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# 白垩纪四足动物足印的生物地层学、生物年代学与遗迹相①

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摘 要：从全球范围来看，白垩纪四足动物的足印多数是非鸟恐龙与鸟类留下的痕迹；少量足印来自翼龙、鳄鱼、龟、哺乳动物和其他四足动物。白垩纪的足迹化石以东亚(尤其是中国和朝鲜)和北美西部的最为人所知。南美(主要是阿根廷和巴西)也有一定数量广泛分布的足迹化石，欧洲、非洲与澳大利亚的白垩纪足迹组合则鲜为人知。以白垩纪四足动物的足印记录为基础，我们对两个全球足印生物年代重新进行了检查。早白垩世生物年代以蜥脚类与鸟脚类的足迹为特征。晚白垩世生物年代中的蜥脚类足迹较少，但是鸭嘴龙、暴龙和角龙的足迹增多了。另外，白垩纪足印化石的记录中记载了许多重要的生物地层学信息，如北美白垩纪中期蜥脚类恐龙的消失，以及白垩纪末恐龙的绝灭。越来越多来自东亚的白垩纪足印记录使我们对更精细的地方性白垩纪足印生物年代学有了初步印象。因此，以地方性四足恐龙(包括鸟类)遗迹属的地层分布为基础，可以识别出三个或四个足印生物年代。 种类丰富并具有地方性特色的东亚的白垩纪鸟类动物的遗迹群，可能指示白垩纪时东亚存在着一个独特而繁盛的鸟类动物群。以足印化石为基础的这一假说有待进一步的验证。

关 键 词：生物地层学，足印，四足动物，白垩纪，亚洲，北美洲，南美洲
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# CRETACEOUS TETRAPOD FOOTPRINT BIOSTRATIGRAPHY, BIOCHRONOLOGY, AND ICHNOFACIES

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**Abstract** The global record of Cretaceous tetrapod footprints is dominated by the tracks of non-avian dinosaurs and birds; fewer tracks are known of pterosaurs, crocodylians, turtles, mammals, and other tetrapods. The Cretaceous track record is best known from East Asia (especially China and Korea) and western North America. A moderately extensive record is also known from South America (primarily Argentina and Brazil), but Cretaceous track assemblages from Europe, Africa, and Australia are much more poorly known. Here, we re-examine two global footprint biochrons based on the Cretaceous tetrapod footprint record. An Early Cretaceous biochron is characterized by sauropod and ornithopod tracks. A Late Cretaceous biochron has fewer sauropod tracks but adds the tracks of hadrosaurs, tyrannosaurids, and

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ceratopsians. Furthermore, the Cretaceous footprint record documents many important biostratigraphic data points, such as the mid-Cretaceous extirpation of sauropod dinosaurs in North America and the terminal Cretaceous extinction of dinosaurs. A growing Cretaceous footprint record from eastern Asia also provides the first glimpse of a more refined, provincial Cretaceous footprint biochronology, in which three or four Cretaceous footprint biochrons based on the stratigraphic distributions of endemic theropod dinosaur (including bird) ichnogenera may be recognizable. The abundance and endemism of this east Asian Cretaceous avian ichnofauna may indicate that a unique and prolific avian fauna existed in eastern Asia during the Cretaceous, a footprint-based hypothesis that merits further testing.

**Key words** biochronology, footprints, tetrapoda, Cretaceous, Asia, North America, South America

## 1 Introduction

As noted by Lucas (2007), tetrapod footprints have a fossil record in rocks of Devonian–Neogene age, and they have a long tradition of use in biostratigraphy and biochronology that extends at least back to Marsh (1891), especially for the late Paleozoic and the Mesozoic Eras. Their uses in biostratigraphy and biochronology (palichnostratigraphy), however, are generally understood to be constrained by three principal factors: 1) the validity or invalidity of ichnotaxa, which is based on whether the tracks are true tracks that show reliable morphological correspondence with the feet of their track makers (bioichnotaxa) or unreliable tracks that are extramorphological variants and/or compromised by poor preservation, 2) relatively slow apparent evolutionary turnover rates, and 3) facies restrictions.

The tetrapod ichnology of the entire Cretaceous is too large a subject to be covered exhaustively in a single paper. We therefore focus the analysis presented herein on the distributions of Cretaceous tracks in space and time; within this age-constrained subset, we also limit our analysis to tracks that are sufficiently well preserved (factor [1]) to have useful ichnotaxonomic labels that help identify the distributions of their track makers with reasonable confidence and therefore provide reliable information on the affinities of those track makers. While various ichnotaxa may have slow apparent evolutionary turnover rates, when their biostratigraphic ranges are analyzed (factor [2])—for example, both outside and within the Cretaceous —distinctive ichnotaxa may nevertheless appear and disappear abruptly. Such changes require careful analysis to determine, if possible, whether the changes are evolutionary (factor [2]) or the results of facies succession changes (factor [3]).

Information pertaining to factor [3] may be of limited biochronological utility because instead of the same ichnotaxa appearing in different areas in rocks of the same age, thus allowing correlations, different ichnotaxa may appear in rocks of the same age due to facies differences. Nevertheless, facies-ichnofauna, or "ichnofacies", relationships are useful for paleoecology and ichnofacies analysis. Abrupt evolutionary turnovers and extinction events may also be recorded: for example, the extinctions at both the Triassic–Jurassic and Cretaceous-Paleogene boundaries involve faunal changes that also show up in the ichnological record (e.g., Lockley & Hunt, 1994a; Olsen et al., 2002; Lucas & Tanner, 2008). In the final analysis, the distributions of well-preserved Cretaceous tracks in space and time can be described with some confidence: however, the significances of such distributions in relation to evolutionary dynamics, paleoecology, facies or habitat preferences, and endemism are matters of interpretation, and we treat these areas of conjecture more tentatively.

As also noted by Lucas (2007), and strongly related to apparently slow rates of evolutionary turnover (factor [2]), tracks rarely can be assigned with any confidence to a genus or species known from the body-fossil record; at best, an ichnogenus can be assigned to a higher taxon that is based on body fossils. Ichnogenera thus necessarily have much longer temporal ranges, and, therefore, slower apparent evolutionary turnover rates, than do taxa based on body fossils. While such factors limit the utility of tracks in refining biochronologies, footprints are abundant and thus should record some trends. In some important stratigraphic units (e.g., the Cretaceous Dakota Group of the western USA), they provide the dominant or only evidence of vertebrates. In addition, while statements about the relatively long stratigraphic ranges of many ichnotaxa (factor [2]) may be generally true, a number of ichnotaxa have very limited distributions in space and time; whether these are the results of sampling limitations or genuine reflections of limited distributions due to endemism or evolutionary history is presently unclear. We address these alternate considerations in the analyses that follow.

The tetrapod footprint record is facies controlled to some degree—as repeatedly noted in the ichnological literature, tracks represent valuable, *in situ* records of animals associated with particular environments. They therefore have considerable paleoecological utility, which, in turn, has led to the concept of vertebrate (especially tetrapod) ichnofacies (Lockley et al., 1995; Hunt & Lucas, 2007a; Lockley, 2007). The thrust of this paper, as was that of Lucas (2007), is to identify some general, broadly-applicable distribution patterns of vertebrate ichnotaxa both in space and time and in relation to facies. However, we also examine these distribution patterns on finer, regional scales, and analyze the extent to which regional track distribution patterns conform to the larger biochronogical scheme of Lucas (2007).

While it is already clear that there were major changes in faunal and ichnofaunal distributions across the Jurassic–Cretaceous and Cretaceous–Paleogene boundaries that confirm the broader utility of their corresponding biochronogical boundaries, current evidence suggests variations in the distributions of Cretaceous tetrapod ichnofaunas that may reflect evolution, endemism, paleoecology, sampling bias, and other variables. Therefore, we emphasize the Cretaceous tetrapod track records for selected areas that have become relatively well known in recent years. These include western North America (Lockley & Hunt, 1995a), East Asia (Matsukawa et al., 2006b; Lockley & Matsukawa, 2009), Europe (Lockley & Meyer, 2000), and South America (Leonardi, 1994). For completeness, we include brief discussions of the poorly known Cretaceous track record in Africa and the sparse record from Australia (the only Mesozoic tracks thus far reported from Antarctica pertain to Early Triassic dicynodonts [Hunt & Lucas, 2007b; MacDonald et al., 1991]). Such regional-scale analyses allow us to determine the extent to which the biochrons of Lucas (2007) may be understood in more detail, and the extent to which new reports published since 2007 alter or modify the global picture.

As a framework, we refer to the Early Cretaceous and Late Cretaceous global ichnological biochrons identified (and numbered 12 and 13, respectively) by Lucas (2007), which were bracketed by the preceding Early and Middle–Late Jurassic biochrons (numbered 10 and 11, respectively) and the succeeding Paleogene biochron (number 14) in Lucas (2007). In stratigraphic order, these are:

Paleogene (14)
Late Cretaceous (13)
Early Cretaceous (12)
Middle–Late Jurassic (11)
Early Jurassic (10)

Lucas (2007) stated that his conclusions were "mostly negative" with respect to the biostratigraphic utility of footprints for correlation and biochronological zonation. However, he allowed that tracks have value in establishing biostratigraphic data points pertaining to the temporal dimensions of tetrapod evolution. He also stressed that, unlike invertebrate ichnology, which concerns itself with evidence of behavior and not the presences or absences of specific biological taxa, vertebrate ichnology treats tetrapod footprints as proxies of biological taxa, and therefore permits ichnologists to draw useful inferences from footprints about tetrapod distributions in time and space (Lockley, 1998). These inferences, in turn, permit biostratigraphic correlations; this practice has been referred to as "palichnostratigraphy" (Haubold & Katzung, 1978).

## 2 Jurassic footprint biostratigraphy and biochronology

In order to place the Cretaceous tetrapod track record in context, it is helpful to briefly review the Jurassic track record, which, as noted above, Lucas (2007) divided into the Early Jurassic (his biochron 10) and Middle–Late Jurassic (biochron 11).

The Early Jurassic biochron is largely synonymous with the classic tetrapod ichnofaunas of the Connecticut Valley (Hitchcock, 1858; Lull, 1953), characterized by *Grallator*, *Eubrontes*, *Anomoepus*, *Otozoum*, and *Batrachopus*, which distinguish the ichnofaunas from older, Triassic, chirotheriid-dominated ichnofaunas (Olsen, 1980; Haubold, 1984; Olsen & Baird, 1986;

Olsen & Padian, 1986; Silvestri & Szajna, 1993; Lockley & Hunt, 1995a; Szajna & Silvestri, 1996; Lockley & Meyer, 2000; Rainforth, 2003; Lucas et al., 2006). As Lucas (2007) pointed out, this *Grallator-Eubrontes-Anomoepus-Otozoum-Batrachopus* assemblage has a global distribution. Early Jurassic tetrapod footprint assemblages are theropod-dinosaur dominated, a fact that has some significance when comparing them with certain Early Cretaceous ichnofaunas (see below), especially those of East Asia (Matsukawa et al., 2006b).

The Middle–Late Jurassic biochron (sensu Lucas, 2007) is generally quite different from its predecessor in that most of the Early Jurassic ichnogenera (*Grallator*, *Eubrontes*, *Anomoepus*, *Otozoum*, and *Batrachopus*) become rare or are absent, and are replaced by two new kinds of tracks: sauropod tracks (e.g., *Brontopodus* and *Parabrontopodus*), which are rare or absent in most Early Jurassic ichnofaunas, and pterosaur tracks (*Pteraichnus*), which are unknown before the Late Jurassic. Thyreophoran tracks of likely stegosaurian affinity (*Deltapodus*) are also relatively common in the Middle–Late Jurassic but rare or absent in most Early Jurassic deposits. Few common, Middle–Late Jurassic ichnogenera are entirely unknown in the Early Cretaceous, although some Early Cretaceous ichnogenera have not been identified in the Middle–Late Jurassic. Ostensibly, this indicates that the track record more reliably documents the appearance of new track-making taxa rather than the disappearance of older track makers (or older pedal morphologies).

## 3 Overview of the global Cretaceous track record

### 3.1 Introduction

In order to compare our analysis of Cretaceous ichnofaunas with that of Lucas (2007), we briefly review his main points and add new information published since 2007 (see Appendix). Again, for consistency, we treat the Early and Late Cretaceous ichnofaunas separately wherever age data allow.

Lucas (2007) noted that Cretaceous tetrapod tracks are widely distributed on all continents except Antarctica (Fig. 1). Dinosaur footprints, especially large ornithopod tracks, dominate many assemblages. The latter are rare in the Jurassic; their dominance begins quite abruptly in basal Cretaceous deposits. Ankylosaur tracks, hitherto unknown with certainty in the Jurassic, also occur widely in the Early and Late Cretaceous; especially good examples come from an Albian acme zone in North America (McCrea et al., 2001b). Sauropod tracks occur in both the Jurassic and Cretaceous strata; both wide-gauge *Brontopodus* and narrow-gauge

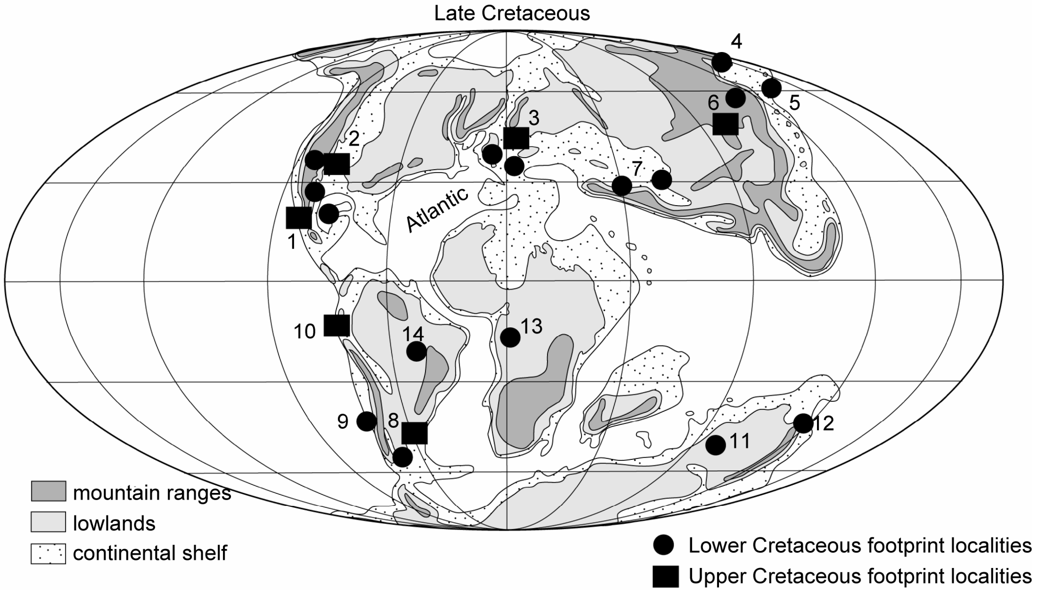


**Fig. 1 Distribution of principle global Cretaceous tracksites** (after Lucas, 2007, Base map after Wings & Sues, 1992)

1. southwestern United States; 2. western Canada; 3. western Europe; 4. Korea; 5. Japan; 6. China; 7. Tadjikistan; 8. Argentina; 9. Chile; 10. Bolivia; 11. western Australia; 12. Queensland, Australia; 13. Cameroon

*Parabrontopodus* tracks are well known in the Jurassic, but *Parabrontopodus* becomes comparatively rare in the Cretaceous (Lockley et al., 1994a). Sauropod tracks tend to be associated with low-latitude, carbonate facies, a fact that gave rise to the concept of a *Brontopodus* ichnofacies that contrasts with an ornithopod-dominated ichnofacies associated with higher-latitude, clastic facies. However, the sample on which this conclusion originally was based (Lockley et al., 1994c) was relatively small compared with that available today, and the geographical and facies distributions of sauropods and ornithopods would benefit from further analysis.

Cretaceous bird tracks are increasingly well known from lakeshore facies, especially in Asia (Lockley & Harris, 2010). Similarly, the Cretaceous pterosaur track record is also becoming increasingly well known (Lockley et al., 2008a). In contrast, Cretaceous mammal tracks remain rare, and are presently restricted to North America (e. g., McCrea & Sarjeant, 2001; Stanford & Lockley, 2002; Lockley & Foster, 2003; Stanford et al., 2007) and South America (Leonardi 1977, 1994; Leonardi et al., 2007).

It is important to note that the Cretaceous is a relatively long geological time period, spanning 80 million years, from ≈145~65 Ma; both the Early and Late Cretaceous are also long—the Early Cretaceous spans 45 million years, from 145~100 Ma, and the Late Cretaceous spans 35 million years, from 100~65 Ma. However, in many areas, standard biostratigraphic indicators are not available, rendering differentiation of Early and Late Cretaceous units problematic; this is particularly true in the terrestrially dominated sequences in Asia. In other regions, distinguishing between ichnofaunas of different ages within a given epoch can be useful. For example, in many parts of North America, tetrapod ichnofaunas from the Early Cretaceous are poorly known from the Berriasian–Hauterivian, but are well known from Barremian–Albian formations (see below and Appendix). In the sections that follow, such distinctions are made where relatively precise age determinations can be made.

### 3.2 Early Cretaceous of North America

Most of the important ichnofaunas from the Cretaceous of North America are found in the western part of the continent, especially in western Canada (Sternberg, 1932; McCrea, 2000), Colorado (Mehl, 1931; Lockley et al., 1992a; Lockley et al., 2006, 2009), and Texas (Bird, 1939, 1941, 1944, 1953, 1954, 1985), though at least one significant ichnofauna was reported quite recently from the eastern USA (Stanford et al., 2004, 2007), and a few Early Cretaceous ichnofaunas have been reported from Mexico (Rodríguez-de la Rosa et al., 2004). Most of these are post-Neocomian (Figs. 2, 3); the most important exceptions come from basal Cretaceous units in western Canada, such as the Mist Mountain Formation (Fig. 3), which has yielded *Neoanomoepus* (Lockley et al., 2009c) and the first sauropod tracks known from Canada (McCrea et al., 2005).

Most western American ichnofaunas are distinctly facies related. For example, the Texas ichnofaunas in carbonate platform facies of the Glen Rose Formation are dominated by *Brontopodus* and large theropod tracks (Bird, 1941, 1944; Farlow et al., 1989; Farlow, 1992, 1993, 2001), whereas the Colorado and western Canadian ichnofaunas are ornithopod dominated, accompanied by other, rarer ornithischian tracks (e.g., *Tetrapodosaurus*, of presumed ankylosaurian affinity; McCrea et al., 2001b), bird tracks (Mehl, 1931; Currie, 1981; McCrea & Sarjeant, 2001; Lockley et al., 2009a),

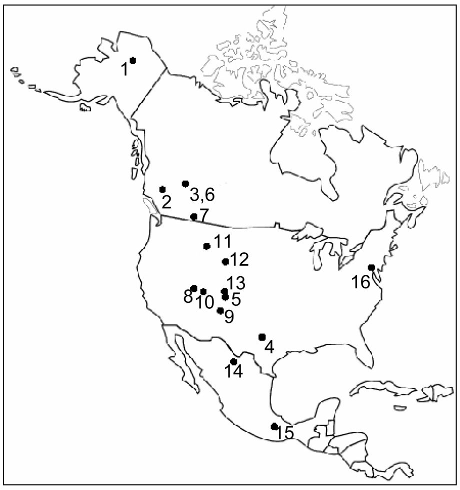


**Fig. 2 Distribution of principal Cretaceous tracksites of North America**

1. Alaska (Upper Cretaceous); 2. Gething Formations, British Columbia, Canada (Berriasian–Aptian); 3. Gates Formation, Alberta, Canada (Albian); 4. Glen Rose Formation, Texas, USA (Aptian–Albian); 5. Dakota Group, Colorado–New Mexico–Oklahoma, USA (Albian–Cenomanian); 6. Dunvegan Formation, Alberta, Canada (Cenomanian); 7. Milk River Formation, Alberta, Canada (Santonian–Campanian); 8. Mesaverde Formation, Utah, USA (Campanian); 9. Raton Formation, New Mexico, USA (Maastrichtian); 10. Cedar Mountain Formation, Utah (Barremian–Albian); 11. Harebell Formation, Wyoming (Maastrichtian); 12. Lance Formation, Wyoming (Maastrichtian); 13. Laramie Formation, Colorado, (Maastrichtian); 14. Cerro del Pueblo Formation, Coahuila (Campanian–Maastrichtian); 15. San Juan Raya Formation, Puebla (Albian); 16. Patuxent Formation, Maryland, USA (Aptian)

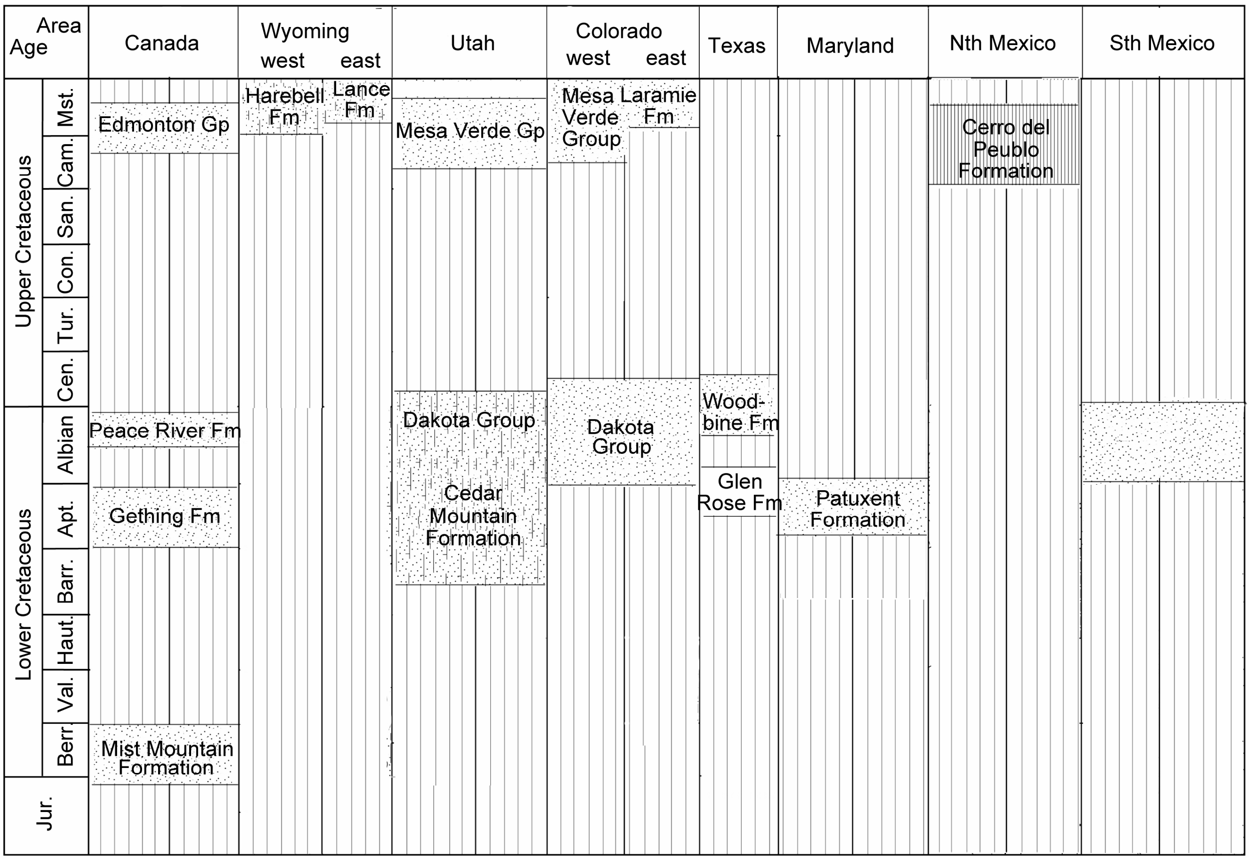


**Fig. 3 Relative ages and facies of important, track-bearing stratigraphic units in North America**

and crocodylian tracks (Lockley et al., 2010a) in siliciclastic facies. Similar ichnofaunas are present in siliciclastic facies at other, less well-known, western American localities in South Dakota (Lockley et al., 2001) and Utah (Lockley et al., 2004b).

Most of the Texas ichnofaunas, made famous by Bird, (1941, 1944) and assigned to the *Brontopodus* ichnofacies (sensu Lockley et al., 1994b; Lockley, 2007) are associated with lower-latitude, carbonate facies (Pittman, 1989, 1992). In contrast, the western Canada, Colorado, and South Dakota ichnofaunas have been characterized as ornithopod dominated (i.e., the ornithopod- or *Caririchnium* ichnofacies (sensu Lockley et al., 1994b; Lockley, 2007), and are associated with well-vegetated, locally coal-bearing, siliciclastic facies of the Western Interior seaway coastal plain systems, particularly in the widely distributed Dakota Group. Collectively, sites in these latter areas have been referred to as the "dinosaur freeway" (Lockley et al., 1992a). Theropod tracks from western Canada, such as *Irenichnites* and *Irenesauripus*, which were named by Sternberg (1932), are also in coal-bearing facies, but have not been identified with confidence south of the 49th Parallel, although Lockley et al. (1998b) noted similarities between these Canadian ichnotaxa and tracks from the Aptian–Albian of Texas, Croatia, and Spain. These similarities and distributions, and their potential ichnotaxonomic and ichnostratigraphic implications, are in need of further study.

Although this general pattern of geographical separation between ornithopod- and sauropod-dominated ichnofaunas can be observed on a global scale, local situations can vary substantially. For example, mixed sauropod and ornithopod ichnofaunas are known from the Cedar Mountain Formation of Utah, USA, where they co-occur with deinonychosaur tracks (Cowan et al., 2010). Similarly mixed and diverse ichnofaunas occur in Maryland in the eastern USA (Stanford et al., 2004, 2007). The apparent late Albian turnover in western American track faunas, from sauropod dominated to ornithopod dominated, was used by Lucas & Hunt (1989) to mark a Cretaceous extirpation of sauropods in North America that lasted until a Maastrichtian

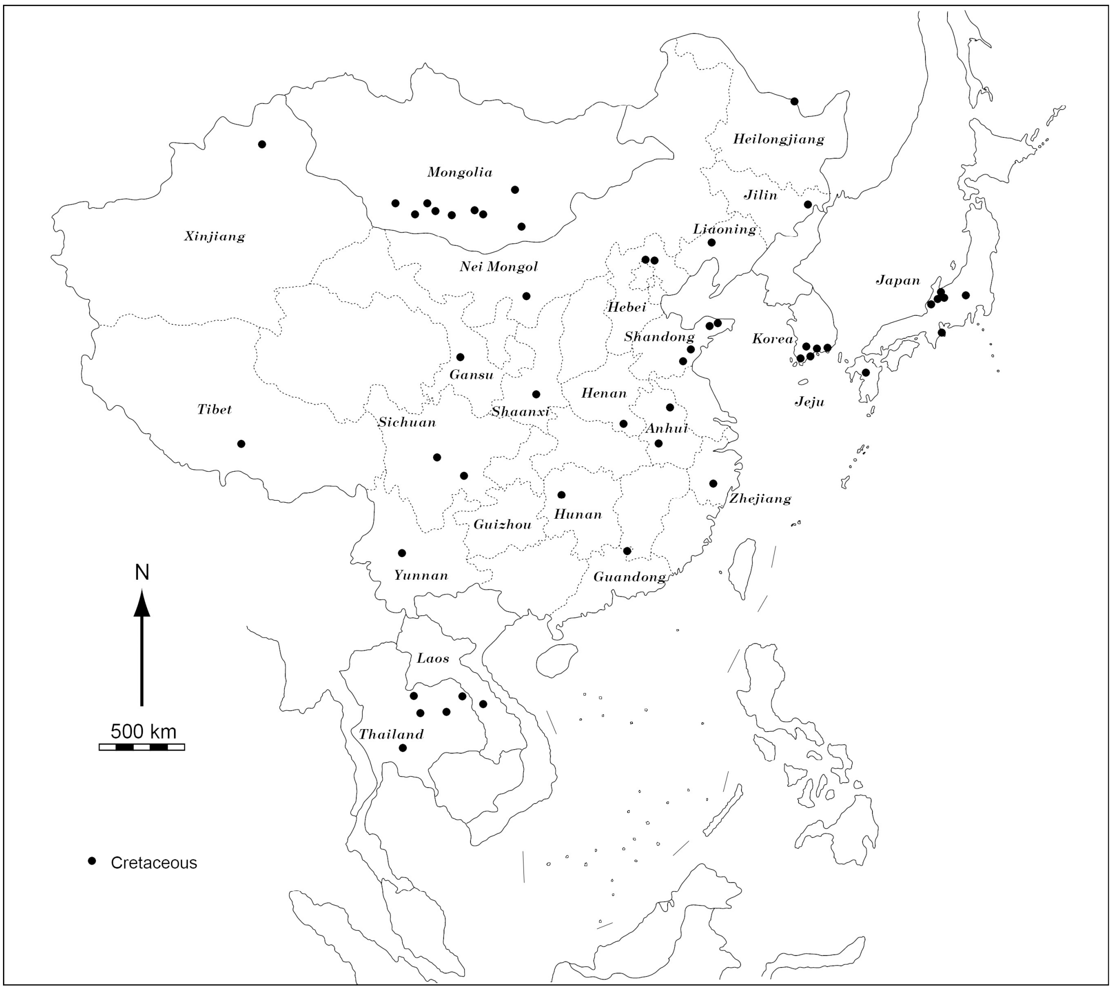


**Fig. 4 Distribution of principal Cretaceous tracksites of east Asia**

immigration (from South America?) brought a low-diversity sauropod fauna back to the continent (Lucas & Sullivan, 2000; D'Emic et al., 2010).

Bird tracks constitute a notable component of Early Cretaceous ichnofaunas in western North America. Ichnotaxa thus far recognized are *Ignotornis* (Mehl, 1931; Lockley et al., 2009a), *Aquatilavipes* (Currie, 1981; Lockley et al., 2001), and *Koreanaornis* (Anfinson et al., 2009). These tracks are associated with siliciclastic facies and are as yet unknown from carbonate facies. The siliciclastic facies, best represented by the Dakota Group, also produce abundant crocodylian swim tracks pertaining to the ichnotaxon *Hatcherichnus* (Foster & Lockley, 1997); these are sometimes associated with rarer turtle and pterosaur swim tracks (Houck et al., 2010; Kukihara et al., 2010; Lockley et al., 2010a; Kukihara & Lockley, 2011). Trackways of walking crocodylians (*Mehliella* sensu Lockley, 2010) are known but also rare.

### 3.3 Early Cretaceous of Asia

In many parts of Asia, distinguishing between Early and Late Cretaceous ichnofaunas has proven difficult, if not wholly impossible, because of the absence either of useful fossils that can be correlated with the standard marine timescale (Chen et al., 2006; Matsukawa et al., 2006b) or of material than can be dated radiometrically. Here we update the data presented by Chen et al. (2006) and expand it to include other parts of east Asia (Figs. 4, 5). In recent years, Early Cretaceous ichnofaunas from east Asia, notably China, Japan, Korea, and Thailand, have become increasingly well known (Lockley & Matsukawa, 2009). In these ichnofaunas, the footprints of major dinosaur groups (theropods, ornithopods, and sauropods) are well represented, but they are found in stratigraphic units that are not as well dated as in North America. Moreover, they are associated with different sedimentary facies. As a result, the ichnofaunas are often markedly different

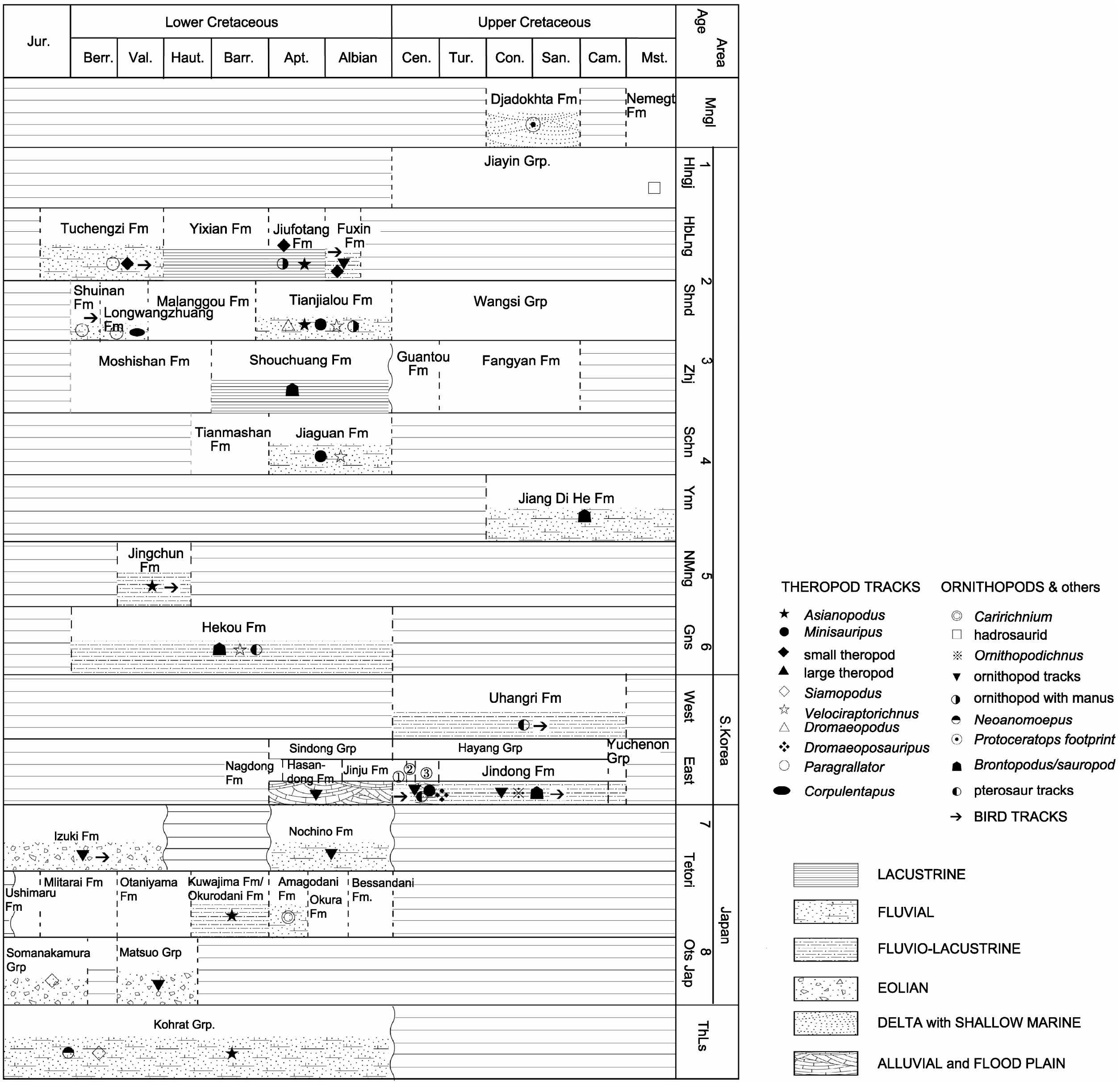


**Fig. 5 Relative ages and facies relationship for Cretaceous sites in Asia** (See separate box for key. Compare with Figure 3)

from those found in North America, at least locally. Where possible below (and in the Appendix), we differentiate between Early and Late Cretaceous Asian ichnofaunas, but we warn the reader that such age assignments are, in all too many cases, tentative and subject to future change.

**3.3.1** China The most important and prolific Early Cretaceous ichnofaunas from China are those reported from the Tuchengzi Formation of Liaoning and Hebei provinces, the Jingchuan Formation of Nei Mongol Province, the Hekou Formation of Gansu Province, and the Tianjialou Formation of Shandong Province (Fig. 5). Of these units, the Tuchengzi Formation is the oldest (Matsukawa et al., 2006a) and is close in age to, and likely spans, the Jurassic-Cretaceous boundary (≈145 Ma) (Lockley et al., 2006b, 2009b; Sullivan et al., 2009; Xing et al., 2009c, 2011a). Tracks in the unit are preserved at a number of sites, of which the Yangshan locality is the best known (Yabe et al., 1940; Zhen et al., 1989; Matsukawa et al., 2006b). Many sites in the unit are dominated by the tracks of small theropods (grallatorid type) assigned to the ichnospecies *Grallator ssatoi.* Recently, Xing et al. (2011a) reported larger theropod tracks from the Tuchengzi Formation that have been identified as *Megalosauripus* and *Therangospodus*, though it is unclear whether the quality of the material warrants such assignments. Likewise, the quality of preservation of purported didactyl tracks from this area is poor, casting doubt on the validity of the ichnogenus *Menglongipus* (Xing et al., 2009c). Bird tracks of the ichnogenus *Pullornipes*, which are among the oldest bird tracks in the world, are known only from a single location in this area, but are well preserved (Lockley et al., 2006b, 2009b).

To the west, in Nei Mongol (Inner Mongolia), in somewhat younger Neocomian strata, at least 16 track localities have been documented in the Jingchuan Formation. Almost all exclusively preserve bird and other saurischian dinosaur tracks (Lockley et al., 2002b, 2011c; Li et al., 2006b, 2009), including the sauropod ichnotaxon *Brontopodus*, the theropod ichnotaxa *Chapus* (Li et al., 2006b) and *Asianopodus*, and the bird track *Tatarornipes* (Lockley et al., 2011c). The latter occurs in abundance at many sites. However, as is the case in the Tuchengzi Formation, many of the theropod ichnotaxonomic assignments lack reliability.

Farther west, in Gansu Province, is a large site in the Hekou Group that has yielded sauropod, theropod (including deinonychosaur and bird), ornithopod, and pterosaur tracks from multiple levels (Li et al., 2002, 2006a; Zhang J. et al., 2006). Xing et al. (2011c) reported bird-dominated ichnofaunas even farther west in the Tugulu Group of Xinjiang Province that also preserve numerous small (footprint length 11~18 cm) theropod tracks assigned to *Asianopodus*, *Kayentapus*, and cf. *Jialingpus*. Bird tracks, which are also abundant at this site, were assigned to *Koreanaornis*, *Goseongornipes*, and the recently named *Moguiornipes*.

In the Longwangzhuang Formation in northeastern Shandong Province, the crocodylian ichnogenus *Laiyangpus* (Lockley et al., 2010b) occurs with the bird ichnogenus *Tatarornipes* (Lockley et al., 2011c) and the problematic theropod ichnogenus *Paragrallator* (Li & Zhang, 2000). To the southwest, around Zhucheng, a large assemblage of grallatorid tracks (cf. *Paragrallator*) occurs in association with the distinctive, theropod ichnogenus *Corpulentapus* and a few sauropod tracks (Li et al., 2011). Farther to the southwest, near Junnan, the younger Tianjialou Formation preserves a highly distinctive and diverse ichnofauna of theropod (including bird) and ornithopod tracks. Among the theropod tracks are *Minisauripus* and *Asianopodus* (Lockley et al., 2008b), the deinonychosaurian morphotypes *Dromaeopodus* and *Velociraptorichnus* (Li et al., 2007), and two avian ichnotaxa: *Koreanaornis* and the highly distinctive *Shan dongornipes* (Lockley et al., 2007b), the latter of which is not known anywhere else in the world. The co-occurrence of *Velociraptorichnus*, *Minisauripus*,and *Koreanaornis* is reminiscent of a less-well-known ichnofauna from Sichuan Province (Zhen et al., 1994) that may also be Early Cretaceous in age.

The facies associations of the Chinese tetrapod ichnofaunas are locally variable, but they are generally associated with fluvio-lacustrine systems, many of which were deposited in isolated inland basins. Many of these basins also include lacustrine deposits that typically yield body fossils of plants, arthropods (insects, ostracods, conchostracans), fishes, and miscellaneous tetrapods (Chen et al., 2006). In the Fuxin Formation of northern Hebei and western Liaoning provinces, as well as the Tongfosi Formation of Jilin Province, coal-bearing facies are developed locally. The absence of ichnofaunas associated with extensively-correlated carbonate or siliciclastic coastal plain systems contrasts sharply with the roughly coeval record in North America.

**3.3.2** Korea　Early Cretaceous Korean ichnofaunas are distinct from coeval North American and Chinese ichnofaunas. The most abundant ichnological assemblages have been reported from the Haman and Jindong formations, which were deposited in siliciclastic, foreland basin lake and floodplain paleoenvironments (Yang et al., 2003; Huh et al., 2009). The ichnofaunas preserve theropod (including bird), sauropod, ornithopod, and pterosaur tracks in considerable, sometimes extreme, abundance all across the Korean peninsula, but especially along the southern coast, which has been dubbed the Korean Cretaceous Dinosaur Coast (KCDC; see Lockley et al., 2012b for summary).

In the Jindong Formation, sauropod and ornithopod tracks are both abundant, though mostly occurring in different horizons (Lim et al., 1994; Hwang et al., 2002b; Lockley et al., 2006c). Most of the sauropod tracks pertain to *Brontopodus* (Lockley et al., 2006c; Kim & Lockley, 2012). Most of the ornithopod tracks pertain to *Caririchnium*, though a few have been attributed to the ichnotaxon *Ornithopodichnus* (Kim et al., 2009); most of the ornithopod tracks were made by animals progressing bipedally, but in rare cases quadrupedally (Lim et al., 2012). In sharp contrast to the Chinese assemblages, theropod tracks are generally rare, and except for *Minisauripus* and *Dromaeosauripus* (Kim et al., 2008; Lockley et al., 2008b; Kim et al., 2012a), few have been named. Korean Early Cretaceous sauropod tracks (*Brontopodus*), ornithopod tracks (*Caririchnium*), and small pterosaur tracks (*Pteraichnus*) are not easily distinguished from those found in other regions. However, the bird tracks are both distinctive and abundant; the avian ichnofauna comprises *Koreanaornis*, *Jindongornipes*, *Ignotornis*, and *Goseongornipes* (Kim et al., 2012b; Kim et al., 2006; Lockley et al., 1992b). With the exception of *Koreanaornis*, the other ichnogenera are not widely known elsewhere in the world.

**3.3.3** Japan and Thailand Early Cretaceous ichnofaunas from Japan and Thailand, while certainly important and interesting in their own rights, add relatively little to the overall picture emerging from east Asia. The theropod ichnogenus *Asianopodus* was originally named from the Kuwajima Formation of Japan (Matsukawa et al., 2005), and *Siamopodus* is a distinctive theropod ichnogenus from the Khorat Group of Thailand (Lockley et al., 2006e). The small ornithischian ichnotaxon *Neoanomoepus*, though based on type material from Canada, has been identified in the basal Cretaceous of Thailand (Lockley et al., 2009c). Other assemblages are dominated by small cf. *Asianopodus* theropod tracks (Matsukawa et al., 2006a). Recently, Le Loeuff et al. (2009) reviewed the Thailand ichnofaunas and showed that the Cretaceous sites are dominated by theropod tracks (q.v. Matsukawa et al., 2006a). Le Loeuff et al. (2009) also identified crocodylian tracks similar to *Batrachopus* in the Khok Kruat Formation, despite the fact that *Batrachopus* is traditionally considered an Early Jurassic ichnogenus.

Japanese Early Cretaceous ichnofaunas are mainly associated with braided stream alluvial facies in a back-arc setting (Matsukawa et al., 2006b). Likewise, Le Loeuff et al. (2009) described the theropod and crocodylomorph tracks from the Khok Kruat Formation in Thailand as associated with predominantly fluvial deposits.

### 3.4 Early Cretaceous of Europe

The European Early Cretaceous tetrapod track record is dominated by ornithopod tracks, especially in the Wealden of England and Germany where the tracks have historically been attributed to *Iguanodon* (footprint ichnogenus *Iguanodontipus*) or a similar track maker (Sarjeant et al., 1998; Wright et al., 1998; Lockley & Meyer, 2000; Lockley & Wright, 2001). In Germany, these ornithopod tracks are associated with various theropod tracks, including as-yet undescribed, didactyl deinonychosaurian theropod tracks (van der Lubbe et al., 2009). The ornithopod tracks normally occur in siliciclastic facies, but in Switzerland they occur in carbonates (Meyer & Thüring, 2003), and in Spain they occur in a variety of facies (Moratalla et al., 1992, 2004; Moratalla & Hernán, 2010) in which they are associated with sauropod and theropod tracks at various sites (Moratalla et al., 1994a; Barco et al., 2004). Ezquerra et al. (2007) reported large swim tracks attributable to theropods in Spain.

Tracks of other ornithischians, especially ankylosaurs, have rarely been reported in the European Early Cretaceous. Potentially important specimens, such as the holotype of the tetradactyl, possibly ankylosaurian ichnotaxon *Metatetrapous* (Haubold, 1971), are currently being re-examined. Purported basal ornithopod ("hypsilophodontid") tracks have been reported from the basal Cretaceous of Spain (Leonardi, 1979b), although this attribution is controversial (Long, 1998; McCrea et al., in press). Theropod and sauropod tracks from the Early Cretaceous of Europe have also proven to be ichnotaxonomically controversial, as in the cases of the theropod track *Buckeburgichnus* (Kuhn, 1958; Lockley, 2000; Thulborn, 2001) and the sauropod track *Rotundichnus* (Hendricks, 1981), which was declared a *nomen dubium* by Lockley et al. (1994a).

Large theropod and sauropod tracks from Lower Cretaceous (Barremian and Albian) carbonates in Croatia (Dalla Vecchia, 2000, 2001, 2002) are abundant but generally poorly preserved. Although tracks from this Adriatic region are from carbonate ichnofacies, in contrast to similar tracks in siliciclastic ichnofacies to the north, few ichnotaxa have been positively identified. As a result, it has been difficult to make all but gross ichnotaxonomic comparisons with other regions. Nevertheless, large and medium-sized theropod tracks are abundant, locally occurring alongside sauropod tracks, but there are few confirmed reports of ornithischian tracks. In this regard, the assemblages appear to be part of the *Brontopodus* ichnofacies (sensu Lockley et al., 1994a) and are therefore comparable to those found in the Early Cretaceous of Texas.

Non-dinosaurian tracks, including *Pteraichnus*, have been found at several localities in Spain (Lockley et al., 1995; Sánchez-Hernández et al., 2009), as have the crocodylian track *Crocodylopodus* (Fuentes Vidarte & Meijide Calvo, 2001; Lockley & Meyer, 2004) and tetrapod trackways of uncertain affinity (Moratalla et al., 1995). Spanish tracks named *Archaeornithipus* (Fuentes Vidarte, 1996) were originally considered avian, but this identification is doubtful and the tracks probably pertain to non-avian coelurosaurian theropods (Lockley & Harris, 2010).

Unusual, high-latitude ornithopod and theropod tracks from the Early Cretaceous of the Arctic island of Spitsbergen in the Svalbard archipelago shed important light on dinosaur distributions and migrations (de Lapparent, 1962; Edwards et al., 1978; Lockley & Meyer, 2000; Hurum et al., 2006). These tracks, like those in northern North America, are from siliciclastic sediments.

### 3.5 Early Cretaceous of South America

In South America, definite Early Cretaceous footprints have been reported from Argentina, Chile, and Brazil (Leonardi, 1981a, 1981b, 1989, 1994). Brazilian Early Cretaceous track assemblages from the state of Paraíba are diverse: Leonardi, 1979a, 1979b, 1984) reported footprints of sauropods, theropods, and large ornithopods. Notably, he erected two ornithopod ichnotaxa: *Sousaichnium* (Leonardi, 1979a) for a large, bipedal ornithopod, and *Caririchnium* (Leonardi, 1984) for a quadrupedal ornithopod (though initially he attributed the ichnogenus to a stegosaur). The latter has a broad distribution in North America and Asia. In Chile, however, tracks named *Iguanodonichnus* that were originally attributed to ornithopods (Casamiquela & Fasola, 1968) are actually misnamed sauropod tracks (Sarjeant et al., 1998; Moreno & Benton, 2005). Likewise, Casamiquela (1964) also described the ichnogenus *Camptosaurichnus*, although there is no compelling evidence that it is of ornithopod origin; it may, in fact, be theropod, but is best considered a *nomen dubium* (Sarjeant et al., 1998). At the time when Leonardi (1989, 1994) compiled many of his data, South American sauropod tracks were only known from São Domingos in Brazil. Since then, however, they have been reported from other parts of South America, including *Sauropodichnus* from Argentina (Calvo, 1991; Calvo & Mazzetta, 2004).

For the reasons given above, the statistics presented by Leonardi (1989, 1994) that document the proportion of different track types found in different regions of South America during different time periods requires updating, as is done herein by the addition of relevant, post-1994 citations. Even though few distinctive theropod tracks have been named, both the initial observations of Leonardi (1989, 1994) and updated data summarized herein (Appendix) indicate that theropod tracks dominate in the Cretaceous, as well as in the Jurassic, of South America.

Among non-dinosaurian ichnotaxa, pterosaur tracks (*Pteraichnus* isp.) are also known from the Early Cretaceous of Argentina (Calvo & Lockley, 2001). Lull (1942) reported the crocodylomorph ichnogenus *Batrachopus* from San Luis Province, Argentina; the source beds were originally thought to be Triassic, but subsequently interpreted as Neocomian by Leonardi (1994), who noted that regardless of their stratigraphic context, the specimens likely are crocodylian. These tracks recall the also-seemingly anachronistic Cretaceous *Batrachopus* tracks from Thailand mentioned above (Le Loeuff et al., 2009).

### 3.6 Early Cretaceous of Australia

Theropod tracks (ichnogenus *Megalosauropus*) were reported from Early Cretaceous sandstones in the Broome area of western Australia (Colbert & Merrilees, 1967). Subsequently, Thulborn et al. (1994) and Long (1998) documented sauropod tracks and possible co-occurrences of ornithopod and stegosaur tracks from the same strata. Recently, McCrea et al. (in press) have confirmed the presence of abundant theropod and sauropod tracks, as well as a few ornithopod tracks, but argued that the purported stegosaur tracks are likely of ankylosaur affinity.

### 3.7 Early Cretaceous of Africa

Though the overall African track record is depauperate, dinosaur tracks have been discovered in Early Cretaceous strata in the northwestern part of the continent. The best documented are theropod tracks from Cameroon (Dejax et al., 1989; Jacobs et al., 1989), which are associated with fluvial deposits associated with early rifting, concomitant with the opening of the South Atlantic. For this reason, Jacobs et al. (1989) considered the tracks to be biostratigraphically significant, an inference elaborated by the claim that the tracks are similar to those found in the Lower Cretaceous of Brazil. Sauropod and theropod tracks from argillaceous strata of both early Early Cretaceous (possibly Late Jurassic) and late Early Cretaceous age in Niger were briefly described and figured by Ginsburg et al. (1966) and Taquet (1976, 1977), but require more study.

## 4 Comparing Early Cretaceous ichnofaunas

In North America, South America, and Europe, small, grallatorid tracks are rare, but in China, grallatorid morphotypes (*Grallator* and *Paragrallator*), as well as *Asianopodus*, are abundant and even dominant in many assemblages. Strangely, such tracks are absent from almost all Korean assemblages (Fig. 6). Perhaps, at least in part, this is a function of the fact that most east Asian Cretaceous tetrapod ichnotaxonomy has been devoted to the footprints of small theropods and birds, with comparatively little attention to tracks pertaining to other groups (Matsukawa et al., 2006b). Uniquely, these small-theropod-dominated assemblages produce *Minisauripus* and *Velociraptorichnus*, both of which are currently unknown outside Asia. They also include abundant bird tracks, some of which (e.g., *Shandongornipes*) are also unknown elsewhere. These track assemblages, therefore, are generally distinct from those found outside Asia. The *Batrachopus*-like form in Thailand, together with *Neoanomoepus*, suggest several possibilities: 1) that at least some Asian track makers were morphologically convergent with Early Jurassic taxa, 2) that some of the Early Cretaceous ichnofaunas and, perhaps, faunas of east Asia have an archaic aspect, 3) that at least some ichnofaunal and faunal elements are endemic to east Asia and absent in North America and other regions, although *Batrachopus* also has been reported from the Neocomian of South America (Leonardi, 1989), or 4) facies controls: North American ichnofaunas are associated mostly with extensive, coastal-plain systems (clastic in the north and carbonate in the south), but many Asian ichnofaunas, especially those in China, are associated with isolated, inland, fluvio-lacustrine basins, so the ichnofaunas from either region may have sampled different faunas with different paleoecologies. Furthermore, as indicated above, while post-Neocomian ichnofaunas from North America are generally quite well dated, the precise ages of many Asian ichnofaunas are uncertain. It is therefore also possible that differences in ichnotaxonomic composition among Asian ichnofaunas and between Asian and other ichnofaunas are due to differences in age.

As noted above, the distributions of tetrapod tracks in space and time are most useful if patterns can be discerned—if the distributions are not random. Sauropod track research provides a potentially useful case study. Farlow (1992) discussed sauropod track distributions in relation to latitude, and Lockley et al. (1994b) considered them in relation to both latitude and facies, demonstrating a statistically significant relationship to low-latitude carbonate substrates. Both studies looked at the distributions of wide- and narrow-gauge sauropod trackways, concluding that some patterns are evident: wide-gauge forms become dominant in the Cretaceous (Lockley et al., 1994a), a conclusion supported independently by Wilson & Carrano (1999). If such conclusions are confirmed for sauropod and other ichnotaxa across broad areas, they would be useful for distinguishing ichnological changes across the Jurassic-Cretaceous boundary.

Lockley (2001, 2008) also discussed the relationship between wide- and narrow-gauge sauropod tracks and large- and small-manus forms, respectively, claiming a positive correlation between narrow-gauge tracks and small manus in the Jurassic and wide-gauge and small manus in the Cretaceous, as larger, wider-bodied, and more front-heavy titanosauriform sauropods became dominant over the diplodocoids of the Late Jurassic. Henderson (2004) also examined these differences but from a biomechanical viewpoint. Falkingham et al. (2011) also reached very similar conclusions concerning the shift.

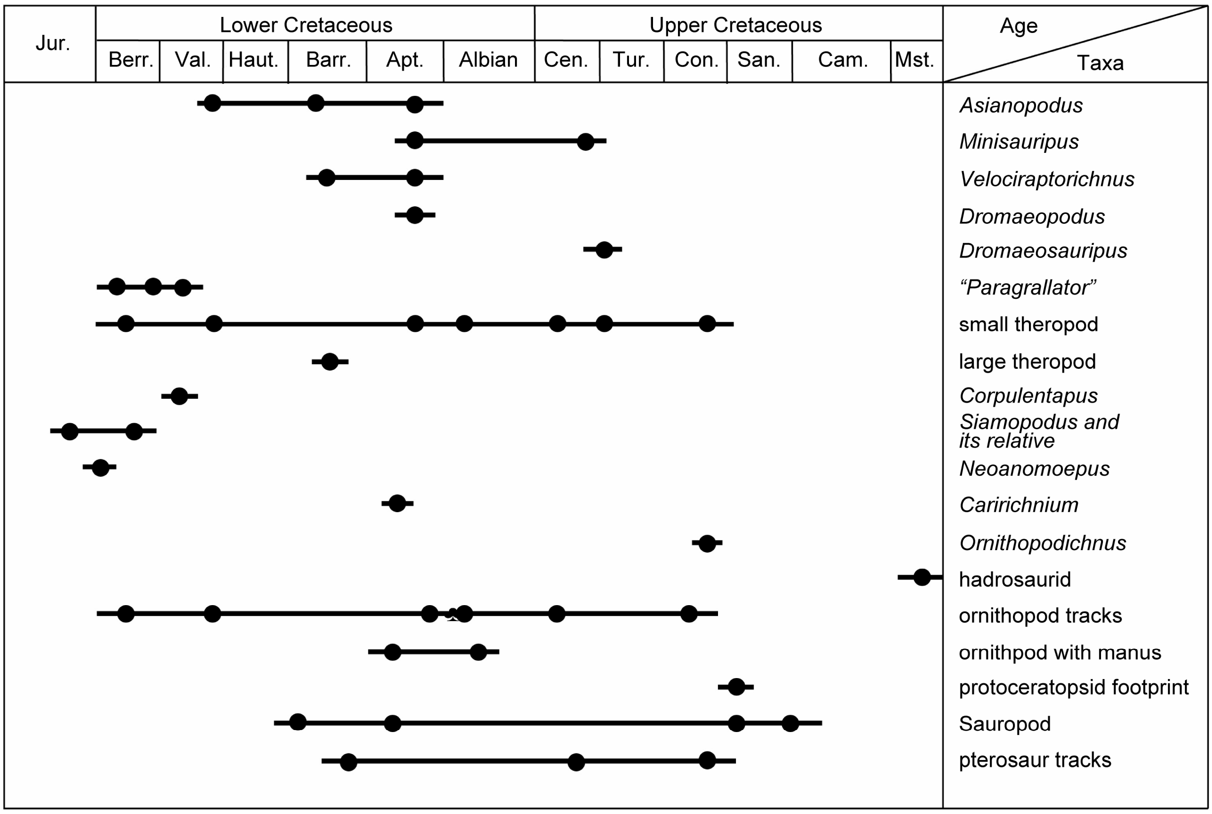


**Fig. 6 Age ranges of dinosaur and pterosaur ichnotaxa in the Cretaceous of Asia**

Other studies have examined the distributions of different sauropod track types in space and time by attempting to correlate track types with track makers at low taxonomic levels (e.g., Carrano & Wilson, 2001). As noted by Lucas (2007), such efforts have so far met with limited success and often lead to ambiguous and inconclusive results. In a similar vein, Wright (2005) attempted to mix sauropod ichnology with cladistics, in some cases using hypothetical, "predicted" track morphologies. However, other than confirming the predominance of wide-gauge trackways in the Cretaceous, this study lacked any very specific conclusions. Clearly, if the polarities between these track types are related to differences between sauropod clades (e.g., Titanosauriformes v. non-Titanosauriformes), as is generally inferred, the case for using trackways to distinguish the distributions of sauropod track makers in space and time is supported, at least at this basic level. Whether or not similar cases can be established for other dinosaur ichnotaxa and clades remains to be seen.

## 5 Late Cretaceous

### 5.1 North America

As noted by Lucas (2007), the Late Cretaceous track record in North America is heavily skewed toward Campanian–Maastrichtian rocks from western Canada and the USA. Ornithopod—ostensibly hadrosaurid-track types dominate in western Canada (Langston, 1960; Currie, 1983; Currie, 1989) and the coal-bearing "Mesaverde Group" and equivalents in Utah and Colorado (e.g., Lockley et al., 1983, 2011a; Parker & Rowley, 1989; Carpenter, 1992), which are generally considered classic examples of wave-dominated, deltaic, coastal plain systems, where ornithopod ichnofacies predominate (Lockley et al., 1994a). Tracks of the probably hadrosaurid ichnotaxon *Hadrosauropodus* from the Maastrichtian of western Canada and the USA (Lockley et al., 2004a) sometimes are well-enough preserved to have skin impressions that match those from body fossils (Currie et al., 1991). In the past, large hadrosaurid track morphotypes have been mistakenly attributed to tyrannosaurids, which as yet have no attributed tracks with skin impressions. *Tyrannosauripus*, from the Maastrichtian interval of the Raton Formation in New Mexico (Lockley & Hunt, 1994a), is the only named ichnotaxon that can be attributed with any confidence to *Tyrannosaurus* (Lockley et al., 2011b).

Ceratopsian tracks are still comparatively rare, although they have been found in the Iron Springs Formation of western Utah (Milner et al., 2006), the "Mesaverde Group" in western Colorado and Utah (Parker & Rowley, 1989), and the Laramie Formation in eastern Colorado, which is the type locality of *Ceratopsipes* (Lockley & Hunt, 1994b, 1995b), the only named ceratopsian ichnotaxon. In the latter two cases, the ceratopsian tracks are associated with other rare track types, including mammal tracks of the ichnogenus *Schadipes* (Lockley & Foster, 2003), champsosaur tracks of the ichnogenus *Champsosaurichnus* (Lockley & Hunt, 1995b), and, at scattered locations, bird, frog, and pterosaur tracks (Lockley, 1999; Robison, 1991). Again, all such occurrences represent wet, coastal plain systems. This association of ceratopsians with wet substrates has been supported independently by the paleosol studies of Retallack (1997).

The Laramie and Harebell formations in Wyoming have also produced the distinctive, gracile theropod track type *Saurexallopus* (Harris et al., 1996; Harris, 1997; Lockley et al., 2004a), which may be of oviraptosaurian affinity (Gierliński & Lockley, in press). *Ornithomimipus* (Sternberg, 1926) is also a distinctive, gracile theropod ichnogenus found in both Canada and the western USA (Gangloff et al., 2004). *Ornithomimipus*, as well as *Magnoavipes* (Lee, 1997; Lockley et al., 2006d) and *Columbosauripus* (Sternberg, 1932), also from western Canada and the USA, have been attributed to gracile coelurosaurians and classified along with *Ornithomimipus* in the ichnofamily Ornithomimipodidae (Lockley et al., 2011a). None of these ichnotaxa have been reported unambiguously outside North America (though tracks from the Late Cretaceous of Peru were referred to *Ornithomimipus* by Jaillard et al. [1993]). Farther north, in western Canada and Alaska, various dinosaur (including ceratopsian and bird) and pterosaur tracks have been reported (Roehler & Stricker, 1984; Gangloff, 1998; McCrea et al., 2001b; Fiorillo & Parrish, 2004; Fiorillo et al., 2007, 2009; Fiorillo et al., 2010a, 2010b). Rylaarsdam et al. (2004) note that track-bearing facies provide a glimpse of Turonian terrestrial environments in which dinosaurs frequented strandplain, beach-ridge, freshwater-lake, and brackish-lagoon habitats during a global eustatic highstand. Body fossils are exceptionally rare in North America from this time period, so tracks once again provide important information about vertebrate diversity and paleoecology that would otherwise be wholly absent.

In the Raton Basin of Colorado, tracks of hadrosaurids and ceratopsians occur only 0.37~2.00 m below the Cretaceous-Paleogene boundary as determined by palynology and the iridium-bearing clay layer, and bird tracks have been found both just above and below that boundary (Lockley, 1991; Pillmore et al., 1994) in the coal-bearing ornithopod ichnofacies sensu Lockley et al. (1994b) and Lockley (2007). Such finds demonstrate the utility of ichnology in documenting the distributions of avian and non-avian dinosaurs immediately before and after the end-Cretaceous extinction event. As noted below, the influx of avian ichnofaunas in the earliest Cretaceous may also indicate an important evolutionary turnover event.

Late Cretaceous ichnofaunas of Mexico are far more abundant than those reported from this region in the Early Cretaceous, but they have received only scant description thus far. Rodríguez-de la Rosa et al. (2004) reported nine ichnofaunas that collectively have yielded tracks representing most major dinosaur groups except sauropods, as well as tracks of turtles, pterosaurs, and crocodylians. These ichnofaunas are associated with lacustrine and low-gradient, mud-dominated, lower coastal plain systems.

### 5.2 Asia

**5.2.1** China and Mongolia As noted above, uncertainty about dating makes it difficult or impossible to distinguish between some Early and Late Cretaceous tracksites in Asia, particularly in the "middle" Cretaceous. A few tracksites in China have been described as "middle and Late" Cretaceous. For example, Xing et al. (2007) described the theropod track *Wupus*, the ornithopod tracks *Caririchnium* and *Laoyingshanpus*, and the ankylosaur track *Qijiangpus* from the "middle" Cretaceous of Chongqing. Other than *Caririchnium*, none of these ichnogenera have been recognized elsewhere; *Qijiangpus*, if correctly attributed, is the only ankylosaurian track currently known in China. *Laoyingshanpus* is purported to be of hadrosauroid affinity. Other Chinese tracks from this interval have been attributed to "hadrosaurs" (though whether this refers to the narrowly construed Hadrosauridae or broader Hadrosauroidea or

Hadrosauriformes is rarely made clear): Dong et al. (2003) named *Jiayinosauropus* from Heilongjiang and Xing et al. (2009a) named a new ichnospecies of *Hadrosauropodus* from Guangdong. These large ornithopod tracks, as well as unnamed/unassigned specimens from the famous Nemegt Formation in Mongolia (Currie et al., 2003), are attributed with a high degree of certainty to hadrosaurids that walked on mudstones and sandstones deposited on the floodplain of a meandering fluvial system. The Mongolian tracks are quite common and have been known for some time (Suzuki & Watabe, 2000; Watabe & Suzuki, 2000a, 2000b), but only recently have some been examined in detail (Ishigaki et al., 2009). Regardless of the validity of the different ichnogenera, together these reports document the widespread distribution of large ornithopod tracks in the Late Cretaceous of Asia. However, as demonstrated by Currie et al. (2003), some hadrosaurid tracksites also yield sauropod and theropod tracks. Thus, inferring that these ichnofaunas are always dominated by hadrosaurid or other large ornithopod tracks is presently impossible. Nevertheless, in the absence of independent age indicators, hadrosaurid tracks are the most useful indicators of a Late Cretaceous age.

**5.2.2** Korea Tracks from the Late Cretaceous Uhangri Formation in the southwestern part of South Korea include the distinctive, duck-like avian tracks *Uhangrichnus*, which has traces of fully developed webbing, and *Hwangsanipes*, which is similar to *Ignotornis* (Yang et al., 1995; Lockley & Harris, 2010; Lockley et al., 2012c). Co-occurring with these tracks at the same site are large pterosaur tracks of the ichnogenus *Haenamichnus* (Hwang et al., 2002a) and large ornithopod and/or theropod tracks (Hwang et al., 2008) that were previously misinterpreted as sauropod swim tracks (Lee & Huh, 2002). Tracks from the Hwasun area reveal a quite different, non-avian-theropod-dominated ichnofauna (Huh et al., 2006), although a few sauropod and ornithopod tracks are present (Lockley et al., 2012a). Abundant ornithopod tracks from the Yeosu Island Archipelago, as well as associated bird, theropod, and sauropod tracks, have also been interpreted as Late Cretaceous (Huh et al., 2012; Lockley et al., 2012d). The Yeosu facies were mud-dominated, lacustrine basin systems similar in many respects to the Lower Cretaceous facies of the Haman and Jindong formations described above.

### 5.3 Late Cretaceous of Europe

There have been relatively few notable Late Cretaceous tracksites documented in Europe (Lockley & Meyer, 2000). A notable exception is the large and visually spectacular Fumanya site in Cataluna, Spain, first documented by Schulp & Brokx (1999). The site is dominated by the tracks of wide-gauge sauropods of presumed titanosaurian affinity. The large, tridactyl tracks *Ornithopodichnites* and *Orcauichnites* from the site (Llompart et al., 1984) are probably best considered *nomina dubia* and are likely of theropod affinity (Lockley & Meyer, 2000). They are too poorly preserved to be of ichnotaxonomic utility.

Nicosia et al. (2006) provided a useful summary of the distribution of tracks in the Cretaceous in the Periadriatic region and discussed the fact that many occurrences of dinosaur tracks in platform carbonates, which were previously considered submarine deposits, have forced a reassessment of the regional geodynamics and the facies in which dinosaurs were capable of registering their footprints (Bosellini, 2002). Ichnotaxonomically important, Late Cretaceous tracks from the region include the possibly ankylosaurian ichnotaxon *Apulosauripus* (Nicosia et al., 1999).

### 5.4 Late Cretaceous of South America

Leonardi (1994) reported a number of important tetrapod track localities from the Upper Cretaceous of South America. These include so-called *Hadrosaurichnus* tracks (Alonso & Marquillas, 1986; Alonso, 1989), which are in fact theropod tracks, and the bird track *Patagonichnornis* (Leonardi, 1994), both from Argentina. More recently, González Riga & Calvo (2009) named the new sauropod ichnogenus *Titanopodus* from the Late Cretaceous of Argentina.

Several Late Cretaceous sites are known in Bolivia, of which the Toro Toro and Cal Orcko sites are the most famous. Based on a spectacular, lengthy trackway from the Toro Toro site, Leonardi (1984) erected the ichnogenus *Ligabueichnium* and suggested that it may have been made by an unusually large ankylosaur. The Cal Orko site is one of the largest tracksites in the world, dramatically exposed on a vertical quarry wall 1 km long. Until recently, this surface also displayed a pair of spectacular sauropod trackways (Lockley & Peterson, 2002; Lockley et al., 2002a) that unfortunately were destroyed when the wall collapsed in 2010. The site also yielded several ankylosaur trackways (Mc-

Crea et al., 2001b) as well as various theropod track types. A third site, at Humaca, reveals yet another set of parallel sauropod trackways (Lockley et al., 2002a). Interestingly, the Toro Toro and Humaca sites are in siliciclastic, lacustrine and alluvial plain sediments, but the Cal Orcko site is in a lacustrine carbonate unit, yet all sites preserve similar ichnofaunas. The proximity of the alkaline lake system (rather than a shoreface-foreshore marine system) to more typical, fluvial-dominated paleoenvironments may explain this exception to the frequent distinction between ichnofacies seen elsewhere.

Leonardi (1994) reported 23 Cretaceous track localities from Brazil, none of which can be definitively dated as Late Cretaceous. Carvalho (2001) later reported Cenomanian theropod and sauropod tracks in estuarine deposits in eastern Brazil. Jaillard et al. (1993) and Noblet et al. (1995) also reported theropod and ornithopod tracks from the Late Cretaceous of Peru.

### 5.5 Australia

In Australia, numerous small theropod and ornithopod tracks from Cenomanian, siliciclastic strata of Winton, Queensland have been assigned to the ichnogenera *Wintonopus* and *Skartopus*, respectively (Thulborn & Wade, 1979, 1984). The site also preserves a set of large, tridactyl tracks that have alternately been attributed to a theropod (Thulborn & Wade, 1984; Thulborn, 2011) and an ornithopod (Romilio & Salisbury, 2010). *Skartopus* has not been reported anywhere outside Australia. Tracks resembling *Wintonopus* were reported from the Early Cretaceous of China (Li et al., 2006a), and the name has been used casually for tracks from the Lower Cretaceous Broome Sandstone in western Australia, where, as noted above, the somewhat older ichnofauna is quite different (Long, 1998; McCrea et al., in press); otherwise, this ichnotaxon, too, is endemic to Australia. Since no other comparable ichnofauna has been identified elsewhere, this meager record from eastern Australia may, therefore, indicate a provincial ichnofauna.

### 5.6 Late Cretaceous of Africa

Taquet (1976) reported, but did not describe, vertebrate traces from several Upper Cretaceous units in Niger, and whether or not any of these traces pertains to a dinosaur remains unknown. Ambroggi & de Lapparent (1954) described an assemblage of small tracks from near Agadir, Morocco, that included tracks of sandpiper-like shorebirds, enigmatic dinosaur tracks, and footprints attributed to a lizard. The latter were named *Agadirichnus.* These tracks have been tentatively interpreted as the tracks of pterosaurs (Billon-Bruyat & Mazin, 2003).

## 6 Comparing Late Cretaceous ichnofaunas

Characteristic Late Cretaceous ichnofaunal elements, such as hadrosaurid tracks, occur in siliciclastic facies in western North America and Asia, although in North America their association with coastal plain systems is evidently different from the floodplain associations reported from Asia. However, these morphotypes are evidently rare or absent from other regions, either due to provincialism or a paucity of sample sites. Large ceratopsian (presumably ceratopsid) tracks are present in western North America in Campanian and Maastrichtian coastal plain deposits, but as yet have not been identified unambiguously from other regions in deposits of this age. A single, isolated report of a protoceratopsian track (Niedzwiedzki et al., 2011) was recently reported from older (Coniacian−Santonian) eolian deposits, thus indicating a different facies association from that observed for large North American ceratopsids. Few of the formally named hadrosaurid and ceratopsian tracks have been reported from anywhere other than their type localities; *Hadrosauropodus* is the only ichnogenus reported from both North America and China.

The Late Cretaceous Korean record is ambiguous because of the difficult problems surrounding the dating of individual units and correlating strata between isolated basins, similar to the problems that plague track studies in China. The Korean assemblage ostensibly includes a suite of bird tracks that differs from its Early Cretaceous counterparts from the same region, but other track types, including the large pterosaur tracks and sauropod and ornithopod tracks, are essentially similar to those reported from the Early Cretaceous.

Though sparse, the European Late Cretaceous track record documents the continued presence of sauropod tracks in lacustrine carbonate facies; these are similar to tracks found in South America, where they co-occur with ankylosaur tracks in lacustrine carbonates. Purported ankylosaur tracks also occur in the Late Cretaceous of China (Xing et al., 2007) and Europe (Nicosia et al., 1999), but they have been assigned to different ichnogenera. In general, all of these records are too scattered to suggest any meaningful patterns in the distribution of ichnofaunas.

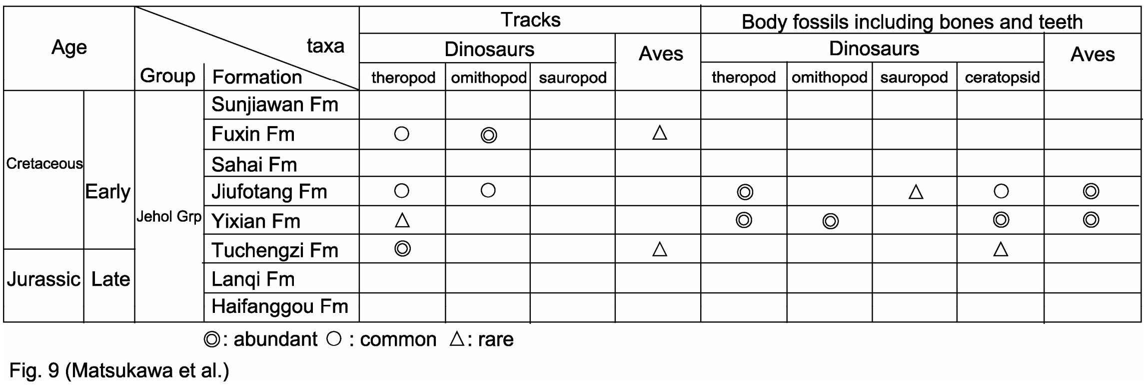
## 7 Tracks across the K/T boundary

Paleogene tetrapod tracks are known mainly from North America and are mostly the footprints of primitive perissodactyls, artiodactyls, and carnivorans. Amphibian, reptile, and bird tracks are also known, but are either too rare (amphibian and reptile tracks) or scattered (bird tracks) to be of any current use in biostratigraphy and biochronology. No dinosaur footprints are known from Paleogene strata. Therefore, the contrast between dinosaur (including bird)-dominated Cretaceous tetrapod ichnofaunas with mammal-dominated Paleogene tetrapod ichnofaunas is clear, paralleling the underlying extinction of dinosaurs at the end of the Cretaceous and subsequent Paleogene diversification of mammals. Indeed, the stratigraphically youngest dinosaur footprints (such as of the aforementioned *Tyrannosauripus* tracks from the upper Maastrichtian of the Raton basin) provide biostratigraphic data points as valid as those of the stratigraphically highest dinosaur bones.

## 8 Discussion

The utility of footprints increases where skeletal remains are rare or absent, as is the case in certain Cretaceous units in the western United States—for example, the track-rich Dakota Group of the western USA and the Glen Rose Formation (and correlative units) in Texas and Arkansas have yielded little body fossil material. The tracks from these units nevertheless document that faunas comprising dinosaurs, pterosaurs, crocodylians, and other tetrapods persisted from preceding time periods. In units where skeletal remains are more abundant, such as the Cedar Mountain Formation of Utah, tracks remain useful, but tend to provide supporting evidence for the presence of groups already recognized from body fossils (Lockley et al., 2004b; Cowan et al., 2010). In some such cases, however, tracks still can document the presence of lower-level taxa unknown from body fossils: for example, *Saurexallopus* tracks from the terminal Cretaceous of Wyoming do not obviously match body fossils of any currently described theropod from either western North America or anywhere else in the world (but see Gierliński and Lockley in press, for possible interpretation).

Lockley & Hunt (1994b) proposed a scheme for comparing the relative abundances of tetrapod trace and body fossils in various formations that retains the potential for wide application. Matsukawa & Lockley (2011) made such an attempt to describe and compare the distributions of tetrapod trace and body fossils in northeast Asia (Fig. 6). They inferred that, in this region, Early Cretaceous dinosaur ichnofaunas are dominated by slender-toed, small theropod and ornithopod tracks, suggesting that a more or less provincial or endemic dinosaur fauna was established in east Asia after the breakup of Pangea. Based on the stratigraphy in northeast China, Upper Jurassic to Lower Cretaceous strata can be divided into eight units: in ascending order, the Haifanggou, Lanqi, Tuchengzi, Yixian, Jiufotang, Shahai, Fuxin, and Sunjiawan formations. Tetrapod tracks occur in four of the eight formations, whereas skeletal remains occur in only three. Dinosaur and bird tracks in both the Tuchengzi and Fuxin formations respectively predate and postdate the earliest and latest skeletal occurrences of these groups in the units. Theropod tracks predominate over those of ornithopods in the lower units (Tuchengzi Formation), but the situation reverses in the upper units (Fuxin Formation; Chen et al., 2006). This may indicate that small theropods appear to have been the first to establish their ecological niches, whereas ornithopods established theirs later. The body fossil record from the Jehol Group shows a similar pattern (Fig. 7): the Yixian Formation is dominated by feathered theropod dinosaurs and early birds; ornithopods, while present, are comparatively rare. In contrast, in the Jiufotang Formation (and its lateral equivalent, the Xiguayuan Formation), ornithischian dominance increases—no ornithischian body fossils have been described, but most, if not all, of the tracks described from the unit pertain to ornithopods (You & Azuma, 1995). Track records with long time spans thus can be as useful as body fossil records for demonstrating such patterns. Moreover, the endemicity of both the ichno



| Age | | taxa | | Tracks | | | | Body fossils including bones and teeth | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Dinosaurs | | | Aves | Dinosaurs | | | | Aves |
| | | Group | Formation | theropod | omithopod | sauropod | | theropod | omithopod | sauropod | ceratopsid | |
| Cretaceous | Early | Jehol Grp | Sunjiawan Fm | | | | | | | | | |
| | | | Fuxin Fm | ○ | ◎ | | △ | | | | | |
| | | | Sahai Fm | | | | | | | | | |
| | | | Jiufotang Fm | ○ | ○ | | | ◎ | | △ | ○ | ◎ |
| | | | Yixian Fm | △ | | | | ◎ | ◎ | | ◎ | ◎ |
| | | | Tuchengzi Fm | ◎ | | | △ | | | | △ | |
| Jurassic | Late | | Lanqi Fm | | | | | | | | | |
| | | | Haifanggou Fm | | | | | | | | | |

◎: abundant ○ : common △: rare

Fig. 9 (Matsukawa et al.)

**Fig. 7 Dinosaur (including bird) track and bone distributions in the Early Cretaceous of northeastern China**

(After Matsukawa & Lockley (2011)

faunas and body fossil faunas from this region provides an interesting opportunity to more closely examine potential track maker-track affiliations (Xing et al., 2009b).

As this review indicates, the global record of Cretaceous tetrapod footprints is dominated by the tracks of dinosaurs, including birds, with many fewer tracks of pterosaurs, crocodylians, turtles, mammals, and other tetrapods. The Cretaceous track record is best known from East Asia (especially China and Korea) and western North America. A moderately extensive record is also known from South America (mostly Argentina and Brazil), but the Cretaceous track assemblages known from Europe, Africa and Australia are much less extensive.

The biochrons proposed by Lucas (2007) maintain their validity, at least at a gross level, even with the addition of new data. The Early Cretaceous biochron is characterized by sauropod and ornithopod tracks; the Late Cretaceous biochron is characterized by fewer sauropod tracks but adds more numerous tracks of large ornithopods, plus tracks of tyrannosaurids and ceratopsians. Furthermore, the Cretaceous footprint record parallels the body fossil records for many important biostratigraphic data points, such as the mid-Cretaceous extirpation of sauropod dinosaurs in North America, the early Cretaceous radiation of birds and the terminal Cretaceous extinction of dinosaurs.

Lucas (2007) also noted that, by the Cretaceous, global vertebrate faunas begin to exhibit increasing provincialization, which, in turn, necessitates provincial, rather than global, vertebrate biochronologies for Cretaceous time. The data presented here support this conclusion. However, Lucas (2007) continued by explicitly stating that unlike the body fossil record, the track record does not demonstrate provincialism. The reason for this apparent dichotomy lies, in part, with the fact that in many areas, ichnofaunas can only be characterized in general terms, distinguishing only broad categories, such as "theropod-", "sauropod-", or "ornithopod tracks". This is particularly true in the Late Cretaceous. However, since 2007, a number of distinctive ichnofaunas have been reported, especially from the Lower Cretaceous of Asia, and the balance of current evidence supports the tentative conclusion that Cretaceous ichnofaunas indeed show some degree of provincialism, at least regionally. For example, dozens of ichnotaxonomically diverse bird track sites now are known from the Early Cretaceous of China, Korea, and Japan, yet none are known from contemporaneous strata in Europe or Australia, and those reported from the relatively small North and South American samples have mostly been assigned to different ichnotaxa.

Indeed, the growing Cretaceous footprint record from eastern Asia (Figs. 5, 6) provides the first glimpse of the potential to construct a more refined, provincial footprint biochronology. In east Asia, three or four footprint biochrons may be recognizable based on the stratigraphic distributions of endemic theropod dinosaur and bird ichnogenera: 1) a Berriasian–early Valanginian "*Paragrallator*" biochron, to which *Siamopodus* and *Neoanomoepus* are restricted; 2) a late Valanginian–early Aptian *Asianopodus* biochron, to which *Velociraptorichnus* is restricted; 3) a late Aptian–Turonian *Minisauripus-Dromaeosauripus* biochron; and 4) a less distinctive, Coniacian–Maastrichtian biochron characterized by hadrosaurid (large ornithopod) tracks. We emphasize, though, that stillunresolved issues with the ages of some of the Asian footprint localities, plus pending resolution of ichnotaxonomic issues, make such a biochronology tentative for the moment. However, the increasingly robust footprint record in the Asian Cretaceous presages recognition of more than two provincial footprint biochrons. Notwithstanding the difficulties of establishing refined and unequivocal ages and ichnotaxonomies for the avian ichnofaunas now known from Asia, it is clear that a shorebird ichnofacies (sensu Lockley et al., 1994b) became well-established in Asia by earliest Cretaceous times, mostly in lacustrine settings. As noted by Lockley and Harris (2010), this ichnofacies is not necessarily attributed to the activity of "shorebirds" as defined by the osteological classifications of contemporary ornithologists and paleornithologists: rather, it indicates the evolution of shorebird-like track makers or species otherwise highly convergent with modern shorebirds *sensu stricto*. Current evidence suggests that the ichnological record is important in underscoring a major radiation of birds early in the Cretaceous. Given the concentration of known tracksites in East Asia, this region may have been an endemic center for this evolutionary radiation.

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## APPENDIX

Cretaceous crocodyliform/crocodylian, pterosaurian, and dinosaurian (including avian) track reports and localities. Track names (ichnogenera) listed are as reported in cited literature; many listed ichnotaxa are likely synonyms of other ichnotaxa—listings here do not necessarily connote endorsement of validity. Ages of rock units and tracks as reported in cited literature. Cited references include representative, recent, and/or most thorough documentation and are not necessarily exhaustive lists of relevant literature. Abbreviations (in chronological order): E. Early; L. Late; Ti. Tithonian; Be. Berriasian; Va. Valanginian; Ha. Hauterivian; Ba. Barremian; Ap. Aptian; Al. Albian; Ce. Cenomanian; Tu. Turonian; Co. Coniacian; Sa. Santonian; Ca. Campanian; Ma. Maastrichtian; U/U. unnamed/unassigned

| **TAXON** | **E. CRETACEOUS (BE–BA)** | **"MIDDLE" CRETACEOUS (AP–CE)** | **E. CRETACEOUS UNDIFFERENTIATED** | **L. CRETACEOUS (TU–MA)** | **L. CRETACEOUS UNDIFFERENTIATED** |
|---|---|---|---|---|---|
| **CROCODYLIFORMES/ CROCODYLIA** | Ti–Be: Purbeck Limestone Fm., England—**U/U swim tracks** (Ensom, 2007) | Ap–Al: Khok Kruat Fm., Thailand—**U/U** (Le Loeuff et al., 2010) | | Ca: Muerto Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Ti–Be: Villar del Arzobispo Fm. & Oncala Gp., Spain—***Crocodylopodus*, U/U** (Fuentes Vidarte & Meijide Calvo, 2001; Pérez-Lorente & Ortega, 2004) | Al: Mesa Rica Sandstone, Dakota Gp., NM, CO, KS—***Hatcherichnus*, *Mehliella*, U/U** (Bennett, 1992; Houck et al., 2010; Kukihara et al., 2010; Lockley et al., 2006d, 2010a; McAllister, 1989) | | Ca: Cerro del Pueblo Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Be: Huerteles Fm., Spain—**U/U** (Pascual Arribas et al., 2005) | | | Ca: Wahweap Fm., UT—**cf. *Crocodylopodus*** (Simpson et al., 2010a) | |
| | Ha–Ba: Calizas de la Huerguina Fm., Spain—**U/U** (Moratalla et al., 1995) | | | Ma: Lance Fm.,WY— **U/U** (Falkingham et al., 2010) | |
| | Ha–Ba?: Sousa Fm., Brazil—**U/U and swim tracks** (Nascimento Campos et al., 2010) | | | Ma: Olmos Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Ba: Laiyang Fm., China—***Laiyangpus*** (Lockley et al., 2010b) | | | | |
| | Ba–Ap: Enciso Gp., La Rioja, Spain—**U/U** (Ezquerra & Pérez-Lorente, 2004) | | | | |
| | Be–Ha: La Cantera Fm., Argentina—***Batrachopus*** (Leonardi, 1989; Lull, 1942) | | | | |
| **PTEROSAURIA** | Ti–Be: Oncala Gp., Spain—***Pteraichnus*** (Fuentes Vidarte et al., 2004; Sánchez-Hernández et al., 2009) | Ap: Urbion Gp., Spain—***Pteraichnus*** (Moratalla et al., 1994c) | | Ca: Cerro del Pueblo & Muerto fms., Mexico—***Pteraichnus*** (Rivera-Sylva et al., 2006; Rodriguez-de la Rosa, 2003) | |
| | Be: Purbeck Limestone Fm., England—***Purbeckopus*** (Wright et al., 1997) | Ap: Patuxent Fm., Potomac Gp., MD—***Pteraichnus*** (Stanford et al., 2007) | | Ca–Ma: Cantwell Fm., AK—***Pteraichnus*** (Fiorillo et al., 2009) | |
| | Ha–Ba?: Hekou Gp., Gansu, China—***Pteraichnus*** (Li et al., 2006a; Peng et al., 2004; Zhang et al., 2006a) | Ap–Al: Haman & Hasandong fms., Korea—***Pteraichnus*** (Kim et al., 2006; Lee et al., 2008) | | Ma: North Horn Fm., UT—***Pteraichnus*** (Lockley, 1999) | |
| | Ha–Ba: Okurodani (= Kitadani) & Kuwajima fms., Tetori Gp., Japan—***Pteraichnus*** (Lee et al., 2009) | Al–Ce: Candeleros Mbr., Rio Limay Fm., Argentina—***Pteraichnus*** (Calvo & Lockley, 2001) | | Ma: unnamed unit, Morocco—***Agadirichnus***(Ambroggi & de Lapparent, 1954; Billon- Bruyat & Mazin, 2003) | |
| | Ba–Ap: Enciso Gp., La Rioja, Spain—***Pteraichnus*** (Moratalla & Hernán, 2009) | Al–Ce: Dakota Fm., CO—**U/U** (Lockley et al., 2007a) | | Ma: Blackhawk Fm., UT—**U/U** (Lockley et al., 2008a; Parker & Balsley, 1989) | |
| | | Ce: Uhangri Fm., Korea—***Haenamichnus*** (Hwang et al., 2002a; Kim et al., 2003; Lockley et al., 1997) | | | |
| | | Ce: Dunvegan Fm., AB—**U/U** (Lockley & Rainforth, 2002) | | | |
| | | early L. Cretaceous: Fangyan Fm., Zhejiang, China—**U/U** (Lü et al., 2010) | | | |
| **STEGOSAURIA** | Ti–Be: El Castellar Fm., Spain—***Deltapodus*** (Cobos et al., 2010) | | | | |
| | Be–Va: Broome Sandstone, Australia—**U/U** (Thulborn et al., 1994)[1] | | | | |
| | L. Jurassic–E. Cretaceous: La Puerta Fm., Bolivia—**U/U** (Apesteguía & Gallina, 2011) | | | | |

(To be continued)

(Continued)

| **Taxon** | **E. Cretaceous (Be–Ba)** | **“Middle” Cretaceous (Ap–Ce)** | **E. Cretaceous Undifferentiated** | **L. Cretaceous (Tu–Ma)** | **L. Cretaceous Undifferentiated** |
|---|---|---|---|---|---|
| **Ankylosauria** | Ti–Be: Lulworth Fm.,. Purbeck Limestone Gp., England—**U/U** (Ensom, 1987; McCrea et al., 2001b; Wright et al., 1998) | Ap: Patuxent Fm., MD & VA—**U/U** (Stanford et al., 2007) | | Tu–Co: Calcare di Altamura, Italy—**U/U** (Conti et al., 2005; Dal Sasso, 2003) | |
| | L. Jurassic–E. Cretaceous: La Puerta Fm., Bolivia—**U/U** (Apesteguía & Gallina, 2011) | Ap: Calcare di Bari Fm., Italy—**U/U** (Petti et al., 2010; Sacchi et al., 2008) | | Sa: Calcare di Altamura, Italy—***Apulosauripus*** (Gierliński et al., 2005; Nicosia et al., 1999) | |
| | Be: Buckeburg Fm., Germany—***Metatetrapous*** (McCrea et al., 2001b) | Ap–Al: Ruby Ranch Mbr., Cedar Mountain Fm., UT—**U/U** (Lockley et al., 2004b; Santucci & Kirkland, 2010) | | Ca: Djadokhta Fm., Mongolia—***Tetrapodosaurus*** (Ishigaki et al., 2009) | |
| | Be–Va: Wessex Fm., Wealden Gp., England—**U/U** (Radley, 1994; Wright et al., 1998) | Ap–Al: Gething Fm., BC—***Tetrapodosaurus*** (Carpenter, 1984; McCrea et al., 2001b) | | Ca: Toro Toro Fm., Bolivia—***Ligabueichnium*** (Leonardi, 1984; McCrea et al., 2001b) | |
| | | Al: Gates Fm., AB—***Tetrapodosaurus*** (Currie, 1989; McCrea, 2000; McCrea & Currie, 1998; McCrea et al., 2001b) | | Ca–Ma: Horseshoe Canyon Fm., AB—***Tetrapodosaurus*-like** (Currie, 1989)$^2$ | |
| | | Al–Ce: Mussentuchit Mbr., Cedar Mountain Fm., UT—**U/U** (Kirkland et al., 1997; Lockley et al., 1999; McCrea et al., 2001b) | | Ca–Ma: Wapiti Fm., AB—**U/U** (Currie, 1989) | |
| | | Al–Ce: Dakota Gp., CO—**U/U** (Kurtz et al., 2001; Lockley et al., 2006a; McCrea et al., 2001b; Schumacher, 2003) | | Ma: Blackhawk Fm., UT—**U/U** (McCrea et al., 2001b; Parker & Balsley, 1989; Parker & Rowley, 1989) | |
| | | Al–Ce: Chandler Fm., AK—***?Tetrapodosaurus*** (McCrea et al., 2001b) | | Ma: El Molino Fm., Bolivia—**U/U** (McCrea et al., 2001b) | |
| | | Al–Ce: Tantalus Fm., Yukon—***Tetrapodosaurus*** (Gangloff et al., 2004; Long et al., 2001) | | Ma: Scollard Fm., AB—**U/U** (Currie, 1989) | |
| | | Ce: Dunvegan Fm., BC—***Tetrapodosaurus*** (Currie, 1989) | | | |
| | | “middle” Cretaceous: Jiaguan Fm., Chongqing, China—***Qijiangpus*** (Xing et al., 2007) | | | |
| **Ceratopsia** | | Al: Nanushuk Fm., AK—**U/U** (Fiorillo et al., 2010a) | | Sa?: Iron Springs Fm., UT—**U/U** (Milner et al., 2006) | |
| | | | | Ca: Djadokhta Fm., Mongolia—**U/U** (Niedzwiedzki et al., 2011) | |
| | | | | Ca: Wahweap Fm., UT—**U/U** (Hamblin & Foster, 2000) | |
| | | | | Ma: Lance Fm., WY—**U/U** (Smith, 2002) | |
| | | | | Ma: Blackhawk Fm., UT—**U/U** (Parker & Rowley, 1989) | |
| | | | | Ma: Laramie Fm., CO—***Ceratopsipes*** (Lockley & Hunt, 1995b) | |
| **“Small” Ornithopoda: basal ornithopods (“hypsilophodontids”–basal dryomorphans** | L. Jurassic–E. Cretaceous: Botucatu Fm., Brazil—***Unespichnium*** (Bertini & Carvalho, 2003) | Ap: Patuxent Fm., MD & VA—***Hypsiloichnus*** (Stanford et al., 2004) | | Ma: Xiaoyan Fm., Anhui, China—**U/U** (Yu et al., 1999) | |
| | Be?–Ba?: Enciso Gp., La Rioja, Spain—***Dinehichnus*, U/U** (Aguirrezabala et al., 1985; Lockley et al., 1998a, 2009c; Moratalla et al., 1988) | Ce: Winton Fm., Australia—***Wintonopus*** (Thulborn & Wade, 1984) | | Ma: Olmos Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Be: Mist Mountain Fm., BC—***Anomoepus*** (Currie, 1989) | | | | |
| | Va: Gorman Creek Fm., BC—**U/U** (Lockley et al., 2009c) | | | | |

(To be continued)

(Continued)

| Taxon | E. Cretaceous (Be–Ba) | “Middle” Cretaceous (Ap–Ce) | E. Cretaceous Undifferentiated | L. Cretaceous (Tu–Ma) | L. Cretaceous Undifferentiated |
|---|---|---|---|---|---|
|  | Va–Ha: Urbion Gp., Spain—***Dinehichnus*** (García-Ortiz de Landaluce et al., 2009; Lockley & Meyer, 2000) |  |  |  |  |
|  | Ha–Ba?: Hekou Gp., Gansu, China—***?Wintonopus*** (Li et al., 2006a) |  |  |  |  |
|  | Be–Ba: Phra Wihan Fm., Thailand—***Neoanomoepus*** (Le Loeuff et al., 2009; Lockley et al., 2009c) |  |  |  |  |
|  | Ba–Ap: Vectis Fm., England—**U/U** (Martill & Naish, 2001; Radley et al., 1998) |  |  |  |  |
|  | Ba–Ap: Zhidan Gp., Nei Mongol, China—**U/U** (Azuma et al., 2006) |  |  |  |  |
| **“large” Ornithopoda: Ankylopollexia–Hadrosauriformes** | Ti–Be: Purbeck Limestone Fm., England—***Iguanodontipus*** (Ensom, 2007; Sarjeant et al., 1998; Wright et al., 1998) | Ap: Schrattenkalk Fm., Switzerland—***Iguanodontipus*** (Meyer & Thüring, 2003) | E. Cretaceous: Urbion Gp., Spain—**U/U** (Ansorena et al., 2008; Moratalla et al., 1994b) | Ce–Tu: Kaskapau Fm., BC—**U/U** (Rylaarsdam et al., 2006) |  |
|  | Ti–Be: Villar del Arzobispo Fm., Spain—**U/U** (Cuenca-Bescós et al., 1999) | Ap: Patuxent Fm., MD & VA—**U/U** (Stanford et al., 2007) | E. Cretaceous: Olivan Gp (“Weald”), Spain—**U/U** (Casanovas Cladellas et al., 1990a) | Ce–Tu: Kem-Kem Beds, Morocco—**U/U** (Sereno et al., 1996) |  |
|  | Ti–Be: Oncala Gp., Spain—***Iguanodontipus*, “*Brachyiguanodonipus*,” “*Iguanodonipus*,” U/U** (Fuentes Vidarte et al., 2005a; Lockley & Meyer, 2000; Moratalla, 1993; Sanz et al., 1999) | Ap: Calcare di Bari Fm., Italy—**U/U** (Petti et al., 2008; Sacchi et al., 2008) | E. Cretaceous: Yangjiazhuang Fm., Laiyang Gp., Shandong, China—**U/U** (Xing et al., 2010a) | Tu: Cardium Fm., BC—**U/U** (Currie, 1989) |  |
|  | Callovian–Be: Amran Gp., Yemen—**U/U** (Schulp et al., 2008) | Ap: Amagodani (= Akaiwa, = Okura) & Nochino fms., Tetori Gp., Japan—***Caririchnium*, U/U** (Matsukawa et al., 2005, 2006a) | Be–Ap: Chacarilla Fm., Chile—**U/U** (Moreno et al., 2011) | Tu: Ferron Sandstone Mbr., Mancos Shale, UT—**U/U** (Jones, 2001) |  |
|  | L. Jurassic–E. Cretaceous: Botucatu Fm., Brazil—**U/U** (Leonardi et al., 2007) | Ap–Al: Haman, Geonchori, Jindong, & Sagog fms., Korea—***Caririchnium,* U/U** (Huh et al., 2003; Lee et al., 2001; Lim et al., in press) |  | Sa–Ca: Cleary Coal Mbr., Menefee Fm., NM—***Caririchnium*** (Lucas & Hunt, 2006) |  |
|  | Be: Obernkirchen Sandstone—***Iguanodontipus*** (Diedrich, 2004; Richter et al., 2007) | Ap–Al: Gething Fm., BC—***Gypsichnites, Amblydactylus*, *Columbosauripus*** (Currie, 1995; Sternberg, 1932) |  |  |  |
|  | Be: Huerteles, Villar del Arzobispo, & Rupelo fms. & Oncala Gp., Spain—**U/U** (Fuentes Vidarte et al., 2005a; Latorre Macarrón et al., 2006; Pérez-Lorente et al., 1997; Platt & Meyer, 1991) | Ap–Al: Hensel Fm/Glen Rose Limestone, TX—***Gypsichnites***, **U/U** (Langston, 1974; Pittman, 1989) |  | Sa: Yong’ancun Fm., Heilongjiang, China—***Jiayinosauropus*** (Dong et al., 2003) |  |
|  | Be: Ashdown Beds, Hastings Beds, England—**U/U** (Woodhams & Hines, 1989) | Ap–Al: Ruby Ranch Mbr., Cedar Mountain Fm., UT—**U/U** (Lockley et al., 1999, 2004b) |  | Sa: John Henry Mbr., Straight Cliffs Fm., UT—**U/U** (Hamblin & Foster, 2000) |  |
|  | Be: Buckeburg Fm., Germany—***Iguanodontipus*** (Diedrich, 2004; Lockley et al., 2004c; Richter, 1998; Wings et al., 2005) | Ap–Al: “Gres Superieurs” (=Khok Kruat Fm), Laos—**U/U** (Allain et al., 1997) |  | Sa?: Iron Springs Fm., UT—**U/U** (Milner et al., 2006) |  |
|  | Be–Va: Wessex Fm., Wealden Gp., England—**U/U** (Wright et al., 1998) | Ap–Al: Khok Kruat Fm., Thailand—***Caririchnium*** (Le Loeuff et al., 2009) |  | Ca: Milk River Fm., AB—**U/U** (Currie, 1989) |  |
|  | Be–Va: Izuki Fm., Tetori Gp., Japan—***Shiraminesauropus*, *Gigantoshiraminesauropus*, U/U** (Matsukawa et al., 2005, 2006a) | Ap–Al: “Complexo gresoso de Olhos Amarelos e Pousio da Galeota”, Portugal—**U/U** (Mateus & Antunes, 2003) |  | Ca: Judith River, Oldman, & Belly River fms., AB—**U/U** (Currie, 1989) |  |
|  | Va: Tunbridge Wells Sandstone, Hastings Beds, England—**U/U** (Woodhams & Hines, 1989) | Ap–Al: Tianjialou Fm., Shandong, China—**U/U** (Li et al., 2005a) |  | Ca: Fruitland Fm., NM—***Caririchnium*, U/U** (Hunt & Lucas, 2003; Lucas et al., 2000, 2011) |  |
|  | Be?–Ba?: Enciso Gp., La Rioja, Spain—**U/U** (Álvarez et al., 2000; Casanovas Cladellas et al., 1990b; Moratalla & Hernán, 2008; Moratalla et al., 1988; Sanz et al., 1985) | Ap–Al: Enciso Gp., Spain—***Iguanodontipus,* U/U** (Jiménez Vela & Pérez-Lorente, 2008; Moratalla & Hernán, 2008; Pérez-Lorente & Jiménez Vela, 2008; Requeta Loza et al., 2008) |  | Ca: Cerro del Pueblo Fm., Mexico—**U/U** (Rodríguez-de la Rosa, 2007) |  |

(To be continued)

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| TAXON | E. CRETACEOUS (BE–BA) | "MIDDLE" CRETACEOUS (AP–CE) | E. CRETACEOUS UNDIFFERENTIATED | L. CRETACEOUS (TU–MA) | L. CRETACEOUS UNDIFFERENTIATED |
|---|---|---|---|---|---|
| | Be–Ba: Sousa, Piranhas, & Antenor Navarro fms., Brazil: **U/U, *Sousaichnium, Staurichnium, Caririchnium*** (Leonardi, 1979a, 1987b; Leonardi & de Souza Carvalho, 2007; Leonardi & dos Santos, 2004) | Al: San Juan Raya Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006; Rodríguez-de la Rosa et al., 2011) | | Ca: Mesaverde Gp., CO, UT, WY—**U/U** (Carpenter, 1992; Lockley et al., 1983) | |
| | Ha: Tongfosi Fm., Yanji Gp., Jilin, China—**U/U** (Matsukawa et al., 1995) | Al: Dakota Gp (incl. Mojado & Pajarito fms.), NM & OK—***Amblydactylus, Caririchnium*** (Kappus & Cornell, 2003; Lucas et al., 1989) | | Ca: Wahweap Fm., UT—**U/U** (Hamblin & Foster, 2000) | |
| | Ha: Ladeiras Fm., Portugal—***Iguanodon*, U/U** (Antunes, 1976) | Al: Bhuj Fm., India—**U/U** (Loyal et al., 1996) | | Ca: Kaiparowits Fm., UT—**U/U** (Hamblin & Foster, 2000) | |
| | Ha: El Castellar & Pinilla de los Moros fms., Spain—**U/U** (Fernández-Baldor et al., 2006; Ruiz-Omeñaca et al., 2004) | Al: unnamed unit, Croatia—**U/U** (Dalla Vecchia et al., 2002) | | Ca–Ma: Chignik Fm., AK—**U/U** (Fiorillo & Parrish, 2004) | |
| | Ha–Ba: Enciso Gp., Spain—**U/U, *Iguanodontipus*, & *Hadrosaurichnoides*** (Aguirrezabala et al., 1985; Casanovas Cladellas et al., 1993b; Lockley & Meyer, 2000; Moratalla & Hernán, 2008) | Al: Luchak Fm., Tadjikistan—***Akmechetosauropus*, *Babatagosauropus*** (Dzhalilov & Novikov, 1993; Nessov, 1995) | | Ca–Ma: Aguilillas Sandstone, Mexico—**U/U** (Rivera-Sylva et al., 2006; Rodríguez-de la Rosa et al., 2004) | |
| | Ha–Ba: unnamed unit, Cameroon—**U/U** (Dejax et al., 1989; Jacobs et al., 1989, 1996) | Al–Ce: Mussentuchit Mbr., Cedar Mountain Fm., UT—**U/U** (Kirkland et al., 1997; Lockley et al., 1999) | | Ca–Ma: Wapiti Fm. AB—***Amblydactylus*** (Currie, 1989; Tanke, 2004) | |
| | Ha–Ba?: Hekou Gp., Gansu, China—**cf. *Caririchnium*** (Li et al., 2006a) | Al–Ce: Tantalus Fm., Yukon—***Amblydactylus, Gypsichnites*** (Gangloff et al., 2004; Long et al., 2001) | | Ca–Ma: unnamed unit, Korea—**U/U (*Caririchnium*–like)** (Huh & Hwang, 2004; Paik et al., 2006) | |
| | Ha–Ba: Hasandong & Jinju fms., Korea—***Caririchnium*, U/U** (Huh et al., 2003; Kim et al., 2002, 2009) | Al–Ce: Candeleros Fm., Argentina—***Limayichnus* (=*Bonapartichnium*), *Sousaichnium*** (Calvo, 1991, 1999, 2007) | | Ca–Ma: St. Mary River & Horseshoe Canyon fms., AB—***Hadrosauropodus*, U/U** (Currie, 1989; Lockley et al., 2004a) | |
| | Ha–Ba:Okurodani (= Kitadani) & Kuwajima fms., Tetori Gp., Japan—***Hadrosaurichnus* (=*Shiraminesauropus*, = *Gigantoshiraminesauropus*, = Ornithopod type A[3]), *Caririchnium*** (Azuma, 2003;Azuma & Takeyama, 1991; Matsukawa et al., 2005, 2006a) | Al–Ce: Chandler and Corwin fms., AK—**cf. *Amblydactylus*, U/U** (Gangloff, 1998; Roehler & Stricker, 1984) | | Ca–Ma: Upper unit, Vilquechico Gp., Peru—***Hadrosaurichnus*** (Jaillard et al., 1993) | |
| | Ba: Yellow Cat Mbr., Cedar Mountain Fm., UT—**U/U** (Lockley et al., 1999) | Ce: Mesa Rica Sandstone, Dakota Gp., CO, NM—***Caririchnium*** (Lockley, 1987; Lucas et al., 2000; Matsukawa et al., 2001; Schumacher, 2003) | | Ma: Nemegt Fm., Mongolia—**U/U** (Currie et al., 2003; Watabe et al., 2010) | |
| | Ba: Lakota Fm., SD—**U/U** (Lockley et al., 2001) | Ce: Woodbine Fm., TX—***Caririchnium*** (Lee, 1997; Pittman, 1989) | | Ma: Lance Fm., WY—***Hadrosauropodus*, U/U** (Lockley et al., 2004a; Smith, 2002) | |
| | Ba: Alacon Fm., Spain—**U/U** (Auqué Sanz et al., 1986; Weishampel et al., 2004) | Ce: Uhangri Fm., Korea—***Caririchnium*, U/U** (Huh et al., 2003; Yang et al., 1997) | | Ma: Tremp Fm., Spain—***Orcauichnites***[5], ***Hadrosauropodus*** (Casanovas et al., 1987; Llompart, 2006; Suñer et al., 2008) | |
| | Ba: unnamed unit, Portugal—***Iguanodontipus*** (dos Santos et al., 2008) | Ce: Itapecuru Gp., Brazil—**U/U** (Carvalho, 2001) | | Ma: Nemegt Fm. Mongolia—**"*Amblydactylus*"- & "*Caririchnium*"– type** (Currie et al., 2003; Ishigaki et al., 2009) | |
| | Ba–Ap: Festningen Sandstone Mbr., Helvetiafjellet Fm., Svalbard Isl.—**U/U** (Hurum et al., 2006) | Ce?[4]—Jindong Fm., Korea—**U/U** (Lim et al., 1989; Paik et al., 2001) | | Ma: Mexcala Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Ba–Ap: Vectis Fm., England—**U/U** (Beckles, 1851; Radley et al., 1998) | "middle" Cretaceous: Jiaguan Fm., Sichuan & Chongqing, China—***Iguanodontipus, Caririchnium, Laoyingshanpus*** (Xing et al., 2007, 2009a; Zhen et al., 1994) | | Ma: Laramie Fm., CO—**U/U** (Lockley & Hunt, 1995a) | |

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| **Taxon** | **E. Cretaceous (Be–Ba)** | **“Middle” Cretaceous (Ap–Ce)** | **E. Cretaceous Undifferentiated** | **L. Cretaceous (Tu–Ma)** | **L. Cretaceous Undifferentiated** |
|---|---|---|---|---|---|
| | Ba–Ap: Cadomin Fm., BC—***Amblydactylus*** (Currie, 1989) | early L. Cretaceous: Fangyan Fm., Zhejiang, China—**U/U** (Lü et al., 2010) | | Ma: Blackhawk Fm., UT—**U/U (“*Dinosauropodes*”)** (Parker & Rowley, 1989) | |
| | Ba–Ap: Zhidan Gp., Nei Mongol, China—**U/U** (Azuma et al., 2006) | | | Ma: Raton Fm., NM—**U/U** (Lockley et al., 2000) | |
| | Ha–Ap: Yangjiazhuang Fm., Laiyang Gp., Shandong, China—**U/U** (Xing et al., 2010a) | | | Ma: Aren Fm., Spain—**U/U** (Barco et al., 2001) | |
| | Va–Ap: Helvetiafjellet Fm., Spitsbergen—**U/U** (de Lapparent, 1960, 1962; Edwards et al., 1978) | | | Ma: Arcillas Grises, Spain—***Ornithopodichnites***[5]**, *Orcauichnites***[5] (Llompart et al., 1984) | |
| | Be–Ha: Matsuo Gp., Japan—**U/U** (Matsukawa et al., 2005; Saka, 2001) | | | Ma: El Molino Fm., Bolivia—**U/U** (Lockley et al., 2002a) | |
| | Be–Ba: Phra Wihan Fm., Thailand—**U/U** (Le Loeuff et al., 2005) | | | Ma: Xiaoyan Fm., Anhui, China—**U/U** (Yu et al., 1999) | |
| | Ba–Ap: Xiguayuan (= Jiufotang) Fm., Hebei, China—**U/U** (Chen et al., 2006; Lockley & Wright, 2001; You & Azuma, 1995) | | | Ma: Zhutian Fm., Guangdong, China—***Hadrosauropodus*** (Xing et al., 2009a) | |
| | Be–Ap: Corda Fm., Brazil—**U/U** (Leonardi & Sarjeant, 1986) | | | Ma: “Gaizes,” Poland—**U/U** (Gierliński, 2009; Gierliński et al., 2008) | |
| | | | | Ma: Yacoraite Fm., Argentina—***Taponichnus*, *Telosichnus*** (Alonso, 1989; Alonso & Marquillas, 1986) | |
| | | | | Ma: Wagad Fm., India—**U/U** (Ghevariya & Srikarni, 1990; Weishampel et al., 2004) | |
| **Sauropoda** | Callovian–Be: Amran Gp., Yemen—**U/U** (Schulp et al., 2008) | Ap: Calcare di Bari Fm., Italy—**U/U** (Petti et al., 2008; Sacchi et al., 2008) | E. Cretaceous: Chacarilla Fm., Chile—**U/U** (Leonardi, 1989; Rubilar-Rogers et al., 2008) | Ce–Tu: Kem-Kem Beds, Morocco—**U/U** (Sereno et al., 1996) | |
| | Ti–Be: Oncala Gp., Spain—***Parabrontopodus*, *Brontopodus*** (Fuentes Vidarte et al., 2005a; Meijide Fuentes et al., 2001, 2004) | Ap: Patuxent Fm., MD & VA—**U/U** (Stanford et al., 2004, 2007) | | Tu–Co: Jiangdihe Fm., Yunnan, China—***Brontopodus* (= *Chuxiongpus*)** (Chen & Huang, 1993; Lockley et al., 2002b) | |
| | Ti–Be: Villar del Arzobispo & Hirgueles fms., Spain—**U/U** (Blanco et al., 2000; Cuenca-Bescós et al., 1999; Royo-Torres et al., 2009) | Ap–Al: El Rhaz Fm., Niger—**U/U** (Ginsburg et al., 1966; Taquet, 1976, 1977) | | Ca: Toro Toro/Chaunaca Fm., Bolivia—**U/U** (Lockley et al., 2002a) | |
| | Ti–Be: Mist Mountain Fm., BC—***Brontopodus*** (McCrea et al., 2005) | Ap–Al: Glen Rose Limestone, TX & De Queen Fm., AR—***Brontopodus*** (Bird, 1939, 1954; Farlow, 1987; Langston, 1974; Pittman & Gillette, 1989) | | Ca–Ma: Loncoche Fm., Argentina—***Titanopodus*** (Gonzalez Riga, 2011; González Riga & Calvo, 2009) | |
| | Be: Buckeburg Fm., Germany—***Rotundichnus*, U/U** (Lockley et al., 2004c; Richter, 1998) | Ap–Al: “Gres Superieurs” (= Khok Kruat Fm), Laos—**U/U** (Allain et al., 1997; Le Loeuff et al., 2009) | | Ca–Ma: unnamed unit, Korea—**U/U** (Paik et al., 2006) | |
| | Be: Huerteles & Rupelo fms., Spain—**U/U** (Latorre Macarrón et al., 2006; Moratalla, 2009; Pascual Arribas & Sanz Pérez, 2000; Platt & Meyer, 1991) | Ap–Al: Haman, Jindong, & Sagog fms., Korea—**U/U** (Kim et al., 2010; Lee et al., 2001; Lim et al., 1994; Paik et al., 2001) | | Ma: Mexcala Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Be–Va: Broome Sandstone, Australia—***Brontopodus*** (Thulborn et al., 1994) | Ap–Al: Ruby Ranch Mbr., Cedar Mountain Fm., UT—***Brontopodus*** (Lockley et al., 1999, 2004b) | | Ma: Nemegt Fm., Mongolia—***”Brontopodus”*–type** (Currie et al., 2003; Ishigaki et al., 2009) | |
| | Be–Va: Wessex Fm., Wealden Gp., England—**U/U** (Radley, 1994; Wright et al., 1998) | Ap–Al: Enciso Gp., Spain—***Titanosaurimanus*, U/U** (Moratalla & Hernán, 2008; Pérez-Lorente & Jiménez Vela, 2008; Requeta Loza et al., 2008) | | Ma: North Cape Fm., New Zealand—**U/U** (Browne, 2009) | |

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| Taxon | E. Cretaceous (Be–Ba) | "Middle" Cretaceous (Ap–Ce) | E. Cretaceous Undifferentiated | L. Cretaceous (Tu–Ma) | L. Cretaceous Undifferentiated |
|---|---|---|---|---|---|
| | Be–Ba: Sousa & Antenor Navarro fms., Brazil—**U/U** (Leonardi, 1989; Leonardi & de Souza Carvalho, 2007; Leonardi & dos Santos, 2004) | Ap–Al: Khok Kruat Fm., Thailand—**U/U** (Le Loeuff et al., 2005) | | Ma: Tremp Fm., Pyrenees (Spain)—**U/U** (Bates et al., 2008; Le Loeuff & Martinez-Rius, 1997; López-Martinez et al., 1997; Schulp & Brokx, 1999; Vila et al., 2008) | |
| | Be–Ba: Phra Wihan Fm., Thailand—**U/U** (Le Loeuff et al., 2002, 2005, 2009) | Al: San Juan Raya Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006; Rodríguez-de la Rosa et al., 2004) | | Ma(?): Zhutian Fm., Guangdong, China—**U/U** (Zhang X et al., 2006a)$^{7,8}$ | |
| | Ha: unnamed unit, Portugal—***Brontopodus*** (Antunes, 1976; dos Santos et al., 2008; Lockley et al., 1994a) | Al: Utrillas Monte Grande fms., Spain—**U/U** (Moratalla et al., 1994a; Pérez-Lorente et al., 2006) | | Ma: Arcillas Grises, Spain—**U/U** (Llompart et al., 1984) | |
| | Ha: El Castellar & Pinilla de los Moros fms., Spain—**U/U, *Brontopodus*** (Cuenca-Bescós et al., 1999; Fernández-Baldor et al., 2006; Ruiz-Omeñaca et al., 2004) | Al: Luchak Fm., Tadjikistan—***Chorrokhsauropus*** (Dzhalilov & Novikov, 1993; Nessov, 1995) | | Ma: El Molino Fm., Bolivia—**U/U** (Lockley et al., 2002a) | |
| | Ha?: Kysyltash Series, Uzbekistan—**U/U** (Meyer, 1998; Meyer & Lockley, 1997) | Al: Edwards Fm., TX—**U/U** (Weishampel et al., 2004) | | Ma: Xiaoyan Fm., Anhui, China—**U/U** (Yu et al., 1999) | |
| | Ha–Ba?: Hekou Gp., Gansu, China—***Brontopodus*** (Li et al., 2006a; Zhang J et al., 2006) | Al–Ce: unnamed unit, Croaia—***Titanosaurimanus*** (Dalla Vecchia, 2005; Dalla Vecchia et al., 2000) | | Ma: Wagad Fm., India—**U/U** (Ghevariya & Srikarni, 1990; Weishampel et al., 2004) | |
| | Ha–Ba: Calcare del Cellina Fm., Italy—**U/U** (Dalla Vecchia, 2005) | Al–Ce: Candeleros Fm., Argentina—***Sauropodichnus*** (Calvo, 1991, 1999; Calvo & Mazzetta, 2004) | | | |
| | Ha–Ba: unnamed unit, Croatia—**U/U** (Dalla Vecchia, 2005) | Ce: Uhangri Fm., Korea—**U/U** (Hwang et al., 2008; Lee & Huh, 2002; Thulborn, 2004) | | | |
| | Ba: unnamed unit, Portugal—**U/U** (dos Santos et al., 2008) | Ce: unnamed unit, Italy—**U/U** (Dalla Vecchia et al., 2005) | | | |
| | Ba: Alacon Fm., Spain—**U/U** (Auqué Sanz et al., 1986; Weishampel et al., 2004) | Ce: unnamed unit, Portugal—**U/U** (Antunes & Mateus, 2003; dos Santos et al., 2008) | | | |
| | Ba: Yellow Cat Mbr., Cedar Mountain Fm., UT—**U/U** (Lockley et al., 1999) | Ce: Itapecuru Gp., Brazil—**U/U** (Carvalho, 2001) | | | |
| | Ha–Ap: Yangjiazhuang Fm., Laiyang Gp., Shandong, China—**U/U** (Xing et al., 2010a) | Ce: unnamed unit, Croa-tia—**U/U** (Mezga et al.,2006b) | | | |
| | Ha?–Ap?: Mengtuan Fm., Jiangsu, China—***Parabrontopodus*** (Xing et al., 2010b) | | | | |
| | Ba–Ap: Urbion & Enciso gps, Spain—**U/U (*Parabrontopodus*?)** (Ansorena et al., 2008; Moratalla, 2009) | | | | |
| | Ba–Ap: Yijinholo (= Jingchuan) Fm., Nei Mongol, China—***Brontopodus*** (Li et al., 2006b; Lockley et al., 2002b) | | | | |
| | Ba–Ap: Shouchang Fm., Zhejiang, China—**U/U** (Matsukawa et al., 2009) | | | | |
| | Ba–Ap: Xiguayuan (= Jiufotang) Fm., Hebei, China—**U/U** (Ji et al., 2008) | | | | |
| | Be–Ap: Corda Fm., Brazil—**U/U** (Leonardi & Sarjeant, 1986) | | | | |
| | Ba-Al: Puchanghe Fm., Yunnan, China$^{6}$—**U/U** (Fujita et al., 2008) | | | | |
| | L. Jurassic–Ha: Gres d'Assaouas, Niger—**U/U** (Ginsburg et al., 1966; Taquet, 1976) | | | | |
| **non-avian Theropoda** | Ti–Be: Purbeck Limestone Fm., England—"***Iguanodontipus***" (Wright et al., 1998) | Ap: Calcare di Bari Fm., Italy—**U/U** (Petti et al., 2008; Sacchi et al., 2008) | E. Cretaceous: Urbion Gp., Spain—**U/U** (Ansorena et al., 2008) | Ce–Tu: Mifune Gp., Japan—**U/U** (Matsukawa et al., 2005) | L. Cretaceous: Xiaodong (= Jinjiang) Fm., Hunan, China—***Hunanpus, Xiangxipus*** Geological Bureau of Hunan, 1982) |

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(Continued)

| TAXON | E. CRETACEOUS (BE–BA) | "MIDDLE" CRETACEOUS (AP–CE) | E. CRETACEOUS UNDIFFERENTIATED | L. CRETACEOUS (TU–MA) | L. CRETACEOUS UNDIFFERENTIATED |
|---|---|---|---|---|---|
| | Ti–Be: Villar del Arzobispo & Hirgue-les fms., Spain—**U/U** (Cobos et al., 2005; de Santisteban et al., 2009; Pérez-Lorente & Herrero Gascón, 2007; Pérez-Lorente & Ortega, 2004; Pérez-Lorente & Romero Molina, 2001) | Ap: Glen Rose Limestone, TX—"***Eubrontes***" (= ***Megalosauropus*****), *Ireni sauripus*** (= "***Grallator***"**)** (Farlow, 1987; Hawthorne et al., 2002; Langston, 1974; Rogers, 2002; Shuler, 1917) | E. Cretaceous: un named unit, Republ. Georgia—***Satapliasaurus*** (Gabuniya, 1951; Vekua & Mchedlidze, 2005) | Ce–Tu: Kem-Kem Beds, Morocco—**U/U** (Sereno et al., 1996) | L. Cretaceous: Aguilillas Sandstone, Mexico—**U/U** (Rivera-Sylva et al., 2006; Rodríguez-de la Rosa et al., 2004) |
| | Ti–Be: Oncala Gp., Spain—***Therangospodus*****, *Filichnites*, "*Yanguanosaurus*,"** **U/U** (Fuentes Vidarte et al., 2005a, 2005b; Lockley & Meyer, 2000; Moratalla, 1993*; Sanz et al., 1999) | Ap: Patuxent Fm., MD & VA—**U/U** (Stanford et al., 2007) | E. Cretaceous: Caiua Fm., Brazil—**U/U** (Leonardi, 1989) | Tu: Moreno Hill Fm., NM—**U/U** (Wolfe, 2006) | |
| | L. Jurassic–E. Cretaceous: Botucatu Fm. & Areado Gp., Brazil—**U/U** (de Souza Carvalho & da Silva Kattah, 1996; Leonardi et al., 2007) | Ap: Amagodani (= Akaiwa, = Okura) & Nochino fms., Tetori Gp., Japan—**U/U** (Matsukawa et al., 2005) | | Tu–Co: Jiangdihe Fm., Yunnan, China—***Yunnanpus*** (Chen & Huang, 1993) | |
| | L. Jurassic–E. Cretaceous: La Puerta Fm., Bolivia—**U/U** (Apesteguía & Gallina, 2011) | Ap–Al: El Rhaz Fm., Niger—**U/U** (Ginsburg et al., 1966; Taquet, 1976) | | Sa?: Iron Springs Fm., UT—**U/U** (Milner et al., 2006) | |
| | L. Jurassic–E. Cretaceous: Takutu Fm., Guyana—**U/U** (McConnell et al., 1969) | Ap–Al: Enciso Gp., Spain—***Theroplantigrada*****,** **U/U** (Álvarez et al., 2000; Casanovas Cladellas et al., 1993a; Ezquerra et al., 2007; Moratalla & Hernán, 2008; Pérez-Lorente & Jiménez Vela, 2008; Requeta Loza et al., 2008) | | Sa: John Henry Mbr., Straight Cliffs Fm., UT—**U/U** (Hamblin & Foster, 2000) | |
| | L. Jurassic–E. Cretaceous: Quebrada Monardes Fm., Chile—**U/U** (Bell & Suárez, 1989) | Ap–Al: Haman Fm., Korea—***Minisauripus, Dromaeosauripus*** (Kim et al., 2008; Lockley et al., 2008b) | | Ca: "Mesaverde Gp.," UT—***Ornithomimipus*****,** ***Grallator*****-like** (Lockley et al., 2011a) | |
| | Be: Oncala Gp., Spain—**U/U, *Kalohipus*** (Barco et al., 2005; Fuentes Vidarte & Meijide Calvo, 1998) | Ap–Al: Tianjialou Fm., Shandong, China—***Dromaeopodus*****, *Velociraptorichnus*, *Minisauripus*** (Li et al., 2005a, 2007; Lockley et al., 2008b) | | Ca: Muerto Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Be: Tuchengzi Fm., Liaoning, China—***Grallator, Menglongipus, Anchisauripus*****, *Therangospodus*, *Megalosauripus*** (Fujita et al., 2007; Sullivan et al., 2009; Xing et al., 2009c, 2011c; Zhang et al., 2004) | Ap–Al: Fuxin Fm., Liaoning, China—***Changpeipus*****,** **U/U** (Chen et al., 2006; Young, 1960) | | Ca: Judith River Fm., AB—**U/U** (Currie, 1989) | |
| | Be: Buckeburg Fm., Germany—***Buckeburgichnus*** (Lockley, 2000; Thulborn, 2001) | Ap–Al: Khok Kruat Fm., Thailand—**U/U** (Le Loeuff et al., 2005) | | Ca: Toro Toro/Chaunaca Fm., Bolivia—**U/U** (Lockley et al., 2002a) | |
| | Be: Obernkirchen Sandstone, Germany— ***Megalosauropus*****,** **U/U** (Diedrich, 2004; Richter et al., 2007; van der Lubbe et al., 2009) | Ap–Al: "Complexo gresoso de Olhos Amarelos e Pousio da Galeota", Portugal—**U/U** (Mateus & Antunes, 2003) | | Ca: Djadokhta Fm., Mongolia—**U/U** **(*Eubrontes*–like)** (Ishigaki, 2010) | |
| | Be: Huerteles & Sierra del Pozo fms. & Oncala Gp., Spain—***Archaeornithipus***, ***Therangospodus*****,** **U/U** (Barco, 2006; Fuentes Vidarte, 1996; García-Hernández et al., 2004; Pascual Arribas & Sanz Pérez, 2000; Platt & Meyer, 1991) | Ap–Al: Gething Fm., BC—***Columbosauripus*****, *Irenisauripus*, *Ornithomimipus* (= *Irenichnites*)** (Kool, 1981; Sternberg, 1932) | | Ca–Ma: Aguililla Sandstone, Mexico—**U/U** (Rodríguez-de la Rosa et al., 2004) | |
| | Be–Va?: Yangjiazhuang (?= Shuinan) Fm., Shandong, China—***Therangospodus*****, *Megalosauripus*** (Xing et al., 2010a) | Al: San Juan Raya Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006; Rodríguez-de la Rosa et al., 2004) | | Ca–Ma: Upper unit, Vilquechico Gp., Peru—***Ornithomimipus*** (Jaillard et al., 1993) | |
| | Be–Va: Broome Sandstone, Australia—***Megalosauropus*** (Colbert & Merrilees, 1967; Thulborn et al., 1994) | Al: Eumeralla Fm., Australia—**U/U** (Martin et al., 2011) | | Ca–Ma: unnamed unit, Korea—**U/U (*Irenisauri- pus*–, *Megalosauripus*–, and *Magnoavipes*–like)** (Paik et al., 2006) | |
| | | | | | |

(To be continued)

*Moratalla J J. 1993. Restos Indirectos de Dinosaurios del Registro Español: Paleoichnología de la Cuenca de Cameros (Jurasíco Superior–Cretácico Inferior) y Paleoología del Cretácico Superior [Ph.D. dissertation]. Madrid: Universidad Autónoma. 1-727

(Continued)

| Taxon | E. Cretaceous (Be–Ba) | "Middle" Cretaceous (Ap–Ce) | E. Cretaceous Undifferentiated | L. Cretaceous (Tu–Ma) | L. Cretaceous Undifferentiated |
|---|---|---|---|---|---|
| | Be–Va: Wessex Fm., Wealden Gp., England—**U/U** (Wright et al., 1998) | Al: unnamed unit, Croatia—**U/U** (Mezga et al., 2006a) | | Ca–Ma: Cantwell Fm., AK—***Magnoavipes***, **U/U** (Fiorillo et al., 2010b; Santucci et al., 2006) | |
| | Be–Va: Izuki Fm., Tetori Gp., Japan—***Itsukisauropus***, **U/U** (Azuma & Takeyama, 1991; Matsukawa et al., 2005) | Al: Dakota Gp (incl. Mojado & Pajarito fms. & Anapra Sandstone), NM—***Magnoavipes*** (Kappus & Cornell, 2003; Kappus et al., 2003; Lucas et al., 1989) | | Ca–Ma: Horseshoe Canyon Fm., AB—***Ornithomimipus*** (Currie, 1989; Lockley et al., 2004a) | |
| | Be–Va: Mist Mountain Fm., BC—**U/U** (Currie, 1989) | Al: Gates Fm., AB—***Irenisauripus*** (Currie, 1989; McCrea, 2000; McCrea et al., 2002) | | Ca: Wahweap Fm., UT—**U/U** (Simpson et al., 2010b) | |
| | Va–Ha: Piedrahita de Muñó Fm., Spain—**U/U** (Platt & Meyer, 1991) | Al: Shirabad Fm., Tadjikistan—***Macropodosaurus*** (Nessov, 1995; Sennikov, 2006; Zakharov, 1964) | | Ma: unnamed unit, Morocco—**U/U** (Ambroggi & de Lapparent, 1954) | |
| | Ha: El Castellar & Pinilla de los Moros fms., Spain—**U/U** (Fernández-Baldor et al., 2006; Ruiz-Omeñaca et al., 2004) | Al: Jindong, Jemgog, Geoncheonri, & Sagog fms., Korea—**U/U** (Lee et al., 2000, 2001) | | Ma: Nemegt Fm., Mongolia—***Asianopodus***, "***Grallator***"–&"***Eubrontes***"–**type** (Currie et al., 2003; Ishigaki et al., 2009) | |
| | Ha: Ladeiras Formation, Portugal—***Eutynichnium*** (Antunes, 1976; Antunes & Mateus, 2003; Lockley et al., 1998b) | Al: Fort Terrett Fm., TX—**U/U** (Pittman, 1989) | | Ma: Olmos Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Ha: unnamed unit, Italy—**U/U** (Dalla Vecchia & Venturini, 1995) | Al–Ce: Winton Fm., Australia—**cf. *Tyrannosauropus***[10], ***Skartopus*** (Thulborn, 2011; Thulborn & Wade, 1984) | | Ma: Lance Fm., WY—***Saurexallopus***, ***Ornithomimipus*–like**, **U/U** (Lockley et al., 2004a; Smith, 2002) | |
| | Ha?: Yanji Fm., Jilin, China—**U/U** (Matsukawa et al., 1995) | Al–Ce: unit unknown, Croatia: **U/U** (Kržič, 2010) | | Ma: Blackhawk Fm., UT—**U/U** (Parker & Rowley, 1989) | |
| | Ha–Ba?: Shuinan Fm., Shandong, China—**cf. *Grallator* or *Paragrallator*** (Li et al., 2011) | Al–Ce: Tantalus Fm., Yukon—***Irenisauripus***, ***Columbosauripus***, ***Ornithomimipus*** (Gangloff et al., 2004; Long et al., 2001) | | Ma: Raton Fm., NM—***Tyrannosauripus*** (Lockley & Hunt, 1994a; Lockley et al., 2000) | |
| | Ha–Ba: Longwangzhuang Fm., Laiyang Gp., Shandong, China—***Paragrallator***, ***Corpulentapus*** (Li et al., 2011; Li & Zhang, 2000) | Al–Ce: Candeleros Fm., Argentina—***Abelichnus***, ***Deferrariischnium***, ***Bressanichnus***, ***Picunichnus***, **U/U** (Calvo, 1989, 1991, 1999; Calvo & Mazzetta, 2004) | | Ma: Tremp Fm., Pyrenees (Spain)—**U/U** (Llompart, 2006; Vila et al., 2004, 2008) | |
| | Ha–Ba?: Hekou Gp., Gansu, China—**U/U** (Azuma et al., 2009; Li et al., 2006a; Zhang J et al., 2006) | Al–Ce: Dakota Fm./Gp., CO, KS—***Magnoavipes***, **U/U** (Liggett, 2005; Schumacher, 2003) | | Ma: Xiaoyan Fm., Anhui, China—**U/U** (Yu et al., 1999) | |
| | Ha–Ba: Tugulu Gp., China—***Jialingpus, Asianopodus, Kayentapus*** (Xing et al., 2011b) | Al–Ce: Cazaderos Fm., Ecuador—**U/U** (Leonardi, 1994) | | Ma: "Gaizes, " Poland—***Irenisauripus***, ***Macropodosaurus***, ***Saurexallopus***, ***Velociraptorichnus*** (Gierliński, 2008, 2009; Gierliński et al., 2008) | |
| | Ha–Ba: Okurodani (= Kitadani) & Kuwajima fms., Tetori Gp., Japan—***Asianopodus***, ***Byakudansauropus***, ***Kuwajimasauropus***, **U/U** (Azuma, 2003; Azuma & Takeyama, 1991; Manabe et al., 1989; Matsukawa et al., 1997, 2005) | Al–Ce: Segovia Fm., TX—**U/U** (Pittman, 1989) | | Ma: Harebell Fm., WY—***Saurexallopus*** (Harris, 1997; Harris et al., 1996) | |
| | Ha–Ba: Xiguayuan Fm., Hebei, China—**U/U** (You & Azuma, 1995) | Ce: Judea Gp., Israel—**U/U** (Avnimelech, 1966) | | Ma: Hell Creek Fm., Montana—**U/U** (Manning et al., 2008) | |
| | Ha–Ba: San Giovanni Rotondo Fm., Italy—**U/U** (Dal Sasso, 2003; Gianolla et al., 2000) | Ce: unnamed unit, Portugal—**U/U** (Antunes & Mateus, 2003; dos Santos, 1998; dos Santos et al., 2008) | | Ma: Laramie/Arapahoe Fm., CO—**U/U** (Lockley & Hunt, 1995b) | |
| | Ba: unnamed unit, Croatia—**U/U** (Mezga et al., 2006a) | Ce: Uhangri Fm., Korea—**U/U** (Huh et al., 2003; Huh et al., 1997) | | Ma: Yacoraite Fm., Argentina—***Salfitichnus*** (Alonso, 1989; Alonso & Marquillas, 1986) | |
| | Ba: Yellow Cat Mbr., Cedar Mountain Fm., UT—**U/U** (Lockley et al., 1999) | Ce: unnamed unit, Italy—**U/U** (Dalla Vecchia et al., 2005) | | Ma: Santa Lucia Fm., Bolivia—**U/U** (Leonardi, 1989) | |

(To be continued)

(Continued)

| TAXON | E. CRETACEOUS (BE–BA) | "MIDDLE" CRETACEOUS (AP–CE) | E. CRETACEOUS UNDIFFERENTIATED | L. CRETACEOUS (TU–MA) | L. CRETACEOUS UNDIFFERENTIATED |
|---|---|---|---|---|---|
| | Ba–Ap: Cadomin Fm., BC—***Irenisauripus*** (Currie, 1989) | Ce: Itapecuru Gp., Brazil—**U/U** (Carvalho, 2001; de Souza Carvalho & Pedrão, 1998) | | Ma: Red Beds (?= Soncco) Fm., Peru—**U/U** (Noblet et al., 1995; Weishampel et al., 2004) | |
| | Ba–Ap: Yixian Fm., Liaoning, China—***Grallator* (= *Jeholosauripus*)** (Azuma & Fujita, 2005; Xing et al., 2009b) | Ce: Woodbine Fm., TX—***Magnoavipes*, *Fuscinapedis*** (Lee, 1997) | | | |
| | Ba–Ap: Donghe Gp., Shaanxi, China—***Megalosauripus*** (Hu et al., 2011) | Ce: Dunvegan Fm., AB—***Columbosauripus*** (McCrea et al., 2001a; Storer, 1975) | | | |
| | Ba–Ap: Vectis Fm., England—**U/U** (Radley et al., 1998) | Ce: Raritan Fm., NJ—**U/U** (Baird, 1989) | | | |
| | Ba–Ap: Yijinholo (=Jingchuan) Fm., Nei Mongol, China: ***Chapus*** (Azuma et al., 2006; Li et al., 2006b) | "mid–Cretaceous": Jiaguan and Wotoushan fms., Sichuan, Chongqing, & Guizhou, China: ***Wupus*, *Minisauripus*, *Velociraptorichnus*, *Grallator*, cf. *Irenisauripus*** (Lockley et al., 2008b; Xing et al., 2007, 2011a; Zhen et al., 1994) | | | |
| | Ba–Ap?: Phu Phan Fm., Thailand—**U/U** (Le Loeuff et al., 2005) | early L. Cretaceous: Fangyan Fm., Zhejiang, China—**U/U** (Lü et al., 2010) | | | |
| | Ba–Ap: Xiguayuan (= Jiufotang) Fm., Hebei, China—**U/U** (Chen et al., 2006; Ji et al., 2008; You & Azuma, 1995) | | | | |
| | Ba-Al: Puchanghe Fm., Yunnan, China[6]—**U/U** (Fujita et al., 2008) | | | | |
| | Ha?–Ap?: Mengtuan Fm., Jiangsu, China—**U/U** (Xing et al., 2010b) | | | | |
| | Be–Ba: Sousa, Piranhas, & Antenor Navarro fms., Brazil—***Moraesichnium***[9]**, U/U** (Calvo et al., 2002; Leonardi, 1987b, 1989; Leonardi & de Souza Carvalho, 2007; Leonardi & dos Santos, 2004) | | | | |
| | Be-Ba: Phra Wihan Fm., Thailand—***Siamopodus*** (Le Loeuff et al., 2009; Lockley et al., 2006e) | | | | |
| | Be–Ap: Chacarilla Fm., Chile—**U/U** (Moreno et al., 2011; Rubilar-Rogers et al., 2008) | | | | |
| | Va–Ap: Helvetiafjellet Fm (Festningsodden Sandstone), Spitsbergen—**U/U** (de Lapparent, 1960, 1962; Edwards et al., 1978) | | | | |
| | Neocomian: Hualhuani Formation, Chile—**U/U** (Moreno et al., 2011) | | | | |
| AVES | Ti–Be: Oncala Gp., Spain—**U/U** (Fuentes Vidarte et al., 2005a) | Ap–Al: Gething & Gladstone fms., BC—***Aquatilavipes*** (Currie, 1981; Lockley & Rainforth, 2002; McCrea et al., 2004) | | Ca: Anacleto Fm., Argentina—***Ignotornis*, *Barro sopus*, *Aquatilavipes*** (Calvo, 2007; Coria et al., 2002) | L. Cretaceous: Qiuzhuang (Chiou Chuang) Fm., Anhui, China—***Aquatilavipes*** (Jin & Yan, 1994) |
| | Be: Tuchengzi Fm., Liaoning, China—***Pullornipes*** (Lockley et al., 2006b) | Ap–Al: Haman & Jindong fms., Korea—***Jindongornipes, Hwangsanipes, Koreanaornis, Goseongornipes, Uhangrichnus*** (Lim et al., 2000; Lockley et al., 2006c) | | Ca: Cerro del Pueblo Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006) | |
| | Be: Oncala Gp., Spain—***Archaeornithipus***[11] (Fuentes Vidarte, 1996) | Ap–Al: Tianjialou Fm., Shandong, China—***Shandongornipes*** (Li et al., 2005b; Lockley et al., 2007b) | | Ca–Ma: Cantwell Fm., AK—***Aquatilavipes*, *Ignotornis*, *Gruipeda*, *Uhangrichnus*** (Fiorillo et al., 2010b) | |
| | Be: Mist Mountain Fm., BC—**U/U** (McCrea et al., 2001a) | Al–Ce: upper Nanushuk Gp., AK—**U/U**[12] (Ahlbrandt et al., 1979; Davies, 1987) | | Ca–Ma: St. Mary River & Horseshoe Canyon fms.,AB—***Jindongornipes*– and *Aquatilavipes*–like** (McCrea et al., 2001a) | |

(To be continued)

(Continued)

| Taxon | E. Cretaceous (Be–Ba) | “Middle” Cretaceous (Ap–Ce) | E. Cretaceous Undifferentiated | L. Cretaceous (Tu–Ma) | L. Cretaceous Undifferentiated |
|---|---|---|---|---|---|
| | Be–Va: Izuki (=Itsuki) Fm., Tetori Gp., Japan—***Aquatilavipes*** (Azuma et al., 2002; Lockley et al., 1992b) | Al–Ce: Dakota Gp., CO, UT—***Koreanaornis, Ignotornis*** (Anfinson et al., 2009; Lockley et al., 1992b, 2009a) | | Ma: Blackhawk Fm., UT—**U/U** (Lockley & Rainforth, 2002; Robison, 1991) | |
| | Ha: Pinilla de los Moros Fm., Spain—**U/U** (Fernández-Baldor et al., 2006) | Ce: Uhangri Fm., Korea—***Uhangrichnus*, *Hwangsanipes*** (Yang et al., 1995, 1997) | | Ma: North Horn Fm., UT—**U/U** (Lockley, 1999) | |
| | Ha–Ba?: Hekou Gp., Gansu, China—**U/U** (Li et al., 2006a; Zhang J et al., 2006) | “middle” Cretaceous: Jiaguan Fm., Chongqing, China—***Koreanaornis* (= *Aquatilavipes sinensis*)** (Lockley & Harris, 2010; Lockley et al., 1992b; Xing et al., 2007) | | Ma: Lance Fm., WY—***Sarjeantopodus*, U/U** (Lockley et al., 2004a) | |
| | Ha–Ba: Tugulu Gp., China—***Koreanaornis, Goseongornipes, Aquatilavipes, Moguiornipes*** (Xing et al., 2011b) | early L. Cretaceous: Fangyan Fm., Zhejiang, China—***Aquatilavipes*** (Lü et al., 2010) | | Ma: Olmos Fm., Mexico—**U/U** (Rivera-Sylva et al., 2006; Rodríguez-de la Rosa et al., 2004) | |
| | Ha–Ba: Okurodani (= Kitadani) & Kuwajima fms., Tetori Gp., Japan—**U/U** (Azuma, 2003) | | | Ma: Yacoraite Fm., Argentina—***Yacoraitichnus*** (Alonso, 1989; Alonso & Marquillas, 1986) | |
| | Ba: Yellow Cat Mbr., Cedar Mountain Fm., UT—**U/U** (Wright et al., 2006) | | | Ma: unknown/unnamed unit, Argen-tina—**”*Patagonichornis*”** (Chiappe, 1996; Leonardi, 1987a, 1994) | |
| | Ba: Lakota Fm., SD—**U/U** (Lockley et al., 2001) | | | Ma: Raton Fm., NM—**U/U** (Lockley & Hunt, 1995a) | |
| | Ba–Ap: Yijinholo (= Jingchuan) Fm., Nei Mongol, China—***Tatarornipes*** (Lockley et al., 2011c) | | | Ma: unnamed unit, Morocco—**U/U** (Ambroggi & de Lapparent, 1954) | |
| | Ha–Ap: Yangjiazhuang Fm., Laiyang Gp., Shandong, China—**U/U** (Xing et al., 2010a) | | | | |

# MISSING LIST OF FOOTNOTES FOR THE APPENDIX:

[1] McCrea et al. (in press) discuss the possibility that these tracks may be ankylosaurian. [2] Listed as ceratopsian in origin. [3] Per Matsukawa et al. (2005). [4] Possibly Santonian in age per Lockley et al. (2006c). [5] Considered possibly theropodan and a *nomen dubium* by Lockley & Meyer (2000) and Lockley et al. (2004a). [6] Age from Hayashi (2006). [7] These may be the “theropod” or “hadrosaur” tracks from the same region mentioned by Erben et al. (1995). [8] Maastrichtian age of track-bearing unit per Zhang et al. (2006c). [9] Reported as theropodan in Calvo (1991). [10] cf. *Tyrannosauripus* tracks considered to be *Amblydactylus* (ornithopod) by Romilio & Salisbury (2010). [11] Considered to pertain to a non-avian theropod by Lockley & Harris (2010). [12] Track described as pertaining to a bird or a small, non-avian theropod.