

First chirothere and possible grallatorid footprint assemblage from the Upper Triassic Baoding Formation of Sichuan Province, southwestern China



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ABSTRACT

Trackways of archosaurs have recently been discovered in sandstones of the Upper Triassic (Norian–Rhaetian) Baoding Formation of Panzhihua City in southern Sichuan Province, China. Based on their overall-morphology, pes imprints are of characteristic chirotheriid shape showing a compact and symmetrical anterior group of digit traces II–IV with the trace of digit III being the longest, and a posterolaterally positioned, long and slender trace of digit V. Imprints of digit I and the manus are not preserved. This could be related to substrate conditions and the relatively shallow impressions, even if peculiarities in the gait such as overstep of the manus by the pes or bipedal movement cannot completely be excluded. Ichnotaxonomically, the imprints are assigned tentatively to cf. *Chirotherium*. There are some similarities with the type ichnospecies *C. barthii* from the Middle Triassic that has a global distribution and that was described also from the Guanling Formation (Middle Triassic) of adjacent Guizhou Province. However, the long and slender digit V that lacks a distinct large oval basal pad, the relatively short stride/step length, the low pace angulation, and the slight inward rotation of the imprints toward the mid-line are different. The peculiar shape of digit V and the lack of digit I in all imprints also preclude an assignment to the common Late Triassic ichnogenus *Brachychirotherium* or similar ichnotaxa such as *Pseudotetrasauropus*. An isolated tridactyl footprint on the same surface is different in shape from the chirotheriid ones by the stronger mesaxony and narrower digit divarication. It is considered here as a possible large grallatorid. This is the first occurrence of tetrapod footprints in the Baoding Formation of Sichuan Province and the second record of chirotheriids in the Triassic of China. The Baoding Formation has also yielded a characteristic Upper Triassic flora with cycads, filicopsids, ginkgos, and conifers as well as bivalve fossils. The depositional environment can be designated as fluvial-lacustrine with occasional opening to marine areas. Considering biostratigraphic and palaeobiogeographic aspects, the late occurrence of chirotheriids cf. *Chirotherium* in China supports the view that basal crown-group archosaurs with a distinct tendency toward a functionally tridactyl pes developed and dispersed in parallel to typical tridactyl dinosaurs.

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1. Introduction

Sichuan Province is the sole region in China that yielded Late Triassic vertebrate tracks. These include theropod and mammal-like tetrapod footprints (Xing et al., 2013a), and an archosaur trackway indicating a possible bipedal trackmaker (Xing et al., in press). Thus far they have been the single clue for understanding Late Triassic vertebrate assemblages from the Sichuan Basin. Middle Triassic *Chirotherium barthii*

trackways were also discovered in the neighboring Guizhou Province (Xing et al., 2013b). Compared with the footprint record from Jurassic and Cretaceous deposits of China, the Triassic evidences are rare.

In 2012, following a hint from the local villagers, Xuezhi Li (the chairman of the Photography Association of Panzhihua City) and Wei Wu, visited the Doudi (“beans place”) tracksite near Panzhihua, southern Sichuan in order to investigate large footprints which they considered to be those of dinosaurs. After the report of Li and Wu, the major authors (Xing L. and Kan Z.) of this paper studied the tracksite again in November, 2013. Here we describe the first tetrapod tracks from the Panzhihua area and the fourth record from the Triassic of China.

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2. Geologic setting

The Baoding Basin is situated at the southwest of Panzhihua City in southern Sichuan Province (Fig. 1A–B). Geotectonically, the basin lies on The Chuan–Dian–Qian (Sichuan–Yunnan–Guizhou) rhombic massif at the western border of the Yangtze paraplatform (Shao et al., 2008). From base to top, deposits of the Baoding Basin are divided into the Bingnan Formation (Lower Triassic), the Daqiaodi Formation (Upper Triassic) and the Baoding Formation (Upper Triassic), of which the Daqiaodi Formation is mainly a coal-bearing unit (Mao, 2004).

The tracks were discovered on the surface of a fine quartz sandstone in the upper part of the Upper Member of the Upper Triassic Baoding Formation (Gu and Liu, 1997), near Doudi, Baoanying Village in Renhe District of Panzhihua City, Sichuan Province (Fig. 1C). Characteristic features of the track-bearing layer are indistinct parallel bedding, ripple marks and invertebrate traces that have not been studied yet. The sedimentary environment of the upper Baoding Formation varies from meandering river delta to lacustrine (Shao et al., 2008). The Baoding Formation can be compared with the Baiguowan Formation of the Xichang area and the Xujiahe Formation of the Sichuan Basin in stratigraphy and age (Gu and Liu, 1997). It originates from the Daqing Layer that represents the upper part of the Nalaqing Coal Series (Zeng, 1945) quarried at the Baoding coal mine of western Panzhihua City and consists mainly of a series of sandstones and mudstones formed in a fluvio-lacustrine depositional environment (Ma et al., 2001). The Baoding Formation is widely distributed in the Panzhihua area. Tectonically, there is a parallel unconformity between the Baoding Formation and the underlying Daqiaodi Formation with the eastern portion of the Panzhihua Fracture Zone covering the Lower Triassic Bingnan Formation or other strata (Xu et al., 1979a,b; Ma et al., 2001). In the Baoanying area the

Baoding Formation covers palaeoproterozoic rocks with biotite-quartz diorite, and is conformably overlain by a mudstone–siltstone succession of the Lower Jurassic Yimen Formation (Fig. 1C).

The Daqiaodi Formation beneath the Baoding Formation is mainly distributed in the Baoding and Hongni basins and is the major coal-bearing unit in the Panzhihua area. The thickness of the Daqiaodi Formation is 2260 m. Its lithology is dominated by gray, gray–green, dark gray fine–coarse feldspathic quartz sandstone, conglomerate mixed with siltstone, mudstone, shale and coal beds. Conglomerates, sandstones, siltstones and mudstones commonly form a rhythmic layering, the upper layer being mixed with a coal bed that yielded rich plant fossils.

2.1. Biostratigraphy and age

The Late Triassic Daqiaodi and Baoding formations of the Panzhihua area are rich in plant fossils, which pertain to the Baoding flora assigned by Xu et al. (1979a,b). The Baoding flora can be divided into two floral associations, i.e. the Daqiaodi floral association yielded from the Daqiaodi Formation and the Daqing floral association yielded from the Baoding Formation. The Daqiaodi floral association is composed of more than 50 genera and approximately 130 species of plant fossils, all pertaining to Pteridophyta and Gymnospermae, dominated by cycads, followed by filicopsids, while other plant types are rare. Biostratigraphically the assemblage is characteristic of the early–middle Carnian–Norian (Late Triassic) interval. The diversity of the Daqing floral association is lower, all in all 15 genera and 24 species are known, Filicopsida account for 50% of all taxa, cycads are less dominant compared with the Daqiaodi floral association. Coniferales and Ginkgoales occur with several new species. It is a unique tropical flora, which is comparable with the Keuper flora from the Alps region in southern Europe. Especially the presence

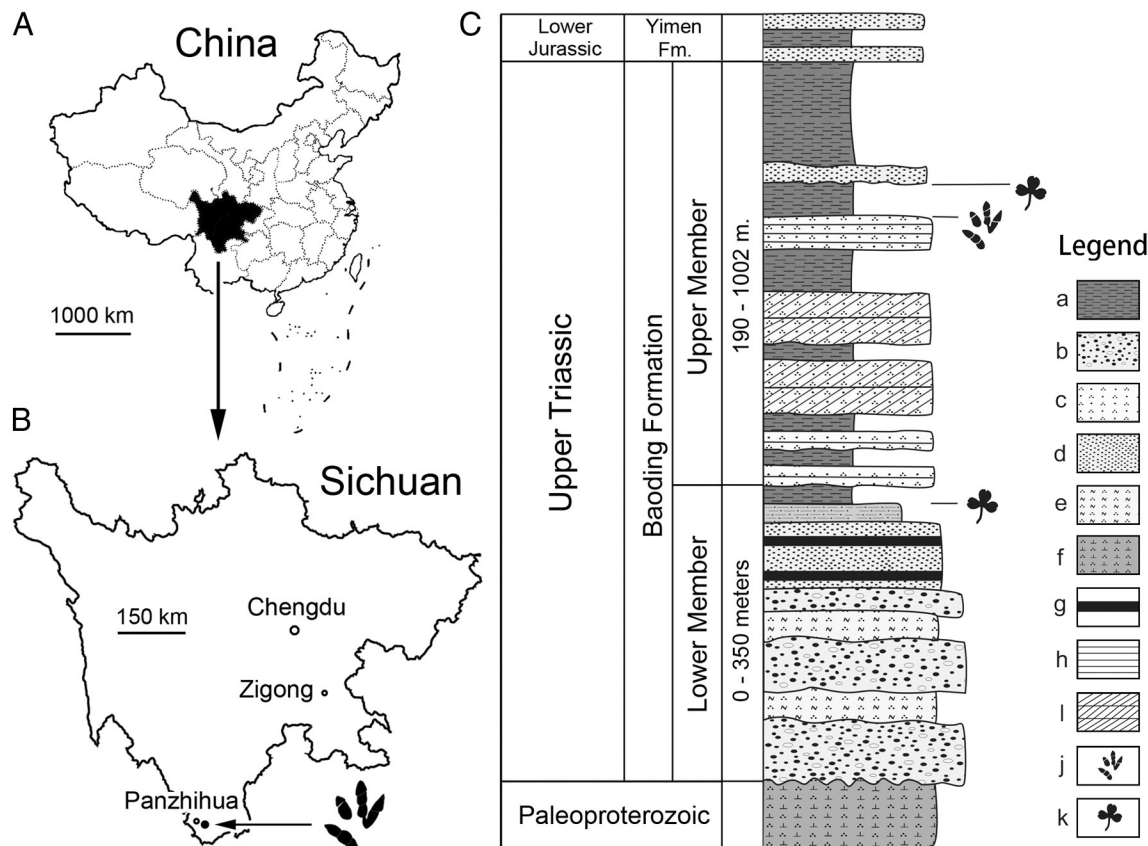


Fig. 1. A–B, map with study area and position of the Panzhihua track locality. C, section with the Baoding Formation showing levels with tracks and plant fossils. Legend: a, mudstone; b, conglomerate; c, quartz sandstone; d, siltstone; e, feldspathic quartz sandstone; f, biotite-quartz diorite; g, coal; h, parallel bedding; i, low angle cross bedding; j, footprints; k, plant fossils.

of different *Podozamites* species is in contrast with the Daqiaodi floral association, indicating that the geological age is younger than that of the Daqiaodi floral association. The profile is akin to the Late Triassic Xujiahe Formation flora at Ya'an, Guangyuan of the Sichuan Basin (Li, 1964; Hu, 1974; PTFMS, 1982). Also, characteristic Early Jurassic plants such as the index fossil *Coniopteris hymenophylloides* have not been found, suggesting a pre-Jurassic, probably middle–late Late Triassic (late Norian–Rhaetian) age.

Furthermore, the dark gray and gray black shale and the silty shale of the middle–lower part of the Baoding Formation of the Panzhihua area indicate brackish water, and provided a small fossil sample with a saline water bivalve fauna containing *Pergamidia*, *Grammatodon*, *Modiolus* and *Thracia*. After Ma et al. (2001), the assemblage indicates a Late Triassic (Norian or Norian–Rhaetian) age. The determined taxa are common in the purported coeval Xujiahe Formation of the Sichuan Basin.

In general, the Baoding Formation is equal to the Baiguowan Formation of the Xichang area and the Xujiahe Formation of the Sichuan Basin after data from sequence stratigraphy and by the geological age being middle–late Late Triassic (late Norian–Rhaetian).

2.2. Sedimentary environment

Lithological associations and sedimentary features of the Baoding Formation, indicate that it is basically a fluvio-lacustrine succession, while estuarine sediments are less well represented at a few stratigraphic intervals. While the Lower Member is dominated by fluvial and flood-generated paludal sediments, the Upper Member is lacustrine. The sandstones of the latter are mostly shoreline lacustrine deposits, while front delta sediments were recognized only locally. The siltstone and some fine-sandstone and mudstone can be designated as shallow lacustrine, whereas the dark deep mudstone and the silty mudstone containing siderite concretions mostly represent deeper lacustrine sediments. Based on the wide distribution and deposition on palaeoproterozoic rocks, the dominating sedimentary environment of the Baoding Formation can be designated as a large lake basin with occasional marine influence and connection to the ocean, the latter being indicated by a bivalve fauna (PTFMS, 1982; see above).

3. Materials and methods

The material comprises an in situ surface of ~8 m² with 13 pes imprints including 3 trackway segments and 4 isolated imprints, and a loose block with 2 pes imprints that constitute a partial trackway. The former was left in the field, the tracks given the identification numbers PT1–T3 (P = Panzhihua locality, T = Trackway). The latter was collected and is now housed under PT0 at the Liujian Paleontology Museum. All tracks, preserved as concave epireliefs, come from a locality situated along the road at Baoanying Village and have been exposed for more than a decade. The loose block was found at a distance of about ten meters from the larger surface, and shows a similar lithology. The minor weathering suggests that it fell down more recently and the time of exposure has been quite short. When removing the overlying mud from the surface of the rocks, a map of the distribution of tracks was made on transparency film. Photographs were taken under natural light in the field. Unfortunately, shadows on the surface resulting from the surrounding trees could not be completely avoided.

4. Systematic paleoichnology

4.1. Ichnofamily Chirotheriidae Abel, 1935

4.1.1. cf. *Chirotherium* Kaup, 1835a

4.1.1.1. *Referred specimens.* 2 trackways with 4 successive pes imprints (PT1–T2) and 1 trackway with 3 successive pes imprints (PT3) on a

single surface; a partial trackway (PT0) representing one step on a fallen block; 3 isolated pes imprints (PI1, PI2, PI3) (Figs. 2–6).

4.1.1.2. *Description.* Large pes imprints with a length that ranges from 25 cm to 43.5 cm and a width that ranges from 32 cm to 41 cm, depending on their completeness and absence/presence of a digit V trace (Table 1). Considering the anterior digit group as a reference, all imprints are of similar length (25–27 cm). Only digits II–V are impressed, a trace of digit I is missing. A small “digit-like” structure near the medial margin of PTOL1 (Fig. 2) is a sedimentary feature and not related to a digit impression. Digits II–IV form a symmetrical anterior digit group with digit III being longest. Digits are moderately spread with the angle between digits II and IV being 54° on average (range 43°–60°). In well-preserved specimens such as PTOL1 and PT1R1 digits II and III seem to be more closely aligned at their base whereas digit IV is strictly separated (Figs. 2, 5). Digits are cigar-like, or spindle to fusiform in shape, tapering at their distal ends, in digits II–IV suggesting the presence of triangular claws (Fig. 2). Digit V is slender and elongated, slightly curved outward, and similar in width to other digits. Pad traces are more distinctly preserved in the second imprint of PT0 (Fig. 2). In digits II, III and V these are three elongated-oval impressions, the most proximal ones in digits II and V possibly representing traces of the metatarsophalangeal pads. Digit IV is only impressed by a short distal portion and indistinctly shows two phalangeal pads. The trace of the basal pad in digit V is not enlarged in width compared with the more distal parts of the digit. A trace of the manus is missing. The trackway shows a narrow pattern with a pace angulation of up to 175° and a relatively short stride and pace length of 172.5 cm and 91 cm, respectively (Table 1). Imprints are slightly turned inward along digit III and relative to the midline by 4°–15°.

4.1.1.3. *Preservational features.* Wrinkle structures characterized by crescent bulges and preserved in positive epirelief on top of the track level can be observed along with the footprints (Fig. 5). Such phenomena have generally been related to the presence of microbial mats (Hagadorn and Bottjer, 1997; Noffke et al., 2002). In the Panzhihua tracks wrinkles are distinctly ruptured and concentrated on the more proximal portion of the tracks whereas the tiptoes of digits II, III and IV lack these completely. This is due to the different weight distribution during progression causing the tiptoes breaking through the surface. The influence of microbial mats and early cementation in the formation and preservation of vertebrate tracks has been examined by various authors (Marty et al., 2009; Carmona et al. 2011; Carvalho et al., 2013).

4.1.1.4. *Discussion.* The overall-shape of the imprints resembles typical pentadactyl chirotheriids of the ichnogenus *Chirotherium* (Kaup, 1835a,b). *Chirotherium* is characterized by a pronounced anterior digit group II–IV with digit III being longest and digit I being strongly reduced and/or posteriorly shifted and digit V being positioned posterolaterally to other digits with a distinct outward or backward curvature. *Chirotherium* is distinguished by these features from other chirotheriids that have a pronounced digit group I–IV and digit proportions with (1) digits II and III dominating while I and IV are short (*Isochirotherium*), (2) digit IV shorter than II (*Brachychirotherium*), (3) digit IV relatively long being longest or subequal with III (*Synaptichnium*) or slightly shorter than III (*Protochirotherium*) (Haubold, 1971a,b, 2006; Karl and Haubold, 1998; Haubold and Klein, 2002; Klein and Haubold, 2003, 2004; Fichter and Kunz, 2004; Klein et al., 2013). Whereas the digit proportions of the Panzhihua tracks preclude an assignment to *Isochirotherium*, *Synaptichnium* and *Protochirotherium*, the relatively broad shape of some imprints, the robust, rounded digits and their proportions with digit IV being (in some cases) shorter than I, also slightly resembles the ichnogenus *Brachychirotherium* and *Pseudotetrasauropus*. However, in the latter two the digit V trace is reduced to a short oval impression lacking a separated phalangeal portion, a feature that is diagnostic of *Brachychirotherium* (Karl and Haubold,

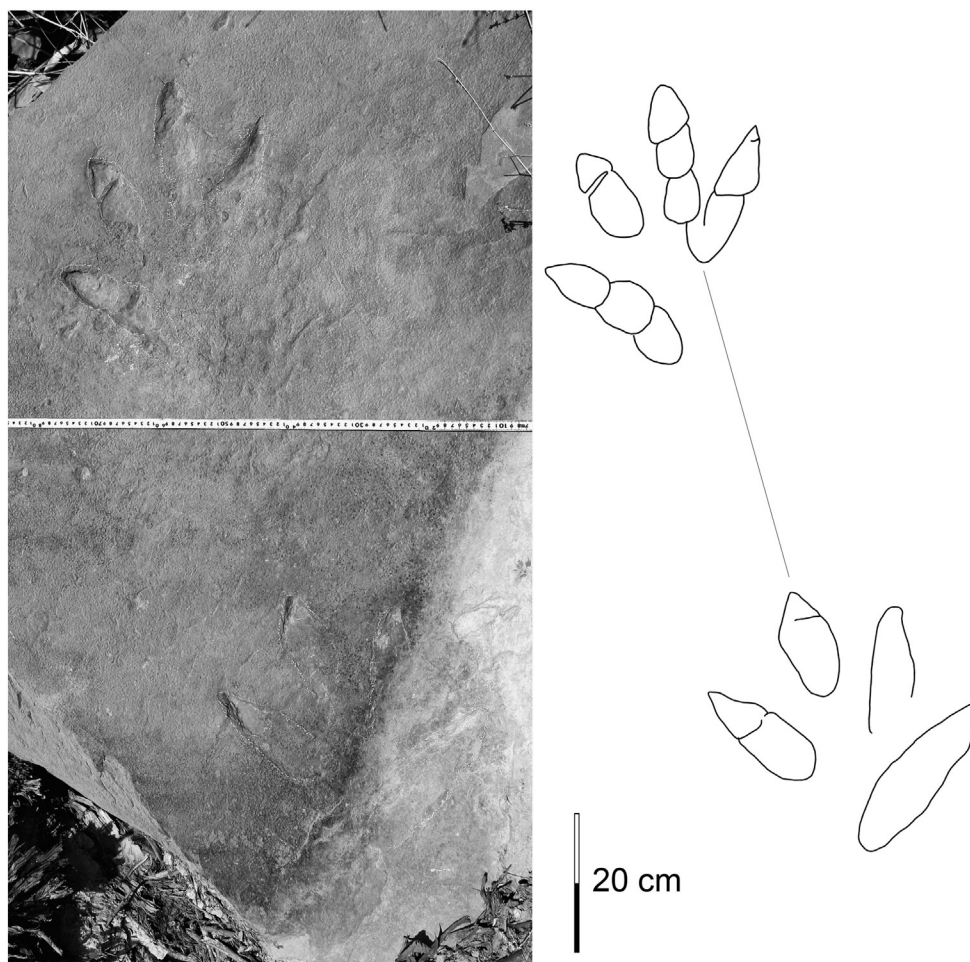


Fig. 2. Photograph and sketch of partial trackway on a fallen block (PT0) with two successive pes tracks assigned here to cf. *Chirotherium* from the Panzhihua locality. Notice shallow impressions and lack of traces of digit I and the manus.

1998). Contrary, well-preserved chirotheriid tracks from Panzhihua locality display distinct pads of digit V, probably including a phalangeal portion (Fig. 2). In *Brachychirotherium*, as in the Panzhihua tracks, the relatively robust digit I can occasionally be missing, but would be expected to occur at least in some imprints on the surface. Observations

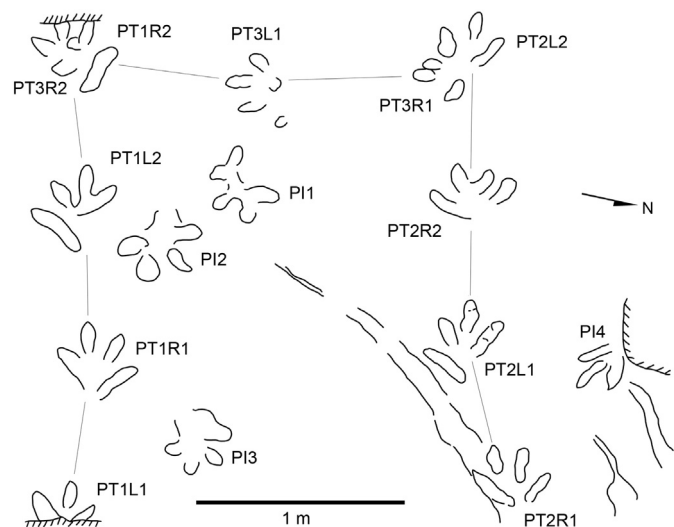


Fig. 3. Map of track surface at Panzhihua locality with different trackways and isolated imprints assigned here to cf. *Chirotherium*. Notice possible large gallatorid pes imprint (PI4) at right.

based on *Brachychirotherium* from strata providing the type material indicate that the complete lack of pedal digit I in the imprints is generally the exception (see Karl and Haubold, 1998). Therefore an assignment to the ichnogenus is less plausible. On the other hand especially *Chirotherium barthii* and morphologically similar forms such as *Sphingopus* and *Parachirotherium* (Demathieu, 1966, fig. 1; Haubold and Klein, 2000, figs. 3, 6, 9G–I, 2002, figs. 4A, 6, 7, 8A, 9) are comparable to the Panzhihua tracks by their overall-shape. Interestingly, the Panzhihua tracks show a close alignment of digits II and III at their base (see above). Haubold (1971a, p. 445) lists a large basal pad connecting the basis of pedal digits II and III as a diagnostic feature of *C. barthii*. However, in *C. barthii* digit V shows a massive rounded to oval basal pad, a feature missing in the Panzhihua tracks, whereas in the latter digit V is slender along its total length. In *Sphingopus* and *Parachirotherium*, digit V is more strongly reduced but occasionally shows a small backward curved phalangeal portion. The Panzhihua tracks also differ from typical chirotheriids by the lack of a digit I impression, by the trackway pattern with relatively short stride and pace lengths (Table 1), the slight rotation of the pes imprints toward the midline (along digit III) which in the latter are more or less turned outward, and by the lack of a distinct manus trace. It has to be noted that in *Sphingopus*, pedal digit I is mostly absent except of a trace of the claw tip (Demathieu, 1966, fig. 1, 1970, fig. 61; Haubold and Klein, 2002, figs. 6B–C, 7). The lack of the traces of a massive basal pad of digit V, digit I and the manus in the Panzhihua tracks could possibly be explained by the shallow impressions and/or the presence of undertracks (Milàn and Bromley, 2006, 2008; Castanera et al., 2013). However, this cannot be proved presently and further material from this locality is

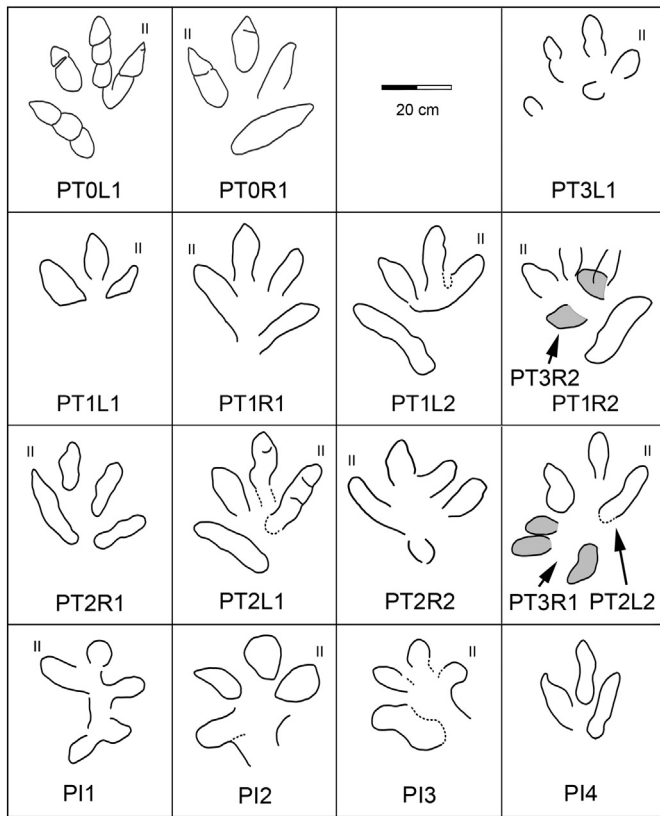


Fig. 4. Sketches showing details of chirotheriid footprints cf. *Chirotherium* and possible grallatorid track (PI4) from the Panzhihua locality.

needed to test this. Alternatively, the lack of a manus could be due to a bipedal progression, or the manus having been overstepped by the pes. The slender digit traces of the imprints and the overall-shape slightly resemble also some chirotheriid tracks from the Middle Triassic of Guizhou (southwestern China) (Xing et al., 2013a,b, figs. 3–7) that have been determined by the present authors as *C. barthii*. Despite the

observed differences to other known trackways, the overall-morphology of the Panzhihua tracks is typically chirotheriid. By the pronounced and symmetrical anterior digit group II–IV with digit III being longest and by the posterolaterally positioned, long and outward curved digit V they are determined here tentatively as cf. *Chirotherium* considering the prevailing congruence with the ichnogenus as well as some remarkable differences. Nevertheless we cannot exclude the possibility that future findings and supplementary material make it necessary to establish a new chirotheriid taxon. The distinct pattern of the Panzhihua tracks is possibly the expression of an evolutionary trend in the pes of some basal archosaurs between the Middle and Upper Triassic, in this case perhaps the reduction of pedal digit I. Chirotheriid footprints that are otherwise characteristic for Middle Triassic assemblages have been described recently from Upper Triassic deposits of Morocco (Lagnaoui et al., 2012). It is well known that the degree of anterior or posterior emphasis represented by chirotherian and other archosaurian trackmakers can be gaged by looking at the relative size of the manus and pes (Peabody, 1948; Avanzini and Lockley, 2002; Lockley, 2007). Therefore the morphological spectrum from bipedal to small manus to large manus forms reflects degree of anterior emphasis and weight distribution relative to the pelvic and pectoral girdles.

4.1.1.5. Trackmaker affinities. Chirotheriid tracks have been attributed to basal archosaurs such as non-crown-group archosauriforms, stem-group crocodylians and basal members of the dinosaur-bird-line (Avenetatarsalia sensu Benton, 1999) (Haubold, 1967, 1971a,b, 2006; Demathieu and Haubold, 1974; Haubold and Klein, 2000, 2002; Heckert et al., 2010; Lucas and Heckert, 2011; Desojo et al., 2013; Farlow et al., 2014). Contrary to other chirotheriids the ichnogenus *Chirotherium* shows an early trend toward the mesaxonian tridactyl morphology of the pes seen in Dinosauriforma by the reduction of digits I and V (Haubold and Klein, 2000, 2002). However, Farlow et al. (2014) recently demonstrated that some crocodile-line archosaurs such as the poposauroid *Poposaurus gracilis* in parallel developed a very dinosaur-like pes and that members of this latter species probably left footprints of dinosaur-like shape. Obviously the mesaxonian tridactyl pes evolved independently in different archosaur groups, though with apparently similar or “convergent” morphodynamic trends at least in

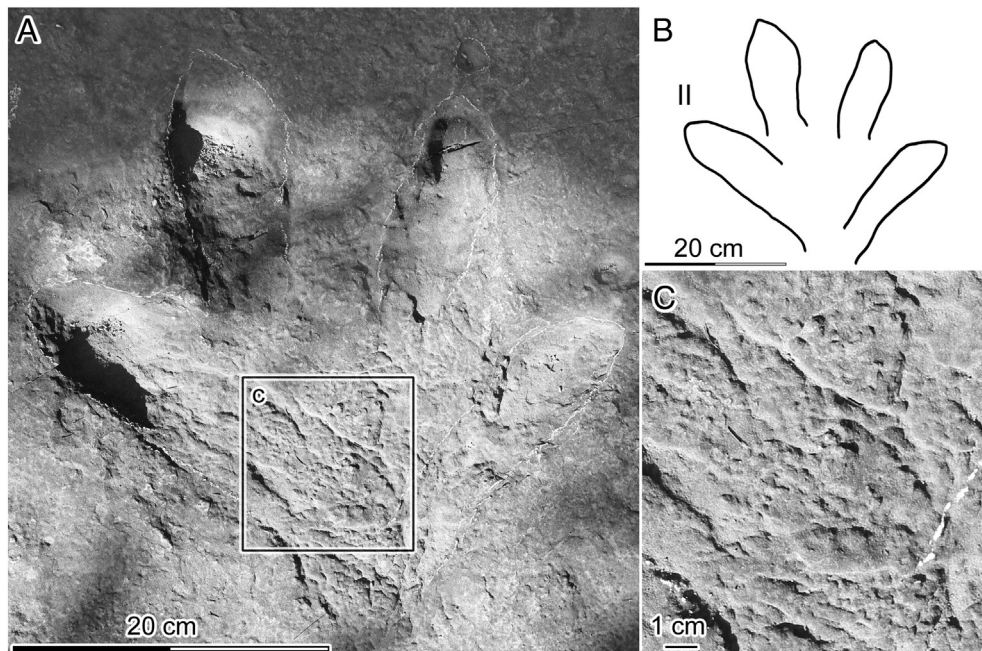


Fig. 5. Photographs (A, C) and sketch (B) showing details with microbial mat structures in chirotheriid footprint cf. *Chirotherium* (PT1R1) from the Panzhihua locality. Position of C demarcated in A by rectangle. Notice lack of microbial mat structures in tiptoes II, III and IV.

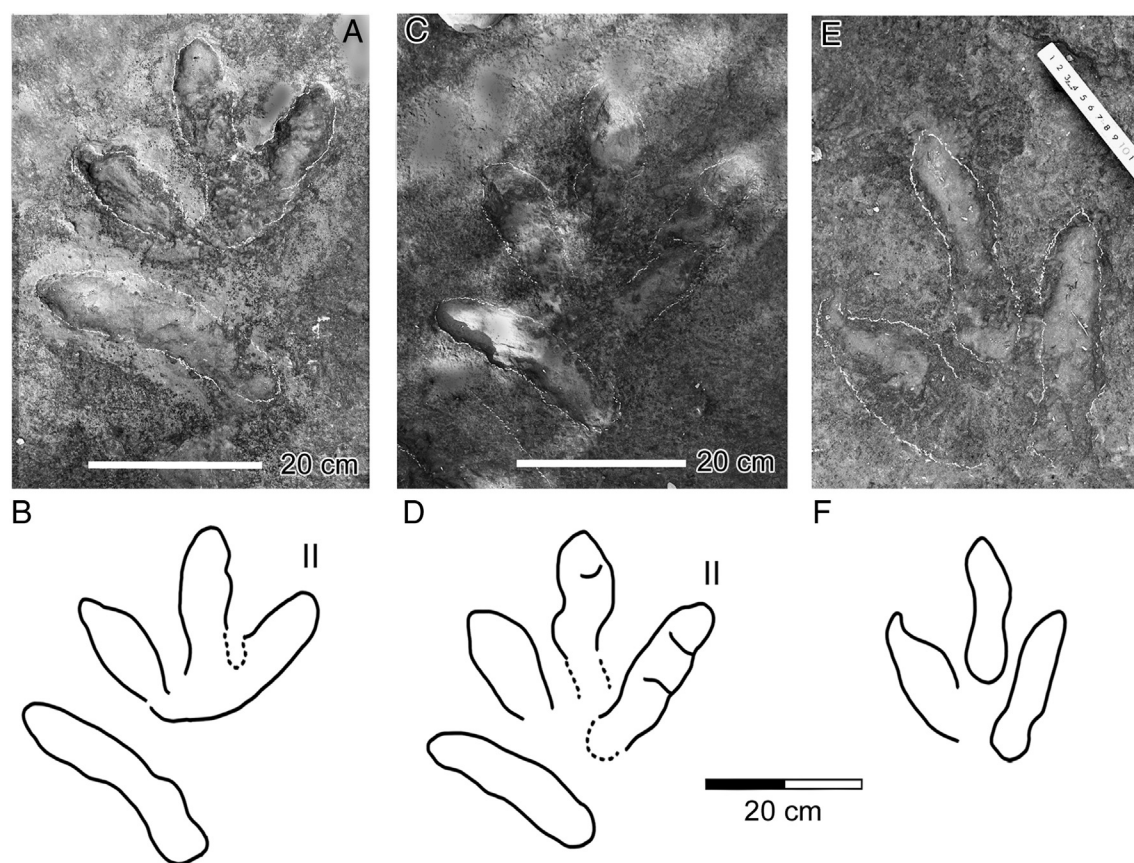


Fig. 6. Photographs and corresponding sketches of chirotheriid footprints cf. *Chirotherium* PT1L2 (A–B) and PT2L1 (C–D), and of possible large grallatorid footprint PI4 (E–F). Notice differences in mesaxony and digit divarication of both morphotypes.

some cases (Lockley, 2007, 2009). Therefore the Panzhihua tracks are attributed here to basal archosaurs without a concrete specification.

4.2. Possible grallatorid

4.2.1. Referred specimen

An isolated pes imprint (PI4) (Figs. 3–4, 6E–F).

4.2.2. Description

The footprint is 27 cm long and 22 cm wide. It is tridactyl and symmetrical along digit III which is the longest. The supposed digit II shows

a sharp claw trace that points slightly outward. If interpreted correctly, digit IV displays a distinct circular metatarsophalangeal pad proximally.

4.2.3. Discussion

Despite its position close to an escarpment in the surface, it seems that this footprint lacks a digit V. It shows a stronger mesaxony compared with the chirotheriid imprints as well as a smaller divarication of digits, appearing more slender in overall-shape. Morphologically it is similar to the typical grallatorid forms of the *Grallator*–*Anchisauripus*–*Eubrontes*-plexus (Olsen et al., 1998) and after its size would match the ichnogenus *Eubrontes*. However, its length is the same as that of the

Table 1

Measurements (in centimeters and degrees) of cf. *Chirotherium* tracks from the Doudi tracksites. Abbreviations: LD II: length of digit II; LD III: length of digit III; LD IV: length of digit IV; LD V: length of digit V; ML: maximum length; MW: maximum width*; PA: Pace angulation; PL: Pace length; SL: Stride length; II–IV: angle between digits II and IV; II–V: angle between digits II and V; L/W: Maximum length/Maximum width.

Number	ML	MW*	LD II	LD III	LD IV	LD V	II–IV	II–V	PL	SL	PA	L/W
PT0L1	41.0	37.0	22.5	21.5	14.5	23.5	43°	73°	78.0	–	–	1.1
PT0R1	39.0	39.0	19.0	15.5	19.0	26.0	51°	83°	–	–	–	1.0
PT1L1	>20	–	–	–	–	–	–	–	78.5	154.0	–	–
PT1R1	39.0	38.0	24.0	16.0	15.5	23.5	57°	89°	76.0	147.5	174°	1.0
PT1L2	43.5	41.0	23.0	15.5	17.0	30.5	48°	74°	72.0	–	–	1.1
PT1R2	>36.5	38.5	>12.5	>10	12.0	26.5	–	–	–	–	–	–
PT2R1	32.0	37.0	26.5	14.5	17.0	17.5	52°	94°	72.5	140.5	–	0.9
PT2L1	41.0	39.5	21.0	16.0	16.5	25.5	54°	85°	67.5	142.0	175°	1.0
PT2R2	28.0	38.5	23.5	14.5	14.0	29.0	58°	78°	75.0	–	166°	0.7
PT2L2	26.0	–	19.0	13.5	15.0	–	–	–	–	–	–	–
PT3R1	25.0	–	13.5	11.5	10.0	–	–	–	91.0	172.5	–	–
PT3L1	>30.0	35.0	19.5	13.5	13.5	6.0	–	–	82.0	–	–	–
PI1	38.0	34.0	17.5	12.0	11.0	20.5	59°	79	–	–	–	–
PI2	36.0	39.5	15.0	13.0	15.0	23.0	–	–	–	–	–	0.9
PI3	32.0	32.0	9.5	13.0	11.5	28.0	60°	88°	–	–	–	1.0
PI4	27.0	–	18.0	18.5	17.5	–	–	–	–	–	–	1.1

* Tracks measured as distance between the tips of digits II and V.

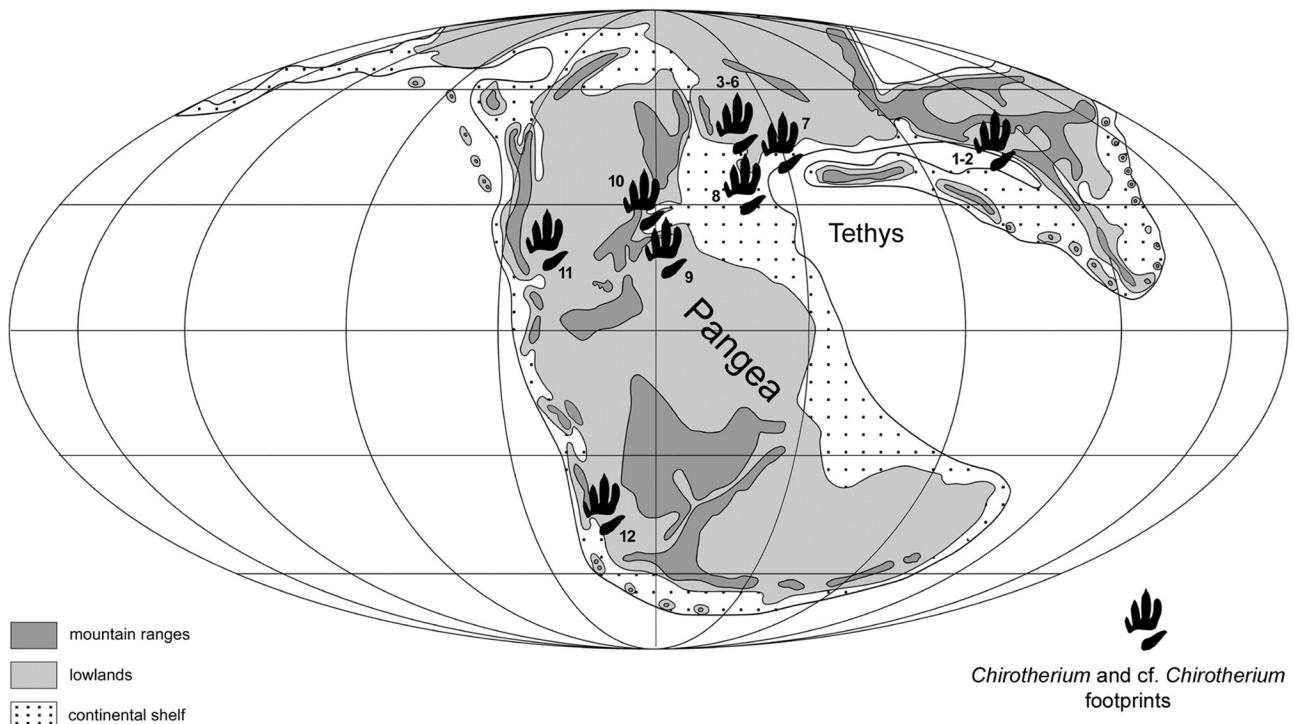


Fig. 7. Map showing the distribution of the ichnogenus *Chirotherium* (including cf. *Chirotherium* described in this study) on Triassic Pangea. 1–2, Ghuizou and Sichuan provinces, China; 3–6, Great Britain, France, Germany, Poland; 7, Italy; 8, Spain; 9, Argana Basin, Morocco; 10, eastern USA; 11, western USA; 12, Argentina. Base map after [Wing and Sues \(1992\)](#).

anterior digit group II–IV of the chirotheriid tracks, and therefore it cannot be completely excluded that this is simply an incomplete chirotheriid lacking digit V. If this is truly a large grallatorid, this is the second report of theropod tracks from the Late Triassic of Sichuan Province and China. From the Upper Triassic Xujiahe Formation of the Sichuan Basin large theropod tracks that belong to the ichnogenus *Pengxianpus* were described ([Xing et al., 2013a](#)).

5. Biostratigraphic and palaeobiogeographic indications from the footprints

In the recent years tetrapod footprints have been progressively used for biostratigraphy and biochronology of the Triassic and different sequences of footprint assemblages were proposed by various authors ([Lucas, 2003, 2007](#); [Hunt and Lucas, 2007](#); [Klein and Haubold, 2007](#); [Klein and Lucas, 2010](#)). [Klein and Lucas \(2010\)](#) established five biochrons in the Triassic, one of them, the “*Chirotherium barthii* biochron” was defined between the first appearance datum (FAD sensu [Lucas, 1998, 2010](#)) of *C. barthii* near the Lower/Middle Triassic (Olenekian–Anisian) boundary and the first appearance datum of *Atreipus–Grallator–plexus* footprints in the Early Middle Triassic (Anisian). The upper stratigraphic range of *C. barthii* and morphologically similar footprints such as *Sphingopus* and *Parachirotherium* into the Late Anisian–Ladinian and even into the Late Triassic (Carnian) has been documented in the recent years ([Haubold and Klein, 2000, 2002](#); [Avanzini and Wachtler, 2012](#); [Lagnaoui et al., 2012](#)). Obviously, chirotheriid tracks with a pronounced symmetrical (“grallatorid”) digit group II–IV, a strongly reduced (or absent) digit I and a posterolaterally positioned digit V in the pes, a characteristic morphotype of the Middle Triassic, continued into the Late Triassic. Their range overlaps the *Brachychirotherium* biochron which is demarcated by the first appearance datum of the ichnogenus *Brachychirotherium* at the beginning of the Late Triassic.

Paleobiogeographically, chirotheriid trackmakers with a functionally tridactyl pes had a wide distribution on Triassic Pangea ([Fig. 7](#)). The

global dispersal of trackmakers proceeded in parallel to that of dinosaurs between the Middle and Upper Triassic. These were probably basal crown-group archosaurs that belong to crocodylian stem and/or dinosaur–bird line groups. The late representatives of a characteristic Middle Triassic morphotype in the Upper Triassic of China support this view.

6. Conclusions

Chirotheriid tracks from the Upper Triassic Baoding Formation of Sichuan Province increase the scarce reports of track sites from the Triassic of China as well as the stratigraphic range of a typical Middle Triassic morphotype reflecting a functionally tridactyl pes. The new discoveries are assigned tentatively to cf. *Chirotherium* considering morphological congruences and differences to the ichnogenus that is known with the ichnospecies *Chirotherium barthii* also from Middle Triassic deposits of Ghuizhou Province. The lack of pedal digit I and a manus might be an extramorphological feature or anatomically/gait related. Together with peculiarities in the trackway pattern such as the short stride/step and the slight inward rotation of the pes imprints this could also point to a new ichnotaxon, however further material is needed to evaluate this. Trackmakers were basal archosaurs, either stem-crocodylians such as poposauroids and basal representatives of the dinosaur–bird-line.

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