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The First Late Cretaceous Footprints from the Nemegt Locality in the Gobi of Mongolia

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In September 2001, large ornithopod footprints were found in the Nemegt Formation at the locality known as Nemegt in the Gobi of Mongolia. Additional hadrosaur ichnites, plus footprints of sauropods and theropods, have been recovered since then. The Nemegt Formation is known for the number and diversity of dinosaur skeletons found there, but footprints have never before been reported. Footprints were noted in three horizons within the formation, and occur at the top of upward-fining successions of floodplain sandstones and mudstones of a meandering fluvial paleoenvironment. Most of the footprints are preserved as natural casts that show good preservation of detail. Skin impressions are found on some, and many have slide marks. The vast majority of the footprints can be identified as having been made by *Saurolophus*, but two footprints each of *Tarbosaurus* and *Opisthocoelicaudia* were also recovered. Three hadrosaur footprints were found in the quarry of a *Tarbosaurus* skeleton. It appears that after the *Tarbosaurus* had died and been partially buried, its skeleton was trampled by a hadrosaur. The overwhelming domination of hadrosaurs at the footprint levels suggests there are preservational biases acting on the fossilization of Nemegt skeletons to produce abnormally high predator/prey ratios.

Keywords Mongolia, Nemegt Formation, footprints, hadrosaur, sauropod, theropod

INTRODUCTION

One of the richest, most diverse dinosaur faunas known is from the Nemegt Formation of the southern Gobi (Fig. 1) of Mongolia (Jerzykiewicz and Russell, 1991). Although famous for the number of dinosaur skeletons and diversity of species, it is only recently that footprints have been recognized in the Nemegt Formation. **Fig. 1**

Dinosaur footprints were reported from a dozen sites in Mongolia by the Mongolian-Hayashibara expeditions (Watabe and Suzuki, 2000). Of these, hadrosaur footprints were found in the Djadokhta Formation at Khongil and Yagaan Khovil, and in the Nemegt Formation at Bugiin Tsav, Hermiin Tsav and Guriliin Tsav (Ishigaki, 1999; Watabe and Suzuki, 2000). None of these footprints have been described.

In September 2001, the authors, in conjunction with Nomadic Expeditions, led their fourth expedition into the Gobi to collect specimens for the Paleontological Center of the Mongolian Academy of Sciences. At the Nemegt locality, the expedition participants were surprised to discover a large, well-preserved dinosaur footprint close to their campsite. Nemegt is one of the classic Mongolian sites that has been visited numerous times by the authors and virtually all other major expeditions since its discovery by the Soviet expeditions in 1946 (Efremov, 1955; Gradzinski et al., 1968-1969; Kielan-Jaworowska, 1969; Lavas, 1993). No footprints were then reported, although most of the deformational structures referred to by Gradzinski (1970) were in fact probably dinosaur ichnites. Once the first footprint was identified, tens of other footprints were quickly found in the immediate region. Furthermore, during the excavation of a skeleton of a juvenile *Tarbosaurus* (MPD 107/5), a trackway of three footprints was found in the quarry (Fig. 2). **Fig. 2**
One large hadrosaur had apparently even stepped on the skull of the Tarbosaurus, which already at that time was dead and shallowly buried in wet sand. The weight of the trackmaker disarticulated some of the skull bones and pushed them deeply into the sediments, but caused relatively little damage to the bones.

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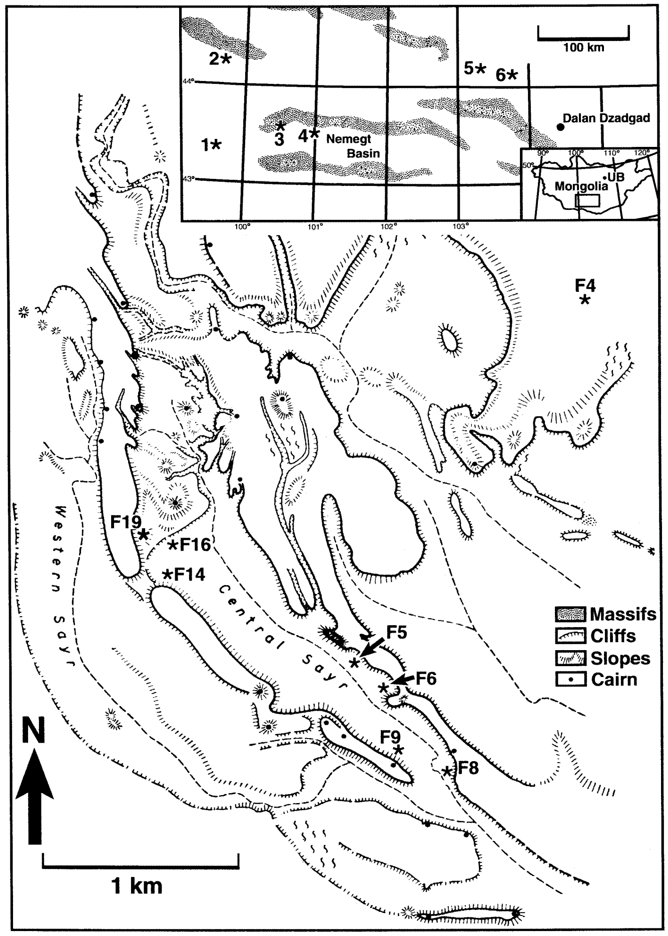

FIG. 1. Map of the Nemegt locality in Mongolia, showing Footprint Sites mentioned in the text. The exceptions are F15, which is immediately to the left of F14, and F17, which is positioned underneath F19. 1, Hermiin Tsav; 2, Bugiin Tsav; 3, Altan Uul; 4, Nemegt; F2-F6, F8, F10, F13, F14, F16, F18, F19, Footprint sites; UB, Ulaan Baatar. Adapted after maps in Gradzinski et al. (1968/1969) and Kielan-Jaworowska (1975).

All footprints seen in 2001 were from the same type of animal, although the smallest ones are less than half the size of the largest. A return to Nemegt by the 2002 expedition revealed that the lowest footprint horizon is very extensive and can be traced from camp for 2.5 km to the southeast (to Footprint Site 8), and 2.2 km to the northeast (Footprint Site 4). The distribution of footprints in this layer is consistent, and there are few areas where this level fails to produce tracks. The second level of ichnites is more localized, but is productive near the camp (Footprint Site 17) and in two other places (Footprint Sites 3 and 14), 1.8 and 0.4 km to the southeast. The third and highest level (Footprint Site 18) has only been seen in the vicinity of the camp, but extends for more than 100 meters on both sides of a narrow ridge and on the west side of a narrow gully. The linear distance of this horizon is about 250 meters, and more than 50 footprints (all hadrosaur) were counted at that level.

Because the strata erode in nearly vertical cliffs, it has not been possible to see trackways of single dinosaurs so far. The footprints found on talus slopes below the cliffs are all in blocks too small to include more than one footprint.

Nineteen footprint sites were identified in 2002 at the Nemegt locality. The coordinates of these sites are available to qualified researchers through the authors.

The spellings of Mongolian geographic and stratigraphic names follows those of Benton et al. (2000), and the chronostratigraphic framework is from Jerzykiewicz and Russell (1991).

INSTITUTIONAL ABBREVIATIONS

MPD, Paleontological Center of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia.

SEDIMENTOLOGY

The footprints can be seen in at least three horizons within the Nemegt Formation at Nemegt. Common sedimentary features of the footprint beds include scoured surfaces with local pebbles and gravels, resting lags, upward-fining grain size, composite inclined stratification, trough cross-stratification, and climbing ripple structures representing channel talweg deposits. Most sand- and silt-grade sediments were deposited as point bars and channel bars. Overbank or topstratum deposits are represented by siltstones, sometimes with intercalations of fine-grained sands. Mudstones of limited lateral persistence might have been deposited from suspension onto the surfaces of the floodplain, in ephemeral lakes and swales between point bars or in abandoned channels.

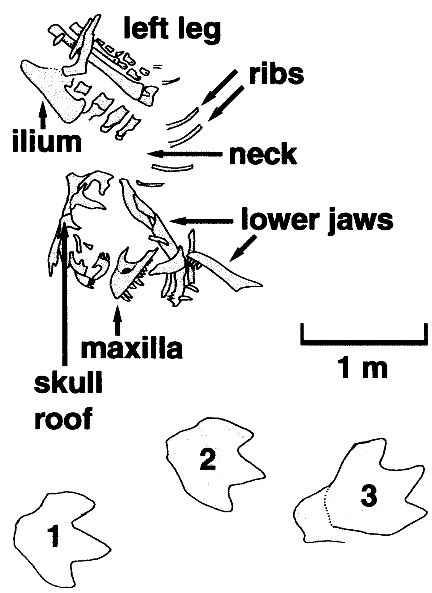

FIG. 2. Hadrosaur footprints and associated Tarbosaurus skeleton, Nemegt Locality.

The alternation of beds of sand- and silt-grade sediments, often seen in composite layers, indicates frequent changes of hydrodynamic conditions within the channel. These changes resulted from frequent changes in river levels, which in turn suggests the existence of seasonal rains in the source area and also in the area of deposition (Gradzinski, 1970). The horizons with footprints occur in the top sediments of ephemeral lakes and swales of meandering fluvial deposits. In these levels are what have previously been interpreted as abundant load cast deformations or sole markings, but almost all are clearly ichnites. In the measured section (Fig. 3), the so-called load structures occur in three levels together with unmistakable footprints.

Fig. 3

The load structures and footprints are generally preserved on the underside of sandstone layers overlying mudstone. The sole markings on the bottom of the sandstones are infillings (variously referred to as counterparts, convex hyporeliefs, molds or casts) of the original footprints that were left in the mud. With the exception of the foot impressions in the *Tarbosaurus* quarry (Fig. 2), all footprints encountered were infillings.

Most of the footprints were made by large animals that sunk to varying depths into the mud. MPD 100F/15 is 45 cm across, but the mud substrate was firm enough that only the claws and anterior parts of the toes sunk into it. Most footprints, however, sunk to depths of 20 to 40 cm below the surface that the animals stepped onto. One large, uncollected hadrosaur ichnite at Footprint Site 18 is 114 cm deep (Fig. 4E), and includes a strongly inclined mark of the lower leg. In most cases, the mud had enough integrity to maintain the shape of the footprints without appreciable backflow, collapse or distortion even when the toes undercut the mud (Fig. 4B). Vertical grooves were frequently left in the mud by the scales on the backs and sides of the feet as they slid into the sediment. Scale impressions may be common, although it is usually difficult to distinguish them from erosional surfaces. In two footprints, skin impressions (MPD 100F/12 and a sauropod footprint from Footprint Site 6) are unequivocal. The common presence of these surface markings is a good indication that there are no subtraces. The feet continued to press into the mud until the sediment was capable of supporting the weight of the animal.

Fig. 4

The sediment that filled in the footprints was coarser grained than the substrate that the animal stepped into, and often included balls of clay that were presumably ripped up from the underlying sediments, plus pebbles and bones. At Footprint Site 14, two *Gallimimus* skeletons (MPD 100/122 and 100/123) were found above the track level in the same layer of sandstone that was responsible for preserving the footprints. The muddy surfaces were presumably present for extended periods of time, because in most cases they were heavily marked by the tracks and trails of invertebrates (Fig. 4A, C). However, the new surfaces made by the bottoms of the dinosaur feet must have been buried rapidly because in most cases they lack any indication of invertebrate activity (Fig. 4A).

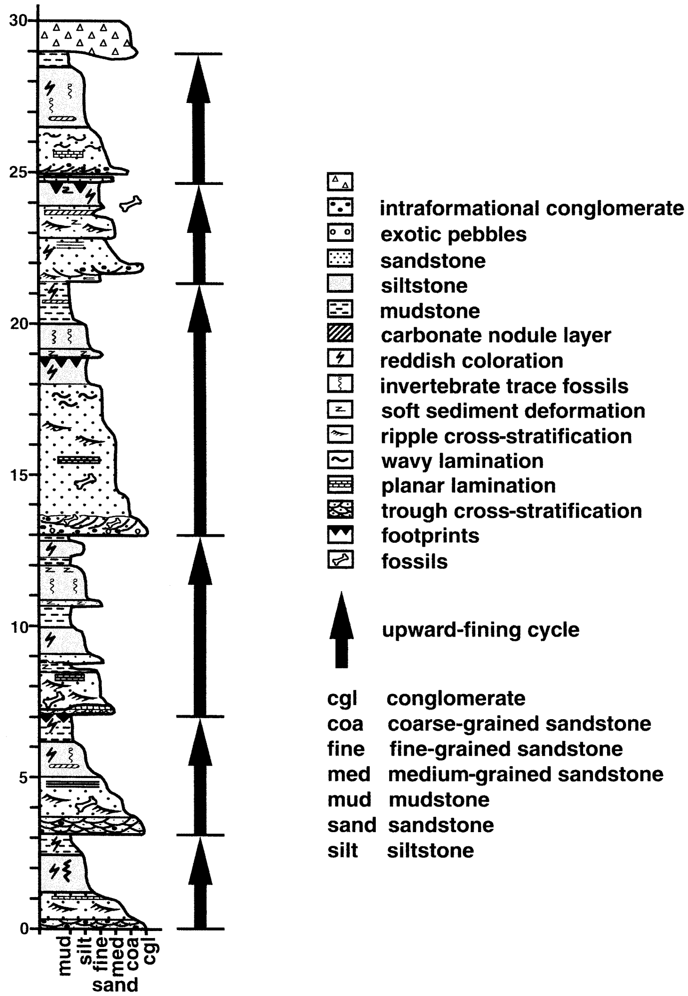

FIG. 3. Nemegt Formation geological profile.

DESCRIPTION

Theropod, sauropod, and hadrosaur ichnites have all been recovered from the Nemegt locality. Two large theropod ichnites and at least two sauropod footprints were identified at Nemegt. The vast majority of ichnites at Nemegt, however, are those of hadrosaurs.

Theropod Footprints

Only two theropod footprints (MPD 100F/12, 100F/14) have been collected, and no others were identified with certainty in the field.

The best preserved theropod footprint (MPD 100F/12, Fig. 5A–C) is an incomplete specimen that lacks one of the toes and was collected on a talus slope. It is 61 cm in length, including the claw impression of the third digit. If this is indeed *Tarbosaurus bataar* Maleev 1955 it was made by a large individual. Assuming that the ichnite includes the impression of the end of the third metatarsal, the third digit was probably about 45 cm

Fig. 5

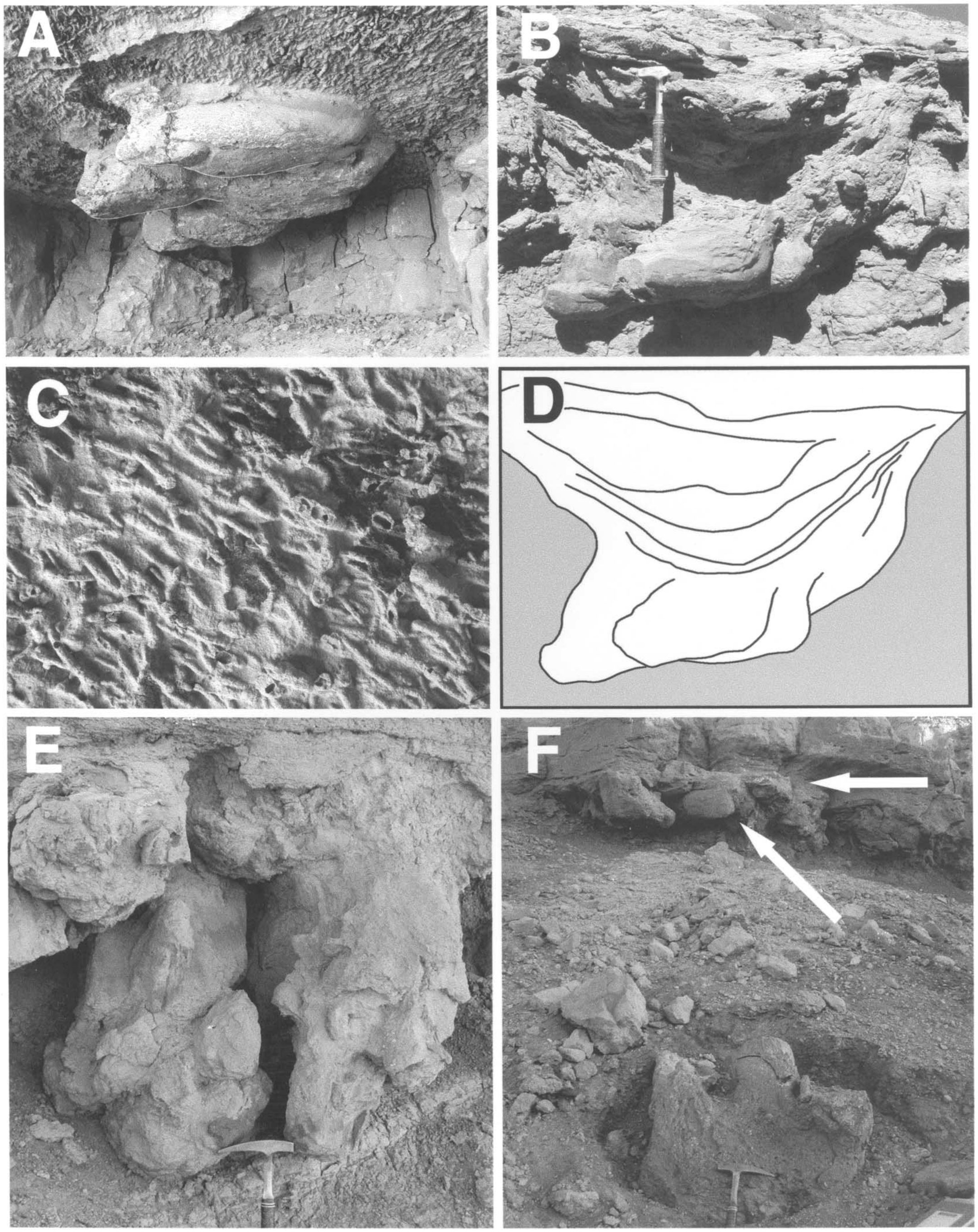

FIG. 4. Preservation of footprints at the Nemegt locality, Mongolia. **A**. Ventrolateral view of small hadrosaur footprint *in situ* at Footprint Site 16. **B**. Uncollected footprint in lateral view at Footprint Site 18. **C**. Closeup of invertebrate traces seen in A. **D**. Diagramatic representation of footprint seen in B. Gray coloration represents the underlying siltstone. **E**. Uncollected, deeply impressed hadrosaur footprint from Footprint Site 18. **F**. Uncollected footprint on talus slope below Footprint Site 14. Lower arrow points to layer this block came from, and has other footprints exposed in lateral view. Upper (horizontal) arrow is pointing to *Gallimimus* skeleton (100/123).

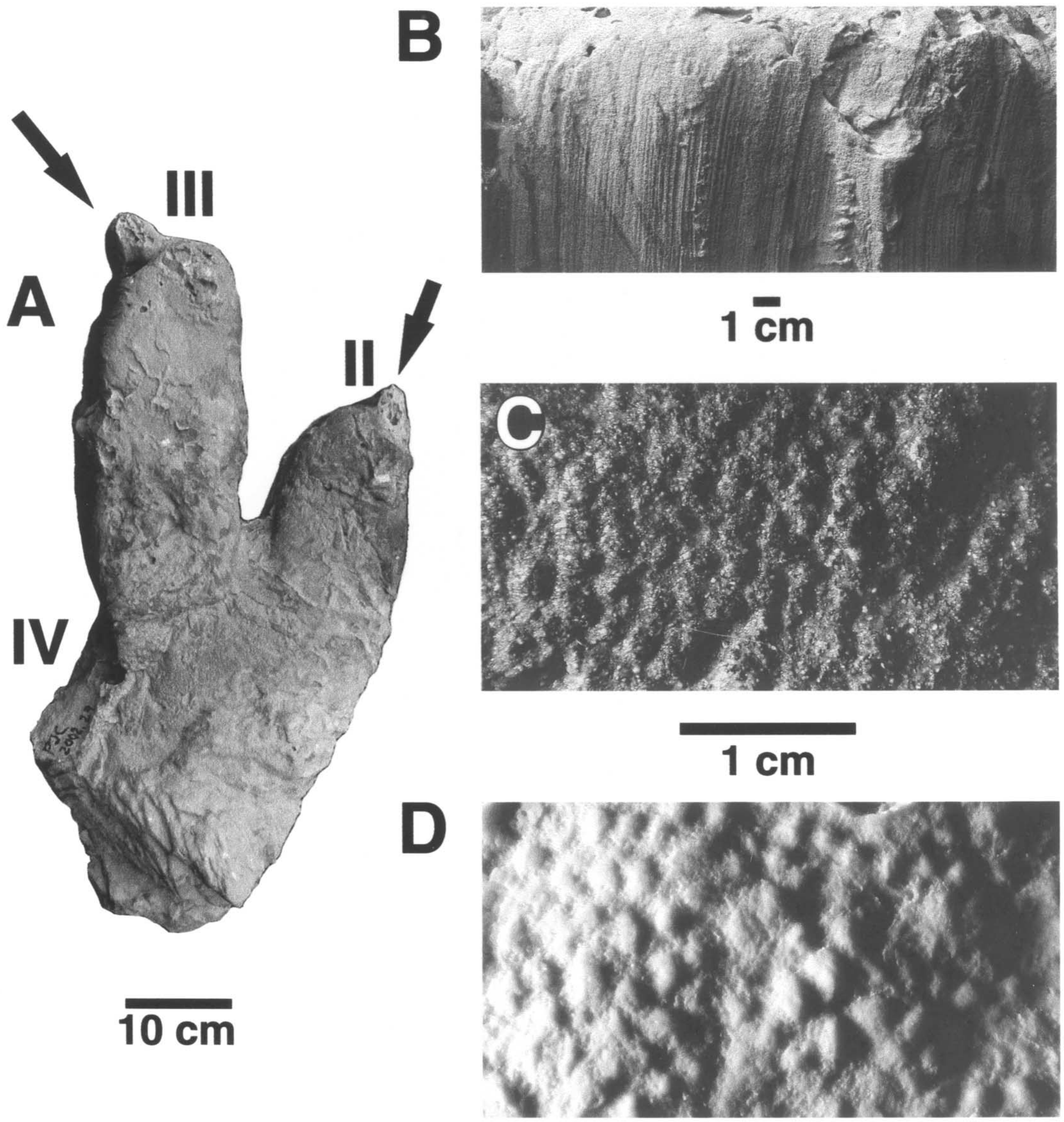

FIG. 5. Theropod ichnites from the Nemegt Formation of Mongolia. **A**. MPD 100F/12, left footprint of *Tarbosaurus* bataar. **B**. slide marks left by skin along the side of footprint MPD 100F/12. **C**. skin impressions from the central region of footprint MPD 100F/12. **D**. skin impressions (MPD 107/6A) associated with a *Tarbosaurus* skeleton from Bugiin Tsav (same scale as Fig. 5C). Roman numerals represent digit numbers. Arrows point to impressions of the claws.

long. A large *Tarbosaurus* skeleton (MPD 107/2) has a 41 cm long third toe, stands 2.5 m high at the hips and is 9.5 m long as mounted.

The two preserved toes of MPD 100F/12 are more elongate and slender than those of hadrosaurs of equivalent size. The free part of the third digit is 35 cm long and has a maximum width of 13.5 cm. The other toe (digit II or IV) has a free portion of 22 cm and a maximum width of 12.5 cm. Unlike hadrosaurs, there were no large pads under the toes, but the third toe expanded in the interphalangeal regions between the first and second, and the second and third phalanges. The positions of the interphalangeal impressions suggest that phalanx III-1 was about 14 cm long, and III-2 was about 10 cm long. Comparison with *Tyrannosauripus pillmorei* (Lockley and Hunt, 1994) indicates that the other toe is most likely the second digit. The base of the missing toe is more divergent, which suggests that it is the fourth. The impression of this toe displays no obvious interphalangeal expansions. If these two lines of reasoning are correct, then MPD 100F/12 is a right foot. Divarication between digits II and III is only slightly more than 20°.

The two digits of MPD 100F/12 include sharp claw impressions, the tips of which were unfortunately broken before the specimen was found. The claw of the second digit is aligned with the medial margin of the foot and points more or less forward. However, the claw of the third digit points as much laterally as it does forward. It is unknown whether this is the normal position of the claw, whether it represents an abnormal but temporary twist at the joint, or whether the end of the toe is pathologic.

The theropod foot sunk uniformly about 12 cm into the mud when MPD 100F/12 was made. Surface detail is excellent, and scale or tubercle impressions are preserved in almost half of the area behind the toes, and in large patches on the toes themselves. The scales also left parallel vertical slide marks (Fig. 5B) as the foot sunk into the mud. Each scale is about 2 mm wide, so it is consistent that there are 5 to 6 vertical slide marks per centimeter. Some of the scales on the bottom of the specimen (especially on the medial edge of digit II) are continuous with the vertical slide marks. These striae, which can also be seen on many of the hadrosaur footprints, have also been reported for ichnites in Cretaceous beds in Alberta (Nadon, 1993) and Utah (Difley and Ekdale, 2002).

The finely pebbled skin of this footprint (MPD 100F/12, Fig. 5C) is the same as the skin reported from other tyrannosaurids. Skin impressions (MPD 107/6A, Fig. 5D) were recovered from a *Tarbosaurus* skeleton destroyed by poachers at Bugiin Tsav (N43° 52.164′, E100° 00.605′). In this specimen, which is a large individual with a frontal width at the interorbital slot of 81 mm, the scales have an average diameter of 2.4 mm. The skin impression was recovered from the thoracic region of the body, although the damage done to the specimen makes it impossible to know exactly which region it covered. Other tyrannosaurid (*Albertosaurus*, *Daspletosaurus*, *Gorgosaurus*) skin impressions have been recovered from Alberta and Montana, and show the same lightly pebbled surfaces.

A second incomplete theropod footprint (MPD 100F/14) also was collected from the talus slope below Footprint Site 5. Using the same criteria as with the other footprint, this ichnite was probably made by a left foot. The metatarsal impression, the bases of digits III and IV, and all of digit II are preserved. Digit IV is 50 cm long, suggesting the animal that made the footprint was slightly larger than the one that made MPD 100F/12. The estimated divarication between digits III and IV is 35°, and that between digits II and IV is 55°. The fourth digit terminates in a sharply pointed claw impression, and the maximum width of the toe is 13 cm. Unfortunately, the specimen had been subject to extensive erosion so that no surface details were preserved.

Sauropod Footprints

Two sauropod pedal ichnites were identified at Nemegt, although only one (MPD 100F/15) was collected. The better preserved footprint (Fig. 6A–C) will be excavated in 2003 from Footprint Site 6. Other sauropod ichnites from manus and pes seem to be present at the same site, but further excavation is required.

Fig. 6

The best preserved sauropod pes ichnite (Fig. 6A–C) is 63 cm across. The infilling of the footprint is part of a massive sandstone block that broke from the cliff and fell onto the talus slope. The ventral surface of the footprint is damaged (Fig. 6C) and provides no details other than the outline. However, the vertical surfaces of the specimen are as well preserved as some of the best sauropod footprints known (Meyer et al., 1994). The pedal ichnite includes four distinct digital impressions, of which at least two toes (but no more than three) bore claws. The foot that made the impression was digitigrade and elephantine, and unlike the hadrosaur tracks the medial, anterior, and lateral margins of the impressions were nearly vertical. The posterior margin of the footprint was indistinct, which makes it difficult to estimate how long the foot would have been. However, it appears to have been slightly longer than wide. There are very distinct, nearly vertical slide marks that were left as the foot pushed down into the mud. Once the weight of the animal was supported by the substrate, the leg pivoted forward and left an impression of the skin (Fig. 6B) above the impression of the first toe. As in other sauropod skin specimens (Czerkas, 1994), the scales are shallow polygons that do not overlap. On average, they are 14 mm across. The smallest one has a diameter of 8 mm, and the largest is double that size.

A shallowly impressed ichnite (MPD 100F/15) from Footprint Site 2 shows well-preserved details of the ends of the digits (Fig. 6D–E). The mud was apparently firm enough that the outer and posterior margins of the foot did not leave an impression. The three largest toes are almost exactly the same size as those of the previously described impression, with the innermost one 230 mm long, the next 210 mm, and the third 170 mm. The first two digits had large, deep claws, although the distal tips of both impressions were damaged before the specimen was found. The impression of the first claw suggests it was 12 cm in dorsoventral height and 4 cm wide. The second is 9 by 3 cm near the base. Because neither claw was fully impressed into the sediment, and because the claws were imbedded in the fleshy pads, both may have had even larger dimensions at the base. Both claw impressions are inclined outwards at angles of about 30° from vertical. The interphalangeal pad behind the claw of the middle digit is well preserved, and has a diameter of 15 cm.

Hadrosaur Footprints

Hadrosaur footprints (Fig. 7) at Nemegt number in the thousands, and range in known size from 35 to more than 80 centimeters long (Table 1). The depositional environment did not seem to favor the preservation of footprints smaller than about 30 cm.

Fig. 7

Table 1

MPD 100F/11 (Fig. 7A–C) was the first of the Nemegt footprints recognized and was recovered from Footprint Site 18. Like most other ichnites, it is the infilling (natural cast of the bottom of the foot) of a footprint and was made by a very large hadrosaur. The morphology of the ichnite, when compared with other hadrosaur footprints, suggests that it was made by a left foot. The infilling is 80 cm long (88 cm including the slide mark of the back of the foot), and has a maximum width of 81 cm. The distance between the distal ends (the claw impressions) of digits II and IV is 75 cm. The impression of digit II is

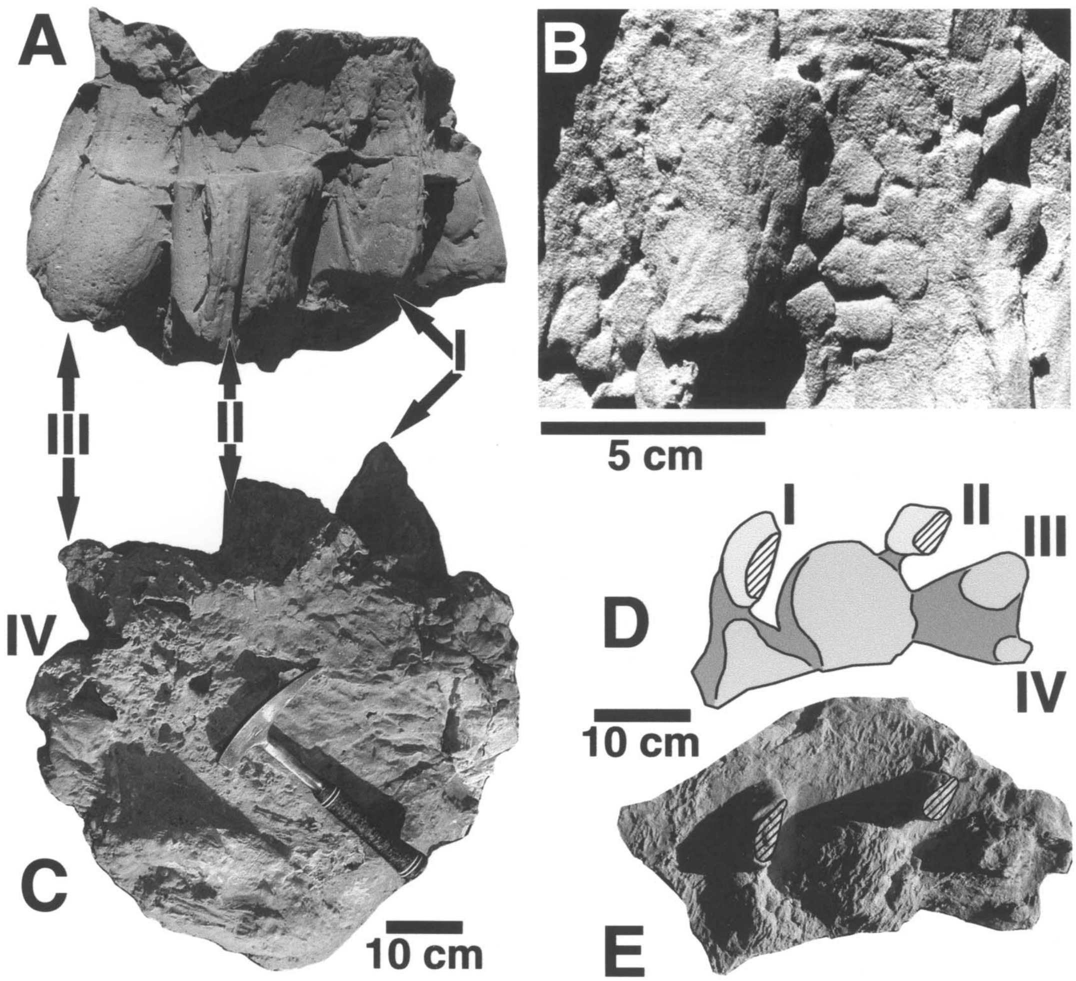

FIG. 6. Sauropod footprints from Nemegt Locality, Mongolia. **A**. anterior view of sauropod ichnite from Footprint Site 6. **B**. closeup of skin impressions of same footprint. **C**. ventral view of same footprint. **D**, **E**. partial footprint of sauropod MPD 100F/15 showing two claw and several digital pad impressions. Cross-hatching represents broken surfaces where the ends of the claw impressions were lost. Light gray shading highlights the terminal regions of the four digits and the digital pads, and the darker shading represents the depressed regions between the pads.

71 cm long (measured from the middle of the back margin of the metatarsal impression), which is 2 cm shorter than digit IV. Digit III is 31 cm at its maximum width midway along the toe. The divarication between digits II and IV is 70°, which is well within the range of other ornithopods (Lockley et al. 1983; Lockley 1987; Leonardi, 1994; Currie, 1995). In contrast with *Amblydactylus*, the "heel" pad is not a single concave impression but is closer to a large hadrosaur footprint from beds of equivalent age in Canada (Currie et al., 1991) in that the back of the footprint is asymmetrically bilobed to reflect the impression of the distal end of the metatarsus. The hoof-like claw impressions show that the unguals of the second and fourth digits were smaller, narrower, and more tapered than that of the third toe. The ungual impression of the third digit is 18 cm across, while those of the second and fourth digits are 12 cm. The footprint is 13.5 cm deep at the front and 18.5 cm at the back.

An uncollected hadrosaur ichnite (Fig. 7F) from Footprint Site 10 is closer to the average size of the Nemegt hadrosaur footprints. It is 56 cm long (the other digital impressions are 51 and 52 cm long), and the claw impressions of digits II and IV are separated by 62 cm. Divarication between digits II and IV is 75°. A smaller print, MPD 100F/13 (Fig. 7E), is distorted, and there is a huge bulbous expansion under the fourth toe. Although this may be some kind of deformity in the sediments, possibly caused by the shifting weight of the animal, it might also indicate that the trackmaker had an infected foot. The latter interpretation is supported by the reduced angle between the second and third toes, and by the fact that the third toe curls down and towards the fourth toe. Finally, there is a double drag mark behind the footprint, and the larger and deeper one is continuous with the apparent deformity.

There is abundant evidence to suggest that animals frequently stepped in the same footprints of other animals. One

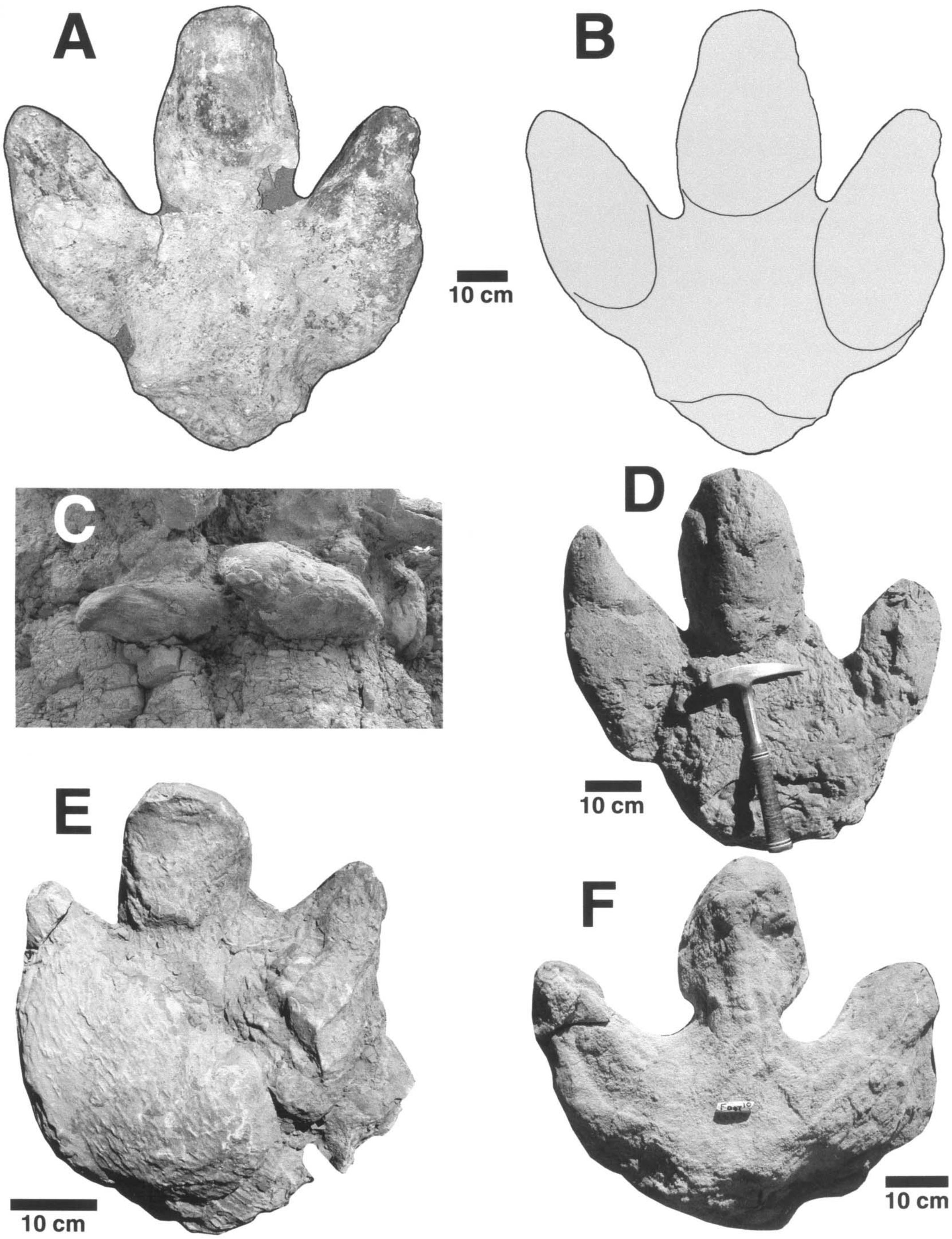

FIG. 7. *Hadrosaur* footprints from Nemegt Locality, Mongolia. **A**. MPD 100F/11 from Footprint Site 18. **B**. outline of same footprint. **C**. MPD 100F/11 as it was first seen *in situ*. **D**. uncollected hadrosaur footprint from Footprint Site 19. **E**. MPD 100F/13 from Footprint Site 5. **F**. uncollected footprint from Footprint Site 10.

TABLE 1
Selection of hadrosaur footprint measurements from Nemegt.

	100F/11	100F/13	2002.41	FS 10	FS 13	FS 14	FS 15	FS 16	FS 18	FS 19
Length	80	44	37	56	67	—	—	48	80	68
Width	81	41	35	65	66	62	63	50	—	67
II–IV div	70	55	75	75	—	—	—	—	—	54
Le digit L	71	38	—	52	—	—	—	44	—	65
Le digit W	25	12	—	15	—	—	—	—	—	17
Digit III W	30.5	14	11	20	—	—	—	—	—	22
R digit L	69	42	34	51	—	—	—	42	—	53+
R digit W	27	12	9	15	—	—	—	—	—	18
Le-III div	40	20	40	33	—	—	—	—	—	21
III-R div	30	35	35	42	—	—	—	—	—	33
Depth ant	13.5	26	12	27	—	—	—	12	82	18
Depth pos	18.5	17	12	—	—	—	—	—	71	—

Abbreviations: ant, anterior; div, divarication in degrees; FS, Footprint Site; L, length; Le, left; post, posterior; R, right; W, width; II, III, IV, digit numbers.

example at Footprint Site 15 seems to be a double impression of a single footprint 63 cm wide. It appears as if the foot twisted and thrust deeper into the mud as the animal shifted all of its weight onto that leg.

Numerous small hadrosaur footprints were found, but only one (MPD 100F/16) has been collected so far. This ichnite includes a long slide mark, and the total length of the specimen is 51 cm. The slide mark is continuous with the back of the footprint, the actual length of which is probably about 35 cm. This is the same as the width of the footprint. However, one of the toes is broken distally and therefore the width may have been slightly more.

Three hadrosaur footprints of a single trackway (Fig. 2) were found during the excavation of a juvenile *Tarbosaurus* skeleton (MPD 107/5). These footprints were not as well preserved, and could not be collected because they were found in relatively soft, unconsolidated sandstone. Their outlines, fortunately, were obvious because the depressions had been infilled by a dark red, friable claystone. A fourth depression was found at the same level as the other ichnites, but was positioned directly over the facial bones of the *Tarbosaurus* skull. It would appear that another hadrosaur or other large dinosaur stepped on the skull, disarticulating the lower jaws, premaxillae, maxillae and at least one jugal, and pushing these bones 10 to 15 cm into the wet sediments. The tyrannosaur skeleton was presumably already mostly buried because the top of the skull remained on its left side in articulation with the neck. The fact that the bones separated without significant breakage suggests that the *Tarbosaurus* carcass was largely decomposed.

The three ichnites in the trackway are tridactylous and large (preserved length is 60 cm, width on average is 65 cm). Pace angulation is 118°, pace is 122 cm, and stride is 239 cm.

DISCUSSION

Most of the footprints at the Nemegt locality are deep impressions, indicating that the mud was soft when they were made. Nevertheless, there was relatively little distortion of the mud as the foot was pulled away, and the footprints are so well preserved that the sides of the casts are often striated and can even include skin impressions. The mud was therefore firm enough to hold its shape until it was filled in by water-borne sand. The presence of invertebrate traces on the surface of the mud and the absence of mud cracks suggest that the sediments never had a chance to dry out. The extensive nature of the track-bearing levels suggests that the marshy floodplain environments were extensive and were subject to rapid flooding events. Similar depositional environments have been described for the St. Mary River Formation of southern Alberta and numerous other Mesozoic sites worldwide (Nadon, 1993).

The theropod footprints are easily differentiated from hadrosaur tracks by their long, narrow toes that terminate in the sharply tapering impressions of claws in MPD 100F/12. Based on their large sizes, MPD 100F/12 and 100F/14 could only have been made by *Deinocheirus*, *Tarbosaurus*, or *Therizinosaurus*, among the known Nemegt Formation theropods. *Therizinosaurus* is an unusual dinosaur from the Nemegt Formation with absurdly large manual claws (Maleev, 1954). *Therizinosaurus* can be eliminated as the trackmaker because it would have produced a pedal ichnite with four toe impressions (Perle 1982). *Deinocheirus* was collected from Altan Uul III, a locality that is only 40 kilometers to the west of Nemegt. Unfortunately, most of the skeleton, including the pes, of this animal is unknown and its affinities are uncertain. Regardless of whether it is an ornithomimid or a therizinosaurid (Currie, 2000), the feet of these animals are sufficiently different from those of tyrannosaurids to eliminate *Deinocheirus* as the trackmaker. A single footprint of *Tyrannosaurus rex* Osborn 1905 has been described (Lockley and Hunt, 1994), and is sufficiently close in morphology to the two theropod tracks from Nemegt to indicate that they were made by a tyrannosaurid, which at this site must have been *Tarbosaurus bataar* Maleev 1955.

Three sauropods are known from Mongolia, although none on the basis of complete specimens. *Nemegtosaurus* was established on the basis of a single skull (Nowinski, 1971), *Opisthocoelicaudia* is known from a nearly complete skeleton that lacks a skull (Borsuk-Bialynicka, 1977), and *Quaesitosaurus* is based on an incomplete skull. Isolated sauropod teeth (including MPD 100/410) are sometimes recovered from the Nemegt Formation at the Nemegt locality but can be referred to *Nemegtosaurus*. A partial tail (MPD 100/406) from the same location is identifiable as *Opisthocoelicaudia*. Although *Nemegtosaurus* and *Quaesitosaurus* have been frequently assigned to the Diplodocidae, and *Opisthocoelicaudia* to the Camarasauridae (Maryanska, 2000), recent cladistic analyses (Salgado et al., 1997; Salgado and Calvo, 1997; Wilson and Sereno, 1998) have identified all of these genera as titanosaurids. It is highly probable that *Nemegtosaurus* and *Opisthocoelicaudia* represent the same genus, as both have similar morphology and have been recovered from the Nemegt Formation. However, this cannot be proven without the recovery of a specimen with both skull and postcranial skeleton. *Quaesitosaurus* from the underlying Baruun Goyot might ultimately also prove to be congeneric with *Nemegtosaurus*.

The foot structure of *Opisthocoelicaudia* (see Plate 14 of Borsuk-Bialynicka, 1977) correlates perfectly with the sauropod footprints from Nemegt. This dinosaur had an asymmetrical foot, and three deep, narrow pedal unguals, the medial surfaces of which faced somewhat downward. The first, second, and third toes of the ichnites are 23, 21, and 17 cm long, respectively, compared with 21, 24, and 19 cm in the only known skeleton (the holotype) with a preserved foot. The sum of the distal widths of the metatarsals of the holotype of *Opisthocoelicaudia* is 46 cm, which gives a minimum width for the footprint it would have made. The distal ends would have been somewhat spread apart, and the soft tissue would also have added to the width of the foot. Still, it seems probable that the footprints were made by a slightly larger animal than the holotype. It is unlikely that there was more than one type of sauropod living in the Nemegt ecosystem, and along with the morphological similarity this justifies referral of these footprints with a high degree of confidence to *Opisthocoelicaudia*. Ultimately, it is possible that specimens will be found to demonstrate the congeneric status of *Opisthocoelicaudia* with *Nemegtosaurus*, at which point the latter name will become valid.

Borsuk-Bialynicka (1977) speculated that the pes was semiplantigrade in *Opisthocoelicaudia*. Adding the lengths of the third metatarsal to the third toe produces a sum of 44 cm, which is slightly shorter than the estimated width of the foot. Although we do not know how much length was added to the ichnite by soft anatomical features, the dimensions are consistent with those of the ichnite (Fig. 6C), suggesting the stance hypothesized by Borsuk-Bialynicka (1977) might be correct. However, evidence from other sauropod ichnites (e.g., Farlow et al., 1989) suggests that sauropods had very large sub-metatarsal pads. Furthermore, the deeply impressed ichnite from Footprint Site 6 has a nearly vertical anterior margin with skin impressions. This indicates that *Opisthocoelicaudia* was completely digitigrade when it started to lift its foot from the substrate. Unlike the Lower Cretaceous sauropod tracks from Texas (Farlow et al., 1989), the “heel” is not deeply impressed in MPD 100F/15 (in fact it apparently did not leave any impression in the substrate), although it is similar in that digit I was clearly bearing a disproportionate amount of the animal’s weight.

The first hadrosaur ichnite (MPD 100F/11) collected at the Nemegt locality is large (80 cm), but is not as large as some hadrosaur tracks from other Nemegt sites, which are apparently up to 115 cm in length (Ishigaki, 1999). Unfortunately, it is not known whether this length measurement includes the drag mark. A hadrosaur footprint from Colorado is 86 cm long (Brown, 1938; Russell and Béland, 1976). Hadrosaur footprints have also been identified from numerous other sites around the world (Langston, 1960; Lockley et al., 1983; Currie, 1995; Currie et al., 1991; Leonardi, 1994), but are rarely this large.

At present, two species of hadrosaurs have been identified from the Nemegt Formation. Many skeletons of *Saurolophus angustirostris* Rozhdestvenskii 1952 have been recovered from the Nemegt formation (Rozhdestvenskii, 1957, 1965; Maryanska and Osmólska, 1981b, 1984; Norman and Sues, 2000; Watabe and Suzuki, 2000). To date, only one specimen of *Barsboldia sicinskii* Maryanska and Osmólska 1981a was found in the Northern Sayr of the Nemegt Locality. Although *Saurolophus* and *Barsboldia* are both collected from Nemegt, the latter is a rarer and smaller animal than the former. Size alone suggests a high probability that the majority of footprints were made by *Saurolophus*, although the smaller hadrosaur footprints may have been left by either hadrosaur.

Hand impressions are seen in association with many of the hadrosaur pedal ichnites, but none has been collected. They are crescentic traces (Currie et al., 1991) but never seem to be as deeply impressed as the footprints of the hind limbs.

The majority of footprints at all of the Nemegt footprint sites are of hadrosaurs, and the largest can be attributed with confidence to *Saurolophus*. Of the hundreds of ichnites examined, only two are considered to have been produced by *Tarbosaurus*, and two by a sauropod. Although more thorough prospecting will certainly increase the number of non-hadrosaur prints, it is clear that hadrosaurs strongly dominate the ichnite faunas.

The association of such large footprint sites with rich recovery of bones and skeletons is almost unprecedented. In most cases, preservational biases favor the preservation of either ich-

TABLE 2
Hind limb length measurements for *Saurolophus*.

Species	Specimen	Femur L	Tibia L	Mt III L	Digit III	Leg L
Saurolophus angustirostris	PIN 551-8	1200	1000	330		
Saurolophus angustirostris	ZPAL MgD-I/17			300	247	
Saurolophus osborni	AMNH 5220	1170	1000	370	310	2540

Measurements for AMNH 5220 and PIN 551-8 are taken from Brown (1913) and Rozhdestvenskii (1957), respectively.

QY: Author: Need Table 2 callout in text.

nites or bones. For example, only two identifiable footprints have been recovered from Dinosaur Provincial Park (Alberta, Canada), one of the richest sites for Campanian dinosaur skeletons (Currie, 1987). Most of the richest footprint sites in the world have no bones or very few bones. Nemegt is unique in that the two types of resources are found together. Isolated bones and skeletons are found in the layers immediately above the footprints, and footprints are even found in the same layers as the bones (as in the case of MPD 107/5). This is important because the two types of resources can provide complementary information. For example, it has often been noted that the number of *Tarbosaurus* skeletons in the Nemegt Formation is exceptionally high when compared with the number of herbivore skeletons. This is at odds with other Late Cretaceous formations that suggest tyrannosaurids were numerically rare in comparison with herbivores. Nemegt clearly shows that depositional environments favoring the preservation of footprints were areas that were overwhelmingly dominated by hadrosaurs. This suggests that there are biases against the fossilization and recovery of hadrosaur skeletons in the Nemegt Formation. Perhaps *Tarbosaurus* was very effective at cleaning up the carcasses of dead herbivores, or perhaps the chemical environment of the sediments was more favorable for the preservation of the denser bone of theropods.

However, the Nemegt footprint sites clearly have biases of their own. All of the footprints found so far were made by relatively large animals, even though the surfaces of the footprint-bearing levels are rich in small invertebrate traces. This, and the fact that the large footprints were impressed into what must generally have been very soft, wet mud, suggest that the sediments may have been covered by enough water to prevent smaller animals from leaving their footprints. The fact that the surfaces of the mudstones are covered with invertebrate trace fossils suggests that small footprints were not removed by scouring.

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