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1        **TRACKING DINOSAURS IN COARSE-GRAINED SEDIMENTS FROM THE**  
2                    **UPPER TRIASSIC OF ARDÈCHE (SOUTHEASTERN FRANCE)**

3        LEO SZEWCZYK<sup>1,2</sup>, EMMANUELLE VENNIN<sup>1</sup>, JEAN-DAVID MOREAU<sup>1</sup>, GEORGES  
4                    GAND<sup>1</sup>, MICHEL VEROLET<sup>3</sup>, NICOLAS KLEE<sup>4</sup> AND EMMANUEL FARA<sup>1</sup>

5        <sup>1</sup>*Biogéosciences, UMR CNRS 6282, Université de Bourgogne Franche Comté, 6 Boulevard*  
6                    *Gabriel, 21000 Dijon, France*

7        <sup>2</sup>*MINES ParisTech, PSL Research University, Centre de Géosciences, 35 rue St Honoré*  
8                    *77305 Fontainebleau Cedex, France*

9                    <sup>3</sup>*Saint-Julien-du-Serre, France*

10                    <sup>4</sup>*Parc Naturel Régional des Monts d'Ardèche, Jaujac, France*

11        *email: leo.szewczyk@mines-paristech.fr*

12        *RRH: UPPER TRIASSIC DINOSAUR TRACKS IN COARSE-GRAINED SEDIMENTS*

13        *LLH: SZEWCZYK ET AL.*

14        **Abstract**

15        **Coarse-grained sediments deposited in high-energy environments are usually considered**  
16        **as unfavorable to the preservation of fossil tracks. Here we report on dinosaur**  
17        **footprints showing a good physical preservation despite being found in coarse-grained**  
18        **sandstones of alluvial origin from the Upper Triassic of Ardèche, southeastern France.**  
19        **The ichnoassemblage, dominated by *Grallator* isp., raises questions about the processes**  
20        **leading to the formation and preservation of tracks in coarse-grained sediments. The**  
21        **track-bearing surface is a medium- to coarse-grained quartz arenite that is**  
22        **microconglomeratic locally. The average grain size ranges from 0.2 to 2 mm and**  
23        **numerous pebbles are present. It is overlain by a succession of thin, intercalated layers**  
24        **of clays and silts, themselves covered by a mix of silts and coarse-grained sandstones.**

We interpret this succession as a progressive decrease in energy due to a meandering channel migration culminating in channel abandonment, followed by channel reactivation and infill by coarse-grained sediments. Sedimentological and taphonomic observations indicate that the trackmakers walked on the layer of silts and clays and their passage deformed the underlying coarse-grained sands, forming transmitted undertracks. The fine-grained layer helped record the pedal anatomy of the trackmakers and contributed to protecting the transmitted undertracks from destruction just after their formation. Overall, this suggests that the fossil footprints were preserved by abiotic processes only, the main factor being the lithological contrast between successive sedimentary layers. The exceptional preservation of tracks in coarse-grained deposits contrasts sharply with the prevailing models involving fine-grained sediments and microbial mats present in low-energy environments. This unusual phenomenon may have been relatively frequent in the Upper Triassic sandstones in Ardèche.

**Key-words:** dinosaur tracks, preservation, abandoned channel, Triassic, Geopark.

## INTRODUCTION

The formation and preservation of fossil tracks involve numerous biotic and abiotic processes. The substrate properties controlling track formation (or track registration, *sensu* Marchetti et al. 2019) include the nature of the lithology and the grain size of the surface trampled (Laporte and Behrensmeyer 1980; Allen 1997; Alcalá et al. 2014; Pérez-Lorente 2015), the sediment water saturation (Allen 1997; Gatesy et al. 1999; Milàn and Bromley 2006, 2008; Jackson et al. 2009, 2010), the lithological contrast between the different sedimentary layers deformed by the trackmaker (Laporte and Behrensmeyer 1980; Paik et al. 2001; Falkingham et al. 2011; da Silva et al. 2012; Pérez-Lorente 2015) and, potentially, the presence of

microbial mats (Marty et al. 2009; Carmona et al. 2011, 2012; Cariou et al. 2014; Carvahlo et al. 2013; Prescott et al. 2014). The shape, size and depth of the tracks are also controlled by factors linked to the trackmaker, such as anatomy, weight, speed, gait, behavior and, more generally, the force applied on the sediment by the animal (Heyler and Lessertisseur 1963; Allen 1997; Falkingham et al. 2011; Gatesy and Falkingham 2017; Marchetti et al. 2019).

The preservation of tracks reflects the balance between various processes that enhance or reduce the likelihood of the tracks being preserved (Cohen et al. 1991; Carmona et al. 2011).

After their formation, tracks usually have an estimated lifespan of hours or days at most, depending on the substrate on which they are formed (Cohen et al. 1991; Marty et al. 2009; Carmona et al. 2011). The processes impacting on whether tracks are preserved include their being infilled or buried (Paik et al. 2001; Romano and Whyte 2003; Milàn and Loope 2007; Huerta et al. 2012; Xing et al. 2015a, b), early cementation induced by microbial mats (Scott et al. 2008; Carmona et al. 2011), substrate desiccation (Cohen et al. 1991; Allen 1997), little or no reworking (Maples and Archer 1989); precipitation of evaporites (Cohen et al. 1991; Scott et al. 2010; Alcalá et al. 2014), fluids circulation and pedogenesis (Paik et al. 2001; Phillips et al. 2007; Tunik et al. 2009; Pazos et al. 2012; Cariou et al. 2014). Depending on local conditions, a single process can induce the long term preservation of tracks or on the contrary accelerate their degradation (Allen 1997; Scott et al. 2010).

Taphonomic studies show that some combinations of processes have a greater potential for track formation and preservation than others. For example, fine-grained sediments combined with a 10 to 20% water saturation appears optimal for tracks' formation (Laporte and Behrensmeyer 1980; Allen 1997; Jackson et al. 2009, 2010; Alcalá et al. 2014; Pérez-Lorente 2015). Also, the combination of fine-grained sediments and non-mineralized microbial mats that stabilize the sediments (Decho 2000; Noffke 2000; Schreiber et al. 2007; Dai et al. 2015; Davies et al. 2016), is considered as one of the most important factors. However, these mats

seem to develop only in low-energy environments such as lakes, lagoons or tidal-flats (Noffke 1998; Gerdes et al. 2000; Porada and Bouougri 2007; Marty et al. 2009; Bouton et al. 2016; Prieto-Barajas et al. 2018). Their fossil analogs, the Microbially Induced Sedimentary Structures (MISS, Noffke et al. 2001), are principally found in finely grained sediments (Porada and Bouougri 2007; Sheldon 2012; Souza Carvahlo et al. 2013; Davies et al. 2016), although some MISS can occasionally occur in medium- to coarse-grained sandstones (Prave 2002; Schieber et al. 2007; Carvahlo et al. 2013; Prescott et al. 2014; Wilmeth et al. 2014; Tu et al. 2016).

Overall, the major role played by fine-grained sediments in track formation and preservation has led many authors to suggest that coarse-grained sediments are extremely unlikely to host vertebrate fossil tracks (e.g., Laporte and Behrensmeyer 1980; Allen 1997; Carvahlo 2004; Carvahlo et al. 2013; Alcalá et al. 2014; Pérez-Lorente 2015). Although this is intuitive and generally correct, researchers usually do not indicate precisely what grain size is associated with the described ‘coarse’ sediments, relative to grain size scales for clastic sediments (Wentworth 1922). Although grain size can be coarse in several sedimentary contexts (alluvial/fluvial systems), specific track-bearing layers are nearly always finer grained (Tucker and Burchette 1977; Lockley and Conrad 1989; Carvahlo 2004) and preferentially preserved in mud-dominated floodplain sedimentary facies (Buatois and Mángano 2011). In rare exceptions tracks made in fine-grained sediments can be filled by coarse grains (up to 1 cm of diameter) that form convex hyporeliefs in sheet-flood deposits (Tucker and Burchette 1977; Moreau et al. 2012).

We report here on an exceptional dinosaur tracksite characterized by abundant footprints preserved in coarse-grained (0.2 to 2 mm) fluvial sandstones from the Upper Triassic of Ardèche (south-eastern France). This range of grain size is larger than those reported in other cases of tracks found in “coarse” sediments (Courel and Demathieu 2000; Milàn and Loope

2007; Seiler and Chan 2008; Jackson et al. 2010; Xing et al. 2015b). Our aim is to identify the biosedimentary processes that contributed to form and preserve tracks in this coarse-grained substrate. We describe the associated facies, sedimentary context and specific layers involved in the tracks' formation, to generate an ichnotaphonomical model.

## GEOLOGICAL CONTEXT

The Triassic deposits from the Ardèche region are known worldwide for their remarkable ichnological abundance and richness (Blanc 1962; Montenat 1968; Finelle 1981; Cula 1987; Gand and Demathieu 2005; Gand et al. 2007; Klein and Haubold 2007: Fig 11). These deposits are exposed along the southeastern border of the Massif Central, on the western edge of the subalpine basin (Courel et al. 1980, 1998; Razin et al. 1996). They form a 50 km long, 2 to 6 km wide strip of continental detrital sedimentary rocks with a NE-SW orientation (Fig. 1A). These deposits, dated palynologically (*Tradispora*, *Cameroporites secatus*) (Rouire et al. 1980; Elmi et al. 1996; Poli 1998), have an uncomfortable contact with the Upper Paleozoic rocks and the Hercynian basement of the Massif Central. The oldest Triassic deposits correspond to the “Formation Arkosique et Conglomératique” (Fig. 1b). They are Middle Triassic (Anisian-Ladinian) in age and contain fluvial conglomerates and sandstones with ventifacts (Durand 2006). These deposits are interpreted as having formed in braided rivers and lagoonal environments (Courel et al. 1984; Poli et al. 1994; Elmi et al. 1996). Locally, they yield halite pseudomorphs, desiccation cracks and vertebrates tracks, implying an arid climate (Evans 1911; Bourquin et al. 2006, 2007). The fossil vertebrate tracks and trackways document pseudosuchian-dominated faunas typical of the Middle Triassic (Demathieu and Samama 1968; Courel and Demathieu 1976; Gand and Demathieu 2005; Gand et al. 2007).

The Upper Triassic is represented by the “Formation Argilo-Carbonatée”, the “Formation Bariolée d’Ucel” and the “Grès Roux” (Fig. 1B). The “Formation Argilo-Carbonatée”, dated from the Ladinian-Carnian, is composed of two black argillite units interbedded with massive

dolomite beds, interpreted as having been deposited in a lagoonal setting (Courel et al. 1980, 1984; Poli et al. 1994; Elmi et al. 1996; Razin et al. 1996). The Carnian-Norian “Formation Bariolée d’Ucel” contains sandstones, microconglomerates and some argillite layers that formed in a fluvial environment (Poli et al. 1994; Razin et al. 1996; Courel et al. 1998). The sandstone beds of the “Formation Bariolée d’Ucel” yield the tracks studied here. The ichnofauna is dinosaur-dominated and has been studied extensively (Courel and Demathieu 1963, 1976, 2000; Demathieu and Samama 1968; Gand et al. 2007). The Rhaetian “Formation de la Croix Blanche” contains sandstones with flaser bedding and bivalves, and was deposited in a tidally influenced marine environment (Reineck and Wunderlich 1968; Elmi and Mouterde 1965; Elmi et al. 1996; Courel et al. 1998). These deposits mark the beginning of a marine transgression that continued until the Early Jurassic (Elmi et al. 1996; Razin et al. 1996).

The site studied here is in the town of Ucel in the Ardèche department, southeastern France. Discovered by one of us (M.V.) in 2007, this site was only briefly mentioned once in Gand et al. (2007, p.22) under the local name “La Bourzède” (misspelled “La Burzède”). It is now a new referenced geosite within the Monts d’Ardèche UNESCO Global Geopark, and is more appropriately called “Le Sartre”. Gand et al. (2007) provided a preliminary report on footprints assigned to *Grallator* isp. and to *Otozoum grandcombensis*. The site is currently being extended for public access. A detailed ichnotaxonomic analysis of the tracks from Le Sartre is on-going and will be described in detail elsewhere. At present, the ichnoassemblage is composed of more than 300 tracks among which footprints of *Grallator* isp. dominate.

## MATERIAL AND METHODS

The sedimentary facies described and depositional settings inferred are based on observations made at Le Sartre together with data obtained from the macroscopic and microscopic study of

10 lithological samples. For the purpose of facies description and taphonomical observations, six thin sections were made in substrate and track samples prior observation with an AZ100 Nikon optical microscope. We use Dott's (1984) classification of sandstones, and Wentworth's (1922) grain size classification.

After the first investigation by two of us (G.G. and M.V.) in 2007-2008, about 200 footprints were found during the first field session in 2016. Other field sessions were conducted after the exposed track-bearing surface was enlarged using heavy machinery in April and November 2019. The extension of the exposed surface revealed more than 100 additional tracks. These tracks were used to do a more detailed taphonomic study, as they have not been exposed to weathering before April 2019. The last survey was made in November 2019. All tracks were labelled and photographed, and photogrammetric reconstructions of the track were made using the Agisoft photoscan Professional software (v1.2.4). The 3D models and Digital Elevation Models (DEM) of the tracks presented in this study are available as Supplementary material.

In this paper, the track-bearing surface refers to the level on which tracks are visible today. The tracks, however, can be true tracks, undertracks or overtracks (Hitchcock 1858; Lockley 1991; Allen 1997; Marty et al. 2009; Pérez-Lorente 2015; Marty et al. 2016). The tracking surface is the layer on which the contact between the substrate and the animal's foot occurred (e.g. Pérez-Lorente 2015; Falkingham et al. 2016).

## FACIES AND DEPOSITIONAL ENVIRONMENTS OF LE SARTRE

At Le Sartre, the track-bearing surface is 50 m long and 4- to 8-m-wide and is located on top of a 7 m thick, coarse siliciclastic unit (Unit 1) that dips gently towards the SSE (Fig. 2A-B). This unit is subdivided into two parts. The basal part is 5.5 m thick, massive and made of meter-scale wide amalgamated sandstone channels amongst which decimeter-scale clayey



layers intercalate. The upper part is 1.5 m thick and made of conglomeratic layered sheet-like deposits (Fig. 2B-C). A second unit (Unit 2) starts with a 50 cm thick interval of clay- and siltstones that is overlain by a 3 m thick succession composed of meter-scale wide amalgamated sandstone channels (Fig. 2C). Five facies associations are identified in these two units and presented in Figure 3. They are numbered relative to increasing flow energy. Unit 1 is composed of three facies associations (Fa1, Fa4 and Fa5). Facies association Fa1 consists of argillite-rich lenticular deposits. It contains fine siltstones with a few mm-sized quartz grains organized in discontinuous mm-thick layers. Fa1 is locally incised by channel-shaped sandstone bodies (Fa5) and characterized by horizontally-aligned calcareous concretions (Fig. 2C). Fa5 is composed of grain-supported coarse-grained sandstones to microconglomerates forming 0.5- to 2-m-thick, 10- to 20-m-wide aggrading amalgamated lenticular bodies with erosive bases (Fig. 2B-C). They are locally interlayered with conglomerates made of pebbles up to several cm in diameter, forming 10- to 30-cm-thick matrix-supported intervals. The lenticular bodies can show faint cross-bedding and current ripples and are arranged into upward-fining successions. This Fa5 interval is overlain by 10- to 20-cm-thick, continuous tabular and stacked sandstones beds assigned to Fa4 (Fig. 2 B-C). These sandstones beds are aggrading and each of them are grain-supported with a fining-upwards trend, from 0.2 to 5 mm, with some cm-sized pebbles. The last 4 or 5 beds show a retrograding pattern indicated by successive pluri-cm scale thick lobes (Fig. 4A-B). Each lobe shows a decreasing grain size following the flow direction. Footprints associated with desiccation cracks are observed on top of this sedimentary succession, at the surface of the lobes.

These facies associations record mainly the vertical transition from a possibly high-sinuosity fluvial system (FA5) to its disconnection stage, during which the last bedload deposits were made (FA4). The fluvial system developed upon the floodplain, indicated by the presence of argillites with calcareous root concretions corresponding to paleosols and occasional small-

scale quartz layers interpreted as flooding events (Wolman and Leopold 1957; Miall 1977, 1978; Cant 1978; Cant and Walker 1978; Ramos et al. 1986; Kraus and Aslan 1993). The aggrading to prograding channel beds and sandbars are interpreted as an active, possibly high-sinuosity fluvial system (Fisk 1947; Allen 1964; Cant and Walker 1976; Ramos et al. 1986; Plint and Reading 1995; Miall 1996). The continuous aggrading tabular stacked sandstone beds and the retrograding pattern observed towards its top indicate a reduction of the flow energy (Ashley 1990) that led to channel abandonment (Allen 1964, 1965; Cant & Walker 1976; Plint and Reading 1995; Miall 1996; Collinson and Montney 2019) as indicated here by the presence of desiccation cracks. Each retrograding lobe and its composition indicate a weaken flow energy in paleocurrents that were flowing towards the ENE (Fig. 4A-B).

Unit 2 is composed of two facies associations (Fa2 and Fa3). Facies association Fa2 is subdivided into siltstones to medium-grained sandstones (Fa2a) and thin claystones (Fa2b). Fa2a contains 2- to 20-cm-thick, continuous tabular or lenticular siltstone layers showing desiccation cracks, rare halite pseudomorphs and current ripples. Scarce mm-thick discontinuous layers of fine- to medium-grained sandstones are intercalated in these siltstones. Fa2b is characterized by several 1-5 cm thick discontinuous clay drapes with desiccation cracks (Fig. 5B). This facies association is surmounted by facies association Fa3, which is also subdivided into two facies (Fa3a and Fa3b). Fa3a is formed by 5- to 25-cm-thick, 10- to 30-m-wide prograding siltstone to coarse-grained sandstone sets (Fig. 5A-B). The sets show occasional erosive bases and fining-upward successions. Fa3b contains continuous, 5- to 20-cm-thick claystones that underline prograding sets with rare desiccation cracks.

Unit 2 records a floodplain depositional environment (Fa2b and Fa3b) in which an abandoned channel was reactivated, as indicated by the presence of successive prograding sandy channels (Fa2a and Fa3a). The claystone and siltstone deposits with small current ripples and

desiccation cracks (Fig. 5B) indicate recurrent emersion and flooding episodes, respectively. The presence of claystones indicates low-energy conditions in the abandoned channel, showing its transition to an abandoned stage (Fig. 3). The progradation of the sets is indicative of channel reactivation (Wolman and Leopold 1957; Allen 1964, 1965; Plint and Reading 1995).

## ICHNOTAPHONOMY

Following the recent extension of the track-bearing surface, it currently displays two areas. The first, called the ‘weathered area’ hereafter, is dark and has been exposed and weathered over many decades. The second, called the ‘fresh area’, is light in color and has been exposed only since April 2019 only (Fig. 4A-B). The former displays the coarse-grained (0.2 to 2 mm) sediment track-bearing surface (Fa4), whereas the latter shows this surface locally covered by patches of silts and clays (Fa2) (Fig. 6A). The entire surface yields abundant tridactyl footprints of *Grallator* isp. (Fig. 2A, 4B) and comprise a typical Late Triassic *Grallator* ichnocoenosis (*sensu* Hunt and Lucas 2006, 2007; Buatois and Mángano 2011). The tridactyl morphology of *Grallator* isp. is used here as a template for assessing ichnotaphonomic features and the morphological variability of the footprints. The latter are all preserved as concave epireliefs. Despite the coarseness of the sediment, the track-bearing surface occasionally yields some footprints showing complete digit impressions, claw marks, digital pads and well-defined imprint walls (Fig. 6B-D). The occurrence of such imprints in the weathered area shows that long-term erosion did not alter their quality (Fig. 6B-D).

The fresh area preserves more ichnotaphonomic and sedimentological features. A first generation of desiccation cracks occurs on top of the coarse-grained sandstones, lined by a thin layer of clays and filled by silts (Fig. 6G). These desiccation cracks do not affect the underlying sandstones. They can be found all around the tracks but are erased within them

(Fig. 6H), indicating that the animals walked over this first generation of desiccation cracks. The thin clay- and siltstones were deformed in the footprints and displaced laterally, resulting in mm-scale displacement rims (Fig. 6H, 7A left). In some instances, these fine-grained sediments were locally injected into the underlying coarse-grained sediments. All these footprints and the surrounding sediment are covered by a new duet of clay- and siltstone layers that draped and sealed the whole surface. The entire surface was affected later by a new generation of desiccation cracks that were filled by silts and fine-grained sands, some of which formed in the overtracks (Fig. 7B). Some of these desiccation cracks are so deep that they affect the underlying coarse-grained sandstones at a depth of up to 1 cm. Although sedimentation continued, no tracks were found in the subsequent layers.

These observations on the layers and sedimentary structures provide a relative chronology that help locate the tracking surface. It is bracketed by the two sets of successive clay- and siltstones and by the two generations of desiccation cracks. The animals walked over the first set of fine-grained sediments in which they left their footprints. When preserved, these are therefore true tracks (Fig. 7A left). This implies that most of the tracks observed in the coarse-grained sandstones (Fig. 6B-D) are in fact transmitted undertracks, although a few could be penetrative undertracks. Both the thinness of the first set of clay- and siltstones and the clay injections only observed in the bottom of some tracks indicate that the latter can be interpreted as unsealed penetrative tracks (Fig. 7C).

Could this inference have been made from the weathered area only? In the absence of the fine-grained layers and their associated sedimentary structures, there is still evidence for their role in the track formation processes. The evidence consists of flaked clay coatings forming very small patches in some footprints, particularly at the digit tips and joints (Fig. 6E-F). At the bottom of some tracks, clay injections in the sandstones show the displacement of quartz grains by the clays, inducing a lack of cohesion between quartz grains (Fig. 7D-E). Lateral to

the tracks, when clays are observed in the sandstones, they only infill small pores of an undisturbed sediment. Although inconspicuous on the weathered area, these observations confirm that at least one claystone layer overlaid the coarse-grained sandstones before being trampled.

## DISCUSSION

The combined sedimentological and ichnotaphonomical observations allow us to propose a model involving several phases for track formation and preservation at the ichnosite of Le Sartre (Fig. 8). The first phases involves the deposition of the retrograding lobes corresponding to what became an abandoned channel at the top of Unit 1 (Fig. 8A-B). Each of these lobes tends to show a lateral decrease in grain size towards the ENE. After a decrease in flow energy indicated by the retrogradation pattern (Fig. 8B), the abandoned channel was covered by a clay layer corresponding to the base of Unit 2 (Fig. C). The base of Unit 2 shows several flooding and emersion episodes (Fig. 8C-F). During the emersion of the first clay layer, desiccation cracks were generated (Fig. 8D) and filled by silts during the following flooding event (Fig. 8E). Both the clay and silt layers were formed under water, respectively at low and moderate flow energy. As these deposits covered all the lobes, despite the more recent lobes being topographically higher, the water depth must have been at least several decimeters. The activity by the dinosaurs was recorded on top of the silt (Fig. 8F), deforming the clay and silt layer (Fig. 7A left) and erasing the first generation of desiccation cracks (Fig. 6H). It shows that the sediments of both the base of Unit 2 and the top of Unit 1 were soft and cohesive at that time. The collapsed walls of some tracks (Fig. 7C) and a sliding trace (Fig. 7F) located on the distal part of one of the lobes suggest that the sediment was unevenly cohesive across the site when the animal walked in the channel. The following phases recorded a new increase and a decrease in water level marked by the deposition of clayey sediments, and then another flooding with deposition of silty sediments (Fig. 8G-I). An

episode of emergence between the clayey and silt deposits was marked by deeper desiccation cracks that affected the top of Unit 1 (Fig. 8H), and some of the tracks (Fig. 7B). Sedimentation continued, eventually transitioning from a low-energy floodplain environment to a new active channel dynamic (Fig. 5) and the ichnosite was buried further down. Today the exposed full outcrop shows erosion-resistant transmitted undertracks set in the coarse-grained sandstones on the top of Unit 1 together with erosion-prone true tracks and partially-filled tracks at the base of Unit 2 (Fig. 8J). As of November 2019, only a few (fast deteriorating) true tracks and some overtracks are left on the fresh area.

Overall this model is built invoking only abiotic parameters unlike models that infer a crucial role of microbial mats in the formation and preservation of tracks, as found in many other tracksites worldwide (e.g. Carmona et al. 2011, 2012; Carvahlo et al. 2013; Cariou et al. 2014; Prescott et al. 2014; Dai et al. 2015; Davies et al. 2016). These biotic models rely on the fact that microbial mats increase the cohesiveness of the substrates on which they grow and protect the tracks after their formation by preventing their being eroded in the short-term (e.g., Cuadrado and Pizani 2007). The presence of clayey and silty layers represents an alternative mechanism that favors the formation and preservation of tracks, when placed over competent coarse-grained sediments. Therefore, it seems that this specific lithological superposition is sufficient for the formation and preservation of tracks. As shown here, the coarse-grained sediments (>1-2 mm) observed on the top of Unit 1 were cohesive enough to prevent the disappearance of the tracks thanks to the presence of clay- and siltstones layers. The sedimentation following trackway formation, dominated by fine grains, favored preservation of the tracks. Such an abiotic scenario, invoking contrasts in sediment grain size and rheology, has been proposed previously based field observations and analogic experiments (Laporte and Behrensmeyer 1980; Allen 1997; Paik et al. 2001; Milàn and Bromley 2008; Rainforth and Howard 2008; Buatois and Mángano 2011; Falkingham et al. 2011; da Silva et al. 2012;

Milner and Lockley 2016). However, to our knowledge, the outcome of these scenarios is the formation and preservation of tracks in fine-grained sediments only and mainly in overbank intervals (particularly in floodplains) within a fluvial succession (Maples and Archer 1989; Buatois et al. 1997). In addition, Lockley and Conrad (1989) and Buatois and Mángano (2011) illustrated the formation of densely tracked surfaces impressed on a muddy substrate, and cast by sand, during a subsequent flooding event. Clearly, the occurrence of footprints showing a good physical preservation in coarse-grained sediments results from an unusual combination of factors and makes Le Sartre a remarkable ichnosite. It shows that grain size can on occasion be rejected as being an adequate predictor of preservation quality for vertebrate fossil tracks, and also that microbially-driven processes may not be invariably involved in track preservation. The implication of microbial mats is a hypothesis that cannot be entirely rejected, but there is currently no evidence for it.

It is, of course, unlikely that tracks would be routinely formed and preserved in coarse-grained sediments deposited by high-energy events within dynamic environments. The intuitive notion, however, that such environments are less favorable may lead to an *a priori* bias during ichnological prospection. In this regard, this situation is somehow reminiscent of earlier debates on the preservation of tracks in eolian deposits (McKeever 1991). There are nonetheless some instances of tracks found in “coarse” sediments throughout the world (Milàn and Loope 2007; Seiler and Chan 2008; Jackson et al. 2010; Xing et al. 2015b) and in the Ardèche region (Courel and Demathieu 2000). In these cases, however, the grain sizes reported for the track-bearing surfaces (fine- to medium-grained sands) are smaller than those observed at Le Sartre (medium-grained sand to microconglomerate, >0.2-2 mm, with some pebbles up to several centimetres; Fig. 3).

Beyond the general acceptance that tracks can be formed only exceptionally in coarse sediments, most authors agree that in such cases the fidelity in which the tracks replicate

346 pedal anatomy should be low (Laporte and Behrensmeyer 1980; Lockley and Conrad 1989;  
347 Allen 1997; Carvahlo 2004; Gatesy and Falkingham 2017), or even that the limited  
348 cohesiveness of the substrate makes it impossible to preserve anatomical features such as digit  
349 length, digital pads and claw marks (Alcalá et al. 2014; Pérez-Lorente 2015). Regardless of  
350 grain size, the high number of factors that control track formation and, the complex  
351 interactions among them imply that some tracks will never, or barely, show any anatomical  
352 details, even immediately following their formation. Gatesy and Falkingham (2017) showed  
353 that although such tracks provide almost no information about their maker's anatomy, their  
354 morphology could really be in the exact state and shape in which they were formed. In that  
355 perspective, the recent critical reviews on terminology and preservation scales by Belvedere  
356 and Farlow (2016), Gatesy and Falkingham (2017), Marchetti (2018) and Marchetti et al.  
357 (2019) represent much-awaited contributions for clarifying communication among vertebrate  
358 ichnologists.

359 One of the interesting characteristics of Le Sartre is that many tracks have a high fidelity to  
360 their morphology at the end of their registration. The tracks exhibit a high physical (P-)  
361 preservation *sensu* Marchetti et al. (2019) (Fig. 7C; 7F) but also good M-preservation in some  
362 instances (presence of claw marks and digital pads; Fig. 6C). Another interesting  
363 characteristic of this site is that the first survey of the surface was made in 2016-2017 and two  
364 others in 2019 after the site extension. The tracks found after widening the site had not been  
365 exposed to weathering. This tracksite thus currently presents tracks in two states of  
366 preservation. The best preserved transmitted undertracks on the weathered part of the study  
367 surface still occur in a good state of physical preservation (Fig. 6B-C). While these  
368 remarkable transmitted undertracks admittedly do not meet the optimal criteria for  
369 ichnotaxonomy as proposed by Marchetti et al. (2019), the walls are well defined, some  
370 digital pads are present, and a few claw marks and drag marks can be observed. One might



371 therefore give these transmitted undertracks an M-preservation score of 2.0 according to  
372 Marchetti et al.'s (2019) scale. This is unexpected considering the coarseness of the sediment  
373 in which they are set and the weathering they suffered. Some of the true tracks and  
374 transmitted undertracks found on the fresh part of the track-bearing surface can be attributed  
375 the same M-preservation score. While weathering has little effect on the score of transmitted  
376 undertracks, the rare true tracks show a low preservation potential, or P-preservation (Fig.  
377 7A), as they are rapidly destroyed because the thin clay- and siltstones layers are easily  
378 eroded. This demonstrates once again that in sediments like the ones examined here true  
379 tracks tend to become fragile structures once unearthed (Lockley and Rice 1990; Lockley  
380 1991; Brand and Kramer 1996) and that they can disappear in a few weeks. However, the  
381 former presence of the true tracks is alluded to by the silt and clay injections preserved in the  
382 underlying sandstones and conglomerates that persist longer (and are still evident at present).

383 The dinosaur footprints from Le Sartre can also be discussed at the scale of the depositional  
384 sequence. As proposed by some authors (e.g. Buffard and Demathieu 1969; Tucker and  
385 Burchette 1977; Lockley and Conrad 1989; Reading 1996), the formation and preservation of  
386 tracks in fluvial environments is preferentially observed on top of flood deposited successions  
387 in overbank settings or in abandoned or inactive channel deposits. Our observations are  
388 generally consistent with these conclusions as the tracks from Le Sartre are within a flood-  
389 deposited succession (Fig. 2C) in an abandoned channel (Unit 2, Fig. 3). Although clay drapes  
390 are considered to have played a role in the track preservation after they were formed, we show  
391 here that these drapes can also be involved in the processes responsible for tracks formation.  
392 More precisely, true tracks are set in flood deposits, but the transmitted undertracks are set in  
393 coarse-grained sediments representing active channel deposits. Lockley and Conrad (1989)  
394 mentioned rare examples of tracks from coarse-grained proximal fluvial deposits (with low  
395 preservation quality) and noted that tracks are much more frequently encountered in distal

floodplain environments (see also Buatois and Mángano 2011). At Le Sartre, the very abrupt change in sedimentary regime between the high-energy channel beds, the abandoned channel and the overbank settings allowed the formation and preservation of tracks in an environment considered hitherto by some authors as hostile to tracks formation (e.g., Carvahlo et al. 2013).

## CONCLUSION

The ichnosite of Le Sartre is outstanding as most of its dinosaur footprints are set in a substrate the grain size of which is above the range identified as being favourable to the formation and preservation of fossil tracks. The associated ichnotaphonomic model suggests that dinosaur footprints were preserved by abiotic processes only, the main factor being the lithological contrast between successive sedimentary layers. In turn, this is at odds with the most frequent models that rely heavily on fine-grained sediments, mostly muddy and microbial mats present in low-energy environments.

The tracks from Le Sartre were formed on the coarse-grained bed of an abandoned channel through clay- and siltstones that were being deposited during the channel filling stage. Most of the tracks are transmitted undertracks formed in coarse-grained sands deformed with the clay and silt layers on which the dinosaurs walked. The difference in competency and plasticity between sand, silt and clay influenced the tracks' formation and further drapings by clay and silts enabled their preservation. Weathering likely eroded true tracks over a few weeks, whereas the transmitted undertracks have proved to be more resistant at le Sartre. Current investigations of the Upper Triassic sandstones from Ardèche suggest that such an unusual phenomenon might be present in other, nearby, localities. Some transmitted undertracks preserved in coarse-grained sediments retain sufficient key anatomical features and will lend themselves to at least generic-level ichnotaxonomic assignments in future works.

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771 CAPTIONS

772 FIG. 1 – Geographical and geological context of the Le Sartre track-bearing locality. **A)**  
 773 Simplified geological map of the area based on the 1:50000 Aubenas geological map (Kerrien  
 774 et al. 1989). **B)** Middle and Upper Triassic lithostratigraphic units for the Ucel area. Based on  
 775 Rouire et al. 1980, Elmi et al. 1996 and Courel et al. 1998.

776 FIG. 2 – Sedimentological setting of the Le Sartre outcrop. **A)** View of the track-bearing  
 777 surface and upper layers (Unit2). **B)** Stratigraphic succession under the track-bearing surface  
 778 (Unit 1). **C)** Lithological log of the outcrop defining Units 1 and 2 (see arrowhead in **B** for  
 779 position).

780 FIG. 3 – Facies association descriptions with the main diagnostic features, depositional  
 781 environments and corresponding illustrations of the outcrop at Le Sartre.

782 FIG. 4 – Sedimentary structures of the track-bearing surface (Fa4). **A)** View of the successive  
 783 centimeter-thick lobes indicating the flow direction (dashed lines indicate the limits of each  
 784 lobe; the black arrow indicates flow direction toward ENE). **B)** Detail of two overlapping  
 785 lobes with proximo-distal grain size variation from microconglomerate to medium-grained  
 786 sandstones.

787 FIG. 5 – Sedimentological logs of the deposits covering the track-bearing surface. **A)**  
788 Panorama of the prograding deposits in an overbank setting. Black arrow indicates flow  
789 direction toward the main channel depocenter. **B)** Detailed sedimentological logs illustrating  
790 the clayey and siltstone layers (see **A** for positions).

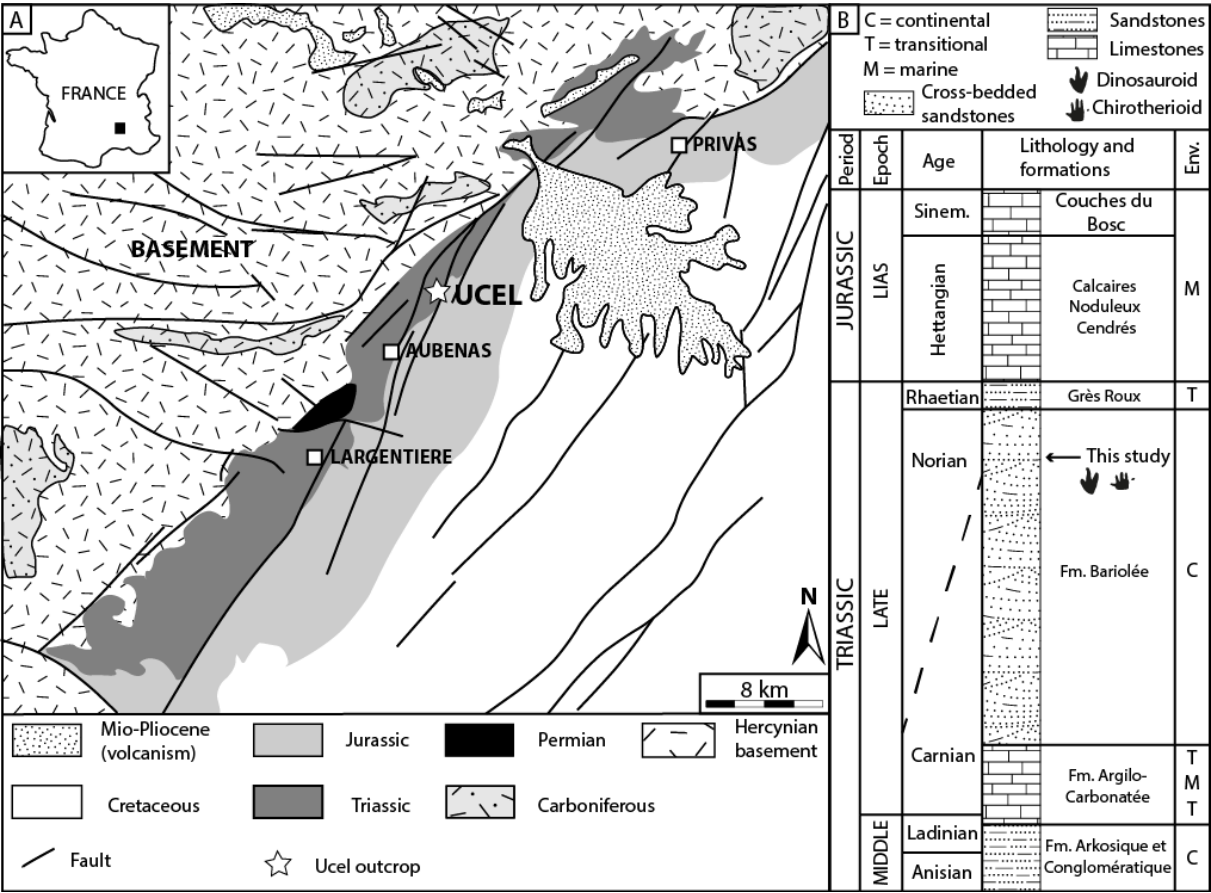
791 FIG. 6 – Sedimentological and taphonomic features of the track-bearing surface. **A)** Part of  
792 the fresh surface showing the coarse-grained sandstones with pebbles (Fa4) (black arrow) and  
793 desiccation cracks (white arrow) filled by clay and silt (Fa2) (red arrow). **B)** Three-toed  
794 footprint (undertrack) (track 44) showing claw marks preserved on the weathered part of the  
795 slab. **C)** Undertrack of a *Grallator* isp. right footprint preserved in very coarse-grained  
796 conglomerate (Fa4). **D)** Pebbles (0.5-4cm long) pushed into the substrate at the bottom and  
797 along the wall base of a three-toed footprint (undertrack) (track 80). **E)** Gravels impressed  
798 into the floor of the tracks and clay coatings infilling the undertrack (track 55). **F)**  
799 Interpretative sketch of Fig. 6E. Black arrows indicate gravels impressed into the track and  
800 red arrow indicates a clay coating. **G)** Close-up view of a first generation desiccation crack.  
801 Cracks occurred in clays (Fa2b; black arrows) and were infilled by silty sediments (Fa2a)  
802 (white arrows). The clays rest on conglomerate to sand-rich deposits (Fa4). Note how cracks  
803 deviate to pass around the gravels. **H)** Large footprint with displacement rim deforming both  
804 clay and silt layers (Fa2) and affecting the desiccation cracks.

805 FIG. 7 – Illustrations of the processes involved in track formation and preservation. **A)** True  
806 track of a three-toed dinosaur foot (track 298) on a silty layer (Fa2a) (white arrow) and  
807 deforming the the silty layer itself, the underlying clay (Fa2b) (red arrow) and sand deposits  
808 (Fa4) in April 2019 (left) and preservation state of the track in November 2019 (right). Note  
809 that all the clay drapes have been eroded leaving only the sandstone surface. **B)** Three-toed  
810 footprint (track 319) filled by clayey and silty (Fa2) sediments showing second generation  
811 desiccation cracks infilled by silts (white arrow). **C)** Three-toed footprint (track 22) showing

that sometimes the dinosaur feet punched through the different layers and that the sediment was cohesive enough not to collapse after the dinosaur withdrew its foot. **D-E)** Vertical thin section and interpretative sketch: below the track bottom, clays show a variable lateral concentration with clay injections. Under the tracks, notice the matrix-supported quartz grains (left) and laterally, grain-supported quartz grains with very little clay under the undisturbed part of the surface (right). **F)** Track of a three-toed footprint showing that the dinosaur slipped (track 226) (white arrow indicates movement direction). White dashed lines highlight sediment that was displaced by the movement and formed a small displacement rim.

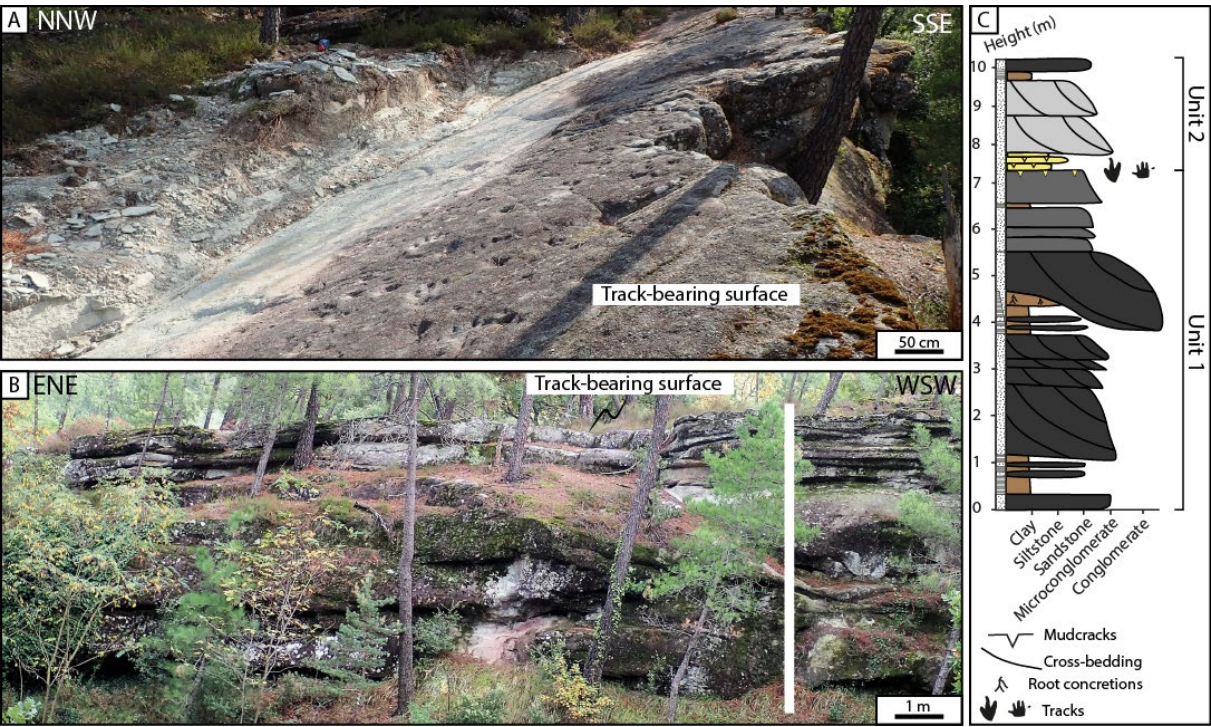
FIG. 8 – Ichnotaphonomic model of track formation at Le Sartre. Water flow is from left to right. **A-F)** Formation of the track-bearing surface. **F)** Track formation. **G-I)** Early phases of the preservation processes. **J)** Current state of the track-bearing surface after differential weathering.

834      FIGURE 1




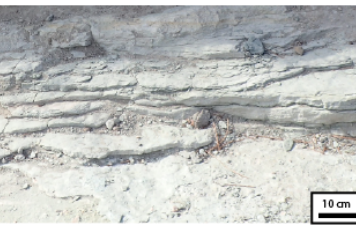


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836      FIGURE 2

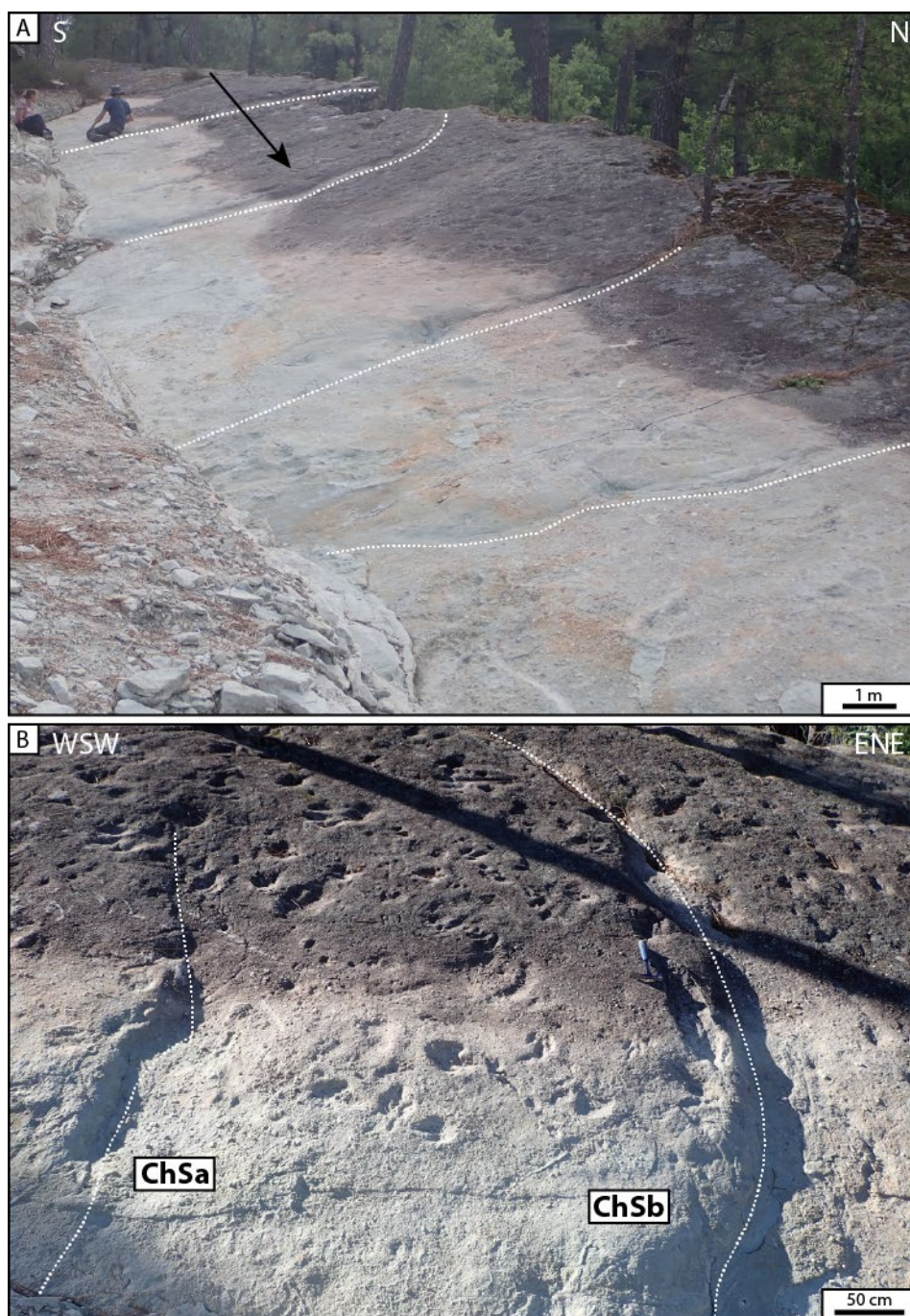


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Facies associations	Beddings, sedimentary structures, granulometry and diagnostic components	Paleoenvironments and main references	Illustrations
<p><b>Fa1</b></p> <p>Argillites</p>	<p>1-1.5 m thick, 2-3 m wide lens. Indurated argillites with a prism-like breaking affected by calcareous root concretions. Very fine (&lt;2 µm) grain size with a few millimeter-sized quartz grains organized in mm thick discontinuous layers.</p>	<p>Floodplain deposits with occasional paleosols. Occasional very low energy flooding.</p> <p>Wolman &amp; Leopold 1957 Miall 1977,1978 Cant 1978 Cant &amp; Walker 1978 Ramos et al. 1986 Kraus &amp; Aslan 1993 Paim 1995</p>	 <p>10 cm</p>
<p><b>Fa2</b></p> <p>Silts to medium sandstones with thin clay layers.</p>	<p><b>Fa2a:</b> 2-20 cm thick, continuous tabular to lenticular silts layers. Quartz arenite with cm to dm current ripples and desiccation cracks infilling with rare halite pseudomorphs. Occasional medium sandstones mm thick layers. <b>Fa2b:</b> 1-5 cm thick discontinuous clay drapes with desiccation cracks.</p>	<p>Shallow to very shallow disconnected channel deposits.</p> <p>Wolman &amp; Leopold 1957 Allen 1964, 1965 Plint &amp; Reading 1995</p>	 <p>10 cm</p>
<p><b>Fa3</b></p> <p>Silts to coarse grain-supported sandstones and clay layers.</p>	<p><b>Fa3a:</b> 5-25 cm thick, 10-30 m wide prograding sets composed of moderately sorted quartz arenite. Occasional erosive bases, upward fining successions with grain sizes between 0.2 and 2 mm. <b>Fa3b:</b> continuous 5-20 cm thick clay layers.</p>	<p>Channel reactivation with low-energy flooding in an abandoned channel or overbank deposits.</p> <p>Allen 1964, 1965 Cant &amp; Walker 1976 Plint &amp; Reading 1995</p>	 <p>50 cm</p>
<p><b>Fa4</b></p> <p>Medium to coarse grain-supported sandstones.</p>	<p>10-20 cm thick, continuous tabular stacked beds of moderately sorted quartz arenite. Upward fining sequences with grain sizes between 0.2 and 5 mm and pebbles up to several cm. Aggrading to retrograding pattern with pluricentimeter scale prograding lobes on the top succession affected by vertebrate tracks and mudcracks. Progradation lobes show a lateral variation of granulometry from coarse to microconglomeratic sandstones in the proximal part to medium low cohesive sandstones in the distal part.</p>	<p>Shallow channel bed aggradation and terminal plugging inducing channel abandonment.</p> <p>Allen 1964, 1965 Cant &amp; Walker 1976 Plint &amp; Reading 1995 Miall 1996</p>	 <p>10 cm</p>
<p><b>Fa5</b></p> <p>Coarse grain-supported sandstones to microconglomerates, with matrix-supported conglomeratic intervals.</p>	<p>0.5-2 m thick, 10-20 m wide amalgamated aggrading lenticular bodies with erosive bases. Poorly sorted quartz arenite with current ripples and faint cross beddings, upward fining successions with grain sizes between 0.2 and 8 mm, and up to several cm pebbles.</p>	<p>Meandering system channel beds and sandbars.</p> <p>Fisk 1947 Allen 1964 Cant &amp; Walker 1976 Ramos et al. 1986 Plint &amp; Reading 1995</p>	 <p>20 cm</p>

841      FIGURE 4



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847 FIGURE 5

