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Forgotten Paleogene limulid tracks: *Xishuangbanania* from Yunnan, China

Li-Da Xing [a,b,c,*], Martin G. Lockley [d], Qing He [a], Masaki Matsukawa [e], W. Scott Persons IV [b], Yin-Wen Xiao [f], Jian-Ping Zhang [a]

[a] *School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China*
[b] *Department of Biological Sciences, University of Alberta, 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada*
[c] *Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China*
[d] *Dinosaur Tracks Museum, University of Colorado at Denver, PO Box 173364, Denver, CO 80217, USA*
[e] *Department of Environmental Sciences, Tokyo Gakugei University, Koganei, Tokyo 184-8501, Japan*
[f] *Independent Researcher, No. 195 Wenxian Road, South of Dali Old Town South Gate, Dali 671003, China*

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Abstract

A re-examination of the problematic ichnotaxon *Xishuangbanania daieuensis* from the Paleogene of Yunnan Province, China, reveals that the type specimen is not a lizard trackway as inferred by C.C. Young in 1979. Instead, the specimen is interpreted as a limulid trackway. The specimen is best referred to the ichnogenus *Kouphichnium* and represents the first discovered limulid tracks in China.

Keywords: Paleogene; Limulid tracks; *Xishuangbanania*; *Kouphichnium*

1. Introduction

Limulids (horseshoe crabs) are aquatic arthropods. Because the overall morphology of modern limulids differs little from extinct forms, limulids are often referred to as "living fossils" (Barale, 1974; Fischer, 1984; Gaillard, 2010). Trace fossils (such as footprints, burrow infills, and feeding traces) may be thought of as "living fossils" in another sense, because trace fossils are records left by an organism during the course of life, rather than after death.

Numerous limulid ichnogenera have been proposed based on trace fossils that exhibit a diverse range of behaviors, including: *Paramphibius* (repichnia – digitate walking imprints) (Willard, 1935), *Limulicubichnus* (cubichnia – resting traces) (Miller, 1982), *Selenichnites* (domichnia – burrowing activity) (Romano and Whyte, 1987, 1990), and *Kouphichnium* (very regular locomotion) (Nopsca, 1923).

Of these ichnogenera, *Kouphichnium* is among the most stratigraphically and geographically widespread (Caster, 1938, 1944; King, 1965; Bandel, 1967; Goldring and Seilacher, 1971; Miller, 1982). The type ichnospecies, *Kouphichnium lithographicum*, consists of straight locomotion traces, and is known from the Upper Jurassic Solnhofen Lithographic Limestone (Bavaria, Germany) and the Upper Kimmeridgian Lithographic Limestones of Cerin (Ain, France). *Kouphichnium* (*Mesolimulus*) *walchi* (Groiss, 1975) is a curved complex trace with disrupted impressions of the telson (Gaillard, 2010). *K. rossendalensis* (referred to *Limulicubichnus* and to *Selenichnites* by Miller [1982] and Romano and Whyte [1990], respectively) consists of lunate prints, and is known from the Carboniferous Upper Haslingden Flags (Lancashire, England) (Hardy, 1970). Other less notable forms include *K. arizonae* from the Upper Triassic of Arizona (USA) (Caster, 1944), *K. gracilis* and *K. variabilis* from the Upper Triassic of Germany (Linck, 1949), and *K.* aff. *variabilis* from the Middle Jurassic of Yorkshire (England) (Romano and Whyte, 2003).

The first trace fossils to be recognized as tracks of a Chinese limulid were discovered along a road cut through the thin-bedded limestone of the Lower Triassic Qinglong Formation, Nanling County, Anhui Province (Bi et al., 1995). Bi et al.

* Corresponding author at: School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China.
E-mail address: xinglida@gmail.com (L.-D. Xing).

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(1995) assigned these limulid tracks to the type ichnospecies *K. lithographicum*.

Earlier, in the summer of 1978, five footprints (IVPP MH.1182-3) were collected near Manmeng Village in Xishuangbanna Dai Autonomous Prefecture by Mr. Yinwen Xiao from the Yunnan Geological Bureau and were sent to the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. Young (1979) interpreted these Manmeng tracks as lizard footprints. The tracks were described as such in a paper that consisted of dual Chinese and English sections (Young, 1979). In the Chinese portion of the paper, the new ichnogenus "*Xishuangbanania daieuensis* gen. et sp. nov." was erected based on the tracks. However, no mention of this new genus was provided in the English portion of the paper. This omission led to the name "*Xishuangbanania*" being unrecognized by most international researchers.

In a review of the vertebrate tracks of East and Southeast Asia, Lockley and Matsukawa (2009) recognized that the Manmeng "lizard" tracks are, in fact, those of a limulid. Lockley and Matsukawa (2009) assigned the tracks to the ichnogenus *Kouphichnium*, but without concrete description or discussion. In 2009, the senior authors of this paper (Xing L.D. and Lockley M.G.) had the opportunity to examine the IVPP track collection, and a thorough description of the Manmeng tracks is now possible.

Institutional abbreviation

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

2. Geological setting

The Manmeng tracksite is located at the China/Burma border, approximately 40 km northeast of Jinghong City (Fig. 1). The track-bearing rock is a fine claystone. Plant fossils associated with the tracksite have been identified as *Cupressus* sp. by the Institute of Botany, Chinese Academy of Sciences (Junrong Tao, pers. commun., 1979.7.4, by Yinwen Xiao).

Young (1979) wrote: "according to the Chinese geological map, the age of the *Xishuangbanania* was most probably Late Cretaceous or Early Tertiary, but it cannot ignore the probability of older age". The Manmeng tracksite belongs to the Lancang River fold zone of the Sanjiang fold series (Ren et al., 1980). The metamorphic rocks of the area are Proterozoic. The claystone containing the limulid tracks and *Cupressus* sp. fossils is an interlayer in a repeating sedimentation and eruptional sequence of the Paleogene Himalayan Tectonic Phase (Geological Team, Bureau of Geology and Mineral Exploration of Yunnan Province, 1979; Mo et al., 2009). The eruptional layers within the sequences

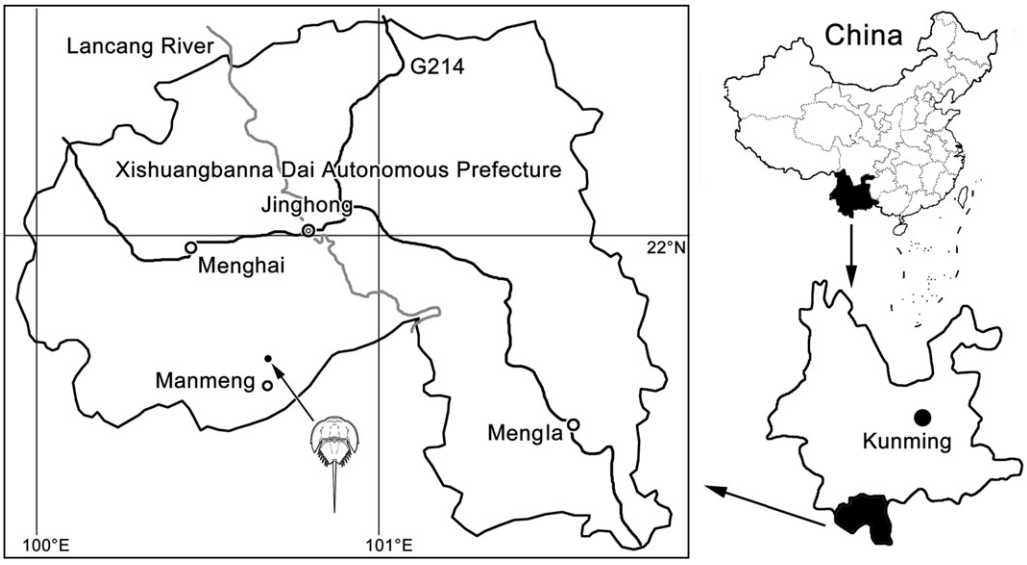

Fig. 1. Location of the Manmeng track locality (indicated by the footprint icon) in Yunnan, China.

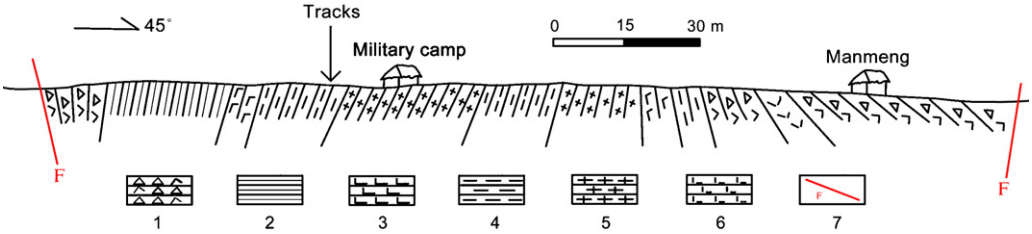

Fig. 2. Stratigraphic section of the Paleogene at the Menglong track locality. Illustration: 1, Tuffaceous breccia; 2, Shale; 3, Spilite; 4, Claystone; 5, Granite; 6, Spilite keratophyre; and 7, Fault.

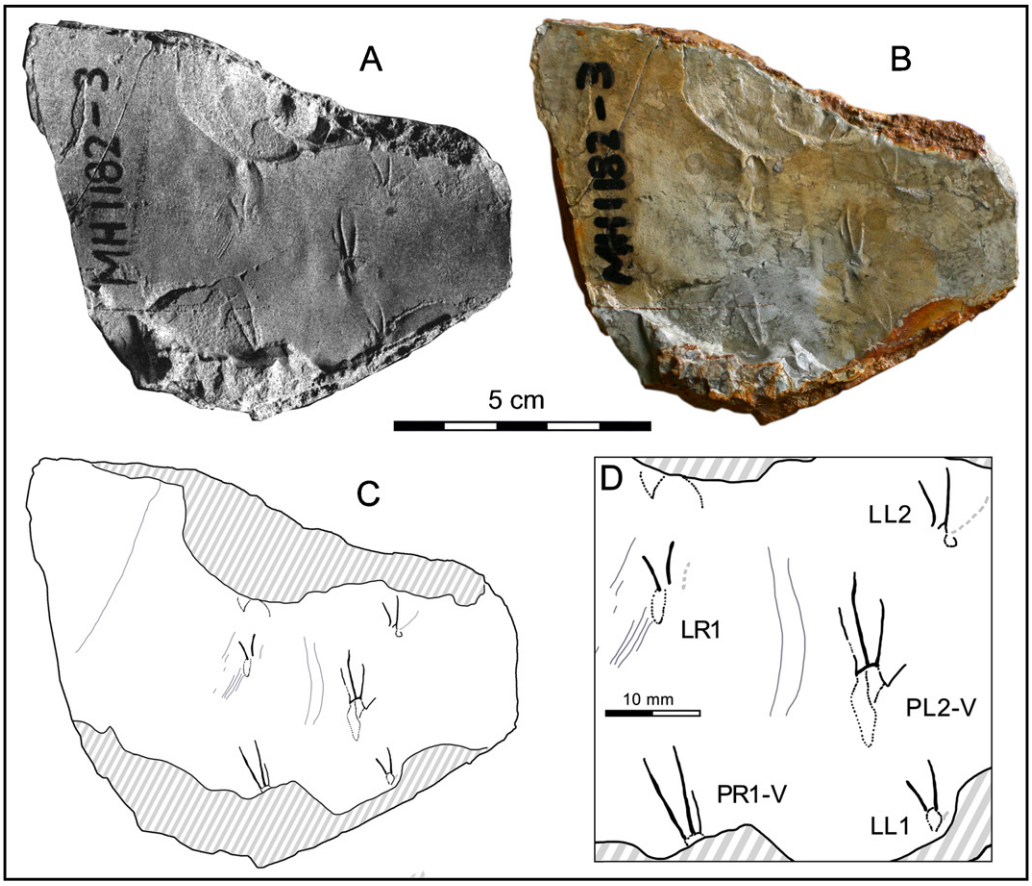

Fig. 3. Menglong limulid tracks IVPP MH.1182-3 from the Menglong tracksite. A, photograph from Young, 1979; B, photograph; C, outline drawing; D, enlarge limulid trackway from C with added specimen numbers. A–C, scale bar = 5 cm; D, scale bar = 10 mm. All specimen numbers begin with the prefix IVPP MH.1182-3. For clarity, tracks are only labeled with their suffixes.

contain large spilite deposits, indicating a marine paleoenvironment (Yinwen Xiao, personal observation; Fig. 2).

3. Systematic ichnology

Material

Five imprints preserved as natural casts on a single slab cataloged as IVPP MH.1182-3 (tracks numbered IVPP MH.1182-3 PR1-V, LL1, LL1, PL2-V, LL2) (Figs. 3 and 4 and Table 1).

Table 1
Measurements (in mm) of limulid tracks from the Menglong tracksite, Yunnan Province, China.

IVPP MH.1182-3	Length	Width	Angle[a]
PR1-V	>10.0	>3.8	–
LR1	8.6	3.1	22°
LL1	7.2	3.0	30°
PL2-V	17.6	7.0	–
LL2	8.0	3.2	30°

[a] The divarication angle between the bifurcate impression in intermediate imprints.

Locality and horizon

Paleogene. Menglong tracksite (21°40′7″N, 100°40′55″E), Jinghong City, Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, China.

Description

Some classifications of limulid appendages recognize six pairs, including one pair of chelicerae and five pairs of heterogeneous legss (Størmer, 1955; Malz, 1964; Gaillard, 2010) (Fig. 3). In such classifications, the chelicerae are numbers as set I and the "pushers" (the longest appendages) are set VI. Here we follow Hantzschel (1975) and excluded the chelicerae from the numbered appendages, considering the "pushers" as appendage set V.

IVPP MH.1182-3 is a roughly symmetric trackway, with two rows of imprints. The right row shows two well preserved intermediate imprints and one main lateral imprint. The left row shows one intermediate imprint and one main lateral imprint (lacking the proximal end). The two main lateral imprints were probably made by the "pushers". The three small intermediate imprints were probably made by one or more of legs I–IV. The single indistinct axial median imprint was probably made by the telson. The distinct V-shaped impressions may have been made

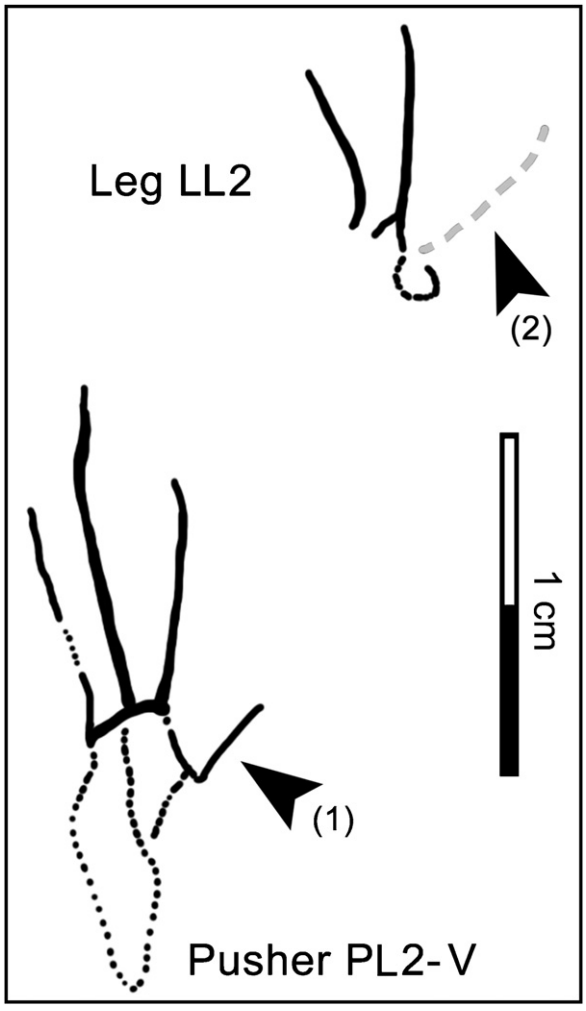

Fig. 4. The outline drawing of Menglong limulid tracks IVPP MH.1182-3 PL2-V and LL2.

by one of the shorter appendage sets, most likely a set close to the pushers (i.e., IV or III). There are no impressions attributable to the prosoma, the front pair of appendages (chelicerae), or from the other appendage pairs (legs II–IV).

Kouphichnium tracks consist of a single pair of main imprints made by the whorled pushing apparatuses on appendage pair V. These hindmost "digitate" tracks have two parts: a "quadrifid" wide anterior part (a fanlike impression made by four digit-like structures) and a reticular posterior part. The "pusher" print PL2-V of IVPP MH.1182-3 is well-preserved, with four slender digit-like structures comprising the anterior portion. The external digit is the shortest and the least distinct. The third digit is the longest and points outward. The other two digits are reduced in size and are slightly curved on their longitudinal axes towards the midline of the trackway. The main imprints of PL2-V differs from those of other *Kouphichnium* main imprints in that the distal end of the prints is indistinct and does not bifurcate. However, this morphology is probably attributable to taphonomic distortion. There are many similarities between the distal end of PL2-V and that of *Kouphichnium* sp. from the Oligocene of Takeo, Japan (Oishi et al., 1993, fig. 7A and B); however, in the latter, the distinct and indistinct bifurcate imprints are preserved (Oishi et al., 1993, fig. 7).

The intermediate imprints of PL2-V have elongate bifid V-shaped impressions or scratch marks that are forwardly directed. Each digitate impression has a different length and is slightly curved towards the axis of the trackway. LL1 and LL2 are nearly the same in size and inclination. Near LR1, external and elongate drag marks are discernible. The mean length of the intermediate prints is 8.0 mm and the mean width is 3.1 mm. The divarication angle of LL1 is the same as the angle of LL2, which suggests that these two simple tracks were left by the same leg of the limulid.

The axial imprint of PL2-V is faint but identifiable as a slightly grooved impression in-between and parallel to the left and right footprint sets. The length of the axial imprint is 17.1 mm and the width is 2.3 mm.

The whole trackway is 37.2 mm long and nearly straight, the internal width is 14.7 mm, and the external width is approximately 26.7 mm. The mean spacing between the main imprints and the intermediate imprints ranges from 14.2 mm (PL2-V–LL2) to 20.6 mm (PR1-V–LR1).

Using the formula $I = W \times 1.5$ and $L = I \times 2.2$ (I: the width of the prosoma; W: the external width of the trackway; L: the length of the trackmaker) (Gaillard, 2010), we calculated the prosoma size of the trackmaker as 4 cm in width and 8.5 cm in length.

Discussion

In Young's (1979) original interpretation of the Menglong tracks as lizard prints, he emphasized that both foot and hand prints are tridactyl. From close observation of PL2-V (considered by Young to be a hind or pes footprint) it is clear that the print has four digitate structures and that LL2 (considered by Young to be a manus print) has bifid scratch marks. The external digit of PL2-V is so short and indistinct (Fig. 4, arrow (1)) that it was overlooked. The external "digit" of LL2 (Fig. 4, arrow (2)) is much shallower than the other digits and is probably an artifact or records the drag of LL2 prior to registration. There is no similar external impression in the other two intermediate imprints (LR1 and LL1).

The Menglong tracks are here referred to *Kouphichnium*. As noted by Caster (1944), a complete or ideal trackway of *Kouphichnium* is composed of two main lateral imprints, eight small intermediate imprints, and one axial median (telson) imprint. The Menglong trackway exhibits two main lateral imprints, three small intermediate imprints, and one telson imprint.

K. lithographicum lacks telson imprints and has "pusher" imprints with distinct "bifid" distal ends (Gaillard, 2010). The characteristics are not present in the Menglong tracks. *Kouphichnium gracilis* is more complete than the Menglong tracks and exhibits no telson drag marks (Linck, 1949). However, the two share two digitate prints and "pusher" prints without posterior virgation. *Kouphichnium walchi* (Barale, 1978; Barthel et al., 1990) differs from the Menglong tracks in possessing prosoma imprints and a sinuous trail.

Like the Menglong tracks, other Chinese limulid tracks from the Qinglong Formation in Nanling, have been assigned to *K. lithographicum* (Bi et al., 1995). The "pusher" prints of Nanling tracks show a bar print with a bifid posterior portion and arc impression, but none of these features are present in the Menglong tracks. There are not enough data to support further comparisons or more precise taxonomic assignment, and in any event Hantzschel (1975, p. 75) stresses that *Kouphichnium* is a characterized by "heteropodus tracks of great variability". The Menglong tracks are most similar to *Kouphichnium*, and are definitely not lizard tracks. The Menglong tracks are best assigned to *Kouphichnium* and, as such, represent the first discovered limulid tracks in China. Thus the ichnogenus *Xishuangbanania* is considered a junior synonym of *Kouphichnium*, with no diagnostic characteristics to distinguish it from *Kouphichnium*, and we here assign the Menglong tracks to *Kouphichnium* isp.

In a recent molecular phylogenetic analysis, Obst et al. (2012) found strong support for a monophyletic Asian genus *Tachypleus* composed of three distinct species, each predicted to have originated from separate speciation events during the Paleogene. The referred *Kouphichnium* from the Paleogene of southwest China and southern Japan (Oishi et al., 1993; Lockley and Matsukawa, 2009) may well have been produced by an early form of *Tachypleus tridentatus*, which Obst et al. (2012) thought most likely migrated on a northeastern route along the southern coast of China towards Japan.

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