

The Paleoenvironmental and Paleoecological Significance of Dinosaur Footprints

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ABSTRACT: Dinosaur tracks were left by dinosaurs when walking on substrates with moderate water content, conglutination and granulation. They were fossilized *in situ* when the substrates were lithified. Ichnology, the study of animal tracks, has unique importance to the study of the paleoenvironment, paleoecology and paleogeography. Tracks provide information about the track makers that bones never could. The present approaches have yielded valuable data on footprints as evidence of (1) animals unknown as body fossils; (2) geographic and geological ranges of vertebrate species, including biostratigraphic zonations by trace fossils; (3) behavior and habitat adaptations of vertebrates; and (4) prevailing environmental conditions. Otog Banner, Inner Mongolia, is famous for preserving abundant dinosaur and bird tracks from the Lower Cretaceous. From more than 1500 dinosaur tracks and more than 100 bird track fossils, 5 ichnotaxa are recognized. By analyzing the tracks and their surrounding rocks it was concluded that a seasonal lake existed in the Chabu area during the Early Cretaceous and that dinosaurs and birds living in the vicinity came to drink in the lake during a certain period of the year. By measuring the distances and relationships between the tracks, the speed of the track maker can be calculated. The fastest speed of a dinosaur so far measured in the world, around 44 km an hour, was found from dinosaur tracks in tracksite 5, Chabu area, Otog Banner. Statistical analysis suggests that at least the sauropod dinosaurs in the Chabu area were gregarious during the Early Cretaceous. The small theropods also lived and hunted together, whereas the large theropod dinosaurs were solitary. In some cases, the study of the assemblage of the tracks can be useful for the palichnostratigraphic correlations.

KEY WORDS: dinosaur tracks, paleoenvironment, paleoecology, Inner Mongolia of China.

INTRODUCTION

Dinosaur tracks are remarkably abundant in many areas. They were left by the dinosaurs when walking on substrates with moderate water content that were firm, fine-grained sediments. They were fossilized *in situ* when the substrates were lithified (Fig. 1). Unlike body fossils, which

are often best preserved when they are buried rapidly, tracks are more likely to be well preserved when they are buried in a relatively slowly. The tracks needs exposure under the sun or dry environment to set for some time before being buried by sediments, allowing them to become harder so as to prevent them from

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damage during burial (Lockley, 1991; Kuban, 1994).

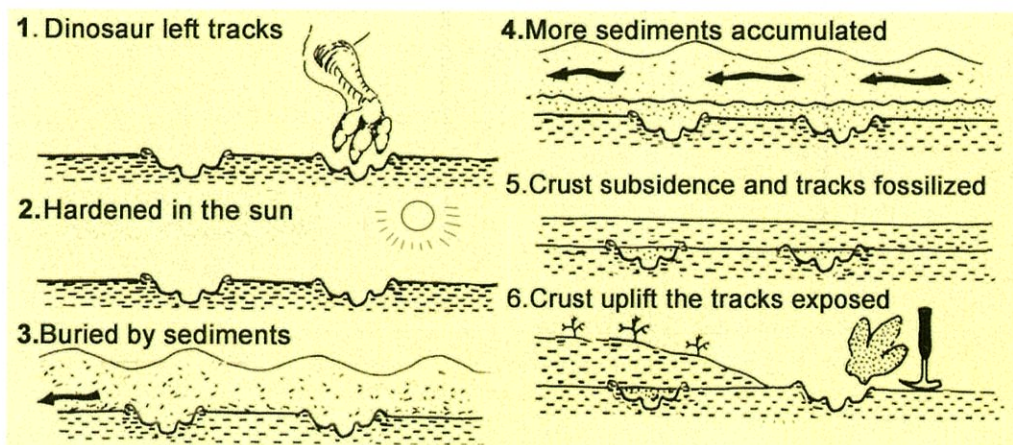


Figure 1. Formation of dinosaur tracks (adapted from Lockley, 1995).

A dinosaur track is a kind of trace fossil. Unlike body fossils, which are the remains of dead bodies, trace fossils record the active movements and behavior of ancient organisms. There are two main differences between fossil tracks and fossil bones. First, the fossil bones were left after the dinosaur died, while the tracks were left when the animals were alive. Second, the bones could be moved before or during the fossilization process, but the tracks always stay in the original position before they were fossilized. Although each animal had only one skeleton, they were able to leave a very large number of tracks during their lifetime. Simply because of these differences, ichnology, the study of tracks makes its own particular contributions to the study of the paleoenvironment, paleoecology and paleogeography. It provides a rich source of information on dinosaur

behavior, locomotion, foot morphology, ecology, chronology, and geographic distribution (Kuban, 1994).

The classification of dinosaur tracks is different from that of the dinosaur body fossils. In ichnology, the lower ichnotaxa, such as ichnofamily, ichnogenus and ichnospecies, are established separately for the fossil tracks or footprints. Those ichnotaxa are then put in the systematic classification system under the order or suborder taxa, implying the potential relationships with the bone fossils (see below).

Otog Banner, Inner Mongolia is famous for preserving abundant dinosaur and bird tracks from the Lower Cretaceous. At present, thousands of tracks are known from 16 different track sites. Dinosaur and bird tracks are found as the concave

footprints, on the upper bedding surface of the sandstones and as natural casts on the under bedding surface. Among more than 1,500 dinosaur tracks and more than 100 bird track fossils, five ichnotaxa have

been recognized, including theropods, *Chapus lockleyi*, *Asianopodus*, *Grallator*, sauropods *Brontopodus birdi* and birds *Tatarornipes chabuensis*.



Figure 2. Geographic position of the fossil locality.

MATERIALS, METHODS AND RESULTS

Geological setting

Otog Banner is located in the northwestern part of the Ordos Basin (Fig. 2), a large successive sedimentological basin developed since the Jurassic (Guo, 1999; Fig. 3). According to the Inner Mongolia Geological Survey Team, there exists a large fault trending north-south in the Ordos Basin, which stretches from Abudatai in the north, via Nalinshili to Uxin Banner. The fault divides the Ordos Basin into two smaller sedimentary basins in the

west and east, respectively. The eastern sedimentary basin mainly comprises deposits of the Yijinhuluo Formation and Dongsheng Formation. The western sedimentary basin mainly comprises deposits of the Zhidan Group that is composed of the Luohandong, Jingchuan, and Lamawan formations of the Lower Cretaceous (Chen, 2003; Chen *et al.*, 2006; No. 1 Territorial Survey Team of Inner Mongolia Geological Bureau, 1980; Wu *et al.*, 2005). In the study area, rocky outcrops containing dinosaur and bird tracks are composed mainly of mottle mudstone, grey green and

purple-red siltstones and sandstones, with some tuffaceous materials, which belong to the Jingchuan Formation, Lower Cretaceous, cover-

ed by grey green and purple red clay stones of the Paleogene and Neogene (Lockley *et al.*, 2002).

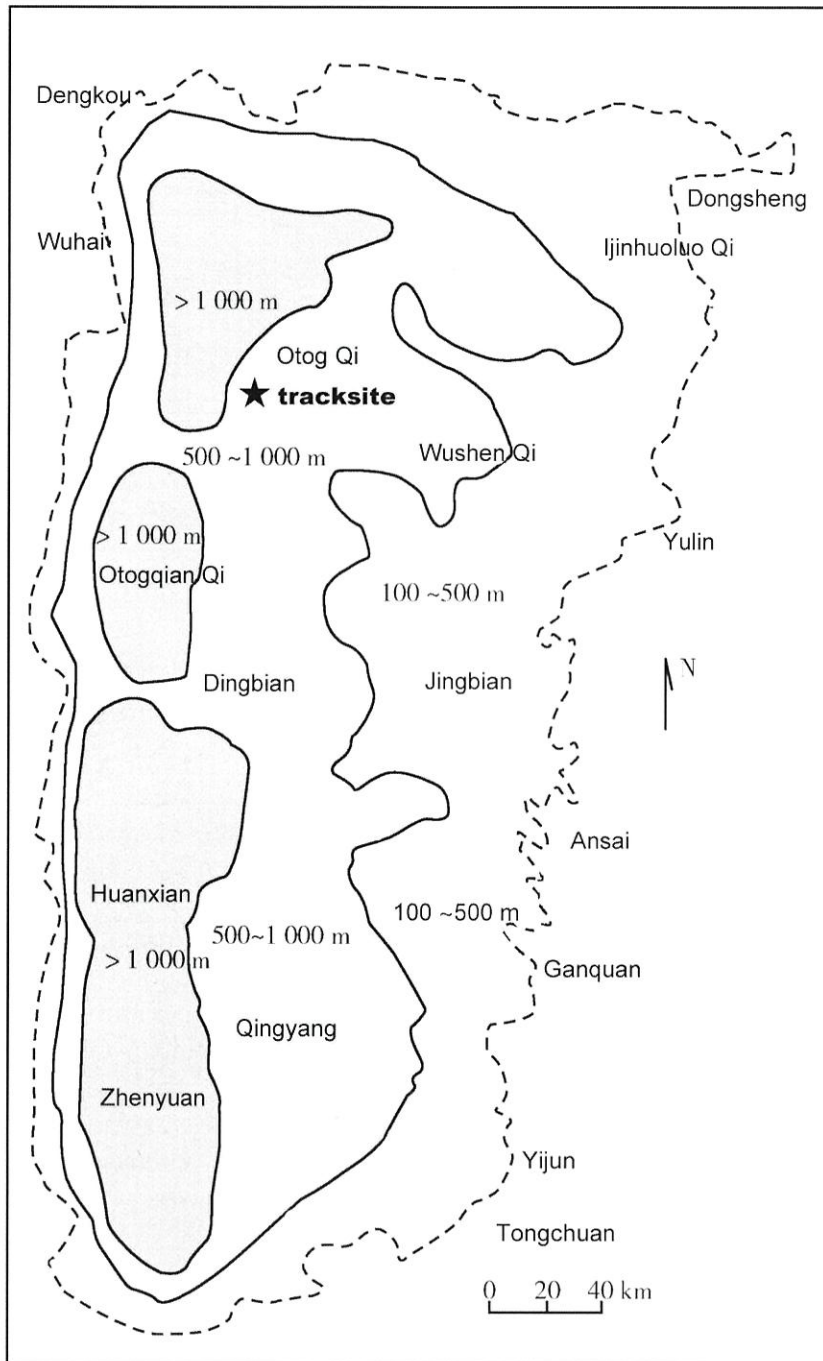


Figure 3. The distribution of the Cretaceous in Odors Basin, the numbers in the figure show the thickness of the sedimentary rocks (from Yang, 2006).

A large number of dinosaur and bird tracks have been found in the Chabu area in the south-western part of Otog Qi. (Lockley *et al.*, 2002; Li *et al.*, 2006). Besides bird and dinosaur tracks, the other fossils found in the Jingchuan formation in the Chabu area include reptiles: *Psittacosaurus youngi*, Hadrosauridae, *Ikchaosaurus* (*Eotomistoma multidentata* Young, 1964), birds: *Otogornis genghisi* (Hou, 1994), *Cathayornis chabuensis* (Li *et al.*, 2008), fish: *Lycoptera woodwardi*, *Lycoptera kansuensis*, *Sinomia zdanskyi*, ostracods: *Cypri-*

dea koskulensis, *Lycopteroocypris circultata*; *Darwinula* sp. *Mongolianna* aff. *almosa*; insects: *Mesolygeus totandocephalus*, *Mesolygeus laiyangensis*, the plant: *Cladophlebis* sp. (Guo, 1999, Chen *et al.*, 2006). These fossils can be well correlated with the members of the Jehol Biota in Western Liaoning. We measured a stratigraphic section near the bird fossil site (Fig. 4) to show the horizontal relationship among bird fossil sites and several dinosaur and bird track sites.

Systematic classification of the dinosaur and bird tracks.

In Otog banner, more than 1,500 dinosaur tracks and more than 100 bird tracks have been studied in detail and 5 ichnotaxa are recognized, including theropods, *Chapus lockleyi* (Li *et al.*, 2006), *Asianopodus* (Li *et al.*, 2011), *Grallator* (Li *et al.*, 2009), sauropod *Brontopodus birdi* (Lockley *et al.*, 2002; Li *et al.*, 2006) and birds *Tatarornipes chabuensis* (Lockley *et al.*, 2012).

Class Reptilia

Order Sauroschia

Suborder Theropoda

Infraorder Canrnosauria

Ichnofamily Eubrontidae Lull, 1904

Ichenogenus *Chapus* Li *et al.* 2006.

Ichnospecies *Chapus lockleyi* Li *et al.* 2006. (Fig. 5)

Diagnosis : Large bipedal, tridactyl tracks, claw acuminate, the angle between toe III and IV larger than that between II and III, the angles between toes are II, 13° III, 35° IV. The length of the footprint is usually greater than 45 cm.

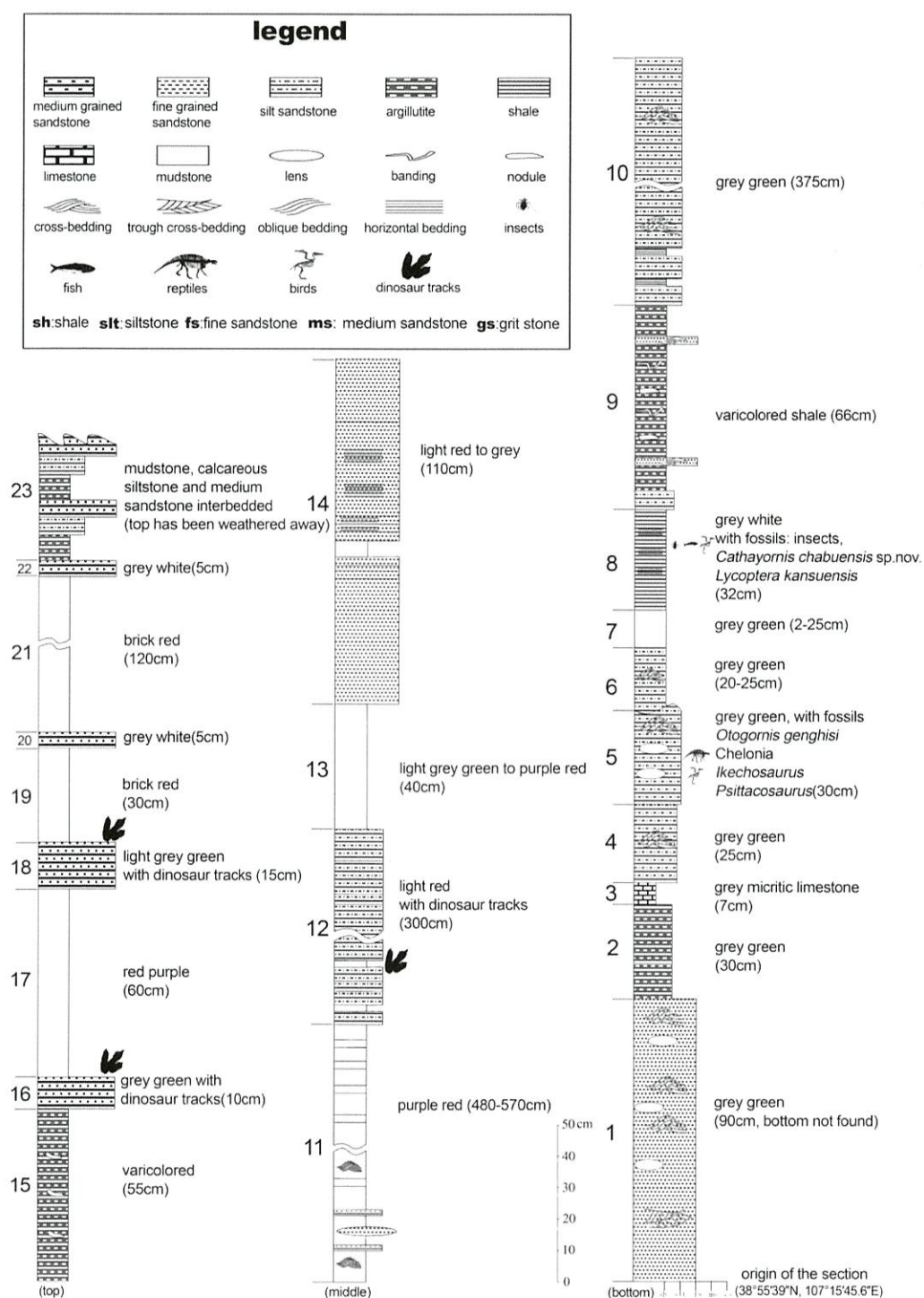


Figure 4. Stratigraphic section of the rock bearing dinosaur and bird tracks (from Li *et al.*, 2008).



Figure 5. *Chapus lockleyi* (from Li *et al.* 2006).

Ichtenogenus *Asianopodus* Matsukawa *et al.*, 2005

Ichnospecies *Asianopodus pulvinicalx* Matsukawa *et al.*, 2005 (Figs. 6, 7)

Diagnosis: Small to medium sized tridactyl, mesaxonic and subsymmetrical tracks with distinct bulbous heel impressions. Track is longer than wide. The digital divaricating angles are rather narrow.



Figure 6. *Asianopodus pulvinicalx* found in Otog Qi.



Figure 7. Trackway of *Asianopodus pulvinicalx*.

Ichnospecies *Asianopodus robustus* Li et al., 2011 (Fig. 8)

Diagnosis: Similar to that of the ichnogenus, while the toes and the metatarsophalangia pad are thicker than that of the type species, *Asianopodus pulvinicalx*, the angles between toes are larger, but the pace is shorter.

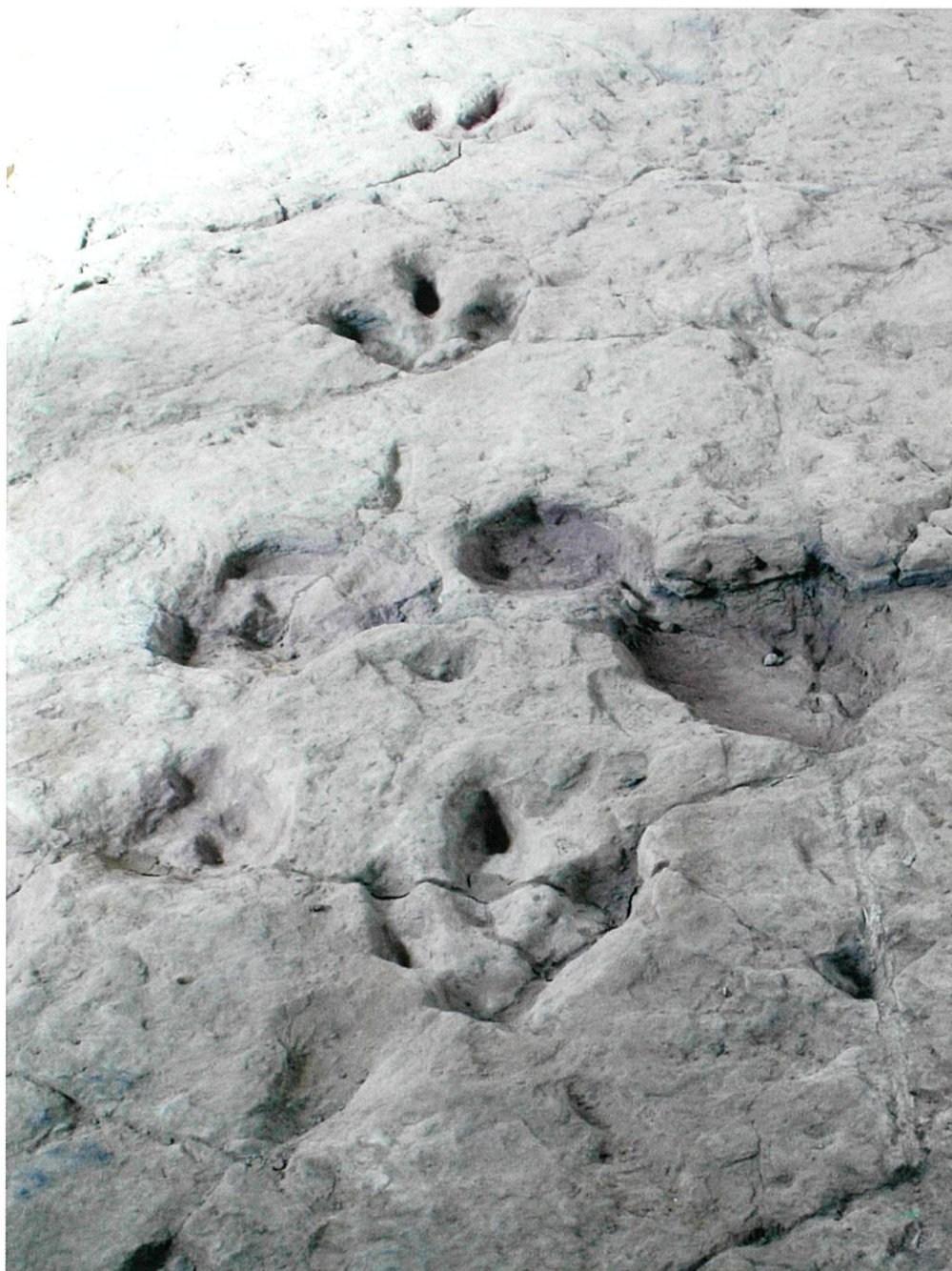


Figure 8. Trackway of *Asianopodus robustus*.

Infraorder Coelurosauria**Ichnofamily Grallatoridae Lull, 1904****Ichnogenus *Grallator* Hitchcock, 1858 (Lull, 1904)****Ichnospecies *Grallator* sp. (Fig. 9)**

Diagnosis: Small tridactyl tracks, digitigrade, tracks longer than wide, tracks are about 10 cm long and 6.5 cm wide, Digit III projection ratio (the projection of digit III beyond the length of the rest on the pes) is about 1, stride length is 92 cm. The dinosaur track ichnogenus *Grallator* is the most widely distributed dinosaur track genus in the world. They have been found on almost all continents. They are small bipedal, tridactyl tracks. because the steps are long the track makers are believed to have had long limbs and small compact feet.



Figure 9. *Grallator* ichnosp. in Otog Banner.

Suborder Sauropoda**Ichnofamily Titanosauridae****Ichnogenus *Brontopodus* Farlow *et al.*, 1989****Ichnospecies *Brontopodus birdi* Farlow *et al.*, 1989**

Diagnosis : Small or large quadrupedal tracks, manus somewhat U-shaped, with digit impression II-IV conjoined into one large pad, I and V slightly separated from the conjoined. Manus tracks are often rotated outward with respect to the direction of travel and are closer to middle line of the trackway. Pes longer than wide, with large, laterally directed claw marks at digits I-III, trackway broad, 1-1.5 times the pes length. The stride is 2-5 times the pes length. Step angle generally 100-120°. Tail drag marks are rare or absent. The track makers were similar to Titanosauri-formes.



Figure 10. Manus of *Brontopodus birdi*.



Figure 11. Trackway of *Brontopodus birdi*.

Class Aves Linnaeus, 1758**Ichnofamily indet.****Ichnogenus *Tatarornipes* Lockley *et al.*, 2012****Ichnospecies *Tatarornipes chabuensis* Lockley *et al.*, 2012
(Figs. 12, 13)**

Diagnosis: Medium sized sub-symmetric functionally tridactyl tracks with wide digit divarication and robust digit traces that are wider proximally than distally. Pad traces may be well defined. Trackway narrow with a relatively long step and little inward rotation. Both the robust width of the proximal digit traces and the long step with little inward rotation distinguishes *Tatarornipes* from other avian ichnotaxa.

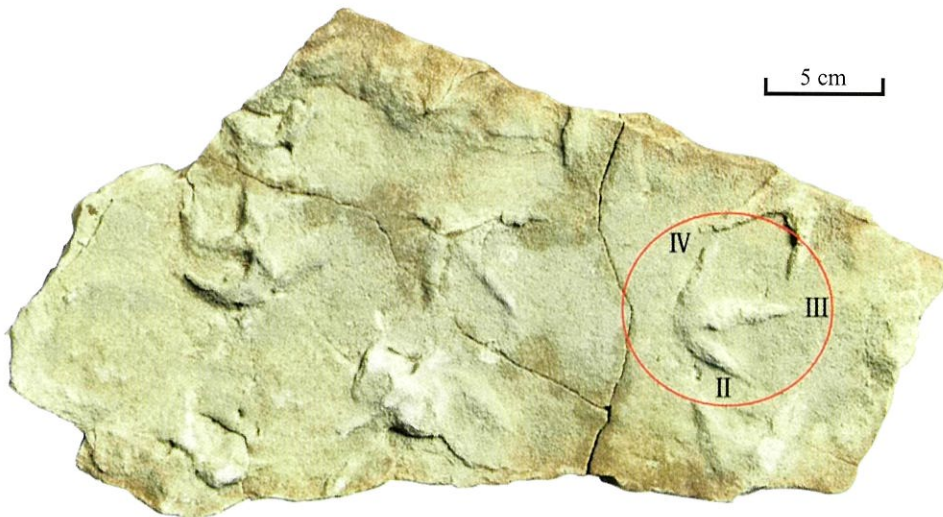


Figure 12. Holotype of *Tatarornipes chabuensis* (from Li *et al.*, 2009).



Figure 13. *Tatarornipes chabuensis* together with *Grallator* sp. (from Li *et al.*, 2011).

DISCUSSION

The importance of the tracks in the paleoenvironment and for determining the behavior of dinosaurs

Because the fossil tracks are preserved in the original position, where the ancient animals actually stepped, the tracks can well indicate the paleoenvironment the dinosaur lived in.

Indication of the edge of a lake

In tracksite 5 of the Chabu area in Otgo Banner, some three dimensionally preserved sauropod tracks

were found. The deep of the tracks could be seen clearly (Fig. 14). As shown in the fig. 14, tracks A1-A4 are four tracks in a trackway. These four tracks are preserved on the bank of a seasonal river so the side view of the tracks can be observed. From A1 to A4, the tracks become shallower and continued to a long trackway with 12 tracks going southeastwards. From these preserved features it is inferred that the track maker walked from the substrate with more moisture to a drier region, or from the lake to land. Then we can suppose that this tracksite shows the edge of a lake (Fig. 15).

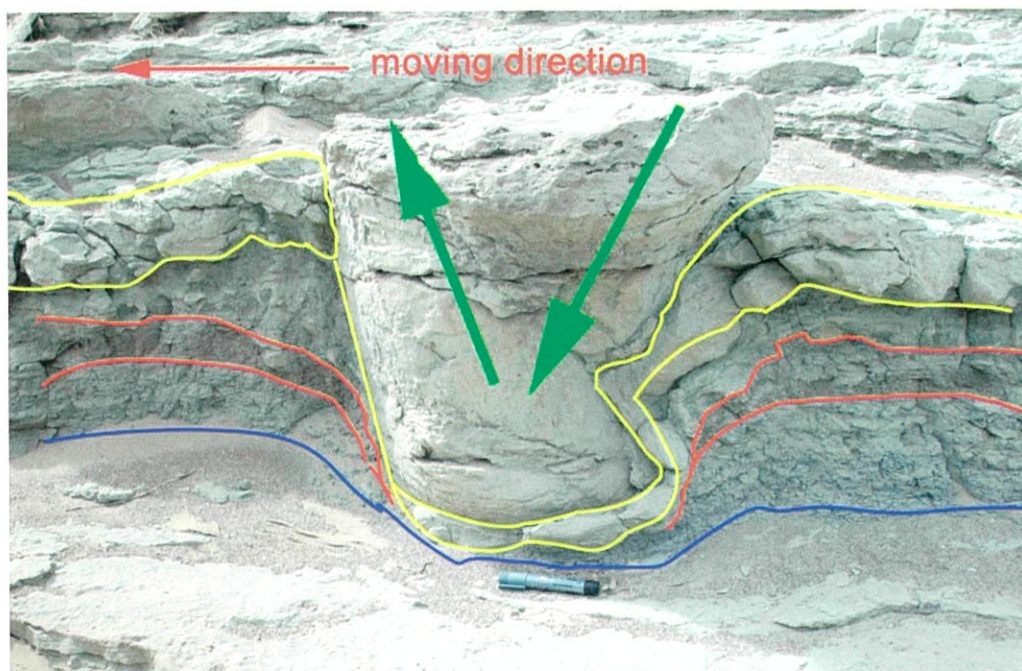


Figure 14. Three dimensional preserved track.

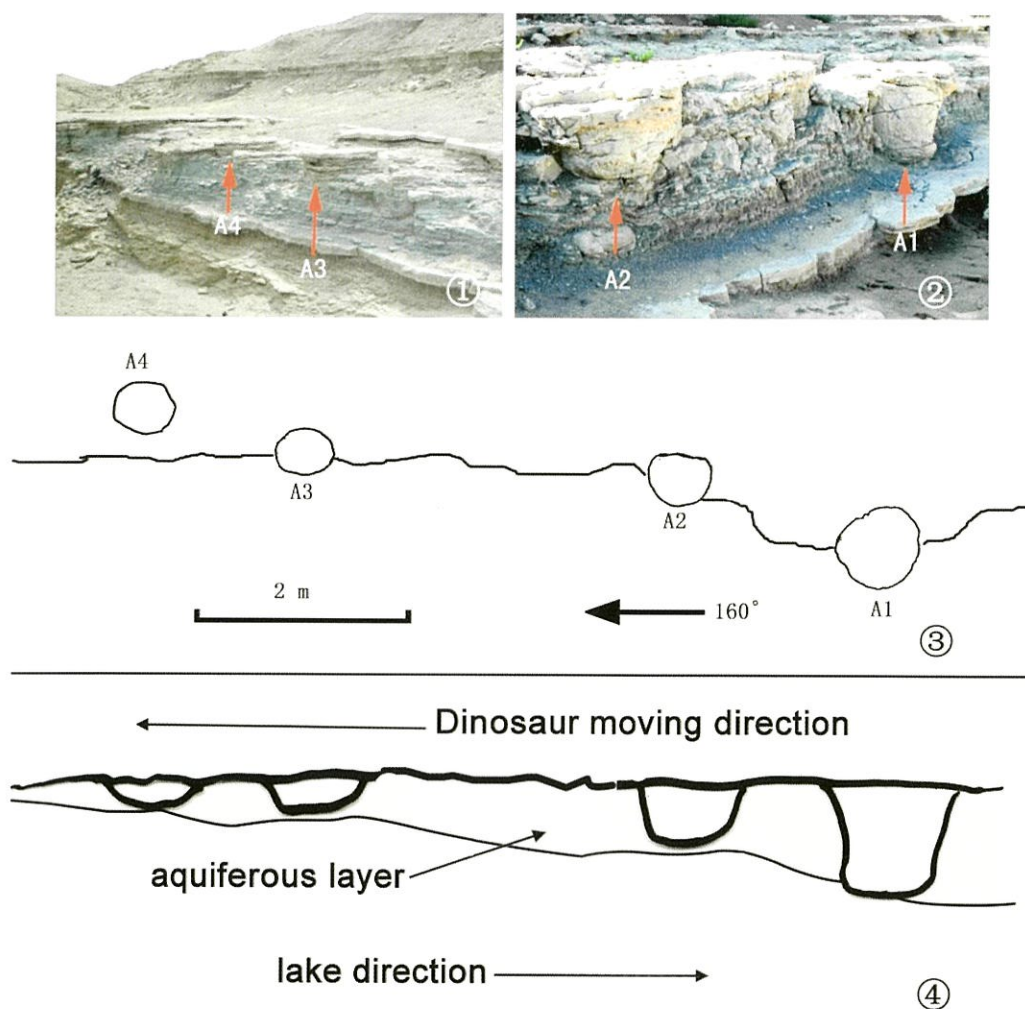


Figure 15. Three dimensional preserved tracks and their environmental importance. ①、② three dimensional preserved tracks, ③ map of the three dimensional preserved tracks; ④ paleoenvironment reconstruction; A1, A2, A3, A4 are four tracks in one trackway (from Li *et al.* 2011).

Gregariousness versus solitary living

Among dinosaur tracks, trackways are often parallel, which means that the dinosaurs that made them walked together in the same direction, indicating a gregarious lifestyle. In Otog Banner, some small theropod trackways, such as *Grallator* (Fig.16),

and sauropods, such as *Brontopodus birdi* (Figs. 17, 18), are found preserved in parallel. We can infer that the sauropods lived gregarious lives and the small theropods hunted in groups, while the large theropods often lived and hunted alone, because few large theropod trackways are found to be preserved in parallel (Figs. 7, 19).

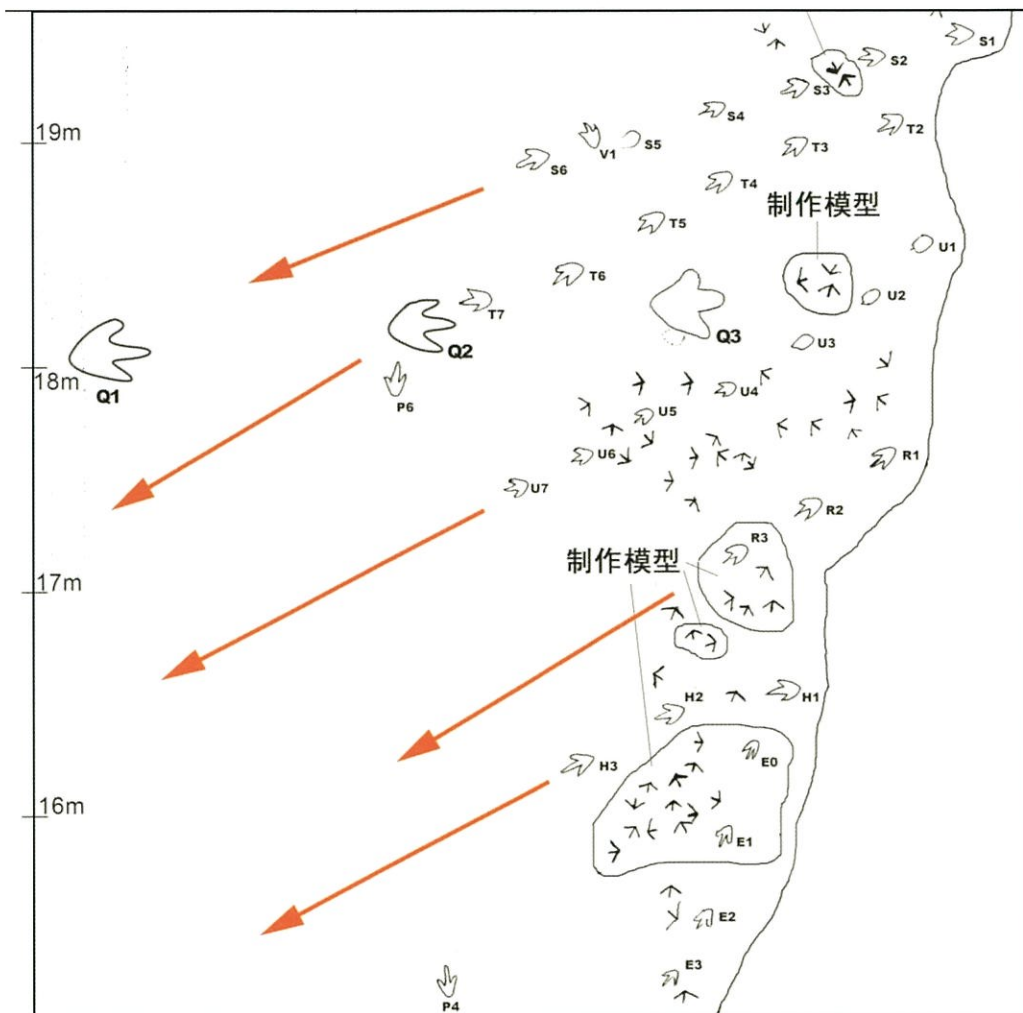


Figure 16. Map of tracksite 15 in Otog Banner showing the parallel trackways of *Grallator*: Red arrows show the direction of small theropod movement, they were in the same direction; the black arrows show the direction of large theropod movement, they were alone. The bird tracks are disorderly and unsystematic (from Li *et al.*, 2011).



Figure 17. Parallel sauropod trackways in tracksite 5 in Otog Banner.

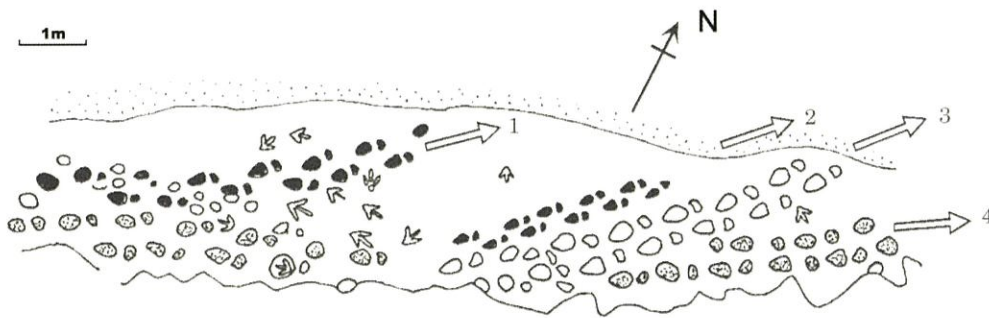


Figure 18. Map of the tracksite 6 in Otog, showing four parallel small sauropod trackways (from Lockley *et al.*, 2002).



Figure 19. Tracksite 16 in Otog, showing two trackways of large theropods that are in different directions.

Estimating the speed of a running dinosaur

It is well known that when we run, the steps are longer than when walking. The faster we run, the longer the steps will be, so with animals. There must be a functional

relationship between the length of the step and the speed of the moving animal. From observations of diverse living animals, including small mammals, humans, horses, elephants and birds, Alexander (1976) provided a formula to estimate the speed of a dinosaur.

$$V = 0.25 \cdot g^{1/2} \cdot \lambda^{1.67} \cdot h^{-1.17}$$

In the formula, (V) stands for the speed of dinosaur, (g) is the acceleration of gravity that roughly equals 9.8 m/s², (λ) is the stride length, which can be measured between the tracks in their original positions in the field, (h) is hip height and equals four times of the foot length, which can be measure from the tracks. Thulborn (1990) suggested another formula for fast running animals.

$$V = [gh(SL/1.8h)^{2.56}]^{0.5}$$

Thulborn also recommended that for trotting gaits the mean of his and Alexander's formula should be used. The University of Sheffield has produced an online Dinosaur Speed Calculator (<http://www.sorbygeo.logy.group.shef.ac.uk/DINOC01/dinocal1.html>), which avoids the need to work out Alexander's rather complex formula by allowing users to input trackway parameters of stride length and foot size. This calculator was used to analyse the data presented here.

At tracksite 5 of Otog Banner we found a dinosaur trackway with very long strides (Fig. 20). The foot length is 0.28 m while the stride is as long as 5.6 m ($g=9.8$; $\lambda=5.6$; $h=4 \times 0.28$). Using Alexander's method we calculated the speed to be 43.85 km/hour, and for Thulborn's calculation, it is 44.14 km/hour. This is so far a world record for the calculated speed of a dinosaur. By

way of comparison, Usain Bolt, the world champion of sprint, widely regarded as the fastest person ever, can attain a speed of 37.38 km/hour.

Inferring the paleoenvironment

From the formation and preservation of the dinosaur tracks described above, we know that after the dinosaurs had left their tracks, they needed strong sunlight for a period of time to solidify before being buried by mud and sand with the next flood. The longer the sun shone on the tracks, the stronger they would be, and the better track fossils would be formed. In Otog Banner, a lot of well-preserved track fossils have been found in the Lower Cretaceous Jingchuan Formation. It can be inferred that Otog Banner got a lot of sunshine in Jingchuan times in the Early Cretaceous, which means that Otog Banner suffered drought conditions when the track makers walked there.

The ichnological associations in the Otog dinosaur track assemblages appears to be saurischian dominated and ornithischian dinosaurs appear to be completely lacking. Sauropod tracks are quite common in fluvio-lacustrine facies associated with inland, semi-arid settings (Lockley *et al.*, 2002). Perhaps the best Jurassic example is the Morrison Formation, where both sauropod body fossils and tracks are common (Dodson *et al.*, 1980; Lockley *et al.*, 1998). As in the Jingchuan formation in Otog Banner, in the Morrison formation theropod

tracks are also abundant and ornithischian tracks are rare. The Morrison Formation comprised arid or semi-arid deposits. Lockley *et al.* (1994) noted the association of inland sauropod ichnofaunas with semiarid

climatic regimes. There is, perhaps, a tendency for saurischian-dominated assemblages to be associated with semi-arid inland basin settings (Lockley *et al.*, 2002), which is supported by the tracks in this study.



Figure 20. Trackway left by the fastest known running dinosaur.

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Dinosaur migration

We measured in detail more than 1,500 dinosaur tracks and more than 100 bird tracks found in Otog. We found that the directions of most tracks are north-east. We draw a rose-diagram to show the directions of the dinosaur and bird tracks in Otog (Fig. 21). The petal pointing the north-east is the longest, indicating that most tracks walking to the north-east direction, only one way. The fact that most dinosaurs walked one direction implies that they were just passing by the Otog and left their tracks here and walked away, i.e. that they subsequently migrated to a place with more water.

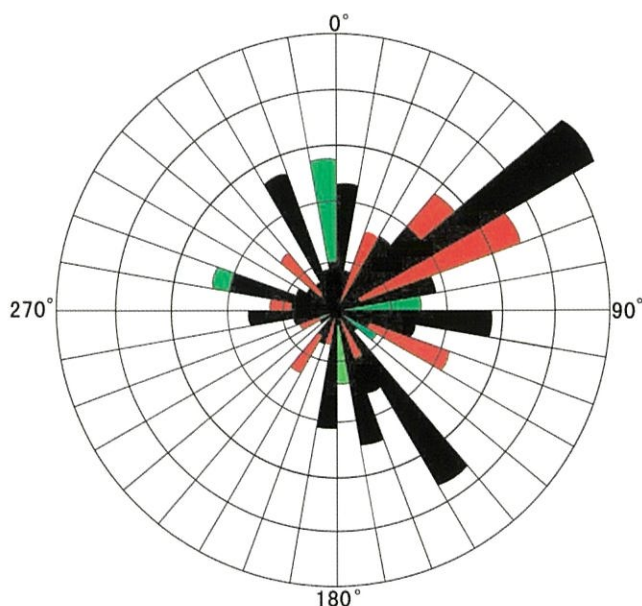


Figure 21. Rose-diagram of dinosaur track direction (From Li *et al.* 2011).

CONCLUSION

Some paleoenvironmental and dinosaur behavioral conclusions have been drawn based on the dinosaur footprints found in Otog Banner, Inner Mongolia. Different depths of the three-dimensionally preserved sauropod tracks informed the understanding of the edge of an ancient lake in tracksite 5 of Otog. Some parallel trackways imply that sauropods and small theropods lived and hunted in groups while large theropods often left single trackways suggesting a solitary lifestyle. Because there is a functional relationship between the length of step and the speed of the animal, dinosaur speed could be estimated by measuring the distances between tracks and the fastest speed of the dinosaurs was nearly 44 km an hour. Otog area suffered arid or semi-arid weather when the tracks were made

in the Jingchuan period in the Early Cretaceous. The tracks were dominated by sauropods and many well preserved tracks were discovered. Because many tracks are unidirectional, at least some dinosaurs migrated during dry seasons.

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