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Ichnology of the Lower Ordovician Landeyran Formation, Montagne Noire, France and criteria for distinguishing simple trace fossils from body fossils

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Fossil sites with exceptional preservation (Lagerstätten) are instrumental in accurately reconstructing ancient ecosystems on Earth. Although Lagerstätten are typically approached from a body fossil perspective, trace fossils can also be associated with these assemblages and provide unique evidence of *in situ* past animal behaviours. In this study, we describe the trace fossils found with the Cabrières Biota, a recently discovered Lagerstätte from southern France. Trace fossils are reported from the mudstone-dominated Lower Ordovician Landeyran Formation and consist of simple horizontal trails (*Helminthoidichnites tenuis*, *Helminthopsis granulata*), passively filled horizontal burrows (*Palaeophycus tubularis*), actively filled burrows (*Alcyonidiopsis longobardiae*, *Planolites montanus*, ?*Torrowangea* isp.), rare vertical burrows (*Skolithos linearis*), isolated faecal pellets (*Coprulus oblongus*), and indiscriminate meiofaunal burrows. Ichnological metrics (e.g. absent to low bioturbation intensity, low ichnodiversity) suggest fluctuations between anoxia and dysoxia in sediments of the shelf (i.e. below the mean storm wave base), which favoured the preservation of soft-bodied organisms. These organisms, such as algae or sponges that can have relatively simple morphologies, are differentiated from trace fossils based on five criteria that we review here, and which can be used by other researchers facing difficulties in identifying fossilized objects regardless of the age or location of the investigated Lagerstätte. ☐ *Bioturbation, Floian, anoxia, dysoxia, outcrop bias*

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Ordovician fossils from the Landeyran Valley in Montagne Noire, southern France, have been the focus of numerous studies since the mid-19th century, given their excellent quality of preservation and abundance (Álvaro & Vizcaïno 2001; Monceret *et al.* this volume). The collection of fossils representing rigid body parts of ancient animals has recently been enhanced by the discovery of a soft-bodied assemblage, making the Cabrières Biota the first Lagerstätte from the Early Ordovician of France (Saleh *et al.* 2024a, b). This discovery was significant as Lagerstätten are less commonly encountered in the Ordovician (Martin *et al.* 2016; Muscente *et al.* 2017; Varejão *et al.* 2025). In that respect, the Landeyran area represents a prime site of investigation to better understand organismal ecosystems of the Ordovician Radiation (also known as the Great Ordovician Biodiversification Event), a major evolutionary event of the history of life on Earth (Sepkoski *et al.* 1981; Servais & Harper 2018; Rasmussen *et al.* 2019; Buatois *et al.* 2020; Saleh *et al.* 2023).

The Cabrières Biota was discovered in the Lower Ordovician (Floian) Landeyran Formation in southern France, within thick mudstone-dominated deposits. The content of this assemblage is not limited to body fossils, and moderately diverse trace fossils are also present, yet their description and interpretation have not been undertaken so far. As trace fossils do represent essential elements of Lagerstätten (Mángano 2011; Kimmig & Schiffbauer 2024), their analysis can provide additional information on the palaeoecology of benthic ecosystems evidenced by the Cabrières Biota.

The objectives of this study are to: (1) describe the ichnotaxa present in the Landeyran Formation; (2) characterize trends in bioturbation intensity, burrow width and depth, ichnodiversity, and ichnodisparity; (3) assess the development of ecological niches and ecosystem engineering; and (4) decipher the different controls imparting on ichnological data. Last, based on the studied material and the recent controversies on whether certain fossils are trace rather than body fossils (Muir & Botting 2024; Saleh *et al.* 2024b), we discuss available criteria for the recognition and identification of simple trace fossils, and elaborate on their potential and limitations in the study of trace fossils in mudstone.

Geological setting

Ordovician deposits investigated in this study are located southwest of Massif Central in the Languedoc lowlands, and compose part of the Mont Peyroux (Fig. 1A, B) and Pic de Vissou units (Álvaro & Vizcaïno 2001; Álvaro *et al.* 2016; Vachard *et al.* 2017). The Mont Peyroux unit is located in a central position on the southern Montagne Noire macrostructural domain (Álvaro *et al.* 2014). The Pic de Vissou unit is in a northeastern position on that domain and corresponds to a fragment of the overturned limb of the Mont Peyroux unit (Vachard *et al.* 2017). During the Early Ordovician, this area was located on the margin of Gondwana close to the South Pole, with sediment eroded from the Panafrican belt and accumulated on the continental shelf (Paris & Robardet 1990; Dabard & Chauvel 1991; Saleh *et al.* 2024a).

In the Mont Peyroux unit, the Floian starts with the ~900 m-thick La Maurerie Formation, which is composed of mudstone and sandy mudstone with intercalated sandstone tempestites representing offshore and open shelf deposits (Fig. 1C; Courtessole *et al.* 1985; Noffke & Nitsch 1994; Vizcaïno *et al.* 2001). The succeeding 150–220 m-thick Cluse de l'Orb Formation has thick-bedded, hummocky cross-stratified sandstone alternating with heterolithic mudstone-sandstone that were previously considered as tempestites accumulated in shoreface and offshore environments (Fig. 1C; Eschard *in* Courtessole *et al.* 1985; Noffke & Nitsch 1994; Vizcaïno & Álvaro 2003). However, recent investigations led Vaucher *et al.* (this volume) to reinterpret this unit as a wave-influenced delta. The overlying 60–100 m-thick Foulon Formation is made of alternating sandstone and mudstone with rare nodules deposited in offshore/prodelta to open shelf environments (Fig. 1C; Courtessole *et al.* 1985; Noffke & Nitsch 1994; Vizcaïno & Álvaro 2003; Vaucher *et al.* this volume).

The Lower Ordovician sequence ends with the Landeyran Formation, a 200–400 m-thick succession composed of mudstone with siliceous nodules that was mainly deposited in the shelf below the reach of storm waves (Fig. 1C; Dean 1966; Dabard & Chauvel 1991; Vizcaïno & Álvaro 2003; Van Iten & Lefebvre 2020; Vaucher *et al.* this volume; see Results section below). Early researchers subdivided the Landeyran Formation into two members, either based on the fossil content or on the colour of strata (e.g. Dean 1966; Courtessole *et al.* 1985; Noffke & Nitsch 1994). Babin *et al.* (1982) noted early that there exists no lithological distinction between members, and Vizcaïno *et al.* (2001) abandoned this scheme. Biostratigraphy suggests that the Landeyran Formation is late Floian (Fl3) and covers two trilobite biozones: an older *Apatokephalus incisus* Zone, and a younger *Hangchungolithus primitivus* Zone (Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003; Ebbestad *et al.* 2020). The Landeyran Formation is identified both in the Mont Peyroux and Pic de Vissou units (Babin *et al.* 1982; Saleh *et al.* 2024a).

Body fossils from the Landeyran Formation are abundant and were described in great detail in numerous studies (e.g. Miquel 1894; Thoral 1935; Dean 1966; Courtessole *et al.* 1981, 1983, 1985; Babin *et al.* 1982; Vizcaïno & Lefebvre 1999; Vizcaïno & Álvaro 2003; Tortello *et al.* 2006; Ebbestad *et al.* 2020; Van Iten & Lefebvre 2020; Saleh *et al.* 2024a, b). They consist of algae, non-biomineralized arthropods, bivalves, brachiopods, cephalopods, cnidarians, echinoderms, gastropods, graptolites, hyoliths, lobopodians, machaeridians, rostroconchs, sponges, trilobites, and worms (Courtessole *et al.* 1985; Vizcaïno *et al.* 2001; Saleh *et al.* 2024a). Trace fossils from the succession were only briefly mentioned in previously published literature. Bonin *et al.* (2007) noted *Skolithos* and *Teichichnus* in intensely bioturbated sandstone, and *Cruziana*, *Nereites*, *Teichichnus*, *Thalassinoides*, and coprolites in mudstone of the *Apatokephalus incisus* Zone. These authors also mentioned that the bulk of investigated strata had limited to absent bioturbation (Bonin *et al.* 2007, fig. 21). Saleh *et al.* (2024b) recently identified *Alcyonidiopsis* and *Planolites* within the same biostratigraphical interval. Muir *et al.* (2019) recorded potential agglutinated tubes (considered by the authors as body fossils) from the *Hangchungolithus primitivus* Zone.

Material and methods

The material investigated in this study was mostly recovered *in situ* from the Landeyran River and Abandoned Vineyard sections, south of Saint-Nazaire-de-Ladarez (Hérault, southern France) (Fig. 1A, B). Additional trace fossils are found at the Road Cut and Lagerstätte sites, which do not have sufficient undeformed strata exposed *in situ* to measure stratigraphical sections.

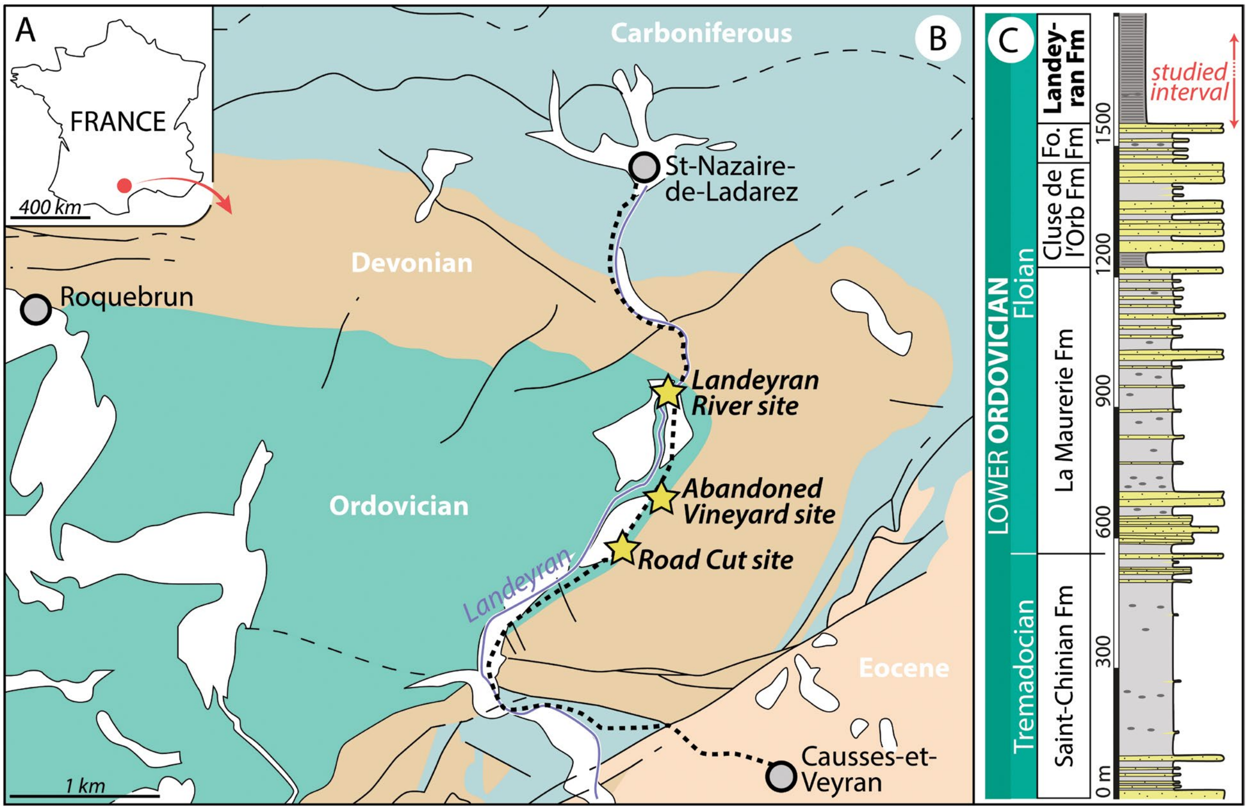

Fig. 1. Maps and stratigraphical context. A, location of the study area in southern France. B, geological map of the Mont Peyroux unit showing three of the four outcrops investigated (yellow stars) near the Landeyran river (blue line) and D136 road (thick dark dashed line). Contour lines of stratigraphical units and faults (thin dark lines) are based on Alabouvette *et al.* (1982). The fourth outcrop is located farther east in the Pic de Vissou unit (see maps in Saleh *et al.* 2024a). C, stratigraphical position of the Landeyran Formation and of the studied interval. From left to right: System and Series; Stage; formations (Fm); synthetic log. Fo. = Foulon. Based on Courtessole *et al.* (1983, table 1).

The Landeyran River site (43°29'46"N, 3°04'39"E) is located 1.3 km south of Saint-Nazaire-de-Ladarez, on the west side of the D136 road, in the Mont Peyroux unit (Fig. 1B). It corresponds to the natural weathering created by the Landeyran stream and is equivalent to sites λ1, λ2, λ3 in Dean (1966, fig. 3) and site 1 in Babin *et al.* (1982, fig. 4). According to Dean (1966), it is the type locality for the lower interval of this unit (*Apatokephalus incisus* Biozone). In our study, the Landeyran River site continuously exposes 105.0 m of strata covering the upper Foulon Formation (basal 6.7 m) and lower Landeyran Formation (the remaining 98.3 m) (Gougeon 2025). Minor faults and gaps of exposure are noted in places, with some intervals highly covered by scree, dust, and vegetation. The section corresponds to a stepped cliff/overhang cliff exposure (*sensu* Shillito & Gougeon 2023) with beds rotated about 85°.

The Abandoned Vineyard site (43°29'26"N, 3°04'37"E) is exposed 600 m southern of the Landeyran River site, on the east side of the D136 road, in the Mont Peyroux unit (Fig. 1B). It corresponds to a trench created between sites λ9 and λ10 of Dean (1966, fig. 3) and south of site 9 in Babin *et al.* (1982, fig. 4), and represents strata of the *Hangchungolithus primitivus* Biozone (Courtessole *et al.* 1981, 1983). The Abandoned Vineyard site is a continuous 44.8 m-thick section that is less affected by faulting than the Landeyran River site and only consists of Landeyran Formation strata (Gougeon 2025). The section ends with a highly folded 2 m-thick portion; strata above this interval are *in situ* and visible, but were not included in this study because folding and faulting were too important and significantly hindered the quality of observations. The section corresponds to an overhang cliff exposure (*sensu* Shillito & Gougeon 2023) with beds rotated about 85°.

The Road Cut site (43°29'13"N, 3°04'24"E) is situated 400 m southwest of the Abandoned Vineyard site, on the east side of the D136 road, in the Mont Peyroux unit (Fig. 1B). Strata are of the *Hangchungolithus primitivus* Biozone (Courtessole *et al.* 1981, 1983) and are oriented subparallel to the road, which does not allow for measuring stratigraphical intervals. Scree and vegetation cover are important. The outcrop is located just north of site 13 in Babin *et al.* (1982, fig. 4).

The *Lagerstätte* site is located at the periphery of the village of Cabrières within a range of 1 km, in the Pic de Vissou unit (see extended data fig. 2 in Saleh *et al.* 2024a for maps). Beds at this locality are lithologically and stratigraphically equivalent to the lower beds of the Landeyran Formation at the Landeyran River site (*Apatokephalus incisus* Biozone; Babin *et al.* 1982; Berard 1986; Vachard *et al.* 2017; Saleh *et al.* 2024a).

Stratal packages were measured by means of a Jacob staff. Naked-eye observations were reported as drawings on stratigraphical columns (logs) in field notebooks, with 6 m of strata per page. The description of sedimentological features focuses on bed geometry, bed thickness, bed grain size, sandstone/mudstone ratio, and sedimentary structures. Mudrock grain scale follows Lazar *et al.* (2015), which uses fine, medium, coarse mudstone, and sandy mudstone categories. Subdivisions of depositional environments on the continental shelf follow MacEachern *et al.* (1999a) and Vaucher *et al.* (this volume). Vertical and bed surface bioturbation are evaluated using the bioturbation index (BI) of Taylor & Goldring (1993) and bedding plane bioturbation index (BPBI) of Miller & Smail (1997), respectively. Trace-fossil taxonomy follows modern standards in the field with the characterization of ichnotaxobases (Bromley 1996; Buatois & Mángano 2011; Bertling *et al.* 2022; Gougeon *et al.* 2025a). Sedimentary logs and ichnological data were then digitized on Adobe Illustrator and are available in Gougeon (2025). For the ecospace utilization analysis, modes of life are evaluated by plotting three parameters on a three-dimensional cube: tiering, feeding mode, and motility (Bambach *et al.* 2007; Buatois *et al.* 2020; Gougeon *et al.* 2025b). For the ecosystem engineering analysis, styles of engineering are identified by plotting three parameters on a three-dimensional cube: tiering, sediment modification mode, and sediment interaction mode (Minter *et al.* 2016; Mángano *et al.* 2024; Gougeon *et al.* 2025b). In addition, about 30 samples were collected from the Landeyran River site within an interval showing increased bioturbation (from 72.6 to 75.6 m in Gougeon 2025) and from the *Lagerstätte* site. Four specimens were cut and polished at the Institut Universitaire Européen de la Mer (IUEM, Plouzané, France) and digitally enhanced following the method detailed in Gougeon *et al.* (2018a). Three specimens were used to prepare thin sections at IUEM. Seven of the collected samples are figured in this work and are housed in the collection of the municipality of Cabrières, with collection numbers UCBL-CAB34 526 to UCBL-CAB34 532. Other material figured in this study was photographed *in situ* and was not collected.

Results

Sedimentology

The sedimentology of the Landeyran Formation was recently reviewed by Vaucher *et al.* (this volume), and only a brief overview is provided here to frame ichnological data within its environmental context. Photographs of facies and sedimentary structures can be found in Vaucher *et al.* (this volume, figs 5, 7). At Landeyran River, the beginning of the Landeyran Formation is placed at the first mudstone-dominated package that is thicker than 0.5 m and that is clearly identifiable (at 6.7 m in Gougeon 2025). The Landeyran River site has the thickest stratal extension of all lower Landeyran Formation deposits (Dean 1966) and will serve as the basis for sedimentological descriptions and interpretations below. Vaucher *et al.* (this volume, fig. 6) subdivided the Landeyran River section into three facies:

1) Mudstone-prone and cross-laminated sandstone (facies 3 in Vaucher *et al.* this volume). This lower interval is 20 metres thick (from 6.7 m to 27.2 m in Gougeon 2025) and is dominated by light grey and brown, heterolithic thinly laminated to medium-bedded, very fine- and fine-grained sandstone alternating with dark-grey, thinly laminated to thin-bedded medium mudstone. In places, mudstone-dominated packages, 0.3–2.7 m thick, are intercalated between heterolithic packages. Sandstone/mudstone ratio therefore varies from 1.5 (heterolithic bedding) to 0 (mudstone-dominated bedding). Mudstone-dominated packages are of the same composition as facies 2 in Vaucher *et al.* (this volume) (see below). Sandstone is tabular to lenticular and is massive, normally graded, or hummocky cross-stratified (HCS). Sandstone bed bases are sharp, with flat or irregular contacts with the underlying strata. Sandstone bed tops are either flat and subhorizontal, undulating if capping HCS, or display symmetrical ripples. Pustular and wrinkled microbially stabilized surfaces are rare. A few sandstone beds show calcite cementation and cone-in-cone diagenetic features. This lower interval is interpreted as deposited in a proximal wave-influenced prodelta (Vaucher *et al.* this volume). HCS and symmetrical ripples are indicative of oscillatory flows (Dott & Bourgeois 1982; Vaucher *et al.* 2017; Jelby *et al.* 2020; Vaucher &

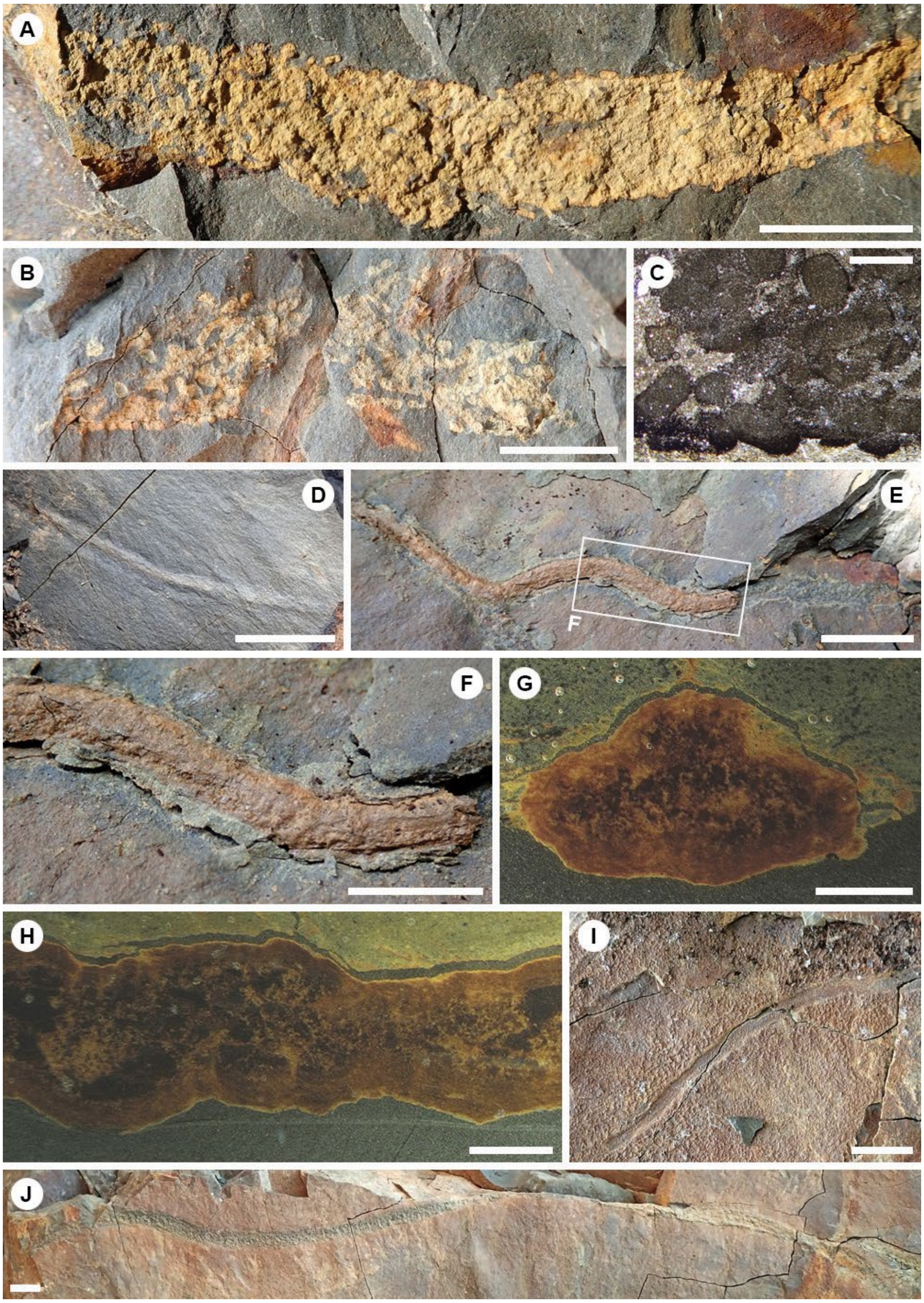

Fig. 2. Alcyonidiopsis longobardiae Massalongo, 1856, *Helminthoidichnites tenuis* Fitch, 1850, and *Helminthopsis granulata* Książkiewicz, 1968 from the Landeyran Formation. Scale bars are 0.1 cm (C, G, H), 0.5 cm (B, F), and 1 cm (A, D, E, I, J). A, *Alcyonidiopsis longobardiae* composed of densely packed pellets within a tubular burrow. Note the important colour contrast of the pellets with the host rock. Full relief, Landeyran River, UCBL-CAB34 526. B, *A. longobardiae* with loose pelletal infill. Full relief, Landeyran River. C, Thin section of *A. longobardiae* (same specimen as in Fig. 2A) showing circular to elongated, well-individualized pellets of *Coprulus oblongus*, and distinctive diagenetic halo (darker colour at the bottom of lower pellets). UCBL-CAB34 527. D, *Helminthoidichnites tenuis* with a straight to slightly curved course. Note the bulged median area flanked by narrow grooves. Positive hyporelief, Road Cut. E, *Helminthopsis granulata* with a gently meandering course. Note the loss of infill preserved at the right end, unravelling a cast with tuberculate texture. Positive and negative relief (found on a loose slab), *Lagerstätte* site. F, close-up from Figure 2E, showing the tuberculate texture on the burrow outline and few longitudinal ridges. G, thin section of *H. granulata* in transversal elevation view, revealing the absence of pellet fill. Note highly recrystallized infill. Full relief, Landeyran River, UCBL-CAB34 528. H, thin section of *H. granulata* in longitudinal elevation view (same specimen as in Fig. 2G), revealing an absence of pellet fill. UCBL-CAB34 529. I, *H. granulata* associated with a pustular microbially textured surface. Negative epirelief, Landeyran River. J, *H. granulata* extending over an impressive length. Note the tuberculate nature of the burrow outline and the gently meandering course. Negative epirelief, Landeyran River.

Dashtgard 2022), and erosive sandstone bases followed by normal grading are interpreted as distal low-density turbidites (Vaucher *et al.* this volume). Mudstone is deposited via suspension fallout in the waning stage of storms and hyperpycnal flows (Mulder & Alexander 2001; Bhattacharya & MacEachern 2009; Biddle *et al.* 2025).

2) Laminated mudstone with lenticular bedding (facies 2 in Vaucher *et al.* this volume). This middle interval is about 30 metres thick (Vaucher *et al.* this volume; from 27.2 m to 57.2 m in Gougeon 2025) and is dominated by dark-grey, massive, and thinly laminated to thin-bedded medium mudstone. Vaucher *et al.* (this volume) noted very rare, very fine-grained sandstone lenses. Based on its facies description and stratigraphical position, this interval is interpreted as deposited in distal prodelta-to-offshore, with mud accumulated via suspension fallout and rare low-density turbidity currents (Vaucher *et al.* this volume).
3) Massive to laminated mudstone (facies 1 in Vaucher *et al.* this volume). This upper interval is about 48 metres thick (from 57.2 m to 105.0 m in Gougeon 2025) and is composed of dark, massive, and thinly laminated to thin-bedded fine mudstone. Based on its facies description and stratigraphical position, this interval is interpreted as deposited in a shelf (*stricto sensu*; cf. MacEachern *et al.* 1999a), with mud accumulated via suspension fallout (Vaucher *et al.* this volume).

The Abandoned Vineyard section is dominated by thinly laminated to thin-bedded medium mudstone. In places, lenticular and tabular thinly laminated to thin-bedded very fine-grained sandstone is present. Sandstone displays HCS and both symmetrical and asymmetrical bed tops. Normal grading, from very fine-grained sandstone or coarse mudstone to medium mudstone following sharp erosive bases, is notably common. Tool marks are in places noted on sandstone bed bases. Small nodules are found at intervals. The Road Cut site poorly exposes fractured bed bases of medium mudstone, without any obvious sedimentary structure displayed. The Lagerstätte site presents rare bed surfaces exposed and common loose slates that are composed of thinly laminated fine mudstone.

Ichnology

Stratigraphical occurrence and relationship to sedimentary facies. – Although trace fossils are recorded within the three intervals of the Landeyran River site, their occurrence is limited to few stratigraphical levels. The lower interval hosts passively filled burrows (*Palaeophycus tubularis*, *Skolithos linearis*) that are not observed in succeeding facies. Simple horizontal trails (*Helminthoidichnites tenuis*) are present and were also found higher in the section. The middle interval is extremely poor in trace fossils, with only *Helminthopsis granulata* and *Planolites montanus* recorded. The upper interval shows the appearance of *Alcyonidiopsis longobardiae* alongside *H. granulata* and *P. montanus*. Because trace fossils typically occur as monospecific suites (rarely paucispecific), and because of the low number of trace fossils recorded, the analysis below will focus on individual ichnotaxa rather than on the identification and recurrence of trace fossil assemblages.

Ichnodiversity. – Trace-fossil diversity of the Landeyran Formation is moderate as a whole, but low per stratigraphical level (Fig. 4A, B). It consists of *Alcyonidiopsis longobardiae*, *Helminthoidichnites tenuis*, *Helminthopsis granulata*, *Palaeophycus tubularis*, *Planolites montanus*, *Skolithos linearis*, ?*Torrowangea* isp., and indiscriminate meiofaunal burrows. *Coprulus oblongus* is not a trace fossil *per se* (Knaust 2020) but is also described. For the stratigraphical positions of the trace fossils mentioned below, 'LR' and 'AV' refer to the Landeyran River and Abandoned Vineyard sections, respectively, and the number(s) that follow these acronyms relate to the exact stratigraphical level(s) where ichnotaxa were found (see Gougeon 2025 for detailed logs).

Alcyonidiopsis longobardiae Massalongo, 1856 is a simple burrow filled with small faecal pellets (Fig. 2A–C, and Saleh *et al.* 2024b, fig. 1f; Uchman 1995; Paz *et al.* 2023). The course is straight, curved, to bent, and it is preserved as full relief on bed bases and tops. Branching is absent. A diagenetic halo, resulting from a geochemical gradient, can be observed in burrows tightly filled with pellets. The halo is thin and internal to the pellets (see lower pellets in Fig. 2C). Pellets are homogeneous, rounded, and ellipsoidal, and correspond to *Coprulus oblongus*. Pellets are composed of yellowish fine mudstone and are easy to distinguish from the dark fine to medium mudstone host rock. Pellets are typically in contact, in places tightly squeezed and leaving no space between them. Less commonly, they present gaps of darker mudstone material between them that is similar to the host rock. Rarely, a red burrow fill is observed, which highly contrasts with the dark mudstone host rock. Burrow width is 4–10 mm, pellets are 0.5–2.2 mm wide or long, pellet width/length ratio is 1/1 to 1/2.5, and maximal burrow length is 110 mm. *Alcyonidiopsis longobardiae* is distinguished from *A. pharmaceus* by smaller burrow sizes and smaller pellet sizes. Although size is usually considered a poor ichnotaxobase, it is, in rare cases, accepted if measures reveal distinct groups while considering larger assemblages (Bertling *et al.* 2022; see also Paz *et al.* 2023). The size specificities remain to be statistically tested in *Alcyonidiopsis* ichnospecies, but we follow previous authors (e.g. Chamberlain 1977; Pickerill & Narbonne 1995; Uchman 1995; Orr 1996; Schlirf 2000) and provisionally use burrow and pellet sizes as key ichnotaxobases until further analyses on the type materials are done. This trace fossil is abundant in a restricted interval at Landeyran River (from LR 73.6 to 75.6). It was also found at the Road Cut and Lagerstätte sites (Saleh *et al.* 2024b, fig. 1f).

Helminthoidichnites tenuis Fitch, 1850 is a simple horizontal trail that has a straight to gently curving course (Fig. 2D; Gougeon *et al.* 2018b, 2025a). It is preserved as positive epirelief and positive hyporelief. Branching and lining are absent, and the medium mudstone infill is similar to the host rock. Trail width is 1–2 mm, and maximal length is 31 mm. This trace fossil is found at Landeyran River and Abandoned Vineyard at seven stratigraphical levels (LR 13.2, 13.5 and AV 8.8, 9.4, 13.1, 24.7, 42.3). It was also observed at the Road Cut site.

Helminthopsis granulata Książkiewicz, 1968 is a simple horizontal trail that has a gently meandering course and a tuberculate surficial ornamentation (Fig. 2E–J; Han & Pickerill 1995). Longitudinal ridges can be visible on the outline, which are also present on the type material from the Lower Cretaceous of Poland (Książkiewicz 1968, 1977; Uchman 1998). It is preserved as positive and negative epirelief and positive and negative hyporelief. Branching is absent. A lining is not distinctly observed, and the contact with the host rock is sharp. The morphology varies depending on the arrangement of tubercles on the outline, from specimens with straight sides (and poor tubercle development) to highly irregular sides (and high tubercle development). Infill is highly recrystalized which precludes characterizing its original composition. Thin sections (Fig. 2G, H) demonstrate that the tuberculate texture on the outer surface is not related to a putative pelletal infill (which makes it diagnostically distinctive from *Alcyonidiopsis longobardiae*; Uchman 1998), but more likely represents the loose packing of excreted material after its passage into the digestive tract of the animal. Trail width is 2–3 mm, and maximal length is about 280 mm. This trace fossil is found at Landeyran River at eight stratigraphical levels (LR 54.8, 66.2, 72.8, 73.6, 74.1, 74.3, 74.5, 97.7) and at the Lagerstätte site.

Palaeophycus tubularis Hall, 1847 is a simple subhorizontal burrow with a thin lining (Fig. 3A, B; Gougeon *et al.* 2025a). It is preserved as full relief on bed bases and tops. The course is straight to gently curved. Branching is absent. A lining is either observed, especially in elevation view, or is inferred based on the sharp contact with the host rock. Infill is massive and is either composed of very fine-grained sandstone different from the medium mudstone host rock, or is similar to it. Burrow width is 5–6 mm, and maximal length is 38 mm. This trace fossil is found at Landeyran River at three stratigraphical levels (LR 10.5, 18.3, 18.7).

Planolites montanus Richter, 1937 is a simple subhorizontal burrow without lining (fig. 1e in Saleh *et al.* 2024b; Pemberton & Frey, 1982). It is preserved as full relief, typically on bed bases and tops. The course is short and typically curved, rarely meandering. Vertical changes in depth within the substrate and the presence of a relief (either as a depression or bulge of the burrow) are diagnostic. Branching and lining are absent. The contact with the host rock is typically diffuse. Infill is massive, made of fine or medium mudstone similar in lithology to the host rock. However, a red burrow fill can contrast with the grey or dark host rock. Burrow width is 1–5 mm, and maximal length is 24 mm. This trace fossil is found at Landeyran River and Abandoned Vineyard at six stratigraphical levels (LR 18.7, 54.8, 72.6, 74.3, 75.4 and AV 21.4). It was also observed at the Road Cut and Lagerstätte sites.

Skolithos linearis Haldeman, 1840 is a simple vertical burrow (Fig. 3C; Knaust *et al.* 2018). It is preserved as full relief. The course is straight and can be slightly oblique from the horizontal bed top. Burrow width is mostly constant, with rare bulges along the course. The cross-section as observed on bed top is perfectly circular. Branching is absent. It is unlined, but the contact with the host rock is sharp. Infill is massive, composed of fine-grained sandstone similar to the host rock. Burrow width is 2–5 mm, and maximum burrow depth is 57 mm. This trace fossil is found at Landeyran River at two stratigraphical levels: LR 6.4 (within the uppermost Foulon Formation) and LR 10.4.

?*Torrowangea* isp. is a simple horizontal burrow with potential constrictions (Fig. 3D). Only one specimen was found at the Abandoned Vineyard section (AV 24.7), of moderate quality, which precludes a convincing assignment to *Torrowangea* Webby, 1970. It is preserved as positive hyporelief. The course is slightly curved. Branching and lining are absent. Infill either seems to be composed of transverse menisci, or of irregular pads that bulge along the course. Constrictions that are diagnostic of *Torrowangea* are therefore not clearly observed, but are mostly inferred. The overall morphology is superficially reminiscent of previously described *Torrowangea rosei* Webby, 1970 (the type ichnospecies of *Torrowangea*) from the type locality in Australia (compare with Webby 1970, fig. 18A–D). Burrow width is 1 mm, and burrow length is 19 mm. An affinity to *Helminthopsis granulata* is ruled out because this ichnotaxon never develops menisci or sediment pads along its course (see above).

Meiofaunal burrows are simple structures that are significantly smaller in scale than any other trace fossil found in the Landeyran Formation (between 0.01 and 1 mm in width; Martínez *et al.* 2025), and are found in association with an algal body fossil (Fig. 3E, F). They are either straight, curved, or bent, and are preserved as full relief on a bed surface. They are observed as horizontal strings, but their short lengths and in places tortuous courses suggest that a vertical component is also present. Lining and branching are absent. The red infill superficially appears as backfilled at first sight, with pseudo-pads of sediment separated from one another and deforming the burrow outlines (Fig. 3E). However, close inspection suggests that the rugosities of the rock surface affected the morphology of the trace fossils; rare burrow intervals that are better preserved on flat areas do not evidence backfill (Fig. 3F). Although their tortuous pattern suggests an affinity to *Planolites montanus*, we prefer to keep these structures in open nomenclature due to the difficulties in assessing their infill type. Burrow width is less than 0.5 mm. Meiofaunal burrows were only found at the *Lagerstätte* site.

Coprulus oblongus Mayer, 1952 is a rounded individual pellet with homogeneous fill that is not associated with any burrow (Fig. 3G, H; Knaust 2008, 2020). On bed surfaces, pellets can be either circular, pseudo-circular with slight angular outlines, to elongated in cross-section. Pellets are isolated or form aggregates, in places in contact with one another. A lining appears absent, and the contact with the host rock is sharp. Infill is massive and composed of yellowish fine mudstone that is easy to distinguish from the dark fine to medium mudstone host rock. Pellets are 0.5–2.5 mm wide or long, with a width/length ratio of 1/1 to 1/3. *Coprulus oblongus* is found abundantly within a restricted interval at Landeyran River (from LR 73.6 to 74.8) and at two other levels at the same locality (LR 102.5, 103.1).

Ichnodisparity. – Although seven ichnospecies are formally described in this study, ichnodisparity (i.e. the development of architectural designs in ichnotaxa; Buatois *et al.* 2017) is lower and represents five categories: (1) simple horizontal trails (*Helminthoidichnites tenuis*, *Helminthopsis granulata*); (2) passively filled horizontal burrows (*Palaeophycus tubularis*); (3) simple actively filled (massive) horizontal to oblique structures (*Planolites montanus*, ?*Torrowangea* isp.); (4) simple actively filled (pelletoidal) horizontal burrows (*Alcyonidiopsis longobardiae*); and (5) vertical unbranched burrows (*Skolithos linearis*).

Vertical bioturbation intensity. – Bioturbation intensity observed in elevation view is, overall, very low across all sites visited (Gougeon 2025). At Landeyran River, the lower interval is mostly characterized by an absence of vertical bioturbation (BI = 0 for n = 27 data points), with rare low values at a few stratigraphical levels associated with *Palaeophycus tubularis* and *Skolithos linearis* in heterolithic sandstone-mudstone deposits (BI = 1–2 for n = 6). The middle interval at this locality is overarchingly dominated by an absence of vertical bioturbation (BI = 0 for n = 25), with a sole record of very low bioturbation intensity from *Planolites montanus* (BI = 1). The upper interval at Landeyran River is also typified by an absence of vertical bioturbation (BI = 0 for n = 26); rare intervals show low to moderate values of vertical biogenic disruption from *Alcyonidiopsis longobardiae* and *Coprulus oblongus* (BI = 2–4 for n = 3). The Abandoned Vineyard section displays an absence of vertical bioturbation for any of the stratigraphical levels investigated (BI = 0 for n = 49).

Bedding plane bioturbation intensity. – Bed surface bioturbation is mostly in accordance with observations made on vertical bioturbation, with few exceptions. The lower interval at Landeyran River is characterized by an absence of bed surface bioturbation (BPBI = 1 for n = 17 data points), with low values recorded at intervals from *Helminthoidichnites tenuis* and non-descript trace fossils (BPBI = 2–3 for n = 10). Low values of BPBI are not specifically associated with heterolithic strata, contrary to observations made on BI (see above). The middle interval shows an absence of bed surface bioturbation (BPBI = 1 for n = 16), except at one stratigraphical level with *Helminthopsis granulata* (BPBI = 2). The upper interval at Landeyran River evidences a good balance between values depicting no bed surface bioturbation (BPBI = 1 for n = 14) and low bioturbation from *Alcyonidiopsis longobardiae*, *Coprulus oblongus*, *H. granulata*, and *Planolites montanus* (BPBI = 2 for n = 14). The Abandoned Vineyard section is typified by an absence of bed surface bioturbation (BPBI = 1 for n = 44) and lesser low values associated with *Helminthoidichnites tenuis*, *P. montanus*, and ?*Torrowangea* isp. (BPBI = 2 for n = 8).

Burrow width. – Across all sites, burrow width is low and is kept below 1.0 cm. Variations depend on the ichnotaxa recovered, with the lowest values expressed in simple grazing trails (0.1–0.2 cm

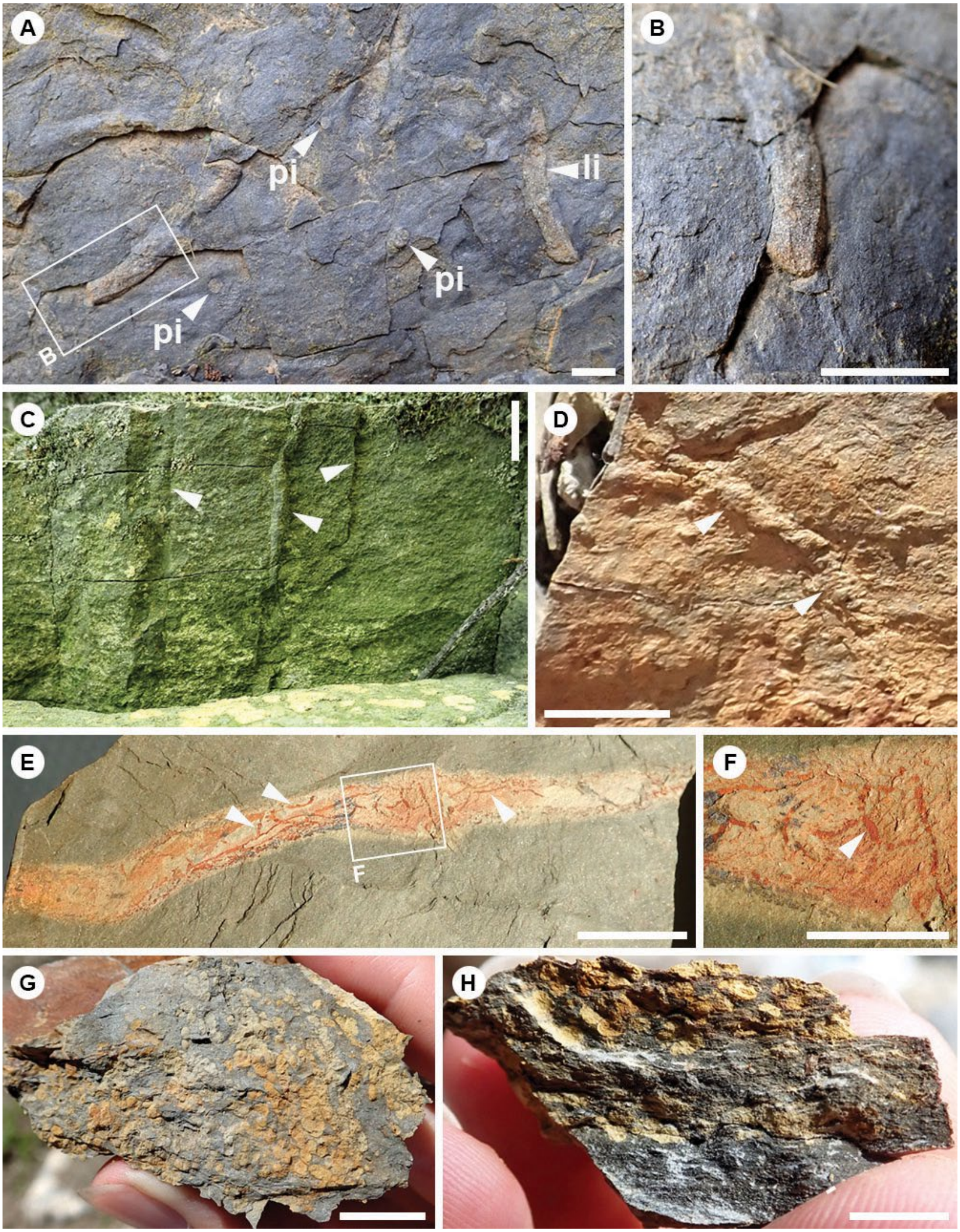

Fig. 3. *Palaeophycus tubularis* Hall, 1847, *Skolithos linearis* Haldeman, 1840, ?*Torrowangea* isp., meiofaunal burrows, and *Coprulus oblongus* Mayer, 1952 from the Landeyran Formation. Scale bars are 0.5 cm (D, F, H) and 1 cm (A–C, E, G). A, *Palaeophycus tubularis* with distinct lining (li). Note the pits (pi) of uncertain affinity. Full relief on bed top, Landeyran River. B, close-up from Figure 3A showing the three-dimensional morphology, the sharp contact with the host rock, and the massive infill. C, *Skolithos linearis* (arrows) in a sandstone bed. Full relief, Landeyran River. D, ?*Torrowangea* isp. oriented horizontally, with bulges along the course, and transverse pseudo-pads visible at intervals (arrows). Positive hyporelief, Abandoned Vineyard. E, meiofaunal burrows (some are arrowed) on an algal remain. Full relief on bed surface (found on a loose slab), Lagerstätte site, UCBL-CAB34 530. F, close-up from Figure 3E showing the irregular outlines of most burrows, although one specimen (arrow) has distinct straight outlines and does not evidence backfill. G, aggregate of *Coprulus oblongus* on a surface showing round to elongate morphologies. Landeyran River, UCBL-CAB34 531. H, *C. oblongus* within its sedimentary fabric. Landeyran River, UCBL-CAB34 532.

for *Helminthoidichnites tenuis*) and simple actively filled burrows (<0.05 cm for meiofaunal burrows, 0.1 cm for ?*Torrowangea* isp.). Burrow width slightly increases in passively filled burrows (0.3–0.6 cm for *Palaeophycus tubularis*), simple vertical burrows (0.2–0.5 cm for *Skolithos linearis*), some simple grazing trails (0.4–0.6 cm for *Helminthopsis granulata*), and some simple actively filled burrows (0.4–1.0 cm for *Alcyonidiopsis longobardiae*, 0.1–0.5 cm for *Planolites montanus*).

Burrow depth and tiering. – Measured burrow depth values are low (n = 8), reaching 0.3 cm for *Palaeophycus tubularis* and 0.3–0.4 cm for *Planolites montanus*. The only exception is *Skolithos linearis,* showing a recorded depth of 3.5 cm in the lowermost Landeyran Formation (LR 10.4 m) at a level that follows another recorded depth of 5.7 cm in the uppermost Foulon Formation (LR 6.4 m). In mudstone-dominated intervals, tiering is poorly developed, and trace fossils are constrained within the first centimetres of the substrate. *Helminthoidichnites tenuis* and *Helminthopsis granulata* are semi-infaunal burrows (preferential occupation of the 0.1–0.5 cm depth of the substrate) (Buatois *et al.* 2020; Gougeon *et al.* 2025b). ?*Torrowangea* isp. is a very shallow tier burrow (0.6–3.0 cm) (Buatois *et al.* 2020; Gougeon *et al.* 2025b). *Palaeophycus tubularis* and *Planolites montanus* do not have strong vertical components in the Landeyran Formation and are interpreted as very shallow tier (0.6–3.0 cm) (Gougeon *et al.* 2025b). *Alcyonidiopsis longobardiae* is the largest burrow recorded in the succession and is interpreted as a shallow tier trace fossil (3.1–6.0 cm) (Buatois *et al.* 2020). *Coprulus oblongus* is not usually included in schemes about tiering because it is not a trace fossil *per se*. The filling of *Alcyonidiopsis longobardiae* with *Coprulus oblongus* suggests the latter is also a structure emplaced in the shallow tier. Although *Skolithos linearis* is typically regarded as a deep tier burrow (12.0+ cm) (Buatois *et al.* 2020), it is here considered as shallow tier because of its maximum recorded depth of 5.7 cm.

Ecospace utilization and ecosystem engineering. – In the succession, modes of life are moderately advanced (n = 8) and dominate the semi-infaunal to shallow tiers (Fig. 3C). Feeding modes consist of suspension feeding, deposit feeding, and predation, and tracemakers are either motile (for animals actively filling their trails and burrows, e.g. *Alcyonidiopsis longobardiae*, *Helminthopsis granulata*) or facultatively motile (for animals constructing permanent open burrows, e.g. *Palaeophycus tubularis*, *Skolithos linearis*). The styles of engineering are low to moderately advanced in the succession (n = 5) (Fig. 3D). Gallery biodiffusors and conveyors are the preferential sediment modification modes, representing animals interacting with their surrounding sediment via compression and backfilling.

Discussion

Comparison with previously published ichnological data on the Landeyran Formation

Previous ichnological studies on the Landeyran Formation are scarce because of the rarity of trace fossils. Bonin *et al.* (2007) reported a fairly diverse trace-fossil suite in the finest-grained deposits of the succession (their facies 5) that was not illustrated and that differs from our observations by the presence of bilobate burrows (*Cruziana*), complex backfilled horizontal burrows (*Nereites*), vertical spreiten burrows (*Teichichnus*), and gallery systems (*Thalassinoides*). *Cruziana* is almost exclusively recovered as casts (positive hyporelief) on sandstone bed bases (Seilacher 1985). Therefore, its presence in homogeneous mudstone deposits of the Landeyran Formation is very unlikely. *Thalassinoides* forms three-dimensional galleries characterized by Y-shaped junctions (Bromley & Frey 1974) that we did not observe, but that can be mistaken with overlapping *Palaeophycus* burrows on bed surfaces. In elevation view, circular and well-defined *Palaeophycus* can resemble *Thalassinoides* depending on the position of the cross-section (Chamberlain 1978; Knaust 2017). *Nereites* and *Teichichnus* are potentially valuable additions to the list of trace fossils described in our study, but we could not confirm their presence. Both ichnotaxa are regularly reported in mudstone deposits of the shelf and represent sub-surface deposit-feeding strategies that are also evidenced by *Alcyonidiopsis* and *Planolites* reported here. Our study concurs with observations made by Bonin *et al.* (2007) in that most of the Landeyran Formation deposits have absent to very low bioturbation levels. Potential agglutinated tubes described by Muir *et al.* (2019, figs 6C, D, 7A, B) from the upper interval of the Landeyran Formation are composed of loose and unorganized shell pieces of variable sizes, without clear burrow outlines, without tube lumen, and with important variations in width, which are atypical of armoured burrows as reported elsewhere (e.g. Kern 1978; Ettensohn 1981; Rigby *et al.* 1998; Monaco *et al.* 2005; Jach *et al.* 2011).

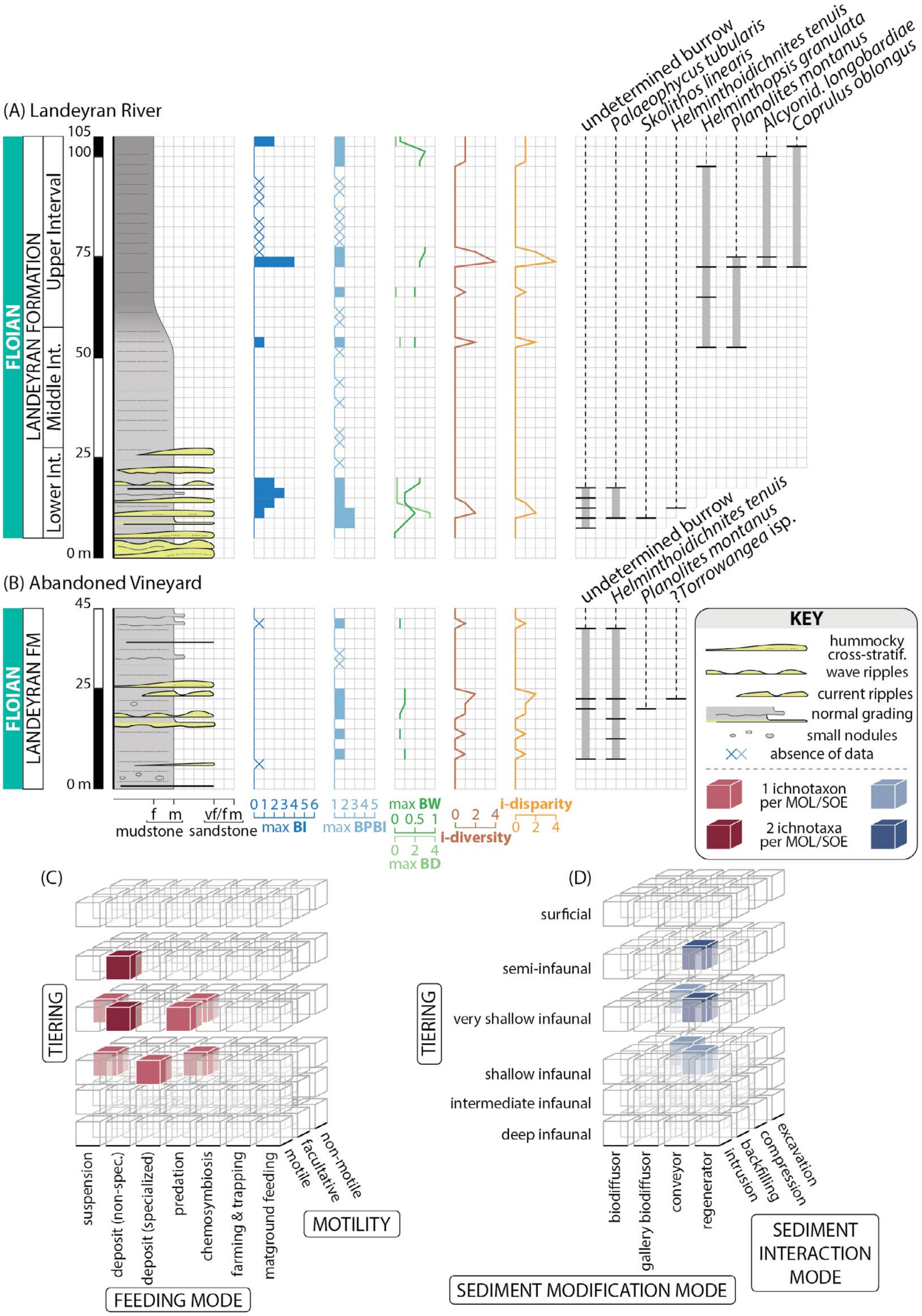

Fig. 4. Summary of data from the Landeyran Formation at the Landeyran River and Abandoned Vineyard sections. *Alcyonid.* = *Alcyonidiopsis*; spec. = specialized; stratif. = stratification. A, B, from left to right: age; formation; stratigraphical interval; sedimentology (in metres); vertical bioturbation intensity (maximum Bioturbation Index, or BI); bed surface bioturbation intensity (maximum Bedding Plane Bioturbation Index, or BPBI); maximum burrow width (BW); maximum burrow depth (BD); ichnodiversity; ichnodisparity; and stratigraphical occurrences of ichnotaxa. Undetermined burrows correspond to trace fossils that could not be affiliated to any ichnotaxa because their morphological features were not ideally expressed. C, multidimensional ecospace utilization cube analysis showing moderate advances in modes of life (MOL) (n = 8). (D) Multidimensional ecosystem engineering cube analysis showing moderate advances in styles of engineering (SOE) (n = 5).

Impact of outcrop exposure on ichnological and sedimentological observations

The type of outcrop exposure has recently been recognized as a major control on the quality of ichnological observations made within a succession and on the related dataset recovered (Shillito & Davies 2020, 2021; Gougeon *et al.* 2023, 2025a, c; Shillito & Gougeon 2023). The Landeyran Formation outcrops are exposed inland either in a dried-out river stream (Landeyran River), on the side of a forested hill (Lagerstätte site), or in artificial cuts (Abandoned Vineyard, Road Cut). Inland sites of this type are not ideal for reporting accurate ichnological and sedimentological observations because vegetation and dust are highly common while fine-grained material weathers as scree (Dean 1966), all resulting in important covering of the rock surfaces. In addition, mudstone tends to lack colour and lithological contrasts between burrow fills and the casting medium, hindering ichnological observations as well (Paz *et al.* 2023; Biddle *et al.* 2025). These features explain the low quality of data points reported on bioturbation intensities and the low number of values reported on burrow depth in the Landeyran Formation, despites the optimal dipping of beds and the continuous exposure of strata (Fig. 5). In those situations, it is essential to look for coeval sections that possess different rock exposure types and have information that will complement original observations, to obtain the full picture of ichnological features depicted within a succession (Gougeon *et al.* 2023). This approach was performed in this study with the investigation of two coeval sections at Landeyran River and Abandoned Vineyard: the former section provides data on bed tops that are lacking in the latter section, and the latter section possesses better quality data from elevation views than in the former section (Fig. 5).

Ichnofacies

At Landeyran River, the base of the Landeyran Formation is transitional with lower shoreface deposits of the Foulon Formation, and is characterized by heterolithic mudstone-sandstone evidencing a proximal prodelta or an offshore environment (Vaucher *et al.* this volume). Then, the bulk of the succession is dominated by shelf sediments (*sensu* MacEachern *et al.* 1999a) deposited via suspension fallout and low-density turbidity currents (Vaucher *et al.* this volume). Trace fossils demonstrate a transition from open burrows made by suspension feeders and passive predators (*Palaeophycus*, *Skolithos*) toward semi-infaunal grazers (*Helminthoidichnites*, *Helminthopsis*) and sub-surface deposit feeders (*Alcyonidiopsis*, *Planolites*) (Figs 4, 6B). This transition highlights a switch from a Skolithos Ichnofacies into potential Cruziana/Phycosiphon and Zoophycos ichnofacies

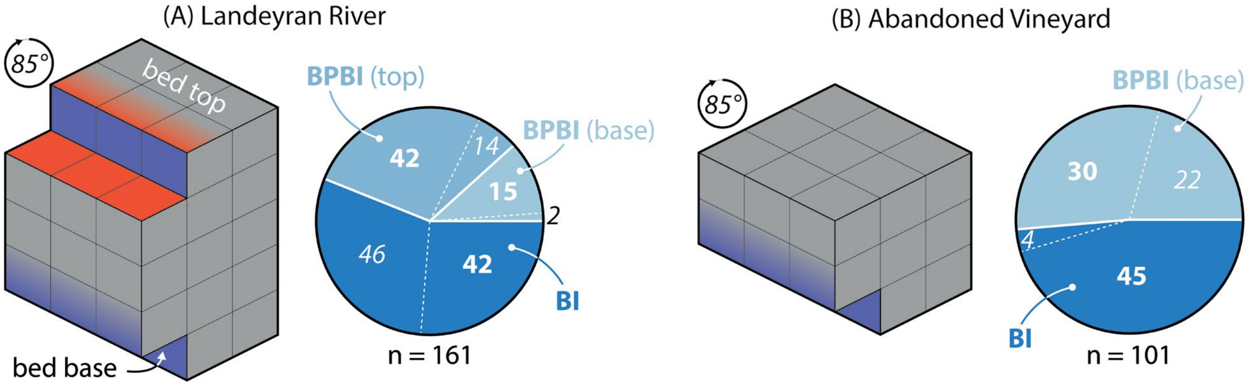

Fig. 5. Evaluation of outcrop bias and its impact on datasets. Block diagrams are based on Shillito & Gougeon (2023) and characterize the types of outcrop exposure and outcrop areas available for vertical (purple colour) or horizontal (red colour) ichnological observations. Grey colour corresponds to areas inaccessible for investigation. Top-left numbers in circular arrows correspond to the rotation of strata from the horizontal plane (dip). Pie charts are designed after Gougeon *et al.* (2023, 2025a) and provide overviews of data collected on Bioturbation Index (BI) and on Bedding Plane Bioturbation Index (BPBI) (with discrimination of data recovered either from bed tops or bases for the latter). Numbers in bold correspond to the recovery of confident values, and numbers in italics to uncertain values (see Gougeon 2025 for complete dataset). A, the Landeyran River section is a stepped cliff/overhang cliff with common elevation views available for study. However, bed surfaces can be significantly covered by scree, dust, and vegetation, which hinders observations on trace fossils and impacts negatively on the quality of data recovered, evidenced by the record of a high number of uncertain values for bioturbation indices (only 48% of the values on BI represent confident observations). B, the Abandoned Vineyard section does not expose bed tops, and the section is an overhang cliff. The quality of data for bioturbation indices is better than at Landeyran River, especially for observations made in elevation view (92% of the values on BI represent confident observations).

(Fig. 6B; MacEachern *et al.* 2012; MacEachern & Bann 2020; Buatois & Mángano 2021). In our study, because the rock surfaces are regularly covered by scree, dust, and vegetation, the identification of a broad range of ichnotaxa that typically compose the Cruziana or Phycosiphon ichnofacies is rendered difficult, precluding definitive conclusions. Regarding the identification of a potential Zoophycos Ichnofacies, rock-surface covering also played a role, but other impediments can be invoked: (1) the lack of lithological contrast between the burrow fill and the host rock in mudstone that hampers trace-fossil identification (MacEachern *et al.* 1999b; MacEachern & Bann 2008); and (2) the difficulty in recognizing this ichnofacies in the Palaeozoic because it mostly relies on the identification of *Zoophycos* itself, which had a broad environmental tolerance at that time (Osgood & Szmuc 1972; Bottjer *et al.* 1988; Zhang *et al.* 2015; Paz *et al.* 2023; Wenger *et al.* 2025). Nevertheless, in the Landeyran Formation, a Zoophycos Ichnofacies can be inferred because (see also Paz *et al.* 2023): (1) semi-infaunal grazing trails (*Helminthopsis*) and sub-surface deposit feeding structures (*Alcyonidiopsis*, *Coprulus*, and *Planolites*) are the dominant trophic types represented, inferring nutrient-rich sediments; (2) the fauna was mobile; and (3) ethological categories are represented by fodinichnia and pascichnia.

Substrate oxygenation

On the shelf, food is abundant and hydrodynamism is low, rendering oxygenation the main controlling factor on bioturbation (Fig. 6A; Savrda & Bottjer 1986; Ekdale & Mason 1988; Buatois & Mángano 2011; Paz *et al.* 2023). Although shelf deposits can be heavily bioturbated and displaying complex tiering architectures (with shallow-tier *Nereites*, mid-tier *Teichichnus*, and deep-tier *Chondrites* and *Zoophycos*, for instance; Savrda 2007), such settings can conversely demonstrate a complete lack of bioturbation as it may lie within the oxygen minimum zone (Buatois & Mángano 2011; Guilbaud *et al.* 2018). In the Landeyran Formation, bioturbation intensity is diagnostically null to very low in deposits just above and below the storm wave base, with local peaks in biogenic activity correlated to increases in deposit-feeding activity (notably with *Alcyonidiopsis* and *Coprulus* that show disruption of the primary fabric; Fig. 3H) suggesting dysoxia (Fig. 6A). Dysoxia typically results in a reduction of animal body size, ichnodiversity, and burrow depth (Paz *et al.* 2023), which contrasts with the features characterizing climax communities that are formed under stable oxic conditions (Bromley 1996). In the succession, slight improvements in substrate oxygenation are related to low-density turbidity currents that were identified by the sedimentological analysis (Vaucher *et al.* this volume; see also Buatois *et al.* 2000). However, the bulk of shelf strata is inferred to have been deposited under anoxia (Fig. 6A), which is commonly invoked as a prerequisite for the exceptional preservation of soft-bodied animals via authigenic mineralization (Allison & Briggs 1993; Saleh *et al.* 2021; Corthésy *et al.* 2025; Gaines & Droser 2025). Anoxia permitted the proliferation of microbes within the sediment, as evidenced in the Landeyran Formation by pustular microbially stabilized surfaces (Fig. 2I). Such textured substrates are also instrumental in the taphonomy leading to the preservation of soft-bodied organisms (Seilacher *et al.* 1985; Wilby *et al.* 1996; Janssen *et al.* 2022). In any case, micro-ichnological and geochemical analyses are necessary to further support these conclusions (Biddle *et al.* 2025) because the seemingly lack of bioturbation in mudrocks can also result from a taphonomic artifact, with compaction and the absence of lithological contrast potentially making trace fossils invisible to the observer today (MacEachern *et al.* 1999b; MacEachern & Bann 2008).

Comparison with other Lagerstätten *hosting trace fossils*

Trace fossils are not usually the main focus of interest in Lagerstätten studies, but can provide valuable information on taphonomy, palaeoecology, and palaeoenvironments. Buatois *et al.* (2000) emphasized that contrasting taphonomic conditions for trace and body fossils usually lead to the preservation of either one or the other, and that biogenic structures are therefore typically rare in Lagerstätten. For instance, the absence to very low bioturbation observed in elevation views can be characteristic (Allison & Brett 1995; Buatois *et al.* 2000; Saleh *et al.* 2022a; Caron *et al.* 2024), which is also evidenced in the Landeyran Formation, and is explained by environmental stress (oxygen depletion). As a consequence, diminutive sizes in trails and burrows and very shallow infaunal colonization have been noted (Buatois *et al.* 2000; Zhang *et al.* 2007; Mángano 2011; Mángano *et al.* 2012). Although this appears to apply to some of the ichnotaxa recovered in the Landeyran Formation (e.g. widths of 0.1 cm for *Helminthoidichnites tenuis* and *Planolites montanus*), others have sizes around 0.5 cm (*Helminthopsis granulata*), or even reach 1.0 cm in width (*Alcyonidiopsis longobardiae*). This suggests that the tracemakers of *H. granulata* and *A. longobardiae* were either

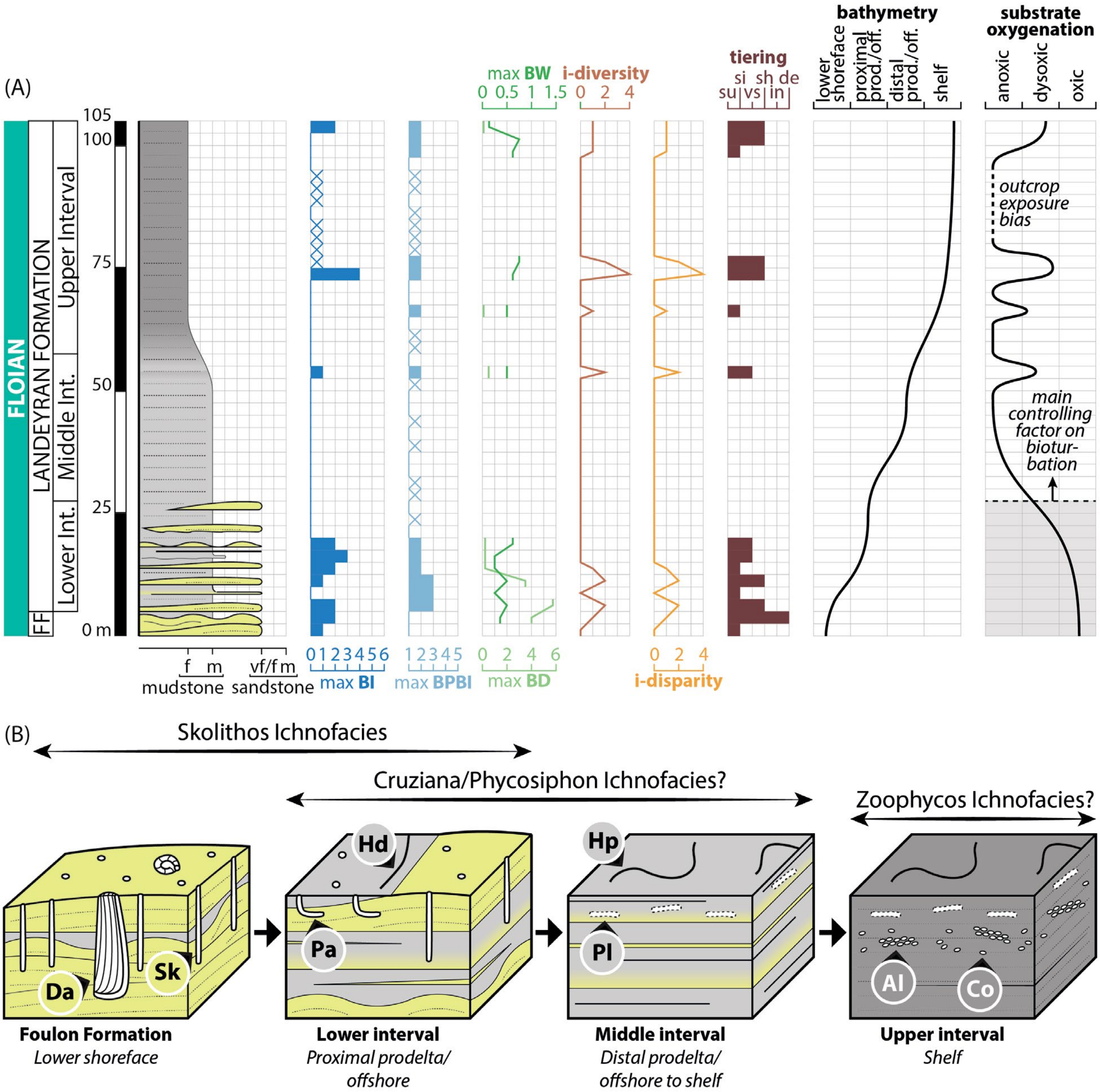

Fig. 6. Environmental controls and palaeoecology. A, summary of ichnological metrics across the upper Foulon Formation (FF)–Landeyran Formation at Landeyran River, and inferred bathymetric and substrate oxygenation curves. Acronyms are the same as in Figure 4. For tiering: su = surficial; si = semi-infaunal; vs = very shallow infaunal; sh = shallow infaunal; in = intermediate infaunal; and de = deep infaunal. Tiering is primarily inferred from ichnotaxa, but is complemented based on bioturbation intensity values for intervals lacking ichnotaxa identified. Off. = offshore; prod. = prodelta. Bathymetric curve is based on sedimentary facies interpretations (see also Vaucher *et al.* this volume). Oxygenation curve follows the method of Savrda & Bottjer (1986) and mostly results from the interpretation of ichnological metrics. Oxygenation became the main controlling factor on bioturbation once the system transitioned from a higher-energetic nearshore with higher sedimentation rates into a lower-energetic shelf. B, block diagrams representing the palaeoecological evolution of animal behaviours evidenced from ichnological data in the Foulon Formation and the three intervals of the base of the Landeyran Formation. A Skolithos Ichnofacies is present in proximal deposits of the Foulon Formation and sandstone-dominated deposits of the lower interval of the Landeyran Formation, characterized by vertical burrows of suspension feeders (Sk = *Skolithos*) and of microbe gardeners (Da = *Daedalus*, only found in the Foulon Formation, see Gougeon 2025). Deposits evidencing lower hydrodynamism in the lower and middle intervals of the Landeyran Formation lack robust ichnological data to confirm assignment to a Cruziana or Phycosiphon ichnofacies; they are nevertheless typified by semi-infaunal microbe grazers (Hd = *Helminthoidichnites*; Hp = *Helminthopsis*), very shallow-tier suspension feeders or passive predators (Pa = *Palaeophycus*), and very shallow-tier deposit-feeders (Pl = *Planolites*). The upper interval could represent an expression of the Zoophycos Ichnofacies, characterized by a community of deposit-feeding animals producing semi-infaunal *Helminthopsis*, very shallow-tier *Planolites*, and shallow-tier *Alcyonidiopsis* (Al) and *Coprulus* (Co).

tolerant to low oxygen levels, targeting untapped organic material buried within the sediment, or were opportunistic and represented the first animals to colonize the substrate after slight improvements in environmental conditions. However, this does not apply to all Lagerstätten as some others have significantly high bioturbation levels, with normal burrow sizes, and still preserve abundant soft-bodied animals (Lin *et al.* 2010). Finally, the association of trace fossils directly on body fossil remains is not unique to the Cabrières Biota (i.e. meiofaunal burrows associated with an alga; Fig. 3E, F). Similar trophic interactions were notably observed in association with animal carcasses/carapaces of the Cambrian Chengjiang Biota (Zhang *et al.* 2007), Sirius Passet (Peel 2010; Mángano *et al.* 2012, 2024), Emu Bay Shale (Schroeder *et al.* 2018), and Burgess Shale (Mángano *et al.* 2019), and the Ordovician Fezouata Biota (Saleh *et al.* 2022b) and Beecher's Trilobite Bed (Boisset *et al.* 2024).

Criteria for distinguishing simple trace fossils from body fossils

The Landeyran Formation hosts a Lagerstätte that is composed of body fossils preserving skeletal parts (e.g. trilobites, echinoderms), soft tissues (e.g. algae, sponges), and trace fossils. This plurality of fossil types requires accurate observations and analyses by experienced researchers coming from different disciplines. Unsurprisingly, misinterpretations can result from difficulties in discriminating between seemingly similar structures. In fact, this long-standing debate started 200 years ago with palaeontologists of the 19th century classifying trace fossils as 'fucoids' (i.e. seaweeds; Brongniart 1823, 1828), until Nathorst (1873, 1881, 1886) convincingly demonstrated their origin as traces of animal activity based on experiments made on plaster casts (therefore ending the 'Age of Fucoids' of Osgood 1975). This question is also faced by palaeontologists dealing with fossils of the Ediacaran, because both trace fossils and body fossils at that time were usually simpler in morphology as a result of primitive body plans (Mángano & Buatois 2020; Gougeon *et al.* 2025a). Going further, the search for life on Mars has recently led specialists to develop criteria to accurately discriminate trace fossils from inorganic structures (Baucon *et al.* 2020a; Genise 2021), a topic of discussion that is rooted in the last century (e.g. Boyd 1975; Ekdale *et al.* 1984).

Combining arguments coming from these different lines of research, we summarize below some of the key features that are essential to understand the formation, preservation, and ultimately, identification of trace fossils in sedimentary rocks, as this is a point of contention that was recently raised by Muir & Botting (2024) for fossils identified in the Cabrières Biota (see also Saleh *et al.* 2024b). The arguments below focus mostly on the identification of simple objects that lack distinctive features that would affiliate them without any doubt to either a trace or a body fossil (e.g. presence of walls, linings, or spreiten in trace fossils; or of anatomical body parts in body fossils). That is, for instance, the distinction of an alga from a simple grazing trail. We acknowledge that there exist counterexamples to each of the five criteria detailed below, which are discussed accordingly. Nevertheless, the following key should be considered as a baseline for the identification of such objects, and should be approached as a whole by giving weight to all of these features together before reaching a conclusion on the origin of a fossil.

1. *Trace fossils are three-dimensional entities.*– Trace fossils can be broadly subdivided into four groups: trails, trackways, burrows, and borings (Fig. 7A; Ekdale *et al.* 1984; Frey & Pemberton 1985; Buatois & Mángano 2011). Of those, only trails and burrows can have morphologies reminiscent of soft-bodied organisms. Trackways are composed of series of individual imprints (Trewin 1994), the nature of which leaves little space for misinterpretation. Borings are made in hardened substrates (Bromley 1994), which is a medium that does not favour burial and preservation of animals lacking skeletons. By definition, burrows possess both horizontal and vertical components while being excavated within unconsolidated substrates, and therefore their fossilized counterparts have diagnostic reliefs either observed within the casting medium (i.e., endichnial preservation), or on bed surfaces (i.e., epichnial and hypichnial preservations; Seilacher 1964; Martinsson 1970). Although trails are subhorizontal, they also display diagnostic reliefs, evidenced either when formed within the substrate (e.g. elliptical outline of internal backfilling in *Psammichnites*; McIlroy & Heys 1997; Mángano *et al.* 2022) or at the sediment-water interface (e.g. concave groove flanked by raised levees in *Archaeonassa*; Jensen 2003; Gougeon *et al.* 2025a). These reliefs made at the time of formation of burrows and trails will typically be preserved in their fossilized counterparts.

   An exception to the rule would be if a trace fossil is preserved in mudstone, which can experience compaction of 50 to 80% (Izumi *et al.* 2017) that will deform and flatten trails and burrows (Fig. 7B). The archetypal example of this is *Chondrites*, which for this reason was the last survivor of the fucoid interpretation of trace fossils (Simpson 1957; Baucon *et al.* 2020b) after being reported, at times, as a flattened structure without any significant relief (e.g. Simpson 1957; D'Alessandro *et al.* 1986; Uchman 1999; Rodriguez-Tovar & Uchman 2004). In such situation, laboratory tools (binocular magnifier, microscope, thin section) can allow the investigator to reach the resolution of analysis necessary to solve the case, because a relief should still be visible while presenting characteristics of flattening (Fig. 7B). In addition, extreme care must be placed in investigating preservational variants that are less compacted and evidence relief, which for instance can be visible in burrow portions along which the fill had been weathered away (e.g. D'Alessandro *et al.* 1986, fig. 4C, D; Uchman 1999, pl. 5, fig. 5). Small-scale structures, such as meiofaunal burrows, also require careful examination as their reliefs will be microscopic and less obvious in naked-eye observations.

Non-skeletal body fossils, especially those with a simpler constitution like a sponge or an alga, will suffer greatly from compactional pressure arising from the pile of sediment accumulating above them during burial. The resulting structure will be highly flattened, losing most of its original relief and representing a two-dimensional view of an original three-dimensional object that will typically not experience lateral expansion (Briggs & Williams 1981; Parry *et al.* 2018). In the Landeyran Formation, some of the algae and sponges described by Saleh *et al.* (2024a, fig. 2a, d, 2024b, fig. 1b) lack significant relief and preserve delicate undeformed features (Saleh *et al.* 2024a, fig. 2a, f), which is different from what can be observed in *Alcyonidiopsis longobardiae*, which is preserved encased within the substrate (Fig. 2A–C), as for individual pellets composing them (Fig. 3G, H), or in *Helminthoidichnites tenuis* and *Helminthopsis granulata* that are preserved as positive and negative hypo- and epireliefs. Although Ediacaran *Helminthoidichnites* has regularly been compared to simple algal body fossils (Jensen *et al.* 2007; Becker-Kerber *et al.* 2021; Runnegar *et al.* 2024), some specimens from the Landeyran Formation display a slight bulge in their median areas that is flanked by narrow grooves (Fig. 2D). These grooves are formed through the pushing of sediment laterally during grazing, which strongly advocates for an ichnological origin for these structures. Soft-bodied animals preserved as semi-reliefs after the decay of the organism's carcass and the opening of a cavity exist under exceptional conditions (Boyd 1975) and notably typify the preservation-style of Ediacaran organisms (Gehling 1999; Bobrovskiy *et al.* 2019). In those cases, attention needs to be placed in identifying other morphological elements that will be diagnostic of body fossils.

2. *Burrows and trails have only minor variations in width.–* Trace fossils are made by organisms that possess fixed body dimensions at the time of formation of the structure. This means that a trail or a burrow made by a deposit feeder, i.e., a structure that was formed through the single passage of an animal, has width dimensions that will mostly be constant along the structure (Ekdale *et al.* 1984). This is notably evident in trails and burrows displaying a massive infill, for instance in *Helminthoidichnites* and *Planolites* (Pemberton & Frey 1982; Gougeon *et al.* 2025a). Backfilled burrows may display slight irregularities in width at the points of junction of sediment pads (e.g. in *Torrowangea*; see Webby 1970) or of internal menisci (e.g. in *Scolicia*; see Buatois *et al.* 2023). These features can easily be identified while looking carefully at taphonomic/preservational variants. Open burrows, however, can present more important variations in width because animals can develop bulges at the end of the structure (e.g. in *Palaeophycus bolbitermilus*; Kim *et al.* 2000), along a tunnel (e.g. in *Bifungites*; Gougeon *et al.* 2025c), or at the point of junction between a tunnel and a shaft in a gallery (e.g. in *Thalassinoides*; Bromley & Frey 1974). In those cases, taphonomic variants and the clear identification of specific ichnotaxobases (e.g. type of infill, presence of a lining) are required to assess convincingly the origin of the structure.

The criterion of a consistent width in trails and burrows led specialists to re-interpret structures previously identified as *Helminthoidichnites* from the Ediacaran of Spain and Brazil as algal filaments or large sulphide-oxidizing bacteria that experienced bending, folding or twisting (Jensen *et al.* 2007; Becker-Kerber *et al.* 2021; see also point 5 below). It is also essential to assess the origin of branching structures, as branching burrows will have tunnels of similar width (e.g. in *Chondrites*, Fig. 8A) whereas branching algae may not (e.g. in *Konglingiphyton*, Xiao *et al.* 2002, fig. 5.13–17; see also Saleh *et al.* 2024b). However, the dimensions of a burrow may be affected by preservational biases, such as tectonic deformation (Chlupáč 1997; Gingras *et al.* 2011; White *et al.* 2025), partial covering of a burrow by an overlying mudstone layer (White *et al.* 2025, fig. 11a, b), or the angle at which a burrow intersects the modern surface of

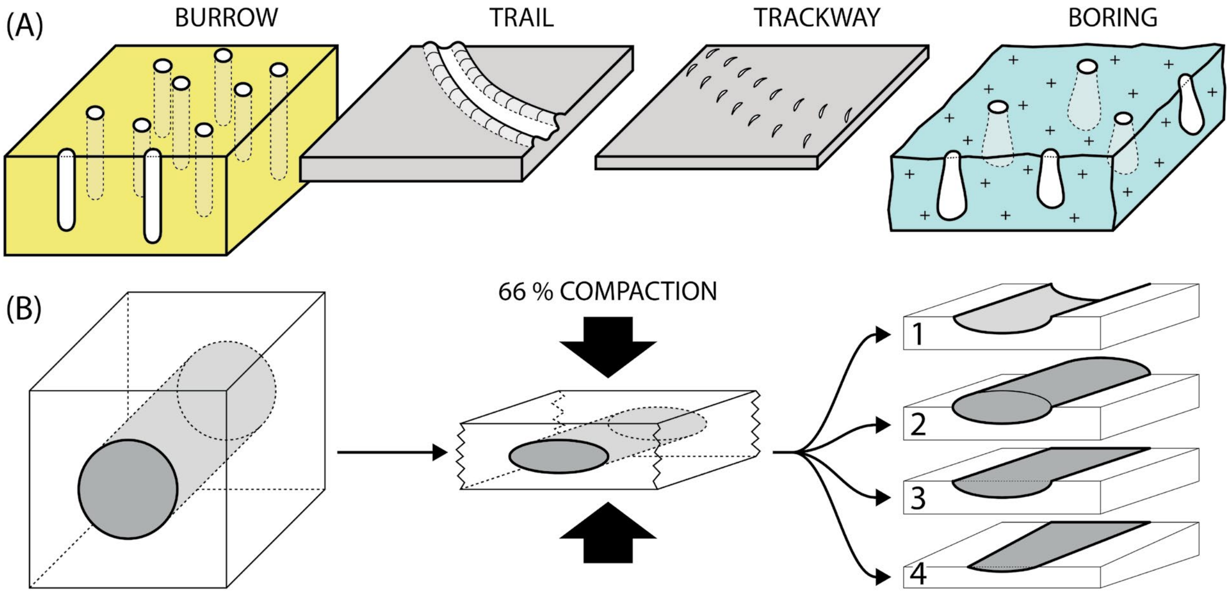

Fig. 7. Terminology and role of compaction. A, common types of trace fossils encountered in the geological record. See Pemberton & Frey (1985) and Buatois & Mángano (2011, pp. 5–8) for further discussion. A burrow is an excavation made in unconsolidated sediment (e.g. *Skolithos*). On the sediment surface, a trail is a continuous groove produced during locomotion (e.g. *Archaeonassa*). Within the sediment, a trail is a continuous structure produced by an animal traveling from one point to another. A trackway is a succession of animal appendage impressions (i.e. tracks) left on the sediment during a single excursion (e.g. *Diplichnites*). A boring is a structure produced mechanically or biochemically in a rigid substrate (e.g. *Gastrochaenolites*). B, compaction of a cylindrical burrow will flatten the structure, which can be up to 80% in mudstone. The resulting structure can show a negative relief (1), a positive relief (2), or no relief at all on the bed surface if affected by longitudinal (3) or oblique (4) weathering. Cases 1 to 3 demonstrate that after compaction, a significant vertical component is still visible in elevation view, characterized by gently curved outlines (inferring an original cylindrical shape); micro-analytical approaches (thin section, microscope) have to be employed in case of important weathering (4) to better characterize the original shape. Cases 1 to 3 demonstrate that burrow width remains constant after compaction, but can change in case of oblique weathering (4). See Vayda *et al.* (this volume, fig. 7) for comparative taphonomic pathways in algal filaments.

exposure (Fig. 7B; Chamberlain 1978, fig. 1), all of which requiring careful assessments.

3. *Simple elongated trace fossils can extend over great lengths on surface areas.*– Trails epitomize the sub-horizontal locomotion of an animal moving from a point A to a point B (Frey & Pemberton 1985; Buatois & Mángano 2011), which can be recovered in the fossil record as extremely long structures. Some of the most iconic trails of this sort are meandering grazing structures of the Nereites Ichnofacies, which are made by animals carefully processing the sediment in search of food (e.g. *Nereites*, *Scolicia*), or looping structures made by arthropods (e.g. *Cruziana*) or extinct sediment bulldozers (e.g. *Psammichnites*) (Delgado 1910; Seilacher 1997, 2007). In any of these cases, the animal had a short body profile that was significantly smaller than the resulting structure, characterized by high manoeuvrability skills (Wang *et al.* 2025) notably evidenced at the turning points of meandering systems. This suggests that structures extending over great lengths, such as *Helminthopsis granulata* reported from the Landeyran Formation (Fig. 2J), most likely correspond to the trace of activity of an animal, and not to the animal itself (see also Runnegar *et al.* 2024, p. 944 for similar conclusions). This criterion can help discriminate annelid body fossils from trace fossils, which present relatively short body profiles and can even be preserved along their elongated trails (Chen *et al.* 2019; Vannier *et al.* this volume). However, this argument is less convincing for filamentous algae which can also extend over great distances. In this case, other morphological features have to be considered, such as the preservation style of constitutive organic material (Fig. 8B) or the presence of kinks and folds along the structure (e.g. Xiao *et al.* 2002, fig. 7.16, 18, 19; Vayda *et al.* this volume, fig. 1D) (see also point 4 below).

4. *Burrow fill does not weather as delicate and fragmentary elements.*– A burrow or trail can be actively filled by an animal manipulating sediment, or be passively filled through gravitational processes (Bromley 1996; Buatois & Mángano 2011).

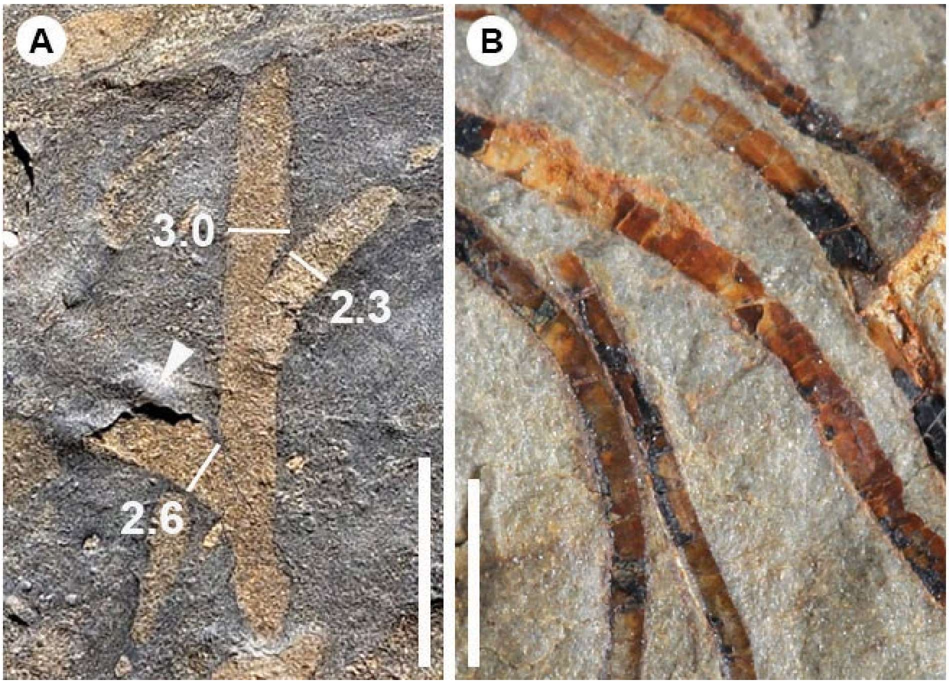

Fig. 8. Application of the criteria to identify a trace fossil (A) and a body fossil (B). Scale bars are 0.3 cm (B) and 1 cm (A). A, branching burrow (*Chondrites* from L'Armorique Formation, Devonian, France) encased in mudstone showing limited variations in branch width (values in millimetres), and presence of a cast in lieu of the weathered infill (arrow) highlighting three-dimensionality. The specimen was not collected, and was photographed in the field. B, algal filaments from the Cabrières Biota showing that organic material composing the fossil weathers as fragmented pieces. *Lagerstätte* Site, UCBL-FSL717 888.

Active infill is done by deposit feeders, with faecal material being stuffed into the burrow after the passage of the animal. Passive infill is typical of dwelling structures of suspension feeders and passive predators. In both cases, either the structure was formed along a sand-mud interface and will result in a positive or negative semi-relief, or was formed within homogeneous sediment and a full relief structure will be created (Seilacher 1964). Semi-reliefs leave little doubt about their ichnological origin, as detailed in point 1 above. For full reliefs, diagenesis and compaction typically result in the tight encasement and crystallization of the sediment within its host rock.

On a bed surface, full reliefs can be exposed as cross-sections through the burrow or trail. The crystallization of the infill will typically result in its solid inclusion within the host rock, and weathering will simply polish both the fill and the host rock (Fig. 8A). In some cases, the internal burrow fill can be partially or fully weathered away whereas the encasing rock is less affected, as can be seen in some *Chondrites* (Fig. 8A; e.g. D'Alessandro *et al.* 1986, fig. 4C, D; Uchman 1999, pl. 5, fig. 5; Uchman *et al.* 2012, fig. 3). In those situations, attention must be placed: (1) in identifying a relief in lieu of the lost fill (see also point 1 above); and (2) in analysing other elements associated to the structure (e.g. the presence of two ichnospecies of *Chondrites* and *Taenidium* burrows on the same sample in Uchman *et al.* 2012, fig. 3, favouring an ichnological interpretation). On the contrary, body fossils made of fragile constituents, such as algae or sponges, can weather as delicate and fragmentary elements. This was observed in specimens from the Cabrières Biota (Saleh *et al.* 2024a, 2a, d, f, 2024b, fig. 1b) and is strikingly expressed in Ediacaran–Cambrian fossils (e.g. Walter *et al.* 1976; Steiner 1994; Xiao *et al.* 2002; Handle & Powell 2012). It is important to note that in the case of algal body fossils, a cast may not be revealed in lieu of the original fossil after weathering; they can display a simple halo or show nothing at all (e.g. Xiao *et al.* 2002, figs 7.19, 8.1), which is also evidenced in some specimens from the Cabrières Biota (e.g. Saleh *et al.* 2024a, fig. 2d).

5. *Body fossils can present evidence of stretching and twisting.*– Although soft-bodied animals with a complex anatomical organization (e.g. annelids) are typically squashed without being significantly deformed during fossilization (Briggs & Williams

1981), stretching can happen in simpler organisms such as algae. For instance, the Ediacaran index fossil *Harlaniella podolica* is composed of oblique elements that can be more or less elongated depending on the curvature of the object (Jensen 2003; personal observations of R.G.). The twisting of algal filaments is also commonly encountered in Ediacaran specimens and is used as a diagnostic criterion to discriminate the trace *versus* body fossil origin by specialists (Jensen *et al.* 2007; Becker-Kerber *et al.* 2021). Stretching and twisting will typically result in a gentle tapering and a width reduction along extended intervals of the fossil, a key feature that is inconsistent with an ichnological origin (see also point 2 above).

Conclusions

The Landeyran Formation hosts moderately diverse trace fossils composed of simple grazing trails (*Helminthoidichnites tenuis*, *Helminthopsis granulata*), simple subhorizontal open burrows (*Palaeophycus tubularis*), actively filled burrows (*Alcyonidiopsis longobardiae*, *Planolites montanus*, ?*Torrowangea* isp.), rare vertical burrows (*Skolithos linearis*), and isolated faecal pellets (*Coprulus oblongus*). Most of the prodelta/offshore and shelf deposits appear seemingly unbioturbated, suggesting anoxic to dysoxic conditions in the sediment which aided in the preservation of soft tissues of diverse organisms of the Cabrières Biota. However, a bias in outcrop exposure, resulting from the important covering of rock surfaces by scree, dust, and vegetation, negatively impacted on the quality of ichnological observations made, and advocates for the need of complementary geochemical and micro-scale analyses to reinforce these interpretations. Simple trace fossils can readily be discriminated from body fossils following observational guidelines and in agreement with distinctive taphonomic pathways. Therefore, our study demonstrates that the diverse trace fossils associated with previously discovered body fossils of the Cabrières Biota make the Montagne Noire an excellent area of focus to untangle early Ordovician ecosystems.

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