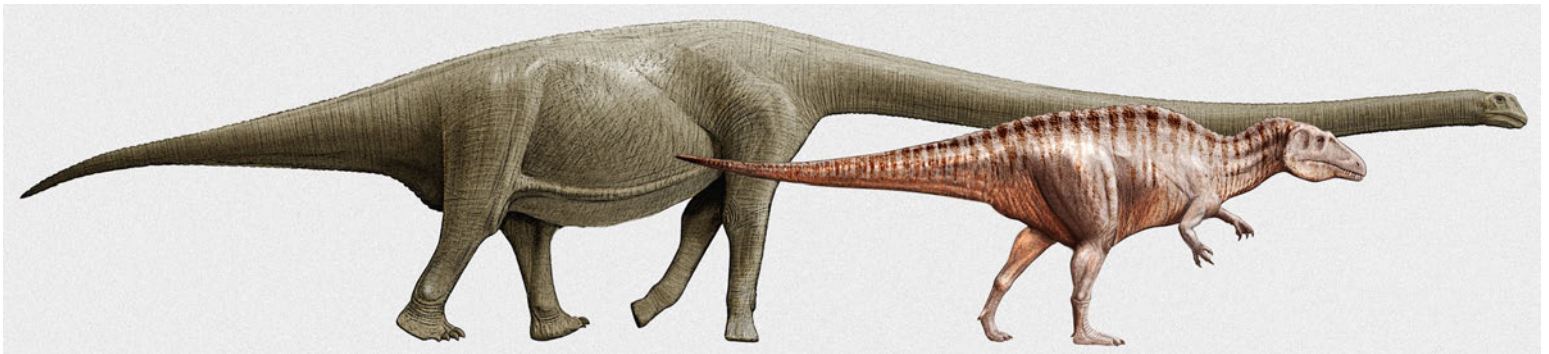


# Early- and Mid-Cretaceous Archosaur Localities of North-Central Texas



Guidebook for the field trip held October 13, 2015 in conjunction with  
the 75<sup>th</sup> Annual Meeting of the Society of Vertebrate Paleontology in  
Dallas, Texas

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2015



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## FIELD TRIP OVERVIEW

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### INTRODUCTION

The transect from the Jones Ranch Quarry, west of the town of Glen Rose, to the Arlington Archosaur Site, in the heart of the Dallas–Fort Worth Metroplex, spans 20 million years of the middle Cretaceous. These sediments lie at the base of a larger section in north-central Texas with near continuous sedimentation to the end of the Maastrichtian. At an even grander scale this is a small part of Cretaceous strata that crop out extensively across the state, forming a broad band roughly parallel with the present day coast of the Gulf of Mexico (Figure 1).

This field trip visits Cretaceous strata in the Fort Worth Basin (Figure 2), that are one of the three main archosaur fossil-bearing regions of the state, the others being in West Texas at Trans-Pecos and Big Bend Park (Jacobs, 1995). The Fort Worth Basin extends south to the Llano Uplift, north to the Red River Arch and Muenster Arch. The basin is bound to the west



Figure 1. Generalized extent of Cretaceous strata (green) in Texas. Shaded rectangle enlarged in Figure 2. Data from Google Earth 2015 and USGS.

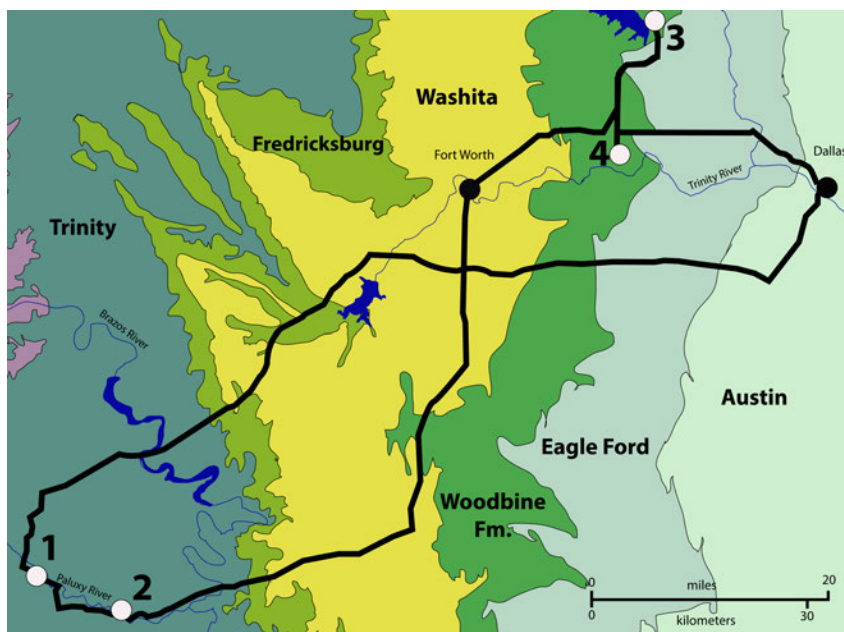


Figure 2. Generalized geologic map of field trip area, Fort Worth Basin. Stops: 1-Jone’s Ranch, 2-Dinosaur Valley State Park, 3-Grapevine Lake, 4-Arlington Archosaur Site. Geologic units in bold. Quaternary deposits are excluded. Modified from Barnes et al. (1972).

by Bend Arch, and to the east by the Paleozoic Ouachita thrust belt, remnants of the mountains found in present day Oklahoma and Arkansas that resulted from the collision of North American and South America as Pangea assembled (Pollastro et al., 2007). The basin is best known for the petroleum-rich Paleozoic strata that lie beneath the Cretaceous section. Wastewater injection into one of these units, the Barnett Shale, has been linked to recent seismic activity northwest of Fort Worth (Hornbach, 2015).

The fossil producing strata visited are the Twin Mountains, Glen Rose, and Woodbine Formations (Figure 3), subdivisions of the Lower Cretaceous Comanchean and Upper Cretaceous Gulfian series, part of the chronostratigraphic framework originally pioneered by R.T. Hill (1887, 1901). Biostratigraphic correlation places the contact between the Twin Mountains and Glen Rose Formation at the Aptian-Albian boundary, 113 Ma in age (Winkler and Rose, 2006; Rose, 2007; Gradstein et al., 2012), and places the Woodbine Formation in the Late Cenomanian, about 95 Ma (Jacobs and Winkler, 1998; Jacobs et al., 2006). This window into the Early to Late Cretaceous transition provides a glimpse into significant changes in the components of vertebrate faunas and floras.

While the oldest known angiosperm fossils date back to the early Cretaceous at 130 Ma (Gomez et al., 2015), they did not become a dominant component of ecosystems globally until the Cenomanian (Dilcher, 2001). Global climate changed significantly during this interval, culminating in one of the warmest periods known, the Cretaceous thermal maximum during the Late Cenomanian-Turonian (Grossman, 2012; Friedrich et al., 2012). Significant carbon isotope excursions, the Cretaceous oceanic anoxic events, at the Aptian-Albian Boundary (Jones Ranch and Glen Rose tracksites), and at the Cenomanian-Turonian Boundary reflect perturbations in marine productivity. Connections between these oceanic events on terrestrial climates and environments are still unfolding (Ludvigson et al., 2015). These patterns also have the potential to enhance age determination of these strata (Jacobs et al., 2005). These environmental changes provide a context to understand some of the changes in the fauna and flora found in the localities visited in this trip.

### ROUTE AND STOP OVERVIEW

At first glance, the low topographic relief and gentle eastward dips of the strata may give the impression that the Cretaceous geology is not exceptional. However, the rich history of stratigraphic and paleontological fieldwork of the sporadic exposures has proved otherwise (Denison et al., 2003). From Dallas to Glen Rose, the Blackland Prairie (and suburban environment) that surrounds much of the

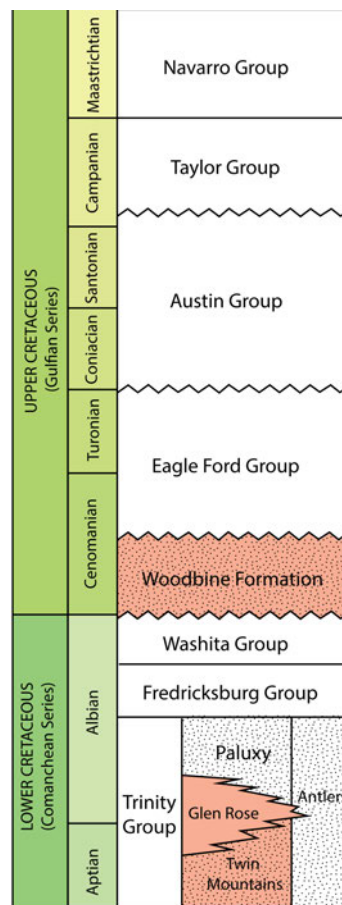


Figure 3. Generalized Cretaceous stratigraphy of North-central Texas. Archosaur-bearing units of focus colored peach. Terrestrial deposits identified by dotted regions. Modified from Winkler et al. (1989) and Jacobs et al. (2013).

eastern part of the DFW Metroplex gives way to a mixed savannah-woodland that is the southern extension of the Cross Timbers, the boundary between the Coastal Plains and the Great Plains to the west. Just west of Dallas, the Balcones Escarpment capped by the Austin Chalk provides the first topographical hints of structural changes in the area (Reaser, 1961; Jacobs et al, 2013). The most striking change from the Blackland Prairie vegetation is near Stops 1 and 2, where the Glen Rose limestone crops out, inhibiting the growth of dense vegetation.

The first stop is Jones Ranch (see Adams, Chapter 2), a quarry that has produced abundant sauropod remains and a diverse assemblage that includes a crocodyliform, numerous microvertebrates, and abundant conifer fossils. The second stop, Dinosaur Valley State Park (see Farlow et al., Chapter 3), contains numerous dinosaur trackways in the Glen Rose Formation that were made famous by R. T. Bird, and have been the focus of continued research since. The

last two stops are within the Woodbine Formation (see Noto, Chapter 4), first at the Grapevine Lake, where fossil bones and tracks of dinosaurs, including remains of the oldest confirmed North American bird, *Flexomornis howei*, was discovered, and at the Arlington Archosaur Site, which continues to produce a diverse assemblage of crocodyliforms, dinosaurs, turtles, mammals, amphibians, fish, and plants.

## PROLOGUE TO THE OPENING RECEPTION

The Perot Museum of Nature and Science, where the SVP Annual Meeting welcome reception is held, there are many exhibits directly relating to the localities on this trip. These include a *Brontopodus birdi* track collected from Glen Rose, a composite and interactive digital model of the *Eubrontes(?) glenrosensis* footprint digitally scanned from the bandstand in the town of Glen Rose (Adams et al, 2010), a cast reconstruction of the *Protohadros byrdi* holotype skull, a model of *Flexomornis howei*, and fossil cones of the conifer *Frenelopsis ramosissima* found in abundance at Jones Ranch. There are numerous other archosaur-centered exhibits, including dinosaurs from Texas and the North Slope of Alaska, the latter including tracks. The Rose Hall of Birds features many taxidermied specimens on display from the museum's extensive ornithological collection. Beyond fossils and rocks, the museum has numerous interactive STEAM exhibits that have drawn a remarkable turnout from the region since opening in December 2012.

## LITERATURE CITED

Adams, T. L., C. Strganac, M. Polcyn, and L. L. Jacobs, 2010. High resolution three-dimensional scanning of the type specimen of *Eubrontes (?) glenrosensis* Shuler, 1935 from the Comanchean (Lower Cretaceous) of Texas: implications for digital archiving and preservation. *Palaeontologica Electronica*, 13:3, 1T.

Barnes, V. E., J. H. McGowen, C. V. Proctor, W. T. Haenggi, D. F. Reiser, R. J. Cordell, E. G. Wermund, R. L. Laury, W. J. Nolte, L. Hendricks and E. Heuer. 1972. *Geologic Atlas of Texas*, Dallas Sheet. University of Texas at Austin, Bureau of Economic Geology.

Denison, R. E., N. R. Miller, R. W. Scott, and D. F. Reaser. 2003. Strontium isotope stratigraphy of the Comanchean Series in north Texas and southern Oklahoma. *Geological Society of America Bulletin*, 115(6): 669-682.

Dilcher, D. L. 2001. Paleobotany: some aspects of non-flowering and flowering plant evolution. *Taxon*, 50 (2): 697-711.

Friedrich, O., R. D. Norris, and J. Erbacher. 2012. Evolution of middle to Late Cretaceous oceans-A 55 m.y. record of Earth's temperature and carbon cycle. *Geology*, 40(2): 107-110.

Gomez, B., V. Daviero-Gomez, C. Coiffard, Carles Martin-Closas, and D. L. Dilcher. 2015. *Montsechia*, an ancient

aquatic angiosperm. *Proceedings of the National Academy of Sciences*, 112(35): 10985-10988.

Gradstein, F. M., J. G. Ogg, M. D. Schmitz, and G. M. Ogg. 2012. *The Geologic Time Scale 2012*: Boston, USA, Elsevier, DOI: 10.1016/B978-0-444-59425-9.00004-4

Grossman, E. L. 2012. Oxygen isotope stratigraphy. In Gradstein, F.M., Ogg, J.G., Schmitz, M., and Ogg, G., eds., *The Geologic Time Scale 2012*, Elsevier, p. 195-220.

Hill, R. T. 1887. The topography and geology of the Cross Timbers and surrounding regions in northern Texas. *American Journal of Science* 3: 1-303.

Hill, R. T. 1901. *Geography and Geology of the Black and Grand Prairies, Texas: With Detailed Descriptions of the Cretaceous Formations and Special Reference to Artesian Waters*. U.S. Geological Survey, 21<sup>st</sup> Annual Report 1899-1900, 666 p.

Hornbach, M. J., H.R. DeShon, W. L. Ellsworth, B. W. Stump, C. Hayward, C. Frolich, H. R. Oldham, J. E. Olson, M. B. Magnani, C. Brokaw, and J. H. Luetgert. 2015. Causal factors for seismicity near Azle, Texas. *Nature Communications*, 6:6728, DOI: 10.1038/ncomms7728

Jacobs, L.L. 1995. *Lone Star Dinosaurs*. Texas A&M University Press, College Station, Texas. 160 pp.

Jacobs, L. L., and D. A. Winkler. 1998. Mammals, archosaurs, and the Early to Late Cretaceous transition in north-central Texas; pp. 253-280 in Y. Tomida, L. J. Flynn, and L. L. Jacobs, (eds.), *Advances in Vertebrate Paleontology and Geochronology*. National Science Museum, Tokyo.

Jacobs, L. L., M. J. Polcyn, D. A., Winkler, T. S. Myers, J. G., Kennedy, and J. B. Wagner. 2013. Late Cretaceous strata and vertebrate fossils of North Texas. *The Geological Society of America Field Guide* 30.

Jacobs, L.L., K. Ferguson, M.J. Polcyn, and C. Rennison. 2005. Cretaceous  $\delta^{13}\text{C}$  stratigraphy and the age of dolichosaurs and early mosasaurs. *Netherlands Journal of Geosciences* 84: 257-268.

Ludvigson, G. A., R. M. Joeckel, L. R. Murphy, D. F. Stockli, L. A. González, C. A. Suarez, J. I. Kirkland, A. Al-Suwaidi. 2015. The emerging terrestrial record of Aptian-Albian global change. *Cretaceous Research*, 56: 1-24.

Pollastro, R. M., D.M. Jarvie, R.J. Hill, and C.W. Adams. 2007. Geologic framework of the Mississippian Barnett Shale, Barnett-Paleozoic total petroleum system, Bend arch-Fort Worth Basin, Texas. *American Association of Petroleum Geologists Bulletin*, 91(4): 405-436.

Reaser, D. F. 1961. Balcones fault system: Its northeast extent. *AAPG Bulletin*, 45(10):1759-1762.

Rose, P. J. 2007. A new titanosauriform sauropod (Dinosauria: Saurischia) from the Early Cretaceous of central Texas and its phylogenetic relationships. *Palaeontologica Electronica* 10: 2,8A.

Winkler, D. A., and P. J. Rose. 2006. Paleoenvironment at Jones Ranch, an Early Cretaceous sauropod quarry in Texas, U.S.A. *Journal of the Paleontological Society of Korea* 22: 77-89.

Winkler, D. A., P. A. Murry, and L. L. Jacobs. 1989. *Field guide to the vertebrate paleontology of the Trinity Group, Lower Cretaceous of Central Texas*. Society of Vertebrate Paleontology 49th Annual Meeting field trip, Institute for the Study of Earth and Man, Southern Methodist University, Dallas, Texas.

## STOP 1

# ARCHOSAURS OF THE LOWER CRETACEOUS TRINITY GROUP OF CENTRAL AND NORTH CENTRAL TEXAS WITH A STOP AT THE JONES RANCH QUARRY

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## INTRODUCTION

The Lower Cretaceous Trinity Group (Aptian–Albian) in Texas is exposed as a broad band of Cretaceous rocks that crop out from northeast to southwest across Texas (Fig. 1). It preserves a diverse terrestrial vertebrate fauna represented by both body and trace fossils (Langston, 1974; Farlow, 1987; Winkler et al., 1990, 1995; Jacobs and Winkler, 1998; Winkler, 2006; D’Emic, 2013; Adams, 2013, 2014). The diverse biota includes cartilaginous and bony fishes, salamanders, frogs, lizards, turtles, crocodylians, dinosaurs, mammals, numerous invertebrates, and plants. Few localities produce more than isolated elements of small or large vertebrates (Winkler et al., 1990). Nevertheless, there are some very notable exceptions, particularly among the archosaurs.

The first dinosaur fossils discovered in Texas were from the Trinity Group (Hill, 1887; Langston, 1974). However, their fossil occurrences are scattered throughout central and north central Texas due to poor exposures and low relief (Jacobs and Winkler, 1998). Since their discovery, dinosaur tracks from the Glen Rose Formation have been an integral part of the human and geological history of north central Texas (Bird, 1985; Jacobs, 1997; Jasinski 2008; Adams et al., 2010). Dinosaur footprints from this middle portion of the Trinity were first described by Shuler in 1917 and made famous by Roland T. Bird with his field work and publications (Albritton, 1942; Bird, 1985; Farlow, 1987). New taxa of neosuchian crocodyliforms from the late Aptian Twin Mountains Formation have expanded the taxonomic diversity of the Early Cretaceous units of Central Texas and increased our knowledge on the evolutionary patterns within Crocodylomorpha (Adams, 2013, 2014; Turner, 2015).

**Institutional Abbreviations**—FWMSH, Fort Worth Museum of Science and History, Fort Worth, Texas, U.S.A. ; SMU, Southern Methodist University Shuler Museum of Paleontology, Dallas, Texas, U.S.A. ; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.

## STRATIGRAPHY

The Trinity Group comprises in ascending order the Twin Mountains, Glen Rose, and Paluxy formations. This sequence is characterized by a complex interfingering of terrestrial and transitional marine environments (Hill, 1901; Sellards et al., 1932). In central and north central Texas the Glen Rose Formation pinches out to the west and north and the Twin Mountains and the Paluxy formations merge as the Antlers Formation landward of the Glen Rose maximum transgression. (Fig. 2; Fisher and Rodda, 1966). Preceding the Trinity Group (mid-Albian onward), Cretaceous rocks in central and north-central Texas are primarily marine with the exception of the terrestrial facies of the Cenomanian (94 Ma) Woodbine Formation (see Noto, this volume).

### **Twin Mountains Formation**

The Twin Mountains Formation is the basal unit of the Lower Cretaceous in central and north-central Texas, and is overlain by the Glen Rose Formation (Fig. 1; Young, 1967; Winkler et al., 1990, 1995; Jacobs and Winkler, 1998). It rests unconformably on westward-dipping Pennsylvanian and Permian strata. The type section of the Twin Mountains Formation is named for two small peaks approximately 43 km north-northeast of Proctor in northern Erath County (Fisher and Rodda, 1966). It is 46 m thick at its type locality and varies from 38 to 68.5 m in thickness in central Texas. The formation is characterized by



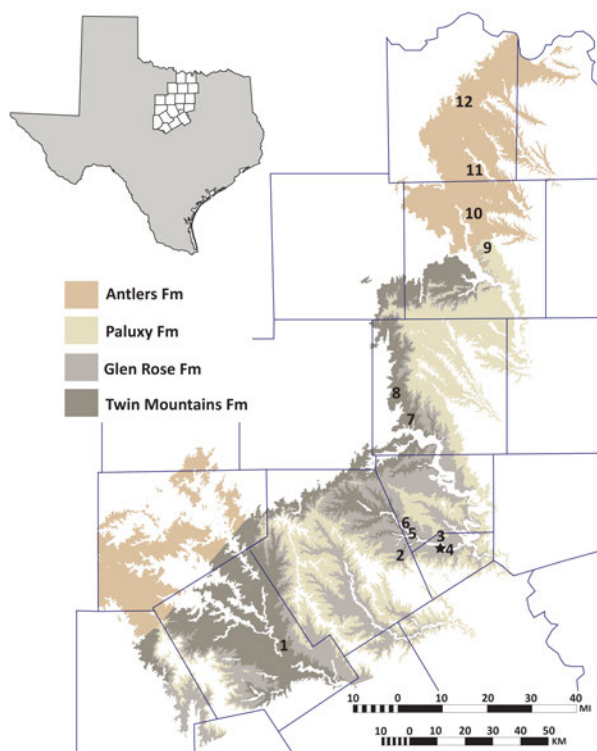


FIGURE 1. Geologic map of Lower Cretaceous Trinity Group strata of central and north-central Texas. Important archosaur localities: Proctor Lake, 1; SMU locality 331, 2; Comanche Peak Nuclear Power Plant, 3; Glen Rose, 4; Jones Ranch, 5; Paluxy Church, 6; Doss Ranch, 7; Hobson Ranch, 8; Decatur, 9; Butler Farm, 10; Greenwood Canyon, 11; Forestburg, 12 (See text for archosaurs identified at each locality). Dinosaur Valley State Park indicated by star.

terrestrial to transitional marine facies, with its fauna distributed a few tens of kilometers (Jones Ranch) to perhaps 150 km (type locality) from the paleoshoreline of a shallow marine shelf (Winkler et al., 1990, 1995). Although the age of the Twin Mountains Formation is not constrained at its base, marine units just above the base that are lateral and downdip equivalents of the formation have been dated as lower and upper Aptian (Young, 1967, 1974). The Twin Mountains-Glen Rose contact is biostratigraphically correlated with the Aptian-Albian boundary (Young, 1974; Winkler et al., 1990, 1995; Jacobs and Winkler, 1998; Gradstein et al., 2004) in north-central Texas (Fig. 2).

**Glen Rose Formation**

The Glen Rose Formation represents the transgression phase of a transgressive-regressive sequence within the Lower Cretaceous Trinity Group (Upper Aptian – Lower Albian) of Central Texas (Jacobs and Winkler, 1998). As a result, the base of the formation is time transgressive as it pinches out to the

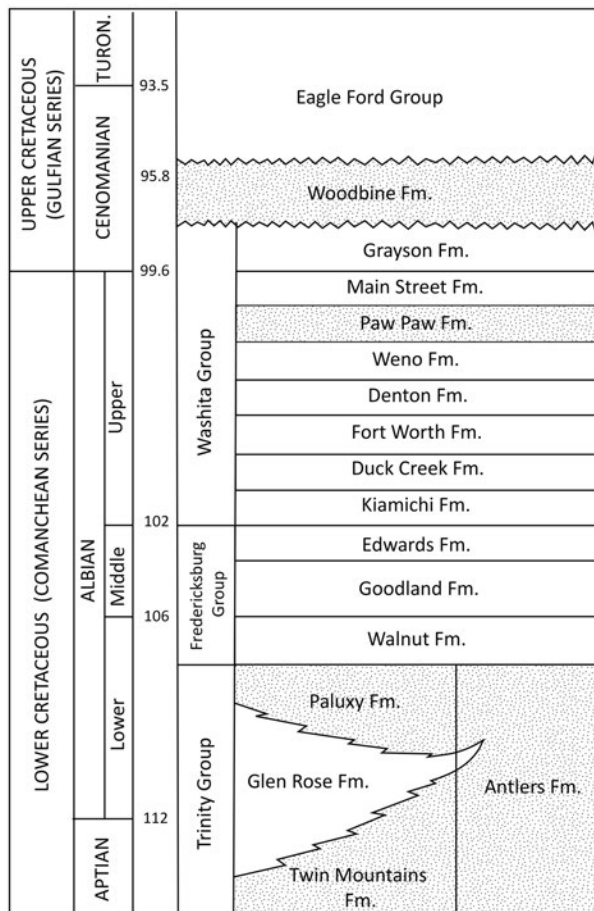


FIGURE 2. Stratigraphic column for the Cretaceous of central and north central Texas showing the position of the Trinity Group relative to timescale and adjacent geologic units. Stippled intervals represent terrestrial deposits. Time scale based on Gradstein et al. (2004). Modified from Jacobs and Winkler (1998).

west and north (Fig. 2; Davis, 1974; Perkins, 1987; Pittman, 1989; Winkler et al., 1989). At the type locality in Somervell County, Texas, the Glen Rose Formation is approximately 75 m thick and is considered earliest Albian in age (Rodgers, 1967; Young, 1967; Perkins, 1987; Winkler et al., 1989; Jacobs and Winkler, 1998). The Glen Rose Formation is subdivided into three members. The upper member consists of alternating limestones and marls. The middle Thorpe Spring member is the most extensive unit, consisting of lime mudstones, wackestones, and calcarenites. The lower member consists of alternating arenaceous limestones and mudstones (Winkler et al., 1989; Hawthorne, 1990). Sediments in the lower member formed on shallow subtidal to tidal flats (Hawthorne, 1990), preserving extensive tracks of theropods and sauropods, as well as rare ornithopod tracks in the type area (Pittman, 1989; Hawthorne, 1990; Farlow, 1987, this volume).

### Paluxy Formation

The Paluxy Formation, the uppermost formation of the Trinity Group, is a relatively thin and continuous stratigraphic unit composed of sand, silt, clay and caliche. Deposits represent fluvial meanderbelt to strandplain, coastal barrier and deltaic facies (Atlee, 1962; Boone, 1968; Caughey, 1977). It is the most variable of the units and ranges from beds, which are loosely cemented to resistant layers of sandstone, topographically being either a ridge or valley-former. The formation ranges from about 60 to over 120 meters in thickness (Caughey, 1977). The marine Walnut Formation of mid Albian age laterally replaces the Paluxy near Waco (Atlee, 1962; Boone, 1968; Caughey, 1977), but overlies it in much of central Texas and northward.

### Antlers Formation

The Antlers Formation of north Texas and southeastern Oklahoma consists of sandstones and claystones interpreted as having been deposited in fluvial deltaic and strandplain environments on the margins of the East Texas Embayment (Fisher and Rodda, 1966). The southern boundary of the Antlers Formation is marked by the landward pinch out of the Glen Rose Limestone (Fig 2). Maximum thickness of the Antlers Formation in outcrop is 183 m (Bullard and Cuyler, 1930).

### STRATIGRAPHIC DISTRIBUTION OF ARCHOSAURS

Although attention has focused primarily on archosaurs from the Twin Mountains Formation, several

important localities are also found within the Glen Rose, Paluxy, and Antlers formations of central and north central Texas (Table 1; Fig. 1; Thurmond, 1971, 1974; Langston, 1974; Winkler et al., 1990, 1995; Jacobs and Winkler, 1998; Winkler, 2006). Cifelli et al. (1997) has provided a complementary faunal list for the Antlers Formation of Oklahoma.

### Crocodyliformes

Crocodyliforms have been recognized as some of the most abundant tetrapods in the Trinity Group, but their remains are typically fragmentary, dominated by teeth and osteoderms (Langston, 1974; Winkler et al., 1990; Adams, 2013). Most are inadequately described, with the exception of three neosuchian taxa. *Wannchampsus kirpachi* from Proctor Lake in the Twin Mountains Formation is a derived paralligatorid eusuchian that reflects the early changes leading to Eusuchia (Adams, 2014; Turner, 2015). A small and yet undescribed skull (USNM 22039), designated the 'Glen Rose Form', from the Greenwood Canyon locality in the Antlers Formation, is considered to have closer affinities to *Wannchampsus kirpachi* and is referable to the that genus (Langston, 1974; Adams, 2014). A second crocodyliform taxon, represented by partial skeleton, was collected as a single small block from Proctor Lake (Winkler et al., 1988; Winkler and Murry, 1989; Adams, in prep).

*Paluxysuchus newmani* from the Jones Ranch locality in the Twin Mountains Formation represents a more basal neosuchian exhibiting features typically associated with longirostrine taxa (Fig. 3; Adams, 2013). Rogers (2003) described and named a small crocodyliform from the Glen Rose Formation in Earth



FIGURE 3. Early Cretaceous reconstruction of north central Texas with the crocodyliform *Paluxysuchus*, juvenile euornithopod, *Tenontosaurus*, *Sauroposeidon*, dromaeosaurid and cryptodire turtle *Glyptops*. Artwork by Karen Carr.

Table 1. Faunal list of archosaur body fossils (by formation) from the Trinity Group of central and north-central Texas. Langston, 1974; Winkler et al., 1989, 1990; Jacobs and Winkler, 1991; Rogers, 2003; Winkler, 2006; D'Emic, 2013; Andres and Myers, 2013; Adams, 2013, 2014.

	Twin Mts.	Glen Rose	Paluxy	Antlers
Crocodyliformes				
<i>Paluxysuchus newmani</i>	x			
<i>Wannchampsus kirpachi</i>	x			x
<i>Pachycheilosuchus trinquei</i>		x		
cf. <i>Bernissartia</i> sp.	x			x
Pholidosauridae, indet.	x			
Atoposauridae, indet.	x			
Goniopholididae, indet.				x
Crocodyliformes, indet.	x	x	x	x
Saurischia				
<i>Acrocanthosaurus atokensis</i>	x			x
Dromaeosauridae, indet.	x			
Theropoda, indet.	x			
<i>Sauroposeidon proteles</i>	x			
<i>Astrophocaudia slaughteri</i>			x	
<i>Cedarosaurus weiskopfae</i>			x	
Sauropoda, indet.		x		
Ornithischia				
<i>Tenontosaurus dossi</i>	x			
<i>Tenontosaurus tilletti</i>		x	x	
<i>Tenontosaurus</i> sp.			x	x
Iguanodontia indet.	x			
Euornithopod, new gen. et sp.	x			
Pterosauria				
<i>Radiodactylus langstoni</i>		x		
Dsungaripteridae				x
Pterosauria indet.		x		

County, Texas (SMU locality 331) as *Pachycheilosuchus trinquei*, and a member of Hylaeochampsidae (Buscalioni et al., 2011).

Several tooth morphologies from the Paluxy Church locality in Hood County, Texas have been assigned to Pholidosauridae, Atoposauridae, and cf. *Bernissartia* (Winkler et al., 1990; Jacobs and Winkler, 1998). Reevaluations of some of these teeth morphologies suggest that they represent more recently described taxa. The atoposaurid tooth figured by Winkler et al. (1990:fig. 9) is indistinguishable with that of *Wannchampsus kirpachi*, while those identified as pholidosaurid share similarities with *Paluxysuchus newmani*. The button shaped teeth from the Paluxy Church assigned to cf. *Bernissartia* are also a common occurrence at the Butler Farm locality in the Antlers Formation. Additional fragmentary material, including a partial right maxilla and osteoscutes belonging to Goniopholididae, has been collected in abundance from the Paluxy and Antlers formations (Langston, 1974).

### Pterosauria

Only three occurrences of pterosaur fossils are recognized from the Lower Cretaceous Trinity Group (Langston, 1974; Jacobs and Winkler, 1998; Murry et

al., 1991; Andres and Myers, 2013). Andres and Myers (2013) described the azhdarchid *Radiodactylus langstoni* from the Glen Rose Formation near the Comanche Peak Nuclear Power Plant, Somervell County. An indeterminate wing bone from the Glen Rose Formation near the town of Glen Rose was also assigned to Pterosauria by Murry et al. (1991). A Dsungaripteridae is documented from the Antlers Formation near Forestburg in Montague County (Langston, 1974; Jacobs and Winkler, 1998; Andres and Myers, 2013).

### Saurischia

From the upper Twin Mountains Formation in Parker County, Texas, the remains of an *Acrocanthosaurus atokensis* were found at the Hobson Ranch (Harris, 1998). Isolated theropod teeth and fragmentary post cranial material occur throughout exposures of the Trinity Group in north central Texas. Few have been identified beyond that of Theropoda, indet., although some material has been tentatively referred to *Acrocanthosaurus* extending its range in Texas to the Antlers Formation (Langston, 1974; Jacobs and Winkler, 1998). Teeth that appear to be dromaeosaurid have been recovered from the Twin



FIGURE 4. Early Cretaceous reconstruction of north central Texas with *Sauroposeidon* browsing among the trees at the river edge with footprints on the river bottom below a semionotid fish. Artwork by Karen Carr.

Mountains, Doss Ranch, Jones Ranch, and Proctor Lake localities (Winkler et al., 1988; Winkler and Murry, 1989; Winkler et al., 1997).

The remains of sauropods from at least four individuals of *Sauroposeidon proteles* (= *Paluxysaurus jonesi*) were excavated from the Jones Ranch quarry in Hood County, Texas (Fig. 4; Winkler and Rose, 2006; Rose, 2007; D’Emic, 2013). D’Emic (2013) identified two additional sauropod taxa, *Astrophocaudia slaughteri* and *Cedarosaurus weiskopfae*, from the Paluxy Formation near the town of Decatur in Wise County, north central Texas. A partial skeleton from an unknown sauropod was also recovered from the Glen Rose Formation in Blanco County (Langston 1974).

### Ornithischia

Ornithopod dinosaurs represent some of the more complete skeletal remains from the Lower Cretaceous rocks of the Trinity Group of Texas, with at least four taxa present (Winkler, 2006). A small primitive ornithopod is known from numerous skeletons at the Proctor Lake dinosaur locality within the lower portion of the Twin Mountains Formation in east-central Comanche County (Winkler and Murry, 1989; Winkler et al., 1988, 1990). The presence of several size groups representing a range of growth stages and the concentration of juveniles in surface depressions suggest that Proctor Lake may have been a dinosaur nesting site. Two articulated skeletons of *Tenontosaurus dossi* were excavated from the Doss Ranch in the upper Twin Mountains Formation in Parker County, Texas (Winkler et al., 1997). *Tenontosaurus tilletti* occurs just west of the Doss Ranch in the Paluxy Formation. *Tenontosaurus* sp. has been designated for isolated teeth and fragmentary post cranial elements that occur throughout the Paluxy and Antlers formations (Winkler,

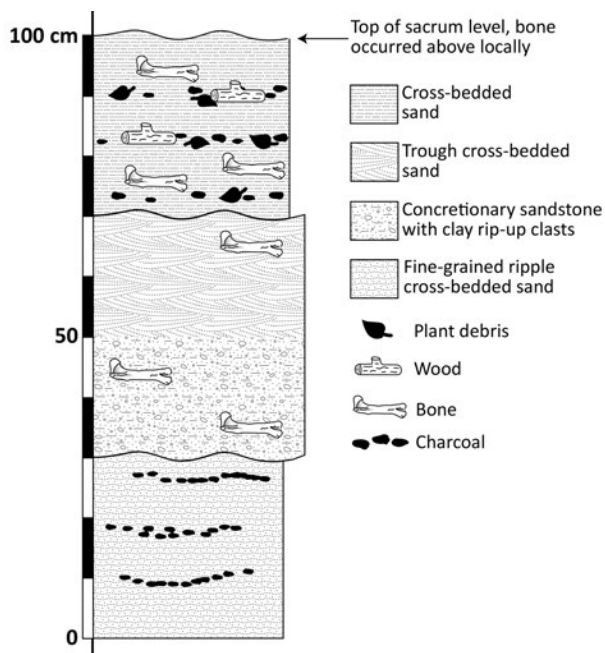


FIGURE 5. Measured section 9 m south and 1 m east of datum. Bone occurs throughout the section beginning with the densely cemented clay clast rich sandstone. Lenses of plant debris, wood, and charcoal are abundant in the upper sand unit of this section. Modified from Winkler and

2006). An indeterminate iguanodontian ornithopod, larger than *Tenontosaurus*, has also been reported from the Antlers Formation of Montague County (Langston, 1974; Jacobs and Winkler, 1998).

### STOP 1: JONES RANCH QUARRY

(32.2801°N, -97.947533° W)

The Jones Ranch quarry (SMU Locality 282; FWMSH 93B-10) in Hood County, Texas occurs in the Lower Cretaceous Twin Mountains Formation (latest Aptian- early Albian, approximately 112 Ma; Jacobs and Winkler, 1998; Winkler and Rose, 2006; Rose, 2007). The locality is stratigraphically less than 10 meters below the overlying Glen Rose Formation and less than 15 km from the well-known track sites at Dinosaur Valley State Park (Fig. 1). The quarry was deposited in a seasonally dry fluvial environment, and consists of unconsolidated channel fills and calcite-cemented sandstone concretions (Fig. 5). The presence of clay rip-up clasts, charcoal and plant debris filled scours, and calcareous soil nodules indicate a semi-arid climate at the Jones Ranch locality (Winkler and Rose, 2006). Fossils are commonly invisible within concretions in the field.

Bones occur throughout approximately 1.5 m of vertical section across approximately 400 square meter of quarry area (Fig. 6). The base of the bone-

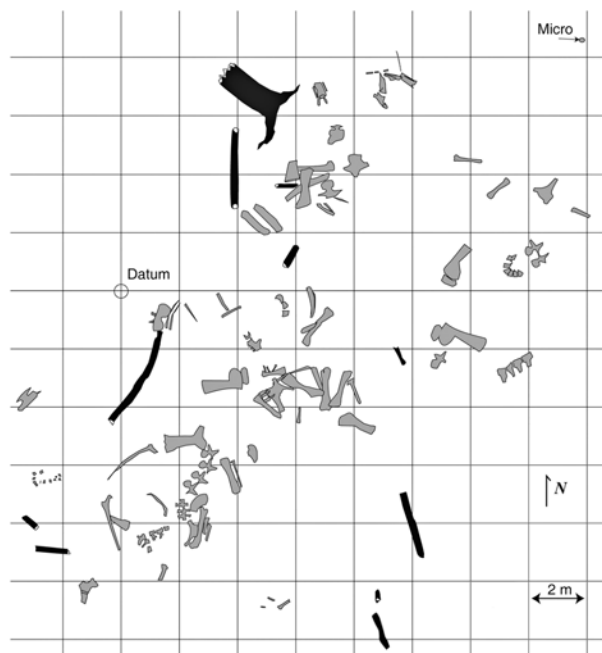


FIGURE 6. Quarry map of Jones Ranch (SMU loc. v282; FWMSH 93B10) showing selected sauropod bone elements (gray) and larger petrified logs (black). Grid is 2 m square. Microvertebrate concentrations begin at point indicated on map and continue northeast along with *Paluxysuchus newmani* skull material and fragmentary sauropod remains. Modified from Winkler and Rose, 2006.

bearing units is low in the south and west edge of the quarry and rises toward the northeast. The primary

elements are isolated bones and partial skeletons representing a minimum of 4 individuals of the sauropod dinosaur *Sauroposeidon proteles* (= *Paluxysaurus jonesi*; Winkler and Rose, 2006; Rose, 2007; D’Emic, 2013). Skeletal elements within the quarry are isolated or in partly articulated segments, with bones of different individuals juxtaposed (Fig. 6 and 7) The only other major vertebrate remains recovered in the quarry come from the crocodyliform *Paluxysuchus newmani*, known from partially articulated and disarticulated elements of two skulls found in close association with sauropod bones (Fig. 8; Winkler and Rose, 2006; Adams, 2013). In addition, an abundant microfauna was discovered in the northeastern section of the quarry, including at least one other crocodyliform taxon, based on isolated teeth (Table 2; Winkler and Rose, 2006).

Plant fossils include logs, wood fragments, cones and leaves, mainly of the conifer *Frenelopsis ramosissima* from the family Cheirolepidiaceae (Fig. 9; Axsmith and Jacobs, 2005). Some of the large logs have preserved lengths of approaching six meters. One large tree is represented by a 3 meter long stump with its top roughly fractured and a root mass more than 2.5 m wide at its base. Many bones and logs are stacked in multiple layers, and commonly encased in massive concretions. Neither logs nor long bones appear to have a preferred long axis orientation. Emplacement of bones and plants by episodes of flooding in a sandy ephemeral stream channel has been established (Winkler and Rose, 2006; Rose, 2007).

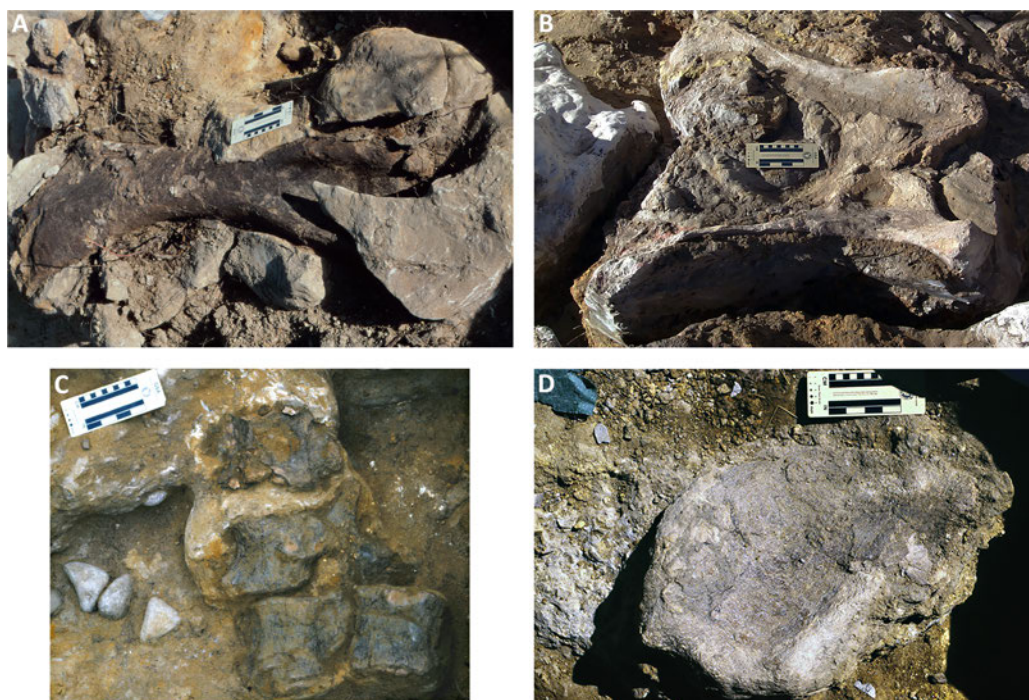


FIGURE 7. Selected elements of *Sauroposeidon proteles* in quarry at Jones Ranch. **A**, right humerus in anterior view. **B**, articulated left pubis and ischium in lateral view. **C**, caudal vertebrae in semi-articulated series. **D**, right coracoid in medial view. Images courtesy of D. Winkler.



FIGURE 8. **A**, Northeast section of Jones Ranch Quarry showing *Paluxysuchus newmani* skull material. **B**, cranial elements of *P. newmani* (SMU 76601) in dorsal view, **C**, 3D digital reconstruction of the skull of *P. newmani* in dorsal view. Scales in centimeters. Quarry Image courtesy of D. Winkler.

#### LITERATURE CITED

Adams, T. L. 2013. A new neosuchian crocodyliform from the Lower Cretaceous (Late Aptian) Twin Mountains Formation of north-central Texas. *Journal Vertebrate Paleontology* 33:85–101.

Adams, T. L. 2014. Small crocodyliforms from the Lower Cretaceous (Late Aptian) of central Texas and their systematic relationship to the evolution of Eusuchia. *Journal of Paleontology* 88: 1031–1049.

Adams, T. L., C. Strganac, M. Polcyn, and L. L. Jacobs, 2010. High resolution three-dimensional scanning of the type specimen of *Eubrontes (?) glenrosensis* Shuler, 1935 from the Comanchean (Lower Cretaceous) of Texas: implications for digital archiving and preservation.

Palaeontologica Electronica, 13:3, 1T.

Albritton, C.C., Jr. 1942. Dinosaur tracks near Comanche, Texas. *Field and Laboratory*, 10:160–181.

Andres, B. and T. S. Myers. 2012. Lone star pterosaurs. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103:1–16.

Atlee, W. A. 1962. The Lower Cretaceous Paluxy Sand in central Texas. *Baylor Geological Studies, Bulletin* 2, 25 pp.

Axsmith, B. J. and B. F. Jacobs. 2005. The conifer *Frenelopsis ramosissima* (Cheirolepidiaceae) in the Lower Cretaceous of Texas: phylogenetic, biogeographical and paleoecological implications. *International Journal of Plant Sciences* 166:327–337.

Bird, R.T. 1985. Bones for Barnum Brown: Adventures of a Dinosaur Hunter. Theodore Schreiber, V. (ed.), Texas



FIGURE 9. Partially excavated silicified log associated with *Frenelopsis ramosissima*. Scale in centimeters. Image courtesy of D. Winkler.

- Christian University Press, Fort Worth.
- Boone, P. A. 1968. Stratigraphy of the basal Trinity (Lower Cretaceous) Sands of Central Texas. *Baylor Geological Studies, Bulletin 15*, 62 pp.
- Bullard, F. M., and R. H. Cuyler. 1930. Preliminary report on the geology of Montague County, Texas. *The University of Texas Bulletin 3001*, pp. 57–76.
- Buscalioni A. D., P. Piras, R. Vullo, M. Signore, C. Barbera. 2011. Early eusuchia crocodylomorpha from the vertebrate-rich Plattenkalk of Pietraroia (Lower Albian, southern Apennines, Italy). *Zoological Journal of the Linnean Society 163*:199–227.
- Caughey, C. A. 1977. Depositional systems in the Paluxy Formation (Lower Cretaceous), Northeast Texas—oil, gas, and groundwater resources. *The University of Texas, Bureau of Economic Geology, Geological Circular 77–8*, 59 pp.
- Cifelli, R. L., J. D. Gardner, R. L. Nydam, and D. L. Brinkman. 1997. Additions to the vertebrate fauna of the Antlers Formation (Lower Cretaceous), southeastern Oklahoma. *Oklahoma Geology Notes 57*:124–131.
- Davis, K. W. 1974. Stratigraphy and depositional environments of the Glen Rose Formation, north-central Texas. *Baylor Geological Studies, Bulletin 26*, 43 pp.
- D’Emic, M. D. 2013. Revision of the sauropod dinosaurs of the Early Cretaceous Trinity Group, southern USA, with the description of a new genus. *Journal of Systematic Palaeontology 11*:707–726.
- Farlow, J. O. 1987. Lower Cretaceous dinosaur tracks Paluxy River Valley, Texas. *Field Guide, South Central Section, Geological Society of America, Baylor University*, 50 pp.
- Fisher, W. L., and P. U. Rodda. 1966. Nomenclature revision of basal Cretaceous rocks between the Colorado and Red rivers, Texas. *The University of Texas, Bureau of Economic Geology, Report of Investigations No. 58*, 20 pp.
- Gradstein, F. M., J. G. Ogg, A. G. Smith, F. P. Agterberg, W. Bleeker, R. A. Cooper, V. Davydov, P. Gibbard, L. Hinnov, M. R. House, L. Lourens, H. -P. Luterbacher, J. McArthur, M. J. Melchin, L. J. Robb, J. Shergold, M. Villeneuve, B. R. Wardlaw, J. Ali, H. Brinkhuis, F. J. Hilgen, J. Hooker, R. J. Howarth, A. H. Knoll, J. Laskar, S. Monechi, J. Powell, K. A. Plumb, I. Raffi, U. Röhl, P. Sadler, A. Sanfilippo, B. Schmitz, N. J. Shackleton, G. A. Shields, H. Strauss, J. Van Dam, J. Veizer, Th. van Kolfschoten, and D. Wilson. 2004. *A Geologic Time Scale 2004*. Cambridge University Press, U. K., p. 500.
- Harris J. D. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science, Bulletin, 13*:1-75.
- Hawthorne, J.M. 1990. Dinosaur track-bearing strata of the Lampasas Cut Plain and Edwards Plateau, Texas, *Baylor Geological Studies*, 49.
- Hill, R. T. 1 887. The topography and geology of the Cross Timbers and surrounding regions in northern Texas. *American Journal of Science 3 3*:29 1–303.
- Hill, R. T. 1901. Geography and geology of the Black and Grand Prairies, Texas. *U.S. Geological Survey 21st Annual Report, Part 7*, 666 pp.
- Jacobs, L.L. 1997. The making of Dinosaur Valley State Park, Glen Rose, Texas, USA, p.226–232. In Yang, S.Y., Huh, M., Lee, Y.-N., and Lockley, M.G. (eds.), *International Dinosaur Symposium for the Uhangri Dinosaur Center and Theme Park in Korea*. *Journal of Paleontological Society of Korea, Special Publication no. 2*.
- Jacobs, L. L., and D. A. Winkler. 1998. Mammals, archosaurs, and the Early to Late Cretaceous transition in north-central Texas; pp. 253–280 in Y. Tomida, L. J. Flynn, and L. L. Jacobs, (eds.), *Advances in Vertebrate Paleontology and Geochronology*. National Science Museum, Tokyo.
- Jasinski, L.E. 2008. *Dinosaur Highway: A History of Dinosaur Valley State Park*. TCU Press, Fort Worth, Texas.
- Langston, W. L., Jr. 1974. Nonmammalian Comanchean tetrapods. *Geoscience and Man, 8*:7–102.
- Murry, P. A., D. A. Winkler, and L. L. Jacobs. 1991. An azhdarchid pterosaur humerus from the Lower Cretaceous Glen Rose Formation of Texas. *Journal of Paleontology 65*:167–70.
- Perkins, B. F. 1987. Alternating marine and terrestrial environments in the Comanche Cretaceous lower Glen Rose Formation, Somervell and Hood counties, Texas. *Field Trip Guide, 1987 Southwest Section American Association of Petroleum Geologists Convention, Field Trip #1*, pp. 9–37.
- Pittman, J.G. 1989. Stratigraphy, lithology, depositional environment, and track type of dinosaur track-bearing beds of the Gulf Coastal Plain, p. 135–153. In Gillette, D.D. and Lockley, M.G., (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, New York.
- Rogers, J. V. II. 2003. *Pachycheilosuchus trinquei*, a new procoelous crocodyliform from the Lower Cretaceous (Albian) Glen Rose Formation of Texas. *Journal of Vertebrate Paleontology 23*:128–145.
- Rodgers, R. W. 1967. Stratigraphy of Glen Rose Limestone, central Texas; pp. 1 19–130 in L. Hendricks (ed.), *Comanchean (Lower Cretaceous) stratigraphy and paleontology of Texas*. Permian Basin Section, Society of Economic Paleontologists and Mineralogists, Publication No. 67–8.
- Rose, P. J. 2007. A new titanosauriform sauropod (Dinosauria: Saurischia) from the Early Cretaceous of central Texas and its phylogenetic relationships. *Palaeontologia Electronica 10*:2,8A.
- Sellards, E. H., W. S. Adkins, and F. B. Plummer. 1932. *The geology of Texas, Vol. I, Stratigraphy*. The University of Texas Bulletin, No. 3232, 1007 pp.
- Shuler, E. W. 1917. Dinosaur tracks in the Glen Rose Limestone near Glen Rose, Texas. *American Journal of Science 44*:294–297.
- Thurmond, J. T. 1971. Cartilaginous fishes of the Trinity Group and related rocks (Lower Cretaceous) of north central Texas. *Southeastern Geology 13*:207–227.
- Thurmond, J. T. 1974. Lower vertebrate faunas of the Trinity Division in north-central Texas. *Geoscience and Man 8*:103–129.
- Turner A. H. 2015. A review of *Shamosuchus* and *Paralligator* (Crocodyliformes, Neosuchia) from the Cretaceous of Asia. *PLoS ONE 10*(2): e0118116. doi:10.1371/journal.pone.0118116.

- Winkler, D. 2006. Ornithopod dinosaurs from the Early Cretaceous Trinity Group, Texas, USA; pp. 169–181 in J. C. Lü, Y. Kobayashi, D. Huang, and Y.-N. Lee (eds.), Papers from the 2005 Heyuan International Dinosaur Symposium, Heyuan City, Guangdong Province, China, 8–12 April 2005. Geological Publishing House, Beijing.
- Winkler, D. A., and P. A. Murry. 1989. Paleoeecology and hypsilophodontid behavior at the Proctor Lake dinosaur locality (Early Cretaceous), Texas, p. 55–61. In J. O. Farlow (ed.), Paleobiology of the Dinosaurs. Geological Society of America Special Paper 238.
- Winkler, D. A., and P. J. Rose. 2006. Paleoenvironment at Jones Ranch, an Early Cretaceous sauropod quarry in Texas, U.S.A. *Journal of the Paleontological Society of Korea* 22:77–89.
- Winkler, D. A., P. A. Murry, and L. L. Jacobs. 1989. Field guide to the vertebrate paleontology of the Trinity Group, Lower Cretaceous of Central Texas. Society of Vertebrate Paleontology 49th Annual Meeting field trip, Institute for the Study of Earth and Man, Southern Methodist University, Dallas, Texas.
- Winkler, D. A., P. A. Murry, and L. L. Jacobs. 1990. Early Cretaceous (Comanchean) vertebrates of central Texas. *Journal of Vertebrate Paleontology* 10:95–116.
- Winkler, D. A., P. A. Murry, and L. L. Jacobs. 1997. A new species of *Tenontosaurus* (Dinosaurian: Ornithopoda) from the Early Cretaceous of Texas. *Journal of Vertebrate Paleontology* 17:330–348.
- Winkler, D. A., L. L. Jacobs, Y.-N. Lee, and P. A. Murry. 1995. Sea level fluctuation and terrestrial faunal changes in North-Central Texas; pp. 175–177 in A. Sun and Y. Wang (eds.), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers. China Ocean Press, Beijing.
- Winkler, D. A., P. A. Murry, L. L. Jacobs, W. R. Downs, J. R. Branch, and P. Trudel. 1988. The Proctor Lake dinosaur locality, Lower Cretaceous of Texas. *Hunteria*, 2:1–8.
- Young, K. 1967. Comanche Series (Cretaceous), South Central Texas, pp. 9–29; in L. Hendricks, (ed.), Comanchean (Lower Cretaceous) Stratigraphy and Paleontology of Texas. Permian Basin Section, Society of Economic Paleontologists and Mineralogists, Publication 67.
- Young, K. 1974. Lower Albian and Aptian (Cretaceous) ammonites of Texas. *Geoscience and Man* 8:175–228.



## STOP 2

# **DINOSAUR FOOTPRINTS FROM THE GLEN ROSE FORMATION (PALUXY RIVER, DINOSAUR VALLEY STATE PARK, SOMERVELL COUNTY, TEXAS)**

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## **INTRODUCTION**

Dinosaur footprints are found in the Glen Rose Formation and other Lower Cretaceous stratigraphic units over much of central Texas (Pittman, 1989; Rogers, 2002; Farlow et al., 2006). Dinosaur tracks were discovered in the rocky bed of the Paluxy River, near the town of Glen Rose, Texas, early in the 20<sup>th</sup> Century (Jasinski, 2008; Farlow et al., 2012b). Ellis W. Shuler of Southern Methodist University did pioneering studies on the dinosaur tracks (Shuler 1917, 1935, 1937), and Langston (1974) summarized much of the early literature.

What really put the dinosaur footprints of the Paluxy River on the map, though, were the herculean efforts that Roland T. Bird of the American Museum of Natural History made to secure trackway slabs for display at that institution and at the Texas Memorial Museum in Austin (Bird, 1985; Jasinski, 2008). In 1970 Dinosaur Valley State Park was created to protect the dinosaur footprints.

This guidebook briefly summarizes earlier work, and also serves as an interim report of research of our group still in progress, concerned with identifying the makers of the Paluxy River footprints, and determining what those animals were up to as they made their tracks. We will offer some comparisons of

the dinosaur tracks of the Glen Rose Formation with those from other ichnofaunas around the world. The last quarter-century has seen an explosive increase in the technical literature dealing with dinosaur footprints, and we cannot possibly cite all of the relevant studies. For the sake of brevity we will emphasize publications from the present century, and summary papers and books, as much as possible. Even with this restriction, however, the literature is so vast that the literature-cited “tail” of this report starts to wag the “dog” of the text.

## **GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE OF TRACKSITES**

As the Paluxy River flows eastward across Somervell County, Texas toward its eventual junction with the larger Brazos River, it makes a northerly and then a southerly loop west of the town of Glen Rose (Fig. 1A). Much of the northern loop is within the boundaries of Dinosaur Valley State Park. The river has cut into rocks of the Trinity Group, and the main track occurrences are in the lower member of the Glen Rose Formation (Fig. 1B; within the town of Glen Rose itself, well away from the river, there is an interesting dinosaur tracksite much higher in the section [Blair et al., 2012a, b]).

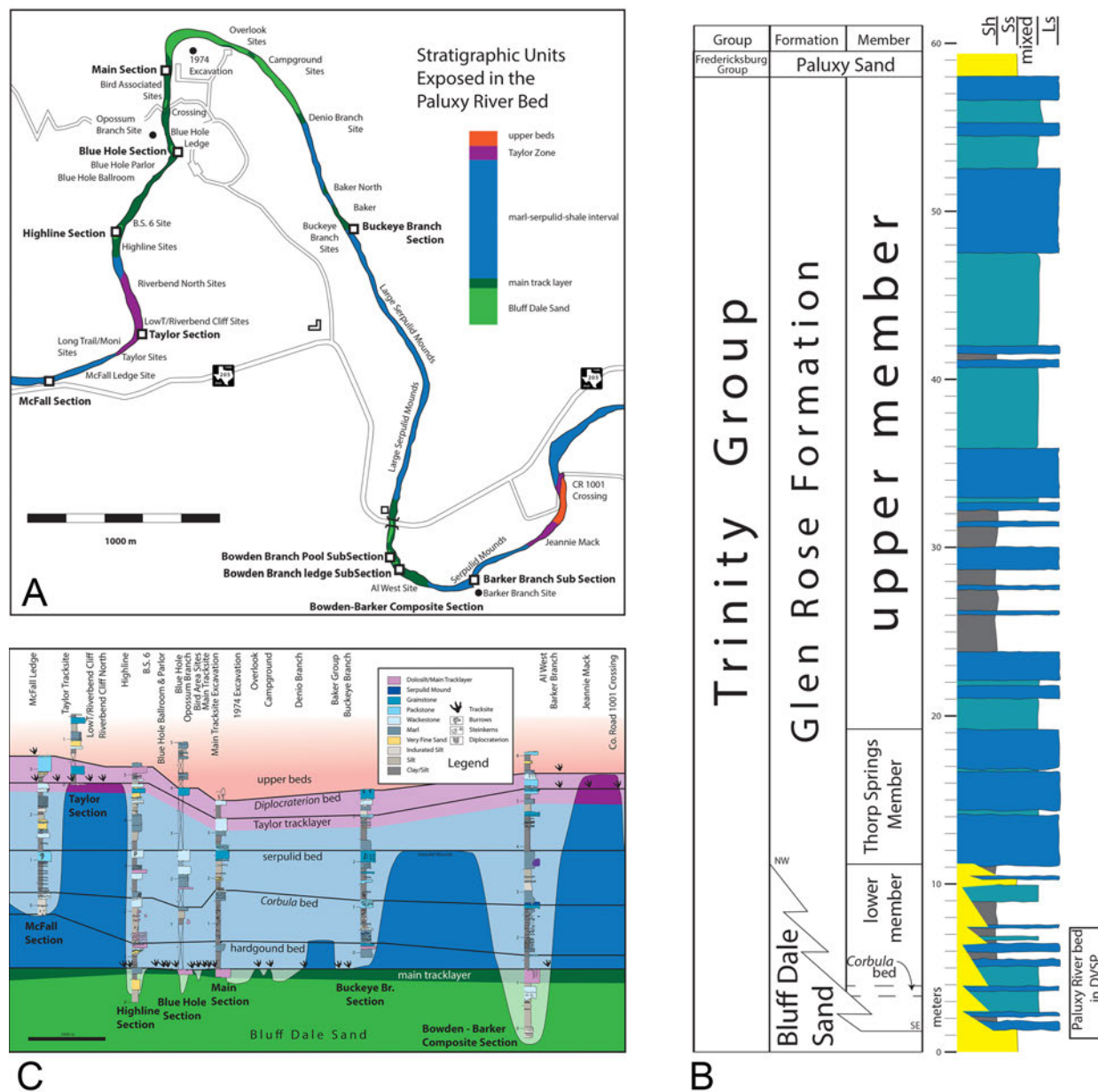


FIGURE 1. Location and stratigraphic occurrence of major Paluxy River dinosaur tracksites and other significant sites (Dattilo et al., 2014); A, the river flows from right to left as shown here. Individual horizons exposed in the river bed coded by color. B, the Glen Rose Formation stratigraphic section in the Glen Rose region. The tracklayers in and around Dinosaur Valley State Park are in the lower member of the formation; C, correlation of the footprint-bearing and other layers; dinosaur tracks occur in the Main Tracklayer, the Taylor Tracklayer, and the *Diplocraterion* bed.

The stratigraphy and sedimentology of the local section has been described in considerable detail (Dattilo et al., 2014 and references therein), and so will receive only brief treatment here, emphasizing the dinosaur trace fossils. Dinosaur footprints have been found at three levels over a roughly 6-meter interval in the lower member of the Glen Rose Formation, separated by beds containing a diverse benthic marine

paleobiota (Feldman et al., 2011; Dattilo et al., 2014; Martin et al., 2015). The track-bearing intervals are designated the Main Tracklayer, the Taylor Tracklayer, and the *Diplocraterion* bed. The units in the Paluxy River section are not perfectly flat, but gently undulate up and down along the length of the river (Fig. 1C).

Fieldwork on the Paluxy's tracksites is not without challenges. During rainy weather the tracksites

may be underwater for days or weeks on end, and at times the river flow may be so deep and fast as to be dangerous. Measuring and photographing footprints underwater can be tricky. During the summer, if water levels are high enough to cover the tracks, as temperatures warm in the afternoon, breezes begin to blow, creating ripples on the water through which the footprints are difficult to see. During dry spells the river may break up into a series of isolated pools. Wading around the prints at such times will kick up sediment that takes several minutes to settle out, and the rock surfaces underwater are very slippery. At those times when the river is almost or completely dry, air temperatures may shoot above the century (Fahrenheit) mark. Snakes are common in the river, and some of them are venomous, but this merely adds to the fun.

### DISTINCTIVE FEATURES OF PALUXY RIVER TRACKSITES

**Main Tracklayer** (Figs. 2, 3A-G)—This unit is a 10-30 cm thick, homogeneous, sandy dolomitic wackestone (Dattilo et al., 2014). The surface of the unit is thickly dotted with small, U-shaped *Arenicolites* burrows, presumably made by benthic crustaceans or polychaetes (Figs. 2H, 3E, 5B, F, 6). R. T. Bird's trackway quarry was in this unit (Figs. 2A-E), and all of the unambiguous sauropod trackways occur in the Main Tracklayer (Figs. 2-4). Particularly impressive tracksites (Fig. 1A) occur in a stretch of river between the Main Tracksite and a rough road crossing to the south of Bird's quarry site (most of which is shown in Fig. 2A), at the Blue Hole, the Blue Hole Ballroom, and at the mouth of Denio Branch. However, many of these sites are often underwater or covered by coarse river sediment, and the Denio site is being actively eroded by the river.

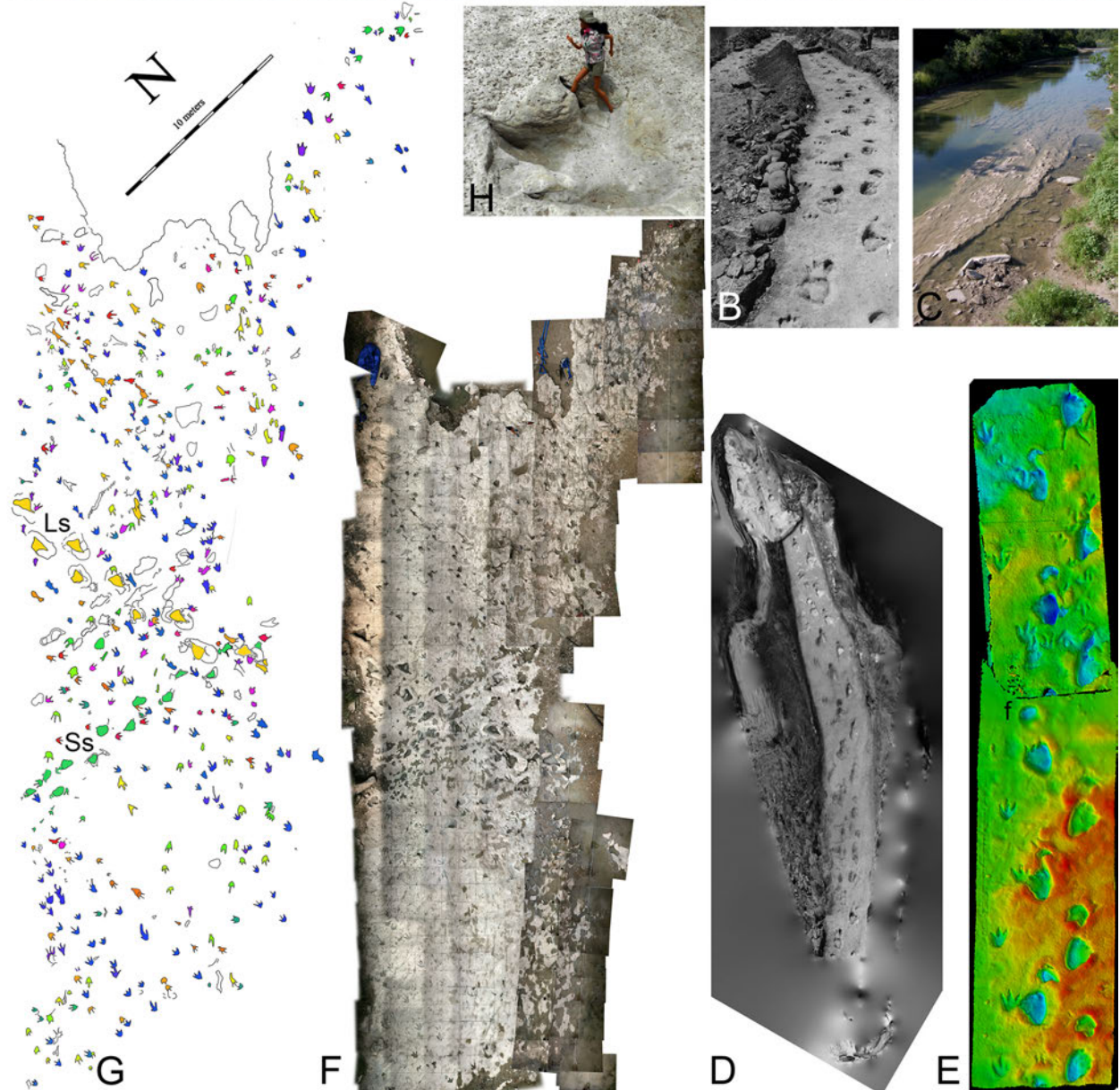
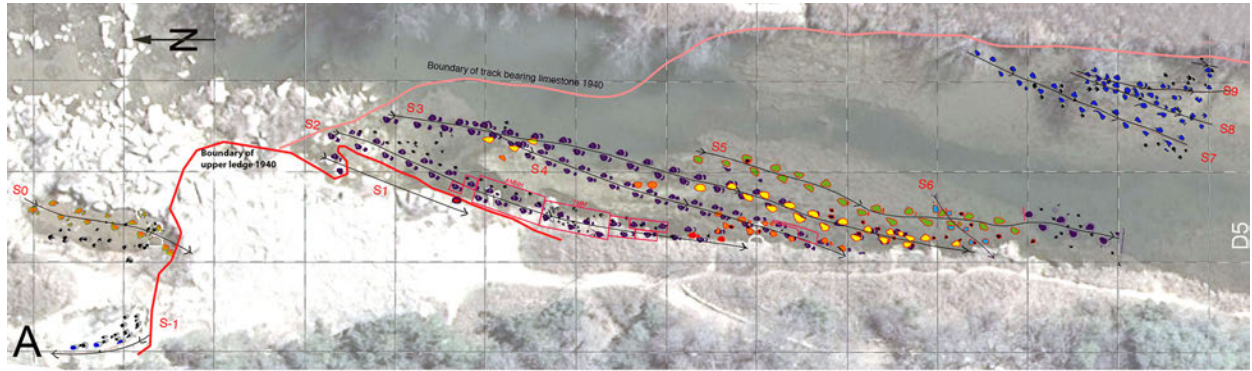
Dinosaur footprints in the Main Tracklayer are often quite deep (up to c. 25-30 cm), and some tracks pass through the layer to the underlying Bluff Dale Sand. The trackmakers had themselves to have been carrying most or all of their body weight, without being buoyed up by water, in order to make such deep footprints.

However, there are some intriguing prints that suggest that their makers were floating or swimming. One of these is a set of two parallel slash marks in the rock at the west bank portion of the Main Tracksite (Fig. 3E, F). These are claw marks only, and decrease dramatically in depth from one end to the other. Footprints attributed to swimming (or possibly swimming) bipedal dinosaurs have been described from a number of tracksites around the world (Whyte and Romano, 2001; Farlow and Galton, 2003; Moreno et al., 2004; Milner et al., 2006a, b; Ezquerro et al., 2007; Xing et al. 2011b, 2013a; Fujita et al., 2012; Romilio et al., 2013; Lockley and Tempel, 2014; Lockley et al., 2014b), and some of these are very similar to the prints described here. A second interesting set of traces consists of a discontinuous series of arcuate slash marks at one end of part of the Main Tracksite (Fig. 3A, G), also possibly made by a swimming animal.

If the Main Tracklayer contains footprints of both floating and walking dinosaurs, then water depth fluctuated (by a few meters?) over the interval during which it recorded footprints. Small but densely populated U-shaped burrows (*Arenicolites*) on the top surface of the Main Tracklayer also indicate a subaqueous environment, as these likely belong to suspension feeders. These burrows must have preceded the dinosaurs, though, as they are compressed within or otherwise deformed by the tracks.

Another interesting feature of the Main Tracklayer is a common mode of preservation of tridactyl prints in which the toe marks penetrate the rock further forward beneath the surface of the rock layer than at the surface, forming "toe tunnels" (Fig. 3D), suggesting a rather plastic consistency of the sediment at the time the tracks were made; Farlow has found it entertaining to watch little fishes swimming in and out of such tunnels, but he is of course very easily amused. Footprints of this kind may indicate something about the kinematics of the foot-substrate interaction of mud-slogging bipedal dinosaurs (cf. Platt and Meyer, 1991; Avanzini et al., 2012; Huerta et al., 2012; Falkingham and Gatesy, 2014). In some tridactyl footprints from the Main Tracklayer there was backflow of sediment into footprints, and even complete collapse of footprints,

FIGURE 2 (next page). Distinctive features of the Paluxy River Main Tracklayer; **A**, View of the Main Tracksite area (left: GPS 32.25324, -97.81883), the Bird Site (middle: 32.25260, -97.81869), and the East Bank (Ozark) Site (32.25221, -97.81856), with R. T. Bird's Rye Chart (Farlow et al., 1989) and other trackway maps superimposed (modified from Farlow et al., 2012). Individual sauropod trackways labeled S0 – S9. Much of the track-bearing bed in the river channel has been destroyed by erosion since 1940; **B – E**, R. T. Bird's sauropod-theropod "chase sequence"; **B**, 1940 Bird photograph of the two trackways; **C**, location of Bird's quarry along the west bank of the river; **D**, digital reconstruction of the two trackways in plan view created from Bird's photographs (Falkingham et al., 2014); **E**, digital model of a portion of the two trackways, created by LiDAR scanning of the American Museum slab (bottom, below seam) and the Texas Memorial Museum slab (above seam). The final sauropod manus print in the American Museum slab (f) is a fabrication; the actual manus is seen immediately above the seam in the Texas Memorial Museum slab; **F, G**, photomosaic and interpretive map of the Blue Hole Ballroom (32.24777, -97.81913). Note prints of a large sauropod (Ls) moving diagonally from left to right as illustrated here, and a small sauropod (Ss) moving diagonally from right to left; **H**, large theropod footprint showing distinct claw marks. Note numerous *Arenicolites* burrows. Paleontologist Dr. Barbara Mattel is about 30 cm tall.



after the footprint was lifted from the substrate. Very commonly, but not always, there is a linear gash at the rock surface indicating where the mud squeezed together after a toe was withdrawn from the sediment. The surface expression of roofed over and collapsed footprints can give the misleading impression of toe marks that are short, broad, and blunt, which has led to misidentification of theropod footprints as those of ornithopods.

**Taylor Tracklayer** (Figs. 3H-J, 5G-M)—This grainstone is about 6 meters stratigraphically above the Main Tracklayer. It crops out in the river bed at and above the upstream end of Dinosaur Valley State Park, and again downstream of the Main Tracklayer exposures, beyond the park boundaries (fig. 1A). In places it consists of a series of very thin beds. Mudcracks and/or microripples are present, but the huge *Arenicolites* aggregations so typical of the Main Tracklayer are absent.

The Taylor layer contains numerous trails of elongate tracks with metatarsal impressions, many of which are largely infilled with a bluish-grey secondary sediment, which oxidizes to rusty-brown upon exposure (Kuban, 1989a, b). The infillings reduce the topographic relief of these tracks (Fig. 3H-J), sometimes leaving indistinct oblong depressions, which under some viewing conditions can resemble human tracks (Fig. 3I), an illusion often mistaken as real by creationists. However, when well cleaned, and especially clean and wet, the contrasting color and texture of the infilling material clearly demarcates the original track shapes and tridactyl digit patterns (Fig. 3H, J, 5K, L). Cores taken at the margin of the infillings show that the original tracks were several cm deep before the infilling episode. Some of the well oxidized infillings have become harder than the surrounding

rock, causing the limestone to erode around them, creating “raised” relief (Fig. 5K).

As with the Main Tracklayer, tridactyl footprints of bipedal dinosaurs are most common, and possibly include ornithopod (Fig. 3J) as well as the usual theropod footprints. Sauropod footprints are at best rare. Tridactyl footprints sometimes occur in very long trackways (e.g. Fig. 5H), and relatively small tridactyl prints (Fig. 5I, J) are prominent at some sites.

**Diplocraterion Bed** (Fig. 3K, L, 5N)—Immediately above the Taylor Trackway is one of the most fascinating units of the local section, a resistant packstone dominated by large, U-shaped *Diplocraterion* burrows (Martin et al., 2015). Like the smaller *Arenicolites* of the Main Tracklayer, the *Diplocraterion* traces were probably made by benthic worms or crustaceans (Martin, 2013; Martin et al., 2015), but whether by larger individuals of the same species as the *Arenicolites*-maker, or a different form, is unknown. Only one dinosaur trackway is presently known from this unit, a series of morphologically nondescript tridactyls at the McFall Ledge Site (Figs. 1, 5N).

## TRACKS AND TRACKMAKERS

**Sauropods** (Figs. 2, 3A, B, 4)—These are, of course, what caught R. T. Bird’s attention (Bird 1985 and references therein), and made the Paluxy River tracksites famous. Sauropod trackways are abundant in the Main Tracklayer, although even in that unit there are many more trackways of tridactyl dinosaurs.

Well-preserved manus prints have a double-U or horseshoe shape (Fig. 4F), and are deepest around the medial, anterior, and lateral rim, and shallowest at the center of the back part of the print. Bird made the

FIGURE 3 (next page). Distinctive features of the Paluxy River exposures. **A – G**, additional features of the Main Tracklayer. **A**, photomosaic of the portion of the Main Tracksite containing sauropod trackway S0 (Fig. 2, panel A) with 1-meter grid; south toward the top. A set of interesting arcuate traces (panel G) are seen at the top end of the image; **B**, digital model of the west bank portion of the Main Tracksite, with north toward the top of the image. The footprints shown in panels D – F are located toward the bottom of the model as shown here. Note unusual trackway of a northbound sauropod (animal [S-1], Fig. 2A); **C**, tridactyl footprint emerging from beneath overlying beds at the west bank portion of the Main Tracksite; **D**, digital model of a negative copy (cast) of a large tridactyl print (scale faintly visible at bottom of image) from near the south end of the west bank portion of the Main Tracksite. The toe marks punch deeply forward as tunnels into the rock; **E, F**, possible print of a swimming dinosaur (?) at the south end of the west bank portion of the Main Tracksite; **E**, the print in situ, shown as two parallel slashes in the rock to the right of the scale. Also note numerous *Arenicolites* traces (small dots in the rock surface); **F**, negative copy (cast) of the track and associated features. Note the triangular shadows associated with the slash marks, indicating that the trackmaker’s toes poked deep into the substrate before being pulled progressively more shallowly backward; **G**, digital model of discontinuous arcuate traces near the south edge of a portion of the Main Tracksite (near sauropod trackway S0 at the top of panel A). Meter stick provides scale; **H – I**, sequences of elongate footprints of bipedal dinosaurs, Taylor Tracklayer, Taylor Site (32.23842, -97.82181); **H**, particularly nice trackway; inset is overhead view of one of the prints; **I**, photomosaic of the classic “man track” trackway of creationists (Kuban 1989a, b) at a time when the color distinctions marking the toes were not distinct (cf. Fig. 5L for the same trackway viewed under ideal conditions); **J**, possible ornithopod trackway from the Taylor Site (inset is overhead view of single footprint); **K – L**, *Diplocraterion* traces, *Diplocraterion* bed. **K**, traces in surface view upstream (32.24237, -97.82119) from the Low T/Riverbend Cliff Site; **L**, vertical section through burrow at the Buckeye Branch Site (32.24433, -97.80690).

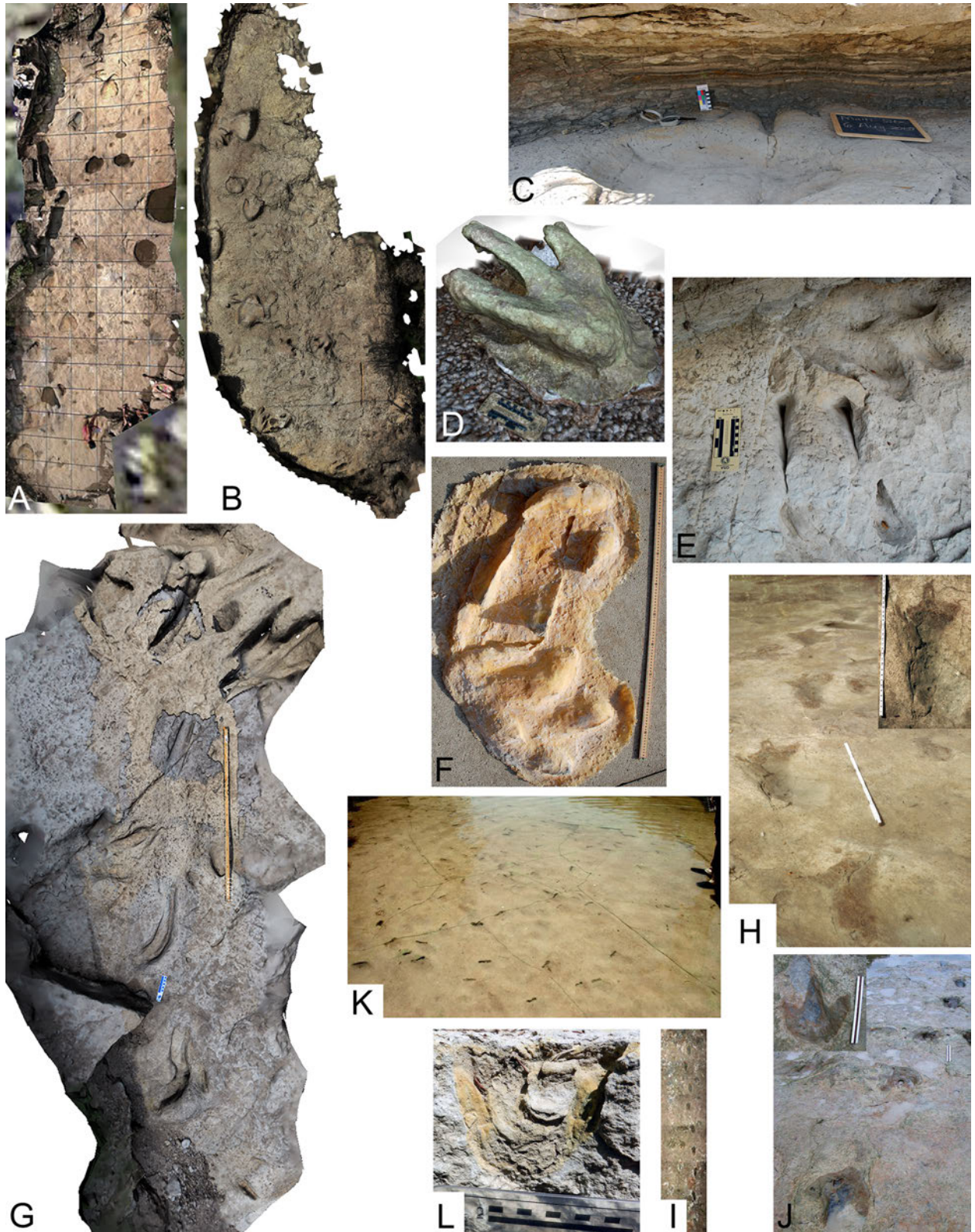
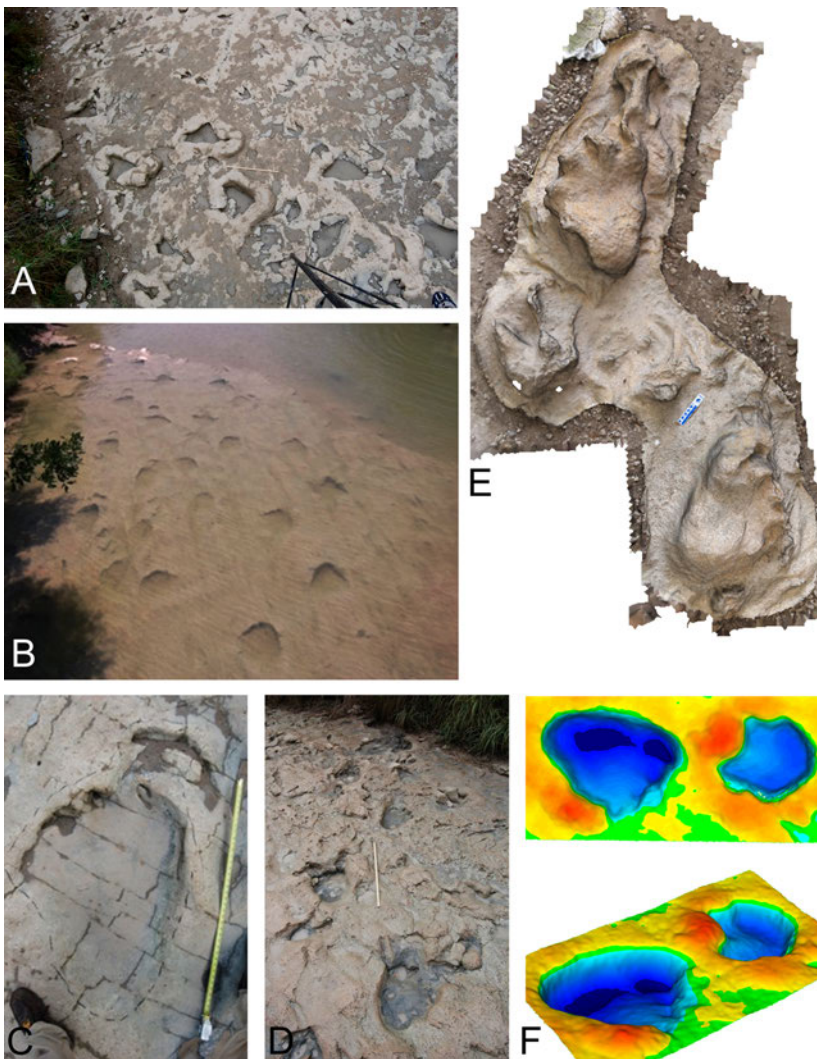


FIGURE 4. Sauropod trackways; **A**, pes-only footprints of a large sauropod with conspicuous pressure ridges (Fig. 2F, G), and numerous associated tridactyl prints, Blue Hole Ballroom; **B**, three sauropod trackways (moving away from the viewer), East Bank (Ozark) Site. The trackway on the right is pes-only; **C**, Left manus-pes set, Bird Site (1 meter of tape is exposed). The manus is rather poorly preserved; **D, E**, portion of the trackway of a small sauropod, Blue Hole Ballroom (Fig. 2F, G); **D**, the trackway in situ; **E**, digital model of a negative copy (cast) of part of the trackway, with an associated tridactyl print. Note distinct claw or nail marks along the front and lateral margins of the pes prints; **F**, digital model showing depth distribution of very well-preserved right manus-pes set from the American Museum slab. The manus print is deepest along its front and its medial and lateral margins. The pes is deepest along its inner margin, and is as deep or deeper than the manus print.



reasonable suggestion that digits II-IV of the forefoot were bound together by soft tissue, and offset from digits I and V. There is no suggestion of a claw mark on digit I. Commonly, however, manus prints were distorted during emplacement of the hindfoot. Sometimes the sediment squashed the manus print from the rear, causing it to be little more than a semicircular mark or depression (Figs. 4B, C), and sometimes the pes overprinted and obliterated the manus print (Figs. 4A, B).

The hindfoot print is larger (as much as a meter or more in length) than the forefoot print, and is roughly triangular in shape. In well-preserved pes prints, there are three or four laterally-directed claw marks, and a nubbin mark corresponding to digit V (cf. Tschoop et al., 2015). Pes prints are deepest on the inner side of the print, particularly near the base of the mark for digit I and at the heel of the print (Fig. 4F), and pes prints are always as deep as, or deeper than, manus prints. There are often conspicuous displacement rims (pressure

ridges) around the edge of pes prints (Figs. 4A, C, 5F). The outer edge of the pes print defines the outer edge of Paluxy sauropod trackways, and usually the inner edge of pes prints does not intersect the trackway midline (Figs. 2E, G, 4A, B, D, E).

R. T. Bird had hoped to describe his sauropod footprints under the name *Brontopodus*, but did not live to do so, and so Farlow et al. (1989) named these trace fossils *Brontopodus birdi* in his honor. Being a railroad enthusiast, Farlow (1992) characterized *Brontopodus* trackways as wide-gauge, in contrast with some other sauropod trace fossils (e.g. *Breviparopus*) that were dubbed narrow-gauge, but noted that the difference was more degree than kind. The distinction was further developed by Lockley et al. (1994), who suggested that narrow-gauge and wide-gauge sauropod trackways differ in relative size of manus and pes prints as well as in relative trackway width. Wilson and Carrano (1999) proposed that wide-gauge sauropod trackways could be interpreted as having been made by titanosaurs and their

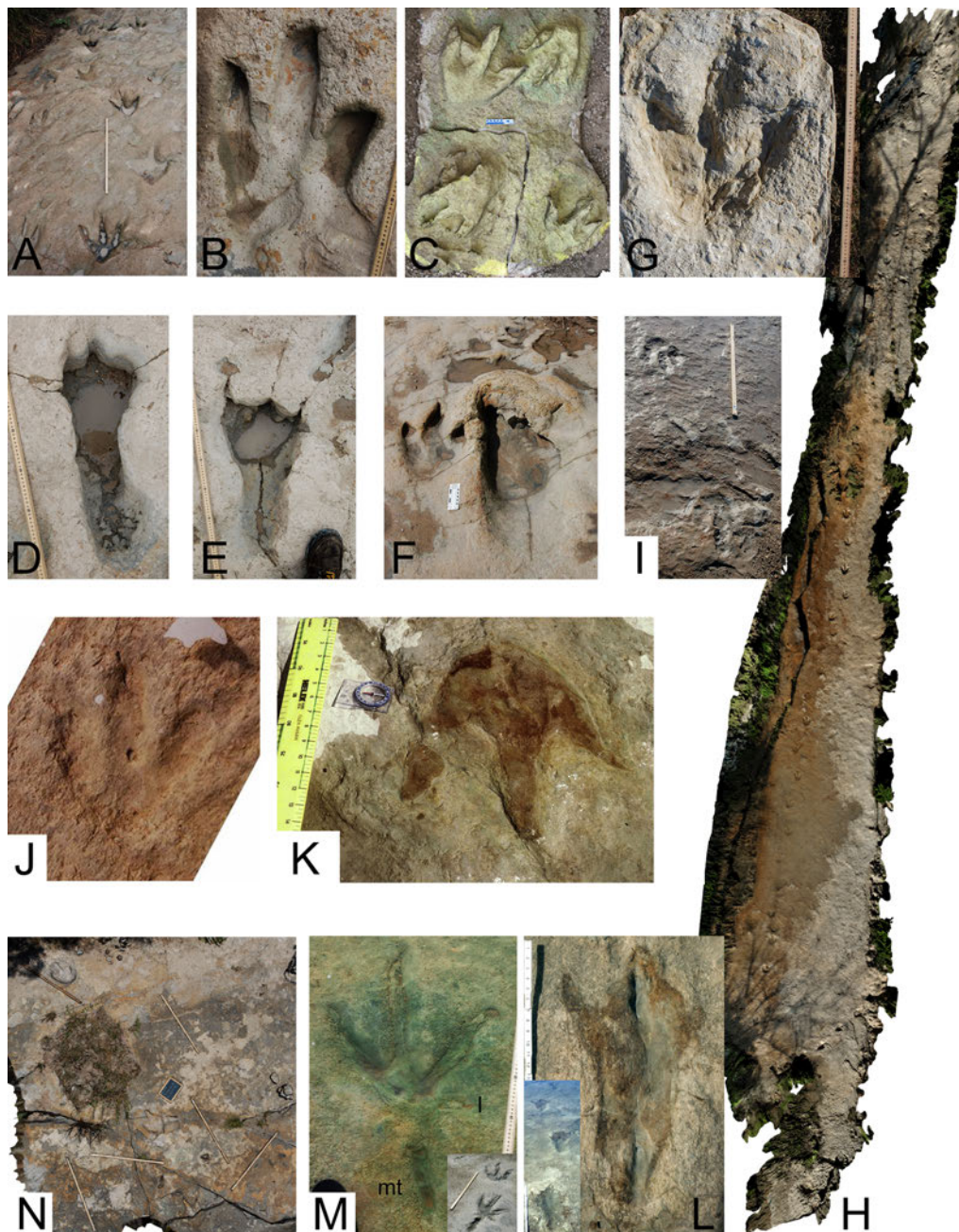


FIGURE 5. Tridactyl footprints. Meter stick (or portions thereof) provides scale in most images; **A – F**, footprints in the Main Tracklayer; **A**, well-preserved theropod prints near the south end of the Blue Hole Ballroom (Fig. 2F, G); **B**, large theropod footprint, Blue Hole. Note the many dot-like indentations in the rock surface (*Arenicolites* traces), a characteristic feature of the Main Tracklayer; **C**, digital model of negative copy of four well-preserved theropod prints, Opossum Branch Site; **D – E**, elongate tracks, Blue Hole Ballroom. Note suggestion of three toe marks at the ends of the prints, and the lack of any suggestion of a digit I mark; **F**, large theropod print associated with sauroprint pes print, Bird Site; **G – M**, footprints in the Taylor Tracklayer; **G**, positive copy of single footprint of large theropod, part of the long trackway illustrated in panel H; **H**, digital model of the McFall Ledge site (32.23733, -97.82449), showing a long trackway of a large theropod; **I**, sequence of footprints of a small bipedal dinosaur, Dattilo Station 754 (32.24230, -97.82122); **J**, individual small (length 25 cm) tridactyl print, Low T/Riverbend Cliff Site (32.23990, -97.82023); **K – L**, color-delimited tridactyls, Taylor Site; **L**, footprint from the classic “man track” sequence under ideal viewing conditions, showing tridactyl nature (Fig. 3H); inset shows portion of the trackway; **M**, very large elongate print with metatarsal (mt) and digit I (I) impressions, Low T/Riverbend Cliff; inset shows oblique view of the same print and another nearby large tridactyl; **N**, digital model of medium-sized tridactyl dinosaur trackway, *Diplocraterion* bed, McFall Ledge site. The animal marches diagonally from lower right to upper left across the image. A rectangular gap marks where a single footprint was removed from the trackway by a person unknown.



close relatives. Trackway gauge continues to be reported in descriptions of sauropod ichnites, albeit with modifications, reservations, and recognition that the differences between narrow- and wide-gauge trackways are not hard and fast (Dalla Vecchia et al., 2000; Lockley and Meyer, 2000; Lockley et al., 2002a, b, 2004, 2006b, 2008, 2014; Marty et al., 2003, 2006; 2010, 2013; Romano and Whyte, 2003; Meijide Fuentes et al., 2004; Moreno and Benton, 2005; Pascual Arribas et al., 2005; Wright, 2005; Le Lœuff et al., 2006; Zhang et al., 2006; Mezga et al., 2007; Romano et al., 2007; Bessedik et al., 2008; González Riga and Calvo, 2009; Moratalla, 2009; Pieńkowski et al., 2009; Santisteban et al., 2009; Santos et al., 2009, 2015; Xing et al., 2010, 2011a, 2013c, 2014a, 2015a, b, d, e, 2016; Castanera et al., 2011, 2012; Diedrich, 2011; Kim and Lockley, 2012; Masrour et al., 2013; Schumacher and Lockley, 2014; Fernández-Baldor et al., 2015; González Riga et al., 2015; Mesa and Perea, 2015; Pérez-Lorente, 2015; Tschopp et al., 2015); de Valais et al. 2015; Xing 2015c, f).

Identifying the kind(s) of sauropod responsible for Paluxy River *Brontopodus* has turned out to be more challenging than first thought. The trackmaker was initially—and without any great enthusiasm—interpreted as *Pleurocoelus* (Langston, 1974; Gallup, 1989; Farlow et al., 1989; Pittman, 1989; Farlow, 1992). Over the following years, a greater diversity of sauropod candidates for the Paluxy trackmaker turned up. *Sauroposeidon* was described by Wedel et al. (2000a, b), and then the Texan formerly known as *Pleurocoelus* was given the splendid name *Paluxysaurus* (Rose, 2007), only to have that name turn out (bummer!) to be a likely junior synonym of *Sauroposeidon* (D’Emic and Foreman, 2012; D’Emic, 2013). By latest tabulation, there may be as many as three distinct sauropod taxa in the Trinity Group and correlative units in the region, with the genera *Astrophocaudia* and *Cedarosaurus* as well as *Sauroposeidon* (D’Emic, 2013). So which of these skeletal taxa (if any) was the *Brontopodus*-maker, or whether more than one of them was responsible for such trackways in the Glen Rose Formation, remains to be determined (if it can be). However, it is worth noting that the pes of *Cedarosaurus* (Gallup, 1989, D’Emic, 2013) seems to match the morphology of the Paluxy River sauropod hindfoot prints. The phalangeal skeleton of *Sauroposeidon* and *Astrophocaudia* is unknown.

The Paluxy River sauropod footprints may have implications for interpreting some distinctive sauropod trace fossils from other sites. R. T. Bird (1985 and references therein) saw a sauropod trackway from the Glen Rose Formation on the Mayan Ranch in South Texas that consisted mainly of manus prints. He concluded that the trackmaker had been half-floating, pulling itself along by its forefeet, its hindquarters supported by the water. Lockley and Rice (1990)

proposed an alternative hypothesis: that manus-only and manus-dominated sauropod trackways are artifacts of undertrack formation. Walking sauropods are interpreted as having carried a greater concentration of weight per unit surface area on the sole of the manus than on the pes, such that deformation of sediment layers beneath that on which the dinosaurs trod was effected only by impression of the manus. Most (Vila et al., 2005; Lockley 2014c, e; Falkingham et al., 2011, 2012), but not all (Ishigaki and Matsumoto, 2009) workers have supported the undertrack hypothesis, and for most sauropod manus-dominated trackways the present authors also find it compelling.

But perhaps not for sauropod trackways from the Glen Rose Formation. In sauropod trackways from the Paluxy River and elsewhere in Texas that preserve both manus and pes prints, hindfoot prints are always as deeply impressed, or more deeply impressed, than manus prints (Fig. 4F), an observation inconsistent with differential autopodial pressure as the sole explanation for manus-dominated trackways (Farlow et al., 2012a). Conceivably such trackways were in fact made by wading or punting sauropods (Wilson and Fisher, 2003; Henderson, 2004).

**Bipedal dinosaurs**—Even in the Main Tracklayer, but especially in the Taylor Tracklayer, tridactyl footprints of bipedal dinosaurs numerically dominate the Paluxy River ichnofauna (Figs. 2F, G, 5, 6). Well-preserved large (c. 45-55 cm long) tridactyls (Fig. 5A-C, F-H, 6) have long, narrow toe marks, often with indications of sharp claw tips (Fig. 2H). The digit III impression sometimes shows a slight sigmoidal curvature along its length (Fig. 6). These footprints sometimes preserve indications of digital pads, but not often. Compared with skeletal taxa, these trackmakers would have been comparable in size to large allosaurs and medium-sized tyrannosaurs (Fig. 7C).

In addition to the large tridactyls, there seems to be a second concentration of smaller footprints (c. 25-40 cm long) that is particularly evident in the Taylor Tracklayer (fig. 5I, J) and the *Diplocraterion* bed (Fig. 5N). If their makers were theropods, they would have been roughly the size of *Dilophosaurus*, *Aucasaurus*, *Allosaurus*, and large ornithomimids (Fig. 7C).

For trackmakers from the Glen Rose Formation and other Early Cretaceous formations from Texas more generally, there seems to be a trimodal distribution of trackmaker sizes, with peaks at roughly 25, 35-40, and 45-50 cm (Fig. 7D). Intriguingly, for a worldwide sample of trackways attributed to theropods, a footprint length of 30 cm is the most common size class, at least for putative theropod trackways of Cretaceous age, with the suggestion of a much smaller secondary mode at footprint lengths of about 50 cm. So the Paluxy River bipedal dinosaur footprint assemblage, if dominated by theropods, seems roughly consistent with what is seen

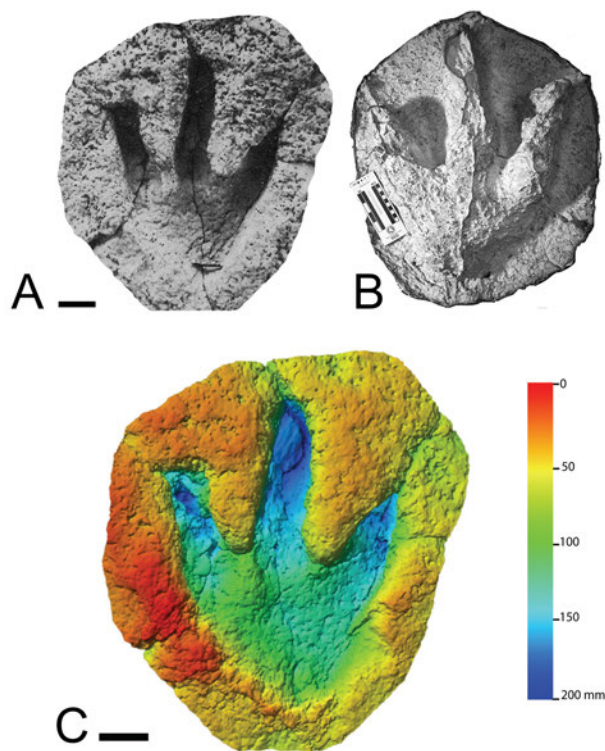


FIGURE 6. The Glen Rose bandstand footprint (Shuler, 1935), the type of *Eubrontes (?) glenrosensis*. **A**, Shuler's photograph of the print, from Adams et al. (2010); **B**, negative copy (cast) of the print; **C**, digital depth-coded image of the print (Adams et al., 2010).

elsewhere.

Skeletal data (Farlow et al., 2006, 2012a, 2014; cf. Fanti et al., 2013) show a clear difference between theropods and bipedal or potentially bipedal ornithischians in relative width of digits (Fig. 7A), with theropods having relatively skinnier toes, especially at large sizes. The large Paluxy tridactyls are clearly theropod-like in this feature, and are longer than broad, which is usually interpreted as a theropod feature in tridactyl footprints. A good candidate for the maker of the big tridactyls is the allosaur *Acrocanthosaurus* (Langston, 1974; Pittman, 1989; Currie and Carpenter, 2000; Farlow, 2001).

The smaller Paluxy tridactyls are also longer than broad, and sometimes preserve digital pad impressions. They have a theropod-like appearance, but the morphological differences between the feet and footprints of theropods and ornithopods become blurred at smaller sizes (Castanera et al., 2013a, b; Escaso et al., 2014; Farlow et al., 2014). Consequently, although we suspect that most or all of these prints were also made by theropods, we cannot be certain of this.

A striking feature of some tridactyl trackways in both the Main Tracklayer and the Taylor Tracklayer is the presence of an elongate depression behind the

digital portion of the footprint (Kuban, 1989a; Figs. 3H, 5D, E, L, M). Such elongate prints have been reported from numerous other dinosaur tracksites around the world (Leonardi, 1979; Calvo, 1991; Kvale et al., 2001; Dalla Vecchia et al., 2002; Lockley et al., 2003, 2006a, 2013, 2014a, b, d; Milner et al., 2006a; Rodríguez-de la Rosa et al., 2004; Conti et al., 2005; Gand et al., 2007; Nicosia et al., 2007; Petti et al., 2008a; Rubilar-Rogers et al., 2008; Gierliński et al., 2009; Ishigaki et al., 2009; Ishigaki, 2010; Li et al., 2010; Xing et al., 2011c, 2014e, 2015c, g; Boutakiout et al., 2012; Moreno et al., 2012; Lockwood et al., 2014; McCrear et al., 2014b; Citton et al., 2015; Pérez-Lorente, 2015). Some of these prints may be slip or skid marks, but most of them (including those from the Paluxy River) record the impression of the metatarsal region of the foot in the substrate. Footprints with metatarsal impressions could be made when the trackmaker was sitting, of course, but many trackways composed of such elongate prints show forward locomotion of the animal, and—very strangely—the step length of the dinosaur seems not much to have been affected by this unusual mode of progression. Whether the creation of such “elongate”, “metatarsal”, or “semplantigrade” footprints reflects deliberate foraging behavior on the part of crouching animals (Kuban, 1989a), or merely an adjustment to substrate conditions (e.g., Pérez-Lorente, 2015), is uncertain.

In any case, registry of the metatarsal region in some Paluxy River footprints provides additional clues to the trackmakers (Farlow et al., 2013). In those ornithischians that retain a digit I, this toe is generally longer, relative to the length of digit III, than in theropods (Fig. 7B). Consequently the presence of a very short digit I impression in a large tridactyl footprint from the Taylor Tracklayer (Fig. 5M) supports the interpretation that the trackmaker was a big theropod; similar footprints have been reported elsewhere (e.g. Nicosia et al., 2007). In contrast, the absence of a digit I impression in some of the elongate footprints from both the Main and Taylor Tracklayers (Fig. 5D, E) suggests that the maker of such prints was a form that had lost this toe, perhaps an ornithomimosaur (cf. Lockley et al., 2006a; Petti et al. 2008a). Hunt (2003) described a probable theropod foot skeleton from the Early Cretaceous Trinity Group of Arkansas, the exact affinities of which are uncertain, but whose erstwhile owner might be a candidate for the maker of many of the Paluxy elongate tracks that lack a digit I impression. More speculatively, we might consider a bipedal ornithischian with a foot like that of the dryosaurid *Eousdryosaurus* (Escaso et al., 2014), although bigger—should such a dinosaur ever turn up.

Some of the elongate tracks made by smaller dinosaurs from the Taylor Tracklayer do show a hallux impression, however, and so there may have been more

than one kind of trackmaker responsible for the elongate prints. The same may be true for the smaller Paluxy bipedal dinosaurs more generally; they may have included adults of relatively small-bodied species, but also smaller, immature individuals of the large theropod species.

Trackways with elongate footprints from the Taylor Tracklayer have become (in)famous as having been interpreted as made by giant humans that supposedly coexisted with dinosaurs (Hastings, 1987; Kuban, 1989a, b; Farlow et al., 2012b). One of the more renowned such trackways (Figs. 3I, 5L) consists of footprints that sometimes have a humanoid appearance (Fig. 3I), but even these show shallow but definite indications of a tridactyl configuration at the front end of the footprint, and under the best viewing conditions color differences (due to differences between the material that filled in the tracks vs. the surrounding rock) display three distinct toe marks (Fig. 5L). Just as the Paluxy River sauropod footprints were first identified by locals as elephant tracks (Farlow et al., 1989), and typical tridactyl dinosaur footprints from around the world are commonly first interpreted as bird prints (cf. Shuler, 1917), the Paluxy River “man track” story seems to have begun as a case of folk natural history, but one that metastasized.

Weirdness of the elongate tracks notwithstanding, the bipedal trackmakers of the Paluxy River and other sites in the Glen Rose Formation seem to have been very similar to other bipedal dinosaurs in their typical locomotion. The stride length of Glen Rose bipeds, relative to footprint length, is very similar to that of trackways attributed to theropods from the entire Mesozoic of the whole world (Fig. 7F). There is a “main sequence” of trackways in which stride length increases with increasing trackmaker size, but starts to level off

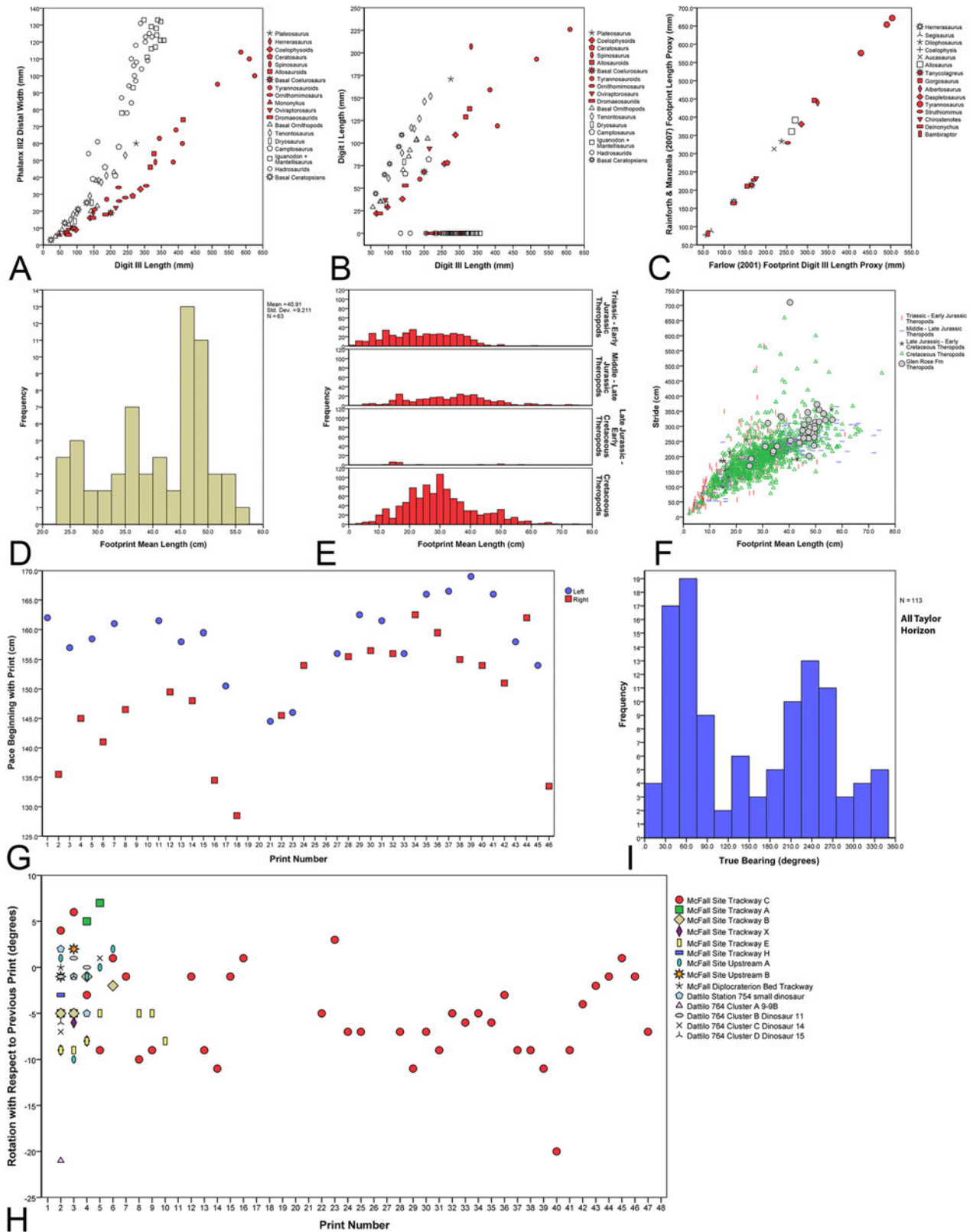
among the biggest trackmakers. This presumably defines the normal stride length: footprint length relationship of dinosaurs going about their business in no particular hurry. Above the main sequence are scattered points that presumably correspond to running dinosaurs, with the maximum stride length seen among animals with a footprint length of about 40 cm.

Long trackways provide especially useful information about trackmaker locomotion (Dalla Vecchia et al., 2001; Mossman et al., 2003; Day et al., 2004; Huh et al., 2006; Kim and Huh, 2010; Wings et al., 2012; Xing et al., 2015c). The long theropod trackway from the McFall Ledge site (Fig. 5H) shows an interesting pattern of step (pace) lengths (Fig. 7G): the animal generally took longer paces when stepping off from its left as opposed to its right foot. Disparity in pace lengths initiated with the left as opposed to the right foot is also seen in the longest tridactyl dinosaur trackway known from the Paluxy River (extending for more than 150 steps, making it one of the longest dinosaur trackways in North America), which also occurs in the Taylor Tracklayer. Dinosaur trackways with unequal step lengths have been reported from other ichnofaunas (e.g. Ishigaki and Matsumoto, 2009; Ishigaki and Lockley, 2010; Foster, 2015; McCrea et al., 2015). The usual interpretation for such trackways is the trackmaker had been injured and was limping, but McCrea et al. (2015) hypothesized that many such cases may have more to do with animal psychology than pathology, being examples of the more general phenomenon of laterality in tetrapods.

Most Paluxy River bipedal trackmakers walked with their footprints angling slightly inward with respect to their direction of travel (negative rotation; Fig. 7H).

A bewildering assortment of ichnotaxonomic names has been applied to tridactyl dinosaur footprints

FIGURE 7 (next page). Interpreting tridactyl dinosaur footprints. **A**, relative width of digit III of bipedal or potentially bipedal dinosaurs. At small sizes, there is little difference between ornithischians and theropods, but with increasing size ornithopods have relatively stout toes, and theropods relatively narrow toes; **B**, digit I length vs. digit III length. Most theropods have a relatively shorter digit I than do most ornithischians, but some members of both groups completely lose digit I (plotted as length of zero in this graph); **C**, comparison of two skeletal proxies of footprint size in theropods. For prints where the proximal end of the digit III impression is well-preserved, Farlow (2001) suggested that a skeletal proxy would be half the length of phalanx 1 plus the combined lengths of phalanges 2-4. Rainforth and Manzella (2007) suggested that a proxy for overall footprint length would be the total lengths of all the phalanges of digit III plus the difference in length between metatarsals III and IV. The two proxies are graphed to show how one proxy is related to the other in the same specimen; **D**, size frequency distribution of trackways of bipedal (mostly theropod?) dinosaurs from Lower Cretaceous sites in Texas. There seem to be three modes, at about 25-30, 35-40, and 45-50 cm footprint length. **E**, worldwide size-frequency distribution for trackways attributed to non-avian theropods from all intervals of the Mesozoic; data cases are trackways represented by at least one stride measurement. For the Cretaceous, the most common size class (length 30 cm) is close to one of the modes for the Texas size-frequency distribution; **F**, stride length as a function of footprint length in trackways attributed to non-avian theropods. The maximum stride length occurs at footprint lengths of about 40 cm; Glen Rose Formation trackways nicely match the pattern for all trackways; **G**, pace lengths along the long trackway from the McFall Ledge Site (Fig. 5H). The dinosaur generally took longer paces when stepping off from the left as opposed to the right foot; **H**, footprint rotation relative to the overall direction of travel of Taylor Tracklayer bipedal dinosaur trackways. For each print, rotation is measured by comparing the azimuth of the individual print with the average of that azimuth and that of the preceding print (the average indicating the overall direction of movement); negative rotation means that the footprint turns inward relative to the animal's movement direction; **I**, direction of travel of Taylor Horizon dinosaurs. Each data case is either the mean for a trackway, or the value for an isolated print.



from around the world (Calvo, 1991; Lockley and Meyer, 2000; Thulborn, 2001; Farlow and Galton, 2003; Calvo and Mazzetta, 2004; Clark et al., 2004; Day et al., 2004; Diedrich, 2004, 2011; Gangloff et al., 2004; Barco et al., 2005, 2006; Getty, 2005; Huh et al., 2006; Li et al., 2006; Lü et al., 2006; Lucas et al., 2006; Gand et al., 2007; Lockley et al., 2007, 2008, 2011, 2013; 2014a, c, e, 2015b, c; Rainforth, 2007; Wings et al., 2007; Bessedik et al., 2008; Fujita et al., 2008; Boutakiout et al., 2009; Sullivan et al., 2009; Belvedere et al., 2010; Li et al., 2010; Niedzwiedzki, 2011; Nouri et al., 2011; Xing et al., 2011b, c; 2013b, 2014a, b, c, d, e, f, h, 2015a, c, e, 2016; Moreau et al., 2012, 2014; Wagensommer et al., 2012; Fanti et al., 2013; Cobos et al., 2014; Fiorillo et al., 2014; McCrea and Pigeon, 2014; McCrea et al., 2014a, b; Foster, 2015; Li et al., 2015; Lallensack et al., 2015; Weems and Bachman, 2015). Criteria used to discriminate among these footprint taxa include relative toe lengths, angles between toes, the footprint width/length ratio, the extent to which the distal impression of digit III extends beyond the distal impressions of digits II and IV, the shape of a triangle defined by the tips of the marks of digits II-IV, and the configuration of the back of the footprint. Ichnotaxa are sometimes distinguished by bivariate characters, sometimes by multivariate analyses, sometimes by geometric morphometrics, and sometimes by the qualitative “gestalt” of the footprints.

Shuler (1917, 1935) applied two names to tridactyl footprints from the Glen Rose Formation in Somervell County. The first (1917) was the tongue-twisting *Eubrontes (?) titanopelopatidus*, for which no type specimen seems to have been secured. In 1935 Shuler applied the more euphonious name *Eubrontes (?) glenrosensis* to a splendid Main Tracklayer footprint which was installed in a bandstand on the town square in Glen Rose (Fig. 6), where it has remained ever since, but has regrettably undergone a certain amount of degradation (Adams et al., 2010) due to exposure to the elements. Langston (1974) suggested that the Paluxy large tridactyls might better fit under the moniker *Irenesauripus*, a name originally applied to footprints from the Early Cretaceous of British Columbia.

Our group has thus far deliberately refrained from discussing names for the Glen Rose Formation tridactyls, but will eventually offer an opinion on this matter. It is probably fair to say, however, that there is a diversity of opinion among us as to how meaningful such names are. Footprints are three-dimensional records of the interaction of a foot with a substrate. Apart from the issue of the extent to which the surface expression of footprint outlines, or linear measures and angles, can capture that complexity, there is the matter of whether or to what extent the vagaries of footprint emplacement, preservation, and modern erosion (Platt and Meyer, 1991; Kvale et al., 2001; Nadon, 2001;

Gatesy, 2003; Manning, 2004, 2008; Henderson, 2006; Graverson et al., 2007; Milàn and Bromley, 2006, 2008; Falkingham et al., 2010; Jackson et al., 2009, 2010; Avanzini et al., 2012; Huerta et al., 2012; Thulborn, 2012; Santos et al., 2013; Razzolini et al., 2014; Carvalho et al., 2013; Alcalá et al., 2014; Cariou et al., 2014; Falkingham, 2014; Falkingham and Gatesy, 2014; Lockley and Xing, 2015; Pérez-Lorente, 2015) render the characters thought to be useful in defining different tridactyl footprint morphotypes and ichnotaxa unreliable. Even the more optimistic members of our group confess to a nagging worry that the ichnotaxonomy of tridactyl dinosaur footprints may be, to borrow the words of an ancient sage, “futile and pursuit of wind” (Ecclesiastes 1:14, Jewish Study Bible).

## TRACKMAKER BEHAVIOR AND ECOLOGY

### Behavior—What were the trackmakers doing?

For the most part, it seems, nothing particularly interesting. In both the Main Tracklayer (Farlow et al., 2012b) and the Taylor Tracklayer (Fig. 7F), the bipedal dinosaurs were moving in roughly the same numbers either northward or southward, presumably walking along the local shoreline. This pattern provides no evidence for group behavior on the part of the carnivorous dinosaurs. Interestingly, theropod trackways in the Taylor Tracklayer are most commonly oriented northeast-southwest, similar to linear trends of *Diplocraterion* burrow tops in the overlying *Diplocraterion* bed (Martin et al., 2015). This coinciding of burrow trends and trackways may reflect the presence of a northeast-southwest shoreline that shifted laterally with a slight rise in relative sea level between deposition of Taylor Tracklayer and *Diplocraterion* bed sediments (Martin et al., 2015).

In contrast, tracksites which show a pronounced single direction of trackmaker travel are usually interpreted as showing animals moving together (Lingham-Soliar et al., 2003; Barco et al., 2006; McCrea et al., 2014; Moreno et al., 2012; García-Ortiz and Pérez-Lorente, 2014; Lockley et al., 2015b; but see Roach and Brinkman, 2007; Getty et al., 2015). In the Main Tracklayer, nearly all of the sauropods were traveling to the south (Fig. 2A), in contrast to the trackways attributed to theropods. Farlow et al. (2012b) therefore hypothesized that (most of?) the sauropods, unlike the theropods, were not routine occupants of the footprint sites, but rather a herd of animals passing through the area at one time.

The two trackway slabs collected by R. T. Bird for the American Museum and the Texas Memorial Museum may record a dramatic story. A large theropod stepped along the trackway of a large sauropod, repeatedly treading upon the big herbivore’s footprints;

at one point both trackways bend to the left (Figs. 2B, D, E). Bird (1985) thought the meat-eater actually attacked the sauropod, but Farlow et al. (2012b) hypothesized the predator was only following the herbivore—at least over the preserved portions of the two trackways.

**Ecology**—The association of footprints of sauropods with those of large or small theropods is a recurrent theme in dinosaur footprint assemblages (Calvo, 1991; Dalla Vecchia et al., 2000, 2001; Lockley and Meyer, 2000; Moreno and Pino, 2002; Romano and Whyte, 2003; Ahmed et al., 2004; Calvo and Mazzetta, 2004; Day et al., 2004; Leonardi and dos Santos, 2004; Moreno et al., 2004; Hernández Medrano et al., 2005-2006; Foster and Lockley, 2006; Bessedik et al., 2008; Belvedere et al., 2010; Nicosia et al., 2007; Petti et al., 2008b; Ishigaki et al., 2009; Sacchi et al., 2009; Xing et al., 2010, 2013c, 2014a, f, 2015a, c, e, 2016; Diedrich, 2011; Hornung et al., 2012; Wagensommer et al., 2012; Bravo Cuevas, 2013; Cariou et al., 2014; Lockley et al., 2014b, 2015b; Schumacher and Lockley, 2014; González Riga et al., 2015; Pérez-Lorente, 2015), and not terribly surprising, given the common co-occurrence of such animals in skeletal assemblages. Perhaps more interesting is the fact that the theropod-sauropod association is frequently seen in carbonate environments (Lockley, 2007). Given the huge size of the Paluxy River sauropods and theropods, it is unlikely that their habitat was limited to the carbonate mudflats in which their tracks were preserved, an inference supported by the occurrence of skeletal material of the presumed trackmakers in more inland clastic settings, as well as the apparently large geographic ranges of these animals (Wedel et al., 2000a, b; Rose, 2007; D’Emic et al., 2012, 2013; D’Emic and Foreman, 2012), and by the broader worldwide paleoenvironmental occurrences of related forms (Mannion and Upchurch, 2010).

The greater abundance of footprints and trackways attributed to theropods than of sauropods in the Glen Rose Formation, a seemingly unexpected situation given the usual relative abundance of large herbivores and carnivores (cf. Hatton et al., 2015), is also seen in many (Leonardi, 1989; Foster and Lockley, 2006; Lockley et al., 2015a; Pérez-Lorente, 2015) but not all (Weems and Bachman, 2015) other dinosaur track assemblages. Leonardi (1989) suggested that this reflected greater activity on the part of carnivorous than herbivorous dinosaurs, an interpretation endorsed by Farlow (2001) by analogy with the movement ecology of extant large mammals. *Acrocanthosaurus* was a huge meat-eater, with large adults possibly weighing as much as 5000-6000 kg (Henderson and Snively, 2004; Bates et al., 2009). Individual theropods that big might have had home ranges covering tens of thousands of square kilometers (Farlow, 2001), and patrolled long distances

in a single day, giving them ample opportunity to make lots of footprints in suitable environments.

Some workers (e.g. Hunt and Lucas, 2007; Lockley, 2007 [and references therein]) have proposed recognition of tetrapod trace fossil ichnofacies analogous to the ichnofacies recognized by ichnologists working on traces of benthic invertebrates (cf. Martin, 2013 [and references therein]). The details of how such ichnofacies are to be defined differ, but in both schemes one of the ichnofacies was named after *Brontopodus*. Lockley (2007 [and earlier]) associated his *Brontopodus* ichnofacies with platform carbonate situations. Hunt and Lucas (2007: Table 2) went further, defining a *Brontopodus* “archetypal tetrapod ichnofacies” associated with “coastal plain, clastic or carbonate marine shoreline” environments, and characterized by footprint assemblages in which the “majority of tracks are terrestrial, quadrupedal herbivores with small quantity (generally > 10% of terrestrial carnivore tracks)”. Lockley’s *Brontopodus* ichnofacies was interpreted by Hunt and Lucas as one of the constituent ichnocoenoses within their more inclusive ichnofacies; as interpreted by Hunt and Lucas, their *Brontopodus* ichnocoenosis, like Lockley’s ichnofacies of the same name, is associated with “carbonate marine shorelines” (Hunt and Lucas 2007:66). What made their *Brontopodus* ichnofacies “archetypal” is that it is not restricted to a particular time interval, and so ranges from the Late Jurassic through the Recent; *Brontopodus* itself, the ichnogenus after which the ichnofacies was named, therefore does not have to be present.

Which these concepts will catch on, if any, is still up in the air. Defining the *Brontopodus* archetypal ichnofacies as being characterized by a “small” number of predator trackways, which at the same time constitute > 10% of the trackway assemblage, seems rather odd. We would have thought that the “> 10%” was a typographical error that should have read “< 10%”, except that the phrase appears more than once in Hunt and Lucas (2007). Be that as it may, if the *Brontopodus* ichnofacies is defined as having substantially fewer carnivore than herbivore trackways, this would seem to disqualify the Glen Rose Formation of Texas, the type formation for *Brontopodus*, from membership therein. Can’t win them all.

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## LITERATURE CITED

- Adams, T. L., C. Strganac, M. J. Polcyn, and L. L. Jacobs. 2010. High resolution three-dimensional laser-scanning of the type specimen of *Eubrontes (?) glenrosensis* Shuler, 1935, from the Comanchean (Lower Cretaceous) of Texas: implications for digital archiving and preservation. *Palaeontologia Electronica* 13(3); [http://palaeo-electronica.org/2010\\_3/226/index.html](http://palaeo-electronica.org/2010_3/226/index.html).
- Ahmed, A. A.-K., T. Lingham-Soliar, and T. J. Broderick. 2004. Giant sauropod tracks from the Middle-Late Jurassic of Zimbabwe in close association with theropod tracks. *Lethaia* 37:467-470.
- Alcalá, L., F. Pérez-Lorente, L. Luque, A. Cobos, R. Royo-Torres, and L. Mampel. 2014. Preservation of dinosaur footprints in shallow intertidal deposits of the Jurassic-Cretaceous transition in the Iberian Range (Teruel, Spain). *Ichnos* 21:19-31.
- Avanzini, M., L. Piñuela, and J. C. García-Ramos. 2012. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lethaia* 45:238-252.
- Barco, J. L., J. I. Canudo, and J. Ruiz-Omeñaca. 2006. New data on *Therangospodus oncalensis* from the Berriasian Fuentesalvo tracksite (Villar del Río, Soria, Spain): an example of gregarious behaviour in theropod dinosaurs. *Ichnos* 13:237-248.
- Barco, J. L., J. I. Canudo, J. I. Ruiz-Omeñaca, and J. L. Rubio. 2005. Evidencia icnológica de un dinosaurio terópodo gigante en el Berriasiense (Cretácico Inferior) de Laurasia (Las Villasecas, Soria, España). *Revista Española de Paleontología* 10:59-71.
- Bates, K. T., P. L. Manning, D. Hodgetts, and W. I. Sellers. 2009. Estimating mass properties of dinosaurs using laser imaging and 3D computer modelling. *PLoS One* 4(2): e4532. doi:10.1371/journal.pone.0004532.
- Belvedere, M., P. Mietto, and S. Ishigaki. 2010. A Late Jurassic diverse ichnocoenosis from the siliciclastic Iouaridène Formation (Central High Atlas, Morocco). *Geological Quarterly* 54:367-380.
- Bessedik, M., C. Mammeri, L. Belkebir, M. Mahboubi, M. Adaci, H. Hebib, M. Bensalah, B. Mansour, and M. E. H. Mansouri. 2008. Nouvelles données sur les ichnites de dinosaures de la région d'el Bayadh (Cretace Inferieur, Algerie). *Palaeovertebrata* 36:7-35.
- Bird, R. T. 1985. *Bones for Barnum Brown: Adventures of a Dinosaur Hunter*. Texas Christian University Press, Fort Worth, Texas, 225 pp.
- Blair, M., B. Dattilo, A. J. Martin, and J. O. Farlow. 2012a. Microstratigraphic analysis of burrow-reworked dinosaur track bed at Joanna's Track Site, Cretaceous Glen Rose Formation, Glen Rose, Texas. 2012 Annual Meeting, Geological Society of America, abstract 158-17.
- Blair, M., B. Dattilo, J. O. Farlow, L. Mark, J. Jacene, and S. McFadin. 2012b. Taphonomy of the Joanna Track Site, Cretaceous Glen Rose Formation: Is the shrimp mightier than the dinosaur? North-Central Section, Geological Society of America, abstract 24-4.
- Boutakiout, M., M. Hadri, J. Nouri, I. Díaz-Martínez, and F. Pérez-Lorente. 2009. Rastrilladas de icnitas terópodos gigantes del Jurásico Superior (Sinclinal de Iouaridène, Marruecos). *Revista Española de Paleontología* 24:31-46.
- Boutakiout, M., J. Nouri, L. Ladel, I. Díaz-Martínez, and F. Pérez-Lorente. 2012. Contenido anómalo de icnitas semiplantigrados terópodos en el yacimiento de Oumzawrou (361GR) del Atlas Marroquí. *Geogaceta* 52:173-176.
- Bravo Cuevas, V. M. 2013. El registro de huellas de dinosaurios de los Estados de Oaxaca, Michoacán, y Puebla. *Paleontología Mexicana* 3:66-71.
- Calvo, J. O. 1991. Huellas de dinosaurios en la Formación Rio Limay (Albiano-Cenomaniano?), Picn Leufú, Provincia de Neuquén, Republica Argentina. (*Ornithischia-Saurischia: Sauropoda-Theropoda*). *Ameghiniana* 28:241-258.
- Calvo, J. O., and G. V. Mazzetta. 2004. Nuevo hallazgos de huellas de dinosaurios en la Formación Candeleros (Albiano-Cenomaniano), Picún Leufú, Neuquén, Argentina. *Ameghiniana* 41:545-554.
- Cariou, E., N. Olivier, B. Pittet, J.-M. Mazin, and P. Hantzpergue. 2014. Dinosaur track record on a shallow carbonate-dominated ramp (Louille section, Late Jurassic, French Jura). *Facies* 60:229-253.
- Carvalho, I. de S., L. Borghi, and G. Leonardi. 2013. Preservation of dinosaur tracks induced by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil. *Cretaceous Research* 44: 112-121.
- Castanera, D., J. Colmenar, V. Sauqué, and J. I. Canudo. 2014. Geometric morphometric analysis applied to theropod tracks from the Lower Cretaceous (Berriasian) of Spain. *Palaeontology* 58:183-200.
- Castanera, D., C. Pascual, J. I. Canudo, N. Hernández, and J. L. Barco. 2012. Ethological variations in gauge in sauropod trackways from the Berriasian of Spain. *Lethaia* 45:476-489.
- Castanera, D., J. L. Barco, I. Díaz-Martínez, J. H. Gascón, F. Pérez-Lorente, and J. I. Canudo. 2011. New evidence of a herd of titanosaurian sauropods from the lower Berriasian of the Iberian range (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 310:227-237.
- Castanera, D., C. Pascual, N. L. Razzolini, B. Vila, J. L. Barco, and J. I. Canudo. 2013a. Discriminating between medium-sized tridactyl trackmakers: tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). *PLoS One* 8(11): e81830. doi:10.1371/journal.pone.0081830.
- Castanera, D., B. Vila, N. L. Razzolini, P. L. Falkingham, J. I. Canudo, P. L. Manning, and A. Galobart. 2013b. Manus track preservation bias as a key factor for assessing trackmaker identity and quadrupedalism in basal ornithopods. *PLoS One* 8(1): e54177. doi:10.1371/journal.pone.0054177.
- Citton, P., U. Nicosia, I. Nicolosi, R. Carluccio, and M. Romano. 2015. Elongated theropod tracks from the Cretaceous Apenninic Carbonate Platform of southern Latium (central Italy). *Palaeontologia Electronica* 18.3.49A:1-12.
- Clark, N. D. L., P. Booth, C. Booth, and D. A. Ross. 2004. Dinosaur footprints from the Duntulm Formation (Bathonian, Jurassic) of the Isle of Skye. *Scottish Journal of Geology* 40:13-21.
- Cobos, A., M. G. Lockley, F. Gascó, R. Royo-Torres, and L. Alcalá. 2014. Megatheropods as apex predators in the

- typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 399:31-41.
- Conti, M. A., M. Morsilli, U. Nicosia, E. Sacchi, V. Savino, A. Wagensommer, L. Di Maggio, and P. Gianolla. 2005. Jurassic dinosaur footprints from southern Italy: footprints as indicators of constraints in paleogeographic interpretation. *Palaios* 20:534-550.
- Currie, P. J., and K. Carpenter. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas* 22:207-246.
- Dalla Vecchia, F. M., A. Tarlao, G. Tunis, and S. Venturini. 2000. New dinosaur track sites in the Albian (Early Cretaceous) of the Istrian Peninsula (Croatia). *Memorie di Scienze Geologiche* 52:193-292.
- Dalla Vecchia, F. M., G. Tunis, S. Venturini, and A. Tarlao. 2001. Dinosaur track sites in the upper Cenomanian (Late Cretaceous) of Istrian Peninsula (Croatia). *Bolletino della Società Paleontologica Italiana* 40:25-53.
- Dalla Vecchia, F. M., I. Vlahović, L. Posocco, A. Tarlao, and M. Tentor. 2002. Late Barremian and Late Albian (Early Cretaceous) dinosaur track sites in the main Brioni/Brijun Island (SW Istria, Croatia). *Natura Nacosta* 25:1-36.
- Dattilo, B. F., S. C. Howald, R. Bonem, J. Farlow, A. J. Martin, M. O'Brien, M. G. Blair, G. Kuban, L. K. Mark, A. R. Knox, W. N. Ward, and T. Joyce. 2014. Stratigraphy of the Paluxy River tracksites in and around Dinosaur Valley State Park, Lower Cretaceous Glen Rose Formation, Somervell County, Texas; pp. 307-338 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Day, J. J., D. B. Norman, A. S. Gale, P. Upchurch, and H. P. Powell. 2004. A Middle Jurassic dinosaur trackway site from Oxfordshire, UK. *Palaeontology* 47:319-348.
- D'Emic, M. D. 2013. Revision of the sauropod dinosaurs of the Lower Cretaceous Trinity Group, southern USA, with the description of a new genus. *Journal of Systematic Paleontology* 11:707-726.
- D'Emic, M. D., and B.Z. Foreman. 2012. The beginning of the sauropod dinosaur hiatus in North America: insights from the Lower Cretaceous Cloverly Formation of Wyoming. *Journal of Vertebrate Paleontology* 32:883-902.
- D'Emic, M. D., K. M. Melstrom, and D. R. Eddy. 2012. Paleobiology and geographic range of the large-bodied Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 333-334:13-23.
- Diedrich, C. 2004. New important iguanodontid and theropod trackways of the Tracksite Obernkirchen in the Berriasian of NW Germany and megatracksite concept of central Europe. *Ichnos* 11:215-228.
- Diedrich, C. 2011. Upper Jurassic tidal flat megatracksites of Germany—coastal dinosaur migration highways between European islands, and a review of the dinosaur footprints. *Palaeodiversity and Palaeoenvironments* 91:129-155.
- Escaso, F., F. Ortega, P. Dantas, E. Malafaia, B. Silva, J. M. Gasulla, P. Mocho, I. Naváez, and J. L. Sanz. 2014. A new dryosaurid ornithopod dinosaur (Dinosauria, Ornithischia) from the Late Jurassic of Portugal. *Journal of Vertebrate Paleontology* 34: 1102-1112.
- Ezquerria, R., S. Doublet, L. Costeur, P. M. Galton, and F. Pérez-Lorente. 2007. Were non-avian theropod dinosaurs able to swim? Supportive evidence from an Early Cretaceous trackway, Cameros Basin (La Rioja, Spain). *Geology* 35:507-510.
- Falkingham, P. L. 2014. Interpreting ecology and behavior from the vertebrate fossil track record. *Journal of Zoology* 292:222-229.
- Falkingham, P. L. and S. M. Gatesy. 2014. The birth of a dinosaur footprint: substrate 3D motion reconstruction and discrete element simulation reveal track ontogeny. *Proceedings of the National Academy of Sciences of the United States of America* 111:18279-18284.
- Falkingham, P. L., K. T. Bates, and J. O. Farlow. 2014. Historical photogrammetry: Bird's Paluxy River dinosaur chase sequence digitally reconstructed as it was prior to excavation 70 years ago. *PLoS One* 9(4): e93247. doi:10.1371/journal.pone.0093247.
- Falkingham, P. L., L. Margetts, and P. L. Manning. 2010. Fossil vertebrate tracks as paleopenetrometers: confounding effects of foot morphology. *Palaios* 25:356-60.
- Falkingham, P. L., K. T. Bates, L. Margetts, and P. L. Manning. 2011. Simulating sauropod manus-only trackway formation using finite-element analysis. *Biology Letters* 7:142-145.
- Falkingham, P. L., K. T. Bates, and P. D. Mannion. 2012. Temporal and palaeoenvironmental distribution of manus- and pes-dominated sauropod trackways. *Journal of the Geological Society, London* 169:365-370.
- Fanti, F., P. R. Bell, and R. L. Sissons. 2013. A diverse, high-latitude ichnofauna from the Late Cretaceous Wapiti Formation, Alberta, Canada. *Cretaceous Research* 41:256-269.
- Fanti, F., M. Contessi, A. Nigarov, and P. Esenov. 2013. New data on two large dinosaur tracksites from the Upper Jurassic of eastern Turkmenistan (Central Asia). *Ichnos* 20:54-71.
- Farlow, J. O. 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. *Zubia* 10:89-138.
- Farlow, J. O. 2001. *Acrocanthosaurus* and the maker of Comanchean large-theropod footprints; pp. 408-427 in D. H. Tanke, K. Carpenter and M. W. Skrepnick (eds.), *Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Phillip J. Currie*. Indiana University Press, Bloomington, IN: Indiana.
- Farlow, J. O., and P. M. Galton, P. M. 2003. Dinosaur trackways of Dinosaur State Park, Rocky Hill, Connecticut pp. 248-263 in P. M. Letourneau and P. E. Olsen (eds.), *The Great Rift Valleys of Pangea in Eastern North America, Volume Two: Sedimentology, Stratigraphy, and Paleontology*. Columbia University Press, New York.
- Farlow, J. O., G. J. Kuban, and P. J. Currie. 2013. On the makers of "metatarsal" tridactyl dinosaur footprints of the Paluxy River (Glen Rose Formation, Dinosaur Valley State Park, Somervell County, Texas). North-Central Section, Geological Society of America, abstracts with program 45(4):22.



- Farlow, J. O., J. G. Pittman, and J. M. Hawthorne. 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the U.S. Gulf Coastal Plain; pp. 371-394 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, UK.
- Farlow, J. O., R. E. Chapman, B. Breithaupt, and N. Matthews. 2012a. The scientific study of dinosaur footprints; pp. 712-759 in M. K. Brett-Surman, T. R. Holtz, Jr., and J. O. Farlow (eds.), *The Complete Dinosaur*. Indiana University Press, Bloomington, Indiana.
- Farlow, J. O., E. R. Schachner, J. C. Sarrazin, H. Klein, and P. J. Currie. 2014. Pedal proportions of *Poposaurus gracilis*: convergence and divergence in the feet of archosaurs. *The Anatomical Record* 297:1022-1046.
- Farlow, J. O., W. Langston, Jr., E. E. Deschner, R. Solis, W. Ward, B. L. Kirkland, S. Hovorka, T. L. Reece, and J. Whitcraft. 2006. *Texas Giants: Dinosaurs of the Heritage Museum of the Texas Hill Country*. Heritage Museum of the Texas Hill Country, Canyon Lake, Texas, 105 pp.
- Farlow, J. O., M. O'Brien, G. J. Kuban, B. F. Dattilo, K. T. Bates, P. L. Falkingham, L. Piñuela, A. Rose, A. Freels, C. Kumagai, C. Libben, J. Smith, and J. Whitcraft. 2012b. Dinosaur tracksites of the Paluxy River valley (Glen Rose Formation, Dinosaur Valley State Park, Somervell County, Texas); pp. 41-69 in *V Actas de las Jornadas Internacionales Paleontología de Dinosaurios y Su Entorno, Salas de los Infantes, Burgos, Spain*.
- Feldman, R. M., C. E. Schweitzer, B. F. Dattilo, and J. O. Farlow. 2011. Remarkable preservation of a new genus and species of limuline horseshoe crab from the Cretaceous of Texas, USA. *Palaeontology* 54:1337-1346.
- Fernández-Baldor, F. T., I. Díaz-Martínez, R. Contreras, P. Huerta, D. Montero, and V. Urién. 2015. Unusual sauropod tracks in the Jurassic-Cretaceous interval of the Cameros Basin (Burgos, Spain). *Journal of Iberian Geology* 41:141-154.
- Fiorillo, A. R., M. Contessi, Y. Kobayashi, and P. J. McCarthy. 2014. Theropod tracks from the lower Cantwell Formation (Upper Cretaceous) of Denali National Park, Alaska, USA with comments on theropod diversity in an ancient, high-latitude terrestrial ecosystem; pp. 429-439 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Foster, J. R. 2015. Theropod dinosaur ichnogenus *Hispanosauropus* identified from the Morrison Formation (Upper Jurassic), western North America. *Ichnos* 22:183-191.
- Foster, J. R., and M. G. Lockley, 2006. The vertebrate ichnological record of the Morrison Formation (Upper Jurassic, North America); pp. 203-216 J. R. Foster and S. G. Lucas (eds.). *Paleontology and Geology of the Upper Jurassic Morrison Formation*. New Mexico Museum of Natural History and Science Bulletin 36, Albuquerque, New Mexico.
- Fujita, M., Y.-N. Lee, Y. Azuma, and D. Li. 2012. Unusual tridactyl trackways with tail traces from the Lower Cretaceous Hekou Group, Gansu Province, China. *Palaios* 27:560-570.
- Fujita, M. Z. Wang, Y. Azama, M. Shibata, and Z. Dong. 2008. First dinosaur track site from the Lower Cretaceous of Yunnan Province, China. *Memoir of the Fukui Prefectural Dinosaur Museum* 7:33-43.
- Gallup, M. R. 1989. Functional morphology of the hindfoot of the Texas sauropod *Pleurocoelus* sp. indet.; pp. 71-74 in J. O. Farlow (eds.), *Paleobiology of the Dinosaurs*. Geological Society of America Special Paper 238, Boulder, Colorado.
- Gand, G., G. Demathieu, and C. Montenat. 2007. Les traces de pas d'amphibiens, de dinosaures et autres reptiles du Mésozoïque Français: inventaire et interprétations. *Palaeovertebrata* 2007:1-149.
- Gangloff, R. A., K. C. May, and J. E. Storer. 2004. An early Late Cretaceous dinosaur tracksite in central Yukon Territory, Canada. *Ichnos* 11:299-309.
- García-Ortiz, E., and F. Pérez-Lorente. 2014. Palaeoecological inferences about dinosaur gregarious behaviour based on the study of tracksites from La Rioja area in the Cameros Basin (Lower Cretaceous, Spain). *Journal of Iberian Geology* 40:113-127.
- Gatesy, S. M. 2003. Direct and indirect track features: What sediment did a dinosaur touch? *Ichnos* 10:91-98.
- Getty, P. R. 2005. Excavated and *in situ* dinosaur footprints from the Murray Quarry (Early Jurassic East Berlin Formation), Holyoke, Massachusetts, USA. *Ichnos* 12:163-178.
- Getty, P. R., L. Hardy, and A. M. Bush. 2015. Was the *Eubrontes* track maker gregarious? Testing the herding hypothesis at Powder Hill Dinosaur Park, Middlefield, Connecticut. *Bulletin of the Peabody Museum of Natural History* 56:95-106.
- Gierliński, G. D., M. G. Lockley, and G. Niedźwiedzki. 2009. A distinctive crouching theropod trace from the Lower Jurassic of Poland. *Geological Quarterly* 53:471-476.
- González Riga, B. J., and J. O. Calvo. 2009. A new wide-gauge sauropod track site from the Late Cretaceous of Mendoza, Neuquén Basin, Argentina. *Palaeontology* 52:631-640.
- González Riga, B. J., L. D. Ortiz David, M. B. Tomaselli, C. R. dos Anjos Candeiro, J. P. Coria, and M. Prámparo. 2015. Sauropod and theropod tracks from the Upper Cretaceous of Mendoza (Argentina): trackmakers and anatomical evidences. *Journal of South American Earth Sciences* 61:134-141.
- Graverson, O., J. Milàn, and D. B. Loope. 2007. Dinosaur tectonics: A structural analysis of theropod undertracks with a reconstruction of theropod walking dynamics. *Journal of Geology* 115:641-654.
- Hastings, R. J. 1987. New observations on Paluxy tracks confirm their dinosaurian origin. *Journal of Geoscience Education* 35(4):4-15.
- Hatton, I. A., K. S. McCann, J. M. Fryxell, T. J. Davies, M. Smerlak, A. R. E. Sinclair, and M. Lorean. 2015. The predator-prey power law: biomass scaling across terrestrial and aquatic biomes. *Science* 349:aac6284-1 through aac6284-13.
- Henderson, D. M. 2004. Tippy punters: sauropod dinosaur pneumaticity, buoyancy and aquatic habits.
- Henderson, D. M. 2006. Simulated weathering of dinosaur tracks and the implications for their characterization. *Canadian Journal of Earth Sciences* 43:691-704.
- Henderson, D. M., and E. Snively. 2004. *Tyrannosaurus* en pointed: allometry minimized rotational inertia of large

- carnivorous dinosaurs. *Proceedings of the Royal Society B (Supplement)* 271:S57-S60.
- Hernández Medrano, N., C. Pascual Arribas, P. Latorre Macarrón, and E. Sanz Pérez. 2005-2006. Contribución de los yacimientos de icnitas Sorianos al registro general de Cameros. *Zubia* 23-24:79-119.
- Hornung, J. J., A. Böhme, T. van der Lubbe, M. Reich, and A. Richter. 2012. Vertebrate tracksites in the Obernkirchen Sandstone (late Berriasian, Early Cretaceous) of northwest Germany—their stratigraphical, palaeogeographical, palaeoecological, and historical context. *Paläontologische Zeitschrift* 86:231-267.
- Huerta, P., F. T. Fernández-Baldor, J. O. Farlow, and D. Montero. 2012. Exceptional preservation processes of 3D dinosaur footprint casts in Costalomo (Lower Cretaceous, Cameros Basin, Spain). *Terra Nova* 24:136-141.
- Huh, M., I. S. Paik, M. G. Lockley, K. G. Hwang, B. S. Kim, and S. K. Kwak. 2006. Well-preserved theropod tracks from the Upper Cretaceous of Hwasun County, southwestern South Korea, and their paleobiological implications. *Cretaceous Research* 27:123-138.
- Hunt, A. P. and S. G. Lucas. 2007. Tetrapod ichnofacies: a new paradigm. *Ichnos* 14:59-68.
- Hunt, R. 2003. An Early Cretaceous theropod foot from southwestern Arkansas. *Proceedings Journal of the 2003 Arkansas Undergraduate Research Conference*: 87-103.
- Ishigaki, S. 2010. Theropod trampled bedding plane with laboring trackways from the Upper Cretaceous Abdrant Nuru fossil site, Mongolia. *Hayashibara Museum of Natural Sciences Research Bulletin* 3:133-141.
- Ishigaki, S., and M.G. Lockley. 2010. Didactyl, tridactyl and tetradactyl theropod trackways from the Lower Jurassic of Morocco: evidence of limping, laboring and other irregular gaits. *Historical Biology* 22:100-108.
- Ishigaki, S., and Y. Matsumoto. 2009. Re-examination of manus-only and manus-dominated sauropod trackways from Morocco. *Geological Quarterly* 53:441-448.
- Ishigaki, S., M. Watabe, K. Tsogtbaatar, and M. Saneyoshi. 2009. Dinosaur footprints from the Upper Cretaceous of Mongolia. *Geological Quarterly* 53:449-460.
- Jackson, S. J., M. A. Whyte, and M. Romano. 2009. Laboratory-controlled simulations of dinosaur footprints in sand: a key to understanding vertebrate track formation and preservation. *Palaios* 24:222-238.
- Jackson, S. J., M. A. Whyte, and M. Romano. 2010. Range of experimental dinosaur (*Hypsilophodon foxii*) footprints due to variation in sand consistency: How wet was the track? *Ichnos* 17:197-214.
- Jasinski, L. E. 2008. *Dinosaur Highway: A History of Dinosaur Valley State Park*. Texas Christian University Press, Fort Worth, Texas, 212 pp.
- Kim, B. S., and M. Huh. 2010. Analysis of the acceleration phase of a theropod dinosaur based on a Cretaceous trackway from Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 293:1-8.
- Kim, Y. J., and M. G. Lockley. 2012. New sauropod tracks (*Brontopodus pentadactylus* ichnosp. nov.) from the Early Cretaceous Haman Formation of Jinju area, Korea: implications for sauropods manus morphology. *Ichnos* 19:84-92.
- Kuban, G. J. 1989a. Elongate dinosaur tracks; pp. 57-72 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, UK.
- Kuban, G. J. 1989b. Color distinctions and other curious features of dinosaur tracks near Glen Rose, Texas; pp. 427-440 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, UK.
- Kvale, E. P., G. D. Johnson, D. L. Mickelson, K. Keller, L. C. Furrer, and A. W. Archer. 2001. Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksites, Bighorn Basin, Wyoming, USA. *Palaios* 16:233-254.
- Lallensack, J. N., P. M. Sander, N. Knötschke, and O. Wings. 2015. Dinosaur tracks from the Langenberg Quarry (Late Jurassic, Germany) reconstructed with historical photogrammetry: evidence for large theropods soon after insular dwarfism. *Palaeontologia Electronica* 18.2.31A:1-34.
- Langston, W. Jr. 1974. Nonmammalian Comanchean tetrapods. *Geoscience and Man* 8:77-102.
- Le Lœuff, J., C. Gourrat, P. Landry, L. Hautier, R. Liard, C. Souillat, E. Buffetaut, and R. Enay. 2006. A Late Jurassic sauropod tracksite from southern Jura (France). *Comptes Rendus Palevol* 5:705-709.
- Leonardi, G. 1979. Nota preliminar sobre seis pistas de dinossauros Ornithischia da Bacia do Rio do Peixe, em Sousa, Paraíba, Brasil. *Anais Academia Brasileira de Ciências* 51:501-516.
- Leonardi, G. 1989. Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation; pp. 165-178 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, UK.
- Leonardi, G., and M. F. C. F. dos Santos. 2004. New dinosaur tracksites from the Sousa Lower Cretaceous basin (Paraíba, Brasil). *Studi Trentini di Scienze Naturali Acta Geologica* 81:5-21.
- Li, J.-J., B. H. Zhang, B.-L. Hu, and L.-H. Gao. 2006. A new type of dinosaur tracks from Lower Cretaceous of Chabu, Otog Qi, Inner Mongolia. *Acta Palaeontologica Sinica* 45:221-234 (In Chinese with English summary).
- Li, J., Z. Bai, M. Lockley, B. Zhou, J. Liu, and Y. Song. 2010. Dinosaur tracks in Wulatezhongqi, Inner Mongolia. *Acta Geologica Sinica* 84:723-742 (In Chinese with English summary).
- Li, R., M. G. Lockley, M. Matsukawa, and M. Liu. 2015. Important dinosaur-dominated footprint assemblages from the Lower Cretaceous Tianjialou Formation at the Houzuoshan Dinosaur Park, Junan County, Shandong Province, China. *Cretaceous Research* 52:83-100.
- Lingham-Soliar, T., T. Broderick, and A. A. K. Ahmed. 2003. Closely associated theropod trackways from the Jurassic of Zimbabwe. *Naturwissenschaften* 90:572-576.
- Lockley, M. G. 2007. A tale of two ichnologies: the different goals and potentials of invertebrate and vertebrate (tetrapod) ichnotaxonomy and how they relate to ichnofacies analysis. *Ichnos* 14:39-57.
- Lockley, M., and C. Meyer. 2000. *Dinosaur Tracks and Other Fossil Footprints of Europe*. Columbia University Press, New York, 323 pp.

- Lockley, M. G., and A. Rice. 1990. Did “*Brontosaurus*” ever swim out to sea? Evidence from brontosaur and other dinosaur footprints. *Ichnos* 1:81-90.
- Lockley, M., and J. Tempel. 2014. “Fossil Trace” trace fossils: the historic, scientific and educational significance of Triceratops Trail—a controversial Upper Cretaceous tracksite complex in the Laramie Formation, Golden, Colorado; pp. 441-457 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Lockley, M. G., and L. Xing. 2015. Flattened fossil footprints: implications for paleobiology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 426:85-94.
- Lockley, M. G., J. O. Farlow, and C. A. Meyer. 1994. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia* 10:135-145.
- Lockley, M. G., G. D. Gierliński, and S. G. Lucas. 2011. *Kayentapus* revisited: notes on the type material and the importance of this theropod footprint ichnogenus; pp. 330-336 in R. M. Sullivan, S. G. Lucas, and J. A. Spielmann (eds.), *Fossil Record 3*. New Mexico Museum of Natural History and Science Bulletin 53, Albuquerque, New Mexico.
- Lockley, M. G., M. Matsukawa, and J. Li. 2003. Crouching theropods in taxonomic jungles: ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. *Ichnos* 10:169-177.
- Lockley, M. G., M. Matsukawa, and D. Witt. 2006a. Giant theropod tracks from the Cretaceous Dakota Group of northeastern New Mexico’ pp. 83-88 in S. G. Lucas and R. M. Sullivan (eds.), *Late Cretaceous vertebrates from the Western Interior*. New Mexico Museum of Natural History and Science Bulletin 35, Albuquerque, New Mexico.
- Lockley, M. G., R. T. McCrea, and L. G. Buckley. 2015a. A review of dinosaur track occurrences from the Morrison Formation in the type area around Dinosaur Ridge. *Palaeogeography, Palaeoclimatology, Palaeoecology* 433:10-19.
- Lockley, M., M. Triebold, and P. R. Janke. 2014a. Dinosaur tracks from the Hell Creek Formation (Upper Cretaceous, Maastrichtian), South Dakota; pp. 459-468 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Lockley, M. G., J. L. Wright, and D. Thies. 2004. Some observations on the dinosaur tracks at Mönchshagen (Lower Cretaceous), Germany. *Ichnos* 11:261-274.
- Lockley, M. G., J. C. Garcia-Ramos, L. Piñuela, and M. Avanzini. 2008. A review of vertebrate track assemblages from the Late Jurassic of Asturias, Spain with comparative notes on coeval ichnofaunas from the western USA: implications for faunal diversity in siliciclastic facies assemblages. *Oryctos* 8:53-70.
- Lockley, M. G., R. Kurihara, L. Ponek, and A. Delgalvis. 2014b. A survey of new fossil footprint sites from Glen Canyon National Recreation Area (western USA), with special reference to the Kayenta-Navajo transition zone (Glen Canyon Group, Lower Jurassic); pp. 157-179 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Lockley, M. G., G. D. Gierliński, Z. Dubicka, B. H. Breithaupt, and N. A. Matthews. 2014c. A preliminary note on a new dinosaur tracksite in the Cedar Mountain Formation (Cretaceous) of eastern Utah; pp. 279-285 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Lockley, M. G., K. Houk, S.-Y. Yang, M. Matsukawa, and S.-K. Lim. 2006b. Dinosaur-dominated footprint assemblages from the Cretaceous Jindong Formation, Hallyo Haesang National Park area, Goseong County, South Korea: evidence and implications. *Cretaceous Research* 27:70-101.
- Lockley, M. G., J. Lires, J. C. García-Ramos, L. Piñuela, and M. Avanzini. 2007. Shrinking the world’s largest dinosaur tracks: observations on the ichnotaxonomy of *Gigantosauroopus asturiensis* and *Hispanosauroopus hauboldi* from the Upper Jurassic of Asturias, Spain. *Ichnos* 14:247-255.
- Lockley, M. G., A. S. Schulp, C. A. Meyer, G. Leonardi, and D. K. Mamani. 2002a. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research* 23:383-400.
- Lockley, M. G., J. Li, R. Li, M. Matsukawa, J. D. Harris, and L. Xing. 2013. A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology. *Acta Geologica Sinica* 87:1-20.
- Lockley, M. G., R. McCrea, L. Alcala, K. Cart, J. Martin, and G. Hadden. 2015b. A preliminary report on an assemblage of large theropod tracks from the Cretaceous Dakota Group, Western Colorado: evidence for gregarious behavior; pp. 179-183 in R. M. Sullivan and S. G. Lucas (eds.), *Fossil Record 4*. New Mexico Museum of Natural History and Science Bulletin 67, Albuquerque, New Mexico.
- Lockley, M. G., R. Li, M. Matsukawa, L. Xing, J. Li, M. Liu, and X. Xu. 2015c. Tracking the yellow dragons: implications of China’s largest dinosaur tracksite (Cretaceous of the Zhucheng area, Shandong Province, China). *Palaeogeography, Palaeoclimatology, Palaeoecology* 423:62-79.
- Lockley, M. G., J. Wright, D. White, M. Matsukawa, J. Li, L. Feng, and H. Li. 2002b. The first sauropod trackways from China. *Cretaceous Research* 23:363-381.
- Lockley, M., K. Cart, J. Martin, R. Prunty, K. Houck, K. Hups, J.-D. Lim, K. S. Kim, and G. Gierliński. 2014d. A bonanza of new tetrapod tracksites from the Cretaceous Dakota Group, western Colorado: implications for paleoecology; pp. 393-409 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Lockley, M. G., G. D. Gierliński, K. Houk, J.-D. Lim, K. S. Kim, D.-Y. Kim, T. H. Kim, S.-H. Kang, R. H. Foster, R. Li, C. Chessser, R. Gay, Z. Dubicka, K. Cart, and C.

- Wright. 2014e. New excavations at the Mill Canyon dinosaur tracksite (Cedar Mountain Formation, Lower Cretaceous) of eastern Utah; pp. 287-300 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Lockwood, J. A. F., M. G. Lockley, and S. Pond. 2014. A review of footprints from the Wessex Formation (Wealden Group, Lower Cretaceous) at Hanover Point, the Isle of Wight, southern England. *Biological Journal of the Linnean Society* 113:707-720.
- Lü, J., Y. Azama, T. Wang, S. Li, and S. Pan. 2006. The first discovery of dinosaur footprint from Lufeng of Yunnan Province, China. *Memoir of the Fukui Prefectural Dinosaur Museum* 5:35-39.
- Lucas, S. G., H. Klein, M. G. Lockley, J. A. Spielmann, G. D. Gierliński, A. P. Hunt, and L. H. Tanner. 2006. Triassic-Jurassic stratigraphic distribution of the theropod footprint ichnogenus *Eubrontes*; pp. 86-93 in J. D. Harris, S. G. Lucas, J. A. Spielmann, M. G. Lockley, A. R. C. Milner, and J. I. Kirkland (eds.), *The Triassic-Jurassic Terrestrial Transition*. New Mexico Museum of Natural History and Science Bulletin 37, Albuquerque, New Mexico.
- Manning, P. L. 2004. A new approach to the analysis and interpretation of tracks: examples from the Dinosauria; pp. 93-123 in D. McIlroy (ed.), *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*. Geological Society of London, London.
- Manning, P. L. 2008. *T. rex* speed trap; pp. 204-231 in P. Larson and K. Carpenter (eds.), *Tyrannosaurus rex, the Tyrant King*. Indiana University Press, Bloomington, Indiana.
- Mannion, P. D., and P. Upchurch, P. 2010. A quantitative analysis of environmental associations in sauropod dinosaurs. *Paleobiology* 36:253-82.
- Martin, A. J. 2013. *Life Traces of the Georgia Coast: Revealing the Unseen Lives of Plants and Animals*. Indiana University Press, Bloomington, Indiana, 692 pp.
- Martin, A. J., M. Blair, B. F. Dattilo, S. Howald, and J. O. Farlow, 2015. The ups and downs of *Diplocraterion* in the Glen Rose Formation (Lower Cretaceous), Dinosaur Valley State Park, Texas (USA). *Geodinamica Acta* 27: DOI: 10.1080/09853111.2015.1037151.
- Marty, D., Strasser, A. and Meyer, C. A. 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. *Ichnos* 16: 127-42.
- Marty, D., C. A. Meyer, M. Belvedere, J. Ayer, and K. L. Schäfer. 2013. Rochefort-Les Grattes: an early Tithonian dinosaur tracksite from the Canton Neuchâtel, Switzerland. *Revue de Paléobiologie, Genève* 32:373-384.
- Marty, D., W. A. Hug, A. Iberg, L. Cavin, C. A. Meyer, and M. G. Lockley. 2003. Preliminary report on the Courtedoux dinosaur tracksite from the Kimmeridgian of Switzerland. *Ichnos* 10:209-219.
- Marty, D., C. A. Meyer, and J.-P. Billon-Bruyat. 2006. Sauropod trackway patterns expression of special behaviour related to substrate consistency? An example from the Late Jurassic of northwestern Switzerland. *Hantkeniana* 5:38-41.
- Marty, D., M. Belvedere, C. A. Meyer, P. Mietto, G. Paratte, C. Lovis, and B. Thuring. 2010. Comparative analysis of Late Jurassic sauropod trackways from the Jura Mountains (NW Switzerland) and the central High Atlas Mountains (Morocco): implications for sauropod ichnotaxonomy. *Historical Biology* 22:109-133.
- Masrour, M., F. Pérez-Lorente, S. Ferry, N. Içame, and D. Grosheny. 2013. First dinosaur tracks from the Lower Cretaceous of the western High Atlas (Morocco). *Geogaceta* 53:33-36.
- McCrea, R. T., and T. S. Pigeon. 2014. Replication and description of a large theropod and large ornithopod trackway from the Upper Minnes Group (Lower Cretaceous: Valanginian) of the Peace River region of northeastern British Columbia, Canada; pp. 269-277 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- McCrea, R. T., L. G. Buckley, J. O. Farlow, M. G. Lockley, P. J. Currie, N. A. Matthews, and S. G. Pemberton. 2014a. A 'terror of tyrannosaurs': the first trackways of tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. *PLoS One* 9(7): e103613. doi:10.1371/journal.pone.0103613.
- McCrea, R. T., L. G. Buckley, A. G. Plint, P. J. Currie, J. W. Haggart, C. W. Helm, and S. G. Pemberton. 2014b. A review of vertebrate track-bearing formations from the Mesozoic and earliest Cenozoic of western Canada with a description of a new theropod ichnospecies and reassignment of an avian ichnogenus; 5-93 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- McCrea, R. T., D. Tanke, L. G. Buckley, M. G. Lockley, J. O. Farlow, L. Xing, N. Matthews, C. W. Helm, S. G. Pemberton, and B. H. Breithaupt. 2015. Vertebrate ichnopathology: pathologies inferred from dinosaur tracks and trackways from the Mesozoic. *Ichnos* 22:235-260.
- Meijide Fuentes F., C. Fuentes Vidarte, M. Meijide Calvo, and M. Meijide Fuentes. 2004. Rastro de un dinosaurio saurópodo en el Weald de Soria (España). *Brontopodus oncalensis* nov. icnsp. *Celtiberia* 54:501-515.
- Mesa, V., and D. Perea. 2015. First record of theropod and ornithopod tracks and detailed description of sauropod trackways from the Tacuarembó Formation (Late Jurassic-Early Cretaceous) of Uruguay. *Ichnos* 22:109-121.
- Mezga, A., B. C. Tešović, and Z. Bajraktarević. 2007. First record of dinosaurs in the Late Jurassic of the Adriatic-Dinaric carbonate platform (Croatia). *Palaios* 22:188-199.
- Milàn, J. and R. G. Bromley. 2006. True tracks, undertracks, and eroded tracks: experimental work with tetrapod tracks in field and laboratory. *Palaeogeography, Palaeoclimatology, Palaeoecology* 231:253-64.
- Milàn, J., and R. G. Bromley. 2008. The impact of sediment consistency on track and undertrack morphology: experiments with emu tracks in layered cement. *Ichnos* 15:18-24.
- Milàn, J., M. Avanzini, B. Clemmensen, J. C. García-Ramos, and L. Piñuela, L. (2006). Theropod foot movements recorded by Late Triassic, Early Jurassic, and Late

- Jurassic fossil footprints; pp. 352-364 in J. D. Harris, S. G. Lucas, J. A. Spielmann, M. G. Lockley, and A. R. C. Milner (eds.), *The Triassic-Jurassic Transition*. New Mexico Museum of Natural History and Science Bulletin 37, Albuquerque, New Mexico.
- Milner, A. R. C., M. G. Lockley, and S. B. Johnson. 2006a. The story of the St. George Dinosaur Discovery Site at Johnson farm: an important new Lower Jurassic dinosaur tracksite from the Moenave Formation of southwestern Utah; pp. 329-344 in J. D. Harris, S. G. Lucas, J. A. Spielmann, M. G. Lockley, and A. R. C. Milner (eds.), *The Triassic-Jurassic Transition*. New Mexico Museum of Natural History and Science Bulletin 37, Albuquerque, New Mexico.
- Milner, A. R. C., M. G. Lockley, and J. I. Kirkland. 2006b. A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George; pp. 315-328 in J. D. Harris, S. G. Lucas, J. A. Spielmann, M. G. Lockley, and A. R. C. Milner (eds.), *The Triassic-Jurassic Transition*. New Mexico Museum of Natural History and Science Bulletin 37, Albuquerque, New Mexico.
- Moratalla, J. J. 2009. Sauropod tracks of the Cameros Basin (Spain): identification, trackway patterns and changes over the Jurassic-Cretaceous. *Geobios* 42:797-811.
- Moreau, J.-D., G. Gand, E. Fara, and A. Michelin. 2012. Biometric and morphometric approaches on lower Hettangian dinosaur footprints from the Rodez Strait (Aveyron, France). *Comptes Rendus Palevol* 11:231-239.
- Moreau, J.-D., V. Trincal, G. Gand, D. Néraudeau, G. Bessière, and B. Bourel. 2014. Deux nouveaux sites à traces de pas dinosauroïdes dans la Formation Dolomitique de l'Hettangien de Lozère, Languedoc-Roussillon, France. *Annales de Paléontologie* 100:361-369.
- Moreno, K., and M. J. Benton. 2005. Occurrence of sauropod tracks in the Upper Jurassic of Chile (redescription of *Iguanodonichmus frenki*). *Journal of South American Earth Sciences* 20:253-257.
- Moreno, K., and M. Pino. 2002. Huellas de dinosaurios en la Formación Baños del Flaco (Titoniano-Jurásico Superior), VI Región, Chile: paleoetología y paleoambiente. *Revista Geológica de Chile* 29:191-206.
- Moreno, K., N. Blanco, and A. Tomlinson. 2004. Nuevas huellas de dinosaurios del Jurásico Superior en el norte de Chile. *Ameghiniana* 41:535-544.
- Moreno, K., S. de Valais, N. Blanco, A. J. Tomlinson, J. Jacay, and J. O. Calvo. 2012. Large theropod dinosaur footprint associations in western Gondwana: behavioural and palaeogeographic implications. *Acta Paleontologica Polonica* 57:73-83.
- Mossman, D. J., R. Brüning, and H. P. Powell. 2003. Anatomy of a Jurassic theropod trackway from Ardley, Oxfordshire, U.K. *Ichnos* 10:195-207.
- Nadon, G. C. 2001. The impact of sedimentology on vertebrate track studies; pp. 395-407 in D. H. Tanke, K. Carpenter and M. W. Skrepnick (eds.), *Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Phillip J. Currie*. Indiana University Press, Bloomington, IN: Indiana.
- Nicosia, U. F. M. Petti, G. Perugini, S. D'Orazi Porchetti, E. Sacchi, M. A. Conti, and N. Marotti. 2007. Dinosaur tracks as paleogeographic constraints: new scenarios for the Cretaceous geography of the Periadriatic region. *Ichnos* 14:69-2007.
- Niedźwiedzki, G. 2011. A Late Triassic dinosaur-dominated ichnofauna from the Tomanová Formation of the Tata Mountains, central Europe. *Acta Palaeontologica Polonica* 56:291-300.
- Nouri, J., I. I. Díaz-Martínez, and F. Pérez-Lorente. 2011. Tetradactyl footprints of an unknown affinity theropod dinosaur from the Upper Jurassic of Morocco. *PLoS One* 6(12): 326882. Doi:10.1371/journal.pone.0022882.
- Pascual-Arribas, C., and N. Hernández-Medrano. 2010. Nuevos datos sobre el yacimiento icnítico de las Cuestas I (Santa Cruz de Yanguas, Soria, España). *Studia Geológica Salmanticensia* 46:121-157.
- Pascual Arribas, C., P. Latorre Macarrón, N. Hernández Medrano, and E. Sanz Pérez. 2005. Las huellas de dinosaurios de los yacimientos del Arroyo Miraflores (Fuentes de Magaña-Cerbón-Magaña, Soria). *Celtiberia* 55:413-442.
- Pérez-Lorente, F. 2015. *Dinosaur Footprints & Trackways of La Rioja*. Indiana University Press, Bloomington, Indiana, 363 pp.
- Petti, F. M., M. A. Conti, S. D'Orazi Porchetti, M. Morsilli, U. Nicosia, and P. Gianolla. 2008a. A theropod dominated ichnocoenosis from late Hauterivian-early Barremian of Borgo Celano (Gargano Promontory, Apulia, southern Italy). *Rivista Italiana di Palaeontologia e Stratigrafia* 114:3-17.
- Petti, F. M., S. D'Orazi Porchetti, M. A. Conti, U. Nicosia, G. Perugini, and E. Sacchi. 2008b. Theropod and sauropod footprints in the Early Cretaceous (Aptian) Apenninic Carbonate Platform (Esperia, Lazio, central Italy): a further constraint on the palaeogeography of the central-Mediterranean area. *Studi Trentini di Scienze Naturali Acta Geologica* 83:323-334.
- Pieńkowski, G., M. E. Popa, and A. Kędzior. 2009. Early Jurassic sauropod footprints of the southern Carpathians, Romania: palaeobiological and paleogeographical significance. *Geological Quarterly* 53:461-470.
- Pittman, J. G. 1989. Stratigraphy, lithology, depositional environment, and track type of dinosaur track-bearing beds of the Gulf Coastal Plain; pp. 135-153 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, UK.
- Platt, N. H., and C. A. Meyer. 1991. Dinosaur footprints from the Lower Cretaceous of northern Spain: their sedimentological and palaeontological context. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85:321-333.
- Rainforth, E. C. 2007. Ichnotaxonomic updates from the Newark Supergroup; pp. 49-59 in E. C. Rainforth (ed.), *Contributions to the Paleontology of New Jersey (II): Field Guide and Proceedings*. Geological Association of New Jersey 24<sup>th</sup> Annual Conference and Field Trip, East Stroudsburg University, East Stroudsburg, Pennsylvania.109-126.
- Rainforth, E. C., and M. Manzella. 2007. Estimating speeds of dinosaurs from trackways: a re-evaluation of assumptions; pp. 41-48 in E. C. Rainforth (ed.), *Contributions to the Paleontology of New Jersey (II): Field Guide and Proceedings*. Geological Association of New Jersey 24<sup>th</sup>

- Annual Conference and Field Trip, East Stroudsburg University, East Stroudsburg, Pennsylvania.109-126.
- Razzolini, N. L., B. Vila, D. Castanera, P. L. Falkingham, J. L. Barco, J. I. Canudo, P. L. Manning, and A. Galobart. 2014. Intra-trackway morphological variations due to substrate consistency: the El Frontal dinosaur tracksite (Lower Cretaceous, Spain). *PLoS One* 9(4): e93708. doi:10.1371/journal.pone.0093708.
- Roach, B. T., and D. L. Brinkman. 2007. A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. *Bulletin of the Peabody Museum of Natural History* 48:103-138.
- Rodríguez-de la Rosa, R. A., M. C. Aguillón-Martínez, J. López-Espinoza, and D. A. Eberth. 2004. The fossil record of vertebrate tracks in Mexico. *Ichnos* 11:27-37.
- Rogers, J. V. II. 2002. Theropod dinosaur trackways in the Lower Cretaceous (Albian) Glen Rose Formation, Kinney County, Texas. *Texas Journal of Science* 54:133-142.
- Romano, M., and M. A. Whyte. 2003. Jurassic dinosaur tracks and trackways of the Cleveland Basin, Yorkshire: preservation, diversity and distribution. *Proceedings of the Yorkshire Geological Society* 54:185-215.
- Romano, M., M. A. Whyte, and S. J. Jackson. 2007. Trackway ratio: a new look at trackway gauge in the analysis of quadrupedal dinosaur trackways and its implications for ichnotaxonomy. *Ichnos* 14:257-270.
- Romilio, A., R. T. Tucker, and S. W. Salisbury. 2013. Reevaluation of the Lark Quarry dinosaur tracksite (late Albian-Cenomanian Winton Formation, central-west Queensland): no longer a stampede? *Journal of Vertebrate Paleontology* 33:102-120.
- Rose, P. J. 2007. A new titanosauriform sauropod (Dinosauria: Saurischia) from the Early Cretaceous of central Texas and its phylogenetic relationships. *Palaeontologia Electronica* 10(2); [http://palaeo-electronica.org/paleo/2007\\_2/00063/index.html](http://palaeo-electronica.org/paleo/2007_2/00063/index.html).
- Rubilar-Rogers, D., K. Moreno, N. Blanco, and J. O. Calvo. 2008. Theropod dinosaur trackways from the Lower Cretaceous of the Chacarilla Formation, Chile. *Revista Geológica de Chile* 35:175-184.
- Sacchi, E., M. A. Conti, S. D'Orazi Porchetti, A. Logoluso, U. Nicosia, G. Perugini, and F. M. Petti. 2009. Aptian dinosaur footprints from the Apulian Platform (Bisceglie, southern Italy) in the framework of periadriatic ichnosites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 271:104-116.
- Santisteban, C. de, M. Suñer, and B. Vila. 2009. El yacimiento de icnitas de dinosaurios de Cañada Paris, Alpuente, Valencia. *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, Salas de los Infantes, Burgos, Spain* pp. 301-309.
- Santos, V. F., P. M. Callapez, and N. P. C. Rodrigues. 2013. Dinosaur footprints from the Lower Cretaceous of the Algarve Basin (Portugal): new data on the ornithopod palaeoecology and palaeobiogeography of the Iberian Peninsula. *Cretaceous Research* 40:158-169.
- Santos, V. F., J. J. Moratalla, and R. Royo-Torres. 2009. New sauropod trackways from the Middle Jurassic of Portugal. *Acta Palaeontologica Polonica* 54:409-422.
- Santos, V. F., P. M. Callapez, D. Castanera, F. Barroso-Barcenilla, N. P. C. Rodrigues, and C. A. Cupeto. 2015. Dinosaur tracks from the Early Cretaceous (Albian) of Parede (Cascais, Portugal): new contributions for the sauropod palaeobiology of the Iberian Peninsula. *Journal of Iberian Geology* 41:155-166.
- Schumacher, B., and M. G. Lockley. 2014. Newly documented trackways at "Dinosaur Lake," the Purgatoire Valley dinosaur tracksite; pp. 261-267 in M. G. Lockley and S. G. Lucas (eds.), *Fossil Footprints of Western North America*. New Mexico Museum of Natural History and Science Bulletin 62, Albuquerque, New Mexico.
- Shuler, E. W. 1917. Dinosaur tracks in the Glen Rose Limestone near Glen Rose, Texas. *American Journal of Science* 44:294-298.
- Shuler, E. W. 1935. Dinosaur track mounted in the bandstand at Glen Rose, Texas. *Field and Laboratory* 4:9-13.
- Shuler, E. W. 1937. Dinosaur tracks at the fourth crossing of the Paluxy River near Glen Rose, Texas. *Field and Laboratory* 5:33-36.
- Sullivan, C., D. W. E. Hone, T. D. Cope, Y. Liu, and J. Liu. 2009. A new occurrence of small theropod tracks in the Houcheng (Tuchengzi) Formation of Hebei Province, China. *Vertebrata Palasiatica* 47:35-52.
- Thulborn, T. 2001. History and nomenclature of the theropod dinosaur tracks *Bueckeburgichnus* and *Megalosauripus*. *Ichnos* 8:207-222.
- Thulborn, T. 2012. Impact of sauropod dinosaurs on lagoonal substrates in the Broome Sandstone (Lower Cretaceous), Western Australia. *PLoS One* 7(5); e36208. doi: 10.1371/journal.pone.0036208.
- Tschopp, E., O. Wings, T. Frauenfelder, and W. Brinkmann. 2015. Articulated bone sets of manus and pedes of *Camarasaurus* (Sauropoda, Dinosauria). *Palaeontologia Electronica* 18.2.44A:1-65.
- Valais, S. de, C. R. Candeiro, L. F. Tavares, Y. M. Alves, and C. Cruvinel. 2015. Current situation of the ichnological locality of São Domingos from the Corda Formation (Lower Cretaceous), northern Tocantins state, Brazil. *Journal of South American Earth Sciences* 61:142-146.
- Vila, B., O. Oms, and A. Galobart. 2005. Manus-only titanosaurid trackway from Fumanya (Maastrichtian, Pyrenees): further evidence for an underprint origin. *Lethaia* 38:211-218.
- Wagensommer, A., M. Latianno, G. Leroux, G. Cassano, and S. D'Orazi Porchetti. 2012. New dinosaur tracksites from the Middle Jurassic of Madagascar: ichnotaxonomical, behavioural and palaeoenvironmental implications. *Palaeontology* 55:109-126.
- Wedel, M. J., R. L. Cifelli, and R. K. Sanders. 2000a. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Palaeontologica Polonica* 45:343-388.
- Wedel, M. J., R. L. Cifelli, and R. K. Sanders. 2000b. *Sauroposeidon proteles*, a new sauropod from the Early Cretaceous of Oklahoma. *Journal of Vertebrate Paleontology* 20:109-114.
- Weems, R. E., and J. M. Bachman. 2015. The Lower Cretaceous Patuxent Formation ichnofauna of Virginia. *Ichnos* 22:208-219.
- Whyte, M. A., and M. Romano. 2001. A dinosaur ichnocoenosis from the Middle Jurassic of Yorkshire, UK. *Ichnos* 8:233-254.

- Wilson, J. A., and M. T. Carrano. 1999. Titanosaurs and the origin of “wide gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* 25:252-267.
- Wilson, J. A., and D. Fisher. 2003. Are manus-only sauropod trackways evidence of swimming, sinking, or wading? *Journal of Vertebrate Paleontology* 23(3):111A.
- Wings, O., D. Falk, N. Knötschke, and A. Richter. 2012. The Early Cretaceous dinosaur trackways in Münchehagen (Lower Saxony, Germany)—the Natural Monument ‘Saurierfähren Münchehagen’ and the adjacent Wesling quarry; pp. 113-142 in A. Richter and M. Reich (eds.), *Dinosaur Tracks 2011*. Universitätsverlag Göttingen, Göttingen, Germany.
- Wings, O., R. Schellhorn, H. Mallison, B. Thuy, W. Wu, and G. Sun. 2007. The first dinosaur tracksite from Xinjiang, NW China (Middle Jurassic Sanjianfang Formation, Turpan Basin)—a preliminary report. *Global Geology* 10:113-129.
- Wright, J. L. 2005. Steps in understanding sauropod biology: the importance of sauropod tracks; pp. 252-284 in K. A. Curry Rogers and J. W. Wilson (eds.), *The Sauropods: Evolution and Paleobiology*. University of California Press, Berkeley, California.
- Xing, L.-D., J. D. Harris, and P. J. Currie. 2011a. First record of dinosaur trackway from Tibet, China. *Geological Bulletin of China* 30:173-2011.
- Xing, L.-D., J. D. Harris, and G. D. Gierliński. 2011b. *Therangospodus* and *Megalosauripus* track assemblage from the Upper Jurassic-Lower Cretaceous Tuchengzi Formation of Chicheng County, Hebei Province, China and their paleoecological implications. *Vertebrata Palasiatica* 49:423-434.
- Xing, L.-D., J. D. Harris, and C.-K. Jia. 2010. Dinosaur tracks from the Lower Cretaceous Mengtuan Formation in Jiangsu, China and Morphological diversity of local sauropod tracks. *Acta Palaeontologica Sinica* 49:448-460.
- Xing, L.-D., J. D. Harris, G. D. Gierliński, W.-M. Wang, Z.-Y. Wang, and D.-Q. Li. 2011c. Mid-Cretaceous non-avian theropod trackways from the southern margin of the Sichuan Basin, China. *Acta Palaeontologica Sinica* 50:470-480.
- Xing, L., M. G. Lockley, J. Zhang, H. Klein, W. S. Persons IV, and H. Dai. 2014a. Diverse sauropod-, theropod-, and ornithopod-track assemblages and a new ichnotaxon *Siamopodus xui* ichnosp. nov. from the Feitianshan Formation, Lower Cretaceous of Sichuan Province, southwest China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 414:79-97.
- Xing, L., M. G. Lockley, D. Marty, L. Píñuela, H. Klein, J. Zhang, and W. S. Persons IV. 2015a. Re-description of the partially collapsed Early Cretaceous Zhaojue dinosaur tracksite (Sichuan Province, China) by using registered video coverage. *Cretaceous Research* 52:138-152.
- Xing, L.-D., G. Niedzwiedzki, M. G. Lockley, J.-P. Zhang, X.-F. Cai, W. S. Persons IV, and Y. Ye. 2014b. *Asianopodus*-type footprints from the Hekou Group of Honggu District, Lanzhou City, Gansu, China and the “heel” of large theropod tracks. *Palaeoworld* 23:304-131.
- Xing, L., G. Peng, M. G. Lockley, Y. Ye, H. Klein, J. Zhang, and W. S. Persons IV. 2015b. Early Cretaceous sauropod and ornithopod trackways from a stream course in Sichuan Basin, southwest China; pp. 319-325 in R. M. Sullivan and S. G. Lucas (eds.), *Fossil Record 4*, New Mexico Museum of Natural History and Science Bulletin 68, Albuquerque, New Mexico.
- Xing, L.-D., M. G. Lockley, J.-P. Zhang, A. R. C. Milner, H. Klein, D.-Q. Li, W. S. Persons IV, and J.-F. Ebi. 2013a. A new Early Cretaceous dinosaur track assemblage and the first definite non-avian theropod swim trackways from China. *Chinese Science Bulletin* 58:2370-2378.
- Xing, L.-D., G.-Z. Peng, Y. Ye, M. G. Lockley, R. T. McCrea, P. J. Currie, J.-P. Zhang, and M. E. Burns. 2014c. Large theropod trackway from the Lower Jurassic Zhenzhucheng Formation of Weiyuan County, Sichuan Province, China: review, new observations and special preservation. *Palaeoworld* 23:285-293.
- Xing, L.-D., M. G. Lockley, Z.-D. Li, H. Klein, J.-P. Zhang, G. D. Gierliński, Y. Ye, W. S. Persons IV, and L. Zhou. 2013b. Middle Jurassic theropod trackways from the Panxi region, southwest China and a consideration of their geologic age. *Palaeoworld* 22:36-41.
- Xing, L. D., Y. Q. Liu, H. W. Kuang, H. Klein, J. P. Zhang, M. E. Burns, J. Chen, M. W. Wang, and J. Hu. 2014d. Theropod and possible ornithopod track assemblages from the Jurassic-Cretaceous boundary Houcheng Formation, Shangyi, northern Hebei, China. *Palaeoworld* 23:200-208.
- Xing, L.-D., M. G. Lockley, H. Klein, G. D. Gierliński, J. D. Divay, S.-M. Hu, J.-P. Zhang, Y. Ye, and Y.-P. He. 2014e. The non-avian theropod track *Jialingpus* from the Cretaceous of the Ordos Basin, China, with a revision of the type material: implications for ichnotaxonomy and trackmaker morphology. *Paleoworld* 23:187-199.
- Xing, L., M. G. Lockley, G. Yang, J. Cao, R. T. McCrea, H. Klein, J. Zhang, W. S. Persons IV, and H. Dai. 2016. A diversified vertebrate ichnite fauna from the Feitianshan Formation (Lower Cretaceous) of southwestern Sichuan, China. *Cretaceous Research* 57:79-89.
- Xing, L.-D., M. G. Lockley, T. Miyashita, H. Klein, T. Wang, W. S. Persons IV, S.-G. Pan, J.-P. Zhang, and Z.-M. Dong. 2014f. Large sauropod and theropod tracks from the Middle Jurassic Chuanjie Formation of Lufeng County, Yunnan Province and palaeobiogeography of the Middle Jurassic sauropods tracks from southwestern China. *Palaeoworld* 23:294-303.
- Xing, L., M. G. Lockley, M. F. Bonnan, D. Marty, H. Klein, Y. Liu, J. Zhang, H. Kuang, M. E. Burns, and N. Li. 2015c. Late Jurassic-Early Cretaceous trackways of small-sized sauropods from China: new discoveries, ichnotaxonomy and sauropod manus morphology. *Cretaceous Research* 56:470-481.
- Xing, L., M. G. Lockley, D. Marty, H. Klein, L. G. Buckley, R. T. McCrea, J. Zhang, G. D. Gierliński, J. D. Divay, and Q. Wu. 2013c. Diverse dinosaur ichnoassemblages from the Lower Cretaceous Dasheng Group in the Yishu fault zone, Shandong Province, China. *Cretaceous Research* 45:114-134.
- Xing, L.-D., M. G. Lockley, C. Wei, G. D. Gierliński, J.-J. Li, W. S. Persons IV, M. Matsukawa, Y. Yong, M. K. Gingras, and C.-W. Wang. 2013d. Two theropod track assemblages from the Jurassic of Chongqing, China, and the Jurassic stratigraphy of Sichuan Basin. *Vertebrata Palasiatica* 51:107-130.

- Xing, L., M. G. Lockley, J. Zhang, H. Klein, D. Marty, G. Peng, Y. Ye, R. T. McCrea, W. S. Persons IV, and T. Xu. 2015d. The longest theropod trackway from east Asia, and a diverse sauropod-, theropod-, and ornithopod-track assemblage from the Lower Cretaceous Jiaguan Formation, southwest China. *Cretaceous Research* 56:345-362.
- Xing, L., J. Zhang, M. G. Lockley, R. T. McCrea, H. Klein, L. Alcalá, L. G. Buckley, M. E. Burns, S. B. Kummel, and Q. He. 2015e. Hints of the early Jehol Biota: important dinosaur footprint assemblages from the Jurassic-Cretaceous boundary Tuchengzi Formation in Beijing, China. *PLoS One* 10(4): e0122715. doi:10.1371/journal.pone.0122715.
- Xing, L.-D., H. Klein, M. G. Lockley, A. Wetzel, Z.-D. Li, J.-J. Li, G. D. Gierliński, J.-P. Zhang, M. Matsukawa, J. D. Divay, and L. Zhou. 2014g. *Changpeipus* (theropod) tracks from the Middle Jurassic of the Turpan Basin, Xinjiang, northwest China: review, new discoveries, ichnotaxonomy, preservation and paleoecology. *Vertebrata Palasiatica* 52:233-259.2014.
- Xing, L., M. G. Lockley, J. Zhang, H. Klein, J. Y. Kim, W. S. Persons IV, M. Matsukawa, X. Yu, J. Li, G. Chen, and Y. Hu. 2014h. Upper Cretaceous dinosaur track assemblages and a new theropod ichnotaxon from Anhui Province, eastern China. *Cretaceous Research* 49:190-204.
- Xing, L., D. Marty, K. Wang, M. G. Lockley, S. Chen, X. Xu, Y. Liu, H. Kuang, J. Zhang, H. Ran, and W. S. Persons IV. 2015f. An unusual sauropod turning trackway from the Early Cretaceous of Shandong Province, China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 437:74-84.
- Xing, L., G. Yang, J. Cao, M. G. Lockley, H. Klein, J. Zhang, W. S. Persons IV, H. Hu, H. Shen, X. Zheng, and Y. Qin. 2015g. Cretaceous saurischian tracksites from southwest Sichuan Province and overview of Late Cretaceous dinosaur track assemblages of China. *Cretaceous Research* 56:458-469.
- Zhang, J., D. Li, M. Li, M. G. Lockley, and Z. Bai. 2006. Diverse dinosaur-, pterosaur-, and bird-track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. *Cretaceous Research* 27:44-55.



## STOPS 3 and 4

# ARCHOSAUR FOSSIL LOCALITIES IN THE WOODBINE FORMATION (CENOMANIAN) OF NORTH CENTRAL TEXAS

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## INTRODUCTION

The Woodbine Formation is a body of Late Cretaceous fossiliferous rock extending through north central Texas. Famed Texas geologist R.T. Hill, who first mapped its exposures during his geological survey from Big Bend to North Texas, named the formation for the town of Woodbine in Cooke County (Hill, 1901). It represents the oldest Upper Cretaceous unit in the Gulf Coastal Plain (Hedlund, 1966; Oliver, 1971). The Woodbine is exposed along a line extending between Temple in central Texas northward to Lake Texoma in southern Oklahoma, cropping out as a narrow and irregular band from Johnson to Cooke counties (Figure 1) (Dodge, 1969; Johnson, 1974; Oliver, 1971; Trudel, 1994). Exposures are up to 32 km wide at the surface and 100 meters deep, thinning to the south and east (Dodge, 1969; Johnson, 1974). The formation unconformably overlies the Grayson Marl of the Washita Group and is unconformably overlain by the Eagle Ford Group (Johnson, 1974; Oliver, 1971). There is a period of marine deposition over a duration of at least ten million years separating the Woodbine Formation from the earlier terrestrial depositional systems characterizing the Lower Cretaceous Trinity Group (Winkler et al., 1995).

During the Cretaceous, Woodbine sediments originated from the Ouachita Mountains in southern Oklahoma and were deposited in a series of near shore environments within the subsiding East Texas Basin (Figure 2) (Dodge, 1952; Oliver, 1971). Woodbine deposits represent primarily terrigenous near shore and shallow marine depositional systems, including shelf, deltaic, and fluvial environments (Main, 2005, 2013; Oliver, 1971; Trudel, 1994).

**Institutional Abbreviation**—DMNH, Perot Museum on Nature and Science, Dallas, Texas, U.S.A.

## AGE AND GEOLOGIC SETTING

A minimum age of early middle Cenomanian for the Woodbine Formation is established through ammonite biostratigraphy. Upper Woodbine Formation deposits and the Tarrant Formation of the lower Eagle Ford Group contain the ammonite *Conlinoceras tarrentense*, a zonal marker for the base of the middle Cenomanian, indicating a minimum age of 95-96 MY (Jacobs and Winkler, 1998; Kennedy and Cobban, 1990; Lee, 1997a).

Stratigraphic subdivision of the Woodbine Formation has undergone multiple revisions and the number and composition of members varies with location (Figure 3). Hill originally divided the Woodbine Formation into two units: the upper Lewisville beds and the lower Dexter beds (Hill, 1901). Dodge designated a series of four members visible in the Dallas–Fort Worth area, in ascending order: the Rush Creek, Dexter, Lewisville, and Arlington Members (C. F. Dodge, 1968). The Rush Creek Member was first defined by Bergquist (Bergquist, 1949) as a shale unit between the overlying Dexter Member and underlying Grayson Marl. This was later amended by Johnson (1974) to recognize interfingering shale and sandstone, forming two distinct provinces separated by the Denton-Tarrant county line. The northern province contains lower shoreface and estuarine facies, while the southern province is composed of offshore bars and lagoon deposits (Johnson, 1974).

The Dexter Member is composed of a ferruginous fluvial sandstone, the uppermost portion of which is composed of a multicolored clay; originally

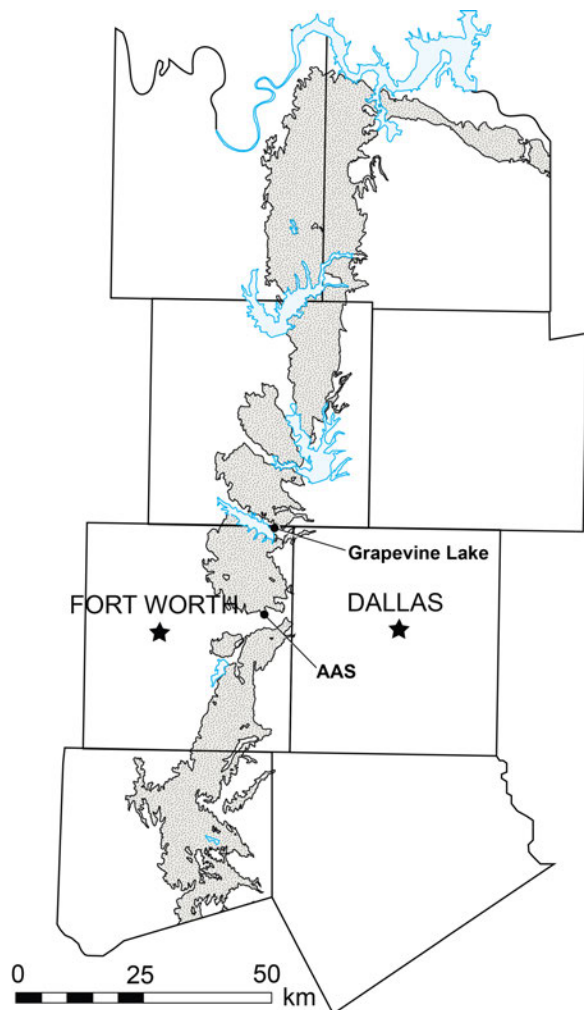


FIGURE 1. Surface exposures of the Woodbine Formation (gray) in north central Texas, with locations of the Arlington Archosaur Site (AAS) and Grapevine Lake. Map created by Thomas Adams.

defined as a separate member called the Rainbow Clay (Bergquist, 1949). Sediments represent primarily fluvio-deltaic environments including tributary facies and coarse-grained meander-belt facies (Oliver, 1971). The Dexter Member is exposed primarily in Grayson County, with some southern outcrops in Tarrant County (Trudel, 1994).

The Lewisville Member represents a coastal, marginal marine environment consisting of mudstones and shales deposited along a coastline, proximal to active delta systems (Main, 2005, 2013; Oliver, 1971; Trudel, 1994). The Lewisville Member is highly fossiliferous and organic-rich, containing an abundance of arenaceous foraminifers, mollusks, and ammonites, including the ammonite *C. tarrantense* (Kennedy and Cobban, 1990; Trudel, 1994). Exposures of the Lewisville Member are dominated by blue-gray to black, finely laminated to massive-bedded mud and

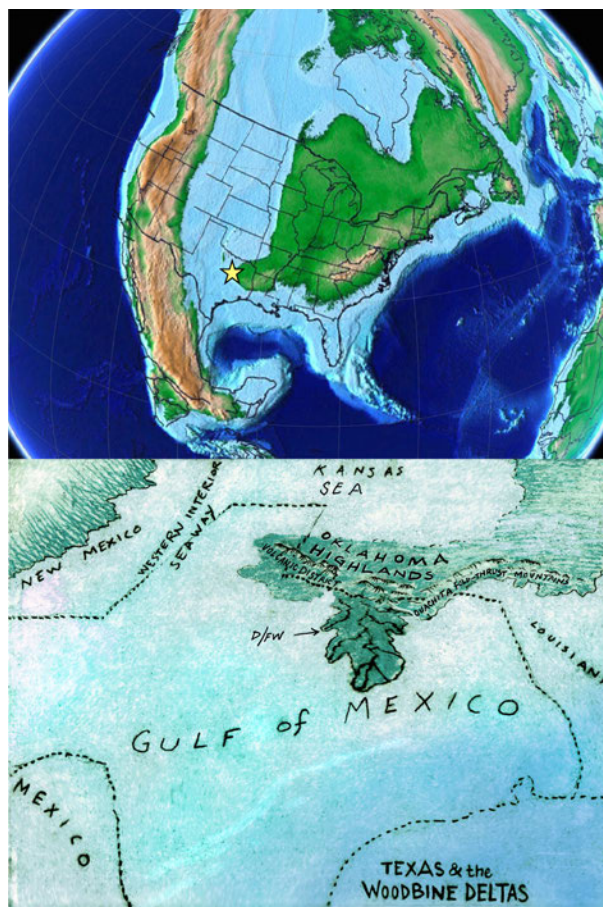


FIGURE 2. The top image is a paleogeographic map of the Cenomanian-Turonian boundary, showing the location of the Woodbine Formation (yellow star). Paleogeographic map created by Chris Scotese. The bottom image shows the Texas peninsula during the Cenomanian, including sediment sources and location of Woodbine Formation delta plains (D/FW). Artwork by Clinton Crowley.

shale interspersed with glauconitic sandstone lenses (Main, 2005; Oliver, 1971; Trudel, 1994). The member is characterized by numerous shallow marine fossils, primarily the oyster *Ostrea soleniscus* (Bergquist, 1949; Trudel, 1994). Bergquist (1949) originally recognized the basal beds consisting of lenticular, cross-bedded ferruginous sandstone and localized lignite deposits as the separate Red Branch Member. This unit is now included as part of the Lewisville Member (Dodge, 1969; Trudel, 1994).

The overlying Arlington Member is a relatively thin (<3 m) unit that occurs primarily in North Texas as exposures in Denton, Johnson, and Tarrant counties (Murlin, 1975). The Arlington Member consists of massive beds of fine-grained, heavily oxidized cross-bedded sandstone interbedded with thinner laminated siltstone beds (Murlin, 1975). The presence of transgressive lags within the Arlington Member

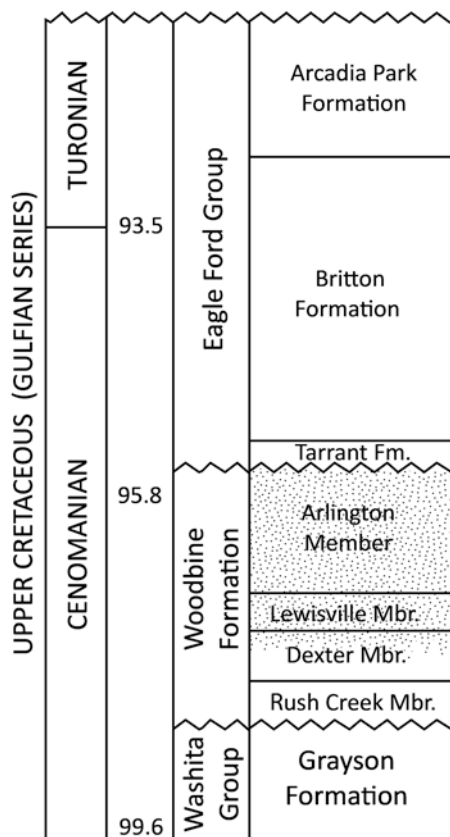


FIGURE 3. Stratigraphic column for the Cretaceous of central and north central Texas showing the position of the Woodbine Formation relative to timescale and adjacent geologic units. Stippled intervals represent terrestrial deposits. Time scale based on Gradstein et al. (2004). Modified from Adams et al. (2011).

indicates a low-lying coastal delta plain depositional environment (Murlin, 1975; Powell, 1968). These areas of the upper Woodbine Formation were likely modified by a series of small, repeating transgressive and regressive events prior to the major transgression marking deposition of the Eagle Ford Group (Lee, 1997a).

### STOP 3: GRAPEVINE LAKE

Grapevine Lake rests on public land in the far northeast corner of Tarrant County, administered by the United States Army Corps of Engineers (USACE). Woodbine Formation exposures around the lake are extensive, including Rock Ledge Park, Murrell Park, and the Grapevine Lake Dam Spillway.

#### Murrell Park (32.995208° N, -97.092072° W)

Exposures of the Woodbine Formation surrounding Grapevine Lake around Murrell Park belong to the lower Arlington Member and include

muds, fine grained bioturbated sandstones, and coarser cross-bedded sandstones (Lee, 1997b; Jacobs et al., 2013; Main, 2013). Cross-bedded and bioturbated sands belong to Woodbine foreshore deposits, including crab feeding balls, burrows, and petrified wood (Jacobs et al., 2013).

Isolated dinosaur remains attributed to a large ornithomimid, most likely *Protohadros*, have been found in Murrell Park and nearby Rock Ledge Park (Main, 2005). The holotype of the hadrosauroid *Protohadros byrdi* was found within a few kilometers of this site in Flower Mound (Head, 1998). Lee (1997b) described a spectacular array of dinosaur tracks exposed on the lake shore of Murrell Park assigned to theropods (*Fuscinapedis woodbinensis*), hadrosaurs (*Caririchnium protohadrosaurichnos*), and large birds (*Magnavipes lowei*) (Figure 4). These trackways have since been covered for their protection (Jacobs et al., 2013).

#### Dam Spillway (32.980505° N, -97.057212° W)

The exposures around the Dam Spillway belong to the underlying Lewisville Member and consist of interbedded fine sands and silts with interspersed sandy channel and levee deposits with abundant carbonized and petrified wood pieces, typical of a coastal plain environment (Figure 5) (Tykoski and Fiorillo, 2010). These deposits are similar to those found at the Arlington Archosaur Site and the nearby *Protohadros* type locality (Head, 1998).

Fossils from the Dam Spillway beds include the enantiornithine *Flexomornis howei* (DMNH 18137), considered the oldest bird in North America (Tykoski and Fiorillo, 2010). Dinosaurs include undescribed remains of a juvenile *Protohadros* surangular (DMNH 18169), partial coelurosaur manual ungual (DMNH 18159), and theropod pubis (DMNH 18139)(Figure 5). Numerous additional remains of sharks, bony fishes, turtles, and crocodyliforms have also been recovered (Tykoski and Fiorillo, 2010). Recently new theropod and hadrosaur tracks were exposed in the Dam Spillway vicinity following the torrential rains of Spring 2015, discovered by land managers of the USACE. Tracks are morphologically similar to those described from Murrell Park (Lee, 1997b) representing large individuals moving over a tidal flat, but occur in exposures of the lower Lewisville Member. These specimens are deposited in Perot Museum of Nature and Science collections awaiting further study.

#### STOP 4: THE ARLINGTON ARCHOSAUR SITE (32.810555° N, -97.079094° W)

##### History of Discovery

The Arlington Archosaur Site (AAS) is a North Texas fossil locality located in the suburban enclave of Arlington, Tarrant County, Texas, between the cities of

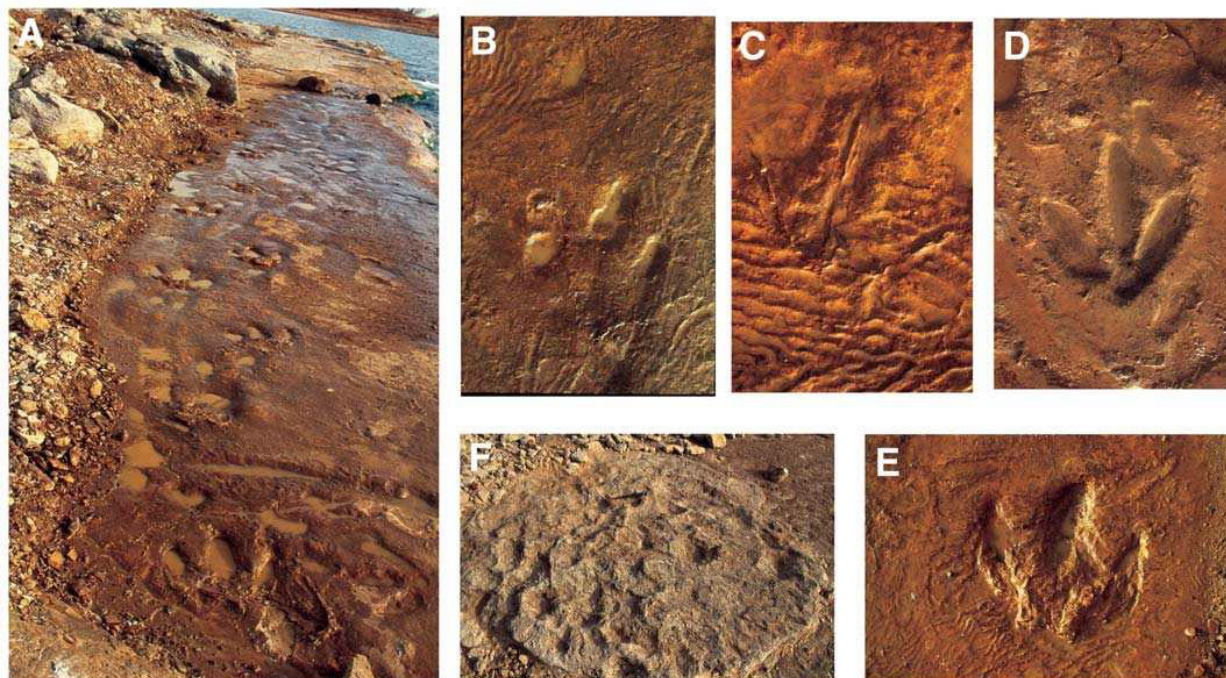


FIGURE 4. Dinosaur tracks exposed on the shore of Grapevine Lake in Murrell Park. **A**, trackway exposed *in situ* on lake shoreline. **B**, footprint of the hadrosaur *Caririchnium protohadrosaurichnos*. **C**, footprint belonging to the large bird *Magnoavipes lowei*. **D**, footprint of theropod *Fuscinaipedis woodbinensis*. **E**, another *Caririchnium protohadrosaurichnos* track. **F**, heavily bioturbated (dinoturbated) surface. Figure from Jacobs et al., 2013.

Dallas and Fort Worth (Figure 1). It preserves a diverse and abundant marginal marine ecosystem deposited during the Cenomanian as part of the Woodbine Formation. Local fossil collector Art Sahlstein and University of Texas–Arlington students Phil Kirchoff and Bill Walker, who independently found

fossils there in 2003, share credit for discovery of the site. Kirchoff presented some of these remains to Dr. Christopher Scotese at UT-Arlington, who handed them off to his new graduate student, Derek Main. Main identified the remains as belonging to a crocodyliform and a hadrosauroid, possibly *Protohadros*. It was based

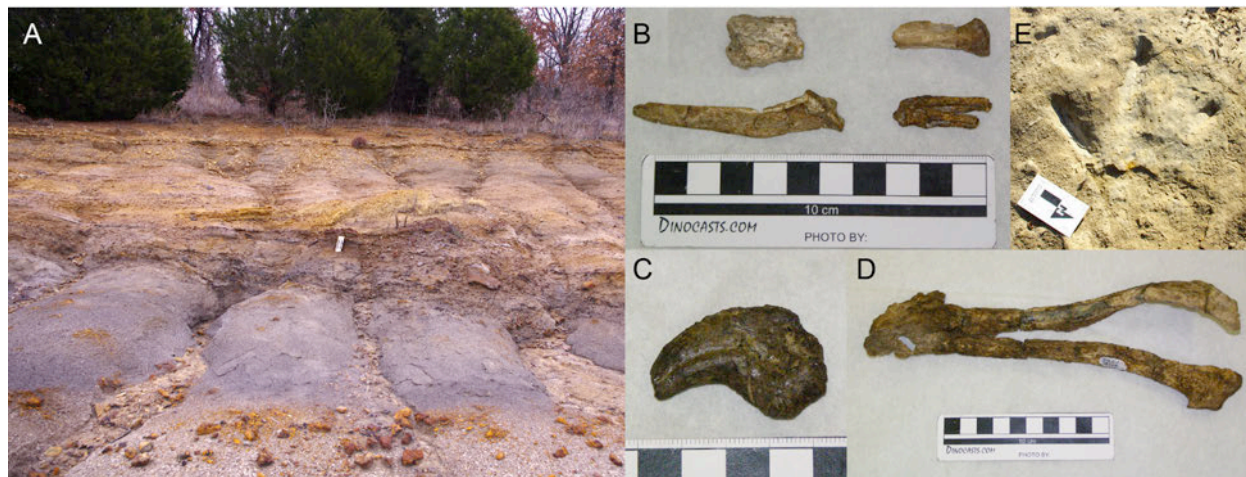


FIGURE 5. Sedimentary beds and archosaur fossils of the Woodbine Formation found at the Grapevine Lake Dam Spillway. **A**, Outcrop exposure showing bulk gray mud, overlain by interbedded fine sands and silts, including a fluvial channel deposit (center by scale bar), indicative of the Lewisville Member. **B**, Type material of *Flexomornis howei*, DMNH 18137 (Tykoski and Fiorillo, 2011). **C**, Manual ungual of a coelurosaur theropod, DMNH 18159. **D**, Paired pubes of indeterminate theropod, DMNH 18139. **E**, Isolated theropod track discovered recently in vicinity of spillway from Lewisville Member; approximate length is 50 cm. Photos B-D courtesy of Kris Howe.

on these initial IDs that he first coined the name for the site. However, organized excavation was stymied between 2003 and 2007 because the landowner at the time refused access. The situation changed in 2006 when the Huffines family purchased the area to build the Viridian housing development. Formal excavation and study was initiated in 2007-2008 through an agreement between Viridian and UT-Arlington, under the direction of Scotese and Main. Work at the AAS continued uninterrupted until 2013, when Derek Main unexpectedly passed away. Chris Scotese retired from UT-Arlington in 2011. Unable to continue curating the growing fossil collection and lacking the scientific expertise to continue its study, UT-Arlington donated the collection to the Perot Museum of Nature and Science in July 2013. Excavation at the site resumed in 2014 directed by the author under the auspices of the Perot Museum and Viridian development owners.

### Stratigraphy and Paleoenvironments

The Arlington Archosaur Site preserves a diverse coastal community of vertebrates, invertebrates, and plants deposited in a lower delta plain system created during a regressive phase along the southeastern margin of the Western Interior Seaway (Adams and Carr, 2010; Main, 2005; Noto et al., 2012; Oliver, 1971). The AAS is placed within the Lewisville Member of the Woodbine Formation based on lithostratigraphic and biostratigraphic criteria. The presence of the invertebrates *Anchura* and *Gyrodus* place the AAS in the lower to middle strata of the Lewisville Member (Stephenson, 1952).

Exposures consist of a hillside 200 m in length, with approximately 50 m representing the main fossil quarry (Figure 6). South of the hillside patches of sandstone at ground level containing shark teeth, trace fossils representing the *Skolithos* ichnofacies, and ripple marks were exposed (Main, 2013; Seilacher, 2007). While their precise relation to hillside exposures is uncertain, the sandstone appears to sit lower in section. The majority of these shallow marine facies south of the main hillside have subsequently been lost to housing development, though samples are preserved in Perot Museum collections. The following description includes the four most common and laterally extensive facies of the hillside exposure. Substantial lateral variation exists along the hillside. The description and interpretation of the main facies differs from Main (2013), here focusing on the hillside exposures with observable contacts. Many fossils were collected as float from the southern field exposures, thus their exact provenance within the Woodbine Formation is uncertain.

Facies A forms the primary fossil quarry, which contains the majority of specimens recovered to date. It consists of a dark brown sandy siltstone at least 50 cm deep overlain by a dark gray carbonaceous sandy

siltstone 30-40 cm thick, the upper portion of which contains slickensides. Sulfur bands, gypsum, and pyrite are prevalent throughout this layer. Abundant plant material is preserved including a high abundance of terrestrial palynomorphs (Main, 2013). The palynomorphs, well-preserved microscopic organic matter, rare dinoflagellates, absence of foraminifera, lungfish toothplates, nonmarine turtles, and lissamphibians, indicates fluvial deposition with minor marine input (Main, 2013). Fragmentary remains of elasmobranchs and osteichthyans representing individuals a meter or more in length suggests the nearby presence of deeper water. Invertebrate remains consist mainly of shells and contain a mixture of freshwater and brackish groups (Main, 2013). Facies A is interpreted as a low-energy freshwater or brackish system, such as a tidal coastal wetland proximal to a river channel (Rabenhorst, 2001).

Facies B is a 40-50 cm thick blocky gray sandy siltstone. Large, intersecting slickensides, root traces, and possible infilled desiccation cracks or clastic dikes are common. The top 5-10 cm changes color to a light brown and contains an abundance of charcoal and invertebrate burrows. Large root systems are preserved in situ as charcoal and encased in carbonate mineral concretions (mainly siderite) (Main et al., 2010). Hadrosauroid fossils attributed to *Protohadros byrdi* are described from this layer (Noto et al., 2013; Main et al., 2014). Rare shells of aquatic invertebrates are present. Facies B represents a paleosol with a seasonally-variable water table, possibly a vertisol or gleysol, that was proximal to a fluvial channel (Retallack, 2001).

Facies C consists of siderite-cemented silt nodules up to 10 cm in diameter or coarse-grained siderite-cemented slabs 2-5 cm thick with an erosional base. The layer is laterally extensive and can be traced up to 100 m west along the hillside. Some slabs are densely packed with invertebrate burrow traces that penetrate the underlying layer. Deformation of overlying bedding indicates the siderite precipitated postdeposition. Fossils are rare but when present belong to predominantly brackish or marine taxa. This rapid transition in section from terrestrial to marine environments may represent an unconformity brought on by subsidence under a prograding delta front.

Facies D is formed from a ~1 m thick interbedded fine white sand and gray siltstone alternating in layers 0.1-0.5 cm thick, with occasional interspersed layers of sand 5-10 cm thick, some of which contain ripple marks. Fossils in this facies are rare and belong to marine invertebrates. Facies D is a marine-influenced environment of active, cyclic deposition. Alternating sand-silt systems are not uncommon in prograding deltas and this facies may represent a mudflat from the intertidal zone or a distal bar/distributary mouth bar in the subaqueous delta plain

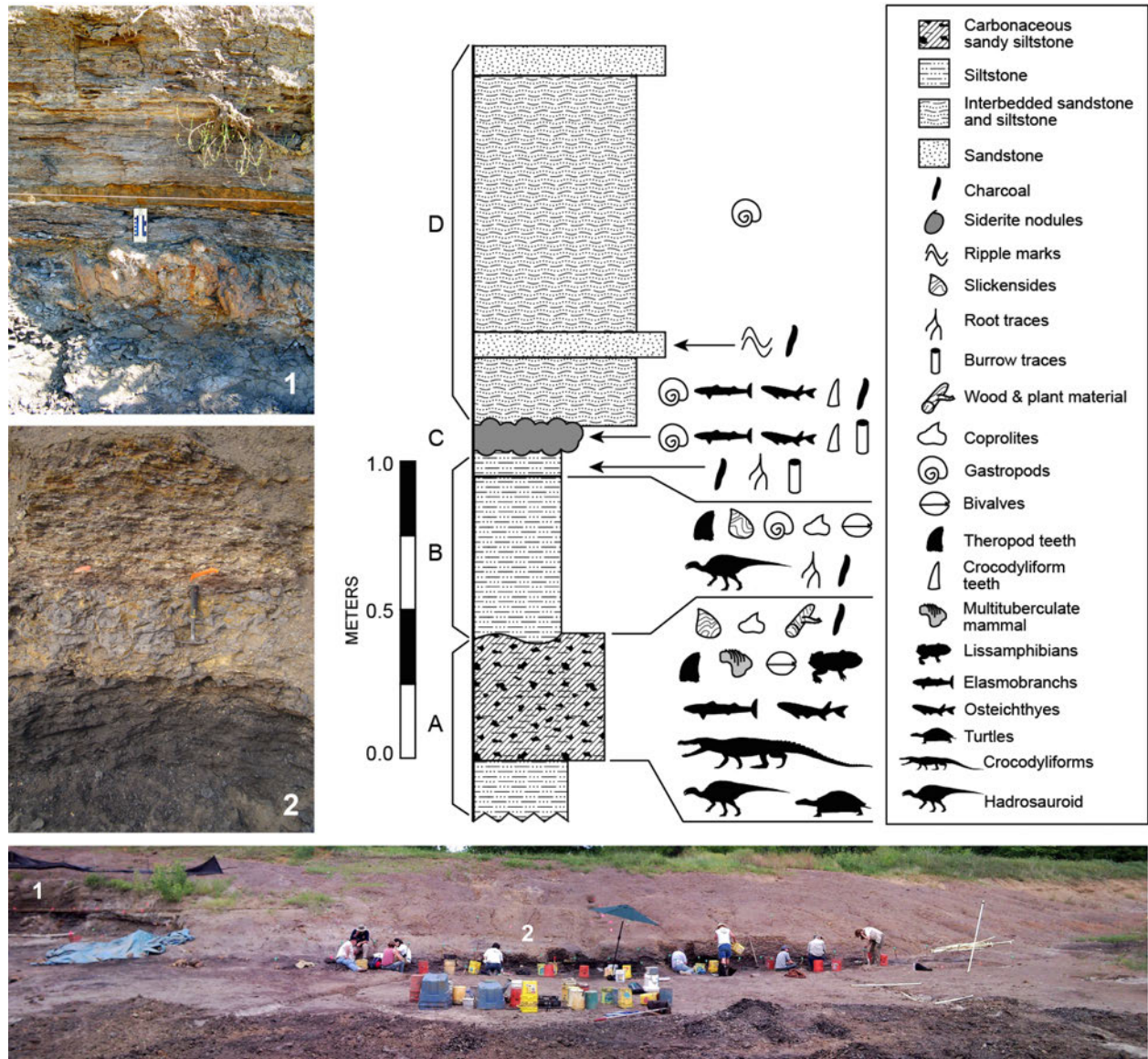


FIGURE 6. Composite stratigraphic section of AAS, based mainly on exposures from area of photo 1. Photo 1 is located in the far west end of the quarry and shows Facies B–D. Photo 2 is a section located near the datum and shows Facies A–D. The photo of the dig was taken around 2009. North is straight ahead in the lower photo.



FIGURE 7. Arrangement of crocodyliform fossils in Facies A at the time of their discovery in 2009. Note complete disarticulation of remains. Derek Main is shown at right.

(Coleman and Prior, 1981; Fan and Li, 2002). In both cases the thicker, sand-dominated layers may represent storm deposition.

**Taphonomy**

The taphonomy of the fossiliferous beds differs considerably. Vertebrate remains in Facies A are well preserved yet almost completely disarticulated, with some elements separated by 2 to 3 meters (Figure 7). When associated, elements are often contorted out of anatomical position. There is little evidence of long-distance aqueous transport or prolonged subaerial weathering features, indicating a parautochthonous origin. Some specimens possess crocodyliform bite marks, whose feeding behavior contributed to the disarticulation of remains and overall macrovertebrate accumulation in this area (Noto et al., 2012). Bite marks occur on only a small number of bones and therefore cannot explain the widespread disarticulation. A more likely mechanism involves tidally forced water level fluctuations displacing remains short distances,

disarticulating and spreading them over time with minimal transport-induced damage. Closely packed wetland plants may have prevented long distance transport by forming barriers that captured and held remains. The fragmentary meso- and microvertebrates preserved in this layer display a variety of preservation modes, suggestive of an allochthonous origin, likely deposited during periodic flooding from storm surges, increased wet season run off, or extreme high tides. Postburial, seasonal shrink-swell cycles in the overlying paleosol (Facies B) contributed further to disarticulation via pedoturbation as well as the distortion of remains close to the paleosol contact.

Facies B contains a disarticulated mass of primarily dense bones from the axial column and limbs attributed to the hadrosauroid *Protohadros*. Bones demonstrate weathering stages 2–4 (Behrensmeier, 1978). Upon death the carcass experienced prolonged episodes of subaerial exposure that alternated with episodes of short-distance hydraulic transport and sorting due to sporadic, low-energy flooding from a

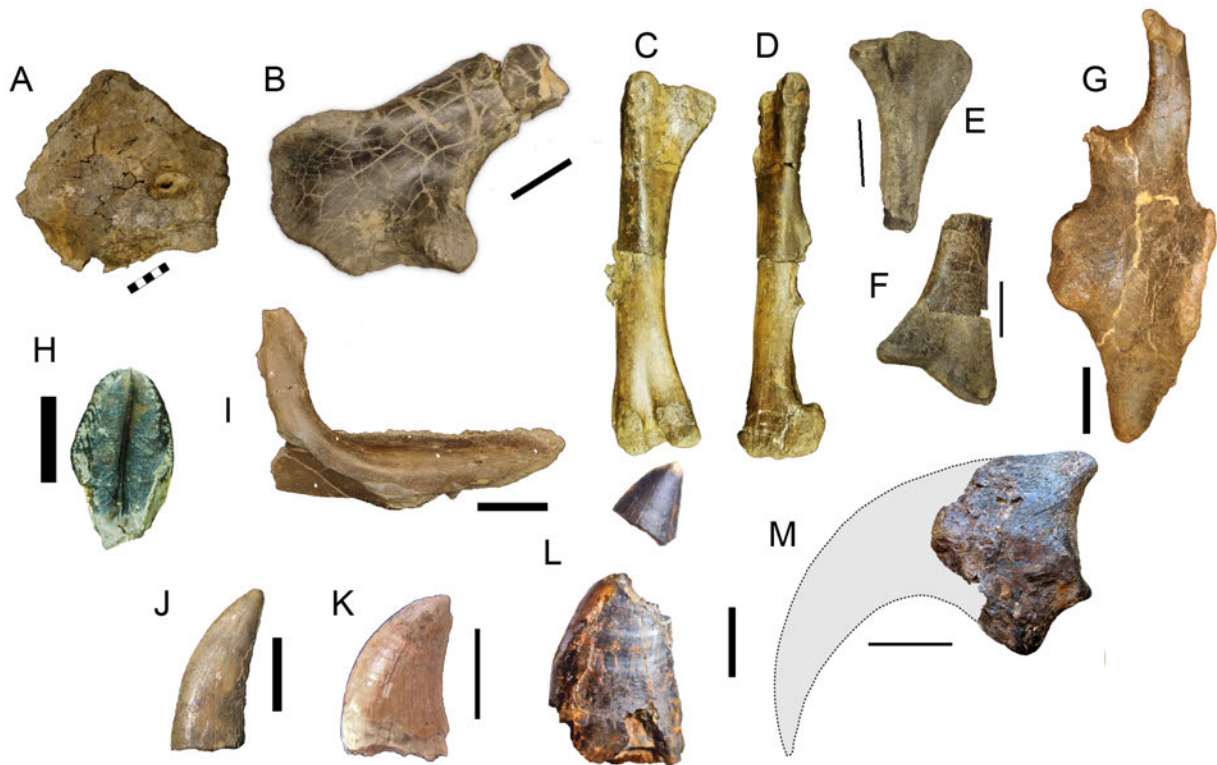


FIGURE 8. Examples of dinosaur remains found at the AAS attributed to the hadrosauroid *Protohadros* (A–I) and theropods (J–M). **A**, left coracoid in lateral view, scale bar equals 5 cm. **B**, partial left scapula in lateral view, scale bar equals 10 cm. **C**, juvenile right femur in anterior view, scale bar equals 10 cm. **D**, juvenile right femur in medial view, scale bar equals 10 cm. **E**, juvenile proximal tibia, scale bar equals 10 cm. **F**, subadult distal tibia, scale bar equals 10 cm. **G**, left ilium in lateral view, scale bar equals 10 cm. **H**, unworn dentary tooth crown, scale bar equals 1 cm. **I**, juvenile right dentary in lateral view, scale bar equals 10 cm. **J**, Theropod tooth morphotype C, scale bar equals 50 mm. **K**, Theropod tooth morphotype A, scale bar equals 1 cm. **L**, Theropod tooth morphotype B, scale bar equals 1 cm. **M**, Theropod manual ungual assigned to Allosauroidea indet. with reconstruction, scale bar equals 5 cm.



FIGURE 9. Examples of crocodyliform remains found at the AAS. **A**, Assembled cranial material of new taxon *Deltasuchus motherali*, scale bar in 10 cm increments **B**, Isolated shed crowns, scale in mm. **C**, juvenile *D. motherali* left dentary in lateral view, scale in cm. **D**, Left humerus attributed to *D. motherali*, scale in cm. **E**, Large dorsal osteoderm. **F**, Right dentary of unnamed eusuchian crocodyliform in lateral view, scale in cm.

nearby distributary channel. Upon final burial in muds, climatic seasonality and soil-forming processes resulted in extensive plastic deformation of the elements. Brittle deformation of elements resulted from later lithostatic compression by overlying strata (Main et al., 2014).

#### Fossil Overview

**Dinosaurs**—Dinosaur remains from the AAS are relatively rare, consisting mainly of elements referable to *Protohadros* and scant remains of large and small theropods (Figure 8; Table 1). *Protohadros* material discovered at the AAS includes a dentary, teeth, scapula, coracoid, humeri, ilia, ischium, pubis, femora, tibiae, metapodials, ribs, ossified tendons, an axis, and cervical, dorsal, and caudal vertebrae (Main et al., 2014). This represents the first postcranial material known for this taxon. Remains represent an MNI of at least 5 individuals including multiple ontogenetic stages from hatchling to subadult/adult. Bones of younger individuals are found in Facies A, while those of larger/older individuals in overlying Facies B. The AAS specimens are assigned to *Protohadros byrdi* because the dentary possesses a distinct medial horizontal shelf underlying the alveoli (Head, 1998). Theropod material consists mainly of teeth and fragmentary postcrania (Main, 2013; Main et al., 2011). At least three different morphotypes of teeth are represented. Morphotype A belongs to a large-bodied dromaeosaurine similar in size to *Deinonychus*. Morphotype B includes multiple

broken crowns attributed to a large tetanuran, an allosauroid or possibly a basal tyrannosauroid. Morphotype C is a small indeterminate theropod tooth. Postcrania include the distal end of a pedal phalanx from a small, gracile theropod and partial manual ungual from a large allosauroid tetanuran.

**Crocodyliforms**—There are three or more taxa of crocodyliform present in the main Facies A quarry (Figure 9). A majority of the remains belong to a new genus and species of large neosuchian crocodyliform named *Deltasuchus motherali* (Main, 2013; Adams et al., in prep). This taxon is represented by the cranial and postcranial remains of numerous individuals from a range of ontogenetic stages including hatchlings, juveniles, subadults, and adults. With a reconstructed skull length of 80-85 cm, adults reached at least 6 m in length. Tooth marks present on *Protohadros* and turtle bones are attributed to the feeding behavior of this taxon (Noto et al., 2012). A series of procoelous vertebrae, keeled rectangular osteoderms, globidont teeth, and a partial dentary indicate the presence of a small-bodied eusuchian crocodyliform. Additional remains of a longirostrine form have been identified, which may belong to *Woodbinesuchus* or *Terminonaris*, both known from the Woodbine Formation (Adams et al., 2011; Lee, 1997a).

**Turtles**—Numerous specimens representing multiple taxa of cryptodire turtle are commonly found in Facies A. Shell material is largely broken and scattered





FIGURE 10. Examples of chelonian remains found at the AAS. **A**, Three of the largest complete turtle humeri found to date, dorsal view. **B**, Robust mandible, dorsal view. **C**, One of the few articulated turtles found at the site. **D**, Section of carapace showing surface sculpturing, dorsal view. **E**, Section of carapace from lateral margin of a robust shell, arrow denotes crocodyliform tooth marks (Noto et al., 2012).

(Noto et al., 2012) with a few complete or near-complete shells, while limb material is generally more intact (Figure 10). Cranial material, including a complete skull and two mandibles, has been recovered. Most remains belong to individuals 35–45 cm carapace length, with some limb and shell pieces belonging to gigantic individuals with a carapace length of a meter or more. Preliminary identification suggests that the AAS turtles represent members of the Trionychoidea and Baenoidea, and possibly *Glyptops* (Main, 2013). All are non-marine, semiaquatic groups.

**Mammals**—To date only two mammal specimens have been recovered: an isolated lower fourth premolar and a partial dentary, both assigned to multituberculates. The AAS specimens differ from mammal material previously described from the Woodbine Formation and likely represent new taxa (Jacobs and Winkler, 1998; Krause and Baird, 1979).

**Amphibians and Other Reptiles**—A broad series of remains referable to multiple amphibian groups have been recovered through bulk screenwashing in Facies A. These include a possible cryptobranchid salamander and indeterminate anurans and caudates (Main, 2013). One vertebra may belong to an indeterminate saurian.

**Fish**—The fragmentary remains of bony and cartilaginous fish, represented principally by scales, teeth, and vertebrae, have been collected from all

exposed facies and as surface float. Osteichthyan specimens include jaw fragments of pycnodontid cf. *Paleobalistum* sp., isolated gar scales (*Lepisosteus* sp.?), the base of a subtriangular tooth that may belong to the enigmatic teleost *Stephanodus*, and multiple toothplates from a new species of lungfish, *Ceratodus carteri* (Main, 2013; Main et al., in press). Condriichthyans are represented by rostral teeth of *Oncopristsis dunklei*, *Cretodus* sp. teeth and vertebrae, hybodont shark spines, and teeth referable to the ray *Pseudohypolophus* sp. (Main, 2013; McNulty and Slaughter, 1962).

**Invertebrates**—Invertebrate fossils represent taxa common to brackish coastal environments, including gastropods and bivalves. The gastropod *Gyrodes*, a fresh water to intertidal carnivore, is the most common genus (Stephenson, 1952). Negative molds of burrow traces on multiple wood specimens are attributed to *Teredolites*, a wood burrowing mollusk typical of brackish water estuaries and coast plains (Bromley et al., 1984; Gingras et al., 2004; Hasiotis, 2002).

**Plants**—Abundant plant material is preserved within hillside exposures as well as adjacent localities on the Viridian property. In Facies A plant material is found in the form of broad, lenticular mats of featureless coalified remains up to 4 cm thick, compressed but well-preserved coalified tree sections 15–20 cm wide, small charcoaled fragments, and pieces of

TABLE 1. Vertebrate fauna from the Arlington Archosaur Site in the Woodbine Formation, Tarrant County, Texas. Modified from Main, 2013.

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Chondrichthyes	
	Hybodontidae indet.
	<i>Cretodus</i> sp.
	<i>Squalicorax</i> sp.
	<i>Onchopristis dunklei</i>
	<i>Pseudohypolophus (Hypolophus) mcnultyi</i>
Osteichthyes	
	cf. <i>Paleobalistum geiseri</i>
	Pycnodontidae indet.
	cf. <i>Lepisosteus</i> sp.
	cf. <i>Stephanodus</i> sp.
	Dipnoi
	<i>Ceratodus carteri</i>
Amphibia	
	Caudata indet.
	Cryptobranchidae indet.
	Anura indet.
Reptilia	
	Chelonia
	Baenidae indet.
	Trionychoidea indet.
	cf. <i>Glyptops</i> sp.
	Chelonia indet.
	Crocodyliformes
	<i>Deltasuchus motherali</i>
	Eusuchia indet.
	cf. <i>Bernissartia?</i> sp.
	cf. <i>Terminonaris?</i> sp.
	cf. <i>Woodbinesuchus?</i> sp.
	Dinosauria
	Theropoda
	Dromaeosaurinae indet.
	Allosauroidae indet.
	Tetanurae indet.
	Theropoda indet.
	Ornithopoda
	<i>Protohadros byrdi</i>
Mammalia	
	Multituberculata indet.

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permineralized wood (Main, 2013). Much of the coalified remains are preserved as vitrain. In 2008 a large conglomeration of over 20 coalified trees trunks 0.5–4 m long was discovered near the base of Facies A. Aligned in a NE-SW direction, these trunks likely represent transported debris (Main, 2013). Charcoalified remains dominate plant material from Facies B, including a series of 20–30 cm wide in situ root systems and abundant fragments throughout the bed. Multiple palynomorphs are present in Facies A

including *Dichastopollenites* and *Stellatopollis*, typical mid-Cenomanian angiosperm taxa (Main, 2013; May, 1975).

*Coprolites*—Hundreds of coprolites have been recovered, mainly from Facies A, ranging in size from 22 to 170 mm long. Small (< 5 cm) spiral coprolites are attributed to fish and sharks, large (> 6cm) spiral and scroll coprolites with a dome/cylinder morphology are attributed to crocodyliforms, while large (>10 cm) ovoid coprolites were likely made by herbivorous dinosaurs (Chin, 2007; Sawyer, 1981, 1998; Thulborn, 1991).

## PALEOECOLOGY

The majority of fossil accumulation occurred in a tidal freshwater or brackish coastal wetland followed by soil development in a proximal floodplain of a lower delta plain. The mixture of terrestrial, freshwater, brackish, and marine taxa reflects the proximity of the site to the paleocoastline (Cumbaa et al., 2010; McNulty and Slaughter, 1968; Russell, 1988). The area was densely vegetated with small and medium trees, ferns, and some angiosperms. The leaf morphologies are all representative of subtropical climates and brackish coastal plain environments (Main, 2013). Slickensides, desiccation cracks, and clastic dikes are indicative of a seasonally dry climate (DiMichele et al., 2006; Retallack, 2001). Dry seasons were marked by periodic wildfires, represented by at least three distinct charcoal-bearing horizons including clastic debris-flow, in-situ burned root systems, and abundant small charcoal fragments (Main et al., 2010). Wildfires were widespread and frequent in the Cretaceous and likely played a large role in structuring the AAS community (Brown et al., 2012). Crocodyliforms, particularly *Deltasuchus*, were the top predators in this environment, consuming turtles and the occasional unwary dinosaur that journeyed too close to the water’s edge (Figure 11).

## CONCLUSIONS

The Woodbine Formation represents one of the few records of early Late Cretaceous terrestrial fossils in Appalachia. Correlative deposits, such as the Cedar Mountain Formation, provide a detailed and growing picture of what was happening on Laramidia, west of the Cretaceous Interior Seaway (Zanno and Makovicky, 2013). To date little is known of faunal and floral dynamics “across the pond” in Appalachia. Diverse and fossiliferous localities like the Arlington Archosaur Site provide an unparalleled glimpse into the new ecosystems that evolved immediately following the completion of the seaway that separated the two landmasses. Future work will continue to elucidate this poorly known interval.



Figure 11. Late Cretaceous reconstruction of the AAS ecosystem, including a deadly encounter between a juvenile *Protohadros* and apex predator *Deltasuchus*. Artwork by Jacek Major.

## ACKNOWLEDGEMENTS

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## LITERATURE CITED

- Adams, R. L., and J. P. Carr. 2010. Regional depositional systems of the Woodbine, Eagle Ford, and Tuscaloosa of the US Gulf Coast.
- Adams, T. L., M. J. Polcyn, O. Mateus, D. A. Winkler, and L. L. Jacobs. 2011. First occurrence of the long-snouted crocodyliform *Terminonaris* (Pholidosauridae) from the Woodbine Formation (Cenomanian) of Texas. *Journal of Vertebrate Paleontology*, 31(3):712-716.
- Behrensmeyer, A. K. 1978. Taphonomic and Ecologic Information from Bone Weathering. *Paleobiology*, 4(2):150-162.
- Bergquist, H. R. 1949. Geology of the Woodbine formation of Cooke, Grayson, and Fannin Counties, Texas, Oil and Gas Inventory. Preliminary Map OM-98. USGS.
- Bromley, R. G., S. G. Pemberton, and R. A. Rahmani. 1984. A Cretaceous Woodground: The *Teredolites* Ichnofacies. *Journal of Paleontology*, 58(2):488-498.
- Brown, S. A. E., A. C. Scott, I. J. Glasspool, and M. E. Collinson. 2012. Cretaceous wildfires and their impact on the Earth system. *Cretaceous Research*, 36(0):162-190.
- Chin, K. 2007. The paleobiological implications of herbivorous dinosaur coprolites from the Upper Cretaceous Two Medicine Formation of Montana: why eat wood? *Palaio*, 22(5):554-566.
- Coleman, J. M., and D. B. Prior. 1981. Deltaic environments of deposition, p. 139-178. *In* P. A. Scholle and D. Spearing (eds.), *Sandstone depositional environments*. AAPG Memoir 31.
- Cumbaa, S. L., K. Shimada, and T. D. Cook. 2010. Mid-Cenomanian vertebrate faunas of the Western Interior Seaway of North America and their evolutionary, paleobiogeographical, and paleoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 295(1-2):199-214.

- Dimichele, W. A., N. J. Tabor, D. S. Chaney, and W. J. Nelson. 2006. From wetlands to wet spots: environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. *Geological Society of America Special Papers*, 399:223-248.
- Dodge, C. F. 1952. Stratigraphy of the Woodbine Formation in the Arlington area. Tarrant County, Texas: Field and Laboratory, 20(2):66-78.
- Dodge, C. F. 1968. Stratigraphic Nomenclature of the Woodbine Formation Tarrant County, Texas p. 107-125. In C. F. Dodge (ed.), Field trip Guidebook, South Central Section, Stratigraphy of the Woodbine Formation, Tarrant County, Texas. Geological Society of America.
- Dodge, C. F. 1969. Stratigraphic nomenclature of the Woodbine Formation Tarrant County, Texas. *Texas Journal of Science*, 21:43-62.
- Fan, D., and C. Li. 2002. Rhythmic deposition on mudflats in the mesotidal Changjiang Estuary, China. *Journal of Sedimentary Research*, 72(4):543-551.
- Gingras, M. K., J. A. Maceachern, and R. K. Pickerill. 2004. Modern perspectives on the Teredolites ichnofacies: observations from Willapa Bay, Washington. *Palaaios*, 19(1):79-88.
- Gradstein, F. M., J. G. Ogg, and A. G. Smith. 2004. A geologic time scale 2004. Cambridge University Press, UK, 86, 500 p.
- Hasiotis, S. T. 2002. Continental Trace Fossils. *SEPM Short Course Notes*, 51:1-131.
- Head, J. J. 1998. A new species of basal hadrosaurid (Dinosauria, Ornithischia) from the Cenomanian of Texas. *Journal of Vertebrate Paleontology*, 18(4):718-738.
- Hedlund, R. W. 1966. Palynology of the Red Branch Member of the Woodbine Formation (Cenomanian), Bryan County, Oklahoma. *Oklahoma Geological Survey Bulletin*, 112:1-69.
- Hill, R. T. 1901. Geography and Geology of the Black and Grand Prairies, Texas: With Detailed Descriptions of the Cretaceous Formations and Special Reference to Artesian Waters. U.S. Geological Survey, 21<sup>st</sup> Annual Report 1899-1900, 666 p.
- Jacobs, L. L., and D. A. Winkler. 1998. Mammals, archosaurs, and the Early to Late Cretaceous transition in north-central Texas, p. 253-280. In Y. Tomida, L. J. Flynn, and L. L. Jacobs (eds.), *Advances in Vertebrate Paleontology and Geochronology*. Volume 14. National Science Museum Monographs, Tokyo.
- Jacobs, L. L., M. J. Polcyn, D. A. Winkler, T. S. Myers, J. G. Kennedy, and J. B. Wagner. 2013. Late Cretaceous strata and vertebrate fossils of North Texas, in Hunt, B. B., and Catlos, E. J., eds., *Late Cretaceous to Quaternary Strata and Fossils of Texas: Field Excursions Celebrating 125 Years of GSA and Texas Geology*, GSA South-Central Section Meeting, Austin, Texas, April 2013. The Geological Society of America Field Guide 30, p. 1-13.
- Johnson, R. O. 1974. Lithofacies and depositional environments of the Rush Creek Member of the Woodbine Formation (Gulfian) of North Central Texas, University of Texas, Arlington, 158 p.
- Kennedy, W. J., and W. A. Cobban. 1990. Cenomanian ammonite faunas from the Woodbine Formation and lower part of the Eagle Ford Group, Texas. *Palaontology*, 33(1):75-154.
- Krause, D. W., and D. Baird. 1979. Late Cretaceous Mammals East of the North American Western Interior Seaway. *Journal of Paleontology*, 53(3):562-565.
- Lee, Y.-N. 1997a. The Archosauria from the Woodbine Formation (Cenomanian) in Texas. *Journal of Paleontology*, 71(6):1147-1156.
- Lee, Y.-N. 1997b. Bird and dinosaur footprints in the Woodbine Formation (Cenomanian), Texas. *Cretaceous Research*, 18(6):849-864.
- Main, D. J. 2005. Paleoenvironments and Paleocology of the Cenomanian Woodbine Formation of Texas, Paleobiogeography of the Hadrosaurs (Dinosauria: Ornithischia), University of Texas, Arlington, 304 p.
- Main, D. J. 2013. Appalachian Delta Plain Paleocology Of The Cretaceous Woodbine Formation At The Arlington Archosaur Site, North Texas, University of Texas at Arlington, unpublished Ph.D dissertation, 548 p.
- Main, D. J., C. R. Noto, and C. R. Scotese. Coastal Cretaceous forest fires, paleosols, and dinosaur paleocology from the Arlington Archosaur Site, North Texas. Geological Society of America Annual Meeting, Denver, CO, 42(5):175.
- Main, D. J., C. R. Noto, and C. R. Scotese. New theropod material from the Cenomanian Woodbine Formation at the Arlington Archosaur Site and Cretaceous biogeography. Society of Vertebrate Paleontology Annual Meeting, Las Vegas, NV.
- Main, D. J., C. R. Noto, and D. B. Weishampel. 2014. Postcranial anatomy of a basal hadrosauroid (Dinosauria: Ornithomimidae) from the Cretaceous (Cenomanian) Woodbine Formation of North Central Texas. , p. 77-95. In D. A. Eberth and D. C. Evans (eds.), *Hadrosaurs*. Indiana University Press, Bloomington, IN.
- Main, D. J., D. C. Parris, B. G. Grandstaff, and B. Carter. in press. A new lungfish (Dipnoi; Ceratodontidae) from the Cretaceous Woodbine Formation, Arlington Archosaur Site, North Texas. *Texas Journal of Science*, 63(3).
- May, F. 1975. *Dichastopollenites reticulatus*, gen. et sp. nov.: Potential Cenomanian Guide Fossil from Southern Utah and Northeastern Arizona. *Journal of Paleontology*:528-533.
- McNulty, C. L., and B. H. Slaughter. 1962. A new sawfish from the Woodbine Formation (Cretaceous) of Texas. *Copeia*, 4:775-776.
- McNulty, C. L., and B. H. Slaughter. 1968. Fishbed conglomerate fauna, Arlington Member, Woodbine Formation (Cenomanian) of Texas, p. 68-73, Fieldtrip Guidebook, South-Central Section, Stratigraphy of the Woodbine Formation, Tarrant County, Texas. Geological Society of America, Denver.
- Murlin, J. R. 1975. Stratigraphy and Depositional Environments of the Arlington Member, Woodbine Formation (Upper Cretaceous), Northeast Texas. M.S. Thesis, University of Texas at Arlington, Arlington, 214 p.
- Noto, C. R., D. J. Main, and S. K. Drumheller. 2012. Feeding traces and paleobiology of a Cretaceous (Cenomanian) crocodyliform: example from the Woodbine Formation of Texas. *Palaaios*, 27(2):105-115.
- Oliver, W. B. 1971. Depositional systems in the Woodbine Formation (Upper Cretaceous), northeast Texas: The University of Texas at Austin. Bureau of Economic Geology Report of Investigations, 73:28.

- Powell, J. D. 1968. Woodbine-Eagle Ford transition, Tarrant Member, p. 27-43. *In* C. F. Dodge (ed.), Field trip Guidebook, South Central Section, Stratigraphy of the Woodbine Formation, Tarrant County, Texas. Geological Society of America.
- Rabenhorst, M. C. 2001. Soils of Tidal and Fringing Wetlands, p. 301-315. *In* J. L. Richardson and M. J. Vepraskas (eds.), *Wetland Soils: Genesis, Hydrology, Landscapes, and Classification*. CRC Press, Boca Raton, Florida.
- Retallack, G. J. 2001. *Soils of the Past*. Blackwell Science, Malden, MA, 404 p.
- Russell, D. A. 1988. A checklist of North American marine Cretaceous vertebrates including fresh water fishes. Occasional Paper of Tyrrell Museum of Palaeontology, 4:1-57.
- Sawyer, G. T. 1981. A Study of Crocodylian Coprolites from Wannagan Creek Quarry (Paleocene-North Dakota): Ichnofossils II. Science Museum of Minnesota Monograph, 5(2):1-29.
- Sawyer, G. T. 1998. Coprolites of the Black Mingo Group (Paleocene) of South Carolina. *Transactions of the American Philosophical Society, New Series*, 88(4):221-228.
- Seilacher, A. 2007. *Trace fossil analysis*. Springer-Verlag, New York, 240 p.
- Stephenson, L. W. 1952. Larger Invertebrate Fossils of the Woodbine Formation (Cenomanian) of Texas. USGS Professional Paper, 242:1-225.
- Thulborn, R. A. 1991. Morphology, preservation and palaeobiological significance of dinosaur coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 83(4):341-366.
- Trudel, P. 1994. Stratigraphic sequences and facies architecture of the Woodbine–Eagle Ford interval, Upper Cretaceous, North Central Texas. unpublished Master's thesis, Tarleton State University, 105 p.
- Tykoski, R. S., and A. R. Fiorillo. 2010. An enantiornithine bird from the lower middle Cenomanian of Texas. *Journal of Vertebrate Paleontology*, 30(1):288-292.
- Winkler, D., L. Jacobs, Y. Lee, and P. Murry. 1995. Sea level fluctuation and terrestrial faunal change in North-Central Texas, p. 175-177. *In* A. Sun and Y. Wang (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press, Beijing.
- Zanno, L. E., and P. J. Makovicky. 2013. Neovenatorid theropods are apex predators in the Late Cretaceous of North America. *Nat Commun*, 4.

## Notes