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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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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

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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.

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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 conifer 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 tersi* 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*.

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Ichnogenus BATRACHOPUS Hitchcock, 1845

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*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  $40^\circ$ . Round to oval phalangeal pads and pointed marks of claws are well marked. The largest  
396 of the two superimposed tridactyl tracks is  $\approx 14$  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  $41^\circ$ . 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  $83^\circ$ .

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 =  $40^\circ$ ) 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  $39^\circ$  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 ( $II$ – $IV = 49.0^\circ$ – $(51.5^\circ)$ – $54.0^\circ$ )  
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*)

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*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 *Talmontonopus* 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 *Talmontonopus* 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

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690

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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).

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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).

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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.

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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.

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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).

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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).

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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.

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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.

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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.

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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.

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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).

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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

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

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					