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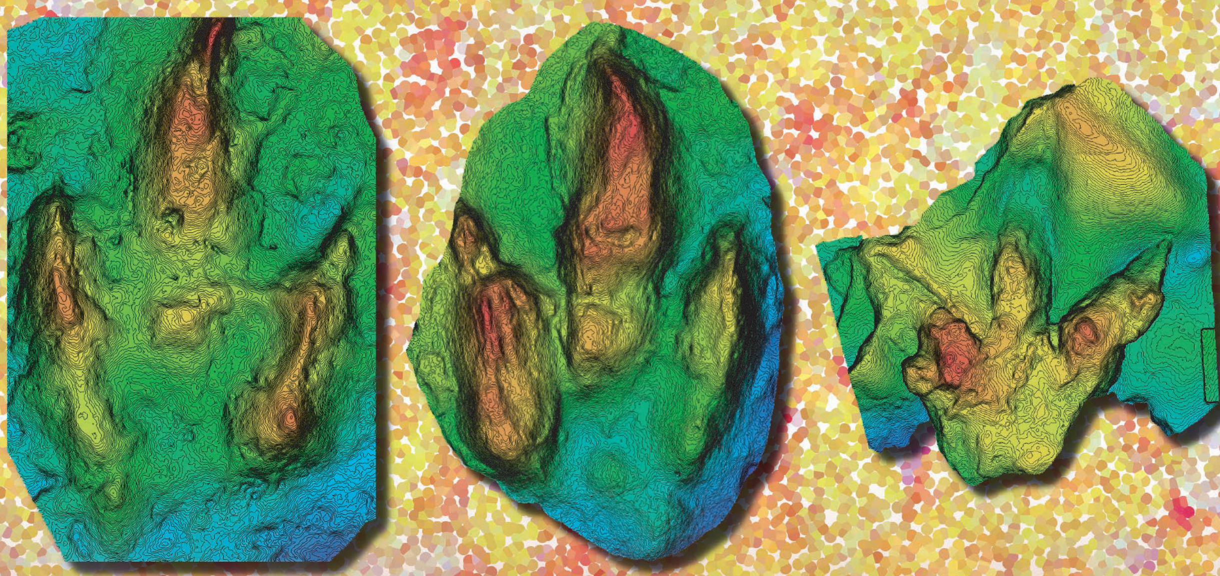

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Crocodylomorph and dinosaur tracks from the lowermost Jurassic of Le Veillon (western France): ichnotaxonomic revision of the type material (Lapparent collection)

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ABSTRACT

The coastline of Le Veillon (western France) has become a key tracksite for the study of Early Jurassic archosaurs from Europe since the second half of the 20th century. Amongst the thousand dinosaur footprints recovered from this locality, some tracks became historical and ichnotaxonomical comparative references in many studies. However, the type material from Le Veillon has never been revised. Here, we reinvestigate the type specimens from Albert-Félix de Lapparent's collection using morphometry and 3D imaging photogrammetry. Amongst the eight ichnospecies historically created at Le Veillon, only two are considered valid, i.e. *Grallator olonensis* Lapparent & Montenat, 1967 and *Grallator variabilis* Lapparent & Montenat, 1967. "*Batrachopus gilberti*" Lapparent & Montenat, 1967, "*Eubrontes veillonensis*" Lapparent & Montenat, 1967 and "*Grallator maximus*" Lapparent & Montenat, 1967 are subjective junior synonyms of *Batrachopus deweyi* (Hitchcock, 1843) Hitchcock,

KEY WORDS
Theropod footprints,
crocodylomorph tracks,
Hettangian,
Talmont-Saint-Hilaire,
Vendée.

1845, *Eubrontes giganteus* Hitchcock, 1845 and *Grallator minusculus* (Hitchcock, 1858) Demathieu, Gand, Sciau & Freytet, 2002, respectively. The ichnogenus "*Talmontopus*" Lapparent & Montenat, 1967 is a subjective senior synonym of *Kayentapus* Welles, 1971, and its type ichnospecies ("*T. tersi*" Lapparent & Montenat, 1967) is regarded as a *nomen dubium*. "*Anatopus*" Lapparent & Montenat, 1967 (and its type ichnospecies "*A. palmatus*" Lapparent & Montenat, 1967) and "*Saltopoides*" Lapparent & Montenat, 1967 (and its type ichnospecies "*S. igalensis*" Lapparent & Montenat, 1967) are considered as *nomina dubia*. The tracks initially ascribed to *Dahutherium* Montenat, 1968 are here reinterpreted as *Batrachopus* isp. and indeterminate grallatorid tracks. The ichnoassemblage from Le Veillon is more similar to tracks from the Grands Causses area (southern France) than to any other Lower Jurassic ichnoassemblage in Europe. Although contemporaneous body fossils remain unknown in Vendée, the archosaur tracks from Le Veillon confirm the co-occurrence of crocodylomorphs and theropods in littoral environments from the central part of Laurasia during the Hettangian.

RÉSUMÉ

Empreintes de crocodylomorphes et de dinosaures du Jurassique inférieur du Veillon (ouest de la France): révision ichnotaxonomique du matériel type (Collection Lapparent).

Depuis la seconde moitié du XXe siècle, le littoral du Veillon (ouest de la France) est devenu un site capital pour l'étude des traces de pas d'archosaures du Jurassique inférieur d'Europe. Parmi le millier d'empreintes de dinosaures découvertes dans ce secteur, certaines traces historiques sont devenues des références ichnotaxonomiques dans de nombreuses études comparatives. Cependant, le matériel type du Veillon n'a jamais été révisé. Ici, nous réexaminons les spécimens types de la Collection Albert-Félix de Lapparent en utilisant la morphométrie et l'imagerie 3D par photogrammétrie. Parmi les huit ichnoespèces historiquement créées au Veillon, seulement deux sont valides, i.e. *Grallator olonensis* Lapparent & Montenat, 1967 et *Grallator variabilis* Lapparent & Montenat, 1967. "*Batrachopus gilberti*" Lapparent & Montenat, 1967, "*Eubrontes veillonensis*" Lapparent & Montenat, 1967 et "*Grallator maximus*" Lapparent & Montenat, 1967 sont respectivement des synonymes juniors subjectifs de *Batrachopus deweyi* (Hitchcock, 1843) Hitchcock, 1845, *Eubrontes giganteus* Hitchcock, 1845 et *Grallator minusculus* (Hitchcock, 1858) Demathieu, Gand, Sciau & Freytet, 2002. L'ichnogenre "*Talmontopus*" Lapparent & Montenat, 1967 est un synonyme senior subjectif de *Kayentapus* Welles, 1971, et son ichnoespèce type ("*T. tersi*" Lapparent & Montenat, 1967) est considérée comme *nomen dubium*. "*Anatopus*" Lapparent & Montenat, 1967 (et son ichnoespèce type "*A. palmatus*" Lapparent & Montenat, 1967) et "*Saltopoides*" Lapparent & Montenat, 1967 (et son ichnoespèce type "*S. igalensis*" Lapparent & Montenat, 1967) sont considérés comme des *nomina dubia*. Les traces initialement attribuées à *Dahutherium* Montenat, 1968 sont ici réinterprétées comme *Batrachopus* isp. et des traces grallatoroïdes indéterminées. A l'échelle européenne, parmi les ichnoassemblages du Jurassique inférieur, c'est avec celui des Grands Causses (sud de la France) que les traces du Veillon montrent le plus de similitudes. Bien que leurs restes squelettiques soient encore inconnus en Vendée, les traces d'archosaures du Veillon confirment la co-occurrence de crocodylomorphes et de théropodes dans les environnements littoraux de la partie centrale de la Laurasia durant l'Hettangien.

MOTS CLÉS
Empreintes de théropodes, empreintes de crocodylomorphes, Hettangien, Talmont-Saint-Hilaire, Vendée.

INTRODUCTION

In 1935, the naturalist Edmond Bocquier (1881-1948) mentioned the presence of "human foot-like" concavities forming alignments on the surface of sandstones from the tidal area of Talmont-Saint-Hilaire, in Vendée, western France (Bocquier 1935; Godard 2003; Viaud & Godard 2008). However, he did not correctly interpret these structures and suggested they were probably produced by marine erosion. It is only in 1963 that Gilbert Bessonnat first interpreted these depressions as archosaur tracks (Lapparent & Montenat 1967). Several field prospecting trips and scientific excavations were undertaken in 1963, 1966 and between 1986 and 1987 (Lapparent & Montenat 1967; Viaud & Duclous 2003). Bessonnat *et al.* (1965) mentioned more than two hundred tracks. In their monograph, Lapparent & Montenat (1967) estimated that the tidal flat would bear around a thousand crocodylomorph and dinosaur tracks. They provided the first and only detailed ichnological analysis of this tracksite. In this work, they erected three ichnogenera (i.e. "*Anatopus*" Lapparent & Montenat, 1967, "*Saltopoides*" Lapparent & Montenat, 1967 and "*Talmontopus*" Lapparent & Montenat, 1967) and eight ichnospecies (i.e. "*Anatopus palmatus*" Lapparent & Montenat, 1967, "*Batrachopus gilberti*" Lapparent & Montenat, 1967, "*Eubrontes veillonensis*" Lapparent & Montenat, 1967, "*Grallator maximus*" Lapparent & Montenat, 1967, *Grallator olonensis* Lapparent & Montenat, 1967, *Grallator variabilis* Lapparent & Montenat, 1967, "*Saltopoides igalensis*" Lapparent & Montenat, 1967 and "*Talmontopus tersi*" Lapparent & Montenat, 1967). The validity of some of these ichnotaxa was questioned by several authors (e.g. Lockley & Meyer 2000; Demathieu 2003), but the type material was never revised.

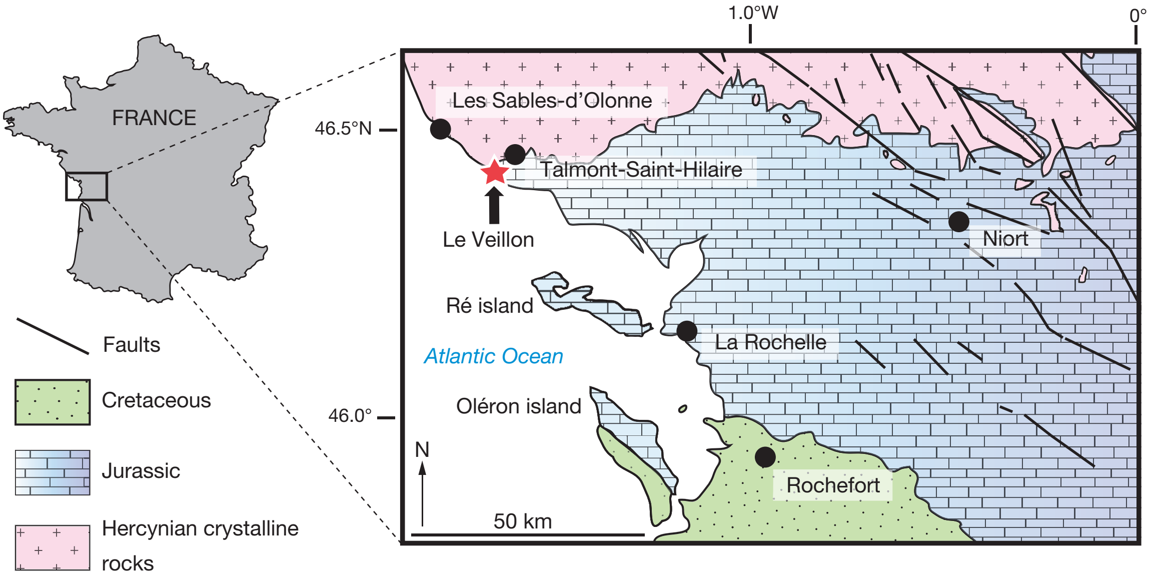

Fig. 1. — Simplified geological map of the study area and location of the tracksite of Le Veillon.

Amongst the many academic institutions and museums housing archosaur tracks from Le Veillon (see the complete list of institutions in Viaud 2003), from a scientific point of view, the collection of the Institut Polytechnique UniLaSalle (Beauvais, France) appears to be the most important. It includes all the type specimens that Lapparent & Montenat (1967) used to erect and describe their ichnotaxa. This collection was constituted by the geologist and palaeontologist Albert-Félix Cochon de Lapparent (1905-1975). As the tracksite of Le Veillon is strongly altered by marine erosion and massive excavations (Viaud 2003), this collection represents an outstanding heritage for this locality. Here we reinvestigate the type material of Lapparent & Montenat (1967) using morphometry and 3D imaging photogrammetry in order to revise the validity of the ichnotaxa from Le Veillon.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The tracksite is located 5 km south-west of Talmont-Saint-Hilaire, in the northwesternmost part of the Aquitaine Basin (Fig. 1), along the southern edge of the Armorican Massif (northwestern France), in the Vendée department. The tracksite is located along a 700-800 m long portion of the Atlantic coastline between the beach from Le Veillon and Port Bourgenay. The tracksite is only visible during low tide. Most of the tracks of the Lapparent collection were collected at the "Pointe du Veillon" and the "Anse de la République". The Hettangian deposits from the Talmont-Saint-Hilaire coastline can be divided into two informal formations: 1) a detrital Formation; and 2) a Dolomitic and Limestone Formation. The former, only visible during low tide, consists of lenticular green sandstones that alternate with green claystones or argillites. All tracks analysed in this study were collected by Lapparent & Montenat (1967) in this formation. However, rare tracks were observed in the overlying Dolomitic and Limestone Formation (Lapparent & Montenat 1967; Montenat & Bessonnat 2002). At Le Veillon, the Detrital Formation yielded abundant conifer remains including leafy axes (*Brachyphyllum* sp., *Hirmeriella airelensis* Muir & van Konijnenburg-van Cittert, 1970, *Pagiophyllum araucaricum* (Schimper, 1870) Salfeld emend. Barale, 1981 and *Pagiophyllum peregrinum* (Lindley & Hutton, 1833) Schenk emend. Kendall, 1948) and pollen grains (*Classopollis* H.D. Pflug, 1953) (Thévenard *et al.* 2003). The Dolomitic and Limestone Formation is mainly exposed in the cliffs along the coastline. The lower part of this formation consists of massive, yellowish-brownish to reddish dolomite beds that alternate with green to blue claystones. The upper part of the Dolomitic and Limestone Formation consists of grey to yellowish coquinas and dolomitic/calcarenitic limestone beds. First regarded as Rhaetian by Lapparent & Montenat (1967), the age of the Detrital Formation was debated by Montenat & Bessonnat (2002) and later challenged by Thévenard *et al.* (2003) who proposed a Hettangian age (Early Jurassic) based on the plant assemblage. The composition of the Detrital Formation ichnoassemblage that we re-evaluate here corroborates this dating. The malacofauna from the coquinas of the limestone levels further attests a Hettangian age (Ters 1961).

MATERIAL AND METHODS

In 2022 and 2023, we investigated the Lapparent collection at the Institut Polytechnique UniLaSalle (Beauvais, France). The largest part of this collection corresponds to archosaur tracks from the Early Jurassic sandstones of Talmont-Saint-Hilaire. It consists of tetradactyl/pentadactyl crocodylomorph tracks and tridactyl dinosaur tracks. Their preservation is variable, from exquisitely preserved tracks to poorly preserved tracks.

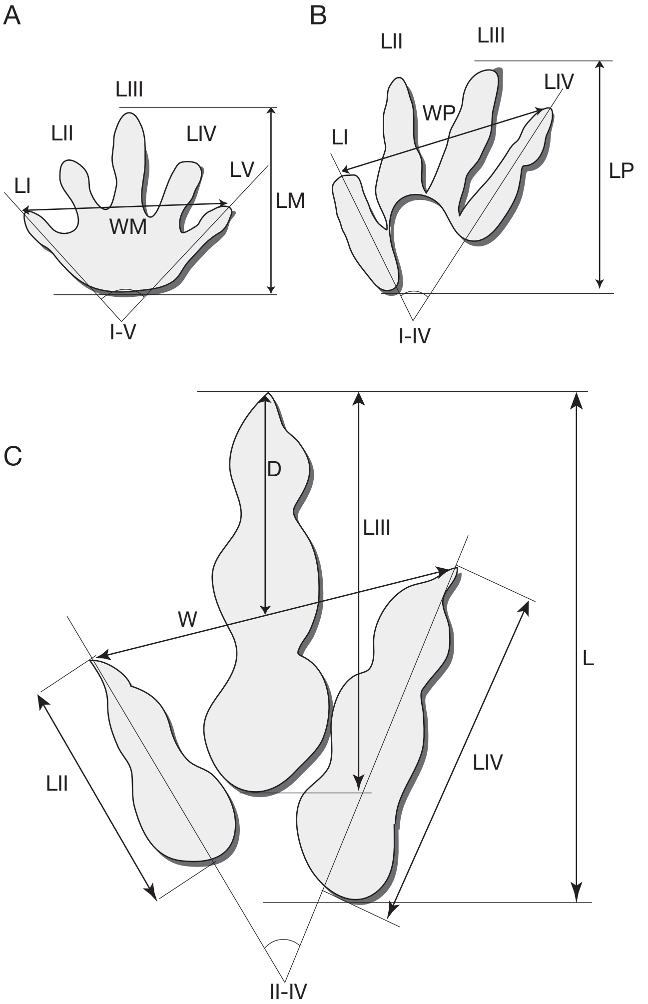

Fig. 2. — Measurements taken on tracks from the Lapparent collection: **A**, for crocodylomorph manus imprint; **B**, for crocodylomorph pes track; **C**, for dinosaur footprint. Abbreviations: **L**, length of footprint (for dinosaur tracks); **LM**, **LP**, length of manus and pes tracks, respectively (for crocodylomorph tracks); **W**, width of footprint (for dinosaur tracks); **WM**, **WP**, width of manus and pes tracks, respectively (for crocodylomorph tracks); **LI**, **LII**, **LIII**, **LIV**, **LV**, lengths of digits I, II, III, IV and V, respectively; **D**, length of the free part of digit III ; **I-V**, **I-IV**, **II-IV**, divarication angles between digits I and V, digits I and IV, then digits II and IV, respectively.

The Lapparent collection includes the type material used to erect the following ichnotaxa: "*Anatopus palmatus*" (ULB-04C15_B, holotype), "*Batrachopus gilberti*" (ULB-04C10_A, holotype), "*Eubrontes veillonensis*" (ULB-04D21_A, plaster cast of the holotype), "*Grallator maximus*" (ULB-04C13_B, plaster cast of the holotype), *Grallator olonensis* (ULB-04D19_A and ULB-04C12_A syntypes), *Grallator variabilis* (ULB-04C08_D, plaster cast of the holotype; ULB-04C05_A and ULB-04C08_A, paratypes), "*Saltopoides igalensis*" (ULB-04C01_B, plaster cast of one footprint from the type trackway) and "*Talmontopus tersi*" (ULB-04C02_A, holotype). A list of the type specimens is given in Tables 1 and 2.

One hundred specimens from the Lapparent collection were measured. The descriptive terminology and measured parameters used to describe crocodylomorph and dinosaur tracks largely follow those from Leonardi (1987), Demathieu *et al.* (2002) and Milàn & Hedegaard (2010). In the section "Palaeoichnology" below, the morphometric parameters are described by giving three values: the minimum, the average (in brackets) and the maximum. Twenty-seven crocodylomorph tracks (Table 1) and seventy-three dinosaur tracks (Table 2) were measured.

The measured values of the tracks from the Lapparent collection were compared with a large dataset including measurements of 406 tridactyl dinosaur tracks from various Early Jurassic strata of the United States (based on data from Weems 1992, 2019; Demathieu *et al.* 2002 and Gand *et al.* 2018) and the Causses Basin, southern France (based on data from Demathieu *et al.* 2002 and Moreau *et al.* 2021). Locomotion speed and height of the hip were estimated based on the formulas of Alexander (1976) and Thulborn (1990). In order to generate 3D-photogrammetric reconstructions of each slab-bearing tracks, the software Agisoft PhotoScan Professional 1.2.4 was used to align and combine multiple digital photographs taken with a Nikon D5200 camera coupled with an AF-S NIKKOR 18-105 mm f/3.5-5.6G ED camera lens. The same software was used to produce 3D-photogrammetric textured meshes and digital elevation models (DEMs) in false colours.

Abbreviations

L	length of footprints (for dinosaur tracks);
LM	length of manus tracks (for crocodylomorph tracks);
LP	length of pes tracks (for crocodylomorph tracks);
W	width of footprints (for dinosaur tracks);
WM	width of manus tracks (for crocodylomorph tracks);
WP	width of pes tracks (for crocodylomorph tracks);
LI	length of digit I;
LII	length of digit II;
LIII	length of digit III;
LIV	length of digit IV;
LV	length of digit V;
I-V	divarication angle between digits I and V;
I-IV	divarication angle between digits I and IV;
II-IV	divarication angle between digits II and IV;
D	length of the free part of digit III *sensu* Demathieu *et al.* (2002) (for tridactyl dinosaur footprints).

SYSTEMATIC PALAEOICHNOLOGY

Amongst the ichnotaxa erected by Lapparent & Montenat (1967) we distinguish: 1) the valid ichnotaxa *Grallator olonensis* and *Grallator variabilis*; and 2) the invalid ichnotaxa "*Anatopus palmatus*", "*Batrachopus gilberti*", "*Eubrontes veillonensis*", "*Grallator maximus*", "*Saltopoides igalensis*" and "*Talmontopus tersi*". Lapparent & Montenat (1967) also described additional and problematic tracks that they identified as "*Dahutherium* sp.", "Unnamed track n°1", and "Unnamed track n°2". All these tracks are revised here.

Nomenclatural remarks

The ichnotaxonomy of the "classic" Early Jurassic tridactyl footprints such as *Anchisauripus* Lull, 1904, *Grallator* Hitchcock, 1858 and *Eubrontes* Hitchcock, 1845 is complex and remains in the centre of many debates. According to Olsen & Galton (1984), the difference in size of these three kinds of

Table 1. — Values measured on Hettangian crocodylomorph tracks from Le Veillon. Abbreviations: **LM**, **LP**, length of manus and pes tracks, respectively; **WM**, **WP**, width of manus and pes tracks, respectively; **I-V**, divarication angle between digit I and digit V; **I-IV**, divarication angle between digit I and digit IV (all in cm except I-IV and I-V in degrees).

Specimens	Lapparent & Montenat 1967	This study	Pes/manus	LM	WM	I-V	LP	WP	I-IV
04C02_B_1	*B. gilberti* (pl. I.3)	*B. deweyi*	Pes	–	–	–	3.9	–	–
04C02_B_2	*B. gilberti* (fig. 4A; pl. I.3)	*B. deweyi*	Pes	–	–	–	3.1	3.2	–
04C02_B_3	*B. gilberti* (pl. I.3)	*B. deweyi*	Pes	–	–	–	3.5	3.1	73
04C02_B_4	*B. gilberti* (pl. I.3)	*B. deweyi*	Manus	1.7	1.8	–	–	–	–
04C04_A_2	*B. gilberti* (fig. 4Bb; pl. VIII)	*B. deweyi*	Pes	–	–	–	3.9	3.1	57
04C04_A_3	*B. gilberti* (pl. VIII)	*B. deweyi*	Manus	1.3	1.8	–	–	–	–
04C09_B	–	*B. deweyi*	Pes/manus set	2.1	2	–	–	–	–
04C10_A_1	*B. gilberti* (fig. 4A; pl. I.1) Holotype	*B. deweyi*	Pes/manus set	2	1.9	–	3.8	3.1	60
04C10_A_2	*B. gilberti* (fig. 4A; pl. I.1) Holotype	*B. deweyi*	Pes/manus set	–	–	–	3.1	2.9	64
04C14_A	*B. gilberti* (fig. 4Bc)	*B. deweyi*	Manus	1.1	1.6	–	–	–	–
04C14_C	*B. gilberti* (pl. I.2)	*B. deweyi*	Pes/manus set	1.7	–	–	3	3.8	44
04C14_D	–	*B. deweyi*	Pes	–	–	–	2.7	2.4	
04C14_F	–	*B. deweyi*	Pes/manus set	1.9	1.6	–	3.4	2.8	36
04C14_G	–	*B. deweyi*	Pes/manus set	1.8	1.7	–	2.9	2.1	–
04C14_H	–	*B. deweyi*	Pes	–	–	–	3.1	–	–
ULB-04C10_E	–	*B. deweyi*	Pes P1	–	–	–	2.9	3.2	79
ULB-04C10_E	–	*B. deweyi*	Pes P3	–	–	–	3	3	80
ULB-04C10_E	–	*B. deweyi*	Manus M4	2.2	2.2	–	–	–	–
ULB-04C10_E	–	*B. deweyi*	Pes P5	–	–	–	2.9	3.2	82
ULB-04C10_E	–	*B. deweyi*	Manus M5	2.4	–	–	–	–	–
ULB-04C14_I	Unnamed track n°1 (fig. 18)	*Batrachopus* isp.	Pes	–	–	–	3.3	3.2	–
ULB-04C17_A	Unnamed track n°1 (fig. 18)	*Batrachopus* isp.	Pes	–	–	–	3.6	2.8	–
ULB-04C15_A	*Dahutherium* sp. (fig. 5bis)	*Batrachopus* isp.	Pes	–	–	–	3	3.9	83

tracks reflects an ontogenetic series and justifies the use of a single ichnotaxon: *Grallator, Anchisauripus* and *Eubrontes* are small-, medium- and large-sized tracks, respectively, i.e. less than 15 cm, about 20 cm long and up to 25 cm long, respectively, according to Olsen *et al.* (1998). Olsen (1980) and Olsen & Galton (1984) recommended considering *Anchisauripus* and *Eubrontes* as subjective junior synonyms of *Grallator*. In addition, Weems (1992) could not see any significant morphological difference between *Grallator* and *Anchisauripus*, and he rejected the junior name *Anchisauripus*. While Klein & Lucas (2021) agree in principle to argue that *Grallator*, *Anchisauripus* and *Eubrontes* should be one ichnogenus, they continue to use the three ichnogeneric names as useful terms to identify theropod tracks of different sizes. Because of the wide use of these names in the literature, Klein & Lucas (2021) propose to group them in the *Grallator-Anchisauripus-Eubrontes* (GAE) plexus. Although Olsen *et al.* (1998) considered *Anchisauripus*, *Grallator* and *Eubrontes* as distinctive ichnogenera, Demathieu (1993), Demathieu & Sciau (1992) and Demathieu *et al.* (2002) did not used *Anchisauripus* for medium-sized tridactyl tracks (i.e. L = 15-30 cm) from the Early Jurassic deposits of France. They justified this choice by the systematic absence of a hallux track which is an occasional character of *Anchisauripus* (Lull 1904). Accordingly, Demathieu *et al.* (2002) emended the diagnosis of *Grallator* in the following term: "*Tridactyl footprints II-IV, from some centimetres to up to a little over 30 cm long, with slender digits in small forms and wider ones in the largest. Digits are often separated from each other and bear well-marked pads. Length of the free part of III smaller as track-size increases. L/D varies from 2.24 to 2.78 at the 5% threshold. Angle II-IV up to 57°*" (translated from French). The ichnological assemblage from Le Veillon shares strong similarities with tracks found in the Early Jurassic of the Causses Basin, this is why we follow here Demathieu *et al.* (2002) and use *Grallator* for medium-sized tridactyl footprints.

VALID ICHNOTAXA

Ichnogenus *Grallator* Hitchcock, 1858

Grallator olonensis Lapparent & Montenat, 1967 (Fig. 3)

Grallator olonensis Lapparent & Montenat, 1967: 14-16, pl. III.1-2, fig. 6.

Syntypes. — ULB-04D19_A1 to ULB-04D19_A13. Lapparent & Montenat (1967) defined the "type" of *G. olonensis* as a surface bearing 25 footprints (surface "B1" in Lapparent & Montenat, 1967). A fragment of this surface is conserved in the Lapparent collection. It consists of the slab ULB-04D19_A (Fig. 3A, B) which bears thirteen tracks preserved as concave epireliefs. The slab ULB-04C12_A ("B1bis" in Lapparent & Montenat, 1967) corresponds to the convexe hyporeliefs of the slab ULB-04D19_A.

Examined material. — ULB-04C03_B, ULB-04C03_C, ULB-04C03_D, ULB-04C03_E, ULB-04C03_F, ULB-04C05_C, ULB-04C07_A, ULB-04C08_C, ULB-04C08_E, ULB-04C08_G, ULB-04C09_A, ULB-04C09_C, ULB-04C11_A, ULB-04C17_E, ULB-04C19_A, ULB-04D17_A, ULB-04D17_B, ULB-04D17_C, ULB-04D22_B.

Diagnosis. —Tridactyl, very small-sized tracks (L = 3-5 cm), longer than wide and with a long projection of the trace of digit III (L/D = 2.1 in average). L/W ratio quite variable (1.2-2.5). Well-defined, very thin, elongated and often separated impressions of digits.

Table 2. — Measured values on Hettangian tridactyl theropod tracks from Le Veillon. Abbreviations: **L**, length of the trace; **W**, width of the trace; **D**, length of the free part of digit III; **II-IV**, divarication angle between digit II and digit IV (all in cm except II-IV in degrees).

Specimens	Lapparent & Montenat (1967)	This study	L	W	D	II-IV
ULB-04C03_B_1	–	*G. olonensis*	3.7	3	2	35
ULB-04C03_B_2	–	*G. olonensis*	3.9	2.5	1.7	37
ULB-04C03_B_3	–	*G. olonensis*	–	–	–	–
ULB-04C03_C	–	*G. olonensis*	4.6	3.2	1.9	37
ULB-04C03_D_1	–	*G. olonensis*	4.4	2.2	2	36
ULB-04C03_D_2	–	*G. olonensis*	–	–	–	–
ULB-04C03_E	–	*G. olonensis*	–	–	–	–
ULB-04C03_F	–	*G. olonensis*	4.5	2.7	2.2	44
ULB-04C05_C	–	*G. olonensis*	3.8	2.5	1.6	42
ULB-04C07_A_1	*G. olonensis* (fig. 6B)	*G. olonensis*		2.4	2	24
ULB-04C07_A_2	–	*G. olonensis*	4.2	2.4	1.9	40
ULB-04C08_C	–	*G. olonensis*	4.9	2.9	2.6	35
ULB-04C08_E_1	–	*G. olonensis*	3.8			
ULB-04C08_E_2	–	*G. olonensis*	4.4	2	2.1	25
ULB-04C08_G	–	*G. olonensis*	–	–	–	–
ULB-04C09_A	–	*G. olonensis*	–	–	–	–
ULB-04C09_C	–	*G. olonensis*	–	–	–	–
ULB-04C11_A_1	–	*G. olonensis*	3.3	2.3	1.7	36
ULB-04C11_A_2	–	*G. olonensis*	4	2.6	2	44
ULB-04C11_A_3	–	*G. olonensis*	3.6	1.8	1.5	25
ULB-04C11_A_4	*G. olonensis* (fig. 6A; pl. III.3)	*G. olonensis*		2.5	1.5	33
ULB-04C11_A_5	*G. olonensis* (fig. 6A; pl. III.3)	*G. olonensis*	4	2.5	2	31
ULB-04C11_A_6	*G. olonensis* (fig. 6A; pl. III.3)	*G. olonensis*	4.8	3.1	2.3	40
ULB-04C11_A_7	*G. olonensis* (fig. 6A; pl. III.3)	*G. olonensis*		2.7	1.5	41
ULB-04C11_A_8	–	*G. olonensis*	4.5	2.4	2.2	27
ULB-04C11_A_9	–	*G. olonensis*	4.5	2.8	2.1	33
ULB-04C17_E	–	*G. olonensis*	4.4	2.5	2.1	34
ULB-04C19_A_1	–	*G. olonensis*	4.8	3.3	2.2	41
ULB-04C19_A_2	–	*G. olonensis*	3.5	2.7	1.7	40
ULB-04C19_A_3	–	*G. olonensis*	3.6	1.8	2	36
ULB-04C19_A_4	–	*G. olonensis*	4.4	2.4	2.2	33
ULB-04C19_A_5	–	*G. olonensis*	4.3	2.4	2	36
ULB-04C19_A_6	–	*G. olonensis*	4.7	2.4	2.1	34
ULB-04D17_A_1	–	*G. olonensis*	4.5	2.5	2.4	38
ULB-04D17_A_2	–	*G. olonensis*	4.3	2.9	1.9	39
ULB-04D17_A_3	–	*G. olonensis*	4.6	2.4	2	31
ULB-04D17_A_4	–	*G. olonensis*	4.5	2.6	2.2	29
ULB-04D17_B_1	–	*G. olonensis*	4.6	2.8	2.2	37
ULB-04D17_B_2	–	*G. olonensis*	4.3	2.5	2.2	37
ULB-04D17_C_1	–	*G. olonensis*	3.4	1.5	1.7	24
ULB-04D17_C_2	–	*G. olonensis*	4.5	2.7	2	
ULB-04D17_C_3	–	*G. olonensis*	4	2.7	1.8	38
ULB-04D19_A_1	*G. olonensis* (fig. 6A; pl. III.1) “Type”	*G. olonensis* Syntype	4.8	2.5	2.4	34
ULB-04D19_A_2	*G. olonensis* (fig. 6A; pl. III.1) “Type”	*G. olonensis* Syntype	4.2	2.5	1.9	31
ULB-04D19_A_3	*G. olonensis* (fig. 6A; pl. III.1) “Type”	*G. olonensis* Syntype	4.6	2.8	2	33
ULB-04D19_A_4	*G. olonensis* (fig. 6A; pl. III.1) “Type”	*G. olonensis* Syntype	4.3	2.5	2.2	25
ULB-04D19_A_5	*G. olonensis* (fig. 6A; pl. III.1) “Type”	*G. olonensis* Syntype	4.5	2.3	2.1	34
ULB-04D19_A_6	*G. olonensis* (fig. 6A; pl. III.1) “Type”	*G. olonensis* Syntype	3.7	1.9	1.8	25
ULB-04D19_A_7	*G. olonensis* (fig. 6A; pl. III.1) “Type”	*G. olonensis* Syntype	–	–	–	–
ULB-04D22_B_1	–	*G. olonensis*	4.2	2.5	2	30
ULB-04D22_B_2	–	*G. olonensis*	4.2	2.5	1.8	34
ULB-04C05_A	*G. variabilis* (pl. III.3) Paratype	*G. variabilis* Paratype	12.3	6.6	4.4	34
ULB-04C05_B	–	*G. variabilis*	8.6	5.2	4.1	40
ULB-04C08_A	*G. variabilis* (pl. IV.1) Paratype	*G. variabilis* Paratype	13.1	7.2	4.6	42
ULB-04C08_B	*G. variabilis* (pl. V.1b)	*G. variabilis*	9.7	6.5	4.1	33
ULB-04C08_D	*G. variabilis* (fig. 7A) plaster cast of the holotype	*G. variabilis* plaster cast of the holotype	–	–	–	–
ULB-04C08_F	*G. variabilis*	*G. variabilis*	–	–	–	–
ULB-04C13_A	*G. variabilis* (pl. XIII.2)	*G. variabilis*	8.8	5.5	4.1	33
ULB-04C14_J_1	–	*G. variabilis*	10	7.7	4.5	35
ULB-04C14_J_2	–	*G. variabilis*	10.5	7.3	4.4	33
ULB-04C15_D	–	*G. variabilis*	–	–	–	–
ULB-04C15_E_1	*G. variabilis* (pl. IV.2)	*G. variabilis*	11.3	8	4.5	45
ULB-04C17_C	–	*G. variabilis*	12			29
ULB-04C17_D	–	*G. variabilis*	10.6	6.8	4.6	30
ULB-04C17_G	–	*G. variabilis*	10.4	6.5	4.3	24
ULB-04C18_B	*Dahutherium* sp. (fig. 5; pl. II)	*G. variabilis*	12.2	7.2	5.1	40
ULB-04C18_C	–	*G. variabilis*	11.3	7.6	4.5	46
ULB-04D18_A	*G. variabilis* (pl. V.1a)	*G. variabilis*	8.6	6.2	4.8	27

Table 2. — Continuation.

Specimens	Lapparent & Montenat (1967)	This study	L	W	D	II-IV
ULB-04D18_B	–	*G. variabilis*	12.9	7.5	4.3	31
ULB-04D18_C	*G. variabilis* (pl. XIII.1)	*G. variabilis*	13.6	8	4.8	36
ULB-04D18_D	–	*G. variabilis*	11.7	7.2	4.7	38
ULB-04D22_A	Unnamed track n°2 (fig. 15C; pl. XIII.5)	*G.* cf. *variabilis*	≈ 11	≈ 7	–	29
ULB-04C04_A_1	–	*G. minusculus*	26.2	17.7	8.2	37
ULB-04C06_A	–	*G. minusculus*	27.5	17.5	9.4	32
ULB-04C10_B	–	*G. minusculus*	26	15.5	8.3	30
ULB-04C13_B	*G. maximus* (fig. 11B; pl. XXI.1) plaster cast of the holotype	*G. minusculus*	27.7	15.9	9.2	33
ULB-04C18_B	*Dahutherium* sp. (fig. 5; pl. II)	*Grallator* isp.	≥ 14	12	–	41
ULB-04C02_A	*T. tersi* (fig. 17; pl. XXII.1) Holotype	*Kayentapus* isp.	26	21.5	9.3	64
ULB-04D21_A	*E. veillonensis* (fig. 12B; pl. XXI.3) plaster cast of the holotype	*E. giganteus*	34	26.5	10	40
ULB-04C10_C	*A. palmatus* (fig. 16B2)	*nomen dubium*	–	–	–	–
ULB-04C15_B	*A. palmatus* (fig. 16A; pl. XII.3) Holotype	*nomen dubium*	8.5	9.5	5.2	–
ULB-04C15_C	*A. palmatus* (fig. 16B1)	*nomen dubium*	–	7.5	–	55
ULB-04C01_A.	*S. igualensis* (fig. 15C; pl. XII.4)	*nomen dubium*	16.5	12.5	6.4	54
ULB-04C01_B	*S. igualensis* (fig. 15A, B) plaster cast of the holotype	*nomen dubium*	15.5	11	5	49

Impression of digit III longer than traces of digits II and IV. Trace of digit III often curved distally. Traces of digits III and IV quite similar in length. Bases of digits II and IV proximally located at the same height. Variable but low divarication angle II-IV (35° in average). Tiny, oval and well-marked phalangeal pads. Tiny marks of acuminate claws.

Description

The material includes two trackways (T1-Go and T2-Go) preserved on the same slab and each composed of at least three consecutive footprints (ULB-04D19_A; Fig. 3A, B). The longest trackway (T1-Go) is 43.5 cm long. The stride is 34.0-(36.7)-39.5 cm long and the pace is 15.1-(17.8)-20.5 cm long. Tracks form a narrow angle with the trackway midline. The material also includes several partial trackways (ULB-04C19_A, ULB-04D17_A, ULB-04D19_A). The tracks are tridactyl, very small-sized, 3.3-(4.3)-4.9 cm long and 1.5-(2.5)-3.3 cm wide (Fig. 3C-H; Table 2). Tracks are longer than wide and show a long projection of the traces of digit III. The L/W and L/D ratios are quite variable, being 1.2-(1.8)-2.5 and 1.8-(2.1)-2.4, respectively. Impressions of digits are well defined, very thin, elongated and often separated. The impression of digit III is longer than those of digits II and IV. The trace of digit III is often curved distally. The traces of digits II and IV are quite similar in length. Typically, the bases of digits II and IV are proximally located at the same height. The position of the digito-metatarsal pad of digit IV is rarely more proximal than that of digit II. The angle between digits II and IV is 24°-(34°)-44°. Phalangeal pads are tiny, oval and commonly well marked. Tracks commonly bear tiny marks of acuminate claws.

Remarks

Based on material from Le Veillon, Lapparent & Montenat (1967) erected *G. olonensis.* Although they defined a type and describe the material, they did not erect a formal diagnosis. In France and throughout the world, *G. olonensis* was only reported from Le Veillon. Other very small-sized tridactyl tracks assigned to distinct ichnospecies of *Grallator* were described from Early Jurassic strata in Connecticut (Lull 1953): *G. cursorius* Hitchcock, 1858*, G. gracilis* Hitchcock, 1865 (synonym of *G. tuberosus* according to Weems 1992) and *G. tenuis* Hitchcock, 1858. *G. cursorius* differs from *G. olonensis* in showing more slender, longer tracks (type material with L = 7.0-7.9 cm according to Weems 1992) and a base of IV much more proximal than II (Fig. 4). Although *G. gracilis* falls in the range size of *G. olonensis*, it differs from the latter in showing lower projection of III (type material with L/D = 2.6 according to Weems 1992; Fig. 4). *G. tenuis* differs from *G. olonensis* in showing longer tracks (type material with L = 6.4-6.6 cm according to Weems 1992) and the base of IV which is more proximal than II (Fig. 4). *G. olonensis* is strongly smaller than *G. cuneatus* Hitchcock, 1858, *G. variabilis* and *G. formosus* Hitchcock, 1858.

Grallator variabilis Lapparent & Montenat, 1967 (Fig. 5)

Grallator variabilis Lapparent & Montenat, 1967: 16-20, pls III.3, IV-VII, IX, XII.2, XIII.1-2, figs 7, 9-10. — Demathieu & Sciau 1992: 1565, fig. 3B. — Sciau 1998: 18; 2003: 27, 84; 2012: 54. — Demathieu *et al.* 2002: 79, pls I.1, V.

Holotype. — ULB-04C08_D (plaster cast; Fig. 5A-C).

Paratypes. — ULB-04C05_A (Fig. 5D-F) and ULB-04C08_A.

Examined material. — ULB-04C05_B, ULB-04C08_B, ULB-04C08_F, ULB-04C13_A, ULB-04C14_J, ULB-04C15_D, ULB-04C15_E, ULB-04C17_C, ULB-04C17_D, ULB-04C17_G, ULB-04C18_B, ULB-04C18_C, ULB-04D18_A, ULB-04D18_B, ULB-04D18_C, ULB-04D18_D.

Emended diagnosis. — Tridactyl, small-sized tracks (L = 8-14 cm), longer than wide (L/W = 1.6 in average). Quite long projection of the

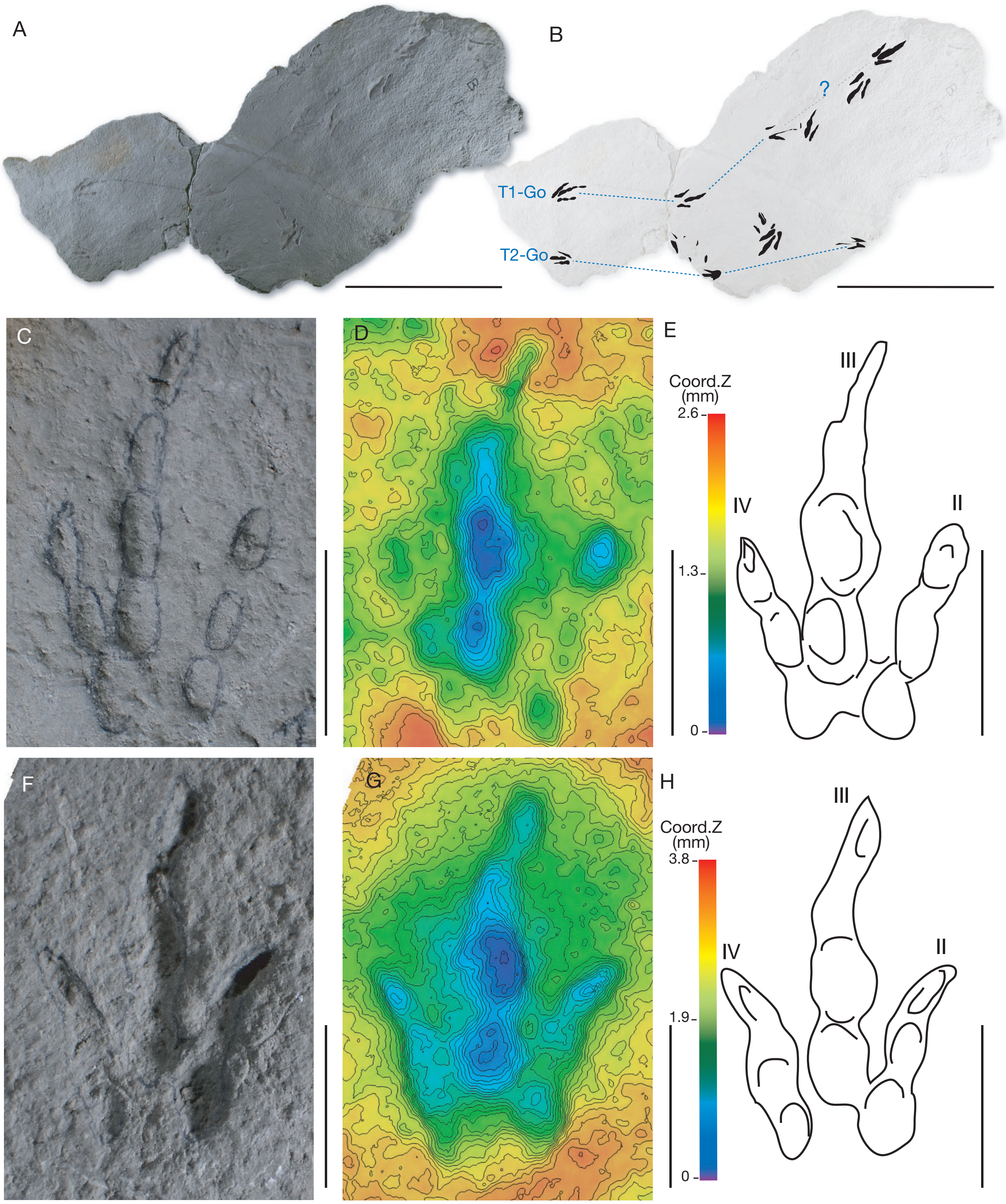

FIG. 3. — *Grallator olonensis* Lapparent & Montenat, 1967: **A**, **B**, slab ULB-04D19 bearing the trackway T1-Go, as well as T2-Go; photograph (**A**) and interpretative sketch (**B**); **C**-**E**, track 04D19_A_4 (syntype) of the trackway T1-Go, photograph (**C**), DEM and false-colour depth map (**D**) and interpretative sketch (**E**); **F**-**H**, ULB-04C11_A_6, photograph (**F**), DEM and false-colour depth map (**G**) and interpretative sketch (**H**). Scale bars: A, B, 20 cm; C-H, 2 cm.

trace of digit III (L/D = 2.5 in average). Well-defined, thin, elongated and often separated impressions of digits. Traces of digits II and III are the shortest and the longest, respectively. Base of the digito-metatarsal pad of digit IV more proximal than trace of digit II. Variable divarication angle II-IV (35° in average). Round to oval phalangeal pads. Pointed marks of claws oriented outward on digits II and IV.

Description

The tracks are tridactyl, small-sized, longer than wide (L/W = 1.3-(1.6)-1.9), 8.6-(11.0)-13.6 cm long and 5.2-(6.9)-8.0 cm wide (Fig. 5A-I; Table 2). The trace of digit III shows a long free part (L/D = 1.8-(2.4)-3). Impressions of digits are very well

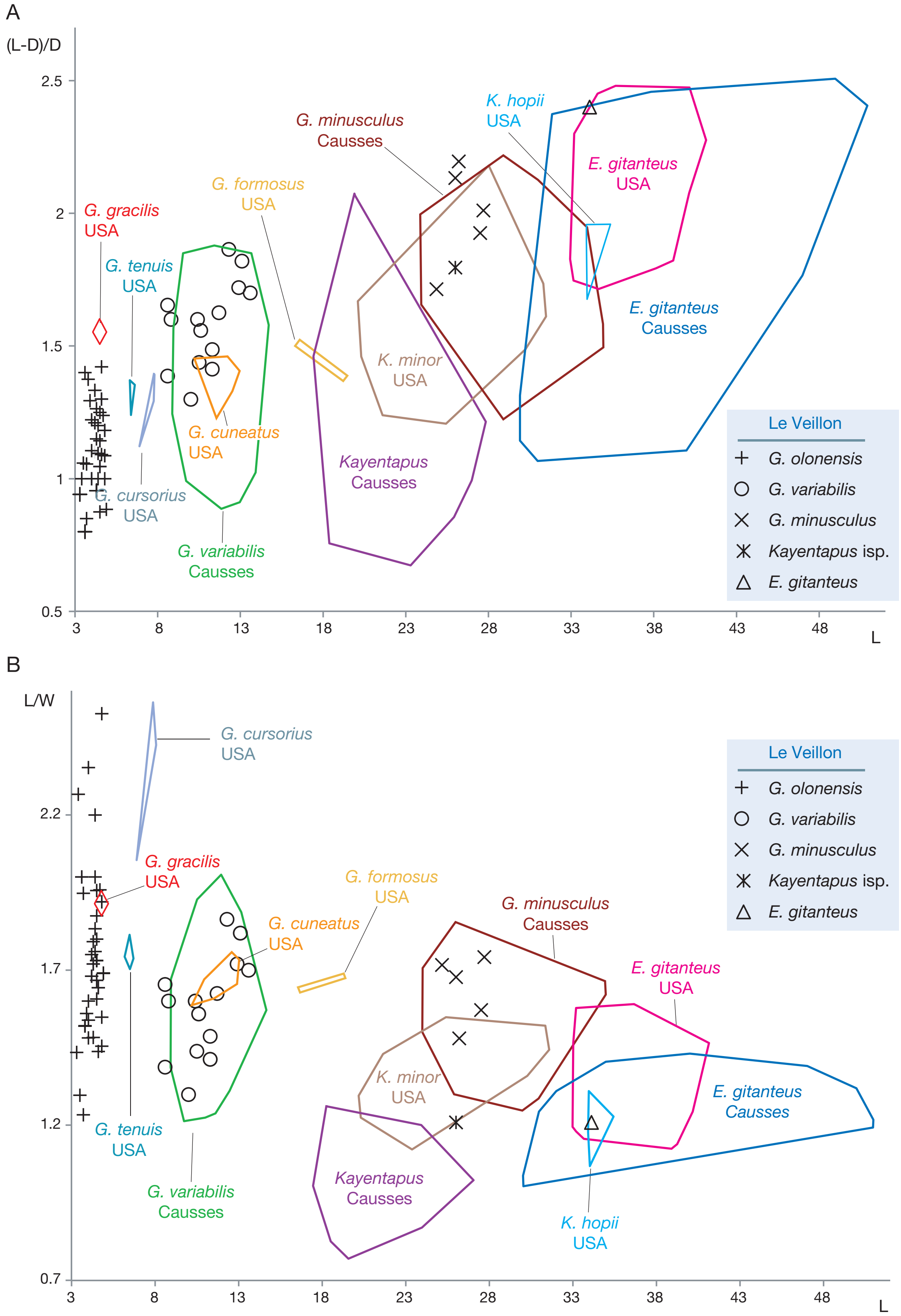

Fig. 4. — Footprints from Le Veillon compared to tridactyl tracks from the Early Jurassic of the Causses Basin (based on data from Demathieu *et al.* 2002; Moreau *et al.* 2021) and the Early Jurassic of the eastern United States (based on data from Weems 1992, 2019; Gand *et al.* 2018): **A**, bivariate diagram L vs (L–D)/D; **B**, bivariate diagram L vs L/W. L in metres.

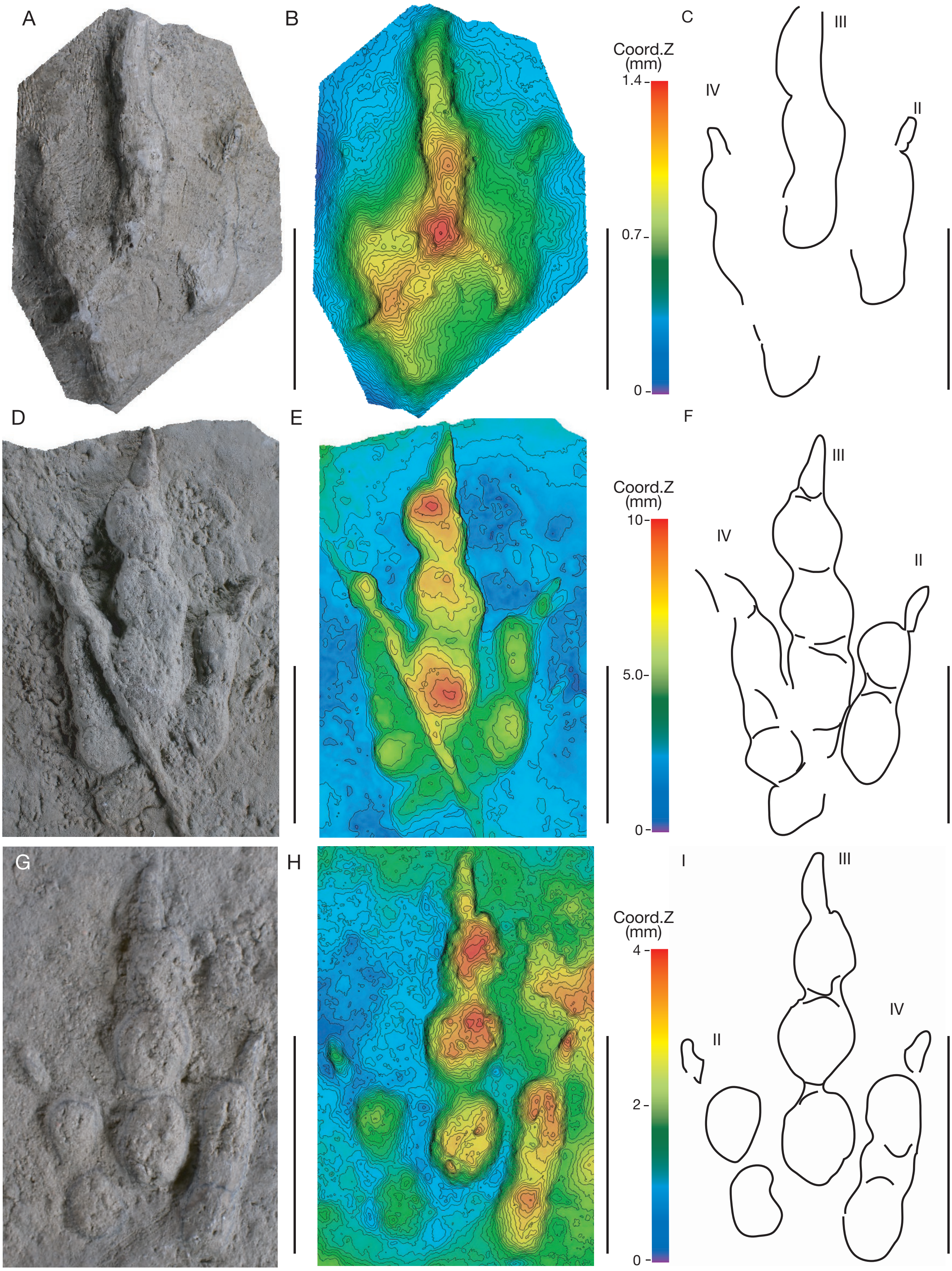

Fig. 5. — *Grallator variabilis* Lapparent & Montenat, 1967: **A**-**C**, plaster cast of the holotype, ULB-04C08_D, photograph (**A**), DEM and false-colour depth map (**B**) and interpretative sketch (**C**); **D**-**F**, paratype, ULB-04C05_A, photograph (**D**), DEM and false-colour depth map (**E**) and interpretative sketch (**F**); **G**-**I**, track ULB-04C13_A, photograph (**G**), DEM and false-colour depth map (**H**) and interpretative sketch (**I**). Scale bars: 5 cm.

defined, thin, elongated and often separated. The impression of digit III is longer than traces of digits II and IV. Traces of digits II are the shortest. At the base of the trace of digit IV, the position of the digito-metatarsal pad is more proximal than that of digit II. The divarication angle II-IV is 24°-(35°)-46°. Round to oval phalangeal pads and pointed marks of claws are commonly very well marked. Marks of claws on the traces of digits II and IV are clearly oriented outward.

Remarks

G. variabilis was erected by Lapparent & Montenat (1967) based on tracks from Le Veillon. This ichnospecies was abundantly reported in coeval tracksites from the Hettangian-Sinemurian deposits of the Causses Basin, in southern France (Demathieu & Sciau 1992; Sciau 1992; Demathieu *et al.* 2002; Gand *et al.* 2007), as well as in northern Africa (Bessedik *et al.* 2008). As mentioned by Lapparent & Montenat (1967), the morphology of *G. cuneatus* from the Connecticut is very close to that of *G. variabilis* from Le Veillon. Morphometric and statistical analyses made by Demathieu *et al.* (2002) and Gand *et al.* (2007) on *G. variabilis* from the Causses Basin confirmed that this last ichnospecies shows close morphological affinities with *G. cuneatus* (Fig. 4). According to Weems (1992), *G. cuneatus* is a synonym of *G. tenuis*. However, this ichnospecies is smaller than *G. variabilis* from Le Veillon and from the Causses Basin; L = 6.4-6.6 cm; Fig. 4). Since the case of *G. cuneatus* remains unclear, Demathieu *et al.* (2002) did not synonymise *G. variabilis* with this ichnospecies. Considering *G. variabilis* as valid, Demathieu *et al.* (2002) erected the following diagnosis (translated from the French): "*Fingers are thin with well-marked phalangeal pads. The median digit is very elongated, the lateral digits are tightened and slightly tilted. There are three pads on digits III and IV, and two on digit II. There is no heel but digit IV is slightly prolonged posteriorly. Claws are elongated and sharp forming cuneiform marks. The ratio stride/pace corresponds to an elongated stride. The paces are arranged on a same line, the median digit in the axis of the trackway, its claw oriented inwards*". The morphology of *G. variabilis* differs from the other *Grallator* ichnospecies from the United States (Lull 1953). *G. cursorius* differs from *G. variabilis* in showing more slender tracks with a higher L/W ratio (Fig. 4). *G. gracilis* is strongly smaller than *G. variabilis* whereas *G. formosus* is larger (Fig. 4).

INVALID AND PROBLEMATIC ICHNOTAXA

Ichnogenus "*Anatopus*" Lapparent & Montenat, 1967

"***Anatopus palmatus***" Lapparent & Montenat, 1967 (*nomen dubium*) (Fig. 6)

Anatopus palmatus Lapparent & Montenat, 1967: 27-29, pl. XII.3, fig. 16.

Examined material. — Holotype: ULB-04C15_B. —Other specimens: ULB-04C10_C, ULB-04C15_C.

Description

The material includes three, isolated and very poorly preserved tracks. Tracks ULB-04C15_B (Fig. 6A-C) and ULB-04C15_C (Fig. 6D-F) are tridactyl whereas ULB-04C10_C is a partial footprint and only preserves two traces of digits. Lapparent & Montenat (1967) included tracks with two kinds of morphologies in this ichnotaxon.

ULB-04C15_B is small-sized and wider than long (L = 8.5 cm, W = 9.5 cm; Fig. 6A-C; Table 2). The trace of digit III shows a long free part (L/D = 1.6). Impressions of digits are thin, elongated, separated and apically sharp. The impression of digit III is markedly longer than traces of digits II and IV that are not fully impressed (proximal part not marked). Marks of claws are well marked. They are oriented outward on traces of digits II and IV.

ULB-04C15_C is small-sized, 7.5 cm wide (Fig. 6D-F; Table 2). Even if the proximal part of ULB-04C15_C is broken, the footprint is longer than wide. The trace of digit III is thin, elongated, shows a long free part and rounded to oval phalangeal pads. The divarication angle II-IV is 55°.

Remarks

Lapparent & Montenat (1967) justified the erection of "*Anatopus palmatus*" (without establishing its diagnosis) by 1) the occasional presence of a skin mark forming a web between tracks of digits II, III and IV; and 2) traces of digits II and IV very short compare to digit III (Fig. 6A, B). Lapparent & Montenat (1967) indicated that only the holotype (ULB-04C15_B; Fig. 6A-C) shows the mark of a web. After reinvestigation of the holotype, we are not convinced by the description of Lapparent & Montenat (1967) (Fig. 6B, C). The structure considered by Lapparent & Montenat (1967) as the border of a web clearly shows a sedimentary origin (structure propagated beyond the track). The holotype of "*Anatopus palmatus*" consists of an undertrack, explaining why the marks of digits II and IV are so short. The sketch of ULB-04C15_C proposed in fig. 16B1 of Lapparent & Montenat (1967) does not correspond to the morphology of the track, which actually looks more like a grallatorid footprint; however, it is too poorly preserved for a specific attribution. We thus consider "*Anatopus palmatus*" as a *nomen dubium.*

Ichnogenus *Batrachopus* Hitchcock, 1845

"***Batrachopus gilberti***" Lapparent & Montenat, 1967 (Fig. 7)

Batrachopus gilberti Lapparent & Montenat, 1967: 11-13, pl. I, fig. 4.

Status. — Subjective junior synonym of *Batrachopus deweyi* (Hitchcock, 1843) Hitchcock, 1845.

Examined material. — Holotype: ULB-04C10_A. — Other specimens: ULB-04C02_B, ULB-04C04_A, ULB-04C09_B, ULB-04C10_E, ULB-04C14_A, ULB-04C14_C, ULB-04C14_D, ULB-04C14_F, ULB-04C14_G, ULB-04C14_H.

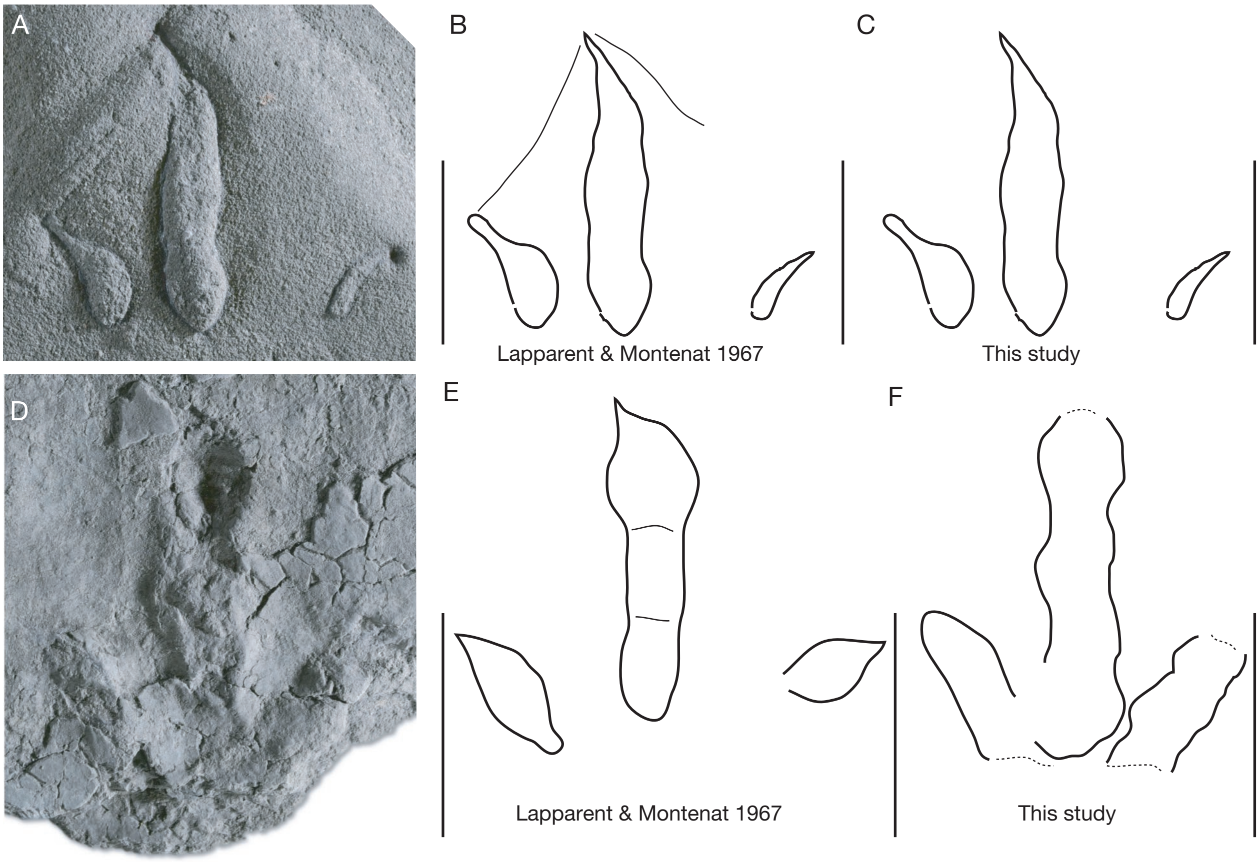

Fig. 6. — "*Anatopus palmatus*" Lapparent & Montenat, 1967, that is here invalidated: **A**-**C**, ULB-04C15_B (holotype of "*A. palmatus*"), photograph (**A**), interpretative sketch of Lapparent & Montenat (1967: fig. 16A and pl.XII.3) (**B**), and our interpretation (**C**); **D**-**F**, ULB-04C15_C, photograph (**D**), interpretative sketch of Lapparent & Montenat (1967: fig. 16B1) (**E**), and our interpretation (**F**). Scale bars: 5 cm.

Description

The material includes a single trackway (ULB-04C10_E; Fig. 7A-C) and several isolated pes/manus sets (Fig. 7D-L; Table 1). The trackway is narrow, 76 cm long and 8 cm wide and is composed of five consecutive pes/manus sets. Pes and manus track strides are 33.0-(35.5)-38.0 cm long. Pes track and manus track pace is 16.0-(17.7)-19.5 cm long. Pes and manus tracks show a small positive rotation angle relative to the trackway axis (15-(20)-25°). Pes and manus tracks show a pronounced heteropody. Pes imprints are digitigrade and functionally tetradactyl, longer than wide to as wide as long (2.7-(3.2)-3.9 cm long and 2.1-(3.0)-3.8 cm wide; Table 1). The ratio PL/PW varies from 0.8 to 1.4. On pes tracks, impressions of digits are clearly marked, straight to curved, and short to quite elongated. Their apices are rounded and can sometimes bear tiny marks of claws. On pes tracks, impression of digit III is always the longest, and impression of digit I the smallest (Fig. 7D-L). Track of digit II is often the second longest. The divarication angle of digits I-IV strongly varies (36-(64)-82°). On pes tracks, the traces of digits II and III are the deepest. Pes tracks can show a short and large plantar-like impression. Manus tracks are pentadactyl and smaller than pes tracks, wider than long to as long as wide, 1.1-(1.8)-2.4 cm long and 1.6-(1.8)-2.2 mm wide (ML/MW = 0.7-(0.)-1.9). On manus tracks, digit imprints are very short and rounded. When preserved, digit V is oriented posteriorly.

Remarks

These tracks were first ascribed to *Cheirotherium* (synonym of *Chirotherium* Kaup, 1835) by Bessonnat *et al.* (1965). This Triassic ichnogenus differs from the tracks from Le Veillon in showing larger tracks, pentadactyl pes tracks with a trace of digit V much more proximal than the group I-IV. Based on the following morphological characters, tracks from Le Veillon can be confidently ascribed to *Batrachopus* Hitchcock, 1845 (see the emended diagnosis in Olsen & Padian 1986): small quadrupedal trackway; pes tracks are digitigrade and functionally tetradactyl; digit III of the pes is the longest and digit I the shortest; pentadactyl and digitigrade manus, usually rotated so that digit II points forward, digit IV points laterally, and digit V points posteriorly; and manus much smaller than the pes.

The gross morphology of *Batrachopus* is close to those of *Antipus* Hitchcock, 1858 and *Crocodylopodus* Fuentes Vidarte & Meijide Calvo, 1999. Olsen & Padian (1986) considered *Antipus* as a subjective synonym of *Batrachopus*. However, Coombs (1996) and Lockley & Meyer (2004) rejected this proposition. According to Lockley & Meyer (2004), *Antipus* differs from *Batrachopus* in showing: much longer impressions of digits on the manus tracks; slender, tapering, quite curvated digit tracks with higher divarication angles and narrow claw impressions. The tracks from

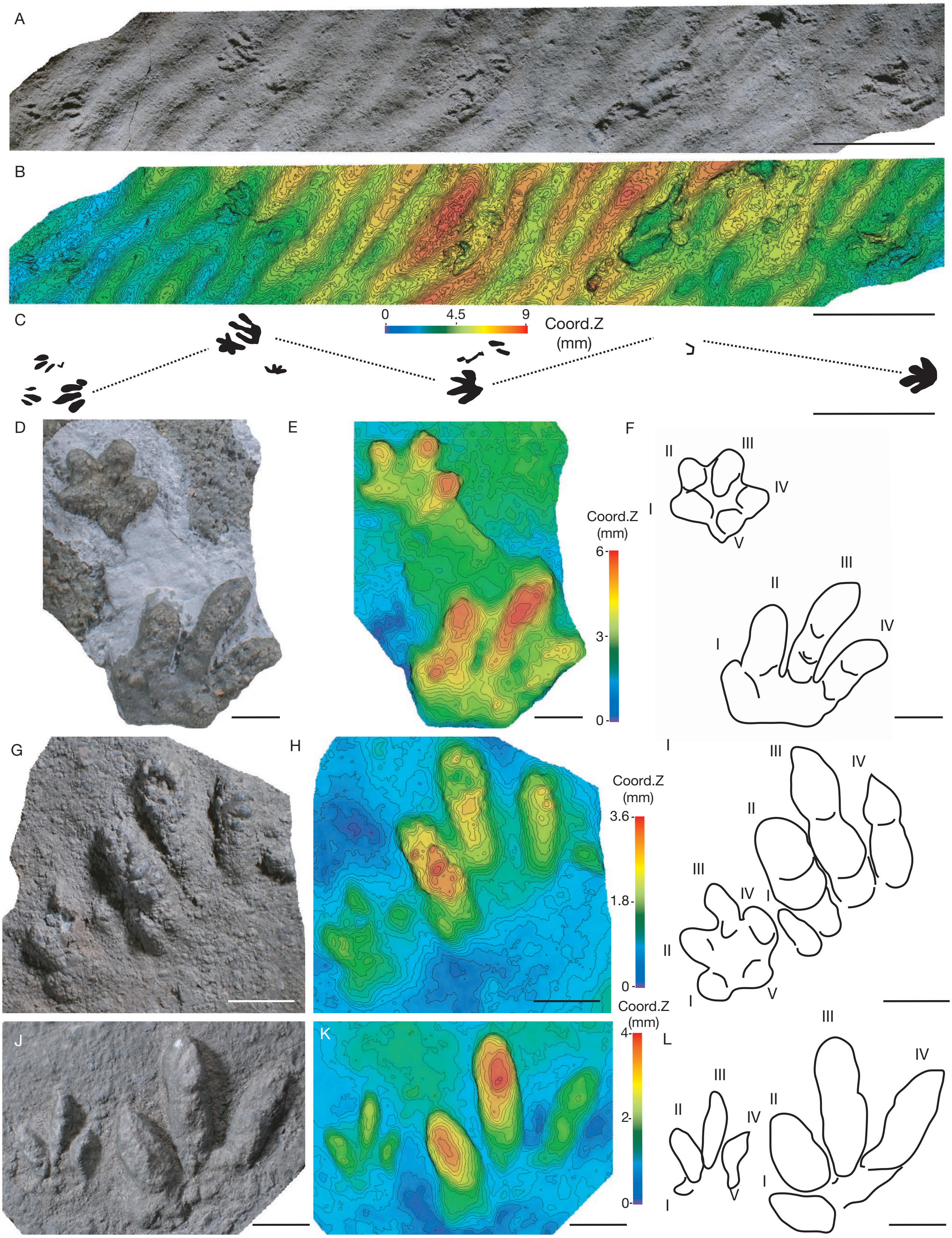

FIG. 7. — *Batrachopus deweyi* (Hitchcock, 1843) Hitchcock, 1845: **A**-**C**, trackway ULB-04C10_E, photograph (**A**), DEM and false-colour depth map (**B**) and interpretative sketch (**C**); **D**-**F**, pes/manus set 04C10_A_1 (holotype of "*B. gilberti*" that is here invalidated), photograph (**D**), DEM and false-colour depth map (**E**) and interpretative sketch (**F**); **G**-**I**, pes/manus set 04C14_C, photograph (**G**), DEM and false-colour depth map (**H**) and interpretative sketch (**I**); **J**-**L**, pes/manus set 04C14_C, photograph (**J**), DEM and false-colour depth map (**K**) and interpretative sketch (**L**). Scale bars represent: A-C, 10 cm; D-L, 1 cm.

Le Veillon clearly differ from *Antipus* in showing shorter blunt-toed digits. *Crocodylopodus* differs from tracks of Le Veillon in showing more slender and divergent digits, less outward rotation of the pes and more outward rotation of the manus (Lockley & Meyer 2004).

Based on ULB-04C10_A, Lapparent & Montenat (1967) erected *B. gilberti*. The validity of the diverse ichnospecies of *Batrachopus* was strongly debated (Olsen & Padian 1986; Rainforth 2005, 2007). In their revision of *Batrachopus*, Olsen & Padian (1986) considered only three valid ichnospecies for this ichnogenus and emended the diagnosis of each of them: *B. deweyi* (Hitchcock, 1843) Hitchcock, 1845, *B. parvulus* (Hitchcock, 1841) Hitchcock 1845 and *B. dispar* Lull, 1904. Based on the following characters, the tracks from Le Veillon can be confidently ascribed to *B. deweyi* (see emended diagnosis in Olsen & Padian 1986): range size of pes length (between 2 and 6 cm); manus tracks about 75% of the length of the pes; on pes tracks, imprints of digit II and IV are sub-equal in length. We consider "*B. gilberti*" as a junior synonym of *B. deweyi*. *B. parvulus* (see emended diagnosis in Olsen & Padian (1986)) differs from tracks of Le Veillon in showing a very short impression of digit I on pes tracks. According to Rainforth (2005), *B. parvulus* can be synonymised with the type ichnospecies *B. deweyi*. *B. dispar* (see emended diagnosis in Olsen & Padian (1986)) differs from tracks of Le Veillon in showing a stronger heteropody. Rainforth (2005) considered three additional valid ichnospecies: *B. bellus* (Hitchcock, 1858) Lull, 1904, *B. gracilior* (Hitchcock, 1865) Lull, 1904, *B. gracilis* (Hitchcock, 1848) Lull, 1904. It contrasts with Olsen & Padian (1986) who subjectively synonymised these ichnospecies in *B. deweyi*. According to Rainforth (2005), *B. bellus* cannot be synonymised with *B. deweyi* because it differs from this ichnospecies in showing tridactyl pes (not concordant with the sketch of *B. bellus* in fig. 20.2B of Olsen & Padian (1986)). Rainforth (2007) tentatively synonymised *B. gracilior* and *B. gracilis*. Olsen & Padian (1986) explained that "apart from its smaller, longer pace and the lack of impressions of digit V in the pes" *B. gracilis* is identical to *B. deweyi*.

Ichnogenus "*Dahutherium*" Montenat, 1968

"*Dahutherium*" isp.
(*nomen nudum*)
(Fig. 8)

Dahutherium sp. – Lapparent & Montenat 1967: 13-14, pl. II, figs 5-5bis. — Montenat 1968: 373-35, pl. 1.4, 2.2-9. — Demathieu & Haubold 1972: 805, 818, 820, fig. 5.8. — Gand 1974a: 9-10, pl. 8A-D; 1974b: fig. 2G. — Haubold 1984: 150, 152, fig. 102.7.

Examined material. — ULB-04C15_A, ULB-04C18_B.

Description

Lapparent & Montenat (1967) described two isolated tracks including a tetradactyl pes track (ULB-04C18_B; Fig. 8 A-C) and a tridactyl manus track (ULB-04C15_A; Fig. 8D-F) that were collected *ex-situ*. Our interpretation is that the track ULB-04C18_B described as a tetradactyl pes track by Lapparent & Montenat (1967) actually represents two superimposed tridactyl grallatorid footprints (Fig. 8 A-C). The smallest of the two superimposed tracks is longer than wide (L/W = 1.7), 12.2 cm long and 7.2 cm wide. The trace of digit III shows a long free part (L/D = 2.4). Impressions of digits are very well-defined, thin and elongated. The impression of digit III is longer than traces of digits II and IV. The trace of digits II is the shorter. At the base of the trace of digit IV, the position of the digito-metatarsal pad is more proximal than that of digit II. The divarication angle II-IV is 40°. Round to oval phalangeal pads and pointed marks of claws are well marked. The largest of the two superimposed tridactyl tracks is ≈ 14 cm long (value measured on a partial length of track, the apex of the trace of III being not well-marked), 12 cm wide. Impressions of digits are thin, elongated and separated. The divarication angle II-IV is 41°. The impression of digit III is the longest. ULB-04C15_A (Fig. 8D-F) is tetradactyl, not tridactyl as proposed by Lapparent & Montenat (1967). This track is quite wider than long, 3.0 cm long and 3.9 cm wide (Table 1). Impressions of digits are short and their apices are rounded. Traces of digit I are poorly impressed whereas those of II-IV are well marked. Impression of digit III is the longest, and impression of digit I the smallest. The divarication angle of digits I-IV is 83°.

Remarks

The ichnogenus "*Dahutherium*" was formally erected by Montenat (1968) based on material from the Middle Triassic of the Daüs Plateau (Ardèche, southern France). However, Lapparent & Montenat (1967) used this ichnotaxon (erroneously mentioned as "*Dahutherium* Montenat, 1967"), which was not yet available at that time, for the assignment of two isolated tracks from Le Veillon (as "*Dahutherium*" sp.). Adding to the confusion, they also provided the main features characterising the ichnogenus "*Dahutherium*": "*Medium-sized quadrupedal tracks; footprint dimensions = 120 × 80 mm. The difference in size and shape between manus and pes is very marked. The manus track is small, probably tetradactyl, although there are often only three digits observable. The pes is tetradactyl. The digit development order is the same as that of* Batrachopus. *The digit I, very reduced, let an inconspicuous imprint. The digits are oriented medially, little divergent, without differentiated claws* (translated from French)". *Dahutherium* has been reported from several Middle Triassic to Early Jurassic tracksites from France (Montenat 1968; Haubold 1971; Gand 1974a, b). The smallest and the largest of the two superimposed tridactyl tracks (initially interpreted as a tetradactyl "*Dahutherium*" pes by Lapparent & Montenat (1967); ULB-04C18_B) can be ascribed to *G. variabilis* and *Grallator* isp., respectively. Although Lapparent & Montenat (1967) interpreted ULB-04C15_A as a tridactyl manus track of "*Dahutherium*", the morphology and the dimensions of this specimen match with *Batrachopus*. Following Klein & Lucas (2021), "*Dahutherium*" is considered as a *nomen nudum*.

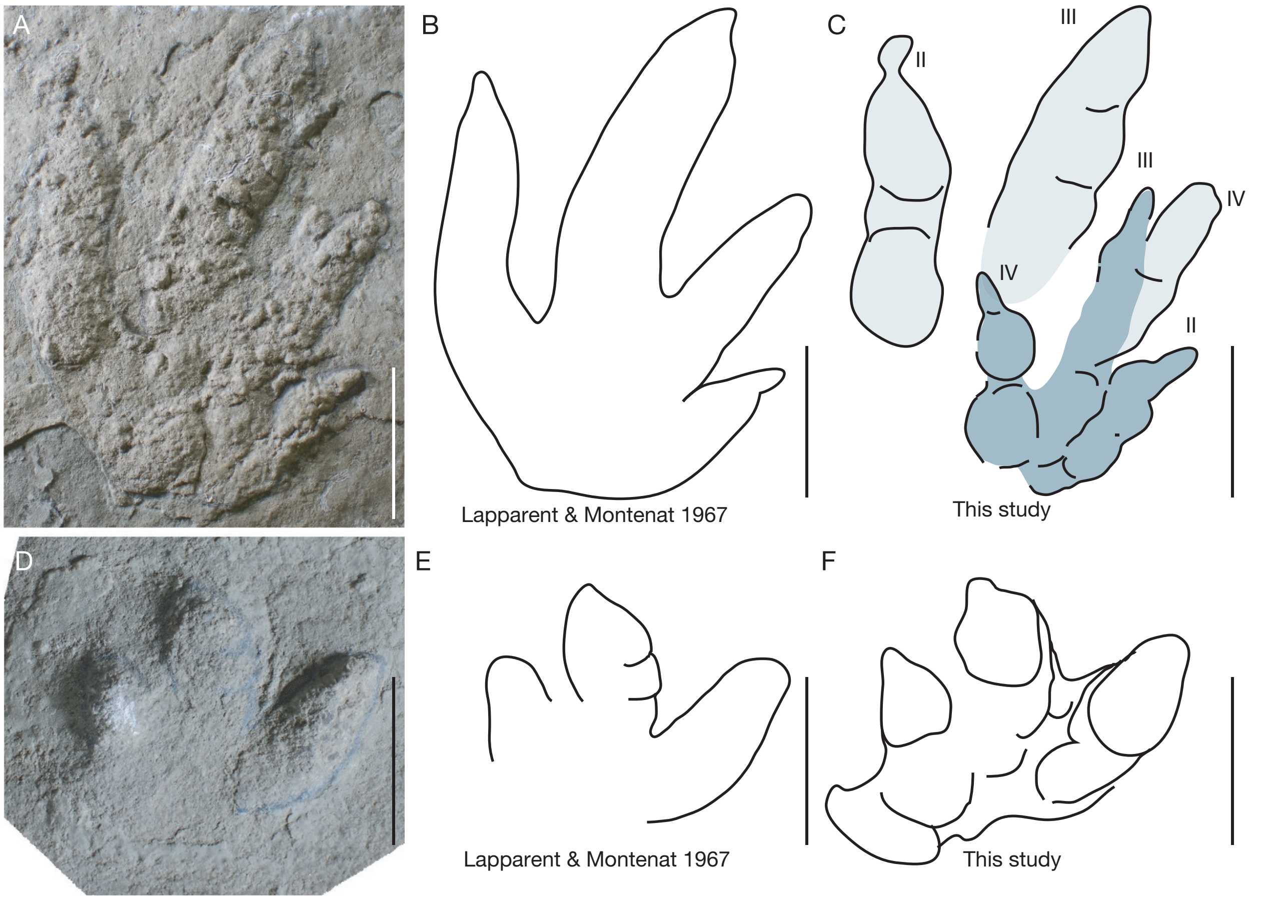

FIG. 8. — Tracks ascribed to *Dahutherium* sp. by Lapparent & Montenat (1967) and that are here reinterpreted: **A**-**C**, two superimposed tridactyl grallatorid footprints, ULB-04C18_B, photograph (**A**), interpretative sketch of Lapparent & Montenat (1967) (**B**), and our interpretation (**C**), showing a small footprint (**dark grey**) and larger footprint (**light grey**); **D**-**F**, *Batrachopus* isp., ULB-04C15_A, photograph (**D**), interpretative sketch of Lapparent & Montenat (1967) (**E**), and our interpretation (**F**). Scale bars: A-C, 5 cm; D-F, 2 cm.

Ichnogenus *Eubrontes* Hitchcock, 1845

"***Eubrontes veillonensis***" Lapparent & Montenat, 1967
(Fig. 9A-C)

Eubrontes veillonensis Lapparent & Montenat, 1967: 23-27, pl. XI.2-4, fig. 12.

STATUS. — Subjective junior synonym of *Eubrontes giganteus* Hitchcock, 1845.

EXAMINED MATERIAL. — Holotype: ULB-04D21_A (plaster cast).

DESCRIPTION

The track is tridactyl, longer than wide (L/W = 1.3), 34 cm long and 26.5 cm wide (Fig. 9A-C; Table 2). The divarication angle between digits II and IV is quite large (II-IV = 40°) and D is short (L/D = 3.5). Impressions of digits are particularly wide with well-distinguished and marked pads. The digito-metatarsal pad of digit IV is more proximal than that of digit II. Tracks display elongated and pointed claw marks.

REMARKS

Based on an *in situ* trackway composed of twelve footprints, Lapparent & Montenat (1967) erected (without diagnosis) the ichnospecies "*Eubrontes veillonensis*". ULB-04D21_A (Fig. 9A-C) is the plaster cast of one of the best-preserved footprints of this trackway. A recent survey in 2022 on the tidal flat from Le Veillon could not relocate the specimen, which was most probably destroyed. *E. giganteus* Hitchcock, 1845 was introduced based on tridactyl tracks from the Early Jurassic rocks of the Dinosaur Footprint Reservation in Holyoke, Massachusetts (Olsen *et al.* 1998). In Fig. 4, ULB-04D21_A is compared with Early Jurassic *Eubrontes giganteus* specimens from France and from the United States. This analysis shows that the *Eubrontes* track from Le Veillon fully falls within the morphological range of this ichnospecies. *E. giganteus* and "*E. veillonensis*" show similar shape of footprints with massive impressions of digits II, III and IV bearing well-marked pads and long claw marks as well as the presence of a well-marked digito-metatarsal pad of digit IV more proximal than that of digit II. Based on these observations we consider "*E. veillonensis*" as a subjective junior synonym of *E. giganteus.*

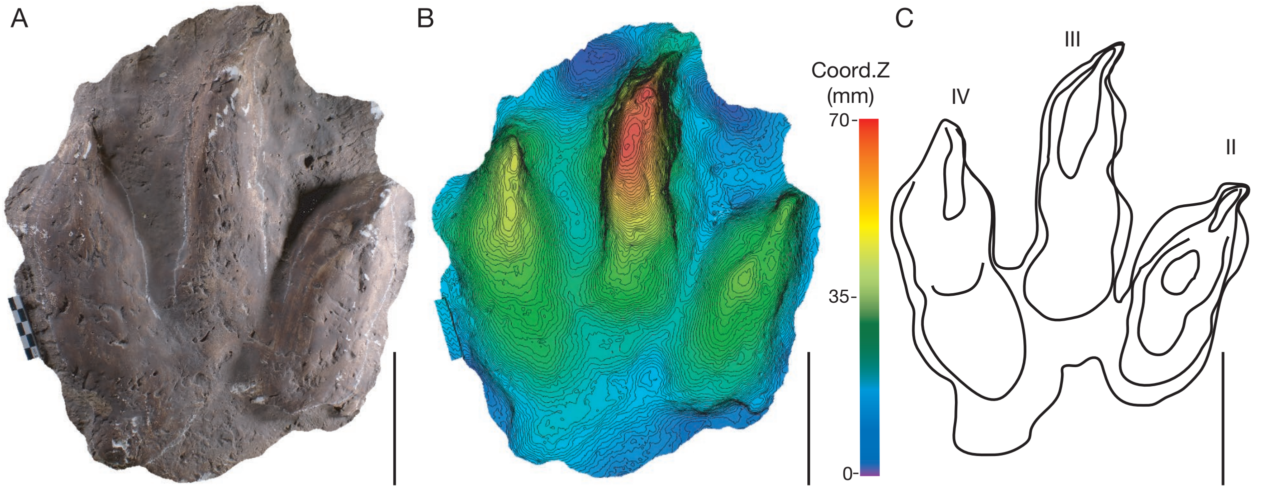

Fig. 9. — *Eubrontes giganteus* Hitchcock, 1845: **A**-**C**, track ULB-04D21_A (plaster cast of the holotype of "*E. veillonensis*" that is here invalidated), photograph (**A**), DEM and false-colour depth map (**B**) and interpretative sketch (**C**). Scale bars: 10 cm.

Ichnogenus *Grallator* Hitchcock, 1858

"***Grallator maximus***" Lapparent & Montenat, 1967 (Fig. 10)

Grallator maximus Lapparent & Montenat, 1967: 20-22, pls X, XI.1, fig. 11.

Status. — Subjective junior synonym of *Grallator minusculus* (Hitchcock, 1858) Demathieu, Gand, Sciau & Freytet, 2002.

Examined material. — Holotype: ULB-04C13_B (plaster cast). — Other specimens: ULB-04C04_A_1; ULB-04C06_A; ULB-04C10_B.

Description

The tracks are tridactyl, longer than wide (L/W = 1.5-(1.6)-1.7), 26.0-(26.8)-27.5 cm long and 15.5-(16.6)-17.7 cm wide (Fig. 10A-F; Table 2). D is quite long (L/D = 2.9-(3.0)-3.2). Impressions of digits are large, separated, well defined and elongated. The traces of digits II and III are the smallest and the longest, respectively. The angle between digits II and IV is 30°-(33°)-37° (Table 2). Impressions of digital pads are well preserved and are circular to oval. The position of the digito-metatarsal pad of digit IV is more proximal than that of digit II (Fig. 10A-F).

Remarks

Based on this material, Lapparent & Montenat (1967) erected (without diagnosis) the ichnospecies "*Grallator maximus*". These tracks being similar to *G. minusculus* (Fig. 4), we consider "*G. maximum*" as a subjective junior synonym of this ichnospecies. Based on footprints from the Jurassic of the United States, Hitchcock (1858) first described such large tridactyl tracks under the name *Brontozoum minusculum* Hitchcock, 1858 that were renamed *Anchisauripus minusculus* Lull, 1904 by Lull (1904). Based on material from the Hettangian-Sinemurian of the Causses Basin, Demathieu (1993) identified tracks that show similarities with the type material of *Anchisauripus minusculus*. Since *Anchisauripus* is characterised by the occasional presence of a hallux trace (Lull 1904), which is always absent in the material from France, Demathieu (1993), Demathieu & Sciau (1992) and Demathieu *et al.* (2002) used *Grallator minusculus* rather than *Anchisauripus minusculus*. Demathieu *et al.* (2002) emended the diagnosis of *G. minusculus* as follows: "*Large tridactyl tracks II-IV of bipeds with L × l = ca 300 × 200 mm, with large digits and well-marked pads. Claws are weakly developed and the digito-metatarsal pad of digit IV is often marked. The angle II-IV is 39° in average. The projection of III is low with a III/D ratio around 1.93*" (translated from French).

Ichnogenus "*Saltopoides*" Lapparent & Montenat, 1967

"***Saltopoides igualensis***" Lapparent & Montenat, 1967 (*nomen dubium*) (Fig. 11)

Saltopoides igualensis Lapparent & Montenat, 1967: 27, pl. XII.4, fig. 15.

Examined material. — Holotype: ULB-04C01_B (plaster cast). — Other specimen: ULB-04C01_A.

Description

The tracks are tridactyl, longer than wide (L/W = 1.32-(1.36)-1.40), 15.5-(16)-16.5 cm long and 11-(11.75)-12.5 cm wide; Fig. 11; Table 2). Impressions of digits are quite wide with well-distinguished claw marks. The free part of III is quite short (L/D = 2.6-(2.8)-3.1). The divarication angle between digits II and IV is large (II-IV = 49.0°-(51.5°)-54.0°) and D is short (L/D = 1.31-(1.36)-1.41). The digito-metatarsal pad of digit IV is much more proximal than that of digit II.

Remarks

Based on a poorly preserved trackway composed of three tridactyl footprints (only the distal parts of digits are partially preserved), Lapparent & Montenat (1967) erected "*Saltopoides igalensis*"

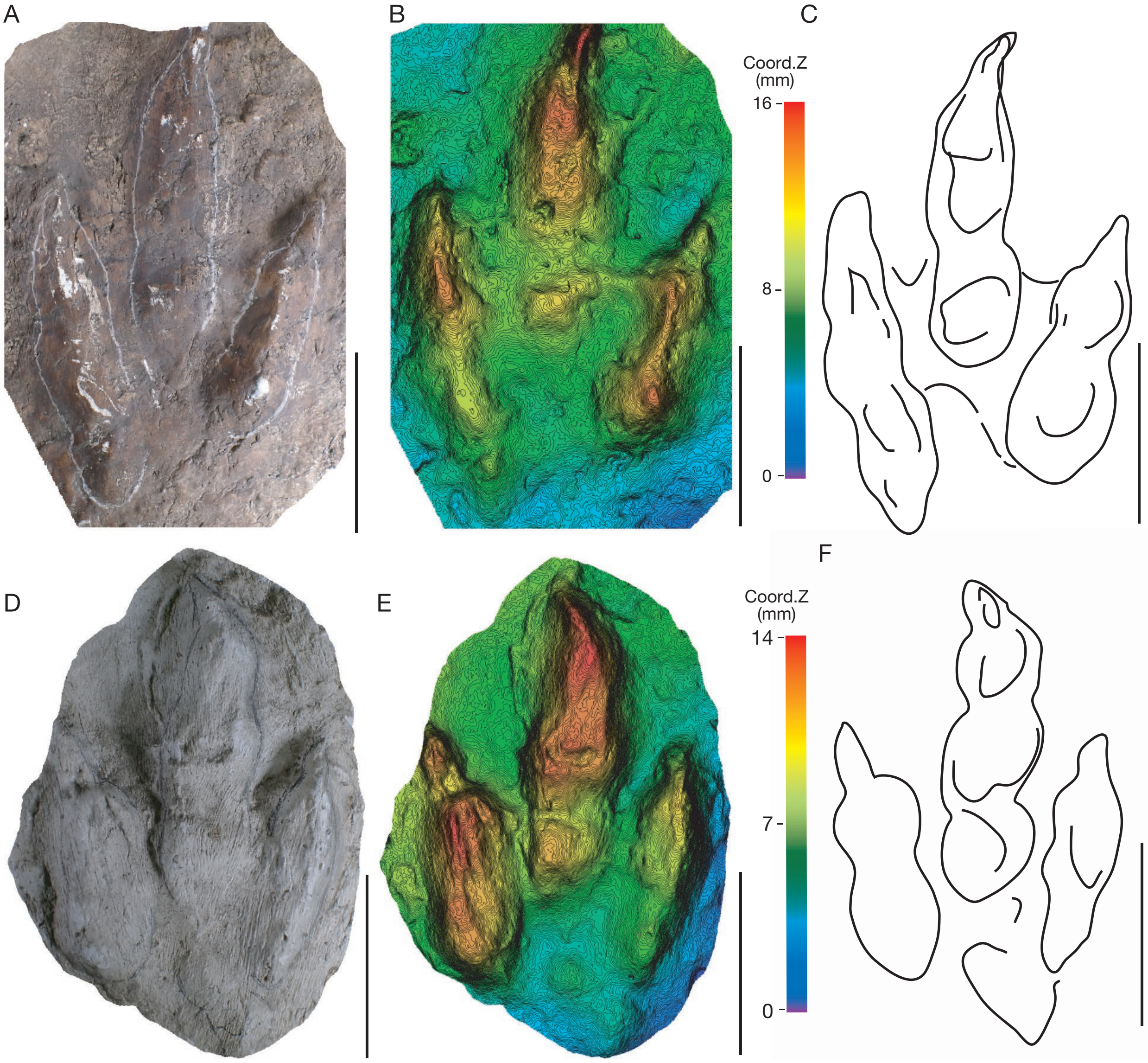

Fig. 10. — *Grallator minusculus* (Hitchcock, 1858), Demathieu, Gand, Sciau & Freytet, 2002: **A**-**C**, track ULB-04C13_B (plaster cast of the holotype of "*G. maximus*" that is here invalidated), photograph (**A**), DEM and false-colour depth map (**B**) and interpretative sketch (**C**); **D**-**F**, track ULB-04C10_B, photograph (**D**), DEM and false-colour depth map (**E**) and interpretative sketch (**F**). Scale bars: 10 cm.

and (without providing any diagnosis). Lapparent & Montenat (1967) justified the erection of the ichnogenus "*Saltopoides*" by an asymmetry of the footprint and the particularly long length of the pace between footprints. Lapparent & Montenat (1967) suggested that the trackmaker was a "jumping dinosaur". A recent survey in 2022 on the tidal flat of Le Veillon could not the find the type trackway of "*S. igalensis*" that has most probably eroded away. It appears that measured characteristics of ULB-04C01_A and ULB-04C01_B (plaster cast of one of the footprints of the type trackway) differ from other tridactyl tracks from Le Veillon that do not show such a proximal base of digit IV compared to digit II. However, without any possibility to revise the now-destroyed type trackway, the ichnotaxonomic validity of "*S. igalensis*" remains questionable.

Ichnogenus "*Talmontopus*" Lapparent & Montenat, 1967

Talmontopus Lapparent & Montenat, 1967: 29-30, pl. XII.1, fig. 17.

Status. — Subjective senior synonym of *Kayentapus* Welles, 1971.

"***Talmontopus tersi***" Lapparent & Montenat, 1967
(*nomen dubium*) (Fig. 12A-C)

Talmontopus tersi Lapparent & Montenat, 1967: 29-30, pl. XII.1, fig. 17.

Status. — Subjective senior synonym of *Kayentapus* isp.

Examined material. — Holotype: ULB-04C02_A.

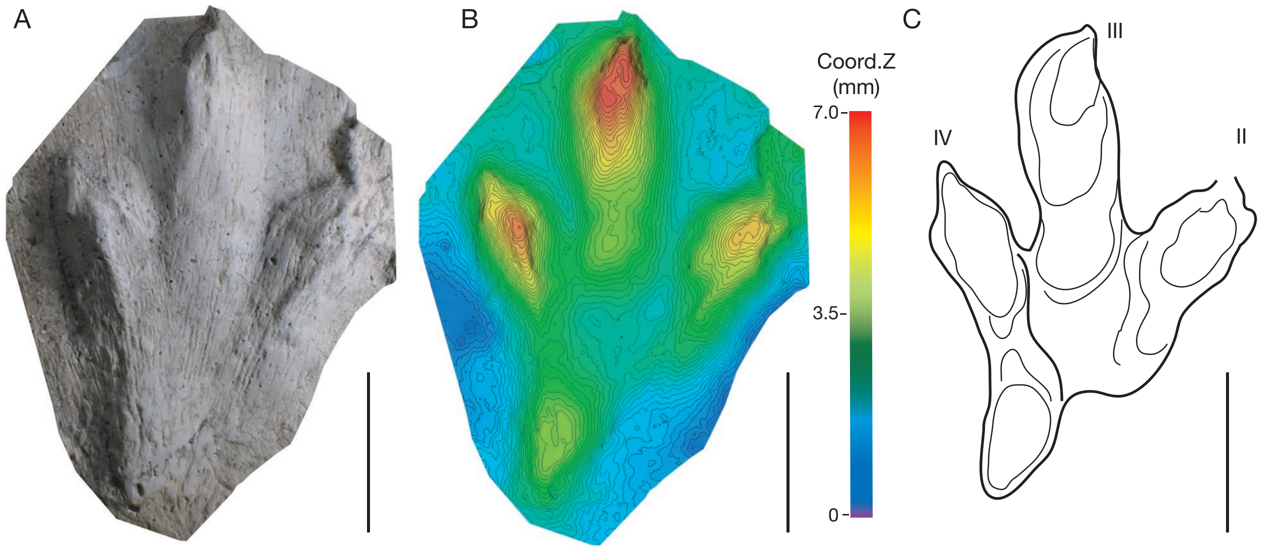

Fig. 11. — Plaster cast of one footprint from the type trackway of "*Saltopoides igalensis*", that is here invalidated: **A**-**C**, track ULB-04C01_B, photograph (**A**), DEM and false-colour depth map (**B**) and interpretative sketch (**C**). Scale bars: 5 cm.

Description

The track ULB-04C02_A consists of a single, slightly longer than wide (L/W = 1.2), 26 cm long and 21.5 cm wide tridactyl track (Fig. 12A-C; Table 2). The angle between II and IV is large (II-IV = 64°). Digit imprints are quite thin and pointed. The traces of digits II and IV are straight and quite similar in length. The trace of digit III is the longest and is slightly curved. The digito-metatarsal base of digit IV is slightly more proximal than that of digit II. The free part of III is quite short (L/D = 2.8). The imprints of pads and claws are only poorly marked.

Remarks

Based on the track ULB-04C02_A, Lapparent & Montenat (1967) erected *Talmontopus tersi*. They justified the creation of "*T. tersi*" by a very high T value between thin tracks of digits, and the presence of a putative web mark. We consider the web mark drawn in fig. 17 of Lapparent & Montenat (1967) as a sedimentary structure that corresponds to a slight thickening of sediment preserved between the traces of digits (see also plate XII.1 in Lapparent & Montenat 1967; ULB-04C02_A). Since ULB-04C02_A shows many characters of *Kayentapus* Welles, 1971, we consider "*Talmontopus*" as a subjective senior synonym of this ichnogenus. *Kayentapus* differs from *Grallator* and *Eubrontes* in showing larger divarication angle II-IV and a smaller L/W ratio. *Kayentapus* was erected by Welles (1971) based on the type ichnospecies *K. hopii* Welles, 1971 from the Early Jurassic Kayenta Formation in Arizona. Two other ichnospecies were later described from Early Jurassic strata of the United States and Poland: *K. minor* (Lull, 1953) Weems, 1987 and *K. soltykovensis* (Gierliński, 1991) Gierliński, 1996 (firstly named *Grallator* (*Eubrontes*) *soltykovensis* in Gierliński 1991 and Gierliński & Ahlberg 1994), respectively (Weems 1987; Gierliński 1996). Based on its D/W and (L-D)/W ratios (0.43 and 0.78, respectively), the track ULB-04C02_A fully falls within the morphological space of *K. hopii* (Gierliński 1996: fig. 1 and Lockley *et al.* 2011: fig. 6B). However, *K. hopii* is clearly larger (L = 34.0-35.5) than ULB-04C02_A (Fig. 4). It also differs from ULB-04C02_A in showing traces of digits that are slender and well individualised, and digito-metatarsal pads of the digit IV much more proximal. ULB-04C02_A is close to *K. minor* (Fig. 4), however, it seems to differ from this ichnospecies in showing a higher D/W ratio (see Gierliński 1996: fig. 1 and Lockley *et al.* 2011: fig. 6B). *K. slotykovensis* differs from ULB-04C02_A in showing a smaller (L-D)/W ratio (see Gierliński 1996: fig. 1 and Lockley *et al.* 2011: fig. 6B).

"Unnamed track n°1"
(Fig. 13A-C)

Unnamed track n°1 – Lapparent & Montenat 1967: 30, fig. 18.

Status. — Specimens here identified as *Batrachopus* isp.

Examined material. — ULB-04C14_I, ULB-04C17_A.

Description

The two tracks described by Lapparent & Montenat (1967) under the name "Unnamed track n°1" are poorly preserved. They are tetradactyl, small-sized, as long as wide, 3.3-(3.4)-3.6 cm long and 2.8-(3.0)-3.2 cm wide (Fig. 13A-C; Table 1). Traces of digits are short. They show rounded phalangeal pads and their apices bear tiny marks of claws. A large plantar-like impression is present on ULB-04C14_I.

Remarks

In their description of "Unnamed track n°1", Lapparent & Montenat (1967) made a mistake by considering that both tracks are tridactyl. However, a thorough examination of the material reveals the presence of a poorly marked fourth digit. The morphology and the dimensions of "Unnamed track n°1" match with the ichnogenus *Batrachopus*.

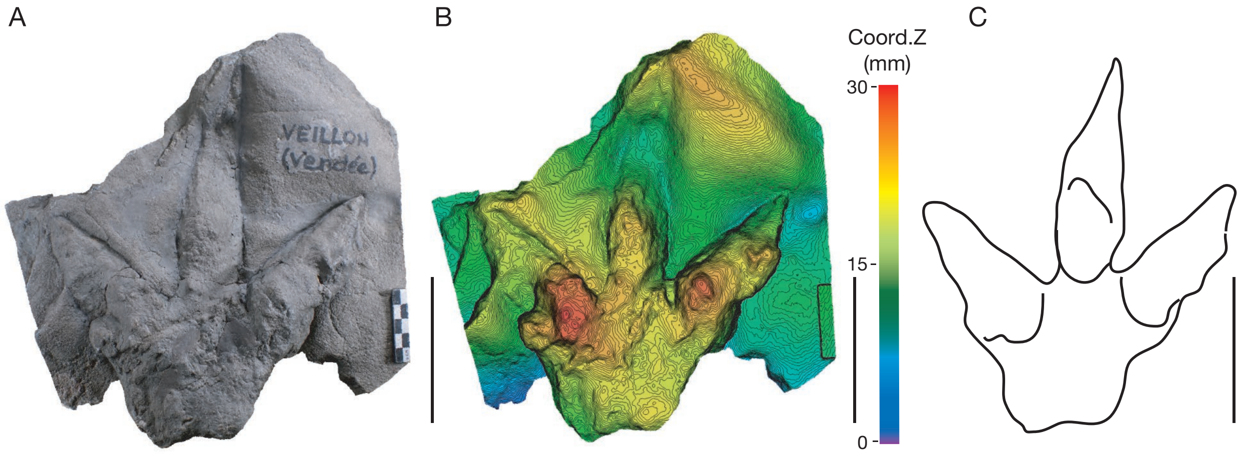

Fig. 12. — *Kayentapus* isp.: **A**-**C**, track ULB-04C02_A (holotype of "*Talmontopus tersi*" that is here invalidated), photograph (**A**), DEM and false-colour depth map (**B**) and interpretative sketch (**C**). Scale bars: 10 cm.

"Unnamed track n°2"
(Fig. 13D-F)

Unnamed track n°2 – Lapparent & Montenat 1967: 30, pl. XIII.5.

Status. — Specimen here identified as *G.* cf. *variabilis*.

Examined material. — ULB-04D22_A.

Description

The track is tridactyl, small-sized, longer than wide, approximatively 11 cm long and 7 cm wide (Fig. 13D-F; Table 2). Impressions of digits are elongated. The impression of digit III is the longest. At the base of the trace of digit IV, the position of the digito-metatarsal pad is more proximal than that of digit II. The divarication angle II-IV is 29°. Round to oval phalangeal pads and pointed marks of claws are commonly very well marked. Marks of claws on the traces of digits II and IV are clearly oriented outward.

Remarks

In their description of this track, Lapparent & Montenat (1967) considering the traces of digits II, III and IV as being parallel and of the same length. However, the reexamination of this track indicates that it matches with the ichnogenus *Grallator*. Despite its poor preservation, ULB-04D22_A shares some similarities with the *G. variabilis* ichnospecies.

DISCUSSION

Comparison with other ichnotaxa from Coeval tracksites

Early Jurassic crocodylomorph tracks were reported from southern Africa, Argentina, Colombia, Europe and the United States, where they have been mainly ascribed to the ichnogenus *Batrachopus* (e.g. Hitchcock 1845; Lapparent & Montenat 1967; Olsen & Galton 1984; Olsen & Padian 1986; Mojica & Macia 1987; Demathieu & Sciau 1992; Olsen 1995; Popa 1999; Lockley *et al.* 2004; Milner *et al.* 2006; Dalman 2012). In Europe, lowermost Jurassic (Hettangian-Sinemurian) crocodylomorph tracks are quite rare (Lockley & Meyer 2000), being only known from France (Lapparent & Montenat 1967; Sciau 1992; Moreau *et al.* 2019) and Romania (Popa 1999).

Early Jurassic tridactyl tracks of dinosaurs were reported from many areas of Australia, Africa, America, Asia and Europe (e.g. Gierliński & Ahlberg 1994 ; Olsen *et al.* 1998; Demathieu *et al.* 2002; Lucas *et al.* 2006; Dalman 2012; Xing *et al.* 2014; Wagensommer *et al.* 2016; Sciscio *et al.* 2017 ; Romilio 2021). The co-occurrence of *Grallator*, *Kayentapus* and *Eubrontes* was observed in various Early Jurassic tracksites from several areas in Europe: France (Moreau *et al.* 2018), Hungary (Gierliński 1996), Italy (Avanzini *et al.* 2006) and Poland (Pacyna *et al.* 2022). The ichnoassemblage from Le Veillon shares many similarities with the historical Early Jurassic American tracksites described by the palaeoichnologist Edward Hitchcock (Hitchcock 1841, 1845, 1858). *Batrachopus*, *Grallator* and *Eubrontes* were introduced based on material from New England, eastern United States (Hitchcock 1841, 1845, 1858). The ichnogenus *Kayentapus* was first described based on material from Arizona (Welles 1971; Lockley *et al.* 2011).

Among the international record of Early Jurassic archosaur tracksites, the ichnoassemblage from Le Veillon shares most similarities with that of the Grands Causses area (southern France). The Hettangian-Sinemurian deposits from the Causses Basin have yielded more than 60 archosaur tracksites. In this area, Sinemurian crocodylomorph tracks were ascribed to *Batrachopus deweyi* by Demathieu & Sciau (1992) and Demathieu *et al.* (2002), while Lockley & Meyer (2004) saw resemblances to *Antipus*. These tracks differ from the specimens assigned to *B. deweyi* from Le Veillon in showing more slender traces of digits and wider divarication angle. In France, Le Serre tracksite (Lozère, northern part of the Causses Basin) is the only other Hettangian tracksite yielding crocodylomorph tracks (Moreau *et al.* 2019).

Although very small-sized tridactyl tracks such as *G. olonensis* remain unknown from the Hettangian-Sinemurian deposits

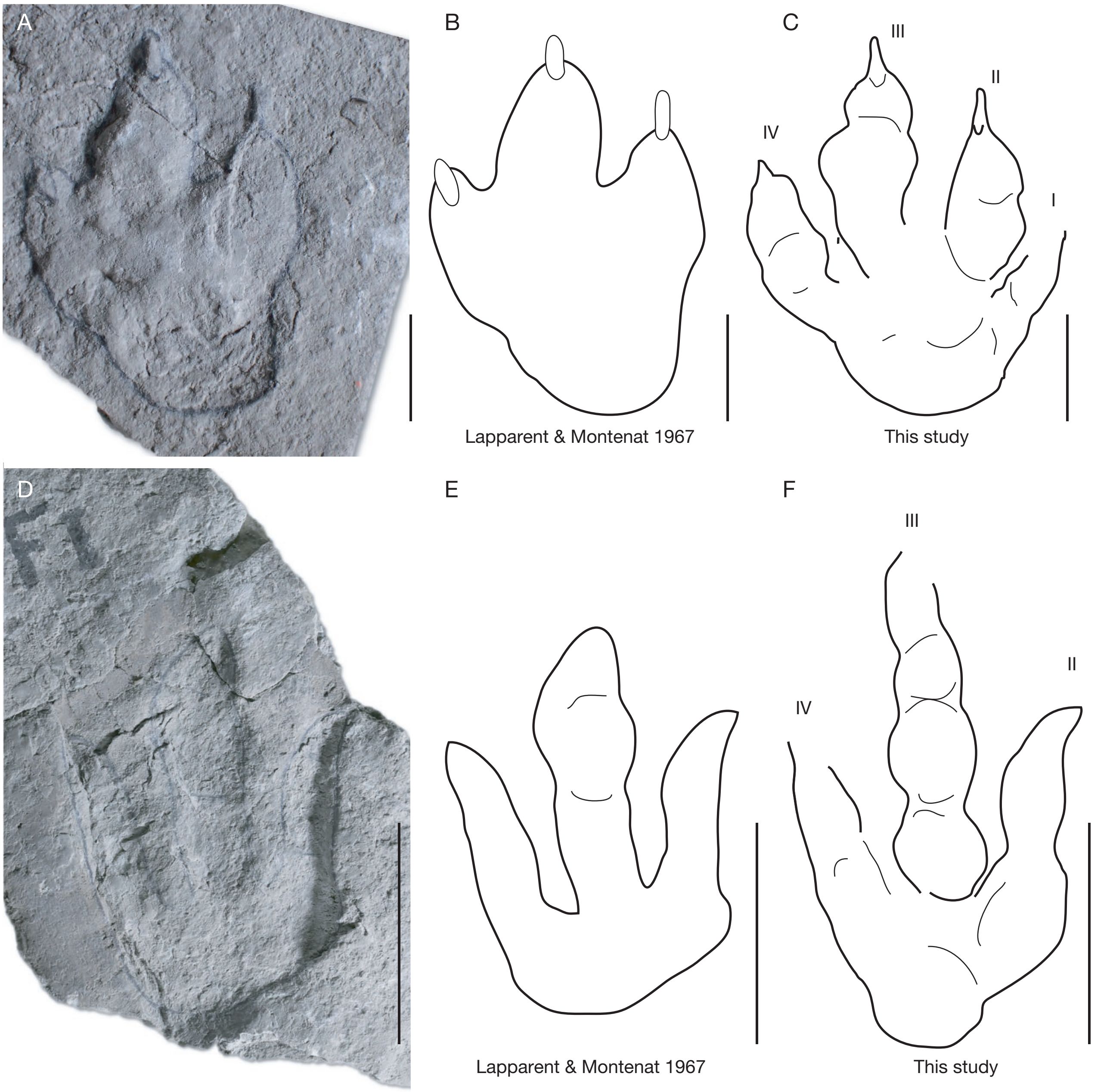

FIG. 13. — Other problematic tracks in Lapparent & Montenat 1967: **A**-**C**, *Batrachopus* isp., ULB-04C14_I, photograph (**A**), interpretative sketch of Lapparent & Montenat (1967) (**B**) ("Unnamed track n°1" in Lapparent & Montenat 1967: fig. 18), and our interpretation (**C**); **D**-**F**, *Grallator* cf. *variabilis*, ULB-04D22_A, photograph (**D**), interpretative sketch of Lapparent & Montenat (1967) (**E**) ("Unnamed track n°2" in Lapparent & Montenat 1967: fig. 18 and pl. XIII.5), and our interpretation (**F**). Scale bars: A-C, 1 cm; D-F, 5 cm.

of the Causses Basin, this area yields abundant specimens of *Grallator variabilis* and *Grallator minusculus*. Comparisons among tracks from Le Veillon and those from the Causses Basin show that the occupied morphological spaces are similar for each of these two ichnospecies in both regions (Fig. 4). Early Jurassic archosaur tracksites from the Causses Basin also yield two additional *Grallator* ichnospecies that are absent from the Lapparent collection: *Grallator lescurei* Demathieu, 1990 and *Grallator sauclierensis*. In the Hettangian tracksites from the Causses Basin, two ichnospecies of *Eubrontes* were identified, *Eubrontes divaricatus* Hitchcock, 1865 (Demathieu & Sciau 1999) and *Eubrontes giganteus* (Demathieu *et al.* 2002; Sciau 2003; Moreau *et al.* 2021). Since the revision of the ichnogenus *Eubrontes* by Olsen *et al.* (1998), Demathieu *et al.* (2002) suggested to use only *Eubrontes giganteus* for the material from this area. Although *Dilophosauripus williamsi* Welles, 1971 was broadly used to describe tracks from the Causses Basin (e.g. Demathieu & Sciau 1992; Sciau 1992, 2003; Demathieu 1993; Demathieu *et al.* 2002; Gand *et al.* 2007; Moreau *et al.* 2014), its validity was strongly debated (Lucas *et al.* 2006; Lockley *et al.* 2011). Recent morphometrical comparisons made by Gand *et al.* (2018) suggested that tracks ascribed to *Dilophosauripus* Welles, 1971 in the Causses Basin are similar to those of *Kayentapus* and can be attributed to that ichnogenus. Their morphology is quite close to that of the *Kayentapus* tracks from Le Veillon but they are smaller. In France, with the exception of the Le Veillon tracksite and the Causses Basin, Early Jurassic tridactyl dinosaur tracks were also reported from Lot (Lange-Badré & Lafon 2000), Dordogne (Gand *et al.* 2007) and Var (Ellenberger 1965).

Trackmakers

Crocodylomorph and dinosaur body fossils remain unknown in the Early Jurassic deposits from Vendée. Olsen & Padian (1986) proposed that the trackmakers of *Batrachopus* were crocodyliform protosuchians (see fig. 20.11 in Olsen & Padian 1986). The osteological architectures of manus and pes of *Protosuchus* Brown, 1934 (Colbert *et al.* 1951) match with the morphology of *Batrachopus* (Olsen & Padian 1986). The trackmaker of *Batrachopus* should have been a crocodylomorph with a reduced pedal digit V (Olsen & Padian 1986). Earliest Jurassic crocodylomorphs were small and fully terrestrial (Frey 1988; Olsen 1995). Body fossils of crocodylomorphs are almost unknown from the earliest Jurassic of Europe, with only a few isolated remains from Great Britain assignable to indeterminate sphenosuchians (Whiteside *et al.* 2016).

The phalangeal formula (type 3, 4 and 5 for toes II, III and IV, respectively) of the tridactyl tracks *Eubrontes, Grallator* and *Kayentapus* matches with the pes of theropod dinosaurs. Body fossils of earliest Jurassic theropods were ascribed to Coelophysoidea and Ceratosauria and reported from Africa, Antarctica, China, Europe and United States (Weishampel *et al.* 2004; Smith *et al.* 2007; Xing *et al.* 2013). In Europe, rare theropod remains have been discovered in the Hettangian-Sinemurian deposits of Great Britain, France, Italy and Luxembourg (Larsonneur & Lapparent 1966; Benton *et al.* 1995; Carrano & Sampson 2004; Delsate & Ezcurra 2014; Martill *et al.* 2016; Dal Sasso *et al.* 2018). The Moon-Airel Formation (Normandie, northwestern France), yielded the only known earliest Jurassic theropod from France (Larsonneur & Lapparent 1966), i.e. the coelophysoid *Lophostropheus airelensis* Cuny & Galton, 1993 (Cuny & Galton 1993; Ezcurra & Cuny 2007). Using the formula of Alexander (1976) and Thulborn (1990), the hip height of the smallest theropods from Le Veillon varies from 18 to 21 cm (trackmakers of *G. olonensis*). The speed of the trackmakers of *G. olonensis* varies from 2.9 to 4.4 km/h, suggesting a walking gait. Lapparent & Montenat (1967) attributed the trackmaker of "*Talmontopus*" to an ornithopod. As this ichnogenus is here reinterpreted and renamed (*Kayentapus*), its trackmaker must be regarded as a medium-sized theropod. Lapparent & Montenat (1967) mentioned that they observed several tail marks of theropods associated with track-bearing tridactyl tracks. However, they specified that it was not possible to link tail marks and footprints. We interpret the single specimen figured in Lapparent & Montenat (1967; pl.4, fig.2 in Lapparent & Montenat 1967; ULB-04C15_E) as a large desiccation crack, not a tail mark.

CONCLUSION

The ichnotaxonomic revision of the type material from Le Veillon, a historical earliest Jurassic tracksite in western France, allows identification of valid and invalid/problematic ichnotaxa. Amongst the eight ichnospecies erected by Lapparent & Montenat (1967), only two are considered as valid: *Grallator olonensis* and *Grallator variabilis*. The diagnosis of *Grallator olonensis* is here formally established. "*Batrachopus gilberti*", "*Eubrontes veillonensis*" and "*Grallator maximus*" are regarded as subjective junior synonyms of *Batrachopus deweyi*, *Eubrontes giganteus* and *Grallator minusculus*, respectively. "*Anatopus*" and "*Saltopoides*" are considered as *nomina dubia*. The ichnogenus "*Talmontopus*" is considered as a subjective senior synonym of *Kayentapus*. The tracks initially assigned by Lapparent & Montenat (1967) to "*Dahutherium* sp." are here reinterpreted and identified as *Batrachopus* isp., *Grallator variabilis* and *Grallator* isp. The two unassigned tracks described by Lapparent & Montenat (1967), i.e. "Unnamed tracks n°1 and n°2", are referred to *Batrachopus* isp. and *G.* cf. *variabilis*, respectively. The Hettangian ichnoassemblage from Le Veillon shares strong similarities with the Early Jurassic archosaur ichnoassemblage from the Causses Basin area in southern France. Although contemporaneous body fossils remain unknown in Vendée, the tetrapod tracks from Le Veillon confirms the co-occurrence of crocodylomorphs and theropods in the central part of Laurasia, along the Tethyan border (near the latitude 30° N) during the Hettangian.

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REFERENCES

Alexander R. McN. 1976. — Estimates of speeds of dinosaurs. *Nature* 261: 129-130. https://doi.org/10.1038/261129a0

Avanzini M., Piubelli D., Mietto P., Roghi G., Romano R. & Masetti D. 2006. — Lower Jurassic (Hettangian-Sinemurian) dinosaur track megasites, southern Alps, northern Italy. *New Mexico Museum of Natural History and Science Bulletin* 37: 207-216 [reterievd from https://nmdigital.unm.edu/digital/collection/bulletins/id/216/rec/1].

Benton M. J., Martill D. M. & Taylor M. A. 1995. — The first Lower Jurassic dinosaur from Scotland: limb bone of a ceratosaur theropod from Skye. *Scottish Journal of Geology* 31: 177-182. https://doi.org/10.1144/sjg31020177

Bessedik M., Mammeri C., Belkebir L., Mahboubi M., Adaci M., Hebib H., Bensalah M. & Mansouri M. E. H. 2008. — Nouvelles données sur les ichnites de dinosaures de la région d'El Bayadh (Crétacé inférieur, Algérie). *Palaeovertebrata* 36: 7-35. https://doi.org/10.18563/pv.36.1-4.7-35

Bessonnat G., Lapparent A. F. de, Montenat C. & Ters M. 1965. — Découverte de nombreuses empreintes de pas de reptiles dans le Lias inférieur de la côte de Vendée. *Comptes rendus hebdomadaires des séances de l'Académie des sciences* 260: 5324-5326. https://gallica.bnf.fr/ark:/12148/bpt6k4020b/f699.item

Bocquier E. 1935. — Observations sur quelques témoins d'anciens rivages dans le Talmondais (Vendée). *Annuaire de la Société d'Émulation de la Vendée* 1935: 17-26. https://gallica.bnf.fr/ark:/12148/bpt6k9741931k/f23.item

Carrano M. T. & Sampson S. D. 2004. — A review of coelophysoids (Dinosauria: Theropoda) from the Early Jurassic of Europe, with comments on the late history of the Coelophysoidea. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 9: 537-558.

Colbert E. H., Mook C. C. & Brown B. 1951. — The ancestral crocodilian *Protosuchus*. *Bulletin of the American Museum of Natural History* 97: 149-182. https://doi.org/10.1086/399139

Coombs W. P. Jr 1996. — Redescription of the ichnospecies *Antipus flexiloquus* Hitchcock, from the Early Jurassic of the Connecticut Valley. *Journal of Paleontology* 70: 327-331. https://doi.org/10.1017/s0022336000023416

Cuny G. & Galton P. M. 1993. — Revision of the Airel theropod dinosaur from the Triassic-Jurassic boundary (Normandy, France). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 187: 261-288.

Dalman S. G. 2012. — New data on small theropod footprints from the Early Jurassic (Hettangian) Hartford Basin of Massachusetts, United States. *Bulletin of the Peabody Museum of Natural History* 53: 333-353. https://doi.org/10.3374/014.053.0201

Dal Sasso C., Maganuco S. & Cau A. 2018. — The oldest ceratosaurian (Dinosauria: Theropoda), from the Lower Jurassic of Italy, sheds light on the evolution of the three-fingered hand of birds. *PeerJ* 6: e5976. https://doi.org/10.7717/peerj.5976

Delsate D. & Ezcurra M. D. 2014. — The first Early Jurassic (late Hettangian) theropod dinosaur remains from the Grand Duchy of Luxembourg. *Geologica Belgica* 17: 175-181 [retrieved from https://popups.uliege.be/1374-8505/index.php?id=4569].

Demathieu G. 1993. — Empreintes de pas de dinosaures dans les Causses (France). *Zubía* 5: 229-252.

Demathieu G. 2003. — Comparaison des ichnopopulations des Grands Causses (Sud de la France) et du Veillon (Vendée). *Le Naturaliste Vendéen* 3: 59-60.

Demathieu G. & Haubold H. 1972. — Stratigraphische Aussagen der Tetrapodenfährten aus der terrestrischen Trias Europas: *Geologie* 21: 802-836.

Demathieu G. & Sciau J. 1992. — Des pistes de dinosaures et de crocodiliens dans les dolomies de l'Hettangien du Causse du Larzac. *Comptes rendus hebdomadaires des séances de l'Académie des sciences* 315: 1561-1566. https://gallica.bnf.fr/ark:/12148/bpt6k6296920w/f663.item

Demathieu G. & Sciau J. 1999. — De grandes empreintes de pas de dinosaures dans l'Hettangien de Peyre (Aveyron, France). *Geobios* 32: 609-616. https://doi.org/10.1016/s0016-6995(99)80010-2

Demathieu G., Gand G., Sciau J. & Freytet P. 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

Ellenberger P. 1965. — Découverte de pistes de vertébrés dans le Permien, le Trias et le Lias inférieur, aux abords de Toulon (Var) et d'Anduze (Gard). *Comptes rendus hebdomadaires des séances de l'Académie des sciences* 260: 5856-5860. https://gallica.bnf.fr/ark:/12148/bpt6k4020b/f1247.item

Ezcurra M. D. & Cuny G. 2007. — The coelophysoid *Lophostropheus airelensis*, gen. nov.: a review of the systematics of "*Liliensternus*" *airelensis* from the Triassic-Jurassic outcrops of Normandy (France). *Journal of Vertebrate Paleontology* 27: 73-86. https://doi.org/10.1671/0272-4634(2007)27[73:tclagn]2.0.co;2

Frey E. 1988. — The carrying system of crocodilians a biomechanical and phylogenetical analysis. *Stuttgarter Beiträge zur Naturkunde* 426: 1-60.

Gand G. 1974a. — Les traces de vertébrés Triasiques de l'Autunois et du nord du Charollais. *Bulletin de la Société d'Histoire naturelle d'Autun* 69: 7-24.

Gand G. 1974b. — Sur les niveaux a empreintes de pas de vertébrés triasiques. Des carrières de St-Sernin-du-Bois (Saône-et-Loire). *Bulletin de la Société d'Histoire naturelle du Creusot* 32: 12-22.

Gand G., Demathieu G. & Montenat C. 2007. — Les traces de pas d'amphibiens, de dinosaures et 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., Caravaca G., Moreau J.-D., Baret L., Andre D., Lefillatre R., Passet A., Wienin M. & Gely J.-P. 2018. — Les pistes d'archosauriens : *Kayentapus ubacensis* nov. isp. (théropodes) et crocodylomorphes du Bathonien des Grands-Causses (France). Conséquences paléo-biologiques, environnementales et géographiques. *Annales de Paléontologie* 104: 183-216. https://doi.org/10.1016/j.annpal.2018.06.002

Gierliński G. 1991. — New dinosaur ichnotaxa from the Early Jurassic of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85: 137-148. https://doi.org/10.1016/0031-0182(91)90030-u

Gierliński G. 1996. — Dinosaur ichnotaxa from the Lower Jurassic of Hungary. *Geological Quarterly* 40: 119-128 [retrieved from https://gq.pgi.gov.pl/article/view/8168].

Gierliński G. & Ahlberg A. 1994. — Late Triassic and Early Jurassic dinosaur footprints in the Höganäs Formation of southern Sweden. *Ichnos* 3: 99-105. https://doi.org/10.1080/10420949409386377

Godard G. 2003. — Histoire de la géologie en Talmondais (Vendée, France). *Le Naturaliste Vendéen* 3: 13-28.

Haubold H. 1971. — *Encyclopedia of Paleoherpetology*. Part 18. *Ichnia Amphibiorum et Reptiliorum fossilium*. Verlag Dr. Friedrich Pfeil: 1-124 (Handbook of Palaeoherpetology).

Haubold H. 1984. — *Saurierfährten*. Die Neue Brehm-Bücherei, Wittenberg, Ziemsen, 231 p.

Hitchcock E. 1841. — *Final Report on the Geology of Massachusetts*. J. H. Butler, Northampton, 831 p.

Hitchcock E. 1845. — An attempt to name, classify, and describe the animals that made the fossil footmarks of New England, *in* Proceedings of the 6th Meeting American Association of Geologists and Naturalists. Association of American Geologists and Naturalists: 23-25.

Hitchcock E. 1858. — *Ichnology of New England: a Report on the Sandstone of the Connecticut Valley Especially its Fossil Footmarks, Made to the Government of the Commonwealth of Massachusetts*. William White, Boston, 220 p.

Klein H. & Lucas S. G. 2021. — The Triassic tetrapod footprint record. *New Mexico Museum of Natural History and Science Bulletin* 83: 1-194.

Lange-Badré B. & Lafon J.-P. 2000. — Découverte de pistes de dinosaures théropodes dans le Lias inférieur des environs de Figeac (Lot). *Comptes Rendus de l'Académie des sciences, série 2a, Sciences de la terre et des planètes de Paris* 330 (5): 379-384. https://doi.org/10.1016/S1251-8050(00)00160-9

Lapparent A. F. de & Montenat C. 1967. — Les empreintes de pas de reptiles de l'Infralias du Veillon (Vendée). *Mémoires de la Société géologique de France* 46: 1-43.

Larsonneur C. & Lapparent (de) A. F. 1966. — Un dinosaurien carnivore, *Halticosaurus*, dans le Rhétien d'Airel (Manche). *Bulletin de la Société linnéenne de Normandie* 10: 108-116.

Leonardi G. 1987. — *Glossary and Manual of Tetrapod Footprint Palaeoichnology*. Publicacão do Departemento Nacional da Produção Mineral, Brasília, 75 p.

Lockley M. G. & Meyer C. 2000. — *Dinosaur Tracks and Other Fossil Footprints of Europe*. Columbia University Press, New York, 327 p.

Lockley M. G. & Meyer C. 2004. — Crocodylomorph trackways from the Jurassic to Early Cretaceous of North America and Europe: implications for ichnotaxonomy. *Ichnos* 11: 167-178. https://doi.org/10.1080/10420940490428832
Lockley M. G., Kirkland J. & Milner A. R. C. 2004. — Probable relationships between the Lower Jurassic crocodilomorph trackways *Batrachopus* and *Selenichnus*: Evidence and implications based on new finds from the St. George area southwestern Utah. *Ichnos* 11: 143-149. https://doi.org/10.1080/10420940490442340
Lockley M. G., Gierliński G. & Lucas S. G. 2011. — *Kayentapus* revised: notes on the type material and the importance of this theropod footprint ichnogenus. *New Mexico Museum of Natural History and Science Bulletin* 53: 330-336 (retrieved from https://nmdigital.unm.edu/digital/collection/bulletins/id/1423/rec/1].
Lucas S. G., Lockley M. G., Hunt A. P., Milner A. R. & Tanner, L. H. 2006. — Tetrapod footprint biostratigraphy of the Triassic-Jurassic transition in the American southwest. *New Mexico Museum of Natural History and Science Bulletin* 37: 105-108 [retrieved from https://nmdigital.unm.edu/digital/collection/bulletins/id/201/rec/1].
Lull R. S. 1904. — Fossil footprints of the Jura-Trias of North America. *Memoirs of the Boston Society of Natural History* 5: 461-557.
Lull R. S. 1953. — *Triassic life of the Connecticut Valley*. State Geological and Natural History Survey, Hartford, 331 p.
Martill D. M., Vidovic S. U., Howells C. & Nudds J. R. 2016. — The oldest Jurassic dinosaur: A basal neotheropod from the Hettangian of Great Britain. *PloS One* 11: e0145713. https://doi.org/10.1371/journal.pone.0145713
Milàn J. & Hedegaard R. 2010. — Interspecific variation in tracks and trackways from extant crocodylians. *New Mexico Museum of Natural History and Science Bulletin* 51: 15-29 [retrieved from https://nmdigital.unm.edu/digital/collection/bulletins/id/1861/rec/1].
Milner A. R. C., Lockley M. G. & Kirkland J. I. 2006. — A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah. *New Mexico Museum of Natural History and Science Bulletin* 37: 315-328 [retrieved from https://nmdigital.unm.edu/digital/collection/bulletins/id/231/rec/1].
Mojica J. & Macia C. 1987. — Nota preliminar sobre la improntas de vertebrados (*Batrachopus* sp.) en sedimentitas de la Formación Saldaña, región de Prado-Dolores, valle superior del Magdalena, Colombia. *Geología Colombiana* 16: 89-94. https://repositorio.unal.edu.co/handle/unal/41344
Montenat C. 1968. — Empreintes de pas de reptiles dans le Trias moyen du plateau du Daüs près d'Aubenas (Ardèche). *Bulletin scientifique de Bourgogne* 25: 369-389.
Montenat C. & Bessonnat G. 2002. — Le gisement d'empreintes de pas de reptiles du Veillon (Vendée) : paléobiologie d'un estuaire infraliasique. *Actes des Congrès nationaux des Sociétés historiques et scientifiques* 124: 337-351.
Moreau J.-D., Trincal V., Gand G., Néraudeau D., Bessière G. & Bourel B. 2014. — Two new dinosaur tracksites from the Hettangian Dolomitic Formation of Lozère, Languedoc-Roussillon, France. *Annales de Paléontologie* 100: 361-369. https://doi.org/10.1016/j.annpal.2014.04.001
Moreau J.-D., Trincal V., Andre D., Baret L., Jacquet A. & Wienin M. 2018. — Underground dinosaur tracksite inside a karst of southern France: Early Jurassic tridactyl traces from the Dolomitic Formation of the Malaval Cave (Lozère). *International Journal of Speleology*, 47: 29-42. https://doi.org/10.5038/1827-806X.47.1.2149
Moreau J.-D., Fara E., Néraudeau D. & Gand G. 2019. — New Hettangian tracks from the Causses Basin (Lozère, southern France) complement the poor fossil record of earliest Jurassic crocodylomorph in Europe. *Historical Biology* 31: 341-552. https://doi.org/10.1080/08912963.2017.1370587
Moreau J.-D., Sciau J., Gand G. & Fara E. 2021. — Uncommon preservation of dinosaur footprints in a tidal breccia: *Eubrontes giganteus* from the Early Jurassic Mongisty tracksite of Aveyron, southern France. *Geological Magazine* 158: 1403-1420. https://doi.org/10.1017/S0016756820001454
Olsen P. E. 1980. — *Fossil Great Lakes of the Newark Supergroup in New Jersey*. In Field studies of New Jersey geology and guide to field trips: New York State Geological Association, 52nd Annual Meeting, Rutgers University: 352-398.
Olsen P. E. 1995. — *Paleontology and Paleoenvironments of Early Jurassic Age Strata in the Walter Kidde Dinosaur Park (New Jersey, USA)*. Field Guide and Proceedings of the Twelfth Annual Meeting of the Geological Association of New Jersey. William Patterson College, Wayne: 156-190.
Olsen P. E. & Galton P. M. 1984. — A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia Africana* 25: 87-100.
Olsen P. E. & Padian K. 1986. — Earliest records of *Batrachopus* from the southwestern United States, and a revision of some Early Mesozoic crocodylomorph ichnogenera *in* Padian K. (ed), *The Beginning of the Age of Dinosaurs*. Cambridge University Press: 259-273.
Olsen P. E., Smith J. H. & Mc Donald N. G. 1998. — Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus* and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). *Journal of Vertebrate Paleontology* 18: 586-601. https://www.jstor.org/stable/4523930
Pacyna G., Ziaja J., Barbacka M., Pieńkowski G., Jarzynka A. & Niedźwiedzki G. 2022. — Early Jurassic dinosaur-dominated track assemblages, floristic and environmental changes in the Holy Cross Mountains region, Poland. *Geological Quarterly* 66: 66-29. https://doi.org/10.7306/gq.1660
Popa M. E. 1999. — First finds of Mesozoic tetrapod tracks in Romania. *Acta Palaeontologica Romaniae* 2: 387-390.
Rainforth E. C. 2005. — *Ichnotaxonomy of the Fossil Footprints of the Connecticut Valley (Early Jurassic, Newark Supergroup, Connecticut and Massachusetts)*. Columbia University, New York, 1301 p.
Rainforth E. C. 2007. — Ichnotaxonomic updates from the Newark Supergroup, *in* Contributions to the Paleontology of New Jersey (II): Field Guide and Proceedings. Geological Association of New Jersey, Trenton: 49-59.
Romilio A. 2021. — Additional notes on the mount Morgan dinosaur tracks from the Lower Jurassic (Sinemurian) Razorback beds, Queensland, Australia. *Historical Biology* 33: 2005-2007. https://doi.org/10.1080/08912963.2020.1755853
Sciau J. 1992. — *Sur la piste des dinosaures des Causses*. Association des Amis du Musée de Millau, Millau, 31 p.
Sciau J. 1998. — *Dinosaures et reptiles marins des Causses*. Association des Amis du Musée de Millau, Millau, 56 p.
Sciau J. 2003. — *Dans les pas des dinosaures des Causses, inventaire des sites à empreintes*. Association des Amis du Musée de Millau, Millau, 107 p.
Sciau J. 2012. — *Présence des tétrapodes terrestres dans les Causses - Des amphibiens aux dinosaures*. Association paléontologique des Causses, Millau, 76 p.
Sciscio L., Bordy E. M., Abrahams M., Knoll F. & Mcphee B. W. 2017. — The first megatheropod tracks from the Lower Jurassic upper Elliot Formation, Karoo Basin, Lesotho. *PloS One* 12: e0185941. https://doi.org/10.1371/journal.pone.0185941
Smith N. D., Makovicky P. J., Hammer W. R. & Currie P. J. 2007. — Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. Zoological Journal of the Linnean Society 151: 377-421. https://doi.org/10.1111/j.1096-3642.2007.00325.x

TERS M. 1961. — *La Vendée littorale : étude de géomorphologie*. Oberthur, Rennes-Paris, 578 p.
THÉVENARD F., DESCHAMPS S., GUIGNARD G. & GOMEZ B. 2003. — Les plantes fossiles du gisement hettangien de Talmont-Saint-Hilaire (Vendée, France). *Le Naturaliste vendéen* 3: 69-87.
THULBORN T. 1990. — *Dinosaur Tracks*. Chapman & Hall, London, 410 p.
VIAUD J.-M. 2003. — Un site géologique remarquable à protéger et à valoriser: le Veillon à Talmont-Saint-Hilaire (Vendée, France). *Le Naturaliste Vendéen* 3: 101-103.
VIAUD J.-M. & DUCLOUS S. 2003. — Journées d'étude des 28 et 29 mars 2002 à Talmont-Saint-Hilaire (Vendée) : les sites à traces de pas de vertébrés vers la limite Trias-Jurassique. *Le Naturaliste Vendéen* 3: 3-11.
VIAUD J.-M. & GODARD G. 2008. — Edmond Bocquier (1881-1948) et la géologie. *Le Naturaliste Vendéen* 8: 57-69.
WAGENSOMMER A., LATIANO M., MOCKE H. B. & D'ORAZI P. 2016. — Dinosaur diversity in an Early Jurassic African desert: the significance of the Etjo Sandstone ichnofauna at the Otjihaenamaparero locality (Namibia). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 281: 155-82. https://doi.org/10.1127/njgpa/2016/0593
WEISHAMPEL D. B., DODSON P. & OSMOLSKA H. 2004. — *The Dinosauria*. University of California Press, Berkeley, 862 p.
WEEMS R. E. 1987. — A Late Triassic footprint fauna from the Culpeper basin northern Virginia (USA). *Transactions of the American Philosophical Society* 77: 1-79. https://doi.org/10.2307/1006417
WEEMS R. E. 1992. — A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper, Virginia, *in* Proceedings 26th Forum on the Geology of Industrial Minerals. Virginia Division of Mineral Resources Publication 119: 113-127.
WEEMS R. E. 2019. — Evidence for bipedal prosauropods as the likely *Eubrontes* track-makers. *Ichnos* 26: 187-215. https://doi.org/10.1080/10420940.2018.1532902
WELLES S. P. 1971. — Dinosaur footprints from the Kayenta Formation of northern Arizona. *Plateau* 44: 27-38.
WHITESIDE D. I., DUFFIN C. J., GILL P. G., MARSHALL J. E. A. & BENTON M. J. 2016. — The Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: Stratigraphy and setting. *Palaeontologia Polonica* 67: 257-287.
XING L., BELL P. R., ROTHSCHILD B. M., RAN H., ZHANG J., DONG Z., ZHANG W. & CURRIE P. J. 2013. — Tooth loss and alveolar remodeling in *Sinosaurus triassicus* (Dinosauria: Theropoda) from the Lower Jurassic strata of the Lufeng Basin, China. *Chinese Science Bulletin* 58: 1931-1935. https://doi.org/10.1007/s11434-013-5765-7
XING L. D., PENG G. Z., YE Y., LOCKLEY M. G., MCCREA R. T., CURRIE P. J., ZANG J.-P. & BURNS M. E. 2014. — Large theropod trackway from the Lower Jurassic Zhenzhuchong Formation of Weiyuan County, Sichuan Province, China: review, new observations and special preservation. *Palaeoworld* 23: 285-293. https://doi.org/10.1016/j.palwor.2014.10.010

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