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EXCEPTIONAL AND STRIKING 3D TRACK-DETACHED UNDERTRACK SPECIMENS FROM THE UPPER JURASSIC OF ASTURIAS (N SPAIN)

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Abstract: Vertebrate palaeoichnology often aims at the identification of the trackmaker by associating diagnostic features from the known taxa's skeletal anatomy with its inferred footprint morphology, but deep penetrative tracks and/or deep detached undertracks (DDU) are providing conflicting morphological/extra-morphological information, bringing into question the initially assumed close anatomical correlation.

Penetrative footprints produced in fluvial-dominated deltaic facies from Upper Jurassic Lastres Formation are very frequent in the coastal cliffs of Asturias (N Spain). Some of them consist of non-avian theropod track casts associated with "ornithopod-like" detached undertracks. Some criteria are suggested to distinguish the latter when such an association does not exist.

Moreover, we describe an exceptional theropod footprint preserved as a sandstone cast along with its respective deep detached sandstone undertrack (DDSU). The specimen records the foot movement through the sediment, entailing striking morphologic changes in outline along four different levels of depth. The uppermost level 1 shows an apparent stegosaur hind track morphology; level 2 resembles an avian-theropod print; level 3 represents the true non-avian theropod pedal morphology of the trackmaker; the lowermost level 4 corresponds to the deep detached sandstone undertrack (DDSU), which could be interpreted as either a track of a graviportal theropod or an ornithopod-like footprint.

In light of this new evidence, it becomes clear that vertebrate ichnotaxonomy should not be based solely on the supposed trackmaker identification. Furthermore, biogeographic and evolutionary studies linked to this core information should be considered unsupported, along with many ichnotaxonomical assignations based on taphonomic processes, such as the case exemplified herein, the *Iguanodontipus* ichnogenus.

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Introduction

Vertebrate palaeoichnology has provided a great number of ichnotaxa over the years, an activity that has increased in recent times. Numerous ichnologists have identified this abundance of data as a problem (Ellenberger 1983a, 1983b; Boy & Fichter 1988; Haubold 1996; Leonardi 1997; Lucas 2001, 2007; Manning 2004; Farlow 2018; Farlow et al. 2012, 2015; Lockley et al. 2013; Piñuela Suárez 2015; Marchetti et al. 2019; Gatesy & Falkingham 2020; Lallensack et al. 2020; Leonardi & Carvalho 2021). It has been suggested (Moratalla García 1993) that probably 70-80% of the ichnogenera should be abolished if, by means of searching for a correlation with the skeletal record, we make a true effort to integrate the pedal dynamics, substrate consistency and the preservation bias of each resultant footprint morphology left by tetrapod species. Fifty-three vertebrate ichnogenera from the Mesozoic of China have been meticulously reviewed (Lockley et al. 2013), considering only thirty-six valid. Similarly, 44 ichnospecies of large ornithopods were reviewed (Díaz-Martínez et al. 2015) and only eight were considered valid.

Throughout the history, approaches to invertebrate and vertebrate ichnology have been different (Bromley 2004; Lucas 2005, 2019; Lockley 2007; Marchetti et al. 2019; Melchor 2021). While ichnologists working on invertebrates have successfully focused their interpretations on the animal's behaviour and on its sedimentary environment, vertebrate ichnologist have contrasting views. Some are trying to build up a trackmaker census through time (Lockley 2007; Lucas 2007), while others believe that the morphology of the tracks is related to the processes of their formation and preservation and does not faithfully reflect the morphology of the trackmakers' feet (Sarjeant 1990; Sarjeant & Langston 1994; Mc Keaver & Haubold 1996; Manning 2004; Farlow et al. 2012; Falkingham et al. 2016; Leonardi & Carvalho 2021; Carvalho & Leonardi 2024).

The question is: how much change in footprint outline shape is sufficient to erect a new ichnotaxon, considering that many of these features may be extramorphological? (Peabody 1948). Indeed, footprint morphology variations are due to a large extent to complex ichnotaphonomic processes that can easily mask the trackmaker's pedal morphology, because it depends on (Marchetti et al. 2019): 1) the original substrate properties; 2) the animal's behaviour, such as pedal movement (especially the sequential stages of entry, support and exit of the foot and locomotory speed; 3) the subsequent physical and biological disturbances of the substrate; 4) interaction of the lower and upper sedimentary layers with the track; 5) diagenetic processes, and 6) degree of weathering of the outcrops.

The problem becomes even more complex if the record of undertracks is added to the discussion, particularly in the case of deep detached undertracks (DDU) centimetric in thickness (Piñuela Suárez 2015), which are quite frequent in the fossil record, but often ignored. The abundant presence of undertracks was already recognized in the 19th century (Hitchcock 1858), although most of them were recently reinterpreted as penetrative tracks (Gatesy & Falkingham 2020). These undertracks do not reflect the anatomy of the trackmaker's autopodium in detail (Hitchcock 1858; Gatesy & Falkingham 2020) because these ichnites tend to be enlarged and modified toward the subjacent layers, hence, they can be confused with different ichnospecies (Hitchcock 1858). Furthermore, "it is possible that many footprints attributed to ornithopods might actually correspond to theropod subtraces" (Leonardi 1997). Recently, theropod undertracks with ornithopod-like morphology were described from the Early Jurassic of Utah (Milner et al. 2023).

Indeed, many authors agree that the distinction between ornithopod and theropod footprints is an ongoing issue in dinosaur palaeontology (Dalla Vecchia et al. 2002; Moratalla et al. 1988; Lockley 2009; Farlow et al. 2012; Schulp & Al-Wosabi 2012; Piñuela Suárez 2015; Lallensack et al. 2016, 2020, 2022; Piñuela et al. 2016). Therefore, the only way to obtain a suitable trackmaker identification, meaningful enough to be used in palaeobiogeography and evolutionary inferences, is to somehow control for these abundant sources of footprint variation (Piñuela 2012; Piñuela et al. 2012; Piñuela Suárez 2015; Marchetti et al. 2019; Lallensack et al. 2022).

Herein, we describe several exceptional dinosaur tracks from the Lastres Formation (Asturias, N Spain), Kimmeridgian in age, preserved as 3-D sandstone casts along with their corresponding deep detached sandstone undertracks (DDSU). One of them provides striking evidence of up to four footprint outlines, resembling those of stego-

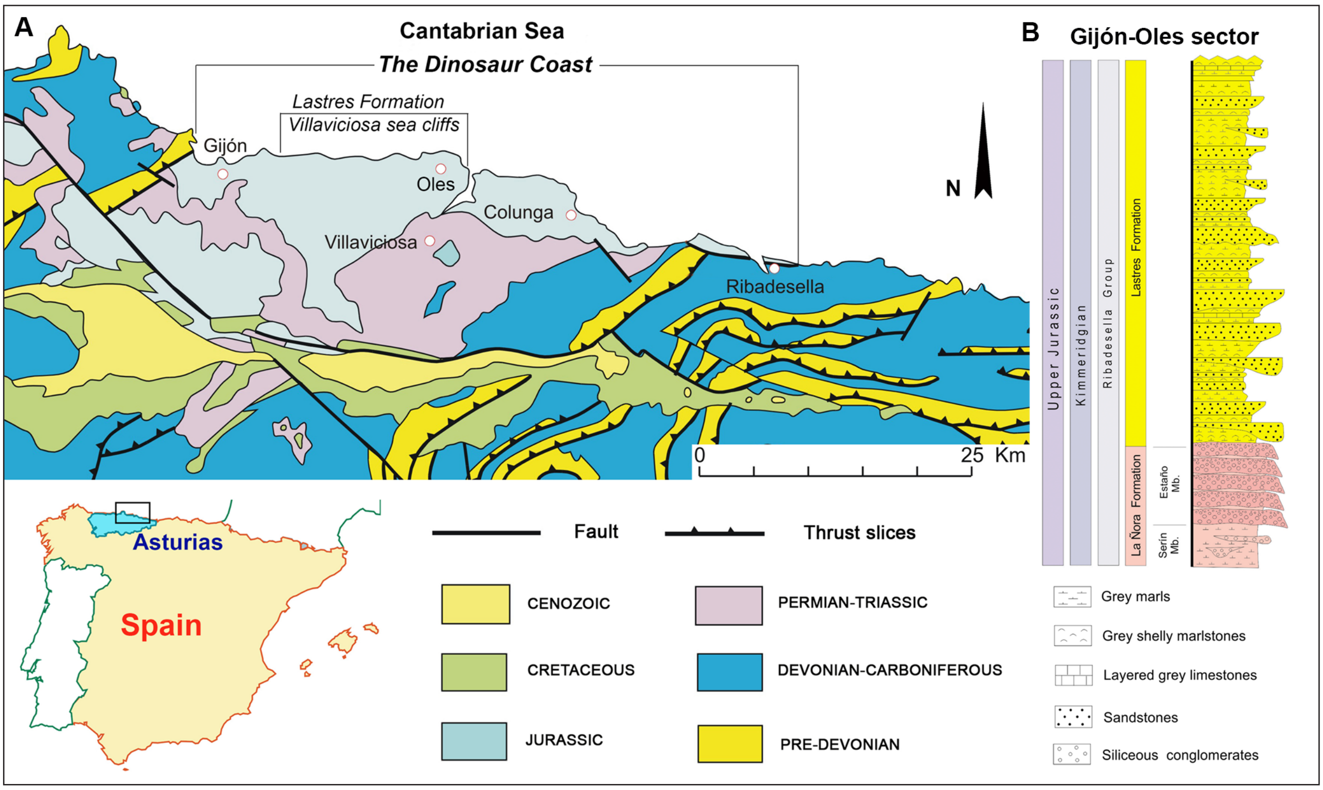


Fig. 1 - A) Geological map of central-eastern area of Asturias (N Spain; modified from García-Ramos & Gutierrez Claverol (1995) showing the location of the Lastres Formation (Upper Jurassic) on Villaviciosa sea cliffs where the specimens were found. B) General stratigraphic log (not to scale) of the Gijón-Oles sector (modified from García-Ramos et al. 2011).

saur-, bird-, theropod- and ornithopod- tracks, in four different levels, which was generated by a single theropod trackmaker. In addition, we put forward several criteria to recognize deep undertracks when they are not directly associated with the true print. Based on these deep Asturian undertracks, it is suggested, that the *Iguanodontipus* ichnogenus can also be a deep detached undertrack (DDU) produced by a theropod.

Location and geological context

The tracks were found in the coastal cliffs of Villaviciosa Municipality (Asturias, northern Spain; Fig. 1A), which is part of the so-called "The Dinosaur Coast", an exposure of about 57 km long Jurassic outcrops where abundant vertebrate tracks belonging to dinosaurs, crocodiles, lizards, pterosaurs, turtles and fishes have been found (García-Ramos et al. 2002, 2004a, 2004b, 2006; Avanzini et al. 2005, 2007, 2008, 2010, 2012; Piñuela et al. 2016; Piñuela Suárez 2015; Rauhut et al. 2018). The large amount and variety of vertebrate footprints, especially those of dinosaurs and pterosaurs, are particularly striking (Piñuela Suárez 2015). At present, the Jurassic Museum of Asturias (MUJA) houses 747 dinosaur footprint specimens attributed to theropods, sauropods, ornithopods and stegosaurs, in which the preservation quality varies from poor to exceptional, some of them showing exquisite detail of skin impressions.

The studied footprints come from the Lastres Formation (Fig. 1B), which is 400 m thick. It consists mainly of interbedded grey sandstones, marlstones and mudstones, including occasional shell beds and conglomeratic layers (García-Ramos et al. 2011).

The Lastres Formation was dated as Late Jurassic (Kimmeridgian) based on scarce ammonoids (Olóriz et al. 1988; Dubar & Mouterde 1957; Suárez Vega 1974).

This unit represents a fluvial-dominated lagoonal delta, sourced by high-sinuosity channels. Different depositional facies are observed in this succession, including delta plains, distributary channels, interdistributary bays, crevasse-splays and levees, sandy mouth bars and prodelta. Small transgressive events (delta-abandonment facies) repeatedly disrupted the sedimentation, recording extensive shell beds dominated mainly by bivalves and gastropods (García-Ramos et al. 2011).

Although some of the natural casts studied were found *ex situ*, and it is not possible to specify more about the sedimentary facies in which they were produced, this type of preservation shown here is very frequent in the sandstone/marly mudstone alternations of crevasse-splay and levee facies along "The Dinosaur Coast".

Materials and methods

The footprints described here were found in Villaviciosa Municipality belonging to "The Dinosaur Coast" (Asturias, N Spain) and are included also in the "Yacimientos de Icnitas" Natural Monument and Special Conservation Zone. All specimens come from the Upper Jurassic (Kimmeridgian) Lastres Formation. Some of them (with MUJA acronym) were incorporated into the Jurassic Museum of Asturias (MUJA) collection.

Footprints were photographed with a Huawei 20pro Leica camera and a Google Pixel 8 (2023) smartphone camera for photogrammetry. Images were processed with the software RealityCapture.

A particular preservation case of Asturian dinosaur footprints

The Asturian Jurassic dinosaur tracks are frequently represented by sandstone casts, often associated with the respective displaced portion of the sandstone bed located below the surface stepped by the trackmakers; the latter were named as undertrack casts (Piñuela Suárez 2015) and herein referred to detached sandstone undertracks (Figs 2, 3). This peculiar type of preservation was usually due to the following inferred taphonomical processes: 1) the dinosaur walked through a soft to stiff, muddy substrate producing a true track; 2) the foot reached the underlying semi-consolidated (cohesive) sandy bed, breaking it and displacing it downward (detached undertrack); 3) the true track was subsequently infilled by newly deposited sandy sediment, which finally becomes a sandstone cast.

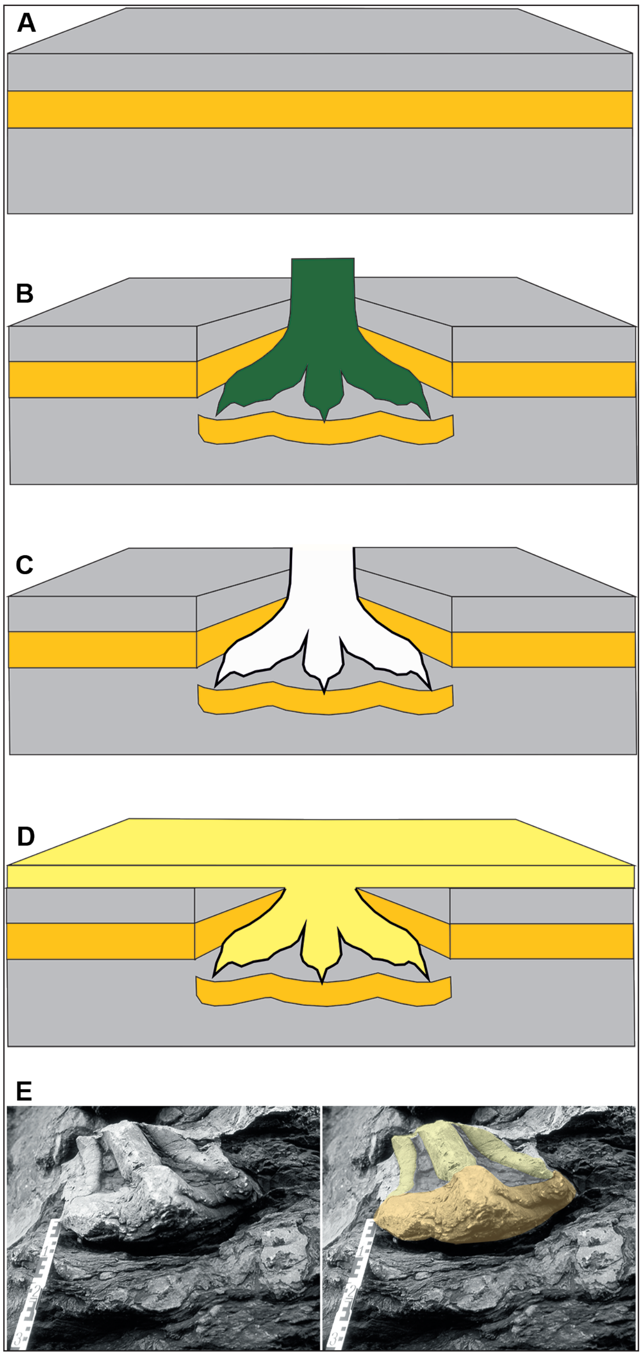


Fig. 2 - Formation of the sandstone track cast and deep detached sandstone undertrack (DDSU), the latter was produced when the dinosaur reached the underlying cohesive sandy bed, breaking and displacing it down (modified from Piñuela Suárez 2015). The sandstone track cast (yellow) is confidently assigned to a theropod, while the resulting DDSU (orange) could be attributed to an ornithopod footprint (specimen from Argüero, Villaviciosa).

Detached sandstone undertracks

Shallow detached sandstone undertracks (SDSU). The displaced portion of the sandstone bed is less than a centimetre thick (Fig. 3A). It is still possible to recognize the morphologic details of the pes or manus of the trackmaker. In this case, the footprint could be useful in parataxonomy (Piñuela 2012; Piñuela Suárez 2015; Piñuela et al. 2012) and/or to suggest a potential trackmaker.

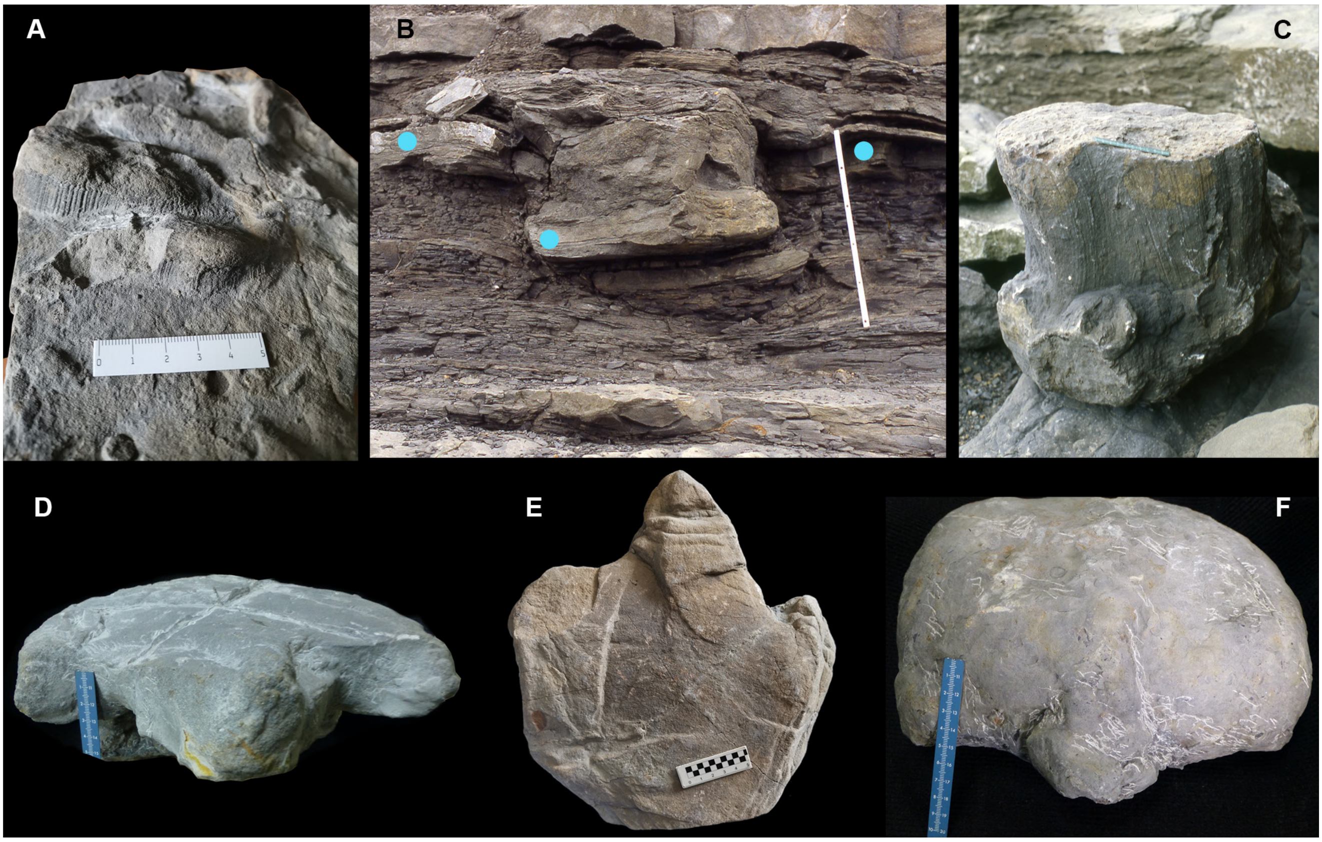


Fig. 3 - Dinosaur detached sandstone undertracks from the Upper Jurassic of Asturias. A) Theropod footprint MUJA-1070 showing striations on the vertical walls of digits II and III produced by the skin scales, which striations end against the SDSU (< 1 cm thick). As being a shallow undertrack, the pedal morphology is still recognizable and it is possible to assign it to the *Grallator* ichnogenus. B) Sauropod sandstone track cast associated to its DDSU. Blue dots indicate the broken sandstone bed that was displaced down. Oles coastal cliffs, Villaviciosa. C) Sandstone track cast of a quadrupedal dinosaur associated to the DDSU. Note the striations produced by skin scales during entry and exit of the hindfoot in the muddy sediment. These structures are only preserved on the vertical walls of the sandstone track cast. Quintueles sea cliffs, Villaviciosa. D) DDSU specimen MUJA-1036 showing a flat sole surface. E) DDSU specimen MUJA-1184 showing a flat sole surface with staggered (microfaults) structures. F) DDSU specimen MUJA-1193 showing very convex sole surface and very short digit impressions. Note that the specimens A, D-F are overturned.

Deep detached sandstone undertracks (DDSU). The displaced portion of the sandstone bed is several centimetres thick (Piñuela Suárez 2015). In this case, it is difficult to recognize the autopod's anatomical details (Figs 2, 3B-F). Hence, DDSU should not be used for nomenclature or to suggest a potential trackmaker.

Association sandstone track cast-detached sandstone undertrack

When both the sandstone track cast and the detached sandstone undertrack are associated, it is often possible to establish the boundary between the two. The detached undertrack is larger than the track cast (Avanzini et al. 2012; Piñuela et al 2012; Piñuela Suárez 2015), increasing in horizontal dimensions (Henderson 2006; Marty 2008; Milàn & Bromley 2006), mainly the width, in the case of bipedal dinosaurs (Figs 2, 3B-F). This enlargement can be explained by the pressure exerted by the dinosaur foot, which is transferred radially outwards (Allen 1997; Manning 2004; Falkingham et al. 2009, 2010). Specifically, in the case presented here this pressure affects the width of the digit impressions more than its length. While the claw impressions reached the distal edge of the detached undertrack, large differences are observed in the digit print width, between the sandstone track cast and the DDSU (Figs 2, 3B-F); in the latter, this digit print width can be from 1.5 up to 4 times greater than in that of the sandstone track cast.

The entry and exit striations generated by the pedal scales, when present, are located on the vertical walls of the sandstone track casts and end abruptly against the larger detached sandstone undertracks located below (Fig. 3A, C); evidently, the latter do not show skin grooves on the walls, as these were not touched by the dinosaur foot.

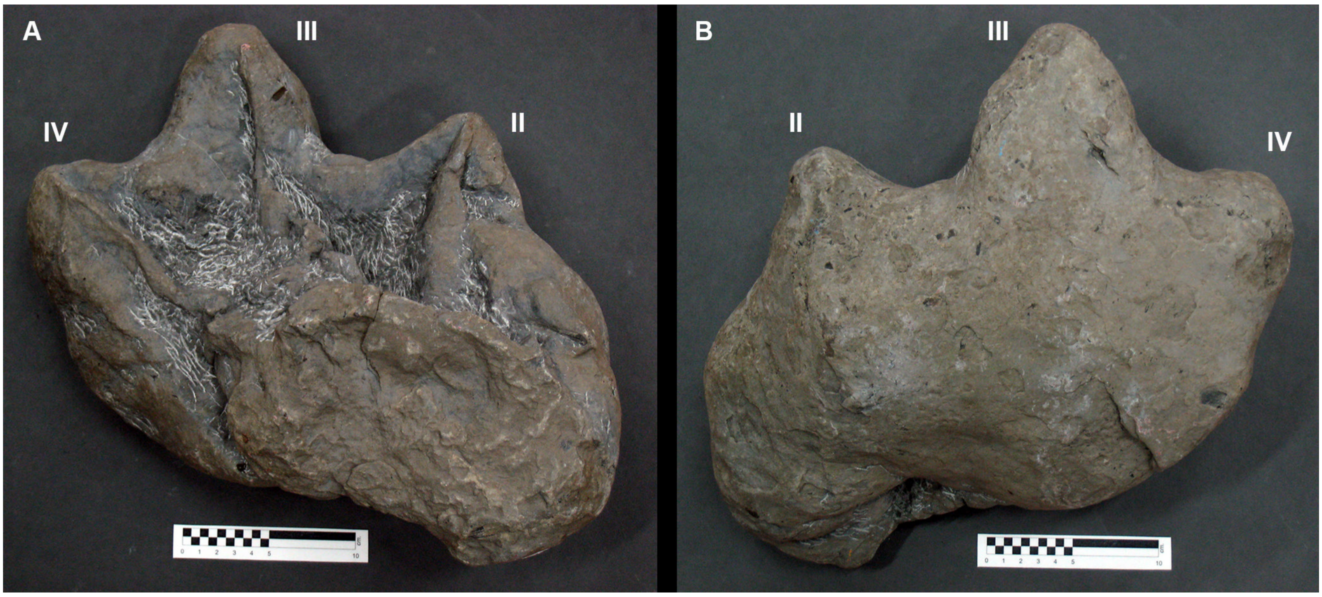


Fig. 4 - Theropod sandstone track cast associated to its respective DDSU (MUJA-1200). A) Top view of the cast showing three very narrow and long digit impressions produced in a soft to stiff muddy sediment. Note the claw mark and the subtle digital pad impressions on digit II. In addition, it is possible to observe a "false quadruped manus-like print" (posterior-medial part), on top, probably shaped during the foot extraction phase. B) Bottom view of DDSU showing the same track with its DDSU showing three very broad and short digit impressions, produced when the theropod foot reached and detached the semi-consolidated (cohesive) sandy bed located below the stepped muddy sediment, resembling an ornithopod footprint.

In this regard, a frequent case observed in the Asturian Jurassic outcrops is deep sandstone track casts with three long and narrow digits, ending in claws and in which it is possible to recognize some foot pads overlying the respective DDSU (Fig. 4A); this type of footprint is correctly attributed to theropods. In contrast, if its associated DDSU is observed from the bottom surface, it shows short and broad digits without claw or pad impressions (Fig. 4B); these features could be erroneously attributed to an ornithopod footprint.

The presence of at least 86 tridactyl theropod footprints at MUJA showing associated sandstone track cast-DDSU, from many different beds of the Lastres Formation, which is 400 m thick, suggests that this phenomenon is very frequent in the Jurassic of Asturias. We have also observed this association in the type series of *Iguanodontipus* from the Cretaceous of England, therefore, probably that could appear in other heterolytic series of the Mesozoic record.

Furthermore, the preservation of deep detached undertracks (DDU) is not exclusive to siliciclastic rocks; they have also been observed in the Upper Jurassic carbonate successions of Asturias (Tereñes Formation), although they are not the subject of the present study.

Criteria for recognizing isolated detached sandstone undertracks

Therefore, when it is not possible to observe a cross-sectional view or both sandstone cast and detached undertrack are not associated, it is in fact difficult to differentiate them. Certainly, shallow detached sandstone undertracks (SDSU) do not constitute a problem in this respect, because they can closely reflect the morphology of the autopod, but there is a problem with the DDSU, since it does not reflect such morphology; in this latter case, the presence of a flat or highly convex sole surface (Fig. 3D-F), sometimes associated with small, radial or concentric microfaults (staggered structures; Fig. 3E), can be a convincing criterion to recognize them. In addition, the relatively distal position of the hypices or their more U-shaped than V-shaped outline as well as the preservation of short, blunt and poorly defined digit impressions may also indicate that a footprint can be a DDSU (Figs 3D-F, 4).

An exceptional 3D theropod track (MUJA-4363)

The studied specimen consists of a sandstone track cast attached to a DDSU, both with remarkably distinctive morphologies (Fig. 5; https://www.museojurasicoasturias.com/muja-4363).

Indeed, different outlines can be observed at different levels, and these are related to the pedal kinematics and its interaction with the soft to stiff substrate.

Description

Four successive footprint outlines are distinguished with depth, from top to bottom:

Level 1. It represents the uppermost part of the sandstone cast (Figs 5A, E; 6). Outline 1 is characterized by an elongated and sub-triangular tridactyl footprint with very short, wide, blunt and forwardly oriented digit impressions. Digit III trace is the longest and widest. The divarication angle (II^IV) is very low. The posterior part of the footprint is elongated, relatively symmetrical, and its proximal edge is rounded. Outline 1 shape approaches the morphology of a stegosaur pes print (White & Romano 2001; García-Ramos et al. 2002; Cobos et al. 2010; Xing et al. 2013; Piñuela Suárez 2015).

Level 2. It is located in the middle part of the sandstone cast (Figs 5A, E; 6). Outline 2 represents a tridactyl track with very narrow and relatively long digit impressions. Although the proximal part of the digit traces is not visible because they are partially truncated by the exit trajectories, the digit III trace is the longest. There is no evidence of digital pad and claw marks. The divarication angle is higher than in the outline 1. The morphology resembles an avian-like theropod footprint, due to a its narrow digits, and it is similar to leptodactyl (Hitchcock 1836) or penetrative tracks (Gatesy & Falkingham 2020).

Level 3. It represents the lower part of the sandstone cast (Figs 5A, E; 6). Outline 3 shows the shape of a tridactyl footprint with long and relatively narrow digit impressions (but wider than those in outline 2) ending in easily distinguishable claw marks. Subtle digital pad impressions were preserved in the three digit traces. The distal end of the digit III impression is slightly medially oriented. In lateral, medial and distal views (Fig. 5C-E), the digit exit trajectories can be observed. This footprint is similar to that produced by the right hind foot of a non-avian theropod.

Level 4. It corresponds to the sandstone DDSU (Figs 5A, B; 6). Outline 4 represents the shape of a tridactyl track of similar length and width. The digit impressions are shorter and wider than in outlines 2 and 3 and have relatively sharp endings although no claw marks can be distinguished. The divarication angle is slightly higher than in previous outlines. Hypices are in a much more distal position than in outline 3. The proximal part of the footprint shows a notch in the posterior-medial margin, behind the digit II impression. This morphology is more robust than in outline 3, hence it could be attributed to a more graviportal theropod or even an ornithopod.

Interpretation

Many of the Asturian theropod footprints were produced in relatively stiff and thick, muddy substrates, which were later infilled with sand and preserved as sandstone casts (Fig. 2). These tracks show several morphological details such as the striations produced by the scales, claw marks and entry or exit trajectory structures of digits. Certainly, this remarkable record constitutes excellent material to study dinosaur pedal kinematics, but the foot morphology is difficult to recognize (Avanzini et al. 2012).

Large Asturian theropod tracks (Avanzini et al. 2012), but also small ones (Piñuela Suárez 2015), tend to increase the interdigital angle when the trackmaker walked in a relatively deep and muddy soft to stiff sediment. Usually, the entry and exit trajectories of the digits are oblique in these deep tridactyl footprints, and the interdigital angles vary progressively along these trajectories (Avanzini et al. 2012; Milan et al. 2006).

In this scenario, the trackmaker of MUJA-4363 should have slipped its foot forward, separating its digits while entering deeply into a soft to stiff muddy substrate. During the sliding, the foot produced the elongated “heel” impression of outline 1. The separation of digits resulted in an avian-like footprint with high divarication angle and very narrow digit impressions in outline 2. In addition, the extreme narrowness of the digit traces was produced by the subsequent collapse of the mud and probably was accentuated due to the suction effect during the pedal extraction phase (Figs 5A, E; 6).

When the foot reached the deepest part of this muddy sediment, touching the boundary with the underlying cohesive sandy bed, produced outline 3, which preserved relatively narrow and long digit impressions, clear claw marks but subtle digital

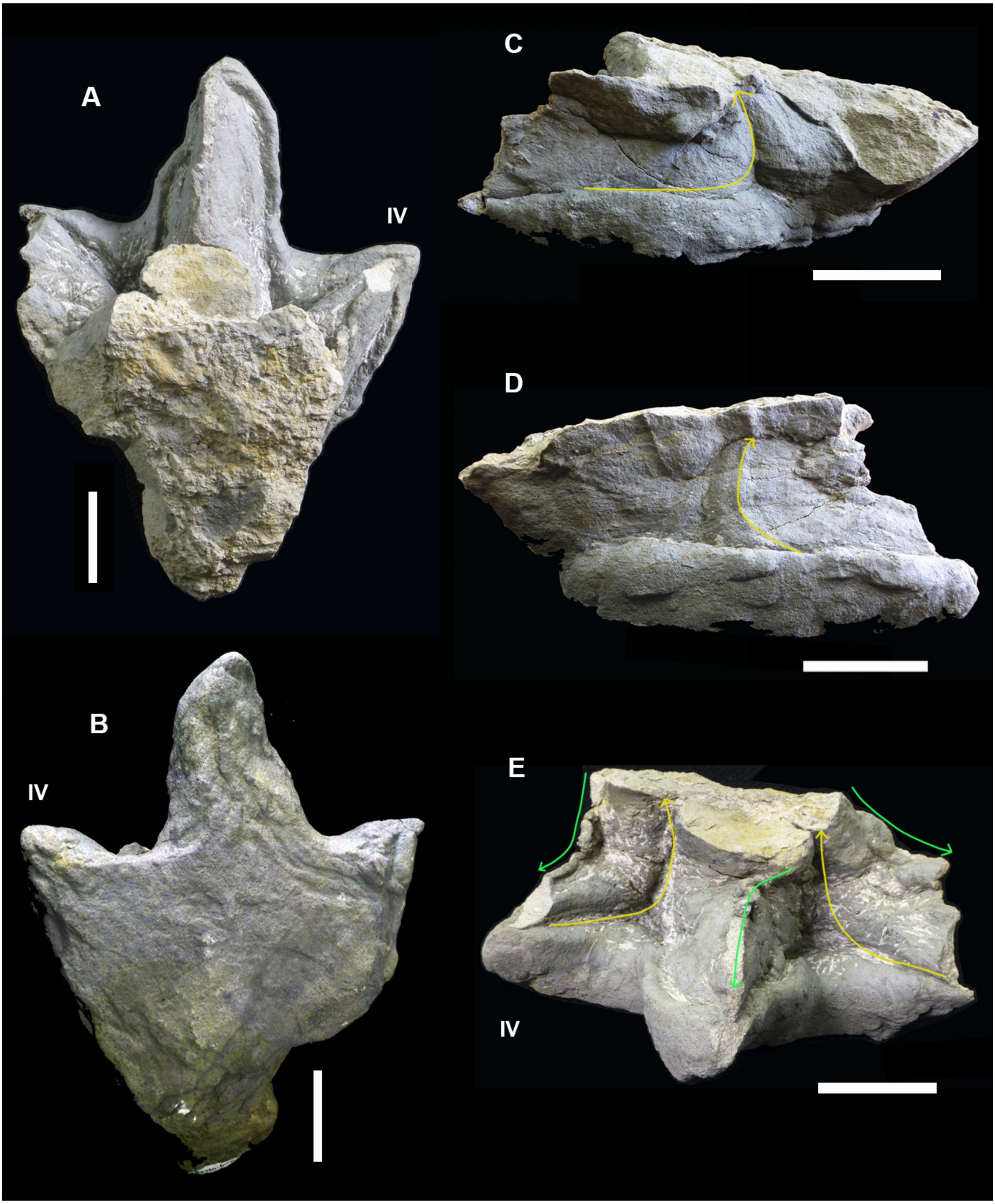
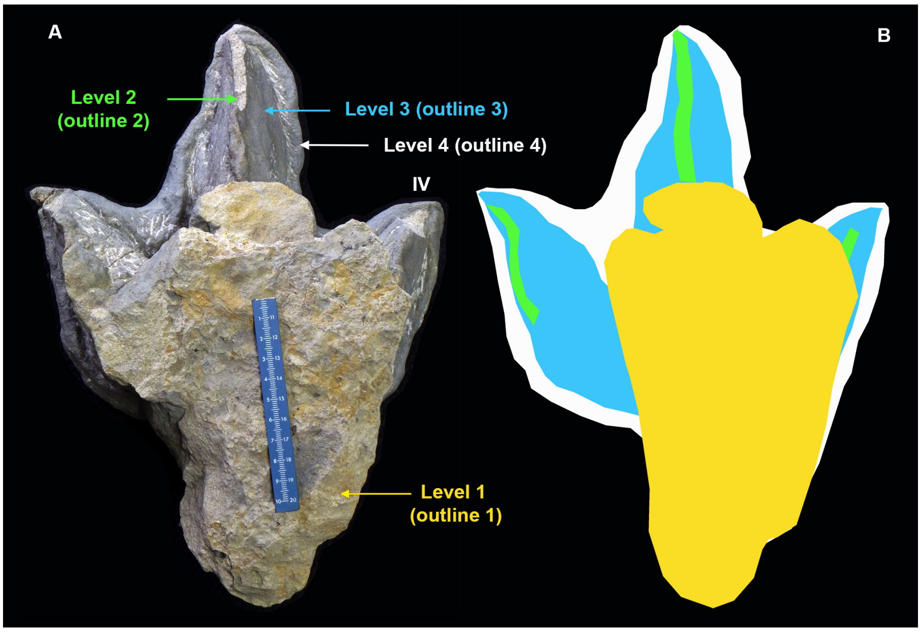


Fig. 5 - Exceptional specimen of a deep 3D theropod footprint (MUJA-4363). A) Top view. B) Bottom view. Note the staggered (microfaults) structures usually related to a semi-consolidated (cohesive) substrate. C) Medial view. D) Lateral view. E) Distal view. Green arrows indicate the entry trajectories of digits and yellow ones the exit trajectories. Scale bars: 5 cm.

pad traces in the three digits (Figs 5A; 6). Hence, outline 3 is the one that reflects the pedal anatomical details of the trackmaker with more precision. The specimen MUJA-4363 can be confidently as-

Fig. 6 - Four different outlines can be identified in the tridactyl theropod footprint specimen MUJA-4363, viewed through four levels of depth. A) Picture of the original specimen in top view. B) Interpretative drawing. Outline 1 shows a morphology apparently attributable to a stegosaur pes print (yellow). Outline 2 is similar to an avian theropod track (green). Outline 3 reveals the most accurate theropod footprint morphology (blue). Outline 4 shows the DDSU, which resembles a more graviportal theropod or might be mistaken with an ornithopod-like footprint (white).



signed to the right pedal footprint of a medium-sized non-avian theropod trackmaker.

At the time of maximum pressure, the theropod´s foot reached the semi-consolidated (cohesive) sandy bed located below the muddy tracked level, breaking it and displacing it downward. The result is a more robust tridactyl footprint (outline 4), characterized by a shorter and wider digital impressions and high interdigital angles (Figs 5A, B; 6). Looking at the bottom surface, this DDSU would have normally been assigned to a more graviportal theropod or even to an ornithopod trackmaker. This eventual identification as an ornithopod is also very evident in other similar cases (see examples in figures 3D-F and 4A-B).

The foot starts the extraction phase, initially moving backward, then upward and finally forward. In Fig. 5E, the exit trajectory of digits II and IV (indicated by the yellow arrows) appears as a continuous structure extending from the top of Level 4 (bottom) to Level 1 (top). These structures (exit trajectories of digits) go initially backward, while approaching digit III and thus progressively decreased the interdigital angle (Fig. 5E), then become vertical and in their last part, they go slightly forward. In this last phase, the dorsal side of the toes displaced the upper part of muddy substrate giving rise to three very short, wide, blunt and distally oriented digital impressions similar to those that would leave a stegosaur foot. So, the upper part of the penetrative footprint infill currently observed as a stegosaur track, like *Deltapodus* (Figs 5A, E; 6), consists of two undifferentiated parts: a posterior one corresponding to the entry of the foot sliding forward ("heel"), and an anterior one produced by the dorsal side of the theropod's digits during exit phase ("false stegosaur digits").

Some consequent considerations about *Iguanodontipus*

The type series of *Iguanodontipus* housed at the Geological Museum of Bournemouth Natural Science Society -BNSS- England, consist of seven natural casts (Sarjeant et al. 1998). The letters of the footprints from the original paper (Sarjeant et al. 1998) are kept herein, but in lowercase. Five of them, including the holotype, display an ornithopod-like track outline (prints B-F, figs. 12 and 13 in Sarjeant et al. 1998; herein tracks c-f Fig. 7A), but the other two are more similar to theropod-like tracks (prints A, G, figs 12 and 13 in Sarjeant et al. 1998; herein track g, Fig. 7A).

Considering the specimen MUJA-4363 (Figs 5, 6) and many other similar examples of the Jurassic of Asturias (Figs 2-5), it is reasonably to suggest that this type of preservation (association track cast-DDU) is present also in some footprints of the *Iguanodontipus* type series (Piñuela et al. 2016).

Looking at the vertical sections of those tracks C and D – the latter is the holotype – in Sarjeant et al. (1998) (herein tracks c-d Fig. 7C, D) it is possible to identify the boundary between the track

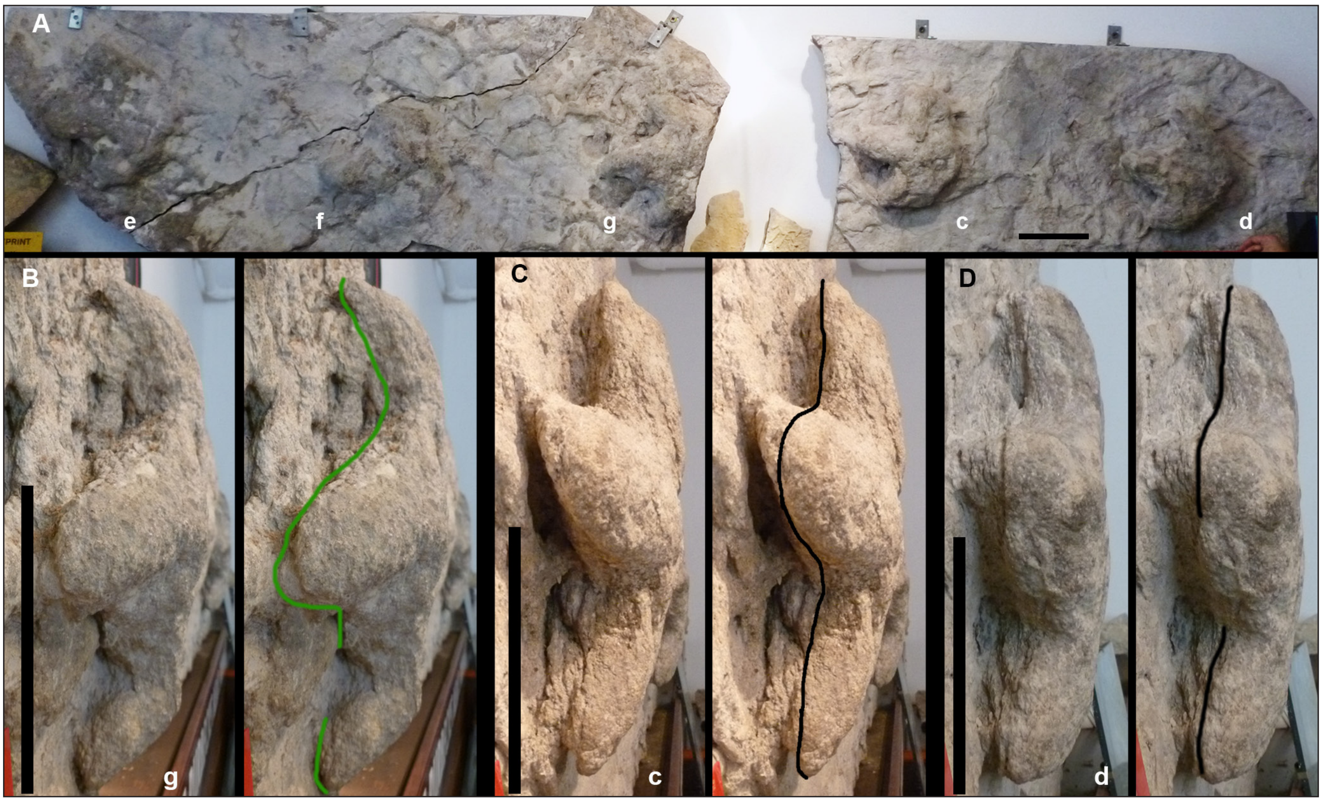


Fig. 7 - A) Part of the type series of *Iguanodontipus* (Sarjeant et al. 1998) exposed at the Geological Museum of Bournemouth Natural Science Society (BNSS) in the south of England. The letters of the footprints from the original paper (Sarjeant et al. 1998) are kept herein, but in lowercase. B) Print g, with an outline more similar to that of a theropod, corresponds apparently to a track cast (green line). C, D) Tracks c and d (the latter is the holotype) look-like ornithopod footprints, but it is possible to observe the boundary between the track cast and the DDU in both (black lines). Scale bars: 15 cm. Note that in B-D the digit III points towards the observer.

cast and the DDU, the latter being several centimeters thick. In both specimens, C and D, the hypices are positioned in a more distal position than those of A and G, resulting in tracks with proportionally shorter and wider digit impressions, similar to those produced by ornithopods.

On the contrary, A and G in Sarjeant et al. (1998) have longer and narrower digital impressions with lower interdigital angles than the other five (herein track g Fig. 7A, B). These features are typical of theropod footprints; moreover, in the vertical section, track cast G in Sarjeant et al. (1998) (herein track g Fig. 7B) apparently has no DDU associated. Hence, in the light of the evidence presented here, this print most probably could have been produced by a theropod.

In the original *Iguanodontipus* description (Sarjeant et al. 1998) the following diagnostic characters were considered: a narrow trackway, a long stride and low interdigital angles in prints A and G; these features should support also a theropod trackmaker.

Other authors think similarly: "either *Iguanodontipus* includes theropod tracks, or trackway parameters and some footprint features are of little use in distinguishing between large theropod and ornithopod tracks" (Dalla Vecchia et al. 2002). In addition, following Bertling et al. (2006), the name of the supposed producer should not have been used to name the ichnotaxon.

The *Iguanodontipus* ichnogenus was revised on a morphological basis and considered a valid ichnotaxon by Díaz-Martínez et al. (2015). Effectively, the outlines of *Iguanodontipus* tracks match the ornithopod footprints, but that morphology does not reflect the anatomy of the trackmaker´s foot because some of these tracks are DDSUs. So, this morphology is a consequence of a taphonomic process during the track registration and should not be considered an ichnotaxobase (Marchetti et al 2019). In our opinion, *Iguanodontipus* is a taphotaxon (cf. Lucas 2001) and for this reason, we suggest that these tracks should not be further used for comparison with either ornithopod or theropod footprints.

The loose correlation between bone and ichnological taxonomy could be frequent in other examples, such as the ichnogenus *Amblydactylus* (Sternberg 1932; Currie & Sarjeant 1979) that could probably also represent DDU example and may be theropodan in origin. Certainly, this could easily be true for other vertebrate ichnotaxa across the fossil record.

Conclusions

The Upper Jurassic succession of the Asturian Basin reveals an abundant record of theropods walking in a relatively soft to stiff and thick muddy sediment producing, in a lower level, deep detached sandstone undertracks (DDSU) showing ornithopod-like footprint morphologies. This raises up an uncomfortable questioning for palaeoichnologists about the trackmaker identification for Theropoda and Ornithopoda, when analysing a DDSU that is not associated with its track cast. Indeed, this record, viewed on as a whole, provides extensive data about the pedal kinematics and its taphonomic process, but little about the taxa census. It becomes highly probable that this problem extends to other vertebrate tracks.

There is a large complexity for the interpretation of footprints, just as seen in MUJA-4363. Depending on the horizontal plane considered, four different footprint morphologies will be seen. This means that if the track was preserved *in situ* and depending on the depth to which it was affected by current erosion on the outcrop, it could have been attributed to up four ichnotaxa and/or morphotypes produced by four different kinds of dinosaurs belonging to both Saurischia and Ornithischia.

Outline 1 would be assigned to a stegosaur; outline 2 could be considered an avian-like theropod; outline 3 would be attributed to a non-avian theropod (this is the real trackmaker) and outline 4 could be identified as a more graviportal non-avian theropod or even an ornithopod. The differences in the divarication angles of these four outlines along with the measurements taken in deep tridactyl dinosaur footprints, provide subjective values that can lead to errors.

The abundance of these peculiar deep footprints in many levels of the Lastres Formation suggests that this phenomenon could be common in other terrigenous successions of the geological record. Therefore, it seems that in deep prints, only careful studies allow an accurate interpretation of the trackmaker.

In addition, after our review of the type series of the ichnogenus *Iguanodontipus*, it seems evident that some of these footprints correspond to DDUs that were probably produced by a theropod. Although the outline matches that of ornithopod footprints, they are deep detached undertracks (DDU) and considered here to be a taphotaxon, so we do not recommend the use of this ichnogenus.

Data Availability Statement

The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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