






Dinosaur Footprints from the Lower Cretaceous, Batá Formation, Colombia (South America), and the Possible Interchange of Large Ornithopods between Southern Laurasia and Northern Gondwana

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Abstract Dinosaur remains from northwestern South America are rare, with only extremely scarce fossil evidence recovered from Colombia. Here we report six dinosaur footprints preserved on a sub-vertical bedding plane of the upper Valanginian – lower Hauterivian Batá Formation, Santa María, Boyacá Department, Colombia. The Batá Formation consists of a thick succession of conglomerates and sandstones with shale intercalations interpreted as deposited along the palaeoshoreline of an epicontinental seaway. Four of the footprints form a trackway made by a single dinosaur, which is interpreted as a sub-adult ornithopod, estimated at 8 m in length, weighing around 2.5 metric tons, and travelling at an average walking speed of almost 5 km/h. The footprints are assigned to the ichnogenus *Iguanodontipus*, and were probably produced by an iguanodontian dinosaur. Prior to this work, *Iguanodontipus* was considered an exclusively European taxon, making this a unique record of the ichnogenus in Gondwana. The presence of *Iguanodontipus* in northern South America suggests an Early Cretaceous sweepstake, with dinosaurs crossing Tethys Ocean into modern-day northern Africa, and migrating along the northern shores of Gondwana into modern-day South America. Range extension of iguanodontian ornithopods southwards into Gondwana during the Early Cretaceous was apparently prevented by the Central Gondwana Desert Belt, possibly as a result of the palaeoecology of these dinosaurs, which seem to have had an affinity for environments rich in water and lush vegetation. A migration route across Tethys and the Central Gondwana Desert Belt helps explain similarities between northern Gondwanan and southern Laurasian dinosaurs, and the differences between northern and southern Gondwanan faunas, during the Early Cretaceous.

Keywords: dinosaur, ichnofossils, Lower Cretaceous, Gondwana, Laurasia, faunal interchange.

Resumen Los restos de dinosaurio del noroeste de Suramérica son raros, con muy pocas evidencias fósiles recuperadas en Colombia. Aquí reportamos seis huellas de dinosaurio preservadas en una capa subvertical del Valanginiano superior–Hauteriviano inferior de la Formación Batá, Santa María, departamento de Boyacá, Colombia. La Formación

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Batá consiste en una secuencia espesa de conglomerados y areniscas con intercalaciones de lodolitas interpretadas como depósitos de la línea de costa de un antiguo mar epicontinental. Cuatro de las huellas forman una pista dejada por un único dinosaurio, interpretado como un ornitópodo subadulto, con una longitud estimada de 8 m, un peso de 2,5 toneladas métricas y que viajaba a un ritmo normal de casi 5 km/h. Las huellas se asignaron al icnogénero *Iguanodontipus*, y fueron probablemente hechas por un dinosaurio tipo iguanodontiano. Antes de este trabajo, *Iguanodontipus* se consideraba como un taxón exclusivamente europeo, por lo que este registro sería el único en Gondwana. La presencia de *Iguanodontipus* en el norte de Suramérica sugiere la existencia de una comunicación terrestre durante el Cretácico Temprano, con dinosaurios cruzando el océano Tetis hacia el norte de África actual, y migrando a lo largo de la costa norte de Gondwana hasta lo que hoy es Suramérica. La extensión del rango de los ornitópodos iguanodontes hasta el sur de Gondwana durante el Cretácico Temprano no ocurrió debido a la presencia del Cinturón del Desierto de Gondwana Central, posiblemente como un resultado de la paleoecología de los ornitópodos, los cuales tenían afinidad por el agua y la vegetación exuberante. Una ruta de migración a través del Tetis y una barrera en el Cinturón del Desierto de Gondwana Central explicarían las similitudes entre los dinosaurios del norte de Gondwana y el sur de Laurasia, y las diferencias entre las faunas de norte y sur de Gondwana, durante el Cretácico Temprano.

Palabras clave: dinosaurio, icnofósiles, Cretácico Inferior, Gondwana, Laurasia, intercambio faunístico.

1. Introduction

Considering the first evidence for dinosaurs from South America came from Colombia (Buffetaut, 2000; Degenhardt in Mahlmann, 1840), body and trace fossils of these large terrestrial Mesozoic reptiles are tantalizingly rare in this country. Most South American dinosaurs are known from Argentina and Brasil (e.g., Bittencourt & Langer, 2011; Costa da Silva et al., 2012; de la Fuente et al., 2007; Díaz-Martínez et al., 2016; Francischini et al., 2015; Leonardi, 1989; Pazos et al., 2012; Weishampel et al., 2004), and indicate taxonomic dissimilarity from Laurasian dinosaurs (Cox, 1974; Gheerbrant & Rage, 2006; Canudo et al., 2009). This leaves a considerable gap in our understanding of the dinosaurs from northwestern Gondwana, and their relationships with the more southerly Gondwanan and southern Laurasian realms. Here, we report on the discovery of six footprints from the Lower Cretaceous Batá Formation of Colombia, northern South America, four of which are attributed to a large ornithopod dinosaur. The Batá Formation footprints apparently demonstrate affinities with Laurasian iguanodontian ichnofossils, rather than with dinosaur footprints from southern South America, therefore these findings have important implications for the palaeobiogeography of Early Cretaceous ornithopod dinosaurs.

1.1. Dinosaurs in Colombia

The first evidence for dinosaurs in South America were footprints reported in the *Gesellschaft für Erdkunde zu Berlin* (the

Berlin Society for Geography) on the 17 March 1839 (Buffetaut, 2000; Degenhardt in Mahlmann, 1840). Although originally correctly cited as originating from Colombia, subsequent reports erroneously indicated the footprints had been discovered in México (Degenhardt, 1840; Winkler, 1886; see also Buffetaut, 2000). These tracks were never figured, and were originally described as the footprints of giant birds (Degenhardt in Mahlmann, 1840). However, this was prior to Richard OWEN coining the term Dinosauria (Owen, 1841), so the Colombian footprints were almost certainly traces of dinosaurs (Buffetaut, 2000). These ichnofossils, now lost, came from a Lower Cretaceous locality near Oiba, Santander Department, Colombia (Degenhardt in Mahlmann, 1840), and remain one of only a handful of reports of dinosaur body and trace fossils from Colombia (Table 1).

Skeletal remains of Colombian dinosaurs are rare, with confirmed reports limited to Late Jurassic/Early Cretaceous sauropods (Carballido et al., 2015; Langston, 1953; Langston & Durham, 1955) and Late Cretaceous theropods (Table 1; Ezcurra, 2009). However, dinosaur footprints, although rare, are more common, with reports (in addition to those of Degenhardt in Mahlmann (1840)) of unidentified footprints from the Jurassic; titanosaurid sauropod, theropod, and rare ornithopod footprints from the uppermost Jurassic/lowermost Cretaceous; and theropod footprints from the Lower Cretaceous (Moreno-Sánchez & Gómez-Cruz, 2013; Moreno-Sánchez et al., 2011). Hence, most dinosaurs reported from Colombia have been attributed to Saurischia, either members of Theropoda or Sauropoda (although some of these taxonomic assignments have been

Table 1. Tabulation of dinosaur remains discovered in Colombia, showing the year of discovery, fossil type, material discovered, location of discovery, the geological formation, and geological age of the find, and the published reference to the discovery.

Year	Type	Material	Locality	Fm/Age	Reference(s)/Notes
1839	T	'Bird footprints' ?Theropod.	Summit of 'Cuchillas de las Pezuñas del Venado', Oiba, Santander.	Cretaceous, probably Paja Fm.	[1, 2]
1937	B	?Theropod, teeth.	Huila and Payandé, Tolima.	Cretaceous, unspecified Fm.	[3], considered crocodylian [4].
1943	B	Sauropod, anterior/mid-thoracic vertebra, UCMP 37689	East of La Paz, Cesar valley, Magdalena.	Pre-upper Aptian (Cretaceous), probably La Luna Fm.	[4]
1949	B	3 Theropod teeth, (2 abelisauridae, 1 ?dromaeosaurid), UCMP 39649a, b (2 teeth), UCMP 39650.	Upper Magdalena Basin, near Ortega, Tolima.	Late Cretaceous (?Maastriichtian), Fm. not specified (probably La Tabla Fm. or Oliní Group).	[5–7]
2008	T	Ornithopod, theropod and titanosaurid sauropod, footprints.	Santuario de Fauna y Flora de Iguaque, Chíquiza, Boyacá	Pre-Valanginian (uppermost Jurassic – Lower Cretaceous), Arcabuco Fm.	[8]
–	T	Theropod, footprints.	Circa de Villa de Leyva, Boyacá.	Aptian, Paja Fm; identification questionable as Paja Fm. is fully marine [9].	[8, 10]
–	T	Dinosaur, footprints.	Near Zapatoca, Santander.	Jurassic, Girón Fm.	[8, 10]
–	T	Theropod, footprints.	A quarry near Alpujarra, Tolima, Upper Magdalena Valley.	Early Cretaceous (?Barremian), Alpujarra Fm. [11], now Honda y Loma Fm.	[8, 10]
–	B	?Dinosaur, bone fragments.	Dolores Sector, Tolima.	Yaví Fm., ?Jurassic – Early Cretaceous.	[8]
–	B	?Ornithopod, bone fragments.	North of Media Luna Syncline, Aipe.	?Jurassic – Early Cretaceous, Yaví Fm.	[8, 10]
–	B	Theropod, ?tooth.	South of Cuiza Fault, Alta Guajira.	Early Cretaceous, Moina Fm.	[8]
–	T	Ornithopod, traces.	Venado River, Huila.	Jurassic, Saldaña Fm.	[10]
–	B	Sauropod, 14 vertebrae, 'JACVM 0001', correctly MJACM 1 [9].	'La Tordolla', vereda Monquirá, Villa de Leyva, Boyacá; La Tordolla lies within vereda El Roble [9].	Late Barremian, Paja Fm.	<i>Padillasaurus leivaensis</i> a brachiosaurid [12]; a non-titanosauriform somphospondyliian [13].
2020	T	Large iguanodontid footprints	Río Batá, Santa María, Boyacá	Early Cretaceous, Batá Fm.	This work

References: [1] Degenhardt (1840); [2] Buffetaut (2000); [3] Botero-Arango (1937, 39, pls 64, 65); [4] Langston & Durham (1955); [5] Ezcurra (2009); [6] Langston (1953); [7] Langston (1965); [8] Moreno-Sánchez et al. (2011); [9] Noè & Gómez-Pérez (2020); [10] Moreno-Sánchez & Gómez-Cruz (2013); [11] Flórez & Carrillo (1994); [12] Carballido et al. (2015); [13] Mannion et al. (2017).

(B) Body fossil (skeletal remains); (Fm.) Formation; (T) trace fossil.

questioned; de Valais et al., 2015), whereas only a small number of footprints have been ascribed to small- or medium-sized ornithopods (Moreno-Sánchez et al., 2011).

1.2. The Cretaceous World

The Cretaceous was a time of profound, but often poorly understood, global tectonic and environmental change, both on land and within the marine realm (Lehmann et al., 2015; Tennant et al., 2016). The break-up of Pangaea, which commenced in the Early Jurassic, continued apace (McLoughlin, 2001). During

the Early Cretaceous, Laurasia remained essentially complete, whereas the opening and widening of the Central Atlantic, and its connection to Tethys Ocean separated Gondwana from Laurasia (Canudo, 2006; Cox, 1974; Rage, 1988; Riccardi, 1991; Sereno et al., 1994; Tennant et al., 2016), producing an equatorial marine seaway along the northern margin of Gondwana (Rage, 1988), extending from modern-day Indonesia to México, linking the Central Atlantic to both western and eastern Panthalassa (Riccardi, 1991). The Central Atlantic-Tethys connection thereby acted as a barrier that apparently brought about continental isolation of Laurasia from Gondwana, breaking the

former terrestrial connection between modern-day Europe and North America, and northern Africa and South America by at least the earliest Cretaceous (Serenó *et al.*, 1994; however, see also Bosellini, 2002).

The complex and gradually accelerating breakup of Gondwana occurred throughout the Cretaceous (Heine *et al.*, 2015; McLoughlin, 2001; Sereno *et al.*, 1994; Torsvik & Cocks, 2017). This initially led to the separation of western Gondwana (Africa and South America) (Gheerbrant & Rage, 2006) from southeastern Gondwana (Antarctica, Australia, India, and Madagascar) through the opening of the South Atlantic, and later to the gradual development of essentially modern continental configurations (Torsvik & Cocks, 2017). The breakup of Gondwana led to constantly moving plates with significantly increased absolute velocities compared to earlier in the Mesozoic (Torsvik & Cocks, 2017). At various times in the Cretaceous, Gondwana was subjected to extensive plume related volcanic activity, doming and rifting, Large Igneous Provinces (LIPs), emplacement of kimberlites, subduction, orogenesis, and occasional meteorite impacts (Jaillard *et al.*, 1995; McLoughlin, 2001; Tennant *et al.*, 2016; Torsvik & Cocks, 2017).

Cretaceous climates were generally warm and humid, with relatively high global temperatures and high atmospheric partial pressures of carbon dioxide ($p\text{CO}_2$) (McLoughlin, 2001; Torsvik & Cocks, 2017). For much of the Cretaceous, the world exhibited high global sea levels, with extensive epicontinental seaways (Cox, 1974), caused in part by long mid-ocean ridges with rapid spreading rates, and in Gondwana by movement of the plates to areas of lower dynamic topography (Torsvik & Cocks, 2017). Hence, superimposed over typically high sea levels, were complex patterns of transgression and regression, which led to constantly changing continental shelves, and the repeated opening (flooding) and closure (isolation or draining) of epicontinental seaways (Cox, 1974; Gheerbrant & Rage, 2006; Lehmann *et al.*, 2015; Tennant *et al.*, 2016). In addition, Early Cretaceous seas and oceans were affected by global or regional oceanic anoxic events (OAEs), leading to widespread deposition of black shales (Erba *et al.*, 2004; Owens *et al.*, 2018; Tennant *et al.*, 2016).

1.2.1. The Early Cretaceous

The Berriasian, Valanginian, and Hauterivian (“Neocomian” of previous authors; Lockley *et al.*, 2009; Torsvik & Cocks, 2017) were times of major global upheaval, and increasing continental isolation of Gondwana (Serenó *et al.*, 1994). During the Valanginian – Hauterivian interval, globally important events included emplacement of the Paraná–Etendeka continental flood basalts (LIP volcanism) in Brasil and Namibia (Erba, 2004; McLoughlin, 2001; Svensen *et al.*, 2018), which initiated rifting of the South Atlantic, and ultimately led to a marine link between the South and Central Atlantic (Rage, 1988; Tennant *et al.*, 2016).

This rifting produced eastward doming of the future South American continental landmass (Jaillard *et al.*, 1995), leading to the deposition of the Batá Formation and other diachronous Lower Cretaceous sediments over the Palaeozoic basement in Colombia (Moreno *et al.*, 2009). On the northern margins of Gondwana, in the Mediterranean realm, there was subduction, folding, emplacement of ophiolites, rotation and rifting of the Iberian Peninsula, and flexure of the Arabian Plate (Gong *et al.*, 2008; Torsvik & Cocks, 2017).

Early Cretaceous, global sea levels were highly variable, falling in the Valanginian – Hauterivian to their lowest for the entire Cretaceous, but rising thereafter, which produced substantial continental flooding (Heine *et al.*, 2015; Lehmann *et al.*, 2015; Miller *et al.*, 2005; Tennant *et al.*, 2016; Torsvik & Cocks, 2017). During the Early Cretaceous, there was a general increase in global temperatures, with the first true greenhouse (globally warm and humid) climatic conditions commencing during the late Valanginian – early Hauterivian (Erba, 2004; Gröcke *et al.*, 2005). However, during the Early Cretaceous there were major climatic fluctuations (Meissner *et al.*, 2015; Tennant *et al.*, 2016), with the general warming punctuated by shorter, cooler episodes. Hence, although many authors consider the Early Cretaceous to have been entirely ice free (e.g., Canudo, 2006; McLoughlin, 2001; Torsvik & Cocks, 2017), there is increasing evidence for dramatically cooler climatic intervals, including sub-freezing temperatures and ice advances during the Valanginian – Hauterivian (Alley *et al.*, 2019; Tennant *et al.*, 2016). Although sea level changes in the Cretaceous are not generally attributed to glaciations (Canudo, 2006; Torsvik & Cocks, 2017), some authors consider Early Cretaceous sea level rises and falls, at least in the Central Atlantic Tethyan realm, the result of global, but relatively time-restricted, ice advances and retreats (Gröcke *et al.*, 2005; McLoughlin, 2001; Tennant *et al.*, 2016).

1.2.2. The Río Batá Footprints: Geological and Palaeoenvironmental Setting

During the Mesozoic, modern-day Colombia straddled the palaeo-equator, and during the Early Cretaceous lay on the northern shores of the rapidly dividing supercontinent of Gondwana. The dinosaur footprints reported here were discovered in a deep gorge of the Río Batá, Boyacá Department, Colombia (Figure 1), in the Batá Formation (Ulloa & Rodríguez, 1979; Etayo–Serna *et al.*, 2003). The Batá Formation forms part of the Lower Cretaceous in Colombia, although these rocks were long considered Early Jurassic in age (Bürgl, 1958, 1964; Irving, 1975; Mojica & Kammer, 1995). The type section of the Batá Formation lies in the valley of the Río Batá, and along the adjacent Guateque–Santa María road, close to Santa María, Boyacá (Ulloa & Rodríguez, 1979). The Batá Formation (Ulloa & Rodríguez, 1979) was formally designated for beds originally described by Bürgl (1958),

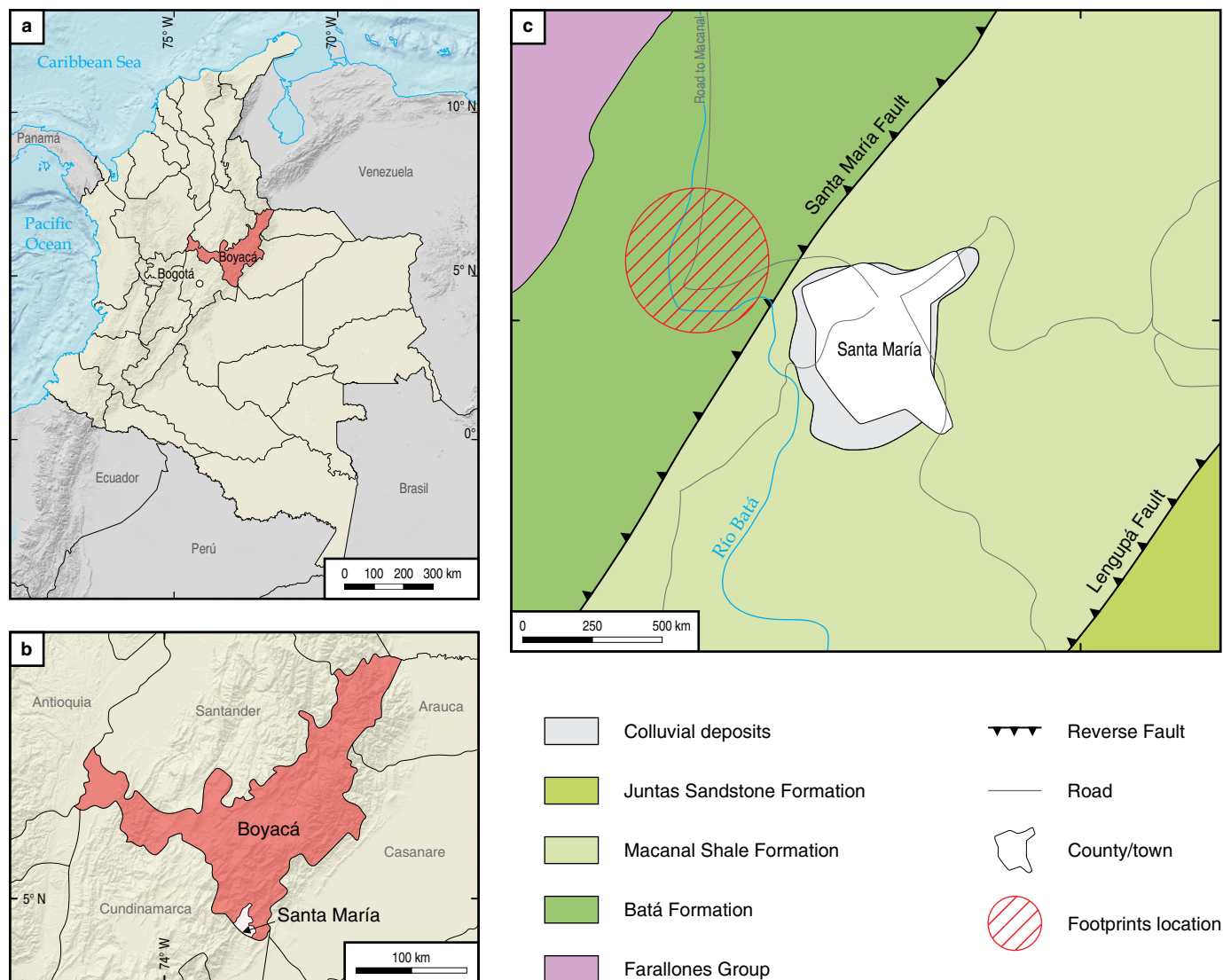


Figure 1. Geographical location of the Río Batá dinosaur footprints. **(a)** Political map of Colombia showing the locations of the capital Bogotá and Boyacá Department. **(b)** Geographical map of the Boyacá Department showing the locality of the municipality of Santa María. **(c)** Geological map of the region around the town of Santa María (modified from Montoya et al., 2008), indicating the approximate position of the dinosaur footprints (hatched red circle).

although previously the name “Batá Formation” had been used informally (Geyer, 1967, 61). At the type locality, the Batá Formation unconformably overlies the Palaeozoic Farallones Group, and is separated from the overlying Cretaceous Macanal Formation by the Santa María Fault (Terraza et al., 2013). The Batá Formation consists of more than 1000 m of conglomerates, quartz arenites, siliceous siltstones, claystones, and mudstones, and is divided into four units lettered A–D from base to top (Ulloa & Rodríguez, 1979). The Batá Formation sediments indicate alternating terrestrial to shallow marine palaeoenvironments (Etayo–Serna et al., 2003; Ulloa & Rodríguez, 1979), with the dinosaur ichnofossils formed along a tidally influenced palaeo–shoreline on the margin of an epicontinental seaway. The palynological evidence is indicative of a warm and humid regional climate (Etayo–Serna et al., 2003).

2. Materials and Methods

There are six dinosaur footprints, here designated DF1–DF6 (Figure 2), four of which (DF1–4) form a single trackway; the remaining two footprints (DF5–6) are isolated, and lie approximately perpendicular to the trackway. The footprints are preserved on a sub–vertical bedding surface above a deep rock pool of the Río Batá, and although additional footprints may be preserved below the water line, no further footprints were observed higher on the cliff face. Due to the difficulty of accessing the site, descriptions and measurements were obtained from field sketches and scaled photographs taken during two site visits. The trackway and footprints were described using standard variables (both metrical and non–metrical) for large tridactyl dinosaur footprints (Figures 3, 4; following Castanera et al., 2013; Lockley, 1991,

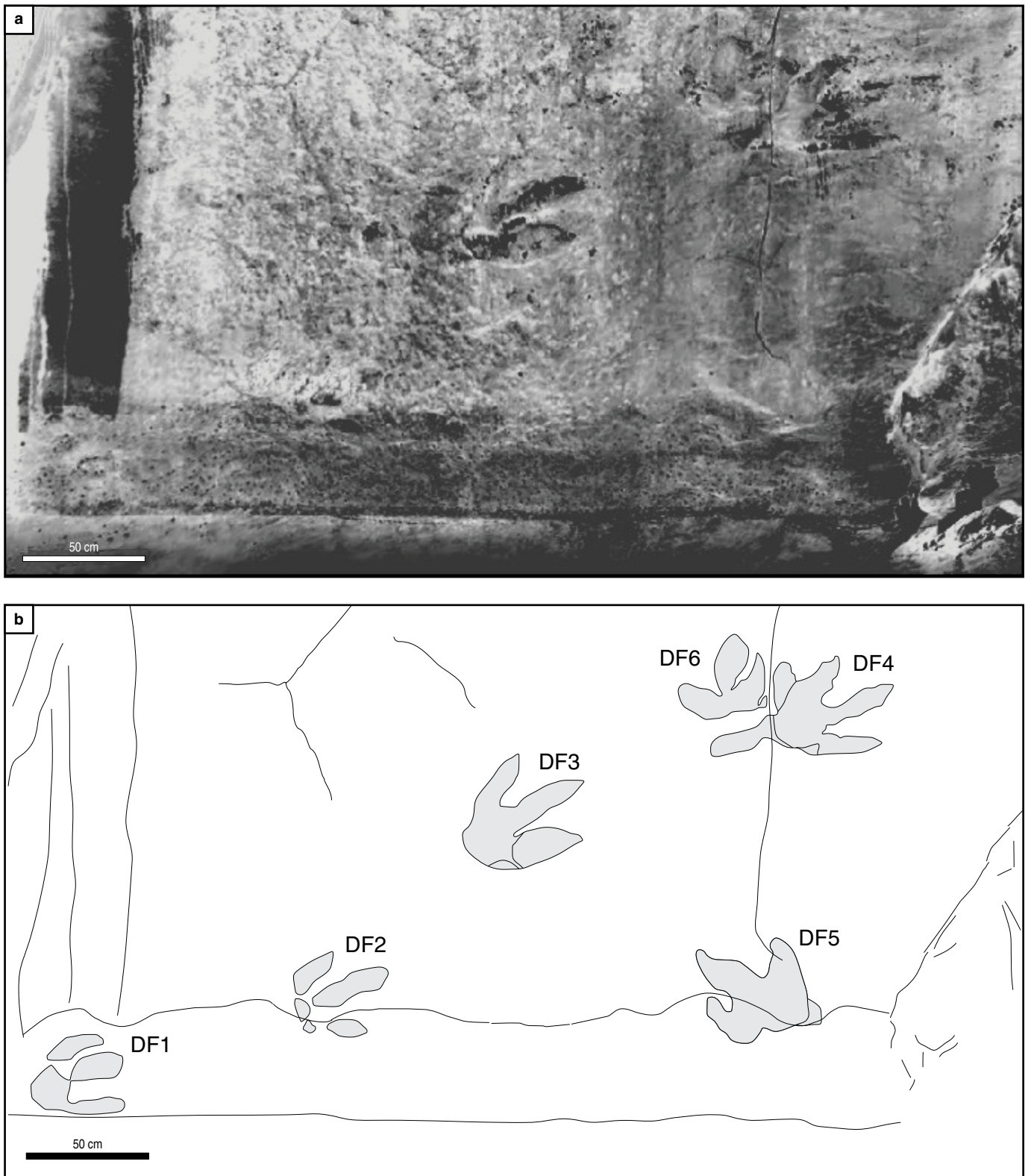


Figure 2. The Río Batá dinosaur footprints. **(a)** Photograph of the outcrop showing the dinosaur footprints preserved in convex hyporelief on the underside of a thick, subvertical, sandstone bed within segments C–D (Ulloa & Rodríguez, 1979) of the Lower Cretaceous (upper Valanginian – lower Hauterivian) Batá Formation. The footprints are exposed along the Río Batá, Boyacá Department, on the eastern flank of the Eastern Cordillera of Colombia. **(b)** Interpretive drawing of the footprints. The dinosaur footprints are indicated with the acronym DF, DF1–4 belong to a single trackway.

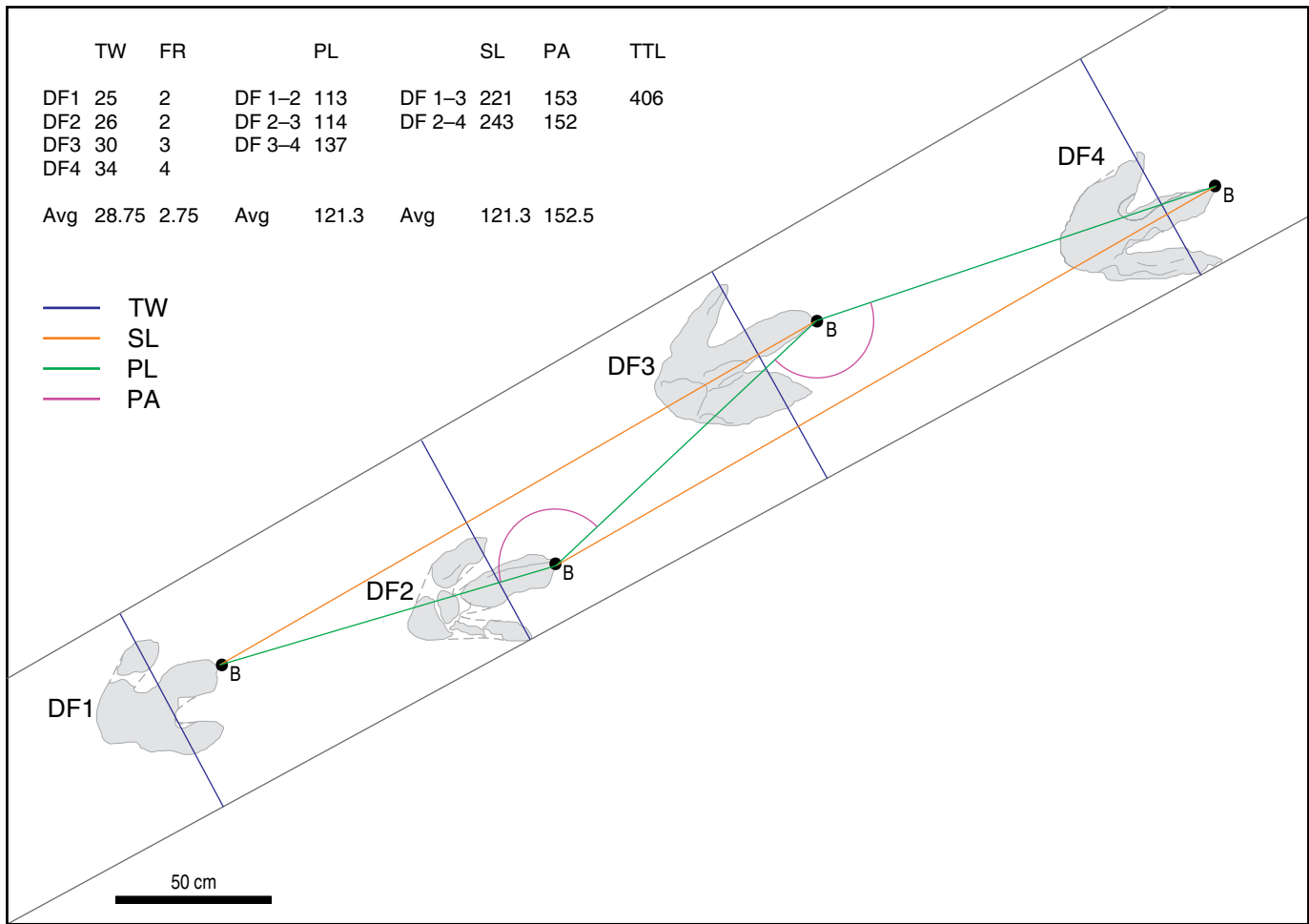


Figure 3. Metrics used to study the Río Batá dinosaur trackway, superimposed over a map of footprints DF1–4 with measurements (in cm) of the footprints. (DF1–4) Dinosaur footprints forming the trackway; (B) tip of digit III; (TW) trackway width; (FR) footprint rotation (not illustrated); (PL) pace length; (SL) stride length; (PA) pace angulation; (TTL) total trackway length; (Avg) average (arithmetic mean). Details of metrics given in the Abbreviations section of the text.

2009; Lockley et al., 2014; Martínez et al., 2015; Moratalla et al., 1988; Romilio & Salisbury, 2011; Thulborn, 1990).

The Río Batá dinosaur footprints remain in situ and are an important part of Colombian National Heritage, protected by the Colombian Constitution (1991) and Decree 1353 (2018). The competent national and regional authorities (the Servicio Geológico Colombiano (SGC), and the Alcaldía, or local mayor of Santa María) have been informed of the exact location to aid their long-term preservation.

3. Systematic Ichnology

3.1. Ichnofamily

Iguanodontipodidae Vialov, 1988 sensu Lockley et al., 2014, and as emended by Martínez et al., 2015.

Diagnosis: Tridactyl, mesaxonic, and subsymmetrical pedal imprints of a digitigrade dinosaur; tracks typically as wide or wider than long; when preserved, one digital pad impression per

digit, longer than wide, and one metatarsophalangeal pad forming the “heel”; well-developed notches on the latero-proximal margins of digits II and IV; manus tracks when present are much smaller than pedal tracks (modified from Martínez et al., 2015; see also Lockley et al., 2014; Martínez et al., 2015).

3.2. Ichnogenus

Iguanodontipus Sarjeant et al., 1998, as emended by Martínez et al., 2015: 23.

Diagnosis: Iguanodontipodidae tracks with a metatarsophalangeal (“heel”) pad impression that is small (only as wide as the proximal impression of digit III), rounded, centred, and narrow; digits long and narrow; digits with sharp distal ends (modified from Martínez et al., 2015).

3.3. Type Ichnospecies

Iguanodontipus burreyi Sarjeant et al., 1998.

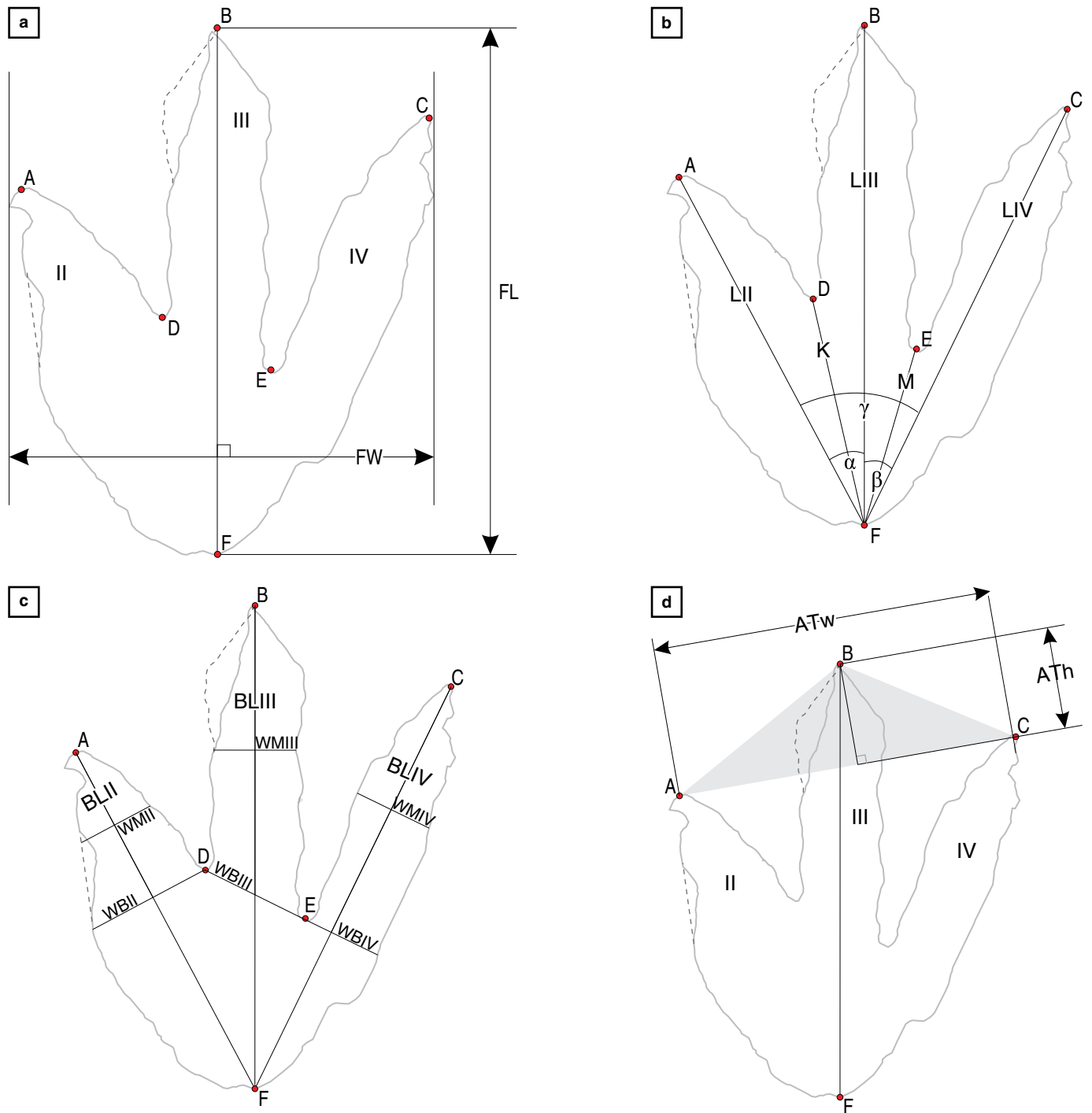


Figure 4. Parameters used to study the Río Batá dinosaur footprints, superimposed over an illustration of footprint DF4. **(a)** Footprint length, width, and key landmarks. **(b)** Digit lengths and angular measurements. **(c)** Digit free segment lengths. **(d)** Anterior triangle. (A, B, C, D, E, F) key footprint landmarks; (ATh, ATw) height and width of the anterior triangle; (BLII, BLIII, BLIV) length of free segment of toe; (FL) footprint length; (FW) footprint width; (LII, LIII, LIV) digit lengths; (K, M) length to hypex; (WBII, WBIII, WBIV) width at base of free segment of toe; (WMII, WMIII, WMIV) width at middle of free segment of toe; (II, III, IV) digit numbers; (α , β , γ) divarication angles. Details of metrics given in the Abbreviations section of the text, and numerical values in Tables 2, 4.

Diagnosis: *Iguanodontipus* is a monotypic ichnospecies containing only *Iguanodontipus burreyi*, which has the same diagnosis as the ichnogenus (Martinez et al., 2015).

3.3.1. Referred Material

Six ornithopod dinosaur footprints, DF1–DF6 (Figure 2).

3.3.2. Emended Distribution

Iguanodontipus: Cretaceous, Berriasian to Hauterivian of western Europe and northern South America. Prior to this work, *Iguanodontipus burreyi* was only known from the Lower Durlston Beds (Berriasian) of England, UK; the Bückeberg Formation (Berriasian) of Germany; and the Oncala Group (Berriasian – Valanginian) of Spain (Castanera et al., 2013; Díaz–Martínez et al., 2015; Lockley et al., 2004; Pascual–Arribas et al., 2009; Sarjeant et al., 1998). The new find extends the geographic range to the Batá Formation (Valanginian – Hauterivian) of Colombia, northern South America.

3.3.3. Locality and Horizon

The referred dinosaur footprints are exposed on the original underside of a now sub–vertically oriented massive sandstone bed within the upper part (segments C–D) of the Lower Cretaceous Batá Formation along Río Batá, Boyacá Department, on the eastern flank of the Eastern Cordillera of Colombia (Figure 1). Segments C and D of the Batá Formation consist of a series of fining–upward successions, commonly including ripple marked sandstone levels, some of which preserve bivalve fossils and palynomorphs (Etayo–Serna et al., 2003; Terraza et al., 2008). The bedding plane preserving the footprints strikes NE–SW is now sub–vertical and elevated to a present–day altitude of 840 m above sea level due to the uplift of the northern Andes. Exact geographic coordinates of the locality are withheld to aid site preservation, but are available from the Servicio Geológico Colombiano upon request.

3.3.4. Geological Age

Late Valanginian to early Hauterivian, ca. 132.9 Ma (Cohen et al., 2013; updated 2019/05). Based on the presence of the bivalve *Syrotrigonia*, palynomorphs, and other unspecified fossils, segments C and D of the Batá Formation were assigned a late Valanginian to early Hauterivian age (Etayo–Serna et al., 2003; although Berriasian is also mentioned without context, page 115). Recently, the Batá Formation has been considered Berriasian in age, based on stratigraphic and unspecified biostratigraphic comparison with the Cumbre Formation of the Middle Magdalena River valley (Moreno et al., 2009; Terraza et al., 2008, 2013). However, it is likely that the Batá and Cumbre Formations are of different ages due to diachronic Early Cretaceous transgression and deposition over underlying Palaeozoic basement of the Farallones Group (Terraza et al., 2013). Hence, here we accept the late Valanginian to early Hauterivian age for the Batá Formation based on the published palaeontological evidence (Etayo–Serna et al., 2003, page 115, arguments 1, 3), rather than the less well supported (and largely unpublished) comparisons with the more spatially

distant Cumbre Formation (Etayo–Serna et al., 2003, page 115, argument 2).

4. Description

The Río Batá dinosaur footprints are tridactyl and digitigrade pedal tracks with no evidence for manus prints, tail drag marks, or interdigital webbing (Figure 2). The orientations of the two isolated footprints DF5 and DF6 make it highly unlikely these form part of a second trackway. The relative timings of production of the trackway and the isolated footprints are unclear, despite footprints DF4 and DF6 partially coinciding.

4.1. Preservation

The Río Batá footprints are preserved in convex hyporelief (Lockwood et al., 2014); i.e., as natural infills of the original footprints (the trace fossils), or as natural casts of the foot of the original dinosaur track maker. The topographically lower footprints (DF1, 2) are less well preserved than those higher up the cliff face (DF3, 4), as they have been partially eroded by running water from Río Batá. As preservation of the footprints on the lower surface of a massive sandstone bed, it is improbable that they are underprints; the Río Batá footprints thereby most likely represent natural casts of “true tracks” (Lockley, 1991; Platt et al., 2018). However, preservation of the Río Batá footprints is sub–optimal, as no distinct metatarsophalangeal “heel” pad, hallux prints, or skin impressions are preserved. DF4 exhibits what may be a “heel” drag mark (Thulborn, 1990), or much less likely a metatarsal impression (Farlow et al., 1995). However, the close proximity of DF4 to DF6, and their similar size, suggests that the “drag mark” may be the “heel” impression of DF6, or possibly the remnants of another poorly preserved footprint coinciding with both DF4 and DF6 (Figure 2). The aligned footprints (DF1–4) were produced by a single individual dinosaur, but show morphological variation along the trackway. This variation may be the result of differences in original footprint morphology (natural differences between the left and right feet), influenced by extra–morphological effects such as dinosaur behaviour (including locomotion pattern and speed), substrate characteristics (including type, consistency, humidity, and local irregularities), taphonomy, or recent subaerial weathering and erosion (Lockley, 2009; Lockley et al., 2014; Moratalla et al., 1988; Pazos et al., 2012; Romilio & Salisbury, 2011), all of which may be applicable to the Río Batá footprints.

4.2. Trackway (DF1–4)

The four aligned footprints form an approximately four metres long trackway. This trackway exhibits average (arithmetic mean) values of: stride length, 2.32 m; pace length, 1.21 m; pace angulation, 152.5°; external track width, 0.38 m; and slight positive

(outward) footprint rotation (sensu Lockley, 1991; we note that Thulborn, 1990 uses the terminology in the opposite sense) of 2–4° (Figure 3). After correction for subsequent tilt of the sub-vertically orientated bedding plane on which the footprints are preserved, the direction of travel (estimated to 5° increments) for the trackway is 255°; and the orientations of footprints DF5 and DF6 are 5° and 325° from north respectively.

4.3. Footprints

Footprints DF3 and DF4 are the best preserved, and therefore are used as the basis for this description (Figure 4). The footprints are large, measuring an average of 51.5 cm from the anterior tip of digit III to rear of the metatarsophalangeal “heel”, and are tridactyl, with no digit I (laterally directed hallux) or digit V impressions preserved. The digits are generally straight, although the distal end digit III of DF3 is curved slightly medially; other toes may also exhibit a slight curvature. Digit III is the longest and forms the anteroposterior axis of the footprints. Digits II and IV are arranged approximately symmetrically either side of, and shorter than, digit III, but sub-equal in length to each other; the mesaxonic condition. Digit II is the widest, stout, robust, and tapering; digit IV is narrower and tapered, and as preserved, is slightly longer than digit II in DF4 but shorter in DF3; digit III is intermediate in form, with approximately sub-parallel lateral and medial margins. None of the digits are constricted. Footprints DF3–4 are longer than wide, with an average length:width ratio of 1.22, an average total digital (II–IV) divarication of 58.5° and individual interdigital angles of 26–33°. The average height:width ratios of the anterior triangles (Lockley, 2009) of DF1–2 are 0.41 (Table 4).

The distal ends of the digits are bluntly tapered, with sub-acute (pointed) tips, and no distinct ungual (hoof or claw) impressions. The hypices (the posterior-most points of separation between the toes) in DF3 are rounded, but the angle is slightly more acute between digits II and III. In DF4, the hypex between digits II and III is more deeply incised but this is likely an artefact of preservation, whereas between digits III–IV it is similar to DF3. In both DF3 and DF4, the lateral margin of the posterior of digit IV (somewhat posterior of the level of the hypices) preserves what may be a slight lateral notch (Martinez *et al.*, 2015). However, this is of a different form, and in a slightly different position in the two footprints, so may be an artefact of preservation. The posterior margin of the metatarsophalangeal “heel” pad impression is rounded in DF4, but sub-quadrangular in DF3, although both metatarsophalangeal pads lack marked medial or lateral indentations.

5. Interpretation and Discussion

Individual footprints represent the original foot morphology of the dinosaur trackmaker (Moratalla *et al.*, 1988), although

the footprint is modified by the effects of behaviour, substrate consistency, preservation, diagenesis, and recent and ancient weathering, requiring considerable caution in interpretation. However, extra-morphological variation in ichnology can be minimized by utilizing data from a series of aligned footprints (a trackway), where available (e.g., Lockley, 1991; Thulborn, 1990). The Río Batá footprints only preserve a short trackway segment (DF1–4) and two additional prints (DF5, 6), so here we focus on metrics from the two best-preserved trackway footprints (DF3–4), supplemented by data DF1–2. We cautiously compare the trackway to the isolated footprints (DF5, 6), although these were most likely produced by one or more different individuals or taxa.

A large ornithopod or theropod dinosaur produced the Río Batá dinosaur footprints. Size definitions are inherently arbitrary, general categories (Lallensack *et al.*, 2016), however, the term “large” for tridactyl dinosaur footprints is only loosely defined. In ichnological studies, organism size is determined by footprint length (FL), and “large” has been considered both >30 cm and >25 cm (Thulborn, 1990 pages 52, 265, 268), although FL >25 cm has also been consistently used (Dalla-Vecchia, 1998, 2008). Medium size for tridactyl dinosaur footprints has been regarded as FL = 20–30 cm (Castanera *et al.*, 2013), implying a large animal has a FL >30 cm. However, other authors (e.g., Martinez *et al.*, 2015) appear to consider large as >25 cm (following Thulborn, 1990), although no clear definition is provided. Here we define “large” tridactyl dinosaur footprints as exhibiting FL >300 mm.

5.1. Ornithopod vs. Theropod Footprints

Distinguishing between large, tridactyl footprints produced by bipedal ornithopod and theropod dinosaurs has frequently proven problematic (e.g., Lallensack *et al.*, 2016; Lockwood *et al.*, 2014; Moratalla *et al.*, 1988; Platt *et al.*, 2018; Romilio & Salisbury, 2011). This difficulty is due to the similar, although osteologically distinct, original foot morphology, which in both groups is digitigrade, functionally 3-toed with the central digit (III) most prominent, and digits II and IV shorter than digit III (Lockley *et al.*, 2009). Hence, the trace fossils produced by both ornithopods and theropods are similar: Relatively wide, tridactyl, and mesaxonic. The difficulty in distinguishing ornithopod from theropod ichnites applies especially to isolated footprints, short trackway segments, or when preservation is sub-optimal (e.g., Moratalla *et al.*, 1988; Thulborn, 1990), all of which apply to the Río Batá footprints.

A number of studies have attempted to resolve the problems of distinguishing between large ornithopod and theropod footprints, however there is no single, unique criterion that clearly separates the trace fossils of these two groups of dinosaurs (Lallensack *et al.*, 2016; Moratalla *et al.*, 1988). Here we use two approaches in an attempt to determine the most likely

Table 2. Measurements for the Río Batá dinosaur footprints, in cm.

Track	Digit length			Free segment length			Basal toe width			Mid-toe width			Hypicities		Divicariance				
	FL	FW	LII	LIII	LIV	BLII	BLIII	BLIV	WBII	WBIII	WBIV	WMII	WMIII	WMIV	K	M	α	β	γ ($\alpha+\beta$)
DF1	44	41	40	44	34	16	25	17	10	17	8	10	12	10	24	18	33	31	64
DF2	52	38	39	52	39	21	35	23	10	8	7	9	10	6	18	17	27	26	53
DF3	56	45	48	56	41	22	31	20	17	13	10	12	11	7	27	23	29	30	59
DF4	54	44	43	54	50	18	33	31	14	13	9	9	9	9	25	20	28	26	54
DF5	48	45	35	48	36	18	28	11	15	15	14	8	12	11	19	25	41	30	71
DF6	37	40	29	37	28	18	22	10	12	11	11	11	13	8	13	19	52	34	86

Note: (DF with number) Río Batá footprint number; (FL) footprint length; (FW) footprint width; (LII, LIII, LIV) digit lengths; (BLII, BLIII, BLIV) length of free segment of toe; (WBII, WBIII, WBIV) width at base of free segment of toe; (WMII, WMIII, WMIV) width at middle of free segment of toe; (K, M) length to hypex; (α , β , γ) divarication angles.

See Figure 4 for locations of metrics; details of metrics given in the Abbreviations section of the text.

track maker for the Río Batá footprints. Firstly, a compilation of ichnological characteristics, based on an updated version of parameters used to distinguish ornithopod from theropod footprints (Dalla-Vecchia & Tarlao, 2000), and modified in the light of subsequent research. Secondly, we compare the Río Batá footprints to ornithopod–theropod threshold values for a series of bivariate ratios (Moratalla et al., 1988).

A compilation of ichnological characteristics (Dalla-Vecchia & Tarlao, 2000), indicates the Río Batá footprints forming the trackway (DF1–4), share more than half (12/21) of the features characterizing large ornithopod dinosaur footprints. However, two features are indicative of large theropods, and slightly more than one-third (7/21) cannot be applied to the Río Batá footprints (Table 3). Of the features indicative of ornithopod footprints digits relatively straight with little curvature, the rounded to quadrangular metatarsophalangeal “heel”, sub-symmetrical footprint, and trackway pace angulation (PA) $<160^\circ$, fall within the typical ornithopod range (Table 3, coloured green). However, other features show overlap between the ornithopod and theropod values, and require discussion. For the best preserved footprints (DF3–4), the height:width ratio of the anterior triangle (Table 4) is within the range reported for large ornithopods (Lockley, 2009). However, when all four footprints in the trackway (DF1–4) are averaged, the value slightly exceeds the ornithopod maximum. Nevertheless, the lowest value for DF3–4 also lies outside the reported theropod range, although the average value is higher, it lies at the extreme lower range for large theropods. Hence, the best preserved, and therefore probably most reliable, data indicates ornithopod affinity, whereas the probably less reliable aggregated data lies at the lower end of the large theropods range. As a result of the above, we consider the anterior triangle data more indicative of ornithopod than theropod dinosaurs. The pedal footprint length:width ratio (FL:FW) is greater than one, indicating a footprint that is longer than wide, a feature considered typical

of theropod dinosaurs (Thulborn, 1990). However, DF3–4 fall within the ornithopod range, although considering all footprints in the trackway, the average does not fall within the ornithopod range. Stride length to foot length (SL:FL) lies within the range most common for ornithopods, but outside that considered most frequently associated with theropods, although the ranges for both groups exhibit considerable overlap (Thulborn, 1990).

Another relevant feature is a notch between digit II and the metatarsophalangeal “heel”, considered a theropod feature. However, the “notch” in Río Batá footprints occurs between digit IV and the “heel”. This is probably a poorly preserved remnant of the double notch observed in ornithopod dinosaur footprints (Martinez et al., 2015). The digits in the Río Batá footprints are relatively long and somewhat pointed; this is often considered a typical theropod feature. However, this is also characteristic of Group 1 ornithopods (Martinez et al., 2015). Hence, many parameters (digit curvature; “heel” shape; trackway pace angulation; anterior triangle height:width ratio; footprint length:width ratio), exhibit overlap between footprints considered to belong to ornithopods and theropods, although for the Río Batá footprints many of these features are closer to the ornithopod state.

Two features of the Río Batá trackway falls within the normal theropod range (Table 3, coloured red). A total divarication between digits II and IV of $<60^\circ$ is considered typically theropodan, although one of the less well-preserved footprints (DF1) shows a typical ornithopod total divarication 64° (Table 2). However, divarication of the digits varies with numerous factors including original foot morphology, substrate consistency, and patterns of behaviour (Platt et al., 2018). In addition, variation is seen when a large number of footprints form a track single attributable to the same individual (Lallensack et al., 2016). Footprint rotation is normally negative (inward facing) in ornithopod dinosaurs, but is weakly positive (outwardly directed) in theropods; the Río Batá footprints exhibit thero-

Table 3. Characteristics of the Río Batá dinosaur footprints compared to a range of criteria used to differentiate large ornithopod from large theropod dinosaur ichnofossils.

Footprint characteristic	Large ornithopod footprints	Río Batá footprints	Large theropod footprints
Anterior triangle, h:w ratio.	Low (0.28–0.47)	Low (0.30–0.36/0.49)	High (0.31–1.43)
Bipedality	Manus prints sometimes present	Manus prints absent	Manus prints almost always absent
Claw impressions	Blunt, “hooves”.	Absent	Sharp, laterally compressed.
Digit impressions (especially DIII)	Wider, parallel-sided, often u-shaped, with a relatively short free segment.	DII wide, tapering; DIII–IV relatively narrow, parallel-sided, u-shaped.	Slender, tapered, often v-shaped, with relatively long free segment.
Digit relative lengths	DIII slightly longer, DII and DIV subequal in length.	DIII slightly longer, DII and DIV subequal in length.	DIII substantially longer, DII shorter and wider than DIV.
Digit I (hallux) impression, medially directed at base of DII.	Lacking in most	Absent	Occasionally present
Digit III form	Symmetrical, straight, with little or no curvature.	Symmetrical, straight, with little or no curvature.	May be curved, sinuous or with a marked medial displacement.
Digital curvature medially, distal.	Little or none	Little, slight in DIII of DF3.	Frequent in DIII, less in DIV, sometimes in DII.
Digital offsets	Digit IV frequently offset and widely divergent	None	Digit II offset from DIII–IV
Divarication, DII–DIII: DIII–DIV.	Angles between DII–DIII and DIII–DIV similar	DII–DIII, 28–29° (27–33°); DIII–DIV, 26–30° (31°).	DII–DIII (35–39°) > DIII–DIV (20–37°)
Divarication, total (DII–DIV)	Wider (?>60°)	54°–59° (64°)	Narrower, usually <60°
Footprint rotation (orientation of DIII)	Normally inward (–ve)	Slightly +ve, ≤4°	Normally weakly +ve
Footprint symmetry	Symmetrical	Symmetrical	Asymmetrical
Heel shape	Relatively large, symmetrical, u-shaped.	Rounded to quadrangular, u-shaped.	Relatively small, elongate, asymmetrical, v-shaped.
Indent medially between DII and heel	Absent	Absent	Present
Pes print FL:FW ratio	FW=FL or FW>FL, range 0.92–1.36	FW>FL 1.23–1.24 (1.07–1.37)	FL>FW, range 1.03–2.64
Phalangeal pad impressions	Almost always lacking when FL>30 cm	Absent	Often well-defined
PL:SL	Shorter	1.91	Longer
PA	Lower, ?<160°	152–153°	High, 160–180°
SL:FL (much overlap)	Low	4.14–4.30 (5.27)	High
TW	Consistently wider	68 cm	Consistently narrower

Source: Data from Dalla-Vecchia & Tarlao (2000) and modified with additions from Hasiotis et al. (2007), Lallensack et al. (2016), Lockley (2009), Milner et al. (2006), Moreno et al. (2012), and Thulborn (1990).

Note: The Río Batá footprints exhibit 12/21 characteristics that indicate an ornithopod affinity (highlighted in green), whereas only 2/21 coincides with the characteristics that indicate a theropod footprint (highlighted in red); seven characteristics are not comparable (not highlighted). See text for further details. (h) Height; (w) width; (D with roman numeral) digit number; (FL) footprint length; (FW) footprint width; (PL) pace length; (SL) stride length; (+ve) positive; (–ve) negative; (PA) pace angulation; (TW) trackway width.

See Figures 3, 4 for locations of metrics; details of metrics given in the Abbreviations section of the text.

pod-like positive rotation, although this also varies depending on speed of locomotion (Day et al., 2002).

Seven of the 21 characteristics are non-applicable (Table 3, uncoloured). Of these features, three cannot be compared with certainty due to lack of excellent preservation (presence/absence of manus prints; claw impressions; presence/absence of a hallux mark), one is a feature which does not match the

diagnostic features of either group (digital offsets), and two lack sufficient comparable metrics in the literature (PL:SL and TW). Hence, on balance (12 features to two in favour, with seven not comparable) we consider the values exhibited by the Río Batá trackway footprints, most likely, to be ornithopod in nature.

Our second approach is to compare the Río Batá footprints to ornithopod–theropod threshold values for a series of bivar-

Table 4. Measurements of the anterior triangle (Lockley, 2009) for the Río Batá dinosaur footprints, in cm.

Track	ATh	ATw	ATh/ATw
DF1	13	40	0.33
DF2	17	35	0.49
DF3	16	45	0.36
DF4	13	43	0.30
DF5	19	41	0.46
DF6	16	39	0.41

Note: Green, large ornithopod range (0.28–0.47); orange, ambiguous (overlaps both large ornithopod and large theropod ranges); red, large theropod range (0.31–1.43); threshold values from Lockley (2009).

(ATh) anterior triangle height; (ATw) anterior triangle width.

See Figure 4d for locations of metrics; details of metrics given in the Abbreviations section of the text.

iate ratios (Figure 5; Table 5; Moratalla et al., 1988). These ratios have been applied graphically by a variety of authors (Figueiredo et al., 2017; Mateus & Milán, 2008; Platt et al., 2018; Romilio & Salisbury, 2011), and have the advantage of utilizing ratios, which minimize the effects of organism size on the analysis (Lallensack et al., 2016). Comparison between the threshold values proposed (Moratalla et al., 1988) and those for the Río Batá trackway, show that the two best-preserved footprints (DF3–4) fall within the ornithopod thresholds for just 3/9 values, whereas 6/9 are considered typically theropodan (Table 5). Including data from all four trackway footprints (DF1–4), shows no unequivocally ornithopod features, 6/9 exhibit overlap between ornithopod and theropod values, and 3/9 indicate a theropod trackmaker. However, the two isolated footprints, DF5 (values for DF6 in brackets) are more clearly ornithischian with 6/9 (8/9) indicating an ornithischian trackmaker, and only 3/9 (1/9) indicating a theropod trackmaker. The second technique would therefore suggest that the trackway was produced by a theropod dinosaur, and the two isolated footprints are ornithischian in nature.

Based on the first of the two techniques employed, we attribute the Río Batá footprints to a large ornithopod dinosaur, whereas the results of the second technique indicate the trackway was produced by a large theropod. We interpret this to indicate that a wide range of descriptive and metrical characteristics are more reliable than comparison to a small sample of time restricted and tentatively proposed threshold values (Moratalla et al., 1988). This is despite the Río Batá footprints concurring in geological age (Early Cretaceous) and organism size (“large” dinosaur) comparable with the original sample (Moratalla et al., 1988); although the Colombian footprints lie outside the original geographical range studied. Hence, our analysis appears to question the applicability of threshold values as a technique to

determine dinosaur affinities in ichnological studies (e.g., as used by Figueiredo et al., 2017; Lallensack et al., 2016; Mateus & Milán, 2008; Platt et al., 2018; Romilio & Salisbury, 2011), as previously argued (Thulborn, 2013). In addition, despite compensating for body size using ratios, biological scaling affects (e.g., allometry, ontogeny; Castanera et al., 2013; Lockley, 2009) may have an important effect on this type of analysis.

5.2. Attribution to Ichnotaxon and Taxon

The somewhat confusing ichnotaxonomy of large ornithopod tracks has recently been revised (Martinez et al., 2015; see also Lockley et al., 2014). Based on the small, rounded metatarsophalangeal “heel” pad (rather than a large rounded or bilobed “heel”), and relatively elongate, narrow digits (as opposed to short, wide digits), the Río Batá footprints can be attributed to the Group 1 ornithopod morphology (Martinez et al., 2015). Group 1 contains only the ichnogenus *Iguanodontipus* and ichnospecies *I. burreyi*. The only other valid ichnospecies, formerly within *Iguanodontipus*, was “*I.*” *billsarjeanti*, now attributed to the ichnogenus *Caririchnium* (Martinez et al., 2015). Thus, the Colombian footprints, as tridactyl, mesaxonic, and subsymmetrical pedal imprints of a digitigrade ornithischian dinosaur, can be attributed to the ichnofamily Iguanodontipodidae, based on the morphological characteristics available (Martinez et al., 2015). However, the tracks are somewhat longer than wide, and do not preserve pad or manus impressions, and only faintly show (on the lateral margins of DF3–4) evidence for the well-developed notches on the latero-proximal margins of digits II and IV, characteristic of the ichnofamily (Martinez et al., 2015). Nevertheless, this lack of data are most likely a result of preservational biases. However, with regard to the ichnogenus *Iguanodontipus*, the “heel” impression of the Río Batá footprints is relatively narrow, rounded, and centred, and the digits are long and narrow with somewhat pointed distal ends, matching the diagnosis of the ichnogenus (Martinez et al., 2015).

Iguanodontipus ichnofossils are universally attributed iguanodontid (or iguanodontian) ornithischian dinosaur track makers (e.g., Lockley et al., 2014; Lockwood et al., 2014; Martinez et al., 2015; Santos et al., 2013; Sarjeant et al., 1998). Body fossils of iguanodontian ornithopods are widely distributed across Laurasia and Gondwana, and have been recovered from the Upper Jurassic to uppermost Cretaceous rocks (Llandres-Serrano et al., 2013; Norman, 2004, 2013). However, prior to this work, the geographic and temporal distribution of *Iguanodontipus* was strictly limited, with the ichnogenus only reported from the Berriasian – Valanginian of Europe (Díaz-Martínez et al., 2015). Hence, the Río Batá *Iguanodontipus* ichnofossils were likely produced by a large iguanodontian ornithischian dinosaur, and thereby have important palaeogeographical implications for dinosaur biogeography.

Thresholds

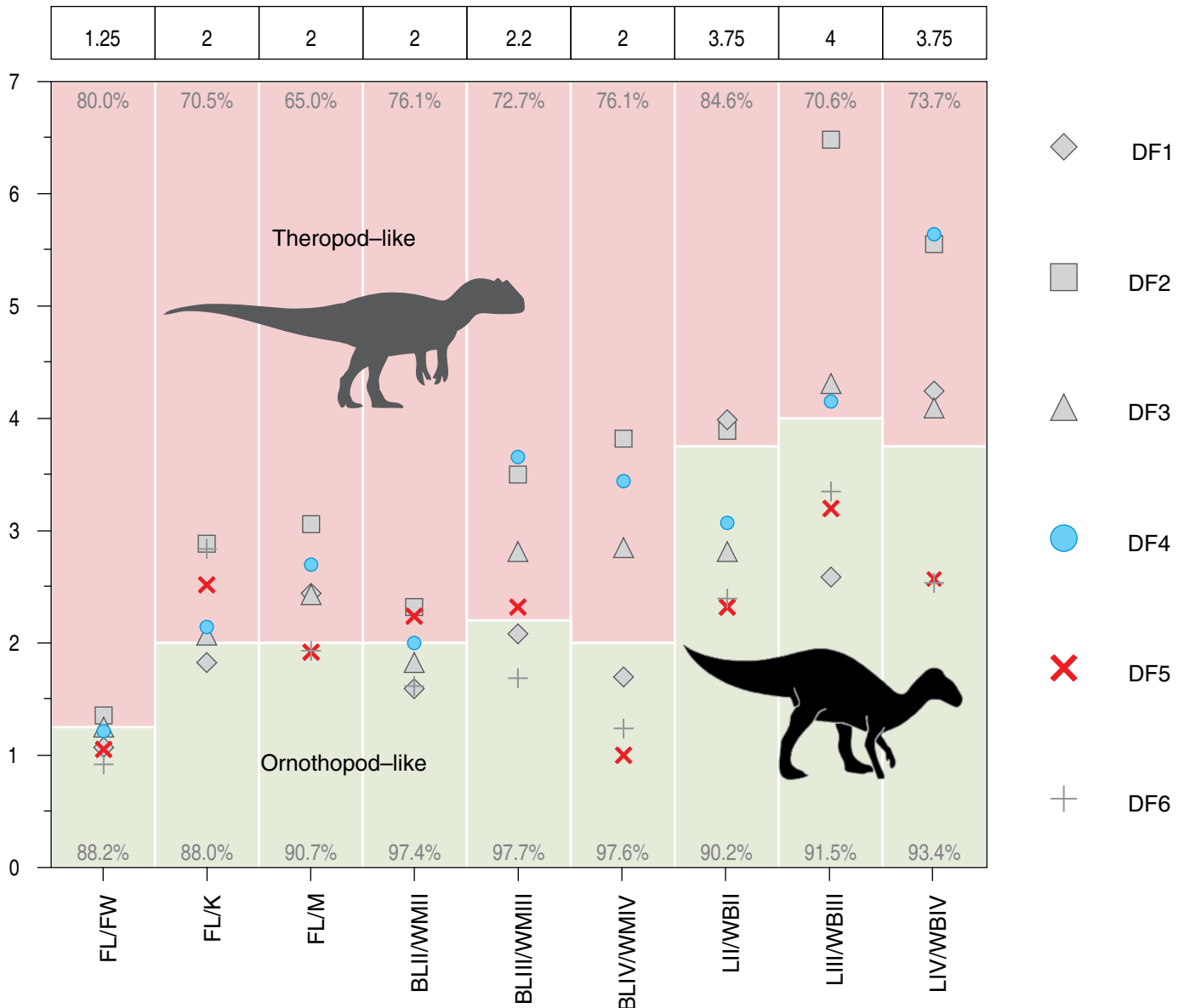


Figure 5. Ratios from the Río Batá footprints (DF1–6) shown as a graphical representation (modified from Romilio & Salisbury, 2011) for comparison to the proposed threshold values (top) used to distinguish between ornithopod and theropod dinosaur footprints (Moratalla et al., 1988). Green, large ornithopod range; red, large theropod range. (BLII, BLIII, BLIV) Length of free segment of toe; (DF1–6) dinosaur footprints; (FL) footprint length; (FW) footprint width; (LII, LIII, LIV) digit lengths; (K, M) length to hypex; (WBII, WBIII, WBIV) width at base of free segment of toe; (WMII, WMIII, WMIV) width at middle of free segment of toe. See Figure 4 for locations of metrics; details of metrics given in the Abbreviations section of the text. See Table 5 for numerical values for the ratios presented.

5.3. Size and Speed Estimates

Ichnofossils can be used to determine the approximate body size and speed of movement of the Río Batá trackmaker by using foot length to obtain hip height, and incorporating stride length (Hutchinson, 2005; Lockley, 1991; Thulborn, 1990). Hip height (HH) can be estimated by assuming the hip was an average of four times the length of the footprint (FL) (McNeil Alexander, 1976; Henderson, 2003). However, although a

range of metrics have been proposed for different dinosaurian groups (Thulborn, 1990), $HH = FL \times 4$ is the most widely used metric (Platt et al., 2018), and is considered the most accurate for large dinosaurs (Henderson, 2003). The Río Batá trackway has an average FL (DF1–4) = 51.5 cm, which produces an estimated $HH = 2.06$ m (Table 6). Comparison with well-known skeletons of the Barremian iguanodontian ornithopod *Iguanodon bernissartensis* provides a body length estimate of approximately 8.0 m and an estimated body mass of 2.500

Table 5. Ratios from the Río Batá footprints for comparison to the proposed threshold values (beneath each metric) for ornithopod and theropod dinosaur footprints (Moratalla et al., 1988), for individual footprints (DF1–6), the range for the best preserved footprints in the trackway (DF3–4), and the range for all footprints in the trackway (DF1–4).

Track	FL:FW 1.25	FL:K 2.0	FL:M 2.0	BLII:WMII 2.0	BLIII:WMIII 2.2	BLIV:WMIV 2.0	LII:WBII 3.75	LIII:WBIII 4.0	LIV:WBIV 3.75
DF1	1.07	1.83	2.44	1.60	2.08	1.70	4.00	2.59	4.25
DF2	1.37	2.89	3.06	2.33	3.50	3.83	3.90	6.50	5.57
DF3	1.24	2.07	2.43	1.83	2.82	2.86	2.82	4.31	4.10
DF4	1.23	2.16	2.70	2.00	3.67	3.44	3.07	4.15	5.56
DF5	1.07	2.53	1.92	2.25	2.33	1.00	2.33	3.20	2.57
DF6	0.93	2.85	1.95	1.64	1.69	1.25	2.42	3.36	2.55
DF3–4	1.23–1.24	2.07–2.16	2.43–2.70	1.83–2.00	2.82–3.67	2.86–3.44	2.82–3.07	4.15–4.31	4.10–5.56
DF1–4	1.07–1.37	1.83–2.89	2.43–3.06	1.60–2.33	2.08–3.67	1.70–3.83	2.82–4.00	2.59–6.50	4.10–5.57

Note: Green, large ornithopod range; orange, ambiguous (overlaps both large ornithopod and large theropod ranges); red, large theropod range; threshold values, shown in bold beneath the headings, from Moratalla et al. (1988).

(DF with number) Río Batá dinosaur footprint number; (FL) footprint length; (FW) footprint width; (K, M) length to hypex; (BLII, BLIII, BLIV) length of free segment of toe; (WMII, WMIII, WMIV) width at middle of free segment of toe; (LII, LIII, LIV) digit lengths; (WBII, WBIII, WBIV) width at base of free segment of toe.

See Figures 3, 4 for locations of metrics; details of metrics given in the Abbreviations section of the text. See Figure 5 for a graphical representation of the data for the individual footprints.

Table 6. Trackway metrics the Río Batá footprints, showing the values used, and the results obtained, for the velocity calculations, using $V \approx 0.25g^{0.5} \cdot SL^{1.67} \cdot HH^{-1.17}$ (McNeil Alexander, 1976).

Track	FL (m)	SL (m)	HH (m)	SL/HH	V m/s	V km/h
DF1	0.44		1.76			
DF2	0.52		2.08			
DF3	0.56		2.24			
DF4	0.54		2.16			
DF1–3		2.21	2.03	1.09	1.29	4.64
DF2–4		2.43	2.16	1.13	1.40	5.04
Avg	0.52	2.32	2.06	1.13	1.37	4.93

Note: (DF with number) Río Batá dinosaur footprint number; (FL) footprint length, in metres; (SL) stride length, in metres; (m) metres; (HH) hip height ($4 \times FL$), in metres; (V) velocity of the trackmaker in both m/s and km/h; (m/s) metres per second; (km/h) kilometres per hour; (Avg) arithmetic mean (average); g, acceleration due to gravity (9.81 m/s).

kg for the Río Batá ornithopod (Henderson, 2003; Norman, 1980; Seebacher, 2001). This would indicate that the Colombian iguanodontian was of moderate to large size, possibly a small adult or a sub-adult approaching adult size, depending upon the species of original trackmaker.

The speed of travel for the Colombian dinosaur can be estimated from the Río Batá trackway (DF1–4), using average (arithmetic mean) trackway metrics, SL (2.32 m) and calculated HH (2.06 m) (Table 6). As average SL/HH (1.13) is ≤ 2.0

(walking pace; Thulborn, 1990), it is appropriate to use $V \approx 0.25g^{0.5} \cdot SL^{1.67} \cdot HH^{-1.17}$ (McNeil Alexander, 1976), where V = velocity in m/s, g = acceleration due to gravity (9.81 m/s), SL = stride length in metres, and HH = hip height in metres. However, this equation is thought to underestimate dinosaur locomotion rates at moderate speeds (Thulborn, 1990). Using the velocity equation above, the estimated speed of the Río Batá trackmaker is 1.37 m/s (or 4.93 km/h) (Table 6). This is within the range of estimated average walking speeds for iguanodontian dinosaurs of 4.61–5.27 km/h (Thulborn, 1990). The apparent lack of manus prints along the Río Batá trackway indicates the animal was travelling either bipedally, or with little weight upon the manus. Adult iguanodontians were probably facultatively bipedal, but may have walked quadrupedally, using their hands in locomotion only at very slow speeds, or when running at greater velocities (Norman, 1980, 2004).

5.4. Dinosaur Biogeography

During the Jurassic, dinosaurs were widely distributed (Barrett et al., 2011; Canudo, 2006; Carballido et al., 2012; Cox, 1974; Rage, 1988; Sereno et al., 1994), with biotic interchange of terrestrial organisms possible due to the geographic competency of Pangaea. However, the latest Jurassic witnessed the opening of the Central Atlantic, which severed the previously persistent Jurassic land connection between Laurasia and Gondwana (Cox, 1974; Rage, 1988; Riccardi, 1991; Tennant et al., 2016). In addition, extinctions at the end of the Jurassic led to major ecosystem upheavals and terrestrial biotic reor-

ganization (Tennant et al., 2016). Tethys ocean thereby began to act both as a conduit for the east–west migration of marine organisms, and as an increasingly effective barrier to the north–south migrations of terrestrial fauna and flora (Canudo, 2006; Gheerbrant & Rage, 2006; Torsvik & Cocks, 2017). As a result, faunal exchanges continued across the northern (Laurasian) and southern (Gondwanan) continents, whereas free faunal exchange between the northern and southern continents was largely precluded (Cox, 1974; Canudo, 2006; Canudo et al., 2009; Francischini et al., 2015; Rage, 1988).

With the isolation of Laurasia and Gondwana, differences began to develop in the Early Cretaceous between the faunas and floras of the two continental landmasses (Cox, 1974; Canudo et al., 2009; Rage, 1988). Hence, continental isolation is seen by many as both a major impediment to north–south dinosaur migrations (e.g., Mao et al., 2012; Sereno et al., 1994), and as a driver of vicariance between the faunas of Gondwana and Laurasia (Canudo, 2006). However, although differences are generally recognised between the Early Cretaceous faunas of Laurasia and Gondwana (Canudo et al., 2009; Cox, 1974; Sereno et al., 1994), a simplistic view of organismal distributions, primarily driven by plate tectonics, is constantly being questioned (e.g., Gheerbrant & Rage, 2006; Rage, 1988). Despite the separation of Gondwana and Laurasia, by perhaps as much as several 100 km of deep ocean in the Early Cretaceous (Canudo et al., 2009), there is a growing body of evidence for faunal and floral exchanges between the northern and southern landmasses (Ezcurra & Agnolín, 2012; Gheerbrant & Rage, 2006; Rage, 1988). This makes the simple distinction between the Early Cretaceous faunas of Laurasia and Gondwana an oversimplification (Gheerbrant & Rage, 2006). However, distinguishing between vicariance–evolution from an ancestral stock following continental separation (Canudo, 2006; Carballido et al., 2012) – and migrations, can prove problematic, especially with an incomplete fossil record and flux in the taxonomy and phylogeny of dinosaurian and other groups. However, between the latest Jurassic and the Barremian – Aptian transition there is growing fossil evidence for biotic exchanges between Gondwana and Laurasia (Canudo et al., 2009).

5.4.1. Migration Routes and Barriers to Dispersal

Limits to continental organismal migrations typically include physical barriers such as deep ocean basins and mountain ranges; and to a lesser extent epicontinental seas and continental flood basalts (Canudo, 2006; Cox, 1974; Lehmann et al., 2015; Sereno et al., 1994). However, climatic gradients such as temperature, water availability, and desert belts also exert profound effects on organismal distributions (Canudo, 2006; Cox, 1974; Gallina et al., 2014). Hence, a deep and wide Tethys Ocean between Laurasia and Gondwana would have acted as an effective

barrier to dinosaur migrations (Canudo, 2006). However, increasing data suggests at least an intermittent connection between Laurasia and Gondwana (Barrett et al., 2011; Canudo et al., 2009; de Klerk et al., 2000; Gallina et al., 2014; Gheerbrant & Rage, 2006; Naish et al., 2004; Nicosia et al., 2007; Rage, 1988), even though this goes against current palaeogeographic received wisdom (e.g., Torsvik & Cocks, 2017). Even if faunal exchanges occurred, it is clear that there was not complete homogenization of northern and southern continental faunas during the Early Cretaceous (Gheerbrant & Rage, 2006), although the reasons for this remain unclear.

Three routes crossing between Laurasia and Gondwana have been hypothesised, although the detailed connections between Mesozoic landmasses are often poorly constrained (Ezcurra & Agnolín, 2012; Rage, 1988). The first is a western corridor via modern–day southern North America and northern South America; the second is a central route between modern–day Europe and northern Africa; and the third is an eastern route between modern–day Asia and Australia (Cox, 1974; Ezcurra & Agnolín, 2012; Gheerbrant & Rage, 2006). Although favoured by some palaeobiogeographic models based on phylogenetic inferences (Barrett et al., 2011; Poropat et al., 2016), the Australia–Asia route has no support based on past or current palaeogeographic continental reconstructions for the Mesozoic (e.g., Scotese & Golonka, 1992; Smith et al., 1994; Torsvik & Cocks, 2017). The long–standing hypothesis that the North America–South America route was more likely than the circuitous route through Europe and Africa (Cox, 1974; Ezcurra & Agnolín, 2012) seems to be the most likely for the dinosaurs forming the Río Batá footprints. However, a North America–South America migration route is not supported by the well–studied dinosaur bearing beds of North America, that lack evidence for *Iguanodontipus* footprints. Hence, despite assertions to the contrary (Cox, 1974; Mao et al., 2012), there is little evidence for migrations across the southwestern margin of Laurasia (modern–day North America) into north–western Gondwana (modern–day northern South America) during the Early Cretaceous (e.g., Torsvik & Cocks, 2017).

The third route suggest dinosaurs migrated across Tethys from modern–day Europe into northern Africa. This route has the greatest support, although sampling remains poor (Dalla–Vecchia, 1998; Ezcurra & Agnolín, 2012; Pazos et al., 2012; Rage, 1988). It has been hypothesised that the most likely routes were through Apulia and/or Alboran, possibly via the Iberian Peninsula (Bosellini, 2002; Canudo, 2006; Gallina et al., 2014; Gheerbrant & Rage, 2006). Dinosaurs could have crossed oceanic Tethys, onto the passive north African margin (Torsvik & Cocks, 2017) and there is growing evidence for temporary connections between European Laurasian and African Gondwana (Canudo et al., 2009; Dalla–Vecchia, 1994, 2008; Nicosia et al., 2007). This migration route is supported by the apparently substantial Laurasian origin of Early Creta-

ceous Gondwanan (northern African) organisms (Gheerbrant & Rage, 2006) and recent palaeogeographic reconstructions (van Hinsbergen et al., 2020). This suggests biotic exchanges occurred between Gondwana and Laurasia (Ezcurra & Agnolín, 2012), although prior to the Barremian the faunas of the two supercontinents remain distinct (Barrett et al., 2011; Canudo et al., 2009). However, it has also been argued that dispersal prior to the division of Pangaea, followed by later independent evolution, is a more plausible explanation for observed dinosaur distributions (Poropat et al., 2016; Sereno et al., 1994).

During the Early Cretaceous, Europe was an archipelago within a shallow epicontinental sea (Canudo, 2006; Canudo et al., 2009; Gheerbrant & Rage, 2006), and dinosaur movements between these islands could have been facilitated by global climatic and environmental changes (Kujau, 2012). Periodically lowered Early Cretaceous sea levels, possibly due to polar ice sheets (Canudo, 2006), would have produced a complex series of emergent land masses that facilitated movement of terrestrial organisms across Tethys in the Central Atlantic region between modern-day Europe and North Africa (Bosellini, 2002; Dalla-Vecchia, 2008; Gheerbrant & Rage, 2006). Although there was no land bridge across Tethys, Gondwana and Laurasia were in relatively close proximity (Rage, 1988). Island hopping across now accreted or subducted microcontinents, volcanic islands, or emergent carbonate platforms may have been possible via the mid-Tethys sill (Canudo, 2006; Canudo et al., 2009; Dalla-Vecchia, 1994, 1998; Ezcurra & Agnolín, 2012; Mao et al., 2012), or Greater Adria (van Hinsbergen et al., 2020). This would indicate biotic exchange across Tethys was a temporary sweepstake between islands, facilitated by lowered sea levels, during times of climatic cooling and may have allowed large animals, such as dinosaurs, to occasionally wade or swim across the intervening body of water. This would have produced an inconsistent, perhaps somewhat directional (north to south), intercontinental selective filter between the two major Early Cretaceous landmasses (Canudo et al., 2009; Ezcurra & Agnolín, 2012; Gheerbrant & Rage, 2006; Rage, 1988).

Considering all the evidence, a Europe–North Africa migration route across Tethys is currently the most plausible explanation for the presence of iguanodontians in northern South America. Hence, the Río Batá footprints would indicate an Early Cretaceous ornithischian dinosaur migration route westwards along the northern shores of Gondwana from modern-day Africa into Colombia. This scenario would predict the future discovery of Lower Cretaceous *Iguanodontipus* footprints, and iguanodontian skeletal remains, in northern Africa and elsewhere in modern northern South America (Figure 6).

5.4.2. Dinosaur Palaeobiology

The remains of dinosaurs are some of the best-studied fossils of the Early Cretaceous (Tennant et al., 2016), and there are

undoubted similarities between the ornithischian dinosaurs of central–southern Laurasia and northern–central Gondwana (Canudo, 2006; Canudo et al., 2009; Gheerbrant & Rage, 2006). Following the end–Jurassic extinctions, terrestrial vertebrate numbers declined, however, the ornithischian dinosaurs were only moderately affected, the ornithopods were virtually unaffected, and the iguanodontians became abundant in the Early Cretaceous (Tennant et al., 2016). It has been hypothesised that the dinosaurs that survived the end–Jurassic extinctions had key morphological adaptations, and possibly more generalized morphologies (Tennant et al., 2016). In addition, terrestrial life may have benefited from the generally warm and humid conditions during times of climatic amelioration, which produced widespread vegetation cover (Charbonnier et al., 2017; McLoughlin, 2001; Mao et al., 2012). This may have allowed the surviving herbivorous dinosaurs to radiate during the Early Cretaceous, taking advantage of broadly distributed, gymnosperm dominated, vegetation (Charbonnier et al., 2017; Mao et al., 2012).

The ecology of the iguanodontian dinosaurs may also have improved their chances of crossing Tethys. The iguanodontian, and other dinosaurian, fauna lived on an archipelago (modern Europe), which led to frequent migrations along coastal areas (Dalla-Vecchia, 1994, 1998; Santos et al., 2013), and probably necessitated occasional or regular wading or swimming between islands. This may have given these dinosaurs a propensity to cross shallow seas (Canudo, 2006), which at appropriate times may have included crossing Tethys. Indeed the Río Batá footprints, many *Iguanodontipus* and Lower Cretaceous dinosaur ichnofossils more generally, are commonly found on or close to palaeoshoreline or other water-rich deposits (e.g., Castanera et al., 2013; Dalla-Vecchia & Tarlao, 2000; Farlow et al., 1995; Kim et al., 2009; Pazos et al., 2012; Santos et al., 2013). In addition, during periods of Early Cretaceous cooling, there may have been additional environmental pressure for dinosaurs to move southwards towards more equatorial climates, thereby tracking both ecological and vegetational changes.

5.4.3. Gondwanan Dinosaur Provincialism

A migration route across Tethys for large, mobile dinosaurs such as iguanodontians fails to explain the absence of *Iguanodontipus* footprints in the more southerly parts of Gondwana. The best-known Gondwanan dinosaur faunas are those from southwest South America: Argentina and Brasil (e.g., Bittencourt & Langer, 2011; Costa da Silva et al., 2012; de la Fuente et al., 2007; de Valais et al., 2015; Moreno et al., 2012; Pazos et al., 2012). However, Gondwanan dinosaurs are also known from South Africa (de Klerk et al., 2000; Haughton, 1915) and Australia (Poropat et al., 2016; Romilio & Salisbury, 2011; Thulborn, 2016), whereas the dinosaurian faunas from northern South America are much more poorly known (Sereno et al., 1994; Weishampel et al., 2004). As a result of substantial connections between the southern continental

Ornithopoda Lower Cretaceous occurrences

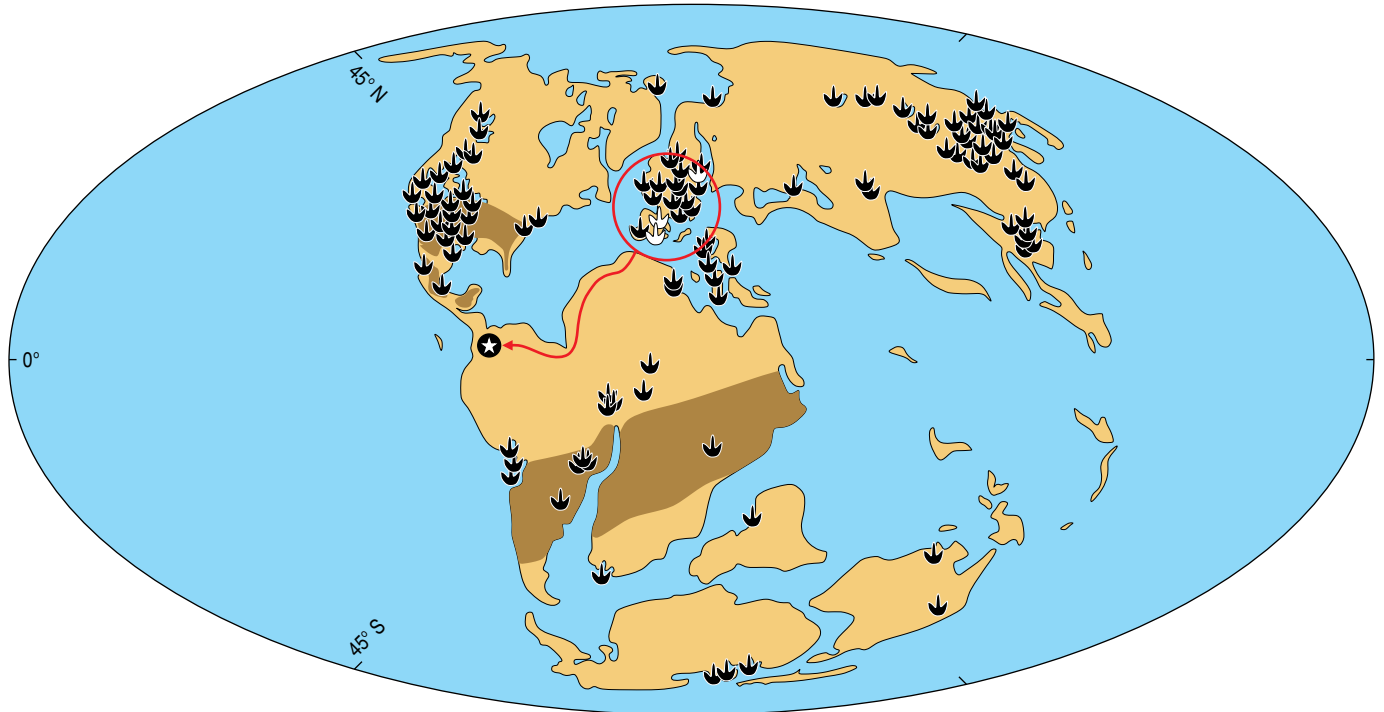


Figure 6. Early Cretaceous palaeogeographic map showing global distribution of ornithopod dinosaurs (footprint symbols, *Iguanodontipus* in white) and proposed migration route for the Río Batá *Iguanodontipus* trackmakers from the European archipelago (red circle), across Tethys Ocean, and along the northern shores of modern-day Africa and South America (red line), and into the modern-day Río Batá locality in Colombia (white star in black circle). Note the Central Gondwanan Desert Belt (dark brown) that probably restricted free southward migration of iguanodontians into southern Gondwana, which has its own endemic dinosaurian fauna, and the desert in the modern southern USA and Central America that precluded the water-adapted iguanodontians from migrating to South America via North America. Dinosaur data from downloaded from The Palaeobiology Database (<https://paleobiodb.org/#/>) using the clade name “Ornithopoda” (04 June 2018); Early Cretaceous base map from Matthews et al. (2016). Blue, water bodies; pale brown, land; dark brown, desert belts.

landmasses during the Early Cretaceous (de Klerk et al., 2000), it has often been assumed Gondwanan dinosaurs were widely distributed, continuing the trend from the Jurassic (e.g., Barrett et al., 2011; Cox, 1974; Sereno et al., 1994). Indeed there is good evidence for a broad distribution of high latitude southern Gondwanan dinosaurian taxa (Gallina et al., 2014) with migrations possible between modern southern South America, South Africa, Antarctica, and Australia, and probably encompassing India and Madagascar (Gheerbrant & Rage, 2006). This was despite (or perhaps because of) strong annual photoperiod variations and a flattened thermal gradient (McLoughlin, 2001; Poropat et al., 2016). On the other hand, there is relatively limited direct evidence for south–north migrations across Gondwana, although these have often been hypothesised based on taxonomic or phylogenetic evidence (e.g., Barrett et al., 2011; Naish et al., 2004). However, during much of the Jurassic, and continuing into the Early Cretaceous, Gondwana extended from the palaeo–equator to southern high latitudes, and the continent is known to have exhibited a well–marked, latitudinally determined, climatic gradient (McLoughlin, 2001).

Across a supercontinent the size of Gondwana, it is inconceivable that climatic gradients did not affect dinosaur distributions and migrations. This would lead to regional variations in dinosaurian faunas (Francischini et al., 2015), controlled by climate and geographical barriers, as with global faunal distributions today (Davies et al., 2011). During the Early Cretaceous, continuing from earlier in the Jurassic, there is considerable evidence for a Central Gondwanan Desert Belt (Gallina et al., 2014; de Valais et al., 2015; Francischini et al., 2015; McLoughlin, 2001; Naish et al., 2004; Philippe et al., 2004; Remes et al., 2009; Svensen et al., 2018). The Central Gondwanan Desert Belt was centred around 30 degrees south of the equator (Philippe et al., 2004, Figure 1), coinciding with the modern descending limbs of the Hadley and Ferrell atmospheric cells (Ziegler et al., 2003). This is in contrast to the northern hemisphere, where an extensive Laurasian (northern) desert belt did not develop, possibly due to widespread epicontinental seaways (e.g., the proto–Western Interior Sea, the central (European) archipelago, and the Turgai Sea), although desert conditions were present in the southern extent of western Laurasia (Philippe

et al., 2004). In Gondwana, the extensive Central Gondwanan Desert Belt crossed the continent from what are today northern Argentina, Uruguay, Paraguay, Brasil, and Namibia (Francischini et al., 2015; Gallina et al., 2014; Iglesias et al., 2011) and undoubtedly restricted the latitudinal migrations of dinosaurs, although occasional faunal interchanges were possible during periods of climatic amelioration (Gallina et al., 2014). Hence, the environment across the wide latitudinal geographic spread of Gondwana was uneven, undoubtedly affected biotic interchanges between northern and southern Gondwana, and prevented the southward migration of the possibly water-loving iguanodontians into southern Gondwana.

6. Conclusions

Six dinosaur footprints discovered in the upper Valanginian to lower Hauterivian Batá Formation along the Río Batá, Boyacá Department, Colombia, South America are interpreted as formed by a large (>30 cm foot length) ornithischian dinosaur. Four footprints form an approximately four metre long trackway generated by a dinosaur attributed to the ichnospecies *Iguanodontipus burreyi*, which prior to this work was an exclusively Laurasian ichnogenus. The trackmaker is interpreted as an iguanodontian dinosaur with a hip height of greater than two metres, possibly suggesting a sub-adult individual of approximately eight metres in length and weighting 2.5 metric tons. The dinosaur was moving at an average walking pace for iguanodontians of almost five kilometres per hour. The Río Batá dinosaur footprints are the first evidence for large ornithopod dinosaurs in Colombia, and represent the best-preserved dinosaur footprints, yet discovered in the country.

The Río Batá footprints, situated close to the northern shore of west Gondwana, suggest biotic interchange across Tethys Ocean between southern Laurasia (modern Europe) and northern Gondwana (modern North Africa), despite many modern palaeogeographic reconstructions showing no direct land connection during the Early Cretaceous. The separation of Pangaea during the latest Jurassic into northern Laurasia and southern Gondwana coincided in time with the end-Jurassic mass extinction event. This resulted in the radiation of iguanodontian dinosaurs into vacant ecological space during the Early Cretaceous. These dinosaurs appear to have been adapted to water-rich environments in the European archipelago and variable climates during the Early Cretaceous, probably related to relatively small-scale ice advances and retreats, which resulted in lowered global sea levels that permitted iguanodontian dinosaurs to cross Tethys Ocean, perhaps via the Iberian Peninsula, Apulia and/or Albora or Greater Adria.

Once in Gondwana, the iguanodontian dinosaurs probably tracked lush tropical vegetation and water-rich environments along the northern margins of the continent. However, a lack of evidence for *Iguanodontipus* footprints in southern Gondwana

implies a geographical barrier between northern and southern Gondwana. To the south lay the Central Gondwanan Desert Belt, which posed a considerable, and possibly impenetrable, barrier to southward movements of the water-loving iguanodontians, and precluded range extension into southern Gondwana. Hence, a variety of geographic and climatic factors drove Early Cretaceous northern Gondwanan dinosaur distributions, and as a result, we predict the discovery of both iguanodontian dinosaur skeletal remains, and further *Iguanodontipus* ichnofossils, in northern Africa and northern South America, but not in southern Gondwana.

The discovery of large ornithopod footprints along the Río Batá thereby adds considerably to the evidence for Colombian and northwestern South American dinosaurs and their movements. The identification of these footprints as attributable to the ichnogenus *Iguanodontipus*, is the first evidence for this ichnotaxon outside modern Europe, and has important implications for the palaeogeographic distribution of *Iguanodontipus* trackmakers. The Río Batá footprints thereby indicate we have much to learn about the palaeobiology, palaeoecology, and palaeogeography of Early Cretaceous dinosaurs in northern South America.

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Explanation of Acronyms, Abbreviations, and Symbols:

α, β, γ	Divarication angles (between II–III, III–IV, II–IV (= total divarication) respectively)	LFN LII, LIII, LIV	Leslie Francis NOÈ Digital lengths (lengths of II, III, and IV along A–F, B–F, and C–F respectively)
A, B, C	Anterior–most points of II, III, IV respectively	LIPs	Large Igneous Provinces
AC–G	Alejandro CORRALES–GARCÍA	MG–P	Marcela GÓMEZ–PÉREZ
AT	Anterior triangle (triangle connecting points A, B, C)	OAE PA	Oceanic anoxic events Pace angulation (angle between points B of three consecutive footprints)
ATh	Anterior triangle height (length of the line passing through B and perpendicular to A–C)	pCO ₂ PL	Partial pressures of carbon dioxide Pace length (line joining points B of consecutive left and right footprints)
ATw	Anterior triangle width (length A–C)	SGC	Servicio Geológico Colombiano
Avg	Average	SL	Stride length (the line joining points B on consecutive footprints on the same (left or right) side)
BLII, BLIII, BLIV	Length of toe free segment (A, B, C along lines A–F, B–F, C–F to the intersection with lines through D (perpendicular to A–F), D–E, E (perpendicular to C–F) respectively)	TA	Trackway axis (the line midway between the lateral–most points of the left and right footprints)
D, E	Posteriormost points of hypices (between II–III, III–IV respectively)	TTL	Total trackway length (distance from F of DF1 to B of DF4)
DF (with number)	Río Batá dinosaur footprints	TW	External trackway width (distance between the lines joining the lateral–most point of the footprints forming the trackway, and approximately parallel to TA)
F	Rear of metatarsophalangeal (“heel”) pad impression (the posterior–most point of the footprint)	WBII, WBIII, WBIV	Width at base of free segment of toe (length of line passing through D perpendicular to A–F, D–E, length of line passing through E perpendicular to C–F)
FA	Footprint axis (line B–F)	WGC–M	William G. CARANTON–MATEUS
FL	Footprint length (distance B–F [\equiv LIII])	WMII, WMIII, WMIII	Width at middle of free segment of toe (length half way between BLII, BLIII, BLIV, and perpendicular to A–F, B–F, C–F, respectively)
FR	Footprint rotation (the angle between FA and TA)		
FW	Footprint width (maximum width perpendicular to FL)		
HH	Hip height (4 \times FL)		
II, III, IV	Digit number (also prefixed by B)		
JVR–J	José Vicente RODRÍGUEZ		
K, M	“heel”–hypex lengths (D–F, E–F respectively)		

Authors' Biographical Notes



Leslie F. NOË is a vertebrate palaeontologist, stratigrapher, and historian of science, with special interests in the palaeobiology and evolution of the Sauropterygia. Leslie undertook his undergraduate studies in the School of Environmental and Applied Sciences at the University of Derby, UK, and graduated with honours with a Combined Subjects (Biology, Geology, and

Physical Geography) degree. Leslie subsequently undertook doctoral studies, at the University of Derby, under the supervision of Dr. Don SMITH, Dr. Arthur CRUICKSHANK (Leicester Museums), and Dr. Derek WALTON, and wrote his PhD thesis on the cranial osteology of the Callovian (Middle Jurassic) Oxford Clay Formation pliosaurian genera *Liopleurodon*, *Simolestes*, and *Pachycostasaurus*. Leslie gained a wide range of experience during seven years in the Sedgwick Museum, University of Cambridge, UK, as well as undertaking undergraduate and postgraduate supervision, and undergraduate teaching in both the Department of Earth Sciences and the Department of Zoology. A curatorship at Thinktank, the Birmingham Science Museum, UK, followed, together with an honorary position at the University of Birmingham. Leslie returned to Cambridge as curator of the globally important Harland Collection of rocks, fossils, and minerals, before moving to Colombia, where he is currently Associate Professor in the Departamento de Geociencias, Universidad de los Andes in Bogotá. As the first geologist in the newly formed Geociencias Department, Leslie has written numerous undergraduate courses, and continues to publish on Mesozoic marine reptiles, with special reference to Colombian Cretaceous faunas.



Marcela GÓMEZ-PÉREZ is a vertebrate palaeontologist and sedimentary geologist with special interests in pliosauromorph marine reptiles, museology, and geological outreach. Marcela undertook her undergraduate studies in the Departamento de Geociencias of the Universidad Nacional de Colombia Sede Bogotá, where she graduated with honours. Marcela then received the Joven Investigador Colciencias and worked for the Departamento de Geología of the Universidad EAFIT, Medellín, implementing the Alkennon protocol for surface seawater temperatures during the Holocene.

Marcela worked on a voluntary basis at the Sedgwick Museum of Earth Sciences in Cambridge, where her enthusiasm for museology started. She joined the Department of Earth Sciences, University of Cambridge, UK, for her doctoral studies under the supervision of Dr. David NORMAN with a prestigious Gates Cambridge Scholarship and a UK government Overseas Research Fellowship, at Newnham College. Following completion of her PhD studies, Marcela worked as a sedimentologist for CASP in Cambridge, before returning to Colombia to work on fine-grained sediment geochemistry for oil prospectation. Marcela undertook post-doctoral research work, focusing on Colombian plesiosaur faunas, and teaching, in the Departamento de Geociencias, Universidad de los Andes. Currently Marcela is the vertebrate palaeontologist in the Museo Geológico José Royo y Gómez of the Servicio Geológico Colombiano in Bogotá, contributing to the development of vertebrate palaeontology and professionalizing all aspects of the museum.



José Vicente RODRÍGUEZ received a BS degree in geology and a MEng in materials from the Universidad Nacional de Colombia in Bogotá. He has extensive first-hand knowledge of Colombian geology which stems from wide-ranging field-work experience including geological mapping, stratigraphy, and sampling. He also has laboratory expertise in sedimentological core studies of Colombian Cretaceous rocks, and on magnetic fabric studies of igneous rocks. His most recent work is related to a tectonic study of the Triassic Pueblo Pluton in the Central Cordillera, and participation in the discovery of a section crossing the Cretaceous – Paleogene boundary in the easternmost Pacific (Gorgona Island).



Alejandro CORRALES-GARCÍA is an undergraduate student in the Departments of Geosciences and Biology at Universidad de los Andes, Bogotá. Alejandro is interested in palaeontology, geochronology, taxonomy, arthropods, reptiles, and amphibians. Starting in his first semester, Alejandro worked in the Museo de Historia Natural ANDES at Universidad de los Andes. For his undergraduate thesis Alejandro worked on the palaeoecology of Cambrian trilobites.



William G. CARANTON-MATEUS

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La Venta Palaeontology project, which focused on primates along the Magdalena valley, Colombia, supported by the National Geographical Society and directed by Siobhan COOKE, PhD in physical anthropology at City University, New York. For his undergraduate thesis, William studied deformation events in the northwest margin of the Sierra Nevada de Santa Marta.

