geodiversitas

2022 • 44 • 31

New data on the Permian ecosystem of the Rodez Basin: ichnofauna (traces of protostomians, tetrapods and fishes), jellyfishes and plants from Banassac-Canilhac (Lozère, southern France)

Jean-David MOREAU & Georges GAND

art. 44 (31) — Published on 10 November 2022
www.geodiversitas.com

PUBLICATIONS SCIENTIFIQUES

MUSÉUM NAL HIST NATURELLE

Couverture / *Cover* :
Réalisée à partir des Figures de l'article/*Made from the Figures of the article*.

Geodiversitas est indexé dans / Geodiversitas *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Physical, Chemical, and Earth Sciences®
- Scopus®

Geodiversitas est distribué en version électronique par / Geodiversitas *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par /
Articles and nomenclatural novelties published in Geodiversitas *are referenced by:*
- ZooBank® (http://zoobank.org)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:* ***Adansonia***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie***, ***Comptes Rendus Palevol***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

New data on the Permian ecosystem of the Rodez Basin: ichnofauna (traces of protostomians, tetrapods and fishes), jellyfishes and plants from Banassac-Canilhac (Lozère, southern France)

Jean-David MOREAU
Georges GAND
UMR CNRS 6282 Biogéosciences, Université de Bourgogne Franche-Comté,
6 boulevard Gabriel, F-21000 Dijon (France)
jean.david.moreau@gmail.com (corresponding author)
georgesb.gand@orange.fr

Submitted on 3 December 2021 | accepted on 7 April 2022 | published on 10 November 2022

urn:lsid:zoobank.org:pub:008AF7BE-28B6-4FB5-A007-45BAB4337BAC

Moreau J.-D. & Gand G. — New data on the Permian ecosystem of the Rodez Basin: ichnofauna (traces of protostomians, tetrapods and fishes), jellyfishes and plants from Banassac-Canilhac (Lozère, southern France). *Geodiversitas* 44 (31): 975-987. https://doi.org/10.5252/geodiversitas2022v44a31. http://geodiversitas.com/44/31

ABSTRACT
The tetrapod tracksite from Le Bousquet (Permian, Red Sandstone Group from the Rodez Basin, southern France) was discovered during the second half of the 20th century. At this time, the tracksite was only weakly prospected and underestimated. Deposits exposed near Le Bousquet were recently re-investigated. New prospections led to: 1) enlargement of the tetrapod ichnofauna (*Amphisauropus latus* Haubold, 1970, *Batrachichnus salamandroides* Geinitz, 1861, *Characichnos* isp., *Ichniotherium* isp. and *Varanopus* isp.); and 2) discovery of protostomian traces (*Diplopodichnus biformis* Brady, 1947, *Scoyenia gracilis* White, 1929), swimming traces of fishes (*Undichna* cf. *britannica* Higgs, 1988), rare freshwater jellyfishes (*Medusina atava* (Pohlig, 1892) Walcott, 1898) as well as terrestrial plant remains including leafy axes of conifers (cf. *Walchia*). Such a palaeontological assemblage is for the first time reported from the Permian deposits of the Rodez Basin. The depositional environment is interpreted as a fluvial zone periodically flooded and emergent, corresponding to a lake/playa system bordered by conifer-dominated forests. Ichnofossils suggest that the tetrapod fauna from Le Bousquet was mainly composed of anamniotes (diadectomorphs, seymouriamorphs, temnospondyls) whereas amniotes (captorhinid reptiles) were less common.

KEY WORDS
Rodez Basin,
Permian,
Tetrapod tracks,
invertebrate traces,
Cisuralian,
photogrammetry.

RÉSUMÉ
Nouvelles données sur l'écosystème permien du Basin de Rodez : ichnofaune (traces de protostomiens, tétrapodes et poissons), méduses et plantes de Banassac-Canilhac (Lozère, Sud de la France).
Le site à traces de pas de tétrapodes du Bousquet (Permien, Groupe du Grès Rouge, Bassin de Rodez, Sud de la France) a été découvert durant la seconde moitié du XXème siècle. Sous-estimé, il n'a été que très peu prospecté durant cette période. Le site du Bousquet a récemment été réinvestigué. De nouvelles prospections ont permis de : 1) compléter l'ichnofaune de tétrapodes (*Amphisauropus latus* Haubold, 1970, *Batrachichnus salamandroides* Geinitz, 1861, *Characichnos* isp., *Ichniotherium* isp. et *Varanopus* isp.) ; et 2) découvrir des traces de protostomiens (*Diplopodichnus biformis* Brady, 1947, *Scoyenia gracilis* White, 1929), des traces de nage de poissons (*Undichna* cf. *britannica* Higgs, 1988), de rares méduses d'eau douce (*Medusina atava* (Pohlig, 1892) Walcott, 1898) ainsi que des restes de plantes terrestres incluant des axes feuillés de conifères (cf. *Walchia*). Un tel assemblage paléontologique est pour la première fois signalé dans le Permien du Bassin de Rodez. L'environnement de dépôt est interprété comme une zone fluviale périodiquement immergée puis émergée, qui correspondait à un système de lac/playa bordé par des forêts de conifères. Les ichnofossiles suggèrent que la faune de tétrapodes du Bousquet était principalement composée de non amniotes (diadectomorphes, seymouriamorphes et temnospondyles) alors que les amniotes (reptiles captorhinidés) étaient moins communs.

MOTS CLÉS
Bassin de Rodez,
Permien,
traces de tétrapodes,
traces d'invertébrés,
Cisuralien,
photogrammétrie.

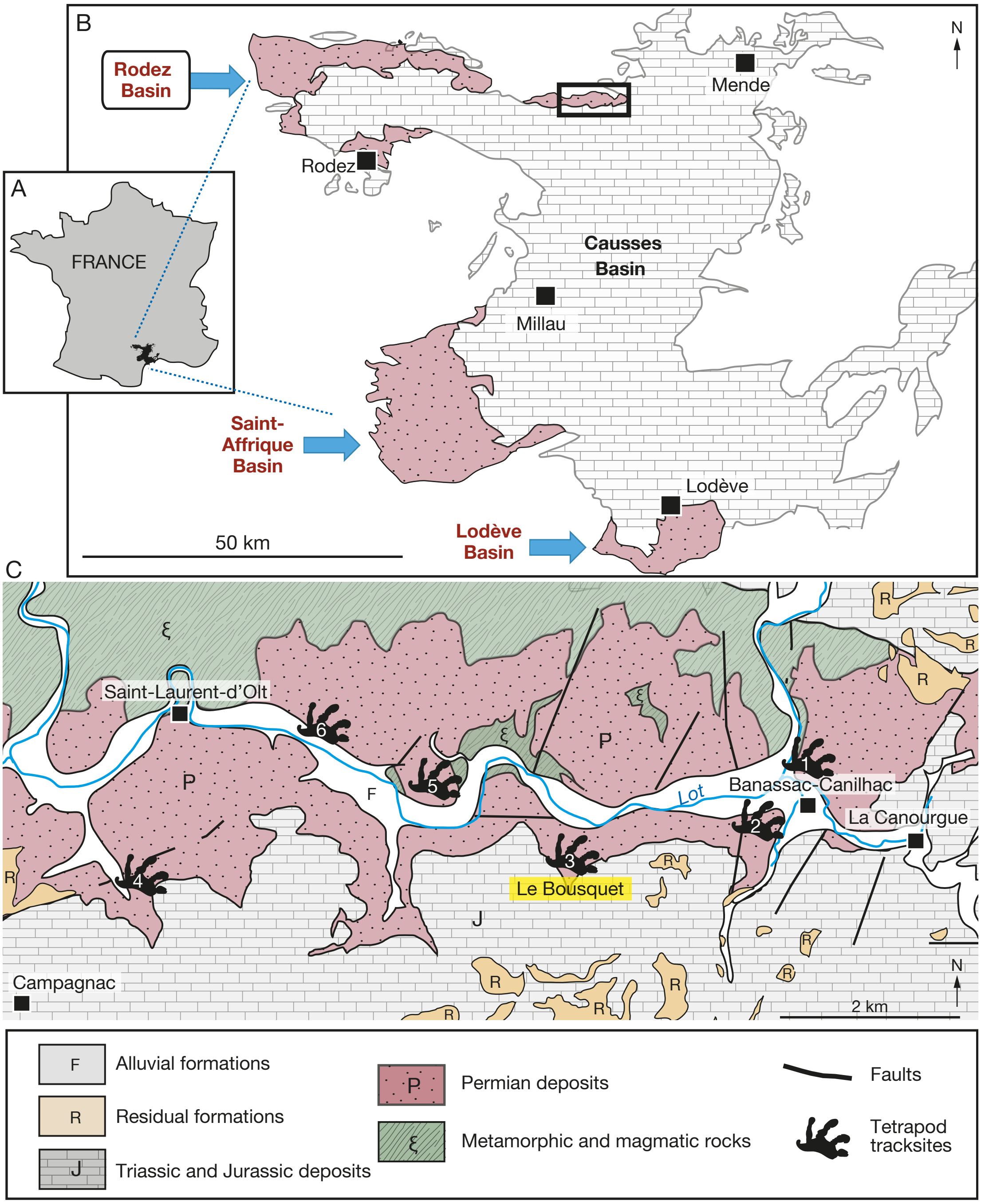

Fig. 1. — Geographical and geological context: **A**, Location of the study area in France; **B**, Location of the Rodez Basin, and location of La Canourgue/Campagnac area (indicated by the black rectangle); **C**, Simplified geological map of La Canourgue/Campagnac area (modified after Defaut *et al.* 1990) and location of tracksites mentionned in Gand (1987): **1**, La Forêt; **2**, Cantacoyou; **3**, Le Bousquet; **4**, Route du Viaduc; **5**, Malvezy; **6**, Saint-Laurent.

INTRODUCTION

Permian basins of France are known to yield ichnofossils that are a key for the reconstruction of late Palaeozoic faunas (Gand 1987; Gand & Durand 2006). Dozens of tracksites were reported from the Autun (Heyler 1984), Blanzy-Le Creusot (Gand 1981), Brive-la-Gaillarde (Gand 1991), Largentière (Gand 1993a), Lodève (Ellenberger & Ellenberger 1959; Heyler & Lessertisseur 1963; Ellenberger 1983a, b, 1984; Gand 1986, 1994; Gand *et al.* 2000, 2008; Mujal & Marchetti 2020), Provence (Gand 1980; Demathieu *et al.* 1992; Gand *et al.* 1995; Logghe *et al.* 2021), Rodez (Gand 1987) and Saint-Affrique basins (Gand & Haubold 1984; Gand 1985, 1993b). The largest amount of tracks was discovered in southern France, especially in the southern part of the Massif Central where the Permian red beds from the Lodève, Rodez and Saint-Affrique basins yield diverse vertebrate and invertebrate trackways (Fig. 1A, B). Whereas tracksites from Lodève and Saint-Affrique were greatly studied during many decades (Ellenberger & Ellenberger 1959; Heyler & Lessertisseur 1963; Ellenberger 1983a, b; Gand 1986, 1994; Gand *et al.* 2000, 2008) those from the Rodez Basin appear to have been less deeply investigated (Gand 1987).

Since the second half of the 19th century, the Rodez Basin has been known to yield tetrapod tracks (Fabre 1872). Three areas from the Rodez Basin show tracksites, La Canourgue/Campagnac, Rodez and Sermels (Gand 1987; Fig. 1C). It is near La Canourgue/Campagnac that the largest number of tracksites were discovered (Gand 1987). One of these tracksites, called "Le Bousquet", was recently re-investigated. The new prospecting revealed a diversified palaeontological assemblage showing the co-occurrence of tetrapod, protostomian and fish trails with jellyfishes and terrestrial plants. This discovery considerably enlarges the fossil diversity of the site. Here, we describe in detail this new and uncommon palaeontological assemblage in order to discuss the palaeoecosystem and palaeoenvironment of the Permian red beds from the area of La Canourgue/Campagnac.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Rodez Basin is a large graben constituting an enclave of sedimentary rocks inside metamorphic and plutonic rocks of the south of the Massif Central (southern France; Fig. 1A, B). Being oriented East-West, 80 km long and 20 km wide, the basin covers an area of about 1500 km^2 (Châteauneuf & Gand 1989; Fig. 1B). The age of its sedimentary rocks ranges from the Carboniferous to the Jurassic (Becq-Giraudon 1986). Jurassic deposits extend toward the East in the Causses Basin (Fig. 1B). The Permian deposits of the Rodez Basin are divided into two groups, the Salabru Group and the Red Sandstone Group (Bourges 1988). The first consists of sandstones and conglomerates alternating with black pelites and dolomites (Defaut *et al.* 1990). The second consists of red pelites, sandstones and conglomerates alternating with rare dolomitized beds (Defaut *et al.* 1990).

The area of La Canourgue/Campagnac is located in the easternmost part of the Rodez Basin (Fig. 1B, C). Tracksites from this area are located in the Red Sandstone Group (Gand 1987; Becq-Giraudon & Fuchs 1989). At La Canourgue/Campagnac, fossils are rare in this group (Alabouvette *et al.* 1989), being limited to plant remains and tracks. Fabre (1872) was the first to report indeterminate plant remains and tetrapod tracks at Malvesy (Fig. 1C). Over a century later, and based on specimens from the private collection of D. Naudin, Gand (1987) reported five additional Permian tracksites at La Canourgue/Campagnac: Cantacoyou, La Forêt, Le Bousquet, Route du Viaduc, and Saint-Laurent (Fig. 1C).

The material presented here comes from Le Bousquet. This tracksite is located in the Lozère department, 3.5 km west of Banassac-Canilhac (Fig. 1C). The tracksite is located in a small ravine near the hamlet of Le Bousquet. At this place, without describing it, Gand (1987) briefly mentioned vertebrate tracks he assigned to *Anthichnium salamandroides* Geinitz, 1861 (synonym of *Batrachichnus salamandroides*), *Ichniotherium cottae* Pohlig, 1885 and *Varanopus* isp.

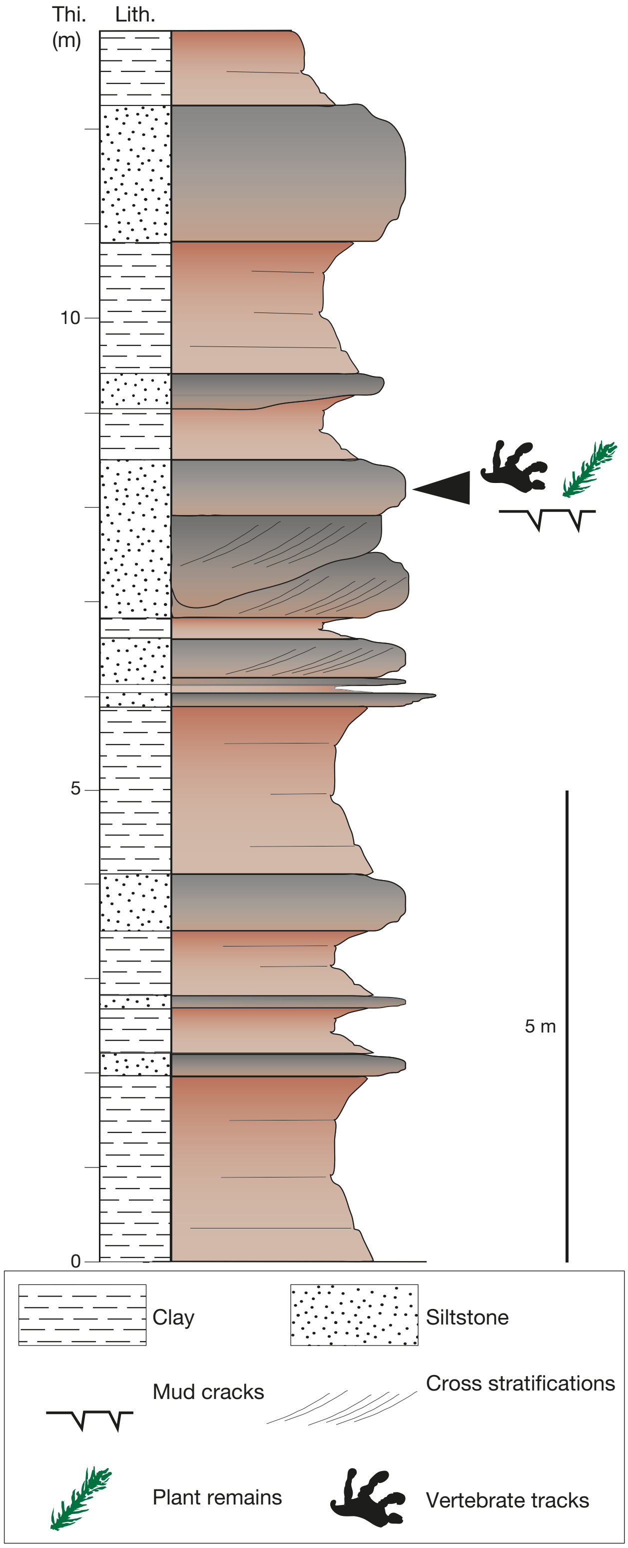

Fig. 2. — Stratigraphic section of Le Bousquet and location of the fossiliferous bed. Abbreviations: **Thi.**, thickness; **Lith.**, lithology.

MATERIAL AND METHODS

At Le Bousquet, a 13 m high outcrop shows an alternation of reddish argillites and pelites (Fig. 2). Prospecting led by one of us (JDM) in 2020 and 2021 revealed a fossiliferous layer between 8.0 and 8.5 m (Fig. 2). The bed consists of a reddish pelitic layer organised in thinly laminated and planar slabs bearing mudcracks that form polygons. It yields abundant invertebrate traces, tetrapod trackways and fish trails. Conifer leafy axes as well as rare jellyfishes co-occur on track-bearing surfaces. The specimens are housed in the palaeontological collections of the Musée du Gévaudan (Mende, Lozère).

The descriptive terminology and biometric parameters used to study the tetrapod tracks follow Haubold (1971) and Leonardi (1987). We used the following standard abbreviations: ML, length of manus track; MW, width of manus track; ML/MW, length to width ratio of manus track; PL, length of pes track; PW, width of pes track; and PL/PW, length to width ratio of pes track.

3D photogrammetric reconstructions (Matthews *et al.* 2016) were produced with the software Agisoft PhotoScan Professional 1.2.4. The same software was used to produce photogrammetric digital elevation models and contours. Pictures of the surfaces were taken with a Nikon D5200 camera coupled with an AF-S Nikkor 18-105 mm f/3.5-5.6G ED lens.

SYSTEMATIC PALAEONTOLOGY

Jellyfishes

Family indet.
Genus *Medusina* Walcott, 1898

Medusina atava (Pohlig, 1892) Walcott, 1898
(Fig. 3A, B)

Material examined. — One specimen; M486_2022.1.9.

Description

The specimen is umbrella-shaped and 16 mm in diameter. The velum is locally visible, forming an up to 3.3 mm wide marginal thickening. The jellyfish bears 10, thin, quite straight and radially arranged furrows originating from the centre and corresponding to radial canals (Fig. 3A, B). Most furrows join the periphery of the jellyfish. The centre of the jellyfish shows an up to 8 mm wide, star-shaped and concave structure corresponding to the manubrium (Fig. 3A, B).

Remarks

Medusina atava was reported in Permian deposits from France (Gand *et al.* 1996), Germany (Schüppel 1984) and Italy (Ronchi & Santi 2003). In the Saint-Affrique Basin, both species *Medusina atava* and *Medusina limnica* Müller, 1978 are known from some Permian sites (Gand *et al.* 1996). However, *Medusina* is for the first time reported in the Permian deposits of the Rodez Basin. *M. limnica* is mainly distinguished from *M. atava* by showing a maximum of four radial canals. Amongst *M. atava* the number of radial canals is variable and can reach a number of ten (Schüppel 1984; Gand *et al.* 1996).

Traces of protostomians

Ichnogenus *Diplopodichnus* Brady, 1947

Diplopodichnus biformis Brady, 1947
(Fig. 3C, D)

Material examined. — Seven traces; four traces preserved as convex hyporeliefs on slab M486_2022.1.1; three traces preserved as convex hyporeliefs on slab M486_2022.1.2.

Description

Traces are horizontal, unbranched, straight to curved, run in different directions and up to 3.0 mm wide. The longest course is 72 mm. The traces consist of two thin and up to 1.4 mm wide parallel hypichnial ridges separated by a central groove that is up to 0.8 mm wide (Fig. 3C, D).

Remarks

The ichnogenus *Diplopodichnus* Brady, 1947 is reported from the Late Proterozoic to the Early Jurassic (Buatois *et al.* 1998; Uchman *et al.* 2011 and references therein). *D. biformis* is widely recorded in Palaeozoic deposits including many occurrences in Permian formations worldwide (e.g. Brady 1947; Lucas *et al.* 2004, 2005; Contardi & Santi 2009; Avanzini *et al.* 2011a; Lima & Netto 2012; Moreau *et al.* 2020).

Ichnogenus *Scoyenia* White, 1929

Scoyenia gracilis White, 1929
(Fig. 3C, D)

Material examined. — Two burrows; one is preserved as concave epirelief on slab M486_2022.1.3; the other is preserved as convex hyporelief on slab M486_2022.1.2.

Description

Burrows are unbranched, and straight to slightly curved. They are circular to oval in transverse section, up to 15 mm in diameter and horizontally, obliquely to vertically oriented (Fig. 3C, D). The surface of burrows shows longitudinal striations. Longitudinal sections of burrows show prominent meniscate backfills (Fig. 3C, D).

Remarks

Scoyenia gracilis is a very common ichnospecies in non-marine Permian deposits (Buatois *et al.* 1997). This ichnotaxon was abundantly reported from some Permian tracksites of the basins of Saint-Affrique and Lodève (e.g. Lopez *et al.* 2008).

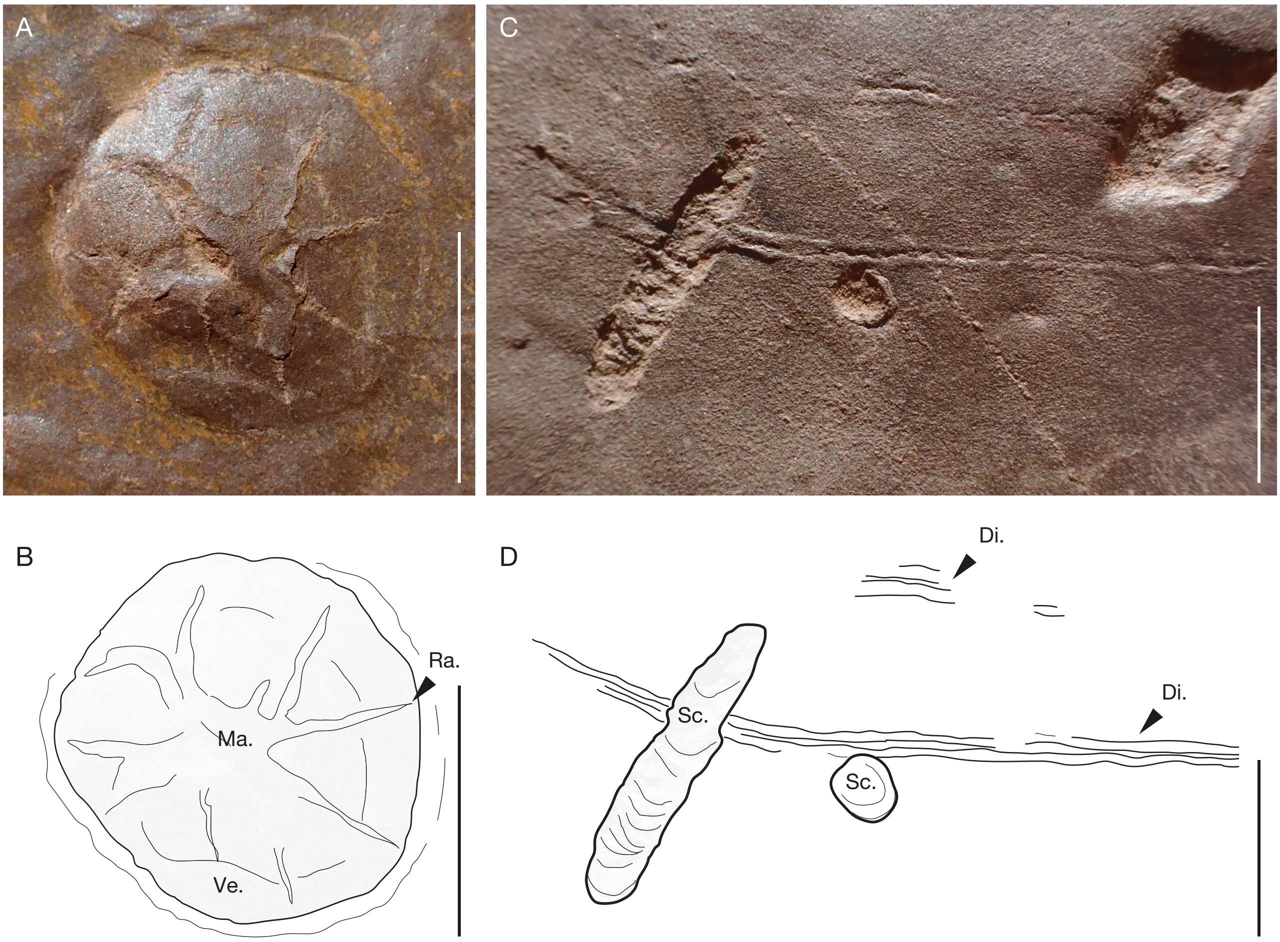

Fig. 3. — Jellyfish and protostomian traces: **A, B**, *Medusina atava* (Pohlig, 1892) Walcott, 1898, photograph (**A**) and interpretative sketch (**B**), specimen M486_2022.1.9; **C, D**, *Diplopodichnus biformis* Brady, 1947 (**Di.**) and *Scoyenia gracilis* White, 1929 (**Sc.**); photograph (**C**) and interpretative sketch, specimen M486_2022.1.2. Abbreviations: **Ma.**, manubrium; **Ra.**, radial canals; **Ve.**, velum. Scale bars: 1 cm.

Tracks of tetrapods

Ichnogenus *Amphisauropus* Haubold, 1970

Amphisauropus latus Haubold, 1970
(Fig. 4)

Material examined. — Eight tracks preserved as concave epireliefs on slab M486_2022.1.5.

Description

The trackway is 13 cm long, 6 cm wide and composed of four consecutive pes/manus sets (Fig. 4A, B). Pes and manus stride is 6.4-6.5 cm long. The manus tracks are more internal than pes tracks. Both are small sized and semi-plantigrade. Pes imprints are pentadactyl and wider than long (PL = 1.1 cm, PW = 1.8-2.0 cm; Fig. 4). The PL/PW ratio is equal to 0.6. Digit imprints are short, straight to slightly curved and end in an enlarged rounded tip (Fig. 4C-E). Pes tracks show a short, large and poorly impressed sole with concave proximal margin. The manus tracks are strongly oriented inward, forming an angle of up to 120° with the trackway axis. Manus imprints are pentadactyl and wider than long (ML = 0.9-1.1 cm; MW = 1.6-1.9 cm; ML/MW = 0.6). Imprints of digits are short and end in a small enlarged rounded tip. The manual digits II-III bent inwards. The divarication angle of digits I-V is up 153°.

Remarks

As noted by Gand *et al.* (2000) *Amphisauropus* Haubold, 1970 shares similarities with *Merifontichnus* Gand, Garric, Demathieu & Ellenberger, 2000. Tracks from Le Bousquet differ from this latter by smaller size and the pedal digit I not parallel to the proximal margin of the sole. Although tracks from Le Bousquet share some similarities with *Dolomitipes* Marchetti, Voigt & Klein, 2017, this ichnogenus differs in showing manus tracks placed in line or slightly external to the pes, and pedal tracks longer than wide or about as wide as long and 40 to 250 mm long (Marchetti *et al.* 2019). *Amphisauropus* represents a widespread Permian ichnogenus that has been reported from many areas including Africa (Voigt *et al.* 2011; Hminna *et al.* 2012; Moreau *et al.* 2020); Argentina (Melchor & Sarjeant 2004); Canada (Mossman & Place 1989; van Allen *et al.* 2005); Europe (e.g. Gand & Haubold 1984; Gand 1987; Haubold 1971; Santi & Krieger

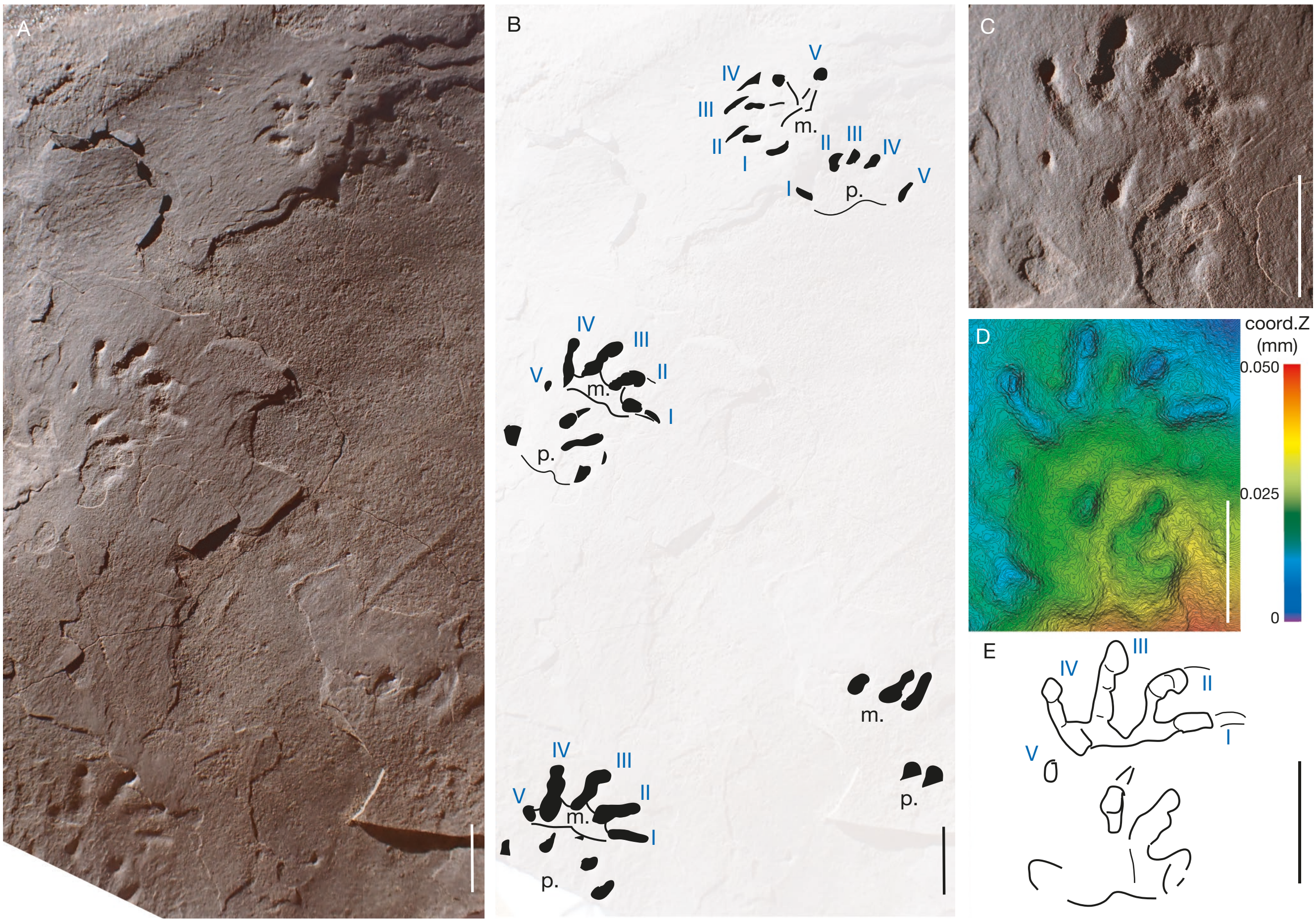

Fig. 4. — *Amphisauropus latus* Haubold, 1970: **A, B**, slab bearing a trackway with four consecutive pes/manus sets, photograph (**A**) and interpretative sketch (**B**). **C-E**, pes/manus set; photograph (**C**), digital elevation model in false colours (**D**) and interpretative sketch (**E**). Concave epireliefs, specimen M486_2022.1.5. Abbreviations: **p.**, pes track; **m.**, manus track. Scale bars: 1 cm.

2001; Ptaszyński & Niedźwiedzki 2004; Voigt 2005; Avanzini *et al.* 2008; Voigt *et al.* 2012; Marchetti *et al.* 2015) and the United States (Lucas *et al.* 2001). In France, *Amphisauropus* was previously reported from the Lodève Basin (Gand & Durand 2006) and the Rodez Basin (Gand 1987). Although Gand (1987) reported *Amphisauropus* in several localities near Banassac-Canilhac this ichnogenus is here for the first time reported from Le Bousquet.

Ichnogenus *Batrachichnus* Woodworth, 1900

Batrachichnus salamandroides Geinitz, 1861
(Fig. 5)

Material examined. — Six tracks; four tracks preserved as concave epireliefs and convex hyporeliefs on slabs M486_2022.1.6A and M486_2022.1.6B, respectively; two tracks preserved as concave epireliefs on slab M486_2022.1.7.

Description

The tracks are small, plantigrade to semi-plantigrade. Pes imprints are pentadactyl and longer (PL = 1.5-4.0 mm) than wide (PW = 1.3-3.8 mm; Fig. 5A-E) to as long as wide. The ratio PL/PW varies from 1.0-1.2. Digit imprints are straight and end in an enlarged, rounded tip (Fig. 5C-E). The divarication angle of digits I-V is up 85°. Pes tracks show a large rounded and well-marked sole (Fig. 5C-E). Manus imprints are tetradactyl, smaller than pes tracks and as long (ML=1.3-2.3 mm) as wide (MW=1.3-2.8 mm) to slightly wider than long. The ML/MW ratio varies from 0.8 to 1.0. Digit imprints are straight and end in an enlarged, rounded tip. The divarication angle of digits I-IV varies from 46° to 73°. Manus tracks show a short and large sole with a concave proximal margin (Fig. 5A, B).

Remarks

The presence of the tetradactyl manus imprints as well as the rounded digit apex are characteristic of the ichnogenera *Batrachichnus* Woodworth, 1900 and *Limnopus* Marsh, 1894. The two ichnogenera are distinguished based on their sizes. Manus imprints of *Batrachichnus* are less than 40 mm in length whereas tracks of *Limnopus* are larger (up to 200 mm in length; Voigt & Lucas 2018). Regionally, the ichnospecies *Batrachichnus salamandroides* was reported from the Saint-Affrique Basin (Gand 1987, 1993b; Gand & Haubold 1984), the Lodève Basin (Ellenberger 1983b; Gand & Durand 2006) and the Rodez Basin (Gand 1987). The ichnospecies *Batrachichnus*

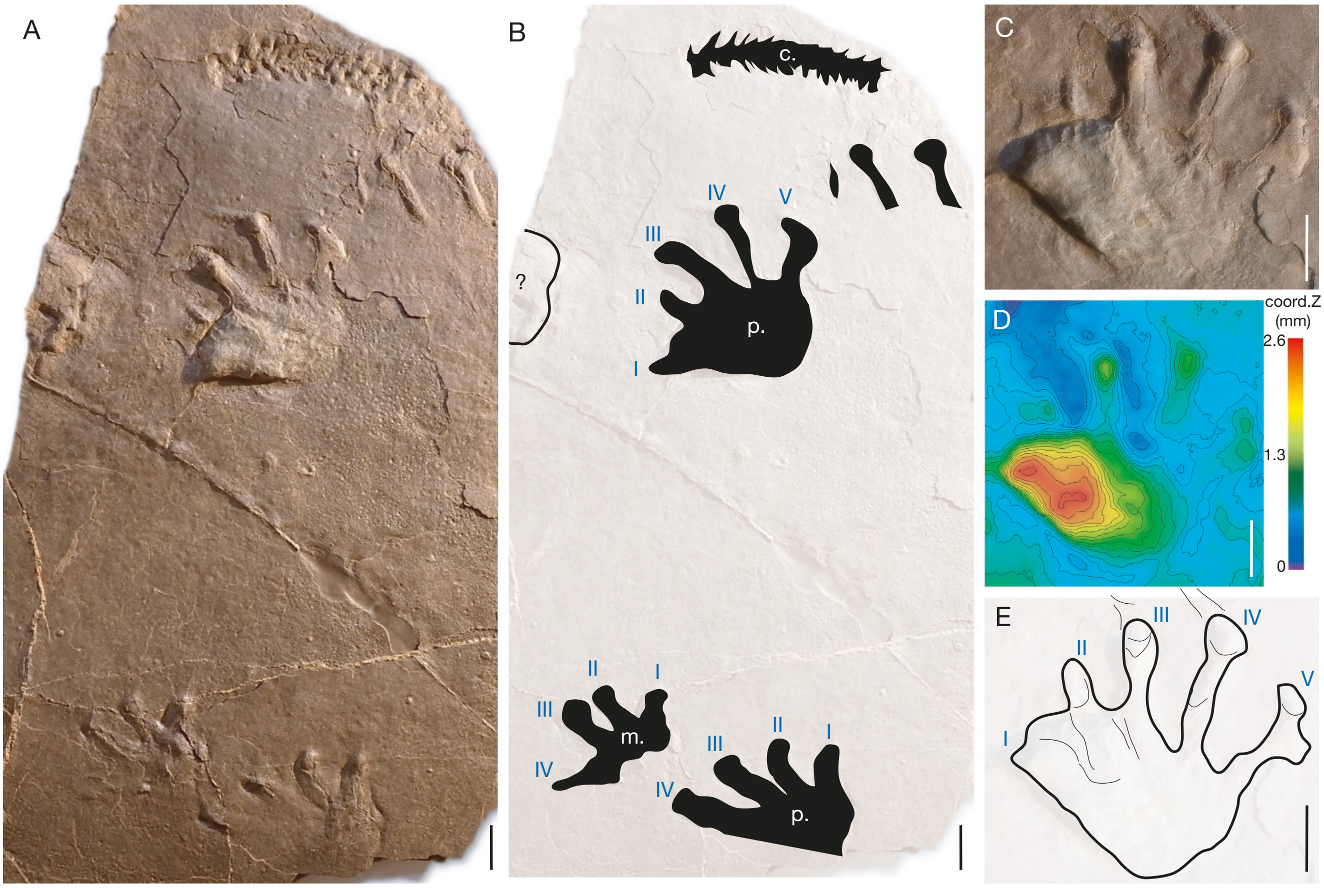

Fig. 5. — *Batrachichnus salamandroides* Geinitz, 1861: **A**, **B**, slab bearing a trackway with pes (**p.**) and manus (**m.**) track (a pes/manus set in visible in the bottom part of the picture), and co-occurring with a conifer leafy axis (**c**) (cf. *Walchia*, in the top of the picture), photograph (**A**) and interpretative sketch (**B**); **C-E**, pes track, photograph (**C**), digital elevation model in false colours (**D**) and interpretative sketch (**E**). Convex hyporeliefs, M486_2022.1.6B. Scale bars: 1 cm.

salamandroides was also reported from southeastern France, in the Estérel Basin (Provence; Gand & Durand 2006). This ichnospecies is for the first time reported from Le Bousquet.

Ichnogenus *Ichniotherium* Pohlig, 1892

Ichniotherium isp. (Fig. 6)

Material examined. — Two tracks preserved as concave epireliefs and convex hyporeliefs on slabs M486_2022.1.4A and M486_2022.1.4B, respectively.

Description

The material includes a single pes/manus set (Fig. 6A, B). The tracks are medium sized and plantigrade. The pes track is pentadactyl and as long as wide to wider than long (PL = 5.8 cm, PW = 6.3 cm). The PL/PW ratio is equal to 0.9. On the pes track, digit impressions are only impressed distally, forming a rounded tip (Fig. 6A, B). The manus track is pentadactyl, smaller than pes track and wider than long (ML = 3.8 cm; MW = 5.2 cm; ML/MW = 0.7). Digit impressions increase in length from I to IV. Proximally digits show transverse and thin grooves. The divarication angle of digits I-V is 81°. On the manus track, digit imprints are short, large, straight and end in an enlarged rounded termination. Digits are more impressed distally. The impression of digit IV is the deepest. Both pes and manus tracks show a short and large sole that is distinctly separated from the digit impressions (Fig. 6A, B).

Remarks

The presence of: 1) pentadactyl manus and pes tracks showing enlarged digit tips and large soles; 2) pes imprints as long as wide; and 3) manus imprints wider than long, are characteristic of *Ichniotherium* Pohlig, 1892. This ichnogenus was reported from upper Carboniferous to lower Permian deposits of many localities throughout the world (e.g. Canada, Brink *et al.* 2012; France, Gand 1987; Germany, Voigt & Ganzelewski 2010; England, Buchwitz & Voigt 2018; Morocco, Lagnaoui *et al.* 2018; Poland, Voigt *et al.* 2012; United States, Voigt *et al.* 2005). In France, *Ichniotherium* was reported from the Lodève Basin (Gand 1987; Gand & Durand 2006; Mujal & Marchetti 2020), the Rodez Basin (Gand 1987) and the Saint-Affrique Basin (Gand & Haubold 1984). Although Gand (1987) briefly mentioned *Ichniotherium* at Le Bousquet (based on the private collection of D. Naudin), he did not describe or illustrate the specimens.

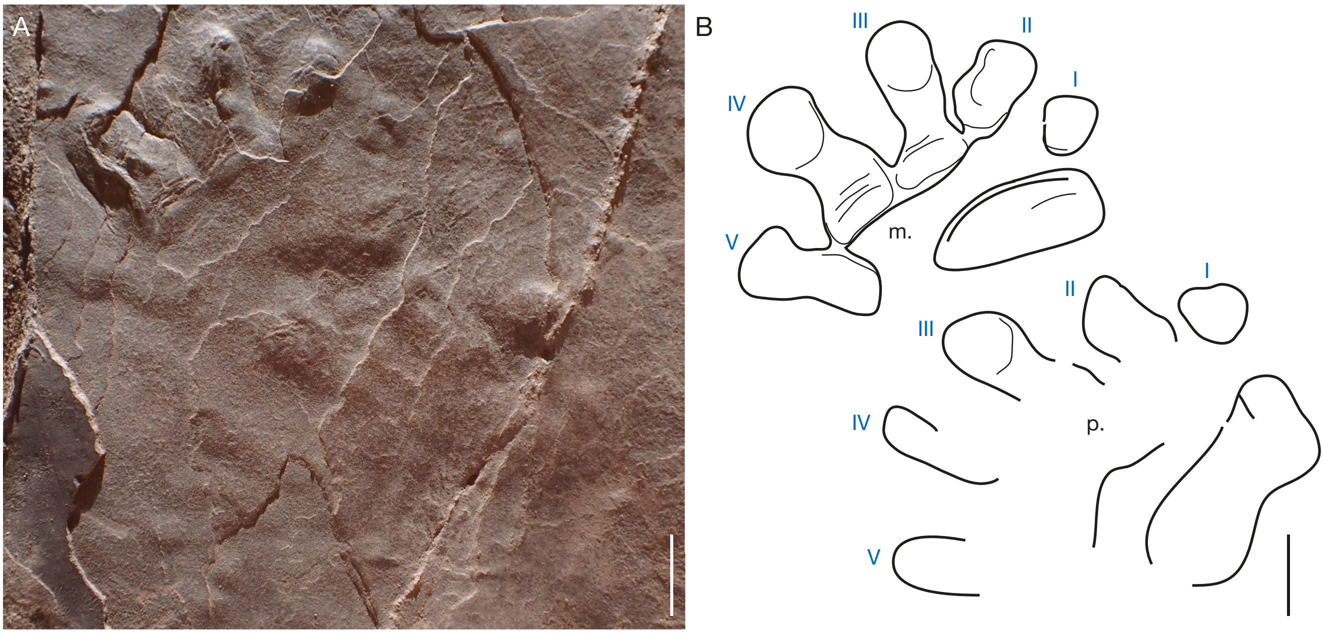

Fig. 6. — *Ichniotherium* isp.: **A, B**, pes/manus set, photograph (**A**) and interpretative sketch (**B**). Convex hyporeliefs, M486_2022.1.4B. Abbreviations: **p.**, pes track; **m.**, manus track. Scale bars: 1 cm.

Ichnogenus *Characichnos* Whyte & Romano, 2001

Characichnos isp.
(Fig. 7A-C)

Material examined. — M486_2022.1.8, slab with numerous tracks preserved as convex hyporeliefs.

Description

The slab M486_2022.1.8 bears numerous swimming tracks of tetrapods (Fig. 7A-C). They are small, up to 14 mm long and up to 9 mm wide. Some of them are aligned showing a trackway-like pattern (Fig. 7C). Morphology of individual tracks vary a lot. They show two to four parallel, elongated, thin and straight to strongly curved furrows. Some of the tracks seem to bear claw traces. Imprints of sole are absent.

Remarks

Characichnos shows a wide stratigraphic range (Carboniferous to Cretaceous) and was reported from several Permian tracksites throughout the world (e.g. Argentina, Melchor & Sarjeant 2004; Spain, Mujal *et al.* 2016; United States, Lucas & Spielmann 2009; Lerner & Lucas 2015; Morocco, Moreau *et al.* 2020). This ichnogenus is for the first time reported in the Permian deposits from the Rodez Basin. These tracks can be interpreted as pes and manus imprints of small tetrapods half-floating and swimming in shallow water. Here, only the tips of the digits touched the substrate. On the slab M486_2022.1.8, these swimming tracks co-occur with abundant fish trails ascribed to *Undichna* cf. *britannica* Higgs, 1988 (Fig. 7D-G).

Tracks of fishes

Ichnogenus *Undichna* Anderson, 1976

***Undichna* cf. *britannica* Higgs, 1988**
(Fig. 7A-G)

Material examined. — M486_2022.1.8, slab bearing numerous trails preserved as convex hyporeliefs.

Description

The slab bears many wavy, horizontal, intermittent, sharp and up to 1.0 mm wide ridges (Fig. 7A, B, D). Some of these ridges form trails consisting of two intertwined and out-of-phase waves (Fig. 7E-G). The longest trail is 145 mm long. Waves show a wavelength of up to 40 mm and an amplitude of up to 5 mm. In some trails, one of the waves shows a low amplitude, whereas the other shows a greatest amplitude (Fig. 7F). Some trails show outer marks that are parallel to central waves (Fig. 7E, G).

Remarks

The presence of wavy, intertwined, horizontal, and intermittent, grooves/ridges is characteristic of several *Undichna* Anderson, 1976 ichnospecies (e.g. *Undichna quina* from the Permian deposits of the Falkland Island, Trewin 2000; *Undichna britannica* from the Carboniferous deposits of England, Higgs 1988). Since ridges are out-of-phase in specimens from Le Bousquet it should be tempting to see similarities with *U. britannica* (see Higgs 1988 and Minter & Braddy 2006). In contrast, amongst *U. quina* ridges are in phase (see Trewin 2000). On trails showing strong variation of amplitude between the two waves (Fig. 7F), the wave with the lowest amplitude was probably made by the anal fin

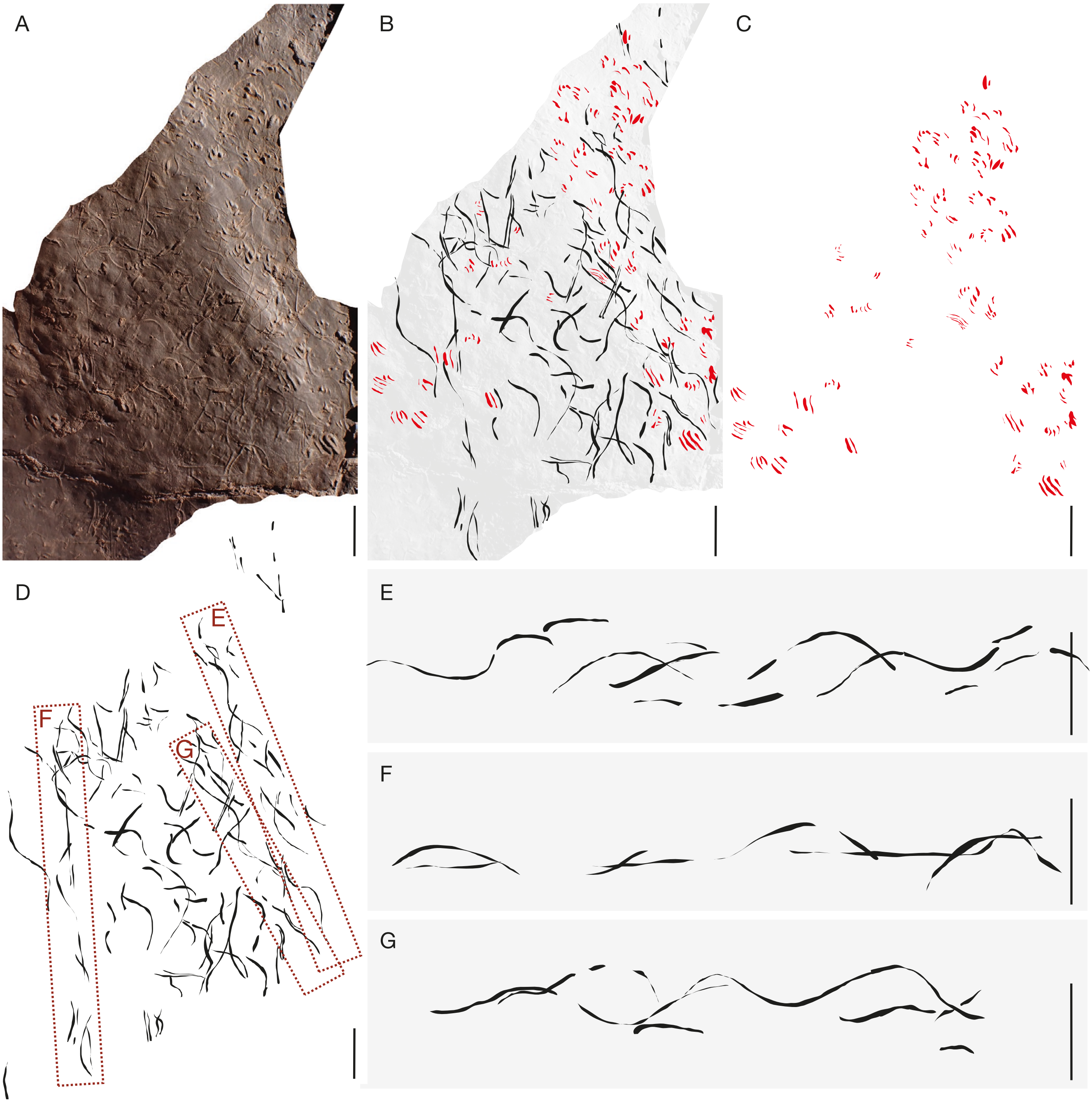

Fig. 7. — Slab showing the co-occurrence of tetrapod swimming tracks (*Characichnos* isp.) and fish trails (*Undichna* cf. *britannica* Higgs, 1988): **A**, photograph; **B**, interpretative sketch showing tetrapod swimming tracks (in red) and fish trails (in black); **C**, interpretative sketch showing only tetrapod swimming tracks; **D**, interpretative sketch showing only fish trails; **E-G**, details of fish trails. M486_2022.1.8. Scale bars: 2 cm.

whereas the wave with a greatest amplitude was probably made by the caudal fin. Outer marks were probably made by pelvic fins.

Plants

Genus *Walchia* Sternberg, 1825

cf. *Walchia* (Fig. 5A, B)

Material examined. — M486_2022.1.6, slab with one specimen. M486_2022.1.10, slab with numerous specimens.

Description

The longest shoot is 90 mm long. Leafy shoots are up to 17 mm in diameter, and straight to slightly curved (Fig. 5A, B). Leaves are helically arranged. They are quite elongated and show a long free part that forms an angle of up to 45° with the main axis of the shoot (Fig. 5A, B). Leaves are falcate in sagittal section. They are up to 12 mm long. The apex of leaves is acute and commonly slightly curved inward. Occasionally, the apex of leaves is slightly recurved outwards.

Remarks

Plant remains are quite common in the fossiliferous bed from Le Bousquet. However, the plant assemblage is only composed of cf. *Walchia* leafy axes. Regionally, the conifer *Walchia* Sternberg, 1825 was previously reported from the basins of Saint-Affrique (Gand *et al.* 1996) and Lodève (Galtier & Broutin 2008; Gand *et al.* 2013).

DISCUSSION

Age of the tracksite

Due to the general lack of biostratigraphic markers, the age of the Red Sandstone Group was strongly debated (Fuchs 1969; Gand 1987; Bourges 1988; Rolando *et al.* 1988; Châteauneuf & Gand 1989; Diego-Orozco *et al.* 2002). Based on palynomorphs collected near Campagnac in the Red Sandstone Group, Châteauneuf & Gand (1989) proposed an "Autunian" age (= lower Permian). Gand (1987) and Châteauneuf & Gand (1989) tentatively correlated tracksites from La Canourgue/Campagnac with the Permian series from the Lodève Basin. They proposed that tracksites can be correlated with deposits exposed at Mas d'Alary and Vialas, corresponding to the end of the Tuilières-Loiras Formation and the Viala Formation (= "Autunian Group" *sensu* Lopez *et al.* 2008), which are Cisuralian in age (Sakmarian-Artinskian according to Michel *et al.* (2015).

Since *Batrachichnus* ranges from the Carboniferous to the Lower Triassic (e.g. Woodworth 1900; Voigt 2005; Gand & Durand 2006; Lucas & Spielmann 2009; Voigt & Lucas 2018; Marchetti *et al.* 2018) and *Amphisauropus* ranges from the lower Permian (e.g. Lucas *et al.* 2001; Santi & Krieger 2001; van Allen *et al.* 2005; Avanzini *et al.* 2011b; Voigt *et al.* 2012) to the upper Permian (e.g. Melchor & Sarjeant 2004; Ptaszyński & Niedźwiedzki 2004; Hminna *et al.* 2012) these ichnogenera are not relevant to discuss the age of the Red Sandstone Group. However, the Permian occurrences of *Ichniotherium* are restricted to lower Permian deposits (Voigt & Lucas 2018) ranging from the Asselian to the Kungurian (Mujal & Marchetti 2020). In the Lodève Basin, *Ichniotherium* only occurs in the Usclas-Saint-Privas, Tuilières-Loiras and Viala formations (Gand & Durand 2006; Mujal & Marchetti 2020), which are Asselian-Artinskian according to Michel *et al.* (2015). It could be tempting to give a similar age for the deposits exposed at Le Bousquet. However, considering the uncertainties and pending more dating arguments, it remains difficult to propose a more precise age than Cisuralian.

Tracemakers and their palaeoenvironment

The *Scoyenia* ichnogenus is interpreted as a feeding or a combined feeding and locomotion trace (burrow), produced by arthropods or annelids (Bromley & Asgaard 1979; Frey *et al.* 1984). Trackmakers of *Diplopodichnus biformis* are commonly attributed to diplopods or other myriapods (Buatois *et al.* 1998). The tetrapod tracks suggest that the fauna from Le Bousquet was mainly composed of anamniotes. *Batrachichnus* is usually referred to stegocephalians such as temnospondyls (Voigt 2005). Trackmakers of *Amphisauropus* are supposed to be seymouriamorphs (Haubold 2000), whereas those of *Ichniotherium* are supposed to be basal diadectomorphs (Voigt & Lucas 2018). In addition to the ichnotaxa we reported here, Gand (1987) briefly mentioned the presence of *Varanopus* isp. at Le Bousquet (based on unfigured specimens from the private collection of D. Naudin). Although we do not know if tracks from the private collection of D. Naudin (see Gand 1987) were collected from the same bed as the tracks we collected here, *Varanopus* Moodie, 1929 suggests the presence of amniote tetrapods (captorhinid reptiles) in the Permian ecosystem from Le Bousquet. Whereas bones of tetrapods are still unknown in the Permian deposits from the Campagnac/La Canourgue area, Sigogneau-Russell & Russell (1974) and then Reisz *et al.* (2011) reported remains of caseids (*Ruthenosaurus russellorum* Reisz, Maddin, Fröbisch & Falconnet, 2011, *Euromycter rutenus* (Sigogneau-Russell & Russell, 1974), Reisz, Maddin, Fröbisch & Falconnet, 2011) in the Red Sandstone Group from the western part of the Rodez Basin. Trails of fishes are for the first time reported in the Permian deposits from the Rodez Basin. Although body fossils of fishes are still unknown in the Cisuralian layers from the area of Banassac-Canilhac, we may notice that Higgs (1988) proposed that tracemakers of *Undichna britannica* were possibly palaeoniscid fishes.

The presence of protostomian burrows and traces with tetrapod tracks matches with the *Scoyenia* ichnofacies. This latter is observed in non-marine formations commonly interpreted as subaqueous freshwater sediments (Buatois & Mángano 1995; Buatois *et al.* 1997). The presence of *Medusina atava* attests to freshwater conditions (Gand *et al.* 1996; Contardi & Santi 2009). The co-occurrence of continental protostomian traces, tetrapod tracks (both walking and swimming tracks), tracks of fishes, jellyfishes, as well as the lithological features of the track-bearing level (channelized and thinly laminated pelitic layers bearing mudcracks, and alternating with argillites), suggest that the depositional environment was a lake/playa system periodically flooded and emerged (Bourges 1988). The presence of abundant conifer leafy axes indicates the relative proximity to forests.

CONCLUSIONS

The deposits exposed at Le Bousquet show the co-occurence of protostomian traces, tetrapod tracks, trails of fishes, jellyfishes and plants.

Freshwater jellyfishes and trails of fishes are for the first time reported in Permian deposits from the Rodez Basin.

The tetrapod ichnoassemblage suggests that the tetrapod fauna from Le Bousquet was mainly composed of anamniotes whereas amniotes were fewer.

The depositional environment is interpreted as a lake/playa system periodically flooded and emerged, and bordered by conifer-dominated forests.

Acknowledgements

We thank Nour-Eddine Jalil and Spencer G. Lucas for their constructive and thoughtful reviews of the manuscript.

REFERENCES

Alabouvette B., Burg J.-P., Lefavrais-Raymond A., Leyreloup A.-F. & Delor C.-P. 1989. — *Notice explicative, carte géologique au 1/50.000 de la France, feuille de Rodez (884)*. Bureau de Recherches géologiques et minières, Orléans, 47 p.

Avanzini M., Neri C., Nicosia U. & Conti M. A. 2008. — A new Early Permian ichnocoenosis from the "Gruppo vulcanico atesino" (Mt. Luco, Southern Alps, Italy). *Studi trentini di scienze naturali, Acta geologica* 83: 231-236.

Avanzini M., Contardi P., Ronchi A. & Santi G. 2011a. — Ichnosystematics of the Lower Permian invertebrate traces from the Collio and Mt. Luco basins (North Italy). *Ichnos* 18: 95-113. https://doi.org/10.1080/10420940.2011.573604

Avanzini M., Bernardi M. & Nicosia U. 2011b. — The Permo-Triassic tetrapod faunal diversity in the Italian southern Alps. *Earth and Environmental Sciences, Intech Open Access*, 591-608. https://doi.org/10.5772/27233

Becq-Giraudon J.-F. 1986. — Le Stéphanien de la bordure nord du détroit de Rodez (Aveyron) et ses relations avec l'Autunien. *Géologie de la France* 3: 293-307.

Becq-Giraudon J.-F. & Fuchs Y. 1989. — Détroit de Rodez, carte géologique, *in* Châteauneuf J. -J. & Farjanel G. (eds), Synthèse géologique des bassins permiens français. *Mémoire du Bureau de Recherches géologiques et minières* 128: 94-99.

Bourges P. 1988. — *Sédimentation alluviale et tectonique extensive dans le Permien du Détroit de Rodez (Aveyron-France)*. Unpublished PhD thesis, University of Toulouse III, 186 p.

Brady L. F. 1947. — Invertebrate tracks from the Coconino Sandstone of northern Arizona. *Journal of Paleontology* 21: 466-472. https://www.jstor.org/stable/1299441

Brink K. S., Hawthorn J. R. & Evans D. C. 2012. — New occurrences of *Ichniotherium* and *Striatichnium* from the Lower Permian Kildare Capes Formation, Prince Edward Island, Canada: palaeoenvironmental and biostratigraphic implications. *Palaeontology* 55: 1075-1090. https://doi.org/10.1111/j.1475-4983.2012.01178.x

Bromley R. & Asgaard U. 1979. — Triassic freshwater ichnocoenoses from Carlsberg Fjord, east Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 28: 39-80. https://doi.org/10.1016/0031-0182(79)90112-3

Buatois L. A. & Mángano M. G. 1995. — The paleoenvironmental and paleoecological significance of the lacustrine Mermia ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage. *Ichnos* 4: 151-161. https://doi.org/10.1080/10420949509380122

Buatois L. A., Mángano M. G. & Maples C. G. 1997. — The paradox of nonmarine ichnofaunas in tidal rhythmites; integrating sedimentologic and ichnologic data from the Late Cretaceous of eastern Kansas, USA. *Palaios* 12: 467-481. https://doi.org/10.2307/3515384

Buatois L. A., Mángano M. G., Maples C. G. & Lanier W. P. 1998. — Taxonomic reassessment of the ichnogenus *Beaconichnus* and additional examples from the Carboniferous of Kansas, USA. *Ichnos* 5: 287-302. https://doi.org/10.1080/10420949809386427

Buchwitz M. & Voigt S. 2018. — On the morphological variability of *Ichniotherium* tracks and evolution of locomotion in the sistergroup of amniotes. *PeerJ* 6: e4346. https://doi.org/10.7717/peerj.4346

Châteauneuf J.-J. & Gand G. 1989. — Stratigraphie, *in* Châteauneuf J. -J. & Farjanel G. (eds), Synthèse géologique des bassins permiens français. *Mémoire du Bureau de Recherches géologiques et ginières* 128: 159-179.

Contardi P. & Santi G. 2009. — New observations on the invertebrate ichnofossils of the Lower Permian basins from Southern Alps (Northern Italy). *Revue de Paléobiologie* 28: 333-347.

Defaut B., Burg J.-P., Leyreloup A.-F., Romney F., Fuchs Y., Alabouvette B. & Lefavrais-Raymond A. 1990. — *Notice explicative, carte géologique au 1/50.000 de la France, feuille de Sévérac-le-Château (885)*. Bureau de Recherches géologiques et minières, Orléans, 58 p.

Demathieu G., Gand G. & Toutin-Morin N. 1992. — La palichnofaune des bassins permiens provençaux. *Geobios* 25: 19-54. https://doi.org/10.1016/S0016-6995(09)90036-5

Diego-Orozco A., Chen Y., Henry B. & Becqgiraudon J.-F. 2002. — Paleomagnetic results from the Permian Rodez basin implications: the Late Variscan tectonics in the southern French Massif Central. *Geodinamica Acta* 15: 249-260. https://doi.org/10.1016/S0985-3111(02)01091-4

Ellenberger P. 1983a. — Sur la zonation ichnologique du Permien moyen (Saxonien) du bassin de Lodève (Hérault). *Comptes Rendus de l'Académie des Sciences, Paris,* série II, 297: 553-558. https://gallica.bnf.fr/ark:/12148/bpt6k5653757z/f557.item

Ellenberger P. 1983b. — Sur la zonation ichnologique du Permien inférieur (Autunien) du bassin de Lodève (Hérault). *Comptes Rendus de l'Académie des Sciences, Paris,* série II, 297: 631-636. https://gallica.bnf.fr/ark:/12148/bpt6k5653757z/f635.item

Ellenberger P. 1984. — Données complémentaires sur la zonation ichnologique du Permien du Midi de la France : bassins de Lodève, Saint-Affrique et Rodez. *Comptes Rendus de l'Académie des Sciences, Paris,* série II, 299: 581-586. https://gallica.bnf.fr/ark:/12148/bpt6k6328301d/f593.item

Ellenberger F. & Ellenberger P. 1959. — Quelques pistes de vertébrés du Permien inférieur de Lodève. *Comptes Rendus de l'Académie des Sciences, Paris*, 248: 437-439. https://gallica.bnf.fr/ark:/12148/bpt6k32002/f449.item

Fabre G. 1872 — Matériaux pour servir à la description géologique du département de la Lozère. *Bulletin de la Société d'Agriculture, Industrie Sciences et arts du département de la Lozère* 23: 35-61. https://gallica.bnf.fr/ark:/12148/bpt6k408911h/f417.image

Frey R. W., Pemberton S. G. & Fagerstrom J. A. 1984. — Morphological, ethological, and environmental significance of the ichnogenera *Scoyenia* and *Ancorichnus*. *Journal of Paleontology* 58: 511-528. https://www.jstor.org/stable/1304799

Fuchs Y. 1969. — *Contribution à l'étude géologique, géochimique et métallogénique du Détroit de Rodez*. Unpublished PhD thesis, University of Nancy, 245×p.

Galtier J. & Broutin J. 2008. — Floras from red beds of the Permian Basin of Lodève (Southern France). *Journal of Iberian Geology* 34 (1): 57-72.

Gand G. 1980. — Description d'une piste de vertébré dans le Permien de l'Esterel (Var, France). *Bulletin du Muséum national d'histoire naturelle, section C, Sciences de la Terre, Paléontologie, Géologie, Minéralogie* 4: 436-440. https://www.biodiversitylibrary.org/page/55610655

Gand G. 1981. — Découverte de traces de reptiles cotylosauriens dans le Permien du bassin de Blanzy-Le Creusot (Saône-et-Loire, France). Une étape dans la succession des palichnofaunes de vertébrés tétrapodes. *Comptes Rendus de l'Académie des Sciences de Paris* 292: 163-167.

Gand G. 1985. — Significations paléobiologique et stratigraphique de *Limnopus zeilleri* dans la partie nord du bassin de St-Affrique. *Geobios* 18: 215-227. https://doi.org/10.1016/S0016-6995(85)80015-2

Gand G. 1986. — Interprétations paléontologique et paléoécologique de quatre niveaux à traces de vertébrés observés dans l'Autunien Du Lodévois (Hérault). *Géologie De La France* 2: 155-176.

Gand G. 1987. — *Les traces de vertébrés tétrapodes du Permien français : paléontologie, stratigraphie, paléoenvironnements*. Unpublished PhD thesis, Bourgogne University, Dijon, 341 p.

Gand G. 1991. — Premières découvertes de traces de pas de vertébrés tétrapodes dans le bassin permien de Brive-la-Gaillarde (Corrèze). *Géologie de la France* 3: 43-51.

Gand G. 1993a. — Les empreintes animales et végétales du bassin permien de Largentière : (Ardèche, France). Conséquences stratigraphiques et paléoenvironnementales. *Bulletin trimestriel de la Société d'Histoire naturelle et des Amis du Muséum d'Autun* 146: 8-41.

Gand G. 1993b. — La palichnofaune de Vertébrés tétrapodes du bassin permien de St-Affrique (Aveyron) : comparaisons et conséquences stratigraphiques. *Géologie de la France* 3-4: 41-56.

Gand G. 1994. — Ichnocoenoses à *Isopodichnus furcosus* nov. ichnosp. dans le Permien du Bassin de Lodève (Massif Central, France). *Geobios 27*: 73-86. https://doi.org/10.1016/S0016-6995(06)80214-7

Gand G. & Durand M. 2006. — Tetrapod footprint ichno-associations from French Permian basins. Comparisons with other Euramerican ichnofaunas. *Geological Society, London, Special Publications* 265: 157-177. https://doi.org/10.1144/GSL.SP.2006.265.01.07

Gand G. & Haubold H. 1984. — Traces de vertébrés du Permien du bassin de Saint-Affrique (description, datation, comparaison avec celles du bassin de Lodève). *Géologie méditeranéenne* 11: 321-348. https://doi.org/10.3406/GEOLM.1984.1333

Gand G., Demathieu G. & Ballestra F. 1995. — La palichnofaune de vertébrés tétrapodes du Permien supérieur de l'Estérel (Provence, France). *Palaeontographica, Abteilung A* 235: 97-139.

Gand G., Garric J., Schneider J., Sciau J. & Walter H. 1996. — Biocœnoses à méduses du Permien français (bassin de Saint-Affrique, Massif Central). *Geobios* 29: 379-400. https://doi.org/10.1016/S0016-6995(96)80001-5

Gand G., Garric J., Demathieu G. & Ellenberger P. 2000. — La palichnofaune de vertébrés tétrapodes du Permien Supérieur du bassin de Lodève (Languedoc-France). Palaeovertebrata 29: 1-82.

Gand G., Garric J., Schneider J., Walter H., Lapeyrie J., Martin C. & Thiery A. 2008. — *Notostraca* trackways in Permian playa environments of the Lodève basin (France). *Journal of Iberian Geology* 34: 73-108.

Gand G., Galtier J., Garric J., Teboul P. A. & Pellenard P. 2013. — Discovery of an Autunian macroflora and lithostratigraphic re-investigation on the western border of the Lodève Permian Basin (Mont Sénégra, Hérault, France). Paleoenvironmental implications. *Comptes Rendus Palevol* 12: 69-79. https://doi.org/10.1016/j.crpv.2013.01.003

Haubold H. 1971. — Ichnia amphibiorum et reptiliorum fossilium. *Handbuch der Paläoherpetologie* 18: 1-124.

Haubold H. 2000. — Tetrapodenfährten aus dem Perm – Kenntnisstand und Progress 2000. *Hallesches Jahrbuch für Geowissenschaften* B 22: 1-16.

Heyler D. 1984. — *Margennipes pansioti*, ng, nsp : empreinte d'un vertébré tétrapode dans l'Autunien supérieur du bassin d'Autun. *Bulletin de la Société d'Histoire naturelle, d'Autun* 111: 27-36.

Heyler D. & Lessertisseur J. 1963. — *Pistes de Tétrapodes permiens dans la région de Lodève (Hérault)*. Muséum national d'Histoire naturelle, Paris, 96 p. (Mémoires du Muséum national d'Histoire naturelle, sér. C – Sciences de la Terre ; 11 [2]). https://www.biodiversitylibrary.org/page/58216767

Higgs R. 1988. — Fish trails in the Upper Carboniferous of south-west England. Palaeontology 31: 255-272.

Hminna A., Voigt S., Saber H., Schneider J. W. & Hmich D. 2012. — On a moderately diverse continental ichnofauna from the Permian Ikakern Formation (Argana Basin, western High Atlas, Morocco). *Journal of African Earth Sciences Palaeoecology* 68: 15-23. https://doi.org/10.1016/j.jafrearsci.2012.03.011

Lagnaoui A., Voigt S., Belahmira A., Saber H., Klein H., Hminna A. & Schneider J. W. 2018. — Late Carboniferous tetrapod footprints from the Souss Basin, Western High Atlas Mountains, Morocco. *Ichnos* 25: 81-93. https://doi.org/10.1080/10420940.2017.1320284

Leonardi G. 1987. — *Glossary and Manual of Tetrapod Footprint Palaeoichnology*. Departemento Nacional da Producao Mineral, Brasilia, 117 p.

Lima J. H. D. & Netto R. G. 2012. — Trace fossils from the Permian Teresina Formation at Cerro Caveiras (S Brazil). *Revista Brasileira de Paleontologia* 15: 5-22. https://doi.org/10.4072/RBP.2012.1.01

Lerner A. J. & Lucas S. G. 2015. — A *Selenichnites* ichno-association from the Early Permian tidal flats of the Prehistoric Trackways National Monument of south-central New Mexico, *in* Lucas S. G. & Dimichele W. A. (eds), Carboniferous-Permian Transition in the Robledo Mountains, Southern New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 65: 141-152.

Logghe A., Mujal E., Marchetti L., Nel A., Pouillon J.-M., Giner S., Garrouste R. & Steyer J.-S. 2021. — *Hyloidichnus* trackways with digit and tail drag traces from the Permian of Gonfaron (Var, France): new insights on the locomotion of captorhinomorph eureptiles. *Palaeogeography, Palaeoclimatology, Palaeoecology* 573: 110436. https://doi.org/10.1016/j.palaeo.2021.110436

Lopez M., Gand G., Garric J., Körner F. & Schneider J. 2008. — The playa environments of the Lodève Permian basin (Languedoc-France). *Journal of Iberian Geology* 34: 29-56.

Lucas S. G. & Spielmann J. A. 2009. — Tetrapod footprints from the lower Permian Abo Formation near Bingham, Socorro county, New Mexico. *New Mexico Geolological Society, Guidebook, 60th Field Conference, Geology of the Chupadera Mesa Region*: 299-304.

Lucas S. G., Lerner A. J. & Haubold H. 2001. — First record of *Amphisauropus* and *Varanopus* in the Lower Permian Abo Formation, central New Mexico. *Hallesches Jahrbuch für Geowissenschaften* B 23: 69-78.

Lucas S. G., Lerner A. J. & Hunt A. P. 2004. — Permian tetrapod footprints from the Lucero uplift, central New Mexico, and Permian footprint biostratigraphy. *New Mexico Museum of Natural History and Science Bulletin* 25: 291-300.

Lucas S. G., Smith J. A., Hunt A. P. 2005. — Tetrapod tracks from the Lower Permian Yeso Group, central New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 31: 121-124.

Marchetti L., Ronchi A., Santi G. & Voigt S. 2015. — The Gerola valley site (Orobic basin, northern Italy): a key for understanding late Early Permian tetrapod ichnofaunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 439: 97-116. https://doi.org/10.1016/j.palaeo.2015.02.032

Marchetti L., Petti F. M., Zoboli D. & Pillola G. L. 2018. — Vertebrate and invertebrate trace fossils in the Late Pennsylvanian (Carboniferous) fluvio-lacustrine San Giorgio Basin (South-West Sardinia): remarks on the oldest continental ichnoassociation of Italy. *Ichnos 25*: 94-105. https://doi.org/10.1080/10420940.2017.1337572

Marchetti L., Klein H., Buchwitz M., Ronchi A., Smith R. M. H., De Klerk W. J., Sciscio L. & Groenewald G. H. 2019. — Permian-Triassic vertebrate footprints from South Africa: ichnotaxonomy, producers and biostratigraphy through two major faunal crises. *Gondwana Research* 72: 139-168. https://doi.org/10.1016/j.gr.2019.03.009

Matthews N., Noble T. & Breithupt B. H. 2016. — Close-Range photogrammetry for 3D ichnology: the basics of photogrammetric ichnology, *in* Falkingham P. L., Marty D. & Richter A. (eds), *Dinosaur Tracks: The Next Steps*. Indiana University Press, Bloomington and Idianapolis: 29-55.

Melchor R. N. & Sarjeant W. A. S. 2004. — Small amphibian and reptile footprints from the Permian Carapacha basin, Argentina. *Ichnos* 11: 57-78. https://doi.org/10.1080/10420940490428814

Michel L. A., Tabor N. J., Montañez I. P., Schmitz M. D. & Davydov V. I. 2015. — Chronostratigraphy and paleoclimatology of the Lodève Basin, France: evidence for a pan-tropical aridification event across the Carboniferous-Permian boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 430: 118-131. https://doi.org/10.1016/j.palaeo.2015.03.020

Minter N. J. & Braddy S. J. 2006. — The fish and amphibian swimming traces *Undichna* and *Lunichnium*, with examples from the Lower Permian of New Mexico, USA. *Palaeontology* 49: 1123-1142. https://doi.org/10.1111/j.1475-4983.2006.00588.x

Moreau J.-D., Benaouiss N., Tourani A., Steyer J.-S., Laurin M., Peyer K., Béthoux O., Ali Aouda, A. & Jalil N.-E. 2020. — A new ichnofauna from the Permian of the Marrakech High Atlas of Morocco. *Journal of African Earth Sciences Palaeoecology* 172: 103973. https://doi.org/10.1016/j.jafrearsci.2020.103973

Mossman D. J. & Place C. H. 1989. — Early Permian fossil vertebrate footprints and their stratigraphic setting in megacyclic sequence II red beds, Prim Point, Prince Edward Island. *Canadian Journal of Earth Sciences* 26: 591-605. https://doi.org/10.1139/e89-050

Mujal E. & Marchetti L. 2020. — *Ichniotherium* tracks from the Permian of France, and their implications for understanding the locomotion and palaeobiogeography of large diadectomorphs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 547: 109698. https://doi.org/10.1016/j.palaeo.2020.109698

Mujal E., Fortuny J., Oms O., Bolet A., Galobart À. & Anadón P. 2016. — Palaeoenvironmental reconstruction and early Permian ichnoassemblage from the NE Iberian Peninsula (Pyrenean basin). *Geological Magazine* 153: 578-600. https://doi.org/10.1017/S0016756815000576

Ptaszyński T. & Niedźwiedzki G. 2004. — Late Permian vertebrate tracks from the Tumlin Sandstone, Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 49: 289-320.

Reisz R. R., Maddin H. C., Fröbisch J. & Falconnet J. 2011. — A new large caseid (Synapsida, Caseasauria) from the Permian of Rodez (France), including a reappraisal of "*Casea*" *rutena* Sigogneau-Russell & Russell, 1974. *Geodiversitas* 33: 227-246. https://doi.org/10.5252/g2011n2a2

Rolando J.-P., Doubinger J., Bourges P. & Legrand X. 1988. — Identification de l'Autunien supérieur, du Saxonien et du Thuringien inférieur dans le bassin de Saint-Affrique (Aveyron, France). Corrélations séquentielles et chronostratigraphiques avec les bassins de Lodève (Hérault) et de Rodez (Aveyron). *Comptes Rendus de l'Académie des Sciences de Paris* 307: 1459-1464. https://gallica.bnf.fr/ark:/12148/bpt6k63314703/f335.item

Ronchi A. & Santi G. 2003. — Non-marine biota from the Lower Permian of the central Southern Alps (Orobic and Collio basins, N Italy): a key to the paleoenvironment. *Geobios* 36: 749-760. https://doi.org/10.1016/j.geobios.2003.01.004

Santi G. & Krieger C. 2001. — Lower Permian tetrapod footprints from Brembana valley-Orobic basin (Lombardy, Northern Italy). *Revue de Paléobiologie* 20: 45-68.

Schüppel D. 1984. — Abdrücke von Hydromedusen aus dem UnterRotliegenden des Erzgebirgischen Beckens. *Freiberger Forschungshefte* C 395: 38-47.

Sigogneau-Russell D. & Russell D. E. 1974. — Étude du premier caséidé (Reptilia, Pelycosauria) d'Europe occidentale. *Bulletin du Muséum national d'Histoire naturelle*, sér. 3, *Sciences de la Terre* 38, 230: 145-216. https://www.biodiversitylibrary.org/page/55496342

Trewin N. H. 2000. — The ichnogenus *Undichna*, with examples from the Permian of the Falkland Islands. *Palaeontology* 43: 979-997. https://doi.org/10.1111/1475-4983.00158

Uchman A., Hu B., Wang Y. & Song H. 2011. — The trace fossil *Diplopodichnus* from the Lower Jurassic lacustrine sediments of central China and the isopod *Armadillidium vulgare* (Pillbug) lebensspuren as its recent analogue. *Ichnos* 18: 147-155. https://doi.org/10.1080/10420940.2011.601372

van Allen H. E., Calder J. H. & Hunt A. P. 2005. — The trackway record of a tetrapod community in a walchian conifer forest from the Permo-Carboniferous of Nova Scotia. *New Mexico Museum of Natural History and Science Bulletin* 30: 322-332.

Voigt S. 2005. — *Die Tetrapodenichnofauna des kontinentalen Oberkarbon und Perm im Thüringen Wald: Ichnotaxonomie, Paläoökologie und Biostratigraphie*. Cuvillier Verlag, Göttingen, 305 p.

Voigt S. & Ganzelewski M. 2010. — Toward the origin of amniotes: Diadectomorph and synapsid footprints from the early Late Carboniferous of Germany. *Acta Palaeontologica Polonica* 55: 57-72. https://doi.org/10.4202/app.2009.0021

Voigt S. & Lucas S. G. 2018. — Outline of a Permian tetrapod footprint ichnostratigraphy. *Geological Society, London, Special Publications* 450, 387-404. https://doi.org/10.1144/SP450.10

Voigt S., Small B. J. & Sanders F. 2005. — A diverse terrestrial ichnofauna from the Maroon Formation (Pennsylvanian-Permian), Colorado: Biostratigraphic and paleoecological significance. *New Mexico Museum of Natural History and Science Bulletin* 30: 342-351.

Voigt S., Lagnaoui A., Hminna A., Saber H. & Schneider J. W. 2011. — Revisional notes on the Permian tetrapod ichnofauna from the Tiddas Basin, central Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 302: 474-483. https://doi.org/10.1016/j.palaeo.2011.02.010

Voigt S., Niedźwiedzki G., Raczyński P., Mastalerz K. & Ptaszyński T. 2012. — Early Permian tetrapod ichnofauna from the Intra-Sudetic basin, SW Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 313, 173-180. https://doi.org/10.1016/j.palaeo.2011.10.018

Woodworth J. B. 1900. — Vertebrate footprints on Carboniferous shales of Plainville, Massachusetts. *Geological Society of America Bulletin* 11: 449-454. https://doi.org/10.1130/GSAB-11-449

Submitted on 3 December 2021;
accepted on 7 April 2022;
published on 10 November 2022.