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EUBRONTES OUT WEST (AND BEYOND)—DISTRIBUTION, MORPHOLOGY, ICHNOTAXONOMY, AND ASSOCIATED ICHNOFAUNA OF FOOTPRINTS OF LARGE, EARLY JURASSIC THEROPOD TRACKMAKERS

Martin G. Lockley, James O. Farlow, Andrew R.C. Milner, and Jack Davidson

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Cover

Left: Two **Dilophosaurus** *producing* **Eubrontes** *footprints. Portion of an illustration called the "Kayenta Timeline" by Brian Engh, LivingRelicProductions.com, commissioned by the St. George Dinosaur Discovery Site. Right: Three* **Eubrontes** *tracks in a trackway in the lower Kayenta Formation at the Warner Valley Tracksite, Washington County, Utah. Photograph by Andrew Milner.*

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Eubrontes Out West (And Beyond)—Distribution, Morphology, Ichnotaxonomy, and Associated Ichnofauna of Footprints of Large, Early Jurassic Theropod Trackmakers

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ABSTRACT

The large theropod ichnogenus *Eubrontes* (footprint length >30 cm) has been reported from 168 sites in the Upper Triassic–Lower Jurassic Glen Canyon Group of the Western United States, mostly from Utah. At most sites, the associated ichnofauna and their possible producers include one or more of the following ichnogenera: *Grallator* (small theropods), *Kayentapus* (medium-sized to large theropods), *Anomoepus* (small ornithischians), *Batrachopus* (crocodyliforms), and more rarely, *Otozoum* (“prosauropod” sauropodomorphs), *Moyenisauropus* (large ornithischians), and *Brasilichnium* (mammaliaforms), and also other synapsid ichnomorphotypes requiring further study. These are collectively considered representative of a globally widespread Early Jurassic tetrapod footprint biochron. Although tridactyl in almost all cases, *Eubrontes* tracks occasionally show hallux (digit I) traces, inviting comparison with *Gigandipus* (possibly a variant of *Eubrontes*), which has been tentatively identified at a single site in the Western United States. The common attribution of the Late Triassic–Early Jurassic *Eubrontes* trackmaker to *Dilophosaurus* is plausible but not proven; we reject the hypothesis that the *Eubrontes* trackmaker was a “prosauropod.” The ‘eponymous’ track *Dilophosauripus* is also a likely subjective junior synonym of *Eubrontes* or *Kayentapus*. Previous studies of these latter two ichnogenera suggest that they are distinct and separable on morphometric grounds, although this has been contested. Glen Canyon Group theropod tracks, including those in the allometric *Grallator-Anchisauripus-Eubrontes* plexus, are variable, with smaller morphotypes being more elongate and more strongly mesaxonic than larger morphotypes. These three ichnogenera, but especially the end members, *Grallator* and *Eubrontes*, probably do not represent the same species of trackmaker. Thus, with *Kayentapus* also considered, the Glen Canyon Group track record suggests a diversity of theropod trackmakers, in a theropod-dominated ecosystem, in which non-theropodan trackmakers were generally minor elements, even if locally abundant. The *Eubrontes* morphotype has been reported from some pre- and post-Jurassic tracksites. We compare and contrast footprint proportions of *Eubrontes* with those of other ichnotaxa attributed to large theropods and consider possible osteological correlates of the digit III and “heel” region proportions. Most notably, the Late Triassic–Early Jurassic *Eubrontes* differs from the larger Middle-Late Jurassic *Megalosauripus* in having proportionally a longer digit III and less well-developed “heel” pad.

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INTRODUCTION

This report has two parts. We begin by updating information about the distribution of the theropod ichnogenus *Eubrontes* reported from some latest Triassic and many Lower Jurassic tracksites in the Western United States, mostly from the broadly defined Glen Canyon Group. We then consider the associated vertebrate ichnotaxa in order to characterize the make-up and diversity of the ichnofaunas of which *Eubrontes* was a conspicuous component, and compare the distribution, facies relationships, and stratigraphic range of *Eubrontes*-rich ichnofaunas in the Western United States.

Because of its importance as one of the earliest formally described large theropod ichnogenera, *Eubrontes* has been a touchstone for nearly all subsequent descriptions of large theropod ichnotaxa. The second part of this report consequently evaluates ichnomorphological variability within and beyond *Eubrontes,* comparing and contrasting this ichnogenus with footprints that have been described under different ichnotaxonomies, not just from the Upper Triassic–Lower Jurassic, but also from later epochs. We then consider how differences between *Eubrontes* and other large theropod ichnotaxa may relate to skeletal morphology of the trackmakers.

THE GENUS *EUBRONTES*: AN HISTORICAL OVERVIEW

Originally named by Hitchcock (1845) based on tracks from the Lower Jurassic of New England, *Eubrontes* has long been recognized, almost universally, as the tracks of a large theropod (cf., Thulborn, 1990; Lockley, 1991; Olsen et al., 1998; Lucas et al., 2006a; Getty and Thomas, 2017; Farlow et al., 2018, 2022, 2025; but see Weems, 2003, 2019, for an alternative view) with footprint lengths (L) in the broad range of 30 to 40 cm, thus representing one of the largest theropods known from this epoch. According to Lull (1904, 1915, 1953), who was the first to revise Hitchcock's work on *Eubrontes* and associated theropod ichnogenera from New England, "Five species are now included in the genus *Eubrontes*, of which *Eubrontes giganteus* is the genotype" (Lull, 1953, p. 179). According to Chure and McIntosh (1989) at least 17 other *Eubrontes* ichnospecies have been named, including three, *E. dananus*, *E. gracillimimus*, and *E. tuberosus*, originally named by Hitchcock (1845), and later assigned to *Anchisauripus,* and *E. divaricatus, E. platypus*, and *E. tuberatus* named by Lull (1904, 1915). As noted by Chure and McIntosh (1989, p. 157) some reports do not contain diagnoses, and we note that many names have rarely been used. Thus, those names are of dubious value. Farlow et al. (2018), explicitly stated that their goal was to describe the morphometric variation in *Eubrontes* and other tridactyl (mostly theropod) tracks. However, they used various nominal *Eubrontes* ichnospecies names applied by previous workers (particularly Rainforth, 2005) to identify individual specimens, almost all of which also have specimen numbers. Farlow et al. (2018) did not comment on the validity of these ichnospecies' names. Likewise, many *Eubrontes* specimens from the Western United States also have specimen numbers, even though no ichnospecies names have been applied.

In contrast to the apparent historical over-splitting of the ichnogenus *Eubrontes*, Olsen (1980) compared the classic Hitchcockian theropod ichnotaxa *Grallator, Anchisauripus*, and *Eubrontes*, using simple morphometric parameters, to show that these three ichnogenera differed in length and width proportions, implying differences in trackmaker foot structure, with smaller tracks (*Grallator*) being narrower and the larger forms (*Eubrontes*) being wider (Figure 1). However, based on the application of allometric principles, Olsen (1980) concluded that the three ichnogenera could be considered part of a *Grallator-Anchisauripus-Eubrontes* or GAE plexus. Thus, Olsen downgraded the ichnogenera into sub-ichnogenera "lumped" into the super ichnogenus *Grallator,* as *Grallator* (*Grallator*)*, Grallator* (*Anchisauripus*), and *Grallator* (*Eubrontes*) as the "GAE plexus." This proposal was followed, briefly, by a few ichnologists (Gierliński, 1991; Gierliński and Ahlberg, 1994), and Rainforth (2005) took a similar "lumping" approach in assigning all to ichnogenus *Eubrontes*. However, Olsen et al. (1998, p. 586) subsequently reversed the earlier interpretation with the statement that the original three ichnotaxa (*Grallator, Anchisauripus*, and *Eubrontes*) could be treated as "distinct ichnogene-

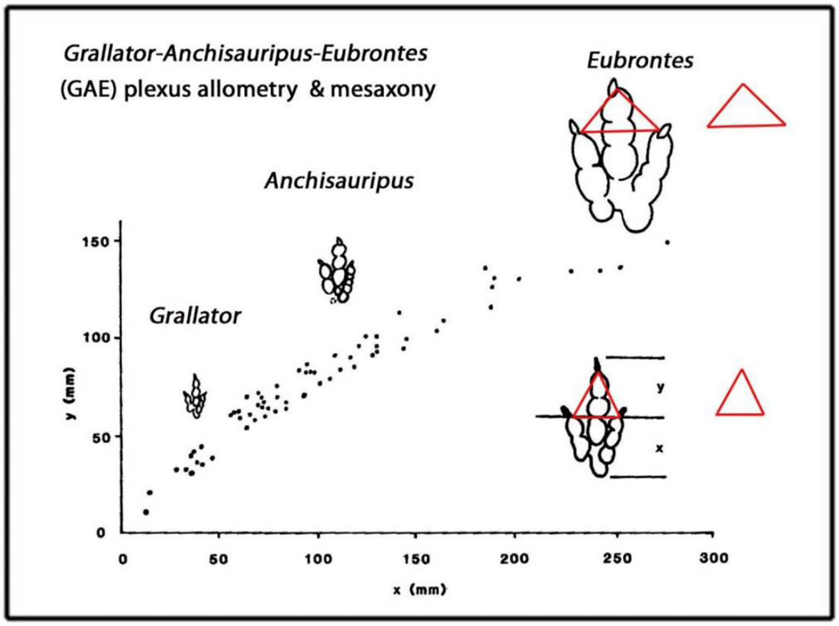


Figure 1. The *Grallator-Anchisauripus-Eubrontes plexus*. Modified after Olsen (1980, Figure 21); and Lockley and Hunt (1995, their Figure 4.6). End members (*Eubrontes* above and *Grallator* below) shown at the right, with the anterior triangle defined by the distal ends of digits II–IV illustrated. Note the increase in relative width of tracks with increasing size, and the associated decrease in relative ichnological mesaxony, as the anterior triangle also becomes relatively wider.

ra" thanks to "the rigorous establishment of these classic ichnological forms." They also opined (op. cit. p. 586) that "it is possible that their major proportional differences derive from allometric growth with individuals of several related species in one genus or even within one species of trackmaker." This suggests that the original suggestion that the trackmakers of GAE plexus could represent a single genus or species, might still be a possibility, notwithstanding these authors' willingness to separate the three ichnogenera. We consider this "one trackmaker species hypothesis" unlikely based on Farlow et al. (2018), who showed that morphological variation within *Eubrontes* and related forms is greater than the "within" species (intraspecies) variation recorded from morphometric analysis of the footprints of a single extant avian species, the emu (*Dromaius novaehollandiae*).

Olsen et al. (1998) regarded *E. giganteus* as a valid ichnospecies and the type of *Eubrontes*, represented by "Appleton Cabinet" specimen ACM-ICH 15/3 from the Portland Formation at Holyoke, Massachusetts. This, confusingly, is not the same specimen as either ACM-ICH 45/8 substituted for the type of *E. giganteus* by Hitchcock (1865), or ACM-ICH 45/1, which Lull (1904, 1915, 1953) referred to as the type. For a discussion of the historic confusion over the type specimens, see Olsen et al. (1998, p. 592).

Given the complexities surrounding *Eubrontes* and GAE plexus ichnotaxonomy in general, it is not surprising that the label *Eubrontes* is frequently used without any ichnospecies assignment, implying *Eubrontes* isp., as in Chure and McIntosh (1989, p. 167), *Eubrontes* ichnosp. indet., cf. *Eubrontes*, or more generally *Eubrontes sensu lato*. This lumper (non-splitter) approach is particularly relevant to the present study, which aims to survey reports of *Eubrontes* in the Upper Triassic–Lower Jurassic of the Western United States, where it is both abundant and relatively ubiquitous.

INSTITUTIONAL, LOCATION, AND SPECIMEN ABBREVIATIONS

Institutions and Locations

ACM-ICH, Beneski Museum of Natural History, Amherst, Massachusetts, USA (abbreviated AC); **AGB**, Anhui Geological Museum, Hefei, Anhui Province, China; **AMNH**, American Museum of Natural History, New York, USA; **AODF**, Australian Age of Dinosaurs Museum, Winton, Queensland, Australia; **Bandstand**, tridactyl print mounted in the downtown bandstand, Glen Rose, Texas, USA; **BHI**, Black Hills Institute of Geological Research, Hill City, South Dakota, USA; **BIBE**, Big Bend National Park collection, Perot Museum of Science and Nature, Dallas, Texas, USA; **BMNHC**, Beijing Museum of Natural History, China; **BPM**, Beipiao Paleontological Museum, Liaoning, China; **BSP**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **BYUMP**, Brigham Young University Museum of Paleontology, Provo, Utah, USA; **CAGS**, Chinese Academy of Geological Sciences, Beijing, China; **CANY,** Canyonlands National Park, Utah, USA; **CEUM**, Utah State University Eastern Prehistoric Museum, Price, Utah, USA; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; **CMC**, Cincinnati Museum Center, Cincinnati, Ohio, USA; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **CP,** Los Corrales del Pelejón tracksite, Teruel, Spain; **CPI**, Centro de Interpretación Paleontológico de La Rioja, Igea, Spain; **CR,** Copper Ridge tracksite, Grand County, Utah, USA; **Culp**, Culpeper Quarry, Virginia, USA; **DeQueen**, CertainTeed Gypsum Mine, Howard County, Arkansas, USA; **DNHM**, Dalian Natural History Museum, Dalian, China; **DSP**, Dinosaur State Park, Rocky Hill, Connecticut, USA; **DVSP**, Dinosaur Valley State Park, Glen Rose, Texas, USA; **EME PV**, Vertebrate Paleontology Collection, Transylvanian Museum Society, Cluj-Napoca, Romania; **F6**, F^6 Ranch tracksite, Kimble County, Texas, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **FPMN**, Fukui Prefecture Museum Fukui, Japan; **GLCA**, Glen Canyon National Recreation Area, Page, Arizona, USA; **Hell**, Hell's Revenge tracksite, Grand County, Utah, USA; **HMNS**, Houston Museum of Natural Science, Houston Texas; **IGB**, Institute of Geology, National Academy of Sciences, Bishkek, Kyrgyzstan; **IVPP**, Institute of Paleontology and Paleoanthropology, Beijing, China; **JME**, Jura-Museum Eichstätt, Germany; **JPM**, Jinzhou Paleontological Museum, Jinzhou, Liaoning, China; **KOKM**, Kuzbass State Museum of Local Lore, Russian Federation; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California; **MB R**, Museum für Naturkunde, Berlin, Germany; **MCCM-LH**, Museo de Paleontológia de Castilla-La Mancha, Cuenca, Spain; **MCF-PVPH**, Museo Carmen Funes, Neuquén, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MiWG**, Museum of Isle of Wight Geology, England; **MMCh-PV**, Museo Municipal "Ernesto Bachmann," Villa El Chocón, Neuquén, Argentina; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **MOR**, Museum of the Rockies, Bozeman, Montana, USA; **MPC, MPC-D,** Institute of Paleontology, Mongolian Academy of Science, Ulaanbaatar, Mongolia**; MPCN**, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina; **MPEF**, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **MUJA**, Museo del Jurasico de Asturias – Colunga, Spain; **MWC**, Museums of Western Colorado, Fruita, Colorado, USA; **Nash**, Nash Dinosaur Tracksite, Granby, Massachusetts, USA; **NCSM**, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA; **NGMC**, **NGMV**, National Geological Museum of China, Beijing, China; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **NSM**, National Museum of Nature and Science, Tsukuba, Ibaraki, Japan; **Penaportillo**, Peñaportillo tracksite, La Rioja, Spain; **PIN**, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **PKUP**, Peking University, Beijing, China; **Purgatoire**, Purgatoire tracksite, Colorado, USA; **RMM**, Red Mountain Museum, Birmingham, Alabama, USA; **ROM**, Royal Ontario Museum, Toronto, Canada; **SGDS**, St. George Dinosaur Discovery Site at Johnson Farm, St. George, Utah, USA; **SM,** Sirindhorn Museum, Department of Mineral Sciences, Kalasin, Thailand; **SMA**, Sauriermuseum Aathal, Switzerland; **SMNS,** Staatliches Museum für Naturkunde, Stuttgart, Germany; **St Mary**, St Mary River Formation tracksite, Alberta, Canada; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **TPII** (abbreviated Tp), Museum of Ancient Life, Thanksgiving Point, Lehi, Utah, USA; **TxVP**, Texas Vertebrate Paleontology Collections, University of Texas, Austin, Texas, USA; **TY**, Teyaeyaneng tracksite, NW Lesotho, southern Africa; **UAM**, University of Arkansas Museum, Fayetteville, Arkansas, USA; **UALVP**, University of Alberta, Edmonton, Alberta, Canada; **UCM**, University of Colorado Natural History Museum, Boulder, Colorado, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA; **UCMZ,** University of Calgary Museum of Zoology, Alberta, Canada; **UFH**, Utah Field House, Vernal, Utah, USA; **UMNH**, Natural History Museum of Utah, Salt Lake City, Utah, USA; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; **Warner**, Warner Valley tracksite, Washington County, Utah, USA; **WH**, Museum Victoria, Australia; **XIY**, Xiyang, Yunnan, China; **YPM**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; **ZCDM**, Zhucheng Dinosaur Museum, Zhucheng, Shandong, China; **ZIN PH**, Paleoherpetology Collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; **ZLJ**, Lufeng World Dinosaur Valley, Lufeng, China; **ZPAL Mg-D,** Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Species Name Abbreviations for Non-Coelurosaurian Skeletal Taxa

Af, *Allosaurus fragilis*; **Aj**, *Allosaurus jimmadseni*; **Ak**, *Alpkarakush kgyrgyzicus*; **Asp**, *Allosaurus sp.*; **Cb**, *Coelophysis bauri*; **Cc**, *Concavenator corcovatus*; **Cn**, *Ceratosaurus nasicornis*; **Dw**, *Dilophosaurus wetherilli*; **Eb**, *Elaphrosaurus bambergi*; **Eub,** *Eucoelophysis baldwini*; **Gs**, *Gualicho shinyae*; **Ki**, *Koleken inakayali*; **Kl**, *Kyacursor longipes*; **Ns**, *Neovenator salerii*; **Rl**, *Riojavenatrix lacustris*; **Sd**, *Sinraptor dongi*; **Sb,** *Skorpiovenator bustingorryi;* **Tt**, *Torvosaurus tanneri*.

EUBRONTES OUT WEST

Tracksites and Research History

Eubrontes and other tridactyl dinosaur footprints occur in the broadly defined Glen Canyon Group represented by the Wingate, Moenave, Kayenta, and Navajo Formations over a wide region (Appendix A; Figures 2 through 4), including large parts of Arizona, Utah, and more localized regions in Colorado. Similarly aged rock units, such as the Nugget Sandstone of Utah, Idaho, Wyoming, and Colorado, and the Aztec Sandstone of Nevada and California, apart from two localities in northeastern Utah (localities 30 and 31 on Figures 2 and 3, and Appendix A), to date lack localities with confidently identified *Eubrontes*. (We use "locality" in the sense of a cataloged/numbered fossil locality and so has the same meaning as "site" or "tracksite" [Figure 3 and Appendix A]).

Gregory (1917, p. 56, plate IXC) described beds between the Wingate and Navajo Sandstones in the Navajo Canyon area, Arizona (locality 14-1 on Figure 3 and Appendix A), containing tracks which, he wrote, "Prof. Lull" had suggested resembled "*Eubrontes giganteus*, but…larger and more robust" with "an immensely thick middle digit" reaching a length of 22 inches (about 55 cm) compared with only 10 to 15 inches (25–37.5 cm) in the Connecticut Valley forms. Apparently, this was the first report of *Eubrontes* from the Western United States by a professional geologist/paleontologist. Gregory (1917) indicated that the site also yielded smaller theropod tracks, which Lull compared with *Anchisauripus*. Whether the *Eubrontes* label is appropriate, or not, cannot be determined without analysis of the original material.

Welles (1971, p. 27) introduced the names *Kayentapus hopii* (Figures 5H and 6B) and *Dilophosauripus williamsi* (Figures 5G and 6D) for large theropod tracks from the Kayenta Formation near Tuba City in north-central Arizona (locality 13 on Figures 2 and 3, and Appendix A), commenting that "a complete study of the Plateau Province footprints would well repay the effort involved." Welles described *Dilophosauripus* tracks, which are not well preserved with regard to pad impressions, from footprints 27 feet (8.2 m) above the base of the Kayenta Formation (locality 13-2 on Figure 3 and Appendix A), and *Kayentapus* footprints, which are well preserved (Lockley et al., 2011), from near the top of the formation 412 feet (125.6 m) above the *Dilophosauripus* level (locality 13-3 on Figure 3 and Appendix A). Welles (1971) reported the length (L) and width (W) of *Dilophosauripus* as 32.5 cm and 28.0 cm (L/W = 1.16), respectively, with a step or pace of 106 cm and a digit II-IV divarication of 54°. The corresponding measurements of *Kayentapus* were 34.0 to 35.5 cm (L) and 29.0 to 29.5 cm (W) (L/W = 1.17 to 1.20), with a step of 188 to 191 cm and digit divarication (II to IV) of 60 to 72°. Welles (1971) placed both new ichnotaxa in the ichnofamily Grallatoridae (Lull, 1904), even though ichnofamily Eubrontidae was available. In fact, Welles (1971) compared *Kayentapus* with *Grallator formosus*, an ichnospecies with a footprint length of about 17 cm,

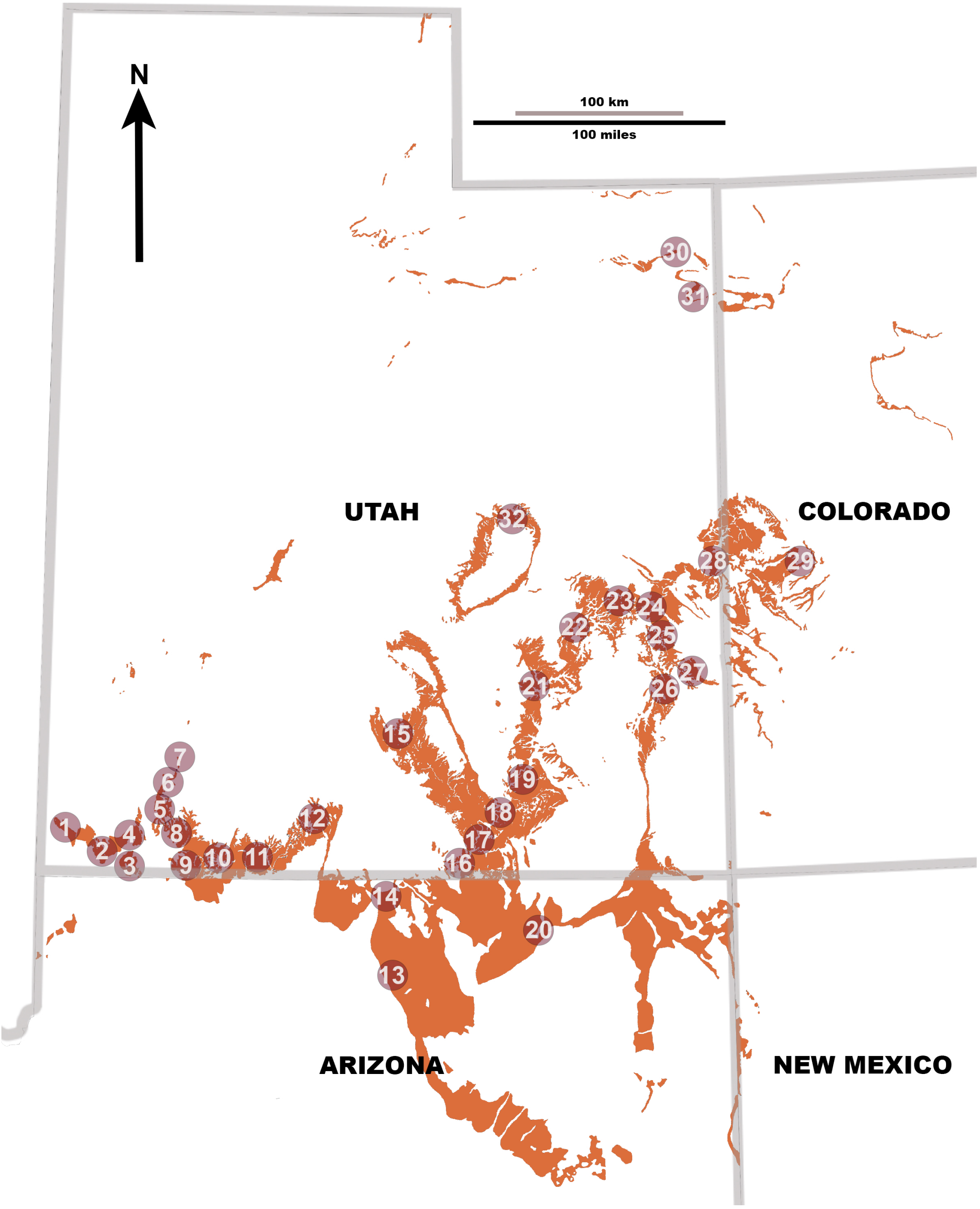


Figure 2. Distribution of *Eubrontes* and/or *Eubrontes*-like theropod tracks from the Lower Jurassic Glen Canyon Group and equivalent Nugget Sandstone (both represented in orange) across the American Southwest with localities in Utah, Colorado, and Arizona. Locality (site) numbers tie in with stratigraphic distributions (see Figure 3) and Appendix A.

half the size of *Kayentapus*. Welles did not compare *Dilophosauripus* or *Kayentapus* to each other or say why they were different at the ichnogenus level. As shown in the original illustrations (Welles, 1971), the most obvious differences are in the preservation of pad traces and greater and more variable digit divarication in *Kayentapus* (Lockley et al., 2011). Lockley (1986, p. 16) casually noted that tracks similar to *Kayentapus* from near Moab, Utah, are "close to tracks from the Connecticut Valley referred to as *Eubrontes* and *Anchisauripus*."

As summarized by Lockley et al. (2014d, p. 216), "Eriksen (1979a, 1979b) reported tracks of *Grallator tenuis* and *Eubrontes giganteus* from Cactus Park, Colorado (locality 29 in Figures 2 and 3, and Appendix A), supposedly from the Entrada Formation," which would make them of Middle to Late Jurassic age. Whereas the identification is not necessarily disputed, restudy of the site by Lockley and Hunt (1995, p. 115–117, their Fig-

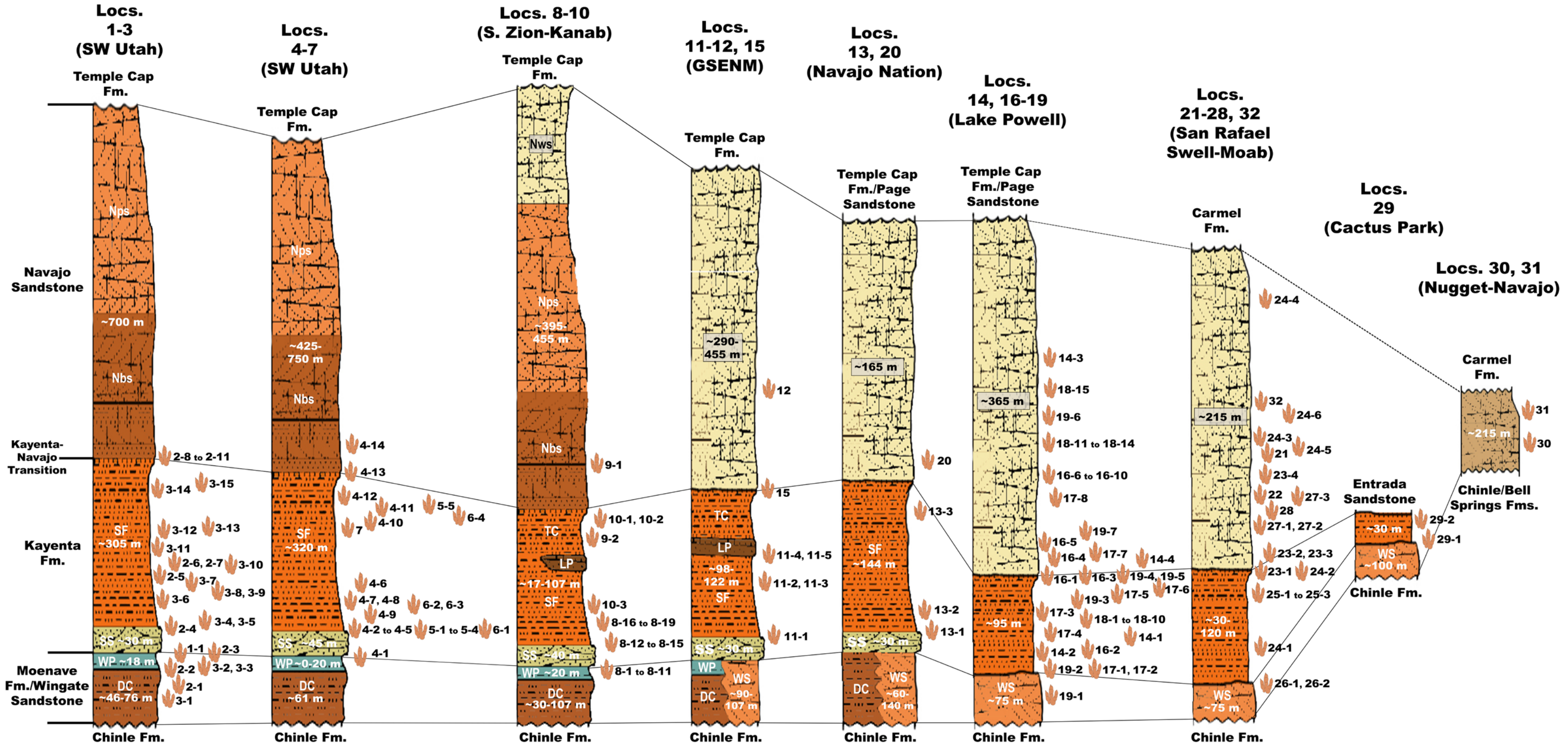


Figure 3. Generalized stratigraphic sections that correspond with regional locality (site) numbers in Figure 2 and estimated stratigraphic distribution of tracksites discussed in text and Appendix A. Regional locality numbers above each section: 1-3; 4-7; 8-10; 11-12, 15; 13, 20; 14, 16-19; 21-28, 32; 29; and 30-31. Modified from DeBlieux et al. (2006, their Figure 3). Specific locality numbers from Appendix A are positioned to the right of each stratigraphic section. Note that some stratigraphic sections are estimates and generalized over significant distances, whereas others may rely upon core log data. Abbreviations: DC = Dinosaur Canyon Member, Moenave Formation; LP = Lamb Point Tongue of Navajo Sandstone; Nbs = brown subunit of Navajo Sandstone; Nps = pink subunit of Navajo Sandstone; Nws = white subunit of Navajo Sandstone; SF = Silty Facies or Main Body of Kayenta Formation; SS = Springdale Sandstone Member, Kayenta Formation (some consider as upper member of Moenave Formation); TC = Tenney Canyon Tongue of Kayenta Formation; WP = Whitmore Point Member, Moenave Formation; WS = Wingate Sandstone.

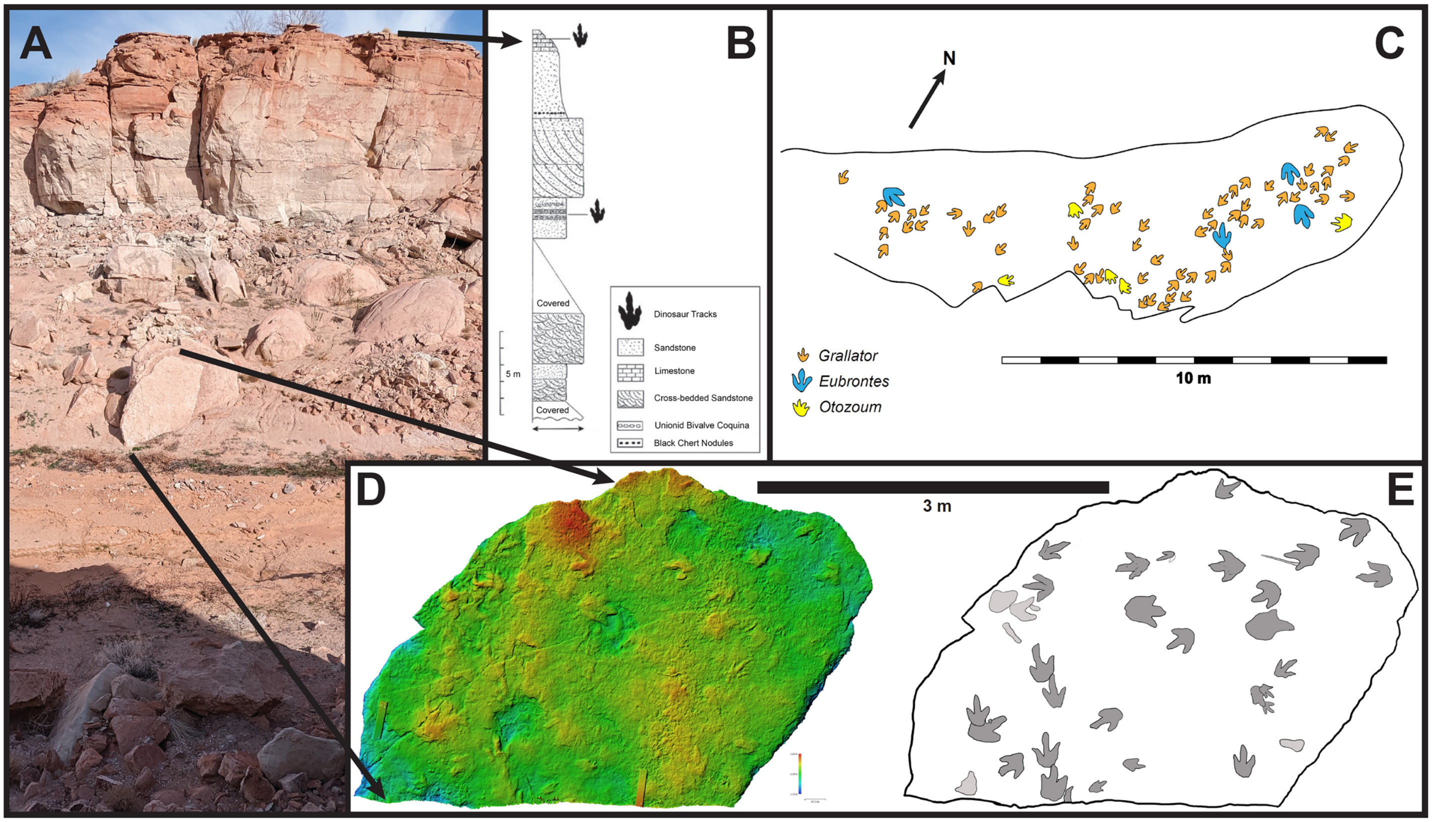


Figure 4. Representative tracksite maps and photographs of *Eubrontes*-bearing surfaces in the Kayenta–Navajo transition zone of the Slick Rock Canyon area, Lake Powell. After Lockley et al. (2014e, their Figure 4). (A) Outcrop and (B), the stratigraphic section corresponding to the photograph. (C) Map of an in situ surface near the top of the cliff. (D) False color depth map, generated from a photogrammetry model, of a large fallen block from the same stratigraphic level as C. (E) Line-drawing map of the fallen block. Note the dominance of tridactyl theropod tracks (*Grallator* and *Eubrontes*). B and C modified from Lockley et al. (2014, their Figure 4), and D and E modified from Milner et al. (2024, their Figure 15).

ure 4.5) suggested that it was "likely Early Jurassic in age, probably from the Wingate Formation," and further study unequivocally demonstrated that this and another nearby site represented the pre-Entrada, Kayenta Formation (Lockley et al., 2014d). Thus, arguably we can cite 1979 as the date of the second report of *Eubrontes* from the Western United States, in units of the Glen Canyon Group.

By the late 1980s and early 1990s it was becoming clear that tracksites were abundant in the Western United State (Gillette and Lockley, 1989; Thulborn, 1990; Lockley, 1991). Among them the Lower Jurassic Warner Valley Tracksite in southwestern Utah (Miller et al., 1989; localities 3 and 4 on Figures 2 and 3, and Appendix A); 19 trackways of a small morphotype (*Grallator*), and four trackways of a larger morphotype (*Eubrontes*), the latter with footprint lengths from 40.2 to 48.0 cm and widths between 24.3 to 36.3 cm (Figure 7). See Birthisel et al. (2011) for an update. Lockley and Conrad (1989, their Figure 14.6) indicated that the Glen Canyon Group is track-rich with *Eubrontes,* particularly abundant in interdune deposits.

By the mid and late 1990s an increasing number of Lower Jurassic tracksites yielding *Eubrontes* had been reported from the Western United States, including several such as the Troutwater Creek site, which had been mapped and collected (Lockley and Hunt, 1995, their Figure 4.8; locality 25-3 on Figure 3 and Appendix A), as well as what is today the Poison Spider Trailhead site (Lockley and Hunt, 1995, their Figure 4.13; locality

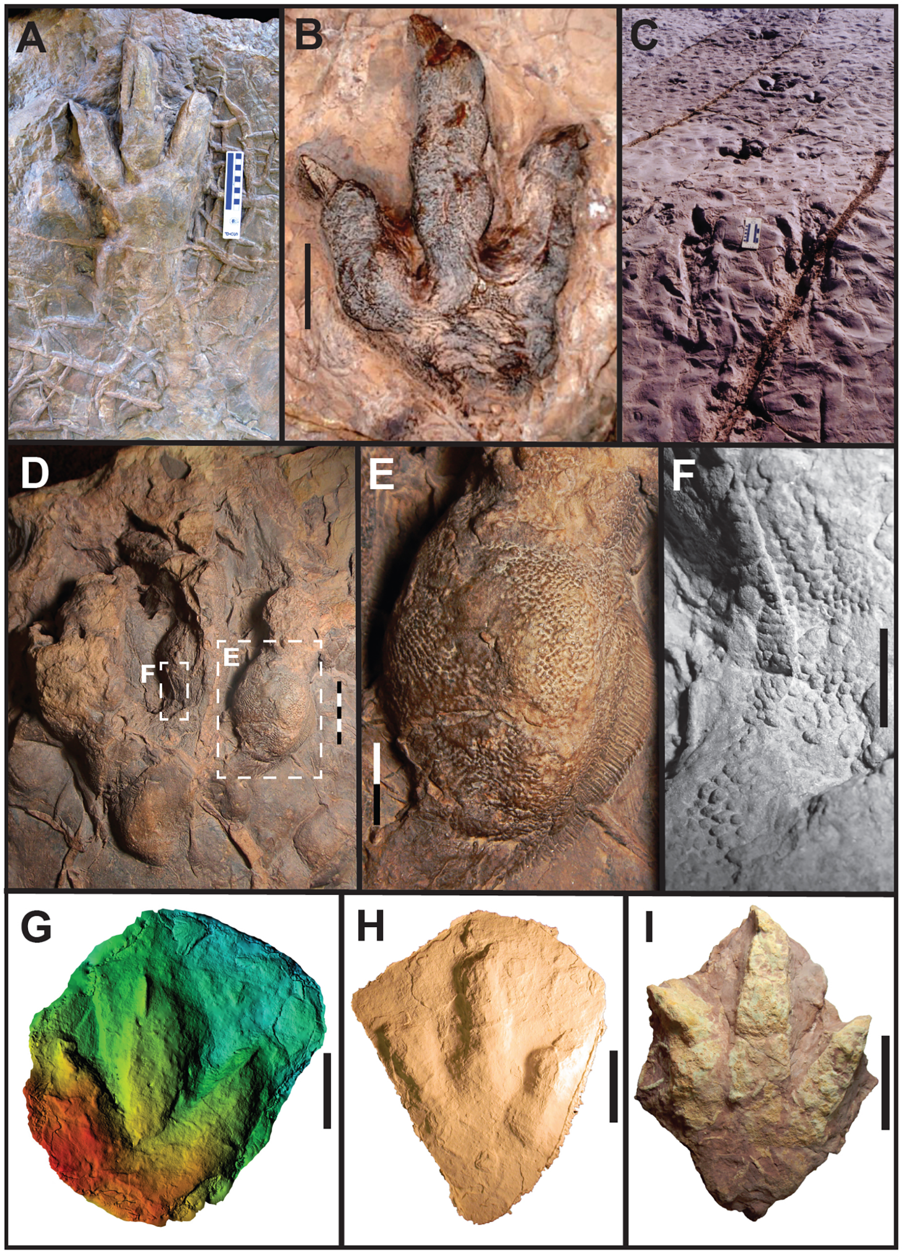


Figure 5. Selected large theropod tracks from the Western United States. (A) Natural cast of left Eubrontes track with elongate metatarsal trace and digit I impression from the "Main Track Layer," lower Whitmore Point Member, Moenave Formation, St. George Dinosaur Discovery Site (SGDS), southwest Utah (SGDS 8). (B) Exceptionally preserved left natural cast Eubrontes giganteus track from the SGDS (SGDS 9). Photograph courtesy Dan Whalen. (C) Resting Eubrontes trace and associated trackway from the "Top Surface Tracksite," SGDS (SGDS 18-T1). (D) Partial right natural cast Eubrontes track (SGDS 15) from the SGDS preserving skin impressions, and boxes (E and F) showing close-up images of skin traces and scale scratch lines on proximal phalangeal pad of digit II (E), and scale traces of proximal digit III pad (F). (G) Color contour image of holotype Dilophosauripus williamsi left track plaster replica from the Kayenta Formation near Tuba City, Arizona (UCMP 79690-4; UCM 124-10). (H) Plaster replica of a right track from holotype trackway (UCMP 83668; UCM 124-12) of Kayentapus hopii. This track is from the lower Kayenta Formation near Tuba City, Arizona. (I) Left natural cast Eubrontes track (GLCA 25456) discovered and salvaged by Michael Callihan and Andrew Milner in 2019 from the Kayenta–Navajo transition, Slick Rock Canyon area, Lake Powell, Utah. Scale for A though C, G through I = 10 cm, D = 5 cm, E = 2 cm; F = 1 cm.

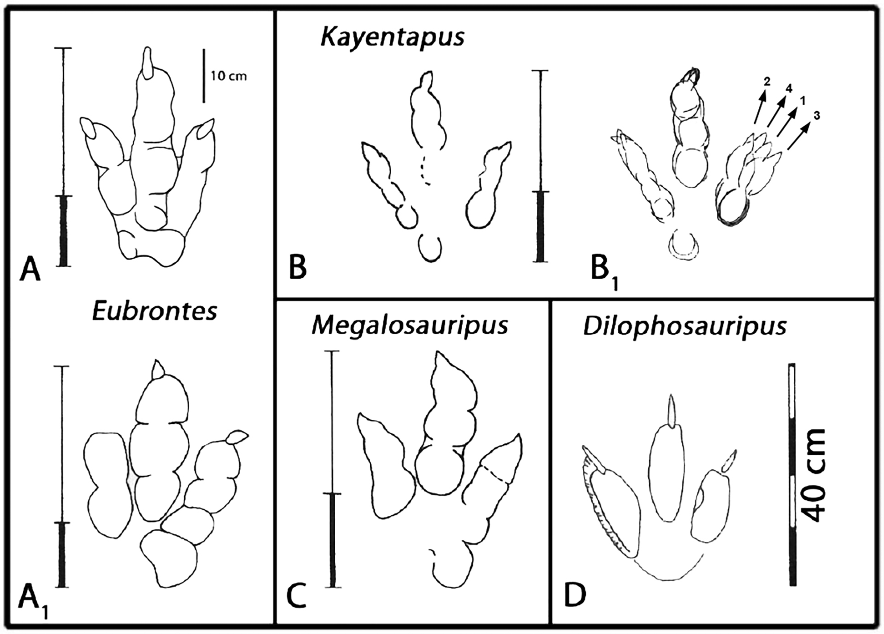


Figure 6. (A) *Eubrontes giganteus* after Olsen et al. (1998, their Figure 5A). (A_1) *Eubrontes* cf. *giganteus* after Lockley et al. (2000, their Figure 5). (B, B_1) *Kayentapus hopii* after Welles (1971, Welles' Figure 2) and Lockley et al. (2011, their Figures 2A and 5). (C) *Megalosauripus* after Lockley et al. (2000, their Figure 11). (D) *Dilophosauripus williamsi* after Welles (1971, Welles' Figure 1). The line segments in panels A through C show the relative lengths of the impressions of digit III (narrow lines) and the "heel" region (thicker lines); total footprint length is the sum of the thin and thick line segments for each footprint.

24-2 on Figure 3 and Appendix A herein), both from the Moab area of Utah in the Kayenta Formation.

Sites were also reported from the Navajo-Nugget Sandstone of the Dinosaur National Monument and Red Fleet Reservoir areas of northeastern Utah (Lockley et al., 1992; Hamblin and Bilbey, 1999; Hamblin et al., 2000; Lockley, 2011a; localities 31 and 30, respectively, on Figures 2 and 3, and Appendix A). Tracks from the Dinosaur National Monument site were referred to *Grallator* (*sensu lato*) by Lockley (2011a, p. 316), but at least one large tridactyl track (op. cit., figure 5) might be labeled cf. *Eubrontes*. Tracks attributable to *Eubrontes* from the Navajo-Nugget at Red Fleet Reservoir (locality 30 on Figures 2 and 3, and Appendix A) include specimens with this label in UCM collections, i.e., UCM 184.1, 184.3, and T134 (Appendix B; the prefix letter "T" indicates a tracing of the footprint outline), and specimens in the UFH collections (specimens UFH-87-6-6 and 87-6-8 as well as several uncatalogued examples).

Eubrontes was also identified from several of the 35 fossil footprints localities reported from the Glen Canyon National Recreation Area (GLCA), also known as Lake Powell, by Lockley et al. (1998). At that time, 20 of the 35 reported localities were identified as representing the Glen Canyon Group (3 Wingate, 5 Kayenta, and 12 Navajo). Among these, sites at Mike's Mesa (locality 18-7 on Figure 3 and Appendix A), Explorer Canyon (localities 18-6, 18-8, and 18-9 on Figure 3 and Appendix A), Rainbow Bridge (locality 16-1 on Figure 3 and Appendix A), and Glen Canyon Dam (Stokes, 1978; locality 14-3 on Figure 3 and Appendix A) were identified as having yielded *Eubrontes* (or cf. *Eubrontes*) tracks. Many more *Eubrontes* sites have been identified in this large area since the 1990s, thus considerably expanding the previous Lockley et al. (1998) database.

The 2000s decade saw more significant reports and studies of *Eubrontes* tracksites. Arguably the most important new discoveries were those made in the track-rich Moenave Formation in and around St. George, Washington County, southwestern Utah, namely the St. George Dinosaur Discovery Site at Johnson Farm (SGDS; localities 2-1 and 2-2 on Figure 3 and Appendix A). See Milner et al. (2006a, 2006b, 2009, 2012); Milner and Spears (2007); Harris and Milner (2015); Martz et al. (2017) and Hurtado et al. (2024). Many other significant *Eubrontes*-yielding tracksites have been discovered nearby (Hamblin et al., 2006; Lockley et al., 2006b; Milner et al., 2012). Apart from the large number of *Eubrontes* tracks discovered at the SGDS site, preserved on multiple stratigraphic levels, mostly as well-preserved natural casts (Figures 5A, 5B, and 5D), some with skin impressions (Figures 5E and 5F; Hendrickx et al., 2022), the site has proved especially important for a trackway

(SGDS 18-T1; Figure 5C) of a dinosaur that squatted down, leaving manus traces and intermittent tail traces (Milner et al., 2009). The SGDS site has also been a center for the study of exceptionally well-preserved theropod swim traces, including those large enough to have been produced by a *Eubrontes* trackmaker (Milner et al., 2006a, 2006b; Milner and Lockley, 2016).

A follow up survey of the track-rich Lake Powell area (GLCA) was conducted in the mid-2000s to take advantage of low water levels that exposed many previously submerged sites. As a result, the aforementioned total of about 20 Glen Canyon Group tracksites was increased considerably to 92, bringing the total of all fossil footprint sites in that area to more than 110. Additional sites have since been reported, but most have not been described in detail in the literature (cf., Lockley et al. [2014e]; Delgalvis [2015]; Lockley [2017]). The large number of localities from the Glen Canyon Group reflects the dominant outcrop in this vast area, extending about 160 miles (~257 km) from the downstream end of the lake at Page, Arizona, to the upstream end near Hite, Utah, with many side canyons in between. According to a locality report submitted by the University of Colorado Denver to the National Park Service (NPS) in the mid-2000s, *Eubrontes* was recognized at no fewer than 35 of these 92 Glen Canyon Group sites (9 of 16 in the Kayenta Formation, 12 of 30 in the Navajo-Kayenta transition zone, and 14 of 42 in the Navajo Sandstone); that number is increased in the present study to 45 *Eubrontes* localities. Note that much or all of what is referred to as the Navajo-Kayenta transition zone of Lockley et al. (2014e) is considered part of the Navajo Sandstone by Kirkland et al. (2011).

From 2010 through the present, Milner has followed in the wake of Lockley, with continued surveys of the track-rich Glen Canyon Group around Lake Powell (Milner et al., 2024), an area large enough to allow much survey work in 'new' areas. This has resulted in the discovery and documentation of several important tracksites dominated by *Eubrontes*. Three of the more important sites include Little Cave Cove in the Wingate Sandstone (Wood et al., 2021; Milner et al., 2024; locality 19-1 on Figure 3 and Appendix A), and the John Wesley Powell Track Block (Lockley et al., 2014e, their Figure 26; Lockley and Xing, 2015, their Figure 4; Milner et al., 2016, 2023b, 2024; locality 16-5 on Figure 3 and Appendix A) and Andre's Alcove Tracksite, both in the Navajo Sandstone (Bennett et al., 2023; Milner et al., 2024; locality 17-7 on Figure 3 and Appendix A), have been subject to extensive study, including well-preserved *Eubrontes* with associated *Batrachopus* from Andre's Alcove (Milner et al., 2024, their Figures 22A and 22B).

On a cautionary note, alleged footprints from a "tracksite" described as a trampled, wet interdunal surface containing abundant *Eubrontes* footprints from the Navajo Sandstone in the Coyote Buttes area of northern Arizona (Seiler and Chan, 2008), are in fact erosional potholes, and not the tracks of theropod dinosaurs (Breithaupt et al., 2021). Abundant, real tracksites have been recorded nearby, but none to date preserves *Eubrontes* (Milàn et al., 2008).

Given the large number of GLCA sites (45) with *Eubrontes* (Figure 4), as well as sites from other regions, all representing the Glen Canyon Group or its equivalents, there is clearly a large database surrounding this ichnogenus, and associated ichnotaxa, in the Western United States, to say nothing of its global distribution (Lucas, 2007).

Tracksite Configurations: Large vs. Small and Single vs. Multiple Surfaces

Among the total of 168 localities from which *Eubrontes* and/or *Eubrontes*-like tracks has/have been identified (Appendix A), a significant number represent large surfaces (30 feet [10 m] or more—sometimes hundreds of feet—across their largest expanse), which have been mapped (or remain to be mapped), to show the configuration of *Eubrontes* and other associated trackways. Some sites (e.g., SGDS) reveal multiple track-bearing levels (20 stratigraphic horizons; see Kirkland et al., 2014), and not all levels at a "*Eubrontes* locality" will reveal that ichnogenus. Ideally for census purposes it should be possible to list the number of tracks and trackways of each ichnotaxon, for each level. However, this is not always possible, and so generalized statements are made, identifying two or more ichnotaxa, without giving the proportions identified either as individual footprints or trackways.

Published site maps are available for the following sites in roughly ascending stratigraphic order: (1) a single Wingate Sandstone tracksite named Little Cave Cove by Lake Powell, Utah (Wood et al., 2021, their Figure 4; Milner et al., 2024, their Figure 12; locality 19-1 on Figure 3 and Appendix A); (2) several track horizons at SGDS in the Moenave Formation (Milner et al., 2006a, 2006b, 2012, their Figures 13, 15, 17; Williams et al., 2006, their Figure 4; locality 2-2 on Figure 3 and Appendix A); (3) the Warner Valley Tracksite (locality 3-4 on Figure 3 and Appendix A) in the lower Kayenta Formation, formerly considered to be in the Moenave Formation (Miller et al., 1989); Birthisel et al., 2011; Miller et al., 2012, their Figure 59); (4) the Grapevine Pass Wash or Spectrum Tracksite from a single surface at the top of the Springdale Sandstone Member of the Kayenta Formation (Hamblin et al., 2006, Figure 3; locality 2-4 on Figure 3 and Appendix A), and five sites from three different levels of the Kayenta Formation at the Desert Tortoise (DT) site designated as the DT1 level, DT2 through DT5 levels (Lockley et al., 2006a; Milner and Spears, 2007; localities 4-3 to 4-6 on Figure 3 and Appendix A); (5) a partial tracksite map of the Hamblin (Ws206T) Tracksite from roughly the middle part of the Kayenta Formation partly illustrated in Milner et al. (2012, their Figure 58; locality 3-13 on Figure 3 and Appendix A) but has not yet been formally described; and (6) the Washington City Water Tank Tracksite (Hamblin et al., 2006, their Figure 5; locality 2-7 on Figure 3 and Appendix A).

The utility of these maps, some of which represent quite large areas, is that they give an indication of track density over large areas; e.g., 13 trackways were registered in an area about 60 x 225 feet (20 x 75 m) at site DT2, whereas 31 trackways were registered in a similar sized area (about 45 x 240 feet [15 x 80 m]) at site DT4. The Flag Point Tracksite (Lockley et al., 2006a; locality 11-2 on Figure 3 and Appendix A), is also mapped in the Kayenta Formation near Kanab, Utah. (7) Two large surfaces (Flat Iron Mesa sites 1 and 2) have been mapped in the Kayenta Formation near Moab (Lockley et al., 2018d; localities 25-1 and 25-2 on Figure 3 and Appendix A), but many of the large theropod tracks here might be referable to *Kayentapus*. (8) The small Kane Creek site (no longer accessible, due to road widening; locality 24-1 on Figure 3 and Appendix A), and (9) the multi-surface Poison Spider sites (locality 24-2 on Figure 3 and Appendix A), also near Moab, were first mapped in the 1980s (Lockley, 1986; see Lockley and Hunt, 1995, for update), and the (10-11) Cactus Park sites in Colorado (Lockley and Hunt, 1995; Lockley et al., 2014d; localities 29-1 and 29-2 on Figure 3 and Appendix A) also represent the Kayenta Formation. The (12) Granite Creek site was also mapped (Lockley et al., 2014c; locality 28 on Figures 2 and 3, and Appendix A). At least five (13-17) Kayenta-Navajo transition zone sites from GLCA have been mapped, including sites from Slick Rock Canyon (Figure 4; localities 18-1 to 18-5 on Figure 3 and Appendix A; see also Milner et al., 2024, their Figure 15) from known stratigraphic levels, and other sites from (18-20) Explorer Canyon (localities 18-6, 18-8 to 18-10 on Figure 3 and Appendix A) and the (21) mouth of Escalante Canyon (locality 17-1 on Figure 3 and Appendix A), which represent fallen blocks (Lockley et al., 2014e).

Large mapped tracksites in the Navajo Sandstone include the (22) Mail Station Dinosaur Tracksite (Breithaupt et al., 2020; Lockley et al., 2021; locality 27-2 on Figure 3 and Appendix A), which is being used by the U.S. Bureau of Land Management (BLM) as an educational site, and maps of the (23) John Wesley Powell Track Block (Lockley et al., 2014e, their Figure 26; Milner et al., 2016, 2023b, their Figure 2B; locality 19-1 on Figure 3 and Appendix A). The afore-listed sites for which maps are available represent about 1/5 (about 30/168) of the known *Eubrontes* sites.

Reports from the 1980s and 1990s predated the widespread use of GPS and three-dimensional (3D) imaging technology. Records of tracks, trackways, and tracksites used traditional methods of documentation such as two-dimensional (2D) photography, track measurements, tracing on transparent overlays, compass and tape mapping of sites, and replication. These methods are still used to varying degrees and may still be the most effective where tracks have little or no relief. With the growth of the Internet, traditional forms of documentation, including simple 2D photography, can be disseminated through this medium.

Paleoecology: Ichnofacies, Faunas, and Biochrons

Eubrontes is abundant throughout most of the Glen Canyon Group of the Colorado Plateau region, mostly at sites in Utah, but also in northern Arizona and western Colorado. The 168 sites that have been discovered, reported, and collected, mostly since the late 1980s, do not include other known Glen Canyon Group sites that have not, or not yet, yielded *Eubrontes*. Thus, the rate of discovery of *Eubrontes* sites has been at least two per year, and is accelerating, with an "approximately" equal number of other non-*Eubrontes* tetrapod Glen Canyon Group tracksites. This contrasts with a relatively sparse body fossil record throughout most of the group, especially in the predominantly "sandy facies" (Galton, 1971; Colbert, 1981; Irmis, 2005; Sertich and Loewen, 2010; Milner et al., 2023a, 2024; Marsh et al., 2024). The "silty facies" of the Kayenta Formation is richer in body fossils (Brady, 1936; Colbert and Mook, 1951; Crompton and Smith, 1980; Welles, 1984; Rowe, 1989; Sues et al., 1994; Tykoski et al., 2002; Marsh and Rowe, 2018, 2020; Milner et al., 2023a, 2024).

All of these tracksites sample the Lower Jurassic faunas of this region. Like other fossil tracks, many have biostratigraphic utility and help delineate biochrons, which are simply defined as fossil faunas or floras with relatively short time ranges. They are the time equivalents of biostratigraphic zones.

The so-called Lower Jurassic "Tetrapod Footprint Biochron" (*sensu* Lucas, 2007) has been characterized as the first globally widespread tetrapod footprint biochron, consisting of dominant elements (*Grallator* and *Eubrontes*) and persistent, but less abundant, elements like *Otozoum, Anomoepus, Moyenisauropus*, and *Batrachopus* in the fluvio-lacustrine and interdune facies, and *Brasilichnium* (with small grallatorids) in the dune facies (Rainforth and Lockley, 1996a, 1996b; Irmis, 2005), as well as the purported small sauropodomorph track *Navahopus* (Baird, 1980; Milàn et al., 2008; Breithaupt et al., 2021; Milner et al., 2024; Foster et al., 2025). This evidence of sedimentary facies preferences is another argument for regarding dune-frequenting small *Grallator* trackmakers (footprint length [FL] about 3.5 cm according to Rainforth and Lockley, 1996a) as unrelated to small *Eubrontes,* which registered few tracks in the dunes, but rather, frequented interdune settings (Lockley, 2005). However, one exception is the North Moccasin Mountain Tracksite in the Navajo Sandstone near Kanab, Utah (locality 9-1 on Figures 2 and 3, and Appendix A), which preserves *Eubrontes,* cf. *Kayentapus, Grallator, Otozoum,* cf. *Anomoepus,* cf. *Brasilichnium,* and *Batrachopus* (Milner et al., 2012).

Throughout the Glen Canyon Group, the composition of ichnofaunas is similar from locality to locality, consisting of between one and seven of the afore-named ichnogenera. This consistency over a wide region and representing a significant span of time gives a high degree of confidence that the track record consistently samples the Lower Jurassic communities of the region (Lockley and Hunt, 1995; Irmis, 2005), even if it does not sample traces made by all animals, for reasons related to preservation bias or other factors.

Assuming the validity of the inferences made about the likely identity of the trackmakers at higher (supra-generic/familial) taxonomic levels, the reliability of track assemblages as representative of the regional fauna facilitates understanding of the paleoecology. For example, it is clear that the fauna was dominated by small and large theropods, the former with typical 5 to 10 cm footprint lengths, indicating hip heights on the order of 22.5 to 45.0 cm, and body lengths on the order of only 60 to 120 cm, according to the formulae of Alexander (1976) and Thulborn (1990) for hip height, and Xing et al. (2009) for body length (see Lockley and Xing, 2021) for discussion). By contrast, the equivalent size estimates for the *Eubrontes* trackmaker hip heights range up to about 2.2 m, and body lengths of up to about 5.8 m (Xing et al., 2009). Size estimates for the largest *Otozoum* trackmaker would be similar to those for the largest *Eubrontes* trackmakers. However, other tracks suggest the presence of various bipedal, intermediate-sized theropods and the small- and intermediate-sized *Anomoepus* (Lockley and Gierliński, 2006) and *Moyenisauropus,* representing ornithischians. The *Batrachopus* trackmaker was a small crocodylomorph quadruped (Olsen and Padian, 1986) with footprint lengths in the range of about 3.0 to 8.0 cm (Lockley et al., 2018a), and the *Brasilichnium* trackmaker was a small mammaliaform quadruped with track lengths in the range of 1.0 to 5.0 cm (Lockley, 2011), although other undescribed mammaliaform ichnotaxa likely produced by tritylodontids and possibly true mammals are known (Milner et al., 2024, p. 308, their Figures 20 and 21).

Lastly, we note that Hunt and Lucas (2007, 2016) proposed the naming of a Lower Jurassic *Eubrontes* ichnocoenosis that was a component of a larger "archetypal" *Grallator* ichnofacies associated with lacustrine margins. According to this definition, the *Eubrontes* ichnocoenosis is characteristic of the Lower Jurassic, and comparable to other Jurassic and post-Jurassic ichnocoenoses in which the tracks of bipedal avian and non-avian theropods dominate. In simplest terms, a tetrapod or vertebrate ichnocoenosis is a local or regionally recurrent assemblage of traces deemed to represent a biological community, usually associated with a particular environment (sedimentary facies), whereas an ichnofacies is a larger, more conceptual entity. For example, as used by Hunt and Lucas (2007, 2016) tetrapod or vertebrate ichnofacies have more global distributions and may be comprised of multiple ichnocoenoses (cf. Klein and Lucas, 2025). To cite examples mentioned above, dune and interdune ichnofaunas may be considered to represent *Brasilichnium* and *Eubrontes* ichnocoenoses, respectively. However, in each case they may also represent larger ichnofacies; e.g., dune ichnofacies are reported from the Pennsylvanian (Rowland et al., 2020) to Holocene and subsumed under the broad label of *Chelichnus* ichnofacies, in this case often with similar invertebrate traces.

EUBRONTES AND BEYOND: MORPHOMETRICS OF LARGE THEROPOD FOOTPRINTS

Footprints, Footprint Tracings, and Foot Skeletons

The University of Colorado Museum (UCM) is the repository of a collection of 266 GLCA specimens (originals, molds, and replicas) collected over a period of about 25 years. The UCM specimen catalog has 37 entries for *Eubrontes*, closely matching the aforementioned locality catalog.

Over a period of about 35 years, Lockley made full-sized tracings, as well as photographs with scale bars, of many of the better-preserved (greater anatomical fidelity; cf. Belvedere and Farlow, 2016; Marchetti et al., 2019) tracks from the above-described localities. These are reposited in the UCM; tracings have the prefix T; Figures 7 through 9). From these tracings comparative morphological measurements can be obtained (albeit with the caveat that such tracings have a degree of inherent subjectivity, due to the way the person tracing the footprints "sees" them). Some tracings correspond to collected specimens; others do not. However, since many tracings predate the introduction and widespread use of 3D photogrammetry and surface laser scanning, most (but not all) of the specimens are not represented by 3D images, unless restudied, and redescribed in later publications.

The UCM tracings collection comprises dozens of tracings, which represent the best-preserved tracks found at given sites; i.e., well-preserved pad impressions, thus ranking as 3, at the top of the 0-1-2-3 preservation scale proposed by Belvedere and Farlow (2016; see Marchetti et al. [2019] for updates). The UCM traces are a primary data source for much of the data analyzed in this study. As a general rule, we have only illustrated and reported reliable measurements for purported *Eubrontes* tracks that show all diagnostic theropod pad impressions and therefore score as number 3 on the aforementioned preservation scale, showing the 2-3-4 phalangeal pad configuration corresponding to digits II, III, and IV. We bear in mind that some pad traces may not be discretely separated due to size-related variability in track morphology (Thulborn, 1990; Lockley, 2000a; Farlow et al., 2018); i.e., fusion of pads, obscuring pad-separating creases, may be a primary morphological feature (cf. Lockley, 2000a), albeit uncommon in most well-preserved *Eubrontes*. Almost all of the UCM tracings were made by the same person (Lockley) (Figures 6 through 9) and so have a measure of consistency that might be lacking if multiple observers were draw-

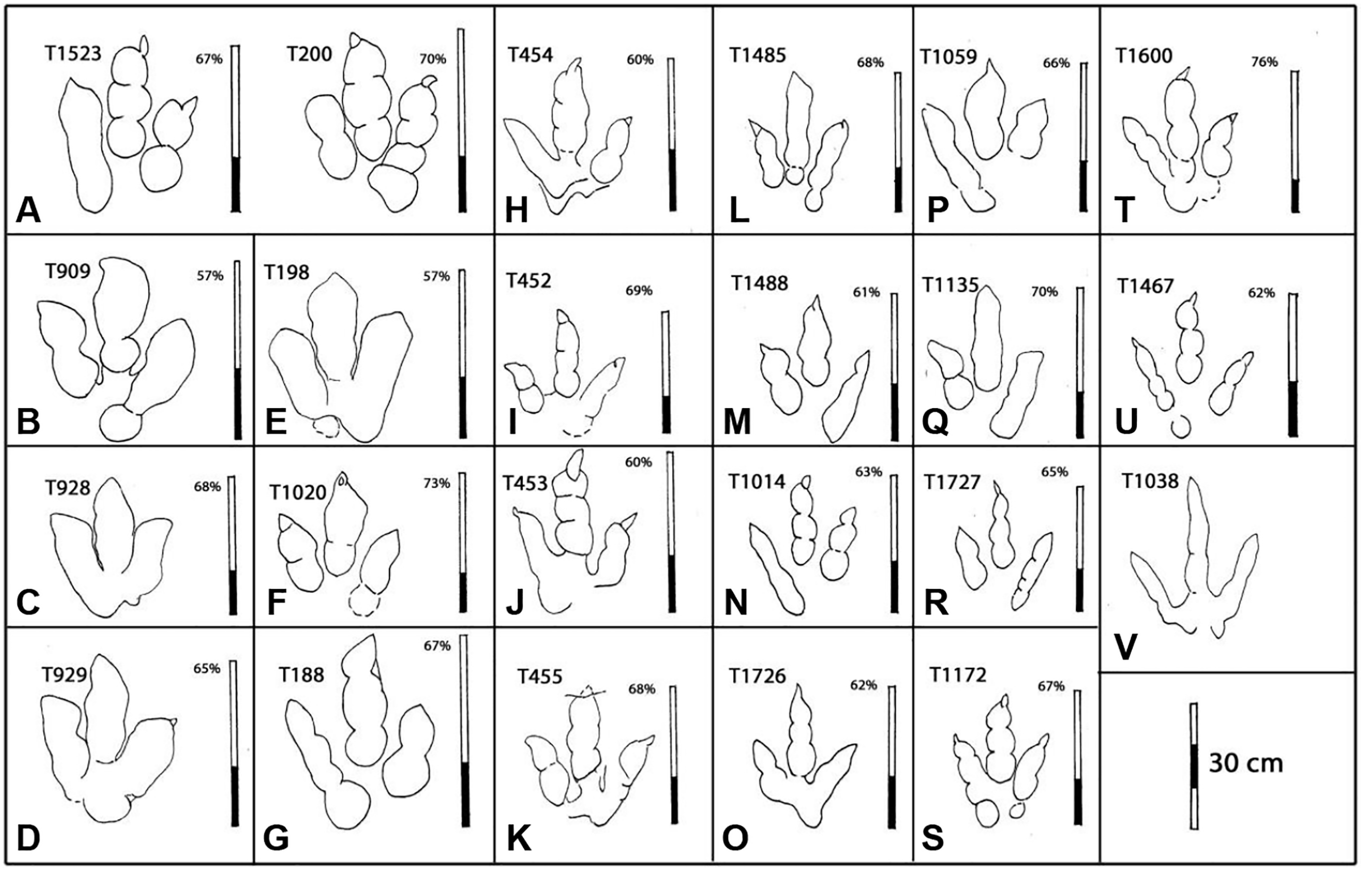


Figure 7. Tracings of 22 well-preserved purported *Eubrontes* tracks (A through T; preservation grade 3 of Belvedere and Farlow, 2016) from the Glen Canyon Group, with *Kayentapus* type specimen (U) and unidentified tridactyl track (V) for comparison. (A) Two *Eubrontes* from the lower Kayenta Formation, Warner Valley, southwestern Utah. (B) *Eubrontes* from the Navajo Sandstone, Sand Flats, Moab, east-central Utah. (C through E) *Eubrontes* from the Kayenta Formation, Explorer Canyon, Lake Powell (GLCA), Utah. (F) *Eubrontes* from the Kayenta-Navajo transition, Escalante Canyon, Lake Powell (GLCA), Utah. (G) *Eubrontes* from Hog Canyon, Kanab, Utah. (H through K) *Eubrontes* from the Moenave Formation, St. George, southwestern Utah. (L and M) *Eubrontes* from the Kayenta Formation, Cactus Park, Colorado. (N) *Eubrontes* from the Kayenta-Navajo transition, Slick Rock-Iceberg Canyons (GLCA), Utah. (O) *Eubrontes* from the Kayenta Formation, Flat Iron Mesa, Utah. (P) *Eubrontes* from the Navajo Sandstone, Moqui Man site (GLCA), Utah. (Q) *Eubrontes* from the Kayenta Formation, Flag Point, Utah. (R) *Eubrontes* from the Kayenta Formation, Flat Iron Mesa, Utah. (S) *Eubrontes* from northern Lake Powell (GLCA), Utah. (T) *Eubrontes* from the Navajo Sandstone, Granite Creek, Utah. (U) Type specimen *Kayentapus* from the Kayenta Formation, northern Arizona. (V) Slender-toed tridactyl from Choal Canyon 1 site (GLCA), Utah. All drawn to the same scale from the UCM tracings catalog (numbers with T prefix also listed in Appendix B). Vertical bars show length of digit III trace (white) as a percentage of total track length, with remaining "heel" region in black. See Appendix B for length (L), width (W), L/W anterior triangle, and divarication of these and other tracks. Compare with Figure 8. The 30 cm scale applies to all footprints.

ing outlines, as in the experiment reported by Thulborn (1990, Thulborn's Figure 4.15).

In addition to tracings of *Eubrontes*, the UCM collection includes tracings of other large tridactyl footprints, both from the early Mesozoic of the Western United States and from ichnofaunas from around the world. These tracings will be used as sources of measurement for comparison with *Eubrontes*. Lockley's full-size tracings are used to derive or check measurements of footprint length parallel to print long axis (L), maxi-

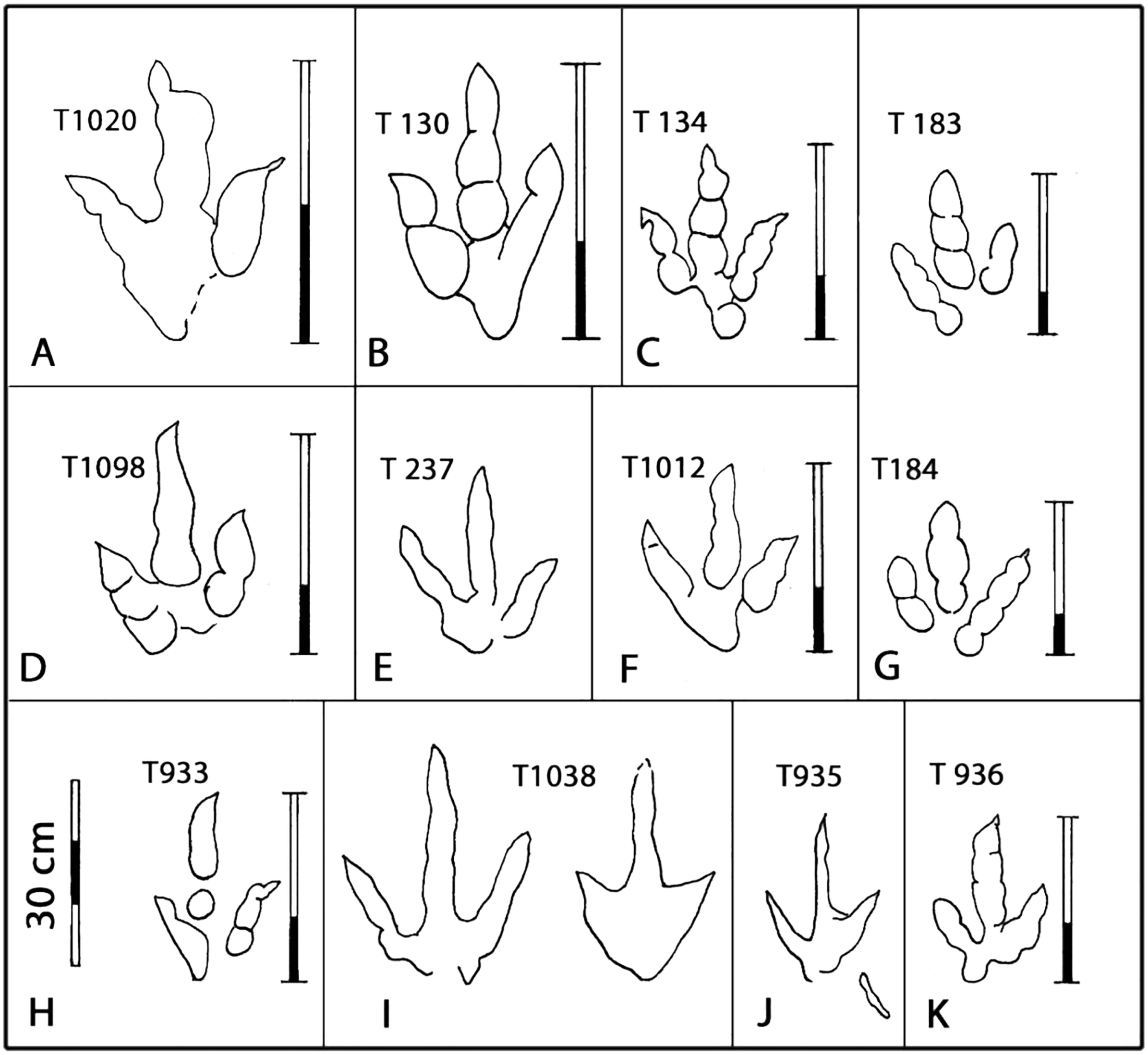


Figure 8. Tracings of 13 theropod tracks from *Eubrontes* localities in the Western United States. A through G, putative *Eubrontes* tracks. (A) Escalante site, Lake Powell (GLCA), Utah. (B) Elongate track from Dead Horse Point area, Utah. (C) Red Fleet Reservoir, Utah. (D) Modified from Trackway #9 of Desert Tortoise Tracksite (DT-4, Locality Ws342T), Utah (T1098; SGDS 1713; Lockley et al., 2006b, their Figures 8 and 10C). (E) Nokai Dome site (GLCA), Utah. (F) Slick Rock-Iceberg Canyons site (GLCA), Utah. (G) Desert Tortoise Tracksite, Washington County, Utah. (H and I) Theropod tracks with slender digit traces and strong mesaxony. (H) Choal Canyon 1 site (GLCA), Arizona. (I) Two tracks from Choal Canyon 1 site (GLCA), Arizona. (J) Track from Navajo National Monument, Arizona. (K) Slick Rock Canyon site (GLCA), Utah. All drawn to same scale from UCM tracings catalog. Note strong mesaxony of footprints in lower row (panels H through K). Vertical bars show length of digit III trace (white) as a percentage of total track length, with remaining "heel" region in black. See Appendix B for length (L), width (W), L/W anterior triangle, and divarication of these and other tracks. Compare with Figure 7.

mum footprint width (W), and the length/width (L/W) ratio of the anterior triangle (Appendix B; Figures 1 and 6 through 8); in many of the figures, footprint outlines are printed at the same size to facilitate comparison.

We use the UCM tracings to graphically depict the ratio of the length of digit III to that of the whole track (LdIII/L, Figures 6 through 8 [cf., Demathieu 1990; Lockley et al., 2000]). These measurements were made by Lockley. In most cases (Figures 6 through 8 [*Eubrontes* and *Megalosauripus* from Western North America])

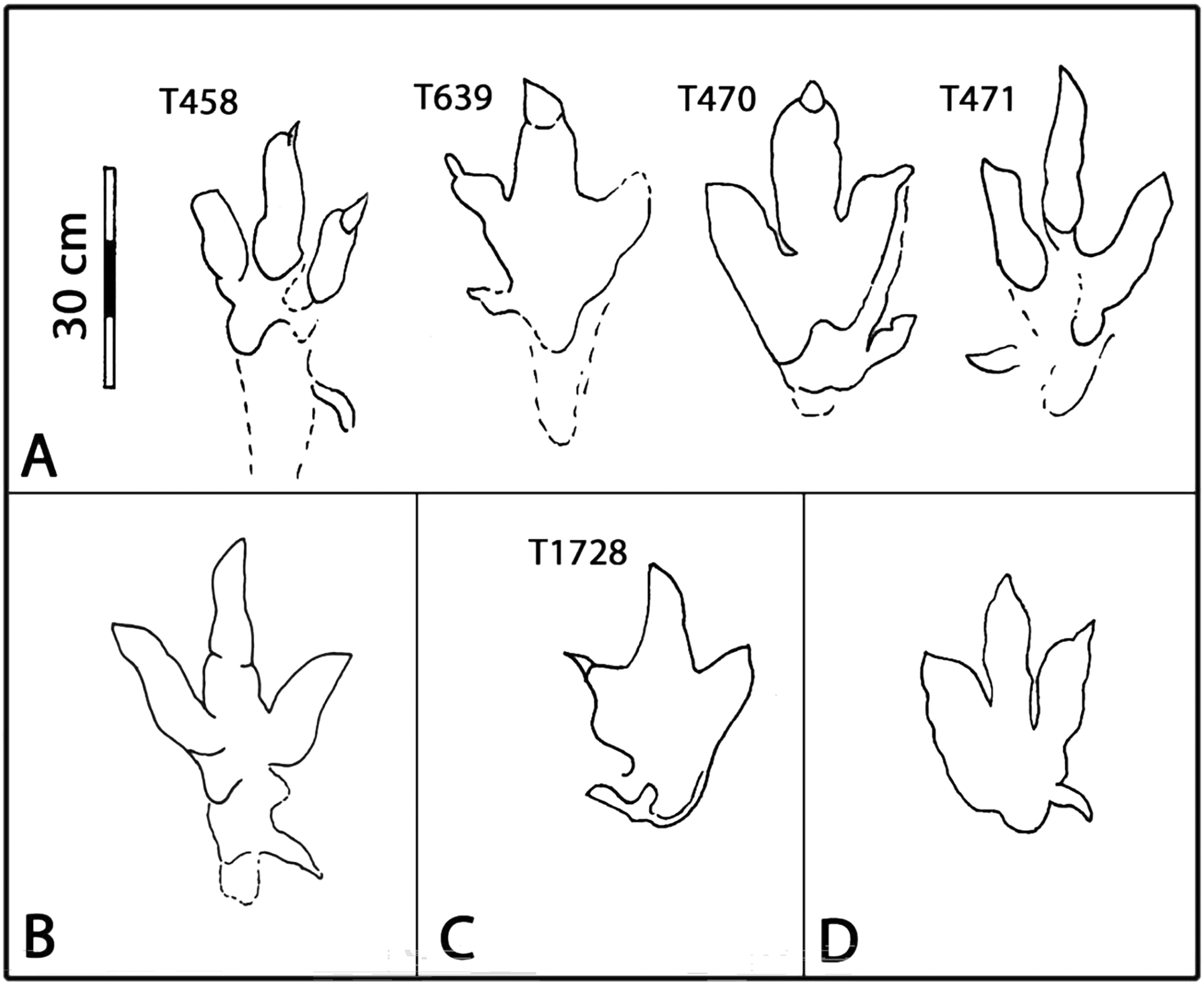


Figure 9. *Eubrontes* tracks with hallux (digit I) traces drawn to scale. (A) Four tracks from the St. George Dinosaur Discovery Site (SGDS), Utah; left to right T458 = SGDS 8; T639 = SGDS 24; T470 = SGDS 50; and T471 = SGDS # uncertain. (B) Single track from Hole in the Rock, Lake Powell (GLCA), Utah, after Lockley et al. (1998, their Figure 20B). (C) Single tracks from Flat Iron Mesa site, Utah. (D) *Gigandipus* after Lull (1953, Lull's Figure 53) and Milner et al. (2009, their Figure 6B).

digit III length was measured parallel to the long axis of the toemark, from the proximal base of the first digital pad to the tip of the claw mark. For prints in which a distinct crease separating the claw mark from the fleshy part of the digit III impression was observed, however (*Megalosauripus* from Europe), the length of the claw mark was not included in the lengths of digit III or the overall footprint length. Differences in the LdIII/L ratio when including vs. excluding the length of the claw mark are trivial.

An objection might be raised, however, to include the claw mark as part of digit III length for such analyses. The length of the claw impression admittedly can be highly variable, reflecting exigencies of the interaction of the claw with the recording sedimentary substrate (which is, of course, why the length of the claw mark is often excluded in comparisons of digit and footprint length). However, recognizing a boundary between the distal end of the terminal digital pad and the base of the claw mark of digit III also is often problematic, especially in large theropod prints. Furthermore, when the claw mark is deemed to be reasonably well-registered in a footprint, including it as part of digit III length allows closer comparison with the size of its potential skeletal correlate or proxy—the aggregate length of the pedal phalanges of digit III (cf. Farlow et al., 2018, 2022).

Independently of Lockley, Farlow made measurements of tridactyl dinosaur footprints from the prints themselves, or casts or other 3D replicas thereof (cf. Farlow et al., 2018, 2022, 2025). Farlow's dataset (available from Farlow on request) includes a few of the same western specimens traced by Lockley, but also includes footprints from around the world, particularly the Early Jurassic Newark Supergroup of Eastern North America and the Lower Cretaceous of Texas. Farlow's digit III and overall footprint length measurements were made as similarly as possible to Lockley's and include the length of the digit III claw mark (cf. Farlow et al., 2025, their Figure 9). These data are used to complement those of Lockley throughout this study, as appropriate.

Olsen (1980) defined a measure of "projection;" i.e., "the length to which digit III extends anteriorly beyond a line drawn transversely from the tip of digit II to the tip of digit IV" (cf. Lockley 2000, p. 282–283, Figure 1 here). This digit III projection ("P;" *sensu* Olsen et al., 1998; de Valais, 2011) or toe extension ("te," *sensu* Weems, 1992) is the height of the anterior triangle.

As traditionally understood in vertebrate zoology (Osborn, 1893; Woodward, 1898; Romer, 1933; Leonardi, 1987; cf. Romano et al., 2020), the term "mesaxonic" refers to a foot in which the axis of symmetry passes through the central digit (III), which is enlarged because most of the weight of the animal is carried on that toe. Theropods typically have a mesaxonic hindfoot in this traditional sense. This contrasts with the conditions of entaxony or ectaxony, in which the inner or outer digits, respectively, are the longest.

Lockley (2009) focused on an aspect of this condition in describing the shape of tridactyl dinosaur footprints, characterizing ichnological mesaxony as being 'strong' versus 'weak' on the basis of the shape of the anterior triangle. Mesaxony in this ichnological sense is the extent to which the middle digit (III in theropods) projects farther anteriorly than the inner (II) and outer (IV) digits (Lallensack et al., 2025). The relative length of "te" or "P" (compared to the width of the footprint), or alternatively, the L/W ratio of the anterior triangle (Figure 1), quantifies whether ichnological mesaxony is strong (larger values of the ratio) or weak (smaller values). The two ratios are closely related (Figure 10). Therefore, elongate tracks are more strongly mesaxonic, with more elongate triangles.

In the present study we follow Thulborn (1990) in arbitrarily including only "large" (L greater than 25 cm) theropod tracks in the UCM sample (for a discussion of footprint shape across a wider size range see Farlow et al., 2025). Smaller footprints attributed to theropods are, however, included in some of our present comparative analyses that use Farlow's data.

For reasons that will become apparent below, we consider the possibility that a key feature that seems to distinguish *Eubrontes* from footprints assigned to a later Jurassic theropod ichnotaxon (*Megalosauripus*) may have osteological correlates in the distal metatarsus of candidate large theropod trackmakers, and/or may be related to body size. In the present study Davidson and Farlow therefore collected measurements of the straight-line lengths, and distal articular anteroposterior (dorsoventral) depths, and distal articular mediolateral widths, of metatarsals III and IV of theropods across a wide range of body sizes. Where possible, measurements were made on actual bones, or casts of bones, but we also extracted measurements (including measurements made on published figures) from the literature.

The Big Picture: Comparing *Eubrontes* and Other Large Theropod Ichnotaxa

Eubrontes, *Kayentapus*, and *Gigandipus*

Tracings (Figures 6 through 9) of about 40 well-preserved tracks from the Glen Canyon Group show the diagnostic footprint morphology of *Eubrontes*. In addition, less well-preserved tracks have also been recorded from the various sites, some of which represent *Kayentapus* (Figure 7U) or other ichnotaxa (Figures 7V and 8H

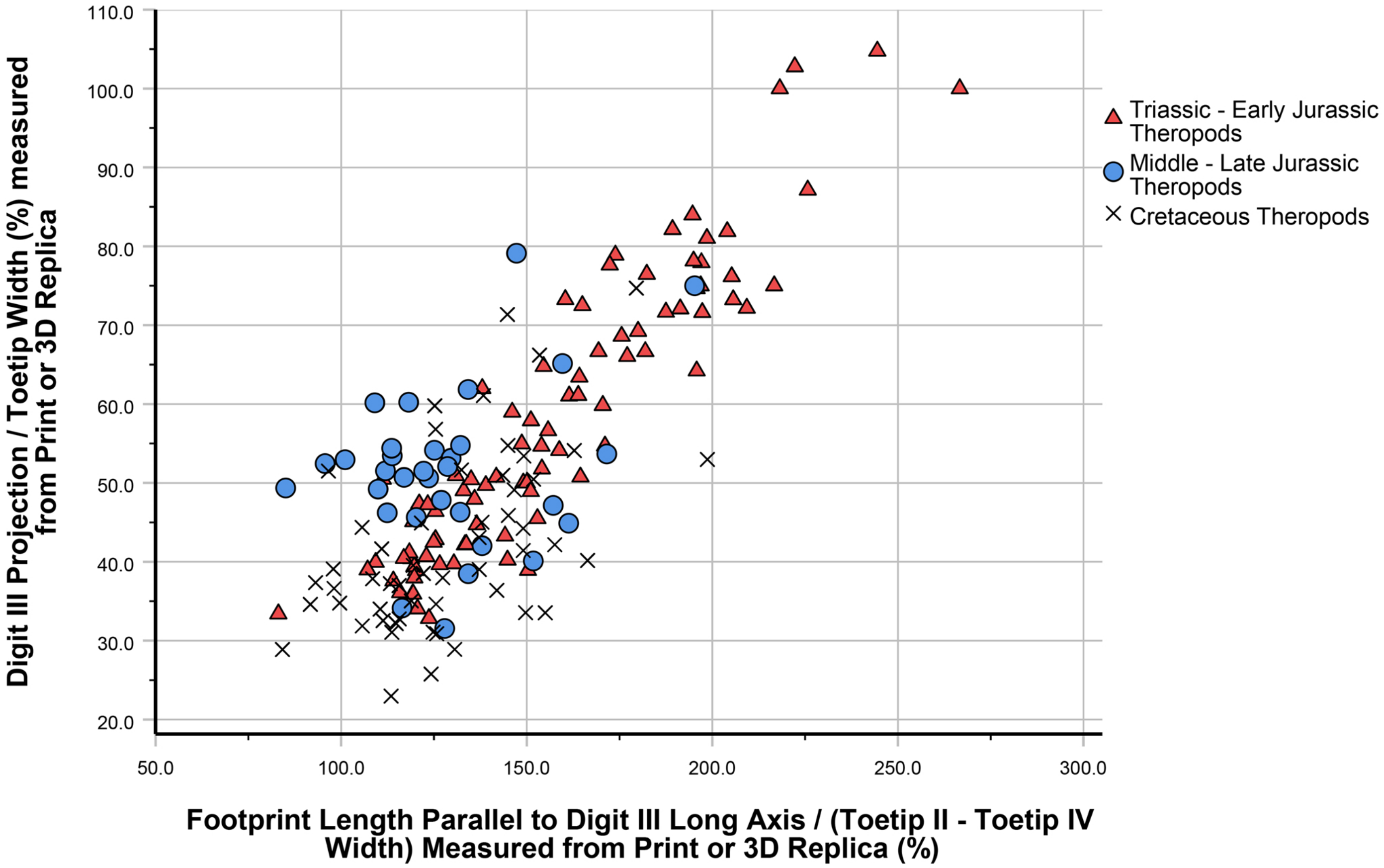


Figure 10. Comparison of two measures of footprint shape, using Farlow's dataset of footprint measurements of footprints attributed to theropods. Data cases are mean values, when more than one footprint in a trackway was measurable, or measurements of individual footprints (either isolated singletons or only one measurable footprint in the trackway).

through 8K). *Eubrontes* co-occurs with other theropod, ornithischian, and other tetrapod tracks with different morphologies and ichnotaxonomies (Appendix A).

The question of variation among large theropod tracks from the Early Jurassic in the Western United States has not previously been addressed in any definitive way. The track labeled T1467 (Figures 6B and 7U, and Appendix B) is, by definition, *Kayentapus* (Welles, 1971; Lockley et al., 2011). Footprints T1726 and T1727 (Figures 7O and 7R) from the Flat Iron Mesa sites have also recently been assigned to *Kayentapus* (Lockley et al., 2018c), their labels in the caption to Figure 7 notwithstanding, although we note that distinguishing between *Kayentapus* and *Eubrontes* at these sites is problematic (cf. Foster et al., 2025). These three tracks are somewhat more elongate (mean L/W 1.44), with more elongate anterior triangles (mean anterior triangle L/W 0.63) than the mean for typical *Eubrontes* tracks (L/W 1.30, range 1.07 to 1.61; N = 35) and anterior triangle (L/W 0.45, range 0.26 to 0.73; N = 33). The five largest tracks in order of decreasing length from 46.0 to 41.5 cm (T188, T909, T1523, T198, and T200) have mean L/W ratios only slightly below average (1.28) and mean anterior triangle ratios also slightly below average (0.44). Six tracks (Figures 8A, 8D, and 8H through 8K) show strong mesaxony (relative digit III toe extension), with anterior triangle values of 0.69 to 0.90 (mean 0.7;: N = 6).

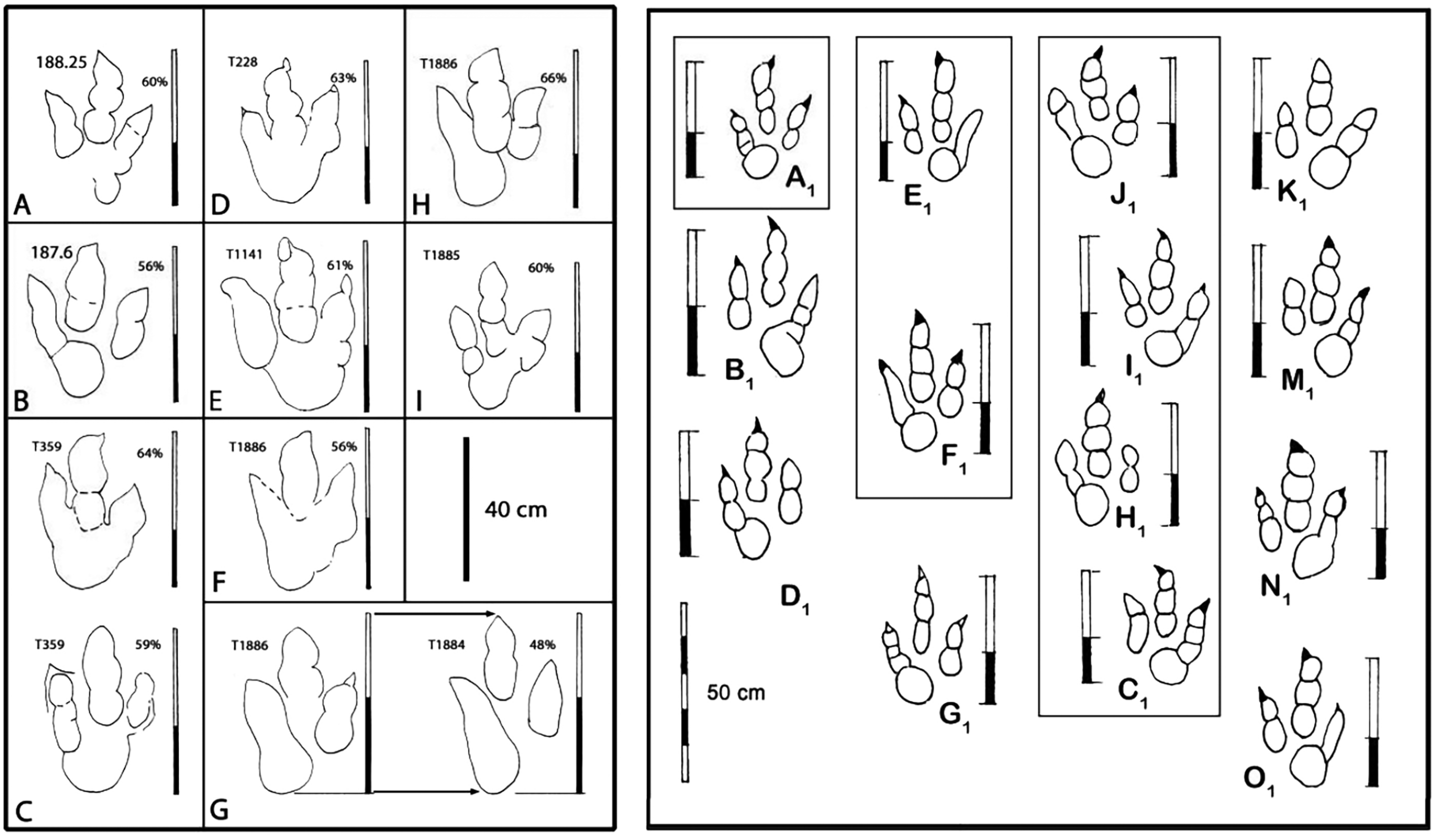
There are at least ten reports of western footprints identified as *Eubrontes* that show hallux (digit I) traces (Figures 5A and 9); at least 26 from the SGDS (Milner et al., 2006b; locality 2-2 in Figure 3 and Appendix A), one each from Hole in the Rock site (Lockley et al., 1998; locality 16-3 in Figure 3 and Appendix A), and from Flat Iron Mesa (Lockley et al., 2018c; locality 25-1 in Figure 3 and Appendix A). As noted by Milner et al. (2009), *Gigandipus* from the Newark Supergroup of Eastern North America (Figure 9D) was originally diagnosed and distinguished from *Eubrontes* in part (Lull, 1953, p. 184) from the presence of a "half rotated" hallux, registered in three consecutive (right, left, right) tracks in the type trackway, which also contains a prominent tail trace. Lull (1904, 1915, 1953) also stated that the generic character of *Eubrontes* is that there is "no indication of a hallux, with one possible exception" (Lull, 1953, p. 179), that being ACM-ICH 15/1 of *E. giganteus* (Lull, 1904, p. 510). Milner et al. (2009, p. 4) noted that, "there has been some speculation that *Gigandipus* is an extramorphological variant of *Eubrontes* in which the trackmaker's foot sank deep enough into the substrate to bring the normally elevated hallux into contact with the substrate …, but some *Eubrontes* tracks that lack hallux impressions are apparently deeper than some *Gigandipus* tracks …, so foot substrate interactions cannot universally explain these differences" (for further discussion see Farlow et al., 2018; Weems, 2019; Foster et al., 2025, p. 337–338). There is, then, uncertainty about whether the trackmakers of *Gigandipus* and *Eubrontes* represent large theropod species with different digit I morphologies (Xing et al., 2014; Foster et al., 2025, p. 338), or whether the variability in hallux registration is an extramorphological feature influenced by substrate variability (Gatesy et al., 1999).

Post-Lower Jurassic *Eubrontes* vs. Other Large Theropod Ichnotaxa

Although clearly an important Lower Jurassic theropod ichnogenus, *Eubrontes* has also been reported from the Late Triassic (Lucas et al., 2006a, 2006b, 2006c; Klein and Lucas, 2021, p. 10 and 13; Klein and Lucas, 2025, p. 222–223) and from the Middle Jurassic to Lower Cretaceous (Foster et al., 2025; Xing et al., 2025). The earliest published report from the Cretaceous is Shuler (1935), who named *Eubrontes* (?) *glenrosensis,* using the question mark to indicate uncertainty, a doubt underscored by the reassignment of the questionable ichnospecies to *Irenesauripus glenrosensis* (Langston, 1974). Mostly, however, later Mesozoic footprints made by large theropods are assigned to other ichnogenera, including *Megalosauripus* (Lockley et al., 1996, 2000; Lockley and Meyer, 2000; Thulborn, 2001; Razzolini et al., 2017), *Hispanosauropus* (Mensink and Mertmann, 1984; Avanzini et al., 2011; Foster, 2015), *Iberosauripus* (Cobos et al., 2014), *Jurabrontes* (Marty et al., 2018), and *Irenesauripus* (Sternberg, 1932; McCrea et al., 2014a; Lockley et al., 2014a, 2014b, 2015).

Although a thorough revision of large theropod ichnotaxa is beyond the scope of this report, we will make preliminary morphometric comparisons of *Eubrontes* with a selected series of later Mesozoic forms (cf. Minguez Ceniceros et al., 2022). At least four large theropod ichnogenera have been named from the Late Jurassic (*Megalosauripus*, *Hispanosauropus*, *Iberosauripus*, and *Jurabrontes*), and five from the Cretaceous (*Irenesauripus*, *Asianopodus, Chapus, Bellatoripes*, and *Tyrannosauripus*), which invite careful comparison with *Eubrontes*. While not comprehensive, this list constitutes nine reasonably well-defined, and/or well-documented ichnogenera based on Late Jurassic through Cretaceous holotype and paratype samples, that provide data for comparative studies.

***Eubrontes* vs. *Megalosauripus* (Figures 11 through 13; Appendices B and C)**: *Megalosauripus* (spelled with an 'i') has long been known as a problematic ichnogenus, due to having been inadequately defined by Lessertiseur (1955), based on a lost ?Cretaceous holotype from Europe, that was soon after renamed as *Bueckeburgichnus maximus* (Kuhn, 1958; see Lockley et al., 1996, 2000; Lockley, 2000b; Lockley and Hunt, 2000; Thulborn, 2001; Razzolini et al., 2017, for extensive discussion). Ichnotaxonomic uncertainly was not helped when Colbert and Merrilees (1967) defined the Cretaceous ichnogenus *Megalosauropus* (spelled with an 'o') based on the ichnospecies *M. broomensis* from Australia. Haubold (1971) placed the Cretaceous Texas *Eubrontes*? *glenrosensis* in new combination as *Megalosauropus glenrosensis*, and two new Late Jurassic ichnospecies of *Megalosauropus* were subsequently named, *M. teutonicus* from Germany (Kaever and Lapparent, 1974; Meyer et al., 2021) and *M. uzbekistanicus* from Uzbekistan (Gabuniya and Kurbatov, 1982). Howev-



***Megalosauripus* Upper Jurassic North America**

***Megalosauripus* Upper Jurassic Europe**

Figure 11. Upper Jurassic tracks assigned to ichnogenus *Megalosauripus* from North America and Europe. North American tracks (left: A through I) from the Entrada, Curtis, and Summerville Formations of Utah are larger than *Eubrontes* by an average of 18% of foot length and have larger (fleshier) "heel" pads, and shorter digit III traces. Compare this with Figures 7 and 8; see text and Appendix C for details. Tracks F, G, and H correspond to specimens MWC 9421, 9420 and 9422. Modified after Lockley (2021. Lockley's Figure 16). European tracks (right: A_1 through O_1) assigned to ichnospecies *Megalosauripus transjuranicus* from the Reuchenette Formation of Switzerland are slightly larger than *Eubrontes* and have larger "heel" pads. The digit III/L ratio is only 0.58 compared with 0.67 in *Eubrontes* (see Appendix C); compare with Figures 7 and 8. See Castanera et al. (2023) and Blakesley et al. (2025) for additional European footprints attributed to *Megalosauripus*.

er, these ichnotaxa have been, or can be shown to be morphologically distinct from the Australian specimen (Lockley et al., 1996, 2000), thus raising doubts as to whether the *Megalosauropus* label applied in these cases. For example, Meyer et al. (2021) consider *M. teutonicus* to be more like *Jurabrontes* than *Megalosauropus*.

Lockley et al. (1996, 2000) argued that *Megalosauripus,* as ill-defined by Lessertiseur (1955) was a *nomen nudum*, as distinct from better- and later-defined Australian *Megalosauropus* and so was available for use. *Megalosauripus* had originally been introduced with the generally vague intent of describing Late Jurassic and Early Cretaceous theropod tracks (with hallux traces) from Portugal and Germany, respectively, that could 'possibly' have been made by the Jurassic dinosaur *Megalosaurus* (Buckland, 1824) or a relative. These *Megalosauripus* specimens belonged to poorly documented and dispersed collections, from which holotypes could not be confidently identified. The German material appeared to have been lost, besides having been labelled *Bueckeburgichnus* by Kuhn (1958) with no tangible holotype matching the original "description-less" *Megalosauripus* illustration selected by Lessertiseur (1955). Thus, *Megalosauripus* was considered available to ac-

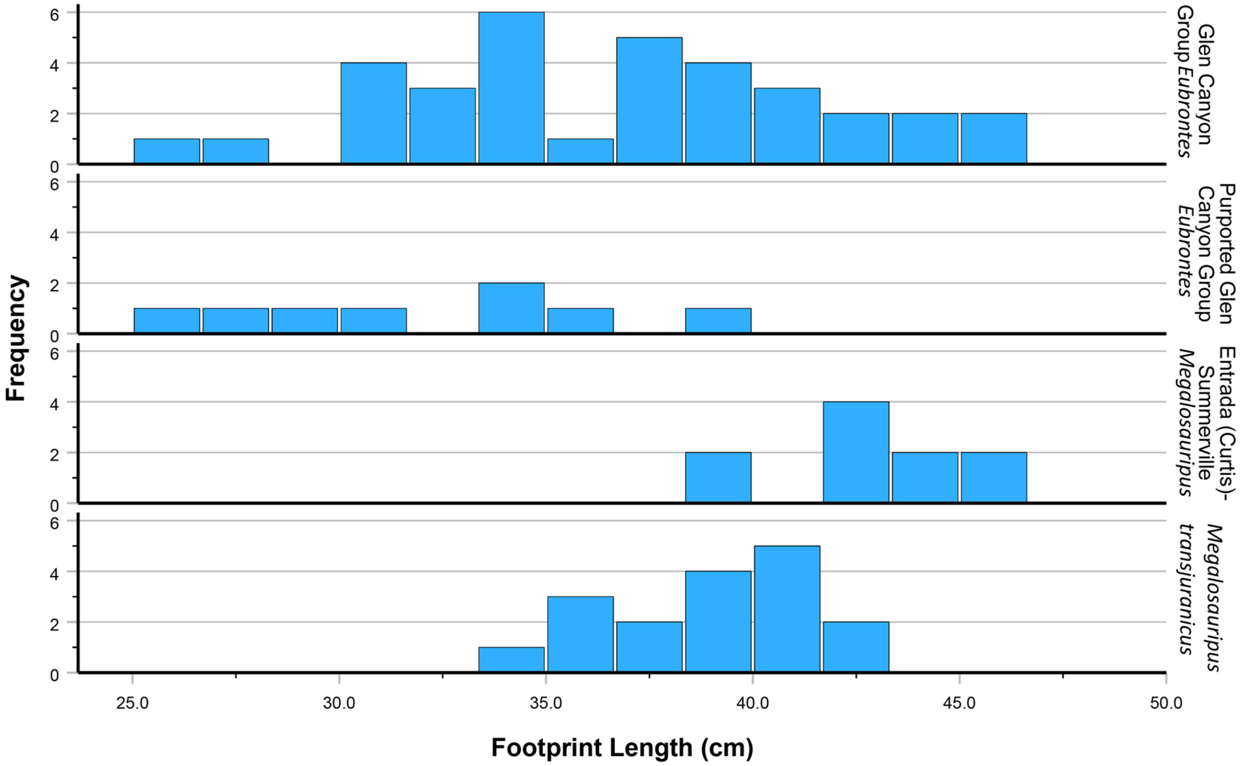


Figure 12. Size-frequency distribution of *Eubrontes* from the Glen Canyon Group with *Megalosauripus* from the Entrada (Curtis)-Summerville Formations of the Western United States and *Megalosauripus transjuranicus* from Europe (Appendices A and B). *Eubrontes* prints in the sample span a larger size range than *Megalosauripus*. Although the size-frequency distributions overlap, *Megalosauripus* prints (especially those in the Entrada [Curtis-Summerville] sample) average larger than *Eubrontes*.

commodate the aforementioned Late Jurassic *M. teutonicus* from Germany (Kaever and Lapparent, 1974) and *M. uzbekistanicus* from Uzbekistan (Gabuniya and Kurbatov, 1982), as well as other tracks with similar *Megalosauripus*-like morphology (sensu Lockley et al., 2000). Thulborn (2001, p. 210) stated that Lockley et al. (1996) had "salvaged the name *Megalosauripus*." Thulborn presented detailed counter arguments for alternate ichnotaxonomic interpretations, which proposed that *B. maximus* (Kuhn, 1958) should be formalized in the combination *Megalosauripus maximus*, thus recognizing the illustrated, but lost, Cretaceous track from Germany as the holotype. Thulborn (2001) implied that the label *Megalosauripus* should not be extended or salvaged to describe different morphotypes from the Jurassic unless, one presumes, they are shown to be morphologically the same, or similar enough at the ichnogenus level. This is a crucial point because the use of either *Megalosauripus* or *Megalosauropus* to describe tracks other than the original "types" requires judgement calls based on comparative study, and interpretation of the International Code of Zoological Nomenclature (ICZN). Thulborn's analysis of *Bueckeburgichnus* and the *Megalosauripus-Megalosauropus* problem is commendably conscientious and corrects a specimen identification error in Lockley (2000b), and also a detailed, if differently nuanced, discussion of the extraordinary ichnotaxonomic complexities surrounding the history and usage of *Megalosauripus*, and other related morphotypes. Thulborn's arguments remain cogent around the original naming of *Megalosauripus* and *Bueckeburgichnus* but, crucially, they have not turned up a lost type specimen, and they have not prevented or significantly influenced the widespread usage of the "salvaged" *Megalosauripus* label (with an 'i') to identify a growing number of Late Jurassic tracks from Europe

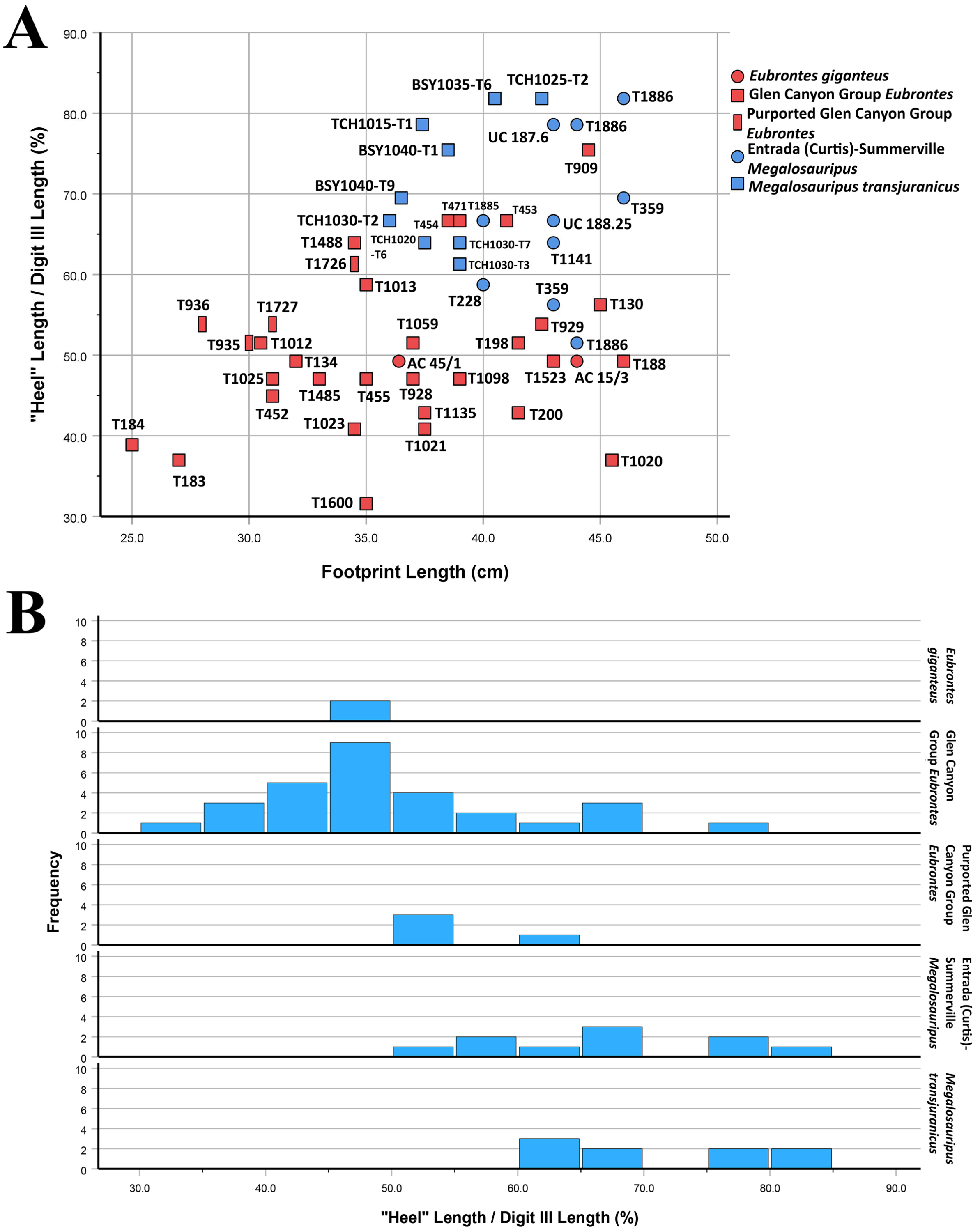


Figure 13. Length of the "heel" region relative to digit III length in *Eubrontes* and *Megalosauripus* (ratio calculated from data in Appendices A and B). (A) "Heel" region length/digit III length vs. overall footprint length. (B) Frequency distribution of the same ratio plotted in panel A. *Megalosauripus* prints tend to have a higher "heel" region length/digit III length than *Eubrontes*. Although there is overlap in relative "heel" region length in the two ichnogenera (especially between larger specimens of *Eubrontes* with *Megalosauripus*), the latter has a longer average relative "heel" region length.

(notably Razzolini et al., 2017; Castanera et al., 2023; Blakesley et al., 2025), Asia, and North America (Lockley et al., 2000; Lockley and Gierliński, 2014; Schumacher and Lockley, 2022), to distinguish them from type *Megalosauropus* (with an 'o') from the Cretaceous of Australia.

Footprints in our sample identified as *Eubrontes* from the Glen Canyon Group (excluding "purported" specimens) span a greater size range, and have a lower average footprint length (range 25 to 46 cm, median 37.0 cm, mean 36.8 cm, standard deviation 5.22 cm, N = 34), than *Megalosauripus* from the Entrada (Curtis)-Summerville interval (range 40 to 46 cm, median 43.0 cm, mean 43.2 cm, standard deviation 2.04 cm, N = 10) (Figures 12 and 13A), although the narrower range of values for *Megalosauripus* could be a matter of sample size. Glen Canyon Group *Eubrontes* are similar in size to *Megalosauripus transjuranicus* (range 34 to 42 cm, median 39.0 cm, mean 38.9 cm, standard deviation 2.45 cm, N = 17).

Lockley et al. (2000, p. 329; and Figures 6 and 11 herein) made the preliminary observation that "the relative length of digit III" trace is much longer in *Eubrontes* than in *Megalosauripus*, a hypothesis we examine here with larger sample sizes. We consider the length of the digit III impression in two ways: (1) as a proportion of the overall length of the footprint, and (2) compared with the length of the portion of the footprint behind (proximal to) the digit III impression, the "heel" region of the footprint. (But keep in mind that this informal usage is only for convenience; the anatomical heel of these animals [the region where the foot met the ankle] would only contact the substrate, and leave an impression, under unusual circumstances [Lallensack et al., 2022]).

Comparing the dIII/L ratio for our sample of *Megalosauripus* and *Eubrontes* tracks from Western North America, as well as a sample of *Megalosauripus transjuranicus* from Europe (described by Razzolini et al., 2017), confirms (Figure 11) a measurable difference in the dIII/L ratio: mean values of 0.58 for European and 0.60 for North American *Megalosauripus* versus 0.67 for *Eubrontes* from the Western United States; compare Appendices B and C. This difference 7% to 9% in percentage values appears related to the relatively larger "heel" pad seen in many *Megalosauripus* tracks (Figure 11), which can further be visualized by comparing the ratio of "heel" region length to digit III length (Figure 13).

Excluding "purported" western *Eubrontes* specimens from the comparison but including *Eubrontes* specimens from Eastern North America, as well as a specimen of *M.* cf. *transjuranicus* (Castanera et al., 2023) in the comparison, the "heel" region length/digit III length ratio does not show the same distribution of values across the three footprint categories (Independent Samples Kruskal-Wallis Test Statistic 23.008, p less than 0.001, N = 48). Pairwise comparisons show the European and North American *Megalosauripus* to be significantly different (larger) than *Eubrontes* (p less than 0.001), but not from each other (p = 0.594).

There are also notable differences in the mean footprint length/width ratio (1.3) and mean II-IV digit divarication angle between western *Eubrontes* and North American and European *Megalosauripus.* The mean L/W ratio for *Eubrontes* is 1.33 (range 1.1 to 1.6); that of North American *Megalosauripus* is 1.43 (range 1.3 to 1.5), and that of *M. transjuranicus* is 1.56 (range 1.4 to 1.9). Mean digit divarication angles are 49° (range 36° to 66°) for western *Eubrontes*, 40° (range 27° to 51°) for North American *Megalosauripus*, and also 40° (range 25° to 59°) for *M. transjuranicus*. Thus, the *Eubrontes* footprint reveals a wider digit divarication related to a less elongate (broader) foot.

***Eubrontes* vs. *Hispanosauropus*, *Iberosauripus*, and *Jurabrontes* (Figure 14, Appendix D)**: The illustrated and tabulated size and morphometric distinctions between *Eubrontes* and *Megalosauripus* outlined above are based on relatively large samples (Figures 11 and 13, Appendices B and C). The samples for *Hispanosauropus* (Mensink and Mertmann, 1984; Avanzini et al., 2011; Foster, 2015) and *Iberosauripus* (Cobos et al., 2014) are small, although the sample for *Jurabrontes* (Marty et al., 2018) is larger. For consistency we provide the same measurements (Appendix D) and similar illustrations (Figure 14) to facilitate comparisons (Figures 6 through 8 and 11). *Hispanosauropus, Iberosauripus*, and *Jurabrontes* are

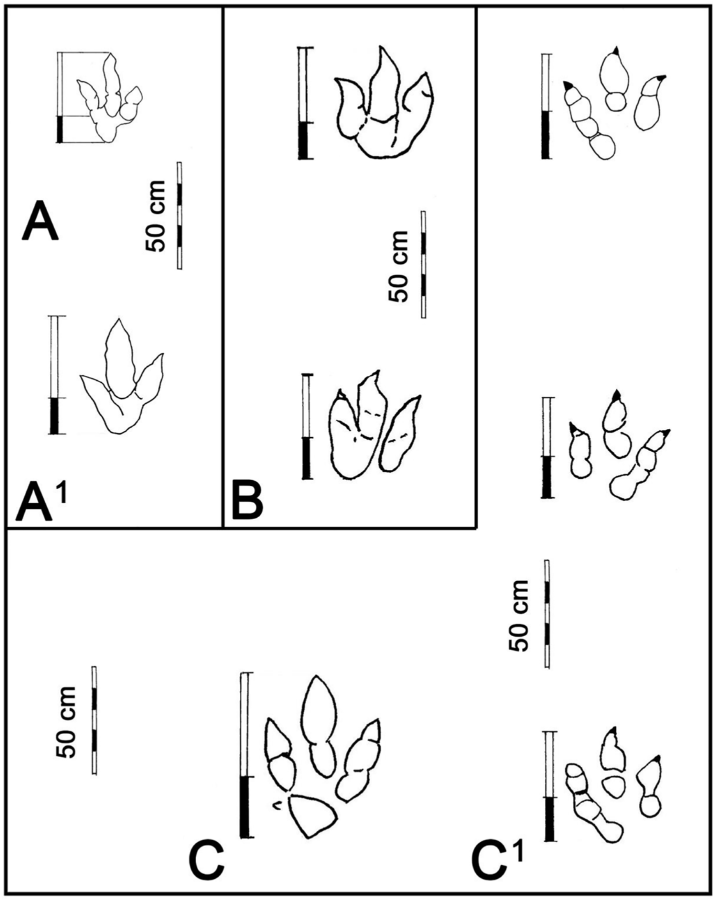


Figure 14. Upper Jurassic tracks assigned to the ichnogenera *Hispanosauropus*, *Iberosauripus*, and *Jurabrontes*. (A, A_1) *Hispanosauropus* from Spain and Utah, respectively. After Avanzini et al. (2011, their Figure 1C) and Foster (2015, Foster's Figure 3B). (B) Two consecutive tracks of *Iberosauripus* from Spain. After Cobos et al. (2014, their Figure 3B). (C) Large isolated *Jurabrontes* track. (C_1) *Jurabrontes* trackway. After Marty et al. (2018, their Figure 6). Digit III/L proportions are shown in all cases for comparison with Figures 6, 7, 8, 11, and 15 through 17.

here discussed in the order in which they were named.

Unfortunately, the holotype of *Hispanosauropus hauboldi* designated by Mensink and Mertmann (1984) is thought to have been lost to erosion (Lockley et al., 2007; Foster et al., 2025). Fortunately, however, similar tracks have been investigated in the type area in Spain (Lockley et al., 2007, 2008; Avanzini et al., 2011), and the ichnogenus has been recognized in North America (Foster, 2015). This latter paper summarizes the morphometric parameters for three specimens, two from Spain and one from Utah (Appendix D), and makes comparisons with representative, but isolated tracks identified as *Eubrontes*, *Megalosauripus*, and *Irenesauripus*. The conclusion that *Hispanosauropus* is distinct from these other ichnogenera, including *Megalosauripus*, based on the dIII/L ratio, and wider digit divarication angle than some other theropod tracks (Foster, 2015), is consistent with the conclusion of Lockley et al. (2007, p. 254) that "*Hispanosauropus* should provisionally be retained as a valid name." Based on the combined data *Hispanosauropus* is a typical, moderately large theropod track (38.0 to 52.0 cm long, mean L/W = 1.38) with an anterior triangle L/W of 0.50 and a mean digit divarication of about 50°. The relative length of digit III (dIII/L) is 0.67. These parameters suggest a greater similarity to *Eubrontes* (Appendix B) than to *Megalosauripus* (Appendix C). Noting that the Utah *Hispanosauropus* originates from the Upper Jurassic Morrison Formation, from which many large theropods have been excavated, "it is a reasonable, if provisional, hypothesis that the [Utah] *Hispanosauropus* trackway was made by an *Allosaurus*" (Foster, 2015, p. 189).

Turning to *Iberosauripus,* our sample consists of the type trackway (Cobos et al., 2014) from the Villar del Arzobispo Formation (Kimmeridgian–Berriasian) and a referred specimen from the Berriasian Oncala Group of Spain (Barco et al., 2005). The type trackway reveals a wide track (mean L, W, and L/W = 56.0 cm, 43.5 cm, and 1.27, respectively) with weak ichnological mesaxony (anterior triangle L/W = 0.295) and low digit divarication angles (29.3°). The isolated track described by Barco et al. (2005) is much larger (L = 69.0 cm, W = 56.0 cm), but the L/W, anterior triangle and digit divarication values are similar to the type. The pooled digit III/L value is 0.60. These data show notable differences between smaller, more elongate and a more strongly mesaxonic, *Hispanosauropus,* and a more transverse *Iberosauripus*. The latter is reported as a younger ichnotaxon found near the Jurassic–Cretaceous boundary. The morphological differences led Cobos et al. (2014) to differentiate two "Ichno-Groups" (1 and 2), inferred to represent different megatheropod clades (Megalosauridae and Allosauridae).

Jurabrontes curtedulensis was described by Marty et al. (2018) from the Kimmeridgian Reuchenette Formation in northwestern Switzerland (a second species, *Jurabrontes melphicticus*, was later described from the Lower Cretaceous of Italy (Antonelli et al., 2023). The Swiss sample is based on three trackways with mean L, W, and L/W values of 57.7 cm, 43.2 cm, and 1.33, respectively. The mean anterior triangle L/W is 0.44, the mean divarication is 47.4º, and the digit III/L ratio is 0.60. The latter parameter as well as the overall size and L/W ratio are similar to *Iberosauripus*. As shown in Appendix D, both *Jurabrontes* and *Iberosauripus* are characterized by short, relatively wide tracks (L/W about 1.20). Both also have a fleshy appearance, and although inter-pad creases are illustrated in the original publications, they are not always clearly defined. As noted by Lockley (2000a) this reduced separation or fusing of pad traces appears to be characteristic of many larger theropod tracks, and suggests a fleshier foot, presumably consistent with weight-bearing adaptations (cf., Farlow et al., 2018).

***Eubrontes* vs. *Irenesauripus*, *Asianopodus*, *Chapus*, *Bellatoripes*, and *Tyrannosauripus* (Figures 15 and 16)**: Turning to large theropod tracks named on the basis of well-known and adequately described Cretaceous holotypes, the following ichnogenera deserve attention: *Irenesauripus, Asianopodus, Chapus, Bellatoripes*, and *Tyrannosauripus*. The first three are associated with the Lower Cretaceous and the latter two with the Upper Cretaceous. *Irenesauripus* is one of the first-named Cretaceous ichnogenera attributed to large theropods, based on the type trackway described by Sternberg (1932, p. 60) from the "Gething Member of the Bullhead Mountain" Formation (now the Aptian Gething Formation) of British Columbia. Soon after Sternberg named *Irenesauripus*, Shuler (1935) described *Eubrontes* (?) *glenrosensis* from the Albian Glen Rose Formation of Texas. Interestingly, Langston (1974) renamed the Texas tracks as *Irenesauripus glenrosensis* based on a number of explicitly stated morphological characters, which ostensibly demonstrate its similarity to *Irenesauripus* and difference from *Eubrontes* (see Appendices E and F, and Figure 15). Langston (1974) also suggested the tracks could be attributed to *Acrocanthosaurus*, and this interpretation was repeated by Farlow (2001) and Farlow et al. (2012) with respect to Texan tracks, and by Lockley et al. (2014a, 2014b) and Foster (2015) with respect to well-preserved Albian tracks from a large Cedar Mountain tracksite in Utah (Appendix E). Rather than simply state that *Irenesauripus* and *Eubrontes* are different, as now implied in the literature, the data presented in Appendices B through F allow morphological differences between these two, and other theropod ichnogenera, to be compared in more detail. Inspection of the holotype of *Irenesauripus* (*I. mclearni*; CMN 8548) suggests suboptimal preservation, and it was originally drawn, in outline, with no discernible digital pad traces (see McCrea, 2000). However, Lockley's own observations of the type specimen indicate that pad traces were registered (Figure 15B). Thus, the utility of the trackway for ichnotaxonomic study is not dismissed out of hand. Moreover, McCrea (2000) reviewed occurrences of *I. mclearni* from Canada and illustrated examples where pad traces are clear and digit divarications are as high as 90°. McCrea summarized the conclusion that two other ichnospecies of *Irenesauripus* named by Sternberg (1932) are invalid, with *I. occidentalis* having been declared a synonym of the ornithopod track *Amblydactylus* by Currie (1995), and *I. acutus* being a subjective synonym of *I. mclearni*. Thus, *I. mclearni* appears to be the only *Irenesauripus* ichnospecies presently accepted and reported from a number of Lower Cretaceous formations in Canada (McCrea et al., 2014a). *Irenesauripus* has also been reported from several sites in the Dakota Sandstone (Albian-Cenomanian) of

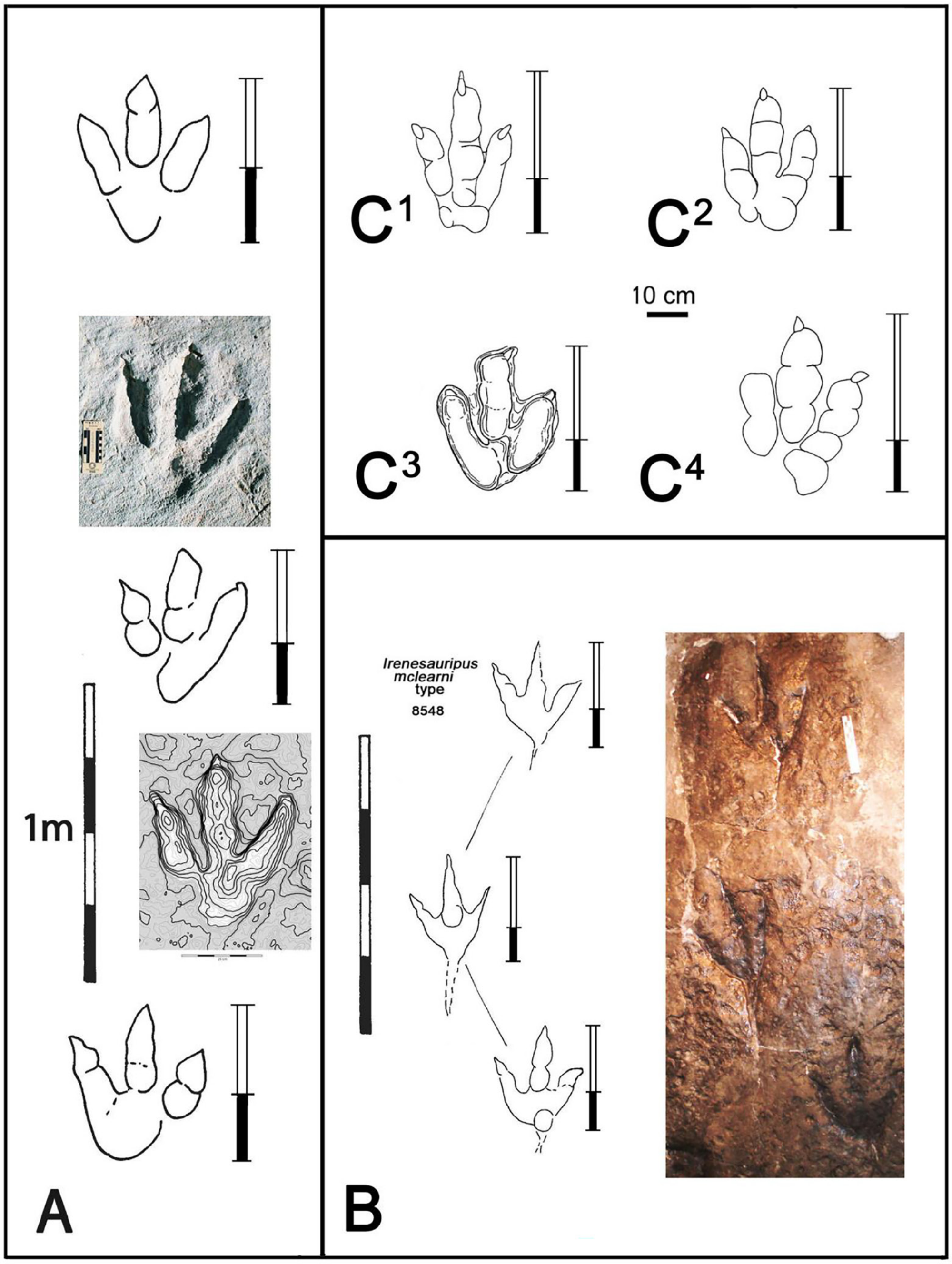


Figure 15. Comparisons between *Irenesauripus* and *Eubrontes*. (A) *Irenesauripus* from the Cedar Mountain Formation of Utah. After Lockley et al. (2014a, their Figures 5A and 6). Also see Lockley et al. (2014b). (B) Type *Irenesauripus* trackway (CMN 8548) outline and photograph at same scale. (C_{1-4}) Various examples of *Eubrontes*. (C_1) Type of *E. giganteus*. After Olsen et al. (1998, their Figure 5A). (C_{2-3}) *E. giganteus* as figured by Lull (1953, Lull's Figure 47) and Ishigaki and Fujisaki (1989, their Figure 48.1). (C_4) *Eubrontes* from Warner Valley, Utah; compare with Figure 7A.

the United States (Lockley et al., 2015; Lockley, 2018).

The ichnogenera *Asianopodus* (three ichnospecies) and *Chapus* (one ichnospecies) were described based on large theropod tracks from Japan (Matsukawa et al., 2005) and China (J. Li et al., 2006, 2011; Y. Li et al., 2020). In addition, *Eubrontes* has also been reported from the Lower Cretaceous of China. As reported by Xing et al. (2021a), various tracks labeled *Eubrontes* isp. indet. have been reported from several sites in the Cretaceous of China, but only recently has a new ichnospecies, *E. nobitai*, been reported from the Jiaguan Formation of Sichuan Province. According to Xing et al. (2021b), who compared this track with 16 Jurassic and 6 Cretaceous theropod tracks, including all those, both Jurassic and Cretaceous, named as *Eubrontes* from China, *Eubrontes nobitai* is the best example of Chinese Cretaceous *Eubrontes* currently known. It differs from *Asianopodus* in a number of features, most notably in

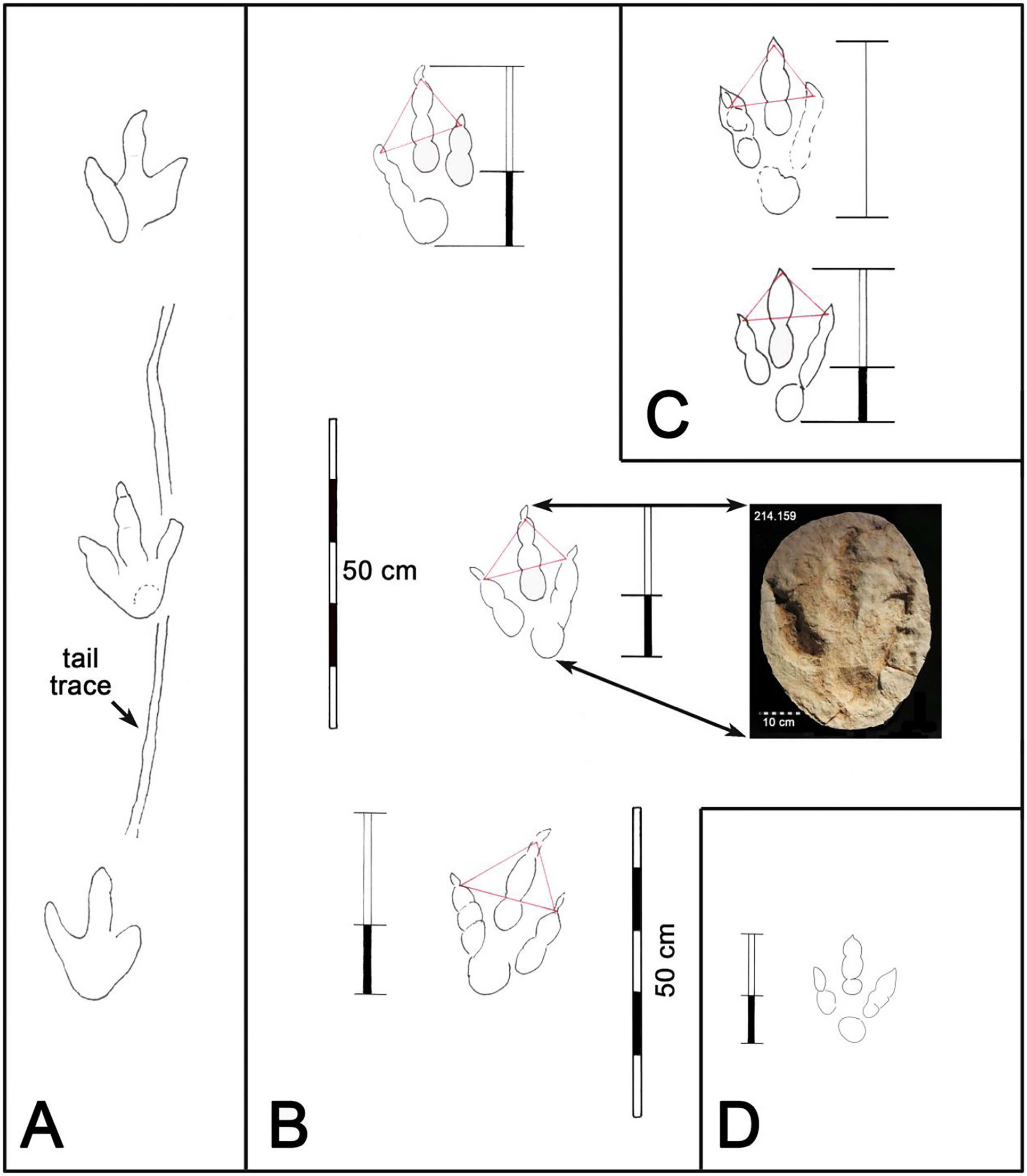


Figure 16. Large Cretaceous theropod tracks from China. (A) Unnamed topotype of *Chapus* from type locality. After Lockley et al. (2018b, their Figure 5D). (B) Holotype of *Chapus*. Modified after J. Li et al. (2006, their Figure 3) and Lockley et al. (2018b) with insert of replica UCM 214.159. (C) Holotype of *Asianopodus niui*. Redrawn after Y. Li et al. (2020, their Figure 3). (D) Holotype of *Asianopodus robustus*. After J. Li et al. (2011).

having a well-developed metatarsophalangeal pad II (MTP II) adjacent to MTP IV, whereas *Asianopodus* is characterized by a single large MT heel pad (MTP IV) and no separate MTP II pad. With respect to the large heel pad, *Asianopodus* resembles *Megalosauripus*, a feature reflected in the digit III/L ratios (Appendix F).

There are three described *Asianopodus* ichnospecies. The ichnogenus was defined on the basis of the Japanese ichnospecies *A. pulvinicalx*, represented by a short partial holotype trackway (Matsukawa et al., 2005). *Asianopodus robustus* (J. Li et al., 2011) is based on a single track similar in size to *A. pulvinicalx*, and with similar ichnological mesaxony and digit III/L ratios (Figure 16). *Asianopodus robustus* was named by J. Li et al. (2011) evidently following the suggestion of Lockley et al. (2002) and Matsukawa et al. (2005), who had illustrated it, and in the latter paper compared it with *A. pulvinicalx*.

The third *Asianopodus* ichnospecies, *A. niui* (Y. Li et al., 2020), is based on a larger track (L = 47.0 cm), which was poorly described; Xing et al. (2021c) suggested the track was not like *Asianopodus* and could equally well have been compared with *Chapus* (J. Li et al., 2006). The difference between type *Chapus* and type *Asianopodus* is perhaps subtle, except that the former ichnotaxon is almost twice as large as the latter and lacks a large heel pad. Otherwise, other morphometric parameters are similar (Appendices E and F) and could benefit from further investigation. Abundant and generally small *Asianopodus* have been recognized from the Lower Cretaceous of Shandong Province (R. Li et al., 2015), where a sample of almost 100 trackways has yielded a print mean length of about 22.0 cm, and the two largest (lengths = 30.0 and 32.0 cm) conform to the sizes of *A. pulvinicalx* and *A. robustus.*

Additional detailed comments on *Chapus* (type ichnospecies *C. lockleyi*) are unnecessary beyond stating that the line drawings in the original paper are misleading (compare J. Li et al. [2006, Figures 2 and 3] with Figure 16 herein and their photographs [op. cit., plate 1]). Figure 16B herein includes a correction of a reversed image of the *Chapus* trackway illustrated by Lockley et al. (2018b, their Figure 5C). Moreover, the UCM collections contain replicas of tracks from the original *Chapus* holotype trackway now preserved in situ in a protected building. These replicas were illustrated by Lockley et al. (2018b, their Figure 5A). The UCM collections also contain replicas of the types of both *A. pulvinicalx* and *A. robustus*, the latter also illustrated by Lockley et al. (2018b, their Figure 5E).

Few large theropod tracks have been formally named from the Upper Cretaceous. The two most important examples, in stratigraphic order, are *Bellatoripes fredlundi* from the Campanian–Maastrichtian of British Columbia (McCrea et al., 2014b), and *Tyrannosauripus pilmorei* (Lockley and Hunt, 1994) from the latest Maastrichtian of New Mexico. Both were placed in the new ichnofamily Tyrannosauripodidae by McCrea et al. (2014b). Both are very different from *Eubrontes* and from each other. *Bellatoripes* is the relatively broadest of the theropod tracks reviewed here (L/W = 1.12, Figure 17) and lacks clear digital pad impressions (cf. Lockley, 2000a). In contrast, *Tyrannosauripus* is much larger and more elongate (L/W = 1.34), with a pronounced hallux trace.

Theropod Footprint Proportions: Stoutness of the “Heel” Region

Summarizing the overall size and proportions of the theropod ichnotaxa we have discussed, an interesting pattern can be seen (Figure 17): as footprints become larger, digit III makes up a decreasing proportion of overall print length. A further way of examining the relative length of digit III is by comparing it not with the length of the entire footprint, but rather with the length of that portion of the footprint proximal to (behind) the digit III impression, the “heel” region. Using a dataset created by Farlow et al. (2025) independently of Lockley’s measurements (Figure 18A), the decrease in relative digit III length seen in Figure 17 is corroborated and extended.

For the digit III length/“heel” region length ratio to become less in bigger footprints, either digit III must become a relatively shorter proportion of total foot length with increasing size, or the length of the “heel” region must become relatively longer. In theropod foot skeletons (if the highly specialized dromaeosaurids are

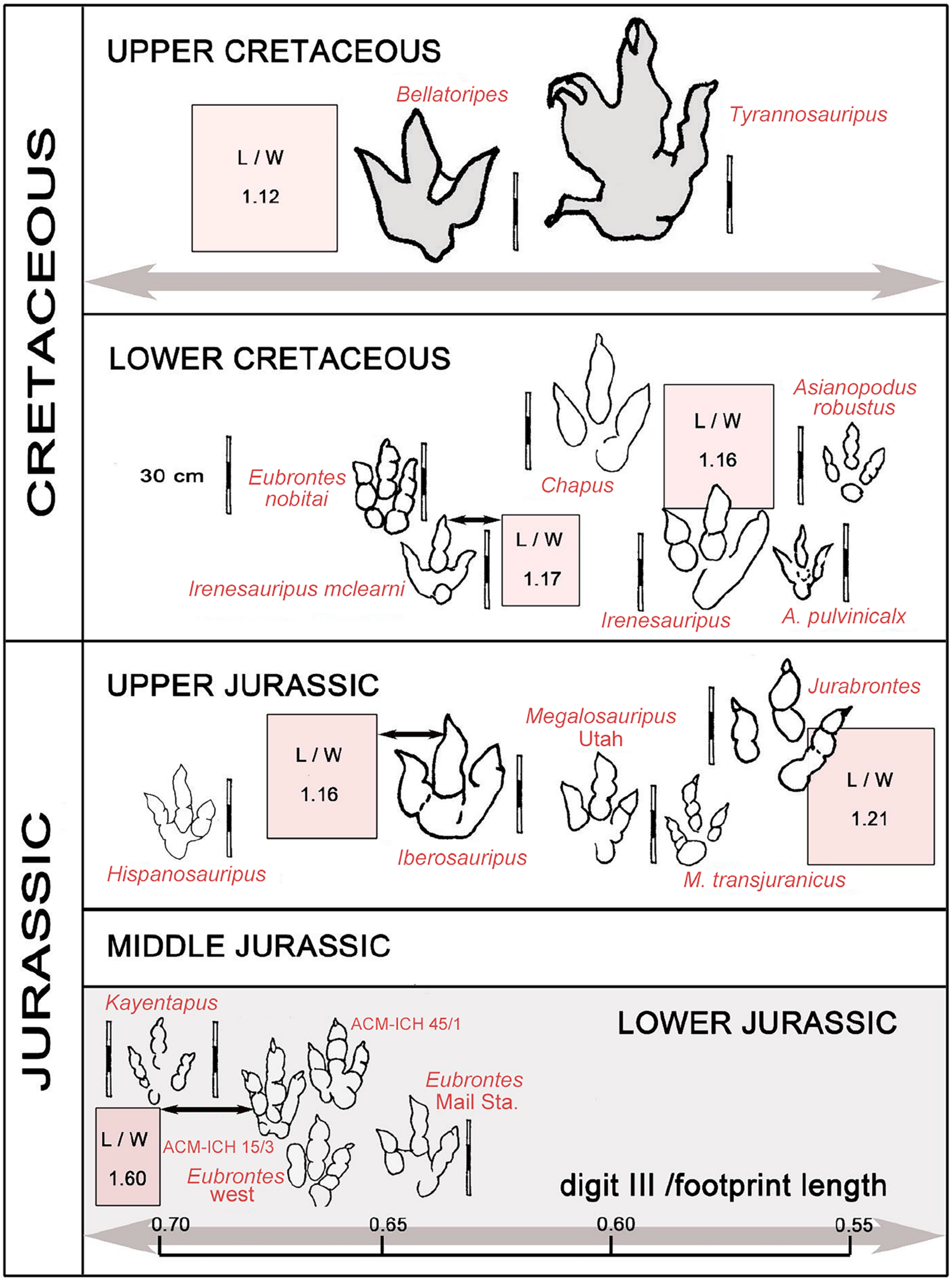


Figure 17. Comparison of *Eubrontes* and *Kayentapus* from the Lower Jurassic with 13 other theropod ichnotaxa from the Upper Jurassic and Cretaceous (Appendix F). All tracks are shown at the same scale and arranged from left to right in order of decreasing digit III/L ratios between 0.70 and 0.55. See text for details. With increasing footprint size, the relative length of digit III decreases.

excluded from the comparison), the aggregate length of the phalanges of digit III, relative to the length of metatarsal III, shows no tendency to decrease as the overall length of the foot (metatarsus III length + digit III length) increases (Figure 18B, Appendix G). In fact, in tyrannosauroids, the relative length of digit III increases as the foot gets bigger (cf. McCrea et al., 2014b; Farlow et al. 2018; Figure 18B here). If digit III does not become relatively shorter in bigger theropod feet, then the length of the "heel" impression must become relatively larger in order for the digit III impression/"heel" length ratio in larger footprints to decrease.

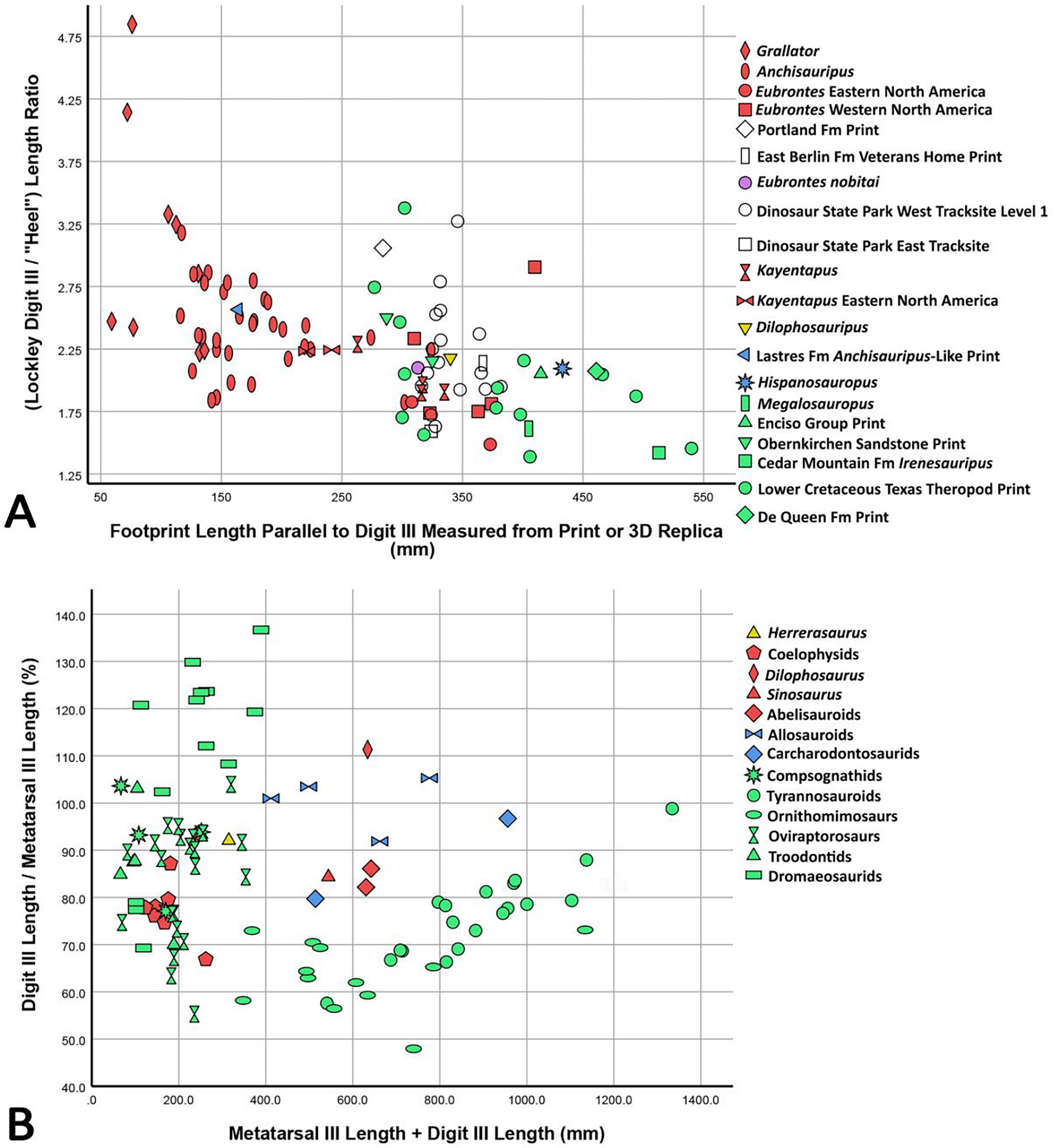


Figure 18. Size and shape comparisons of footprints attributed to theropod dinosaurs, and of theropod foot skeletons. (A) Relative length of the digit III and "heel" impressions in footprints; measurements made independently of Lockley's footprint measurements. Most or all of the footprints from Dinosaur State Park and the Veterans Home (both in Rocky Hill, Connecticut), and the Portland Formation (Hartford Basin, Connecticut and Massachusetts) would likely be classic *Eubrontes* as recognized in Eastern North America (Farlow et al., 2025). The digit III length/"heel" region length ratio decreases with increasing footprint size (cf. Figure 17). (B) The digit III length/metatarsal III length ratio as a function of total foot length (metatarsal III length + digit III length; Appendix G). Considering theropods other than dromaeosaurids, there is no systematic decrease in the metatarsal/digit length ratio with increasing animal size, and the ratio actually increases with increasing size in tyrannosaurs.

Comparing *Eubrontes*, *Megalosauripus*, and other large theropod prints (Figure 19A), the relatively longer "heel" in *Megalosauripus* compared with most *Eubrontes* is again apparent, and there is a positive but not very impressive correlation between the "heel" region length/digit III length ratio and footprint length (Spearman's rho = 0.358, p = 0.002, N = 73). However, Farlow's data for the same relationship, which span a greater range of footprint lengths (Figure 19B), show a stronger relationship between the two variables (Spearman's rho = 0.550, p less than 0.001, N = 115).

In principle, a relatively longer "heel" in footprints of progressively larger theropods might be explained by a progressively less vertical carriage of the metatarsus, such that the metatarsus impressed over a relatively greater proportion of its distal end in bigger dinosaurs. This explanation seems unlikely, however, given anatomical evidence for a more erect limb carriage in large as opposed to small theropods (cf. Gatesy et al., 2009; Bates et al., 2012; Bishop et al., 2018; Hutchinson et al., 2005, 2011; Hutchinson 2021).

Lockley (2000a, 2007, 2021) inferred from footprints an increase in stoutness of the posterior region of the digital portion of the foot as saurischian trackmakers became larger through time. Large theropods tended to have "fleshier" feet, with more coalesced digital pads. Farlow et al. (2018) described from skeletal evidence how large theropods have stouter toes than their smaller kin, and Farlow et al. (2025) reported an increase in relative breadth across the more proximal region (behind the toe impressions) of large as opposed to small footprints attributed to theropods. The relative increase in the length of the "heel" region in progressively larger footprints is arguably part of the same overall trend toward more massively constructed feet in bigger theropods. Just such a disproportionate increase in the surface area of the "heel" region has been hypothesized to have occurred ontogenetically in tyrannosaurs (Enriquez et al., 2021).

The "heel" region of theropod footprints—the portion proximal to (behind) the digital impressions—reflects impression of the metatarsophalangeal region of the foot, particularly around digits III and IV (Baird, 1957; Thulborn, 1990; Farlow et al., 2000). The "heel" region of theropod footprints conceivably finds an osteological correlate in the stoutness of the distal ends of metatarsals III and IV, expressed as the ratios of each of two dimensions across the distal end of the metatarsal to the length of the metatarsal. The two distal measurements are the dorsoventral (anteroposterior) depth and the mediolateral width (Appendix H).

If we treat theropod pedal skeletons in a simple-minded manner that ignores phylogenetic relationships (including congeneric and conspecific relationships of taxa), stoutness of the distal dorsoventral (anteroposterior) depth of metatarsal III (Figure 20A) has a weakly positive correlation with metatarsal length (Spearman's rho = 0.329, p = 0.036, N = 41). Stoutness of the distal mediolateral width of metatarsal III (Figure 20B) shows a stronger positive correlation with metatarsal length (Spearman's rho = 0.526, $p < 0.001$, N = 93).

Stoutness of the distal dorsoventral (anteroposterior) depth of metatarsal IV (Figure 21A) shows a significant positive correlation with metatarsal length (Spearman's rho = 0.433, p = 0.007, N = 38). Stoutness of the distal mediolateral width of metatarsal IV (Figure 21B) shows a nearly significant weakly positive correlation with metatarsal length (Spearman's rho = 0.221, p = 0.058, N = 74).

All four measures of distal metatarsal stoutness show marked separation of larger coelurosaurs (ornithomimosaurs plus tyrannosaurs) from more basal theropods; ornithomimosaurs and tyrannosaurs show distinctly more gracile distal metatarsals than other theropods of comparable size. Among more basal theropods, allosauroids (the sample dominated by a presumed ontogenetic series of *Allosaurus* itself) suggest a particularly strong size-related increase in metatarsal stoutness, and at all sizes include many of the stouter distal metatarsals of theropod metatarsals of a given length.

We hypothesize, then, that *Megalosauripus* may show a relatively longer "heel" region than *Eubrontes* in part because the *Megalosauripus*-makers – at least the form from the American Southwest, but likely not the European form – tended to be larger dinosaurs than the *Eubrontes*-makers (Figure 12). An even more important contributing factor may have been differences

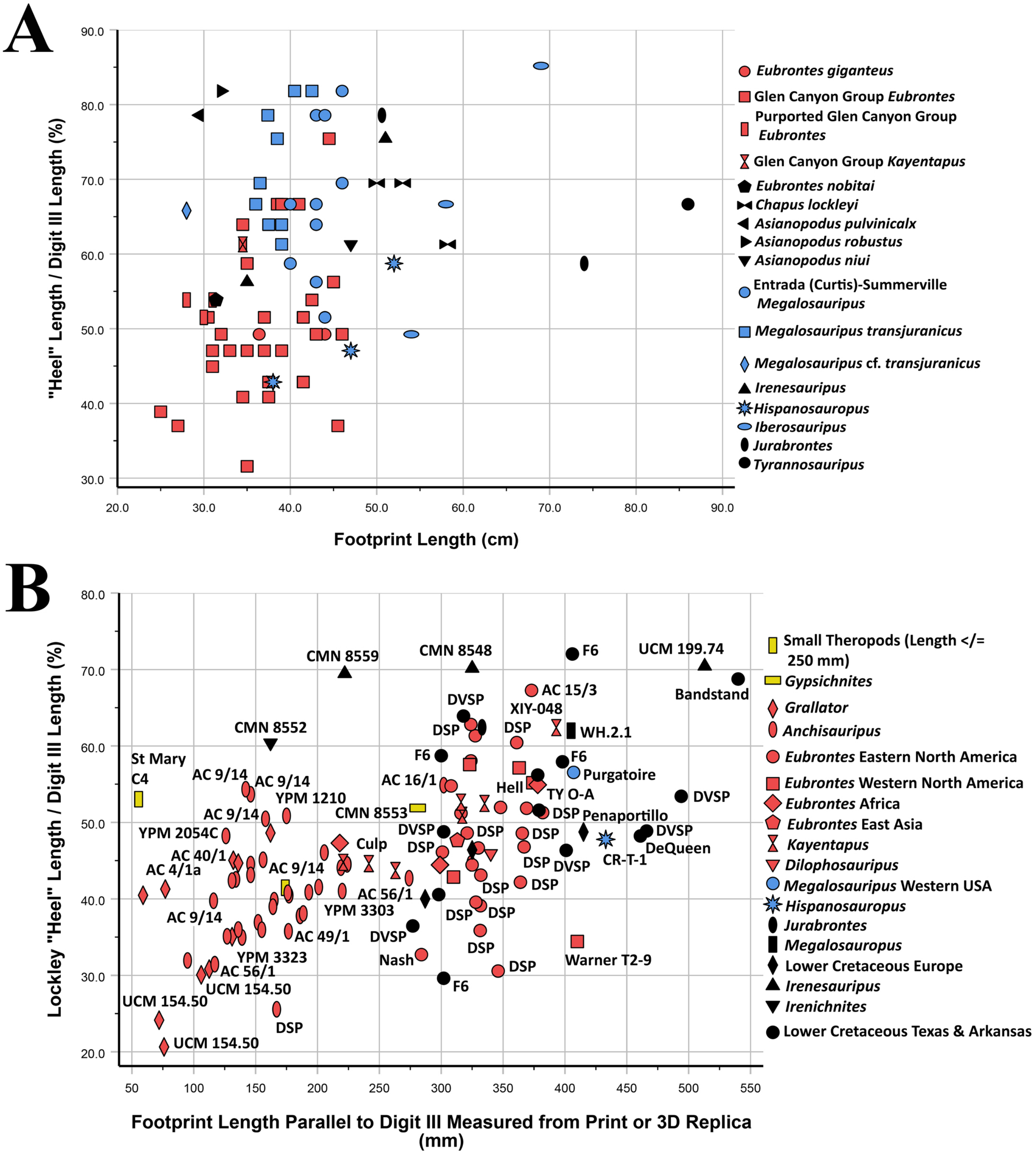


Figure 19. Length of the "heel" region relative to digit III length in *Eubrontes*, *Megalosauripus*, and other footprints attributed to theropod dinosaurs. (A) Measurements mostly made by Lockley (ratio calculated from data in Appendices A through D, which also provide keys to specimen labels); measurements of *Megalosauripus* cf. *transjuranicus* made by Farlow for this study from 3D replica of a footprint (cf. Castanera et al., 2023). (B) Measurements independently made by Farlow et al. (2025; see that paper for additional information about the sources of these footprints) across a larger size range, with many footprints not measured by Lockley.

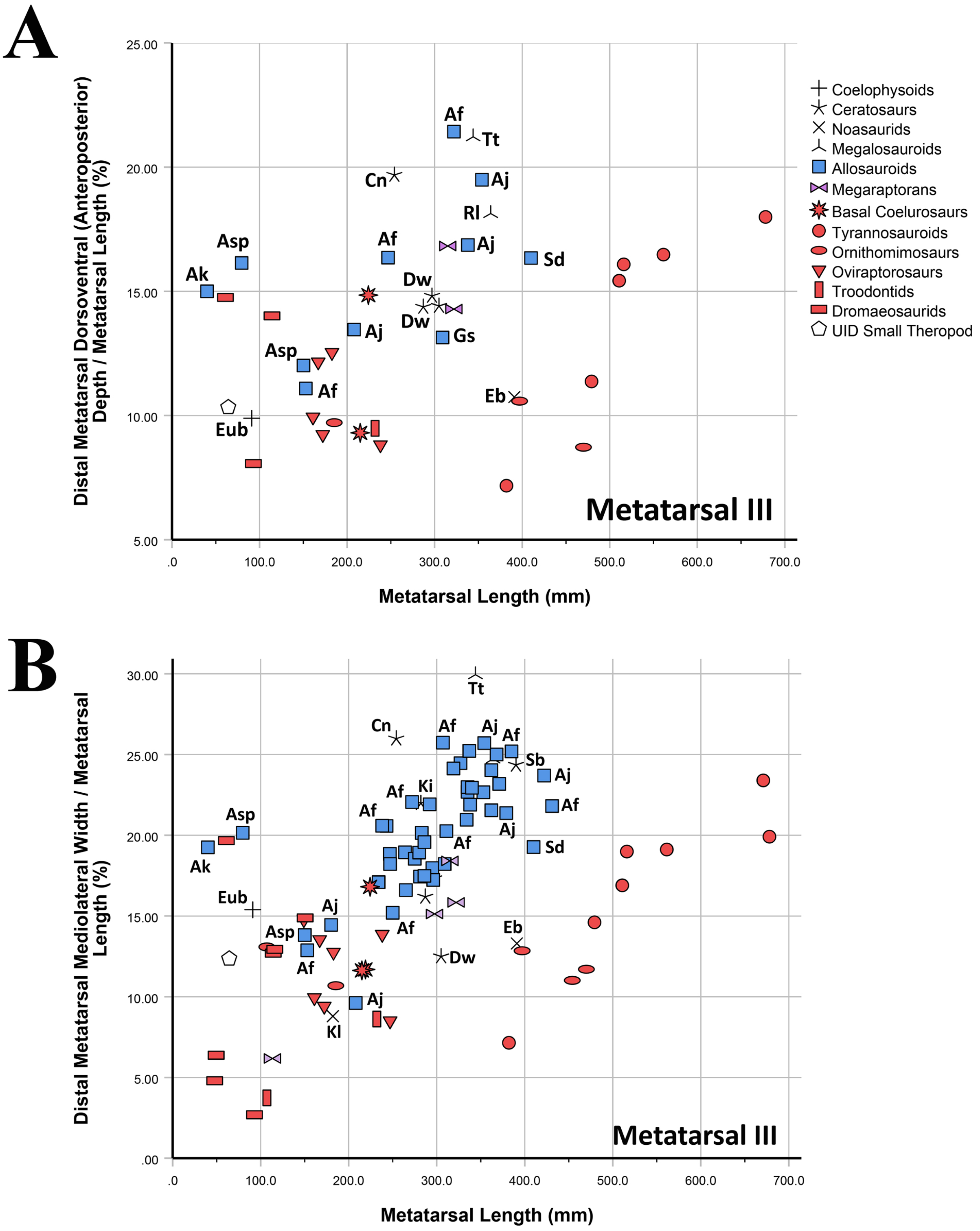


Figure 20. Relative stoutness of the distal end of metatarsal III (% of metatarsal length) in theropod dinosaurs (Appendix H). (A) Dorsoventral (anteroposterior) depth of distal end. (B) Mediolateral width of distal end. Non-coelurosaur points are labeled with species abbreviations, which are provided in the INSTITUTIONAL, SPECIMEN, AND LOCATION ABBREVIATIONS section.

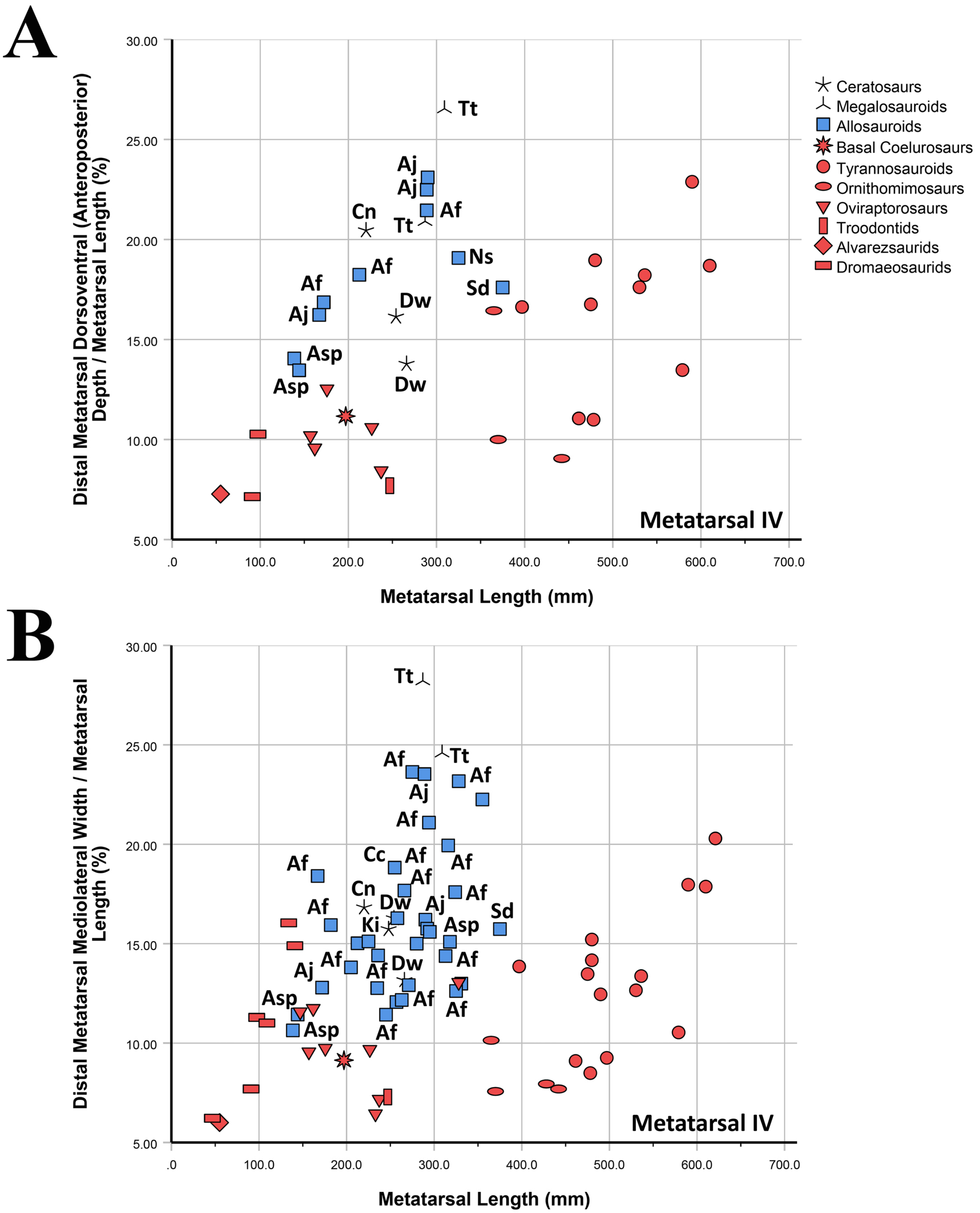


Figure 21. Relative stoutness of the distal end of metatarsal IV (% of metatarsal length) in theropod dinosaurs (Appendix H). (A) Dorsoventral (anteroposterior) depth of distal end. (B) Mediolateral width of distal end. Non-coelurosaur points are labeled with species abbreviations which are provided in the INSTITUTIONAL, SPECIMEN, AND LOCATION ABBREVIATIONS section.

in the systematic affinities of the *Eubrontes*-makers and the *Megalosauripus*-makers. *Dilophosaurus*, a candidate for the Glen Canyon Group *Eubrontes*-maker, may have less stout distal metatarsals than allosauroids and megalosauroids of comparable size, the latter groups including plausible candidates for the *Megalosauripus*-maker (Figures 20 and 21). The same considerations of overall footprint size and trackmaker affinities may account for the relatively longer "heel" region—and of course the relatively shorter digit III length—in some (but not all? – note the more gracile distal metatarsals of tyrannosauroids) of the later, even bigger theropod trackmakers.

We end with some interesting questions. The *Megalosauripus*-maker and the *Eubrontes*-maker (and all other theropods) hatched from eggs and so would have started life as considerably smaller animals than adults. Consequently, at some stages in their lives, theropods that as fully grown individuals would have impressed *Megalosauripus* prints would have been comparable in size to the smaller, typical *Eubrontes*-makers. Although there is overlap in the spread of points of relative length of the "heel" region of prints of comparable size of the two ichnogenera (Figures 13A and 19A), *Megalosauripus* tends to have a relatively longer "heel" region than *Eubrontes* over the range of footprint sizes in our sample. But given the relationship between relative "heel" length and overall footprint length across a wider size range (Figure 19B), would the difference in relative "heel" length and footprint size between the two ichnogenera remain true for very small footprints—say, those 10 cm or less in length?

And even acknowledging the size-related, and/or skeletal taxon-related, differences in the relative lengths of the digit III and "heel" region impressions among the large-theropod footprints examined in this study, are these differences enough to warrant recognition of all of the different forms as distinct ichnogenera? Recent morphometric analyses of large-theropod morphotypes (Lallensack et al., 2019; Farlow et al., 2025; Lallensack, 2025) have questioned whether the diversity of names applied to large-theropod footprints is justified.

However these questions are resolved—on the optimistic assumption that they can be resolved—the ichnogenus *Eubrontes* will likely be involved in answering them.

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APPENDIX A

Eubrontes and *Eubrontes*-like track bearing sites reported from Glen Canyon Group and Nugget Sandstone in the Western United States with a total of 168 localities (BENM = Bears Ears National Monument; CANY = Canyonlands National Park; Em = Emery County; Ga = Garfield County; Gr = Grand County; GSENM = Grand Staircase-Escalante National Monument; In = Iron County; Ka = Kane County; GLCA = Lake Powell and surrounding Glen Canyon National Recreation Area; RCRA = Red Cliffs Recreation Area; Sa = San Juan County; SGDS = St. George Dinosaur Discovery Site at Johnson Farm; Un = Uintah County; Wn = Wayne County; Ws = Washington County; ZION = Zion National Park. Note "Site Number" corresponds to regions before hyphen on Figure 3), and number after the hyphen are subsites within each region on Figure 3.

Site Name/State (Locality Number)	**Site Number**	**Unit**	**Associated Ichnofauna**	**References**
Motoqua Road Tracksite (Ws536), Utah	1-1	Whitmore Point, Moenave	*Grallator*	
Jensen Ridge Tracksite (Ws528), SGDS, Utah	2-1	Dinosaur Canyon, Moenave	*Grallator, Batrachopus*	
St. George Dinosaur Discovery Site at Johnson Farm (SGDS, Ws199), Utah	2-2	Dinosaur Canyon-Whitmore Point, Moenave	*Grallator, Kayentapus, Gigandipus, Anomoepus, Batrachopus, Selenichnus, Characichnos,* eucynodont tracks	Kirkland et al. (2002, 2014), Lockley et al. (2004), Kirkland and Milner (2006), Milner et al. (2006a, 2006b), Williams et al. (2006), Milner and Spears (2007), Harris and Milner (2015), Milner and Lockley (2006, 2016), Hendrickx et al. (2022), Hurtado et al. (2024)
Dixie Lube Site (Ws351), Utah	2-3	Whitmore Point, Moenave	*Grallator*	Milner and Kirkland (2006)
Grapevine Pass Wash Tracksite (Ws201, aka, Spectrum Tracksite), Utah	2-4	Springdale, Kayenta		Hamblin (2006), Hamblin et al. (2006), Milner and Spears (2007), Milner et al. (2012, their Figure 57)
I-9 Roadcut Tracksite (Ws680), Utah	2-5	Kayenta		
Washington City Water Tank Tracksite 2 (Ws152), Utah	2-6	Kayenta		
Washington City Water Tank Tracksite (Ws143), Utah	2-7	Kayenta	*Grallator*	Hamblin et al. (2006), Milner and Spears (2007)
Red Hills Parkway Tracksite (Ws537, aka, Red Hills Desert Garden), Utah	2-8	Kayenta-Navajo	*Kayentapus, Grallator, Batrachopus, Characichnos,* cf. sauropodomorph swim tracks	Milner et al. (unpublished data)
AM11-24 (Ws545, Red Hills Parkway Project), Utah	2-9	Kayenta-Navajo		

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
AM11-25 (Ws546, Red Hills Parkway Project), Utah	2-10	Kayenta-Navajo		
Mader Tracksite 1 (Ws376), Utah	2-11	Kayenta-Navajo	*Grallator*	
Kayenta Wash Tracksite, Utah (UGS loc.# WS801)	2-12	Whitmore Point, Moenave	cf. *Kayentapus*, *Grallator*	
Olsen Canyon Tracksite (Ws496), Utah	3-1	Dinosaur Canyon, Moenave	*Grallator, Anomoepus, Batrachopus*	Milner et al. (2012), Suarez et al. (2017)
Mader Moenave Tracksite 1 (Ws476), Utah	3-2	Whitmore Point, Moenave	*Grallator*	
Mader Moenave Tracksite 2 (Ws477), Utah	3-3	Whitmore Point, Moenave	*Grallator*	
Warner Valley Tracksite (Ws135), Utah	3-4	Kayenta	*Grallator, Anomoepus*	Miller et al. (1989), Birthisel et al. (2011), Milner et al. (2012, their Figure 59)
CPCP Tracksite (Ws473), Utah	3-5	Kayenta		
ARCM07-WC38 (Ws433), Utah	3-6	Kayenta		Miller et al. (1989)
AM09-01 (Ws503), Utah	3-7	Kayenta		
Ws538 Site (aka, Southern Parkway Plant Site), Utah	3-8	Kayenta	*Grallator, Anomoepus, Batrachopus, Characichnos,* cf. *Moyenisauropus, Undichna*	Milner et al. (2012 and unpublished data)
Red Reef Tracksite (Ws684), Utah	3-9	Kayenta	*Grallator, Anomoepus, Characichnos*	
GSA 1 Tracksite (Ws446), Utah	3-10	Kayenta		
GSA 2 Tracksite (Ws447), Utah	3-11	Kayenta		
AM11-33 (Ws550, Southern Parkway Project), Utah	3-12	Kayenta		
Hamblin Tracksite (Ws206T; Southern Parkway Project), Utah	3-13	Kayenta	*Kayentapus, Grallator, Anomoepus, Batrachopus*	Milner et al. (2012, their Figure 58)
Overkamp Tracksite (Ws654), Utah	3-14	Kayenta	*Kayentapus, Grallator*	
East Sand Mountain Tracksite (Ws478), Utah	3-15	Kayenta	*Grallator*	

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
ARCM05-06 (Ws373), Utah	4-1	Whitmore Point, Moenave		
Virgin River Tracksite 1 (Ws328), Hurricane, Utah	4-2	Kayenta	*Grallator*	
Desert Tortoise Tracksite 1 (Ws342; aka, “Site 9-23-05”), Utah	4-3	Kayenta	*Grallator*	Lockley et al. (2006b), Milner and Spears (2007), Milner et al. (2012)
Desert Tortoise Tracksite 2 (Ws377; aka, Plant Pot Site), Utah	4-4	Kayenta		Lockley et al. (2006b)
Desert Tortoise Tracksite 4 (Ws378; aka, Mader Tracksite 2), Utah	4-5	Kayenta		Lockley et al. (2006b)
Babylon 5 Tracksite (Ws393; aka, Desert Tortoise Tracksite 5), Utah	4-6	Kayenta	*Grallator*	Milner and Spears (2007)
Desert Tortoise South Tracksite 6 (Ws386), Utah	4-7	Kayenta	*Grallator*	
Desert Tortoise South Tracksite 8 (Ws385), Utah	4-8	Kayenta		
ARCM06-WC7 (Ws390), Utah	4-9	Kayenta		
Voyles Tracksite (Ws684), RCRA, Utah	4-10	Kayenta	*Grallator, Anomoepus,* cf. *Characichnos*	
DD Cottonwood Canyon – 10 (Ws591), RCRA, Utah	4-11	Kayenta		
RCRA 4 (Ws397), Utah	4-12	Kayenta	*Grallator*	Milner and Spears (2007, their Figures 30C and 30D)
RCRA Campground Site 1 (Ws356), Utah	4-13	Kayenta-Navajo	*Kayentapus, Grallator*	Milner and Spears (2007, their Figure 29)
Silver Reef Trail Tracksite (Ws160), RCRA, Utah	4-14	Kayenta-Navajo		Milner and Spears (2007, their Figure 30B)
DD Cottonwood Canyon-01 (Ws583), RCRA, Utah	4-15	Navajo	*Grallator, Brasilichnium*	
Wallace Ranch Tracksite (Ws470), Utah	5-1	Kayenta	*Grallator*	
Black Wash Tracksite 1 (Ws650; aka, Zack's Tracks), Utah	5-2	Kayenta		
Black Wash Tracksite 2 (Ws651; aka, Shelley Oden Tracks), Utah	5-3	Kayenta		
Smith Mesa Road Tracksite (Ws687), Utah	5-4	Kayenta		

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
Subway Tracksite (Ws002), ZNP, Utah	5-5	Kayenta		Stokes and Bruhn (1960), DeBlieux et al. (2006, their Figure 20), Milner et al. (2012, their Figure 40B)
KBRDT-2 (Ws244), ZNP, Utah	6-1	Kayenta	*Grallator*	DeBlieux et al. (2006, their Figures 22B and 22C)
KBRDT-1 (Ws245), ZNP, Utah	6-2	Kayenta	*Grallator*	DeBlieux et al. (2006, their Figure 22A)
Kolob Canyons Float Track Casts (Ws578), ZNP, Utah	6-3	Kayenta	*Grallator*	
Don's Kolob Track Block (Ws731), ZNP, Utah	6-4	Kayenta	*Grallator*	Milner et al. (2012, their Figures 40D and 40E)
Cedar City Overlook (In160), Utah	7-1	Kayenta		
Red Hollow Bridge Tracksite L1 #1 (In193), Utah	7-2	Kayenta	*Grallator,* cf. *Kayentapus*, cf. *Anomoepus*	
Red Hollow Bridge Tracksite L1 #3 (In194), Utah	7-3	Kayenta	cf. *Kayentapus*, cf. *Anomoepus*	
Red Hollow Bridge Tracksite L2 #1 (In195), Utah	7-4	Kayenta	cf. *Grallator*	
Red Hollow Bridge Tracksite L2 #2 (In196), Utah	7-5	Kayenta		
Red Hollow Bridge Tracksite L2 #3 (In197), Utah	7-6	Kayenta		
Red Hollow Bridge Tracksite L2 #4 (in198), Utah	7-7	Kayenta	cf. *Grallator*	
Red Hollow Bridge Tracksite L2 #5 (In199), Utah	7-8	Kayenta		
DD Canaan Mountain-02 (Ws616), Utah	8-1	Whitmore Point, Moenave	cf. *Characichnos*	
ZPS00.32 (Ws337), ZION, Utah	8-2	Whitmore Point, Moenave		
ZPS00.33 (Ws338), ZION, Utah	8-3	Whitmore Point, Moenave	*Grallator*	

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
ZION 1997 Survey (Ws157), ZION, Utah	8-4	Whitmore Point, Moenave	*Grallator*	
Bridge Mountain 1 (Ws161), ZION, Utah	8-5	Whitmore Point, Moenave	*Grallator*	
Bridge Mountain 2 (Ws162), ZION, Utah	8-6	Whitmore Point, Moenave		DeBlieux et al. (2006, their Figure 24D)
ZCTR03-1 (Ws260), ZION, Utah	8-7	Whitmore Point, Moenave		DeBlieux et al. (2006, their Figure 15), Milner et al. (2012, their Figure 40A)
ZCTR03-2 (Ws261), ZION, Utah	8-8	Whitmore Point, Moenave		
Oak Creek Tracksite (Ws211), ZION, Utah	8-9	Whitmore Point, Moenave		
Parunaweap Canyon 2002-1 (Ws313), ZION, Utah	8-10	Whitmore Point, Moenave	*Grallator, Anomoepus*?	DeBlieux et al. (2006, their Figure 17)
Watchman Trail 5 (Ws181), ZION, Utah	8-11	Whitmore Point, Moenave		DeBlieux et al. (2006, their Figure 24E)
Fire Station 2 (Ws187), ZION, Utah	8-12	Springdale, Kayenta		
Oak Creek 1 (Ws188), ZION, Utah	8-13	Springdale, Kayenta		DeBlieux et al. (2006, their Figures 19A and 19B, 24E)
Pine Creek single track (Ws213), ZION, Utah	8-14	Springdale, Kayenta		
Bridge Mountain Amphitheatre (Ws255; BAT03 -1), ZION, Utah	8-15	Springdale, Kayenta		DeBlieux et al. (2006, their Figure 19C)
ZION 1997 Survey (Ws158), ZION, Utah	8-16	Kayenta	*Grallator*	
ARCM07-WC33 (Ws426), ZION, Utah	8-17	Kayenta		
BAT03-3 (Ws257), ZION, Utah	8-18	Kayenta		DeBlieux et al. (2006, their Figure 21E)
Blacks Canyon 2 (Ws166), ZION, Utah	8-19	Kayenta		
North Moccasin Mountain Dinosaur Tracksite (Ka1023), Utah	9-1	Navajo	*Grallator, Kayentapus, Otozoum, Brasilichnium, Batrachopus*	Milner et al. (2012)

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
Hog Canyon Dinosaur Tracksite (Ka221), Utah	9-2	Kayenta		
GSENM 2007 Paleo Survey Locality (Ka3475; 13UTKA-8), GSENM, Utah	10-1	Kayenta	*Kayentapus*	
GSENM 2007 Paleo Survey Locality (Ka3055; MKZ-2007-1), Utah	10-2	Kayenta		
Vermillion Cliffs large dinosaur tracks (Ka006), Utah	10-3	Kayenta		
Harry Barber Tracksite (Ka621), GSENM, Utah	11-1	Kayenta		
Flag Point Dinosaur Tracksite (Ka002), GSENM, Utah	11-2	Kayenta	*Grallator*	Hamblin and Foster (2000), Foster et al. (2001), Lockley et al. (2006a)
Flag Point II Tracksite (Ka568), GSENM, Utah	11-3	Kayenta	*Anomoepus*?	Foster et al. (2001)
Flag Point III Tracksite (Ka567), GSENM, Utah	11-4	Kayenta		Foster et al. (2001)
Flag Point V Tracksite (Ka1214), GSENM, Utah	11-5	Kayenta		
West Swag Tracksite (Ka570), GSENM, Utah	12	Navajo	*Anomoepus*?	Foster et al. (2001, their Figure 11)
Tuba City Tracksite, Arizona	13-1	Springdale, Kayenta		
Dilophosauripus Type Locality, Arizona	13-2	Kayenta		Welles (1971)
Kayentapus Type Locality, Arizona	13-3	Kayenta		Welles (1971), Lockley et al. (2011)
Navajo Canyon, GLCA, Arizona	14-1	Kayenta?		Gregory (1917)
Neskla Nizadi, GLCA, Utah	14-2	Kayenta?		Hall (1934), Lockley et al. (2014e, their Figure 18)
Dam Site, GLCA PalLoc_0445, Arizona	14-3	Navajo		Stokes (1978), Lockley et al. (1998)
Choal Canyon 1 (aka, OK Site), GLCA PalLoc_0700, Arizona	14-4	Kayenta-Navajo	cf. *Kayentapus, Batrachopus*	Jones and Ward (1991), Lockley et al. (1998, 2014e, their Figure 18)
Kayenta Kiva Koffeehouse (Ka322; aka, Kayenta Koffeehouse Tracksite), GSENM, Utah	15	Kayenta	*Grallator, Brasilichnium*	Hamblin and Foster (2000), Foster et al. (2001)

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
Rainbow Bridge (Sa372) (RABR PalLoc_0001), GLCA, Utah	16-1	Kayenta		Lockley et al. (1998)
San Juan 2, GLCA PalLoc_0503, Utah	16-2	Kayenta	*Grallator, Anomoepus*?	
Hole in the Rock south side, GLCA PalLoc_0475, Utah	16-3	Kayenta-Navajo		
Confluence Overlook, GLCA PalLoc_0442, Utah	16-4	Navajo		
John Wesley Powell Track Block (Sa002), GLCA PalLoc_0001, Utah	16-5	Navajo	*Grallator, Batrachopus*	Lockley et al. (2014e, their Figure 26), Lockley and Xing (2015, their Figure 4), Tweet and Santucci (2018, their Figure 3E), Milner et al. (2023b, 2024, their Figure 14L)
Driftwood Canyon, GLCA PalLoc_0447, Utah	16-6	Navajo	*Grallator*	Lockley et al. (1998)
Hole in the Rock 1, GLCA PalLoc_0400, Utah	16-7	Navajo		Lockley et al. (1998)
Hole in the Rock 2, GLCA PalLoc_0401, Utah	16-8	Navajo		Lockley et al. (1998)
Hole in the Rock 3, GLCA PalLoc_0450, Utah	16-9	Navajo		Lockley et al. (1998)
Reflection Canyon, GLCA PalLoc_0454, Utah	16-10	Navajo		Lockley et al. (2014e)
Escalante Mouth 1, GLCA PalLoc_0485, Utah	17-1	Kayenta	*Grallator*	Lockley et al. (2014e, their Figure 14B)
Delgalvis Low water site, GLCA, Utah	17-2	Kayenta		Lockley et al. (2014e, their Figure 2); site is in the Lockley's Cove vicinity, just south and down-section from David's Camp localities
Delgalvis Crouching *Grallator* Site 1, GLCA_PalLoc 0068, Utah	17-3	Kayenta	*Grallator*	Gierliński et al. (2009), Lockley et al. (2014e, their Figure 14), Tweet and Santucci (2018, their Figure 3F), Milner et al. (2024, their Figures 17A through 17C)
Big Bend 1, GLCA PalLoc_0511, Utah	17-4	Kayenta		
Down-lake from mile 68, GLCA PalLoc_0483, Utah	17-5	Kayenta-Navajo	*Grallator*	
Fence Canyon, GLCA PalLoc_0474, Utah	17-6	Kayenta-Navajo		Barnes (1986)
Andre's Alcove Tracksite, GLCA PalLoc_0069, Utah	17-7	Navajo	*Grallator, Anomoepus, Navahopus*	Bennett et al. (2023), Milner et al. (2024, their Figure 22A and unpublished data)

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
Camp Site Tracksite (Ka1181), GLCA PalLoc_0047, Utah	17-8	Navajo	*Brasilichnium*	
Slick Rock Canyon 1, GLCA PalLoc_0516, Utah	18-1	Kayenta		Lockley et al. (1998)
Slick Rock Canyon 2, GLCA PalLoc_0266, Utah	18-2	Kayenta	*Grallator, Otozoum*	Lockley et al. (2014e, their Figure 4)
Slick Ice 3 (also known as Lockley Cove 4), GLCA PalLoc_0054, Utah	18-3	Kayenta	*Grallator*	Lockley et al. (2014e, their Fgure 5)
Slick Ice 9, GLCA PalLoc_0506, Utah	18-4	Kayenta		
Slick Ice 11, GLCA PalLoc_0496, Utah	18-5	Kayenta	*Grallator*	
Explorer Canyon 1, GLCA PalLoc_0498, Utah	18-6	Kayenta		Lockley et al. (1998)
Mikes Mesa, GLCA PalLoc_0513, Utah	18-7	Kayenta		Lockley et al. (1998)
Explorer Canyon 2, GLCA PalLoc_0499, Utah	18-8	Kayenta		Lockley et al. (2014e, their Figure 16)
Explorer Canyon 3, GLCA PalLoc_0500, Utah	18-9	Kayenta	*Grallator*	
Explorer Canyon, GLCA PalLoc_0510, Utah	18-10	Kayenta		Edwards (1967)
Halls Crossing, GLCA PalLoc_0449, Utah	18-11	Navajo		
Moqui Man 1, GLCA PalLoc_0462, Utah	18-12	Navajo	*Grallator*	
Moqui Man 2, GLCA PalLoc_0463, Utah	18-13	Navajo		
Annie's Canyon (also known as *Eubrontes* Beach), GLCA PalLoc_0532, Utah	18-14	Navajo	*Grallator, Otozoum*	Lockley et al. (1998)
(Nokai Dome, GLCA, Utah	18-15	Navajo		
Little Cave Cove, GLCA, PalLoc_0078 Utah	19-1	Wingate	*Grallator, Kayentapus,* cf. *Characichnos*	Wood et al. (2021), Milner et al. (2024, their Figure 12)
Good Hope Bay 1, GLCA PalLoc_0507, Utah	19-2	Kayenta		
Delgalvis Crouching Dinosaur 2, GLCA PalLoc_0084, Utah	19-3	Kayenta		Milner et al. (2024, their Figures 17D and 17E)

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
North of Cedar Canyon 1, GLCA PalLoc_0479, Utah	19-4	Kayenta-Navajo		
North of Cedar Canyon 2, GLCA PalLoc_0478, Utah	19-5	Kayenta-Navajo		
Tapestry Wall Tracksite (Ga853), GLCA PalLoc_0046, Utah	19-6	Navajo	cf. *Grallator*	Lockley et al. (1998)
South of Knowles Canyon, GLCA PalLoc_0464, Utah	19-7	Navajo		
Navajo National Monument, Arizona	20	Navajo		
Sunset Pass Big Track Block (Ga2172), Utah	21-1	Kayenta		
Tracksite near Land's End (Ga2171), GLCA, Utah	21-2	Navajo		
Leprechaun Canyon Dinosaur Tracksite (Ga186), Utah	21-3	Navajo		
Horseshoe Canyon West Rim Trailhead Dinosaur Tracks (Wn118), Utah	22-1	Navajo		DeBlieux et al. (2024)
Horseshoe Canyon Great Gallery Dinosaur Tracks (Wn119), Utah	22-2	Navajo		
A1 Lithium (Gr1328), Utah	23-1	Kayenta		
Big Mesa Campground (Gr588), Utah	23-2	Navajo		Wilkens (2008)
Dead Horse Point Road, Utah	23-3	Navajo		
Martin Lockley 2004 BLM Report (Gr918; UCD 05), Utah	23-4	Navajo		
Kane Creek, Utah	24-1	Kayenta		Lockley (1986)
Poison Spider Trailhead (Gr011), Utah	24-2	Navajo	*Grallator, Anomoepus*	Lockley and Hunt (1995, their Figure 4.13)
Hell's Revenge Dinosaur Tracksite (Gr664), Utah	24-3	Navajo		
Sand Flats Site, Utah	24-4	Navajo		
Track below Hell's Revenge (Gr979), Utah	24-5	Navajo		
Morning Glory Arch Tracks (Gr990), Utah	24-6	Navajo		

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Site Name/State (Locality Number)	Site Number	Unit	Associated Ichnofauna	References
Flat Iron Mesa 1 (Sa1452), Utah	25-1	Kayenta	*Grallator*	Lockley et al. (2018c)
Flat Iron Mesa 2 (Sa1465), Utah	25-2	Kayenta	*Grallator, Otozoum, Kayentapus*	Lockley et al. (2018c)
Troutwater Creek Dinosaur Tracksite (Sa285), Utah	25-3	Kayenta		Lockley and Hunt (1995, their Fgure 4.8)
Linda's Track Block (Sa1279), BENM, Utah	26-1	Wingate	*Grallator, Anomoepus*?	
AM15-32 (Sa1103), BENM, Utah	26-2	Wingate or Kayenta?		
Martin Lockley 2014 BLM Report: Lisbon Valley Turnoff (Sa908; UCD 60), Utah	27-1	Navajo	cf. *Anomoepus*	
Mail Station Tracksite, Utah	27-2	Navajo		Lockley et al. (2021; and this study)
Casa Colorado Site, Utah	27-3	Navajo		
Granite Creek, Utah	28	Navajo	*Grallator, Brasilichnium*	Lockley et al. (2014c, their Figure 6)
Cactus Park 1, Colorado	29-1	Kayenta	*Grallator*	Lockley and Hunt (1995)
Cactus Park 2, Colorado	29-2	Kayenta	*Grallator*	Lockley et al. (2014d)
Red Fleet Reservoir Dinosaur Tracksite (Un425), Utah	30	Navajo-Nugget		Hamblin and Bilbey (1999), Hamblin et al. (2000)
Dinosaur National Monument, Utah	31	Navajo-Nugget		Lockley (2011a, Lockley's Figure 5)
Buckhorn Draw Dinosaur Track Locality (Em0015), Utah	32	Navajo		Stokes (1978)

APPENDIX B

Morphometric parameters of Lower Jurassic *Eubrontes* and a few associated large tracks (footprint length greater than 30 cm, except for T 935 and T 936) from the Glen Canyon Group, Western United States (Figures 6 through 8). The letter prefix "T" indicates that the measurements are made from tracings of footprint outlines. All tracks are well preserved, i.e., 2 and 3 on the scale of Belvedere and Farlow (2016). Tracks with asterisk* have not been identified as *Eubrontes*. Track numbers in bold are represented by mean values. L = footprint length (cm), W = footprint width (cm), Ant Tri = ratio of length to width of the anterior triangle, dIII/L = ratio of digit III length to overall footprint length, and Div II–IV = divarication (interdigital) angle between digits II and IV (degrees).

Track	L	W	L/W	Ant Tri	dIII/L	Div II–IV	Comments
T 130	45.0	28.0	1.61	0.73	0.64	41°	Dead Horse Point, E Utah
T 132	36.0	32.0	1.13	0.42	-	66°	Hole in the Rock (GLCA), Utah
T 134	32.0	24.0	1.33	0.45	0.67	42°	Red Fleet Res., NE Utah
T 183	27.0	21.0	1.29	0.59	0.73	45°	Washington Co., SW Utah
T 184	25.0	23.0	1.09	0.44	0.72	55°	Washington Co., SW Utah
T 188	46.0	34.0	1.35	0.53	0.67	45°	Hog Canyon, Kanab, Utah
T 198	41.5	34.0	1.22	0.42	0.66	47°	Explorer Canyon (GLCA), Utah
T 200	41.5	31.0	1.34	0.48	0.70	38°	Warner Valley, SW Utah
T 237	31.0	27.0	1.15	-	-	59°	Nokai Dome (GLCA), Utah
T 452	31.0	29.0	1.07	0.39	0.69	55°	SGDS, SW Utah
T 453	41.0	29.0	1.41	0.53	0.60	38°	SGDS, SW Utah
T 454	38.5	26.5	1.45	0.44	0.60	59°	SGDS, SW Utah
T 455	35.0	30.0	1.57	0.47	0.68	52°	SGDS, SW Utah
T 470 (SGDS 50)	39.0	26.0	1.50	0.46	-	44°	SGDS, SW Utah
T 471	39.0	27.5	1.60	0.57	0.60	46°	SGDS, SW Utah
T 639 (SGDS 24)	38.0	28.0	1.36	0.50	-	66°	SGDS, SW Utah
T 909	44.5	39.0	1.14	0.37	0.57	57°	Sand Flats, E Utah
T 928	37.0	29.5	1.25	0.33	0.68	48°	Explorer Canyon (GLCA), Utah

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Track	**L**	**W**	**L/W**	**Ant Tri**	**dIII/L**	**Div II–IV**	**Comments**
T 929	42.5	33.0	1.29	0.47	0.65	55°	Explorer Canyon (GLCA), Utah
T 933*	30.0	20.0	1.50	0.90	0.66	47°	Choal Canyon 1 (GLCA), Arizona
T 935*	26.5	17.5	1.51	0.70	-	62°	Navajo National Monument, Arizona
T 936*	28.0	19.0	1.47	0.69	0.65	64°	Slick Rock Canyon (GLCA), Utah
T 1012	30.5	25.5	1.20	0.48	0.66	58°	Slick Rock-Iceberg Canyons (GLCA), Utah
T 1013	35.0	26.5	1.32	0.44	0.63	49°	Slick Rock-Iceberg Canyons (GLCA), Utah
T 1020	35.0	29.5	1.19	0.32	-	53°	Escalante (GLCA), Utah
T 1020	45.5	35.0	1.30	0.51	0.73	44°	Escalante (GLCA), Utah
T 1022	37.5	24.0	1.56	0.62	0.71	46°	Slick Rock-Iceberg Canyons (GLCA), Utah
T 1023	34.5	29.0	1.19	0.43	0.71	60°	Slick Rock-Iceberg Canyons (GLCA), Utah
T 1025	31.0	24.0	1.29	0.50	0.68	44°	Escalante (GLCA), Utah
T 1038*	40.0	30.5	1.31	0.50	-	52°	Choal Canyon 1 site (GLCA), Utah
T 1038*	35.0	22.0	1.59	0.89	-	60°	Choal Canyon 1 site (GLCA), Utah
T 1059	37.0	30.5	1.21	0.26	0.66	53°	Moqui Man (GLCA), Utah
T1098 (SGDS 1713)	39.0	26.0	1.50	0.75	0.68	42°	Desert Tortoise Tracksite 1, SW Utah
T 1135	37.5	28.0	1.34	0.58	0.70	51°	Flag Point, Utah
T 1172	32.0	23.0	1.39	0.46	0.67	47°	N Lake Powell (GLCA), Utah

APPENDIX B

Track	**L**	**W**	**L/W**	**Ant Tri**	**dIII/L**	**Div II–IV**	**Comments**
T 1467*	34.5	28.5	1.21	0.48	0.62	58°	*Kayentapus* type, N Arizona
T 1485	33.0	23.0	1.43	0.63	0.68	36°	Cactus Park 2, W Colorado
T 1488	34.5	24.0	1.44	0.47	0.61	49°	Cactus Park 1, W Colorado
T 1523	43.0	32.0	1.34	0.42	0.67	38°	Warner Valley, SW Utah
T 1600	35.0	27.0	1.30	0.37	0.76	54°	Granite Creek, E Utah
T 1726*	34.5	24.0	1.44	0.50	0.62	58°	Flat Iron Mesa, Utah
T 1727*	31.0	23.0	1.35	0.52	0.65	46°	Flat Iron Mesa, Utah
T1728	36.0	24.0	1.50	0.54	-	53°	Flat Iron Mesa, Utah
Means	**36.8**	**28.2**	**1.30**	**0.49**	**0.67**	**50.7**	

APPENDIX C

Measurements from *Megalosauripus* tracks (1 through 10) from the Middle to Upper Jurassic Entrada (Curtis)–Summerville Formations interval in Utah. Numbers without T prefix are UCM specimens. T prefix indicates tracing. Specimens 11 through 14 represent European *M. transjuranicus* after Razzolini et al. (2017). For parameter abbreviations see Appendix B. Numbers in **bold** indicate mean values for trackways.

No. Track	**L**	**W**	**L/W**	**Ant Tri**	**dIII/L**	**Div II–1V**	**Comments**
Megalosauripus UT							
1 188.25	43.0	30.0	1.43	0.47	0.60	51°	
2 187.6	43.0	33.0	1.30	0.34	0.56	41°	Bull Canyon site
3 T359	43.0	30.0	1.43	0.56	0.64	34°	
4 T359	46.0	30.0	1.53	0.55	0.59	27°	
5 T228	40.0	28.0	1.43	0.38	0.63	43°	
6 T1141	43.0	34.0	1.26	0.43	0.61	39°	
7 T1886	44.0	29.0	1.52	0.38	0.56	38°	Duma Point
8 T1886	46.0	31.0	1.48	0.55	0.55	41°	Duma Point
9 T1886	44.0	30.0	1.47	0.39	0.66	37°	Duma Point
10 T1885	40.0	28.0	1.43	0.50	0.60	46°	
Means 1-10	**43.2**	**30.3**	**1.43**	**0.46**	**0.60**	**39.7°**	
Megalosauripus transjuranicus							
11 BEB5000-TR7	**36.2**	**26.4**	**1.40**	**0.50**		**58.8°**	
12 SCR1000-T23	**41.0**	**25.7**	**1.60**	**0.50**		**33.0°**	
13 BSY1035-T6	40.5	22.5	1.80	0.60	0.55	25.0°	
14 BSY1040-T1	**38.5**	**20.1**	**1.50**	**0.50**	**0.57**	**38.5°**	
15 BSY1040-T9	36.5	26.0	1.40	0.50	**0.59**	41.0°	
16 TCH1000-TR1	**38.7**	**25.7**	**1.50**	**0.50**		**36.3°**	
17 TCH1000-TR2	**40.3**	**26.7**	**1.40**	**0.40**		**35.7°**	
18 TCH1015-T1	**37.4**	**21.5**	**1.70**	**0.50**	**0.56**	**30.0°**	
19 TCH1020-T1	34.0	23.5	1.40	0.60		52.0°	
20 TCH1020-T2	**41.1**	**31.4**	**1.40**	**0.50**		**40.0°**	
21 TCH1025-T1	40.5	22.5	1.80	0.50		26.0°	
22 TCH1025-T2	42.5	30.0	1.40	0.40	0.55	48.0°	
23 TCH1030-T1	43.0	26.0	1.70	0.60		46.0°	
24 TCH1030-T2	**36.0**	**22.5**	**1.60**	**0.60**	**0.60**	**41.3°**	
25 TCH1030-T3	39.0	25.5	1.50	0.50	0.62	41.0°	
26 TCH1030-T6	37.5	25.0	1.50	0.60	**0.61**	51.0°	Holotype
27 TCH1030-T7	39.0	20.5	1.90	0.70	**0.61**	30.0°	
Means 11-24	**39.0**	**24.8**	**1.57**	**0.52**	**0.58**	**39.7°**	

APPENDIX D

Measurements of *Hispanosauripus*, *Iberosauripus*, and *Jurabrontes* tracks based on published sources, with minor modifications based on the authors' notes and measurements of specimens and tracings. For parameter abbreviations see Appendix B.

No. Track	L	W	L/W	Ant Tri	dIII/L	Div II–1V	Comments
Hispanosauripus							
paralectotype	52.0	38.0	1.36	0.45	0.63	54°	Lockley et al. (2007)
MUJA 1055	38.0	26.0	1.46	0.52	0.70	50°	Avanzini et al. (2011)
Copper Ridge, Utah	47.0	35.0	1.34	0.53	0.68	56°	Foster (2015)
Grand mean	**45.7**	**33.0**	**1.38**	**0.50**	**0.67**	**50.3°**	
Iberosauripus							Cobos et al. (2014)
ICB1-4	54.0	42.0	1.28	0.30	0.67	25°	
ICB1-5	58.0	45.0	1.28	0.29	0.60	37°	
ICB1-6	54.0?	43.0	1.25	-	-	26°	
mean	**56.0**	**43.5**	**1.27**	**0.295**	**0.635**	**29.3°**	
Las Villasecas	69.0	56.0	1.23	0.32	0.54	33°	Barco et al. (2005)
Grand mean	**59.3**	**46.6**	**1.26**	**0.30**	**0.60**	**30.2°**	This study
Jurabrontes							Marty et al. (2017)
BSY 1050-TR1	48.5	40.0	1.21	0.48		52 °	paratype
BSY 1050-TR2	74.0	47.8	1.56	0.47	0.63	44.3 °	paratype
SRC 1500-T1	50.6	41.8	1.21	0.38	0.56	46 °	holotype
Mean	**57.7**	**43.2**	**1.33**	**0.44**	**0.60**	**47.4 °**	

APPENDIX E

Comparison of the type material of the Lower Cretaceous theropod ichnogenera, *Irenesauripus* from North America and *Chapus* and the three ichnospecies of *Asianopodus* from Asia. Table modified after Xing et al. (2021a, 2021b). Abbreviations: L = maximum length, W = maximum width, PL = pace length, SL = stride length, M = mesaxony, and L/W is dimensionless.

Track #	**L**	**W**	**L/W**	**M**	**Digit III/L**	**II–IV**	**PL/SL**	**Source**
Irenesauripus 1	35	30	1.17	0.40	0.64	62°	75.0/135.0	Type specimen
Irenesauripus 2	51.0	44.0	1.16	0.33	0.57	55°	155/310	Foster (2015)
C. lockleyi L1	58.2	42.6	1.36	0.53	0.62	57 °	—	Li et al. (2011); Lockley et al. (2018c)
C. lockleyi R1	50.0	39.0	1.28	0.45	0.59	61°	—	Li et al. (2011); Lockley et al. (2018c)
C. lockleyi L2	53.0	40.0	1.32	0.45	0.59	60 °	—	Li et al. (2011); Lockley et al. (2018c)
***C. lockleyi* mean**	**53.7**	**40.5**	**1.32**	**0.48**	**0.60**	**59.3°**	126.6/233	Li et al. (2011); Lockley et al. (2018c)
A. pulvinicalx	29.5	20.5	1.44	0.45	0.56	30.0°	91.0/—	Matsukawa et al. (2005)
A. robustus	32.0	26.0	1.23	0.40	0.55	55.0°	—	Li et al. (2011); Lockley et al. (2018c)
A. niui holotype	56.0	42.0	1.33	0.64	—		172/332	Li et al. (2020); taxon regarded as a *nomen dubium* by Xing et al. (2021c)
A. niui paratype	47.0	31.0	1.52	0.52	0.62		—	Li et al. (2020)
E. nobitai	31.4	22.5	1.4	0.37	0.65	47°	82.7/164.4	Xing et al. (2021b)

APPENDIX F

Comparison of type specimens and type material used to define the important theropod ichnogenera discussed in this paper, listed in order of geological age from Early, Middle, and Late Jurassic (J1, J2, J3) to Early and Late Cretaceous (K1 and K2). Abbreviations: L = maximum length, W = maximum width, L/W = length to width ratio, PL = pace length, SL = stride length, M = mesaxony (i.e., anterior triangle L/W), dIII/L = ratio of length between digit III and whole track, II–IV = divarication between digits II and IV. M, dIII/L, and L/W are dimensionless ratios. When published, morphometric information was not available, especially for ratios M and dIII/L, parameters were measured from, and checked against, original illustrations or original specimens. For consistency the measurements were collected by the same observer (M. Lockley). Note also that morphometric data for western *Eubrontes* (*Eubrontes* west) are new, summarized in Appendix B, and compared with a large single site sample from the Mail Station (Mail Sta.) site in Utah. Likewise, asterisk * denotes that morphometric data for *Megalosauripus* 1 and 2, from the Western United States and Europe respectively are pooled from the large samples detailed in Appendix C. *Irenesauripus* 2 refers to tracks from the Cedar Mountain Formation site, Utah (Figure 15).

Track #	Age	L	W	L/W	M	dIII/L	II–IV	PL/SL	Source
Eubrontes ACM-ICH 15/3	J1	44.0	28.0	1.57	0.47	0.67	35.0°	-	Olsen et al. (1998)
Eubrontes ACM-ICH 45/1	J1	36.4	22.8	1.60	0.44	0.67	32.0°	105/206.5	Olsen et al. (1998)
Eubrontes west	J1	36.7	28.2	1.30	0.49	0.67	50.7°	-	This study
Eubrontes Mail Sta.	J1	37.5	28.9	1.31	0.44	0.64	46.2°	181.5/360.7	Lockley et al. (2021)
Kayentapus	J1	36.5	29.0	1.26	0.47	0.70	57.0°	191.0/382.0	Lockley et al. (2011)
Megalosauripus 1*	J3	43.2	30.3	1.50	0.46	0.60	39.7°	-	This study
Megalosauripus 2*	J3	39.0	24.8	1.57	0.52	0.58	39.7°	107.5/ -	Razzolini et al. (2017)
Hispanosauropus	J3	38.0	26.0	1.46	0.52	0.70	50.0°	-	Avanzini et al. (2011)
Iberosauripus	J3	56.0	43.5	1.27	0.295	0.635	29.3°	178/355.5	Cobos et al. (2014)
Jurabrontes	J3	50.6	41.8	1.21	0.38	0.56	46.0°	151.6/303.5	Marty et al. (2017)
Irenesauripus type	K1	35.0	30.0	1.17	0.40	0.64	62.0 °	75.0/135.0	Type specimen
Irenesauripus 2	K1	51.0	44.0	1.16	0.33	0.57	55.0 °	155/310	Lockley et al. (2014d, 2014e)
Asianopodus type	K1	29.5	20.5	1.45	0.45	0.56	30.0°	91.0/ -	Matsukawa et al. (2005)
A. robustus	K1	32.0	26	1.23	0.40	0.55	55.0°	-	Li et al. (2011)
Chapus type	K1	53.7	40.5	1.32	0.48	0.60	59.3°	126.6/233.0	Li et al. (2006)
Eubrontes nobitai	K1	31.2	22.5	1.40	0.37	0.65	47.0°	82.7/164.4	Xing et al. (2021b)
Bellatoripes	K2	57.9	51.9	1.12	0.40	-	36.0°	173/346	McCrea et al. (2014b)
Tyrannosauripus	K2	86.0	64.0	1.34	0.44	0.60	50.0°	-	Lockley and Hunt (1994)

APPENDIX G

Relative proportions of metatarsal III and digit III in theropod dinosaurs. Measurements were made from actual specimens, casts thereof, or illustrations in published sources. Note: different authors likely measured metatarsals and pedal phalanges slightly differently, introducing some artificial variability in the data.

Group	**Specimen**	**Metatarsal III Length + Digit III Length (mm)**	**Digit III Length / Metatarsal III Length Ratio (%)**	**Source of Data**
Herrerasaurus	*H. ischigualastensis* PR 1895 PVSJ 373	315	92.1	P.J. Currie (pers. comm.)
Coelophysoids	*Coelophysis bauri* AMNH 7223	243,8	93.5	Colbert (1989)
	Coelophysis bauri MNA V3318	146	78.0	Colbert (1989) and Open Dinosaur Project
	Coelophysis bauri CM 81766	180.6	87.2	Rinehart et al. (2009)
	Coelophysis bauri CM 81767	175.8	79.6	Rinehart et al. (2009)
	Coelophysis bauri CM 81770	144.6	76.1	Rinehart et al. (2009)
	Coelophysis bauri NMMNH P-42352	167.3	74.6	Rinehart et al. (2009)
	Procompsognathus triassicus SMNS 12591	123.4	77.8	Ostrom (1981)
	Segisaurus halli UCMP 32101	181	82.8	This study; measured YPM VP 055662 (cast)
	Limusaurus inextricabilis IVPP V15923	262	66.9	P.J. Currie (pers. comm.)
Dilophosaurus	*D. wetherilli* UCMP 37302	642	116.2	Marsh and Rowe (2020: digit III length estimated from Figure 25)
	D. wetherilli TxVP 43646-1	567	82.9	Digit III length this study; Marsh and Rowe (2020)
Sinosaurus	*S. triassicus* ZLJ0057 (LDM L10)	543.8	84.3	P.J. Currie (pers. comm.)

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Group	Specimen	Metatarsal III Length + Digit III Length (mm)	Digit III Length / Metatarsal III Length Ratio (%)	Source of Data
Abelisauroids	*Aucasaurus garridoi* MCF-PVPH-236	630.3	82.2	P.J. Currie (pers. comm.)
	Skorpiovenator bustingorryi MMCh-PV-48	642	86.1	J.I. Canale (pers. comm.)
Allosauroids	*Allosaurus fragilis* AMNH 680	776	105.3	P.J. Currie (pers. comm.)
	Allosaurus fragilis Burkhart Pohl specimen	412	101.0	P.J. Currie (pers. comm.)
	Allosaurus fragilis Ciotka specimen Berlin Museum	514	79.7	P.J. Currie (pers. comm.)
	Allosaurus jimmadseni MOR 693	662	91.9	P.J. Currie (pers. comm.)
	Allosaurus jimmadseni SMA 0005	685	91.9	This study
	Concavenator corcovatus MCCM-LH 6666	514	79.7	Cuesta Fidalgo et al. (2018)
	Meraxes gigas MMCh-PV-65	956	96.7	Canale et al. (2022)
Compsognathids	*Beipiaognathus jii* AGB4997	252	93.8	Hu et al. (2016)
	Compsognathus longipes BSP AS I 563	108.2	93.4	Ostrom (1978)
	Sinosauropteryx prima NGMC GMV 2124	170	77.1	P.J. Currie (pers. comm.)
	Juravenator starki JME Sch 200	67.2	103.6	Chiappe and Gölich (2010)
Tanycolagreus	*T. topwilsoni* TPII 2000-09-29	416	92.6	This study
Tyrannosauroids	*Albertosaurus sarcophagus* CMN 11315	796.5	79.0	P.J. Currie (pers. comm.)
	Albertosaurus sarcophagus TMP 1985.98.1	830	74.7	P.J. Currie (pers. comm.)
	Albertosaurus sp. MOR 657	918	74.9	This study
	Gorgosaurus libratus FMNH PR 866 (2211)	540.5	57.6	P.J. Currie (pers. comm.)

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Group	Specimen	Metatarsal III Length + Digit III Length (mm)	Digit III Length / Metatarsal III Length Ratio (%)	Source of Data
	Gorgosaurus libratus CMN 2120	1103	79.3	P.J. Currie (pers. comm.)
	Gorgosaurus libratus CMN 11593	1137	87.9	P.J. Currie (pers. comm.)
	Gorgosaurus libratus ROM 1247	906	81.2	P.J. Currie (pers. comm.)
	Gorgosaurus libratus TMP 91.36.500	813	78.3	P.J. Currie (pers. comm.)
	Gorgosaurus libratus TMP 99.33.1	882.2	73.0	P.J. Currie (pers. comm.)
	Gorgosaurus libratus USNM 12814	970	83.0	P.J. Currie (pers. comm.)
	Gorgosaurus libratus TMP 2000.12.14	713.5	68.7	P.J. Currie (pers. comm.)
	Gorgosaurus cf. *libratus* Indianapolis Children's Museum 2001.89.1	955.9	77.7	P.J. Currie (pers. comm.)
	Daspletosaurus horneri MOR 590	842	69.1	This study & P.J. Currie (pers.comm.)
	Daspletosaurus sp. TMP 85.62.1	1000	78.6	P.J. Currie (pers. comm.)
	Tarbosaurus bataar MPC 940823-Bgt-1	687	66.7	P.J. Currie (pers. comm.)
	Tarbosaurus bataar MPC-D100/61	815	66.3	P.J. Currie (pers. comm.)
	Tarbosaurus bataar MPC-D107/02	973	83.6	P.J. Currie (pers. comm.)
	Tarbosaurus bataar PIN 551-2	945	76.6	Maleev (1974) via P.J. Currie (pers. comm.)
	Tarbosaurus bataar PIN 552-2	709	68.8	Maleev (1974) via P.J. Currie (pers.comm,)
	Tyrannosaurus rex FMNH PR 2081	1334	98.8	P.J. Currie (pers. comm.)
	Tyrannosaurus rex LACM 23845	897	84.9	This study

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Group	Specimen	Metatarsal III Length + Digit III Length (mm)	Digit III Length / Metatarsal III Length Ratio (%)	Source of Data
	Tyrannosaurus rex USNM 555000	1280	91.0	This study
	Tyrannosaurus rex BHI 6230 (now HMNS.PV.1505)	1177	78.1	This study
Ornithomimosaurs	*Dromiceiomimus brevetertius* CMN 12068	557	56.5	P.J. Currie (pers.comm.)
	Gallimimus bullatus ZPAL MdG-I/94	348	58.2	P.J. Currie (pers.comm.)
	Gallimimus bullatus MPC-D100/138	739.7	47.9	P.J. Currie (pers.comm.)
	Gallimimus bullatus MPC-D100/121	497	63.0	P.J. Currie (pers.comm.)
	Gallimimus bullatus Gaston Design Cast	693	47.4	This study
	Struthiomimus altus ROM 1790	493.1	64.4	P.J. Currie (pers.comm.)
	Struthiomimus altus BHI 1266	785	65.3	P.J. Currie (pers.comm.)
	Struthiomimus altus TMP 90.26.1	607.4	62.0	P.J. Currie (pers.comm.)
	Struthiomimus altus UCMZ (VP) 1980.1	634	59.3	P.J. Currie (pers.comm.)
	Struthiomimus altus AMNH 5339	589	55.4	This study (measured cast TMP 85.8.3)
	Ornithomimus edmontonicus ROM 851	525	69.4	P.J. Currie (pers.comm.)
	BHI Fort Peck ornithomimid	633	62.3	This study
	Sinornithomimus dongi IVPP V11797-10	368.4	73.0	Kobayashi and Lü (2003)
	Deinocheirus mirificus MPC-D100/127 KID 447	1134	73.1	P.J. Currie (pers.comm.)
Oviraptorosaurs	*Chirostenotes pergracilis* CMN 8538	445	93.5	This study
	Avimimus portentosus PIN 3907/1	236	55.3	P.J. Currie (pers.comm.)

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Group	Specimen	Metatarsal III Length + Digit III Length (mm)	Digit III Length / Metatarsal III Length Ratio (%)	Source of Data
	Protarchaeopteryx sp. NGMV 2125	160	88.2	P.J. Currie (pers.comm.)
	Caudipteryx dongi IVPP 12344	211.6	70.6	P.J. Currie (pers. comm.); cf. Zhou and Wang (2000)
	Caudipteryx zhoui NGMC 97-9-A	189	76.6	P.J. Currie (pers. comm.)
	Caudipteryx zhoui NGMC 98-7-8	185.3	76.5	P.J. Currie (pers. comm.)
	Caudipteryx zhoui private collection	195.8	73.3	P.J. Currie (pers. comm.)
	Caudipteryx zhoui BPM 0001	189	67.3	Zhou et al. (2000)
	Caudipteryx sp. IVPP 12430	183	63.4	Zhou et al. (2000)
	Citipati osmolskae MPC-D100/978	353.9	84.3	P.J. Currie (pers. comm.)
	Citipati sp. MPC-D100/42	345	91.7	P.J. Currie (pers. comm.)
	Khaan mckennai IGM MPC D-100/1002	204.3	92.7	P.J. Currie (pers. comm.)
	Corythoraptor jacobsi JPM-2015-001	320.2	103.9	Lü et al. (2017)
	Conchoraptor gracilis MPC-D110/03	233.2	92.7	P.J. Currie (pers. comm.)
	Oksoko avarsan MPC-D102/110 # 1	237.9	86.6	P.J. Currie (pers. comm.)
	Oksoko avarsan MPC-D102/110 # 2	225.2	90.8	P.J. Currie (pers. comm.)
	Oksoko avarsan MPC-D100/33	236.7	90.1	P.J. Currie (pers. comm.)
	Heyuannia (= *Ingenia*) *yanshini* MPC-D102/03	233.2	92.7	P.J. Currie (pers. comm.)
	Heyuannia (= *Ingenia*) *yanshini* MPC-D100/32	255.6	93.6	P.J. Currie (pers. comm.)

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Group	Specimen	Metatarsal III Length + Digit III Length (mm)	Digit III Length / Metatarsal III Length Ratio (%)	Source of Data
	Heyuannia (= *Ingenia*) *yanshini* MPC-D100/34	145.2	91.6	P.J. Currie (pers. comm.)
	Heyuannia (= *Ingenia*) *yanshini* MPC-D100/36	199.3	95.0	P.J. Currie (pers. comm.)
	Yulong mini Henan Geological Museum field #L08-39-1a	69.7	74.7	P.J. Currie (pers. comm.)
	Yulong mini Henan Geological Museum 41HIII-0107	82.1	89.6	P.J. Currie (pers. comm.)
	Xingtianosaurus ganqui IVPP V13390	175	95.2	Qiu et al. (2019)
Troodontids	*Sinornithoides youngi* IVPP V9612	188.7	70.0	P.J. Currie (pers. comm.)
	Anchiornis huxleyi BMNHC PH823	96.0	87.5	Pei et al. (2017)
	Anchiornis huxleyi PKUP V1068	104.6	103.1	Pei et al. (2017)
	Anchiornis huxleyi Henan Geological Museum 41HIII-0404	99.1	87.7	Guo et al. (2018)
	Anchiornis huxleyi Henan Geological Museum 41HIII-0515	66.0	84.9	Guo et al. (2018)
	Talos sampsoni UMNH VP 19479	271	55.7	This study
Dromaeosaurids	*Bambiraptor feinbergi* AMNH FARB 30556 (FIP 000001)	161.9	102.4	P.J. Currie (pers. comm.)
	Halszkaraptor escuilliei MPC D-102/109	112.8	120.7	Cau et al. (2017)
	Deinonychus antirrhopus AMNH 3015	314.5	108.3	Ostrom (1969)
	Deinonychus antirrhopus MCZ 4371	369.1	136.7	Ostrom (1969)

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Group	Specimen	Metatarsal III Length + Digit III Length (mm)	Digit III Length / Metatarsal III Length Ratio (%)	Source of Data
	Deinonychus antirrhopus Citoka lab Hong Kong Museum of Science	375	119.3	P.J. Currie (pers. comm.)
	Deinonychus antirrhopus MOR 747	294	100.0	This study
	Velociraptor mongoliensis MPC-D 100/0025	251.4	123.5	P.J. Currie (pers. comm.)
	Velociraptor mongoliensis MPC-D 100/0054	231.9	129.8	P.J. Currie (pers. comm.)
	Velociraptor sp. UALVP49389, 49390	240.9	121.8	P.J. Currie (pers. comm.)
	Saurornitholestes langstoni UALVP 55700	263.9	123.6	P.J. Currie (pers. comm.)
	Microraptor gui Wendy1 IMMNH-PV00731	119	69.3	P.J. Currie (pers. comm.)
	Daurlong wangi	228	107.3	Wang et al. (2022)
	Wulong bohaiensis DNHM D2933	101.8	78.9	Poust et al. (2020)

APPENDIX H

Measurements of metatarsals of theropod dinosaurs. Data extracted from the literature are either specifically reported measurements, or estimates made by the present authors from figured specimens in cited publications.

Taxon	Specimen	Metatarsal	Length (mm)	Distal Dorso-Ventral (Anteroposterior) Articular Depth (mm)	Distal Mediolateral Articular Width (mm)	Source of Data
Coelophysoids						
Eucoelophysis baldwini	NMMNH P-22298	III	91	9	14	Sullivan and Lucas (1999)
Ceratosaurs						
Dilophosaurus wetherilli	UCMP 37302	Left III	297	44	51	Marsh and Rowe (2020); Welles (1984)
		Left IV	254	41	41	
	UCMP 77270	Right III	287	41	46	Marsh and Rowe (2020)
	TxVP 43646-1	Left III	305	43.95	38.1	
		Left IV	266	36.65	35	
Ceratosaurus nasicornis	USNM 4735	Left III	254	50	66	Gilmore (1920)
		Left IV	220	45	37	
Koleken inakayali	MPEF-PV-10826	Right III	282		62	Pol et al. (2024)
		Right IV	248		39	
Skorpiovenator bustingorryi	MMCh-PV 48	III	390		95	Cerroni et al. (2022)
Noasaurids						
Elaphrosaurus bambergi	MB R 4960	III	391	42	52	Rauhut and Carrano (2016)
Kyacursor longipes	KOKM 5542	III	182		16	Averianov et al. (2024)
Megalosauroids						
Torvosaurus tanneri	BYUVP 5280	Left III	344	73	103	Britt (1991, Britt's Figure 24)
	BYUVP 5278	Left IV	309	82	76	
	FMNH PR 3060	Left IV	287	60	81	Hanson and Makovicky (2014)
Riojavenatrix lacustris	CPI 1640	Left III	364	66	90	Isasmendi et al. (2024)
Allosauroids						
Allosaurus jimmadseni	Sauriermuseum Aathal 0005	Right III	354	69	91	This study; measurements of cast
		Right IV	289	65	68	
	MOR 693	Right III	338	57	74	This study; measurements of cast
		Right IV	290	67	47	
	Western Paleontology Labs, Lehi, Utah	Right III	208	28	20	This study; measurements of cast
		Right IV	172	29	22	
	BYU 725-16543	Right III	180		26	Loewen (2009

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Taxon	Specimen	Metatarsal	Length (mm)	Distal Dorso-Ventral (Anteroposterior) Articular Depth (mm)	Distal Mediolateral Articular Width (mm)	Source of Data
	BYU 725-16680	Right III	422		100	
Allosaurus fragilis	CMC VP9221	Left IV	167	27.1	30.7	This study
	CMC VP9216	Right? III	152.9	16.9	19.7	
	CMC VP16236	Right III	246.8	40.4	46.5	This study; measurements of cast
	CMC VP12637	Right IV	212.4	38.7	31.9	
	CMC VP3028	Left III	322	69		This study; measurements of cast of composite foot
		Left IV	289	62		
	AMNH 6125	Left III	371		86	Loewen (2009)
		Left IV	316		63	
	AMNH 680	Left III	385		97	
		Left IV	328		76	
	AMNH 290	Right III	431		94	
	USNM 4734	Left III	327		80	Gilmore (1920)
		Left IV	275		65	
	USNM 8423	Left III	353		80	
		Left IV	324		57	
	CM 11844	Left III	362		87	Loewen (2009)
		Left IV	294		62	
	UMNH VP 6629	Left III	243		50	
	UMNH VP 7055	Right III	234		40	
	UMNH VP 7054	Right III	265		44	
	UMNH VP 7058	Left IV	182		29	
	UMNH VP 7059	Right IV	205		28.3	
	UMNH VP 7060	Left IV	235		30	
	UMNH VP 7061	Left IV	225		34	
	UMNH VP 7753	Left III	247		45	
	UMNH VP 7055	Right III	234		40	
	UMNH VP 7793	Left III	250		38	
	UMNH VP 9399	Left IV	331		43	
	UMNH VP 9400	Left IV	292		46	
	UMNH VP 9401	Right IV	313		45	
	UMNH VP 9885	Right IV	258		42	
	UMNH VP 9887	Left IV	295		46	
	UMNH VP 9888	Left IV	263		32	
	UMNH VP 9889	Left IV	245		28	
	UMNH VP 9890	Right IV	257		31	
	UMNH VP9891	Right IV	266		47	
	UMNH VP 9892	Left IV	271		35	
	UMNH VP 9894	Right III	272		60	
	UMNH VP 9895	Right III	286		56	

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Taxon	Specimen	Metatarsal	Length (mm)	Distal Dorso-Ventral (Anteroposterior) Articular Depth (mm)	Distal Mediolateral Articular Width (mm)	Source of Data
	UMNH VP 9896	Right III	280		53	
	UMNH VP 9897	Right III	295		53	
	UMNH VP 9898	Left III	275		51	
	UMNH VP 9900	Left III	283		57	
	UMNH VP 9901	Right III	296		51	
	UMNH VP 9902	Left III	281		49	
	UMNH VP 10136	Left III	307		79	
	UMNH VP 10374	Left III	335		77	
	UMNH VP 10376	Left III	337		85	
	UMNH VP 10377	Left III	334		70	
	UMNH VP 10378	Left III	340		78	
	UMNH VP 10380	Right III	311		63	
	UMNH VP 10382	Left III	362		78	
	UMNH VP 10386	Right III	335		76	
	UMNH VP 16036	Left III	292		64	
	UMNH VP 16037	Right III	319		77	
	UMNH VP 16038	Left III	264		50	
	YPM 4679	Left IV	280		42	
	YPM 4944	Left III	238		49	
		Left IV	236		34	
Allosaurus sp.	CMC VP8593	Left IV	138.6	19.5	14.7	This study (same individual as CMC VP9029?)
	CMC VP8592	Left? III	150.1	18.0	20.7	This study (same individual as CMC VP 9216?)
	CMC VP9029	Right IV	144.1	19.4	16.5	This study (same individual as CMC VP8593?)
	CMC VP157796	Right? III	79.6	12.9	16	This study
	MOR 637	Right III	379		81	
		Right IV	318		48	
Sinraptor dongi	IVPP 10600	Right III	410	67	79	Currie and Zhao (1993)
		Right IV	375	66	59	
Concavenator corcovatus	MCCM-LH 6666	III	286		50	Cuesta et al. (2018)
		IV	255		48	
Gualicho shinyae	MPCN FV 0001	Left III	309	40.6	56.3	Apestiguia et al. (2016)
Neovenator salerii	MIWG 6348	Left IV	325	62	41	Brusatte et al. (2008)
Alpkarakush kyrgyzicus	IGB 2-43	Right III	40	6	7.7	Rauhut et al. (2024)

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Taxon	Specimen	Metatarsal	Length (mm)	Distal Dorso-Ventral (Anteroposterior) Articular Depth (mm)	Distal Mediolateral Articular Width (mm)	Source of Data
Unidentified allosauroid	IVPP V18060	Left IV	355		79	He et al. (2013)
Basal Coelurosaurs						
Tanycolagreus topwilsoni	TP II 2000-09-29	Right III	215	20	25	This study; measurements of cast
		Right IV	197	22	18	
Kileskus aristotocus	ZIN PH 11/117	Left III	219		25.6	Averianov et al. (2010)
Zuolong salleei	IVPP V15912	III	224.3	33.3	37.7	Choiniere et al. (2010)
Megaraptorans						
Fukuiraptor kitadaniensis	FPMN 9712223	III	297.5		45	Azuma and Currie (2000)
Australovenator wintonensis	AODF 604	Right III	322	46	51	White et al. (2013)
Phuwiangvenator yaemniyorni	SM-PW9A	Left III	315	53	58	Samathi et al. (2022)
Jaculinykus yaruui	MPC-D 100/209	Right III	113.35		7	Kubo et al. (2023)
Tyrannosauroids						
Dryptosaurus aquilunguis	AMNH FARB 2438	IV	397	66	55	Carpenter et al. (1997)
Appalachiosaurus montgomeriensis	RMM 6670	Right IV	579	78	61	Carr et al. (2005)
Alectrosaurus olseni	AMNH FARB 6554	Right IV	478.2	52.5	40.6	Carr et al. (2023)
Albertosaurus sarcophagus	CMN 11315	Left III	479.2	54.5	70	This study
		Left IV	461.5	51	42	
	TMP 2000.054.001	III	382	27.4	27.3	P.J. Currie (pers. comm.)
Judith River tyrannosaurid	MOR 657	Left IV	480		73	This study
Daspletosaurus horneri	MOR 590	Left III	510.8	78.8	86.3	Carr et al. (2017)
		Left IV	475.1	79.6	64	
	MOR 1130	Right IV	530.3	93.4	67.1	Carr et al. (2017)
Tarbosaurus bataar	Gaston Designs Cast	Right III	516	83	98	This study
		Right IV	480	91	68	
Unidentified tyrannosaurid	BIBE 45850	Right III	561.3	92.5	107.3	T. Adams (pers. comm.)
		Right IV	536.3	97.7	71.7	
Mesaverde Group tyrannosaurid	UMNH VP 16395.4	IV	490		61	Thomson et al. (2013)
Tyrannosaurus rex	MOR 555	Left IV	590	135	106	This study; measurements of cast
	BHI-6230	Right III	678	122	135	
		Right IV	610	114	109	

APPENDIX H

Taxon	Specimen	Metatarsal	Length (mm)	Distal Dorso-Ventral (Anteroposterior) Articular Depth (mm)	Distal Mediolateral Articular Width (mm)	Source of Data
	(now MNS.PV.1505)					
	FMNH PR2081	Right III	671		157	Brochu (2002)
		Right IV	621		126	
Nanotyrannus lancensis	BHI-6437 (now NCSM 40000)	Left IV	497		46	This study; measurements made from cast
Ornithomimosaurs						
Arkansaurus fridayi	UAM-74-16-1	Right III	397	42	51	Hunt and Quinn (2018)
		Right IV	365	60	37	
Nedcolbertia justinhoffmani	CEUM 5071	Right III	107		14	This study; measurements of cast
Struthiomimus sedens	BHI 1266	Left III	454		50	This study; measurements of cast
		Left IV	428		34	
Unidentified Hell Creek ornithomimid	BHI Uncatalogued	Right IV	370	37	28	This study; measurements of cast
Gallimimus bullatus	Gaston Designs Cast	Left III	470	41	55	This study
		Left IV	442	40	34	
Unidentified ornithomimid	TMP 2000.012.0008	III	185.3	18	19.8	Funston et al. (2016); identified by those authors as *Leptorhynchos* elegans
Troodontids						
Tochisaurus nemegtensis	PIN 551-224	III	232	22	20	Kurzanov and Osmolska (1991)
		IV	247	19	18	
Saurornithoides mongoliensis	IVPP V10597	Left III	107		4	Currie and Peng (1993)
Oviraptorosaurs						
Chirostenotes pergracilis	CMN 8538	III	238.1	21	33	This study
		IV	226.5	24	21.9	
	TMP 1993.036.0181	Right IV	237.1	20	17	
Elmisaurus rarus	MPC-D-102/006	III	182.7	22.9	23.3	Funston et al. (2016)
		IV	175.7	22	17.1	
	MPC-D-102/007	IV	161.9	15.5	19	
	ZPAL Mg-D-1/172	III	149		22	Osmólska (1981)
		IV	147		17	

APPENDIX H

Taxon	Specimen	Metatarsal	Length (mm)	Distal Dorso-Ventral (Anteroposterior) Articular Depth (mm)	Distal Mediolateral Articular Width (mm)	Source of Data
Citipes elegans	TMP 1982.016.0006	III	172.2	15.9	16.2	Funston et al. (2016)
	ROM 781 (4758 Ct)	Left III	161	16	16	Parks (1933)
		Left IV	157	16	15	
cf. *Anzu wyliei*	NSM PV 21055	Right IV	328		42.8	Tsujimura et al. (2021)
Eoneophron infernalis	CM 96523	Right III	247		21	Atkins-Wellman et al. (2024)
		Right IV	233		15	
Anomalipes zhaoi	ZCDM V0020	III	167	20.3	22.6	Yu et al. (2018)
Alvarezsaurids						
Parvicursor remotus	PIN 4487/25	Right IV	55	4	3.3	Averianov and Lopatin (2021)
Dromaeosaurids						
Dromaeosaurus sp.	CMN 40776	Right III	114.2	16	14.5	This study
		Right IV	97.4	10	11	
Deinonychus antirrhopus	AMNH 3015	Left IV	134		21,5	Ostrom (1969)
	YPM 5205	Left IV	141		21	
	YPM 5207	Right III	150.5		22.4	
Saurornitholestes sp.	MOR 660	Left III	116		15	This study
		Left IV	109		12	
Microraptor zhaoianus	CAGS 20-7-004	Left III	47.8		2.29	Hwang et al. (2002)
		Left IV	46.76		2.91	
	CAGS 20-8-001	Left III	49.39		3.15	
Sinornithosaurus millenii	IVPP V 12811	Right III	93	7.5	2.5	Xu and Wang (2000)
		Right IV	91	6.5	7	
Balaur bondoc	EME PV 313	Right III	61	9	12	Brusatte et al. (2013)
Unidentified Theropod						
Unidentified Morrison Fm small theropod	CMC VP8780	III?	64.3	6.6	7.9	This study