



A review of large Cretaceous ornithopod tracks, with special reference to their ichnotaxonomy

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Trackways of ornithopods are well-known from the Lower Cretaceous of Europe, North America, and East Asia. For historical reasons, most large ornithopod footprints are associated with the genus *Iguanodon* or, more generally, with the family Iguanodontidae. Moreover, this general category of footprints is considered to be sufficiently dominant at this time as to characterize a global Early Cretaceous biochron. However, six valid ornithopod ichnogenera have been named from the Cretaceous, including several that are represented by multiple ichnospecies: these are *Amblydactylus* (two ichnospecies); *Caririchnium* (four ichnospecies); *Iguanodontipus*, *Ornithopodichnus* originally named from Lower Cretaceous deposits and *Hadrosauropodus* (two ichnospecies); and *Jiayinosauropus* based on Upper Cretaceous tracks. It has recently been suggested that ornithopod ichnotaxonomy is oversplit and that *Caririchnium* is a senior subjective synonym of *Hadrosauropodus* and *Amblydactylus* is a senior subjective synonym of *Iguanodontipus*. Although it is agreed that many ornithopod tracks are difficult to differentiate, this proposed synonymy is questionable because it was not based on a detailed study of the holotypes, and did not consider all valid ornithopod ichnotaxa or the variation reported within the six named ichnogenera and 11 named ichnospecies reviewed here. We therefore emphasize the need to base comparisons between ichnotaxa on type material, and not on selected referred material. It is concluded that there is considerable variation in the morphology of the holotypes, as well as variation in size and quality of the samples and the mode of preservation. Conversely, there is considerable overlap in morphology among other tracks that have been informally attributed to these ichnotaxa. These factors make it difficult to synonymize any of the existing ichnotaxa without detailed revision of the samples from which the type material originates. Nevertheless, a review of the type material of all ichnotaxa is presented as a basis for further discussion and, as a first step, the ichnofamily Iguanodontipodidae is proposed to accommodate *Amblydactylus*, *Caririchnium* and *Iguanodontipus*, © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **113**, 721–736.

ADDITIONAL KEYWORDS: footprints – ichnology – iguanodontids – vertebrate ichnology.

INTRODUCTION

Ornithopod tracks are extraordinarily abundant in the Cretaceous, giving rise to the suggestion that they are characteristic of a Lower Cretaceous biochron (Lucas, 2007). Indeed, Lucas (2007: 22) states that ‘Cretaceous

tetrapod footprints can be distinguished from Jurassic tracks primarily by the abundance and near ubiquity of large ornithopod tracks’. However, as yet, there is no firm consensus about which of the several ichnotaxonomic names, including *Amblydactylus*, *Caririchnium*, *Iguanodontipus*, *Hadrosauropodus*, and *Ornithopodichnus*, are applicable to given track morphologies. Lockley *et al.* (2013) noted that, in addition to the five aforementioned ichnogenera, a sixth,

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Jiayinosauropus, was named by Dong, Zhou & Wu (2003). Both *Hadrosauropodus* and *Jiayinosauropus* are Late Cretaceous ichnogenera of presumed hadrosaurid affinity, whereas the others are reported from the Lower to 'mid' Cretaceous, with many of the better documented occurrences being confined to units dated as Berriasian to earliest Cenomanian.

Lucas (2007) refers to *Amblydactylus*, *Iguanodontipus*, and *Caririchnium* as the three names applied to Early Cretaceous morphotypes, with the former two being strictly bipedal, whereas *Caririchnium* represents a quadruped. As discussed below, this summary requires elaboration to include *Ornithopodichnus*, which was named after 2007. Moreover, Lucas *et al.* (2011: 357) have recently suggested that only two ichnogenera may be valid: '*Caririchnium* (= *Hadrosauropodus*) and *Amblydactylus* (= *Iguanodontipus*)'. Again this conclusion does not address the position of *Ornithopodichnus* or *Jiayinosauropus* already known at the time that this interpretation was proposed. Thus, although we agree with Lucas *et al.* (2011: 361) that 'further study of the ichnotaxonomy of large ornithopod footprints is needed', we consider their suggestions premature and in need of further scrutiny. We therefore review the usage of these names and the morphological criteria used in their definition.

The informal and taxonomically incorrect name '*Iguanodon* tracks' was applied as early as the 1860s to describe tracks inferred to have been made by *Iguanodon*. However, as noted by Sarjeant, Delair & Lockley (1998), this name, referring to an osteological taxon, is invalid as an ichnotaxon. As a result, these authors proposed the name *Iguanodontipus*, based on ornithopod track casts from the Lower Cretaceous of England where so-called *Iguanodon* tracks were first reported. These authors also dismissed the name *Iguanodonichnus* (Casamiquela & Fasola, 1968) as a *nomen dubium* and an egregious misidentification of a sauropod track, probably similar to *Brontopodus* (Farlow, Pittman & Hawthorne, 1989). This conclusion was supported by Moreno & Benton (2005).

Sternberg (1932) named the new ichnogenus *Amblydactylus* based on the type ichnospecies *Amblydactylus gethingi* from the Lower Cretaceous of Canada. Although he mentioned tracks, he only illustrated one. The description of this ichnospecies was revised by Currie & Sarjeant (1979), who recognized the morphotype as a slightly elongate track (length/width ratio = 1.08) with relatively sharp terminations to the digit traces. They also inferred that the trackmaker was a biped. By contrast, they erected the ichnospecies *Amblydactylus kortmeyeri* for a more transverse track (length/width = 42/43 cm = length/width ratio 0.98). Several *A. kortmeyeri* were described based on isolated specimens and trackway

segments indicating bipedal progression. However, neither holotype is based on a trackway.

Leonardi (1984) named the ichnospecies *Caririchnium magnificum* based on the trackway of a quadruped from the Lower Cretaceous of Brazil. The ichnotaxon was based on a trackway indicating quadrupedal progression, a pes track with a distinctive quadripartite morphology, and a relatively large irregular manus. Leonardi (1984) inferred the trackmaker to have been a stegosaur but, subsequently, on seeing similar tracks in Colorado, he reinterpreted the Brazilian tracks as ornithopodan (Lockley, 1986). The Colorado tracks were subsequently named *Caririchnium leonardii* from North America by Lockley (1987), as also discussed by Lockley & Wright (2001), and additional ichnospecies, *Caririchnium lotus* and *Caririchnium protohadrosaurichnos* were subsequently erected on the basis of Lower and 'mid' Cretaceous tracks from Texas and China (Lee, 1997 and Xing *et al.*, 2007).

Iguanodontipus was named by Sarjeant *et al.* (1998), ostensibly to address the 'iguanodon tracks' problem outlined above. *Jiayinosauripus* was named by Dong *et al.* (2003) without reference to any of the previously named ichnogenera. However, as noted by Lockley *et al.* (2013), the report of this ichnogenus has been ignored until recently. This brief introduction to the ichnotaxonomy of large Cretaceous ornithopod tracks establishes an historical context for further analysis of each ichnotaxon and leads us to question whether a careful analysis of the six aforementioned ichnogenera (*Amblydactylus*, *Caririchnium*, *Iguanodontipus*, *Hadrosauropodus*, *Ornithopodichnus*, and *Jiayinosauropus*) and their various ichnospecies, are distinct and valid, or in need of some measure of synonymy, as suggested by Lucas *et al.* (2011). As will be shown, it is difficult to fully evaluate the suggestions of Lucas *et al.*, (2011) because they only discuss the first four of the above listed ichnogenera (*Amblydactylus*, *Caririchnium*, *Iguanodontipus*, and *Hadrosauropodus*), and their analysis is remarkably brief. Moreover, they present their inference that '*Hadrosauropodus* is a junior subjective synonym of *Caririchnium*' (Lucas *et al.*, 2011: 361) and that *Amblydactylus* (= *Iguanodontipus*) as more of a casual suggestion than a formal ichnotaxonomic statement or revision.

Although we acknowledge that large ornithopod tracks occur ubiquitously in the Cretaceous and that individual tracks attributed to any of the ichnogenera may be convergent in morphology, it is important to be clear about the morphological characteristics of the type specimens, as opposed to other specimens, that may have been casually or informally labelled with a given ichnogenus or ichnospecies name. In this regard, Lucas *et al.* (2011) make a number of questionable assumptions, if not significant missteps, that

compromise the strength of their argument. For example, their fig. 5, purports to show the type specimens of *Amblydactylus*, *Caririchnium*, *Iguanodontipus*, and *Hadrosauropodus*, with the caption 'Type specimens of selected large ornithopod footprint ichnogenera, drawn to be approximately the same size. *Amblydactylus* after Currie (1995); *Iguanodontipus* after Lockley & Meyer (2000); *Hadrosauropodus* after Lockley *et al.* (2003) [sic]; and *Caririchnium* after Leonardi (1994)'. However, the fact is that this illustration does not show the type specimen of either *Caririchnium*, *Iguanodontipus* or *Amblydactylus* but, instead, compares paratypes or referred specimens. [The reference is also Lockley, Nadon & Currie, 2004, and not 2003]. Moreover, they fail to cite the original description of *A. gethingi* (Sternberg, 1932) or the revisions of that ichnospecies, and the erection of the new ichnospecies *A. kortmeyeri* by Currie & Sarjeant (1979). These are significant omissions that present obstacles to any attempt to synonymize any of these ichnogenera.

ICHNOTAXONOMY OF LARGE CRETACEOUS ORNITHOPODS

Given that ichnotaxonomy observes the rules of priority, we review established ornithopod ichnogenera (and included ichnospecies) from the Lower Cretaceous in the order that they were named:

Amblydactylus gethingi (Sternberg, 1932)
Amblydactylus kortmeyeri (Currie & Sarjeant, 1979)
Caririchnium magnificum (Leonardi, 1984)
Caririchnium leonardii (Lockley, 1987)
Caririchnium protohadrosaurichnos (Lee, 1997)
Caririchnium lotus (Xing *et al.*, 2007)
Iguanodontipus burreyi (Sarjeant *et al.*, 1998)
Ornithopodichnus masanensis (Kim *et al.*, 2009)

Similarly, the history of naming Upper Cretaceous ichnotaxa is:

Jiayinosauripus johnsoni (Dong *et al.*, 2003)
Hadrosauropodus langstoni (Lockley, Nadon & Currie 2004a)
Hadrosauropodus nanxiongensis (Xing *et al.*, 2009)

Note that, in the above list, all second or third assignments of new ichnospecies to an existing ichnogenus were made several years or decades after the original ichnogenus was erected.

We are fully aware that separating Early and Late Cretaceous ichnotaxa is a matter of convenience. In the sections that follow, discussions of ichnotaxa morphology are presented independent of considerations of their age. However, age is considered a factor when discussing possible trackmakers and other factors such as geological context. In this regard, it is worth noting that there is some precedent in the literature

for recognizing the significant time gap separating the occurrences of the afore-listed ichnogenera (Fig. 1). Lucas (2007), for example, recognizes separate Lower and Upper Cretaceous biochrons, although these are differentiated on the basis of the overall ichnoassemblages not on the basis of ornithopod ichnotaxa alone.

For historical reasons the first three named ichnogenera *Amblydactylus*, *Caririchnium*, and *Iguanodontipus*, have all, at one time, been attributed to *Iguanodon*, or iguanodontian track makers. We also argue that all three ichnogenera are more similar to each other than to the other ichnogenera, which are based on smaller samples, in some cases based on suboptimally preserved material. We therefore propose the new ichnofamily Iguanodontipodidae. The concept of ichnofamilies or 'morphofamilies' (*sensu* Lull, 1904; Sarjeant & Kennedy, 1973; Sarjeant and Langston, 1994) is very broad, and essentially informal with respect to the International Code of Zoological Nomenclature. The label Iguanodontipodidae, proposed here, recognizes the long history of scientific debate on the subject of the footprints of *Iguanodon* and similar track makers. Such suprageneric categories are useful as indicators of morphological similarity. Moreover, they can be employed without 'lumping' or synonymizing ichnogenera prematurely, and may also serve as a ready-made category to which other existing or new ichnotaxa may be assigned.

ICHNOFAMILY IGUANODONTOPODIDAE (FIGS 2, 3, 4A, 5)

Diagnosis: Large, subsymmetric tridactyl pes tracks lacking digital phalangeal pad traces but sometimes divided by inter-digital creases into a quadripartite configuration, indicating three, fleshy, sub-oval digits and a heel pad, and sometimes with broad ungual traces. Heel may be rounded or posteriorly bilobed. Manus small, rounded, oval to semi-circular or crescentic, when present, and typically situated anterior to anteriolateral. Trackway typically with short step and inwardly rotated pes.

AMBLYDACTYLUS STERNBERG 1932

The original description of *A. gethingi* by Sternberg (1932) is relatively simple, referring to a holotype plaster cast (catalogue number 8555) 64 cm long and 59 cm wide (length/width ratio = 1.08) and corresponding field photograph (Sternberg, 1932, plate IV, fig. 2) of an original impression (concave epirelief). The track lacks discrete pad impressions but has a digit divarication, between II and IV of 56° (Fig. 2A). According to Sternberg (1932: 72) who cites Beckles (1856), the track 'nearly resembles those of the Wealdon (*sic*) of Europe, which are generally regarded as *Iguanodon*'.

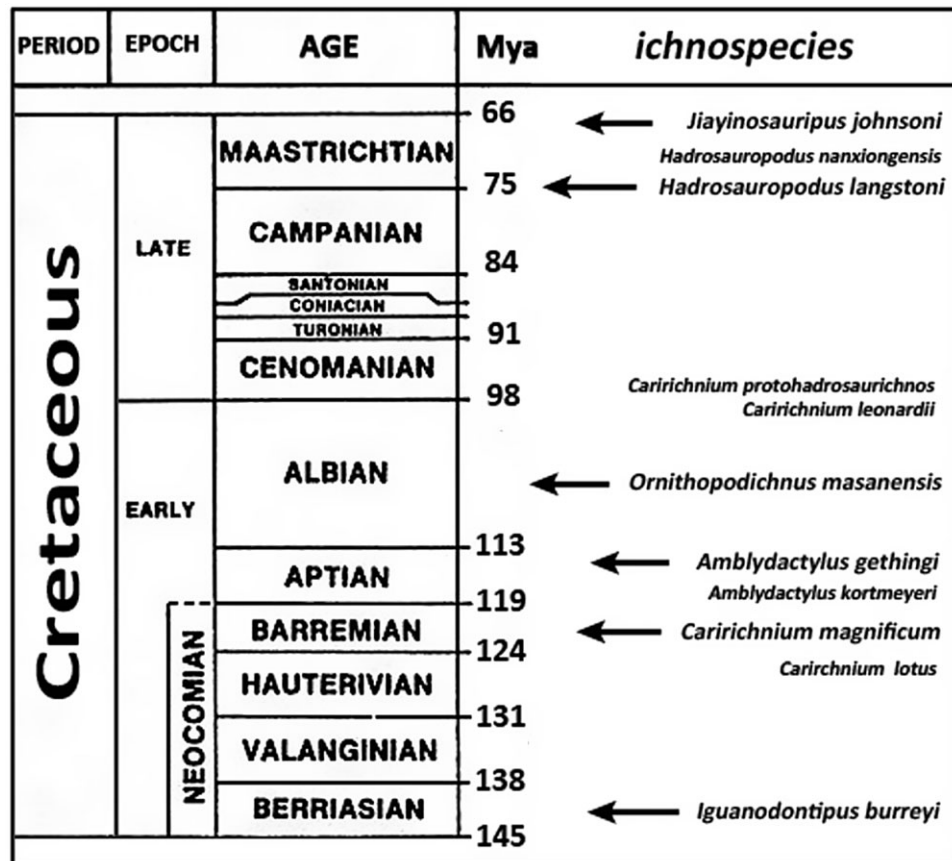


Figure 1. Stratigraphic occurrence of named ichnotaxa of large ornithopods from the Cretaceous.

Sternberg also compares the Canadian tracks with 'The Triassic Genus *Eubrontes*' and *Eubrontes* (?) *titananopelopatidus* from the Cretaceous of Texas, suggesting, rather ambiguously, that the track more closely resembles the former than the later ichnotaxon.

In their revisions of *Amblydactylus*, Currie & Sarjeant (1979) did not refer in any detail to the type specimen reported by Sternberg as catalogue number 8555 and stated (Currie & Sarjeant, 1979: 105) that 'no further footprints of this type have so far been recovered. The holotype was discovered at a stratigraphical level now generally submerged beneath the Peace River'. This stratigraphical level is the Gething Formation, which is Aptian to Albian in age (Currie, 1989). Comparisons between type *Amblydactylus* and other ichnotaxa are compromised by the lack of a well-defined holotype.

By contrast to *A. gethingi*, which is rather poorly defined, Currie & Sarjeant (1979) defined a new ichnospecies *A. kortmeyeri*, which they described in great detail (Fig. 2B). It also originates from the Gething Formation. The holotype is based on a left pes 42 cm long and 43 cm wide (length/width ratio = 0.98). They designated five much smaller paratypes (I–V)

with the length/width ratios: 0.90, 0.93, 0.89, 0.95, and 1.00. (Paratypes III and IV belong to the same trackway, with a mean length/width ratio = 0.93.) After pooling the values for III and IV, the mean length/width ratio for all six tracks (presumably representing 5 trackways) is 0.95. In their diagnosis Currie & Sarjeant (1979) recognize *A. kortmeyeri* as wider than long but consider digit divarication (70–80°) difficult to define and misleading because the angle subtended between the heel and the tips of digits II and IV does not follow the longitudinal axes of the digits, which are almost parallel to the footprint axis. Instead, the tracks have a definite tendency towards the quadripartite configuration of three padded toes and a heel, as described below for other named and unnamed ornithopod morphotypes. They also describe a digit III unguis trace and a hypex between digits III and IV shallower than between II and III, which they interpreted as evidence for webbing.

It is interesting that paratype I of *A. kortmeyeri* is less than half the size of the holotype (length 19 cm) and paratypes II–V are approximately one quarter the size (length 11.2–12.0 cm). These specimens all lack well-defined hypices, which may either be interpreted

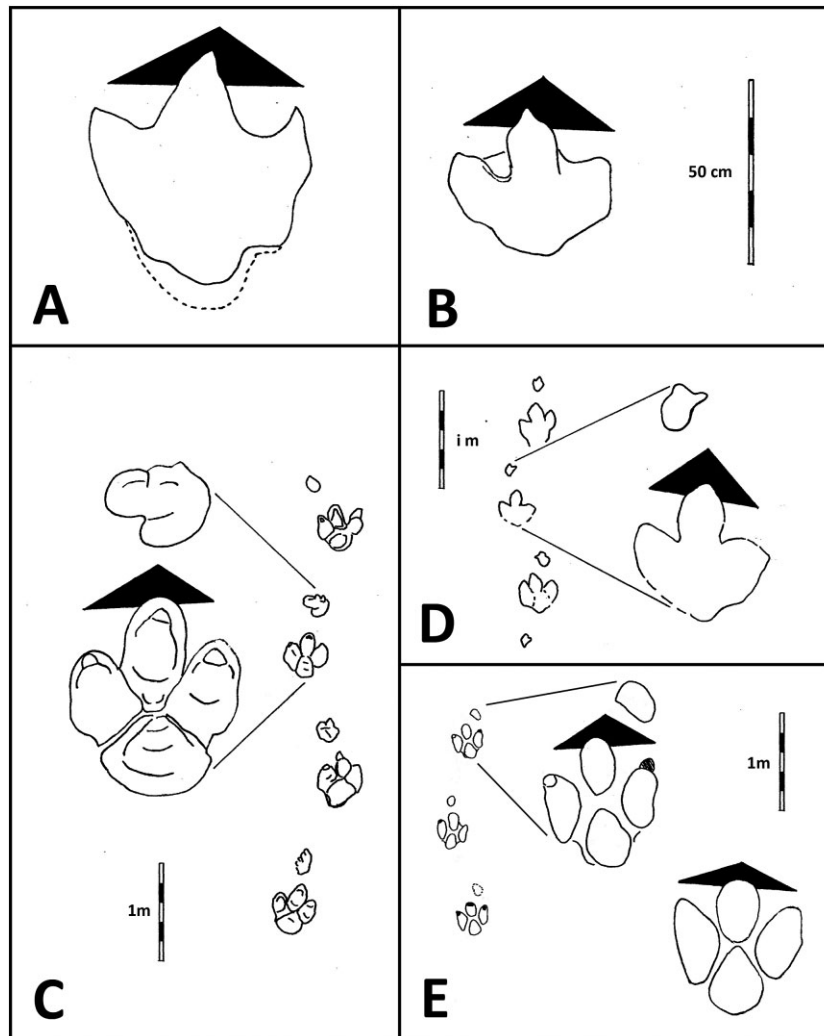


Figure 2. Holotypes of ichnospecies of *Amblydactylus* and *Caririchnium* ichnospecies drawn to the same scale. A, *Amblydactylus gethingi* sensu Sternberg (1932). B, *Amblydactylus korymeyeri* sensu Currie & Sarjeant (1979). C, *Caririchnium magnificum* sensu Leonardi (1984) showing trackway and detail of second left manus-pes set. D, *Caririchnium leonardii* sensu Lockley (1987) showing detail of left manus pes set. E, isolated pes of *Caririchnium lotus* sensu Xing *et al.* (2007) with detail of holotype trackway added. Shape of anterior triangles shown in black. *Caririchnium protohadrosaurichnos* Lee (1997) not shown. See text for details.

as webbing (*sensu* Currie & Sarjeant, 1979) or as sub-optimal preservation, an interpretation that we prefer.

It might originally have appeared that the *Amblydactylus* trackmakers represented exclusively bipedal animals as implied by the description of the two ichnospecies, based only on pes tracks (incomplete samples). Currie (1983: 63) explicitly stated that the ‘most common ichnogenus in the Peace River Canyon is *Amblydactylus*, a large bipedal herbivore’ making up 50% of the trackways and 90% of the isolated footprints. He continued (Currie, 1983: 63) that ‘The morphology of the hand and footprints suggest that the tracks and trackways were made by hadrosaurs, and the ichnites might represent the

earliest record of these dinosaurs’. This reference to the ‘hand’ clearly indicates that sometimes *Amblydactylus* occurs in trackways indicating quadrupedal progression. This observation was explicitly confirmed by Currie (1995) when he illustrated a trackway of four consecutive pes footprints, three of which show associated manus tracks (Fig. 3). In each case, the manus is arcuate in shape with a concave posterior margin. Detailed illustration of the first manus in the sequence shows that three digit traces corresponding to digits II, III, and IV are clearly seen (Fig. 3). McCrea *et al.* (2014) also report trackways of *A. gethingi* that were clearly made by quadrupeds. This reference reiterates the reports by Currie (1995).

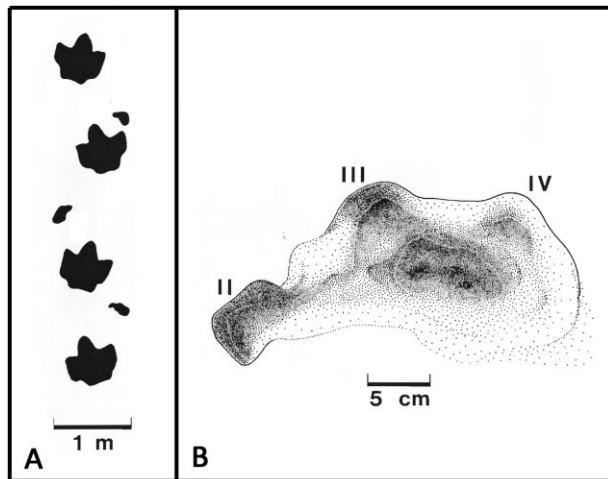


Figure 3. A, trackway of *Amblydactylus* isp. indet. from the Gething Formation indicating quadrupedal progression. B, detail of arcuate manus with traces of digits II, III and IV clearly shown. Modified from Currie (1995).

There are a number of implications arising from Currie's description and discussion of this trackway (Fig. 3). First, he says that it is difficult to distinguish *A. gethingi* from *A. kortmeyeri* so the trackway, by default, is simply referred to as *Amblydactylus* (implying *Amblydactylus* isp. indet.). He also described manus track morphology in some detail, noting that it differs from *Caririchnium* from Brazil. So a difference is explicitly noted, although Currie (1995: 432) stated that 'this characteristic cannot be used by itself to distinguish them [*Caririchnium* manus tracks] from *Amblydactylus* . . .' continuing that 'It is probable that *Caririchnium* is a junior synonym of *Amblydactylus*'. All these points are debatable, especially because Currie does not give a reason why differences in the manus are not of ichnotaxonomic significance at the ichnogenus level. As indicated below, all three holotype trackways of *Caririchnium* have distinctive quadripartite pes morphologies. Thus, the difference, based on holotypes, does not stand 'by itself' on the basis of manus morphology alone. Another pertinent factor in trying to distinguish *Amblydactylus* and *Caririchnium*, is the fact that Currie's description of an admittedly distinctive trackway, under the nonspecific ichnogenus label *Amblydactylus* is not a formal revision or amendment of either of the two aforementioned ichnospecies (*A. gethingi* or *A. kortmeyeri*). Thus, the possibility or probability of synonymy (technically a subjective synonymy) of this trackway, with either of the type specimens, remains open.

Finally, even though the exact location of the type track (or trackway) from which the original

Amblydactylus holotype (*A. gethingi*) was recovered is not precisely known, it originates from the same region and formation as *A. kortmeyeri* and the *Amblydactylus* trackway referred to by Currie (1995). Thus, the latter falls in the general category of an *Amblydactylus* 'topotype' and, because it reveals details of the trackway, configuration is a useful addition to our knowledge of the ichnogenus.

CARIRICHNIUM LEONARDI 1984

We now turn to *Caririchnium*, originally defined by Leonardi (1984) on the basis of the Brazilian ichnospecies *C. magnificum*, from the Antenor Navarro Formation (Fig. 2C) in the lower part of the pre Aptian Rio do Peixe Group (Leonardi, 1989). The type specimen is based on a well preserved trackway of a quadruped that exhibits a subsymmetric, pes trace with quadripartite morphology consisting of impressions of three digits and a heel pad separated by pronounced ridges, which, in life, represented well-defined concave-up creases that separated the convex-down pads. Ungual traces are also shown within, not distal to, the traces of digits II–IV. The manus traces of *C. magnificum* are irregular in size and shape ranging from a crude and rather large, irregular 'L' shaped trace to oval or subcircular, with the trace of an antero-medially, protruding digit in some cases. The 25-m long trackway is designated as an *in situ* holotype with a representative 'plastotype' ('Plastotypus') of the first manus pes set preserved in the Museu Câmara Cascudo del-l'Università, Federale di Natal.

The question of whether Leonardi (1984: 178) made adequate comparisons with other ichnotaxa, such as *Amblydactylus*, is interesting because, as noted below, he did not initially attribute it to an ornithopod track maker. However, he did state that it undoubtedly was of ornithischian affinity ('Non c'è dubbio che si tratta di un ornitisco'), and he devoted several paragraphs of careful discussion to its possible affinities. We consider his attempts to compare *Caririchnium* with other ichnotaxa more than adequate given the literature available at the time, which included little reference to trackways of large quadrupedal ornithopods.

This distinctive morphology (quadripartite pes and small oval manus with protruding digit trace) of *C. magnificum* is also seen in *C. leonardii* from Colorado (Lockley, 1987; Lockley, Hook & Taylor, 2001) (Fig. 2D), which originates from the upper part of the Dakota Group dated as near the Albian-Cenomanian transition (Fig. 1). A similar morphology is reported in *C. lotus* from China (Xing *et al.*, 2007) (Fig. 2E), which was originally illustrated on the basis of the pes and manus. Similar to the *C. magnificum*

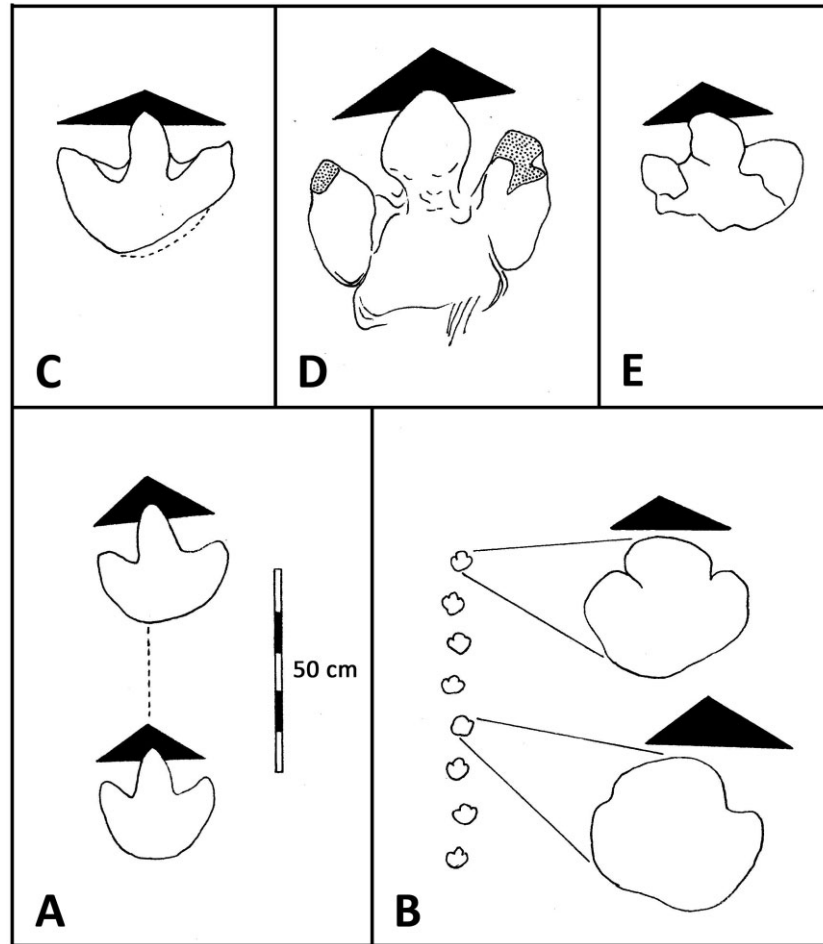


Figure 4. Type ichnospecies of *Iguanodontipus* and *Ornithopodichnus* (A, B) from the Lower Cretaceous, and *Jiayinosauripus* and *Hadrosauropodus* (C, D, E) from the Upper Cretaceous drawn to the same scale. A, *Iguanodontipus burreyi* sensu Sarjeant *et al.* (1998). B, *Ornithopodichnus masanensis* sensu Kim *et al.* (2009), C, *Jiayinosauripus johnsoni* sensu Dong *et al.* (2003), D, *Hadrosauropodus langstoni* sensu Lockley *et al.* (2004a). E, *Hadrosauropodus nanxiongensis* sensu Xing *et al.* (2009).

holotype, the *C. lotus* holotype trackways and several topotype trackways also reveal manus and pes unguial traces. The holotype of ichnospecies *Caririchnium protohadrosaurichnos* (Lee, 1997), from the Cenomanian of Texas also represents a quadruped. It is similar to *C. leonardii* except for less defined quadrupartite pes and a more elongate manus.

Caririchnium leonardii differs from *C. magnificum* in the configuration of the manus and the shape of the heel. All ichnospecies are represented by trackways. Lucas *et al.*, (2011: fig. 5) incorrectly referred to a track from the Dakota Group of Colorado as type *Caririchnium* (i.e. *C. magnificum*) and labelled it 'after Leonardi (1994)'. This track, (UCM 201.1), the only *Caririchnium* reported with skin impressions, was originally illustrated by Lockley (1989), Currie, Nadon & Lockley (1991) and Lockley & Hunt (1994, 1995)

under the label *C. leonardii*. Moreover it is not from the *C. leonardii* type locality and so cannot be considered a topotype or paratype of that ichnospecies, even though the label *C. leonardii* is appropriate.

It is noteworthy that all *Caririchnium* ichnospecies are based on trackways with similar configurations (Fig. 2C, D, E). When Lockley (1987) named *C. leonardii*, based on the holotype from Dinosaur Ridge, Colorado, he was influenced in part by Leonardi's field identification of the track as belonging to ichnogenus *Caririchnium* (Lockley, 1986). This ichnogenus label has subsequently been applied, almost universally, to ornithopod tracks from the Dakota Group, as well as elsewhere, notably in Asia (Lockley *et al.*, 2006). One exception was the informal use of the label *Amblydactylus* to describe an ornithopod manus pes set from the Dakota Group of New Mexico (Lucas,

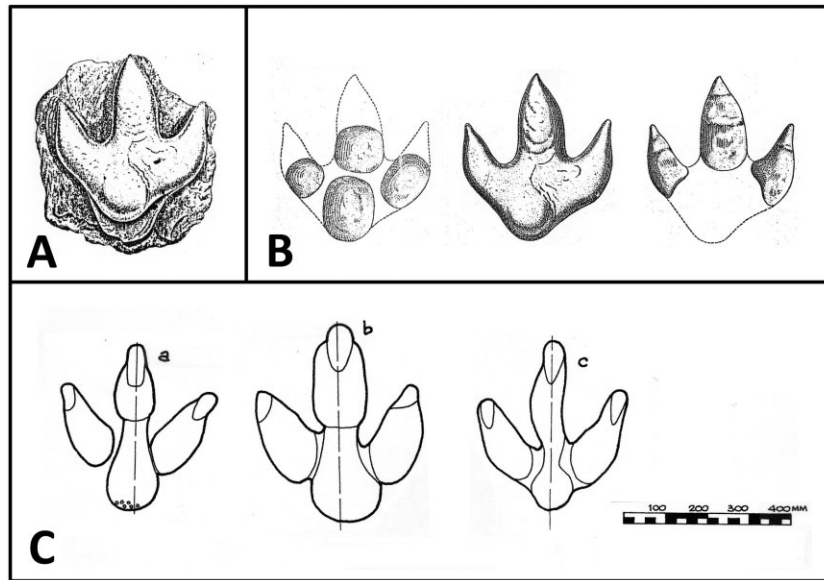


Figure 5. *Iguanodon* footprint casts from the Wealden beds of southern England, all showing tendency towards a quadripartite morphology. A, *sensu* Beckles 1856, from Bexhill area near Hastings. B, three modes of preservation illustrated by Dollo (1906) interpreted, from left to right as resting ('repos'), walking ('marche'), and running ('course'). C, tracks from Hastings Beds at Fairlight Cove near Hastings, *sensu* Woodhams & Hines (1989), with their scale, and numbers a, b, and c. Note that all show clear unguis traces and 'a' shows skin impressions on the heel.

Hunt & Kietze, 1989), although these same tracks were later labelled as *Caririchnium* (Lockley & Hunt, 1995). The specimen illustrated under the label *Amblydactylus* (Lucas *et al.*, 1989: fig. 22.4d) has a strongly quadripartite pes morphology and a strongly bilobed heel, which does not immediately align the morphology with either of the type ichnospecies of *Amblydactylus*. Thus, the identification remains debatable, and we are left to conclude that, although *Amblydactylus* and *Caririchnium* are similar, and may be difficult to distinguish in some cases (Lockley *et al.*, 1992; Currie, 1995), descriptions of the type specimens are significantly different.

The paper by Lucas *et al.* (2011) reveals a problematic practice in ichnotaxonomy (i.e. the informal substitution of nontype material for the purposes of ichnotaxonomic comparison). This raises the problem of an informally referred specimen, as subjectively judged to be a better exemplar than the holotype, not being able to substitute for the holotype, without a formal revision, even if the type is of inferior quality, as well as representing an annoying obstacle to understanding variation within the ichnotaxon. The embellished description of *Amblydactylus s.l.* by Currie (1995) is a good example of this practice. Because this was not a formal amendment of the ichnogenus (or either of its two ichnospecies), the suggestion of 'probable' synonymy carries no formal ichnotaxonomic weight. The same is true for the

casual suggestions of Lucas *et al.* (2011). The exposition given here is also 'informal' below the level of ichnofamily Iguanodontipodidae, and aims only to review the ichnotaxonomic arguments thoroughly, so that any further formal revisions might be undertaken judiciously.

IGUANODONTIPUS SARJEANT *ET AL.*, 1998

Sarjeant *et al.* (1998) described, in considerable detail, the process of selecting a type for ichnogenus *Iguanodontipus*, represented by the ichnospecies *I. burreyi*, which they proposed as an ichnotaxonomic solution to the problem of labelling ubiquitous ornithopod tracks from the Wealden and associated deposit in England as *Iguanodon* footprints, without a designated type. *Iguanodontipus* was erected as a monospecific ichnogenus, and remains so at present. As part of their study, they rejected the ichnogenus *Iguanodonichnus* (Casamiquela & Fasola, 1968), which was shown to be a *nomen dubium* with no diagnostic characteristics linking it to the Ornithopoda or the Iguanodontidae. Indeed, they inferred that the tracks represented a sauropod, an interpretation later confirmed by Moreno & Benton (2005).

The choice of the *I. burreyi* holotype was a pair of track casts, in sequence (Fig. 4A), from the Middle

Purbeck Beds at Norman's Quarry in Dorset, which is dated as earliest Cretaceous (Berriasian) (i.e. a pre-Wealden deposit, representing a non-Wealden sedimentary facies). The chosen 'type series' (*sensu* Sarjeant *et al.*, 1998) consisted of seven specimens (A to G) from Paines Quarry near Herston Dorset: respective length/width ratios are 1.16, 0.89, 0.86, 0.85, 1.07, 1.07, and 0.90 (mean length/width ratio = 0.97). The holotype trackway consisting of tracks C and D is represented by the two widest tracks (respective length and width of 23.5 and 27.5 cm for C and 24.1 and 28.2 cm for D). Thus, they have the lowest length/width ratios (0.86 and 0.85). Both consist of relatively well-preserved natural casts, indicating relatively deep and well-defined footprints. However, despite the good preservation, there is no indication of the quadripartite morphology seen in many ornithopod tracks. Nevertheless, it is relevant to note that so-called *Iguanodon* tracks with quadripartite configuration have been reported abundantly by Beckles, (1856, 1862), Dollo (1906) and subsequent workers (Woodhams & Hines, 1989) as a result of investigations of the Wealden beds (Fig. 5). These tracks are generally larger and morphologically different from *Iguanodontipus*.

ORNITHOPODICHNUS KIM *ET AL.*, 2009

Ornithopodichnus masanensis was named by Kim *et al.* (2009) from the track-rich Jindong Formation of Korea, which is considered to have been deposited during the Albian stage. *Ornithopodichnus* was erected as a monospecific ichnogenus, and remains so at present. It is based on a large sample of at least a dozen trackways of which six, each containing between five and eight consecutive footprints, were removed from a construction site near Masan city to the Natural Heritage Center in Daejeon city, where the slabs were given the numbers NHC 1001 (the holotype) through to NHC 1005. This sample can be considered the 'type' or 'topotype' series. Kim *et al.* (2009) also labelled NHC 1001 as trackway 2 (TW2) and trackways 1, 3, 4, 4', and 5 as paratypes. They incorrectly stated that TW5 is the holotype (*contra* their Figs 4, 5, 6). There are multiple photographs and line drawings of the trackways, including individual tracks A and B from Trackway TW2 (Fig. 4B) and measurements are given for each individual track. A summary of the mean measurements for each trackway is provided in Table 1, indicating a range of length width ratios from extremely transverse (0.640 in TW1 and 0.748 in TW5) to slightly elongate (1.187 in TW3). However, the mean for all six trackways is 0.899.

It should be noted that the preservation of these trackways is suboptimal, with some tracks still par-

Table 1. Mean measurements for length (L), width (W), and L/W for all *Ornithopodichnus* trackways in the type series

Trackway number	N	Length (L)	Width (W)	L/W
TW1	7	35.85	56.00	0.640
TW2	8	42.75	47.75	0.895
TW3	5	43.20	36.4	1.187
TW4	6	36.33	39.66	0.916
TW4'	4	35.75	35.50	1.007
TW5	5	42.20	56.40	0.748

Grand L/W means for all six trackways is 0.899.

tially filled, as noted by Kim *et al.* (2009). This is not unusual, although it is also worth noting that some of the tracks and digit traces are so broad and rounded as to make digit traces and the hiccups that separate them difficult to see clearly (i.e. the toe traces are extremely blunt). This raises the question as to whether the toes traces reflect blunt toes or extramorphological, preservational factors. As noted by Kim *et al.* (2009) preservational factors likely play a role, which may need to be taken into consideration when making comparisons with trackways where better preservation is evident.

JIAYINOSAURIPUS JOHNSONI DONG *ET AL.*, 2003

Jiayinosauripus johnsoni is based on a single natural cast, illustrated and briefly described by Dong *et al.* (2003), from the Yongancun Formation of the Jiayin Group, exposed near the Cretaceous–Tertiary boundary, also now referred to as the Cretaceous–Paleogene boundary. A second partial specimen is considered a paratype. The track is large and transverse according to measurements given by Xing *et al.* (2009), where the length is 35.94 cm and the width is 42.81 cm, giving a length/width ratio of 0.84.

HADROSAUROPODUS LOCKLEY *ET AL.*, 2004A

Hadrosauropodus langstoni was erected on the basis of a very well preserved natural cast of a large hadrosaur track (TMP 87.76.7), from the Upper Cretaceous St Mary River Formation of possibly Campanian–Maastrichtian age (Lockley *et al.*, 2004a). *Hadrosauropodus* was originally erected as a monospecific ichnogenus but now accommodates a second ichnospecies *H. nanxiogensis* erected by Xing *et al.* (2009) for an Upper Cretaceous trackway from and the Zhutian Formation of Guandong Province, China.

Hadrosauropodus langstoni is unequivocally identified as a true track as a result of well-preserved skin

impressions. The block from which it originated also shows an associated manus impression (Fig. 3D), although a trackway sequence is not evident. Both pes and manus tracks are included as part of the formal description. The pes track is wider (60 cm) than long (55 cm), giving a length/width ratio of 0.917. Although the pes track has a distinctive quadripartite configuration, it has an extraordinarily wide bilobed heel that makes up approximately two-thirds (67%) of track width. The manus is slightly triangular, with its anterior margin situated approximately 55 cm anterior of pes digit IV and outwardly rotated by approximately 45°. Overall manus length is approximately 15 cm and width is approximately 25 cm. The manus is not preserved on the block containing the pes and, to the best of our knowledge, remains in the field.

Hadrosauropodus nanxiongensis was erected by Xing *et al.* (2009) for an Upper Cretaceous trackway from the Zhutian Formation of Guangdong Province, China. The dimensions for the holotype (given as NDM.F1) are 40.38 cm and 51.32 cm, respectively, for total length and width, giving a length/width ratio of 0.786. The tracks occur in a trackway indicating bipedal progression, with steps approximately 2 × footprint length, and slight inward rotation.

COMPARATIVE ANALYSIS

Many factors need to be considered when evaluating and comparing the ichnotaxonomy of the ten ichnospecies listed above that have been attributed to large ornithopods. These factors include but are not limited to:

1. Quality and preservation of the of type material
2. Size and variability of the sample
3. Comparative morphology
4. Labelling of nonholotype and nontopotype tracks
5. Ichnotaxon age and facies relationships

PRESERVATION AND QUALITY OF THE TYPE MATERIAL

A brief visual survey of Figures 2 and 4, which illustrate the type specimens of 10 of the 11 ichnospecies discussed here, indicates considerable variation in the quality and preservation of samples selected as the basis of holotypes. Holotypes of both *Amblydactylus* ichnospecies are based on isolated pes tracks that were named by different workers almost 50 years apart. According to Currie & Sarjeant (1979), the ichnogenotype of *Amblydactylus* chosen by Sternberg (1932) as catalogue number 8555 (Fig. 2A) originates from an unspecified locality in an area where the ichnogenus is extraordinarily abundant both as trackways and isolated casts. The *A. gethingi* holotype is not particularly well preserved, whereas

the *A. kortmeyeri* holotype is better preserved but still an isolated specimen. Both are associated with a large sample of trackways that indicate trackmakers progressing both bipedally and quadrupedally, as later noted by Currie (1995).

By contrast, the holotypes of *Caririchnium* are all based on continuous trackway segments preserved as natural impressions (concave epireliefs). According to Peabody (1955) and Sarjeant (1989), it is preferable to base new ichnotaxa on trackways, not isolated tracks, wherever possible. All holotype *Caririchnium* trackways also preserve both manus and pes tracks, indicating quadrupedal trackmakers. Moreover, the type material remains available for study.

The holotypes of both *Iguanodontipus* and *Ornithopodichnus* are both based on trackway segments and moderately large samples (Fig. 3A, B). However, the holotype trackway of *Iguanodontipus* is preserved as natural casts (convex hyporeliefs), indicating moderately deep tracks, whereas the holotype trackway of *Ornithopodichnus* is based on natural impressions (concave epireliefs) that are partly filled. For this reason, it can be argued that *Ornithopodichnus* is not well preserved. Both ichnotaxa were erected on the basis of pes tracks only.

The holotypes of the remaining three ichnotaxa from the Upper Cretaceous are essentially based on very small samples. The holotype of *Jiayinosauripus* is based on an isolated natural cast (convex hyporeliefs) and partial paratype. Type *H. langstoni* is a very well preserved natural cast (convex hyporeliefs) of a pes showing skin traces. An associated manus cast made by the same animal is included in the description of the type. Type *H. nanxiongensis* is based on a rather poorly-preserved trackway of natural impressions (concave epireliefs) of the pes only.

In summary, four ornithopod track holotypes (*A. gethingi*, *A. kortmeyeri*, *J. johnsoni*, and *H. langstoni*) are based on isolated natural casts, pes specimens in the case of the former three, and a manus pes set in the case of the latter. All other holotypes, with the exception of *I. burreyi*, are based on tracks or trackways preserved as natural impressions. *Iguanodontipus burreyi* is associated with a few other natural casts in a similar state of preservation.

Finally, as noted by Lockley & Hunt (1994), tracks made in mud, and subsequently preserved as natural sandstone casts, often have very different cross-sections and depths from those made as natural impressions on sandy substrates that are less easily compacted. It is uncertain how these differences may affect the measurement of morphological features, on which differences in ichnotaxonomy might be based. However, it is known that gross morphology, such as the presence or absence of quadripartite morphology, can be preserved in either medium. This means that

such major morphological differences cannot be entirely attributed to preservation differences. It is also worth noting that natural sandstones cast very often represent true tracks, frequently showing striations where the integument of the foot was in contact with the muddy sediment in which the tracks were made: but see Avanzini, Pinuela & Garcia-Ramos (2012) for other cases.

SIZE AND VARIABILITY OF THE SAMPLE

As implied above, all four *Caririchnium* ichnospecies are based on relatively large trackway samples. Although only one *C. magnificum* trackway has been described, from Brazil (Leonardi, 1984, 1994), the topotype sample of *C. leonardii* from Colorado is based on a large sample documented in numerous studies (Lockley, 1987; Lockley & Hunt, 1994, 1995; Lockley *et al.*, 2001). Similarly, the topotype samples of *C. protohadrosaurichnos* and *C. lotus* from Texas and China (Lee, 1997 and Xing *et al.*, 2007 respectively) are large and well preserved and currently under further study. In all four *Caririchnium* samples, track shape is quite uniform, although, as noted below, there is sometimes variation in the morphology of the pes heel trace and pes unguis traces. The *Iguanodontipus* topotype sample consists of seven tracks comprising three trackway segments, all the tracks are fairly uniform in size and shape, and are explicitly referred to by Sarjeant *et al.*, 1998) as part of a single 'type series'. By contrast, there is considerable variation in the topotype sample, or type series, of *Ornithopodichnus*, which, as noted above, may be a result of suboptimal and/or extramorphological preservation.

Little can be said about the size and variability of other type specimens because the samples are so small. However, this does not preclude the possibility of obtaining more topotype material from some of the type localities, or reexamining the tracks on which the original descriptions were based.

COMPARATIVE MORPHOLOGY

According to the 'Ten Ichnological Commandments' proposed by Sarjeant (1989: 369), no new ichnotaxon should be named without making 'a thorough Literature search' for comparative material (commandment II). Related to this Sarjeant (Sarjeant, 1989: 370, commandment VIII) stresses the need to write diagnoses that are 'sufficiently tight to leave no ambiguity in the mind of the reader and to permit no confusion with types of footprints described earlier'. Although this has not always been done in the past, it is possible, as in the present study, to review existing diagnoses, and explicitly identify differences that facilitate meaningful comparison

between ichnotaxa. Specifically, comparison between ornithopod ichnotaxa can be based on the following morphological track and trackway characteristics typically described in the literature:

1. Length/width ratios of pes tracks
2. Degree of pes mesaxony (*sensu* Lockley, 2009a)
3. Pes digit termination characteristics (pointed toes, unguis traces, etc.)
4. Pes digital pad characteristics (quadripartite, or nonquadripartite configuration)
5. Pes heel shape (rounded, oval, triangular, bilobed)
6. Shape of manus tracks
7. Pes and manus skin trace characteristics (if present)
8. Presence or absence of manus tracks (indicating biped or quadruped)
9. Rotation of pes and manus traces in trackway
10. Trackway width and pace angulation

It is evident that the above list of potentially diagnostic features deals both with individual tracks morphology (characteristics 1–7) and trackway characteristics (8–10).

Once concerns pertaining to preservation and sample size have been considered, morphology becomes the most important factor to address in any comparative analysis of the validity and utility of ichnotaxa. We use the above morphological criteria in the ichnotaxonomic discussion presented below.

LABELLING OF NONHOLOTYPE AND NONTOPOTYPE TRACKWAYS

Many nontopotype tracks are assigned ichnotaxonomic labels. Ideally, these assignments are based on one or more of the morphological criteria listed in the previous section. However, it is not good practice to compare the ichnotaxonomic names given to different nontopotype samples if they are not at the same time compared to the holotypes. In other words, one cannot designate a nonholotype track as more representative of the ichnotaxon than the holotype without making and justifying a formal revision.

ICHNOTAXON AGE AND GEOLOGICAL FACIES RELATIONSHIPS

In theory, ichnotaxon age and facies relationships have little or no direct bearing on the practice of ichnotaxonomy, which should be based exclusively on morphological analysis. In practice, however, age and geological facies may have an indirect bearing on ichnotaxonomy in so far as tracks may be named to reflect inferences about trackmaker identity (e.g. *Iguanodontipus* and *Hadrosauropodus*), geological and

geographical provenance, and other nonmorphological factors. However, the ichnotaxonomic names themselves should be conceptually independent of their morphological diagnoses and descriptions.

DISCUSSION

As noted above, once we exclude *Iguanodonichnus*, an inappropriately named sauropod track (Sarjeant *et al.*, 1998; Moreno & Benton, 2005), *Ornithopodichnites* (Llompart, 1984), a probable theropod track that is poorly preserved (Lockley & Meyer, 2000), and *Hadrosaurichnus* (Alonso, 1980) another inappropriately named theropod track, we are left with only the 11 ichnospecies in the six ichnogenera introduced above. Questions arising from this synthesis include: are all the ichnotaxa valid? And, if not, can we justify casual synonymies of the type proposed by Lucas *et al.*, (2011: 358) ‘that all large ornithopod footprints should be referred to two ichnogenera, *Amblydactylus* and *Caririchnium*’, and that *Amblydactylus* (= *Iguanodontipus*), and that *Hadrosauropodus* is a junior subjective synonym of *Caririchnium*? Or should we defer judgment pending further study.

Regardless of the fact that Lucas *et al.* (2011) did not illustrate the holotypes of three of the four ichnogenera, we can agree that *Amblydactylus* and *Caririchnium* are the first two ichnogenus names introduced in large ornithopod ichnotaxonomy, and could potentially have priority in any thorough revision of ornithopod ichnotaxonomy. We also agree that their questions about differences between ornithopod ichnogenera are pertinent, if we wish to avoid undue ‘splitting’. However, we cannot agree that *Amblydactylus* = *Iguanodontipus* on the basis of the criteria given by Lucas *et al.* (2011: 358) namely that ‘its more gracile digit imprints . . . are usually more laterally directed, and [it has a] more tapered (narrower) heel’. We have shown that *Amblydactylus* represents a large trackmaker approximately twice the size of the *Iguanodontipus* trackmaker. *Amblydactylus* also often represents a quadruped. Because the two *Amblydactylus* type ichnospecies are based only on pes tracks they can be interpreted three ways: (1) that the trackmaker was a biped; (2) that trackmaker overstepped the manus with the pes (Paul, 1991); and (3) the holotype samples are far too incomplete to prove definitively which gait is represented. By contrast, the argument that *Iguanodontipus* represents a biped is far more convincing, based on a more ample ‘type series’, and can only be doubted or challenged by suggesting that the pes tracks possibly overlap the manus tracks, as suggested by Paul (1991). We note, however, that the tracks ‘tentatively referred to as *Iguanodontipus*’

(Lockley *et al.*, 2004b: 267) occur in the Purbeck equivalent beds of Northern Germany, and mostly represent bipeds but indicate quadrupedal locomotion and a distinctive tripartite manus in a few cases.

Given the lack of trackway evidence for type *Amblydactylus* the afore-cited suggestion by Lucas *et al.* (2011) that the digit imprints are laterally directed is not supported. The argument that the heel is more tapered (narrower) is also questionable, especially because Lucas *et al.* (1989) and Currie (1995) show bilobed heels in *Amblydactylus*. Similarly, Lucas *et al.* (2011), note considerable variation stating that in *Caririchnium* ‘the heel is blunt – either slightly rounded, transverse and, in some specimens slightly bilobed because of a posterior concave indentation’. Although it is true that heels of this description have been recognized in some samples of *C. leonardii* from North America, this morphology is not recognizable to any degree in any of the three type trackways (Fig. 2C, D, E) all of which have more or less oval to sub triangular heels.

We endorse the efforts of Lucas *et al.* (2011) to provoke a very interesting discussion. However, we argue that its resolution may lie in a different direction. A large number of so called *Iguanodon* tracks from the Wealden of England are highly convergent with type *Caririchnium* (Figs 2, 5). Moreover, the most distinctive feature of many of these tracks is that they are much larger and more differentiated into a quadripartite configuration than *Iguanodontipus*. Moreover, both *Caririchnium* (Fig. 2) and the Wealden morphotypes illustrated here (Fig. 5) often show similar ungual traces.

It is interesting to note that, consistent with this interpretation, McCrea *et al.* (2014) independently report ‘*Iguanodontipus* ichnosp. from the older Mist Mountain Formation, (and) *Amblydactylus* ichnosp., known from the younger Gething Formation’. These two formations are age equivalent, respectively, to the older Purbeck and younger Wealden units in England. They also explicitly refer to *A. gethingii* tracks and trackways with associated manus footprints (Currie, 1983, 1995). Similarly, the report of *Iguanodontipus* in the Minnes Group (~Valanginian) is another relatively early Lower Cretaceous occurrence (McCrea & Pigeon, 2014). Thus, although we conclude on the basis of morphology and the distribution of type and topotype material in space and time that *Iguanodontipus* is differentiated from *Caririchnium*, as Lucas *et al.* (2011) suggest, *Amblydactylus* is not a senior subjective synonym of *Iguanodontipus* but rather is much closer to *Caririchnium*. It is worth noting that *Iguanodontipus* has also recently been reported from the basal Cretaceous of Spain (Castenera *et al.*, 2013), as discussed elsewhere (Lockley *et al.*, 2014).

Regarding the proposal of Lucas *et al.* (2011) to synonymize *Hadrosauropodus* with *Caririchnium*, we argue that the wide bilobed heel is highly developed in type *Hadrosauropodus*, although this feature is not a part of the formal diagnosis of any *Caririchnium* ichnospecies. Also, the type descriptions and illustrations indicate differences in the manus that provisionally justify retaining two separate ichnogenera. There are also notable differences in size, as well as the non-morphological criterion of age. Lastly, the type *Hadrosauropodus* reveals a distinctive, well-preserved skin impression, which admittedly is similar to that described for a single less well-preserved nontopotype *Caririchnium* track (Lockley, 1989; Currie *et al.*, 1991). However, as yet, skin traces from Lower Cretaceous ornithopod tracks are almost unknown, or undescribed in detail (Woodhams & Hines, 1989), and therefore not useful for comparative analysis.

We consider the morphology of *Jiayinosauripus* (Dong *et al.*, 2003) insufficiently known to permit formal synonymy with the three ichnogenera, *Amblydactylus*, *Caririchnium*, and *Iguanodontipus*, named prior to 2003, even though the similarities are sufficient to place them in the same ichnofamily. Similarly, *Ornithopodichnus* does not obviously fall into any other ichnogenus. However, it has been argued that tracks assigned to *Ornithopodichnus* from the type series in Korea, and other locations (Lockley, Huh & Kim, 2012), are sufficiently distinct from all the aforementioned ornithopod ichnogenera to suggest a distinctive trackmaker with correspondingly weak mesaxony (Kim *et al.*, 2009; Lockley, 2009a). Presently, the stratigraphic range of *Ornithopodichnus* appears to be similar to that of *Amblydactylus* and *Caririchnium* (i.e. Barremian to Albian or early Cenomanian) (Fig. 1). This chronostratigraphic range (Fig. 1) appears to be distinct from the range of *Iguanodontipus* (Berriasian). This conclusion is supported by the suggestion of Castenera *et al.* (2013) that many tracks previously identified as type *Therangosopodus* from the Berriasian of Spain are better accommodated in *Iguanodontipus*(?), which is similar in size and general morphology to type *Iguanodontipus* from England. Several criteria have been used in arriving at this conclusion, including the presence of rare manus traces (Lockley, 2009b). This report, similar to the one from Germany (Lockley *et al.*, 2004b), indicates that *Iguanodontipus* may not always indicate bipedal progression.

Finally, it should be noted that Gierlinski & Sabath (2008) formally revised the ichnotaxonomy of *Stegopodus* (Lockley & Hunt, 1998), originally described on the basis of a manus track, to include the description of an associated pes track. This track has a slight resemblance to *Iguanodontipus*, although it is generally blunter toed and less symmetric.

CONCLUSIONS

The proposed synonymy of four large Cretaceous ornithopod ichnogenera, suggested by Lucas *et al.* (2011) is:

Amblydactylus (= *Iguanodontipus*) ~ Berriasian to Albian
Caririchnium (= *Hadrosauropodus*) ~ late Neocomian to Maastrichtian
 Other ichnogenera not considered

We suggest an alternative scheme, with the approximate age range of ichnogenera also shown:

Iguanodontipus ~ Berriasian – ?Valanginian
Caririchnium (quite similar to *Amblydactylus*) ~ Barremian – Cenomanian
Hadrosauropodus ~ Campanian – Maastrichtian
 Other ichnogenera considered but not assigned to a group:
Jiayinosauripus and *Ornithopodichnus*

Although individual track occurrences may fall outside these age ranges, we suggest that the latter scheme is more coherent for two important reasons. First, the holotypes were evaluated in detail morphologically. Second, based on morphology, including size, we appear to be able to discriminate three different ornithopod ichnofaunas with potential biochronological significance: one in the basal Cretaceous (Berriasian), one in the late Early to 'mid' Cretaceous (~Barremian – Cenomanian), and the last in the uppermost Cretaceous.

Although we recognize that there is considerable variation in ornithopod track morphology, both within holotype trackways, topotypes and type series, some trends are apparent. This includes the small size of basal Cretaceous forms in Europe (Lockley, McCrea & Matsukawa, 2009; Lockley, 2009b), which appear dominantly bipedal, and their replacement by generally larger and often quadrupedal forms in the late Early Cretaceous (~Barremian – Cenomanian) in Europe, Asia, and the Americas. This is followed by the appearance of even larger forms in the Late Cretaceous.

Finally, and again in the spirit of recognizing that there is considerable variation in ornithopod track morphology, we have proposed that *Amblydactylus*, *Caririchnium*, and *Iguanodontipus* be united in ichnofamily Iguanodontipodidae. We do not doubt that an argument could be made for including some of the other ornithopod ichnogenera in this ichnofamily.

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REFERENCES

- Alonso R. 1980.** Icnitas de dinosaurios (Ornithopoda, Hadrosauridae) en el Cretácico Superior del norte de Argentina. *Acta Geologica Lilloana* **15**: 55–63.
- Avanzini M, Pinuela L, Garcia-Ramos JC. 2012.** Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lehaia* **45**: 238–252.
- Beckles SH. 1856.** On the Orthichnites of the Wealdon. *Proceedings of the Geological Society of London* **X**: 456–464.
- Beckles SH. 1862.** On some natural casts of reptilian footprints in the Wealden Beds of the Isle of Wight and Swanage. *Quarterly Journal Geological Society, London* **18**: 443–447.
- Casamiquela RM, Fasola A. 1968.** Sobre pisadas de dinosaurios del Cretácico Inferior de Colchagua (Chile). *Publicaciones, Departamento de Geología, Chile Universidad* **30**: 1–24.
- Castanera D, Pascual C, Razzolini NL, Vila B, Barco JL, Canudo JI. 2013.** Discriminating between medium-sized tridactyl trackmakers: tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). *PLoS ONE* **8**: e81830.
- Currie PJ. 1983.** Hadrosaur trackways from the Lower Cretaceous of Canada. *Second symposium on Mesozoic Terrestrial ecosystems*. Jadwisin 1981. *Acta Paleontologica Polonica* **28**: 63–73.
- Currie PJ. 1989.** Dinosaur footprints of western Canada. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. New York, NY: Cambridge University Press, 293–300.
- Currie PJ. 1995.** Ornithopod trackways from the Lower Cretaceous of Canada. In: Sarjeant WA, ed. *Vertebrate fossils and the evolution of scientific concepts*. Singapore: Gordon and Breach Publishers, 431–443.
- Currie PJ, Nadon G, Lockley MG. 1991.** Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado. *Canadian Journal of Earth Sciences* **28**: 102–115.
- Currie PJ, Sarjeant WAS. 1979.** Lower Cretaceous dinosaur footprints from the Peace River Canyon, British Columbia, Canada. *Paleogeography, Paleoclimatology, Paleoclimatology* **28**: 103–115.
- Dollo ZL. 1906.** Les Allures des Iguanodons. *Bulletin Biologique de la France et de la Belgique* **40**: 1–12.
- Dong ZM, Zhou ZL, Wu SY. 2003.** Note on hadrosaur footprint from Heilongjiang River area of China. *Vertebrata Palasiatica* **41**: 324–326. (in Chinese with English abstract).
- Farlow JO, Pittman JG, Hawthorne JM. 1989.** *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the US Gulf Coastal Plain. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 371–394.
- Gierlinski GD, Sabath K. 2008.** Stegosaurian footprints from the Morrison Formation of Utah and their implications for interpreting other ornithischian tracks. *Oryctos* **8**: 29–46.
- Kim JY, Lockley MG, Kim HM, Lim JD, Kim SH, Lee SJ, Woo JO, Park HJ, Kim HS, Kim KS. 2009.** New Dinosaur Tracks from Korea, *Ornithopodichnus masanensis* ichnogen. et ichnosp. nov. (Jindong Formation, Lower Cretaceous): implications for polarities in ornithopod foot morphology. *Cretaceous Research* **30**: 1387–1397.
- Lee Y-N. 1997.** Bird and dinosaur footprints in the Woodbine Formation (Cenomanian) Texas. *Cretaceous Research* **18**: 849–864.
- Leonardi G. 1984.** Le impronte fossili di dinosauri. In: Bonaparte JF, Colbert EH, Currie PJ, de Rocles A, Kielan-Jaworowska Z, Leonardi G, Morello N, Taquet P, eds. *Sulle ormi di dinosauri*. Venice: Editio Editrice, 165–186.
- Leonardi G. 1989.** Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological significance. In: Gillette D, Lockley MG, eds. *Dinosaur tracks and traces*. New York, NY: Cambridge University Press, 165–179.
- Leonardi G. 1994.** *Annotated atlas of South America tetrapod footprints (Devonian to Holocene)*. Brasilia: República Federativa do Brasil Ministério de Minas e Energia Companhia de Pesquisa de Recursos Minerais.
- Llompart C. 1984.** Un nuevo yacimiento de icnitas de dinosaurios en las facies Garumnienses de la Conca de Tremp (Leida Espana). *Acta Geologica Hispanica* **19**: 143–147.
- Lockley MG. 1986.** *Dinosaur Tracksites*: a field guide published in conjunction with the first international symposium on dinosaur tracks and traces. *University of Colorado at Denver, Geology Department Magazine Special Issue* **1**: 1–56.
- Lockley MG. 1987.** Dinosaur footprints from the Dakota Group of Eastern Colorado. *Mountain Geologist* **24**: 107–122.
- Lockley MG. 1989.** Summary and prospectus. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. New York, NY: Cambridge University Press, 41–447.
- Lockley MG. 2009a.** New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. *Geological Quarterly* **53**: 415–432.
- Lockley MG. 2009b.** Some comparisons between Dinosaur-dominated footprint assemblages in North America and Europe. In: Huerta P, Torcida-Fernandez-Baldor F, eds. *Actas de Las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Burgos: Salas de los Infantes, 121–138.
- Lockley MG, Holbrook J, Hunt AP, Matsukawa M, Meyer C. 1992.** The dinosaur freeway: a preliminary report on the Cretaceous Megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains; Colorado, Oklahoma and New Mexico. In: Flores R, ed. 39–54. *Mesozoic of*

- the western interior, *SEPM midyear meeting fieldtrip guidebook*. Denver, CO: SEPM.
- Lockley MG, Hook N, Taylor A. 2001.** A brief history of paleontological research and public education on dinosaur ridge. In: Lockley MG, Taylor A, eds. *Dinosaur Ridge: celebrating a decade of discovery*. *Mountain Geologist* **38**: 87–89.
- Lockley MG, Houck K, Yang SY, Matsukawa M, Lim SK. 2006.** Dinosaur-dominated footprint assemblages from the Cretaceous Jindong Formation, Hallyo Haesang National Park area, Goseong County, South Korea: evidence and implications. *Cretaceous Research* **27**: 70–101.
- Lockley MG, Huh M, Kim BS. 2012.** *Ornithopodichnus* and pes-only sauropod trackways from the Hwasun tracksite Cretaceous of Korea. *Ichnos* **19**: 93–100.
- Lockley MG, Hunt AP. 1994.** *Fossil Footprints of the Dinosaur Ridge Area*. A publication of the Friends of Dinosaur Ridge and the University of Colorado at Denver Dinosaur Trackers Research Group, with the Morrison Museum of Natural History.
- Lockley MG, Hunt AP. 1995.** *Dinosaur tracks and other fossil footprints of the Western United States*. New York, NY: Columbia University Press.
- Lockley MG, Hunt AP. 1998.** A probable stegosaur tracks from the Morrison Formation of Utah. In: Carpenter K, Chure D, Kirkland J, eds. *The Upper Jurassic Morrison Formation: an interdisciplinary study*. *Modern Geology* **23**: 331–342.
- Lockley MG, Li J, Li RH, Matsukawa M, Harris JD, Xing L. 2013.** A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology. *Acta Geologica Sinica* **87**: 1–20.
- Lockley MG, McCrea RT, Matsukawa M. 2009.** Ichnological evidence for small quadrupedal ornithischians from the basal Cretaceous of southeast Asia and North America: implications for a global radiation. In: Buffetaut E, Cuny G, Le Loeuff J, Suteethorn V, eds. *Late palaeozoic and mesozoic continental ecosystems of SE Asia*. London: Geological Society of London, v. 315: 251–265.
- Lockley MG, Meyer CA. 2000.** *Dinosaur tracks and other fossil footprints of Europe*. New York, NY: Columbia University Press.
- Lockley MG, Nadon G, Currie PJ. 2004a.** A diverse dinosaur-bird footprint assemblage from the Lance Formation, Upper Cretaceous, Eastern Wyoming: implications for ichnotaxonomy. *Ichnos* **11**: 229–249.
- Lockley MG, Wright JL. 2001.** The trackways of large quadrupedal ornithopods from the Cretaceous: a review. In: Carpenter K, Tanke D, eds. *Mesozoic vertebrate life. New research inspired by the Paleontology of Philip J. Currie*. Bloomington, IN: Indiana University Press, 428–442.
- Lockley MG, Wright JL, Thies D. 2004b.** Some observations on the dinosaur tracks at Münchehagen (Lower Cretaceous), Germany. *Ichnos* **11**: 261–274.
- Lockley MG, Xing L, Kim JY, Matsukawa M. 2014.** Tracking Lower Cretaceous dinosaurs in China: a new database for comparison with ichnofaunal data from Korea, the Americas, Europe, Africa and Australia. *Biological Journal of the Linnean Society* **113**: 770–789.
- Lucas SG. 2007.** Tetrapod footprint biostratigraphy and biochronology. *Ichnos* **14**: 5–38.
- Lucas SG, Hunt AP, Kietze KK. 1989.** Stratigraphy and age of Cretaceous dinosaur footprints in northeastern New Mexico and northwestern Oklahoma. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*, 9th edn. Cambridge: Cambridge University Press, 217–221.
- Lucas SG, Sullivan RM, Jasinski SE, Ford T. 2011.** Hadrosaur footprints from the Upper Cretaceous Fruitland Formation, San Juan Basin, New Mexico, and the ichnotaxonomy of large ornithopod footprints. *New Mexico Museum of Natural History Bulletin* **53**: 357–362.
- Lull RS. 1904.** Fossil footprints of the Jura-Trias of North America. *Memoirs Boston Society Natural History* **5**: 461–557.
- McCrea RT, Buckley LG, Plint AG, Currie PJ, Haggart JW, Helm CW, Pemberton SG. 2014.** A review of vertebrate track-bearing formations from the Mesozoic and earliest Cenozoic of western Canada with a description of a new theropod ichnospecies and reassignment of an avian ichnogenus. *New Mexico Museum of Natural History and Science, Bulletin* **62**: 5–93.
- McCrea RT, Pigeon TS. 2014.** Replication and description of a large theropod and large ornithopod trackway from the upper Minnes Group (Lower Cretaceous: Valanginian) of the Peace Region of northeastern British Columbia, Canada. *New Mexico Museum of Natural History and Science, Bulletin* **62**: 269–277.
- Moreno K, Benton MJ. 2005.** Occurrence of sauropod dinosaur tracks in the Upper Jurassic of Chile (redescription of *Iguanodonichnus frenki*). *Journal of South American Earth Sciences* **20**: 253–257.
- Paul G. 1991.** The many myths, some old, some new of dinosaurology. *Modern Geology* **16**: 69–99.
- Peabody F. 1955.** Taxonomy and the footprints of Tetrapods. *Journal of Paleontology* **29**: 915–918.
- Sarjeant WAS. 1989.** Ten Paleoichnological commandments: a standardized procedure for the description of fossil vertebrate footprints. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 369–370.
- Sarjeant WAS, Langston W. 1994.** Vertebrate footprints and invertebrate traces from the Chadronian (Late Eocene) of Trans-Pecos Texas. *Texas Memorial Museum Bulletin* **36**: 1–86.
- Sarjeant WAS, Delair JB, Lockley MG. 1998.** The footprints of *Iguanodon*: a history and taxonomic study. *Ichnos* **6**: 183–202.
- Sarjeant WAS, Kennedy WJ. 1973.** Proposal of a code for the nomenclature of trace fossils. *Canadian Journal of Earth Sciences*. **10**: 460–475.
- Sternberg CM. 1932.** Dinosaur tracks from the Peace River, British Columbia. *National Museum of Canada Annual Report for 1930*, p. 59–85.

- Woodhams KE, Hines JS. 1989.** Dinosaur footprints from the Lower Cretaceous of Sussex, England. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 301–307.
- Xing L, Harris JD, Dong Z, Lin Y, Chen W, Guo S, Ji Q. 2009.** Ornithopod (Dinosauria: Ornithischia) tracks from the Upper Cretaceous Zhutian Formation in the Nanxiong basin, Guangdong China and general observations on large Chinese ornithopod footprints. *Geological Bulletin of China* **28**: 829–843.
- Xing L, Wang F, Pan S, Chen W. 2007.** The discovery of dinosaur footprints in the middle Cretaceous Jianguan Formation of Qijiang County, Chongqing City. *Acta Geologica Sinica* **81**: 1591–1603.