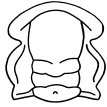




# The Cabrières Biota inhabited a polar wave-influenced delta

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## LETHAIA



The recent discovery of the Cabrières Biota provides a unique insight into a complex, polar community of the Early Ordovician. This biota was found in the southeastern part of the Montagne Noire, in the Landeyran Formation, within the Pic de Vissou unit (Hérault, France). Although there is general agreement on the marine affiliation of the strata yielding the Cabrières Biota, the detailed processes driving sedimentation during its lifetime, which may have influenced its ecological distribution and preservation, remain unknown. In this study, we examined a stratigraphical succession from the nearby Mont Peyroux unit, which includes the Cluse de l'Orb (Floian; early Fl2), Foulon (Floian; late Fl2), and Landeyran (Floian; early Fl3) formations, and is coeval with the fossil-bearing unit. These sedimentary formations are well exposed along the Rieuberlou and Landeyran rivers, and a 350 m thick composite section was logged and analysed for sedimentary facies. The results indicate that the studied interval records a wave-influenced delta flanked by shoreface environments. The facies yielding the fossils correspond to the most distal part of the system, likely in prodelta/offshore to shelf environments, where mud settling and low-density turbidity currents influenced deposition, thus aiding the exceptional preservation of the Cabrières Biota. □ *Sedimentology, stratigraphy, lagerstätte, shoreface, Montagne Noire*

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Palaeoenvironmental reconstructions are essential for understanding the evolution, adaptation, distribution, and exceptional preservation of organisms throughout the Earth history. The Early Ordovician marks a pivotal period in the history of life, particularly with the so-called 'Great Ordovician Biodiversification Event', which represents the major radiation of all the phyla that were established during the 'Cambrian Explosion' (Mángano *et al.* 2016; Servais & Harper 2018; Saleh *et al.* 2023; Servais *et al.* 2023). In this context, the recent discovery of the Early Ordovician (Floian, Fl3) Cabrières Biota in Montagne Noire (France) is of prime importance and has revealed unique communities that once thrived near the palaeo-South Pole (Saleh *et al.* 2024c) during a time when Earth experienced a hothouse climate (Judd *et al.* 2024). The faunal assemblages consist of both bio-mineralized and soft-bodied organisms belonging to groups such as but not limited to sponges, algae, and arthropods (Saleh *et al.* 2024c) (Fig. 1).

In this study, we present a detailed facies analysis of a Lower Ordovician composite stratigraphical

section that encompasses the Cluse de l'Orb (Floian, Fl2), Foulon (Floian, Fl2), and Landeyran (Floian, Fl3) formations in the Roquebrun area, Hérault, France (Fig. 2). Our results refine the depositional environment and associated sedimentary processes in which the Cabrières Biota was discovered. Previous studies dealing with the sedimentology and stratigraphy of the area were conducted a few decades ago by Courtessole *et al.* (1985) and Noffke & Nitsch (1994), both of which predate the discovery of the Cabrières Biota. While these studies suggested a marine environment, they primarily focused on lithofacies characteristics and attempted to explain stratigraphical patterns without clearly defining the palaeoenvironment, and detailed analyses based on recent advances in shallow-marine clastic sedimentology have yet to be conducted. These analyses are crucial for precisely constraining the conditions in which the Cabrières Biota lived, which will, in turn, help to understand its distribution and taphonomy, as it was recently achieved for other sites with soft tissue preservation such as the early Cambrian Chengjiang Biota in China

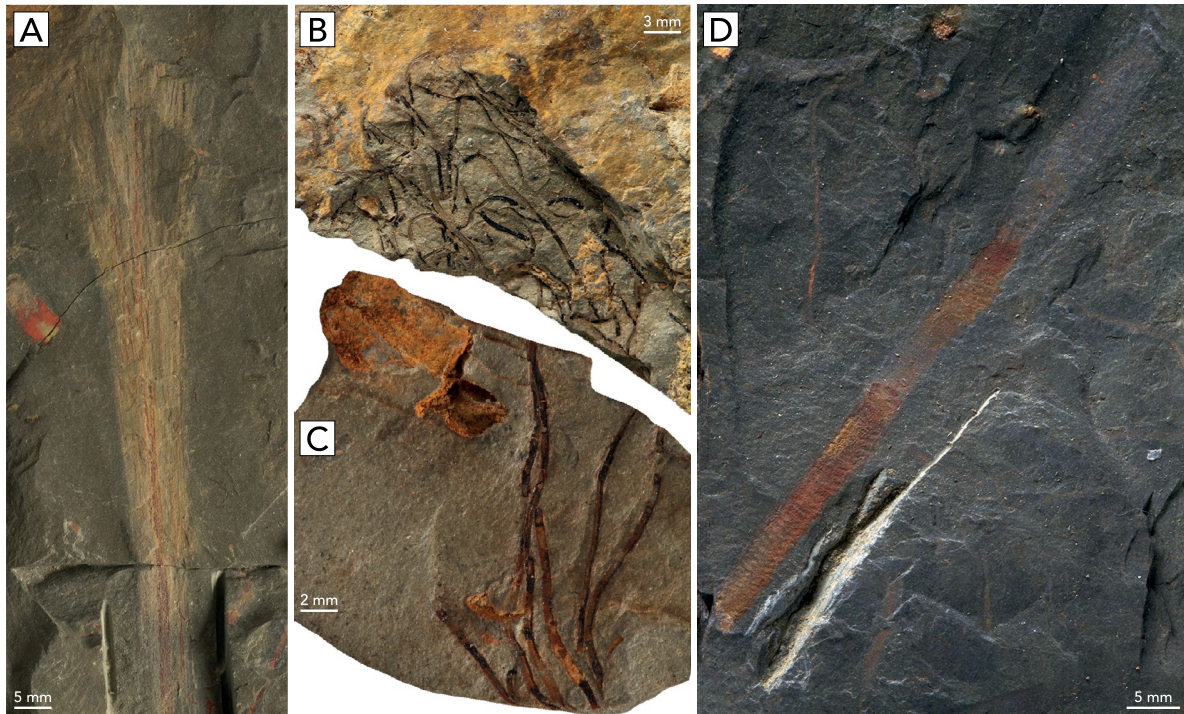


Fig. 1. Cabrières Biota, lower part of the Landeyran Formation, *Apatokephalus incisus* trilobite Zone (late Floian). A, elongated sponge spicules, UCBL-FSL-717-878. B, C, black, coalified, filamentous remains likely belonging to algae, UCBL-FSL-717-888. D, annulated worm, UCBL-FSL-717-862.

(Saleh *et al.* 2022c), or the Ediacara Biota in Namibia, for example (O'Connell *et al.* 2025).

While fossil remains provide invaluable insights into ancient animal communities (e.g. Balseiro & Waisfeld 2013; Saleh *et al.* 2021b; 2023; Serra *et al.* 2021), Early Ordovician exceptionally preserved fossils have a limited stratigraphical and geographical distribution (Van Roy *et al.* 2015; Martin *et al.* 2016a; Saleh *et al.* 2020a; 2024c) and are crucial for understanding both the organisms and their palaeoecosystems (e.g. Briggs 2001; Muscente *et al.* 2017). While our knowledge of the palaeobiology of Early Ordovician communities has greatly improved over the last few decades, studies focusing on sedimentary environments to understand the habitats and environmental influences on these biotas remain scarce (Varejão *et al.* 2025).

In comparison with Lower Ordovician Lagerstätten, studies focusing on sedimentary processes characterizing Cambrian Lagerstätten are more common, such as those of the Emu Bay Shale (Australia; Gaines *et al.* 2024), Chengjiang (China; e.g. MacKenzie *et al.* 2015; Saleh *et al.* 2022c), and the Burgess Shale (Canada; e.g. Gabbott *et al.* 2008; Collom *et al.* 2009; Bath Enright *et al.* 2017; 2021). These studies highlight how burial through gravity-flow deposits was a key step in initiating exceptional preservation of organisms. In the case of Lower Ordovician Lagerstätten, the Fezouata Biota (Early Ordovician, Morocco) is an exception, as it has been

the most extensively investigated site in terms of sedimentary processes, helping to constrain the exceptional preservation of fossils to specific sedimentary facies (e.g. storm- and turbidity-induced deposits) in offshore to shelf environments (Martin *et al.* 2016a; 2016b; Vaucher *et al.* 2016; 2017; Saleh *et al.* 2020c; 2021; 2022b).

## Geological setting

The Montagne Noire is a Variscan tectonostratigraphical unit located in the southern part of the French Massif Central (Fig. 2A). It was formed as a result of a complex fold-and-thrust belt transpressive movement, which was linked to the Cévennes fault (see Chardon *et al.* 2020 for a comprehensive reappraisal of the Montagne Noire tectonics). The traditional subdivision of the Montagne Noire into three distinct units is based on lithological, metamorphic and structural arguments (Gèze 1949; Montmartin *et al.* 2021; Lefebvre *et al.* 2023). These units are the Axial zone, bounded by the Northern and Southern flanks (Fig. 2C). The Axial zone is an elongated migmatized orthogneiss of Ordovician affinity (Roger *et al.* 2004) considered to be a parautochthonous unit displaced from its original northern position (i.e. the most proximal facies belt in term of palaeogeography) through the emplacement of recumbent folds. The Northern flank is characterized

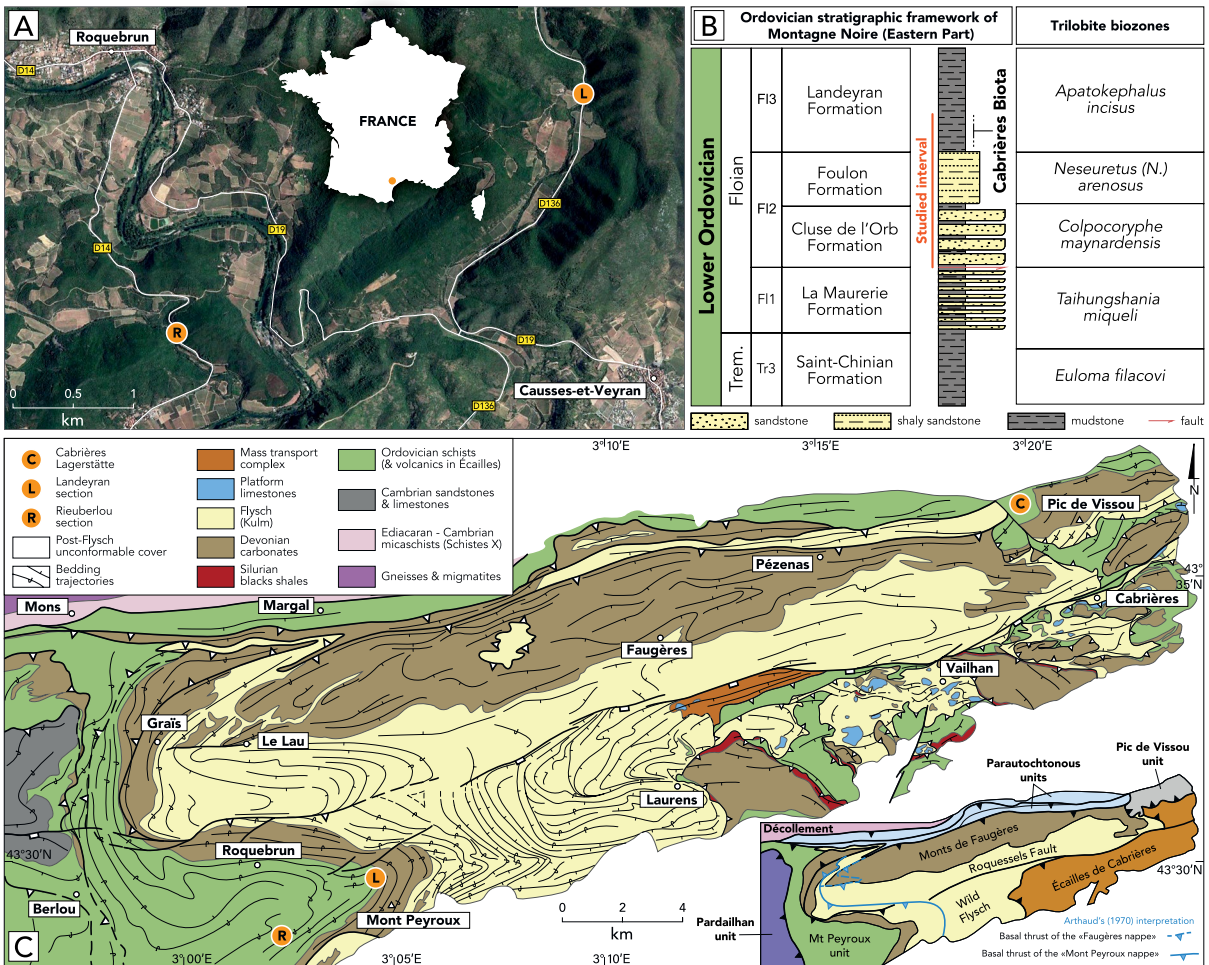


Fig. 2. Geological context. A, map of the study area in southern France (Hérault) near the cities of Roquebrun and Causses-et-Veyran. The locations of the studied sections are marked with orange circles: R-Rieuberlou; L-Landeyran. B, simplified Ordovician stratigraphical framework of the eastern part of the Montagne Noire with the general lithological evolution. Formations, ages, and biozones are shown. This figure is modified from Vizcaïno and Álvaro (2002) and Saleh *et al.* (2024c). C, geological map of the Southern flank of Montagne Noire modified from Chardon *et al.* (2020 and references therein). According to Engel *et al.* (1980) the overturned Pic de Vissou and the overturned Mont Peyroux units have stratigraphical affinities. The inset shows the main units composing the Montagne Noire.

by imbricated folds and thrust sheets consisting of low-grade metamorphosed Palaeozoic rocks. The Southern flank is primarily composed of recumbent folded nappes with similar facies (i.e. the most distal facies belt) and stratigraphical affinity, including the Minervois, Pardailhan, Mont Peyroux and Faugères nappes (Fig. 2C). In most cases, the only preserved component of these nappes is the inverted limb, which gives most exposures an overturned tectonic expression. In the northeastern part of the Southern flanks, the Cabrières nappe preserves the so-called 'Écailles de Cabrières', which have been interpreted as slabs of Ordovician to lower Carboniferous strata transported upon the so-called 'wildflysch' (Gèze 1949).

This study focuses on the Rieuberlou and Landeyran sections, which are located in the Mont

Peyroux unit. The selected sections encompass the Lower Ordovician Cluse de l'Orb, Foulon, and Landeyran formations, which extend from the upper part of the *Colpocoryphe maynardensis* to the *Apatokephalus incisus* trilobite biozones (Fig. 2). In the studied area, the Landeyran Formation represents the uppermost Lower Ordovician stratigraphical unit, which is unconformably overlain by Lower Devonian sedimentary rocks (e.g. Vizcaïno & Álvaro 2002). In terms of palaeogeography, the Montagne Noire was located on the western margin of Gondwana in the vicinity of the South Pole during the Early Ordovician (Álvaro *et al.* 2003; Saleh *et al.* 2024c). The Cabrières Biota is found in a restricted stratigraphical interval of the Landeyran Formation exposed in the Pic de Vissou unit (Fig. 2C) (Saleh *et al.* 2024b; 2024c).

## Material and methods

In the Pic de Vissou Unit (Fig. 2C), the Landeyran Formation yielding the Cabrières Biota only crops out in small patches due to dense vegetation cover, which prevents a thorough sedimentological study in that area. For this reason, we selected a time-equivalent (*Apatokephalus incisus* biozone) and lithologically similar section further west in the Mont Peyroux unit (Fig. 2C). The selected sections offer a more complete exposure, not only of the Landeyran Formation but also of the underlying Cluse de l'Orb and Foulon formations. The excellent exposure of these additional formations

provides an opportunity to study a broader range of depositional environments, allowing for a more comprehensive understanding of the sedimentary processes operating within the basin during the Early Ordovician.

The 270-m-thick and 70-m-thick studied stratigraphical sections crop out along the Rieuberlou and Landeyran rivers, respectively (Fig. 2B), near Roquebrun, Hérault, France. The sections mostly comprise interbedded mudstone and sandstone. The Rieuberlou section mostly displays the Cluse de l'Orb Formation and finishes with the lower part of the Foulon Formation (Figs 3, 4). The section along the Landeyran River starts with the upper part

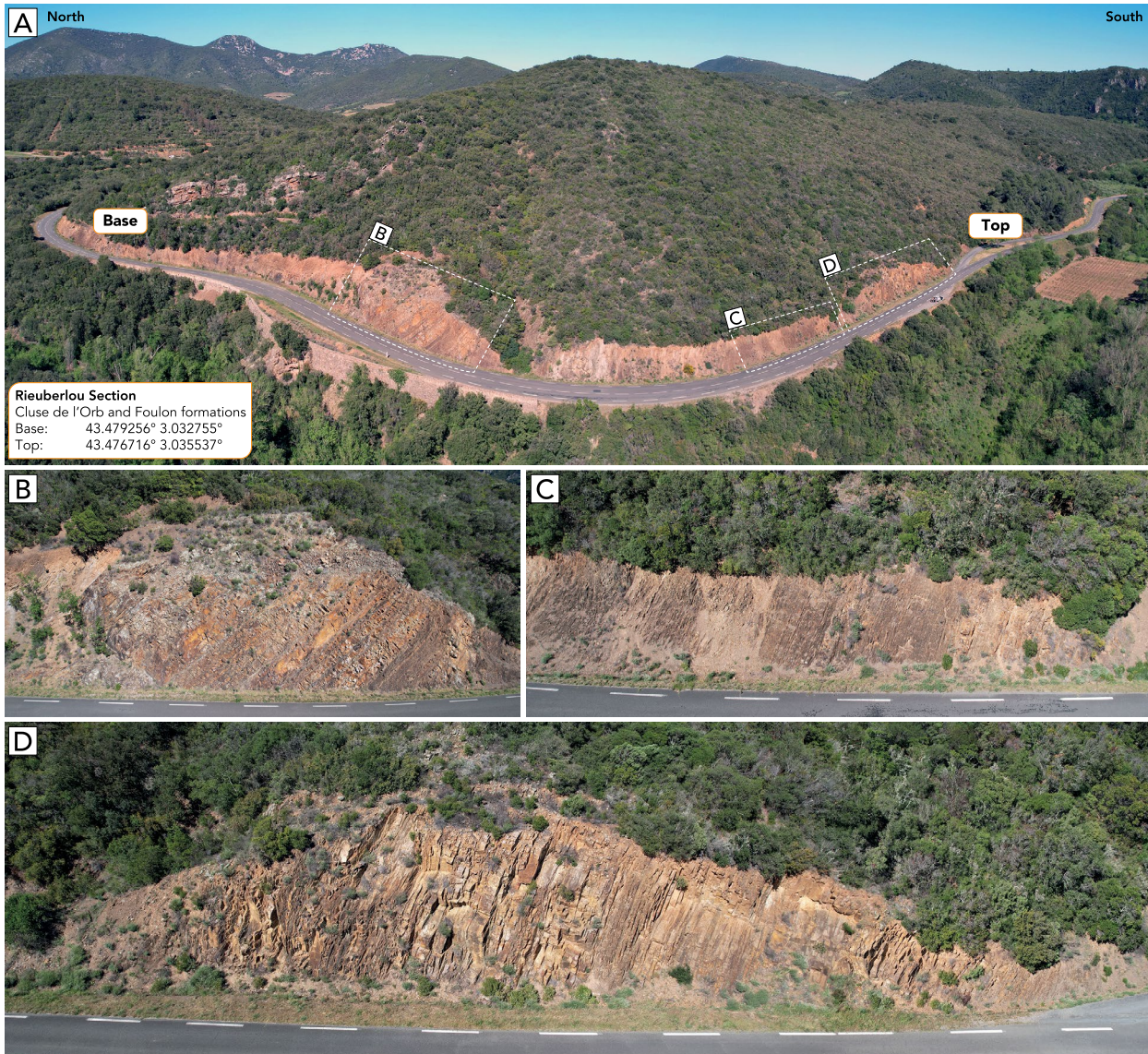


Fig. 3. Rieuberlou section. A, aerial view of the entire stratigraphical interval studied along the road. B, zoom into the first sandstone-dominated interval with overturned beds. C, overview of a mudstone-prone interval interbedded with hummocky cross-stratified sandstone beds. D, overview of the last sandstone-rich interval along this section, which shows mostly amalgamated hummocky cross-stratified and planar laminated sandstone.

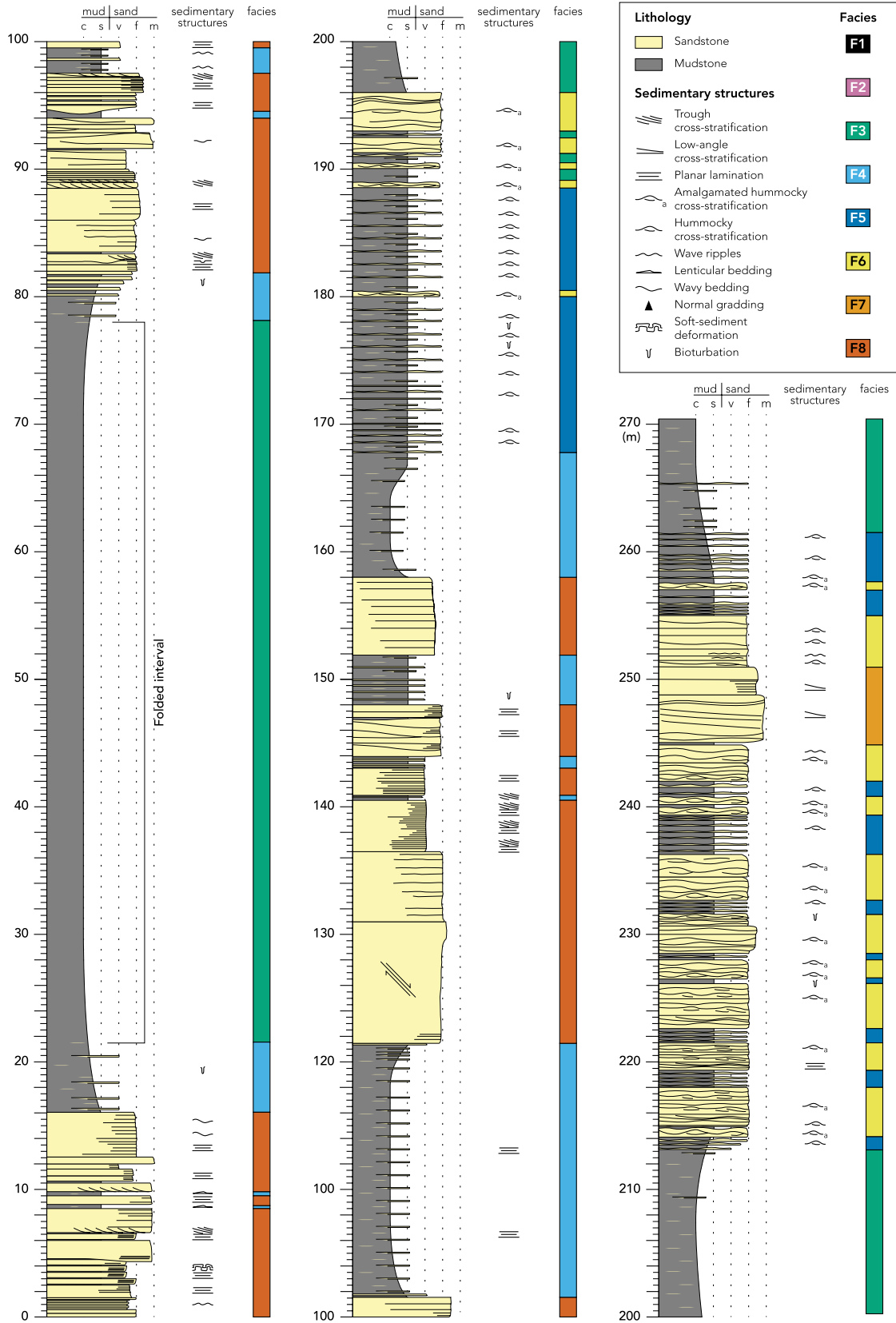


Fig. 4. Stratigraphical log of the Rieuberlou section. The 270-m-thick section of the Cluse de l'Orb and Foulon formations records shallow-marine environments. River processes are dominant up to 158 m, while above wave processes are the main depositional processes. The main sedimentary structures and facies are shown.

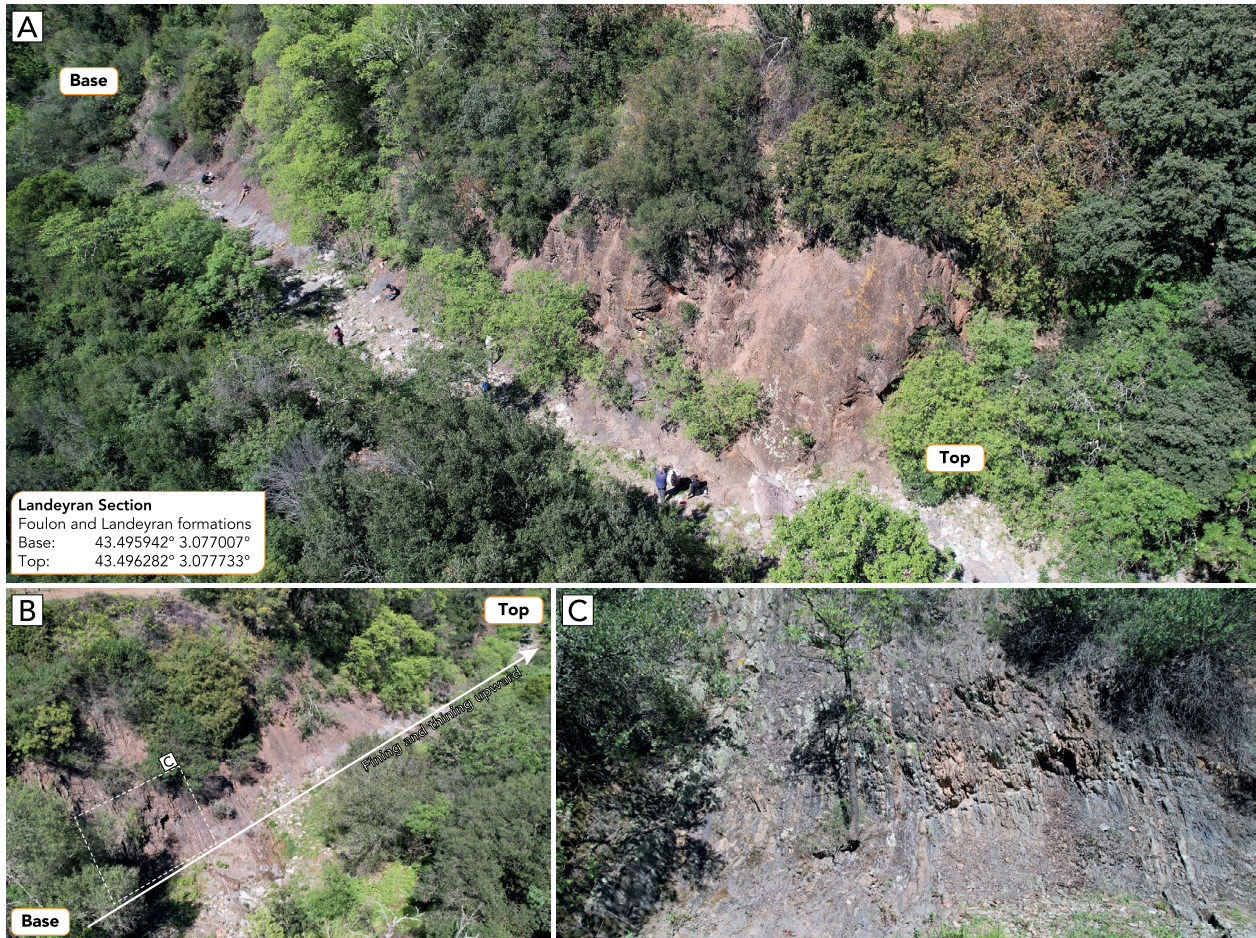


Fig. 5. Landeyran section. A, aerial view of the entire stratigraphical interval studied along the Landeyran riverbed. Overview (B) and detail (C) of the lower part of the section, showing a general trend of fining and thinning upward from sandstone-dominated to heterolithic to mudstone-dominated.

of the Foulon Formation and transitions upward into the Landeyran Formation (Figs 5, 6). Due to folding, overturning, and vegetation, the exact thickness of the Foulon Formation is unknown; however, estimates suggest a thickness of 60 to 100 m (Vizcaino *et al.* 2001). The interval was logged at a decimetre scale. Stratal thicknesses were measured using a Jacob's staff, and descriptions were made of bed geometries, bounding contacts, grain size, sedimentary structures, and body fossils (Figs 3, 5). Information on trace fossils is provided from other studies (for the discussion). Drone photographs were acquired using a DJI Mavic Air 2S.

## Results

The Cluse de l'Orb, Foulon, and Landeyran formations consist of silty claystone, siltstone, and sandstone (Figs 3–9). Eight sedimentary facies were

identified (Table 1), which are grouped into two facies assemblages. These facies assemblages represent environments ranging from the shelf (distal; below the mean storm wave base) to the coastline (proximal) and reflect shallow-marine environments either characterized by river (prodelta, delta-front) or wave/storm (offshore, shoreface) processes. Here, the offshore and prodelta are defined as environments located between the mean storm wave base and the mean fair-weather wave base, while the shoreface and delta front are situated above the mean fair-weather wave base (e.g. Pemberton *et al.* 1992; Catuneanu 2006; Dashtgard *et al.* 2021). While trace fossils have been reported from the studied interval (Courtessole *et al.* 1981; 1985; Dabard & Chauvel 1991; Noffke & Nitsch 1994; Noffke *et al.* 2022), the ichnological content is not described here and is the focus of another study for the Landeyran Formation (Gougeon *et al.* this issue).

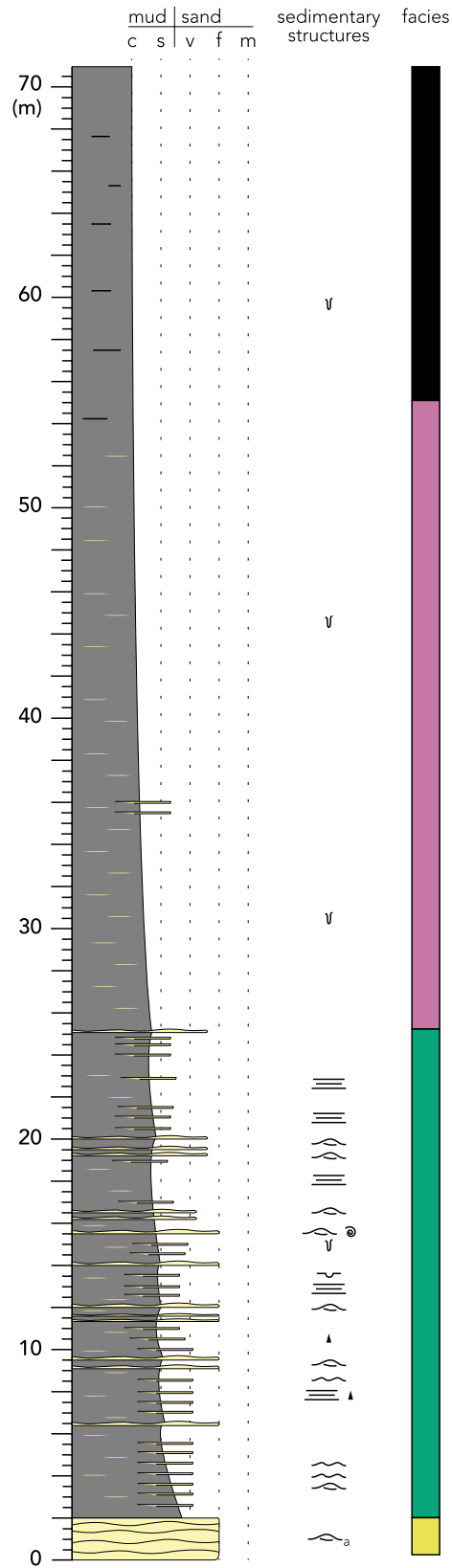
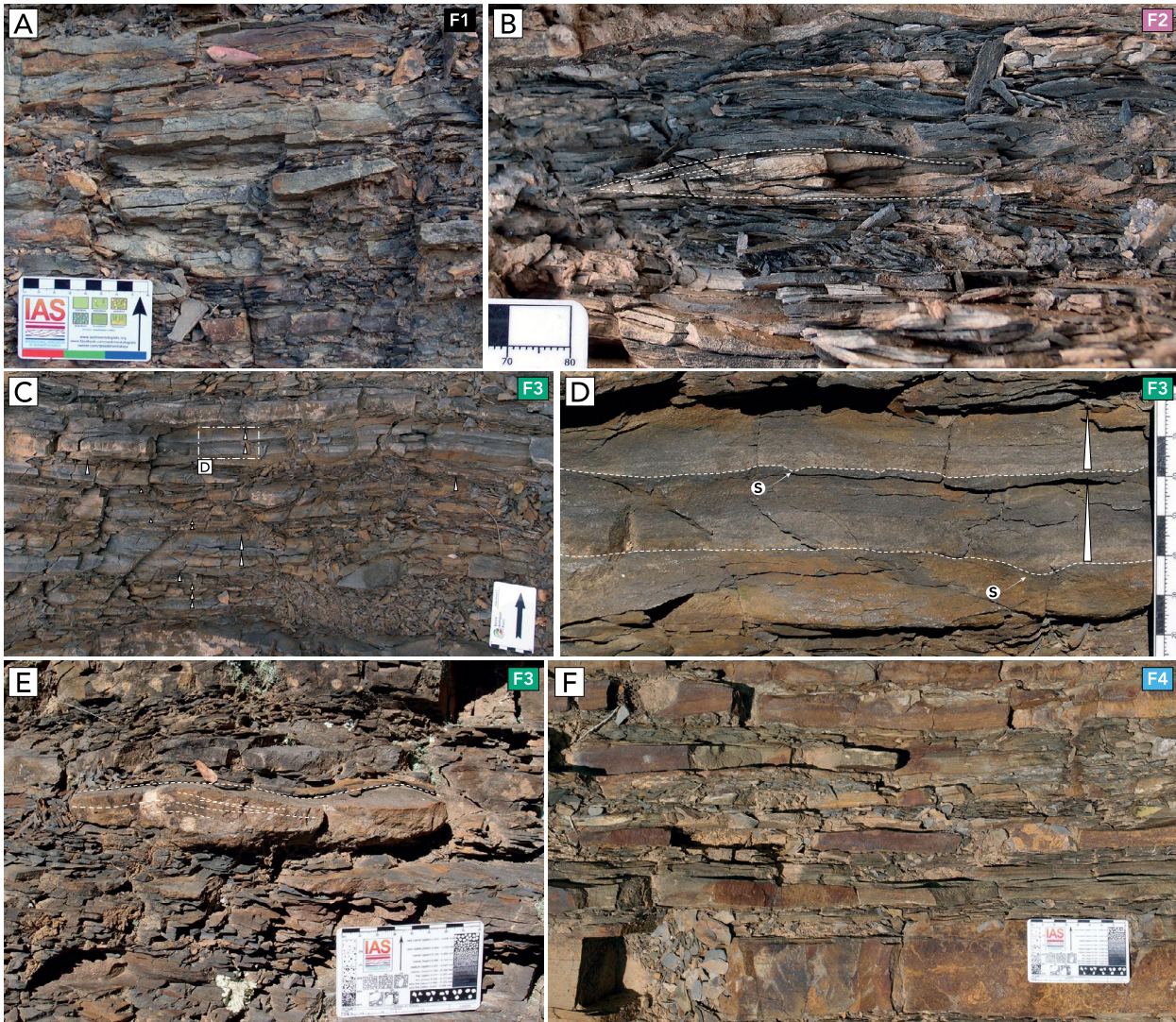


Fig. 6. Stratigraphical log of the Landeyran section. The 70 - m-thick section of the Foulon and Landeyran formations records shallow-marine environments. The main sedimentary structures and facies are shown (key can be found in Figure 4).

*Distal shallow-marine environments (F1–F5) – shelf, and offshore to prodelta*

*Description.* – The first facies assemblage consists of five sedimentary facies (F1–F5; Figs 7, 8; Table 1). Facies 1 and 2 are composed of very dark grey mudstone, with grain sizes ranging from clay to silt. Facies 1 is massive to thinly laminated and exhibits sharp bases (Fig. 7A). Facies 2 is similar to F1; however, it includes thin lenticular bedding with very fine-grained sandstone lenses (Fig. 7B). Facies 3 and 4 are more siltstone-rich, containing a higher

proportion of sandstone, and range in colour from dark to light grey. Facies 3 displays lenticular bedding composed of very fine-grained sandstone, with scours associated with normal grading (Fig. 7C, D), as well as very fine- to fine-grained hummocky cross-stratified (HCS) sandstone characterized by centimetre-scale wavelengths (i.e. micro-HCS *sensu lato*) interbedded with siltstone (Fig. 7E). Facies 4 consists of siltstone with lenticular bedding of very fine-grained sandstone, alternating with very fine- to fine-grained planar-laminated sandstone. Some sandstone beds in Facies 4 exhibit symmetrical ripple



*Fig. 7.* Sedimentary facies. A, tabular dark massive to laminated mudstone. B, thinly laminated dark mudstone with lenticular cross-laminated fine-grained sandstone. C, laminated dark grey mudstone with millimetric greyish fine-grained sandstone intercalations displaying normal grading, highlighted with white triangles. D, close-up of (C) showing the erosive bases of very fine-grained sandstone layers with scours (s) and normal grading. These beds are interpreted as distal low-density turbidites. E, brownish fine-grained symmetrical cross-laminations interstratified within thinly laminated dark mudstone. F, brownish very fine- to fine-grained quasi tabular planar-laminated sandstone.

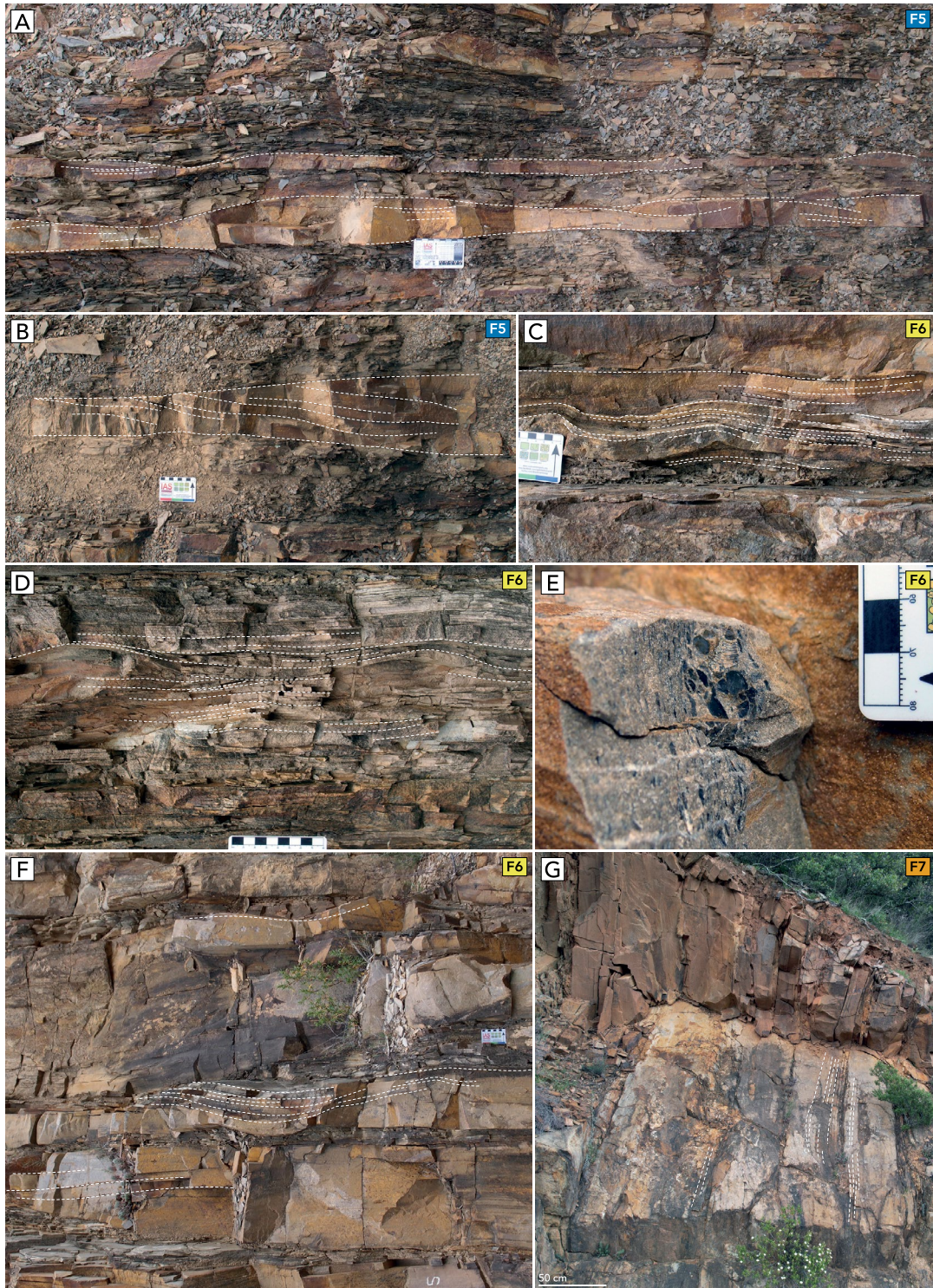


Fig. 8. Sedimentary facies. A, alternating brownish fine-grained isotropic hummocky cross-stratified sandstone beds and thinly laminated greyish mudstone to siltstone. B, brownish fine-grained anisotropic hummocky cross-stratified sandstone interbedded with thinly laminated greyish mudstone to siltstone. The cross-stratified sandstone beds in (A) and (B) are interpreted as storm deposits. C, asymmetrical cross-laminated light brown fine-grained sandstone beds with symmetrical and planar lamination. E, shelly beds consisting mainly of brachiopods (locally known as 'lingules') occurring within facies F6. F, overview of the uppermost sandstone-prone interval of the Cluse de l'Orb Formation showing an alternation of amalgamated hummocky cross-stratified to planar laminated fine-grained brownish sandstone beds. G, interval composed of fine- to medium-grained sandstone showing low-angle cross-stratification and reactivation surfaces.

Table 1. Sedimentary facies and detailed characteristics observed in the Lower Ordovician (Fl2–Fl3) Cluse de l'Orb, Foulon and Landeyran formations along the Rieuberlou and Landeyran rivers near Roquebrun, Hérault, France.

Facies	Grain size	Bed thickness	Description	Processes interpretation	Facies sketch	
<b>F1</b>	Massive to laminated siltstone	Clay-silt	Centimetre scale	Massive to thinly laminated very dark grey silty claystone to clayey siltstone. Clayey siltstone present possible sharp base.	<i>Shelf.</i> – Suspension settling of mud and silt and dilute turbidity currents.	
<b>F2</b>	Laminated siltstone with lenticular bedding	Silt to very fine sand	Centimetre scale	Massive to thinly laminated dark grey clayey siltstone with lenticular bedding made of very fine-grained sandstone.	<i>Distal prodelta-to-offshore.</i> – Suspension settling of mud and silt punctuated by low-density turbidity current.	
<b>F3</b>	Siltstone-prone and cross-stratified sandstone	Silt to fine sand	Centimetre to decimetre scale	Massive to thinly laminated dark grey clayey siltstone with lenticular bedding made of very fine-grained sandstone. Sharp- or scour-based very fine- to fine-grained sandstone displaying isotropic HCS with centimetre-scale wavelength, planar lamination, and/or normal grading.	<i>Proximal wave-influenced prodelta.</i> – Fluctuating energy conditions. Alternation between suspension settling of mud and silt, and distal storm-induced deposits and low-density turbidity current.	
<b>F4</b>	Siltstone-prone and planar-laminated sandstone	Silt to very fine sand	Centimetre to decimetre scale	Massive to thinly laminated dark to light grey clayey siltstone with lenticular bedding made of very fine-grained sandstone. Sharp-based very fine- to fine-grained planar-laminated sandstone. Minor symmetrical ripples are also present.	<i>Proximal prodelta.</i> – Fluctuating energy conditions. Repeated high-velocity unidirectional flows punctuated by low-energy conditions allowing mud and silt settlement.	
<b>F5</b>	Heterolithic cross-stratified sandstone and siltstone	Fine sand	Decimetre scale	Massive to thinly laminated light grey clayey siltstone with lenticular bedding made of light brown to grey very fine-grained sandstone. Sharp- or scour-based very fine- to fine-grained light brown to grey sandstone displaying isotropic and anisotropic HCS with a decimetre-scale wavelength are present.	<i>Proximal offshore.</i> – Fluctuating energy conditions. Alternation between suspension settling of mud and silt, and storm-induced deposits.	
<b>F6</b>	Amalgamated hummocky cross-stratified sandstone	Fine sand	Decimetre to metre scale	Sharp-based amalgamated HCS fine-grained brown sandstone with decimetre-to metre-scale wavelength. Symmetrical and combined-flow cross-laminated sandstone are also observed. Shell layers are present.	<i>Lower shoreface.</i> – Storm deposits formed by oscillatory and combined flows. Aggrading ripples suggest high sediment supply.	
<b>F7</b>	Low-angle cross-stratified sandstone	Fine to medium sand	Decimetre to metre scale	Sharp-based low-angle cross-stratified to planar-laminated fine- to medium-grained brown sandstone. Symmetrical and combined-flow cross-laminated sandstone are also observed. Reactivation surfaces are also present.	<i>Upper shoreface to foreshore.</i> – Sustained high-energy oscillatory and combined flow conditions.	
<b>F8</b>	Tabular massive to trough cross-stratified sandstone	Fine to medium sand	Decimetre to metre scale	Sharp- to channelized-based massive or tangential trough cross-stratified to planar-laminated fine- to medium-grained brown to grey sandstone interbedded with laminated siltstone. Double and single mud drapes are present on the foresets. Wavy bedding is also observed. Soft-sediment deformation occurs in some sandstone beds.	<i>Delta-front.</i> – Unidirectional flow with variable velocities. Soft-sediment deformation suggests rapid deposition of sandy material. Mud drapes suggest variable flow speeds.	

cross-laminations. Facies 5 is a heterolithic, light brown to grey facies (Fig. 8A, B). Facies 5 displays an alternation between massive to thinly laminated siltstone and sharp- or scour-based, very fine- to fine-grained sandstone with isotropic and anisotropic HCS at decimetre-scale wavelength.

*Interpretation.* – Sharp mudstone bed bases observed in Facies 1 suggest recurrent deposition from low-density turbidity currents (Bhattacharya & MacEachern 2009; Boulesteix *et al.* 2022; Biddle *et al.* 2025). Facies 1 likely represents shelf settings where mud and silt settled from suspension, along with dilute turbidity currents, and is the deepest marine environment recognized in the studied interval. The lenticular bedding in Facies 2 indicates an introduction of sand into an otherwise quiet background environment during episodic storms or floods, likely within a distal prodelta/offshore setting (Buatois *et al.* 2012; La Croix & Gingras, 2021; Hsieh *et al.* 2025). The increase in sandstone beds in Facies 3, displaying either normal grading or micro-HCS, points to low-density turbidity currents associated with distal river discharges or storm-induced (oscillatory and combined flows) currents in proximal prodelta settings influenced by waves and storms (Tinterri 2011; Collins *et al.* 2017; Saleh *et al.* 2022c; Vaucher *et al.* 2023; Hsieh *et al.* 2025). In contrast, the dominance of sharp-based planar-laminated sandstone beds in Facies 4 interbedded with laminated siltstone suggests repeated waning density currents via hyperpycnal flows in a proximal prodelta environment (Bhattacharya *et al.* 2020; Zavala *et al.* 2024). Finally, the predominance of isotropic or anisotropic HCS characterized by decimetre-scale wavelengths in sandstone beds with either erosional or sharp bases interbedded with laminated siltstone in Facies 5 suggests deposition under storm-induced currents in proximal offshore settings (Myrow & Southard 1996; Tinterri 2011; Collins *et al.* 2017; Vaucher *et al.* 2017; Jelby *et al.* 2020; Dashtgard *et al.* 2021; Grundvåg *et al.* 2021). In turn, Facies 1 and 2 represent the most distal parts of the system, where the clear identification of the triggering processes of sedimentation becomes blurred, as both storm- and gravity-induced currents could lead to the formation of similar sedimentary patterns. Facies 3, 4, and 5, on the other hand, are bathymetrically equivalent, evidencing variations in the dominant hydrodynamic processes at play. Facies 4 is river-dominated (prodelta), Facies 5 is wave-dominated (offshore), and Facies 3 represents a transitional zone between the two (wave-influenced prodelta).

### *Proximal shallow-marine environments (F6–F8) – shoreface to delta-front*

*Description.* – The second facies assemblage consists of three sedimentary facies (F6–F8; Figs 8, 9; Table 1). Facies 6 consists of brown fine-grained brown sandstone displaying amalgamated HCS characterized by decimetre- to metre-scale wavelengths with symmetrical and combined-flow ripple cross-lamination, in places showing an aggrading pattern (Fig. 8C–F). Facies 7 features sharp-based, low-angle cross-stratified to planar-laminated brown fine- to medium-grained sandstone, with occasional symmetrical wave and combined-flow ripple cross-lamination, as well as large erosional surfaces (Fig. 8G). Facies 8 displays sharp-based to channelized, massive or tangential trough cross-stratified to planar-laminated brown to grey fine- to medium-grained sandstone, interbedded with laminated siltstone (Fig. 9). The foresets of Facies 8 in places exhibit single and double mud drapes (Fig. 9A, B), and some sandstone beds in Facies 8 show convolute beddings.

*Interpretation.* – The interval characterized by sandstone with amalgamated HCS, wave ripples, and combined-flow ripples, as seen in Facies 6, indicates lower shoreface settings subject to oscillatory and combined flows during either storms of variable intensity or fair-weather wave processes (Hampson & Storms 2003; Pemberton *et al.* 2012; Dashtgard *et al.* 2021). Some ripples display climbing lamina architecture, suggesting sporadic increases in sediment supply, likely due to storm-induced back-currents or high sediment input from nearby rivers via hyperpycnal discharge (Dumas & Arnott 2006; Jelby *et al.* 2020; Vaucher *et al.* 2023). The presence of low-angle cross-stratified to planar-laminated sandstone in Facies 7, along with wave and combined-flow ripples, suggests a shallower environment compared to Facies 6. In Facies 7, the oscillatory motion of incoming waves begins to break, forming either upper-stage plane beds or ripples, depending on the local topography or the intensity of waves (Clifton 2006; Vaucher *et al.* 2017; 2018b; Isla *et al.* 2020; Vaucher & Dashtgard 2022). In Facies 7, the large erosional surfaces potentially reflect phases of erosion due to large waves during storm events close to the shoreline (Inman & Guza 1982; Vaucher *et al.* 2017). The alternation of laminated siltstone and trough cross-bedded to planar-laminated tabular sandstone displaying either sharp or channelized bases, accompanied by current ripples, occasional soft-sediment deformation, indicates proximal delta-front settings with variable river

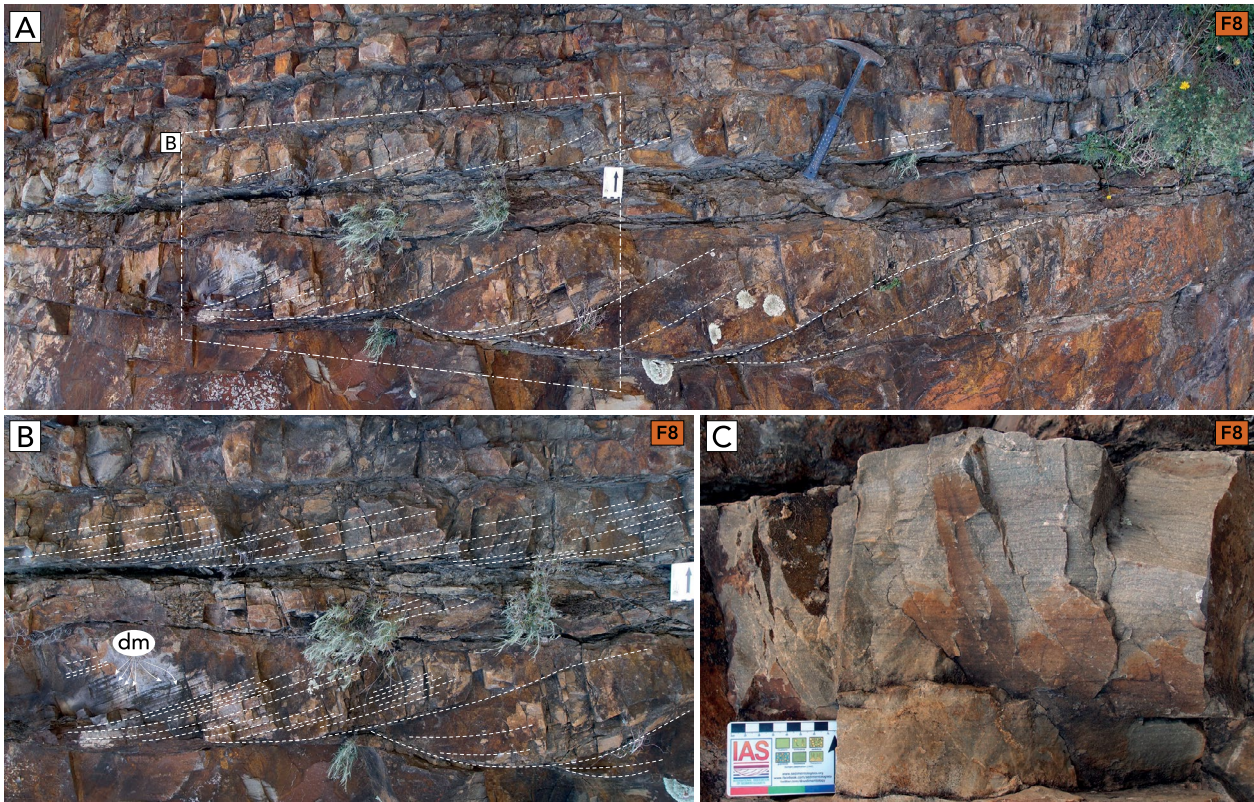


Fig. 9. Sedimentary facies. A, overview of a brownish sandstone-prone interval with minor mudstone-siltstone levels. Sandstone beds are either massive or cross-stratified (see the white dashed lines). B, close-up of (A). Tangential cross-stratified fine- to medium-grained sandstone beds. Double mud drapes (dm) are present on some foresets. C, planar-stratified fine-grained light grey sandstone beds.

discharge as seen in Facies 8 (van Yperen *et al.* 2020; Dillinger *et al.* 2021; Vaucher *et al.* 2025). The variability in flow intensity in Facies 8 is evidenced by the alternation between upper-stage plane beds, sinuous-crested dunes, and current ripples (Vaucher & Dashtgard 2022). A possible tidal influence in Facies 8 is suggested by the presence of single or double mud drapes on some dune foresets (Allen & Homewood 1984; Fenies *et al.* 2002).

## Discussion

### *Wave-influenced delta*

The sedimentary facies analysis reveals variability in the dominance of depositional processes throughout the studied stratigraphical section. The lower part of the composite section (from 0 to 158 m; Fig. 10) primarily shows evidence of gravity and traction currents. Siltstone interbedded with thin, normally graded planar-laminated sandstone with scour or sharp bases reflect low-density turbidity currents in

a prodelta environment, likely linked to hyperpycnal flow during flood discharges (Mulder *et al.* 2003; Bhattacharya & MacEachern 2009; Bhattacharya *et al.* 2020; Jelby *et al.* 2020; Grundvåg *et al.* 2021). Thick, planar to cross-bedded sandstone records upper-stage plane beds and sinuous-crested dunes, respectively (Vaucher & Dashtgard 2022), suggesting variable water flow discharge in delta-front settings, likely corresponding to mouth bar deposits (van Yperen *et al.* 2020; Vaucher *et al.* 2020; Dillinger *et al.* 2021). Additionally, the associated soft-sediment deformation likely indicates rapid sediment deposition on a water-saturated seafloor, plausibly linked to river flooding events (Owen *et al.* 2011).

The upper part of the composite section (from 158 to 324 m; Fig. 10) shows a shift in sedimentary facies, depicting structures ranging from thin, symmetrical cross-laminated sandstone to amalgamated HCS sandstone. The hydrodynamic processes responsible for generating HCS or HCS-like sedimentary structures are varied. These processes include oscillatory, unidirectional, combined flows, and gravity currents interacting with topography, for example, all of which

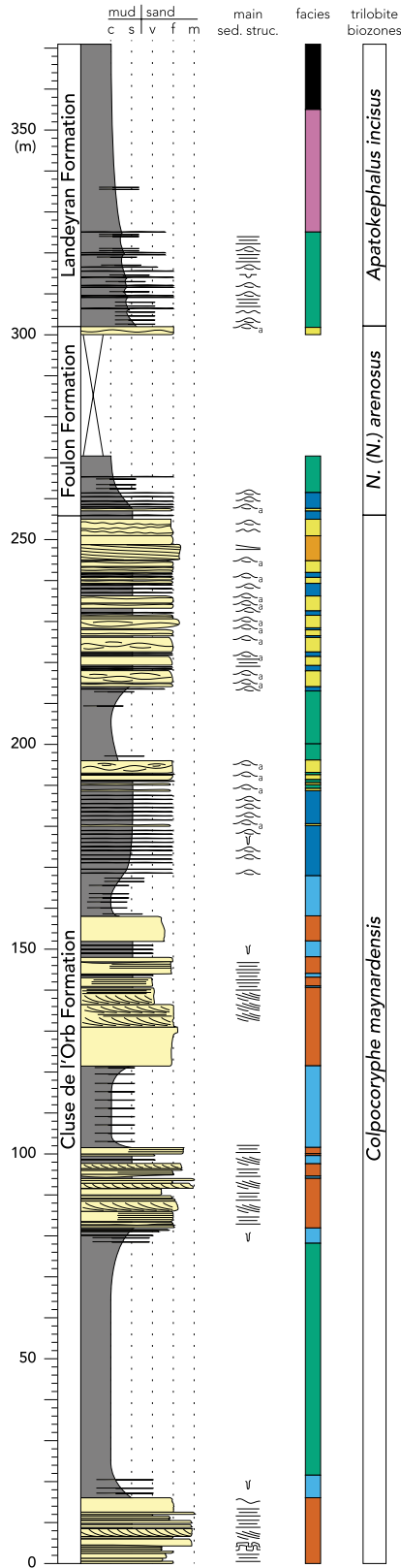


Fig. 10. Synthetic composite log of the studied interval based on the Rieuberlou and Landeyran sections. The main sedimentary structures along with the sedimentary facies and the trilobite biozones are shown. The colour scheme and sedimentary facies correspond to those in Figure 4 and Table 1.

can generate such structures across different depositional environments (e.g. Mutti *et al.* 2000; Dumas & Arnott 2006; Mulder *et al.* 2009; Quin 2011; Tinterri 2011; Perillo *et al.* 2014; Vaucher *et al.* 2018a; Keavney *et al.* 2024; Privat *et al.* 2024). In our study, we observed a gradual increase in the wavelength of the HCS, from discrete, centimetre-scale in Facies 3, to decimetre-scale in Facies 5, and then to amalgamated, decimetre- to metre-scale in Facies 6, sometimes capped by Facies 7 (upper-shoreface/foreshore deposits), but not by Facies 8 (delta-front deposits). The increase in HCS wavelength, alongside the coarsening and thickening-upward trends, likely reflects a stronger influence of oscillatory and combined flows associated with waves and storms (e.g. Yang *et al.* 2006; Perillo *et al.* 2014), indicating a facies sequence typical of a prograding wave-dominated shoreline (e.g. Clifton 2006; Dashtgard *et al.* 2021). Therefore, symmetrical ripples and amalgamated HCS likely reflect varying oscillatory and combined-flow conditions at different water depths during both fair and storm weather in offshore to shoreface settings (Myrow & Southard 1996; Vaucher *et al.* 2017; Jelby *et al.* 2020; Dashtgard *et al.* 2021). In this interval, the clearer signature of wave and storm actions is predominantly found in more proximal environments, while more distal and deeper environments typically record the combined influence of traction, gravity, oscillatory and combined flows. These changes in sedimentary structures indicate a transition from more river-dominated environments to wave-dominated settings, with wave processes becoming more prominent as the depositional environment becomes shallower.

Previous studies have reported the trace fossil content in the Cluse de l'Orb Formation, including *Cruziana*, *Planolites*, and *Phycodes* in the finer-grained intervals, and *Daedalus* and *Skolithos* in the coarser-grained intervals (Courtessole *et al.* 1981; 1985; Dabard & Chauvel 1991; Noffke & Nitsch 1994). The Foulon Formation contains *Planolites* and *Phycodes* (Noffke & Nitsch 1994), while the Landeyran Formation hosts *Alcyonidiopsis*, *Helminthoidichnites*, *Helminthopsis*, *Palaeophycus*, *Planolites*, *?Torrowangea*, meiofaunal burrows, and *Coprulus fecal pellets* in mudstone intervals, with rare sandstone beds displaying *Skolithos* (Saleh *et al.* 2024b; Gougeon *et al.* this issue). Interestingly, *Daedalus* was observed in high abundance in the wave-dominated part of the Cluse de l'Orb Formation, while it is absent in the lower 158 m of strata of the section, evidencing traction current processes (Dabard & Chauvel 1991; Noffke *et al.* 2022). *Daedalus* typically forms in nearshore environments where clean, well-oxygenated, and porous substrates are present, which

is characteristic of high-energy, wave-dominated settings (Neto de Carvalho *et al.* 2016; Noffke *et al.* 2022). The fact that *Daedalus* is only found in the wave-dominated part of the succession suggests that different environmental factors controlled the distribution of trace fossils in the river-dominated part of the studied interval. Trace fossils from the Landeyran Formation suggest that deposit-feeding and grazing strategies were common inferring good nutrient supplies in the system, which is typical of the Cruziana/Phycosiphon and Zoophycos ichnofacies (MacEachern & Bann 2008; 2020; Buatois & Mángano 2021; Gougeon *et al.* this issue).

Overall, the stratigraphical record of the Cluse de l'Orb, Foulon, and Landeyran formations suggests that both river and wave processes played key roles during deposition. While parts of the section are either river-dominated (i.e. the lower part) or wave-dominated (i.e. the upper part), deeper water environments consistently record both processes. The dominance of wave and storm processes in the upper part of the Cluse de l'Orb Formation, evidenced by thick packages of amalgamated HCS sandstone, could reflect either an intensification of storm events that obscured the preservation of river processes (e.g. Zuchuat *et al.* 2023) or an avulsion of the river, with the stratigraphical section recording the shoreface flanking the sides of the delta (e.g. Bhattacharya & Giosan 2003; Bhattacharya 2011; Anthony 2015; Ainsworth *et al.* 2017).

The identified deltaic system in this study developed along a passive margin which was fed by rivers transporting sediment associated with the erosion of metamorphic and plutonic rocks from the Pan-African range (Dabard & Chauvel 1991). While river avulsion is an autogenic process that can occur with varying frequency (Colombera & Mountney 2022), it is very likely that during the Early Ordovician – a time period without widespread vegetation to stabilize riverbanks – channel mobility via avulsion processes occurred more frequently (Gibling & Davies 2012), and probably even more so during hothouse conditions (Prieur *et al.* 2024). Such a scenario would explain the identified shift from river dominance to wave-dominated conditions, and therefore, we propose that the studied section represents the stratigraphical expression of a wave-influenced delta that shifted its point-source locus through time (Fig. 11).

While wave and storm processes were identified in these formations in earlier works (Courtessole *et al.* 1985; Noffke & Nitsch 1994), the recognition of deltaic processes had yet to be described. Interestingly, Dabard & Chauvel (1991) recognized along-strike thickness variability in the river-dominated interval we identify

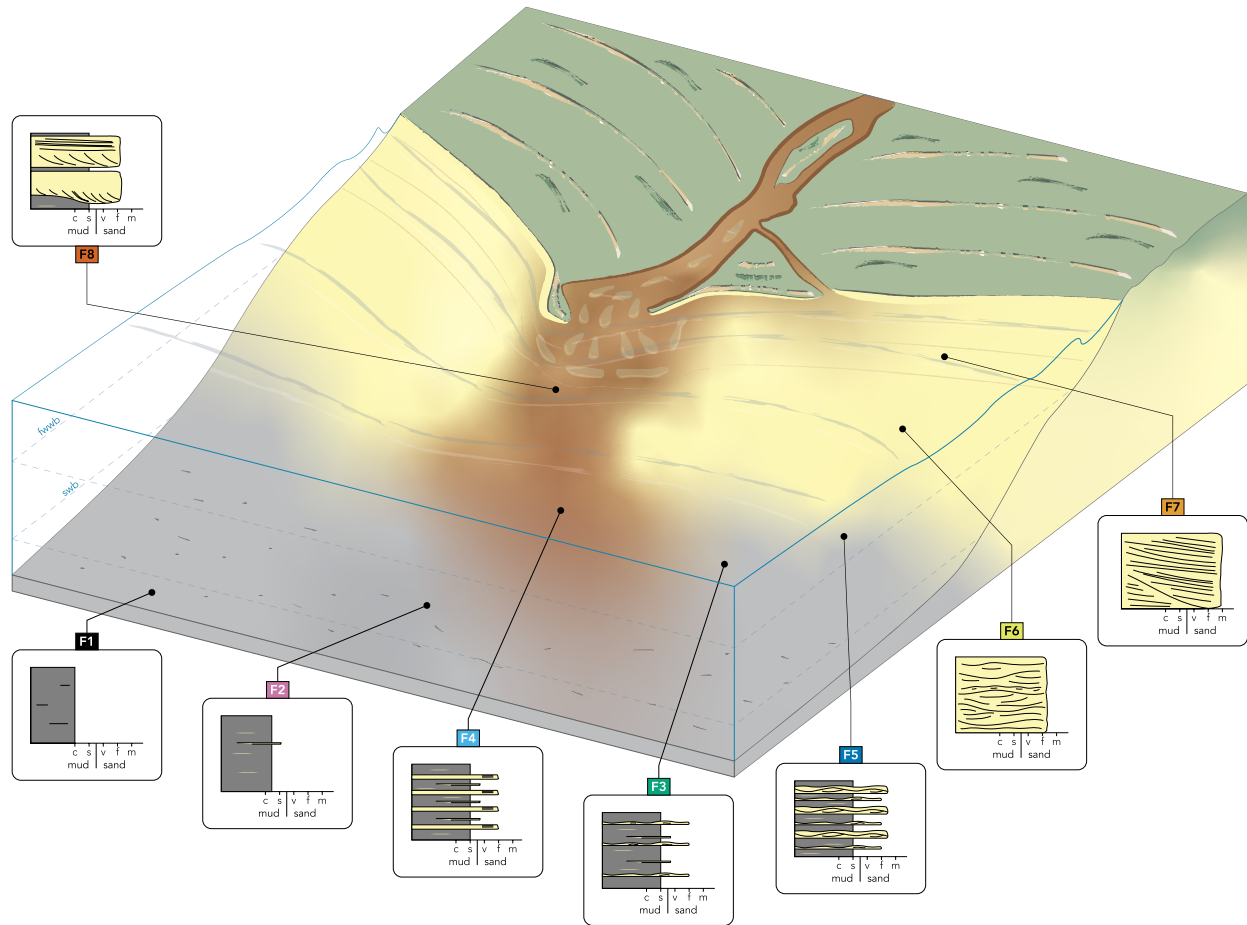


Fig. 11. Conceptual model of deposition during the Early Ordovician (Floian) for the Roquebrun area in Montagne Noire, Hérault, France. The sedimentary facies and their associated sketches are shown and were recognized in the Cluse de l'Orb, Foulon, and Landeyran formations. The wave-influenced delta is illustrated, with the main river mouth and flanking shoreface, explaining the facies variability observed in the studied stratigraphical section. The colour scheme and sedimentary facies correspond to those in Figure 4 and Table 1. FWWB: fair-weather wave base; SWB: storm wave base.

here, which is potentially related to the lobate shape of the deltaic environments (e.g. Bhattacharya & Giosan 2003; Bhattacharya 2011; van Yperen *et al.* 2020; Vaucher *et al.* 2020) and/or to its asymmetry (e.g. Bhattacharya & Giosan 2003; Ayranci & Dashtgard 2016), a common characteristic in wave-influenced deltas experiencing alongshore drift, as demonstrated in modern examples such as the São Francisco Delta, Brazil (e.g. Bhattacharya & Giosan 2003; Anthony 2015).

### *Sedimentary flux and its influence on the biota*

The identification of an avulsion-prone, wave-influenced delta system during the Floian in Montagne Noire has several implications for the fauna that inhabited these environments and their preservation. While evidence of life in the studied sedimentary interval

has been observed through biomineralized body fossils and trace fossils, the exceptionally well-preserved soft-bodied fauna of the Cabrières Biota has only recently been discovered (Saleh *et al.* 2024c), further increasing the diversity and the importance of this Early Ordovician ecosystem. Biomineralized fossils primarily include trilobites, echinoderms, molluscs, brachiopods, hyoliths, and conulariids, all of which were found in the fine-grained intervals of the studied stratigraphical section, with the exception of brachiopods and eocrinoids, which are also found in the coarser sandstone intervals (Courtessole *et al.* 1981; 1985; Dabard & Chauvel 1991; Noffke & Nitsch 1994; Vizcaïno & Lefebvre 1999; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2002; Nardin 2007; Ebbestad *et al.* 2020; Van Iten & Lefebvre 2020). The high diversity of the organisms in the Cabrières Biota can, at least in part, be attributed to the deltaic setting, which

provides a high input of nutrients and oxygen delivered by rivers, during a period when oceanic oxygen levels were likely lower (e.g. Pohl *et al.* 2022). A similar pattern in biodiversity distribution is observed at other sites with exceptional fossil preservation, such as the Chengjiang Biota, which was also preserved in a deltaic context (Saleh *et al.* 2022c).

Within this deltaic system, the fossils are not evenly distributed throughout the stratigraphical interval, as a higher diversity of both biomineralized and soft-bodied organisms is found in more distal environments, particularly within the mudstone-rich intervals corresponding to prodelta/offshore and shelf settings. This increase in diversity from proximal to distal settings may be attributed to differences in environmental conditions between these settings. For instance, proximal settings in deltas are more prone to environmental stress than distal ones, as they are frequently subjected to turbidity and salinity fluctuations (e.g. MacEachern & Bann 2020; 2022). As previously demonstrated, even though trilobites did colonize deltas and estuaries during the Early Ordovician (Mángano *et al.* 2021), their diversity increased further away from terrestrial influences (Serra *et al.* 2021). Salinity and turbidity stresses are also detrimental to animals like echinoderms, which could explain why these organisms are very rare in the Cabrières Biota (Saleh *et al.* 2022c). The increase in diversity from proximal to distal settings may also be linked to taphonomic biases, as distal settings are more favourable for the preservation of labile anatomies than high-energy proximal sites. Distal settings are often richer in clays, which play a significant role in stabilising anatomies during decay. Some clays have antibacterial properties, while others can initiate the replication of soft tissues by minerals that are resistant over geological timescales (McMahon *et al.* 2016; Anderson *et al.* 2018; Saleh *et al.* 2019; Corthésy *et al.* 2024; 2025).

The rather low bioturbation intensity associated to the Cabrières Biota deposits (Gougeon *et al.* this issue) also suggests limited substrate oxygenation waters and/or high sediment supply, which likely aided in soft tissue preservation. Exceptional preservation seems to be limited to two specific sedimentary facies (F1 and F2), where trace-fossils analysis and the presence of microbially textured surfaces suggest anoxic to dysoxic conditions (Gougeon *et al.* this issue). Although the lack of oxygen is not enough on its own to guarantee exceptional fossil preservation, as some tissues decay faster under anoxic conditions than in the presence of oxygen (Hancy & Antcliffe 2020), anoxia can limit scavengers from recycling carcasses. Reducing conditions are also essential for the replication of certain anatomies by minerals like

pyrite (Gabbott *et al.* 2004; Saleh *et al.* 2020b; 2022a; El Khoury *et al.* 2025a; 2025b), which can, in turn, increase the preservation potential of soft tissues over geological time (Saleh *et al.* this issue).

In the deeper water environments of the Cabrières Biota, laminated mudstone occasionally displays millimetric to centimetric-thick normally graded very-fine to fine-grained sandstone layers (Figs 7, 11) and is associated with null to very low bioturbation levels (Gougeon *et al.* this issue). This suggests that a sustained and significant low-density sedimentary flux reached the prodelta/offshore to shelf environment (Bhattacharya & MacEachern 2009; Boulesteix *et al.* 2022; Saleh *et al.* 2022c; Zavala *et al.* 2024; Biddle *et al.* 2025). These sedimentary fluxes were essential to bury the organisms and isolate them from the chemical conditions of the water column, as is often the case in other Lagerstätten (Collom *et al.* 2009; Gaines *et al.* 2012; 2024; Bath Enright *et al.* 2017; 2021; Muscente *et al.* 2017; Saleh *et al.* 2022c). For example, fast burial through storm- and gravity-flow deposits are also among the main factors for the exceptional preservation of the Early Ordovician Fezouata Biota in bathymetrically equivalent environments (Martin *et al.* 2016a; 2016b; Vaucher *et al.* 2016; 2017; Saleh *et al.* 2020c; 2021; 2022b). These sedimentary facies provide evidence of relatively high sedimentary flux in the system, linked to deltaic activity and likely enhanced by storm events (Fig. 11). Consequently, the loci of deposition that favoured exceptional preservation may have shifted geographically over time in response to river avulsion.

### *Tempo of burial?*

An interesting pattern in the Cabrières Biota is that most animals are fragmented (Saleh *et al.* 2024b; 2024c), suggesting they may have either suffered post-mortem decay on the seafloor before the arrival of burial material or been transported by sedimentary flows over prolonged distances. In deeper water settings (i.e. prodelta/offshore, shelf), only the most powerful events are capable of transporting sediment to bury organisms (Saleh *et al.* 2018; 2020c). This implies that, when animals die on the seafloor, they may remain exposed to decay processes until burial material arrives (Saleh *et al.* 2020a; 2021a; 2022d). To constrain the timing of post-mortem decay, a comparison with other sites exhibiting soft tissue preservation, such as the Fezouata Biota, will be necessary. Additionally, the Chengjiang Biota, which inhabited comparable environmental conditions to the Cabrières Biota, may provide valuable insights (Saleh *et al.* 2022b). Given the limited thickness of the event

beds observed in F1 and F2 (Table 1), it seems plausible that the animals were already dead on the seafloor before burial (e.g. Saleh *et al.* 2021a; 2022b; 2024a). Otherwise, the animals would likely have been able to escape sediment burial and form fugichnia, which was not observed. However, this hypothesis still requires further testing. Due to the scope of this study, we were unable to investigate the effects of transport on preservation, such as whether carcasses are found within or beneath obrution deposits.

## Conclusion

The Lower Ordovician (Floian; F12–F13) Cluse de l'Orb, Foulon, and Landeyran formations were investigated for their sedimentological and stratigraphical content. The detailed analysis of these strata allows for a refined interpretation of the depositional environment, which has generally been regarded as a storm-dominated platform. In this study, we show that, in addition to the storm influence, river processes also played a significant role and were the dominant processes in several intervals of the stratigraphical succession. These river processes are primarily evidenced by traction and gravity flow-related sedimentary structures, such as proximal to distal turbidites in shallow-marine settings, as well as evidence of mouth bar deposits in more proximal settings. With the variable influence of storms recorded throughout the sections, and most notably recognized through the presence of hummocky cross-stratified sandstone, either as isolated or amalgamated beds, we propose that the sedimentary successions record the expression of a wave-influenced delta. Consequently, the recently discovered Cabrières Biota inhabited a wave-influenced delta, with exceptional preservation of fossils occurring in the deeper water prodelta/offshore-to-shelf environments. Research into the mechanisms and modes of preservation of the Cabrières Biota is still in its early stages, with this study serving as a cornerstone for subsequent, more detailed taphonomic investigations.

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