

THE JOHN WESLEY POWELL FOSSIL TRACK BLOCK—THEROPOD TRACKS WITH ORNITHOPOD-LIKE MORPHOLOGY FROM THE EARLY JURASSIC NAVAJO SANDSTONE, GLEN CANYON NATIONAL RECREATION AREA, UTAH

Andrew R.C. Milner, Vincent L. Santucci, John R. Wood, Tylor A. Birthisel, Erica Clites, and Martin G. Lockley



This is an open-access article in which the Utah Geological Association permits unrestricted use, distribution, and reproduction of text and figures that are not noted as copyrighted, provided the original author and source are credited. Email inquiries to GIW@utahgeology.org.



GEOLOGY OF THE INTERMOUNTAIN WEST

President

Treasurer

Secretary

President-Elect

Program Chair

Past President

an open-access journal of the Utah Geological Association ISSN 2380-7601

2023

Volume 10

Editors

Douglas A. Sprinkel Azteca Geosolutions 801.391.1977 GIW@utahgeology.org dsprinkel@gmail.com

Bart J. Kowallis Brigham Young University 801.380.2736 bkowallis@gmail.com

Steven Schamel GeoX Consulting, Inc. 801.583-1146 geox-slc@comcast.net

Thomas C. Chidsey, Jr. Utah Geological Survey 801.824.0738

tomchidsey@gmail.com John R. Foster

Utah Field House of Natural History State Park Museum 435.789.3799 johnfoster@utah.gov

Production

Cover Design and Desktop Publishing Douglas A. Sprinkel

Cover

Two hypothetical, Eubrontes-producing theropods walking across a sandy, water-saturated, microbial-matrich interdunal playa during an early phase of the Navajo erg in the Early Jurassic. This restoration was created based on the spectacular undertracks preserved on the John Wesley Powell Fossil Track Block. The ornithopodlike undertracks now visible on the track block were registered in horizons situated below stromatolitic or endoevaporitic layers (represented in green). These undertracks display different morphologies than the true tracks, which would have resembled Eubrontes. Artwork by Brian Engh (dontmesswithdinosaurs.com).



Geology of the Intermountain West (GIW) is an open-access journal in which the Utah Geological Association permits unrestricted use, distribution, and reproduction of text and figures that are not noted as copyrighted, provided the original author and source are credited.

2023-2024 UGA Board

Eugene Szymanski	eugenes@utah.gov	801.537.3364
Keilee Higgs	keileeann@utah.gov	801.678.3683
Chris Stallard	cstallard@utah.gov	801.386.0976
Aubry DeReuil	aubry@zanskar.us	850.572.2543
Trae Boman	tbowman@teamues.com	801.648.5206
Rick Ford	rford@weber.edu	801.915.3188

UGA Committees

Environmental Affairs	Craig Eaton	eaton@ihi-env.com	801.633.9396
Geologic Road Sign	Greg Gavin	greg@loughlinwater.com	801.541.6258
Historian	Paul Anderson	paul@pbageo.com	801.364.6613
Outreach	Greg Nielsen	gnielsen@weber.edu	801.626.6394
Public Education	Zach Anderson	zanderson@utah.gov	801.537.3300
	Matt Affolter	gfl247@yahoo.com	
Publications	Paul Inkenbrandt	paulinkenbrandt@utah.gov	801.537.3361
Publicity	Paul Inkenbrandt	paulinkenbrandt@utah.gov	801.537.3361
Social/Recreation	Roger Bon	rogerbon@xmission.com	801.942.0533

AAPG House of Delegates

David A. Wavrek dwavrek@petroleumsystems.com 2024-2026 Term 801.322.2915 State Mapping Advisory Committee Bill Loughlin bill@loughlinwater.com UGA Representative 435.649.4005 Earthquake Safety Committee Grant Willis gwillisgeol@gmail.com Chair 801.537.3355 UGA Website — www.utahgeology.org paulinkenbrandt@utah.gov Paul Inkenbrandt Webmaster 801 537 3361 **UGA** Newsletter Bill Lund Newsletter Editor uga.newsletter@gmail.com 435.590.1338

Become a member of the UGA to help support the work of the Association and receive notices for monthly meetings, annual field conferences, and new publications. Annual membership is \$30 and annual student membership is only \$5. *Visit the UGA website at www.utahgeology.org for information and membership* application.

The UGA board is elected annually by a voting process through UGA members. However, the UGA is a volunteer-driven organization, and we welcome your voluntary service. If you would like to participate please contact the current president or committee member corresponding with the area in which you would like to volunteer.

Utah Geological Association formed in 1970 from a merger of the Utah Geological Society, founded in 1946, and the Intermountain Association of Geologists, founded in 1949. Affiliated with the American Association of Petroleum Geologists.



The John Wesley Powell Fossil Track Block—Theropod Tracks with Ornithopod-Like Morphology from the Early Jurassic Navajo Sandstone, Glen Canyon National Recreation Area, Utah-Arizona

Andrew R.C. Milner¹, Vincent L. Santucci², John R. Wood³, Tylor A. Birthisel⁴, Erica Clites⁵, and Martin G. Lockley⁶ ¹St. George Dinosaur Discovery Site at Johnson Farm, St. George, UT 84790 USA; arcmilner@gmail.com ²National Park Service, Geologic Resources Division, Washington, DC 20005 USA; vincent_santucci@nps.gov ³National Park Service, Geologic Resources Division, Natural Resources Stewardship and Science Directorate, Lakewood, CO

USA 80225; jack_wood@nps.gov

⁴Natural History Museum of Utah, Salt Lake City, UT 84108-1214 USA; tbirthisel@nhmu.utah.edu ⁵Michigan State University Extension, Detroit, MI 48238 USA; eclites@gmail.com

⁶Dinosaur Trackers Research Group, University of Colorado Denver, Denver, CO 80217-3364 USA; martin.lockley@ucdenver.edu

ABSTRACT

A large fallen block of Early Jurassic Navajo Sandstone located at Lake Powell, within Glen Canyon National Recreation Area, south-central Utah, displays natural casts of vertebrate tracks. The footprints occur on at least three track-bearing horizons preserved on and between stromatolitic sandstone beds. Two large, parallel trackways, plus a third, divergent trackway, on the main track layer (MTL) superficially resemble ornithopod footprints; however, they were produced by large-sized theropod dinosaurs, rather than ornithischians, and we identify these as *Eubrontes*.

Small coelophysoid theropod tracks (*Grallator*) are the most common vertebrate ichnofossils on all track-bearing horizons, with approximately 50 footprints preserved on the MTL, six on the highest surface, and three on thinner float slabs stratigraphically lower in section. An additional 12 tracks in three trackways of *Anchisauripus* size occur on the MTL, but they superficially resemble *Kayentapus* in having wider divarication angles than typical *Anchisauripus*. The MTL also preserves at least five closely associated tetradactyl footprints that we identify as cf. *Brasilichnium*. A nearby, smaller fallen block preserves distinct *Batrachopus* tracks, which are rare in eolian environments.

The microbial (possibly endoevaporitic) mats and stromatolitic horizons on which the animals had walked produced a distinct ichnomorphologic variation because of substrate consistency and the elastic properties of the mats, resulting in differential compaction of the bedding surfaces. Lithic compaction of the finer-grained sediments between denser, more resistant sandstone beds pre- and/or post-lithification resulted in additional deformation of the tracks, followed by natural erosion. We interpret these natural cast footprints on the MTL as possible transmitted tracks. The track-bearing, microbial-mat surfaces represent interdunal pooling of water, probably during periods of increased precipitation and/or rising water tables during wet seasons.

Citation for this article.

Milner, A.R.C., Santucci, V.L., Wood, J.R., Birthisel, T.A. Clites, E., and Lockley, M.G., 2023, The John Wesley Powell Fossil Track Block theropod tracks with ornithopod-like morphology from the Early Jurassic Navajo Sandstone, Glen Canyon National Recreation Area, Utah-Arizona: Geology of the Intermountain West, v. 10, p. 185–222, https://doi.org/10.31711/giw.v10.pp185-222.

INTRODUCTION

Glen Canyon National Recreation Area (GLCA) preserves an incredible abundance of tetrapod trace fossils, especially those of dinosaurs, because of extensive exposures of Late Triassic-Early Jurassic Chinle Formation and Glen Canyon Group strata (Lockley and others, 1998, 2014). These strata were deposited in paleoenvironmental conditions conducive to track preservation, such as fluvial, lacustrine, and eolian environments. Many important tracksites submerged by and around Lake Powell have been recorded by two of us (VLS and MGL), the National Park Service (NPS), and others (Lockley and Hunt, 1995; Lockley and others, 1998, 2014; Santucci and others, 2009; Santucci and Kirkland, 2010; Kirkland and others, 2010; Delgalvis, 2015; Tweet and Santucci, 2018; Bennett and others, 2023).

One such example, which is the focus of this paper, is a large, approximately 7-m-tall fallen block (NPS locality # GLCA 10) of Early Jurassic Navajo Sandstone we have designated as the John Wesley Powell Fossil Track Block (PFTB), honoring Major John Wesley Powell, who perilously explored the Colorado River along its length on two occasions in 1869 and 1871-1872, including the Glen Canyon area in which man-made Lake Powell Reservoir now lies. The PFTB was discovered in 2009 by Jessalyn Imdieke and reported to the Office of the State Paleontologist at the Utah Geological Survey (UGS) by Stuart Havenstrite. The locality was then reported by Dr. James Kirkland (UGS) to the NPS. It was subsequently investigated in a joint effort between the NPS and UGS in 2009. The block was reported and illustrated for the first time in an internally distributed NPS document (Kirkland and others, 2010, figure 32), and later figured and partially described on other occasions (Lockley and others, 2014, figure 26; Lockley and Xing, 2015, figure 4; Tweet and Santucci, 2018, figure 3E).

The site is located along the eastern shore of Lake Powell, near the San Juan confluence within GLCA (figure 1). Because of high levels of tourism in the Lake Powell area and the need to protect this valuable fossil resource from potential damage, specific locality information about the site is withheld here, but will be

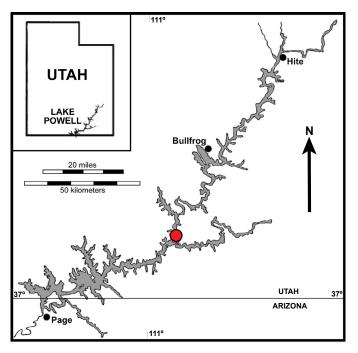


Figure 1. Approximate location (red circle) of the John Wesley Powell Fossil Track Block Site (GLCA #10).

made available to qualified researchers upon request. The PFTB preserves a spectacular assemblage of tracks (figure 2), primarily produced by bipedal theropod dinosaurs, although two of the trackways superficially resemble ornithopod tracks. Approximately 85 footprints are preserved on three identified track-bearing horizons exposed on the vertically oriented block and nearby associated float slabs. The most prominent tracks lie on a horizon referred to as the Main Track Layer (MTL); other tracks present at the site occur on, or on float slabs originating from, both a higher and a lower stratigraphic horizon.

During the original inspection of the PFTB, the ornithopod-like tracks were recognized as morphologically unusual, prompting the question of whether some unknown large ornithopod dinosaurs may have produced them. However, this hypothesis seems unlikely because the PFTB tracks are significantly older than the oldest-known body fossils of even small ornithopods, such as the dryosaurid *Callovosaurus* from the Middle Jurassic of the United Kingdom (Ruiz-Omeñaca and others, 2007; Díaz-Martinez and others, 2015), and *Kulindadromeus* from the Middle–Late Jurassic of Russia (Godefroit and others, 2014), which was recovered as

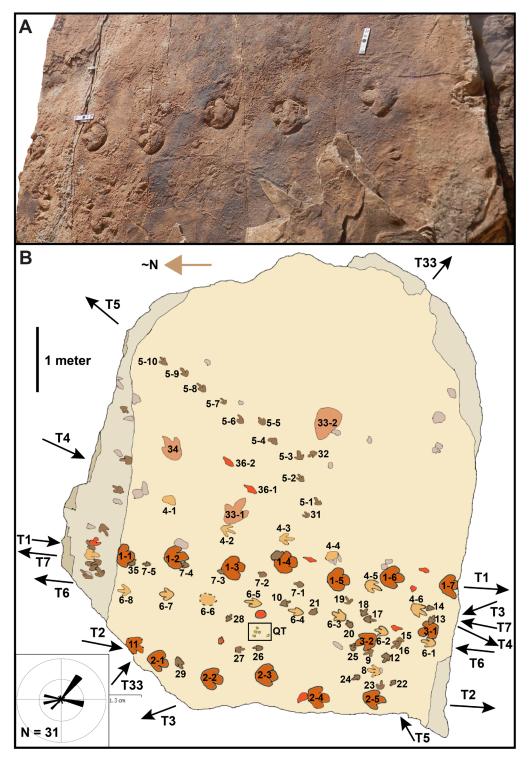


Figure 2. The John Wesley Powell Fossil Track Block (PTFB) at locality GLCA #10. (A) Photograph of track block looking to the west. (B) An inverted map of the middle and upper track-bearing surfaces. Tracks have been assigned unique track and trackway numbers. Arrows indicate directions of travel of individual trackmakers; the inset rose diagram shows the prevalence of travel directions relative to the estimated north orientation of the PFTB. Tracks have been colored: dark orange = *Eubrontes*; brown = *Grallator*; light orange = medium-size theropod tracks (*Anchisauripus*-sized tracks); red = cf. *Grallator*; In box marked QT = *Brasilichnium*; light purple = unidentified tracks. Scale = 1 m.

an ornithopod by Dieudonné and others (2022). Moreover, the oldest recorded tracks assigned to ornithopod dinosaurs (which, from an ichnological perspective, has been used as something of a wastebasket) are Middle Jurassic (Milàn and others, 2020) and Late Jurassic in age, including the ichnotaxa Camptosauropus vialovi from Tajikistan (Gabunia and Kurbatov, 1988), Wealdenichnites iguanodontoides (Kuhn, 1958) from Germany, Sinoichnites youngi (Kuhn, 1958) from China, and ostensible ornithopod tracks from the Morrison Formation in the western United States (Foster and Lockley, 2006). Note that Sinoichnites was identified as Late Jurassic, but because its source locality is unknown, the proposed age is suspect (Díaz-Martinez and others, 2015). Additionally, Li and others (2012) found evidence that Sinoichnites might be a thyreophoran track with some resemblance to Moyenisauropus. All of these ichnotaxa were considered nomina dubia by Díaz-Martinez and others (2015).

Moreno and others (2012) defined ornithopod tracks as, "tridactyl, mesaxonic, with lengths of digits II, III, and IV only slightly different; wide digits with rounded ends; digits converge proximally into a broad metatarsophalangeal impression ('heel pad'). Ornithopod ichnites are similar in anteroposterior and mediolateral dimensions, and their general shapes resemble a clover." Following closer examination of the PFTB tracks, we agree with Lockley and Xing (2015) in inferring a saurischian (specifically theropod), rather than ornithischian, origin for these footprints. Lockley and Xing (2015, p. 87–88, figure 4) assigned these tracks to Eubrontes and interpreted the "fleshy" appearance of the footprints as a result of compaction and deformation of the track casts due to extensive loading on finer-grained and softer beds between thick, dense, eolian sand layers. While we agree this is, in part, correct, we expand on this hypothesis below.

Following Martin (2014, p. 71), additional points should be considered in attributing tracks to specific clades of trackmakers, especially with tridactyl dinosaur tracks, *in*clude: (1) the overall shapes of digit impressions (thin, medium, robust) relative to entire track length; (2) the distal ends of digits—are they blunt and rounded or do they possess discreet claw marks?; (3)

the shape of the proximal portion of track (i.e., "heel"); (4) the kind(s) of substrate on which the tracks are preserved and how this may have affected overall track morphology; (5) track morphology subject to behavioral differences (e.g., stopping, turning, speed, etc.); (6) sediment collapse into the tracks after foot extraction, changing overall track morphology; (7) the substrate drying after the track was formed, which can alter overall track morphology; and (8) whether or not the visible track actually is an "undertrack," or more precisely a transmitted track and how far below the surface the undertrack was transmitted (Thulborn, 1990). In this study, we consider all these points along with the shapes of the anterior triangles of the tracks (how far the digit III trace extends distally beyond the ends of the digit II and IV traces—i.e., the degree of mesaxony or the "toe extension" measurement of some authors) (Olsen, 1980; Lockley and Hunt, 1995; Lockley, 2009; Farlow and others, 2018) and the dimensions of the proximal proportions of the tracks, following Farlow and others (2018).

MATERIALS AND METHODS

Logistics, Tracksite Mapping, and Site Excavation

Our initial detailed documentation of the PFTB in 2010 was complicated by the vertical orientation and large size of the block, making accessing much of the MTL difficult. The initial investigation employed a 6-ft (1.8-m) ladder to access higher areas of the block, but we were still limited on how much of the track surface we could physically access and examine in detail. Unstable float slabs (rock debris broken off from the PFTB and its adjacent source cliff) at the base of the block made positioning the ladder difficult, and maintaining balance safely was an issue (figures 3A and 3B). Many of the float slabs in front of the PFTB also contain dinosaur tracks from layers underlying the MTL, and these tracks could easily be damaged when walked or climbed on. Initially we were unable to map the lowermost part of the PFTB because the float slabs partially obscured the lower tracks and trackways. These slabs were systematically recorded (positionally and stratigraphically), excavated, and removed with the assistance of NPS

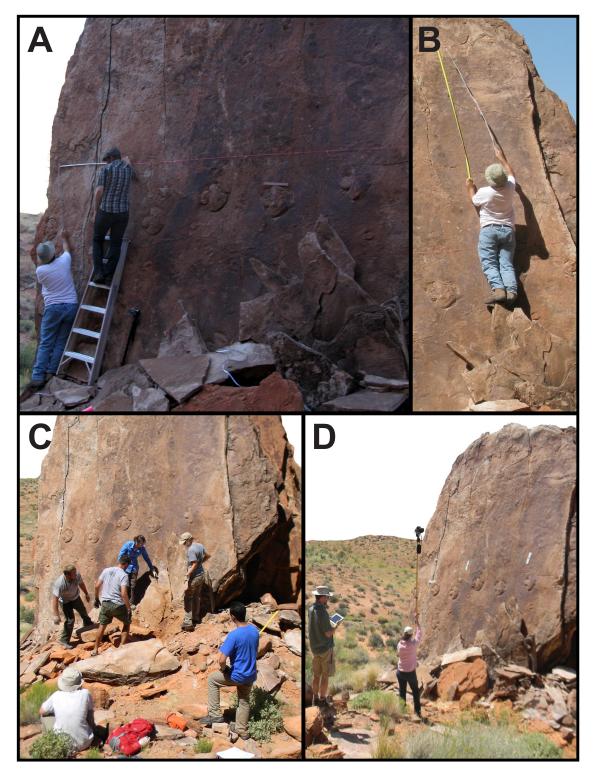


Figure 3. Methods used in John Wesley Powell Fossil Track Block (PTFB) tracksite documentation. Gridding PFTB for mapping. (A) Dan Whalen working on a ladder to place pink string datum line in place above *Eubrontes* trackway 1. (B) Tylor Birthisel chalking upper part of the PFTB while standing on precarious rock. (C) NPS crew excavating the covered part of the track block in which tracks were found in situ on lower horizons. (D) September 2014 photogrammetry of track block; left to right: John "Jack" Wood and Sarah Doyle.

staff (figure 3C) in June 2015. This led to the confirmation of a slightly older track horizon several centimeters below the MTL.

PHOTOGRAMMETRY AND DATA PROCESSING METHODS

We generated high-quality, three-dimensional models of the track-bearing surface of the PFTB to enhance mapping and morphological assessments. To accomplish this, structure-from-motion (SfM) photogrammetry was employed following Matthews (2008) and Mallison and Wings (2011). Additional details on photogrammetry methods for the PFTB location were presented by Wood and others (2021, figure 1B).

The imagery for the photogrammetry was collected with two different digital cameras at two different times. The initial effort, in September 2014, targeted the upper section of the block because the lower part had not yet been revealed (Supplementary file: https://irma.nps.gov/ DataStore/Reference/Profile/2299562). This initial phase captured 92 images using a Nikon D800 35 mm digital, single reflex lens camera with a 28 mm f/2.4 prime lens (figure 3D). Horizontally and vertically spaced images were taken in a gridded pattern with the aid of a 7-m telescopic camera mast and a CamRanger remote triggering system. The mast was a "home-made" rig, comprised of an aluminum tree-saw pole with a swivel/tilt camera tripod head attached. The construction of the mast allowed the camera positions to change between landscape and portrait positions (rotated to 90° and 270°).

The lower portion of the PFTB was photographed in June 2015 by the first author after removal of the debris at the base of the block (Supplementary file: https:// irma.nps.gov/DataStore/Reference/Profile/2299562). This second phase captured 131 images using a Nikon CoolPix L110 with a fixed Nikkor 15X wide optical zoom VR (5.0–75.0 mm) lens. The lens zoom settings were set to emulate a 35 mm camera set for a 28 mm focal length to match the first-phase photographs. Handheld photography was completed with the camera rotated between landscape and portrait orientations.

Finally, photogrammetric images of the small cf.

Brasilichnium tracks on the MTL were taken in March 2023 by Conner Bennett using a Nikon D800 35 mm digital single reflex lens camera with a 28 mm f/2.4 prime lens. A total of 58 images were taken. Several 28 cm control sticks were used, calibrated to \pm 0.23 mm (Supplementary file: https://irma.nps.gov/DataStore/Reference/Profile/2299562).

Images were processed with the photogrammetry package PhotoScan (now known as MetaShape) v. 1.2.6 build 2834 by AGIsoft, LLC. Raw Nikon (.nef) images for the upper part were pre-processed for color, exposure, vignetting, and spherical aberration in Adobe Bridge as a batch process. Lens distortion was corrected as part of the photograph alignment and sparse-cloud processing with PhotoScan. Once the two sections of the PFTB were processed to dense cloud models, the two portions were merged within the software to create a uniform surface for the full 7-m-high, track-bearing surfaces (Supplementary file: https://irma.nps.gov/ DataStore/Reference/Profile/2299562). The model is internally scaled using control sticks of 30 and 50 cm lengths, calibrated to \pm 0.1 mm. Calibration for these scales was completed by comparing the distances between the printed targets with an ASTM certified ruler. The estimated error reported from the processing of the model is ± 0.4 mm, which instills high confidence in the fidelity of model feature measurements.

Both high-definition digital cinematography and high-resolution digital photography are essential elements to the future of monitoring paleontological sites. Digital documentation provides data for historical sideby-side and overlay comparisons of high-quality images and real-time footage (Wood and others, 2021). The collected images and footage can be used to monitor natural or man-made changes to sites, *in*cluding vandalism, theft, and erosion, for new and existing paleontological sites. Implementing digital technology is a vital and essential component for raising public awareness, minimizing impact, and preserving paleontological resources.

Measurements of Tracks and Trackways

Individual track measurements were recorded (after

Olsen and others, 1998; Farlow and others, 2018; figure 4A) including total track length, maximum track width, estimated track depth, estimated lengths of digits II, III, and IV, divarication angles between digits II to IV, II to III, and III to IV, anterior track length (ATL), anterior track width (ATW), and indication of symmetry (i.e., were tracks produced by left or right feet?).

Some of the aforementioned measurements could only be estimated because most footprints at the site are not exceptionally well preserved: following the 0-1-2-3 preservation scale established by Belvedere and Farlow (2016) and later modified by Marchetti and others (2019), tracks on the PFTB mostly score "1." Most tracks on the PFTB do not show digit pads; nearly all have been impacted by modern-day weathering (e.g., exfoliation) and have some form of lithic deformation, which is discussed in more detail below. Some Grallator tracks can be scored "2" because track outlines are sharp, and some toe pads can be discerned. Finally, two overlapping Batrachopus pedal tracks found at the site on a smaller float block we consider elite tracks, or "3" on the preservation scale. Consequently, most measurements taken for digit lengths, divarication angles, anterior triangle lengths, and anterior triangle widths are necessarily estimates.

In addition to individual track measurements, the following measurements were recorded for bipedal trackways (after Lockley, 1991; Farlow and others, 2018; figure 4B): pace, stride, pace angulation, trackway width, footprint rotation, and direction of travel.

Generally, trackway orientations are recorded using a compass when preserved in situ; however, on the PFTB, this could not be accomplished because the track surfaces are ex situ. Nevertheless, we were able to orient the estimated position of the block with the adjacent, *in* situ cliff, and we were able to estimate directions of travel.

Specific ichnological terminologies and definitions are used based on standards summarized by Marty and others (2016).

INSTITUTIONAL ABBREVIATIONS

ACM-ICH, "Appleton Cabinet," Beneski Museum

of Natural History (formerly Pratt Museum of Amherst College), Amherst, Massachusetts; GLCA, Glen Canyon National Recreation Area, Page, Arizona; SGDS, St. George Dinosaur Discovery Site at Johnson Farm, St. George, Utah; UCM, University of Colorado at Boulder, Boulder, Colorado; UCMP, University of California, Museum of Paleontology, Berkeley, California.

GEOLOGY

Stratigraphy

The Glen Canyon Group within GLCA is composed, in stratigraphic order from oldest to youngest, of the Wingate Sandstone, Kayenta Formation, and Navajo Sandstone. The Wingate Sandstone (about 75 m thick), which holds the Triassic-Jurassic boundary (in part, laterally equivalent to the Moenave Formation to the west and southwest), overlies the Upper Triassic Church Rock Member (or Rock Point Member of some authors) of the Chinle Formation (or Chinle Group of some authors). The Kayenta Formation overlies the Wingate, but it is thin (about 95 m thick) and sandy in GLCA compared to its siltier lithology in north-central Arizona and southwestern Utah, where it measures approximately 144 m and 305 to 320 m thick, respectively. Above the Kayenta Formation, the Navajo Sandstone ranges from 350 to 400 m thick; it is unconformably overlain by the Middle Jurassic Carmel Formation of the San Rafael Group within most of GLCA, and the Middle Jurassic Temple Cap Formation (formerly Page Sandstone) in the southern and western parts of the park (Doelling and others, 2013).

As in drainage basins during the Late Triassic through Early Jurassic, represented by the Chinle, Wingate Sandstone, Moenave, and Kayenta Formations, most river systems flowed from the southeast toward the northwest through the Navajo erg depositional basin (figure 5). The braided fluvial systems of the Kayenta Formation brought in massive accumulations of sand with increased aridity, leading to the formation of the Navajo erg (Blakey, 1994, 1996; Peterson, 1994; Bryant and Miall, 2010), the largest sand sea known in Earth history (Kocurek and Dott, 1983). The upper part of the Kayenta and lower Navajo Sandstone are both grada-

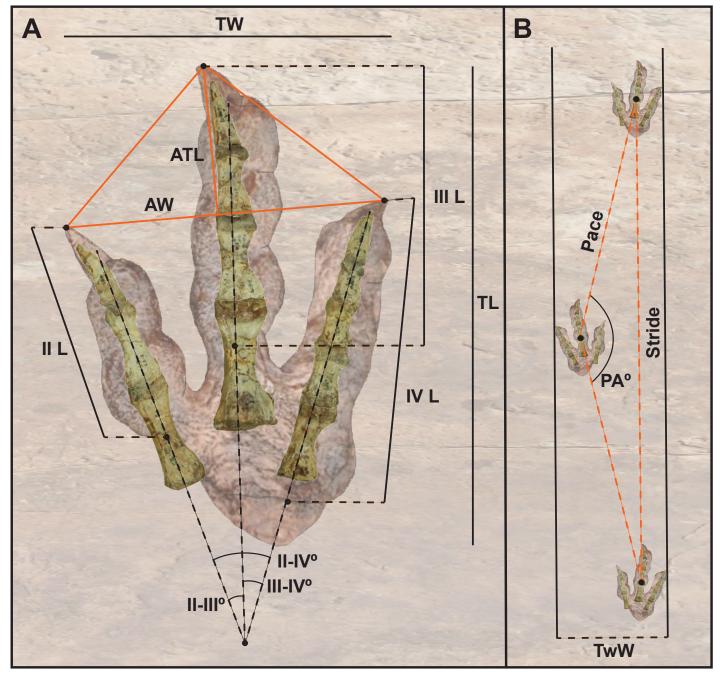
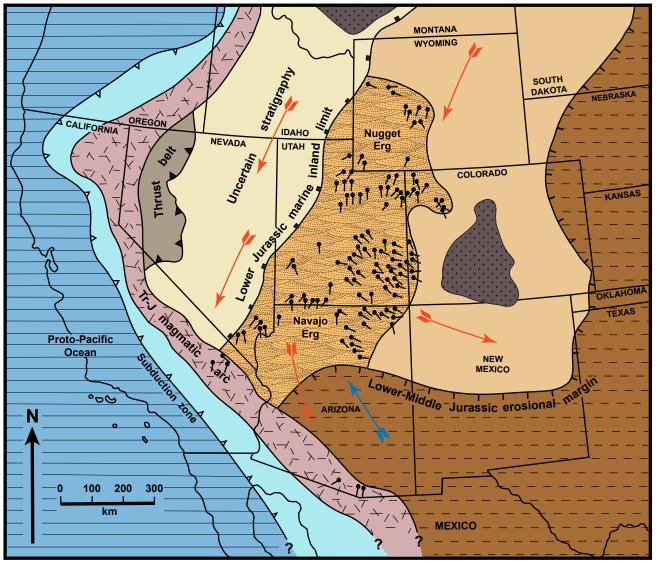


Figure 4. Track and trackway measurements taken. (A) Individual *Eubrontes* footprint showing measurements used in this paper. (B) Bipedal dinosaur trackway showing pace or step, stride, trackway width, and pace angulation. Modified from Lockley (1991). **II**, **III**, **IV** = digits; **II**–**III**° = divarication angle between digits II and III; **II**–**IV**° = divarication angle between digits II and IV; **III**–**IV**° = divarication angle between digits III and IV; **III** L = digit III length; **IV** L = digit IV length; **ATL** = anterior track length; **AW** = anterior track width; **PA**° = pace angulation; **TL** = total track length; **TW** = total track width.

tional and intertongue substantially with one another over large areas, and we observe this same interfingering between fluvial and eolian systems on a smaller scale within the vicinity of, and immediately below the PFTB. We follow other authors and refer to this sequence as the Kayenta–Navajo transition (Harshbarger and oth-

The John Wesley Powell Fossil Track Block—Theropod Tracks with Ornithopod-Like Morphology from the Early Jurassic Navajo Sandstone, Glen Canyon National Recreation Area, Utah-Arizona



Milner, A.R.C., Santucci, V.L., Wood, J.R., Birthisel, T.A. Clites, E., and Lockley, M.G.

Figure 5. Depositional and structural features during the Early Jurassic and onset of the Navajo erg. Tadpole symbols indicate location (dot) and average foreset dip directions (tails). Dark gray represents eroded basement rocks during the Early Jurassic. Red arrows indicate estimated wind directions based on sand dune data. Blue arrow represents predominant fluvial flow directions during Late Triassic-Early Jurassic (figure modified from Bryant and Miall, 2010, and Bryant and others, 2016; data after Blakey, 1994; Parrish and Peterson, 1988; Peterson, 1994; Dickinson and Gehrels, 2003).

ers, 1957; Middleton and Blakey, 1983; Sansom, 1992; Herries, 1993, Blakey, 1996; Lockley and others, 2014).

The Navajo Sandstone was deposited in a low-latitude erg that was situated on the western margin of Pangaea during the Early Jurassic (Pliensbachian-Toarcian; approximately 180 to 190 million years ago; Loope and others, 2001). Although uncommon, interdunal carbonate beds in the Navajo Sandstone, especially in south-central and southeastern Utah, are more prominent in the lower half of the formation (Marzolf, 1983), but these beds rarely measure greater than 1 m in thickness. These carbonate beds can span areas of over 1 km (Doelling and other, 1989; Stokes, 1991; Bryant and others, 2016), and many are made up of dolostone and cherty limestone deposited between dune sets along interdunal surfaces. Vertebrate tracks and invertebrate traces can be locally abundant on and within these interdunal carbonates. Additionally, stromatolites and

microbial mat surface are quite common in some areas, *including many localities within GLCA*.

Sedimentology

The track-bearing horizons at the PFTB are in the lower part of the Navajo Sandstone, approximately 15.8 m above the conformable contact between the "sandy facies" of the Kayenta Formation and Navajo Sandstone (figure 6A). Due to rough terrain, vegetation, and poor exposures, a "clean" stratigraphic section had to be measured several hundred meters to the south of the PFTB locality where the Kayenta–Navajo transition could be observed up to a traceable, laterally extensive interdunal/paleoerosional parting ("crack") extending between both sites (figure 6A).

Three additional sections were measured at the PFTB locality: (1) the in situ cliff face adjacent to the PFTB (figures 6B and 6C); (2) the south side of the PFTB (figure 6D); and (3) the north side of the PFTB (figure 6E). All three of these short sections have nearly identical stratigraphic features that can easily be correlated with one another.

The wavy-laminated beds preserving the tracks within the cliff (figures 6B and 6C) compare well with measurements taken from both sides of the PFTB (figures 6D and 6E): in the cliff, the thickness from the base of a dark brown, oxidized unit to the bottom of the track-bearing unit measures 1.86 m. Another oxidized, brown bed below the wavy-laminated track-bearing unit is about 30 cm thick and is composed of poorly sorted, fine-grained sandstone nearly identical to the cross-bedded layers below it that are dune sequences.

The section measured on the south side of the PFTB comprises lower wavy-laminated beds; middle massive beds; and upper thick, planar-laminated beds (figure 6D). The thinner track-bearing beds pinch out toward the top of the block, and similar sets of sandstones were observed in situ within the cliff next to the PFTB (figures 6B and 6C). Whereas wavy-laminated beds, as well as localized chert and carbonate beds, are present in a laterally traceable layer continuing for several hundred meters to the north (figures 7B through 7D) and south of the PFTB in the cliff, the thickest parts of these beds

are found in situ near the PFTB.

The stratigraphic section measured on the north side of the PFTB is 5.25 m thick (figure 6E). The main track-bearing surface lies at the base of the section, starting with approximately 0.5 m of wavy, fine- to very fine, well-cemented sandstone. We recognize three track horizons located on some of these carbonate-rich, wavy-laminated surfaces, which are stromatolitic (figures 6F, 6G, and 7B). Microbial mats certainly were present when animals walked across the surfaces judging from the pitted texture of the MTL, as well as some other horizons. Above the MTL is approximately 25 cm of massive to poorly laminated, coarse-grained sandstone that shows evidence of soft-sediment deformation. An additional 25 cm of finely laminated, medium-grained sandstone that is oxidized to a dark brown are followed by about 4 m of planar-laminated, fine to very fine sandstone making up the lower part of a dune sequence. Float blocks between the exposed track surfaces of the PFTB and the cliff face mostly pertain to additional beds that were present below the MTL.

The wavy-laminated beds bearing the tracks formed during a time of wet conditions in which substantial water, either a rise in the water table during a wet season and/or during a monsoon season (Loope and others, 2001), would have been able to accumulate and pool on flats between dunes (i.e., *in*terdunal playas). The resulting carbonate-rich beds commonly preserve microbial laminates and even large stromatolites at some localities (Eisenberg, 2003; Parrish and Falcon-Lang, 2007; Dorney, 2009; Dorney and Parrish, 2009; Chure and others, 2014; Parrish and others, 2017).

Although some parts of the PFTB surfaces are heavily weathered, the majority is well-preserved, exhibiting sedimentary structures such as small mudcracks (figure 8A), and the aforementioned pitted, rugose texture likely formed by microbial mats. Branching horizontal structures that may represent poorly preserved invertebrate grazing trails, and unidentified larger, mudcrack-like structures were also observed and mapped (figure 8B), but we have not been able to definitively identify any of these sedimentary structures with confidence.

Additionally, several float blocks contain invertebrate burrows, but their exact stratigraphic positions

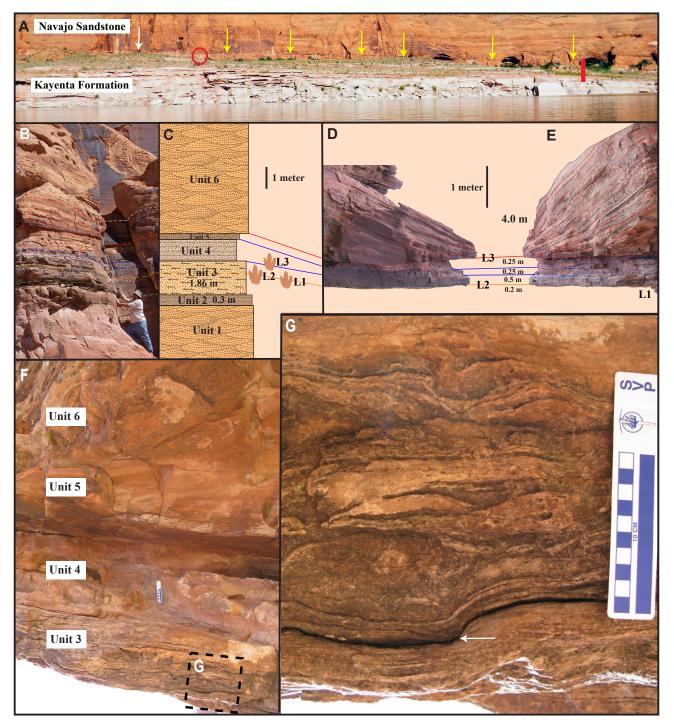


Figure 6. Stratigraphy and lithology of the John Wesley Powell Fossil Track Block (PTFB). (A) View of PFTB location (red circle) from the lake looking east. Red line indicates where stratigraphic section was measured to determine distance above the Kayenta–Navajo contact; yellow arrows point to interdunal surface that traces to the top of the main track-bearing, stromatolitic beds; the white arrow points to northern exposure of track beds north of the PFTB. (B) In situ cliff adjacent to PFTB. (C) Corresponding stratigraphic section of in situ cliff (B), and comparison with the PFTB (in D and E). Track-bearing layers are designated L1–L3. (D) Stratigraphy of the south side of the PFTB. (E) Stratigraphy on the north side of the PFTB. (F) Close-up of distinct units on north side of PFTB. Dashed box indicates area shown in G. (G) Close-up of track-bearing, stromatolitic, wavy laminated carbonate-rich sandstone beds. White arrow points to possible track in cross section.



Figure 7. (A) Medium-grained, stromatolitic sandstones bearing *Grallator* tracks in track layer 1 (see figure 6 for the position of this layer), the oldest tracks identified at the John Wesley Powell Fossil Track Block (PTFB). (B) In situ track-bearing stromatolitic beds with cherty layers immediately below, located north of the PFTB. (C) Another track surface in situ north of the PFTB. White arrow points to tracksite surface under overhang. (D) Close-up of overhang in C; white arrows point to in situ natural cast tracks; red arrows point to unidentified sedimentary structures.

below the track-bearing surfaces are uncertain. These back-filled burrows resemble *Taenidium barretti* (figure 8C; see Keighley and Pickerill, 1994; Matt Stimson, New Brunswick Museum, personal communication, 2022).

Structural fractures, which are aligned approximately 90° to larger scale joint orientations, can be recognized on the track block surface. Using the orientations of joint and fracture trends in the approximate location of the rockfall, and because the orientation of joints and varying stratigraphy from one side of the block to the other, we can safely estimate the in situ position of the PFTB, thereby allowing us to also estimate travel orientations of track producers (figure 2B, *in*set).

PALEONTOLOGICAL DESCRIPTION OF THE POWELL FOSSIL TRACK BLOCK

A total of 104 footprints were observed on the main track block itself, preserved on at least three track horizons (figures 2 and 6C). Tracks indicate a moderately

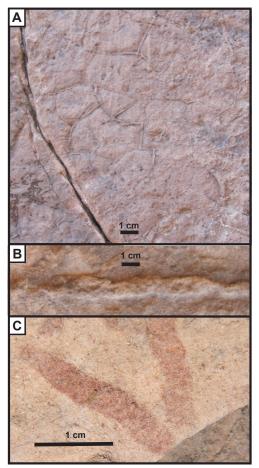


Figure 8. Sedimentary structures on the main track surface of the John Wesley Powell Fossil Track Block (PTFB). (A) Small mudcracks and possible horizontal, branching burrows. (B) Large, rope-like structures that could be mudcracks. (C) Back-filled invertebrate burrows (cf. *Taenidium barretti*) found in float between the PFTB and cliff where the block originated.

diverse ichnofauna including three to four theropod dinosaur size groups, crocodylomorphs, and possible cynodont synapsids.

Grallator and Grallator-Like Tracks (Figures 9 and 10, Tables 1 to 3)

We identify small tracks and trackways of bipedal theropods from the PFTB as *Grallator* (Hitchcock, 1858) or *Grallator*-like because of their size, general outline, and trackway configuration. *Grallator* is the most abundant track type at the PFTB, with a total of 49 individual tracks, 22 of which are within three distinct trackways. These small theropod footprints range from 4.5 to 22 cm in length and 4.0 to 12.5 cm in width, and average 13.3 cm long and 9.2 cm wide (table 1).

Grallator trackway T5 (figures 2B, 9A, and 9B, tables 1 and 2) comprises 10 footprints, starts near the middle of the PFTB, and ends in the upper right corner. The trackway shows a very slight left turn where the animal changed its pace and stride: the first three footprints following the turn (T5-4 to T5-6) have shorter stride and wider pace angulation values (i.e., minimum of 62.5 cm and average of 122.3°) followed by longer stride and narrower pace angulation values (averaging 75.1 cm and 166.3°) nearly identical to those displayed prior to the direction change. This individual was travelling toward the northeast. The best preserved footprint in this trackway is T5-10, which is a left print (figure 10A).

Grallator trackway T7 was traveling toward the north, opposite to the direction of *Eubrontes* trackway T1 (figures 2B, 9C, and 9D) and at a later time than *Eubrontes* T1 because T7-3 overprints T1-3, and T7-4 overprints the displacement rim of T1-2. T7 is one of the smallest theropod trackways preserved on the PFTB, having an average footprint length of 12 cm and width of 7.4 cm. The best-preserved print in this trackway is T7-4, a right track with some indication of a 2-3-4 toe pad arrangement, as is typical for *Grallator*, visible in the photogrammetric images (figure 10B). Trackway T7 has an average stride of 140 cm, an average trackway width of 13.4 cm, and an average pace angulation of 172° (table 2).

Grallator-like trackway T36 consists of only two poorly preserved tracks that average 21.8 cm long and 9.7 cm wide (figure 2B; table 1). The lengths of these tracks may have been exaggerated by metatarsal traces, but this cannot be confirmed due to poor preservation.

Grallator tracks on the MTL of the PFTB, *in*cluding those of trackway T7, are "inflated" or "expanded" in a similar way to those of the larger theropod tracks, though not as exaggerated. Examples of this "inflation" include the distal end of the trace of digit II in track T7-4 (figure 10B), isolated left track T12 (figure 10E), and left track T7-1 (figure 10C); the latter has an identifiable *Grallator* shape, but the distal end of the trace of digit II is missing, and the intersection between the The John Wesley Powell Fossil Track Block—Theropod Tracks with Ornithopod-Like Morphology from the Early Jurassic Navajo Sandstone, Glen Canyon National Recreation Area, Utah-Arizona

Milner, A.R.C., Santucci, V.L., Wood, J.R., Birthisel, T.A. Clites, E., and Lockley, M.G.

Track #	Sym.	TL	TW	ATL	ATW	Digit II L	Digit III L	Digit IV L	II-IVº	II-IIIº	III-IVº	TD
T 5-1	Right	13.0	9.8	5.5	7.8	5.9	12.0	8.3	40	26	14	N/A
T 5-2	Left	11.5	10.5	4.4	8.7	6.0	10.5	9.5	50	22	28	N/A
T 5-3	Right	10.5	8.6	4.6	8.4	—	_	—	83	41	43	N/A
T 5-4	Left	9.2	7.7	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 5-5	Right	13.2	8.3	N/A	7.1	N/A	N/A	N/A	44	20	25	N/A
T 5-6	Left	13.5	10.7	6.2	8.1	7.5	12.5	9.6	N/A	N/A	N/A	N/A
T 5-7	Right	13.0	11.0	6.4	9.5	7.5	12.3	9.5	N/A	23	N/A	N/A
T 5-8	Left	13.4	11.0	N/A	8.6	N/A	N/A	N/A	46	28	18	N/A
Т 5-9	Right	16.0	11.5	6.4	8.6	7.9	15.0	10.0	69	34	37	N/A
T 5-10	Left	13.6	10.7	6.1	9.1	6.4	12.5	8.6	45	18	27	N/A
Avg.		12.7	10.0	5.7	8.4	6.9	12.5	9.3	54	27	27	N/A
T 7-1	Left	12.8	7.6	5.9	6.7	5.7	11.5	8.0	50	25	25	1.0
T 7-2	Right	12.2	7.6	N/A	5.9	N/A	N/A	N/A	46	26	20	2.5
T 7-3	Left	12.1	6.5	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	2.0
T 7-4	Right	11.7	7.6	4.2	6.0	7.1	10.1	8.6	47	26	21	0.5
T 7-5	Left	11.0	7.8	N/A	N/A	N/A	N/A	N/A	41	29	15	N/A
Avg.		12.0	7.4	5.1	6.2	6.4	10.8	8.3	46	27	20	1.5
T 38-1	N/A	23.5	9.6	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 38-2	N/A	20.1	9.7	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Avg.		20.1	9.7 9.7	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 9	Right	16.0	10.9	6.5	8.7	8.0	14.0	9.5	59	31	28	~0.5
T 10	Right	15.3	10.9	6.8	8.9	6.5	14.0	9.3	55	26	28	N/A
	-											
T 12	Left	15.0	9.5	7.0	8.8	7.5	12.5	9.3	50	26	24	1.0
T 13	Right	14.1	8.4	5.2	6.9	8.8	12.8	9.0	47	24	23	N/A
T 14	Right	12.4	7.9	4.5	6.7	6.5	10.3	10.7	33	19	14	N/A
T 15	Left?	12.0	11.0	5.8	8.5	N/A	N/A	N/A	64	28	34	1.0
T 16	Left?	14.0	12.6	6.3	10.1	N/A	N/A	N/A	58	29	33	1.0
T 17	Right	9.7	6.0	3.5	6.0	3.9	9.2	6.3	48	28	24	N/A
T 18	N/A	12.4	11.5	4.7	7.9	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 19	N/A	12.0	11.5	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 20	Left	8.9	5.3	3.5	4.7	3.8	7.1	5.0	33	20	14	N/A
T 21	Right?	12.4	7.3	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 22	N/A	8.5	6.6	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 23	N/A	8.7	7.3	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 24	Right	14.3	10.5	5.5	7.7	6.2	11.4	11.5	63	24	40	N/A
T 25	N/A	9.5	7.9	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 26	Left	11.5	7.8	4.6	4.9	5.4	10.0	7.4	30	12	18	N/A
T 27	Right	16.0	10.0	6.3	7.8	7.4	13.3	9.5	35	13	21	N/A
T 28	NA	4.5	4.0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 29	Left	17.4	12.5	5.5	11.8	10.3	14.0	12.5	49	29	23	N/A
T30	N/A	22.0	12.5	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 31	Right?	12.0	8.9	4.8	8.6	6.2	10.2	7.8	63	35	38	N/A
T 32	Left	16.0	12.5	7.0	11.0	8.3	15.5	12.5	47	19	28	N/A
T 35	Left	16.5	10.5	8.3	7.0	8.5	15.0	10.5	N/A	N/A	N/A	N/A
T 36	N/A	9.9	6.5	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
T 37	Right	11.6	9.5	6.5	7.0	N/A	N/A	N/A	57	36	21	N/A
T 40	Right?	16.5	10.9	7.6	10.6	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Table 1 caption is on the next page.

Table 1 is on the previous page. Measurements (cm) of 44 individual *Grallator* tracks on the main track layer of the John Wesley Powell Fossil Track Block. ATL = anterior triangle length; ATW = anterior triangle width; Avg. = average; Digit II, III, and IV L = digit II, III, and IV lengths; II–IV, II–III, and III–IV = divarication angles between digits II–IV, II–III, and III–IV; N/A = no data; Sym. = symmetry (i.e., left or right tracks); TD = track depth; TL = track length; TW = track width.

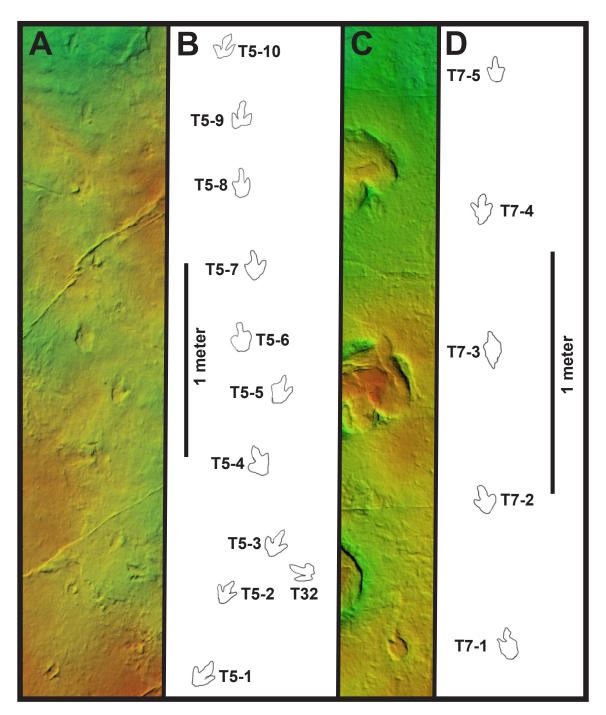


Figure 9. *Grallator* trackways on the John Wesley Powell Fossil Track Block (PFTB). (A–B) Inverted trackway T5, which shows a change in pace/stride of the trackmaker due to very slight change in travel direction: (A) photogrammetry, (B) interpretive map of trackway. (C–D) Natural cast trackway 7: (C) photogrammetry, (D) interpretive map of trackway.

, , ,		1	1					
Track #	Sym.	PL	SL	PA°	TW	FR		
T 5-1	Right	N/A	N/A	N/A	N/A	N/A		
Т 5-2	Left	44.0	80.1	154	20.2	N/A		
Т 5-3	Right	38.5	72.0	112	29.8	N/A		
Т 5-4	Left	48.0	79.0	135	21.5	N/A		
Т 5-5	Right	38.0	62.5	120	27.7	N/A		
Т 5-6	Left	34.5	73.5	143	26.2	N/A		
Т 5-7	Right	37.0	73.0	167	18.3	N/A		
Т 5-8	Left	37.0	76.5	169	17.4	N/A		
Т 5-9	Right	42.0	77.5	163	16.9	N/A		
Т 5-10	Left	36.7	N/A	N/A	N/A	N/A		
Average		39.5	74.3	145	22.3	N/A		
Т 7-1	Left	N/A	N/A	N/A	N/A	N/A		
Т 7-2	Right	62.8	145.0	174	14.8	9		
Т 7-3	Left	62.9	140.0	167	12.6	5		
Т 7-4	Right	58.1	135.0	175	12.8	4		
Т 7-5	Left	59.5	N/A	N/A	N/A	N/A		
Average		60.8	140.0	172	13.4	6		

Table 2. Two *Grallator* trackway measurements (cm) on the main track layer of the John Wesley Powell Fossil Track Block. FR = footprint rotation; N/A = no data; PA = pace angle; PL = pace length; SL = stride length; Sym. = symmetry; TW = trackway width.

traces of digits II and III is not visible. This print was underlain by a thicker layer of sand, and its "inflated" morphology possibly is a result of the transfer of sticky, sandy sediment from one foot strike to the next.

Better preserved *Grallator* tracks on surfaces directly below the MTL (Track Layer 1; figure 10D) exhibit more typical overall shapes for *Grallator* than many of those on the MTL. Only a few theropod tracks were identified during the excavation of float slabs in front of the PFTB, all of which pertain to *Grallator*.

Several *Grallator* tracks on the youngest track surface preserved on the right side of the PFTB have a lower quality of preservation due to dinoturbation and significant erosion of the exposed parts of the tracksite. For these reasons, many of the tracks on this surface cannot be properly identified. A total of ten tracks have been identified as *Grallator* and have length and width ranges between 10.2 to 19.7 cm and 5.9 to 17.6 cm, respectively (table 3).

Grallator tracks from the Navajo Sandstone would

have been produced by contemporaneous, small, coelophysid-like theropods, such as *Segisaurus halli*, which is known only from the Navajo Sandstone of northern Arizona (Camp, 1936; Carrano and others, 2005).

Medium-Sized Tridactyl cf. *Kayentapus* Tracks (Figure 11; Tables 4 and 5)

Medium-sized theropod tracks on the MTL comprise two trackways (T4 and T6) and a single isolated track (T8) (figure 2B). T4 consists of six footprints with average pace and strides of 85.9 and 173.3 cm (table 5). The maximum trackway width is 27.4 cm and pace angulation of approximately 164°. Individual tracks in T4 have an average length and width of 24.8 and 18.5 cm, respectively (table 4).

Trackway T6 (figures 2B and 11) is made up of eight footprints, but T6-6 is nearly unrecognizable, represented only by an elongate mound. Tracks in this trackway have an average length and width of 21.9 cm and 16.7

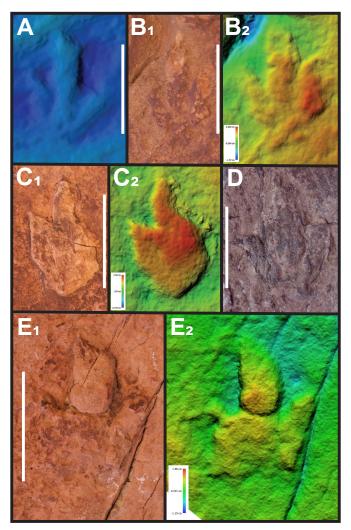


Figure 10. Natural cast *Grallator* tracks on the John Wesley Powell Fossil Track Block (PFTB). (A) Close-up photogrammetry of left natural cast track T5-10. (B₁) Photograph of T7-4 and (B₂) photogrammetry of T7-4. (C₁) Photograph of T7-1 and (C₂) photogrammetry of T7-1. (D) *Grallator* natural cast track from oldest PFTB track surface. (E₁) Photograph of isolated *Grallator* track T12 and (E₂) photogrammetry of T12. All scale bars = 10 cm.

cm, respectively. The average divarication angles between the traces of digits II–IV in T4 and T6 are 51° and 40°, respectively. Like the holotype tracks of *Kayentapus hopii* (UCMP 83668; figure 15C), the PFTB tracks are strongly mesaxonic, with an estimated anterior triangle length compared to entire track length of 40% in the holotype, whereas for PFTB tracks in trackway T4 is 40% and T6 is 38%. Finally, the pace angulation of the holotype trackway is narrow at approximately 174 to 175° (Welles, 1971), which is close to those of PFTB trackways T4 and T6 that average 164° and 170°.

The PFTB cf. Kayentapus tracks bear some morphological similarities to those in the holotype trackway of Kayentapus from the Kayenta Formation near Tuba City, Navajo Nation, Arizona (Welles, 1971; Lockley and others, 2011); our tentativeness in firmly assigning the PFTB tracks to Kayentapus stems from the lower quality of preservation of tracks at the PTFB (i.e., lacking toe pads) and deformation/inflation (expansion) of the digit traces. Additionally, the divarication angles between traces of digits II-IV across the tracks in T6 are consistently lower by about 10° than those in the holotype trackway. The holotype tracks were identified as "slight" undertracks by Lockley and others (2011, p. 333), as is our interpretation of the PFTB tracks. Several authors have suggested that Kayentapus is a junior synonym of Eubrontes and that its apparent morphological distinction is due to the poor preservation of the holotype tracks (Rainforth, 2005; Lucas and others, 2006). Paul Olsen (Columbia University, personal communication, 2017) suggested that Kayentapus tracks are partially penetrative Eubrontes tracks, and that the partial penetration splayed the digits, resulting in wider divarication angles, and gave the digits a narrower appearance. This may be partially true, but the holotype tracks of Kayentapus are shallow and not penetrative, and many examples of clear Eubrontes exist that are also partial or fully penetrative in a variety of substrates. Despite these concerns, many still consider Kayentapus valid (Lockley and Hunt, 1995; Gierliński, 1996; Piubelli and others, 2005; Weems, 2006 and many citations therein; Lockley, 2009; Xing and others, 2020; Lockley and others, 2011; Farlow and others, 2018).

Medium-sized theropod tracks on the MTL superficially resemble *Kayentapus*, so we refer to them here as cf. *Kayentapus*. However, aside from these tracks having larger sizes than the above-mentioned *Grallator* and *Grallator*-like tracks, the anterior track length/track length ratios and divarications angles between digits II-IV do not differ significantly between all these footprint categories. Therefore, the cf. *Kayentapus* could be considered large cf. *Grallator* tracks as well. A thorough

Table 3. Ten Grallator-like individual track measurements (cm) from uppermost track horizon on the John Wesley Powell
Fossil Track Block. ATL = anterior triangle length; ATW = anterior triangle width; Avg. = average; Digit II, III, and IV L =
digit II, III, and IV lengths; II–IV, II–III, and III–IV = divarication angles between digits II–IV, II–III, and III–IV; N/A = no
data; Sym. = symmetry (i.e., left or right tracks); TD = track depth; TL = track length; TW = track width.

Track #	Sym.	TL	TW	ATL	ATW	Digit II L	Digit III L	Digit IV L	II-IVº	II-IIIº	III-IVº
L1	Right	10.2	5.9	4.6	4.6	3.5	6.6	6.2	50.0	25.0	25.0
L2	N/A	16.5 (18)	11.3	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
L3	Right	17.6	13.8	5.5	9.5	11.5	11.7	12.6	48.0	30.0	18.0
L4	Left	23.7	15.8	9.8	11.0	10.0	18.3	16.6	59.0	42.0	18.0
L5	Left?	11.3	8.5	5.0	5.9	N/A	N/A	N/A	N/A	N/A	N/A
L6	Right?	19.7	17.6	6.8	13.4	N/A	N/A	N/A	N/A	N/A	N/A
L7	Right?	17.7	10.5	8.8	8.6	N/A	N/A	N/A	N/A	N/A	N/A
L8	N/A	16.0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
L9	N/A	17.0	7.7	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
L10	N/A	17.5	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

differentiation between *Kayentapus* and *Grallator* (and *Anchisauripus*) is beyond the scope of this report.

No potential trackmakers of the size required to make the cf. *Kayentapus* tracks are known currently from body fossils from the Navajo Sandstone; however, *Dilophosaurus* was found near the *Kayentapus* type locality, so juveniles or subadults of this larger taxon could have been the trackmaker (Welles, 1954, 1970, 1984; Marsh and Rowe, 2020).

Eubrontes (A.K.A., "Ornithopod-Like Tracks") (Figures 12 and 14; Tables 6 and 7)

By far the most prominent and eye-catching footprints on the PFTB are the two parallel, "ornithopod-like" natural cast trackways arranged horizontally across the MTL (T1 and T2; figures 2, 12, and 13). A third trackway (T3) only preserves two footprints (figures 2B and 14A through 14G). These three trackways, produced by large bipedal dinosaurs, have average track lengths of 34.3, 34.5, and 35.8 cm, respectively. The average widths are 35.2, 32.1, and 37.5 cm (table 6), respectively. After close examination of these tracks, and through the use of photogrammetry, we agree with Lockley and Xing

(2015) that these tracks pertain to *Eubrontes*. Although the overall track morphologies, which display "inflated" digit traces and exaggerated track widths, are "ornithopod-like," we propose that these footprints may not be distorted solely by sediment load compaction and deformation following lithification. The deformation of muddy, and potentially spongy microbial mats and/or endoevaporitic substrates by the feet will often produce steep-walled mud rims around the footprints, as seen in trackways T1 and T2 (figures 12 and 13). Additionally, the transfer of wet, sticky substrate from one track to the next into successive tracks may also be a contributing factor to the "bulkiness" of the digit impressions. Also, overgrowth of microbial mats into and over tracks following their formation could have occurred, further distorting the footprints and distorting overall track morphology (Marty and others, 2009). Studies of modern bird tracks (emus and domestic chickens) through controlled experimentation also show incredible variations in track preservation from poor to exceptional based on sediment type and quantities (i.e., percentages of different sediment types such as clay and sand), as well as water content or lack thereof (Milàn, 2006; Falk and others, 2017; Farlow and others, 2018). Farlow and others (2018, p. 166) even suggest how a theropod foot

Table 4. Measurements (cm) of 15 *Kayentapus*-like individual theropod tracks on the John Wesley Powell Fossil Track Block. **ATL** = anterior triangle length; **ATW** = anterior triangle width; **Avg.** = average; **Digit II, III, and IV L** = digit II, III, and IV lengths; **II–IV, II–III, and III–IV** = divarication angles between digits II–IV, II–III, and III–IV; **N/A** = no data; Sym. = symmetry (i.e., left or right tracks); **TL** = track length; **TW** = track width.

Track #	Sym.	TL	TW	ATL	ATW	Digit II L	Digit III L	Digit IV L	II-IVº	II-IIIº	III-IV°
T 4-1	Left	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Т 4-2	Right	25.0	17.5	N/A	N/A	N/A	N/A	N/A	53	27	26
Т 4-3	Left	22.5	18.5	8.8	13.4	12.0	21.2	16.5	60	28	32
T 4-4	Right	28.0	20.0	10.6	15.0	13.5	22.5	19.0	N/A	N/A	N/A
Т 4-5	Left	26.0	17.5	11.3	15.6	12.5	24.5	16.5	45	22	23
Т 4-6	Right	22.5	19.0	8.7	15.9	14.5	17.5	14.2	44	24	20
Avg.	_	24.8	18.5	9.9	15.0	13.1	21.4	16.6	51	25	25
T 6-1	Right	20.0	16.2	9.0	15.0	12.5	17.5	11.7	32	18	16
Т 6-2	Left	22.5	17.2	7.5	14.3	17.0	20.0	12.5	38	18	20
Т 6-3	Right	22.5	17.0	9.0	16.1	11.5	18.5	14.5	44	21	23
T 6-4	Left	22.0	15.5	N/A	N/A	N/A	N/A	N/A	49	22	27
Т 6-5	Right	21.0	16.2	7.9	14.5	12.5	20.5	14.2	39	24	15
Т 6-6	Left	18.5	16	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Т 6-7	Right	21.8	17.0	7.3	15.0	12.9	19.4	17.0	67	34	33
Т 6-8	Left	23.5	16.5	8.3	14.5	15.0	20.5	16.5	57	38	19
Avg.	—	21.9	16.7	8.2	14.9	13.6	19.4	14.4	47	25	22
Т 8	Right	22.5	18.0	8.0	15.2	13.8	18.7	15.8	40	21	19

interacting with the right substrate conditions could produce a footprint that is ornithopod-like, especially if the main sediment was a sand with lower water content resulting in sediment collapse into the track. So, rather than ornithopod-like dinosaurs being the track producers at the PFTB, more likely the producers were medium-sized theropods similar in size to *Dilophosaurus*, which is known from the underlying Kayenta Formation of north-central Arizona and possibly Utah (Welles, 1954, 1970, 1984; Madsen and others, 2012; Marsh and Rowe, 2020).

In T1, the trackway width is approximately 42 cm wide from footprints T1-1 to T1-3, and about 43 cm wide from T1-5 to T1-7. However, at T1-4, the trackway width expands to 53 cm. Also, at T1-4, the foot rotation increased, and the animal toed out with the left foot as the pace angulation decreases by a couple of degrees toward the right between footprints T1-4 and T1-5. We

speculate that this slight alteration was due to slippage and/or a reaction to sediment consistency. Deformation on the outside edge of T1-4 track wall is marked by an unidentified, subrectangular, poorly preserved track (cf. *Grallator*; figure 12). Trackway T1 preserves seven footprints with average pace and strides of 87.1 and 170.0 cm, respectively (table 7). The maximum trackway width is 47.6 cm, and the average pace angulation is approximately 167°.

In trackway T2 (figures 2 and 13), track T2-5 displays an elongated and tapered digit III trace, and traces of digits II and IV are not as rounded and do not divaricate as widely like those in the preceding footprints in this trackway. Tracks T2-1 to T2-4 look more like those in T1 (figures 2 and 13), whereas T2-4 preserves a sharp claw mark on the trace of digit III that is only visible through the use of photogrammetry. An elongated digit III trace and the presence of sharp claws would be exThe John Wesley Powell Fossil Track Block—Theropod Tracks with Ornithopod-Like Morphology from the Early Jurassic Navajo Sandstone, Glen Canyon National Recreation Area, Utah-Arizona

Milner, A.R.C., Santucci, V.L., Wood, J.R., Birthisel, T.A. Clites, E., and Lockley, M.G.

Table 5. Kayentapus-like trackway T4 and T6 measurements (cm) on the main track layer of the John Wesley Powell Fossil
Track Block. Avg. = Average; FR = footprint rotation; N/A = no data; PA = pace angle; PL = pace length; SL = stride length;
Sym. = symmetry; TW = trackway width.

Track #	Sym.	PL	SL	PA°	TW	FR
T 4-1	Left	N/A	N/A	N/A	N/A	N/A
Т 4-2	Right	96.0	183.0	160	N/A	11
Т 4-3	Left	93.0	172.0	165	23.8	11
Т 4-4	Right	81.0	160.0	162	28.4	N/A
Т 4-5	Left	78.0	158.0	170	30.1	N/A
T 4-6	Right	81.5	N/A	N/A	N/A	N/A
Avg.		85.9	173.3	164	27.4	11
T 6-1	Right	N/A	N/A	N/A	N/A	N/A
Т 6-2	Left	78.0	149.0	172	20.8	0
Т 6-3	Right	70.8	139.0	161	26.2	12
Т 6-4	Left	68.8	136.0	172	20.7	0
Т 6-5	Right	67.7	126.0	172	N/A	0
T 6-6	Left	57.8	137.0	175	N/A	N/A
T 6-7	Right	83.3	125.0	N/A	N/A	0
T 6-8	Left	62.5	N/A	N/A	N/A	N/A
Avg.		69.8	135.3	170	22.6	2

pected of theropod tracks. Trackway T2 consists of five tracks with average pace and strides of 88.4 and 173.3 cm (table 7). The maximum trackway width is 57.1 cm, and the average pace angulation is approximately 159°.

The first footprint in T3 (T3-1) is a left track, although it is not well preserved (figure 14). T3-1 and T3-2 have track lengths of 35.5 and 33.0 cm, and widths of 26.5 and 27.0 cm, respectively (table 6). Like those of T1 and T2, both tracks in T3 appear ornithopod-like, although T3-1 has a clear, sharp claw impression preserved on digit II, and track T3-2 has a sharp claw mark on digit III. Both of these tracks are also narrower than all of the footprints of T1 and T2, with the exception of T2-5. Like tracks T2-4 and T2-5, the presence of sharp claws in narrower tracks strongly suggests that they were made by theropod dinosaurs, and the unusual, inflated morphology is likely the result of sediment compaction (Lockley and Xing, 2015), weathering, and/or sediment consistency as mentioned above, and discussed in more detail below. The step between these two tracks is 100

cm (table 7).

The common orientation and lack of overlap of the two longer trackways, T1 and T2, suggests possible gregarious behavior by the trackmakers (Hamblin and others, 2006; Lockley and others, 2006; Getty and others, 2015). Such social behavior is well-established for later ornithischian dinosaurs from both body fossil and track records, but not for Early Jurassic ornithischians based on tracks such as Anomoepus (but see Olsen and Rainforth [2003] for a contrary perspective). Gregarious behavior has been well documented in Early Jurassic theropods, however (Ostrom, 1972; Raath, 1977; Colbert, 1989; Currie, 1993; Lockley and Matsukawa, 1999; Hamblin and others, 2006; Lockley and others, 2006; Milner and others, 2006; Currie and Eberth, 2010). In fact, theropod dinosaurs in general, throughout their existence from the Late Triassic to the Late Cretaceous, show strong evidence of at least occasional gregarious behaviors (Hitchcock, 1836; Hamblin and others, 2006; Lockley and others, 2006), although some tracksites

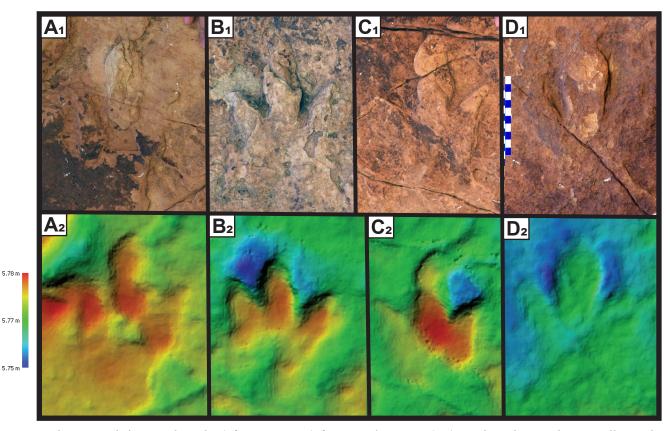


Figure 11. Medium-sized theropod tracks (cf. *Kayentapus*) from trackway six (T6) on the John Wesley Powell Fossil Track Block (PFTB) shown as photographs (above) and color contour photogrammetry images (below): (A_{1-2}) T6-1, (B_{1-2}) T6-2, (C_{1-2}) T6-3, (D_{1-2}) T6-7. Scale = 10 cm for all pictures. Contour color relief to left of box.

from the Newark Supergroup of eastern North America do not support this claim (Getty and others, 2015).

Early Jurassic ornithischian trackways, such as those of *Anomoepus* and *Moyenisauropus*, show the trace of pedal digit III toeing inward; occasionally, these trackways also include manus impressions (Lockley and Gierliński, 2006; Wilson and others, 2009; Milner and others, 2012, figure 58). The tracks in T1 have digit III traces either parallel with the trackway axis or toeing outward slightly, a characteristic more indicative of a saurischian than an ornithischian trackmaker (Day and others, 2002; Lockley, 2003), although examples do exist of theropods toeing inward (Day and others, 2002).

Additional support for the interpretation of a *Eubrontes* affinity for trackways T1, T2, and T3 is based upon mesaxony, which by two-dimensional ichnological definition (Lockley, 2009; Romano and others, 2018) measures the general proportionality of the greater dis-

tal projection of digit III anterior to the distal tips of digits II and IV (a.k.a., toe extension), as measured by the shape of the anterior triangle (Olsen, 1980). Mesaxony has been used by many authors in morphometric analysis of theropod tracks (e.g., Weems, 1992; Lockley and others, 2014, p. 174; Farlow and others, 2018; Abrahams and others, 2022). Anterior triangles that are strongly mesaxonic, meaning that they have digit III impressions that project well beyond the distal ends of the traces of digits II and IV (Lockley, 2009), show that the shape difference of the anterior triangle has a consistent relationship to overall track shape (length/width ratio), and is not simply the result of variation in digit divarication angles, which is often extramorphologically controlled by substrate consistencies (Lockley and others, 2014).

The natural cast holotype *Eubrontes giganteus* (ACM-ICH-15/3; figure 15A) from the Early Jurassic Portland Formation of Holyoke, Massachusetts, has a

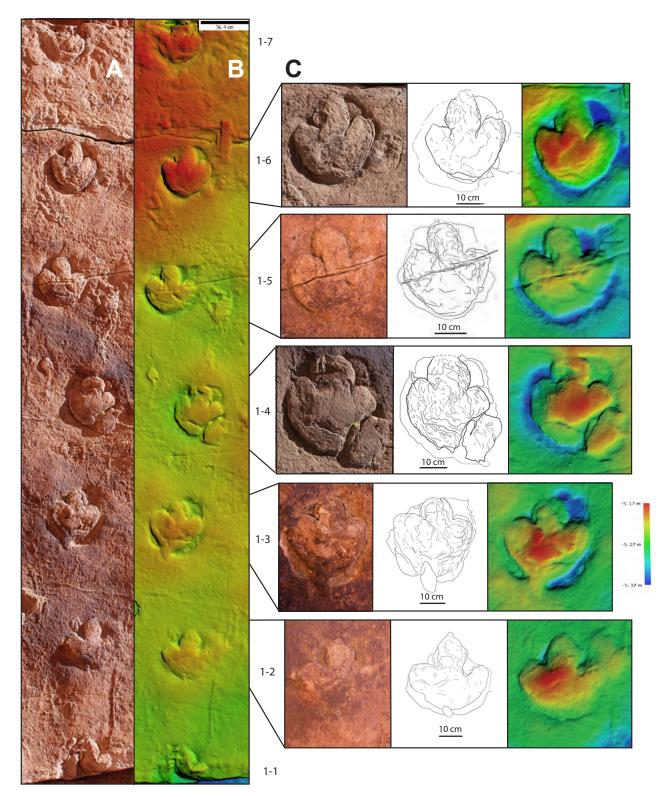


Figure 12. *Eubrontes* natural cast trackway T1 on the John Wesley Powell Fossil Track Block. (A) Photograph of complete trackway. (B) Photogrammetry of trackway shown in color relief with 1 mm contours. (C) Close-ups of individual tracks. From left to right: photographs; drawings; and photogrammetric image with color relief and 1 mm contour lines. Tracks T1-1 to T1-7 are incomplete.

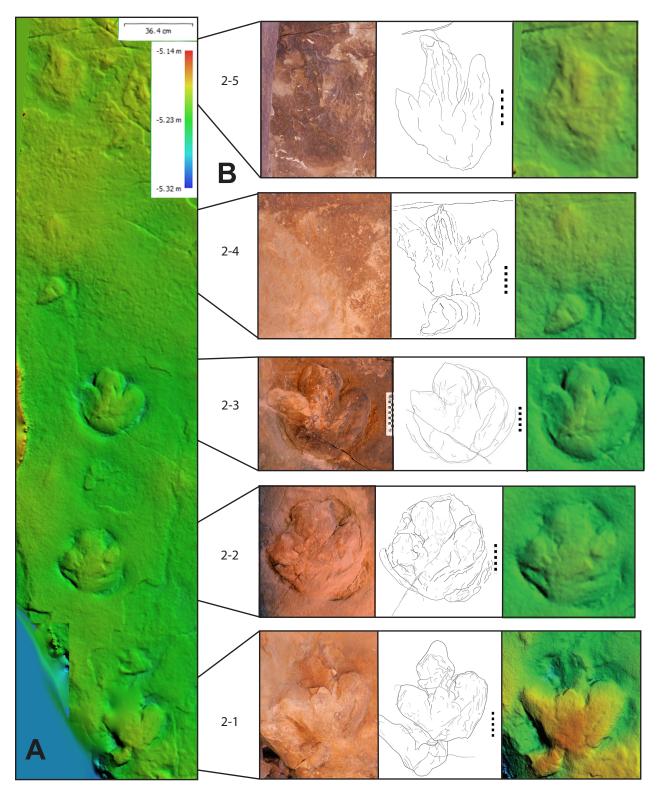


Figure 13. *Eubrontes* natural cast trackway T2 on the John Wesley Powell Fossil Track Block. (A) Photogrammetry of trackway shown in color relief with 1 mm contours. (B) Close-up photographs (left), interpretive sketches (center), and photogrammetric images (right) of individual tracks; drawings with 10 cm scale bars; and photogrammetric images with color relief and 1 mm contour lines.

Table 6. Measurements (cm) of 17 large, "ornithopod-like" theropod individual tracks (i.e., *Eubrontes*) on the main track layer of the John Wesley Powell Fossil Track Block (GLCA #10). **ATL** = anterior triangle length; **ATW** = anterior triangle width; **Avg.** = average; **Digit II, III, and IV L** = digit II, III, and IV lengths; **II–IV, II–III, and III–IV** = divarication angles between digits II–IV, II–III, and III–IV; **N/A** = no data; **Sym.** = symmetry (i.e., left or right tracks); **TD** = track depth; **TL** = track length; **TW** = track width.

Track #	Sym.	TL	TW	ATL	ATW	Digit II L	Digit III L	Digit IV L	II-IV°	II-IIIº	III- IVº	TD
T 1-1	Right	25.7 (28)	36.5	17.5	28.5	N/A	N/A	N/A	58	31	27	3.5
Т 1-2	Left	35.5	35.9	13.5	27.2	20.5	32.0	23.0	48	23	25	3.0
T 1-3	Right	36.2	37.2	11.8	30.1	25.7	33.0	26.3	59	27	32	2.5
T 1-4	Left	36.8	34.5	11.1	26.8	26.5	31.5	22.5	45	18	27	3.5
T 1-5	Right	34.5	36.5	11.7	29.1	20.0	31.3	24.5	50	21	29	3.0
T 1-6	Left	36.0	35.0	12.5	29.9	20.5	33.0	27.0	49	23	26	3.5
Т 1-7	Right	29 (34)	30.5	5 (9)	26.9	20.0	28 (24)	23.5	54	22	32	4.0
Avg.		35.8	35.2	12.1	28.4	22.2	28.2	24.5	52	24	28	3.3
Т 2-1	Left	34.5	32.6	19.7	25.9	24.0	32.0	25.0	48	24	24	1.0
Т 2-2	Right	33.5	31.7	12.7	24.8	17.5	32.5	19.7	50	24	26	N/A
Т 2-3	Left	35.0	34.7	11.2	26.3	22.5	31.7	27.0	45	18	27	3.5
Т 2-4	Right	33.0	32.0	N/A	N/A	N/A	N/A	N/A	42	20	22	N/A
Т 2-5	Left	37.0	29.5	18.8	26.8	19.0	32.0	24.5	44	22	22	3.0
Avg.		34.6	32.1	15.0	26.0	20.8	31.9	25.8	46	22	24	2.5
Т 3-1	Left	35.5	26.5	11.3	24.6	20.5	29.0	27.0	56	33	23	3.5
Т 3-2	Right	33.0	27.0	11.0	24.4	18.0	27.0	24.5	47	25	22	2.5
Avg.		34.3	26.8	11.2	24.5	19.3	28.0	25.8	52	29	23	3.0
Т 33-1	Left	45.0	34.5	14.5	26.6	26.1	40.4	35.0	53	30	24	N/A
Т 33-2	Right	48.0	40.4	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Avg.		46.5	37.5	14.5	26.6	26.1	40.4	35.0	53	30	24	N/A
T 11	Left?	29.5	29.5	N/A	N/A	N/A	N/A	N/A	50	22	28	N/A

total track length of 35.7 cm, digit tip width of 24.4 cm, digit II–IV divarication of 45°, and the anterior triangle length (i.e., toe extension) is 11.1 cm (Farlow and others, 2018, p. 559–560; Jim Farlow, Purdue University, personal communication, 2023). Specimen SGDS 9 (figure 15B) from the Early Jurassic (Hettangian) Whitmore Point Member of the Moenave Formation of St. George, Utah, has similar proportions to the *Eubrontes* holotype with a total track length of 37.5 cm, total track width of 28.5 cm, anterior track length of 13.0 cm, and digit II–IV divarication of 35°. As mentioned above, *Kayentapus hopii* has an average track length of 33.5 cm, track width of 29 cm, anterior triangle length range of 12.0 to 13.5 cm, and digit II–IV divarication of 52°. *Dilophosauripus williamsi* type (UCMP 79690-4; figure 15D; Welles, 1971), which has been synonymized with *Eubrontes*, is a natural cast with a length of 32.5 cm and width of 28.0 cm, with sharp claw traces, and a digit

Table 7. Three <i>Eubrontes</i> trackway measurements (cm) on the main track layer of the John Wesley Powell Fossil Track Block.
FR = footprint rotation; N/A = no data; PA = pace angle; PL = pace length; SL = stride length; Sym . = symmetry; TW =
trackway width.

Track #	Sym.	PL	SL	PA°	TW	FR
T 1-1	Right	N/A	N/A	N/A	N/A	N/A
Т 1-2	Left	84.5	174.0	172	42.0	3
Т 1-3	Right	90.5	173.0	166	50.0	2
Т 1-4	Left	84.0	167.0	161	53.0	3
Т 1-5	Right	86.5	167.0	167	50.0	4
Т 1-6	Left	83.5	175.0	171	43.0	3
Т 1-7	Right	93.5	N/A	N/A	N/A	N/A
Average		87.1	171.0	167	47.6	3
T 2-1	Left	N/A	N/A	N/A	N/A	N/A
Т 2-2	Right	87.0	171.0	162	48.7	4
Т 2-3	Left	83.0	174.0	153	62.2	15
Т 2-4	Right	94.5	175.0	161	60.4	3
Т 2-5	Left	89.0	N/A	N/A	N/A	N/A
Average		88.4	173.3	159	57.1	7
Т 3-1	Left	N/A	N/A	N/A	N/A	N/A
Т 3-2	Right	100.0	N/A	N/A	N/A	N/A
Average		100.0	N/A	N/A	N/A	N/A

II–IV divarication of 54° (Welles, 1971). James Farlow (Purdue University, personal communication, 2023) measured this same type footprint with somewhat similar results – length as 34.5 cm, track width of 28.2 cm, anterior track length of 9.6 cm, and digit II-IV divarication of 60°. The overall shape of *Dilophosauripus* is very similar to the ornithopod-like *Eubrontes* tracks on the PFTB (figures 13E through 13G).

Additionally, Weems (2003, 2019) suggested *Eubrontes* tracks were produced by a basal sauropodomorph (a.k.a., "prosauropod") as well as attributing *Otozoum* (figure 15L) to a sauropodomorph: we agree with the latter, but not the former interpretation. These two ichnotaxa are clearly morphologically distinct from one another, even in overall shape (figure 15). The lengths of the traces of digits I to IV and arrangements of *Eubrontes* tracks do not match those of *Otozoum*, or any other ostensible sauropodomorph footprints (e.g., *Na*- *vahopus* from the Navajo Sandstone; Baird, 1980; Milàn and others, 2008; Farlow and others, 2022; Lockley and others, 2023). Therefore, sauropodomorphs from the Navajo Sandstone can be ruled out as producers of the ornithopod-like tracks from the PFTB.

Comparisons with the PFTB ornithopod-like tracks and known ornithischian footprints from the Early Jurassic must be considered. Both *Moyenisauropus* (figure 15J) and *Anomoepus* (figure 15K) are known from the Navajo Sandstone, but once again, overall track morphology does not compare well with the PFTB *Eubrontes* footprints. Finally, comparisons with the younger ichnogenus *Caririchnium* (figure 15L), for example, *C. lotus* from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of China (Xing and others, 2015), has similar rounded digits, but does not display sharp claws like those seen on the PFTB. Additionally, the worldwide geologic range of large "ornithopod" tracks

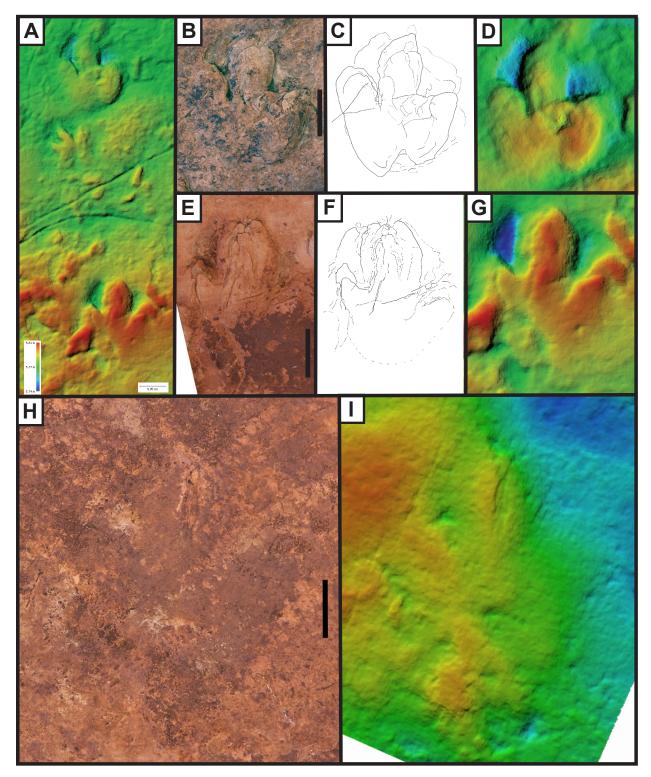


Figure 14. Other large theropod natural cast tracks on the John Wesley Powell Fossil Track Block. (A) Photogrammetry of *Eubrontes* trackway 3. (B) Close-up photograph of T3-2. (C) Sketch of T3-2. (D) Photogrammetric image of T3-2. (E) Close-up photograph of T3-1. (F) Sketch of T3-1. (G) Photogrammetric image of T3-1. (H) Photograph of large cf. *Eubrontes* track T33-1. (I) Photogrammetry of T33-1. Color relief and 1 mm contour lines in A, D, G, and I. Scale bars in B, E, and H equal 10 cm.

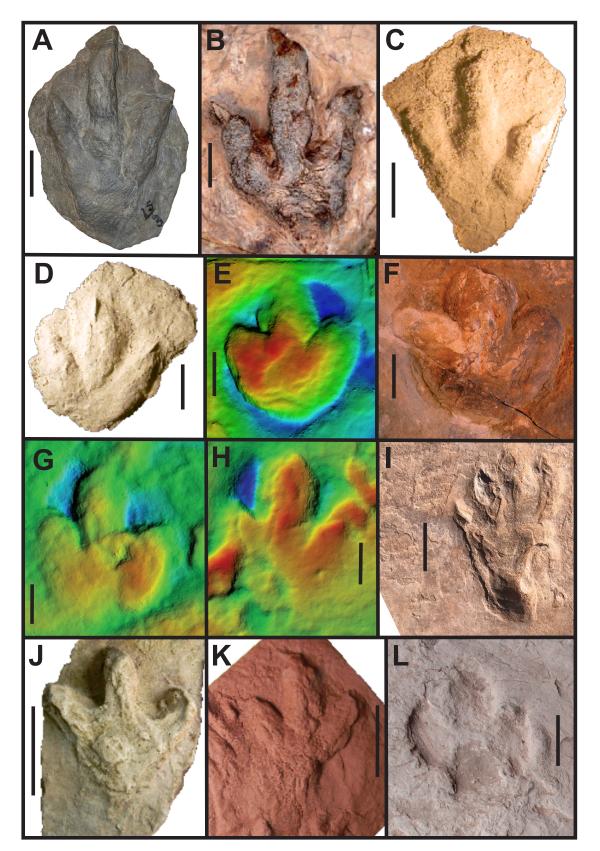


Figure 15 caption is on the next page.

Figure 15 is on the previous page. Comparison of ornithopod-like *Eubrontes* tracks with other known Early Jurassic dinosaur tracks, including *Eubrontes, Kayentapus, Dilophosauripus, Otozoum, Moyenisauropus*, and *Anomoepus*, and Early Cretaceous *Caririchnium*. (A) ACM-ICH-15/3, holotype *Eubrontes giganteus* from the Portland Formation of Holyoke, Massachusetts (photograph courtesy of James O. Farlow). (B) SGDS 9, *Eubrontes* from the "Main Track Layer," lower Whitmore Point Member, Moenave Formation, St. George Dinosaur Discovery Site, southwest Utah. (C) Plaster replica of a right track from *Kayentapus hopii* holotype trackway (UCMP 83668), lower Kayenta Formation, Tuba City area, Arizona. (D) Plaster replica of holotype *Dilophosauripus williamsi* left track from the Kayenta Formation near Tuba City, Arizona (UCMP 79690-4). (E) Photogrammetry of *Eubrontes* T1-6 from PFTB. (F) *Eubrontes* T2-3 from PFTB. (G) Photogrammetry of *Eubrontes* T3-2 from PFTB. (H) Photogrammetry of *Eubrontes* T3-1 from PFTB. (I) *Otozoum moodii* sauropodomorph track from Navajo Sandstone, GLCA Loc. 359, Utah (photograph courtesy of Jim L. Williams). (J) SGDS 1321, replica of *Anomoepus* isp. ornithischian tracks from the Lower Jurassic Zagaje Formation, Poland. (K) SGDS 1296, replica of *Anomoepus* isp. ornithischian track from Kayenta-Navajo transition, Red Hills Desert Garden, St. George, Utah. (L) *Caririchnium* from Qijiang Tracksite, Jiaguan Formation, China (photograph courtesy of Jerry D. Harris). Scale equals 10 cm in all figures except K which equals 5 cm.

is much younger than those preserved in the Navajo Sandstone.

No potential trackmakers of the size required to make the *Eubrontes* tracks are known currently from body fossils in the Navajo Sandstone. The trackmaker was presumably a medium-sized neotheropod similar to *Dilophosaurus*.

We speculate that most, if not all the tracks preserved on the PFTB could be transmitted tracks (Leonardi, 1987; Gatesy, 2003), and the transfer of substrate from one footprint to the next may have resulted in a lower quality of track preservation. Also, the collapse of sediment back into footprints as suggested by Martin (2014, p. 71), or the regrowth of microbial mats within and over tracks could also result in the loss of footprint details (Marty and others, 2009; Dai and others, 2015). Growth of microbial mats over footprints is a good possibility based on our examination of the photogrammetry of T2-4 (figure 13) that shows the same pustulate, pitted texture often produced by microbial mats (Simpson and others, 2022).

Microbial mats aid in the preservation of tracks (Thulborn, 1990; Cohen and others, 1991; Kvale and others, 2001; Marty, 2008; Marty and others, 2009; Wilson and others, 2009; de Souza Carvalho and others, 2013; Dai and others, 2015; Simpson and others, 2022). The elasticity of cyanobacterial laminites (Avanzini, 1998) and the compaction of tracks following burial due to loading (Lockley and Xing, 2015) are likely both responsible for the deformation of tracks on all three

track horizons recorded at PFTB. Suitable wet environments for the formation of microbial mats that assist in track-making conditions have been documented previously in the Navajo Sandstone (Gilland, 1979; Peterson and Pipiringos, 1979; Middleton and Blakey, 1983; Herries, 1992; Sansom, 1992; de Souza Carvalho and others, 2013; Simpson and others, 2022).

Finally, three very large, but poorly preserved, tracks (figures 14H and 14I) probably also made by large theropods occur on the PFTB. The best of these tracks is T33-1, a left footprint measuring approximately 45 cm long and 34.5 cm wide (table 6). Surprisingly, this track is very shallow considering the size and weight of the theropod that must have produced it. It is possible that this track was produced at a later point in time after wet sediment had dried, making the track-maker less able to register a deeper track.

Quadruped Tracks cf. *Brasilichnium* (Figures 16A through 16D; Supplementary File: https://irma.nps.gov/ DataStore/Reference/Profile/2299562)

Five or six small tracks (figures 2B and 16A through 16D) are preserved on the PFTB MTL surface. Although very difficult to see in natural lighting, photogrammetry has greatly assisted in interpretation of these footprints (figure 16A). The better-preserved example of these tracks, a left footprint (QT1), measures 3.5 cm long by 3 cm in width. It displays four digits, with digit IV being

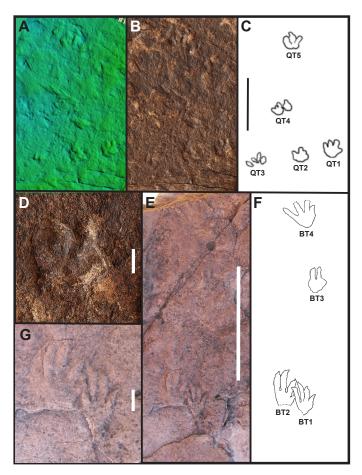


Figure 16. Quadruped natural cast footprints from localities GLCA #10 and GLCA #209. (A–D) Unidentified quadruped footprints (cf. *Brasilichnium*) from the John Wesley Powell Fossil Track Block (GLCA #10). Photogrammetry (A), photograph (B), interpretive sketch (C), and close-up of track QT1 (D). (E-G) Well-preserved *Batrachopus* natural cast trackway (GLCA #209). Photograph of trackway (E) and interpretive sketch (F), and close-up of two overlapping pes tracks BT1 and BT2 (G). D, G scale bar =1 cm; C, E scale bar = 10 cm.

slightly longer than digit III, and digits II and V of similar length (figures 16A and 16B).

These small tracks, possibly of the ichnotaxon *Brasilichnium*, were likely produced by quadrupedal tritylodont synapsids whose footprints are commonly preserved on eolian dune surfaces in the Navajo Sandstone, *including within GLCA* (Lockley and others, 1996, 2014; Lockley, 2011a, 2011b) and at localities near the PFTB. Winkler and others (1991) recorded a partial tritylodont skeleton from the Navajo Sandstone in northern Arizona, but the vast majority of Early Ju-

rassic tritylodont body fossils within the Glen Canyon Group come from the underlying Kayenta Formation (Kermack, 1982; Lewis, 1986; Sues, 1986a, 1986b; Sues and others, 1994; Irmis, 2005; Sues and Jenkins, 2006), from which there is a much greater yield of body fossils associated with the silty facies. However, in March 2023, one of us (ARCM) discovered a tritylodont bone bed with interdunal facies of the Kayenta-Navajo transition in relatively close proximity and stratigraphic distance to the PFTB. Nearby, and stratigraphically lateral to this bone bed, within interbedded, thin carbonate sandstones, siltstones, and mudstones, abundant tracks were found including cf. Brasilichnium, Eubrontes, and Grallator. These cf. Brasilichnium tracks provide stronger support for tritylodonts being the presumptive trackmakers.

Batrachopus (Figures 16E through 16G)

An associated float slab (locality GLCA #209) from an uncertain stratigraphic horizon, located immediately south of the PFTB, has 11 poorly preserved natural cast tracks, *in*cluding two trackways (figures 16E and 16F) that we refer to the crocodylomorph ichnotaxon *Batrachopus*. Two of these tracks are well preserved and show overlapping pes tracks (figure 16G). This is the only record of *Batrachopus* from the beds at the PFTB locality. Possible producers of *Batrachopus* are basal protosuchian crocodyliforms resembling *Protosuchus* (Colbert and Mook, 1951). Fragmentary protosuchian skeletons were recovered from the Navajo Sandstone to the southwest of the PFTB locality in northern Arizona (Rinehart and others, 2001), documenting the existence of such a potential trackmaker.

Very few *Batrachopus* are known from eolian environments, although they are not that uncommon in wet, *in*terdunal environments as reported for the Lake Powell area by Lockley and others (2014) based on UCM collections especially from the Kayenta-Navajo transition. An example of *Batrachopus* tracks in an eolian environment occurs at the North Moccasin Mountain Tracksite in the Navajo Sandstone close to Coral Pink Sand Dunes State Park near the town of Kanab, Kane County, Utah (Milner and others, 2012).

PALEONTOLOGICAL RESOURCE MANAGEMENT, PROTECTION, AND POTENTIAL SITE DEVELOPMENT FOR PUBLIC INTERPRETATION

The size and weight of the PFTB, as well as its remote location, make field collection or removal of this massive block for preservation, conservation, or protection impossible. In situ management and study of the block would benefit from long-term monitoring of the stability and condition of its ichnological resources. Both natural processes and, potentially, human activities may contribute to the loss or deterioration of the track block over time. Through the development of a cyclic monitoring strategy, any changes or impacts to the track block can be documented and help to inform park management regarding future preservation and protection of the PFTB.

The first assessment and documentation of the PFTB by the National Park Service and the Utah Geological Survey occurred in 2009 during an initial attempt to develop a strategy for monitoring in situ paleontological resources at GLCA (Kirkland and others, 2010, 2011). This project represented a prototype effort for the National Park Service to implement recommendations and guidance developed for monitoring in situ paleontological resources (Santucci and Koch 2003; Santucci and others, 2009).

To monitor any changes in the track-bearing layers of the PFTB, two crack sensors were placed on the south of the PFTB face in 2009. Since their placement, no movement was detected when checked in 2017. As evidenced by the hollow sound of the rock surface and wider cracks on the south side of the block, this part of the PFTB will eventually fall off within years. A visit to the site in March 2023 revealed that both crack monitors were broken, and this crack may have widened slightly, or weathering caused the monitors to break. Because of its uniqueness, replication of the large ornithopod-like theropod trackway is recommended. Replication can be accomplished through the use of photogrammetry data and rapid prototyping technologies. With this recently detected deterioration, we also highly recommend some sort of artificial stabilization to ensure longevity of this unique track site. Additionally, the collection of isolated track slabs at the base of the PFTB from the older track surface could be useful for further study, exhibits, and preservation of specimens in a proper museum as a partial record of the locality.

Given public knowledge of the PFTB, the park may want to consider the installation of a remote camera to monitor visitor activity at the fossil locality. Theft, vandalism, and other paleontological resource crimes have been documented at fossil localities within GLCA, and the scientific and educational values of the PFTB warrant some ability to monitor this important fossil vertebrate tracksite.

Public interpretation of the PFTB has been discussed by NPS staff. Careful planning for any interpretation, such as installation of an interpretive wayside exhibit, should consider resource protection of the fossil locality. Any interpretation of a paleontological locality should incorporate a resource protection message about non-renewable resources and that the collection or disturbance of fossils, *including* replication, is prohibited unless undertaken through a scientific research and collecting permit.

CONCLUSIONS

The John Wesley Powell Fossil Track Block preserves approximately 104 tracks on three different track horizons, all preserved on stromatolitic surfaces. This ichnoassemblage includes abundant *Grallator*, possible *Kayentapus*, large ornithopod-like tracks attributed to *Eubrontes*, three large cf. *Eubrontes*, possible *Brasilichnium*, and rare *Batrachopus*.

The most noticeable footprints are those of two large, parallel trackways that superficially resemble ornithopod footprints. Closer examination of these two trackways, and a third consisting of only two footprints, show that they were produced by medium-sized theropod dinosaurs, rather than ornithischians. The presence of sharp claw marks, and narrower digits on some of the tracks made more visible through the use of photogrammetry, clearly show these footprints pertain to *Eubrontes* (figure 17).



Figure 17. Two hypothetical, *Eubrontes*-producing theropods walking across a sandy, water-saturated, microbial-mat-rich interdunal playa during an early phase of the Navajo erg in the Early Jurassic. This restoration was created based on the spectacular undertracks preserved on the John Wesley Powell Track Block. The ornithopod-like undertracks now visible on the track block were registered in horizons situated below stromatolitic or endoevaporitic layers (represented in green). These undertracks display different morphologies than the true tracks, which would have resembled *Eubrontes*. Artwork by Brian Engh (dontmesswithdinosaurs.com).

Additionally, abundant, small coelophysoid theropod tracks we identify as *Grallator* and *Grallator*-like are the most common forms on all track-bearing horizons. Medium-sized theropod tracks that superficially resemble *Kayentapus* by having wider divarication angles than typical other theropod tracks recorded at the site are the least common ichnomorphotype. At least five small, closely associated tetradactyl footprints that we identify as *Brasilichnium*-like occur on the MTL of the PFTB. On a nearby fallen block, also made up of microbial laminites, distinct trackways of *Batrachopus* occur. *Batrachopus* tracks are rare in eolian environments.

The presence of microbial (possibly endoevaporitic)

mats and stromatolitic horizons the animals had walked upon produced a distinct ichnomorphologic variation likely due to substrate consistency and the elastic properties of the mats, resulting in differential compaction of the beds. The possible transfer of sediment from one footprint to the next, and overgrowth of the tracks by microbial mats could also have been a contributing factor to the poor preservation of track details and distortion of overall track shapes. Microbial mats formed on interdunal surface where water pooled to produce lakes and ponds, likely during periods of increased precipitation and/or rising water tables during wet seasons.

ACKNOWLEDGMENTS

The PFTB is within the ancestral homelands of the Nuwuvi (Southern Paiute) and Dine' (Navajo) peoples. We would like to thank the NPS and SGDS DinosaurAH!Torium Foundation for funding fieldwork and research efforts. Thank you to NPS/GLCA staff, including John Spence, Taryn Preston, Matthew Miller, Mark Anderson, Ann Miller, Maria Rodriguez, and many others for transporting us to the site, assisting with logistics and excavation, and for their great hospitality. Special thanks to Sarah Doyle (GLCA paleontology intern) who assisted us in the field with stratigraphy, collection of locality data, photogrammetry, and her boating skills. Thank you to James I. Kirkland (Utah Geological Survey) for lengthy discussions about this locality and Jerry D. Harris (Utah Tech University) for reviewing an earlier version of this manuscript. Thank you to Jim Farlow (Purdue University Fort Wayne), Tom Chidsey (Utah Geological Survey), and Justin Tweet (National Park Service) for their helpful reviews that greatly improved this manuscript. A special thanks to Brian Engh (dontmesswithdinosaurs.com) for providing his beautiful artwork. Thank you to Conner Bennett (former SGDS intern) for photographing and creating the photogrammetry of the small cf. Brasilichnium tracks on PFTB. Thanks to Don DeBlieux and Scott Madsen from the Utah Geological Survey for their early assessment of the PFTB. Thank you to Neffra Matthews (BLM, Denver) and Mike Santella (former SGDS volunteer) for helping with preliminary photogrammetry. We thank Matt Stimson (New Brunswick Museum, Saint John, New Brunswick, Canada) for assistance with invertebrate trace identifications. Thanks to Dan W. Whalen (SGDS volunteer) for documenting all our 2010 fieldwork through photography and videography, and to SGDS volunteer David L. Slauf for assistance in the field. Thank you to Jaleesa Buchwitz (SGDS Deputy Curator) for her assistance with the graphics in figure 5. Appreciation to Jim Farlow (Purdue University Fort Wayne) for providing the photo in figure 15A, Jim Williams (SGDS volunteer) for providing the photograph for figure 15I, and Jerry D. Harris for figure 15L. Finally, thank you to editor, Doug Sprinkel (Utah Geological Survey), for his patience and help in editing this paper.

REFERENCES

- Abrahams, M., Bordy, E.M., Knoll, F., and Farlow, J.O., 2022, Theropod tridactyl tracks across the Triassic–Jurassic boundary in southern Africa—implications for pedal morphology evolution: Frontiers in Ecology and Evolution, v. 10, p. 1–18.
- Avanzini, M., 1998, Anatomy of a footprint—bioturbation as a key to understanding dinosaur walk dynamics: Ichnos, v. 6, no. 3, p. 129–139.
- Baird, D., 1980, A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona, *in* Jacobs, L.L., editor, Aspects of vertebrate history: Flagstaff, Museum of Northern Arizona Press, p. 219–230.
- Belvedere, M., and Farlow, J.O., 2016, A numerical scale for quantifying the quality of preservation of vertebrate tracks, *in* Falkingham, P.L., Marty, D., and Richter, A., editors, Dinosaur tracks—the next steps: Bloomington and Indianapolis, *in*diana University Press, p. 92–99.
- Bennett, C., Milner, A.R.C., and Harris, J., 2023, A glimpse through time—preliminary report of the Andre's Alcove Tracksite, Lower Jurassic Navajo Sandstone, Glen Canyon National Recreation Area, Utah: Curiosity: Interdisciplinary Journal of Research and Innovation, 9 p.
- Blakey, R.C., 1994, Paleogeographic and tectonic controls on some Lower and Middle Jurassic erg deposits, Colorado Plateau, *in* Caputo, M.V., Peterson, J.A., and Francsyk, K.J., editors, Mesozoic systems of the Rocky Mountain region, USA: Society for Sedimentary Geology (SEPM), Rocky Mountain Section, p. 273–298.
- Blakey, R.C., 1996, The Kayenta-Navajo transition—a critical environmental change in Lower Jurassic rocks of the Colorado Plateau, *in* Morales, M, editor, The continental Jurassic: Museum of Northern Arizona Bulletin, v. 60, p. 477–478.
- Bryant, G., Cushman, R., Nick, K., and Miall, A., 2016, Paleohydrologic controls on soft-sediment deformation in the Navajo Sandstone: Sedimentary Geology, v. 344, p. 205–221.
- Bryant, G., and Miall, A., 2010, Diverse products of near-surface sediment mobilization in an ancient eolianite—outcrop features of the Early Jurassic Navajo Sandstone: Basin Research, v. 22, p. 578–590.
- Camp, C.L., 1936, A new type of small bipedal dinosaur from the Navajo Sandstone of Arizona: University of California Publications, Bulletin of the Department of Geological Sciences, v. 24, p. 39–56.

- Carrano, M.T., Hutchinson, J.R., and Sampson, S.D., 2005, New information on *Segisaurus halli*, a small theropod dinosaur from the Early Jurassic of Arizona: Journal of Vertebrate Paleontology, v. 25, no. 4, p. 835–849.
- Chure, D.J., Engelmann, G.F., Britt, B.B., and Good, T.R., 2014, It's not your parents' erg deposit anymore—fossil management implications of a paleontological study of the Nugget Sandstone in northeastern Utah: Proceedings of the 10th Conference on Fossil Resources, Rapid City, South Dakota, Dakoterra, v. 6, p. 140–154.
- Cohen, A., Lockley, M., Halfpenny, J., Michel, A.E., 1991, Modern vertebrate track taphonomy at Lake Manyara, Tanzania: Palaios, v. 6, p. 371–389.
- Colbert, E.H., 1989, The Triassic dinosaur *Coelophysis*: Museum of Northern Arizona Bulletin, v. 57, 160 p.
- Colbert, E.H., and Mook, C.C., 1951, The ancestral crocodilian *Protosuchus*: American Museum of Natural History Bulletin, v. 97, no. 3, p. 149–182.
- Currie, P.J., 1993, Hadrosaur trackways from the Lower Cretaceous of Canada: Acta Palaeontologica Polonica, v. 28, no. 1-2, p. 63–73.
- Currie, P.J., and Eberth, D.A., 2010, On gregarious behavior in *Albertosaurus*: Canadian Journal of Earth Science, v. 47, no. 1, p. 1277–1289.
- Dai, H., Xing, L., Marty, D., Zhang, J., Persons IV, W.S., Hu, H., and Wang, F., 2015, Microbially-induced sedimentary wrinkle structures and possible impact of microbial mats for the enhanced preservation of dinosaur tracks from the Lower Cretaceous Jiaguan Formation near Qijiang (Chongqing, China): Cretaceous Research, v. 53, p. 98–109.
- Delgalvis, A., 2015, The lost tracks—a journey of discovery: Studio 2138, Grand Junction, Colorado, 160 p.
- de Souza Carvalho, I., Borghi, L., and Leonardi, G., 2013, Preservation of dinosaur tracks induced by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil: Cretaceous Research, v. 44, p. 112–121.
- Díaz-Martínez, I., Pereda-Suberbiola, X., Pérez-Lorente, F., and Canudo, J.I., 2015, Ichnotaxonomic review of large ornithopod dinosaur tracks—temporal and geographic implications: PLoS ONE, v. 10, no. 2, e0115477.
- Dickinson, W.R.G., and Gehrels, G.E., 2003, U–Pb ages of detrital zircons from Permian and Jurassic eolian sandstones of the Colorado Plateau, USA; paleogeographic implications: Sedimentary Geology, v. 163, p. 29–66.

- Dieudonné, P.-E., Cruzado-Caballero, P., Godefroit, P., and Tortosa, T., 2022, A new phylogeny of cerapodan dinosaurs: Historical Biology, v. 33, no. 10, p. 2335–2355.
- Doelling, H.H., Davis, F.D., and Brandt, C.J., 1989, The geology of Kane County, Utah: Utah Geological and Mineral Survey Bulletin, v. 124, 192 p.
- Doelling, H.H., Sprinkel, D.A., Kowallis, B.J., and Kuehne, P.A., 2013, Temple Cap and Carmel Formations in the Henry Mountains Basin, Wayne and Garfield Counties, Utah, in Morris, T.H., and Ressetar, R., editors, The San Rafael Swell and Henry Mountains Basin-geologic centerpiece of Utah: Utah Geological Association Publication 42, p. 279–318.
- Dorney, L.J., 2009, Carbonate lakes and mounds in the Jurassic Navajo Formation of southeastern Utah: University of Idaho, Moscow, Idaho, M.S. thesis, 81 p.
- Dorney, L.J., and Parrish, J.T., 2009, Carbonate mound structures in the Jurassic Navajo Sandstone of southeastern Utah [abs.]: Geological Society of America Abstracts with Programs, v. 41, no. 6, 40 p.
- Eisenberg, L., 2003, Giant stromatolites and a supersurface in the Navajo Sandstone, Capitol Reef National Park, Utah: Geology, v. 31, no. 2, p. 111–114.
- Falk, A.R., Hasiotis, S.T., Gong, E., Lim, J.-D., and Brewer, E.D., 2017, A new experimental setup for studying avian neoichnology and the effects of grain size and moisture content on tracks—trials using the domestic chicken (*Gallus gallus*): Palaios, v. 32, no. 11, p. 689–707.
- Farlow, J.O., Coroian, D., and Currie, P.J., 2018, Noah's Ravens—interpreting the makers of tridactyl dinosaur footprints: Bloomington, Indiana University Press, 644 p.
- Farlow, J.O., Lallensack, J.N., Müller, R.T., and Hyatt, J.A., 2022, Pedal skeletal proportions of bipedal and potentially bipedal dinosaurs and other archosaurs—interpreting the makers of early Mesozoic footprints: Bulletin of the Peabody Museum of Natural History, v. 63, p. 33–90.
- Foster, J.R., and Lockley, M.G., 2006, The vertebrate ichnological record of the Morrison Formation (Upper Jurassic, North America): New Mexico Museum of Natural History and Science Bulletin, v. 36, p. 203–216.
- Gabunia, L.K., and Kurbatov, V., 1988, Jurassic dinosaur tracks in the south of central Asia, *in* Bogdanova, T.N., Khozatsky, L.I., and Istchenko, A.A., editors, Fossils traces of vital activity and dynamics of the environment in ancient biotopes: Transactions of the XXX Session of

All-Union Paleontological Society and VII Session of the Ukrainian Paleontological Society, Kiev, Naukova Dumka, p. 45–57.

- Gatesy, S.M., 2003, Direct and indirect track features—what sediment did a dinosaur touch?: Ichnos, v. 10, p. 91–98.
- Getty, P.R., Hardy, L., and Bush, A.M., 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, v. 56, no. 1, p. 95–106.
- Getty, P.R., Olsen, P.E., LeTourneau, P.M., Gatesy, S.M., Hyatt, J.A., Farlow, J.O., Galton, P. M., Falkingham, P., and Winitch, M., 2017, Exploring a real Jurassic Park from the dawn of the age of dinosaurs in the Connecticut Valley: Geological Society of Connecticut, Guidebook No. 9, Spring Fieldtrip, 82 p.
- Gierliński, G., 1996, Dinosaur ichnotaxa from the Lower Jurassic of Hungary: Geological Quarterly, v. 40, no. 1, p. 119–128.
- Gilland, J.K., 1979, Palaeoenvironment of a carbonate lens in the lower Navajo Sandstone near Moab, Utah: Utah Geology, v. 6, p. 29–48.
- Godefroit, P., Sinitsa, S.M., Shouailly, D., Bolotsky, Y.L., Sizov, A.V., McNamara, M.E., Benton, M.J., and Spagna, P., 2014, A Jurassic ornithischian dinosaur from Siberia with both feathers and scales: Science, v. 345, no. 6195, p. 451–455.
- Hamblin, A.H., Lockley, M.G., and Milner, A.R.C., 2006, More reports of theropod dinosaur tracksites from the Kayenta Formation (Lower Jurassic), Washington County, Utah implications for describing the Springdale megatracksite: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 276–281.
- Harshbarger, J.W., Repenning, C.A., and Irwin, J.H., 1957, Stratigraphy of the uppermost Triassic and the Jurassic rocks of the Navajo country: U.S. Geological Survey Professional Paper 291, 74 p.
- Herries, R.D., 1992, Contrasting styles of fluvial-aeolian interaction at a downwind erg margin—Jurassic Kayenta-Navajo transition, northeastern Arizona, USA, *in* North, C.P., and Prosser, F.J., editors, Characterization of fluvial and aeolian reservoirs: Geological Society Special Publication No. 73, p. 199–218.
- Hitchcock, E., 1836, Ornithichnology—description of the foot marks of birds, (Ornithichnites) on New Red Sandstone in Massachusetts: American Journal of Science, v. 29, p. 307–340.

- Hitchcock, E., 1858, Ichnology of New England—a report on the sandstone of the Connecticut Valley, especially its fossil footmarks: Boston, W. White, Printer of the State, 220 p.
- Irmis, R.B., 2005, A review of the vertebrate fauna of the Lower Jurassic Navajo Sandstone in Arizona, *in* McCord, R.D., editor, Vertebrate paleontology of Arizona: Mesa Southwest Museum Bulletin, no. 11, p. 55–71.
- Keighley, D.G., and Pickerill, R.K., 1994, The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*: Palaeontology, v. 37, no. 2, p. 305–337.
- Kermack, D.M., 1982, A new tritylodontid from the Kayenta Formation of Arizona: Zoological Journal of the Linnean Society, v. 76, 17 p.
- Kirkland, J.I., Madsen, S.K., DeBlieux, D.D., Ehler, B., Weaver, L., and Santucci, V.L., 2010, Final report for paleontological resources inventory and monitoring at Glen Canyon National Recreation Area, Utah: Unpublished NPS report under cooperative agreement #H2360097080, 171 p., 2 plates, scale 1:125,000.
- Kirkland, J.I., S.K. Madsen, D., DeBlieux, D., and Santucci, V.L., 2011, Establishing a paleontological monitoring test site at Glen Canyon National Recreation Area, *in* Olstad, T., and Aase, A., editors, Proceedings of the 9th Conference on Fossil Resources,: Brigham Young University Geology Studies, v. 49 (A), p. 51–60.
- Kocurek, G., and Dott, R.H., Jr., 1983, Jurassic paleogeography and paleoclimate of the central and southern Rocky Mountain region, *in* Reynolds, M.W., and Dolly, E.D., editors, Mesozoic paleogeography of west-central United States: Society for Sedimentary Geology (SEPM), Rocky Mountain Section, p. 101–116.
- Kuhn, O., 1958, Die Fährten der vorzeitlichen Amphibien und Reptilien: Verlagshaus Meisenbach, 64 p.
- Kvale, E.P., Johnson, G.D., Mickelson, D.L., Keller, K., Furer, L.C., and Archer, A.W., 2001, Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksites, Bighorn Basin, Wyoming, U.S.A: Palaios, v. 16, p. 233–254.
- Leonardi, G. (editor), 1987, Glossary and manual of tetrapod footprint palaeoichnology: Departmento Nacional da Produção Mineral, Brasilia, Brazil, 75 p.
- Lewis G.E., 1986, *Nearctylodon broomi*, the first Nearctic tritylodont, *in* Hotton, N, III, MacLean, P.D., Roth, J.J., and Roth, E.C., editors, The ecology and biology of mammal-like reptiles: Washington, Smithsonian Institution Press, p. 295–303.

- Li, J., Lockley, M.G., Zhang, Y., Hu, S., Matsukawa, M., and Bai, Z., 2012, An important ornithischian tracksite in the Early Jurassic of the Shenmu region, Shaanxi, China: Acta Geologica Sinica, v. 86, no. 1, 10 p.
- Lockley, M.G., 1991, Tracking dinosaurs—a new look at an ancient world: New York, Cambridge University Press, 238 p.
- Lockley, M.G., 2003, Trackways—dinosaur locomotion, *in* Briggs, D.E.G., and Crowther, P.R., editors, Palaeobiology II: Malden, Blackwell Science Ltd., p. 408–412.
- Lockley, M.G., 2009, New perspectives on morphological variation in tridactyl footprints—clues to widespread convergence in developmental dynamics: Geological Quarterly, v. 53, p. 415–432.
- Lockley, M.G., 2011a, The ichnotaxonomic status of *Brasilichnium* with special reference to occurrences in the Navajo Sandstone (Lower Jurassic) in the western USA: New Mexico Museum of Natural History and Science Bulletin, v. 53, p. 306–315.
- Lockley, M.G., 2011b, Theropod- and prosauropod-dominated ichnofaunas from the Navajo-Nugget Sandstone (Lower Jurassic) at Dinosaur National Monument—implications for prosauropod behavior and ecology: New Mexico Museum of Natural History and Science Bulletin, v. 53, p. 315–320.
- Lockley, M.G., Kukihara, R., Pionek, L., and Delgalvis, A., 1994, 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): New Mexico Museum of Natural History and Science Bulletin, v. 62, p. 157–179.
- Lockley, M.G., and Gierliński, G.D., 2006, Diverse vertebrate ichnofaunas containing *Anomoepus* and other unusual trace fossils from the Lower Jurassic of the western United States—implications for paleoecology and palichnostratigraphy: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 176–191.
- Lockley, M.G., Gierliński, G.D., and Lucas, S.G., 2011, *Kayentapus* revisited—notes on the type material and the importance of this theropod footprint ichnogenus: New Mexico Museum of Natural History and Science Bulletin, v. 53, p. 330–336.
- Lockley, M.G., and Hunt, A.P., 1995, Dinosaur tracks and other fossil footprints of the western United States: New York, Columbia University Press, 338 p.
- Lockley, M.G., Hunt, A.P., Meyer, C., Rainforth, E.C., and

Schultz, R.J., 1998, A survey of fossil footprint sites at Glen Canyon National Recreation Area (western USA)—a case study in documentation of trace fossil resources at a national preserve: Ichnos, v. 5, p. 177–211.

- Lockley, M.G., Kukihara, R., Pionek, L., and Delgalvis, A., 2014, 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): New Mexico Museum of Natural History and Science Bulletin, v. 62, p. 157–179.
- Lockley, M.G., Lallensack, J.N., Sciscio, L., and Bordy, E.M., 2023, The early Mesozoic saurischian trackways *Evazoum* and *Otozoum*—implications for 'prosauropod' (basal sauropodomorph) gaits: Historical Biology, DOI: 10.1080/08912963.2022.2163170.
- Lockley, M.G., and Matsukawa, M., 1999, Some observations on trackway evidence for gregarious behavior among small bipedal dinosaurs: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 150, p. 25–31.
- Lockley, M.G., Milner, A.R.C., Slauf, D., and Hamblin, A.H., 2006, Dinosaur tracksites from the Kayenta Formation (Lower Jurassic) "Desert Tortoise Site," Washington County, Utah: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 269–275.
- Lockley, M.G., and Xing, L., 2015, Flattened fossil footprints implications for paleobiology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 426, p. 85–94.
- Loope, D., Eisenberg, L., and Waiss, E., 2004, Navajo sand sea of near-equatorial Pangea—tropical westerlies, slumps, and giant stromatolites, *in* Nelson, E.P., and Erslev, E.A., editors, Field trips in the southern Rocky Mountains, USA: Geological Society of America Field Guide 5, 13 p.
- Lucas, S.G., Lockley, M.G., Hunt, A.P., Milner, A.R.C., and Tanner, L.H., 2006, Tetrapod footprint biostratigraphy of the Triassic-Jurassic transition in the American Southwest: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 105–108.
- Madsen, S.K., Kirkland, J.I., DeBlieux, D.D., Santucci, V.L., *in*kenbrandt, P., and Tweet, J.S., 2012, Paleontological resources inventory and monitoring, Arches National Park, Utah: Utah Geological Survey Contract Deliverable Cooperative Agreement #H230097080, 163 p.
- Mallison, H., and Wings, O., 2014, Photogrammetry in paleontology—a practical guide: Journal of Paleontological Techniques, v. 12, 31 p.

- Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, S., Melchor, R., and Farlow, J.O., 2019, Defining the morphological quality of fossil footprints—problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present: Earth Science Reviews, v. 193, p. 109–145, DOI: 10.1016/j.earscirev.2019.04.008.
- Marsh, A.D., and Rowe, T.B., 2020, A comprehensive anatomical and phylogenetic evaluation of *Dilophosaurus wetherilli* (Dinosauria, Theropoda) with descriptions of new specimens from the Kayenta Formation of northern Arizona: Journal of Paleontology Memoir, v. 78, 103 p.
- Martin, A.J., 2014, Dinosaurs without bones: New York, Pegasus Books, 460 p.
- Marty, D., 2008, Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez–Combe Ronde tracksite, NW Switzerland)—insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology: GeoFocus, v. 21, 278 p.
- Marty, D., Falkingham, P.L., and Richter, A., 2016, Dinosaur track terminology—a glossary of terms, *in* Falkingham, P.L., Marty, D., and Richter, A., editors, Dinosaur tracks—the next steps: Bloomington, *in*diana University Press, p. 399–402.
- 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, v. 16, p. 122–142.
- Marzolf, J.E., 1983, Changing wind and hydrologic regime during deposition of the Navajo and Aztec Sandstones, Jurassic (?), southwestern United States, *in* Brookfield, M.E., and Ahlbrandt, T.S., editors, Eolian sediments and processes: Amsterdam, Elsevier, p. 635–660.
- Matthews, N.A., 2008, Aerial and close-range photogrammetric technology—providing resource documentation, *in*terpretation, and preservation: Technical Note 428, U.S. Department of the Interior, Bureau of Land Management, National Operations Center, Denver, Colorado, 42 p.
- Middleton, L.T., and Blakey, R.C., 1983, Processes and controls on the intertonguing of the Kayenta and Navajo Formations, northern Arizona, *in* Brookfield, M.E., and Ahlbrandt, T.S., editors, Eolian sediments and processes: Developments in Sedimentology, v. 38, p. 613–634.
- Milàn, J., 2006, Variation in the morphology of Emu (*Dromai-us novaehollandiae*) tracks reflecting differences in walk-

ing pattern and substrate consistency—ichnotaxonomic implications: Palaeontology, v 49, p. 405–420.

- Milàn, J., and Bromley, R.G., 2006, True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 231, p. 253–264.
- Milàn, J., Loope, D.B., and Bromley, R.G., 2008, Crouching theropod and *Navahopus* sauropodomorph tracks from the Early Jurassic Navajo Sandstone of USA: Acta Palaeontologica Polonica, v. 53, no. 2, p. 197–205.
- Milàn, J., Falkingham, P.L., and Mueller-Töwe, I.J., 2020, Small ornithopod dinosaur tracks and crocodilian remains from the Middle Jurassic Bagå Formation, Bornholm, Denmark—important additions to the rare Middle Jurassic vertebrate faunas of northern Europe: Bulletin of the Geological Society of Denmark, v. 68, p. 245–253.
- Milner, A.R.C., Lockley, M.G., and Johnson, S.B., 2006, 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: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 329–345.
- Milner, A.R.C., Birthisel, T.A., Kirkland, J.I., Breithaupt, B.H., Matthews, N.A., Lockley, M.G., Santucci, V.L., Gibson, S.Z., DeBlieux, D.D., Hurlbut, M., Harris, J.D., and Olsen, P.E., 2012, Tracking Early Jurassic dinosaurs across southwestern Utah and the Triassic-Jurassic transition: Nevada State Museum Paleontological Papers, v. 1, 107 p.
- Moreno, K., de Valais, S., Blanco, N., Tomlinson, A.J., Jacay, J., and Calvo, J.O., 2012, Large theropod dinosaur footprint associations in western Gondwana—behavioural and palaeogeographic implications: Acta Palaeontologica Polonica, v. 57, no. 1, p. 73–83.
- Olsen, P., 1980, Fossil great lakes of the Newark Supergroup in New Jersey, *in* Manspeizer, W., editor, Field studies of New Jersey geology and guide to field trips: New York State Geological Association, New York, p. 352–398.
- Olsen, P.E., and Rainforth, E.C., 2003, The Early Jurassic ornithischian dinosaurian ichnogenus Anomoepus, in Letourneau, P.M., and Olsen, P.E., editors, The Great Rift Valleys of Pangea in eastern North America, Volume 2: Sedimentology, Stratigraphy, and Paleontology: New York, Columbia University Press, p. 314–368.
- Olsen, P.E., Smith, J.B., and McDonald, N.G., 1998, Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Ju-

rassic, Hartford and Deerfield Basins, Connecticut and Massachusetts, U.S.A.): Journal of Vertebrate Paleontology, v. 18, no. 3, p. 586–601.

- Ostrom, J.H., 1972, Were some dinosaurs gregarious?: Palaeogeography, Palaeoclimatology, Palaeogeography, v. 11, p. 287–301.
- Parrish, J.T., and Falcon-Lang, H.J., 2007, Coniferous trees associated with interdune deposits in the Jurassic Navajo Sandstone Formation, Utah, USA: Palaeontology, v. 50, no. 4, p. 829–843.
- Parrish, J.T., Hasiotis, S.T., and Chan, M.A., 2017, Carbonate deposits in the Lower Jurassic Navajo Sandstone, southern Utah and northern Arizona: Journal of Sedimentary Research, v. 87, p. 740–762.
- Parrish, J.T., and Peterson, F., 1988, Wind directions predicted from global circulation models and wind directions determined from eolian sandstones of the western United States—a comparison: Sedimentary Geology, v. 56, p. 261–282.
- Peterson, F., 1994, Sand dunes, sabkhas, streams and shallow seas—Jurassic paleogeography in the southern part of the Western Interior Basin, *in* Peterson, J.A., Caputo, M.V., and Franczyk, K.J., editors, Mesozoic systems of the Rocky Mountain region, USA: Society for Sedimentary Geology (SEPM), Rocky Mountain Section, p. 233–272.
- Peterson, F., and Pipiringos, G.N., 1979, Stratigraphic relations of the Navajo Sandstone to Middle Jurassic formations, southern Utah and northern Arizona: U.S. Geological Survey Professional Paper, v. 1035-B, 43 p.
- Piubelli, D., Avanzini, M., and Mietto, P., 2005, The Early Jurassic ichnogenus *Kayentapus* at Lavini di Marco ichnosite (NE Italy)—global distribution and palaeogeographic implications: Bollettino della Società Geologica Italiana, v. 124, p. 259–267.
- Raath, M.A., 1977, The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokesauridae) and a consideration of its biology: Salisbury, South Africa, Rhodes University, Ph.D dissertation, 233 p.
- Rainforth, E., 2005, Ichnotaxonomy of the fossil footprints of the Connecticut Valley (Early Jurassic, Newark Supergroup, Connecticut and Massachusetts: New York, Columbia University, Ph.D. dissertation, 1301 p.
- Rinehart, L.F., Heckert, A.B., Bryant, G., Lucas, S.G., and Cushman, R., 2001, Protosuchid crocodylomorphs from the Lower Jurassic Navajo Sandstone of north-central Ar-

izona, *in* McCord, R.D., and Boaz, D., editors, Western Association of Vertebrate Paleontologists and Southwest Paleontological Symposium—Proceedings: Mesa Southwest Museum Bulletin, v. 8, p. 25–31.

- Romano, M., Citton, P., and Avanzini, M., 2018, A review of the concepts of 'axony' and their bearing on tetrapod ichnology: Historical Biology, v. 32, no. 5, p. 611–619.
- Ruiz-Omeñaca, J.I., Pereda Suberbiola, X., and Galton, P.M., 2007, *Callovosaurus leedsi*, the earliest dryosaurid dinosaur (Ornithischia: Euornithopoda) from the Middle Jurassic of England, *in* Carpenter, K., editor, Horns and beaks—ceratopsian and ornithopod dinosaurs: Bloomington, *in*diana University Press, p. 3–16.
- Sansom, P.J., 1992, Sedimentology of the Navajo Sandstone, southern Utah, USA, volume I: text and appendices: Oxford, United Kingdom, University of Oxford, Ph.D. dissertation, 168 p.
- Santucci, V.L., Kenworthy, J.P., and Mims, A.L., 2009, Monitoring in situ paleontological resources, *in* Young, R., and Norby, L.I., editors, Geological monitoring: Geological Society of America Specialty Book https:// doi.org/10.1130/9780813760322, p. 189–202, https://doi. org/10.1130/2009.monitoring(08).
- Santucci, V.L., and Kirkland, J.I., 2010, An overview of National Park Service paleontological resources from the parks and monuments in Utah, *in* Sprinkel, D.A., Chidsey, T.C., Jr., and Anderson, P.B., editors, Geology of Utah's parks and monuments: Utah Geological Association Publication 28, p. 565–599.
- Santucci, V.L., and Koch, A.L., 2003, Paleontological resource monitoring strategies for the National Park Service: Park Science, v. 22, no. 1, p. 22–25.
- Simpson, E.L., Wizovich, M.C., Pittinger, D., Rogers, G., and Lazer, K., 2022, Microbially induced sedimentary structures and the preservation of vertebrate tracks on the Colorado River delta in Lake Powell, Hite, Utah: Geology of the Intermountain West, v. 9, p. 131–151.
- Stokes, W.L., 1991, Petrified mini-forests of the Navajo Sandstone, east-central Utah: Utah Geological and Mineral Survey, Survey Notes, v. 25, p. 14–19.
- Sues, H.-D., 1986a, The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America: Bulletin of the Museum of Comparative Zoology, v. 151, no. 3, p. 217–268.

Sues, H.-D., 1986b, Relationships and biostratigraphic sig-

nificance of the Tritylodontidae (Synapsida) from the Kayenta Formation of northeastern Arizona, *in* Padian, K., editor, The beginning of the age of dinosaurs—faunal change across the Triassic-Jurassic boundary: New York, Cambridge University Press, p. 179–284.

- Sues, H.-D., Clark, J.M., and Jenkins, F.A., Jr., 1994, A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest, *in* Fraser, N.C., and Sues, H.-D., editors, In the shadow of the dinosaurs—Early Mesozoic tetrapods: New York, Cambridge University Press, p. 284–294.
- Sues, H.-D., and Jenkins, F.A., Jr., 2006, The postcranial skeleton of *Kayentatherium wellesi* from the Lower Jurassic Kayenta Formation of Arizona and the phylogenetic significance of postcranial features in tritylodontid cynodonts, *in* Carrano, M.T., Gaudin, T.J., Blob, R.W., and Wible, J.R., editors, Amniote paleobiology—perspectives on the evolution of mammals, birds, and reptiles: Chicago, University of Chicago Press, p. 114–152.
- Thulborn, T., 1990, Dinosaur tracks: London, Chapman and Hall, 410 p.
- Tweet, J.S., and Santucci, V.L., 2018, An inventory of non-avian dinosaurs from National Park Service areas: New Mexico Museum of Natural History and Science Bulletin, v. 79, p. 703–730.
- Weems, R.E., 1992, A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper, Virginia, *in* Sweet, P.C., editor, Proceedings of the 26th Forum on the Geology of Industrial Minerals: Virginia, Division of Mineral Resources, (May 14–18, 1990), p. 113–127.
- Weems, R.E., 2003, *Plateosaurus* foot structure suggests a single trackmaker for *Eubrontes* and *Gigandipus* footprints, *in* Letourneau P.M., and Olsen P.E., editors, The Great Rift Valleys of Pangea in eastern North America, Volume 2: Sedimentology, Stratigraphy, and Paleontology: New York, Columbia University Press, p. 293–313.
- Weems, R.E., 2006, Locomotor speeds and patterns of running behavior in nonmaniraptoriform theropod dinosaurs—the

Triassic-Jurassic terrestrial transition: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 379–389.

- Weems, R.E., 2019, Evidence for bipedal prosauropods as the likely *Eubrontes* track-makers: Ichnos, v. 26, no. 3, p. 187–215.
- Welles, S.P., 1954, New Jurassic dinosaur from the Kayenta Formation of Arizona: Geological Society of America Bulletin, v. 65, p. 591–598.
- Welles, S.P., 1970, *Dilophosaurus* (Reptilia, Saurischia), a new name for a dinosaur: Journal of Paleontology, v. 44, p. 989.
- Welles, S.P., 1971, Dinosaur footprints from the Kayenta Formation of northern Arizona: Plateau, v. 44, p. 27–38.
- Welles, S.P., 1984, *Dilophosaurus wetherilli* (Dinosauria, Theropoda)—osteology and comparisons: Palaeonto-graphica Abteilung A, v. 185, p. 84–180.
- Wilson, J.A., Marsicano, C. A., and Smith, R. M. H., 2009, Dynamic locomotor capabilities revealed by early dinosaur trackmakers from southern Africa: PLoS ONE, v. 4, no. 10, e7331.
- Winkler, D.A., Jacobs, L.L., Congleton, J.D., and Downs, W.R., 1991, Life in a sand sea—biota from Jurassic interdunes: Geology, v. 19, p. 889–892.
- Wood, J.R., Bozek, M.A., Milner, A.R.C., Mims, A.L., Frost, F., and Santucci, V.L., 2021, Structure from motion photogrammetry enhances paleontological resources documentation, research, preservation and education efforts for National Park Service areas: New Mexico Museum of Natural History and Science Bulletin, v. 82, p. 513–523.
- Xing, L., Dai, H., Wei, G., Lockley, M.G., Klein, H., Persons, W.S., Wang, M., Jing, S., and Hu, H., 2020, The Early Jurassic *Kayentapus* dominated tracks from Chongqing, China: Historical Biology, v. 33, no. 10, p. 2067–2073.
- Xing, L., Lockley, M.G., Mart, D., Zhang, J., Wang, Y., Klein, H., McCrea, R.T., Buckley, L.G., Belvedere, M., Mateus, O., Gierliński, G.D., Piñuela, L., Persons, W.S., IV, Wang, F., Ran, H., Dai, H., and Xie, X., 2015, An ornithopod-dominated tracksite from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, south-central China—new discoveries, ichnotaxonomy, preservation and palaeoecology: PLoS ONE, v. 10, no. 10, e0141059.