

THE FOSSIL RECORD OF CROCODYLIAN TRACKS AND TRACES: AN OVERVIEW

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Abstract—This volume fills a gap in the ichnological literature on crocodylian tracks and other traces (bite marks and coprolites). The definition of Crocodylia is presently in flux as both crown-based and stem-based definitions are present in the literature. The present volume provides articles focused on reports of new crocodylian track records from the Triassic, Jurassic, Cretaceous and Miocene, crocodylian neoichnology and new occurrences of crocodylian coprolites and bite marks. The global geographic distribution of crocodylian tracks is summarized, and the influence of *Characichnos* and *Hatcherichnos* ichnocoenoses/ichnofacies on global archetypal ichnofacies is discussed.

PREFACE

Crocodyles (or crocodyles, crocodylians or crocodylomorphs) are, together with birds, the only extant groups of archosaurs, and are the closest living relatives of dinosaurs and pterosaurs (Fig. 1). A close relationship between crocodiles and other Mesozoic reptiles was hypothesized in the early 1800s when the first reported dinosaurs and marine reptiles (mosasaurs) were reconstructed and classified as crocodile-like creatures. Likewise, crocodiles and other “primitive” aquatic “monsters” (e.g., labyrinthodont amphibians) were considered among the prime candidates as the makers of the first found and first classified fossil footprints: the famous Triassic “hand beast” tracks known as *Chirotherium* (Fig. 2). Despite almost two centuries of further paleontological research into the evolutionary history and fossil record of crocodiles, which has substantially increased our understanding of their skeletal record, we still know relatively little about crocodile tracks and traces. This volume is a significant step forward in documenting the hitherto neglected, or at best sporadically documented, trace fossil record of crocodylians.

INTRODUCTION

Vertebrate ichnology has had a renaissance in the last two decades, initiated by the publication of several volumes and books, especially on dinosaur tracks (Leonardi, 1987, 1994; Gillette and Lockley, 1989; Thulborn, 1990; Lockley 1991; Lockley and Hunt, 1995; Lucas and Heckert, 1995; Lockley and Meyer, 2000) in addition to a rapid increase in the number of published tracks and tracksites from all over the world. In recent years, growing numbers of more specialized volumes and reviews of Cenozoic tracks (Lucas et al., 2007), hominid ichnology (Kim and Lockley, 2008, 2009), pterosaur ichnology (Lockley et al., 2008), and avian ichnology (Lockley and Harris, 2010) have appeared. However, until now, the subject of crocodylian ichnology has not been treated as a discrete subdiscipline.

Crocodylians and their allies, as defined below, are a major group of archosaurs that have a fossil record extending back to the Triassic. Inasmuch as dinosaurs were archosaurs of the land, and pterosaurs archosaurs of the air, extant crocodylians are archosaurs of the water (Lockley, 2007). Obviously, this threefold division is biased by the Recent: when scrutinized in detail, a number of early crocodile-line archosaurs, such as various basal pseudosuchians, members of the “Sphenosuchia,” and non-crown-group crocodyliforms, included fully terrestrial forms. (Fig. 3). Many of these taxa were undoubtedly track makers, some of which were responsible for making a variety of long-studied “chirothere” tracks. As a result, they have, since their first discovery (Kaup, 1835)

and interpretation (Soergel, 1925; Peabody 1948), attracted considerable attention in the ichnological community. Thus, for historic reasons many of the better known tracks reported from the early Mesozoic (Triassic and Early Jurassic) are attributed to terrestrial track makers such as pseudosuchians and sphenosuchians, which are paleoecologically very distinct from modern crocodylians.

Whereas “chirothere” tracks are certainly attributable to pseudosuchian archosaurs, such as rauisuchids, aetosaurs, and their allies, there has been a problematic tendency to attribute various non-crocodylomorph and non-crocodylian tracks to crocodylomorph and crocodylian trackmakers. For example, Haubold (1984) attributed the probable prosauropod track *Otozoum* to a crocodylian (“protosuchid”). Another classic example was the incorrect attribution of the Late Jurassic pterosaur track *Pteraichnus* (Stokes, 1957; Lockley et al, 1995, 2008) to a crocodylian (Padian and Olsen, 1984). There is even a reverse case where crocodylian tracks (Bennett, 1992) had previously been incorrectly attributed to pterosaurs (Gillette and Thomas, 1989). Likewise, very similar crocodylian tracks (Kukihara, 2006; Kukihara et al., 2010) had previously been incorrectly attributed to dinosaurs (McAllister, 1989a,b). In another interesting case, a large sauropod trackway from near the Jurassic-Cretaceous boundary in Spain (Lockley, 2009) was incorrectly attributed to a giant crocodile (Perez-Lorente and Ortega, 2003).

Thus, it appears, at least superficially, that there has been considerable historical confusion surrounding the probable makers of different archosaurian tracks (including those of variously defined Crocodylia). However, in recent years the renaissance in tetrapod ichnology has shed considerable light on the morphology and distribution of dinosaur and pterosaur tracks (the archosaurs of land and air), while, ironically, there has been less progress in the documentation of the tracks of crocodylians – the one group with extant representatives! [Birds are now also considered dinosaurs and therefore extant archosaurs]. Even though it is accepted that ichnologists cannot assign tracks to track makers with high levels of confidence (i.e., at lower taxonomic levels such as genus or species, often by a process of elimination), track maker correlations are being made with increasing confidence.

In this volume, we continue in the tradition of a maturing ichnology by filling a significant gap in the literature on crocodylian tracks and other traces (bite marks and coprolites). Contributors to the volume, independent of any editorial persuasion, have primarily elected to submit papers on the tracks and traces of late Mesozoic through Recent crocodylians. The volume comprises 31 papers from 33 authors, covering topics including new Mesozoic tracksite ichnology, neoichnology, bite marks and coprolites.



FIGURE 1. An 1848 duo-tone lithograph by David Roberts entitled “Scene on the Nile near Wady Dabod, with crocodiles” from a book entitled “Views from Egypt, Nubia and the Holy Land.”

DEFINING THE CROCODYLIA

In the contributions to this volume various different names for groups (clades) of organisms are sometimes used even when the content of the group being discussed is the same. This is because, over the years, original Linnean nomenclature has been modified by developments in modern paleontology, neontology, and phylogenetic research, sometimes with limited consensus. To understand different frameworks, we briefly outline the philosophies underlying alternative nomenclatural systems (Fig. 3) of interest to the specialist, and conclude with a working summary scheme (Fig. 4) that provides a framework for the ichnological contributions presented here.

Crocodylia as Crown Group, Crocodylomorpha and Crocodyliformes as Stem Groups

Although Linneus and Salvii (1758) initially placed *Crocodylus* in their Lacerta, Gmelin (1789) separated out Crocodylia as an ordinal-level group. At the time of their classification, Gmelin and Linnaeus were only aware of extant species of Crocodylia. Because early systematists worked without knowledge or understanding of fossils or evolution, Linnean groups consisted only of extant taxa - groupings that today would be termed “crown groups” in phylogenetic terms. In a strict application of modern phylogenetic rules, these groupings, if monophyletic, should be preserved without any change in concept or membership. To preserve the stability of the name and the original membership encompassed by the name, larger groupings that encompass crown group taxa plus extinct (fossil) members outside the crown group would require new names.

Crocodylia received its first modern, phylogenetic definition from Benton and Clark (1988) who, to preserve the Linnean concept, restricted the term to the crown group. To accommodate more inclusive clades to which the crown-group Crocodylia belonged, new terms were erected: Crocodylomorpha was given to the clade that includes the Crocodylia plus all of the most closely related taxa from the Late Triassic onward — essentially all “sphenosuchians,” “protosuchians,” “mesosuchians,” and eusuchians (Benton and Clark, 1988). A smaller, less inclusive clade, the Crocodyliformes, encompassed all of the latter except the “sphenosuchians” (Benton and Clark, 1988). In this system, then, Crocodylia is a small subset of several other larger, more inclusive clades (Fig. 3A).

Crocodylia as Stem Group

Despite the logic underlying this “crown group-centric” philosophy, the modern understanding of phylogenetic relationships between extinct and extant organisms creates problems with group names (Mook, 1934). Less than 40 years after the Crocodylia (Gmelin, 1789), Owen (1842) specifically stated that his “Crocodylia” included members that extended as far back as the Early Jurassic (“Lias”), including *Teleosaurus* and *Steneosaurus*, both described nearly 20 years earlier by Geoffroy Saint-Hilaire (1825) in a paper whose title, “Du crocodile fossile de Caen” (“On the fossil crocodile from Caen”), explicitly indicates no hesitation in including these fossil taxa in the same group (Crocodylia) as extant, crown-group taxa.

The question of whether nomenclatural “stability” is best served by a Linnean “crown group” is complex. Cuvier (1809) and de la Beche

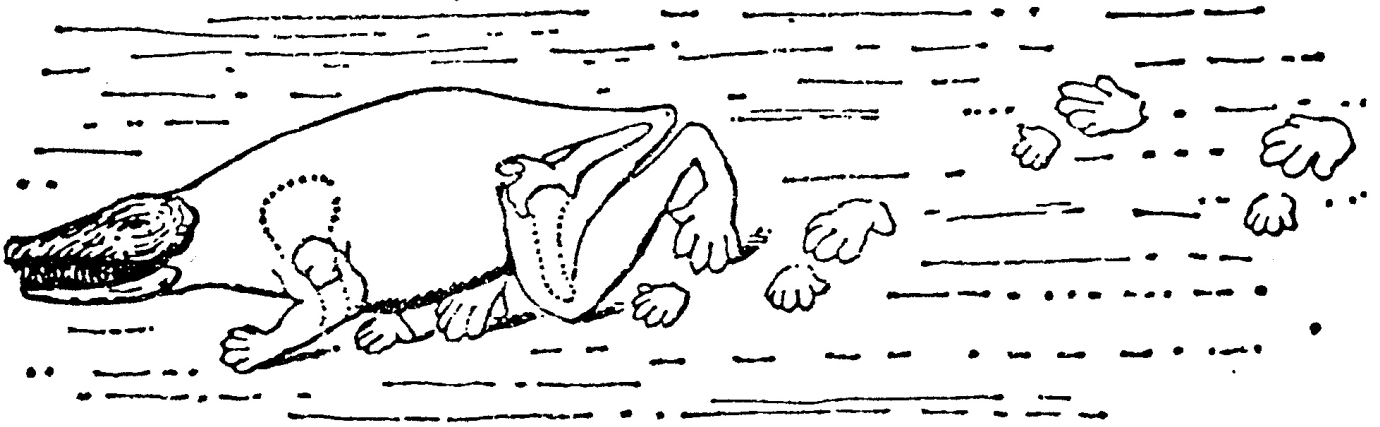


FIGURE 2. An early depiction of a the Triassic trackmaker of *Chirotherium* footprints, shown as a sprawling crocodile-like creature – actually inferred to be a labyrinthodont amphibian in this reconstruction attributed to Charles Lyell.

and Conybeare (1821) placed fossils radically different from anything extant within crown group Crocodylia. So, it seems the systematic Zeitgeist, even in “Linnean” times, was *not* to restrict groupings to extant organisms (Martin and Benton, 2008). In the case of Crocodylia, this historically-precedented philosophy espouses using Crocodylia in a broader sense - essentially to encompass anything “croc-like,” regardless of whether or not it falls within the crown group.

Martin and Benton (2008) supported using Crocodylia Gmelin, 1789 as a senior synonym of Crocodyliformes Benton and Clark, 1988 because: (1) crown groups are not more inherently stable than stem groups, and (2) the use of Crocodylia in a stem-group sense was more widely published and disseminated. They argued that attempting to redefine the term to include *only* the crown-group would cause *more*, not *less*, confusion. Following the stem-group paradigm virtually all “croc” clades are subsets of Crocodylia (Fig. 3B), much the inverse of the crown-group Crocodylia perspective (Fig. 3A).

From a long-term historical perspective, Martin and Benton (2008) are correct that Crocodylia as a stem-group, including probably hundreds of fossil taxa of varying evolutionary “grades,” has predominated. However, Brochu et al. (2009) argued for the alternate, “stable crown-group philosophy” because use of the crown-group Crocodylia has been much more prevalent than the stem-group concept between 1988 and 2006. Presumably this reflects increased publication rates during this recent period! Brochu et al. (2009) argue that the crown group paradigm creates more stability than an ever-labile stem-group Crocodylia.

This brief overview of different meanings of the term “Crocodylia,” and its shorthand “crocodylian” (and, colloquially, even “croc”) provides readers with the background to distinguish between Crocodylia used in the crown-group or stem-group sense: see Figure 4 for a simplified scheme that uses the stem group nomenclature, while also delineating where the crown-group definition would fit within it. The authors of this and other papers in this volume have different preferences, and for this reason both classifications are presented. As tracks of extinct forms cannot, with certainty, be correlated with extinct track maker species, an unambiguous definition Crocodylia is arguably of less concern than it might be in a review based on the osteological record.

Crocodylia as it Relates to Ichnology

This semantic debate is potentially important, even in ichnological circles, because of the implications for track maker behavior and locomotor style. The oldest crown-group crocodylians are Campanian (Late Cretaceous) in age, or perhaps a little older (Brochu, 2003). If Crocodylia is perceived as crown group-only, then pre-Upper Cretaceous tracks cannot be crocodylian, though they could be crocodyliform. For ex-

ample, tracks from Upper Jurassic strata could pertain to a “goniopholidid,” but Goniopholididae is not within crown-group Crocodylia, so the tracks would not be crocodylian. Such distinctions are avoided here by using the more inclusive stem group concept while acknowledging the crown group, including all extant forms, as a distinctive clade within it (Fig. 4).

The concept of crown-group Crocodylia naturally evokes images of extant aquatic, “ectothermic,” semi-sprawling animals whose ontogenies, physiologies, and, most important for ichnology, locomotor behaviors are fairly well understood. Although there may be a tendency to infer that tracks described as “crocodylian” only indicate a crown group crocodylian, they may, as the broader definition allows (Fig. 4), have been made by various stem group representatives, with either relatively similar or quite different foot morphologies. As noted above, early “crocs” (“sphenosuchians” and “protosuchians”) were radically unlike extant crocodylians in many fundamental respects, including erect limb posture and narrower, parasagittal stance (Parrish, 1987). Like more basal pseudosuchians (Fig. 3), their tracks were probably more chirothere-like and unlike those of extant crocodylians. Thus, the reader should exercise discrimination in understanding which terms are being used in any given case, and which foot morphologies and locomotor styles could fit the tracks

Clearly, since the Triassic, there has been considerable evolutionary change in the crocodylian/crocodylomorph Bauplan, as well as in behavior and locomotion. In ichnology, tracks should be interpreted strictly and “primarily” from the morphologies of the ichnites rather than by making assumptions about track maker characteristics. Where “secondary” attempts to infer or name the track maker are made, such morphological evidence should help clarify whether tracks are assignable to taxa with similar foot structures and locomotor styles as narrower (crown group) or broader, more inclusive (stem group) clades. In the latter case, it is already established on the basis of ichnological and osteological evidence that many non-crown-group taxa were unlike modern crocodylians in morphology, behavior, and/or locomotor styles.

CROCODYLOMORPH BODY FOSSIL RECORD AND EVOLUTION

Fossils of the earliest members of the Crocodylomorpha (“sphenosuchians”) are from Upper Triassic and Lower Jurassic strata, among them taxa well-known from complete/nearly complete cranial and postcranial material, such as *Hesperosuchus*, *Sphenosuchus*, *Saltoposuchus*, *Dibothrosuchus*, and *Protosuchus* (e.g., Colbert, 1952; Crush, 1984; Parrish, 1991; Sereno and Wild, 1992; Colbert and Mook, 1951; Wu and Chatterjee, 1993; Lucas et al., 1998; Clark et al., 2004).

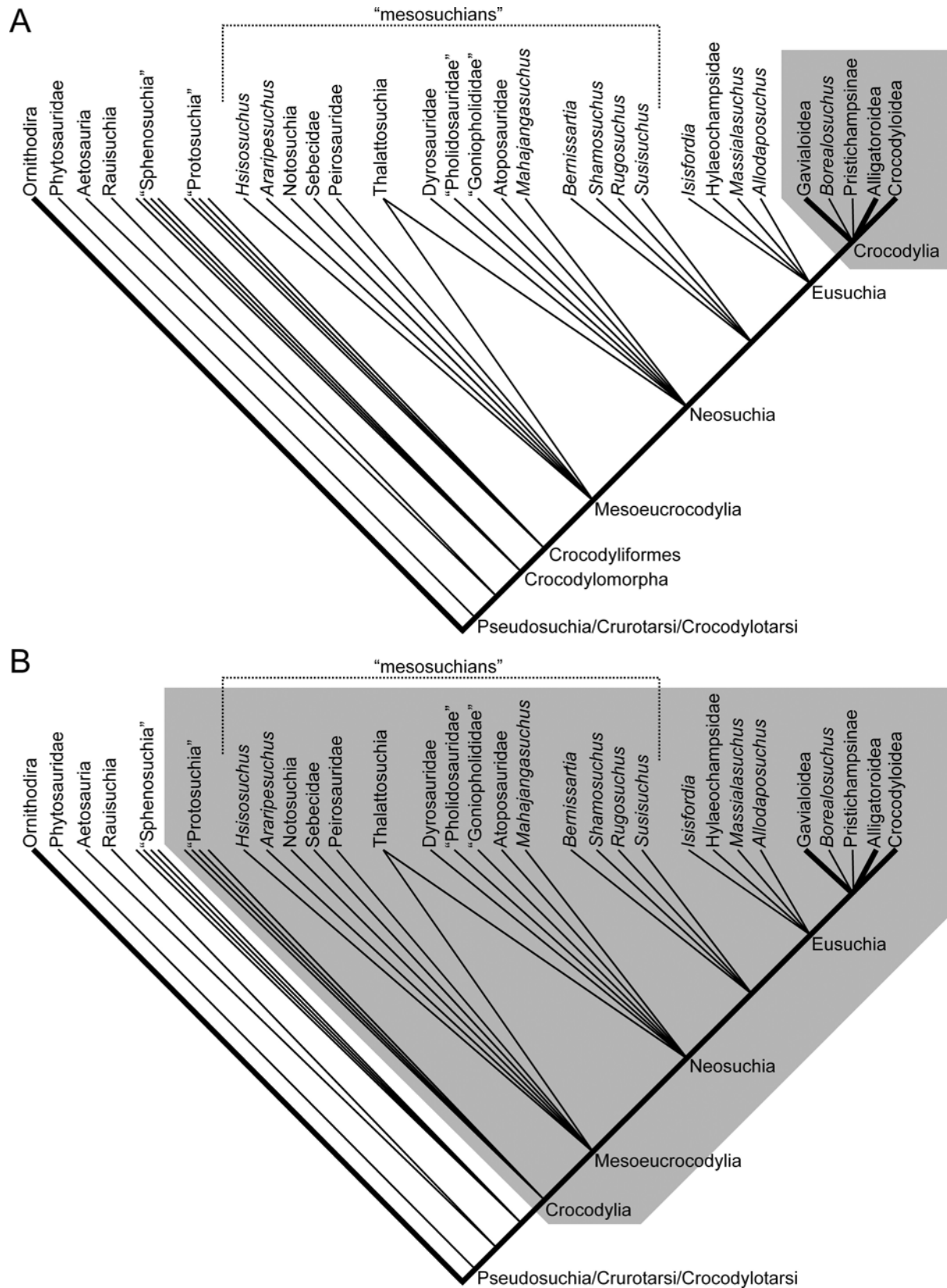


FIGURE 3. Cladograms depicting different definitions and memberships for Crocodylia (modified from Brochu et al., 2009). Dark, thick lines denote extant organisms, thin, light lines denote extinct taxa, and gray areas encompass all taxa that are included in Crocodylia. **A**, Crocodylia as a crown group. In this system, only gavialoids, pristichampsines, alligatoroids, and crocodyloids are crocodylians; all other listed taxa above the node Crocodylomorpha but below Crocodylia, such as "protosuchians," notosuchians, sebecids, dyrosaurids, atoposaurids, and hylaeochampsids, are non-crocodylian crocodylomorphs. **B**, Crocodylia as stem group. In this system, Crocodylia has a much larger (and more diverse) membership than in the crown group sense, including not only extant taxa but all crocodylomorphs since the earliest Jurassic.

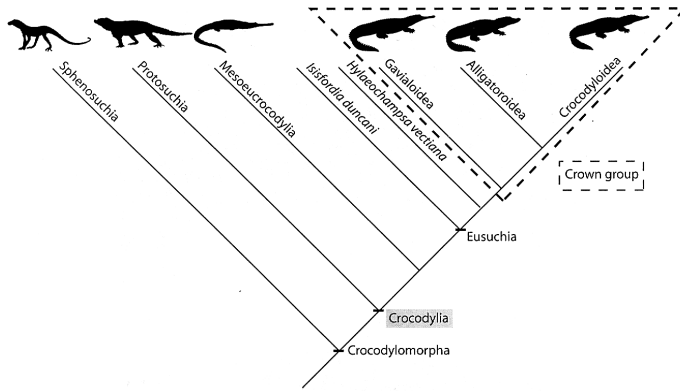


FIGURE 4. A simplified crocodylomorph cladogram (after Marin and Benton, 2008) showing “crown group Crocodylia” nested within “stem group Crocodylia” allows a conceptual integration (superposition) of the two cladistic models shown in Figure 3. It is unlikely, with our present state of knowledge that crocodylian track makers can be convincingly identified at taxonomic levels higher than those used here. Where such inferences are made one may refer to Figure 3, and the terminology therein. See text for details.

These early crocodylomorphs were lightly built, terrestrial forms. Aquatic adaptations are unknown for Triassic taxa and apparently evolved in more derived crocodyliforms during the Jurassic. Indeed, during the Late Triassic, the modern crocodylian ecological niches were filled primarily by more basal pseudosuchians: the phytosaurs (e.g., Hunt, 1989; Fig. 3).

Most Jurassic crocodylians, in the stem group sense discussed above (Figs. 3-4), were “mesosuchians” and “protosuchians,” two groups of primitive crocodyliforms that include the oldest obviously aquatic crocodylians. These groups have an extensive, nearly global fossil record, as do the oldest eusuchian crocodylians, which appeared during the Early Cretaceous (Clark and Norell, 1992; Pol et al., 2009). By the end of the Cretaceous, the three main branches of crown-group crocodylians, alligatoroids, gavialoids and crocodyloids, had appeared (Brochu, 2003). Their extensive Late Cretaceous and Cenozoic body fossil record is well known from most of the continents.

THE STRATIGRAPHIC DISTRIBUTION OF CROCODYLOMORPH FOOTPRINTS

Triassic

Tracks of crocodylomorphs are not common in the Triassic. The oldest definitive records of crocodylomorph tracks are *Batrachopus*-like footprints in strata of the Newark Basin of Pennsylvania, USA of latest Triassic age (Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Szajna and Hartline, 2003), a few meters below the stratigraphically lowest Newark basalt (see Lucas and Tanner, 2007). However, as noted here, Avanzini et al. (2010a) argue that some Late Triassic *Brachychirotherium eyermani* Baird, 1957 footprints from the Italian Southern Alps show possible “sphenosuchian” affinities. Similarly, Bernardi et al. (2010) interpret a webbed archosaur footprint from the Upper Triassic of the Italian Southern Alps as having been made by a quadrupedal crocodylomorph showing possible aquatic adaptations. Conversely, Klein and Lucas (2010) re-evaluate the Triassic footprint record of crocodylomorphs and conclude that the oldest definitive ichnological evidence of crocodylomorph tracks is of latest Triassic age (the Newark record cited above), and that these tracks represent sphenosuchians or protosuchians.

Early to Middle Jurassic

The ichnogenus *Batrachopus* is common in Lower Jurassic strata in many regions (Fig. 5). It was first named on the basis of material from New England (Hitchcock, 1845; Olsen and Padian, 1986), and subse-

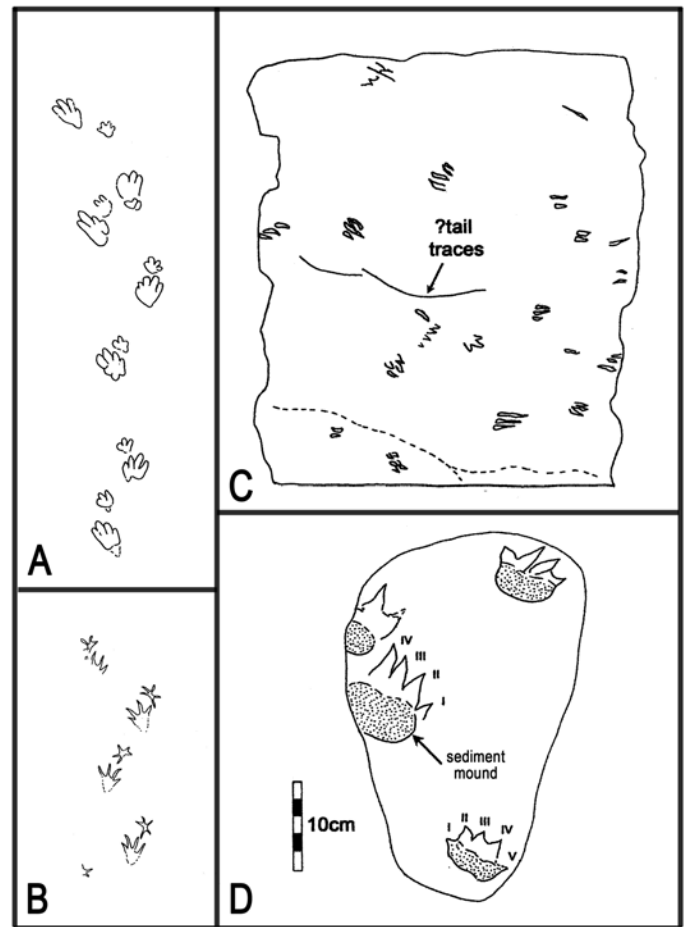


FIGURE 5. Named ichnogenera attributed to crocodylians. **A**, *Batrachopus*. **B**, *Crocodylopodus*. **C**, *Laiyangpus*. **D**, *Kuangyuanpus*. Compare with Figure 6, see text for details. The affinity of *Laiyangpus* is somewhat doubtful due to a missing type specimen. See text and Lockley et al. (2010) for details.

quently recognized in Europe (Lapparent and Montenant, 1967; Popa, 1999; Lockley and Meyer, 2000; 2004); it is relatively common, though little documented, in western North America (Olsen and Padian, 1986; Lockley et al., 2004; Milner et al., 2006). Here, again, there has been historical confusion regarding the affinity of various tracks, including those first attributed to pterosaurs (Stokes and Madsen, 1979), before being re-labelled first as *Batrachopus* (Leonardi, 1987) and subsequently as *Brasilichnium* (see Lockley and Hunt, 1995 for a review).

A number of Early Jurassic ichnotaxa proposed by Ellenberger (1972, 1974) based on material from southern Africa are probably of crocodylomorph affinity and many may be synonymous with *Batrachopus*. Although the Chinese ichnogenus *Kuangyuanpus* (Young, 1943; Fig. 5 herein) was assigned to *Batrachopus* by Zhen et al. (1989), this attribution is incorrect according to Lockley et al. (2010b) who consider *Kuangyuanpus* tracks similar to the crocodylian “swim track” *Hatcherichnus* (Foster and Lockley, 1997). Romano and Whyte (2010) report crocodylian and turtle tracks from the Middle Jurassic of Yorkshire already known for dinosaur walking and swim traces, including the ichnogenus *Characichnos* (Whyte and Romano, 2001) that lends its name to a swim track ichnofacies (Hunt and Lucas, 2007).

Late Jurassic

The Late Jurassic crocodylomorph footprint record is not extensive, certainly when compared to the coeval dinosaur footprint record. The first crocodylomorph tracks reported and named from the Late

Jurassic were *Hatcherichnus sanjuanensis* (Foster and Lockley, 1997) from the Morrison Formation of Utah, USA (Fig. 6). Since then, three other Morrison localities with crocodylomorph tracks have been reported, some with distinctive tail traces. The most recent is described herein (Lockley and Foster, 2010). Likewise, several Late Jurassic crocodylomorph tracksites have been reported from the Asturias, Spain (Garcia Ramos et al., 2002, 2006; Avanzini et al., 2007). Avanzini et al. (2010b) discuss several morphotypes, including the ichnogenera *Crocodylopodus* (Fig. 5) and *Hatcherichnus*. Mateus and Milàn (2010) also report the first records of crocodylian (and pterosaur) tracks from the Upper Jurassic (Kimmeridgian) of Portugal.

Cretaceous

The Cretaceous crocodylomorph footprint record, like that of the Late Jurassic, is also not extensive in comparison with the dinosaur footprint record. The ichnospecies *Crocodylopodus meijidei* (Fuentes Vidarte and Meijide Calvo, 2001) was described from the Jurassic-Cretaceous (Tithonian-Berriasian) boundary in Spain on the basis of a well-preserved trackway. Since then, another, near-coeval Spanish trackway attributed to *C. meijidei* has also been reported from the basal Cretaceous of Spain (Pascual Arribas et al., 2005). As noted above, claims of a giant crocodylian trackway from the Tithonian-Berriasian of Galve, Spain (Perez-Lortente and Ortega, 2003) are refuted by Lockley (2009), who demonstrated its sauropod affinity.

Campos et al. (2010) report body imprints and tracks produced by large crocodylians from the Lower Cretaceous Sousa Formation of Brazil. The crocodylian traces are interpreted as subaqueous traces possibly produced by Mesoeucrocodylia engaged in half-swimming and resting behavior next to the margin of a lake. This is the first record of a crocodylian track from Brazil. Le Loeuff et al. (2010) report a very interesting, Early Cretaceous tracksite in Thailand including crocodylomorph footprints apparently indistinguishable from *Batrachopus*. This is the youngest occurrence of tracks so closely resembling this ichnogenus. A large, isolated track of probable crocodylian origin is also known from another Cretaceous site in Thailand (Matsukawa et al., 2006, fig. 10F)

Due to the large number of sites now known from the Albian-Cenomanian Dakota Group of Colorado, Kansas, and New Mexico, many documented here for the first time, the “mid” Cretaceous crocodylian track record is much more extensive than that of the earlier Cretaceous or Jurassic. Lockley et al. (2010a) report a total of 70 documented Dakota Group tracksites, including 19 with crocodylian tracks (~26% of localities). Numerically, therefore, crocodylian tracks are the second most abundant tetrapod track type in this unit and make up ~16% of the total numerical track sample. A large percentage of these are “swim tracks.” A swim track assemblage from Kansas, discovered in the 1930s was initially, albeit tentatively, attributed to *Dakotasuchus* (Lane, 1946), before being controversially misinterpreted as the traces of swimming dinosaurs (McAllister, 1989a,b). This misinterpretation was investigated in detail by Kurihara (2006) and Kurihara et al. (2010), who show that the tracks cannot be reasonably interpreted as dinosaurian.

Lockley (2010) reports on the reinvestigation of a historically important Dakota site near Golden, Colorado, that is the type locality of *Mehliella jeffersonensis* Strand (1932). Because Mehl did not reposit the type material (plaster casts) at the University of Missouri, as stated in his paper (Mehl, 1931), he created what is dubbed the “*Mehliella* mystery” solved herein (Lockley, 2010).

Houck et al. (2010) also document a newly-discovered “walking” crocodylian trackway from another site (North Golden) that originates from near the original, now-lost, *Mehliella* locality. The trackway represents a smaller individual (~2m long) and is similar to those reported from a site in New Mexico (Bennett, 1992). The abundant traces of swimming and walking crocodylians from the Dakota Group have considerable implications for our understanding of the tetrapod ichnofacies along the “Dinosaur Freeway.”

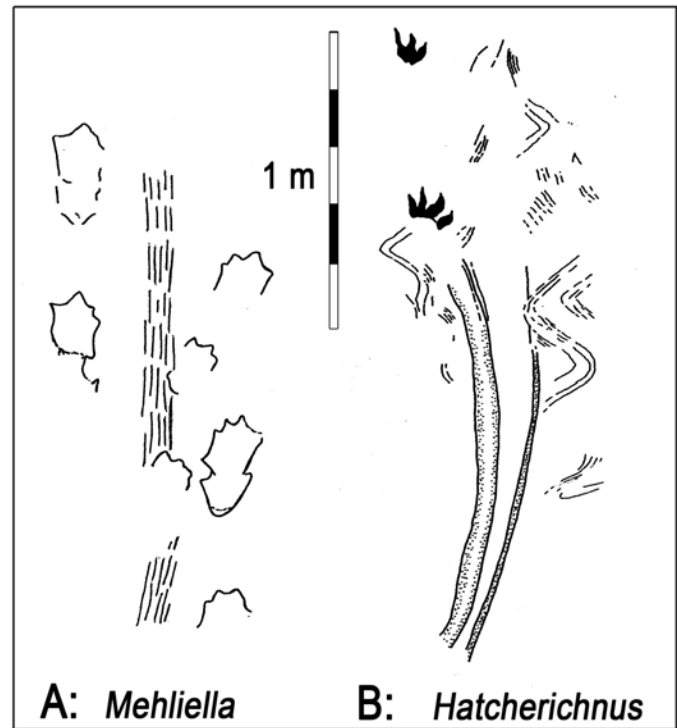


FIGURE 6. Named ichnogenera attributed to crocodylians. **A**, *Mehliella*. **B**, *Hatcherichnus*. Compare with Figure 5, see text for details.

Late Cretaceous crocodylian tracks are far less common than those reported from the Late Jurassic and Early to “mid” Cretaceous, and two articles in this volume represent most of the known record. Simpson et al. (2010) report an isolated, cf. *Crocodylopodus* pes track from the Campanian, capping sandstone member of the Wahweap Formation, Grand Staircase-Escalante National Monument, southern Utah. Falkingham et al. (2010) document a 1.5-m-long, double sinusoidal trace of crocodylian origin from the Maastrichtian Lance Formation of Wyoming.

Cenozoic

Reports of fossil crocodylian footprints of Cenozoic age are not common. However, two recent Paleocene reports (McCrea et al., 2004; Erikson, 2005) both named new ichnogenera. The former study named swim tracks from Alberta *Albertasuchipes russellia*. The latter study named basking crocodylian traces *Borealosuchipus hanksi*. Only one article in this volume adds to this meager record: Mikuláš (2010) documents series of three to four parallel ridges from Miocene lacustrine sandstones of the Zliv Formation at Zahájí, Czech Republic. The *Characichnos* tracks probably represent swim traces of large crocodylians.

NEOICHOLOGY

Extant crocodylians comprise Crocodylidae (14 species), Alligatoridae (8 species) and Gavialidae (1 species). This volume not only attempts to redress neglect of the crocodylomorph/crocodylian trace fossil record, but attempts are also made to document the tracks and traces of modern representatives of Crocodylia to facilitate meaningful comparison with fossil tracks.

Four papers in this volume address the topic of crocodylian footprint neoichnology. Milàn and Hedegaard (2010) compare tracks and trackways from 12 species of extant crocodylians and map out the morphological variation found in their tracks and traces, while Farlow and Elsegy (2010) take an in-depth look at tracks and trackways of American alligators, *Alligator mississippiensis*, in the wild. Kumagi and Farlow

(2010) examine the traces of the American crocodile *Crocodylus acutus* in its natural habitat, and Kubo (2010) examines the effect of different locomotion postures and gaits on crocodylian trackways. Together, these studies show that even though extant crocodylians share a conservative body plan, there are important differences in their tracks and trackways resulting from differences in progression speed and gait, and the consistency of the sediment during track making.

Neochronological studies prove very valuable for the interpretation of fossil tracks and traces. For example, even in the Dakota Group, the most crocodylian track-rich unit hitherto reported, only three of 19 sites reveal “walking” trackways. Modern examples illustrated by Milàn and Hedegaard (2010) help identify very similar examples in the Cretaceous that had previously proved difficult to interpret due to the lack of well-described modern analogs.

Clearly, the rarity of walking trackways in comparison to the abundance of swim tracks provides significant behavioral evidence. Kumagai and Farlow (2010) illustrate examples of the sporadic distribution of tracks in intertidal, estuarine environments that are identical to many Cretaceous swim tracks.

BITE MARKS

Acts of predation and scavenging often leave physical evidence in the form of bite marks in the remains of the victims, and while it can sometimes be difficult to establish the affinity of the bite marks, they provide important paleoecological information. In the first of four papers here, Vasconcellos and Carvalho (2010) deal with a Late Cretaceous ichnoassociation around *Baurusuchus*, where severe bite marks in its skull and bones are associated with coprolites and gastroliths. In a second contribution, Schwimmer (2010) examines large bite marks in turtle and dinosaur bones made by the giant, Late Cretaceous crocodylian *Deinosuchus*. Mikuláš (2010) examines possible crocodylian bite marks in Miocene bones from the Czech Republic, and Milàn et al. (2010) examine bite marks in the turtle shells made by dwarf caimans, *Paleosuchus palpebrosus*. These papers demonstrate the variety of bite marks attributed to crocodylians and their appearance in fossil and recent material.

COPROLITES

Coprolites are commonly encountered in the fossil record, and can provide important information about the diets of their makers. In this volume, Souto (2010) describes the extensive and well-preserved crocodylian coprofauna from the Upper Cretaceous of Brazil and the many coprolite morphotypes encountered there. A similarly diverse crocodylian coprofauna is described by Harrell and Schwimmer (2010) from the Late Cretaceous of Georgia, USA, including giant coprolites attributed to *Deinosuchus* as well as several specimens from smaller crocodylians. Milàn (2010) describes a coprofauna from the Danian (Early Paleocene) of Denmark, including coprolites from fish, sharks, and crocodylians. Finally, Hunt and Lucas (2010) provide a comprehensive review of the global record of crocodylian coprolites. In all, this section, together with the modern crocodile scat described by Milàn and Hedegaard (2010), provides a good reference base for identifying crocodylian coprolites.

GEOGRAPHIC DISTRIBUTION OF CROCODYLOMORPH FOOTPRINTS

The majority of well documented, Jurassic through Cretaceous crocodylomorph track sites, including many of those noted above and described in this volume, have been reported from the Northern Hemisphere. The first named crocodylian tracks (*Batrachopus* Hitchcock, 1845) were from North America, and it is from there that the majority of crocodylian tracksites (at least ~50) are known (Table 1). The sample of sites (~12) with documented crocodylomorph tracksites from the Jurassic through Cretaceous of Europe is considerably smaller (Table 2), and the number reported from Asia fewer still (Table 3).

DEPOSITIONAL ENVIRONMENTS AND PALEOECOLOGY

In the papers in this volume by Farlow and Elsey and Kumagai and Farlow, crocodylian tracks are described from natural coastal plain and estuarine habitats in Louisiana and Costa Rica, respectively. The known distribution of modern crocodylians – in aquatic tropical and subtropical environments, such as deltas, lakes, large river systems, estuaries, and other coastal plain environments – makes it possible to propose general inferences about the paleoenvironments and climates that prevailed where fossil crocodylian tracks are present. This presupposes that crocodylian habitat preferences have not changed markedly since the Mesozoic, and while this holds true mainly for crown group crocodylians, it is less so for more archaic stem group forms, many of which had different adaptations. On a more local scale, tracks, trackways, and other traces made by basking, low-walking, high-walking, subaqueously-walking and swimming crocodylians can help distinguish between emergent and shallow water environments and may, in some cases, even be relatively precise indicators of water depth.

The association of crocodylian tracks with those of other vertebrates and invertebrates, reported in several papers here, allows inferences about the paleoecology of the track makers. Clearly, coprolites and bite marks have the potential to provide direct evidence of predator-prey relationships. Both tracks and skeletal remains may also suggest at least indirect evidence of paleoecological relationships in the form of ratios between predator and prey taxa. For example, in the Cretaceous Dakota Group, despite the large number of herbivorous ornithomimid tracks, there is an absence of tracks indicative of large predatory dinosaurs; tracks of relatively small, gracile, coelurosaurian (probably ornithomimid) dinosaurs evidently do not represent a top predator species. Therefore, Lockley et al. (2010a) suggest that the hitherto unrecognized abundance of crocodylian tracks, many representing large individuals, is suggestive of the important ecological role they may have played as predators in that ecosystem.

ICHTNOFACIES

Previously, there has been little in-depth study of vertebrate or tetrapod ichnofacies, and it is fair to say that the field is still in its infancy. Preliminary studies (Lockley et al., 1994; Hunt and Lucas, 2007; Lockley, 2007) have defined various recurrent, tetrapod-dominated ichnological associations in particular sedimentary facies as ichnocoenoses and/or ichnofacies. The majority of these are characterized by the trackways of animals that habitually walked on emergent surfaces “on land.” However, some are characterized by “swim tracks,” and one of these, the *Hatcherichnus* ichnocoenosis (*sensu* Hunt and Lucas, 2007), was named using a crocodylian ichnotaxon. This suggests certain pertinent questions, some of which are explored in contributions to this volume (e.g., Lockley et al., 2010a, b). For example, two of the most obvious questions are:

- 1) Do crocodylian tracks (track assemblages) always, or at least typically, occur in similar, recurrent associations and facies, and how, therefore, are their spatial and temporal distributions defined?
- 2) Have crocodylian tracks been found in associations and facies that already have ichnocoenoses or ichnofacies labels?

The answer to the first question is yes. The only very common crocodylian tracks, which, by definition, occur with sufficient frequency to allow the recognition of recurrent associations, are *Batrachopus* and *Hatcherichnus*. The former is represented almost exclusively by “walking” trackways, and the latter by swim tracks. Also, it is worth noting that, with the exception of the Thailand occurrence (Le Loeuff et al. 2010), all *Batrachopus* occurrences are pre-Cretaceous (indeed, pre-Middle Jurassic), whereas all *Hatcherichnus* occurrences are post-Middle

TABLE 1. Documented crocodylomorph tracksites from the Triassic, Jurassic, Cretaceous, and Cenozoic of North America. The estimated minimum number of sites is ~50.

Unit and location	Age	Taxon	Reference
Newark Supergroup	Late Triassic	<i>cf. Batrachopus</i>	Silvestri and Szajna, 1993 Szajna and Silvestri, 1996 Szajna and Hartline, 2003
Multiple sites in New England	Early Jurassic	<i>Batrachopus</i>	Hitchcock, 1845 Olsen & Padian, 1986
Multiple sites in western USA	Early Jurassic	<i>Batrachopus</i>	Lockley et al., 2004 Milner et al., 2006
4 sites in the Morrison Formation	Late Jurassic	<i>Hatcherichus</i>	Lockley and Foster, 2010
19 sites in the Dakota Group	'mid' Cretaceous	<i>Hatcherichus</i> and <i>Mehliella</i>	Mehl 1931; Lockley et al., 2010; Lockley 2010
Wahweap Fm., Utah	Late Cretaceous	<i>Crocodylopodus</i>	Simpson et al., 2010
Lance Fm, Wyoming	Late Cretaceous	crocodylian	Falkingham et al., 2010
Alberta	Paleocene	<i>Albertasuchipes</i>	McCrea et al., 2004
North Dakota	Paleocene	<i>Borealosuchipus</i>	Erickson, 2005

Jurassic.

Most *Batrachopus* occurrences are associated with lacustrine shoreline habitats where there may or may not have been local fluvial influence. In such settings, the associated tetrapod tracks are predominantly those of small theropods (especially *Grallator*), with a lesser number of tracks of other small (*Anomoepus*) and larger dinosaurs (*Eubrontes*, *Otozoum*). Because *Batrachopus* is mostly restricted to the Early Jurassic, the associated ichnofaunas are therefore characteristic of this epoch or biochron (sensu Lucas, 2007) as well as being representative of particular habitats. Based on the definitions of Hunt and Lucas (2007), *Batrachopus*-rich ichnofaunal associations are intimately associated with the lake margin *Grallator* ichnofacies. Based on the recurrence of *Batrachopus*-bearing assemblages, it is possible to recognize, and herein define, a *Batrachopus* ichnocoenosis that forms part of the *Grallator* ichnofacies (sensu Hunt and Lucas, 2007). This does not imply that all authors of this paper necessarily agree with the concept of the archetypal *Grallator* ichnofacies or its global distribution. However, it does imply that it is possible to recognize that recurrent *Batrachopus*-bearing assemblages (the *Batrachopus* ichnocoenosis) are intimately associated with a more broadly distributed *Grallator* ichnofacies. It remains to be seen whether other sporadic occurrences of *Batrachopus* in both space and time conform to the recurrent pattern of association noted in North

America.

The *Hatcherichnus* ichnocoenosis (Hunt and Lucas, 2007), compared to the *Batrachopus* ichnocoenosis, is based on significantly different assemblages, which in turn represents a conceptually different ichnofacies concept. First, the *Hatcherichnus* ichnocoenosis is already defined as representative of facies dominated by swim tracks: i.e., the *Characichnos* ichnofacies (sensu Hunt and Lucas, 2007), which is associated with "shallow lacustrine" environments. Technically, the *Hatcherichnus* ichnocoenosis was based on two very small assemblages from fluvial deposits (in the Upper Jurassic Morrison Formation of Utah and Colorado). However, by implication, the ichnocoenosis can be considered to include other similar ichnofaunas from similar facies. This wider distribution is confirmed by the report of two more *Hatcherichnus* occurrences in the same formation, in similar fluvial facies, as well as similar occurrences in fluvial settings in Europe (Avanzini et al., 2010b, c).

The identification of multiple, *Hatcherichnus*-dominated assemblages in the Dakota Group (Lockley et al., 2010a) not only extends the concept of the *Hatcherichnus* ichnocoenosis in space and time, but also permits a re-evaluation of its facies relationships, which, by definition, are a key component of ichnocoenosis and ichnofacies philosophy. While the *Hatcherichnus*-dominated Dakota Group assemblages are clearly all

TABLE 2. Documented crocodylomorph tracksites from the Jurassic and Cretaceous of Europe. All reports except Asturias represent single sites. Estimated minimum number of sites is ~12.

Site and location	Age	Taxon	Reference
La Viellon, France	Hettangian	<i>Batrachopus</i>	Lapparent and Montenat, 1967
Causses, France	Hettangian	<i>Batrachopus</i>	Lockley and Meyer, 2004
Resita Basin, Romania	Hettangian-Sinemurian	<i>Batrachopus</i>	Popa, 1999
Yorkshire, England	Aalenian-Bathonian	—	Whyte and Romano, 2003 Romano and Whyte, 2010
Praia de Peralta, Portugal	Kimmeridgian	cf. <i>Hatcherichnus</i>	Mateus and Milan, 2010
Asturias	Kimmeridgian	Four types including <i>Crocodylopodus</i> & <i>Hatcherichnus</i>	Avanzini et al., 2007, 2010
Valdevilla, Spain	Berriasian	cf. <i>Crocodylopodus</i>	Pascual Arribas et al., 2005
Villar del Rio, Spain	Tithonian- Berriasian	<i>Crocodylopodus meijidei</i> type	Fuentes Vidarte and Meidije Calvo, 2001
Aldanueva de Cameros, Spain	?Berriasian	?crocodylian	Moratalla et al., 2002
Las Hoyas, Spain	Hauterivian- early Barremian	?crocodylian	Moratalla et al., 1999

indicative of swimming activity in subaqueous settings, they do not, strictly speaking, represent shallow lacustrine settings, either in the Morrison Formation or the Dakota Group. Instead, they represent fluvial channel systems in the Morrison, and a complex of fluvial, delta plain and estuarine (paralic) deposits in a coastal plain setting in the Dakota Group. This suggests the need for an alternate treatment of the *Hatcherichnus* ichnocoenosis, including one or more of the following options:

- 1) The *Hatcherichnus* ichnocoenosis could be elevated to the *Hatcherichnus* ichnofacies associated with the suite of fluvial-coastal plain facies.
- 2) The *Hatcherichnus* ichnocoenosis could be subsumed under a different ichnofacies, which is characteristic of fluvial-coastal plain facies (e.g., the *Batrachichnus* ichnofacies of Hunt and Lucas, 2007) associated with “tidal flat-fluvial plain” environments, or even with their *Brontopodus* ichnofacies, which is associated with coastal plain environments.

3) The *Hatcherichnus* ichnocoenosis could be retained in the *Characichnos* ichnofacies, only if the inferred environmental (facies) context is much more broadly defined.

It is not our intention here to provide an unequivocal solution to any of these complex questions, but merely to show some of the issues that require attention in any ichnofacies analysis. Lockley et al. (2010a) note that a preference for the former solution (#1) - i.e., defining vertebrate ichnofacies more narrowly - leans towards the “ichnofacies split-

TABLE 3. Documented crocodylomorph tracksites from the Jurassic and Cretaceous of Asia. All reports represent single sites. Reported total = 4.

Site and location	Age	Taxon	Reference
Sichuan, China	Middle Jurassic	<i>Kuangyuanpus</i>	Young, 1943 Lockley et al., 2010b
Shandong, China	Early Cretaceous	<i>Laiyangpus</i>	Young, 1960 Lockley et al., 2010b
Thailand	Early Cretaceous	cf. <i>Batrachopus</i>	Le Leouff et al., 2010
Thailand	Early Cretaceous	large ?crocodylian tracks	Matsukawa et al., 2006

ting” paradigm (cf. Lockley 2007), whereas the “ichnofacies lumping” camp is also a defensible paradigm (Hunt and Lucas, 2007).

Regardless of the merits of either ichnofacies philosophy, more can be said about vertebrate ichnofacies, and we conclude here with the problem of “degree of overlap” between named ichnocoenoses and ichnofacies (using examples cited above). In theory, every ichnocoenosis or ichnofacies should be clearly defined. However, this does not necessarily create clear-cut boundaries in space and time, or prevent ichnocoenoses and ichnofacies from overlapping in various complex ways. Again, the *Batrachopus* and *Hatcherichnus* ichnocoenoses are instructive because they represent different types of evidence. The *Batrachopus* ichnocoenosis, as noted and defined above, is part of the *Grallator* ichnofacies, and does not overlap with any other ichnofacies. Thus, it need not be considered further here. In contrast, as noted by Lockley et al. (2010a), the *Hatcherichnus* ichnocoenosis was not only defined as part of the *Charicichnos* ichnofacies, but in the Cretaceous Dakota Group, it co-occurs in the *Charirichnium* ichnofacies (Lockley et al., 1994; Lockley 2007), characterized as the *Charirichnium* ichnocoenosis by Hunt and Lucas (2007). As originally defined, the “dinosaur-dominated” *Charirichnium* ichnofacies is co-extensive with the Dinosaur Freeway in the upper part (Sequence 3) of the Dakota Group. The studies of this group presented herein indicate that the Dinosaur Freeway ichnofaunas are a complex mix of dinosaur “walking” tracks and crocodylian “swim tracks” assemblages that represent two quite distinct ichnofacies. Thus, the Western Interior Coastal plain system was a dinosaur freeway interlaced with “crocodile waterways” - a complex mosaic of emergent and subaqueous environments.

This conclusion raises further conceptual questions. First, is it possible to define two interpenetrating ichnocoenoses or ichnofacies that are entirely co-extensive in a given area? By definition, ichnocoenoses should represent recurrent assemblages of a “particular” type in “similar” facies. Thus, it would be logical, where two “particular” ichnocoenoses

or ichnofacies are coextensive, to combine the labels in some way. At this stage in ichnofacies research, it is probably inadvisable to introduce any formal terminology for areas where two or more pre-defined ichnofacies (or ichnocoenoses) overlap. As suggested above, the overlap or interpenetration can simply be noted and the nature of the overlap and interpenetration examined. For example, in such cases the two ichnofacies/ichnocoenoses may occur in facies that are subtly different on a local scale. Second is the problem of scale. While it is argued that recognition of the interpenetration of the *Charirichnium* and *Hatcherichnus* ichnocoenoses can be described and understood at the “ichnocoenosis” level (*sensu* Hunt and Lucas, 2007), there are pitfalls to describing such overlapping ichnocoenoses at the “ichnofacies level.” As a result, Lockley et al (2010a) have reservations about describing the Dakota Group ichnocoenoses as an overlap or interpenetration of the *Brontopodus* and *Characichnos* ichnofacies. This is not just because the ichnogenus labels may create conceptual problems and confusion between original and revised definitions, but also because the sedimentary facies and the habitats they represent are too broadly defined at this higher, global, archetypal or ichnofacies level. Third, one must consider whether such ichnofacies overlap is inherently more common or predictable in some settings, and less so in others. For example, there is agreement between the ichnofacies “lumper” and “splitter” camps (Hunt and Lucas 2007; Lockley 2007) regarding the definitions and extents of some vertebrate ichnofacies (e.g., *Chelichnus*), but not others.

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A Gharial from the KrokodilleZoo in Denmark. Photo by Jesper Milán.