Original article

Dinosaur footprints from the Early Jurassic of Le Mazel (Lozère, Southern France)

Empreintes de pas de dinosaures du Jurassique Inférieur du Mazel (Lozère, Sud de la France)

Jean-David Moreau[a,*], Vincent Trincal[b], Louis Baret[c], Benjamin Bourel[d], Alain Jacquet[c]

[a] *Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France*
[b] *LMDC, INSAT/UPS Génie Civil, 135 Avenue de Rangueil, 31077 Toulouse cedex 04, France*
[c] *Association Paléontologique des Hauts Plateaux du Languedoc, 14 chemin des Ecureuils, 48000 Mende, France*
[d] *Institut Méditerranéen de Biodiversité et d'Ecologie–IMBE (Aix Marseille Univ, Avignon Université, CNRS, IRD), Europôle de l'Arbois, avenue Philibert, Bât. Villemin, 13545 Aix-en-Provence, France*

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ABSTRACT

During the 20th century, the first dinosaur tracks of the Causses Basin were identified at Saint-Laurent-de-Trèves, in the Parc National des Cévennes (southern France). A recent excavation reveals a new theropod tracksite in the Hettangian deposits from Le Mazel, 2 km from the historical tracksite at Saint-Laurent-de-Trèves. The tracks are here described combining a biometric approach and 3D imaging photogrammetry. The main track-bearing surface bears 64 *in situ* tridactyl footprints preserved as concave epireliefs. Two morphotypes were identified, a *"Grallatorid"* morphotype and a "*Kayentapus"* morphotype. Footprints belonging to the first morphotype are closely similar to *Grallator lescurei*, *Grallator minusculus*, and *Grallator sauclierensis*. This study shows the difficulty to distinguish quite similar tridactyl tracks from an ichnotaxonomic point of view and highlights the importance of detailed biometric comparisons. Tracks are preserved in a brown to yellowish dolomudstone showing abundant cryptalgal laminites and mud cracks. These deposits were accrued in shallow environments such as intertidal and supratidal zones of a tidal flat.

Mots clés :
Empreintes de pas de théropodes
Jurassique Inférieur
Hettangien
Bassin des Causses
Lozère

RÉSUMÉ

Durant le XXe siècle, les premières empreintes de pas de dinosaures du Bassin des Causses furent identifiées à Saint-Laurent-de-Trèves, dans le Parc National des Cévennes (Sud de la France). Une fouille récente a révélé une nouvelle dalle à traces de théropodes dans les dépôts hettangiens du Mazel, à 2 km du site historique de Saint-Laurent-de-Trèves. Les empreintes sont ici analysées en combinant une approche biométrique avec de l'imagerie 3D par photogrammétrie. La surface principale porte 64 traces tridactyles qui sont conservées *in situ* sous forme d'épireliefs concaves. Deux morphotypes sont identifiés : « *Grallatorid* » et « *Kayentapus* ». Les empreintes de pas du premier montrent de fortes similitudes avec *Grallator lescurei*, *Grallator minusculus* et *Grallator sauclierensis*. Cette étude montre la difficulté à distinguer des traces tridactyles similaires du point de vue ichnotaxonomique et met en évidence l'importance de comparaisons biométriques détaillées. Les empreintes sont imprimées dans une dolomie brune à jaunâtre portant d'abondantes laminites cryptoalgaires et des prismes de dessiccation. Ces dépôts ont été formés dans un environnement peu profond correspondant à un platier tidal.

* Corresponding author.
E-mail address: jean.david.moreau@gmail.com (J.-D. Moreau).

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1. Introduction

Skeletal remains of Early Jurassic theropods being extremely sparse in Europe (Larsonneur and Lapparent, 1966; Carrano and Sampson, 2004; Delsate and Ezcurra, 2014; Dal Sasso et al., 2018) and throughout the world (Weishampel et al., 2004; Smith et al., 2007; Xing et al., 2013), tracksites are important tools to reconstruct dinosaurs from this time period and their palaeoecosystems. Since many Hettangian-Sinemurian archosaur trackways were discovered in the Causses Basin (southern France), the tracksites from this area became capital for the study of Early Jurassic ichnofaunas (Ellenberger, 1988; Demathieu, 1990; Demathieu and Sciau, 1992, 1999; Sciau, 1998, 2003, 2019; Demathieu et al., 2002; Gand et al., 2007; Moreau, 2011; Moreau et al., 2012a, 2014, 2018, 2019a, 2021a). Historically, the first dinosaur tracksite mentioned in the Causses Basin was that from Saint-Laurent-de-Trèves, which is located at Cans-et-Cévennes, in the Parc National des Cévennes (Monod, 1935; Fig. 1). During the first half of the 20th century, tracks from this locality were interpreted as footprints of a "*prehistoric beast*" (Monod, 1935). It was only during the second half of the 20th century that they were first analysed by the palaeontologist Louis Thaler (1930-2002) from the University of Montpellier (southern France; Thaler, 1962). The Saint-Laurent-de-Trèves tracksite contains over 30 dinosaur footprints and consists of the single tracksite from the Parc National des Cévennes which is equipped for the accessibility to the public (Moreau et al., 2019b).

A recent excavation reveals a new dinosaur tracksite at Le Mazel, 2 km from the historical trackways from Saint-Laurent-de-Trèves (Fig. 1). This new palaeontological locality yields more abundant and better preserved footprints than those from Saint-Laurent-de-Trèves. Here, we describe the tracks using morphometry and 3D imaging photogrammetry, after that the track assemblage is compared with data from other coeval tracks of the Causses Basin.

2. Geographical and geological setting

The tracksite is located south of the Massif Central (southern France), in the Lozère department, 5 km south of Florac, near the hamlet of Le Mazel (Fig. 1). The exposed deposits at Le Mazel are Hettangian in age. In Lozère, Hettangian deposits are divided into two informal formations (Brouder et al., 1977; Briand et al., 1979; Gèze et al., 1980): (1) the Detrital Sandstones-Variegated Mudstones Formation and (2) the Dolomitic Formation.

The first formation consists of rubefied lenticular and channelised sandstones that alternate with variegated argillites or marls. Based on pollen grains, this formation was dated from the Rhaetian-Hettangian to Hettangian (Grignac and Taugourdeau-Lantz, 1982). Near Florac, the Detrital Sandstones-Variegated Mudstones Formation is poorly developed (a few metres thick) or missing (Gèze et al., 1980; Fig. 1C) and is largely dominated by white or ferruginous sandstones. In the northern part of the Causses Basin, this formation yields rare fossils. They mainly consist of plant impressions (Malafosse, 1873; Saporta, 1891; Moreau and Thévenard, 2018) ascribed to bennettitaleans (*Otozamites latior* Saporta, *Weltrichia fabrei* Saporta emend. Moreau & Thévenard) as well as dinosaur tracks (Demathieu et al., 2002; Sciau, 2003; Moreau et al., 2012b).

The Dolomitic Formation consists of brown to yellowish dolomite organised in thin or massive layers, as well as dolomitic laminites alternating with green and black argillites or marls that are locally lignitic (Gèze et al., 1980). The tracksite of Le Mazel is stratigraphically located in this formation (Fig. 1C). Based on rare ammonites (e.g. *Psiloceras planorbis* Sowerby), the lowermost part of the Dolomitic Formation was dated as Hettangian (Brouder et al., 1977). In the area of Florac, the formation is 80 to 100 metres thick. Locally, in Lozère, the Dolomitic Formation shows plant-bearing beds yielding conifers (*Brachyphyllum paparelii* Saporta and *Pagiophyllum peregrinum* (Lindley & Hutton) A. Schenk emend. Kendall), pteridosperms (*Thinnfeldia rhomboidalis* Ettingsh) Cycadales (*Ctenopteris* Brongn. ex Saporta), Filicales (*Clathropteris platyphylla* Brongn.) and Ginkgoales (*Eretmophyllum caussenense* Thévenard; Saporta, 1873, 1884; Ressouche, 1910; Roquefort, 1934; Thévenard, 1992, 1993; Moreau et al., 2019c, 2021b) as well as archosaur tracks including dinosaur and crocodylomorph trackways (Demathieu, 1990; Sciau, 2003; Demathieu et al., 2002; Moreau, 2011; Moreau et al., 2012a, 2014, 2018, 2019a).

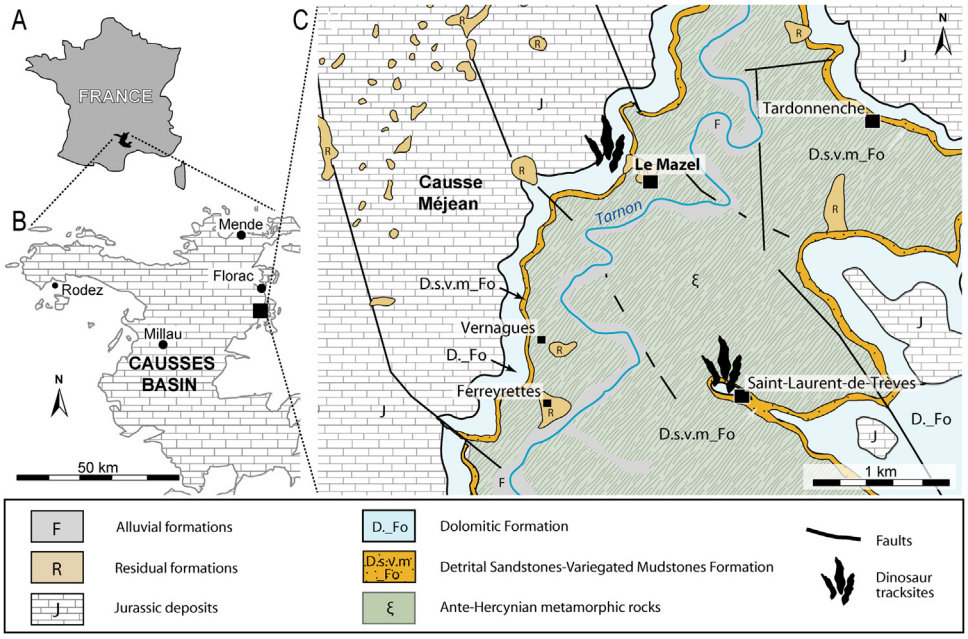


Fig. 1. A, Location of the Causses Basin in France. B, Causses Basin and location of the study area (black square). C, Simplified geological map of the study area and location of Le Mazel tracksite.



Fig. 2. Illustrations of Le Mazel tracksite. A, Southern part of the tracksite during the excavation. B, Northern part of the tracksite after excavation. C, Southern part of the tracksite after excavation. D, Track-bearing surface (by night) showing deep footprints and mud cracks.

3. Material & methods

The tracksite of Le Mazel was fortuitously discovered by Roger Almies during the 1960s. At that time, he extracted some large blocks of rock for the construction of a fireplace lintel in the small hamlet of Le Mazel. During many decades the location of the tracksites was only known of some residents of the hamlet and a few regional naturalists. In 2012, two of us (JDM and LB) made the first observations after Daniel André and Raymond Lefillatre indicated to us the tracksite location. Only 12 dinosaur tracks were visible on a small outcrop a few metres wide. In July 2018, the Association Paléontologique des Hauts Plateaux du Languedoc (A.P.H.P.L.) organised an excavation (Fig. 2A). Thanks to this excavation, an area of up to 4.5 m wide and up to 22 m long was cleaned, representing a surface of 50 m^2 (Figs. B–C, 3). The main track-bearing surface bears 64 *in situ* tridactyl footprints preserved as concave epireliefs (Fig. 3).

The descriptive terminology and biometric parameters are taken from Leonardi (1987), Dematheiu (1990), Dematheiu 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* Dematheiu et al. (2002; Fig. 4). In the section "Palaeoichnology" below, these morphometric parameters are described by giving three values; the minimum, the average (in brackets) and the maximum. The biometric values of the tracks from Le Mazel were compared with a large dataset including measurements of 427 tridactyl tracks from the Early Jurassic of the Causses Basin (based on data from Dematheiu et al., 2002 and Moreau et al., 2012a, 2014, 2018, 2021a). 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 (e.g. 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 (DEM) in false colours.

Rock samples were taken from several levels (Fig. 5; Table 1) in order to perform mineralogical analyzes. Thin sections were

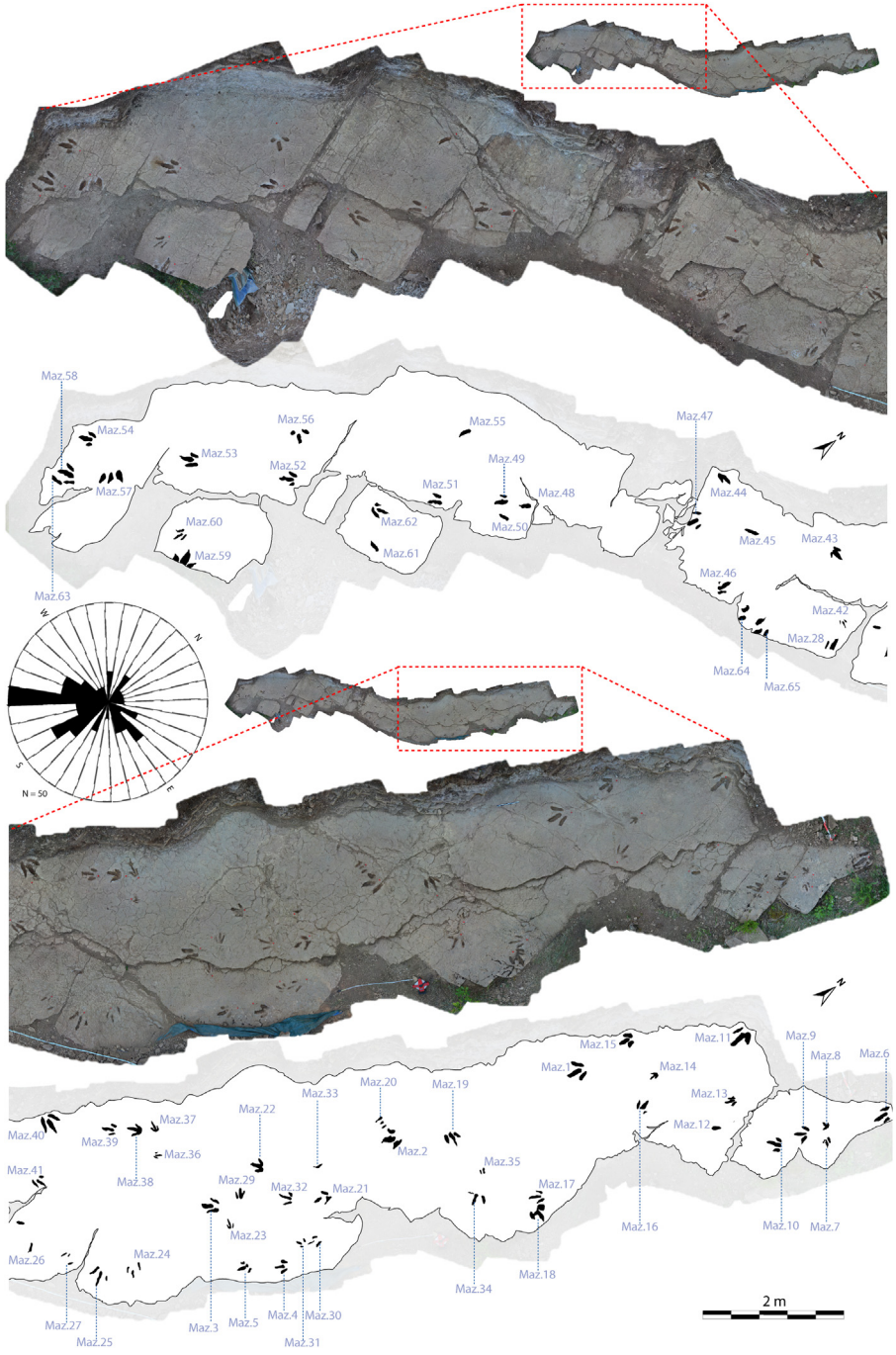


Fig. 3. Le Mazel tracksite and location of footprints. Photographs and interpretative sketches of both southern (top of the figure) and northern (bottom of the figure) parts.

made for the microscopic observations, powdered for the XRD analyzes. Samples were crushed manually in an agate mortar until a powder with particles < 80 μm (sieve control) was obtained. The diffractometer was a Bruker D8 Advance using a copper X-ray tube, equipped with a vertical theta/theta goniometer and a LynxEye XE-TTM high-speed linear detector. A motorised anti-scattering knife was used. The acquisition of the diffractograms was carried out at 40 kV and 40 mA, from 7° to 70° 2θ with an interval of 0.02° 2θ and a total acquisition time of 2h30 per sample. Minerals were identified using the Bruker-AXS DIFFRACplus Eva v4 software and the 2015 ICDD PDF database. Mineralogical quantification was performed by Rietveld calculation with DIFFRACplus Topas v5 following rules described in Trincal et al. (2014).

4. Results

4.1. Sedimentology and track preservation

The excavation conducted in 2018 exposed a 1.7 m high outcrop (Fig. 5). The lithology is quite constant along the stratigraphic section. Exposed beds mainly consist of homogenous centimetre- to decimetre-thick layers of brown to yellowish dolomudstone (94.5 to 98.9 wt% of dolomite and 0.2 to 4.9 wt% of calcite; Fig. 6A, Table 1). It mainly shows a non-porous fabric, however, dolomudstone is sometimes bioturbated (possible root casts; Fig. 6B). Microbial laminites are locally observed (cryptalgal laminites; between 0.4 and 0.7 m; Fig. 5). They are millimetre-thick, parallel to the bedding

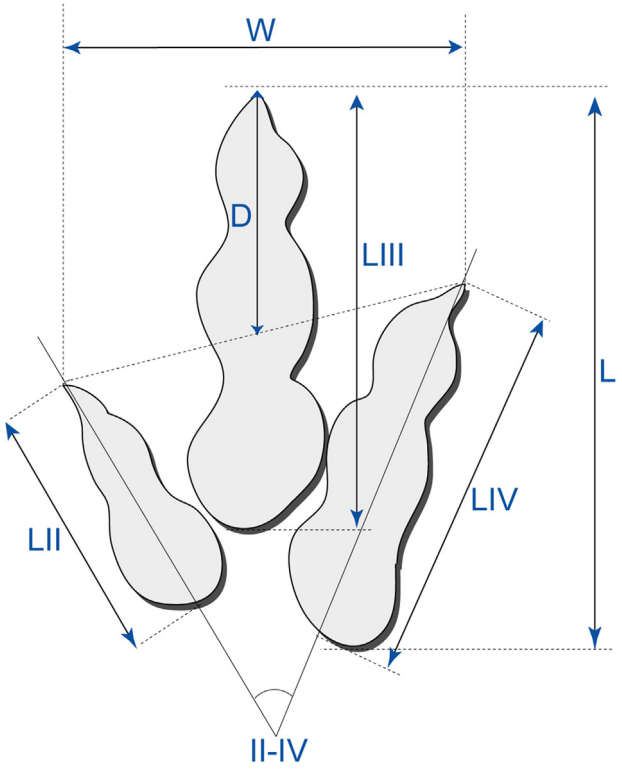


Fig. 4. Morphometric measurements taken on tridactyl tracks. L, length; W, width; D, length of the free part of digit III; LII, LIII and LIV, digit lengths; T, angle between the two external digits.

planes, wavy to planar and show alternating micrite and sparite layers. Mud cracks are abundant (between 0.7 m and 1.1 m; Fig. 6C), whereas ripple marks are less common (only observed at 1.05 m; Fig. 6D).

At the Mazel, five stratigraphic surfaces (S1 to S5) bear dinosaur footprints (Fig. 5). The *in-situ* footprints exposed on the large track-bearing surface (Fig. 3) are stratigraphically located in S1 to S4. The surface S5 yielded a single track that was extracted during the excavation. Tracks from S1 are covered by a 0 to 2 cm thick lens of dolomite bearing S2. Tracks from S2 are covered by a 0 to 5 cm thick lens of dolomite bearing S3. S3 is overlapped by another 0 to 5 cm thick lens of dolomite bearing S4. The lateral extension of the surfaces S2 and S4 is limited to the northern part of the outcrop. Surfaces S3 and S4 are directly covered by a 1-centimeter-thick layer of clayey dolomite (80.8 wt% of dolomite and almost 14 wt% of phyllosilicates, sample Maz.S6 in Table 1). Since tracks deform a single bed and are not propagated into the underlying layer, they are all interpreted as true tracks. Some of the tracks are exquisitely preserved showing details of pads and claws.

4.2. Palaeoichnology

Among the complete traces, two morphotypes were distinguished: a *"Grallatorid"* morphotype and a *"Kayentapus"* morphotype. Due to the partial preservation of many footprints, only 33 of the 64 tracks can be confidently assigned to a morphotype.

***"Grallatorid"* morphotype.** The first morphotype is represented by 26 tridactyl II–IV footprints. A single short trackway composed of four footprints is identified

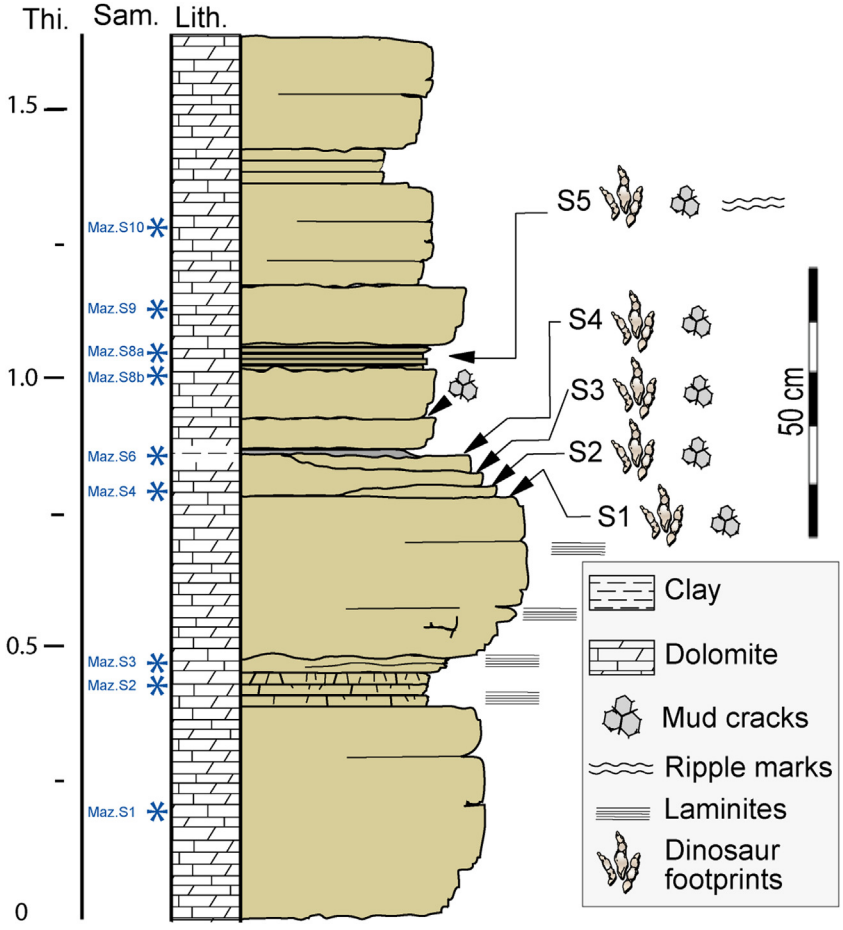


Fig. 5. Stratigraphic section of Le Mazel tracksite and location of the track-bearing surfaces. "Thi." = thickness (in metres); "Sam." = rock samples; "Lith." = lithology.

Table 1
Mineralogical composition of Le Mazel samples obtained by XRD analyses (in weight %). Accuracy of the measurement is estimated by multiplying the goodness of fit (GOF) by the standard deviation given by Rietveld software.

Samples	Calcite	Dolomite	Quartz	Rutile	Illite + Mica	Kaolinite	Rwp	GOF
Maz.S1	4.9 ± 0.4	94.5 ± 0.5	0.6 ± 0.2	0.0 ± 0.2	–	–	8.96	5.89
Maz.S2	0.3 ± 0.2	98.1 ± 0.4	1.6 ± 0.2	0.1 ± 0.2	–	–	8.84	5.74
Maz.S3	1.3 ± 0.3	97.9 ± 0.3	0.8 ± 0.2	0.0 ± 0.1	–	–	8.04	5.30
Maz.S4	0.2 ± 0.2	98.9 ± 0.3	0.8 ± 0.2	0.1 ± 0.2	–	–	8.03	5.33
Maz.S6	0.5 ± 0.3	80.8 ± 0.3	4.6 ± 0.4	0.4 ± 0.3	12.3 ± 4.4	1.5 ± 0.7	8.30	5.56
Maz.S8a	0.9 ± 0.3	97.4 ± 0.5	1.5 ± 0.2	0.2 ± 0.3	–	–	8.98	5.92
Maz.S8b	1.1 ± 0.3	97.7 ± 0.5	1.1 ± 0.2	0.2 ± 0.2	–	–	8.94	5.87
Maz.S9	1.3 ± 0.3	97.2 ± 0.4	1.5 ± 0.2	0.0 ± 0.1	–	–	9.05	5.98
Maz.S10	0.7 ± 0.3	98.5 ± 0.4	0.7 ± 0.2	0.1 ± 0.2	–	–	8.79	5.74

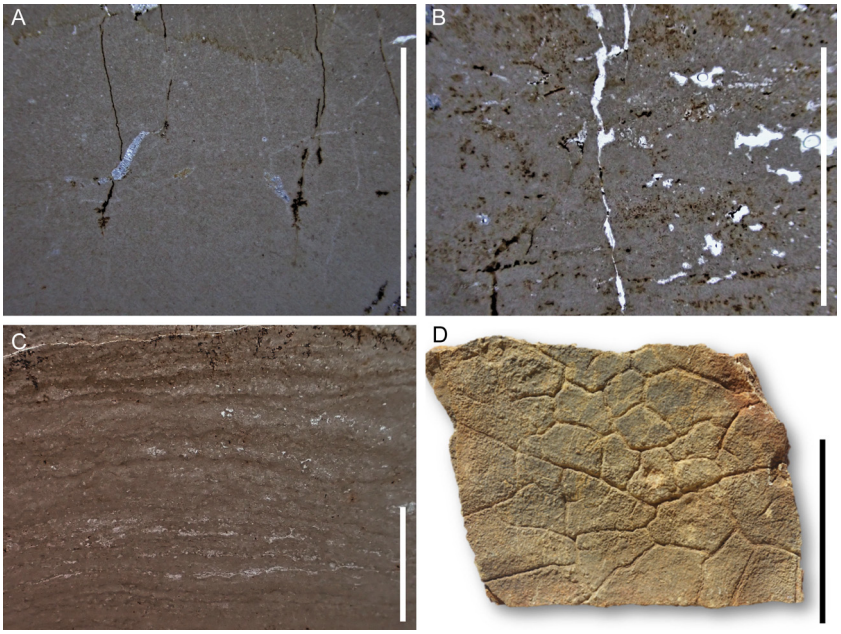


Fig. 6. Microfacies and sedimentary structures. A, Dolomudstone. B, Dolomudstone with porous fabric. C, Cryptalgal laminites. D, Mud cracks. Scale bars: A–C = 5 mm, D = 10 cm.

(Maz-51–Maz-54); Fig. 7). Pace length is 135–136 cm, and the stride is 271 cm long. Pes tracks are aligned with the trackway midline (Fig. 7). Tracks are small- to medium-sized and mainly longer than wide (L/W = 0.9–(1.2)–1.5), 10.0–(21.1)–29.0 cm long and 10.5–(17.2)–27 cm wide (Fig. 8, Table 2). The angle between II and IV is quite small (T = 29.0–(41.3)–52.0°). Digit imprints are well individualised and elongated. Impressions of digits III and II are the longest and the shortest, respectively. The free part of III is quite long (L/D = 1.8–(2.1)–2.8). The position of the digito-metatarsal pad of digit IV is more proximal than for digit II. On some tracks, marks of pads are well preserved and are circular to oval. There is no plantar impression.

***"Kayentapus"* morphotype.** The second morphotype consists of 7 footprints. One partial trackway composed of two consecutive tridactyl II–IV tracks (MAZ-1–MAZ-2; Fig. 3) displays a 260 cm pace length. Footprints are as long as wide (L/W = 1.0–(1.0)–1.1), 19.0–(22.9)–28.5 cm long and 18.0–(22.2)–29.5 cm wide (Fig. 8, Table 2). The angle between II and IV is large (T = 44.0–(60.7)–76.0°; Table 2). Digit imprints are moderately elongated and well-individualised. In some tracks, the traces of digits II and IV are quite similar in length. The free part of III is quite long (L/D = 2.0–(2.2)–2.5). The imprints of pads are absent or poorly marked but impression of claws are well-marked.

5. Discussion

5.1. Comparison with tridactyl tracks from the Causses Basin

Six ichnospecies of tridactyl footprints were described from the Lower Jurassic formations of the Causses Basin (Dematheiu, 1990; Dematheiu and Sciau, 1992; Dematheiu et al., 2002): *Dilophosauripus williamsi* Welles, *Eubrontes giganteus* Hitchcock, *Grallator variabilis* Lapparent & Montenat, *Grallator lescurei* Dematheiu, *Grallator minusculus* Hitchcock, and *Grallator sauclierensis* Dematheiu & Sciau. *D. williamsi* was established based on tracks from the Lower Jurassic of United States of America (Welles, 1971). The validity of this ichnotaxon has been strongly debated (Lucas et al., 2006; Lockley et al., 2011). Some authors consider *Dilophosauripus* Welles as a junior synonym of *Eubrontes* (see references in Lucas et al., 2006; Lockley et al., 2011). *D. williamsi* was broadly used to describe tracks from the Causses Basin (e.g. Dematheiu and Sciau, 1992; Sciau, 1992, 2003; Dematheiu, 1993; Dematheiu et al., 2002; Gand et al., 2007; Moreau et al., 2014). However, recent morphometrical comparisons made by Gand et al. (2018) suggested that *Dilophosauripus* is a synonym of *Kayentapus* Welles.

Based on the parameters L, T, L/W and (L-D)/D, Fig. 9 shows bivariate diagrams for the diverse ichnospecies from the Lower

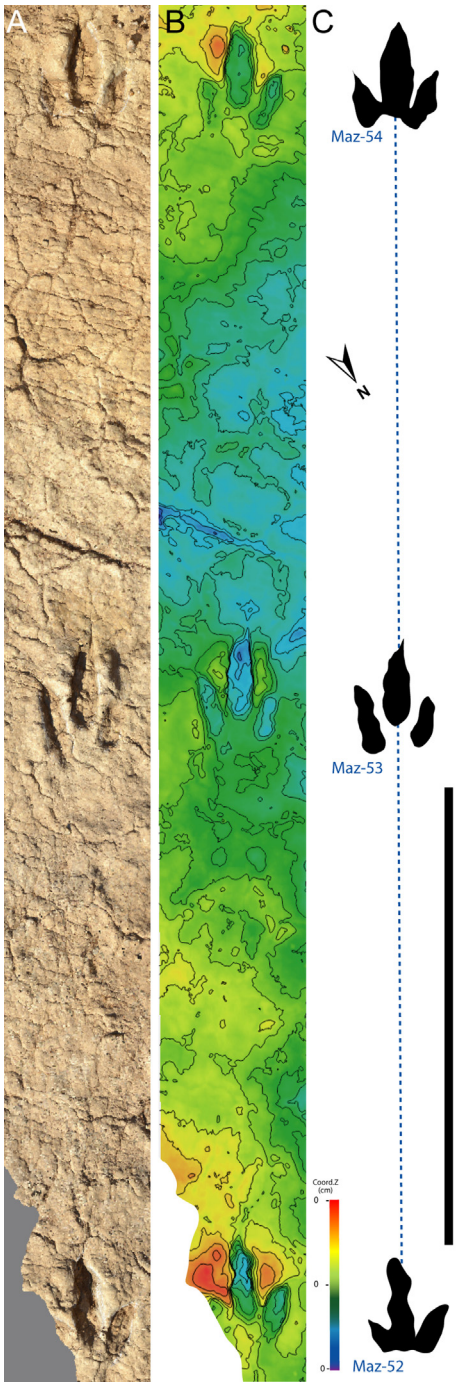


Fig. 7. *"Grallatorid"* morphotype trackway (Maz-52–Maz-54). A, 3D-photogrammetric mesh with texture. B, DEM in false-colour depth map. C, Interpretative sketch. Scale bar = 1 m.

Jurassic of the Causses Basin. The two morphotypes from Le Mazel are clearly smaller than the large tracks *E. giganteus* (L > 30 cm in the diagnosis of Olsen et al., 1998). The *"Grallatorid"* morphotype from Le Mazel shows a broad range of length values (L = 10.0–(21.1)–29.0) and shares similarities with several *Grallator* Hitchcock ichnospecies from the Lower Jurassic of the Causses Basin. Some tracks of the *"Grallatorid"* morphotype (Maz-7, Maz-8, Maz-14, Maz-23, Maz-36 and Maz-42; Table 2) fall in the range size of *G. variabilis* (L = 9.0–(11.3)–14.7; Demathieu et al., 2002). However, they mainly differ from this ichnospecies by a shorter free part of digit III ((L-D)/D of *G. variabilis* = 0.9–(1.3)–1.9; Demathieu et al., 2002). Some of the tracks (e.g. Maz-23; Fig. 8A) are similar to *G. sauclierensis*, which mainly differs from *G. variabilis* by smaller L/W values (L/W = 1.3 and 1.5 in average, respectively) and higher II–IV values (51.1° and 39.4° in average, respectively). *G. sauclierensis* was erected by Demathieu and Sciau (1992) based on tracks from the Sauclières quarry in Aveyron (Causses Basin, southern France). Most of the largest tracks of the *"Grallatorid"* morphotype from Le Mazel (e.g. Maz-62; Table 2) clearly fall in the morphometric space of *G. lescurei*, which was erected by Demathieu (1990) based on tracks from Saint-Léons in Aveyron (Causses Basin, southern France). The large size (L = 28 cm) and the small II–IV value (II–IV = 30°) of Maz-53 suggest similarities with of *G. minusculus* (Fig. 8C, Table 2). So, the *"Grallatorid"* morphotype from Le Mazel is

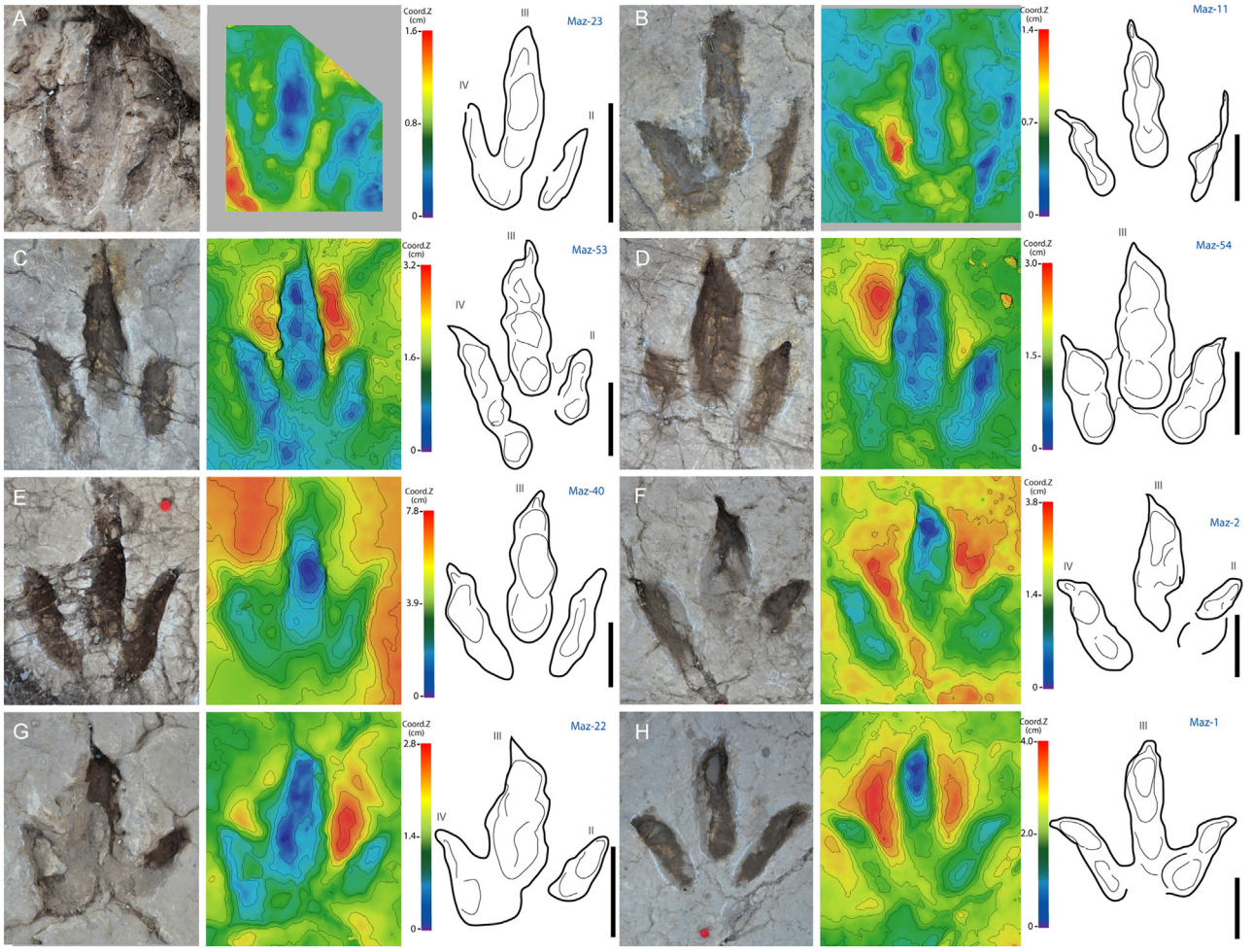


Fig. 8. Tridactyl footprints from Le Mazel tracksite; photographs, DEM in false-colour depth map and interpretative sketch for each track (from left to right). A–E, *"Grallatorid"* morphotype. F–H, *"Kayentapus"* morphotype. All scale bars = 10 cm.

closely similar to *Grallator lescurei*, *Grallator minusculus*, and *Grallator sauclierensis*.

The *"Kayentapus"* morphotype from Le Mazel shares strong similarities with *Kayentapus* tracks previously described in the Causses Basin (= *Dilophosauripus* in Demathieu et al., 2002): medium sized (L = 19.0–(22.9)–28.5 and 17.5–(21.5)–27.9, respectively) and as long as wide (L/W = 1.0–(1.0)–1.1 and 0.8–(1.0)–1.3, respectively) tracks with high values of the angle II–IV (II–IV = 44.0–(60.7)–76.0° and 35–(68)–98°, respectively). The morphometric spaces of *Kayentapus* and *G. lescurei* from the Causses Basin are partially overlapping (Fig. 9). However, *G. lescurei* differs from *Kayentapus* by tracks that are as longer than wide (L/W = 1.0–(1.3)–1.9 and 0.8–(1.0)–1.3, respectively) and having lower II–IV values (II–IV = 30–(49.8)–80° and 35–(68)–98°, respectively).

5.2. Depositional environment and trackmakers

The abundance of vertebrate tracks and mud cracks co-occurring with ripple marks shows that the depositional environment was regularly flooded then emerged. Cryptalgal laminites are characteristic of shallow environments such as intertidal and supratidal zones of a tidal flat (Matysik, 2016). At Mende (30 km North from Le Mazel; Fig. 1B) and Marvejols (50 km North-West from Le Mazel), halite pseudomorphs were reported, attesting to evaporitic conditions (Moreau, 2011; Moreau et al., 2019b). Such restricted life conditions could explain the absence of invertebrate remains at Le Mazel and their extreme rarity in the Dolomitic Formation.

Based on the osteological architecture deduced from the morphology of the tracks, many authors consider trackmakers of *Grallator* and *Kayentapus* as theropod dinosaurs (Baird, 1957; Olsen et al., 1998; Demathieu et al., 2002; Gand et al., 2018). Using the formula of Alexander (1976) and Thulborn (1990), the hip height of the trackmakers of the *"Grallatorid"* morphotype from Le Mazel varies from 1.2 to 1.4 m. Their speed varies from 5.9 to 6.7 km/h, suggesting a walking gait (based on the trackway Maz-51–Maz-54). Although more than 60 theropod tracksites were reported from the Hettangian–Sinemurian sediments of the Causses Basin, body remains of theropods are unknown in the Lower Jurassic from this area. In France, only the Hettangian Moon-Airel Formation from Normandie (northwestern France) yielded theropod body remains. They were ascribed to Coelophysoidea, *Lophostropheus airelensis* Cuny & Galton (Larsonneur and Lapparent, 1966; Cuny and Galton, 1993; Ezcurra and Cuny, 2007). Near Marjevols, Moreau et al. (2019a) reported an ichnoassemblage with the co-occurrence of *Batrachopus* Hitchcock and *Grallator* attesting the presence of terrestrial crocodylomorphs in littoral ecosystems during the Hettangian.

Based on more than 60 tracksites, the ichnological record of the Dolomitic Formation suggests that the lowermost Jurassic dinosaur communities from the Causses Basin were mainly composed of theropods. They probably crossed the tidal flats in order to hunt along the coastline. Moreover, the tidal flats of the Causses Basin

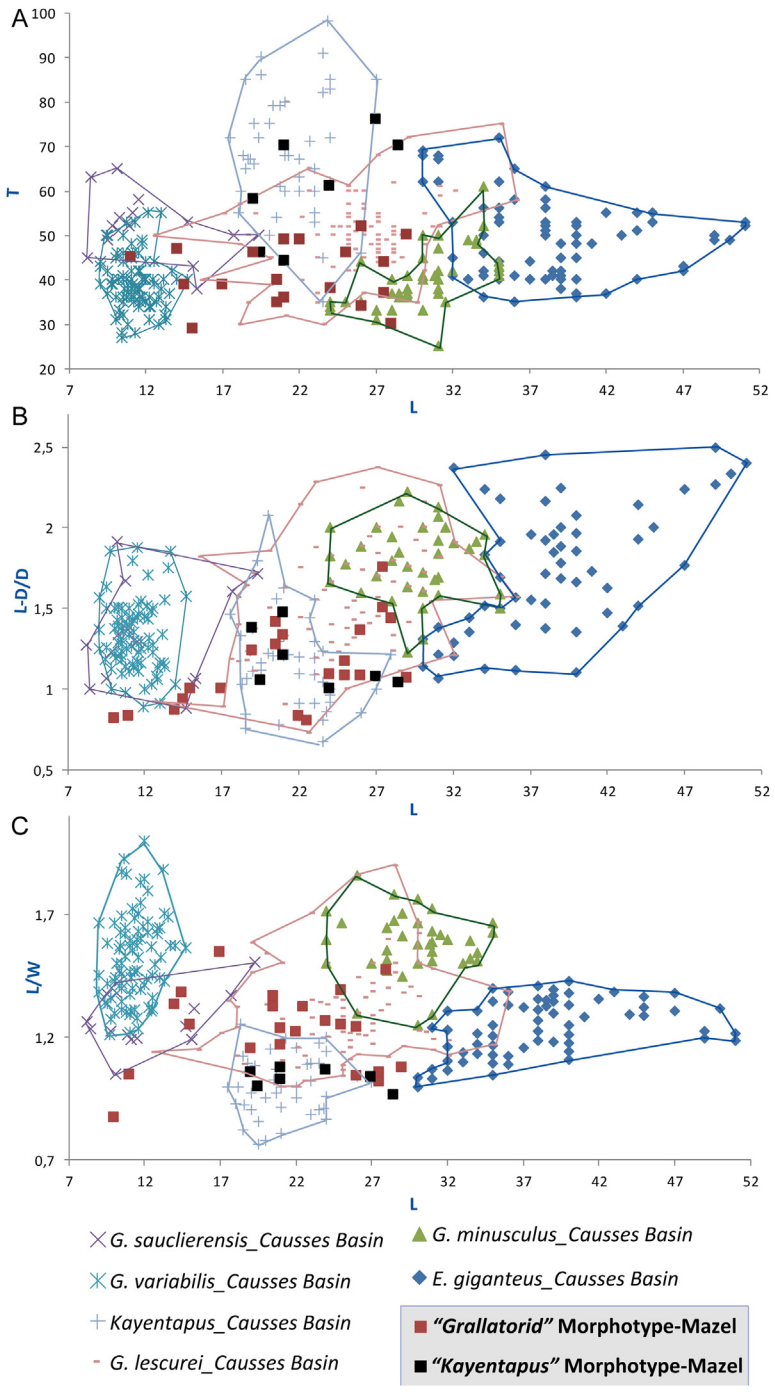


Fig. 9. Footprints from Le Mazel tracksite compared to tridactyl tracks from the Early Jurassic of the Causses Basin (based on data from Demathieu et al., 2002; Moreau et al., 2012a, 2014, 2018, 2021a). A, Bivariate diagram L vs T. B, Bivariate diagram L vs. (L−D)/D. C, Bivariate diagram L vs L/W (C). L in metres and T in degrees.

probably corresponded to a way of migration that theropods used to join innermost environments from the Massif Central where they could found nesting and hunting areas.

Wood, pollen and foliar remains collected in the lignitic layers of the Dolomitic formation (Barale, 1981; Thévenard, 1993; Moreau et al., 2019c, 2021b) suggest that the Hettangian tidal flats were bordered by littoral forests. Although cycadales, ginkgoales and pteridosperms are present in Hettangian plant assemblage from the Causses Basin, the cuticle remains as well as the pollen strongly suggest that the flora was dominated by conifers (mainly Cheirolepidiaceae; Thévenard, 1993; Moreau et al., 2021b). Barale et al. (1981) and Thévenard (1992) estimated that the conifers constituted nearly 98% of cuticles remains. Palaeoecophysiological analyses of cuticles demonstrated that the conifers (*Brachyphyllum* Brongn., *Pagiophyllum* Heer emend Harris) from the Dolomitic Formation display xerophytic characters (fleshy shoots, adapted leaf morphology, thick cuticle, and sunken stomata apparatuses limiting the water-loss) which are typical of plants adapted to withstand coastal environments under a tropical climate with contrasted seasons, cyclically dry then humid (Thévenard, 1993; Moreau et al., 2021b).

Table 2
Values measured on Hettangian tridactyl tracks from Le Mazel. 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 N°	L	W	D	LII	LII	LIV	II-IV	L/W	L/D	(L-D)/D	Morphotypes
Maz-1	28.5	29.5	14	16.5	21.5	17	70	1.0	2.0	1.0	"*Kayentapus*" Morphotype
Maz-2	27	26	13	8	21	17.5	76	1.0	2.1	1.1	"*Kayentapus*" Morphotype
Maz-15	21	20.5	9.5	10	15.5	13	70	1.0	2.2	1.2	"*Kayentapus*" Morphotype
Maz-16	19.5	19.5	9.5	9	15.5	13.5	46	1.0	2.1	1.1	"*Kayentapus*" Morphotype
Maz-22	19	18	8	9	13.5	11	58	1.1	2.4	1.4	"*Kayentapus*" Morphotype
Maz-21	24	22.5	12	12.5	–	16	61	1.1	2.0	1.0	"*Kayentapus*" Morphotype
Maz-4	21	19.5	8.5	11.5	13.5	12.5	44	1.1	2.5	1.5	"*Kayentapus*" Morphotype
Maz-5	21	17	9.5	–	–	–	49	1.2	2.2	1.2	"*Grallatorid*" Morphotype
Maz-7	14	10.5	7.5	5	12	8.5	47	1.3	1.9	0.9	"*Grallatorid*" Morphotype
Maz-8	10	11.5	5.5	–	–	–	–	0.9	1.8	0.8	"*Grallatorid*" Morphotype
Maz-10	25	18	12	–	19	12		1.4	2.1	1.1	"*Grallatorid*" Morphotype
Maz-11	27.5	27	11	16	21.5	17	44	1.0	2.5	1.5	"*Grallatorid*" Morphotype
Maz-14	14	10.5	–	–	–	–	–	1.3	–	–	"*Grallatorid*" Morphotype
Maz-17	22	18	12	12	18	11	49	1.2	1.8	0.8	"*Grallatorid*" Morphotype
Maz-23	14.5	10.5	7.5	6.5	11	9.5	39	1.4	1.9	0.9	"*Grallatorid*" Morphotype
Maz-25	26	25	12.5	–	22	15	34	1.0	2.1	1.1	"*Grallatorid*" Morphotype
Maz-30	20.5	15	9	–	–	10.5	40	1.4	2.3	1.3	"*Grallatorid*" Morphotype
Maz-36	11	10.5	6	3.5	10.5	6.5	45	1.0	1.8	0.8	"*Grallatorid*" Morphotype
Maz-37	17	11	8.5	7	14	9	39	1.5	2.0	1.0	"*Grallatorid*" Morphotype
Maz-38	21	18	9	–	14	–	36	1.2	2.3	1.3	"*Grallatorid*" Morphotype
Maz-39	19	16.5	8.5	8.5	14	9	46	1.2	2.2	1.2	"*Grallatorid*" Morphotype
Maz-40	29	27	14	20	25	23	50	1.1	2.1	1.1	"*Grallatorid*" Morphotype
Maz-42	15	12	7.5	7	12	8.5	29	1.3	2.0	1.0	"*Grallatorid*" Morphotype
Maz-43	22.5	17	12.5	–	19.5	–		1.3	1.8	0.8	"*Grallatorid*" Morphotype
Maz-46	24	19	11.5	–	–	12.5	38	1.3	2.1	1.1	"*Grallatorid*" Morphotype
Maz-50	–	–	–	–	–	–	–	–	–	–	"*Grallatorid*" Morphotype
Maz-51	–	–	–	–	–	–	–	–	–	–	"*Grallatorid*" Morphotype
Maz-52	26	–	–	–	26	16	–	–	–	–	"*Grallatorid*" Morphotype
Maz-53	28	19	11.5	12	21	18.5	30	1.5	2.4	1.4	"*Grallatorid*" Morphotype
Maz-54	25	20	11.5	13	20	14	46	1.3	2.2	1.2	"*Grallatorid*" Morphotype
Maz-58	27.5	26	10	14.5	23.5	18	37	1.1	2.8	1.8	"*Grallatorid*" Morphotype
Maz-60	20.5	15.5	8.5	11.5	–	12.5	35	1.3	–	1.4	"*Grallatorid*" Morphotype
Maz-62	26	21	11	11.5	19	16	52	1.2	2.4	1.4	"*Grallatorid*" Morphotype

Disclosure of interest

The authors declare that they have no competing interest.

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