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Research paper

Early cretaceous bird-dominated and dinosaur footprint assemblages from the northwestern margin of the Junggar Basin, Xinjiang, China

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Abstract

Here we describe a number of mostly isolated bird and non-avian dinosaur footprints from the Huangyangquan track site in the Lower Cretaceous Lower Layer of the Tugulu Group near Huangyangquan Reservoir in the Wuerhe District, Karamay, Xinjiang Uyghur Autonomous Region, China. Bird footprints at the site pertain to *Koreanaornis dodsoni* n. ichnosp., *Goseongornipes* isp., *Aquatilavipes* isp., and *Moguiornipes robusta* n. ichnogen. n. ichnosp. *Moguiornipes* tracks may be the products of a bird with lobed feet. These shorebird-morph tracks are the first solid evidence of birds in the Tugulu Group, and greatly enrich the known faunal diversity of the Lower Layer of the Tugulu Group. The Huangyangquan avian ichnofauna is comparable to those of the Jindong Formation, Korea and the Dakota Formation, USA. Non-avian dinosaur footprints at the site pertain to cf. *Jialingpus* isp., *Asianopodus* isp., and *Kayentapus* isp. This is the first report of *Jialingpus* from Lower Cretaceous strata. The discoveries of *Asianopodus* isp. and *Kayentapus* isp. increase the known ranges of these two ichnogenera.

Keywords: *Koreanaornis dodsoni*; *Goseongornipes* isp.; *Aquatilavipes* isp.; *Moguiornipes robusta*; Lower layer of the Tugulu Group; Lower Cretaceous

1. Introduction

Research on dinosaur tracks from Xinjiang Uyghur Autonomous Region has lagged far behind research on dinosaur body fossils from the same region. Numerous dinosaur body fossils have been recovered from Middle Jurassic through Lower Cretaceous strata in Xinjiang, but the only tracks thus far described come from the Middle Jurassic Sanjianfang Formation of the Turpan Basin (Wings et al., 2007). Tracks from the Middle Jurassic Xishanyao Formation of the southern Junggar (Dsungar) Basin were mentioned by Deng et al. (2003) but as yet lack formal description.

In 2002, dinosaur footprints were discovered by An Jianfu, the curator of the Moguicheng Dinosaur And Bizarre Stone Museum of the 137th Regiment, 4th Division, Xinjiang Production and Construction Corps, along the shore of Huangyangquan ("yellow goat spring") Reservoir in the Wuerhe (Wuerho or Urho) District. Subsequently, a set of these footprints were collected in July 2009.

The Wuerhe District is located in the northwestern part of the Junggar Basin, where Lower Cretaceous strata (Tugulu Group) are well exposed in part as a result of wind erosion. The Early Cretaceous *Dsungaripterus*-*Psittacosaurus* fauna (Dong, 2001) is well known in the Junggar Basin. A few fossil fishes (Lucas, 2001), the pterosaur *Dsungaripterus weii* (Young, 1964), and the stegosaur *Wuerhosaurus homheni* (Dong, 1973, 1990) all

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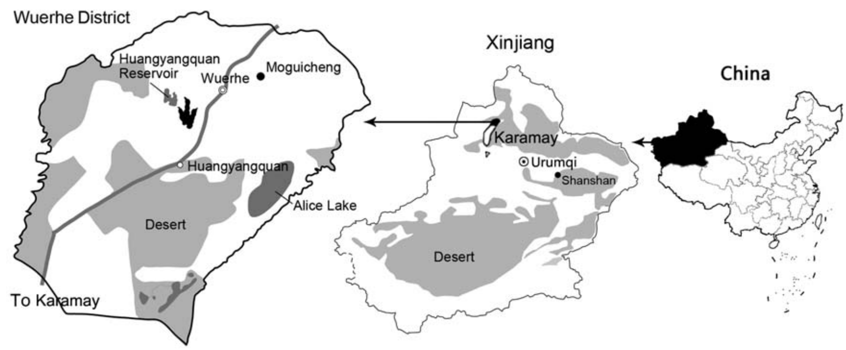

Fig. 1. Location of the Huangyangquan track locality (indicated by the footprint icon) in Xinjiang, China.

come from the Upper or Grey-green Layers of the group. The theropods *Kelmayisaurus petrolicus*, *Phaedrolosaurus ilikensis* (a nomen dubium per Rauhut and Xu, 2005), *Tugulusaurus faciles* (Dong, 1973), and *Xinjiangovenator parvus* (Rauhut and Xu, 2005), as well as the sauropod cf. *Asiatosaurus mongoliensis* (Dong, 1973), were recovered from the Upper or Grey-green Layer of Tugulu Group. The fossil assemblage from the Lower Layer of the Tugulu Group is sparse, consisting only of the ostracode *Cypridea* (*Ulwellia*) (Regional Survey Team of the Bureau of Geology of the Xinjiang Uygur Autonomous Region, 1980), *Dsungaripterus* isp., *Wuerhosaurus* isp. (Dong Z.M., pers. comm.), and tracks. Other taxa from the Tugulu Group in the Junggar Basin, but from unspecified strata, include several turtles (Maisch et al., 2003; Matzke and Maisch, 2004; Rabi et al., 2010), the pterosaur *Lonchognathosaurus* (Maisch et al., 2004), the protosuchian crocodyliform *Edentosuchus* (Wings et al., 2010), and the basal ceratopsian *Psittacosaurus* (Brinkman et al., 2001).

2. Institutional abbreviation

MGCM = Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China; MPD = Paleontological Center of the Mongolian Academy of Sciences, Ulan Baatar, Mongolia; HDT = Huaxia Dinosaur Tracks Research and Development Center, Gansu, China; ZDRC = Zhucheng Dinosaur Research Center, Shandong, China.

3. Geological setting

The Wuerhe District lies 110 km northeast of the city of Karamay (Kelamayi). The track site is on the margin of Huangyangquan Reservoir (Fig. 1). The tracks initially discovered were distributed along the bank, but in 1989, when the base of the reservoir was reinforced by heavy equipment, the trace fossils were destroyed. The track sites reported here, which produce isolated dinosaur and bird tracks, were exposed only in the last two decades as a result of wind and water weathering and erosion.

The Tugulu Group along the northwestern margin of the Junggar Basin is difficult to divide into the subunits that are more easily demarcated along the southern and eastern margins of the basin (in ascending order the Qingshuihe, Hutubihe, Shengjinkou, and Lianmuqin formations). Presently, it can only be divided as Upper, Grey-green, and Lower layers, none of which are readily correlated with the four formations from the southern and eastern margins of the basin (Academy of Prospecting and Developing, Xinjiang Bureau of Petroleum, 1977, 1996, 1997). The footprints reported here come from the Lower Layer of Tugulu Group, which is Barremian in age (Currie and Zhao, 1993). Lower Layer sediments, which are grey, sandy mudstones and light green-grey sandstones, were deposited in deltaic, shore-shallow lake, and semi-deep lake environments (Gu et al., 2003). The Lower Layer at this locality is overlain by 1–10 m of upper Pleistocene–Holocene, alluvial and eolian, poorly sorted alluvium (Fig. 2).

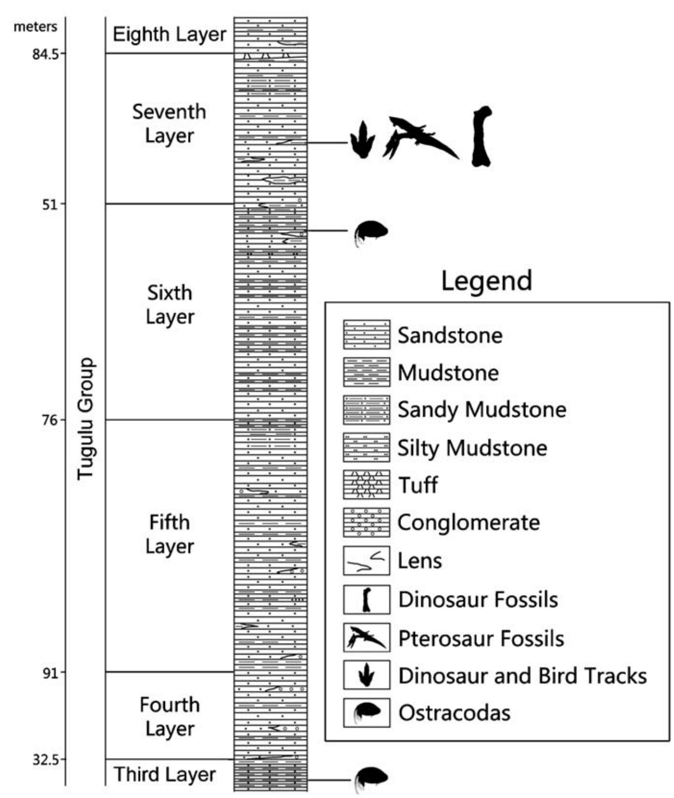

Fig. 2. Stratigraphic section of the Lower Layer of the Tugulu Group at the Huangyangquan track locality (emended from Qi et al., 1995).

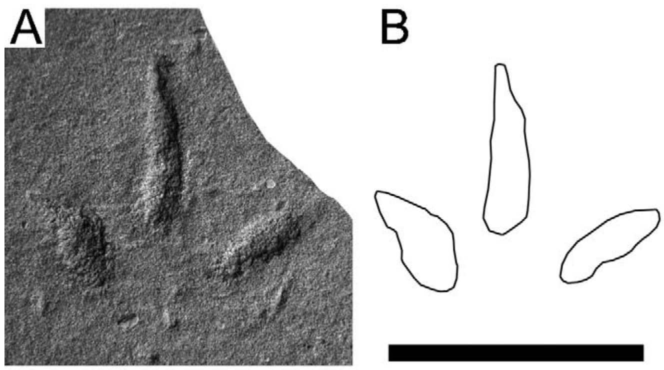

Fig. 3. *Koreanaornis dodsoni* MGCM.H14 from the Huangyangquan track site. A, photograph; B, outline drawing. Scale bar = 5 cm.

4. Systematic ichnology

4.1. Bird tracks

4.1.1. Koreanaornis morphotype

Koreanaornipodidae Lockley et al., 2006a

Koreanaornis Kim, 1969

Type ichnospecies: *Koreanaornis hamanensis* Kim, 1969, Lockley et al., 1992 emend.

Diagnosis: Small, tetradactyl bird tracks with small hallux impressions occasionally present. Digit traces typically separate (i.e., not connected proximally). Claw traces variably present, slender, and obscure. Trackways exhibit inward (positive) rotation of the tracks. Tracks wider than long, with widths ranging from 2.5 to 4.4 cm. Divarication between digits II and IV averaging about 120° (Lockley et al., 1992).

Koreanaornis dodsoni n. ichnosp.

Etymology: The ichnospecies name "*dodsoni*" is in honor of Peter Dodson, a famous dinosaur paleontologist.

Holotype: A complete natural mold, cataloged as MGCM.H14, from the Huangyangquan track site (Fig. 3; Appendix A).

Referred material: One hundred sixteen complete natural casts and molds on seven slabs cataloged as MGCM.H10 (2), H11 (25), H16 (32), H17 (8), H18 (15), H19 (15), and H20 (19) (numbers in parentheses indicate numbers of tracks on each slab; tracks lettered on each slab [e.g., MGCM.H10a, MGCM.H10b, etc.]) (Fig. 4A, B, D–F; Appendix A).

Locality and horizon: Lower Layer of the Tugulu Group, Lower Cretaceous. Huangyangquan track site (46°4′25″N, 85°34′57″E), Huangyangquan Reservoir, Wuerhe District, Xinjiang Uyghur Autonomous Region, China.

Diagnosis: Different from *K. hamanensis* tracks in having smaller divarication angles between digits II and IV, greater overall track length and width, persistent absence of digit I, and absence of digital pad impressions.

Description: Medium and large, tridactyl bird tracks lacking hallux impressions. Digit III is the longest digit; digits II and IV are subequal in length. Digital pad impressions are absent. Digit II is broader than digits III and IV. The divarication angles between digits II and III are smaller than those between digits III and IV.Tracks on slabs MGCM.H10, H11, and H16-H20 typically are not connected proximally. Average length:width ratio 0.9 (range 0.67–1.24). Average maximum length is 4.6 cm (range 3.0–6.3 cm); average maximum width is 5.1 cm (range 3.2–6.8 cm). Average divarication angle between digits II and IV 87° (range 58°–109°). The pace angulation of the only distinct trackway, H111a-H111c, is 160°. Tracks in the trackway exhibit slight positive (inward) rotation.

Discussion: Most characteristics of MGCM.H14 match those of Koreanaornipodidae (Kim, 1969; Lockley et al., 2006a), such as small, wide (2.5–3.0 cm), sub-symmetric, functionally tridactyl tracks with slender digit impressions and wide (90°–115°) divarication angles between digits II and IV. Koreanaornipodid trackways also exhibit positive rotation (Lockley et al., 2006a). But the overall size of the Huangyangquan tracks is slightly larger than holotypic koreanaornipodid tracks. In comparison, the hallux of *Pullornipes aureus* is preserved more frequently than in the MGCM specimens.

Based on these characteristics, the MGCM tracks are referred to *Koreanaornis*. However, the divarication angles between digits II and IV of the tracks are markedly smaller than the 120° of *Koreanaornis hamanensis*; the tracks furthermore exceed *K. hamanensis* in length and width. The small hallux impression occasionally present in *K. hamanensis* tracks is absent in the MGCM tracks. The greater width of digit II than digits III and IV of the MGCM tracks and the absence of distinct digital pad impressions further differentiate the Huangyangquan tracks from *K. hamanensis*. These differences are also seen in *Koreanaornis* cf. *hamanensis* tracks (Anfinson et al., 2009), and support placement of the MGCM tracks in a new ichnospecies.

4.1.2. Goseongornipes isp.

Material: Six complete natural casts on a single slab cataloged as MGCM.H13 (tracks numbered MGCM.H13a-f) (Fig. 5; Appendix A).

Locality and horizon: Lower Layer of the Tugulu Group, Lower Cretaceous. Huangyangquan track site (46°4′25″N, 85°34′57″E), Huangyangquan Reservoir, Wuerhe District, Xinjiang Uyghur Autonomous Region, China.

Description: Medium and large, tetradactyl bird tracks with small hallux impression occasionally present (faintly visible on H13a and H13b); when present, it is oriented caudally about 180° from digit III. Digit III is the longest of the three digits. Digital pad impressions are absent. Average length:width ratio is 0.73 (range 0.66–0.79). Average maximum length is 4.0 cm (range 3.8–4.4 cm); average maximum width is 5.5 cm (range 4.8–6 cm). Mean divarication angle between digits II and IV is 120° (range 101°–152°). The pace angulation of trackway sequence H13a-c is 140°. These tracks exhibit slight positive (inward) rotation.

Discussion: Most characteristics of MGCM.H13 tracks match those of *Goseongornipes* (Lockley et al., 2006a), including being tetradactyl, having widely splayed digits II–IV and a small, caudally directed hallux, and being slightly semipalmate with subtle webbing traces at the proximal hypeces between digits III and IV. Due to the small sample size, it is difficult to

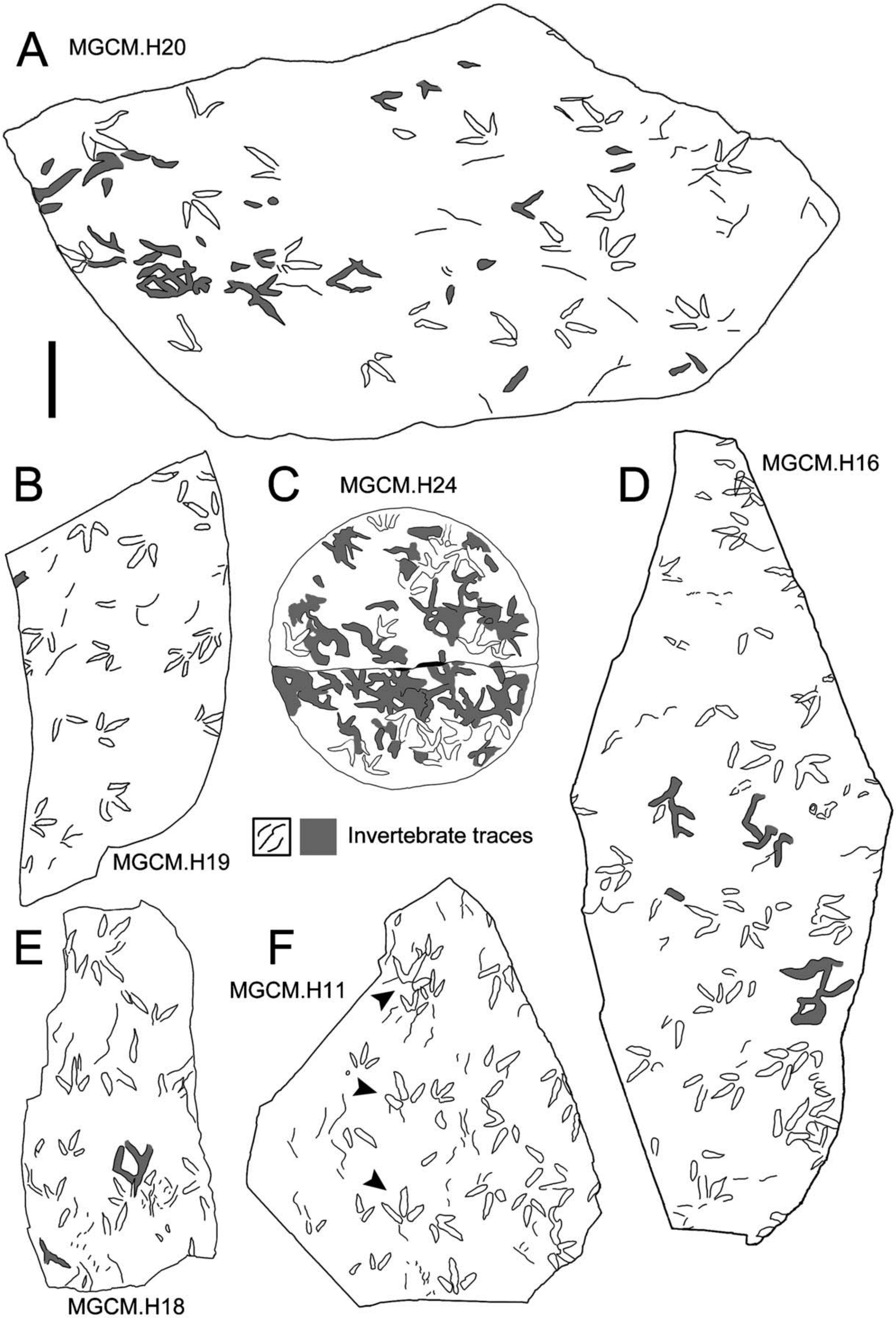

Fig. 4. Bird footprints from the Huangyangquan track site. (A) MGCM H20; (B) MGCM H19; (C) MGCM H24; (D) MGCM H16; (E) MGCM H18; (F) MGCM H11. Scale bars = 10 cm.

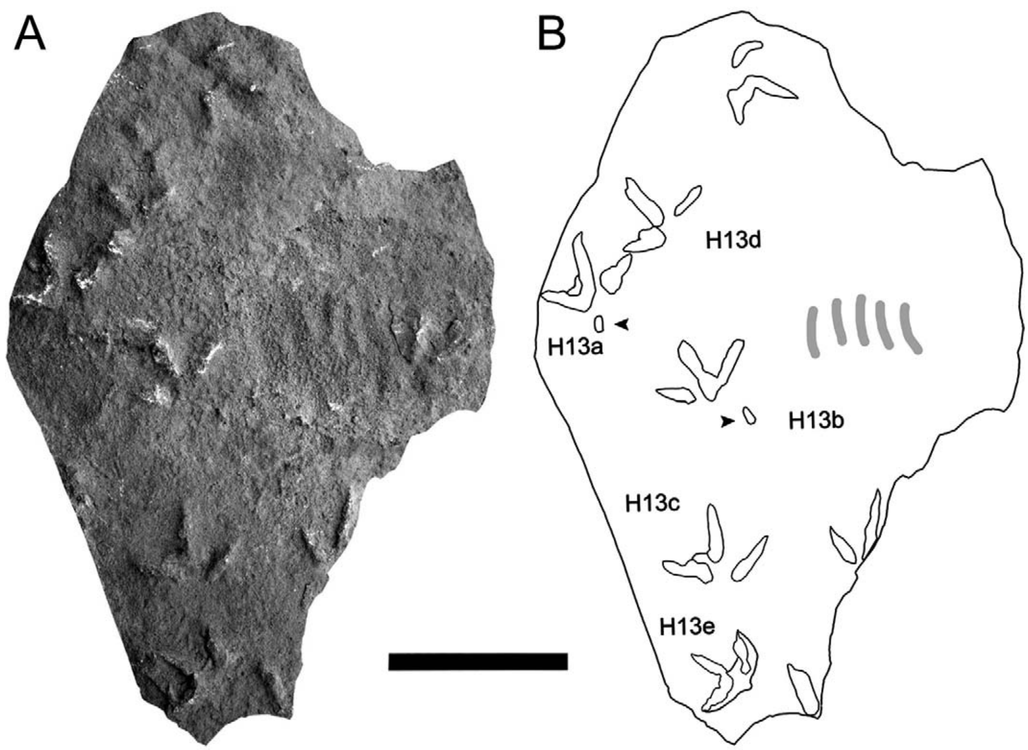

Fig. 5. *Goseongornipes* isp. MGCM.H13 from the Huangyangquan track site. (A) photograph; (B) outline drawing. Scale bar = 10 cm.

discern systematic features, and thus the material is referred to *Goseongornipes* isp.

4.1.3. Aquatilavipes isp.

Material: Twenty-two complete natural casts on two slabs cataloged as MGCM.H24 (16), H26 (6) (numbers in parenthesis indicate numbers of tracks on each slab; tracks lettered on each slab [e.g., MGCM.H24a, MGCM.H24b, etc.]) (Figs. 4C, 6; Appendix A).

Locality and horizon: Lower Layer of the Tugulu Group, Lower Cretaceous. Huangyangquan track site (46°4′25″N, 85°34′57″E), Huangyangquan Reservoir, Wuerhe District, Xinjiang Uyghur Autonomous Region, China.

Description: Medium, tridactyl bird tracks. Digit III is the longest of the three digits. Digital pad impressions are absent. Average length:width ratio is 0.9 (range 0.76–0.96). Average maximum length is 4 cm (range 2.8–4.5 cm); average maximum width is 4.4 cm (range 3.7–4.7 cm). Average divarication angle between digits II and IV is 104° (range 85°–120°). A complete metatarsophalangeal region is preserved for most tracks; for tracks made in firmer sediments, it is low and flat, but in partial tracks it is elongated.

Discussion: *Aquatilavipes* has been incorrectly used as a catch-all ichnogenus both in North America and in Asia (Anfinson et al., 2009). Presently, *Aquatilavipes* includes at least *A. swiboldae* (Currie, 1981) and *A. izumiensis* (Azuma et al., 2002). *A. curriei* (McCrea and Sarjeant, 2001) may belong to a new ichnogenus (Lockley and Harris, 2010), and *A. sinensis* (Zhen et al., 1994) is a synonym of *Koreanaornis* (Lockley et al., 2008). With the exclusion *A. sinensis*, the only record of *Aquatilavipes* in China is from Inner Mongolia (Lockley and Rainforth, 2002).

Tracks on MGCM.H24 and H26 differ from other sorts of bird tracks at the Huangyangquan site by possessing low, flat metatarsophalangeal regions, no hallux impressions, and slender digits, all of which are characteristics of *Aquatilavipes* (Currie, 1981). Furthermore, the 104° divarication angle between digits II and IV is close to the 100° angle of *A. swiboldae* (Currie, 1981) but less than the 120° angle of *A. izumiensis* (Azuma et al., 2002). The slabs on which the Huangyangquan tracks are preserved are heavily bioturbated, limiting comparisons, so the material is referred to only as *Aquatilavipes* isp.

4.1.4. Moguiornipes

Moguiornipes robusta n. ichnogen. n. ichnosp.

Etymology: From the Chinese "mogui" meaning demon; and from the Latin "orni" and "pes" meaning bird and foot, respectively. Mogui refers to the local famous resort Demon City (Mogui Cheng). The species name "*robusta*" is from the Latin, meaning the tracks are robust.

Holotype: A complete natural cast, cataloged as MGCM.H25a, from the Huangyangquan track site (Fig. 7A and C; Appendix A).

Paratypes: MGCM.H25b-d, three additional natural casts on the same slab (MGCM.H25) as the holotype, which bears more than 25 tracks (Fig. 8; Appendix A); MGCM.H27a (Fig. 7B and D; Appendix A), one natural cast.

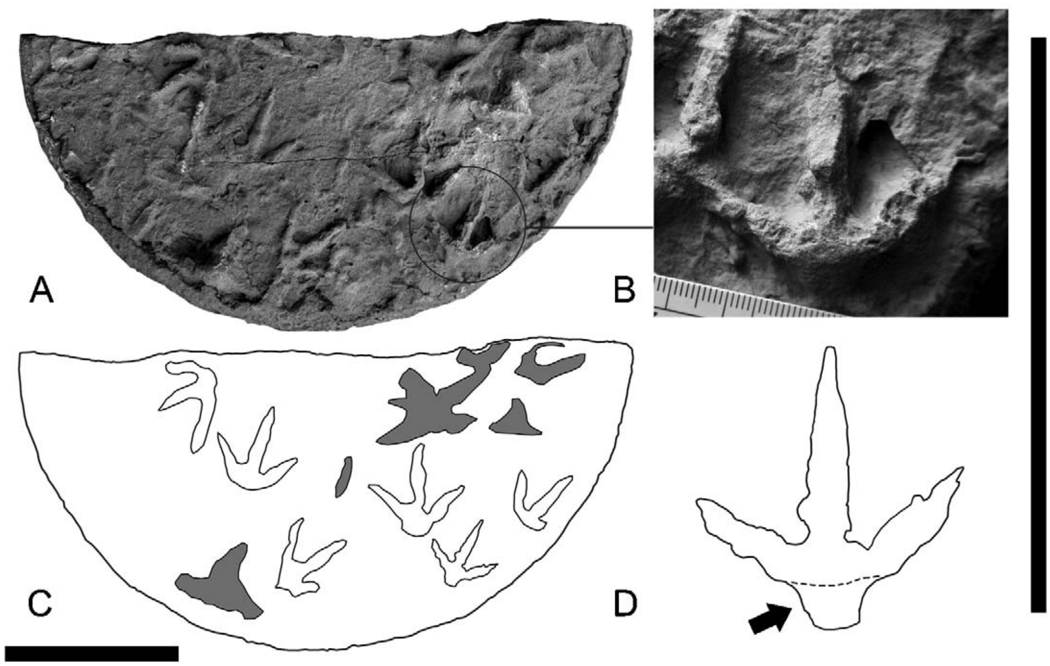

Fig. 6. *Aquatilavipes* isp. MGCM.H26 from the Huangyangquan track site. (A) and (B) photograph; (C) and (D), outline drawing. Arrows in (D) point to elongate metatarsophalangeal region. Scale bar = 10 cm.

Locality and horizon: Lower Layer of the Tugulu Group, Lower Cretaceous. Huangyangquan track site (46°4′25″N, 85°34′57″E), Huangyangquan Reservoir, Wuerhe District, Xinjiang Uyghur Autonomous Region, China.

Diagnosis: Medium size, short, wide (5–6.3 cm), tridactyl tracks with stocky digit impressions and wide divarication angles

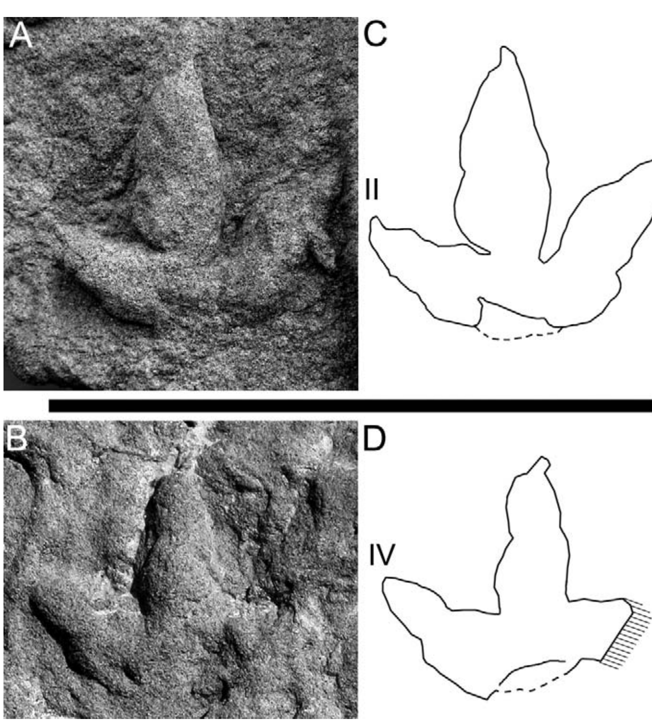

Fig. 7. *Moguiornipes* MGCM.H25a (A) and (C) and MGCM.H27a (B and D) from the Huangyangquan track site. (A) and (B), photograph; (C) and (D) outline drawing. Scale bar = 10 cm.

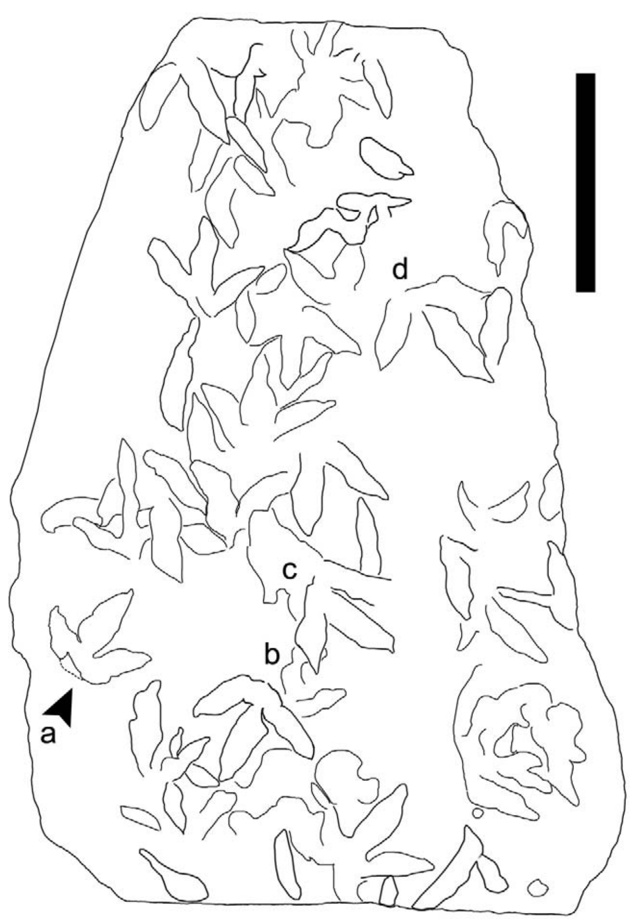

Fig. 8. Outline drawing of *Moguiornipes* track-bearing slab MGCM.H25. Scale bar = 10 cm.

between digits II and IV (90°–99°). No hallux or webbing impressions. Digit III impressions have two short digital pads. The length:width ratio of each digit is less than 3.0.

Description: The following description is based primarily on the holotype, but the paratype specimens are very similar in all respects. The length:width ratio is 0.9. Digit II is the shortest of the three digits; digits III and IV are subequal in length. Each of the three digits has at least two faint digital pads. Digit IV is narrower than digits II and III. The divarication angles between digits II and III are greater than those between digits III and IV. The length:width ratios of each digit are: II = 1.6, III = 2.2, and IV = 2.3. The proximal ends of the digits are not separate from the metatarsophalangeal region. The metatarsophalangeal regions are concave caudally. Close to the intersection point of the axes of digits II and IV, at the caudal end of the track, the topography of the track decreases, sloping toward the plane of the surrounding substrate.

There are at least 25 footprints on slab MGCM.H25, some of which are incomplete, but all of which exhibit two distinct digital pads on digit III. MGCM.H27a lacks the impression of digit II.

Discussion: Except for the thick digit impressions, features of *Moguiornipes* tracks characterize bird tracks in general, including their small size, high divarication angles (110°–120°) between digits II–IV, and length:width ratios $\leq$1.0 (Lockley et al., 1992; McCrea and Sarjeant, 2001). The thick digit III impressions distinguish MGCM.H25 tracks from *Koreanaornis* tracks at the Huangyangquan track site, for which the length:width ratios of each digit range from 3.3 to 4.0, significantly greater than the ratios of 2.2–3.0 of MGCM.H25 tracks. All currently described Mesozoic bird ichnotaxa are characterized by slender digits (Lockley and Harris, 2010); the stocky digit impressions of MGCM.H25a are therefore rather unprecedented. The length:width ratios of most unwebbed bird tracks are greater than those of MGCM.H25a. This supports placing the MGCM.H25 tracks in a new ichnotaxon.

Although only faintly discernible, *Moguiornipes* tracks have at least two proximodistally short digital pads on each digit. Among modern birds, feet that would be capable of registering *Moguiornipes* tracks are similar to those of some semi-aquatic birds that have lobed feet, such as grebes (Podicipediformes) and coots (*Fulica* spp.). The toes of lobed feet have stiff, scale-covered flaps that provide a surface analogous to webbing for better propulsion during foot-propelled swimming and diving. It is possible that the *Moguiornipes* track maker had either lobed feet or expanded digital pads for similar function and that would explain the great digit impression widths.

4.2. Shorebird tracks at the Huangyangquan track site

4.2.1. Comparisons to bird tracks from the Jindong Formation (Korea) and Dakota Formation (USA)

Mesozoic–Cenozoic shorebird tracks constitute a widespread "shorebird ichnofacies" (Lockley et al., 1994). The co-occurrence of *Koreanaornis dodsoni*, *Goseongornipes* isp., *Aquatilavipes* isp., and *Moguiornipes robusta* at the Huangyangquan track site denotes sympatry of a variety of shorebird-morph taxa, and expands the known distribution of the Koreanaornipodidae in the Early Cretaceous of Asia. The discovery of the Huangyangquan bird tracks greatly enriches the known faunal and ichnofaunal diversity of the Lower Layer of the Tugulu Group. The tracks are the first solid evidence of birds in the Tugulu Group; the only previous report of a possible avian (Young, 1964) was later recognized as pertaining to a dsungaripterid pterosaur (Buffetaut, 1996).

Although *Pullornipes* is a koreanaornipodid (Lockley et al., 2006b), the Huangyangquan specimens of *Koreanaornis* and *Goseongornipes* are the first reported instances of those ichnogenera in China. In morphology and size, *Koreanaornis dodsoni* and *Goseongornipes* isp. correspond with koreanaornipodid, ignotornid, and jindongornipodid tracks from South Korea (Kim et al., 2006). These types of tracks therefore span a substantial amount of time from the Early Cretaceous into the Late Cretaceous (Paik et al., 2007).

Aquatilavipes and *Koreanaornis* have been previously noted to coexist in the late Early Cretaceous (Barremian–Aptian). The presence of *Aquatilavipes* isp. at the Huangyangquan track site coincides with the known temporal range for the ichnotaxon. The avian ichnofauna from the Lower Layer of the Tugulu Group is comparable to that of the Lower to "mid" Cretaceous Dakota Formation of North America (Anfinson et al., 2009).

4.2.2. Paleoecology, track makers, and behavior

The strata at the Huangyangquan track site were deposited in shallow lake and lake shore environments (Gu et al., 2003). Abundant invertebrate traces accompany the bird tracks: small traces are dominated by *Cochlichnus* and *Helminthoidichnites*, whereas large traces pertain to as-yet undetermined ichnotaxa. *Cochlichnus* grazing traces were probably made by nematodes (Chamberlain, 1975; Buatois et al., 1997) while *Helminthoidichnites* fodichnia were made by either nematodes or larval insects (Buatois et al., 1997). The co-occurrence of bird and invertebrate traces at the Huangyangquan track site suggests that the assemblage was a feeding site and that the *Cochlichnus* and *Helminthoidichnites* trace makers were an abundant food source.

Modern shorebirds can be divided into visual and tactile foragers. Visual foraging is hindered by the presence of other individuals or species, so visual foragers, such as members of Charadriidae, tend to forage individually or in low densities (Kober, 2004). Tactile foraging is less hindered by the presence of other organisms, so tactile foragers, such as members of Scolopacidae, can forage in groups (Conklin and Colwell, 2008). Bird tracks at the Huangyangquan track site occur both isolated (e.g., *Koreanaornis zhoui*, *Aquatilavipes* isp.) and in groupings (e.g., *Goseongornipes* isp.). More broadly, isolated shorebird tracks are common, e.g., *Aquatilavipes swiboldae* (Currie, 1981) and *Aquatilavipes izumiensis* (Azuma et al., 2002). Shorebird tracks that occur in groups include *Pullornipes* (Lockley et al., 2006b), *Ignotornis yangi* (Kim et al., 2006), *Koreanaornis* cf. *hamanensis* (Anfinson et al., 2009), and *Ignotornis mcconnelli* (Lockley et al., 2009). Isolated tracks may suggest closer ecological (but not necessarily phylogenetic) affinities between the track makers and charadriids, whereas the grouped tracks may suggest closer ecological affinities between the track makers and extant scolopacids.

The Huangyangquan shorebird trackways exhibit noticeable trends with respect to ripple marks on the track-bearing surfaces. *Goseongornipes* isp. trackways (Fig. 5) run parallel to the ripple crests, a phenomenon also noted for *Koreanaornis* cf. *hamanensis* tracks (Anfinson et al., 2009). *Pullornipes* tracks also run subparallel to the trend of ripple crests (Lockley et al., 2006b). Grant (1984) indicated that the probe marks of *Limnodromus* were significantly more abundant on the crests than in the troughs of tidally formed sand ripples. This suggests ripple crests are tied to the foraging activities of shorebirds. Movement parallel or subparallel to the ripple crests in the fossil tracks at the Huangyuanquan site may therefore be tied to foraging activity.

Huangyangquan site *Koreanaornis dodsoni* tracks vary widely in size (3.2–6.8 cm), spanning a similar range of sizes as the entire *Koreanaornis*-*Goseongornipes*-*Jindongornipes* assemblage from the Jindong Formation of South Korea (2.5–7.5 cm; Lockley et al., 2006a). Yet large and small *K. dodsoni* specimens do not otherwise differ morphologically. This could mean that there were several tracks making species that had similar foot morphologies, or, alternatively, various age groups of the same track-making species. The modern dunlin (*Calidris alpina*) is known to feed in mixed-age groups that are typically dominated by adults (Serra et al., 1998), though groups dominated by juveniles have also been documented (Yosef and Meissner, 2006).

Moguiornipes tracks may be the products of a bird with lobed feet, which would be unique among known Mesozoic birds. If correct, the *Moguiornipes* track maker may have been more amphibious than aquatic, swimming actively in the Lower Layer shallow lake.

4.3. Non-avian Theropod tracks

4.3.1. Jialingpus

Jialingpus Zhen et al., 1983

Type ichnospecies: *Jialingpus yuechiensis* Zhen et al., 1983

Amended Diagnosis: Medium-size, tridactyl theropod tracks, manus and tail traces occasionally present, hallux rarely impressed (only appear in BNHM-SCFP 24), pad formula of 2-2–3–3-x; the length:width ratios is 1.86, divarication angles between digits II and IV range from 44° to 52°. Pad I of digit II is larger than the pads of digit IV, and almost as large as the metatarsophalangeal pad. The distance between the proximal ends of digits II and III to metatarsophalangeal region apparently larger than that between the proximal end of digit IV to metatarsophalangeal region.

cf. *Jialingpus* isp.

Material: Six complete natural casts on a single slab cataloged as MGCM.H1–4, 7, and 8, from the Huangyangquan track site (Fig. 9A–D, G–H; Appendix A).

Locality and horizon: Lower Layer of the Tugulu Group, Lower Cretaceous. Huangyangquan track site (46°4′25″N, 85°34′57″E), Huangyangquan Reservoir, Wuerhe District, Xinjiang Uyghur Autonomous Region, China.

Description: Medium size, tridactyl theropod tracks that lack manus and tail traces. All specimens are isolated; no trackways are identifiable. The length:width ratios of MGCM.H1, 2, 7, and 8 range from 1.76 to 2.29. Digit III is directed cranially, and digit IV is similar in length to digit II. The divarication angles between digits II and IV range from 36° to 56°. Track H7, which is the most complete and serves as an exemplar of the sample, has a pad formula of x-2–3–3-x. Pads 1–3 of digit III each taper from proximal to distal. A sub-ovoid metatarsophalangeal region lies nearly in line with the axis of digit III, close to the proximal end of digit IV.

Discussion: The ichnotaxon *Jialingpus yuechiensis* was based on several well-preserved tracks from the Upper Jurassic Penglaizhen Formation of Sichuan Province (Zhen et al., 1983, 1989; Yang and Yang, 1987) that are now reposited at the Beijing Natural History Museum, Chongqing Natural History Museum, and Institute of Vertebrate Paleontology and Paleoanthropology (IVPP, Chinese Academy of Sciences) in Beijing. Zhen et al. (1989) considered the tracks similar to the ornithischian ichnotaxon *Anomoepus*, but their narrow divarication angles led Lockley et al. (2003) to attribute them to a theropod.

In general morphology, *Jialingpus* tracks are of the *Grallator* morphotype. The length:width ratio of the type specimen (BNHM-SCFP 24) is 1.86; the divarication angles between digits II and IV range from 44° to 52°. Specimen BNHM-SCFP 24 is unique in possessing both a hallux impression, a larger and more elongate metatarsophalangeal pad, and a manus impression with 4–5 digits than the other specimens. The length:width ratios of the IVPP specimens (no catalog numbers, Temp 1) range from 1.73 to 1.75; all of the IVPP and BNHM specimens possess sub-ovoid metatarsophalangeal regions. In *Jialingpus*, digit II generally projects farther forward than digit IV, though not as far as digit III. *Jialingpus* tracks have a pad formula of 2–2–3–3–x. The distance between the proximal ends of digits II and III and the metatarsophalangeal region is apparently larger than that between the proximal end of digit IV to the metatarsophalangeal region.

The aforementioned proportions and morphological characteristics also occur in the Huangyangquan specimens. However, Huangyangquan specimens MGCM.H4 and H7, which have distinct digit pad impressions, possess less well-developed digit II impressions than the IVPP and BNHM specimens of *Jialingpus* (Fig. 9). Furthermore, pad I of digit II in other *Jialingpus* tracks is larger than the pads of digit IV, and almost as large as the metatarsophalangeal pad. Although pads I of digit II of MGCM.H4 and H7 are relatively large, the largest digit pads are pads I of digit III. The Huangyangquan specimens are therefore referred to only as cf. *Jialingpus* isp. (see Fig. 10).

Jialingpus has also been reported from the Late Jurassic of Poland (Gierliński et al., 2009). Gierliński (1994) treated *Jialingpus* as a junior synonym of *Grallator*, but subsequently (Gierliński et al., 2009) retained ichnotaxonomic distinction based on the V-shaped caudal end of the track and the position of the metatarsophalangeal pad caudal to digit III. However,

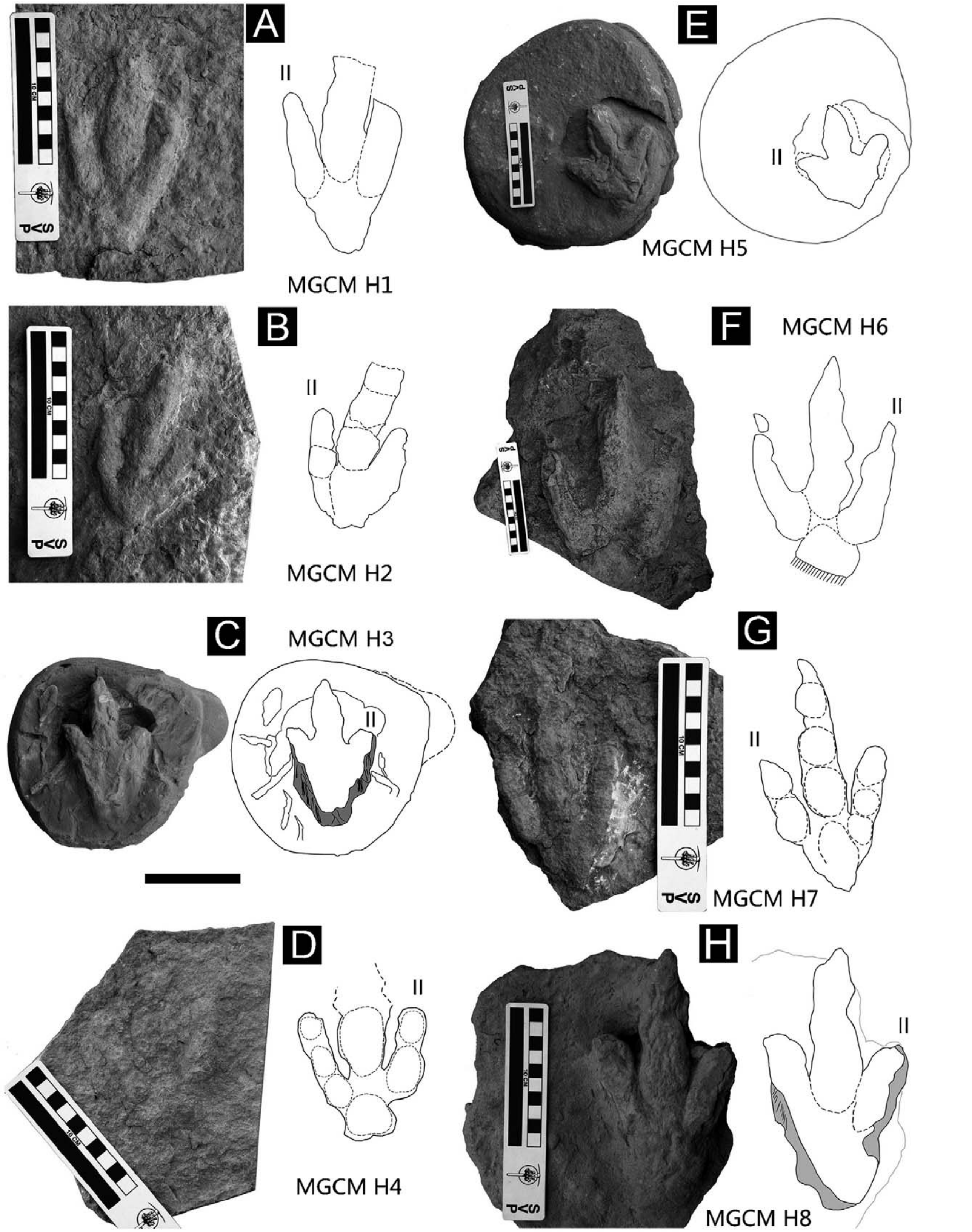

Fig. 9. Dinosaur footprints from the Huangyangquan track site. (A) MGCM H1; (B) MGCM H2; (C) MGCM H3; (D) MGCM H4; (E) MGCM H5; (F) MGCM H6; (G) MGCM H7; (H) MGCM H8. Scale bar = 10 cm.

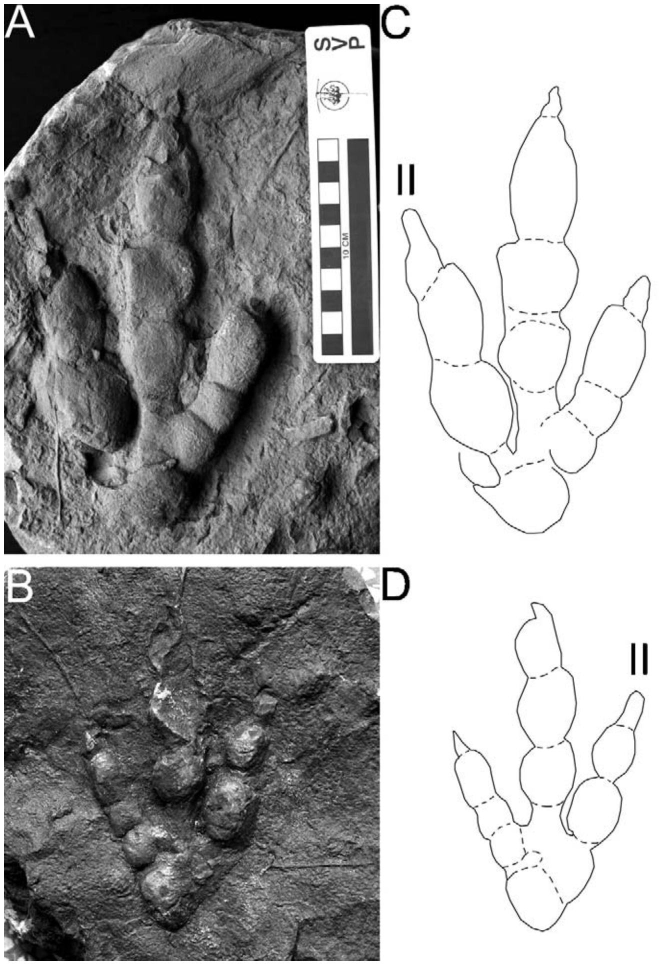

Fig. 10. *Jialingpus* IVPP specimens (no catalog numbers, Temp 1) from the Huanglong track site. (A) and (B) photographs; (C) and (D) outline drawings. All to the same scale 10 cm.

Gierliński et al. (2009) based their analysis on a poorly preserved footprint (BNHM-SCFP 21, Gierliński et al., 2009; Fig. 8A), in which the proximomedial region is faint. Furthermore, it is uncommon in *Jialingpus* that the metatarsophalangeal pad is V-shaped caudally. Therefore, whether or not the Polish tracks are truly attributable to *Jialingpus* isp. remains to be seen.Tracks MGCM.H3 and H8 (Fig. 9C and H) are the deepest theropod tracks at the Huangyangquan track site. The medial side of MGCM H8, from digit II to the metatarsophalangeal region, protrudes farther outward from the track midline more than the lateral sides of the tracks. This feature suggests that the center of gravity of the track maker leaned medially while the animal was moving; it may have been in the process of turning. Milàn et al. (2006) believe that different theropods adopted different walking strategies at the Late Triassic, Early Jurassic and Late Jurassic. Tracks MGCM.H3 and H8 show an outward deformation, the digits II and IV slope outward, which are close to the Late Jurassic type (Milàn et al., 2006).

4.3.2. *Asianopodus* isp.

Material: One complete natural cast, cataloged as MGCM.H6, from the Huangyangquan track site (Fig. 9F; Appendix A).

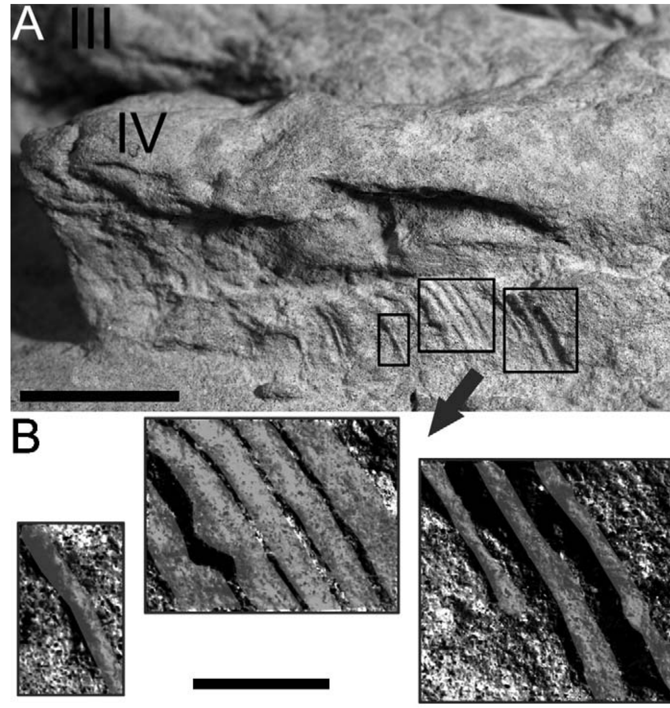

Fig. 11. Scale scratch lines along the side of MGCM H8. (A) scale bar = 2 cm; (B) scale bar = 5 mm.

Locality and horizon: Lower Layer of the Tugulu Group, Lower Cretaceous. Huangyangquan track site (46°4′25″N, 85°34′57″E), Huangyangquan Reservoir, Wuerhe District, Xinjiang Uyghur Autonomous Region, China.

Description: The length:width ratio is 1.61. Digit II is the shortest of the three digits; digit III is the longest. Digit IV is narrower than digits II and III. The divarication angle between digits II and IV is 41°. The divarication angle between digits II and III is nearly equal to that between digits III and IV. Despite the similarities in divarication angles, the distance between digits II and III is nearly twice of that between digits III and IV, but this characteristic may be a preservational artifact. The proximal ends of the digits are distinctly separate from the metatarsophalangeal region. The caudal end of the metatarsophalangeal pad is incomplete, but it appears to be ovoid.

Discussion: MGCM.H6 is similar to *Asianopodus* tracks based on the following characteristics: the distinct, bulbous heel impression, the length:width ratio (ranges from 1.43 to 1.54 for the ichnogenus), and divarication angles (from digits II to IV ranges from 42° to 59° for the ichnotaxon) (Matsukawa et al., 2005). However, the greater distance between digits II and III than between digits III and IV differs from *Asianopodus pulvinicalx*. The specimen is referred to *Asianopodus* isp.

The discovery of *Asianopodus* at the Huangyangquan track site increases the known range of *Asianopodus*, which was previously known from Japan (Matsukawa et al., 2005), Thailand (Lockley et al., 2006c), and, in China, Hebei Province (Matsukawa et al., 2005) and Inner Mongolia (Lockley et al., 2002); the latter is the closest locality, but still over 2000 km away. This suggests that *Asianopodus* may be a common component of Early Cretaceous Asian dinosaurian ichnofaunas.With a length of 30.4 cm, MGCM.H6 is the largest theropod track from the Huangyangquan track site. The smallest theropod track at the site, MGCM.H4 (Fig. 9C), which pertains to *Jialingpus*, measures only 12 cm. The sizes of theropod track makers represented at the site vary considerably. Assuming a foot/hip height ratio in the range of 4–4.9 for large theropods (Thulborn, 1990; Henderson, 2003), the average hip height:body length ratio of is 1:2.63 (Xing et al., 2009). Based on this mean, the body length of the *Asianopodus* track maker is estimated at 3.2–3.9 m.

4.3.3. *Kayentapus* isp.

Material: One complete natural cast, cataloged as MGCM.H5, from the Huangyangquan track site (Fig. 9E; Appendix A).

Locality and horizon: Lower Layer of the Tugulu Group, Lower Cretaceous. Huangyangquan track site (46°4′25“N, 85°34′57”E), Huangyangquan Reservoir, Wuerhe District, Xinjiang Uyghur Autonomous Region, China.

Description: The length:width ratio is 1.26. Digit II is the shortest of the three digits; digit III is the longest. Digit IV is narrower than digits II and III. The divarication angles between digits II and III and between digits III and IV are both 35°. The proximal ends of digits are not distinctly separated from the metatarsophalangeal region. The caudal end of the metatarsophalangeal region is V-shaped. The surface on which the track is located is covered with circular impressions interpreted as raindrop impressions.

Discussion: The lone *Kayentapus* track from the Huangyangquan track site has a wide divarication angle (70°) and lacks a large, round metatarsophalangeal pad, differentiating it from the *Jialingpus* and *Asianopodus* morphotypes. The divarication angles, as well as the length of the track (13.4 cm), accord with some characteristics of *Kayentapus* (Welles, 1971; Gierliński, 1996; Piubelli et al., 2005; Milner et al., 2009). However, the V-shaped distal end of the metatarsophalangeal region and the lack of other comparative specimens make it difficult to attribute MGCM.H5 to a particular ichnospecies with certainty, so the specimen is referred to merely as *Kayentapus* isp.Scale scratch lines on cf. *Jialingpus* isp. tracksSome cf. *Jialingpus* tracks, such as MGCM.H3 and MGCM.H8 (Fig. 9C and H), preserve scale scratch lines made when individual pedal scales dragged through the sediment as the tracks were registered (Fig. 11). The scale scratch lines of digits IV average 1.3 mm wide, and there are 6–7 lines per centimeter, and the directions conform to the fact that entry striations of the pads of digits II and IV mostly slid forward after contact (Gatesy, 2001). Scale scratch lines are also known from theropod tracks from the Lower Jurassic Moenave Formation, Utah (Milner et al., 2006) and the Upper Cretaceous St. Mary River Formation, Alberta (Nadon, 1993), North Horn Formation, Utah (Difley and Ekdale, 2002), and Nemegt Formation, Mongolia (Currie et al., 2003). Among the Mongolian tracks, MPD 100F/12 is 68.9 cm long, and has 5 to 6 scratch lines per centimeter (Currie et al., 2003).

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Appendix A. Measured data of the well-preserved Huangyangquan theropod and bird tracks

Number MGCM	Right/left	Maximum length (cm)	Maximum width* (cm)	Length of digit II (cm)	Length of digit III (cm)	Length of digit IV (cm)	Angle between digits II and III (°)	Angle between digits III and IV (°)	Angle between digits II and IV (°)	FL/FW	Measured by digit pad
H1	R	13.5	5.9	6.4	8.5	7.2	15	21	36	2.29	Y
H2	R	>11.4	5.5	3.8	>7.5	4.7	15	25	40	>2.07	N
H3	R	13.7	7.8	2.2	6.5	2.3?	30	26	56	1.76	N
H4	R	>12	7.2	5.8	8?	6.7	22	25	47	–	Y
H5	L	13.4	10.6	3	6.4	3.6	35	35	70	1.26	N
H6	R	30.4	18.9	17.8	23.7	18.9	20	21	41	1.61	Y
H7	L	14.9	7.2	5.5	10.1	6.1	23	21	44	2.07	Y
H8	R	18.4	9.3	6.9	11.8	6.9	18	24	42	1.98	N
H10a	L	4.2	6.3	1.3	3.6	3	48	54	102	0.67	Y
H10b	L	4	5.3	1.5	2.9	1.2	49	55	104	0.75	Y
H11a	R	3	3.7	2.2	2.7	2.5	36	36	72	0.81	Y
H111a	R	5.9	5.5	2.6	4.1	3.1	41	47	88	1.07	Y
H111b	L	5.2	5.2	3.1	4	3	48	40	88	1	Y
H111c	R	5.2	5.3	2.8	4	3.3	36	44	80	0.98	Y
H11c	L	3.4	3.2	1.7	2.6	2.5	32	26	58	1.06	Y
H11d	L	3.5	3.4	2.1	2.7	2.2	32	31	63	1.03	Y

Number MGCM	Right/left	Maximum length (cm)	Maximum width* (cm)	Length of digit II (cm)	Length of digit III (cm)	Length of digit IV (cm)	Angle between digits II and III (°)	Angle between digits III and IV (°)	Angle between digits II and IV (°)	FL/FW	Measured by digit pad
H11e	L	3.5	3.8	2	3.2	1.9	39	41	80	0.92	Y
H12	L	3.2	3.2	2.3	3	2.3	34	34	68	1	Y
H13a	R	4.4	5.6	2.4	3.5	2.8	45	70	115	0.79	Y
H13b	L	3.8	5.8	2.3	3.8	3.9	53	48	101	0.66	Y
H13c	R	4.3	6	3.1	3.2	2.9	52	57	109	0.72	Y
H13d	L	3.8	5.5	2.4	3.2	2.2	67	85	152	0.69	Y
H13e	R	3.8	4.8	2.4	2.7	2.3	63	59	122	0.79	Y
H14	L	4.4	5.7	2.3	3.7	2.4	40	51	91	0.77	Y
H15a	L	4.5	5	2.4	3.8	2.8	34	44	78	0.9	Y
H15b	L	4.7	3.8	1.9	3.2	2.2	30	32	62	1.24	Y
H15c	R	4.2	5.5	2.8	3.2	3.7	41	34	75	0.76	Y
H15d	R	5.1	4.9	3	4.5	3.9	45	46	91	1.04	Y
H15e	R	4.2	5.2	2.4	3.2	3.3	34	42	76	0.81	Y
H16a	L	6.3	5.5	2.3	4.9	2.9	38	38	76	1.15	N
H16b	L	4.8	5.5	2.9	4.1	3.1	43	50	93	0.87	Y
H16c	L	4.2	5.7	2.1	3.5	3.1	47	62	109	0.74	N
H16d	R	4.5	5.4	1.8	3.1	2.4	53	43	96	0.83	N
H17	R	4.5	5.4	2	4.2	2.6	51	50	101	0.83	Y
H18a	R	4.3	4.6	2.6	3.8	2.9	32	43	75	0.93	Y
H18b	L	3.4	4	2.2	2.7	2.1	53	51	104	0.85	Y
H19a	L	4.4	5.4	2.1	3.7	3	42	51	93	0.81	Y
H19b	L	4.9	5	2.1	4.1	3.2	36	39	75	0.98	Y
H19c	L	4.4	5	2.2	3.4	2	56	44	100	0.88	N
H19d	R	3.4	3.9	2.1	2.8	2.4	45	37	82	0.87	Y
H19e	R	4.5	4.8	2.3	3.9	2.5	57	46	103	0.94	Y
H20a	R	5.2	6.8	3	4.3	3.9	46	49	95	0.76	Y
H20b	R	5.4	5.6	2.2	4	2.8	57	47	104	0.96	Y
H20c	L	4.6	5.9	3.1	4.1	3.1	40	37	77	0.78	N
H20d	L	6.1	6	2.8	4.6	2.9	46	52	98	1.02	N
H20e	R	4.6	6.1	2.9	3.6	3.6	44	43	87	0.75	Y
H20f	R	5.5	6.5	3	4.8	3.6	45	55	100	0.85	N
H20g	R	5.1	6.4	2.8	4.2	3.8	43	46	89	0.8	Y
H20h	R	4.5	5.4	3	3.9	3.1	40	36	76	0.83	Y
H20i	L	5.6	5.4	2.8	4.1	1.9	50	55	105	1.04	N
H24a	R	4.3	4.6	1.7	3.2	1.7	53	67	120	0.93	N
H24b	L	2.8	3.7	1.6	2.1	1.4	50	65	115	0.76	N
H25a	L	4.5	5	2.5	3.3	3.3	48	42	90	0.9	Y
H25b	L	4.6	6	3.6	3.8	3.2	54	39	93	0.77	Y
H25c	R	4.9	–	3.4	4.3	–	50	–	–	–	Y
H25d	R	5.8	6.3	3.2	4.3	–	57	42	99	0.92	Y
H26b	R	4.5	4.7	2.3	3.5	2.5	40	45	85	0.96	N
H26c	R	4.3	4.7	2.1	3	1.9	44	53	97	0.91	N
H27a	R	4	–	–	3	2.6	–	50	–	–	Y

MGCM.H 1–8 are theropod tracks; others are bird tracks.
* Maximum width (distance between the tips of digits II and IV).

References

Academy of Prospecting and Developing, Xinjiang Bureau of Petroleum, 1977. Editorial Group of the Regional Stratigraphic Scale of Xinjiang Uygur Autonomous Region (internal publications). Vol. 1 (Altay and Junggar).

Academy of Prospecting and Developing, Xinjiang Bureau of Petroleum, 1996. Achievements in the Study on Cretaceous Biostratigraphy of the Junggar Basin, Xinjiang (internal publications).

Academy of Prospecting and Developing, Xinjiang Bureau of Petroleum, 1997. Annual Reports for 1996 (Exploration Volume) (internal publications).

Anfinson, O.A., Lockley, M.G., Kim, S.H., Kim, K.S., Kim, J.Y., 2009. First report of the small bird track *Koreanaornis* from the Cretaceous of North America: implications for avian ichnotaxonomy and paleoecology. Cretaceous Research 30, 885–894.

Azuma, Y., Tomida, Y., Currie, P.J., 2002. Early Cretaceous bird tracks from the Tetori Group, Fukui Prefecture, Japan. Memoir of the Fukui Prefectural Dinosaur Museum 1, 1–6.

Brinkman, D.B., Eberth, D.A., Ryan, M.J., Chen, P.J., 2001. The occurrence of Psittacosaurus xinjiangensis Sereno and Chow, 1988 in the Urho area, Junggar Basin, Xinjiang, People's Republic of China. In: Currie, P.J. (Ed.), The Sino-Canadian Dinosaur Project 3. Canadian Journal of Earth Sciences 38, 1781–1786.

Buatois, L.A., Jalfin, G., Acenolaza, F.G., 1997. Permian nonmarine invertebrate trace fossils from southern Patagonia, Argentina: ichnologic signatures of substrate consolidation and colonization sequences. Journal of Paleontology 71 (2), 324–336.

Buffetaut, E., 1996. The "ornithurine" from the Lower Cretaceous of Changji, Xinjiang (China), bird or pterosaur? Cretaceous Research 17, 505–508.

Chamberlain, C.K., 1975. Recent lebensspurren in nonmarine aquatic environments. In: Frey, R.W. (Ed.), The Study of Trace Fossils. Springer-Verlag, New York, pp. 431–458.

Conklin, J.R., Colwell, M.A., 2008. Individual associations in a wintering shorebird population: do Dunlin have friends? Journal of Field Ornithology 79 (1), 32–40.

Currie, P.J., 1981. Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of Northeastern British Columbia, Canada. Journal of Vertebrate Paleontology 1, 257–264.

Currie, P.J., Zhao, X.J., 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30, 2037–2081.

Currie, P.J., Badamgarav, D., Koppelhus, E.B., 2003. The first Late Cretaceous footprints from the Nemegt locality in the Gobi of Mongolia. Ichnos 10, 1–13.

Deng, S., et al., 2003. Jurassic System in the North of China (Vol.I) – Stratum Introduction. Petroleum Industry Press, pp. 85.

Difley, R.L., Ekdale, A.A., 2002. Footprints of Utah's last dinosaurs: track beds in the Upper Cretaceous (Maastrichtian) North Horn Formation of the Wasatch Plateau, central Utah. Palaios 17, 327–346.

Dong, Z.M., 1973. Dinosaurs from Wuerho. Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropolgy. Academia Sinica 11, 45–52.

Dong, Z.M., 1990. Stegosaurs of Asia. In: Carpenters, K., Currie, P.J. (Eds.), Dinosaur Systematics. Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 255–268.

Dong, Z.M., 2001. Mesozoic fossil vertebrates from the Junggar Basin and Turpan Basin, Xinjiang, China. In: Sun, G., Mosbrugger, V., Ashraf, A.R., Wang, Y. (Eds.), The Advanced Study of Prehistory Life and Geology of Junggar Basin, Xinjiang China. Proceedings of Sino-German Cooperation Symposium on the Prehistory and Geology of Junggar Basin, Xinjiang, Urumqi, pp. 95–103.

Gatesy, S.M., 2001. Skin impressions of Triassic theropods as records of foot movement. Bulletin of the Museum of Comparative Zoology 156 (1), 137–149.

Gierliński, G., 1994. Early Jurassic theropod tracks with the metatarsal impressions. Przegląd Geologiczny 42, 280–284.

Gierliński, G., 1996. Dinosaur ichnotaxa from the Lower Jurassic of Hungary. Geological Quarterly 40, 119–128.

Gierliński, G., Niedźwiedzki, G., Nowacki, P., 2009. Small theropod and ornithopod foot prints in the Late Jurassic of Poland. Acta Geologica Polonica 59 (2), 221–234.

Grant, J., 1984. Sediment microtopography and shorebird foraging. Marine Ecology Progress Series 19, 293–296.

Gu, Y.F., Ma, M.F., Su, S.L., Xu, H.M., Hu, B., Yao, W.J., 2003. Lithofacies paleogeography of the Cretaceous in the Junggar Basin. Petroleum Geology and Experiment 25 (4), 337–347.

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

Kim, B.K., 1969. A study of several sole marks in the Haman Formation. Journal of the Geological Society of Korea 5, 243–258.

Kim, J.Y., Kim, S.H., Kim, K.S., Lockley, M.G., 2006. The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation Changseon and Sinsu Islands): more evidence of high avian diversity in east Asia. Cretaceous Research 27, 56–69.

Kober, K., 2004. Foraging Ecology and Habitat Use of Wading Birds and Shorebirds in the Man-Grove Ecosystem of the Caeté Bay, Northeast Pará, Brazil. Dissertation Centre for Tropical Marine Ecology. University of Bremen, Bremen, Germany, 178 pp.

Lockley, M.G., Harris, J.D., 2010. On the trail of early birds: a review of the fossil footprint record of avian morphological and behavioral evolution. In: Ulrich, P.K., Willett, J.H. (Eds.), Trends in Ornithology Research. Nova Publishers, Hauppauge, pp. 1–63.

Lockley, M.G., Rainforth, E.C., 2002. The track record of Mesozoic birds and pterosaurs: an ichnological and paleoecological perspective. In: Chiappe, L.M., Witmer, L.M. (Eds.), Mesozoic Birds: Above the Heads of Dinosaurs. University of California Press, Berkeley, pp. 405–418.

Lockley, M.G., Yang, S.Y., Matsukawa, M., Fleming, F., Lim, S.K., 1992. The track record of Mesozoic birds: evidence and implications. Philosophical Transactions: Biological Sciences 336 (1277), 113–134.

Lockley, M.G., Hunt, A.P., Meyer, C., 1994. Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy. In: Donovan, S. (Ed.), The Paleobiology of Trace Fossils. John Wiley and Sons, Chichester, pp. 241–268.

Lockley, M.G., Wright, J., White, D., Matsukawa, M., Li, J.J., Feng, L., Li, H., 2002. The first sauropod trackways from China. Cretaceous Research 23, 363–381.

Lockley, M.G., Matsukawa, M., Li, J.J., 2003. Crouching theropods in taxonomic jungles: ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. In: Pemberton, S.G., McCrea, R.T., Lockley, M.G. (Eds.), William Antony Swithin Sarjeant (1935–2002): A Celebration of His Life and Ichnological Contributions Volume 1. Ichnos 10, 169–177.

Lockley, M.G., Houck, K., Yang, S.Y., Matsukawa, M., Lim, S.K., 2006a. Dinosaur-dominated footprint assemblages from the Cretaceous Jindong Formation, Hallyo Haesang National Park area, Goseong County, South Korea: evidence and implications. Cretaceous Research 27 (1), 70–101.

Lockley, M.G., Matsukawa, M., Ohira, H., Li, J., Wright, J.L., White, D., Chen, P., 2006b. Bird tracks from Liaoning Province, China: new insights into avian evolution during the Jurassic–Cretaceous transition. Cretaceous Research 27, 33–43.

Lockley, M.G., Matsukawa, M., Sato, Y., Polahan, M., Daorerk, V., 2006c. A distinctive new theropod dinosaur track from the Cretaceous of Thailand: implications for theropod track diversity. Cretaceous Research 27, 139–145.

Lockley, M.G., Kim, J.Y., Kim, K.S., Kim, S.H., Matsukawa, M., Li, R., Li, J., Yang, S.Y., 2008. *Minisauripus*—the track of a diminutive dinosaur from the Cretaceous of China and South Korea: implications for stratigraphic correlation and theropod foot morphodynamics. Cretaceous Research 29, 115–130.

Lockley, M.G., Chin, K., Houck, K., Matsukawa, M., Kukihara, R., 2009. New interpretations of Ignotornis, the first-reported Mesozoic avian footprints: implications for the paleoecology and behavior of an enigmatic Cretaceous bird. Cretaceous Research 30, 1041–1061.

Lucas, S.G., 2001. Chinese Fossil Vertebrates. Columbia University Press, New York, 375 pp.

Maisch, M., Matzke, A., Sun, G., 2003. A new sinemydid turtle (Reptilia: Testudines) from the Lower Cretaceous of the Junggar Basin (NW China). Neues Jahrbuch für Geologie und Paläontologie Monatshefte 12, 705–722.

Maisch, M.W., Matzke, A.T., Sun, G., 2004. A new dsungaripteroid pterosaur from the Lower Cretaceous of the southern Junggar Basin, north-west China. Cretaceous Research 25 (5), 625–634.

Matsukawa, M., Shibata, K., Kukihara, R., Koarai, K., Lockley, M.G., 2005. Review of Japanese dinosaur track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. Ichnos 12 (3), 201–222.

Matzke, A.T., Maisch, M.W., 2004. New information and specimens of *Wuguia hutubeiensis* (Reptilia: Testudines) from the Lower Cretaceous Tugulu Group of the southern Junggar Basin (NW China). Neues Jahrbuch für Geologie und Paläontologie Monatshefte 8, 473–495.

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

Milàn, J., Avanzini, M., Clemmensen, L.B., Garciá-Ramos, J.C., Piñuela, L., 2006. Theropod foot movement recorded from Late Triassic. Early Jurassic and Late Jurassic fossil footprints. New Mexico Museum of Natural History and Science Bulletin 37, 352–364.

Milner, A.R.C., Lockley, M.G., Kirkland, J.I., 2006. A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah. In: Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C., Kirkland, J.I. (Eds.), The Triassic–Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin 37, 315–328.

Milner, A.R.C., Harris, J.D., Lockley, M.G., Kirkland, J.I., Matthews, N.A., 2009. Bird-like anatomy, posture, and behavior revealed by an Early Jurassic theropod dinosaur resting trace. PLoS One 4 (3), e4591.

Nadon, G.C., 1993. The association of anastomosed fluvial deposits and dinosaur tracks, eggs, and nests: implications for the interpretation of floodplain environments and a possible survival strategy for ornithopods. Palaios 8, 31–44.

Paik, I.S., Huh, M., So, Y.H., Lee, J.E., Kim, H.J., 2007. Traces of evaporites in Upper Cretaceous lacustrine deposits of Korea: origin and paleoenvironmental implications. Journal of Asian Earth Sciences 30, 93–107.

Piubelli, D., Avanzini, M., Mietto, P., 2005. The Early Jurassic ichnogenus Kayentapus at Lavini di Marco ichnosite (NE Italy). Global distribution and palaeogeographic implications. Bollettino della Società Paleontologica Italiana 124, 259–267.

Qi, X.F., Cheng, X.S., Yang, J.L., 1995. Jiamuhe section of Wuerhe area. Academy of prospecting and developing. Xinjiang Bureau of Petroleum (internal publications).

Rabi, M., Joyce, W.G., Wings, O., 2010. A review of the Mesozoic turtles of the Junggar Basin (Xinjiang, Northwest China) and the paleobiogeography of Jurassic to Early Cretaceous Asian testudinates. In: Martin, T., Sun, G., Mosbrugger, V. (Eds.), Triassic–Jurassic Biodiversity, Ecosystems, and Climate in the Junggar Basin, Xinjiang, Northwest China. Palaeobiodiversity and Palaeoenvironments 90 (3), 259–273.

Rauhut, O.W.M., Xu, X., 2005. The small theropod dinosaurs *Tugulusaurus* and *Phaedrolosaurus* from the Early Cretaceous of Xinjiang, China. Journal of Vertebrate Paleontology 25 (1), 107–118.

Regional Survey Team of the Bureau of Geology of the Xinjiang Uygur Autonomous Region, 1980. Geological map L-45-XIV, scale 1:200 000. Ministry of Geology and Mineral Resources, Beijing.

Serra, L., Baccetti, N., Cherubini, G., Zenatello, M., 1998. Migration and moult of Dunlin *Calidris alpina* wintering in the central Mediterranean. Bird Study 45, 205–218.

Thulborn, T., 1990. Dinosaur Tracks. Chapman and Hall, New York, 410 pp.

Welles, S.P., 1971. Dinosaur footprints from the Kayenta Formation of northern Arizona. Plateau 44, 27–38.

Wings, O., Schellforn, R., Heinrich, M., Thuy, B., Wu, W.H., Sun, G., 2007. The first dinosaur track site from Xinjiang, NW China (Middle Jurassic Sanjianfang Formation. Turpan Basin)—a preliminary report. Global Geology 10 (2), 113–129.

Wings, O., Schwarz-Wings, D., Pfretzschner, H.U., Martin, T., 2010. Overview of Mesozoic crocodylomorphs from the Junggar Basin, Xinjiang, Northwest China and description of isolated crocodyliform teeth from the Late Jurassic Liuhuanggou locality. In: Martin, T., Sun, G., Mosbrugger, V. (Eds.), Triassic–Jurassic Biodiversity, Ecosystems, and Climate in the Junggar Basin, Xinjiang, Northwest China. Palaeobiodiversity and Palaeoenvironments 90 (3), 283–294.

Xing, L.D., Harris, J.D., Feng, X.Y., Zhang, Z.J., 2009. Theropod (Dinosauria: Saurischia) tracks from Lower Cretaceous Yixian Formation at Sihetun, Liaoning Province. China and possible track makers. Geological Bulletin of China 28 (6), 705–712.

Yang, X.L., Yang, D.H., 1987. The Dinosaur Footprints from Mesozoic of Sichuan Basin. Sichuan Scientific and Technological Publishing House, Chengdu, 110 pp.

Young, C.C., 1964. On a new Pterosaurian from Sinkiang. Vertebrate PalAsiatica 8, 221–225.

Yosef, R., Meissner, W., 2006. Seasonal age differences in weight and biometrics of migratory Dunlins (*Calidris alpina*) at Eilat, Israel. Ostrich 77 (1–2), 67–72.

Zhen, S.N., Li, J.J., Zhen, B.M., 1983. Dinosaur footprints of Yuechi, Sichuan. Memoirs of Beijing Natural History Museum 25, 1–19.

Zhen, S.N., Li, J.J., Rao, C.G., Mateer, N., Lockley, M.G., 1989. A review of dinosaur footprints in China. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaurs: Past and Present. Cambridge University Press, Cambridge, pp. 187–197.

Zhen, S.N., Li, J.J., Zhang, B.K., Chen, W., Zhu, S.L., 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan. Memoirs of Beijing Natural History Museum 54, 105–120.