

Small sauropod tracks in the Hettangian of Southern France – A case of ichnite fossilization in an intertidal zone

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Abstract: This paper presents the description and the interpretation of recently discovered traces on a Lower Hettangian dolomitic outcrop in the Bédarieux area, Southern France. One trace set immediately attracted the attention by its resemblance to a small sauropod pes-manus couple but no trackway was visible. As the other traces have a variety of shapes with no obvious significance, it took a thorough examination of the 3D and sedimentological data to come to the conclusion that most traces likely were sauropod tracks made under diverse conditions. Sedimentological and ichnological data indicate that the tracks have been made in the intertidal zone of a carbonated tidal flat shortly before an emersion period. It appears that that the variety of trace shapes is due to a variety of water depths: the sauropods were punting when the water level was high. The lack of trackways seems due to the combination of an underprint situation, buoyancy effects and the small size of the track-bearing slab. Several hypotheses can be considered for explaining the very small size of the tracks, such as insular dwarfism or the immaturity of the trackmakers.

Keywords: Tracks, Sauropods, Lower Jurassic, Intertidal Zone, Bédarieux, Southern France

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INTRODUCTION

The tracks studied here are located on a Lower Hettangian dolomitic outcrop 3 kilometers southwest of Bédarieux, Occitanie, France. The area is covered by the Bédarieux and Lodève geological maps (Fig. 1A). The trace-bearing slab is located on private property at the top of a dolomite bed close to the greenhouse of the Saint Raphael Farm and was discovered by the farmer J.P. Raymond.

Numerous tetrapod tracks have been found over the years (and the centuries) within a 50 km radius of the site, mainly: amphibian and reptile tracks in the Permian (Bogdanoff et al., 1984; Gand et al., 2000), a variety of archosaur tracks (including many chirotherioïd and a few dinosauroïd tracks) in the Middle Triassic (Gand & Demathieu, 2005; Gand et al., 2007), and tridactyl dinosaur tracks in the Hettangian and Lower Sinemurian (Bogdanoff et al., 1984; Demathieu et al., 2002; Gand et al., 2007).

However, the study presented here is quite different from usual ichnological studies. In a vast majority of tetrapod track sites it is obvious upfront that the tracks considered are tetrapod tracks. Here, the situation is totally different. Although one trace set strongly resembles a small sauropod pes-manus couple, no trackway is visible and the other traces have a variety of shapes with no obvious significance. It took a thorough examination of the 3D shapes and sedimentological data to come to the conclusion that all traces likely were sauropod tracks made under a variety of water depths.

GEOLOGICAL SETTING OF THE TRACKS IN THE BEDARIEUX AREA

Fig. 2A shows the lithostratigraphic column of the Rhetian and Liassic deposits in the Bedarieux basin (Bogdanoff et al., 1984). Figs. 2B and 2C exhibit a detailed section of the Lower Hettangian (11) in the outcrop with dinosaur tracks close to the greenhouse of the Saint Raphael Farm and of the Upper Hettangian (12) close to the Bédarieux roundabout. Some pictures of the diverse facies and thin sections of 11 and 12 are shown in Fig. 3. The Bédarieux geological map (Bogdanoff et al., 1984) exhibits a monoclinal of Liassic with a northward dip, but our new mapping shows tectonic slices (Fig. 1B) with diverse dips northwards or southwards, six longitudinal faults and three transversal faults. The outcrop is located in a tectonic zone (Fig. 1B) limited in the south by Les Aires fault that is a multiphase fault with a recent normal displacement increasing the thickness of alluvial deposits in the Orb valley, a reverse displacement during a Pyrenean phase (Upper Eocene) with a thrust between the Paleozoic and the Jurassic north of Tantajo and a tardi-hercynian sinistral strike-slip displacement (Bogdanoff et al., 1984).

The Lower Hettangian (11)

The 11 is dolomitic and its thickness is from 20 m to 30 m in the Bédarieux map (Bogdanoff *et al.*, 1984). The dolomite of the Lower Hettangian passes laterally towards the north-East to the Parlatges limestone constituted of thin mudstone and wackestone with ripples (20 m) in the Pas de l'Escalette

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section (Lopez, 1992; Hamon, 2004). The classifications of Dunham (1962) and Folk (1962) were used for the description of carbonates.

South of Bédarieux, near the Saint Raphael Farm the 11 is a tectonic slice (Fig. 1B). The cross-section under the trace-bearing layer is 1.4 m thick (Figs. 2B and 3A) from base to top: dolomitic breccia, three fenestral dolomicritic beds with round pink vacuoles filled with sparite (Fig. 3E, thin section Sr7) in a grey dolomicrite, a dolomicritic bed, a peldolomicrosparite (packstone, Fig. 3F, thin section Sr5) that is a mixture of poorly and well sorted micritic pellets and intraclasts, a laminated micritic dolomite that presents wave ripples with cross-laminations (Figs. 3C and D) and then the dinosaur tracks are located at the top of the laminated dolomite. Above the bed with dinosaur tracks begin a deposit of dolomitic breccia in a small syncline 10 to 20 m thick).

The complete sequence (0.6 m thick) of the 11 can be drawn with this succession of dolomitic facies from base to top: homogeneous dolomicrite (0.2 m thick), laminated dolomite

(0.1 m to 0.2 m thick, Fig. 3A) and dolomitic breccia (0.2 m thick, Fig. 3A). The dinosaur tracks are located at the top of the laminated dolomite. This laminated micritic dolomite presents wave ripples with cross-laminations (Figs. 3C and D). Another section 50 m west of the dinosaur trace-bearing layer (Fig. 3B) exhibits laminated micritic dolomite (0.4 m thick) with wave ripples and stromatolites on the basal dolomitic breccia observed in the eastern section (Fig. 3A). Dolomicrite passes laterally to wavy dolomicrite from east to west. It can be estimated that approximately 0.6m up to the dinosaur tracks bed was eroded in this western section. A synsedimentary normal microfault fossilized by upper laminae is visible on the Sr1 thin section (Fig. 3G). Domal stromatolites are present in the 11 under the railway bridge along the Orb River and the desiccation cracks close to the plant nursery of Bédarieux along the Orb River in the 11, but not in the Saint Raphael Farm.

After James (1984) and Flügel (2012), homogeneous dolomicrite can be interpreted as a deposit of a subtidal lagoon. The fenestral facies present round vacuoles named birdseyes

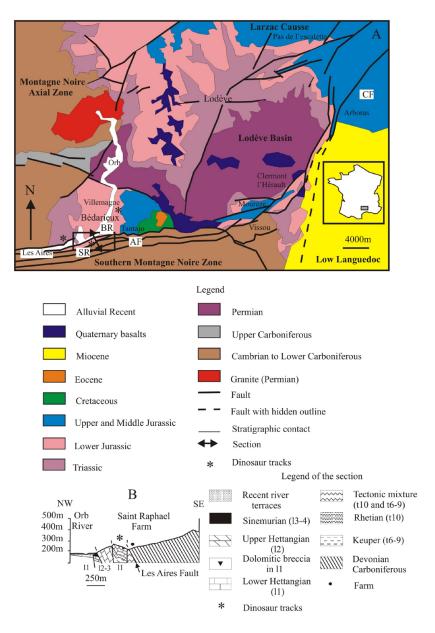


Figure 1. Geological map of the Bédarieux and Lodève area (A) and section (B). AF: Les Aires Fault, BR: Bédarieux Roundabout, CF: Cévennes Fault, and SR: Saint Raphael Farm. The rectangle represents the field of study.

formed during water evaporation or methane degasification and filled with blocky sparite during diagenesis. The interpretation of laminated dolomite is more difficult. It can be a laminated dolomicrite deposited in the lagoon shore with wave ripples (Figs. 3C and D) or a building of cyanobacteria (laminated stromatolites, Elf-Aquitaine, 1975, page 170) in the intertidal zone of the tidal flat. The observation of thin dark and clear laminae and clotted peloidal micrite are known as proofs of the stromatolite building from the Shark Bay intertidal zone (Australia: Collins & Jahnert, 2014 and Suosaari *et al.*, 2016). Prados Andrès & Badenas Lago (2015) defined smooth (planar), wavy (domal) and crinkly (with mud cracks) stratiform stromatolites intercalated with mudstone and packstone in the Liassic of Spain.

This succession of facies constitutes a shallowing upward sequence from lagoon to land. The detailed section (Fig. 2b) shows from base to top: sediments of the intertidal and supratidal zone, then subtidal lagoon, supratidal and intertidal zone below the tracks without mud cracks (which would be

formed during an emersion) and finally supratidal. There are two types of tidal flat, a hypersaline tidal flat in a desertic climate as the modern Persian Gulf and a normal tidal flat in a humid climate similar to the modern Bahamas. The low content of evaporites allows to choose a tidal flat with alternation of dry and wet periods (Hamon, 2004).

The dolomitic breccia above the bed with dinosaur tracks could be interpreted as a local dry period inside the Lower Hettangian or before the Upper Hettangian deposition or as a tectonic or a eustatic event. This dolomitic breccia can be followed hundred meters westward to the tunnel of the old railroad, and eastward in the 11 outcrop close to Palagret village. If this breccia is local, it can be interpreted rather as a period of tectonic uplift in this faulted zone. But this breccia could correspond to an eustatic lowstand because the eustatic curve of the Jurassic (Haq *et al.*, 1988; Haq, 2017) shows three marine sequences during the Hettangian with sequence boundaries at the base of Lower Hettangian (*Psiloceras planorbis* Sowerby), Middle Hettangian (*Alsatites liasicus* d'Orbigny)

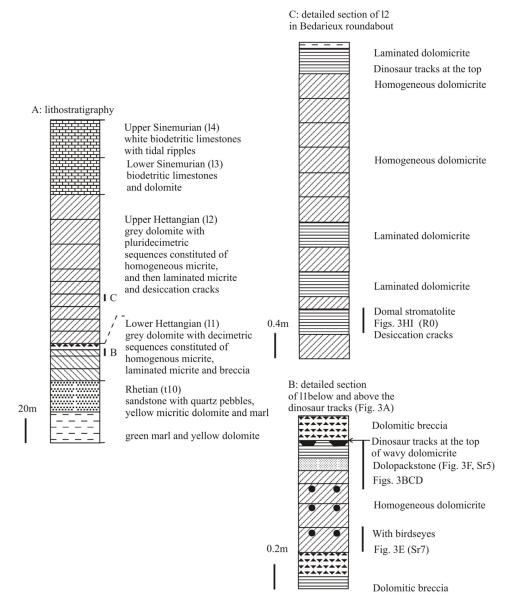


Figure 2. Lithostratigraphic column in the Bédarieux area (A) and detailed sections of Lower Hettangian (11) below and above the dinosaurs tracks close to the Saint Raphael Farm (B) and Upper Hettangian (12) in the Bédarieux roundabout (C).

and Upper Hettangian (*Schlotheimia angulata* Schlotheim). Hamon (2004) described a paleokarst at the boundary of Lower and Middle Hettangian in the Pas de l'Escalette (Le Caylar map). This thick breccia could correspond to this paleokarst during the lowstand.

In summary, the dolomitic breccia and sands that we observe today above the trace-bearing layer are probably the result of a succession of transformations: a paleokarst during the Liassic; a karst during the quaternary; and finally, anthropic erosion.

The Upper Hettangian (12)

The 12 is dolomitic and its thickness is 120 m (Bogdanoff *et al.*, 1984) in the Bédarieux map with increase of bed thickness in the upper part. The 12 is also dolomitic (200 m) in the Pas de l'Escalette (Hamon, 2004).

A section (5 m thick) was drawn on the Fig. 2C in the Bédarieux roundabout with from base to top an alternation of homogeneous and laminated dolomicrite with domal stromatolites (Fig. 3H) and desiccation cracks. The thin section R0 (Fig. 3I) shows thick (1.5 mm) and thin (0.1 mm) couplets

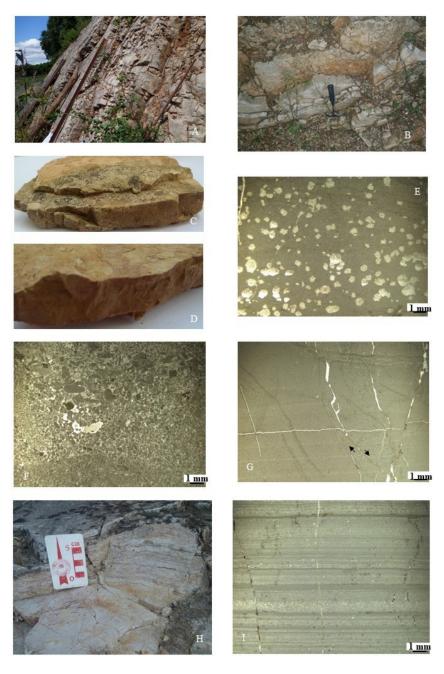


Figure 3. Pictures of Lower (11) and Upper (12) Hettangian deposits south of Bédarieux. A. Section across the dolomites (1 m thick) from the Lower Hettangian (11) stage below the dinosaur tracks bed with a dip (60°, N170) located close to the greenhouse of the Saint Raphael Farm at the east of the trace-bearing layer. B. Dolomitic breccia capped by cross-laminated dolomite (0.4 m thick at the west of the trace-bearing layer). C. wave ripples with cross-laminations (1 cm thick) in micritic bed below the dinosaur tracks. D. small wave ripples (5 mm thick) draping the troughs and crests of the ripples (picture C) in micritic bed below the dinosaur tracks. E. Sr7 thin section located in Fig. 2B, fenestral micrite (birdseyes filled with blocky calcite in grey micrite) at the top of the micritic dolomicrite (0.2 m thick) located 0.7 m below the dinosaur tracks. F. Sr5 thin section located in Fig. 2B, dolopackstone with micritic pellets and intraclasts. G. Sr1 thin section located in Fig. 2B, synsedimentary normal microfault with open fractures filled with calcite in a wavy dolomicrite. H. Domal stromatolites in the roundabout from Bédarieux. I. R0 thin section located in Fig. 2C, thick and thin couplets of pale grey and dark grey dolomicrites in the stromatolitic dome (Fig. 3H).

constituted of pale grey and dark grey micrite laminae. The thick couplet passes upwards to multiple thin couplets. The complete sequence (1 m thick) presents from base to top: homogeneous dolomicrite (0.4 m thick), an emersion surface with a possible tridactyl dinosaur track and mud cracks, then laminated dolomite (0.4 m thick) and claystone (0.1 m thick).

Homogeneous dolomicrite can be interpreted as a deposit of a subtidal lagoon; laminated dolomite as a micritic deposit or a building of cyanobacteria (laminated and domal stromatolites, Fig. 3H, thin section R0, Fig. 3I) in the intertidal zone of the tidal flat; mud cracks as desiccation cracks in the intertidal and supratidal zone of the tidal flat. The domal stromatolite facies was described by Prados Andrès & Badenas Lago (2015) in their figure 4 and interpreted as domal laminated stromatolites. Collins & Jahnert (2014) measured after ¹⁴C a stromatolite growth from 0.1 to 0.5 mm/year in the recent Shark bay (Australia) stromatolites. The duration of a thick couplet in thin section R0 can be multiannual and of a thin couplet is annual. An isolated bipedal dinosaur footprint was found in 12 South of Hérépian (Bogdanoff *et al.*, 1984).

Microstratigraphy under the tracks

The upper part of the laminated micrite under the tracks were reworked by wave ripples under water. The ripple height (H) is 1 cm (Fig. 3C) and the ripple length (L) measured on 5 samples varies from 10 cm below the tracks east of the track-bearing layer (Fig. 3A) to 60 cm at 1 m below the tracks west of the track-bearing layer (Fig. 3B). The Ripple index (RI) is equal to L/H=10 and the Ripple symmetry index RSI (RSI) is equal to the length ratio between the stoss side and the lee side of the ripple=6/4=1.5. Ripples can be done by waves (RI<4 and RSI<2.5) or currents (RI>15 and RSI>3) after Collinson & Thompson (1984). Therefore these ripples are wave ripples. Small wave ripples (Fig. 3D, 5 mm thick) drap the troughs and crests of the wave ripples (1cm thick) and fill partially the tracks. Both ripples (C and D) were probably deposited during the same flood tide. The direction of ripple crests is north-south with a west-east wind fetch direction. There are no traces of emersion such as mud cracks near the level of the tracks.

METHODS, EQUIPMENT, and CONVENTIONS

All photographs of the tracks were taken with a Sony RX100 II camera. The photogrammetric software used was 3DF Zephyr in its free version. The presentation of the 3D data (depth maps and vertical profiles) was made using ParaView 5.8.0.

Unless indicated otherwise, all measurements are in centimeters (cm) or degrees ($^{\circ}$).

Azimuths (Az) are counted as 0 for the north (N); 90 for the east (E); 180 for the south (S); and 270 for the west (W). If not indicated with an azimuth, directions are indicated by a combination of the letters N, E, S, W, e.g. NW means northwest.

When referring to the traces, horizontal means parallel to the stratification plane and vertical perpendicular to the stratification plane.

DESCRIPTION OF THE TRACKS

The dolomitic trace-bearing surface

The dolomitic trace-bearing surface (Fig. 4) is approximately

2 meters by 3 meters and has a dip of 60° toward Azimuth 170. This surface is part of a multi-layered dolomitic outcrop approximately 2.2 meters high and extending horizontally over approximately 50 meters. The layers outcropping in the immediate vicinity of the trace-bearing layer are below this layer. All layers are fractured and their surfaces are weathered.

The traces

The traces are concave epireliefs in the laminated dolomite. The names given to the traces (A to I) as presented in Fig. 4 are arbitrary, with the limited exception of traces A1 and A2. This exception is due to historical reasons: it is the similarity of the A1 –A2 set to a sauropod pes-manus couple that attracted the attention to the site.

Despite this initial sauropod analogy, the poor quality of the traces due to weathering and fractures, the variety of shapes and the lack of obvious trackways did not allow a straightaway response to the question of the origin of the traces. Many examples are known where traces of a variety of origins, such as cavities left by tree stumps or erosion, were first interpreted as sauropod tracks (e.g. Gand *et al.* 2018). Therefore, a prudent step by step analysis of all observable data appeared necessary.

The outlines of the traces can be organized in three categories: ovoid, partly ovoid (meaning: generally ovoid but with a locally undefined border), and crescentic. In the ovoid class (traces A1 and G, Fig. 5) an arc-shaped area close to the border of the trace is deeper than the other areas of the trace; the arc on the opposite area of the trace is shallower than the other areas of the trace. In the partly ovoid class (traces B, C, and H, Fig. 5), in one area the border is clearly defined next to an arc of maximum depth, and at the opposite end of the trace the border is undefined. In the crescentic class (traces D, E, F and I, Fig. 6) the arc-shaped area of maximum depth is in the middle of the trace, close to the concave border of the crescent (this feature is undefined in crescentic trace A2, Fig. 5).

Several cases of backfilling are visible: in trace A2 (Fig. 5) nearly half of the cavity of the trace has been backfilled by a light-colored dolomite with a roundish surface - which seems worth noting: most features are angular in the sediments of this site. This phenomenon is visible in the field, and on the stereoscopic views, but invisible on the photogrammetry results. At the bottom of traces A1, B and H (Fig. 5) some similar backfilling occurred, but with very limited volumes. In trace F (Fig. 6), little plates of dolomite seem to have been deposited at the bottom of the hollow after its making. Some of these plates seem to be partly one on top of the other. The stratigraphic background and the shape of the backfilled material suggest that the situation in A2 and to a lesser extent B and H is due to a mobilization of dolomitic mud when the trace was made, followed by re-sedimentation in the hollow shortly afterwards. The situation in F is somewhat different: it seems small dolomitic plates were dislodged when the trace was made and slipped into the cavity afterwards.

Measurements are presented in Table 1. We used the following conventions: for ovoid or partly ovoid traces ${\bf L}$ is the length of the trace measured along the plane of symmetry. For crescentic traces, ${\bf L}$ is the distance between the middle of the convex border and the line joining the two ends of the crescent. ${\bf W}$ is the width of the trace measured perpendicularly to the plane of symmetry. ${\bf D}$ is the depth of the trace, measured as the elevation difference between the deepest point of the trace and the closest slab surface outside the trace.

The poor quality of the traces has been a difficulty throughout the study. Three specific cases should be noted: the NE part of trace B seems to be the result of a disruption by a phenomenon having nothing to do with the main part of trace B-may be a case of overprinting. Traces H and I are cut by very significant fractures; we included them in the study to be as thorough as possible.

DISCUSSION

IDENTIFICATION OF THE TRACES AS SAUROPOD TRACKS

Identification of the A1-A2 set as a sauropod pes-manus couple

The A1-A2 set has a usual sauropod pes-manus outline. In addition, the 3D shape of the footprint indicates that the digit area is slightly deeper than the heel area, which is consistent with a usual walking gait. That the NW side of the digit area is deeper than the E side suggests that A1 is a right foot, as in sauropod autopods digits are asymmetric, digit I being the stoutest. Then we can conclude that the manus is outwardly oriented, with an angle between pes and manus axes of ca. 35°, which is consistent with many sauropod pes-manus relative positions. The heteropody defined as the manus/pes area ratio

is approximately 1:3.2, which is within the normal heteropody range for sauropods and can be considered as moderately elevated.

It should be noted that the 3D view of the manus presented in Fig. 5 indicates a very shallow imprint, which is incorrect: as we have seen above, the manus hollow has been partially backfilled by dolomitic mud mobilized when the autopod crushed the sediments. As the photogrammetric process providing the 3D view takes only into account the geometry of the current surface, the stereoscopic view examination is necessary to see that the manus imprint was deeper before backfilling.

The A1-A2 set strongly resembles sauropod tracks from the Early and Middle Hettangian of Poland presented in Gierliński (1997), Gierliński *et al.* (1998, 1999 and 2004), and Niedwiedzki *et al.* (2004) (see Fig. 7). The morphology of the pes is similar: maximum width in the digit area, narrow heel, footprint longer than wide; the shape, relative size and position of the manus are similar too. Thanks to the discovery of several tracks and trackways, the authors identified the tracks as *Parabrontopodus* Lockley, Farlow and Meyer (1994) despite the smaller size of the tracks.

The original diagnosis of the *Parabrontopodus* ichnogenus reads as follows: "Narrow sauropod trackway of medium to large size (footprint length about 50-90 cm), characterized by no space between trackway midline and inside margin of pes



Figure 4. The trace-bearing layer and the trace names. Scale indicator: 2 meters.

	Ovoid		Partly Ovoid			Crescentic				
	A1	G	В	C	Н	A2	D	E	F	I
L	14.5	15	?	?	?	6	11	12	10.5	10?
W	11	14	15.5	12	13?	10	19	15	14.5	16?
D	5.5	4	3	2.5	7.5	2+	6.5	8.5	6	9

Table 1. Measurements of the tracks. In centimeters (cm). Due to the poor quality of the traces, differences of 0.5 cm should not be considered significant.

tracks. Pes footprint longer than wide with long axis rotated outward. Pes claw impressions, corresponding to digits I, II and III show strong outward rotation. Manus track semicircular and small in comparison with pes track (i.e. pronounced heteropody)."

The general pes and manus morphology of A1-A2 as well as their relative sizes match the *Parabrontopodus* diagnosis. The heteropody of 1:3.2 is not significantly different from the Podole measurement of 1:4.2. But on several important parameters, such as trackway width and claw orientation, we have no information. By overall shape similarity to the coeval tracks from Poland we may tentatively identify the A1 – A2 set as *Parabrontopodus* sp., but obviously this identification could be revised if additional similar tracks are found in the area.

The size issue

The most striking feature when comparing the tracks of this site

to other sauropod or prosauropod tracks is their very small size. The pedal length of track A1 is approximately 14.5 cm. This is extremely small compared to most known sauropod tracks.

In most Middle Jurassic and later sites the foot lengths are in the 50 cm to 1 meter range. In the Kimmeridgian megatracksite discovered in Switzerland when preparing for the construction of Federal Highway A16, among thousands of sauropod tracks up to 1.10 meter in length a few tiny tracks in the 10 to 20 cm range were found – suggesting that the trackmakers were "baby sauropods" (Marty *et al.*, 2009b). Thus the author proposed the following size classification, PL being the acronym for Pes Length: Tiny (PL < 25 cm), Small (25< PL < 50 cm), Mediumsized (50 < PL < 75 cm) and Large (PL > 75 cm) (Marty, 2008).

In most Lower Jurassic sites, pes lengths exceed 30 cm, both in the ichnological and paleontological records. From the ichnological record we can mention the ca. 32 cm pes length of the prosauropod *Lavinipes* Avanzini, Leonardi, & Mietto

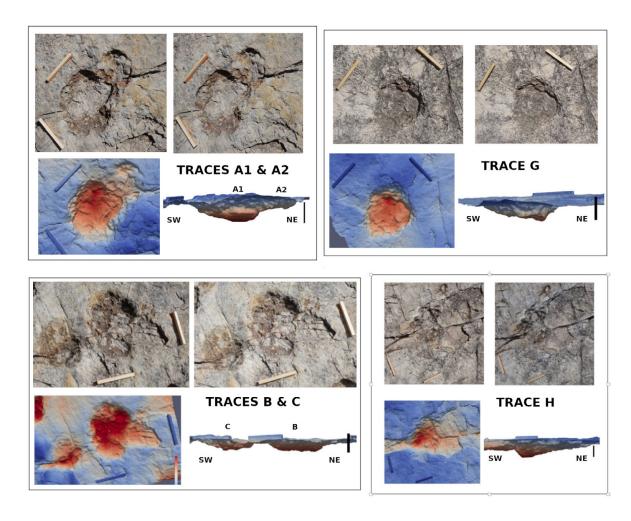


Figure 5. Traces A1 and A2, ovoid trace G, and partly ovoid traces B, C and H. Note that the A2 imprint was originally deeper than it appears, due to backfilling. For each trace, the figure includes: a stereoscopic couple of photographs; a depth map resulting from the photogrammetric processing; and, a vertical profile along the plane of symmetry resulting from the same photogrammetric processing. Surface is in blue, deepest areas in red. The photographs are oriented as observed in the field (i.e. top of the page toward the top of the outcrop). Horizontal scale bars are 10 cm long and have a square cross section of 0.9 x 0.9 cm. Vertical scale bars are 5 cm long.

2003 from the Sinemurian of Italy (Avanzini et al., 2003) and several sauropod pes lengths in the 33 to 36 cm range from the Early Jurassic of China (Xing et al., 2016). In the paleontological record, the *Vulcanodon karibaensis* Raath reconstruction presented in Cooper 1984 indicates a foot length of approximately 50 cm. Very few sauropod footprints have been found so far with pedal lengths in the 20 - 25 cm range. This includes the *Parabrontopodus* sp. tracks from the Early Hettangian of Poland described above, the smallest one being the Podole track with a pes length of 17 cm. The authors considered several hypotheses for explaining the small sizes, mainly: juvenile or even younger trackmakers, and/ or dwarfism due to locally difficult conditions (Gierliński et al., 2009, Niedwiedzki & Pienkowski, 2004).

In the Bedarieux area insular dwarfism cannot be excluded: in Hettangian times Western France was an island isolated from the main emerged continental masses (Scotese, 2021). The juvenile hypothesis cannot be excluded either - the Hettangian fauna of the region includes bigger predators, as exemplified by 20 to 30 cm long *Grallator* or *Dilophosauripus* footprints (Demathieu *et al.*, 2002).

For the Hettangian there is not as many data as for the Kimmeridgian, but it seems reasonable to assume that the classes proposed by Marty (2008) should be significantly scaled down – for the tracks studied here we feel that "tiny"

may be exaggerated and we think appropriate to classify them as "small".

Identification of the other traces as sauropod tracks made under a variety of water depths

Although the other traces have very diverse shapes, their sizes are of the same order of magnitude, which suggests a common origin. A prudent step by step analysis led us to the conclusion that it is very likely that most of them have been made by trackmakers similar to the A1-A2 trackmaker.

In a first step we may note that several features suggest that most of the other traces are tetrapod tracks as opposed to other potential origins such as tree stump cavities, hollows made by erosion or sedimentary features: in the close vicinity of several traces surface laminae are bent down, which is indicative of a downward thrust (this phenomenon is particularly visible in traces B, F, G, and H, Figs. 5 and 6); the 3D volumes of the traces have an overall vertical plane of symmetry which bisects the outline and the arc of maximum depth – most of the other potential origins would be associated with radial symmetries or no symmetry at all; and, the presence of other features such as lignite, traces of erosion with similar shapes, periodic phenomena, were looked for but not found.

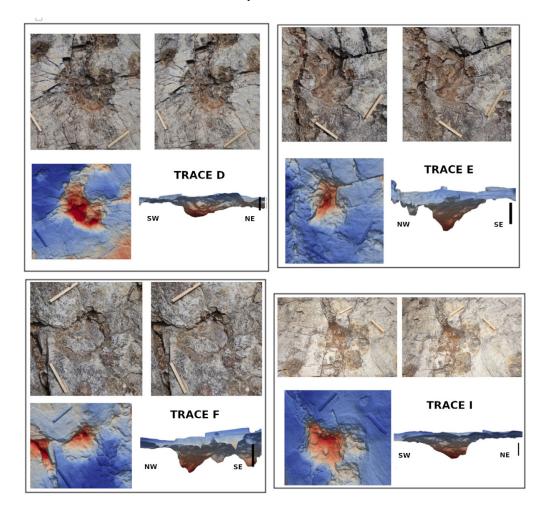


Figure 6. Crescentic traces **D**, **E**, **F** and **I**. Note that the crescentic trace A2 is presented in Fig. 5 as it is associated with ovoid trace A1. For each trace, the figure includes: a stereoscopic couple of photographs; a depth map resulting from the photogrammetric processing; and, a vertical profile along the plane of symmetry resulting from the same photogrammetric processing. Surface is in blue, deepest areas in red. The photographs are oriented as observed in the field (i.e. top of the page toward the top of the outcrop). Horizontal scale bars are 10 cm long and have a square cross section of 0.9 x 0.9 cm. Vertical scale bars are 5 cm long.

Ovoid and crescentic tracks are commonly observed in sauropod trackways. However, the 3D shapes of the crescentic tracks observed here are unusual. Generally the tracks with crescentic shapes are manual tracks because the manus skeleton has a crescentic structure (Bonnan, 2003); in such case the arc of maximum depth is near the convex border of the track. In the crescentic tracks D, E, F and I the arc of maximum depth is in the middle or near the concave part of the track, which is consistent with a very oblique footfall as illustrated in Fig. 8. For the E and F imprints the angles between the sole of the autopod and the horizontal plane are in the order of 55° (as can be measured on Fig. 6), which means that the horizontal component of the thrust provided by the autopods was greater than its vertical component. This is consistent with a punting gait, the weight of the trackmaker being compensated by buoyancy and the main effort being a push forward against water resistance.

This conclusion that several tracks were made underwater is also very consistent with the sedimentological background presented above.

The swimming or partly-swimming sauropod hypothesis was generally considered in the years 1940 – 1950, and well-illustrated by Roland Bird's famous 1944 drawing (republished in Bird, 1985). In the decades that followed this hypothesis has often been rejected, but recently re-considered in a few cases. Farlow *et al.* (2019) present a very detailed discussion of manus-only trackways and punting situations.

We may note that swimming traces are very different from punting tracks – see for instance the review and categorization of numerous swimming traces left by Triassic archosaurs presented in Thomson and Lovelace (2014).

THE SEARCH FOR TRACKWAYS OR OTHER ASSOCIATIONS

Pes-Manus couples

In addition to the A1-A2 set, the B-C set attracted the attention as a potential additional pes-manus couple. Several independent features are consistent with this hypothesis: the general outlines of B and C, their relative positions and their very shallow depths. These shallow depths are quite different from the depths of all other tracks of the site, indicating that B and C were made at a time when the ground was harder.

Two additional parameters can be considered to assess further the likelihood of this interpretation: the heteropody and the relative orientation of the manus and pes imprints. For B and C we cannot calculate areas, as the rear borders are undefined, but as a substitute for heteropody we may compare the widths. Despite the difficulty that the NE part of B is unclear, the width ratio is approximately 1:1.5 for C/B and 1:1.4 for A2/A1. This shows that there is no significant difference between the two. The angle between the axes of B and C is approximately 20°. The depth asymmetry in B suggests that B is a left pes, thus C is outwardly oriented. In conclusion, all parameters suggest that B and C constitute a pes-manus couple.

Table 2. Orientations of the tracks. Az is the azimuth in degrees (°) as defined in the text. If it can be estimated, R indicates a right autopod and L a left one. Due to the poor quality of the traces, differences of 10° should not be considered significant.

Orientations as a tool for associating the tracks

The orientation of each track is defined by two parameters: the axis of symmetry of the outline and the curvature of the arc of maximum depth, which allow the differentiation of the digit area from the heel. In Table 2 the orientation of the autopod is indicated by its azimuth Az. In a few cases the asymmetry in the position of the deepest point suggests a differentiation between right (R) and left (L) autopods given the fact that in sauropods the internal digits are the stoutest.

The result is that the tracks are oriented toward three very different directions: 5 tracks (B, C, D, H, I) are oriented toward the Southwest; 3 tracks (A1, A2, G) are oriented toward the Northeast; and, 2 tracks (E, F) are oriented toward the Southeast. These differences in directions are significant, they substantially exceed usual orientation differences between two feet of the same trackmaker.

Correlation between orientations and depth patterns

The correlation between track orientations and depth profiles suggests that:

Tracks D and I have been made by punting sauropods (or: one sauropod) going to the Southwest. A punting situation indicates a high water level: a major part of the body must be in water to trigger a buoyancy effect and a very oblique footfall.

Tracks E and F have been made by punting sauropods (or: one sauropod) going to the Southeast, thus in high water too.

Tracks A1-A2 and G have been made by sauropods (or: one sauropod) walking to the Northeast on moderately soft ground. A1-A2 must have been made in some level of water to account for the re-sedimentation of displaced dolomitic mud after the track was made. The level of water should not have significantly exceeded half the mid-limb as no buoyancy effect is observed. It seems difficult to tell if water was present or not when track G was made.

Track H has been made by a sauropod walking toward the West / Southwest on relatively soft ground, possibly in a moderate depth of water.

The B-C group is a pes-manus couple of a sauropod walking to the Southwest on relatively dry ground, as the imprints are significantly shallower than all others.

Other potential associations

In addition to the pes manus couples A1-A2 and B-C discussed above, let us examine the potential for additional tracks made by the same animal.

The D-I Group: D and I are relatively close. With the lack of a third track, it seems difficult to ascertain if they are from the same animal or not. If they were from the same animal track I would be the imprint of the right pes and D the left. It would be a Wide-Gauge trackway: the Inner Trackway Width would be approximately equal to the Pes Width. The Pace Length would be close to 40 cm, which is within usual proportions, but the axes of the two pes prints are practically parallel, which is unusual. However, because of strong buoyancy effects, the parameters observed here may differ from the trackway

	Ovoid		Partly Ovoid			Crescentic				
	A1	G	В	C	Н	A2	D	E	F	I
Az	20	20	240	220	240	55	220	100	130	225
R or L	R	R?	L		L?		R?	R	R	

parameters made by the same animal in a normal walking situation – the wide-gauge stance with parallel feet might be a reaction to random water movements. In conclusion, it seems possible that D and I are a left pes- right pes set of the same animal, but it should be noted that the two trackway parameters observed, pace length and gauge, may not be representative of normal walking conditions.

The E-F Group: the relative position of E and F is similar to the one observed with D and I, i.e. they are relatively close but significantly separated laterally. As we have seen, the angles of the soles with the horizontal plane are very similar – in the order of 55°, which indicates very similar biomechanical conditions. The depth asymmetry of the imprints suggests that they both are right autopods, which would lead to the conclusion that they are from two different animals. But E and F are so similar in shape and size that we feel compelled to examine the hypothesis that they could have been made by the same animal anyway - a potential scenario is that the depth asymmetry originated from a reaction to a lateral water movement, not by right/ left pes morphology differential. In such a case E would be the imprint of the left pes, F the right. The Inner Trackway Width would be approximately 1.3 times the Pes Width, which would be an extremely Wide-Gauge situation. The pace length is ca. 40 cm, which fits normal proportions and is practically identical to the D-I distance. The angle between the axes is approximately 30°, in a usual sauropod trackway pattern. In conclusion, it seems very possible that E and F constitute a left pes-right pes set of the same animal, but as for D and I, due to buoyancy effects the two trackway parameters observed may not be representative of normal walking conditions.

The relative positions of the A1-A2 set and G could be compatible with the hypothesis of the same-animal origin. But they are very far apart and G seems to have been made in a bipedal stance, so it seems difficult to ascertain any relation. Track H seems isolated.

Potential explanations for the lack of trackways

The "missing tracks phenomenon" is frequently observed in sauropod ichnology. Various hypotheses have been considered through the years (e.g. Lockley & Conrad 1989, Marty *et al.*, 2009b, Moreau *et al.*, 2020).

In the site studied here, underprinting may have played some role: the disruptions of laminae indicate that the autopods went through several layers of sediments and several features suggest that the current track-bearing surface may not be the ground surface on which the sauropods walked. The current surface has a significantly eroded aspect and by comparison

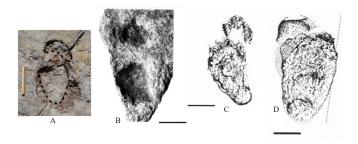


Figure 7. Comparison with Hettangian tracks from Poland. **A.** The A1-A2 set, this study. **B.** The Podole track, Middle Hettangian, copied from Niedwiedski & Pienkowski (2004). **C and D.** the Gromadzice tracks, Lower Hettangian, copied from Gierlinski (1997). All scale bars are 10 cm long.

with other areas of the outcrop it seems possible that a few centimeters of very fragile laminated dolomite separated the current surface from the overlaying breccia.

Some of the tracks made by the trackmakers of the horizontal or sub-horizontal tracks (A1, A2, B, C, G, H) may be missing due to differential penetration followed by erosion.

The trackmakers of the punting tracks (D, E, F, I) were subject to strong buoyancy effects and, in addition, they may have switched between punting and swimming in a random manner. Farlow *et al.* (2018) studied the footfall pattern of an underwater bottom-walking crocodile and observed pes strides longer and more variable than in normal walking conditions. In their review of swimming traces, Thomson and Lovelace (2014) observed the frequent lack of traceways.

Other potential phenomena seem to have played a limited role. Overprinting may have been involved on the NE part of track B. Undertrack situations are not likely to be encountered here, as clear-cut disruptions of the dolomitic laminae are much larger than any plastic deformations.

Last but not least, it must be remembered that the track-bearing surface is small, approximately 2 meters by 3 meters. Associated tracks may have been out of the currently existing area.

QUADRUPEDAL OR BIPEDAL STANCE

A majority of pes imprints

Considering the discussions above regarding the oblique footfall origin of the crescentic tracks; the straight rear border of track F; the morphology of track G with the absence of an associated manus; and the consistency of the widths and shapes of the crescentic tracks, it seems that we can conclude with some level of confidence that most tracks, with the exceptions of tracks A2 and C, are pes tracks.

Quadrupedal or bipedal stance

Couples A1-A2 and B-C indicate that the trackmaker was quadrupedal. It is difficult to tell whether the lack of manus associated to the other tracks is due to a temporary bipedal stance or other phenomena mentioned above such as underprinting, differential penetration or random switching between punting and swimming. Anyway, it seems very likely that small basal sauropods had good bipedal capabilities - studies have shown that even some of the heaviest sauropods were able to use a bipedal stance (Wilson *et al.*, 1999).

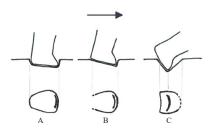


Figure 8. Footfalls and track shapes. **A.** Ovoid tracks A1 and G. **B.** Partly ovoid tracks B, C and H. C. Crescentic tracks D, E, F and I.

Major role of the hindlimbs

For tracks E, D, F and I, even if the forelimbs touched the ground, it is clear that the main locomotion thrust came from the hindlimbs. Roland Bird's famous 1944 drawing mentioned above presented a late-Jurassic sauropod punting with its forelimbs. In contrast, here, all parameters suggest than most tracks were made by Hettangian basal sauropods punting with their hindlimbs.

PALEOENVIRONMENT AND TAPHONOMY

Estimated water depths

As we have seen, the tracks at the Saint Raphael Farm were made under water, with the exception of the last ones, B and C. The water depth may be estimated by two independent methods: from ripple marks measurements and from ichnological data.

The ripple measurements indicated in Section "Microstratigraphy under the tracks" allow some calculations. Numerical estimates of ancient waves and water depth were done by Tanner (1971) and Diem (1985). The equations of Diem (1985) applied to the sample with L= 0.10 m below the tracks (Fig. 3A) indicate that the water depth was between 0.4 m and 1.06 m. These values fit well with the lowest values from ripples in the Lower Marine Molasse (Oligocene) from Switzerland (Diem, 1985). Applying the same equations to L=0.20 m indicates a water depth between 0.6m and 1 m below the tracks on the western section (Fig. 3B). With the equations of Tanner (1971), the water depth is 1 m for L=0.10 m.

For interpreting the ichnological data in terms of elevation above the ground we can consider the *Vulcanodon* reconstruction mentioned above. *Vulcanodon* is dated Pliensbachian-Toarcian according to Yates (2004), thus more recent than the trackmakers of this study, but it seems to have one of the best known post-cranial skeleton among early sauropods. The key dimension ratios of *Vulcanodon* are presented in Table 3 and estimated water depths in Table 4. These are only orders of magnitude: the Hettangian trackmakers may have had different proportions.

The water depth estimates obtained are consistent with the calculation made from the ripple marks: a maximum water depth in the order of 1 meter. In addition, the ichnological data illustrates that the water depths varied: the water depth was in the 60 cm to 1 meter range when tracks D, E, F and I were made; liquid water was present but with a depth less than 80 cm when tracks A1, A2, G and H were made; and, there was no liquid water when tracks B and C were made. These results are very consistent with the upper part of an intertidal zone.

Table 3. Estimated key parameters for *Vulcanodon*. PL = Pes Length.

Body ratios of Vulcanodon					
Elevation of the highest part of the back above the ground	4.6 PL				
Acetabulum elevation above the ground	3.2 PL				
Mid-limb elevation above the ground	1.7 PL				

Behavior and estimated corresponding water depth Swimming Above 5 PL Punting Between 4 PL and 5 PL Walking Below 4 PL

Preservation of the tracks

It seems that the preservation of the dinosaur prints in a soft dolomitic mud was made possible by the combined presence of a microbial mat providing some level of cohesion and partially lithified sediments providing some level of rigidity. The sediments under the dinosaur tracks in the Saint-Raphael Farm were a sandwich of semi-liquid mud (wavy mudstone) and quasi-elastic sandy packstone and mudstone. The sands and muds have a quasi-elastic behavior under a low deformation, but non-elastic under a large deformation (Tatsuoka & Shibuya, 1991). When underwater, this composite ground reacted as a soft fragile solid: it was sufficiently unconsolidated to be crushed over several centimeters by the autopods of a buoyed trackmaker (thus much lighter than the same trackmaker in a walking situation), but sufficiently consolidated to keep the shape of the hollow afterwards. The semi-liquid mud filling the vacuoles of the matrix was mobilized when the autopods crushed the sediment - its re-sedimentation is visible (see above).

Avanzini *et al.* (1997) described in the Early Hettangian from Northern Italy dinosaur tracks that were preserved by early dolomitization under a semi-arid climate on a tidal flat characterized by alternation periods of sea-water influx and dryness. They also wrote that the sediments under the dinosaur tracks were a sandwich of partially lithified plastic sediments, elastic cyanobacteria laminae and semi-liquid mud.

Marty et al. (2009a) investigated the formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments. The footprints are shallow and well-defined in moist mats, present high variability on water-unsaturated mats, poorly defined in water-saturated mats and rare (poorly defined with modifications with the growth recovery of the microbial mat) in consolidated or partially lithified mats. The lithification by early diagenesis seems preclude the track formation. The B and C tracks were certainly done on a moist or water-unsaturated, but not fully lithified soil.

Avanzini *et al.* (1997) in Northern Italy and Hamon & Merzeraud (2007) in Pas de l'Escalette measured depleted values of d¹³C and d¹⁸O due to early meteoric diagenesis in subaerial exposure facies that can explain the partial lithification of dolomite and enriched values in marine facies by marine water. Depleted values of isotopes are measured in third order sequence boundary and not in high frequency sequence boundary. It can be explained because the duration of emersion at the limit of high frequency sequence is shorter than for the third order sequence (Joachimski, 1994; Hamon & Merzeraud, 2007). As the track-bearing slab is below a thick dolomitic breccia corresponding to a third order sequence boundary, the diagenesis during this event was important and

Table 4. Estimated Water Depth from Ichnological data. Orders of magnitude of the water depths based on pes lengths in the 15 to 20 cm range.

Tracks	Behavior	Water Depth Estimate		
No tracks made	Swimming	More than 1 meter		
D-I	Sauropods (or: a sauropod) punting toward the southwest, very soft ground, elevated water level	60 cm to 1 meter		
E-F	Sauropods (or: a sauropod) punting toward the southeast, very soft ground, elevated water level	60 cm to 1 meter		
A1-A2- G	Sauropods (or: a sauropod) walking toward the northeast, soft ground, shallow water	Less than 80 cm		
Н	A sauropod walking toward the Southwest on relatively soft ground	Less than 80 cm		
В-С	A sauropod walking toward the southwest on relatively hard ground	No liquid water		
No observable tracks remaining	Sauropods walking on hard ground. No imprints or the extremely shallow imprints have been eroded	No liquid water		

can explain the track preservation. But, this event hid the early diagenesis before the tracks were done. Rameil (2008) studied the dolomitization and dedolomitization in the Late Jurassic/ Early Cretaceous from Jura and distinguished type 1 dolomite formed by seepage reflux of brine capped by type 2 laminated dolomite formed by tidal/evaporating pumping at the tidal flat margin during a highstand and in all the lagoon during a lowstand of a high frequency sequence (100 ka). The time for generating a dolomite cap can probably last from a thousand to ten thousand years. But the time interval between the tracks made underwater (most of the tracks) and the tracks made on an unsaturated ground surface (tracks B and C) is certainly short because Marty *et al.* (2009) showed that tracks cannot be done on a fully lithified soil.

Environments favored by sauropods

Meyer & Pittman (1994) showed in the Upper Jurassic of Switzerland and Portugal and the Cretaceous of Texas that the environments where sauropods left their tracks are often calcareous coastal marine environments, while theropods left tracks in more in-land environments. The site studied here and the finding of tridactyl footprints in the Hettangian a few kilometers north of the site suggest a similar situation. However, in the Glen Rose Formation (Lower Cretaceous) in Texas, Dattilo et al. (2014) observed theropod and rare sauropod tracks at the top of coastal marine dolomudstone with serpulids or clams. In addition, as discussed in Meyer & Pittman (1994) and Gierliński & Pienkowski (2004) these observations could also be the result of biased preservation. We may note that very different sedimentological settings were involved: the tracks in Switzerland and Portugal are located at the top of a lagoonal limestone and are overlain by stromatolitic bed or mudcracks, while the tracks in Texas penetrated the stromatolitic algal-laminated limestone. Avanzini et al. (1997) observed in an Early Triassic tidal flat from northern Italy more theropod footprints in a sector capped by mud-cracked stromatolithe bindstone and more sauropod footprints in another sector with fenestral mudstone. At the Saint-Raphael Farm, we observed sauropod traces on wavy mudstone and pellets sands.

CONCLUSION

Sedimentological and ichnological examinations of recently discovered traces on a Lower Hettangian dolomitic outcrop in the Bédarieux area, Southern France, led to the conclusion that these were tracks made by small basal sauropods in an intertidal zone within a shallowing upward sequence from lagoon to land. All parameters indicate that the variety of track shapes is due to the variability of the water depths: the sauropods were walking, wading, punting, and maybe swimming, depending on the water depth. In contrast with previous sauropod punting hypotheses in which the main thrust was provided by the forelimbs, here the main thrust was provided by the hindlimbs. One pes-manus set strongly resembles coeval ichnites found in Poland and determined there as Parabrontopodus, but the lack of trackways and the poor quality of the imprints precluded further ichnological taxonomic analysis. The lack of trackways seems mainly due to underprint conditions, buoyancy effects and the small size of the track-bearing slab.

Given the weathered and fractured conditions of the trackbearing layer, we initially hesitated writing this article. Finally, we wrote it for two different reasons: (1) to preserve the memory of this site in case additional related discoveries are made in the region, and (2) because it may bring some additional level of contribution to several interesting topics. Even given the limitations discussed above, we think this study will provide:

- Some additional data regarding the earliest sauropods, a subject on which the ichnological and paleontological records are scarce.
- Some additional data regarding sauropod gaits in a variety of water depths.
- A picture of a Hettangian intertidal zone. Many ichnological studies have been dedicated to tidal flats, however most of them were related to the constantly emerged upper parts of the tidal flats.
- A contribution to the regional inventory of the Hettangian ichnofauna. Up to now the regional ichnological record indicated an overwhelming percentage of carnivorous dinosaurs (e.g. Demathieu *et al.*, 2002, p.111).
- An additional example of the importance of integrating

- sedimentological and ichnological analyses in complex ichnological situations such as tracks made underwater.
- An additional opportunity to compare the contributions of different methods in paleoichnology, specifically photogrammetry and stereoscopic photographs. The use of photogrammetry in ichnology has been increasing in recent years (e.g. Mallison *et al.*, 2014, Mujal *et al.*, 2020). In this study, photogrammetry and a 3D image manipulation software enabled us to "see through the stone", i.e. to look at the hollow of the tracks from the side and from below. It also provided 3D results that can easily be shared, compared and classified. On the other hand, stereoscopic views enabled the recording and sharing of important micro-morphological details that were visible in situ but not in the photogrammetric data, such as in the case of backfilling.

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BIBLIOGRAPHY

- Avanzini, M., Frisia, S., Van den Driesche, K., Koppens, E., 1997.

 A dinosaur tracksite in an Early Triassic tidal flat in northern Italy: Paleoenvironment reconstruction from Sedimentology and Geochemistry. Palaios 12:538-551. https://doi.org/10.2307/3515410
- Avanzini, M., Leonardi, G., Mietto, P., 2003. Lavinipes cheminii ichnogen. ichnosp. nov., a possible sauropodomorph track from the Lower Jurassic of the Italian Alps. Ichnos, 10:179-193. https://doi.org/10.1080/10420940390256195
- Bird, R., 1985. Bones for Barnum Brown; adventures of a dinosaur hunter. Texas Christian University Press, Fort Worth. 225p.
- Bogdanoff, S., Donnot, M., Ellenberger, F., 1984. Notice explicative de la feuille Bédarieux à 1/50000. Editions du BRGM, France, 105p.
- Bonnan, M.F., 2003. The evolution of manus shape in sauropod dinosaurs: Implications for functional morphology, forelimb orientation, and phylogeny. Journal of Vertebrate Paleontology, 23:595-613. https://doi.org/10.1671/A1108
- Cooper, M. 1984. A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria:Saurischia) and the origin of the Sauropoda. Palaeontologia Africana, 25:203-231. https://doi.org/10.1017/S009483730001407X
- Collins, L.B., Jahnert, R.J., 2014. Stromatolites in the Shark Bay word heritage area. WA Science. Journal of the Royal Society of Western Australia, 97:189-214.
- Collinson, J.D., Thompson, D.B., 1984. Sedimentary structures. George Allen & Unwin, 194p.
- Datillo, B.F., Howald, S.C., Bonem, R., Farlow, J., Martin, A.J., O'Brien, M., Blair, M.G., Kuban, G., Mark, L.K., Knox, A.R., Ward, W.N., Joyce, J., 2014. Stratigraphy of the Paluxy River tracksites in around Dinosaur Valley State Park, Lower Cretaceous Glen Rose Formation, Somervell County, Texas. In: Lockley, M.G. and Lucas, S.G. (Eds.), Fossil footprints of Western North America, Bulletin 62, New Mexico Museum of Natural History and Science, pp. 307-338.
- Demathieu, G., Gand, G, Sciau, J., Freytet, P., Garric, J., 2002. Les traces de pas de dinosaures et autres archosaures du Lias inférieur

- des Grands Causses, sud de la France. Palaeovertebrata, 31:1-143. https://doi.org/10.18563/pv.31.1-4.1-143
- Diem, B., 1985. Analytical method for estimating paleowave climate and water depth from wave ripple marks. Sedimentology, 32:705-720. https://doi.org/10.1111/j.1365-3091.1985. tb00483.x
- Dunham, R.J., 1962. Classification of carbonate rocks according to depositional texture – Classification of Carbonate rocks, a symposium. American Association of Petroleum Geologists, Memoir 1:108-121. https://doi.org/10.1306/M1357
- Elf-Aquitaine, 1975. An attempt at sedimentological characterization of carbonate deposits. Elements d'analyse, 173p.
- Farlow, J.O., Robinson, N.J., Turner, M.L., Black, J., Gatesy, S.M., 2018. Footfall pattern of a bottom-walking crocodile (*Crocodylus acutus*). Palaios, 33:406-413. https://doi.org/10.2110/palo.2018.037
- Farlow, J.O., Bakker, R. Dattilo, B., Deschner, E., Falkingham, P., Harter, C., Solis, R., Temple, D., Ward, W., 2019. Thunder lizard handstands: Manus-only sauropod trackways from the Glen Rose Formation (Lower Cretaceous, Kendall County, Texas). Ichnos, 27:167-199. https://doi.org/10.1080/1042094 0.2019.1698424
- Flügel, E., 2012. Microfacies of Carbonate Rocks: Analysis, Interpretations and Applications. Springer Verlag.
- Folk, R.L., 1962. Spectral subdivisions of limestones types Classification of Carbonate rocks, a symposium. American Association of Petroleum Geologists, Memoir 1:62-84.
- Gand, G., Garric, J., Demathieu, G., Ellenberger, P., 2000. La palichnofaune de vertébrés tétrapodes du Permien Supérieur du bassin de Lodève (Languedoc, France). Palaeovertebrata, 29:1-82.
- Gand, G., Demathieu, G., 2005. Les pistes dinosauroïdes du Trias moyen français: interprétation et réévaluation de la nomenclature. Geobios, 38:725-749. https://doi.org/10.1016/j.geobios.2005.04.001
- Gand, G., Demathieu, G., Montenat, C., 2007. Les traces de pas d'amphibiens, de dinosaures et d'autres reptiles du Mésozoïque français: inventaire et interprétations. Palaeovertebrata, 35:1-149. https://doi.org/10.18563/pv.35.1-4.1-149
- Gand, G., Fara E., Durlet C., Moreau J-D., Caravaca G., Baret L., André D., Lefillatre R., Passet A., Wiénin M., Gély J-P, 2018. Les pistes d'archosauriens : Kayentapus ubacensis nov. isp. (théropodes) et crocodylomorphes du Bathonien des Grands-Causses (France). Conséquences paléobiologiques, environnementales et géographiques. Annales de Paléontologie, 104:183-216. https://doi.org/10.1016/j.annpal.2018.06.002
- Gierliński, G. 1997. Sauropod tracks in the Early Jurassic of Poland. Acta Palaeontologica Polonica, 42:533-538.
- Gierliński, G., Sawicki, G., 1998. New sauropod tracks from the Lower Jurassic of Poland. Geological Quarterly, 42:477-480.
- Gierliński, G., Pienkowski, G. 1999. Dinosaur track assemblages from the Hettangian of Poland. Geological Quarterly, 43:329-346.
- Gierliński, G., Pienkowski, G. 2004. Tetrapod Track Assemblage in the Hettangian of Soltykow, Poland, and its Paleoenvironmental Background. Historical Biology, 11:195-211. https://doi.org/10.1080/10420940490444861
- Gierliński, G., Niedźwiedzki, G., Nowacki, P., 2009. Small theropod and ornithopod footprints in the Late Jurassic of Poland. Acta Geologica Polonica, 59:221-234.
- Hamon, Y., 2004. Morphologie, évolution latérale et signification géodynamique des discontinuités sédimentaires. Exemple de la marge ouest du bassin du Sud-Est (France). PhD Thesis, Université de Montpellier II, 294p.
- Hamon, Y., Merzeraud, G., 2007. C and O isotope stratigraphy in shallow-marine carbonate: a tool for sequence stratigraphy (example from the Lodève region, peritethyan domain). Eclogae Geologia Helvetica 100:1-14. https://doi.org/10.1007/s00015-007-1206-4
- Haq, B.U., 2017. Jurassic Sea-Level Variations: A Reappraisal. GSA Today, 28:4-10. https://doi.org/10.1130/GSATG359A.1

- Haq, B.U., Hardenbol, J., Vail, P.R., 1988. Mesozoic and Cenozoic chronostratigraphy and eustatic cycles. In: Wilgus, C.K., Posamentier, H., Ross, C.K., Kendall, C.G. St.C. (Eds.), Sea-level Changes: An integrated Approach, Tulsa, SEPM Publication 42:71-108. https://doi.org/10.2110/pec.88.01.0071
- James, N.P., 1984. Shallowing upward sequences in carbonates. In: Walker R.G. (Ed), Facies models, second edition. Geosciences Canada, Reprint series 1: 213-244.
- Joachimski, M.M., 1994. Subaerial exposure and deposition of shallowing-upward sequences: evidence from stable isotopes of Purbeckian peritidal carbonates (basal Cretaceous), Swiss and French Jura Mountains. Sedimentology, 41:805-824. https://doi.org/10.1111/j.1365-3091.1994.tb01425.x
- Lockley, M.G., Conrad, K., 1989. The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the western USA. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces, Cambridge University Press, pp.121-134.
- Lockley, M.G., Farlow, J.O., Meyer, C.A., 1994. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wideand narrow-gauge sauropod trackways. In: Lockley, M.G., dos Santos, V.F., Meyer, C.A., Hunt, A. (Eds.), Aspects of Sauropod Paleobiology, Gaia 10, 135-145.
- Lopez, M., 1992. Arrêt I-1: La transition Rhétien-Lias: modalité du passage d'un appareil terrigène à une plate-forme carbonatée. In: Bodeur, Y., Livret-guide (84 p.) et Documents sur le Jurassique au Sud des Cévennes (129 p.), Excursion en Languedoc (21-22-23 septembre 1992): Du seuil Caussenard au Bassin Languedocien. Groupe Français d'étude du Jurassique, Université de Nantes.
- Mallison, H., Wings, O., 2014. Photogrammetry in Paleontology a practical guide. Journal of Paleontological Techniques 12, 1-31.
- Marty, D., 2008. Sedimentology, taphonomy and ichnology of Late Jurassic dinosaurs' tracks from the Jura carbonate platform (Chevenez-Combe Ronde tracksite, NW Switzerland).
 Insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion and palaeoecology. PhD Thesis, Fribourg University, GeoFocus 21, 278 p.
- Marty, D., Strasser, A., Meyer, C.A., 2009a. Formation and taphonomy of human footprints in microbial mats of presentday tidal-flat environments: implications for the interpretation of fossil footprints. Ichnos, 16:127-142. https://doi. org/10.1080/10420940802471027
- Marty, D., Billon-Bruyat, J.-P., 2009b. Field trip to the excavations in the Late Jurassic along the future Transjurane highway near Porrentruy (Canton Jura, NW Switzerland): dinosaur tracks, marine vertebrates and invertebrates Guide. In: Billon-Bruyat, J.-P., Marty, D., Costeur, L., Meyer, CA, Thüring, B., (Eds.), 5th International Symposium on Lithographic Limestone and Plattenkalk, Abstracts and Field Guides. Société Jurassienne d'Emulation, actes 2009 bis, 109 p.
- Meyer, C., Pittman, J., 1994. A comparison between the *Brontopodus* ichnofaciès of Portugal, Switzerland and Texas. Gaia, 10:125-133.
- Moreau, J-D., Trincal, V., Fara, E., Baret, L., Jacquet, A., Barbini, C., Flament, R., Wienin, M., Bourel, B., Jean, A., 2020. Middle Jurassic tracks of sauropod dinosaurs in a deep karst cave in France. Journal of Vertebrate Paleontology, 39:e1728286. https://doi.org/10.1080/02724634.2019.1728286

- Mujal, E., Marchetti, L., Schoch, R.R., Fortuny, J., 2020. Upper Paleozoic to Lower Mesozoic tetrapod ichnology revisited: photogrammetry and relative depth pattern inferences on functional prevalence of autopodia. Frontiers in Earth Science 8:248. https://doi.org/10.3389/feart.2020.00248
- Niedwiedzki, G., Pienkowski, G., 2004. A dinosaur track association from the Early Jurassic deltaic deposits of Podole near Opatów, Poland. Geological Quarterly 48: 333-338.
- Prados Andrés, G.M., Badenas Lago, B., 2015. Sedimentary factors controlling thickness of stratiform stromatolites, from laminae to meter thick package (Sinemurian, Iberian basin). Revista de la Sociedad Geológica de España, 28(2):3-14.
- Rameil, N., 2008. Early diagenetic dolomitization and dedolomitization of late Jurassic and early Cretaceous platform carbonates: a case study from the Jura Mountains (NW Switzerland and E France). Sedimentary Geology, 212:70-85. https://doi.org/10.1016/j.sedgeo.2008.10.004
- Scotese, C.R., 2021. An atlas of Phanerozoic paleogeographic maps: the seas come in and the seas go out. Annual Review of Earth and Planetary Sciences, 49:679-728. https://doi.org/10.1146/annurev-earth-081320-064052
- Suosaari, E.P., Reid, E.P., Playford, P.E., Foster, J.S., Stolz, J.F., Casaburi, G., Hagan, P.D., Chirayath, V., Macintyre, I.G., Planavsky, N.J., Eberli, G.P., 2016. New multi-scale perspectives on the stromatolites of Shark Bay, Western Australia. Scientific Reports, 6:20557. https://doi.org/10.1038/srep20557
- Tanner, W.F., 1971. Numerical estimates of ancient waves, water depth and fetch. Sedimentology, 16:71-88.
- Tatsuoka, F., Shibuya, S., 1991. Deformation characteristics of soils and rocks from field and laboratory. Keynote Lecture for Session 1, Proceeding 9th Asian Regional Conference on SMFE, Bangkok, volume 2.
- Thomson T., Lovelace D., 2014. Swim track morphotypes and new track localities from the Moenkopi and Red Peak formations (Lower-Middle Triassic) with preliminary interpretations of aquatic behaviors. In: Lockley, M.G., Lucas, S.G., (Eds), Fossil footprints of Western America, New Mexico Museum of Natural History & Science Bulletin 62:103-128.
- Wilson, J. A., Carrano. M.T., 1999. Titanosaurs and the origin of "wide-gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. Paleobiology, 25:252-267. https://doi.org/10.1017/S0094837300026543
- Xing, L., Lockley, M.G., Marty, D., He, J., Hu, X., Dai, H., Matsukawa, M., Peng, G., Ye, Y., Klein, H., Zhang, J., Hao, B., Persons, S., 2016. Wide-gauge sauropod trackways from the Early Jurassic of Sichuan, China: oldest sauropod trackways from Asia with special emphasis on a specimen showing a narrow turn. Swiss Journal of Geosciences, 109:415-428. https://doi.org/10.1007/s00015-016-0229-0
- Yates, A., Hancox, J., Rubidge, B., 2004. First record of a sauropod dinosaur from the upper Elliot Formation (Early Jurassic) of South Africa. South African Journal of Science, 100: 504-506.