

TETRAPOD ICHNOFACIES OF THE CRETACEOUS

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Abstract—Fundamental terms in ichnology are: ichnocoenosis—a trace fossil assemblage produced by a biological community that can be characterized by morphological criteria; and ichnofacies—recurrent ichnocoenoses that represent a significant portion of Phanerozoic time. There are five archetypal vertebrate ichnofacies for nonmarine environments (*Chelichnus*, *Grallator*, *Brontopodus*, *Batrachichnus*, *Characichichnos*), of which four are present in the Cretaceous: (1) *Grallator* ichnofacies (*Jindongornipes* and *Megalosauripus* ichnocoenoses); (2) *Batrachichnus* ichnofacies (*Pteraichnus* ichnocoenose); (3) *Brontopodus* ichnofacies (*Ceratopsipes*, *Carichnium*, *Brontopodus*, *Parabrontopodus*, *Dinehichnus*, and *Tetrapodosaurus* ichnocoenoses); and (4) *Characichichnos* ichnofacies (*Chelonichnium* ichnocoenosis).

INTRODUCTION

There is a very large database of Cretaceous tetrapod tracks, which are known from five continents (North America, South America, Europe, Asia, Australasia: Fig. 1). Tracks range in age from the earliest to the latest Cretaceous and include some very large and well studied tracksites such as Lark quarry in Australia and Dinosaur Ridge in the United States (Thulborn and Wade, 1979, 1984; Lockley et al., 1992; Lockley and Hunt, 1995a). Lucas (2006) has recently provided a synthesis of the biochronology and biostratigraphy of these ichnofaunas. The purpose of this paper is to provide an overview of Cretaceous tracks from an ichnofacies perspective. Thus, we discriminate broad ichnofacies and ichnocoenoses in the context of the archetypal ichnofacies concept (Hunt and Lucas, 2006b).

TETRAPOD ICHNOCOENOSES AND ICHNOFACIES

An ichnocoenose can be defined as a trace fossil assemblage produced by a biological community that can be characterized by morphological criteria (independent of depositional environment or biological affinities) (e.g., Bromley, 1996; McIlroy, 2004; Hunt and Lucas, 2006b).

Seilacher (1964, p. 303) introduced the term ichnofacies for “general trace associations, or types of ichnocoenoses, representing certain facies with a long geologic range.” These high-level ichnofacies are referred to as archetypal (Frey and Pemberton, 1987), and there is consensus that ichnofacies should refer to recurrent ichnocoenoses that represent a significant portion of Phanerozoic time (Hunt and Lucas, 2006a). Seilacher named six archetypal invertebrate ichnofacies after typical ichnofossils (Seilacher, 1964, 1967), and this work stimulated numerous studies of invertebrate ichnofacies (Hunt and Lucas, 2006b). Lockley et al. (1994c) provided a cogent synthesis and discussion of tetrapod ichnofacies. Subsequently, Hunt and Lucas (2006b) defined five archetypal tetrapod ichnofacies for nonmarine environments: *Chelichnus*, *Grallator*, *Brontopodus*, *Batrachichnus* and *Characichichnos* ichnofacies (Table 1). Hunt and Lucas (2006b) argued that all tetrapod ichnofacies defined prior to 2005 should be considered ichnocoenoses, as they represent the traces of specific communities that lack the stratigraphic and geographic range that would warrant their consideration as archetypal ichnofacies. Hunt and Lucas (2006a, c) have applied this scheme of tetrapod ichnofacies to Permian and Late Jurassic ichnofaunas.

CRETACEOUS TETRAPOD TRACK RECORD

Introduction

Cretaceous tetrapod tracks, mostly of dinosaurs, have a nearly global distribution, being known from all of the continents except Antarctica (Lucas, 2006; Fig. 1). In addition, Cretaceous tracks are represented by a number of very large individual tracksites, several stratigraphic units that yield large sample sizes and several megatracksites.

Differences Between Late Jurassic and Cretaceous Track Records

Cretaceous tetrapod footprints can be distinguished from Jurassic footprints primarily by the abundance and near ubiquity of large ornithopod tracks in the Cretaceous strata and their virtual absence in the Jurassic (Lucas, 2006). In addition, in the Early Cretaceous there are facies differences between sauropod-dominated and ornithopod-dominated footprint assemblages (Lockley et al., 1994a). Turtle and pterosaur tracks and the sauropod ichnogenus *Parabrontopodus* are much more common in the Jurassic than the Cretaceous. In contrast, birds tracks are unknown in the Jurassic and are locally abundant in the Cretaceous (Lockley and Rainforth, 2002).

Thyreophoran tracks also become locally abundant in the Cretaceous, notably ankylosaur tracks in the Early Cretaceous (McCrea et al., 2002). Neoceratopsian tracks are locally common in the Maastrichtian (Lockley and Hunt, 1995b).

Late Jurassic ichnofaunas are globally cosmopolitan (Lucas, 2006; Hunt and Lucas, 2006c). The Early Cretaceous track record reflects the increased provinciality of dinosaur faunas.

Track Types

The majority of Cretaceous tetrapod tracks represent dinosaurs. Mammal tracks of Cretaceous age are rare, restricted to North America, and some records are of doubtful affinity (Sarjeant and Thulborn, 1986; Sarjeant, 2000; McCrea and Sarjeant, 2002; Stanford and Lockley, 2002; Lockley and Foster, 2003; Lucas, 2006). Bird footprints have their lowest occurrence in the Lower Cretaceous, and almost all Cretaceous bird tracks are from lakeshore or seashore facies (Lockley et al., 1992b; Lockley and Rainforth, 2002). Most new ichnofaunas of Cretaceous bird tracks have received new ichnogenetic names, and there is a need for ichnotaxonomic revision. The Cretaceous pterosaur track record is similar to that of birds (Lockley and Rainforth, 2002). With a few exceptions (e.g., *Purbeckopus*), most specimens can be referred to *Pteraichnus*. Turtle tracks are less common than in the Jurassic, but they occur locally (e.g., Spain: Lockley and Meyer, 2000).

Some of the earliest large theropod tracks are Berriasian in age, and they can be assigned to the Jurassic taxon *Therangospodus* (Lockley and Meyer, 2000). Younger Early Cretaceous theropod tracks include *Buckeburgichnus* in Europe and *Magnoavipes* in North America (Hunt and Lucas, 1998; Lockley and Meyer, 2000). There is less synthetic work on the ichnotaxonomy of the diverse Late Cretaceous theropod tracks (e.g., Lockley and Hunt, 1995b), but they include some unusual forms such as *Saurexallopus* and the presumed track of *Tyrannosaurus*, *Tyrannosauripus* (Lockley and Hunt, 1994).

Sauropod tracks are abundant in the Late Jurassic (Hunt and Lucas, 2006c). In Lower Cretaceous deposits, sauropod tracks are abundant in low latitude, carbonate platform, sabkha and lacustrine deposits (Lockley

et al., 1994c). Sauropod tracks are much less common in Lower-Middle Jurassic and in Upper Cretaceous deposits than in Upper Jurassic-Lower Cretaceous deposits (Farlow, 1992; Lockley et al., 1994c). Narrow gauge sauropod trackways are far more abundant in the Jurassic than the Cretaceous. In the Cretaceous, large sauropod footprints and large ornithopod footprints rarely co-occur, and Lockley et al. (2002a) noted the generally low-paleolatitude distribution of sauropod tracksites versus the higher paleolatitudes of many ornithopod tracksites. A conservative ichnotaxonomy of Jurassic-Cretaceous sauropod tracks assigns almost all of them to two ichnogenes, *Brontopodus* (wide-gauge trackway) and *Parabrontopodus* (narrow-gauge trackway), with large and small manus, respectively. Virtually all Middle-Late Jurassic and Cretaceous sauropod tracks can be assigned to these two ichnogenes because sauropod foot morphology is generalized and conservative (e.g., Farlow et al., 1989; Farlow, 1992; Lockley et al., 1994a).

Large Early Cretaceous ornithopod tracks are assigned three principal ichnogenes, *Iguanodontipus* (the putative track of *Iguanodon*), *Amblydactylus* and the quadrupedal *Caririchnium*. There is not a widely-used ichnotaxonomy for Late Cretaceous tracks of ornithopods (principally hadrosaurs), although *Amblydactylus* has been used for some (e.g., Hunt and Lucas, 2003). Lockley et al. (2003) provided the name *Hadrosauropodus* as a possible name for hadrosaur tracks. There are several problems with the ichnotaxonomy of Cretaceous ornithopod tracks including: (1) naming of poorly preserved specimens that lack diagnostic features (e.g., Sarjeant et al., 1998); (2) inadequate differential diagnoses (Lockley et al., 2003); and (3) a rationale that Late Cretaceous tracks must pertain to a different ichnogenus than Early Cretaceous ones, because they pertain to hadrosaurs, not iguanodontians (e.g., Lockley et al., 2003). There is need for a thorough review of the ichnotaxonomy of large Cretaceous ornithopod tracks. Some small ornithopods from the Early Cretaceous of Spain are assigned to the Jurassic ichnogenus *Dinehichnus* (Lockley and Meyer, 2000).

Ankylosaur tracks are rare in the Jurassic (McCrea et al., 2002; Lockley and Meyer, 2000; Gierlinski et al., 2005). In the Cretaceous they have their lowest occurrence in the Early Cretaceous, but their record, though widespread (North America, South America, Europe and Asia) is not extensive. They appear to have an Albian acme (McCrea et al., 2002; Lucas, 2006). Ankylosaur tracks are generally rare, but a single documented tracksite in Alberta preserves thousands of ankylosaur tracks (ichnogenus *Tetrapodosaurus*), and there are other similar, undocumented sites (McCrea, 2000).

Ceratopsian tracks are not common until late in the Cretaceous and then they are only locally abundant in the Laramie Formation of Colorado (Lockley and Hunt, 1995b).

Track Sites

Early Cretaceous

Lower Cretaceous sauropod tracks are known in Chile, Croatia, Germany, Australia, Brazil, Korea, Utah, Spain, Portugal, Korea, Tajikistan, Texas and Argentina (Calvo, 1991; Farlow, 1992; Pittman, 1992; Moratalla, 1992; Moratalla et al., 1994; Lockley et al., 1994c). In contrast, Late Cretaceous sauropod track records come from Croatia, Spain, Bolivia and China (Lockley et al., 1994b, 2002a, b).

Early Cretaceous tracksites are abundant in the southwestern United States, especially in Texas, New Mexico and Colorado (Pittman, 1989, 1992; Lockley and Hunt, 1995a). Sites of early to middle Albian age, concentrated in Texas and adjoining Arkansas and Oklahoma, are sauropod dominated—these are the classic Trinity Group tracks made famous by the work of Roland T. Bird (1941, 1944) and much studied since (e.g., Pittman, 1989, 1992). There are some Early Cretaceous (pre-late Albian) ornithopod tracks in Utah (Lockley and Hunt, 1994a). However, slightly younger (mostly late Albian) ornithopod-dominated tracksites are widely distributed from central Colorado into western Oklahoma, Nebraska and northeastern New Mexico and comprise the so-called “dinosaur freeway” (Lockley et

al., 1992). The evident late Albian turnover in the western American track fauna, from sauropod dominated to ornithopod dominated, was used by Lucas and Hunt (1989) to mark the Cretaceous extirpation of sauropods in North America, which lasted until the late Campanian immigration (from South America?) of sauropods back into the continent (Lucas and Sullivan, 2000).

In western Canada, Lower Cretaceous tracksites in British Columbia and Alberta yield tracks of large ornithopods, theropods, birds, ankylosaurs and mammals (e.g., Currie, 1983, 1989; McCrea, 2000; McCrea and Sarjeant, 2002). Ankylosaur tracks are generally rare, but a single documented tracksite in Alberta preserves thousands of tracks of *Tetrapodosaurus* (McCrea, 2000).

The European Early Cretaceous record is ornithopod dominated, but it also includes tracks of theropods, sauropods, pterosaurs and ankylosaurs. An extensive Early Cretaceous track record is known from the Purbeck and Wealden strata of England and correlatives in the Cameros basin of Spain (e.g., Wright et al., 1998; Lockley and Meyer, 2000; Moratalla et al., 2003). Similar Early Cretaceous tracks are also known from Germany (Hendricks, 1981), Switzerland (Meyer and Thuring, 2003) and Portugal (Lockley et al., 1994c). Early Cretaceous (Barremian and Albian) tracks from Croatia are of large theropods, ornithopods and sauropods (Dalla Vecchia and Tarlao, 2000; Dalla Vecchia et al., 2002). Theropod and ornithopod tracks are also known from the Lower Cretaceous of Svalbard (Lapparent, 1962; Edwards et al., 1978; Lockley and Meyer, 2000).

Lower Cretaceous tracksites from eastern Asia (China, Korea, Japan and Thailand) are dominated by large ornithopods and theropods (Zhen et al., 1987; Matsukawa and Obata, 1994; Lim et al., 1994; Lockley and Matsukawa, 1998; Lee and Huh, 2002). The most extensive Asian Early Cretaceous record is from Korea, especially in the Jindong Formation, and also includes sauropod and bird tracks (e.g., Hwang et al., 2002a, b).

In South America, Lower Cretaceous footprints are known from Argentina, Chile and Brazil. In Argentina, these are tracks of theropods and crocodylomorphs (ichnogenus “*Batrachopus*”) from San Luis Province (Lull, 1942). In Chile, ornithopod tracks have been attributed to an iguanodont (Casamiquela and Fasola, 1968). In Brazil, sauropod tracks are known from São Domingos in the northernmost part of the country, but most of the Brazilian Lower Cretaceous tracks are in the state of Paraíba and are records of sauropods, theropods and large ornithopods (*Caririchnium*) (Leonardi, 1979, 1984). In southern Brazil, large theropod and ornithopod tracks are also present (Leonardi, 1994). In the Australian Lower Cretaceous, large and small theropod tracks are known in the western part of the country (Colbert and Merrilees, 1967; Flannery and Rich, 1981). In Cameroon, west Africa, theropod tracks are present in Lower Cretaceous strata (Jacobs et al., 1989).

Late Cretaceous

Tracks of Late Cretaceous age are essentially global in distribution (Fig. 1) and differ from Early Cretaceous tracks in a lesser number of sauropod tracks and in the presence of ceratopsian, tyrannosaurid and hadrosaurid tracks.

Relatively few tracks are known from the Upper Cretaceous of Europe. They are sauropod tracks from the Cenomanian of Carenque in Portugal, sauropod and theropod tracks from the Cenomanian of Istria in Croatia and sauropod tracks from the Maastrichtian at Fumanya in Spain (Lockley and Meyer, 2000).

Western North America has an extensive track record of Late Cretaceous age, mostly in Campanian-Maastrichtian rocks. These include hadrosaur tracks from western Canada (Langston, 1960; Currie, 1989), extensive assemblages of hadrosaurian, theropod and some mammal footprints in the Wahweap, Kaiparowits and Straight Cliffs formations and the coal-bearing Mesaverde Group of Utah and Colorado (Lockley et al., 1983; Parker and Rowley, 1989), ceratopsian tracks in the Laramie Formation of Colorado (Lockley and Hunt, 1995b) and the apparent footprint of *Tyrannosaurus rex* from the Maastrichtian interval of the Raton Formation in New Mexico (Lockley and Hunt, 1994b). Indeed, the tracks of hadrosaurs

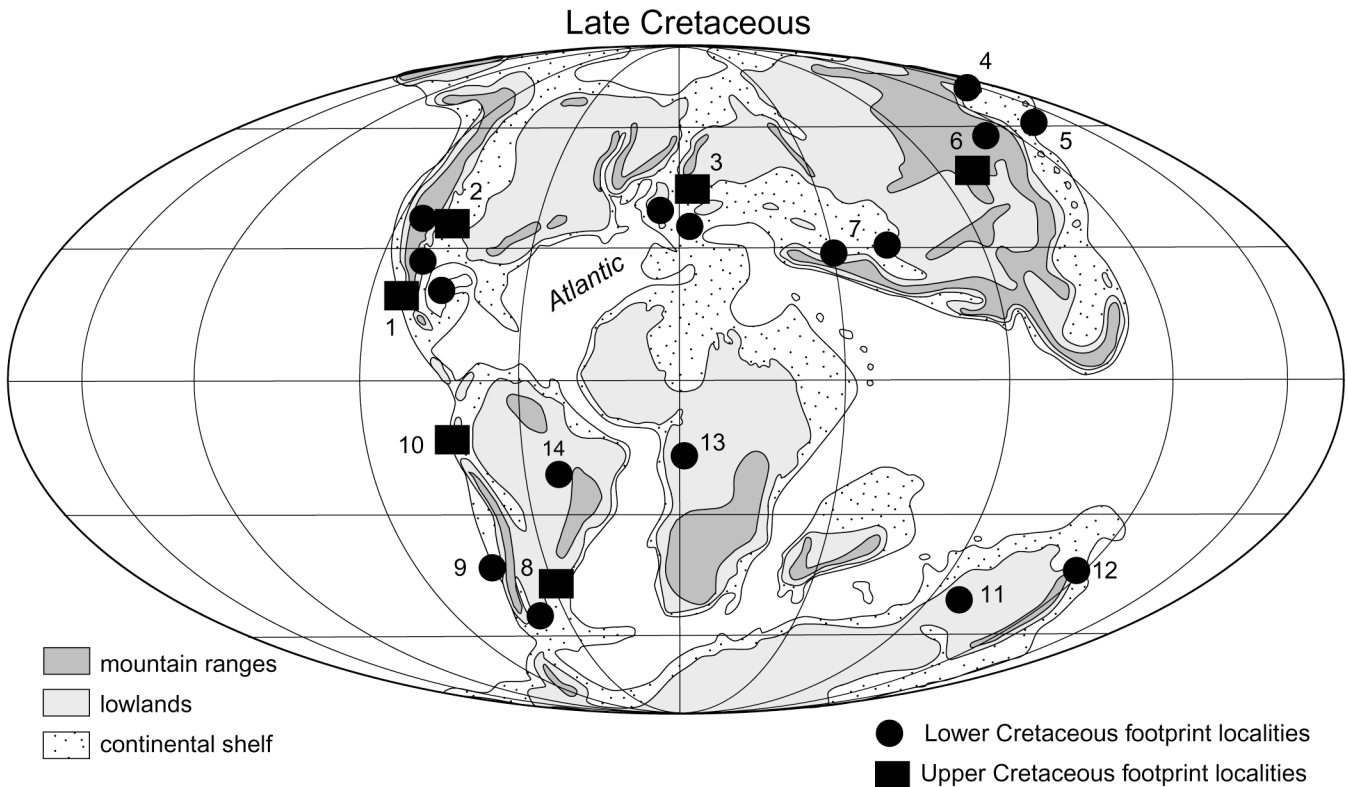


FIGURE 1. Distribution of principal Cretaceous tracksites. Locations are 1, southwestern United States; 2, western Canada; 3, western Europe; 4, Korea; 5, Japan; 6, China; 7, Tadjikistan; 8, Argentina; 9, Chile; 10, Bolivia; 11, western Australia; 12, Queensland, Australia; 13, Cameroon. Base map after Wing and Sues (1992).

and ceratopsians in the Raton Formation are within 37 cm of the Cretaceous-Paleogene boundary, as determined by palynology and the iridium layer, and thus provide a valuable biostratigraphic datum to establish the stratigraphically highest occurrence of dinosaurs in the Cretaceous (Lockley, 1991a). In South America, Late Cretaceous footprint records are mostly from Argentina, where theropod, ornithopod and bird tracks are known, mostly from Maastrichtian strata (Casamiquela, 1964; Alonso, 1980, 1989; Leonardi, 1994). In Bolivia, Late Cretaceous theropod and ankylosaur tracks are present (Leonardi, 1981a, 1984). In Australia, numerous small theropod and ornithopod tracks are known from the Cenomanian of Winton, Queensland (Thulborn and Wade, 1979, 1984). Late Cretaceous tracks from Asia, mainly from China and Korea, are mostly of theropods and sauropods (Zhen et al., 1989; Lockley et al., 2002a).

CRETACEOUS TETRAPOD ICHNOFACIES AND ICHNOCOENOSES

History of Study

Lockley et al. (1994c) named a *Brontopodus* “ichnofacies” (ichnocoenosis of current usage) to include ichnoassemblages of Jurassic and Cretaceous age dominated by sauropod tracks. This “ichnofacies” explicitly included Morrison ichnofaunas. Hunt and Lucas (2006b) defined an archetypal *Brontopodus* ichnofacies to include all ichnocoenoses that are dominated by the tracks of terrestrial herbivores.

Lockley et al. (1994c) also named a *Caririchnium* ichnocoenosis (“ichnofacies” of their usage) for Early Cretaceous ornithopod-track ichnofaunas from North America and a *Jindongornipes* ichnocoenosis (“ichnofacies” of their usage) for Early Cretaceous bird-track ichnofaunas of Korea. Subsequently, Hunt and Lucas (2006b) named the *Ceratopsipes* ichnocoenosis for the Late Cretaceous ceratopsid “ichnofacies” of Lockley et al. (1994).

Cretaceous Ichnofacies and Ichnocoenoses

Brontopodus Ichnofacies

Hunt and Lucas (2006b) proposed the *Brontopodus* ichnofacies for medium diversity ichnofaunas in which the majority of tracks are of terrestrial herbivores with a small quantity (generally > 10%) of terrestrial carnivore tracks. This ichnofacies includes coastal plain-marine shoreline environments and some lacustrine shorelines, and it ranges from Late Permian to Recent in age. Hunt and Lucas (2006b) recognized several constituent ichnocoenoses of the *Brontopodus* ichnofacies.

The *Brontopodus* ichnocoenosis was first defined as an ichnofacies (Lockley et al., 1994c; Hunt and Lucas, 2006b). This ichnocoenosis was originally defined to include ichnofaunas dominated by sauropod tracks (Lockley et al., 1994c). Hunt and Lucas (2006b) restricted the ichnocoenosis to ichnofaunas dominated by wide-gauge *Brontopodus*. This ichnocoenosis extends into the Late Jurassic and temporally overlaps the *Parabrontopodus* ichnocoenosis, which encompasses ichnofaunas dominated by the narrow-gauge *Parabrontopodus* (Hunt and Lucas, 2006b). In the Cretaceous, the vast majority of ichnofaunas are referable to the *Brontopodus* ichnocoenosis (e. g., Early Cretaceous of North America; Early-Late Cretaceous of Europe; Early-Late Cretaceous of South America; Late Cretaceous of East Asia). The *Parabrontopodus* ichnocoenosis does occur in the Cretaceous, particularly in lower part, but it is not common (e. g., Valdemurillo locality in Spain: Lockley and Meyer, 2000).

There is a clear *Caririchnium* ichnocoenosis in the Early Cretaceous of South and North America that may extend into the Late Cretaceous ornithopod-track ichnofaunas from North America (Lucas and Hunt, 2006). The Jurassic *Dinehichnus* ichnocoenosis (Hunt and Lucas, 2006c) occurs locally in the basal Cretaceous of Spain (Lockley and Meyer, 2000). Further work on large ornithopod ichnotaxonomy may result in the discrimination of an *Iguanodontipus* ichnocoenosis in the Early Cretaceous of Europe (Sarjeant et al., 1998) and a *Hadrosauropodus* ichnocoenosis,

TABLE 1. Archetypal tetrapod ichnofacies (Hunt and Lucas, 2006) and representative Cretaceous ichnocoenoses.

Archetypal Tetrapod Ichnofacies	Predominant trace fossil types	Constituent Cretaceous ichnocoenoses	Inferred environment
<i>Chelichnus</i>	Low diversity ichnofaunas (less than 4 ichnogenera) of tetrapod tracks that have equant shape with subequal manual and pedal impressions and short digit impressions	None	Eolian crossbeds
<i>Batrachichnus</i>	Majority of tracks are of quadrupedal carnivores; medium-high diversity (4-8 ichnogenera)	<i>Pteraichnus</i> (Lockley and Meyer, 2000)	Tidal flat-fluvial plain
<i>Brontopodus</i>	Majority of tracks are terrestrial herbivores with small quantity (generally > 10%) of terrestrial carnivore tracks; medium-high diversity (4-8 ichnogenera)	<i>Ceratopsipes</i> (Hunt and Lucas, 2006b) <i>Carichnium</i> (Lockley et al., 1994c) <i>Brontopodus</i> (Lockley et al., 1994c) <i>Parabrontopodus</i> (Hunt and Lucas, 2006c) <i>Dinehichnus</i> (Hunt and Lucas, 2006c) <i>Tetrapodosaurus</i> (herein)	Coastal plain, clastic or carbonate marine shoreline
<i>Grallator</i>	Medium-high diversity ichnofaunas (5-8 ichnogenera) with tracks (usually dominant) of tridactyl avian and non-avian theropods	<i>Jindongornipes</i> (Lockley et al., 1994) <i>Megalosauripus</i> (Hunt and Lucas, 2006c)	Lacustrine margin
<i>Characichnos</i>	Parallel scratch marks and fish swimming trails (<i>Undichna</i>)	<i>Chelonichnium</i> (Lockley and Meyer, 2000)	Shallow lacustrine/aquatic

which may have a global distribution (e. g., Lockley et al., 2003).

Cretaceous ichnofaunas are only locally dominated by the tracks of quadrupedal ornithischians. Some Late Cretaceous ichnofaunas can be assigned to the *Ceratopsipes* ichnocoenosis (Hunt and Lucas, 2006b). Some Early Cretaceous ichnofaunas are dominated by the tracks of ankylosaurs (McCrea, 2000; McCrea et al., 2002; Lockley et al., 2006; Lucas, 2006). We name the *Tetrapodosaurus* ichnocoenosis for these ichnofaunas after the most common ichnogenus in the Canadian ichnofaunas. This ichnocoenosis may have an Albian acme (McCrea et al., 2002; Lucas, 2006).

Grallator Ichnofacies

Hunt and Lucas (2006b) proposed the *Grallator* ichnofacies for medium to high diversity ichnofaunas (five to eight ichnogenera) dominated by tracks of tridactyl avian and non-avian theropods (usually dominant) or of other habitual bipeds. Tracks of bipedal and quadrupedal ornithischians, sauropods and herbivorous mammals are also locally common in this ichnofacies. This ichnofacies extends from the Late Triassic to the Recent and often characterizes lacustrine margin environments. There is a need for an ichnotaxonomic review of Cretaceous theropod tracks, so we cannot distinguish many ichnocoenoses. The Jurassic *Megalosauripus* ichnocoenosis (represented by *Therangospodus*) of Hunt and Lucas (2006c) occurs in the Berriasian of Europe (Lockley and Meyer, 2000). It may be possible to distinguish Early Cretaceous ichnocoenoses based upon distinctive ichnogenera such as *Buckeburgichnus* in Europe and *Magnoavipes* in North America (Lockley and Meyer, 2000). Similarly, Late Cretaceous ichnofaunas include distinctive ichnotaxa whose distribution is poorly understood (e. g., *Saurexalopus*).

Currently there is one defined ichnocoenosis for Cretaceous bird tracks – the *Jindongornipes* ichnocoenosis (Lockley et al., 1994; Hunt and Lucas, 2006b). Most new ichnofaunas of Cretaceous bird tracks have received new ichnogenetic names. We conservatively assign all these ichnofaunas to the *Jindongornipes* ichnocoenosis, but we expect that a more precise ichnotaxonomy will allow the discrimination of several ichnocoenoses. This ichnocoenosis has two Cretaceous acmes—in the Aptian-Cenomanian and the Campanian-Maastrichtian (Lockley and Rainforth, 2002, fig. 17.2).

Batrachichnus ichnofacies

Hunt and Lucas (2006b) proposed the *Batrachichnus* ichnofacies for ichnofaunas in which the majority of tracks are of quadrupedal carnivores with a moderate-high diversity (four to eight ichnogenera). This ichnofacies represents tidal flat-fluvial plain environments from the Devonian to the Cretaceous.

Hunt and Lucas (2006c) placed the *Pteraichnus* ichnocoenosis of Hunt and Lucas (2006b) (= *Pteraichnus* ichnofacies of Lockley and Meyer, 2000) within the *Batrachichnus* ichnofacies because it is dominated by the tracks of quadrupedal carnivores. This ichnocoenosis occurs in the Early Cretaceous of Europe and is most notable in the Iberian peninsula (Lockley and Meyer, 2000; Lockley and Rainforth, 2002). Other Cretaceous examples of this ichnocoenosis occur in the Early Cretaceous of England and Maryland and the Late Cretaceous of Korea, Canada and the United States (Lockley and Rainforth, 2002).

Characichnos ichnofacies

Hunt and Lucas (2006b) proposed the *Characichnos* ichnofacies for medium diversity ichnofaunas in which the majority of tracks are swimming traces (parallel scratch marks) and fish swimming trails (*Undichna*). This ichnofacies represents shallow lacustrine (and tidal) environments. Lockley and Meyer (2000) recognized a *Chelonichnium* ichnocoenosis (ichnofacies in their definition) characterized by ichnoassemblages dominated by turtle swimming tracks of the ichnogenus *Chelonichnium*. This ichnocoenosis occurs locally such as in the Enciso Group of Spain (Moratalla, 1992; Lockley and Meyer, 2000). Ichnofaunas dominated by swimming tracks occur in the “Dakota Group” of western North America, and these can be assigned to the *Characichnos* ichnofacies (McAllister, 1989; Lockley and Hunt, 1995a).

Chelichnus ichnofacies

Hunt and Lucas (2006b) proposed the *Chelichnus* ichnofacies for ichnofaunas that have a low diversity (less than five ichnogenera) of tetrapod tracks in which manus and pes tracks are equant in shape of subequal size and have short digit impressions. This ichnofacies is recurrent in dune faces of eolian environments (Fig. 1), and it extends from the Early Permian to the Early Jurassic. The *Chelichnus* ichnofacies is not present in the Cretaceous.

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