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Dinosaur footprints from the Upper Cretaceous of Mongolia

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We report new data on 18 dinosaur footprint localities discovered in the Upper Cretaceous of the Gobi Desert of Mongolia, where we have recognized more than 20 000 footprints of dinosaurs. There are at least four types of dinosaur footprints, attributed to theropod, ornithopod, ankylosaurid and sauropod trackmakers. We have also recognized abundant footprints of unidentified trackmakers from each locality. Coexistence of footprints and many skeletal remains in the same and/or nearby beds is a remarkable feature of these Mongolian sites. Analyses of dinosaur footprints and associated body fossil remains for each locality reveal that even in the same beds, the ichnofauna differ from the fauna reconstructed on the basis of body fossils of dinosaurs. The results demonstrate that dinosaur faunal assemblages reconstructed from body fossil or footprint evidence solely should be considered very carefully.

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INTRODUCTION

Mongolia is one of the most important countries yielding abundant dinosaur remains. Expedition parties by American, Russian (and the former USSR), and Polish researchers in partnership with Mongolian researchers have discovered large numbers of dinosaur skeletons in the Gobi Desert. The first discovery of dinosaur footprints in Mongolia was made by Namnandorzhi (1957). In this paper he reported the occurrence of 14 tridactyl and 20 oval dinosaur footprints from the Lower Cretaceous sandstones at the bottom of Mt. Sayzhrakh, 250 km west of Ulaanbaatar. After Namnandorzhi (1957), several dinosaur footprints were reported from the Gobi Desert. Obata and Matsukawa (1996) and Matsukawa *et al*. (1997) reported dinosaur footprints which are 11 oval concave depressions from the Lower Cretaceous of Khuren Dukh, 260 km SSE of Ulaanbaatar. Loope *et al*. (1998) reported dinosaur footprints from the eolian sand deposit of the Ukhaa Tolgod locality (Upper Cretaceous). Currie *et al*. (2003) reported footprints of large ornithopods, theropods and sauropods at the Nemegt locality (Upper Cretaceous). Matsukawa *et al*. (2006) introduced the Khuren Dukh and Nemegt tracksites together with other Asian Cretaceous tracksites. Gierliński *et al*. (2008) reported a footprint of *Protoceratops* inside the field jacket collected from Flaming Cliffs in 1965 by the Polish-Mongolian joint expedition.

In 1995, the Hayashibara Museum of Natural Sciences — Mongolian Paleontological Center Joint Paleontological Expedition (HMNS-MPC Expedition) discovered abundant dinosaur footprints in the Upper Cretaceous of Shar Tsav, 275 km east of Dalanzadgad, South Gobi Aimag (Suzuki and Watabe, 2000*a*). A total of about 18 000 footprints were discovered at Shar Tsav. By the 2008 field season, the HMNS-MPC Expedition had discovered 18 new dinosaur tracksites and more than 20 000 dinosaur footprints from the Upper Cretaceous of Mongolia (Ishigaki, 1999; Suzuki and Watabe, 2000*b*; Watabe and Suzuki, 2000*a–c*; Watabe and Tsogtbaatar, 2004; Watabe *et al*., 2004; Ishigaki *et al*., 2004; Ishigaki *et al*., 2008).

Here we present an overview of these newly found footprint localities, describe the morphology of representative footprints and interpret the possible trackmakers. It is remarkable that in those Mongolian sites, both bone remains and footprints are rich. Sites with rich bone and track remains together are very rare in the world. Thus we present a preliminary result of comparison between ichnofauna and body fossil remains from the same bed and locality.

GEOLOGICAL SETTING

The Upper Cretaceous of Mongolia is subdivided into four "formations" ("svitas" is the Russian stratigraphic term): in ascending order, the Bayn Shire, Djadokhta, Barun Goyot, and the Nemegt formations (Gradziński *et al.*, 1968; Jerzykiewicz and Russell, 1991; Jerzykiewicz, 2000; Shuvalov, 2000). The Bayn Shire Formation is comprised of fluvio-lacustrine deposits (Jerzykiewicz and Russell, 1991; Jerzykiewicz, 2000). The Djadokhta Formation consists predominantly of eolian deposits with rare intercalations of fluvio-lacustrine deposits (Fastovsky *et al.*, 1997; Jerzykiewicz, 2000). The Barun Goyot Formation consists of eolian and fluvio-lacustrine (playa) deposits (Gradziński and Jerzykiewicz, 1974; Jerzykiewicz, 2000). The Nemegt Formation is composed of mainly fluvio-lacustrine deposits with minor eolian deposits (Gradziński, 1970; Jerzykiewicz and Russell, 1991; Ishii *et al.*, 1995; Jerzykiewicz, 2000). The age of each formation has been estimated from dinosaurian and invertebrate faunas, palaeomagnetic analysis and physical data of intercalated igneous rocks (Jerzykiewicz and Russell, 1991; Hicks *et al.*, 1999; Jerzykiewicz, 2000; Shuvalov, 2000). The Bayn Shire Formation age is estimated as being from Cenomanian to Santonian; the Djadokhta Formation as Santonian to Campanian; the Barun Goyot Formation as Santonian to Campanian; and the Nemegt Formation as Maastrichtian.

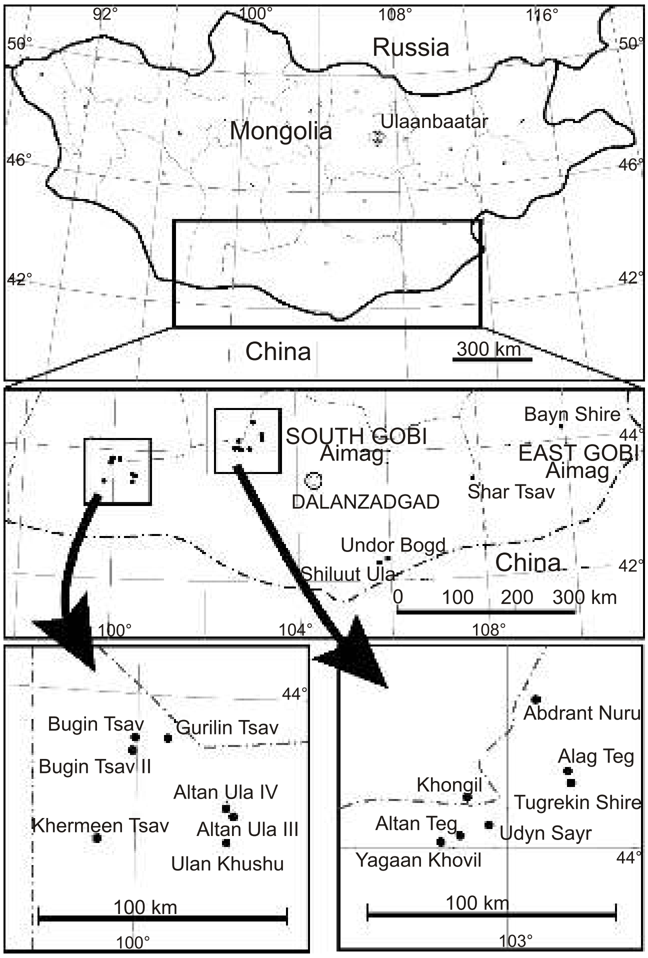


Fig. 1. Locality map of newly-discovered dinosaur tracksites from the Gobi Desert, Mongolia

LOCALITIES

In this paper we report 18 localities of dinosaur footprints. They are located in the Gobi Desert of Southern Mongolia (Fig. 1). These are as follows: Bayn Shire, Shar Tsav, Tugrekin Shire, Abdrant Nuru, Alag Teg, Udyn Sayr, Khongil, Altan Teg, Yagaan Khovil, Altan Ula III, Altan Ula IV, Ulan Khushu, Gurilin Tsav, Bugin Tsav, Bugin Tsav II, Khermeen Tsav, Shiluut Ula, and Undor Bogd. To relocate the geographical positions of these sites, we refer to Gradziński *et al.* (1968), Shuvalov and Chkhikvadze (1975), Sochava (1975) and Ivakhnenko and Kurzanov (1988). The names of the footprint-bearing formations at each locality are: the Bayn Shire Formation at Bayn Shire; the Djadokhta Formation at Abdrant Nuru, Alag Teg, Tugrekin Shire, Khongil and Udyn Sayr; the Barun Goyot Formation at Shiluut Ula; and the Nemegt Formation at Shar Tsav, Yagaan Khovil, Altan Ula III, Altan Ula IV, Ulan Khushu, Gurilin Tsav, Bugin Tsav, Bugin Tsav II and Khermeen Tsav (Shuvalov and Nikolaeva, 1985; Jerzykiewicz and Russel, 1991; Mikhailov *et al.*, 1994; Jerzykiewicz, 2000; Shuvalov, 2000). The stratigraphic positions of the footprint-bearing beds in Altan Teg and Undor Bogd are not fully known. Footprints are preserved in eolian deposits at Tugrekin Shire and are preserved in fluvio-lacustrine deposits at the other localities. The geographical information of each locality is shown in Table 1.

DINOSAUR FOOTPRINTS

More than 20 000 dinosaur footprints have been discovered. We have classified the dinosaur footprints found in these new localities into four groups, along with indeterminate forms: Type A, B, C, D and "indeterminate".

TYPE A

Localities: Abdrant Nuru, Alag Teg, in the Djadokhta Formation, and Shar Tsav, Yagaan Khovil, Bugin Tsav, Bugin Tsav II and Khermeen Tsav in the Nemegt Formation.

Characteristics: tridactyl or tetradactyl footprints with long, slender and separated digital impressions. Digit III impression is the longest. The width/length ratio of the footprints is less than 0.9 (Fig. 2A–K).

Table 1

Newly-discovered dinosaur tracksites from the Gobi Desert, Mongolia

Area in the Gobi Desert	Locality	Approximate coordinate of locality		Belonging formation of footprint bearing beds	Depositional environments	Quantity of footprints				
		Latitude	Longitude			Type A	Type B	Type C	Type D	Indeterminate
South-east	Bayn Shire	44°17’ N	109°55’ E	Baynshire	flu-lac	–	5	–	–	5
	Shar Tsav	43°34’ N	107°46’ E	Nemegt?	flu-lac	3 000	–	200	–	15 000
Central	Tugrekin Shire	44°14’ N	103°18’ E	Djadokhta	eolian	–	–	–	–	10
	Abdrant Nuru	44°32’ N	103°09’ E	Djadokhta?	flu-lac	120	2	150	–	100
	Alag Teg	44°15’ N	103°18’ E	Djadokhta	flu-lac	15	–	–	–	30
	Udyn Sayr	44°06’ N	102°55’ E	Djadokhta	flu-lac	–	–	–	–	10
	Khongil	44°11’ N	102°47’ E	Djadokhta?	flu-lac	–	3	12	–	20
	Altan Teg	44°03’ N	102°45’ E	?	flu-lac	–	–	–	–	5
	Yagaan Khovil	44°04’ N	102°40’ E	Nemegt?	flu-lac	5	20	–	10	20
West	Altan Ula III	43°36’ N	100°30’ E	Nemegt	flu-lac	–	–	–	–	5
	Altan Ula IV	43°36’ N	100°27’ E	Nemegt	flu-lac	–	–	–	–	10
	Ulan Khushu	43°29’ N	100°27’ E	Nemegt	flu-lac	–	–	–	–	10
	Gurilin Tsav	43°51’ N	100°08’ E	Nemegt	flu-lac	–	300	5	–	50
	Bugin Tsav	43°52’ N	100°01’ E	Nemegt	flu-lac	20	300	30	2	1 000
	Bugin Tsav II	43°49’ N	99°59’ E	Nemegt	flu-lac	10	10	5	–	10
	Khermeen Tsav	43°28’ N	99°50’ E	Nemegt	flu-lac	20	–	10	–	100
South	Undor Bogd	42°21’ N	105°59’ E	?	flu-lac	–	–	10	–	10
	Shiluut Ula	42°18’ N	105°44’ E	Barun Goyot?	flu-lac	–	–	–	–	100
					Total	3 190	640	422	12	16 495
								Grand total		20 759

Description: footprints with impressions of digits II, III and IV. Digit I impression is preserved in some deeply imprinted medium sized footprints (Figs. 2C and 3C). Digit II and IV impressions are similar to each other in length. Digit III impressions are the longest and straight. Pointed tips are printed at the distal end of each digital impression in well-preserved footprints. The width/length ratio of the footprints ranges from 0.6 to 0.9. In well-preserved footprints, impressions of digital pads counts 2 in the digit II, 3 in the digit III and 3–4 in the digit IV. Divarication angles of the digits II–IV vary from 40 to 70°. The values of the divarication angles of the digits II–III and III–IV are similar to each other. The length of footprints ranges from 6 to 70 cm (Fig. 2A–K). Elongated footprints with metatarsal impressions have been discovered in Shar Tsav and Abdrant Nuru (Fig. 2C). Trackway width is small, and the pace angulation ranges from 135 to 170° (Fig. 3A–F). The footprint axis is almost parallel or rotated slightly outwards (less than 10°) from the trackway midline. There is no tail dragging impression.

Ichnotaxonomy: there are footprints with *Asianopodus*-type (Matsukawa *et al.*, 2005) outline (Fig. 2E). However, the impression of the heel pad is not isolated from the digit IV impression. Thus we must be cautious before attributing them to *Asianopodus*. The small footprints with relatively long digit III (Fig. 2F–H and K) from Shar Tsav are *Grallator*-type (Lull, 1953), and medium to semi-large sized footprints (Fig. 2B) are morphologically *Eubrontes*-type (Lull, 1953). As *Eubrontes* and *Grallator* are established as Trias–Jurassic taxa, we use the name with “-type” for describing the outline morphology of the Type A footprint. The ichnotaxonomy of Type A tracks should be discussed precisely in the future study using the best preserved materials.

Trackmaker: morphology and trackway patterns of Type A footprints indicate that their trackmakers are variously-sized theropod dinosaurs. The precise taxonomic positions of the trackmakers are unknown. However, there are two examples that suggest identical relationships between footprints and body fossils.

One example is a group of small footprints with “tear-drop shaped outlines” from the Shar Tsav locality and the skeletal remains of a small theropod, *Avimimus*. From the largest exposure of the footprint-bearing bedding plane in Shar Tsav, abundant small footprints (10–12 cm in length) with “tear-drop shaped outlines” have been discovered (Fig. 2G and K). Digit III impression is very long. The divarication angle between digits II and IV is small (40°). Digit II and IV impressions are almost the same length. The overall outline of the footprint is symmetrical. The skeletal remains of *Avimimus* were discovered in the stratigraphic zone just below the main footprint-bearing layers of Shar Tsav. (Kurzanov, 1981, 1987; Watabe and Suzuki, 2000*a*; Watabe *et al*., 2004). The morphological characteristics of these small footprints such as the very long digit III impression and the symmetrical morphology are concordant with the pes mor-

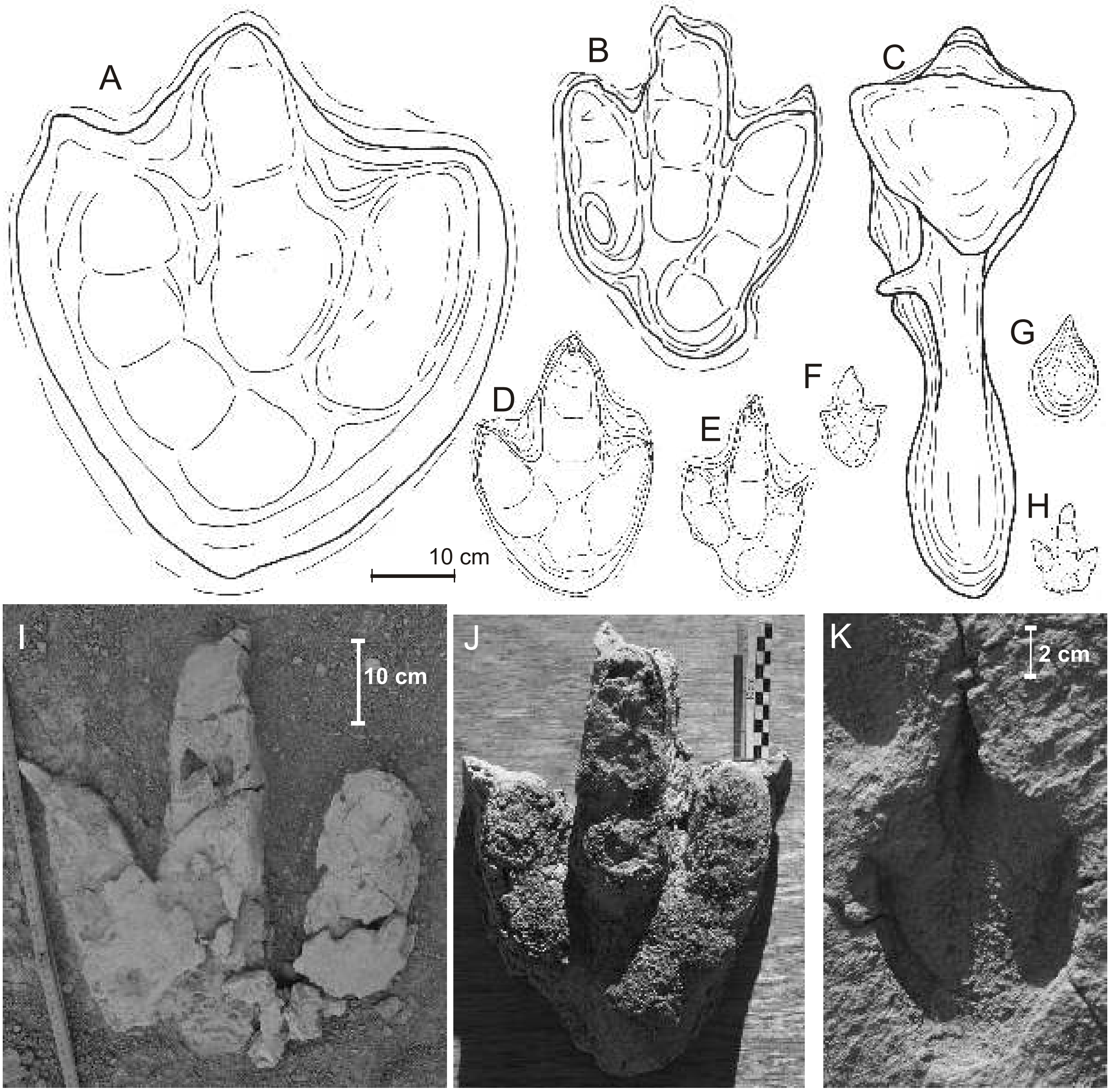


Fig. 2. Drawings and photos of Type A footprints

A, **B**, **D**, **E**, **F**, **G**, **H**, **K** — concave molds from Shar Tsav (B is the 2nd footprint in Figure 3A, D belongs to one of the parallel trackways in Figure 3F, F is the 5th footprint in Figure 3E); **C** — sole view of elongated natural cast with digit I impression from Abdrant Nuru; **I** — top surface view of very large natural cast from Bugin Tsav; **J** — sole view of very well-preserved natural cast from Shar Tsav; scale is 10 cm

phology of *Avimimus*. These data suggest that these small footprints are attributable to *Avimimus*.

Another example is *Tarbosaurus* and the large natural casts of footprints around 55 cm in length found at Bugin Tsav and Bugin Tsav II. The impressions of each digit of the footprints are well separated showing clear claw marks (Fig. 2I). These footprints were found in the stratigraphic zone that yields many skeletal and isolated body remains of *Tarbosaurus* (Maleev, 1955; Kramarenko, 1974). Among the theropods described from the Nemegt Formation of the Gobi Desert, especially of Bugin Tsav, *Tarbosaurus* is the only candidate to be a trackmaker of the large footprints. The characteristics of the large footprints are concordant with the pes morphology of *Tarbosaurus*. These data suggest that the footprints were left by individuals of *Tarbosaurus*.

TYPE B

Localities: Bayn Shire in the Bayn Shire Formation, Abdrant Nuru and Khongil in the Djadokhta Formation, and Yagaan Khovil, Gurilin Tsav, Bugin Tsav and Bugin Tsav II in the Nemegt Formation.

Characteristics: tridactyl footprints with three broad digital impressions. The digit III impression is the longest. The

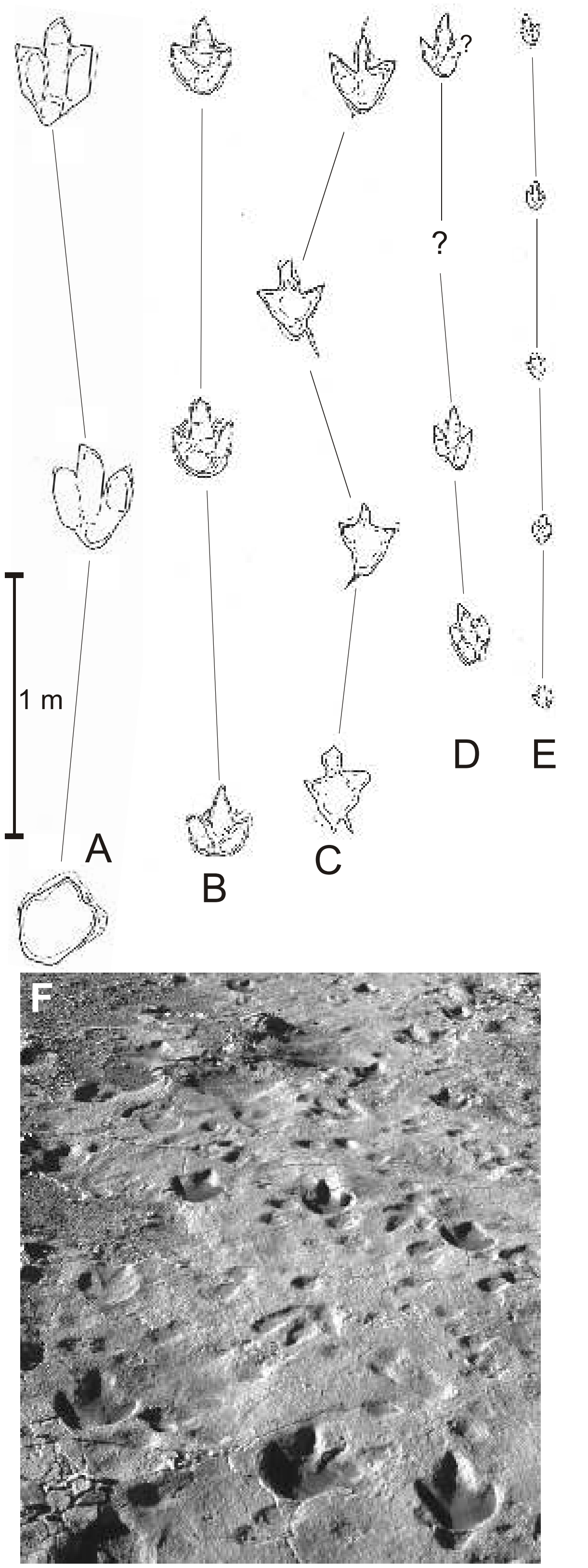


Fig. 3. Drawings and photo of Type A trackways

A, **B**, **D**, **E** — trackways from Shar Tsav; **C** — trackway with digit I impression from Abdrant Nuru; **F** — photo of parallel trackways from Shar Tsav, footprint length: 28 cm, stride length: 285 cm, B is a drawing of the part of one trackway in this photo

footprint is almost symmetrical. The width/length ratio of the footprints is equal to or slightly larger than 1.0.

Description: footprints with digit II–IV impressions. Impressions of each digit are broad. The distal end of the digital impressions show rounded outlines. There are no pointed tips. Digit II and IV impressions are similar in length. Digit III impression is the longest. Inside the digital impressions, there are no traces of digital pads. The footprint width is equal to or slightly larger than the length. Footprint length varies from 25–115 cm (Fig. 4A–G), averaging 65 cm. The divarication angle between digits II–IV varies from 40 to 90°, mostly around 50–60°. The values of divarication angles between digits II–III and III–IV are similar. The overall outlines of the footprints of Type B are almost symmetrical. All of the findings are natural casts of sandstone, or massive hard sandstone layers (underprints) under the true prints. An exceptionally large specimen, 115 cm in both width and length, was discovered in the Nemegt Formation at Gurilin Tsav (Fig. 4A).

A footprint axis of this type is rotated slightly inward (around 10°) from the trackway midline. The trackway width is small, and the pace angulation ranges mostly from 155–170° (Fig. 5A–D). No manus prints are observed. There is no tail dragging impression.

Ichnotaxonomy: most of the footprints of Type B in this paper (Figs. 4 and 5) are provisionally assigned to the *Amblydactylus*-type (e.g., Sternberg, 1932; Currie and Sarjeant, 1979) which is typically known from North America. There are some footprints with *Caririchnium*-type characteristics such as bilobate heels (Figs. 4D and 5B). However, there are no traces of the manus at all.

Trackmaker: footprint morphology and trackway patterns suggest that all Type B footprints are attributable to various-sized ornithopod dinosaurs. Precise taxonomic positions of the trackmakers are unknown. However, there is one example that suggests identical relationships between footprints and body fossils. At Bugin Tsav, Bugin Tsav II and Gurilin Tsav, Type B footprints exceeding 50 cm in length are abundant. In those localities, abundant skeletal remains of *Saurolophus* have been unearthed from the same or nearby stratigraphic horizons of footprints (Rozhdestvenskii, 1952, 1957; Maryańska and Osmólska, 1984; Norman and Sues, 2000; Suzuki and Watabe, 2000*a*, *b*; Watabe and Suzuki, 2000*c*). The characteristics of those large footprints are concordant with the pes morphology of *Saurolophus* (Rozhdestvenskii, 1952, 1957). This evidence suggests that these footprints are attributable to *Saurolophus.* Currie *et al*. (2003) also reported natural casts of large ornithopod footprints from the Nemegt locality. They also attributed these types of footprints to *Saurolophus.*

The largest footprint of this category is 115 cm in length and width (Fig. 4A). It was discovered at Gurilin Tsav. The specimen is a natural cast. It is isolated and does not form a trackway. The value of the divarication angle between digits II and IV (90°) is very large among this type. We consider that the trackmaker of this large print might have spread its digits widely when stepping on to the muddy substrate. This behaviour might have caused the exaggeration of footprint size and

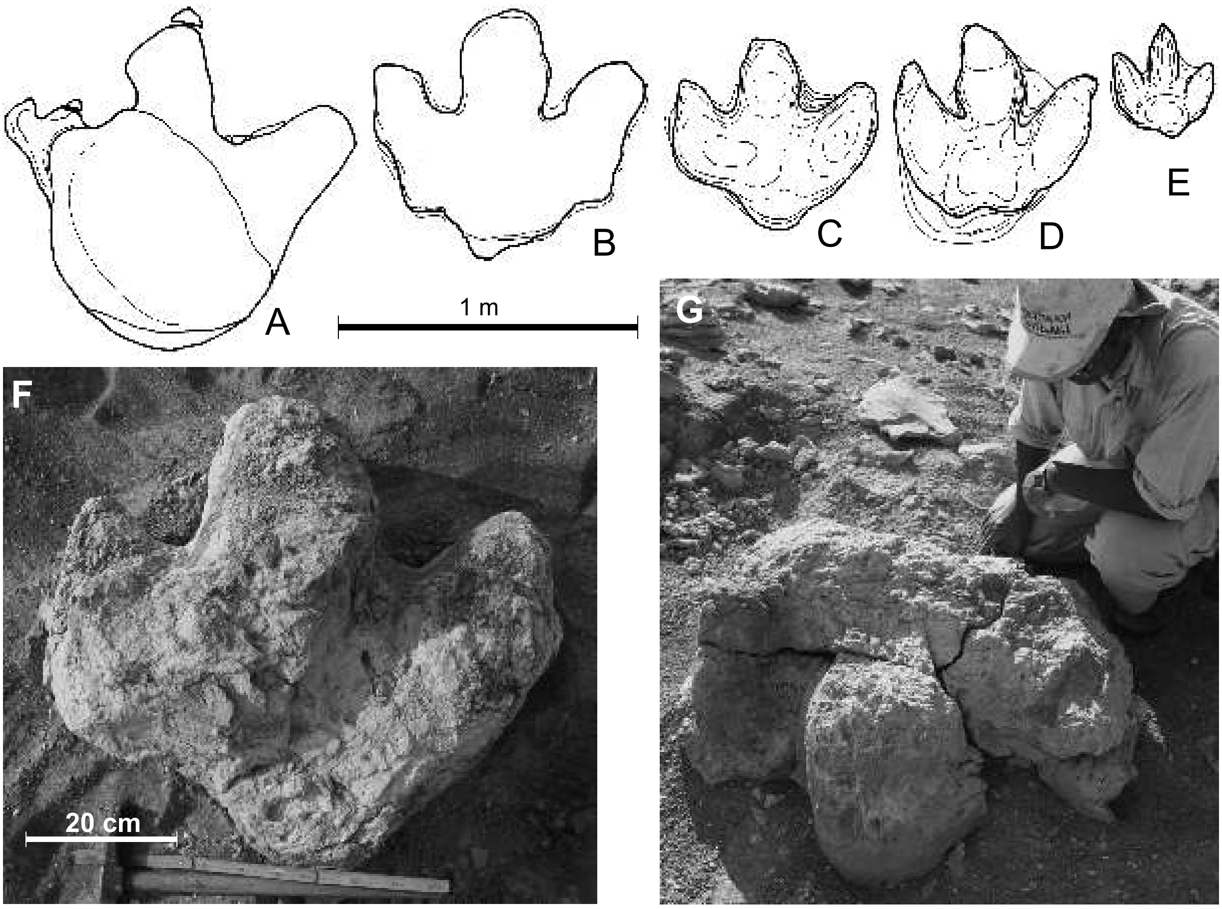


Fig. 4. Drawings and photos of Type B footprints from Bugin Tsav (B–G) and Gurilin Tsav (A) (all natural casts)

A, **B** — drawings of top surface view of natural casts; **C**–**E** — drawings of sole view of natural cast; **F**, **G** — photos of sole view of natural cast

the large divarication angle. The mean length and width of this large footprint is estimated to be about 90 cm, which is the maximum size among the footprints from Bugin Tsav, Bugin Tsav II and Gurilin Tsav belonging to this type.

TYPE C

Localities: Abdrant Nuru in the Djadokhta Formation, Shar Tsav and Bugin Tsav in the Nemegt Formation.

Characteristics: oval or round footprints of a quadrupedal animal. Wide gauge trackway. Small pace angulation around 83°.

Description: oval or round footprints with footprint length ranging from 30 to 90 cm. In the case of oval footprints, the long axis of the footprints is almost parallel to the trackway midline (Fig. 6A). All of the findings are natural casts or platy hard sandstone blocks with underprints formed in the underlying beds beneath the true prints. Strongly weathered trackways appear as a chain of damaged stepping stones (Fig. 6B and C). Three blunt impressions can be observed in the anterior part of better preserved materials (Fig. 6C and E) and they are considered as traces of digits. No manus prints were preserved among the investigated trackways belonging to Type C. But one isolated footprint was found at Abdrant Nuru. It is a half-moon-shaped natural cast with five blunt digital impressions. Its width is 47 cm and the length is 32 cm (Fig. 6D).

Almost all of the footprints form trackways. 26 trackways were observed and 15 trackways have been mapped. Values of the pace angulation of the trackways range from 71 to 94°. The average value of pace angulation of all trackways is 83°. The trackway is wide (Fig. 6A–C). Some of the trackways are in the category of “wide gauge” (Farlow, 1992; Wilson and Carrano, 1999). The value of trackway ratio (T/R) of those trackways ranges from 33 to 45%. This calculation of trackway ratio is based on the formula by Romano *et al*. (2007). There is no tail-dragging impression.

Ichnotaxonomy: most of the footprints belonging to Type C are poorly preserved and difficult to discuss taxonomically. Only one well-preserved large manus footprint is provisionally assigned to *Tetrapodosaurus* (Sternberg, 1932) (Fig. 6D). *Tetrapodosaurus*-type footprints have been reported from the Lower Cretaceous of Japan (Fujita *et al*., 2003), but have not been reported from China or Korea (McCrea *et al*., 2001; Matsukawa *et al*., 2006). So this is the first discovery report of this type from Continental Asia.

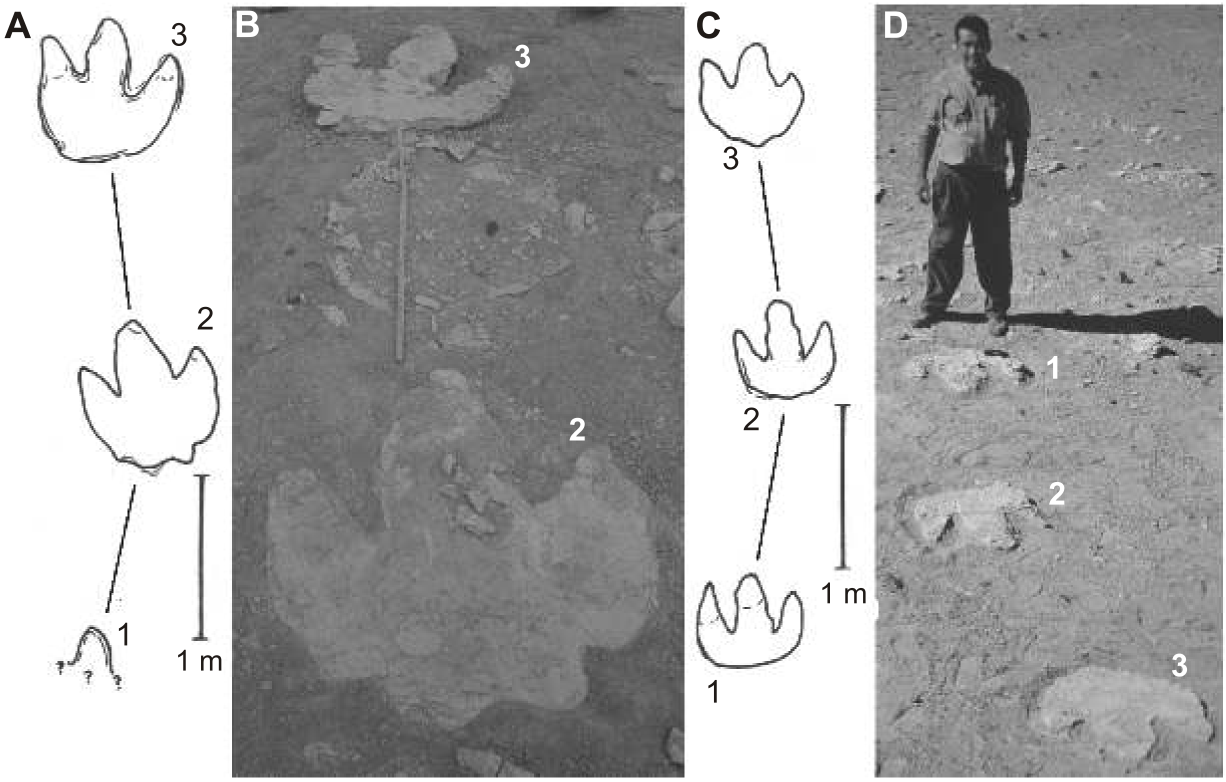


Fig. 5. Drawings and photos of Type B trackways from Bugin Tsav (all natural casts)

A, **B** — drawing and photo of the same trackway of large individual;
C, **D** — drawing and photo of the same trackway of a middle-sized individual

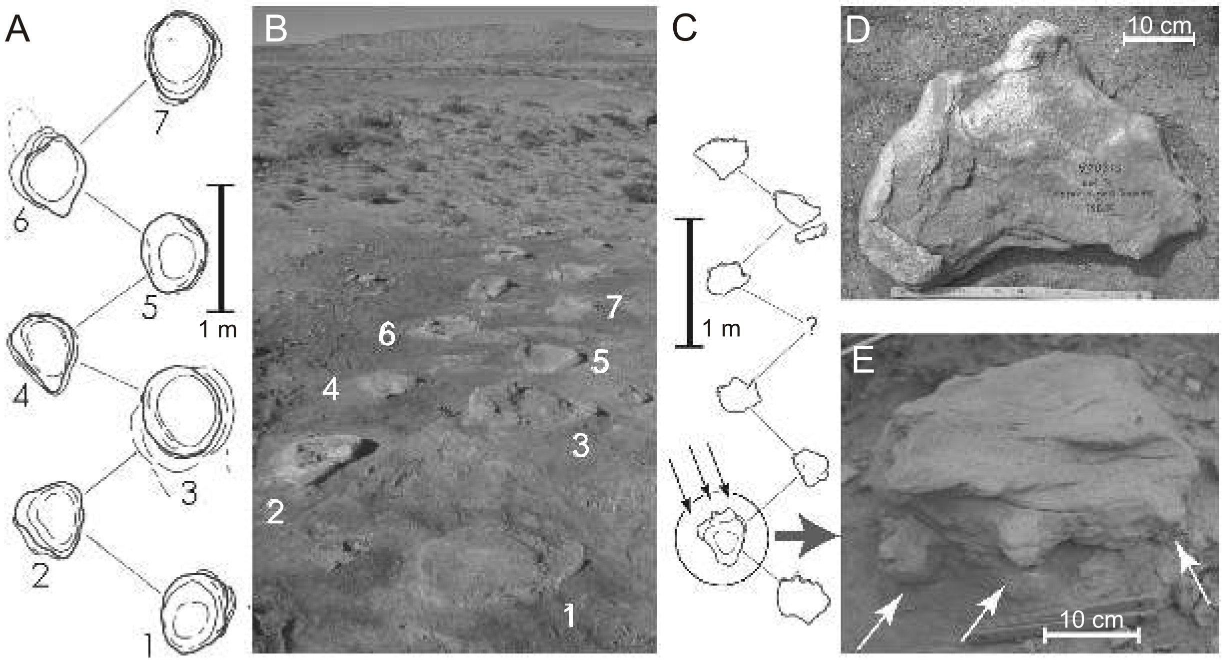


Fig. 6. Drawings and photos of Type C trackways and footprints from Abdrant Nuru (all natural casts)

A, **B** — drawing and photo of the same trackway; **C** — drawing of small trackway (strongly weathered); arrows indicate three blunt digit marks; **D** — photo of isolated natural cast of manus print; **E** — photograph of anterior part of a pes print from trackway C; arrows indicate three blunt digit marks

Trackmaker: the main characteristics of the Type C trackways are the wide gauge and small pace angulation. There were no bipedal animals that imprinted such large (30–90 cm in length) footprints with such wide gauge trackways in the Upper Cretaceous of Mongolia. Therefore the trackmakers of Type C trackways are quadrupedal animals. The lack of manus prints in these trackways may have been caused by the overlapping of posterior footprints on the anterior ones, as the low pace angulation values suggest. The quadrupedal dinosaur body remains from the Upper Cretaceous of the Gobi Desert are sauropod, ankylosaurid and ceratopsid. The pace angulation of sauropod trackways generally ranges from 100 to 140° (e.g., Thulborn, 1990; Lockley, 1991; Lockley and Hunt, 1995; Lockley and Meyer 2000; Romano *et al*., 2007). The pace angulation of Type C is around 83° which is significantly less than in sauropod trackways. Therefore, there is less probability that sauropod dinosaurs were the trackmakers of Type C footprints.

The wide gauge, small trackway ratio and small pace angulation of Type C trackways suggests that the trackmakers had dorsoventrally flattened body shapes. Animals with short limbs and a large distance between left and right limbs could have left the Type C trackways. The animals of this kind of body morphology might have been large individuals of the Ankylosauria or Neoceratopsia. However, body fossils of the latter animals have not been reported from Mongolia. Therefore the most likely trackmakers of the Type C footprints are ankylosaurid dinosaurs.

Leonardi (1984) reported a trackway with similar characteristics of Type C from the Upper Cretaceous in Toro Toro, Bolivia, South America. Leonardi (1984) and McCrea *et al.* (2001) attributed them to an ankylosaurid dinosaur. McCrea *et al.* (2001) reported other trackways that have similar characteristics to Type C from the Upper Cretaceous of Bolivia, Canada and the USA, attributing them to ankylosaurid dinosaurs.

There are two other pieces of evidence that support this attribution of Type C footprints. The existence of three blunt impressions of digit tips in some better preserved natural casts (Fig. 6C and E) and morphological characteristics of a natural cast of manus (Fig. 6D) are important evidence. Three or four blunt digit tips on a pes impression are typical characteristics of previously discovered ankylosaurid hind footprints (McCrea *et al.*, 2001). Half moon-shaped large manus impressions with five blunt digit marks are also identified as ankylosaurid.

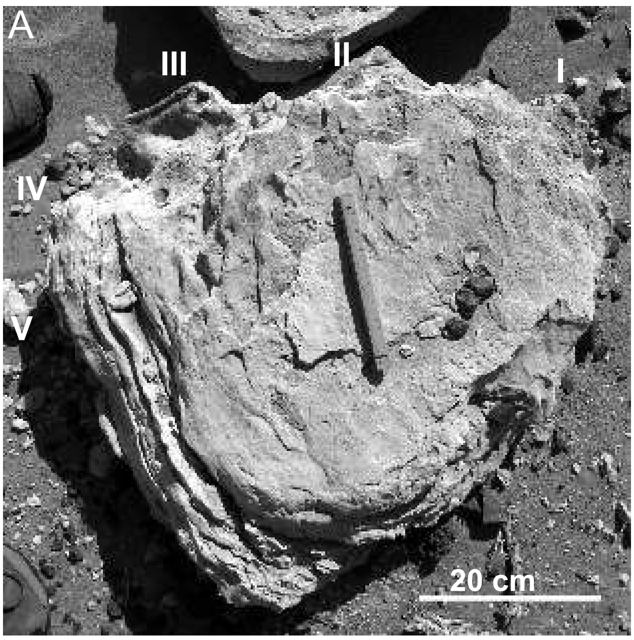
Further evidence is the coexistence of skeletal remains of ankylosaurids and Type C footprints in a single bed. In the Djadokhta Formation at Abdrant Nuru, one large skeleton and many disarticulated bones of ankylosaurids (*Pinacosaurus* and other forms) were discovered from the same stratigraphic layers that yielded rich footprints of Type C (Watabe and Suzuki, 2000*b*). These data suggest that the footprints are attributable to ankylosaurid dinosaurs.

TYPE D

Localities: Yagaan Khovil and Bugin Tsav in the Nemegt Formation.

Characteristics: large, oval to semi-triangular outline, four to five impressions of pes digits in the anterior rim of the footprints.

Description: several large, thick and massive natural casts of hard sandstone were discovered at Yagaan Khovil. The outline of these footprints is semi-triangular (one angle is at the posteriormost point of the footprint). Footprint length and width are almost the same. One well-preserved natural cast is 65 cm in length, 63 cm in width and 25 cm in thickness (Fig. 7A and B). Very clear slipping traces of the claws of digits I, II and III, and more ambiguous slipping traces of digits IV and V are imprinted. They are preserved at the lateral surface of the anterior part of the natural cast. The traces left by the slipping motion measure about 20 cm in length. The slipping traces are not vertical to the bedding plane (top surface of the natural cast) but are inclined laterally outwards (Fig. 7B).



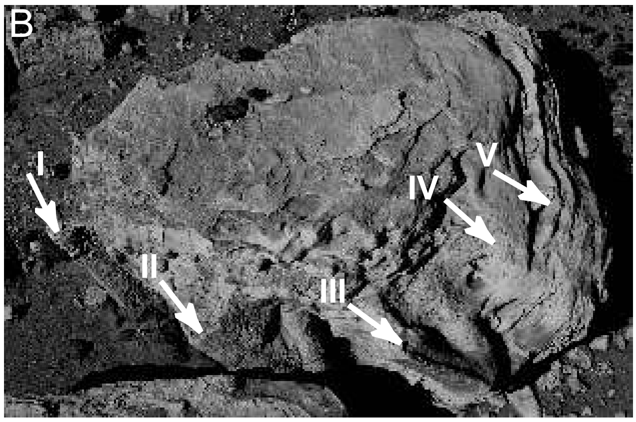


Fig. 7. Photos of Type D footprint (natural cast) from Yagaan Khovil

A — top surface view of natural cast; **B** — slipping traces of claws on the same specimen (lateral view from front-left direction)

Two large platy natural casts were discovered at Bugin Tsav. Their anteroposterior length is larger than their width. Their overall shape is oval. The length of the longest axis of the footprints is 75–85 cm. They are slab-like sandstone plates. Claw impressions are observed at the anterior part of the footprints.

These footprints from Yagaan Khovil and Bugin Tsav are all isolated, not forming a trackway. Manus prints are not preserved. There are no tail-dragging impressions.

Ichnotaxonomy: the Type D pes prints from Yagaan Khovil are morphologically of *Brontopodus*-type (Fig. 7A). In Central Asia, *Brontopodus*-type footprints have been reported from the Lower and Upper Cretaceous beds of China (Lockley *et al.*, 2002; Li *et al*., 2006). They are also reported from the Cretaceous of Korea (e.g., Lockley *et al*., 2006; Lee and Lee, 2006). As the materials in this paper are isolated natural casts of pes prints, there is no manus print information or trackway data. To compare Type D footprints with material from other areas of the world, it is desirable to find well-preserved complete manus-pes trackways.

Trackmaker: the main characteristics of the Type D footprints are their large size, oval to semi-triangular outlines and clear impressions of claws and digits counting 4 or 5 in the anterior part of the footprints. The size and overall morphology of the footprints of Type D from Bugin Tsav and Yagaan Khovil are attributable to the pes of sauropods. The fossiliferous beds of Bugin Tsav and Yagaan Khovil are correlated with the Nemegt Formation. The sauropod taxa *Nemegtosaurus* and *Opisthocoelicaudia* were discovered in the Nemegt Formation of the Nemegt Basin (Nowiński, 1971; Borsuk-Białynicka, 1977). Footprint-bearing beds of the Nemegt Formation in Bugin Tsav and Yagaan Khovil yield disarticulated bones and teeth of a sauropod. From the Nemegt locality, Currie *et al*. (2003) reported natural casts with similar characteristics of Type D and also attributed them to sauropods. Those data support the attribution of Type D footprints to sauropod dinosaurs.

All of the findings of Type D are, at present, isolated natural casts, and their trackways have not yet been recognized in the field. Further discovery of their trackways and manus footprints are very important for the reconstruction of limb anatomy, locomotion and behaviour.

INDETERMINATE FOOTPRINTS

Localities: indeterminate footprints occur in all four named formations at Bayn Shire, Shar Tsav, Tugrekin Shire, Abdrant Nuru, Alag Teg, Udyn Sayr, Khongil, Altan Teg, Yagaan Khovil, Altan Ula III, Altan Ula IV, Ulan Khushu, Gurilin Tsav, Bugin Tsav, Bugin Tsav II, Khermeen Tsav, Shiluut Ula and Undor Bogd.

Characteristics: poorly preserved materials with no identical characteristics of the Types A–D.

Description and comments: a large amount of poorly preserved material that is unassignable to types A–D exist at all 18 of these newly-found localities. At the localities except Tugrekin Shire, they are preserved as natural casts and as hard sandstone underprints. Based on sedimentological and ichnological data, it is possible to identify them as "footprints". They are abundant in Shar Tsav and Bugin Tsav where they total more than 16 000 (Table 1). At Tugrekin Shire, the footprints are found in fine-grained sorted eolian sandstone beds, which are soft, loose, inclined foreset beds. Due to the special character of substrates, the footprints are ambiguous and cannot be categorized into the Types A–D.

DISCUSSION AND CONCLUSION

At the well-known dinosaur body fossil-rich localities in the world, it is common that there are few or no dinosaur tracks. It is also common that the best known dinosaur ichnosites yield few or no body fossils. By contrast, the newly found tracksites described in this paper have been well-known as dinosaur body fossil sites. Frequent coexistence of footprints and skeletal remains in the same and/or nearby beds is a remarkable feature of these Mongolian sites. That makes possible the detailed comparative analyses of footprints and body fossil remains. Identical relationships between body fossils and footprints are observed in the cases of *Tarbosaurus*, *Avimimus* and *Saurolophus.*

We first anticipated that the fauna based on body fossils and the fauna based on footprints (ichnofauna) from a single locality might be similar in their taxonomic compositions and also in the frequency ratio of occurrence in each taxon. However, the data reveal that the inferred dinosaur faunal assemblages based on footprints are different from those based on the body fossil remains, even in the same stratigraphic zone at the same locality.

For example, in the footprint-bearing beds of the Nemegt Formation at Bugin Tsav and Gurilin Tsav, Type A (theropod) footprints are rare while Type B (ornithopod) are abundant (Table 1). By contrast, many theropod body fossils have been unearthed there, together with ornithopod body fossils in the same layer as contain the footprints at these sites (Chudinov, 1966; Suzuki and Watabe, 2000*a*). Although there is no precise numerical data regarding the exposed body fossil remains, theropod fossils are more abundant and frequently observed than ornithopod fossils in the field.

At the Shar Tsav locality, where the footprint-bearing beds might be correlated with the Nemegt Formation, the majority of the footprints discovered are Type A (theropod) of various sizes (Table 1 and Fig. 1). There are some Type C (ankylosaurid) footprints, but no Type B (ornithopod) nor Type D (sauropod) footprints. However, no body fossil remains of medium to large sized theropods or ankylosaurids have been recovered from this site. Only small theropods and sauropod body fossil remains have been discovered (Kurzanov and Bannikov, 1983; Watabe and Suzuki, 2000*a*).

At the Abdrant Nuru locality, both body remains of ankylosaurids and Type C (ankylosaurid) footprints are abundant. This association seems to be reasonable. However, body fossils of theropods are very rare compared to the frequent discovery of Type A (theropod) footprints at the same site.

These preliminary observations indicate that, even in the same bed and site, the dinosaur faunal assemblage based on footprints differs from that on body fossil remains. Currie *et al.*

(2003) reported a similar example from the Nemegt locality. Based on their observations at Nemegt, they inferred biases against the fossilization and recovery of hadrosaur skeletons compared to theropod skeletons. Currie *et al.* (2003) noted the possibility that *Tarbosaurus* was very effective at scavenging the carcasses of dead hervivores. They suggested that the chemical environment of the sediment influences the relative preservation of ornithopod and theropod bones. Such interpretations could be applicable at Bugin Tsav and Gurilin Tsav. However, they may not be applicable to other sites. The processes preserving body fossils and footprints must be influenced by many factors. The results demonstrate that dinosaur faunal assemblages should be considered very carefully and wherever possible, include evidence from both footprints and body fossil remains to form a complete analysis.

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REFERENCES

BORSUK-BIAŁYNICKA M. (1977) — A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from Upper Cretaceous of Mongolia. Palaeont. Pol., **37**: 5–64.

CHUDINOV P. K. (1966) — A unique site for late Cretaceous reptiles in Bayan Khongor Aimag (in Russian). In: Materialy po Geologii Mongol'skoi Narodnoi Respubliki (ed. N. A. Marinov): 74–78. Moscow, Nedra.

CURRIE P., BADAMGARAV D. and KOPPELHUS E. B. (2003) — The first Late Cretaceous footprints from the Nemegt locality in the Gobi of Mongolia. Ichnos, **10**: 1–12.

CURRIE P. and SARJEANT W. A. S. (1979) — Lower Cretaceous dinosaur footprints from the Peace river Canyon, British Columbia, Canada. Palaeogeogr. Palaeoclimat. Palaeoecol., **28**: 103–115.

FARLOW J. O. (1992) — Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. Zubia, **10**: 89–138.

FASTOVSKY D. E., BADAMGARAV D., ISHIMOTO H., WATABE M. and WEISHAMPEL D. B. (1997) — The paleoenvironments of Tugrekin Shire (Gobi Desert, Mongolia) and aspects of the taphonomy and paleoecology of *Protoceratops* (Dinosauria: Ornithischia). Palaios, **12** (1): 59–70.

FUJITA M., AZUMA Y., GOTO M., TOMIDA Y., HAYASHI S. and ARAKAWA Y. (2003) — First ankylosaur footprints in Japan and their significance. J. Vertebr. Paleontol., **23** (3 Suppl.): 52A.

GIERLIŃSKI G. D., LOCKLEY M. G., SINGER T. and NIEDŹWIEDZKI G. (2008) — Protoceratopsid skeleton and track association from the Upper Cretaceous of Mongolia. Second International Congress on Ichnology, Kraków, Poland 2008, Abstract Book, Pol. Geol. Inst.

GRADZIŃSKI R. (1970) — Sedimentation of dinosaur-bearing Upper Cretaceous deposits of the Nemegt Basin, Gobi Desert. Palaeontol. Pol., **21**: 147–229.

GRADZIŃSKI R. and JERZYKIEWICZ T. (1974) — Sedimentation of the Barun Goyot Formation. Palaeont. Pol., **30**: 111–146.

GRADZIŃSKI R., KAŹMIERCZAK J. and LEFELD J. (1968) — Geographical and geological data from the Polish-Mongolian Palaeontological Expeditions. Palaeont. Pol., **19**: 33–82.

HICKS J. F., BRINKMAN D. L., NICHOLS D. J. and WATABE M. (1999) — Paleomagnetic and palynologic analyses of Albian to Santonian strata at Bayn Shire, Burkhant, and Khuren Dukh, eastern Gobi Desert, Mongolia. Cret. Res., **20**: 829–850.

ISHIGAKI S. (1999) — Abundant dinosaur footprints from Upper Cretaceous of Gobi Desert, Mongolia. J. Vertebr. Paleont., **19** (3 Suppl.): 54A.

ISHIGAKI S., WATABE M. and TSOGTBAATAR K. (2008) — Dinosaur footprints from Mongolia, an overview. Second International Congress on Ichnology, Krakow, Poland 2008, Abstract Book, Pol. Geol. Inst.

ISHIGAKI S., WATABE M., TSOGTBAATAR K. and BARSBOLD R. (2004) — Footprint evidence of gregarious theropod dinosaurs from the Upper Cretaceous of Shar Tsav, South Gobi Aimag, Mongolia. J. Vertebr. Paleont., **24** (3 Suppl.): 74A.

ISHII K., BARSBOLD R. and Hayashibara Museum of Natural Sciences-Geological Institute, Academy of Natural Sciences of Mongolia joint Paleontological Expedition Team (1995) — Cretaceous sediments and occurrence of dinosaur fossil in the Gobi Desert, Mongolia (in Japanese). J. Geol. Soc. Japan., **101** (3): ix–x.

IVAKHNENKO M. F. and KURZANOV S. M. (1988) — Geological structure and age of Udan-sayr and Shara-Tsav localities (in Russian). In: Iskopaemye reptilii i ptitsy Mongolii, Soviet-Mongolia Joint Paleontol. Exped. Transac., **34**: 100–105.

JERZYKIEWICZ T. (2000) — Lithostratigraphy and sedimentary settings of the Cretaceous dinosaur beds of Mongolia. In: The Age of Dinosaurs in Russia and Mongolia (eds. M. J. Benton *et al.*): 279–296. Cambridge Univ. Press. Cambridge.

JERZYKIEWICZ T. and RUSSELL D. A. (1991) — Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. Cret. Res., **12**: 345–377.

KRAMARENKO N. N. (1974) — On works of the Joint Soviet — Mongolian Paleontological Expedition (in Russian). Soviet-Mongolia Joint Paleontol. Exped. Transac., **1**: 9–18.

KURZANOV S. M. (1981) — On the unusual theropods from Upper Cretaceous of Mongolia (in Russian with English summary). Soviet-Mongolia Joint Paleontol. Exped. Transac., **15**: 39–50.

KURZANOV S. M. (1987) — Avimimidae and the problem of the origin of birds (in Russian with English title and contents). Soviet-Mongolia Joint Paleontol. Exped. Transac., **31**: 5–92.

KURZANOV S. M. and BANNIKOV A. F. (1983) — A new sauropod from the Upper Cretaceous of Mongolia (in Russian). Paleontologichekii Zhurnal, **2**: 90–96.

LEE Y.-N. and LEE H.-J. (2006) — A sauropod trackway in Donghae-Myeon, Goseong county, Soouth Gyeongsang province, Korea and its paleobiological implications of Uhangri manus-only sauropod tracks. J. Paleont. Soc. Korea, **22** (1): 1–14.

LEONARDI G. (1984) — Le impronte fossili di dinosauri (in Italian). In: Sulle Orme dei Dinosauri (eds. J. F. Bonaparte *et al.*): 165–186. Errizo Editrice. Venice.

LI D., AZUMA Y., FUJITA M., LEE Y.-N. and ARAKAWA Y. (2006) — A preliminary report on two new vertebrate track sites including dinosaurs from the early Cretaceous Hekou Group, Gansu province, China. J. Paleont. Soc. Korea, **22** (1): 29–49.

LOCKLEY M. G. (1991) — Tracking Dinosaurs. Cambridge Univ. Press. Cambridge.

LOCKLEY M. G., HOUCK K., YANG S.-Y., MATSUKAWA M. and LIM S.-K. (2006) — Dinosaur-dominated footprint assemblages from the Cretaceous Jidong Formation, Hallyo Haesang National Park area, Goesong County, South Korea: evidence and implications. Cret. Res., **27**: 70–101.

LOCKLEY M. G. and HUNT A. P. (1995) — Dinosaur tracks and other fossil footprints of the Western United States. Columbia Univ. Press. Cambridge.

LOCKLEY M. G. and MEYER C. (2000) — Dinosaur tracks and other fossil footprints of Europe. Columbia Univ. Press. New York.

LOCKLEY M. G., WRIGHT J., WHITE D., MATSUKAWA M., JIANJUN L., LU F. and HONG L. (2002) — The first sauropod trackways from China. Cret. Res., **23**: 363–381.

LOOPE D. B., DINGUS L., SWISHER III C. C. and MINJIN C. (1998) — Life and death in a Late Cretaceous dune field, Nemegt Basin Mongolia. Geology, **26** (1): 27–30.

LULL R. S. (1953) — Triassic life of the Connecticut Valley. State Geol. and Natu. Hist. Surv. Bull., **81**. State of Connecticut, Hartford.

MALEEV E. A. (1955) — New carnivorous dinosaur from the Upper Cretacous of Mongolia. Dokl. Akad. Nauk SSSR, **104**: 779–782.

MARYAŃSKA T. and OSMÓLSKA H. (1984) — Postcranial anatomy of *Saurolophus angustirostris* with comments on other hadrosaurs. Palaeontol. Pol., **46**: 119–141.

MATSUKAWA M., LOCKLEY M. G. and JIANJUN L. (2006) — Cretaceous terrestrial biotas of East Asia, with special reference to dinosaur-dominated ichnofaunas: toward a synthesis. Cret. Res., **27**: 39–21.

MATSUKAWA M., NAGATA H., TAKETANI Y., KHANDA Y., KHOSBAJAR P., BADAMGARAV D. and OBATA I. (1997) — Dinosaur-bearing lower Cretaceous deposits in the Choir basin, SE Mongolia — stratigraphy and sedimentary environments. J. Geol. Soc. Philippines, **52** (3–4): 99–114.

MATSUKAWA M., SHIBATA K., KURIHARA R., KOARAI K. and LOCKLEY M. (2005) — Review of Japanese Dinosaur Track Localities: Implications for Ichnotaxonomy, Paleogeography and Stratigraphic Correlation. Ichnos, **12**: 201–222.

MCCREA R. T., LOCKLEY M. G. and MEYER C. A. (2001) — Global distribution of purported ankylosaur track occurrences. In: The Armored Dinosaurs (ed. K. Carpenter): 413–454. Indiana Univ. Press. Bloomington.

MIKHAILOV K., SABATH K. and KURZANOV S. (1994) — Eggs and nest from the Cretaceous of Mongolia. In: Dinosaur Eggs and Babies. (eds. K. Carpenter, K. F. Hirsch and J. R. Horner): 88–115. Cambridge Univ. Press, Cambridge.

NAMNANDORZHI O. (1957) — Traces of huge lizards in Mongolia (in Russian). Priroda, **44** (5): 110–111.

NORMAN D. B. and SUES H. D. (2000) — Ornithopods from Kazakhstan, Mongolia and Siberia. In: The age of Dinosaurs in Russia and Mongolia (eds. M. J. Benton *et al*.): 462–479. Cambridge Univ. Press, Cambridge.

NOWIŃSKI A. (1971) — *Nemegtosaurus mongoliensis* n. gen., sp. (Sauropoda) from the Uppermost Cretaceous of Mongolia. Palaeont. Pol., **25**: 57–81.

OBATA I. and MATSUKAWA M. (1996) — Kyouryuu no michi (Road of dinosaur) (in Japanese). Catalogue for the special exhibit. Nakazato Village, Gunma Prefecture, Japan.

ROMANO M., WHYTE M. A. and JACKSON S. J. (2007) — Trackway Ratio: a new look at trackway gauge in the analysis of quadripedal dinosaur trackways and its implications for Ichnotaxonomy. Ichnos, **14** (3): 257–270.

ROZHDESTVENSKII A. K. (1952) — A new representative of the duck-billed dinosaurs from the Upper Cretaceous deposits of Mongolia (in Russian). Dokl. Akad. Nauk SSSR, **86**: 405–408.

ROZHDESTVENSKII A. K. (1957) — Duckbilled dinosaur *Saurolophus* from the Upper Cretaceous of Mongolia (in Russian with English abstract). Vert. PalAsiat., **1**: 129–149.

SHUVALOV V. F. (2000) — The Cretaceous stratigraphy and paleobiogeography of Mongolia. In: The Age of Dinosaurs in Russia and Mongolia (eds. M. J. Benton *et al*.): 256–278. Cambridge Univ. Press. Cambridge.

SHUVALOV V. F. and CHKHIKVADZE V. M. (1975) — New data on Late Cretaceous turtle of southern Mongolia (in Russian). Soviet-Mongolia Joint Paleontol. Exped. Transac., **2**: 214–229.

SHUVALOV V. F. and NIKOLAEVA T. V. (1985) — On age and areal distribution of Cenozoic basalts in south of Mongolia (in Russian). Vestnik Leningradtskogo Gosudarstvennogo Univ., **14**: 52–59.

SOCHAVA A. V. (1975) — Stratigraphy and lithology of Upper Cretaceous deposits of Southern Mongolia (in Russian). In: Stratigrafia Mezozoiskikh otlozhenii Mongolii (eds. G. G. Martinson). Soviet-Mongolia Joint Paleont. Exped. Transac., **13**: 113–182.

STERNBERG C. M. (1932) — Dinosaur tracks from Peace River, British Columbia. Annu. Rep. Natl. Mus. Canada, **1930**: 59–85.

SUZUKI S. and WATABE M. (2000*a*) — Report on the Japan–Mongolia Joint Paleontological expedition to the Gobi Desert, 1995. Hayahsibara Mus. Natur. Sc. Res. Bull., **1**: 45–57.

SUZUKI S. and WATABE M. (2000*b*) — Report on the Japan–Mongolia Joint Paleontological expedition to the Gobi Desert, 1998. Hayahsibara Mus. Natur. Sc. Res. Bull., **1**: 83–98.

THULBORN T. (1990) — Dinosaur tracks. Chapman and Hall, London.

WATABE M. and SUZUKI S. (2000*a*) — Report on the Japan–Mongolia Joint Paleontological expedition to the Gobi Desert, 1996. Hayahsibara Mus. Natur. Sc. Res. Bull., **1**: 58–68.

WATABE M. and SUZUKI S. (2000*b*) — Report on the Japan–Mongolia Joint Paleontological expedition to the Gobi Desert, 1997. Hayahsibara Mus. Natur. Sc. Res. Bull., **1**: 69–82.

WATABE M. and SUZUKI S. (2000*c*) — Cretaceous fossil localities and a list of fossils collected by the Hayashibara Museum of Natural Sciences and Mongolian Paleontological Center Joint Paleontological Expedition (JMJPE) from 1993 through 1998. Hayahsibara Mus. Natur. Sc. Res. Bull., **1**: 99–108.

WATABE M. and TSOGTBAATAR K. (2004) — Report on the Japan-Mongolia Joint Paleontological expedition to the Gobi Desert, 2000. Hayahsibara Mus. Natur. Sc. Res. Bull., **2**: 45–67.

WATABE M., TSOGTBAATAR K., ICHINOROV N. and BARSBOLD R. (2004) — Report on the Japan–Mongolia Joint Paleontological expedition to the Gobi Desert, 2001. Hayahsibara Mus. Natur. Sc. Res. Bull., **2**: 69–96.

WILSON J. A. and CARRANO M. T. (1999) — Titanosaurs and the origin of wide gauge trackways — a biomechanical and systematic perspective on sauropod locomotion. Paleobiology, **25**: 252–267.