

The fastest-running theropod trackway in the Cretaceous from Ordos, Inner Mongolia, China

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Abstract The maximum locomotor capabilities of theropod dinosaurs have long been a subject of considerable scholarly, primarily due to the lack of contemporary species for direct comparison. Biomechanical modeling and the analysis of dinosaur trackways have yielded significant theoretical insights into this area of research. This study investigates the running speed of a mid-sized theropod dinosaur trackway recently identified in the Otog region of Inner Mongolia, and it juxtaposes these findings with other running theropod trackways from diverse various global locations utilizing standardized inference methodologies. The results indicate that the trackmaker was capable of achieving a running speed of 45 or 41±4.9 km/h, thereby establishing it as the fastest-running theropod trackway documented from the Cretaceous period. Additionally, this paper reviews biomechanical investigations concerning the maximum running speeds of theropod dinosaurs and illustrates that the inferred speed of this mid-sized theropod aligns with the predictions of the majority of biomechanical models, thereby providing compelling new evidence to enhance our understanding of the locomotor capabilities of mid-sized theropods.

Keywords Theropod trackway, Running speed, Cretaceous, Inner Mongolia, China

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1. Introduction

The maximum running speed of non-avian theropod dinosaurs has long been a subject of considerable interest within the scholarly community, given that locomotor capabilities, especially running speed, are essential for both predation and evasion from predators (Sellers and Manning, 2007; Dececchi et al., 2020; Navarro-Lorbés et al., 2021). Researchers have made considerable progress utilizing various methodologies, with current estimates of the maximum running speed of theropod dinosaurs primarily derived from two

main sources of evidence: (1) biomechanical analyses and (2) trackway examinations.

Biomechanical investigations into the running capabilities of theropod dinosaurs have their origins in comparative anatomy. Coombs (1978), by examining the locomotor abilities and anatomical traits of extant vertebrates, concluded that small bipedal dinosaurs were likely more agile than their larger counterparts, though probably not as fast as contemporary bipedal species such as kangaroos and ostriches. Thulborn (1982), using known relationships between speed, gait, and body size (primarily derived from mammals), supplemented by comparative anatomy and dinosaur trackway data, estimated that small bipedal dinosaurs could

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achieve speeds of 35–40 km/h, whereas larger bipedal dinosaurs were likely limited to walking or slow jogging, with maximum speeds of approximating 15–20 km/h. Subsequent research has employed a diverse array of methodologies, including bone strength analysis, safety factor assessments, ground reaction forces, musculoskeletal modeling, interactive B-spline models, inverse dynamics biomechanical analyses, general scaling models, multibody dynamics analyses, and bone stress evaluations, to estimate the maximum running speeds of theropod dinosaurs (Coombs, 1978; Thulborn, 1982; Farlow et al., 1995; Alexander, 1996; Blanco and Mazzetta, 2001; Hutchinson and Garcia, 2002; Hutchinson, 2004; Hutchinson et al., 2007, 2011; Sellers and Manning, 2007; Bates et al., 2009; Hirt et al., 2017; Sellers et al., 2017; Dececchi et al., 2020).

Although it has been suggested that using trackway analysis to estimate the speed of trackmakers may be inaccurate based on data from extant birds (Prescott et al., 2025), this estimation method has become a standard research approach, as both stride length and relative stride length (the ratio of stride length to hip height) are intricately linked to the locomotion speed and walking gait of the trackmaker (Alexander, 1976; Thulborn, 1990; González Riga, 2011). Alexander (1976) conducted empirical observations on various contemporary species, including horses, jirds, elephants, and ostriches, establishing a correlation among speed, hip height, and stride length. Furthermore, the ratio of stride length (SL) to hip height (h) serves as a valuable indicator for inferring the locomotion patterns of the trackmaker. In a subsequent study, Alexander et al. (1977) focused on the rapid locomotion of ungulates, such as zebras, giraffes, warthogs, and seven species of bovids, suggesting that the equation formulated in 1976 was more applicable to slower running speeds, leading to the development of a new formula tailored for faster locomotion. Thulborn (1990) contended that the equation proposed by Alexander (1976) is relevant for slow walking and proposed an alternative formula that is more appropriate for the rapid movement of the trackmaker. Ruiz and Torices (2013) also validated the accuracy of the equation by analyzing a dataset pertaining to human walking and running. Although the coefficient in their formula was marginally lower, the range they provided still encompassed the range of the formula proposed by Alexander (1976). While inferring the speed of dinosaurs from their trackways provides a useful methodology, it does not ascertain whether these speeds represent the maximum capabilities of the trackmakers. Presently, instances of fast-running trackways are infrequent globally, predominantly attributed to small- to medium-sized theropod dinosaurs (Lapparent and Montenat, 1967; Farlow, 1981; Thulborn and Wade, 1984; Irby, 1996; Kim, 2002; Zhang et al., 2004; Weems, 2006; Kim and Huh, 2010; Li et al., 2011; Bordy, 2021; Lockley et al., 2021; Navarro-Lorbés et al., 2021; Xing et al., 2021; Dececchi et

al., 2024). Some of these trackways indicate speeds that may reflect the upper limits of running capabilities in dinosaurs (Farlow, 1981; Kim, 2002; Kim and Huh, 2010; Li et al., 2011; Lockley et al., 2021; Navarro-Lorbés et al., 2021).

In a recent resource survey conducted by Wang Xiaolin and his research team in the Otog region of Inner Mongolia, a new footprint site was identified near the original Chabu 5. This discovery includes four trackways and two isolated footprints. Of particular interest is a unique trackway attributed to a mid-sized theropod dinosaur, which comprises five consecutive footprints exhibiting a notable stride length of 5.3 m. This measurement indicates that the trackmaker was moving at a high rate of speed. Utilizing advanced research methodologies, the team conducted comprehensive analyses of the morphological features of the footprints, as well as the speed and gait of the trackmaker. The findings provide significant insights into the estimation of the height and body length characteristics of the trackmaker, the maximum running speed of mid-sized theropod dinosaurs, and their behavioral habits, thereby providing valuable support for biomechanical interpretations.

2. Materials and methods

The specimens described here are all natural molds (concave hyporeliefs) *in situ*, found on the grayish-white sandstone located in the Otog region, Ordos City, China. The newly discovered Chabu 5⑦ is located approximately 400 m northeast of the previously documented Chabu 5⑤ (Figure 1). The footprint layer belongs to the Lower Cretaceous Jingchuan Formation, which is characterized as a fine-grained sedimentary layer within the Lower Cretaceous Zhidan Group. The lower part is predominantly composed of sandstone, while the upper part is primarily made up of bluish-gray mudstone interbedded with thin layers of conglomerate, sandstone, and limestone. Numerous typical fossils from the Jehol biota, including *Lycoptera* and ostracods, have been found in the shale of the Chabu area (Guo et al., 2006). The Jingchuan Formation is chiefly noted for its shallow lacustrine deposits, which exhibit relatively gentle strata dips. Differential weathering has led to the extensive exposure of the more resilient sandstones, which in turn have preserved a significant number of tracks, including those of non-avian dinosaurs, birds, and turtles (Li et al., 2011; Lockley et al., 2012, 2018).

Photogrammetric images were produced through the acquisition of multiple digital photographs captured from various perspectives utilizing a Canon EOS 5D Mark III camera. Subsequently, these images were then processed using Agisoft Photoscan Professional to create a scaled and highly accurate 3D textured mesh model (Falkingham et al., 2018). The resultant final false-color depth maps were ren-

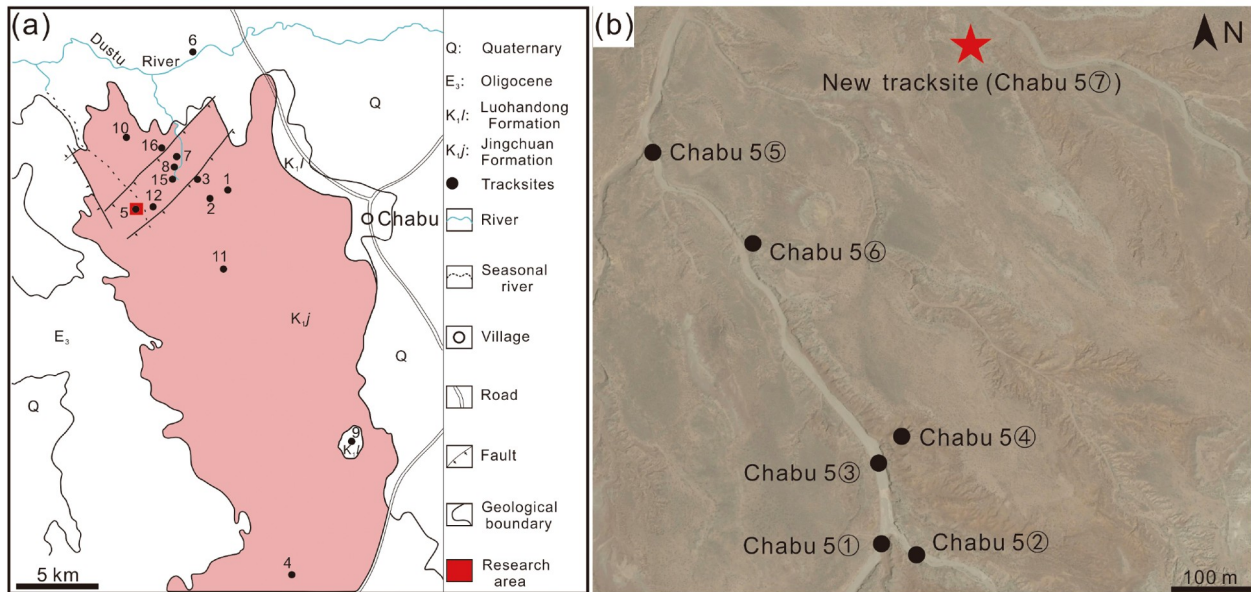


Figure 1 Distribution map of tracksites in the Chabu area, Otog Banner, Inner Mongolia. (a) Location map of the research area and reported tracksites (modified from Lockley et al., 2018), (b) detailed location map of the research area, the red five-pointed star indicates the location of the newly discovered tracksite.

dered using CloudCompare.

Utilizing the classification methodology established by Marty (2008), the tracks have been classified into distinct size classes based on pes length (FL) as follows: minute (<10 cm), small ($10\text{ cm} < \text{FL} < 20$ cm), medium ($20\text{ cm} < \text{FL} < 30$ cm), and large (>30 cm). The footprint length and width, length/width ratio and divarication angles between digit traces were conducted in accordance with established standards (Olsen, 1980; Thulborn, 1990). Furthermore, the length/width ratio of the anterior triangle was calculated according to the method proposed by Lockley (2009). The hip height is estimated using the formula proposed by Alexander (1976) that the hip height is four times the length of the footprint. This study does not incorporate the variable hip height ratios suggested by Thulborn (1990) for various sizes and types of dinosaurs, as the four-times ratio is widely used by scholarly community when estimating hip height (Navarro-Lorbés et al., 2021). The body length of the trackmaker is determined according to the methodologies proposed by Henderson (2003) and Xing et al. (2009).

The estimation of body weight follows the method established by Weems (2006), which suggests that weight is approximately proportional to the cube of 4.73 times the hip height. In assessing the speed of the trackmaker, this study employs and compares two methodologies. The first is the empirical formula introduced by Thulborn (1990), which is suitable for fast running gaits. The second is a modified version of the equation proposed by Alexander (1976), as adapted by Ruiz and Torices (2013) and Navarro-Lorbés et al. (2021), which offers a range of uncertainty that encompasses the outcomes derived from Alexander's original

equation. Together, these two methods cover the full range of speed estimates for fast-running trackways suggested by various scholars. The total footprint length is calculated based on the average length of the footprints observed within the trackway.

3. Tracks and trackways

The trackway T1 consists of five consecutive footprints. In each instance, the deepest impressions are located at the distal ends of the digits, while the proximal ends are either absent or exhibit shallower impressions. Some footprints preserve distal claw marks, which are shallower than the digit impressions and are sharper (Figure 2, Figure 3, Figure 4). Among the five footprints, only two preserve very shallow heel impressions, namely T1-2R and T1-4R (Figure 4). The T1-2R footprint measures 25.5 cm in length and 22.5 cm in width, resulting in a length-to-width ratio of 1.13. Notably, the middle digit is slightly longer than the outer digits, and the anterior triangle length-to-width ratio is 0.60. The angle between the outer digits is 52.29° . The distal ends of digits II and IV exhibit relatively sharp claw marks, with the deepest impressions found at the distal ends of digits II and III, which gradually decrease in depth toward the proximal end. The digit IV only shows relatively shallow claw marks and deeper impressions at the distal end of the digit. The T1-4R footprint measures 25.0 cm in length and 22.8 cm in width, resulting in a length-to-width ratio of 1.10. Notably, the middle digit is slightly longer than the lateral digits, and the anterior triangle length-to-width ratio is 0.58. The angle between the outer

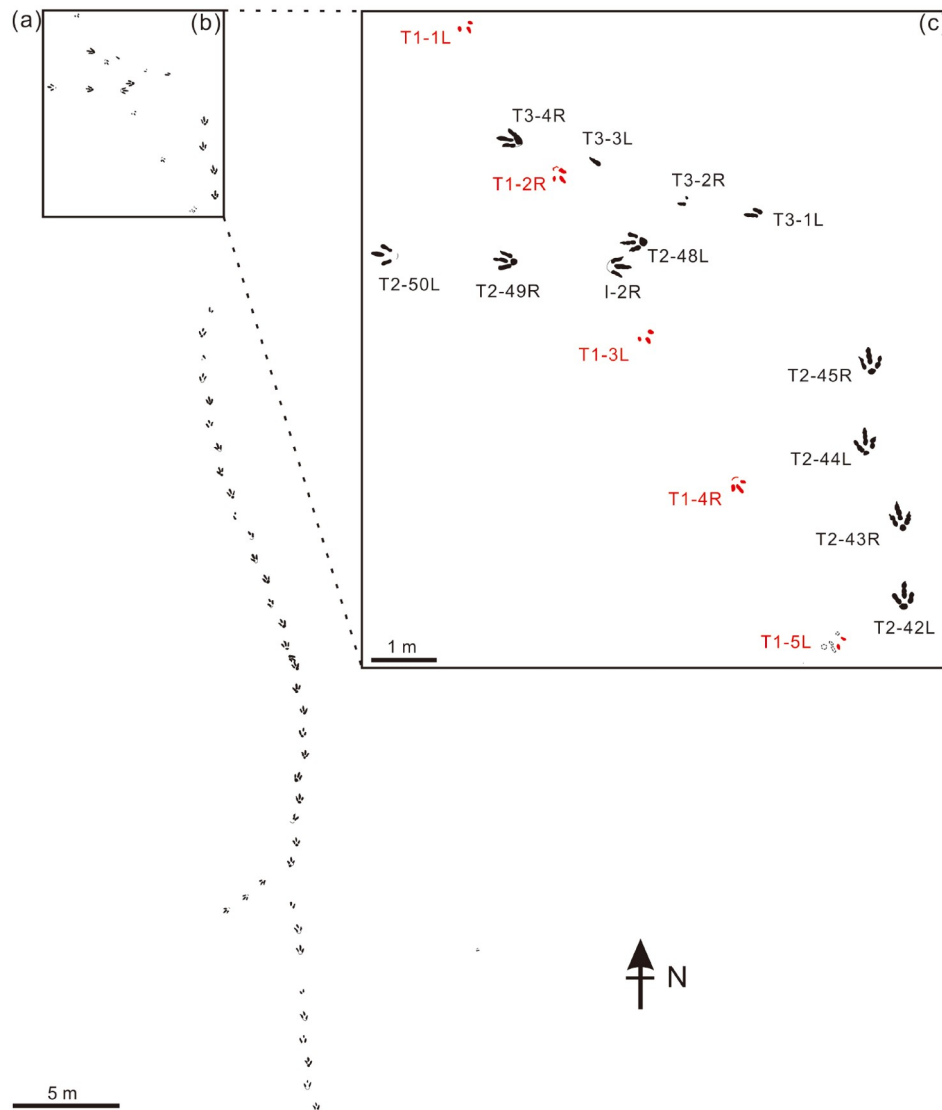


Figure 2 Composite map of footprint distribution and enlarged detail of running trackway at Chabu5(7). (a) Footprints distribution map, (b) distribution map of trackway T1 and nearby footprints, (c) magnified view of region (b), with the red color represents the fast-running trackway T1.

digits is 72.57° . Additionally, the distal end of the digit IV preserves relatively sharp claw marks, while the distal impressions of digits II and IV are deeper, and the digit III shows signs of partial weathering, with only one digit pad preserving a deeper impression. Based on the footprint length exceeding 25 cm, sharp claws, broad digital impressions, and small anterior triangle length-to-width ratios, these characteristics align with those of footprints from the Eubrontidae.

The trackway T1 exhibits a nearly straight line, characterized a large pace and stride lengths. The average pace length is 2.65 m, which is 10.50 times the average footprint length, while the stride length is 5.3 m, which is 20.99 times the average footprint length. The pace argulation ranges from 176° to 178° , with an average of 177° , close to 180° (Figure 3).

There are also 59 large theropod dinosaur footprints on the same layer, including three trackways and two isolated footprints (Figure 2). The morphological features of these footprints are uniform, exhibiting large theropod footprints with a tridactyl shape. Notably, there are no traces of tail and manus impressions are observed. The footprints are relatively large, with a length greater than the width; the average length is approximately 44.92 cm, and the width is about 34.85 cm. The length-to-width ratio is relatively low, calculated at 1.29. The middle digit is slightly longer than the two lateral digits and is oriented towards the digit IV. The claw impressions are blunt, especially the claw on the middle digit, which is distinctly pronounced. The anterior triangle length-to-width ratio is small, approximately 0.44. Based on the large size, the low length-to-width ratio, the low anterior triangle length-to-width ratio, the middle digit being slightly

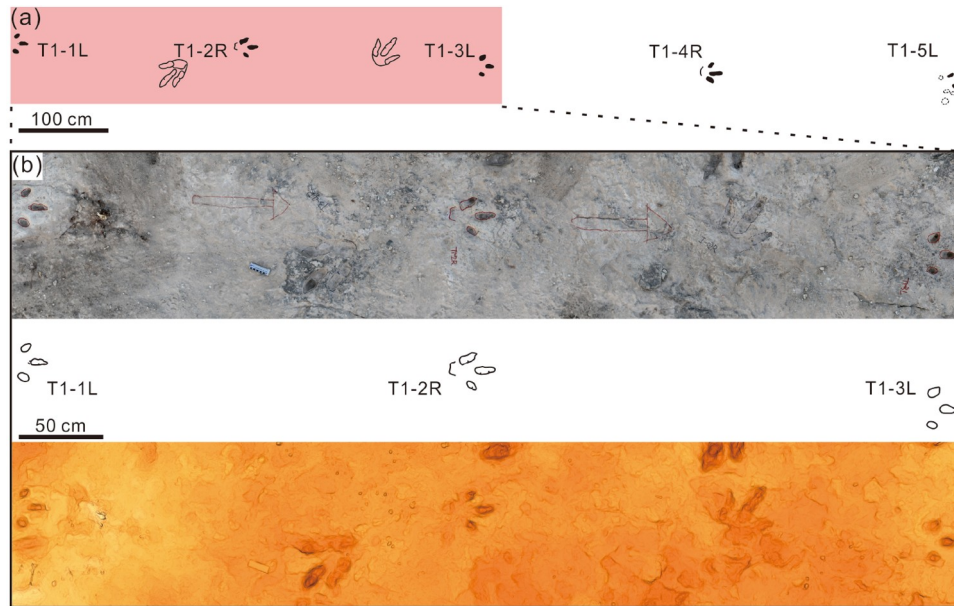


Figure 3 Distribution map of fast-running theropod trackway. (a) Distribution map showing the trackway T1 and nearby footprints, (b) photograph, line drawings, and false-colored depth maps of the first three footprints of T1 (with colors ranging from yellow to brown indicating increasing footprint depth).

longer than the lateral digits and pointing toward the digit IV, and the blunt claws of the middle digit, the footprints share characteristics with those of *Chapus lockleyi*.

Trackway T2 reveals a series of footprints extending over a distance of 60 m, consisting of 50 footprints. The initial segment of the trackway is covered by soil, suggesting that further excavation may uncover additional footprints. The average pace length is relatively short, about 125 cm, approximately 2.74 times the footprint length (about 45.6 cm), while the stride length is noted to be 245 cm. Trackway T3 is composed of four footprints, of which the first three footprints exhibit poor preservation. The fourth footprint, however, is better preserved, measuring 40.5 cm in length and 30.0 cm in width. The average pace length is approximately 128 cm, about 3.16 times the length of the footprint, and the stride length is about 246 cm. Trackway T4 consists of three footprints, with footprint T4-2R being well-preserved. This footprint measures 36.5 cm in length and 29.5 cm in width, with a pace length of 130 cm and a stride length of 260 cm.

4. Speed analysis and the size of the track-maker

In trackway T1, only T1-2R and T1-4R preserve shallow impressions of the heel, with an average length of 25.25 cm for these two footprints. Following the methodology proposed by Alexander (1976), it is assumed that the hip height is four times the total length of the footprint, resulting in an estimated hip height of 101 cm. Furthermore, as indicated by Henderson (2003) and Xing et al. (2009), the body length of

theropod dinosaurs is 2.63 times the hip height, resulting in a body length of 265.63 cm for the trackmaker. The calculation of body weight is derived from the formula presented by Weems (2006), which states that weight is 4.73 times the cube of the hip height, yielding an estimated body weight of about 109 kg, which, according to Hutchinson (2004), corresponds to a mid-sized theropod dinosaur.

The answer to whether the trackmaker of trackway T1 was in a fast running state, approaching the maximum running speed, is affirmative. The reasons are as follows: (1) The relative stride length of the trackway can be used to scientifically infer the gait of the trackmaker. It is widely accepted that if $SL/h \leq 2$, the trackmaker is in a normal walking gait; if $2 < SL/h \leq 2.9$, the trackmaker is in a trotting gait; if $2.9 < SL/h$, the trackmaker is in a running gait (Alexander, 1976; Thulborn, 1990). The stride length of trackway T1 is 5.3 m, with a hip height is 1.01 m, resulting in a relative stride length of 5.25, which signifies a fast running state. (2) Trackway T1 is nearly a straight line, coupled with a pace angulation approaches 180° . Research has indicated that theropod dinosaurs tend to adjust their pace angulation to near 180° during rapid locomotion (Day et al., 2002; Kim and Huh, 2010). This adaptation allows the trackmaker's feet are close to or placed near the midline of the body, thereby maximizing the effective stride length and minimizing energy wasted due to lateral displacement of the center of mass, thus optimizing movement efficiency (Day et al., 2002). (3) When the trackmaker is in a fast running state, the center of mass shifts forward, causing deeper impressions at the tips of the digits and either shallow or absent impressions at the heel. This phenomenon indicates that the trackmaker is "running on

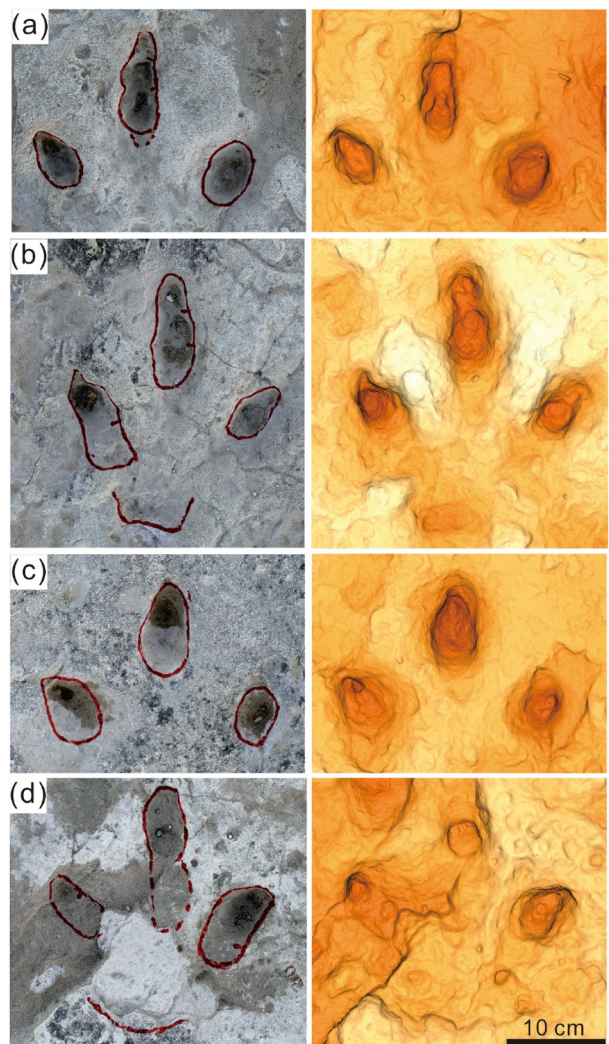


Figure 4 The details of the photographs and false-colored depth maps of well preserved footprints of T1(with colors ranging from yellow to brown indicating increasing footprint depth). (a) T1-1L, (b) T1-2R, (c) T1-3L, (d) T1-4R.

tiptoe”, which allows the trackmaker to lengthen the stride and achieve a “full extension” running posture (Thulborn and Wade, 1979; Thulborn, 1982; Lockley et al., 2021; Navarro-Lorbés et al., 2021). (4) Some scholars have proposed that achieving a relative stride length of around 5.0 is very difficult, and thus, a relative stride length of around 5.0 represents the maximum running speed of dinosaurs (Thul-

born, 1981, 1990; Thulborn and Wade, 1984; Kim and Huh, 2010).

To calculate the running speed of the trackmaker for trackway T1, we applied the formulas improved by Thulborn (1990) and Ruiz and Torices (2013), which encompass the range of running speeds inferred by scholars for fast-running trackways. In the calculations, the acceleration is taken as 9.8 m/s^2 . Using the formula proposed by Thulborn (1990), the running speed of the trackmaker is calculated to be 12.38 m/s (approximately 45 km/h). Conversely, the formula established by Ruiz and Torices (2013) yields a range, with the running speed of the trackmaker estimated at $11.33\pm1.36\text{ m/s}$ ($41\pm4.9\text{ km/h}$) (Table 1).

In this study, the relative stride length and speeds of the other three trackways (T2–T4) were calculated using Ruiz and Torices (2013) formula. The relative stride length of trackways T2–T4 were 1.32, 1.52 and 1.78, all of which are significantly less than 2, indicating a normal walking gait. The speeds were 6 ± 0.7 , 7 ± 0.8 , and $8\pm1.0\text{ km/h}$, respectively (Table 1).

5. Provide evidence for biomechanical research

Direct evidence of the maximum running speed of non-avian theropod dinosaurs cannot be obtained from skeletal fossil analyses, however, biomechanics research, along with continuous advancements, provides a basis for estimating the maximum running speed of dinosaurs (Coombs, 1978; Farlow et al., 1995; Alexander, 1996; Blanco and Mazzetta, 2001; Hutchinson and Garcia, 2002; Hutchinson, 2004; Hutchinson et al., 2007, 2011; Sellers and Manning, 2007; Bates et al., 2009; Hirt et al., 2017; Sellers et al., 2017; Dececchi et al., 2020). A limited number of biomechanical studies provide evidence supporting the hypothesis that large theropod dinosaurs possessed the capability for rapid locomotion. Coombs (1978) examined the running capabilities and anatomical features of extant vertebrates, categorizing their running abilities into four levels (graviportal, mediportal, subcursorial, cursorial). This classification was then applied to dinosaurs, indicating that bipedal dinosaurs generally exhibited greater running potential, with small bipedal dinosaurs being faster runners than large ones. The running

Table 1 Footprint lengths, hip heights and speed of trackways in Chabu 5⑦^{a)}

Trackway	Footprint length (m)	Hip height (m)	Stride length (m)	Speed 1 (km/h)	Speed 2 (km/h)
T1	0.2525	1.01	5.30	45	41 ± 4.9
T2	0.456	1.82	2.45		6 ± 0.7
T3	0.405	1.62	2.46		7 ± 0.8
T4	0.365	1.46	2.60		8 ± 1.0

a) Speed 1 is determined utilizing the formula established by Thulborn (1990), whereas Speed 2 is derived from the equation proposed by Ruiz and Torices (2013).

ability of large theropod dinosaurs falls within the mid-level, with studies suggesting that the maximum speed of *Tyrannosaurus* could reach 64 km/h. Blanco and Mazzetta (2001), by considering the strength of the femur and establishing stability indicators, estimated that large theropod dinosaurs, such as the South American giant theropod *Giganotosaurus carolinii*, could attain a maximum speed of approximately 50.4 km/h. In a subsequent study, Hutchinson et al. (2011) employed evolutionary computation methods to analyze the running ability of the large bipedal dinosaur *Tyrannosaurus*, estimating a maximum potential running speed of 56.52 km/h within biologically plausible parameters.

Numerous biomechanical analyses indicate that large theropod dinosaurs were not fast runners, primarily relying on walking or slow running gaits, whereas smaller and mid-sized theropods exhibited the capacity for higher maximum running speeds. Thulborn (1982) estimated the locomotor speeds of 62 dinosaur species (representing 51 genera) by applying known relationships between speed, gait, and body size (mostly derived from mammals), supplemented by comparative anatomy and relevant information from dinosaur footprints. The study concluded that small bipedal dinosaurs could attain running speeds of 35–40 km/h. The maximum speed of the so-called “ostrich-like dinosaurs” was below 60 km/h, with probable values of 35–40 km/h. Furthermore, larger bipedal dinosaurs (those weighing over 800 kg) were likely close to or exceeded a critical point where they could no longer support running and could only walk or move at a slow jog, with a maximum speed of about 15–20 km/h. Farlow et al. (1995) conducted an analysis of a slender *Tyrannosaurus* specimen (MOR 555) housed at the Museum of the Rockies, focusing on the reconstruction of its weight and measuring the length, anteroposterior diameter, and circumferences of the femur and shaft. Employing strength indices proposed by Alexander (1989), which quantify the capacity of long bones to resist bending stress during vigorous activity, it was concluded that the impact force and deceleration produced by a *Tyrannosaurus* running at high speeds (72 km/h) could potentially result in fatal injuries. This led to the assertion that the species likely exhibited a slower mode of locomotion, with an estimated maximum speed of around 36 km/h for adult individuals. In a commentary published in Nature, Alexander (1996) concurred with the assertion that the inference based on leg bone strength that *Tyrannosaurus* could not run fast was correct. Hutchinson and Garcia (2002) introduced a methodology for evaluating running ability by estimating the minimum mass of the extensor muscles (supportive muscles) required for fast running. Their findings suggested that smaller dinosaurs were efficient runners, whereas even under lenient assumptions, adult *Tyrannosaurus* would require an exceptionally large mass of extensor muscles. Hutchinson (2004), using

inverse dynamic biomechanical analyses previously validated for extant bipedal animals, calculated the minimum active muscle mass required for fast bipedal running in several extinct dinosaur groups. This research reinforced the conclusion that large theropods like *Tyrannosaurus* could not run fast, while smaller and medium-sized theropods excelled at running. Hutchinson et al. (2007) proposed an interactive B-spline method for estimating and visualizing biomechanical parameters of animal body segments, which strongly supported the notion that *Tyrannosaurus* was not a fast runner. Sellers and Manning (2007) established musculoskeletal models for various animals and estimated the maximum running speeds of theropods of differing sizes, revealing that maximum speed diminished with increasing body weight, particularly beyond approximately 1000 kg, with *Tyrannosaurus* estimated to have a maximum speed of merely 28.8 km/h. Bates et al. (2009), utilized laser scanning (LiDAR) and computer modeling to create 3D weight models of five non-avian dinosaur specimens, concluding that *Tyrannosaurus* was not a fast runner. Hirt et al. (2017) proposed a general scaling model to elucidate the relationship between maximum speed and body weight, indicating that non-avian dinosaurs weighing between 100–1000 kg could still achieve relatively high top speeds, while larger species like *Tyrannosaurus* were likely to be slow runners. Sellers et al. (2017) integrated two independent biomechanical techniques (multibody dynamics analysis and bone stress analysis) to demonstrate that the running gait of *Tyrannosaurus* could result in bone stresses that would be unacceptable, biomechanically limiting this species to walking gaits. Dececchi et al. (2020) suggested that there was a significant divergence between small/medium and large theropods in terms of maximizing running potential, indicating that theropods of different sizes adopted two distinct strategies in limb elongation. For small and medium theropods, increased limb length seemed associated with higher maximum speeds, while for large species (weighing over 1000 kg), limb elongation appeared to be related more to energy efficiency and reducing foraging costs. Consequently, it was proposed that large theropods primarily relied on walking gaits, while small and medium-sized theropods were capable of achieving high speeds.

Based on the results of various biomechanical models analyzed above, the majority of these models support the notion that large theropod dinosaurs (especially those weighing over 1000 kg) primarily moved with a walking gait or at slow running speeds, while small and medium-sized theropods were capable of attaining higher maximum running speeds (Hutchinson, 2004; Sellers and Manning, 2007; Hirt et al., 2017; Dececchi et al., 2020). Notably, a fast-running trackway discovered in the Otog region of Inner Mongolia, attributed to mid-sized theropods, recorded a speed of 45 or 41 ± 4.9 km/h. This running speed aligns clo-

sely with biomechanically inferred speeds for mid-sized theropods (Thulborn (1982) estimated speeds of 35–40 km/h, Hutchinson (2004) estimated speeds of 39.6–50.4 km/h, Sellers and Manning (2007) estimated speeds around 40 km/h, and Hirt et al. (2017) estimated speeds of 40.752–54.54 km/h), providing corroborating evidence for biomechanical research (Table 2). Additionally, there are also trackways of larger theropod dinosaur activity in the same footprint layer, leading to the hypothesis that the possible reason the trackmaker ran fast was partly for hunting prey and partly to avoid predation by larger theropods. This suggests that these mid-sized theropods faced significant selective pressures, necessitating the attainment of high maximum speeds and rapid acceleration to facilitate escape (Dececchi et al., 2020).

6. The fastest-running theropod trackway in the Cretaceous

Records of running non-avian theropod dinosaur trackways are relatively scarce globally. Presently, instances of fast-running theropod dinosaur trackways have been discovered in China, Republic of Korea, the United States, France, Australia, South Africa, and Spain, with the highest concentration of discoveries occurring in China and the United States (Table 3). The majority of these trackways consist of small to medium-sized footprints, and the lengths of the trackways are generally short (Lapparent and Montenat, 1967; Farlow, 1981; Thulborn and Wade, 1984; Irby, 1996; Kim, 2002; Zhang et al., 2004; Weems, 2006; Kim and Huh, 2010; Li et al., 2011; Bordy, 2021; Lockley et al., 2021; Navarro-Lorbés et al., 2021; Xing et al., 2021; Dececchi et al., 2024). This suggests that medium or small theropod dinosaurs may only be capable of maintaining high-speed locomotion for a limited duration (Weems, 2006; Kim and Huh, 2010). This study collected data on the footprint length, hip height (four times the foot length), and stride length of all running trackways (Table 3, Figure 5), using formulas from Thulborn (1990) and Ruiz and Torices (2013) for calculations. Utilizing a consistent calculation approach and accounting for the same margin of error, the analysis revealed that the T18 trackway, discovered by Lockley et al. (2021) in the United States, currently represents the fastest-running theropod trackway in the world from the Early Jurassic, with speeds reaching 49 or 45 ± 5.4 km/h. Additionally, the second fastest-running theropod dinosaur trackway is discovered in this study (45 or 41 ± 4.9 km/h), which is slightly higher than the trackway reported by Li et al. (2011), but they are essentially comparable (44 or 40 ± 4.8 km/h), representing a new fastest-running trackway in the Cretaceous period. This provides an intuitive understanding of the maximum running speed of mid-sized theropod dinosaurs.

Table 2 Biomechanical assessment of the estimated maximum running speeds of theropod dinosaurs

Taxon	Speed (km/h)	Notes
<i>Tyrannosaurus</i>	64	Coombs, 1978
<i>Antrodemus</i>	67	Coombs, 1978
<i>Dromiceiomimus</i>	97	Coombs, 1978
<i>Deinonychus</i>	74	Coombs, 1978
<i>Compsognathus</i>	12–16	Thulborn, 1982
<i>Podokesaurus</i>	15–20	Thulborn, 1982
<i>Compsognathus</i>	19–26	Thulborn, 1982
<i>Coelophysis</i>	20–26	Thulborn, 1982
<i>Ornitholestes</i>	26–34	Thulborn, 1982
<i>Coelophysis</i>	27–36	Thulborn, 1982
<i>Gallimimus</i>	27–36	Thulborn, 1982
<i>Deinonychus</i>	32–42	Thulborn, 1982
<i>Dromiceiomimus</i>	35–47	Thulborn, 1982
<i>Struthiomimus</i>	38–50	Thulborn, 1982
<i>Dromiceiomimus</i>	38–51	Thulborn, 1982
<i>Gallimimus</i>	42–56	Thulborn, 1982
<i>Teratosaurus</i>	10–14	Thulborn, 1982
<i>Megalosaurus</i>	10–15	Thulborn, 1982
<i>Ceratosaurus</i>	11–16	Thulborn, 1982
<i>Antrodemus</i>	13–18	Thulborn, 1982
<i>Albertosaurus</i>	14–20	Thulborn, 1982
<i>Tyrannosaurus</i>	16–23	Thulborn, 1982
<i>Tyrannosaurus</i>	36	Farlow et al., 1995
<i>Giganotosaurus carolinii</i>	50.4	Blanco and Mazzetta, 2001
<i>Tyrannosaurus</i> (Young)	39.6–50.4	Hutchinson, 2004
<i>Coelophysis</i>	32.4	Hutchinson, 2004
<i>Compsognathus</i>	64.08	Sellers and Manning, 2007
<i>Velociraptor</i>	38.88	Sellers and Manning, 2007
<i>Dilophosaurus</i>	37.8	Sellers and Manning, 2007
<i>Allosaurus</i>	33.84	Sellers and Manning, 2007
<i>Tyrannosaurus</i>	28.8	Sellers and Manning, 2007
<i>Tyrannosaurus</i>	56.52	Hutchinson et al., 2011
<i>Velociraptor</i>	54.54	Hirt et al., 2017
<i>Allosaurus</i>	40.752	Hirt et al., 2017
<i>Tyrannosaurus</i>	27.036	Hirt et al., 2017

7. Conclusion

The newly discovered running trackway from the Cretaceous Jingchuan Formation in Otog, Inner Mongolia, consists of

Table 3 The speed analysis of running theropod trackways worldwide^{a)}

Tracks	FL (m)	Hip height (m)	Stride length (m)	Speed 1 (km/h)	Speed 2 (km/h)	Location	Horizon	Notes
Track#1–5	0.075	0.30	0.97	13	10±1.2	South Africa	Jurassic	Bordy, 2021
T5	0.15	0.60	1.85	17	13±1.6	China	Jurassic	Zhang et al., 2004
T6	0.17	0.68	2.06	18	13±1.6	China	Jurassic	Zhang et al., 2004
T3	0.13	0.52	1.76	18	14±1.7	China	Jurassic	Zhang et al., 2004
T7	0.14	0.56	2.35	25	21±2.5	China	Jurassic	Zhang et al., 2004
T8	0.39	1.56	5.38	32	25±3.0	America	Jurassic	Lockley et al., 2021
C1	0.28	1.12	4.92	37	32±3.8	America	Jurassic	Irby, 1996
<i>Saltopoides igalensis</i>					34±4.1	France	Jurassic	Lapparent and Montenat, 1967 Navarro-Lorbés et al., 2021
T7	0.36	1.44	6.33	42	36±4.3	America	Jurassic	Lockley et al., 2021
T18	0.30	1.20	6.31	49	45±5.4	America	Jurassic	Lockley et al., 2021
<i>Skartopus</i>					10±1.2	Australia	Cretaceous	Thulborn and Wade, 1984 Navarro-Lorbés et al., 2021
LS-T7	0.14	0.56	1.98	20	16±1.9	China	Cretaceous	Xing et al., 2021
BLV→A3	0.37	1.48	5.385	34	27±3.2	America	Cretaceous	Farlow, 1981
Trackway A	0.33	1.32	5.00	34	27±3.2	China	Cretaceous	Li et al., 2011
La Torre 6A	0.33	1.32	5.23	36	29±3.5	Spain	Cretaceous	Navarro-Lorbés et al., 2021
Trackway B	0.21	0.84	3.93	35	31±3.7	Republic of Korea	Cretaceous	Kim and Huh, 2010
86→0–82	0.38	1.52	6.589	43	36±4.3	America	Cretaceous	Farlow, 1981
La Torre 6B	0.29	1.16	5.57	43	38±4.6	Spain	Cretaceous	Navarro-Lorbés et al., 2021
Q94→Q48	0.29	1.16	5.656	43	39±4.7	America	Cretaceous	Farlow, 1981
5–3	0.28	1.12	5.60	44	40±4.8	China	Cretaceous	Li et al., 2011
T1	0.2525	1.01	5.30	45	41±4.9	China	Cretaceous	This paper

a) Speed 1 is determined utilizing the formula established by Thulborn (1990), whereas Speed 2 is derived from the equation proposed by Ruiz and Torices (2013).

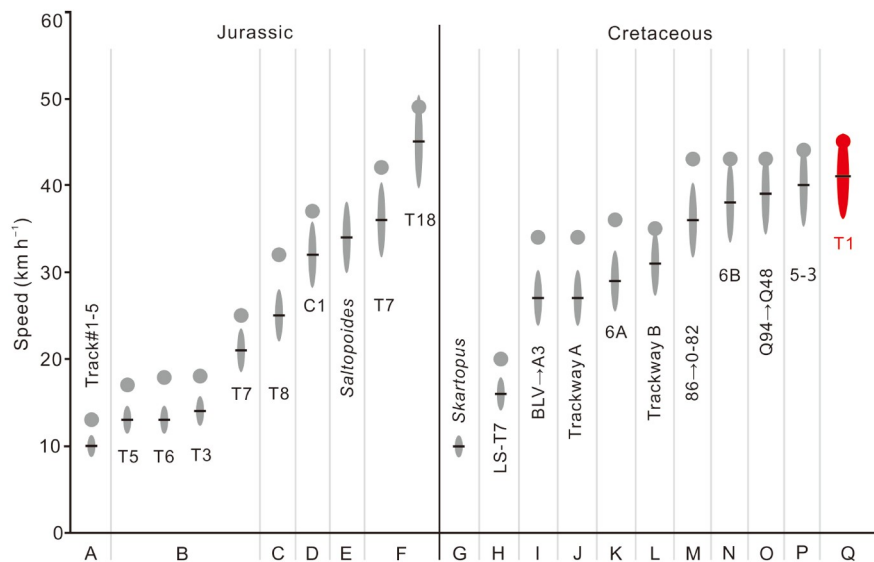


Figure 5 Speed comparison of Jurassic and Cretaceous running theropod trackways. The circles show speeds calculated using Thulborn (1990), while the ellipses represent speeds based on Ruiz and Torices (2013). The red symbols indicate the running trackway discovered in this study. The data A is from Bordy (2021), B is from Zhang et al. (2004), C is from Lockley et al. (2021), D is from Irby (1996), E is from Lapparent and Montenat (1967), Navarro-Lorbés et al. (2021), F is from Lockley et al. (2021), G is from Thulborn and Wade (1984), Navarro-Lorbés et al. (2021), H is from Xing et al. (2021), I is from Farlow (1981), J is from Li et al. (2011), K is from Navarro-Lorbés et al. (2021), L is from Kim and Huh (2010), M is from Farlow (1981), N is from Navarro-Lorbés et al. (2021), O is from Farlow (1981), P is from Li et al. (2011), Q is from this paper.

five consecutive footprints. A comprehensive morphological analysis has classified the trackway T1 into the ichnofamily Eubrontidae. Utilizing empirical formulas, the hip height of the trackmaker was estimated to be 101 cm, with a body length of 265.63 cm and an approximate body weight of 109 kg, indicating a mid-sized theropod dinosaur. Based on estimates of hip height and stride length, the trackmaker's running speed could reach 45 or 41 ± 4.9 km/h. This speed represents the fastest known theropod trackway in the Cretaceous period. Biomechanical modeling consistently indicates that large theropod dinosaurs (particularly those weighing over 1000 kg) typically employ walking or low-speed running gaits, whereas small and mid-sized theropods are capable of achieving greater running speeds. The running speed of the mid-sized theropod identified in this study aligns with predictions from existing biomechanical models for dinosaurs of comparable size, thereby providing substantial support for biomechanical research and further enhancing our comprehension of the locomotor capabilities of theropod dinosaurs.

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References

- Alexander R M N. 1976. Estimates of speeds of dinosaurs. *Nature*, 261: 129–130
- Alexander R M. 1989. Dynamics of Dinosaurs and Other Extinct Giants. New York: Columbia University Press. 167
- Alexander R M N. 1996. *Tyrannosaurus* on the run. *Nature*, 379: 121
- Alexander R M N, Langman V A, Jayes A S. 1977. Fast locomotion of some African ungulates. *J Zool*, 183: 291–300
- Bates K T, Manning P L, Hodgetts D, Sellers W I, Beckett R. 2009. Estimating mass properties of dinosaurs using laser imaging and 3D computer modelling. *PLoS ONE*, 4: e4532
- Blanco R E, Mazzetta G V. 2001. A new approach to evaluate the cursorial ability of the giant theropod *Giganotosaurus carolinii*. *Acta Palaeontol Pol*, 46: 193–202
- Bordy E M. 2021. Darting towards storm shelter: A minute dinosaur trackway from southern Africa. *S Afr J Sci*, 117, <http://doi.org/10.17159/sajs.2021/9145>
- Coombs W P. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Q Rev Biol*, 53: 393–418
- Day J J, Norman D B, Upchurch P, Powell H P. 2002. Dinosaur locomotion from a new trackway. *Nature*, 415: 494–495
- Dececchi T A, Mloszewska A M, Holtz T R, Habib M B, Larsson H C E, Cuff A. 2020. The fast and the frugal: Divergent locomotory strategies drive limb lengthening in theropod dinosaurs. *PLoS ONE*, 15: e0223698
- Dececchi T A, Kim K S, Lockley M G, Larsson H C E, Holtz Jr. T R, Farlow J O, Pittman M. 2024. Theropod trackways as indirect evidence of pre-avian aerial behavior. *Proc Natl Acad Sci USA*, 121: e2413810121
- Farlow J O. 1981. Estimates of dinosaur speeds from a new trackway site in Texas. *Nature*, 294: 747–748
- Farlow J O, Smith M B, Robinson J M. 1995. Body mass, bone “strength indicator,” and cursorial potential of *Tyrannosaurus rex*. *J Vertebrate Paleontology*, 15: 713–725
- Falkingham P L, Bates K T, Avanzini M, Bennett M, Bordy E M, Breithaupt B H, Castanera D, Citton P, Díaz-Martínez I, Farlow J O, Fiorillo A R, Gatesy S M, Getty P, Hatala K G, Hornung J J, Hyatt J A, Klein H, Lallensack J N, Martin A J, Marty D, Matthews N A, Meyer C A, Milàn J, Minter N J, Razzolini N L, Romilio A, Salisbury S W, Sciscio L, Tanaka I, Wiseman A L A, Xing L D, Belvedere M, McIlroy D. 2018. A standard protocol for documenting modern and fossil ichnological data. *Palaeontology*, 61: 469–480
- González Riga B J. 2011. Speeds and stance of titanosaur sauropods: Analysis of *Titanopodus* tracks from the Late Cretaceous of Mendoza, Argentina. *An Acad Bras Ciênc*, 83: 279–290
- Guo Q Y, Li Z Y, Yang S B, Yang L Z. 2006. Sedimentary characteristics of Cretaceous in northwestern Ordos basin (in Chinese). *Uran Geol*, 22: 143–150
- Henderson D. 2003. Footprints, trackways, and hip heights of bipedal dinosaurs—testing hip height predictions with computer models. *Ichnos*, 10: 99–114
- Hirt M R, Jetz W, Rall B C, Brose U. 2017. A general scaling law reveals why the largest animals are not the fastest. *Nat Ecol Evol*, 1: 1116–1122
- Hutchinson J R. 2004. Biomechanical modeling and sensitivity analysis of bipedal running ability. II. Extinct taxa. *J Morphology*, 262: 441–461
- Hutchinson J R, Garcia M. 2002. *Tyrannosaurus* was not a fast runner. *Nature*, 415: 1018–1021
- Hutchinson J R, Ng-Thow-Hing V, Anderson F C. 2007. A 3D interactive method for estimating body segmental parameters in animals: Application to the turning and running performance of *Tyrannosaurus rex*. *J Theor Biol*, 246: 660–680
- Hutchinson J R, Bates K T, Molnar J, Allen V, Makovicky P J, Claessens L. 2011. A computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontogeny, and growth. *PLoS ONE*, 6: e26037
- Irby G V. 1996. Paleoichnological evidence for running dinosaurs worldwide. In: Morales M, ed. The Continental Jurassic. Flagstaff: Museum of Northern Arizona
- Kim B S. 2002. Speeds and gaits of dinosaurs from the Cretaceous of Korea: With reference to the Hwasun Dinosaur site. Dissertation for Doctoral Degree. Gwangju: Chonnam National University
- Kim B S, Huh M. 2010. Analysis of the acceleration phase of a theropod dinosaur based on a Cretaceous trackway from Korea. *Palaeogeogr Palaeoclimatol Palaeoecol*, 293: 1–8
- Lapparent A F, Monténat C. 1967. Les empreintes de pas de reptiles de l'Infralias du Veillon (Vendée). Paris: Société géologique de France
- Li J J, Bai Z Q, Wei Q Y. 2011. On the Dinosaur Tracks from the Lower Cretaceous of Otog Qi, Inner Mongolia (in Chinese). Beijing: Geological Publishing House. 109
- Lockley M G. 2009. New perspectives on morphological variation in tri-dactyl footprints: Clues to widespread convergence in developmental dynamics. *Geol Q*, 53: 415–432
- Lockley M G, Li J J, Matsukawa M, Li R H. 2012. A new avian ichnotaxon from the Cretaceous of Nei Mongol, China. *Cretac Res*, 34: 84–93
- Lockley M G, Li J J, Xing L D, Guo B, Matsukawa M. 2018. Large theropod and small sauropod trackmakers from the Lower Cretaceous Jingchuan Formation, Inner Mongolia, China. *Cretac Res*, 92: 150–167
- Lockley M G, Breithaupt B H, Matthews N A, Shibata K, Hunt-Foster R. 2021. A preliminary report on an Early Jurassic *Eubrontes*-dominated tracksite in the Navajo Sandstone Formation at the Mail Station Di-

- nosaur tracksite, San Juan County, Utah. *N M Mus Nat Hist Sci Bull*, 82: 195–208
- Marty D. 2008. Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez3-Combe Ronde tracksite, NW Switzerland): Insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology. *GeoFocus*, 21: 1–278
- Navarro-Lorbés P, Ruiz J, Díaz-Martínez I, Isasmendi E, Sáez-Benito P, Viera L, Pereda-Suberbiola X, Torices A. 2021. Fast-running theropods tracks from the Early Cretaceous of La Rioja, Spain. *Sci Rep*, 11: 23095
- Olsen P E. 1980. Fossil great lakes of the Newark supergroup in New Jersey. In: 52nd Annual Meeting of the New York State Geological Association. Newark
- Prescott T L, Griffin B W, Demuth O E, Gatesy S M, Lallensack J N, Falkingham P L. 2025. Speed from fossil trackways: Calculations not validated by extant birds on compliant substrates. *Biol Lett*, 21: 20250191
- Ruiz J, Torices A. 2013. Humans running at stadiums and beaches and the accuracy of speed estimations from fossil trackways. *Ichnos*, 20: 31–35
- Sellers W I, Manning P L. 2007. Estimating dinosaur maximum running speeds using evolutionary robotics. *Proc R Soc B*, 274: 2711–2716
- Sellers W I, Pond S B, Brassey C A, Manning P L, Bates K T. 2017. Investigating the running abilities of *Tyrannosaurus rex* using stress-constrained multibody dynamic analysis. *PeerJ*, 5: e3420
- Thulborn R A. 1981. Estimated speed of a giant bipedal dinosaur. *Nature*, 292: 273–274
- Thulborn R A. 1982. Speeds and gaits of dinosaurs. *Palaeogeogr Palaeoclimatol Palaeoecol*, 38: 227–256
- Thulborn T. 1990. *Dinosaur Tracks*. London: Chapman & Hall
- Thulborn R A, Wade M. 1979. Dinosaur stampede in the Cretaceous of Queensland. *Lethaia*, 12: 275–279
- Thulborn R A, Wade M. 1984. Dinosaur trackways in the Winton Formation (Mid-Cretaceous) of Queensland. *Mem Queensl Mus*, 21: 413–517
- Weems R. 2006. Locomotor speeds and patterns of running behavior in non-maniraptoriform theropod dinosaurs. *N M Mus Nat Hist Sci Bull*, 37: 379–389
- Xing L D, Harris J D, Sun D H, Zhao H Q. 2009. The earliest known deinonychosaur tracks from the Jurassic-Cretaceous boundary in Hebei Province, China. *Acta Palaeontol Sin*, 48: 662–671
- Xing L D, Lockley M G, Mao Z F, Klein H, Gu Z F, Bai C D, Qiu L, Liu Y S, Romilio A, Scott Persons Iv W, Wan X Q. 2021. A new dinosaur track site from the earliest Cretaceous (Berriasian) part of the Tuchengzi Formation, Hebei Province, China: Implications for morphology, ontogeny and paleocommunity structure. *Palaeogeogr Palaeoclimatol Palaeoecol*, 580: 110619
- Zhang Y Z, Zhang J P, Wu P, Zhang X B, Bai S. 2004. Discovery of dinosaur track fossils from the Middle-Late Jurassic Tuchengzi Formation in the Chaoyang Area, Liaoning Province (in Chinese). *Geol Rev*, 50: 561–566, 667

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