

An Unusual Trackway of a Possibly Bipedal Archosaur from the Late Triassic of the Sichuan Basin, China

Authors: Xing, Lida, Peng, Guangzhao, Marty, Daniel, Ye, Yong, Klein, Hendrik, et al.

Source: Acta Palaeontologica Polonica, 59(4) : 863-871

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2012.0087>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

An unusual trackway of a possibly bipedal archosaur from the Late Triassic of the Sichuan Basin, China

LIDA XING, GUANGZHAO PENG, DANIEL MARTY, YONG YE, HENDRIK KLEIN, JIANJUN LI, GERARD D. GIERLIŃSKI, and CHUNKANG SHU



Xing, L., Peng, G., Marty, D., Ye, Y., Klein, H., Li, J., Gierliński, G.D., and Shu, C. 2014. An unusual trackway of a possibly bipedal archosaur from the Late Triassic of the Sichuan Basin, China. *Acta Palaeontologica Polonica* 59 (4): 863–871.

The Longguan dinosaur tracksite in the Sichuan Basin (China) is described. It is located in the uppermost part of the Upper Triassic Xujiahe Formation and displays a single, unusual trackway consisting of 19 deeply impressed pes imprints. All tracks have suffered from erosion over many years of exposure, but they still reveal interesting details such as conspicuous elongated grooves, interpreted here as toe and claw drag marks. The trackmaker, a medium-sized archosaur, was walking in a thick and relatively soft layer of sand. The elongated, oval shape of the footprints resembles the ichnogenus *Eosauropus* from North America and Europe, assigned to facultative bipedal sauropodomorphs. The Chinese track differs by inward rotation of the footprints toward the midline, whereas in *Eosauropus*, these are turned strictly outward. Other ichnotaxa and possible trackmakers are discussed, but presently, a distinct assignment cannot be given. The Longguan trackway enlarges the scarce footprint record from the Triassic of China.

Key words: Vertebrate ichnology, archosaur trackway, deep tracks, Triassic, Xujiahe Formation, Sichuan Province, China.

Lida Xing [xinglida@gmail.com], School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China;

Guangzhao Peng [pguangzhao@yahoo.com.cn], Yong Ye [yeyozdm@126.com], and Chunkang Shu [sckang@yahoo.cn], Zigong Dinosaur Museum, Zigong 643013, Sichuan, China;

Daniel Marty [daniel.marty@palaeojura.ch], Office de la Culture-Paléontologie A16, Hôtel des Halles, P.O. Box 64, 2900 Porrentruy 2, Switzerland;

Hendrik Klein [Hendrik.Klein@combyphone.eu], Saurierwelt Paläontologisches Museum, Alte Richt 7, D-92318 Neumarkt, Germany;

Jianjun Li [lj5681@126.com], Department of Paleontology, Beijing Natural History Museum, 126 Tian Qiao South Street, Beijing 100050, China;

Gerard D. Gierliński [gierlinski@yahoo.com], JuraPark, ul. Sandomierska 4, 27-400 Ostrowiec Świętokrzyski, Poland, and Polish Geological Institute, Rakowiecka 4, 00-975 Warszawa, Poland.

Received 7 August 2012, accepted 17 February 2013, available online 19 February 2013.

Copyright © 2014 L. Xing et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The Sichuan Basin, also called the “Red Basin”, is located in SW China (Fig. 1) and is renowned for its Middle and Late Jurassic dinosaur fauna in the Zigong area. Triassic deposits are relatively rare, and in the western Sichuan Basin mainly belong to the Upper Triassic Xujiahe Formation (Peng et al. 2005). Apart from bony fishes such as *Shuniscus* and *Jialingichthys* (Su 1983), the Xujiahe Formation has not yet revealed many vertebrate fossils, even though, in Fushun County, southeast of Zigong City, the tracks described herein have been known for a few hundred years at least,

and local people have called them “Rhinoceros Footprints” (Xing et al. 2011).

More recently discovered tracks include tridactyl tracks attributed to the theropod ichnotaxon *Pengxianpus* (Yang and Yang 1987), tracks of a mammal or mammal-like reptile in Peng County (Yang and Yang 1987; Lockley and Matsukawa 2009; Xing et al. 2013), and theropod tracks in Tianquan County (Gou 1996; Wang et al. 2005), which have not been studied in detail so far. Moreover, in 2009, Guangzhao Peng and a colleague from the Zigong Dinosaur Museum have discovered a new dinosaur tracksite with a single trackway on the Longguan Mountain (also known as Luoguan Mountain),

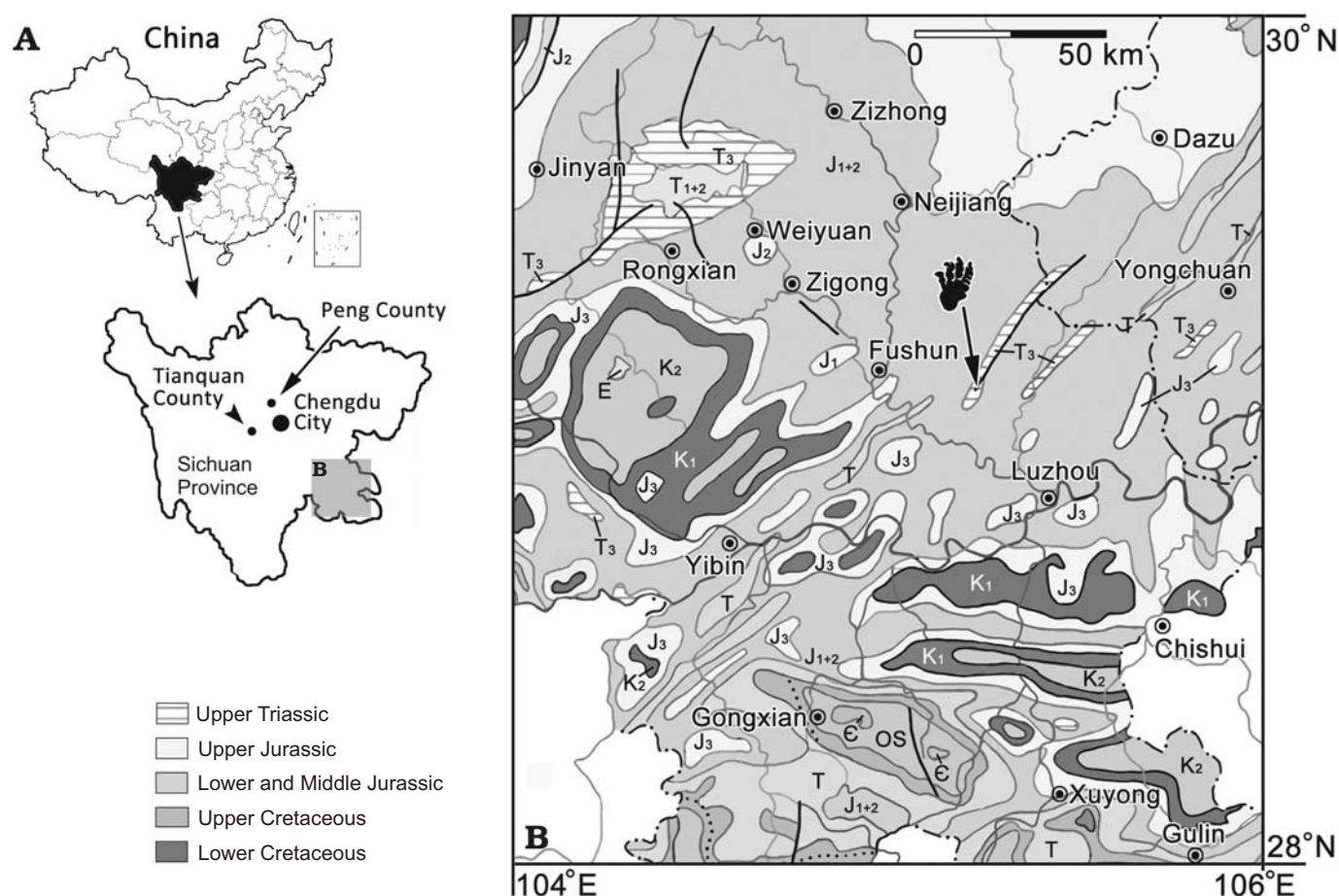


Fig. 1. Geographical (A) and geological (B) setting of the Fushun tracksite (indicated by the footprint icon) within the Sichuan Province, China. Abbreviations: T, Triassic; T1, Lower Triassic; T2, Middle Triassic; T3, Upper Triassic; J1, Lower Jurassic; J2, Middle Jurassic; J3, Upper Jurassic; K1, Lower Cretaceous; K2, Upper Cretaceous; E, Paleogene; OS, Ordovician and Silurian; C, Cambrian.

Fushun County, southeast of Zigong City (Fig. 1). In summer 2011, Lida Xing, Jianjun Li, Guangzhao Peng, and other colleagues studied this site in greater detail and the description and interpretation of the trackway from the Longguan tracksite is in the focus of the present work.

Abbreviations.—FS, Fushun tracksite, Zigong, Sichuan Province, China.

Geological setting

The Longguan tracksite is located on a slope with a dip of 13° about 50 m from the peak of Longguan Mountain (400 m), Zhixi Township, Tongsi Town, Fushun County, southeast of Zigong City, Sichuan Province (Fig. 1).

Most of the outcrops around the Longguan tracksite belong to the Lower Jurassic Zhenzhuchong Formation, which is characterized by cross-bedded, rather thin sandstone and without any thick sandstone beds (Peng et al. 2005). The Upper Triassic (Rhaetian, sensu Qiao et al. 2012) Xujiahe Formation, on the other hand, consists mainly of thick sandstone beds, mudstone, and interlayered coal seams, which form rhythmic sequences of different thicknesses, from a few hun-

dred to 3000 m, often rich in plants and bivalve fossils (Fig. 2; Gu et al. 1997). The Longguan tracksite is located on top of a thick sandstone unit, showing typical features of the Xujiahe Formation and can be assigned to the 4th out of six members. This is further confirmed by field mapping, the Zigong City geological map (Sichuan Bureau of Geology and Mineral Resources 1990), analyses of satellite images, and aerial photographs. The 4th member of the Xujiahe Formation is made up of delta plain and delta-front deposits (Hu and Bao 2008), which formed under a warm and dry climate (Xu et al. 2010).

Trackway preservation and description

Nineteen tracks were identified and attributed to a single trackway (Figs. 3–5, Table 1). They are labelled as FS-1 to FS-19, where FS is the abbreviation for the Longguan (from Fushun) tracksite. The original tracks all remain in the field, and the Zigong Dinosaur Museum plans to make a cast of the whole trackway in the near future.

Due to the exposure of the tracksite, possibly for several tens to hundreds of years, weathering of the surface and

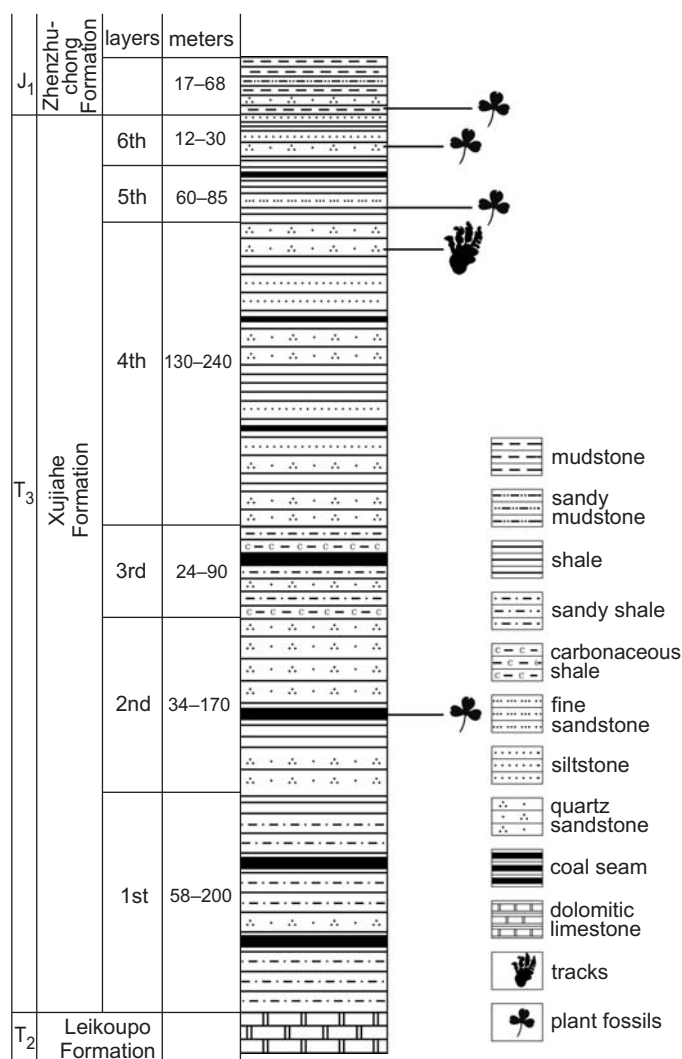


Fig. 2. Stratigraphical setting of the Fushun tracksite. Abbreviations: J1, Lower Jurassic; T3, Upper Triassic; T2, Middle Triassic.

tracks is severe. The surface and the tracks have deteriorated to different degrees by growth of plant roots and circulating water. Several carved and washed-out straight or rounded grooves can be observed on the surface and between the tracks. The most noticeable of these grooves can be observed between FS-6 and FS-7, FS-7 and FS-8, FS-10 and FS-12, and between FS-14 and FS-15 (Fig. 3A, 5C). Rather than tail drag impressions (see Platt and Hasiotis 2008 for classification), we interpret these grooves as erosional dissolution features around roots, because most are straight, not exclusively associated with tracks, and also can be observed elsewhere on the surrounding surface.

The tracks are preserved as up to 30 cm deep impressions (negative epirelief) in a single, thick sandstone layer. Because none of the tracks contains any track fill, and because the track-bearing surface is the uppermost bed in the outcrop, the track infilling material and the original preservational state of the tracks is unknown. Important original track features may have been eroded away or may at least have been modified. Nevertheless, some of the tracks are still reason-

ably well preserved and reveal some morphological characteristics such as scratch marks. For this reason, the tracks are interpreted as (deep) true tracks or more precisely (deep) underprints *sensu* Marty et al. (2009).

All tracks have a relatively shallow wall and a deeper floor of the track (Figs. 4, 5A, Table 1). The wall includes occasional impressions at the rear of some of the tracks and elongated grooves in the anterior part that follow the slope. The floor is thought to correspond approximately to the dimensions of the trackmaker's foot, whereas the wall is related to the whole movement (impact) of the foot.

The mean length of the floor is 211 mm and the mean width 153 mm. The length to width ratio of the floor varies between 1.0–1.9, with an average of 1.4, indicating that the trackmaker's foot was longer than wide.

In some of the tracks (notably FS-5, FS-6, FS-9, FS-12; Fig. 4), elongated grooves are connected with the anterior part of the shallow peripheral depressions, and they are interpreted as toe and claw drag marks. On the anterior part of the right pes track FS-12 (Fig. 4), the two best-preserved elongated grooves can be observed, where the exterior (right) groove has a length of 193 mm and a width of 51 mm, and the internal (left) groove a length of 133 mm, and a width of 52 mm, respectively. Both grooves on FS-12 are proximally wider, and narrow distally into fairly sharp tips. Similar to FS-12, the left tracks FS-5 and FS-9 have an anteriorly elongated groove (Figs. 4, 5A). Possibly these grooves were initially made up of several (at least two) grooves but this is now difficult to decipher, because of their washed-out appearance.

The right track FS-10 and the left track FS-11 are connected, which suggests that the trackmaker was sliding backwards with its left foot towards the impression of its right foot. FS-5, FS-6, and FS-19 are distinctly elongated backwards. This is interpreted as the trackmaker's foot sliding forward on the slippery substrate into the final position (Fig. 5A).

All tracks are rotated slightly inward (towards the trackway midline), but otherwise, the Fushun trackway is characterized by an irregular configuration. Pace length varies between 558 and 859 mm (695 mm on average), stride length between 948 and 1351 mm (1142 mm on average), and pace angulation between 102° and 144° (123° on average) (Table 1). For instance, the pace length between FS-1 and FS-2 is 859 mm, immediately dropping to 656 mm between FS-2 and FS-3, and later on fluctuating between 600 and 700 mm. The shortest pace lengths are located between FS-9 and FS-13 being associated with a slight turn in the trackway, and with a distinct sliding movement between FS-10 and FS-11. These tracks are also the deepest tracks of the trackway.

Discussion

Ichnotaxonomy and trackmaker identification.—Because the Fushun trackway consists of substrate-kinematics-dominated, unusually deep tracks, that furthermore have

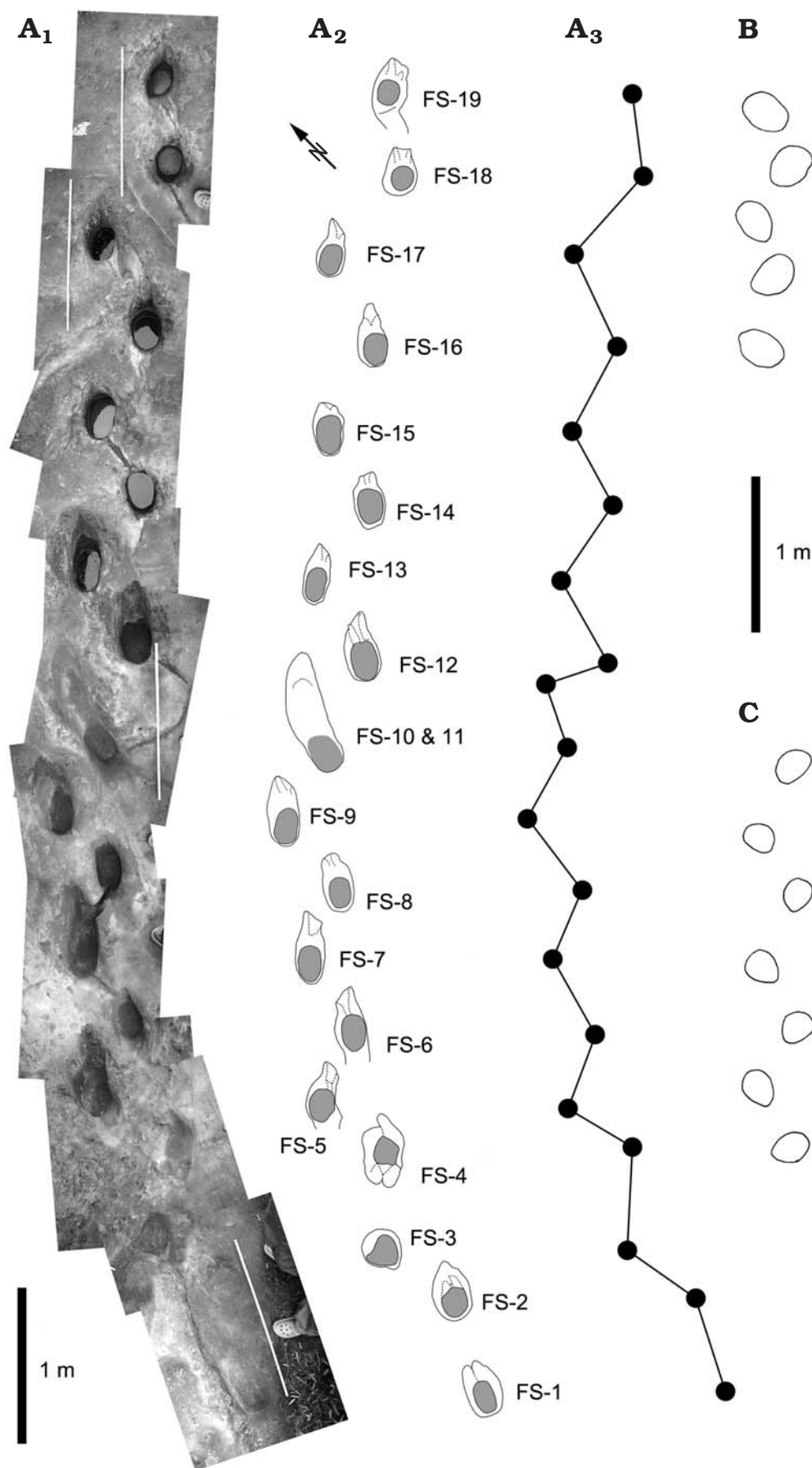


Fig. 3. A. Overview of the Late Triassic Fushun archosaur trackway. Stitched photograph (A₁), interpretative outline drawing (A₂), pace lines connecting the reference points (intersection of long and wide axes) of each track (A₃). Note that the reference point of FS-11 is ambiguous, because the foot was possibly sliding backwards into FS-10. B. *Eosauropus* trackway from the Utah West tracksite (Lockley et al. 2011: fig. 6). C. *Eosauropus* trackway from the Knowles Canyon tracksite (Lockley et al. 2011: fig. 6).

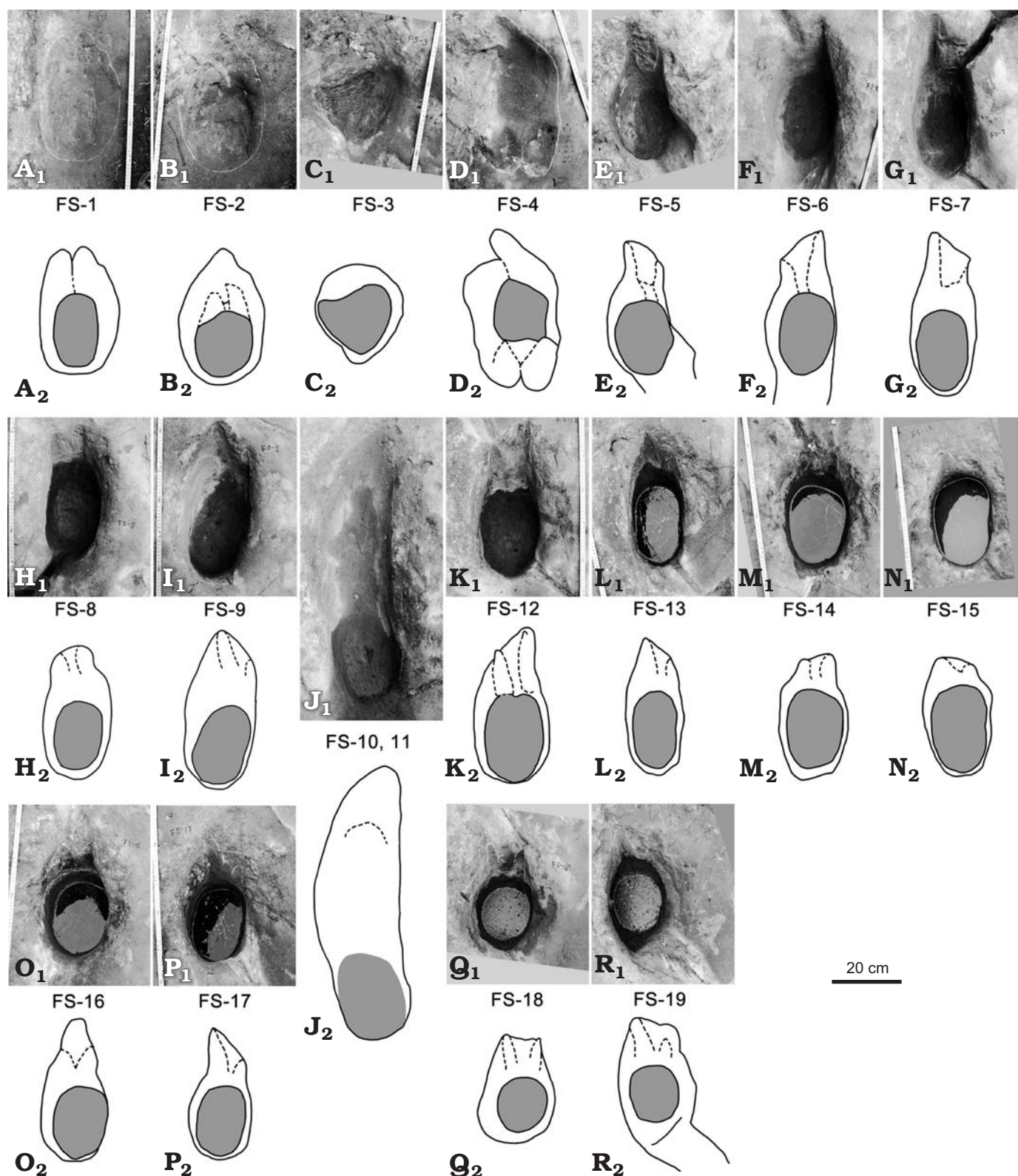


Fig. 4. Photographs (A_1 – R_1) and outline drawings (A_2 – R_2) of the Late Triassic Fushun archosaur tracks FS-1 to FS-19. All tracks are oriented in walking direction (upwards). Note that the two tracks FS-10 and FS-11 are connected to each other, interpreted as the left foot sliding backwards into the previously left impression of the right foot.

suffered from recent weathering, it is difficult to assign it to an ichnotaxon. Furthermore, it is not certain whether it was made by an animal moving bipedally or if the manus imprints

were simply destroyed or overprinted by the pes. The size and orientation of the pes imprints and the relatively narrow trackway pattern indicate an archosaur as the trackmaker.

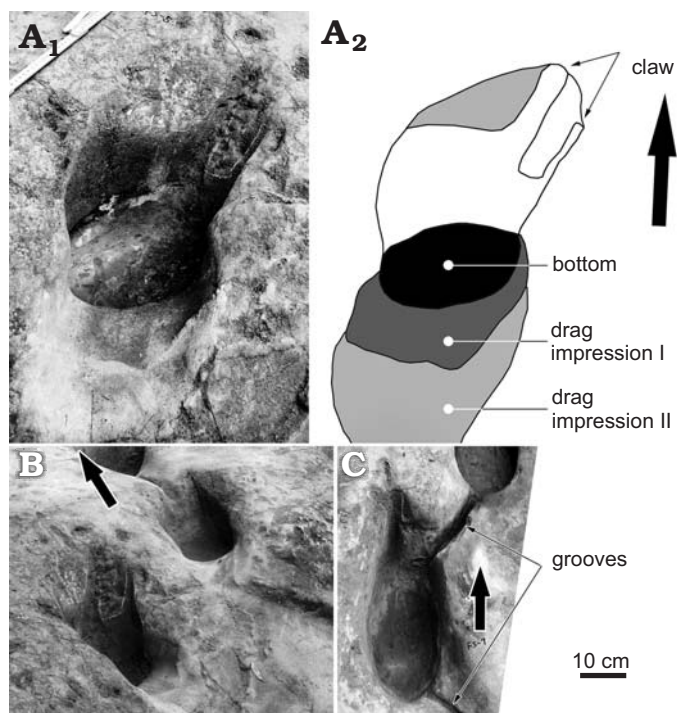


Fig. 5. Close-up photographs highlighting characteristic the Late Triassic Fushun archosaur track features. A. Photograph (A₁) and outline drawing (A₂) of FS-5 exhibiting a large impression at the rear of the track, which is inclined towards the deepest part of the track, and two elongated grooves in the anterior part of the track. The impression at the rear of the track is interpreted as being related to the foot sliding on the substrate into its final position, and the two elongated anterior grooves as toe and claw drag marks after foot withdrawal. B. Low-angle light photograph of FS-5 and FS-6. Note the two elongated grooves in the anterior part of FS-5, interpreted as toe and claw drag marks. C. Straight and washed out grooves between FS-6 and FS-7, and FS-7 and FS-8, interpreted as erosional dissolution features around roots and/or of draining water. Arrows indicate walking direction.

The two anterior, elongated grooves, as notably observed in FS-12 (Fig. 4), represent drag marks of (at least) two separated long digits. Interestingly, this “didactyl” pattern occurs continuously in all imprints. It seems that the trackmaker had a pes with two digits dominating by their length and/or robustness. Therefore, typical symmetrical, tridactyl theropods can be excluded. Deep theropod tracks, described for example from the Lower Cretaceous of the Paluxy River (Kuban 1989), show three digits and a long metatarsal impression (“heel”) that is much narrower compared with the Longguan tracks. Also, in the former, the digits are more widely spread. The same is true for ornithischians with a tridactyl to tetradactyl pes that also would have left three distinct digits when being deeply impressed.

A look at sauropodomorphs as possible trackmakers reveals different similarities. Late Triassic–Early Jurassic trackways of bipedal and/or facultative bipedal archosaurs (possibly sauropodomorphs) with impressions of separated, long digits are known by the ichnotaxa *Kalosauropus* (Ellenberger 1970), *Agrestipus* (Weems 1987), *Evazoum* (Nicosia and Loi 2003), *Pseudotetrasauropus* (Ellenberg-

er 1972), and *Otozoum* (Rainforth 2003), that have been included in the OPEK plexus and the ichnofamily Otozoidae (Lull 1904), respectively, by Lockley et al. (2006b). In particular the trackmakers of *Pseudotetrasauropus* and *Otozoum* footprints could possibly have left footprints of oval shape, similar to those seen in the Longguan trackway, when walking on a moist, deep substrate (Fig. 6A–C). Besides sauropodomorphs, there are further suggestions about the trackmakers of the OPEK plexus footprints: an indeterminate archosaur (Olsen and Galton 1984) or ornithischian (Gierliński 1997) for *Pseudotetrasauropus*, a small aetosaur (Weems 2006) for *Agrestipus*, a dinosauriform archosaur such as the herbivorous *Silesaurus* (Dzik 2003; Piechowski and Dzik 2010) or the poposaurid archosaur *Effigia* (Nesbitt 2007) for *Evazoum* (D’Orazi Porchetti et al. 2008).

A further ichnotaxon attributed to sauropodomorph trackmakers is *Eosauropus* (Lockley et al. 2006a, 2011) (Figs. 3B, C, 6D), which shows some similarities with the trackway from Longguan, particularly in the elongate, oval shape of the imprints. *Eosauropus* was originally described as the track of a quadruped (Lockley et al. 2006a), but has also been documented by pes-only versions (Lockley et al. 2011). The latter could be due to bipedal movement and facultative bipedality, as well as to the overstep of the manus by the pes (Lockley et al. 2011). It has to be noted here, that if the Longguan trackmaker was a facultative biped, it would probably have used its forelegs while walking on unstable substrates. Nevertheless, there is a distinct difference in the trackway pattern between *Eosauropus* and the specimen from Longguan. In the former, the imprints are strongly outward rotated relative to the midline, whereas in the latter, these point inward (compare Fig. 3A₁, A₂ and B, C). This cannot be explained by variation of the gait on the slippery and deep substrate. It is more likely that it is an anatomical signal. Therefore, the Longguan trackway cannot be assigned to *Eosauropus*.

Non-dinosaurian archosaurs have to be considered as well. A distinct feature in all imprints of the Longguan trackway is that the outer digit trace is the longest. It is curved outward due to the dynamics of the pes. It is likely, that it represents digit IV, which is the outermost of the anterior digit group in the archosaur pes. A more laterally positioned digit would probably have left a further trace, but this cannot be observed. If this interpretation is correct, and if digit IV in the pes was longest, this indicates a more primitive archosaur. For example, semi-aquatic phytosaurs, which were common on Late Triassic Pangaea, have a pes with digit IV longest or subequal with III. Their tracks have been identified as the ichnogenus *Apatopus* (Baird 1957; Padian and Pchelnikova 2010; Klein and Lucas 2013), which shows a plantigrade to semi-plantigrade pes with digit IV longest and often with an outward curved trace of the latter. However, as in the comparison with *Eosauropus*, the trackway pattern is different by the “toed-in” orientation of the imprints that are outward rotated in *Apatopus*. Also, *Apatopus* has a manus imprint that is positioned anterior to the pes, whereas the

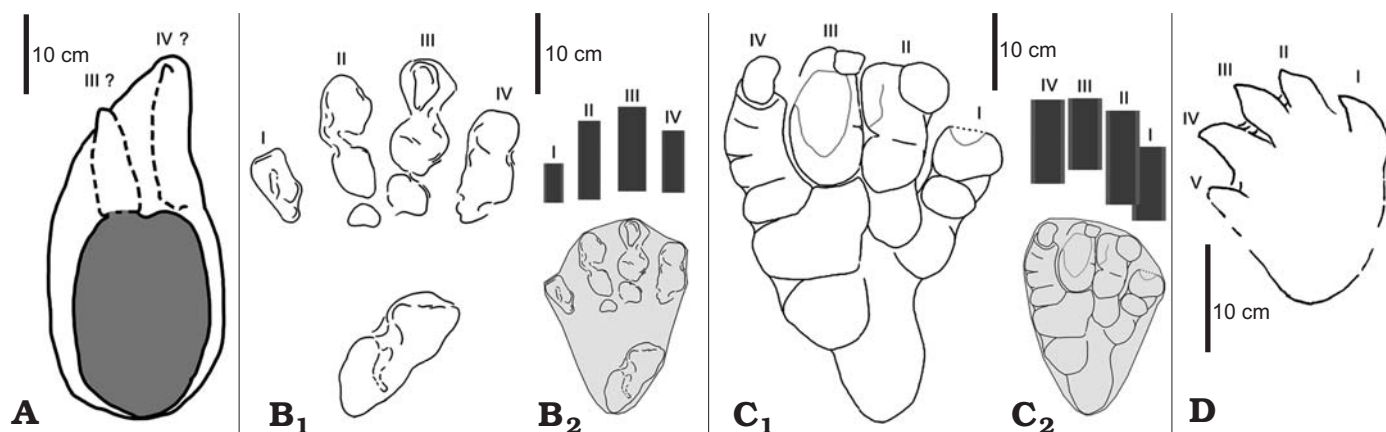


Fig. 6. Comparison of the Fushun archosaur trackway with *Pseudotetrasauropus*, *Otozoum*, and *Eosauropus*. **A.** Outline drawing of the right pes FS-12 of the Fushun trackway. **B.** *Pseudotetrasauropus bipedoida* Ellenberger, 1972 (modified from D'Orazi Porchetti and Nicosia 2007: fig. 9). **C.** *Otozoum moodii* Rainforth, 2003 (mirrored and modified from Rainforth 2003: fig. 3C). **D.** *Eosauropus cimarronensis* Lockley, Lucas, and Hunt, 2006 (Lockley et al. 2006a: fig. 4A). In B₂, C₂ the gray-scale sketches show the connected outer edges; the black bars the length of the four digits. The digits of *P. bipedoida* are well separated while those of *O. moodii* are relatively compact. However, during foot withdrawal out of deep substrate, both could result in the anterior, elongated grooves as observed in FS-12, and these could correspond to digits III and IV.

trackway described here lacks this feature (but see possible explanation above). Presently, it is impossible to assign the trackway from Longguan to any distinct archosaur group.

Track formation and foot kinematics.—The Fushun trackway is unusual in that the tracks are very deep, having been made in a thick layer of unstable substrate. In the ternary track classification diagram of Padian and Olsen (1984), the Fushun tracks would plot into the substrate-kinematics

dominated field. Thus, they are not useful for ichnotaxonomic purposes, but they can reveal information about foot kinematics in a deep substrate. The irregular trackway configuration indicates that the trackmaker performed a particular locomotion style, adapted to cross an unstable substrate. This involved the foot sliding forward several times over the slippery substrate into the final position of the foot, forming the major and deepest part (floor) of the tracks. During foot withdrawal, the toes and claws produced the anterior,

Table 1. Trackway parameters (in cm) of the Fushun trackway. Abbreviations: DF, deeper floor (Internal diameter, corresponding approximately to the trackmaker's foot dimensions); MD, maximum depth; ML, maximum length; MW, maximum width; PA, pace angulation; PL, pace length; SL, stride length; SW, shallow wall (external diameter); R/L, right/left; "—", measurement not possible or not applicable.

Number	R/L	SW			DF			MD	SL	PL	PA
		ML	MW	ML/MW	ML	MW	ML/MW				
FS-1	L	36.9	22.8	1.6	20.9	12.8	1.6	9	135.1	85.9	144°
FS-2	R	39.2	24.8	1.6	19.1	16.1	1.2	10	113.0	65.6	122°
FS-3	L	28.6	25.5	1.1	19.7	20.7	1.0	11	112.4	67.9	120°
FS-4	R	45.7	25.5	1.8	17.7	15.0	1.2	12	94.8	66.6	102°
FS-5	L	42.9	21.9	2	21.6	16.6	1.3	27	105.1	64.5	129°
FS-6	R	49.8	20.7	2.4	23.8	15.6	1.5	21	112.8	59.5	128°
FS-7	L	47.3	18.8	2.5	23.4	14.7	1.6	25	108.1	70.3	122°
FS-8	R	38.2	19.2	2	19.4	13.8	1.4	22	99.1	55.8	115°
FS-9	L	45.4	20.7	2.2	22.7	13.9	1.6	17	101.7	68.3	130°
FS-10	R	78.7	25.3	—	25.3	18.7	1.4	15	72.3?	49.1?	91°?
FS-11	L	—	—	—	22.6?	—	—	—	80.6?	54.8?	79°?
FS-12	R	44.9	21.9	2.1	25.0	17.6	1.4	25	113.7	67.6	117°
FS-13	L	39.4	16.4	2.4	21.6	12.0	1.9	27	112.3	76.0	117°
FS-14	R	36.1	19.9	1.8	21.7	16.2	1.3	22	118.7	65.5	123°
FS-15	L	34.3	19.9	1.7	24.6	15.7	1.6	25	132.8	78.0	127°
FS-16	R	40.9	19.1	2.1	20.6	15.6	1.3	26	125.5	77.1	114°
FS-17	L	38.0	18.0	2.1	20.1	13.3	1.5	30	127.3	78.6	132°
FS-18	R	29.8	21.4	1.4	16.1	13.7	1.2	26	—	65.1	—
FS-19	L	46.1	23.0	2.0	16.0	14.0	1.1	28	—	—	—

elongated grooves interpreted here as drag marks. There is no evidence for a (partial) collapse of the tracks, indicating that the substrate was coherent enough to retain the shape of the tracks, before they were filled and covered up. The slight turn between FS-9 and FS-13 and the documented sliding movement between FS-10 and FS-11 are interpreted as the trackmaker was slowing down to turn, being unstable for a moment, before it moved on and accelerated again.

The Late Triassic Xujiahe Formation ichnocoenosis on a Chinese and global scale.—Vertebrate tracks from the Xujiahe Formation include: (i) the archosaur trackway of unknown affinity, described in the present work; (ii) large-sized tridactyl tracks named *Pengxianpus* from Peng County and attributed to theropods (Yang and Yang 1987; Lockley and Matsukawa 2009; Xing et al. 2013); the *Pengxianpus* tracks lack detailed comparisons and interpretations and only two successive tracks are known, representing a single pace with a length of 93 cm; these tracks were first attributed to a prosauropod (Yang and Yang 1987), but Lockley and Matsukawa (2009) considered them to be similar to the North American ichnotaxon *Atreipus*, attributed to theropods (Thulborn 1993), ornithopods (Olsen and Baird 1986) and dinosauromorphs (Haubold and Klein 2000; D'Orazi Porchetti et al. 2008); for assignments see also Xing et al. (2013) and Lockley et al. (2013); (iii) small tridactyl tracks from Tianquan County (Gou 1996; Wang et al. 2005; Xing et al. 2013), having a mean length of 11 cm and attributed to theropods; (iv) mammal or mammal-like reptile tracks from Peng County, on the same slab as *Pengxianpus*, but without any detailed description provided as yet (Lockley and Matsukawa 2009; Xing et al. 2013).

Conclusions and outlook

The Longguan trackway was left by a medium-sized to large archosaur that was either a quadruped overstepping its forefeet impressions with its hindfeet, or an obligate/facultative biped. An assignment to a distinct trackmaker or ichnotaxon cannot be given. Together with the presence of small and large-sized theropod tracks, and footprints of mammal-like tetrapods, the record indicates a larger ichno- and vertebrate diversity for the Upper Triassic Xujiahe Formation than previously assumed (Gu et al. 1997). A future task is further prospecting for tracks in the Xujiahe Formation and to revise and describe the Xujiahe Formation ichnocoenosis in more detail. Thus, it may be compared on a more global scale with other Upper Triassic track-bearing localities of eastern North America (e.g., Weems 1987, 1992; Lockley and Hunt 1995), Europe (e.g., Haubold 1984; Lockley and Meyer 2000; Klein and Lucas 2010), southern Africa (e.g., Ellenberger 1972; Olsen and Galton 1984), northern Africa (Lagnaoui et al. 2012), and South America (e.g., Marsicano and Barredo 2004; Melchor and de Valais 2006; Marsicano et al. 2007). These are generally dominated by *Brachychi-*

rotherium tracks and tridactyl tracks of the *Grallator–Eubrontes* type (Klein and Lucas 2010). How far the assemblage from the Xujiahe Formation is distinctive or matches other localities, also in a biostratigraphic context, has to be explored.

Acknowledgements

We thank Martin G. Lockley (Dinosaur Tracks Museum, University of Colorado Denver, USA) and Simone D'Orazi Porchetti (Sapienza Università di Roma, Italy) for their constructive comments and reviews, as well as Christian A. Meyer (Natural History Museum Basel, Switzerland) and Julien D. Divay (University of Alberta, Alberta, Canada) for their suggestions and comments on an earlier version of the manuscript. This research project was supported by the Zigong Dinosaur Museum.

References

- Baird, D. 1957. Triassic reptile footprint faunules from Milford, New Jersey. *Bulletin of the Museum of Comparative Zoology* 117: 449–520.
- D'Orazi Porchetti, S. and Nicosia, U. 2007. Re-examination of some large early Mesozoic tetrapod footprints from the African collection of Paul Ellenberger. *Ichnos* 14: 219–245.
- D'Orazi Porchetti, S., Nicosia, U., Mietto, P., Petti, F.M., and Avanzini, M. 2008. *Atreipus*-like footprints and their co-occurrence with *Evazoum* from the upper Carnian (Tuvanian) of Trentino-Alto Adige. *Studi Trentino Scienze Naturali Acta Geologica* 83: 277–287.
- Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 23: 556–574.
- Ellenberger, P. 1970. Les niveaux paléontologiques de première apparition des mammifères primordiaux en Afrique du Sud et leur ichnologie. Etablissement de zones stratigraphiques détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias Supérieur à Jurassique). In: S.H. Haughton (ed.), *Second Symposium on Gondwana Stratigraphy and Palaeontology, International Union of Geological Sciences*, 343–370. Council for Scientific and Industrial Research, Pretoria.
- Ellenberger, P. 1972. Contribution à la classification des pistes de vertébrés du Trias: les types du Stormberg d'Afrique du Sud (I Partie). *Palaeovertebrata, Mémoire Extraordinaire* 104: 1–152.
- Gierliński, G. 1997. Sauropod tracks in the Early Jurassic of Poland. *Acta Palaeontologica Polonica* 42: 533–538.
- Gou, Z.H. 1996. Stratigraphic features of the Xujiahe formation in the Tianquan Lushan Baoxing area, Sichuan. *Regional Geology of China* 4: 321–329.
- Gu X., Liu, X., and Li, Z. 1997. *Stratigraphy (lithostratic) of Sichuan Province*. 417 pp. China University of Geosciences Press, Wuhan.
- Haubold, H. 1984. *Saurierfahrten*. 231 pp. Ziemsen, Wittenberg.
- Haubold, H. and Klein, H. 2000. Die dinosauroiden Fahrten *Parachirotherium–Atreipus–Grallator* aus dem unteren Mittelkeuper (Obere Trias: Ladin, Karn, ?Nor) in Franken. *Hallesches Jahrbuch für Geowissenschaften B* 22: 59–85.
- Hu G., and Bao Z. 2008. Sedimentary facies of fourth and fifth members of upper Triassic Xujiahe formation, Sichuan basin. *Journal of Liaoning Technical University (Natural Science Edition)* 27: 508–511.
- Klein, H. and Lucas, S.G. 2010. Tetrapod footprints—their use in biostratigraphy and biochronology of the Triassic. In: S.G. Lucas (ed.), *The Triassic Timescale. Geological Society of London Special Publications* 334: 419–446.
- Klein, H. and Lucas, S.G. 2013. The Late Triassic tetrapod ichnotaxon *Apatopus lineatus* (Bock 1952) and its distribution. *New Mexico Museum of Natural History and Science, Bulletin* 61: 313–324.

- Kuban, G.J. 1989. Elongate dinosaur tracks. In: D.D. Gillette and M.G. Lockley (eds.), *Dinosaur Tracks and Traces*, 57–72. Cambridge University Press, Cambridge.
- Lagnaoui, A., Klein, H., Voigt, S., Hminna, A., Saber, H., Schneider, J.W., and Werneburg, R. 2012. Late Triassic tetrapod-dominated ichnoassemblages from the Argana Basin (Western High Atlas, Morocco). *Ichnos* 19: 238–253.
- Lockley, M.G. and Hunt, A.P. 1995. *Dinosaur Tracks and other Fossil Footprints of the Western United States*. 338 pp. Columbia University Press, New York.
- Lockley, M.G. and Matsukawa, M. 2009. A review of vertebrate track distributions in East and Southeast Asia. *Journal Paleontological Society of Korea* 25: 17–42.
- Lockley, M.G. and Meyer, C.A. 2000. *Dinosaur Tracks and other Fossil Footprints of Europe*. 360 pp. Columbia University Press, New York.
- Lockley, M.G., Hups, K., Cart, K., and Gerwe, S. 2011. A zone of sauropodomorph footprints in the basal Wingate Sandstone (Latest Triassic) of western Colorado and eastern Utah: is *Eosauropus* a common ichnogenus in this region? *New Mexico Museum of Natural History and Science, Bulletin* 53: 337–343.
- Lockley, M.G., Li, J., Li, R., Matsukawa, M., Harris, J.D., and Xing, L. 2013. A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology. *Acta Geologica Sinica* 87: 801–840.
- Lockley, M.G., Lucas, S.G., and Hunt, A.P. 2006a. *Eosauropus*, a new name for a Late Triassic track: further observations on the Late Triassic ichnogenus *Tetrasauropus* and related forms, with notes on the limits of interpretation. *New Mexico Museum of Natural History and Science, Bulletin* 37: 192–198.
- Lockley, M.G., Lucas, S.G., and Hunt, A.P. 2006b. *Evazoum* and the renaming of Northern Hemisphere “*Pseudotetrasauropus*”: implications for tetrapod ichnotaxonomy at the Triassic–Jurassic boundary. In: J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner, and J.I. Kirkland (eds.), *The Triassic–Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science, Bulletin* 37: 199–206.
- Lull, R.W. 1904. Fossil footprints of the Jura–Trias of North America. *Memoirs of the Boston Society of Natural History* 5: 461–558.
- Marsicano, C.A. and Barredo, S.P. 2004. A Triassic tetrapod footprint assemblage from southern South America: palaeobiogeographical and evolutionary implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203: 313–335.
- Marsicano, C.A., Domnanovich, N.S., and Mancuso, A.C. 2007. Dinosaur origins: evidence from the footprint record. *Historical Biology* 19: 83–91.
- Marty, D., Strasser, A., and Meyer, C.A. 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. *Ichnos* 16: 127–142.
- Melchor, R.N. and de Valais, S. 2006. A review of Triassic tetrapod track assemblages from Argentina. *Palaeontology* 49: 355–379.
- Nesbitt, S.J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History* 302: 1–84.
- Nicosia, U. and Loi, M. 2003. Triassic footprints from Lericci (La Spezia, northern Italy). *Ichnos* 10: 127–140.
- Olsen, P.E. and Baird, D. 1986. The ichnogenus *Atreipus* and its significance for Triassic Biostratigraphy. In: K. Padian (ed.), *The Beginning of the Age of Dinosaurs*, 61–87. Cambridge University Press, Cambridge.
- Olsen, P.E. and Galton, P.M. 1984. A review of the reptile and amphibian assemblages from the Stormberg of Southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia Africana* 25: 87–110.
- Padian, K. and Olsen, P.E. 1984. The fossil trackways *Pteraichnus*: not pterosaurian, but crocodilian. *Journal of Paleontology* 58: 178–184.
- Padian, K., Li, C., and Pchelnikova, J. 2010. The trackmaker of *Apatopus* (Late Triassic, North America) implications for the evolution of Archosaur stance and gait. *Palaeontology* 53: 175–189.
- Peng, G.Z., Ye, Y., Gao, Y.H., Jiang, S., and Shu, C.K. 2005. *Jurassic Dinosaur Faunas in Zigong*. 236 pp. Peoples Publishing House of Sichuan Province, Chengdu.
- Piechowski, R. and Dzik, J. 2010. The axial skeleton of *Silesaurus opolenensis*. *Journal of Vertebrate Paleontology* 30: 1127–1141.
- Platt, B.F. and Hasiotis, S.T. 2008. A new system for describing and classifying tetrapod tail traces with implications for interpreting the dinosaur tail trace record. *Palaios* 23: 3–13.
- Qiao, X., Guo, X., Li, H., Gou, Z., S, D., Tang, Z., Zhang, W., and Yang, G. 2012. Soft-sediment deformations in the Late Triassic and the Indosinian tectonic movements in Longmenshan. *Acta Geologica Sinica* 86: 132–156.
- Rainforth, E.C. 2003. Revision and re-evaluation of the Early Jurassic dinosaurian ichnogenus *Otozoum*. *Palaeontology* 46: 803–838.
- Sichuan Bureau of Geology and Mineral Resources 1990. *Geological Report of Zigong City Area*. Unpublished Report.
- Su, D.Z. 1983. Late Triassic actinopterygians from East Sichuan, China. *Vertebrata Palasiatica* 21: 275–285.
- Thulborn, R.A. 1993. A tale of three fingers: ichnological evidence revealing the homologies of manual digits in theropod dinosaurs. *New Mexico Museum of Natural History and Science, Bulletin* 3: 461–463.
- Wang, Q.W., Kan Z.Z., Liang, B., and Cai, K. 2005. Discovery of track fossils of dinosaurs in Late Triassic strata of Tianquan, Sichuan, China. *Geological Bulletin of China* 24: 1179–1180.
- Weems, R.E. 1987. A Late Triassic footprint fauna from the Culpeper Basin, northern Virginia (U.S.A.). *Transactions of the American Philosophical Society, New Series* 77: 1–79.
- Weems, R.E. 1992. A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper, Virginia. In: P.C. Sweet (ed.), *Proceedings 26th Forum on the Geology of Industrial Minerals. Virginia Division of Mineral Resources Publication* 119: 113–127.
- Weems, R.E. 2006. The manus print of *Kayentapus minor*: its bearing on the biomechanics and ichnotaxonomy of early Mesozoic saurischian dinosaurs. In: J.D. Harris, J.I. Kirkland, and A.R.C. Milner (eds.), *The Triassic–Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin* 37: 369–378.
- Xing, L.D., Mayor, A., Chen, Y., Harris, J.D., and Burns, M.E. 2011. The folklore of dinosaur trackways in China: Impact on Paleontology. *Ichnos* 18: 213–220.
- Xing, L.D., Klein, H., Lockley, M.G., Chen, W., Ye, Y., Matsukawa, M., and Zhang, J. 2013. Earliest records from China of theropod and mammal-like tetrapod footprints in the Late Triassic of Sichuan Basin. *Vertebrata Palasiatica* 51 (3): 184–198.
- Xu, Z.H., Wang, Z.C., Hu, S.Y., Zhu, S.F., and Jiang, Q.C. 2010. Paleoclimate during depositional period of the Upper Triassic Xujiahe Formation in Sichuan Basin. *Journal of Palaeogeography* 12: 415–424.
- Yang, X.L. and Yang, D.H. 1987. *Dinosaur Footprints of Sichuan Basin* [in Chinese]. 30 pp. Sichuan Scientific & Technical Publisher, Chengdu.