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Chirotherium Trackways from the Middle Triassic of Guizhou, China

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Triassic tetrapod footprints from China are less well known than those from the Jurassic and Cretaceous. Archosaurian trackways of the ichnogenus *Chirotherium* were found in the Middle Triassic Guanling Formation in Zhenfeng County (Guizhou Province) at the southwestern edge of the Yangtze plate in the early 1960s but were not correctly identified and adequately described until 40 years later. Here we give a detailed re-description and review of the trackways, which are known from two localities near the villages of Niuchang and Longchang. They occur on the bedding surface of a mud-cracked argillaceous dolostone deposited in a near-shore, shallow-water environment. Their morphology and general trackway pattern indicate that they pertain to the ichnospecies *Chirotherium barthii*, well known from Middle Triassic track surfaces of Europe, North and South America, and northern Africa. A peculiarity of the trackways from China are the low pace angulation and stride length, reflecting slow-moving trackmakers, which were basal crown-group archosaurs, possibly early representatives of the dinosaur-bird line or, alternatively, stem-group crocodylians. These tracks constitute the only chirotheriid record known from Asia thus far and indicate a Pangea-wide distribution for this ichnotaxon. Biostratigraphically, assemblages with *C. barthii* are characteristic of the early Anisian, an age assignment already supported for the Guanling Formation based on conodont and bivalve biostratigraphy. In contrast, however, radiometric data from an interlayered ash bed indicate a Ladinian age.

Keywords *Chirotherium barthii*, Middle Triassic, Basal archosaurs, Guanling Formation

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INTRODUCTION

Pentadactyl footprints of quadrupedal basal archosaurs (chirotheriids) are the main component of numerous Triassic ichnoassemblages and are known from continental deposits with a Pangea-wide distribution. The early evolution of crocodile- and dinosaur-stem tetrapod groups is reflected in chirotheriid forms, the pes prints of which are characterized by a compact, anterior digit group I–IV and the posteriorly positioned, reduced digit V that sometimes has a thumb-like shape. Narrow trackways indicate that the extremities of the trackmakers were held under the body and the limb movement was directed in a parasagittal plane. Manus imprints that are much smaller than their associated pes imprints indicate distinct tendencies toward bipedality (Haubold, 1971a, b). The locomotory pattern is characteristic for archosaurs and distinguishes chirotherian trackmakers from those of lacertoid groups (e.g., *Rhynchosauroides*, *Procolophonichnium*) with a sprawling posture.

Chirotheriid footprints are known from Lower-Upper Triassic deposits of Europe, North America, South America, northern and southern Africa, and China (Klein and Haubold, 2007; Klein and Lucas, 2010a). The ichnospecies *Chirotherium barthii* and *C. sickleri* from the Thüringischer Chirotheriensandstein (Solling Formation, early Anisian) of Thuringia, Germany, were the first scientifically named tetrapod footprints (Kaup, 1835a, b). Thus far, about 75 chirotherian ichnospecies have been described. Most of them are synonyms and/or extramorphological (substrate-related) variations of perhaps 35 valid ichnotaxa. The excellent preservation of *C. barthii* and *C. sickleri* trackways makes these two ichnospecies some of the best-documented Triassic footprints.

Chirotheriids are subdivided in different ichnogenera. By their morphology and stratigraphic range they reflect different stages of the development of the pes in the course of archosaur evolution: *Protochirotherium* (Early Triassic), *Synaptichnium* (Early–Middle Triassic), *Chirotherium* (Middle Triassic), *Isochirotherium* (Middle Triassic), and *Brachychirotherium* (Late Triassic). Other ichnogenera of similar morphology such as *Parachirotherium* and *Sphingopus* from the Middle Triassic are basically of chirotheriid shape but show transition to tridactyl *Atreipus* and G*rallator* along trackways of facultative bipeds (Haubold and Klein, 2002).

The global distribution pattern of *Chirotherium* (for overviews, see Klein and Lucas, 2010a; Klein et al., 2011) suggests that they were made by successful archosaurian track makers whose habitats were not restricted to distinct latitudes.

Chirotherium from the Guanling Formation of Gouizhou Province, China (Fig. 1) is the only evidence of this ichnogenus, and of chirotheriids from Asia thus far. Numerous trackways and imprints at the Longchang and Niuchang localities exhibit the characteristic pattern of the ichnogenus in both the morphologies of the pes and manus as well as the relative positions of the imprints. We review the research on these footprints since their discovery. We outline the geology of the footprint-bearing strata and describe and discuss the material in detail in order to clarify their ichnospecific assignment.

HISTORY OF RESEARCH

Early in the 1960s, villagers from Shangba Village, Niuchang Townlet (later renamed Beipanjiang Town), Zhenfeng County, discovered some strange "ghostly handprints" while constructing a grain-sunning ground (Fig. 1). These were believed to have been left by deities of ancient China. In April 1988, the Bureau of Municipal and Rural Construction invited the Museum of Guizhou Province to examine these footprints (Wang, 1996). In May 1988, Xuehua Wang and Ji Ma from Regional Geological Survey Teams, Bureau of Geology and Mineral Resources of Guizhou Province, also examined them. Wang and Ji (1989) briefly described the tracks and assigned them to *Chirotherium* sp. but mistook *Chirotherium* as a kind of pentadactyl dinosaur track.

A field crew from the Beijing Museum of Natural History subsequently explored the tracksite. Zhen et al. (1996) mentioned the discoveries and first translated the name *Chirotherium* into Chinese language, meaning "hand beast."

In November 2003, another *Chirotherium* trackway was discovered at the side of the Xingyi Highway at Longchang Village, Zhenfeng County (Fig. 1). Lü et al. (2004) described *Chirotherium* from both the Longchang and Niuchang tracksites, but no ichnospecific assignment was given.

In their review of vertebrate track distributions in east and Southeast Asia, Lockley and Matsukawa (2009) considered

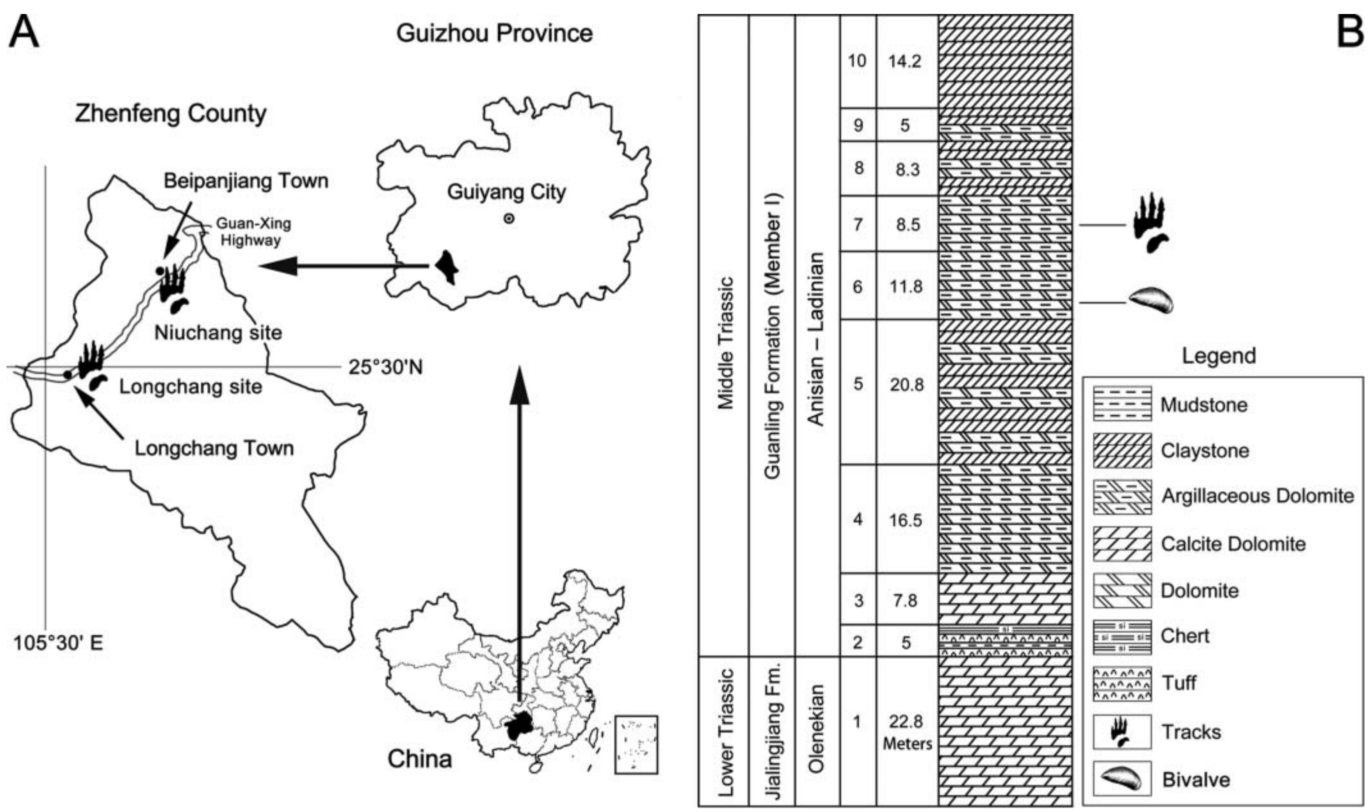

FIG. 1. **A.** Geographic map showing the location (footprint icon) of the Niuchang and Longchang tracksites locality in Zhenfeng County, Guizhou Province, China. **B.** Stratigraphic section of the Lower–Middle Triassic in the study area, showing the Guanling Formation and the position of the trackbearing strata.

the *Chirotherium* tracks from Guizhou Province as similar to those found in Europe and North America. Klein and Lucas (2010a) referred the Niuchang tracks to *Chirotherium barthii*. The identification of the ichnospecies in China lends further support to a late Olenekian–early Anisian *Chirotherium barthii* biochron within a global biostratigraphic framework based on tetrapod footprints. Klein and Lucas (2010a, fig. 6e) figured a left pes-manus set (NC19) but did not give a description.

As the lone *Chirotherium* exemplars discovered in China, valuable information may be derived from the Zhenfeng trackways. The major authors (LX and JX) of this paper explored the Longchang and Niuchang tracksites again in 2011.

MATERIAL AND METHODS

The material described herein comes from two localities in Zhenfeng County (Qianxi'nan Buyei and Miao Autonomous Prefecture) in Guizhou Province (Fig. 1): (1) the Niuchang locality (L-00612; 25°34′28.26″N, 105°39′4.50″E) near Shangba Village, Beipanjiang Town and (2) the Longchang locality (L-00613; 25°28′14.58″N, 105°30′53.82″E) at the roadside of Guanling to Xingyi Highway near Longchang Village, Longchang Town. All footprints are preserved as concave epireliefs.

The Niuchang locality preserves 60 natural molds in three trackways (A–C); the Longchang locality preserves 10 imprints in a single trackway. Only trackway A is presently visible at the Niuchang tracksite, others are covered now by road and farmland. The Longchang trackway is badly weathered and only briefly mentioned here.

Outline-drawings of footprints were carried out on transparency film and digitalized with vector-based drawing software. Latex molds were taken from the main trackway at the Niuchang locality and from individual imprints at the Longchang locality; these replicas are stored at the University of Colorado Dinosaur Tracks Museum at Denver, Colorado, in the United States, and at the Institute of Earth Resources and Information, University of Petroleum, China. Measurements were taken according to the standard methods proposed by Leonardi (1987) and Haubold (1971b).

Institutional Abbreviations

NC: Niuchang locality. LC: Longchang locality. CU: University of Colorado Dinosaur Tracks Museum, Denver, Colorado, USA. "A"–"C" refer to different trackways at Niuchang locality, "m" and "p" to manus and pes, respectively. "L" in locality numbers refers to data of CU.

Ichnological Abbreviations

R, Right footprint of a trackway; L, left footprint of a trackway; ML, maximum length of pes; MW, maximum width of pes; PA, pace angulation of pes; PL, pace length of pes; SL, stride length of pes; TW, trackway width; II–IV: angle between pedal digits II and IV; L/W, maximum length/ maximum width ratio of pes.

GEOLOGICAL SETTING–LITHOSTRATIGRAPHY AND BIOSTRATIGRAPHY

Overview of Stratigraphy

The Niuchang and Longchang tracksites are located at the southwestern edge of the Yangtze Plate and very close to the northwestern edge of the Triassic Youjiang Flysch Basin. The tracks occur in the Middle Triassic Guanling Formation (Wang and Ji, 1989; Lü et al., 2004). The Guanling Formation conformably contacts both the Lower Triassic Jiangling Formation below and the Middle Triassic Liujing Formation above (Guizhou Bureau of Geology and Mineral Resources, 1987; Fig. 1B).

Guanling Formation

The Guanling Formation is located in the lower part of the Middle Triassic succession in Guizhou Province and is mainly composed of limestone, dolostone, and minor claystone strata; its total thickness ranges from 440 m to 810 m. The Guanling Formation is divided into two members: Songzikan (lower member) and Shizishan (upper member) (Guizhou Bureau of Geology and Mineral Resources, 1987; Dong, 1997). The *Chirotherium* trackways are preserved on the bedding surface of the mud-cracked argillaceous dolostone of the Songzikan Member (Fig. 1B) (Wang and Ji, 1989; Lü et al., 2004).

The Songzikan Member (Fig. 1B) is composed of dolostone and variegated claystone. A coarse-grained green pisolite that is rich in volcanic ash (Zhu, 1994) at its base is widely distributed in southwestern China and a pronounced marker for the basal Guanling Formation (Zhu, 1994; Wan, 2002; Xiao and Hu, 2005). ^{40}Ar/^{39}Ar dating of ash in the green pisolite in the Zunyi region, Guizhou Province is 238–239 Ma (Hu et al., 1996). After recent radio-isotopic data by Mundil et al. (2010) this corresponds to the Ladinian. However biostratigraphic data point to an Anisian age. The Songzikan Member yields abundant conodont and bivalve faunas that suggest an early Anisian age throughout southern China (Wang et al., 2005, 2009; Zhang et al., 2009). The lower part of the Songzikan Member that is composed of grey, light grey, yellow grey, and red-flesh-colored micrite dolostone, calcarenite dolostone, and argillaceous dolostone, interbedded with brecciated dolostones, contains the bivalves ? *Leptochondria* sp., *Costatoria goldfussi, Pleuromya* sp. and others (Dong, 1997). Vertebrates are very rare in this unit, except of the sauropterygians, *Chinchenia* and *Sanchiaosaurus,* that show affinities with the eastern Pacific realm as well as the western Tethys (Rieppel, 1999; Li, 2006). *Chinchenia* is closely related to *Corosaurus* from the Alcova Limestone of the Chugwater Group of Wyoming. However, the exact geological age of the Alcova Limestone is uncertain and therefore these remains cannot be used presently for a biostratigraphic correlation.

The Shizishan Member is mainly composed of grey thin to middle bedded vermiformed limestone and argillaceous limestone (Guizhou bureau of geology and mineral resources, 1987; Lü et al., 2004). The Paxian biota (Wang et al., 2009) occurs in this unit and is of middle Anisian (Pelsonian) age based on conodonts of the *Nicoraella kockeli* Zone (Zhang et al., 2009). It contains also numerous tetrapods (ichthyosaurs, nothosaurs, pistosaurs, protorosaurs and archosaurs) and fishes. The divergence of radio-isotopic and biostratigraphic data is an unsolved problem. More data from the Guanling Formation are needed.

PALEOENVIRONMENT

The two tracksites were registered in similar environments. Except for the different overall-sizes and preservation (one has broad digits, the other has slender digits), all characteristics are generally consistent. The facies is typical for an intertidal paleoenvironmental zone (but see Li, 2006). This is indicated by microbial mats, current ripples, and bird-eyes structures (S. Voigt, personal communication, December 9, 2012). The observations conflict with the hypothesis advanced by Lockley and Hunt (1995) that chirotherian footprints are mostly preserved in continental sandstone and mudstone deposits accompanied by intense mud crack formation. The occurrence of chirotheriid footprints in intertidal deposits is rare and reported only from a few localities in Europe (Diedrich, 2009).

SYSTEMATIC PALEOICHNOLOGY

Ichnofamily Chirotheriidae Abel, 1935
Ichnogenus *Chirotherium* Kaup, 1835

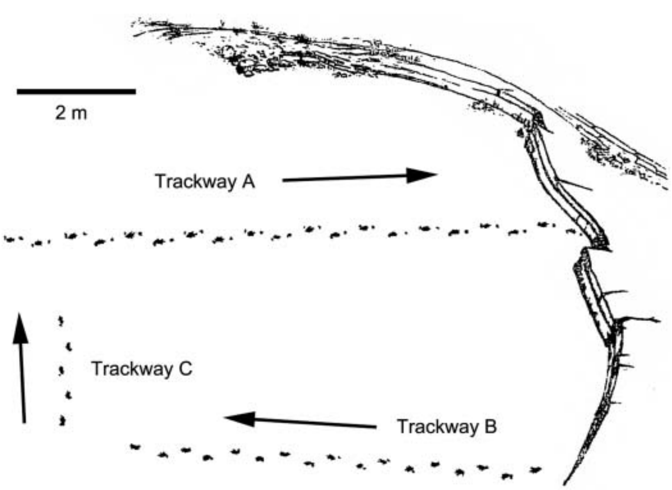

FIG. 2. Map showing the relative positions of the *Chirotherium barthii* trackways (**A**–**C**) on surface at the Niuchang locality. Note that manus imprints are preserved only in trackway A.

Type ichnospecies: *Chirotherium barthii* Kaup, 1835.

Diagnosis: (emended after Peabody, 1948; Haubold, 1971a, b): Medium-size to large chirotheriids, showing low trackway widths, an average pes angulation of 170°, and relatively low stride length values. Manus more strongly turned outward than the pes. Pedal digit group I–IV relatively long and slender, with II–IV forming a symmetrical unit of which digit III is the longest. Digit I reduced, thinner than the other digits and slightly posteriorly shifted. Proximal pads of digits I–IV form a posteriorly concave margin. Digit V with a large oval basal pad positioned in line with digit IV, and with a distinct, thin phalangeal portion that is strongly recurved. Manus with digit III longest; II and IV shorter and subequal to each other. Digits I and V short and occasionally absent. Digits IV and V laterally spread.

Material:

Niuchang locality (Figs. 2–5, Table 1). Three trackways (A–C; Fig. 2). Trackway A, cataloged as NC1–21, has 20 pes and 18 manus imprints that remain in situ (Figs. 3, 4 A–C, 5A–D). CU 140.17 is a latex mold and replica of trackway A. An uncataloged artificial mold is stored at the Institute of Earth Resources and Information, University of Petroleum, China. Trackways B–C have 17 and 5 pes imprints, respectively; no manus prints are preserved in either of these two trackways.

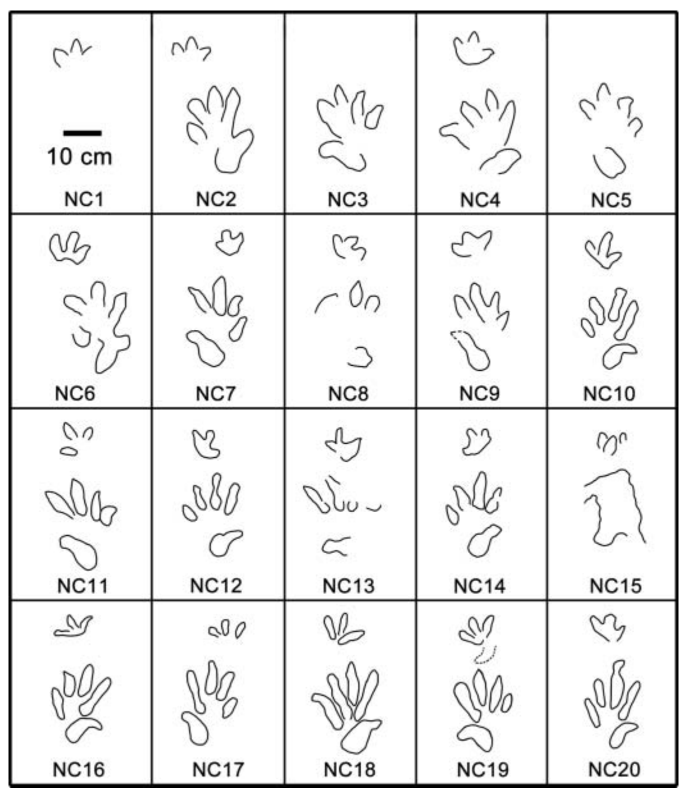

FIG. 3. Sketches of pes and manus imprints of trackway A (NC1–21) at the Niuchang locality. Note slender digit shapes and absence of digits I and V in the manus of most imprints.

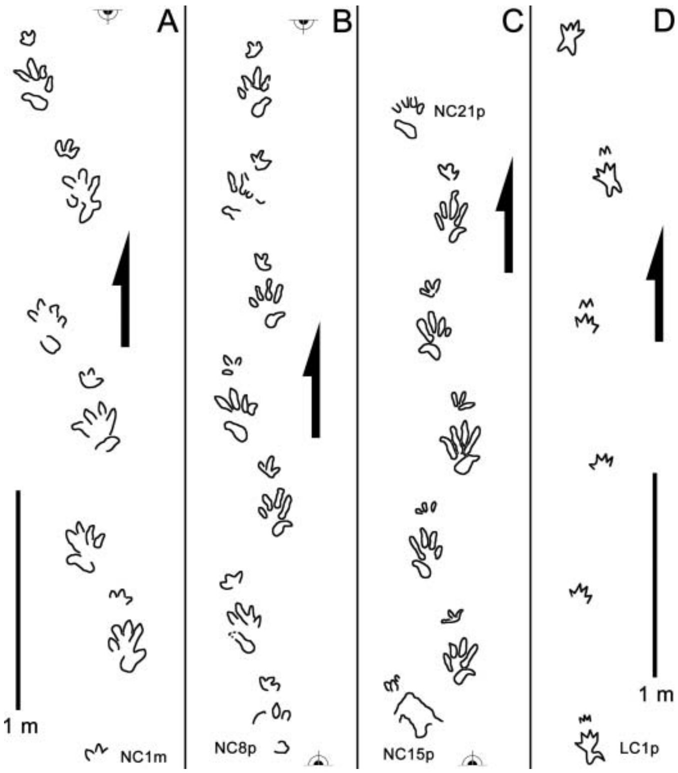

FIG. 4. Sketches of trackways. **A–C.** Trackway A (NC1–21) at the Niuchang locality. **D.** Trackway catalogued as LC1p–7p at the Longchang locality(from Lü et al., 2004). Note, that only six successive sets were mapped by Lü et al. (2004).

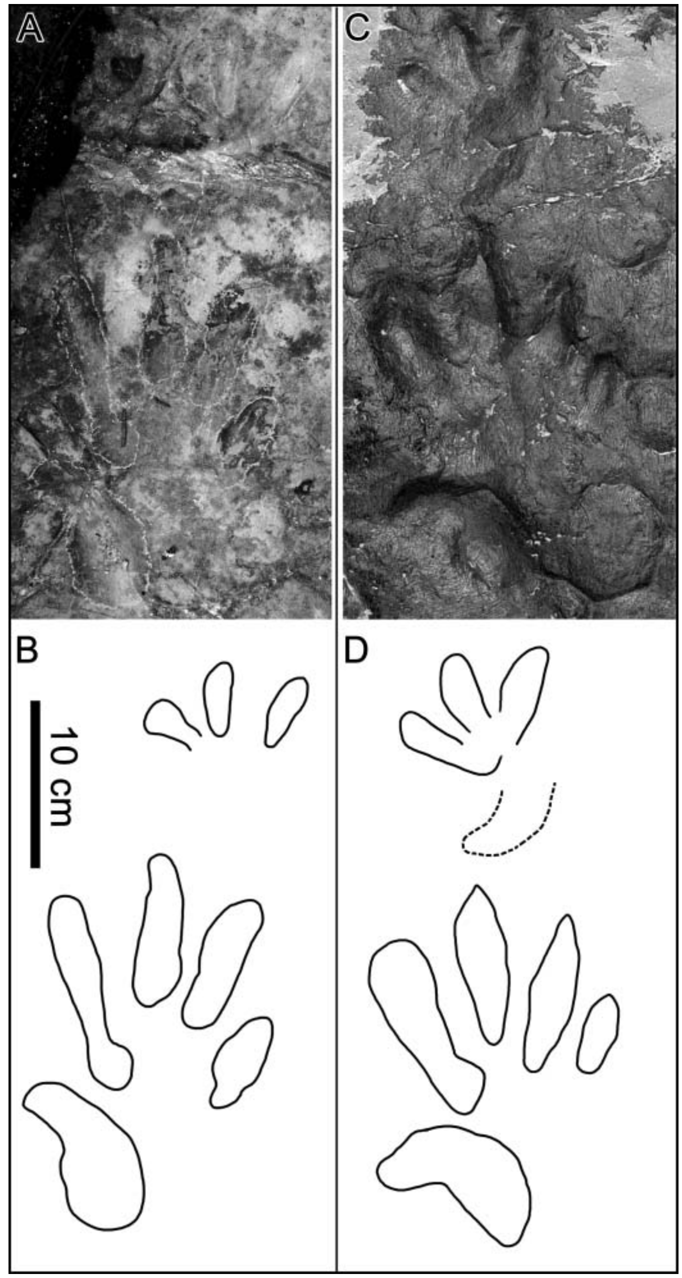

FIG. 5. Photograph and sketch with detail of trackway A (NC1–21) at the Niuchang locality showing two left pes–manus sets. **A–B**. NC17. **C–D.** NC19. Photograph in C by Lü Hongbo.

Locality and horizon: Member I of Guanling Formation, Middle Triassic (Anisian–Ladinian). Niuchang locality, Guizhou, China (L-00612).

Description: Trackway A is 10 m long, B is 9 m long, and C is 2 m long. The trackways pertain to medium-size to large individual trackmakers with pentadactyl, semi-digitigrade pes imprints 22–25 cm long. Digit imprints slender and often isolated from each other. In the pes, digit III is the longest, followed by digits IV, II, and I. A metatarsophalangeal pad of digit IV can be observed in some imprints, whereas others have only the phalangeal impressions. Claws are indicated by tapering distal ends of the digit impressions. The manus imprints in trackway A are positioned anterior to the pes. The trackway width for the pedes (distance between digit III bases perpendicular to the midline) is 7–15 cm. Stride length is 86–109 cm and the pace angulation of the pes 143–164°. Pes imprints are slightly, and manus imprints are more strongly turned outward relative to the midline (approximately 11° and 20°, respectively).

Longchang locality (Figs. 4D, 6–7). At least seven pes imprints, plus one manus imprint, constituting a trackway, cataloged as LC1p–7p and left in situ (Figs. 4D, 6–7 A, B). LCxp is a right pes-manus set originally belonging to the same trackway but now covered (Fig. 7C–D); its original position in the trackway is unknown.

***Locality and horizon*:** Member I of Guanling Formation, Middle Triassic (Anisian – Ladinian). Longchang locality, Guizhou, China (L-00613).

***Description*:** LC1p–7p is a narrow trackway. The pes imprints show similar proportions as in those from the Niuchang locality, but they are smaller (15 cm pes length on average) and both the digits and tracks as a whole are much broader.

TABLE 1
Measurements (in cm) of the *Chirotherium* tracks from Niuchang tracksite and Longchang tracksite

Number	R/L	ML	MW	II-IV	TW	SL	PL	PA	L/W
NC1m	L	10	10	—	—		67	—	1
NC1p	L	—	—	—	—	—	—	—	—
NC2m	R	8	9.8	90.5°	—	101		—	0.8
NC2p	R	23	15.5	31°	14.2	98.5	51	148°	1.5
NC3m	L	—	—	—	—	—	—	—	—
NC3p	L	23.5	16	31°	12.5	98.5	51.5	152°	1.5
NC4m	R	9	10	89.5°	—	96		—	0.9
NC4p	R	22.5	18	36°	6.6	99	50.1	158°	1.3
NC5m	L	—	—	—	—	—	—	—	—
NC5P	L	24.5	17.5	35.5°	9.5	100	50.8	164°	1.4
NC6m	R	8	9	89°	16	96	50.5	142°	0.9
NC6P	R	23.5	16	41°	12.8	98.2	51	151°	1.5
NC7m	L	7	7.5	80°	18.2	98	51	138°	0.9
NC7P	L	23.5	16.9	38°	14.9	97	50.5	146°	1.4
NC8m	R	7	9.4	81°	19.4	101	54	138°	0.7
NC8P	R	23	16.5	—	13.3	99.5	51	150°	1.4
NC9m	L	6.5	11.5	91°	18.7	100.5	54.2	139°	0.6
NC9P	L	23.3	15	31.5°	13.2	98	52	150°	1.6
NC10m	R	10	9	80°	17.7	94	53	138°	1.1
NC10P	R	22.2	15.3	35°	13.1	96.5	49.5	150°	1.5
NC11m	L	8.5	9.5	105°	9.7	93	47.5	156°	0.9
NC11P	L	25	19	35°	13.0	101	50.5	151°	1.3
NC12m	R	7.4	9	95°	5.0	98	47.5	168°	0.8
NC12P	R	22.6	15	43°	16.3	97.5	53.8	143°	1.5
NC13m	L	9	9	74°	7.3	107	51	164°	1
NC13P	L	22	20.6	—	7.4	109	49	164°	1.1
NC14m	R	6.4	8.6	107°	13.1	97.5	57	149°	0.7
NC14P	R	23	15.5	36°	6.8	98	61	163°	1.5
NC15m	L	7	8	—	9.6	92.5	44	156°	0.9
NC15P	L	20	—	—	11.3	86	38	150°	—
NC16m	R	6.5	10.5	111°	11.1	98	50.5	154°	0.6
NC16P	R	22	15	36°	12.1	96	51	152°	1.5
NC17m	L	6	10	100°	14.4	99	50	148°	0.6
NC17P	L	23	15	31.5°	12.1	97	48	152°	1.5
NC18m	R	8.5	11	85°	13.8	101	53.1	149°	0.8
NC18P	R	24.5	17	30.5°	10.1	101	52	157°	1.4
NC19m	L	8	9.5	86°	—	—	51.6	—	0.8
NC19P	L	22	14	33°	15.0	97.5	51	146°	1.6
NC20m	R	8.5	9.5	72°	—	—	—	—	0.9
NC20P	R	24	15.5	35°	—	—	51	—	1.5
NC21m	L	—	—	—	—	—	—	—	—
NC21P	L	—	21	—	—	—	—	—	—
LC1p	R	13.5	11.2	58°	10	135	71.5	163°	1.2
LC2p	L	>7.3	—	—	12	132	65	159°	—
LC3p	R	>7.8	13.5	—	11	142	69.3	162°	—
LC4p	L	14.7	12.2	54°	14	142	74.4	158°	1.2
LC5m	R	3.0	>3.1	—	—	—	—	—	—
LC5p	R	13.2	9.8	51°	—	—	70.3	—	1.3
LC6p	L	14.1	11.3	62°	—	—	—	—	1.2
LC7p	R	17?	11.0	—	—	—	—	—	—
LCxm	R	>1.1	>2.7	—	—	—	—	—	
LCxp	R	15.1	11.0	54°	—	—	—	—	1.4

Abbreviations: R/L: Right/Left; ML: maximum length; MW: maximum width; PA: pace angulation; PL: pace length; SL: stride length; TW: trackway width; II–IV: angle between digits II and IV; L/W: maximum length/ maximum width.

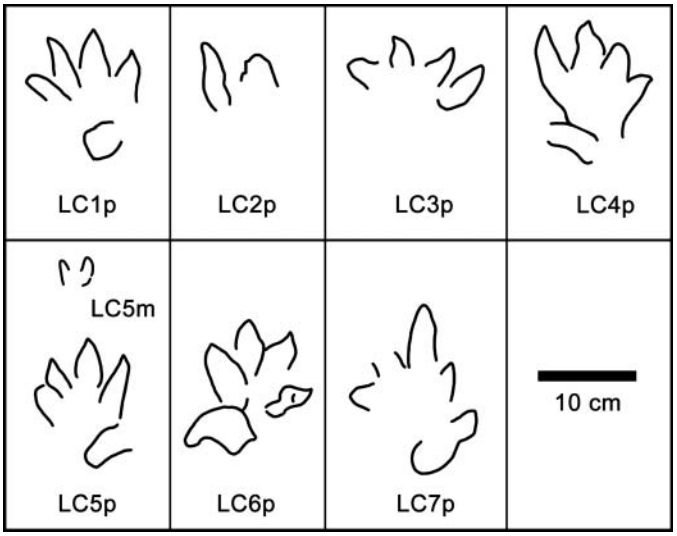

FIG. 6. Sketches of imprints from trackway catalogued as LC1p–7p at Longchang locality. Note broader digits than in imprints from the Niuchang locality (Figs. 3, 5). Only LC5p has an associated manus.

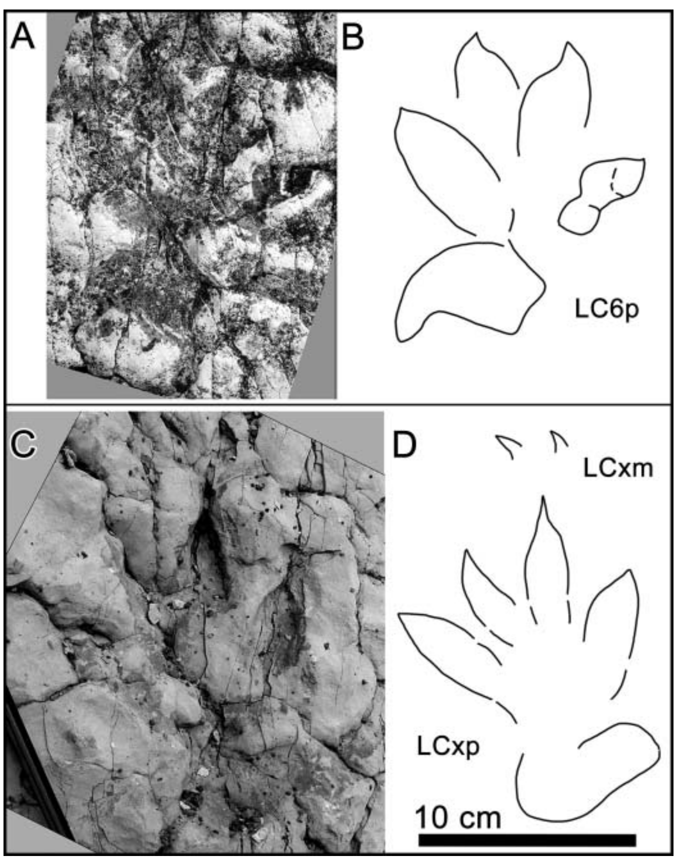

FIG. 7. Photographs and sketches of footprints from trackway LC1p–7p at Longchang locality. **A**–**B.** Pes imprint LC6p. **C**–**D.** Pes imprint and associated manus imprint (LCXp, LCxm) that preserves only two digits. This set belongs to the same trackway. The position of the track is unknown because this part is now covered. Photograph in C by Y.X. Zhang.

Compared with NC 1–21 (Figs. 3, 4A–C, 5), digit impressions are generally less isolated from each other. A manus imprint is only visible in LC5p (Fig. 6). It is incomplete and possesses only two digits (? II–III). The best preserved pes print is LC6p that shows distinct rounded pads of digit I (Figs. 6, 7A–B). Digit V has a massive proximal base. A right pes-manus set (LCxp), originally belonging to the same trackway is now covered (Fig. 7C–D; Lü, 2004, fig. 2). Its original position in the trackway is unknown. It has a relatively long and massive digit I. However, this is due to extramorphological (substrate-related) factors. An incomplete manus imprint is visible anterior to digit III and preserved only by two slender digit impressions (? II, III) that are curved inward and strongly tapering at their distal ends.

DISCUSSION

The footprints described here have different digital proportions from those specified by Haubold (1971a, b) and share no similarities with the chirotheriid ichnogenera *Isochirotherium*, *Brachychirotherium*, *Synaptichnium,* or *Protochirotherium*. The narrow trackways from the Niuchang and Longchang localities are congruent with the general pattern observed in *Chirotherium barthii* from the type locality at Heßberg near Hildburghausen in southern Thuringia, Germany (Fig. 8A), which were studied and extensively detailed by Haubold (1971a, 2006). This concerns the dominant digit group II–IV with digit III longest and II slightly shorter than IV as well as the backward shifted digit I and the recurved, thumb-like digit V. The divarication angle between digits II and IV is relatively large (35° on average, with a maximum of 43°; Table 1). This distinguishes these imprints from similar but more slender Middle Triassic forms such as *Sphingopus* (Haubold and Klein, 2002) that have divarication angles of < 30°. *Parachirotherium*, another Middle Triassic ichnogenus of chirotheriid shape, also has a wider divarication but differs from the Chinese footprints by having more strongly reduced pedal digits I and V (Haubold and Klein, 2002). Interestingly, the trackways from China show low pace angulations (144°) and stride length values (98 cm) compared with those of *Chirotherium barthii* from the type locality (170° and 120 cm, respectively) in footprints of similar size (compare with Haubold, 1971b). In comparison with those from other localities in Europe, northern Africa, and North America, the values from the Chinese trackways are very low (Peabody, 1948; Haubold, 1971b; King et al., 2005; Klein and Lucas, 2010b; Klein et al., 2011). However, this may be due to variations of gait and velocity. Possibly, the trackmakers of the footprints described here moved very slowly. Because the differences between the Chinese specimens and other tracks of *C. barthii* are minor and are possibly functions of locomotory mode, the tracks from the Niuchang and Longchang localities are referred here to this ichnospecies.

TRACKMAKERS

Chirotheriids have been assigned to pseudosuchians as well as to stem archosaurs (Soergel, 1925; Peabody, 1948;

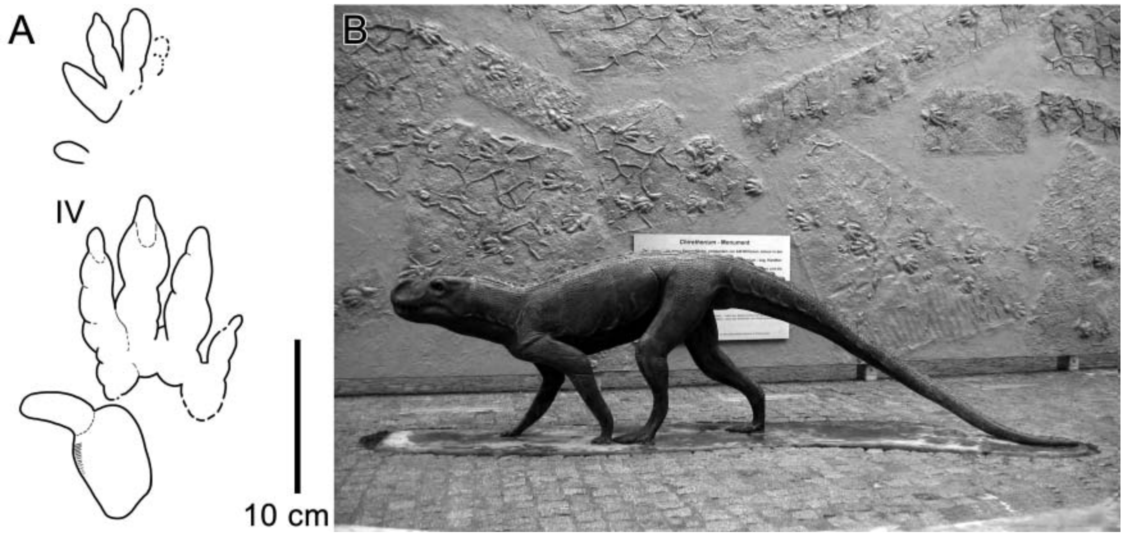

FIG. 8. *Chirotherium barthii*. **A.** Schematic diagram of a pes–manus set from the type surface at Hildburghausen, Thuringia, Germany. **B.** Life-size reconstruction of the trackmaker and replica of the type surface (background) by H. Haubold and M. Kroniger. On display at Chirotherium–Monument, Hildburghausen. Sketch in A after Haubold (1971a). Photograph in B by G. Rudloff and R. Werneburg.

Baird, 1957; Haubold, 1971a, b; Haubold and Klein, 2002). Krebs (1965) reconstructed the footprint of the "rauisuchian" archosaur *Ticinosuchus ferox* from the Middle Triassic of Switzerland based on a nearly complete pes skeleton; the track had a distinct chirotheriid morphology but differed from *Chirotherium barthii* in its digit proportions, as was noted also by Krebs (1965). *Chirotherium barthii* is generally considered to reflect a basal crown-group archosaur (Haubold, 1971a, b, 2006; Fig. 8B). The digit proportions of the pes, dominated by a nearly symmetrical digit group II–IV with digit III longest, the reduced, posteriorly shifted digit I, and the narrow posterior end with overlapping metatarsal pads II–IV, point to an advanced form close to the base of the dinosaur-bird line (Avemetatarsalia *sensu* Benton, 1999) (Haubold and Klein, 2002; Brusatte et al., 2010, 2011; Klein et al., 2011; Nesbitt, 2011). This is also supported by the narrow, curved posterior margins behind digits I–IV in the pes tracks, which suggest slender and appressed metatarsals. Furthermore, manual digit IV is strongly reduced and laterally spread, a feature that can be observed in dinosaurs. The similar morphology in other Middle Triassic ichnogenera such as *Sphingopus* and *Parachirotherium* as well as the co-occurrence of tridactyl footprints indicates an early radiation of avemetatarsalian/ dinosauromorph archosaurs (Haubold and Klein, 2002; Brusatte et al., 2011; Klein et al., 2011). On the other hand, convergent evolutionary developments might have occurred also in some stem-group crocodylians that cannot be excluded as trackmakers.

CONCLUSIONS

The trackways from the Middle Triassic (Anisian–Ladinian) Guanling Formation of Niuchang and Longchang localities (Guizhou Province, China) are assigned to the ichnospecies *Chirotherium barthii* based on characteristic features of the pes and manus imprints and by the general trackway pattern. Trackmakers were basal, crown-group archosaurs, possibly early members of the dinosaur–bird-line (Avemetatarsalia), though stem-group crocodylians cannot be excluded.

The record from China is the first one from Asia and extends the distribution of the ichnospecies, thus far known from Europe, North America, South America and North Africa. Biostratigraphically, assemblages with *Chirotherium barthii* are characteristic for the Early Anisian (Lucas, 2007; Klein and Haubold, 2007; Klein and Lucas, 2010a). This corresponds with independent data from body fossils in the Guanling Formation but conflicts with radiometric data that point to a Ladinian age.

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