

CHONDRITES-CLADICHNUS ICHNOCOENOSIS FROM THE DEEP-SEA DEPOSITS OF PIERFRANCESCO (CRETACEOUS; ITALY): OXYGEN- OR NUTRIENT-LIMITED?

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Abstract. The Italian Northern Apennines are acknowledged as the place where ichnology was born, but there is comparatively little work about their ichnological record. This study bridges this gap by describing two new ichnosites from the locality of Pierfrancesco, which preserve an abundant, low-disparity trace-fossil assemblage within the Late Cretaceous beds of the M. Cassio Flysch. Results show that lithofacies and ichnotaxa are rhythmically organized. The base of each cycle consists of *Megagraption*-bearing calciclastic turbidites, which are overlain by marlstone beds with an abundant, low-disparity assemblage of trace fossils. This includes *Chondrites intricatus*, *C. patulus*, *C. targionii*, *C. recurvus* and *Cladichnus fischeri*. The cycle top consists of mudstones with no distinct burrows. The rhythmic pattern of Pierfrancesco reflects a deep-sea ecological succession, in which species and behaviour changed as turbidite-related disturbances altered the seafloor. This study opens the question of whether the *Chondrites-Cladichnus* ichnocoenosis represents low-oxygen or nutrient-poor settings.

INTRODUCTION

“The hills around Parma and Piacenza show abundant molluscs and bored corals still attached to the rocks”.

Leonardo da Vinci (ca. 1505)

The Northern Italian Apennines is regarded as the cradle of palaeontology (Baucon 2009,

2010). Here, on the hills between Parma and Piacenza, certain peasants collected bored fossil shells and brought a huge bagful of them to Leonardo da Vinci. Leonardo used borings (bioerosional trace fossils) to demonstrate the biological origin of the fossil shells, at a time when body fossils were considered sports of nature. As such, Leonardo da Vinci established a line of continuity between the two main branches of palaeontology – body fossil palaeontology and ichnology (Baucon 2009, 2010). Da Vinci focused also on fossil burrows (bioturbational

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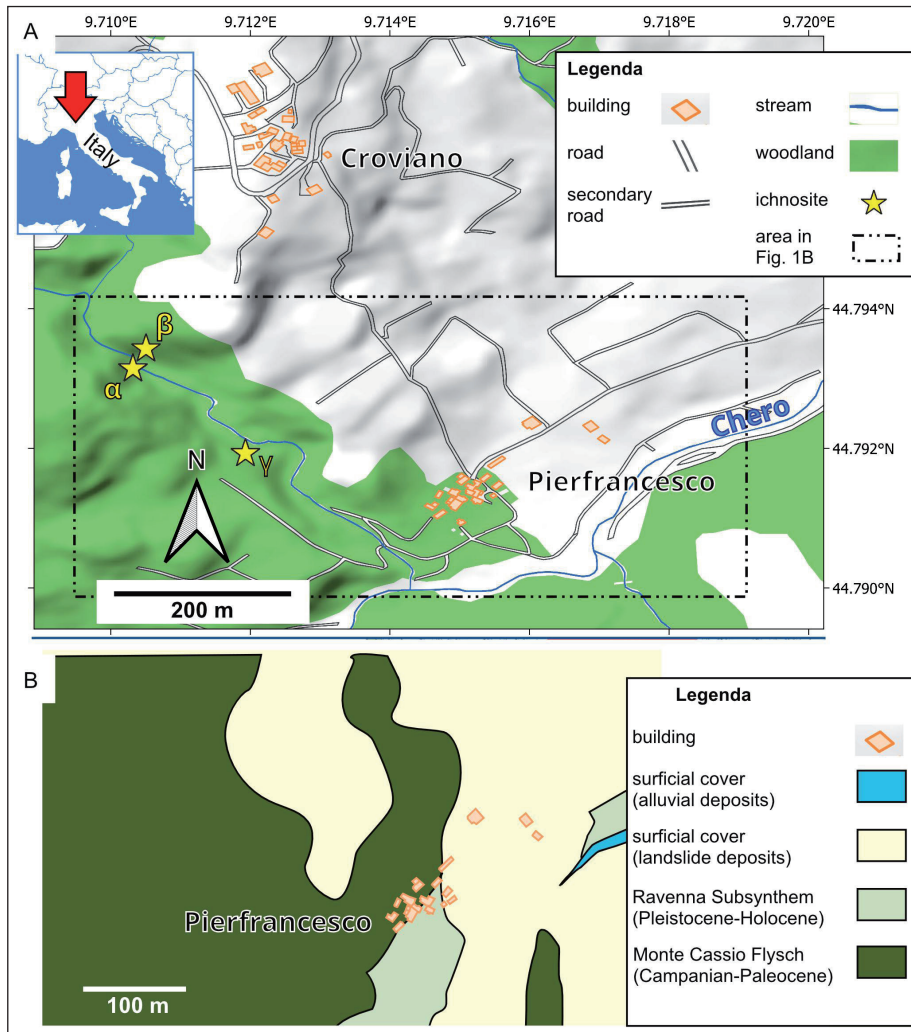


Fig. 1 - Geographic and geologic setting of the ichnosites at Pierfrancesco. A) Geographic setting of the Pierfrancesco ichnosites (α , β and γ). B) Geologic setting, based on geological maps of Regione Emilia-Romagna (2020a, 2020b, 2020c) and original field survey.

trace fossils), although he did not specify the locality where he studied them. However, it is plausible that Leonardo observed the burrows of the Apennines flyschs (Baucon 2010), some of which are so rich in trace fossils to be collectively known as ‘Helminthoid Flysch’ (see Conti et al. 2020).

It is therefore to some extent surprising that the trace fossils of the Northern Apennines are incompletely studied. Remarkably few studies have been designed to analyse the trace fossils of the area between Parma and Piacenza, which has been recognized as an ichnologically-rich territory since the Leonardo da Vinci times. Exceptions include the Pliocene-Pleistocene deposits in the Piacenza surroundings (Uchman & Pervesler 2007; Pervesler & Uchman 2009; Pervesler & Uchman 2009; Pervesler et al. 2011; Crippa et al. 2018), whereas there is virtually no ichnological work about the ‘Helminthoid Flysches’ of the Piacenza Apennine. Localities rich in trace fossils have been studied in the Liguria region (Uchman 2007a, 2007b; Uchman

& Rattazzi 2016, 2018) which is however outside of the area between Parma and Piacenza cited by Leonardo.

This study aims to fill this gap by describing the ichnological content of the Helminthoid Flysch outcropping at Pierfrancesco, a small locality located between Parma and Piacenza. The objectives of this work are describing the trace fossil suites and interpreting the depositional environment.

GEOLOGICAL SETTING

The trace fossil-rich area is located in the surroundings of Pierfrancesco, a village in the North Italian Apennines located 30 km south of Piacenza and 50 km north of Parma. Three major ichnosites are documented (α , β and γ in Fig. 1). Here, trace fossils are found in the scree derived from vertical cliffs, belonging to the Late Cretaceous M. Cassio Flysch.

The M. Cassio Flysch pertains to the Helminthoid Flysch of the Northern Apennines, which is an informal group of geological units named after the abundance of trace fossils (see Conti et al. 2020). The Helminthoid Flysch was deposited in the Piedmont-Ligurian Ocean, a small oceanic basin that opened in the Jurassic and closed in the Eocene (Marroni et al. 2002). The calcareous nanofossil biostratigraphy shows that flysch sedimentation started during the late Campanian and ended between the Palaeocene and Middle Eocene (Daniele & Plesi 2000). The compilation of igneous, sedimentary, and metamorphic geochronological data of the past 300 Ma shows that there is no magmatic record of subduction initiation and closure of the Piedmont-Liguria ocean in the Alps, i.e., the closure of rift basins forming the Piedmont-Liguria ocean did not follow a classical Wadati-Benioff-type subduction (McCarthy et al. 2018).

The deposition of the Helminthoid Flysch is related to the Adria microplate, a Gondwana-derived terrane that drifted northward to collide with Europe (Jacobs et al. 2018). In the Late Cretaceous, Europe started to subduct underneath Adria, resulting in the formation of the Alps during Oligocene-Miocene continental collision; to the south, the Adria plate subducted underneath the Corsica-Sardinia block of the Europe plate, resulting in the Apennines (Jacobs et al. 2018). The Helminthoid Flysch pertains to the part of the Ligurian-Piedmont Ocean close to the continental margin of the Adria microplate, which corresponds to the External Ligurian Domain of the Ligurian Units (Conti et al. 2020). In other words, the Helminthoid Flysch represents the infilling of an oceanic trench during plate convergence (Vescovi et al. 1999).

The M. Cassio Flysch consists of a more than 1500 m thick succession of distal turbidites, Campanian-Palaeocene in age (Di Dio et al. 2005). It comprises grey marlstones alternating with thin sandstone layers and marly-silty clays (Di Dio et al. 2005). Mud-rich turbidites have a SW provenance, whereas sand-rich turbidites arrived from the NW (Vescovi et al. 1999). The hemipelagic horizons of the M. Cassio Flysch are devoid of calcium carbonate and calcareous forams, for which reason the depositional environment has been interpreted as deeper than the carbonate compensation depth (CCD) (Sagri & Marri 1980; Vescovi et al. 1999).

MATERIAL AND METHODS

The Pierfrancesco ichnosites were investigated in 2013 and 2020. Georeferenced field pictures were taken using a Nikon AW150 camera. Bioturbation intensity has been quantified using the bioturbation index (BI) (Taylor & Goldring 1993), which however has the shortcoming of using unequally distributed degrees (Knaust 2021). Percent of bioturbation is also reported, using the percent categories of Knaust (2021) because of their linear distribution. Morphometric measurements have been performed on 43 burrow branches, which have been selected for their excellent preservation. The measured parameters include (1) branch width; (2) branch length, i.e., the distance between the tip of a branch and the closest branching point; (3) total dichotomous angle, i.e., the angle of dichotomy formed by a pair of adjacent branches; (4) root angle, that is the angle between the lowest-order branch (root) and one of its child branches. These parameters have been previously discussed in Baucon et al. (2020a) for *Chondrites*. The measured values are presented in Table 1.

Rock specimens were collected and deposited at the Natural History Museum of Piacenza. All specimens were photographed using a DSLR camera (Canon EOS 1100D) equipped with a Canon Zoom lens 18/55 mm f 1:3.5-5.6 and a Sigma Macro lens 105 mm f 1:2,8. The photography setup included a Durst M301 stand with micrometric slide, four 10W led lamps and a cold light source (Starlight LED 3). Information about each specimen (i.e., ichnogenus, ichnospecies, author, collector, locality, stratigraphical unit, storage unit and image) was entered in a Visual dBase-supported database. To date, the database records information about 249 specimens and 30 ichnogenera from the Piacenza territory. Every specimen is associated with a unique ID number (e.g., NHMP#229), to which we refer in this article.

FACIES OF THE M. CASSIO FLYSCH AT PIERFRANCESCO

The logged section consists of a turbidite succession with a total thickness of about 40 m (Fig. 2A). The succession exhibits three lithofacies, which are typically arranged in a rhythmic, fining-upward pattern (Fig. 3). Each cycle typically consists of calciclastic turbidites (facies CC) at the base, white marlstone (facies WM) in the middle part, and dark blue-grey mudstones (facies DBG) at the top. Occasionally, the WM facies is lacking.

Calciclastic turbidites (CC turbidites)

Description. Normally graded thick and very thick-bedded (up to 1.5 m) turbidites (Fig. 2B) showing a thin, medium-grained sandstone followed by a few centimetres-thick, fine-grained sandstone interval, with even lamination, grading into a thick interval of white silty marlstone (WB beds). The most ubiquitous sedimentary structure is horizontal lamination. It is very rarely displayed in the basal parts and is much more common in the higher

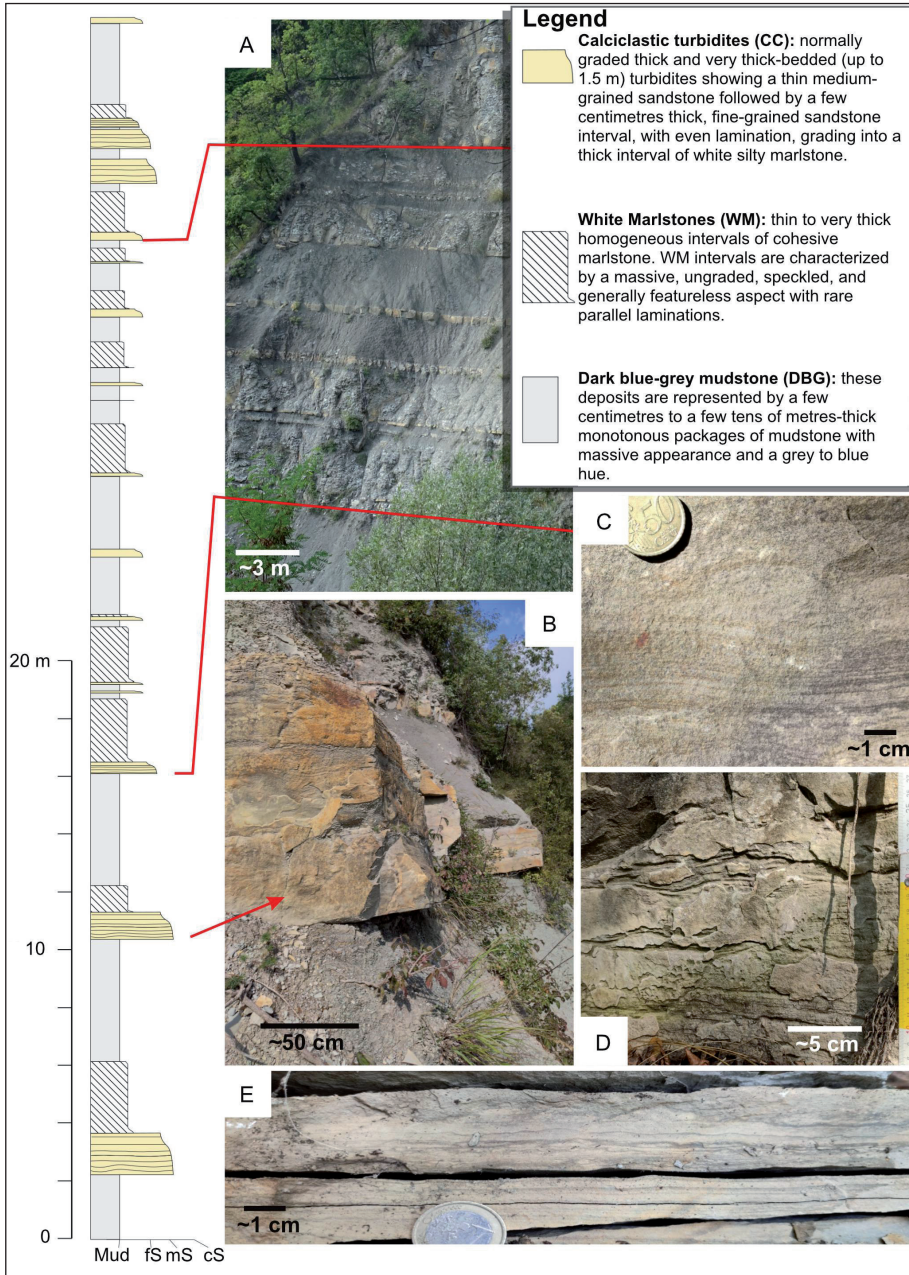


Fig. 2 - The Pierfrancesco section. The location of the stratigraphic section corresponds to the ichnosite β in Fig. 1. A) Exposure of the Pierfrancesco section and correlation within the measured sedimentological log. B) Medium-grained, very thick calciclastic turbidite showing a massive sandstone followed by a few cm thick, fine-grained sandstone interval, with even lamination, grading into a thick interval of white silty marlstone (WB beds). C) Small-scale undulated lamination. D) Small-scale ripple lamination. E) Rare parallel laminations observed in WM (white marlstones) beds. Laminae are arranged in centimetre- to decimetre-thick stacks of alternating fine silt and clayey silt. Primary sedimentary structures are partly destroyed by moderate but relatively continuous bioturbation.

finer grained parts of almost all beds. Small-scale undulated lamination is found (Fig. 2C). Ripple lamination is widespread (Fig. 2D). Most of the cross-lamination is poorly developed rarely being over 3 cm per set. These bedded turbidites are petrographically characterized by a lithic QFL (quartz-feldspar-lithic fragments) mode with the Rock Fragments population dominated by carbonate grains.

Interpretation. Massive and graded lower divisions are here interpreted as deposits of the most concentrated underflow, while the upper divisions showing traction and traction-plus-fallout structures were probably deposited by a turbulent overflow (F8-F7 of Mutti 1992).

White marlstone (WM)

Description. This facies consists of thin to very thick homogeneous intervals of cohesive white marlstone. It overlies in sharp vertical transition the CC turbidites and pass abruptly to dark blue-grey mudstone intervals (DBG mudstone) toward the top, from which they can be distinguished by their texture, lighter colour (Fig. 2A), greater carbonate content (25% to 45). Our observations indicate that the WM intervals are characterized by a massive, ungraded, speckled, and generally featureless aspect with rare parallel lamination from 0.2 mm to 1.0 mm in thickness (Fig. 2E). Laminae can also

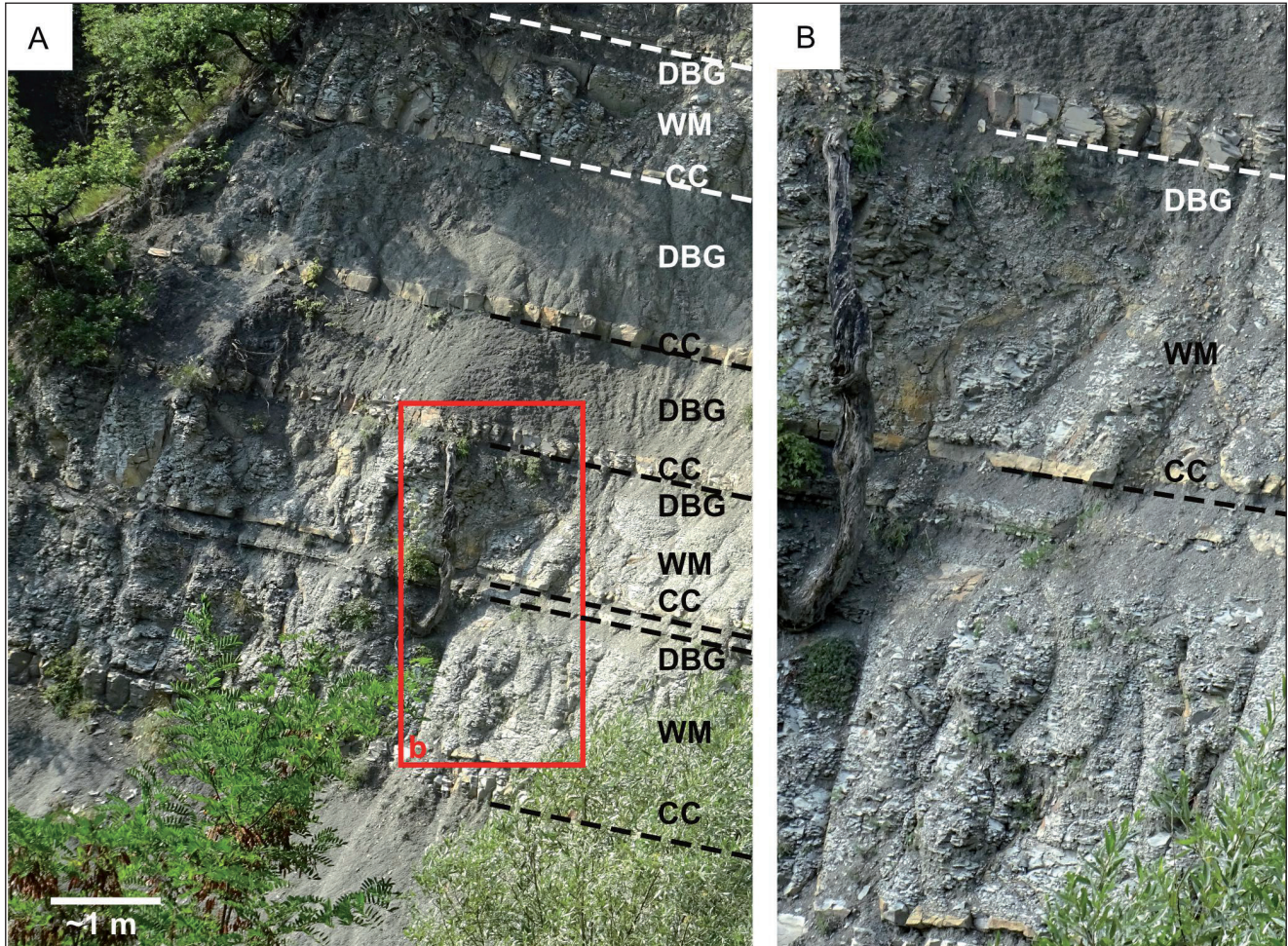


Fig. 3 - Rhythmic organization of the Pierfrancesco sedimentary succession. A) Rhythmical stacking pattern. The dashed line shows the base of each cycle. Facies are indicated by CC (calciclastic turbidites), WM (white marlstones), DBG (dark blue-grey mudstones). The 'b' rectangle indicates the area photographed in B. B) Close-up of A showing a typical CC-WM-DBG cycle.

be arranged in centimetre- to decimetre-thick stacks of alternating fine silt and clayey silt. The carbonate content of the WM intervals is represented chiefly by planktonic foraminifera and coccoliths, and rare benthic foraminifera.

Interpretation. The WM intervals could have been derived from the settling of suspension clouds produced from waning turbidity currents (hemiturbidites *sensu* Stow & Wetzel 1990; homogenites *sensu* Mulder et al. 2009). During a turbidity-current event, thick and relatively diluted turbulent flows could have detached from the basal and denser part of the flow along an axial flow path. A turbidite origin implies that the flows, after dropping the heavier terrigenous load, began depositing lighter particles, e.g., abundant carbonate shells such as coccoliths and other hydraulically-equivalent clay-size carbonate particles and phyllosilicates. This indicates that the WM intervals

may have resulted from hydraulic sorting of the finer and lighter particles toward the upper part of the flow.

Dark blue-grey mudstone (DBG mudstone)

Description. These deposits are represented by a few centimetres to a few tens of metres-thick monotonous packages of mudstone with massive appearance and a grey to blue hue (Fig. 2A), intercalated by rare millimetric very-fine sandstone and siltstone beds. Bioturbation structures are almost absent (bioturbation intensity 10%, i.e., B1 = 1), especially compared to what is observed in the WM deposits (bioturbation intensity 30-50%, i.e., BI = 2-3). The sedimentary packages comprised of these DBG mudstone are laterally continuous across the outcrop area, thereby separating subsequent turbidite beds.

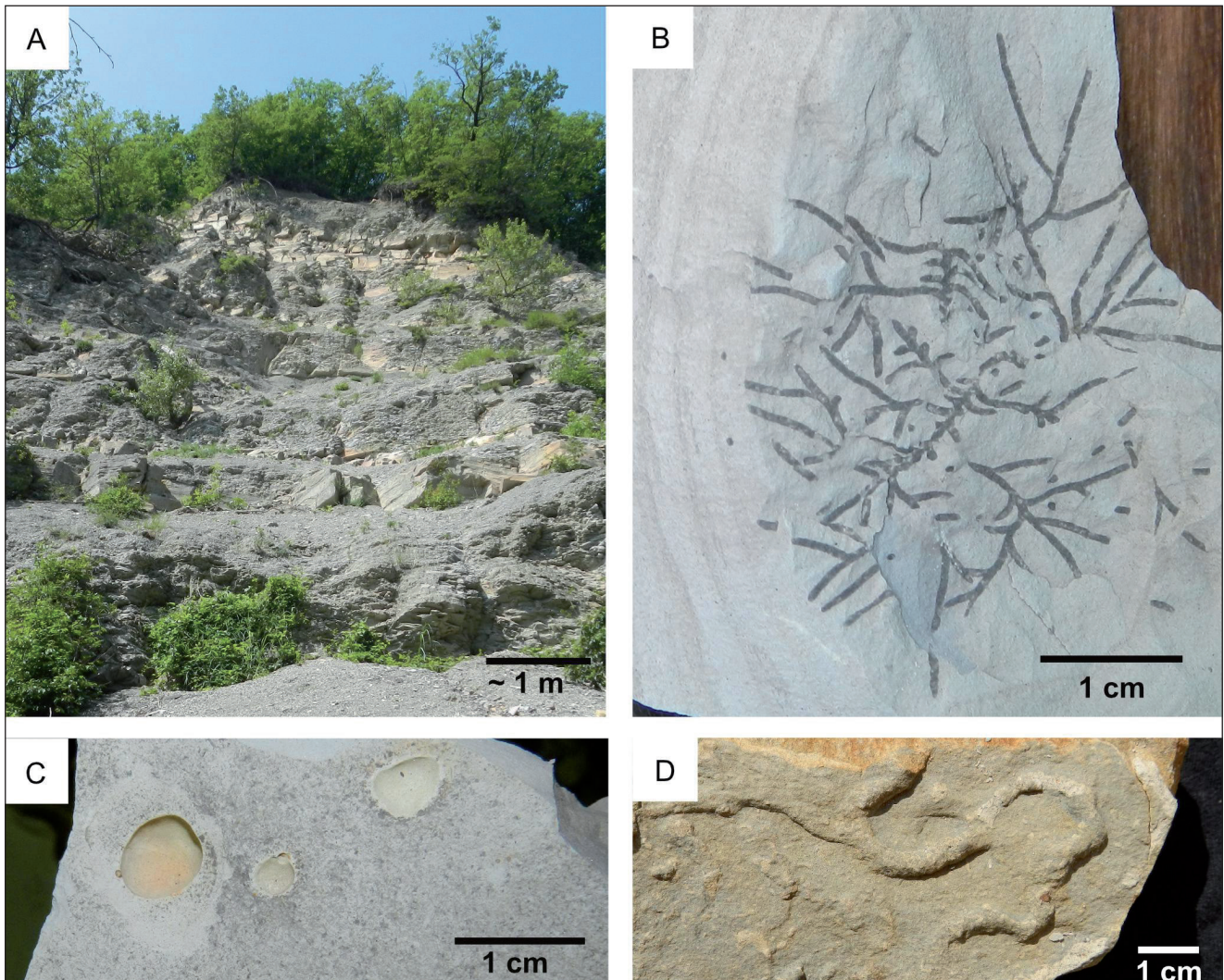


Fig. 4 - Geological and ichnological features of the study area. A) Vertical cliff showing alternating marlstone and sandstone layers. The approximate height of the cliff is 30 m. B) Laminated marlstone with *Chondrites intricatus* preserved as full relief. The specimen has been retrieved from scree material, therefore bedding polarity is unknown. C) Possible weathered nodules. The specimen has been retrieved from scree material, therefore bedding polarity is unknown. D) Sandstone with a specimen of *Megagraption* isp. preserved as hyporelief.

Interpretation. These mudstones are interpreted to be dominated by continued hemiplegic fall-out or, alternatively, they could represent the distal product of dilute turbidites.

TRACE FOSSILS

The trace fossil-bearing outcrops of Pierfrancesco consist of light-coloured marlstones (WM intervals) alternating with decimetric sandstone layers (CC turbidites; Fig. 4A). Mudstone layers (DBG mudstone) usually do not display bioturbation structures. Marlstones can be laminated and preserve full-relief burrows (Fig. 4B). They frequently comprise millimetric spherical depressions, at times filled

by limonitic sediments (Fig. 4C). These depressions plausibly represent weathered nodules or, alternatively, body fossils. Sandstone layers preserve hyporelief trace fossils (Fig. 4D). The Monte Cassio Flysch at Pierfrancesco includes six ichnospecies, belonging to the ichnogenera *Chondrites*, *Cladichnus* and *Megagraption*. Overall, bioturbation intensity is low, typically ranging from BI = 0 (no bioturbation) to BI = 2 (5–30% of the bedding plane/parting surface disrupted).

Chondrites intricatus (Brongniart, 1823)

Fig. 4B, 5

Description. Branching tunnel system forming a dendritic network; the dichotomous branching angle is typically less than 50° (Table 1). The network

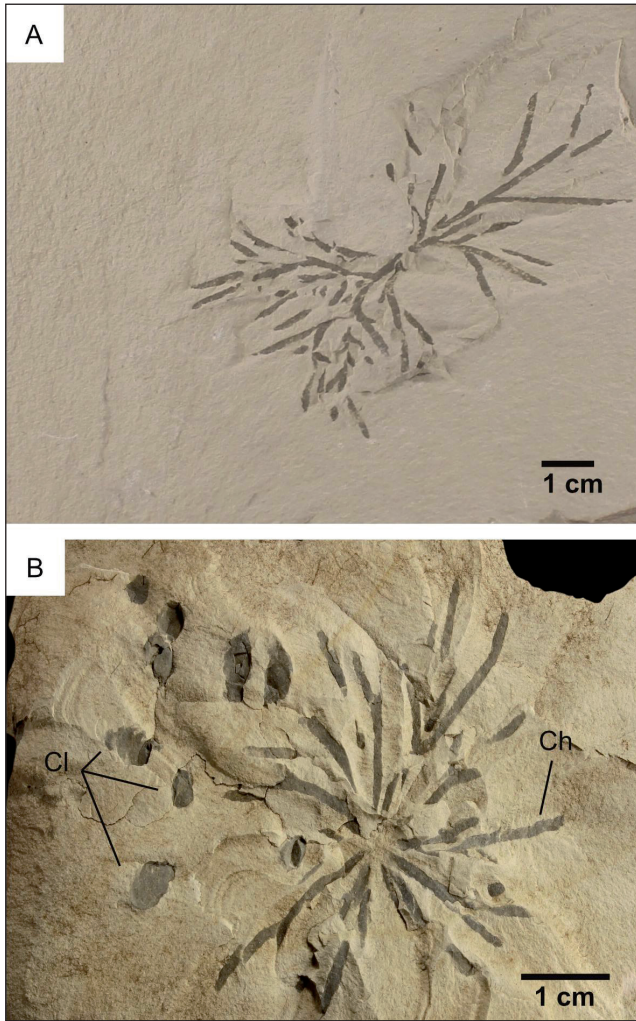


Fig. 5 - *Chondrites intricatus*. A) Specimen NHMP#200. B) Association between *Chondrites intricatus* (Ch) and *Cladichnus fischeri* (Cl). Specimen NHMP#62.

appears to be constrained by the horizontal plane, but this is likely to be an artifact due to compaction. Burrow fill contrasting with the host rock. Average burrow width is 1.0 mm.

Facies. WM intervals.

Remarks. The studied trace fossils fit with the recently revised diagnosis of *Chondrites* (Baucon et al. 2020a), including dendritic networks of regularly branching tunnel systems. Specifically, they fit with *C. intricatus* because of the branching angle less than 45° (Uchman 1998) (Fig. 5A). At Pierfrancesco, *C. intricatus* is the only ichnospecies of *Chondrites* known to occur together with *Cladichnus fischeri* (Fig. 5B, C). The colour contrast between the fill and the host rock apparently indicates an active fill, but it should be noted that *Chondrites* presents a wide variety of fill microtextures, which were produced in a passive or active manner (Baucon et al. 2020a).

Ichnospecies	Branch width (mm)			Branch length			Length/width ratio			Angle ($^\circ$) (dichotomous angle: d; root angle: r)			
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Circular mean	Max	N
<i>Chondrites intricatus</i>	0.5	1.0	1.5	2.6	13.7	28.8	4.3	14.6	23.3	7	d: 47.8	d: 64	d: 6
<i>Chondrites patulus</i>	0.4	0.5	0.6	3.4	9.0	14.6	6.6	18.0	28.5	6	d: 54.5; r: 70	d: 63; r: 87	d: 2; r: 2
<i>Chondrites targionii</i>	3.2	4.6	5.7	25.3	29.7	34.0	4.5	5.7	7.0	2	d: 77; r: 54*	d: 77; r: 54	d: 1; r: 1
<i>Chondrites recurvus</i>	0.7	1.1	2.2	3.8	10.6	16.1	5.0	10.0	19.5	6	r: 50	r: 62.1	r: 7
<i>Cladichnus fischeri</i>	2.7	3.1	3.6	17.4	19.0	20.6	6.1	6.3	6.5	4	d: 46	d: 46	d: 1
<i>Megagraption isp.</i>	0.7	1.6	4.3	-	-	-	-	-	-	-	-	-	-

Tab. 1 - Morphometric parameters. Width and length refer to leaf branches, i.e., branches with no child branches.

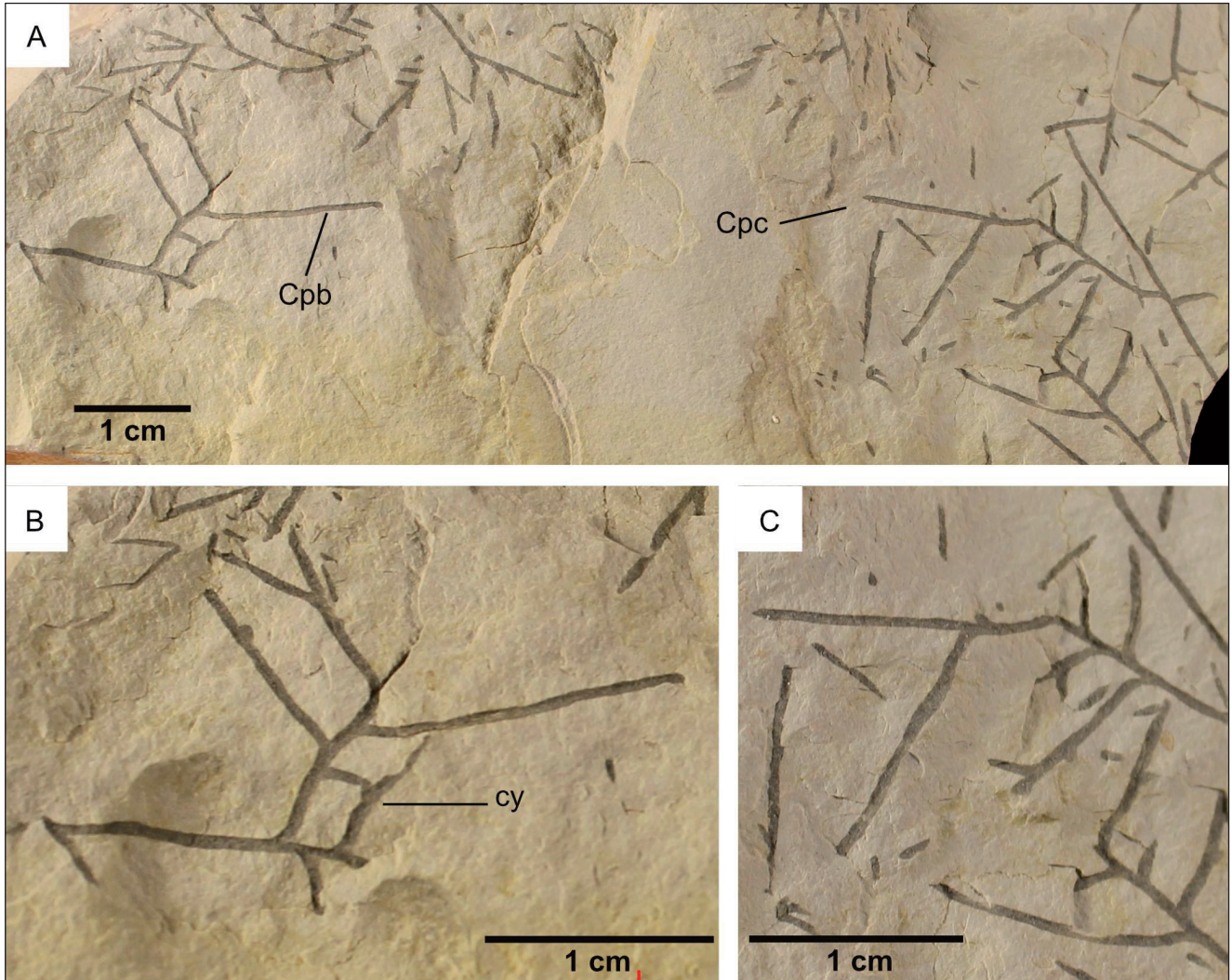


Fig. 6 - *Chondrites patulus*. A) Specimen NHMP#35. Arrows point to the specimens detailed in B (Cpb) and C (Cpc). B) Detail of A showing a cycle (cy) (l). C) Detail of A.

Chondrites patulus Fischer-Ooster, 1858

Fig. 6

Description. Branching tunnel system with long tunnels forming wide ($>50^\circ$) angles. Branch width is typically sub-millimetric (average: 0.5 mm; Table 1). The tunnels are usually slender, being on average 18 times longer than wide (Table 1).

Facies. WM intervals.

Remarks. The studied burrow shares its major features with *Chondrites patulus*, formed by long and straight tunnels branching at an obtuse angle with the main branch (Uchman 1998; Baucon et al. 2020a). *Chondrites* can be modelled as a network consisting of a set of nodes (branching points and tips) and links (branches). *Chondrites* typically does not form cycles ('loops') that are sequences of adjacent links starting and ending at the same node (Baucon et al. 2020a).

However, one specimen of *C. patulus* from Pierfrancesco forms a cycle, which is interpreted to be due to behavioural (true branching) factors (Fig. 6B). It should be noted that compressed tunnels on close levels may look like fused. Besides the specimen of Pierfrancesco, the only observed cyclic *Chondrites* is another specimen of *C. patulus* (Uchman 2007a, fig. 2F). This may suggest that the presence of occasional cycles is characteristic of *C. patulus*.

Chondrites recurvus (Brongniart, 1828)

Fig. 7

Description. Branching tunnel system with curved branches only at one side of the master branch. Master branches can be radially arranged. Branch width ranges between 0.7 and 2.2 mm (Table 1).



Fig. 7 - *Chondrites recurvus*. A) *C. recurvus* (Chr) associated with *C. intricatus* (Chi) and *C. targionii* (Cht). Specimen NHMP#61. B) *C. recurvus* (Chr) showing radial arrangement of branches. Detail of branch (br) is provided in C. Specimen NHMP#58. C) Master branch with branching at only one side. Detail of B.

Facies. WM intervals.

Remarks. The studied burrows share their major features with the ichnogenus *Chondrites*, recently emended by Baucon et al. (2020a). Branching only at one side is characteristic of *Chondrites recurvus* (Uchman 1998; Seilacher 2007).

Chondrites targionii (Brongniart, 1828)

Fig. 8

Description. Branching tunnel system with dichotomous branches. Only one order of branching is observed. Branches are relatively wide (up to

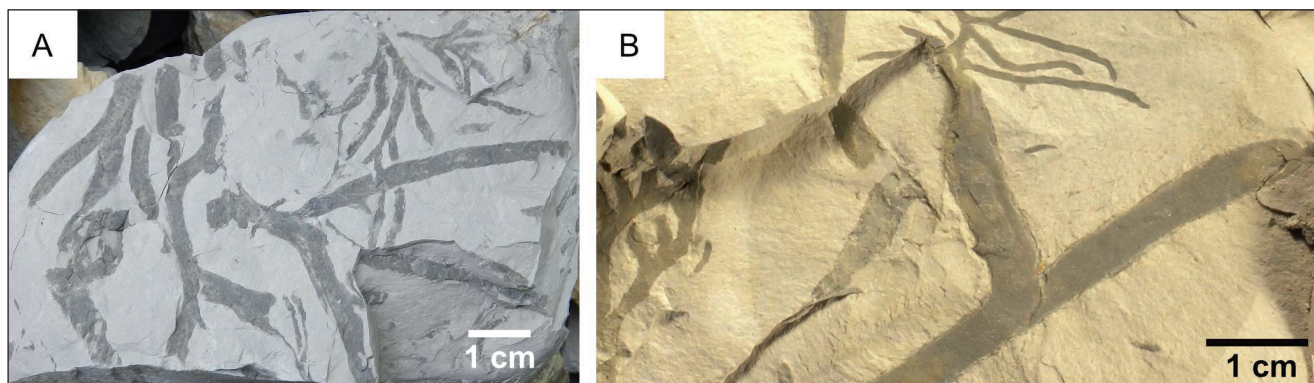


Fig. 8 - *Chondrites targionii*. A) Field photograph showing numerous specimens. B) Specimen NHMP#61. For an overview of the specimen see Fig. 7A.

5.7 mm; Table 1) compared to other ichnospecies of *Chondrites* from Pierfrancesco (e.g., the widest branch of *C. patulus* is 0.6 mm).

Facies. WM intervals.

Remarks. The studied burrows share their major features with *Chondrites targionii*, being characterized by well-expressed primary branches, often curved (Uchman 1999).

Cladichnus fischeri (Heer, 1877)

Fig. 5B,C; Fig. 9

Description. Branched, radial burrow systems consisting of annulated or moliniform (i.e., resembling a string of beads) tunnels. Tunnels are unlined and consist of meniscate packets (Fig. 9A-D). Fill is darker than the host rock and, occasionally, consisting of distinct faecal pellets of millimetric size (Fig. 9E, F). One order of branching is documented. The width of the tunnels within each burrow system is consistent and, on average, is 3.1 mm (Table 1). Branches are usually 6 times longer than wide (Table 1). The burrow is associated with *Chondrites intricatus*, but not to other ichnospecies of *Chondrites*.

Facies. WM intervals.

Remarks. This burrow system is assigned to the ichnogenus *Cladichnus*, with which it shares branched geometry, moliniform or annulated tunnels, and the absence of lining (Wetzel & Uchman 2013). *Cladichnus* comprises four ichnospecies, which are characterized by the centre of radiation being (1) within the branching plane (*C. radiatum*), (2) above the branching plane (*C. fischeri*), (3) absent (no centre of radiation; *C. parallelum*), (4) and showing tangentially-arranged pellets (*C. aragonen-*

sis). *Cladichnus lusitanicum* (Neto De Carvalho et al., 2016a) is better assigned to the ichnogenus *Hillichnus* because it is composed of a series of lined tubes curving upward into a nearly vertical position by branching from the basal tube (Knaust 2017, fig. 5.63; see also Bromley et al. 2003). The centre of radiation of the Pierfrancesco specimens is above the branching plane, thus they correspond to *C. fischeri*.

Megagraption submontanum (Azpeitia Moros, 1933)

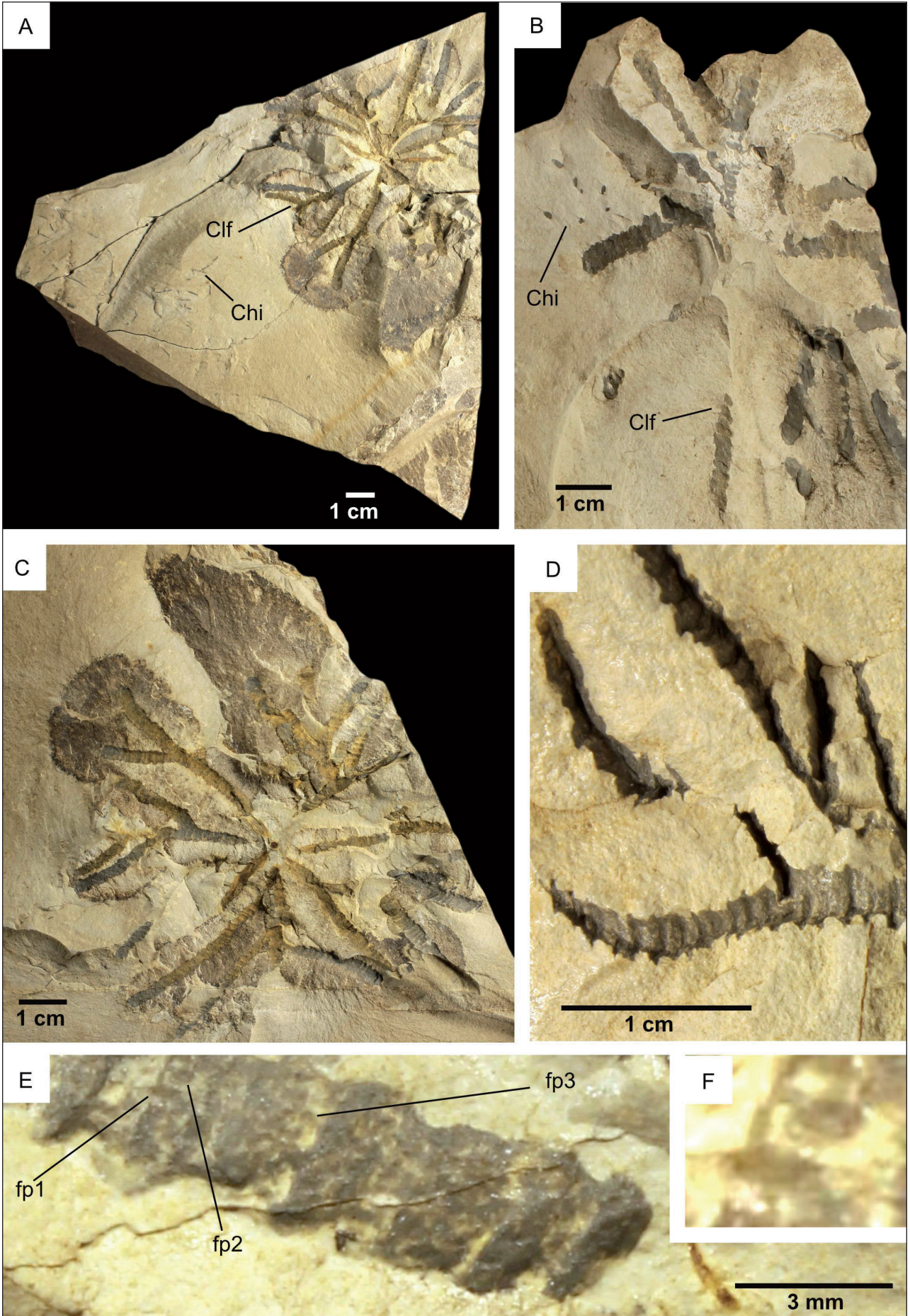
Fig. 4D, Fig. 10

Description. Branched, horizontal burrow network consisting of winding tunnels. The fill contrasts in colour with the host rock and appears enriched in iron oxides with respect to the host rock. Branch width can be as wide as 4.3 mm, but typically it is smaller (average: 1.6 mm; Table 1).

Facies. WM, CC facies.

Remarks. *Megagraption* comprises an irregular net with meshes bordered by slightly winding strings that branch at nearly right angles (Wetzel et al. 2007; see Uchman 1998 for more taxonomic details). *Megagraption* is rarely found at Pierfrancesco, occasionally in association with *Chondrites intricatus*.

Fig. 9 - *Cladichnus fischeri*. A) *C. fischeri* (Clf) associated with *Chondrites intricatus* (Chi). Specimen NHMP#69. B) *C. fischeri* (Clf) with *C. intricatus* (Chi). Specimen NHMP#62. C) *C. fischeri*. Specimen NHMP#63. D) Detail of *C. fischeri*. Specimen NHMP#168. E) Faecal pellets (fp1-3) in the fill of *C. fischeri*. Specimen NHMP#168. F) Detail of E showing the faecal pellets fp1 and fp2. Contrast and brightness have been increased to improve visibility of the structures.



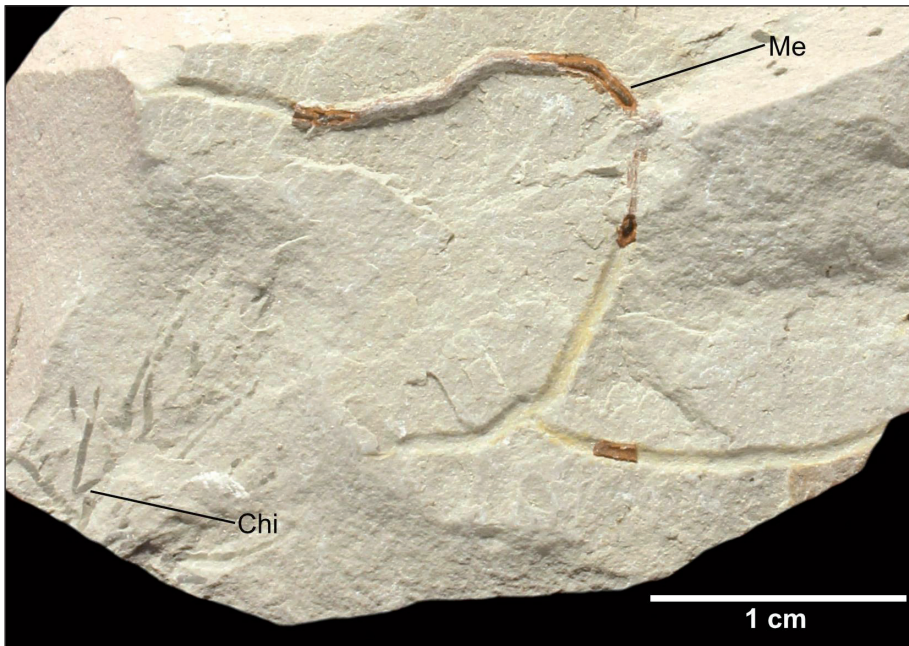


Fig. 10 - *Megagraption* (Me) associated with *Chondrites intricatus* (Chi).

DISCUSSION

The ichnosites at Pierfrancesco are intrinsically important for their scientific, historical, cultural value. The importance of the studied ichnoassemblage is primarily given by its geodynamic and ecological setting, that is, an oceanic trench palaeoenvironment (see Vescovi et al. 1999 for a geodynamic framework). Modern trenches are ecologically poorly known because they are poorly sampled, therefore our knowledge of ecological structure and functioning of this environment remains rudimentary (Jamieson et al. 2010). This increases the importance of the ichnoassemblage at Pierfrancesco, providing insight into the ecology of a Cretaceous trench.

The importance of the Pierfrancesco ichnosites relies also in its astrobiological potential. Oceanic trenches are extreme environments (Jamieson 2011; Nagano & Nagahama 2012; Coker 2019), therefore, they can help to define the boundaries for the search of life in the Universe (see Amils et al. 2007; Rotschild 2007; Preston & Dartnell 2014; Merino et al. 2019). For these reasons, astrobiologists strive to obtain biological information from such environments (Martins et al. 2017; George 2020), which are however logistically difficult to access. By contrast, the Pierfrancesco ichnosites allow direct observation of a fossil trench ecosystem. The importance of Pierfrancesco is also heightened by the fact that ichnology is a

new frontier in astrobiology (Baucon et al. 2017).

Moreover, the ichnosites at Pierfrancesco are found in the area where ichnology was born, therefore they are inherently important localities offering not only insights into the evolution of the Earth, but also potential information on the history of science. This view fits into the definition of *Geoheritage* (Brocx & Semeniuk 2007) and is supported by recent works on the *Geoheritage* value of trace fossils (Neto de Carvalho 2011, 2014; Francischini et al. 2015; Martínez-Graña et al. 2016; Baucon et al. 2020c;).

It should be noted that the studied ichnoassemblage does not represent an ichnocoenosis, that is, an ecologically pure assemblage of trace fossils (Bromley 1996). In fact, an assemblage of trace fossils comprises all the trace fossils occurring within a single unit of rock (Baucon et al. 2015), but it can represent more than one community of organisms. This is the case of the ichnoassemblage at Pierfrancesco, which comprises either pre- or post-depositional suites of trace fossils. According to Książkiewicz (1954), Kern (1980) and Bromley (1990), these terms are used especially for semi-relief trace fossils occurring on soles of turbidites and storm beds. A pre-depositional suite corresponds to trace fossils that were emplaced in a background mud prior to a sudden erosion or depositional event and thus, frequently show erosional features; the burrow is cast on the sole of the sand unit. A post-depositional suite

Ichnocoenosis	Ichnotaxa	Intensity of bioturbation	Pre-depositional or post-depositional?	Environment
<i>Megagraption</i>	<i>Megagraption</i> , <i>Chondrites intricatus</i> ?	BI = 1 ($\leq 10\%$)	Pre-depositional	Oligotrophic abyssal plain
<i>Chondrites</i>	<i>Chondrites intricatus</i> , <i>C. patulus</i> , <i>C. recurvus</i> , <i>C. targionii</i>	BI = 2-3 (30-50%)	Post-depositional	Dysoxic and/or oligotrophic abyssal plain
<i>Chondrites-Cladichnus</i>	<i>Chondrites intricatus</i> , <i>Cladichnus fischeri</i>	BI = 2 (30%)	Post-depositional	Dysoxic and/or oligotrophic abyssal plain

Tab. 2 - Ichnocoenoses of Pierfrancesco. Intensity of bioturbation is reported using BI (Taylor and Goldring, 1993) and the percent categories of Knaust (2021).

was formed after an erosive or freshly deposited turbidites, so frequently the trace fossils are well preserved and intersect a pre-depositional suite (Książkiewicz 1954; Kern 1980; Bromley 1990; Buatois & Mángano 2011; Uchman & Wetzel 2011).

Three ichnocoenoses can be observed at Pierfrancesco (Table 2): (1) *Megagraption* ichnocoenosis, (2) *Chondrites* ichnocoenosis, (3) and *Cladichnus-Chondrites* ichnocoenosis. Their ecology is evaluated by first grouping ichnotaxa based on the inferred behaviour, trophic group and tier (ichnoguild approach; Bromley 1996), and then evaluating the environmental significance of ichnological properties (bioturbation intensity, diversity, disparity, among others).

Megagraption ichnocoenosis

The *Megagraption* ichnocoenosis at Pierfrancesco is dominated by the mesh-like burrow *Megagraption*. The assemblage represents the activity of shallow tier, agrichnial stationary organisms. In fact, *Megagraption* represents a graphoglyptid, a class of ornamental, highly-patterned trace fossils interpreted as microbial gardens (agrichnia) (Bromley 1996; Uchman & Wetzel 2011). *Megagraption* is a typical pre-depositional trace fossil that was produced prior to turbidite sedimentation (Uchman & Wetzel 2011). In general, pre-depositional traces may be preserved in full relief in background mud or convex hyporeliefs on event-bed soles (Savrda 2007). At Pierfrancesco, both cases are represented by *Megagraption*, which is preserved as full relief in marly facies and as hyporelief on sandstone beds. Simple *Planolites*-like trace fossils are associated with *Megagraption*, although their fragmentary nature precludes a sound taxonomic attribution. Further studies are needed to confirm the pres-

ence of *Planolites* because of the fragmentary nature of the *Planolites*-like burrows at Pierfrancesco.

Ichnological characteristics of the *Megagraption* ichnocoenosis suggest a deep-sea environment characterized by hydrodynamically quiet, oligotrophic conditions. In fact, the low diversity of trace fossils dominated by a single patterned dwelling net occupying a shallow tier, suggest poor conditions like low food supply and redox discontinuity close to the water bottom interface limiting the permanent occupation of the substrate (Crimes et al. 1981; Uchman 2007c; Wetzel & Uchman 2007). Low-diversity suites can indicate environmental stress or taphonomical processes (Bromley 1996; Gingras et al. 2011; Buatois & Mángano 2013; Baucon et al. 2015; Neto de Carvalho et al. 2016b). The presence of pre-depositional traces preserved in full relief (*Megagraption*) is suggestive of the stress hypothesis because it implies that the mixed layer was poorly bioturbated. In fact, in the case of intense shallow-tier bioturbation, graphoglyptids would have been obliterated by bioturbation itself. This interpretation relies on the traditional assumption that graphoglyptids are shallow-tier structures (e.g., Buatois et al. 2017).

Megagraption is rare at Pierfrancesco. Calciturbidites commonly lack graphoglyptids and other pre-depositional traces that are common in siliciclastic turbidites (Savrda 2012) because turbidity currents carrying carbonate mud may be less energetic than those transporting siliciclastics (Uchman 2007a). This is explained by the fact that particles of the marly oozes consist mostly of coccospheres and foraminifer tests, having a much higher buoyancy than siliciclastic grains (Uchman 2007a). Consequently, calciturbidites lack the erosive power to exhume, cast and preserve graphoglyptids (Uchman 2007a).

***Chondrites* ichnocoenosis**

The *Chondrites* ichnocoenosis typically includes *C. intricatus*, *C. patulus* and/or *C. recurvus*, whereas *C. targionii* is rare. This ichnocoenosis represents the activity of deep-tier, deposit feeding and/or chemosymbiotic stationary organisms. This interpretation is supported by several lines of evidence: first, *Chondrites* is typically depicted as a deep-tier burrow, colonizing the transition- and the historical-layer (Savrda 2007). It can penetrate previously deposited beds, being a typical post-depositional trace fossil, produced after turbidite deposition (Uchman 2007a; Uchman & Wetzel 2011). Second, the trace makers built *Chondrites* to obtain food (Baucon et al. 2020a): (1) vermiform deposit feeders produced *Chondrites* searching for food in the sediment (fodinichnion), (2) asymbiotic bivalves built *Chondrites* for cultivating and directly ingesting bacteria (agrichnion), (3) and chemosymbiotic bivalves produced *Chondrites* to provide symbionts with chemical agents (agr-ichnion: chemichnion). At present, there are no morphological means to attribute a given specimen of *Chondrites* to one of the aforementioned behavioural classes. However, it should be highlighted that chemosymbiotic thyasirid bivalves have been observed near the bottom of the Japan Trench (7326 m deep) (Fujikura et al. 1999), which is a geodynamic setting compatible with that of the Helminthoid Flysch (Vescovi et al. 1999). The Japan Trench is not a perfect parallel of the trench of the Helminthoid Flysch, which deposited in a smaller oceanic basin with abundant sedimentary input (Marroni et al. 2002). Notwithstanding the differences, this is an intriguing parallel because thyasirid bivalves have been proposed as the trace makers of *Chondrites* (Fu 1991; Bromley 1996; Baucon et al. 2020a). The small size of *C. intricatus* is comparable with that of *Parathyasira* burrows (fig. 17 in Baucon et al. 2020a), although this does not falsify the hypothesis of a worm-like producer for *Chondrites*. Further studies on *Chondrites* are required to test this hypothesis.

The ichnological characteristics of the *Chondrites* ichnocoenosis reflect a stressful, hydrodynamically quiet basin plain. In fact, low-diversity assemblages (e.g. *Chondrites*-*Zoophycos* ichnoguild) or monogeneric *Chondrites* assemblages are a good proxy for dysoxic porewater, i.e. dissolved oxygen between 0.2 and 1 ml/l (Bromley & Ekdale 1984;

Knaust 2017; Baucon et al. 2020a). An apparent single tier with a simple historical layer is characteristic of *Chondrites* oxygen-related ichnocoenosis (Wetzel & Uchman 2012). Although *Chondrites* is commonly associated with organic-rich, dysoxic settings (Boyer et al. 2014; Bednarz & McIlroy 2015; Neto de Carvalho et al. 2016c), it should be noted that its producer also tolerated nutrient-poor environments (Wetzel & Uchman 2001).

***Chondrites*-*Cladichnus* ichnocoenosis**

This assemblage is dominated by *Chondrites intricatus* and *Cladichnus fischeri*, representing the work of typically deep-tier, deposit feeding and chemosymbiotic animals. Together, three characteristics of *Cladichnus* indicates that the burrow has been actively filled by the trace maker: (1) meniscate fill; (2) colour contrast with the host rock; (3) darker colour of the burrow fill, suggesting a richer content of organic matter, therefore, a possible faecal nature of the fill. Similar observations have been made by Wetzel & Uchman (2013).

The faecal nature is confirmed by the pellet-like fill observed in several specimens of *Cladichnus* at Pierfrancesco (Fig. 9E, F). Specifically, the fill of some specimens of *Cladichnus* consist of sub-millimetric ellipsoidal particles (Fig. 9E, F), which are interpreted as faecal pellets. A higher carbon content in the burrow fill than in the host rock may sound controversial because deposit-feeding trace makers ingest sediment and extract organic content from it during digestion. Accordingly, one might expect that excreta would be poorer in organic carbon than the ingested sediment, not richer. This paradox is explained as the result of selective uptake of organic-rich particulate matter as well by the refractory character of the ingested food (Wetzel & Uchman 2016; Baucon et al. 2020b). An additional explanation, which can be alternative or complementary to the previous one, is that organic matter may be better preserved within the burrow than outside. The texture fill appears to confirm the notion that *Cladichnus* is the result of selective surface deposit feeding (Wetzel & Uchman 2013) and/or bacterial harvesters. The occurrence at Pierfrancesco also supports the observation by Uchman (2011) that *C. fischeri* is restricted to marly sediments. In this regard, it should be noted that *Cladichnus* is especially common in WM intervals, which are in-

terpreted as hemiturbidites *sensu* Stow and Wetzel (1990). Accordingly, *Cladichnus* colonized deposits resulted from hydraulic sorting of the finer and lighter particles (e.g., coccoliths and clay-size carbonate particles), therefore a question might arise: Did the *Cladichnus* producer colonize hemiturbidites because of trophic or substrate preferences? At present, we do not have enough data to prefer one hypothesis over the other.

The *Chondrites-Cladichnus* ichnocoenosis represents the work of a community colonizing a stressful deep-sea trench. There is indeed wide agreement that diverse trace-fossil suites record optimal environmental conditions, whereas low ichnodiversity indicates environmental stress (Gingras et al. 2011; Buatois & Mángano 2013; Baucon et al. 2015; Neto De Carvalho et al. 2016b). Low ichnodiversity can also reflect taphonomical processes, as result of stable conditions promoting the establishment of deep-tier climax communities (Bromley 1996; Buatois & Mángano 2013). However, no evidence (e.g., climax trace fossils) in this regard has been observed at Pierfrancesco. Rather, the low ichnodiversity is interpreted to reflect oxygen-depleted environments, which are suggested by the occurrence of *Chondrites* in low-diversity assemblages (Bromley & Ekdale 1984; Knaust 2017; Baucon et al. 2020a). However, it should be noted that *Chondrites* is also associated to nutrient-poor settings (Wetzel & Uchman 2001), therefore oligotrophy can also explain the low ichnodiversity.

Chondrites and *Cladichnus* are unlined and probably originated in a deep-tier stiff substrate. Although exceptions are known (e.g., softground *Planolites*), it is generally agreed that the presence of a lining is commonly related to shifting substrates, whereas deep-tier ichnogenera, and particularly those in compacted (dewatered or stiff) sediment typically lack linings (Gingras et al. 2011). Based on this interpretation, the specimens of *Chondrites* and *Cladichnus* at Pierfrancesco colonized deep-tier stiff substrates. *Chondrites* is typically depicted as a transition- and historical-layer trace (Savrda 2007), thus supporting this interpretation. Unfortunately, no cross-cutting relationships have been observed between the different ichnotaxa, hence it is not possible to exactly reconstruct the tiering pattern. According to Uchman (2007a: fig. 12), *Chondrites* penetrated deeper than *Cladichnus fisheri*

into the sediment. This interpretation is also supported by the ichnodisparity viewpoint. Whereas ichnodiversity refers to ichnotaxonomic richness, ichnodisparity is a measure of the variability of morphological plans in biogenic structures (Buatois & Mángano 2013). The concept of ichnodisparity centres on the definition of categories of architectural designs (Buatois et al. 2017), according to which the Pierfrancesco ichnoassemblage comprise 1-2 categories. In fact, in their paper about architectural designs in trace fossils, Buatois et al. (2017) attributed *Cladichnus* and *Chondrites* to different architectural categories, namely “Radial to rosetted structures” and “Burrows with shaft or bunch with downwards radiating probes”. It should be noted that, at a coarser morphological resolution, both traces are branched radial burrows.

The occurrence of *Chondrites* and *Cladichnus* at Pierfrancesco is not an isolated case. In fact, this associated occurrence is frequently reported from the Cretaceous (e.g. Kropivnik Fucoïd Marls, Poland: Leszczyński 2004; Monte Antola Formation, Italy: Uchman 2007a; San Bartolomeo Formation near Sanremo, Italy: Baucon et al. 2020a, fig. 7C; and the Eocene (e.g. Scisti Varicolori, Italy: Checconi 2008), and may be tracked back at least to the Middle Ordovician (Neto de Carvalho et al. 2016c). This encourages further studies on the evolutionary and palaeoenvironmental significance of this recurring association of trace fossils.

Ecological succession in a deep-sea trench: oxygen- or nutrient-limited?

The ichnosites at Pierfrancesco show a alternating stacking pattern of lithofacies and ichnocoenoses. The base of each cycle consists of calciclastic turbidites (facies CC) with trace fossils of the *Megagraption* ichnocoenosis preserved on the lower bedding planes. This interval is overlain by White marlstone (facies WM) with the *Chondrites* and/or *Chondrites-Cladichnus* ichnocoenoses preserved as full reliefs. The top of each cycle is represented by dark blue-grey mudstones (facies DBG) with no distinct burrows.

This rhythmic pattern is interpreted to reflect the change in the species structure, behaviour, and physico-chemical parameters over time. Specifically, the *Megagraption* ichnocoenosis reflects the interval of time prior to turbidite deposition,

as it is implied by its hyporelief preservation. The fact that the graphoglyptid *Megagraption* is found as a semi-relief at the base of turbiditic sandstone beds (Fig. 4D; facies CC) indicates that the corresponding burrows have been scoured and casted by turbidity currents. *Megagraption* is also preserved in full-relief, indicating its post-depositional occurrence (Fig. 10).

This interpretation is supported by Uchman and Wetzel (2012), suggesting that during the long periods between the deposition of successive turbidites the slowly deposited background sediment is colonized by the producers of graphoglyptids. The preservation of the graphoglyptid burrows clearly indicate that the *Megagraption* ichnocoenosis was followed by turbidite deposition, whereas the overlying facies WM represents the deposits of the suspension clouds produced from waning turbidity currents. *Phycosiphon* and *Nereites* are expected to be followed by graphoglyptids if the porewater is sufficiently oxygenated (Wetzel & Uchman 2001; Uchman & Wetzel 2012), but this is not the case of the Pierfrancesco ecological succession. Turbidites normally import considerable amounts of organic matter from shallower areas and, when just deposited, they are fully oxygenated (Wetzel & Uchman 2001). Accordingly, the abundance of nutrients favours opportunistic deposit feeders, whereas oxygenated porewaters allow the establishment of burrows with no connection to the oxygenated seafloor. These strategies are typically represented by *Phycosiphon* and *Nereites* (Uchman & Wetzel 2012). However, the Pierfrancesco ichnoassemblage partially departs from this model because it does not comprise *Phycosiphon*, *Nereites* or other horizontal trace fossils with no connection to the seafloor, besides possible *Planolites*-like horizontal burrows. This implies that the newly deposited turbidites of Pierfrancesco were nutrient- and/or oxygen-poor, being colonized by the trace makers of the *Chondrites-Cladichnus* ichnocoenosis.

The *Chondrites* ichnocoenosis probably reflects a further impoverishment in oxygen and/or nutrients, which excluded the *Cladichnus* trace maker from the seafloor community. In fact, pore water of newly deposited turbidites is well-oxygenated; successively, the lower part of newly deposited turbidites becomes dysoxic because oxygen consumption exceeds oxygen replacement by

diffusion, whereas on the seafloor, organic matter is oxidized while exposed to the more oxygenated bottom water (Wetzel & Uchman 2001). Either a low-oxygen or a low-nutrient scenario would have been unfavourable for the producer of *Cladichnus*, which is a surface deposit feeder (Wetzel & Uchman 2013). By contrast, the trace makers of *Chondrites* are extremotolerant, capable of colonizing nutrient-poor layers (Wetzel & Uchman 2001) and environments with oxygen levels well below levels needed for survival of other animals (Savrda & Bottjer 1986, 1989; Baucon et al. 2020a;). Finally, the *Chondrites* ichnocoenosis was followed by the *Megagraption* one, which represents the return to the normal background conditions of the basin plain.

To date, we cannot establish whether low nutrient levels (Fig. 11) or low oxygen levels were the major ecological control in the palaeoenvironment. It is tempting to apply known oxygenation models (Savrda & Bottjer 1989; Martin 2004), according to which low-diversity assemblages dominated by *Chondrites* correspond to dysoxic porewaters. However, it should be noted that oceanic trenches are often characterized by a limited food supply and an oxygenated seafloor (Jamieson et al. 2010; Jamieson 2011). This interpretation is supported by the light colour of WM intervals, which suggests a low content in organic carbon. In general, the grey-black colour spectrum is controlled by the total organic carbon content, i.e., the lighter the colour, the lower the organic carbon content (Myrow 1978). It should be noted that oxidative loss of carbon is non-reversible (i.e., lighter colours with time; Myrow 1978), therefore the colour-based estimate of TOC provides only a lower constraint to the original organic matter content of WM intervals. Specifically, diagrams relating rock colour and organic carbon (Myrow 1978, figs. 1, 2; Potter et al. 1980, fig. 1.25; Sandberg & Gutschick 1984, fig. 15) suggest a 0-0.3% content in organic carbon for the WM intervals.

Therefore, a question might arise: Do *Chondrites* and *Cladichnus* reflect behavioural adaptations to low food supply? To answer this question, more research in modern and fossil trenches is needed. In addition, ethology of *Cladichnus* should be better constrained, testing the hypothesis that its tunnels filled with organic matter represented a food cache in an oligotrophic environment (sequestrichnia model of Wetzel & Uchman 2016).

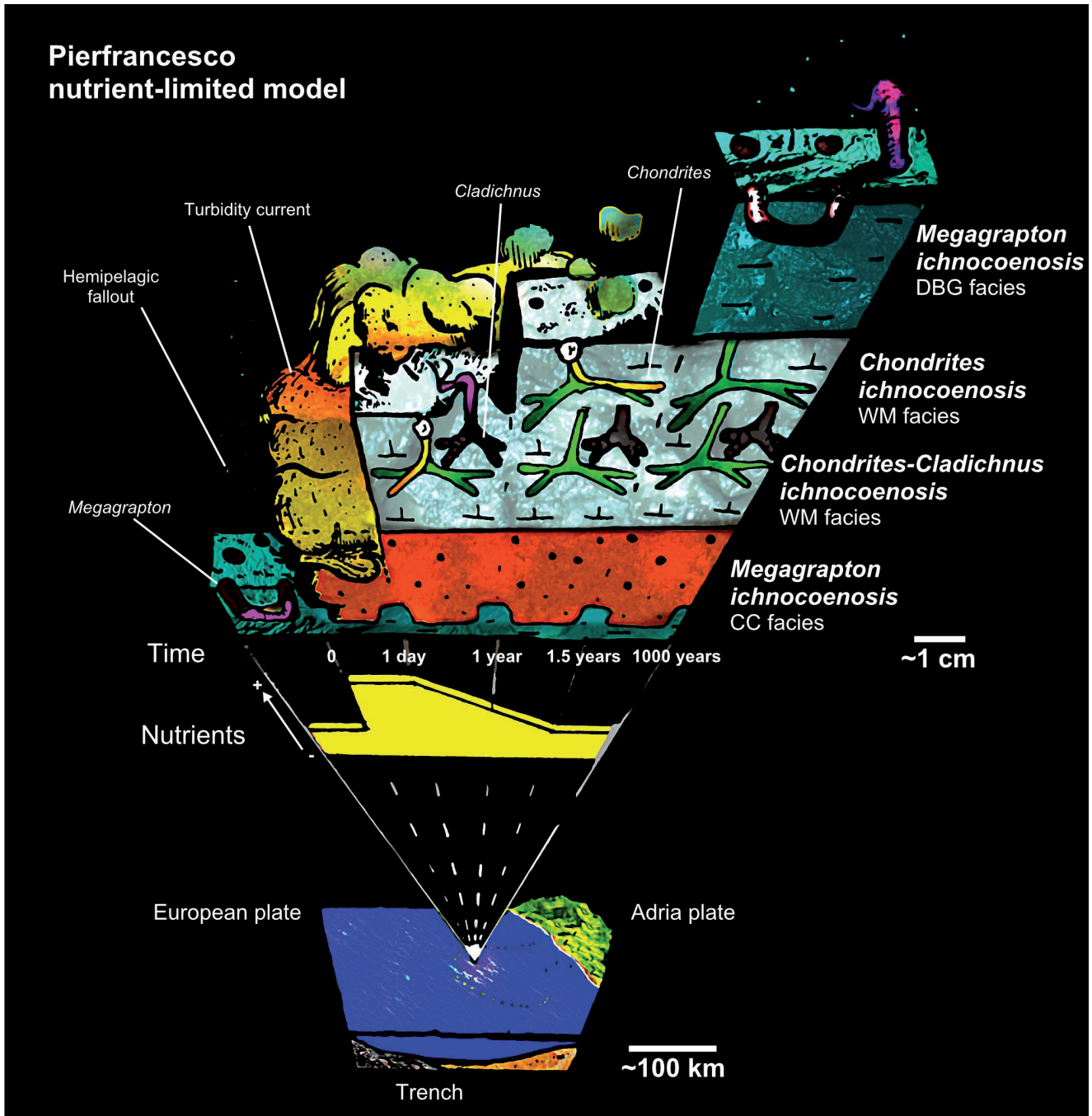


Fig. 11 - Nutrient-limited model explaining the rhythmic organization of ichnoassemblage observed at Pierfrancesco. The ichnocoenoses are stacked on the top of each other, e.g., the *Chondrites* ichnocoenosis is stacked on the top of the *Chondrites-Cladichnus* ichnocoenosis.

CONCLUSIONS

An ichnoassemblage from the Monte Casio Formation at Pierfrancesco is described for the first time. It contains trace fossils belonging to three well-defined ichnogenera and their ichnospecies, which are *Megagraption* isp., *Chondrites intricatus*, *C. patulus*, *C. targionii*, *C. recurvus* and *Cladichnus fischeri*. This ichnoassemblage is interpreted to represent a trench environment characterized by

low oxygen and/or nutrient levels. As such, the ichnoassemblage at Pierfrancesco represented the activity of organisms colonizing a deep-sea extreme environment, being particularly informative for constraining the range of what might be regarded as a habitable environment beyond Earth. Further studies on the astrobiological potential of the Pierfrancesco trace fossils are therefore required. The ichnoassemblage is rhythmically organized, representing an ecological succession in which

species and behaviours changed as turbidite-related disturbances modified the seafloor ecosystem. The graphoglyptid *Megagraption* characterized the time intervals between deposition of successive turbidites, whereas the producers of *Chondrites* and *Cladichnus* colonized hemiturbidites under decreasing oxygenation and/or nutrient levels. In this regard, this study raised the question of whether the *Chondrites-Cladichnus* ichnocoenosis represented oxygen-poor or low-nutrients settings. Previous work indicates that *Chondrites* and *Cladichnus* are recurrently associated, suggesting the application of this ichnocoenose as a palaeoenvironmental proxy. Consequently, this study encourages further ichnological investigations on *Chondrites-Cladichnus* associations in order to decipher a more precise palaeoenvironmental significance of this association.

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