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Palaeoenvironmental reconstruction and early Permian ichnoassemblage from the NE Iberian Peninsula (Pyrenean Basin)

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Abstract – Recent finds of tetrapod ichnites in the red-bed and volcaniclastic succession of the Iberian Pyrenean Basin permits an assessment of the faunal diversity and palaeoenvironment of a late early Permian setting. The tetrapod ichnoassemblage is inferred with the aid of photogrammetry and constituted by *Batrachichnus salamandroides*, *Limnopus* isp., cf. *Amphisauropus* (these three ichnotaxa present associated swimming traces, assigned to *Characichnos*), cf. *Ichniotherium*, *Dromopus* isp., cf. *Varanopus*, *Hyloidichnus* isp. and *Dimetropus leisnerianus*. These ichnotaxa suggest the presence of temnospondyls, seymouriamorphs, diadectomorphs, araeoscelids, captorhinids and synapsid pelycosaurs as potential trackmakers. These faunas correlate to the late early Permian. Two ichnoassociations correspond to two different palaeoenvironments that were permanently or occasionally aquatic (meandering fluvial systems and unconfined runoff surfaces, respectively). Ichnotaxa in the fluvial system is more diverse and abundant than in the runoff surfaces system. The Iberian Pyrenean ichnoassemblage reveals the faunistic connection and similarities among nearing basins (Spain, southern France and Morocco) differing from the Central European basins (i.e. German Tambach Formation). Based on the palaeogeography and the climate models of the early Permian, we suggest the correlation of ichnofaunal composition with different palaeoclimate biomes. This results in a diffuse boundary of Gondwana–Laurasia land masses, indicating no geographic barriers but a possible climate control on the faunal distribution. Further studies, integrating data from distant tracksites, should refine these biome boundaries.

Keywords: late Palaeozoic, Pyrenees, tetrapod ichnology, Central Pangaea, photogrammetry.

1. Introduction

The Permian continental record of the Iberian Pyrenees represents a well-known red-bed and volcaniclastic succession (e.g. Mey *et al.* 1968; Martí, 1983, 1996; Gisbert, 1986; Gascón & Gisbert, 1987; Galé, 2005). However, vertebrate footprints are restricted to the late Cisuralian Peranera Formation tracksites studied here (see also Voigt & Haubold, 2015) and the younger Palanca de Noves locality (Ribera d'Urgellet, Alt Urgell, Catalonia; Robles & Llompart, 1987; Fortuny *et al.* 2010, 2011), presumably of middle Permian age or younger. In the rest of the Iberian Peninsula and in the Balearic islands, two additional Permian fossil sites are known: Peña Sagra in the Cantabrian Mountains (Gand *et al.* 1997; Demathieu *et al.* 2008) and Cala Pilar in Menorca island (Pretus & Obrador, 1987). The location of the Pyrenean Basin at the Gondwana–Laurasia boundary is critical to better understand the faunal distribution across Pangaea during Permian time. The scarcity of tetrapod body fossils can be compensated with the presence of tetrapod footprints, by far more abundant during late Palaeozoic time and reliable faunistic indicators at the family level (Falcon-Lang *et al.* 2010). The potential use of trace fossils as environmental indicators is explored here for a better understanding of the faunistic response to the low-latitude aridization processes occurring during latest Carboniferous – late Permian times (Chumakov & Zharkov, 2002; Gibbs *et al.* 2002; Roscher & Schneider, 2006; Benton & Newell, 2014; Michel *et al.* 2015). Voigt & Haubold (2015) recently published material from the Peranera Formation in the Vall de Manyanet area (Pallars Jussà, Catalonia), mainly focusing on ichnotaxonomy and tetrapod footprint biostratigraphy. Our field prospections in this formation largely improve the Pyrenean ichnological record, allowing a reliable palaeoenvironmental reconstruction based on the integration of ichnology and facies analyses.

The aim of the present work is to expand on and provide new insights on the Pyrenean ichnotaxa, particularly on the Peranera Formation. The new findings reveal a noteworthy tetrapod diversity and distribution during early Permian time and allow the palaeoenvironmental settings in Central Pangaea to be reconstructed. Our aim is to compare our findings with other

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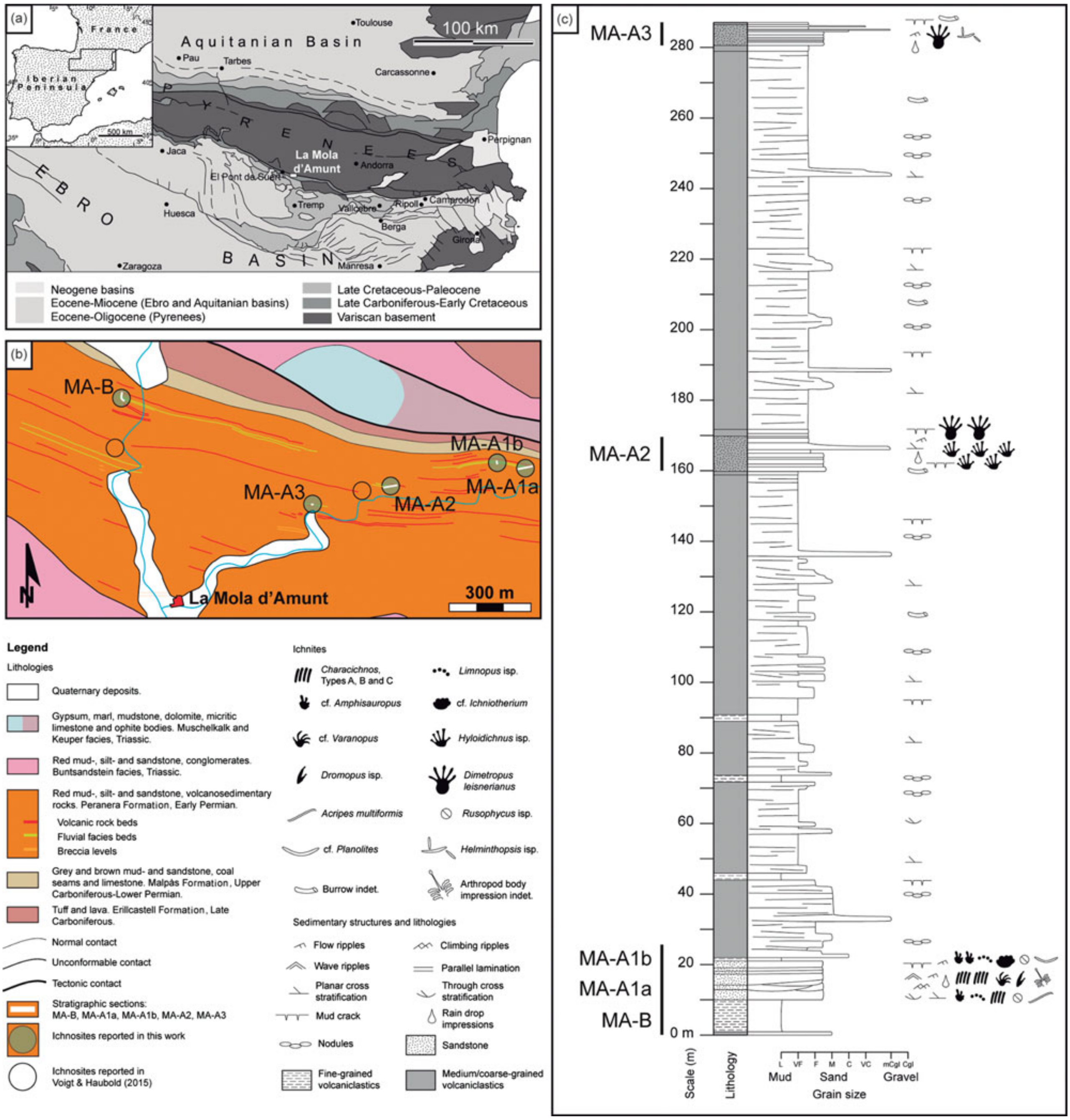

Figure 1. (Colour online) Geographical and geological setting. (a) European situation and regional geology. (b) Geological map of the studied area based on field observations, maps from Zwart (1979) and orthophoto (scale 1:5000) obtained from Institut Cartogràfic de Catalunya webpage (ICC; http://www.icc.cat). (c) Synthetic stratigraphic section (at 114 m from the base of the Peranera Formation) including sequences of tetrapod footprints. Note the differences between different ichnoassociations.

nearby ichnoassociations, to evaluate their uniformity and distribution. Photogrammetry has recently been revealed as a powerful tool in palaeoichnology, mostly applied in order to study large dinosaur footprints in detail (e.g. Petti *et al.* 2008; Castanera *et al.* 2013) and other associated tetrapod footprints (Belvedere *et al.* 2013). Our study is the first to apply photogrammetry to Permian tetrapod ichnites in order to assist in an enhanced morphological characterization and to minimize the effects of substrate conditions and the behaviour of the trackmakers, allowing reliable taxonomic attributions.

2. Material and methods

2.a. Fieldwork

The present work was developed in two outcrops situated north of Les Esglésies and La Mola d'Amunt towns, on the roads to Benés and Avellanos villages respectively, on Vall de Manyanet at Pallars Jussà region (south-central Pyrenees, Catalonia, Iberian Peninsula; Fig. 1a, b). In this work, we use lithostratigraphy (Fig. 1b) by Mey *et al.* (1968), Nagtegaal (1969), Zwart (1979) and Martí (1983), although other nomenclatures at the Pyrenean scale exist (e.g. depositional units of

Gascón & Gisbert, 1987; Galé, 2005). Further studies are needed for a detailed global correlation of the depositional units, so the lithostratigraphic divisions are used here instead. The studied outcrops correspond to a sequence at 114 m from the base of the Peranera Formation in the El Pont de Suert-Sort Permian Basin (Zwart, 1979; Martí, 1983), and the localities with trace fossils are referred to as La Mola d'Amunt-Avellanos (MA-A) and La Mola d'Amunt-Benés (MA-B).

Five stratigraphic sections were measured: one at MA-B (Section MA-B) and four at MA-A (from east to west and from the stratigraphically lower to higher: MA-A1a, MA-A1b, MA-A2 and MA-A3; Fig. 1b, c; see also supplementary Appendix S1, Fig. S1, available at http://journals.cambridge.org/geo). These five sections include all the footprints described here and have been used to characterize the palaeoenvironmental setting and succession. The field tracking of strata (assisted with photointerpretation) allowed the five sections to be correlated to produce a synthetic section (Fig. 1b, c). In order to reconstruct the fluvial and volcanosedimentary palaeoenvironments of the ichnites-bearing rocks described in the area, a sedimentological study determination (based on lithologic succession, sedimentary structures and lateral variations) was carried out. A correlation between lithofacies associations and ichnoassociations can provide information on the palaeoenvironmental setting.

2.b. Ichnological study

Organism dynamics and substrate cohesion have an important influence on tracks and trackways shape and patterns (Hasiotis *et al.* 2007; Falkingham, 2014), giving a wide range of extramorphological variation (i.e. morphologies not depending on the shape of the limbs). As a consequence, a single trackmaker could imprint many different forms, complicating the identification and classification of ichnites (e.g. Petti *et al.* 2014).

The quantitative and qualitative parameters analysed in 78 vertebrate tracks and 4 trackways follow Haubold (1971), Leonardi (1987) and Hasiotis *et al.* (2007). Considering the sample, we selected the best-preserved footprints for a correct ichnotaxonomic determination following the suggestions of Haubold *et al.* (1995), Haubold (1996) and Bertling *et al.* (2006). The descriptions were made by direct observation of the specimens (both in the field and in the laboratory) and also by digital photographs with different light positions. Biometric measurements were made with ImageJ software (version 1.46r, available for download from http://rsbweb.nih.gov/ij/). In this work, ichnite refers to both tetrapod and invertebrate trace fossils, while footprint and track only refer to tetrapod trace fossils. We also provide additional figures (see supplementary Appendix S1, Figs S1–S5, available at http://journals.cambridge.org/geo) and the parameters measured on tetrapod footprints of all the analysed taxa (supplementary Appendix S2, Tables S1–S11), as well as the systematic ichnology of the invertebrate trace fossils (supplementary Appendix S3). The tetrapod swimming traces (scratches), which represent a large sample of the ichnoassemblage, are described as specific ichnotaxa. The possible association with footprints is discussed in Section 4.b.6 (see Melchor & Sarjeant, 2004 for further discussion, and Petti *et al.* 2014 for an alternative nomenclature).

2.c. Photogrammetry

In order to analyse tetrapod footprints, 3D photogrammetric models of 18 specimens have been generated following the procedures of Matthews (2008) and Falkingham (2012). Photographs were taken with digital compact camera Sony DSC-T200 8.1 megapixels. Three different software programs were used: VisualSFM v0.5.22 (http://www.ccwu.me/vsfm/) and MeshLab v.1.3.2 (http://meshlab.sourceforge.net/) to generate the 3D models; and ParaView v.3.98.1 (http://www.paraview.org) to elaborate the depth maps and contour lines (see also Falkingham, 2012; Belvedere *et al.* 2013).

2.d. Permits, repositories and material

Most of the studied material is on outcrop (*in situ*) and still remains in the field. On the other hand, several specimens (*ex situ*) were legally collected by the authors during field works in July 2012 (under the permit PINTER 8432) and July 2013 (under the permit 213K121N-080–450–563–760–610–787–823–871–2013–1–9833); both permits were issued by Departament de Cultura of the Generalitat de Catalunya (Catalan local government). Several silicone moulds and synthetic resin replicas of some tetrapod footprints were also made. The collected specimens, as well as the footprint moulds and replicas, are stored at the Museum of the Institut Català de Palaeontologia Miquel Crusafont (Sabadell, Spain). Tetrapod footprints collections from Museum für Naturkunde (MfN; Berlin, Germany), Musée Fleury (MFL; Lodève, France), Muséum National d'Histoire Naturelle (MNHN; Paris, France) and Institut des Sciences de l'Evolution-Montpellier (ISE-M, Université Montpellier 2; Montpellier, France) were studied first-hand by one of the authors (E.M.) and are also used for comparison with the Iberian Pyrenean specimens, housed at the Institut Català de Paleonologia (IPS; Sabadell, Spain).

The recovered specimens and the replicas studied here are: IPS-73723, IPS-73724, IPS-73726, IPS-83730, IPS-73739, IPS-73741, IPS-73742, IPS-73743, IPS-73744, IPS-73745, IPS-82604, IPS-82605, IPS-82606, IPS-82607, IPS-82608, IPS-83712 and IPS-83722. Specimens not recovered have no code, but are situated on the relative stratigraphic level and georeferenced.

3. Geological setting

The Catalan Pyrenees expose several Permian volcanic and sedimentary successions aligned in a belt that extends from El Pont de Suert (west) to Camprodon (east) (Fig. 1a). These rocks accumulated in strike-slip continental basins at the end of the Variscan Orogeny, resulting from the amalgamation of Pangaea (Speksnijder, 1985; Martí, 1996). Such rocks, of late Carboniferous – late Permian age, are unconformably overlaid by the Triassic Buntsandstein, Muschelkalk and Keuper facies (Nagtegaal, 1969; Gisbert, 1986; Gascón & Gisbert, 1987; Martí, 1996).

In the studied area, the Peranera Formation mainly consists of a volcanic-siliciclastic sequence composed of alternating deposits of tuffs, ignimbrites, breccia levels and cinerites (ash beds) with edaphic limestone nodules, and with sporadically intercalated fluvial deposits (mudstones, siltstones and sandstones) (see Mey *et al.* 1968; Nagtegaal, 1969; Gisbert, 1986; Martí, 1996; Fig. 1c; supplementary Appendix S1, Fig. S1, available at http://journals.cambridge.org/geo). The volcaniclastic sediments are completely different from its fluvial lithofacies (see Section 4.a below) and broadly display three main lithofacies: (1) clast-supported lithic breccia (facies mlBrf and dblBrf in the sense of Branney & Kokelaar, 2002); (2) volcaniclastic sandstone facies (VSF in the sense of Martí, 1996); and (3) fine-grained ashes and lutites. These deposits are classically attributed to reddish Autunian facies and dated as early Permian in age (Gisbert, 1986; Martí, 1996).

4. Results

4.a. Sedimentology and facies associations

The sections of La Mola d'Amunt-Benés (MA-B) and La Mola d'Amunt-Avellanos (MA-A1a, MA-A1b) are situated 114 m from the base of the Peranera Formation, and contain the fluvial strata which yielded the footprints (Figs 1, 2; supplementary Appendix S1, Fig. S1, available at http://journals.cambridge.org/geo). These sections are correlated by a distinctive basal ignimbrite bed of thickness 1.5–2.5 m. A massive mudstone-texture volcanosedimentary succession (6–12 m thick) lying above this ignimbrite contains five to six thin interbedded cinerites of 5–10 cm thick.

The fluvial beds (Fig. 2a, b) present channels with erosive bases and lateral accretions. A sigmoid-like morphology is recognized in most of the strata (each of thickness 20–30 cm and sets of thickness *c.* 1 m), with several sedimentary structures such as planar and through cross-stratification, lunate, linguoid and straight-crest flow ripples and climbing and wave ripples (Fig. 2b, e, f). These traits are typical of meandering systems. Mudcracks are also present (Fig. 2g), indicating an episodical emersion. The fluvial deposits result from relatively continuous functional perennial systems which were eventually abandoned.

In section MA-B the fluvial deposits are relatively coarse (fine to medium sandstone), whereas in MA-A1a and MA-A1b the deposits are relatively fine grained (fine to very fine sandstone). In all the outcrops the fluvial deposits correspond to confined flows, but in section MA-B the facies correspond to deeper parts of the channel. Raindrop impressions and mudcracks are more abundant on MA-A1a and MA-A1b than on MA-B, so the fluvial system dried more frequently and water level was probably lower than in MA-B.

Sections MA-A2 and MA-A3 (Fig. 2c, d) contain massive tabular ignimbrites (up to 1.5 m thick), and volcaniclastic breccia levels with rough planar cross-stratification. Sections encompass two short intervals of ignimbrite beds covered by millimetric- to centimetric-scale mudstone – very-fine-sandstone layers (Fig. 2i). These thin layers preserve water flow ripples, raindrop impressions (Fig. 2d, h), mudcracks and the ichnites described in Section 4.b. These structures probably indicate sedimentation by unconfined runoff rainwaters which fell after the deposition of the pyroclastic flow. The lack of confinement of these surfaces implies they were comparable to fluvial mudflats or floodplains.

4.b. Systematic ichnology

The tetrapod footprints presented in this work include the following ichnotaxa: *Batrachichnus salamandroides*, *Limnopus* isp., cf. *Amphisauropus*, cf. *Ichniotherium*, *Dromopus* isp., cf. *Varanopus*, *Hyloidichnus* isp. and *Dimetropus leisnerianus* (Figs 3–11). Three different swimming trace morphotypes all assigned to *Characichnos* isp. are associated to the first three ichnotaxa listed above (Fig. 11). Voigt & Haubold (2015) reported from the same formation (see Fig. 1b) the presence of *Batrachichnus*, *Limnopus*, *Dromopus*, *Varanopus* and *Hyloidichnus*. The works by Robles & Llompart (1987) and Fortuny *et al.* (2010) correspond to a completely different Pyrenean tracksite (i.e. different formation and situated in a different basin, in the sense of Galé, 2005), presumably younger. Our data therefore expand the late Cisuralian ichnoassemblage and provide new details on the ichnotaxonomy of most of these ichnotaxa.

4.b.1. Temnospondylian tracks

Ichnogenus *Batrachichnus* Woodworth, 1900
Ichnospecies *Batrachichnus salamandroides*
(Geinitz, 1861)

(Fig. 3; supplementary Appendix S2, Tables S1, S2, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: In section MA-A1a, five fitting slabs *ex situ* with six tracks (marks and casts, i.e. both in concave and convex relief): IPS-73741, IPS-73742, IPS-73743, IPS-73744 and IPS-73745.

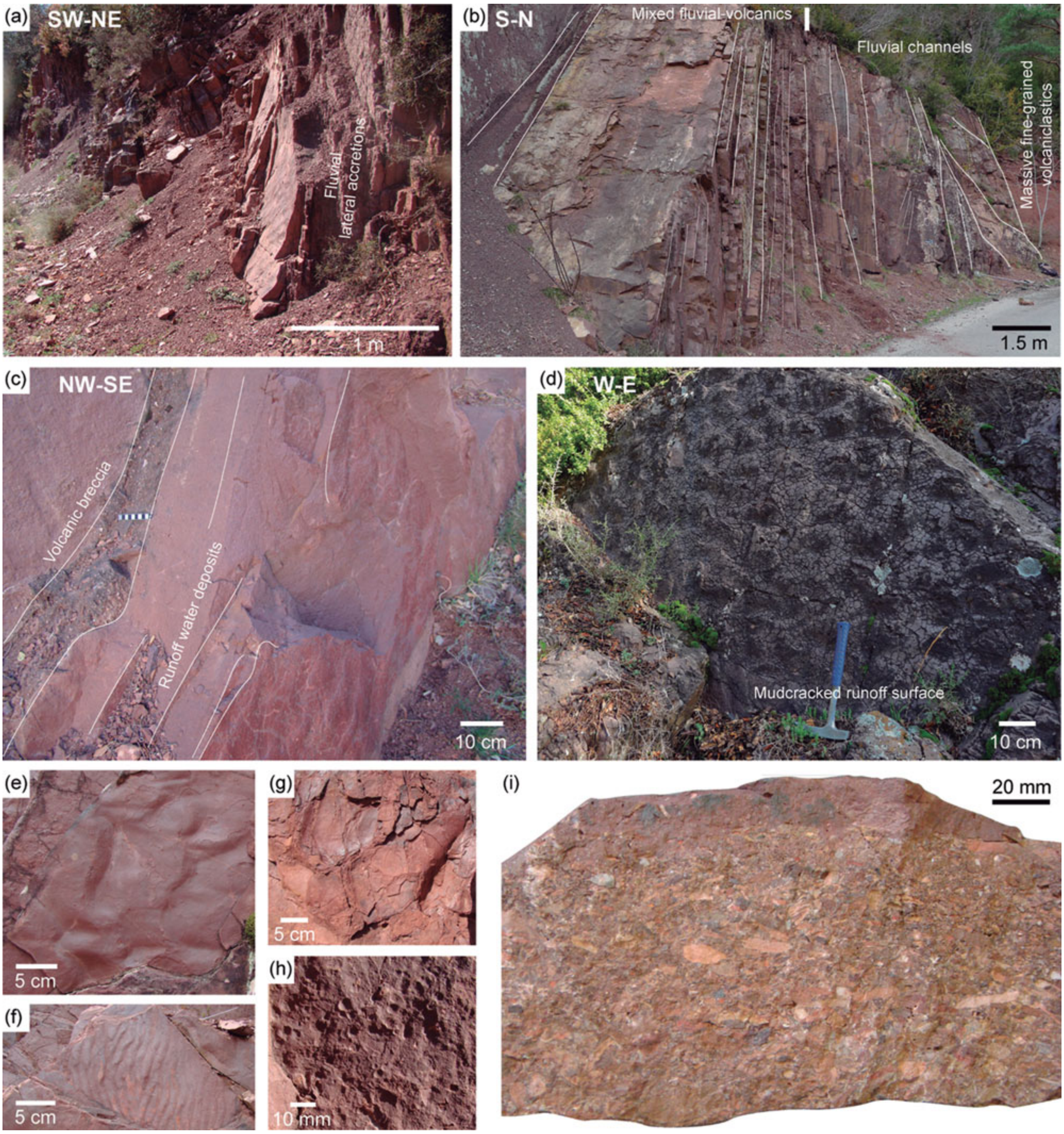

Figure 2. (Colour online) Deposits bearing ichnites. (a) Fluvial interval upper part from the MA-A1a section, top sequence to SSW. (b) Fluvial interval from the MA-B section, top sequence to S; the mixed fluvial-volcanic deposits contain cf. *Ichniotherium*. (c) Unconfined runoff surface, the upper surface is the level with *Hyloidichnus* isp. at MA-A2 7.90 m. (d) Surface subjected to high temperatures from the MA-A3 section. (e) Flow ripples from the MA-B section. (f) Wave ripples from the MA-B section. (g) Mudcracked surface from the MA-A1a section. (h) Raindrop impressions from the MA-A2 section. (i) Hand sample of a volcanic breccia with a mudstone – very-fine-sandstone layer from a runoff water flow.

Description: The footprints are grouped in different manus-pes sets, but only one is nearly complete, settled in a trackway. The footprints are usually digitigrade or semiplantigrade, except for one that is plantigrade. All the ichnites are wider than long and terminate in rounded digit tips without claw marks. Three tracks present a shallow sole impression. In front of all the tracks there are scratches formed when digit tips dragged the surface to advance. Tracks of the manus (6 × 11 mm) are presumably tetradactyl, whereas those of the pedes (8 × 12 mm) are pentadactyl. The relative length of the digits is not significant (supplementary Appendix S2, Table S1, available at http://journals.cambridge.org/geo) and ichnites are rotated either inwards or outwards from the midline, without following any pattern. Pace

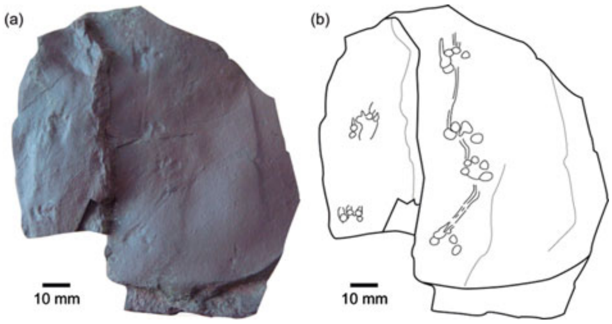

Figure 3. (Colour online) *Batrachichnus salamandroides* specimen (IPS-73741–5) from site MA-A1a. (a) Photo; (b) ichnites outline.

angulations of the manus and the pedes are low (<60º), this being indicative of sprawling locomotion of the trackmaker.

Discussion: The small size of the ichnites (<20 mm), the alternating sets, the low stride angulations, the tetradactyl manus and the rounded digits are diagnostic of the ichnospecies *Batrachichnus salamandroides*, known from Carboniferous – lower Permian deposits of France (Gand & Durand, 2006), Germany (Voigt, 2005), New Mexico (Lucas *et al.* 2005; Voigt & Lucas, 2015), Canada (Falcon-Lang *et al.* 2010; Stimson, Lucas & Melason, 2012) and Poland (Voigt *et al.* 2012). The shape and the size of the extremities and the glenoacetabular distances (30–35 mm) of branchiosaurids and micromelerpetontid temnospondyls and also lepospondyls are comparable to these footprints, so these groups are suggested to be trackmakers of *B. salamandroides* (Gand & Durand, 2006; Voigt, 2012; E.M., personal observation).

Ichnogenus ***Limnopus*** Marsh, 1894
Ichnospecies ***Limnopus*** **isp.**

(Figs 4, 11b–d; supplementary Appendix S1, Figs S2a–c, S3; supplementary Appendix S2, Tables S3, S4, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: In section MA-A1a, numerous tracks in concave epirelief at 10.20–10.50 m and 10.90 m (replica IPS-82606), one trackway composed of two manus-pes sets and one partial manus track (replica IPS-82608), 16 partial tracks at 18.15 m and one slab *ex situ* partially covered with ten tracks (IPS-83730). In section MA-A1b, several tracks in concave epirelief at 12.00–13.00 m. In section MA-B, numerous tracks in convex hyporelief at 15.00–18.00 m, one slab *ex situ* with one manus-pes set (IPS-73724) and one large block *ex situ* not recovered.

Description: Two different track shapes are recognized. The first (Fig. 4a–f) consists of ichnites with rounded, clawless digit tips and shallow oval (wider than longer) palm and sole impressions, some with an expulsion rim. The manus tracks are semiplantigrade to plantigrade, and wider (43–54 mm) than long (32–38 mm). The ichnites are tetradactyl with wide digits. The relative digit length is I<II≤IV<III. The digits I, II and IV are slightly rotated inwards, whereas digit III is straighter. All the digits present a rounded to elliptical shape. The digits I and II are more deeply impressed than the others. The pedes are pentadactyl and plantigrade, slightly wider (50–57 mm) than long (37–48 mm), and with a sole sometimes U-shaped. The digits I–V divarication is over 100°. The digit relative length is I≤V<II<III<IV. The pedes digits are proportionally longer than those of the manus, and digit V is rotated outwards. The digit tips are rounded and deeply impressed. The average width is greater in the manus (53 mm) than in the pes (50 mm). This is probably caused by the uncommon preservation of complete pedes in the larger-size tracks (see Fig. 4a–d; supplementary Appendix S2, Table S3, available at http://journals.cambridge.org/geo). In some sets, the pedes partially overstep the manus (Fig. 4e, f). In the trackway, the manus impressions are rotated inwards and the pedes are deformed (Fig. 4a–d). The low pace angulation (69°) and the relative large trackway external width (322 mm) indicate a sprawling posture of the trackmaker.

The second type of tracks (Figs 4g–i, 11d; 2 in Fig. 11b) is the most abundant: it is generally unguligrade, formed by rounded digit tip prints in groups of two to five (commonly formed by four digit tips), and is spreaded in an arc with widths similar to those of the first track shape (both morphologies present a width/length ratio of 0.6–0.8). Some tip impressions show an expulsion rim in their posterior part. Some tracks appear as semiplantigrade because a very shallow sole or palm impression is preserved. Some digit tip prints are anteriorly elongated and slightly curved inward (i.e. scratches), with a similar track pattern than that of the previously described *Batrachichnus salamandroides*. At 17.75 m in section MA-B, a well-defined trackway is formed by digit tip prints that are in contact with one another and present pace angulations of 92° (supplementary Appendix S1, Fig. S3 and Appendix S2, Table S4, available at http://journals.cambridge.org/geo).

Discussion: The two described track shapes belong to the same ichnotaxon because they present analogue proportions and some transitions between the two morphologies were found; they therefore represent different preservational states (Fig. 4a, h, i). The tetradactyl manus with a wide, large palm impression, the rounded clawless digit tips, the relative digit lengths, the pentadactyl pedes with a shallow impression of digit V and a U-shaped sole, as well as the pace angulations, are diagnostic of the ichnogenus *Limnopus* (e.g. Baird, 1952; Gand, 1988; Tucker & Smith, 2004; Voigt, 2005; Marchetti, Avanzini & Conti, 2013; Voigt & Haubold, 2015). Specimens reported here are different from those assigned to *Batrachichnus salamandroides*; there are two discrete populations of size (supplementary Appendix S2, Tables S1, S3, available at http://journals.cambridge.org/geo), indicating no

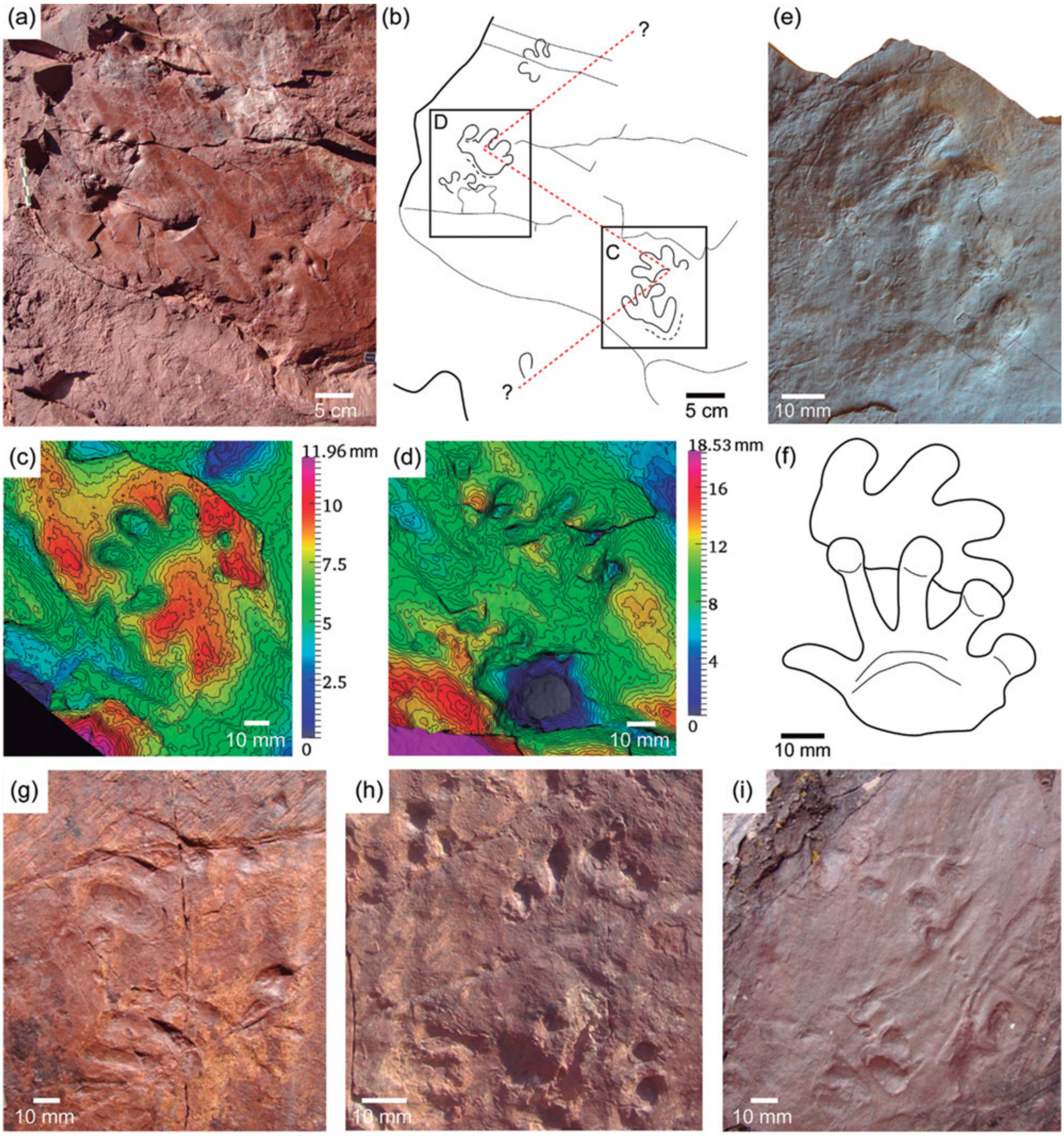

Figure 4. (Colour online) *Limnopus* isp. tracks. (a–d) Trackway and isolated track from MA-A1a 18.15 m. (a) Photograph; (b) ichnites outline; (c) 3D model of the right set; and (d) 3D model of the left set. (e, f) Isolated right set (IPS-73724). (e) Photograph; and (f) ichnites outline. (g–i) Digit tip tracks. (g) Two tracks with trailing digits from section MA-A1a at 10.20 m; (h) pes track and diverse digit tips from section MA-A1a at 10.20 m; and (i) tracks with expulsion rim on the posterior part of the digits from section MA-A1b at 12.00 m.

transition between both ichnogenera. The 3D model analyses reveal that within all tracks the manus digits I and II are the most deeply impressed, probably because they are the most functional as suggested in other ichnogenera (Avanzini *et al.* 2008). This is also indicated by the inwards orientation of the manus footprints, an uncommon feature in the ichnogenus in which the manus is often parallel to the midline (Voigt, 2005; Fig. 4a–f). Similar specimens are found in the upper Carboniferous deposits of England (Tucker & Smith, 2004) and the lower Permian deposits of France (Gand, 1988; Demathieu *et al.* 1992), Italy (Marchetti *et al.* 2015*a*, *b*), Germany (Haubold, 1970, 1971; Voigt, 2005) and North America (Baird, 1952). Haubold (2000) only considered the ichnospecies *L. vagus*, *L. zeilleri* and *L. cutlerensis* (see also Voigt, 2005) to be of possible ichnotaxonomic value. Recently, Lucas & Dalman (2013) identified *L. heterodactylus* as the first described ichnospecies; it should therefore be used instead of *L. vagus* in case of synonymy (see also Marchetti, Avanzini & Conti, 2013). Nevertheless, due to the preservation of the specimens described here, ichnospecies remain

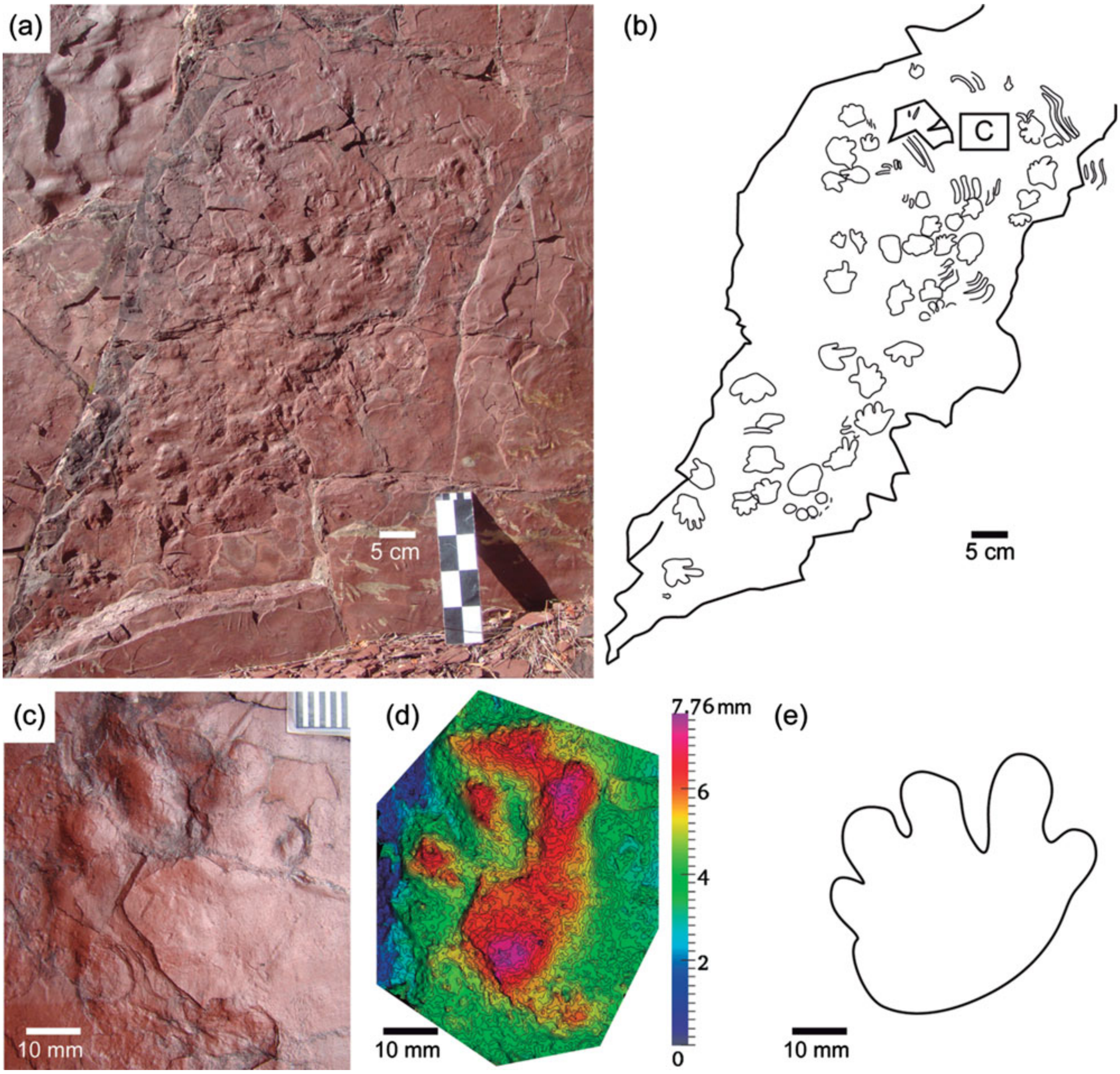

Figure 5. (Colour online) cf. *Amphisauropus* tracks from section MA-B. (a, b) Mass occurrence of tracks in surface at 17.75 m. (a) Photograph; and (b) ichnites outline. (c–e) Manus outlined in (b). (c) Photograph; (d) 3D model; and (e) ichnite outline.

uncertain. The potential trackmakers for *Limnopus* are temnospondyl amphibians similar to eryopsids (Gand, 1988; Van Allen *et al.* 2005; Voigt, 2005; Gand & Durand, 2006).

4.b.2. Seymouriamorph tracks

Ichnogenus cf. *Amphisauropus* Haubold, 1970

(Figs 5, 11c; supplementary Appendix S1, Fig. S2d–l and Appendix S2, Table S5, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: In section MA-B, at 15.00–15.20 m, 16.00 m, 16.50 m, 17.75 m (replica IPS-82605), 21.50 m and 23.80 m, as well as one slab *ex situ* with one manus and three partial pes digits (IPS-73723). All the tracks are in convex hyporelief.

Description: The ichnites are coupled in manus-pes sets. The manus are plantigrade to semiplantigrade and wider (31–52 mm) than long (19–39 mm). They are pentadactyl with short digits terminated in rounded and relatively large clawless digit tips, more deeply impressed than the rest of the footprint (Fig. 5). The digit length increases from digit I to IV. The length of digit V is similar to that of I. The pedes, larger than the manus, are plantigrade to semiplantigrade and pentadactyl. They are longer (32–57 mm) than wide (27–51 mm) and their digit length increases from I to IV. The length of digit V falls between those of I and II. The digits III and IV are the longest. Commonly, digits III and IV are the most deeply impressed followed by digits I and II, while digit V is not always preserved. In sets, the pedes never overstep the manus; the latter are rotated inwards at approximately 90° from the pes

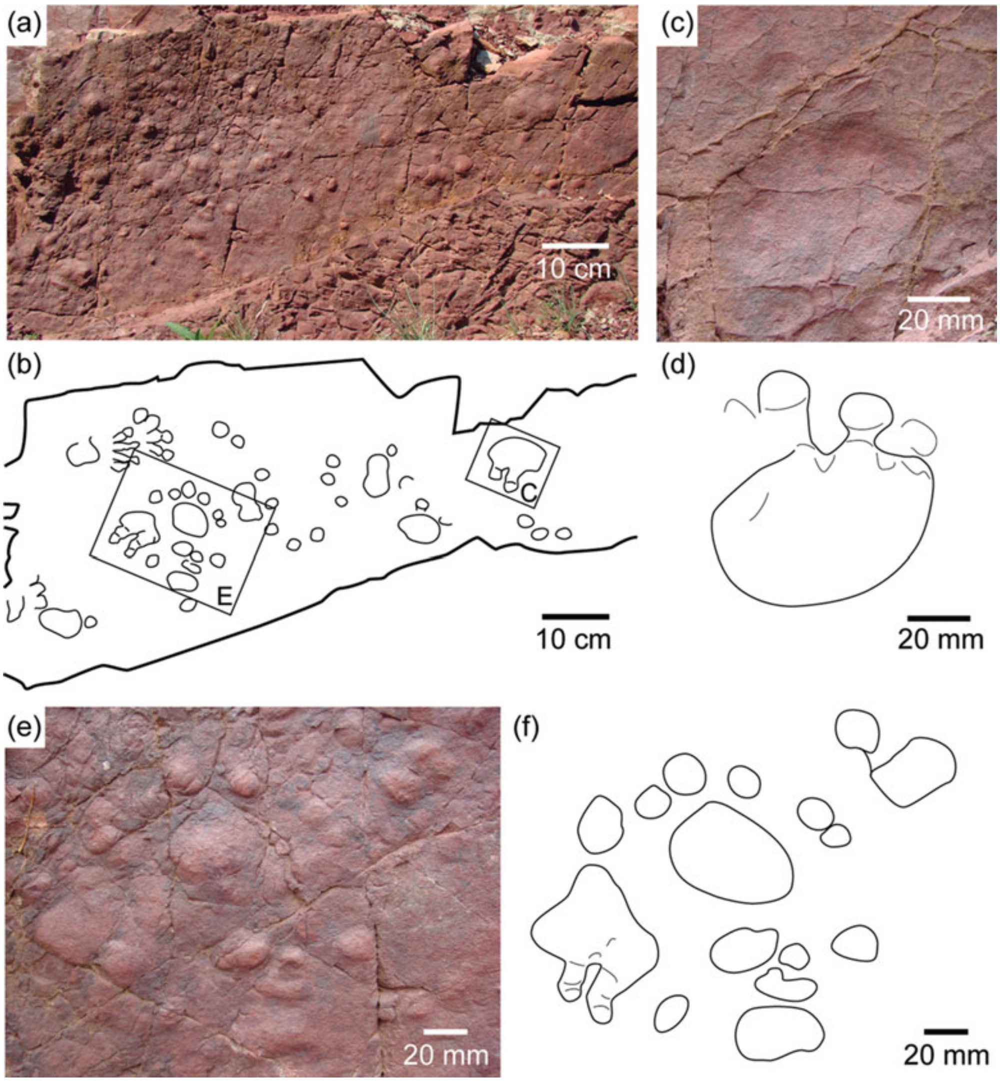

Figure 6. (Colour online) cf. *Ichniotherium* from section MA-B at 22.60 m. (a) Entire surface; (b) ichnites outline; (c) and (e) detail of the ichnites outlined in (b). (d, f) Ichnites outline of (c) and (e), respectively.

orientation (i.e. the manus width axis is aligned with the pes length axis; supplementary Appendix S1, Fig. S2j–l, available at http://journals.cambridge.org/geo).

Discussion: The plantigrade to semiplantigrade pentadactyl tracks with broad sole, the rounded digit tips, the measured relative digit lengths, the manus sensibly wider than long and inwards-oriented with respect to the pes (supplementary Appendix S2, Table S5, available at http://journals.cambridge.org/geo) are diagnostic traits of *Amphisauropus* (see Haubold, 1970; Voigt, 2005). However, this assignation remains tentative due to the lack of trackways, and the overall poor preservation of the specimens. The specimens from the site MA-B present shorter and more robust digits than tracks assignable to *A. kablikae* (the only valid ichnospecies *sensu* Voigt, 2005) described by Haubold (1970, 1971), Gand (1988), Nicosia, Ronchi & Santi (2000), Lucas, Lerner & Haubold (2001), Lucas, Spielmann & Lerner (2009), Van Allen *et al.* (2005), Voigt (2005, 2012), Avanzini *et al.* (2008), Voigt *et al.* (2011*a*, 2012), Marchetti *et al.* (2015*a*, *b*). The Pyrenean specimens are smaller (but similar in shape) than those assigned to *Amphisauropus* isp. by Hminna *et al.* (2012) in the Argana Basin (Morocco). According to Lucas, Lerner & Haubold (2001) and Voigt (2005), the trackmakers of *Amphisauropus* could belong to the seymouriamorph group.

4.b.3. *Diadectomorph tracks*

Ichnogenus cf. *Ichniotherium* Pohlig, 1892

(Fig. 6; supplementary Appendix S2, Table S6, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: In section MA-B, at 23.20 m, at least 16 tracks in convex hyporelief.

Description: The footprints are pentadactyl and plantigrade, with a characteristic oval-shaped laterally expanded sole impression. The digits are preserved as rounded impressions. The tips are the most deeply impressed parts, and often the only preserved parts.

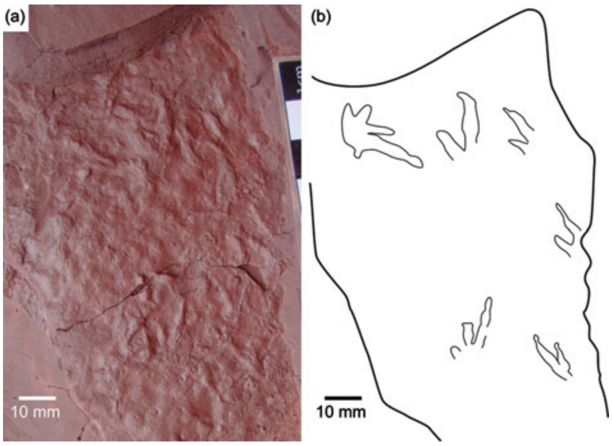

Figure 7. (Colour online) *Dromopus* isp. specimens from section MA-B at 22.40 m. (a) Photograph; and (b) ichnites outline.

Some tracks only preserve the sole or some digit tips. The digits relative length is I<II≤V<III<IV, and the sole impression is opposite to digits II–V. At least two manus-pes sets are preserved and partial trackways can be established, although these groupings remain tentative due to the partial preservation of most of the footprints.

Discussion: The position and shape of the sole and the assumed morphology and length of the digits can be tentatively attributed to cf. *Ichniotherium* (see Voigt, Berman & Henrici, 2007). This ichnogenus, common in German basins (Voigt, 2005; Voigt, Berman & Henrici, 2007), has also been reported in the French basin of Lodève (Gand & Durand, 2006), the Moroccan basin of Khenifra (Voigt *et al.* 2011*b*), Colorado (Voigt, Small & Sanders, 2005), New Mexico (Lucas *et al.* 2011) and Canada (Brink, Hawthorn & Evans, 2012). The specimens described here are preserved in a different substrate (tabular bed, coarser with rough aspect), formed in drier conditions than the rest of the strata bearing footprints, which suggests different palaeoenvironmental conditions associated with this ichnospecies. This is in concordance with the attribution of *Ichniotherium* to inland zones (e.g. Brink, Hawthorn & Evans, 2012), being separated from ichnotaxa commonly found in wetter environments. The trackmakers assigned to *Ichniotherium* are most probably early amniote diadectids (Voigt, Berman & Henrici, 2007).

4.b.4. *Eureptilian tracks*

Ichnogenus *Dromopus* Marsh, 1894
Ichnospecies *Dromopus* isp.

(Fig. 7; supplementary Appendix S2, Table S7, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: In section MA-B, at 22.40 m, six footprints in convex hyporelief.

Description: Of the six isolated footprints described here, four of them preserve only two digit impressions, another is composed of three digits and the last is presumably pentadactyl. The largest ichnite is 22.7 mm in length, and the relative digits length increases from digit II to IV. The digits are relatively long with pointed tips, indicating the presence of claws. The digits are slightly curved inward. The digits III and IV are the most deeply impressed, followed by the digit II. The digit IV is remarkably longer than the digit III. Mean divarication of the digits III and IV is 24.8°.

Discussion: The shape of the digits as well as their relative length (with the digit IV sensibly longer than the digit III) and the deeper impression of digits III and IV are diagnostic traits of the ichnogenus *Dromopus*. It is the most widespread ichnotaxon in early Permian and Carboniferous basins (Voigt, 2005); similar specimens have been reported from German (Voigt, 2005), Polish (Voigt *et al.* 2012), Italian (Avanzini, Bernardi & Nicosia, 2011; Marchetti *et al.* 2015*a*, *b*), French (Gand, 1988; Gand & Durand, 2006), Moroccan (Voigt *et al.* 2011*a*, *b*) and also North American (Van Allen *et al.* 2005; Lucas *et al.* 2011; Voigt & Lucas, 2015) basins. *Dromopus* specimens described here are commonly preserved as incomplete didactyl tracks; there is therefore still no consensus on possible ichnospecific differentiations due to the lack of diagnostic traits. The trackmakers referred to *Dromopus* are small- to medium-sized sauropsids, in particular araeoscelids and bolosaurids (Voigt *et al.* 2012).

Ichnogenus cf. *Varanopus* Moodie, 1929

(Fig. 8; supplementary Appendix S2, Tables S8, S9, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: In section MA-A1a, at 10.50 m (replica IPS-82607), eight tracks settled in a trackway in concave epirelief.

Description: The trackway is composed of eight tracks grouped in four manus-pes sets. The footprints have an expulsion rim, higher in the outer or lateral sides of the trackway than in the inner side. Both manus and pedes are probably pentadactyl and semiplantigrade. The digits I–IV are curved inwards (more in manus than in pes tracks) with pointed and sharply curved tips, indicating the presence of claws. The digit length increases from digit I to IV, digit V length in pedes is uncertain and in manus it is similar to the length of digit I.

The manus tracks are slightly wider than long (39×38 mm) with divarication of digits I–V over 130°, whereas the pedes are longer than wide (24×31 mm) with the divarication of digits I–V less than 90° (supplementary Appendix S2, Table S8, available at http://journals.cambridge.org/geo). The pes tracks appear smaller than the manus tracks, but this corresponds to extramorphological variation (see following discussion). The third set is situated in the surface of the layer below the other ichnites, and therefore corresponds to

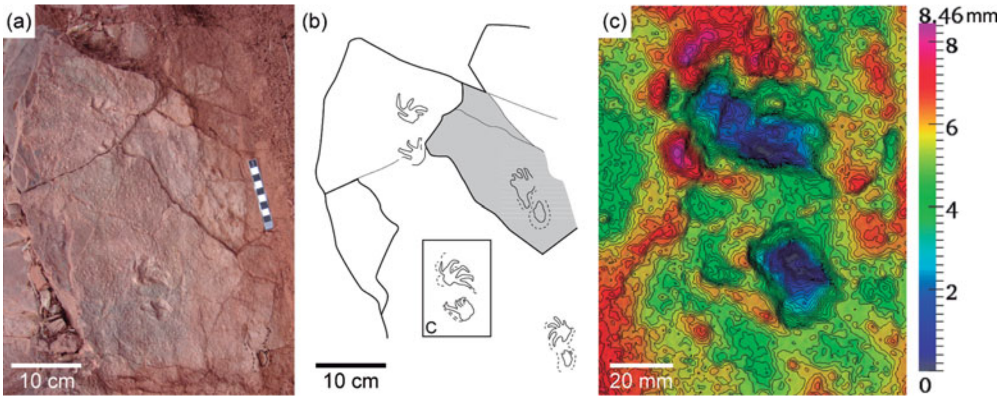

Figure 8. (Colour online) cf. *Varanopus* footprints from section MA-A1a 10.50 m. (a) Trackway; (b) ichnites outline; and (c) 3D model outlined in (b).

an undertrack. The manus is a highly deformed shallow footprint, much longer than wide. The preserved digits are also wider, and the digit tips are sharply curved inwards and pointed as in the other manus ichnites. The pes track is a shallow impression outlined by a low expulsion rim. The manus tracks, on average 47 mm distant from the pedes, are slightly rotated inwards towards the trackway midline. The manus tracks are generally more deeply impressed than the pedes tracks and with higher expulsion rims. The trackway parameters are similar in manus and pedes. The pace angulations indicate a sprawling locomotion (<90°).

Discussion: The shape of the digits (rotated inwards with curved clawed tips), the measured relative lengths of the digits, the divarication of digits I–V, the stride angulation and the stride/pes length proportion (supplementary Appendix S2, Tables S8, S9, available at http://journals.cambridge.org/geo) are diagnostic traits of *Varanopus* (*sensu* Haubold & Lucas, 2003; Voigt, 2005; Voigt & Haubold, 2015), but due to the poor preservation of the tracks the assignation should remain tentative. These tracks resemble those reported by Moodie (1929, p. 364–5) (a single set) or those of further studies (e.g. Haubold, 1971; Gand, 1988; Nicosia, Ronchi & Santi, 2000; Haubold & Lucas, 2001, 2003; Lucas, Spielmann & Lerner, 2009; Voigt, 2005, 2012; Voigt, Small & Sanders, 2005; Marchetti *et al.* 2015*a*, *b*). The sets show that the pes tracks are smaller than the manus tracks, and the manus palms are much deeper than the digits. These traits are probably due to substrate conditions, with a trackmaker possibly advancing on the substrate under water level (on this surface there are also swimming scratches). The elongated manus undertrack from the third set indicates a dragging component of the manus on the substrate surface, due to a strong limb impression of the trackmaker. This ichnotaxon is found in several early Permian localities from Europe and North America and potentially from Morocco (see Voigt *et al.* 2011*a* for discussion). The trackmakers assigned to this ichnotaxon could be eureptiles such as captorhinids (Haubold & Lucas, 2003; Voigt, 2005; Gand & Durand, 2006).

Ichnogenus *Hyloidichnus* Gilmore, 1927
Ichnospecies *Hyloidichnus* isp.

(Fig. 9; supplementary Appendix S2, Table S10, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: In section MA-A2, four tracks in the surface at 7.30 m and ten tracks in the surface at 7.90 m. All the tracks are in concave epirelief.

Description: Four manus-pes sets have been identified. The manus impressions are closer and slightly rotated to a hypothetical trackway midline (although there are no true trackways preserved). The manus lengths and widths are 41–75 mm and 69–84 mm, respectively. The digit V is often not preserved, and track widths cannot always be measured. The pes tracks are slightly larger than the manus tracks (supplementary Appendix S2, Table S10, available at http://journals.cambridge.org/geo). The digits are relatively large and straight with wide and rounded to T-shaped tips. The digit V is directed outwards. The digit relative length is V<I<II<III<IV and the digit depth impression decreases from digit I to V. The ichnites in the surface at 7.90 m are semiplantigrade to plantigrade (Fig. 9a–c) and those at 7.30 m are digitigrade to semiplantigrade (Fig. 9e, f).

Discussion: The two surfaces yield tracks with different preservation, probably because of different substrate conditions at the moment of the track impression; the lower-level surface might have been dryer and harder than the upper level because the ichnites from the former are shallower than those from the latter, and with less features preserved. Despite these differences in preservation, these tracks correspond to the same ichnogenus as they have similar digit morphology, relative length and divarication (supplementary Appendix S2, Table S10, available at http://journals.cambridge.org/geo). Based on the manus/pes proportions, the slender digits with wider tips, the relative digit length (with a relatively short pes digit V) and impression depth and the size

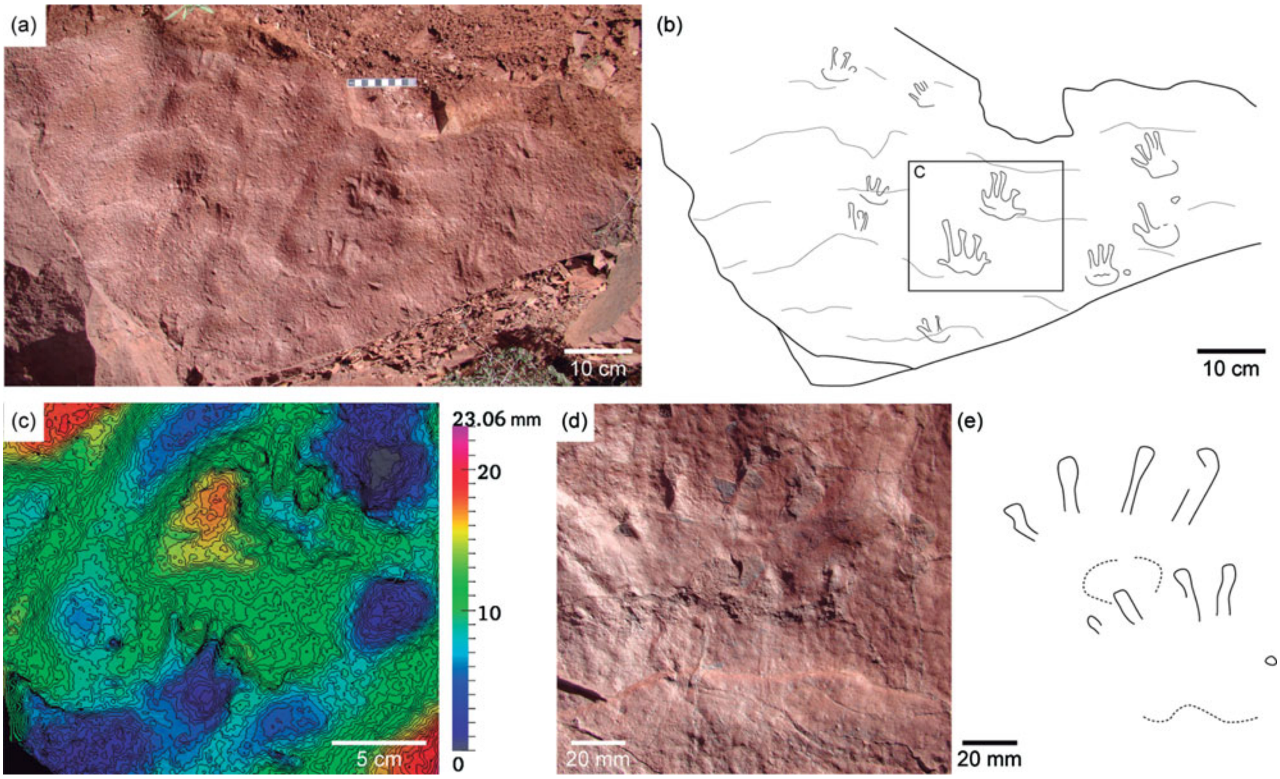

Figure 9. (Colour online) *Hyloidichnus* isp. footprints from section MA-A2. (a) Ichnites from surface at 7.90 m; (b) ichnites outline; (c) 3D model of the manus-pes set outlined in (b); (d) manus-pes set from surface at 7.30 m; and (e) ichnites outline.

of the digits in relation to the shallow sole and palm impressions, these footprints are assigned to *Hyloidichnus* (see Gilmore, 1927; Haubold, 1971; Gand, 1988). Material referred to *Hyloidichnus* was previously described by Voigt & Haubold (2015) in a locality nearby to MA-A2. However, the specimens described here are larger in size (up to lengths of 68.9 mm in the manus and 74.5 mm in the pedes). The ichnospecies identification remains uncertain due to the lack of trackways and because there is still no consensus on the ichnospecific differentiation (e.g. Gand, 1988; Marchetti, Avanzini & Conti, 2013). *Hyloidichnus* has been reported in Permian deposits of Peña Sagra, Spain (Gand *et al.* 1997), Argana, Morocco (Voigt *et al.* 2010; Hminna *et al.* 2012), Italy (Avanzini, Bernardi & Nicosia, 2011; Marchetti, Avanzini & Conti, 2013; Marchetti *et al.* 2015*b*), France (Gand, 1988; Gand, 1993; Gand & Durand, 2006) and North America (Gilmore, 1927; Lucas *et al.* 2013). The possible *Hyloidichnus* trackmakers are captorhinid eureptiles (Voigt *et al.* 2010; Hminna *et al.* 2012).

4.b.5. *Synapsid tracks*

Ichnogenus *Dimetropus* Romer & Prince 1940
Ichnospecies *Dimetropus leisnerianus* (Geinitz, 1863)

(Fig. 10; supplementary Appendix S1, Fig. S2m-o; Appendix S2, Table S11, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: In section MA-A2, two manus-pes sets at 8.60 m. In section MA-A3, one manus-pes set at 4.70 m. All the tracks are in concave epirelief.

Description: The manus-pes sets are formed by plantigrade pentadactyl ichnites. The palm and sole impressions are deep and the digit shape is not well preserved. The tracks are similar in length and width. The pedes impressions (120–135 mm in length) are larger than the manus impressions (102–120 mm in length). The digits of the manus are long (*c.* 40% of track length) and straight with similar divarication. The relative length of the digits is I<II≤V<III<IV. Digits of the manus have the lateral walls collapsed, indicative of a saturated substrate. The digits of the pedes are short in relation to sole length and width, and in digit IV of the second set there is a shallow claw impression. The manus palms and the pedes soles are more deeply impressed than the digits, indicating a strong plantigrade track. The ichnites from section MA-A2 seem to correspond to the same trackway, as the tracks are rotated towards a hypothetical trackway midline (Fig. 10). The footprints from section MA-A3 are deformed (supplementary Appendix S1, Fig. S2m–o, available at http://journals.cambridge.org/geo), but they have been identified because of the similarity in shape to those of MA-A2 although the pes is just a shallow sole impression and in the manus only two digits are well distinguished. The cause of the low preservation quality of the ichnites from section MA-A3 is

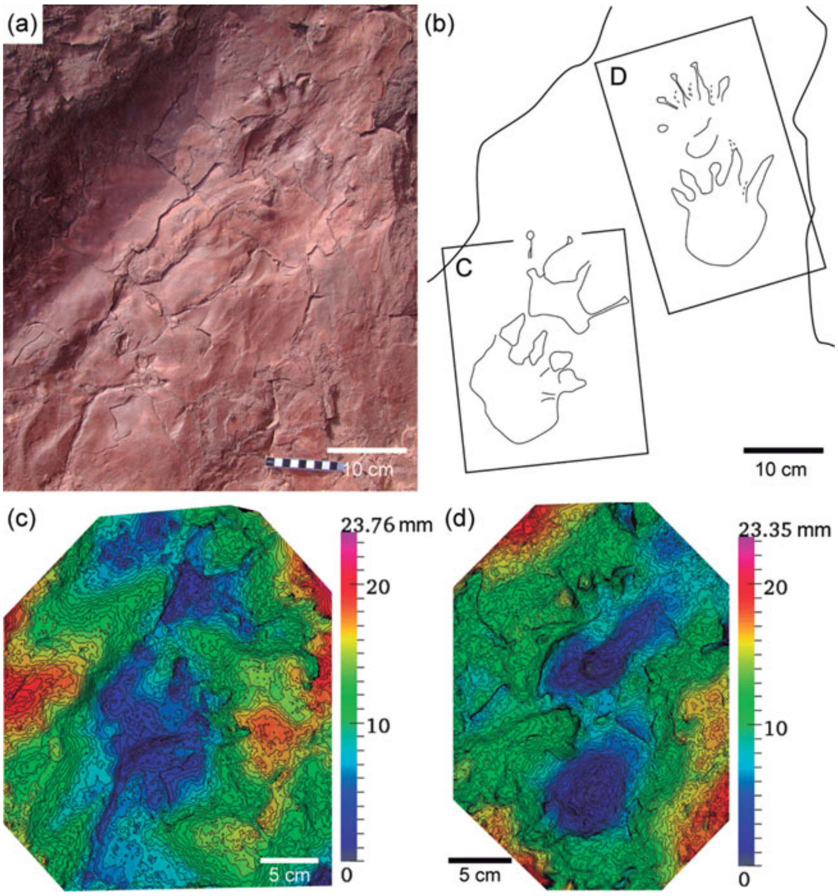

Figure 10. (Colour online) *Dimetropus leisnerianus* footprints from section MA-A2 at 8.60 m. (a) Entire surface; (b) ichnites outline; (c, d) 3D models of the manus-pes sets outlined in (b).

probably due to the runoff water circulation soon after their impression.

Discussion: The size of the plantigrade footprints with large, rounded, deep palm and sole impressions (>50% of track length), the straight digits with claw marks (although shallow), the relative digit length, the divarication of digits I–V and the manus-pes proportion are diagnostic traits of *Dimetropus leisnerianus* (see Voigt, 2005). This ichnogenus is known from Permian tracksites from northern land masses (e.g. Haubold, 1971, 1984; Gand, 1988; Van Allen *et al.* 2005; Voigt, 2005; Lucas *et al.* 2011, 2013; Voigt *et al.* 2012) and also from Tiddas (Voigt *et al.* 2011*a*) and Khenifra basins (Voigt *et al.* 2011*b*) in Morocco. *Dimetropus* also appears in German early Carboniferous sites (Voigt & Ganzelewski, 2010). The pelycosaur synapsids, including caseids, edaphosaurids, ophiacodontids and sphenacodontids, are traditionally considered as the trackmakers of *Dimetropus* (Haubold, 1971, 2000; Gand, 1988; Voigt, 2005; Voigt *et al.* 2011*a*, *b*).

4.b.6. *Tetrapod swimming traces*

Ichnogenus *Characichnos* Whyte & Romano 2001
Ichnospecies *Characichnos* isp.

(Fig. 11; supplementary Appendix S1, Fig. S3, available at http://journals.cambridge.org/geo)

Material and stratigraphic position: Type A (associated with *Batrachichnus salamandroides*): one slab *ex situ* (IPS-73739) from site MA-A1a, the tracks are in convex hyporelief. In section MA-B, numerous tracks in convex hyporelief at 16.80 m, one slab *ex situ* with *Acripes multiformis* and *Rusophycus* isp. at the uppermost surface (IPS-73726) and one slab *ex situ* not recovered. Type B (associated with *Limnopus* isp.): in section MA-A1a, numerous tracks in concave epirelief at 10.20–10.50 m and 10.90 m (replica IPS-82606). In section MA-A1b, several tracks in concave epirelief at 12.00–13.00 m. In section MA-B, numerous tracks in convex hyporelief at 15.00–18.00 m (replica IPS-82604 at 17.50 m), 20.10–20.30 m and 23.00 m, and one large block *ex situ* not recovered. Type C (associated with cf. *Amphisauropus*): in section MA-B, numerous tracks in convex hyporelief at the upper part of the surface at 17.75 m.

Description: Where present, these ichnites are abundant. Three groups of ichnites differing in shape and size can be recognized.

Type A. The tracks are composed of relatively large and narrow (1×5–20 mm) scratches (digit tip prints dragged on the surface). Most of them are sinuous, although some are straight. A hooked end is present in some scratches. The tracks have a maximum of four

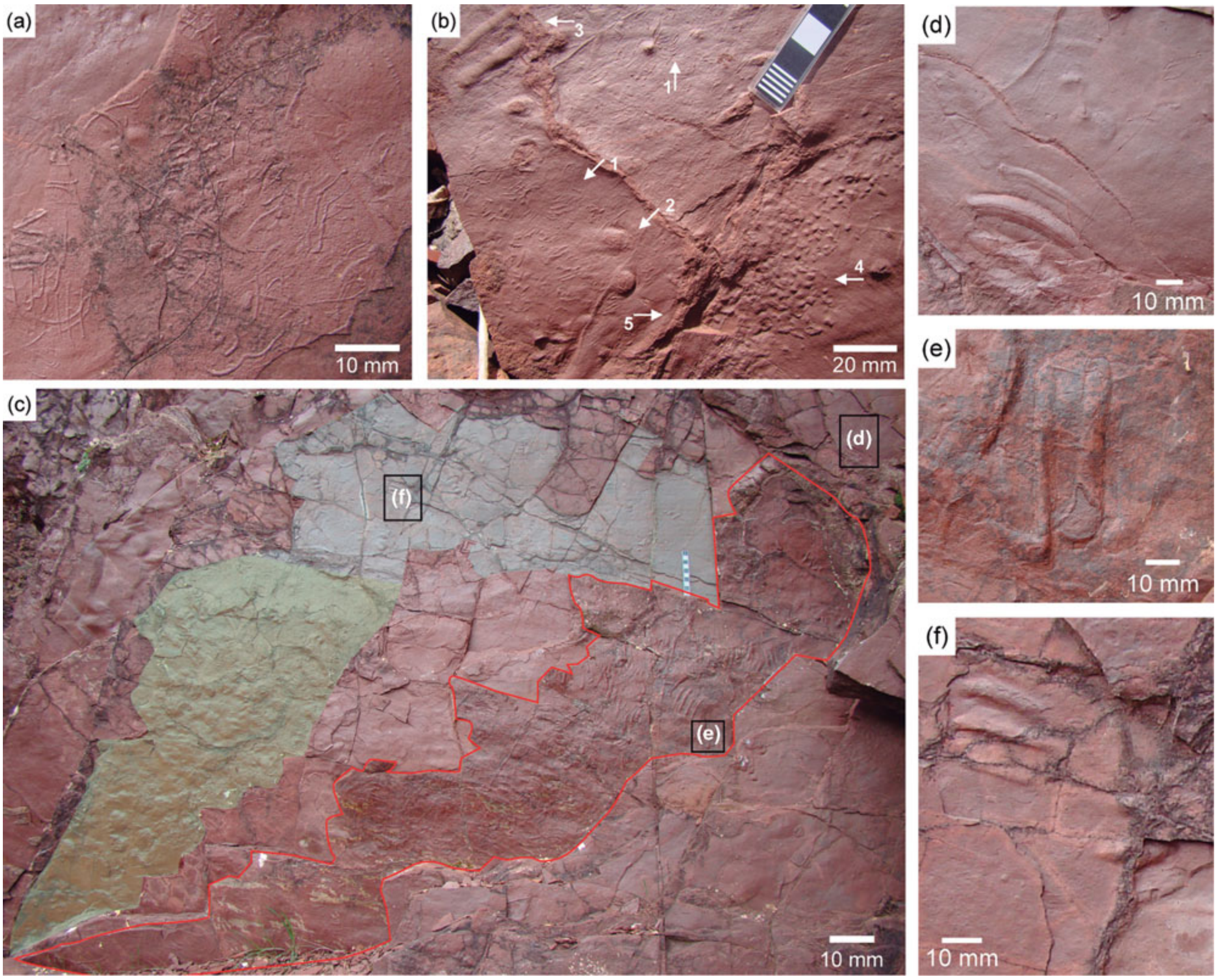

Figure 11. (Colour online) Swimming traces and associated ichnites. (a) *Characichnos* Type A. (b) *Characichnos* Type A (1), *Limnopus* isp. digit tip footprints (2), *Characichnos* Type B (3), *Rusophycus* isp. (4) and plant remains (5) (MA-B *ex situ* slab not recovered). (c) Section MA-B at 17.50 m with *Limnopus* isp. footprints and *Characichnos* Type B (surface bounded in red), at 17.75 m with cf. *Amphisauropus* footprints and *Characichnos* Type C (in the lower and upper part of the coloured surface, respectively). (d, e) Detail of *Characichnos* Type B outlined in (c). (f) Detail of *Characichnos* Type C outlined in (c).

scratches, but usually three. Two different track sizes are present: 10 mm width or 5–6 mm. Although most of the tracks are aligned in the same direction, no clear groups of tracks or trackway patterns can be identified due to the high abundance of tracks, which usually overstep one another. In some parts in section MA-B at 16.80 m (Fig. 11a) scratches have no preferential directions and are accompanied by invertebrate trace fossils (*Acripes multiformis* and arthropod body impressions; Fig. 1c), and sometimes also by larger scratches of Type B.

Type B. The ichnites are formed by two, three or four digit scratches slightly curved or sinuous (Fig. 11b–e). Tracks with two scratches are usually in contact. The scratch associated with each digit measures 10 mm in width and 30–60 mm in length. In most surfaces these tracks are isolated or accompanied by digit tip tracks of the second morphology of *Limnopus* isp., except in the surface at 17.50 m in section MA-B which is plenty of scratches aligned in the same direction (Fig. 11c). Some scratches present a hooked end (Fig. 11e) such as those of Type A. At 10.35 m in section MA-A1a there are several scratches and digit tip tracks of *Limnopus* isp. displayed in different trackways, demonstrating the association between these swimming traces and *Limnopus* isp. Some of these scratches have a large expulsion rim on the posterior part, suggesting an anteroposterior limb movement.

Type C. These scratches measure in average 5×25 mm. They are usually in groups of three digit scratches, or in some case with a fourth print (Fig. 11c, f). Traces of this morphotype are smaller and relatively narrower than those of Type B. In the surface at 17.75 m from section MA-B there is a transition from cf. *Amphisauropus* to these scratches, in some cases impressed by the same trackmaker individual (Fig. 11c). Swimming traces appear largely abundant, also with some digit tip imprints of *Limnopus* isp. (supplementary Appendix S1, Fig. S3, available at http://journals.cambridge.org/geo).

Discussion: Swimming scratches with the same shapes and range of sizes are referred to the ichnogenus *Characichnos* defined by Whyte & Romano (2001). Scratches similar to Type A have been associated with tracks of *Batrachichnus salamandroides* described by Lucas *et al.* (2011). These three types of scratches are interpreted as swimming traces (Gand, 1989; Whyte & Romano, 2001; Melchor & Sarjeant, 2004; Gand *et al.* 2011; Lucas *et al.* 2011; Lovelace & Lovelace, 2012). The hooked ends observed in Types A and B show the changing direction of the limb when it was being raised up, indicating that the trackmaker was probably swimming close to the substrate. The superimposition of different specimens renders the identification of the trackway pattern impossible due to the contact of trackmakers with substrate, which was not regular. The associations of scratches with *Batrachichnus salamandroides*, *Limnopus* isp. and cf. *Amphisauropus* indicate a transition of walking to swimming locomotion of the trackmakers, probably due to a transition of relatively shallow to relatively deep water. The potential trackmakers of these swimming traces are probably those of the associated walking gait footprints: branchiosaurids and micromelerpetontid temnospondyls and lepospondyls for Type A; large temnospondyls for Type B; and seymouriamorphs for Type C.

5. Discussion

5.a. Ichnoassociations and environmental setting

Two ichnoassociations are observed: (1) one composed of *Batrachichnus salamandroides*, *Limnopus* isp., cf. *Amphisauropus*, cf. *Ichniotherium* cf. *Varanopus* and *Characichnos*, and yielded in the meandering river environment; and (2) the other composed of *Hyloidichnus* isp. and *Dimetropus leisnerianus*, and is yielded in the unconfined runoff surfaces (Fig. 12a).

The thick sandstone–mudstone layers from sections MA-A1a, MA-A1b and MA-B (Fig. 2a, b) represent meandering fluvial deposits. All these three sections present a similar pattern with abundant swimming tracks in the central-lower part and with footprints showing a walking behaviour in the other levels, probably impressed in drier conditions. Most of the ichnites are preserved on the mudstone layers deposited after the channel functionality (i.e. small ponds and oxbow lakes), so trackmakers inhabited channels during quieter environment conditions.

Extramorphological variations in *Limnopus* isp. tracks probably reflect different palaeoenvironments. The first morphology (Fig. 4a–f) may correspond to walking tracks in subaerial conditions (with wet and soft substrate) while the second morphology (Fig. 4g–i) corresponds to a mixture between subaerial and subaquatic conditions. The associated swimming tracks (*Characichnos* Type B; Fig. 11b–e) correspond to shallow-water environments. Section MA-A1a presents a succession from lower levels with abundant tracks of digit tips of *Limnopus* isp. and scratches of *Characichnos* Type B (10.20–10.50 m) to higher levels with *Limnopus* isp. walking gait tracks (18.15 m). Successive tetrapod track associations are observed in section MA-B (from base to top) as follows.

1. *Limnopus* isp. + cf. *Amphisauropus* + *Characichnos* Type B (15.50–16.50 m): tracks impressed in a relatively quiet environment. This association represents subaerial to subaquatic environments, as indicated by both walking and swimming tracks.
2. *Limnopus* isp. + *Characichnos* Types A and B + cf. *Amphisauropus* (16.50–17.50 m): abundant tracks of swimming gait (scratches) from higher water level interval (i.e. high flow-rate environment).
3. cf. *Amphisauropus* + *Characichnos* Type C + *Limnopus* isp. (17.75 m, track surface with two parts): in one part walking gait tracks without a preferential orientation, similar to those from the first domain, are abundant. These tracks may correspond to the higher part of the fluvial scroll. The other part is dominated by swimming scratches, which are assumed to be impressed in the deeper part of the channel.
4. cf. *Amphisauropus* (21.50 m and 23.80 m) + cf. *Ichniotherium* (23.20 m): tracks impressed in irregular surfaces corresponding to subaerial environments. *Limnopus* isp. tracks are sporadic. The occasional mudcracked surfaces with scratches and surfaces covered with notostracan trace fossils are indicative of channel desiccation after ichnites impression. The strata bearing these footprints are similar to the ignimbrites with unconfined runoff surfaces identified in sections MA-A2 and MA-A3 (Fig. 2a; supplementary Appendix S1, Fig. S1, available at http://journals.cambridge.org/geo).

Tetrapod footprints from sections MA-B and MA-A1a indicate a progressive drying process from the base to the top (from swimming to walking gait footprints). Interestingly, it has been suggested that seymouriamorphs (the potential cf. *Amphisauropus* trackmakers) and diadectomorphs (potential cf. *Ichniotherium* trackmakers) may have had ecological advantages during dry seasons (Falcon-Lang *et al.* 2010; Brink, Hawthorn & Evans, 2012). If confirmed, this could explain the dominance of these ichnotaxa in the upper part (fourth association) in section MA-B. On the other hand, section MA-A1b only yields *Limnopus* isp. tracks in one interval; this is probably due to the lack of surfaces cropping out, limiting palaeoenvironmental inferences.

The invertebrate ichnites (see supplementary Appendix S3, available at http://journals.cambridge.org/geo) from ichnoassociation 1, dominated by notostracan trace fossils (i.e. *Rusophycus* isp. and *Acripes multiformis*), are only identified in section MA-B; they are more abundant in the central part of the fluvial system deposits (supplementary Appendix S1, Fig. S1, available at http://journals.cambridge.org/geo). Trackmakers are likely to have required regular or constant water presence (Buatois *et al.* 1998; Avanzini *et al.* 2011). These conditions would have prevailed in the deepest part of the fluvial channel. Such environments would represent periods of transport inactivity of the channel

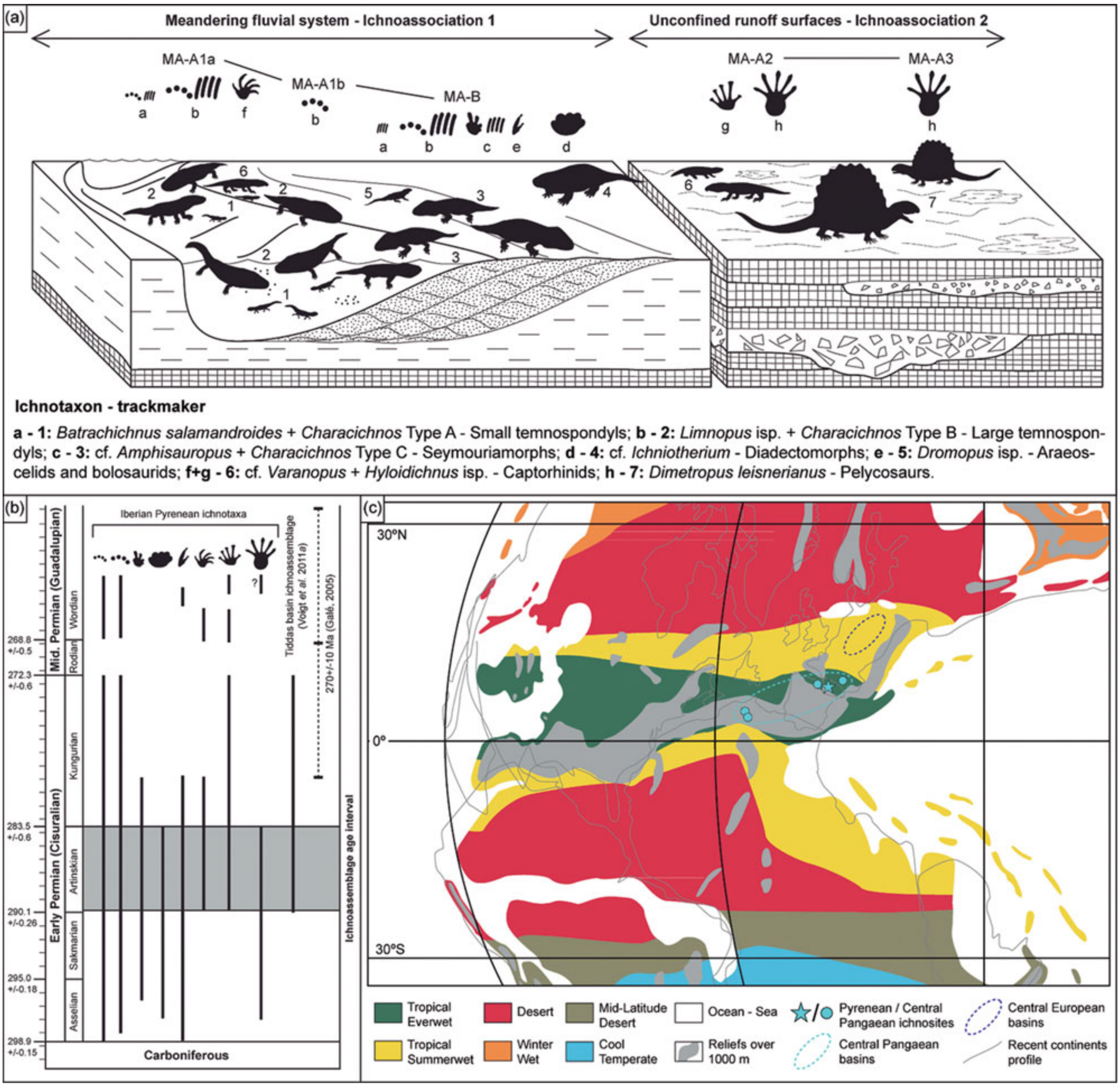

Figure 12. (Colour online) (a) Palaeoenvironments of the Pyrenean tetrapod ichnotaxa and potential trackmakers (tetrapod silhouettes and palaeoenvironmental settings are not scaled). (b) Ichnoassemblage age interval (grey area) for the Iberian Pyrenean tetrapod footprints. The age ranges of different ichnospecies are those of French, Italian, German and North American basins (after Gand & Durand, 2006; Lucas *et al.* 2011; Voigt, 2012; Marchetti *et al.* 2015*a*, *b*; Voigt & Haubold, 2015; Voigt & Lucas, 2015). The Tiddas Basin ichnotaxa, the most similar Moroccan ichnoassemblage to the Pyrenean assemblage, are not differentiated as they are on the same stratigraphic levels (see Voigt *et al.* 2011*a*). Question mark (?) on upper *Dimetropus leisnerianus* interval indicates dubious specimens. The radiometric dating cited in Galé (2005) overlaps with the potential age interval. Footprints intervals are calibrated to the current standard chronostratigraphic scale (available from http://www.stratigraphy.org). Silhouettes of the ichnites as in (a); modified from Gand & Durand (2006). (c) Palaeogeography from Ziegler *et al.* (1997) and palaeoclimate based on Rees *et al.* (2002), map for Artinskian stage (middle early Permian) and approximate positions of Central Pangaean and Central European basins.

due to the avulsion of the meandering system, which is consistent with the observed setting (small ponds and oxbow lakes).

Outwith the fluvial meandering environment, unconfined runoff surfaces are present and correspond to sections MA-2 and MA-A3. They consist of mud-draped ignimbrites, resulting from exposure to water runoff (Fig. 2c, d, i). The tetrapod footprints and trace fossils of *Helminthopsis* isp. are preserved on the surface of mudstone layers, while the undetermined trace fossils burrowed the ignimbrites (supplementary Appendix S1, Fig. S5, available at http://journals.cambridge.org/geo).

The *Hyloidichnus* isp. tracks are interpreted to have formed in humid and warm climate conditions (Gilmore, 1927; Gand, 1988). The flow in temporary water bodies formed ripples, while mudcracks are indicative of subaerial exposure and long dry periods

(Gand *et al.* 1997, 2011; Minter & Braddy, 2009). These features are recognized in the strata containing ichnoassociation 2. The tetrapod footprints could have been impressed both during and after the presence of water flow, when the substrate was soft. *Helminthopsis* isp. and burrows indicate shallow-water palaeoenvironments or moist substrate (Avanzini *et al.* 2011). The *Helminthopsis* isp. specimens overprint flow ripples. Consequently, these traces were formed after runoff flow within the presence of a body of water or a substrate with high water content.

Considering the tetrapod ichnofacies proposed by Hunt & Lucas (2006, 2007), the Iberian Pyrenean ichnoassemblage may correspond to both *Batrachichnus* and *Characichnos* ichnofacies (see also Minter & Braddy, 2009). The environment inferred for the *Batrachichnus* ichnofacies is a fluvial plain, whereas the environment for the *Characichnos* ichnofacies is a shallow lacustrine (see Hunt & Lucas, 2007). These environmental inferences are in accordance with our sedimentological results. Within the ichnoassemblage, *Limnopus* isp. and *Hyloidichnus* isp. are the most abundant specimens in ichnoassociations 1 and 2, respectively (Fig. 1c; supplementary Appendix S1, Fig. S1, available at http://journals.cambridge.org/geo). Ptaszyński & Niedźwiedzki (2004) proposed that such an abundance might be the result of: (1) gregarious behaviour of the trackmakers; or (2) habitat preferences. Otherwise, the high concentration of footprints and also invertebrate trace fossils is restricted to wetter palaeoenvironments during dry seasons (Falcon-Lang *et al.* 2010). Roscher & Schneider (2006) reported wet phases that interrupted the aridization transition from Carboniferous to Permian (see Section 5.d below); deposits from these time intervals may therefore also present a higher concentration of ichnites.

5.b. Ichnofaunal diversity and age

The ichnotaxa found in all the studied sections can be compared with those of other dated basins. *Amphisauropus* appears at the base of the Permian succession in Canada and Germany (Van Allen *et al.* 2005; Voigt, 2012), while the oldest *Ichniotherium* tracks are from Carboniferous deposits of Germany (Voigt & Ganzelewski, 2010) and the youngest tracks from upper lower Permian deposits of Morocco (Voigt *et al.* 2011*b*). *Hyloidichnus* ranges from the upper Artinskian (lower Permian) succession in the Lodève (Gand & Durand, 2006) and Midland basins (Gilmore, 1927; Lucas *et al.* 2011) to the middle–upper Permian deposits of the Argana Basin (Voigt *et al.* 2010), the Lodève Basin (Gand & Durand, 2006) and the Italian Southern Alps (Avanzini, Bernardi & Nicosia, 2011). *Dimetropus* is known from Carboniferous (Voigt & Ganzelewski, 2010) to Cisuralian (lower Permian) deposits (Gand & Durand, 2006; Voigt *et al.* 2011*a*). Haubold & Lucas (2003) and Voigt & Haubold (2015) pointed out that *Batrachichnus*, *Limnopus*, *Amphisauropus*, *Varanopus*, *Dimetropus* and *Dromopus* are characteristic ichnogenera of the Artinskian (upper lower Permian) deposits of Europe, Morocco and North America. The main difference in the Kungurian-aged and younger strata is the lack of *Erpetopus* (e.g. Haubold & Lucas, 2001, 2003; Hminna *et al.* 2012; Marchetti, Bernardi & Avanzini, 2013; Marchetti, Santi & Avanzini, 2014) and therapsid footprints (Gand *et al.* 2000; Avanzini, Bernardi & Nicosia, 2011).

The Peranera Formation base is aged 270 ± 10 Ma according to radiometric dating of calc-alkaline igneous rocks (see Galé, 2005). The underlying Malpàs Formation flora is dated as late Carboniferous – early Permian in age (Álvarez-Ramis & Doubinger, 1987; Talens & Wagner, 1995). Pereira *et al.* (2014) provided absolute ages for the ignimbrites and ignimbritic enclaves older that the studied strata (i.e. Erillcastell Formation and equivalents), resulting in an age range of *c.* 310–273 Ma (late Carboniferous – early Permian). A magmatic activity of *c.* 276–266 Ma (early–middle Permian) was also noted by Pereira *et al.* (2014). These age ranges are in agreement with our biostratigraphic results. Accordingly, the age of the present ichnoassemblage should be late early Permian (Fig. 12b), as pointed out by Voigt & Haubold (2015).

5.c. Footprint biogeography: late early Permian

Only the integrated discussion of ichnofaunal diversity, age and environmental constrictions (Fig. 12a) can support the palaeobiogeography of tetrapod footprints, probably linked to the palaeoclimatic patterns (Fig. 12b, c). The general palaeobiogeographic patterns can be inferred comparing different basins and stratigraphic succession of ichnotaxa (e.g. Gand & Durand, 2006; Voigt *et al.* 2011*a*, *b*).

The late early Permian (Artinskian) vertebrate fauna, based both on skeletal (Lucas, 2006) and ichnological (e.g. Gand & Durand, 2006; Hunt & Lucas, 2006; Voigt *et al.* 2011*a*; Voigt & Haubold, 2015) record, was worldwide uniform. However, the comparison of the Artinskian ichnoassemblages from Spanish, Southern French and Moroccan basins with that from the German Tambach Formation of Central Europe (Voigt, 2012) highlights differences in the presence and the relative abundance of certain ichnotaxa, probably due to environmental/climatic conditions or to an incorrect interpretation of the Tambach Formation age.

Ichnotaxa identified in the Iberian Pyrenean Basin are also present (at least at ichnogenus level) in nearby basins from Central Pangaea of this stage (Gand *et al.* 1997; Gand & Durand, 2006; Voigt *et al.* 2011*a*, *b*). These comparisons infer that the Central Pangaean faunas were dominated by amphibian temnospondyls, captorhinid eureptiles and also subordinated seymouriamorphans and synapsids such as pelycosaurs (Fig. 12a). Diadectomorphs were also present, represented by assumed *Ichniotherium* specimens, but their tracks are scarce and poorly preserved.

The Peña Sagra footprints (northern Spain) are found in a red-bed succession interpreted as shallow-water deposits that underwent frequent subaerial exposure (i.e. mudflat; Gand *et al.* 1997). This is indicated by the abundance and repeated occurrence of mudcracks and raindrop impressions, similarly to the Peranera Formation (Fig. 1c; supplementary Appendix S1, Fig. S1, available at http://journals.cambridge.org/geo). The low ichnotaxa diversity from Peña Sagra, possibly due to sampling bias, is correlated with the Rabejac Formation ichnoassemblage from the Lodève Basin (Gand *et al.* 1997). The palaeoenvironments from the Khenifra Basin middle and upper members (Central Morocco) are considered to belong to a floodplain with minor ponds and small lakes (Voigt *et al.* 2011*b*). The Tiddas Basin (Central Morocco) footprints are preserved in a succession of reddish-brown sandstones, siltsones and mudstones attributed to deposits of an episodically inundated mudflat (Voigt *et al.* 2011*a*). The sedimentological data from the French Permian basins (e.g. Lodève, Saint-Affrique, Gonfaron) indicate lacustrine, playa, fluviatile and floodplain palaeoenvironments for the tracksites (Demathieu, Gand & Toutin-Morin, 1992; Gand & Durand, 2006). Roscher & Schneider (2006) inferred a dominantly fluvial environment for the Lodève Basin, a floodplain setting with periodically water-filled ponds, sheetfloods, braided rivers and adjacent lakes. Homogeneous ichnoassemblages conditions are therefore considered for the Central Pangaean basins of this period, with prevailing mudflat and floodplain palaeoenvironments.

The comparison with Central Europe reveals differences in the proportions of the assumed Artinskian ichnoassemblages, as well as in the presence of some ichnogenera. In Central Pangaea the dominating ichnotaxa are *Batrachichnus* and *Limnopus* (Gand, 1988; Gand & Durand, 2006; Lucas *et al.* 2011), whereas *Ichniotherium* is the most abundant in Central Europe (Germany; see Voigt, 2005, 2012).

Ichniotherium is also reported in Morocco (*I. sphaerodactylum*; Voigt *et al.* 2011*b*), southern France (cf. *Ichniotherium*; Gand, 1989; Gand & Durand, 2006), North America (Voigt, Small & Sanders, 2005), and Canada (Brink, Hawthorn & Evans, 2012). Nevertheless, the presence of *Ichniotherium* is scarce in the low latitudes of Pangaea, in Morocco only a partial track has been reported and in southern France specimens are not abundant and of dubious attribution (see Gand & Durand, 2006). In the present work, assumed *Ichniotherium* specimens (Fig. 6) preserved in a peculiar substrate (medium to fine sandstone with rough aspect) are reported. The ichnogenus *Hyloidichnus* has not been reported in Central Europe (see Voigt, 2005, 2012 for a discussion), but it is present in Central Pangaea except in the Khenifra Basin (Voigt *et al.* 2011*b*).

5.d. Palaeoclimatic ichnoassemblage zones: late early Permian

The trend of the late Palaeozoic global climate was the transition from humid conditions during Carboniferous time to the development of arid and semiarid environments during early–middle Permian time (e.g. Haubold, 1985; Gascón & Gisbert, 1987; Schneider *et al.* 2006). This aridization process, influenced by the distribution of the land masses (i.e. the Pangaea supercontinent), resulted in the development of the globally known red-bed deposits (Chumakov & Zharkov, 2002; Gibbs *et al.* 2002; Roscher & Schneider, 2006; Michel *et al.* 2015). In the upper parts of sections MA-B and MA-A1a (Fig. 1c; supplementary Appendix S1, Fig. S1, available at http://journals.cambridge.org/geo), palaeosols resemble those attributed by Gascón & Gisbert (1987) to a tropical steppe climate with relatively low annual precipitation (250–450 mm/year), which is also in accordance with the low-latitude Permian aridization.

The homogeneity of the Central Pangaean ichnoassemblages and palaeoenvironments indicates a diffuse Gondwana–Laurasia boundary during early Permian time, which might suggest a possible palaeogeographic continuity and widespread palaeoenvironmental conditions. This is in accordance with Roscher & Schneider (2006), who suggested that the Trans-Pangaean Belt did not exist and the Variscan Chain maximum elevation migrated through the continent due to the Gondwanian clockwise rotation. On the other hand, Sinisi *et al.* (2014) pointed out that the more humid conditions (with punctual arid episodes) in Central Pangaea were influenced by the presence of the South European Variscan Chain. The latter could have influenced climate but was not a geographic barrier for faunal distribution in Central Pangaea, as suggested by the similarity of the ichnoassemblages discussed above.

Rees *et al.* (2002) performed a palaeoclimatic model for the Sakmarian and established latitudinal biomes equivalent to present day different climates. In a tentative palaeogeographic (from Ziegler, Hulver & Rowley, 1997) and palaeoclimatic (based on Rees *et al.* 2002) reconstruction during Artinskian time (Fig. 12c), Central Pangaean basins are situated in the tropical everwet biome (in the sense of Rees *et al.* 2002: tropical, humid, minimum of 40 mm of precipitation per month during all year), whereas the Central European basins are in the tropical summerwet biome (in the sense of Rees *et al.* 2002: tropical, humid summers or semihumid, minimum of 40 mm of precipitation per month during summer season; see also Chumakov & Zharkov, 2002; Gibbs *et al.* 2002; Roscher & Schneider, 2006; Schneider *et al.* 2006; Michel *et al.* 2015). These climate variations could explain the differences observed between the Central Pangaean and Central European basins as described in Section 5.c above. We therefore suggest a climatic control for the fauna distribution among Pangaea, as has been previously suggested for the (?)middle–late Permian deposits of Niger (Sidor *et al.* 2005), rather than different environmental conditions or different ages of the tracksites. Nevertheless, these possibilities cannot be discarded at the present state of knowledge.

6. Conclusions

1. The study of diagnostic morphological features of selected material, with the aid of photogrammetric techniques, has enhanced systematic determinations. The Permian Iberian Pyrenean Basin yields unexpected ichnofaunal diversity. This ichnoassemblage comprises *Batrachichnus salamandroides*, *Limnopus* isp., cf. *Amphisauropus*, cf. *Ichniotherium*, *Dromopus* isp., cf. *Varanopus*, *Hyloidichnus* isp., *Dimetropus leisnerianus* and three types of *Characichnos*. Based on biostratigraphic correlations, this ichoassamblage could be late early Permian in age (Artinskian).

2. Two ichnoassociations appear restricted to water-laid deposits within a volcaniclastic succession. The comparison with other ichnoassociations of late early Permian Pangaea allows any biostratigraphic change in the studied sections to be excluded. Instead, each ichnoassociation suggests distinctive palaeoenvironmental conditions. Ichnoassociation 1 is found in meandering fluvial deposits. Water fluctuations are inferred by the type of tetrapod footprints, which suggest both subaqueous (scratches and digit tip tracks) and subaerial palaeoenvironments (plantigrade or semiplantigrade tracks). Ichnoassociation 2 is found in unconfined runoff surfaces (mudflats covering pyroclastic flows), where the tetrapod footprints record a walking gait. Mudcracks and raindrop impressions are present in all sections, suggesting dry seasonal conditions.

3. Our data suggest that the South European reliefs of the Variscan Chain could have influenced climate, but it was not a geographic barrier preventing faunal distribution through different sites of Artinskian Central Pangaea.

4. The ichnites suggest that, at that time, climate was wetter in Central Pangaea than in Central Europe. The Central Pangaean basins are indeed dominated by ichnofauna constricted to wetter environments (i.e. *Batrachichnus* and *Limnopus*), whereas in Central European basins the most common ichnofauna are those from inland drier settings (i.e. *Ichniotherium*). Some common ichnotaxa from Central Pangaea (i.e. *Hyloidichnus*) are also absent from Central Europe. It should be noted that data on assumed late Cisuralian sites of Central Europe are few; further studies are therefore reccomended. The available information supports previous climatic models, stressing the potential of ichnites in palaeoenvironmental and palaeoclimatic reconstructions and suggesting climatic control on faunal distribution within Pangaea.

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Declaration of interest

None.

Supplementary material

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