

A Review of the Tetrapod Track Record in China, with Special Reference to Type Ichnospecies: Implications for Ichnotaxonomy and Paleobiology

Martin G. LOCKLEY^{1,*}, LI Jianjun^{2,*}, LI Rihui³, Masaki MATSUKAWA⁴,
Jerald D. HARRIS⁵ and XING Lida⁶

1 University of Colorado Denver, Dinosaur Tracks Research Group, P.O. Box 173364, Campus Box 172, Denver, CO 80217-3364, USA

2 Beijing Museum of Natural History Museum, 126 Tianqiao, South Street, Beijing 100050, China

3 Qingdao Institute of Marine Geology, China Geological Survey, 62 Fuzhou Road, Qingdao 266071, China

4 Department of Environmental Sciences, Tokyo Gakugei University, Koganei, Tokyo, 184-8501, Japan

5 Department of Physical Sciences, Dixie State College, 225 South 700 East, St. George, Utah 84770

6 Department of Biological Sciences, University of Alberta, 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada

Abstract: “Splitting” and “lumping” are perpetual problems in vertebrate, especially dinosaur, ichnotaxonomy. Chinese dinosaur ichnotaxonomy, which began in 1940, provides a series of interesting case studies, highlighting the dual problems of historical and dubious ichnotaxonomy. Chinese Mesozoic tetrapod track types have been placed into 63 ichnospecies (one Triassic, 28 Jurassic, and 34 Cretaceous), exclusive of other, non-type ichnospecies or ichnotaxa identified from China. Fifty-two (~83%) of these 63 tetrapod ichnospecies were placed in monospecific ichnogenera. At the ichnogenus level, we prune—either by recognizing *nomina dubia* or by synonymy—17 from the list of 53 dinosaurian ichnogenera (a 32% reduction), leaving 36 ichnotaxa that we consider valid. Most of the cuts affect Jurassic theropod ichnotaxa, which are reduced from 23 to only nine because most ichnogenera are subjective junior synonyms of *Grallator* and *Eubrontes*. Fewer Chinese Cretaceous ichnotaxa (only six of 21 ichnogenera) are obvious *nomina dubia* or subjective synonyms, suggesting greater east Asian endemism during this time. Because ichnospecies differences are subtle, we provisionally retain ichnospecies as valid pending detailed comparative analyses of congeneric ichnospecies. This synthesis is long overdue and is necessary to address problems of historical and provincial ichnotaxonomy, which severely hamper comparisons of tetrapod ichnofaunas in space and time.

Key words: Dinosaurs, birds, theropods, ichnotaxonomy, Mesozoic, China

1 Introduction

“Splitting” and “lumping” are perennial problems in vertebrate ichnotaxonomy, particularly in dinosaur ichnotaxonomy. Much splitting has been due to provincial taxonomy: assigning new names to footprint morphologies simply because they come from new areas, localities, and/or formations, and without comparison to similar tracks from other areas and/or time periods. Their novelties in terms of geographic and geological occurrences, rather than any unique morphologies, were used improperly to

justify erecting new ichnotaxa—in short, newness of occurrence does not equate to newness of ichnotaxonomy. Except when the specimens on which the ichnotaxa were based differ markedly in morphology, most ichnologists would subjectively regard most as subjective junior synonyms of ichnospecies named previously from other areas, localities, and/or formations, despite the fact that the Chinese specimens were based on new occurrences. In some cases, such provincial taxonomies are residuals of history, resulting from the publication of ichnotaxonomic descriptions in literature that was, at this time, poorly distributed; often these are regional publications in various languages. Such sources were often unknown, unavailable,

*Corresponding author. E-mail: Martin.Lockley@UCDenver.edu
ljj5681@126.com

or inaccessible to many authors describing new specimens, limiting proper comparisons between ichnotaxa and perhaps falsely leading to the perception that new specimens were morphologically unique. Other ichnotaxa (*nomina dubia*) were based on poorly preserved ichnites that lack adequate diagnostic morphologies and/or involve extramorphological features and therefore do not accurately reflect true pedal morphologies.

Between 1940 and 2012, a total of 63 tetrapod ichnospecies were erected based on Chinese type specimens (Table 1). All are Mesozoic in age; all but a single Triassic type are either Jurassic (28) or Cretaceous (34) in age. Except for one crocodylian and two presumed ornithischian dinosaur ichnospecies, all of the Jurassic ichnotaxa have been attributed to theropod dinosaurs. Similarly, only two of the Cretaceous ichnospecies are non-dinosaurian (one pterosaur and one crocodylian), although unlike in the Jurassic, seven pertain to avian theropods (birds). Among the 25 inferred non-avian dinosaurian ichnospecies, 18 have been attributed to theropods, four to ornithomorphs, two to sauropods, and one, incorrectly, to an ankylosaur.

The primary goal of this paper is to discuss the validity of Mesozoic tetrapod ichnotaxa that are based on Chinese type ichnospecies. Many of these have been previously treated as *nomina dubia* or otherwise had their validities questioned, either formally or informally. For historical reasons, including the aforementioned inaccessibility of relevant literature—a significant problem because of language barriers, academic traditions, and/or limitations of publication distribution—a number of ichnotaxa constitute obvious or suspected subjective synonyms. Certainly, the over-splitting of vertebrate ichnotaxa is by no means a provincial phenomenon restricted to any one particular research tradition or historical chapter in science: the father of ichnology himself (Hitchcock, 1858) was responsible for naming many ichnotaxa that, according to many researchers (e.g., Olsen, 1980; Gierliński, 1994; Rainforth, 2005), include many synonyms. However, revising the extensive work of Hitchcock and of Early Jurassic tracks from eastern and northeastern USA, in order to unequivocally remove invalid or otherwise dubious ichnotaxa, has proved difficult (Olsen et al., 1998). While we are aware of the tendency to over-split that arises from research with a provincial focus and/or limited access to relevant literature, we attempt to avoid the alternate approach of lumping ichnospecies without careful study of the type material, its state of preservation, and the quality of the primary literature.

For these reasons, herein we cannot tackle the monumental task of evaluating every ichnotype for its

validity at the ichnospecies level. However, working at the more general ichnogenus level (Lucas, 2007) has precedents, and we therefore attempt to evaluate the validity of all of the relevant ichnogenera. Therefore, while we transfer many ichnospecies into appropriate ichnogenera, we have not proposed synonymies at the ichnospecies level. This preserves the complete list of Chinese type ichnospecies as a reference catalog, and leaves open the possibility of further analyses of type ichnospecies and their relations at the “ichnospecies level.” Nevertheless, in the sections that follow, we discuss all named Chinese tetrapod ichnospecies in order to objectively assess their validities and where they are best accommodated at the ichnogenus level.

An additional consideration involves the dating of type localities and type specimens (reviewed for the Cretaceous by Matsukawa et al. [2006] and Chen et al. [2006]). The inferred ages of several Chinese sites and specimens are uncertain and, in some cases, have changed over time. While such changes and uncertainty may compromise biostratigraphic comparisons of Chinese tracks with those from other areas, in principle it does not affect evaluation of the ichnotaxonomic validities of specimens themselves based on comparative morphology, analysis of preservation, and the accuracy and quality of primary sources.

Bearing in mind that a few ichnotaxa reported from China are not endemic (i.e., they are based on type materials from other countries), the composition of the list of Chinese type specimens does not accurately reflect the diversity of Chinese track types or inferred track makers, even after we have pruned out inappropriately named ichnotaxa. Stated another way, to accurately understand the complete Chinese track record, other recorded ichnotaxa must be added (see below) and obvious synonyms must be subtracted. Thus, on the one hand, the list of Chinese type ichnospecies discussed herein reflects the history of vertebrate track research in China combined with ichnotaxonomic traditions, geography, and the distribution of track-bearing strata in China. On the other hand, comparison of Chinese tracks to ichnotaxa named elsewhere, as well as additions and amendments to Chinese ichnotaxonomy (especially synonymies), facilitate perception of how the Chinese track record fits into global ichnotaxonomic trends.

2 Ichnotaxonomy

In this section, we review known ichnotaxa to assess whether any are adequately described and/or differentiable from existing ichnospecies, and therefore accommodated in an appropriate ichnogenus. In cases where tracks are so

Table 1 Tetrapod type ichnospecies from China named between 1940 and 2012. Ichnospecies (numbered 1–63) are listed first by age (period and epoch) and second by order of publication

Time Period	#	Ichnotaxon	Ichnospecies Established by
Triassic (1 isp. in 1 igen.)	1	<i>Pengxianpus cifengensis</i>	Yang and Yang, 1987
Early–Middle Jurassic (25 ispp. in 20 igen.)	2	<i>Kuangyuanpus szechuanensis</i> (crocodylan)	Young, 1943
	3	<i>Sinoichnites youngi</i> (ornithischian)	Kuhn, 1958
	4	<i>Changpeipus carbonicus</i>	Young, 1960
	5	<i>Shensipus tungchuanghensis</i>	Young, 1966
	6	<i>Changpeipus luanpingensis</i>	Young, 1979
	7	<i>Grallator limnosus</i>	Zhen et al., 1986
	8	<i>Paracoelurosaurichnus monax</i>	Zhen et al., 1986
	9	<i>Schizograllator xiaohebaensis</i>	Zhen et al., 1986
	10	<i>Youngichnus xiyangensis</i>	Zhen et al., 1986
	11	<i>Zhengichnus jinningensis</i>	Zhen et al., 1986
	12	<i>Zizhongpus wumanensis</i>	Yang and Yang, 1987
	13	<i>Chongqingpus microiscus</i>	Yang and Yang, 1987
	14	<i>Chongqingpus nananensis</i>	Yang and Yang, 1987
	15	<i>Chongqingpus yemiaoxiensis</i>	Yang and Yang, 1987
	16	<i>Tuojiangpus shuinanensis</i>	Yang and Yang, 1987
	17	<i>Chonglongpus hei</i>	Yang and Yang, 1987
	18	<i>Megaichnites jizhaishiensis</i>	Yang and Yang, 1987
	19	<i>Jinlijingpus nianpanshanensis</i>	Yang and Yang, 1987
	20	<i>Chuanchengpus wuhaungensis</i>	Yang and Yang, 1987
	21	<i>Lufengopus dongi</i>	Lü et al., 2006
	22	<i>Changpeipus xuiana</i>	Lü et al., 2007
	23	<i>Weiyuanpus zigongensis</i>	Gao, 2007
	24	<i>Changpeipus pareschequier</i>	Xing et al., 2009a
	25	<i>Kayentapus hailuensis</i>	Li et al., 2010
	26	<i>Shenmuichnus youngteihardorum</i> (ornithischian)	Li et al., 2012
Late Jurassic (3 ispp. in 3 igen.)	27	<i>Yangtzeipus yipingensis</i>	Young, 1960
	28	<i>Jialingpus yuechiensis</i>	Zhen et al., 1983
	29	<i>Huanglongpus shengouensis</i>	Yang and Yang, 1987
Cretaceous (34 ispp. in 30 igen.)	30	<i>Grallator ssatoi</i> (originally <i>Jeholosauripus s-satoi</i>)	Yabe et al., 1940; Zhen et al., 1989
	31	<i>Laiyangpus liui</i> (crocodylan)	Young, 1960; Lockley et al., 2010
	32	<i>Xiangxipus chenxiensis</i>	Zeng, 1982a, b
	33	<i>Xiangxipus youngi</i>	Zeng, 1982a, b
	34	<i>Hunanpus jiuquwanensis</i>	Zeng, 1982a, b
	35	<i>Brontopodus changlinensis</i> (originally <i>Chuxiongpus changlinensis</i>) (sauropod)	Chen and Huang, 1993; Lockley et al., 2002
	36	<i>Brontopodus zheni</i> (originally <i>Chuxiongpus zheni</i>) (sauropod)	Chen and Huang, 1993; Lockley et al., 2002
	37	<i>Yunnanpus huangcaoensis</i>	Chen and Huang, 1993
	38	<i>Velociraptorichnus sichuanensis</i>	Zhen et al. 1994
	39	<i>Minisauripus chuanzhuanensis</i>	Zhen et al. 1994
	40	<i>Grallator emeiensis</i> (originally incorrectly referred to as both <i>G. emeiensis</i> and <i>Neograllator emeiensis</i>)	Zhen et al. 1994
	41	<i>Koreanaornis sinensis</i> (originally <i>Aquatilavipes sinensis</i>) (bird)	Zhen et al. 1994
	42	<i>Iguanodonpus xingfuensis</i> (originally labeled ornithopod, but probably theropod)	Zhen et al., 1996
	43	<i>Aquatilavipes anhuiensis</i> (bird)	Jin and Yan, 1994
	44	“Paragrallator” yangi	Li and Zhang, 2000
	45	<i>Pullornipes aureus</i> (bird)	Lockley et al., 2006
	46	<i>Jiayinosauropus johnsoni</i> (ornithopod)	Dong et al., 2003
	47	<i>Pterichnus yanguoxiaensis</i> (pterosaur)	Peng et al., 2004
	48	<i>Shandongornipes muxiai</i> (bird)	Li et al., 2005; Li et al., 2007
	49	<i>Chapus lockleyi</i>	Li et al., 2006
	50	<i>Caririchnium lotus</i> (ornithopod)	Xing et al., 2007
	51	<i>Qijiangpus sinensis</i> (ankylosaur?)	Xing et al., 2007
	52	<i>Laoyingshanpus torridus</i> (ornithopod?)	Xing et al., 2007
	53	<i>Wupus agilis</i>	Xing et al., 2007
	54	<i>Dromaeopodus shandongensis</i>	Li et al., 2008
	55	<i>Minisauripus zhenshouanani</i>	Lockley et al., 2008
	56	<i>Hadrosauropodus nanxiongensis</i> (ornithopod)	Xing et al., 2009c
	57	<i>Menglongipus sinensis</i>	Xing et al., 2009b
	58	<i>Asianopodus robustus</i>	Li et al., 2011b
	59	<i>Corpulentapus lilasia</i>	Li et al., 2011b
	60	<i>Koreanaornis dodsoni</i> (bird)	Xing et al., 2011
	61	<i>Moguornipes robusta</i> (bird)	Xing et al., 2011
	62	<i>Tatarornipeschabuensis</i> (bird)	Lockley et al., 2012
	63	<i>Dromaeosauripus yongjingensis</i>	Xing et al., 2012

Bold italic print = original Chinese type (ichnogenotype). **Regular italic print** = a subsequently named, new ichnospecies of an aforementioned ichnogenus originally named from China (eight examples). Small, Romanized (non-italic) print = new ichnospecies of an ichnogenus originally named outside of China (12 examples). Synonymies listed were recognized prior to the present analysis; synonymies proposed in this paper are not listed (see text for detail). All tracks pertain to theropods (unless otherwise stated in parentheses).

poorly preserved, or so poorly described and documented as to be undiagnostic, we declare the ichnotaxa *nomina dubia* that should henceforth be abandoned. In cases where the material is better preserved, but appears synonymous with an existing ichnotaxon at the ichnogenus or ichnospecies level, we emend those ichnotaxa accordingly. In such cases, we state explicitly whether there are any legitimate grounds for differentiating the junior and senior synonyms, or refer to previously published analyses. Such procedures do not, however, prevent future researchers from conducting further analyses of the material to retest the validity of the ichnotaxonomies proposed herein.

2.1 Triassic Ichnospecies

Specimens assigned to the widespread ichnogenus *Chirotherium* have been reported from the Middle Triassic of Guizhou Province (Lü et al., 2004), but *Pengxianpus cifengensis* (Yang and Yang, 1987) is the *only* endemic or “type” tetrapod ichnospecies from the Chinese Triassic. We have examined the type specimen in the Chongqing Natural History Museum in Sichuan Province, which consists of two tridactyl tracks, evidently representing a single step by a single track maker (Matsukawa et al., 2006; Lockley and Matsukawa, 2009). The track is not tetradactyl as suggested by Yang and Yang (1987). The preservation of the tracks is good, especially of the first track in the sequence, which possesses localized skin impressions (Lockley and Matsukawa, 2009). Although large, tridactyl tracks of similar size have been reported elsewhere from the Late Triassic (Lucas et al., 2006) and the Jurassic, time periods in which *Eubrontes* is the most common large, tridactyl ichnotaxon (see below), *P. cifengensis* cannot be attributed to *Eubrontes* with any confidence because it lacks the asymmetry and pad configurations of that ichnogenus. Thus, we retain *P. cifengensis* as a valid ichnotaxon.

2.2 Early and Middle Jurassic Ichnospecies

Kuangyuanpus szechuanensis (Young, 1943) is the only

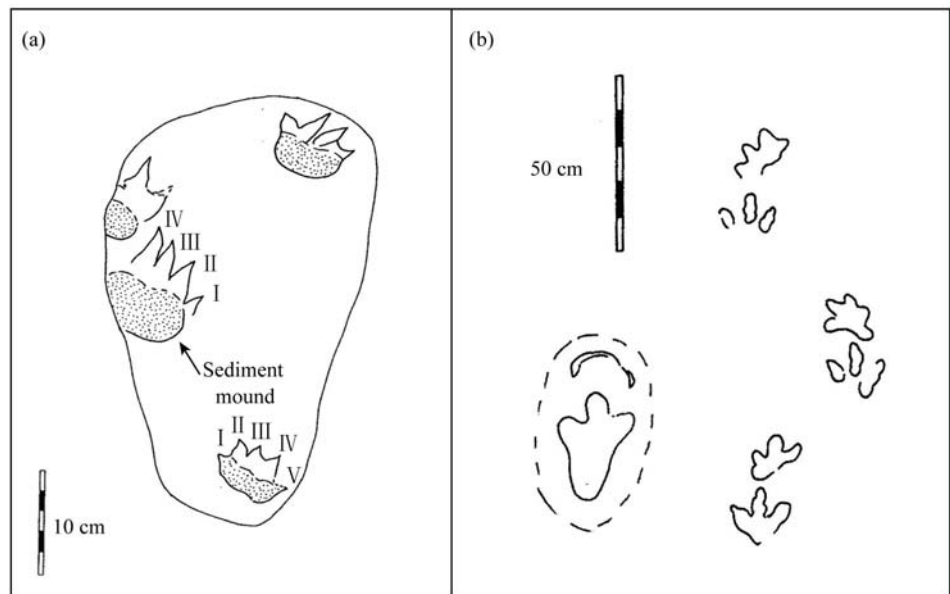


Fig. 1. (a), *Kuangyuanpus szechuanensis* (Young, 1943), modified after Lockley et al. (2010); (b), right, three manus–pes sets in a trackway of well-preserved *Shenmuichnus youngteilharedorum* tracks; left, poorly-preserved manus–pes set of tracks resembling *Sinoichnites youngi* (Kuhn, 1958) (after Li et al. (2012)).

presumed non-dinosaurian type ichnospecies reported from the Jurassic of China (Fig. 1). It was also the first tetrapod ichnospecies formally named from the Jurassic of China, and while it was briefly considered a synonym of *Batrachopus* (Zhen et al., 1989), more recently it has been re-examined and re-described in detail by Lockley et al. (2010), who considered it valid and of presumed crocodylian affinity. The specimen is well-preserved, displaying five sharp digit traces on the presumed manus and four on the pes. The tracks have sediment mounds behind them, suggesting that they are swim tracks. According to Lockley et al. (2010) all these features are diagnostic of crocodylian affinity, although not exclusively so.

All 27 presumed dinosaurian type ichnospecies from the Jurassic of China appear to pertain to theropods (Table 1). Of these, 24 are considered Early or Middle Jurassic in age; 14 (~58%) of these were described in two studies conducted in the 1980s (Zhen et al., 1986; Yang and Yang, 1987). These tracks comprise what can be characterized as the Yunnan and Sichuan ichnofaunas, respectively. Lockley and Matsukawa (2009) compared the ichnotaxa in the Yunnan ichnofauna by illustrating them at the same scales (Fig. 2), concluding that they could all probably be referred to known ichnotaxa, such as *Eubrontes* and *Grallator*. Lockley et al. (2003) reached the same conclusion for the Sichuan ichnofauna. Furthermore, Gierliński (1994) also suggested that these ichnofaunas are seriously oversplit.

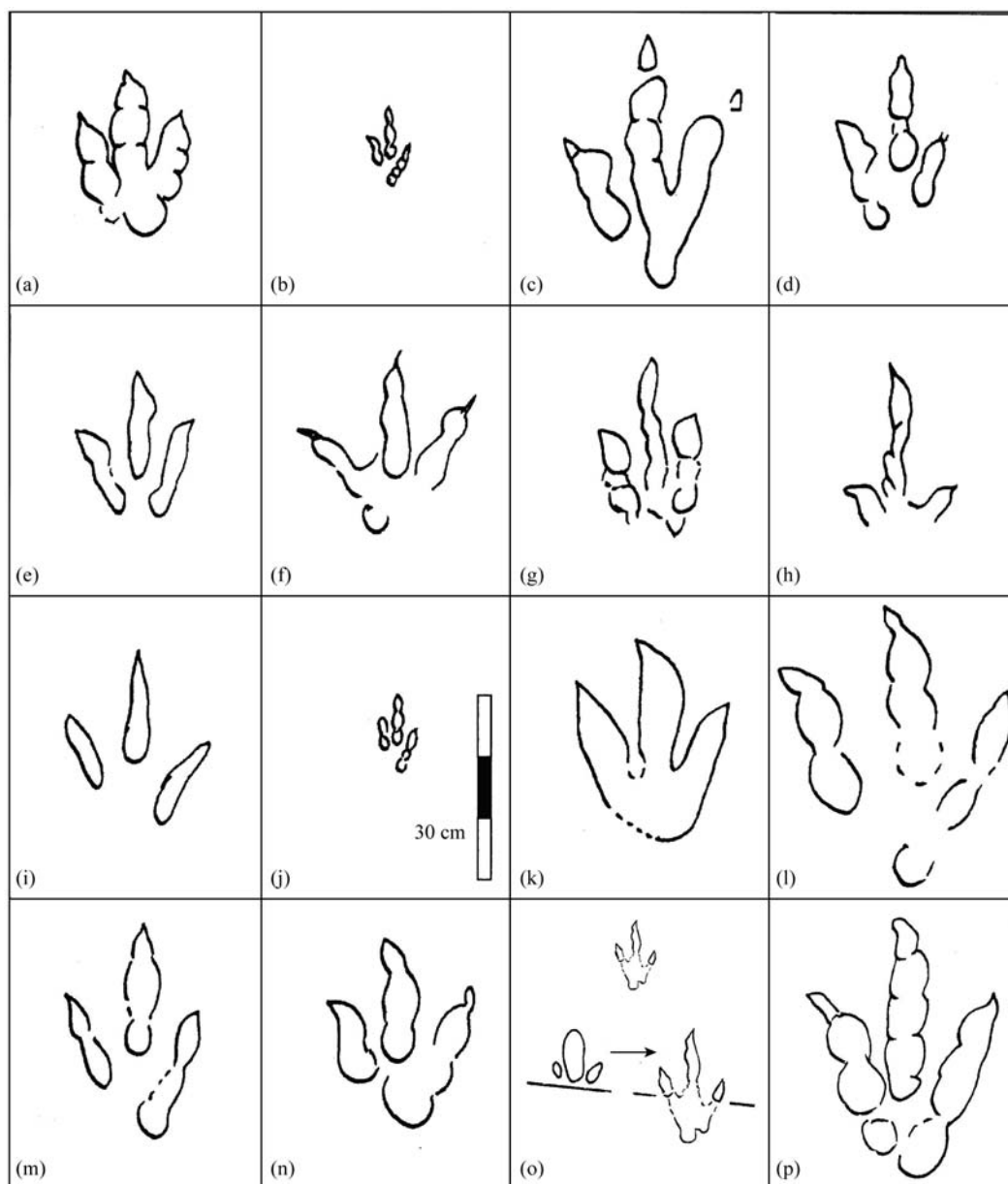


Fig. 2. Exemplar morphologies of the Early Jurassic theropod ichnotaxa *Eubrontes* Hitchcock 1845 (a) and *Grallator* Hitchcock 1858 (b) compared to various theropod tracks from the Lower Jurassic of China (c–p), arranged in chronological order of naming. (c), *Changpeipus carbonicus*; (d), *Grallator limnosus*; (e), *Paracoelurosaurichnus monax*; (f), *Schizograllator xiaohebaensis*; (g), *Youngichnus xiyangensis*; (h), *Zhengichnus jinningensis*. (i), *Zizhongpus wumanensis*; (j), *Chongqingpus microiscus*; (k), *Tuojiangpus shuinanensis*; (l), *Chonglongpus hei*; (m), *Megaichnites jizhaoshiensis*; (n), *Jinlijingpus nianpanshanensis*; (o), *Chuanchengpus wuhuangensis*, with correct outline (top) and enlargement (bottom) showing the differences between illustrations of the type (bottom left) and corrected illustration (bottom right); (p), *Weiyuanpus zigongensis*. All tracks (except for i and k) drawn by the senior author from type material and redrafted to the same scale. c after Young (1960); d–h after Zhen et al. (1983); i–o after Yang and Yang (1987).

Zhen et al. (1986) erected four monospecific ichnogenera from the Lower Jurassic Fengjiahe Formation of Jinning, Yunnan: *Paracoelurosaurichnus monax*, *Schizograllator xiaohebaensis*, *Youngichnus xiyangensis*, and *Zhengichnus jinningensis*. In addition, they recognized a new ichnospecies of *Grallator*, *G. limnosus*,

and the previously named ichnospecies *Eubrontes platypus* (Lull, 1904). The latter ichnospecies is not a Chinese type and so is not included in our lists (Table 1) and analyses. We have examined the type material of each of these ichnotaxa, which were originally illustrated with photos and line drawings. We also note that, at the time

Table 2 Summary of ichnotaxonomic revisions of the six ichnospecies reported from the Lower Jurassic Fengjiahe Formation of Yunnan Province, China by Zhen et al. (1986)

Ichnotaxa of Zhen et al. (1986)	Revised Ichnotaxonomy	Comments
<i>Eubrontes platypus</i>	no change	—
<i>Grallator limnosus</i>	no change	—
<i>Paracoelurosaurichnus monax</i>	<i>Eubrontes monax</i> comb. nov.	—
<i>Schizograllator xiaohebaensis</i>	<i>Kayentapus xiaohebaensis</i> comb. nov.	—
<i>Youngichnus xiyangensis</i>	<i>Eubrontes xiyangensis</i> comb. nov.	—
<i>Zhengichnus jinmingensis</i>	<i>nomen dubium</i>	poor, undiagnostic preservation

Note that the original ichnogenetic diversity of six, mainly provincial, names is reduced to three ichnogenera that have global distributions. See text and Fig. 2.

Table 3 Summary of ichnotaxonomic revisions of the nine ichnospecies reported from the Lower Jurassic Xintiangou and Lower Shaximiao formations of Sichuan Province, China by Yang and Yang (1987)

Ichnotaxa of Yang and Yang (1987)	Revised Ichnotaxonomy	Comments
<i>Zizhongpus wumanensis</i>	<i>Kayentapus wumanensis</i> comb. nov.	—
<i>Tuojiangpus shuinanensis</i>	<i>nomen dubium</i>	poor, undiagnostic material
<i>Chonglongpus hei</i>	<i>Gigandipus hei</i>	see Lockley et al. (2003)
<i>Megaichnites jizhaoshiensis</i>	<i>Kayentapus jizhaoshiensis</i> comb. nov.	—
<i>Chuanchengpus wuhuangensis</i>	<i>Grallator wuhuangensis</i> comb. nov.	—
<i>Jinlijingpus nianpanshanensis</i>	<i>Eubrontes nianpanshanensis</i> comb. nov.	—
<i>Chongqingpus nananensis</i>	<i>Kayentapus nananensis</i> comb. nov.	—
<i>Chongqingpus yemiaoxiensis</i>	<i>Grallator yemiaoxiensis</i> comb. nov.	—
<i>Chongqingpus microiscus</i>	<i>Grallator microiscus</i> comb. nov.	—

the original study was performed, comparative literature was difficult to obtain in China (implied in the acknowledgements in Zhen et al., 1986) and that the globally widespread *Grallator*- and *Eubrontes*-dominated, Early Jurassic ichnofauna (Olsen and Galton, 1984; Lucas, 2007; Lockley et al., 2011a, and references therein) was not widely recognized. Nevertheless, the authors clearly recognized affinities of some of their tracks to already-known ichnotaxa (*Coelurosaurichnus* and *Grallator*, which formed the roots of two of their ichnogenus names). Perhaps unsurprisingly, the four ichnospecies not assigned to either *Grallator* and *Eubrontes* require comparison to ichnospecies of both of these ichnogenera, as well as to other, closely related forms (e.g., *Kayentapus*) named prior to the current renaissance in Chinese ichnology.

The *G. limnosus*, *S. xiaohebaensis*, and *Y. xiyangensis* types were based on trackways, whereas the other Yunnan ichnotaxa were based on individual tracks. We consider *Z. jinmingensis* a *nomen dubium* because it is based on a poorly preserved specimen that is very distorted. *P. monax* and *Y. xiyangensis* are indistinguishable from *Eubrontes* at the ichnogenus level, they have the same digital pad formulae, and similar digit widths and divarication angles. Because no diagnostic features were given to distinguish either ichnospecies from type *Eubrontes*, or any other *Eubrontes* ichnospecies, the erection of the ichnogenera *Paracoelurosaurichnus* and *Youngichnus* were unjustified, and both are therefore assigned here to *Eubrontes* (Table 2). *S. xiaohebaensis* may be distinct from *Eubrontes* and has already been compared favorably with *Kayentapus* (Welles, 1971), both indirectly (Lockley and Hunt, 1995) and directly (Matsukawa et al., 2005; Lockley and Matsukawa, 2009; Lockley et al., 2011a). Thus, based on

these previous suggestions of synonymy, we propose the combination *K. ayentapus xiaohebaensis* comb. nov. to accommodate these specimens. This implies that the Japanese ichnospecies *Schizograllator otariensis* becomes *K. otariensis* comb. nov., although the Japanese ichnospecies is smaller and more elongate than *K. xiaohebaensis* according to Matsukawa et al. (2005). As noted below, it is possible that *Kayentapus* is a subjective junior synonym of *Changpeipus*.

The Sichuan ichnofauna, from the Lower–Middle Jurassic Xintiangou Formation near Zizhou and Jinlijing, was described by Yang and Yang (1987), who erected the following monospecific ichnogenera: *Zizhongpus wumanensis*, *Tuojiangpus shuinanensis*, *Chonglongpus hei*, *Megaichnites jizhaoshiensis*, *Chuanchengpus wuhuangensis*, and *Jinlijingpus nianpanshanensis*. In addition, Yang and Yang (1987) erected three ichnospecies of the new ichnogenus *Chongqingpus*, *C. microiscus*, *C. nananensis*, and *C. yemiaoxiensis*, for tracks from a locality in the Lower Shaximiao Formation in Chongqing City. They also described *Huanglongpus shengouensis* from Upper Jurassic strata near Yuechi (see next section). Based on examination and re-illustration of most of the types, Lockley et al. (2003) and Lockley and Matsukawa (2009) commented on the similarities of these ichnospecies to *Grallator*, *Eubrontes*, and *Kayentapus*, to which they are herein referred (Table 3). In the case of *Chongqingpus*, *C. microiscus*, is assigned to *Grallator microiscus* comb. nov. and *C. yemiaoxiensis* is assigned to *Grallator yemiaoxiensis* comb. nov. (q.v. Lockley and Matsukawa, 2009). *C. nananensis* is assigned to *Kayentapus nananensis* comb. Nov. (Xing et al., in press).

Yang and Yang (1987) provided photos and line

Table 4 Early and Middle Jurassic dinosaur tracks from China not described by Zhen et al. (1986) or Yang and Yang (1987)

Ichnotaxon	Revised Ichnotaxonomy	Comments
<i>Sinoichnites youngi</i> Kuhn (1958)	<i>nomen dubium</i>	undiagnostic; holotype lost
<i>Changpeipus carbonicus</i> Young (1960)	no change	has variously been compared to <i>Grallator</i> , <i>Eubrontes</i> and <i>Kayentapus</i>
<i>Shensipus tuchuanghensis</i> Young (1966)	no change	—
<i>Changpeipus luangpineris</i> Young (1979)	<i>nomen dubium</i>	referred to <i>C. carbonicus</i> by Xing et al. (2009a)
<i>Lufengopus dongi</i> Lü et al. (2006)	cf. <i>Eubrontes</i>	—
<i>Changpeipus xuiana</i> Lü et al. (2007)	<i>Eubrontes carbonicus</i> comb. nov.	referred to <i>C. carbonicus</i> by Xing et al. (2009a)
<i>Weiyuanpus zigongensis</i> Gao (2007)	<i>Eubrontes zigongensis</i> comb. nov.	—
<i>Kayentapus hailuensis</i> Li et al. (2010)	no change	—
<i>Changpeipus pareschequier</i> Xing et al. (2009a)	<i>Eubrontes pareschequier</i> comb. nov.	—
<i>Shenmuichnus youngteihardorum</i> Li et al. (2012)	no change	the only valid, large ornithischian ichnotaxon from the Early Mesozoic of China

drawings of their various type specimens, but as shown by Lockley et al. (2003) and Lockley and Matsukawa (2009), the morphological details in many of the line drawings are incorrect and do not reflect the morphologies of the actual tracks. For example, *Chuanchengpus wuhuangensis* is depicted as having a long, sausage-shaped, clawless digit III and very short digits II and IV (Yang and Yang, 1987, fig. 21). However, based on our examination of the actual specimen, only the anterior half of the actual track was traced (Yang and Yang, 1987, pl. III-1); the complete specimen is a typical *Grallator* track, with a long heel, claw traces, and discrete pad traces. The comparison between the two interpretations is stark (Fig. 2) and *C. wuhuangensis* would have to be considered a *nomen dubium* were it not possible to reinterpret the morphology (Lockley et al., 2003, fig. 6F) and assign the ichnite to ichnogenus *Grallator*. While different researchers may interpret tracks differently, as in the case just described, the absence of a systematic comparison of new ichnotaxa with existing ichnotaxa is also problematic. Given the greatly improved understanding of Early Jurassic theropod ichnotaxa that has evolved since 1987, the fact that not one ichnotaxon in the Sichuan assemblage has been compared with or attributed to the contemporaneous, globally ubiquitous ichnogenus *Grallator*, *Eubrontes*, and *Kayentapus* is surprising, and in our opinion a telling omission. We propose several synonymies (Table 3) based on two bodies of evidence: (1) the comparisons already made with the aid of revised illustrations (Lockley et al., 2003; Lockley and Matsukawa, 2009; Fig. 2 herein) between these well-known ichnogenus and the ichnotaxa erected by Yang and Yang (1987) and (2) the simple fact that all of the Sichuan ichnogenus (except *Chonglongpus*, which is tetradactyl, and *Tuojiangpus*, an obvious *nomen dubium* due to poor preservation and expression of features) have typical theropod digital pad formulae and lack any other diagnostic features that separate them from the more ubiquitous theropod ichnotaxa. *Chonglongpus hei* bears a hallux impression and, therefore, is morphologically distinct from the other ichnotaxa

described by Yang and Yang (1987). We agree with Yang and Yang (1987) that this warrants comparison to *Gigandipus*, and have previously suggested that *Chonglongpus hei* should be referred to *Gigandipus* as *G. hei* comb. nov. (Lockley et al., 2003).

Ten other Early–Middle Jurassic dinosaurian ichnotaxa from China remain for consideration (Table 4). *Sinoichnites youngi* was the first dinosaur track reported from China (Teilhard de Chardin and Young, 1929), although it was not named until later (Kuhn, 1958). Unfortunately, despite its historical importance, the type specimen is lost. Based on photos and descriptions in the original publication, we can only confirm that the track is a tridactyl cast about 33 cm wide and 30 cm long with blunt digit impressions. Lacking diagnostic characters, it is a *nomen dubium*. The type locality is not known precisely, described only as located somewhere near Shenmu City, Shaanxi Province. Although Teilhard de Chardin and Young (1929) suggested its track maker would have been similar to *Iguanodon*, recent work indicates that track-rich units in this area are of Early Jurassic age (Li et al., 2012), substantially predating *Iguanodon* or, indeed, any large ornithopod. Quadrupedal, non-ornithopod ornithischian trackways that resemble *Sinoichnites* include *Deltapodus*; well-preserved trackways from this region have been assigned to the new, *Moyenosauripus*-like ichnotaxon *Shenmuichnus youngteihardorum* (Li et al., 2012).

Changpeipus carbonicus (Young, 1960) is a reasonably well-preserved theropod track that exhibits numerous features, such as its digital pad formula, that ally it to the *Grallator*–*Eubrontes* plexus (sensu Olsen, 1980); indeed, Gierliński (1994) considered it a synonym of *Grallator sensu lato*, a position echoed by Lockley et al. (2003) and indirectly endorsed by Xing et al. (2009a). In particular, *Changpeipus carbonicus* is similar to type *Eubrontes* (sensu Olsen et al., 1998). However, Xing et al. (2009a) considered it closer to *Kayentapus* (Welles, 1971). If *Changpeipus* and *Kayentapus* are indeed indistinguishable at the ichnogenus level, then *Changpeipus* (Young, 1960) has priority. Therefore, we agree with Xing et al. (2009a)

that the absence of a systematic revision of all the relevant ichnotaxa makes it premature to suggest a formal synonymy. However, we may conclude that regarding the type of *Changpeipus* as a junior synonym of *Grallator* or *Eubrontes*, or as a senior synonym of *Kayentapus*, is not a satisfactory conclusion. Thus, further work is warranted.

Changpeipus carbonicus was originally interpreted by Young (1960) as having been made by a quadrupedal theropod with a small tridactyl manus. However, Zhen et al. (1989) declared that the supposed manus print required further study; subsequent workers assumed that the purported manus has no real relationship to the pes either by ignoring the report (Lockley et al., 2003; Lockley and Matsukawa, 2009) or by explicitly attributing it to a different track-making animal (Thulborn, 1990; Xing et al., 2009a).

Xing et al. (2009a) considered *Changpeipus luangpingeris* (Young, 1979) and *Changpeipus xuiana* (Lu et al., 2007) synonyms of *C. carbonicus*. While this reduced the number of accepted *Changpeipus* ichnospecies, Xing et al. (2009a) again increased the number by naming the new ichnospecies *C. pareschequier* based on tracks in which the trace of digit IV bears only two digital pads, giving a pad formula of 2-3-2 rather than 2-3-4. We consider this a misinterpretation of the holotype because, as illustrated, it has most of the characteristics of a typical *Eubrontes* track, better transferred to *Eubrontes pareschequier* comb. nov. (Table 4). Normally, the posterior heel pad traces are continuous with those of the more anterior traces of digit IV; in the case of *C. pareschequier*, this is clearly seen (Xing et al., 2009a, pl. 1), indicating that their drawing (Xing et al., 2009a, fig. 4) does not adequately represent the morphology of the holotype, giving it the exaggerated impression of a large heel pad that is not connected to digit IV.

As is the case with so many Chinese Jurassic theropod tracks, as admitted by Xing et al. (2009a), synonymy is likely: some have proposed synonymy of *Changpeipus* with *Grallator* (Gierliński, 1994). However, for clarification, we note that the synonymy in this case is with *Grallator sensu lato*, which includes *Eubrontes* (Gierliński, 1994). Bearing in mind that *Changpeipus* cannot be synonymized with the later-named *Kayentapus* (Welles, 1971), both because of publication order and because it differs morphologically, it could be considered a synonym of *Eubrontes*. As argued by Gierliński (1994) and reiterated by Lockley et al. (2003), Lockley and Matsukawa (2009), and Xing et al. (2009a), the larger, Early–Middle Jurassic theropod tracks from China cannot be distinguished from *Eubrontes*, or in some cases *Kayentapus*, without resorting to finely delimited, qualitative distinctions, mostly minor digit divarication

angles that may well be attributable to foot-substrate interactions and/or differences in track maker behavior. Attempts to quantify the differences, based on the most rudimentary measurements (footprint length and width) result only in scatter diagrams in which data for each ichnotaxon overlaps with the next, revealing no meaningful morphological distinctions, statistical or otherwise (Lu et al., 2007; Xing et al., 2009a).

Another example of this same kind of problem is *Lufengopus dongi* (Lü et al., 2006), a relatively poorly preserved, isolated track that yielded only one measurement that appears to plot along the same regression line as various other theropod tracks, including *Grallator* and *Eubrontes*. Lü et al. (2007) subsequently plotted *Changpeipus xuiana* on the same graph; it, too, fell within the same field as *Eubrontes*. Neither of these ichnospecies therefore has diagnostic characters that can distinguish them from well-established ichnotaxa, such as *Eubrontes* and *Grallator*.

In summary, with the exception of the probable crocodylian track *Kuangyuanpus* (Young, 1943), the *nomen dubium* *Sinoichnites*, the ornithischian track *Shenmuichnus*, and *Shensipus* (a distinctive and possibly valid ichnotaxon of uncertain affinity), all of the other Early and Middle Jurassic ichnotaxa from China can be assigned to one of only five ichnogenera: *Changpeipus*, *Grallator*, *Eubrontes*, *Kayentapus*, or *Gigandipus*. This simplification brings the Chinese ichnofauna into line with those reported from other parts of the world (reviewed by Lucas, 2007).

2.3 Late Jurassic Ichnospecies

Three dinosaurian ichnospecies have been reported from the Upper Jurassic of China. These are, in the historical order of naming, *Yangtzeipus yipingensis* (Young, 1960; Zhen et al., 1986), *Jialingpus yuechiensis* (Zhen et al., 1983), and *Huanglongpus shengouensis* (Yang and Yang, 1987) (Fig. 3). *Yangtzeipus yipingensis* (Young, 1960) is based on an elongate, tridactyl type specimen that has minimal divarication angles between the digit traces, and has a purported digital pad formula of 2-3-3. Based on the illustrations Young (1960) provided, a formula of 2-3-4 could as easily be inferred, indicating a theropod track maker. Young (1960) also claimed to see “coarsely granulated” skin impressions, although we have been unable to confirm this observation. He also claimed that one of the two other, smaller specimens, although seriously damaged, was certainly a manus trace. This, in turn, suggested to Zhen et al. (1989) that the track might be of ornithopod affinity. However, little, if any, evidence supports this interpretation, and we infer that the type pertains to a bipedal theropod, and that the paratypes have

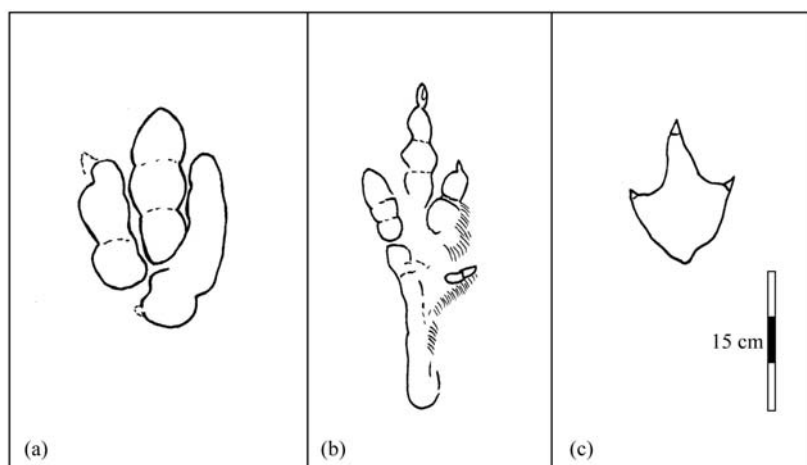


Fig. 3. Late Jurassic theropod tracks of China.

(a), *Yangtzeopus yipingensis* (Young, 1960); (b), *Jialingpus yuechiensis* (Zhen et al., 1983); (c), *Huanglongpus shengouensis* (Yang et al., 1987).

uncertain relationships to the holotype. *Yangtzeopus* has a “fleshy” or well-padded appearance somewhat reminiscent of *Therangospodus*, an Upper Jurassic ichnogenus known from Europe and North America (Lockley et al., 2000) that has recently also been reported from China (Xing et al., 2011a). Because it is based on well-preserved material, and morphological characteristics, (thick, “fleshy” digit traces and low digit divarication angles), *Yangtzeopus* is retained here as a valid ichnotaxon.

Jialingpus is the most distinctive Late Jurassic track reported from China. It is based on a sample of well-preserved natural casts that have well-defined digital pad impressions, reminiscent of *Grallator*; this is true even for an unusual specimen that has a well-defined hallux and metatarsal trace. Because of the hallux and metatarsal trace, Zhen et al. (1989) compared *Jialingpus* to *Anomoepus* and placed it in the ichnofamily Anomoepodidae (Lull, 1953), but without explicitly stating that the tracks were of ornithischian affinity (Lockley and Gillette, 1989). At that time, few theropod tracks with metatarsal and hallux traces had been reported, whereas now they are much better known (Lockley et al., 2003; Gierliński et al., 2009). The anomoeopodid attribution is almost certainly incorrect, as already stated by Lockley et al. (2003), and we infer the ichnogenus pertains to a theropod track maker. Its distinctive morphology of well-preserved pads and hallux and metatarsal traces indicates that *Jialingpus*, is *Grallator*-like. Like so many theropod tracks discussed here, it is in need of detailed comparison with other ichnotaxa, and pending such an analysis, we retain it as valid here. We emphasize that *Grallator* cannot be ruled out as the appropriate ichnotaxon for these specimens solely based on their Late Jurassic age: *Grallator* tracks have also been

reported from Lower Cretaceous strata, especially in China (see below). But more importantly, ichnotaxa are diagnosed by morphological features, not ages or presumed track maker affinities.

Huanglongpus shengouensis (Yang and Yang, 1987) is based on a poorly preserved, elongate, tridactyl track that is 16 cm long. It has sharp claw traces (Yang and Yang, 1987, fig. 19), but lacks diagnostic pad traces. The poor quality of preservation renders *Huanglongpus* a *nomen dubium*.

2.4 Revised Tetrapod Ichnotaxonomy for the Jurassic of China

Aside from the crocodylian *Kuangyuanpus*, the ornithischian *Shenmuichnus* and *Sinoichnites*, and the unassigned *Shensipus*, all other Jurassic ichnotaxa from China that are not *nomina dubia* pertain to theropods. Only three of these ichnospecies were originally placed in non-endemic ichnogenera (*Grallator limnosus*, *Eubrontes platypus*, and *Kayentapus hailuensis*). We conclude that only five theropod ichnogenera are valid and useful for describing Chinese theropod tracks from the Early and Middle Jurassic: *Eubrontes* and *Grallator* (both of which are relatively ubiquitous), *Kayentapus* and *Gigandipus* (which are less common but still known across much of the Northern Hemisphere), and *Changpeipus*, which may be a senior subjective synonym of *Kayentapus*. If further study supports this latter synonymy, the ichnogenetic diversity would shrink further from five to four. Two Late Jurassic theropod ichnogenera that we provisionally retain are the *Therangospodus*-like *Yangtzeopus* and the *Grallator*-like *Jialingpus*. The only well-defined, non-theropod tracks from the Early and Middle Jurassic of China are *Shenmuichnus* and *Kuangyuanpus*, respectively of ornithischian and crocodylian affinities. Four other ichnogenera and ichnospecies constitute *nomina dubia*. Thus, the previous diversity of 28 endemic Chinese Jurassic tetrapod ichnospecies in 23 ichnogenera (excluding non-endemic *Eubrontes platypus*) reduces to only 10 ichnogenera of which seven represent theropods. Sixteen of the 24 unequivocal theropod ichnospecies (~67%) are accommodated in just three ichnogenera (seven in *Eubrontes*, excluding *E. platypus*, four in *Grallator*, and five in *Kayentapus*). All of the ichnogenera compare favorably to other Jurassic ichnogenera from other continents, enhancing their utility for various paleobiological and paleobiogeographical comparison and analyses.

2.5 Cretaceous Ichnospecies: General Comments

Thirty-four tetrapod ichnospecies assigned to 30 ichnogenera have been named from the Cretaceous of China. Of these, 32 pertain to dinosaurs, seven of which are birds, and one each to a pterosaur and a crocodylian. The majority of these 34 are Early Cretaceous in age, but the exact ages of some are uncertain. For this reason, the following descriptions are generally presented in the historical order in which they were described, and readers interested in age estimates should consult the original sources we cite.

2.6 Early Cretaceous Ichnospecies

The first named Cretaceous ichnospecies in China was *Jeholosauripus s-satoi* (Yabe et al., 1940) which at the time was thought to be pre-Cretaceous in age (Fig. 4). The ichnospecies, later renamed *Grallator ssatoi* (the

ichnospecies name emended to reflect the International Code of Zoological Nomenclature dictum against punctuation marks in names) by Zhen et al. (1989), originated from the Tuchengzi Formation, a unit considered Late Jurassic through basal Cretaceous in age, in Liaoning Province. More than 1000 tracks have been documented at the site from which the holotype of *G. ssatoi* came (Matsukawa et al., 2006). Whether or not *G. ssatoi* is readily distinguishable from other *Grallator* ichnospecies remains unclear. However, the synonymy of this ichnotaxon with *Grallator* seems reasonable and uncontroversial on morphological grounds.

Despite the large number of theropod tracksites described from Liaoning Province, few have yielded track assemblages different from those described by Yabe et al. (1940). Although a few theropod tracks from these sites have recently been attributed to previously described

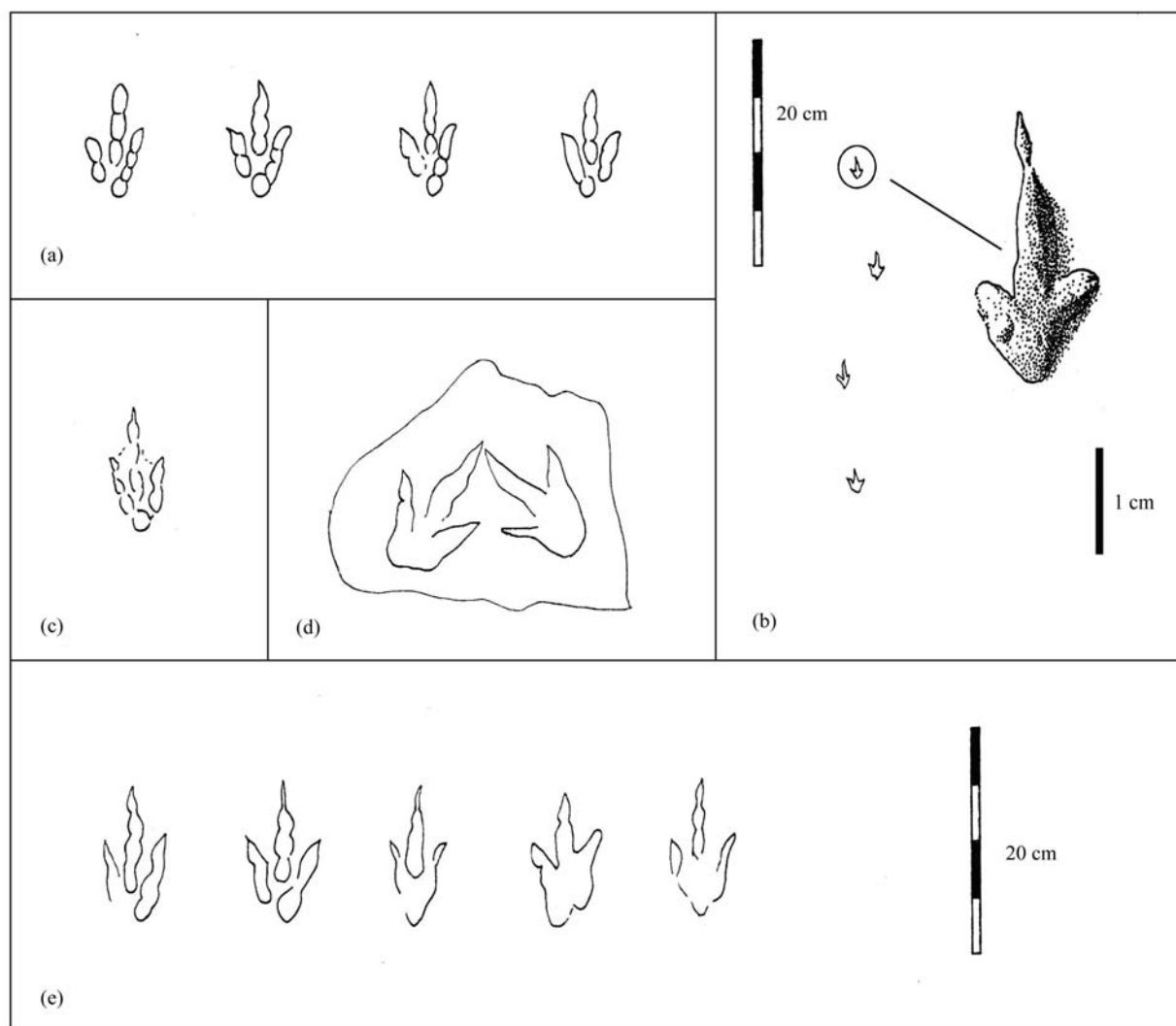


Fig. 4. Grallatorid tracks from the Cretaceous of China.

(a), *Grallator ssatoi* topotypes from Liaoning, (b), *Grallator emeiensis* from Sichuan (after Zhen et al., 1994; Matsukawa et al., 2006); (c), *Paragrallator masiengensis* from the Late Triassic of Lesotho, southern Africa (after Ellenberger, 1972); (d), type specimen of *Paragrallator yangi* (after Lockley et al., 2012), herein referred to *Grallator yangi* comb. nov.; (e): Grallatorid tracks referred to *Paragrallator* by Lockley et al. (2012), referred herein to *Grallator yangi* comb. nov. All tracks drawn to same scale except for detail of *G. emeiensis*.

ichnotaxa, such as *Therangospodus* and *Megalosauripus* (Xing et al., 2011a), only one additional ichnotaxon has been named: *Menglongipus sinensis* (Xing et al., 2009b). *M. sinensis* is based on a poorly preserved trackway of a purportedly didactyl (deinonychosaurian) theropod. Although individual tracks are difficult to distinguish from poorly preserved tridactyl tracks, as admitted by Xing et al. (2009b), the occurrence of a trackway sequence of didactyl traces is sufficient evidence for us to retain this name, at least provisionally.

After *Grallator ssatoi*, the next tetrapod ichnotaxon named was *Laiyangpus liui* (Young, 1960), which was initially interpreted as a theropod track but later reinterpreted as of crocodylian affinity (Lockley et al., 2010). Unfortunately, the type specimen of *L. liui* is lost, so the degree to which it is diagnostic can only be gauged with uncertainty through published photographs and descriptions.

Zeng (1982a, b) reported three new ichnospecies from a single slab from the Cretaceous Xiaodong Formation of Hunan Province (Fig. 5). The first of these, *Hunanpus jiuquwanensis*, is based on a moderately well-preserved, small theropod track similar to others found in situ at the type locality (Matsukawa et al., 2006, fig. 5). The other two tracks, *Xiangxipus chenxiensis* and *X. youngi* were assigned to the same ichnogenus, despite being rather different in appearance. *X. chenxiensis* is a slender-toed, tridactyl track with a wide total digit divarication that resembles a number of ichnotaxa assigned to the Ornithomimipodidae (Lockley et al., 2011b). The two consecutive *X. chenxiensis* tracks differ in mode of preservation, suggesting that while the first in the sequence is clearly tridactyl, the second in sequence, which is technically the type, appears tetradactyl, evidently due to one of the digits having left a double trace (Fig. 5). The differences between the larger *X. chenxiensis* and the smaller *X. youngi*, which also has wide digit divarication angles and wider or more robust digit traces, may be sufficient to place the latter form in a different ichnogenus. As noted below, *X. youngi* is similar in size and digit divarication to *Wupus agilis* (Xing et al., 2007), but even if this synonymy is demonstrable, the question of whether both *Xiangxipus chenxiensis* and *X. youngi* belong in the same ichnogenus is not resolved. However, none of the Hunan tracks are obvious synonyms of ichnotaxa named before 1982, and so the names provisionally stand, although they should be researched further.

Chen and Huang (1993) erected *Chuxiongpus changlinensis* and *C. zheni* for two morphologically similar, indifferently-preserved sauropod tracks from the Cretaceous of Yunnan (Fig. 5). Lockley et al. (2002)

considered *C. zheni* a synonym of *C. changlinensis* and further synonymized the ichnogenus with *Brontopodus*, producing *B. changlinensis* comb. nov. The track of a tridactyl biped named *Yunnanpus huangcaoensis* (Chen and Huang, 1993) is poorly preserved and must be considered a *nomen dubium*.

Zhen et al. (1994) reported an important Cretaceous ichnofauna from the Emei region of Sichuan Province that included four new tetrapod ichnospecies: *Velociraptorichnus sichuanensis*, *Minisauripus chuanzhuensis*, *Grallator emeiensis*, and *Aquatilavipes sinensis*, in addition to so-called *Iguanodon* track; the latter was later formally named *Iguanodonopus xingfuensis* (Zhen et al., 1996). *V. sichuanensis* and *M. chuanzhuensis* are highly distinctive and unlike anything previously reported. The former ichnospecies is universally accepted as the first track to have been correctly attributed to a functionally didactyl, deinonychosaurian theropod. *Minisauripus* was initially attributed to a small ornithopod, but it has since been interpreted as the track of a theropod (Lockley et al., 2008). *G. emeiensis*, mislabeled in the figure caption as *Neograllator emeiensis* (Zhen et al., 1994, fig. 3), is convincingly interpreted as a small theropod. However, *I. xingfuensis* is a poorly preserved, non-diagnostic theropod track, not an ornithopod track as the name and original interpretation proposed. It is here regarded as a *nomen dubium*, in agreement with Xing et al. (2009c). However, we do not agree with the latter authors that it can be transferred to *Iguanodontipus* (Sarjeant et al., 1998) either on the basis of morphology or historical priority. In our opinion, no more precise identification than “grallatorid indet.” is possible. The Emei avian track named *Aquatilavipes sinensis* is more similar to type *Koreanaornis* (Kim, 1969; Lockley et al., 1992; Lockley and Harris, 2010) than to type *Aquatilavipes*, and therefore has been transferred to *Koreanaornis sinensis* (Lockley et al., 2008, 2012).

The “grallatorid” track *Paragrallator yangi* (Li and Zhang, 2000; Li et al., 2002) from Shandong Province is problematic because it was named without reference to the grallatorid track *Paragrallator masiengensis* erected by Ellenberger (1972), albeit without a formal description (making it a *nomen dubium*). Xing et al. (2010) declared *P. yangi* a *nomen dubium*; Lockley et al. (2011) re-illustrated the type material and considered it in need of revision. Although the type specimen is not very well preserved, a large sample of very well-preserved tracks ascribed to *Paragrallator* was described from another Shandong locality (Zhucheng area) by Li et al. (2011). These authors also identified the new and highly distinctive theropod ichnospecies *Corpulentapus lilasia*

from the Zhucheng sample. In light of the “priority” of the *Paragrallator* as poorly applied by Ellenberger (1972), the name cannot be used as the ichnogenus to accommodate the *yangi* ichnospecies, which must either be moved to a suitable existing ichnogenus (e.g., *Grallator yangi*) or put in a new ichnogenus. Pending the results of an in-progress, further study of the abundant material from Shandong, we here make no recommendations regarding these options.

The Early Cretaceous bird track *Pullornipes aureus* (Lockley et al., 2006) from Liaoning Province (Fig. 6) is distinctive: its well-developed hallux, separate (non-connected) digit traces, long step, and slight inward rotation are unlike any avian ichnotaxon previously described, and therefore the ichnotaxon is treated here as valid. Despite the abundance of avian body fossils from Liaoning, this was the first avian ichnospecies named from this region. The

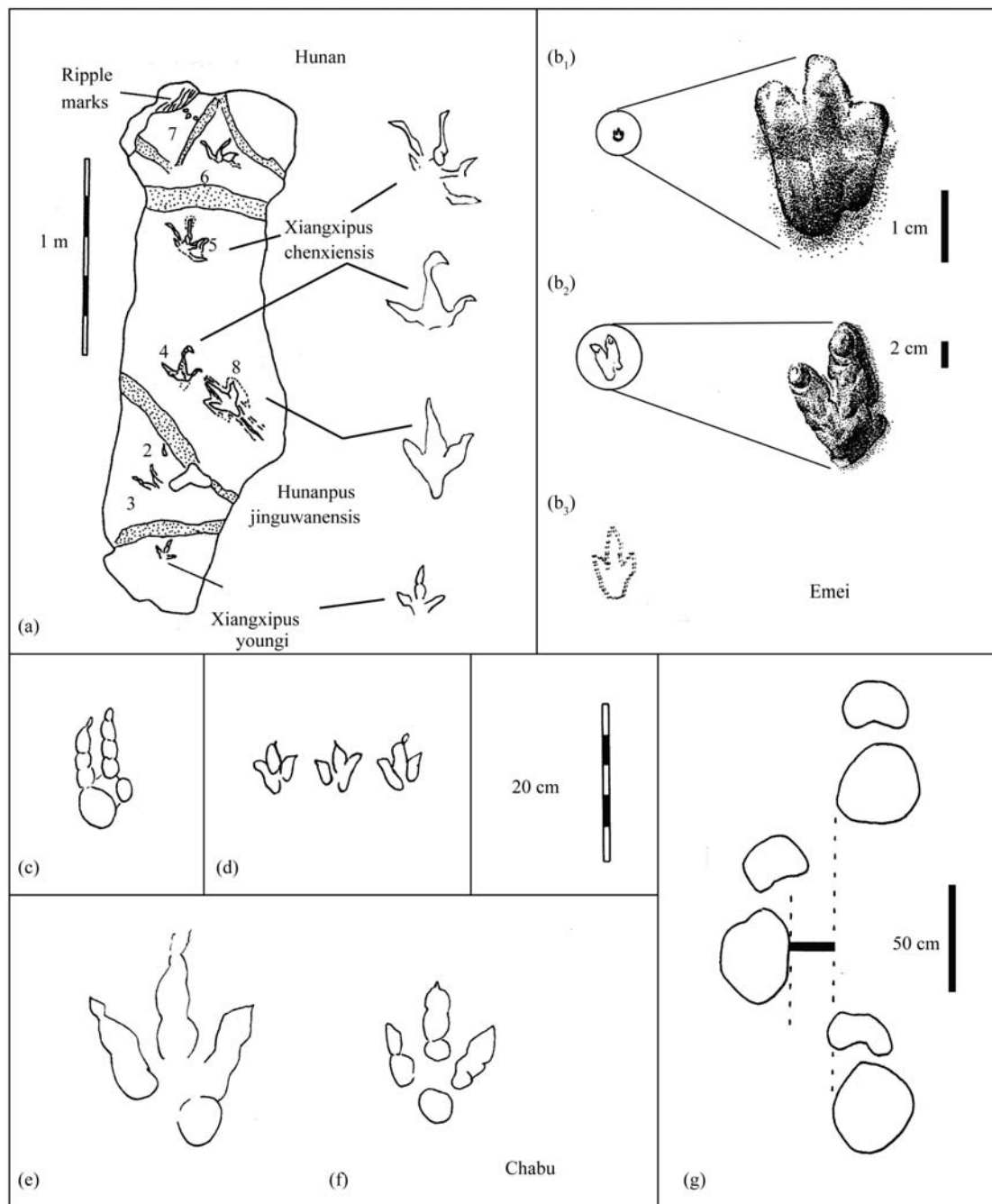


Fig. 5. Early Cretaceous tetrapod ichnofauna of China.

(a), the Hunan ichnofauna, comprising (1) *Xiangxipus chenxiensis* (Zeng, 1982a, b), (2) *Xiangxipus youngi* (Zeng, 1982a, b), and (3) *Hunanpus jinguwanensis* (Zeng, 1982a, b); (b), The Emei ichnofauna, comprising (1) *Minisauripus chuanzhuensis* (Zhen et al., 1994), (2) *Velociraptorichnus sichuanensis* (Zhen et al., 1994), and (3) *Iguanodonpus xingfuensis* (Zhen et al., 1996); (c), *Dromaeopodus shandongensis* (Li et al., 2008); (d), *Corpulentapus lilasia* (Li et al., 2011); (e), *Chapus lockleyi* (Li et al., 2006); (f), *Asianopodus robustus* (Li et al., 2011) from the Chabu ichnofauna; (g), *Brontopodus changlinensis* (Lockley et al., 2002).

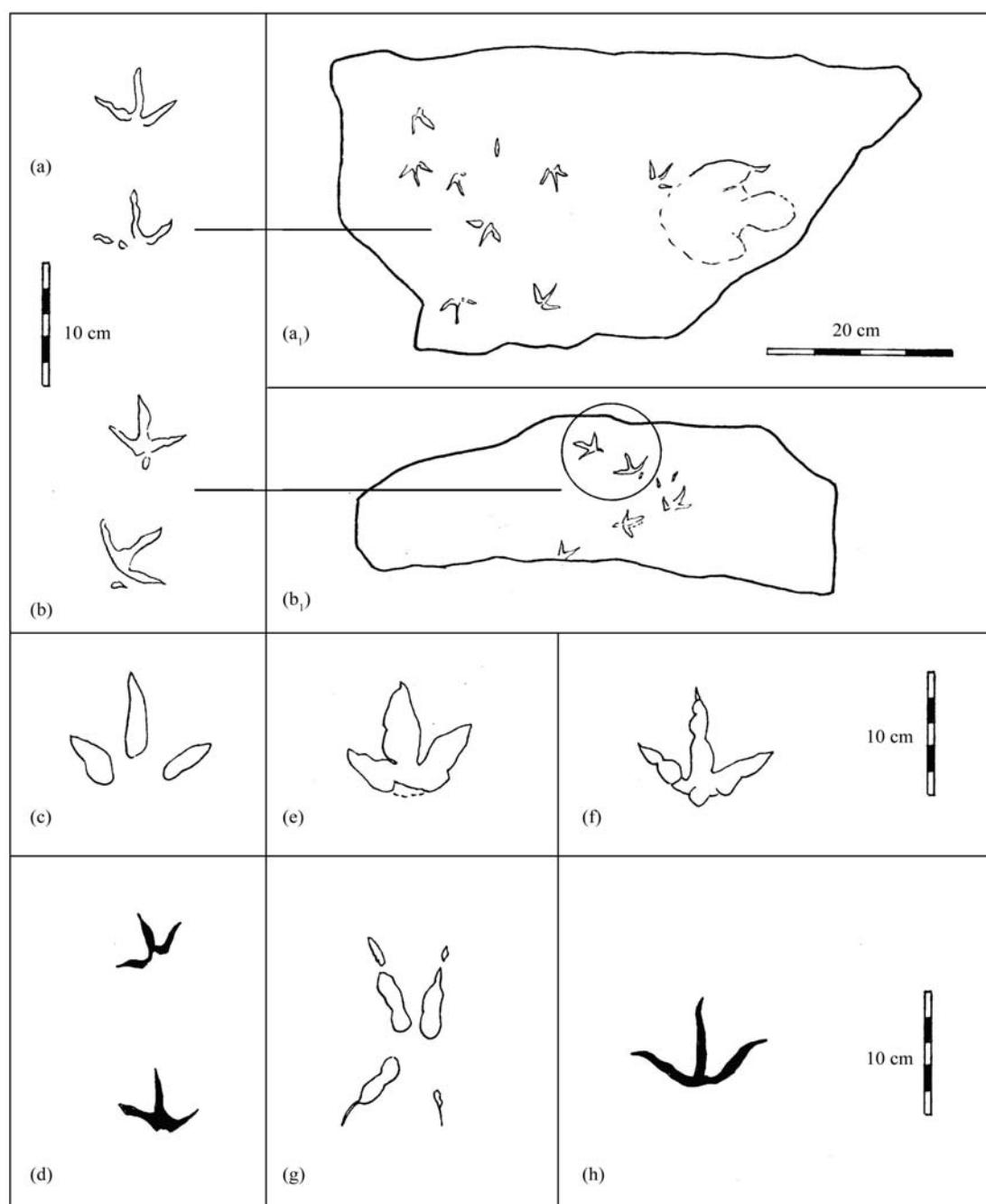


Fig. 6. Bird tracks from the Cretaceous of China.

(a), *Koreanaornis sinensis*, comb. nov. (modified after Matsukawa et al., 2006); (b), *Koreanaornis anhuiensis* comb. nov.; (c), *Koreanaornis dodsoni* (after Xing et al., 2011); (d), *Koreanaornis hamanensis* topotypes from the Early Cretaceous of Korea for comparison with a–c; (e), *Moguiornipes robusta* (after Xing et al., 2011); (f), *Shandongornipes muxiai* after Li et al., 2005; (g), *Aquatilavipes swiboldae* (Currie, 1981) from the Early Cretaceous of Canada for comparison with a–f.

new ichnospecies *Pteraichnus yanguoxiaensis* (Peng et al., 2004) described from the Early Cretaceous of Hekou Group of Gansu Province, was the first pterosaurian ichnotaxon described from China, but is difficult to distinguish from other ichnospecies of *Pteraichnus* (Lockley and Harris, in press). Recently, another ichnospecies from Gansu, the third deinonychosaurian ichnotaxon known from China, was named *Dromaeosauripus yongjingensis* (Xing et al., in

press). Another highly distinctive bird track, *Shandongornipes muxiai* (Li et al., 2005; Lockley et al., 2007) was reported from a site in the Junan area of Shandong Province that also yielded the large, highly-distinctive, and well-preserved, dromaeosaurid track *Dromaeopodus shandongensis* (Li et al., 2008), a new ichnospecies of *Minisauripus*, *M. zhenshounani* (Lockley et al., 2008), and large ornithopod tracks (cf.

Ornithopodichnus).

New ichnospecies have also been reported from the Early Cretaceous of Nei Mongol, including the large theropod track *Chapus lockleyi* (Li et al., 2006), the theropod track *Asianopodus robustus* (Li et al., 2011), and the bird track *Tatarornipes chabuensis* (Lockley et al., 2012), all of which are herein retained as valid.

Most recently, Xing et al. (2011b) reported a bird-dominated ichnofauna in the Tugulu Group of Xinjiang Province associated with tracks assigned to existing theropod ichnogenera (*Asianopodus*, *Kayentapus*, and cf. *Jialingpus*). In addition, these authors erected two new avian ichnospecies: *Koreanaornis dodsoni* and *Moguornipes robusta*. *K. dodsoni* is somewhat larger than other ichnospecies assigned to *Koreanaornis* (Fig. 6). Size is generally a weak character on which to base an ichnotaxonomic diagnosis, and it may be that the ichnospecies belongs in a different combination, e.g., *Aquatilavipes dodsoni*. However, until further work is completed, the *K. dodsoni* is provisionally regarded as a distinct ichnotaxon. *M. robusta*, as the name suggests, has unusually wide digit traces, which arouses suspicion that extramorphological factors may have played a role in the preservation of the tracks. Such variation was examined in detail in the description of *Tatarornipes* from Nei Mongol (Lockley et al., 2012). Pending further investigations, we consider *M. robusta* provisionally valid.

2.7 “Middle” and Late Cretaceous Ichnospecies

Based on current age assessments, the 27 Chinese type ichnospecies discussed in the previous section are all Early Cretaceous in age. The remaining six Cretaceous ichnotaxa are “middle” or Late Cretaceous.

Xing et al. (2007) named four new ichnospecies from the “middle” Cretaceous Jiaguan Formation of Chongqing. These tracks were illustrated with only line drawings, not photographs, and are therefore difficult to assess (Fig. 7). These named ichnotaxa comprise *Wupus agilis*, attributed

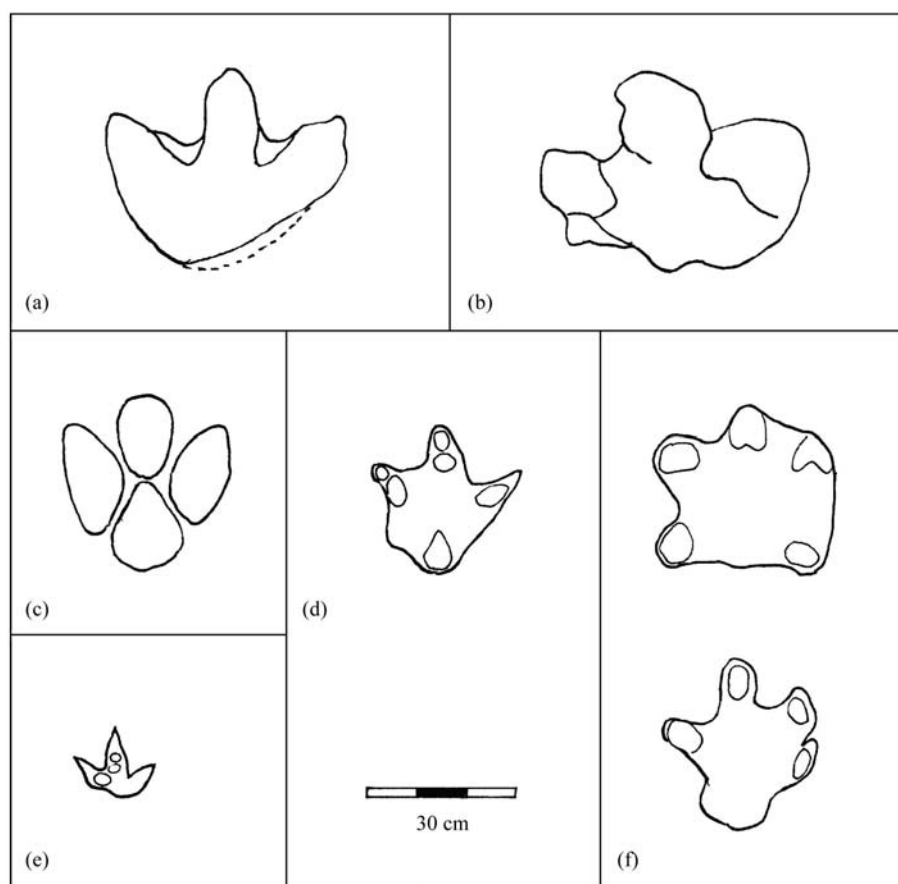


Fig. 7. Tracks assigned to Ornithischia and Theropoda from the Cretaceous of China.

(a), *Jiayinosauropus johnsoni* (Dong et al., 2003); (b), *Hadrosauropodus nanxiongensis* (Xing et al., 2009); (c), *Caririchnium lotus* (Xing et al., 2007); (d), *Laoyingshanpus torridus* (Xing et al., 2007); (e), *Wupus agilis* (Xing et al., 2007); (f), *Qijiangpus sinensis* (Xing et al., 2007). See text for discussion of the affinities of *W. agilis* and *Q. sinensis*.

to a theropod, and *Laoyingshanpus torridus*, *Caririchnium lotus*, and *Qijiangpus sinensis*, all attributed to ornithischians. *W. agilis* is a small but abundant tridactyl track with a long step and wide digit divarication (Wang 2012) that as noted above, could be tentatively compared with *X. youngi* from Hunan Province. *L. torridus*, a functionally tridactyl track with a poorly defined trace of a hallux, appears to be another *nomen dubium*. *C. lotus*, the best-preserved and most abundant track type at the site, pertains to a facultatively quadrupedal ornithopod. The tridactyl pes prints possess the quadripartite pes print morphology typical of the ichnogenus, and smaller manus prints, similar to those of type *Caririchnium leonardii* from Colorado (Lockley, 1987; Lockley et al., 2001). Lastly, *Q. sinensis* was described as the track of an ankylosaur with a tetradactyl manus and a pentadactyl pes. The tracks are poorly preserved and a clear trackway configuration was not reported. The ichnotaxon appears to have no diagnostic features and, based on a re-examination of the type by two of us (MGL and XL) in 2012, we regard it as a *nomen dubium*, as noted below.

A new avian ichnospecies, *Aquatilavipes anhuiensis*, was briefly described (with minimal information) from the Late Cretaceous of Anhui Province (Jin and Yan, 1994). As with the aforementioned Sichuan ichnospecies of *Aquatilavipes*, it is unlike type *Aquatilavipes*, in revealing a small hallux trace (Fig. 6), and we herein transfer it to *Koreanaornis anhuiensis* comb. nov.

Large ornithopod tracks from the Late Cretaceous of Heilongjiang China formed the basis for *Jiayinosauropus johnsoni* (Dong et al., 2003); similar tracks from southern China were named *Hadrosauropodus nanxiongensis* (Xing et al., 2009c) because of their similarity to *Hadrosauropodus langstoni* (Lockley et al., 2004). *H. nanxiongensis* tracks are not well-preserved, although they occur in a trackway. *Jiayinosauropus* is similar to *Hadrosauropodus*; if congeneric, then *Jiayinosauropus* has nomenclatural seniority. However, as pointed out by Xing et al. (2009c) the posterior margin of *Jiayinosauropus* tracks are not clearly defined, rendering diagnostic characteristics difficult to ascertain. In contrast, the type of *H. langstoni* is well preserved, even displaying skin impressions. We provisionally retain *Jiayinosauropus* here as valid pending further investigation.

2.8 Revised Tetrapod Ichnotaxonomy for the Cretaceous of China

In contrast to type Chinese Jurassic ichnotaxa, type Cretaceous ichnotaxa have been named rather more judiciously. We contend that six highly distinctive, well-preserved forms—*Velociraptorichnus*, *Minisauripus*, *Shandongornipes*, *Pullornipes*, *Dromaeopodus*, and *Corpulentapus*—are impossible to assign to any previously established ichnotaxon. In addition, 13 Chinese Cretaceous ichnospecies have been erected in previously established ichnogenera: *Aquatilavipes* (two ispp.), *Asianopodus*, *Brontopodus* (two ispp. referred), *Caririchnium*, *Grallator* (two ispp.), *Hadrosauropodus*, *Koreanaornis*, *Minisauripus*, *Dromaeosauripus* and *Pteraichnus*. Some of these might be subjective junior synonyms of existing ichnospecies, but they otherwise appear secure in the ichnogenera to which they are currently assigned.

Fifteen other ichnotaxa (Table 1) are more problematic. Of these, *Paragrallator* needs to be assigned to either a new or an existing ichnogenus (possibly *Grallator*) because the ichnogenoholotype is a *nomen dubium*. We also consider *Qijiangpus sinensis* a *nomen dubium*. Two of the present authors (MGL and LX) reexamined the type tracks (purported manus and pes) and regard them as poorly preserved, compound tracks made by ornithopods.

The Chinese ichnospecies *Iguanodonopus* is a *nomen dubium*, as are the ichnogenera *Yunnanpus* and

Laoyingshanpus, all due to poor preservation that make identifying diagnostic characters impossible. Leaving aside the type of *Laiyangpus*, which is lost (Lockley et al., 2010), seven ichnogenera and ichnospecies—*Xiangxipus* (two ispp.), *Hunanpus*, *Jiayinosauropus*, *Chapus*, *Tatarornipes*, and *Moguornipes*—are provisionally regarded as valid. However, we suspect that several of these ichnotaxa will require detailed ichnotaxonomic analysis, comparative study, and/or revision in the near future.

As is the case with Jurassic theropod ichnotaxa, differentiating many Cretaceous theropod track ichnotaxa is equally challenging. For example, although globally ubiquitous Early Jurassic forms, such as *Grallator* and *Eubrontes*, are less commonly reported from the Cretaceous, legitimate Cretaceous examples of *Grallator* have been most confidently identified from China, where it is remarkably abundant (Matsukawa et al., 2006). If the mislabeled *Paragrallator* and the grallatorid morphotype *Hunanpus* genuinely are synonyms of *Grallator*, the abundance of *Grallator* in the Cretaceous of China is particularly striking and reduces the apparent global ichnodiversity among Cretaceous theropod tracks. This raises the question as to whether other Jurassic theropod ichnotaxa, such as *Eubrontes*, *Kayentapus*, or *Changpeipus*, are represented in the Cretaceous. It would be constructive, for example, to compare *Chapus* with such Jurassic ichnotaxa. As noted below, the differentiation of non-avian theropod and non-theropod ichnotaxa is less problematic.

3 Discussion and Synthesis

Chinese Mesozoic tetrapod track types have been placed into 63 ichnospecies (one Triassic, 28 Jurassic, and 34 Cretaceous), exclusive of other non-type ichnospecies or ichnotaxa identified from China. Fifty-two (~83%) of these 63 tetrapod ichnospecies were placed in monospecific ichnogenera. Of the 29 Triassic and Jurassic ichnospecies, one track pertains to a crocodylian and two pertain to ornithischian dinosaurs; all the rest (~89%) pertain to non-avian theropods. As has been noted previously, most of these ichnospecies are subjective junior synonyms of various *Grallator* ispp. and *Eubrontes* ispp.; many are best considered synonymous at the ichnogeneric level. Two of the 34 Cretaceous ichnospecies pertain to non-dinosaurs (a crocodylian and a pterosaur); the remaining 32 pertain to dinosaurs, of which 18 (~56%) pertain to non-avian theropods and seven (~22%) to avian theropods (birds). The remaining seven (~22%) pertain to sauropods and ornithischians.

Of the 63 Chinese Mesozoic tetrapod ichnospecies, 53

(~84%) pertain to dinosaurs, and all but 10 to non-avian theropods. Nine of these 10 are Cretaceous in age, and seven of them pertain to birds. Fewer Chinese Cretaceous ichnospecies are obvious *nomina dubia* or subjective synonyms, in sharp contrast to the situation in the Jurassic. Nevertheless, Chinese dinosaur ichnotaxa are oversplit, so making objective decisions about which ichnotaxa are obvious subjective synonyms or *nomina dubia* is difficult without familiarity with the type specimens and both the relevant Chinese and non-Chinese literature. However, the authors of this paper have collectively seen all the type material (except for two holotypes that are lost), in order to arrive at the ichnotaxonomic revisions presented above. At the ichnogenus level, we prune (either by recognizing *nomina dubia* or by synonymy) 17 from the list of 53 dinosaurian ichnogenera (a 32% reduction), leaving 36 valid ichnotaxa. Most of the cuts affect Jurassic ichnotaxa, which are reduced from 23 to only nine. Ichnospecies differences arguably are subtle, so we provisionally retain ichnospecies as valid pending detailed analyses of differences between congeneric ichnospecies. Such a synthesis is long overdue and is necessary to address the problems of historical and provincial ichnotaxonomy, which severely hamper comparisons of tetrapod ichnofaunas in space and time. Identification of such provincial ichnotaxonomic practices strongly cautions against the casual introduction of new names, especially when the workers erecting such ichnotaxa fail to make sufficient comparisons to other published ichnotaxa and/or properly account for foot–substrate interactions and other extramorphological phenomena. We would also advise against using very slight or subtle differences (e.g., small differences in digit divarication angles), that other workers would not also recognize, as the basis for ichnotaxonomic distinctions, especially in the case of small samples.

Of the 63 type tetrapod ichnospecies hitherto identified from the Mesozoic of China, 10 are *nomina dubia*. Of the valid ichnospecies, 37 pertain to non-avian theropods and another seven to avian theropods (birds). This high proportion appears to indicate a genuine abundance of non-avian theropod footprints in the Chinese track record. However, the sheer abundance of such tracks does not necessarily equate to a comparably high ichnodiversity. Despite the relatively conservative nature of the theropod foot, which would logically translate to low ichnotaxonomic diversity, Chinese theropod ichnotaxonomy has historically, but counterintuitively, suggested an apparently high ichnodiversity. As demonstrated particularly in the Jurassic, this apparent high diversity is an artifact of provincial ichnotaxonomy and, as a result, “splitting” single morphologies into numerous ichnotaxa in need of comprehensive revision.

Recent studies (e.g., Gierliński, 1994; Lockley et al., 2003; Lockley and Matsukawa, 2009; Xing et al., 2009a) have taken small steps in this direction. With this in mind, and with the modern ease of access to global ichnologic literature, we therefore appeal to ichnotaxonomists (in China and elsewhere) to exercise caution and restraint when erecting new ichnotaxa. New ichnotaxa (1) should always be based on (preferably multiple) examples of well-preserved, morphologically distinct specimens, and (2) require detailed description, illustration, and thorough, comprehensive comparisons to existing ichnotaxa from all continents and from all time periods (q.v., Sarjeant, 1989). Adherence to this practice avoids ichnotaxa that are either obvious synonyms of existing ichnotaxa, poorly preserved, and/or otherwise undiagnostic. Such ill-conceived ichnotaxa are essentially useless because they hinder understanding of regional and global ichnological trends through time.

The need to conduct careful comparative analyses reminds us that there are a few tetrapod ichnotaxa (ichnogenera and ichnospecies) reported from China that are not endemic types cited herein (Table 1). These include representatives of the ichnogenera *Chirotherium* isp. from the Triassic (Lü et al., 2004), *Anomoepus* (Lockley and Matsukawa, 2009) and *Eubrontes* (Zhen et al., 1986) from the Early Jurassic, *Therangospodus* isp. and *Megalosauripus* isp. from the Late Jurassic (Xing et al., 2011a), *Anchisauripus* from near the Jurassic–Cretaceous boundary (Sullivan et al., 2009), and *Dromaeosauripus* (Xing et al., in press) from the Early Cretaceous. This increases the estimated 35 valid endemic tetrapod ichnogenera reported from the Mesozoic of China by adding about 20% to a combined total of 42 endemic and non-endemic ichnogenera.

New discoveries and further, careful study of Chinese tetrapod ichnotaxa will doubtlessly change these ichnotaxonomic lists and diversity estimates. We recognize that our study is a preliminary synthesis, and that a large part of ichnotaxonomy involves the investigation of subjective synonymies. Therefore, investigating the validity of most ichnospecies is beyond the scope of this paper; similarly, evidence of their variability, if available, is likewise not analyzed, largely because many ichnospecies are based on very small samples. However, as shown above, investigation of Chinese ichnotaxa at the ichnogenus level reveals that a substantial number are morphologically indistinguishable from well-known ichnogenera from other regions that, in most cases, have nomenclatorial priority. Assigning these ichnospecies to appropriate ichnogenera, creating new combinations, is thus relatively easy. In cases where poor preservation (or incorrect morphological interpretation) of

ichnotypes is clearly demonstrable, ill-conceived ichnotypes can be declared *nomina dubia*. As noted above, such weeding out of invalid names is essential to enable progress toward more standardized and useful ichnotaxonomies. As Lucas (2007) suggested, this may involve recognizing that, in the majority of cases, ichnogenera are the most useful “units of currency” for comparative morphology and correlation because differentiating ichnospecies within given ichnogenera is highly subjective, both for specialist and non-specialist ichnologists. Moreover, current literature provides many examples of ichnogenus-level correlations (Lucas, 2007 and references therein), but few, if any, useful or convincing examples of widely used ichnospecies-level correlations, even at the local or regional level. The aim of a more standardized consensus in naming ichnotaxa—beginning, as attempted here, at the ichnogenus level—can only be achieved by imploring vertebrate ichnologists to conduct careful comparative analyses and name new ichnotaxa judiciously and without unwarranted provincial bias.

4 Conclusions

Although this study is preliminary, it is nevertheless sufficiently broad in scope to reach some tentative, quasi-quantitative conclusions regarding both apparent and real Chinese tetrapod ichnodiversity:

(1) The total number of valid Triassic through Cretaceous type ichnogenera from China can be reduced by 35% from 54 to 35. This reduction is quite conservative because it provisionally retains some questionable ichnogenera that are in need of further study.

(2) Seven additional tetrapod ichnogenera based on non-endemic ichnites, named outside China, increases total ichnogenus diversity to 42.

(3) The Chinese Triassic tetrapod track record is sparse, with only one type ichnospecies reported, which is treated as valid herein.

(4) The Jurassic track record reduces, by ~57%, from an initial, perceived ichnogenetic diversity of 23 to 10 ichnogenera of global (or, at least widespread) distribution. This marked reduction in provincial ichnogenera from the Jurassic reflects the general global uniformity of Jurassic ichnofaunas and the widespread distribution of *Grallator*–*Eubrontes*-dominated assemblages (Lucas, 2007), as is expected from greater paleogeographic uniformity in the Jurassic.

(5) The Chinese Cretaceous track record required less drastic pruning than the Jurassic record: based on our analysis, the record reduces, by ~17%, from 30 to 25 ichnogenera by recognizing five *nomina dubia*. Of the

remaining 25 ichnogenera, ten are assigned to ichnogenera whose ichnogenoholotypes are specimens discovered outside China. The remaining 15 (60% of) Cretaceous ichnogenera first described in China appear genuinely endemic to either China or East Asia, and six of these are highly distinctive.

(6) The Cretaceous percentage of endemic ichnotaxa is not such a pronounced expression of provincial ichnotaxonomy as was the case with the Jurassic. Indeed, Cretaceous tetrapod ichnofaunas reflect greater endemism and are apparently more diverse than those from any other region.

(7) The historic practice of naming new provincial ichnotaxa, especially ichnogenera, without careful comparison to ichnofaunas from other areas, has produced far too many junior synonyms, especially in the Jurassic. The result has been serious obstruction of global correlations and comparative analyses.

(8) The present synthesis aims only to eliminate the most obvious ichnogenetic synonyms. Further analysis is necessary to assess the validity of individual ichnospecies.

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