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ORIGINAL RESEARCH

# Dinosaur Tracks from the Lower Jurassic Lufeng Formation of Northern Central Yunnan, China

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**ABSTRACT**
An increasing number of theropod-dominated tracksites have been reported from the Jurassic and Cretaceous of China. These include a significant number from the Lower Jurassic of the Lufeng Basin, famous for its *Lufengosaurus* fauna and known for a typical Lower Jurassic globally-distributed tetrapod footprint biochron. Here we report another localized theropod track occurrence regular of various scattered tracksites from the Lufeng Formation. The tracks are medium-sized tridactyl tracks from the basal member of the Zhangjia'ao Member, Lufeng Formation which shows an unusually wide divarication between the traces of digits III and IV, which suggest several possible interpretations.

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## Introduction

THE DINOSAUR FAUNA of the Lower Jurassic Lufeng Formation is often collectively referred to as the "*Lufengosaurus* fauna" (Dong, 1992). As the best-preserved Early Jurassic dinosaur fauna of East Asia, which also has the most incredible diversity, the *Lufengosaurus* fauna embraces basal sauropodomorphs, basal sauropods, theropods, basal thyreophorans (Xing et al., 2016a, b), and is dominated by the basal sauropodomorph *Lufengosaurus* (Mao et al., 2020). Tracks with high diversity have been reported from the Lower Jurassic stratum in Lufeng Basin, including theropod tracks including *Kayentapus*-type (Xing et al., 2016a), *Changpeipus carbonicus* (Xing et al., 2016b), *Eubrontes pareschequier* (Xing et al., 2009, 2014; Lockley et al., 2013); basal thyreophorans tracks including *Shenmuichnus wangi* (Xing et al., 2016a, b), and *Anomoepus*-type (Xing et al., 2016c). Xing et al. (2016b) considered, from present evidence, that the Lufeng Formation is a Type 3b or Type 4b deposit where both tracks and bones occur, with bones abundant, but indicating an inconsistency in the evidence they provide of faunal elements.

In 2021, staff from Lufeng Land and Resources Bureau went to Wanhailao village, Wande Town, Wuding County in the north-eastern Chuxiong Yi Autonomous Prefecture of Yunnan Province (GPS: 26°2’58.49”N, 102°10’13.71”E) and collected two dinosaur footprints (Fig. 1).

Fossil records in the Wuding area contained a lower jaw of *Lufengosaurus* (Young, 1966); hip, hind limbs, and vertebra of the basal sauropod *Kunmingosaurus wudingi,* which is a *nomen dubium* since it lacks formal description (Young, 1940; Li, 1998; Zhao, 1985; Barrett, 1999, Fang and Li, 2008). Additionally, there are records of the theropod *Sinosaurus triassicus* (Zhao, 1985)

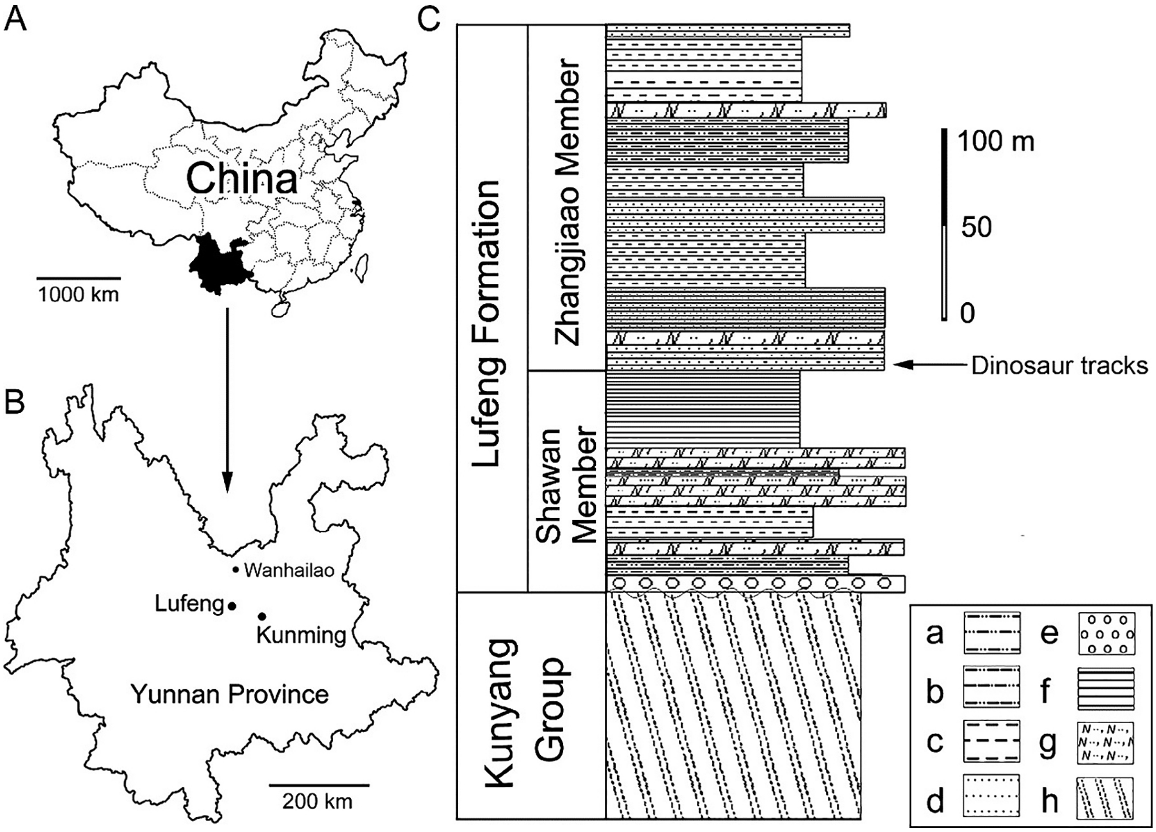


**Figure 1.** Location map. A, B) Location of Wanhailao tracksite in Yunnan Province, China. C) Stratigraphic section of Lower Jurassic–Cretaceous strata in the Lufeng Basin with the position of track-bearing levels. Key: a = pelitic siltstone; b = sandy mudstone; c = mudstone; d = sandstone; e = conglomerate; f = shale; g = orthomicrite; h = fossiliferous orthomicrite. Lithological succession was modified from Fang et al. (2000) and Xing et al. (2016c).

## Methods

The ex-situ surface was photographed (n=36) from various viewpoints with an iPhone 12 Pro Max (5.1 mm lens). Photographs were added to Agisoft Metashape Professional (v.1.6.3) for the creation of a virtual 3D model, which was then scale-corrected before being imported into Meshlab (v 2020.06) and automatically reoriented to the centre of the Cartesian coordinate system (Lallensack et al., 2020; Romilio, 2020). The surface topography was visualized using filters in Paraview (v 5.9.0) and CloudCompare (v 2.10.2), as shown previously (Xing et al., 2021).

## Geological setting

The exposed Red Beds in the Lufeng Basin are from the Lufeng Series, which was previously divided into the Lower Jurassic lower Lufeng Formation (dark purple beds) and the Middle Jurassic upper Lufeng Formation (deep red beds) (Bien, 1941; Sheng et al., 1962). Fang et al. (2000) reduced the stratigraphic range of the "Lufeng Formation" to what was previously known as the lower Lufeng Formation. They divided the redefined Lufeng Formation into the Shawan and Zhangjia'ao Members, which comprise a succession of mudstone, siltstone, sandstone, and limestone deposited in piedmont plain, lake and fluvial environments (Luo & Wu, 1995; Tan, 1997). The Wanhailao tracksite is preserved in a fluvial sandstone layer within the lower part of the Zhangjia'ao Member. According to biostratigraphic correlations, the age of this site belongs to the Early-Middle Early Jurassic (Hettangian–Pliensbachian) (Luo & Wu, 1995). In contrast, magnetostratigraphic analysis indicates a late Sinemurian Toarcian age (Huang et al., 2009).

## Ichnotaxonomy

## Description

There are two unambiguous tracks designated as WHL T1 and T2, preserved as natural casts (Figs. 2&3, Table. 1). Both are interpreted as good footprints with an intermediate quality of preservation: i.e., ~ 2.0 on the four-point (0-1-2-3) scale of Belvedere and Farlow (2016). This score indicates that details of pad traces are present but not considered optimum preservation suitable for detailed ichnotaxonomy analysis. Part of track WHL-T1 overlaps WHL-T2. The claw marks of digit II in WHL-T1 extended to the posterior, proximal side of the digit II trace in WHL-T1. In addition, the impression of WHL-T1 is more profound than WHL-T2, presumably demonstrating different registration times for two footprints of similar size, not attributed to the exact trackway. If WHL-T2 was formed before WHL-T1, the substrate moisture content mushy has increased after the registration of T2.

**Figure 2.** Photograph two theropod tracks from the Wanhailao site in Yunnan Province, China.

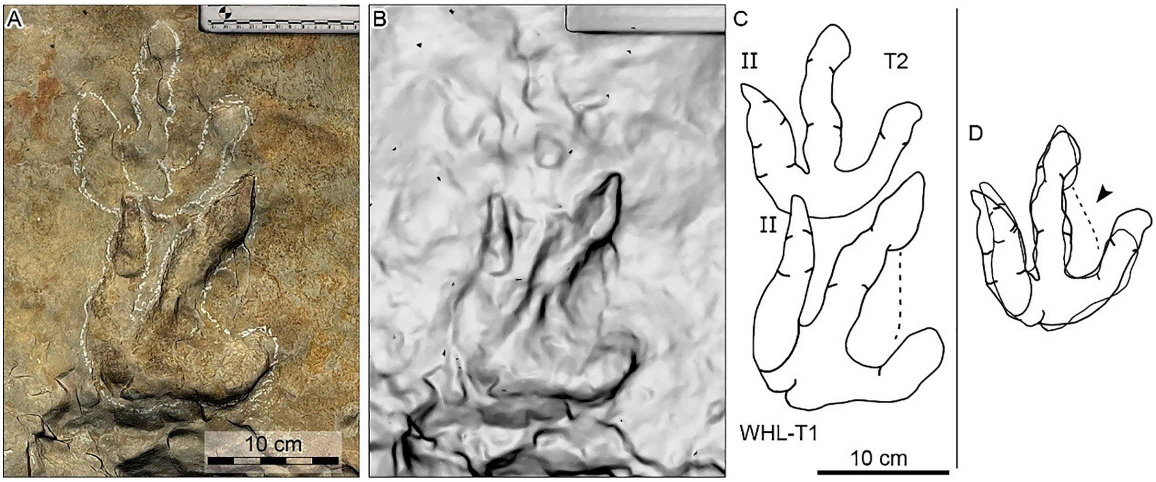


**Figure 3.** Photograph (A), contour map (B), interpretative outline drawing (C), and multiple overlays of track outlines (D) of Wanhailao tracks.

| Number | ML | MW | II-III | III-IV | II-IV | L/W | M |
|---|---|---|---|---|---|---|---|
| WHL-T1 | 20.5 | 15.5 | 28 | 37 | 65 | 1.3 | 0.61 |
| WHL-T2 | 14.7 | 13.8 | 34 | 39 | 73 | 1.1 | 0.47 |

**Table 1.** Measurements (in cm) of the dinosaur tracks from Wanhailao track site, Yunnan Province, China. Note: Abbreviations: ML: Maximum length; MW: Maximum width (measured as the distance between the tips of digits II and IV); II–IV: angle between digit II and IV; L/W is dimensionless; M: mesaxony.

WHL-T1 is the best-preserved track, with a length/width ratio of 1.3. Digit III is the longest, and the digit II trace, apparently showing two robust pad traces plus distal claw traces, is longer than the digit IV trace, with the distal tip of II situated more anteriorly than IV. The trace of digit III reveals only the two more distal pad traces, but the third proximal pad position is inferred at the midpoint of the track. The trace of digit IV has no distinct borders between the phalangeal pads. The metatarsophalangeal pad of digit IV is indistinct, but located in line with the axis of digit III. The divarication between digits II–III (28°) is smaller than that between digits III–IV (37°). The inner hypes between digits II and III is almost equal to the outer hypes between digits III and IV. The space between digits III and IV is notably more expansive than between digits II and III, a feature related to the preservation and the outward splay of digit IV.

WHL-T2 is also tridactyl, with a length/width ratio of 1:1, probably due to the incomplete registration and/or preservation of the heel trace. The 3D imagery highlights relatively narrow distal claw traces on all three digits. WHL-T2 has a wider divarication between digits II–IV (73°) than WHL-T1. The divarication between digits II–III (34°) is slightly smaller than that between digits III–IV (39°).

## Discussion

Theropod ichnotaxonomy is notoriously challenging due to the subtle similarities and variation in foot and track morphology. The field has a long history beginning with the study of Lower Jurassic Tracks in North America: see Hitchcock (1858), Lull (1953) for a summary of early work, and Olsen (1980), Olsen et al. (1998), Weems (1992) Lockley (2000) and Farlow (2018) for more recent treatments. These latter studies deal with the concept of the *Grallator-Anchisauripus-Eubrontes* (GAE) plexus and also recognize *Kayentapus* as a distinctive form (Weems, 1992). All these ichnotaxa have a global distribution in the Early Jurassic (Lucas, 2007). Early studies of well-preserved ichnofaunas from the Lower Jurassic of China named many new ichnotaxa (Zhen et al., 1986; Yang and Yang, 1987) regarded in most cases as cases of over splitting, provincial ichnotaxomomy (Lockley et al., 2013). Comparisons between Lower Jurassic Chinese ichnotaxa indicate that in many cases, they are synonyms of the aforementioned North America ichnotaxa, especially the GAE plexus. As a result, many Chinese ichnotaxa previously only recognized locally and inadequately described were placed in synonymy with more widely distributed and better documented GAE plexus and related forms. This makes ichnologist cautious in the identification and naming of theropod tracks. However, some other ichnogenera, notably *Changpeipus* were not synonymized into the GAE plexus, even though they have been compared with GAE plexus ichnogenera (Lockley et al., 2013).

Although the number of specimens is limited, WHL-T1 and T2 reveal some exciting features highlighted by the 3D imagery. For instance, in WHL-T1 the distance between digits III and IV is more comprehensive than between digits II and III: i.e., the ratio is ~1:3, while in typical tridactyl theropods it is ~1:1 (Lockley et al., 2013). This property, briefly explored here, is reflected in the divarication angles between digits, which may remember morphology, preservation or both. Such differences between digit divarication angles in WHL-T2 are not apparent. With only two available specimens, further inferences are not helpful for these specimens, even though such differences may be diagnostic in other trackways.

Digit divarication differences have been observed in living birds, such as emus *(Dromaius novaehollandiae),* in which digits II and IV almost share the same length. Still, the angle and space between digits III–IV are more comprehensive than the digits II–III angle (Milàn, 2006). The disparity between the interior angle and the lateral angle may link to the center of gravity when the animal is walking. Research on flightless fossil birds like emus has mainly focused on the foot and hip joints (e.g., Abourachid, 1991, Goetz et al., 2008) rather than foot morphology. But the parallelism between extant avian and non-avian theropod feet and footprints is well known (Farlow2018).

*Kayentapus* originally applied to relatively large (pes length ~35 cm) tridactyl tracks of a bipedal theropod dinosaur first described from the Lower Jurassic Kayenta Formation of Arizona (Welles, 1971). *Kayentapus* has narrower, more slender digit traces, with wider digit divarication (60–75° between digit II and IV in the holotype) than *Eubrontes* (Lockley et al., 2011). The wider digit divarication and mesaxony of Wanhailao materials are similar to *Kayentapus.* However, the Wanhailao materials lacked the essential identifying characteristics of *Kayentapus*: the preservation of the metatarsophalangeal pad of digit IV well separated from the rest of the digit impressions (Welles, 1971; Lockley et al., 2011).

The spacing between digits III and IV in WHL-T1 and somewhat in WHL-T2 is potentially reminiscent of *Lockleypus.* The spacing between digits III and IV in WHL-T1 and, to a lesser extent, in WHL-T2 is potentially reminiscent of *Lockleypus.* Xing et al. (2018) described some isolated theropod tracks from the Lower Cretaceous Dabeigou Formation of the Luanping Basin, Hebei Province, China. They named them *Lockleypus luanpingeris,* representing a medium-sized (~25 cm long), robust tridactyl theropod track type with unusual characteristics. The free length of digit IV is twice as long as the free length of digit II. The morphology of *Lockleypus* is significantly different from *Changpeipus* (Young, 1979), the latter which was generally used to describe Jurassic dinosaur tracks in Northern China.

However, the materials from the Wanhailao site are not abundant or well-preserved enough to suggest an ichnotaxonomic identification and the ichnogenus level. Moreover, to offer potential addition to the Early Jurassic theropod track record in Lufeng Basin would be speculative given the fact that the common Jurassic track types so far recognized include *Kayentapus*-type (Xing et al., 2016a), *Changpeipus carbonicus* (Xing et al., 2016b), and *Eubrontes paresche-quier* (Xing et al., 2009, 2014; Lockley et al., 2013).

There are two known theropods based on skeletal remains from the Lufeng area and its vicinity: the neotheropod *Sinosaurus* (Young, 1948, Hu, 1993; Xing, 2012) and the coelophysid *Panguraptor* (You et al., 2014). *Shuangbaisaurus* described by Wang et al. (2017), was thought to fall within the range of specimens assigned to *Sinosaurus triassicus* (Currie et al., 2019). This hints at the possibility that theropod track types are more diverse and abundant than skeleton records, which indicates the importance of track records to paleoecological biodiversity. Indeed the abundance, size range and diversity of theropod track morphotype in the Lower Jurassic of Yunnan Province, and more widely across China, strongly supports the inference that the track record indicates a variety more significant than that currently proven by the skeletal record in these same regions.

## Conclusion

A new tracksite occurrence from the Zhangjia'ao Member of the Lufeng Formation in Yunnan Province adds another theropod track occurrence to the Lower Jurassic ichnological record of the region. The tracks are challenging to identify ichnotaxonomically with any certainty. They come from the Lower Jurassic biochron zone in which the *Grallator-Eubrontes* plexus, *Kayentapus* and *Changpepus* tracks are known. These taxa are difficult to identify from small samples that are not optimally preserved. However, we note the large divarication between the traces of digits III and IV show a certain parallelism with certain large extant birds.

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