The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2014, **113**, 770–789. With 3 figures

Tracking Lower Cretaceous Dinosaurs in China: a new database for comparison with ichnofaunal data from Korea, the Americas, Europe, Africa and Australia

MARTIN G. LOCKLEY[1]*, LIDA XING[2], JEONG YUL KIM[3] and MASAKI MATSUKAWA[4]

[1]*Dinosaur Trackers Research Group, University of Colorado Denver, CB 172, PO Box 173364, Denver, CO 80217-3364, USA*
[2]*School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China*
[3]*Department of Earth Science Education, Korea National University of Education, Cheongwon, Chungbuk 363-791, Korea*
[4]*Department of Environmental Sciences, Tokyo Gakugei University, Koganei, Tokyo 184-8501, Japan*

Received 1 February 2014; revised 11 March 2014; accepted for publication 12 March 2014

Following the recent rapid increase in the reports of tetrapod tracksites in the Cretaceous, especially from the Lower Cretaceous, of China and other parts of East Asia, notably South Korea, a review of the ichnofaunal database from these regions is presented as the basis for comparisons with other Lower Cretaceous ichnofaunas that are abundant and reasonably well documented. These areas include parts of North and South America, especially the western USA, and parts of Europe, including the United Kingdom, Northern Germany, Spain, Italy and Croatia. The Chinese database presently includes about 70 Cretaceous sites, the majority of which are Early Cretaceous in age. Although abundant data are available from many regions, much of it has yet to be synthesized in detail or in standard formats. Moreover, ichnotaxonomy may be variable (provincial) between different regions. Thus, while comprehensive lists of sites are available for some regions (China and South America), in other regions such as South Korea and the western USA data have been compiled primarily on a formation by formation basis. The record for Europe is moderately good, but scattered in the primary literature and in need of further synthesis. The record for Australia and Africa is sparse and also in need of synthesis. The most notable regional differences between ichnofaunas appears to be in the relative abundance of distinctive bird and pterosaur track ichnotaxa in China and Korea in comparison with their scarcity or absence in other regions. The distinctive ichnogenus *Minisauripus* is also known only in China and Korea as are the majority of known dromaeosaurid track occurrences. Ornithopod-dominated and ornithopod-rich ichnofaunas are widespread and particularly abundant in the late Early Cretaceous Barremian to Albian, of some regions. Most well documented Early Cretaceous ichnofaunas are associated with siliciclastic facies and evidently differ from those associated with carbonate facies.

ADDITIONAL KEYWORDS: China – Cretaceous – dinosaurs – footprints – tetrapods.

INTRODUCTION

In this paper we review what is currently known of dinosaur and other tetrapod tracksites in the Early Cretaceous of China and other footprint-rich regions including Korea, the Americas and Europe. Due to variability and limitations in available databases, only brief discussion of African and Australian track records is possible. It is well known that the rate of discovery of dinosaurs, both avian and non-avian, in China has been impressive in recent years, due not least to the steady increase in reports of feathered dinosaurs from northeastern China. The majority of these come from the Yixian Formation, which is essentially devoid of footprints, evidently because the facies is unsuitable for footprint registration (see Matsukawa *et al*., 2014). However, this does not

*Corresponding author. E-mail: martin.lockley@ucdenver.edu

mean that tracksites are rare in the Early Cretaceous of China. On the contrary, we now know of about 70 sites reported from most of the 31 provinces, regions and municipalities of China. Here we summarize the data available from these sites and compare the results with summaries derived from other areas well-known for abundant Early Cretaceous tracksites including Korea, North and South America and Europe. We also discuss the differences between databases obtained from different regions by different methods.

Impetus for the present study derives from several sources. First, it is a contribution to the Jehol-Wealden International Conference, held in England in September 2013 (see acknowledgements). Second, is the opportunity to showcase the rapid development of Early Cretaceous tetrapod ichnology in China in the last decade. Third, the study provides an opportunity to compare the most important Early Cretaceous ichnofaunas from China with those known from other parts of East Asia, the Americas, Europe and elsewhere. As discussed, these databases are very variable and incomplete in some regions.

PREVIOUS WORK

The first attempts to summarize the fossil footprint record of China, in the English literature, was by Zhen *et al*. (1989, fig. 19.1) who identified a total of 22 'principal dinosaur footprint localities' of which only eight were reported as being Cretaceous in age. This number was more than doubled when Matsukawa, Lockley & Li (2006) reported 52 principal sites from China, including 29 in the Cretaceous, as well as an additional 20 mostly Cretaceous sites elsewhere in East Asia. Between 1999 and 2006, much of this work was spear-headed by two of the present authors (MGL and MM) culminating in short reviews (e.g. Lockley & Matsukawa, 2009). Presently this work is being continued (2007-present) under the leadership of LX and MGL, with continued participation by the other authors. As noted below these lists are always underestimates, and always in need of updating. This is because they often deal only with principal sites, or treat previously defined tracksite regions, where several discrete sites occur in close proximity, as single sites. Efforts to list tetrapod tracksites in China and East Asia have been fairly consistent, at least in style of presentation. The map produced by Zhen *et al*. (1989) formed the basis of subsequent maps (Matsukawa *et al*., 2006; Lockley *et al*., 2012a) and is again used here (Fig. 1). However, as noted above, the number of tetrapod tracksites reported from China has increased rapidly in recent years and is now in excess of 100, with about 70 being known from the Cretaceous (Table 1). There have been recent efforts to simplify the 'over-split' ichnotaxonomy of Chinese tetrapod tracks (Lockley *et al*., 2013). One outcome of this study has been to conclude that Jurassic tetrapod ichnotaxonomy was even more over-split than Cretaceous ichnotaxonomy. Nevertheless 34 Chinese tetrapod ichnospecies have been named to date (Lockley *et al*., 2013, Table 1; Table 1 herein). As noted in the following sections work on important tracksites in Korea, the Americas and Europe has been ongoing at least since the 1980s, if not earlier in some regions. However, due to the difference in size of study areas, geology and research methods (traditions), the emergent data have proved quite variable.

MATERIAL AND METHODS

Despite the aforementioned studies that review the distribution of ichnofaunas in China and East Asia, the potential data base is vast, especially when comparative data from Korea, the Americas and Europe is included. Ideally a complete database should include a list of all sites, and the number of track types and trackways reported from each. While such data are available for some sites, reliable data are by no means readily available for all sites. This is to say nothing of the variability employed in naming various track morphotypes either at the ichnospecies, ichnogenus or less-precise higher taxonomic levels. Moreover the published record is always in need of re-evaluation, as some sites are enlarged, others removed or diminished by erosion or human impact, and yet others re-evaluated by re-naming or re-surveying the various ichnotaxa, and their relative abundance. With increase interest in geoheritage studies, and the creation of national and international geoparks and World Heritage sites in areas with significant fossil footprint sites, efforts are underway to find consistent methods for evaluating the importance of tracksites, because such comparative analyses are required for such nominations and designations. Thus, several studies, pertaining to World Heritage site nominations have created lists of the globally most important tetrapod tracksites based on a number of factors: size of site, number of trackways, diversity of track types, preservation quality, and other features. These factors cannot be discussed in detail here. However, it is important to note that many factors must be considered in measuring importance, including those listed above. These factors may be of similar or different importance in evaluating sites for scientific study and for geoheritage designations. For example, large sites may appear high on the global list of importance, whereas small sites do not. Nevertheless, small sites may be of scientific significance and it is important to include all sites in databases if possible.

Table 1. List of 72 tetrapod tracksites from China, referred to as Cretaceous in at least one published source. Note that some may be associated with the Jurassic–Cretaceous boundary and some may be Upper Cretaceous in age. Holotype occurrences also noted (light green shading; light grey in print). Thero, theropod; sauro, sauropod; ornith, ornithioschian; ptero, pterosaur; croc, crocodilian

	Site	Province	Age	Fm or Gp	Thero	Bird	Sauro	Ornith	Ptero	Croc	Turtle	Holotype
1	Tongfosi	Jilin	Cret	Tongfosi	x			Ornithopod				
2	Sijiazi	Liaoning	Tith-Ber	Tuchengzi	X							*Grallator ssatoi*
3	Nanpachazu	Liaoning	Tith-Ber	Tuchengzi	x							
4	KanJiaTun	Liaoning	Tith-Ber	Tuchengzi		X						*Pullornipes aureus*
5	Fuxin coalmine	Liaoning	Early Cret	Fuxin	X							*Changpeipus carbonicus*
7	Qiaomaigonmen	Hebei	Early Cret	Jiufotang	x			*Caririchnium*				
8	Sangyuan	Hebei	Early Cret	Jiufotang	x	x		Ornithopod				
9	Shuinan Laiyang	Shandong	Early Cret	Longwang-zhuang	X							*Paragrallator yangi*
10	Huangyandi	Shandong	Early Cret	Shuinan						x		*Laiyangpus liui*
11	Shaojian	Shaanxi	Early Cret	Fengjiashan	X							*Magnoavipes asiaticus*
14	Yuanjiatun	Yunnan	Tur-Con	Jiangdihe			X					*Brontopodus changlingensis*
15	Fangjiahe hill	Yunnan	Tur-Con	Jiangdihe	X							*Yunnanpus huangcaoensis.*
16	Yuanjiatun 2	Yunnan	Tur-Con	Jiangdihe			x					
17	Yuanjiatun 3	Yunnan	Tur-Con	Jiangdihe	x		x					
18	Yuanjiatun 4	Yunnan	Tur-Con	Jiangdihe			x					
23	Guanyingchong	Sichuan	Early Cret	Jiaguan	X							*Yangtzepus yipingensis*
24	Xingfu cliff Emei	Sichuan	Cret	Daergun	XXXX	X						*Grallator emeiensis, Velociraptorichnus sichanensis, Minisauripus chuanzhuensis, Aquatilavipes sinensis, Iguanodopus xingfuensis*
31	Hingwei village	Hunan	Late Cret	Xiaodong	XXX							*Hunanpus jiuquwanensis, Xiangpus chenxiensis, Xianxipus youngi*
32	Xiahutian	Anhui	Late Cret	Qiuzhang	x			?ornithopod				
33	Shangshagen	Anhui	Late Cret	Qiuzhang	x	x						
34	Minguan	Anhui	Late Cret	Qiuzhang		X						*Aquatilavipes anhuiensis*
36	Chabu 1	Nei Mongol	Early Cret	Jianchuan	x	x						
37	Chabu 2	Nei Mongol	Early Cret	Jianchuan	x		x					
38	Chabu 3	Nei Mongol	Early Cret	Jianchuan	x							
39	Chabu 4	Nei Mongol	Early Cret	Jianchuan	x		x					
40	Chabu 5	Nei Mongol	Early Cret	Jianchuan	x		x					
41	Chabu 6	Nei Mongol	Early Cret	Jianchuan	X		x					*Asianopodus robustus*
42	Chabu 7	Nei Mongol	Early Cret	Jianchuan	x	x						
43	Chabu 8	Nei Mongol	Early Cret	Jianchuan	X		x					*Chapus lockleyi*
44	Chabu 9	Nei Mongol	Early Cret	Jianchuan	x	x						
50	Yanguoxia	Gansu	Early Cret	Hekou Group	x		x	x	x			
51	Xiaguan	Henan	Early Cret	Sangping				X				

52	Yangmeikeng	Guandong	Late Cret	Nanxiong				X			*Hadrosauropodus nanxiongensis*
53	Sihetun	Liaoning	Early Cret	Yixian	x						
54	Qianjiadian	Beijing	Early Cret	Tuchengzi	x		x				
55	Luofengpo	Hebei	Early Cret	Tuchengzi	x						
56	Siliang	Hebei	Early Cret	Tuchengzi	x						
57	Hailiutu	Hebei	Early Cret	Tuchengzi	x			?			
61	Shaojian	Shaanxi	Early Cret	Donghe Group	x						
62	Bawangzhuang	Shaanxi	Early Cret	Luohe	x						
63	Dijiaping	Shaanxi	Early Cret	Luohe	x						
65	Guyuan	Ningxia	Early Cret	Liwaxia	X		x				*Ningxiapus liupanshanensis*
67	Huazhuang	Gansu	Early Cret	Hekou Group	x						
68	Xiapujia	Gansu	Early Cret	Hekou Group		x					
69	Zhingpu	Gansu	Early Cret	Hekou Group	x		x				
71	Wuerhe	Xinjiang	Early Cret	Tugulu Group	x	x		Stegosaur	x	x	*Deltapodus curriei, Koreanaornis dodsoni, Moguiornipes robusta*
72	Asphaltite	Xinjiang	Early Cret	Tugulu Group	x	x			x		
73	Weuxiyuan	Shandong	Early Cret	Qugwzhang	x	x			x		
74	Zhangzhuhewang	Shandong	Early Cret	Tianjialou		x	x	x			
75	Huanglonggou	Shandong	Early Cret	Longwangzhuang	X	x				x	*Corpulentapus lilasia*
76	Junan	Shandong	Early Cret	Tianjialou	XXX	x		x			*Dromaeopodus shandongensis, Shandongornipes muxiai, Minisauripus zhenshounani*
77	Linshu	Shandong	Early Cret	Tianjialou	x	?	x	Ornithischian			
78	Qingquansi	Shandong	Early Cret	Tianjialou			x				
79	Malingshan	Shandong	Early Cret	Tianjialou	x		x				
81	Lishui	Zhejiang	Early Cret	Shouchang			x				
82	Dongyang	Zhejiang	Late Cret	Jinhua	x	x		x	x		
83	Gushi	Guandong	Late Cret	Nanxiong				x			
86	Hemenkou	Yunnan	Early Cret	Puchnaghe	x		x	?			
89	Sanbiluoga	Sichuan	Early Cret	Feitianshan	x		x	x	x		
90	Jeufanggou	Sichuan	Early Cret	Feitianshan			x				
91	Yangmozou	Sichuan	Early Cret	Feitianshan	x						
95	Lotus	Sichuan	Early Cret	Jiaguan	X?	x	?	X	x		*Caririchnium lotus, Wupus agilis*
96	Baoyuan	Sichuan	Early Cret	Jiaguan	x						
98	Yongnan	Heilongjiang	Early Cret	Yong'ancun				x			*Jiayinosauripus johnsoni*
99	Chabu 10	Nei Mongol	Early Cret	Jianchuan	x						
100	Chabu 11	Nei Mongol	Early Cret	Jianchuan	x						
101	Chabu 12	Nei Mongol	Early Cret	Jianchuan	x						
102	Chabu 13	Nei Mongol	Early Cret	Jianchuan	x						
103	Chabu 14	Nei Mongol	Early Cret	Jianchuan	x						
104	Chabu 15	Nei Mongol	Early Cret	Jianchuan	x	x					
105	Chabu 16	Nei Mongol	Early Cret	Jianchuan	x						

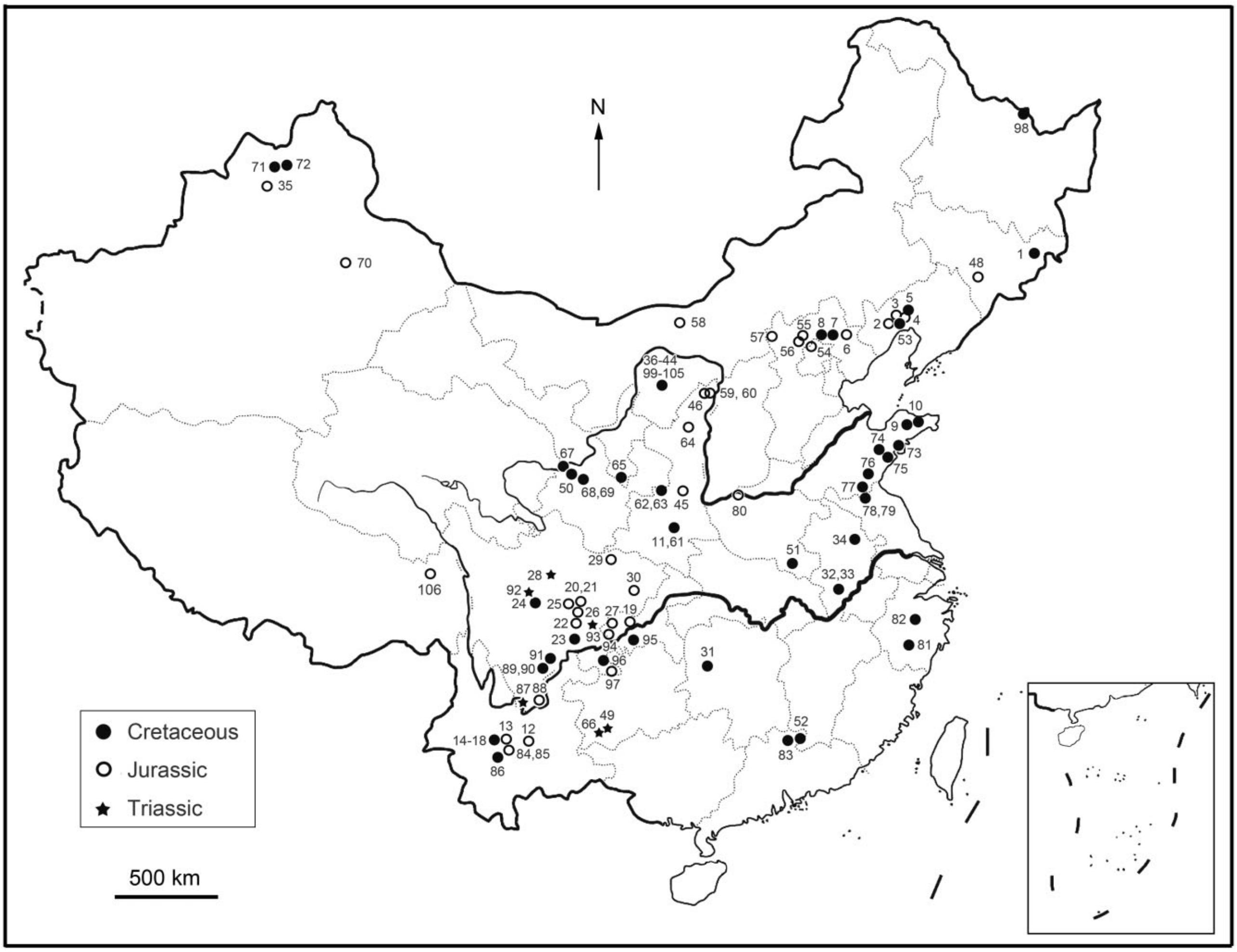

Figure 1. Mesozoic tetrapod tracksites in China. Note separate symbols for Triassic, Jurassic and Cretaceous sites. To date the present authors have recorded at least 106 Mesozoic sites. About 70 of these are Cretaceous in age (see Table 1). Precise dating is not available for all sites. Thus, differentiating which sites are just above or below the Jurassic–Cretaceous and Lower to Upper Cretaceous boundaries is difficult in some cases.

As noted above, researchers studying Chinese tetrapod tracksites have been relatively consistent in compiling lists of tracksites, often with precise GPS coordinates, name of track-bearing unit (formation or group) and comments on the track types present, especially holotypes: see, for example, the appendix of 52 Chinese sites provided by Matsukawa *et al*. (2006 pp. 19–20). However, the number of trackways of any given type has not been reported for many of these sites, and may not be precisely known from the primary literature. Nevertheless, for consistency, the current updated list of Chinese sites is based on a significant expansion of the 2006 list, and also includes formation or group name, and reference to holotypes and known track types. In order to protect sites GPS information is not published here, although it may appear in other publications and be obtainable from the authors for *bona fide* research purposes. Such consistency makes comparative study easier, allowing us to compare Chinese sites with those from other regions, from which comprehensive data are available. These regions, in approximate order of publication include South America (Leonardi, 1989, 1994), North America (Lockley *et al*., 2006a, 2010a) South Korea (Lockley *et al*., 2006a, 2012a, b; Lockley, Huh & Kim, 2012c) and Europe. Lockley *et al*. (2012a) also compiled a list of all significant Cretaceous tracksites, but did not number the sites, or break them down into regional groupings. The methods used in compiling data, the geographical areas included in the studies, and the stratigraphic precision with which they have been recorded are summarized as follows.

South Korea is a relatively small area in comparison with neighboring China, and the track-bearing regions of North and South America discussed below. Nevertheless it has yielded hundreds of tracksites since the first were reported in the early 1980s. One of the distinctive features of the Korean sites is that many occur in close proximity at different stratigraphic levels in small geographical areas. For example Lockley *et al*. (2006b) compiled measurements for ~300 individual dinosaur trackways from several hundred horizons in the Jindong Formation at four named locations within the Goseong Tracksite, a geographic stretch of coastline only about 3 km long (see Houck & Lockley, 2006: table 2 here). This, compilation was exclusive of dozens of bird tracks from at least 30 horizons identified in the same outcrops. As noted below, this type of data is comparable with data obtained from single track-rich formations in other regions. However, in the case of Korea it is only part of the picture as there are many other tracksites in other Cretaceous formations throughout the whole country.

The work of Leonardi (1989, 1994) is truly continental in scope and his data is comparable in scale and stratigraphic range to the compilations reported for China. Leonardi (1989) reported 28 principal Cretaceous tracksites of which 23 are identified as Early Cretaceous. This number was considerably increased in a more detailed compilation (Leonardi, 1994) which referred to about 38 sites. In this latter publication map locations and approximate coordinates, formation names and track types were given for all sites, and individual trackways were counted in many cases. As noted below, it has been possible to update the data of Leonardi (1994) by adding information from a number of new Cretaceous tracksite reports published during the last 2 decades.

By contrast, the data available for North America are of a different order. The most comprehensive compilations of data currently available are for various track-rich formations that have been intensively studied. For example, Lockley *et al*. (2010a) compiled the number of track types and trackways from 70 ‘Mid’ Cretaceous Dakota Group tracksites east of the continental divide in Colorado, New Mexico, Kansas and Utah. Recently, this number was increased to 80, and an additional 40 sites have been reported from west of the Continental Divide (Lockley *et al*., 2014a). Likewise Pittman (1989) reported 42 tracksites from the Comanche Series of Texas, mostly from the well known Glen Rose Formation. The number of track types and trackways recorded from many of these sites, as well as additional sites reported since 1989, is known from scattered literature sources but such data have not been compiled into a coherent database. Finally, any reference to Cretaceous tetrapod tracksites from North America must include reference to the abundant, sites reported from western Canada. These are scattered geographically as well as stratigraphically (McCrea *et al*., 2014).

RESULTS

Early Cretaceous Tetrapod Ichnofaunas in China

As shown in Table 1, ~70 tetrapod tracksites localities (locs.) are known from the Cretaceous of China, and to date have been identified from all but four provinces (the exceptions being Qinghai, Guangxu, Fujian and Hubei: see Fig. 1). The precise age of many formations is uncertain, according to primary sources. Nevertheless, in most cases age determinations or estimates exist in the literature and are used here. As expected the distribution of geological formations causes some areas to have higher concentrations of tracksites. Likewise the variation in age, facies and ichnological content of these formations results in significant variation in track types and significance of tracksites in different regions. For these reasons, we focus attention on the more important tracksite regions (C1–C6) and track-bearing units as follows:

C1: Northeastern China. This region is historically important for having produced some of the first named dinosaur tracks from China. These include *Grallator ssatoi* (formerly named *Jeholisauripus s satoi*) an abundant small theropod track from the Tuchengzi Formation (Yabe, Inai & Shikama, 1940; Matsukawa *et al*., 2006) in Liaoning Province. This unit is currently considered to represent the Jurassic-Cretaceous (Tithonian-Berriasian) transition, and thus may include some of the oldest Cretaceous ichnofaunas in Asia (locs. 2–4 of Fig. 1), for example bird tracks (*Pullornipes aureus*) reported by Lockley *et al*. (2006c) may be among the oldest known from Asia. Saurischian tracks occur in this formation elsewhere in the region including Hebei Province (Xing *et al*., 2009a; Xing, Harris & Gierliński, 2011a) and the Beijing Municipality, where sauropod tracks also occur in the recently designated Yanqing International Geopark (loc. 54) (Zhang *et al*., 2012).

C2: Shandong Province. Tetrapod tracks were first reported from Shandong province by Young (1960) who named *Laiyangpus liui* from the Shuinan Formation (loc 10), and mistakenly assigned it to theropod dinosaur, when it is likely of crocodile affinity (Lockley *et al*., 2010b). Since 1960, other tracks found at the site include bird tracks (ichnogenus *Tatarornipes*: Lockley *et al*., 2011). Small theropod tracks are also abundant in Shandong including the problematic ichnotaxon *Paragrallator yangi* (cf. *Grallator*), from loc. 9, and have been found at most of the other localities known in the province (Fig. 1). The most important localities reported to date include the Junan site (loc. 76) which has yielded a high diversity of forms from multiple levels in the Tianjialou

Formation, which is thought to be Barremian-Aptian in age. These include both large and small dromaeosaur tracks, *Dromaeopodus* and *Velociraptorichnus* respectively (Li *et al*., 2007, 2014), highly distinctive small theropod track *Minisauripus* (Lockley *et al*., 2008), the unique roadrunner-like track *Shandongornipes* (Lockley *et al*., 2007) and more typical bird tracks (*Koreanaornis*). Ornithopod tracks also occur at this site. Recent studies of other Tianjialou tracksites in the region report other dromaeosaur tracks, sauropod tracks and possible psittacosaur tracks (Xing *et al*., 2013a). Another very important site occurs at Huanglongou (Yellow Dragon Valley) in the Lower Cretaceous Longwangzhuang Formation near Zhucheng, here (loc. 75) more than 2000 tracks have been mapped on a single surface including abundant *Grallator* tracks, the distinctive theropod track *Corpulentapus* (Li *et al*., 2011b; Lockley *et al*., 2012d), sauropod tracks and some of the first turtle tracks reported from China (Lockley *et al*., 2012e). Pterosaur tracks have also been reported from the Qugezhuang Formation (Xing *et al*., 2012). Collectively the above-listed Shandong sites have yielded among the most diverse ichnofaunas reported from the Chinese Lower Cretaceous.

C3: Inner Mongolia. The Ordos Basin region of Inner Mongolia (Nei Mongol) has yielded at least 17 tracksites (locs. 36–44 and 99–105) in the Chabu region near Otog Qi (Li *et al*., 2009; Li, Bai & Wei, 2011a). These occur mainly in the Jianchuan Formation and include assemblages dominated by saurischian tracks including the non-avian theropod tracks *Chapus* and *Asianopodus* (Li *et al*., 2006, 2011a respectively), the sauropod track *Brontopodus* (Lockley *et al*., 2002) and the bird (avian theropod) track *Tatarornipes* (Lockley *et al*., 2011).

C4: Gansu Province. A number of tracksites have been reported from the Hekou Group in the Yellow River (Hwang He) valley near Lanzhou in Gansu Province. The two largest sites occur side by side at Yangouxia National Geopark (loc. 50). They reveal a remarkable diversity of track types including tridactyl and didactyl theropod tracks, the latter representing the first reported *Dromaeosauripus* from China (Xing *et al*., 2013b), unusually large sauropod tracks, ornithopod tracks, pterosaur tracks (*Pteraichnus*) which were the first reported from China (Peng *et al*., 2004; Zhang *et al*., 2006) and bird tracks (cf. *Aquatilavipes*).

C5: Sichuan Province and Chongqing City. Until recently the Xingfu Cliff site in Emei County has been regarded as one of the best known and most important Cretaceous tracksites in China. It is a very small site (Loc. 24), but it has yielded the type material for the well known ichnogenera *Minisauripus* and *Velociraptorichnus*, as well as new ichnospecies of *Aquatilavipes* and *Grallator* (Zhen, Li & Zhang, 1994) The ichnogenus *Iguanodonopus* has been declared a *nomen dubium*. (Xing *et al*., 2009b; Lockley *et al*., 2013). In contrast to the Emei County site, new tracksites in the Zhaojue area reveal very large surfaces associated with large copper mine excavations. These sites reveal with very long trackways of theropods, sauropods, ornithopods and a few pterosaurs. The Lotus site in the Qijiang area (Chongqing City) is also a large tracksite associated with a historically famous cliff fortress. It has yielded well preserved quadrupedal *Caririchnium*, and the bird-like track *Wupus* (Xing *et al*., 2007) and pterosaur tracks (Xing *et al*., 2013c). The Sanbiluoga site in the Zhaojue County also reveals theropod, sauropod ornithopod and pterosaur tracks (Xing *et al*., 2013c), including the first definitive non-avian theropod swim trackway from China (Xing *et al*., 2013d).

C6: Xinjiang Autonomous Region China. Xinjiang is a huge region of western China that remains largely unexplored for its tetrapod tracks potential (Fig. 1). However in recent years two important tetrapod tracksites have been described from the region. The first, the Wuerhe site has yielded a diverse assemblage of non-avian and avian theropod, thyreophoran (*Deltapodus*), pterosaur and turtle tracks. This is first record of *Deltapodus* from the Cretaceous of China (Xing *et al*., 2013e). The second, the Asphaltite site also yields non-avian and avian theropod tracks together with pterosaur tracks (He *et al*., 2013; Xing *et al*., 2013f). The area has huge potential for more tracksite discoveries.

Early Cretaceous Tetrapod Ichnofaunas in Korea

Since the discovery of Cretaceous dinosaur tracks in Korea in the early 1980s (Yang, 1982) the rate of report of diverse tetrapod ichnofaunas, all pertaining to the Cretaceous, has increased rapidly. In fact the abundance of sites, especially at localities along the southern coast has led to the concept of the Korea Cretaceous Dinosaur Coast (KCDC). Probably the most accessible summaries of the many discoveries since 1982 are found in the special issue of *Ichnos*, vol. 19 (1–2), entitled *Tracking on the Korean Cretaceous Dinosaur Coast: 40 years of vertebrate ichnology in Korea* (Lockley *et al*., 2012b) and the Mesozoic terrestrial ecosystems of the Korean Cretaceous dinosaur coast: a field guide to the excursions of the 11th Mesozoic Terrestrial Ecosystems Symposium (Lockley *et al*., 2012c). Lee *et al*. (2000) also provided summary information on Korean dinosaur tracksites.

As is the case in China, many of the Cretaceous deposits in Korea have proved difficult to date, partly because of the widespread effects of thermal and regional metamorphism (Houck & Lockley, 2006). However, we may summarize the present state of knowledge as follows. The majority of track-bearing deposits have been reported from the Gyeongsang Supergroup of the Gyeongsang Basin which occupies much of the southeastern sector of the Korean peninsula (Fig. 2). The Gyeongsang Supergroup is divided into three groups: the predominantly sedimentary lower and middle groups, the Sindong and Hayang Groups respectively, which succeed each other conformably and the upper, predominantly volcanic Yucheon Group which overlies the older sequences unconformably. Recent literature has dated the track-rich Sindong and Hayang Groups as Hauterivian to Albian (Houck & Lockley, 2006) or as somewhat younger, Aptian to Campaninan (Paik *et al*., 2012). In the southwestern sector of the Korean peninsula there are a number smaller basin with track-rich deposits, that have tended to yield Late Cretaceous dates, but many of the stratigraphic sequences in this area remain unnamed.

In recent years tetrapod tracks from the region have become very well-known. As indicated in Table 2, there have been relatively few important tracksites reported from the older Sindong Group, which has however, yielded some tetrapod body fossils (Fig. 2A). The more significant reports include the oldest Korean report of pterosaur tracks (*Pteraichnus*, Lee *et al*., 2008) from the Hasandong Formation and the oldest *Dromaeosauripus* from the Jinju Formation Kim *et al*. (2012a). However, the vast majority of significant tracksites has been reported from the overlying Hayang Group, much of which is made up of the track-rich Haman and overlying Jindong Formations usually dated as Aptian-Albian (Houck & Lockley, 2006). As indicated in Table 2 and the aforementioned summary publications (Lockley *et al*., 2012b, c) the Haman Formation has yielded six tetrapod track holotypes attributable to avian and non-avian theropods, sauropods and pterosaurs. These are assigned to the avian ichnogenera *Koreanaornis* (Kim, 1969), *Ignotornis* (Kim *et al*., 2006; Kim *et al*., 2012b), dromaeosaurids (*Dromaeosauripus* Kim *et al*., 2008), sauropods (*Brontopodus*) (Kim & Lockley, 2012) and pterosaurs (*Haenamichnus*) (Kim *et al*., 2012c). The Haman Formation has also produced a relatively large number of reports of the small theropod ichnogenus *Minisauripus* (Lockley *et al*., 2008; Kim *et al*., 2012d), which is currently only known from the Cretaceous of China and Korea.

The Jindong Formation is perhaps even richer in tracks than the Haman Formation. The southwestern part of Goseong County referred to as the Samcheonpo tracksites (Fig. 2B) is also designated as Korea Natural Monument 411, and is also referred to as the Goseong Tracksite, although it is one of many tracksite areas in Goseong County. In this area (Monument 411) hundreds of track-bearing levels have been documented in great detail (Lockley *et al*., 2006b; Houck & Lockley, 2006). Several avian theropod (bird) holotypes have been named and assigned to the ichnogenera *Jindongornipes* (Lockley *et al*., 1992), *Goseongornipes* (Lockley *et al*., 2006b) and *Gyeongsangornipes* (Kim *et al*., 2013). In addition the ornithopod ichnogenus *Ornithopodichnus* (Kim *et al*., 2009) is from the Jindong Formation. For more information on bird tracks see Lim *et al*. (2000, 2002).

There are a number of other important tetrapod tracksites in the Cretaceous of Korea, including three, like the Goseong area, which are designated as Korea Natural Monuments 394, 434 and 487. All three of these sites have been reported as Upper Cretaceous in age, or of uncertain age, and so are not included here in Table 2. Briefly they are as follows: Natural Monument 394 is the Haenam Tracksite where ornithopod (*Caririchium*) pterosaur (*Haenamichnus*) (Lockley *et al*., 1997) and bird tracks (*Hwangsanipes* and *Uhangichnus*) occur in the Uhangri Formation. The latter tracks show traces of a fully developed interdigital web and are convergent with small ducks (Yang *et al*., 1995; Lockley & Harris, 2010). Natural Monument 434 is the Yeosu Tracksite associated with an unnamed formation yielding theropod, sauropod ornithopod and bird tracks (Huh *et al*., 2012; Lockley *et al*., 2012b, c, f, g). The Hwasun tracksite, Natural Monument 487 yields theropod, sauropod and ornithopod tracks from the Jingdong Tuff (Huh *et al*., 2006; Lockley, Huh & Kim 2012c, h).

Although other tracksites occur in elsewhere in southeast Asia, they are not abundant. For example, Matsukawa *et al*. (2006) reported only nine tracksites from Japan and five from Thailand, and this number has not increased significantly as a result of new reports. However, it is worth noting that some of these ichnofaunas contain named ichnotaxa that are not reported from other ichnofaunas discussed here. For example, the distinctive theropod ichnogenus *Siamopodus* (Fig. 3) is currently known only from Thailand (Lockley *et al*., 2006d), and small theropod ichngenus *Toyamasauripus* is known from Japan. *Asianopodus*, also a theropod ichnogenus, originally based on a Japanese holotype (Matsukawa *et al*., 2005), is also abundant at some sites in Thailand. The only known Cretaceous report of *Batrachopus* is also from Thailand (Le Loeuff *et al*., 2010), as is the only known Asian report of *Neoanomoepus* (Lockley, McCrea & Matsukawa, 2009). Most other dinosaur tracksites from Japan and Thailand have yielded only small assemblages of theropod and ornithopod tracks few of which have been named. Sauropod tracks occur at one locality in Laos (Matsukawa *et al*., 2006).

Early Cretaceous Tetrapod Ichnofaunas in South and Central America

It is outside the scope of this review to outline the work of Leonardi (1989, 1994) in detail. Initially, in 1989 he reported 23 Cretaceous sites, increasing this number to 38 in a later compilation (Leonardi, 1994). The majority of these (about 28) are Lower to Mid-Cretaceous in age His continent-wide survey is comparable to the compilation presented here for China which identified 105 tracksites. In the case of South

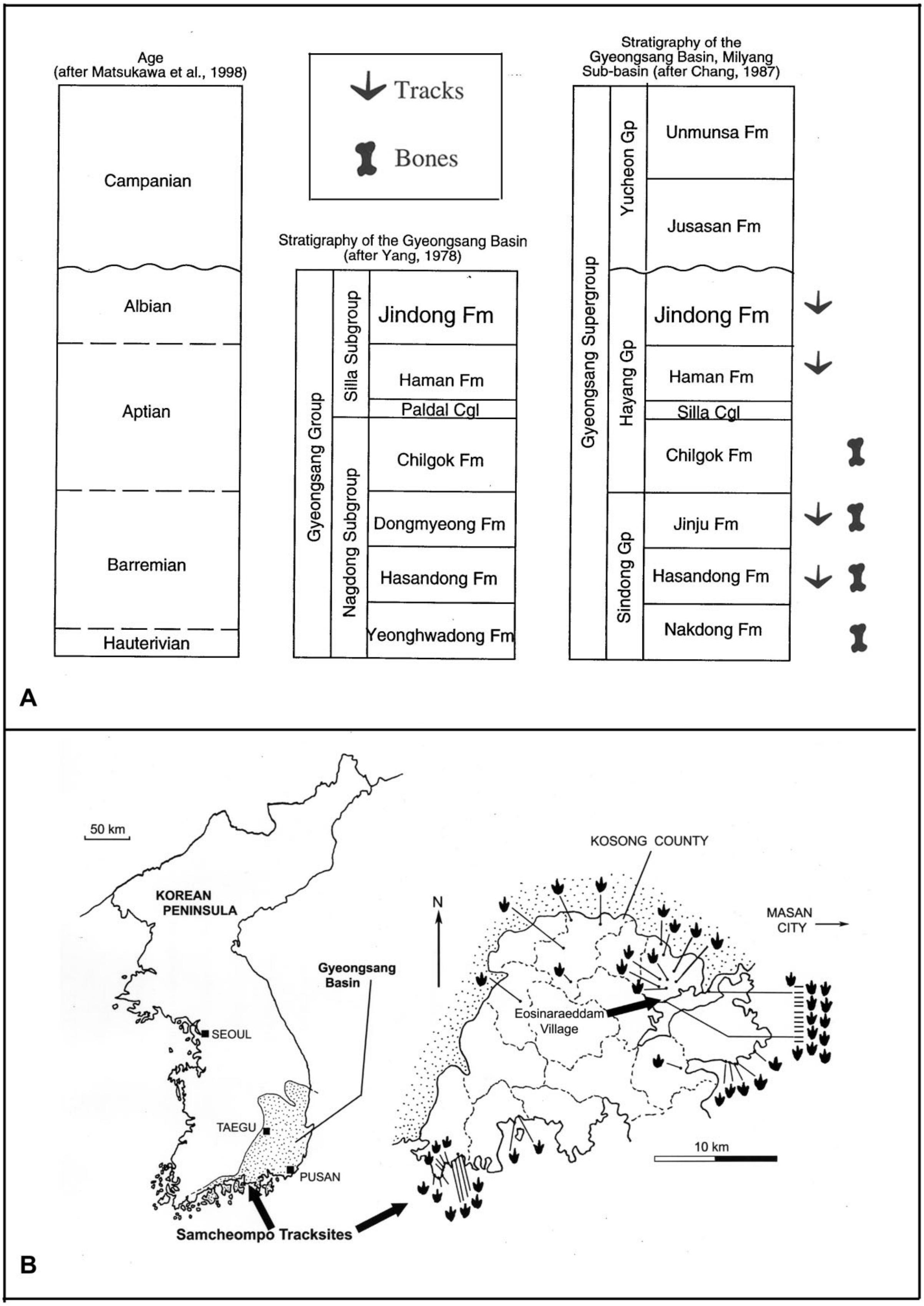
Age
(after Matsukawa et al., 1998)
Campanian
Albian
Aptian
Barremian
Hauterivian
Tracks
Bones
Stratigraphy of the Gyeongsang Basin
(after Yang, 1978)
Gyeongsang Group
Silla Subgroup
Nagdong Subgroup
Jindong Fm
Haman Fm
Paldal Cgl
Chilgok Fm
Dongmyeong Fm
Hasandong Fm
Yeonghwadong Fm
Stratigraphy of the
Gyeongsang Basin, Milyang
Sub-basin (after Chang, 1987)
Gyeongsang Supergroup
Yucheon Gp
Hayang Gp
Sindong Gp
Unmunsa Fm
Jusasan Fm
Jindong Fm
Haman Fm
Silla Cgl
Chilgok Fm
Jinju Fm
Hasandong Fm
Nakdong Fm
A
50 km
KOREAN
PENINSULA
SEOUL
Gyeongsang
Basin
TAEGU
PUSAN
Samcheompo Tracksites
N
KOSONG COUNTY
MASAN
CITY
Eosinaraeddam
Village
10 km
B

Figure 2. Aspects of the stratigraphy and distribution of tracksites in the Cretaceous of Korea. A: the main track-bearing formations in the Sindong and Hayang Groups Gyeongsang Basin. Note that the age of these formations is debated in the literature (see text for details). B: distribution of tracksites in Goseong County, with special reference to the Samcheompo tracksite also designated as the Goseong Tracksite and Korea Natural Monument 411. Compare with Table 2.

and Central America Leonardi (1994) identified 115 sites including 88 that are reported as Mesozoic in age. Since 1994 approximately 16 Cretaceous sites have been added for a total of about 54 sites: data were taken from Lockley *et al*. (2012a) and other sources. Approximately ten of the newly added site are Lower or Mid-Cretaceous in age, giving an estimated total of about 38 Lower to 'Mid' Cretaceous sites.

The largest concentration of Early Cretaceous sites is in the Sousa Basin of Brazil, where Leonardi (1994) listed 18 sites. All but one reveal theropod tracks with seven sites yielding ornithopod tracks, including the important type specimen of ichnogenus *Caririchnium* (Leonardi, 1984) which has been widely identified on other continents, and five sites also yielding sauropod tracks. None of the other sites shows strong geographical concentrations or highly distinctive ichnofaunas. Bird tracks are conspicuous by their absence in the Lower Cretaceous although there are three reports from the Upper Cretaceous (Lockley & Harris, 2010). Pterosaur tracks are also scarce (Calvo & Lockley, 2001).

Early Cretaceous Tetrapod Ichnofaunas in North America

Important Early Cretaceous tetrapod ichnofaunas from North America are mostly known from the western USA and western Canada. In both regions there are major gaps in the Neocomian successions, leaving only the Aptian and Albian well represented. Only one significant ichnofauna is known from the eastern USA containing a diverse assemblage of mostly small tracks of theropods, ornithopods, sauropods and pterosaurs (Stanford, Lockley & Weems, 2007) from the Aptian Patuxent Formation. The size-frequency of the track assemblage is biased by the unusual preservation in small pieces of reworked sediment. In the western USA the oldest significant in situ assemblages are those reported from the Cedar Mountain Formation (Aptian-Albian) of eastern Utah. Relatively few sites are known but they show a high diversity of tracks attributed to birds (*Aquatilavipes*) and non-avian theropods (*Dromaeosauripus* and *Irenesauripus*), sauropods (*Brontopodus*) and ornithischians (*Caririchnium* and *Deltapodus*) (Lockley *et al*., 2014a, b).

In contrast to the diverse Patuxent and Cedar Mountain ichnofaunas associated with clastic fluvio-lacustrine facies, the Albian Glen Rose Formation ichnofaunas occur in carbonate platform sequences in Texas. These were described by Pittman (1989) as dominated by ichnites of large, theropods, attributed to *Acrocanthosaurus*, (Farlow, 2001) and large wide gauge (*Brontopodus*) trackways described in some detail by Farlow, Pittman & Hawthorne (1989) and attributed to titanosauriform sauropods.

Again in contrast to the Texan ichnofaunas the slightly younger (Late Albian-Cenomanian) track-rich siliciclastic, coal-bearing facies of the Dakota Group is rich in ornithischian tracks, and apparently devoid of sauropod tracks, despite reports of at least 120 sites (Lockley *et al*., 2014c). This lack of sauropod evidence is apparently due to facies differences and what has been referred to as the North American 'sauropod hiatus' (Lucas & Hunt, 1989) beginning in the Late Albian. The dominant ornithischian tracks are of ornithopod affinity (*Caririchnium*) especially in eastern Colorado and northeastern New Mexico, but ankylosaur tracks (*Tetrapodosaurus*) are more common in western Colorado. Theropod tracks, especially *Magnoavipes*, probably representing a gracile ornithomimid, are moderately common, and crocodilian swim tracks (*Hatcherichnus*) are also common. Bird tracks (*Ignotornis* and *Koreanaornis*) are rare (Mehl, 1931; Lockley & Harris, 2010), but tracks of small and large pterosaurs (cf., *Pteraichnus*) are moderately common. According to a regional synthesis of more than 1000 trackways from ~70 Dakota tracksites (Lockley *et al*., 2010a, table 6), across the then-known eastern outcrops the dominant track type is *Caririchnium*, representing ornithopod trackmakers. This ichnogenus outnumbers all other tracks types by an order of magnitude (i.e. by at least 10:1, or more). Preliminary study of at least 40 tracksites across the western outcrops indicates that the ornithopods were far less dominant and that ankylosaur trackmakers were common (Lockley *et al*., 2014c).

While the ichnofaunas from the four stratigraphic units outlined above (Patuxent, Glen Rose, Cedar Mountain and Dakota) are representative of well-studied and locally or regionally track-rich deposits from the lower 48 states of the USA, many other track-rich Cretaceous deposits are known from western Canada. These were recently reviewed by McCrea *et al*. (2014). It is outside the scope of this paper to discuss these ichnofaunas in detail.

Table 2. Distribution of Early (–'Mid') Cretaceous track types in main units of the Sindong and Hayang Groups (Gyeongsang Basin) Korea, with associated holotype occurrences. Thero, theropod; sauro, sauropod; ornith, ornithioschian; ptero, pterosaur; croc, crocodilian. Note that tracksite occurrences in other basins, where purported Upper Cretaceous tracks are reported, are not included. See text for details

Site or section	Age	Strat unit	Track levels	Thero tways	Bird tways	Sauro tways	Ornitho tways	Ptero tways	Holotypes	Reference
Goseong 1 Silbawi	Early Cret.	Jindong	65	1	n	20	14			Lockley *et al*., 2006b
Goseong 2 Bongwhagol	Early Cret.	Jindong	17		n	6	17			Lockley *et al*., 2006b
Goseong 3 Dekmyeong-ri	Early Cret.	Jindong	79	2	n	31	76		*Jindongornipes kimi Goseongornipes markjonesi Geongsangornipes lockleyi*	Lockley *et al*., 1992, Lockley *et al*., 2006b, Kim *et al*., 2013
Goseong 4 Sangjok	Early Cret.	Jindong	57	1	n	38	92			Kim *et al*., 2013
Goseong 5 Donghae-myeon	Early Cret.	Jindong	6	4		28	35			Lee *et al*., 2000
Goseong 6 Hoewha-myeon	Early Cret.	Jindong	9	1		39	21			Lee *et al*., 2000
Masan site	Early Cret.	Jindong	1				12		*Ornithopodichnus masanensis*	Kim *et al*., 2009
Docheon-ri	Early Cret.	Jindong	1			10				Hwang *et al*., 2004
Subtotals		**All jindong**	**235**	**9**	**N**	**172**	**267**			
Yongsan-myeon	Early Cret.	Haman			N				*Koreanaornis hamanensis*	Kim, 1969
Changseon Island Gain-ri	Early Cret.	Haman			11				*Ignotornis yangi*	Kim *et al*., 2006
Sinsu Island	Early Cret.	Haman						3		Kim *et al*., 2006
Changseon Island Gain-ri	Early Cret.	Haman		1		1	2	5	*Haenamichnus gainensis*	Kim *et al*., 2012c
Changseon Isle Buyun-ri	Early Cret.	Haman		38						Kim *et al*., 2012d
Changseon Island Godu	Early Cret.	Haman		5						Kim *et al*., 2012d
Changseon & Adu isles	Early Cret.	Haman						1		Kim *et al*., 2012c
Changseon & Chu isles	Early Cret.	Haman		1					*Dromaeosauripus hamanensis*	Kim *et al*., 2008
Gajin-ri	Early Cret.	Haman		1	$N = 100$ s	2			*Brontopodus pentadactylus, Ignotornis gajinensis*	Kim & Lockley 2012
Bito Island	Early Cret.	Jinju		1					*Dromaeosauripus jinjuensis*	Kim *et al*., 2012a
Hadong	Early Cret.	Hasandong						1	*Pteraichnus koreanensis*	Lee *et al*., 2008

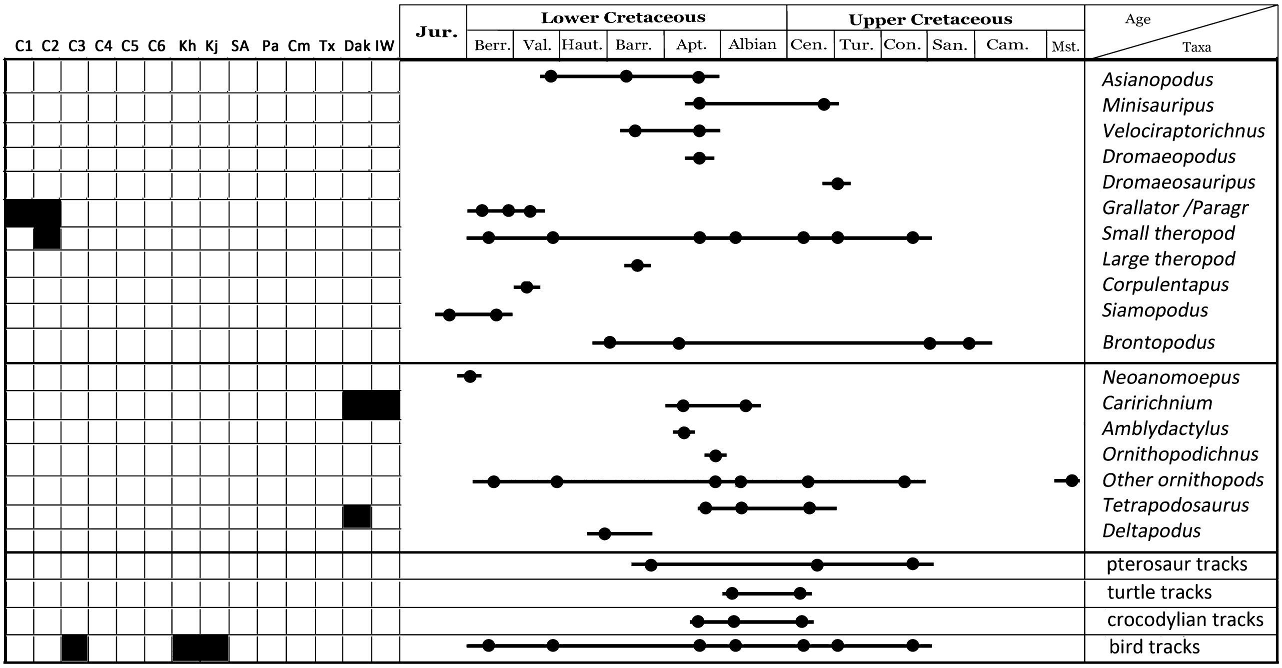

Figure 3. Distribution of track types in areas with abundant Lower Cretaceous ichnofaunas: C1–C6 refer six areas in China discussed in text. Kh and Kj respectively refer to the Jindong and Haman Formations of Korea. SA: South America, Pa: Patuxent Fm, eastern USA, Cm: Cedar Mountain Fm, western USA, Tx: Texas, western USA, Dak: Dakota Group, western USA, IW: Isle of Wight, UK. Black square indicate high abundance of a given ichnotaxon or track type; dots indicate occurrences. Ranges of selected ichnotaxa are given. Modified after Lockley *et al.* (2012a). Note that exact age of UK and USA ichnofaunas is well established, but the age of some Asian ichnofaunas is uncertain or in dispute.

However, it is worth noting that the following ichnofaunas are significant and historically important for the global discussion. First, the Canadian Cretaceous contains a number of track-rich units associated with the Jurassic-Cretaceous (Tithonian-Berriasian) transition including the Mist Mountain Formation which has yielded a diverse ichnofauna including the *Neoanomoepus* holotype (Lockley *et al.*, 2009), Canada's oldest sauropod tracks and various other dinosaurian and non-dinosaurian tetrapod ichnites ranging from large and small non-avian theropod tracks to probable avian theropod, pterosaur and aquatic tetrapod swim tracks. Second, the slightly younger (Berriaasian-Valanaginian) Gorman Creek Formation also yields a diverse ichnofauna including *Neoanomoepus* and *Tetrapodosaurus*. Third, after a significant gap in the Neocomian succession the next significant western Canada ichnofauna is that reported from the historically famous Gething Formation (Sternberg, 1932; Currie & Sarjeant, 1979; Currie, 1995; McCrea *et al.*, 2014), which is dominated by tracks of miscellaneous non-avian theropods, ornithischians (type specimens of *Amblydactylus* and *Tetrapodosaurus*) with several reports of bird tracks (McCrea *et al.*, 2014) including the type of *Aquatilavipes* (Currie, 1981). Forth, in the Lower Cretaceous succession, a similar ichnofauna, with abundant *Tetrapodosaurus* and avian and non-avian theropod tracks occurs in various slightly younger units including the early Albian Gates Formation through the early Cenomanian Dunvegan Formation (see McCrea *et al.*, 2014 for summary).

Early Cretaceous Tetrapod Ichnofaunas in Europe

As noted above, the impetus for the present study derives from the Jehol-Wealden International Conference, held in England in September 2013. Ideally it would have been desirable to have similar databases for the two regions, but this is not the case for several reasons, including the vast size differences in the regions studied and differences in quality of tracksite exposure. Nevertheless, this contribution, which began with a review of the Lower Cretaceous ichnofaunas of China, includes brief reference to Lower Cretaceous ichnofaunas from the Wealden Group in England, and equivalent deposits elsewhere in western Europe.

As outlined elsewhere in this volume (Lockley *et al.*, 2014; Lockwood, Lockley & Pond, 2014; Pond *et al.*,

2014) ichnofaunas from the Wealden Group are among the first ever reported from the Lower Cretaceous. Historically most reports refer to *Iguanodon* tracks, which appear to be the dominant track type (Lockwood *et al*., 2014). However, because the rules of the International Code of Zoological Nomenclature (ICZN) do not permit use of a genus name based on skeletal material to describe trace fossils, Sarjeant, Delair & Lockley (1998) erected the ichnogenus *Iguanodontipus*, based on relatively small pre-Wealden ichnites from the Purbeck Group (Tithonian-Berriasian). These are significantly different from the Barremian age Wealden Group ornithopod tracks which have mostly been assigned to *Caririchnium*. Thus, in essence the Purbeck and Wealden ornithopod footprints mostly represent the two distinct, respective ichnogenera named above (Lockley *et al*., 2014). Few other ichnotaxa from the Wealden Group have been described in detail, but it appears that tracks of theropod, sauropods and other ornithischians (ichnogenera *Tetrapodosaurus* and possibly *Deltapodus*) are also represented.

Ichnofaunas from the Berriasian deposits of northern Germany include unnamed ornithopod (iguanodontid tracks) which resemble *Iguanodontipus* (Lockley, Wright & Thies, 2004). This ichnogenus has recently been identified in rocks of the same age in Spain (Castanera *et al*., 2013), where, like the German tracks a small proportion show manus prints. It is possible that quadrupedal progression was less common among Tithonian-Berriasian ornithopods than among larger varieties represented by younger (Barremian-Albian) trackmakers. However, we admit that this inference is speculative. As noted below a recent review by Moratalla & Hernán (2010) of Spanish ichnofaunas from the Cameros Basin provides useful data on the proportion of theropod, ornithopod and sauropod tracks found in the Lower Cretaceous (Berriasian) Huérteles Formation and the much younger (Aptian) Enciso Group.

Other Lower Cretaceous tracksites reported from Europe include those associated with carbonate platform paleoenvironments in Switzerland (Meyer & Thuring, 2004), Italy (Sacchi *et al*., 2009; Petti *et al*., 2010) and Croatia (Dalla Vecchia, 2008). Collectively these reports deal with quite different paleoenvironments from those described from the clastic facies of the Wealden Group and equivalent beds of England, Germany and Spain. Thus, we can generally differentiate between clastic facies in northern European and carbonate facies in southern Europe. In the case of the Swiss site from the Albian Schrattenkalk Formation an iguanodontid trackway, similar to *Caririchnium*, but not explicitly attributed to that ichnogenus, was reported as an unusual example of this track type in association with a carbonate substrate, which typically yields theropod-sauropod assemblages characteristic of the *Brontopodus* ichnofacies (sensu Lockley *et al*., 1994). The Italian sites have yielded a number of trackways of quadrupedal dinosaurs of uncertain ichnotaxonomic affinity. According to Sacchi *et al*. (2009, fig. 13) theropod, sauropod ornithopod and thyreophoran footprints are all represented in the Lower Cretaceous, although in most cases these are all very poorly preserved, and in our opinion there is no definitive evidence of ornithopods, or strong evidence to differentiate the purported trackways of ankylosaurs and sauropods. In this regard the ichnogenus *Apulosauripus* reported by Nicosia *et al*. (1999) from Upper Cretaceous carbonates of Italy and attributed to a hadrosaurian track makers, was reinterpreted as being of likely ankylosaurian affinity (Gierlinski & Sabath, 2008). Petti *et al*. (2010) described purported ankylosaur trackway, but again this identification is uncertain. Dalla Vecchia (2008) has identified many theropod and sauropod tracks from the Lower Cretaceous of Croatia. Such assemblages are consistent with the theropod-sauropod assemblage typical of the *Brontopodus* ichnofacies associated with carbonate platforms. The combined reports of tracksites from these three areas (Switzerland, Italy and Croatia) indicate that tracks are abundant in the Lower Cretaceous carbonates of the region, as well as in the Upper Cretaceous. However, in general they are poorly preserved and saurischian (theropod and sauropod dominated) with reports of ornithischians (ornithopods and ankylosaurs) generally being either rare, uncertain or both.

Early Cretaceous Tetrapod Ichnofaunas in Africa

Relatively few Lower Cretaceous dinosaur tracksites are known from Africa, although recent studies have indicated that several sites are known in North Africa, some extending into the 'Mid' Cretaceous (Cenomanian). As reported by Bellair & Lapparent (1948) Mid-Cretaceous tridactyl (theropod) tracks have been known from Algeria since 1880. Recent studies in this region have identified well preserved theropod tracks of Valanginian age (Bensalah *et al*., 2005). Other significant Lower Cretaceous sites include those reported from Morocco including a theropod-sauropod tracksite from the Barremian-Aptian Tazought Formation northeast of Agadir (Masrour *et al*., 2013) and two sites theropod-sauropod tracksites from the Mid-Cretaceous (Cenomanian) Kem Kem Formation (Belvedere *et al*., 2013; Ibrahim *et al*., 2014). The former report also documents turtle and crocodilian swim tracks. There are a few other reports of confirmed Mid-Cretaceous age including a report of bird tracks from Tunisia (Contessi & Fanti, 2012). Jacobs *et al*. (1989) reported well preserved theropod tracks from Cameroon in West Africa. Thus, despite recent reports, the African track record for the Early Cretaceous remains very sparse and scattered.

Early Cretaceous Tetrapod Ichnofaunas in Australia

Relatively few tetrapod tracksites are known from the Cretaceous of Australia (Long, 1998). Moreover, the few that are known, although significant, are also very controversial making track identification problematic. According to Thulborn (2013) and Thulborn & Wade (1984) the well-known Lark Quarry site, from the 'Mid' Cretaceous Winton Formation in Queensland, yielded two ichnogenera *Wintonopus* and *Skartopus* representing small ornithopods and small theropods respectively. Both track types were reported as abundant, and interpreted as evidence of a stampede. Neither ichnogenus has been reported outside Australia. However, according to Romilio, Tucker & Salisbury (2013) these are swim tracks and *Skartopus* is not a valid ichnotaxon: i.e., it is a junior synonym of *Wintonopus*. Romilio & Salisbury (2010) also reinterpreted large-theropod tracks as ornithopodan. Thus there is no consensus on the ichnotaxonomy, trackmaker identity or trackmaker behavior. Tracks from the Broome Sandstone in western Australia include only one named, uncontroversial ichnogenus, *Megalosauropus* (Colbert & Merrilees, 1967). Almost all other tracks, although representing unnamed theropod, sauropod and ornithischian ichnotaxa (Long, 1998) are associated with heavily trampled substrates (Thulborn, 2012), and have not been described in detail. Martin, Vickers-Rich & Vazquez-Propkopec (2012) recently described theropod tracks and first Cretaceous bird tracks (Martin *et al*., 2014) from Victoria, Australia. Thus, the entire Lower Cretaceous track record from Australia is concentrated in three widely-separated regions and consists of three named, tridactyl, non-avian dinosaur tracks, including one in dispute, a few avian theropod (bird) tracks and unnamed mostly poorly preserved sauropod and ornithischian tracks. Even assuming disputes over track interpretation can be resolved, this database is very sparse in comparison with that available from other continents.

DISCUSSION

Among the aims of contributions to this volume are comparison between the Lower Cretaceous faunas of China and the Wealden Group in England. Comparisons based on the ichnofaunas of the two regions are possible, but hampered by various uncertainties. The most significant problems relate to the uncertain age of many of the Chinese deposits, due to the complex structure of Cretaceous basins across China and East Asia in general (Haggart, Matsukawa & Ito, 2006). Nevertheless, there is no shortage of new ichnological data emerging from China and elsewhere in the region (notably Korea and Thailand). Given that the Wealden ichnofaunas are heavily ornithopod dominated it is easy to a select a few examples of ornithopod-dominated ichnofaunas, such as the *Caririchium* -dominated Qijiang ichnofauna (Xing *et al*., 2007) or the Jindong ichnofauna where *Caririchium* is also abundantly represented. In general however, many of the Chinese ichnofaunas are not ornithopod dominated, even though numerically ornithopod trackways represent a small or intermediate component in many. As cited elsewhere in this volume Lucas (2007: 22) suggested that 'Cretaceous tetrapod footprints can be distinguished from Jurassic tracks primarily by the abundance and near ubiquity of large ornithopod tracks'. This statement deserves analysis, because while it is true that large ornithopod tracks are relatively ubiquitous, not 'near ubiquitous', they are only abundant in certain regions and deposits, including the Wealden and Dakota Groups (Fig. 3). Lockley *et al*. (2012a) have already suggested that East Asian ichnofaunas are significantly different in composition, being dominated in many regions by an abundance of small non-avian theropod (grallatorid) tracks (*Grallator s.l.* and *Asianopodus*), and avian theropod (bird) tracks as well as forms like *Minisauripus* and various dromaeosaurid tracks (*Velociraptorichnus*, *Dromaeopodus* and *Dromaeosauripus*) which are apparently rare or absent in all other regions. In this regard it is interesting to note that the South American ichnofaunas are also heavily theropod-dominated, as are the Spanish ichnofaunas, and in both these examples these conclusions are based on substantial data sets.

Although vertebrate ichnology has progressed rapidly in recent decades, there have been relatively few efforts to synthesize the large volume of data now available. We have cited the Chinese data set (Table 1) as an example of a comprehensive compilation of tracksites, comparable to the South American data set provided by Leonardi (1994). However, we stress that other comprehensive data sets such as those provided by Lockley *et al*. (2006b) for the Jindong Formation of Korea, by Lockley *et al*. (2010a) for the Dakota Group of the western USA and by Moratalla & Hernán (2010) for the Cameros Basin of Spain are regional in scope, and refer to discrete stratigraphic units. However, in these cases as well as counting tracksites, the number of individual trackways have been recorded allowing a quantitative assessment of the proportion of different track types, rather than simple presence/absence data. Ultimately such relative abundance data is necessary in order to better characterize the ichnofaunas and their facies relationships.

As an example of this potential to show quantitative trends we cite the evidence for an increase in the proportion of ornithopods between the basal Early Cretaceous (Berriasian) and the later Early Cretaceous (Aptian-Albian). This trend was recorded independently in Spain (Moratalla & Hernán, 2010) and northeastern China (Matsukawa *et al*., 2014). This trend can also be inferred in Korea (Table 2, Fig. 2) where the abundance of ornithopods in the Jindong Formation is far greater than in any of the underlying (older) units. Likewise the trend is evident in Canada (McCrea *et al*., 2014) where track-rich formations from both intervals are available for study, and where track-rich formations from both intervals are available for study and where Currie (1995) has stated that ornithopod tracks are very abundant (dominant) in the Aptian Gething Formation. As hinted above, the increase in abundance of large ornithopods may also correlate with an increase in average size during the Early Cretaceous.

Such differences in the types of data available for widely different regions make for very generalized syntheses. Here we claim only to provide an overview of track-bearing Lower Cretaceous deposits from which relatively abundant data is available (Fig. 3). It is beyond the scope of the present study to extract data in a standardized format for all regions discussed; indeed it is doubtful that anything more than presence/absence data can be extracted from some of the primary literature (see appendix in Lockley *et al*., 2012a). These obstacles to a standardized approach are compounded by the lack of consistency in ichnotaxonomic practice. However, ichnologists are aware of this problem and have attempted to address the problem of 'over-splitting', especially in the case of Chinese ichnotaxonomy (Lockley *et al*., 2013). In short it is necessary to have a consistent ichnotaxonomy before making meaningful comparative analyses. Elsewhere in this volume for example, the ichnotaxonomy of large ornithopod tracks is reviewed (Lockley *et al*., 2014), with a view to highlighting both obvious and subtle differences, and moving towards a manageable ichnotaxonomy that is useful in practice. For example, while acknowledging that there are subtle differences of opinion regarding the similarities and differences between *Amblydactylus* and *Caririchnium* (the latter ichnogenus being represented by four different ichnospecies on three continents) there seems to be little dispute over the fact that both ichnogenera represent large facultatively bipedal ornithopods, that are abundantly represented in the post-Neocomian Early Cretaceous (Aptian–Albian). In contrast *Iguanodontipus* is more typical of the basal Cretaceous.

Finally it is important to note that while Early Cretaceous ichnofaunas are quite distinct from those for other epochs, causing Lucas (2007) to recognize a distinct Lower Cretaceous biochron, many ichnofaunas are facies-controlled, or facies-related. The best example among the ichnofaunas cited here would be the differentiation between the Texas (Pittman, 1989) and southern European ichnofaunas associated with carbonate platform facies (Dalla Vecchia, 2008; Sacchi *et al*., 2009) and all others associated with diverse clastic facies. Lockley, Hunt & Meyer (1994a) suggested that such differences are evidence of distinctive vertebrate ichnofacies, later also referred to as tetrapod ichnofacies (Hunt & Lucas, 2007; Lockley, 2007). Ichnofacies may be controlled by regional and global scale environmental factors such as latitude, climate and depositional environment (Lockley, Hunt & Meyer, 1994b). In short, ichnofacies, like sedimentary facies, are variable and may intergrade in complex ways. All these factors, as well as age, and the dynamics of evolutionary turnover, influence the composition and distribution of ichnofaunas on a global scale. In many regions tracks are extremely abundant, and the compilation of data sets is potentially very useful, especially when the age of the ichnofaunas, their ichnotaxonomy and facies relations are well understood and provide well documented context. As stressed here, uncertainties about the age, ichnotaxonomy and other factors may compromise the utility of data and comparative analyses, at least in the short term. However, as we hope to have shown, in the long term, databases are growing steadily in volume and quality, as is their potential utility for ichnofaunal analysis.

ACKNOWLEDGEMENTS

We thank Gareth Dyke for his efforts to organize the Jehol-Wealden International Conference, held at Southampton University, England, in September 2013. Support to attend this conference was provided to the senior author (MGL) by the offices of the Dinosaur Trackers Research Group (University of Colorado Denver). We also thank Richard McCrea for providing access to in press information on the Canadian ichnofaunas. We thank Stuart Pond, University of Southampton and Matteo Belvedere, University of Padova for their helpful reviews.

REFERENCES

Bellair P, Lapparent A-F. 1948. Le Crétacé et les empreintes de pas de Dinosauriens d'Amoura (Algérie). *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* **39:** 168–175.

Belvedere M, Jalil N-E, Breda A, Gattolin G, Bourget H, Khaldoune F, Dyke GJ. 2013. Vertebrate footprints from the Kem Kem beds (Morocco): a novel ichnological approach to faunal reconstruction. *Palaeogeogr Palaeclim Palaeoecol* **383–384:** 52–58.

Bensalah M, Adaci M, Hebib H, Bessedik M, Belkebir L, Mahboubi M, Mansouri MEH, Mammeri C, Mansour B. 2005. Presence d'empreintes de pas de dinosauriens dans le Cretace au nord d'el Bayadh (Djebel Amour, Algerie). *Sciences and Technologie* **23:** 107–109.

Calvo JO, Lockley MG. 2001. The first pterosaur track record in Gondwanaland. *Cretaceous Research* **22:** 585–590.

Castanera D, Pascual C, Razzolini NL, Vila B, Barco JL, Canudo JI. 2013. Discriminating between medium- sized tridactyl trackmakers: tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). *PLoS ONE* **8:** e81830. doi:10.1371/journal.pone.0081830.

Colbert EH, Merrilees D. 1967. Cretaceous dinosaur footprints from Western Australia. *Journal of the Royal Society of Western Australia* **50:** 21–25.

Contessi M, Fanti F. 2012. First record of bird tracks in the late Cretaceous (Cenomanian) of Tunisia. *Palaios* **27:** 455–464.

Currie PJ. 1981. Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. *Journal of Vertebrate Paleontology* **1:** 257–262.

Currie PJ. 1995. Ornithopod trackways from the Lower Cretaceous of Canada. In: Sarjeant WA, ed. *Vertebrate Fossils and the Evolution of Scientific Concepts*. Singapore: Gordon and Breach Publishers, 431–443.

Currie PJ, Sarjeant WAS. 1979. Lower Cretaceous dinosaur footprints from the Peace River Canyon, British Columbia, Canada. *Paleogeography, Paleoecology, Paleoclimatology* **28:** 103–115.

Dalla Vecchia FM. 2008. The impact of dinosaur palaeoichnology in palaeoenvironmental and palaeogeographic reconstructions: the case of the Periadriatic carbonate platforms. *Oryctos* **8:** 89–106.

Farlow JO. 2001. *Acrocanthosaurus* and the maker of Comanchean large-theropod footprints. In: Tanke DH, Carpenter K, eds. *Mesozoic vertebrate life*. Bloomington: Indiana University Press, 408–427.

Farlow JO, Pittman J, Hawthorne MJ. 1989. Brontopodus birdi Lower Cretaceous sauropod Footprints from the US Gulf Coastal Plain. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 371–394.

Gierlinski GD, Sabath K. 2008. Stegosaurian footprints from the Morrison Formation of Utah and their implications for interpreting other ornithischian tracks. *Oryctos* **8:** 29–46.

Haggart J, Matsukawa M, Ito M. 2006. Paleogeographic and paleoclimatic setting of Lower Cretaceous basins in east Asia and western North America, with reference to nonmarine strata. *Cretaceous Research* **27:** 149–167.

He Q, Xing L, Lockley MG, Klein H, Persons WS IV, Qi L, Jia C. 2013. New Early Cretaceous pterosaur-bird track assemblage from Xinjiang, China: paleoethology and paleoenvironment. *Acta Geologica Sinica* **87:** 1477–1485.

Houck K, Lockley MG. 2006. Life in an active volcanic arc: petrology and sedimentology of the dinosaur track beds of the Jindong Formation (Cretaceous), Gyeongsang basin, South Korea. *Cretaceous Research* **27:** 102–122.

Huh M, Lockley MG, Kim KS, Kim JY, Gwak SG. 2012. First reports of *Aquatilavipes* from Korea: new reports from the Yeosu islands archipelago. *Ichnos* **19:** 43–49.

Huh M, Paik IS, Lockley MG, Hwang KG, Kwak SK. 2006. Well-preserved theropod tracks from the Upper Cretaceous of Hwasun County, southwestern South Korea and their paleobiological implications. *Cretaceous Research* **27:** 114–130.

Hunt AP, Lucas SG. 2007. Tetrapod ichnofacies: a new paradigm. *Ichnos* **14:** 59–68.

Hwang KG, Huh M, Paik SI. 2004. Sauropod trackways from the Cretaceous Jindong Formation at Docheon-ri, Changnyeon-gun, Geongsagnam-do, Korea. *Journal of the Geological Society of Korea* **40:** 145–159.

Ibrahim N, Varricchio DJ, Sereno PC, Wilson JA, Dutheil DB, Martill DM, Baidder L, Zouhri S. 2014. Dinosaur footprints and other ichnofauna from the Cretaceous Kem Kem Beds of Morocco. *PLoS ONE* **9:** e90751. doi:10.1371/journal.pone.0090751.

Jacobs LJ, Flanagan KM, Brunet M, Flynn LJ, Dejax J, Hell JV. 1989. Dinosaur footprints from the Lower Cretaceous of Cameroon, West Africa. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 349–351.

Kim BK. 1969. A study of several sole marks in the Haman Formation. *Journal of the Geological Society of Korea* **5:** 243–258.

Kim JY, Kim KS, Lockley MG, Yang SY, Seo SJ, Choi HI, Lim JD. 2008. New didactyl dinosaur footprints (*Dromaeosauripus hamanensis* ichnogen. et ichnosp. nov.) from the Early Cretaceous Haman Formation, south coast of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* **262:** 72–78.

Kim JY, Kim MK, Oh MS, Lee CZ. 2013. A new semipalmate bird track, *Gyeongsangornipes lockelyi* ichnogen. et ichnosp. nov., and *Koreanaornis* from the Early Cretaceous Jindong Formation of Goseong County, southern coast of Korea. *Ichnos* **20:** 72–80.

Kim JY, Kim SH, Kim KS, Lockley MG. 2006. The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu islands): more evidence of high avian diversity in East Asia. *Cretaceous Research* **27:** 56–69.

Kim JY, Lockley MG. 2012. New sauropod tracks (*Brontopodus pentadactylus* ichnosp. nov.) and from the

Early Cretaceous Haman Formation of Jinju area, Korea: implications for sauropods manus morphology. *Ichnos* **19:** 84–92.

Kim JY, Lockley MG, Kim HM, Lim JD, Kim SH, Lee SJ, Woo JO, Park HJ, Kim HS, Kim KS. 2009. New dinosaur tracks from Korea, *Ornithopodichnus masanensis* ichnogen. et ichnosp. nov. (Jindong Formation, Lower Cretaceous): implications for polarities in ornithopod foot morphology. *Cretaceous Research* **30:** 1387–1397.

Kim JY, Lockley MG, Kim KS, Seo SJ, Lim JD. 2012c. Enigmatic giant pterosaur tracks and associated ichnofauna from the Cretaceous of Korea: implications for bipedal locomotion. *Ichnos* **19:** 50–65.

Kim JY, Lockley MG, Seo SJ, Kim KS, Kim SH, Baek KS. 2012b. A paradise of Mesozoic birds: the world's richest and most diverse Cretaceous bird track assemblage from the Early Cretaceous Haman Formation of the Gajin tracksite, Jinju, Korea. *Ichnos* **19:** 84–92.

Kim JY, Lockley MG, Woo JO, Kim SH. 2012a. Unusual didactyl traces from the Jinju Formation (Early Cretaceous, South Korea) indicate a new ichnospecies of *Dromaeosauripus*. *Ichnos* **19:** 75–83.

Kim KS, Lockley MG, Kim JY, Seo SJ. 2012d. The smallest dinosaur tracks in the world: occurrences and significance of *Minisauripus*. *Ichnos* **19:** 66–74.

Le Loeuff J, Lauptasert K, Suteethorn S, Souillat C, Suteethorn V, Buffetaut E. 2010. Late Early Cretaceous crocodyliform trackways from Thailand. In*:* Milàn J, Lucas SG, Lockley MG, Spielmann JA. (eds.), Crocodyle tracks and traces. *New Mexico Museum of Natural History and Science Bulletin* **51:** 99–108.

Lee YN, Lee HJ, Lu J, Kobayasi Y. 2008. New pterosaur tracks from the Hasandong Formation (Lower Cretaceous) of Hadong, County, South Korea. *Cretaceous Research* **29:** 345–353.

Lee YN, Yang SY, Seo SJ, Baek KS, Lee DJ, Park EJ, Han SW. 2000. Distribution and paleobiological significance of dinosaur tracks in the Jindong Formation (Albian) in Kosong County, Korea. *Paleontological Society of Korea, Special Publication* **4:** 1–12.

Leonardi G. 1984. Le impronte fossili di dinosauri. In: Bonaparte JF, **Coauthors, ed.** *Sulle Orme dei Dinosauri*. Venice: Erisso Edetrice, 163–186.

Leonardi G. 1989. Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 165–178.

Leonardi G. 1994. *Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene)*. Rio de Janeiro: República Federativa do Brasil, Ministério de Minas e Energia, Companhia de Pesquisa de Recursos Minerais, 1–247.

Li J, Bai Z, Wei Q. 2011a. *On the dinosaur tracks from the Lower Cretaceous of Otog Qi, Inner Mongolia*. Beijing, China: Geological Publishing House. 109 p. 8 Pls.

Li J, Bater M, Zhang W-H, Hu B-L, Gao L-H. 2006. A new type of dinosaur tracks from Lower Cretaceous Otog Qi, Inner Mongolia. *Acta Palaeontologica Sinica* **45:** 221–234. (in Chinese with English summary).

Li J, Lockley MG, Bai Z, Zhang L, Wei Q, Ding Y, Matsukawa M, Hayashi K. 2009. New bird and small theropod tracks from the Lower Cretaceous of Otog Qi, Inner Mongolia, P. R. China. *Memoirs of the Beijing Museum of Natural History* **61:** 51–79.

Li R, Lockley MG, Makovicky PJ, Matsukawa M, Norell MA, Harris JD, Liu M. 2007. Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China. *Die Naturwissenschaften* **95:** 185–191.

Li R, Lockley MG, Matsukawa M, Liu M. 2014. Important Dinosaur-dominated footprint assemblages from the Lower Cretaceous Tianjialou Formation at the Houzuoshan Dinosaur Park, Junan County, Shandong Province, China. *Cretaceous Research* **52:** 83–100.

Li R, Lockley MG, Matsukawa M, Wang K, Liu M. 2011b. An unusual theropod track assemblage from the Cretaceous of the Zhucheng area, Shandong Province, China. *Cretaceous Research* **32:** 422–432.

Lim JD, Martin LD, Zhou Z, Baek KS, Yang SY. 2002. The significance of Early Cretaceous bird tracks. In: Zhou Z, Zhang F, eds. *Proceeding of the 5th Symposium of the Society of Avian Paleontology and Evolution*. Beijing: The Society of Avian Paleontology and Evolution, 157–163.

Lim JD, Zhou Z, Martin LD, Baek KS, Yang SY. 2000. The oldest known tracks of web-footed birds from the Lower Cretaceous of South Korea. *Die Naturwissenschaften* **87:** 256–259.

Lockley MG. 2007. A tale of two ichnologies: the different goals and missions of vertebrate and invertebrate ichnology and how they relate in ichnofacies analysis. *Ichnos* **14:** 39–57.

Lockley MG, Cart K, Martin J, Prunty R, Houck K, Hups K, Lim JD, Kim KS, Gierlinski G. 2014c. A bonanza of new tetrapod tracksites from the Cretaceous Dakota Group, western Colorado: implications for paleoecology. *New Mexico Museum of Natural History and Science Bulletin* **62:** 393–409.

Lockley MG, Fanelli D, Honda K, Houck K, Mathews NA. 2010a. Crocodile waterways and dinosaur freeways: implications of multiple swim track assemblages from the Cretaceous Dakota Group, Golden area, Colorado. *New Mexico Museum of Natural History and Science, Bulletin* **51:** 137–156.

Lockley MG, Gierlinski GD, Dubicka Z, Breithaupt BH, Matthews NA. 2014a. A preliminary report on new dinosaur Tracksite in the Cedar Mountain Formation (Cretaceous) of Eastern Utah. *New Mexico Museum of Natural History and Science, Bulletin* **62:** 279–285.

Lockley MG, Gierlinski GD, Houck K, Lim JD, Kim KS, Kim DY, Kim TK, Kang SH, Hunt Foster R, Li R, Chesser C, Gay R, Dubicka Z, Cart K, Wright C. 2014b. New excavations at the Mill Canyon Dinosaur Track site (Cedar Mountain Formation, Lower Cretaceous) of Eastern Utah. *New Mexico Museum of Natural History and Science, Bulletin* **62:** 287–300.

Lockley MG, Harris JD. 2010. On the trail of early birds: a review of the fossil footprint record of avian morphological and behavioral evolution. In: Ulrich PK, Willett JH, eds. *Trends in ornithology research*. Hauppauge: Nova Publishers, 1–63.

Lockley MG, Holbrook J, Kukihara R, Matsukawa M. 2006a. An ankylosaur-dominated dinosaur tracksite in the Cretaceous Dakota Group of Colorado and its paleoenvironmental and sequence stratigraphic context. *New Mexico Museum of Natural History and Science, Bulletin* **35:** 95–104.

Lockley MG, Houck K, Yang SY, Matsukawa M, Lim SK. 2006b. Dinosaur dominated footprint assemblages from the Cretaceous Jindong Formation, Hallayo Haesang National Park, Goseong County, South Korea: evidence and implications. *Cretaceous Research* **27:** 70–101.

Lockley MG, Huh M, Kim BS. 2012h. *Ornithopodichnus* and pes-only sauropod trackways from the Hwasun tracksite Cretaceous of Korea. *Ichnos* **19:** 93–100.

Lockley MG, Huh M, Kim JY. 2012c. Mesozoic terrestrial ecosystems of the Korean Cretaceous Dinosaur Coast: a field guide to the excursions of the 11th Mesozoic Terrestrial Ecosystems Symposium (August 19–22). A publication supported by the Korean Federation of Science and Technology Societies, 81p.

Lockley MG, Huh M, Kim JY, Lim JD, Kim KS. 2012b. Recent Advances in Korean vertebrate ichnology: the KCDC comes of age. *Ichnos* **19:** 1–5.

Lockley MG, Huh M, Kwak SK, Hwang KG, Paik IS. 2012f. Multiple tracksites with parallel trackways from the Cretaceous of the Yeosu City area, Korea: implications for gregarious behavior in ornithopod and sauropod dinosaurs. *Ichnos* **19:** 105–114.

Lockley MG, Huh M, Lim SK, Yang SY, Chun SS, Unwin D. 1997. First report of pterosaur tracks from Asia, Chollanam Province, Korea. *Journal of the Paleontological Society of Korea, Special Publication* **2:** 17–32.

Lockley MG, Hunt AP, Meyer C. 1994a. Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy. In: Donovan S, ed. 241–268. *The paleobiology of trace fossils*. New York: Wiley and Sons, Inc., vi+308 p.

Lockley MG, Hunt AP, Meyer CA. 1994b. Vertebrate Tracks and the Ichnofacies Concept: implications for Paleoecology and Palichnostratigraphy. In: Donovan S, ed. *The paleobiology of trace fossils*. New York: Wiley and Sons, Inc, 241–268.

Lockley MG, Kim JY, Kim KS, Kim SH, Matsukawa M, Li R, Li J, Yang SY. 2008. *Minisauripus* – the track of a diminutive dinosaur from the Cretaceous of China and South Korea: implications for stratigraphic correlation and theropod foot morphodynamics. *Cretaceous Research* **29:** 115–130.

Lockley MG, Li J, Li RH, Matsukawa M, Harris JD, Xing L. 2013. A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology. *Acta Geologica Sinica* **87:** 1–20.

Lockley MG, Li J, Matsukawa M, Li R. 2011. A new avian ichnotaxon from the Cretaceous of Nei Mongol, China. *Cretaceous Research* **34:** 84–93.

Lockley MG, Li R, Harris JD, Matsukawa M, Liu M. 2007. Earliest zygodactyl bird feet: evidence from Early Cretaceous roadrunner-like tracks. *Die Naturwissenschaften* **94:** 657–665.

Lockley MG, Li R, Matsukawa M, Li J. 2010b. Tracking Chinese crocodylians: *Kuangyuanpus*, *Laiyangpus*, and implications for naming crocodylian and crocodylian-like tracks and associated ichnofacies. In: Milàn J, Lucas SG, Lockley MG, Spielmann JA. (eds.), Crocodyle tracks and traces. *New Mexico Museum of Natural History and Science Bulletin* **51:** 99–108.

Lockley MG, Li R, Matsukawa M, Li J, Liu M, Wang K, Zhang XX, Xing X. 2012d. The importance of the Huanglonggou or 'Yellow Dragon Valley' dinosaur tracksite (Early Cretaceous) of the Zhucheng area, Shandong Province China. In: Huh M, Kim HJ, Park JY, eds. 315–317. *The 11th Mesozoic Terrestrial Ecosystems*. Abstracts volume (August 15–18), Kwangju: Korea Dinosaur Research Center, Chonnam National University, 461p.

Lockley MG, Lim JD, Kim JY, Kim KS, Huh M, Hwang KG. 2012g. Tracking Korea's early birds: ichnological insights into avian evolution and behavior. *Ichnos* **19:** 17–27.

Lockley MG, Lucas SG, Matsukawa M, Harris JD. 2012a. Cretaceous tetrapod footprint biostratigraphy, biochronology and ichnofacies. *Journal of Stratigraphy* **36:** 503–550.

Lockley MG, Matsukawa M. 2009. A review of vertebrate track distributions in east and southeast Asia. *Journal of the Paleontological Society of Korea* **25:** 17–42.

Lockley MG, Matsukawa M, Ohira H, Li J, Wright J, White D, Chen PJ. 2006c. Bird tracks from Liaoning Province, China: new insights into avian evolution during the Jurassic–Cretaceous transition. *Cretaceous Research* **27:** 33–43.

Lockley MG, Matsukawa M, Sato Y, Polahan M, Daorerk V. 2006d. A distinctive new theropod dinosaur track from the Cretaceous of Thailand: implications for ichnological diversity. *Cretaceous Research* **27:** 139–145.

Lockley MG, McCrea RT, Matsukawa M. 2009. Ichnological evidence for small quadrupedal ornithischians from the basal Cretaceous of southeast Asia and North America: implications for a global radiation. In: Buffetaut E, Cuny G, Le Loeuff J, Suteethorn V, eds. *Late palaeozoic and Mesozoic continental ecosystems of SE Asia*. London: Geological Society of London, **315:** 251–265.

Lockley MG, Meyer C, Hunt AP, Lucas SG. 1994b. The Distribution of sauropod tracks and trackmakers. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural, Lisbon* Portugal **10:** 233–248.

Lockley MG, Wright J, White D, Matsukawa M, Li J, Feng L, Li H. 2002. The first sauropod trackways from China. *Cretaceous Research* **23:** 363–381.

Lockley MG, Wright JL, Thies D. 2004. Some observations on the dinosaur tracks at Münchehagen (Lower Cretaceous), Germany. *Ichnos* **11:** 261–274.

Lockley MG, Xing L, Li J, Li R, Matsukawa M. 2012e. First records of turtle tracks in the Cretaceous of China. In: Huh M, Kim HJ, Park JY, eds. 311–313. *The 11th Mesozoic Terrestrial Ecosystems*. Abstracts volume (August 15–18), Kwangju: Korea Dinosaur Research Center, Chonnam National University, 461p.

Lockley MG, Xing L, Lockwood JAF, Pond S. 2014. A review of large Cretaceous ornithopod tracks, with special reference to their ichnotaxonomy. *Biological Journal of the Linnean Society* **113:** 721–736.

Lockley MG, Yang SY, Matsukawa M, Fleming F, Lim SK. 1992. The track record of Mesozoic birds: evidence and implications. *Philosophical Transactions of the Royal Society of London B* **336:** 113–134.

Lockwood JAF, Lockley MG, Pond S. 2014. A review of footprints from the Wessex Formation (Wealden Group, Lower Cretaceous) at Hanover Point, the Isle of Wight, southern England. *Biological Journal of the Linnean Society* **113:** 707–720.

Long J. 1998. *Dinosaurs of Australia and New Zealand*. Sydney: UNSW Press.

Lucas SG. 2007. Tetrapod footprint biostratigraphy and biochronology. *Ichnos* **14:** 5–38.

Lucas SG, Hunt AP. 1989. *Alamosaurus* and the sauropod hiatus in the Cretaceous of the North American Western Interior. *Geological Society of America Special Paper* **238:** 75–85.

Martin AJ, Vickers-Rich P, Rich TH, Hall M. 2014. Oldest known avian footprints from Australia: Eumeralla Formation (Albian), Dinosaur Cove, Victoria. *Palaeontology* **57:** 7–19.

Martin AJ, Vickers-Rich P, Vazquez-Propkopec G. 2012. A polar dinosaur-track assemblage from the Eumeralla Formation (Albian), Victoria, Australia. *Alcheringa* **36:** 171–188.

Masrour M, Pérez-Lorente F, Ferry S, Içame N, Grosheny D. 2013. First dinosaur tracks from the Lower Cretaceous of the Western High Atlas (Morocco). *Geogaceta* **53:** 33–36.

Matsukawa M, Lockley M, Li J. 2006. Cretaceous terrestrial biotas of East Asia, with special reference to dinosaur-dominated ichnofaunas: towards a synthesis. *Cretaceous Research* **27:** 3–21.

Matsukawa M, Shibata K, Kukihara R, Koarai K, Lockley MG. 2005. Review of Japanese dinosaur track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. *Ichnos* **12:** 201–222.

Matsukawa M, Shibata K, Sato K, Xing X, Lockley MG. 2014. The Early Cretaceous terrestrial ecosystems of the Jehol Biota based on food-web and energy-flow models. *Biological Journal of the Linnean Society* **113:** 836–853.

McCrea RT, Buckley LG, Plint AG, Currie PJ, Haggart JW, Helm CW, Pemberton SG. 2014. A review of vertebrate track-bearing formations from the Mesozoic and earliest Cenozoic of western Canada with a description of a new theropod ichnospecies and reassignment of an avian ichnogenus. *New Mexico Museum of Natural History and Science Bulletin* **62:** 5–93.

Mehl MG. 1931. Additions to the vertebrate record of the Dakota Sandstone. *American Journal of Science* **21:** 441–452.

Meyer CA, Thuring B. 2004. The first iguanodontid dinosaur tracks from the Swiss Alpes (Schrattenkalk Formation, Aptian). *Ichnos* **10:** 221–228.

Moratalla JJ, Hernán J. 2010. Probable palaeogeographic influences of the Lower Cretaceous Iberian rifting phase in the Eastern Cameros Basin (Spain) on dinosaur trackway orientations. *Paleogeography, Paleoecology, Paleoclimatology* **295:** 116–130.

Nicosia U, Marino M, Mariotti N, Muraro C, Panigutti S, Petti FM, Sacchi E. 1999. The Late Cretaceous dinosaur tracksite near Altamura (Bari, southern Italy). *Geologica Romana* **35:** 237–247.

Paik IS, Lee YI, Kim HJ, Huh M. 2012. Time, space and structure on the Korea Cretaceous Dinosaur Coast: Cretaceous stratigraphy, geochronology and paleoenvironments. *Ichnos* **19:** 6–16.

Peng BX, Du YS, Li DQ, Bai ZC. 2004. The first discovery of the Early Cretaceous pterosaur track and its significance in Yanguoxia, Yongjing County, Gansu Province. *Earth Science: Journal of China University of Geosciences* **29:** 21–24. (in Chinese).

Petti FM, D'Orazi Porchetti S, Sacchi E, Nicosia U. 2010. A new purported ankylosaur trackway in the Lower Cretaceous (lower Aptian) shallow-marine carbonate deposits of Puglia, southern Italy. *Cretaceous Research* **31:** 546–552.

Pittman J. 1989. Stratigraphy, lithology depositional environment and tracks type of dinosaur track-bearing beds of the Gulf Coastal Plain. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 135–153.

Pond S, Lockley MG, Lockwood JAF, Breithaupt BH, Matthews NA. 2014. Tracking dinosaurs on the Isle of Wight: a review of tracks, sites, and current research. *Biological Journal of the Linnean Society* **113:** 737–757.

Romilio A, Salisbury SW. 2010. A reassessment of large theropod dinosaur tracks from the Mid-Cretaceous (late Albian-Cenomanian), Winton Formation of Lark Quarry, central-western Queensland, Australia: a case for mistaken identity. *Cretaceous Research* **32:** 135–142.

Romilio A, Tucker RT, Salisbury SW. 2013. Reevaluation of the Lark Quarry dinosaur tracksite (late Albian-Cenomanian Winton Formation, central-western Queensland, Australia): no longer a stampede? *Journal of Vertebrate Paleontology* **33:** 102–120.

Sacchi E, Conti MA, D'Orazi Porchetti S, Logoluso A, Nicosia U, Perugini G, Petti FM. 2009. Aptian dinosaur footprints from the Apulian platform (Bisceglie, Southern Italy) in the framework of periadriatic ichnosites. *Palaeogeography, Palaeoclimatology, Palaeoecology* **271:** 104–116.

Sarjeant WAS, Delair JB, Lockley MG. 1998. The footprints of Iguanodon: a history and taxonomic study. *Ichnos* **6:** 183–202.

Stanford R, Lockley MG, Weems R. 2007. Diverse dinosaur dominated ichnofaunas from the Potomac Group (Lower Cretaceous) Maryland. *Ichnos* **14:** 155–173.

Sternberg CM. 1932. Dinosaur tracks from the Peace River, British Columbia. *National Museum of Canada Annual Report* for 1930, p. 59–85.

Thulborn RA. 2013. Lark Quarry revisited: a critique of methods used to identify a large dinosaurian track-maker in the Winton Formation (Albian–Cenomanian), western Queensland, Australia. *Alcheringa*. Available at: http://dx.doi.org/10.1080/03115518.2013.748482

Thulborn RA, Wade M. 1984. Dinosaur trackways in the Winton Formation (Mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum* **21:** 413–517.

Thulborn T. 2012. Impact of sauropod dinosaurs on lagoonal substrates in the Broome Sandstone (Lower Cretaceous), Western Australia. *PLoS ONE* **7:** e36208. doi:10.1371/journal.pone.0036208.

Xing L, Harris JD, Dong ZM, Lin YL, Chen W, Guo SB, Ji Q. 2009b. Ornithopod (Dinosauria: Ornithischia) tracks from the Upper Cretaceous Zhutian Formation in the Nanxiong Basin, Guangdong, China and general observation on large Chinese ornithopod footprints. *Geological Bulletin of China* **28:** 829–843.

Xing L, Harris JD, Gierliński G. 2011a. *Therangospodus* and *Megalosauripus* track assemblage from the Upper Jurassic–Lower Cretaceous Tuchengzi Formation of Chicheng County, Hebei Province, China and their paleoecological implications. *Vertebrata PalAsiatica* **49:** 423–434.

Xing L, Harris JD, Gierliński GD, Gingras MK, Divay JD, Tang YG, Currie PJ. 2012. Early Cretaceous Pterosaur tracks from a 'buried' dinosaur tracksite in Shandong Province, China. *Palaeoworld* **21:** 50–58.

Xing L, Harris JD, Jia CK, Luo ZJ, Wang SN, An JF. 2011b. Early Cretaceous bird-dominated and dinosaur footprint assemblage from the northwestern border of the Junggar Basin, Xinjiang, China. *Palaeoworld* **20:** 308–321.

Xing L, Harris JD, Sun DH, Zhao HQ. 2009a. The earliest known deinonychosaur tracks from the Jurassic–Cretaceous boundary in Hebei Province, China. *Acta Palaeontologica Sinica* **48:** 662–671.

Xing L, Li D, Harris JD, Bel PR, Azuma Y, Fujita M, Lee Y-N, Currie PJ. 2013b. A new *Dromaeosauripus* (Dinosauria: Theropoda) ichnospecies from the Lower Cretaceous Hekou Group, Gansu Province, China. *Acta Paleontological Polonica* **58:** 723–730.

Xing L, Lockley MG, Klein H, Zhang J. He Q, Divay JD, Qi L-Q, Jia C-K. 2013f. Dinosaur, bird and pterosaur footprints from the Lower Cretaceous of Wuerhe asphaltite area, Xinjiang, China, with notes on overlapping track relationships. *Paleoworld* **22:** 42–51.

Xing L, Lockley MG, Marty D, Klein H, Buckley LG, McCrea RT, Zhang JP, Gierliński GD, Divay JD, Wu QZ. 2013a. Diverse dinosaur ichnoassemblages from the Lower Cretaceous Dasheng Group in the Yishu fault zone, Shandong Province, China. *Cretaceous Research* **45:** 114–134.

Xing L, Lockley MG, McCrea RT, Gierlinski GD, Buckley L, Zhang J, Qi L, Jia C. 2013e. First record of *Deltapodus* tracks from the Lower Cretaceous of China. *Cretaceous Research* **42:** 55–65.

Xing L, Lockley MG, Piñuela L, Zhang JP, Klein H, Li DQ, Wang FP. 2013c. Pterosaur trackways from the Lower Cretaceous Jiaguan Formation, Qijiang District, Chongqing Municipality, China. *Palaeogeography, Palaeoclimatology, Palaeoecology* **392:** 177–185.

Xing L, Wang F, Pan S, Chen W. 2007. The discovery of dinosaur footprints from the Middle Cretaceous Jiaguan Formation of Qijiang County, Chongqing City. *Acta Geologica Sinica* **81:** 1591–1602. (in Chinese with English abstract).

Xing LD, Lockley MG, Zhang JP, Andrew RCM, Klein H, Li DQ, Persons WS, Ebi JF. 2013d. A new Early Cretaceous dinosaur track assemblage and the first definite non-avian theropod swim trackway from China. *Chinese Science Bulletin (Engl Ver)* **58:** 2370–2378.

Yabe H, Inai Y, Shikama T. 1940. Discovery of dinosaurian footprints from the Cretaceous (?) of Yangshan, Chinchou. Preliminary note. *Proceedings of the Imperial Academy of Tokyo* **15:** 560–563.

Yang SY. 1982. On the dinosaur's footprints from the upper Cretaceous Gyeongsang Group, Korea. *Journal of the Geological Society of Korea* **18:** 138–142. (in Korean with English Abstract).

Yang SY, Lockley MG, Greben R, Erikson BR, Lim SY. 1995. Flamingo and duck-like bird tracks from the Late Cretaceous and Early Tertiary: evidence and implications. *Ichnos* **4:** 21–34.

Young CC. 1960. Fossil footprints in China. *Vertebrata PalAsiatica* **4:** 53–67.

Zhang J, Li D, Li M, Lockley MG, Bai Z. 2006. Diverse dinosaur-, pterosaur- bird track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, Northwest China. *Cretaceous Research* **27:** 44–55.

Zhang JP, Xing L, Gierliński GD, Wu FD, Tian MZ, Currie PJ. 2012. First record of dinosaur trackways in Beijing, China (in Chinese). *Chinese Science Bulletin (Chin Ver)* **57:** 144–152.

Zhen S, Li J, Rao C, Mateer NJ, Lockley MG. 1989. A review of dinosaur footprints in China. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 187–197.

Zhen S, Li J, Zhang B. 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan, China. *Memoirs of the Beijing Natural History Museum* **54:** 105–120.