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Upper Cretaceous dinosaur track assemblages and a new theropod ichnotaxon from Anhui Province, eastern China

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ABSTRACT

Several noteworthy Cretaceous tracksites are known in the Huizhou District (Huangshan City) in the Yangtzee valley of southern Anhui Province. These include some that have been known since the late 1970s but have not been studied in detail until now. The footprints described here occur in siliciclastic fluvial deposits in three distinct horizons. The Xiaohutian tracksite in the Upper Cretaceous Xiaoyan Formation is the most interesting, being situated at a historically famous location used as a Taoist and Buddhist shrine. The Xiaohutian tracksite yields an assemblage with three different morphotypes of non-avian theropod tracks including the new ichnotaxon *Paracorpulentapus zhangsanfengi* that can be attributed to a theropod with relatively short "fleshy" toes showing convergence with the footprints of small ornithopods. A further diagnostic feature is the trackway pattern with relatively short steps. Associated ichnofossils are invertebrate traces that can be assigned to eurybathic forms such as *Palaeophycus* and ?*Planolites* or ?*Scoyenia*. Thus far skeletal remains from the Xiaoyan Formation have proved the pachycephalosaur *Wannanosaurus* and indeterminate sauropods. The ichnoassemblages enlarge the known dinosaur fauna by small- to medium-sized theropods that are identified here as the trackmakers and that are otherwise rare in Upper Cretaceous deposits of eastern China. The Shangshangen locality is another significant tracksite which has yielded small bird tracks (cf. *Koreanaornis*) in association with small tracks of non-avian theropods.

1. Introduction

Dinosaur tracks from Lower Cretaceous deposits are abundant throughout China and have been well documented by many authors (Matsukawa et al., 2006; Xing, 2010; Lockley et al., 2013). However, dinosaur tracks from Upper Cretaceous deposits of this region are comparatively rare, and the only known well-preserved specimens are those from the Jiuquwan tracksite of Hunan Province (Xiaodong Formation) (Zeng, 1982; Zhao, 1985; Matsukawa et al., 2006) and the Xiaohutian tracksite of Anhui Province (Xiaoyan Formation) (Yu, 1998, 1999; Yu et al., 1999; Matsukawa et al., 2006) (Fig. 1). There are a few other scattered reports, but among putative type specimens (ichnospecies) from the Upper Cretaceous of China, only *Jiayinosauropus johnsoni* (Dong et al., 2003; Xing et al., 2009a; Lockley et al., 2013) is unequivocally dated as Late Cretaceous. The tracks of the Xiaohutian tracksite exceed those of the Jiuquwan tracksite in both quantity and quality of preservation. Dinosaur skeletal fossils are rare in Upper Cretaceous deposits of Eastern China, and the Xiaohutian tracks are, therefore, important for the reconstruction of the local dinosaur fauna.

It is not uncommon for theropod tracks of different sizes and morphologies to be preserved at the same tracksite. Li et al. (2011)

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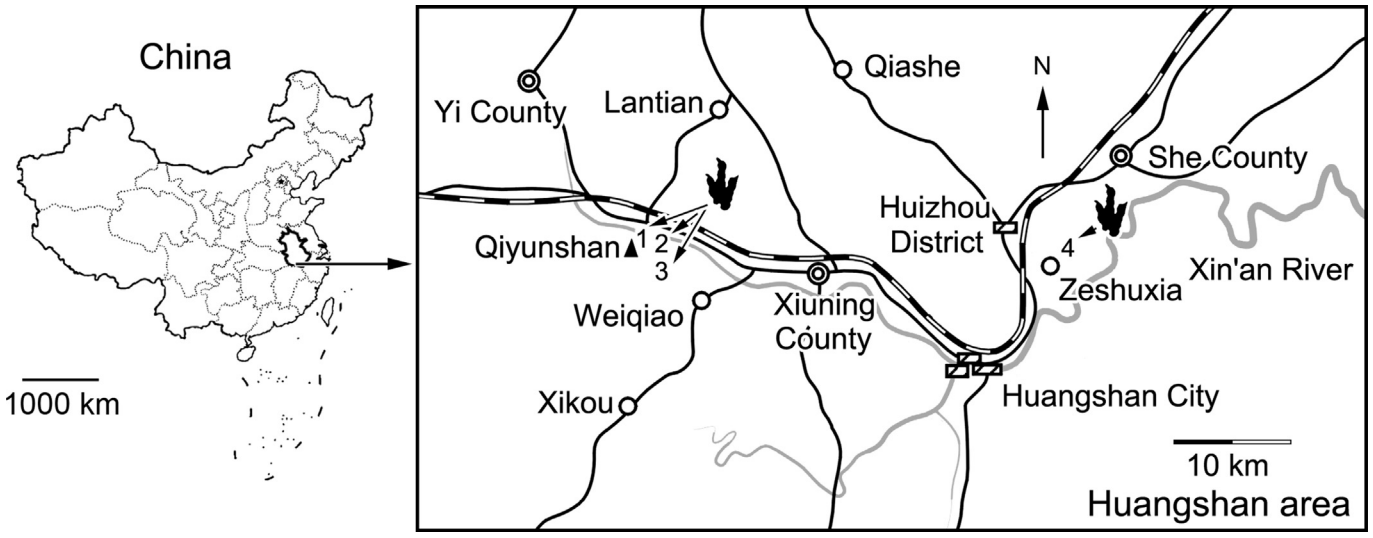

Fig. 1. Geographic map showing the location (footprint icon) of the dinosaur tracksites in Huangshan area, Anhui Province, China. 1, Xiaohutian; 2, Yujundong; 3, Shangshangen; 4, Zeshuxia tracksites.

described an unusual theropod track assemblage from the Lower Cretaceous of the Zhucheng area, Shandong Province, China, that included *Corpulentapus* and medium-sized grallatorid tracks (*Paragrallator*). These two theropod tracks show striking differences in their morphology and demonstrate that two distinct medium-sized theropod taxa frequented the same habitat in significant numbers (Li et al. 2011). The Xiaohutian tracksite preserves tracks that resemble those of the Zhucheng theropod track assemblage. The Xiaohutian tracks that resemble *Corpulentapus* were originally attributed to ornithopods (Yu et al., 1999; Matsukawa et al., 2006). While this attribution cannot be disproved completely, *Corpulentapus* type tracks from Xiaohutian are herein interpreted to reflect evolutionary developments in the pes convergent with those of ornithopods, nonetheless manifesting certain theropod characteristics.

Institutional abbreviations

CU = University of Colorado, Denver, USA; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; SS = Shanshan tracksite, Turpan City, Xinjiang, China; SSG = Shangshangen tracksite, Anhui, China; UCM = University of Colorado Museum of Natural History; XHT = Xiaohutian tracksite, Anhui, China; YJD = Yujundong tracksite, Anhui, China

2. History of discovery

In 1970, Lianhai Hou (Institute of Vertebrate Paleontology and Paleoanthropology, IVPP, China) discovered a partial skeleton of a pachycephalosaur as well as the first dinosaur tracks from East China on the outskirts of Zeshuxia Village, Huizhou District, Huangshan City (Hou, 1977). More than twenty years later, the Xiaohutian tracksite was discovered by Junchang Lü and Hailu You (IVPP) at Qiyun Mountain, Anhui Province (Yu, 1998). In 1996, Xinqi Yu et al (No. 332 Geological Survey Team, Anhui Province Geological Exploration Bureau, China) discovered nearby dinosaur tracks at Shangshangen Village, Xiuning County and Yujundong.

Yu (1998) described skeletal material of the coelurosaur *Xiuningpus xintanensis* and the pachycephalosaur *Wannanosaurus yansiensis*. He reported also the ichnotaxa "*Xiuningpus qukouensis*" (a presumed coelurosaur track from Shangshangen Village, Qukou Township) and "*Qiyunshanpus xiaohutianensis*" (a presumed pachycephalosaur track from Xiaohutian, Qiyunshan Town). However, these were not cataloged, illustrated, or morphologically described. Presently, it is impossible to determine to which footprints the names "*Xiuningpus qukouensis*" and "*Qiyunshanpus xiaohutianensis*" were originally intended to apply, and the names must be regarded as invalid (*nomina nuda*). Yu et al. (1999) first described dinosaur tracks from the Xiaohutian tracksite identifying a single theropod track (IVPP V l1875) and a single presumed ornithopod track (IVPP V l1874).

Matsukawa et al. (2006) described theropod and purported ornithopod tracks from the Xiaohutian tracksite (29°48′30.3″ N, 118°1′48.54″E) as well as theropod tracks from the Shangshangen tracksite (29° 47′24.36″N, 118°1′57.78″ E), which they referred to as tracksites 32 and 33 in their list of Chinese tracksites known at that time. As noted below (Fig. 2) the Shangshangen tracksite is positioned in the Huizhou Formation and the Xiaohutian tracksite in the stratigraphically higher Xiaoyan Formation.

In 2011, the first author was invited by the Qiyun Mountain Administrative Committee to investigate the dinosaur tracks at Xiaohutian tracksite again, and in 2012, Qing He and Jian Hu measured the tracks.

3. Geological setting

3.1. The Xiaoyan Formation

Outcrops of the Xiaoyan Formation yield the majority of dinosaur fossils in the southern portion of the Anhui Province (Fig. 2), although, as noted below, tracks are reported also from the older Huizhou Formation. The Xiaoyan Formation has a pseudoconformable contact with the underlying Qiyunshan Formation, and reaches a maximum thickness of 753 m. The Xiaoyan Formation is divided into the upper and lower members. The lower member is composed of purple conglomerate, litharenite, andesitic agglomerate, pyroxene andesite, tuffaceous conglomerate, and sandstone with large-scale cross bedding. The upper member is composed of purplish-grey and brick-red conglomerate interbedded with mixed litharenite and mudstone. The remains of *Wannanosaurus yansiensis* were recovered from the upper member of the Xiaoyan Formation. Both the Xiaohutian and Yujundong tracksites are exposed layers of calcareous sandstone in the uppermost part of the lower member of the Xiaoyan Formation (Yu,

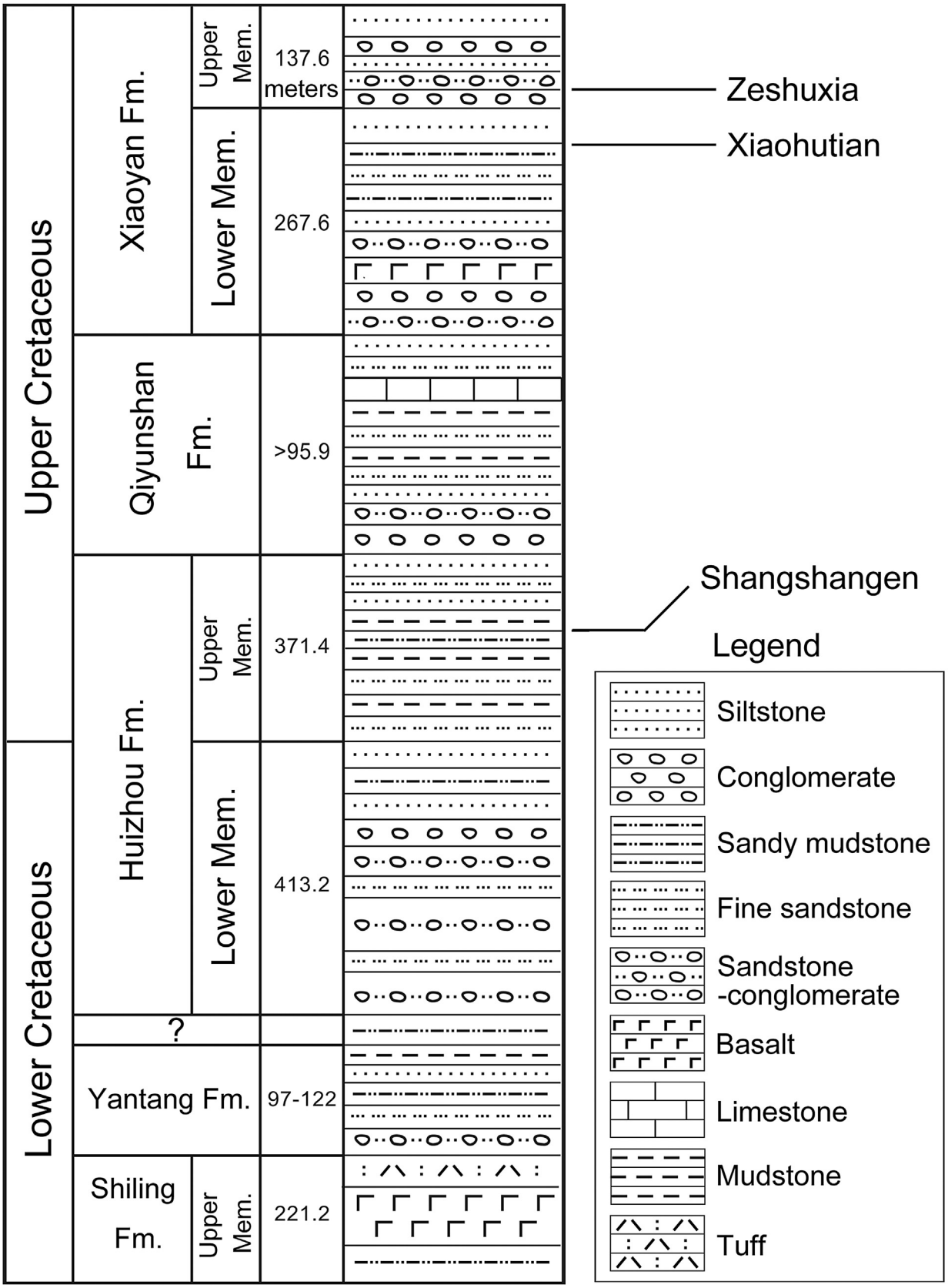

Fig. 2. Stratigraphic section of the Cretaceous sedimentary sequences in the Huangshan area (emended from Yu and Wang, 2001).

1999), not the Qiyunshan Formation as reported by Chen et al. (2006). The geological age of the Xiaoyan Formation is controversial. Chen and Chang (1994) assigned the Xiaoyan Formation to the Campanian based on vertebrate fossils, while Sullivan (2006) tentatively assigned it to the early Maastrichtian based on the pachycephalosaurid record.

The exposures of the Xiaoyan Formation in Yansi differ slightly in lithology from those of the Qiyunshan Formation. In Yansi, the upper member is composed of proportionately less conglomerate and is dominated by thick-layers of sandstone with weathered large-scale cross bedding. Hou (1977) discovered tridactyl dinosaur tracks in thin layers of mudstone in the upper member of the Xiaoyan Formation. They come from a higher position within the Qiyunshan Formation than those from Yansi.

3.2. *Invertebrate traces and paleoecology of the Xiaoyan Formation*

Abundant invertebrate traces are preserved at the Xiaohutian tracksite (Fig. 3), and these are of two general morphologies:

1)?*Planolites*, ?*Scoyenia* (Fig. 3A).

Description: Slightly sinuous, horizontal, and slender trails preserved as convex hyporeliefs on a coarse-grained brown sandstone bedding surface. Trails rang in size up to 85 mm in length and up to 3 mm in diameter. They are characterized by an annulose structure. Annuli are of regular size and spacing. Wall lining is not observed.

Remarks: Despite some similarities an assignment to the ichnogenus *Planolites* is uncertain. *Planolites* is characterized among others by the burrow fill which is differing from the surrounding host sediment. However, this is not distinct in the described trace fossils from the Xiaoyan Formation. Remarkable is the observed annulation, a feature differentiating *Planolites annularius* from the other ichnospecies of *Planolites* (Fillion and Pickerill, 1990).

2) *Palaeophycus tubularis* (Fig. 3B)

Description: Slightly sinuous, generally smooth, horizontal to slightly inclined, large trails preserved as convex hyporelief on a

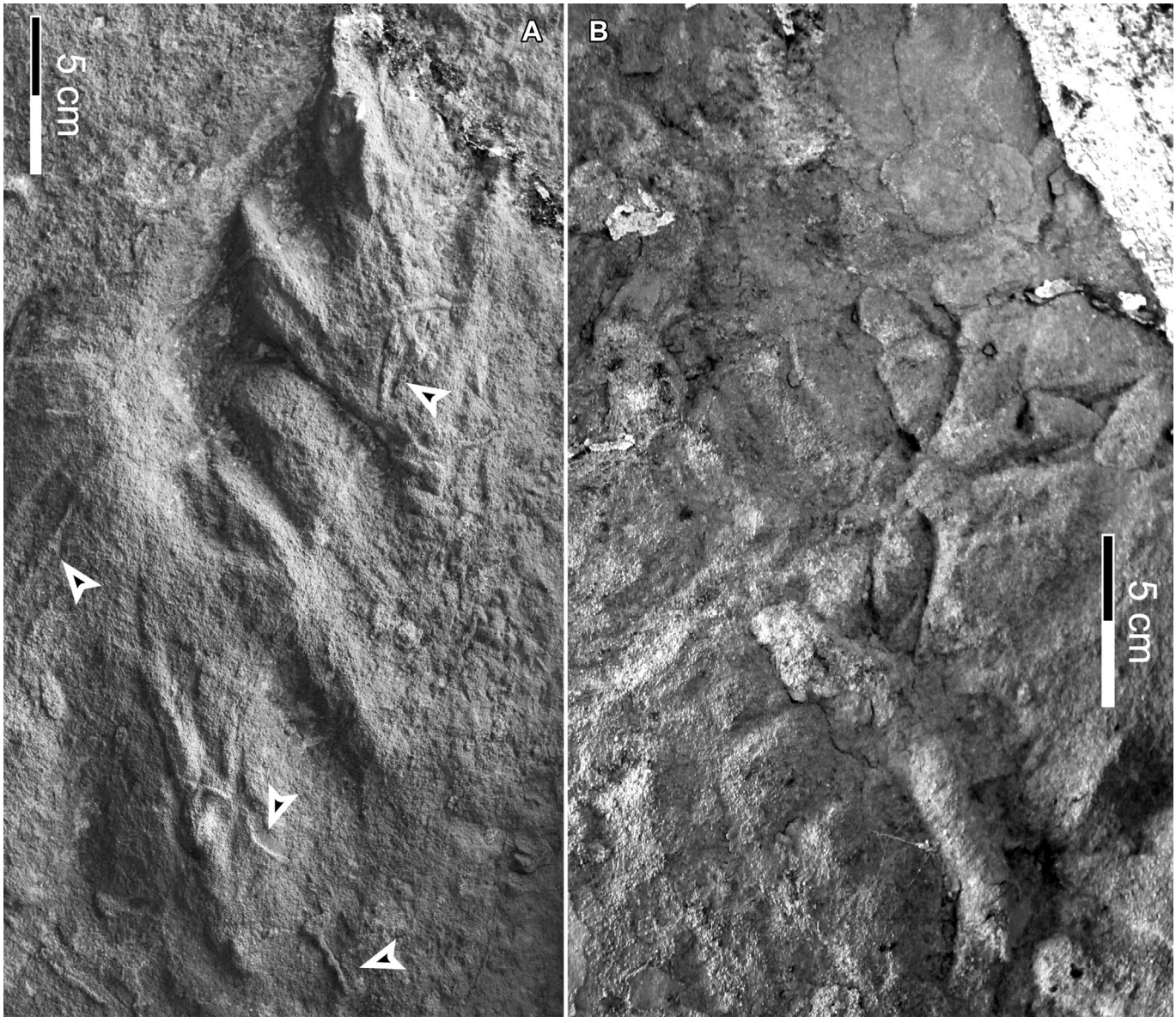

Fig. 3. A–B. Photographs with associated tracks and invertebrate traces from the Xiaohutian tracksite. Arrows in A indicate invertebrate traces.

coarse-grained gray sandstone surface. Trails are thinly-walled. Trail-fill sediments are massive and nearly the same as surrounding deposits. Trails range up to over 20 cm in length and about 10 mm in diameter.

Remarks: Thinly but distinctly lined tube-like features of trails are diagnostic of *Palaeophycus tubularis* (Pemberton and Frey, 1982). However, the tubes are roughly 10 mm in diameter and are larger than previously reported for any *Palaeophycus* ichnospecies.

Planolites and *Palaeophycus* are eurybathic forms reported from the Precambrian to Pleistocene deposits (Fillion and Pickerill, 1990)

3.3. The Huizhou Formation

The Huizhou Formation outcrop area constitutes the main body of the Xiuning-Yansi Mesozoic Red Bed Basin. The lower member is a cyclic sequence that consists of red conglomerate and silty mudstone with calcareous nodules and thick layers of litharenite and siltstone. The upper member is a cyclic sequence that consists of thickly-layered sandstone and siltstone mixed with silty mudstone. The dinosaur tracks at Shangshangen Village, Qukou Township occur in the uppermost part of a thin-layered mudstone at the base of a thick sandstone in the lower part of the upper member of the Huizhou Formation.

4. Distribution of dinosaur tracks

(1). The Xiaohutian tracksite of Qiyunshan, Xiuning County, Huangshan City, is a single exposed sandstone surface near the top of the Xiaoyan Formation. The tracks are exposed as natural casts on the under surface of a massive sandstone bed that creates an overhang or roof in a cave-like horizontal slit eroded into a steep cliff face. The tracksite serves as a shrine for Buddhist pilgrims. The tracks of the Xiaohutian tracksite are the most numerous and best preserved. For these reasons, it is the Xiaohutian tracksite that is given here the greatest consideration.

(2). The Yujundong tracksite of Qiyunshan, Xiuning County, Huangshan City, is a narrow seam of calcareous sandstone in the Xiaoyan Formation. The Yujundong tracksite contains only 10–15 footprints.

(3). The Zeshuxia tracksite of Yansi Town, Huizhou District, Huangshan City, is a previously described locality in the Xiaoyan Formation (Yu et al., 1999). These tracks could not be re-located during the 2012 field expedition. They may have since been weathered or otherwise damaged beyond recognition. The former investigation lacks photography and documentation and therefore this record seems to be lost.

(4). The Shangshangen tracksite of Qukou Township, Xiuning County, Huangshan City, is a single mudstone layer of the Huizhou Formation. No tracks were found at this tracksite during the 2012 field expedition, and it is likely that the tracks formerly present have now been weathered beyond recognition. However, tracks documented and photographed by previous field expeditions are briefly described below. Matsukawa et al. (2006, p. 20) reported that track "specimens are housed in the Hefei Geological Museum" and herein we illustrate three specimens represented by small replicas in the University of Colorado collections.

5. Systematic ichnology of the Xiaohutian tracksite

5.1. General morphotypes

Morphotype A consists of several complete and well-preserved natural casts cataloged as XHT-15, 24, 32, 33, 35, 37, 48, 50, 51 (Figs. 4, 5A, 7B, Table 1). These tracks were not collected and remain in situ. They are small to medium sized (length 13–24 cm) and tridactyl, with an average length/width ratio of 1.3. They resemble the classic theropod footprint genera *Eubrontes*, *Anchisauripus* and *Grallator* from the Late Triassic-Early Jurassic, but they commonly have a wider divarication of digits II–IV (average 56°) compared with the former (10°–40°; Olsen et al., 1998) and sharp claw marks. No distinct trackway of this morphotype was observed. Although, XHT-32 and 33 appear to constitute a single sequential step. A concrete ichnotaxonomic assignment cannot be given.

According to Olsen (1980), Weems (1992), and Lockley (2009), theropod tracks can be differentiated on the basis of mesaxony: i.e., the degree to which the central digit (III) protrudes anteriorly beyond the medial (II) and lateral (IV) digits. Morphotype A is characterized by weak to moderate mesaxony (average 0.49, range 0.46–0.53, $N = 6$), which is typical for footprints of the ichno- or morphofamily Eubrontidae Lull 1904.

Coelurosaurs are known to have proportionately wider feet than less derived theropods (Lockley, 1999; Snively et al., 2004). This suggests that Morphotype A tracks belong to coelurosaurs, whose skeletal fossils show that they have been the prominent theropods throughout China, during the Late Jurassic and Cretaceous (Huh et al., 2006).

Morphotype B consists of medium sized (length 18–21 cm) tridactyl tracks (Figs. 5B, 6A–D, 7A, Table 1) (see 5.2), with very long middle digit and moderate to strong mesaxony (average 0.76, range 0.73–0.81, $N = 3$).

Morphotype C consist of medium sized (length 16 cm) tridactyl tracks (Figs. 5C, 6E, F, 7D, Table 1) (see 5.3), with weak mesaxony (average 0.37, range 0.28–0.44, $N = 7$). These tracks are similar to *Corpulentapus* from Early Cretaceous of the Zhucheng area, Shandong Province, China.

Other material consists of the poorly-preserved and severely weathered tracks, XHT-1, 3, 5, 11, 17, 42 and 54. The major features of these tracks, such as length/width ratio and divarication of digits,

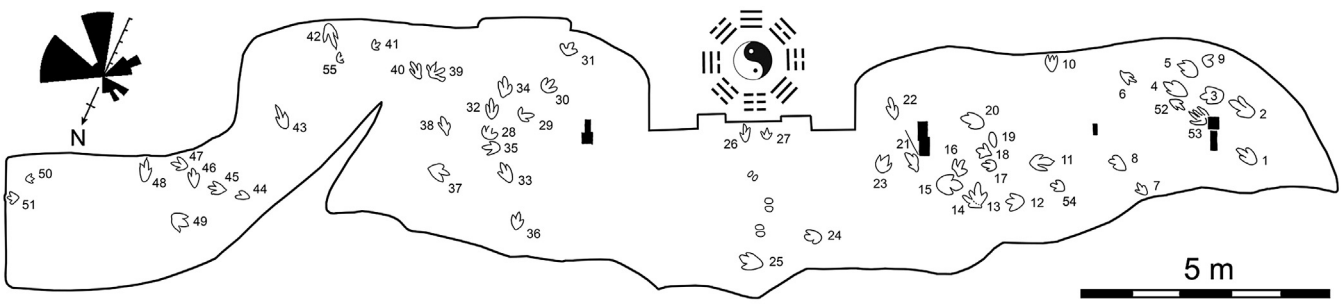

Fig. 4. Map with the distribution of footprints at the Xiaohutian tracksite. The Bagua (eight diagrams) indicate a taoist sculpture.

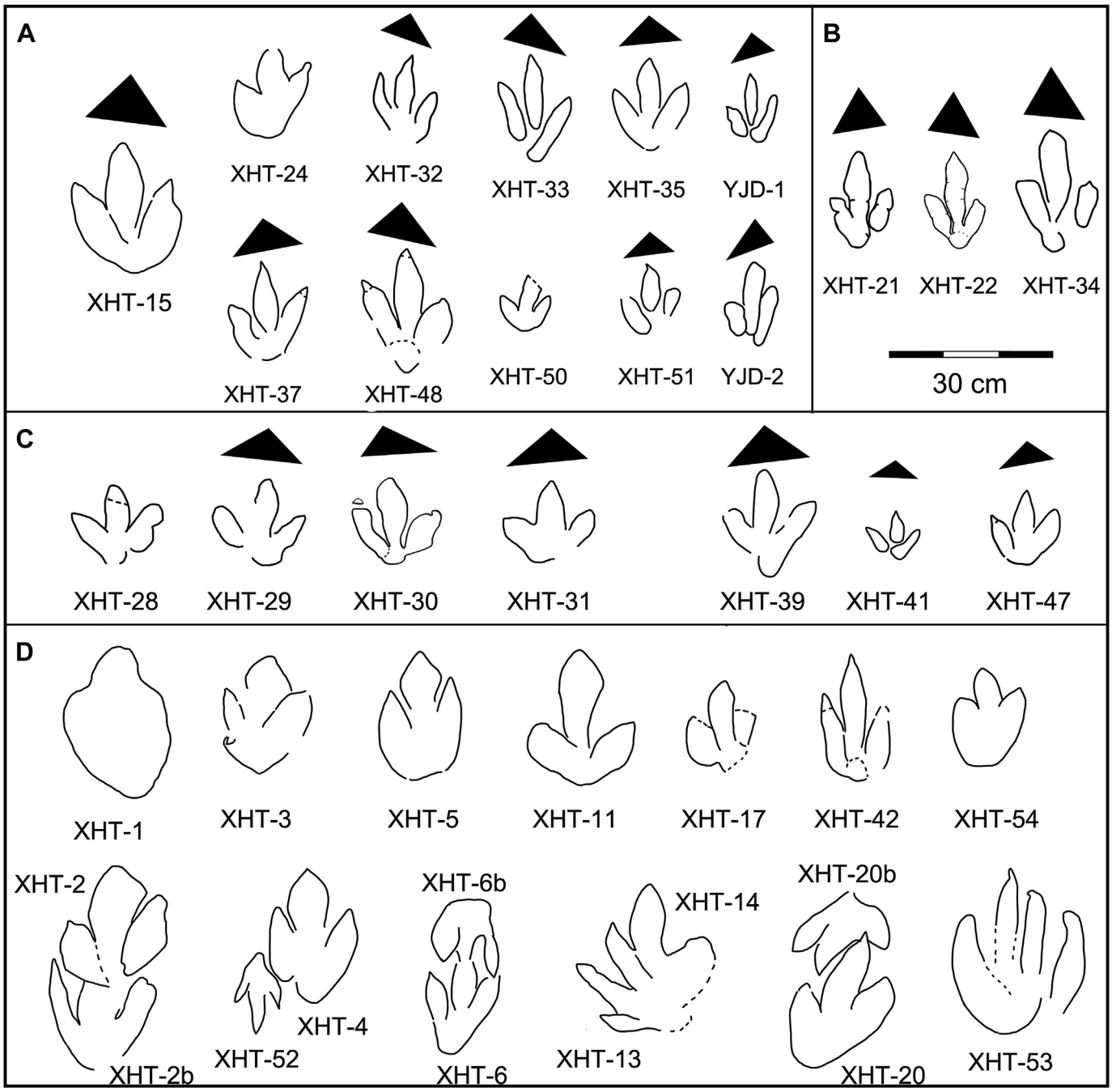

Fig. 5. A–D. Outline drawings of theropod tracks from the Xiaohutian and Yujundong tracksites.

resemble Morphotype A. XHT-4, 5 (Fig. 5, 6G, H) have strong mesaxony (0.68, 0.72 individually), but lack the long middle digit of Morphotype B.

Because of the density of tracks, there are many instances of tracks that overlap (Fig. 5D). For example, XHT-2 overlaps digit III of XHT-2b, XHT-14 digits overlaps a lateral digit of XHT-13. This frequent overlapping indicates a substrate sediment that sustained optimal conditions for track preservation. Obviously, the overlapping of pes tracks of bipedal trackmakers indicates the overlapping of paths traveled by different track makers. A range of print sizes, the frequent overlapping of prints, and the sheer volume of tracks indicate that the Xiaohutian tracksite had once been a location of high dinosaur traffic. The overlapping of XHT-13 and 14 caused Yu et al., (1999) to misidentify these two theropod tracks as a single pentadactyl sauropod track.

In his research on emu tracks, Milàn (2006) concluded that the ideal track cast is most easily formed in deep, semi-firm sediments. The quality of the tracks at the Xiaohutian tracksite indicates preservation conditions near to this ideal, although, based on the track depth, the sediments were probably firmer.

XHT-60 (Fig. 6I, J) is an unusual track that consists of only two parallel digits, probably the middle digit and a lateral digit. XHT-60 is likely an example of a sliding track, and similar prints that form a sliding trail have been reported from the Middle Jurassic Shanshan (Xing et al. in press). Such sliding traces indicate a soft, wet, and slippery substrate.

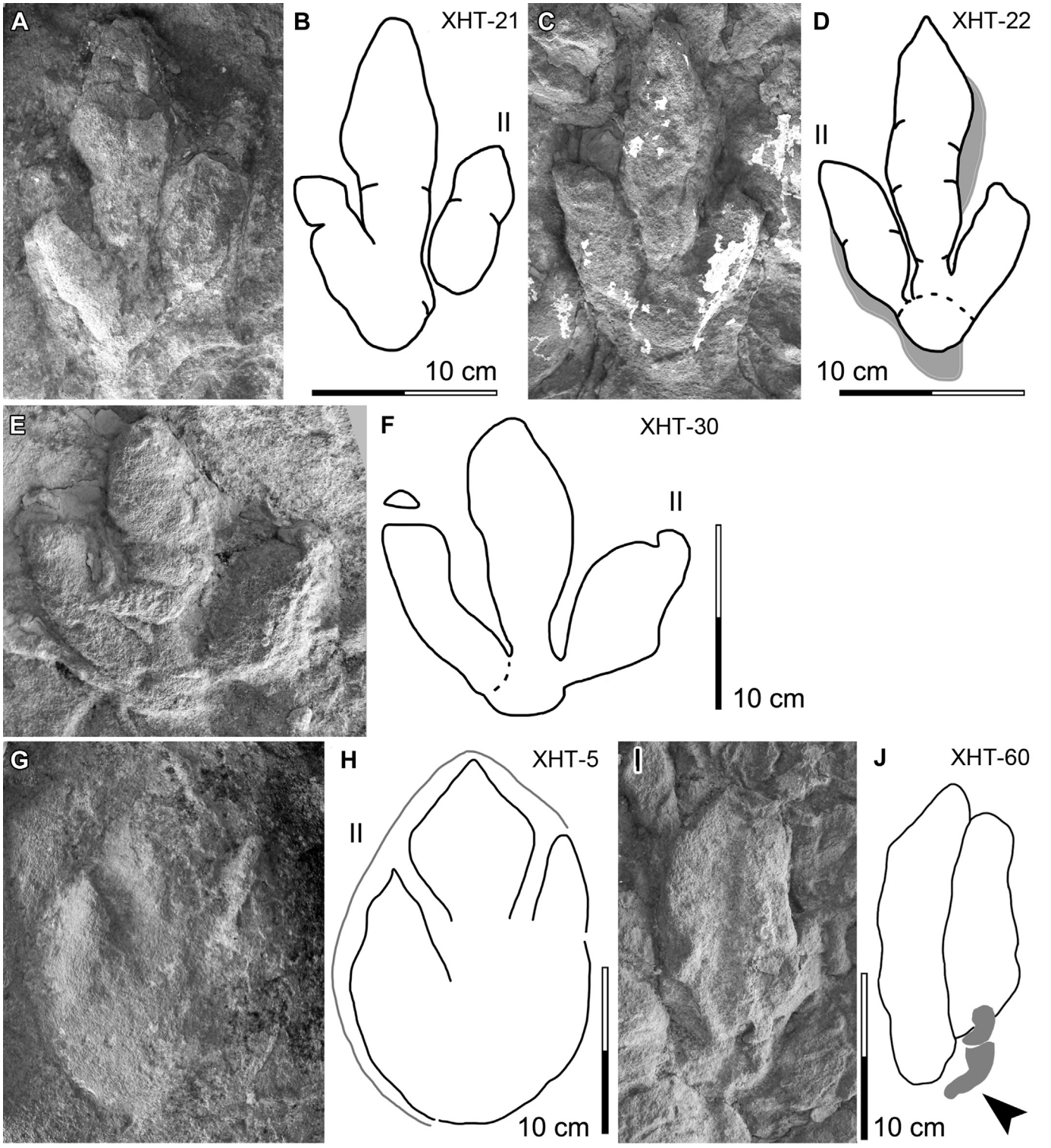

Fig. 6. Photos and outline drawings of theropod tracks XHT-5, 21, 22, 30, and 60 from the Xiaohutian tracksite. E–F. Holotype of *Paracorpulentapus zhangsanfengi* ichnogen. nov. ichnosp. nov.

5.2. Morphotype B

Materials. Two complete pes natural cast tracks constituting a single pace, cataloged as XHT-21 and 22 (CU Denver replica 214. 37 and CU tracing 572: Matsukawa et al., 2006, fig. 4C) from the Xiaohutian tracksite (Figs. 5B, 6A–D, 7A, Table 1). A single isolated natural cast track, cataloged as XHT-34 (Fig. 5B). The original specimens remain in the field.

Locality and horizon. The Xiaoyan Formation, Upper Cretaceous. Xiaohutian tracksite, Huangshan City, Anhui Province, China.

Description. XHT-21 (the first left track in the sequence) and XHT-22 (the right track) are similarly preserved except that end of the

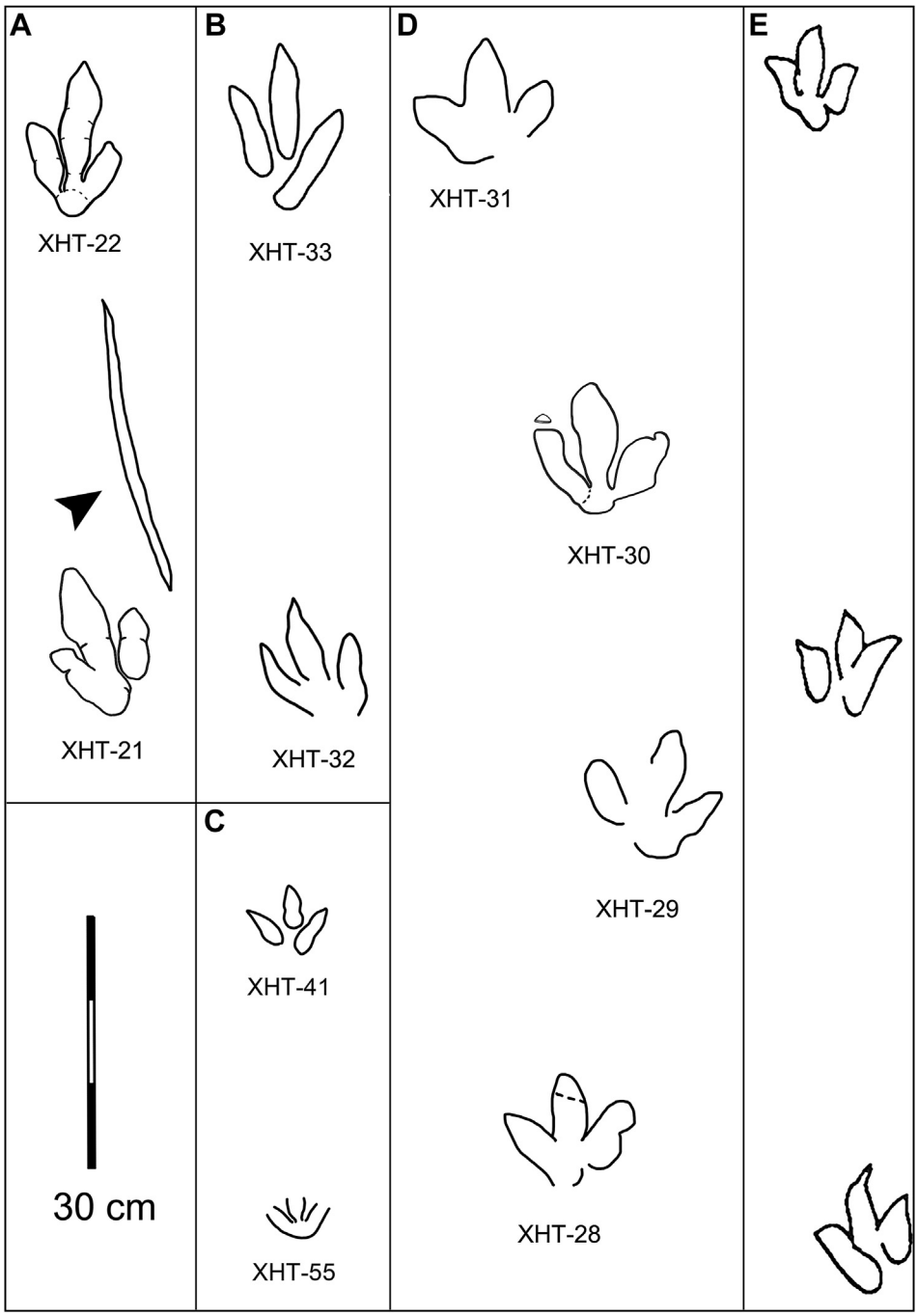

Fig. 7. A–C. Theropod trackways from the Xiaohutian tracksite. D. *Paracorpulentapus zhangsanfengi* ichnogen. nov. ichnosp. nov. holotype trackway. E. *Corpulentapus* trackway from Zhucheng area, Shandong Province, China (after Li et al., 2011).

cast of digit IV in XHT-22 is slightly broken. XHT-21 and XHT-22 constitute a single pace, with a drag mark between the two (Fig. 7A). This indicates a short step length (60.5 cm), only 3.3 times the length of the footprint. XHT-34 (Fig. 5B) is slightly larger than XHT-21 and 22, but similar in overall morphology.

XHT-22 (Figs. 5B, 6C, D, 7A) is the better-preserved example showing clearer pad traces. It has a length/width ratio of 1.8. Digit III is the longest, and digit IV appears the shortest, but has the tip of the cast broken off .The hypex between digits II and III in XHT-21 and XHT-22, is deeper (more posterior) than between digits III and IV, as is typical in theropods. Digits II and III have 2 and 3 digital pads respectively, and digit IV lacks distinct phalangeal pads. A distinct metatarsophalangeal pad trace of digit IV is located on the long axis of digit III. The divarication of digits II–IV (52°) is wider than in the typical Late Triassic–Early Jurassic theropod tracks *Eubrontes*, *Anchisauripus* and *Grallator* (10°–40°), and the divarication of digits II–III is larger than that of digits III–IV. The claw marks of digit III and digit IV are relatively sharp, but generally less than is typical of Late Triassic–Early Jurassic theropod tracks, such as *Eubrontes*, *Anchisauripus*, *Grallator*, and *Kayentapus* as well as of some Early Cretaceous theropod tracks from East Asia, such as *Asianopodus* (Matsukawa et al., 2005). The proximal metatarsophalangeal pad of digit II shows signs of slippage towards the trackway midline and digit III has an associated drag mark, both further indicate that the substrate was wet and slippery.

Table 1
Measurements (in cm) of the best-preserved theropod tracks from Xiaohutian tracksite and Shangshangen tracksite.

Number.	R/L	ML	MW	LD II	LD III	LD IV	II-III	III-IV	II-IV	SL	PL	PA	L/W
XHT-1	—	28.0	18.3	—	—	—	—	—	—	—	—	—	1.5
XHT-2	L	22.1	17.3	—	—	—	—	—	—	—	—	—	1.3
XHT-2b	R	>15.4	17.8	—	—	—	—	—	—	—	—	—	—
XHT-3	R	21.9	14.9	—	—	—	25°	28°	53°	—	—	—	1.5
XHT-4	L	24.7	13.4	13.9	11.3	9.1	18°	24°	42°	—	—	—	1.8
XHT-5	L	23.4	11.4	9.5	10.5	7.0	19°	16°	35°	—	—	—	2.0
XHT-6	L	>17.5	12.7	9.3	—	—	—	—	—	—	—	—	—
XHT-6b	R	>11.6	9.8	6.7	—	7.9	—	—	—	—	—	—	—
XHT-11	R	24.7	18.8	9.1	16.7	9.6	27°	28°	55°	—	—	—	1.3
XHT-13	—	23.0	—	—	—	—	—	—	—	—	—	—	—
XHT-14	—	23.8	17.3	—	—	—	—	—	—	—	—	—	1.4
XHT-15	R	24.2	17.9	11.6	15.7	14.8	27°	28°	55°	—	—	—	1.3
XHT-17	L	15.4	10.7	—	—	—	—	—	—	—	—	—	1.4
XHT-20	R	27.3	14.7	7.8	16.0	6.9	—	—	—	—	—	—	1.9
XHT-20b	—	>16.3	17.1	—	—	—	—	—	—	—	—	—	1.0
XHT-21	R	18.2	10.0	8.3	12.3	7.6	27°	25°	52°	—	60.5	—	1.9
XHT-22	L	18.3	9.7	8.5	13.4	6.0	30°	22°	52°	—	—	—	1.8
XHT-24	L	16.4	13.6	—	—	—	32°	27°	59°	—	—	—	1.2
XHT-28	R	>11.3	15.0	8.7	—	7.5	—	—	—	82.1	43.0	147°	—
XHT-29	L	16.1	16.1	8.6	10.6	7.3	38°	38°	76°	85.3	42.7	177°	1.0
XHT-30	R	16.3	14.4	8.7	11.7	8.3	40°	27°	67°	—	42.7	—	1.1
XHT-31	L	15.6	16.4	5.6	9.2	6.9	45°	35°	80°	—	—	—	1.0
XHT-32	R	>16.3	10.8	—	—	—	—	—	—	—	66.0	—	1.5
XHT-33	L	19.7	13.4	11.4	13.6	9.7	22°	30°	52°	—	—	—	1.5
XHT-34	R	21.1	12.2	8.0	15.9	9.3	28°	23°	51°	—	—	—	1.7
XHT-35	R	16.9	13.2	10.1	9.5	6.9	27°	31°	58°	—	—	—	1.3
XHT-37	L	18.2	14.7	9.1	13.4	6.9	31°	32°	63°	—	—	—	1.2
XHT-39	L	19.6	17.1	7.0	11.1	9.4	32°	32°	64°	—	—	—	1.1
XHT-41	L	9.1	9.9	5.8	5.8	6.6	43°	37°	80°	—	—	—	0.9
XHT-42	R	23.2	11.5	10.5	17.4	14.0	23°	18°	41°	—	—	—	2.0
XHT-47	R	13.5	12.5	7.4	8.2	7.3	30°	36°	66°	—	—	—	1.1
XHT-48	R	22.7	15.7	9.1	15.3	13.4	26°	25°	51°	—	—	—	1.4
XHT-50	L	>10.3	8.8	—	—	—	—	—	—	—	—	—	—
XHT-51	R	13.0	9.7	—	—	—	31°	33°	64°	—	—	—	1.3
XHT-52	L	15.0	8.2	6.8	7.8	4.9	22°	26°	48°	—	—	—	1.8
XHT-53	—	30.4	12.7	—	—	—	—	—	—	—	—	—	2.4
XHT-54	L	17.9	11.3	—	—	—	19°	26°	45°	—	—	—	1.6
YJD-1	L	12.8	9.2	6.7	7.0	9.4	30°	25°	55°	—	—	—	1.4
YJD-2	L	15.5	9.5	6.4	9.4	11.4	30°	20°	50°	—	—	—	1.6
SSG-1	R	9.2	4.2	3.3	6.1	4.1	17°	27°	44°	—	—	—	2.2
SSG-5	R	>7.5	4.4	4.0	5.4	4.3	—	—	—	—	—	—	—
SSG-7	R	8.2	4.5	2.5	6.0	4.0	25°	25°	50°	—	—	—	1.8

Abbreviations: R/L: Right/Left; LD I: length of digit I; LD II: length of digit II; LD III: length of digit III; LD IV: length of digit IV; ML: maximum length; MW: maximum width*; PA: Pace angulation; PL: Pace length; SL: Stride length; II–III: angle between digits II and III; III–IV: angle between digits III and IV; II–IV: angle between digits II and IV; L/W: Maximum length/ Maximum width.

A nearly straight to slightly sinuous and slender trace is observable along the XHT-21 and 22 step. The trace is slightly convex to the left of the trackway and covers most of the step distance between the two consecutive tracks (XHT-21–22). The trace is 36 cm in maximum length, 2 cm in maximum width, and 1 cm in maximum depth. Both ends of the trace are pointed. The trace is U-shaped in cross-section. No surface ornamentation is preserved.

Discussion

Compared with other tracks at the Xiaohutian tracksite, morphotype B is characterized by a long middle digit and stronger mesaxony. Morphotype B theropod tracks are similar to *Therangospodus* (Lockley et al., 1998) in having digits with a rather fleshy appearance and rather indistinct creases between the digital pads. Both are elongated and asymmetric theropod tracks with coalesced, elongated, and oval-shaped digital pads and subtle phalangeal pad traces. However, the anterior triangle (drawn between the tips of the distal ends of digits II, III, and IV [sensu Weems, 1992; Lockley, 2009], indicating the degree of mesaxony) of *Therangospodus* is 0.55 (range 0.47–0.61, based on Lockley et al. 1998: fig. 6 A-G). *Therangospodus* isp is known from the Jurassic–Cretaceous boundary Houcheng (Tuchengzi) Formation in China, such as the Luofenggou tracksite and the Shangyi tracksite in Hebei province (Xing et al., 2013). The morphotype B theropod tracks are most similar to *Therangospodus* isp., from the Shangyi tracksite. Both have robust digits of which the middle digit is long. However, *Therangospodus* isp. from Shangyi has a mean length/width ratio of 1.66, and the mean length/width ratio of the anterior triangle is 0.69, being slightly less than the ratios of morphotype B with1.8 and 0.76. Morphotype B indicates that *Therangospodus*-type theropod tracks have a wider distribution both in age and scope.

XHT-21 and 22 constitute a single step. Assuming that the length of a stride equals that of two steps, we calculate speed (v) using Alexander's (1976) formula: $v = 0.25g^{0.5}.\ SL^{1.67}.\ h^{-1.17}$, where g = gravitational acceleration in m/sec; SL = stride length; and h = hip height, estimated as 4.5 times foot length (FL), using the ratio for small theropods proposed by Thulborn (1990). Based on the length of the step, we estimate a speed of ~1.4 m/s or ~4.9 km/h. The relative stride length (SL/h) is 1.5, implying that the animal was walking, not trotting or running. This speed almost coincides with that calculated for the Shanshan tracks SSIB33 and SSIB41, which were also made in a wet and slippery environment (Xing et al., in press).

On the basis of its occurrence closely associated with a trackway and absence of any groove-like physical features on the surface, the

trace between XHT-21 and 22 is regarded to be a dinosaur tail drag impression left by the same theropod (Kim and Lockley, 2013).

5.3. Morphotype C

Theropoda Marsh, 1881
Ichnofamily indet.
Paracorpulentapus ichnogen. nov.
Type ichnospecies *Paracorpulentapus zhangsanfengi* ichnosp. nov.
Fig. 6E, F

Diagnosis.

Medium-sized (~16.0 cm long and ~15.4 cm wide), robust tridactyl theropod tracks, almost as wide as long; mean divarication between digits II and IV 74°; weak mesaxony; digit traces relatively short and "fleshy" with indistinct creases only between pads and with blunt claws; digits traces separated by a hypex for most of their proximal length; digit IV always the narrowest; digit traces II and III proximally with thin interspace area; metatarsophalangeal pad of digit IV located close to the axis of digit III forming a short rounded "heel"; trackway narrow with short steps; step lengths 2.7 times as much as the track length.

Holotype. A complete pes of natural cast track, cataloged as XHT-30 (CU Denver replica 214. 39 and CU Tracing T 572) from the Xiaohutian tracksite (Figs. 5C, 6E, F, 7D, Table 1). The original specimens remain in the field.

Paratypes. Specimens XHT-28, 29 and 31 (Figs. 5C, 7D) in the same trackway as the holotype. As with the holotype, these specimens remain in the field. XHT-41 (=CU 214.40; Fig. 5C), from another trackway is also designated as a paratype.

Etymology. "para-" Greek, means: "near"; "*Corpulentapus*" is a theropod ichnotaxon introduced by Li et al., 2011.

Type horizon and locality. Xiaoyan Formation, Upper Cretaceous. Xiaohutian tracksite, Huangshan City, Anhui Province, China.

***Paracorpulentapus zhangsanfengi* ichnosp. nov.**

Diagnosis. As for the ichnogenus

Holotype. Same as ichnogenus.

Etymology. Zhang Sanfeng was a legendary Chinese Taoist, according to local superstition the tracks were the palm print left by him or other mythical Taoist figures.

Type horizon and locality. Same as for the ichnogenus.

Description.

XHT-30 (Figs. 5C, 6E, F, 7D) is the best-preserved representative of *Paracorpulentapus zhangsanfengi* within the holotype trackway, and represented by specimen CU 214.39.The tracks are robust tridactyl theropod tracks, with a length/width ratio of 1.1. Digit III is the longest, and digits II and IV of subequal lengths. The two lateral digits have blunt claws. Digit II has two robust phalangeal pads. In digits III and IV there is no distinct border between the phalangeal pads. The metatarsophalangeal pad of digit IV is located close to the axis of digit III. Digits II and III are connected posteriorly. Proximally, digits II and III show a thinner inter-pad space area. The divarication between digit II–III is larger than that between digits III–IV. XHT-28, 29, 31 and the holotype (XHT 30) constitute a single trackway with a slight outward rotation of the footprints. The trackway pattern with the position of the fourth (right) imprint crossing the trackway midline possibly indicates a slight turn to the left. In the footprints, the distal ends of digit III tend to rotate outward away from the long axis of the footprint. The step is more than 2.7 times larger than footprint length.

XHT-39, 41 (CU Denver replica 214. 40) and 47 (Fig. 5C) also from the Xiaohutian tracksite strongly resembles XHT-30, and likely belongs to the same ichnotaxon. They have the same degree of weak mesaxony, 0.44, 0.34 and 0.47, respectively. XHT-41 is merely 9.1 cm in length and possibly the track of a juvenile.

Discussion.

When Li et al. (2011) described *Corpulentapus*, the authors considered *Corpulentapus* to differ from most other theropod tracks in the following characteristics: 1) a distinctive "fleur de lys" shape, 2) robust, "fleshy" digit traces, 3) an absence of well-defined digital pads separated by recognizable creases, 4) a relatively short digit III showing little anterior projection beyond the tips of digits II and IV (=weak mesaxony; Lockley 2009). Except for the "fleur de lys" shape, XHT-30 shares most of the other defining characteristics of *Corpulentapus*. However, the main difference related to the "fleur de lys" shape is that the digits are more strongly separated by greater divarication. XHT-30 is larger than *Corpulentapus* in absolute size (16 cm vs. 11.8 cm), and has slightly stronger mesaxony ($0.37 > 0.32$), wider divarication ($74° > 65°$). Also, the trackway is proportionately wider with shorter step lengths (step length is 5.6 times footprint length in *Corpulentapus* vs. 2.7 times footprint length in the trackway described here). This difference is important because we have a large sample of topotype *Corpulentapus* consistently showing long steps and a very narrow trackway pattern. Thus we regard *Corpulentapus* as sufficiently distinct to merit the erecting of a new ichnotaxon.

Based on Alexander's (1976) formula, we estimate the speed of *Paracorpulentapus* at ~0.9 m/s or ~3.1 km/h. The relative stride length (SL/*h*) is 1.2, implying that the animal was walking.

Yu (1999) attributed these tracks to ornithopods. However, *Paracorpulentapus* has long and narrow claw marks (Fig. 6E, F), and a strong indentation behind digit II, which are major characteristics of theropod tracks (Lockley, 1991). Lockley (2009) considered that there is convergence in the pes development of some short toed theropods and ornithopods especially in the Cretaceous.

Generally speaking as tridactyl bipedal dinosaurs got longer legs they had shorter feet, and longer legged forms have shorter steps. This counter intuitive observation has been discussed in some detail by Lockley, (1999, 2001, 2007) and is supported by Thulborn (1990)'s data on theropod vs. ornithopod foot-leg length ratios, in relation to typical step length. Therefore, *Paracorpulentapus* may have been a short toed form that had long legs.

6. Systematic ichnology of the Yujundong tracksite

The distance between the Yujundong tracksite and the Xiaohutian tracksite is approximately 200 m, and the two tracksites share the same lithology and stratum (Fig. 5). However, the Yujundong specimens are difficult to measure and observe. YJD-1 and YJD-2 are small-sized, ~13 to ~16 cm, mean length/width ratio of 1.5, and the mean length/width ratio of the anterior triangle is 0.6, all coincide with the XHT morphotype C.

7. Systematic ichnology of the Shangshangen tracksite

The Shangshangen tracks can only be analyzed from the original photos (Fig. 8). SSG-1–6 and SSG-7 were located on two isolated slates. SSG-1, 5, and 7 were well-preserved. SSG-1 and 7 are similar to XHT morphotype B, with a mean length/width ratio of 2 and the length/width ratio of the anterior triangle of 0.81. The other Shangshangen tracks are similar to the XHT morphotype C. Yu (1999) provided the outline of the tracks on another slate (Fig. 8E), but without photographs. The outline indicates a length range from 9.5–17 cm, mean length/width ratio of 1.5, mean divarication of digits 57°, and general morphology similar to XHT morphotype C. All tracks appear to have been part of any discernible trackway.

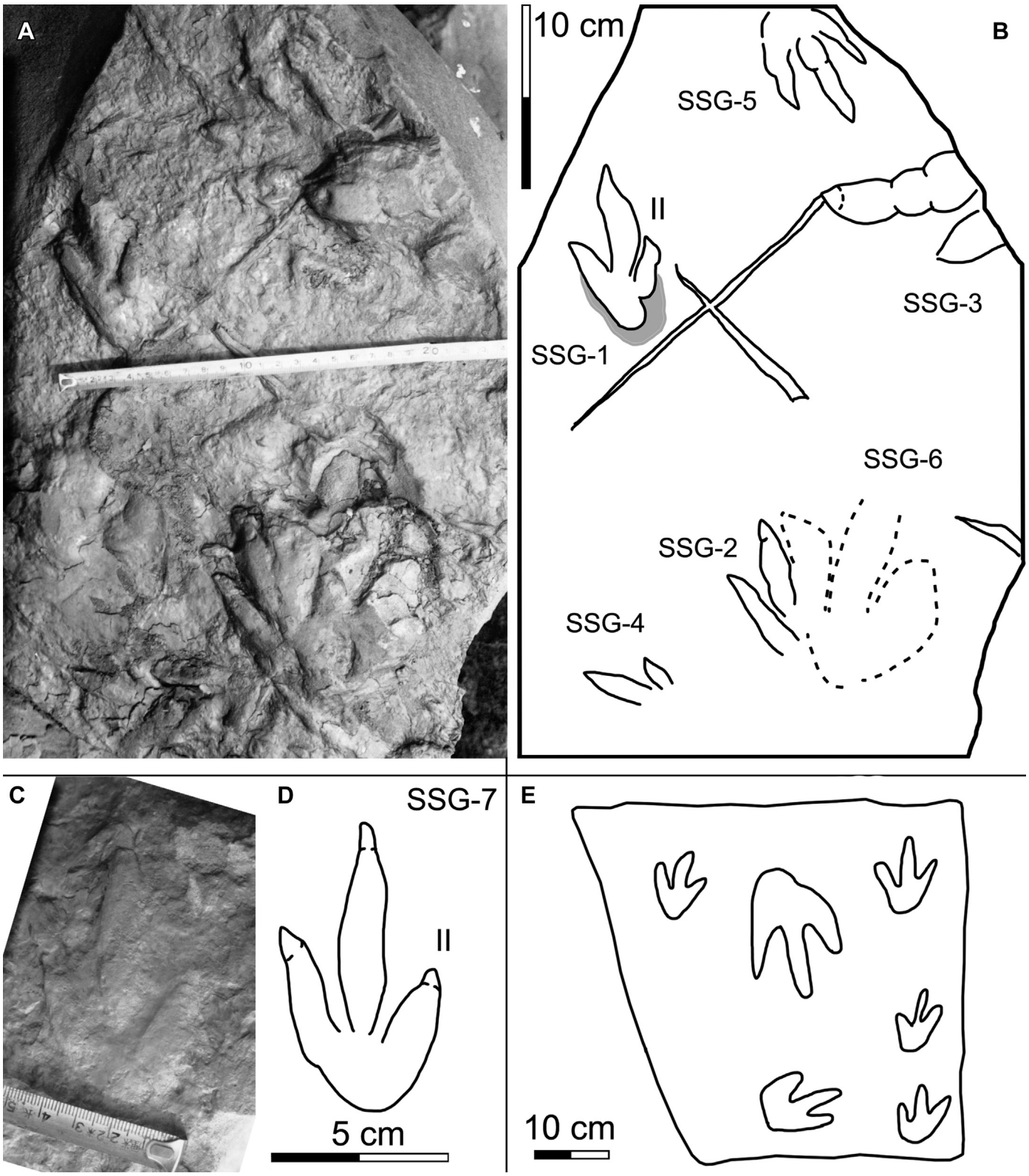

Fig. 8. A–E. Photographs and sketches of theropod tracks from the Shangshangen tracksite.

In 2001, the Shangshangen tracksite was visited and studied by several of the present authors (ML, MM and LJJ). Five loose blocks were observed that revealed small theropod and bird tracks preserved as natural casts (Fig. 9). Only one of these blocks revealed the poorly preserved bird tracks. These specimens were traced (CU tracings T 560–563) and latex molds were made of selected tracks and preserved as specimens CU 214.41 to 214.43: Fig. 9). The preservation of these tracks is not very good. However, more than

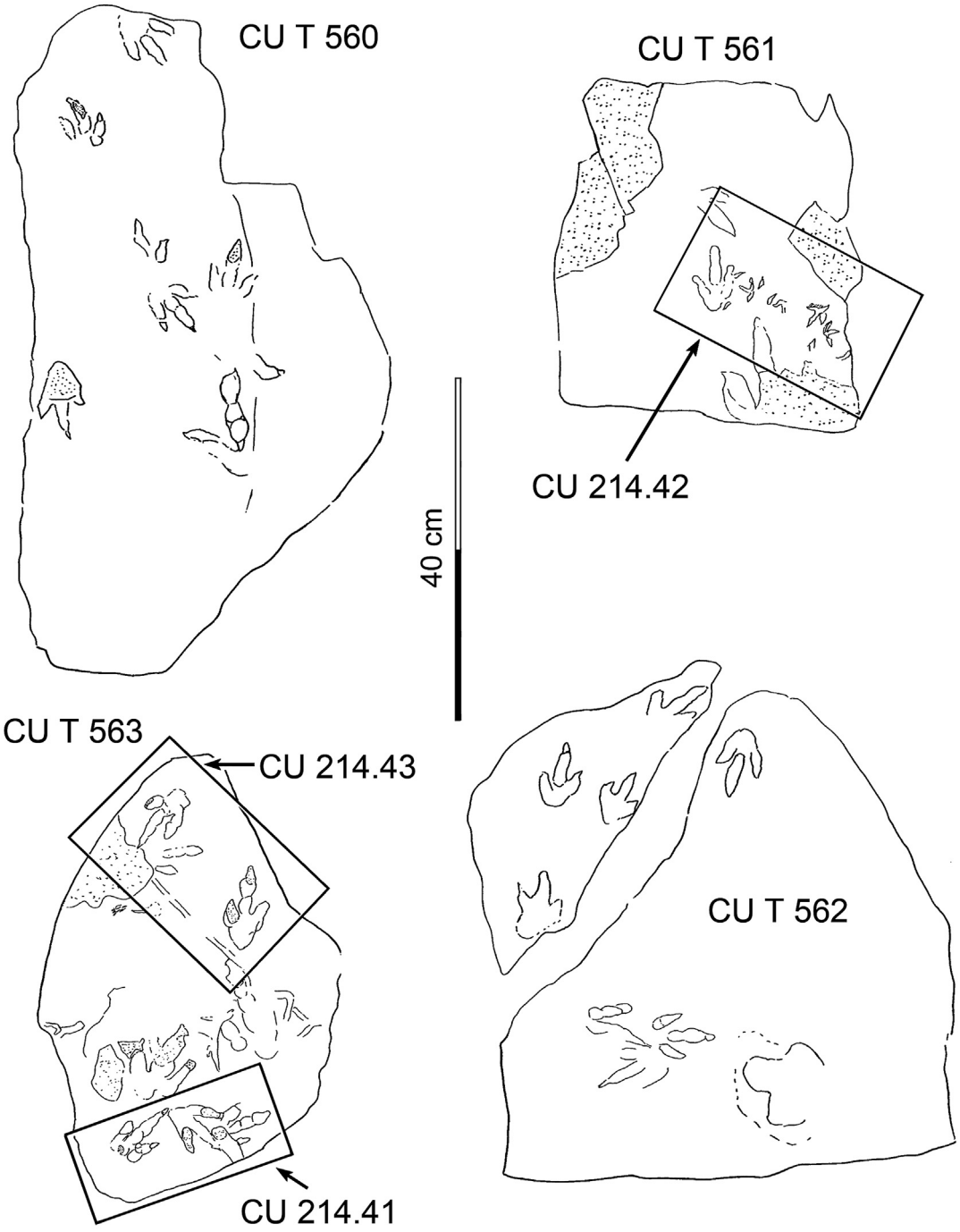

Fig. 9. A–D. Blocks with theropod and bird tracks (B) from the Shangshangen tracksite based on CU tracings T 560–T 563 and representative specimens CU 214.41–214.43. See text for details.

25 complete and partial small theropod tracks were recorded with footprint lengths in the range of ~8–10 cm. We also noted the presence of at least three small (foot width ~3.0 cm) tridactyl bird tracks two of which have very wide digit divarication angles (120–140°). Such small tracks are probably best assigned to *Koreanaornis* (Kim, 1969) although this assignment is tentative. As reported by Matsukawa et al. (2006, p.20) these "specimens are housed in the Hefei (Anhui) Geological Museum" (The Anhui Geological Museum now becomes Anhui Palaeontological Museum in 2012). Unfortunately, these tracks probably have been lost. The first author cannot find them in the Anhui Palaeontological Museum collections.

8. Legends and Tracks

Taoism is a native Chinese religion, with a history that spans nearly 4700 years. Qiyunshan Taoism originated during the reign of Emperor Qianyuan, Tang Dynasty (758–760), and continues to be practiced today. Qiyunshan Mountain is one of four holy tracksites of Taoism. According to Taoism mythology Qiyunshan Mountain was the tracksite of the Taoist ancestor Sanfeng Zhang's rite. The Xiaohutian tracksite is located in an alley (a kind of Chinese temple) in the Ming Dynasty. Inside is a 20 m long, 3.3 m wide, 2.5 m high grotto. The dinosaur tracks are preserved at the apex of the grotto.

For centuries, worshipers have come to the temple and paid homage to the dinosaur tracks (Taoist Temple Tour Editorial Team, 2005), frequently burning incense inside of some of the tracks (Fig. 10A and B). Because the dinosaur tracks are small, with many being roughly the size of a human hand, and because overlapping tracks falsely appear to be single prints with five digits (such as XHT-13 and 14, XHT-53) (Fig. 5, 10C and D), local Taoism followers believed the dinosaur tracks to be the palm prints of ancient Taoists who obtained immortality and could perfume the feat of imprinting their hands into solid stone (Hu, 1996). This offers another example of how some dinosaur tracks influenced the formation of Chinese folk legends (Xing et al., 2011).

9. Dinosaur fauna in the Late Cretaceous of southern Anhui Province

Dinosaur bones in the Upper Cretaceous Xiaoyan Formation of the southern Anhui Province are rare, but include *Wannanosaurus yansiensis* a pachycephalosaur (Hou, 1977) and skeletal remains referred to sauropod indet (Yu, 1998). *Wannanosaurus* was less than one meter in length, and has been considered a flat skull-type pachycephalosaur (Butler and Zhao, 2009), but may also represent a juvenile of the domed skull-type (Longrich et al., 2010). Cervical vertebrae and partial limb girdles of sauropods have been collected from the Xiaoyan Formation. However, this fragmentary material is difficult to assign to a particular sauropod taxon (Hou, 1977). Yu (1999) mentioned that theropod material was also discovered in the lower member of the Huizhou Formation, but provided no detailed descriptions.

The three different theropod track morphotypes represented at the Xiaoyan tracksite confirm the presence of at least three small bodied theropods. The body length of the track maker of the XHT morphotype A, is calculated using the average hip height to body length ratio of 1: 2.63 (Xing et al., 2009b) and the formula: hip height $\approx 4 \times$ footprint length (Henderson, 2003), is approximately 1.4–3.2 m. The body lengths of the track makers of XHT morphotype B and C is 1.9–2.2 m and 1.0–2.1 m respectively. The body lengths of the track makers of the Yujundong and Shangshangen tracks appears to have been roughly the same that of morphotype A.

The Late Cretaceous dinosaur fauna of China is represented by the Hadrosaurid–Titanosaurid assemblage (Dong 1992, Dong and Cheng 1996). In this assemblage, theropod material is rare and largely consists of teeth from large theropods, primarily tyrannosaurids (Dong, 1979; Lü et al., 2009). The most complete theropod fossil is *Zhuchengtyrannus* (Hone et al., 2011), which includes a partial jaw. The adult body length of *Zhuchengtyrannus* is estimated at approximately 11 m. The nearest contemporaneous medium-small sized theropod remains are mostly those found in Inner Mongolia of northern China and Guangdong of southern China. The former contains *Oviraptor* (Osborn, 1924) and *Archaeornithomimus* (Russell, 1972), the latter *Heyuannia* (Lü, 2003) and *Shixinggia* (Lü and Zhang, 2005). There is almost no record of small and medium-sized theropods in East China. The discovery of diverse theropod track assemblages in the Huangshan region of Anhui Province, indicates that a diverse medium-small theropod fauna roamed the region during the time of the deposition of Huizhou and Xiaoyan formations. Medium-and-small sized theropods, pachycephalosaurs, and sauropods constitute a new faunal

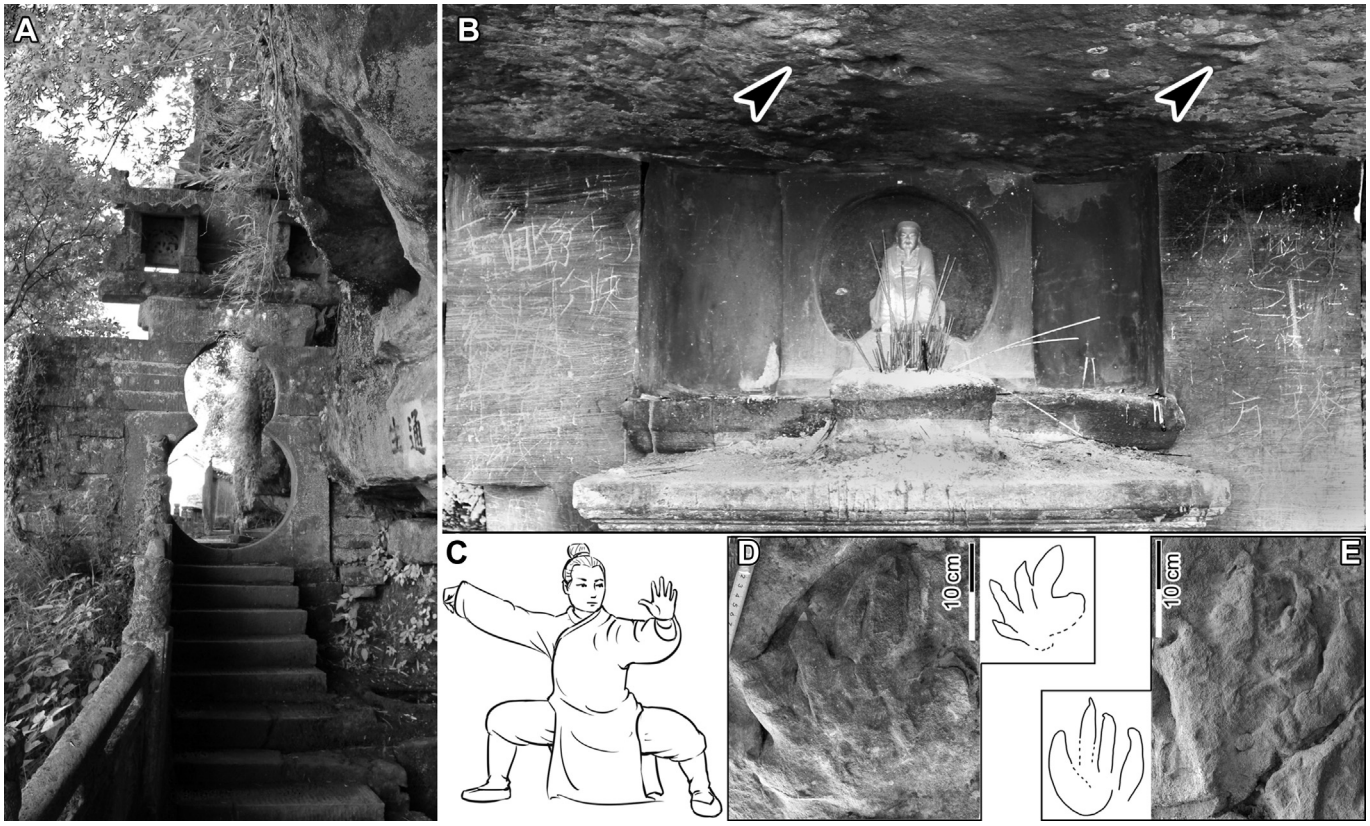

Fig. 10. Dinosaur footprints and historical documents at the Xiaohutian tracksite. A. The grotto in the Xiaohutian tracksite. B. Taoist ancestor Sanfeng Zhang's rite; arrows indicate dinosaur tracks. C. Different postures of hands (like palm-hitting) are important moves of Taiji (Illustration by Feng Liu). D–E. Photographs and sketches of Xiaohutian theropod tracks XHT-13–14 and XHT-53 that falsely appear to be human hand prints with five digits.

assemblage, and contribute to the growing understanding of the rich vertebrate fauna of Late Cretaceous China.

10. Conclusions

Upper Cretaceous tracksites in Anhui Province of eastern China show typical assemblages dominated by small to medium sized tridactyl theropod footprints with the rare occurrence of small bird tracks documented at one locality, At the Xiaohutian tracksite in the Xiaoyan Formation three general morphotypes of theropod tracks can be distinguished by the different mesaxony, divarication of digits and other features. *Paracorpulentapus zhangsanfengi* ichnogen. nov. ichnosp. nov. is described based on diagnostic features such as weak mesaxony, subequal length and width, short, "fleshy" toes, wide digit divarication and short steps. In particular the pes imprint morphology indicates developments convergent with those in typical ornithopods. The assemblage enriches the dinosaur fauna of the Xiaoyan Formation and Eastern China by the presence of small-medium sized theropods. Furthermore, the Xiaohutian tracksite is an interesting example for the close association of ichnological and historical documents.

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