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First Report of Small *Ornithopodichnus* Trackways from the Lower Cretaceous of Sichuan, China

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Trackways of ornithopods are well-known from the Lower Cretaceous of East Asia, particularly in Korea and China. However, most morphotypes have been identified as *Caririchnium* which is characterized by moderate mesaxony, the ratio length = width, or length > width and, in some cases, by a quadrupedal gait. In 2009 the ichnogenus *Ornithopodichnus,* which exhibits distinctively weak mesaxony and a broader, transverse pes imprint with the ratio length < width, was identified in Korea, on the basis of material with suboptimal preservation. The trackmaker was a large ornithopod. Subsequently, in 2009 a second report recognized *Ornithopodichnus* in China, the trackmaker being a moderately large quadruped. In 2012, *Ornithopodichnus* was described on the basis of well-preserved material from the Upper Cretaceous of Korea, in this case left by a small, gregarious biped. Herein we document, a fourth occurrence of *Ornithopodichnus* in the Lower Cretaceous Feitianshan Formation of Sichuan, China which is a further example of trackways that can be attributed to small, bipedal and gregarious ornithopods. Morphology, size, trackway pattern and speed of locomotion correspond well with trackways known from the Korean Hwasun tracksite. Possibly, the occurrence of *Ornithopodichnus* which is restricted to East Asia thus far, is related to ecological and biogeographical pecularities in this area.

Keywords Ornithopod tracks, *Ornithopodichnus*, Lower Cretaceous, China

INTRODUCTION

Tracking Ornithopods

Numerous reports of ornithopod trackways are known from East Asia, especially from Korea and China, including those that represent both bipeds and quadrupeds, and many sites that indicate gregarious behavior. Nevertheless, relatively few Asian examples have been determined at the ichnospecies level and in many cases, ornithopod tracks have been given generalized ichnotaxonomic labels. For example most ornithopod trackways from the footprint-rich Jindong Formation of Korea have been assigned to the ichnogenus *Caririchium* (Lockley et al., 2006), with no ichnospecies designation. The same ichnogenus label has been applied to trackways from the Uhangri Formation (Huh et al., 2003). In both of these, ichnofaunas the trackmakers appear to have been bipeds. *Caririchium* is also recognized in the Lower Cretaceous of China (Xing et al., 2007) where it is represented by the ichnospecies *C. lotus* indicative of a quadrupedal trackmaker and being morphologically similar to *C. leonardii* from the Cretaceous of Colorado (Lockley, 1987; Lockley et al., 2001). However, as noted below, some Cretaceous ornithopod tracks appear to be readily distinguishable from *Caririchium* on morphological grounds (Lockley et al., in press). These include the ichnogenus *Ornithopodichnus*, hitherto reported from two localities in Korea and one in China, as well as from the newly reported locality described here.

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Ornithopodichnus

The ichnogenus *Ornithopodichnus* (type ichnospecies *Ornithopodichnus masanensis*) currently remains as a monoichnospecific ichnogenus. It was originally described by Kim et al. (2009) as a distinctive, robust ornithopod track, which is wider than long (mean length/width [l/w] ratio = ~0.90; range 0.64–1.18), with positive (inward) rotation, and very thick, broad and U-shaped toe impressions creating a trefoil outline with a smoothly rounded hind margin. Lockley (2009) pointed out that *Ornithopodichnus* has a very short middle toe (digit III trace) relative to digits II and IV, thus exhibiting "weak mesaxony" in comparison with other ornithopod ichnotaxa. Although no attempt was made to identify the trackmaker of the Korean footprints at a low ichnotaxonomic level, Kim et al. (2009) pointed out that some Cretaceous ornithopods, including the Asian genus *Zhouchengosaurus,* also exhibit weak mesaxony.

Additional examples of *Ornithopodichnus* with the distinctive low l/w ratio (0.84–0.86) were described from well-preserved trackways as the Hwasun site in Korea (Huh et al.,

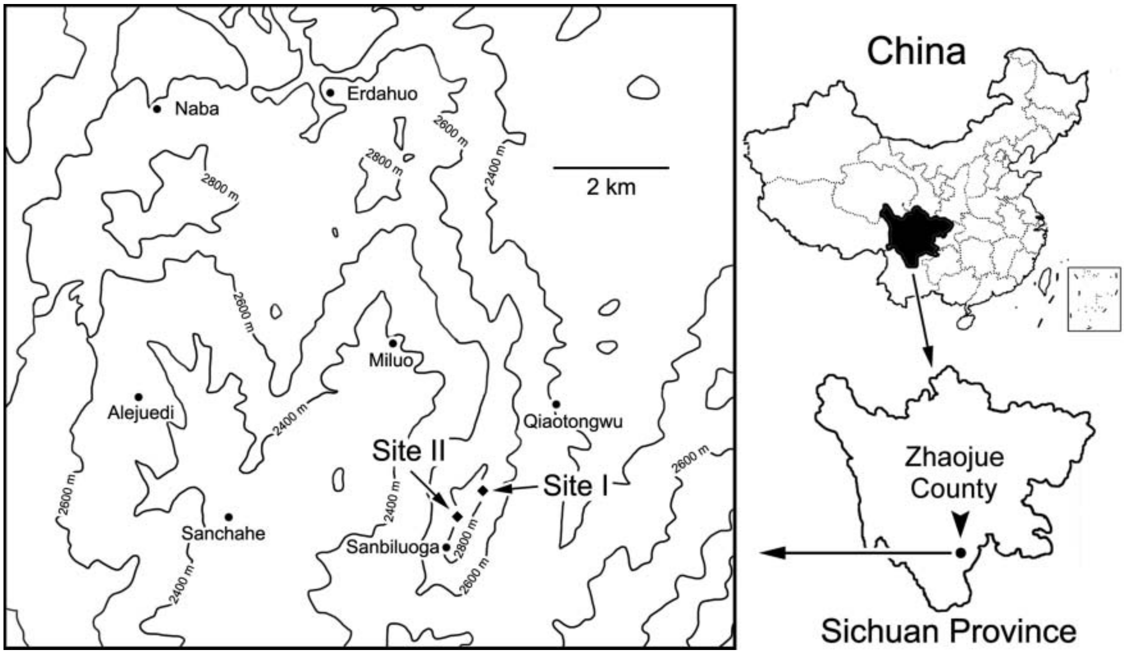

FIG. 1. Geographic map indicating the location of the Zhaojue dinosaur footprint tracksites I and II in Liangshan Yi Autonomous Prefecture, Zhaojue County, Sichuan Province, China.

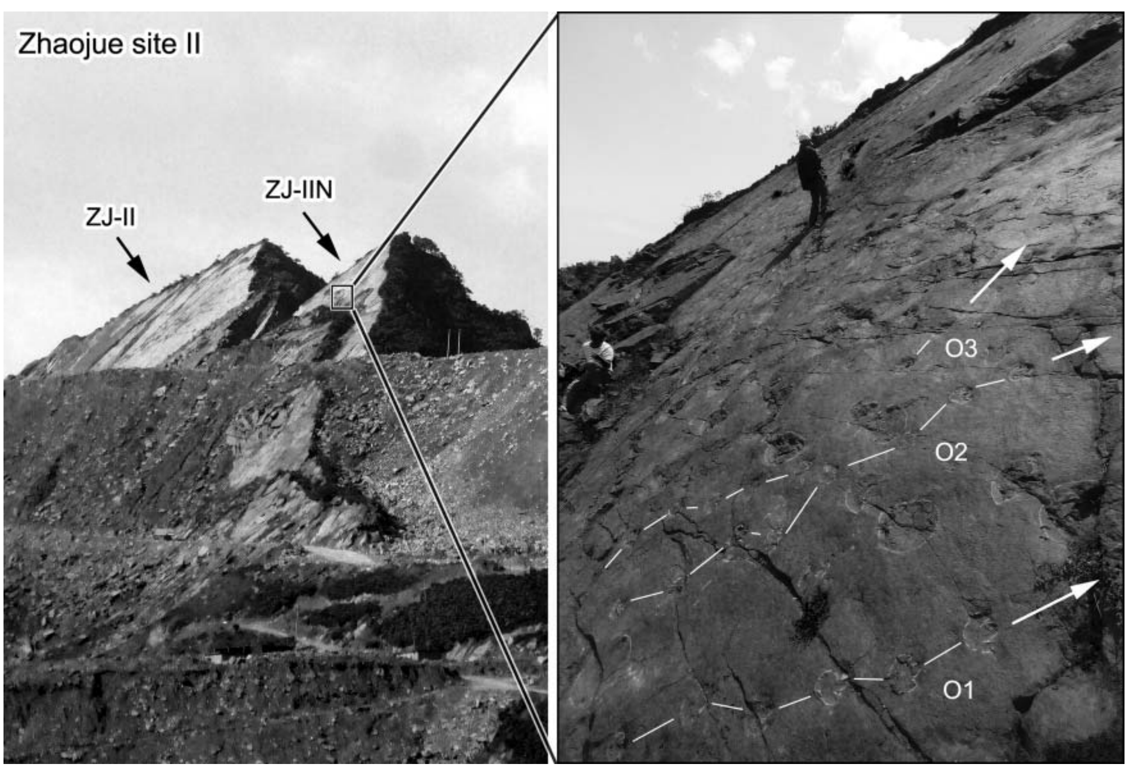

FIG. 2. Zhaojue dinosaur tracksite II. A. Overview of section with steep track surface. B. Track surface with *Ornithopodichnus* trackways.

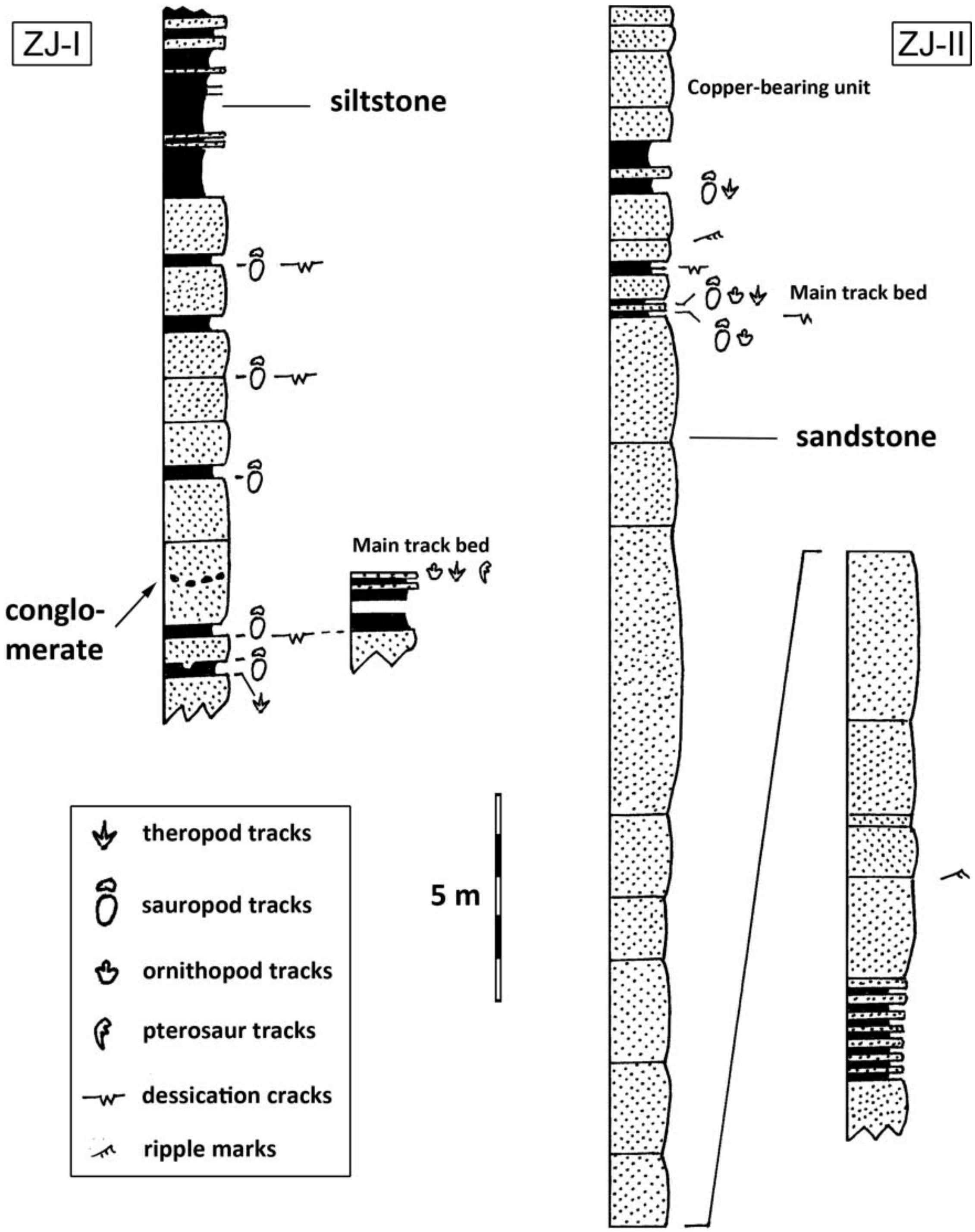

FIG. 3. Stratigraphic sections at Zhaojue dinosaur tracksites I and II.

2006; Lockley et al., 2012a) where they represent small bipedal trackmakers, evidently moving in the same direction as a small group of six individuals. A single large *Ornithopodichnus* track was also recorded at the Hwasun locality having the size of the smallest of the larger tracks from the *O. masanensis* type locality. A similar, large, transverse ornithopod track morphotype, first reported from the Lower Cretaceous, Houzuoshan Dinosaur Park site in Shandong Province by Matsukawa and Lockley (2007), was subsequently given the label *Ornithopodichnus* by Lockley (2009). Two trackways were illustrated, one indicating a bipedal trackmaker, the other a quadruped. In summary, including the present report,

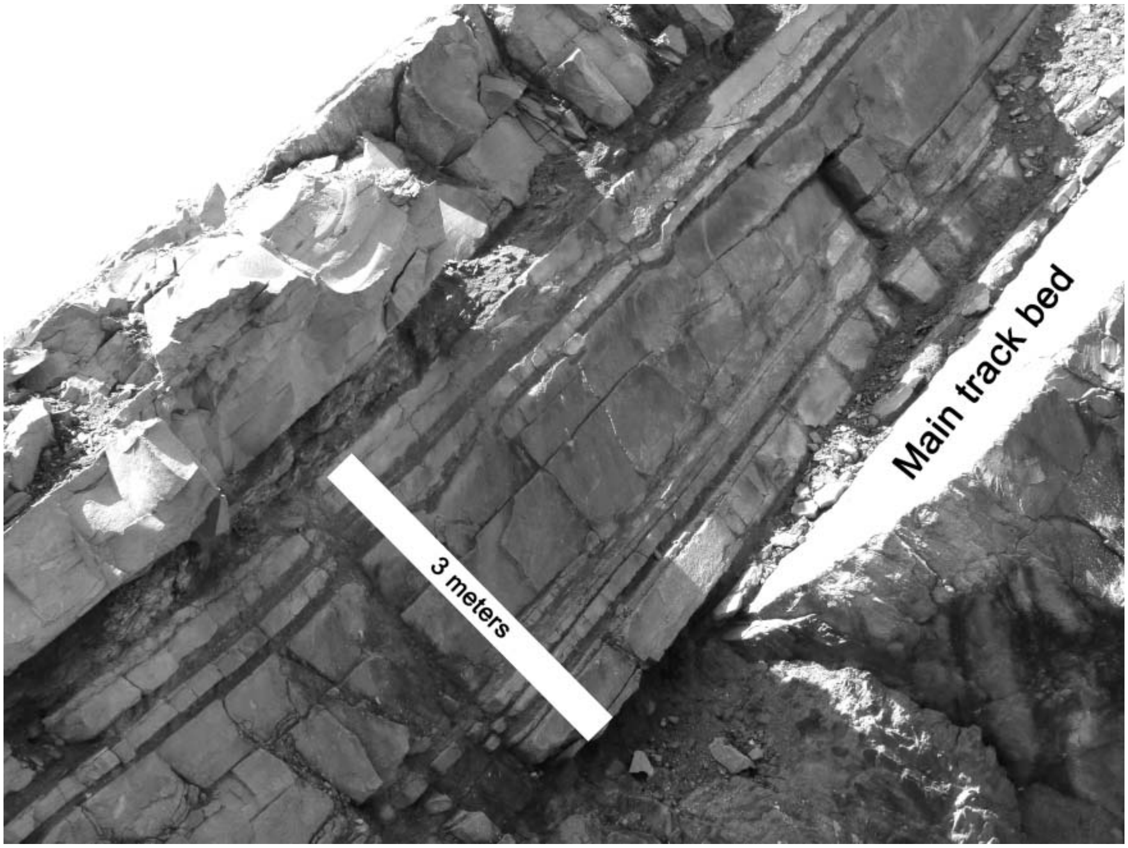

FIG. 4. View of track-bearing section at the Zhaojue dinosaur tracks quarry (site ZJ-II). Note the main track bed is exposed at the top of a massive sandstone overlain by an alternating sequence of muddy red siltstones 5–65 cm thick and sandstones 10–130 cm thick. The uppermost sandstone unit is a rich source of copper.

Ornithopodichnus is known from two localities in Korea and two in China:

- *Ornithopodichnus masanensis*, Jindong Formation (Cretaceous), Masan site, Korea, representing at least six large bipeds (Kim et al., 2009).
- *Ornithopodichnus,* (ichnosp. indet.), Tianjialou Formation (Cretaceous), Houzuoshan Dinosaur Park site, near Junan, Shandong Province, China, representing a large biped and a large quadruped (Matsukawa and Lockley, 2007; Lockley, 2009).
- *Ornithopodichnus* (ichnosp. indet.), unnamed formation (Cretaceous), Hwasun site Korea, representing six small bipeds and one large biped (Lockley et al., 2012a).
- *Ornithopodichnus* (ichnosp. indet.), Feitianshan Formation, China (this study) representing three small bipeds (this article).

The *Ornithopodichus* morphotype is distinguished from ornithopod tracks such as *Caririchnium* (Leonardi, 1984; Lockley, 1987; Lockley and Wright, 2001; Xing et al., 2007) by very weak mesaxony (Lockley, 2008, 2009) which obviously seems to be correlated with variation in the mesaxony that has been observed in the pes skeletons of large ornithopods. For example, Kim et al. (2009) show unequivocally that there is variation in the relative length of the toes of *Iguanodon* species. Thus, *Iguanodon atherfieldensis* can be described as showing much stronger mesaxony (a more prominent digit III) than *Iguanodon bernissartensis*, and that the feet of large ornithopods like *Zhuchengosaurus* (= *Shantungosaurus*; Ji et al., 2011) show extremely weak mesaxony (Zhao et al., 2007). The differences between *I. bernissartensis* and *I. atherfieldenis* were considered by Paul (2007) of sufficient importance to transfer the latter species to the new genus *Mantellisaurus* (i.e., *M. atherfieldensis*). Among the differences between the two former *Iguanodon* species noted by Paul (2007) were the lengths of the fore limbs. Thus, given that Lockley (2007, 2009) has drawn attention to recognizable morphodynamic relationships between limbs and between limb and foot proportions, the inferences of Kim et al. (2009) that discernable morphological differences in the pes might be recognizable in the footprints is plausible.

Thus, tracks such as *Caririchnium* likely represent track makers similar to *Iguanodon atherfieldensis* with well-defined

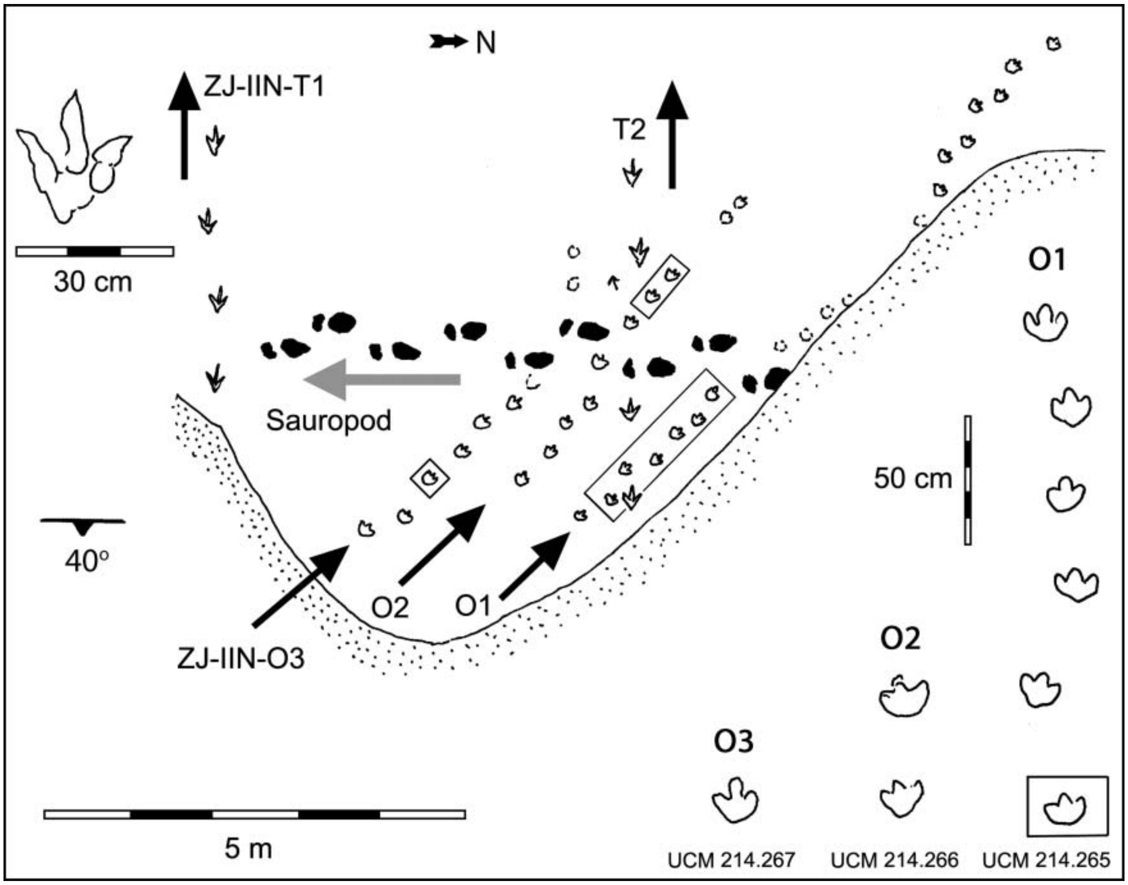

FIG. 5. Map of a part of Zhaojue site ZJ-IIN, showing three parallel *Ornithopodichnus* trackways (O1–O3). Compare with Figure 6.

or stronger mesaxony, whereas *Ornithopodichnus* appears to represent a trackmaker like *Zhuchengosaurus* with much weaker mesaxony. This variation in mesaxony is obviously independent from track size and ontogenetic growth because (weak mesaxonic) *Ornithopodichnus* comprises footprints of large and small individuals. In naming *Ornithopodichnus* Kim et al. (2009) noted that Moratalla (1993) had informally proposed the name '*Brachyguanodonipus prejanensis*' for large ornithopod tracks that are unusually wide (mean length and width values of 53.0 and 64.3 cm respectively) giving a l/w ratio of 0.82 (Lockley, 2009). However, as the name was proposed in an unpublished PhD thesis (in Spanish) it has no formal status in ichnotaxonomy.

In the present study we describe small *Ornithopodichnus* trackways from the northern part of tracksite II (prefix ZJ-IIN), which we infer to be very similar to those reported from the Lower Cretaceous of Korea (Lockley et al., 2012a).

GEOLOGICAL SETTING

The Zhaojue site is a large active copper mine quarry in the Lower Cretaceous Feitianshan Formation (Berriasian–Barremian; Tamai et al., 2004) of Sichuan Province (Figs. 1–3). The outcrops in this area are dominated by thick sandstone sequences with minor siltstones and shale, which alternate with thick brick red shale and siltstone sequences, which in turn contain thin sandstones (Fig. 4). The quarry sequence reveals tracks at several levels including impressions (concave epireliefs) on the surfaces of sandstone beds and natural casts (convex hyporeliefs) on the underside of beds where sand has filled in tracks made in shale or silt beds. The exposed sandstone surfaces are extensive and reveal many tracks, ripple marks, desiccation cracks and other biogenic and non-biogenic sedimentary features. The preservation of tracks is variable but generally good to moderately good.

Tracks found on the most track-rich surfaces include large theropod, sauropod and ornithopod tracks as well as pterosaur footprints. A preliminary report on swim tracks attributable to theropods, has recently be published (Xing et al., 2013), and the pterosaur track occurrence has also been noted elsewhere (He et al., 2013). Xing et al. (2013) referred to two main outcrops, about 450 meters apart, designated as tracksites I and II. Trackways from these sites have the prefixes ZJ-I and ZJ-II, respectively. However, as noted by Xing et al. (2013), the quarry configuration is changing constantly due to active excavation. In the previous, preliminary study attention was focused on swim tracks from tracksite II. Studies are ongoing at both tracksite I and tracksite II, where multiple track-bearing layers have been identified.

MATERIAL AND METHODS

Due to the steepness of the bedding planes (40–50°) at both tracksite I and tracksite II (Xing et al., 2013), it was necessary to use ropes during the study of track-bearing surfaces. In order to make accurate maps, especially in areas destined for destruction by quarry operations, tracks were photographed, outlined in chalk, and traced on large sheets of plastic. In addition a representative area of well-preserved tracks was mapped by hand using a chalk grid (Fig. 5). Several natural casts were collected, and latex molds of representative tracks were made. Additional more detailed tracings of selected tracks were made on transparent acetate film. Due to the difficulty of obtaining accurate trackway measurements from steep slopes, measurements for the present study were taken primarily from the tracings and latex molds of representative tracks from three trackways. Latex molds and plaster replicas are reposited in the Huaxia Dinosaur Tracks Research and Development Center collections (prefix HDT) and in the University of Colorado Museum of Natural History collections, Boulder (USA) (prefix UCM). Tracings are also reposited at both institutions.

Maps of three areas (part of tracksite I and parts of both the northern and southern sectors of tracksite II) have been prepared and will be published elsewhere. A map of the area with the best preserved *Ornithopodichnus* tracks that shows a part of the northern sector of tracksite II was also made as a base map to help reference the tracings and latex molds collected in that sector (Figs. 5 and 6). As shown in Figure 5, three parallel *Ornithopodichnus* trackways have been designated as O1, O2 and O3. At least 21, 8, and 7 footprints are preserved, individually.

Trackway O1 is the longest and most accessible trackway, with the best preserved segments including the tracks designated as O1.1 through O1.6 (Tracing T1611 in the UCM archive). Track O1.6 is the best preserved (Fig. 7). Track O1.1 in this sequence was replicated and is preserved in the UCM collections as 214.265. Two sequential tracks in trackway O2 (i.e. tracks O2.7 and O2.8) were replicated as UCM 214.266, and track O.3.3 from trackway O3 was molded and replicated as UCM 214.267 (see Table 1, and UCM tracing T1613).

DESCRIPTION

As indicated in Table 1, trackway O1 represents a small trackmaker (mean footprint length and width 12.97 and 15.30 cm, respectively), with wide feet (mean 1/w 0.83). Trackway O2, is similar in size and also displays wide tracks (l/w 0.91). Only one reliable measurement was obtained from trackway O3, indicating tracks similar in size to O2 and O3 and about as wide as long (l/w 1.00). Digital pads are absent;

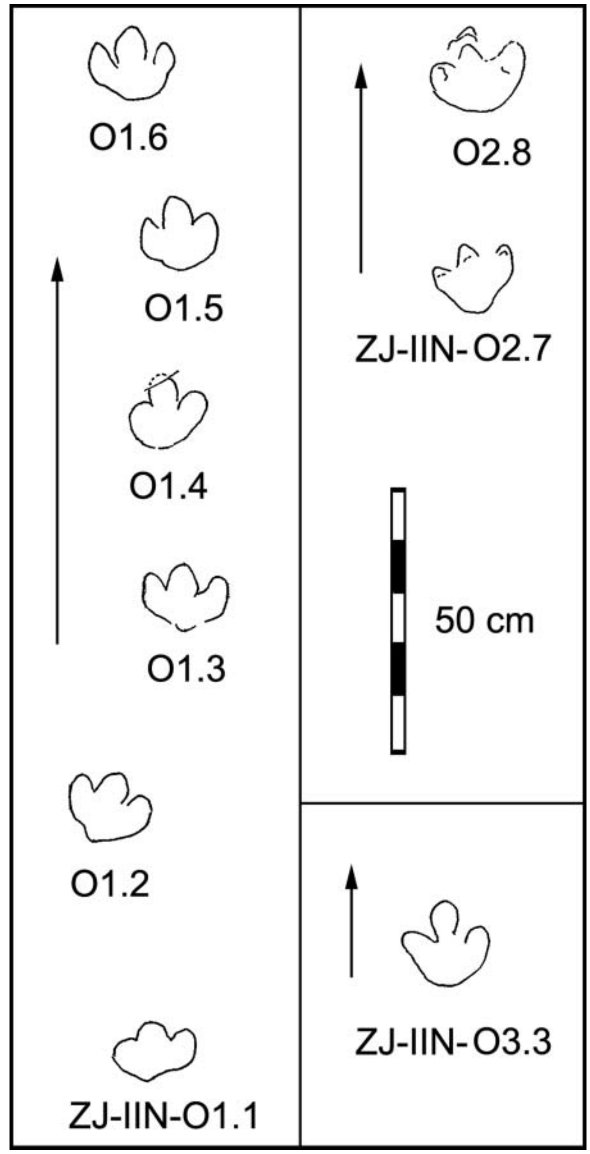

FIG. 6. Sketches with details of *Ornithopodichnus* trackways ZJ-IIN-O1–O3. Compare with Figure 5.

all the distal part of digits are deep, the claw marks are round and blunt. Based on trackway O1, there is consistent inward rotation ranging from 0–26° (mean ~7°). Step averages ~ 40.0 cm (or 2.6 × footprint length) but appears to show a deceleration from 47.2 to 32.0 cm in the segment measured in detail. All three trackways are oriented toward the northwest.

COMPARISONS WITH OTHER *ORNITHOPODICHNUS* TRACKS

As noted above *Ornithopodichnus* from Zhaojue is similar in size and shape (l/w ratio 0.83–1.00: mean 0.91) to *Ornithopodichnus* tracks from the sample described by Lockley et al. (2012a) from the Hwasun site in Korea (mean l/w ratio =

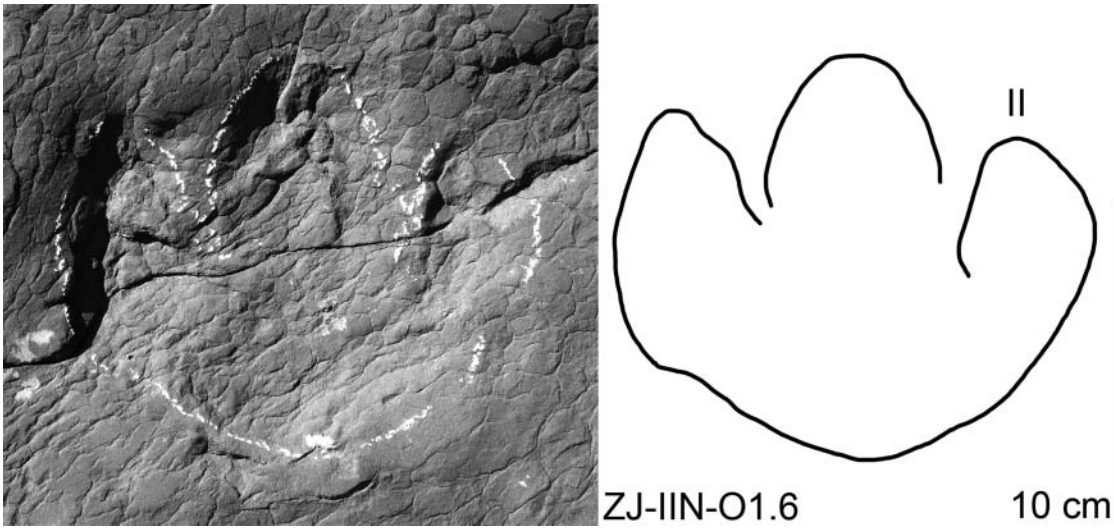

FIG. 7. Photograph and sketch of best preserved *Ornithopodichnus* track ZJ-IIN-O1.6.

0.90; Table 2). It is also similar to the sample of much larger *Ornithopodichnus masanensis* tracks described from the Jindong Formation, Korea (Kim et al., 2009) that show a mean l/w ratio of 0.90 (Table 2). Both samples contain long trackways, which make it possible to verify that the characteristic features of the tracks, notably their transverse shape and tendency to inward rotation, recur repeatedly in long trackways and therefore seem to reflect anatomical peculiarities rather than extramorphology and substrate condition. As noted by Lockley et al. (2012a) the six small *Ornithopodichnus* trackways from Hwasun are particularly well-preserved, and have yielded internally consistent measurements within the sample. The three Zhaojue trackways (Fig. 5, Table 1) are more variable in preservation, and it is difficult to obtain multiple measurements from trackways O2 and O3 due to the difficulty of access on a steep slope and the quality of preservation affected by weathering and trampling by other trackmakers. Nevertheless, the following comparisons support assigning the Zhaojue trackways (O1–3) to *Ornithopodichnus* inferring that they are similar to the Hwasun trackways (O1–O6). First the size and shape (l/w ratio) is similar in the two samples. Thus, the mean length and width values for tracks from the Zhaojue sample are 14.79 and 15.76 cm compared with 11.98 and 13.34 for the Hwasun sample. Thus, on average, the Chinese tracks are 25% longer and 18% wider than the Korean tracks. However, the best preserved Zhaojue trackway (O1) is only slightly larger than the Korean tracks, and we consider this trackway to produce the most reliable data. Likewise the mean step for Zhaojue trackway O1, is 40.04 cm, which is very similar to the mean step of 38.49 cm calculated for the entire Hwasun sample (Table 2). Other notable points of comparison include the similarity in average inward rotation (7.2° for Zhaojue trackway O1 and 10.5° for the Hwasun sample).

Xing et al. (2013) also described several middle-sized, but variably-shaped ornithopod tracks from ZJ-II. The length of these tracks ranges between 18.2 and 28.7 cm, and the L/W ratios are 0.78–1.48. But most of these tracks are poorly preserved and the fills are amalgamated to the tracks, making it difficult to separate them mechanically. These tracks resemble both *Caririchnium* and *Ornithopodichnus* in morphology. Thus larger *Ornithopodichnus* from ZJ-IIN may be present.

SPEED ESTIMATES

As reported by Kim et al. (2009), all *Ornithopodichnus masanensis* trackways are parallel and oriented in the same (southward) direction. They also show consistent intertrack-

TABLE 1
Measurements for small *Ornithopodichnus* tracks from the Zhaojue site II

Track number	Left/ right	length : width	l/w ratio	Rotation	Step
ZJ-IIN-O1.1	R	11.00 : 15.30	0.72	14°	—
ZJ-IIN-O1.2	L	13.50 : 15.30	0.88	16°	47.20
ZJ-IIN-O1.3	R	12.50 : 15.80	0.79	0°	41.50
ZJ-IIN-O1.4	L	13.00 : 14.80	0.88	0°	35.50
ZJ-IIN-O1.5	R	14.30 : 14.40	0.99	9°	34.00
ZJ-IIN-O1.6	L	13.50 : 16.20	0.83	4°	32.00
O1 mean		**12.97 : 15.30**	**0.85**	**7.2°**	**38.04**
ZJ-IIN-O2.7	—	13.90 : 15.50	0.90	—	—
ZJ-IIN-O2.8	—	16.10: 17.50	0.92	—	—
O2 mean		**15.00 : 16.50**	**0.91**	—	**36.00**
ZJ-IIN-O3.3	—	16.40 : 16.40	1.00	—	—

TABLE 2
Mean measurements for small *Ornithopodichnus* trackways from the Cretaceous Zhaojue (China) and Hwasun and Masan tracksites (Korea). O1- O6 and LOT (Large ornithopod trackway) from the Hwasun tracksite, modified after Lockley et al. (2012). TW1–TW5 after Kim et al. (2009).

Trackway no.	Pes length : width	l/w	Step : stride	Rot. ° : pace angle °
ZJ-IIN-O1	12.97 : 15.30	0.83	38.04 : 76.08*	7.20 : —
ZJ-IIN-O2	15.00 : 16.50	0.91	36.00 : 72.00*	—
ZJ-IIN-O3	16.40 : 16.40	1.00	—	—
O1-O3 mean	**14.79: 15.76**	**0.91**	**38.02 : 76.04**	—
O1 Hwasun	12.67 : 14.72	0.86	38.43 : 73.80	5.00 : 161.20
O2 Hwasun	12.07 : 14.03	0.86	40. 53 : 81.95	11.75 : —
O3 Hwasun	(11.65) : 12.80	(0.91)	38.30 : —	—
O4 Hwasun	(12.00) : 12.80	0.94	36.40 : 73.00	—
O5 Hwasun	12.13 : 14.50	0.84	38.30 : 75.75	14.80 : 156.00
O6 Hwasun	11.40 : 11.20	1.01	—	—
O1-O6 mean	**11.98 : 13.34**	**0.90**	**38.39 : 76.12**	**10.52 : 158.60**
LOT	35.10 : 41.70	0.84	114.25 : 225.00	13.80 : 154.30
TW1	35.85 : 56.00	0.64	80.33 : 156.80	— : 153.40
TW2	42.75: 47.75	0.89	95.40 : 189.33	— : 169.83
TW3	43.20 : 36.40	1.18	91.50 : 181.60	— : 165.00
TW4	36.33 : 39.66	0.92	80.60 : 159.75	— : 171.25
TW4’	35.75 : 35.50	1.00	70.00 : 160.50	—
TW5	42.20 : 56.40	0.75	91.00 : 177.67	— : 161.00
TW1-5 mean	**39.35 :45.29**	**0.90**	**84.81 : 170.94**	—

*Indicates stride calculated as 2 £ step. Mean values in parentheses ( ) indicate that approximate measurements from original data have been included in calculations.

TABLE 3
Estimated data of height at the hip and speed of *Ornithopodichnus* producers. Trackways TWI-TW5 refer to the Masan sample (after Kim et al., 2009). Trackways ZJ-IIN-O1–ZO2 refer to the Zhaojue sample and trackways HO1-2, HO4-5 and LOT refer to the Hwasun sample

Trackway no.	L (cm)	SL (cm)	h* (cm)	SL/h	V# (m/s)
TW1	38.0	155.0	217.0	0.72	1.76
TW2	44.0	190.0	251.0	0.76	1.89
TW3	44.0	182.0	251.0	0.73	1.89
TW4	37.0	160.0	211.0	0.76	1.73
TW4′	36.0	160.0	205.0	0.78	1.71
TW5	42.0	177.0	239.0	0.69	1.84
ZJ-IIN-O1	13.0	80.8	59.8	1.35	0.92
ZJ-IIN-O2	15.0	72.0	69.0	1.04	0.99
HO1	12.7	73.8	58.4	1.26	0.91
HO2	12.1	82.0	55.7	1.47	0.89
HO4	12.0	73.0	55.2	1.32	0.89
HO5	12.1	75.8	55.7	1.36	0.89
LOT	35.1	225.0	200.0	1.12	1.69

L: track length, SL: stride length, SL/h: relative stride length (Thulborn, 1990).
*h = 5.7L (height at the hip of large bipedal dinosaurs in general) and = 4.6L (small bipedal dinosaurs in general) after Thulborn, 1990.
#V = $(1.42h)^{0.5}$ (average walking speed of bipedal dinosaurs after Thulborn, 1990).

way spacing (*sensu* Lockley, 1989). Such parallel ornithopod trackways are quite common at Cretaceous sites in Asia (Lockley et al., 2006; Zhang et al., 2006) and in North America (Lockley and Hunt, 1995; Matsukawa et al., 1999) and are usually considered indicative of gregarious behavior. Kim et al. (2009) estimated the size and speed of the *O. masanensis* trackmaker, using relative stride length (stride length/height at the hip, or SL/h), and the equation, $V \approx (1.42h)^{0.5}$ proposed by Thulborn (1990) and references therein. The speed of the Masan *Ornithopodichnus* trackmakers was estimated at 1.71 to 1.89 m/s, a relatively slow rate of progression. For consistency, where reliable stride data are available, we estimated the speeds of the Zhaojue and Hwasun trackmakers using the same formula (Table 3). Zhaojue trackways O1 and O2 indicate estimated speeds between 0.92 and 0.99 m/s, which compare closely with the speeds estimated from small ornithopod trackways from Hwasun (HO1–2 and HO4–5) which range from 0.89–0.91 m/s. The large ornithopod trackway (LOT) from Hwasun gives a speed estimate of 1.69 m/s, which is very similar to the estimates derived from the large trackways in the Masan sample.

DISCUSSION AND CONCLUSIONS

Small short (l< w) ornithopod tracks from the Zhaojue locality represent the fourth report of the ichnogenus

Ornithopodichnus from Asia since it was defined by Kim et al. (2009). Two of these assemblages, one from Masan, Korea, and the other from Junan, China represent large trackmakers. In the Junan sample, one trackway indicates bipedal progression, the other one a quadrupedal movement. The other two samples, from Hwasun, Korea and Zhaojue, China, both represent small trackmakers (footprint length ∼13.0–15.0 cm) that created parallel trackways suggestive of gregarious behavior. Based on footprint length, the hip heights of the dinosaurs from both of these samples is in the range of 55–69 cm. The regularity in step length and speed estimates from both sites indicates that the trackmakers were moving slowly at about 1 meter/second. The Junan sample is the only one to have yielded unequivocal evidence of quadrupedal progression by an *Ornithopodichnus* trackmaker. Thus, although it is not possible to rule out overprinting of the manus by the pes (Paul, 1991), it appears that the majority of samples reflects bipedal progression.

Ornithopod tracks occur abundantly in the Cretaceous. Lucas (2007) therefore used them as indicators of a Lower Cretaceous footprint-based biochron (Lucas, 2007). Six ornithopod ichnogenera, *Amblydactylus, Caririchnium, Iguanodontipus*, *Hadrosauropodus, Jiayinosauropus* and *Ornithopodichnus* have been erected on the basis of Cretaceous ichnites. This list does not include tracks such as *Iguanodonichnus* that have been proven to represent sauropods and *Hadrosaurichnus,* which represents a theropod (Sarjeant et al., 1998). Three of these (*Caririchnium, Jiayinosauropus,* and *Ornithopodichnus*) have been identified in Asia (Lockley et al., 2013), with the latter two being based on Asian holotypes (Dong et al., 2003, and Kim et al., 2009, respectively). To date *Ornithopodichnus* has only been recognized in Asia. Both *Hadrosauropodus* and *Jiayinosauropus* are Late Cretaceous ichnogenera of presumed hadrosaurid affinity. The other ichnotaxa are reported from the Lower to mid Cretaceous.

Lucas et al. (2011, p. 357) recently suggested only two Cretaceous ichnogenera may be valid: "*Caririchnium* (= *Hadrosauropodus*) and *Amblydactylus* (= *Iguanodontipus*)." However, this conclusion does not address the position of *Ornithopodichnus* or *Jiayinosauropus* already known when this interpretation was proposed. For this reason Lockley et al. (in press) have reviewed the ichnotaxonomic status of Cretaceous ichnotaxa attributed to ornithopods and find that the suggestions of Lucas et al. (2011) are in need of re-evaluation. Although reiterating the conclusions of this review is beyond the scope of this study, *Ornithopodichnus* is an ichnotaxon of undoubted ornithopod affinity, which must be considered in any comprehensive review of this group of trackmakers. If the ichnogenus proves to be exclusively or dominantly of Asian affinity, as suggested in preliminary reports, it may support the inference that Lower Cretaceous ichnofaunas from Asia are regionally distinctive (Lockley et al., 2012b). If this is the case the single, global Lower Cretaceous biochron of Lucas (2007) may potentially be differentiated and defined in more detail.

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