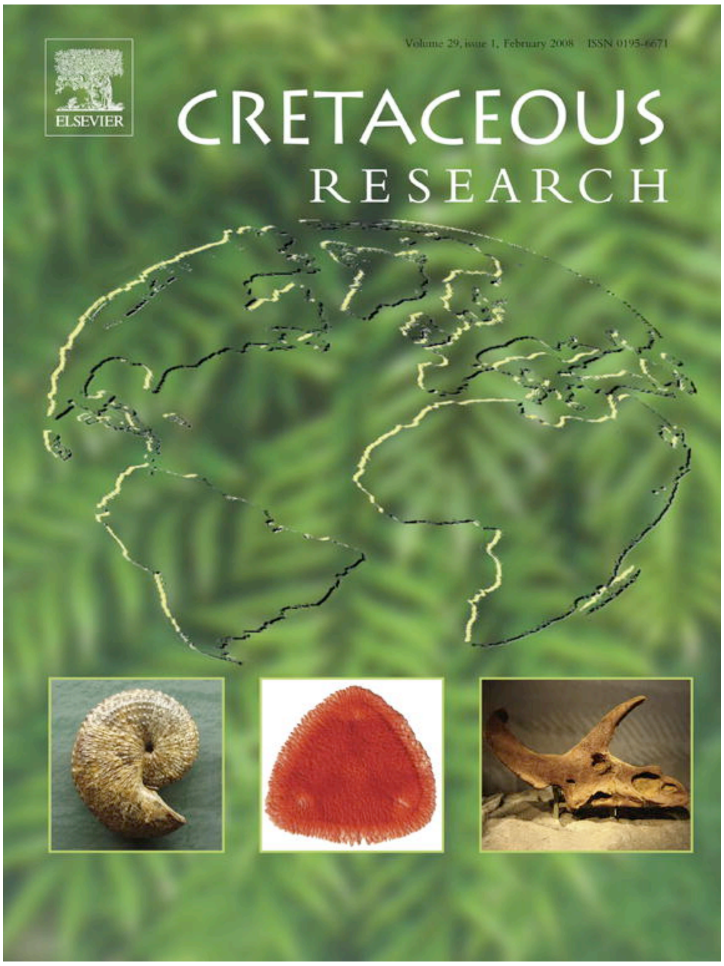
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Minisauripus—the track of a diminutive dinosaur from the Cretaceous of China and South Korea: implications for stratigraphic correlation and theropod foot morphodynamics

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Abstract

The diminutive (2.5–3.0 cm long), Cretaceous dinosaur track ichnogenus *Minisauripus*, previously known only from the type ichnospecies, *M. chuanzhuensis*, from a single locality in Sichuan Province China, is here reported from two new localities in South Korea and one in China. Material from the new Chinese locality is assigned to the new ichnospecies *M. zhenshuonani* on the basis of its distinctive morphology. Most of the new material is well-preserved, revealing narrow asymmetric tracks with claw traces, long step and phalangeal formula (2-3-4 for digits II, III and IV, respectively), suggesting a theropod track maker rather than an ornithischian, as originally inferred for the Chinese type material.

The South Korean samples (eight tracks), from two localities in the Haman Formation, are considered Early Cretaceous (Aptian-Albian) in age, whereas the Chinese type material (21 specimens) has been assigned both an Early and Late Cretaceous age. The former age is probably correct as suggested by a new *Minisauripus* locality (5 specimens) from the Early Cretaceous (Barremian-Albian) of Shandong Province, China.

Other diminutive tracks from the Sichuan fauna include *Aquatilavipes sinensis* (2.5 cm long, a possible junior synonym of *Koreanoris hamanensis*), *Grallator emeiensis* (2 cm long) and *Velociraptorichnus sichuanensis* (10–11 cm), which occur, in various combinations, with *Minisauripus* at both the new Korean and Chinese localities.

In *Minisauripus*, digit III is very short in comparison with other theropods and provides a striking contrast to *G. emeinsis*. This difference has significant implications for standard assumptions about theropod track allometry. Based on the classic Early Jurassic forms *Grallator* and *Eubrontes*, it has long been inferred that relative digit III length shrank with increasing size (up to foot lengths of 30–40 cm). The reiteration of reduction in relative length of digit III in specimens in the size range of 2–3 cm indicates that the allometric or morphodynamic 'program' that influenced development in large theropod clades reiterated fractally in theropod clades a full order of magnitude smaller. This shows that a given allometry can be size-dependent in one clade and size-independent in another. Thus, the developmental program appears 'contracted' or morphologically miniaturized by heterochrony to manifest paedomorphically in some clades and peramorphically in others. This strongly suggests that 'formal' developmental 'programs operated' along similar morphodynamic lines in quite different clades.

Keywords: Early Cretaceous; Stratigraphic correlation; China; Korea; Dinosaur footprints; *Minisauripus*

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1. Introduction

Zhen et al. (1995) described a distinctive ichnological assemblage from the Early Cretaceous of Sichuan Province, China. This ichnofauna included several diminutive ichnotaxa that had not previously been reported, including *Minisauripus chuanzhuensis*, *Aquatilavipes sinensis* (a possible junior synonym of *Koreanornis hamanensis*), *Grallator emeiensis* and *Velociraptorichnus sichuanensis*. With special reference to *Minisauripus*, we herein report the occurrence of three of these ichnotaxa in various combinations at two localities in South Korea and an additional locality in China. Although Chen et al. (2006) recently inferred that the Sichuan locality is Late Cretaceous in age, rather than Early Cretaceous as originally proposed, the discovery of these Sichuan ichnofaunal elements at localities for which an early Cretaceous age is strongly supported (see below) suggests that the original age assignment was correct.

Lower Cretaceous sedimentary rocks of South Korea are well-known for abundant vertebrate tracks. Most of these fall clearly into the following categories: 1. Dinosaurs (Lim et al., 1989, 1994, 1995; Lee et al., 2000, 2001; Yang et al., 2003; Huh et al., 2003, 2006; Lockley et al., 2006a); 2. Birds (Kim, 1969; Lockley et al., 1992; Yang et al., 1995, 1997; Kim et al., 2006; Lockley et al., 2006b); or 3. Pterosaurs (Lockley et al., 1997; Hwang et al., 2002; Kim et al., 2006).

These tracks have been quite intensively studied in recent years, leading to an improved understanding of typical ichnofacies associations. The tracks come from several different geological basins. The largest is the Gyeongsang Basin which contains two extensive units – the Haman and Jindong formations – that are particularly rich in tracks. These have been dated as late Early Cretaceous (Aptian-Albian) by Matsukawa et al. (1998, 2006a), although younger dates have also been proposed by (Huh et al., 2003). The predominant track types are ornithopods (cf. *Caririchnium*) and sauropods (cf. *Brontopodus*), with associated bird tracks (mainly *Koreanornis* and *Jindongornipes*). As discussed below, the large dinosaur tracks from these formations appear to be widespread and have so far only been assigned to the aforementioned ichnogenera, *Caririchnium* and *Brontopodus*, both of which occur in North America as well as Asia (Lockley and Hunt, 1995; Lockley and Matsukawa, 1998). In the case of *Brontopodus*, the record extends to Europe (Lockley and Meyer, 2000) and other continents (Lockley et al., 1994). At most localities, especially in the Gyeongsang Basin, theropod tracks are relatively rare (Lockley et a1., 2006a) though in some of the smaller basins in southwestern Korea, theropod tracks are locally abundant (Huh et al., 2006).

Thus, the discovery of the highly distinctive and diminutive (2.5–3.0 cm long) theropod track ichnogenus *Minisauripus* at two localities in Namhae Province, South Korea, adds significantly to the Korean track record (Figs. 1 and 2). This track type was previously only known from a single locality in Sichuan Province, China (Zhen et al., 1995), but is now also known from a second Chinese site in Shandong Province, where it is primarily represented by larger tracks (5–6 cm long). These discoveries also pose interesting questions about the *Minisauripus* track maker and its distribution. Therefore, the primary purpose of this paper is to describe these tracks and amend the morphological and systematic diagnosis and descriptions. We also discuss the affinity of the track maker, and the implications of the tracks for correlation between South Korea and China. A further objective is to discuss the broader implications of *Minisauripus* morphology for previous ideas about allometric growth patterns in the theropod foot and place these patterns in the framework of heterochrony.

The discoveries of the new *Minisauripus* sites were made by the present authors as the result of three separate studies and expeditions between 2004 and 2006. Following the study of the original discovery site in Sichuan, China (J.L. and colleagues), the new finds, in chronological order, are designated as follows: Korean *Minisauripus* locality 1 (KML1), found by M. G. L. (with S-Y.Y. and M.M.) in 2004 (Lockley et al., 2005) and supplemented by a discovery (by J-Y.K.) in 2006; KML2, found by the J-Y.K., K-S.K. and S-H.K. team in 2005 and 2006, and the new *Minisauripus* tracks from Shandong Province, China found by R.L., M. G. L. and M. M. in 2006. In the interests of scientific consistency and coherence, these three teams have worked collaboratively to describe the new material and assess its morphological variation and implications for ichnotaxonomy. As part of this collaboration, replicas of all available specimens have been assembled in the CU Denver collections (replicas with CU prefix) and distributed as necessary to other institutions with which the authors are affiliated. In some cases, the original material remains in the field.

2. Geological setting and material

2.1. *Minisauripus* type locality and type material

The type of *Minisauripus chuanzhuensis* (Zhen et al., 1995, 1996) originates from the Emei dinosaur track site at Xingfuya, near Chuanzhu town, Emei County, Sichuan Province (Fig. 1: 29° 36′ 12.72″ N, 103° 26′ 34.86″ E). Associated tracks include *Grallator emeiensis*, *Velociraptorichnus sichuanensis*, and *Iguanodonopus xinduensis*. They occur in the Jiaguan Formation, outcrops of which are distributed in the southwestern Sichuan Basin and that was originally assigned an Early Cretaceous age (Zhen et al., 1995) before being assigned to the Upper Cretaceous (Chen et al., 2006) based on the similarity of the ostracodes listed below to those found in the Upper Cretaceous of NW China. The track-bearing sequence comprises brownish-red and lateritic sandstone and siltstone with shale and basal conglomerate in the lower part (391 m) and brownish-red and lateritic mudstone and siltstone intercalated with thin-bedded shale, marl, and gypsum in the upper part (894 m). It unconformably overlies the Lower Cretaceous Tianmashan Formation or Upper Jurassic Penglaizhen Formation, and it yields the ostracodes *Cypridea tera*, *C. gunzulingensis*, *C. enodata*, and *Kaitunia cuneata*. These fossils are also found in Upper Cretaceous strata in northeastern China, but it is unclear whether they are reliable age indicators.

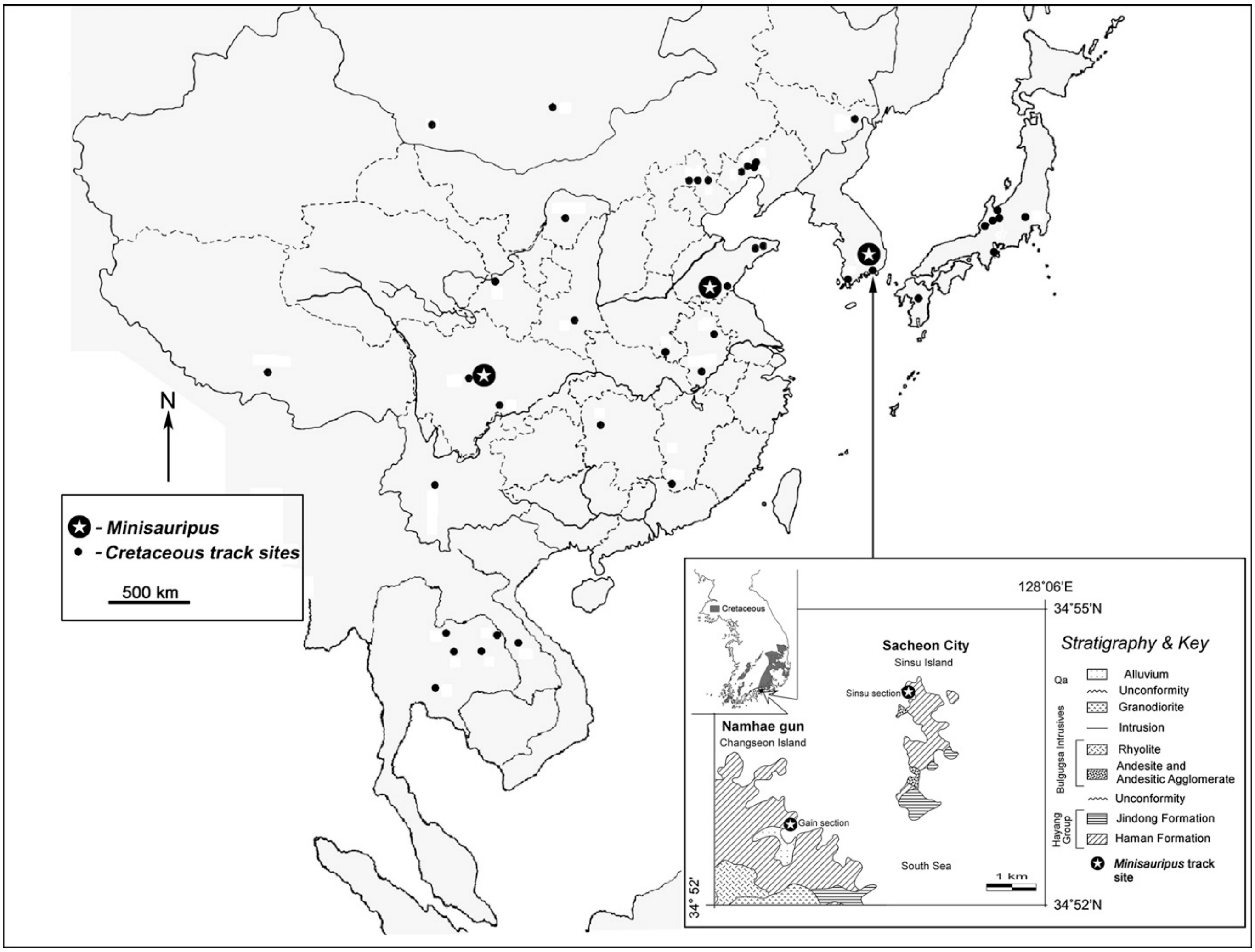

Fig. 1. Locality map for South Korean and Chinese tracksites yielding *Minisauripus*. Inset shows that there are two Korean localities in close proximity. See Fig. 2 for Chinese stratigraphy.

The type material of *Minisauripus chuanzhuensis* consists of specimens CFEC A-1 to A-21 in the Chongqing Natural History Museum. The material originates from the ''Upper Cretaceous'' Jiaguan Formation of Emei County, Sichuan Province, China (Figs. 3 and 4). Prior to this study only the holotype (A-1) had been illustrated. It was not possible to examine this material during the early stages of our study because it was on loan for a traveling exhibit. However, while the paper was in review, one of us (J. L.) was able to obtain molds of the type material which allowed us to verify the published record, (Zhen et al., 1995), make replicas (CU 214.124-214.126), illustrate topotype and paratype material (Fig. 4), and provide all the pertinent information presented herein.

2.2. Korean sites KML1- KML2

The Korean *Minisauripus* localities (KML1-KML2) from the Haman Formation form part of the non-marine Kyongsang Supergroup (Chang, 1975) that has been divided, in ascending stratigraphic order, into the Sindong (Berriasian to Barremian), Hayang (Aptian to middle Albian), and Yucheon groups (upper Albian to Cenomanian) and the Bulgugsa intrusives (Chang, 1982; Fig. 2). Again in these age assignments we follow Matsukawa et al. (1998, 2006a) because of our concerns that younger dates suggested by Huh et al. (2003) may be the result of 'resetting' by regional and thermal metamorphism (Houck and Lockley, 2006). The Sindong Group mainly consists of alluvial fan, floodplain, and lacustrine deposits, the Hayang Group of floodplain and lacustrine sediments intercalated with minor volcaniclastic sediments (Um et al., 1987), and the overlying Yucheon Group of volcanic rocks. The Hayang Group consists, in ascending order, of the Chilgog Formation, Silla Conglomerate, and Haman and Jindong formations. The Haman Formation lies conformably on the Silla Conglomerate. It is mainly composed of reddish shale and sandy shale, and white to greenish and gray sandstones with minor intercalating tuffaceous and pebbly sandstone. They are metamorphosed locally into compact hornfels with a reddish colour in the lower levels and with greenish grey colour in the higher levels of the formation (Chi et al., 1983).

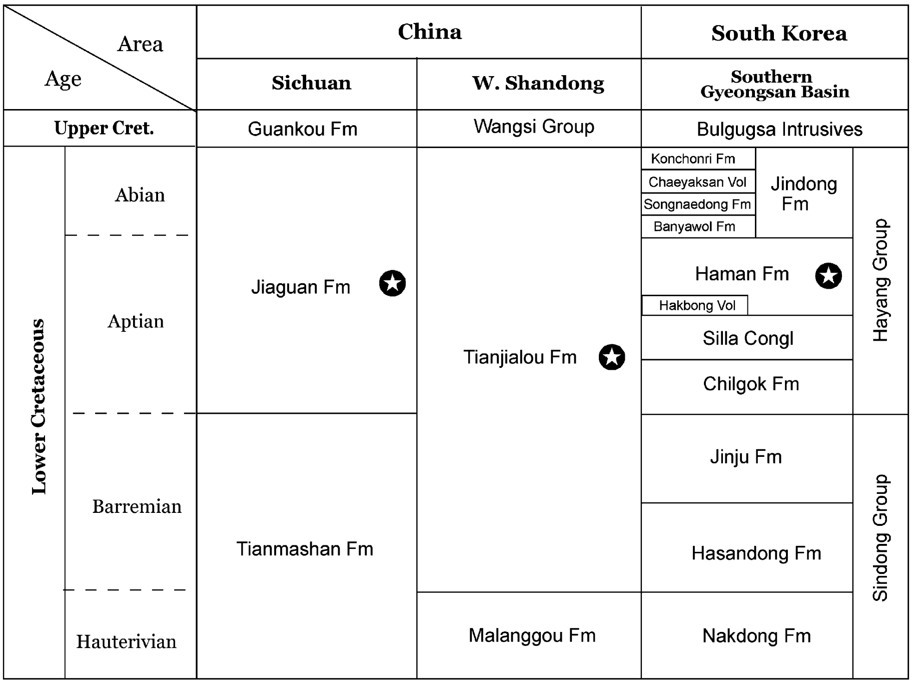

Fig. 2. Simplified stratigraphy for South Korean and Chinese tracksites (modified from Chen et al., 2006; Lockley et al., 2006a).

The Haman Formation generally dips 10°–20° SE and was intruded by the Bulgugsa intrusives. The ichnofauna includes dinosaur footprints and four kinds of bird tracks: *Koreanornis hamanensis* (Kim, 1969; Lockley et al., 1992; Baek and Yang, 1997), *Jindongornipes hamanensis* (Baek and Yang, 1997), *Uhangrichnus chuni* (Baek and Yang, 1997) and *Ignotornis yangi* (Kim et al., 2006). The latter are similar or identical to unnamed tracks of web-footed birds also reported from the Haman Formation (Lim et al., 2000). Together with these footprints, diverse invertebrate trace fossils, ripple marks, mud cracks and raindrop imprints (Seo, 1997; Baek and Yang, 1997) represent a lakeshore environment (Lim et al., 2002).

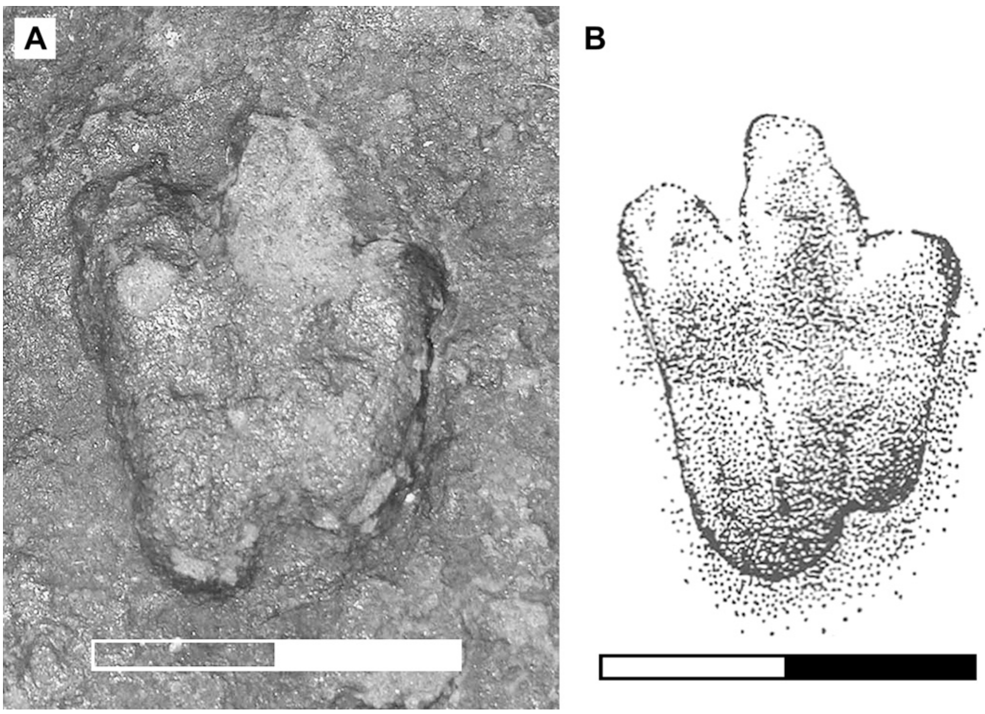

Fig. 3. Photograph (A) and drawing (B) of Chinese type *Minisauripus chuanzhuensis*, from Sichuan. B after Zhen et al. (1995, fig. 6).

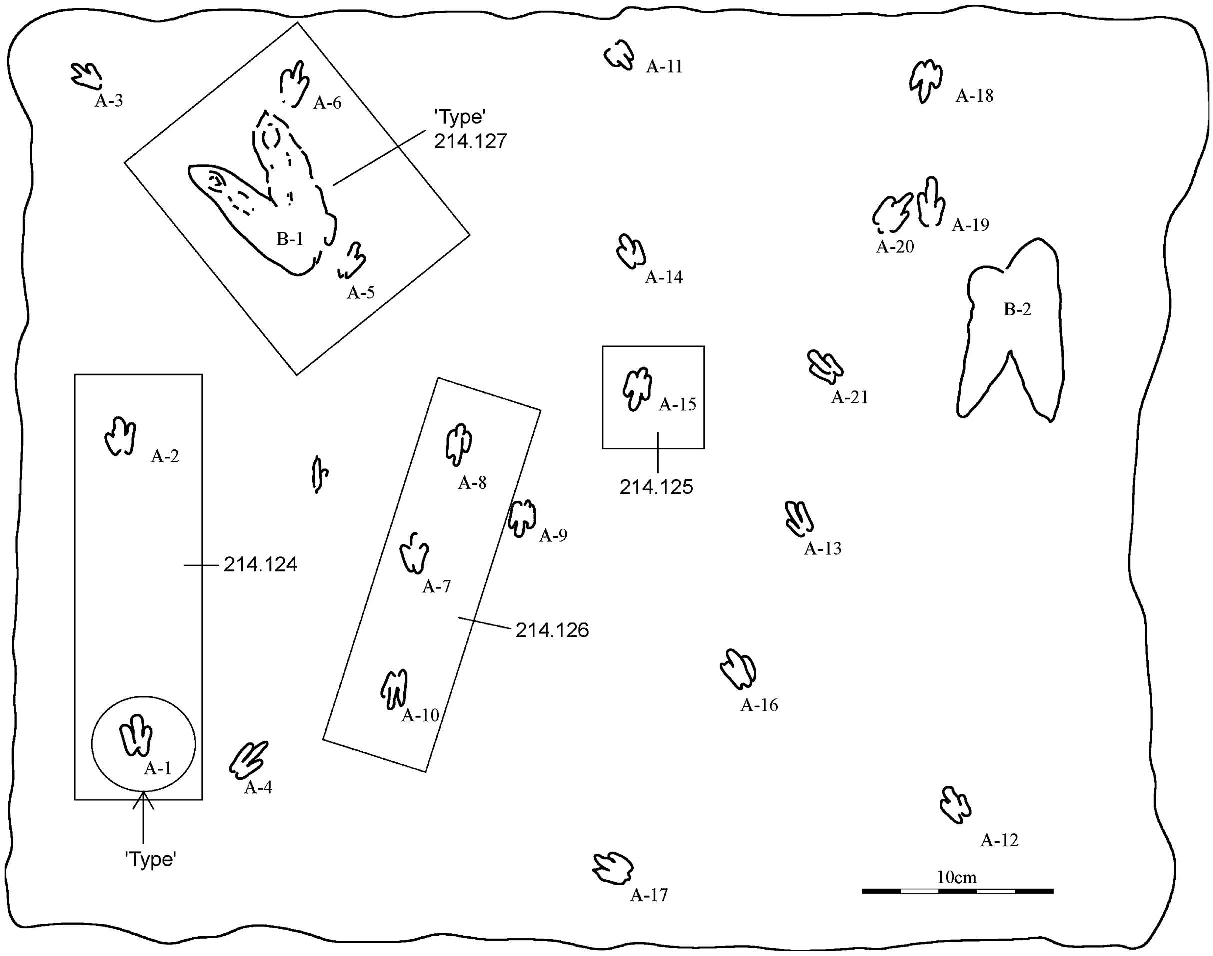

Fig. 4. Line drawing of *Minisauripus* type slab with number on tracks (A-1 to A-21) corresponding to numbering scheme in Zhen et al. (1995). Holotype (A-1) and the following footprint (A-2) represent a step and corresponds to replica CU 214.124. The A-7, A-8, A-10 group is preserved as replica CU 124.126, with A-8 and A-10 representing a step. A-15 corresponds to CU 214.125. This slab also preserves the type of *Velociraptorichnus* (B-1) and paratype (B-2).

2.2.1. KML1: the first Korean discovery

KML1 revealed *Minisauripus* from the Gain section of Changseon Island, Namhae Province, South Korea. These beds are in the middle part of the Haman Formation (Fig. 2), which consists of centimeter-scale rhythmic alternations of fine-grained siliciclastic sediment. Here, in the northeast of Changseon Island, the fine- to medium-grained sandstone frequently exhibits parallel lamination, cross-stratified lamination, convolute bedding, flame structures and ripple marks. Fossil plants, raindrop imprints, and mud cracks are also observed on the bedding planes of the interbedded shale to mudstone.

Specimens herein attributed to cf. *M. zhounanensis*, ichnosp. nov., found by the senior author in the Haman Formation of Changseon Island, consist of two tracks found on a single slab numbered KPE 61010 in the Kyungpook National University collections, Taegu (Figs. 5 and 6). A replica of this specimen is also reposited in the University of Colorado at Denver Dinosaur Tracks Museum collections (specimen number CU 214.101). A preliminary report of this discovery was given by Lockley et al. (2005).

Further investigation of the KML1 site (by J-Y.K.) revealed another *Minisauripus* track cast (Fig. 5). This specimen (CU 214.128) may come from a similar horizon as the two tracks on the loose block of the original discovery. However, the new discovery at this site, unlike the first, is associated with a surface that shows rain drop impressions.

2.2.2. KML2: the second Korean discovery

KML2 reveals *Minisauripus* tracks from the Sinsu section of Sinsu Island, Namhae Province, that occur in the lower middle part of the Haman Formation (Fig. 2), about 340 m stratigraphically lower than the tracks at the first discovered site in the Gain section (Changseon Island). In the section on northwest Sinsu Island, the fine- to medium-grained sandstone frequently exhibits parallel lamination, cross lamination, and ripple marks. Fossil plants, bird footprints, sauropod and theropod tracks, invertebrate trace fossils such as *Palaeophycus* ichnosp. and *Cochlichnus anguineus*, raindrop imprints, and mud cracks are also observed on the bedding plane of the section.

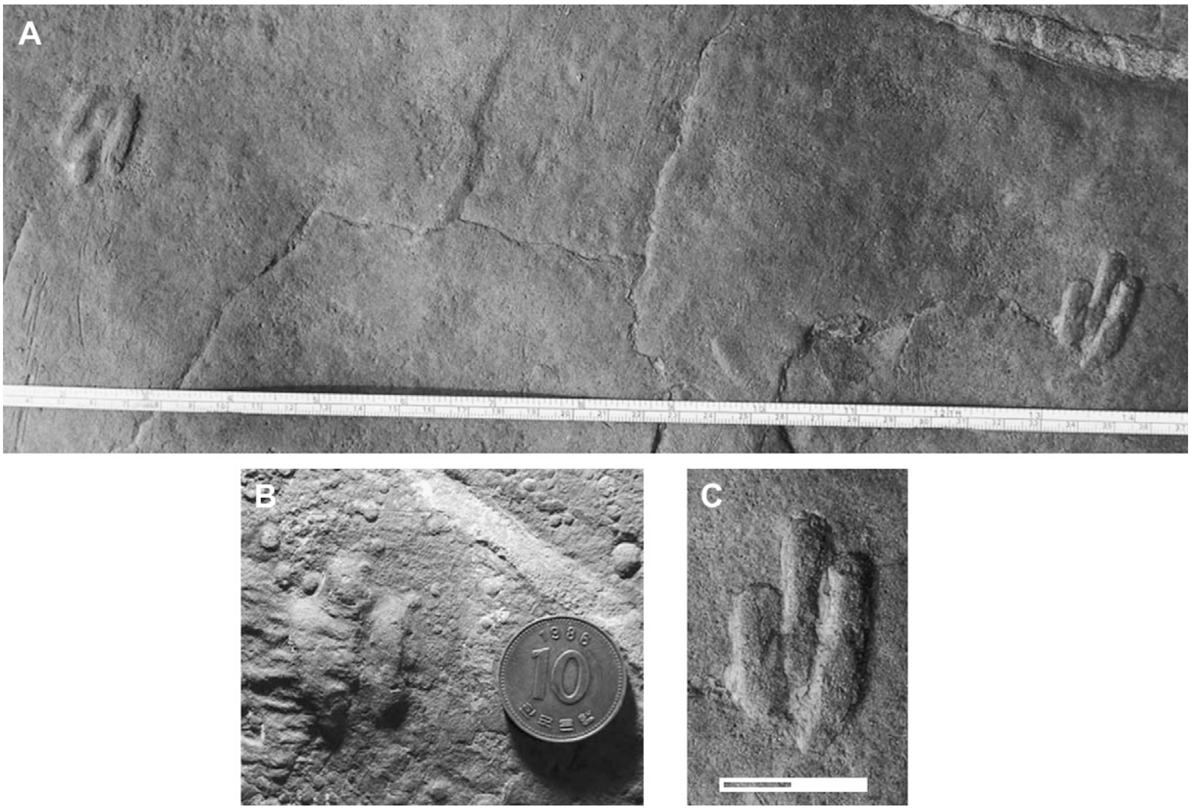

Fig. 5. A, photograph of two *Minisauripus* tracks from KML1 site, Haman Formation, Changseon Island. B, a third *Minisauripus* track from Changseon Island; coin diameter 2.3 cm. C, detail of track shown on right of Fig. 5A. Compare with Fig. 6.

Minisauripus material from this site consists of a single trackway consisting of three steps and four partial tracks, one of which includes claw impressions (Fig. 7). This specimen is designated no. KNUE 051101 in the Korea National University of Education collections (Cheongwon, Chungbuk). It is distinguished from the isolated Changseon 'tracks,' as the first *Minisauripus* 'trackway' found in Korea. A replica of this specimen is also reposited in the University of Colorado at Denver Dinosaur Tracks Museum collections (specimen number CU 214.102). Further investigation of the site (by J-Y.K.) has revealed another specimen consisting of two tracks preserved as impressions in a single trackway (Fig. 8). A replica

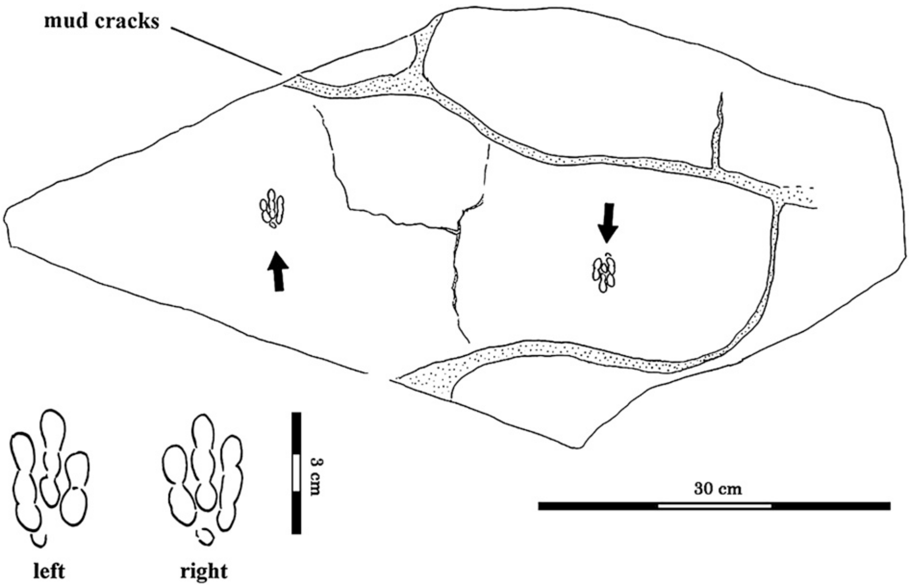

Fig. 6. Drawing of slab with two *Minisauripus* tracks from KML1 site, Haman Formation, Changseon Island, with detail of both tracks (lower left). Black arrows show that the two tracks represent individuals moving in opposite directions. Compare with Fig. 5.

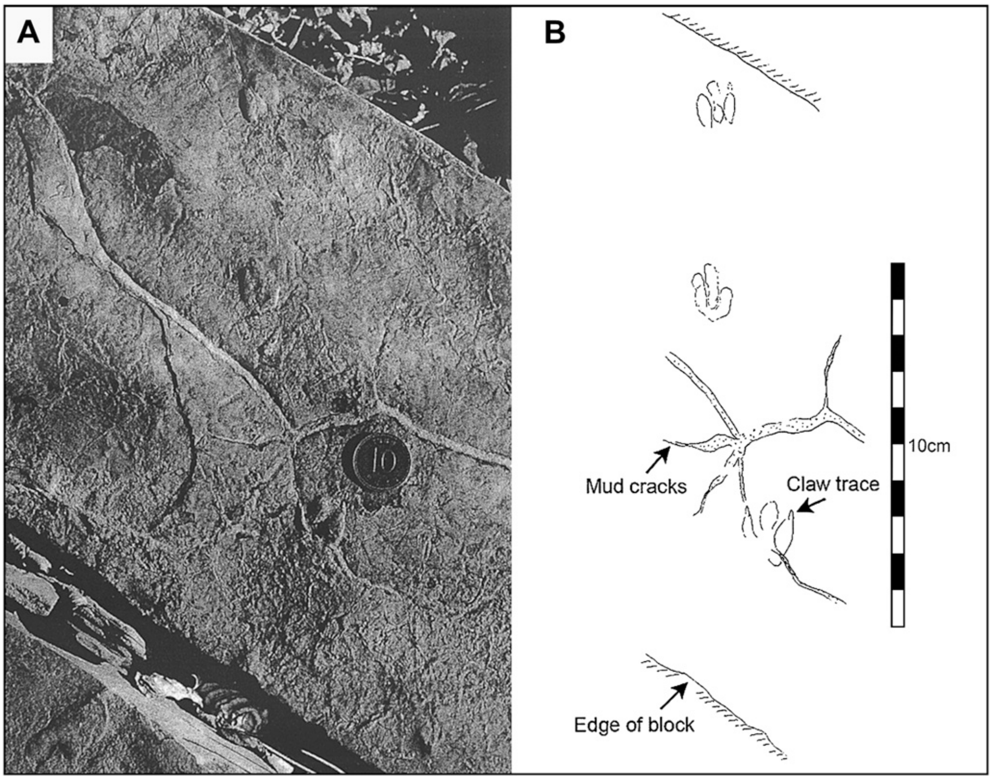

Fig. 7. Photograph and drawing of first discovered South Korean *Minisauripus* trackway from KML2 site, Haman Formation, Sinsu Island.

of this specimen, the second *Minisauripus* trackway from Korea, is preserved in the CU Denver collections as CU 214.129.

2.3. Shandong site

The third new *Minisauripus* site is from bed 12 (*sensu* Li et al., 2005a,b) of the fluvial and lacustrine deposits of the Tianjialou Formation (Early Cretaceous, Barremian-Albian), Houzoushan Dinosaur Park, Linquan town, Junan County, Shandong Province, China. The section in this region has been described by Li et a1. (2005a, p. 1150, 2005b) as consisting of 'light grey purple medium-grained feldspar sandstone, interbedded with dark purple muddy siltstone to form rhythms.' '...well developed sedimentary structures, such as mud cracks, ripple marks;' raindrop impressions also occur. The *Minisauripus* tracks are associated with two thin mudstone laminae or drapes that separate thicker sandstone beds.

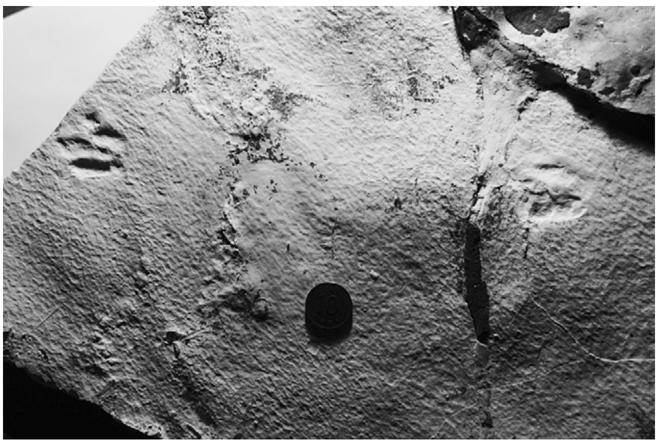

Fig. 8. Photograph of second found South Korean *Minisauripus* trackway from KML2 site, Haman Formation: numbered as replica CU 214.129. Coin diameter 2.3 cm.

The Shandong sample consist of three 'large' tracks (about 6.0 cm) long, two of which occur as part of a trackway, and a single 'small' track (3.0 cm long) that occurs at a different stratigraphic level only about 30 cm above the horizon with the larger tracks (Figs. 9 and 10). The two tracks in sequence are designated CU 214.103 and 214.104, and the other large track from this horizon is CU 214.105. The small track from the upper level is CU 214-106 (Fig. 9D), and its affinity to either of the two *Minisauripus* ichnospecies is uncertain, owing to problems of preservation.

3. Track descriptions and ichnotaxonomy

3.1. General descriptions

Type *Minisauripus chuanzhuensis* tracks from Sichuan Province, China, were originally diagnosed as 'small (less than 3 cm long)' and 'bipedal' with phalangeal pads that are 'not very clear' and 'stride and pace very long' (Zhen et al., 1995, p. 115). In the accompanying description, based on 21 specimens, the length was given as between 2.1 and 3.0 cm and the width as between 1.6 and 1.8. The toes were described as 'thick,' each with 'two phalangeal pads.' The step lengths

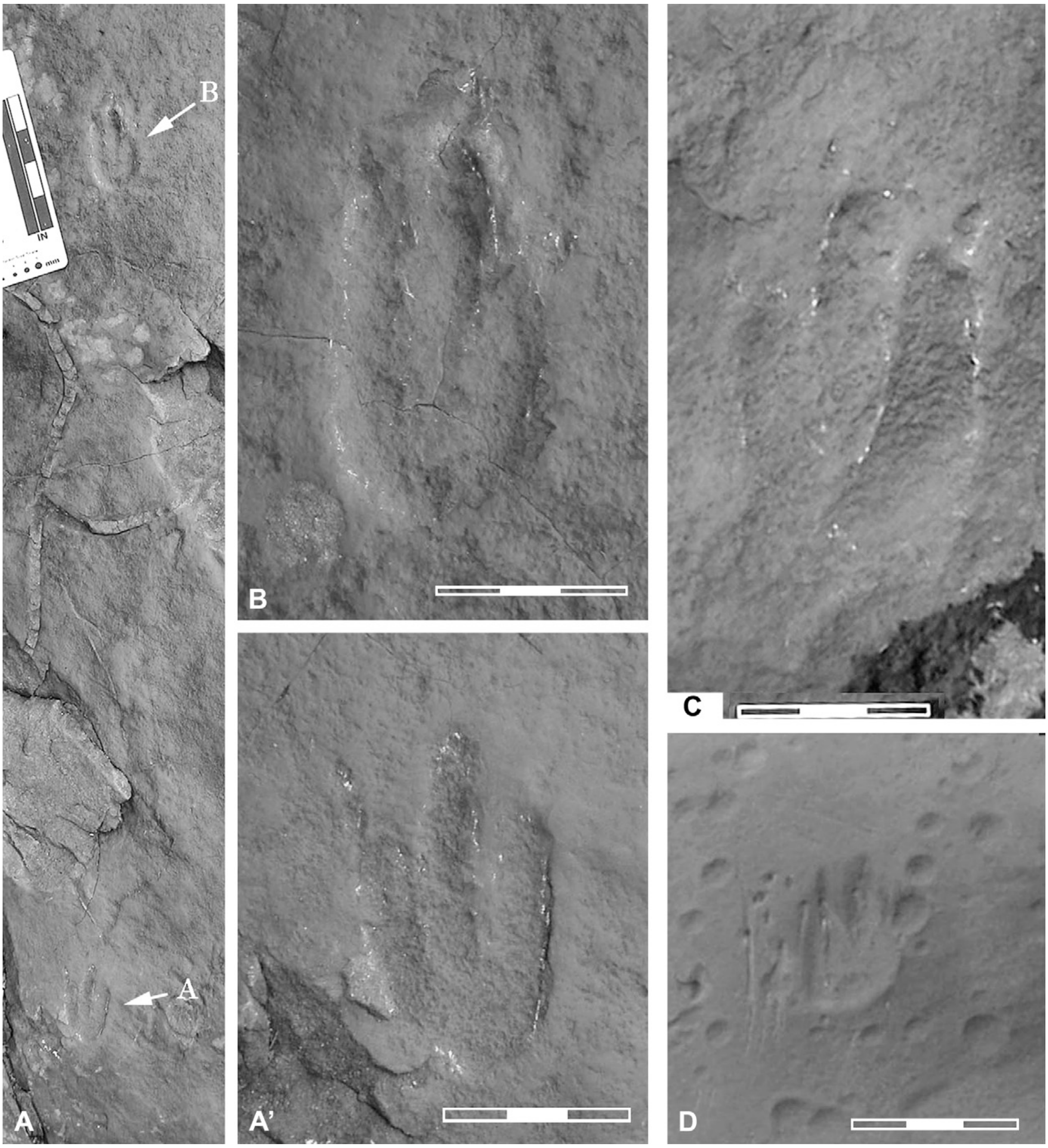

Fig. 9. Photographs of Chinese *Minisauripus* from Shandong. A, A' and B, holotype trackway of *M. zhenshuonani*, with detail of consecutive tracks (A and B). C, topotype track of *M. zhenshuonani*. D, possible small *Minisauripus* track partly obscured by rain drop impressions and vandalism scratch marks. Compare with Fig. 10.

range from 14.0 to 24.5 cm (N = 6). No specific mention is given of the short anterior projection of digit III beyond II and IV, though this is evident from the single illustration, and length measurements for each digit are given. The overall shape of the footprint is described as 'somewhat pentagon shaped' (Fig. 3). Herein, we illustrate the 'type' slab for the first time, showing the high density of tracks (Fig. 4).

The first-discovered Korean sample (KML1) consists of only two tracks, both about 3 cm long and 2 cm wide, preserved as natural casts (Fig. 1). In these specimens, it is clear that it is only digit II that has two pads, while digit III has three pads. Digit IV has three clear larger pads anteriorly and a fourth smaller posterior pad – the metatarsophalangeal pad – that is more medially situated. Thus, it appears that *Minisauripus* has a 2-3-4 phalangeal formula corresponding to digits II, III and IV. The anterior end of the distal phalangeal pad of digit IV projects more anteriorly than the distal end of digit II. Given that the Chinese *M. chuanzhuensis* was described as having a 2-2-2 phalangeal formula, it is ostensibly different from the Korean material and so we are justified in erecting a new ichnospecies. However, we regard it as probable that the differences in pad preservation are more apparent than

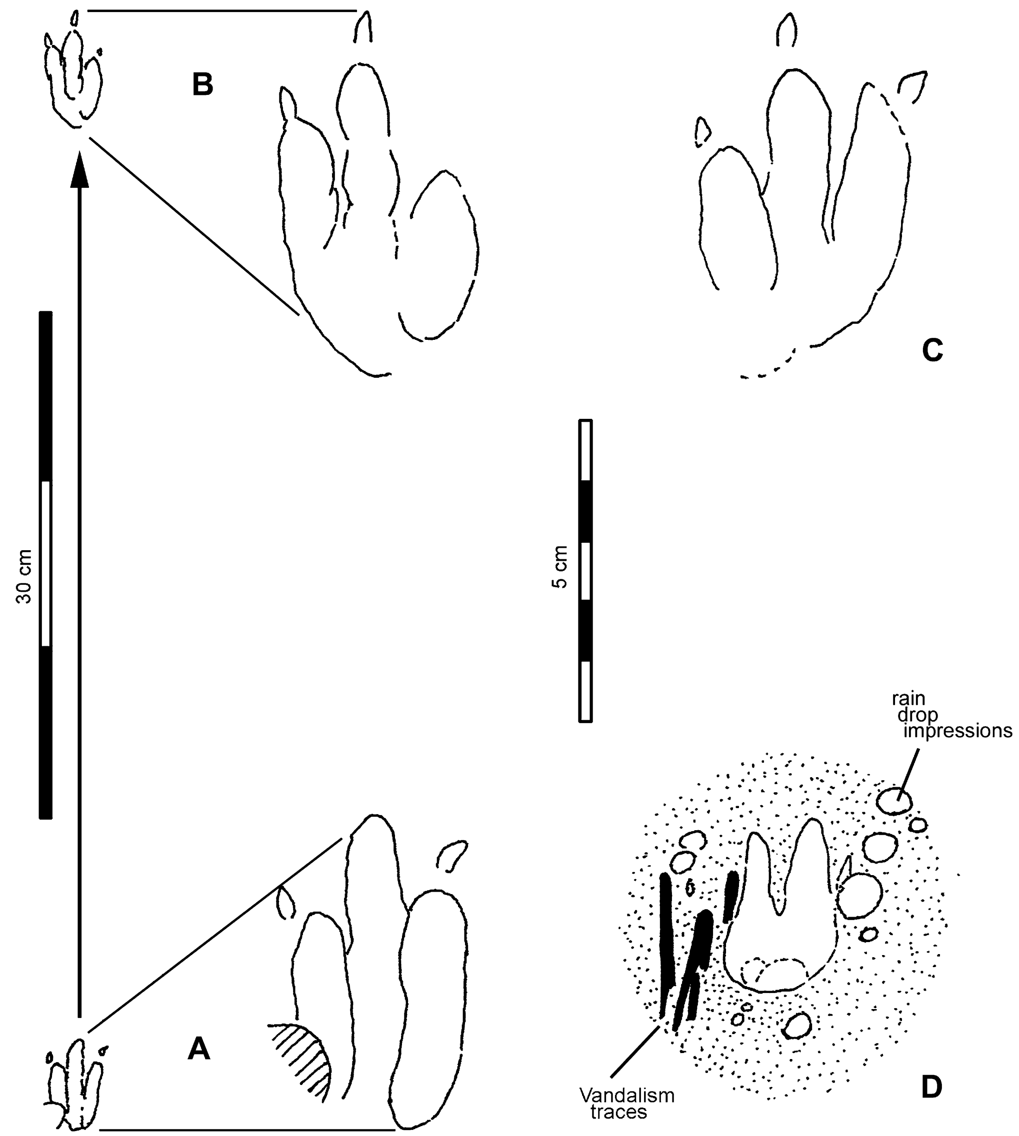

Fig. 10. Drawing of Chinese *Minisauripus* from Shandong. A and B, holotype trackway of *M. zhenshuonani*. C, topotype track of *M. zhenshuonani*. D, possible small *Minisauripus* track partly obscured by rain drop impressions and vandalism scratch marks. Compare with Fig. 9.

real, and due to variable preservation of the Chinese material. Thus, we have no doubt that the tracks from both areas belong to the same ichnogenus.

KML1 material was preserved on a block that was too narrow to preserve consecutive steps. However, as shown in Fig. 6, based on the space both in front of, and behind, the tracks, one specimen had a minimum pace of at least 22.5 cm and the other of at least 13.5 cm. This supports the conclusion that the pace was long relative to foot length. The third specimen recovered from this locality is 3.1 cm long and 2.1 cm wide. It is moderately deep (about 0.2 cm) and occurs on a surface with clear rain drop impressions. However, no additional track is detected for 17 cm behind, or 13 cm in front of, this track. This suggests a long step (minimum step length of 17 cm and stride of 34 cm).

The KML2 sample consists of two trackway segments. The first is a trackway of three relatively complete footprint casts in the sequence right-left-right (Fig. 7). The tracks are about 20% smaller (about 2.3 cm long) than in the KML1 sample. One track shows claw impressions on both digits II and IV and, in the right footprint casts, digit IV clearly projects more anteriorly than digit II. However, digital pad impressions are not well-preserved, though this may in part be due to erosion. The step length is variable (7.5–10.0 cm), but clearly not as long as in the other samples. The second trackway consists of two footprints of which the second in the sequence (a left) is well preserved (Fig. 8) measuring 3.5 cm long and 2.4 cm wide. The step is 22.5 cm.

The Shandong sample is anomalous in that it contains three tracks that are twice the size of all other specimens; these occur on the lower of two surfaces that bear *Minisauripus*, which we call the 'main' *Minisauripus* level. Nevertheless, they show the same diagnostic theropodan features seen in the Korean samples. The larger tracks (length about 6.0–6.1 cm) all show traces of sharp claws, sometimes impressed as isolated traces just beyond the blunt distal ends of the digits impressions (Fig. 9). One trackway segment consists of a right and a left footprint (CU 214.103 and 214.104 respectively) indicating a step of 60 cm, with no appreciable footprint rotation. In the left footprint, digit IV clearly projects distally beyond digit II. A second very similar trackway segment consists of two footprints comprising a step of 64.5 cm. The second track in this sequence, (a right), is designated CU 214.105. The fifth track is an isolated footprint from a level about 30 cm above the main layer. The track is only about 3.0 cm long and exhibits two well-preserved, pointed digit traces, probably digits III and IV, and a clear rim around the posterior margin of heel. Traces of a third digit (probably II) are visible, but they are obscured by a rain drop impression (Fig. 10). This trackway surface, although draped with a smooth layer of mud, is undulating as the result of large, high amplitude crescentic ripple marks. The track was registered on a slight slope and so its outlines are not as clear as those of the tracks on the main layer just below. This undulating surface also contains traces of small tridactyl, grallatorid tracks.

3.2. Systematic implications of variation in the Minisauripus *sample*

Now that multiple *Minisauripus* localities are known, several conclusions can be drawn about the ichnogenus: 1. It is clear that the new *Minisauripus* material (herein designated *M. zhenshuonani*) consistently reveals all the important diagnostic characteristics of a theropod track such as length-greater-than-width and the 2-3-4 phalangeal formula for digits II, III and IV respectively. Also reexamination of the type material, especially track A-15, reveals sharp claw traces. This contrasts with the interpretation of *M. chuanzhuensis* as a blunt-toed ornithopod track. 2. There is a significantly larger size range than previously known. The three Shandong specimens that form the basis of the new ichnospecies *M. zhenshuonani* are about twice the size of the Sichuan specimens of *M. chuanzhuensis* and specimens of similar size from South Korea. 3. It is clear that the step length of *Minisauripus* is quite variable, though long steps (10 times foot length) predominate over short steps (only 3 times foot length). 4. It is debatable as to how much of the track and trackway variation is attributable to diagnostic morphological differences as opposed to preservation; likewise the differences between natural impressions and natural casts, i.e., convex hyporelief, rather than concave epirelief. Nevertheless, it is clear that the new material allows significant revision of the ichnogenus *Minisauripus*, substantially changing our understanding of the morphology of the foot of its track maker(s).

Based on overall morphology – footprint shape, digit proportions and length of stride – there is no justification for erecting a new ichnogenus for material from outside the type locality. However, as noted above, many details of foot morphology reveal significant differences between the type *M. chuanzhuensis* material and the newly discovered footprints. These differences include evidence of pad morphology and claw traces as well as footprint length-width ratios. For example, the larger tracks tend to be more elongate than the small tracks, with more prominent evidence of long slender claws. While such differences may in part be due to preservation, this inference is by no means certain, and it is practically impossible to prove that type *M. chuanzhuensis* tracks from Sichuan reveal the same diagnostic characteristics described for the other material. Therefore, given that morphology is the primary criterion for distinguishing ichnotaxa, we propose, on the basis of these comparative observations, a new ichnospecies *M. zhenshuonani*, based on the larger Shandong specimens. Other material from the Korean localities is referred to as *M.* cf. *zhenshuonani* or *M.* cf. *chuanzhuensis*. For example, we infer that the two elongate tracks (CU 214.101, 214.128) from the Changseon Island site (Figs. 5 and 6) are similar to the Shandong specimens and therefore we tentatively label them as *M. zhenshuonani*. In contrast shorter wide tracks from Sinsu Island (CU 214.102) are more reminiscent of the type material from Sichuan Province China, which we therefore tentatively label as *M. chuanzhuensis*.

3.3. Systematic palaeontology

Ichnogenus *Minisauripus*

Ichnogenoholotype: *Minisauripus chuanzhuensis* Zhen et al., 1995

Minisauripus zhenshuonani ichnosp. nov.

1995 *Minisauripus chuanzhuensis* Zhen et al.
2005 *Minisauripus* Lockley et al.

Amended diagnosis for ichnogenus. Small tridactyl track with sub-parallel, elongate, well-padded digits with blunt distal terminations connected to narrow distal claw traces. Digit III only slightly longer than IV, which is slightly longer than digit II. Phalangeal formula of 2-3-?4 for digits II, III and IV, respectively discernible in well preserved examples. Pace long, 3–10 times footprint length. Trackway narrow.

Type horizon and locality. Lower Cretaceous Jiaguan Formation of Emei County, Sichuan Province, China.

Minisauripus zhenshuonani ichnosp. nov.

Diagnosis. Small, elongate, tridactyl track with parallel, digits with conspicuous claw traces. Track is narrower than *M. chuanzhuensis* with digits less-divergent, and digit II relatively shorter. Pace and stride about 10 times footprint length and typically longer than in *M. chuanzhuensis*. Trackway very narrow.

Description. Small, elongate, tridactyl track, about 50–70% as wide (1.6–3.8 cm) as long (2.5–6.1 cm). Individual digit impressions are parallel-sided, and well-padded with blunt distal terminations, i.e., no distal tapering. Traces of narrow claws sometimes preserved. Digits show minimal distal divergence. Digit III only slightly longer than digit IV, which is in turn significantly longer (more anteriorly projected) and narrower than II. Digital padding indicates a phalangeal formula of 2-3-?4 for digits II, III and IV, respectively. Discrete pad impression are very faintly preserved in digit IV though the shallower proximal metatarsophalangeal pad is clear. Pace long, up to 10 times footprint length.

Type horizon and locality. Lower Cretaceous Tianjialou Formation (Barremian-Albian) Houzoushan Dinosaur Park, Linquan Town, Junan County, Shandong Province, China.

Type specimen. Trackway comprising right and left footprints CU 214.103 and 214.104. Paratype and topotype: CU 214.105.

4. Stratigraphic and palaeogeographic distribution and context of *Minisauripus*

The Cretaceous successions of China and South Korea are dominated by terrestrial deposits that have proved difficult to date biostratigraphically. This is, in part, because the faunas often appear endemic and are thus rarely age diagnostic (e.g., Smith et al., 2001). *Minisauripus* provides a good example. Prior to the discovery of the new Chinese and Korean samples described herein, *Minisauripus chuanzhuensis* appeared to represent part of a highly endemic ichnofauna of small dinosaurian track makers from the Emei locality in Sichuan Province. The associated ichnotaxa include *Grallator emeiensis* (2 cm long) and *Velociraptorichnus sichuanensis* (10–11 cm) and the bird track *Aquatilavipes sinensis,* which may be a junior synonym of *Koreaornis hamanesis* (Kim, 1969). Another tridactyl track from this locality was designated *Iguanodon*, though this is not a valid ichnogenus label (Sarjeant et al., 1998); moreover, we reinterpret this track as that of a theropod. The age of the Emei ichnofaunas was also in dispute, having originally been designated as Early Cretaceous (Zhen et al., 1995) and subsequently interpreted as Late Cretaceous by Chen et al. (2006).

The discovery of *Minisauripus* at various localities in South Korea and China improves our understanding of both the stratigraphic and palaeogeographic distribution of the ichnogenus. Both the Haman Formation in South Korea and the Tianjialou Formation in Shandong Province are inferred to be late Early Cretaceous in age (probably Barremian-Albian). Matsukawa et al. (1998, 2006a) discuss this age assignment in the case of the Korean sequences. In Shandong, as noted by Li et al. (2005a,b), Liu (2003) regarded the Tianjialou Formation, the second oldest of the four formations of the Dasheng Group (Malanggou, Tianjialou, Siqiancun and Mengtuan formations in ascending order) as Barremian-Aptian in age, based on four lines of evidence: 1) isotopic dates ranging from 125∼89 Ma., 2) fossil conchostracans such as *Yanjiestheria sinensis*, *Y. anhwiensis*, *Y. qiancaoensis,* 3) remains of dinosaurs such as *Psittacosaurus sinensis* and *P. youngi*, which Lucas (2006) subsequently placed unequivocally in the Barremian-Albian *Psittacosaurus* biochron, and 4) two successive palynological assemblages consisting of the lower *Cicatricosispor-Classsopollis-Clavatipollenites* assemblage and the upper *Schizaeoisporites—Classopollis–Tricolpite* assemblage. Although Si (2002) suggested a Cenomanian-Turonian age for the Dasheng Group as a whole, on the basis of the *Schizaeoisporites-Ephedripites-Tricolpites* palynological assemblage, this is inconsistent with the aforementioned evidence and, on balance, we regard the evidence for a Barremian-Albian age for the tracks from the Tianjialou Formation as more consistent and convincing.

The Tianjialou ichnofauna is particularly important because it also contains *Velociraptorichnus sichuanensis* and cf. *Aquatilavipes sinensis*. The latter is represented by an endemic ichnospecies diagnosed by the small size of the tracks (length 2.5 cm, width 3.1), that is very similar to the type material from Sichuan (length 3.1 cm and 3.8 cm wide). These tracks, which resemble *Koreanornis hamanensis* (Kim, 1969), are smaller (foot length and width about 2.5 and 3.1 cm) than the type *Aquatilavipes* tracks that pertain to *A. swiboldae* (3.75 cm long and 4.67 wide) from the Early Cretaceous (Aptian) of Canada (Currie, 1981) and from other ichnospecies, including *A. izumiensis* (mean length and width 37.7 and 44.5 mm) from the Early Cretaceous (Berriasian-Valanginian) of Japan first reported by Lockley et al. (1992) and subsequently named by Azuma et al. (2002). Likewise, *Aquatilavipes* isp., (3.2 cm long and 4.3 wide) from the Lower Cretaceous of Gansu Province (Li et al., 2002, 2006; Zhang et al., 2006) is also larger and evidently closer to *Aquatilavipes swiboldae* than to *A. sinensis*, although Li et al. (2006) suggested a similarity with *Koreanornis*. Thus, although there may be species level size variation in Asian *Aquatilavipes*, the ichnogenus is not restricted to the Sichuan site as might have been inferred at the time of the original discovery (Zhen et al., 1987, 1995). We suspect that there are at least three types that have been labeled *Aquatilavipes*, including: (1) the smaller variety (foot length and width typically about 2.5 and 3.0 cm) of the *A. sinensis* type, which may be a junior synonym of *Koreanornis hamanensis* (Kim, 1969); (2) larger forms (foot length and width approaching about 3.8 to 4.7 cm respectively) that are close to type *Aquatilavipes swiboldae* (Currie, 1981); and (3) a much larger form, *A. curriei* (McCrea and Sarjeant, 2001), that is 7.9 cm long and 9.5 wide, that may belong in a different ichnogenus (R. McCrea, personal communication, 2006).

It is beyond the scope of this study to date the *Minisauripus* bearing beds precisely. However, most credible evidence suggests that all the assemblages discussed herein are Early Cretaceous in age, specifically the Barremian-Aptian interval, at least in the Shandong and South Korean assemblages (Liu, 2003; Li et al., 2005a, b).

5. Allometric trends in theropod footprint morphology

Allometry refers to changes in the shape of morphological features in an individual organism, in individuals within a species, or species within a clade (Ridley, 2004). Such a definition is essentially synonymous with the term 'morphodynamic' movement (Lockley, 1999, in press) and cannot be separated from the concept of heterochrony, which recognizes the differential timing of development of organs within individuals, individuals within species, and species within clades. The examples examined here deal with theropod foot shape variation in multi-species clades.

Olsen (1980) set a precedent for this approach when he argued that Early Jurassic tracks traditionally assigned to *Grallator*, *Anchisauripus* and *Eubrontes* form an allometric plexus (*GAE*) best characterized by reducing all three ichnogenera to the status of sub-ichnogenera: i.e. *G*. (*Grallator*), *G*. (*Anchisauripus*) and *G*. (*Eubrontes*). He showed that as the tracks got larger, from small *Grallator* to large *Eubrontes*, they tended to become relatively shorter and wider, with a reduced projection of digit III beyond the tips of digits II and IV. This triangle, formed by the distal extremities of digits II, III and IV (Fig. 11) has since played a pivotal role in theropod track studies and is often used diagnostically to help distinguish ichnotaxa (Olsen, 1980; Weems, 1992; Olsen et al., 1998; Lockley, 2000; Piubelli et al., 2005). In short, Olsen (1980, p. 370) promulgated the simple allometric doctrine that the 'shape of the pes changes continuously with size.' There seems little doubt that such trends in theropod foot morphology (i.e., widening with increased size) are important, and that they correlate with a relative shortening of the medial digit (III) relative to the others (II and IV). We are in agreement with Olsen (1980) that this trend is real, at least for the *GAE* plexus.

However, having recognized this trend, we must ask whether it is universal for theropods, or for dinosaurs in general, and how it might vary across different clades. The comparisons noted above between *Minisauripus* and *Grallator emeiensis* provide an interesting test case now that the theropodan origin of *Minisauripus* is confirmed (Fig. 12). The difference in relative track width and projection of digit III is actually more pronounced in comparisons between there two contemporaneous Cretaceous theropod tracks in the size range of 2–3 cm than it is in the Early Jurassic *Grallator-Eubrontes* comparison covering a size range from about 3–40 cm. Thus, we might infer

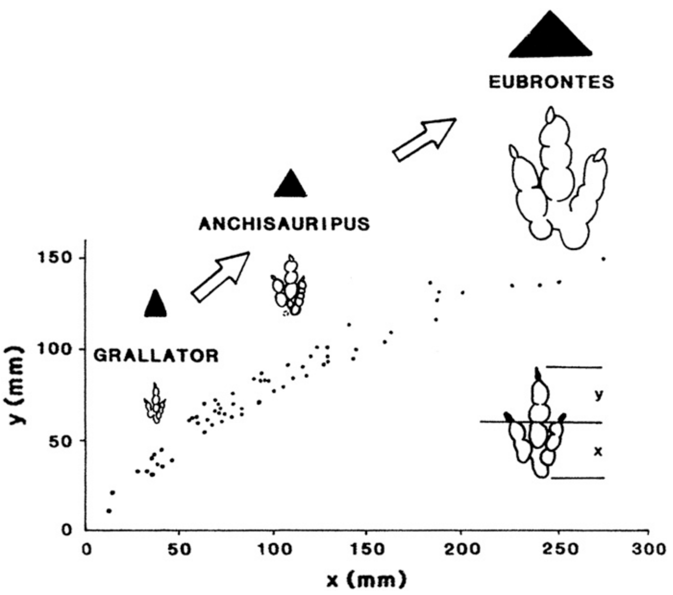

Fig. 11. Allometric relationships between *Grallator* and *Eubrontes* show that with size increase from about 3 to 30 cm, there is a progressive reduction in the relative length of the track and the anterior projection of digit III relative to II and IV. (after Olsen, 1980). Black triangles indicate the anterior toe projection of digit III as defined by the 'anterior' triangle between the distal ends of digits II, III and IV. Compare with Fig. 12.

that the size-related track widening and digit III shortening 'program' contracted or miniaturized itself in these Cretaceous forms. Since the track makers themselves were also diminutive, this inference seems plausible. Expressed in heterochronic terms, the Cretaceous forms became diminutive (paedomorphic) while still maintaining growth 'programs' that expressed relative proportions similar to those observed in larger (peramorphic) forms.

It has been suggested (Lockley, 1999, 2005, in press) that broadening of the foot in larger and more derived dinosaurs, including theropods, is just one example of other, often size-related trends in the broadening of other organs – and, in fact, the whole body – that repeat recursively, or fractally, throughout dinosaur clades. In feet, this broadening, mostly in derived forms relative to a narrowing or central tendency in primitive forms, can be seen as a phenomenon that is related to the relative emphasis of digit III.

All theropods have a mesaxonic pes (i.e., middle digit III is emphasized). If we compare *Grallator* with *Eubrontes* or *Minisauripus,* it is more strongly mesaxonic, and overall the foot is narrower. Therefore, the width of the foot is related to the degree of mesaxony in these cases. In the case of *G. emeiensis*, the two parasagittal digits (II and IV) are very short and the digits are very slender. In contrast, the two parasagittal digits of *Minisauripus* are much longer, though not longer than digit III, and they are wider. Therefore, digit width also correlates with foot width. These morphologies are polar opposites and can be understood in terms of the compensation principle, referred to as 'trade offs' in the language of heterochrony (McNamara, 1997): i.e., in the narrower foot, the elongation is concentrated towards the foot's sagittal plane and reduced in the side toes, whereas in the broader foot, elongation is more emphasized in the lateral parasagittal digits (II and IV), or across the whole foot, with a compensatory loss of emphasis in the central digit.

Whereas the lengths of digits II and IV are similar in *Grallator*, leading to a symmetric (isosceles) anterior triangle between the tips of digits II, III and IV, we also note that in the case of *Minisauripus*, the lengths of digits II and IV are not equal, resulting in an asymmetric (scalene) triangle (Fig. 12). Such observations point to fundamental differences in symmetry between different theropod tracks. Moreover, Lockley (2000) and Lockley et al. (2007) noted a polarity between tracks in which the medial hypex between digits II and III was located anterior to the lateral hypex between digits III and IV and compared it to the reverse case where the medial hypex was situated more posteriorly. In the case of *Minisauripus*, it is difficult to see the hypeces because the toes are not splayed; however, it appears from the relative anterior projection of digits II and IV that the lateral side (III-IV hypex?) is more anteriorly situated (Figs. 3–10, 12).

It has also been noted (Lockley, 1999, in press) that there is a compensatory relationship between foot length and limb length. Thus, in the vast majority of cases, forms with long feet have short limbs and forms with short feet have longer limbs. This is clearly seen in the Saurischia, and pertains to the Dinosauria as a whole. For example, it is well-established

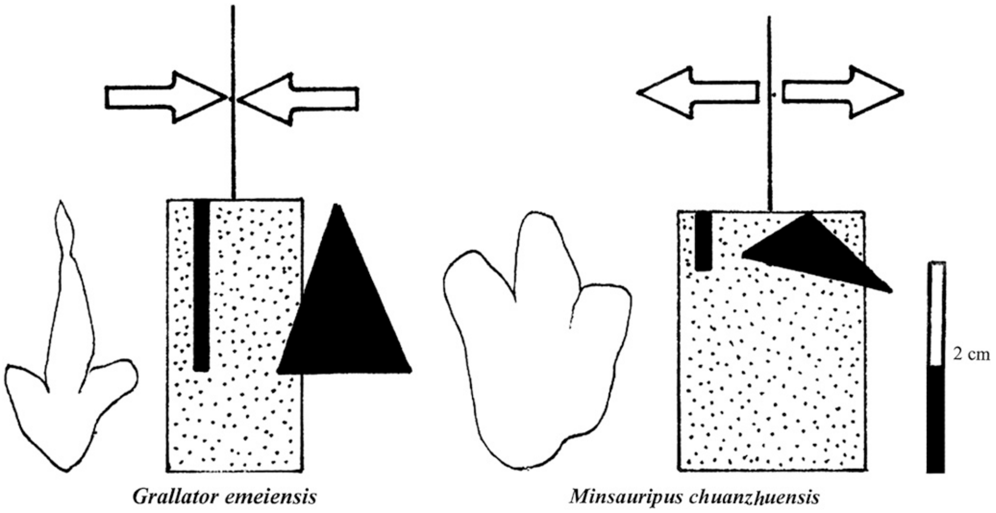

Fig. 12. Comparison between *Grallator emeinsis* and *Minisauripus* to show the relative width of the footprints and the differential lengths of digit III. Stippled boxes represent length and width of tracks with converging and diverging white arrows respectively representing relative lateral compression and lateral expansion of track width. Vertical black lines represent the proportion of track length represented by anterior projection of digit III beyond II and IV. Black triangles represent area of 'anterior' triangle defined by distal tips of digits II, III and IV.

that ornithopods have shorter and wider feet than theropods, but on average they have longer limbs (Thulborn, 1990; Lockley, 1999). This, like all allometric or morphodynamic relationships, can be understood in terms of heterochronic compensations or trade-offs (*sensu* McNamara, 1997). Thus, when small (paedomorphic) vertebrates are compared with larger (peramorphic) relatives, their distal organs (e.g., feet) appear to be larger than their proximal organs (i.e., inner limb bones), as shown in studies of modern birds (Middleton and Gatesy, 2000) and pterosaurs (Kellner, 2003). So a sauropod has relatively longer limbs, but shorter feet, than a primitive theropod. Such consistent allometric or morphodynamic relationships are useful to the ichnologist and allow us to infer that the track makers of small Jurassic *Grallator* tracks were probably relatively short-legged but long-footed ceratosaurs such as *Coelophysis* or *Megapnosaurus* (formerly *Syntarsus*) whereas, in contrast, larger, more derived forms had comparatively shorter feet and longer legs. Thulborn (1990) quantified this allometric relationship with the generalized conclusion that leg/foot length ratios were about 10% greater in large than in small theropods (i.e., hip height was 4.9 × foot length in large theropods but only 4.5 × foot length in smaller forms). These conclusions lead to the inference that the *Minisauripus* track maker may have been longer-limbed than the contemporary *Grallator emeiensis* track maker. This conclusion is perhaps supported by the relatively short step (4–5 × foot length) of the *Grallator emeiensis* track maker (Matsukawa et al., 2006a,b, fig. 6) compared with the step of the *Minisauripus* track maker, which is as much as 10 × foot length. However, we acknowledge that step length is variable and can not be used to infer limb length with any certainty.

6. Discussion

Although the distribution of *Minisauripus* now suggests that it is relatively widespread in east Asia, it may still represent a distinctive, small vertebrate ichnofauna containing relatively rare elements of diminutive size (foot length in the range of 2.5 to about 11 cm). For example, *Velociraptorichnus sichuanensis* and *Aquatilavipes sinensis* are only known from the two Chinese *Minisauripus*-producing localities (Sichuan and Shandong) and *Shandongornipes muxiai* (Li et al., 2005a; Lockley et al., 2007) occurs at only one. Ostensibly, none of these three tracks co-occur in the Korean assemblages with *Minisauripus*, although, as noted above, the likely synonymy of *Koreanornis hamanensis* with *A. sinensis* would strengthen the *Minisauripus* correlation. Based on this rationale, a *Minisauripus*-small shorebird assemblage occurs in both South Korea and China in association with larger dinosaur tracks. However, in general, the Korean assemblages – especially those from the Gyeongsang Basin, which have been well-studied (Lockley et al., 2006a, and references therein) – are dominated by ornithopod and sauropod tracks with few theropod tracks, and differ from the theropod-dominated assemblages from many of the Chinese localities and from elsewhere in Korea (Huh et al., 2006).

It is possible that these differences reflect variation in local distribution patterns or preservational bias. Matsukawa et al. (2006b) noted that the abundance of small theropod and bird tracks in many east Asian ichnofaunas is consistent with the concurrent Early Cretaceous skeletal record. However, Matsukawa et al. (2006b) also noted that large ornithopod and sauropod tracks also co-occur at some localities. Ornithopod tracks appear to be more dominant in the Early Cretaceous of South Korea and northeastern China north of palaeolatitude 30° N, in regions representing continental margins, whereas sauropod and theropod tracks are more abundant in the south and in regions representing inland basins. Current evidence suggests that small vertebrate tracks appear different in the two regions, but that *Minisauripus* and the possible *Koreanornis-Aquatilavipes* correlation suggest links, even though all other bird tracks, and most non-avian dinosaur tracks, are distinct and endemic based on current ichnotaxonomy. Again, such a difference may be attributable to secondary, non-palaeobiological factors such as small sample size and bias against the preservation of small tracks. However, there is ample evidence from the trace fossil record in East Asia that small tracks are well preserved. Likewise, the general ichnological record supports the inference that differences in sedimentary facies and palaeogeography, together with biostratigraphic signatures reflecting succession and turnover of evolutionary faunas, exert a primary 'biological' or ecological influence on the distribution of ichnotaxa in space and time. Thus, we are obliged to read the track record for the primary biological data it encodes, while exercising caution in interpretations requiring recognition of the influence of secondary, non-biological factors such as preservation.

7. Conclusions

1. *Minisauripus* occurs at multiple localities in the Early Cretaceous of China and South Korea.
2. *Minisauripus* can be attributed, with confidence, to a theropod, not an ornithopod. Diagnostic features allow the ichnogenus to be amended and a new, 'large' elongate ichnospecies *M. zhenshuonani* to be erected and distinguished from the smaller, broader type ichnospecies *M. chuanzhuensis*.
3. The size range *of Minisauripus* (foot length 2.5 to approximately 6.0 cm) is greater than previously supposed.
4. Type *Minisauripus* from Sichuan co-occurs with *Velociraptorichus* and *Aquatilavipes sinensi*. All three ichnotaxa co-occur in the Shandong assemblages, suggesting a previously unrecognized correlation.
5. The bird track *A. sinensis* may be a junior synonym of *Koreanornis hamanensis*. If this is the case, then the correlation between the Chinese *Minisauripus* localities and those from the Haman Formation of South Korea is strengthened.
6. By demonstrating that the *Minisauripus* assemblage is not restricted to the type area in Sichuan, the utility of these ichnofaunas for correlation is strengthened. Current evidence suggest that they may all fall within the Barremian-Albian interval.
7. Despite the evidence for a wider distribution for *Minisauripus* and '*Aquatilavipes*' (and/or *Koreanornis*), several associated ichnotaxa are still only known from one or two localities in China. Thus, the evidence for distinctive local or regional ichnofaunas is not fully dispelled.
8. Evidence that many Early Cretaceous ichnofaunas from east Asia are dominated by the tracks of small theropods and birds is consistent with the skeletal record in many regions.

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