

An Unusual, Three-Dimensionally Preserved, Large Hadrosauriform Pes Track from “Mid”-Cretaceous Jiaguan Formation of Chongqing, China

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Abstract: Three-dimensional tracks provide unique insights into the locomotor mechanics of their track makers. An isolated, large hadrosauriform print attributable to *Caririchnium lotus* from the “mid”-Cretaceous Lotus track site (Jiaguan Formation) in China permits reconstruction of the footfall, weight-bearing, and kick-off phases of the step cycle. Large-scale modifications of the pes during the step cycle indicate *C. lotus* trackmakers were capable of locomotory modifications in response to substrate consistency beyond the “expected” shift between bipedal and quadrupedal postures. An unusual curvature to the trace of one of the outer digits indicates substantial transverse mobility. The remaining digits demonstrate lesser degrees of transverse movement accompanied by extension of the digits during footfall. The absence of overprinted scale-scratch marks and toe drags are consistent with a vertical kick-off of the pes and concomitant flexion of the digits. This track suggests that pedal mobility in *C. lotus* track makers was greater than previously suspected and has implications for reconstructions of hadrosauriform locomotion.

Key words: hadrosauriform, locomotion, footprints, Cretaceous, step cycle

1 Introduction

Fossil trackways typically occur as roughly two-dimensional impressions on bedding planes and provide information about the identities and paleobiologies of the track makers. Track relief may be either positive or negative, but is usually limited to a matter of millimeters or centimeters. Of the thousands of fossil trackways known, deep, three-dimensional tracks are relatively rare and difficult to define. In general, three-dimensional tracks are noticeably deeper (decimetres) than common cast tracks and are occasionally accompanied by scale scratch lines (Difley and Ekdale, 2002). Three-dimensional tracks have been described for ceratopsids and hadrosaurids (Difley and Ekdale, 2002; Currie et al., 2003), sauropods (Milàn et al., 2005; Platt and Hasiotis, 2006; Mateus and Milàn, 2008), and theropods (Gatesy et al., 1999; Milàn et al., 2006; Avanzini et al., 2011). Some load cast features

with undefined morphologies have also been interpreted as deep sauropod tracks (Lockley, 2001; Hasiotis, 2004; Li et al., 2011). Most importantly, well-preserved, three-dimensional tracks provide reliable records of the footfall, weight-bearing, and, less frequently, the kick-off phases of the step cycle of their track makers. Such traces can also be used to infer locomotor mechanics of the track makers (Thulborn and Wade, 1984; Milàn et al., 2005).

In 2006, the Qijiang County Bureau of Land and Resources in Chongqing and the Southeast Sichuan Geological Team discovered dinosaur tracks within the “mid”-Cretaceous Jiaguan Formation that crops out on Laoying Mountain, near the town of Sanjiao, Qijiang County. Xing et al. (2007) attributed these tracks to hadrosaurids (*Laoyingshanpus torridus* and *Caririchnium lotus*), ankylosaurids (*Qijiangpus sinensis*), and the small theropod *Wupus agilis*. In 2009, the senior author located several new track-bearing layers from the same tracksite, including three-dimensional tracks.

Only three other examples of three-dimensional tracks

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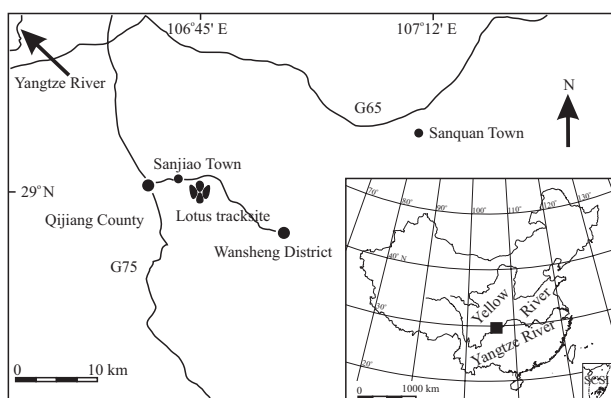


Fig. 1. Geographic map indicating the location (footprint icon) of the Lotus track site locality in Qijiang County, Chongqing City, China.

have been previously discovered in China, none of which have been described. These include: (1) sauropod tracks from the Early Cretaceous Chabu track site, Inner Mongolia (Li et al., 2011); (2) an isolated but well-preserved sauropod manus track from the Early Cretaceous of the Yongjing track site, Gansu (which will be described elsewhere); and (3). Sauropod (?) tracks from the “mid”-Cretaceous Emei track site, Sichuan (Lu et al., in press). The purpose of this study is to describe the hadrosauriform track and discuss the locomotory implications of this trace. The aforementioned sauropod tracks will be described elsewhere.

2 Institutional Abbreviations

QJGM, Exhibition Hall of Qijiang County Bureau of Land and Resources, China; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

3 Locality and Geological Setting

Qijiang Petrified Wood and Dinosaur Footprint National Geological Park is located in Qijiang County, south of Chongqing Municipality near the southeastern border of the Sichuan Basin (Fig. 1). Upper Jurassic (Shangshaximiao, Suining, and Penglaizhen formations) and “mid”-Cretaceous (Jiaguan Formation) rocks crop out within the Park. Petrified wood (Coniferopsida) (Liu et al., 2010), theropod teeth (Wang Feng-ping, pers. comm. 2011), and sauropod remains (*Mamenchisaurus* Fauna; Liu et al., 2010) are known from the Jurassic outcrops within the Park; however, only dinosaur tracks have been discovered in the Cretaceous Jiaguan Formation (Xing et al., 2007).

Four track sites have been identified in fluvial facies of the Jiaguan Formation. Tracks at these sites have been

attributed to small to medium-sized avian and non-avian theropods, medium-sized to large ornithopods, and ankylosaurians (Young, 1960; Zhen et al., 1994; Xing et al., 2007, 2009, 2011). The Lotus track site is preserved within dark magenta sandstones and mudstones (Fig. 2) and comprises at least four track-bearing layers that include shallow cast (positive, in-filled) and mold (negative) type tracks as well as rare, deep, three-dimensional tracks. The three-dimensional (cast) tracks were impressed into fine-grained mud units that were in-filled and overlain by sandy layers. The less resistant mudstones are recessed relative to the bench-forming sandstone units, permitting observation of cast traces on the undersides of these benches.

Li (1995) suggested the Jiaguan Formation ranges between 85–117Ma (Aptian–Santonian) based on electron spin resonance (ESR) dating; however, Gou and Zhao (2001) considered an even longer span (Valanginian–Santonian) based on totaled magnetochronology and ESR dating. Preliminary pollen assays recovered relatively abundant species comparable to extant angiosperm pollen, such as Betulaceae, Cyrillaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Labiatae, Meliaceae, Nyssaceae, Rutaceae, Symplocaceae, and Ulmaceae, typical of Campanian–Maastrichtian assemblages (Wang

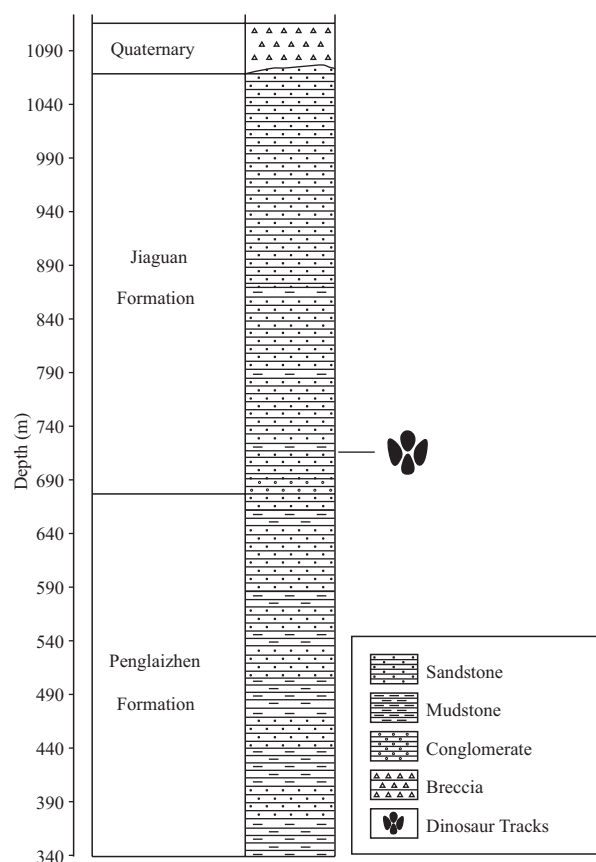


Fig. 2. Stratigraphic column of the Jurassic–Cretaceous strata of the Lotus track site.

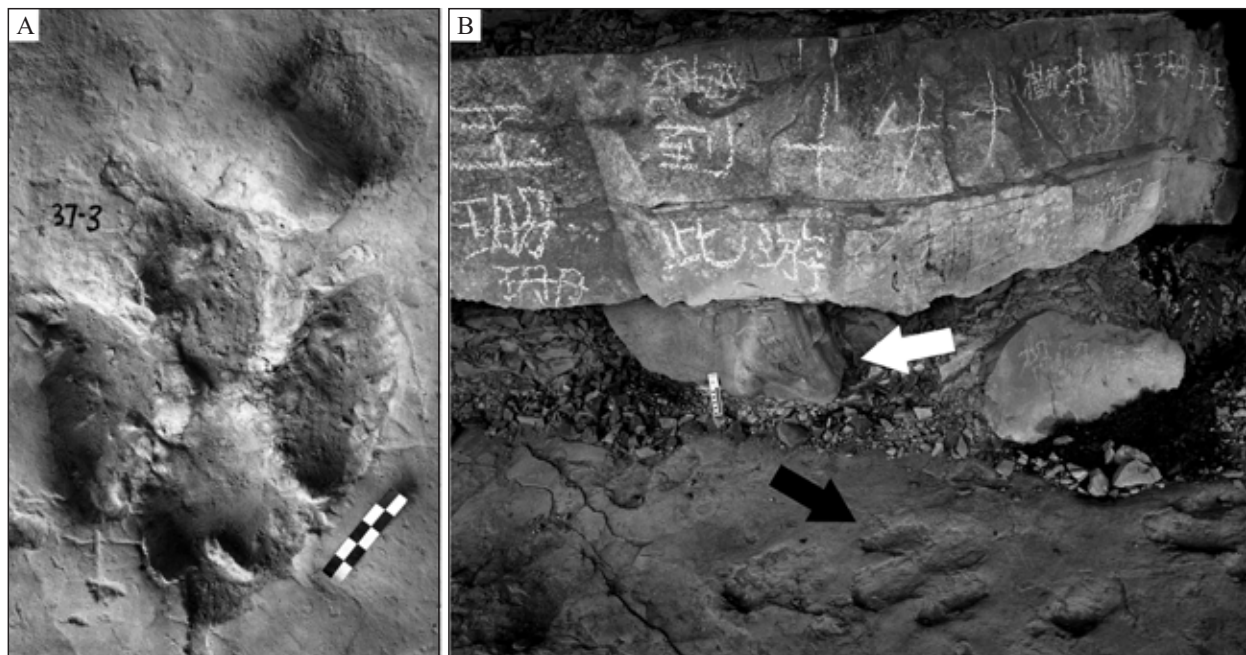


Fig. 3. A. Type specimen of *Caririchnium lotus* QJGM-T37-3; B. Distribution of *Caririchnium lotus* tracks in two layers at the Lotus track site, including *in situ* natural molds tracks (black arrow) and three-dimensional, natural cast track QJGM-C1 in overlying sandstone (white arrow). Scale=10 cm.

Wei-ming pers. comm. 2011). Pending detailed palynological analysis, and following Li (1995) and Gou and Zhao (2001), we regard the Jiaguan Formation as “mid”-Cretaceous.

4 Distribution of Tracks

4.1 *Caririchnium* at the Lotus track site

Caririchnium is a common ichnogenus typically attributed to hadrosauriform and widely distributed across North America, including Colorado (Lockley, 1987), New Mexico (Hunt and Lucas, 1996; Kappus et al., 2003), Oklahoma (Lockley et al., 1992), Texas (Lee, 1997), Virginia (Weems, 2004), and Wyoming (Lockley et al., 2004). *Caririchnium* has also been reported from Brazil (Leonardi, 1984), Korea (Huh et al., 2003), Japan (Matsukawa et al. 2005), and China (Xing et al., 2007). Other typical hadrosauriform tracks include *Amblydactylus* (Sternberg, 1932; Currie and Sargeant, 1979), and *Hadrosauropodus* (Lockley et al., 2003); rarer ichnotaxa include *Jiayinosauropus* (Dong et al., 2003; Xing et al., 2009) and *Ornithopodichnus* (Kim et al., 2009) from China and Korea, respectively. The overwhelming majority of hadrosauriform tracks are simple molds and casts, whereas deep, three-dimensional tracks are considerably less common.

The Lotus track site preserves nearly 200 symmetrical, tridactyl *Caririchnium lotus* tracks (Fig. 3A, Table 1), which include adults (tracks 37-40 cm in length),

Table 1 Measurements (in cm) of *Caririchnium lotus* tracks from the Lotus track site

Specimen #	ML	MW	II	III	IV	Me	L/W
QJGM-T37-3	38.7	28.5	20.0	17.0	20.0	19.5	1.36
QJGM-T100-1	33.5	24.0	18.9	14.3	14.8	>11.8	1.40
QJGM-C1	42.5	34.7	26.3*	—	—	18.9	1.22
QJGM-C2.8	32.2	26.4	18.7	15.9	14.8	11.0	1.22

L/W: Maximum length/maximum width; ML: Maximum length; MW: Maximum width, distance between the tips of digits II and IV; II: Length of digit II; III: Length of digit III; IV: Length of digit IV; Me: Length of metatarsophalangeal pad.*This may be either digit II or IV.

subadults (25-30 cm in length), and young individuals (19-23 cm in length). The length:width ratio of the holotype specimen, QJGM-T37-3, an adult pes print, is 1.36:1. Despite the range of sizes present, track morphology is consistent. Digits II and IV are subequal in length, and essentially identical in morphology: the outline of each digit is ovoid and bears a prominent, but mediolaterally narrow, claw impression at the anterior end. Digit III is slightly shorter than digits II and IV, but protrudes farther anteriorly than these, and is broadly U-shaped at its anterior end. The metatarsophalangeal pad of the type specimen is shaped like a clover-leaf with the edges of the “leaves” corresponding to the base (i.e., proximal part) of each digit; in other specimens at the site, however, the impression is more pear- or teardrop-shaped. The posterior margin of the metatarsophalangeal pad is slightly concave, and a distinct border separates the impression from those of digits II and IV. The divarication angles between digits II and III and digits III and IV are both 25°. Ovoid to subrectangular manus impressions lie in front of the

impressions of pedal digits III and IV (Xing et al., 2007).

Impression tracks of *Caririchnium lotus* are most common on bedding planes at the Lotus track site (Fig. 3A, Table 1), although infilled tracks (Figs. 4-6, Table 1) are also present on the undersides of overlying, bench-forming sandstone layers. Shallow cast tracks are relatively common and occur as isolated prints (Fig. 4) or in complexly overprinted series made by multiple individuals travelling in a variety of directions (Fig. 5). Invertebrate traces are common on the ventral (i.e., plantar) surfaces of cast tracks. At least one cast track shows digit III impressed considerably deeper than digits II and IV, a phenomenon that has been observed in some other hadrosaurid tracks (Currie et al., 2003: fig. 4B, D).

Caririchnium and *Amblydactylus* have been attributed to both iguanodontids and hadrosaurid track makers (Sternberg, 1932; Currie and Sarjeant, 1979; Currie, 1983; Paul, 1987; Lockley, 1985, 1986, 1987; Lee, 1997); however, the absence of skeletal material from the Jiaguan Formation hampers potential identification of the track maker(s). An often-used criterion for differentiating between iguanodontid and hadrosaurid tracks is their respective geological ages; the former were predominately distributed in the early Early Lower Cretaceous, the latter predominately distributed in the Late Cretaceous. However, since those initial studies, understanding of large ornithopod phylogeny has become substantially clearer and more complex (e.g., McDonald et al., 2010a, b; Prieto-Marquez, 2010). Hadrosauridae, as currently understood, is exclusively a late Late Cretaceous clade (Santonian–Maastrichtian); late Early and early Late Cretaceous large ornithopods are members of Hadrosauriformes and Hadrosaurioidea, but not Hadrosauridae. As far as is currently known, most of these taxa would leave similar tracks, including *Caririchnium*. If the late Late Cretaceous age of the Jiaguan Formation suggested by the preliminary palynological analysis (Wang Wei-ming pers. comm. 2011, they will to be described elsewhere) is ultimately supported by more detailed studies, then it is possible that the track maker was a hadrosaurid *sensu stricto*. At present, however, the *C. lotus* track maker (and the makers of *Caririchnium* tracks in general) can only be referred safely to Hadrosauriformes, though it may have been a hadrosaurid.

4.2 Three-dimensional *C. lotus* track

QJFM-C1 is an isolated, three-dimensional cast found *in situ* on the underside of a resistant sandstone layer within the Jiaguan Formation (Fig. 3B). The original track remains in the field, where it is protected within the Qijiang Petrified Wood & Dinosaur Footprint National

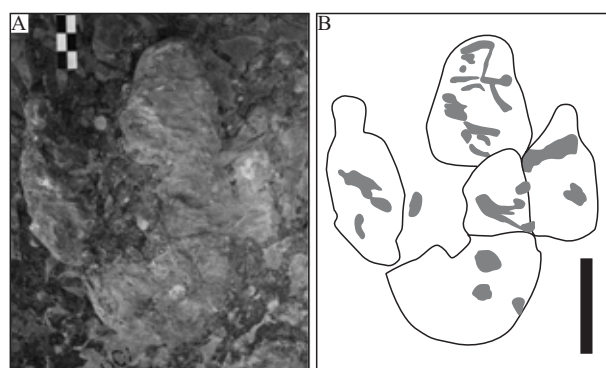


Fig. 4. *Caririchnium lotus* cast track (QJGM-T100-1) from the Lotus track site. A: Photograph; B: Outline drawing. Gray areas indicate invertebrate traces. Scale bar = 10 cm.

Geological Park. A cast is preserved in the Exhibition Hall of Qijiang County Bureau of Land and Resources, China.

The track has a maximum length of 42.5 cm and is 37.1 cm deep, which is nearly the thickness of the mudstone layer in which the actual footprint (i.e., the natural mold) was preserved made. The metatarsophalangeal region and all three digits are preserved. As exposed, it is not possible to differentiate between the medial and lateral digits; these digits are referred to herein as digits A and C, with digit C being the digit closest to, and still partly embedded in, the mudstone outcrop. The trace of the metatarsophalangeal region is columnar and vertically oriented (Fig. 6). There is no defined margin between digit III and the metatarsophalangeal pad plantarily, which is characteristic of *Caririchnium lotus*. The vertical impression made by digit III (Fig. 6) is 37.4 cm in height and angles anteroventrally. Digit C (Fig. 6) measures 39.5 cm in height and is partially obscured by rock. Its vertical axis is anteroventrally oriented, parallel to that of digit III, giving the entire print a somewhat trapezoidal outline in mediolateral aspect (Fig. 6A, B). The trace of digit A (Fig. 6) is unusually curved, tracing a path 49.7 cm in height. In anterior view, the digit trace bulges outward (away from digit III) at mid-height. Ventral (plantar) to that point, it curves dramatically inward to contact the ventral-most part of the trace of digit III.

The surfaces of the digital and metatarsophalangeal region traces of QJGM-C1 preserve elongate, parallel scale scratch lines. The metatarsophalangeal region and the curved trace of digit A have 3–4 scratch lines per centimeter; digit III has 2–3 scratch lines per centimeter.

5 Discussion

The morphology of the hadrosauriform pes deviates from the plesiomorphic morphology seen in much of the Dinosauria (Moreno et al., 2007). This relatively derived

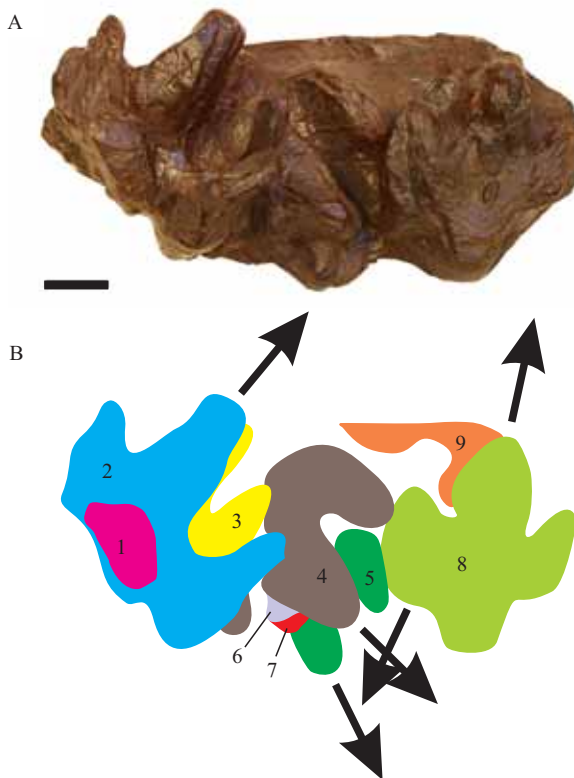


Fig. 5. *Caririchnium lotus* natural cast tracks (QJGM-C2.1-9) from the Lotus track site. A: Photograph; B: Outline drawing. Numerals 1–9 indicate nine discrete tracks. Black arrows indicate the direction of advancement of the discernible tracks. Scale bar = 10 cm

condition (tridactyly, modification of the unguals into hooves, phalanges wider and dorsoventrally thinner than long, absence of collateral ligament fossae, loss of sagittal ridge and tendon attachment processes, and relatively flattened interphalangeal articular surfaces) culminated in a subunguligrade foot posture in hadrosaurids (Moreno et al., 2007). Metatarsals II and IV diverge from metatarsal III, apparently preventing the digits from coming into contact with one another (Horner et al., 2004), and the digits themselves have been interpreted as relatively inflexible (Moreno et al., 2007). The proximal and distal articular surfaces of hadrosauriform pedal phalanges are roughly trapezoidal in articular view and lack the curvatures and sagittal ridges/sulci (i.e., ginglymous articular surfaces) seen in more basal ornithopods such as *Thescelosaurus* and *Camptosaurus* (Moreno et al., 2007); how widespread these features are in non-hadrosaurid hadrosauriforms is unclear. The consequent, more upright (i.e., subunguligrade) stance corresponds to an increase in the weight-bearing capacity of

the pes (Moreno et al. 2007).

Based on the track length (Table 1), the ornithopod responsible for QJGM-C1 probably measured 2.3 m at the hip ($h=5.9 \times$ foot length; Thulborn, 1990). Fine, parallel striae on QJGM-C1 and the lithology of the track-bearing layer suggest the track maker stepped into wet but cohesive mud (Nadon, 1993; Difley and Ekdale, 2002) that maintained the integrity of the print after the track maker had moved on. Parallel striae indicate that the pes was covered in rough tubercles or scales approximately 3 mm in diameter (Gatesy, 2001; Milàn et al., 2006; Avanzini et al., 2011). This is corroborated by intact skin impressions on the pedal skeletal material of some hadrosaurid specimens (Osborn, 1912; Brown, 1914). Irregularities, probably due to wear, on the leading edge of the keratinous claw are presumably responsible for parallel striae visible on the front of digit III.

The most striking feature of QJGM-C1 is the strangely curved path of digit A, which likely formed as a result of transverse movement of the digit during the touchdown and weight-bearing phases of the step. Other possible explanations for the peculiarity of the track include soft-sediment deformation, slippage, or pathological modification of the pes. Soft-sediment deformation is dismissed based on the well-preserved and linear paths of digit III and digit C as well as the preservation of fine details such as scale scratch lines. Any wholesale, post-depositional deformation would be expected to have

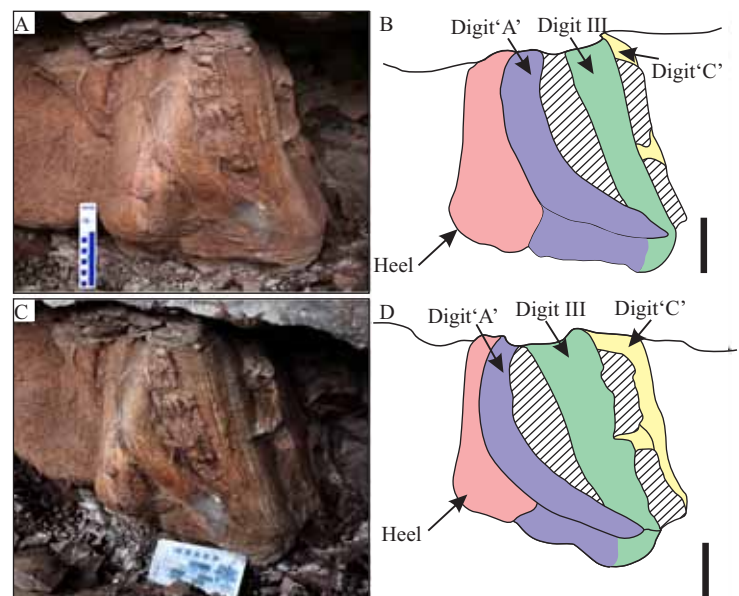


Fig. 6. Three-dimensional, natural cast *Caririchnium lotus* pes track (QJGM-C1) from the Lotus track site. A and C: Photographs, B and D: Outline drawings. Metatarsophalangeal ("heel") trace in red; digit III trace in green, and medial and lateral digits in blue and orange. A, B are in lateral view; C, D are in anterolateral view. Scale bar = 10 cm.

registered across the entire footprint, but this is not the case. Slipping of the foot itself is discredited for the same reason: nothing unusual was observed in the downward passage of the other two digits or the metatarsophalangeal region. Similarly, the scale scratch lines on the edges of the metatarsophalangeal region remain parallel and vertical for the entire height of the impression, indicating that movement during the footfall occurred in a predominantly vertical plane. Rarely-noted, abnormal dinosaur footprints have been attributed to limping individuals and the pathologic loss of digits (Lockley et al., 1994; Tanke and Rothschild, 1998). Examples of “bent” or unevenly spaced toes that result in unusual prints have also been found (Ishigaki, 1986; Helm, 2008). Given that the outline of QJGM-C1 conforms to the typical morphology of *Caririchnium* tracks at the top of the cast (i.e., when the foot first made contact with the substrate), this trace does not reflect a pathologic digit.

Both the depth of the print and corresponding paths of the digits of QJGM-C1 provide rare insight into the locomotor mechanics of the track maker. The vertical path of the metatarsophalangeal region contrasts with the anteroventrally-directed traces of digit III and digit C. This discrepancy can be explained by assuming a gradual outward and forward extension of the digits as the animal transferred its weight on to the foot and as the digits met resistance from the substrate. Large, extant graviportal mammals—whose masses are within the estimated realm of large ornithopods—experience similar phenomena during footfall (Weissengruber et al., 2006, P. Bell pers. obs.) in which elastic properties of the fatty cushion ventral to the pedal skeleton permit the pedal surface area to expand (Weissengruber et al., 2006; Miller et al., 2007). Similarly elastic footpads are occasionally seen other specialized, non-graviportal mammals, such as the dromedary (*Camelus dromedarius*; Arnautovic and Abdalla, 1969; Arnautovic, 1996). In such cases, the role of the footpad is both to spread the load of the animal, thereby preventing unnecessary sinking into unconsolidated substrates, and to act as an energy absorber (Arnautovic and Abdalla, 1969; Arnautovic, 1996; Miller et al., 2007). That large ornithopods possessed similar footpads has been corroborated by both footprint and postural studies, and the pads presumably acted in a similar fashion (Moreno et al., 2007). Extension of the digits during the down-step in QJGM-C1 is consistent with load-bearing adaptations in extant, high-mass mammals; splaying of the digits in QJGM-C1 therefore may have helped spread the weight of the track maker, conferring better stability (and, hence, increased locomotor efficiency) in the thixotropic sediments at the Lotus tracksite. However, the exaggerated curvature of digit A remains anomalous.

The absence of overprinted parallel striae (Difley and Ekdale, 2002) or anteriorly-directed toe-drag marks (Gatesy et al., 1999; Milàn et al., 2005) imply that the digits did not make contact with the surrounding sediments during the kick-off phase of the step cycle. Any horizontal component to the stride clearly did not take place until the foot had been extracted from the deep track. For this to have occurred, following the final part of the load-bearing phase, the toes must have been curled (flexed) as the foot was lifted vertically, such that they did not make further contact with the surrounding substrate. Similar vertical step cycles have been described from isolated sauropod manus prints (Milàn et al., 2005). The isolated nature of QJGM-C1 (and the aforementioned sauropod prints) unfortunately does not permit characterization of the stride of the track maker, but documents a single footfall and take-off in substrate with a specific set of compositional and structural properties. The sequence of this step in QJGM-C1 can be described as follows:

(1) Initial contact of pes with substrate. Pes is in its “normal” state, coinciding with the usual morphology of *Caririchnium lotus* tracks (depth = 0 cm).

(2) As weight was transferred to the foot, the digits began to splay outward as the “heel” pressed vertically into the substrate; the divarication angle between digit A and digit III reached its maximum at a depth of 16.5 cm.

(3) Below a depth of 16.5 cm, the divarication angle between digit A and digit III reduces sharply as the digit moves toward digit III, culminating in contact between the two digits at a depth of 34.8 cm. Digit III and digit C continue to extend outward (anteriorly and transversely).

(4) The pes is depressed further to a depth of 37.1 cm with digits III and A remaining in contact. Digits III and C attain their maximum extension.

(5) The pes is retracted vertically without leaving further impressions.

This interpretation of digital mobility (Fig. 7) paints a picture of a hadrosauriform rather gingerly navigating a thick muddy layer in a river floodplain. It contrasts with the conventional picture of digital inflexibility of the hadrosauriform pes (Moreno et al., 2007). The surprising mobility of the digits in QJGM-C1, particularly that of digit A, indicate a greater degree of pedal flexibility than previously thought, which has important implications for the reconstruction of hadrosauriforms locomotion (Sellers et al., 2009).

Moreover, it suggests *Caririchnium lotus* track makers, and perhaps hadrosauriforms in general, were capable of locomotory modifications in response to substrate consistency beyond the “expected” shift between bipedal and quadrupedal postures (Wilson et al., 2009).



Fig. 7. Schematic of pedal mobility in *Caririchnium lotus* as interpreted from QJGM-C1. All three digits combine transverse as well as anterior (extension/flexion) movement relative to the metatarsophalangeal region as the foot penetrated deeper into the substrate (lighter shades of gray represent increasing depth). Note how lateral digit A (right side of foot) moves to contact digit III. “Normal” footprint silhouette (dark gray) based on holotype QJGM-T37-3.

6 Conclusions

Deep, three-dimensional tracks offer insight into the locomotor mechanics of the trackmaker, including the footfall, weight-bearing, and kick-off phases of the step cycle. QJGM-C1 is a three-dimensional hadrosauriform track attributable to *Caririchnium lotus* from the ‘mid’ Cretaceous Lotus tracksite, south-central China. The track demonstrates modifications in foot posture (extension and increased divarification angle between the digits) took place during the footfall, consistent with adaptations for increased stability and load-bearing in response to unconsolidated substrates. The pes was retracted from the sediments without leaving further impressions, suggesting the digits were flexed somewhat from their position in the load-bearing phase. The track also demonstrates a high degree of mediolateral mobility in at least one of the digits, contradictory to the pedal osteology of the alleged hadrosauriform trackmaker. These findings demonstrate *Caririchnium lotus* track makers, and perhaps hadrosauriforms in general, were capable of locomotory modifications in response to substrate consistency beyond the “expected” shift between bipedal and quadrupedal postures (Wilson et al., 2009).

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References

- Arnautovic, I., 1996. A contribution to the study of some structures and organs of camel (*Camelus dromedarius*). *Journal of Camel Practice and Research*, 4: 287–293.
- Arnautovic, I., and Abdalla, O., 1969. Elastic structures of the foot of the camel. *Acta Anatomica*, 72: 411–428.
- Avanzini, M., Piñuela, L., and García-Ramos, J.C., 2011. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lethaia*. doi: 10.1111/j.1502-3931.2011.00276.x.
- Brown, B., 1914. *Corythosaurus casuarius*, skeleton, musculature, and epidermis. *Bulletin of the American Museum of Natural History*, 35: 709–716.
- Currie, P.J., and Sarjeant, W.A.S., 1979. Lower Cretaceous dinosaur footprints from the Peace River Canyon, British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 28: 103–115.
- Currie, P.J., 1983. Hadrosaur trackways from the lower Cretaceous of Canada. *Acta Paleontologica Polonica*, 28: 63–73.
- Currie, P.J., Badamgarav D., and Koppelhus, E.B., 2003. The first Late Cretaceous footprints from the Nemegt locality in the Gobi of Mongolia. *Ichnos*, 10: 1–13.
- Difley, R.L., and Ekdale, A.A., 2002. Footprints of Utah’s last dinosaurs: track beds in the Upper Cretaceous (Maastrichtian) North Horn Formation of the Wasatch Plateau, central Utah. *Palaios*, 17: 327–346.
- Dong Zhiming, Zhou Zhongli and Wu Shaoyuan, 2003. Note on a hadrosaur footprint from Heilongjiang River area of China. *Vertebrata Palasiatica*, 41: 324–326 (in Chinese with English abstract).
- Gatesy, S.M., Middleton, M.K., Jenkins Jr., F.A., and Shubin, N.H., 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature*, 399: 141–144.
- Gou Zonghai and Zhao Bing, 2001. The Cretaceous and Tertiary systems in Dayi and Chongzhou Regions, Sichuan. *Journal of Stratigraphy*, 25: 28–33, 62 (in Chinese with English abstract).
- Hasiotis, S.T., 2004. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: *Sedimentary Geology*, 167: 177–268.
- Helm, C., 2008. *Exploring Tumbler Ridge*. Publishing Division, Tumbler Ridge News, Tumbler Ridge, BC.
- Horner, J.R., Weishampel, D.B., and Forster, C.A., 2004. Hadrosauridae. In: Weishampel, D.B., Dodson, P. and

- Osmolska, H. (Eds), *The Dinosauria*, 2nd edition. University of California Press, Berkeley, Cali, 438–463.
- Hunt, A.P., and Lucas, S.G., 1996. A reevaluation of the vertebrate ichnofauna of the Mesa Rica Sandstone and Pajarito Formations (Lower Cretaceous: Late Albian), Clayton Lake State Park, New Mexico. *New Mexico Geology*, 18(2): 1–57.
- Huh, M., Hwang, K.G., Paik, I.S., Chung, C.H., and Kim, B.S., 2003. Dinosaur tracks from the Cretaceous of South Korea: distribution, occurrences and paleobiological significance. *The Island Arc*, 12: 132–144.
- Ishigaki, S., 1986. Dinosaur footprints of the Atlas Mountains. *Nature Study*, 32: 6–9.
- Kim, J.Y., Lockley, M.G., Kim, H.M., Lim, J.D., and Kim, K.S., 2009. New dinosaur tracks from Korea, *Ornithopodichnus masanensis* ichnogen. et ichnosp. nov. (Jindong Formation, Lower Cretaceous): implications for polarities in ornithopod foot morphology. *Cretaceous Research*, 30: 1387–1397.
- Kappus, E.J., Lucas, S.G., Hunt, A.P., Heckert, A.B., and Lockley, M.G., 2003. Dinosaur Footprints from the Lower Cretaceous Sarten Member of the Mojado Formation at Cerro de Cristo Rey, Dona Ana County, New Mexico. *Ichnos*, 10: 263–267.
- Lee, Y.N., 1997. Bird and dinosaur footprints in the Woodbine Formation (Cenomanian), Texas. *Cretaceous Research*, 18: 849–864.
- Leonardi, G., 1984. *Le impronte fossili di dinosauri*. In: Bonaparte, J.F. and Bonaparte, J.F. (Eds), *Sulle Orme de Dinosauri* (Venezia: Erizzo). 333.
- Li, J.J., Bai Z.Q., and Wei Q.Y., 2011. *On the Dinosaur Tracks from the Lower Cretaceous of Otog Qi, Inner Mongolia*. Beijing: Geological Publishing House, 1–109 (in Chinese with English abstract).
- Li, Y.L., 1995. Daxi conglomerate and its geological time. *Journal of Chengdu University of Technology*, 22(2): 11–14 (in Chinese with English abstract).
- Liu, Y.S., He, Z.W., Long, X.J., Li, X.Q., Li, N.J., and Gong, L.M. 2010. Characteristics and geological significance of geological relics in Qijiang geopark, Chongqing City. *Chinese Journal of Geological Hazard and Control*, 21(2): 118–124 (in Chinese with English abstract).
- Lockley, M.G., 1985. Vanishing tracks along Alameda Parkway. In: *Environments of Deposition (and Trace Fossils) of Cretaceous Sandstones of the Western Interior*. Society of Economic Paleontology Museum Field Guide, 2nd Annual Meeting, Golden, Colorado, 131–142.
- Lockley, M.G., 1986. A guide to dinosaur tracksites of the Colorado Plateau and American southwest. *University of Colorado Denver Geology Department Magazine Special Issue*, 1: 1–56.
- Lockley, M.G., 1987. Dinosaur footprints from the Dakota Group of eastern Colorado. *The Mountain Geologist*, 24: 107–122.
- Lockley, M.G., 2001. *A Field Guide to Dinosaur Ridge: Denver, Colorado*. Friends of Dinosaur Ridge and University of Colorado at Denver Dinosaur Trackers Research Group. 34.
- Lockley, M.G., Holbrook, J., Hunt, A.P., Matsukawa, M., and Meyer, C., 1992. *The Dinosaur Freeway: a preliminary report on the Cretaceous megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains; Colorado, Oklahoma and New Mexico*. In: *Mesozoic of the Western Interior*, SEPM Midyear Meeting Fieldtrip Guidebook, 39–54.
- Lockley, M.G., Hunt, A.P., Moratalla, J., and Matsukawa, M. 1994. Limping dinosaurs? Trackway evidence for abnormal gaits. *Ichnos*, 3: 193–202.
- Lockley, M.G., Nadon, G., and Currie, P.J., 2003. A diverse dinosaur-bird footprint assemblage from the Lance Formation, Upper Cretaceous, eastern Wyoming: implications for ichnotaxonomy. *Ichnos*, 11: 229–249.
- Lu, T.Q., Wang, Z.L., Yang, X.Y., and Zhang, X.L., In press. Dinosaur tracks in vertical sections from Middle Cretaceous of Emei, Sichuan Province. *Geological Bulletin of China*.
- Manning, P.L., Morris, P.M., McMahon, A., Jones, E., Gize, A., Macquaker, J.H.S., Wolff, G., Thompson, A., Marshal, J., Taylor, K.G., Lyson, T., Gaskell, S., Reamtong, O., Sellers, W.I., van Dongen, B.E., Buckley, M., and Wogelius, R.A., 2009. Mineralized soft-tissue structure and chemistry in a mummified hadrosaur from the Hell Creek Formation, North Dakota (USA). *Proceedings of the Royal Society of London B*, 276: 3429–3437.
- Mateus, O., and Milàn, J., 2008. *Sauropod forelimb flexibility deduced from deep manus tracks*. In: 52th Paleontological Association Annual Meeting. 18th–21st December 2008, University of Glasgow, 67–68.
- Matsukawa, M., Shibata, K., Kukihiro, R., Koarai, K., and Lockley, M., G. 2005. Review of Japanese dinosaur track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. *Ichnos*, 12:201–222.
- McDonald, A.T., Kirkland, J.I., DeBlieux, D.D., Madsen, S.K., Cavin, J., Milner, A.R.C., and Panzarin, L., 2010. New basal iguanodonts from the Cedar Mountain Formation of Utah and the evolution of thumb-spiked dinosaurs. *PLoS ONE* 5(11): e14075 (1–35).
- McDonald, A.T., Wolfe, D.G., and Kirkland, J.I., 2010. A new basal hadrosauroid (Dinosauria: Ornithopoda) from the Turonian of New Mexico. *Journal of Vertebrate Paleontology* 30: 799–812.
- Milàn, J., Christiansen, P., and Mateus, O., 2005. A three-dimensionally preserved sauropod manus impression from the Upper Jurassic of Portugal: implications for sauropod manus shape and locomotor mechanics. *Kaupia*, 14: 47–52.
- Miller, C.E., Ren, L., and Hutchinson, J.R., 2007. An integrative analysis of elephant foot biomechanics. *Journal of Morphology*, 268: 1107.
- Moreno, K., Carrano, M.T., and Snyder, R., 2007. Morphological changes in pedal phalanges through ornithopod dinosaur evolution: a biomechanical approach. *Journal of Morphology*, 268: 50–63.
- Nadon, G.C., 1993. The association of anastomosed fluvial deposits and dinosaur tracks, eggs, and nests: implications for the interpretation of floodplain environments and a possible survival strategy for ornithopods. *Palaio*, 8: 31–44.
- Osborn, H.F., 1912. Integument of the iguanodont dinosaur *Trachodon*. *Memoirs of the American Museum of Natural History* 2: 33–54.
- Paul, G.S., 1987. The science and art of restoring the life appearance of dinosaurs and their relatives: a rigorous how-to guide. In: Czerkas, S.J. and Olson, E.E. (Eds), *Dinosaurs Past and Present*. Volume II. Los Angeles County Museum of Natural History/University of Washington Press, Seattle, 4–49.
- Platt, B.F., and Hasiotis, S.T., 2006. Newly discovered sauropod

- dinosaur tracks with skin and foot-pad impressions from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, U.S.A. *Palaio*, 21: 249–261.
- Prieto-Márquez, A., 2010. Global phylogeny of Hadrosauridae (Dinosauria: Ornithopoda) using parsimony and Bayesian methods. *Zoological Journal of the Linnean Society*, 159: 435–502.
- Sellers, W.I., Manning, P.L., Lyson, T., Stevens, K., and Margetts, L., 2009. Virtual palaeontology: gait reconstruction of extinct vertebrates using high performance computing. *Palaeontologica Electronica* 12: 11A (1–26).
- Sternberg, C.M., 1932. Dinosaur tracks from Peace River, British Columbia. *National Museum of Canada Bulletin* 68: 59–85.
- Tanke, D.H., and Rothschild, B.M., 1998. Paleopathology. In: Currie, P.J. and Padian, K. (Eds), *the Encyclopedia of Dinosaurs*. Academic Press, San Diego, Calif, 525–530.
- Thulborn, R.A., and Wade, M., 1984. Dinosaur trackways in the Winton Formation (Mid Cretaceous) of Queensland. *Memoirs of the Queensland Museum*, 21: 413–517.
- Thulborn, R.A., 1990. *Dinosaur Tracks*. Chapman Hall, London. 410.
- Weems, R.E., 2004. A new dinosaur ichnotaxa on from the Lower Cretaceous Patuxent Formation of Maryland and Virginia. *Geological Society of America Abstracts with Programs*, 36(2): 116.
- Weissengruber, G.E., Egger, G.F., Hutchinson, J.R., Gorenwald, H.B., Famini, D., and Forstenpointner, G., 2006. The structure of the cushions in the feet of African elephants (*Loxodonta africana*). *Journal of Anatomy*, 209: 781.
- Wilson, J.A., Marsicano, C.A., and Smith, R.M.H., 2009. Dynamic locomotor capabilities revealed by early dinosaur trackmakers from South Africa. *PLoS ONE*, 4(10): e7331. doi:10.1371/journal.pone.0007331.
- Xing Lida, Wang Fengping, Pan Shigang and Chen Wei, 2007. The discovery of dinosaur footprints from the Middle Cretaceous Jiaguan Formation of Qijiang County, Chongqing City. *Acta Geologica Sinica* (Chinese edition), 81: 1591–1602 (in Chinese with English abstract).
- Xing, L.D., Harris, J.D., Dong, Z.M., Lin, Y.L., Chen, W., Guo, S.B., and Ji, Q., 2009. Ornithopod (Dinosauria: Ornithischia) Tracks from the Upper Cretaceous Zhutian Formation in Nanxiong Basin, China and General Observations on Large Chinese Ornithopod Footprints. *Geological Bulletin of China*. 28: 829–843.
- Xing, L.D., Harris, J.D., Gierliński, G.D., Wang, W.M, Wang, Z.Y., and Li, D.Q., 2011. Middle Cretaceous non-avian theropod trackways from the southern margin of the Sichuan Basin, China. *Acta Palaeontologica Sinica* 50(4): 470–480.
- Young, C.C., 1960. Fossil footprints from China. *Vertebrata Palasiatica*, 4: 53–66.
- Zhen Shuonan, Li Jianjun, Chen Wei, Zhu Songlin and Zhang Baokun, 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan. *Memoirs of the Beijing Natural History*, 54: 105–120 (in Chinese with English abstract).