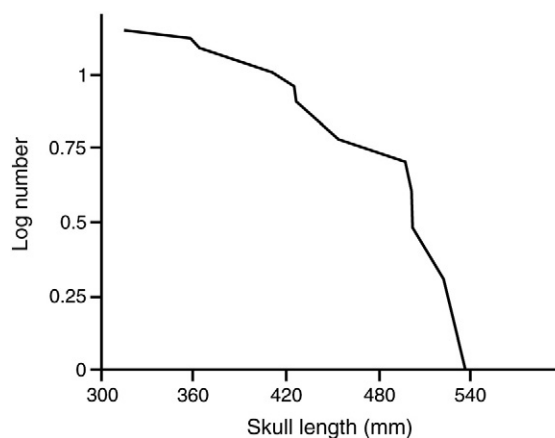

Fig. 8. Survivorship curve based on skulls from Lamy amphibian quarry. LOG_{10} number of survivors is plotted against skull midline length in mm ($N = 14$).

expectation of long life and then die more or less simultaneously after the characteristic life span for the species (Deevey, 1947). However, in the curve for the Lamy metoposaurids, the smallest size is not the hatchling or even a juvenile size, but rather a relatively large size of a presumed adult animal (Fig. 8). This observation appears typical of documented mass death mass death assemblages of metoposaurs (Hunt, 1993), including Rotten Hill, Texas – *Buettneria* population $N>60$; Argana, Morocco, Dutuit's site 13 – *Dutuitosaurus* population $N>70$ (Dutuit, 1976); Krasiejow, Poland – *Metoposaurus* population $N>66$ (Sulej, 2007); all the individuals in these bonebeds are apparently adults (Rinehart et al., 2008).

5. Discussion

5.1. Previous taphonomic analyses

Romer's (1939) idea of a receding pool of water in which the Lamy metoposaurids died was little more than an interesting suggestion presented in a semi-popular article without any real supporting data. At the Lamy amphibian quarry, sedimentological evidence of a pond and features associated with a drought are absent. The evident disassociation and alignment of bones in the MCZ and USNM quarry slabs indicates that some hydrodynamic sorting must have been involved in formation of the bonebed (Hunt and Lucas, 1989, 1995). However, only Zeigler et al. (2002) attempted an analysis of the taphonomy of the Lamy bonebed, prior to the work presented here.

Zeigler et al. (2002) based their analysis on what we would call "forensic taphonomy" – they did not have access to the bonebed or to detailed records from previous collecting and preparation (none was kept that we are aware of), so they had to base their analysis on limited field notes and the published, collected fossils (a similar forensic taphonomic analysis of a Chinle bonebed was presented by Fiorillo et al., 2000). Thus, they relied on 1947 field notes by David Dunkle of the USNM excavation to understand the stratigraphic setting of the quarry (Zeigler et al., 2002, Fig. 2), and on the two collected quarry slabs, one at MCZ the other at USNM (Fig. 2), for which Colbert and Imbrie (1956) published photographs and some metric data.

The "forensic taphonomy" approach of Zeigler et al. (2002) led to the mistaken impression that few limb elements are present in the bonebed because limb elements were removed from the MCZ block and plastered over in the USNM block. The NMMNH block has numerous limb elements (Fig. 5), and many limb elements removed from the Harvard block remain in the MCZ collection. Zeigler et al. (2002, Fig. 4) established rose diagrams for the two excavated blocks, but assigned all the bones present to Voorhies groups I and II. Nevertheless, Zeigler et al.'s (2002, p. 282) overall conclusion that "the

Lamy amphibians died in a catastrophic mortality event and were subsequently transported" is supported by our analysis based on more extensive data.

5.2. Taphonomy of the Lamy metoposaurid bonebed

The Lamy amphibian quarry is a macrofossil bonebed that we see as a physical (hydraulic) concentration using the genetic framework for vertebrate skeletal concentration of Rogers and Kidwell (2007, fig1.1). The total disarticulation of skeletal elements in the bonebed and their evident preferred orientation (=current alignment) is prima facie evidence of hydraulic concentration. However, the near monotaxy of the Lamy amphibian quarry assemblage suggests a biological concentrating mechanism (feeding?/mating?) of a metoposaur population prior to death, disarticulation and hydraulic concentration (Fig. 9). Thus, the Lamy amphibian quarry is a mass death assemblage with a hydraulic overprint (Rogers and Kidwell, 2007, Fig. 1.6). However, as a hydraulic concentration, the Lamy amphibian quarry is unusual because the bones are in mudstone, not in a fluvial channel deposit.

Behrensmeyer (2007) distinguished abiotic from biotic processes in bonebed formation. She argued that abiotically concentrated bonebeds are typically diverse, whereas biotically concentrated bonebeds have low diversity. This fits the idea that the Lamy amphibian quarry reflects an original biotic concentrating mechanism, followed by an abiotic overprint (Fig. 9).

In the Eberth et al. (2007a) classification of bonebeds, the Lamy amphibian quarry can be described as low diversity multitaxic and monodominant (one taxon numerically dominant). This is a fairly common type of bonebed, but Lamy is unusual because of the complete disarticulation of skeletal elements and its sedimentary context. Eberth et al. (2007a, p. 123) note that "monodominant bonebeds most frequently form and develop in settings with low transport and reworking potential" and are often interpreted as catastrophic. This suggests that some sort of gregarious behavior underlies the formation of monodominant bonebeds (also see Currie, 2000).

Significantly, as Brinkman et al. (2007) argue, monodominant bonebeds are very useful for inferring paleobehavior. Thus, they note that "aggregation paleobehavior is frequently cited as an influence in the formation of bonebeds…, especially in those cases where a site contains enormous numbers of individuals of one species…" (Brinkman et al., 2007, p. 231). However, as they note, attritional mortality can lead to monodominant bonebeds and stress (e.g., drought, fire) can cause the aggregation of animals. Indeed, drought is commonly posited as a cause of aggregation (Brinkman et al., 2007, p. 238–239).

We have reviewed geological and taphonomic data on the Lamy bonebed based on the protocols of Eberth et al. (2007b), also see Munthe and McLeod, 1975; Behrensmeyer, 1991). Particularly important data include sedimentary context, sample size, counting individuals, taxonomic representation and relative abundance, age profile, body size, skeletal articulation and association, skeletal completeness, bone orientation and bone modification. These data lead us to posit the following sequence of events leading to formation of the Lamy bonebed (Fig. 9):

1. Aggregation of a large number of metoposaurid amphibians (cause of aggregation unknown) at a site different from the location of the Lamy amphibian quarry, though not distant.
2. Catastrophic mass mortality of the metoposaurids by an unknown agent. Ironically, the drought-death scenario envisioned by Romer (1939) remains a possibility (though direct evidence is lacking) as the agent of death of the Lamy metoposaurids.
3. Complete disarticulation and disassociation of the metoposaurid skeletons.
4. Rapid transport of the disarticulated bones onto a floodplain surface that was undergoing pedogenesis.
5. Rapid burial of the bones by clay, followed by continued pedogenesis.

5.3. Comparison to other Triassic metoposaurid amphibian bonebeds

Lamy is one of four well-known metoposaurid amphibian-dominated bonebeds in Upper Triassic strata; these are records from the Upper Triassic of Morocco and the Upper Triassic of the western USA (Case, 1932; Colbert and Imbrie, 1956; Dutuit, 1976; Romer, 1939). One of these bonebeds, in Morocco, included articulated to associated skeletal material, so it differs fundamentally from the Lamy bonebed. However, the other metoposaurid bonebeds known in the Chinle Group of the western USA, are characterized by totally disarticulated and disassociated bones. The Upper Triassic bonebed at Krasiejow, Poland also contains totally disarticulated and disassociated metoposaurid bones (Sulej, 2007), but this bonebed also includes numerous skulls and other bones of non-metoposaurids (primarily archosaurian reptiles), so we do not compare it to the monodominant and nearly monotaxic metoposaurid bonebeds.

Thus, Dutuit's (1976) Argana, Morocco site 13 apparently preserves a case of a catastrophic death assemblage caused by a drying pond, much as Romer (1939) had suggested for the Lamy bonebed. Dutuit and his crews found a very high density, essentially monospecific assemblage of approximately 70 large individuals of the metoposaur *Dutuitosaurus ouazzoui* in a 30 m^2 area. The quarry itself did not contain mud cracks, but they were seen surrounding the quarry in the same facies. Most of the skeletons were articulated and many were nearly complete. There was no imbrication of the bones or skeletons and no calcrete pebbles were present. Significantly, all of the largest individuals were found in the center of the deposit surrounded by a ring of smaller animals, which had apparently been forced out as the pond decreased in size.
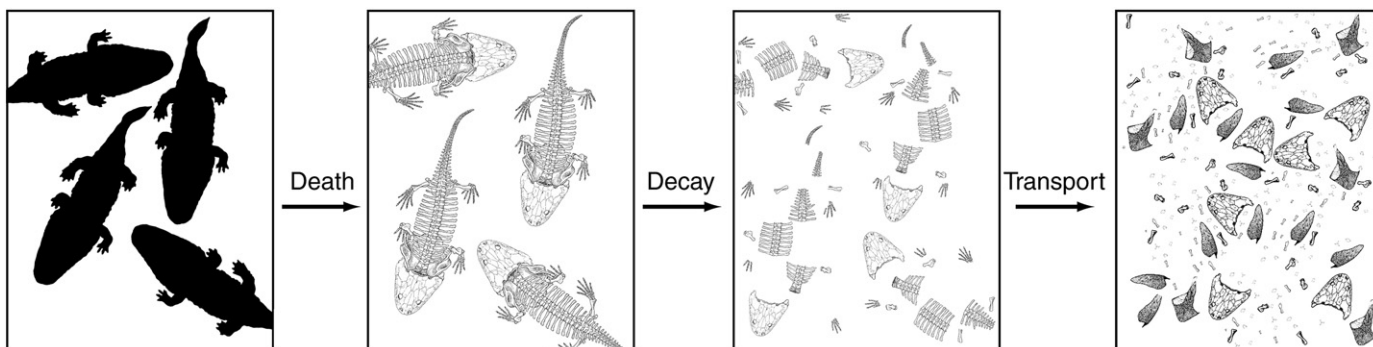

Fig. 9. Schematic representation of events that lead to the formation of the Lamy amphibian bonebed. A population of metoposaurs died at one location, decayed to disarticulated bones, and these bones were transported to the current location of the Lamy amphibian bonebed.

In contrast, the other metoposaurid bonebeds, in Texas–New Mexico, USA, are characterized by disarticulated bones packed into beds that show clear evidence of hydraulic transport and sorting of the bones. The Texas bonebeds (Rotten Hill and Scurry County) preserve the metoposaurid bones in sandy and conglomeratic strata that are clearly fluvially-transported channel deposits. In contrast, the Lamy bonebed preserves the bones in a finer-grained deposit that we interpret as a floodplain surface onto which the bones were transported.

All of these metoposaurid bonebeds are monodominant and nearly monotaxic. They thus imply that metoposaurids aggregated in life to die suddenly and be preserved either at the site of death (Morocco) or to be transported to a final resting place (USA). The cause of aggregation in Morocco seems to have been a drought that forced the animals into a pond, whereas in the USA bonebeds the cause of aggregation is less certain.

The likely cause of aggregation may be indicated by Rinehart et al (2008), who investigated growth and age structure in *Buettneria perfecta* from the Lamy amphibian quarry and from Rotten Hill, in the Tecovas Formation of West Texas. They compared data from the metoposaurs in these mass death assemblages to extant salamander outgroups (e.g., *Andrias*, *Cryptobranchus*, *Chioglossa*, others) and other amphibians to show that growth was indeterminate and that probably only sexually mature adults (marked by size, slow linear growth, and age distribution shape) were present in the fossil assemblages. Their analysis of the Rotten Hill population showed that the diameter of *Buettneria* limb bones grew in strong negative allometry; e.g., the allometric constant for femur length versus midshaft diameter $= 0.78$, where a constant of 1.5 is required to maintain constant stress on the limb bones throughout growth. Thus, the weight-bearing capacity (strength) of the limbs relative to body size (stress) decreased drastically throughout adulthood. Based on these results, Rinehart et al. (2008) hypothesized an ecological separation of juveniles and adults in *Buettneria,* similar to that seen in some extant amphibians. Such a separation probably could have served to reduce competition for food and conspecific predation of the juveniles. The decreasing relative strength of limb bones in the adults may have enforced such an ecological separation by making adults water-bound while the juveniles could have been more terrestrial. The implication of this preliminary investigation is that mass death assemblages of metoposaurids, like that of the Lamy amphibian quarry, probably represent breeding populations.

Acknowledgments

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