



HAL
open science

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

Jean-David Moreau, Romain Vullo, Elsie Bichr, Jérôme Thomas, Georges Gand, Cyril Gagnaison, Pascal Barrier, Didier Néraudeau

► To cite this version:

Jean-David Moreau, Romain Vullo, Elsie Bichr, Jérôme Thomas, Georges Gand, et al.. Crocodylomorph and dinosaur tracks from the lowermost Jurassic of Le Veillon (western France): ichnotaxonomic revision of the type material (Lapparent collection). *Geodiversitas*, 2024, 46 (8), pp.343-366. 10.5252/geodiversitas2024v46a8 . insu-04632523

HAL Id: insu-04632523

<https://insu.hal.science/insu-04632523v1>

Submitted on 4 Dec 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

4

5 JEAN-DAVID MOREAU^{1,*}, ROMAIN VULLO², ELSIE BICHR², JÉRÔME THOMAS¹,
6 GEORGES GAND¹, CYRIL GAGNAISON³, PASCAL BARRIER³ *and* DIDIER
7 NÉRAUDEAU²

8

9 ¹ Biogéosciences, UMR 6282 CNRS, Université Bourgogne, 6 Boulevard Gabriel, 21000
10 Dijon, France; jean.david.moreau@gmail.com.

11 ² Géosciences Rennes, UMR 6118 CNRS, Université Rennes, 263 Avenue du Général
12 Leclerc, F-35000 Rennes, France.

13 ³ Institut Polytechnique UniLaSalle Beauvais, Département Géosciences, Unité Bassins-
14 Réservoirs-Ressources (B2R – U2R 7511), UniLaSalle-Université de Picardie Jules VERNE,
15 19 rue Pierre Waguet – boîte postale 30313, F-60026 Beauvais cedex, France.

16 * Corresponding author

17

18 **Abstract:** The coastline from Le Veillon (western France) has become a key tracksite for the
19 study of Lower Jurassic archosaurs from Europe since the second half of the 20th century.
20 Amongst the thousand dinosaur footprints recovered from this locality, some tracks became
21 historical and ichnotaxonomical comparative references in many ichnological studies.
22 However, the type material from Le Veillon has never been revised. Here, we reinvestigate
23 the ichnogeneric and ichnospecific type material from the Albert-Félix de Lapparent's

24 collection using morphometry and 3D imaging photogrammetry. Amongst the eight ichnotaxa
25 historically created at Le Veillon, only two are considered valid, i.e. *Grallator olonensis* and
26 *Grallator variabilis*. *Batrachopus gilberti*, *Eubrontes veillonensis* and *Grallator maximus* are
27 subjective junior synonyms of *Batrachopus deweyi*, *Eubrontes giganteus* and *Grallator*
28 *minusculus*, respectively. The ichnogenus *Talmontopus* is a subjective junior synonym of
29 *Kayentapus*. *Anatopus* and *Saltopoides* are considered as nomina dubia. The tracks initially
30 ascribed to *Dahutherium* are here reinterpreted as *Batrachopus* isp. and indeterminate
31 grallatorid tracks. The ichnoassemblage from Le Veillon is more similar to tracks from the
32 Grands Causses area (southern France) than to any other Lower Jurassic archosaur
33 ichnoassemblage worldwide. Although contemporaneous body fossils remain unknown in
34 Vendée, the tetrapod tracks from Le Veillon confirms the co-occurrence of crocodylomorphs
35 and theropods in the central part of Laurasia, along the Tethyan border (near the latitude 30°
36 N) during the Hettangian.

37

38 **Keywords:** theropod footprints; crocodylomorph tracks; Hettangian; Talmont-Saint-Hilaire;
39 Vendée.

40

41

42

43

44

45

46 In 1935, the naturalist Edmond Bocquier (1881-1948) mentioned the presence of “human
47 foot-like” concavities forming alignments on the surface of sandstones from the tidal area of
48 Talmont-Saint-Hilaire, in Vendée, western France (Bocquier 1935; Godard 2003; Viaud &
49 Godard 2008). However, he did not correctly interpret these structures and suggested they
50 were probably produced by marine erosion. It is only in 1963 that Gilbert Bessonnat first
51 interpreted these depressions as archosaur tracks (Lapparent & Montenat 1967). Several field
52 prospections and scientific excavations were undertaken in 1963, 1966 and in 1986-1987
53 (Lapparent & Montenat 1967; Viaud & Duclous 2003). Bessonnat *et al.* (1965) mentioned
54 more than two hundred tracks. In their monography published in the “Mémoires de la Société
55 Géologique de France”, Lapparent & Montenat (1967) estimated that the tidal flat would bear
56 around a thousand crocodylomorph and dinosaur tracks. They provided the first and only
57 detailed ichnological analysis of this tracksite. In this work, they erected eight ichnotaxa:
58 *Anatopus palmatus*, *Batrachopus gilberti*, *Eubrontes veillonensis*, *Grallator maximus*,
59 *Grallator olonensis*, *Grallator variabilis*, *Talmontopus tersi* and *Saltopoides igalensis*. The
60 validity of some of these ichnotaxa was questioned by several authors (e.g. Lockley & Meyer
61 2000; Demathieu 2003) but the type material was never revised.

62 Amongst the many academic institutions and museums housing archosaur tracks from
63 Le Veillon (see the complete list of institutions in Viaud 2003), the collection of the Institut
64 Polytechnique UniLaSalle (Beauvais, France) appears the most important from a scientific
65 point of view. It includes all the type specimens that Lapparent & Montenat (1967) used to
66 erect and describe their ichnotaxa. This collection was constituted by the geologist and
67 palaeontologist Albert-Félix Cochon de Lapparent (1905-1975). The tracksite of Le Veillon
68 being strongly altered by marine erosion and massive excavations (Viaud 2003), this
69 collection represents an outstanding heritage for this locality. Here we reinvestigate the type

70 material of Lapparent & Montenat (1967) using morphometry and 3D imaging
71 photogrammetry in order to revise the validity of the ichnotaxa from Le Veillon.

72

73 **GEOGRAPHICAL AND GEOLOGICAL SETTING**

74

75 The tracksite is located in the northwesternmost part of the Aquitaine Basin (Fig. 1), along the
76 southern edge of the Armorican Massif (northwestern France), in the Vendée department, 5
77 km south-west of Talmont-Saint-Hilaire. The tracksite is located along a 700-800 m long
78 portion of the Atlantic coastline between the beach from Le Veillon and Port Bourgenay. The
79 tracksite is only visible during low tides. Most of the tracks of the Lapparent collection were
80 collected at “Pointe du Veillon” and “Anse de la République”. The Hettangian deposits from
81 the Talmont-Saint-Hilaire coastline can be divided into two informal formations: (1) a detrital
82 Formation and (2) a Dolomitic and Limestone Formation. The former, only visible during low
83 tides, consists of lenticular green sandstones that alternate with green clay or argillites. All
84 tracks analysed in this study were collected by Lapparent & Montenat (1967) in this
85 formation. However, rare tracks were observed in the overlying Dolomitic and Limestone
86 Formation (Lapparent & Montenat 1967; Montenat & Bessonnat 2002). At Le Veillon, the
87 Detrital Formation yielded abundant conifers remains including leafy axes (*Brachyphyllum*
88 sp., *Hirmeriella airelensis*, *Pagiophyllum araucaricum* and *Pagiophyllum peregrinum*) and
89 pollen grains (*Classopollis*) (Thévenard *et al.* 2003). The Dolomitic and Limestone Formation
90 is mainly exposed in the cliffs along the coastline. The lower part of this formation consists of
91 massive, yellowish, brownish to reddish dolomite beds that alternate with green to blue clays.
92 The upper part of the Dolomitic and Limestone Formation consists of grey to yellowish
93 coquinas and dolomitic/calcarenitic limestone beds. First regarded as Rhaetian by Lapparent
94 & Montenat (1967), the age of the Detrital Formation was debated by Montenat & Bessonnat

95 (2002) and later challenged by Thévenard *et al.* (2003) who proposed a Hettangian age (Early
96 Jurassic) based on the plant assemblage. The composition of the Detrital Formation
97 ichnoassemblage that we re-evaluate here corroborates this dating. The malacofauna from the
98 coquinas of the limestone levels further attests a Hettangian age (Ters 1961).

99

100 MATERIAL & METHODS

101

102 In 2022 and 2023, we investigated the Lapparent collection at the Institut Polytechnique
103 UniLaSalle (Beauvais, France). The largest part of this collection corresponds to archosaur
104 tracks from the Early Jurassic sandstones of Talmont-Saint-Hilaire. It consists of
105 tetradactyl/pentadactyl crocodylomorph tracks and tridactyl dinosaur tracks. Their
106 preservation is variable, from exquisitely preserved tracks to poorly preserved tracks. The
107 Lapparent collection includes the type material used to erect the following ichnotaxa:

108 *Anatopus palmatus* (ULB-04C15_B, holotype), *Batrachopus gilberti* (ULB-04C10_A,
109 holotype), *Eubrontes veillonensis* (ULB-04D21_A, plastotype), *Grallator maximus* (ULB-
110 04C13_B, plastotype), *Grallator olonensis* (ULB-04D19_A and ULB-04C12_A holotype;
111 ULB-04C11_A, paratype), *Grallator variabilis* (ULB-04C08_D, plastotype; ULB-04C05_A
112 and ULB-04C08_A, paratypes), *Talmontopus tersi* (ULB-04C02_A, holotype) and
113 *Saltopoides igalensis* (ULB-04C01_B, plaster cast of one footprint from the type trackway).

114 A list of the type specimens is given in Tables 1 and 2.

115 One hundred specimens from the Lapparent collection were used to conduct a
116 biometric analysis. The descriptive terminology and biometric parameters used to describe
117 crocodylomorph and dinosaur tracks largely follow those from Leonardi (1987), Demathieu *et*
118 *al.* (2002) and Milàn & Hedegaard (2010). We used the following standard abbreviations (Fig.
119 2): “L”, length of footprint (for dinosaur tracks); “LM” and “LP”, length of manus and pes

120 tracks, respectively (for crocodylomorph tracks); “W”, width of footprint (for dinosaur
121 tracks); “WM” and “WP”, width of manus and pes tracks, respectively (for crocodylomorph
122 tracks); “LI”, “LII”, “LIII”, “LIV” and “LV”: lengths of digits I, II, III, IV and V,
123 respectively; “I–V” “I–IV” and “II–IV”, divarication angles between digits I and V, digits I
124 and V, and digits II and IV, respectively. For tridactyl dinosaur footprints, we also used “D”
125 which corresponds to the length of the free part of digit III *sensu* Demathieu *et al.* (2002). In
126 the section “Palaeoichnology” below, these morphometric parameters are described by giving
127 three values; the minimum, the average (in brackets) and the maximum. Twenty-seven
128 crocodylomorph tracks (Table 1) and seventy-three dinosaur tracks (Table 2) were measured.

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

140

141 **SYSTEMATIC PALAEOICHOLOGY**

142 Amongst the ichnotaxa erected by Lapparent & Montenat (1967) we distinguish (1) the valid
143 ichnotaxa *Grallator olonensis* and *Grallator variabilis*, and (2) the invalid ichnotaxa
144 *Anatopus palmatus*, *Batrachopus gilberti*, *Eubrontes veillonensis*, *Grallator maximus*,

145 *Talmontopus tarsi* and *Saltopoides igalensis*. Lapparent & Montenat (1967) also described
146 additional and problematic tracks that they identified as *Dahutherium* sp., Unnamed track n°1,
147 Unnamed track n°2. All these tracks are revised here.

148

149 *Nomenclatural remarks.* The ichnotaxonomy of the “classic” Early Jurassic tridactyl
150 footprints such as *Anchisauripus*, *Grallator* and *Eubrontes* is complex and remains in the
151 centre of many debates. According to Olsen & Galton (1984), the difference in size of these
152 three types of tracks (*Grallator*, *Anchisauripus* and *Eubrontes* being small-, medium- and
153 large-sized tracks, respectively; i.e., less than 15 cm, about 20 cm long and up to 25 cm long,
154 respectively according to Olsen *et al.* (1998)) reflects an ontogenetic series and justify the use
155 of a single ichnotaxon. Olsen (1980) and Olsen & Galton (1984) recommended to consider
156 *Anchisauripus* and *Eubrontes* as junior synonyms of *Grallator*. In addition, Weems (1992)
157 could not see any significant morphological difference between *Grallator* and *Anchisauripus*,
158 and he rejected the junior name *Anchisauripus*. Although Olsen *et al.* (1998) considered
159 *Anchisauripus*, *Grallator* and *Eubrontes* as distinctive ichnogenera, Demathieu (1993),
160 Demathieu & Sciau (1992) and Demathieu *et al.* (2002) did not use *Anchisauripus* for
161 medium-sized tridactyl tracks (i.e. L= 15-30 cm) from the Lower Jurassic deposits of France.
162 They justified this choice by the systematic absence of a hallux trace which is an occasional
163 character of *Anchisauripus* (Lull 1904). Accordingly, Demathieu *et al.* (2002) emended the
164 diagnosis of *Grallator* in the following term: “*Tridactyl footprints II-IV, from some*
165 *centimetres to up to a little over 30 cm long, with slender digits in small forms and wider ones*
166 *in the largest. Digits are often separated from each other and bear well-marked pads. Length*
167 *of the free part of III smaller as track-size increases. L/D varies from 2.24 to 2.78 at the 5%*
168 *threshold. Angle II-IV up to 57°*” (translated from French). Ichnological assemblage from Le
169 Veillon sharing strong similarities with tracks found in the Lower Jurassic of the Causses

170 Basin, we follow here Demathieu *et al.* (2002) and use *Grallator* for medium-sized tridactyl
171 footprints.

172

173 *Valid ichnotaxa*

174

Ichnogenus GRALLATOR Hitchcock, 1858

175

Grallator olonensis Lapparent & Montenat, 1967

176

Figure 3

177

178

179 *Holotype.* Lapparent & Montenat (1967) defined the holotype of *G. olonensis* as a surface
180 bearing 25 footprints. Here, we limit the holotype to the longest trackway from this surface:
181 trackway T1-Go of the slabs ULB-04D19_A (concave epireliefs; Fig. 3A–B) and ULB-
182 04C12_A (convexe hyporeliefs).

183

184 *Paratype.* Lapparent & Montenat (1967) defined the paratype (that they called “other samples
185 of the type”) of *G. olonensis* as a group of 5 footprints on the slab ULB-04C11_A. Here, we
186 limit the paratype to the footprint ULB-04C11_A6 (Fig. 3F–H).

187

188 *Other material.* ULB-04C03_B, ULB-04C03_C, ULB-04C03_D, ULB-04C03_E,
189 ULB-04C03_F, ULB-04C05_C, ULB-04C07_A, ULB-04C08_C, ULB-04C08_E, ULB-
190 04C08_G, ULB-04C09_A, ULB-04C09_C, ULB-04C17_E, ULB-04C19_A, ULB-04D17_A,
191 ULB-04D17_B, ULB-04D17_C, ULB-04D22_B,

192

193 *Etymology.* Lapparent & Montenat (1967) erected the ichnospecies *G. olonensis* in reference
194 to the Olonne-sur-Mer area (Vendée), close to the tidal area from Le Veillon.

195

196 *Diagnosis.* Tridactyl, very small-sized tracks (L=3–5 cm), longer than wide and with a long
197 projection of the trace of digit III (L/D = 2.1 in average). L/W ratio quite variable (1.2–2.5).
198 Well-defined, very thin, elongated and often separated impressions of digits. Impression of
199 digit III longer than traces of digits II and IV. Trace of digit III often curved distally. Traces
200 of digits III and IV quite similar in length. Bases of digits II and IV proximally located at the
201 same height. Variable but low divarication angle II–IV (35° in average). Tiny, oval and well-
202 marked phalangeal pads. Tiny marks of acuminate claws.

203

204 *Description.* The material includes two trackways (T1-Go and T2-Go) composed of at least
205 three consecutive footprints (ULB-04D19_A; Fig. 3A–B). The longest trackway is 43.5 cm
206 long. The stride is 34.0–(36.7)–39.5 cm long and the pace is 15.1–(17.8)–20.5 cm long.
207 Tracks form a narrow angle with the trackway midline. The material also includes several
208 partial trackways (ULB-04C19_A, ULB-04D17_A, ULB-04D19_A). The tracks are tridactyl,
209 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).
210 Tracks are longer than wide and show a long projection of the traces of digit III. The L/W and
211 L/D ratios are quite variable, being 1.2–(1.8)–2.5 and 1.8–(2.1)–2.4, respectively. Impressions
212 of digits are well defined, very thin, elongated and often separated. The impression of digit III
213 is longer than those of digits II and IV. The trace of digit III is often curved distally. The
214 traces of digits II and IV are quite similar in length. Typically, the bases of digits II and IV are
215 proximally located at the same height. The position of the digito-metatarsal pad of digit IV is
216 rarely more proximal than that of digit II. The angle between digits II and IV is 24°–(34°)–

217 44°. Phalangeal pads are tiny, oval and commonly well marked. Tracks commonly bears tiny
218 marks of acuminate claws.

219

220 *Remarks.* Based on material from Le Veillon, Lapparent & Montenat (1967) erected *G.*
221 *olonensis* and defined the type material but without providing any diagnosis. In France and
222 throughout the world, *G. olonensis* was only reported from Le Veillon. Other very small-sized
223 tridactyl tracks assigned to distinct ichnospecies of *Grallator* were described from Lower
224 Jurassic strata in Connecticut (Lull 1953): *G. cursorius*, *G. gracilis* (= *G. tuberosus* according
225 to Weems 1992) and *G. tenuis*. *G. cursorius* differs from *G. olonensis* in showing more
226 slender, longer tracks (type material with L=7.0–7.9 cm according to Weems 1992) and a
227 base of IV much more proximal than II (Fig. 4). Although *G. gracilis* falls in the range size of
228 *G. olonensis*, it differs from the latter in showing lower projection of III (type material with
229 L/D= 2.6 according to Weems 1992; Fig. 4). *G. tenuis* differs from *G. olonensis* in showing
230 longer tracks (type material with L=6.4–6.6 cm according to Weems 1992) and the base of IV
231 which is more proximal than II (Fig. 4).

232

233 *Grallator variabilis* Lapparent & Montenat, 1967

234 Figure 5

235

236 *Plastotype.* ULB-04C08_D (Fig. 5A–C).

237

238 *Paratypes.* ULB-04C05_A (Fig. 5D–F) and ULB-04C08_A.

239

240 *Other material.* ULB-04C05_B, ULB-04C08_B, ULB-04C08_F, ULB-04C13_A, ULB-
241 04C14_J, ULB-04C15_D, ULB-04C15_E, ULB-04C17_C, ULB-04C17_D, ULB-04C17_G,
242 ULB-04C18_B, ULB-04C18_C, ULB-04D18_A, ULB-04D18_B, ULB-04D18_C, ULB-
243 04D18_D.

244

245 *Description.* The tracks are tridactyl, small-sized, longer than wide ($L/W = 1.3\text{--}(1.6)\text{--}1.9$),
246 $8.6\text{--}(11.0)\text{--}13.6$ cm long and $5.2\text{--}(6.9)\text{--}8.0$ cm wide (Fig. 5A–I; Table 2). The trace of digit
247 III shows a long free part ($L/D = 1.8\text{--}(2.4)\text{--}3$). Impressions of digits are very well defined,
248 thin, elongated and often separated. The impression of digit III is longer than traces of digits
249 II and IV. Traces of digits II are the shortest. At the base of the trace of digit IV, the position
250 of the digito-metatarsal pad is more proximal than that of digit II. The divarication angle II–
251 IV is $24^\circ\text{--}(35^\circ)\text{--}46^\circ$. Round to oval phalangeal pads and pointed marks of claws are
252 commonly very well marked. Marks of claws on the traces of digits II and IV are clearly
253 oriented outward.

254

255 *Remarks.* *G. variabilis* was erected by Lapparent & Montenat (1967) based on tracks from Le
256 Veillon. This ichnospecies was abundantly reported in coeval tracksites from the Hettangian-
257 Sinemurian deposits of the Causses Basin, in southern France (Demathieu & Sciau 1992;
258 Sciau 1992; Demathieu *et al.* 2002; Gand *et al.* 2007), as well as in northern Africa (Bessedik
259 *et al.* 2008). As mentioned by Lapparent & Montenat (1967), the morphology of *G. cuneatus*
260 from the Connecticut is very close to that of *G. variabilis* from Le Veillon. Morphometric and
261 statistical analyses made by Demathieu *et al.* (2002) and Gand *et al.* (2007) on *G. variabilis*
262 from the Causses Basin confirmed that this last ichnospecies and *G. cuneatus* is an
263 ichnospecies with close morphological affinities with *G. variabilis* (Fig. 4). According to
264 Weems (1992), *G. cuneatus* is a synonym of *G. tenuis*. However, this ichnospecies is smaller

265 than *G. variabilis* from Le Veillon and from the Causses Basin; L=6.4–6.6 cm; Fig. 4). Since
266 the case of *G. cuneatus* remains unclear, Demathieu *et al.* (2002) did not synonymize *G.*
267 *variabilis* with this ichnospecies. Considering *G. variabilis* as valid, Demathieu *et al.* (2002)
268 erected the following diagnosis (translated from the French): “*Fingers are thin with well-*
269 *marked phalangeal pads. The median digit is very elongated, the lateral digits are tightened*
270 *and slightly tilted. There are three pads on digits III and IV, and two on digit II. There is no*
271 *heel but digit IV is slightly prolonged posteriorly. Claws are elongated and sharp forming*
272 *cuneiform marks. The ratio stride/pace corresponds to an elongated stride. The paces are*
273 *arranged on a same line, the median digit in the axis of the trackway, its claw oriented*
274 *inwards”.*

275

276 *Invalid and problematic ichnotaxa*

277

278 Ichnogenus ANATOPUS Lapparent & Montenat, 1967

279 *Anatopus palmatus* Lapparent & Montenat, 1967

280 (*nomen dubium*)

281 Figure 6

282

283 *Material.* ULB-04C10_C, ULB-04C15_B (holotype of *A. palmatus*), ULB-04C15_C.

284

285 *Description.* The material includes three, isolated and very poorly preserved tracks. Tracks
286 ULB-04C15_B (Fig. 6A–C) and ULB-04C15_C (Fig. 6D–F) are tridactyl whereas ULB-
287 04C10_C is a partial footprint and only preserves two traces of digits. Lapparent & Montenat
288 (1967) included tracks with two kinds of morphologies in this ichnotaxon.

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

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

298

299 *Remarks.* Lapparent & Montenat (1967) justified the erection of *Anatopus palmatus* (without
300 establishing its diagnosis) by (1) the occasional presence of a skin mark forming a webbing
301 between tracks of digits II, III and IV; and (2) traces of digits II and IV very short compare to
302 digit III (Fig. 6A–B). Lapparent & Montenat (1967) indicated that only the holotype (ULB-
303 04C15_B; Fig. 6A–C) shows the mark of a webbing. After reinvestigation of the holotype, we
304 are not convinced by the description of Lapparent & Montenat (1967) (Fig. 6C). The structure
305 considered by Lapparent & Montenat (1967) as the border of a webbing clearly shows a
306 sedimentary origin (structure propagated beyond the track). The holotype of *Anatopus*
307 *palmatus* consists of an undertrack, explaining why the marks of digits II and IV are so short.
308 The sketch of ULB-04C15_C proposed in fig. 16B1 of Lapparent & Montenat (1967) does
309 not correspond to the morphology of the track, which actually looks more like a grallatorid
310 footprint; however, it is too poorly preserve to propose any precise determination. We thus
311 consider *Anatopus palmatus* as a *nomen dubium*.

312

313

Ichnogenus BATRACHOPUS Hitchcock, 1845

314
315
316
317
318
319
320
321
322
323
324
325
326
327
328
329
330
331
332
333
334
335
336
337
338

Batrachopus gilberti Lapparent & Montecat, 1967

(subjective junior synonym of *Batrachopus deweyi* (Hitchcock, 1843) Hitchcock, 1845)

Figure 7

Material. ULB-04C02_B, ULB-04C04_A, ULB-04C09_B, ULB-04C10_A (holotype of *B. gilberti*), ULB-04C10_E, ULB-04C14_A, ULB-04C14_C, ULB-04C14_D, ULB-04C14_F, ULB-04C14_G, ULB-04C14_H.

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.

339

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

349 The gross morphology of *Batrachopus* is close to those of *Antipus* and
350 *Crocodylopodus*. Olsen & Padian (1986) considered *Antipus* as a synonym of *Batrachopus*.
351 However, Coombs (1996) and Lockley & Meyer (2004) rejected this proposition. According
352 to Lockley & Meyer (2004), *Antipus* differs from *Batrachopus* in showing: much longer
353 impressions of digits on the manus tracks; slender, tapering, quite curved digit tracks with
354 higher divarication angles and narrow claw impressions. The tracks from Le Veillon clearly
355 differ from *Antipus* in showing shorter blunt-toed digits. *Crocodylopodus* differs from tracks
356 of Le Veillon in showing more slender and divergent digits, less outward rotation of the pes
357 and more outward rotation of the manus (Lockley & Meyer 2004).

358 Based on ULB-04C10_A, Lapparent & Montenat (1967) erected *B. gilberti*. The
359 validity of the diverse ichnospecies of *Batrachopus* was strongly debated (Olsen & Padian
360 1986; Rainforth 2005, 2007). In their revision of *Batrachopus*, Olsen & Padian (1986)
361 considered only three valid ichnospecies for this ichnogenus and emended the diagnosis of
362 each of them: *B. deweyi*, *B. parvulus* and *B. dispar*. Based on the following characters, the
363 tracks from Le Veillon can be confidently ascribed to *B. deweyi* (see emended diagnosis in

364 Olsen & Padian 1986): range size of pes length (between 2 and 6 cm); manus tracks about
365 75% of the length of the pes; on pes tracks, imprints of digit II and IV are sub-equal in length.
366 We consider *B. gilberti* as a junior synonym of *B. deweyi*. *B. parvulus* (see emended diagnosis
367 in Olsen & Padian (1986)) differs from tracks of Le Veillon in showing a very short
368 impression of I on pes tracks. According to Rainforth (2005), *B. parvulus* can be synonymized
369 with the type ichnospecies *B. deweyi*. *B. dispar* (see emended diagnosis in Olsen & Padian
370 (1986)) differs from tracks of Le Veillon in showing a stronger heteropody. Rainforth (2005)
371 considered three additional valid ichnospecies: *B. bellus*, *B. gracilior*, *B. gracilis*. It contrasts
372 with Olsen & Padian (1986) who subjectively synonymised these ichnospecies in *B. deweyi*.
373 According to Rainforth (2005), *B. bellus* cannot be synonymised with *B. deweyi* because it
374 differs from this ichnospecies in showing tridactyl pes (not concordant with the sketch of *B.*
375 *bellus* in fig. 20.2B of Olsen & Padian (1986)). Rainforth (2007) tentatively synonymised *B.*
376 *gracilior* and *B. gracilis*. Olsen & Padian (1986) explained that “apart from its smaller, longer
377 pace and the lack of impressions of digit V in the pes” *B. gracilis* is identical to *B. deweyi*.

378

379 Ichnogenus DAHUTHERIUM Montenat, 1968

380 *Dahutherium* sp.

381 (*nomen nudum*)

382 Figure 8

383

384 *Material.* ULB-04C15_A, ULB-04C18_B.

385 *Description.* Lapparent & Montenat (1967) described two isolated tracks including a
386 tetradactyl pes track (ULB-04C18_B; Fig. 8 A–C) and a tridactyl manus track (ULB-
387 04C15_A; Fig. 8D–F) that were collected *ex-situ*. Our interpretation is that the track ULB-

388 04C18_B described as a tetradactyl pes track by Lapparent & Montenat (1967) actually
389 represents two superimposed tridactyl grallatorid footprints (Fig. 8 A–C). The smallest of the
390 two superimposed tracks is longer than wide ($L/W = 1.7$), 12.2 cm long and 7.2 cm wide. The
391 trace of digit III shows a long free part ($L/D = 2.4$). Impressions of digits are very well-
392 defined, thin and elongated. The impression of digit III is longer than traces of digits II and
393 IV. The trace of digits II is the shorter. At the base of the trace of digit IV, the position of the
394 digito-metatarsal pad is more proximal than that of digit II. The divarication angle II–IV is
395 40° . Round to oval phalangeal pads and pointed marks of claws are well marked. The largest
396 of the two superimposed tridactyl tracks is ≈ 14 cm long (value measured on a partial length
397 of track, the apex of the trace of III being not well-marked), 12 cm wide. Impressions of digits
398 are thin, elongated and separated. The divarication angle II–IV is 41° . The impression of digit
399 III is the longest. ULB-04C15_A (Fig. 8D–F) is tetradactyl, not tridactyl as proposed by
400 Lapparent & Montenat (1967). This track is quite wider than long, 3.0 cm long and 3.9 cm
401 wide (Table 1). Impressions of digits are short and their apices are rounded. Traces of digit I
402 are poorly impressed whereas those of II–IV are well marked. Impression of digit III is the
403 longest, and impression of digit I the smallest. The divarication angle of digits I–IV is 83° .

404

405 *Remarks.* Lapparent & Montenat (1967) first introduced the name *Dahutherium* (without
406 diagnosis) for two tracks from Le Veillon while this ichnogenus was actually erected one year
407 later based on material from the Middle Triassic of Ardèche (southern France) (Montenat,
408 1968). The genus *Dahutherium* has been reported from several Middle Triassic to Lower
409 Jurassic tracksites from France (Montenat 1968; Haubold 1971; Gand 1974a, 1974b). The
410 smallest and the largest of the two superimposed tridactyl tracks (initially interpreted as a
411 tetradactyl *Dahutherium* pes by Lapparent & Montenat (1967); ULB-04C18_B) can be
412 ascribed to *G. variabilis* and *Grallator* isp., respectively. Although Lapparent & Montenat

413 (1967) interpreted ULB-04C15_A as a tridactyl manus track of *Dahutherium*, the morphology
414 and the dimension of this specimen match with *Batrachopus*.

415

416 Ichnogenus EUBRONTES Hitchcock, 1845

417 *Eubrontes veillonensis* Lapparent & Montenat, 1967

418 (subjective junior synonym of *Eubrontes giganteus* Hitchcock, 1845)

419 Figure 9A–C

420

421 *Material.* ULB-04D21_A (plaster cast, plastotype of *E. veillonensis*).

422

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

428

429 *Remarks.* Based on an *in situ* trackway composed of twelve footprints, Lapparent & Montenat
430 (1967) erected (without diagnosis) the ichnospecies *Eubrontes veillonensis*. ULB-04D21_A
431 (Fig. 9A–C) is the plastotype replicating one of the best preserved footprints of this trackway.
432 Recent prospecting conducted in 2022 on the tidal flat from Le Veillon did not allow to find
433 the type trackway, which was most probably destroyed. *E. giganteus* was introduced by
434 Hitchcock (1845) based on tridactyl tracks from the Lower Jurassic rocks of the Dinosaur
435 Footprint Reservation in Holyoke, Massachusetts (Olsen *et al.* 1998). In Fig. 4, ULB-
436 04D21_A is compared with Early Jurassic *Eubrontes giganteus* specimens from France and
437 from the USA. This biometric analysis shows that the *Eubrontes* track from Le Veillon fully

438 falls within the morphological range of this ichnospecies. *E. giganteus* and *E. veillonensis*
439 show similar shape of footprints with massive impressions of digits II, III and IV bearing
440 well-marked pads and long claw marks as well as the presence of a well-marked digito-
441 metatarsal pad of digit IV more proximal than that of digit II. Based on these observations we
442 consider *E. veillonensis* as a junior synonym of *E. giganteus*.

443

444 Ichnogenus GRALLATOR Hitchcock, 1858

445 *Grallator maximus* Lapparent & Montenat, 1967

446 (subjective junior synonym of *Grallator minusculus* Hitchcock, 1858 emend. Demathieu,
447 Gand, Sciau & Freytet, 2002)

448 Figure 10

449

450 *Material.* ULB-04C04_A_1; ULB-04C06_A; ULB-04C10_B; ULB-04C13_B (holotype of *G.*
451 *maximus*).

452

453 *Description.* The tracks are tridactyl, longer than wide ($L/W = 1.5\text{--}(1.6)\text{--}1.7$), $26.0\text{--}(26.8)\text{--}$
454 27.5 cm long and $15.5\text{--}(16.6)\text{--}17.7$ cm wide (Fig. 10A–F; Table 2). D is quite long ($L/D =$
455 $2.9\text{--}(3.0)\text{--}3.2$). Impressions of digits are large, separated, well defined and elongated. The
456 traces of digits II and III are the smallest and the longest, respectively. The angle between
457 digits II and IV is $30^\circ\text{--}(33^\circ)\text{--}37^\circ$ (Table 2). Impressions of digital pads are well preserved and
458 are circular to oval. The position of the digito-metatarsal pad of digit IV is more proximal
459 than that of digit II (Fig. 10A–F).

460

461 *Remarks.* Based on this material, Lapparent & Montenat (1967) erected (without diagnosis)
462 the ichnospecies *Grallator maximus*. These tracks being similar to *G. minusculus* (Fig. 4), we
463 consider *G. maximum* as a junior synonym of this ichnospecies. Based on footprints from the
464 Jurassic of the USA, Hitchcock (1858) first described such large tridactyl tracks under the
465 name *Brontozoum minusculum* that were renamed *Anchisauripus minusculus* by Lull (1904).
466 Based on material from the Hettangian-Sinemurian of the Causses Basin, Demathieu (1993)
467 identified tracks that show similarities with the type material of *Anchisauripus minusculus*.
468 Since *Anchisauripus* is characterized by the occasional presence of a hallux trace (Lull 1904),
469 which is always absent in the material from France, Demathieu (1993), Demathieu & Sciau
470 (1992) and Demathieu *et al.* (2002) used *Grallator minusculus* rather than *Anchisauripus*
471 *minusculus*. Demathieu *et al.* (2002) emended the diagnosis of *G. minusculus* as follows:
472 “Large tridactyl tracks II–IV of bipeds with $L \times l = ca\ 300 \times 200\ mm$, with large digits and
473 well-marked pads. Claws are weakly developed and the digito-metatarsal pad of digit IV is
474 often marked. The angle II–IV is 39° in average. The projection of III is low with a III/D ratio
475 around 1.93” (translated from French).

476

477 Ichnogenus SALTOPOIDES Lapparent & Montenat, 1967

478 *Saltopoides igualensis* Lapparent & Montenat, 1967

479 (*nomen dubium*)

480 Figure 11

481

482 *Material.* ULB-04C01_A, ULB-04C01_B (plaster cast, plastotype of *S. igualensis*).

483

484 *Description.* The tracks are tridactyl, longer than wide ($L/W = 1.32\text{--}(1.36)\text{--}1.40$), $15.5\text{--}(16)\text{--}$
485 $16.5\ cm$ long and $11\text{--}(11.75)\text{--}12.5\ cm$ wide; Fig. 11; Table 2). Impressions of digits are quite

486 wide with well-distinguished claw marks. The free part of III is quite short ($L/D = 2.6$ – (2.8) –
487 3.1). The divarication angle between digits II and IV is large (II – $IV = 49.0^\circ$ – (51.5°) – 54.0°)
488 and D is short ($L/D=1.31$ – (1.36) – 1.41). The digito-metatarsal pad of digit IV is much more
489 proximal than that of digit II.

490 *Remarks.* Based on a poorly preserved trackway composed of three tridactyl footprints (only
491 the distal parts of digits are partially preserved), Lapparent & Montenat (1967) erected
492 *Saltopoides igalensis* and (without providing any diagnosis). Lapparent & Montenat (1967)
493 justified the erection of the ichnogenus *Saltopoides* by an asymmetry of the footprint and the
494 particularly long length of pace between footprints. Lapparent & Montenat (1967) suggested
495 that the trackmaker was a “jumping dinosaur”. Recent prospecting conducted in 2022 on the
496 tidal flat of Le Veillon did not allow us to find the type trackway of *S. igalensis* that has most
497 probably eroded away. It appears that biometric characteristics of ULB-04C01_A and ULB-
498 04C01_B (plastotype replicating one of the footprints of the type trackway) differ from other
499 tridactyl tracks from Le Veillon that do not show such a proximal base of digit IV compared
500 to digit II. However, without any possibility to revise the now-destroyed type trackway, the
501 ichnotaxonomic validity of *S. igalensis* remains questionable.

502

503 Ichnogenus TALMONTOPUS Lapparent & Montenat, 1967

504 (subjective junior synonym of *Kayentapus* Welles, 1971)

505 *Talmontopus tersi* Lapparent & Montenat, 1967

506 (*nomen dubium* = *Kayentapus* isp.)

507

508 Figure 12A–C

509

510 *Material.* ULB-04C02_A (holotype of *T. tersi*).

511

512 *Description.* The track ULB-04C02_A consists of a single, slightly longer than wide ($L/W =$
513 1.2), 26 cm long and 21.5 cm wide tridactyl track (Fig. 12A–C; Table 2). The angle between
514 II and IV is large ($II-IV = 64^\circ$). Digit imprints are quite thin and pointed. The traces of digits
515 II and IV are straight and quite similar in length. The trace of digit III is the longest and is
516 slightly curve. The digito-metatarsal base of digit IV is slightly more proximal than that of
517 digit II. The free part of III is quite short ($L/D = 2.8$). The imprints of pads and claws are only
518 poorly marked.

519 *Remarks.* Based on the track ULB-04C02_A, Lapparent & Montenat (1967) erected
520 *Talmontopus tersi*. They justified the creation of *T. tersi* by a very high T value between thin
521 tracks of digits, and the presence of a putative webbing mark. We consider the webbing mark
522 drew in fig. 17 of Lapparent & Montenat (1967) as a sedimentary structure that corresponds
523 to a slight thickening of sediment preserved between the traces of digits (see also plate XII.1
524 in Lapparent & Montenat 1967; ULB-04C02_A). Since ULB-04C02_A shows many
525 characters of *Kayentapus*, we consider *Talmontopus* as a subjective junior synonym of this
526 ichnogenus. *Kayentapus* differs from *Grallator* and *Eubrontes* in showing larger divarication
527 angle II-IV and a smaller L/W ratio. *Kayentapus* was erected by Welles (1971) based on the
528 type ichnospecies *K. hopii* from the Lower Jurassic Kayenta Formation in Arizona. Two other
529 ichnospecies were later described from Lower Jurassic strata of the USA and Poland: *K.*
530 *minor* and *K. soltykovensis* (firstly named *Grallator (Eubrontes) soltykovensis* in Gierliński
531 1991 and Gierliński & Ahlberg 1994), respectively (Weems 1987; Gierliński 1996). Based on
532 its D/W and $(L-D)/W$ ratios (0.43 and 0.78, respectively), the track ULB-04C02_A fully falls
533 within the morphological space of *K. hopii* (see the fig. 1 of Gierliński 1996 and the fig. 6B of
534 Lockley *et al.*, 2011). However, *K. hopii* is clearly larger ($L=34.0-35.5$) than ULB-04C02_A
535 (Fig. 4). It also differs from ULB-04C02_A in showing traces of digits that are slender and

536 well individualized, and digito-metatarsal pads of the digit IV much more proximal. ULB-
537 04C02_A is close to *K. minor* (Fig. 4), however, it seems to differ from this ichnospecies in
538 showing a higher D/W ratio (see the fig. 1 of Gierliński 1996 and the fig. 6B of Lockley *et al.*
539 2011). *K. slotykovensis* differs from ULB-04C02_A in showing a smaller (L-D)/W ratio (see
540 the fig. 1 of Gierliński 1996 and the fig. 6B of Lockley *et al.* 2011).

541

542 Unnamed track n°1
543 (= *Batrachopus* isp.)

544 Figure 13A–C

545

546 *Material.* ULB-04C14_I, ULB-04C17_A.

547

548 *Description.* The two tracks described by Lapparent & Montenat (1967) under the name
549 “Unnamed track n°1” are poorly preserved. They are tetradactyl, small-sized, as long as wide,
550 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
551 short. They show rounded phalangeal pads and their apices bear tiny marks of claws. A large
552 plantar-like impression is present on ULB-04C14_I.

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

557

558 Unnamed track n°2
559 (= *G. cf. variabilis*)

560
561
562
563
564
565
566
567
568
569
570
571
572
573
574
575
576
577
578
579
580
581
582
583

Material. ULB-04D22_A.

Description. The track is tridactyl, small-sized, longer than wide, approximately 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 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) made a mistake by considering that the traces of digits II, III and IV are 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 USA, where they have been mainly ascribed to the ichnogenus *Batrachopus* (e.g. Hitchcock 1845; Lapparent & Montenat 1967; Olsen & Galton 1984; Olsen

584 & Padian 1986; Mojica & Macia 1987; Demathieu & Sciau 1992; Olsen 1995; Popa 1999;
585 Lockley *et al.* 2004; Milner *et al.* 2006; Dalman 2012). In Europe, lowermost Jurassic
586 (Hettangian-Sinemurian) crocodylomorph tracks are quite rare (Lockley & Meyer, 2000),
587 being only known from France (Lapparent & Montenat 1967; Sciau 1992; Moreau *et al.*
588 2019) and Romania (Popa 1999).

589

590 Early Jurassic tridactyl tracks of dinosaurs were reported from many areas of
591 Australia, Africa, America, Asia and Europe (e.g. Gierliński & Ahlberg 1994 ; Olsen *et al.*
592 1998; Demathieu *et al.* 2002; Lucas *et al.* 2006; Dalman 2012; Xing *et al.* 2014;
593 Wagensommer *et al.* 2016; Sciscio *et al.* 2017 ; Romilio 2021). The co-occurrence of
594 *Grallator*, *Kayentapus* and *Eubrontes* was observed in various Early Jurassic tracksites from
595 several areas in Europe: France (Moreau *et al.* 2018), Hungary (Gierliński 1996), Italy
596 (Avanzini *et al.* 2006) and Poland (Pacyna *et al.* 2022). The ichnoassemblage from Le Veillon
597 shares many similarities with the historical Early Jurassic American tracksites described by
598 the palaeoichnologist Edward Hitchcock (Hitchcock 1841, 1845, 1858). *Batrachopus*,
599 *Grallator* and *Eubrontes* were introduced based on material from New England, eastern USA
600 (Hitchcock 1841, 1845, 1858). The ichnogenus *Kayentapus* was first described based on
601 material from Arizona in western USA (Welles 1971; Lockley *et al.* 2011).

602 Among the international record of Early Jurassic archosaur tracksites, the
603 ichnoassemblage from Le Veillon shares most similarities with that of the Grands Causses
604 area (southern France). The Hettangian-Sinemurian deposits from the Causses Basin yielded
605 more than 60 archosaur tracksites. In this area, Sinemurian crocodylomorph tracks were
606 ascribed to *Batrachopus deweyi* by Demathieu & Sciau (1992) and Demathieu *et al.* (2002).
607 These tracks differ from the specimens assigned to *B. deweyi* from Le Veillon in showing
608 more slender traces of digits and wider divarication angle. In France, Le Serre tracksite

609 (Lozère, northern part of the Causses Basin) is the only other Hettangian tracksite yielding
610 crocodylomorph traces (Moreau *et al.* 2019).

611 Although very small-sized tridactyl tracks such as *G. olonensis* remain unknown from
612 the Hettangian-Sinemurian deposits of the Causses Basin, this area yields abundant specimens
613 of *Grallator variabilis* and *Grallator minusculus*. Biometric comparisons among tracks from
614 Le Veillon and those from the Causses Basin show that the occupied morphological spaces
615 are similar for each of these two ichnospecies in both regions (Fig. 4). Early Jurassic
616 archosaur tracksites from the Causses Basin also yield two additional *Grallator* ichnospecies
617 that are absent from the Lapparent collection: *Grallator lescurei* and *Grallator sauclierensis*.
618 In the Hettangian tracksites from the Causses Basin, two ichnospecies of *Eubrontes* were
619 identified, *Eubrontes divaricatus* (Demathieu & Sciau 1999) and *Eubrontes giganteus*
620 (Demathieu *et al.* 2002; Sciau 2003; Moreau *et al.* 2021). Since the revision of the ichnogenus
621 *Eubrontes* by Olsen *et al.* (1998), Demathieu *et al.* (2002) suggested to use only *Eubrontes*
622 *giganteus* for the material from this area. Although *Dilophosauripus williamsi* was broadly
623 used to describe tracks from the Causses Basin (e.g. Demathieu & Sciau 1992; Sciau 1992,
624 2003; Demathieu 1993; Demathieu *et al.* 2002; Gand *et al.* 2007; Moreau *et al.* 2014), its
625 validity was strongly debated (Lucas *et al.* 2006; Lockley *et al.* 2011). Recent morphometrical
626 comparisons made by Gand *et al.* (2018) suggested that tracks ascribed to *Dilophosauripus* in
627 the Causses Basin are similar to those of *Kayentapus* and should be ascribed to that
628 ichnogenus. Their morphology is quite close to that of the *Kayentapus* tracks from Le Veillon
629 but they are smaller. In France, except the Le Veillon tracksite and the Causses Basin, Early
630 Jurassic tridactyl dinosaur tracks were also reported from Lot (Lange-Badré & Lafon 2000),
631 Dordogne (Gand *et al.* 2007) and Var (Ellenberger 1965).

632

633 *Trackmakers*

634
635 Crocodylomorph and dinosaur body fossils remain unknown in the lowermost Jurassic
636 deposits from Vendée. Olsen & Padian (1986) proposed that the trackmakers of *Batrachopus*
637 were crocodyliform protosuchians (see fig. 20.11 in Olsen & Padian 1986). The osteological
638 architectures of manus and pes of *Protosuchus* (Colbert *et al.* 1951) match with the
639 morphology of *Batrachopus* (Olsen & Padian 1986). The trackmaker of *Batrachopus* should
640 have been a crocodylomorph with a pedal digit V reduced (Olsen & Padian 1986). Earliest
641 Jurassic crocodylomorphs were small and fully terrestrial (Frey 1988; Olsen 1995). Body
642 fossils of crocodylomorphs are almost unknown from the earliest Jurassic of Europe, with
643 only a few isolated remains from Great Britain assignable to indeterminate sphenosuchians
644 (Whiteside *et al.* 2016).

645 The phalangeal formula (type 3, 4 and 5 for toes II, III and IV, respectively) of the
646 tridactyl tracks *Eubrontes*, *Grallator* and *Kayentapus* matches with the osteological
647 architecture of theropod dinosaurs. Body fossils of earliest Jurassic theropods were ascribed to
648 Coelophysoidea and Ceratosauria and reported from Africa, Antarctica, China, Europe and
649 USA (Weishampel *et al.* 2004; Smith *et al.* 2007; Xing *et al.* 2013). In Europe, rare theropod
650 remains have been discovered in the Hettangian-Sinemurian deposits of Great Britain, France,
651 Italy and Luxembourg (Larsonneur & Lapparent 1966; Benton *et al.* 1995; Carrano &
652 Sampson 2004; Delsate & Ezcurra 2014; Martill *et al.* 2016; Dal Sasso *et al.* 2018). The
653 Moon-Airel Formation (Normandie, northwestern France), yielded the only known earliest
654 Jurassic theropod from France (Larsonneur & Lapparent 1966), i.e. the coelophysoid
655 *Lophostropheus airelensis* (Cuny & Galton 1993; Ezcurra & Cuny 2007). Using the formula
656 of Alexander (1976) and Thulborn (1990), the hip height of the smallest theropods from Le
657 Veillon varies from 18 to 21 cm (trackmakers of *G. olonensis*). The speed of the trackmakers
658 of *G. olonensis* varies from 2.9 to 4.4 km/h, suggesting a walking gait. Lapparent & Montenat

659 (1967) attributed the trackmaker of *Talmontopus* to an ornithopod. As this ichnogenus is here
660 reinterpreted and renamed (*Kayentapus*), its trackmaker must be regarded as a medium-sized
661 theropod. Lapparent & Montenat (1967) mentioned that they observed several tail marks of
662 theropods associated with track-bearing tridactyl tracks. However, they specified that it was
663 not possible to link tail marks and footprints. We interpret the single specimen figured in
664 Lapparent & Montenat (1967; pl.4, fig.2 in Lapparent & Montenat 1967; ULB-04C15_E) as a
665 sedimentary structure such as a large desiccation crack, not a tail mark.

666

667 CONCLUSION

668

669 The ichnotaxonomic revision of the type material from the Lapparent collection allows to
670 identify valid and invalid/problematic ichnotaxa from Le Veillon, a historical earliest Jurassic
671 tracksite in western France. Amongst the eight ichnotaxa erected by Lapparent & Montenat
672 (1967), only two are considered as valid, *Grallator olonensis* and *Grallator variabilis*. The
673 diagnosis of *Grallator olonensis* is here formally established. *Batrachopus gilberti*, *Eubrontes*
674 *veillonensis* and *Grallator maximus* are regarded as subjective junior synonyms of
675 *Batrachopus deweyi*, *Eubrontes giganteus* and *Grallator minusculus*, respectively. *Anatopus*
676 and *Saltopoides* are considered as nomina dubia. The ichnogenus *Talmontopus* is considered
677 as a subjective junior synonym of *Kayentapus*. The tracks initially ascribed by Lapparent &
678 Montenat (1967) to *Dahutherium* are here reinterpreted and identified as *Batrachopus* isp.
679 *Grallator variabilis* and *Grallator* isp. The two kinds of unnamed tracks described by
680 Lapparent & Montenat (1967) are assigned to *Batrachopus* isp. and *G. cf. variabilis*. The
681 Hettangian ichnoassemblage from Le Veillon shares strong similarities with the Early Jurassic
682 archosaur ichnoassemblage from the Causses Basin area in southern France. The

683 ichnodiversity of the Lapparent collection show that trackmakers were theropod dinosaurs and
684 crocodylomorphs.

685

686 *Acknowledgements.* This work is a contribution to the e-Col+ project funded by the
687 Programme d'Investissements d'Avenir (ANR 21 ESRE 0053) and the Research Infrastructure
688 Récolnat (national network of naturalist collections). We thank Emmanuel Fara for
689 discussions and comments on the first draft of the manuscript.

690

691 *Author contributions.* **Conceptualization** Jean-David Moreau (JDM), Romain Vullo (RV),
692 Didier Néraudeau (DN); **Data Curation** JDM; **Formal Analysis** JDM; **Funding Acquisition**
693 Jérôme Thomas (JT); **Investigation** JDM, JT; **Methodology** JDM; **Project Administration**
694 JDM; **Supervision** JDM; **Validation** RV, Georges Gand (GG), DN; **Visualization** JDM;
695 **Writing – Original Draft Preparation** JDM; **Writing – Review & Editing** RV, Elsie Bichr
696 (EB), JT, GG, Cyril Gagnaison (CG), Pascal Barrier (PB), DN.

697

698 REFERENCES

699

700 ALEXANDER, R. McN. 1976. Estimates of speeds of dinosaurs. *Nature* **261**, 129–130.

701

702 AVANZINI, M., PIUBELLI, D., MIETTO, P., ROGHI, G., ROMANO, R. and MASETTI, D.
703 2006. Lower Jurassic (Hettangian–Sinemurian) dinosaur trackmegasites, southern
704 Alps, northern Italy. *New Mexico Museum of Natural History and Science Bulletin*, **37**,
705 207–216.

706

707 BENTON, M. J., MARTILL, D. M. and TAYLOR, M. A. 1995. The first Lower Jurassic
708 dinosaur from Scotland: limb bone of a ceratosaur theropod from Skye. *Scottish*
709 *Journal of Geology*, **31**, 177–182.

710

711 BESSEDIK, M., MAMMERI, C., BELKEBIR, L., MAHBOUBI, M., ADACI, M., HEBIB,
712 H., BENSALAH, M. and MANSOURI, M. E. H. 2008. Nouvelles données sur les
713 ichnites de dinosaures de la région d'El Bayadh (Crétacé inférieur,
714 Algérie). *Palaeovertebrata*, **36**, 7–35.

715

716 BESSONNAT, G., LAPPARENT (de), A. F., Montenat, C. and Ters, M. 1965. Découverte de
717 nombreuses empreintes de pas de reptiles dans le Lias inférieur de la côte de Vendée.
718 *Comptes Rendus de l'Académie des Sciences de Paris*, **260**, 5324–5326.

719

720 BOCQUIER, E., 1935. Observations sur quelques témoins d'anciens rivages dans le
721 Talmondais (Vendée). *Annuaire de la Société d'Émulation de la Vendée*, 17–26.

722

723 CARRANO, M. T. and SAMPSON, S. D. 2004. A review of coelophysoids (Dinosauria:
724 Theropoda) from the Early Jurassic of Europe, with comments on the late history of
725 the Coelophysoidea. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **9**,
726 537–558.

727

728 COLBERT, E. H., MOOK, C. C. and BROWN, B. 1951. The ancestral crocodylian
729 *Protosuchus*. *Bulletin of the American Museum of Natural History*, **97**, 149–182.

730

731 COOMBS, W. P. Jr. 1996. Redescription of the ichnospecies *Antipus flexiloquus* Hitchcock,
732 from the Early Jurassic of the Connecticut Valley. *Journal of Paleontology*, **70**,327–
733 331
734
735 CUNY, G. and GALTON, P.M. 1993. Revision of the Airel theropod dinosaur from the
736 Triassic-Jurassic boundary (Normandy, France). *Neues Jahrbuch für Geologie und*
737 *Paläontologie, Abhandlungen* **187**, 261–288.
738
739 DALMAN, S. G .2012. New data on small theropod footprints from the Early Jurassic
740 (Hettangian) Hartford Basin of Massachusetts, United States. *Bulletin of the Peabody*
741 *Museum of Natural History*, **53**, 333–353.
742
743 DAL SASSO, C., MAGANUCO, S. and CAU, A. 2018. The oldest ceratosaurian
744 (Dinosauria: Theropoda), from the Lower Jurassic of Italy, sheds light on the evolution
745 of the three-fingered hand of birds. *PeerJ*, **6**, e5976.
746
747 DELSATE, D. and EZCURRA, M. D. 2014. The first Early Jurassic (late Hettangian)
748 theropod dinosaur remains from the Grand Duchy of Luxembourg. *Geologica Belgica*,
749 **17**, 175–181.
750
751 DEMATHIEU, G., 1993. Empreintes de pas de dinosaures dans les Causses (France). *Zubía*,
752 **5**, 229–252.
753
754 DEMATHIEU, G. 2003. Comparaison des ichnopathologies des Grands Causses (Sud de la
755 France) et du Veillon (Vendée). *Le Naturaliste Vendéen*, **3**, 59–60.

756

757 DEMATHIEU, G. and SCIAU, J. 1992. Des pistes de dinosaures et de crocodiliens dans les
758 dolomies de l'Hettangien du Causse du Larzac. *Comptes Rendus de l'Académie des*
759 *Sciences de Paris*, **315**, 1561–1566.

760

761 DEMATHIEU, G. and SCIAU, J. 1999. De grandes empreintes de pas de dinosaures dans
762 l'Hettangien de Peyre (Aveyron, France). *Geobios*, **32**, 609–616.

763

764 DEMATHIEU, G., GAND, G., SCIAU, J. and FREYTET, P. 2002. Les traces de pas de
765 dinosaures et autres archosaures du Lias inférieur des Grands Causses, Sud de la
766 France. *Palaeovertebrata*, **31**, 1–143.

767

768 ELLENBERGER, P. 1965. Découverte de pistes de vertébrés dans le Permien, le Trias et le
769 Lias inférieur, aux abords de Toulon (Var) et d'Anduze (Gard). *Comptes Rendus de*
770 *l'Académie des Sciences de Paris*, **260**, 5856–5860.

771

772 EZCURRA, M.D. and CUNY, G. 2007. The coelophysoid *Lophostropheus airelensis*, gen.
773 nov.: a review of the systematics of “*Liliensternus*” *airelensis* from the Triassic–
774 Jurassic outcrops of Normandy (France). *Journal of Vertebrate Paleontology*, **27**, 73–
775 86.

776

777 FREY, E. 1988. The carrying system of crocodilians a biomechanical and phylogenetical
778 analysis. *Stuttgarter Beiträge zur Naturkunde*, **426**, 1–60.

779

780 GAND, G. 1974a. Les traces de vertébrés Triasiques de l'Autunois et du nord du Charollais.
781 *Bulletin de la Société d'Histoire Naturelle d'Autun*, **69**, 7–24.
782

783 GAND, G. 1974b. Sur les niveaux a empreintes de pas de vertébrés triasiques. Des carrières
784 de St-Sernin-du-Bois (Saône-et-Loire). *Bulletin de la Société d'Histoire Naturelle du*
785 *Creusot*, **32**, 12-22.
786

787 GAND, G., DEMATHIEU, G. and MONTENAT, M. 2007. Les traces de pas d'amphibiens,
788 de Dinosaures et autres Reptiles du Mésozoïque français : inventaire et interpretations.
789 *Palaeovertebrata*, **35**, 1–149.
790

791 GAND, G., FARA, E., DURLET, C., CARAVACA, G., MOREAU, J. -D., BARET, L.,
792 ANDRE, D., LEFILLATRE, R., PASSET, A., WIENIN, M. and GELY, J. -P., 2018.
793 Les pistes d'archosauriens : *Kayentapus ubacensis* nov. isp. (théropodes) et
794 crocodylomorphes du Bathonien des Grands-Causse (France). Conséquences paléo-
795 biologiques, environnementales et géographiques. *Annales de Paléontologie*, **104**,
796 183–216.
797

798 GIERLIŃSKI, G. 1991. New dinosaur ichnotaxa from the early Jurassic of the Holy cross
799 Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **85**, 137–
800 148.
801

802 GIERLIŃSKI, G. 1996. Dinosaur ichnotaxa from the Lower Jurassic of Hungary. *Geological*
803 *Quarterly*, **40**, 119–128.
804

805 GIERLIŃSKI, G. and AHLBERG, A. 1994. Late Triassic and Early Jurassic dinosaur
806 footprints in the Höganäs Formation of southern Sweden. *Ichnos*, **3**, 99–105.
807

808 GODARD, G. 2003. Histoire de la géologie en Talmondais (Vendée, France). *Le Naturaliste*
809 *Vendéen*, **3**, 13–28.
810

811 HAUBOLD, H. 1971, *Ichnia Amphibiorum et Reptiliorum fossilium*. *Encyclopedia of*
812 *Paleoherpetology*, **18**, 1–124.
813

814 HITCHCOCK, E. 1841. *Final Report on the Geology of Massachusetts*. JS & C. Adams. 831
815 pp.
816

817 HITCHCOCK, E. 1845. *An attempt to name, classify, and describe the animals that made the*
818 *fossil footmarks of New England*. Proceedings of the 6th Meeting American
819 Association of Geologists and Naturalists, 23–25.
820

821 HITCHCOCK, E. 1858. *Ichnology of New England: a report on the sandstone of the*
822 *Connecticut valley especially its fossil footmarks, made to the Government of the*
823 *Commonwealth of Massachusetts*. William White, printer, 220 pp.
824

825 KLEIN, H. and LUCAS, S. G. 2021. The Triassic tetrapod footprint record. *New Mexico*
826 *Museum of Natural History and Science Bulletin*, **53**, 1–194
827

- 828 LANGE-BADRE, B. and LAFON, J. -P. 2000. Découverte de pistes de dinosaures théropodes
829 dans le Lias inférieur des environs de Figeac (Lot). *Comptes Rendus de l'Académie*
830 *des Sciences de Paris*, **330**, 379–384.
- 831
- 832 LAPPARENT (de), A. F. and MONTENAT, C. 1967. Les empreintes de pas de reptiles de
833 l'Infralias du Veillon (Vendée). *Mémoires de la Société Géologique de France*, 46, 43
834 pp.
- 835
- 836 LARSONNEUR, C. and LAPPARENT (de), A. F. 1966. Un dinosaurien carnivore,
837 *Halticosaurus*, dans le Rhétien d'Airel (Manche). *Bulletin de la Société Linnéenne de*
838 *Normandie*, **10**, 108–116.
- 839
- 840 LEONARDI, G. 1987. *Glossary and manual of tetrapod footprint palaeoichnology*.
841 Publicação do Departamento Nacional da Produção Mineral Brasil, 75 pp.
- 842
- 843 LOCKLEY, M. G. and MEYER, C. 2000. *Dinosaur Tracks and other fossil footprints of*
844 *Europe*. Columbia University Press, 327 pp.
- 845
- 846 LOCKLEY, M. G. and MEYER, C. 2004. Crocodylomorph trackways from the Jurassic to
847 Early Cretaceous of North America and Europe: implications for
848 ichnotaxonomy. *Ichnos*, **11**, 167–178.
- 849
- 850 LOCKLEY, M.G., KIRKLAND, J. and MILNER, A. R. C. 2004. Probable relationships
851 between the Lower Jurassic crocodylomorph trackways *Batrachopus* and *Selenichnus*:

852 Evidence and implications based on new finds from the St. George area southwestern
853 Utah. *Ichnos*, **11**, 143–149.

854

855 LOCKLEY, M.G., GIERLIŃSKI, G. and LUCAS, S. G. 2011. *Kayentapus* revised: notes on
856 the type material and the importance of this theropod footprint ichnogenus. *New*
857 *Mexico Museum of Natural History and Science Bulletin*, **53**, 330–336.

858

859 LUCAS, S. G., LOCKLEY, M. G., HUNT, A. P., MILNER, A. R. and TANNER, L. H. 2006.
860 Tetrapod footprint biostratigraphy of the Triassic–Jurassic transition in the American
861 southwest. The Triassic–Jurassic Terrestrial Transition. *New Mexico Museum of*
862 *Natural History and Science Bulletin*, **37**, 105–108.

863 LULL, R. S. 1904. Fossil footprints of the Jura-Trias of North America. *Memoirs of the*
864 *Boston Society of Natural History*, **5**, 461–557.

865 LULL, R. S. 1953. Triassic life of the Connecticut Valley. State Geological and Natural
866 History Survey, 331pp.

867 MARTILL, D. M., VIDOVIC, S. U., HOWELLS, C. and NUDDS, J. R. 2016. The oldest
868 Jurassic dinosaur: A basal neotheropod from the Hettangian of Great Britain. *PLoS*
869 *ONE*, **11**, e0145713.

870 MILAN, J. and HEDEGAARD, R. 2010. Interspecific variation in tracks and trackways from
871 extant crocodylians. *New Mexico Museum of Natural History and Science Bulletin*, **51**,
872 15–29.

873

874 MILNER, A. R. C., LOCKLEY, M. G. and KIRKLAND, J. I. 2006. A large collection of
875 well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave

876 Formation, St. George, Utah. *New Mexico Museum of Natural History and Science*
877 *Bulletin*, **37**, 315–328.

878

879 MOJICA, J. and MACIA, C. 1987. Nota preliminar sobre la improntas de vertebrados
880 (*Batrachopus* sp.) en sedimentitas de la Formación Saldaña, región de Prado-Dolores,
881 valle superior del Magdalena, Colombia. *Geología Colombiana*, **16**, 89–94.

882

883 MONTENAT, C. 1968. Empreintes de pas de reptiles dans le Trias moyen du plateau du Daüs
884 près d’Aubenas (Ardèche). *Bulletin Scientifique de Bourgogne*, **25**, 369–389.

885

886 MONTENAT, C. and BESSONNAT, G. 2002. Le gisement d’empreintes de pas de reptiles
887 du Veillon (Vendée): paléobiologie d’un estuaire infraliasique. *Actes des congrès*
888 *nationaux des sociétés historiques et scientifiques*, **124**, 337–351.

889

890 MOREAU, J. -D., TRINCAL, V., GAND, G., NÉRAUDEAU, D., BESSIÈRE, G. and
891 BOUREL, B. 2014. Two new dinosaur tracksites from the Hettangian Dolomitic
892 Formation of Lozère, Languedoc-Roussillon, France. *Annales de Paléontologie*, **100**,
893 361–369.

894

895 MOREAU, J. -D., TRINCAL, V., ANDRE, D., BARET, L., JACQUET, A. and WIENIN, M.
896 2018. Underground dinosaur tracksite inside a karst of southern France: Early Jurassic
897 tridactyl traces from the Dolomitic Formation of the Malaval Cave (Lozère).
898 *International Journal of Speleology*, **47**, 29–42.

899

900 MOREAU, J. -D., FARA, E., NÉRAUDEAU, D. and GAND, G. 2019. New Hettangian
901 tracks from the Causses Basin (Lozère, southern France) complement the poor fossil
902 record of earliest Jurassic crocodylomorph in Europe. *Historical Biology*, **31**, 341–
903 552.

904

905 MOREAU, J. -D., SCIAU, J., GAND, G. and FARA, E. 2021. Uncommon preservation of
906 dinosaur footprints in a tidal breccia: *Eubrontes giganteus* from the Early Jurassic
907 Mongisty tracksite of Aveyron, southern France. *Geological Magazine*, **158**, 1403–
908 1420.

909

910 OLSEN, P. E. 1980. *Fossil great lakes of the Newark Supergroup in New Jersey*. In Field
911 studies of New Jersey geology and guide to field trips: New York State Geological
912 Association, 52nd Annual Meeting, Rutgers University, 352–398.

913

914 OLSEN, P. E. 1995. *Paleontology and paleoenvironments of Early Jurassic age strata in the*
915 *Walter Kidde Dinosaur Park (New Jersey, USA)*. Field Guide and Proceedings of the
916 Twelfth Annual Meeting of the Geological Association of New Jersey. William
917 Patterson College, 156–190.

918

919 OLSEN, P. E., GALTON, P. M. 1984. A review of the reptile and amphibian assemblages
920 from the Stormberg of southern Africa, with special emphasis on the footprints and the
921 age of the Stormberg. *Palaeontologia africana*, **25**: 87–100.

922

923 OLSEN, P. E. and PADIAN, K. 1986. Earliest records of *Batrachopus* from the southwestern
924 United States, and a revision of some Early Mesozoic crocodylomorph ichnogenera.

925 259–273. In PADIAN K. (ed). *The beginning of the Age of Dinosaurs*. Cambridge
926 University Press.

927

928 OLSEN, P. E., SMITH, J. H. and MC DONALD, N. G. 1998. Type material of the type
929 species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus* and
930 *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and
931 Massachusetts, U.S.A.). *Journal of Vertebrate Paleontology*, **18**, 586–601.

932 PACYNA, G., ZIAJA, J., BARBACKA, M., PIEŃKOWSKI, G., JARZYŃKA, A. and
933 NIEDŹWIEDZKI, G. 2022. Early Jurassic dinosaur-dominated track assemblages,
934 floristic and environmental changes in the Holy Cross Mountains region, Poland.
935 *Geological Quarterly*, **66**, 66–29.

936

937 POPA, M. E. 1999. First finds of Mesozoic tetrapod tracks in Romania. *Acta Palaeontologica*
938 *Romaniae*, **2**, 387–390.

939

940 RAINFORTH, E. C. 2005. *Ichnotaxonomy of the fossil footprints of the Connecticut Valley*
941 *(early Jurassic, Newark Supergroup, Connecticut and Massachusetts)*. Columbia
942 University, 1301 pp.

943

944 RAINFORTH, E. C. 2007. Ichnotaxonomic updates from the Newark
945 Supergroup. *Contributions to the Paleontology of New Jersey (II): Field Guide and*
946 *Proceedings. Trenton: Geological Association of New Jersey*, 49–59.

947

948 ROMILIO, A. 2021. Additional notes on the mount Morgan dinosaur tracks from the Lower
949 Jurassic (Sinemurian) Razorback beds, Queensland, Australia. *Historical Biology*, **33**,
950 2005–2007.

951

952 SCIAU, J. 1992. *Sur la piste des dinosaures des Causses*. Association des Amis du Musée de
953 Millau, 31 pp.

954

955 SCIAU, J. 2003. *Dans les pas des dinosaures des Causses, inventaire des sites à empreintes*.
956 Association des Amis du Musée de Millau, 107 pp.

957

958 SCISCIO, L., BORDY, E. M., ABRAHAMS, M., KNOLL, F. and McPHEE, B. W. 2017.
959 The first megatheropod tracks from the Lower Jurassic upper Elliot Formation, Karoo
960 Basin, Lesotho. *PLoS One*, **12**, e0185941.

961

962 SMITH, N. D., MAKOVICKY, P. J., HAMMER, W. R., CURRIE, P. J. 2007. Osteology of
963 *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica
964 and implications for early theropod evolution. *Zoological Journal of the Linnean*
965 *Society*, **151**, 377–421.

966

967 TERS, M. 1961. *La Vendée littorale: étude de géomorphologie*. Oberthur, 578 pp.

968

969 THÉVENARD, F., DESCHAMPS, S., GUIGNARD, G. and GOMEZ, B. 2003. Les plantes
970 fossiles du gisement hettangien de Talmont-Saint-Hilaire (Vendée, France). *Le*
971 *Naturaliste vendéen*, **3**, 69–87.

972

- 973 THULBORN, T. 1990. *Dinosaur Tracks*. Chapman & Hall, 410 pp.
- 974
- 975 VIAUD, J. -M. 2003. Un site géologique remarquable à protéger et à valoriser: le Veillon à
976 Talmont-Saint-Hilaire (Vendée, France). *Le Naturaliste Vendéen*, **3**, 101–103.
- 977
- 978 VIAUD, J. -M. and DUCLOUS, S. 2003. Journées d'étude des 28 et 29 mars 2002 à Talmont-
979 Saint-Hilaire (Vendée): les sites à traces de pas de vertébrés vers la limite Trias-
980 Jurassique. *Le Naturaliste Vendéen* 3, 3–11.
- 981
- 982 VIAUD, J. -M. and GODARD, G. 2008. Edmond Bocquier (1881-1948) et la géologie. *Le*
983 *Naturaliste Vendéen*, **8**, 57–69.
- 984
- 985 WAGENSOMMER, A., LATIANO, M., MOCKE, H. B. and D'ORAZI, P. 2016. Dinosaur
986 diversity in an Early Jurassic African desert: the significance of the Etjo Sandstone
987 ichnofauna at the Otjihaenamaparero locality (Namibia). *Neues Jahrbuch für Geologie*
988 *und Paläontologie-Abhandlungen*, **281**, 155–82.
- 989
- 990 WEISHAMPEL, D. B., DODSON, P. and OSMOLSKA, H. 2004. *The Dinosauria*. University
991 of California Press, 862 pp.
- 992 WEEMS, R. E. 1987. A Late Triassic footprint fauna from the Culpeper basin northern
993 Virginia (USA). *Transactions of the American Philosophical Society*, **77**, 1–79.
- 994
- 995 WEEMS, R. E. 1992. A re-evaluation of the taxonomy of Newark Supergroup saurischian
996 dinosaur tracks, using extensive statistical data from a recently exposed tracksite near

997 Culpeper, Virginia. *Proceedings 26th Forum on the Geology of Industrial Minerals*.
998 *Virginia Division of Mineral Resources Publication*, **119**, 113–127.
999

1000 WEEMS, R. E. 2019. Evidence for bipedal prosauropods as the likely *Eubrontes* track-
1001 makers. *Ichnos*, **26**, 187–215.
1002

1003 WELLES, S. P. 1971. Dinosaur footprints from the Kayenta Formation of northern Arizona.
1004 *Plateau*, **44**, 27–38.
1005

1006 WHITESIDE, D. I., DUFFIN, C. J., GILL, P. G., MARSHALL, J. E. A. and BENTON, M. J.
1007 2016. The Late Triassic and Early Jurassic fissure faunas from Bristol and South
1008 Wales: Stratigraphy and setting. *Palaeontologia Polonica*, **67**, 257–287.
1009

1010 XING, L., BELL, P. R., ROTHSCHILD, B. M., RAN, H., ZHANG, J., DONG, Z., ZHANG,
1011 W. and CURRIE, P. J. 2013. Tooth loss and alveolar remodeling in *Sinosaurus*
1012 *triassicus* (Dinosauria: Theropoda) from the Lower Jurassic strata of the Lufeng Basin,
1013 China. *Chinese Science Bulletin*, **58**, 1931–1935.
1014

1015 XING, L. D., PENG, G. Z., YE, Y., LOCKLEY, M. G., MCCREA, R. T., CURRIE, P. J.,
1016 Zang J. -P. and BURNS, M. E. 2014. Large theropod trackway from the Lower
1017 Jurassic Zhenzhuchong Formation of Weiyuan County, Sichuan Province, China:
1018 review, new observations and special preservation. *Palaeoworld*, **23**, 285–293.
1019
1020

1021 **FIGURE CAPTIONS**

1022

1023 **FIG 1.** Simplified geological map of the study area and location of the tracksite of Le Veillon.

1024

1025 **FIG 2.** Biometric measurements taken on tracks from the Lapparent collection. A, for

1026 crocodylomorph manus imprint. B, for crocodylomorph pes track. C, for dinosaur footprint.

1027 L, length of footprint (for dinosaur tracks); LM and LP, length of manus and pes tracks,

1028 respectively (for crocodylomorph tracks); W, width of footprint (for dinosaur tracks); WM

1029 and WP, width of manus and pes tracks, respectively (for crocodylomorph tracks); LI, LII,

1030 LIII, LIV, LV: lengths of digits I, II, III, IV and V, respectively; D, length of the free part of

1031 digit III ; I–V I–IV and II–IV, divarication angles between digits I and V, digits I and IV, then

1032 digits II and IV, respectively. Scale bars represent: 20 cm (A, B), 2 cm (C–H).

1033

1034 **FIG 3.** *Grallator olonensis*. A–B, slab ULB-04D19 bearing the type trackway T1-Go;

1035 photograph (A) and interpretative sketch (B). C–E, track 04D19_A_4 of the type trackway

1036 T1-Go, photograph (C), DEM in false-colour depth map (D) and interpretative sketch (E).

1037 F–H, paratype, ULB-04C11_A_6, photograph (F), DEM in false-colour depth map (G) and

1038 interpretative sketch (H).

1039

1040 **FIG 4.** Footprints from Le Veillon compared to tridactyl tracks from the Early Jurassic of the

1041 Causses Basin (based on data from Demathieu *et al.* 2002; Moreau *et al.* 2021) and the Early

1042 Jurassic of the eastern USA (based on data from Weems 1992, 2019; Gand *et al.* 2018). A,

1043 bivariate diagram L vs $(L - D)/D$ (A). B, bivariate diagram L vs L/W (B). L in metres.

1044

1045 **FIG 5.** *Grallator variabilis*. A–C, plastotype, ULB-04C08_D, photograph (A), DEM in false-
1046 colour depth map (B) and interpretative sketch (C). D–F, paratype, ULB-04C05_A,
1047 photograph (D), DEM in false-colour depth map (E) and interpretative sketch (F). G–I, track
1048 ULB-04C13_A, photograph (G), DEM in false-colour depth map (H) and interpretative
1049 sketch (I). Scale bars represent 5 cm.

1050

1051 **FIG 6.** *Anatopus palmatus* that is here invalidated. A–C, ULB-04C15_B (=holotype of *A.*
1052 *palmatus*); photograph (A); interpretative sketch of Lapparent & Montenat (1967) (fig. 16A
1053 and pl.XII.3 of Lapparent & Montenat 1967) (B); our interpretation (C). D–F, ULB-
1054 04C15_C; photograph (D); interpretative sketch of Lapparent & Montenat (1967) (fig. 16B1
1055 of Lapparent & Montenat 1967) (E); our interpretation (F). Scale bars represent 5 cm.

1056

1057 **FIG 7.** *Batrachopus deweyi*. A–C, trackway ULB-04C10_E, photograph (A), DEM in false-
1058 colour depth map (B) and interpretative sketch (C). D–F, pes/manus set 04C10_A_1 (=
1059 holotype of *B. gilberti* that is here invalidated), photograph (D), DEM in false-colour depth
1060 map (E) and interpretative sketch (F). G–I, pes/manus set 04C14_C, photograph (G), DEM in
1061 false-colour depth map (H) and interpretative sketch (I). J–L, pes/manus set 04C14_C,
1062 photograph (J), DEM in false-colour depth map (K) and interpretative sketch (L). Scale bars
1063 represent: 10 cm (A–C), 1 cm (D–L).

1064

1065 **FIG 8.** Tracks ascribed to *Dahutherium* sp. by Lapparent & Montenat (1967) and that is here
1066 invalidated. A–C, two superimposed tridactyl grallatorid footprints, ULB-04C18_B;
1067 photograph (A); interpretative sketch of Lapparent & Montenat (1967) (B); our interpretation,
1068 showing a small footprint (dark grey) and larger footprint (light grey) (C). D–F, *Batrachopus*

1069 isp., ULB-04C15_A; photograph (D); interpretative sketch of Lapparent & Montenat (1967)
1070 (E); our interpretation (F). Scale bars represent: 5 cm (A–C), 2 cm (D–F).

1071

1072 **FIG 9.** *Eubrontes giganteus*. A–C, track ULB-04D21_A (= plastotype of *E. veillonensis* that
1073 is here invalidated), photograph (A), DEM in false-colour depth map (B) and interpretative
1074 sketch (C). Scale bars represent 10 cm.

1075

1076 **FIG 10.** *Grallator minusculus*. A–C, track ULB-04C13_B (= plastotype of *G. maximus* that is
1077 here invalidated), photograph (A), DEM in false-colour depth map (B) and interpretative
1078 sketch (C). D–F, track ULB-04C10_B, photograph (D), DEM in false-colour depth map (E)
1079 and interpretative sketch (F). Scale bars represent 10 cm.

1080

1081 **FIG 11.** Plaster cast of one footprint from the type trackway of *Saltopoides igalensis* that is
1082 here invalidated. A–C, track ULB-04C01_B, photograph (A), DEM in false-colour depth map
1083 (B) and interpretative sketch (C). Scale bars represent 5 cm.

1084

1085 **FIG 12.** *Kayentapus* isp. A–C, track ULB-04C02_A (= holotype of *Talmontopus tersi* that is
1086 here invalidated), photograph (A), DEM in false-colour depth map (B) and interpretative
1087 sketch (C). Scale bars represent 10 cm.

1088

1089 **FIG 13.** Other problematic tracks in Lapparent & Montenat 1967. A–C, *Batrachopus* isp.,
1090 ULB-04C14_I; A, photograph; B, interpretative sketch of Lapparent & Montenat (1967) (=
1091 Unnamed track n°1 in fig. 18 of Lapparent & Montenat 1967). C, our interpretation. D–F,
1092 *Grallator* cf. *variabilis*, ULB-04D22_A; D, photograph; E, interpretative sketch of Lapparent

1093 & Montenat (1967) (= Unnamed track n°2 in fig. 18 and pl.XIII.5 of Lapparent & Montenat
1094 1967); F, our interpretation). Scale bars represent: 1 cm (A–C), 5 cm (D–F).

1095

1096

1097

1098

1099

1100

1101

1102

1103

1104

1105

1106

1107

1108

1109

1110

1111

1112

1113

1114

1115

1116

1117 **Table 1.** Biometric values measured on Hettangian crocodylomorph tracks from Le Veillon.
 1118 LM and LP: length of manus and pes tracks, respectively; WM and WP, width of manus and
 1119 pes tracks, respectively; I–V, divarication angle between digit I and digit V; I–IV, divarication
 1120 angle between digit I and digit IV (all in cm except II–IV in degrees).
 1121

Specimens	Lapparent & Montenat 1967	This study	Pes/manus	LM	WM	I– V	LP	WP	I–IV
04C02_B_1	<i>B. gilberti</i> (Pl. I.3)	<i>B. deweyi</i>	Pes	-	-	-	3.9	-	-
04C02_B_2	<i>B. gilberti</i> (Fig. 4A; Pl. I.3)	<i>B. deweyi</i>	Pes	-	-	-	3.1	3.2	-
04C02_B_3	<i>B. gilberti</i> (Pl. I.3)	<i>B. deweyi</i>	Pes	-	-	-	3.5	3.1	73
04C02_B_4	<i>B. gilberti</i> (Pl. I.3)	<i>B. deweyi</i>	Manus	1.7	1.8	-	-	-	-
04C04_A_2	<i>B. gilberti</i> (Fig. 4Bb; Pl. VIII)	<i>B. deweyi</i>	Pes	-	-	-	3.9	3.1	57
04C04_A_3	<i>B. gilberti</i> (Pl. VIII)	<i>B. deweyi</i>	Manus	1.3	1.8	-	-	-	-
04C09_B	-	<i>B. deweyi</i>	Pes/manus set	2.1	2	-	-	-	-
04C10_A_1	<i>B. gilberti</i> (Fig. 4A; Pl. I.1)	<i>B. deweyi</i>	Pes/manus set	2	1.9	-	3.8	3.1	60
	HOLOTYPE								
04C10_A_2	<i>B. gilberti</i> (Fig. 4A; Pl. I.1)	<i>B. deweyi</i>	Pes/manus set	-	-	-	3.1	2.9	64
	HOLOTYPE								
04C14_A	<i>B. gilberti</i> (Fig. 4Bc)	<i>B. deweyi</i>	Manus	1.1	1.6	-	-	-	-
04C14_C	<i>B. gilberti</i> (Pl. I.2)	<i>B. deweyi</i>	Pes/manus set	1.7	-	-	3	3.8	44
04C14_D	-	<i>B. deweyi</i>	Pes	-	-	-	2.7	2.4	
04C14_F	-	<i>B. deweyi</i>	Pes/manus set	1.9	1.6	-	3.4	2.8	36
04C14_G	-	<i>B. deweyi</i>	Pes/manus set	1.8	1.7	-	2.9	2.1	-
04C14_H	-	<i>B. deweyi</i>	Pes	-	-	-	3.1	-	-
ULB-	-	<i>B. deweyi</i>	Pes P1	-	-	-	2.9	3.2	79
04C10_E									
ULB-	-	<i>B. deweyi</i>	Pes P3	-	-	-	3	3	80
04C10_E									

ULB-04C10_E	-	<i>B. deweyi</i>	Manus M4	2.2	2.2	-	-	-	-
ULB-04C10_E	-	<i>B. deweyi</i>	Pes P5	-	-	-	2.9	3.2	82
ULB-04C10_E	-	<i>B. deweyi</i>	Manus M5	2.4	-	-	-	-	-
ULB-04C14_I	Unnamed track n°1 (Fig. 18)	<i>Batrachopus</i> isp.	Pes	-	-	-	3.3	3.2	-
ULB-04C17_A	Unnamed track n°1 (Fig. 18)	<i>Batrachopus</i> isp.	Pes	-	-	-	3.6	2.8	-
ULB-04C15_A	<i>Dahutherium</i> sp. (Fig. 5bis)	<i>Batrachopus</i> isp.	Pes	-	-	-	3	3.9	83

1122

1123

1124

1125

1126

1127

1128

1129

1130

1131

1132

1133

1134

1135 **Table 2.** Biometric values measured on Hettangian tridactyl theropod tracks from Le Veillon.
 1136 L: length of the trace; W: width of the trace; D: length of the free part of digit III; II–IV,
 1137 divarication angle between digit II and digit IV (all in cm except II–IV in degrees).
 1138

Specimens	Lapparent & Montenat 1967	This study	L	W	D	II–IV
ULB-	-	<i>G. olonensis</i>	3.7	3	2	35
04C03_B_1						
ULB-	-	<i>G. olonensis</i>	3.9	2.5	1.7	37
04C03_B_2						
ULB-	-	<i>G. olonensis</i>	-	-	-	-
04C03_B_3						
ULB-	-	<i>G. olonensis</i>	4.6	3.2	1.9	37
04C03_C						
ULB-	-	<i>G. olonensis</i>	4.4	2.2	2	36
04C03_D_1						
ULB-	-	<i>G. olonensis</i>	-	-	-	-
04C03_D_2						
ULB-	-	<i>G. olonensis</i>	-	-	-	-
04C03_E						
ULB-	-	<i>G. olonensis</i>	4.5	2.7	2.2	44
04C03_F						
ULB-	-	<i>G. olonensis</i>	3.8	2.5	1.6	42
04C05_C						
ULB-	<i>G. olonensis</i> (Fig. 6B)	<i>G. olonensis</i>		2.4	2	24
04C07_A_1						
ULB-	-	<i>G. olonensis</i>	4.2	2.4	1.9	40
04C07_A_2						
ULB-	-	<i>G. olonensis</i>	4.9	2.9	2.6	35
04C08_C						

ULB-	-	<i>G. olonensis</i>	3.8				
04C08_E_1							
ULB-	-	<i>G. olonensis</i>	4.4	2	2.1	25	
04C08_E_2							
ULB-	-	<i>G. olonensis</i>	-	-	-	-	
04C08_G							
ULB-	-	<i>G. olonensis</i>	-	-	-	-	
04C09_A							
ULB-	-	<i>G. olonensis</i>	-	-	-	-	
04C09_C							
ULB-	-	<i>G. olonensis</i>	3.3	2.3	1.7	36	
04C11_A_1							
ULB-	-	<i>G. olonensis</i>	4	2.6	2	44	
04C11_A_2							
ULB-	-	<i>G. olonensis</i>	3.6	1.8	1.5	25	
04C11_A_3							
ULB-	<i>G. olonensis</i> (Fig. 6A; Pl. III.3)	<i>G. olonensis</i>		2.5	1.5	33	
04C11_A_4	PARATYPE						
ULB-	<i>G. olonensis</i> (Fig. 6A; Pl. III.3)	<i>G. olonensis</i>	4	2.5	2	31	
04C11_A_5	PARATYPE						
ULB-	<i>G. olonensis</i> (Fig. 6A; Pl. III.3)	<i>G. olonensis</i>	4.8	3.1	2.3	40	
04C11_A_6	PARATYPE	PARATYPE					
ULB-	<i>G. olonensis</i> (Fig. 6A; Pl. III.3)	<i>G. olonensis</i>		2.7	1.5	41	
04C11_A_7	PARATYPE						
ULB-	-	<i>G. olonensis</i>	4.5	2.4	2.2	27	
04C11_A_8							
ULB-	-	<i>G. olonensis</i>	4.5	2.8	2.1	33	
04C11_A_9							
ULB-	-	<i>G. olonensis</i>	4.4	2.5	2.1	34	
04C17_E							

ULB-	-	<i>G. olonensis</i>	4.8	3.3	2.2	41
04C19_A_1						
ULB-	-	<i>G. olonensis</i>	3.5	2.7	1.7	40
04C19_A_2						
ULB-	-	<i>G. olonensis</i>	3.6	1.8	2	36
04C19_A_3						
ULB-	-	<i>G. olonensis</i>	4.4	2.4	2.2	33
04C19_A_4						
ULB-	-	<i>G. olonensis</i>	4.3	2.4	2	36
04C19_A_5						
ULB-	-	<i>G. olonensis</i>	4.7	2.4	2.1	34
04C19_A_6						
ULB-	-	<i>G. olonensis</i>	4.5	2.5	2.4	38
04D17_A_1						
ULB-	-	<i>G. olonensis</i>	4.3	2.9	1.9	39
04D17_A_2						
ULB-	-	<i>G. olonensis</i>	4.6	2.4	2	31
04D17_A_3						
ULB-	-	<i>G. olonensis</i>	4.5	2.6	2.2	29
04D17_A_4						
ULB-	-	<i>G. olonensis</i>	4.6	2.8	2.2	37
04D17_B_1						
ULB-	-	<i>G. olonensis</i>	4.3	2.5	2.2	37
04D17_B_2						
ULB-	-	<i>G. olonensis</i>	3.4	1.5	1.7	24
04D17_C_1						
ULB-	-	<i>G. olonensis</i>	4.5	2.7	2	
04D17_C_2						
ULB-	-	<i>G. olonensis</i>	4	2.7	1.8	38
04D17_C_3						

ULB-04D19_A_1	<i>G. olonensis</i> (Fig. 6A; Pl. III.1)	<i>G. olonensis</i>	4.8	2.5	2.4	34
	HOLOTYPE					
ULB-04D19_A_2	<i>G. olonensis</i> (Fig. 6A; Pl. III.1)	<i>G. olonensis</i>	4.2	2.5	1.9	31
	HOLOTYPE					
ULB-04D19_A_3	<i>G. olonensis</i> (Fig. 6A; Pl. III.1)	<i>G. olonensis</i>	4.6	2.8	2	33
	HOLOTYPE					
ULB-04D19_A_4	<i>G. olonensis</i> (Fig. 6A; Pl. III.1)	<i>G. olonensis</i>	4.3	2.5	2.2	25
	HOLOTYPE	HOLOTYPE				
ULB-04D19_A_5	<i>G. olonensis</i> (Fig. 6A; Pl. III.1)	<i>G. olonensis</i>	4.5	2.3	2.1	34
	HOLOTYPE	HOLOTYPE				
ULB-04D19_A_6	<i>G. olonensis</i> (Fig. 6A; Pl. III.1)	<i>G. olonensis</i>	3.7	1.9	1.8	25
	HOLOTYPE					
ULB-04D19_A_7	<i>G. olonensis</i> (Fig. 6A; Pl. III.1)	<i>G. olonensis</i>	-	-	-	-
	HOLOTYPE	HOLOTYPE				
ULB-04D22_B_1	-	<i>G. olonensis</i>	4.2	2.5	2	30
ULB-04D22_B_2	-	<i>G. olonensis</i>	4.2	2.5	1.8	34
ULB-04C05_A	<i>G. variabilis</i> (Pl. III.3) PARATYPE	<i>G. variabilis</i>	12.3	6.6	4.4	34
		PARATYPE				
ULB-04C05_B	-	<i>G. variabilis</i>	8.6	5.2	4.1	40
ULB-04C08_A	<i>G. variabilis</i> (Pl. IV.1) PARATYPE	<i>G. variabilis</i>	13.1	7.2	4.6	42
		PARATYPE				
ULB-04C08_B	<i>G. variabilis</i> (Pl. V.1b)	<i>G. variabilis</i>	9.7	6.5	4.1	33
ULB-04C08_D	<i>G. variabilis</i> (Fig. 7A)	<i>G. variabilis</i>	-	-	-	-
	PLASTOTYPE	PLASTOTYPE				
ULB-04C08_F	<i>G. variabilis</i>	<i>G. variabilis</i>	-	-	-	-

ULB- 04C13_A	<i>G. variabilis</i> (Pl. XIII.2)	<i>G. variabilis</i>	8.8	5.5	4.1	33
ULB- 04C14_J_1	-	<i>G. variabilis</i>	10	7.7	4.5	35
ULB- 04C14_J_2	-	<i>G. variabilis</i>	10.5	7.3	4.4	33
ULB- 04C15_D	-	<i>G. variabilis</i>	-	-	-	-
ULB- 04C15_E_1	<i>G. variabilis</i> (Pl. IV.2)	<i>G. variabilis</i>	11.3	8	4.5	45
ULB- 04C17_C	-	<i>G. variabilis</i>	12			29
ULB- 04C17_D	-	<i>G. variabilis</i>	10.6	6.8	4.6	30
ULB- 04C17_G	-	<i>G. variabilis</i>	10.4	6.5	4.3	24
ULB- 04C18_B	<i>Dahutherium</i> sp. (Fig. 5; Pl. II)	<i>G. variabilis</i>	12.2	7.2	5.1	40
ULB- 04C18_C	-	<i>G. variabilis</i>	11.3	7.6	4.5	46
ULB- 04D18_A	<i>G. variabilis</i> (Pl. V.1a)	<i>G. variabilis</i>	8.6	6.2	4.8	27
ULB- 04D18_B	-	<i>G. variabilis</i>	12.9	7.5	4.3	31
ULB- 04D18_C	<i>G. variabilis</i> (Pl. XIII.1)	<i>G. variabilis</i>	13.6	8	4.8	36
ULB- 04D18_D	-	<i>G. variabilis</i>	11.7	7.2	4.7	38
ULB- 04D22_A	Unnamed track n°2 (Fig. 15C; Pl. XIII.5)	<i>G. cf. variabilis</i>	≈ 11	≈ 7	-	29

ULB-	-	<i>G. minusculus</i>	26.2	17.7	8.2	37
04C04_A_1						
ULB-	-	<i>G. minusculus</i>	27.5	17.5	9.4	32
04C06_A						
ULB-	-	<i>G. minusculus</i>	26	15.5	8.3	30
04C10_B						
ULB-	<i>G. maximus</i> (Fig. 11B; Pl. XXI.1)	<i>G. minusculus</i>	27.7	15.9	9.2	33
04C13_B	PLASTOTYPE					
ULB-	<i>Dahutherium</i> sp. (Fig. 5; Pl. II)	<i>Grallator</i> isp.	≥ 14	12	-	41
04C18_B						
ULB-	<i>T. tersi</i> (Fig. 17; Pl. XXII.1)	<i>Kayentapus</i> isp.	26	21.5	9.3	64
04C02_A	HOLOTYPE					
ULB-	<i>E. veillonensis</i> (Fig. 12B; Pl. XXI.3)	<i>E. giganteus</i>	34	26.5	10	40
04D21_A	PLASTOTYPE					
ULB-	<i>A. palmatus</i> (Fig. 16B2)	<i>nomen dubium</i>	-	-	-	-
04C10_C						
ULB-	<i>A. palmatus</i> (Fig. 16A; Pl. XII.3)	<i>nomen dubium</i>	8.5	9.5	5.2	-
04C15_B	HOLOTYPE					
ULB-	<i>A. palmatus</i> (Fig. 16B1)	<i>nomen dubium</i>	-	7.5	-	55
04C15_C						
ULB-	<i>S. igualensis</i> (Fig. 15C; Pl. XII.4)	<i>nomen dubium</i>	16.5	12.5	6.4	54
04C01_A.						
ULB-	<i>S. igualensis</i> (Fig. 15A–B)	<i>nomen dubium</i>	15.5	11	5	49
04C01_B	PLASTOTYPE					