Theropod (Dinosauria: Saurischia) tracks from Lower Cretaceous Yixian Formation at Sihetun Village, Liaoning Province, China and possible track makers

辽宁省四合屯下白垩统义县组的兽脚类足迹化石和可能的造迹者

XING Li-da[1], Jerald D. HARRIS[2], FENG Xiang-yang[3], ZHANG Zhi-jun[3]
邢立达[1],杰瑞德 D. 哈里斯[2],冯向阳[3],张志军[3]

1. *Institute of Geology, Chinese Academy of Geological Sciences, Beijing* 100037, *China;*
2. *Physical Sciences Department, Dixie State College, 225 South 700 East, St. George, Utah* 84770, *USA;*
3. *Department of Palaeontology, Geological Museum of China, Beijing* 100034, *China*
1. 中国地质科学院地质研究所,北京 100037;
2. 迪克西州立学院自然科学系,美国 犹他 84770;
3. 中国地质博物馆古生物中心,北京 100034

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Abstract: Herein we describe three and one half footprints that pertain to *Grallator* isp. from the Lower Cretaceous Yixian Formation, Sihetun, Liaoning Province, China. This is the first description of dinosaur footprints from the Yixian Formation. The tracks were left by at least three individual track makers. It is estimated from the tracks that the body lengths of the track makers were 1.51 m, which is the average length of known theropods from the Yixian Formation. The feet of *Caudipteryx* and *Sinosauropteryx* were reconstructed. The former was more similar than the latter to the *Grallator* isp. track outlines. Feet capable of registering *Grallator* morphotype tracks may therefore have been widely distributed in small-medium sized theropods (other than dromaeosaurids and troodontids) from the Yixian Formation.

Key words: Sihetun Village, Liaoning Province; Lower Cretaceous Yixian Formation; *Grallator*; track maker

摘要:记述了辽宁省四合屯下白垩统义县组三个半恐龙足迹,归入似鹤龙足迹(亦译为跷脚龙足迹)一未定种(*Grallator* isp.)。这是义县组恐龙足迹化石的首次描述。该行迹至少由 3 个造迹者所造。从足迹推断恐龙体长 1.51 m,属于义县组兽脚类恐龙较为

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

普遍的体长范围。重建了尾羽鸟(*Caudipteryx*)和中华龙鸟(*Sinosauropteryx*)的足部,前者的足迹轮廓与似鹤龙足迹未定种的吻合度超过后者。根据化石记录,似鹤龙足迹类型可能广泛存在于义县组的各种中小型兽脚类(驰龙类与伤齿龙类除外)中。

关键词:辽宁省四合屯;下白垩统义县组;似鹤龙足迹;造迹者

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1 Introduction

Research on Mesozoic tracks in western Liaoning Province has long history. In 1940, the first formal study was by Yabe et al., who described dinosaur tracks from the Sijiazi (Ssuchiatzu) tracksite near Yangshan, near Chaoyang City[1]. Thereafter, Shikama, Young, Zhen et al. and Matsukawa et al. further studied the track site[2-5]. In 2004, Zhang et al[6]. described dinosaur tracks from the Sijiaban dinosaur track site near Beipiao City, Nanbajiazi County; Fujita et al. described these tracks and the site in greater detail[7]. In 2006, Lockley et al[8]. described the Kangjiatun bird track site near Kangjiatun village, Beipiao City. In northern Hebei Province, bordering western Liaoning Province, Sullivan et al[9]. described a dinosaur track occurrence from the Nanshuangmiao site in Chengde County.

All the aforementioned tracks in Liaoning Province are from the Tuchengzi Formation; the tracks in Hebei Province are from the probably correlative Houcheng Formation. The Tuchengzi Formation and its lateral correlates, while apparently relatively track-rich, have produced comparatively few body fossils [11-12]. In contrast, the overlying, body fossil-rich Yixian Formation has thus far produced only one reported dinosaur track occurrence [13], though tracks were also reported from the possibly correlative [14] Xiguayuan Formation in Hebei Province [15]. The lone Yixian Formation track sample was collected at Sihetun in 1998 by the National Geological Museum of China, at the same time they collected the type specimen of the ornithomimosaur *Shenzhousaurus orientalis*[16]. The tracks are described here for the first time.

2 Institutional abbreviation

CAGS-IG=Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China NGMC=National Geological Museum of China, Beijing, China. BPM=Beipiao Paleontological Museum, China. IVPP=Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China. JMP = Jinzhou Museum of Paleontology, Liaoning , China, NIGP= Nanjing Institute of Geology and Palaeontology, Nanjing, China.

3 Geological setting

Beipiao City is located in the northeast of Chaoyang City, western Liaoning Province, the area includes Dabangou, Libalanggou, Sihetun, Huangbanjigou, Jianshangou to Shangyuan from south to north. The Sihetun area of Beipiao is situated at, and overlaps, the eastern border of the northern end of the larger Jilingsi-Yangshan basin, Liaoning Province (Fig. 1). The Jurassic-Cretaceous boundary Tuchengzi For-

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

mation is the primary unit exposed in the Sihetun area, but the Lower Cretaceous Yixian Formation is exposed unconformably on the Tuchengzi Formation at many localities.

The tracks were found in the lower-Jianshangou bed of the Yixian Formation at Sihetun-i.e., the lowermost part of the formation, immediately overlying the unconformable contact with the Tuchengzi Formation. The sedimentary facies of the site is a stream channel[17]. The ages of these rocks are between 128 Ma and 139 Ma[18].

4 Systematic ichnology

***Grallator* Hitchcock, 1858**

Type ichnospecies

***Grallator parallelus* Hitchcock, 1858**

Revised diagnosis

Small (< 15 cm long) bipedal, functionally tridactyl ichnite. Digit III projects relatively farther cranially (projection ratio 1.3); foot narrower than in *Eubrontes* and *Anchisauripus* (length/width ratio ⩾2, often around 2.2); hallux rarely impressed; divarication of outer digits 10-30°, averaging 28°[19].

***Grallator* isp.**

Figs. 2,3; Table 1.

Material: Three complete and one half natural casts on a single slab (NGMC V2115) housed at the National Geological Museum of China. The tracks on the slab are cataloged individually as NGMC V2115A-D (Figs. 2, 3; Table 1).

Locality and horizon: Sage green siltstone of the lower -Jianshangou bed of the Yixian Formation (Lower Cretaceous), Sihetun fossil site, Beipiao, western Liaoning, China.

Description: All specimens (NGMC V2115A-D) are natural casts. They display typical characteristics of theropod tracks[20-21]: tridactyl, narrow, have tapering digits with V -shaped outlines and impressions of claws, and made by bipeds.

The average length:width ratio of tracks NGMC V2115A-C (the complete specimens) is 1.71. Digit II is the shortest, with two indistinct and discernible digital pads. Digit III is the longest and has three indistinct digital pads. Digit IV is short, bearing three indistinct digital pads that are narrower than those of digits II and III. In all three tracks, the divarication angles between digits II and III are greater than those between digits III and IV (Table 1). The cranial ends of digits II and IV in V2115D are missing, and only the first digital pad is preserved for digit III. In all tracks, two sub -rounded, somewhat indistinct metatarsophalangeal pads are separate from the proximal ends of all three digits. The more medial of the two is typically in line with digit III, implying it may pertain to the metatarsal of that digit. The other impression lies at the base of digit IV.

Short claw drag marks are preserved at the tips of digit II in NGMC V2115B and C. In NGMC V2115B, the mark is 2.11 cm long; in NGMC V2115C, it is 2.39 cm long.

Fig. 2 *Grallator* isp. (NGMC V2115) (Individual tracks A-D) proceed from the bottom of the slab to the top, scale bar=10 cm

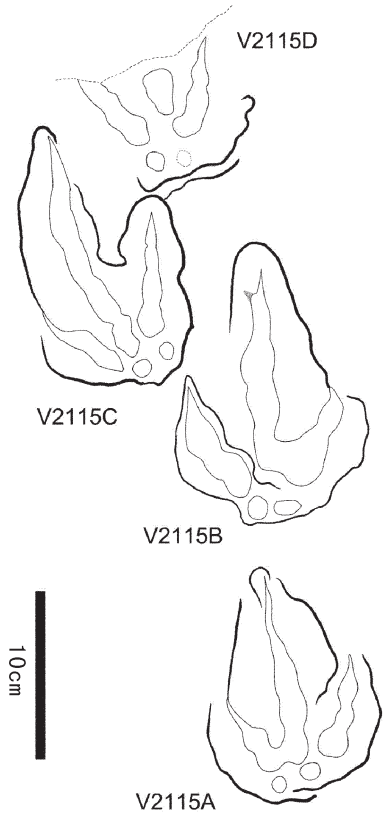

Fig. 3 Outline drawings of *Grallator* isp. NGMC V2115A–D

The black lines around the footprints demarcate the natural outlines around each track of substrate deformed by the mass of the track maker

Discussion: Theropod tracks thus far described from this region in China are primarily from the Tuchengzi Formation. These include tracks originally named *Jeholosauripus s–satoi*[1], but *Jeholosauripus* was later considered a junior synonym of *Grallator* so the specimens were redescribed as *Grallator ssatoi*[4]. Theropod track types A, B, and C from the Sijiaban site are very similar to *Grallator*; type B is particularly similar to *Grallator ssatoi*, but displays a few differences [7]. Generally speaking, the known theropod tracks from the Tuchengzi Formation are basically of the *Grallator* morphotype.

Grallator[19, 22–23] is a common, small (< 15 cm long), narrow, tridactyl track type made by bipedal theropods. Digit III projects relatively farther cranially than the other digits and the foot is narrower than in

Table 1 Measurements of *Grallator* isp. (NGMC V2115)

Measurement	NGMC V2115			
	A	B	C	D
Maximum length*/cm	12.96	14.72	15.45	-
Maximum width*/cm	7.77	8.53	8.87	-
Length of digit II**/cm	6.87	6.25	5.41	6.24***
Length of digit III**/cm	12.56	12.54	14.03	3.22***
Length of digit IV**/cm	7.62	7.74	7.9	5.35***
Angle between digits II and III	27°	29°	35°	-
Angle between digits III and IV	24°	20°	23°	-
Angle between digits II and IV	51°	49°	58°	-

notes: *Maximum length/width plus claw drag marks; Maximum length and width are the distance between the tips of digits Ⅱ and Ⅳ; **Measured to the rear margin of the caudalmost digital node; ***Incomplete

Eubrontes and *Anchisauripus* (length/width ratio ≥ 2). The hallux is rarely impressed and divarication of the outer digits ranges from 10–30°. In terms of the number of specimens and named ichnospecies, *Grallator* is a massive ichnotaxon that encompasses many small, predominantly Late Triassic and Early Jurassic theropod tracks. NGMC V2115 possesses enough characteristics of *Grallator* to warrant placement in this ichnotaxon, including: digit III always the longest, digits II and IV subequal in length[24], and length/width ratio is 1.71. This latter number is substantially smaller than the 2.2 listed for the type ichnospecies (see above), but other tracks also referred to *Grallator* similarly have smaller ratios (see example below). The ratios may reflect differences in locomotion adopted by the track makers and/or differences in foot–substrate interaction; additionally, it may indicate a previously unappreciated ichnotaxonomically useful characteristic.

The NGMC V2115 tracks differ from both *G. ssatoi* and the Sijiaban theropod tracks. The average digit length ratios of NGMC V2115 tracks are 0.47 for digits II–III and 0.59 for digits IV–III, but those of *G. ssatoi* are 0.77 and 0.93, respectively [4]. The mean ratios for Sijiaban track type B specimens are 0.62 and 0.76, respectively[7]. The digit divarication angles of NGMC V2115 average 30° for digits II–III

and 22° for digits III-IV, but are 14° and 13°, respectively, in *G. ssatoi*[4] and 21.7° and 15° in Sijiaban type B tracks[7].

Furthermore, NGMC V2115 differs from representative *Grallator*, particularly the ichnogenotype, *G. parallelus* [22]. The length:width ratio of *G. parallelus* is 2.2, versus 1.71 in NGMC V2115; divarication of the outer digits averages of *G. parallelus* is 28°, but 53° in NGMC V2115. Narrow divarication angles between digits II-IV exemplify most *Grallator* ichnospecies, such as *G. variabilis* (35-39°[25]), *G. limnosus* (35°[26]), *G. andeolensis* (37°[27]), but the same measurements are substantially greater in NGMC V2115. For other *Grallator* ichnospecies, such as *G. emeiensis*[28] and *G. sauclierensis*[29], the angles between digits II-IV are 60° and 54°, respectively, much more similar to the NGMC V2115 tracks. However, the length/width ratios differ (2.17 and 1.39, respectively). The NGMC V2115 *Grallator* tracks therefore represent a comparatively short and wide exemplar of Grallator.

5 Track maker

5.1 A single track maker?

Virtually all theropod trackways have extremely high pace angulations (nearing 180°) and stride lengths. If the NGMC V2115 tracks are interpreted as pertaining to a single trackway, the pace angulation of NGMC V2115A-C is an unusually low 123°. This means that they were probably registered by multiple individuals. However, in tridactyl or tetradactyl dinosaur tracks, the claws of digits II and IV point away from the axis of the foot while the claw of digit III is invariably bent inward toward the midline of the trackway[30]. This situation is apparent in NGMC V2115A-C, especially NGMC V2115B and C, which lies in an alternating right-left-right pattern. Taken at face value, this suggests that the tracks pertain to a single trackway. Additionally, NGMC V2115A-C have very similar length:width ratios-the concomitant differences in the angles between digits II and III and III and IV of NGMC V2115A-C may be attributed to variations of the substrate[31] and/or changes in track maker behavior. Most telling, however, is the peculiar arrangement of tracks in the aforementioned right-left-right pattern of NGMC V2115A-C. In this sequence, the right and left tracks lie on the opposite sides of the "trackway" axis from what would be predicted-to make this pattern, a single track maker would have to swing each foot inward far over the trackway axis, a behavior unknown in any theropod. Were the pattern left-right-left, NGMC V2115A-C could conceivably have been made by a single dinosaur walking very slowly. The trackway pattern instead supports that the small sample on the slab could only have been made by at least three individual track makers.

5.2 Many kinds of possible track makers

The hip height of the track maker can be estimated most accurately using the formula: hip height ? 4x footprint length[32]. From Table 1, the estimates of track maker height for the NGMC V2115 A-C tracks would be 51.8 cm, 58.9 cm, and 61.8 cm, respectively, with a mean of 57.5 cm. To estimate body length from the hip height, ten theropod (or near-theropod, in the cases of *Eoraptor* and *Herrerasaurus*) species from a diverse set of clades and that are known from complete skeletons were analyzed to determine hip height to body length ratios (Table 2); the resultant average ratio of hip height to body length is 1:2.63. Based on this mean, the body length of the track makers of NGMC V2115 is estimated at about 1.51 m.

Theropods in this size range are not unknown in the Yixian Formation. The overall length of the preserved vertebrae and skull of the only known specimen of the ornithomimosaur *Shenzhousaurus orientalis* is 843 mm [16]; assuming similar proportions to other ornithomimosaurs (e.g., *Gallimimus* and *Struthiomimus*[37]), the estimated overall length of *Shenzhousaurus* is 1.37 m. In addition, the basal tyrannosauroid *Dilong paradoxus*[43] has an estimated length of 1.66 m. At 1.2 m, the compsognathid *Huaxiagnathus* is slightly shorter[44], but the compsognathid *Sinocalliopterx* is far larger at 2.4 m [45]. All these

Table 2 Ratios of hip height to body length of nine theropods

Taxa	Hip height∶body length
Deinonychus antirrhopus[33]	1∶2.61
Herrerasaurus ischigualastensis[34]	1∶2.57
Eoraptor lunensis[35]	1∶2.35
Allosaurus fragilis[36]	1∶2.96
Compsognathus longipes[37]	1∶3.20
Sinosauropteryx prima[38]	1∶3.66
Tyrannosaurus rex[37]	1∶2.44
Gallimimus bullatus[39]	1∶2.15
Citipati osmolskae[40-41]	1∶2.16
Microraptor gui[42]	1∶2.18

note:sources of measurements given in parentheses for each taxon

theropods are therefore in the size range expected for the NGMC V2115 track maker. Other Yixian Formation theropods are known only from smaller specimens, such as 67 and 72 cm, respectively, for specimens NGMC 97−4−A and BPM 0001 of the ovirap torosaurian: *Caudipteryx zoui*[46], 77 cm for *Caudipteryx* sp. (IVPP V 12430)[47] and *Protarchaeopteryx robusta*[46], and 71 cm for the compsognathid *Sinosauropteryx prima*[38]. The NGMC V2115 tracks could not have been made by any of the Yixian Formation dromaeosaurids or troodontids because the specialized digits II of members of these clades were held off the ground during locomotion;and therefore would register didactyl, not tridactyl, tracks[48].

Dromaeosaurids and troodontids aside, complete pedes are rarely preserved in theropods from the Yixian Formation. Complete and correlative feet occur in the oviraptorosaurians *Caudipteryx dongi* (IVPP V 12344), *Caudipteryx zoui* (BPM 001), *Caudipteryx* sp. (IVPP V 12430), and *Protarchaeopteryx robusta* (NGM C 2125) and the compsognathids *Sinosauropteryx prima* (NIGP 127587), *Huaxiagnathus orientalis* (CAGS −IG02 −301), and *Sinocalliopteryx gigas* (JMP−V−05−8−01). Incomplete feet are preserved in other theropod specimens such as *Caudipteryx zoui* (NGMC 97−4−A) and *Dilong paradoxus* (IVPP V 11579). *Caudipteryx* sp. (IVPP V 12430) and *Sinosauropteryx prima* (NIGP 127587) were selected

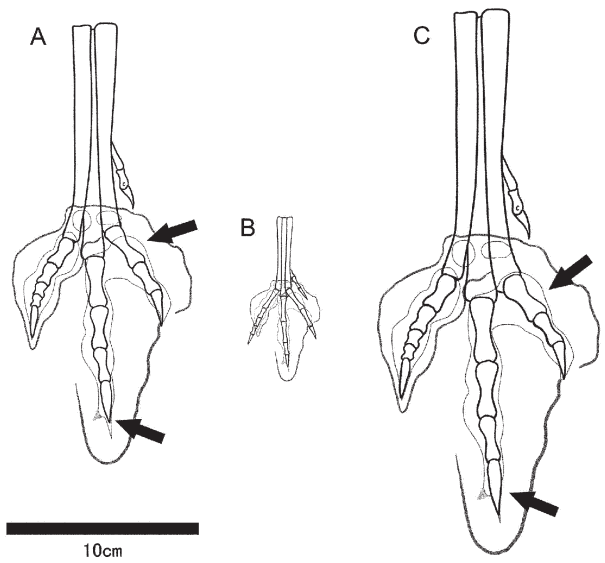

Fig. 4 Comparison between NGMC V2115B and the foot skeletons of selected theropod dinosaurs
A−*Caudipteryx* sp. (IVPP V 12430); B−*Sinosauropteryx prima* (NIGP 127587); C−Foot idealized of NGMC V2115 track maker. Arrows denote the minor differences between A and C

and their in vivo feet reconstructed for comparison with the NGMC V2115 tracks (Fig. 4). An idealized foot of the actual track maker was also reconstructed according to the x−2−3−3−x phalangeal formula of *Caudipteryx* sp. It is well known that digital pads can be both arthral and mesarthral, so digital pads do not necessarily reflect the underlying phalangeal formulae in footprints [19, 49]. However, phalangeal lengths can reflect the approximate lengths of the pedal digits of a track maker. The NGMC V2115 track makers appear to have had feet similar to *Caudipteryx* sp., with two exceptions in the lengths of digits II and III (Fig. 4−A, C). The NGMC V2115 tracks are distinct from the reconstructed pes of *Sinosauropteryx* in the lengths of digits II and IV (Fig. 4−B). These measurements and comparisons, however, cannot determine whether or not the NGMC V2115 track maker was oviraptorosaurian; nor cant hey definitively exclude compsognathids and other theropods. Still, we can at least make the following determinations:

(1) Due to the similarity of the tracks to known pes body fossils, the Yixian *Grallator* isp. track maker

was at least fairly closely related to known small-medium sized Yixian Formation theropods. The *Grallator* morphotype would therefore be expected to have a wide distribution in theropods (aside from dromaeosaurids and troodontids) from the Yixian Formation.

(2) The occurrence of *Grallator* in the Yixian Formation expands the known age range and geographic distribution of the morphotype. Because *Grallator* tracks occur in both the Tuchengzi and Yixian formations, it also suggests similarities in the theropod faunas from these two units.

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References

[1]Yabe H, Inai Y, Shikama T. Discovery of dinosaurian footprints from the Cretaceous of Yangshan, Chinchou: preliminary note[J]. Proceedings of the Imperial Academy, Japan Preliminary, 1940, (16): 560-563.

[2]Shikama T. Footprints from Chinchou, Manchoukuo, of Jeholosauripus, the Eo-Mesozoic Dinosaur[J]. Central National Museum of Manchoukuo, 1942, (3): 21-31.

[3]Young C C. Fossil Footprints in China[J]. Vertebrata Palasiatica, 1960, (4): 53-66.

[4]Zhen S N, Li J J, Rao C G, et al. A review of dinosaur footprints in China[M]//Gillette D D, Lockley M G. Dinosaurs: Past and Present. Cambridge: Cambridge University Press, 1989: 187-197.

[5]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.

[6]Zhang Y Z, Zhang J P, Wu P, et al. Discovery of Dinosaur Tracks from the Middle-Late Jurassic Tuchengzi Formation in the Chaoyang area, Liaoning Province[J]. Geological Review, 2004, (50):561-566.

[7]Fujita M, Azuma Y, Lee Y N, et al. New theropod tracksite from the Upper Jurassic Tuchengzi Formation of Liaoning Province, northeastern China[J]. Memoir of the Fukui Prefectural Dinosaur Museum, 2007, (6): 17-25.

[8]Lockley M G, Matsukawa M, Ohira H, et al. Bird tracks from Liaoning Province, China: new insights into avian evolution during the Jurassic-Cretaceous transition[J]. Cretaceous Research, 2006, 27 (1):33-43.

[9]Sullivan C, Hone D W E, Cope T D, et al. A new occurrence of small theropod tracks in the Tuchengzi Formation of Hebei Province, China[J]. Vertebrata Palasiatica, 2009, in press

[10]Zhao X J, Cheng Z W, Xu X. The earliest ceratopsian from the Tuchengzi Formation of Liaoning, China[J]. Journal of Vertebrate Paleontology, 1999, (19):681-691.

[11]Zhao X J, Cheng Z W, Xu X, et al. A new ceratopsian from the Upper Jurassic Houcheng Formation of Hebei, China[J]. Acta Geologica Sinica (English Edition), 2006, (80):467-473.

[12]Dong Z M. A forefoot of sauropod from the Tuchengzi Formation of Chaoyang area in Liaoning, China[M]// Deng T. Wang Y. Proceedings of the Eighth Annual Meeting of the Chinese Society of Vertebrate Paleontology. Beijing: China Ocean Press, 2001: 29-33.

[13]Ji Q. On the Mesozoic Jehol Biota of China[J]. Geological Review. 2002, 48(3): 290-296.

[14]Zhang H, Yuan H L, Hu Z C, et al. U-Pb zircon dating of the Mesozoic volcanic strata in Luanping of north Hebei and its significance[J]. Earth Science—Journal of China University of Geosciences, 2005, 30(6):707-720.

[15]You H L, Azuma Y. Early Cretaceous dinosaur footprints from Luanping, Hebei Province, China[M]//Sun A, Wang Y. Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers. Beijing: China Ocean Press, 1995:151-156.

[16]Ji Q, Norrell M, Makovicky P J, et al. An Early Ostrich Dinosaur and Implications for Ornithomimosaur Phylogeny[J]. American Museum Novitates, 2003, (3420):1-19.

[17]Zhang L J, Gong E P, Xu D L, et al. Sedimentary facies of the Yixian Formation of Lower Cretaceous in Sihetun Basin of Beipiao, Liaoning Province[J]. Journal of Palaeogeography, 2005, (7):70-78.

[18]Swisher C C, Wang X L, Zhou Z H, et al. Further support for a Cretaceous age for the feathered dinosaur beds of Liaoning, China: new $^{40}Ar/^{39}Ar$ dating of the Yixian and Tuchengzi Formations[J]. Chinese Science Bulletin, 2002, (47):135-138.

[19]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.

[20]Thulborn R A. Dinosaur Tracks[M]. London: Chapman Hall, 1990: 1-410.

[21]Lockley M G. Tracking dinosaurs[M]. New York: Cambridge University Press, 1991:1-238.

[22]Hitchcock E. Ichnology of New England: A report on the sandstone of the Connecticut Valley, especially its fossil foot marks[J]. Boston: W. White, 1858:1-220.

[23]Lull R S. Triassic life of the Connecticut Valley[J]. Bulletin of the Connecticut State Geology Natural History Survey, 1953,(181):1-331.

[24]Olsen P E. Fossil great lakes of the Newark Supergroup in New Jersey[M]//Manspeizer W. Field Studies in New Jersey Geology and Guide to Field Trips. 52nd Ann. Mt. N.Y. State Geol. Assoc., 1980:352−398.

[25]de Lapparent A F, Montenat C. Les empreintes de pas de reptiles de l′Infralias de Veillon (Vendée)[J]. Mémoires de la Société géologique de France, nouvelle série, 1967, (107):1−44.

[26]Zhen S N, Li J J, Rao C G, et al. Dinosaur footprints of Jinning County, Yunnan[J]. Beijing Natural History Museum, 1986, (33): 1−17.

[27]Gand G, Vianey−Liaud M, Demathieu G, et al. Deux nouvelles traces de pas de Dinosaures du Trias supérieur de la bordure cévenole (La Grand−Combe, Gard, France)[J]. Geobios, 2000, (33): 599−624.

[28]Zhen S N, Li J J, Chen W, et al. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan[J]. Memoirs of the Beijing Natural History, 1995, (54):105−120.

[29]Demathieu G, Sciau J. L′ichnofaune Hettangienne d′archausauriens de Sauclieres, Aveyron, France[J]. Bulletin de la Société d′Histoire Naturelle d′Autun, 1995, (151):5−46.

[30]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.

[31]Falkingham P L, Margetts L, Smith I M, et al. Reinterpretation of palmate and semi−palmate (webbed) fossil tracks: insights from finite element modelling[J]. Palaeogeography, Palaeoclimatology, Palaeoecology, 2008, (271): 69−76.

[32]Henderson D M. Footprints, trackways, and hip heights of bipedal dinosaurs−testing hip height predictions with computer models[M]//Pemberton S G, McCrea R T, Lockley M G. William Antony Swithin Sarjeant (1935−2002): A Celebration of His Life and Ichnological Contributions Volume 1. Ichnos 10. 2003:99−114.

[33]Ostrom J H. Dromaeosauridae[M]//Weishampel D B, Dodson P, Osmolska H. The dinosaurian. Berkeley: Univ. California Press, 1990:273.

[34]Sereno P C, Novas F E. The complete skull and skeleton of an early dinosaur[J]. Science, 1992, (258):1137−1140.

[35]Sereno P C, Forster C A; Rogers R R, et al. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosaurs[J]. Nature, 1993, (361):64−66.

[36]Sereno P C. A rationale for phylogenetic definitions, with application to the higher level taxonomy of Dinosauria[J]. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen,1998, (210):41−83.

[37]Paul G S. Predatory dinosaurs of the world[M]. New York: Touchstone, Simon and Schuster Inc., 1988:1−464.

[38]Currie P J, Chen P J. Anatomy of Sinosauropteryx prima from Liaoning, northeastern China [J]. Can. J. Earth Sci., 2001, 38:1705−1727.

[39]Osmólska H, Roniewicz E, Barsbold R. A new dinosaur, Gallimimus bullatus n. gen.n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia[J]. Paleontol. Polonica, 1972, (27):103−143.

[40]Norell M A, Clark J M, Chiappe L M, et al. A nesting dinosaur[J]. Nature, 1995, (378):774−776.

[41]Clark J M, Norell M A, Barsbold R. Two new oviraptorids (Theropoda: Oviraptorosauria), Upper Cretaceous Djadokhta For mation, Ukhaa Tolgod, Mongolia[J]. Journal of Vertebrate Paleontology, 2001, 21(2):209−213.

[42]Xu X, Zhou Z H, Wang X L, et al. Four−winged dinosaurs from China[J]. Nature, 2003, (421): 335−340.

[43]Xu X, Norell M A, Kuang X, et al. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids[J]. Nature, 2004, (431):680−684.

[44]Hwang S H, Norell M A, Ji Q, et al. A large compognathid from the Early Cretaceous Yixian Formation of China[J]. Journal of Systematic Palaeontology, 2004, 2(1):13−30.

[45]Ji S A, Ji Q, Lü J C, et al. A New Giant Compsognathid Dinosaur with Long Filamentous Integuments from Lower Cretaceous of Northeastern China[J]. Acta Geologica Sinica, 2007, 81(1):8−15.

[46]Ji Q, Currie P J, Norell M A, et al.Two feathered dinosaurs from northeastern China[J]. Nature, 1998, (393): 753−761.

[47]Zhou Z H, Wang X L, Zhang F C, et al. Important features of Caudipteryx — evidence from two nearly complete new specimens [J]. Vert Palasiat., 2000,38(4): 241−254.

[48]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): 185−191.

[49]Smith J B, Farlow J O. Osteometric approaches to trackmaker assignment for the Newark Supergroup ichnogenera Grallator, Anchisauripus, and Eubrontes[M]//LeTourneau P M, Olsen P E. The Great Rift Valleys of Pangea in eastern North America, volume 2: Sedimentology, Stratigraphy, and Paleontology. New York: Columbia University Press, 2003: 273−292.