Cretaceous Research 61 (2016) 1–4

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Short communication

A tyrannosaur trackway at Glenrock, Lance Formation (Maastrichtian), Wyoming

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ARTICLE INFO

Article history:
Received 5 September 2015
Received in revised form
20 December 2015
Accepted in revised form 30 December 2015
Available online xxx

Keywords:
Theropod
Ichnofossil
Tyrannosaurs
Tracksite

ABSTRACT

During the Campanian and Maastrichtian ages (86–66 million years ago), tyrannosaurids were the predominant large carnivorous dinosaurs throughout the Northern hemisphere. Despite the abundance of skeletal material, the fossil-footprint record of tyrannosaurids has been limited. Here we report a tyrannosaurid trackway in the Lance Formation, Wyoming. The trackway consists of three sequential tracks on a sandstone surface. Based on the age and size of the footprints, the trackmaker can be identified as either a sub-adult *Tyrannosaurus rex* or a *Nanotyrannus lancensis*. The trackway offers a record of a tyrannosaurid pace length, which permits the speed of the trackmaker to be calculated at 4.5–8.0 km/h. This result discounts previous speculation that tyrannosaurid walking speeds were notably slower than those of other large theropods.

1. Introduction

Although tyrannosaurids were widely distributed across Laurasia, their fossil track record is sparse, even in regions where their skeletal fossils are abundant. Of the few documented tyrannosaurid tracks, most are isolated single prints (Lockley and Hunt, 1994; Lockley et al., 2004; Manning et al., 2008; Lockley et al., 2011), and true tyrannosaurid trackways are extremely rare (McCrea et al., 2014). This ichnological scarcity is all the more frustrating given the many debates surrounding tyrannosaurid behavior and athleticism, to which track data have great potential to contribute. Naturally, of particular interest is the discovery of trackways attributable to the most heavily researched tyrannosaurid: *Tyrannosaurus rex*.

2. Locality and horizon

The Glenrock section of the Lance Formation (Maastrichtian) has lithology that is occasionally conducive to preservation of vertebrate tracks. The Glenrock section is estimated to be 728 m thick (Allen, 1990) and consists of yellow sandstones inter-bedded with gray shales and mudstones. Occasionally, the general lithology is broken by strong ridges capped by layers of fine sandstone secondarily cemented with iron and calcite. The relative hardness of these layers often result in wide exposures. One such exposure, approximately 300 mm thick and 300 m from the base of the formation (GPS coordinates: N 42 °, 52.964 min, West 105°, 51.266 min), contains the Glenrock tracksite (Fig. 1). As with many of the other cemented sandstone layers, ripple marks are prevalent across the tracksite surface. In addition to the theropod trackway described here, the Glenrock tracksite contains isolated large footprints that are identifiable as those of hadrosaurs and ceratopsians.

3. Description and diagnosis

The trackway consists of three large tridactyle tracks. The first of the three tracks is the best preserved (Fig. 2). Latex molds of the tracks are stored in the collection of the Glenrock Paleon Museum (catalog number: GPMtr01-03). The first track measures 470 mm across its anterior–posterior midline, spans 370 mm between the distal tips of digit II and IV, and is 190 mm in depth. The second and third tracks are less well defined and progressively shallower (170 mm and 130 mm deep, respectively). When first discovered, only the first track was fully exposed, while the

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http://dx.doi.org/10.1016/j.cretres.2015.12.020
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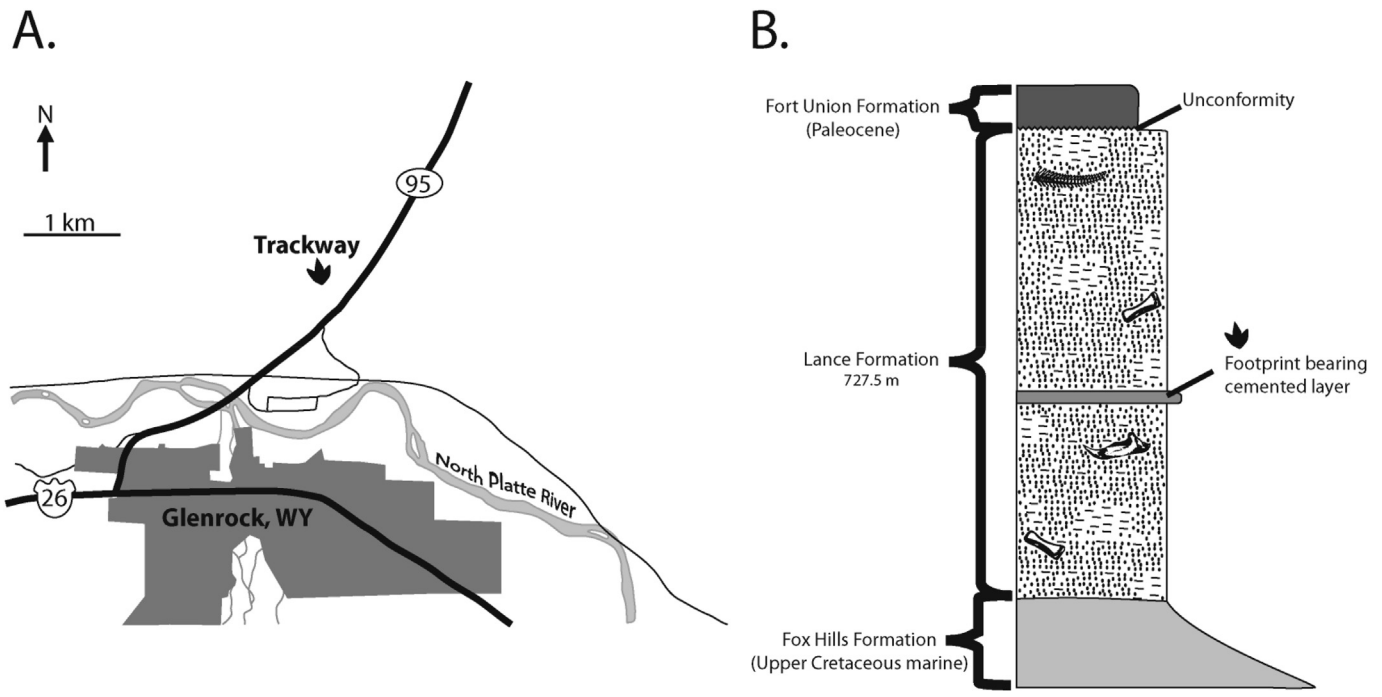

Fig. 1. Geographic and stratigraphic position of the Glenrock Trackway. A. Locality map, the trackway resides roughly two kilometers outside of the town of Glenrock. B. Stratigraphic profile.

second and third were buried in sediment. For this reason, the diminished quality and depth of the second and third tracks is interpreted as most probably reflecting an increase in the competency of the original track substrate across the trail, rather than the result of weathering. The three tracks are interpreted to be part of a single trackway based on the left-right-left arrangement and the similarity of track size, orientation, and spacing. The second track is not directly in line with the first and third, but is

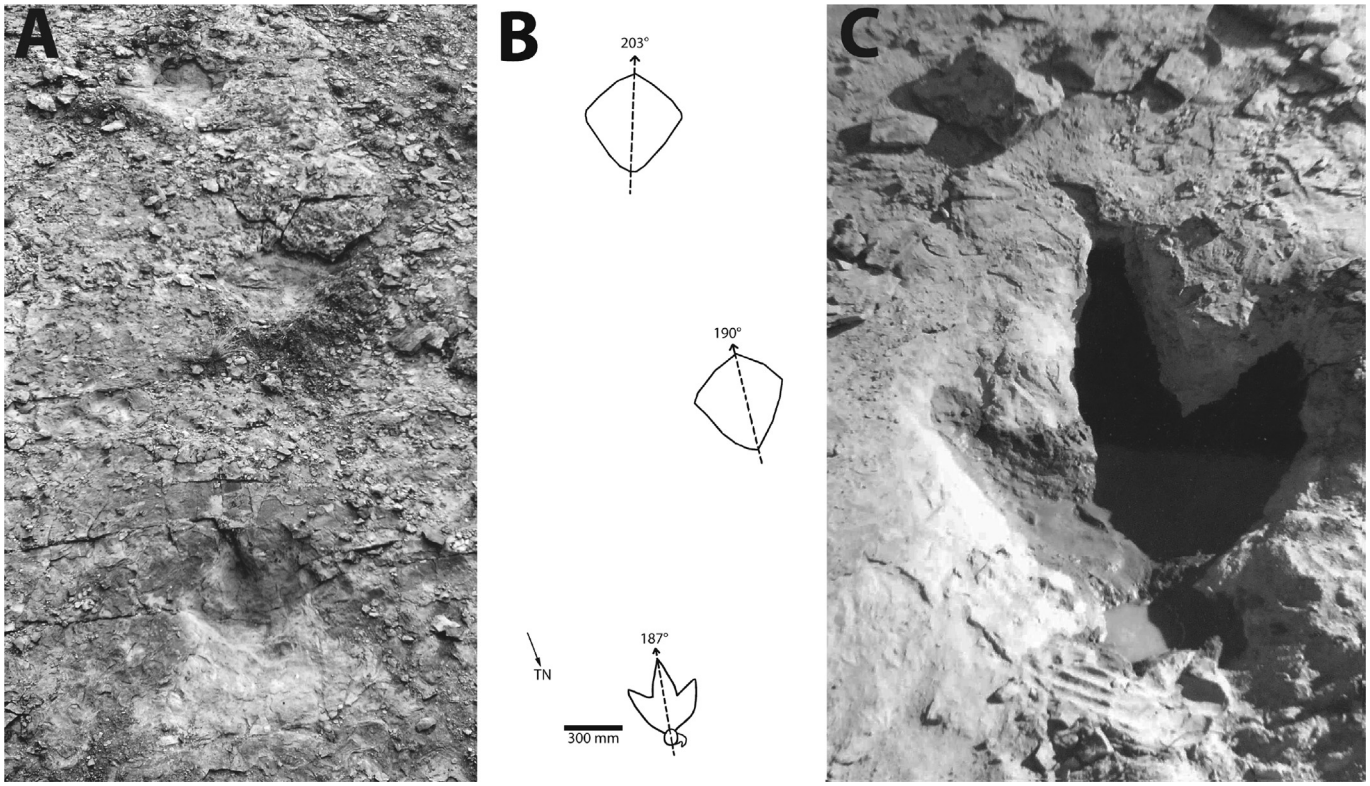

Fig. 2. The Glenrock Trackway. A. Photograph of the sandstone surface bearing the three prints. B. Diagram of the trackway, with track orientations denoted. C. Photograph of the first track, slightly wetted to reveal contours.

offset to the right (pace angulation 136 °), which is indicative of a walking gait (Day et al., 2002). The tracks are diagnosed as those of a theropod based on the following characteristics, as best observed in the first track: digits II, III, and IV are roughly equal in lateral width; digit III is substantially longer than both digit II and IV; all claw impressions have sharply angled tips; a prominent round heel impression is present, and an impression of a rear directed hallux (digit I) is preserved (Manning et al., 2008; Lockley et al., 2011).

The fossil faunas of the Lance Formation and similarly aged North American formations have been extensively worked, and the only know theropod genera large enough to be potential candidates for the trackmaker are the tyrannosaurids *Nanotyrannus* and *Tyrannosaurus*. The validity of the former genus is controversial and is thought by some to be an early ontogenetic stage of the latter (Carr, 1999; Larson, 2013). Putative skeletal material from both *Nanotyrannus* and *Tyrannosaurus* has been found in the Glenrock Section.

Even a conservative hip-height estimation derived for the Glenrock trackmaker exceeds that of the recently described large-bodied oviraptorosaurian *Anzu wyliei* (Lamanna et al., 2014) (see following section), and the presence of a hallux impression rules out the possibility that the track was made by an exceptionally large ornithomimid (Makovicky et al., 2004).

4. Speed estimation and discussion

Based on a range of modern animals, Alexander (Alexander, 1976) derived an equation for estimating the speed of a trackmaker of known hip height and stride length: $V = 0.25\sqrt{g}\cdot L^{1.67}\cdot H^{-1.7}$, where V is the velocity in meters per second, L is the length of the stride, H is the hip height of the trackmaker, and g is acceleration (9.81 m/s2). More recently, Ruiz and Torices (2013) re-examined the challenge of estimating speed from trackways offered a slightly modified equation: $V = 0.226\sqrt{g}\cdot L^{1.67}\cdot H^{-1.7}$. This new equation was derived strictly from a study of human trackmakers (Ruiz and Torices, 2013), but may, therefore, be a better choice for estimating speed in bipedal taxa. To estimate H, Alexander (1976) concluded that the hip height of a theropod trackmaker is generally equal to 4x track midline length. Alexander's method for estimating hip height is by far the most commonly used within the literature and has been supported by latter quantitative study (Henderson, 2003). However, it is an estimation generalized across all theropods. Tyrannosaurids are characterized by hind limbs that are proportionally longer than those of most other equivalently sized theropods (Holtz, 2004), and, to better refine tyrannosaurid track hip-height estimation, McCrrea et al. (2014) proposed the equation: $H = 29.8\cdot(\text{footprint length})^{0.711}$.

Excluding the length of the hallux and metatarsal heel pad, the midline length of the first track of the Glenrock trackway is 390 mm, and the hip height of the Glenrock trackmaker is estimated to be between approximately 1560 mm (as estimated using Alexander's method) and 2070 mm (using McCrrea et al. 's method). Of all reasonably complete Lancian-aged tyrannosaurid specimens, BMR (Burpee Museum of Natural History) P2002.4.1 is nearest in size to the Glenrock trackmaker. BMR P2002.4.1 has an estimated hip height (here measured as the summed length of the femur, tibia, and metatarsal III) of 2120 mm. Proponents of the validity of *Nanotyrannus* have considered BMR P2002.4.1 to be assignable to that genus (Larson, 2013), and BMR P2002.4.1 is the only presently described potential *Nanotyrannus* specimen with nearly complete hindlimb elements. The hip height of *Tyrannosaurus* exceeds 2800 mm among adults. Thus, the size of the Glenrock trackmaker falls near that of known specimens of *Nanotyrannus* but well below that of an adult *Tyrannosaurus*, and the trackmaker may be regarded as a *Nanotyrannus* or as a juvenile *Tyrannosaurus*.

As measured from heel base to heel base, the stride length between the first and the third Glenrock track spans 3330 mm. The speed of the Glenrock trackmaker is estimated at between 1.24 m/s (McCrrea et al.'s equation for estimating hip height and Ruiz and Torices equation for estimating speed) and 2.23 m/s (Alexander's equation for estimating hip height and Alexander's equation for estimating speed).

5. Concluding remarks

Previous walking speed estimations from large theropods (footprint length greater than 300 mm in length) generally range from 1 to 3 m/s (Thulborn, 1984; Day et al., 2002; Lingham-Soliar et al., 2003; Li et al., 2005; Gao, 2007; Li et al., 2011, Moreno, 2011). McCrrea et al. (2014) estimated the speed of another tyrannosaurid trackmaker at 1.84–2.36 m/s. Similarly, working from only an isolated tyrannosaurid track, but one with a lithologically continuous span in front of it, Lockley and Hunt (1994) offered a minimum speed estimation of 1.72–3.05 m/s. The range of speed estimations here reported for the Glenrock trackmaker overlaps that of McCrrea et al. (2014) and Lockley and Hunt (1994). Lockley et. al (2004) reported a segment of a possible tyrannosaur trackway from the Lance Formation, but recognized the doubtfulness of this assessment, because the two, or possibly three, tracks that comprised the alleged trackway are poorly preserved, part of a larger jumble of criss-crossing tracks of various taxa, and were unusually close together, suggesting that the trackmaker had an inordinately short stride. Nonetheless, this interpretation has been taken as evidence supporting the argument that tyrannosaurs were ponderous slow movers (Lockley et al., 2004). Both the tyrannosaurid trackway described by McCrrea et al. (2014) and the Glenrock trackway demonstrates the dubiousness of this prior track interpretation. The tyrannosaurid track record shows that tyrannosaurid stride lengths and walking speeds fell well within the range of other similarly sized theropods and affirms previous trackbases ecological inferences that tyrannosaur stride lengths and walking speeds exceeded those of their presumed hadrosaurid-prey (Currie, 1983, Persons and Currie, 2014).

Acknowledgments

We would like to extend thanks to our two reviewers, Dr. Peter Falkingham and Dr. Eric Snively, and to the editor, Dr. Eduardo Koutsoukos, for their highly constructive critiques.

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