Mud-trapped herd captures evidence of distinctive dinosaur sociality

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A unique dinosaur assemblage from the Cretaceous beds of western Inner Mongolia preserves geologic and paleontologic data that clearly delineate both the timing and mechanism of death. Over twenty individuals of the ornithomimid *Sinornithomimus dongi* perished while trapped in the mud of a drying lake or pond, the proximity and alignment of the mired skeletons indicating a catastrophic mass mortality of a social group. Histologic examination reveals the group to consist entirely of immature individuals between one and seven years of age, with no hatchlings or mature individuals. The *Sinornithomimus* locality supports the interpretation of other, more taphonomically ambiguous assemblages of immature dinosaurs as reflective of juvenile sociality. Adults of various nonavian dinosaurs are known to have engaged in prolonged nesting and post hatching parental care, a life history strategy that implies juveniles spent considerable time away from reproductively active adults. Herding of juveniles, here documented in a Cretaceous ornithomimid, may have been a common life history strategy among nonavian dinosaurs reflecting their oviparity, extensive parental care, and multi-year maturation.

Key words: Dinosauria, Ornithomimosauria, taphonomy, herding, sociality, miring, drought, Cretaceous.

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Introduction

Fossil assemblages from trilobites to tyrannosaurs provide important insight into the sociality and population dynamics of extinct species (Voorhies 1969; Hulbert 1982; Klein 1982; Speyer and Brett 1985; Speyer 1991; Currie 2000; Tinn and Meidla 2003). However, discerning the biological significance of these assemblages requires an unambiguous understanding of the underlying processes governing their formation (Voorhies 1969; Klein 1982; Speyer and Brett 1985; Patterson et al. 2007).

Sites dominated by a single dinosaur species have commonly been used to support hypotheses of herding, sociality and population structure and growth (Gilmore 1917; Currie and Dodson 1984; Ostrom 1986; Norman 1987; Forster 1990; Rogers 1990; Jerzykiewicz et al. 1993; Varricchio and Horner 1993; Schwartz and Gillette 1994; Bilbey 1999; Ryan et al. 2001; Fiorillo and Eberth 2004; Eberth and Getty 2005; Scherzer and Varricchio 2005; Lehman 2006; Zanno and Erickson 2006; Garrison et al. 2007; Gates 2006; Myers and Storrs 2007; C. Suarez et al. 2007; M. Suarez et al. 2007; Zhao et al. 2007). However, these assemblages typically show significant evidence of post-mortem processes such as disarticulation, carcass and bone transport, and bone loss through winnowing, sorting, scavenging, and weathering (e.g., Rogers 1990; Varricchio and Horner 1993; Eberth and Getty 2005; Myers and Storrs 2007). The overprinting of these assemblages by largely abiotic and protracted processes makes determination of both the cause and timing of death impossible or speculative at best and complicates behavioral and ecological interpretations. Some localities may simply reflect attritional and selective processes such as serial predation and agonistic interactions at favored waterholes (Haynes 1988; Roach and Brinkman 2007). The least biased assemblages result from catastrophic and non-selective mortality, in which animals make a rapid transition from the biosphere to the rock record (Voorhies 1985).

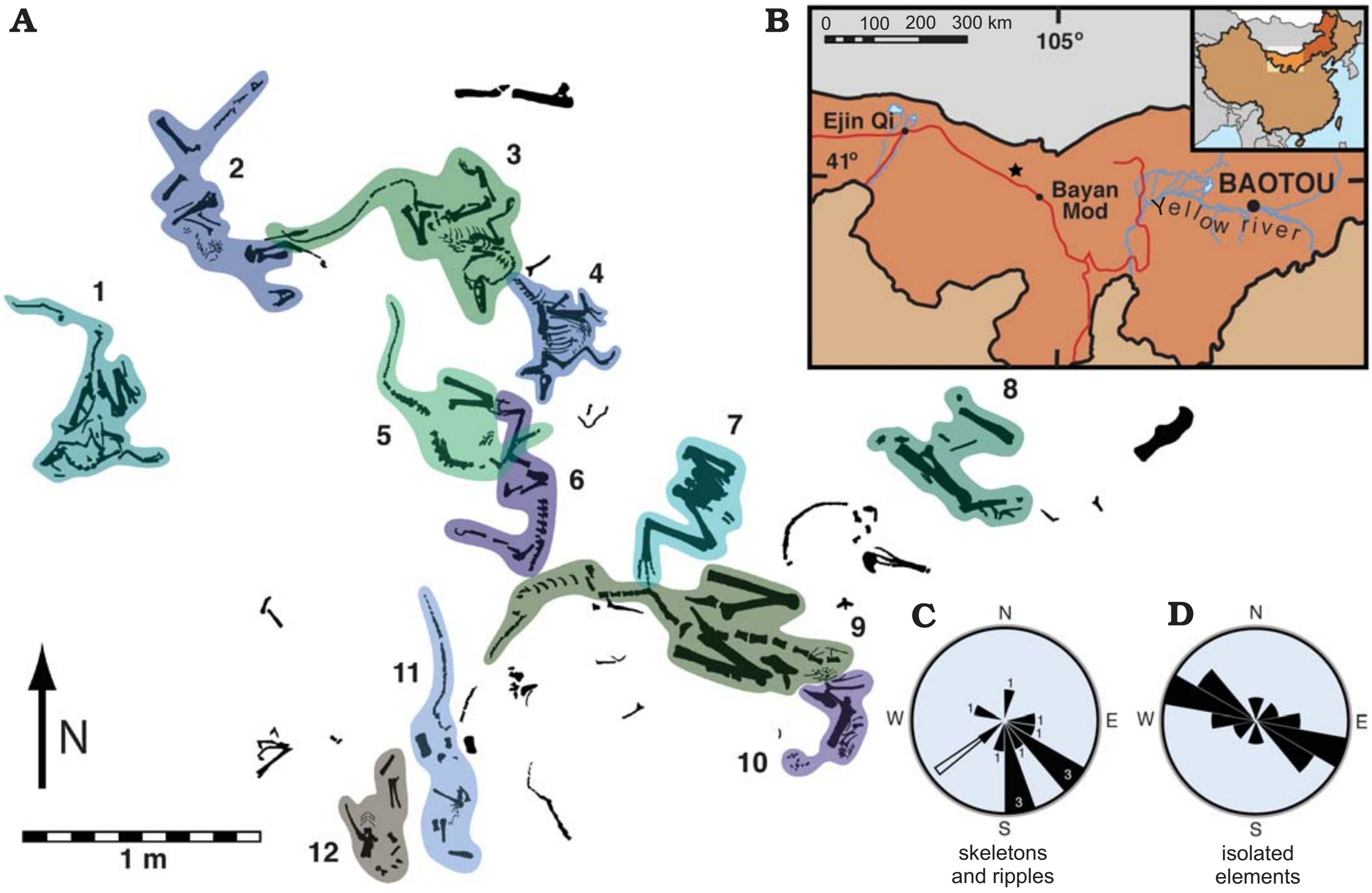

Fig. 1. Suhongtu site, partial quarry map, locality map, and orientation data. **A**. Map of the central and northern portions of site showing the position of 12 of 13 skeletons. Skeletons 3 and 4 enlarged in Fig. 3. **B**. Fossil locality (41°17' 10"N, 103°52'38"E) located 90 km northwest of Bayan Mod, Inner Mongolia, China. **C**. Rose-diagram showing trends for skeletons (black, numbers denote skeleton count) and ripples (white). **D**. Mirror rose-diagram of elongated, isolated elements ($n = 13$). Trends of skeletons have a strong, non-random ($p < 0.002$) alignment to southeast. Flow direction of ripples is roughly perpendicular to that of elongate elements.

A dense, monospecific assemblage of the recently named ornithomimid dinosaur *Sinornithomimus dongi* Kobayashi and Lü, 2003 comes from the Upper Cretaceous Ulansuhai Formation of Inner Mongolia (Fig. 1B). Previous excavations had collected an assemblage of 14 primarily juvenile individuals showing uniform preservation with no weathering and little evidence of post-mortem transport. Although the exceptional preservation of these specimens has been noted (Kobayashi et al. 1999; Kobayashi and Lü 2003), the circumstances surrounding their accumulation have remained elusive. We present evidence that these ornithomimids perished after becoming entrapped along the margins of a drying lake. Their uniform, circumscribed death and aligned arrangement indicates a catastrophic miring of a herd of *Sinornithomimus*, the juvenile age-profile of which we document with long bone measurements and bone histology.

Institutional abbreviation.—LH, Long Hao Institute for Paleontology, Hohhot, Nei Mongol Autonomous Region, China.

Other abbreviation.—LAG, line of arrested growth.

Geological setting

The Upper Cretaceous Ulansuhai Formation crops out in the southern Gobi Desert within the western portion of the Nei Mongol (Inner Mongolia) Autonomous Region, People's Republic of China. The formation unconformably overlies Lower Cretaceous clastics and volcanics (Bureau of Geology 1991). Radiometric dating of these volcanic rocks suggests a maximum age of 92 Ma for the Ulansuhai Formation (Bureau of Geology 1991). Although dominated by red mudstone and siltstone, the formation also contains evaporites, calcretes, and coarser fluvial clastics. The Ulansuhai Formation is one of many rock units representing continental deposition within the Cretaceous Gobi Basin. Through this period the region experienced an increase in overall aridity and a shift from lacustrine and fluvial Lower Cretaceous facies to predominantly aeolian dune and associated interdune facies in the Upper Cretaceous (Jerzykiewicz 2000). The *Sinornithomimus* locality occurs approximately 30 km northwest of the town of Suhongtu, Nei Mongol (Fig. 1B).

Site description

Sedimentology.—The skeletons are preserved within a 1.3 m-thick unit consisting predominantly of red and blue-gray claystone interbedded with siltstone to very fine sandstone (Fig. 2). Although some of the coarser units are tan to reddish tan in color, coloration is otherwise not controlled by grainsize. Blue-gray mottling occurs within red horizons and visa versa. Mottling is often concentrated along contacts between red and blue-gray beds (Fig. 2B). Bed thicknesses, visible even within extensive zones of deformed bedding, range from thinly laminated to very thinly bedded (< 3 to 30 mm thick). Ripple-scale cross-bedding occurs in the very thin sandstone beds (Fig. 2C). Planar exposures reveal at least two horizons with sand-filled mudcracks. Deformed bedding consists either of convoluted or disrupted laminae. In the latter, bedding laminae in a zone several centimeters thick are crosscut by vertical gaps 1–2 cm wide and infilled with red mudstone. Laminae curve downwards as they approach the gap (Fig. 2C).

The upper 12 cm of this unit displays vertical root-traces, clay-lined peds, i.e., aggregates of soil (Retallack 1990), and burrows with reduction halos and grades into the overlying mudstone. This and subsequent overlying massive and blocky mudstone units exhibit a variety of additional pedogenic features, including mottling, slickensides, uncommon calcite concretions, and gilgai microrelief (Retallack 1990). Only 40 cm of the unit underlying the 1.3 m skeleton-bearing unit were exposed. This tan red mudstone exhibited blue-gray mottling concentrated towards its top and burrows with reduction halos.

The bulk of the ornithomimid skeletons lay at the top of a 10 cm-thick zone of deformed bedding and 20 cm above the base of the 1.3 m thick unit (Fig. 2B, C). Abundant blue-gray mottling distinguishes the upper 2–3 cm of mudrock just beneath the bone. Planar exposures of the bone horizon in the northwest portions of the quarry reveal sand-filled mudcracks. Concentrations of ostracods, cf. *Cypridea* or *Pseudocypridea*, up to 5 mm thick, occur in irregular patches some-

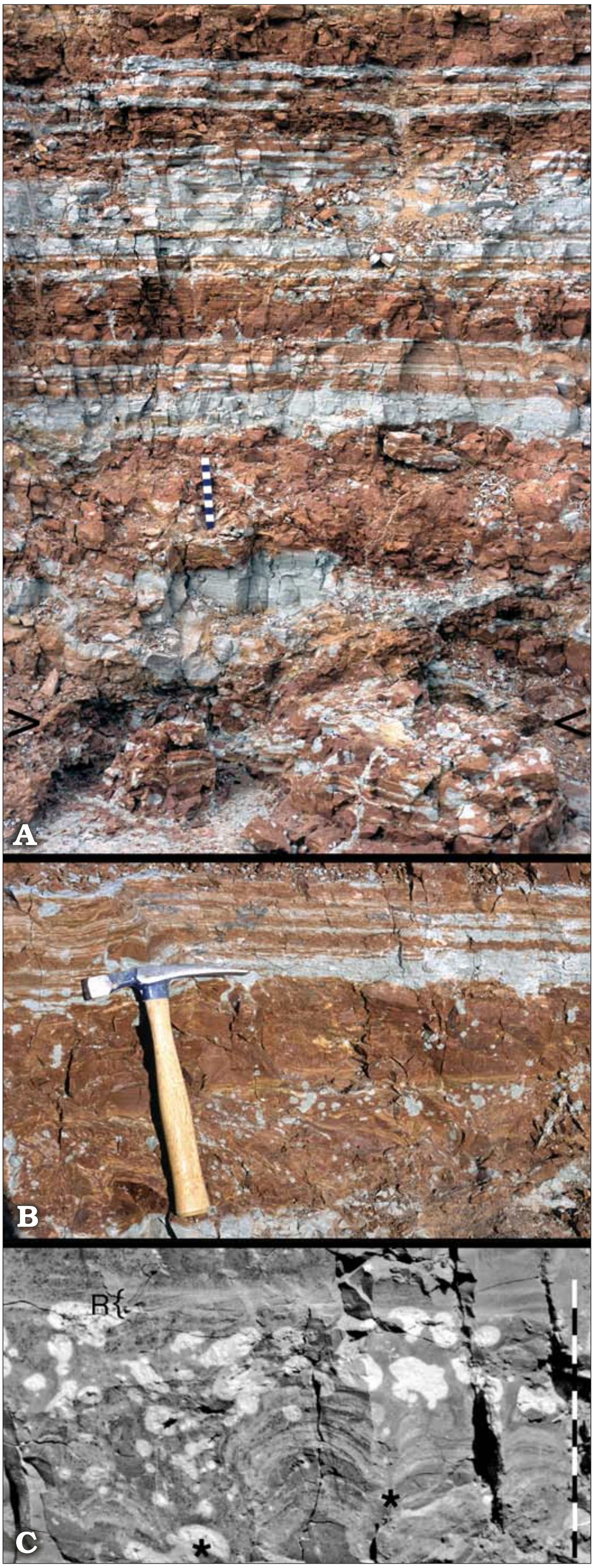

Fig. 2. Sedimentary profile of the Suhongtu quarry. **A**. Laminated to very thinly bedded, red and blue-gray unit with a total thickness of 1.3 m. More massive mudstones (not shown) under- and overlie this unit. Main bone-producing horizon located near base (marked by **> <**) at top of mottled interval. Scale bar 10 cm. **B**. Close-up sedimentary profile of the Suhongtu quarry. The principal bone horizon lies at the midway point of the hammer handle. This unit consists of abundant convoluted bedding and is marked by blue-gray mottling near its top. A thin, light-colored sandstone immediately overlies this unit. Hammer length equals 27.6 cm. **C**. Close-up of main bone-bearing unit with partially collapsed, infilled footprint structures in laminated claystone. Ripple-scale cross-stratification (R) in thin (1 to 2 cm) very fine sandstone that lies immediately above the main bone horizon. A great abundance of mottling occurs near the top of this bone-bearing unit. Asterisks mark the lower ends of V-shaped disruption structures, where footfalls and digits have bisected underlying laminated units. The down curved lamina and uniform fills of these structures suggest the original substrate was soft and only partially consolidated. Scale bar 10 cm.

Table 1. Taphonomic condition of the recently excavated *Sinornithomimus* skeletons from the Upper Cretaceous Suhongtu locality, Nei Mongol. Numbers correspond to Fig. 1A. Femur lengths in cm. Skeletons are fully articulated except for disarticulated associated material or missing elements. Several specimens were in part truncated by recent weathering resulting in bone loss (marked †). Loss of ilia or other pelvic elements, however, cannot be attributed to recent weathering. *Posture* refers to the orientation of the pelvis and hind limbs with *upright* referring to specimens whose hindlimbs and pelvic girdles maintain a life-like orientation and extend deep into underlying strata. Specimens 3, 4, and 9 were sampled for histology.

Skeleton	Repository number	Femur	Trend [°]	Posture	Associated material	Missing elements
1	LH PV8	18.3	168	upright	some ribs	dorsals, some ribs, sacrum, ilia, some proximal caudal arches
2	LH PV9	19.5	226	upright	skull, some ribs, hind limbs	cervicals, dorsals, some caudals, some ribs, ilia
3	LH PV5	21.6	155	upright		ilia, sacral arches, 2 cervical ribs
4	LH PV6	19.4	174	upright, torso on right	some ribs, dorsal centra	some dorsal arches, left ilium
5	LH PV10	~ 20	128	upright, torso on right	some left ribs	skull, cervicals, ilia
6	LH PV11	~18	177	on left	–	skull, right ribs, right ilium
7	LH PV12	~22	128	upright	–	skull, cervicals, dorsals, ribs, gastralia, forelimbs
8	LH PV13	30.5	121	upright	ribs, caudals, ilium	skull, cervicals, dorsals, most ribs, gastralia, forelimbs, ilium, portion of left femur
9	LH PV7	36.4	101	upright	some ribs	cervicals, some dorsals, some ribs, ilia, sacrum, some caudal arches, some caudals†
10	LH PV14	~23	87	upright	partial skull, few ribs,	partial skull cervicals, dorsals, most ribs, ilia, some caudals†
11	LH PV15	~20	188	upright	ribs, gastralia, portions of forelimbs	skull, cervicals, dorsals, some ribs, ilia†
12	LH PV16	~ 20	2	upright	ribs, forelimbs	skull, cervicals, dorsals, most ribs, gastralia, ilia†
13	LH PV17	20.5	201	upright	ribs, forelimb	skull, cervicals, dorsals, some ribs, ilia†

times adjacent to or on top of the uppermost bones. More commonly, a 2-cm thick, very fine sandstone with ripple-scale cross-stratification indicating a current direction of 230° overlies the bones (Fig. 2B, C).

Two additional horizons within the 1.3 m unit produce minor amounts of isolated bones. As with the main bone horizon (Fig. 2B), both sit at the top of a zone of convoluted bedding and are associated with some or all of the following: drab, blue-gray burrows, mudcracks, V-shaped disruption structures, and ostracods.

Bone assemblage.—Recent excavations yielded 13 partially articulated skeletons. Although these vary in their completeness from a minimum of the pelvic girdle with portions of the hind and fore limbs to nearly complete skeletons, they all show a consistent pattern of preservation (Figs. 1A, 3, Table 1). Twelve of the 13 individuals retain an articulated pelvis and hind limbs with most in a life-like crouched posture. All flexed hind limbs, elongate shafts of the ventral pelvis, and some forelimbs plunge down into the sediments as deep as 40 cm crosscutting underlying strata (Fig. 3E, F). Articulated tail sections occur in some specimens and often extend down 25 to 30 cm and occasionally curl back up through the underlying beds. The extraordinary burial depth for such small-sized skeletons and flexed posture of many intact pedes suggest entrapment within deformable mud. Penetration depths likely represent minimum values given normal sediment compaction resulting from burial. One skeleton shows an unusual twisted cervical series (Fig. 3B) rather than the posteriorly arched death pose common to many theropod specimens (Faux and Padian 2007). Throughout, a drab, blue-gray halo, roughly 5 mm thick, surrounds nearly all articulated skeletal elements (Fig. 3E, F) and suggests that decomposition of the trapped carcasses rapidly shifted from aerobic to anaerobic pathways creating reducing conditions in immediately adjacent sediments (Allison 1988).

In contrast to the plunging limbs and tails, skeletal portions on the main bone horizon are more variably preserved. This difference likely reflects their exposure to postmortem disarticulation, scavenging and transport. Final resting posture strongly influenced preservation. For example, skeletons resting on their ventral side retain articulated gastral baskets (Fig.

Fig. 3. Skeletons 3 and 4 (Fig. 1), respectively LH PV5 and LH PV6 (to left), of *Sinornithomimus dongi* Kobayashi and Lü, 2003 at Suhongtu, showing preservational features indicative of catastrophic miring of an immature herd; in plan view (**A**–**D**) and in cross-sectional view (**E**, **F**). **A**. Skeletons overlap and have parallel body axis orientation. **B**. The short snout, unfused neurocentral sutures and estimated age (1–2 years) indicate immaturity. Note the unusual curvature in the neck. **C**. The intact pelvis is missing only the superficially positioned left ilium. **D**. A gastrolith mass and carbonized stomach contents (anterior and posterior to the gastroliths) lie within the ribcage and gastral basket. Left shank and pes (**E**) and forelimb (**F**) with flexed ungual phalanges lodged deep in the claystone in near-vertical orientations. Remaining portions of the skeletons lie above in a horizontal plane that represents the ground surface at the time of miring (marked by **> <**). A bluish-gray halo surrounds all bones. Scale bars 10 cm.

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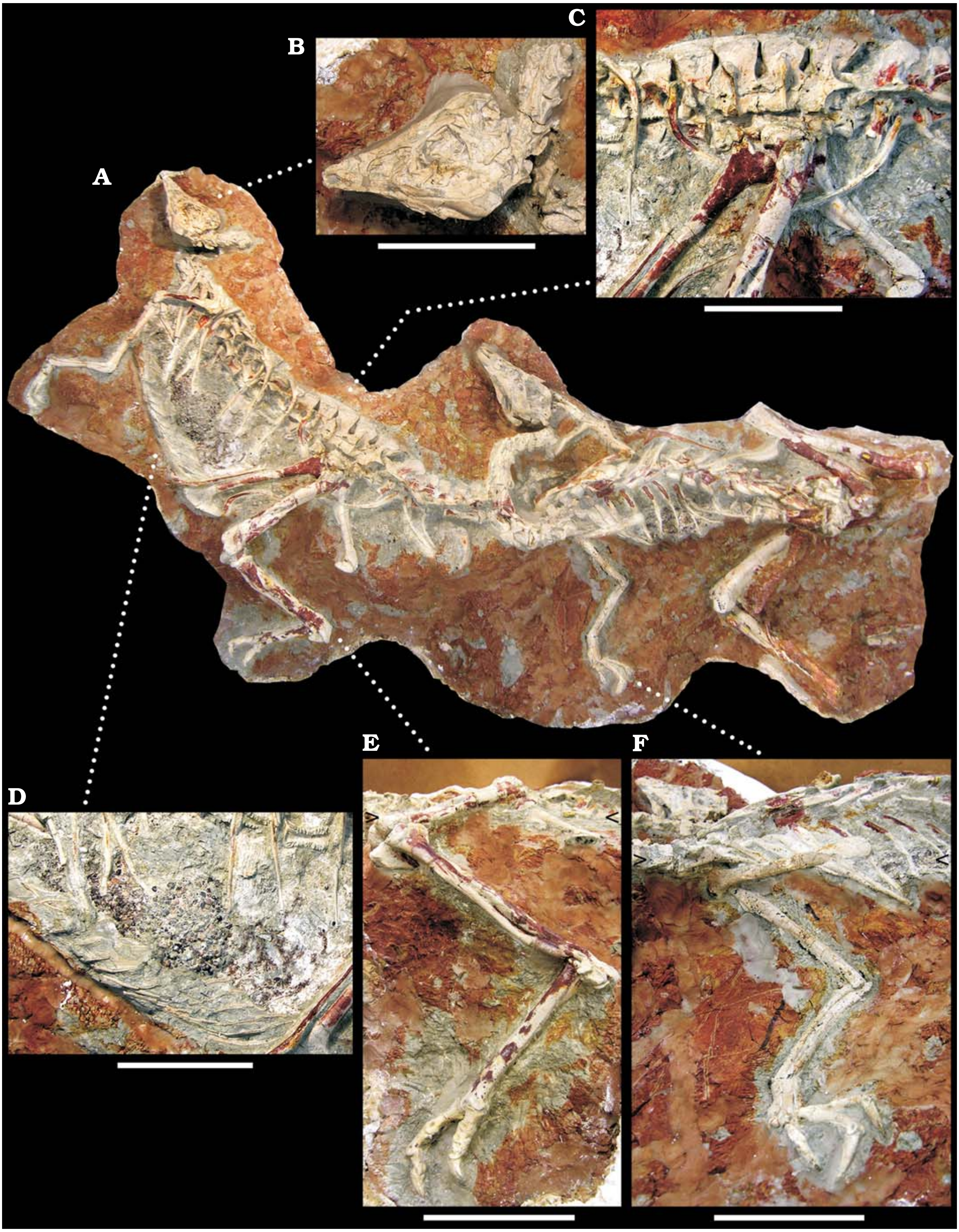
A
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E
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3A) but sometimes lack dorsal vertebrae and ribs. Skeletons lying on their right side, similarly, preferentially preserve the right rib series as compared to the left. Only a few individuals retain full dorsal and cervical vertebral series. More commonly, a scattering of associated bones lies on the main bone horizon anterior to the pelvis. Despite the universal presence of pubes and ischia in natural articulation, few preserve either ilium, a large bone that would have been exposed near the surface (Fig. 3C). Nine of 13 skeletons lack both ilia and several are missing the sacrum as well. Further, evidence of selective bone removal after entrapment includes a series of centra and another of chevrons that remain in life position despite the absence of neural arches and vertebrae, respectively. Nevertheless, several individuals display exceptional preservation. Presence of intact gastrolith masses (Kobayashi et al. 1999), carbonized stomach contents (Fig. 3D), and sclerotic rings within orbits suggests limited subaerial exposure.

Trends of individual skeletons were measured toward the head and perpendicular to a line connecting right and left sides of the pelvis. The skeletons show a strong preferred orientation toward the southeast, with ten of the 13 specimens facing between 87° and 188° (Fig. 1C, Table 1). That this represents chance alignment is extremely improbable ($p < 0.002$).

Additional skeletal material not clearly associated with specific individuals occurs across the main bone horizon. This includes a few articulated sections of caudal and cervical vertebrae, four forelimbs, and isolated elements. The 52 isolated elements consist primarily of vertebrae, centra, ribs and gastralia. Bones of the forelimb, shoulder girdle and skull are rare ($n = 3$) and with the exception of a single ilium, no pelvic or hind limb elements occur. Eleven elements remained unidentifiable in the field. Of the identifiable material, all but one element are assignable to *Sinornithomimus*. This material largely corresponds to elements missing from the articulated skeletons. All lack the drab, blue-gray halo that surrounds the skeletons. Elongate, isolated elements show a preferred orientation, aligning along a west-northwest to east-southeast axis (Fig. 1D, Table 2). Nearly all bones, whether isolated or from articulated skeletons, are well preserved, complete, and un-weathered.

Table 2. Trends and plunges of isolated, elongate elements. Strike and dip of bedding plane measured 80°, 10° N.

Element	Trend [°]	Plunge [°]
rib	268	38
rib	301	15
rib	264	6
rib	255	1
rib	286	4
rib	283	9
chevron	290	6
metacarpal	348	14
metacarpal	18	9
femur	314	16
metatarsus	41	5
unidentified	305	10
unidentified	287	7

Among both articulated and disarticulated material, only four bones clearly show breaks, although final preparation of all specimens may potentially reveal more broken elements. A femur of the most disturbed skeleton is truncated high on the shaft, leaving the proximal end in articulation with the ischium and pubis, while the remainder lies some 40 cm away. A partial femur on another specimen similarly remains in articulation. Two breaks occur within a tibia of an articulated hind limb with the mid shaft slightly displaced. Broken pieces of the sole remaining disarticulated ilium remain in contact; the crushed, abnormal, and concave-up arrangement of these fragments suggests damage by trampling. Although tooth marks and borings were not observed on any bones, elongate irregular masses less than 2 cm wide and consisting of finely macerated bone fragments occur on and below the bone horizon. These may represent coprolites or possibly bone-chipped filled burrows (Paik 2000).

Histology

All of the recently excavated Suhongtu ornithomimids are immature individuals (Figs. 4, 5). The largest retains completely open neurocentral sutures in all preserved vertebrae (dorsal to mid caudal) while the smallest exhibits a proportionately short snout. Using the femur as a rough proxy for body size, most of the skeletons have femora between 18 and 24 cm in length, or less than half the femoral length (48 cm) estimated for the largest known individual (Kobayashi and Lü 2003) (Fig. 5). To assess the ontogenetic age of the ornithomimids, histologic samples of tibia, fibula and rib were obtained for three individuals with femoral lengths of 19.4, 21.6, and 36.4 cm, respectively. Cross-sections were prepared for each element using standard paleohistologic techniques (Wilson 1993; Lamm 1999, 2001), and examined with light microscopy. Age at death was assessed from annual lines of arrested growth (LAGs) (Erickson 2005). Histology of the three elements is largely consistent for each individual. For example, the fibula of the largest individual shows a comparable set of LAGs within the fibrolamellar tissue to that of the tibia. Additionally, the cortex of all elements consists of fibrolamellar bone with primarily longitudinally arranged osteons.

The pair of smaller individuals (Fig. 3A) shows only a single line of arrested growth. The tibia of the slightly larger one (Fig. 3A, right skeleton) bears a circumferential band of laminar bone with a parallel crystal arrangement that likely corresponds with the single LAG in the rib and fibula (Fig. 4A). Presence of a single LAG indicates that these two individuals were between one and two years of age at the time of death. The longer skull length (134 versus 114 mm) of the slightly larger individual suggests that it may belong to an earlier brood from the same breeding season.

The tibia and fibula of the largest individual sampled display four LAGs, but their larger medullary cavity (compared to smaller individuals) suggests that a few initial LAGs may have been lost to endosteal remodeling (Fig. 4B). Spacing of preserved LAGs is consistent between the tibia and fibula and both possess incompletely developed outer osteons with wide osteonal canals (Fig. 4C). The rib bears seven unequally spaced LAGs. A wide region with multiple rows of osteons separates an inner and outer set of more closely spaced LAGs.

Discussion

Depositional environment.—The short stratigraphic section visible at the Sohongtu locality consists of a fine-grained, laminated to very thinly bedded unit sandwiched between more massive, fine-grained units with a variety of soil-related features. These underlying and overlying units lack any architectural elements suggestive of fluvial channels and are more representative of overbank deposition (Miall 1996). The lamination and very thin beds of the intervening unit represent slow deposition under quiet, low-energy conditions and an absence of significant invertebrate or vertebrate bioturbation. Abundance of ostracods like *Cypridea* within this interval favors a freshwater environment such as a pond or lake for the main burial unit. Insufficient outcrop exists at the locality to determine the aerial extent of this ponding environment. However, the short stratigraphic extent and bounding overbank units suggest a temporarily limited feature. The gradual transition of the laminated unit to more massive mudstones with a variety of soil-related features (e.g., slickensides, peds, carbonate nodules) reflects the eventual infilling of the pond or lake. An arid to semi-arid climate is suggested by caliche horizons, evaporites and gilgai structures found either in the Sohongtu locality section or in nearby outcrops of the Ulansuhai Formation (Bureau of Geology 1991).

A striking aspect of the laminated unit is the alternating red and blue-gray coloration (Fig. 2A, B). The color and concentration of blue-gray mottling along specific horizons is consistent with gleization. In this process, the activity of microorganisms depletes stagnant water of oxygen leading to the eventual reduction of minerals by anaerobic microbes (Retallack 1990). A similar process also likely accounts for the blue-gray coloration surrounding articulated skeletons (see below) and the alternating red and blue-gray horizons throughout the unit. The latter suggests the frequent and repeated stagnation of the water body.

We regard the V-shaped deformation structures of the bone-bearing and two additional horizons as partially collapsed, infilled, toe prints that were made in wet laminated clay. The deformed strata match those identified as footprints at other localities (Agenbroad 1984: fig. 4.4; Melchor et al. 2006: fig. 9H, I) and experimentally produced in wet sediments (Milàn and Bromley 2008). The narrow-toed, sharp-

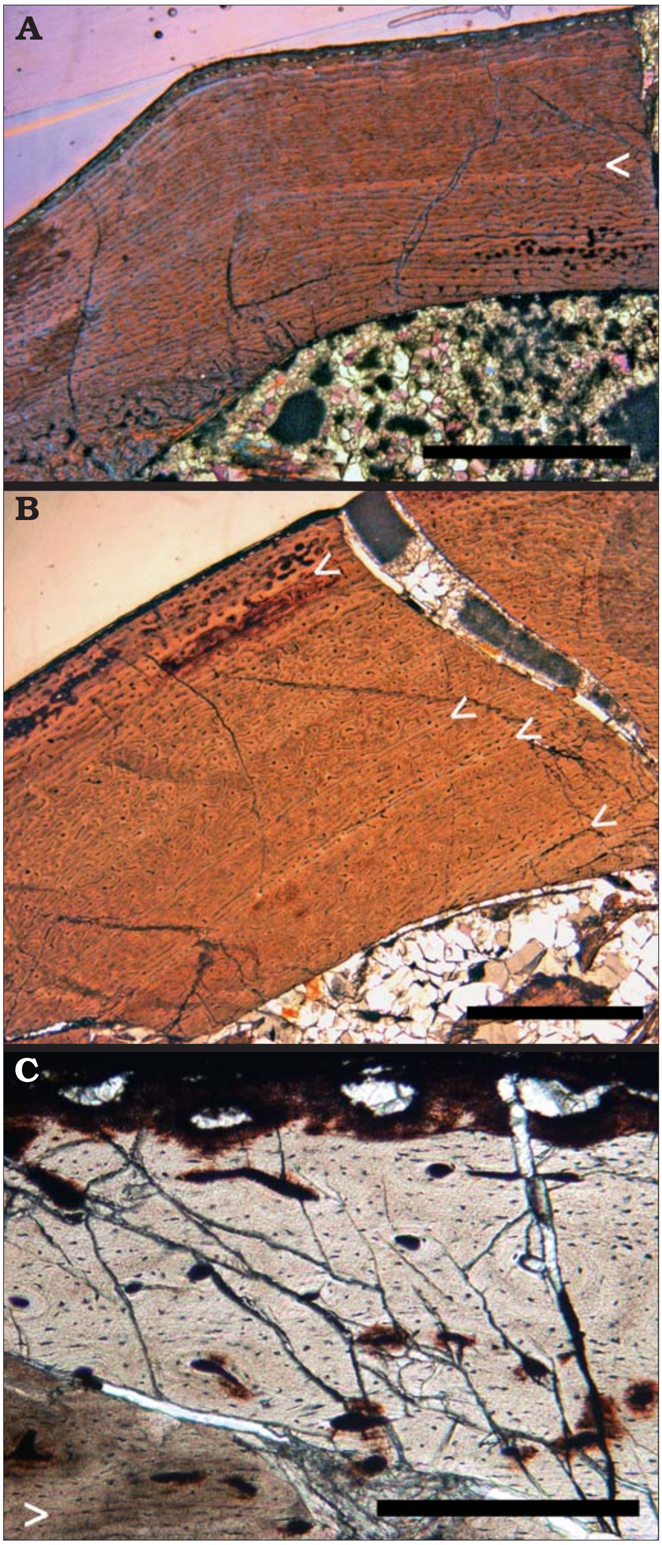

Fig. 4. Histologic cross-sections and age profile of skeletons. **A**. Cross-section of tibial mid shaft from small individual (LH PV5, femur length = 21.6 cm) showing a single band of laminar bone (marked by <) but no LAGs (lines of arrested growth). **B**. Histologic cross-section of tibial mid shaft of the large individual (LH PV7, femur length = 36.4 cm) showing four LAGs (marked by <). **C**. Histologic cross-section showing the exterior of the tibial mid-shaft cortex for the large individual (LH PV7). Note row of developing osteons at the exterior (top of photograph). One LAG visible near bottom of photograph. Scale bar is 2 mm for A, B and 0.25 mm for C.

clawed pedes of the ornithomimids are the appropriate size and shape to have generated these structures.

Taphonomic history.—The Suhongtu site records the catastrophic miring of an ornithomimid herd within a shrinking lake or pond under drying conditions. The mud-anchored carcasses were then scavenged, with some postmortem, low-energy transport of disarticulated elements prior to or during final burial. Although both miring and drought conditions likely contributed to the deaths of the *Sinornithomimus* at this locality, we consider miring as discussed below as the more proximal cause given the more restricted temporal and geographic conditions under which it acts.

Miring.—In modern environments, entrapment in mud is a rare cause of death that requires particular substrate viscosity usually involving the partial drying of water-saturated sediment (Weigelt 1989). Waterlogged initial conditions are evidenced at Suhongtu by the deep penetration of limbs and tails into underlying horizons and the V-shaped footprint disruption structures of these laminae (Fig. 2C). The mud infilling of these footprints indicates the immediate slumping and collapse of the track as the foot was withdrawn, conditions common to waterlogged sediments (Agenbroad 1984; Melchor et al. 2006; Milàn and Bromley 2008). The crosscutting relationship of both the skeletons and footprints with the underlying strata indicates that miring post-dates deposition of these horizons. The coincident die-off of ostracods near and adjacent to the skeletons and sand-filled mudcracks suggest deterioration of the ponding environment and desiccation. Finally, the presence of entrapped ornithomimids (and their associated traces) in a sequence of otherwise finely laminated strata suggests that miring occurred at a time of low water level. Suitable conditions for entrapment are often short-lived, weather dependent, and may last for only days (Weigelt 1989).

Recent and fossil cases of death by miring include a variety of terrestrial vertebrates ranging in size from the foals of feral horses (Berger et al. 2001) to multi-ton dinosaurs (Sander 1992) and include both quadrupeds and bipeds (Stirling 1894; Weigelt 1989; Berger et al. 2001). When trapped in mud, living vertebrates ultimately die from dehydration, starvation and/or predation (Stirling 1894; Weigelt 1989; Berger et al. 2001). Death postures and preservational patterns match those of the Suhongtu ornithomimids and include plunging limbs and preferential preservation of entrapped body parts (Stirling 1894; Weigelt 1989; Sander 1992; Berger et al. 2001) (Fig. 3). Limbs typically extend into the underlying substrate whereas the trunk and head remain at ground level. This condition occurs in 12 of the 13 recently excavated *Sinornithomimus*. Following death, buried limbs remain articulated and intact, while exposed portions experience greater levels and ranges of disarticulation, weathering, and scavenging (Stirling 1894; Weigelt 1989; Sander 1992). The significance of the plunging *Sinornithomimus* tail sections remains ambiguous, but may reflect the struggles of these bipedal animals to free themselves once entrapped.

Variable preservation of the upper portions of the *Sinornithomimus* skeletons suggests a brief period of exposure, decay, and possibly scavenging prior to final burial. Aerobic decay of carcasses requires a large oxygen supply; consequently, most carcasses decompose anaerobically and create reducing conditions and anoxic microenvironments in adjacent sediments (Allison 1988). The drab haloes occurring within the otherwise red and oxic sediments and surrounding the articulated portions of the ornithomimids skeletons (Fig. 3) likely reflect the oxic, then anoxic decay of soft tissue. The absence of such haloes around isolated elements indicates that either scattering occurred after rotting of the flesh or these skeletal portions were of insufficient size to deplete local microenvironments of oxygen. Scavenging may account for the curious absence of ilia and sacra from otherwise articulated pelves. Perhaps carnivores favored the large muscle mass of the hips (Lyman 1994). However, no shed theropod teeth occurred amongst the *Sinornithomimus* skeletons.

Mass mortality.—Several taphonomic attributes of the Suhongtu locality indicate a mass mortality of a social group rather than attritional death of individuals. First, the ornithomimids occur on a single bedding plane. Although some have disarticulated and likely been subjected to scavenging, the absence of weathering on any element indicates minimal subaerial exposure, probably less than one year (Behrensmeyer 1978). Exceptional preservation, including intact gastrolith masses within the ribcage (Kobayashi et al. 1999), carbonized stomach contents (Fig. 3D), and intact sclerotic rings in several individuals, favors relatively rapid burial. Further, miring depends upon specific conditions of water level and substrate viscosity. Any deviations, whether to drier or wetter conditions, would prohibit entrapment. Uniform carcass appearance at modern miring localities reflects both herding behavior and synchronous mortality (Weigelt 1989; Berger et al. 2001). In contrast to the alignment of elongate, isolated bones, the skeletons show a strong orientation to the southeast with ten of the 13 specimens oriented within a 101° arc (Fig. 1C). Similar parallel alignment has been observed in a small flock of flightless birds mired in a Pleistocene lacustrine deposit (Stirling 1894). The consistent preservation, close proximity, and preferred orientation of the *Sinornithomimus* skeletons suggest that these individuals arrived and perished together at this site.

Drought conditions.—Evidence for drying conditions within the lake or pond includes the marginal mudcracks, the associated ostracod assemblages, and the presence of the ornithomimids and their traces. The latter is significant, because the bone-bearing unit consists sequentially of laminated horizons, the mass death horizon, a thin sandstone and a return to laminated strata. The unbioturbated laminae suggest deeper water (Fig. 2A). The presence of the ornithomimids and their traces indicates a time of low water in what was otherwise a deeper water sequence. Although several dinosaur bonebeds have been interpreted as potentially originating due to past drought conditions (Norman 1987; Rogers 1990; Schwartz and Gillette 1994; Gates 2005; Eberth et al. 2006; Myers and Storrs 2007) physical indicators of drought have been limited. Evidence primarily consists of (i) an overall arid to semi-arid paleoenvironment and (ii) the concentration of bones and/or individuals in a flood plain lake or depression. However, these localities may simply represent favorable areas of preservation where weathering rates of bone are slowed and sedimentation rates are higher. Furthermore, most of these assemblages also record significant post-mortem transport of carcasses or bones (Norman 1987; Schwartz and Gillette 1994; Eberth et al. 2006; Myers and Storrs 2007). The Suhongtu locality is unusual in its association with several indicators of drought (ostracod die-off, mudcracks, and footprints in otherwise deeper water deposits) independent of the bone assemblage and a direct linking of mortality (miring) to the drought conditions. The frequent alternation between red and blue-gray horizons within the laminated to thinly bedded unit indicates irregular alternating periods of aeration and stagnation, possibly reflecting wetter and drier conditions. Consequently, the occurrence of three horizons with some combination of footprints, ostracods, and mudcracks within this section suggests a more extreme and uncommon drying within this alternating pattern. The Suhongtu site emphasizes the important role of drought in the fossil record both as an agent of mortality and as a mechanism driving vertebrates into depositional settings where preservation can occur (Shipman 1975; Rogers 1990).

Population structure and sociality.—Histologic examination of the Suhongtu ornithomimids confirms that the absence of neurocentral fusion and small size in these specimens reflects immaturity (Fig. 4). Presence of a single LAG in the small individuals sampled indicates that these two were between one and two years of age at the time of death. The longer skull length of the slightly larger individual suggests that it may belong to an earlier brood from the same breeding season. The rib of the largest individual sampled has seven LAGs, suggesting a minimum age of seven years. This number is consistent with the number of LAGs and the size of the medullary cavity observed in the limb elements. The developing osteons at the periphery of the limb elements indicates that this individual was still undergoing rapid growth at the time of death (Fig. 4C) (Ricqlès 1980). Consequently, the *Sinornithomimus* herd consisted entirely of juveniles and subadults from one to seven years old (Fig. 5).

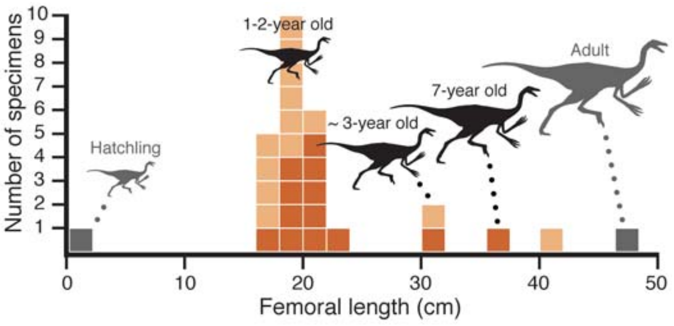

Fig. 5. Size distribution of individuals from the Suhongtu quarry representing a juvenile to subadult herd. Missing hatchling and adult sizes shown in gray. Colors in plot differentiate skeletons from this study (rust) from those excavated previously (orange) (Kobayashi and Lü 2001).

Skeletal assemblages composed predominantly of juveniles have been reported for other nonavian dinosaurs including the therizinosaur *Falcarius* (Zanno and Erickson 2006), a diplodocid sauropod (Myers and Storrs 2007), the ankylosaurid *Pinacosaurus* (Jerzykiewicz et al. 1993), ceratopsians (Gilmore 1917; Lehman 2006; Zhao et al. 2007), and several ornithopods (Forster 1990; Varricchio and Horner 1993; Scherzer 2008; Scherzer and Varricchio 2005; Garrison et al. 2007). However, taphonomic ambiguity concerning the causative agents of these assemblages weakens the interpretation of these sites as reflecting social groups. The *Sinornithomimus* locality suggests that these other assemblages indeed record a true behavioral signal. In general, catastrophic death assemblages of extant vertebrates are highly representative of living social groups (Berger et al. 2001).

In extant archosaurs sociality among juveniles is uncommon. In crocodilians the most common juvenile associations are “pods” that form for several weeks after hatching and are generally accompanied by an adult (Lang 1989). Among some birds more persistent juvenile aggregations occur when sexual maturity is delayed for several years (Boarman and Heinrich 1999; Davies 2002) as in nonavian dinosaurs (Erickson et al. 2008). Ostrich broods often coalesce into large and fairly stable flocks with or without attending males, and large numbers of yearlings with some non-breeding adults form flocks in the greater rhea (*Rhea americana*) (Davies 2002). In the common raven (*Corvus corax*) juveniles and non-breeders maintain foraging crowds and communal roosts (Boarman and Heinrich 1999).

Three life-history attributes would have favored sociality of immature and non-breeding individuals in nonavian dinosaurs: (i) oviparity with relatively small hatchlings, (ii) extensive parental care of eggs and young (Horner 2000), and (iii) a multi-year growth phase prior to sexual maturation (Erickson 2005). Both crocodilians and birds invest significant time to mating, nest building, and parental care. For example, the Orinoco crocodile (*Crocodylus intermedius*) requires nearly six months (Thorbjarnarson and Hernandez 1993) and the ostrich some two to eleven months (Davies 2002). Growing evidence now supports parental care of eggs and young in many dinosaurs (Norell et al. 1995; Horner 2000; Meng et al. 2001; Varricchio et al. 2007) perhaps with the exception of some sauropods (Sander et al. 2008). Time to maturation for nonavian dinosaurs, despite relatively rapid growth rates, remains greater than one year and often more than a decade for larger species (Erickson 2005). Thus, as in modern birds like ostrich and raven, while adults were preoccupied with breeding, nesting, and the care of eggs and hatchlings, non-breeding juveniles and adults may have congregated elsewhere in social groups of mixed age, as preserved by the miring at Suhongtu. Such groups would potentially differ from those of modern birds, e.g., raven. Because fledged birds are nearly the same size as adults, avian aggregations include a much narrower range of body sizes than could potentially be represented by non-avian dinosaur groups. Given the taxonomic diversity of juvenile-dominated assemblages, herding of immature individuals may have been common behavioral pattern among nonavian dinosaurs.

In addition to the ornithomimid locality described here, exclusively or predominantly juvenile assemblages occur among sauropods, theropods, ankylosaurs, ceratopsians, and ornithopods (Gilmore 1917; Forster 1990; Jerzykiewicz et al. 1993; Varricchio and Horner 1993; Scherzer and Varricchio 2005; Zanno and Erickson 2006; Lehman 2006; Garrison et al. 2007; Myers and Storrs 2007). Whether the sociality of immature individuals found in non-avian dinosaurs and modern birds is a shared derived feature remains unclear. However, the rarity of such sociality among extant avians might favor the independent evolution of this behavior. Despite filling similar terrestrial niches in comparison to modern mammals, nonavian dinosaurs exhibited drastically different life history strategies in terms of their reproduction and sociality.

Recently, studies have interpreted *Sinornithomimus* and ornithomimids as unusual among theropods in being herbivorous (White et al. 1998; Kobayashi et al. 1999; Ji et al. 2003; Norell et al. 2004). Whether this shift in diet can be associated with the acquisition of more complex social behavior remains to be determined.

Finally, the age profile of the *Sinornithomimus* assemblage indicates a population with normally high juvenile mortality. This pattern conforms to that suggested for other herbivorous dinosaurs (Varricchio and Horner 1993; Sander et al. 2008) but differs markedly from that of tyrannosaurs (Erickson et al. 2006). The unusual mortality pattern proposed for tyrannosaurs (Erickson et al. 2006) may reflect their distinct ecology as large-bodied predators or may be a non-biologic artefact as the population structure was based upon attritional remains of unclear taphonomic origin (Roach and Brinkman 2007).

Conclusions

- Sedimentary and taphonomic evidence at the Suhongtu locality indicate the mass miring of a juvenile herd of *Sinornithomimus.* Mudcracks, ostracod assemblages, and the occurrence of footprints in otherwise deeper water deposits reflect the deterioration and drying of the lake environment. The deeply plunging limbs and tails that crosscut underlying laminated strata denote death by entrapment within muddy sediments. The variable preservation of the skeletal portions on the main bone horizon reflects their greater exposure to postmortem decay, scavenging, and transport. The uniform preservation, close proximity on a single bedding plane, and parallel alignment of skeletons supports a catastrophic mass mortality of a group rather than attritional death of individuals.
- The Suhongtu site is exceptional among dinosaur bonebeds in preserving several indicators of drought (ostracod assemblages, mudcracks, and footprints in deeper water strata) independent of the bone assemblage.
- The age profile of the *Sinornithomimus* herd represents strictly immature individuals and supports other juvenile-dominated dinosaur bonebeds as biologically real.
- Nonavian dinosaurs differed from modern terrestrial vertebrates in their proclivity to form juvenile herds. This reflects their mobile lifestyle, oviparity, parental care of eggs and hatchlings, and slow (i.e., mutli-year) maturation.
- The population structure of the *Sinornithomimus* herd conforms to those of other herbivorous dinosaurs and suggests high juvenile mortality.

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