·基础地质·

An Early Cretaceous non-avian dinosaur and bird footprint assemblage from the Laiyang Group in the Zhucheng basin, Shandong Province, China

山东诸城盆地下白垩统莱阳群的非鸟恐龙与鸟足迹化石组合

XING Li-da[1,2], JERALD D. Harris[3], WANG Ke-bai[4], LI Ri-hui[5]
邢立达[1,2],杰瑞德 D.哈里斯[3],王克柏[4],李日辉[5]

1. *Department of Biological Sciences, University of Alberta,* 11145 *Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada;*
2. *Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences, PO Box* 643, 100044 *Beijing, China;*
3. *Physical Sciences Department, Dixie State College,* 225 *South* 700 *East, St. George, Utah* 84770, *USA;*
4. *Zhucheng Municipal Bureau of Tourism, Zhucheng* 262200, *Shandong, China;*
5. *Qingdao Institute of Marine Geology, China Geological Survey, Qingdao* 266071, *Shandong, China*
1. 艾伯塔大学生物科学系,加拿大 埃德蒙顿 T6G 2E9;
2. 中国科学院脊椎动物进化系统学开放实验室,北京 100044;
3. 迪克西州立学院自然科学系,美国 犹他 84770;
4. 诸城市旅游局,山东 诸城 262200;
5. 中国地质调查局青岛海洋地质研究所,山东 青岛 266071

Xing L D, Harris J D, Wang K B, Chen S Q, Zhao C J, Li R H. An Early Cretaceous non-avian dinosaur and bird footprint assemblage from the Laiyang Group in the Zhucheng basin, Shandong Province, China. ***Geological Bulletin of China,*** **2010, 29(8):1105-1112**

Abstract: Diverse non-avian dinosaur (sauropod and ornithopod) and bird tracks occur in the Lower Cretaceous Yangjiazhuang Formation at the Zhangzhuhewan Village track site in Zhucheng basin, Shandong Province, China. Non-avian dinosaur tracks at this tracksite are heavily deformed, having been registered in waterlogged sediment. Sauropod pes and manus impressions, made by a slowly advancing track maker, are roughly equal in area. The ornithopod tracks are of the generalized *Iguanodon*-hadrosaur morphotype. The bird tracks are unlike other Mesozoic bird tracks from China, but are similar to the shorebird-like ichnotaxon *Jindongornipes*. Among tracks previously reported from the Laiyang Group, *Laiyangpus* is of uncertain affinity and its type specimen has been lost, and *Paragrallator* is referable to *Anchisauripus* isp. The new tracks described herein further increase the known dinosaur diversity in eastern Shandong Province.

Key words: Zhucheng basin; Early Cretaceous; Yangjiazhuang Formation; Shandong; sauropod tracks; ornithopod tracks, bird tracks

Received on May 6,2010; **revised** on June 18, 2010; **accepted** on June 25, 2010; **published** on August 15, 2010

This study was supported by the Zhucheng Municipal Government

Author: XING Li-da(1982-), male, presently specializes in the Mesozoic vertebrate paleontology and functional morphology. E-mail: Xinglida@gmail.com

摘要:中国山东省诸城盆地张祝河湾村下白垩统杨家庄组发现了非鸟恐龙(蜥脚类和鸟脚类)与古鸟类足迹。该足迹点的非鸟恐龙足迹深受水浸沉积物的影响,发生了强烈变形。蜥脚类足迹的前后足迹面积相近,造迹者行进缓慢。鸟脚类足迹属于禽龙-鸭嘴龙类型的足迹。古鸟类足迹并不类似于中国以往发现的中生代鸟类足迹,而类似于韩国滨水鸟类足迹的金东鸟足迹(*Jindongornipes*)。讨论了莱阳足迹(*Laiyangpus*)和拟跷脚龙足迹(*Paragrallator*,亦译为拟似鹬龙足迹),前者因模式标本遗失而不明确,后者可归入安琪龙足迹未定种(*Anchisauripus* isp)。这批足迹的发现大大增加了山东省东部恐龙的多样性。

关键词:诸城盆地;早白垩世;杨家庄组;山东;蜥脚类足迹;鸟脚类足迹;鸟类足迹

中图分类号:P534.53;Q915.865 **文献标志码**:A **文章编号**:1671-2552(2010)08-1105-08

1 Introduction

Dinosaur track research in the Lower Cretaceous Laiyang Group, Shandong Province, has a long but discontinuous history. The first tracks, found at Beibozi (formerly spelling Peiputze) Village, Muyudian Township, Laiyang City, were studied by Young and named *Laiyangpus*[1]. Young did not mention a specific unit within the "Laiyang Series" as the source of *Laiyangpus*; at the time of his description, the Laiyang Group and its tracks were perceived as Late Jurassic in age. In 2000, more tracks, specifically from the Longwangzhuang Formation in the Laiyang Group, near Longwangzhuang Township, Laiyang City, were named *Paragrallator*[2]. Both *Laiyangpus* and *Paragrallator* pertain to theropod dinosaurs.

The Zhucheng basin lies in the southwest part of the Jiaolai basin and is paleontologically most renowned for its abundance of Late Cretaceous hadrosaurs[3], such as *Shantungosaurus*[4]. In the 1950s, villagers from Zhangzhuhewan discovered fossil tracks in the Lower Cretaceous Yangjiazhuang Formation, Laiyang Group, on the eastern bank of the branch rivers of Wujialou Reservoir in the Village. In 2005, the Village representatively reported the fossil discovery to the Zhucheng Municipal Museum, which investigated and discovered four tracks in July of the following year. In March 2009, the Zhucheng Municipal Bureau of Tourism discovered two assemblages of tracks at the same site. These tracks include tracks made by small-medium sized sauropods, large ornithopods, and birds.

2 Institutional abbreviation

LG=Provisional Collection(Lin-shi Guancang, LG) of Zhucheng Municipal Museum, Shandong Province, China; ZDRC=Zhucheng Dinosaur Research Center, Shandong Province, China.

3 Geological setting

In eastern Shandong Province, the Laiyang Group has been divided into formations according to two systems. In one system, the units are (from the bottom) the Wawukuang, Linsishan, Zhifengzhuang, Shuinan, Longwangzhuang, and Qugezhuang formations; in the other system, the units are the

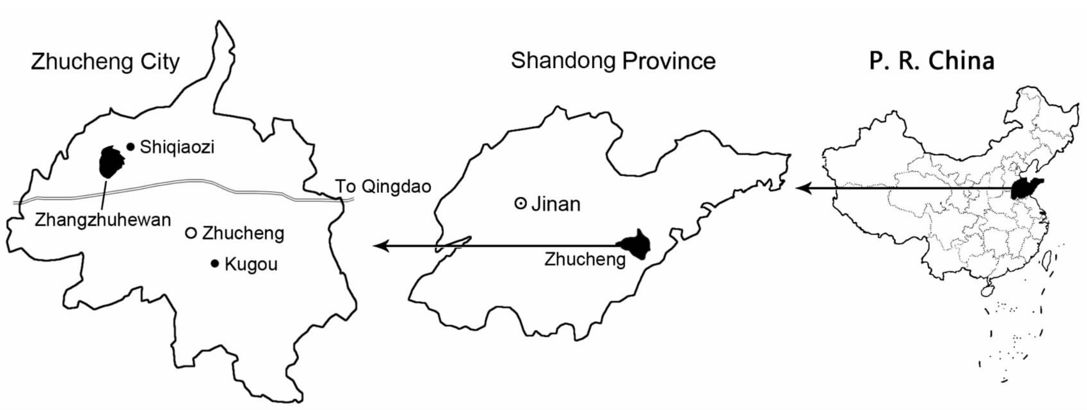


Fig. 1 Geographic position of the dinosaur footprint locality (indicated by the footprint icon)

Wawukuang, Linsishan, Zhifengzhuang, Yangjiazhuang, Ducun, and Fajiaying formations[5]. The Yangjiazhuang Formation, in which the dinosaur tracks reported here occur, appears to be a correlative facies of the Shuinan and Longwangzhuang formations. The lithology of the Yangjiazhuang Formation comprises cyclic coarse, medium-grained, and fine-grained sandstones, siltstone, and shale. The dinosaur tracks occur in a fine-grained sandstone at Zhangzhuhewan Village.

The Laiyang Group comprises fluvio-lacustrine deposits[6]. The Yangjiazhuang Formation comprises fluvial and alluvial deposits from a braided river, with shallow, regional lakes[5] and meandering river deposits[7]. The fluvial deposits contain volcanic material[8].

The substrate of the track site appears to have been, at the time the tracks were registered, very soft and wet; a tract of mud cracks developed near the trackway suggests that the sediment dried subaerially before are buried.

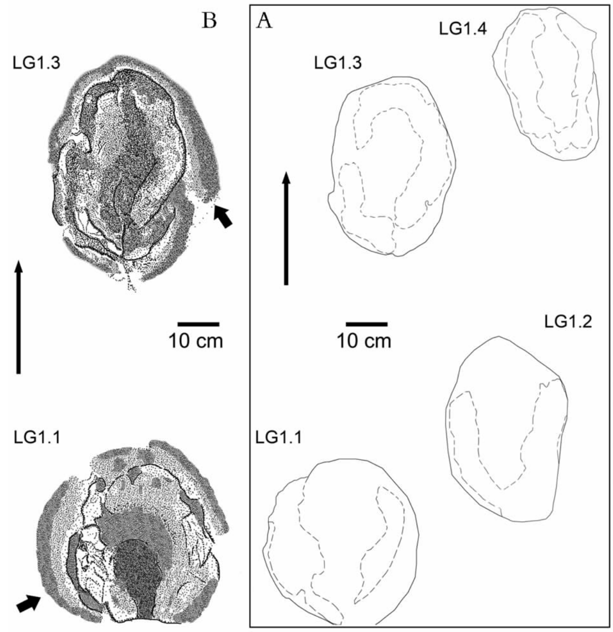


Fig. 2 Sauropod footprints (LG1) from the Zhangzhuhewan tracksite

A—outline drawings; B—interpretative drawings of LG1.1 and LG1.3. long arrows indicate the direction toward which the dinosaurs moved, short arrows indicate the external diameters. scale bar=10cm

4 Description of tracks

4.1 **Sauropod tracks**

(1)Material

Four complete natural molds on a slab reposited at the Zhucheng Municipal Museum. The tracks are cataloged individually as LG1.1-1.4(Fig. 2, Plate Ⅰ-A, Table 1). LG1 is well preserved due to its early discovery. There are also six natural molds on a slab reposited at the Zhucheng Dinosaur Research Center. The tracks are cataloged individually as ZDRC.F1.1-1.6(Plate Ⅰ-B, Table 1). Both are from the Lower Cretaceous Yangjiazhuang Formation, Zhucheng basin, Shandong Province, China.

(2)Description and Discussion

The morphologies of these tracks can be discussed via either or both their internal and external diameters: the internal diameter consists of the track *sensu stricto*, while the external diameter demarcates concentric mud rings around the track. The internal length:width ratios of the four tracks are very similar, ranging from 1.37-1.53, whereas the external length: width ratios vary substantially from 0.98-1.55.

Neither digit nor claw impressions are distinct; the tracks are preserved as simple, ovoid pits. Raised areas in the centers of the tracks represent sediment that adhered to the bottoms of the feet and was pulled back up as the feet were extracted. The tracks lack claw/digit impressions either because the sediment was simply too waterlogged to permit distinct impressions or because the sediment collapsed back inward upon foot extraction. Widths between tracks range from 5.8-7.4 cm.

In both sets of tracks, it is difficult to discriminate between pes and manus impressions. However, it is obvious from the external diameter that the length: width ratios of LG1.1 and LG1.4 are less than those of LG1.2 and LG1.3. Furthermore, the higher parts of the mud rings of LG1.2 and, especially, LG1.3 lean laterally outward, possibly representing deformed impressions of a pedal digit or claw. The higher parts of the mud rings of LG1.1 and LG1.4 lean proximomedially and proximolaterally; these could be deformed

Table 1 Measurements of sauropod footprints from the Zhangzhuhewan tracksite, Yangjiazhuang Formation, Shandong Province, China

Measurement	Internal diameter			External diameter		
	Maximum Length/cm	Maximum Width/cm	F/W	Maximum Length/cm	Maximum Width/cm	F/W
LG1.1	43.6	31.8	1.37	47.3	48.2	0.98
LG1.2	44.5	29.1	1.53	59.1	38.2	1.55
LG1.3	42.7	30.9	1.38	52.7	35.5	1.49
LG1.4	37.4	25.2	1.48	40?	33.9	1.18?
ZDRC.F1.1	"33"	"27"	-	"40"	"31"	-
ZDRC.F1.2	"48"	"23"	-	"60"	"30"	-
ZDRC.F1.3	"37"	"30"	-	"47"	"44"	-
ZDRC.F1.4	"37"	"20"	-	"46"	"27"	-
ZDRC.F1.5	"30"	"25"	-	"54"	"39"	-
ZDRC.F1.6	44	30	1.47	-	-	

note:"－"means not applicable; "?" means uncertain measurement due to trackway without reservation; quotation marks around number: approximate value(the fossils are severely damaged and weathered, making it difficult to ascertain distinct track borders)

impressions of manual digits I and V. Therefore, LG1.1 and LG1.4 are presumed manus impressions and LG1.2 and LG1.3 pes impressions.

Pes－only sauropod trackways are rare; both quadrupedal and apparently bipedal walking can be found in a single sauropod trackway[9]. Pes－only tracks also have been interpreted as the result of relatively fast movement, where the pes overprints the manus[10]. This example is especially noteworthy in *Iguanodonichnus frenki*[11－12]. But LG1 tracks do not possess the elongate shapes that reflect such footprint overlap.

In heteropod sauropod trackways, the area ratios of manus/pes prints range from 1/2－1/3－1/5[13]. In the Zhucheng tracks, the ratios of LG1.1/LG1.3 and LG1.4/LG1.2 are far higher at 3/5－4/5. However, due to the influence of substrate conditions, the manus:pes ratios of sauropods vary frequently: for example, Oxfordshire trackway 14 (original fig.7D)[14] and the Toro Toro trackway (original fig. 12)[15] both have ratios very close to 1.0.

The distances between LG1.1 and LG1.3 and between LG1.4 and LG1.2 are relatively wide, unlike those of typical *Brontopodus birdi* tracks [16], which are much narrower. A similar phenomenon also occurs at sauropod trackways from the Galinba site (original fig.3, left)[17] and Chabu 5 site (original fig.6B) [18]. These differences are attributed to varying velocities of their respective sauropod track makers: slower velocities produce wider distances between the manus and the pes.

ZDRC.F1, a series of poorly preserved tracks, was excavated from a locality about 10 m from LG1. Due to long exposure, the fossils are severely damaged and weathered, making it difficult to ascertain distinct track borders. The lengths and widths of the tracks do not differ from those of LG1, suggesting that the tracks were left by the same type of track maker. Using similar reasoning as explained above for tracks

Table 2 Measurements of bird footprints from the Zhangzhuhewan tracksite, Yangjiazhuang Formation, Shandong Province, China

Measurement	ZDRC.F2.1a	ZDRC.F2.1b	ZDRC.F3
Maximum length	20.3cm	49 cm	3.1 cm
Maximum width†	18.5 cm	33.5 cm	2.9 cm
Length of digit I	-	-	0.7* cm
Length of digit II	-	22.1 cm	1.4* cm
Length of digit III	-	23.6 cm	1.9* cm
Length of digit IV	-	23.3* cm	1.1* cm
Angle between digits II and III	-	37°	64°
Angle between digits III and IV	-	13°	57°
Angle between digits II and IV	-	50°	121°

note: +means distance between the tips of digits II and IV; *means measured the distance from the tip of the digit to a line drawn perpendicular to the digit axis and that is tangent to the adjacent hypex from LG1, ZDRC.F1.1, 1.4, and 1.5 are manus impressions, and 1.2, 1.3, and 1.6 are pes impressions. The pace angulation of the pes impressions is 125°, close to angulations previously reported as characteristic of Sauropoda(100–120°[16]; less than 110°[19]).

Using Alexander´s formula[20], the velocity of the track maker is a slow 0.73 m/s.

4.2 Ornithopod tracks

(1)Material

Three complete natural molds on a slab reposited at the Zhucheng Municipal Museum. The tracks are cataloged individually as ZDRC.F2.1a, b; 2.2b(Fig. 3, Plate Ⅰ-C, Table 2) from the Lower Cretaceous Yangjiazhuang Formation, Zhucheng basin, Shandong Province, China.

(2)Description and Discussion.

ZDRC.F2, which is a part of a long trackway, was excavated from a river bank about 10 m from LG1. Due to weathering, most specimens at this locality are poorly preserved, except ZDRC.F2. Footprint 2.1a is a manus impression; 2.1b and 2.2b are pes impressions.

The length:width ratio of subtriangular manus print 2.1a is 1.1. The manus impression lies cranial to the pes impression, approximately in line with the impression of pedal digit IV, which accords with the manus-pes configuration of most *Iguanodon*-hadrosaur morphotype tracks, e.g. *Caririchnium leonardii*[21], *Amblydactylus* isp.[22], *Caririchnium protohadrosaurichnos*[23], and *Iguanodontipus* isp.[24].

The length:width ratio of pes print 2.1b is 1.46. The step from 2.1b to 2.2b is 108 cm, though 2.2b is indistinct. Digits III and IV are closely appressed, whereas a larger gap separates the impressions of digits II and III. Digit II is the shortest and widest; digit III is longer and wider than digit IV. The metatarsophalangeal region is indistinct, though it seems to have a caudally concave caudal margin, similar to those of *Caririchnium leonardii*[25], *Hadrosauropodus langstoni*[26], and *Hadrosauropodus nanxiongensis*[27]. It is unclear which aspects of the morphology of this pes impression reflect foot morphology and which are functions of foot-substrate interaction.

4.3 Bird track

(1)Material

ZDRC.F3, one natural mold on a slab from the Lower Cretaceous Yangjiazhuang Formation, Zhucheng basin, Shandong Province, China.

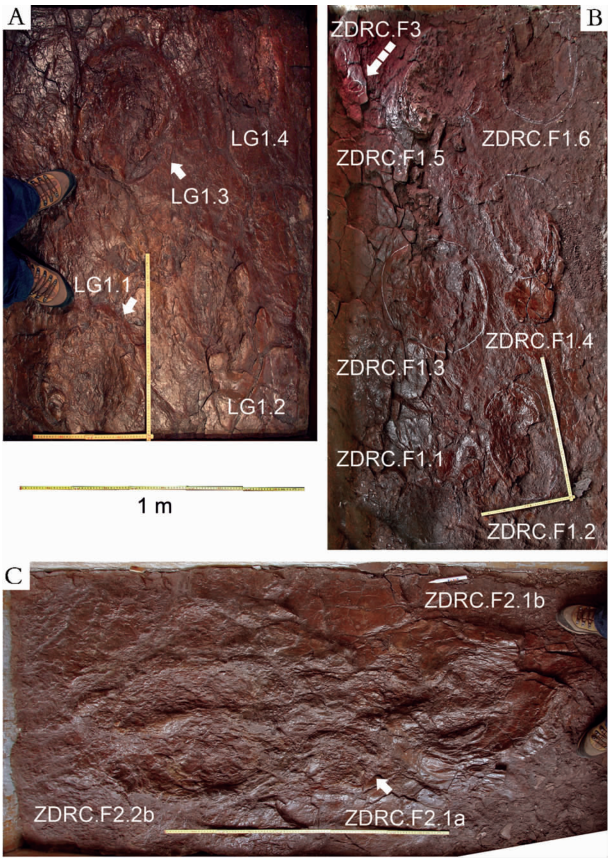
(2)Description and Discussion

ZDRC.F3, a small, tetradactyl bird track (Fig. 4, Table 2), was discovered on the border of the ZDRC.F1 trackway. Originally, it was part of a single trackway, but later damage destroyed all but one track. The length:width ratio of ZDRC.F3 is 1.07. The hallux (digit I) impression is directed caudally; its length is half of that of digit II. Digit III is the longest and, unusually for a bird track, appears to have three pads. Digit II is slightly longer than digit IV. Claw marks are indistinct.

Characteristics of bird tracks include: small size; slender toe impressions with slender claw marks; large (110-120°) divarication angle between digits II-IV; anisodactyly; and length:width ratios ≤1.0[28-29]. ZDRC.F3 exhibits all of these traits.

Currently there are at least 15 formally described Mesozoic bird ichnotaxa(original table 1)[30]. ZDRC.F3 is rather unlike other Mesozoic bird tracks from China, but is quite similar to the shorebird-like ichnotaxon *Jindongornipes* from the Lower Cretaceous Jindong Formation of Korea: both lack webbing traces and possess short, caudally directed hallux impressions. However, the hallux impression of *Jindongornipes* possesses two distal pads and the angle between digits II and IV for *Jindongornipes* is wider than in ZDRC.F3 [28]. Though ZDRC. F3 was preserved in a fluvial en vironment[5,7-8] and *Jindongornipes* tracks in a lake shoreline environment, the Jindong Formation is replete with abundant sauropod, ornithopod, and theropod tracks[28], similar to that of the Yangjiazhuang Formation. Avian track makers in both units therefore presumably had similar paleoecologies. The diversity and abundance of bird tracks from the Early Cretaceous in East Asia are higher than those of other regions[15]; the discovery of ZDRC.F3 supports this contention.

Plate Ⅰ



A—sauropod trackway LG1; B—sauropod trackway ZDRC.F1 and bird track ZDRC.F3.; C—ornithopod trackway ZDRC.F2. scale bar=1m

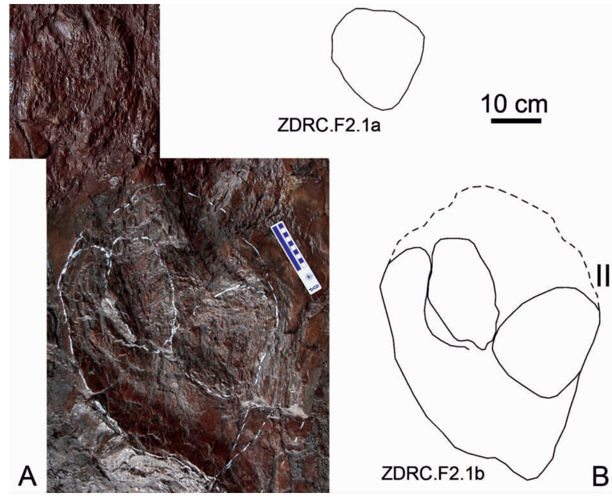


Fig. 3 Ornithopod footprints (ZDRC.F2.1a, b) from the Zhangzhuhewan tracksite

A—photograph; B—outline drawing. dashed lines indicate indistinct footprint borders and the maximum extent of sediment deformed by registration of the track. scale bar=10cm

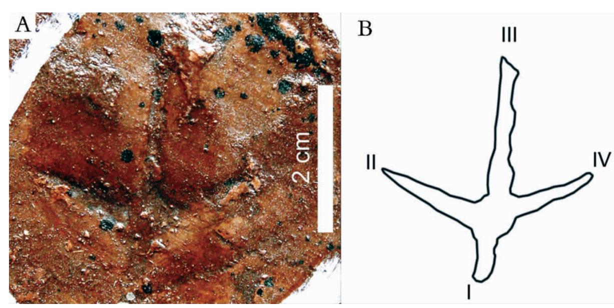


Fig. 4 Bird footprint (ZDRC.F3) from the Zhangzhuhewan tracksite

A—photograph; B—outline drawing

5 Preservational mode of the Zhangzhuhewan track site

The most important factor controlling track formation(morphology)and preservation is moisture content of the substrate[31-32]. The substrate of the Zhangzhu hewan site was probably quite waterlogged —the presence of shorebird tracks suggested that this site was proximal to a body of water. Large track makers, such as sauropods and ornithopods, effectively destroyed the details of their own tracks when sediment stuck to the bottoms of the feet of the track makers and was pulled up by their feet. Smaller, lighter track makers, such as birds, were less subject to this same interaction. Unfortunately, the few known tracks from the locality are not well-preserved. Further excavation may uncover better preserved tracks that may shed more light on track maker identity and diversity.

6 Dinosaur and bird tracks of the Laiyang and Dasheng groups

6.1 *Laiyangpus and Paragrallator*

Previously studied and named tracks from the Laiyang Group differ from any of those discussed herein. *Laiyangpus* was initially attributed to a"coelurosaur"[1], but the morphology of this ichnotaxon cannot be sufficiently reevaluated because the type specimen is missing. Lockley et al. attributed the ichnotaxon to a bird[33]; Matsukawa et al. regarded *Laiyangpus* as an ichnotaxon of uncertain status[34].

The theropod ichnotaxon *Paragrallator*[2] is more problematic. The name "*Paragrallator*" was first used by Ellenberger (p. 49)[35] for Late Triassic tracks from Lesotho, but the ichnotaxon was never formally erected and is therefore a *nomen nudum*. The name was therefore unavailable for the Laiyang Group "*Paragrallator*"[2], so these ichnites lack an ichnogenus. The Lesotho tracks have been regarded as belonging to *Grallator*[36]; *Paragrallator*[2] is closer to *Anchisauripus*[37-38]. Due to their poor preservation, it is difficult to be attribute them to any particular ichnospecies of *Anchisauripus*, so we refer them to *Anchisauripus* isp.

6.2 Dinosaur and bird tracks of the Dasheng Group

The Dasheng Group overlies the Laiyang Group, and formations in the former have also produced fossil tracks. Abundant theropod, ornithopod, and bird tracks were discovered in the Tianjialou Formation (Barremian -Aptian) at Junan County Houzuoshan Dinosaur Park[39]. These include the avian *Shandongornipes muxiai*[40-41] and the non-avian theropod *Dromaeopodus shandongensis*[42] and *Minisauripus zhenshuonani*[43]. Ornithopod tracks occur in this unit, as well[39, 41]. Theropod and sauropod tracks have also been discovered in a stratigraphically higher (Upper Cretaceous) unit, the Mengtuan Formation, in Shanzuokou Village, Donghai County[44]. The new tracks described herein increase still further the known dinosaur diversity in eastern Shandong Province.

Acknowledgements: The authors thank Philip J. Currie (University of Alberta, Edmonton, Alberta, Canada) and Xu Xing (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044, China) for their critical comments and suggestions on early drafts of this paper. Thanks to Li Dunjing from the Zhucheng Dinosaur Museum, Shandong Province for his participation in field research. Thanks to Han Gang from the Zhucheng Dinosaur Museum, Shandong Province for the access to the specimens. Thanks to the Zhucheng Municipal Bureau of Tourism, which provided logistical support.

References

[1]Young C C. Fossil footprints from China[J]. Vertebrata PalAsiatica, 1960, 4(2): 53-66.

[2]Li R H, Zhang G W. New Dinosaur Ichotaxon from the Early Cretaceous Laiyang Group in the Laiyang Basin, Shandong Province[J]. Geological Review, 2000, 46(6): 605-610.

[3]Liu M W, Zhang Q Y, Song W Q. Division of the Cretaceous lithostratigraphic and volcanic sequences of Shandong Province [J]. Journal of Stratigraphy, 2003, 27(3): 247-253.

[4]Hu C C. A new Hadrosaur from the Cretaceous of Chucheng, Shantung[J]. Acta Geologica Sinica, 1973, 2: 179-206.

[5]Zhang Z Q, Liu M W. Lithostratigraphy of Shandong Province[M]. Wuhan: The Press of China University of Geosciences, 1996: 1-328.

[6]Li R H, Zhang G W. A preliminary study of nonmarine trace fossils from the Laiyang group (Early Cretaceous), Laiyang Basin, Eastern China[J]. Acta Palaeontologica Sinca, 2001, 40(2): 252-261.

[7]Zhang Z Q, Zhang Z H, Hu S T, et al. Laiyang Stage of palaeogeography and deposits evolution at the depression of the Lower Cretaceous in Zhucheng, Shandong province[C]//National Important Fruits Essays of Geology in the Ninth Five-Year Plan. 2000:574-580.

[8]Shi W, Zhang Y Q, Dong S W, et al. Tectonic deformation and formation and evolution of the Jiao -Lai basin, Shandong—A case study of a deformation analysis of the Wangshi and Dasheng Groups [J]. Geological Bulletin of China, 2003, 22(5): 325-334.

[9]Lockley M G, Houck K J, Prince N K. North America´s largest dinosaur trackway site: implications for Morrison Formation paleoecology[J]. Bulletin of the Geological Society of America, 1986, 97: 1163-1176.

[10]Meyer C A. Sauropod tracks from the Upper Jurassic Reuchenette Formation (Kimmeridgian, Lommiswil, Kt. Solothurn) of northern Switzerland[J]. Eclogae Heologicae Helvetiae, 1990, 82(2): 389-397.

[11]Casamiquela R M, Fasola A. Sobre pisadas de dinosaurios del Cretácico Inferior de Colchagua (Chile)[J]. Universidad de Chile, Departamento de Geología, 1968, 30: 1-24.

[12]Moreno K, Benton M J. Occurrence of sauropod dinosaur tracks in the Upper Jurassic of Chile (redescription of *Iguanodonichnus frenki*) [J]. Journal of South American Earth Sciences, 2005, 20: 253-257.

[13]Lockley M G, Farlow J O, Meyer C A. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways, Gaia [J]: Revista de Geociencias, Museu Nacional de Historia Natural, Lisbon, Portugal, 1994, 10: 135-146.

[14]Day J J, Norman D B, Gale A S, et al. A Middle Jurassic dinosaur trackway site from Oxfordshire, UK[J]. Palaeontology, 2004, 47(2): 319-348.

[15]Lockley M G, Rainforth E C. The track record of Mesozoic birds and Pterosuars—an Ichnological and Paleoecological Perspective[M] //Chiappe L, Witmer L M. Mesozoic Birds above the Heads of Dinosaurs. Berkeley: University of California Press, 2002: 405-418.

[16]Farlow J O, Pittman J G, Hawthorne J M. Brontopodus birdi, Lower Cretaceous dinosaur footprints from the U.S. Gulf Coastal Plain[M]//Gillette D D, Lockley M G. Dinosaur Tracks and Traces. Cambridge: Cambridge University Press, 1989: 371−394.

[17]dos Santos V F, Lockley M G, Meyer C A,et al. A new sauropod tracksite from the Middle Jurassic of Portugal[J]. GAIA,1994,10: 5−13.

[18]Lockley M G, Schulp A S, Meyer C A, et al. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide−gauge locomotion and gregarious behaviour[J]. Cretaceous Research, 2002, 23: 383−400.

[19]dos Santos V F, Lockley G M, Moratalla J, et al. The longest dinosaur trackway in the world? Interpretations of Cretaceous foot prints from Carenque, near Lisbon, Portugal[J]. Gaia 5, 1992: 18−27.

[20]Alexander R M. Estimates of speeds of dinosaurs[J]. Nature. 1976, 261: 129−130.

[21]Lockley M G. Dinosaur footprints from the Dakota Group of eastern Colorado[J]. The Mountain Geologist, 1987, 24: 107−122.

[22]Currie P J. Ornithopod trackways from the Lower Cretaceous of Canada[M]//Sarjeant W A S. Vertebrate Fossils and the evolution of scientific concepts. Amsterdam:Gordon and Breach Publishers, 1995: 431−443.

[23]Lee Y N. Bird and Dinosaur Footprints in the Woodbine Formation (Cenomanian), Texas[J]. Cretaceous Research, 1997,18:849−864.

[24]Diedrich C. New important iguanodontid and theropod trackways of the tracksite Obernkirchen in the Berriasian of NW Germany and megatracksite concept of central Europe[J]. Ichnos, 2004, 11: 215−228.

[25]Currie P J, Nadon G C, Lockley M G. Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado [J]. Canadian Journal of Earth Sciences, 1991, 28: 102−115.

[26]Lockley M G, Nadon G, Currie P J. A diverse dinosaur−bird footprint assemblage from the Lance Formation, Upper Cretaceous, eastern Wyoming; implications for ichnotaxonomy[J]. Ichnos, 2003, 11:229−249.

[27]Xing L D, Harris J D, Dong Z M, et al. Ornithopod (Dinosauria: Ornithischia) Tracks from the Upper Cretaceous Zhutian Formation in Nanxiong Basin, China and General Observations on Large Chinese Ornithopod Footprints[J]. Geological Bulletin of China, 2009, 28(7): 829−843.

[28]Lockley M G, Yang S Y, Matsukawa M, et al. The track record of Mesozoic birds: Evidence and implications[J]. Philosophical Transactions of the Royal Society of London B, 1992, 336: 113−134.

[29]McCrea R T, Sarjeant W A S. New ichnotaxa of bird and mammal footprints from the lower Cretaceous (Albian) Gates Formation of Alberta[M]//Tanke D H, Carpenter K. Mesozoic Vertebrate Life. Bloomington and Indianapolis: Indiana University Press, 2001:453−478.

[30]Lockley M G, Harris J D. On the trail of early birds: a review of the fossil footprint record of avian morphological and behavioral evolution[M]//Ulrich P K, Willett J H. Trends in Ornithology Research. Hauppauge: Nova Publishers, 2010: 1−63.

[31]Allen J R L. Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S.W. Britain: mechanics of formation, preservation and distribution[J]. Philosophical Transactions of the Royal Society of London B, 1997, 352: 481−518.

[32]Manning P L. A new approach to the analysis and interpretation of tracks: examples from the Dinosauria[M]//McIlroy D. The Application of Ichnology to Palaeoenvironmental and Stratigraphical Analysis. Geological Society of London, Special Publication, 2004,228:93−128.

[33]Lockley M G, Matsukawa M, Li J J. Cretaceous bird tracks from China: their Asian and global context[J]. Journal of Vertebrate Paleontology, 2003, 23(3): 72.

[34]Matsukawa M, Lockley M G, Li J J. Cretaceous terrestrial biotas of East Asia, with special reference to dinosaur−dominated ichnofaunas: towards a synthesis[J]. Cretaceous Research, 2006,(27):3−21.

[35]Ellenberger P. Contribution à la classification des pistes de Vertébrés du Trias : les types du Stormberg d´Afrique du Sud (I) [J]. Palaeovertebrata, Mémoire Extraordinaire, 1972: 1−152.

[36]Knoll F. The tetrapod fauna of the Upper Elliot and Clarens formations in the main Karoo Basin (South Africa and Lesotho)[J]. Bulletin de la Société Géologique de France, 2005, 176(1): 81−91.

[37]Lull R S. Fossil footprints of the Jura−Trias of North America[J]. Memoirs of the Boston Society of Natural History, 1904, 5(11): 461−557.

[38]Olsen P E, Smith J B, McDonald N G. Type material of the type species of the classic theropod footprint genera Eubrontes, Anchisauripus, and Grallator (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.)[J]. Journal of Vertebrate Paleontology, 1998, 18(3): 586−601.

[39]Li R H, Liu M W, Lockley M G. Early Cretaceous dinosaur tracks from the Houzuoshan Dinosaur Park in Junan County, Shandong Province, China[J]. Geological Bulletin of China, 2005, 24:277−280.

[40]Li R H, Lockley M G, Liu M W. A new ichnotaxon of fossil bird track from the Early Cretaceous Tianjialou Formation (Barremian−Albian), Shandong Province, China[J]. Chinese Science Bulletin, 2005, 50:1149−1154.

[41]Lockley M G, Li R H, Harris J D, et al. Earliest zygodactyl bird feet: evidence from Early Cretaceous roadrunner−like tracks [J]. Naturwissenschaften, 2007, 94(8): 657−665.

[42]Li R H, Lockley M G, Makovicky P J, et al. Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China[J]. Naturwissenschaften, 2007, 95(3): 185−191.

[43]Lockley M G, Kim J Y, Kim K S, et al. *Minisauripus*—the track of a diminutive dinosaur from the Cretaceous of China and South Korea: implications for stratigraphic correlation and theropod foot morphodynamics[J]. Cretaceous Research, 2008, 29(1): 115−130.

[44]Xing L D, Harris J D, Jia C K, et al. Dinosaur tracks from the Lower Cretaceous Mengtuan Formation in Jiangsu, China and morphological diversity of local sauropod tracks[J]. Acta palaeontologica Sinica, 2010, in press.