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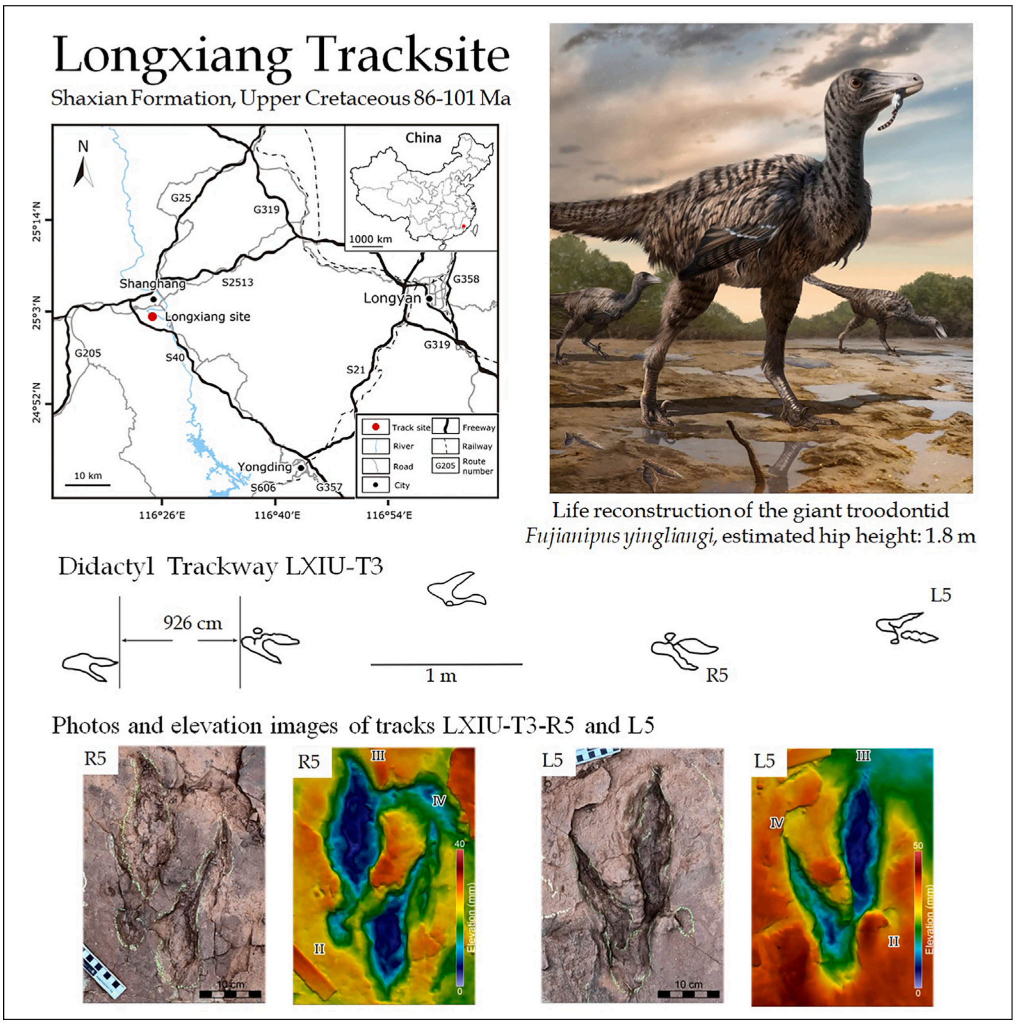

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Highlights

Distinctive two-toed fossil tracks at Longxiang site belong to "raptor" dinosaurs

The larger tracks (~36 cm long) establish a new dinosaur taxon: *Fujianipus yingliangi*

Standing an estimated 1.8 m at the hip, *Fujianipus* is among the largest known raptors

Based on relative toe-proportions, *Fujianipus* is identified as a probable troodontid

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Deinonychosaur trackways in southeastern China record a possible giant troodontid

Lida Xing,[1,2,9,*] Kecheng Niu,[3,4] Martin G. Lockley,[5] Anthony Romilio,[6] Ke Deng,[7] and W. Scott Persons IV[8,*]

SUMMARY

The Longxiang tracksite (lower Upper Cretaceous, Shanghang Basin) includes twelve didactyl deinonychosaur tracks that fall into two morphologies, differentiated by both size and form. The smaller tracks (∼11 cm long) are referable to the ichnogenus *Velociraptorichnus*. The larger tracks (∼36 cm long) establish the ichnotaxon *Fujianipus yingliangi*. Based on the size of the tracks, *F. yingliangi* has an estimated hip height of over 1.8 m, a size comparable to that of the largest known deinonychosaurs, i.e., *Austroraptor* and *Utahraptor*. The reduced form of digit IV, relative to digit III, indicates that *F. yingliangi* is a probable troodontid. Gigantism evidently evolved independently at least four times within the Deinonychosauria and within at least three major lineages: the Eudromaeosauria, Unenlagiidae, and Troodontidae. In the mid-Cretaceous of Asia, the evolution of *F. yingliangi* overlapped with that of early large-bodied tyrannosauroids and with previously established large allosaurids (although the latter may have been in decline).

INTRODUCTION

Due in large part to the group's close evolutionary relationship with Aves, the Deinonychosauria has been an intensely researched theropod clade.[1] As with many coelurosaurian lineages, deinonychosaurs appear to have originated at some point in the Late Jurassic, rose to greatest taxonomic diversity and obtained maximum body size during the Late Cretaceous, and have been recognized as a morphologically diverse group comparatively recently – thanks substantially to a slew of discoveries from eastern Asia.[1–5] Uniquely among non-avian theropods, deinonychosaurs typically held pedal digit II in a raised position. Along with the associated enlarged raptorial phalanx II-3, the raised digit II appears to have been a synapomorphy of the group and was retained in all currently known deinonychosaurian taxa. This characteristic has permitted the ready identification of didactyl theropod tracks as those of deinonychosaurs.[6–10] Didactyl deinonychosaur tracks have been recorded in China, Korea, Iran, Germany, the United States, Canada, Mexico, Argentina, and Bolivia,[7,11] and the deinonychosaur track record includes multiple instances of parallel trackways that have been interpreted as recording the passage of social groups.[6,9]

In the winter of 2020, the main authors of this paper discovered a large dinosaur track assemblage in Fujian Longyan, southeastern China.[12,13] Three main track layers were identified, and the site has been dubbed the Longxiang tracksite. One of the track layers contained three occurrences of didactyl tracks.

RESULTS AND DISCUSSION

The tracksite

Located along the outskirts of Longyan prefecture in the Fujian Province of China (Figure 1), the Longxiang tracksite is an exposure of the lower Shaxian Formation in the Shanghang Basin.[12,13] The Shaxian Formation was deposited in an alluvial fan/braided river/lacustrine environment.[14] Magnetic stratigraphy has dated the Shaxian Formation to 80–105 Ma,[15] and 206Pb/238U radiometric dating has narrowed this range to 86–101 Ma (with a weighted mean of 96.0 ± 4.1 Ma).[16] At the site, fossil tracks are abundantly preserved *in situ* as natural molds across three silty mudstone surfaces. Collectively, these track-bearing surfaces span roughly 1,600 square meters and contain over 240 identifiable dinosaur tracks. This includes tracks from ornithopods (*Hadrosauropodus* and cf. *Ornithopodichnus*), sauropods (cf. *Brontopodus*), and tridactyl theropods (cf. *Tridentigerpe*).[13]

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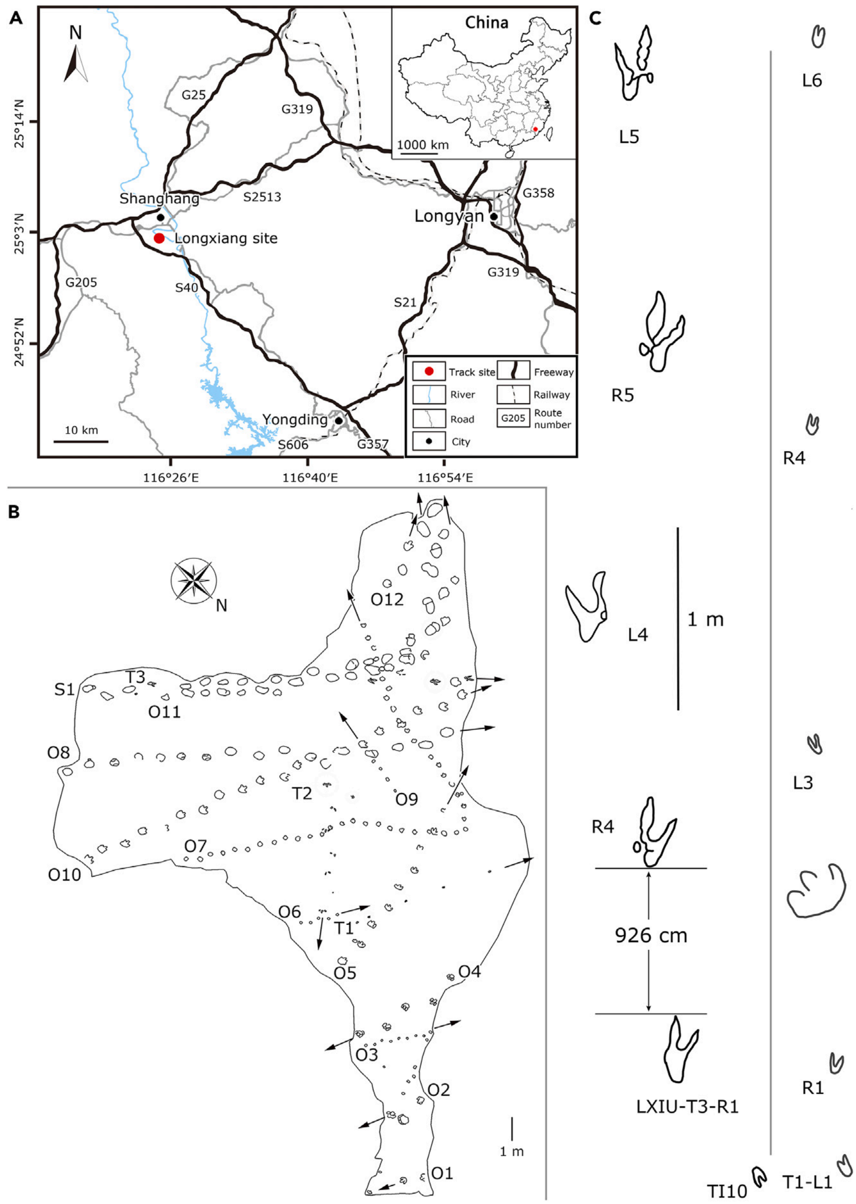

Figure 1. Overview of the Upper Cretaceous Longxiang tracksite

(A) Location of the site, within Fujian Province, China.

(B) Interpretative illustration of track-bearing surface.

(C) Interpretative outline illustrations of trackway LXIU-T3 and LXIU-T1.

Description and identification

The deinonychosaurian tracks preserved at the Longxiang tracksite fall into two size classes: 10–12 cm proximodistal length and 34–39 cm proximodistal length (Figures 2 and 3) (see Table S1). The specific lithology of the didactyl track layer is a light purple-red medium-thin layered muddy siltstone. Compared with the lower layers, the grain size of the track layer is significantly finer. Wavy and horizontal bedding is developed in the track layer, and fine surface features, such as ripple marks, rain marks, and invertebrate burrows, are preserved.[13,14] No tracks were found in the above layer, and the larger sauropod and ornithopod tracks on the same layer have obvious mud rims.[13] As such, the didactyl tracks do not appear to be undertracks and the size of the tracks is here assumed to roughly correspond to the true size of the trackmaker digits.

The smaller didactyl tracks (Figure 2) consist of a five-print trackway (cataloged as LXIU-T1- L1, R1, L3, R4, and L6) and a single isolated track (cataloged as LXIU-TI10). The LXIU-T1 trackway spans 6.3 m; however, the tracks are discontinuous, with L2, R2, R3, L4, L5, and R5 either not

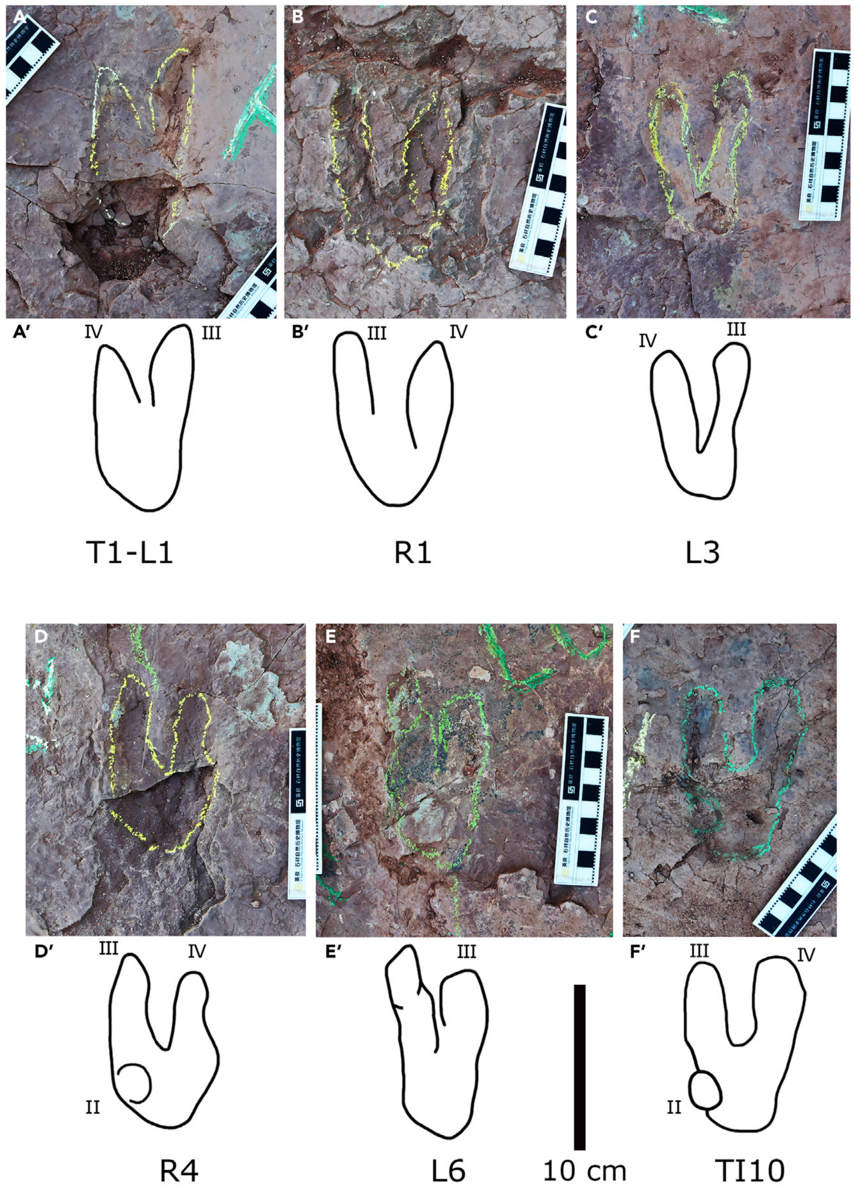

Figure 2. Photographs and interpretive outlines of select smaller didactyl tracks preserved at the Longxiang tracksite
Photographs (A-F) and interpretive outlines (A′-F′) of select smaller didactyl tracks preserved at the Longxiang tracksite.

preserved or obscured by overlapping dinosaur prints. The smaller tracks have an average length of 10.9 cm and a length/width ratio of 2.4. Each track is elongated with a short, rounded heel trace. The impressions of digit III are slightly longer than those of digit IV. There are no recognizable digit pads. All claw impressions are sharp, especially those of digit III. The metatarsophalangeal region is large, semicircular, and is not separated from the digit traces by a distinct border. LXIU-T1-R4 is the best preserved, showing a faint digit II impression that connects with the imprint of digit III at the proximomedial edge. The average divarication angle between digits III and IV is 24°.

Compared to tridactyl theropod tracks, the known diversity of deinonychosaurian ichnotaxa is low (Figure 4). Small deinonychosaurian ichnospecies include *Velociraptorichnus sichuanensis*,[11,17] *Velociraptorichnus zhangi*,[18] *Menglongipus sinensis*,[17] *Dromaeosauripus jinjuensis*,[19] and *Dromaeosauriformipes rarus*[19]—see Lockley et al.[7] for a review. Among these, *Velociraptorichnus zhangi* is inferred to sometimes be represented by tridactyl traces, *Dromaeosauripus jinjuensis* lacks a heel pad, and *Dromaeosauriformipes rarus* and *Menglongipus sinensis* are extremely small (∼1 and ∼6 cm in length, respectively).[17] The small Longxiang didactyl tracks are comparable in size and form to *Velociraptorichnus sichuanensis* (the length of the type specimen being 11 cm) and to most *Velociraptorichnus* isp. previously known from China (typically ∼10 cm long) (see Table S2). *Velociraptorichnus* is characterized by relatively thick digit traces (with digit III of the holotype having a length-to-width ratio of ∼1.9) and by the absence of well-defined digit pad traces—all features present in the smaller Longxiang didactyl

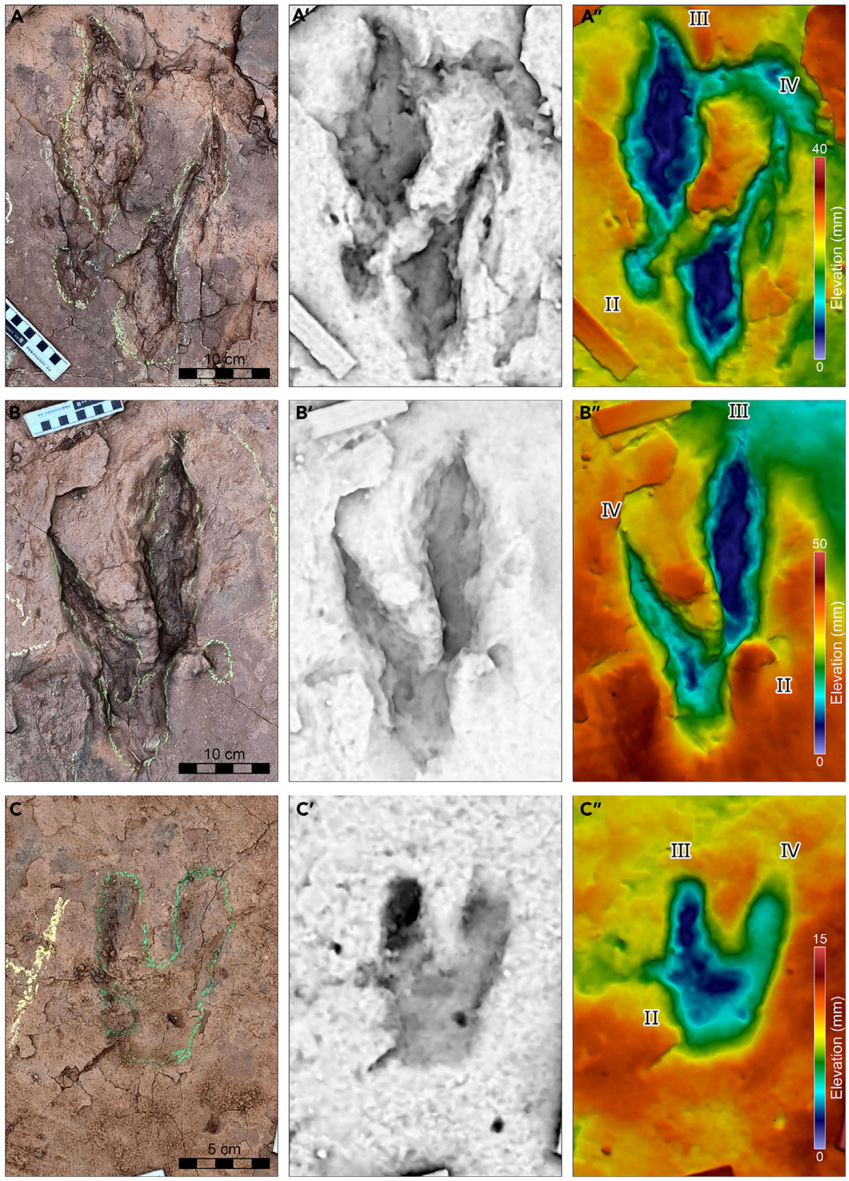

Figure 3. Details of select larger didactyl tracks preserved at the Longxiang tracksite I

Orthographic photographs (A–C), ambient occlusion images (A′–C′), and elevation images (A″–C″) of the deinonychosaur tracks LXIU-T3-R5, L5 and TI10.

tracks. Additionally, the divarication angle between the traces of digits III and IV of *Velociraptorichnus* (24° in the holotype) is consistent, as is the track length/single pace length ratio of *Velociraptorichnus* trackways (~5)[17] and the roughly equal lengths of digits III and IV (both 6.4 cm long in the *Velociraptorichnus* holotype). However, the comparably poorer preservation of the smaller Longxiang tracks makes classification to the ichnospecies level problematic,[20] and LXIU-T1 and LXIU-TI10 are here assigned simply to *Velociraptorichnus* isp.

The five larger Longxiang didactyl tracks all belong to a single trackway (cataloged as LXIU-T3), which spans 14.3 m. The last four tracks are in a continuous sequence, and a gap of over 9 m separates the first track from the others. All LXIU-T3 tracks have the same general morphology, with L5 being the best preserved (Figure 5). The average length of the five tracks is 36.4 cm (from 34.7 to 39 cm), and the average width is 16.8 cm (from 14.2 to 19 cm). The mean step length is 128 cm, and the mean pace angulation is 166°. LXIU-T3-R1 is a significantly deeper track, with a longer and more deeply penetrating digit IV claw trace, indicating the track was left in a region of slightly softer sediments.

In size, the closest named deinonychosaurian ichnospecies is *Dromaeopodus shandongensis*.[6] However, even *D. shandongensis* is roughly 20% smaller and differs in various morphological details: in *D. shandongensis* the digit II traces are not isolated; the proximal portion of the digit II depression is medial to the anterior margin of the heel pad and posteromedial to the margin of digit III; digits III and IV consistently

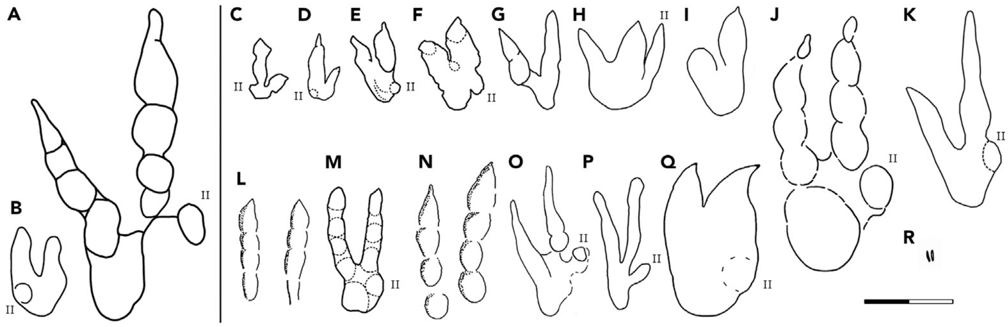

Figure 4. Interpretative outline drawings of deinonychosaur ichnotaxa

All tracks are drawn to the same scale, scale bar = 10 cm.

(A) Deinonychosaur track LXIU-T3-L5 from Longxiang area.

(B) Deinonychosaur track LXIU-TI10 from Longxiang area.

(C) *Menglongipus sinensis* from Hebei (Xing et al., 2009a).

(D) *Menglongipus* isp. from Shandong (Xing et al., 2018a).

(E) *Velociraptorichnus* from Shandong (Li et al., 2008).

(F) *Velociraptorichnus sichuanensis* (Xing et al., 2009a).

(G) *Velociraptorichnus* isp. from Sichuan (Xing et al., 2015a).

(H) *Velociraptorichnus zhangi* from Sichuan (Xing et al., 2015a).

(I) Probable troodontid track from Alberta (Enriquez et al. 2021).

(J) *Dromaeopodus shandongensis* from Shandong (Li et al., 2008).

(K) Troodontid track A2 from Obernkirchen, Germany (Lockley et al., 2016).

(L) *Dromaeosauripus jinjuensis* from Korea (Kim et al., 2012).

(M) *Dromaeosauripus yongjingensis* from Gansu (Xing et al., 2013a).

(N) *Dromaeosauripus hamanensis* from Korea (Kim et al., 2008).

(O) Didactyl tracks from the Plainview Sandstone at Dinosaur Ridge (Lockley et al., 2016b).

(P) *Sarmientichnus* isp. from Shaanxi (Xing et al., 2018b).

(Q) *Dromaeosauripus* isp. from Jishan (Xing et al., 2013b); and (R) *Dromaeosauriformipes rarus* from Korea (Kim et al., 2018). Note: A, C, D, I, K, and O all have a digit IV that is substantially shorter than digit III and, on this basis, may be attributable to troodontids, rather than dromaeosaurids.

curve medially; and the digit III and IV impressions are nearly parallel, are equivalent in length, and have a divarication angle of $\sim$5–10°—vs. 27° in the larger Longxiang didactyl tracks.[6] The larger Longxiang didactyl tracks are morphologically distinct from all previously described ichnogenera and are here used to establish the new taxon *Fujianipus yingliangi* (ZooBank: BA88C3D1-2315-4935-AA2F-08316F2974B0).

Systematic paleontology

Deinonycosauripodidae ichnofam. nov

Referred material "Dromaeopodidae" Li et al., 2008

Remarks

When Li et al.[6] proposed the ichnofamily "Dromaeopodidae", the clear implication was that it encompasses didactyl tracks attributable to dromaeosaurs but not to all other deinonychosaurids. As such, a more inclusive classification is needed for deinonychosaurid tracks that either cannot be confidently identified to a particular deinonychosaurian subgroup (including the Dromaeosauridae) or that can be identified as likely belonging to any non-dromaeosaur deinonychosaurid. To accommodate this current ichnotaxanomic need, the superichnofamily Deinonycosauripodidae is proposed (see the subsequent section). Ichnofamilies are widely regarded (including by the ICZN) as generalized if not informal categories. Nevertheless, it is likely, given the rate at which new instances of didactyl theropod tracks are being discovered, that recognizing further ichnotaxonomic designations for non-dromaeopodid deinonychosaurian tracks—e.g., troodontid tracks = "Troodontipodidae"—will become useful. However, such a new ichnotaxon is not formally proposed here, because, prior to the present study, no ichnogenus or ichnospecies inferred as attributable to troodontids has been named and it is the opinion of the authors that the diagnosis of such an ichnofamily would benefit from delay until additional referable taxa are recognized and described. It is, however, worth noting many previously documented deinonychosaurid tracks, including those referred to existing ichnotaxa, do show the proportionately short digit IV that its suggestive of a troodontid affinity, these include deinonychosaurid tracks from Alberta;[21] Obernkirchen, Germany;[7] and Dinosaur Ridge, USA;[22] and *Menglongipus sinensis* from Hebei;[17] and *Menglongipus* isp. from Shandong[9] (see Figure 4).

Since 2008, Lockley et al.[7,22] have reported 16 deinonychosaurian track occurrences from the Cretaceous of China, Korea, the USA, Canada, Germany, and Poland, and an additional $\sim$15 sites have been reported from China and Korea between 2017 and 2023.[8,12,19,23–26] Although these deinonychosaurian tracks have mostly been attributed to dromaeosaurs, the German and Canadian tracks have been

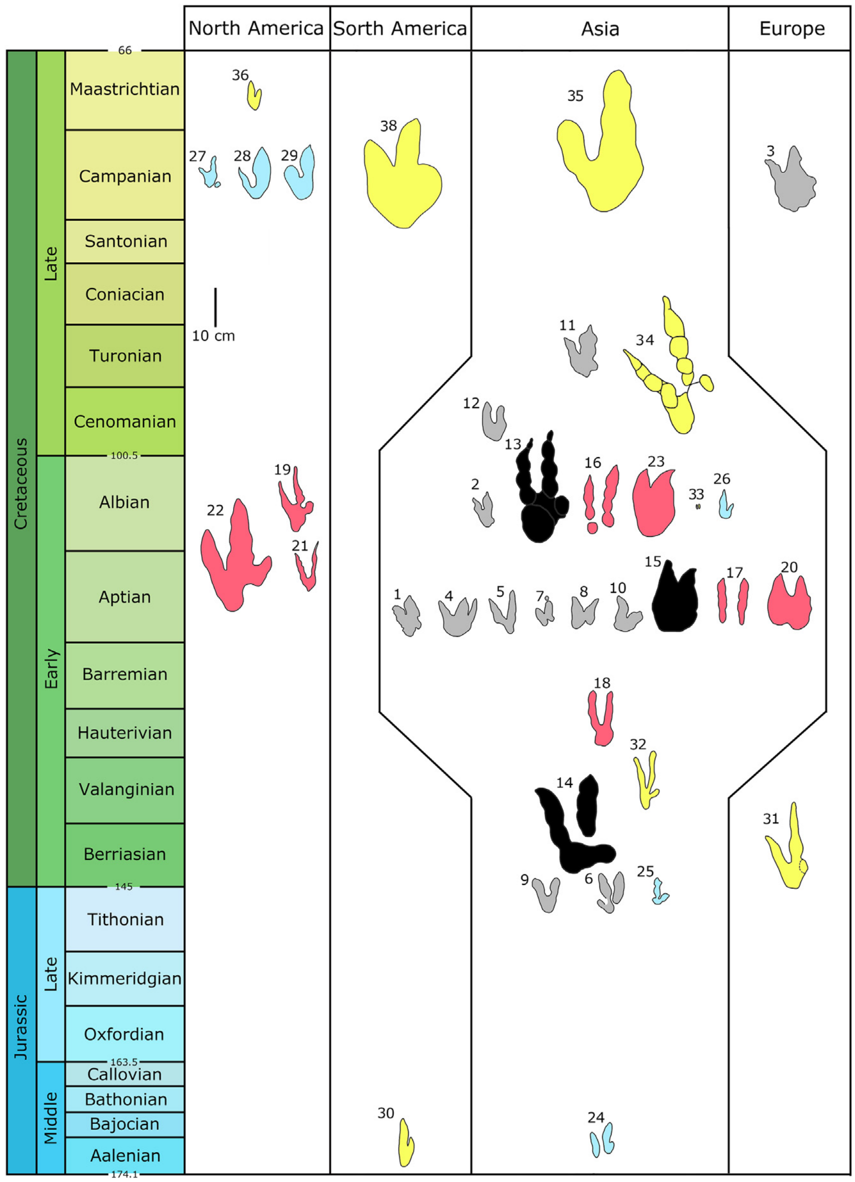

Figure 5. Morphology, age, and geographic distribution of Mesozoic deinonychosaur tracks (numbers correspond to Table S2)

recognized as likely having troodontid affinity.[7,21] The probable troodontid affinity of the large tracks described here highlights the variation in curvature of deinonychosaurian digit traces, which may be due to both actual foot morphology and/or the effects of registration dynamics. The German tracks, like the Longxiang tracks described here, differ from others in having straighter, rather than curved digit traces, although small *Velociraptorichnus* tracks may also have straight digit traces. Thus, digit curvature may be, in part, a function of size and/or preservation as discussed in the following text.

With the exception of *Menglongipus*, which is characterized by uniquely short digit IV impressions,[17] all deinonychosaurian tracks have been accommodated in three ichnogenera (*Velociraptorichnus*, *Dromaeosauripus*, and *Dromaeopodus*). The ichnogenus *Dromeosauriformipes*[19] can be added but it is minute, enigmatic and, as the name and description affirm, only "dromaeosaur-like." With the addition of *Fujianipus* ichnogen. nov. the diversity of deinonychosaurian ichnotaxa remains low (3–5 ichnogenera and ~7 ichnospecies).

Diagnosis of superichnofamily Deinonychosauripodidae

Distinctive didactyl tracks of theropod affinity with narrow trackways, which register only digits III and IV as full, typical impressions. Digit II trace is absent, registered only proximally in the metatarsal phalangeal pad region, or is preserved such that the long and laterally compressed form of the digit II ungual is apparent. Digit III and IV both straight or curved inwards (concave medially). Deinonychosauripodidae includes the previously defined ichnofamily "Dromaeopodidae", which is here amended to sub-ichnofamily status.

Dromaeopodinae Li et al. 2008 amended

"Dromaeopodidae" Li et al.[6] is here amended to the subichnofamily Dromaeopodinae:

Narrow, didactyl tracks of a biped with digit III only slightly longer than IV, and digit II represented by no impression or by a short, round impression posteromedial to free part of digit III.

Deinonycosauripodidae ichnofam. nov

Fujianipus ichnogen. nov. (ZooBank: BA88C3D1-2315-4935-AA2F-08316F2974B0)

Type material

LXIU-T3, a trackway composed of five tracks, four of which are consecutive.

Etymology

Fujianipus means "tracks from Fujian Province," and *yingliangi* acknowledges the Yingliang Group, China, and the Yingliang Stone Natural History Museum, which launched this investigation and houses the resin and digital copies.

Type horizon and locality

Longxiang tracksite I, Shaxian Formation, Longyan City, Fujian Province, China.

Differential diagnosis for ichnogenus

Large functionally didactyl track, up to ~36.0 cm long with digit III and IV traces straight and divergent. Proximal trace of digit II is subrounded to elliptical with the proximal pad not clearly connected to the heel print. Diagnostically distinct from *Dromaeopodus*, the largest previously known deinonychosaurian track, which has curved, sub-parallel digit III and IV traces and larger, more robust heel pad traces.

Fujianipus yingliangi ichnosp. nov (ZooBank: BA88C3D1-2315-4935-AA2F-08316F2974B0)

Description

Large (~36.4 cm long and ~16.9 cm wide) didactyl tracks with slender digit impressions. Digital pad impressions are well developed and with a formula of x-1-3-4-x. Digit III is 1.2 times longer than IV. Digit III traces with a higher forward-facing degree than digit IV. Distinct sharp claw impressions in digit III and IV. Digit II is an elliptic print, with the distal end near the proximal end of digit III and the proximal end not connected to the heel print. A sub-oval heel composes roughly one-fourth of the posterior length. Narrow (27°) divarication angle between digits III and IV. Pes impressions nearly parallel to the trackway axis (~6.5 degrees of rotation).

Two large (28.0 and 39.0 cm long) didactyl tracks have been previously reported from the Late Cretaceous Nanxiong Basin, southwest of the Longxiang tracksite;[27] however, the apparent didactyl nature of these tracks was previously considered ambiguous and possibly attributable to incomplete preservation. In light of the large Longxiang trackway, these morphologically consistent tracks are tentatively referred to cf. *Fujianipus*.

The co-occurrence of the smaller *Velociraptorichnus* isp. and the larger *F. yingliangi* tracks raises the possibility that the trackmaker of the former is a juvenile of the latter. However, this seems unlikely, given the differences in form between the two. Rather, two deinonychosaur taxa of disparate sizes appear to have been concurrent in the region. Similarly, the cooccurrence of *Velociraptorichnus* isp. and *Dromaeopodus* was reported from the Junan County site in Shandong province.[28]

The *Velociraptorichnus* isp. and *F. yingliangi* tracks also appear to represent different major deinonychosaurian groups. Compared with the typical condition in eudromaeosaurians, pedal digit IV of troodontids is reduced relative to digit III. This trait has been previously used to identify probable troodontid trackmakers in the case of didactyl tracks from the Bückeberg,[7,21] Xiaoba,[9] and Wapiti formations.[21] On this basis, the *Velociraptorichnus* isp. tracks are interpreted as eudromaeosaurian and the *F. yingliangi* tracks are interpreted as most probably troodontid.

Size and speed estimation

Alexander[29] proposed the classic formula for estimating dinosaur speed from trackways and associated ratios between footprint length and hip height. Since then, many scholars have proposed more precise ratios specific to different dinosaur groups[30,31] and based on different parameters.[32] Tsukiji et al.[8] used five species of deinonychosaurs to propose the hip-height/foot-length ratios of 4.32 for dromaeosaurids and 5.47 for troodontids. Applying the dromaeosaurid hip-height/foot-length ratio to the Longxiang tracksite *Velociraptorichnus* isp. tracks and the troodontid hip-height/foot-length ratio to the Longxiang tracksite *Fujianipus* tracks, yields estimated average hip heights of ~47 cm and ~197 cm, respectively. Note, because the ratio calculations of Tsukiji et al.[8] were based on typical smaller-sized troodontids and because distal leg length scales at a reduced non-allometric rate with theropod body size,[33] this hip height estimation is, in the case of

Fujianipus, likely an overestimation and is best interpreted as the upper limit of the reasonable size range. Applying the dromaeosaurid hip height/foot length ratio to the *Fujianipus* tracks yields a hip height estimation of ∼156 cm, and applying the standard equation for estimating hip height in small/medium theropods (h = 3.06 FL^1.14) yields an estimation of ∼184 cm. Thus, the hip height of the *Fujianipus* track maker is estimated to fall within the range of 156–197 cm and can be confidently assumed to have exceeded 1.5 m.

An alternative method for estimating the size of the trackmakers is to consider the relationship between foot length and total body length. The ratio between the proximodistal length of phalanges 2–4 of digit III and deinonychosaur body length is 5.11% on average (see Table S3). This value varies for different groups within the deinonychosauria, with the Unenlagiidae having the lowest ratio and the Troodontidae the highest. Using the average ratio, the body length of the *Velociraptorichnus isp*. trackmaker is estimated at ∼1 m (6.5/5.11%) and the *Fujianipus* trackmaker is estimated at ∼5 m (26/5.11%), respectively.

Both the Longxiang site *Velociraptorichnus* isp. and *Fujianipus* trackways have relatively short stride lengths, consistent with walking or trotting gaits. Using the formula of Alexander,[29] the speeds of the trackways are respectively estimated at 7.74 km/h and 7.34 km/h. This speed estimation is not unusual, low speeds are commonly inferred from deinonychosaur trackways and theropod tracks in general.[9,34] This reflects the facts that animals engage in vigorous motion only on rare and brief occasions and that many tracks preserved in the fossil record were initially left in viscous substrates, through which animals were naturally inclined to walk at atypically slow speeds. In the case of *Fujianipus* the tracks are generally deeper than those of *Dromaeopodus,* however, the step/maximum-footprint-length ratio (∼128/36 cm and ∼100/28 cm, respectively) is very similar, at ∼3.5 in both cases.

Deinonychosaur gigantism and troodontid affinity

The oldest and earliest diverging deinonychosaurs come from Late Jurassic deposits and are among the smallest of known non-avian theropods.[35,36] By the Late Cretaceous, the Deinonychosauria was globally distributed and had split into five major non-avian lineages: the Eudromaeosauria, Halszkaraptorinae, Microraptoria, Unenlagiidae, and Troodontidae. Although many early and basal members of these groups were small and the possibility of arboreal/flight capabilities has been proposed as basal for deinonychosaurs,[5,35,37,38] many later forms were larger and predominantly ground-dwelling predators.[39,40] Unusually for a diverse and widely successful clade of carnivorous non-avian theropods, most deinonychosaurs retained relatively small absolute body sizes, with a majority of genera estimated to measure under three meters in total length.

Exceptions to this size restraint include the unenlagiine *Austroraptor* from the Allen Formation (middle Campanian to early Maastrichtian)[41] and the eudromaeosaurians *Achillobator* from the Bayan Shireh Formation (Albian-Santonian),[42] *Dakotaraptor* from the Hell Creek Formation (Maastrichtian),[43] and *Utahraptor* from the Cedar Mountain Formation (Berriasian-Cenomania).[39] *Ulughbegsaurus* from the Bissekty Formation (Turonian) is an additional potential giant deinonychosaur,[44] and isolated troodontid teeth from the Prince Creek Formation (Maastrichtian) suggest another.[45]

Of these, *Achillobator* and its specific lineage is a candidate for the Longxiang site *Fujianipus* trackmaker, as the current temporal range of the Shaxian and Bayan Shireh formations overlap and a biogeographic distribution from Mongolia to southeastern China is entirely feasible for such a large theropod. However, *Achillobator* definitively falls within the Eudromaeosauria (having, among other features, the key synapomorphy of elongate and branching caudal zygapophysial and chevron rods),[42] while the proportionately shorter digit IV of *Fujianipus* indicates a troodontid affinity.

The gigantism of deinonychosaurs implies increased predatory ability and a shift toward larger prey.[39] Based on the track record, *Fujianipus* coexisted with medium-sized iguanodonts, smaller ornithopods, and multiple species of smaller theropods. It is noteworthy that, in early Late Cretaceous Asia both the deinonychosaur and tyrannosauroid lineages were experimenting with increased body size and were invading niches further up the food chain.[46–48] Whether this was an adaptational reaction to an ecological vacuum created by a decline in the prevalence/diversity of allosauroids (which had been the dominant large-bodied carnivores starting in the Late Jurassic) or the result of both deinonychosaurs and tyrannosauroids competitively replacing allosauroids due to some mutually shared coelurosaurian advantages remains unclear. Future work narrowing down the timing of both radiations and of the allosauroid decline is key to answering this question.

Limitations of the study

The specific ages of layers within the Shaxian Formation remain poorly resolved. This lack of temporal resolution limits this study's ability to place the tracksite, and the instance of deinonychosaur gigantism that it records, in larger evolutionary context. The size and speed estimations presented here are based on small sample sizes, and caution should be taken in assuming that the estimations are truly typical for the taxa. The possible affinity between *Fujianipus yingliangi* and *Achillobator giganticus* cannot be directly tested, because complete pedal material is not currently known for *A. giganticus*. As such, it is an assumption of this study that *A. giganticus* conformed to the typical pedal morphology of other dromaeosaurids and did not have a digit IV that was reduced relative to digit III.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact

- ○ Materials availability
- ○ Data and code availability
- ● METHOD DETAILS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.109598.

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AUTHOR CONTRIBUTIONS

L.X. and K.N. conceived the study and conducted fieldwork at the tracksite (including the collection of footprint measurements). K.N. and K.D. conducted the geologic survey. L.X. analyzed the trackway data and performed the biomechanical calculations. L.X. and W.S.P. wrote the original and subsequent manuscript drafts. M.G.L. assisted in manuscript revisions.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Track 3D surface scans	figshare	figshare: LXIU-T3-R3, LXIU-T3-L3, LXIU-TI10
Nomenclatural acts	ZooBank	ZooBank:urn:lsid:zoobank.org:pub:BA88C3D1-2315-4935-AA2F-08316F2974B0

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to the lead contact Lida Xing (xinglida@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- This published work and the nomenclatural acts it contains, have been registered in and is publicly available at ZooBank: http://zoobank.org/References/XXXXXXXXX.
- Data for this study, including 3D surface scans, are publicly available via the digital repository of the University of Queensland Romilio Dinosaur Lab: https://datadryad.org/stash/share/XXXX [please note that the data for this paper are not yet published and this temporary link should not be shared without the express permission of the author].
- This paper does not report original code.

METHOD DETAILS

Digital 3D models were created of the *in situ* track-bearing surface following photogrammetry methods outlined by Romilio[49] and using an Apple iPhone XS Max (focal length 4.25 mm), Agisoft Metashape Professional (v.1.6.3), and Meshlab.[50] The surface topography was visualized using Paraview (v. 2020.06)[51] and CloudCompare (v. 2.10.2; http://www.cloudcompare.org/) filters.

Maximum track length, maximum track width (taken from the tip of digit III to the tip of digit IV), pace length, stride length, pace angulation, and rotation were measured according to the standard methods of Xing et al.[34] Two ratios of the degree of digital prominence (DP) were calculated: 1) the difference in anterior length between digit III and digit IV / the length of digit III, and 2) the difference in anterior length between digit III and digit IV / total track length.

The osteological measurement standards used in this paper are as follows: The traditional length measurement of the digits is from the most prominent point on a proximal joint surface to that of the distal joint surface. The length of an articulated digit is often less than the sum of its individual phalanx lengths. For articulated digits, the authors measured the length of the digit III, digit IV, and the total length of phalanges 2–4 of digit III. For unarticulated phalanges, measurements were taken from the proximal midpoint to the distal end of each phalanx. The length of the keratin sheath is the distance between the tip of the fourth phalanx and the tip of the sheath.

The formula of Alexander[29] was employed to estimate trackmaker speeds from trackways. The methods proposed by Alexander[29] and Thulborn[31,52] were applied to estimate the hip heights. Relative stride length (stride length/hip height) was calculated using the method of Thulborn.[52] For a small theropod (maximum pes length < 25 cm), Thulborn[52] suggests that hip height = 4.5*maximum pes length. The relative stride length (SL/h) may be used to determine whether the animal is walking ($SL/h \leq 2.0$), trotting ($2 < SL/h < 2.9$), or running ($SL/h \geq 2.9$)[29,52] (Alexander, 1976; Thulborn, 1990).