

PALAEOENVIRONMENT AND PALAEOECOLOGY OF THE LATE ALBIAN – EARLY CENOMANIAN THEROPOD-ORNITHOPOD ICHNOASSEMBLAGE OF THE DJEBEL AZZEDDINE TRACKSITE, OULED NAIL MOUNTAINS, ALGERIA

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ABSTRACT

This study examines the Djebel Azzeddine tracksite, in Algeria, providing insights into the palaeoenvironment and the interaction of footprints with litho-, bio- and ichnofacies. The tracksite offers valuable insights into the emersion history of the eastern part of the Saharan Atlas basin, representing the first evidence of widespread emersions in the region after the 'mid'-Cretaceous transgression. It underscores the role of tidal flats as migration routes for dinosaurs during lowstand periods, facilitating exchanges between different land areas in the Saharan Atlas. Furthermore, the coexistence of dinosaurs and invertebrates, particularly worms and crustaceans in such a tidal setting, reflects a complex ecosystem. A comprehensive ichnological and sedimentological analysis presents a genetic model for the tracksite's development, emphasising the significance of water content, sediment firmness, and environmental conditions in preserving dinosaur tracks.

Keywords - Dinosaur footprints - Ichnofacies - Emersions - Tidal flats - Genetic model - Saharan Atlas.

PALÉOENVIRONNEMENT ET PALÉOÉCOLOGIE DE L'ICHNOASSEMBLAGE DES THÉROPODES-ORNITHOPODES DE L'ALBIEN SUPÉRIEUR – CÉNOMANIEN INFÉRIEUR DE L'ICHNOSITE DU DJEBEL AZZEDDINE, MONTS DES OULED NAÏL, ALGERIE

RÉSUMÉ

Cette étude examine l'ichnosite de Djebel Azzeddine en Algérie, offrant des perspectives sur le paléoenvironnement et l'interaction des empreintes avec les litho-, bio- et ichnofaciès. Le site fournit des informations précieuses sur l'histoire de l'émersion de la partie orientale du

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bassin de l'Atlas saharien, représentant la première preuve d'émersions généralisées dans la région après la transgression du 'Crétacé moyen'. Il souligne le rôle des replats de marées en tant que voies de migration pour les dinosaures pendant les périodes de bas niveau marin, facilitant les échanges entre différentes zones terrestres dans l'Atlas saharien. De plus, la coexistence de dinosaures et d'invertébrés, en particulier de vers et de crustacés, dans un tel environnement intertidal reflète un écosystème complexe. L'analyse ichnologique et sédimentologique présente un modèle génétique pour le développement de l'ichnosite, mettant en évidence l'importance de la teneur en eau, de la fermeté des sédiments et des conditions environnementales dans la préservation des empreintes de dinosaures.

Mots-clés - Empreintes de Dinosaures - Ichnofaciès - Emersions - Replats de marées - Modèle génétique - Atlas saharien.

I- INTRODUCTION

More than twenty dinosaur tracksites and megatracksites are known in the eastern and central parts of the Algerian Saharan Atlas Range (Ouled Nail and Djebel Amour Mountains, respectively). They have long been considered as Valanginian to Cenomanian in age (Mahboubi *et al.*, 2007; Regagba *et al.*, 2007; Bessedik *et al.*, 2008, 2020; Mammeri *et al.*, 2011, 2020; Mammeri, 2018). The recent discovery of brachiopod levels from the track-bearing series of the El Bayadh area (Djebel Amour Mountains) allowed attributing numerous sites to the Late Jurassic (Mahboubi *et al.*, 2021, 2023).

In 1880, dinosaur tracks were first discovered in Algeria and Africa within the Cenomanian series of the Ouled Nail Mountains, specifically at Djebel Boukahil in the vicinity of Amoura village (Le Mesle and Péron, 1880). Amoura footprints are the first dinosaur remains discovered in Africa, and the third tracksite found worldwide after the famous site of Connecticut, USA (Hitchcock, 1836) and another one in Colombia (Dagenhardt, 1840).

Le Mesle and Péron (1880) considered these ichnites as traces of giant birds. Ten years later, Gaudry (1890) attributed these 24 cm-long footprints to theropods. A meticulous study of the site was carried out by Bellair and De Lapparent (1948) who identified a total of 140 tracks, divided into two categories, two of them considered as pes prints and the third as manus prints. These tracks were

at two sites (Amoura village and Amoura gorge) and were initially attributed by these authors to *Struthiomimus*. However, a revision conducted by Haubold (1971) led to their reassignment to the new ichnospecies *Columbosauripus amourensis*. It was emphasized that *Struthiomimus* (= *Ornithomimus*) is a characteristic ornithomimid of North America, unknown in Africa, whereas the Amoura ichnites were produced by individuals belonging to Coelurosauria.

A third site (Amoura Gaada) was discovered in the same locality, stratigraphically situated 20 meters below the first tracksite (Mammeri *et al.*, 2011). It consists of around thirty tridactyl footprints of large theropods, which have been compared to the ichnogenera *Megalosauropus* and *Megalosauripus*, and attributed to representatives of Coelurosauria.

Recently, the fourth dinosaur tracksite (Djebel Azzeddine) of the Ouled Nail Mountains was discovered, having a nearly identical age (Naimi *et al.*, 2023). This site is located near Bou Saada, approximately 130 km to the NNE of Amoura. Two morphotypes have been identified. The first one (MT1) is attributed to small theropods and compared to the ichnogenus *Grallator*, while the second one (MT2) is assigned to small ornithopods. These latter ones represent the first ornithischian remains discovered in Algeria.

After the descriptive and ichnotaxonomic study presented in the initial work, this paper aims

to provide insight into the palaeoenvironmental context and the palaeoecology of the tracksite and the relationship between the footprints and lithofacies, biofacies and ichnofacies. It also presents a genetic model concerning the site's development.

II- GEOLOGICAL SETTING AND LOCALITY

The Algerian Alpine chain is composed of two main systems: (i) the Tell to the north and (ii) the Atlas to the south (fig. 1A). The latter is subdivided into many components, i.e., Saharan Atlas, Zibane Mountains, Aures Massif, Tebessa-Nementcha-Negrine Mountains, Tlemcen domain and Oran Meseta (Kazi-Tani, 1986; Aït

Ouali, 1991; Naimi, 2022). The Saharan Atlas which is the focus of the present work is an intracratonic mountain belt, which comprises the Ksour Mountains to the west, the Djebel Amour Mountains in the center, and the Ouled Nail Mountains to the east, between the High Atlas to the west and the Zibane Mountains to the east (Ritter, 1902; Naimi *et al.*, 2021a).

The studied section is located at Djebel Azzeddine (35°12'23" N; 4°09'36" E), near Bou Saada in the Ouled Nail Mountains (Northeastern termination of the Saharan Atlas). The geological series of Djebel Azzeddine is dominated by Late Albian to Early Cenomanian marine carbonate deposits (fig. 1B). It has been subdivided into

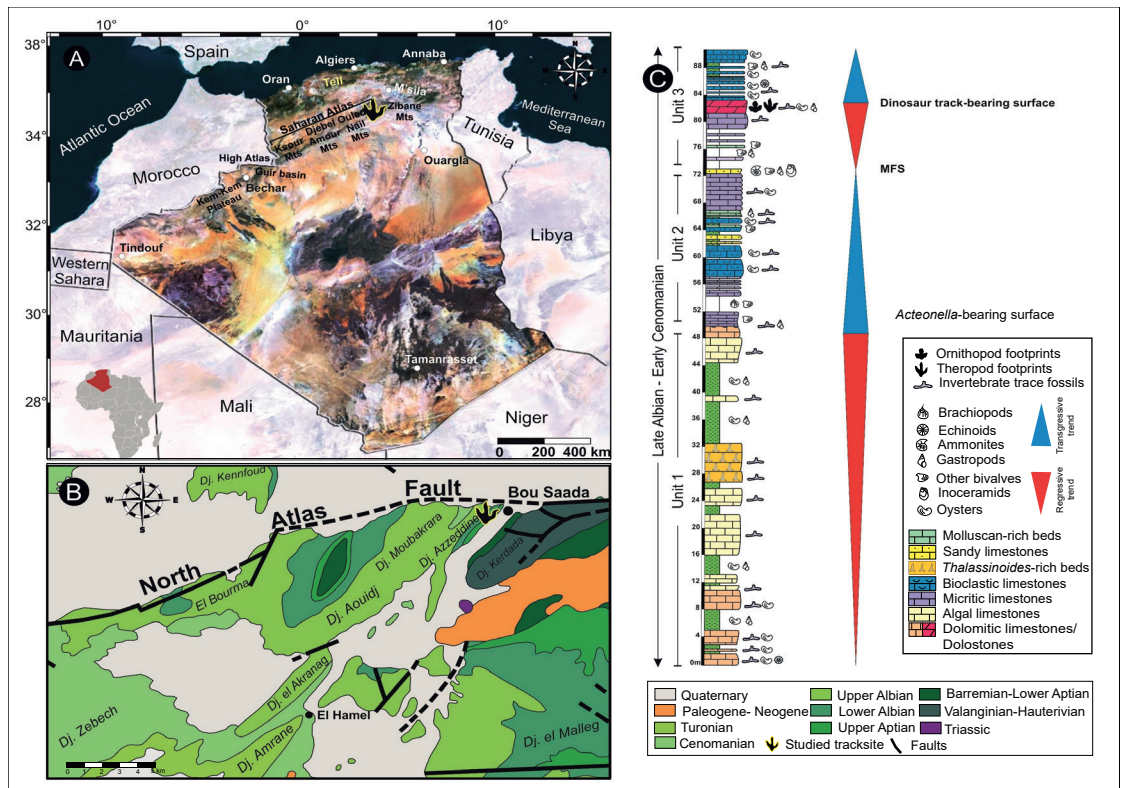


Fig. 1 - A) Satellite image showing the location of the studied tracksite in Algeria; B) Geological map of the study area showing the location of the studied Djebel Azzeddine tracksite; C) Lithostratigraphic column of the Djebel Azzeddine section.

A) Image satellite montrant la localisation de l'ichnosite en Algérie ; B) Carte géologique de la région d'étude montrant la localisation de l'ichnosite du Djebel Azzeddine ; C) Colonne lithostratigraphique de la coupe du Djebel Azzeddine.

three informal units (Naimi and Cherif, 2021) (fig. 1C). The series starts with very shallow marine oyster and echinoid-rich carbonates as well as abundant *Lofer* cyclothems and *Thalassinoides paradoxicus*-bearing levels (Unit 1: Marlstones-algal bioturbated limestones). These deposits are terminated with a hardground characterized by condensed gastropods (*Acteonella delgadoi*) at this section and by abundant borings (*Trypanites*, *Gastrochaenolites* and *Petroxestes pera*), as well as encrusted oysters belonging to *Ostrea falco* at Djebel Arar section, located 6 km to the northwest (Naimi *et al.*, 2021b).

Deeper deposits (Unit 2: Lower marl-stones-shelly limestones) overlay the previous strata, with thick marly levels, interbedded by bivalve and gastropod shell-beds. The maximum flooding surface (MFS) is marked by condensed large ammonites belonging to *Pervinqueria pricei* and *Engonoceras* sp. (Naimi *et al.*, submitted).

The upper part of the section (Unit 3: Upper marlstones-shelly limestones) is characterised by shallow marine deposits. The track-bearing dolostone bed is located in the middle part of the latter.

It should be noted that the North Atlas Fault crosses the Mount Djebel Azzeddine, which separates the Saharan Atlas into two zones: (i) sub-tabular Pre-Atlas zone to the north and (ii) folded Atlas zone (or Saharan Atlas *sensu stricto*) to the south.

III- RESULTS

III.1- Section

Observations

The track-bearing surface terminates at 2 to 3-m-thick hard, oxidised, and brownish to reddish dolostone bed (pl. 1A–D). It consists of an iron-stained emersion surface, unconfor-

mably overlain by bioclastic limestones and marls (fig. 2). The track-bearing surface also encompasses *Skolithos* and *Thalassinoides* burrows (pl. 1D), bivalve and gastropod shells, as well as some calcite-filled vugs.

The overlying bioclastic limestones correspond to biodetrital facies composed of complete or fragmentary oyster, pectinid and gastropod shells, randomly oriented parallel to bedding (pl. 1E). They also display hummocky cross-stratification (HCS) and swaley cross-stratification (SCS). These limestones are interbedded by thin levels of whitish to light grey, soft marlstones, containing bivalves and gastropods. The contact between dolostone and bioclastic limestone is marked by an irregular surface with relief of up to 10 cm. At this level, dinosaur ichnites were observed.

INTERPRETATION

Djebel Azzeddine section presents fifteen facies types (FT1 to FT15) (Naimi and Cherif, 2021). Sedimentological, ichnological and palaeontological data suggest a marginal-littoral with mixed tide/storm energy, indicated also by the co-occurrence of marine bivalves and gastropod fauna as well as dinosaur ichnites. The dolostones are interpreted as deposited within a very shallow marine environment, influenced by tides and storms. The presence of dissolution vugs and oxidised dolostone evidences a subaerial exposure.

The overlying bioclastic limestones refer to a lower shoreface environment, between fair weather and storm wave bases, based on the distribution of molluscan shells and sedimentological features indicating tempestite deposits.

III.2- Tracksite description and ichnofabric analysis

The studied tracksite comprises two surfaces of approximately 18 m² (6 x 3 m) and 7.5 m² (3 x 2.5 m) outcropping at the summit of the Djebel Azzeddine hill. The foot-prints are poorly pre-

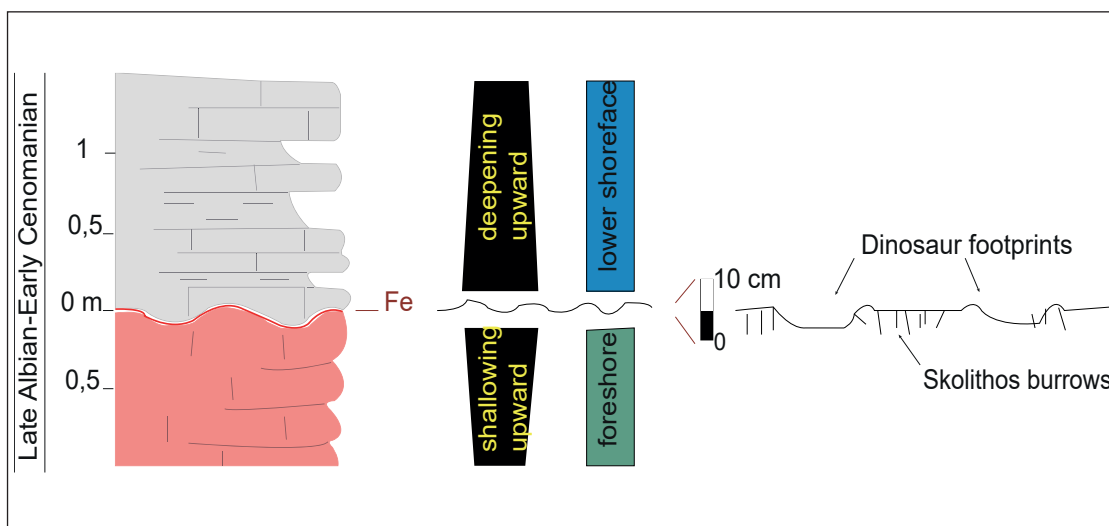


Fig. 2 - Detailed stratigraphic log observed at the track-bearing interval.

Log stratigraphique détaillé de l'intervalle à ichnites de dinosaures.

served, and most occur as rounded depressions (pl. 1B). Better preserved tracks include tridactyl impressions (pl. 1C), preserved as concave epireliefs (epichnia). They are 10 to 30 mm deep, 9 to 22 mm long and 12 to 17 mm wide. They have steep margins with raised rims.

A detailed ichnological analysis allowed for the categorization into two morphotypes, attributed respectively to small-sized theropods (Grallatoridae) and small-sized ornithopods (Naimi *et al.*, 2023).

The surface preserves abundant epichnial *Skolithos* burrows, measuring 2 to 13 mm in width, characterised by circular to slightly oval apertures at the bedding plan surface (pl. 1D). These burrows penetrate entirely the rock and are filled with a brownish sandy material as well as small recrystallised bioclasts.

This dinosaur-*Skolithos* ichnofabric represents intense bioturbation and dinoturbation in very shallow marine carbonate deposits. It forms dense assemblages resembling Early Paleozoic *Skolithos* pipe-rocks. *Skolithos* burrows are closely spaced. Due to the different lithologies, the boundary between the host dolomitic rock and

Skolithos sandy fillings is clearly visible. The ichnofabric index is 4 (ii4, most bioturbated sediment). This index proposed by Droser and Bottjer (1986) is a method used to quantify the degree of bioturbation in a sedimentary facies and involves grading the amount of ichnological activity on a scale of 1 to 6. Common sedimentary deformation on the track-bearing surface is interpreted as dinoturbation. The latter consists of generally slumped to homogenised bedding.

Dinosaur footprints and *Skolithos* burrows are associated with scarce *Thalassinoides* traces consisting of horizontal tunnels inclined to vertical shafts, with diameters ranging from 10 to 30 mm. They are filled with the same material as that of *Skolithos* burrows.

IV- DISCUSSION

Tidal flats favoured the creation and preservation of vertebrate tracks and track-ways. These areas recorded earlier archosaurs and other reptilian footprints from the Early to Mid-Triassic of Central Europe, as well as dinosaur ichnites from the Jurassic of Europe, the Early Cretaceous of the Mediterranean Platform margin and the Late Cretaceous of North Africa and

the Mediterranean Carbonate Platform (Meyer, 1993 ; Dalla Vecchia, 1994, 2008 ; Meyer and Mezga, 2000 ; Gianolla *et al.*, 2000 ; Baucon and Avanzini, 2008; Marty, 2008).

Numerous dinosaur tracksites and mega-tracksites were reported from carbonate tidal flats, especially in mud-cracked biolaminates (e.g., Marty, 2008). They led to focus on the bathymetry and palaeogeography of these tracksites. At the Djebel Azzeddine tracksite, footprints made up a theropod-ornithopod ichnocoenosis in tidal flat carbonate deposits. These track associations are also known from other North African synchronous deposits, such as the terrestrial detrital deposits of the Kem-Kem Plateau further to the southwest (Ibrahim *et al.*, 2014). The presence of dinosaur tracks in the Djebel Azzeddine section constitutes the first evidence of periods of widespread emersions in the eastern part of the Saharan Atlas basin after the 'Mid'-Cretaceous transgression. In the lower part of the section, and before the MFS indicated by a *Pervinquieria*-condensed surface, short emersion phases were individualised based on paleosols and loferitic breccias (Naimi and Cherif, 2021). This subaerial exposure recorded in the Djebel Azzeddine section suggests the existence of a narrow isthmus attached to the emerged area where dinosaurs probably migrated. However, the extension of this putative isthmus remains unknown. Djebel Azzeddine dinosaurs lived along coastal zones and used them most probably as migration highways, in which theropods, ornithopods and sauropods followed a general SW-NE direction. Such direction has been concluded depending on recorded ichnites from synchronous deposits from the central areas of the Saharan Atlas located further to the west (e.g., Mahboubi *et al.*, 2007; Bessedik *et al.*, 2008). These migration routes consist of the Djebel Amour and Ouled Nail sub-basins, characterised by the striking absence of dinosaur skeletal remains and the abundance of their footprints. On the other hand, the typical habitat of the dinosaur trackmakers is terrestrial fluvial environments of the Ksour Mountains,

Guir basin and Kem-Kem Plateau that yielded extremely rich skeletal remains (fig. 1A).

The tidal flats formed periodic bridges between islands and old massifs, allowing dinosaur migrations and interchanges between the different exposed land areas of the Saharan Atlas during lowstand periods. The same case was recorded in Northern Switzerland, where a carbonate platform seems to have formed a bridge between the Central and the Rhenish massifs (Marty, 2008).

Studied ichnites are oriented SE/ESE (Naimi *et al.*, 2023). This indicates that theropods and ornithopods travelled, possibly at the same time, towards land. The displacement of dinosaurs from the sea may have been possible during the low tide, characterised by deposition of a mud layer, filling *Skolithos* burrows and burying the ichnites. The presence of bioclasts could be linked to storm events. However, actuopaleontological experiments carried out in the carbonate tidal flats south of the Arabian Gulf in the United Arab Emirates, using the modern lizard *Iguana* to produce footprints (Diedrich and Gardner, 2004; Diedrich, 2005), showed that storm floods destroyed the tracks immediately. In contrast, the rising tides typically arrive smoothly and immediately cover the tracks and the actively stabilised algal mats with a millimetre thick layer of fresh sediment that adheres directly to the mat surface.

On old and recent tidal flats, the accumulation rate is generally between 0.07 and 2 mm/y (e.g., Marty, 2008). This allows us to consider that the track-bearing interval was formed in a few thousand years. Also, we think that the bioclasts were formed in a deeper environment (i.e., shoreface) and transported later by each new tide that rises across the northern Ouled Nail coast.

On the other hand, the sandy material found in *Skolithos* burrows suggests a dual marine-terrestrial alimentation source. During this period, continental environments were primarily

occupied by fluvial-deltaic deposits of the *Continental Intercalaire* series dating from the Early Cretaceous. Apart from the migration theory, it is highly likely that the presence of carnivorous theropods in this tidal flat indicates their food search, especially given the abundant invertebrate fauna.

The high degree of bioturbation by the *Skolithos* suspension-feeding tracemakers reflects well-developed colonisation windows (Desjardins *et al.*, 2012). Disruption of the modern stabilised tidal flat surfaces may occur at low tide through bioturbation by browsing and grazing by epifaunal feeding or by burrowing infaunal organisms (Kvale *et al.*, 2001). Theropods in a similar context from the Late Jurassic of Portugal moved toward the coast to feed on fish, invertebrates and other vertebrates exposed on the tidal surface (Razzolini *et al.*, 2016). Farlow (1993) and Moreno *et al.* (2012) indicated that theropods were solitary hunters, which is consistent with the behaviour of predators.

In recent tidal flats, such a co-occurrence of vertebrates and worms (*Skolithos* tracemakers), as well as crustaceans (*Thalassinoides* producers), has been reported in Sri Lanka (Balasuriya, 2018), where epibenthic organisms (or epifauna) living on the mud include decapod crustaceans, worms, bivalves (pectinids and oysters), echinoderms, wading birds and shorebirds. We note that in such a setting, the invertebrates provide a food source for wading birds (Miththapala, 2013).

Within tide-dominated settings, intense bioturbation by decapods and polychaetes was observed in both mud flats (Reineck and Singh, 1980) and along the margins of tidal cracks dissecting mat-grounds (Baucon, 2008).

The track preservation occurred most probably in exposed bars in a tidal-channel environment. This context preserves randomly oriented isolated footprints (Carvalho, 2004).

The latter is always associated with fluidisation structures and present superficial colour stains (red in the case of the studied tracksite). This fluidisation around the footprints results from a dinostatic pressure in water-saturated and low cohesive sediments (Carvalho, 1994). This preservational character indicates a behavioural response to a soft substrate.

The integration of ichnological, palaeontological, and sedimentological data enables us to present a genetic model for the development of the Djebel Azzeddine tracksite (fig. 3):

(i) Colonisation of substrate by worms, crustaceans, bivalves and gastropods in a subtidal to lower intertidal environment (fig. 3a);

(ii) Subaerial exposure, which led to the formation of dissolution vugs, substrate oxidation, and dinosaur trampling (fig. 3b). During this phase, the structure and shape of the created tracks depend on the water content in the sediment, applied pressure, as well as mat cohesion (Scrivner and Bottjer, 1986; Allen, 1989; Marty, 2008). Footprints have been impressed when water resides, typically during low tide periods. The initial footprint formation took place when the sediments were sufficiently soft but firm enough to preserve the tracks (Naimi *et al.*, 2023);

(iii) A flooding event led to the deposition of carbonate mud, which contained bioclasts along with terrestrial sandy materials (fig. 3C). The sediments filled *Skolithos* and *Thalassinoides* burrows and buried the footprints, ultimately preserving them.

VI- CONCLUSIONS

The Djebel Azzeddine tracksite has unveiled crucial insights into the palaeoenvironment and dynamics of dinosaur life in the Saharan Atlas basin. This unique site, situated in the eastern part of the basin, not only marks the first evidence of widespread emersions following the

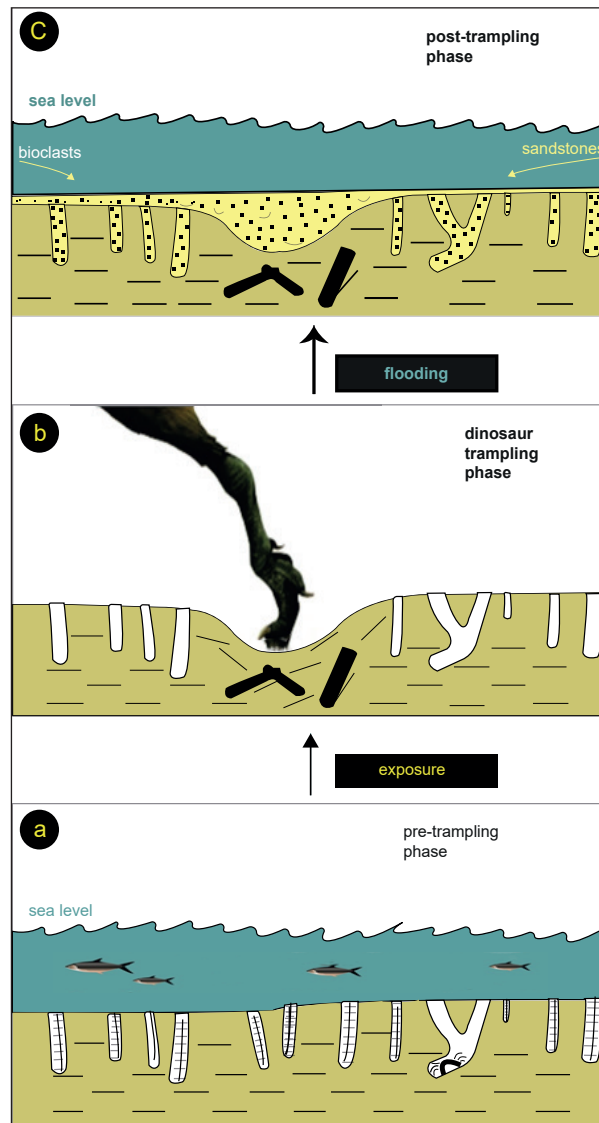


Fig. 3 - Genetic model for the development of the Djebel Azzeddine dinosaur tracksite from oldest below (a) to youngest above (c).

Modèle génétique du développement de l'ichnosite à dinosaures du Djebel Azzeddine du plus ancien en bas (a) au plus récent en haut (c).

mid-Cretaceous transgression but also showcases the pivotal role of tidal flats as migratory highways for dinosaurs during lowstand periods. The study proposes a compelling migration idea, suggesting that theropods, ornithopods, and sauropods may have used these tidal flats as seasonal routes, with tracks aligned in a consistent SW-NE direction. Additionally, the presence of carnivorous theropods in this tidal flat environment aligns with the notion of these creatures actively seeking food,

likely in response to the abundant invertebrate fauna.

The genetic model for the tracksite's development is outlined through distinct steps: (i) colonisation by marine organisms in a subtidal to lower intertidal environment; (ii) subaerial exposure leading to dissolution vugs, substrate oxidation, and dinosaur trampling; and (iii) flooding event depositing carbonate mud, filling burrows, and burying footprints. Track preservation is in-

fluenced by water content, sediment firmness, and environmental conditions.

This study not only enriches our understanding of dinosaur behaviour in a tidal flat setting but also emphasizes the intricate interplay between environmental factors, migration patterns, and feeding behaviours, offering a valuable contribution to the broader field of palaeo-ichnological research.

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Appendice

Plate 1



A- The track-bearing dolostone bed.

Le banc dolomitique renfermant les ichnites.

B-C- The upper surface of the bed shows dinosaur footprints. In B, tracks are poorly preserved, occurring as rounded depressions. In contrast, C shows tridactyl ornithopod footprints (yellow arrows) co-occurring with other small ornithischian ichnites.

La surface supérieure du banc montre des empreintes de pas de dinosaures. En B, les traces de pas sont mal préservées, ayant l'allure de dépressions arrondies. En contrepartie, l'image C montre des ichnites tridactyles d'ornithopodes (flèches jaunes) en association avec d'autres ichnites de petits ornithischiens.

D- Dinosaur track co-occurring with *Skolithos* burrows. We notice that these burrows are present only on the margin of the track and are absent inside.

Empreinte de pas de dinosaure en association avec des traces de Skolithos. On note que ces traces sont présentes uniquement sur la marge de l'empreinte.

E- Bioclastic limestones with abundant fragmented oyster shells.

Calcaires bioclastiques avec d'abondantes coquilles fragmentaires d'huîtres.