Uncommon preservation of dinosaur footprints in a tidal breccia: *Eubrontes giganteus* from the Early Jurassic Mongisty tracksite of Aveyron, southern France

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Abstract

A recent excavation yielded 118 large tridactyl footprints in the Lower Jurassic Dolomitic Formation of the Causses Basin, at Mongisty in southern France. Most of the tracks are ascribed to *Eubrontes giganteus* Hitchcock, 1845. They are preserved on a surface of 53 m^2 and form parallel rows with a preferential orientation towards the north. Such an abundance and density of *E. giganteus* is observed for the first time in the Early Jurassic from the Causses Basin. Sedimentological and ichnotaphonomical analyses show that the footprints were made at different time intervals, thus excluding the passage of a large group. In contrast to all other tracksites from the Dolomitic Formation, where tracks are preserved in fine-grained sediments corresponding to low-energy depositional palaeoenvironments, the tracks from Mongisty are preserved in coarse-grained sediment which is a matrix- to clast-supported breccia. Clasts consist of angular to sub-rounded, millimetric to centimetric-scale (up to 2 cm), poorly sorted, randomly oriented, homogeneous dolostone intraclasts floating in a dolomudstone matrix. Sedimentological analysis shows that the depositional environments of Mongisty varied from subtidal to intertidal/supratidal settings in a large and protected flat marsh. The lithology of the track-bearing surfaces indicates that the mudflat of the Causses Basin was sporadically affected by large mud flows that reworked and redeposited mudstone intraclasts coming from the erosion of upstream, dry and partially lithified mud beds. Throughout the world, this type of preservation of dinosaur tracks in tidal matrix- to clast-supported breccias remains rare.

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1. Introduction

The Causses Basin in southern France is known for its abundant Early Jurassic vertebrate footprints (Demathieu *et al.* 2002; Gand *et al.* 2007). More than 60 archosaur tracksites have been reported in the Hettangian–Sinemurian sediments in this area. The Hettangian Dolomitic Formation from the Causses Basin mainly contains theropod trackways (Ellenberger, 1988; Demathieu, 1990; Demathieu & Sciau, 1992, 1999; Demathieu *et al.* 2002; Sciau, 2003, 2019; Gand *et al.* 2007; Moreau *et al.* 2012*a*, 2014) and rarely crocodylomorph trackways (Sciau, 1998; Demathieu *et al.* 2002; Moreau *et al.* 2019*a*). In all these Hettangian tracksites, ichnofossils are preserved in homogeneous dolomudstone beds or laminites showing abundant microbial mats (Demathieu *et al.* 2002; Moreau *et al.* 2018, 2019*a*). Such sedimentological facies, corresponding to low-energy depositional palaeoenvironments, are usually interpreted as tidal flats.

In the area of Mongisty in the Causses Basin (Aveyron, southern France), Demathieu *et al.* (2002) and Sciau (2003) reported several small outcrops with rare Hettangian dinosaur footprints (*Grallator variabilis* Lapparent & Montenat, 1967 and *Eubrontes giganteus* Hitchcock, 1845). We excavated a new outcrop recently at Mongisty. This paper provides a detailed description of the newly discovered dinosaur tracks. The excavated surface consists of a high density of well-preserved and large tridactyl footprints. In contrast to other tracksites of the Dolomitic Formation, the tracks are preserved in a coarse-grained substrate that constitutes an uncommon track-bearing facies. Here, we characterize the tracks using morphometry and 3D imaging photogrammetry, in association with sedimentological and ichnotaphonomic analyses. The track assemblage is compared with other coeval tracks, and a depositional environment model is proposed.

2. Geographical and geological setting

The dinosaur footprints were discovered in the Dolomitic Formation on the western edge of the Causses Basin, south of the Massif Central (southern France; Fig. 1). The tracksite is located in Aveyron, 10 km west of Millau, near the hamlet of Jouvenet and the ruin of the Mongisty farm.
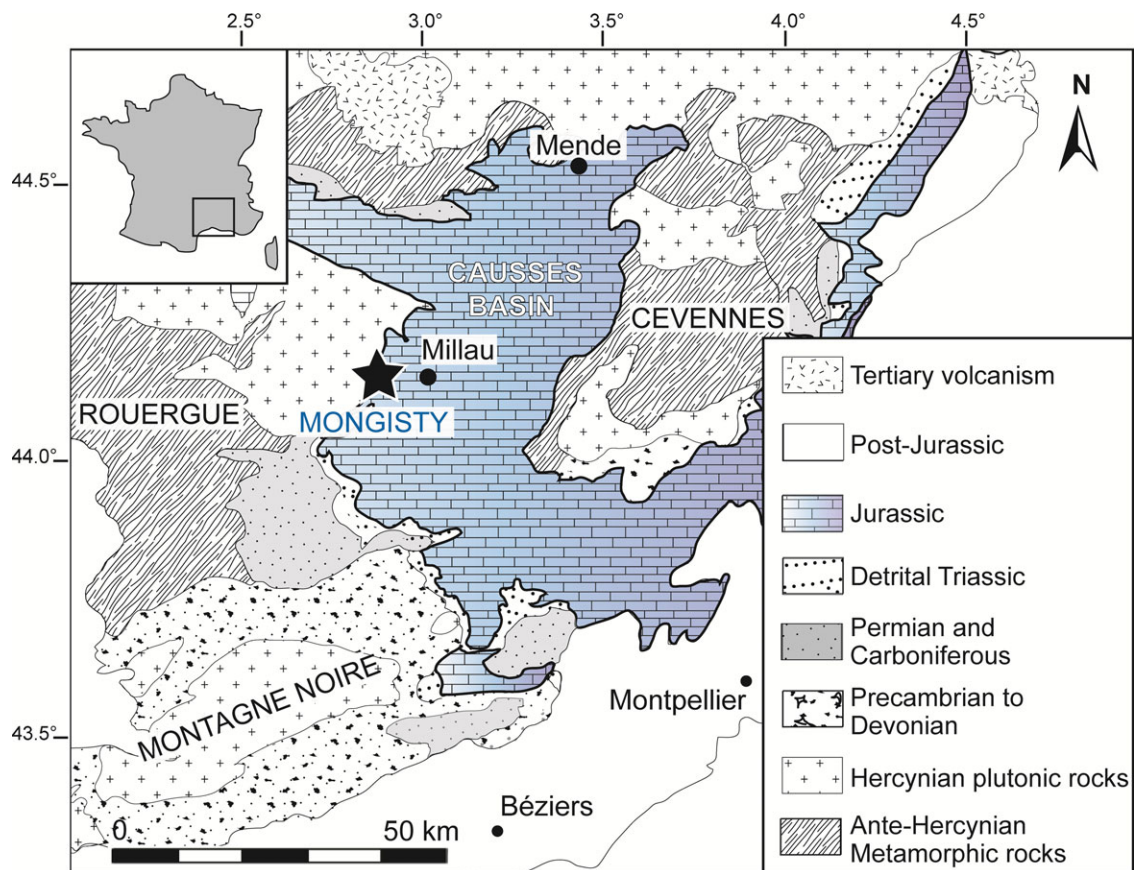
Fig. 1. (Colour online) Simplified geological map of the Causses Basin (modified from Moreau *et al.* 2018) and location of the Mongisty tracksite indicated by the black star.

In the area of Millau, the Dolomitic Formation is 70 to 200 m thick (Mennessier *et al.* 1984, 1986). It mainly consists of grey dolomite organized in centimetric to metric layers, as well as dolomitic laminites alternating with green and black argillites or marls. Locally, the base of the Dolomitic Formation is exposed as conglomerates, sandstones and sandy dolomites (Mennessier *et al.* 1984). The top of the Dolomitic Formation bears plant-bearing beds yielding the conifers *Brachyphyllum paparelii* Saporta, 1884 and *Pagiophyllum peregrinum* (Lindley & Hutton) A. Schenk emend. Kendall, 1948, as well as the pteridosperm *Thinnfeldia rhomboidalis* Ettingsh, 1852 (Roquefort, 1934; Mennessier *et al.* 1984; Thévenard, 1993; Moreau *et al.* 2019b). The Dolomitic Formation has already yielded numerous archosaur tracksites in all the Causses Basin (Ellenberger, 1988; Demathieu, 1990; Demathieu & Sciau, 1992, 1999; Sciau, 1998, 2003, 2019; Demathieu *et al.* 2002; Gand *et al.* 2007; Moreau, 2011; Moreau *et al.* 2012a, 2014, 2018, 2019a). With the exception of vertebrate footprints and terrestrial plants, body fossils are uncommon in the Dolomitic Formation. Some bivalves (e.g. *Cardinia* Agassiz, 1841, *Liostrea* Douvillé, 1904, *Ostrea* Linnaeus, 1758) and external natural casts of unidentified gastropods have been mentioned (Brouder *et al.* 1977; Briand *et al.* 1979; Gèze *et al.* 1980), as well as rare ammonites found at the base of the formation (e.g. *Psiloceras planorbis* Sowerby, 1824; Brouder *et al.* 1977) that give a Hettangian age to the Dolomitic Formation. Demathieu *et al.* (2002) and Sciau (2003) located the Mongisty tracksite in 'Unit IIIA' of Arrondeau (1982) which is considered late Hettangian in age.

The tracksite at Mongisty was discovered in 1998. It was first mentioned briefly by Demathieu *et al.* (2002) in an inventory of the Hettangian–Sinemurian dinosaur tracksites from the Causses

Basin. At Mongisty, tracks are dispersed in several small outcrops separated from each other by several metres. Demathieu *et al.* (2002) mentioned a total of six tridactyl footprints located on two outcrops called Mongisty A and Mongisty B. The main track-bearing surface (Mongisty A) was limited to very small dolomitic slabs located along a dirt road and measuring less than 2 m². This surface yielded four *in situ* footprints referred to *Eubrontes giganteus* (Demathieu *et al.* 2002; Sciau, 2003). Mongisty B yielded two traces referred to *Grallator variabilis* (Demathieu *et al.* 2002; Sciau, 2003). In a recent paper, Sciau (2019) described a third outcrop with two *in situ* tracks referred to *Eubrontes giganteus* (Mongisty C).

In 2018, a fourth outcrop yielding tridactyl tracks was discovered by one of us (J.S.). Here, we describe this new fossiliferous surface which is located 100 m south of the main surface (Mongisty A) described by Demathieu *et al.* (2002) and then by Sciau (2003). We call this new outcrop 'Mongisty D' (Fig. 2). When the tracksite of Mongisty D was discovered in 2018, only two tracks were visible on a surface less than 1 m². After an excavation conducted in 2018–19 and supervised by one of us (J.S.), an area up to 7 m wide and 11 m long was cleaned, representing a surface of 53 m². Today, Mongisty D bears 118 *in situ* tridactyl footprints (Figs 2 and 3).

In addition to the four outcrops with tridactyl footprints (Mongisty A to D), Sciau (2019) mentioned two other outcrops that contain tetradactyl pes impressions and pentadactyl manus impressions which he identified as the first prosauropod trackways from the Lower Jurassic of the Causses Basin. Two of us (J.-D.M and G.G.) have recently reinvestigated these structures that are most probably surfaces bearing microbial crust and mud cracks showing reticular patterns.
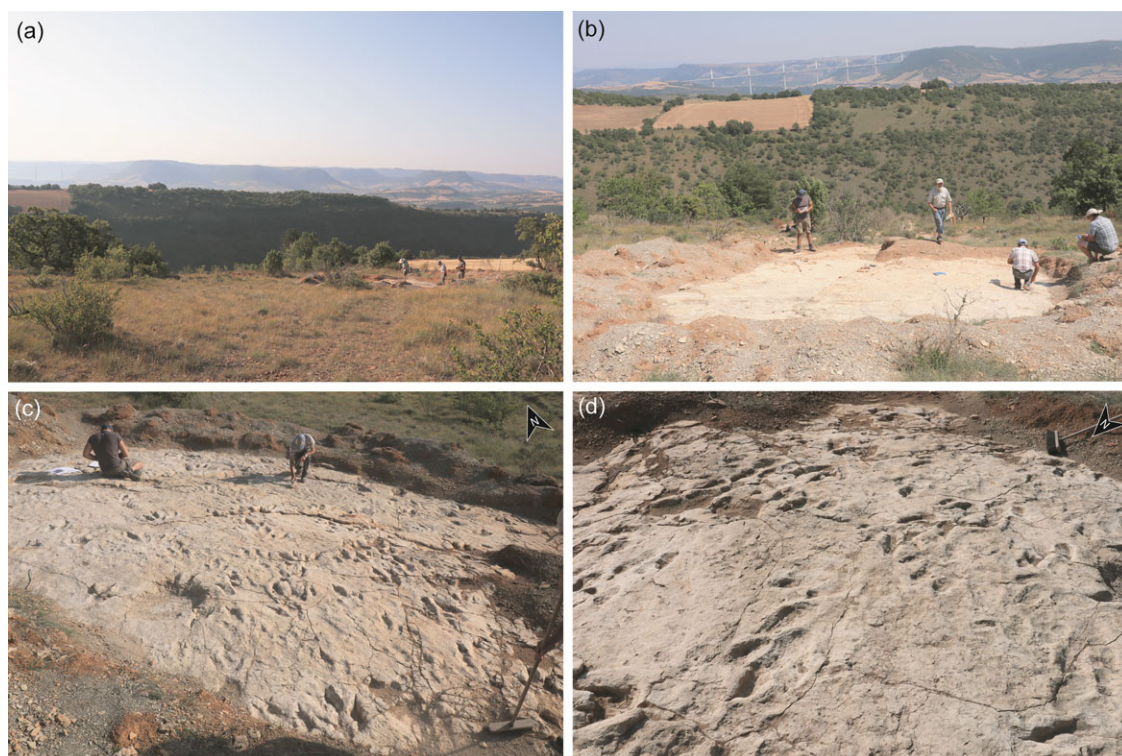
Fig. 2. (Colour online) Illustration of the Mongisty D tracksite (a–b) showing abundant tridactyl dinosaur footprints (c–d).

3. Material and methods

The descriptive terminology and morphometric parameters are taken from Leonardi (1987), Demathieu (1990), Demathieu *et al.* (2002) and Marty (2008). We used the following standard abbreviations (Fig. 4): L, length of the footprint; W, width of the footprint; LII, LIII, LIV, lengths of the digits; II–IV, divarication angle between digit II and digit IV. We also used D, which corresponds to the length of the free part of digit III *sensu* Demathieu *et al.* (2002). In Section 4.b below, we describe these morphometric parameters by giving three values: the minimum, the average (in brackets) and the maximum. None of the specimens were collected. The orientations of tracks were measured on site. The morphometric values of the tracks from Mongisty D were compared with a large dataset including measurements of 431 tridactyl tracks from the Early Jurassic of the Causses Basin (based on data from Demathieu *et al.* 2002 and Moreau *et al.* 2012*a*, 2014, 2018) and of 80 tridactyl tracks from the Early Jurassic of Connecticut and Massachusetts, USA (data from Weems, 2019). Following the diagnosis of *Eubrontes giganteus*, proposed by Olsen *et al.* (1998), we only used tracks that were more than 30 cm long, thus selecting 80 footprints out of the 83 *E. giganteus* footprints in the dataset of Weems (2019). Locomotion speed and height of the hip were estimated based on the formulas of Alexander (1976) and Thulborn (1990). In order to produce 3D-photogrammetric reconstructions of the tracksite (Mallison & Wings, 2014; Matthews *et al.* 2016), the software Agisoft PhotoScan Professional 1.2.4 was used to align and combine multiple digital photographs taken with a Nikon D5200 camera coupled with an AF-S NIKKOR 18–105 mm f/3.5–5.6G ED camera lens. The same software was used to produce 3D-photogrammetric textured meshes and digital elevation models (DEMs) in false colours. The 3D meshes are available online at https://figshare.com.

4. Results

4.a. Sedimentology and track preservation

At Mongisty D, deposits of the Dolomitic Formation are exposed along a 4 m high outcrop. Based on the location of outcrops, we can estimate that the track-bearing surfaces of Mongisty A to C are all in stratigraphic layers located some metres above Mongisty D. Based on the main lithological variations along the stratigraphic section at Mongisty D, we distinguish eight levels (Level 1 to Level 8), and four facies (F1 to F4; Table 1; Figs 5 and 6). At the base of the section, Facies F1 is a yellowish, thinly laminated dolomite forming decimetre-thick beds with abundant hemispherical stromatolites (Fig. 6a–c). Stromatolitic domes are up to 40 cm in diameter (Fig. 6a–b). F2 consists of a grey to yellowish homogeneous dolomudstone forming centimetre- to decimetre-thick layers bearing mud cracks and microbial mats (Fig. 6d–e). F3 is a grey-blue to yellow clayey cryptalgal dolomudstone showing abundant millimetre-thick laminites with mud cracks and microbial mats. The microbial laminae are parallel to the bedding planes and are wavy to planar. F4 corresponds to yellowish matrix- to clast-supported breccia organized in lenticular, 0 to 15 cm thick, successive, and partially overlapping prograded lobes. Clasts consist of angular to sub-rounded, millimetric to centimetric (up to 2 cm), poorly sorted, randomly oriented, homogeneous dolostone intraclasts with a mudstone texture and floating in a dolomudstone matrix (Fig. 7). Clast arrangement is chaotic. Abundance of intraclasts is variable and the latter can be lacking in lobes locally. Thin-sections of samples from Facies F4 show irregular, alveolar, nodular structures similar to those described by Arrondeau *et al.* (1985) in the Hettangian Dolomitic Formation of Aveyron. Arrondeau *et al.* (1985) interpreted such structures as rhizoconcretions. The thin-sections do not reveal the presence of microbial mats in Facies F4.
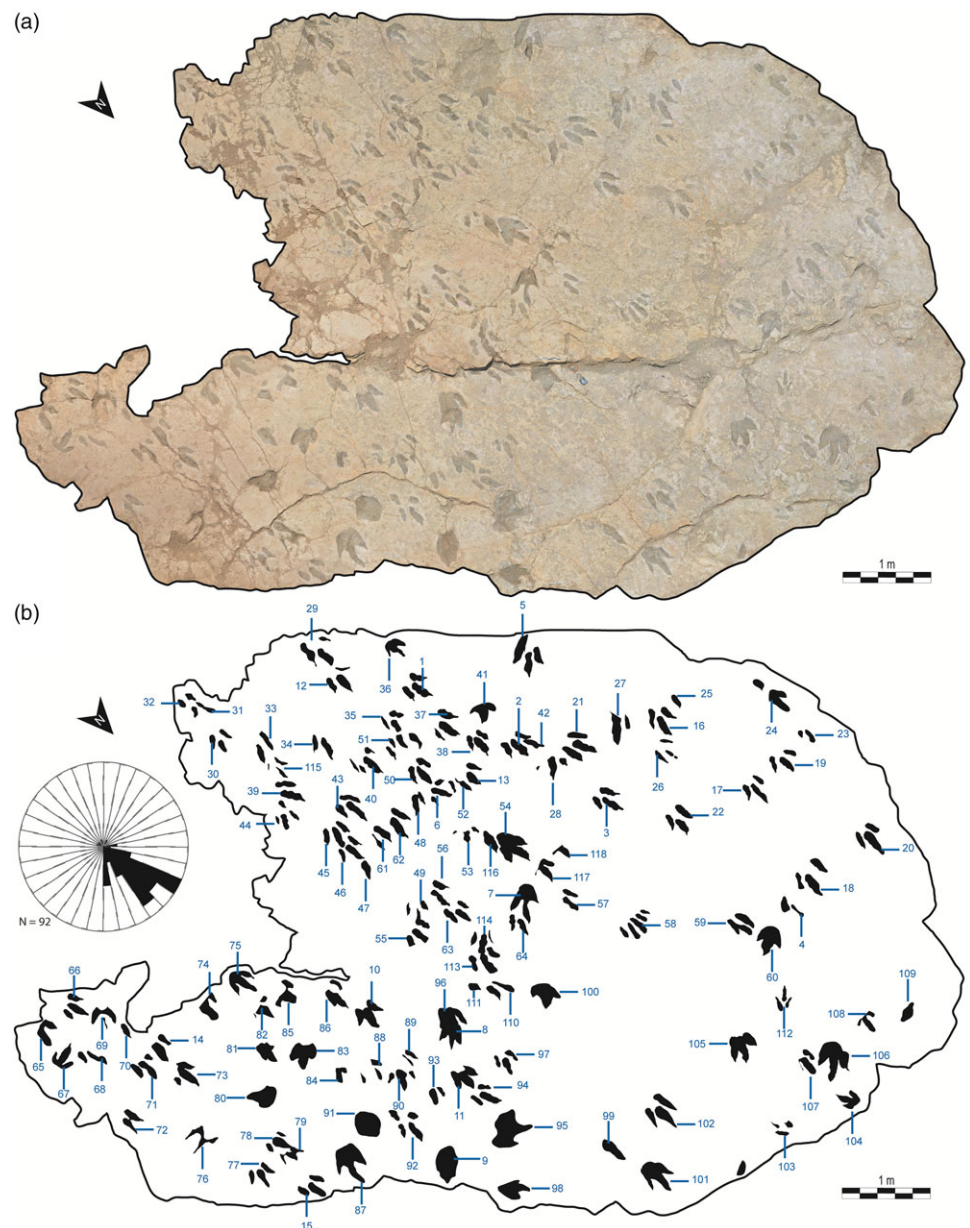
Fig. 3. (Colour online) Mongisty D tracksite showing abundant tridactyl dinosaur tracks preferentially oriented towards the north. (a) Photograph. (b) Interpretative sketch.

Only Level 7 (within Facies F4) yielded tracks. In the upper part of Level 7, six 0–15 cm thick and consecutive lobes (L1 to L6) bear footprints (Fig. 8a–b). All footprints from Mongisty D are concave epireliefs. The lithology is similar for the six lobes (matrix- to clast-supported breccia). The lateral extension of lobe L3 is limited to the northern part of the outcrop (Fig. 8a–b). To the south, L3 is missing but a clay lens (C1), up to 13 cm thick, is present between L2 and L4 (Fig. 8a–f). The lobes L4 to L6 overlap each other towards the south or the southeast, suggesting a progradation in that direction (Fig. 8c–d).

The surfaces of the six lobes L1 to L6 (Facies 4) bear footprints, whereas no tracks have been observed in the clay lens C1. At least four trampled surfaces (TS) can be distinguished. TS-1 to TS-3 correspond to the surface of lobes L1 to L3 respectively, whereas TS-4 corresponds to the surface of the three consecutive and prograded lobes L4 to L6 (Fig. 8a–d).

The trampled surface TS-4 is directly covered by Level 8 which is a clayey cryptalgal dolomudstone showing abundant thin laminites (Facies 3). Level 8 being not deformed by tracks, the tracks from the surface TS-4 are interpreted as true tracks. Most of the tracks deform a single lobe and did not propagate into the underlying lobe. However, some tracks are impressed over the limit of two overlapping lobes (where the overlying lobe is the thinnest) and deform both of them (e.g. limits between lobes L1/L2 and L4/L5). The trampled surface TS-1 bears true tracks and undertracks. True tracks from TS-1 are directly covered by lobe L2 (Fig. 8e–f), whereas under-tracks from TS-1 correspond to tracks made on the surface of lobe L2 and that propagated into lobe L1 (Fig. 8e–f).

Diverse kinds of preservation are observable. Despite the relative coarseness of the sediment, tracks show a good anatomical fidelity and completeness (Fig. 9). Others are poorly marked
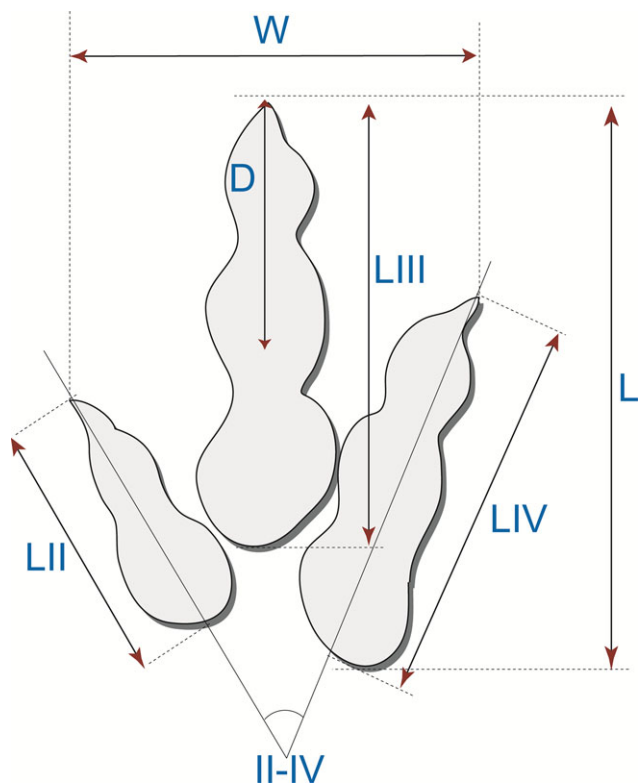
Fig. 4. (Colour online) Morphometric measurements taken on tridactyl tracks. L, length; W, width; D, length of the free part of digit III; LII, LIII and LIV, digit lengths; T: angle between the two most external digits.

Table 1. Microfacies

No.	Facies	Description	Depositional environments
F1	Stromatolites	Yellowish thinly laminated dolomite composed of abundant hemispherical stromatolites.	Subtidal to intertidal.
F2	Dolomudstone	Grey to yellowish homogeneous dolomudstone showing mud cracks and microbial mats.	Intertidal to supratidal zone. Protected tidal flat. Periodic emersions.
F3	Cryptalgal laminites	Grey-blue to yellow clayey cryptalgal dolomudstone showing abundant thin laminites with mud cracks and microbial mats. Microbial laminae parallel to the bedding planes and wavy to planar.	Intertidal to supratidal zone. Protected tidal flat. Periodic emersions.
F4	Matrix- to clast-supported breccia	Yellowish matrix- to clast-supported breccia. Angular to sub-rounded, millimetric to centimetric (up to 2 cm), poorly sorted, randomly oriented, homogeneous dolostone intraclasts floating in a dolomudstone matrix. Rhizoconcretions.	Supratidal zone affected by occasional mud flows. Pedogenesis

and limited to isolated marks of digits (Fig. 9). The tracks exhibit a good physical preservation and a variable morphological preservation *sensu* Marchetti *et al.* (2019). Footprints could get a score of 0.5 to 2.5 according to the morphological preservation scale of Marchetti *et al.* (2019).

4.b. Palaeoichnology

Due to the partial preservation of many traces, only 60 of them (located on the surface of the six lobes L1 to L6) can be ascribed to an ichnotaxon, of which 58 are *Eubrontes giganteus* Hitchcock and 2 are *Grallator* cf. *lescurei* Demathieu, 1990. Due to the high number of overlapping footprints, trackways cannot be easily identified. Although several alignments of two consecutive tracks are observed, a single short trackway composed of three consecutive *E. giganteus* footprints is identified (Mon-1–Mon-3).

Eubrontes giganteus Hitchcock, 1845
Description. The trackway is 290 cm long (Mon-1–Mon-3; Fig. 10). Pace length is 122–(124)–126 cm and the stride is 252 cm long. Pes tracks are aligned with the trackway midline (Fig. 10). Footprints are tridactyl, longer than wide (L/W = 1.1–(1.3)–1.4), 30.0–(36.5)–47.0 cm long and 24.5–(29.5)–36.0 cm wide (Fig. 11; Tables 2 and 3). The divarication angle between digits II and IV is quite large (II–IV = 31.0°–(42.4°)–55.0°) and D is short (D = 9.0–(14.0)–17.5 and L/D = 2.1–(2.6)–3.3). The position of the digito-metatarsal pad of digit IV is commonly more proximal than that of digit II. Some footprints display wide impressions of digits with well-marked pads. When preserved, claw marks are elongated and pointed.

Remarks. The ichnogenus *Eubrontes* Hitchcock, 1845 is well known in diverse Late Triassic – Early Jurassic formations throughout the world (e.g. Lucas *et al.* 2006a and references therein; Dalman, 2012; Lagnaoui *et al.* 2012; Xing *et al.* 2014; Getty & Fox, 2015; Wagensommer *et al.* 2016; Sciscio *et al.* 2017). In the Early Jurassic of France, the ichnogenus *Eubrontes* was reported from Aveyron (Demathieu & Sciau, 1999; Demathieu *et al.* 2002; Moreau *et al.* 2012b), Gard (Sciau, 2003), Lot (Lange-Badré & Lafon, 2000), Lozère (Moreau *et al.* 2014, 2018) and Vendée (Lapparent & Montenat, 1967). Amongst these Hettangian–Sinemurian tracks, the ichnospecies *E. giganteus* was only reported from Aveyron and Gard in the Causses Basin (Demathieu *et al.* 2002; Sciau, 2003). Based on ten large tracks from the site of Peyre, Demathieu & Sciau (1999) were the first to identify the ichnogenus *Eubrontes* in the Hettangian Dolomitic Formation of the Causses Basin. They initially ascribed the tracks to *Eubrontes divaricatus* Hitchcock, 1865. Later, based on the revision of the ichnogenus by Olsen *et al.* (1998), Demathieu *et al.* (2002) renamed the tracks from Peyre *Eubrontes giganteus*. Using the formula of Alexander (1976) and Thulborn (1990), and based on the trackway Mon-1–Mon-3, we estimate the hip height of the track maker between 1.71 and 1.86 m and their speed between 8.47 and 9.28 km h^{-1}, suggesting a walking gait.

Grallator cf. *lescurei* Demathieu, 1990
Description. Tracks are tridactyl, longer than wide (L/W = 1.4), 26 cm long and 18.0 cm wide (Fig. 12; Tables 2 and 4). The angle between digits II and IV is 39°–(40°)–41°. Impressions of digits are
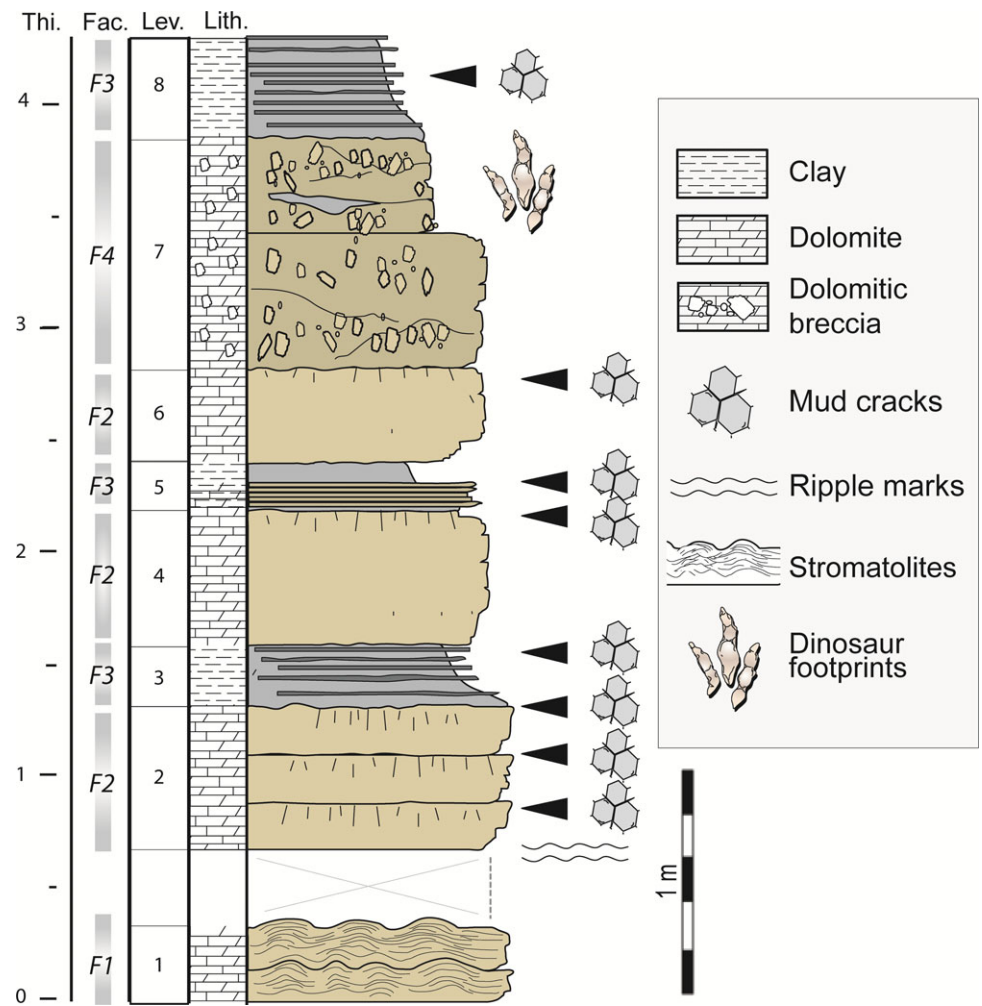
Fig. 5. (Colour online) Stratigraphic section of Mongisty D and location of the track-bearing level (Level 7).

separated, well-defined and elongated. The traces of digits III and IV are similar in length. D is quite long (D = 11.0–(11.5)–12.0). Impressions of digital pads are well preserved and are circular to oval. The position of the digito-metatarsal pad of digit IV is more proximal than that of digit II. There is no plantar impression.

Remarks. Grallator lescurei was erected by Demathieu (1990) based on tracks from Saint-Léons in Aveyron (southern France). In the Early Jurassic of France, *G. lescurei* was only reported from Aveyron, Gard and Hérault (Demathieu, 1990; Demathieu *et al.* 2002; Sciau, 2003). Grallatoroid footprints showing strong similarity with *G. lescurei* were also reported from the Hettangian Dolomitic Formation of Lozère (Moreau *et al.* 2014).

5. Discussion

5.a. Comparison with tridactyl tracks from the Causses Basin

Amongst Hettangian–Sinemurian tridactyl footprints from the Causses Basin, Demathieu *et al.* (2002) described six ichnospecies as currently identified: *Dilophosauripus williamsi* Welles, 1971, *Eubrontes giganteus*, *Grallator variabilis*, *Grallator lescurei*, *Grallator minusculus* Hitchcock, 1868 and *Grallator sauclierensis* Demathieu & Sciau, 1992. It is interesting to note that some authors consider *Dilophosauripus* Welles, 1971 as a junior synonym of *Eubrontes* (see references in Lucas *et al.* 2006*b*; Lockley *et al.* 2011). Recently, based on morphometrical comparisons,

Gand *et al.* (2018) recommended using *Kayentapus* Welles, 1971 rather than *Dilophosauripus* for the lowermost Jurassic tracks of the Causses Basin.

Based on the parameters L, L/W and (L − D)/D, Figure 13 shows bivariate diagrams for the diverse ichnospecies from the Lower Jurassic of the Causses Basin. The two grallatoroid tracks from Mongisty D (Mon-104 and Mon-112) are much longer than the small *Grallator* ichnospecies from the Causses Basin (*Grallator sauclierensis*, *Grallator variabilis*; Fig. 13). They mainly differ from *G. minusculus* by being a longer length of the free part of digit III ((L − D)/D = 1.2–(1.3)–1.4). *Kayentapus* tracks from the Causses Basin differ from *G.* cf. *lescurei* tracks from Mongisty D in being as long as wide (L/W = 0.8–(1.0)–1.3 and 1.4, respectively) and in having higher II–IV values (35–(68)–98° and 39–(40)–41°, respectively). Demathieu (1990) described *G. lescurei* as: '*Digits slender, well specified and separated in the proximal part. Projection of digit III beyond the other toes of moderate size (ratio III/D = 1.70 +/− 0.14); divarication between digits II and IV rather great for this ichnogenus, about 50.9° +/− 4.3° (instead of 24.9 +/− 3.4°, as exhibited by the type species). Differences between digits II and IV higher than G. sillimani. Length/width ratio about 1.2 +/− 0.06.*' Although Demathieu (1990) proposed in the diagnosis of *G. lescurei* a smaller L/W ratio than *G.* cf. *lescurei* from Mongisty D (1.4 on average; Table 4), the data set used to describe this ichnotaxon in Demathieu *et al.* (2002) included values of L/W ratio that range from 1.0 to 1.9. Although Demathieu (1990) diagnosed *G. lescurei*
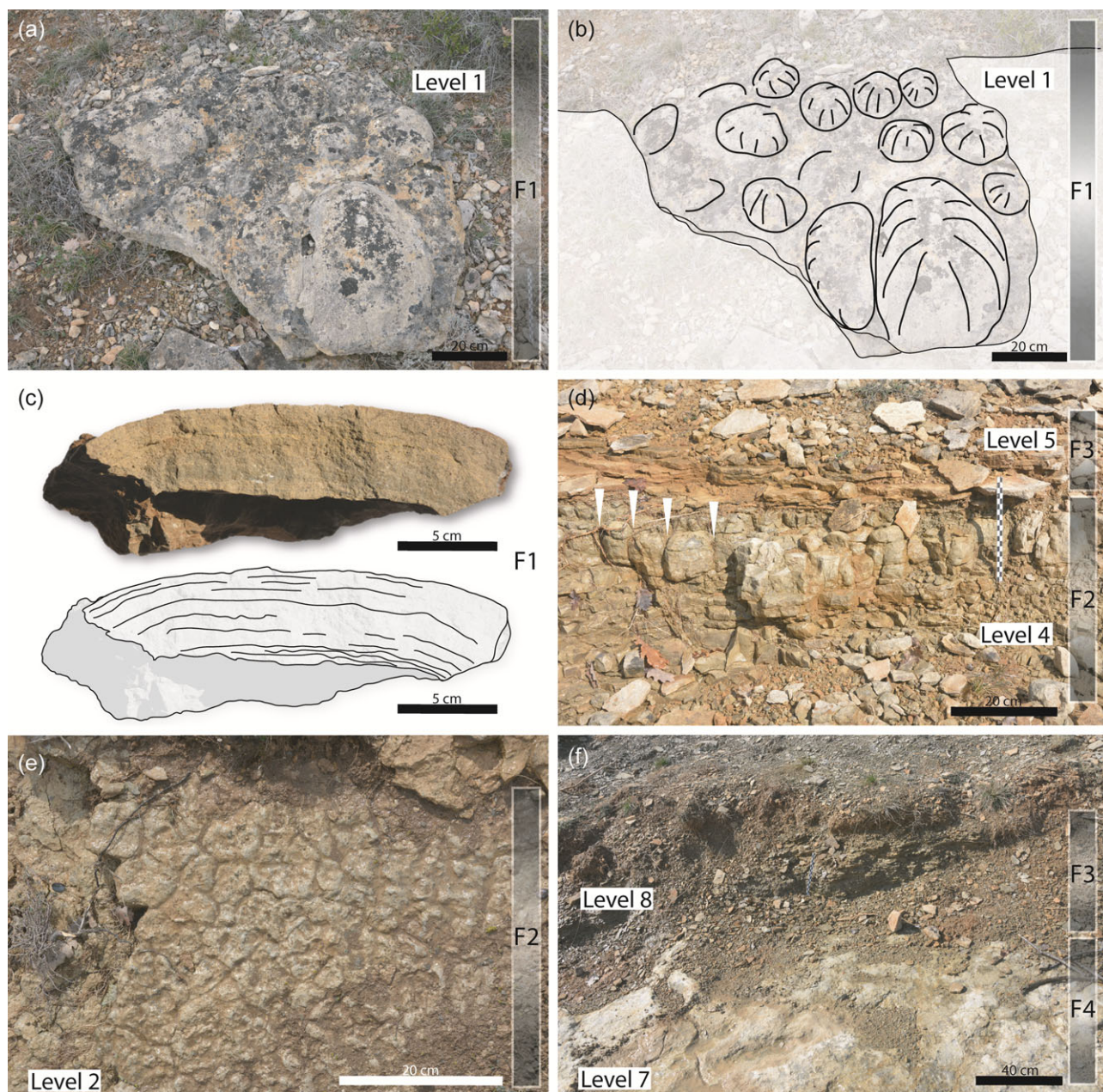
Fig. 6. (Colour online) Facies. (a–b) Hemispherical stromatolites (Facies F1), upper view of Level 1, photograph (a) and interpretative sketch (b). (c) Transversal section of a thinly laminated hemispherical stromatolite (Facies F1) from Level 1, photograph and interpretative sketch. (d) Interface between Levels 4 and 5 with dolomudstone showing vertical mud cracks (white arrows; Facies F2) and dolomudstone laminites (Facies F3). (e) Surface of a dolomudstone slab from Level 2 with mud cracks (Facies F2). (f) Interface between Levels 7 and 8 showing matrix- to clast-supported breccia (Facies F4) and dolomudstone laminites (Facies F3).

with a divarication angle higher than that observed in *G*. cf. *lescurei* from Mongisty D (40° on average), the data set used in Demathieu *et al.* (2002) included values of II–IV that range from 30° to 80°. This demonstrates the broad variability of the divarication angle II–IV, probably depending on the nature and the hydration of substratum, as well as on the speed of the animal (Milàn, 2003; Milàn & Falkingham, 2016).

The morphometric space of the largest *Grallator* Hitchcock, 1858 ichnospecies (*G. lescurei* and *G. minusculus*) and that of *E. giganteus* from Mongisty D are distinct (Fig. 13). Track lengths of *G. lescurei* and *G. minusculus* are shorter (12.5–(25.5)–36.0 and 24.0–(30.1)–35.0 cm, respectively) than the well-preserved tracks of *E. giganteus* from Mongisty D. *G. lescurei* and *G. minusculus*

display digit imprints that seem more slender than *E. giganteus* from Mongisty D, although quantitative values are not available for a formal comparison. *G. minusculus* also shows a higher L/W ratio than *E. giganteus* from Mongisty D (0.9–(1.6)–1.9 and 1.1–(1.3)–1.4, respectively). *Kayentapus* from the Causses Basin differs from *E. giganteus* at Mongisty D by shorter tracks that are as long as wide, and higher II–IV values (35–(68)–98° and 31.0–(42.4)–55°, respectively).

Based on material from the Lower Jurassic of the USA, Olsen *et al.* (1998) described *Eubrontes giganteus* as: '*Large* (>30 cm *long*), *functionally tridactyl ichnite . . . and the length to width ratio is about 1.4 to 1.5; projection of digits II and IV along the axis of digit III about equal; and divarication of outer digits 30°–40°.*' Even if
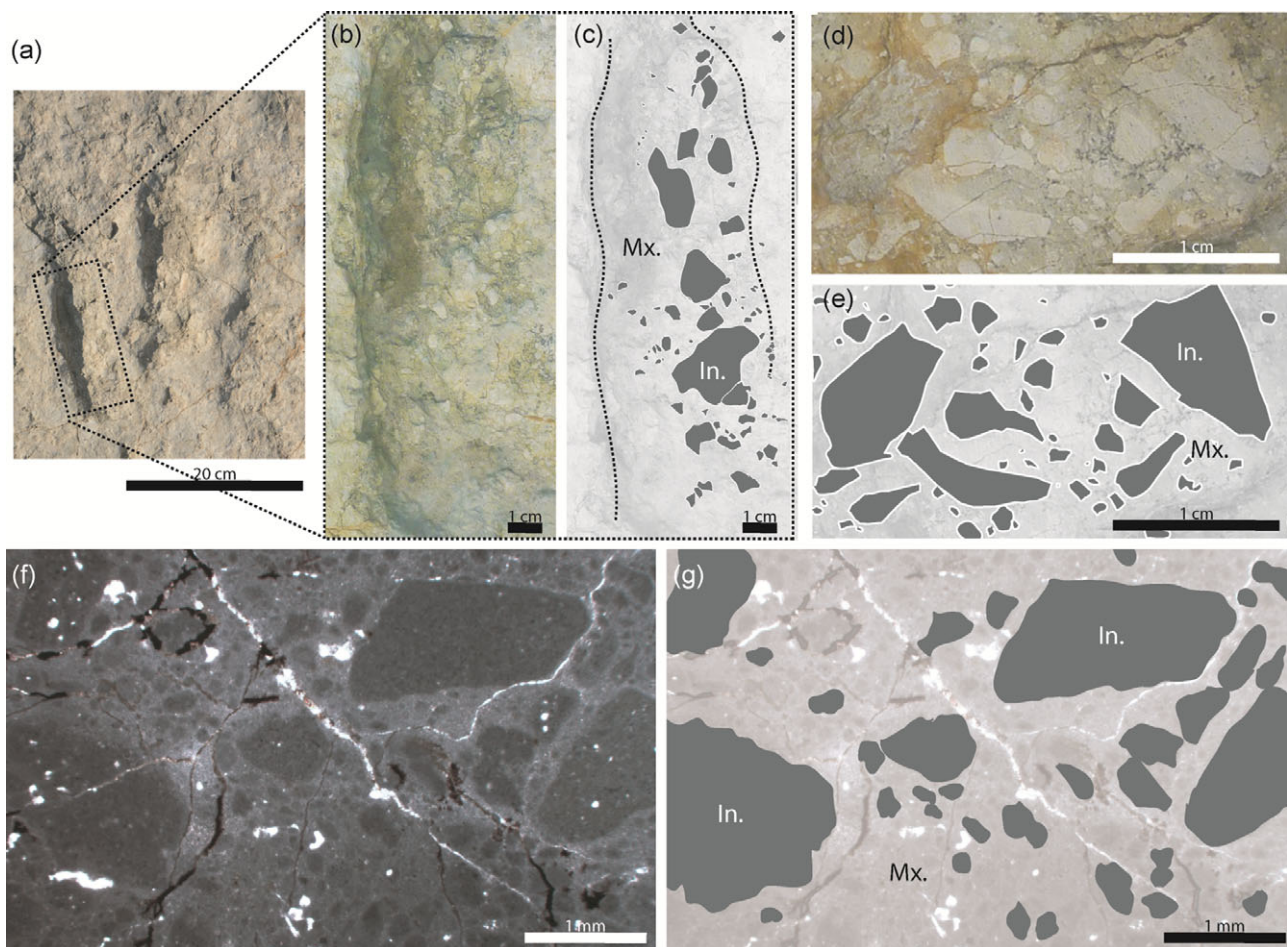
Fig. 7. (Colour online) Details of the matrix- to clast-supported breccia (Facies F4) composing the track-bearing surfaces. (a–c) Tridactyl track Mon-57 (a) and detail of the sediment in an imprint of digit IV (b–c) showing abundant angular to sub-rounded millimetric to centimetric, poorly sorted, randomly oriented, homogeneous dolostone intraclasts floating in a dolomudstone matrix, photograph (b) and interpretative sketch (c). (d–e) Detail of the matrix- to clast-supported breccia, photograph (d) and interpretative sketch (e). (f–g) Microfacies of the track-bearing surfaces showing poorly sorted, randomly oriented, homogeneous dolostone intraclasts (In.) floating in a dolomudstone matrix (Mx.).

they used the ichnospecies *E. giganteus*, Demathieu *et al.* (2002) indicated that the diagnosis of *E. giganteus* proposed by Olsen *et al.* (1998) was not entirely appropriate for the track assemblage from the Causses Basin. Demathieu *et al.* (2002) mentioned that *E. giganteus* tracks from this area differs from those described by Olsen *et al.* (1998) in showing: small claw marks on impressions of digits II, III and IV; pads not well marked or absent; smaller L/W ratio (1.0–1.4); and higher II–IV values (41–72°). The length and width of *E. giganteus* reported by Demathieu *et al.* (2002) and those from Mongisty D are very close (length: 39.0 cm and 36.5 cm respectively on average; width: 31.4 cm and 29.5 cm respectively on average; Fig. 13). However, *E. giganteus* from Mongisty D differs from those reported by Demathieu *et al.* (2002) in having smaller II–IV values (up to 55° and up to 72° respectively; Tables 2 and 3), well-marked phalangeal pads and elongated claw marks. Thus, tracks from Mongisty D fit the diagnosis of *E. giganteus* better than those described in Demathieu *et al.* (2002). In Figure 13, the morphometric space of *E. giganteus* from the Causses Basin and those from the USA largely overlap. However, *E. giganteus* from the USA tend to have shorter length and can have a slightly higher L/W ratio.

In the lowermost Jurassic deposits from France, another ichnospecies of *Eubrontes* was reported from the Hettangian of the Veillon tidal flat, in Vendée: *E. veillonensis* Lapparent &

Montenat, 1967. We may notice that the length, width and L/W ratio of *E. veillonensis* (34 cm, 28 cm and 1.21 respectively) clearly fall within the values of *E. giganteus* from the Causses Basin (Fig. 13). Lapparent & Montenat (1967) erected this new ichnospecies and explained that it is very close to *E. giganteus* from Connecticut (Hitchcock, 1845). They distinguished these two ichnospecies based on a rather subjective criterion, namely that their '*outlines are slightly different*' (Lapparent & Montenat, 1967, p. 26). In the absence of a robust comparison, the authors failed to distinguish *E. veillonensis* from *E. giganteus*. Demathieu & Sciau (1999) indicated that *E. veillonensis* mainly differs from *E. giganteus* by the values of the divarication angle formed by the lateral digits II and IV. However, as observed on specimens from Mongisty D and from other areas in the Causses Basin (Demathieu *et al.* 2002), the divarication angle can be quite variable amongst footprints of *E. giganteus*. Without synonymizing these two ichnospecies, Demathieu (2003) and Gand *et al.* (2007) further suggested that they are very close to each other. Pending a robust comparison, for the time being we agree with these authors.

5.b. Ichnotaphonomy

Vertebrate tracks are commonly impressed in sediments that range from '*clay-mineral or lime muds to siliciclastic or bioclastic-ooid*
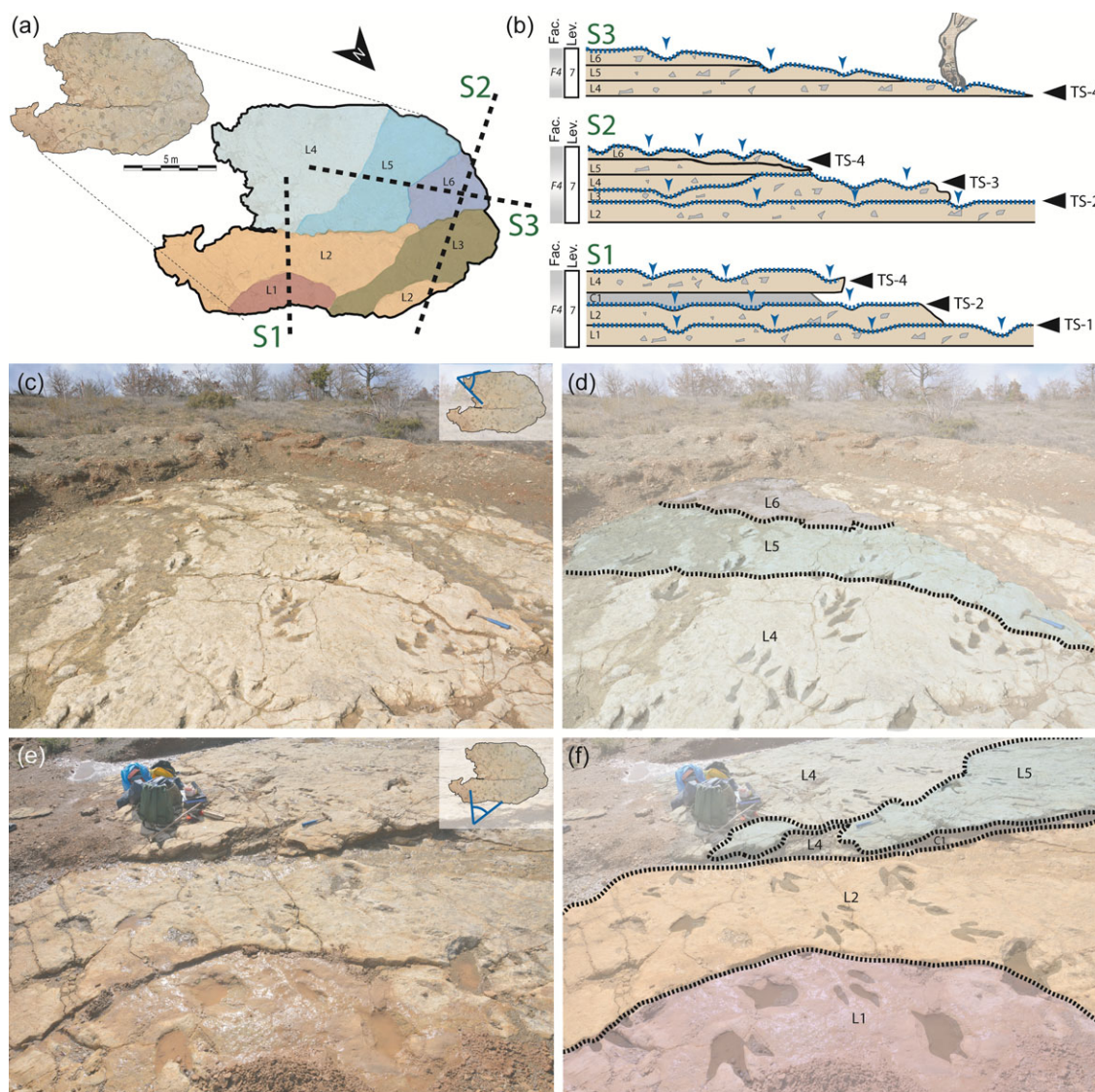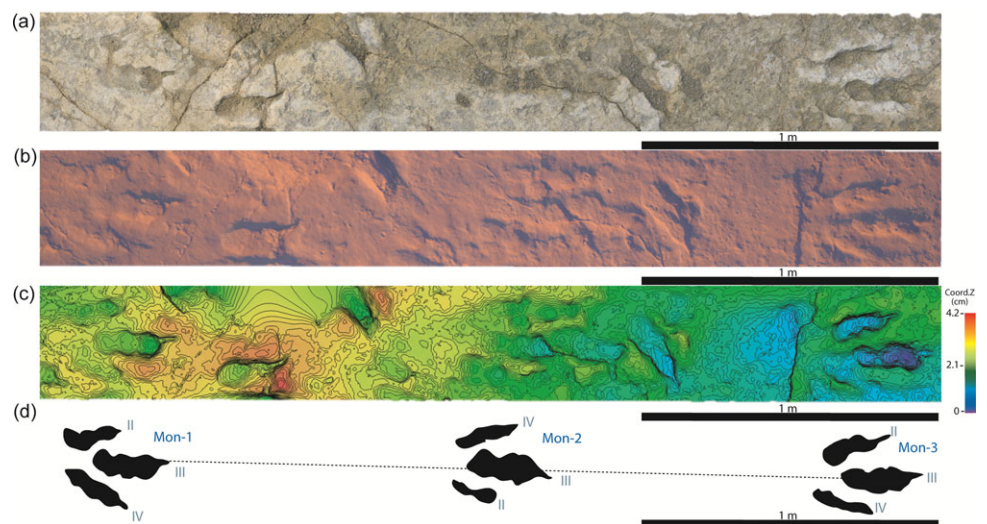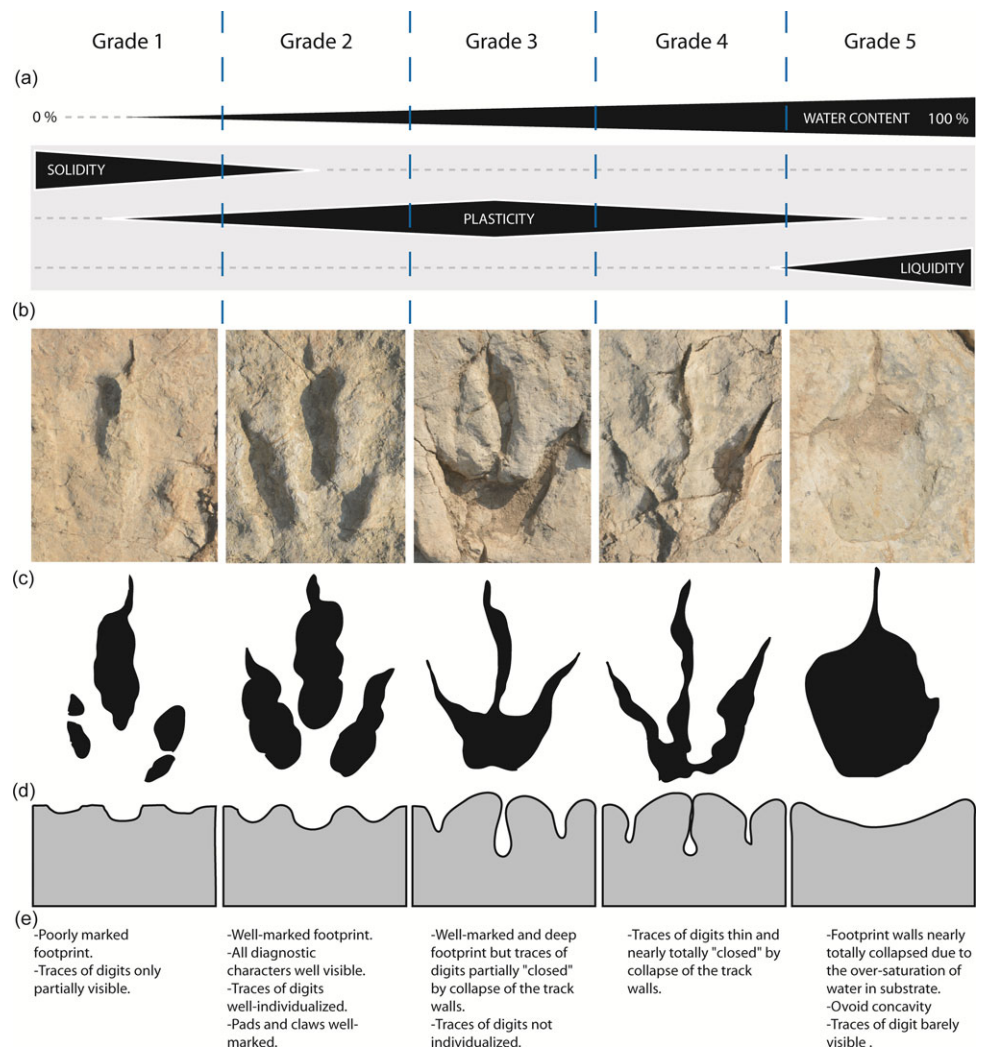
Fig. 8. (Colour online) Sedimentary structures of the tracksite and location of the trampled surfaces. (a) Map of the tracksite showing the location of the six lobes (L1–L6). (b) Three transversal sections (S1–S3) showing the structure of the six lobes (L1–L6) and location of the four trampled surfaces (TS1–TS4); footprints are indicated by blue vertical arrows; trampled surfaces are indicated by dotted blue lines and black arrows; Fac., facies; Lev., level. (c–d) View from the south showing the successive and overlapping decimetre-thick progradation lobes L4–L6; photograph (c) and interpretative sketch (d). (e–f) View from the east showing successive decimetre-thick progradation lobes (L1–L2 and L4–L5) alternating with a thin clay lens (C1); photograph (e) and interpretative sketch (f).

sands' (Allen, 1997, p. 485). They are mainly preserved in fine-grained sediments corresponding to low-energy depositional palaeoenvironments (e.g. Laporte & Behrensmeyer, 1980; Allen, 1997; Alcalá *et al.* 2014). Regionally, in the dozens of tetrapod tracksites reported from the Dolomitic Formation of the Causses Basin so far, footprints are always preserved in homogeneous dolomudstone beds or laminites showing abundant microbial mats without coarse intraclasts or coarse detrital particles (e.g. Demathieu, 1993; Demathieu & Sciau, 1999; Demathieu *et al.* 2002; Sciau, 2003; Moreau *et al.* 2014, 2018, 2019*a*). These track-bearing surfaces were interpreted as tidal flat deposits. As shown by some taphonomic experiences in present-day tidal-flat environments, a track can be consolidated by desiccation or lithification of the mat, or by ongoing growth of the mat (Marty *et al.* 2009). The abundant microbial mats in archosaur tracksites from the Dolomitic Formation of the Causses Basin were probably crucial in the preservation of the frequent vertebrate tracks.

In some tracksites throughout the world, footprints are preserved in coarser sediments that mainly consist of silts or sandstones deposited in alluvial/fluvial (e.g. Tucker & Burchette, 1977; Courel & Demathieu, 2000; Gand & Demathieu, 2005) and aeolian context (e.g. Loope, 2006; Milàn & Loope, 2007; Candia Halupczok *et al.* 2018). In most of these cases, tracks are reported from coarse silts to medium sands. Only very rare sites yield tracks preserved in coarse sands and microconglomerates (Szewczyk *et al.* 2020). In contrast to all tracksites reported from the Lower Jurassic Dolomitic Formation of the Causses Basin, Mongisty D stands as an exceptional locality because footprints are preserved in a relatively coarse sediment (a dolomitic breccia) and in a facies apparently barren of microbial mats.

The morphology and dimensions of footprints depend on several biotic factors, such as the anatomy of the pes, the weight, the speed, the gait, the behaviour and the force applied on the sediment by the track maker (Allen, 1997; Falkingham *et al.* 2011; Gatesy &

Fig. 9. (Colour online) Influence of water saturation on preservation of tracks in tidal breccia. (a) Five grades of water saturation (grade 1 to grade 5) influencing plasticity of substrate; grade 1, track Mon-34 (lobe L4); grade 2, track Mon-3 (lobe L5); grade 3, track Mon-7 (lobe L5); grade 4, track Mon-29 (lobe L4); grade 5, track Mon-91 (lobe L1). (b) Five kinds of preservation of tracks related to the physical properties of substrate. (c) Sketches of tracks. (d) Sketches showing the deformation of substrate in a transversal plan. (e) Characteristics of the different kinds of preservation.

Fig. 10. (Colour online) *Eubrontes giganteus* trackway (Mon-1–Mon-3). (a–d) 3D-photogrammetric mesh with texture (a), 3D-photogrammetric mesh (b), DEM in false-colour depth map (c) and interpretative sketch (d).

Falkingham, 2017). In addition, the formation and the resulting morphology of footprints also depend on substrate properties such as lithology (including the grain size of allochems/clasts), the morphology of the walking surface, its water saturation and the presence of microbial mats. Later erosional processes should also be added to this long list of parameters. At Mongisty D, the preservation of tracks varies a lot within the same trampled surface, and from one trampled surface to another (Fig. 9). As erosional
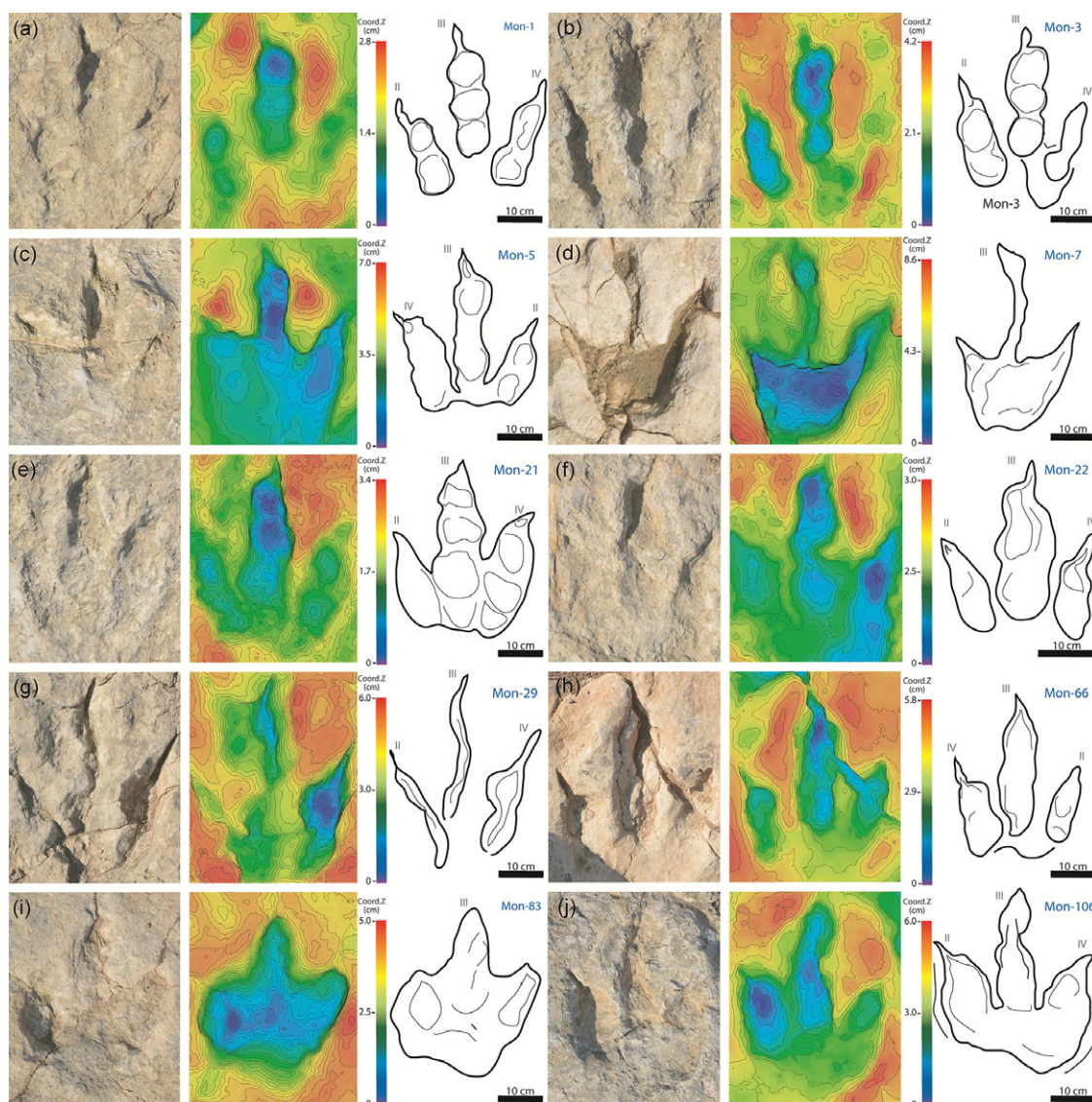
Fig. 11. (Colour online) *Eubrontes giganteus*. (a) Mon-1. (b) Mon-3. (c) Mon-5. (d) Mon-7. (e) Mon-21. (f) Mon-22. (g) Mon-29. (h) Mon-66. (i) Mon-83. (j) Mon-106. For each footprint, photograph, DEMs in false-colour depth map and interpretative sketch are given (from left to right).

processes alone are insufficient to explain such morphological contrasts, this indicates that tracks were made at different moments when the water saturation of sediment was not homogeneous. In Figure 9, we distinguish five grades of water saturation (grade 1 to grade 5) influencing the track preservation and classified from lower to higher water contents and linked with the solidity of substrate. These five grades were distinguished using true tracks only, and a single trampled surface can show several of these grades (for example, the trampled surface TS-4 combines grade 1 to grade 4). For grade 1, as footprints are poorly marked and digit impressions are only partially visible, tracks were made in a consistent/solid and dry sediment with a very low plasticity. For grade 2, as footprints are well marked, the plasticity of the sediment was higher than in grade 1. However, the relatively shallow tracks with well-defined walls revealing foot morphology suggest the water content was not so high. Only the tracks produced in grade 2 conditions exhibit all diagnostic characters of the ichnotaxa and all detailed marks of

digits, pads and claws. The dolomitic breccia with coarse intraclasts was cohesive enough to prevent the disappearance of the tracks thanks to the presence of an abundant matrix between dolostone grains (Fig. 7). For grades 3 and 4, as footprints are very deep with narrow traces of digits without marks of pads and some deformation of the track walls (especially in grade 4, for which digit imprints are nearly 'closed'), footprints were made in a sediment with high water saturation and high plasticity. In grade 5, as footprints consist of ovoid concavities and track walls are nearly totally collapsed (traces of digit barely visible), it appears that the sediment could not remain consistent after the kick-off phase of the track maker's foot. In grade 5, footprints were made in sediment with very high water saturation and very low plasticity. The diverse types of preservation observed on this nearly monospecific track assemblage (*E. giganteus*) highlight the strong influence of the physical properties of the sediment upon track preservation (see also Gatesy & Falkingham, 2017).

Table 2. Values measured on Hettangian tridactyl tracks from Mongisty D. L: length of the trace; W: width of the trace; D: length of the free part of digit III; LII, LIII, LIV: lengths of the digits; II–IV, divarication angle between digit II and digit IV (all in cm except II–IV in degrees); and ratio L/W, L/D and (L − D)/D

Track no.	L	W	D	LII	LIII	LIV	II–IV	L/W	L/D	(L − D)/D	Ichnotaxon
Mon-1	35	30	14	21	28	23	42	1.2	2.5	1.5	*E. giganteus*
Mon-2	36	26		17	25	19	41	1.4			*E. giganteus*
Mon-3	38	27	16	14	27	23	40	1.4	2.4	1.4	*E. giganteus*
Mon-5	47	34	14.5	22	29	29	43	1.4	3.2	2.2	*E. giganteus*
Mon-6	31			17	25						*E. giganteus*
Mon-7	42	31	17	21		27	37	1.4	2.5	1.5	*E. giganteus*
Mon-10	34	29	13.5	17	25	21	36	1.2	2.5	1.5	*E. giganteus*
Mon-14					28						*E. giganteus*
Mon-16	39	30	12	22	27	23	38	1.3	3.3	2.3	*E. giganteus*
Mon-17	34	30	12	19	25	20	42	1.1	2.8	1.8	*E. giganteus*
Mon-18	42	31	16		28		55	1.4	2.6	1.6	*E. giganteus*
Mon-19	32	30	14.5	19	23	20	53	1.1	2.2	1.2	*E. giganteus*
Mon-20	44		17.5	17	31	20	40		2.5	1.5	*E. giganteus*
Mon-21	41	32	15	19	31	25	48	1.3	2.7	1.7	*E. giganteus*
Mon-22	34	28	12	15	24	18	41	1.2	2.8	1.8	*E. giganteus*
Mon-28		29			27						*E. giganteus*
Mon-29	44	34	15		30	22	55	1.3	2.9	1.9	*E. giganteus*
Mon-30	40	28	15	21	26	27	37	1.4	2.7	1.7	*E. giganteus*
Mon-33					22						*E. giganteus*
Mon-36	32	24.5	14	15	23	18	45	1.3	2.3	1.3	*E. giganteus*
Mon-38	31	25	13	15	22	16.5		1.2	2.4	1.4	*E. giganteus*
Mon-39	39				28	24					*E. giganteus*
Mon-40					26.5						*E. giganteus*
Mon-43	40	29	17	20	31	26	40	1.4	2.4	1.4	*E. giganteus*
Mon-45		30									*E. giganteus*
Mon-46		30	9.5		22.5	20	50				*E. giganteus*
Mon-47		30	10	14	22	16.5	55				*E. giganteus*
Mon-48	30					24					*E. giganteus*
Mon-49		25	9	12.5	15	16	46				*E. giganteus*
Mon-50	37	28	14.5	23	29	24	44	1.3	2.6	1.6	*E. giganteus*
Mon-54		30	15.5	21	21	34.5	36				*E. giganteus*
Mon-56	33				25.5	19					*E. giganteus*
Mon-57					19	22					*E. giganteus*
Mon-58											*E. giganteus*
Mon-59	32	27.5			19	14		1.2			*E. giganteus*
Mon-61					24						*E. giganteus*
Mon-62					29						*E. giganteus*
Mon-63	32	26	14	14	21	20	41	1.2	2.3	1.3	*E. giganteus*
Mon-64	32				22						*E. giganteus*
Mon-65											*E. giganteus*
Mon-66	36	27	15	14	24	20	31	1.3	2.4	1.4	*E. giganteus*
Mon-67	34	26	10.5	11	23	12	50	1.3	3.2	2.2	*E. giganteus*
Mon-71	35	26			27	20		1.3			*E. giganteus*
Mon-73	35				26						*E. giganteus*

(Continued)

Table 2. (*Continued*)

Track no.	L	W	D	LII	LIII	LIV	II–IV	L/W	L/D	(L − D)/D	Ichnotaxon
Mon-83	35	31	12	14	14	18.5	40	1.1	2.9	1.9	*E. giganteus*
Mon-85	33	30	14	20.5	25	20	40	1.1	2.4	1.4	*E. giganteus*
Mon-87	39	33	13.5	23	25	32	40	1.2	2.9	1.9	*E. giganteus*
Mon-92	34	29	16	14	25	15	46	1.2	2.1	1.1	*E. giganteus*
Mon-94	36	26	17	16.5	26	16.5	35	1.4	2.1	1.1	*E. giganteus*
Mon-97		25.5									*E. giganteus*
Mon-98	34										*E. giganteus*
Mon-101	33	29	13.5	14	24	19		1.1	2.4	1.4	*E. giganteus*
Mon-102	40	36	15	19	29	22	36	1.1	2.7	1.7	*E. giganteus*
Mon-105	37	32	12.5	20	27	22	40	1.2	3.0	2.0	*E. giganteus*
Mon-106	47	36	17	23	31	33	42	1.3	2.8	1.8	*E. giganteus*
Mon-113		36		19		26	37				*E. giganteus*
Mon-114		34	13								*E. giganteus*
Mon-116											*E. giganteus*
Mon-104	26	18	11	13	19	13.5	41	1.4	2.4	1.4	*G.* cf. *lescurei*
Mon-112	26	18.5	12	12	15	16	39	1.4	2.2	1.2	*G.* cf. *lescurei*

Table 3. *Eubrontes giganteus*. Minimum, maximum, average and standard deviation values for each morphometric parameter (L: length of the trace; W: width of the trace; D: length of the free part of digit III; LII, LIII, LIV: lengths of the digits; II–IV: divarication angle between digit II and digit IV; all in cm except II–IV in degrees) and ratio L/W, L/D and (L − D)/D; *n* = number of measured specimens

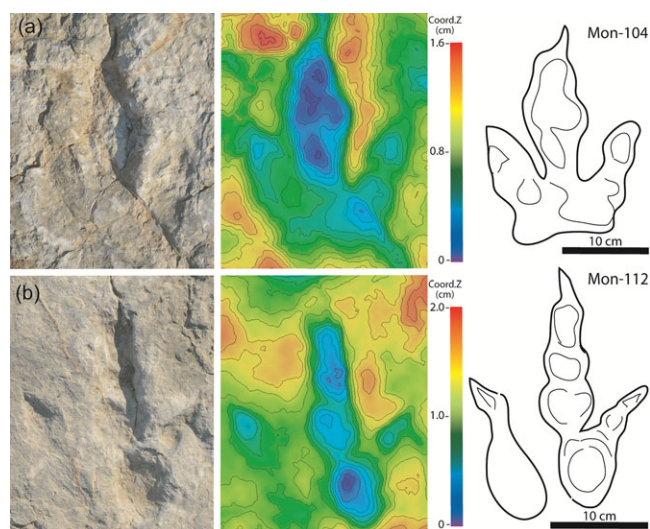|	L	W	D	LII	LIII	LIV	II–IV	L/W	L/D	(L − D)/D
n	40	41	35	34	48	41	34	32	30	30
Min	30.0	24.5	9.0	11.0	14.0	12.0	31.0	1.1	2.1	1.1
Max	47.0	36.0	17.5	23.0	31.0	34.5	55.0	1.4	3.3	2.3
Average	36.5	29.5	14.0	17.8	25.1	21.6	42.4	1.3	2.6	1.6
Standard deviation	4.41	3.12	2.19	3.41	3.79	4.93	6.11	0.10	0.32	0.32

Fig. 12. (Colour online) *Grallator* cf. *lescurei*. (a) Mon-104. (b) Mon-112. For each track, photograph, DEMs in false-colour depth map and interpretative sketch are given (from left to right).

5.c. Depositional environment

The hemispherical stromatolites (Facies F1) present at the base in the Mongisty D section (Fig. 5) are characteristic of a subtidal to intertidal depositional environment (Jahnert & Collins, 2012). Such laminated biosedimentary structures were reported from several Hettangian–Sinemurian archosaur tracksites of the Causses Basin (Demathieu *et al.* 2002; Sciau, 2003; Moreau, 2011). The abundance of mud cracks in Facies F2 and F3 indicates that sediments were deposited in an environment which was periodically exposed or subaerial. The cryptalgal laminites (Facies F3) are characteristic of regularly flooded environments, such as the intertidal and supratidal zones of a tidal flat in which microbial mats are growing (e.g. Alsharhan & Kendall, 2003; Hamon, 2004; Matysik, 2016). The lack of bioclasts and coarse particles in Facies F2 and F3 suggests limited storm-generated transport and a relatively long distance to the subtidal zone. Locally in the Causses Basin, some layers with halite pseudomorphs were reported from the Dolomitic Formation and suggest evaporitic conditions (Moreau, 2011). In contrast to Facies F1 to F3, the nature of Facies 4 (matrix-supported breccia) indicates high-energy events, such as the sudden reworking of

Table 4. *Grallator* cf. *lescurei*. Minimum, maximum, average and standard deviation values for each morphometric parameter (L: length of the trace; W: width of the trace; D: length of the free part of digit III; LII, LIII, LIV: lengths of the digits; II–IV: divarication angle between digit II and digit IV; all in cm except II–IV in degrees) and ratio L/W, L/D and (L − D)/D; *n* = number of measured specimens

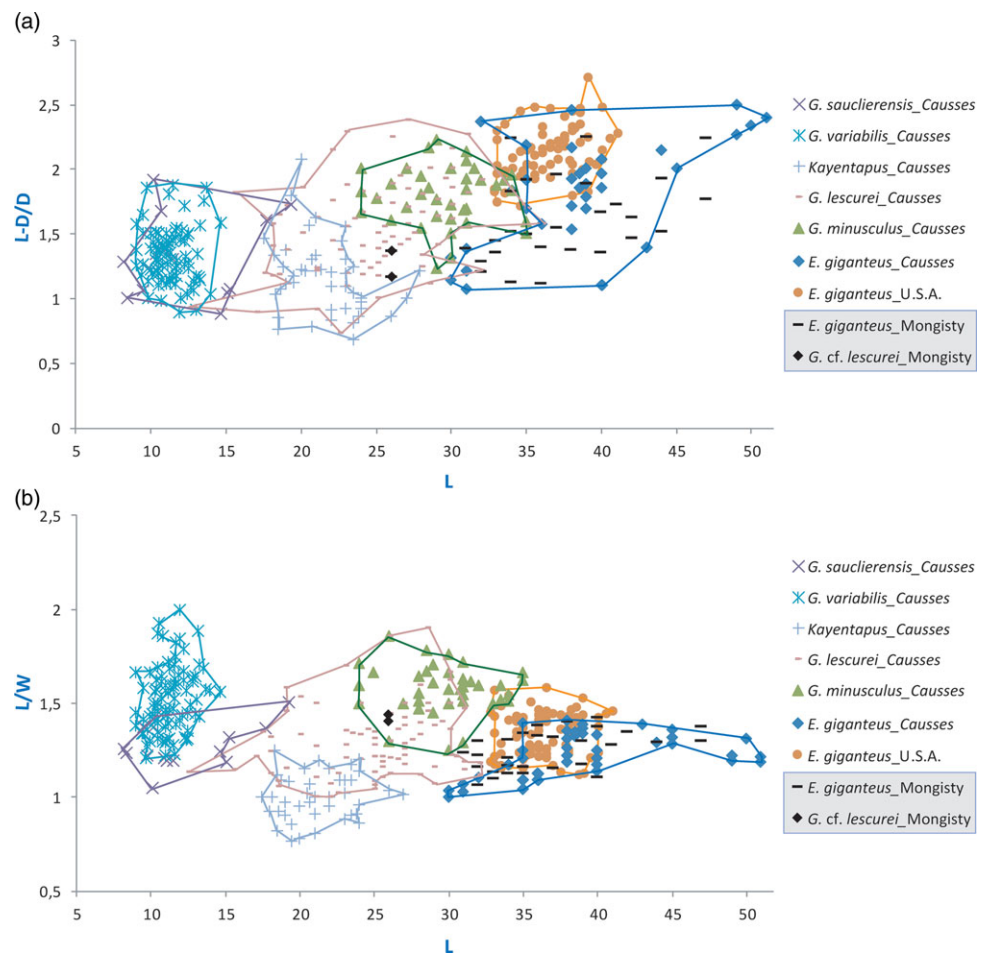|	L	W	D	II	III	IV	II–IV	L/W	L/D	(L − D)/D
n	2	2	2	2	2	2	2	2	2	2
Min	26.0	18.0	11.0	12.0	15.0	13.5	39.0	1.4	2.2	1.2
Max	26.0	18.5	12.0	13.0	19.0	16.0	41.0	1.4	2.4	1.4
Average	26.0	18.3	11.5	12.5	17.0	14.8	40.0	1.4	2.3	1.3
Standard deviation	0.00	0.35	0.71	0.71	2.83	1.77	1.41	0.03	0.14	0.14

Fig. 13. (Colour online) Footprints from Mongisty D compared to tridactyl tracks from the Early Jurassic of the Causses Basin (based on data from Demathieu *et al.* 2002; Moreau *et al.* 2012*a*, 2014, 2018) and the Early Jurassic of the eastern USA (based on data from Weems, 2019), in a bivariate diagram L vs (L− D)/D (a) and in a bivariate diagram L vs L/W (b). L in metres.

material by floods or storms in a supratidal zone. The presence of rhizoconcretions and dinosaur tracks in Facies 4 attests to periods of subaerial exposure and pedogenesis. The dolostone intraclasts present in the matrix-supported breccia are remnants of dry mud beds (partially lithified) that were eroded further upstream and subsequently transported in mud flows. The origin of brecciation could be explained by a phase of dewatering during prolonged subaerial exposure or initial formation of palaeosols (Kendall & Warren, 1987). As observed in diverse sedimentological contexts, the trampling of a surface by large vertebrates may also contribute to brecciation (e.g. Dalla Vecchia *et al.* 2000; Loope, 2006; Marty, 2008; Candia Halupczok *et al.* 2018). Matrix- to clast-supported breccia organized in lenticular lobes (Facies F4) indicates that the

mudflat of the Causses Basin was sporadically affected by large floods that reworked and redeposited intraclasts. The abundance and good preservation of footprints on the trampled surfaces (TS-1 to TS-4) demonstrate that erosion was not so intense during and after each flood (at least locally). The hardening of trampled surfaces after lobes were deposited and emerged was probably crucial in the preservation of tracks. The preservation of tetrapod tracks in such a depositional context remains exceptional. Based on sedimentological and ichnotaphonomical observations, Figure 14 shows a model to explain the formation of the Mongisty D tracksite. Such an occurrence of dinosaur tracks in tidal matrix- to clast-supported breccia remains extremely rare in the world (e.g. Marty, 2008). Overall, all facies suggest that the depositional environments of Mongisty D
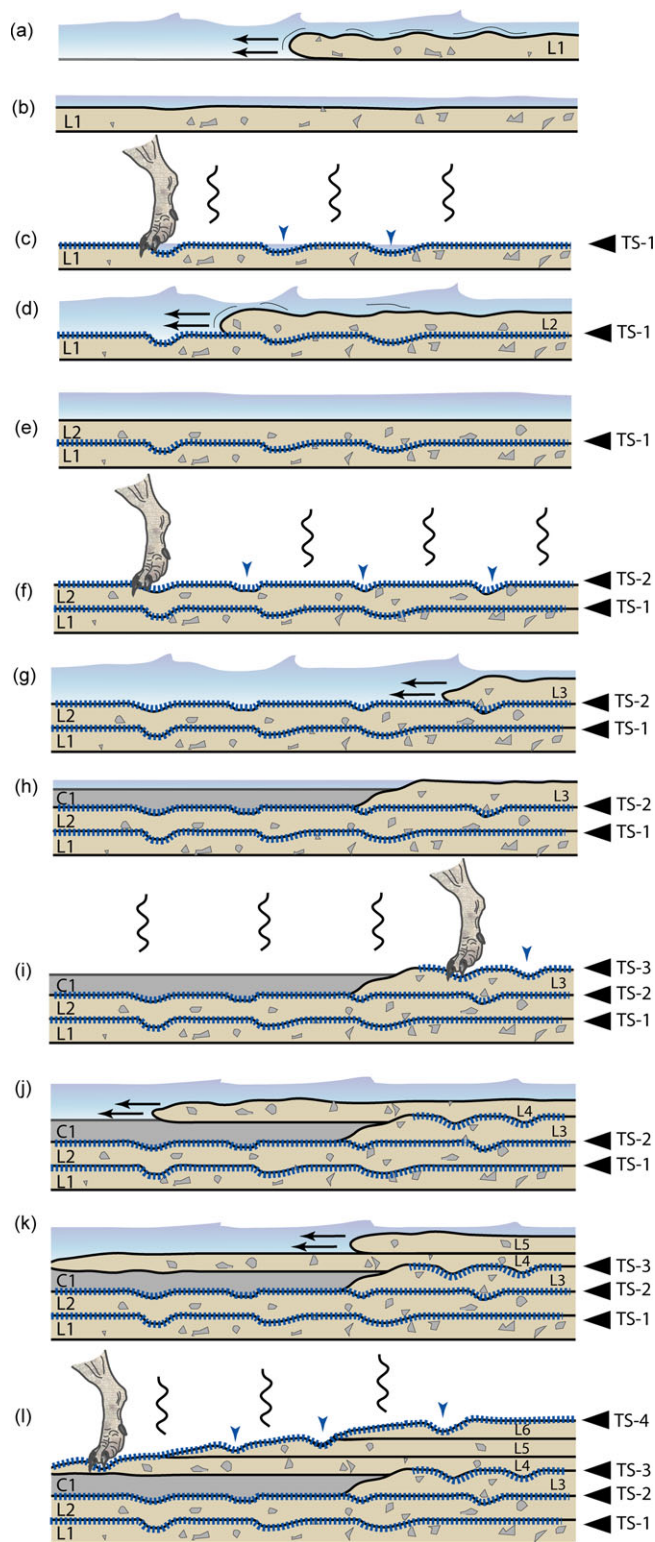
Fig. 14. (Colour online) Ichnotaphonomic model of the formation of the six overlapping decimetre-thick progradation lobes (L1–L6) and the four trampled surfaces (TS1–TS4). (a–c) Progradation and emersion of lobe L1; deformation of its surface by dinosaur tracks (trampled surfaces TS-1). (d–f) Progradation and emersion of lobe L2; deformation of its surface by dinosaur tracks (trampled surfaces TS-2). (g–i) Progradation of lobe L3 followed by the deposition of the clay lens C1; emersion and deformation of the surface of L3 by dinosaur tracks (trampled surfaces TS-3). (j–l) Progradation of the three partially overlapping lobes L4 to L6 followed by an emersion; deformation of the three consecutive lobes L4 to L6 by dinosaur tracks (trampled surfaces TS-4). Blue dotted lines: trampled surfaces; vertical black wavy lines: drying of the substrate; vertical blue arrows: substrate deformed by dinosaur feet.

varied from subtidal to intertidal/supratidal areas in a large and protected flat marsh. The absence of invertebrate skeletal fossils suggests unfavourable life conditions.

5.d. Track makers and their behaviour

Grallator and *Eubrontes* are tridactyl ichnogenera and show a similar phalangeal formula (type 3, 4 and 5 for toes II, III and IV). This osteological architecture corresponds to those of theropod dinosaurs (Baird, 1957; Olsen *et al.* 1998; Demathieu *et al.* 2002). Worldwide, body fossils of Early Jurassic theropods are attributed to Coelophysoidea and Ceratosauria and reported from Africa, Antarctica, China, Europe and the USA (Weishampel *et al.* 2004; Smith *et al.* 2007; Xing *et al.* 2013). In Europe, their body fossils are known from the Hettangian–Sinemurian deposits of England, France, Italy and Luxembourg (Larsonneur & Lapparent, 1966; Carrano & Sampson, 2004; Delsate & Ezcurra, 2014; Dal Sasso *et al.* 2018). In France, Hettangian theropods are only represented by the Coelophysoidea *Lophostropheus airelensis* Cuny & Galton, 1993 from the Moon–Airel Formation in Normandie (northwestern France; Larsonneur & Lapparent, 1966; Cuny & Galton, 1993; Ezcurra & Cuny, 2007) but they are currently unknown in the lowermost Jurassic of the Causses Basin. Although theropods are the most probable track makers of *E. giganteus* from the Hettangian of the Causses Basin, we notice that Weems (2003, 2019) suggested that the track makers of some *E. giganteus* from the Early Jurassic of the USA probably included basal sauropodomorphs.

Based on parallel trackways from the Early Jurassic of the USA, some authors (e.g. Hitchcock, 1848; Ostrom, 1972) suggested that track makers of *E. giganteus* were gregarious. At the Mongisty D outcrop, the high density of tracks that are preferentially oriented to the north (Fig. 3) could be regarded as evidence in favour of such a hypothesis. However, the different types of preservation of true tracks observed among *E. giganteus* (Fig. 9) and the presence of four trampled surfaces (Fig. 14) indicate that the footprints were not made at the same time. There is no evidence for the passage of a large group. Based on material from the USA, the gregarious behaviour of the track makers of *E. giganteus* was debated by Getty *et al.* (2015, 2017) who showed that such a parallel orientation of trackways can be mainly explained by physical barriers, suggesting that the track makers of *E. giganteus* were solitary. In a synthesis of many tracksites from the Hettangian–Sinemurian of the Causses Basin, Demathieu *et al.* (2002) observed that trackways show two preferential and perpendicular orientations at the scale of the basin. These authors proposed that dinosaurs from this area preferentially walked along the shoreline or were walking towards it.

6. Conclusion

Overall, the 118 large tridactyl tracks discovered at Mongisty D are significant for the following reasons:

1) They are preserved on the surface of lobes corresponding to matrix- to clast-supported breccia. This sharply contrasts with all other tracksites from the Dolomitic Formation in the Causses Basin, in which tracks are usually preserved in fine-grained sediments corresponding to low-energy depositional palaeoenvironments. The preservation of dinosaur tracks in such a coarse-grained sediment is also rare at the global scale.

2) Tracks from Mongisty D were formed in a subtidal to intertidal/supratidal setting in a large and protected flat marsh. This

setting was sporadically affected by large mud flows that redeposited mudstone intraclasts.

3) Most of the tracks are ascribed to *Eubrontes giganteus* and they represent the highest abundance and density of this ichnospecies in the Early Jurassic of the Causses Basin. These footprints were not made at the same time, excluding the passage of a large group.

References

Alcalá L, Pérez-Lorente F, Luque L, Cobos A, Roya-Torres R and Mampel L (2014) Preservation of dinosaur footprints in shallow intertidal deposits of the Jurassic-Cretaceous transition in the Iberian Range (Teruel, Spain). *Ichnos* **21**, 19–31.

Alexander R McN (1976) Estimates of speeds of dinosaurs. *Nature* **261**, 129–30.

Allen JRL (1997) Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S.W. Britain: mechanics of formation, preservation and distribution. *Philosophical Transactions of the Royal Society B, Biological Sciences* **352**, 481–518.

Alsharhan AS and Kendall CSC (2003) Holocene coastal carbonates and evaporites of the southern Arabian Gulf and their ancient analogues. *Earth-Science Reviews* **61**, 191–243.

Arrondeau J-P (1982) *Etude sédimentologique du Lias inférieur carbonaté du seuil caussenard et de ses abords (Languedoc)*. Thesis, University of Nantes, Nantes, France. Published thesis.

Arrondeau J-P, Bodeur Y, Cussey R, Fajerwerg R and Yapaudjian L (1985) Indices de pédogenèse et de karstification dans le Lias calcaréo-dolomitique du Causse du Larzac (Languedoc, France). *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* **9**, 373–403.

Baird D (1957) Triassic reptile footprint faunules from Milford, New Jersey. *Harvard College Museum of Comparative Zoology Bulletin* **117**, 449–520.

Briand BG, Couturié J-P, Geffroy J and Gèze B (1979) *Notice explicative, carte géologique au 1/50.000 de la France, feuille de Mende (862)*. Orléans: Bureau de Recherches Géologiques et Minières, 52 pp.

Brouder P, Gèze B, Macquar JC and Paloc H (1977). *Notice explicative, carte géologique au 1/50.000 de la France, feuille de Meyrueis (910)*. Orléans: Bureau de Recherches Géologiques et Minières, 29 pp.

Candia Halupczok DJ, Sánchez ML, Veiga GD and Apesteguía S (2018) Dinosaur tracks in the Kokorkom desert, Candeleros formation (Cenomanian, Upper Cretaceous), Patagonia Argentina: implications for deformation structures in dune fields. *Cretaceous Research* **83**, 194–206.

Carrano MT and Sampson SD (2004) A review of coelophysoids (Dinosauria: Theropoda) from the Early Jurassic of Europe, with comments on the late history of the Coelophysoidea. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **9**, 537–58.

Courel L and Demathieu G (2000) Une nouvelle espèce *Coelurosaurichnus grancieri* du Trias de l'Ardèche, France. *Geodiversitas* **22**, 35–46.

Cuny G and Galton PM (1993). Revision of the Airel theropod dinosaur from the Triassic-Jurassic boundary (Normandy, France). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **187**, 261–88.

Dalla Vecchia FM, Tarlao A, Tentor M, Tunis G and Venturini S (2000) First record of Hauterivian dinosaur footprints in southern Istria (Croatia). *Zbornik Radova* **2**, 143–9.

Dalman SG (2012) New data on small theropod footprints from the Early Jurassic (Hettangian) Hartford Basin of Massachusetts, United States. *Bulletin of the Peabody Museum of Natural History* **53**, 333–53.

Dal Sasso C, Maganuco S and Cau A (2018) The oldest ceratosaurian (Dinosauria: Theropoda), from the Lower Jurassic of Italy, sheds light on the evolution of the three-fingered hand of birds. *PeerJ* **6**, e5976.

Delsate D and Ezcurra MD (2014) The first Early Jurassic (late Hettangian) theropod dinosaur remains from the Grand Duchy of Luxembourg. *Geologica Belgica* **17**, 175–81.

Demathieu G (1990). Problem in discrimination of tridactyl dinosaur footprints, exemplified by the Hettangian trackways, the Causses, France. *Ichnos* **1**, 97–110.

Demathieu G (1993) Empreintes de pas de dinosaures dans les Causses (France). *Zubía* **5**, 229–52.

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

Demathieu G and Sciau J (1992) Des pistes de dinosaures et de crocodiliens dans les dolomies de l'Hettangien du Causse du Larzac. *Comptes Rendus de l'Académie des Sciences de Paris* **315**, 1561–6.

Demathieu G and Sciau J (1999) De grandes empreintes de pas de dinosaures dans l'Hettangien de Peyre (Aveyron, France). *Geobios* **32**, 609–16.

Demathieu G, Gand G, Sciau J and Freytet P (2002) Les traces de pas de dinosaures et autres archosaures du Lias inférieur des Grands Causses, Sud de la France. *Palaeovertebrata* **31**, 1–143.

Ellenberger P (1988) La découverte des pistes de dinosauriens de Camprieu. *Causses et Cévennes* **7**, 139–40.

Ezcurra MD and Cuny G (2007) The coelophysoid *Lophostropheus airelensis*, gen. nov.: a review of the systematics of '*Liliensternus*' airelensis from the Triassic–Jurassic outcrops of Normandy (France). *Journal of Vertebrate Paleontology* **27**, 73–86.

Falkingham PL, Bates KT, Margetts L and Manning PL (2011) The Goldilocks effect: preservation bias in vertebrate track assemblages. *Journal of the Royal Society Interface* **8**, 1142–54.

Gand G and Demathieu G (2005) Les pistes dinosauroïdes du Trias moyen français: interprétation et réévaluation de la nomenclature. *Geobios* **38**, 725–49.

Gand G, Demathieu GR and Montenat C (2007) Les traces de pas d'amphibiens, de dinosaures et autres reptiles du Mésozoïque français: inventaire et interpretations. *Palaeovertebrata* **35**, 1–149.

Gand G, Fara E, Durlet C, Caravaca G, Moreau J-D, Baret L, André D, Lefillatre R, Passet A, Wiénin M and Gély J-P (2018) Les pistes d'archosauriens: *Kayentapus ubacensis* nov. isp. (théropodes) et crocodylomorphes du Bathonien des Grands-Causses (France). Conséquences paléo-biologiques, environnementales et géographiques. *Annales de Paléontologie* **104**, 183–216.

Gatesy SM and Falkingham PL (2017) Neither bones nor feet: track morphological variation and 'preservation quality'. *Journal of Vertebrate Paleontology* **37**, e1314298.

Getty PR, Aucoin C, Fox N, Judge A, Hardy L and Bush AM (2017) Perennial lakes as an environmental control on theropod movement in the Jurassic of the Hartford Basin. *Geosciences* **7**, 13.

Getty PR and Fox N (2015) An isolated *Eubrontes giganteus* trackway from the Gary Gaulin dinosaur track site (Early Jurassic, East Berlin Formation). *Northeastern Geoscience* **33**, 16–21.

Getty PR, Hardy L and Bush AM (2015) Was the *Eubrontes* track maker gregarious? Testing the herding hypothesis at Powder Hill Dinosaur Park, Middlefield, Connecticut. *Bulletin of the Peabody Museum of Natural History* **56**, 95–106.

Gèze B, Pellet J, Paloc H, Bambier A, Roux J and Senaud G (1980). *Notice explicative, carte géologique au 1/50.000 de la France, feuille de Florac (886)*. Orléans: Bureau de Recherches Géologiques et Minières, 52 pp.

Hamon Y (2004) *Morphologie, évolution latérale et signification géodynamique des discontinuités sédimentaires: exemple de la marge Ouest du Bassin du Sud-Est (France)*. Thesis, University of Montpellier II, Montpellier, France. Published thesis.

Hitchcock E (1845) An attempt to name, classify, and describe the animals that made the fossil footmarks of New England. In *Proceedings of the Sixth Annual Meeting of the American Association of Geologists and Naturalists*, New Haven, Connecticut, pp. 23–5.

Hitchcock E (1848) An attempt to discriminate and describe the animals that made the fossil footmarks of the United States, and especially of New England. *Memoirs of the American Academy of Arts and Sciences* **3**, 129–256.

Jahnert RJ and Collins LB (2012) Characteristics, distribution and morphogenesis of subtidal microbial systems in Shark Bay, Australia. *Marine Geology* **303**, 115–36.

Kendall CGStC and Warren J (1987) A review of the origin and setting of tepees and their associated fabrics. *Sedimentology* **34**, 1007–28.

Lagnaoui A, Klein H, Voigt S, Hminna A, Saber H, Schneider JW and Werneburg R (2012) Late Triassic tetrapod-dominated ichnoassemblages from the Argana Basin (Western High Atlas, Morocco). *Ichnos* **19**, 238–53.

Lange-Badré B and Lafon JP (2000) Découverte de pistes de dinosaures théropodes dans le Lias inférieur des environs de Figeac (Lot). *Comptes Rendus de l'Académie des Sciences de Paris* **330**, 379–84.

Laporte LF and Behrensmeyer AK (1980) Tracks and substrate reworking by terrestrial vertebrates in Quaternary sediments of Kenya. *Journal of Sedimentary Research* **50**, 1337–46.

Lapparent AF (de) and Montenat C (1967) Les empreintes de pas de reptiles de l'Infralias du Veillon (Vendée). *Mémoires de la Société Géologique de France* **46**, 1–43.

Larsonneur C and Lapparent AF (de) (1966) Un dinosaurien carnivore, *Halticosaurus*, dans le Rhétien d'Airel (Manche). *Bulletin de la Société Linnéenne de Normandie* **10**, 108–16.

Leonardi G (1987) *Glossary and manual of tetrapod footprint palaeoichnology.* Brasília: Publicacão do Departemento Nacional da Produção Mineral Brasil, 75 pp.

Lockley MG, Gierliński G and Lucas SG (2011) *Kayentapus* revised: notes on the type material and the importance of this theropod footprint ichnogenus. *New Mexico Museum of Natural History and Science Bulletin* **53**, 330–6.

Loope DB (2006) Dry-season tracks in dinosaur-triggered grainflows. *Palaios* **21**, 132–42.

Lucas SG, Klein H, Lockley MG, Spielmann JA, Gierliński GD, Hunt AP and Tanner LH (2006a) Triassic-Jurassic stratigraphic distribution of the theropod footprint ichnogenus *Eubrontes*. *New Mexico Museum of Natural History and Science Bulletin* **37**, 86–93.

Lucas SG, Lockley MG, Hunt AP, Milner AR and Tanner LH (2006b) Tetrapod footprint biostratigraphy of the Triassic–Jurassic transition in the American southwest. *New Mexico Museum of Natural History and Science Bulletin* **37**, 105–8.

Mallison H and Wings O (2014) Photogrammetry in paleontology – a practical guide. *Journal of Paleontological Techniques* **12**, 1–31.

Marchetti L, Belvedere M, Voigt S, Klein H, Castanera D, Díaz-Martínez I, Marty D, Xing L, Feola S, Melchor RN and Farlow JO (2019) Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. *Earth-Science Reviews* **193**, 109–45.

Marty D (2008) Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez-Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology. *Geofocus* **21**, 1–278.

Marty D, Strasser A and Meyer CA (2009) Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. *Ichnos* **16**, 127–42.

Matthews N, Noble T, Breithaupt BH, Falkingham PL, Marty D and Richter A (2016) Close-range photogrammetry for 3-D ichnology: the basics of photogrammetric ichnology. In *Dinosaur Tracks: The Next Steps* (eds PL Falkingham, D Marty and A Richter), pp. 29–55. Bloomington and Indianapolis: Indiana University Press.

Matysik M (2016) Facies types and depositional environments of a morphologically diverse carbonate platform: a case study from the Muschelkalk (Middle Triassic) of Upper Silesia, southern Poland. *Annales Societatis Geologorum Poloniae* **86**, 119–64.

Mennessier G, Collomb P, Astruc J-G, Roche J, Bambier A and Galharague J (1984) *Notice explicative, carte géologique au 1/50.000 de la France, feuille de Millau (935).* Orléans: Bureau de Recherches Géologiques et Minières, 32 pp.

Mennessier G, Collomb P, Astruc J-G, Roche J, Vautrelle C and Galharague J (1986) *Notice explicative, carte géologique au 1/50.000 de la France, feuille de Saint Beauzély (909).* Orléans: Bureau de Recherches Géologiques et Minières, 43 pp.

Milàn J (2003) *Experimental ichnology: experiments with track and undertrack formation using emu tracks in sediment of different consistencies, with comparisons to fossil dinosaur tracks.* Thesis, University of Copenhagen, Copenhagen, Denmark. Published thesis.

Milàn J and Falkingham PL (2016) Experimental and comparative ichnology. In *Dinosaur Tracks: The Next Steps* (eds PL Falkingham, D Marty and A Richter), pp. 14–27. Bloomington and Indianapolis: Indiana University Press.

Milàn J and Loope DB (2007) Preservation and erosion of theropod tracks in eolian deposits: examples from the Middle Jurassic Entrada Sandstone, Utah, U.S.A. *Journal of Geology* **115**, 375–86.

Moreau J-D (2011) *Nouvelles découvertes d'empreintes de dinosaures en Lozère. Analyse biométrique des traces et synthèse paléoenvironnementale de l'Hettangien.* Mende: Association Paléontologique des Hauts Plateaux du Languedoc, 34 pp.

Moreau J-D, Baret L, Trincal V and André D (2012a) Empreintes dinosauroïdes de l'Hettangien de Gatuzières (Lozère, France). In *Ichnologie dinosaurienne du Jurassique de Meyrueis*, pp. 5–11. Mende: Association Paléontologique des Hauts Plateaux du Languedoc.

Moreau J-D, Fara E, Néraudeau D and Gand G (2019a) New Hettangian tracks from the Causses Basin (Lozère, southern France) complement the poor fossil record of earliest Jurassic crocodylomorph in Europe. *Historical Biology* **31**, 341–552.

Moreau J-D, Gand G, Fara E and Michelin A (2012b) Biometric and morphometric approaches on Lower Hettangian dinosaur footprints from the Rodez Strait (Aveyron, France). *Comptes Rendus Palevol* **11**, 231–9.

Moreau J-D, Philippe M and Thévenard F (2019b) Early Jurassic flora from the city of Mende (Lozère): synthesis of the historical sites, new sedimentological, palaeontological and palaeoenvironmental data. *Comptes Rendus Palevol* **18**, 159–77.

Moreau J-D, Trincal V, André D, Baret L, Jacquet A and Wienin M. (2018) Underground dinosaur tracksite inside a karst of southern France: early Jurassic tridactyl traces from the Dolomitic Formation of the Malaval Cave (Lozère). *International Journal of Speleology* **47**, 29–42.

Moreau J-D, Trincal V, Gand G, Néraudeau D, Bessière G and Bourel B (2014) Two new dinosaur tracksites from the Hettangian Dolomitic Formation of Lozère, Languedoc- Roussillon, France. *Annales de Paléontologie* **100**, 361–9.

Olsen PE, Smith JH and McDonald NG (1998) Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus* and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). *Journal of Vertebrate Paleontology* **18**, 586–601.

Ostrom JH (1972) Were some dinosaurs gregarious? *Palaeogeography, Palaeoclimatology, Palaeoecology* **11**, 287–301.

Roquefort C (1934) Contribution à l'étude de l'Infra-Lias et du Lias inférieur des Causses cévenols. *Bulletin de la Société Géologique de France* **5**, 573–94.

Sciau J (1998) *Dinosaures et reptiles marins des Causses.* Millau: Association des Amis du Musée de Millau, 56 pp.

Sciau J (2003) *Dans les pas des dinosaures des Causses. Inventaire des sites à empreintes.* Millau: Association des Amis du Musée de Millau, 107 pp.

Sciau J (2019) *Quelques sites à empreintes de pas de dinosaures connus ou nouveaux.* Millau: Association Paléontologique des Causses, 57 pp.

Sciscio L, Bordy EM, Abrahams M, Knoll F and McPhee BW (2017) The first megatheropod tracks from the Lower Jurassic upper Elliot Formation, Karoo Basin, Lesotho. *PLOS ONE*, **12**, e0185941.

Smith ND, Makovicky PJ, Hammer WR and Currie PJ (2007) Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society* **151**, 377–421.

Szewczyk L, Vennin E, Moreau J-D, Gand G, Verolet M, Klee N and Fara E (2020) Tracking dinosaurs in coarse-grained sediments from the Upper Triassic of Ardèche (southeastern France). *Palaios*.

Thévenard F (1993) Les coniférales du Jurassique inférieur du gisement de Chaldecoste, bassin des Causses (Lozère, France). *Review of Palaeobotany and Palynology* **78**, 145–66.

Thulborn T. (1990) *Dinosaur Tracks*. London: Chapman & Hall, 410 pp.

Tucker M and Burchette T (1977) Triassic dinosaur footprints from south Wales: their context and preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **22**, 195–208.

Wagensommer A, Latiano M, Mocke HB and D'Orazi P (2016) Dinosaur diversity in an Early Jurassic African desert: the significance of the Etjo Sandstone ichnofauna at the Otjihaenamaparero locality (Namibia). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* **281**, 155–82.

Weems RE (2003) *Plateosaurus* foot structure suggests a single trackmaker for *Eubrontes* and *Gigandipus* footprints. In *The Great Rift Valleys of Pangea in Eastern North America* (eds PM Letourneau and PE Olsen), pp. 293–313. New York: Columbia University Press.

Weems RE (2019) Evidence for bipedal Prosauropods as the likely *Eubrontes* track-makers. *Ichnos* **26**, 187–215.

Weishampel DB, Dodson P and Osmolska H (2004) *The Dinosauria*. Berkeley: University of California Press, 862 pp.

Xing L, Bell PR, Rothschild BM, Ran H, Zhang J, Dong Z, Zhang W and Currie PJ (2013) Tooth loss and alveolar remodeling in *Sinosaurus triassicus* (Dinosauria: Theropoda) from the Lower Jurassic strata of the Lufeng Basin, China. *Chinese Science Bulletin* **58**, 1931–5.

Xing LD, Peng GZ, Ye Y, Lockley MG, McCrea RT, Currie PJ, Zhang, JP and Burns ME (2014) Large theropod trackway from the Lower Jurassic Zhenzhuchong Formation of Weiyuan County, Sichuan Province, China: review, new observations and special preservation. *Palaeoworld* **23**, 285–93.