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ORIGINAL PAPER

Swimming trails of fishes from the Permian playa-lake ecosystem of the Salagou Formation (Lodève Basin, southern France)

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Abstract
The Col de Dio palaeontological site yields the first swimming trails of fishes from the continental Permian deposits of the Lodève Basin (southern France). Several morphologies of trails were distinguished, each of them including one, two or four thin, horizontal and sinusoidal grooves/ridges. Trails are ascribed to *Undichna bina*, *Undichna britannica* and *Undichna unisulca.* They co-occur with arthropod body remains (e.g. "conchostracans", triopsids), invertebrate traces (cf. *Cochlichnus*, *Diplichnites*, and *Diplopodichnus*) and swimming tracks of tetrapods (*Characichnos*). The sedimentological analysis conducted at the Col de Dio tracksite indicates the presence of two orders of stratigraphic sequences that rule the alternation of humid and arid cycles in an endorheic terminal mud-dominated floodplain and playa-lake environment. Although body fossils of fishes remain unknown in the Salagou Formation, the presence of *Undichna* shows that ichthyofauna was an abundant component of the palaeoecosystem related to this formation. The diverse shapes of *Undichna* suggest a great diversity of fish morphologies and/or behaviours. This new discovery of fish trails co-occurring with tetrapod and arthropod tracks complements other coeval French tracksites, suggesting that such ichnofaunas were common in Permian terrestrial ecosystems from the Eastern Pangean intertropical zone.

Keywords Fish trails · *Undichna* · Lodève Basin · Palaeoenvironment · Late Palaeozoic · Permian

Introduction

The Grands Causses area (southern France; Fig. 1a) is surrounded by three Permian basins yielding abundant body fossils and ichnofossils that are crucial for the reconstruction of late Palaeozoic continental ecosystems. It consists of the Lodève, Rodez and Saint-Affrique basins (Fig. 1b). Amongst the Permian basins from France, the Lodève Basin (Fig. 1c) was clearly the most prospected from a palaeontological point of view, yielding diverse vertebrate (e.g. Gervais 1859; Heyler 1969; Thévenin 1910; Werneburg et al. 2007; Falconnet 2010), arthropod (e.g. Nel et al. 1999, 2008; Béthoux et al. 2001, 2002, 2003; Béthoux 2008; Prokop et al. 2015; Garrouste et al. 2018) and plant remains (e.g. Doubinger and Kruseman 1965; Galtier and Broutin 1995, 2008). Since at least the first half of the 20th century, Permian deposits from this basin also yielded abundant tetrapod and invertebrate tracks (e.g. Delage 1912; Ellenberger and Ellenberger 1959; Heyler and Lessertisseur 1963; Ellenberger 1983a, 1983b, 1984; Gand 1986, 1987, 1994; Gand et al. 2000, 2008; Gand and Durand 2006; Mujal and Marchetti 2020).

Although continental deposits from the upper part of the Permian series from the Lodève Basin (Rabejac, Salagou and La Lieude formations; Fig. 2) yield abundant body fossils of aquatic organisms, ichthyofaunas remain unknown. Here, we describe the first swimming trails of fishes from the Lodève Basin as well as associated protostomian body fossils and ichnofossils. Body remains of fishes being absent from the deposits yielding trails, the related ichnofaunas as well as their palaeoecosystem and palaeoenvironment are discussed.

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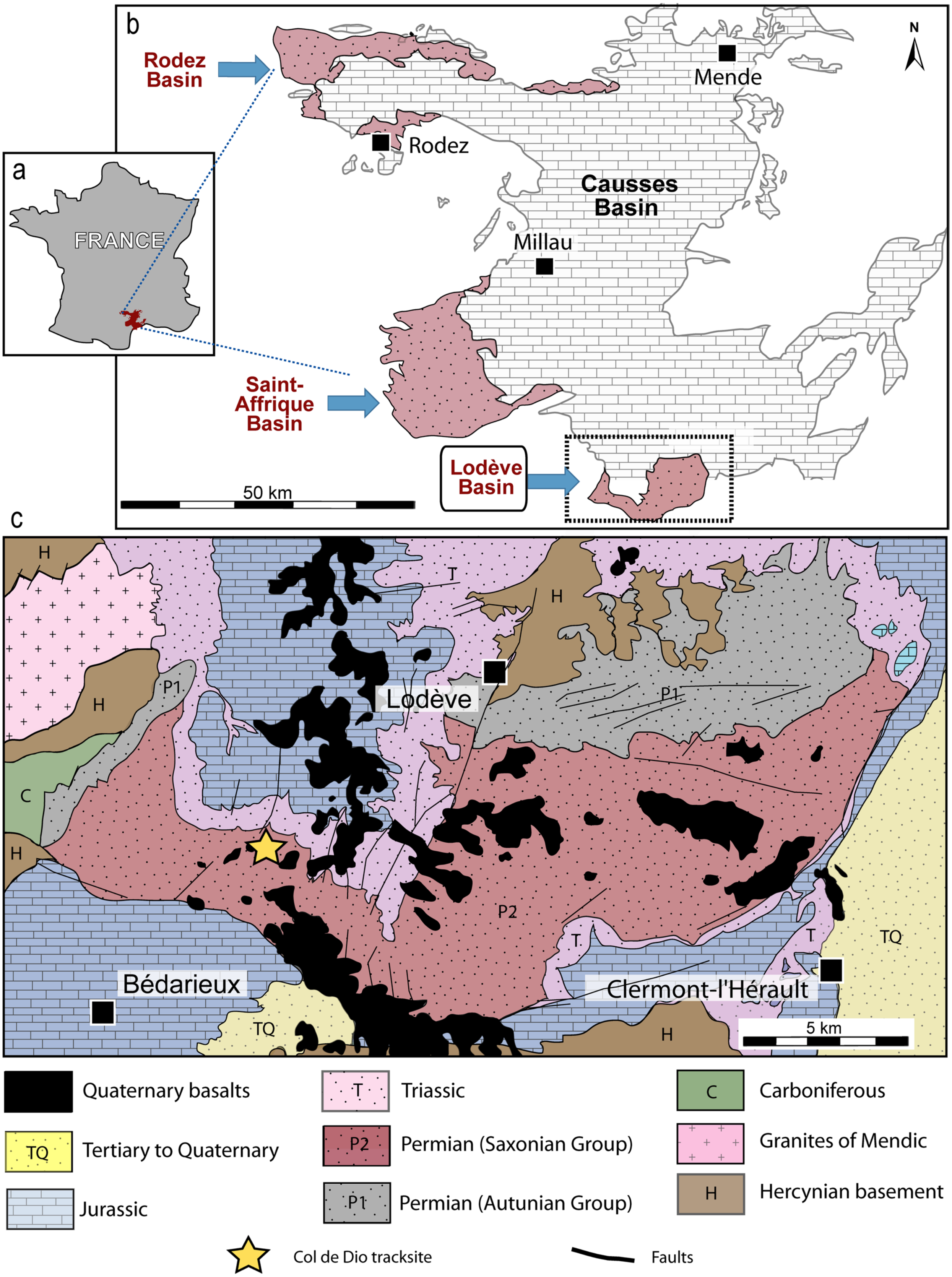


Fig. 1 Geographical and geological context. **a** location of the Causses Basin in France. **b** location of Permian basins around the Causses Basin. **c** simplified geological map of the Lodève Basin and location of the Col de Dio tracksite

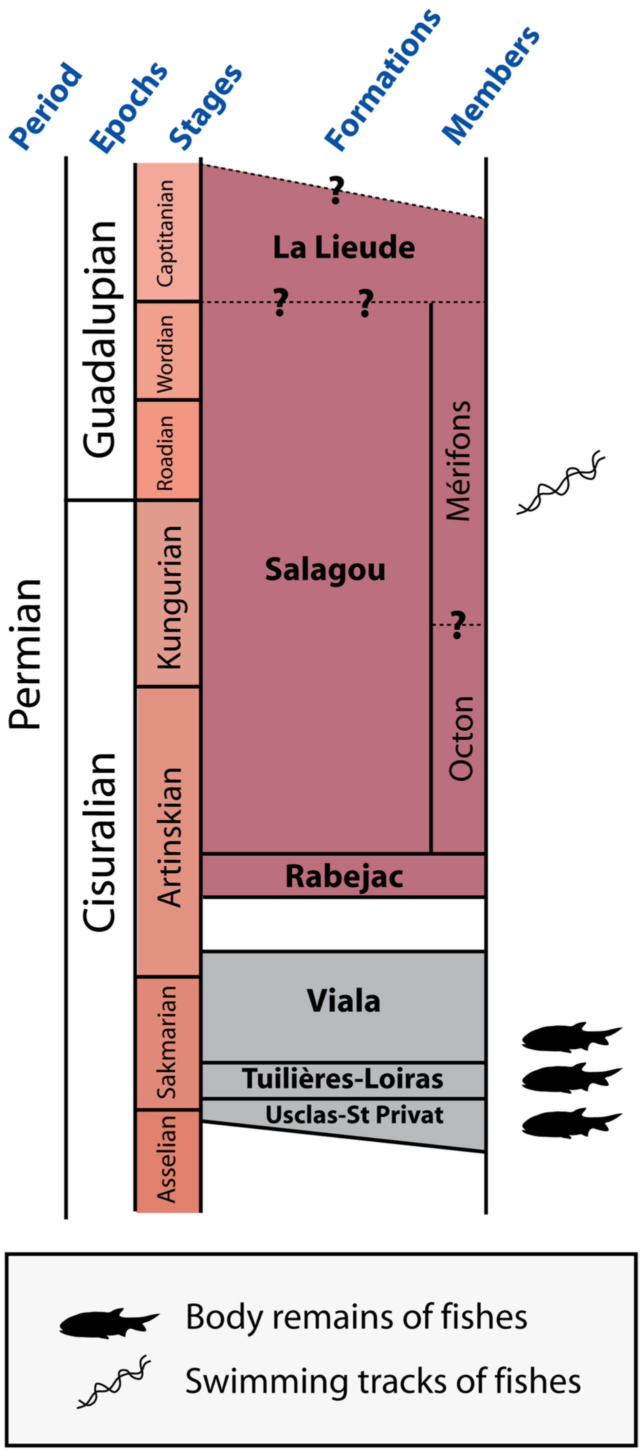


Fig. 2 General stratigraphic column of the Lodève Basin and location of body fossils of fishes and fish trails. Modified after Michel et al. 2015a

Geographical and geological setting

The Lodève Basin is located in southern France (Fig. 1a, 1b). It consists of a half-graben of Permian age spread over about 150 km^2. The basin shows of a 3000 m thick sedimentary series, at the hanging wall of the south bordering fault, which is organised in two major megasequences separated by a slight regional unconformity. The first is 750 metres-thick, was deposited in a pre-rift context and includes three formations (Fm.), the Usclas-Saint Privat Fm., the Tuilières-Loiras Fm. and the Viala Fm. They correspond to an overall shallowing upward sequence from deep anoxic lacustrine systems to low energy river and floodplain deposits. The upper megasequence displays a fan shape geometry relative to the synrift infill of the basin. It consists of an overall fining upward sequence split into two major formations (Lopez et al. 2008), the Rabejac Fm. and the Salagou Fm. The first is about 300 m thick and corresponds to coarse fluvial deposits. The second one is 2000 m thick and mainly composed of red pelites. The Salagou Fm. displays overall facies partitioning from coarse alluvial fan on the hanging wall of the south and western bordering faults (La Tour facies) to ephemeral fluvial systems (La Lieude facies) passing downstream to floodplain (Octon facies) and playa lake systems (Mérifons facies) in the central part of the depocenter (Lopez et al. 2008). However, because a partial stratigraphical superposition tendency, more recent works tend to place the La Lieude facies into a distinct formation at the top of the Permian series and to split the Salagou Fm. into the Octon Member in the lower part and the Mérifons Member in the upper part (Schneider et al. 2006; Michel et al. 2015a; Fig. 2). For convenience, we will follow this stratigraphical succession (Fig. 2) because the tracksite is stratigraphically located in the Mérifons Member of the Salagou Fm., at about 80 to 100 m below the basal sandstones of the la Lieude Fm. near Col de Dio (Dio-et-Valquières; Fig. 1c).

Magnetostratigraphic data indicate that most of the Salagou Formation lies within the Permo-Carboniferous Reversed Superchron (PCRS) with two distinct groups: a lower one consistent with the Octon Member which is mainly Artinskian in age; and an upper one reliable with the Mérifons Member including the Kungurian and possibly part of the Roadian stages (Evans 2012). This assumption was confirmed by complementary magnetostratigraphic data at the base of overlying La Lieude Formation that fall into the reverse interval above the Wordian-N polarity zone indicating at least a Capitanian age (Evans et al. 2014). Moreover U-Pb zircon ages (CA-IDTIMS) from a tuff bed in the upper part of the Octon Member (Sample T12, Michel et al. 2015a; b) show an age of 282.86 ± 0.13 Ma (early Kungurian) compatible with a stratigraphical stage between upper Kungurian and Wordian for the Mérifons Member where this study focus.

Material and methods

The tracksite was discovered at the end of the 20th century by one of us (J.L.) during prospection in the the western part of the Lodève Basin. Specimens were collected at that time. In 2022 and 2023, based on new prospections, a detailed sedimentological analysis was conducted along a 14 metres high section (Fig. 3). Specimens are preserved on surfaces of reddish pelitic slabs. They bear swimming trails of fishes and tetrapods as well as arthropod trackways. Ichnofossils are preserved as both concave epireliefs and convex hyporeliefs. They are associated with "conchostracan" and triopsid body fossils. All specimens are housed in the palaeontological collections (Lapeyrie collection) of the Musée de Lodève (Hérault, southern France). The following specimens were used in the present study: LdLAP-826 to LdLAP-829, LdLAP-840 to LdLAP-842, LdLAP-846, LdLAP-848, LdLAP-850, LdLAP-851. 3D photogrammetric reconstructions 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 Olympus Tough TG-6 camera.

Results

Sedimentological analysis

The Col de Dio sedimentary pile consists of monotonous red splintery pelites alternating with thin greenish blue to red brown massive to thinly laminated silty carbonate bearing mudstones giving a 'barcode' pattern on the landscape over several hundreds of metres in thickness. Here, the stacking pattern of the pile is ruled by two orders of embedded sequences.

The first order consists of 1 to 3 metres thick red pelite dominated facies separated by very continuous 3 to 5 centimetres thick carbonate bearing greenish blue fine to medium siltites (Figs. 3, 4a–b). The siltite layers are relatively hard and relief-shaped compared to softer pelites with a sharp flat to erosive base and display a thin plane horizontal to wavy lamination compatible with 2D current ripples (Fig. 4b). Locally the base of the flat horizontal siltite layers shows well developed desiccation cracks (Fig. 4c) that indicate a time gap and subaerial exposure between the deposition of the pelite mud and the flooding by the silty material. However, the most common geometry at the base of siltite layers is simple to pendulous load casts (Owen 2003) with a diapir protrusion of distorted pelites at the nodes of the loading cells (Fig. 4d–e). These structures indicate a relatively plastic comportment of the underlying pelite mud below the more cohesive silt layer with density inversion and shear thinning compatible with the Rayleigh-Taylor instability when gravity forces overcome elasticity (Harrison and Maltman 2003; Mora et al. 2014; Chakrabarti et al. 2018). Careful analysis of the geometry of the thin lamination preserved in such layers shows that only the basal lamina package is deformed and partly sheared by the loading effect and the gravitational collapse. The intermediate lamina pinch out on the shoulder of the synform and diapir bulge up to compensate the differential sinking of the cohesive material (Fig. 4e). This situation is compatible with a relative quick flooding event after the deposition of the first order pelitic sequence which remain relatively soupy to low-consistent during the deposition of the overlying denser siltite materiel. The top of the carbonate bearing siltite layers is often gradational (Fig. 4b, d–e) with a progressive blue green to red colour change and fining upward trend (Fig. 4e) indicating the transition from diluted tractive current to dense suspension settling.

The second order sequences, packed in the thick pelite interval, show pluri-millimetre to centimetre thick blue green to brown wispy to continuous fine carbonate-rich siltite layers (Figs. 3, 4a–d) locally associated with oscillatory ripples or desiccation cracks. These thin layers are interpreted as temporary drowning of the floodplain by diluted shallow still stand waters during the large first order sequence. Some small yellowish dolocrete nodules are also visible 9 m above the base of the section indicating the possible development of rooted vegetation. Complementarily, two intra-pelitic intervals (9.25 m and 10.70 m from the base of the section) show a cuvette-shape green silty-mudstones described previously as 'rigoles' deposits where abundant fossiliferous remains were identified and interpreted as the focalization point of runoff waters after the surface has dried (Gand et al. 2003a).

Systematic palaeontology

Trails of fishes

Undichna Anderson, 1976
Undichna bina Anderson, 1976
(Fig. 5a–b)

Material: One trail preserved as concave epirelief. LdLAP-840.
Description: The trail is 25.5 cm long, up to 3.7 cm wide. It consists of a pair of wavy, in-phase, and horizontal grooves (Fig. 5a–b). The lateral distance between the waves is up to 2.7 cm long. The amplitude and the wavelength are up to 5 mm high and up to 5 cm long, respectively. The widths of the two grooves are not similar. The narrowest is 0.5 to 3 mm wide whereas the largest is 2 to 7 mm wide.
Remarks: Several ichnospecies of *Undichna* show the presence of two waves: *Undichna britannica* and *U. bina* (Fig. 6a–b; see also Figure 2 in Minter and Braddy 2006). When *U. britannica* shows two waves, it differs from *U. bina* by the intertwined and out-of-phase characters of the waves.

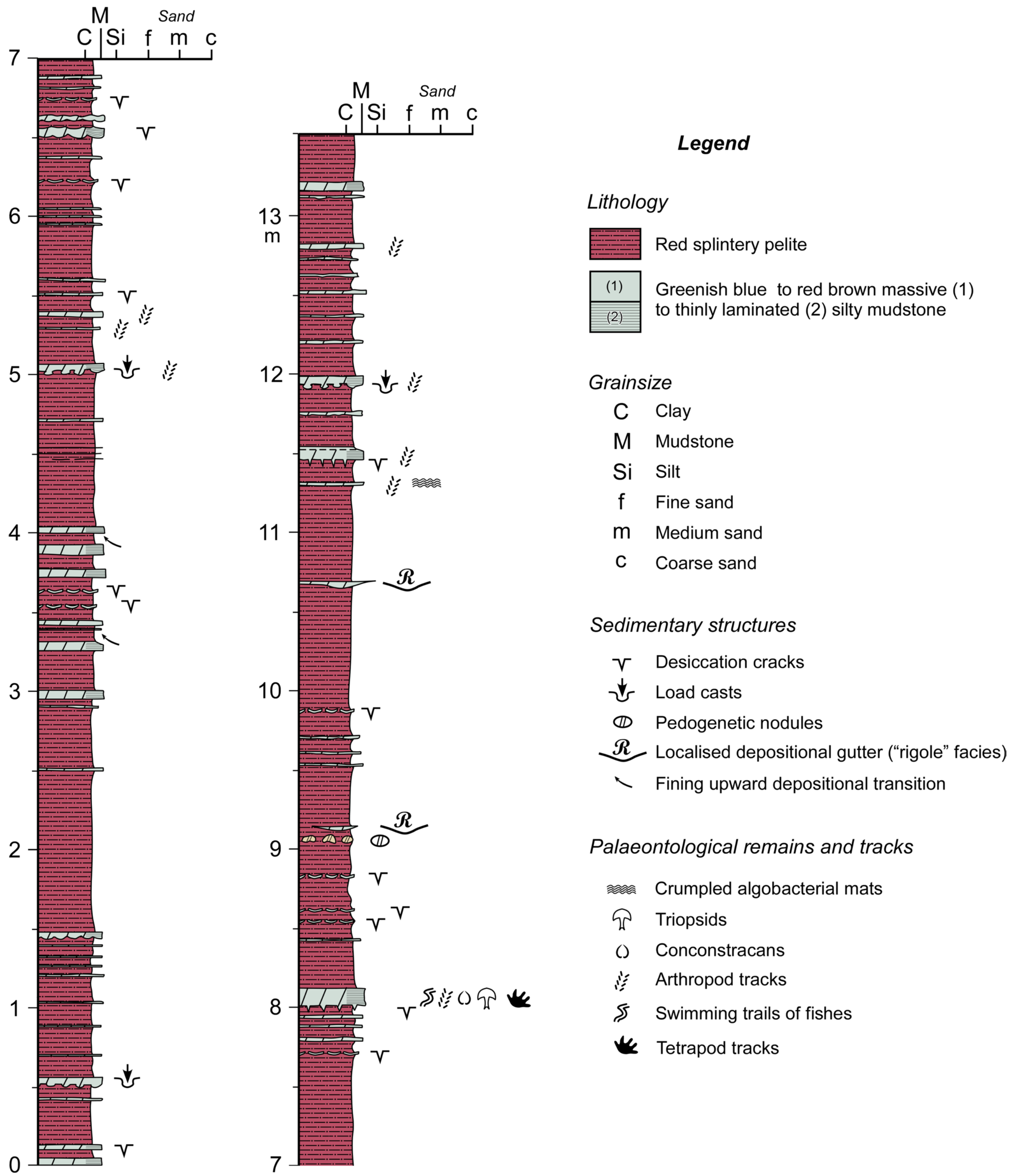


Fig. 3 Detailed sedimentological column of the Col de Dio section

Undichna britannica Higgs, 1988
(Fig. 5c–d)

Material: One trail preserved as convex hyporelief. LdLAP-826.

Description: This trail is 27 cm long, up to 3.5 cm wide and consists of two, wavy, intertwined, out-of-phase, asymmetrical, intermittent and horizontal ridges (Fig. 5c–d). One of the wave shows an amplitude of up to 1.6 cm and

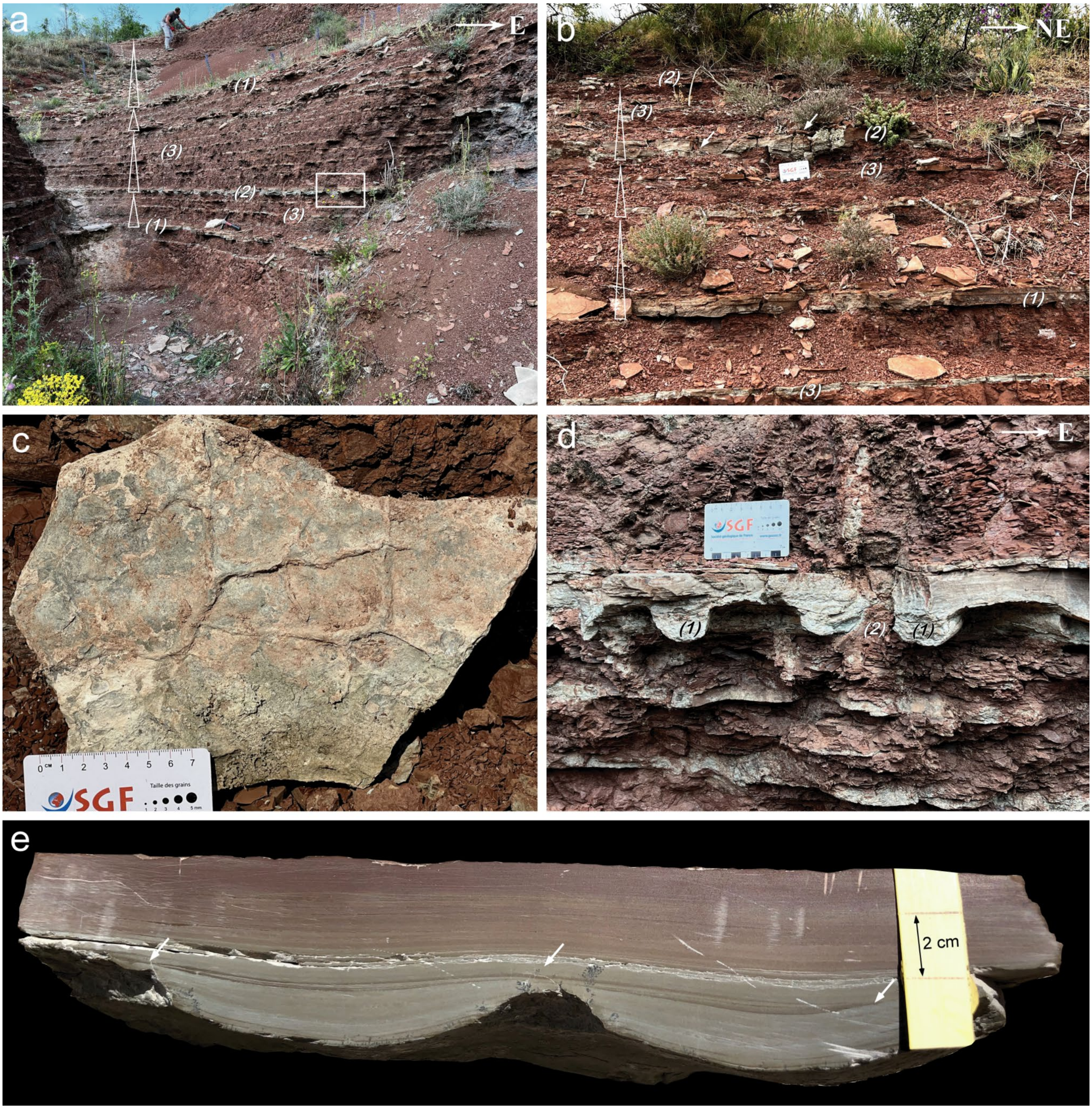


Fig. 4 Sedimentological characteristics of the Col de Dio section. **a** general view of the upper part of the section showing the typical 'bar-code' facies from alternating blue green carbonate bearing siltites and splintery red pelites. Note the flat (1) or wavy (2) character at the base of the thick green siltites layers. The red pelite intervals include very thin but relatively continuous green to brown clayey siltites layers (3) highlighting the rhythmicity of the deposits. White triangle indicates first order sequences. **b** detailed view of laminated carbonate bearing siltites layers sandwiched into red pelites showing both flat to slightly irregular base and flat top (1) and more erosive base topped with large current ripples (2), Some thin silty layers also show a wavy geometry compatible with current ripples; (3) fine laminated muddy siltite thin layer including possible wave ripples and desiccation cracks. **c** desiccation cracks at the base of a flat blue green carbonate layer indicating subaerial exposure during arid periods. **d** close up view of photo a (white rectangle) showing a thinly laminated blue green carbonate bearing siltite layer submitted to density inversion and sub-pendulous load cast (Owen, 2003) development (1) with distorted pelite protrusion (2) at the nodes of the loading cells. **e** sawn transversal section of a carbonate bearing siltite layer submitted to early gravitational loading and lamina collapse during the deposition of the bed in response to density inversion, with sub-pendulous load cast development. The pinch out of the lamina in the shoulder of the synform and flank of the diapir in the middle part of the layer (white arrows) indicates the progressive compensation up to flat horizontal lamina deposition. The progressive upward colour change from green to red in the middle part of the bed indicates the transition from suboxic to oxic environment

Fig. 5 *Undichna* from the Permian tracksite of Col de Dio. **a–b** *Undichna bina*, photograph (**a**) and interpretative sketch (**b**); LdLAP-840. **c–d** *Undichna britannica*, photograph (**c**) and interpretative sketch (**d**); LdLAP-826

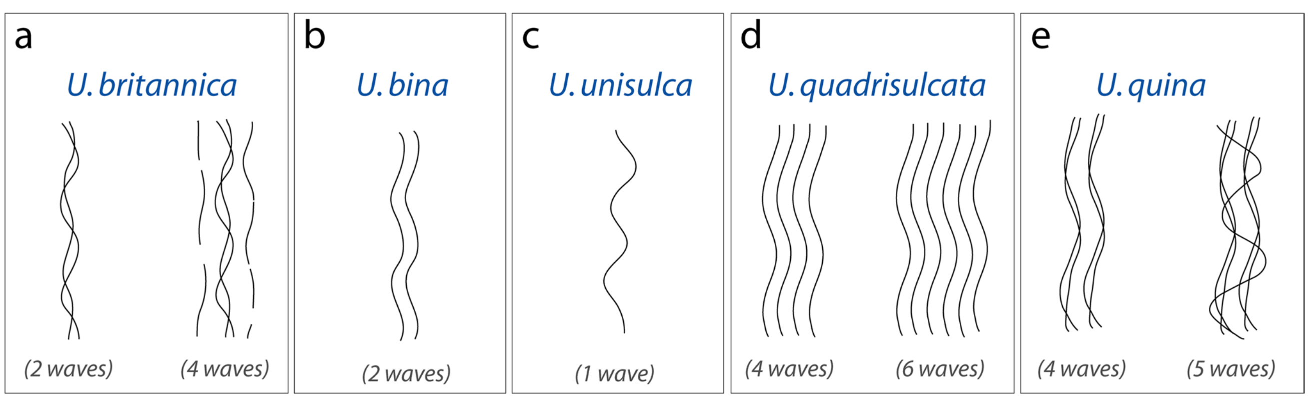


Fig. 6 Diverse morphologies of *Undichna* ichnospecies. **a** *U. britannica* (Higgs 1988). **b** *U. bina* (Anderson 1976). **c** *U. unisulca* (Gibert et al. 1999). **d** *U. quadrisulcata* (Knaust 2019). **e** *U. quina* (Trewin 2000)

a wavelength of up to 5 cm. The other wave shows a lower amplitude and a longer wavelength (not measurable). The width of ridges strongly varies (up to 7 mm wide).

Remarks: Based on the following characters, the trail of the slab LdLAP-826 can be ascribed to *U. britannica*: "trails comprising two out-of-phase, intertwined waves, one of which has a greater amplitude than the other" (see emended diagnosis of the ichnospecies *U. britannica* in Minter and Braddy 2006).

Undichna cf. *britannica* Higgs, 1988
(Fig. 7a–c)

Material: One trail preserved as convex hyporelief. LdLAP-827.
Description: This trail is 20.5 cm long, up to 3.5 cm wide and is composed of two, intertwined, out-of-phase, wavy, asymmetrical and horizontal sharp ridges (Fig. 7a–c). One of the waves is deeply marked whereas the other is poorly marked. The sinuosity is not regular. The crests are asymmetrical, rounded to pointed (Fig. 7a–c). The amplitude and the wavelength are not constant. The amplitude is up to 3.5 cm long whereas the wavelength varies from 3.2 cm to 4.3 cm. The ridges are up to 5 mm wide.
Remarks: Similarly with the trail of the slab LdLAP-826, this track displays two, intertwined, out-of-phase, wavy, and asymmetrical waves. These characters match with *U. britannica.* However, the difference of amplitude between the two waves, which is characteristic of *U. britannica*, is less marked than the specimen of the slab LdLAP-826 (see emended diagnosis *U. britannica* in Minter and Braddy 2006).

Undichna unisulca Gibert et al., 1999
(Fig. 8a–b)

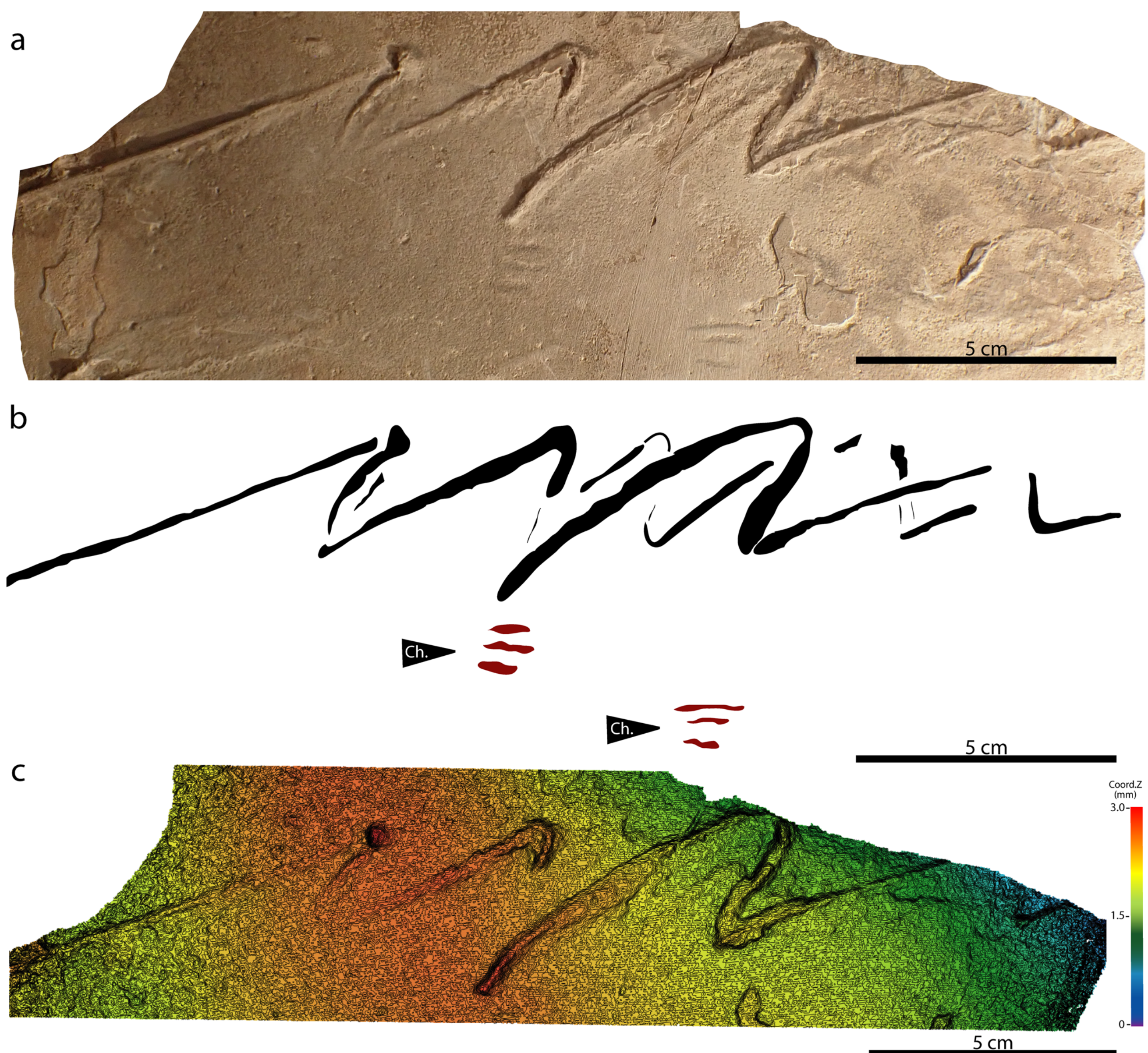


Fig. 7 **a–c** *Undichna* cf. *britannica* and *Characichnos* (indicated by the arrows), photograph (**a**), interpretative sketch (**b**) and digital elevation model in false colours (**c**); LdLAP-827. *Ch. Characichnos*

Material: Two trails preserved as concave epireliefs. LdLAP-841– LdLAP-842.

Description: The longest trail is 27 cm long, up to 2.2 cm wide. Trails are characterised by a single, horizontal, thin, unbranched, asymmetric and sinusoidal wave (Fig. 8a–b). The amplitude varies from 2.5 mm to 9.0 mm whereas the wavelength varies 4.0 cm to 7.6 cm. The groove is up to 4 mm wide.

Remarks: *U. unisulca* was described based on specimens from the Cretaceous of Spain (Gibert et al. 1999). It consists of the simplest form of *Undichna* (Fig. 6c). *U. unisulca* differs from *Cochlichnus* by showing a wavelength which is higher than 20 mm in length (Minter and Braddy 2006).

Undichna isp.
(Fig. 8c–d)

Material: One trail preserved as convex hyporelief. LdLAP-828.

Description: This trail is 27 cm long, up to 3.5 cm wide and consists of four wavy, intertwined, intermittent, sharp, and up to 3 mm wide ridges (Fig. 8c–d). At least two waves are in-phase. They display a 2 cm high amplitude and a 13.5 cm long wavelength.

Remarks: Several ichnospecies of *Undichna* show the presence of four waves (*U. britannica*, *U. quadrisulcata*, *U. quina*; Fig. 6a, d–e; see also Figure 2 in Minter and Braddy 2006). When *U. britannica* shows four waves (Fig. 6a), it differs from LdLAP-828 by the presence of two out-of-phase intertwined waves and two outer parallel waves with lower amplitude. *U. quadrisulcata* differs from LdLAP-828 by trails forming four to six parallel waves (Fig. 6d; Knaust 2019). *U. quina* differs from LdLAP-828 by the presence of in-phase and paired waves (Fig. 6e; see also Figure 2 in Minter and Braddy 2006). *U. quina* can also shows a fifth wave (Fig. 6e).

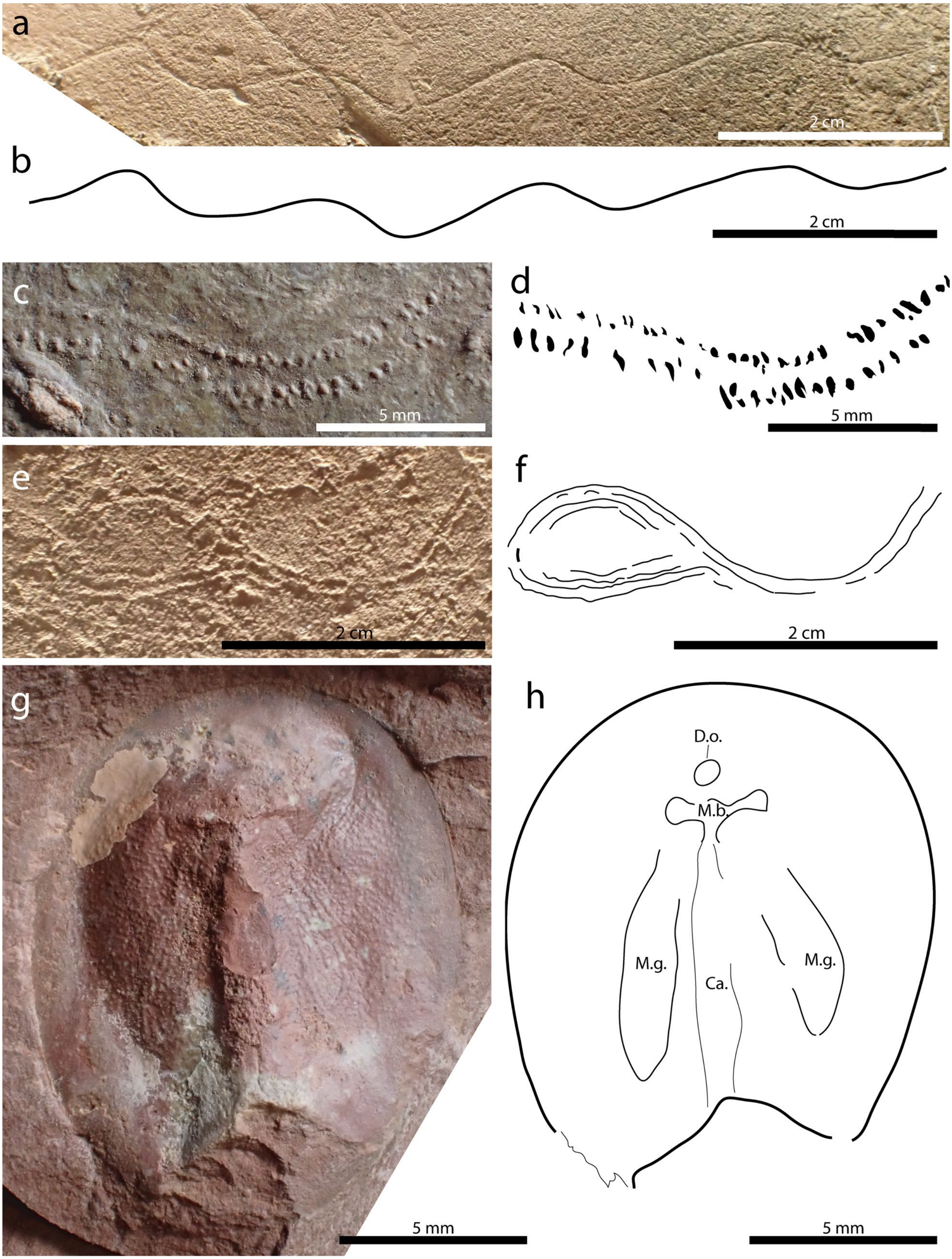
Associated vertebrate and invertebrate tracks

Characichnos Whyte and Romano, 2001
Characichnos isp.
(Fig. 7a–b)

Material: Two tracks preserved as convex hyporeliefs. LdLAP-827.

Description: The slab LdLAP-827 bears two swimming tracks of tetrapods (Fig. 7a–b). They are small, up to 12 mm

Fig. 8 *Undichna* from the Permian tracksite of Col de Dio. **a–b** *Undichna unisulca*, photograph (**a**) and interpretative sketch (**b**); LdLAP-841. **c–d** *Undichna* isp., photograph (**a**) and interpretative sketch (**b**); LdLAP-828


a
2 cm
b
2 cm
c
5 mm
d
5 mm
e
2 cm
f
2 cm
g
5 mm
h
D.o.
M.b.
M.g.
Ca.
M.g.
5 mm

◂**Fig. 9** Associated ichnofossils and invertebrate body remains. **a–b** cf. *Cochlichnus* isp., photograph (**a**) and interpretative sketch (**b**); LdLAP-828. **c–d** *Diplichnites gouldi*, photograph (**c**) and interpretative sketch (**d**); LdLAP-850. **e–f** *Diplopodichnus biformis*, photograph (**e**) and interpretative sketch (**f**); LdLAP-827. **g–h** triopsid *Heidiops permiensis*, photograph (**g**) and interpretative sketch (**h**); LdLAP-846; *Ca.* carina; *D.o.* dorsal organ; *M.b.* mandibular bulge; *M.g.* maxillary glands

long, up to 11 mm wide. Tracks are oriented in the same direction, being probably related to the same trackway. The distance between the two tracks is 40 mm long. They are composed of three parallel, quite elongated, thin and straight marks of digits. Imprints of claw or sole are absent.
Remarks: These tracks can be interpreted as pes or manus imprints of a small tetrapod half-floating and swimming in shallow water. Only the tips of the digits touched the substrate. *Characichnos* is reported from the Carboniferous to the Cretaceous (Whyte and Romano 2001; Weems and Lucas 2021) and was identified in several Permian formations throughout the world (e.g. Argentina, Melchor and Sarjeant 2004; Spain, Mujal et al. 2016; USA, Lucas and Spielmann 2009; Lerner and Lucas 2015; Morocco, Moreau et al. 2020). We may notice that on the surface of LdLAP-827 *Characichnos* isp. co-occurs with a swimming trail of fish.

cf. *Cochlichnus* Hitchcock, 1858
cf. *Cochlichnus* isp.
(Fig. 9a–b)

Material: One trail preserved as concave epirelief. LdLAP-828.
Description: This trail is 8.2 cm long, up to 7 mm wide and consists of an horizontal, thin, unbranched, unornamented and sinusoidal groove (Fig. 9a–b). The amplitude varies from 3.5 mm to 5.0 mm whereas the wavelength varies from 17 mm to 23 mm. The ratio amplitude/wavelength varies from 0.15 to 0.25.
Remarks: The gross morphology of *Cochlichnus* shares some similarities with *Undichna unisulca* (Gibert et al. 1999). Both ichnotaxa are characterised by a single sinusoidal wave. According to Gibert et al. (1999), *Cochlichnus* differs from *U. unisulca* in having smaller amplitude and wavelength values. According to Minter and Braddy (2006), *Cochlichnus* should be reserved for specimens with wavelength around 20 mm (or less) whereas *Undichna unisulca* is used for wavelengths greater than 100 mm.

Diplichnites Dawson, 1873
Diplichnites gouldi Gevers et al., 1971
(Fig. 9c–d)

Material: Two slabs bearing numerous traceways preserved as convex hyporeliefs. LdLAP-850–LdLAP-851.
Description: Trackways are simple, straight to curved and consist of two parallel rows of tiny traces of appendages. The longest trackway is 4.5 cm long. External and internal trackway widths are up to 2.0 mm long and up to 0.8 mm long, respectively. The traces of appendages are numerous, closely spaced and form an angle with the trackway midline that varies from 45° to 90°. The traces of appendages are closely spaced, separated by a distance of up to 0.4 mm. Traces of appendages are up to 1 mm long and up to 0.3 mm wide, and sometimes show a bifid end.
Remarks: *Diplichnites gouldi* was reported from numerous Permian tracksites throughout the world (e.g. Minter et al. 2007; Avanzini et al. 2011; Lucas et al. 2011; Marchetti et al. 2015; Moreau et al. 2020). Such tracks share similarities with *Acripes multiformis* described by Gand et al. (2008) in Permian from Lodève, which includes a very large set of track morphologies. As suggested by Minter et al. (2007), the taxonomy of *Diplichnites* and close relatives (e.g. *Acripes, Asaphoidichnus, Lineatichnus, Merostomichnites, Multipodichnus, Pentapodichnus, Petalichnus, Protichnites, Tasmanadia, Trachomatichnus* and *Umfolozia*) needs to be revised.

Diplopodichnus Brady, 1947
Diplopodichnus biformis Brady, 1947
(Fig. 9e–f)

Material: Three slabs bearing numerous traceways preserved as concave epireliefs (LdLAP-827) and convex hyporeliefs (LdLAP-850–LdLAP-851).
Description: The longest traceway has a length of 10 cm. They are horizontal, unbranched, curved, and up to 1.6 mm wide (Fig. 9e–f). They consist of two thin and up to 0.6 mm wide parallel epichnial grooves separated by a central ridge that is up to 0.6 mm wide (Fig. 9e–f).
Remarks: *Diplopodichnus* shows a wide stratigraphic range, occurring in deposits which are Late Proterozoic to the Early Jurassic in age (Buatois et al. 1998a; Uchman et al. 2011 and references therein). In the Permian basins from France *Diplopodichnus* was reported from the Rodez Basin and the Saint-Affrique Basin (Moreau and Gand 2022; Moreau et al. 2022).

Associated body fossils

Heidiops permiensis (Gand et al., 1997) Werneburg and Schneider, 2022
(Fig. 9g–h)

Material: Two specimens. LdLAP-846, LdLAP-848.
Description: The material includes two fragments of carapaces that are three-dimensionally preserved. One of them is nearly complete (LdLAP-846; Fig. 9g–h). Thorax, telson

and furca are not preserved. The carapace is longer than wide (length = 14 mm; width = 11 mm; length/ratio = 1.3), shield-shaped and shows well-marked median dorsal carina. Anteriorly, the carapace is rounded whereas posterior margin is deeply concave is the median region. The surface of the carapace is finely granulated (small tubercles). The mandibular bulge is well-marked. Maxillary glands are elongated and obliquely oriented upon the anterior part of the carapace, forming an angle of about 30° with the carina. The dorsal organ is quite visible, rounded and located on the anteromedian part of the carapace (slightly anteriorly to the mandibular bulge).

Remarks: Based on material collected in several sites from the Salagou Fm. such triopsids were firstly named *Triops cancriformis permiensis* by Gand et al. (1997). Werneburg and Schneider (2022) recently included this taxon in the monospecific genus *Heidiops*. Triopsids were reported in Permian deposits from France (Gand et al. 1997; Garrouste et al. 2009), Germany (Voigt et al. 2008; Werneburg and Schneider 2022) and the USA (Ruedemann 1922).

Discussion

Palaeoenvironment and associated faunas

The careful analysis of the sedimentary facies and stacking pattern of the Col de Dio fossiliferous section indicates two orders of stratigraphic sequences that rule the alternation of humid and arid cycles in an endorheic terminal mud-dominated floodplain and playa lake environments (Tunbridge 1981, 1984) similar to distributive fluvial systems (Weissmann et al. 2010; Gulliford et al. 2014; Dos Reis et al. 2019) or terminal fluvial fans (Cain and Mountney 2009). The two nested sequences observed along the section can be reported to two-order climatic variations of the Milankovitch band following the works of Schneider et al. (2006), Tabor and Poulsen (2008) and more recently Pfeifer et al. (2020). In particular, these last authors consider the few metre-thick sequences (described here as first order sequences) to high frequency obliquity and/or precession variability. During humid periods, strongly seasonal rainfall led to extensive overland flow and drowning of the terminal flood plain which is submitted to overall high dense silty mud suspension settling. These deposits, at the origin of the red pelite facies, were poorly favourable to the development of life because high turbidity and sedimentation rate in standing waters and soupy consistent mud. During the arid phases, the terminal floodplain was progressively dried up and submitted to desiccation process and periodically invaded by the radial spreading of unconfined diluted Newtonian flow from the termination of ephemeral low sinuous channels or overspill processes in relation to short seasonal rains. This process led to the rapid deposition of laterally extensive plane parallel to rippled laminated blue-green silt material with possible load cast formation on residual soupy areas, and late carbonate precipitation on remaining shallow resting waters reported to ephemeral playa lakes. Based on the abundance of palaeontological remains associated to the carbonate bearing siltites, we suppose that the diluted flow during semi-arid astronomically controlled cycles favoured the colonization of the terminal floodplain by abundant animal and plant life.

The presence of triopsid crustaceans is characteristic of a terrestrial environment with shallow water such as temporary puddles, ponds/lakes and floodplain marshes of hot-dry and temperate climates (Werneburg and Schneider 2022). The co-occurrence of tetrapod swimming tracks and fish trails on the same surfaces suggests that traces were produced in very shallow water probably periodically flooded and emerged (Fig. 10). The dense concentration of *Undichna* at 8 m of the stratigraphic section could suggests that fishes were trapped in shallow ponds or puddles during dry periods. Although body fossils of fishes remain unknown in the Salagou Fm., the diverse shapes of *Undichna* from Col de Dio suggest that such playa-lake ecosystems included fishes showing a great diversity of morphologies and behaviours. According to Higgs (1988), *U. britannica* was produced by palaeoniscid fishes; the wave with the greatest amplitude being attributed to the caudal fin, whereas the other can be attributed to the anal fin. Trailmakers of *U. unisulca* correspond to fishes whose caudal or anal fins project much further below the body than any other fin (Gibert et al. 1999). Based on the very low amplitudes of *U. bina*, Anderson (1976) suggested that this ichnospecies was produced by pectoral fins of actinopterygian fishes. Trewin (2000) suggested that possible trailmakers of *U. bina* include fishes with an anguilliform locomotion where the whole body undulates.

The co-occurrence of fish trails with cf. *Cochlichnus*, *Diplichnites gouldi* and *Diplopodichnus biformis* attests that this terrestrial ecosystem was inhabited by diverse protostomians (Fig. 10). The ichnogenus *Cochlichnus* is interpreted as grazing trails (Buatois et al. 1996). Tracemakers of *Cochlichnus* are either annelid worms, nematodes or larvae of insects (Hasiotis 2004). Even if the specimen LdLAP-828 matches with the diagnosis of *Cochlichnus* isp., its morphology is very close to those of *Undichna*. We cannot exclude that tracemaker of LdLAP-828 was a small or a juvenil fish. The trackmakers of *Diplopodichnus biformis* were diplopods or other myriapods (Buatois et al. 1998a). *Diplichnites* is usually attributed to a locomotion trace of multi-limb arthropods such as crustaceans, myriapods, and euthycarcinoids (Minter et al. 2007).

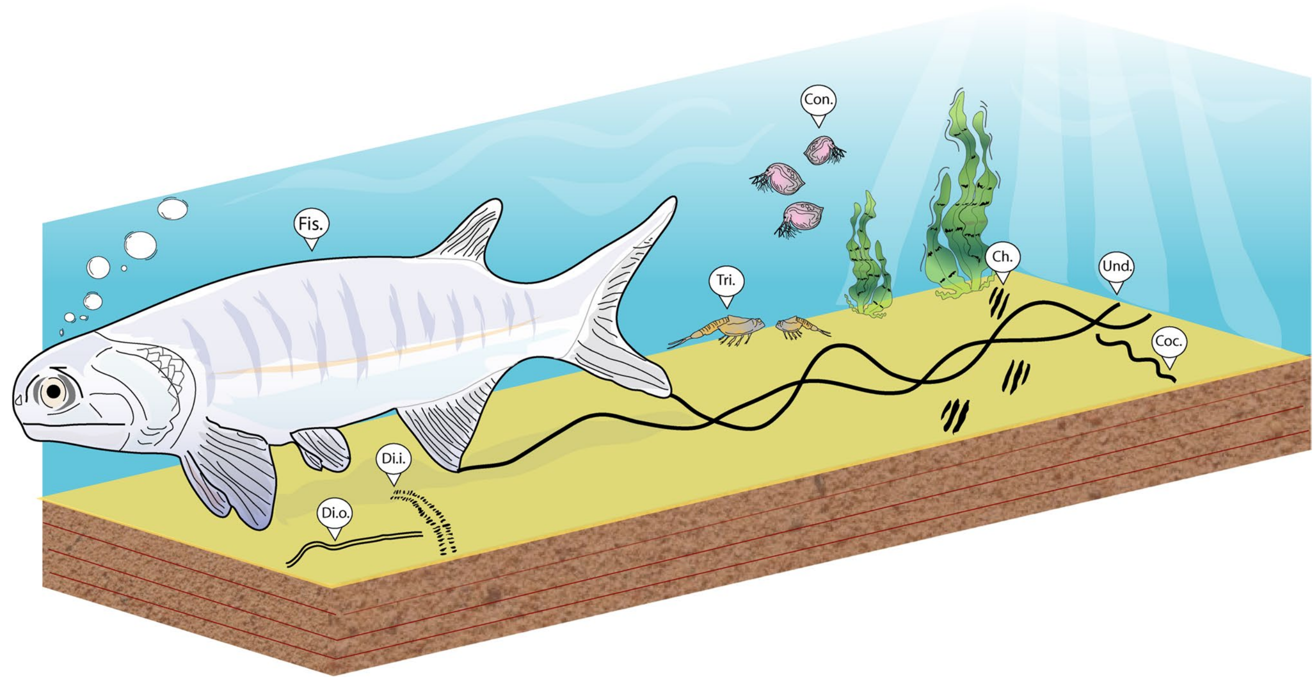


Fig. 10 Schematic reconstruction of the Col de Dio Permian ecosystem with the associated fauna and tracks. *Ch. Characichnos*; *Coc*. *Cochlichnus*; *Con.* "Conchostraca"; *Fis*. fish ; *Di.i Diplichnites*; *Di.o. Diplopodichnus*; *Tri.* Triopsid

Comparison with coeval tracksites

In the Paleozoic record, although such co-occurrence of tetrapod and fish trails is common in Carboniferous deposits (Lucas et al. 2004, 2010; Soler-Gijón and Moratalla 2001; Buatois et al. 1998b; Martin and Pyenson 2005; Fillmore et al. 2011) it seems rarer in Permian tracksites (Minter and Braddy 2006; Lerner and Lucas 2015; Ronchi et al. 2018). Co-occurrences of *Undichna* with tetrapod tracks were reported from Permian sites of Italy (Ronchi et al. 2018) and the United-States (Minter and Braddy 2006; Lerner and Lucas 2015). In France, although Permian tetrapod tracks are known since the 19th century (Fabre 1872), the discovery of swimming trails of fishes is recent (Fara et al. 2022; Moreau and Gand 2022; Moreau et al. 2022). *Undichna* was reported in the Permian deposits from Moulin de Latour, in the Saint-Affrique Basin (Moreau et al. 2022) and Banassac, in the easternmost edge the Rodez Basin (Moreau and Gand 2022). Trails from these areas were ascribed to *Undichna quadrisulcata*, *Undichna* cf. *britannica* and several morphotypes of *Undichna* isp. Additionally, fish trails under study are mentioned in the Permian of Ardèche (Fara et al. 2022). The discovery from the Col de Dio tracksite complements other coeval French tracksites, suggesting that such ichnofaunas showing the co-occurrence of fish trails with tetrapod and arthropod tracks were common in Permian terrestrial ecosystems from the Eastern Pangean intertropical zone.

In the Lodève Basin, several layers yielded body fossils of fishes. They are stratigraphically located in the Usclas-Saint Privat Fm., the Tuilières-Loiras Fm. and the lowermost part of the Viala Fm. (Heyler 1996; Gand et al. 2003b; Lopez et al. 2022; Fig. 2). These fossils were ascribed to the acanthodian *Acanthodes* sp. and to the actinopterygian *Pygopterus* sp. (Heyler 1969, 1977, 1996). Fish remains from the Lodève Basin also include the probable actinopterygian taxon *Usclasichthys macrodens* (Heyler 1977). Additionally, numerous undescribed fishes and elasmobranch coprolites from the Usclas-Saint Privat Fm. are preserved in the palaeontological collections of the Musée de Lodève (Lopez et al. 2022). They include partial and complete skeletons ascribed to undeterminate aeduelliform and palaeonisciform fishes.

In the Rodez, Saint-Affrique and Lodève basins, *Undichna* systematically co-occur with tetrapod and arthropod tracks (Moreau and Gand 2022; Moreau et al. 2022), suggesting that such ichnoassociation is common in Permian deposits from southern France. *Undichna* bearing-surfaces from Rodez and Saint-Affrique basins yielded both amniotes and anamniotes trackways (e.g. *Amphisauropus latus, Batrachichnus salamandroides*, *Dromopus lacertoides, Ichniotherium*; Moreau and Gand 2022; Moreau et al. 2022).

Conclusions

The palaeontological site from the Col de Dio yields the first trails of fishes from the Permian deposits of the Lodève Basin. This discovery reveals that ichthyofaunas were an important component in the periodical playa-lake and dried terminal floodplain ecosystems in which the carbonate bearing siltites of the Salagou Fm. were deposited. These swimming trails of fishes show several morphologies including one, two or four waves. Three ichnospecies of *Undichna* are reported, *U. bina*, *U. britannica* and *U. unisulca,* suggesting a great diversity of fish morphologies and/or behaviours. The co-occurrence of *Undichna* with swimming tracks of tetrapods suggests that fishes were trapped in very shallow ponds/lakes or puddles during dry periods. The ichnoassemblage including *Characichnos*, cf. *Cochlichnus*, *Diplichnites*, *Diplopodichnus*, and *Undichna* as well as the associated body fossils demonstrate that such ecosystem was inhabited by tetrapods, fishes, arthropods (e.g. triopsids, "conchostracans") and other diverse protostomians during semi-arid blooms cycles.

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Data availability The specimens investigated here are housed in the Musée de Lodève.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

References

Anderson, A.M. (1976). Fish trails from the Early Permian of South Africa. *Palaeontology, 19*, 397–409.

Avanzini, M., Contardi, P., Ronchi, A., & Santi, G. (2011). 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

Béthoux, O. (2008). The insect fauna from the Permian of Lodève (Hérault, France): state of the art and perspectives. *Journal of Iberian Geology*, *34*, 109–113.

Bethoux, O., Nel, A., Gand, G., & Lapeyrie, J. (2001). *Surijoka lutevensis* nov. sp.: the first Glosselytrodea (Insecta) from the Upper Permian of France (Lodève Basin). *Geobios*, *34*, 405–413. https://doi.org/10.1016/S0016-6995(01)80004-8

Béthoux, O., Nel, A., Gand, G., Lapeyrie, J., & Galtier, J. (2002). Discovery of the genus *Iasvia* Zalessky, 1934 in the Upper Permian of France (Lodève Basin)(Orthoptera, Ensifera, Oedischiidae). *Geobios*, *35*, 293–302. https://doi.org/10.1016/S0016-6995(02)00027-X

Béthoux, O., Nel, A., Lapeyrie, J., Gand, G., & Galtier, J. (2003). New Martynoviidae from the Permian of Southern France (Lodève basin) (Insecta: Palaeoptera: Diaphanopterodea). *Geobios*, *36*, 131–139. https://doi.org/10.1016/S0016-6995(03)00002-0

Brady, L. F. (1947). Invertebrate tracks from the Coconino Sandstone of northern Arizona. *Journal of Paleontology, 21*, 466–472.

Buatois, L. A., Mángano, M. G., Wu, X., & Zhang, G. (1996). Trace fossils from Jurassic lacustrine turbidites of the Anyao Formation (central China) and their environmental and evolutionary significance. *Ichnos, 4*, 287–303. https://doi.org/10.1080/10420949609380137

Buatois, L. A., Mángano, M. G., Maples, C. G., & Lanier, W. P. (1998a). 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

Buatois, L. A., Mángano, M. G., Maples, C. G., & Lanier, W. P. (1998b). Ichnology of an upper Carboniferous fluvio-estuarine paleovalley: The Tonganoxie sandstone, Buildex quarry, eastern Kansas, USA. *Journal of Paleontology, 72*, 152–180. https://doi.org/10.1017/S0022336000024094

Cain, S. A., & Mountney, N. P. (2009). Spatial and temporal evolution of a terminal fluvial fan system: the Permian Organ Rock Formation, South-east Utah, USA. *Sedimentology*, *56,* 1774–1800. https://doi.org/10.1111/j.1365-3091.2009.01057.x

Chakrabarti, A., Mora, S., Richard, F., Phou, T., Fromental, J. M., Pomeau, Y., & Audoly, B. (2018). Selection of hexagonal buckling patterns by the elastic Rayleigh-Taylor instability. *Journal of the Mechanics and Physics of Solids, 121,* 234–257. https://doi.org/10.1016/j.jmps.2018.07.024

Dawson, J. W. (1873). Impressions and footprints of aquatic animals and imitative markings on Carboniferous rocks. *American Journal of Science, 5*, 16–24.

Delage, A. (1912). Empreintes de pieds de grands quadrupèdes dans le Permien Inferieur de l'Hérault. *Mémoires de l'Académie des Sciences et Lettres de Montpellier, 4*, 221–267.

Dos Reis, A. D., dos Santos Scherer, C. M., do Amarante, F. B., Rossetti, M. D. M. M., Kifumbi, C., de Souza, E. G., Ferronatto, J. P., & Owen, A. (2019). Sedimentology of the proximal portion of a large-scale, Upper Jurassic fluvial-aeolian system in Paraná Basin, southwestern Gondwana. *Journal of South American Earth Sciences*, *95*, 102248. https://doi.org/10.1016/j.jsames.2019.102248

Doubinger, J., & Kruseman, G. P. (1965). Sur la flore du Permien de la région de Lodève ("zone de transition" et Saxonien inférieur). *Bulletin de la Société Géologique de France, 7,* 541–548.

Ellenberger, P. (1983a). Sur la zonation ichnologique du Permien moyen (Saxonien du bassin de Lodève, Hérault. *Comptes Rendus de l'Académie des Sciences de Paris, 297*, 553–558.

Ellenberger, P. (1983b). Sur la zonation ichnologique du Permien inférieur (Autunien du bassin de Lodève, Hérault. *Comptes Rendus de l'Académie des Sciences de Paris, 297*, 631–636.

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 de Paris, 299*, 581–586.

Ellenberger, F., & Ellenberger, P. (1959). Quelques pistes de vertébrés du Permien inférieur de Lodève. *Comptes Rendus de l'Académie des Sciences de Paris, 248,* 437.

Evans, M. E. (2012). Magnetostratigraphy of the Lodève Basin, France: Implications for the Permo-Carboniferous reversed superchron and the geocentric axial dipole. *Studia Geophysica et Geodaetica*, *56*, 725–734. https://doi.org/10.1007/s11200-010-0082-y

Evans, M. E., Pavlov, V., Veselovsky, R., Fetisova, A., (2014). Late Permian paleomagnetic results from the Lodève, Le Luc, and Bas-Argens Basins (southern France): magnetostratigraphy and geomagnetic field morphology. *Physics of Earth and Planetary Interiors, 237*, 18–24. 10.1016/j. pepi.2014.09.002

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.

Falconnet, J. (2010). *Diversification initiale des Amniotes: l'apport des amniotes français* Ph.D. Thesis, (pp. 1–336). Paris: Muséum National d'Histoire Naturelle.

Fara, E., Moreau, J.-D., Szewczyk, L., Gand, G., Mendras, L., Fayolle, R., Klee, N., Jiquel, S., Laffont, R., Poloni, L., Verolet, M., & Vennin, E. (2022). Etude des traces de pas de vertébrés du Permien et du Trias d'Ardèche. *Bulletin de la Société Géologique d'Ardèche, 15*, 43–50.

Fillmore, D. L., Lucas, S.G., & Simpson, E. L. (2011). The fish swimming trace *Undichna* from the Mississippian Mauch Chunk Formation, Eastern Pennsylvania. *Ichnos, 18,* 27–34. https://doi.org/10.1080/10420940.2011.552579

Galtier, J., & Broutin, J. (1995). La flore de la zone de transition de l'Autunien supérieur de Lodève. *Sciences Géologiques, 48*, 83–93.

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

Gand, G. (1986). Interprétations paléontologique et paléoécologique de quatre niveaux à traces de vertébrés observés dans l'Autunien du Lodèvois (Hérault). *Géologie de la France, 2*, 155–176.

Gand, G. (1987). *Les traces de vertébrés tétrapodes du Permien français: paléontologie, stratigraphie, paléoenvironnements* Ph.D. Thesis, (pp. 1–341). Dijon: Université de Bourgogne.

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. In S. G. Lucas, G. Cassinis, & J. W. Schneider (Eds.), *Non-Marine Permian Biostratigraphy and Biochronology*. *Geological Society, London, Special Publications, 265*, 157–177. https://doi.org/10.1144/GSL.SP.2006.265.01.07

Gand, G., Garric, J., & Lapeyrie, J. (1997). Biocénoses à Triopsidés (Crustacea, Branchiopoda) du Permien du Bassin de Lodève (France). *Geobios, 30*, 673–700. https://doi.org/10.1016/S0016-6995(97)80157-X

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., Galtier, J., Garric, J., Schneider, J., Körner, F., & Béthoux, O. (2003a). Les bassins carbonifère de Graissessac et permien de Lodève, (Languedoc-France). Livret-guide de l'excursion n◦3 du 7 mai 2001. *Bulletin de la Société d'Histoire Naturelle d'Autun, 186,* 9–40.

Gand, G., Galtier, J., Garric, J., Schneider, J., Körner, F., & Béthoux, O. (2003b). Les bassins carbonifère de Graissessac et permien de Lodève, (Languedoc-France). Livret-guide de l'excursion n◦3 du 7 mai 2001. *Bulletin de la Société d'Histoire Naturelle d'Autun, 185,* 7–40.

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.

Garrouste, R., Nel, A., & Gand, G. (2009). New fossil arthropods (Notostraca and Insecta: Syntonopterida) in the Continental Middle Permian of Provence (Bas-Argens Basin, France). *Comptes Rendus Palevol, 8,* 49–57. https://doi.org/10.1016/j.crpv.2008.11.008

Garrouste, R., Lapeyrie, J., Steyer, J. S., Giner, S., & Nel, A. (2018). Insects in the Red Middle Permian of Southern France: first Protanisoptera (Odonatoptera) and new Caloneurodea (Panorthoptera), with biostratigraphical implications. *Historical Biology, 30*, 546–553. https://doi.org/10.1080/08912963.2017.1301448

Gervais, P. (1859). Sur un Saurien proprement dit des schistes permiens de Lodève. *Comptes Rendus de l'Académie des Sciences de Paris, 48*, 1–192.

Gevers, T. W., Frakes, L. A., Edwards, L. N., & Marzolf, J. E. (1971). Trace fossils in the Lower Beacon sediments (Devonian), Darwin Mountains, southern Victoria Land, Antarctica. *Journal of Paleontology, 45*, 81–94.

De Gibert, J. M., Buatois, L. A., Fregenal-Martínez, M. A., Mángano, M. G., Ortega, F., Poyato-Ariza, F. J., & Wenz, S. (1999). The fish trace fossil *Undichna* from the Cretaceous of Spain. *Palaeontology, 42*, 409–427.

Gulliford, A. R., Flint, S. S., & Hodgson, D. M. (2014). Testing applicability of models of distributive fluvial systems or trunk rivers in ephemeral systems: reconstructing 3-D fluvial architecture in the Beaufort Group, South Africa. *Journal of Sedimentary Research, 84*, 1147–1169. https://doi.org/10.2110/jsr.2014.88

Harrison, P., & Maltman, A. J. (2003). Numerical modelling of reverse-density structures in soft non-Newtonian sediments. *Geological Society, London, Special Publications*, *216*, 35–50. https://doi.org/10.1144/GSL.SP.2003.216.01.04

Hasiotis, S. T. (2004). Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. *Sedimentary Geology, 167,* 177–268. https://doi.org/10.1016/j.sedgeo.2004.01.006

Heyler, D. (1969). *Vertébrés de l'Autunien de France* (pp. 1–255). Paris: Cahiers de Paléontologie du Centre National de la Recherche Scientifique.

Heyler, D. (1977). Découvertes ichthyologiques dans le Permien de Lodève; une nouvelle structure dentaire. *Géologie Méditerranéenne, 4,* 189–203.

Heyler, D. (1996). Les vertébrés permiens du bassin de Lodève (Hérault) : bilan. *Bulletin de la Société d'Histoire Naturelle d'Autun, 157*, 5–28.

Heyler, D., & Lessertisseur, J. (1963). Pistes de tétrapodes permiens dans la région de Lodève (Hérault). *Bulletin du Muséum national d'Histoire naturelle de Paris, 11*, 125–221. https://www.biodiversitylibrary.org/page/58216767

Higgs, R. (1988). Fish trails in the Upper Carboniferous of southwest England. *Palaeontology, 31*, 255–272.

Hitchcock, E. (1858). *Ichnology of New England: a report on the sandstone of the Connecticut valley especially its fossil footmarks* (pp. 1–220). Boston: William White.

Knaust, D. (2019). The Fish Trail *Undichna quadrisulcata* isp. nov. from the Eocene of Spitsbergen. *Ichnos*, *26*, 178–186. https://doi.org/10.1080/10420940.2018.1532901

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

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.

Lopez, M., Falconnet, J., & Decombeix, A.-L. (2022). *Livret guide Bassin de Lodève* (pp. 1–47). Montpellier: Congrès de l'Association Paléontologique Française.

Lucas, S. G., & Spielmann, J. A. (2009). Tetrapod footprints from the lower Permian Abo Formation near Bingham, Socorro country, New Mexico (pp. 299–304). In V. Lueth, S. G. Lucas, & R. M. Chamberlin (Eds.), *New Mexico Geolological Society, Guidebook, 60th Field Conference, Geology of the Chupadera Mesa Region*.

Lucas, S. G., Lerner, A. J., Bruner, M., & Shipman, P. (2004). Middle Pennsylvanian ichnofauna from eastern Oklahoma, USA. *Ichnos, 11*, 45–55. https://doi.org/10.1080/10420940490442322

Lucas, S. G., Mansky, C., & Calder, J. (2010). Invertebrate ichnology of the Mississippian Horton Bluff Formation at Blue Beach, Nova Scotia, Canada. In GSA Denver Annual Meeting (Oct 31–Nov 3). *Geological Society of America Abstracts with Programs,* paper N°101-41.

Lucas, S. G., Voigt, S., Lerner, A. J., & Nelson, W. J., (2011). Late early Permian continental ichnofauna from Lake Kemp, north-central Texas, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology, 308*, 395–404. https://doi.org/10.1016/j.palaeo.2011.05.047

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

Martin, A. J., & Pyenson, N. D. (2005). Behavioral significance of vertebrate trace fossils from the Union Chapel site (pp. 59–73). In R. J. Buta, A. K. Rindsberg, & D. C. Kopaska-Merkel (Eds.), *Pennsylvanian Footprints in the Black Warrior Basin of Alabama*. Tuscaloosa: Alabama Paleontological Society.

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. (2015a). 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

Michel, L. A., Tabor, N. J., Montañez, I. P., Schmitz, M. D. Davydov, V. I., (2015b). Reply to the comment on "Chronostratigraphy and paleoclimatology of the Lodève Basin, France: Evidence for a pan-tropical aridification event across the Carboniferous-Permian boundary'' by Michel et al., (2015a). *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

Minter, N. J., Krainer, K., Lucas, S. G., Braddy, S. J., & Hunt, A. P. (2007). Palaeoecology of an Early Permian playa lake trace fossil assemblage from Castle Peak, Texas, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *246*, 390–423. https://doi.org/10.1016/j.palaeo.2006.10.009

Mora, S., Phou, T., Fromental, J. M., & Pomeau, Y. (2014). Gravity driven instability in elastic solid layers. *Physical review letters*, *113*, 178301. https://doi.org/10.1103/PhysRevLett.113.178301

Moreau, J.-D., & Gand, G. (2022). New data on the Permian ecosystem from the Rodez Basin: ichnofauna (traces of protostomians, tetrapods and fishes), jellyfishes and plants from Banassac-Canilhac (Lozère, southern France). *Geodiversitas, 44*, 975–987. https://doi.org/10.5252/geodiversitas2022v44a31

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

Moreau, J.-D., Michelin, A., Fara, E., Gand, G., Galtier, J., Puech, G., & Fouché, S. (2022). Ichnofossils and body fossils from the Permian of the Sorgue Valley (Saint-Affrique Basin, southern France): palaeoenvironmental implications. *Historical biology, 36*, 82–95. https://doi.org/10.1080/08912963.2022.2148205

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

Nel, A., Gand, G., & Garric, J. (1999). A new family of Odonatoptera from the continental Upper Permian: the Lapeyriidae (Lodève Basin, France). *Geobios*, *32*, 63–72. https://doi.org/10.1016/S0016-6995(99)80083-7

Nel, A., Fleck, G., Garrouste, R., & Gand, G. (2008). The Odonatoptera of the Late Permian Lodève Basin (Insecta). *Journal of Iberian Geology*, *34*, 115–122.

Owen, G. (2003). Load structures: gravity-driven sediment mobilization in the shallow subsurface. *Geological Society, London, Special Publications*, *216*, 21–34. https://doi.org/10.1144/GSL.SP.2003.216.01.03

Pfeifer, L. S., Hinnov, L., Zeeden, C., Rolf, C., Laag, C., & Soreghan, G. S. (2020). Rock magnetic cyclostratigraphy of permian loess in eastern equatorial pangea (Salagou formation, South-Central France). *Frontiers in Earth Science*, *8*, 241. https://doi.org/10.3389/feart.2020.00241

Prokop, J., Szwedo, J., Lapeyrie, J., Garrouste, R., & Nel, A. (2015). New middle Permian insects from Salagou Formation of the Lodève Basin in southern France (Insecta: Pterygota). *Annales de la Société entomologique de France, 51*, 14–51.

Ronchi, A., Santi, G., Marchetti, L., Bernardi, M., & Gianolla, P. (2018). First report on swimming trace fossils of fish from the Upper Permian and Lower Triassic of the Dolomites (Italy). *Annales Societatis Geologorum Poloniae, 88*, 111–125.

Ruedemann, R. (1922). On the occurrence of an *Apus* in the Permian of Oklahoma. *Journal Geology*, *30*, 311–318.

Schneider, J. W., Körner, F., Roscher, M., & Kroner, U. (2006). Permian climate development in the northern peri-Tethys area—the Lodève basin, French Massif Central, compared in a European and global context. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *240*, 161–183. https://doi.org/10.1016/j.palaeo.2006.03.057

Soler-Gijón, R., & Moratalla, J. J. (2001). Fish and tetrapod trace fossils from the Upper Carboniferous of Puertollano, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology, 171*, 1–28. https://doi.org/10.1016/S0031-0182(01)00257-7

Tabor, N. J., & Poulsen, C. J. (2008). Palaeoclimate across the Late Pennsylvanian–Early Permian tropical palaeolatitudes: a review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *268*, 293–310. https://doi.org/10.1016/j.palaeo.2008.03.052

Thévenin, A. (1910). Les plus anciens quadrupèdes de France. *Annales de Paléontologie, 5*, 1–65.

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

Tunbridge, I. P. (1981). Sandy high-energy flood sedimentation—some criteria for recognition, with an example from the Devonian of SW England. *Sedimentary Geology*, *28*, 79–95. https://doi.org/10.1016/0037-0738(81)90058-0

Tunbridge, I. P. (1984). Facies model for a sandy ephemeral stream and clay playa complex; the Middle Devonian Trentishoe Formation of North Devon, UK. *Sedimentology, 31*, 697–715. https://doi.org/10.1111/j.1365-3091.1984.tb01231.x

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

Voigt, S., Hauschke, N. & Schneider, J. W. (2008). Nachweise fossiler Notostraken in Deutschland — ein Überblick. *Abhandlungen und Berichte für Naturkunde, 31*, 7–24.

Weems, R. E., & Lucas, S. G. (2021). The first record of vertebrate ichnofossils from the Norton Formation (Pennsylvanian, Middle Moscovian) in southwestern Virginia, USA. *New Mexico Museum of Natural History and Science Bulletin*, *83*, 497–504.

Weissmann, G. S., Hartley, A. J., Nichols, G. J., Scuderi, L. A., Olson, M., Buehler, H., & Banteah, R. (2010). Fluvial form in modern continental sedimentary basins: distributive fluvial systems. *Geology, 38*, 39–42. https://doi.org/10.1130/G30242.1

Werneburg, R., & Schneider, J. W. (2022). New branchiopod crustaceans from the late Carboniferous and early Permian of the Thuringian Forest Basin, Germany, with a review of Permian notostracans from the Lodève basin, France. *Semana*, *37*, 57–103.

Werneburg, R., Steyer, J.-S., Sommer, G., Gand, G., Schneider, W., & Vianey-Liaud, M. (2007). The Earliest Tupilakosaurid amphibian with diplospondylous vertebrae from the Late Permian of Southern France. *Journal of Vertebrate Paleontology*, *27*, 26–30. https://doi.org/10.1671/0272-4634(2007)27[26:TETAWD]2.0.CO;2

Whyte, M. A., & Romano, M. (2001). A dinosaur ichnocoenosis from the Middle Jurassic of Yorkshire, UK. *Ichnos, 8*, 223–234.