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ScienceDirect
Palaeoworld 25 (2016) 444–452
Palaeoworld
www.elsevier.com/locate/palwor

A tetrapod footprint assemblage with possible swim traces from the Jurassic–Cretaceous boundary, Anning Formation, Konglongshan, Yunnan, China

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Received 1 December 2014; received in revised form 20 May 2015; accepted 8 June 2015
Available online 18 June 2015

Abstract

A small tetrapod footprint assemblage from the Anning Formation (Upper Jurassic–Lower Cretaceous) at Konglongshan Town, Yunnan Province, China, contains possible swim traces attributable to theropod dinosaurs based on their tridactyl and mesaxonic pes morphology. Morphotypes are tentatively assigned to the ichnogenera *Characichnos* and *Wintonopus*, a third one is similar to *Hatcherichnus*. Due to the inherent variability observed in tetrapod swim tracks, the names are used here informally describing footprints that reflect a distinct trackmaker behavior rather than anatomically accurate images of the pes anatomy. Variation of the imprint shape is obviously due to extramorphological effects and does not indicate taxonomic diversity of trackmakers. Elongate, slender impressions associated with these tracks are discussed here as possible tail traces. Trackmakers were possibly buoyant and active swimming individuals touching and scratching the bottom of deeper waterbodies with the distal ends of their digits. The orientation of the traces perpendicular to preserved ripples suggest cross-current movement and activities.

Keywords: Swim tracks; *Characichnos*; *Wintonopus*; Anning Formation; Yunnan Province

1. Introduction

The Lufeng Basin is well-known for its dinosaur body fossils, especially those of the *Lufengosaurus* fauna from the Lower Jurassic (Young, 1951) and the *Chuanjiesaurus* fauna from the Middle Jurassic (Fang et al., 2004). However, skeletons from the Upper Jurassic and Cretaceous deposits are rare. Fragmentary material attributed to *Mamenchisaurus* has been discovered from the Anning Formation, the lower subdivision of the Upper Jurassic Chuanjie area (Fang et al., 2004). Tyrannosauroid teeth from the Lower Cretaceous Jingxing Formation in Lanping County, Yunnan Province, constitute the sole Cretaceous osteological record (Ye, 1975). Fujita et al. (2008) described the Hemenkou tracksite as the first dinosaur tracksite from the Lower Cretaceous of Yunnan. However, updated research has demonstrated that the Hemenkou tracksite pertains to the Upper Jurassic Shedian Formation.

In June 2014, Tao Wang and Li-Da Xing discovered non-avian theropod tracks in the Anning Formation, which spans the Jurassic–Cretaceous boundary near Ganchong Village, Lufeng County, Yunnan Province (Fig. 1). Based on various morphological characteristics, these tracks were left possibly by swimming animals. It is the first record of possible swim tracks in Yunnan Province, allowing for comparisons with the recent report of swim tracks found in the Lower Cretaceous Zhaojue area of Sichuan Province (Xing et al., 2013). Here we give a

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http://dx.doi.org/10.1016/j.palwor.2015.06.002
1871-174X/

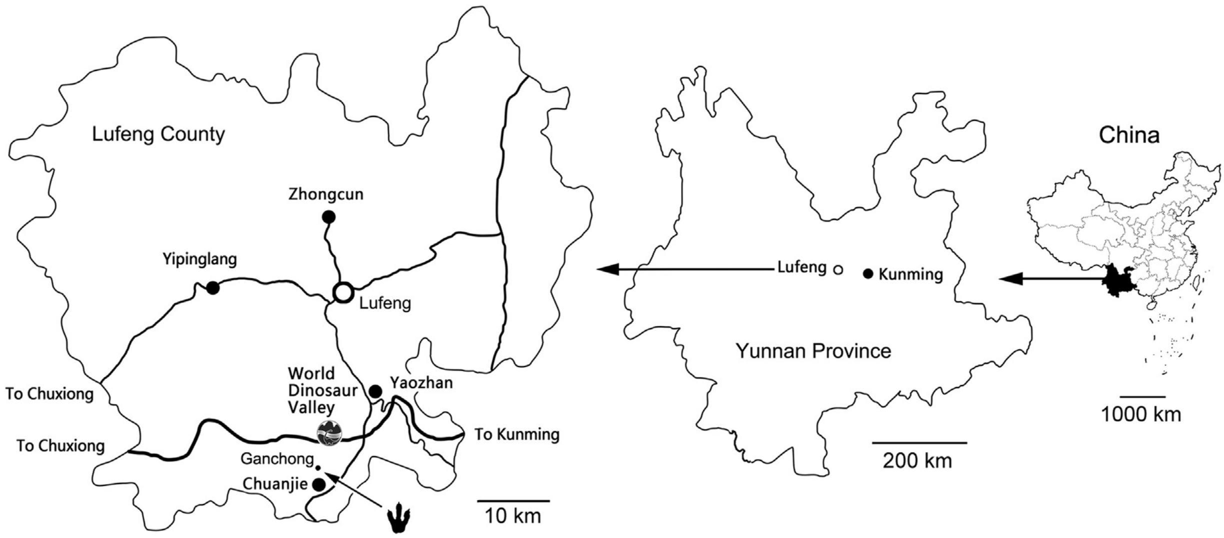

Fig. 1. Maps showing position of study area and Ganchong track locality in Lufeng County, Yunnan Province, China.

detailed description and discussion of this material comparing it with other known swim tracks from the Jurassic–Cretaceous deposits. Additionally, four tridactyl tracks, possibly those of avian theropods and about 3–4 cm in length, have been found at the same locality by Tao Wang (personal communication) in 1997. Unfortunately, no photographs were taken of these specimens, and they were subsequently damaged during road construction. Similar tracks were not discovered during our recent reinvestigation of the site.

Institutional abbreviations and acronyms. Field # SW = swim tracks from St. George Dinosaur Discovery Site at Johnson Farm, Utah, USA; GC = Ganchong tracksite, Yunnan Province, China; NMB = Natural History Museum Braunschweig, Germany.

2. Geological setting

The type section of the Anning Formation is situated in the Anning Basin (the area covers 264 km^2), 32 km west of Kunming City (Bureau of Geology and Mineral Resources of Yunnan Province, 1990). Jiang (1984) divided the Upper Jurassic Anning Formation into lower, middle, and upper units. Lithologically, these are characterized by red, yellow, and variegated mudstone layers. Fang et al. (2000) named the lower unit of the Anning Formation as the Madishan Formation. The middle and upper units are reserved and regarded as the new lower unit and the new upper unit of the Anning Formation. In the Chuanjie area, the Anning Formation lacks the upper unit, and consists of the lower unit only. *Mamenchisaurus* fragments were found in the middle–upper portion of the lower unit (Fang et al., 2000). In the Chuanjie area, there is a disconformity between the Lower Cretaceous Matoushan Formation and the Late Jurassic Anning Formation below (Cheng et al., 2004). On the basis of magnetostratigraphy and conchostracans, Huang et al. (2005) and Li et al. (2008) considered the Jurassic–Cretaceous boundary to be located between the upper and lower units of the Anning Formation. On the basis of the sporopollen record (*Dicheiropollis*), Zhang (1995) argued that the upper unit of the Anning Formation in the Fumin Basin is Berriasian–Barremian in age.

The Ganchong tracksite (24°55′20.60″N, 102°2′6.64″E) is situated along the side of a road, near Ganchong Village, Konglongshan (the former Chuanjie) Town in Lufeng County. The tracks are present on exposures of grey, yellow-green siltstone at the apex of the lower unit of the Anning Formation (Fig. 2). The Ganchong tracks are distributed in two different layers. The first layer (GCI) is 24 cm thick and not completely exposed. It preserves four tracks and two possible tail traces. GCI has well-developed ripple marks on bedding surfaces. The second layer (GCII) exceeds the first layer by 160 cm in thickness. The ripple marks at GCII are well-developed, but only one footprint was discovered here. The ripple marks from GCI and GCII indicate a current flow direction NW to SE and SE to NW, respectively. Unfortunately, due to the dip direction of the strata, most of the tracks are covered by the country road. Further excavation is therefore impossible.

3. Tetrapod swim tracks

3.1. Description

Four tracks from Ganchong tracksite I were cataloged as GCI-1–4 (Figs. 3, 4A, B). One track from Ganchong tracksite II was cataloged as GCII-1 (Fig. 4C, D). All tracks remain *in situ*.

GCI-2 (Fig. 4A, B) is the best-preserved track at Ganchong tracksite I. It is tridactyl and 8.2 cm and 10.4 cm in length and width, respectively (Table 1). Being an isolated track, it is difficult to determine if it is a left or a right pes imprint. The median digit trace is the longest, and the left is nearly equal in length to the right. The right digit trace is nearly parallel oriented to the trace of the median digit. The distal end of each digit trace is sharp, especially that of the median one. The lateral margin of the median digit impression is relatively shallow, and shallowness may record slippage by the track maker. The right side of the median digit impression shows a large displacement rim.

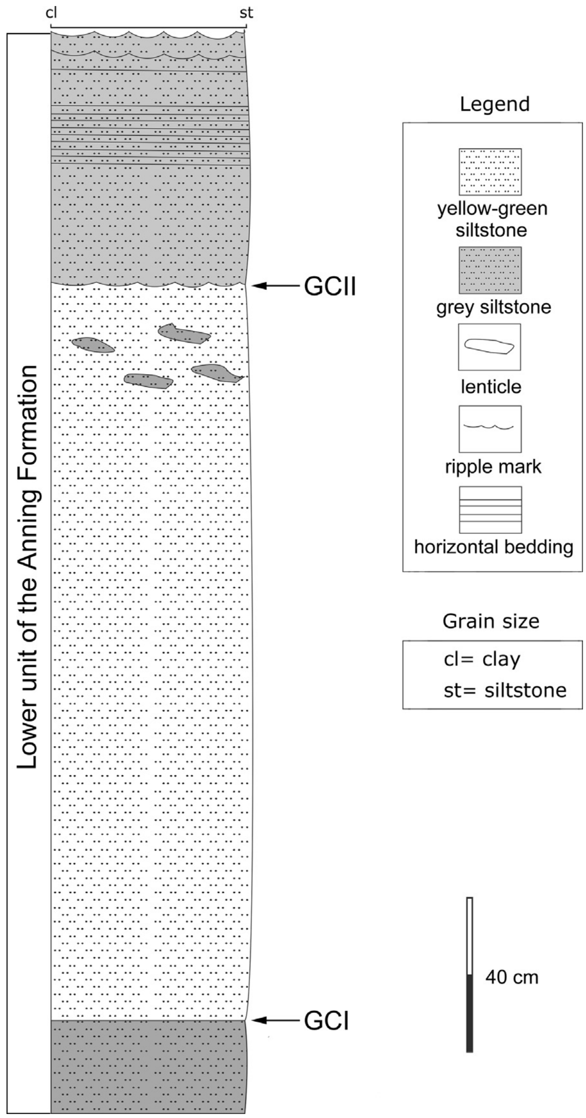

Fig. 2. Stratigraphic section of the lower unit of the Anning Formation at the Ganchong track locality.

The L/W ratio of the anterior triangle formed by the anterior points of the three digit impressions is 0.4.

GCI-3, which is 9.2 cm and 10.5 cm in length and width, respectively, is consistent with GCI-2 in morphology, except that the posterior end of GCI-3 is damaged. GCI-4 is similar to GCI-2 and GCI-3 in overall size, but poorly-preserved. GCI-1 (Fig. 5) shows only two digits, but the third (probably outer) one is broken off along the edge of the slab.

GCII-1, from Ganchong tracksite II (Fig. 4C, D), is tridactyl and well-preserved with three slender digit traces. It is 17.2 cm long and 8.0 cm wide. The left digit is the longest, but the right digit is slightly shorter than the median digit. All three digits show a nearly parallel orientation, with sharp distal ends. The anterior end of the left digit and the posterior end of the median digit show distinct displacement rims. The left digit of GCII-1 appears significantly elongated posteriorly, showing a typical drag mark. In similar tracks, this feature has been interpreted as swim traces by different authors (e.g., Ezquerra et al., 2007, fig. 2; Xing et al., 2013, fig. 3).

3.2. Comparison and discussion

3.2.1. Swim tracks and possible swim tracks from the global record

In the literature numerous tridactyl tracks have been inferred to represent swimming tetrapods, including relatively large morphotypes with footprint lengths and widths in the range of those recorded here: i.e., on the decimeter scale of 10–20 cm. As noted by Lockley et al. (2014) swim tracks are inherently variable, even in cases where there are large assemblages on large surfaces, and repeated or regular patterns indicate swim trackway configurations. The main morphological characters of swim tracks of buoyant tetrapods are: (1) elongated parallel or slightly divergent scratches or imprints of digits and claws; (2) lack of distinct anatomical details such as phalangeal pad impressions or skin texture apart from scale scratch marks; (3) posterior displacement rim or sediment mound behind digits due to the dynamics of the foot when contacting the bottom and pushing back the

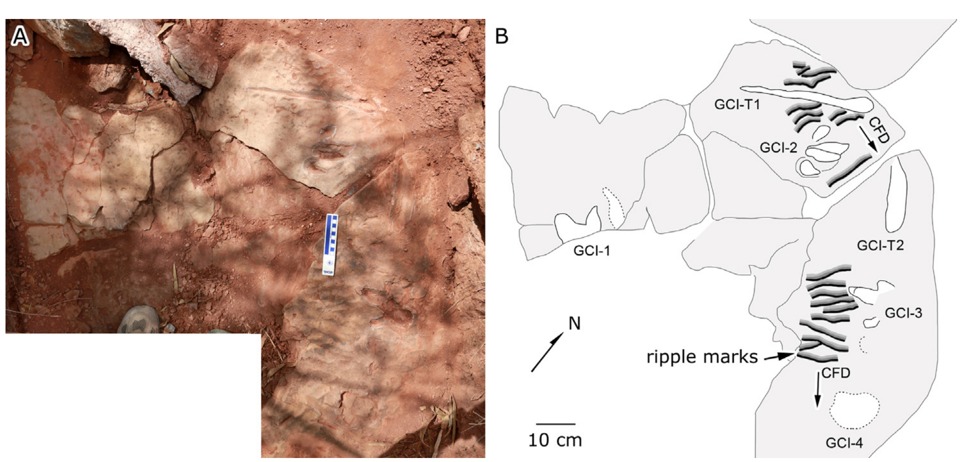

Fig. 3. Overview of track surface at Ganchong locality with the traces of swimming theropods. (A) Photograph; (B) map. Notice elongate impressions discussed here as possible tail traces (GCI-T1, GCI-T2) and ripple marks; the latter are oriented at an angle to the track axis indicating cross-current movement of the trackmakers. CFD, current flow direction.

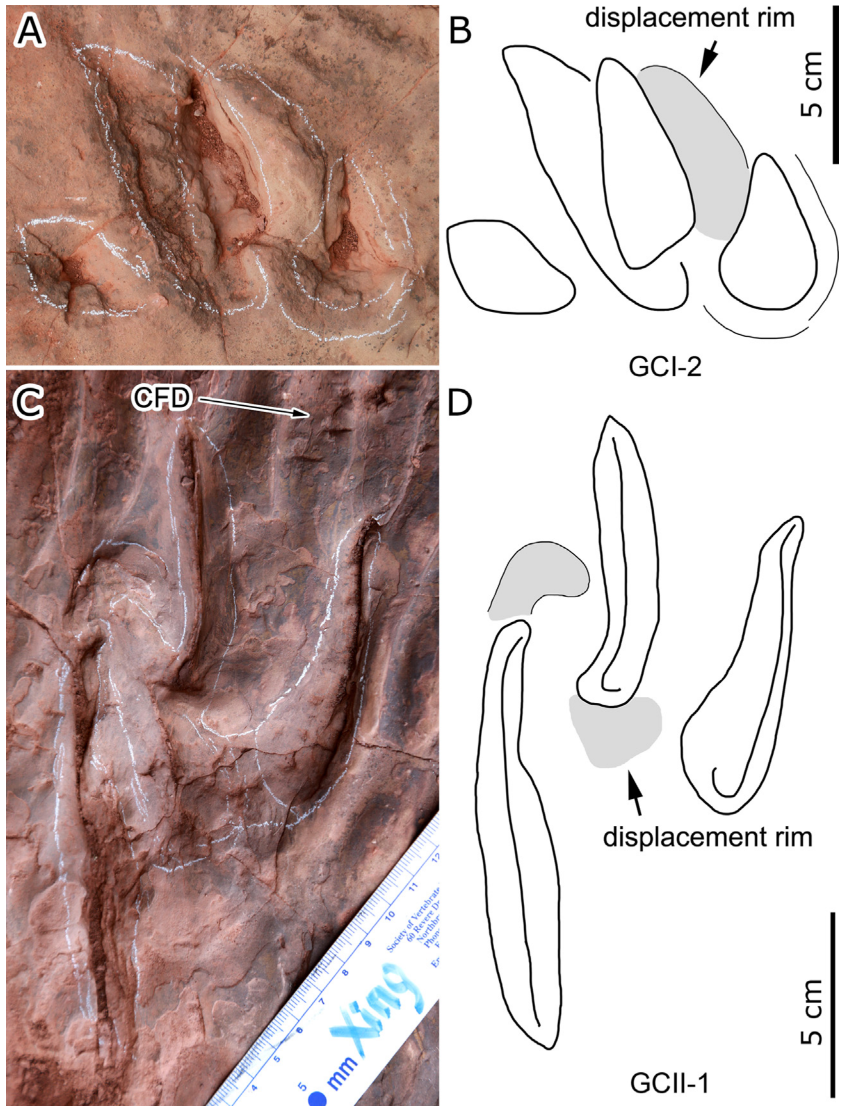

Fig. 4. Possible swim tracks at Ganchong locality showing extramorphological variation due to the more or less intensive contact of digits with the substrate. (A, B) Photograph and sketch of traces with impressed distal portions of digits. (C, D) Photograph and sketch of traces showing elongate digits (scratches). CFD, current flow direction.

sediment (see also McAllister, 1989). Among the ichnogenera that have been most recently been considered as representatives of swimming archosaurs, *Hatcherichnus*, inferred to represent a crocodilian, and *Characichnos* inferred to represent a theropod, are well-known (Foster and Lockley, 1997; Whyte and Romano, 2001; Milner et al., 2006; Xing et al., 2013; Lockley et al., 2014 and references therein).

To this list of swim tracks we may tentatively add the ichnogenus *Wintonopus* (Thulborn and Wade, 1984), which is morphologically similar to *Hatcherichnus*. However,

Table 1
Measurements (in cm and degrees) of the theropod tracks from the Ganchong tracksites.

Number	ML	MW	LLD	LMD	LRD	L-R	M	L/W
GCI-1	>15.9	—	—	12.7	10.3	—	—	—
GCI-2	8.2	10.4	4.6	6.5	5.0	106°	0.4	0.8
GCI-3	9.2	10.5	3.4	6.9	3.5	109°	0.4	0.9
GCI-4	10.3	—	—	—	—	—	—	—
GCI-T1	31	4	—	—	—	—	—	—
GCI-T2	>20	5	—	—	—	—	—	—
GCII-1	17.2	8.0	11.6	7.8	8.3	31°	0.6	2.2

Abbreviations – ML: maximum length; MW: maximum width; LLD: length of left digit; LMD: length of middle digit; LRD: length of right digit; L-R: angle between left digit and right digit; M: mesaxony (length/width ratio for the anterior triangle); L/W: maximum length/maximum width.

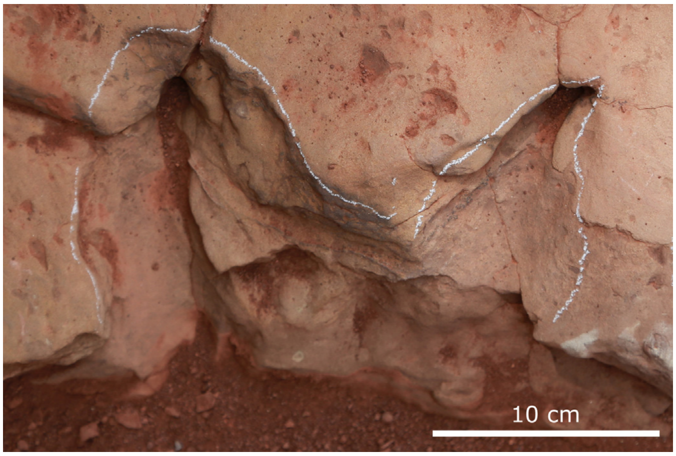

Fig. 5. Close-up photograph of possible swim track GCI-1 from Ganchong locality.

morphological similarity does not imply behavioral similarity or taxonomic similarity between trackmakers, especially in the case of swim tracks. *Wintonopus* is controversial because it was first described from the Lark Quarry dinosaur tracksite of Australia, where it is associated with the ichnogenus *Skartopus* (Thulborn and Wade, 1984), which Romilio et al. (2013) synonymized with *Wintonopus*. Both ichnogenera were originally interpreted as recording a stampede of a mixed herd of small theropod and ornithopod dinosaurs. This implies that tridactyl tracks of running dinosaurs registered only the distal parts of their digits and therefore might be morphologically convergent with tracks of swimming dinosaurs. Other factors pertaining to preservation may lead to the registration of only the distal portion of digits on underlayers (Lockley and Rice, 1990 and references therein). In short, the fact that the Lark Quarry tracks, first inferred to indicate running dinosaurs (Thulborn and Wade, 1984), could be reinterpreted as evidence of swimming dinosaurs (Romilio et al., 2013) is evidence that such tracks are difficult to interpret (cf. Martin, 2014). Thus, so-called "swim tracks" should always be interpreted with considerable caution. Likewise, as noted below, ichnotaxonomic labels should also be used and interpreted with caution, and may not provide unambiguous evidence of trackmaker identity.

3.2.2. Ganchong tracks

GCI-2 is similar to *Hatcherichnus*, whereas GCI-3 could conceivably be compared with *Wintonopus* (Thulborn and Wade, 1984; Romilio et al., 2013). *Hatcherichnus* is characterized by a tetradactyl pes impression consisting of digit-only traces; outside digits (I and IV) are nearly equal in length, as are middle digits (II and III); and the outside digits are shorter than the middle digits by about 25% (Foster and Lockley, 1997; Avanzini et al., 2010). Moreover, *Wintonopus* shows tridactyl, mesaxonic pes traces that are wider than long; digit traces are cranially directed and are short, with digit III being the longest, and digit IV being equivalent to or longer than digit II; both digit II and IV traces extend farther proximally than the digit III trace (Thulborn and Wade, 1984; Romilio et al., 2013). Both GCI-3 and *Wintonopus* are small- to medium-sized (<0.3 m long) tridactyl, mesaxonic pes imprints being wider than long. The digit impressions are short and taper distally; the two lateral digit impressions of each track extend farther proximally than the digit III impression, but a metatarsophalangeal pad impression is absent. On the other hand, by its overall shape, GCI-3 could also represent an incomplete walking track or undertrack. The small sample makes diagnosing of the GCI tracks difficult. If their interpretation as swim traces is correct, by their shape they could be assigned to the ichnogenera *Hatcherichnus* and *Wintonopus* as well as to *Characichnos* (Whyte and Romano, 2001). The latter has the following diagnostic features: two to four elongate digit traces or scratches, their shape being straight, gently curved or slightly sinuous with straight or slightly flexed termination ("hypichnial ridges" and "epichnial grooves", respectively, after Whyte and Romano, 2001). Given that the trace of digit III is the longest in GCI-3 and GCII-1, a tentative label cf. *Characichnos* or cf. *Wintonopus* may be given to these tracks, whereas GC1-2 is more similar to *Hatcherichnus*. However, these are very tentative assignments and they might be based on extramorphological variation rather than anatomical difference. Therefore they should not be taken to indicate a taxonomic diversity of track-makers. They indicate similarities between irregularly-shaped tridactyl tracks that have variously been interpreted as evidence of swimming behavior of archosaurs. On the basis of size and morphology, we can rule out any likelihood that the Ganchong sample represents pterosaurs or turtles: see Lockley et al. (2014) for criteria used to differentiate swim track morphotypes.

We emphasize that the ichnotaxon *Characichnos* is likely not restricted to the description of tridactyl swim tracks of theropods as originally introduced by Whyte and Romano (2001). Thus far authors have assigned this name to any kind of (didactyl-pentadactyl) tetrapod swim tracks. Another example for different dinosaur groups being responsible for a distinct ichno-morphotype, is the ichnotaxon *Dinehichnus* that was erected by Lockley et al. (1998) based on material from the Upper Jurassic Morrison Formation of western North America, and that was attributed to ornithopods. *Dinehichnus* is likely not restricted to the tracks of ornithopods only (Lockley and Foster, 2006). The characteristics of *Wintonopus* probably apply broadly to swim tracks made by both small-sized bipedal ornithopods (Romilio et al., 2013) and theropods. The sharp claw marks of the Ganchong specimens are suggestive of a theropod affinity. *Wintonopus* has also been reported from the Broome tracksite, in Western Australia (Long, 1998). However, McCrea et al. (2012) have reinterpreted some of the Broome *Wintonopus* tracks as cf. *Irenichnites*, and consider the theropod tracks from this locality as evidence of normal walking behavior.

Elongated and parallel digital impressions and sediment mounds at the posterior ends of digit marks are common features of tetrapod swim tracks (McAllister, 1989; Swanson and Carlson, 2002; Milner et al., 2006; Ezquerra et al., 2007; Xing et al., 2013). In all cases, the anterior portions of the impressions are deepest, and the traces become shallower posteriorly. These features indicate that the distal tips of the digits contacted the sediment initially and with the greatest impact force, and that the foot was then lifted, as it moved posteriorly, propelling the animal forward and pushing the sediment backward (Milner et al., 2006; Ezquerra et al., 2007; Romilio et al., 2013). The GCII-1 track coincides with these characteristics.

The tracks described as *Characichnos* from the Middle Jurassic Saltwick Formation of England (Whyte and Romano, 2001) are dinosaur swim tracks likely with theropod affinities. As noted above, the characteristics of GCII-1 are consistent with

Fig. 6. Close-up photographs of elongate impressions discussed here as possible tail traces at Ganchong locality.

Characichnos in having three elongate and parallel epichnial grooves, the terminations of which are sharply reflexed. GCII-1 is therefore tentatively assigned to cf. *Characichnos*.

GCII-1 also slightly resembles "didactyl" theropod tracks from the ?Middle Jurassic of Agadez, Africa (Mudroch et al., 2011), such as NMB-1887-Sp, which were named *Paravipes*. The sole difference is that, in NM-1887-Sp, only two digital impressions are discernable. When reviewing the didactyl tracks, Lockley et al. (in press) argued that the Agadez "didactyl" theropod tracks could be considered as swim tracks.

The swim track *Characichnos* has elongated and parallel digital impressions (Whyte and Romano, 2001; Xing et al., 2013), which may suggest the trackmaker was swimming or buoyant in deeper water (≥hip height), where only distal ends of digits could touch the substrate. While shorter swim tracks, such as GCI-2 and GCI-3, may indicate that the trackmaker moved in more shallow water (≤hip height), where it could reach the substrate with the complete anterior part of the foot (Romilio et al., 2013).

With the exception of GCI-1, the orientations of all GCI and GCII tracks are similar and up to 90° to the direction of flow suggested by the orientation of ripple marks. Cross-current swim track orientations are inferred from some sites. For example, Milner et al. (2006) reported tracks oriented at an angle of approximately 45° to current flow direction. For the Ganchong sample, angles of track orientation relative to ripple crests are: 45° for GCI-2 and GCI-4, 70° for GCI-3, and 90° for GCII-1.

The cross-current possible swim tracks GCI and GCII resemble those seen in the shorebird (*Goseongornipes* isp.) trackway from Xinjiang (Xing et al., 2011) and some non-avian theropod swim tracks (e.g., Field # SW.77) from Utah (Milner et al., 2006). However, they are different from theropod swim tracks of the Cameros Basin (Spain), which are oriented in an up-current direction (Ezquerra et al., 2007), and from non-avian theropod swim tracks from Utah, running in an up-current/down-current direction (Milner et al., 2006, fig. 6A–E).

A swimming trackmaker moving in a cross-cutting current orientation may indicate foraging activity (Xing et al., 2011). There is growing evidence of piscivory among a diverse array theropod groups, including coelophysids (Kirkland et al., 2005; Milner and Kirkland, 2007), ceratosaurids, compsognathids, spinosaurids (Holtz, 1998; Ibrahim et al., 2014), unenlagiines (Gianechini et al., 2009), and microraptorians (Xing et al., 2013). There is, therefore, no reason to rule out foraging activity as an explanation for the observed parallel orientation of tracks and ripple marks at the Ganchong tracksite, although such an explanation remains highly speculative.

The two layers with possible swim tracks at the Ganchong tracksite might suggest that the local depositional environment remained aquatic for an extended period of time and that the inferred dinosaur track makers swam with relative frequency.

If these are truly the traces of swimming tetrapods, at the time they were made, the water depth must have been roughly equivalent to the hip height of the theropod track maker (Xing et al., 2013). Calculations of hip height from a digitigrade pedal posture after the formula of Alexander (1976) requires the presence of a metatarsodigital pad impression. GCI-3 lacks a metatarsodigital pad impression, so applying Alexander's formula will underestimate hip height. However, based on the *Sinosaurus* pedal skeleton in digitigrade and subunguligrade posture (Xing et al., 2014, fig. 8), and on GCI-3 reconfigured to a digitigrade posture, a foot length of ~11.2 cm, and a hip height $h = 4 \times 11.2$ cm = 44.8 cm is calculated (Alexander, 1976).

4. Possible tail traces

Two possible tail traces from Ganchong tracksite I were cataloged as GCI-T1–2 (Fig. 6). All tracks remain *in situ*.

Ganchong tracksite I has two discernable grooves that could be interpreted as tail drag marks even if this is merely speculative. GCI-T1 is 31 cm long and runs parallel to GCI-2. The length of the second one (GCI-T2) is >20 cm. The depth of both grooves is approximately 8 mm. According to the standards for description and comparison of dinosaur tail traces (Kim and Lockley, 2013, table 3): GCI-T1 is short (<1 m), narrow (<5 cm), shallow (<1 cm), u-shaped in cross-section, follows a straight path, has a smooth surface ornamentation, and has a tapered termination. GCI-T2 is less complete, but although slightly wider than GCI-T1, it appears generally consistent in all these characters. In general, the trails (tail traces) of dinosaurs are located at the middle of trackways, or overlap the interior or median digit of the tracks (Kim and Lockley, 2013). Unfortunately, only a few isolated tracks are exposed at the Ganchong tracksite and continuous trackways are missing. Therefore, a repetitive rhythmic pattern that includes impressions of the tail cannot be proved here.

5. Conclusions

The Ganchong track sample shows several features characteristic of tetrapod "swim tracks" even if the presence of walking (?under) tracks in some specimens cannot be completely excluded. Based on the tridactyl morphology of individual prints and the mesaxonic pattern, these are attributable to theropods; however, this cannot be proved with certainty. Ichnotaxonomically they are tentatively related to the ichnogenera *Characichnos* or *Wintonopus*, although at least one is convergent with the morphotype *Hatcherichnus*. The possibility of applying all three of these labels to tracks within a small sample illustrates the problems inherent in the study of most swim tracks: i.e., assemblages often contain several different and irregular morphotypes. Such variable morphologies may indicate small differences in trackmaker locomotion, but are not a reliable indication of track maker diversity where large samples are not available (cf. Lockley et al., 2014). The Ganchong sample does not contain any recognizable trackway segments; however, the orientation of several tracks at a high angle to the flow direction inferred from ripple marks may indicate that several trackmakers were moving in a direction influenced by water currents.

Acknowledgements

Thanks for Anthony Romilio (The University of Queensland, Australia) offering the abundant information of Australian dinosaur tracks; Ignacio Díaz-Martínez (Universidad Nacional de Río Negro, Argentina) and an anonymous reviewer for their helpful reviews of the manuscript. This research project was supported by the 2013 support fund for graduate student's science and technology innovation from China University of Geosciences (Beijing), China. Thanks to Andrew R.C. Milner (St. George Dinosaur Discovery Site at Johnson Farm, Utah, USA) for an early review of the manuscript.

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