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A protoceratopsid skeleton with an associated track from the Upper Cretaceous of Mongolia

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A B S T R A C T

The Djadokhta Formation of the Gobi Desert is known for the number and diversity of dinosaur and other vertebrate bones and skeletons found there, but only theropod, hadrosaur and supposed ankylosaurid footprints have been reported from this stratum. Dinosaur footprints are also noted from the Nemegt Formation, and occur as typical dinosaur track accumulations (tracksites). An articulated protoceratopsid skeleton – specimen ZPAL Mg D-II/3 – was collected by the Polish-Mongolian Expedition of 1965 from the Djadokhta Formation of Flaming Cliffs in Mongolia. Recently, the natural cast of a tetradactyl digitigrade footprint was found underneath the pelvic girdle while the skeleton and matrix were being prepared. This is possibly the first find of a dinosaur track in close association with an articulated skeleton. Although *Protoceratops* is an extremely common dinosaur in Mongolia, its footprints have never previously been reported from the Late Cretaceous of the Gobi Desert.

1. Introduction

Finding a dinosaur dead in its tracks constitutes the holy grail of vertebrate ichnology: the Cinderella Syndrome (Lockley, 1998). Despite discoveries of invertebrates dead in their tracks (Barthel et al., 1990), and the feet of animals mired in place (Spencer et al., 2003), there are no confirmed reports of vertebrates literally dead in their diagnostically identifiable tracks (Lockley, 1998, 1999). A few cases of close correspondence between footprints and trackmaker skeletons are known only from the Pleistocene, as in the case of a jaguar (Simpson, 1941) and *Diprotodon* (Lockley, 1999).

The Gobi Desert in Mongolia is one of the most important paleontological areas yielding abundant vertebrate fossils, including dinosaur, bird and mammal remains (Benton et al., 2001). Expedition parties by American, Russian (and the former USSR), and Polish paleontologists in partnership with Mongolian scientists have discovered large numbers of vertebrate fossils (mainly dinosaur skeletons and mammal remains).

One of the richest and most diverse dinosaur faunas known is from the Late Cretaceous of the Gobi Desert of Mongolia (Jerzykiewicz and Russell, 1991; Benton et al., 2001). Numerous dinosaur footprints were recently reported from several sites from Gobi Desert (Ishigaki et al., 2009).

2. Material studied

Herein we report the discovery of a tetradactyl footprint found by two of us (TS and GN) in close association with an articulated *Protoceratops* (Fig. 1A), while the skeleton and matrix were being prepared (Gierliński et al., 2008). The specimen (ZPAL Mg D-II/3) in the collections of the Institute of Paleobiology, Polish Academy of Sciences was found in the Upper Cretaceous Djadokhta Formation, in Bayn Dzak (known also as Shabarakh Usu or Flaming Cliffs) during the famous Polish-Mongolian expedition of 1965 (Lavas, 1993). The Djadochta Formation (sometimes transcribed Djadokhta) is situated in central Asia (Gobi Desert) and dates from the Late Cretaceous. Laid down in the early Campanian, possibly starting in the latest Santonian, it is dated somewhat uncertainly at about 84–75 million years ago. It preserves an arid habitat of sand dunes, with little fresh water apart from oases and arroyos (Gradziński, 1970; Shuvalov, 2000). Most notable fossil discoveries have been the first confirmed dinosaur eggs (a clutch, probably of

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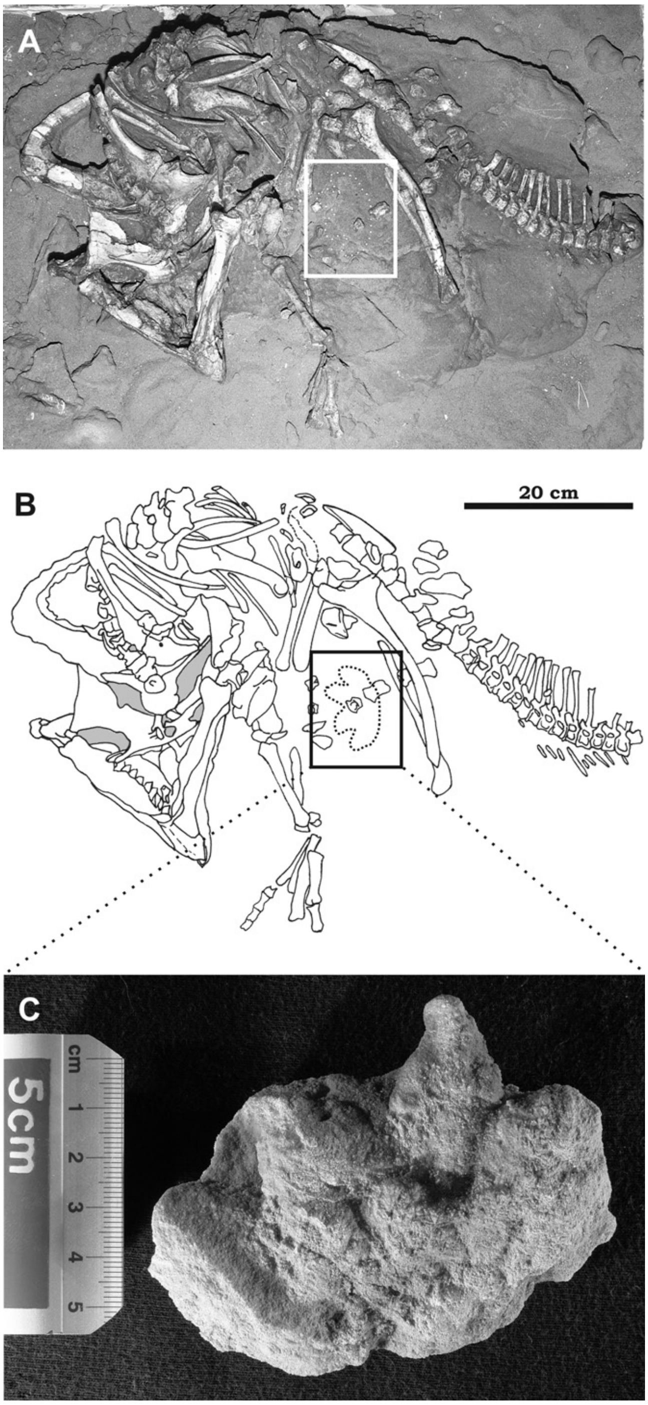

Fig. 1. Subadult *Protoceratops* skeleton and footprint ZPAL Mg D-II/3 from the Djadokhta Formation of Bayn Dzak, Mongolia; A. Ventral view of most of the skeleton with the footprint located underneath the pelvic girdle. B. Isolated footprint close up.

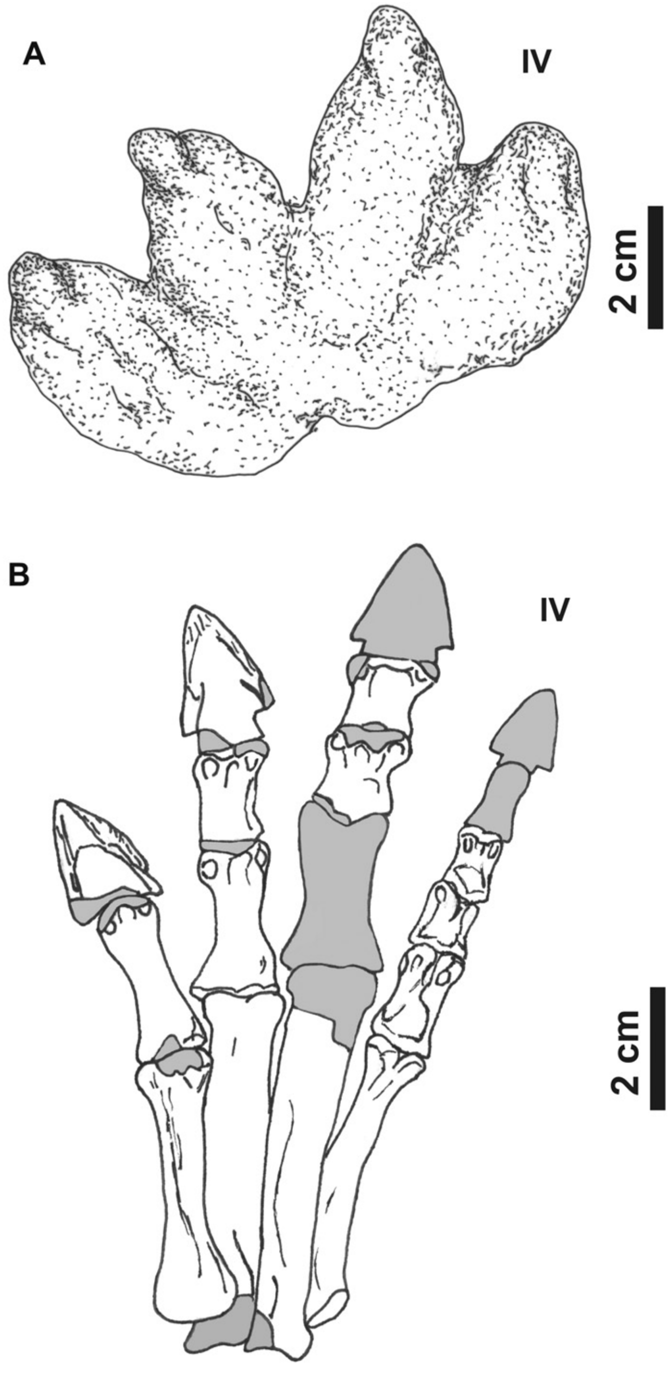

Fig. 2. A. Footprint drawing. B. The foot of *Protoceratops* specimen ZPAL Mg D-II/3.

Oviraptor) and several dinosaurs (*Protoceratops*, *Pinacosaurus* and *Velociraptor* being the most prominent), mammals, birds, lizards and crocodylomorphs (Benton et al., 2001). The footprint, preserved as a natural cast (Figs. 1B and 2B), closely fits *Protoceratops* left pes morphology (Fig. 2A) and was found in the sediments underneath the pelvic girdle. Natural casts are the typical mode of preservation for the tracks from the Late Cretaceous of Mongolia (Ishigaki et al., 2009).

Although famous for the number of dinosaur skeletons and diversity of species, it is only recently that footprints have been recognized in this fossiliferous stratum. Numerous dinosaur footprints were reported from several sites in Mongolia by the Hayashibara Museum of Natural Sciences – Mongolian Paleontological Center Joint Paleontological Expedition (Watabe and Suzuki, 2000a,b,c; Ishigaki et al., 2008, 2009).

The first discovery of dinosaur footprints in Mongolia was made by Namnandorzhi (1957). In that 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. Ishigaki (1999) and Ishigaki et al. (2004, 2008, 2009) reported new data on several new dinosaur footprint localities discovered in the Upper Cretaceous of the Gobi Desert of Mongolia, and they recognized more than 20 000 footprints of dinosaurs. There are at least four types of dinosaur footprints, attributed to theropod, ornithopod, supposed ankylosaurid and sauropod trackmakers.

Until 2009, only hadrosaur footprints were described from the Djadokhta Formation at Khongil and Yagaan Khovil (Ishigaki, 1999; Watabe and Suzuki, 2000a,b,c). In 2009, Ishigaki et al. reported about new tracksites from the Djadokhta Formation. New and spectacular specimens of dinosaur tracks from this formation have been outlined and shortly described by Ishigaki et al. (2008, 2009).

3. Description

The footprint from Djadokhta Formation in question here is tetradactyl, digitigrade, and wider than long, measuring 9.1 cm and 7.8 cm respectively. Toes are slightly projected above the hypex. They are relatively broad and well padded with no discrete phalangeal pads. However, the small rounded claws on digit II and III, and the metatarsophalangeal pad below digit IV, are recognizable. The fourth digit is the longest. Digit length ratios vary as follows: IV/I = 1.17, IV/II = 1.19 and IV/III = 1.04. The angles between the digit axes are: I–II = 29°, II–III = 33° and III–IV = 26°. The track is preserved in reddish-brown sandstone, cemented by carbonate and silica matrix. Interestingly, this footprint looks like a much smaller version of the unnamed ceratopsian footprint CU-MWC 227.1, from the Iron Springs Formation (Upper Cretaceous) of Utah (Milner et al., 2006).

4. Discussion and conclusions

Although *Protoceratops* is an extremely common dinosaur in Mongolia its footprints, like those of its equally-common relative, *Psittacosaurus*, a zonal index fossil (see Lucas, 2006), have never previously been reported. This disparity between the body and trace fossil records may reflect both collecting and/or preservational biases (Lockley and Hunt, 1994a). Coexistence of trace fossils and many skeletal remains in the same beds is a remarkable feature of the Gobi Desert dinosaur record. Recently Ishigaki et al. (2009) show very interesting analyses of the dinosaur ichnorecord and associated body fossil remains from Gobi Desert. Their results clearly demonstrate that ichnofauna differ from the fauna reconstructed on the basis of body fossils.

The common misconception that tracks are only useful if matched with skeletons and skeletal-derived inferences has been challenged on several grounds (Lockley, 1998, 1999). Many taxa based on skeletal remains lack feet and are based on very few specimens. Tracks, however, represent living flesh in dynamic action. Tracks allow consistent comparison of the same elements, identification of skin texture (Gatesy et al., 1999), and estimates of speed, gait (Gatesy, 2001), and population parameters (Matsukawa et al., 2001). ZPAL Mg D-II/3 indicates that the trackmaker was digitigrade and likely in active motion (not passively transported) prior to death. Given that *Protoceratops* was common, we must consider the possibility that the track associated with this skeleton was made by another animal. However, even if this unparsimonious interpretation is considered, it appears highly probable that the trackmaker was another *Protoceratops* of the same size as skeleton ZPAL Mg D-II/3 (see Table 1). *Protoceratops* was approximately 1.6–1.8 m in length and 0.4–0.6 m high at the shoulder, a herbivorous ceratopsian. It was a relatively small dinosaur with a proportionately large skull. The large numbers of specimens found in high concentration suggest that *Protoceratops* lived in herds.

Table 1
Measurements of selected bones from the *Protoceratops* skeleton (specimen ZPAL Mg D-II/3).

Collection no	Identification	Total length
MgD-II/3	Left tibia	143 mm
MgD-II/3	Right ilium	148 mm
MgD-II/3-60	Right ischium	165 mm
MgD-II/3-34	Left Humerus	107 mm
MgD-II/3-51	Left ulna	88 mm
MgD-II/3	Metatarsal I	46 mm
	Metatarsal II	53 mm
	Metatarsal III	52 mm
	Metatarsal IV	47 mm

McCrea et al. (2001) briefly discussed the possible criteria for discriminating some ornithischian tracks. The authors noted that in the foot of the ceratopsid *Centrosaurus* Lambe, 1904 the hallux is not as short (reduced) in comparison with digits II–IV as it became in the nodosaurid *Sauropelta* pes. The *Centrosaurus* foot fits the pedal morphology of *Ceratopsipes* Lockley and Hunt (1995) and an unnamed ceratopsian track described by Milner et al. (2006), where digits I and IV are nearly equally developed.

In contrast, several typical ornithischian morphotypes contain functionally tridactyl footprints, which lack a strong hallux, or have one that is clearly shorter than the main digit group II–IV. According to Gierliński and Sabath (2008), tetradactyl *Tetrapodosaurus* from Cretaceous (Aptian-Cenomanian) is closer to the ceratopsian foot morphology than to ankylosaurian and stegosaurian skeletal pedal patterns, which may even be tridactyl. The first pedal digit was already well developed in the basal neoceratopsians, like *Protoceratops* Granger and Gregory, 1923 (see Brown and Schlaikjer, 1940), *Archaeoceratops* Dong and Azuma, 1997, *Montanoceratops* Brown and Schlaikjer, 1942 and *Cerasinops* Chinnery and Horner, 2007. Such a large hallux impression is present in the described above supposed *Protoceratops* (basal neoceratopsian) track from the Mongolia, which looks like a smaller, more gracile and digitigrade version of a larger and semiplantigrade *Tetrapodosaurus*.

Although tracks rarely indicate the specific or generic identity of trackmakers at low taxonomic levels (Lucas, 2007), there are exceptions. Footprints attributed to the genera *Tyrannosaurus* (Lockley and Hunt, 1994b), *Presbyornis* (Yang et al., 1995), *Australopithecus* (Hay and Leakey, 1982), *Dinornis* (Lockley et al., 2007), *Acrocanthosaurus* (Farlow, 2001), *Orobates*, *Diadectes* (Voigt et al., 2007), and now *Protoceratops* is identified with possibly pes imprint in close association. This growing list of Cinderella candidates indicates the maturation of vertebrate ichnology and the logical necessity that more matches will be found as diagnostic tracks and trackmakers are discovered and compared, especially in recent geologic time where body and trace fossil assemblages are more complete and well-preserved.

References

Barthel, K.W., Swinburne, N.H.M., Conway Morris, S., 1990. Solnhofen: A Study in Mesozoic Palaeontology. Cambridge University Press, Cambridge, 236 pp.

Benton, M.J., Shishkin, M.A., Unwin, D.M., Kurochkin, E.N. (Eds.), 2001. The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, UK, 696 pp.

Brown, B., Schlaikjer, E.M., 1940. The structure and relationships of *Protoceratops*. Annals of the New York Academy of Sciences 40, 133–266.

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.
Farlow, J.O., 2001. *Acrocanthosaurus* and the Maker of Comanchen Large Theropod Footprints. In: Tanke, D.H., Carpenter, K. (Eds.), Mesozoic Vertebrate Life. Indiana University Press, pp. 408–427.
Gatesy, S.M., 2001. Skin impressions of Triassic theropods as records of foot movement. Bulletin of the Museum of Comparative Zoology 156, 137–149.
Gatesy, S.M., Middleton, K.M., Jenkins, F.A.J., 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature 399, 141–144.
Gierliński, G.D., Sabath, K., 2008. Stegosaurian footprints from the Morrison Formation of Utah and their implications for interpreting other ornithischian tracks. Oryctos 8, 29–46.
Gierliński, G.D., Lockley, M.G., Singer, T., Niedźwiedzki, G. 2008. Protoceratopsid skeleton and track association from the Upper Cretaceous of Mongolia. In: Second International Congress on Ichnology, Kraków, Poland 2008, Abstract Book, Polish Geological Institute, vol. 45.
Gradziński, R., 1970. Sedimentation of dinosaur-bearing Upper Cretaceous deposits of the Nemegt basin, Gobi Desert. Palaeontologia Polonica 21, 147–229.
Hay, R.L., Leakey, M.D., 1982. The fossil footprints of Laetoli. Scientific American 246, 38–45.
Ishigaki, S., 1999. Abundant dinosaur footprints from Upper Cretaceous of Gobi Desert, Mongolia. Journal of Vertebrate Paleontology 19, 54A.
Ishigaki, S., Watabe, M., Tsogtbaatar, K., Barsbold, R., 2004. Footprint evidences of Gregarious theropod dinosaurs from the Upper Creatceous of Shar Tsav, South Gobi Aimag, Mongolia. Journal of Vertebrate Paleontology 24, 74A.
Ishigaki, S., Watabe, M., Tsogtbaatar, K., 2008. Gigantic theropod dinosaur footprints from the late Pliensbachian of Poland. In: The Second International Congress on Ichnology, Cracow, Poland, August 29–September 8, 2008. Polish Geological Institute. Abstrakt Book, pp. 94–95.
Ishigaki, S., Watabe, M., Tsogtbaatar, Kh, Saneyoshi, M., 2009. Dinosaur footprints from the Upper Cretaceous of Mongolia. Geological Quarterly 53, 449–460.
Jerzykiewicz, T., Russell, D.A., 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi basin. Cretaceous Research 12, 345–377.
Lavas, J.R., 1993. Dragons From the Dunes: The Search for Dinosaurs in the Gobi Desert, Published by the Author, pp. 1–138.
Lockley, M.G., 1998. The vertebrate track record. Nature 396, 429–432.
Lockley, M.G., 1999. The Eternal Trail: A Tracker Looks at Evolution. Perseus Books, pp. 1–334.
Lockley, M.G., Hunt, A.P., 1994a. A Review of vertebrate ichnofaunas of the western interior United States: evidence and implications. In: Caputo, M.V., Peterson, J.A., Franczyk, K.J. (Eds.), Mesozoic Systems of the Rocky Mountain Region, United States, pp. 95–108.
Lockley, M.G., Hunt, A.P., 1994b. A track of the Giant theropod dinosaur *Tyrannosaurus* from close to the Cretaceous/Tertiary Boundary, Northern New Mexico. Ichnos 3, 213–218.
Lockley, M.G., Gregory, M.R., Gill, B., 2007. The Ichnological record of New Zealand's Moas: A Preliminary Summary. In: New Mexico Museum of Natural History and Science Bulletin, vol. 42, pp. 73–78.
Loope, D.B., Dingus, L., Swisher III, C.C., Minjin, C., 1998. Life and death in a late Cretaceous dune field, Nemegt basin Mongolia. Geology 26, 27–30.
Lucas, S.G., 2006. The *Psittacosaurus* biochron, early Cretaceous of Asia. Cretaceous Research 27, 189–198.
Lucas, S.G., 2007. Tetrapod footprint biostratigraphy and biochronology. Ichnos 14, 5–38.
Matsukawa, M., Nagata, H., Taketani, Y., Khanda, Y., Khosbajar, P., Badamgarav, D., Obata, I., 1997. Dinosaur-bearing Lower Cretaceous deposits in the Choir basin, SE Mongolia – stratigraphy and sedimentary environments. Journal of Geological Society of Philippines 52, 99–114.
Matsukawa, M., Matsui, T., Lockley, M.G., 2001. Trackway evidence of herd structure among ornithopod dinosaurs from the Cretaceous Dakota Group of northeastern New Mexico. Ichnos 8, 197–206.
Matsukawa, M., Lockley, M.G., Jianjun, L., 2006. Cretaceous terrestrial biotas of East Asia, with special reference to dinosaur-dominated ichnofaunas: toward a synthesis. Cretaceous Research 27, 21–39.
McCrea, R.T., Lockley, M.G., Meyer, C.A., 2001. Global distribution of purported ankylosaur track occurrences. In: Carpenter, K. (Ed.), The Armored Dinosaurs. Indiana University Press, Bloomington, pp. 413–454.
Milner, A.R.C., Vice, G.S., Harris, J.D., Lockley, M.G., 2006. Dinosaur tracks from the Upper Cretaceous Iron Spring formation. In: Lucas, S.G., Sullivan, R.M. (Eds.), Late Cretaceous Vertebrates from the Western Interior. New Mexico Museum of Natural History and Science Bulletin, vol. 35, pp. 105–113.
Namnandorzhi, O., 1957. Traces of huge lizards in Mongolia (in Russian). Priroda 44, 110–111.
Obata, I., Matsukawa, M., 1996. Kyouryuu no michi (Road of dinosaur) (in Japanese). Catalogue for the Special Exhibit. Nakazato Village, Gunma Prefecture, Japan.
Shuvalov, V.F., 2000. The Cretaceous stratigraphy and paleobiogeography of Mongolia. In: Benton, M.J., et al. (Eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge Univ. Press, Cambridge, pp. 256–278.
Simpson, G.G., 1941. Discovery of jaguar bones and footprints in a cave in Tennessee. American Museum Novitates 1131, 1–12.
Spencer, L.M., Valkenburgh, B.V., Harris, J.M., 2003. Taphonomic analysis of large mammals recovered from the Pleistocene Rancho La Brea tar seeps. Paleobiology 29, 561–575.
Voigt, S., Berman, D.S., Henrici, A.C., 2007. First well-established track-trackmaker association of Paleozoic tetrapods based on *Ichniotherium* trackways and diadectid skeletons from the Lower Permian of Germany. Journal of Vertebrate Paleontology 27, 553–570.
Watabe, M., Suzuki, S., 2000a. Report on the Japan–Mongolia Joint Paleontological Expedition to the Gobi Desert, 1996. In: Hayahsibara Museum of Natural Sciences, Research Bulletin, vol. 1 58–68.
Watabe, M., Suzuki, S., 2000b. Report on the Japan–Mongolia Joint Paleontological Expedition to the Gobi Desert, 1997. In: Hayahsibara Museum of Natural Sciences, Research Bulletin, vol. 1 69–82.
Watabe, M., Suzuki, S., 2000c. 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. In: Hayahsibara Museum of Natural Sciences, Research Bulletin, vol. 1 99–108.
Yang, S.Y., Lockley, M.G., Greben, R., Erikson, B.R., Lim, S.Y., 1995. Flamingo and Duck like bird tracks from the late Cretaceous and early Tertiary: evidence and implications. Ichnos 4, 21–34.