Two-Toed Tracks through Time: On the Trail of "Raptors" and Their Allies

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THE TWO-TOED, OR DIDACTYL, TRACKS OF DEINONYCHOSAURIAN dinosaurs, popularly known as "raptors," are among the most distinctive theropod tracks known. Including the first confirmed report from China in 1994, a total of 16 tracksites have been recognized, all from Cretaceous strata. These include nine Chinese, two Korean, three North American, and two European occurrences. Many of these tracks have been assigned to four ichnogenera: *Velociraptorichnus* (two ichnospecies), *Dromaeopodus*, *Menglongipus*, and *Dromaeosauripus* (three ichnospecies). Most of the tracks have been attributed to dromaeosaurid theropods, but in the case of the largest sample, from Germany, a troodontid trackmaker is inferred.

Here we review all 16 Cretaceous occurrences, indicating sample size, preservation quality, morphological characteristics, utility for ichnotaxonomy, and trackmaker identification. The size range (foot length) of known deinonychosaurian trackmakers is between ~10 and 28 cm. Most reported instances were made by trackmakers inhabiting fluvio-lacustrine habitats in the later part of the Early Cretaceous (Barremian-Albian).

We also note two reports of pre-Cretaceous, didactyl – or pseudodidactyl – ichnogenera (*Evazoum* and *Paravipes*), both of probable saurischian affinity, with which Cretaceous deinonychosaurian tracks have been compared. In the case of *Evazoum*, we infer a morphological and behavioral convergence with deinonychosaurian morphology, related to the retraction of digit II. In the case of *Paravipes*, morphological similarities are less obvious, and we infer that this ichnogenus likely comprises swim tracks.

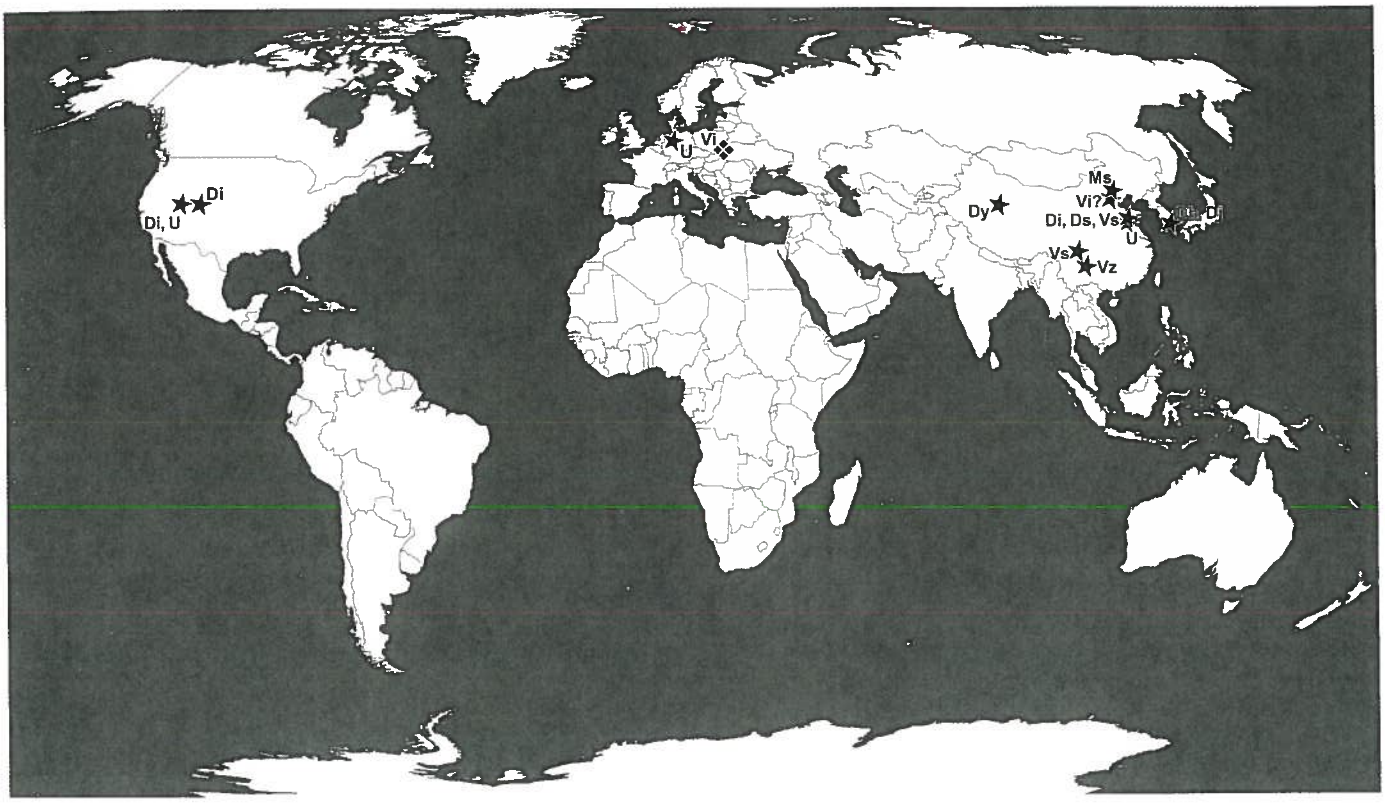
INTRODUCTION

Although the term "raptor" has broad, popular meaning for birds of prey, in popular depictions of nonavian dinosaurian paleontology it has come (thanks to *Jurassic Park*) to refer specifically to deinonychosaurian (dromaeosaurid and troodontid) theropod dinosaurs. These theropods have a distinctive pedal morphology characterized by a retracted pedal digit II that bears a well-developed, hypertrophied 'sickle claw.' Until quite recently, tracks of these Mesozoic 'raptors' were unknown, despite the clade being quite well-represented in the osteological record, especially in the Cretaceous (Turner, Makovicky, and Norell, 2012). In particular, their pedal specialization, well preserved in many specimens (e.g., Ostrom, 1969; Norell and Makovicky, 1997; Xu and Norell, 2004; Gao et al., 2012), indicates that digit II was held raised during locomotion in life.

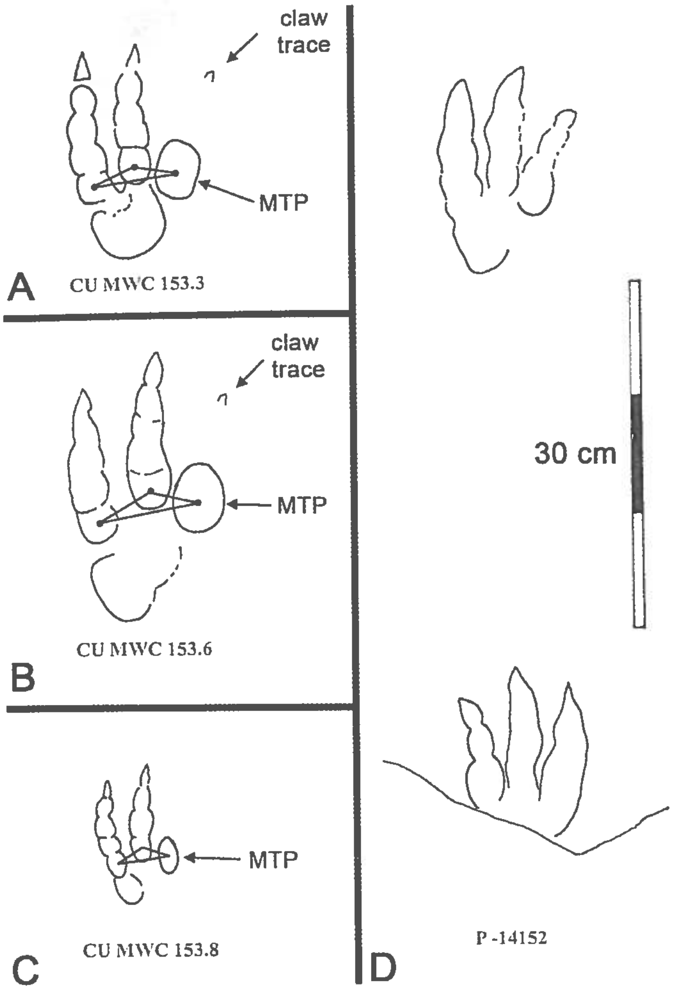
Because deinonychosaurians were known long before their tracks were identified, ichnologists speculated, based on known pedal skeletons, that deinonychosaurian tracks would be didactyl, comprising impressions of only digits III and IV. Tracks pertaining to these dinosaurs were not reported until 1994, when small, didactyl tracks from the Cretaceous of Sichuan Province, China, were described as *Velociraptorichnus* (Zhen et al., 1994). At present, 16 Cretaceous deinonychosaurian track sites have been reported (Fig. 11.1, Table 11.1), including 11 from Asia (9 from China, 2 from Korea), 3 from North America, and 2 from Europe. These are in addition to reports of likely nondeinonychosaurian, didactyl track morphotypes from the Permian, Late Triassic–Early Jurassic, and Middle Jurassic. Here we give a detailed account of all these occurrences and their implications for distinguishing different deinonychosaurian track morphotypes. In this regard, some samples are instructive in pointing to differences between dromaeosaurid and troodontid tracks. We also take into consideration other essential, morphological factors, such as size and relative proportions of digit traces and trackway patterns, as well as nonmorphological factors, such as sample size, substrate preservation, geological age, and paleobiogeography.

PRE-CRETACEOUS DIDACTYL TRACKS

Some pre-Cretaceous, didactyl tracks clearly pertain to nondinosaurian trackmakers. The best known example is *Dromopus didactylus* (Moodie, 1930), which comprises incompletely preserved tracks of a pentadactyl, lacertiform trackmaker from the Permian of Texas that show only the impressions of the longest digits (IV and III). Such tracks are small and



11.1. Map showing the localities of Cretaceous, didactyl tracks worldwide. The star indicates Early-"middle" Cretaceous and the diamond u, Late Cretaceous tracks. Abbreviations: Dh, *Dromaeosauripus hamanensis;* Di, *Dromaeosauripus* isp.; Dj, *Dromaeosauripus jinjuensis*; Ds, *Dromaeopodus shandongensis*; Du, *Dromaeopodus* isp.; Dy, *Dromaeosauripus yongjingensis*; Ms, *Menglongipus sinensis*; U, unnamed/unattributed; Vi, *Velociraptorichnus* isp.; Vs, *Velociraptorichnus sichuanensis;* Vz, *Velociraptorichnus zhangi*.



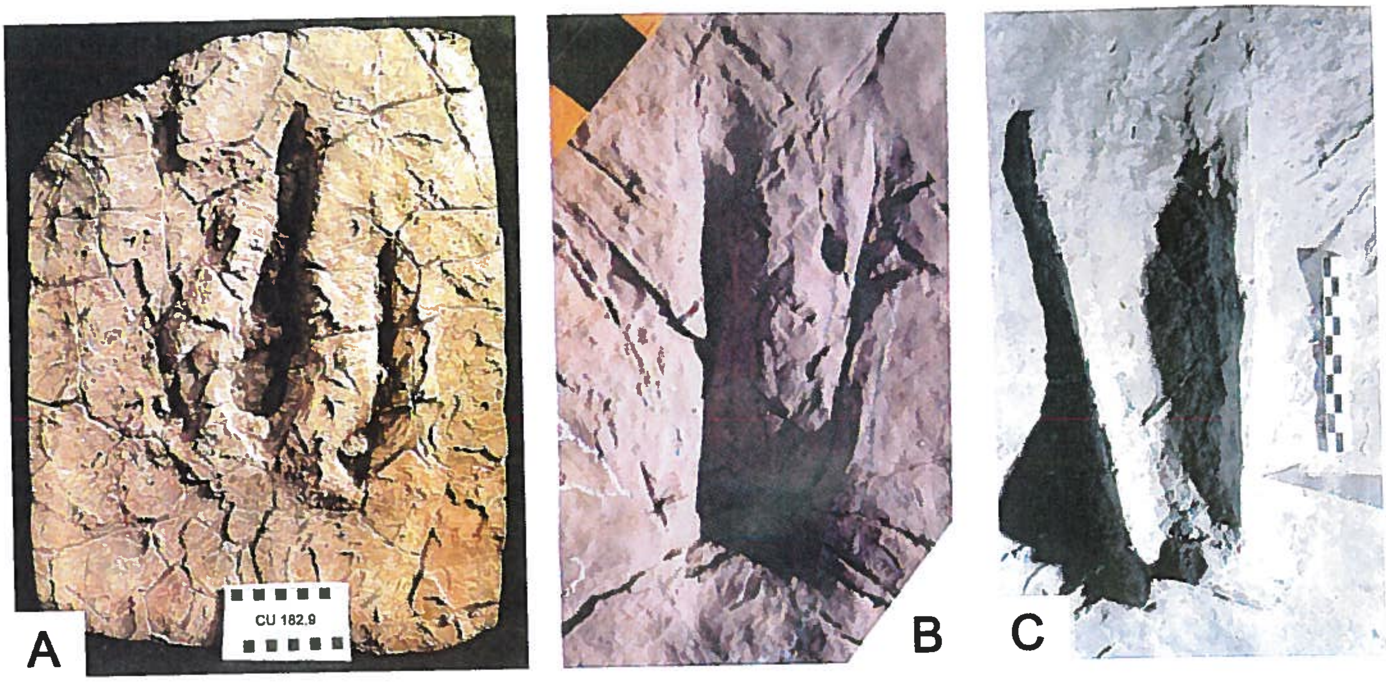
11.2. (A–C) *Evazoum gatewayensis* from the Chinle Group of western Colorado. University of Colorado Museum of Natural History specimens now part of the University of Colorado Denver, Dinosaur Tracks Museum collection (CU): CU MWC 153.3 (holotype, [Museum of Western Colorado collection]) (A), CU MWC 153.6 (B), and CU MWC 153.8 (C). Note the triangular configuration of the metatarsophalangeal pads (MTP) of digits II–IV. (D) An example of a more typical, tridactyl *Evazoum* track (P-14152) from the Late Triassic of New Mexico. *After Lockley and Lucas (2013).*

form part of a suite of trackways made by small, quadrupedal animals that cannot morphologically compare with the tracks of large, bipedal dinosaurs from the Mesozoic. However, they provide important evidence that animals with pentadactyl, tetradactyl, and tridactyl feet are capable of leaving didactyl tracks depending on how substrate conditions and/or locomotory behaviors affect footprint preservation, a subject discussed in some detail by Lockley and Lucas (2013).

Recently, Lockley, Lucas, and Hunt (2006) and Lockley and Lucas (2013) referred to four, Late Triassic–Early Jurassic ichnogenera (*Otozoum*, *Pseudotetrasauropus*, *Evazoum*, and *Kalosauropus*) as the "OPEK plexus." This group is accommodated in the previously named ichnofamily Otozoidae (Lull, 1904), which originally contained only *Otozoum*. Lockley et al. (2006) noted that type *Otozoum* and *Pseudotetrasauropus* (O and P morphotypes) are large tracks, in some cases associated with manus tracks, indicating quadrupedal trackmakers. In contrast, *Evazoum* (Nicosia and Loi, 2003) and *Kalosauropus* (Ellenberger, 1972, 1974) (E and K morphotypes) are both small tracks made by bipeds. Of significance here are reports that *Evazoum* from North America includes a morphotype that is functionally didactyl, or pseudodidactyl, preserving for digit II only a swollen or enlarged, proximal pad trace. This morphotype has been illustrated on a number of occasions (Olsen, Schlische, and Gore, 1989; Gaston et al., 2003; Lockley et al., 2006) and recently formally described as the new ichnospecies *Evazoum gatewayensis* (Lockley and Lucas, 2013) (Fig. 11.2). All ichnotaxa in the OPEK plexus have been attributed to basal sauropodomorphs, if not unanimously then at least by a majority of authors (Ellenberger, 1972; Lockley and Hunt, 1995; Rainforth, 2003; Lockley, Lucas, and Hunt, 2006; D'Orazi Porchetti and Nicosia, 2007; Lockley and Lucas, 2013). Given this interpretation, some *Evazoum* tracks represent a foot morphology and/or locomotory behavior that appears to be a convergent precursor of the morphology of deinonychosaurian tracks that are now increasingly well known in the Cretaceous. The fact that both inferred trackmaking groups (Deinonychosauria and basal Sauropodomorpha) belong to the saurischian clade suggests the possibility of a reiterative developmental pattern or the generation of convergent morphology as a result of similar evolutionary adaptation.

The Middle Jurassic ichnogenus *Paravipus didactyloides*, of presumed theropod affinity, was recently named on the basis of unusual, "didactyl" tracks from Mali, Africa. These enigmatic tracks, described as having been made by a digitigrade, bipedal trackmaker, preserve paired, subparallel impressions assigned to digits III and IV, of which the purported digit III impressions were slightly longer than those of digit IV (Murdoch et al., 2011). Impressions of digit II were occasionally represented by small, round or oval "pad" impressions (Mudroch et al., 2011). These tracks show many similarities to theropod swim tracks from the Early Jurassic of Utah (Milner, Lockley, and Kirkland, 2006) (Fig. 11.3A) and discussed elsewhere in this volume (Milner and Lockley, 2016).

Another locality revealing large, apparently didactyl, tracks was reported by Ishigaki and Lockley (2010) from the Early Jurassic of Morocco. Although some of the individual tracks in this report have a striking didactyl appearance (Figs. 11.3B, 11.3C), these tracks were associated with, and in some cases parts of, trackways of tridactyl theropods. Their didactyl appearance is attributable to postregistration sediment collapse and/or irregular gaits associated with unusual preservational conditions. These tracks have not been named.



11.3. Large "didactyliform" tracks from the Jurassic of Africa. (A) Fiberglass replica of the holotype of *Paravipus didactyloides* from Middle Jurassic of Mali (CU 182.9 [University of Colorado Denver, Dinosaur Tracks Museum collection]). (B–C) Natural impressions and molds of apparently didactyl theropod tracks from the Early Jurassic of Morocco.

DEINONYCHOSAUR TRACK OCCURENCES IN SPACE AND TIME

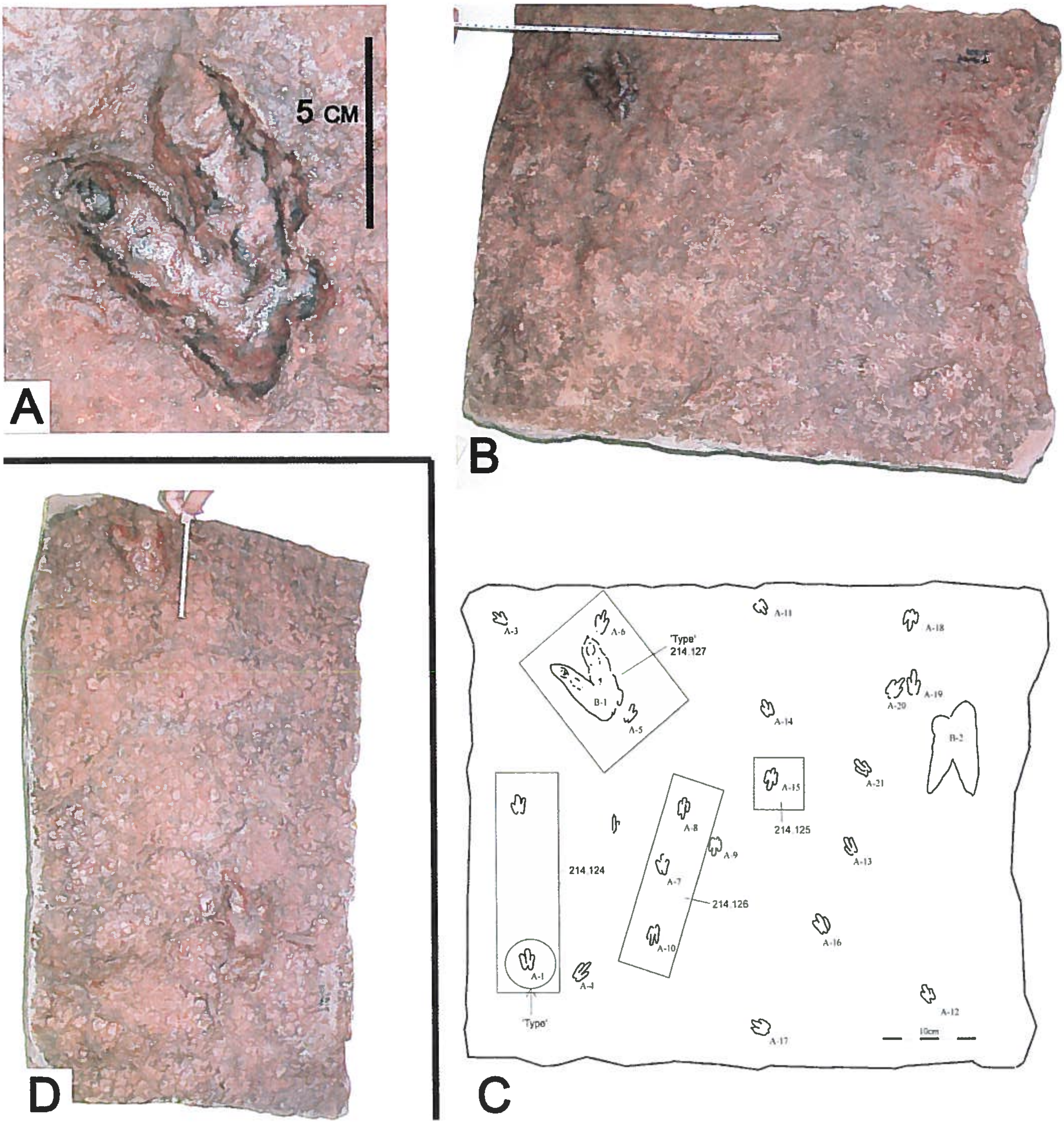
The First Discovery: Velociraptorichnus sichuanensis

The tracks named by Zhen et al. (1994) as *Velociraptorichnus sichuanensis* are part of an important assemblage of small tracks from the Cretaceous Jiaguan Formation of Sichuan Province, China. *Velociraptorichnus sichuanensis* was originally called "*Deinonychosaurichnus*" in an unillustrated abstract (Zhen et al., 1987) and a subsequent citation of this same abstract (Zhen et al., 1989). However, because abstracts are not valid venues in which to erect taxa, this name is not valid, and *V. sichuanensis*, as erected in Zhen et al. (1994), is the valid name. In Zhen et al. (1994), only one track, the holotype (CFEC-B-1 [Chongqing Natural History Museum collection]), was illustrated; two other paratype and topotype tracks (CFEC-B-2 and CFEC-B-3) were only reported (Fig. 11.4). However, measurements were given for all three tracks, which have lengths between 11.0 and 11.5 cm and widths between 6.0 and 6.5 cm.

The slab containing the type of *V. sichuanensis* (Figs. 11.4B–11.4C), also preserves a second, poorly preserved track that we attribute to *V. sichuanensis*. The two consecutive *V. sichuanensis* paratype tracks (Fig. 11.4D) occur on a different slab and have a step length of 55 cm. Neither slab was illustrated by Zhen et al. (1994), who provided only line drawings of the type. Although neither slab has previously been illustrated photographically, except for a small picture of the holotype in a popular book (Xing, 2010:26), the holotype slab was illustrated as a line drawing by Lockley et al. (2008:fig. 4) as part of a restudy of the ichnogenus *Minisauripus*, which is also preserved on the holotype slab (Fig. 11.4C). Likewise, the single step sequence on the holotype slab was illustrated in a line drawing by Lockley et al. (2004:fig. 7C) and Matsukawa, Lockley, and Li (2006:fig. 6). To rectify this situation, the type material is illustrated here photographically for the first time (Fig. 11.4). The main points given in the description of *V. sichuanensis* by Zhen et al. (1994) confirm that the ichnospecies can be unequivocally attributed to a deinonychosaurian theropod dinosaur: the trackmaker was clearly functionally didactyl, with digit II represented only by a small, proximal pad impression. However, whether the attribution by Zhen et al. (1994) of *V. sichuanensis* to a dromaeosaurid trackmaker, as opposed to a troodontid trackmaker, is correct is an open question.

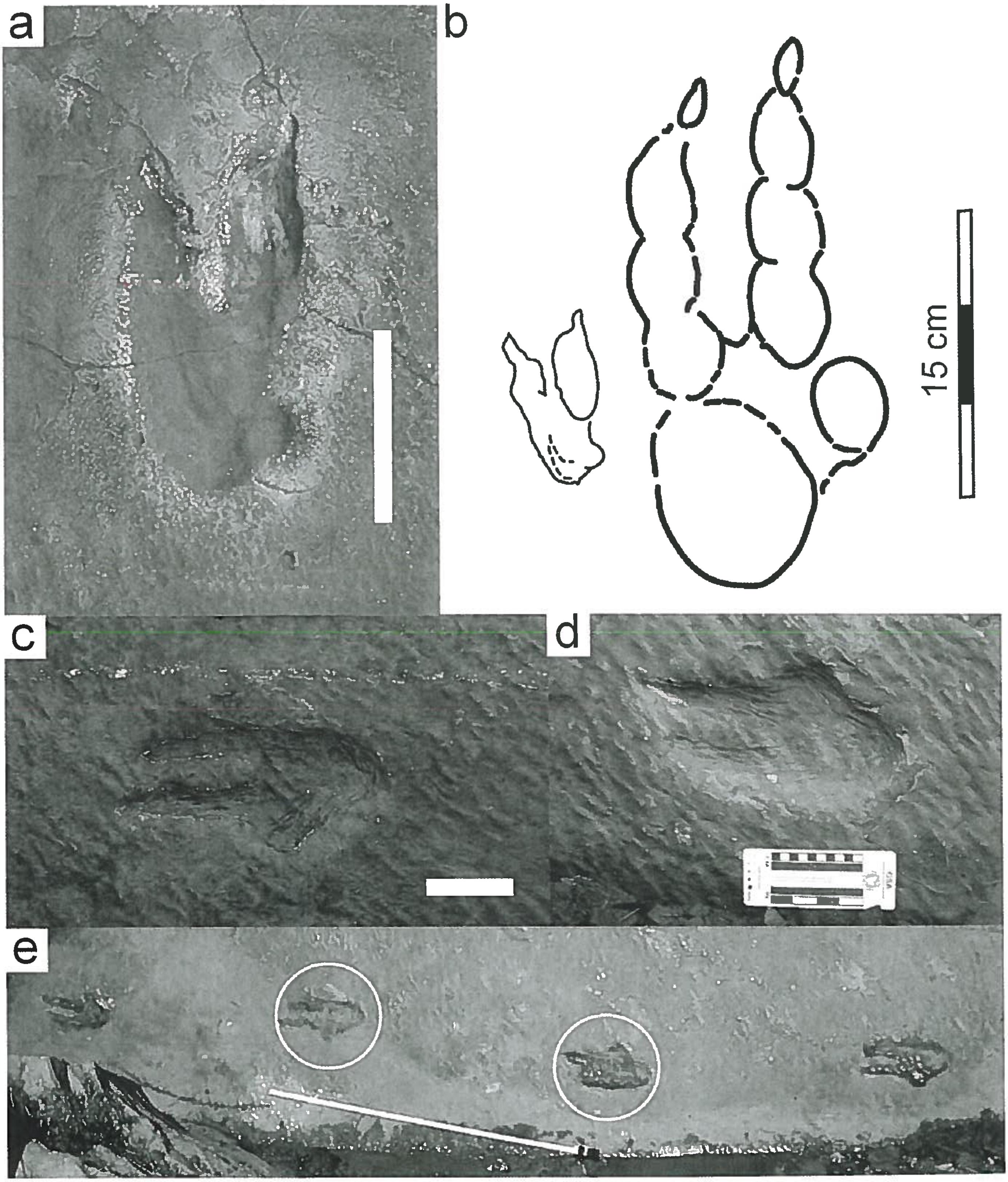
The Perfect Trackway: Dromaeopodus shandongensis, the Spoor of a Big Pack Hunter?

Li and Lockley (2005) first reported large (track length ~28 cm), didactyl, dromaeosaurid trackways from the Lower Cretaceous Tianjalou Formation of Shandong Province China found in association with a rich ichnofauna of bird and other dinosaur tracks (Li, Liu, and Lockley, 2005; Li

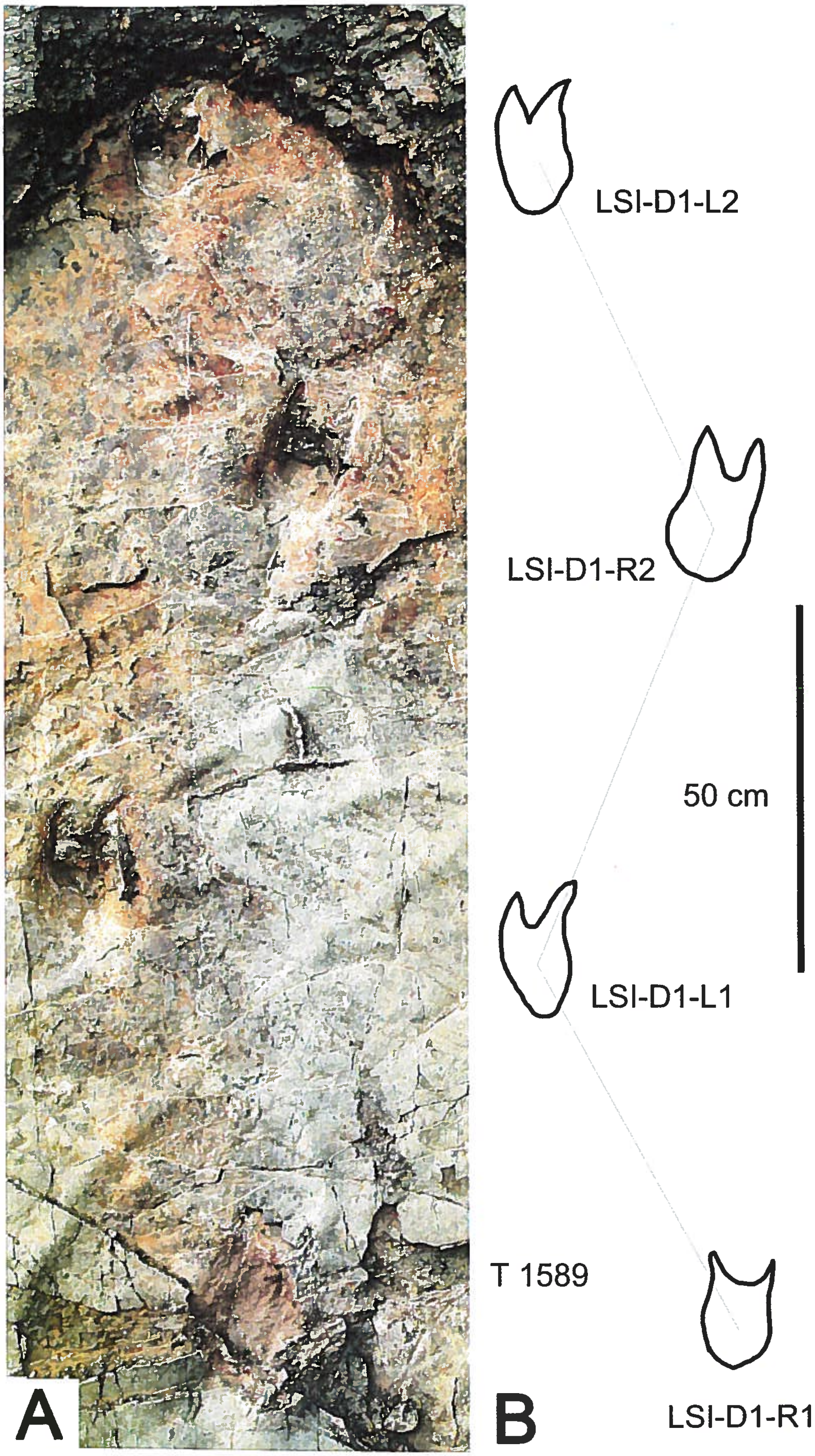


11.4. (A) Photograph of the holotype of *Velociraptorichnus sichuanensis* (CFEC-B-1 [Chongqing Natural History Museum collection]), located in the upper left corner of the type slab. (B) Photograph of the slab bearing the type of *V. sichuanensis*. (C) Map of the slab bearing the type of *V. sichuanensis* (after Lockley et al., 2008:fig. 4). The map also shows the positions of the type and paratypes of *Minisauripus chuanzhuensis*. Replicas of the *V. sichuanensis* holotype (CU 214.127 [University of Colorado Denver, Dinosaur Tracks Museum collection]) and the *M. chuanzhuensis* holotype (CU 214.124) and paratypes (CU 214.125 and 214.126) are reposited in the University of Colorado Museum of Natural History collections. (D) Paratype slab from *V. sichuanensis* type locality showing two consecutive tracks in trackway segment.

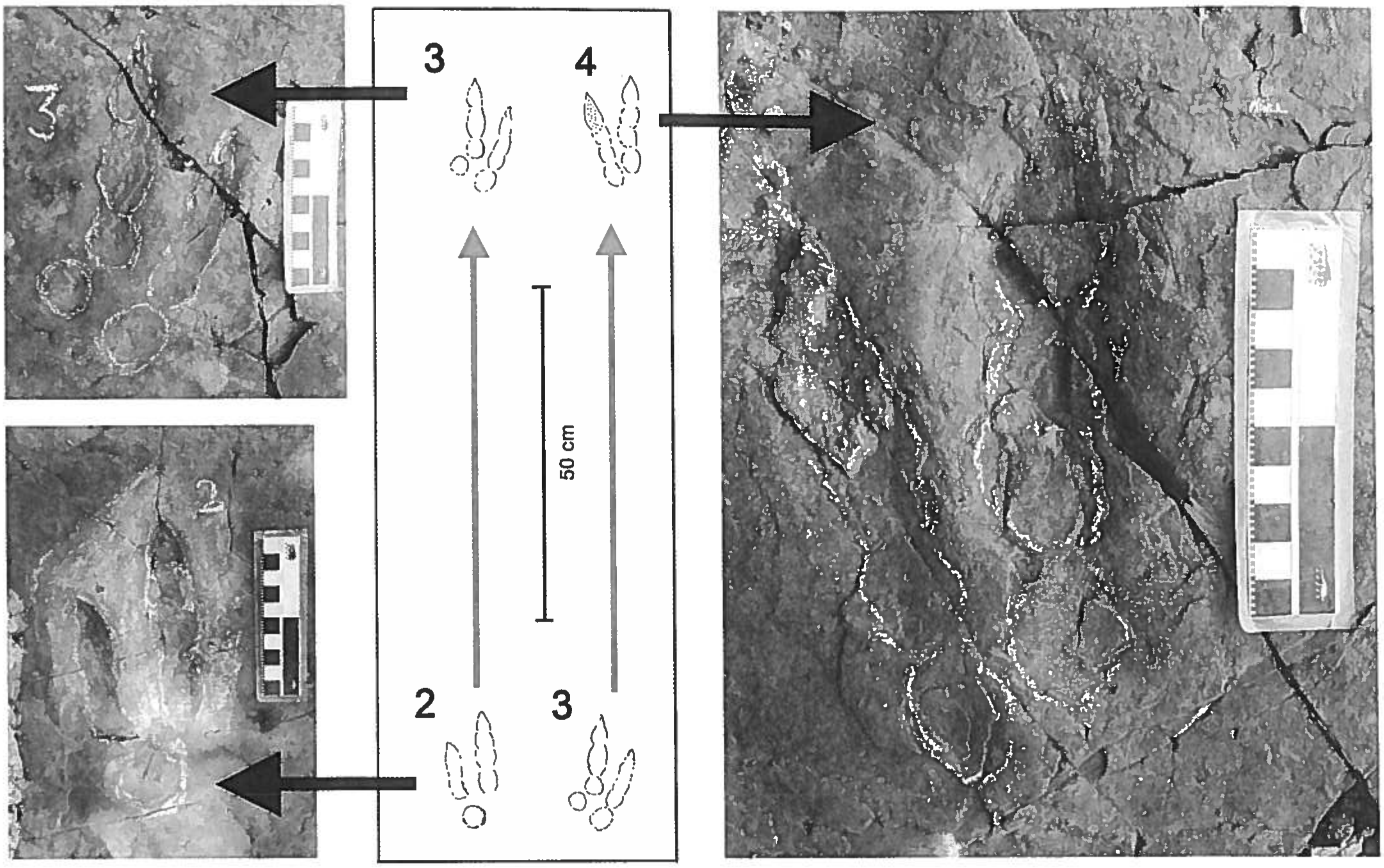
et al., 2008; Lockley et al., 2008). These were subsequently described in detail by Li et al. (2008), who erected for the didactyl tracks the ichnotaxon *Dromaeopodus shandongensis* (Fig. 11.5) based on well-preserved holotype (CU 214.111 [University of Colorado Denver, Dinosaur Tracks Museum collection]) and paratype (CU 214.112) trackways from two different, but closely associated, track-bearing horizons (Li et al., 2008:figs. 1–3). The holotype horizon yielded only one well-preserved *D. shandongensis* trackway, but the paratype horizon yielded six parallel trackways, strongly suggesting



11.5. Didactyl dromaeosaurid tracks from Junan, Shandong Province, China: (A) *Velociraptorichnus* and (C–E) *Dromaeopodus*. (B) Relative sizes and anatomical differences between the smaller *Velociraptorichnus* (left) and larger *Dromaeopodus* (right). (C–D) Close-ups of the middle right (C) and left (D) prints, respectively, from the holotype *Dromaeopodus* trackway (E). Scale bars: A = 5 cm, C = 10 cm, and E = 1 m. *After Li et al. (2008).*



11.6. A newly discovered dromaeosaurid trackway from the Tianjialou Formation of Shandong China. (A) Photograph and (B) line drawing of four consecutive tracks of the Linshu site (LSI): LSI-D1-R1, LSI-D1-L1, LSI-D1-L2, LSI-D1-R2. T 1589 refers to the tracing of this trackway in the catalog in the University of Colorado Denver, Dinosaur Tracks Museum collection. *After Xing, Lockley, et al. (2013).*



11.7. Line drawings and photographs of tracks 2–4 of the *Dromaeosauripus hamanensis* type trackway from the Lower Cretaceous Haman Formation, Korea (after Lockley, Huh, and Kim, 2012). Compare with Figures 11.4–11.6 and 11.8–11.9.

that they were made by a gregarious track-making taxon. This evidence is intriguing because prior to this discovery, dromaeosaurid theropods had speculatively been hypothesized as having engaged in gregarious behavior, possibly including wolf-like, pack-hunting behavior (Ostrom, 1969, 1990; Paul, 1988; Maxwell and Ostrom, 1995; q.v. Roach and Brinkman, 2007).

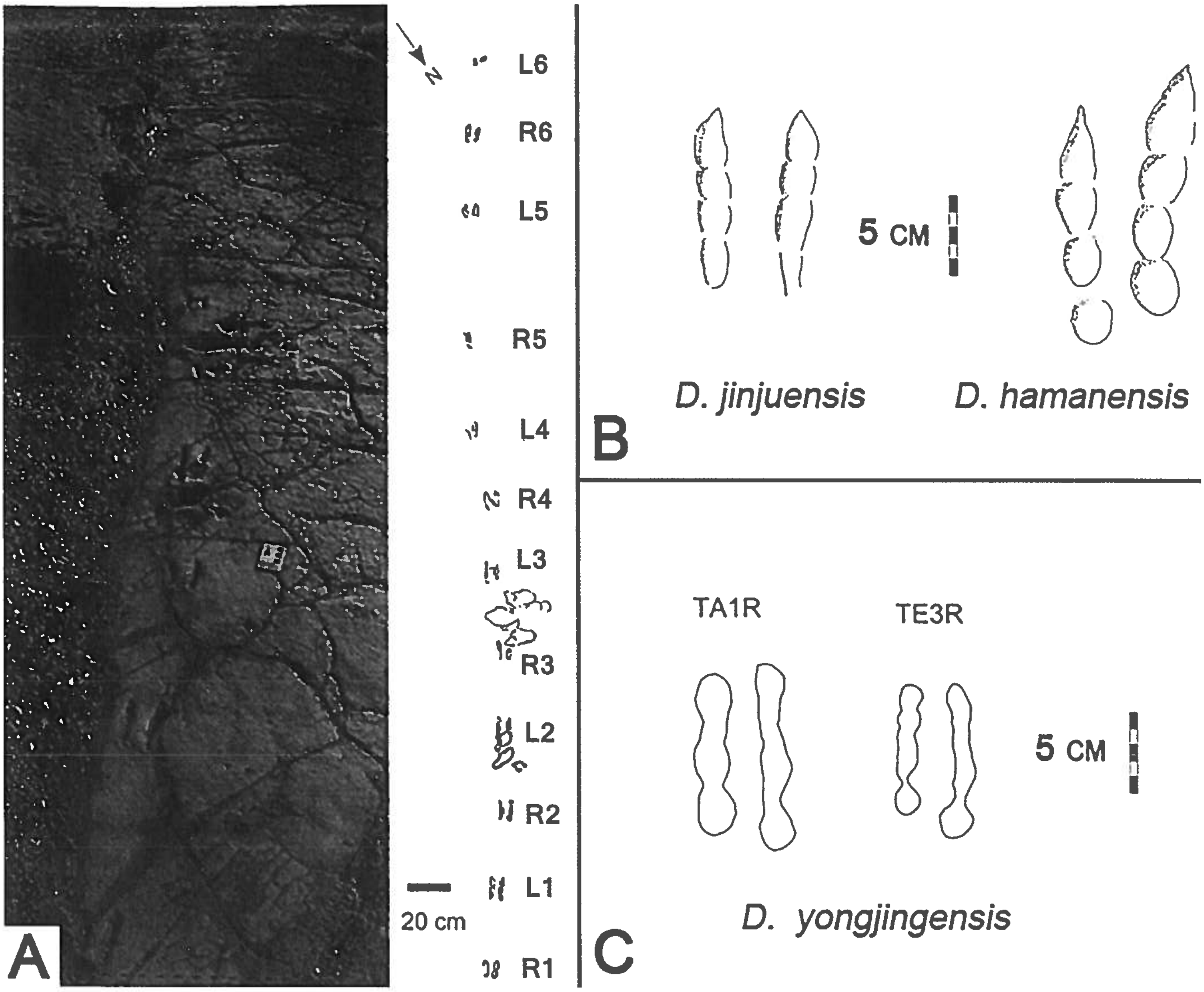
Li et al. (2008) compared *D. shandongensis* to *Velociraptorichnus* (Fig. 11.5), which also occurs at the Shandong site. This comparison emphasized a number of distinctive differences. In addition to the considerable size difference (28 cm vs. 11 cm), *Dromaeopodus* has slightly curved and more parallel digits III and IV traces that were more subequal in length than in the smaller *Velociraptorichnus. Dromaeopodus shandongensis* furthermore has sharp claw impressions, and its heel (metatarsophalangeal) pad and proximal pad of digit II both are well developed, in contrast to *V. sichuanensis*.

Another Dromaeosaurid Trackway from Shandong, China

In November 2012, two of the authors (M.G.L. and L.X.) discovered a new didactyl trackway in the Lower Cretaceous (Aptian-Albian) Tianjialou Formation (Dasheng Group) of Shandong Province (Xing, Li, et al., 2013). The tracks (Fig. 11.6) are deep (~4 cm) and were made in thinly bedded lacustrine sediment. The trackway pertains to a trackmaker with feet about 18 cm long and 10 cm wide, although these measurements may be slightly enlarged as a result of preservational factors. The mean pace length is ~59 cm. This size is intermediate between type *Velociraptorichnus* and type *Dromaeopodus*, both of which, as noted, are known from the same region of China (Li et al., 2008). Although the didactyl morphology of the tracks is clear, details of pad impressions and the traces of the short, proximal portions of digit II seen in *Velociraptorichnus* and *Dromaeopodus* are not visible. It is therefore difficult to attribute this track to either of these ichnogenera. Based on size, they are similar to *Dromaeosauripus*. This new find establishes a considerable size range in dromaeosaurid tracks from Shandong.

More Asian Didactyl Tracks: Dromaeosauripus from the Cretaceous of Korea and China

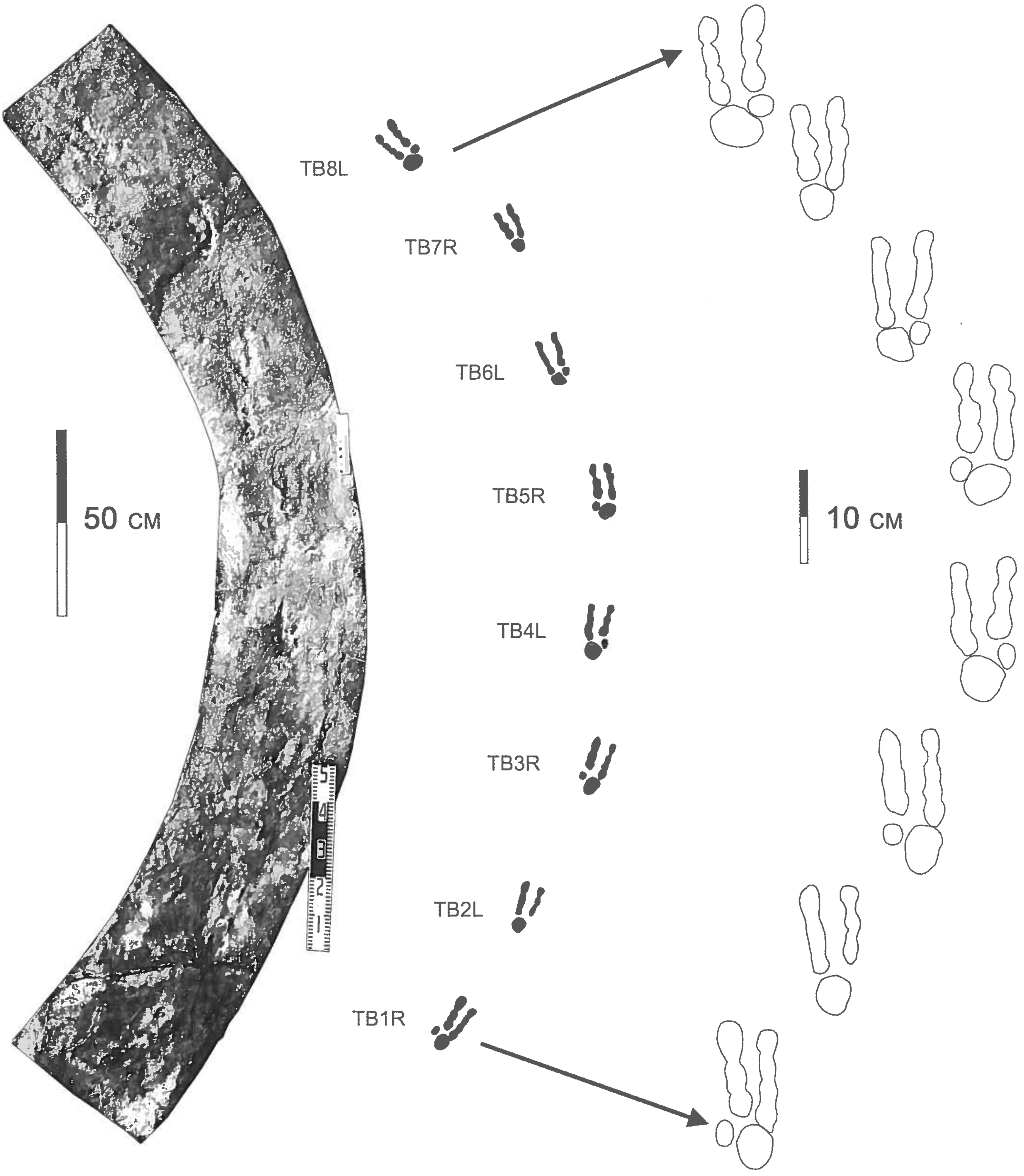
Site 1: The *Dromaeosauripus hamanensis* type Kim et al. (2008) reported the first deinonychosaurian tracks from



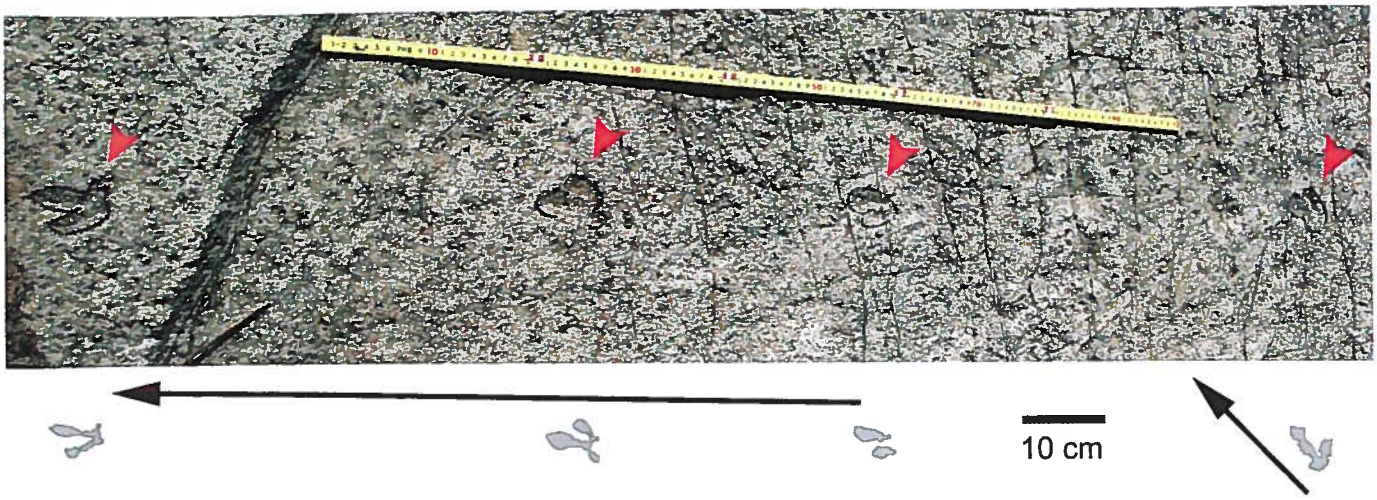
11.8. (A) Photograph and line drawing of the 12 tracks in the holotype *Dromaeosauripus jinjuensis* type trackway from the Lower Cretaceous Jinju Formation, Korea (after Kim et al., 2012). (B) Comparison of individual tracks of *D. jinjuensis* and *D. hamanensis* (after Kim et al., 2012). (C) Examples of *Dromaeosauripus yongjingensis* from the Lower Cretaceous Hekou Group of Gansu Province, China, which are convergent with *D. jinjuensis* (after Xing, Li, et al., 2013). Compare with Figures 11.4–11.7 and 11.9.

Korea: a trackway consisting of four footprints from the Lower Cretaceous Haman Formation. Three of these tracks possess quite good morphological detail. The tracks in this trackway are clearly didactyl and have a mean length of ~15.5 cm, which is intermediate in size between *Velociraptorichnus* and *Dromaeopodus*. As initially reported, the tracks lack the proximal basal pad of digit II and have heel traces that are indistinct and whose precise locations relative to the digit traces are ambiguous. The fourth track in the sequence suggests a phalangeal pad formula for digits III and IV that differ from those of *Dromaeopodus*. These differences prompted Kim et al. (2008) to assign this ichnotaxon to the new ichnogenus and ichnospecies *Dromaeosauripus hamanensis* (Fig. 11.7). The individual digit traces show only slight inward curvature, which is less pronounced than in *Dromaeopodus*.

Subsequent examination of the type trackway (Lockley, Huh, and Kim, 2012) suggested that a faint trace of the basal pad of digit II in track number III can be discerned (Fig. 11.7). Furthermore, the proximal-most digit IV pad trace illustrated by Kim et al. (2008) for the fourth track in the holotype sequence could, in fact, be a faint heel trace. These observations suggest that *Dromaeosauripus* may be morphologically more similar to *Dromaeopodus* and *Velociraptorichnus* than previously supposed. However, this conclusion is tentative, and evidence suggests that the lack of posterior traces (heel and digit II) may reflect a distinctive, digitigrade



11.9. Photograph, schematics, and details of eight tracks of *Dromaeosauripus yongjingensis* in the TB trackway from the Lower Cretaceous Yanguoxia Formation (Hekou Group) of Gansu Province, China (modified after Xing, Lockley, et al., 2013). Compare with illustrations of *D. hamanensis* and *D. jinjuensis*, respectively, in Figures 11.7–11.8.



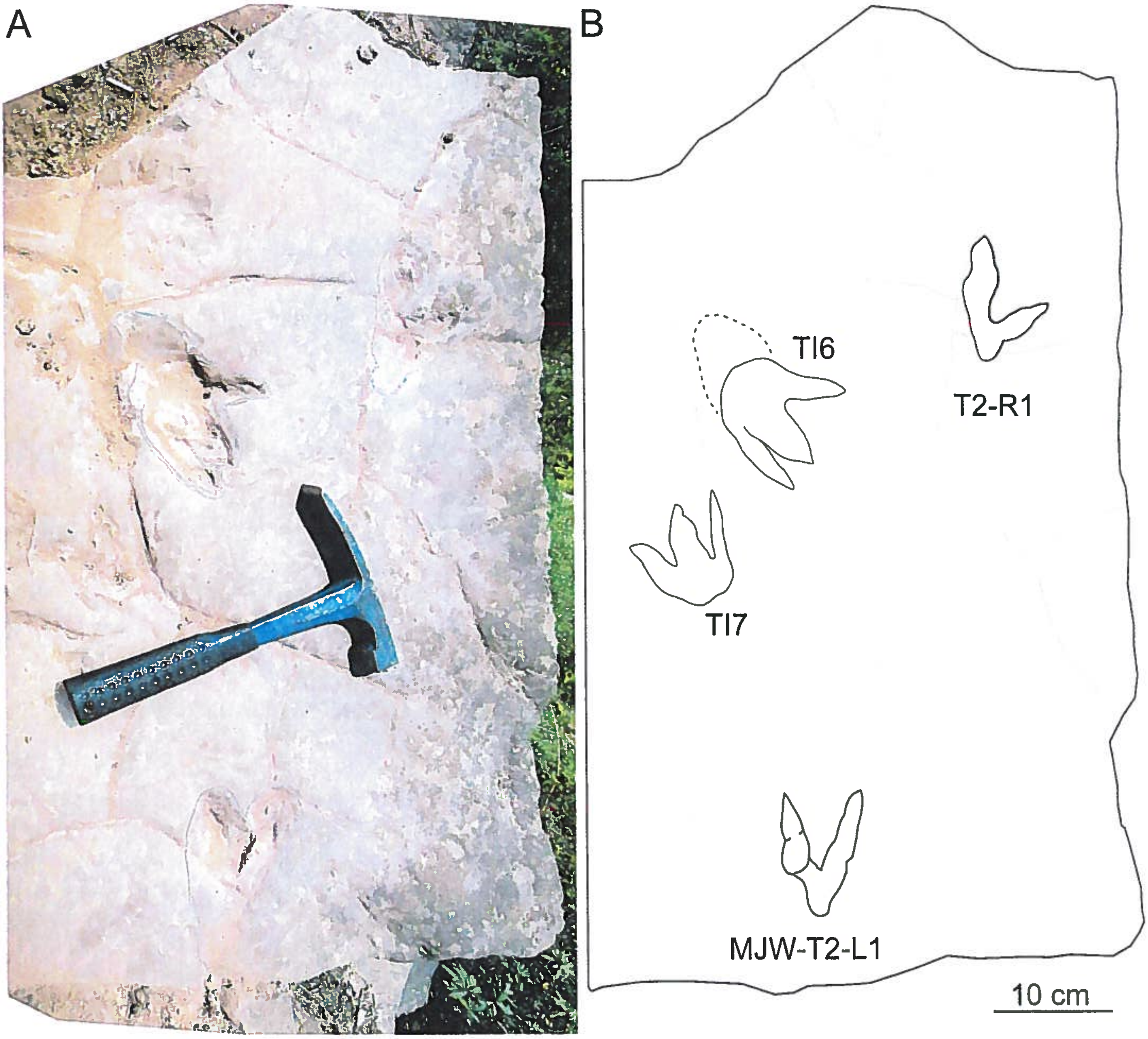
11.10. *Menglongipus* trackway. *After Xing et al. (2009).*

morphology. Replicas of *D. hamanensis* are reposited in the CU collections (CU 214.131 and 214.132).

Site 2: The *Dromaeosauripus jinjuensis* type Kim et al. (2012) described another trackway of a distinctive, didactyl biped from Korea, this time from the Lower Cretaceous Jinju Formation, which is older than the Haman Formation The new trackway comprises a continuous sequence of 12 tracks (Fig. 11.8). This trackway formed the basis for a new ichnospecies, *Dromaeosauripus jinjuensis*, which differs from *D. hamanensis* in a number of details. The tracks are shorter (mean length 9.3 cm) and have wider separations of the proximal digit traces. Thus, there is no sign that the digit traces converge proximally toward any trace of a heel, possibly indicating a distinctive, digitigrade posture. As noted herein, differential preservation may account for these differences. *D. jinjuensis* is represented in the CU collections by CU 214.243.

Site 3: The *Dromaeosauripus yongjingensis* type Xing, Lockley, et al. (2013) described trackways of another ichnospecies of *Dromaeosauripus*, *D. yongjingensis*, from the Lower Cretaceous Yanguoxia Formation (Hekou Group) at the Liujiaxia Dinosaur National Geopark in Gansu Province, China (see also Li et al., 2006). Six trackway segments were recognized, including a turning trackway from which eight consecutive tracks were illustrated (Fig. 11.9). They illustrated 19 individual tracks that show much the same range of variation seen in both Korean ichnospecies (*D. hamanensis* and *D. jinjuensis*). Among these the holotype (GSLTZP-S2-TE4L [Fossil Research and Development Center of the Third Geology and Mineral Resources Exploration Academy of Gansu Province collection]) is also represented by replica UCM 214.279 (University of Colorado Museum of Natural History collection).[1] The tracks are very similar in size (length 14.5–16.0 cm) to *D. hamanensis* and have very similar digit III and IV lengths, but in contrast to the Korean ichnospecies, most of the Chinese tracks have well-developed heel pad traces. However, the basal pad of digit II is poorly impressed in most cases: at best, it is only faintly and inconspicuously illustrated in about half the tracks illustrated. Some tracks lack heel traces and therefore are short, similar to *D. jinjuensis*. These observations suggest that there is considerable variation in the morphology of the tracks so far attributed to ichnogenus *Dromaeosauripus*, and that the Chinese samples demonstrate that differences between the two Korean ichnospecies may, in part, be related to preservation. However, there appear to be genuine, morphological (not extramorphological) differences between *Dromaeosauripus* and the previously named ichnogenera (*Dromaeopodus* and *Velociraptorichnus*), especially in relation to the development of the heel pad and digit II trace.

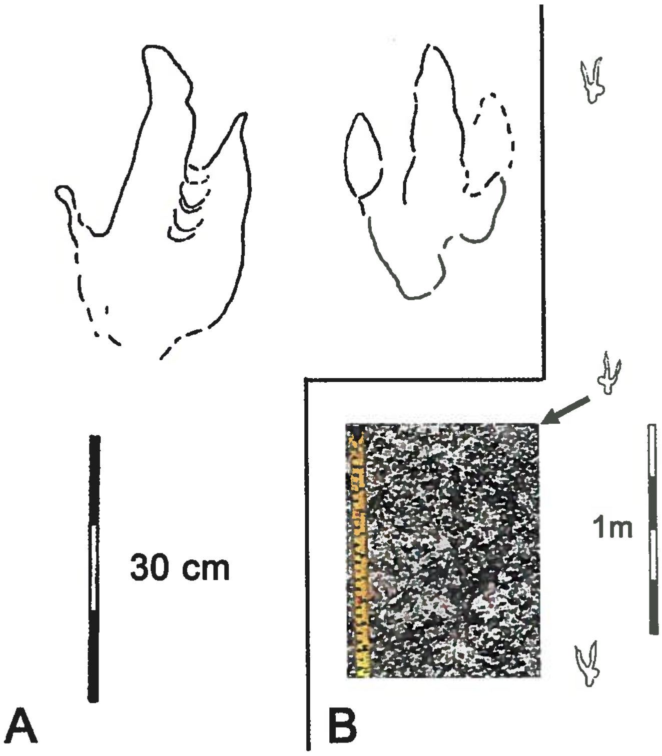
Site 4: A problematic trackway: The *Menglongipus sinensis* type Xing et al. (2009) reported poorly preserved, ostensibly didactyl theropod tracks from a single trackway on a track surface that otherwise preserves only tridactyl *Grallator* tracks from the latest Jurassic or earliest Cretaceous Tuchengzi Formation of Hebei Province, China. They were named *Menglongipus sinensis* (Fig. 11.10). Based on the age of the Tuchengzi Formation, these tracks were proclaimed as the oldest known deinonychosaur tracks. Photogrammetric models of four tracks in a single trackway sequence show that the tracks are variably preserved and that, in all cases, the presumed digit IV is short compared to digit III. If this accurately reflects the pedal morphology of the trackmaker, then it differs from those of the trackmakers of *Velociraptorichnus*, *Dromaeopodus*, and *Dromaeosauripus*, in which digits III and IV are subequal in length. Xing et al. (2009) further illustrated a photogrammetric digital elevation model of one of the *Dromaeosauripus yongjingensis* tracks from



11.11. (A) Photograph and (B) an interpretative outline drawing of didactyl and tridactyl theropod tracks from the Mujiaowu (MJW) tracksite. The tridactyl morphotype has been named *Velociraptorichnus zhangi*. *Modified after Xing et al., 2015.*

the Gansu site (Xing, Lockley, et al., 2013), documenting the different morphology. Coarse-grained substrates in the Tuchengzi Formation preserve, at numerous sites, abundant, tridactyl theropod tracks attributed to *Grallator* (Matsukawa, Lockley, and Li, 2006). For this reason, as well as the poor preservation, *Menglongipus sinensis* could be merely a poorly preserved tridactyl track, which would render it a nomen dubium. However, although the tracks are difficult to distinguish from poorly preserved *Grallator* tracks, their occurrence in a single trackway that does not include tridactyl *Grallator* tracks led Lockley et al. (2013) to retain the validity of the ichnotaxon, at least provisionally. Despite this provisional acceptance of the ichnotaxon, the step is somewhat irregular and the middle toe (digit III) impression of the first footprint in the sequence aligns poorly with the inferred trackway trend. Therefore, the case for the validity of *Menglongipus sinensis* is weaker than those for *Velociraptorichnus*, *Dromaeopodus*, and *Dromaeosauripus*. If it was truly made by a didactyl, presumably deinonychosaurian, trackmaker, the short digit IV suggests that the trackmaker was more likely a troodontid than a dromaeosaurid, though Xing et al. (2009) specifically stated that such a determination was not possible to make.

Site 5: Didactyl and tridactyl traces: *Velociraptorichnus zhangi* ichnosp. nov. type The most recent report of *Velociraptorichnus* comes from the Mujiawa tracksite in the



11.12. (A) Line drawings of two isolated tracks from the Lower Cretaceous Cedar Mountain Formation of Arches National Park, Utah (after Lockley et al., 2004). (B) Schematic diagram and photograph of a representative track from a second Cedar Mountain Formation deinonychosaurian trackway, attributed to *Dromaeosauripus* by Lockley, Gierlinski, Dubicka, et al. (2014).

Cretaceous Xiaoba Formation, Sichuan Province (Xing et al., 2015). The Mujiawa site has yielded both didactyl and tridactyl tracks that we interpret as different expressions of *Velociraptorichnus* caused by sporadic registration of the normally retracted digit II, either due to special substrate conditions or differences in behavior pertaining to degree of claw retraction in different individuals. The tridactyl morphotype has been named *Velociraptorichnus zhangi* (Xing et al., 2015); it possesses a very low divarication angle between the traces of digit II and III (Fig. 11.11).

At least one other Cretaceous tracksite from Sichuan Province that preserves a few didactyl tracks is currently under investigation by two of the authors (M.G.L. and X.L.). Descriptions of the tracks from this site will be published elsewhere.

Deinonychosaurian Tracks in North America

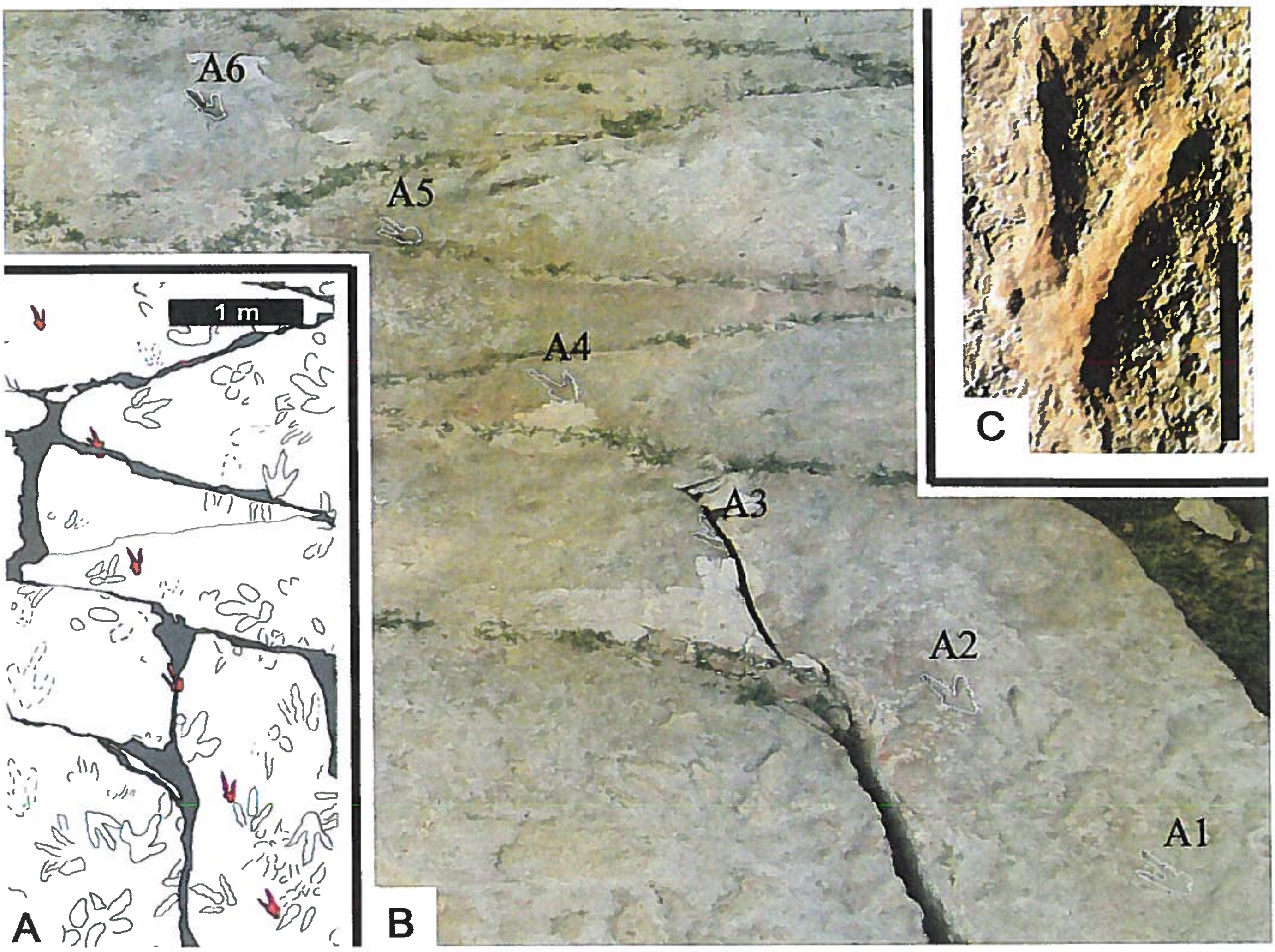
At present, only three North American dinosaur tracksites are known to have yielded deinonychosaurian tracks. Two occur in the Cedar Mountain Formation in eastern Utah, the third occurs in the Dakota Group of Colorado (Table 1). The first-discovered site yielded only isolated footprints, but the second-discovered site yieldes two well-preserved trackways.

Cedar Mountain Formation occurrences of *Dromaeopodus* and associated ichnites from Utah Isolated, possibly didactyl tracks reported from the Ruby Ranch Member of the Lower Cretaceous Cedar Mountain Formation within the boundaries of Arches National Park in eastern Utah were tentatively identified as the first deinonychosaur tracks from North America (White and Lockley, 2002; Lockley et al., 2004). Unequivocal confirmation of such tracks came from a five-track (four-step) trackway at another nearby site known as the Mill Canyon Dinosaur Tracksite, just west of Arches National Park (Lockley, Gierlinski, and Dubicka, et al., 2014). The two best-preserved tracks are represented in the CU collections by UCM 199.67 and 199.68. Further excavation at the site has since exposed another three-track (two-step) trackway (UCM 199.82) illustrated by Lockley, Gierlinski, and Houck, et al. (2014:fig. 8A). The Mill Canyon tracks were originally attributed to *Dromaeopodus* by Cowan, Lockley, and Gierlinski (2010) but have since been restudied and assigned to *Dromaeosauripus* (Lockley, Gierlinski, and Dubicka, et al., 2014; Lockley, Gierlinski, and Houck, et al., 2014). This trackway (Fig. 11.12) pertains to a smaller and more gracile trackmaker than that of the type *Dromaeopodus* from China. The Utah tracks have relatively small, though unequivocal, proximal pad traces on digit II. The tracks are smaller (footprint length 20–21 cm) than the isolated, apparently didactyl tracks reported in 2004 (Fig. 11.12A), which remain enigmatic. Recently, the Bureau of Land Management has installed interpretative signs at the Mill Canyon Dinosaur Tracksite, including one which uses the label *Dromaeosauripus* and shows a reconstructed "raptor" foot, with retracted claw, making a didactyl track.

Deinonychosaurian Tracks in Europe

At present, only two European dinosaur tracksites are reported to have yielded deinonychosaurian tracks. One is associated with the Early Cretaceous of Germany, the other with the late Cretaceous of Poland. The German site yielded a large assemblage of tracks, but it occurred as part of an extensively trampled surface. The Polish sites yielded a single trackway that was not very well preserved.

The Oberkirchen "Chicken Yard" Site Didactyl tracks from the Early Cretaceous (Berriasian) of northern Germany (van der Lubbe, Richter, and Böhme, 2009; van der Lubbe et al., 2012) occur amid a heavily 'trampled' tracksite on the company grounds of the Obernkirchener Sandsteinbrüche near the town of Obernkirchen (See also Richter and Böhme, 2016). The site, which has become popularly known as the Chicken Yard (Hühnerhof) is important not least because it preserves the largest assemblage of deinonychosaurian tracks known anywhere in the world. Their relative abundance



11.13. (A) Partial map and (B) photograph of deinonychosaurian trackway A from the Obernkirchen Chicken Yard site, Lower Cretaceous Obernkirchen Sandstone, Germany.

allows for a detailed description of general track morphology, as well as an opportunity to expand available data on didactyl tracks. The entire Obernkirchen ichnoassemblage will be described in detail elsewhere (e.g., Richter and Böhme, 2016).

A total of 86 didactyl tracks documented to date are preserved as shallow impressions (depths ~0.6–14 mm; average ~6 mm) in silty sandstone. Many of the tracks are well preserved, showing well-defined pad and sharp claw impressions. They generally are very slender, and the digit IV impressions are markedly shorter than those of digit III. A segment of 1 (trackway A) of the 17 didactyl trackways at the site (labeled A–R, omitting I) is illustrated herein (Fig. 11.13). Trackway width is narrow, and pace angulation is 170°–180°. Track sizes range from a total track length 13.0 cm to a maximum of 23.3 cm. Pace and stride lengths are long: the 105 cm average pace length of trackway F corresponds to a track length of 20.9 cm.

A slightly ovoid, almost circular heel impression constitutes the proximal-most part of each track. Digit II is represented by a small, subcircular to ovoid impression positioned slightly posterior to the impression of the first pad of digit III. Digit III impressions consist of three elongate, subrectangular to slightly ovoid pad impressions terminating in long, sharp claw imprints. Digit IV impressions consist of four pad impressions, but they are only well defined in a few specimens. Digit IV claw impressions are rare, and much shorter than those of digit III. Digit IV impressions are rather straight, and, in a single case (A 12), actually curves gently laterally. The angles of divarication between digit III and IV impressions range from 21° to 36° (average ~28°).

Digit III consistently left the deepest impressions (2.5–14 mm), followed by the metatarsal pad impressions (1.5–11.3 mm). The digit IV impressions are, on average, only slightly deeper than those of digit II (6 mm and 5.1 mm, respectively). The maximum value for a digit IV impression depth is 12.5 and the minimum value is 2.5 mm; the same values are 11.5 and 2.1 mm, respectively, for digit II. The morphology and measurements of the tracks are distinctive

Table 11.1. Summary data on 16 reported deinonychosaurian tracksites from the Cretaceous of Asia, North America, and Europe, with ichnotaxonomic designations, details of sample size, track size, quality of preservation, and sources of information

Site	Ichnotaxon	Number of tracks/ trackways	L and W (cm)	Preservation	Reference(s)
Emei County, Sichuan, China	*Velociraptorichnus sichuanensis*	4/3	L ~10 cm	Good, deep casts	Zhen et al. (1994)
Junan County, Shandong, China	*Dromaeopodus shandongensis*, *Velociraptorichnus*	14/7	L 28.0	Excellent molds in type; others variable	Li et al. (2008)
Linshu County, Shandong, China	dromaeosaurid track indet.	5/1	L ~19.0, W ~ 10.5	Fair, deep molds	Xing et al. (2013b)
Chicheng, Hebei, China	*Menglongipus sinensis*	4/1–2	Mean L = 6.3, mean W = 4.3	Poor molds	Xing et al. (2009)
Gansu, China	*Dromaeosauripus yongjingensis*	71/7	L 14.8, W 6.4	Fair to good molds	Xing et al. (2013a)
Chu Island, Korea	*Dromaeosauripus hamanensis*	4/1	mean L = 15.5	Fair, shallow molds	Kim et al. (2008)
Bito Island, Korea	*Dromaeosauripus jinjuensis*	12/1	mean L = 9.3	Deep incomplete molds	Kim et al. (2012)
Arches National Park, Utah	Unnamed, probable deinonychosaurian	2/2	L ~28–?~35	Fair, very deep molds	Lockley et al. (2004)
Mill Canyon site, Utah	*Dromaeosauripus*	4/1	L 21/	Good, shallow molds	Cowan et al. (2009)
Obernkirchen, Germany	Unnamed, probable troodontid	–/86	L = 13-23.3	Good molds	van der Lubbe et al. (2009), (2012)
Mlynarka Mount, Poland	*Velociraptorichnus* isp.	3/1	L 17.0	Poor molds	Gierliński (2007, 2008, 2009)
Mujiaowu, Sichuan, China	*Velociraptorichnus zhangi*, *Velociraptorichnus* isp.	2/0 3/1	L ~10.4, W 9.4 L 11.3	Good molds Good molds	Xing et al. (2015)
Yanqing, Beijing, China	? *Velociraptorichnus*	1/1	L 10.8, W 5.3	Good mold	Xing et al. (2015)
Bajiu, Sichuan, China	cf. *Dromaeopodus*	2/2	L 17.4–24.8, W 5.9–14.5	Good mold	Xing et al. (2016)
Shimiaogou Sichuan, China	*Velociraptorichnus* isp.	5/1	L ~7.1 cm	Fair molds	Xing et al., in press
Dinosaur Ridge	*Dromaeosauripus*	2/2	L ~16.0-17.0	Natural casts	Lockley et al., 2016

Notes: Note that two distinct morphotypes are known from the Junan County site in Shandong province. L, length; W, width.

enough that they could support a new ichnotaxon when fully described.

A Late Cretaceous Track from Poland

Gierlinski (2007, 2008) illustrated two individual tracks attributed to *Velociraptorichnus* from the Late Cretaceous (late Maastrichtian) Mlynarka Mount site in Poland and indicated that a specimen is preserved in the Polish Geological Institute (PIG 1704.11.6). According to the illustrations in these publications, the tracks are about 17 cm long. Later describing the same material in more detail, Gierlinski (2009) suggested that tracks might be more similar to *Dromaeopodus* from China (Li et al., 2008). The first two reports comprise illustrated abstracts that thus provide minimal description of the material. In the later paper, two tracks were shown in a purported trackway sequence, with the first (a right) followed, after a gap of about 1.87 m as measured from the scale of the photograph (Gierlinski, 2009:fig. 7), by a left. Gierlinski (2009) suggested that the tracks compose a portion of a single trackway with a footprint: pace length ratio of 1:12.30, indicating a remarkable speed of about 50 km/hr. Unfortunately, the trackway has since been destroyed (Gierlinski, pers. comm., 2012).

The illustration presented by Gierlinski (2007), which is of the same left footprint illustrated by Gierlinski (2009), does not show the proximal trace of digit II as well defined, but the illustration in Gierlinski (2008) indicates a different track, or differently illuminated view, of a left footprint with the proximal trace of digit II more clearly defined. However, the method of illustrating tracks that the author used in these papers involved isolating the tracks from photographs by cropping the matrix surrounding the tracks. This may have introduced some subjectivity in how the outline or margin of the track is defined.

DISCUSSION

Deinonychosaurian tracks have been reported from 16 Cretaceous tracksites in Asia, North America, and Europe (Fig. 11.1, Table 11.1), including the most recently reported sites from China (Xing et al. 2015a; 2015b; 2016, in press) and Colorado (Lockley et al., unpublished manuscript). With the exception of the German site, the sample sizes are small. The best preserved among these tracks are the types of *Velociraptorichnus* from Sichuan Province and *Dromaeopodus* from Shandong Province, China. The type of *Dromaeopodus* is particularly well preserved and is associated with a nearby assemblage of six other parallel trackways, suggestive of gregarious behavior (Li et al., 2008). The large, German sample consists of 86 tracks, and the preservation is sufficient both to differentiate the tracks from the other named ichnogenera and to suggest that they are of troodontid, rather than dromaeosaurid origin; they remain the only convincingly troodontid tracks known. As noted, the morphological differences between the as-yet unnamed German tracks and other, named tracks, such as *Dromaeopodus*, may well be sufficient to warrant the erecting of a new ichnotaxon. The only other track morphotype currently known that could be attributed to a troodontid, based on the differential lengths of the traces of digits III and IV, is *Menglongipus*. However, such attribution is only conjectural because the poor preservation of the type specimens renders such an inference uncertain.

Known deinonychosaurian tracks range widely in size (Table 11.1), varying from a mean length of only 6.3 cm in *Menglongipus sinensis* to 28 cm in *Dromaeopodus shandongensis*. One very deep track from the Arches National Park site in Utah is about 35 cm long, but its length may have been exaggerated during the registration and extraction of the foot.

Clearly, the footprint evidence complements the skeletal evidence that indicates that deinonychosaurian trackmakers were paleogeographically widespread. The ages of many of the track-bearing units, however, are less certain: not all are reliably dated to the level of epoch or age (Chen et al., 2006; Matsukawa, Lockley, and Li, 2006; Lockley et al., 2013). It is beyond the scope of this chapter to discuss in detail the ages of the formations from which these tracks originate or the resultant implications for the temporal distribution of deinonychosaurian tracksites. In general, most of these tracksites appear to be late Early Cretaceous (post-Neocomian; Barremian-Albian) in age. The Hebei and Yanqing tracksites are ostensibly the oldest, associated with the basal Cretaceous (or Jurassic-Cretaceous transition), and the Polish site is the youngest. The Polish site is also the only one associated with carbonate deposition in a marginal marine setting; all others are associated with fluvio-lacustrine settings.

Following the discovery of *Velociraptorichnus* in 1994, and the uncertain reports of tracks from Utah in 2004, all 14 subsequent discoveries have been reported since 2007. Why the bulk of discoveries have been made in such a short period of time may have to do with increased searching for and recognition of dinosaur tracks globally, but in any case, deinonychosaurian tracks are not as rare as might have previously been assumed. The reports of Li et al. (2008) and van der Lubbe, Richter, and Böhme (2009) and van der Lubbe et al. (2012), respectively, have indicated that it may be possible to differentiate dromaeosaurid from troodontid tracks, at least in some cases. Examinations of the foot skeletons of members of both groups, to see how they might 'best fit' the footprints (Lockley, 1998), would facilitate such distinctions.

Ostrom (1969) interpreted the morphology of pedal digit II of *Deinonychus antirrhopus* as highly specialized for a predatory function such that it did not contact the ground at all under normal circumstances, an interpretation borne out by later discoveries and studies of other dromaeosaurids (Barsbold, 1974, 1998; Norell and Makovicky, 1997; Xu and Norell, 2004; Manning et al., 2005; Gao et al., 2012). The recent report of Xing et al. (2015), suggesting that in some cases traces of digit II (other than its proximal pad) may have registered, indicates that such cases are the exception, not the rule. As summarized in Table 11.1, more than 30 deinonychosaurian trackways have been described from the 16 sites included in this survey. Only two of these indicate occasional registration of the distal part of digit II. In terms of its effect on locomotion, the specialization of digit II shifted, albeit incompletely, the structural, weight-bearing axis of the foot from mesaxonic (along digit III) to ectaxonic (between digits III and IV); this shift is reflected by the subequal lengths of digits III and IV. As noted, digit II impressions have been reported in almost every well-preserved Cretaceous didactyl track documented to date, but with the exception of *V. zhangi* (Xing et al., 2015a), they consist solely of the proximal pad. These traces are not preserved in some examples of ichnogenus *Dromaeosauripus*, notably *D. jinjuensis* (Kim et al., 2012), probably due to preservational factors; the Gansu sample described by Xing, Lockley, et al. (2013) shows that the range of preservation of *Dromaeosauripus yongjingensis* is at least as wide as those of both the Korean ichnospecies (*D. hamanensis* and *D. jinjuensis*). Digit II, therefore, maintained a role, albeit a limited one, during normal locomotion. The depths of the Obernkirchen didactyl tracks suggest that the structural, weight-bearing axes of the feet of their trackmakers indeed had shifted from its normal position along the midline through digit III toward digit IV to a certain degree, confirming the prediction of Ostrom (1969). However, digit III constitutes the most deeply impressed part of the foot in all specimens documented so far and was undoubtedly the primary weight-bearing digit.

The primary character that distinguishes the Obernkirchen tracks from all the other didactyl tracks is the length difference between the impressions of digits III and IV (average ratio of digit IV to III impression length is 0.8). In all other didactyl tracks, except for *Menglongipus* (Xing et al., 2009), digit IV is either subequal to or slightly shorter than digit III, comparing favorably with dromaeosaurid pedal skeletons. The proportions of the pedal skeletons of *Troodon formosus* (Russell and Séguin, 1982), *Sinovenator changii* (Xu et al., 2002; van der Lubbe, pers. obs.), *Mei long* (Xu and Norell, 2004; van der Lubbe, pers. obs.), and *Talos sampsoni* (Zanno et al., 2011) match remarkably well the proportions of the didactyl tracks from Obernkirchen. However, the match is not universal among troodontids: digits III and IV are of subequal length in the pes of the holotype specimen of *Sinornithoides youngi* (Russell and Dong, 1993), which is a juvenile. Among dromaeosaurids, at least *Microraptor* (Xu, Zhou, and Wang, 2000) possesses a digit IV noticeably shorter than digit III (van der Lubbe, pers. obs.). Published data are only of limited use because measurements of unguals were usually made along their outer, and sometimes also inner, curvatures. During track formation, the claw will not imprint along its curvature but rather leave an imprint representing a line from its tip to the proximal end of the keratinous sheath; see Lockley and Lucas (2013) for similar traces in Triassic *Evazoum* tracks. An encompassing study of paravian pedal morphology with a special focus on characters (such as digit lengths) that are potentially relevant for ichnology (Sullivan, van der Lubbe, and Xing, 2012) may show whether the hypothesis briefly presented here can be further elaborated. Nevertheless, the didactyl tracks from Obernkirchen differ from all other published didactyl tracks in a character that is best explained as related to pedal morphology, and they are therefore probably of troodontid origin.

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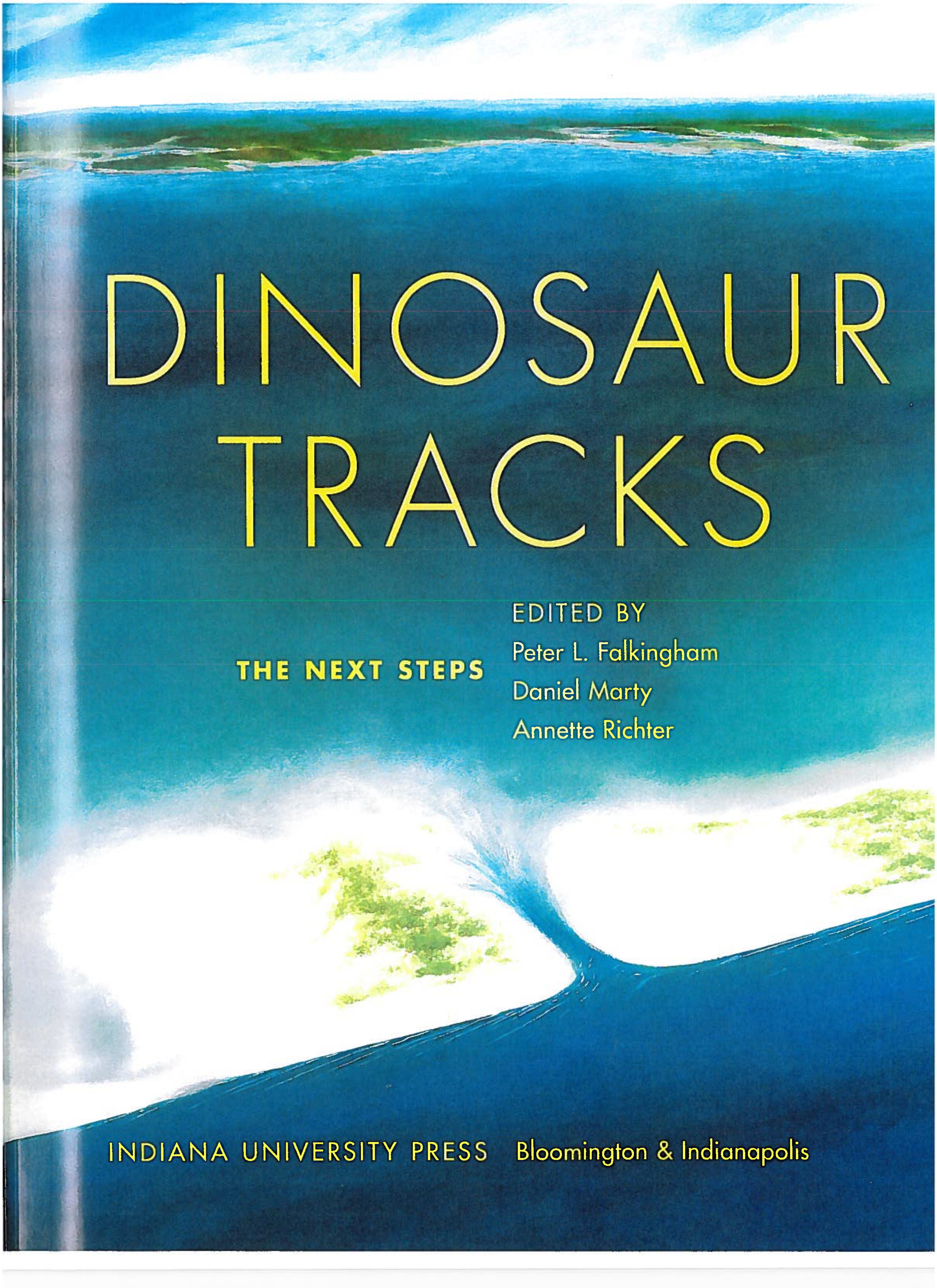
NOTE

1. Beginning in 2012, after the transfer of the CU collection to UCM, this prefix, if used, is synonymous with the CU prefixes cited in many of the publications referenced herein and elsewhere.



DINOSAUR TRACKS

THE NEXT STEPS

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