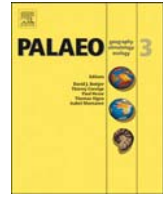




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Life in near-anoxic conditions: A case study of the ichnology and infaunal ecology of Silurian graptolitic black shales from Sardinia, Italy

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ABSTRACT

A trace fossil assemblage from the Silurian (Llandovery) black shales of the Genna Muxerru Formation is reported for the first time. The ichnofossil record is abundant, well-preserved and comprises *Alcyonidiopsis*, *Cochlichnus*, *Phymatoderma*, *Planolites* (large morphotype), *Planolites* (rough morphotype) and a 'Small chondritid'. Sedimentological and ichnological evidence indicates that the bioturbated black shales were deposited in outer shelf (or deeper) settings with severe depletion in oxygen. The seafloor provided a high food supply for the infauna. The palaeoenvironment of the Genna Muxerru Formation is an ancient analogue of modern oxygen-minimum zones. Burrow fills are apparently massive in macroscopic view, whereas observations under the petrographic and stereoscopic microscope show that a lifestyle dominated, i.e. that of pellet-filling sediment-feeders. As such, the Genna Muxerru Formation provides not only a new ethologic reference for low-oxygen settings but also a methodological benchmark for ichnological analysis of black shales. Bioturbation in black shales may be commoner than expected but its recognition requires microscopic observation.

1. Introduction

One of the basic tenets of biology is that animals require oxygen for their metabolic processes (Diaz and Rosenberg, 1995). Marine benthos displays stressed behaviours when oxygen falls below ≤ 2 ml of O_2/l (hypoxia), culminating in mass mortality when dissolved oxygen declines below 0.5 ml of O_2/l (Diaz and Rosenberg, 2008). As such, the rise or expansion of hypoxia and anoxia represent major perturbations to the structure and functioning of modern coastal marine ecosystems (Chan et al., 2008). One of the biological processes that is most intensely influenced by oxygenation is bioturbation, i.e. the process by which organisms rework sediments (Frey and Pemberton, 1985; Sturdivant et al., 2012). In fact, the 0.2 ml O_2/H_2O boundary marks the disappearance of infaunal bioturbators in modern sediments (Tyson and Pearson, 1991; Buatois and Mángano, 2011).

The fossil record mirrors these observations about modern ecosystems. Diversity of trace fossils and intensity of bioturbation decreases with decreasing oxygenation (Bromley and Ekdale, 1984; Savrda and

Bottjer, 1986; Savrda, 1992; Buatois and Mángano, 2011). Oxygen depletion evidence is not only indicated by trace fossils, but also by lithofacies. In this regard, the most iconic low-oxygen facies is represented by dark, laminated and organic-rich mudrocks known as black shales (Föllmi, 2012).

Black shale is a dark-coloured mudrock containing organic matter and silt- to clay-size mineral grains that accumulated together (Tourtelot, 1979; Swanson, 1961; see also Meyer and Kump, 2008). Most shales that meet this colour criterion contain 1% or more organic carbon; 2–10% is a common range (Tourtelot, 1979; Arthur and Sageman, 1994). Black shales are often laminated and characterized by impoverished benthonic faunas, or devoid of metazoan life (Arthur and Sageman, 1994). Following these authors, the most important constituent that differentiates black shales from other mudrocks is organic matter content, which is the major cause of the dark colour in black shales. However, the definition of black shale by organic content will always be arbitrary because of organic content loss during thermal maturation or metamorphism (Arthur and Sageman, 1994). Lamination

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is another fundamental characteristic of black shales but not all black shales are laminated (Arthur and Sageman, 1994).

The most extensive black shale deposits are the product of oceanic anoxic events (OAE), time intervals in which mid- and bottom-water masses became depleted in oxygen (Föllmi, 2012). It should be noted that although OAEs tend to generate black shales, black shales can form in very shallow-water environments as well as deeper environments that are prone to slow circulation and reoxygenation.

Based on this evidence, black shales are expected to be almost unbioturbated. Nevertheless, there are several examples of bioturbated black shales (e.g. Williams and Rickards, 1984; Arthur and Sageman, 1994; Schieber, 2003; Schieber, 2011; Boyer and Droser, 2009; Izumi, 2012; Neto de Carvalho et al., 2016). Bioturbated black shales contrast with the still widespread perception that black shales represent lifeless, anoxic ecosystems (Schieber, 2003). Here we report a novel example of bioturbated black shales from the Genna Muxerru Formation (Silurian; Sardinia-Italy). This case study is particularly significant because bioturbation in the Genna Muxerru Formation can be easily overlooked at the macroscopic scale, but finer scale observations reveal abundant and well-preserved trace fossils.

The goal of this study is to reconstitute the Genna Muxerru palaeoecosystem by answering the following research questions: (a) What are the ichnotaxa of the black shales of the Genna Muxerru Fm.? (b) How did life thrive in the low-oxygen environments of the Genna Muxerru Fm.? (c) What was the depositional environment of the bioturbated black shales?

2. Materials and methods

Trace fossils were studied in a small outcrop (locality GMX-5 of Floris, 2009) located a few km west of Gonnosfanadiga village, in the northwestern flank of Genna Muxerru hill at coordinates 39°28'7.8" N, 8°37'27.1" E (elevation ~415 m; Fig. 1). Here, 36 samples were collected and labelled as GMX#1–36. Samples are housed in the DISTAV palaeontological collection at the University of Genova, Italy. Sample collection was accompanied by ichnological and sedimentological observations.

Rock samples were observed and photographed with a stereoscopic microscope (Konus Diamond 5450). Ten thin sections and ten polished slabs were prepared. One of the polished slabs (GMX#1) was cleaned by ultrasonic cleaning. Thin sections and polished slabs were first wetted with a water sprayer, then observed and photographed in reflected light using a Wild M3C stereoscopic microscope equipped with a Delta Pix Camera (DISTAV). Observation and photographing of thin sections in transmitted light were operated with Olympus BX51 polarizing microscope (DISTAV).

Micro-Raman measurements were conducted with a Horiba Jobin-

Yvon Explora.Plus spectrometer equipped with an Olympus BX41 confocal microscope at the University of Genova (DISTAV). Raman spectra were excited by the 532 nm line of a Nd-YAG solid state laser. The spectrometer was calibrated to the silicon Raman peak at 520.5 cm^{-1} . The instrumental spectral resolution is $\sim 2 \text{ cm}^{-1}$ while the instrumental precision in determining the peak position is approximately 0.5 cm^{-1} . This last value refers to the half of the spectral pixel-pixel distance, which depends from different instrumental factors including CCD detector array, groove density of monochromator gratings and excitation-light wavelength.

XRD scans were collected using a Philips PW1140 diffractometer at DISTAV. Samples were first ground in an agate mortar and then mounted on zero-background silicon plates. The diffractometer was equipped with a radiogenic tube with a Co anode (producing X-rays with a wavelength of 1.78901 Å), the current was set at 20 mA, the voltage at 40 kV. Each sample was scanned between 5° and 70° 2 θ with a step size of 0.02° 2 θ with an acquisition time of 1 s per step.

Qualitative and quantitative chemical analyses, backscattered electron (BSE) images and elemental maps were obtained using a scanning electron microscope equipped with an X-ray energy-dispersion analyser (Tescan Vega 3 LMU with EDAX Apollo X SDD). Operating conditions were: accelerating voltage of 20 kV, beam current of about 2 nA, beam diameter 320 nm, count rate 30 s. Natural and synthetic silicates and oxides were used as standards.

The bedding plane bioturbation index (BPBI) (Miller and Smail, 1997) was used to quantify bioturbation intensity along bedding planes. In other words, the approach consisted of estimating percentage of bedding-plane area bioturbated. The BPBI index consists of 5 categories, each of which indicate the surface area containing biogenic structures (1 = 0%, 2 = 0–10%, 3 = 10–40%, 4 = 40–60% and 5 = 60–100%). Ichnotaxa were classified at the ichnogenus level; morphotypes have been used to distinguish between distinct size classes of the same ichnogenus.

In this paper, we use the oxygenation terms of Table 1, which is based on previous works (Brenchley and Harper, 1988; Buatois and Mángano, 2011; Algeo and Li, 2020).

3. Geological setting

During the middle Palaeozoic Sardinia represented a terrane within the assemblage of the north Gondwana margin known as the Armorican Terrane Assemblage (Torsvik and Cocks, 2013) or the Galatian Terranes (von Raumer and Stampfli, 2008). For a review and discussion of the paleogeographical position of Sardinia refer to Ferretti et al. (2009a). Different sequences are exposed in the southeastern and in the southwestern part of the island: these resemble the coeval sequences of Thuringia and Bohemia, respectively (Ferretti et al., 1998; Corradini and Ferretti, 2009; Corradini et al., 1998, 2009a). The studied area is located in southwestern Sardinia, where Silurian and lowermost Devonian rocks are among the best-known sediments of the whole Palaeozoic sequence of the island. However, despite the richness and the good preservation of the fossil material, outcrops are, in general, quite disappointing, since only a few meters of rocks, normally strongly tectonized, or a group of scattered blocks are exposed here and there, without any undisturbed sections (Barca et al., 1992; Corriga and Corradini, 2008; Corradini et al., 2009a; Ferretti et al., 2009b).

Two formations were formally described by Gnoli et al. (1990) in the Silurian of SW Sardinia: the Genna Muxerru Formation (Llandovery) and the Fluminimaggiore Formation (uppermost Llandovery-lowermost Lochkovian) (Fig. 2). The Genna Muxerru Fm. consists of about 20–25 m of graptolitic, silica-argillaceous and silty shales, interbedded with rarecherts in the lower part (Gnoli et al., 1990). Faulting, cleavage and small-scale folding characterize the whole unit. Graptolites are the only fossils reported (Štorch and Serpagli, 1993; Rickards et al., 1995; Štorch and Piras, 2009b; Floris, 2009, 2014), documenting several Llandovery biozones from the base of the Silurian

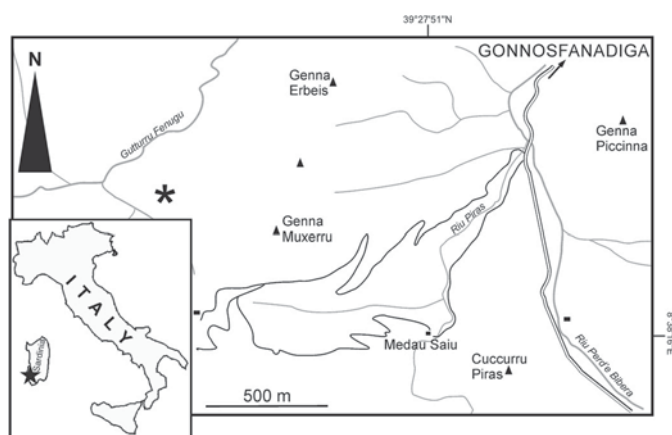


Fig. 1. Location map of the trace-fossil bearing outcrop (asterisk) in southwestern Sardinia. Star in the inset shows position of the study area.

Table 1

Oxygenation terms adopted in this paper. The table is after the reviews of [Brenchley and Harper \(1988\)](#), [Buatois and Mángano \(2011\)](#) and [Algeo and Li \(2020\)](#).

| ml O ₂ /l H ₂ O | Regime | Biofacies | Physiological regime | Reference | Notes |
|---------------------------------------|---------|-----------------|----------------------|--|--|
| 8.0 | Oxic | Aerobic | Normoxic | Tyson and Pearson (1991) | Rhoads and Morse (1971) used the term aerobic (fully oxygenated) to indicate oxygen levels in excess of 1.0 ml O ₂ /l H ₂ O |
| 2.0 | Dysoxic | Dysaerobic | Hypoxic | Tyson and Pearson (1991) | Rhoads and Morse (1971) used the term dysaerobic (poorly oxygenated) to indicate oxygen levels in excess of 1.0 ml O ₂ /l H ₂ O |
| 0.2 | Suboxic | Quasi-anaerobic | | Tyson and Pearson (1991) | The 0.2 ml O ₂ /l H ₂ O marks the disappearance of bioturbation |
| 0.0 | Anoxic | Anaerobic | Anoxic | Tyson and Pearson (1991) | Rhoads and Morse (1971) used the term anaerobic (anoxic) to indicate oxygen levels less than 0.1 ml O ₂ /l H ₂ O |
| - | Euxinic | - | - | Meyer and Kump (2008) | Euxinia is a state of a body of water characterized by the presence of free hydrogen sulphide. Although anoxia frequently evolves into euxinia, the term 'euxinic' primarily refer to toxic levels of hydrogen sulphide. |

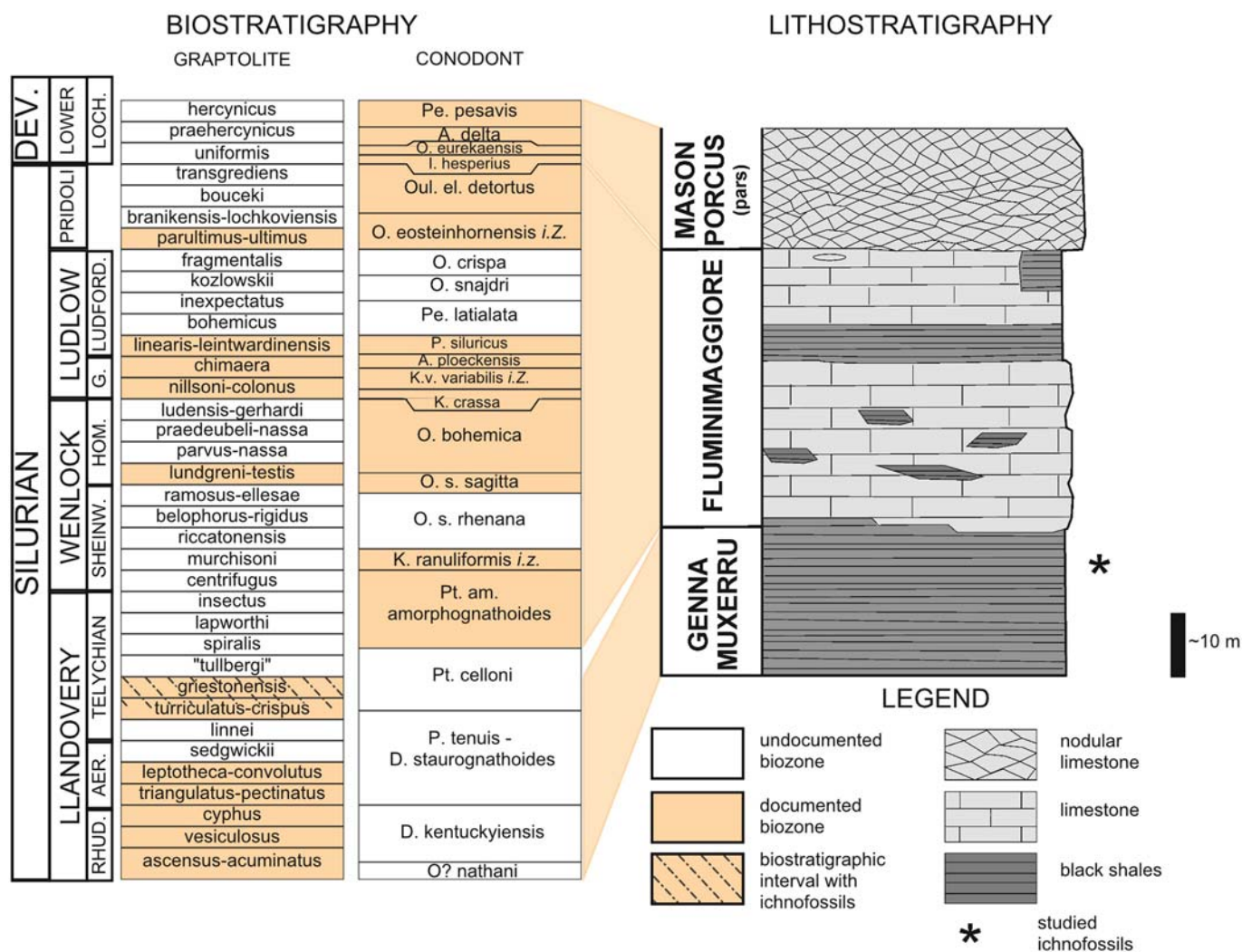


Fig. 2. Sketched stratigraphic scheme of the Silurian and lowermost Devonian of southwestern Sardinia (modified after [Corradini et al., 2009a](#)). The asterisk indicates the stratigraphic level of the trace fossils within the Genna Muxerru Formation. The biostratigraphic scheme lists all established zones for the Silurian, highlighting the biozones that have been identified in SW Sardinia ('documented biozone'). The dash-dot pattern ('biostratigraphic interval with ichnofossils') refers to the age of the here studied outcrop. Graptolites allow to date the ichnofossil-bearing outcrop to an undifferentiated *crispus-griestonensis* Zone of early Telychian (late Llandovery) age. For details on the graptolite and conodont biozones documented in Sardinia refer to [Štorch and Piras \(2009a\)](#) and [Corriga et al. \(2009\)](#). In the chronostratigraphy section, abbreviations refer to Rhuddanian (Rhud.), Aeronian (Aer.), Sheinwoodian (Sheinw.), Homerian (Hom.), Gorstian (G.), Ludfordian (Ludford.), Lochkovian (Loch.), Devonian (Dev.). It should be noted that the biostratigraphy scheme does not refer to the studied locality only, but to a large area (SW Sardinia). Here, conodont zones are documented in limestones, and graptolites in black shales. Since most time intervals are not represented by both rock types, mismatches between graptolite and conodont biozones are documented. Notwithstanding, the studied locality is precisely dated by the graptolites recovered.

up to the *griestonensis* Zone (Štorch and Piras, 2009a).

The Genna Muxerru Fm. seems to grade into the overlying Fluminimaggiore Fm., but the boundary is never exposed (Gnoli et al., 1990). The Fluminimaggiore Fm. roughly corresponds to the “calcarei a *Orthoceras*, *Cardiola*, *Monograptus*, etc.” of the early authors. It is mainly constituted by black calcareous lenses and layers alternating with dark non-calcareous pelites and shales. Carbonate deposition is characterized dominantly by fossiliferous wackestones-packstones, that grade to fossiliferous mudstones. Plastic deformation and cleavage strongly altered the shales, whereas limestone blocks preserve fossils mostly in full three dimensions (Gnoli et al., 1980; Ferretti and Serpagli, 1996; Corradini et al., 2009a, 2009b; and references therein). The black colour and the peculiar bituminous smell reveal a high content of organic matter. The thickness of the Fluminimaggiore Fm. is approximately 40–50 m, but it can be only indirectly estimated, since no sections expose the whole unit due to the strong tectonic deformation (Gnoli et al., 1990; Corradini et al., 2009a). Based on illite crystallinity, a low-grade (anchizone) metamorphic imprint characterizes the Variscan foreland in Sardinia, which includes the Genna Muxerru Formation (Eltrudis et al., 1995; Franceschelli and Puxeddu, 2006; Funedda and Oggiano, 2009).

Trace fossils were collected in a small outcrop corresponding to the locality GMX-5 of Floris (2009), located a few km west of Gonnostrada villa, on the northwestern flank of Genna Muxerru hill, where several outcrops yielded lower Telychian graptolites (Štorch and Serpagli, 1993; Floris, 2009, 2014). However, the tectonic deformation that affected the area, mainly related to a major regional overthrust located a few tens of metres to the north, resulted in heavy deformations: even if black shales crops out widely, no continuous sections are exposed, and only small outcrops of metric thickness are well preserved here and there in the area. The graptolite association from the GMX-5 locality includes *Cochlograptus veles* (Richter), *Monograptus priodon* (Bronn), *Streptograptus loydelli* Štorch and Serpagli and *Torquigraptus* sp., and allow to date the outcrop to an undifferentiated *crispus-griestonensis* Zone of early Telychian (late Llandovery) age.

4. Sedimentology and body fossil palaeontology of the bioturbated black shales

The Genna Muxerru Formation has been investigated for over 20 years (e.g. Gnoli et al., 1990; Štorch and Serpagli, 1993; Rickards et al., 1995; Štorch and Piras, 2009b; Floris, 2009, 2014) but, to date, trace fossils have been documented only at the studied outcrop (locality GMX-5 of Floris, 2009; Fig. 3A). Specifically, trace fossils have been found for the first time in 2009 during a detailed macrofossil survey (Floris, 2009). Other outcrops in the type area (Floris, 2014) and localities have been studied in comparable detail (e.g. Štorch and Serpagli, 1993; Rickards et al., 1995; Štorch and Piras, 2009b), but they did not reveal trace fossils.

The trace-fossil bearing outcrop is represented by dark, laminated, fissile, organic-rich mudstones (black shales sensu Föllmi, 2012) (Fig. 3B). These lithological features are uniform at the outcrop scale and are consistent with the typical lithofacies of the Genna Muxerru Formation (Gnoli et al., 1990; Štorch and Serpagli, 1993; Rickards et al., 1995; Štorch and Piras, 2009b; Floris, 2009, 2014). The palaeontological content of the studied locality comprises both body and trace fossils. Macroscopic body fossils are represented by graptolites, i.e. *Cochlograptus veles*, *Monograptus priodon*, *Streptograptus loydelli* and *Torquigraptus* sp.

Observations under the petrographic microscope show that the bioturbated black shales consist of an organic-rich matrix within which silt-sized grains (mostly mica and quartz) are disseminated. Both grain- and matrix-dominated laminae were observed. Mica flakes often display simultaneous extinction, suggesting that they are oriented in parallel. Quartz grains are rounded and sorted. Some of the quartz grains are reminiscent of recrystallized radiolaria, although further

observations are needed to determine whether their nature is bioclastic or not. Both quartz grains and mica flakes are organized in parallel horizons, which provides a faintly laminated aspect to the specimens (Fig. 3B). In thin section, burrows appear as tiny elliptical structures that are richer in organics than the host matrix. Carbonates or pyrite grains are not documented from the bioturbated black shales (Fig. 4).

Both facies can contain prismatic, elongated, idiomorphic crystals. At the stereoscopic microscope, they are usually contrasting in colour with the host rock and present a length of 1 mm or less (Fig. 4A, B).

Raman results suggest no large differences between the spectra collected on the crystals and those collected on the matrix (Fig. 5). Apparently, a single crystal appears to be composed of at least two different phases and the same is true for the matrix. Importantly, the peak positions of the main bands collected on the matrix and those collected on the crystals look very similar. Finally, based on high-quality Raman spectra, it is possible to determine the presence of water within the analysed material.

SEM observations on specimens GMX#1 and GMX#17 confirm the Raman analysis. They show that the ‘crystals’ possibly represent an intergrowth (topotactically pseudomorphic on undetermined primary mineral phases), that is, they are ghost minerals. Thin section study shows that the morphology of the ghost minerals (Fig. 6C, D) is similar to that of evaporitic minerals such as gypsum, anhydrite, or carbonates.

Frequently, but not exclusively, the idiomorphic crystals are associated with smaller subspherical structures (Fig. 4C, D) of problematic interpretation, herein referred to as “spherules”. These are similar in shape and size to detrital grains, faecal pellets and problematic microfossils (e.g. Silurian/Devonian *Muellerisphaerida* described by Hladil, 2016); further study is required to decipher their origin.

5. Ichnology of the Genna Muxerru Formation

Trace fossils of the Genna Muxerru Formation are commonly observed on parting surfaces of black shales. Bioturbation intensity is on average low (BPBI 2), although a few bedding planes are moderately to intensely bioturbated (BPBI 3 or higher). It should be noted, however, that burrows are poorly visible, hence the bioturbation intensity is often underestimated. The vertical (stratigraphic) distribution of trace fossils is difficult to assess because faults and soil cover preclude the possibility of following bioturbation along a stratigraphic log. However, qualitative estimates can be done. Accordingly, bioturbation distribution is homogeneous at a metrical scale, but at finer observation scales (ca. 10 cm) bioturbation is sporadically heterogeneous (sensu Gingras et al., 2011).

The studied site is the only outcrop of the Genna Muxerru Formation where trace fossils are found, either in the type locality or in other areas of SW Sardinia, thus suggesting a stratigraphically (and/or spatially) abrupt transition from bioturbated to unbioturbated black shales.

In vertical section (Fig. 6), the black shales of the Genna Muxerru Formation frequently display a spotty fabric consisting of unlined structures with elliptical cross-section (width: 0.1–0.5 mm). These structures differ from the subspherical structures of Fig. 4C–D for presenting indistinct boundaries. The spotty structures may represent either trace fossils or the product of metamorphism; further studies on their three-dimensional morphology are required to determine their nature.

Two types of fill are distinguished (Fig. 7). The first type is massive and mud-supported. It may include silt-sized particles, some of which are quartz grains (Fig. 6A, Fig. 7A). SEM-EDS analyses on selected areas show that the trace fills are richer in Mg and Fe than the host rock (see Fig. 7C). TiO₂ rods are present both in the fill and the host rock. These trace fossils resemble the typical “spotty” (Knaust, 2017) appearance of *Chondrites* in cross-section (Bednarz and McIlroy, 2015; Knaust, 2017). However, it should be noted that in cross-section *Chondrites* can be confused with *Planolites* (Knaust, 2017) or faecal pellets. The second type of fill is porous and carbonaceous (Fig. 6B, Fig. 7B). The irregular

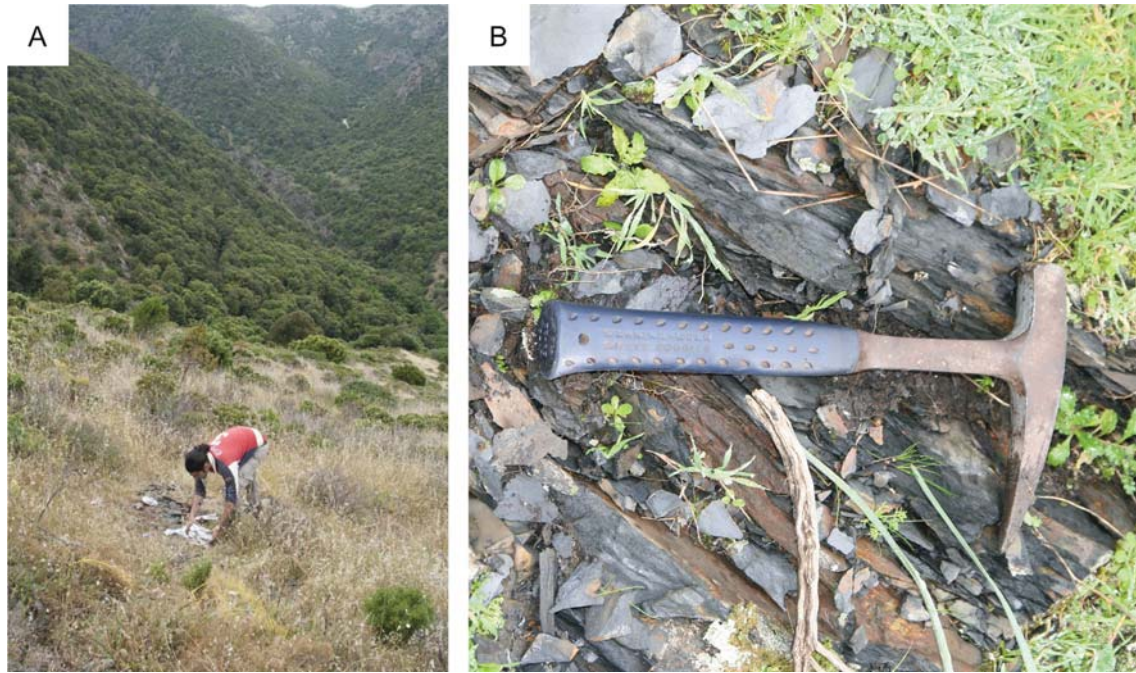


Fig. 3. The trace-fossil bearing outcrop. A. General view of the outcrop. Geologist for scale. B. Dark, laminated mudstone of the Genna Muxerru Formation in the studied outcrop. Hammer for scale.

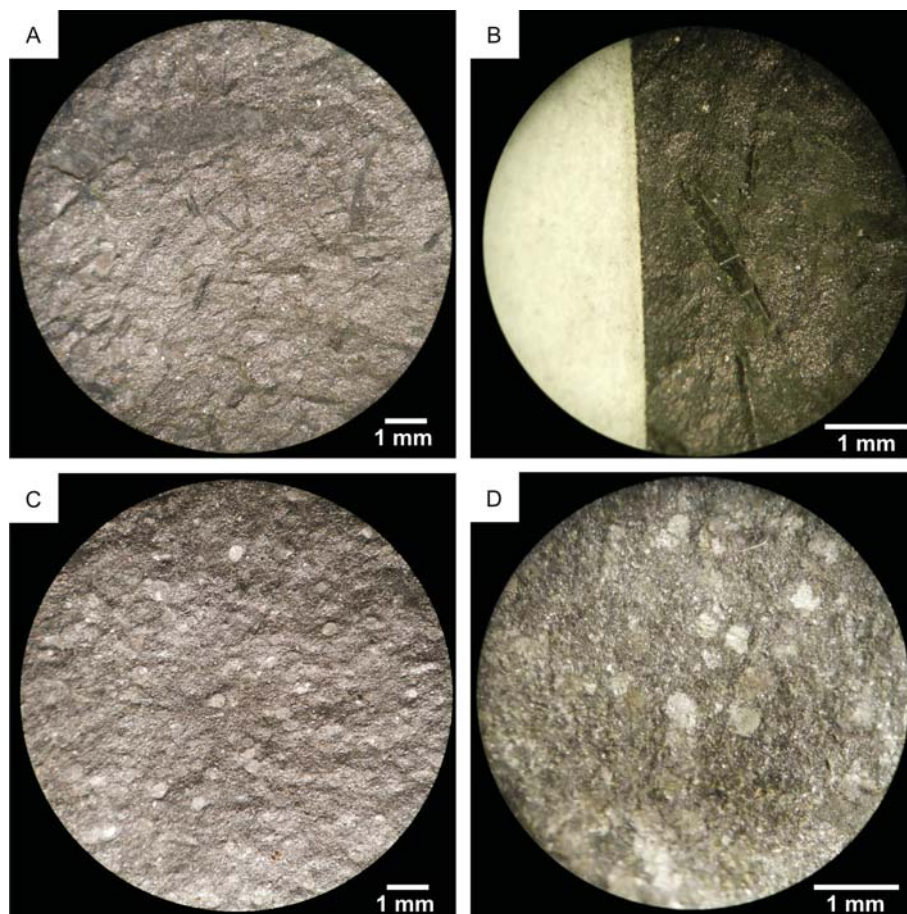


Fig. 4. Bedding plane features of the Genna Muxerru Formation. Stereoscopic microscope photographs. A. Prismatic elongated crystals, sample GMX#20. B. Prismatic elongated crystals (GMX#1), C. Subspherical structures, herein referred as to spherules (GMX#12), D. Spherules (GMX#10).

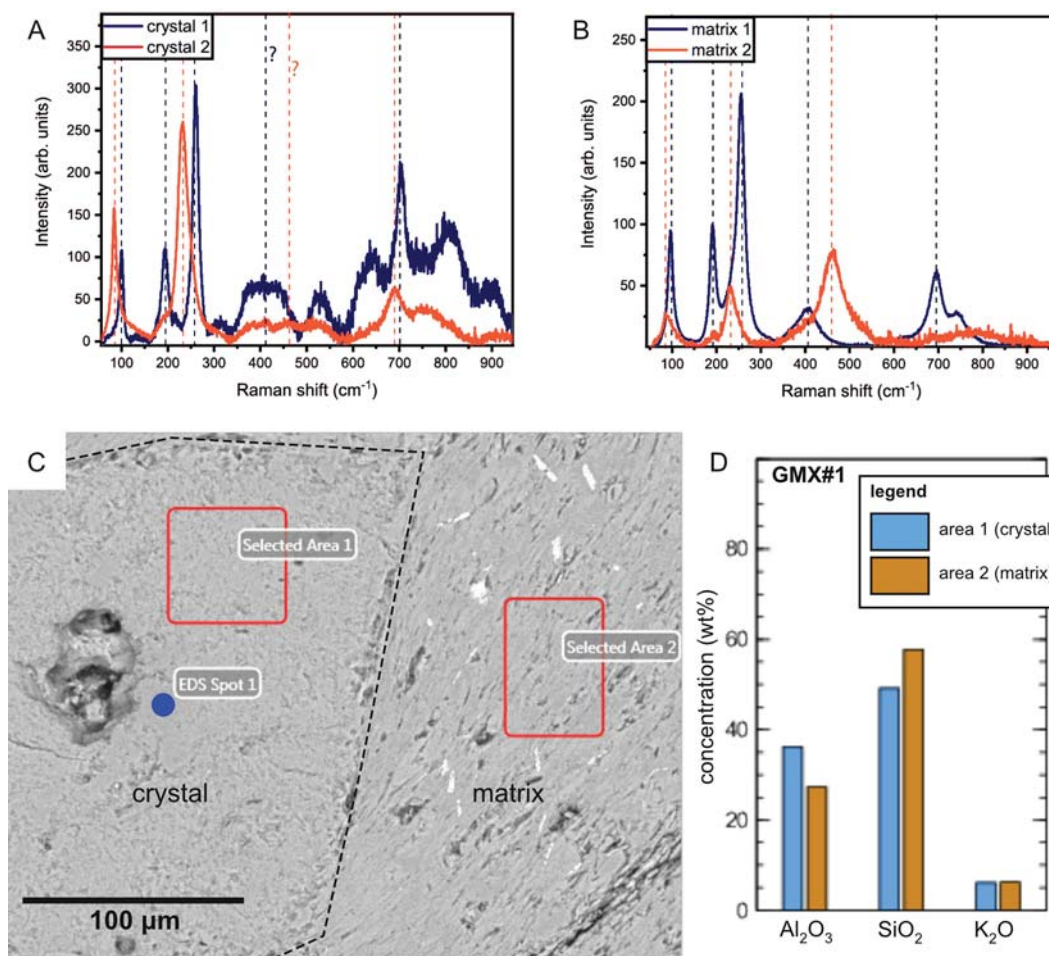


Fig. 5. A-B. Representative Raman spectra collected on one single idiomorphic crystal (in A) and the surrounding matrix (in B). Dashed lines are guidelines to highlight the main Raman spectra. Other signals are probably due to the strong luminescence effects (mainly in the crystals). Question mark (?) indicates supposed Raman peaks deduced by similarity, the signal of which is partially hidden by the luminescence background. C. SEM BSE image reporting the selected analysed areas (area 1: pseudomorphic intergrowth on ghost crystal; Area 2: matrix). Dashed line highlights the boundary between a crystal and the surrounding matrix. D. Representative analysis of the two areas in C. Concentration is expressed as weight percent (wt%). MgO, Na₂O and CaO are always present but in subordinate amounts (< 1 wt%). It should be noted that the plot does not represent the mean of a set of observations, but a single observation obtained from a representative sample.

surface prevents both quantitative and qualitative analyses. However, quartz grains and TiO₂ rods are observed both in the fill and in the host rock.

The ichnofauna presents a moderate-low diversity as it consists of 7 ichnotaxa, described as follows.

5.1. *Alcyonidiopsis isp*

Description: Straight, unlined, horizontal burrows with fill contrasting with the host rock (Fig. 8). Fill consists of microscopic pellets (approximate width: 1/10 mm) (Fig. 8A-C). Burrows are unbranched (Fig. 8A), although branching is suggested by some specimens (Fig. 8D-E). Rare specimens are sinuous. Full relief preservation. Burrow width ranges from 0.5 to 1.3 mm; average width: 0.98 mm ($n = 5$).

Associated structures: *Alcyonidiopsis* is commonly associated with spherules and, possibly, with *Planolites* (large morphotype).

Remarks: The preservation style and the morphology of the here described structures resemble those of fossil algae from the black shales of the Afon Gam and Zuun-Arts lagerstätten (e.g. Botting et al., 2015; Dornbos et al., 2016). The resemblance between algae and trace fossils has historically been the source of many misinterpretations (Oehler and Oehler, 1976; Haines, 2000; Baucon, 2009; Neto de Carvalho et al., 2016a), hence caution must be exercised when interpreting the

structures of the Genna Muxerru Formation. The straight geometry (Fig. 8A) is particularly reminiscent of algae (e.g. Botting et al., 2015; Dornbos et al., 2016), but the pelletal infill (Fig. 8B, C) favours the ichnological interpretation. Algae frequently (but not exclusively) display tapering (e.g. fig. 2D in Fu et al., 2019), which is not displayed by any of the Genna Muxerru Formation structures. This strengthens the ichnological interpretation of the here discussed structures.

This trace shares its major features with the ichnogenus *Planolites*, i.e. horizontal orientation, absence of lining and presence of contrast between burrow fill and the host rock (Pemberton and Frey, 1982). However, the microscopic pellets in the burrow fill attribute the trace to the pellet-filled ichnogenus *Alcyonidiopsis*, whose synonyms include *Tomaculum*, *Halymenites* and *Syncoprulus* (Uchman, 1999; Eiserhardt et al., 2001; Uchman et al., 2005). The pellets of the studied traces bear a superficial resemblance with framboids, but they are not made of pyrite or iron oxides/hydroxides.

Because the fill contrasts with the host rock and consists of pellets, it represents the result of backfilling by ingestion and subsequent excretion (ingestion-and-excretion backfilling sensu Baucon et al., 2014). The modern polychaete *Nereis diversicolor* produces similar pellet-filled traces when dwelling, deposit feeding, and possibly grazing (Kulkarni and Panchang, 2015). For these reasons, our specimens of *Alcyonidiopsis* are interpreted as a feeding/dwelling burrow of a worm-like organism.

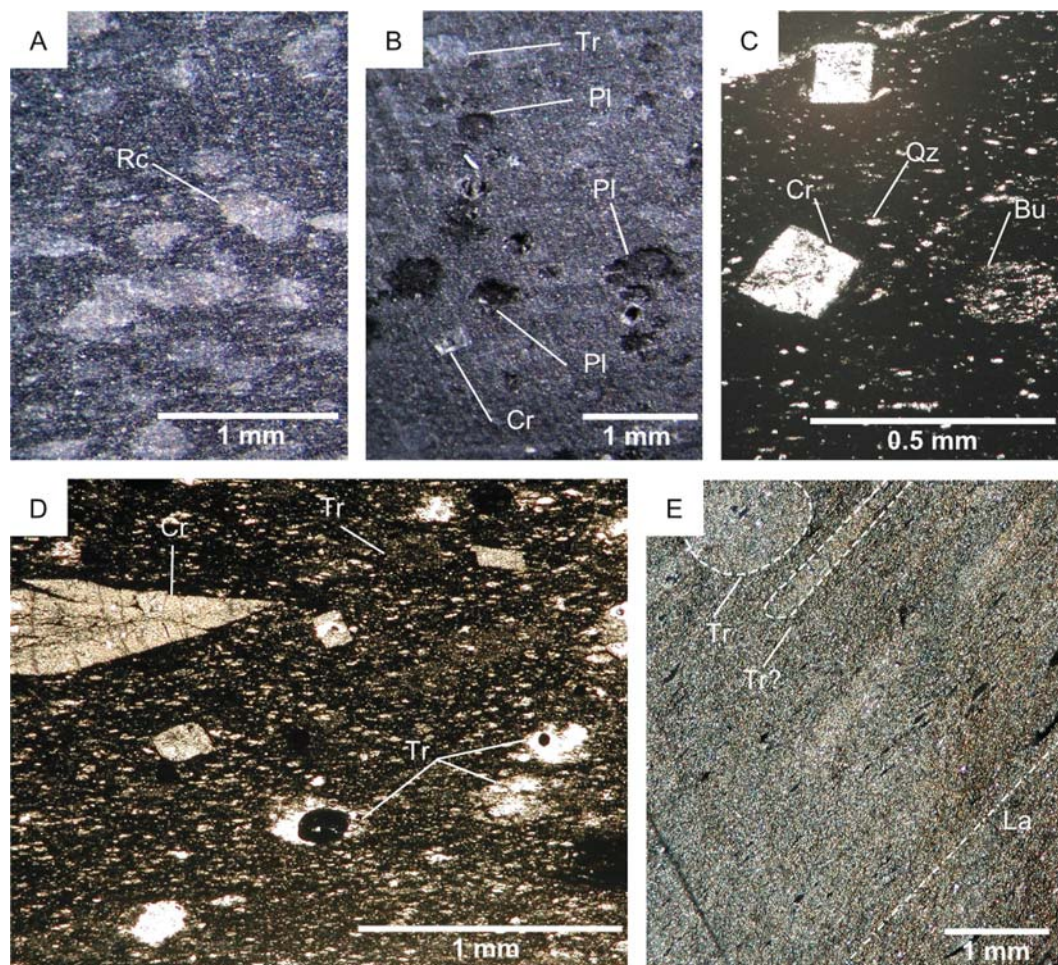


Fig. 6. Ichnofabrics of the Genna Muxerru Formation as seen in thin section. A. Spotty fabric derived by structures with rounded cross-section (Rc). These may represent burrows or low grade metamorphic artefacts. Stereoscopic microscope photograph, reflected light. Specimen GMX#13. B. Ichnofabric derived from *Planolites*-like burrows with carbonaceous fill and traces with rounded cross-section. A ghost crystal is also observable. C. Ichnofabric at the petrographic microscope (crossed nicols). D. Poorly visible trace fossils observed under the petrographic microscope (crossed nicols). The thin section has been rotated. Legend: burrow (Bu), ghost crystal (Cr), quartz grain (Qz), *Planolites*-like burrows with carbonaceous fill (Pl), rounded cross-section structure (Rc), undetermined trace fossils (Tr).

It is however uncertain whether the *Alcyonidiopsis* tracemaker fed at the surface (i.e. detritus feeding) or in the subsurface (i.e. deposit feeding). For example, the polychaete *Nereis diversicolor* produces pellet-filled burrows as a result of deposit feeding (Kulkarni and Panchang, 2015), whereas the pellet-filled traces *Phymatoderma* and *Zoophycos* have been interpreted as the result of an animal feeding at the seafloor (Ekdale and Bromley, 1983; Kotake, 1991; Izumi, 2012).

The pelleted fill of these traces has been suggested to represent a resource (i.e., food cache or bacterial garden) for times of food shortage (Bromley, 1991; Izumi, 2012; García-Ramos et al., 2014; Kotake, 2014; Löwemark, 2015). A similar function is not excluded for the *Alcyonidiopsis* of the Genna Muxerru Formation, although there is no direct evidence to confirm (or reject) this hypothesis. Absence of lining and sharp walls suggests that the sediment was moderately cohesive at the time of tracemaking (Ekdale and de Gibert, 2010).

Without microscope observations, pellets are difficult to distinguish and consequently, the trace would have been attributed to the ichnogenus *Planolites*. Therefore, a practical question is raised here: What practical criterion should we follow to attribute small burrows to *Alcyonidiopsis* or *Planolites*? This adds to the challenge posed by Uchman (1999), i.e. it is likely that most *Planolites* were *Alcyonidiopsis*-like in being pellet-filled, but faecal pellets failed to be preserved. Low oxygenation may play a role in preserving the pellets; this idea is supported by the common presence of pellet-filled burrows in low-oxygen environments (Podhalańska, 2007; Neto de Carvalho et al., 2016b).

5.2. *Cochlichnus isp*

Description: Horizontal, unlined structures with sinusoidal, regularly meandering and winding configuration (Fig. 9). Fill darker than the host rock. Burrow width is less than 1 mm.

Associated structures: The structures are associated with spherules, which are not observed in the burrow fill. *Cochlichnus* is also associated with *Alcyonidiopsis* and 'Small chondritid'.

Remarks: These burrows resemble the ichnogenus *Cochlichnus*, consisting of regularly meandering, horizontal trails and burrows resembling sine curves (Stanley and Pickerill, 1998). It should be noted, however, that typical specimens of *Cochlichnus* differ from our traces by displaying more regular meanders and a larger wavelength/amplitude ratio (see fig. 4a of Uchman et al., 2009).

In the Genna Muxerru specimens, the contrast between the host rock and the fill suggest ingestion-and-excretion backfilling (sensu Baucon et al., 2014) by a deposit-feeding worm. Producers of *Cochlichnus* include annelids lacking well-developed parapodia, nematodes lacking circular muscles, and, in subaerial deposits, insect larvae (Stanley and Pickerill, 1998).

5.3. *Phymatoderma isp*

Description: branched network consisting of subhorizontal tunnels (Fig. 10). Fill is lighter than the host rock (Fig. 10A-C) and apparently

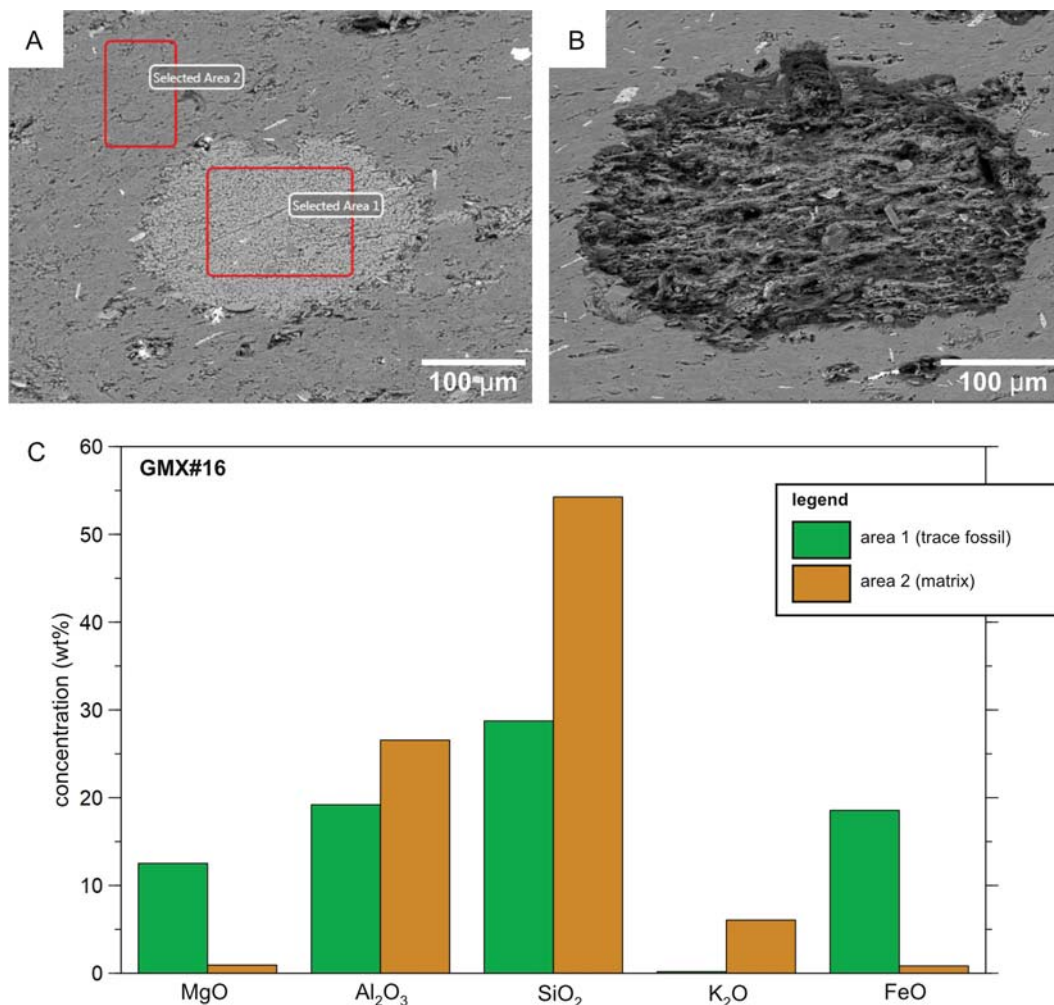


Fig. 7. Types of fill. A. Massive fill. SEM image of specimen GMX#16. Selected areas refer to the areas analysed in C. B. Carbonaceous fill. SEM image of specimen GMX#17. C. Elemental analysis of the trace fossil and the matrix (host rock) figured in Fig. 7A. Concentration is expressed as weight percent (wt%). Other elements are always in subordinate or trace amounts (< 1 wt%). It should be noted that the plot does not represent the mean of a set of observations, but a single observation obtained from a representative sample.

structureless, but some specimens show pellets organized in meniscate packets (Fig. 10C). Wall is unlined, burrow margin is smooth. Full relief preservation. Burrow width is 3–4 mm. Similar features have been documented from a single, dark-filled specimen which, however, does not show evidence of pellets and menisci (Fig. 10D).

Associated structures: *Alcyonidiopsis*.

Remarks: The light-filled burrows are comparable with the ichnogenus *Phymatoderma*, which is distinguished from the morphologically similar ichnogenus *Chondrites*, except for the presence of pelletal infill (Izumi, 2012). Pelletal infill can be discerned only in some specimens of the Genna Muxerru Formation (Fig. 10C). This fits with observations of other authors (Uchman and Gaździcki, 2010), according to whom pellets can be only locally preserved in *Phymatoderma*. The here described structures are branched, whereas the similar pellet-filled burrow *Alcyonidiopsis* is unbranched (Knaust, 2012). Accordingly, the here described structures are assigned to the ichnogenus *Phymatoderma*. It should be however noted that other authors (Rodríguez-Tovar and Uchman, 2004) describe *Alcyonidiopsis* as a branched burrow. These authors highlight the similarity between *Alcyonidiopsis* and *Phymatoderma granulatum*, which is filled with faecal pellets like *Alcyonidiopsis*, but displays tree-like branching. The branching of the here described structure is tree-like, which therefore support their attribution to the ichnogenus *Phymatoderma*. *Phymatoderma granulata* is interpreted as a product of an animal that ingested seafloor sediments and excreted

faecal pellets in the subsurface (Izumi, 2012). The sharp colour contrast of the Genna Muxerru specimens is compatible with an animal feeding at the surface and excreting in the subsurface. *Phymatoderma* occurs mostly in outer shelf or deeper environments (Uchman and Gaździcki, 2010). *Phymatoderma* is commonly associated with black shales (Izumi, 2012). It reflects oxygenated bottom water and low- oxygen porewater (Izumi, 2012; Lima and Netto, 2012; Baucon et al., 2015).

The dark-filled trace without pellets and menisci (Fig. 10D) is a chondritid but a more precise attribution is problematic because of the availability of only a single specimen.

5.4. *Planolites* (large morphotype)

Description: Horizontal to oblique, unbranched burrows. The wall is unlined, although microscopic observations reveal a discontinuous horizon surrounding the burrow fill. It probably consists of iron hydroxides. The host sediment is deformed around the trace. Wall is generally smooth and often characterized by longitudinal engravings (bioglyphs). Straight to gently sinuous configuration. When preserved, fill is carbonaceous and contrasts with the host rock. The burrow fill is often divided into smaller partitions separated by septa-like structures. Observations under the petrographic microscope show that probable iron hydroxides are associated with the burrow. Septa-like structures create a texture that is comparable with that of mineral-filled cracks of

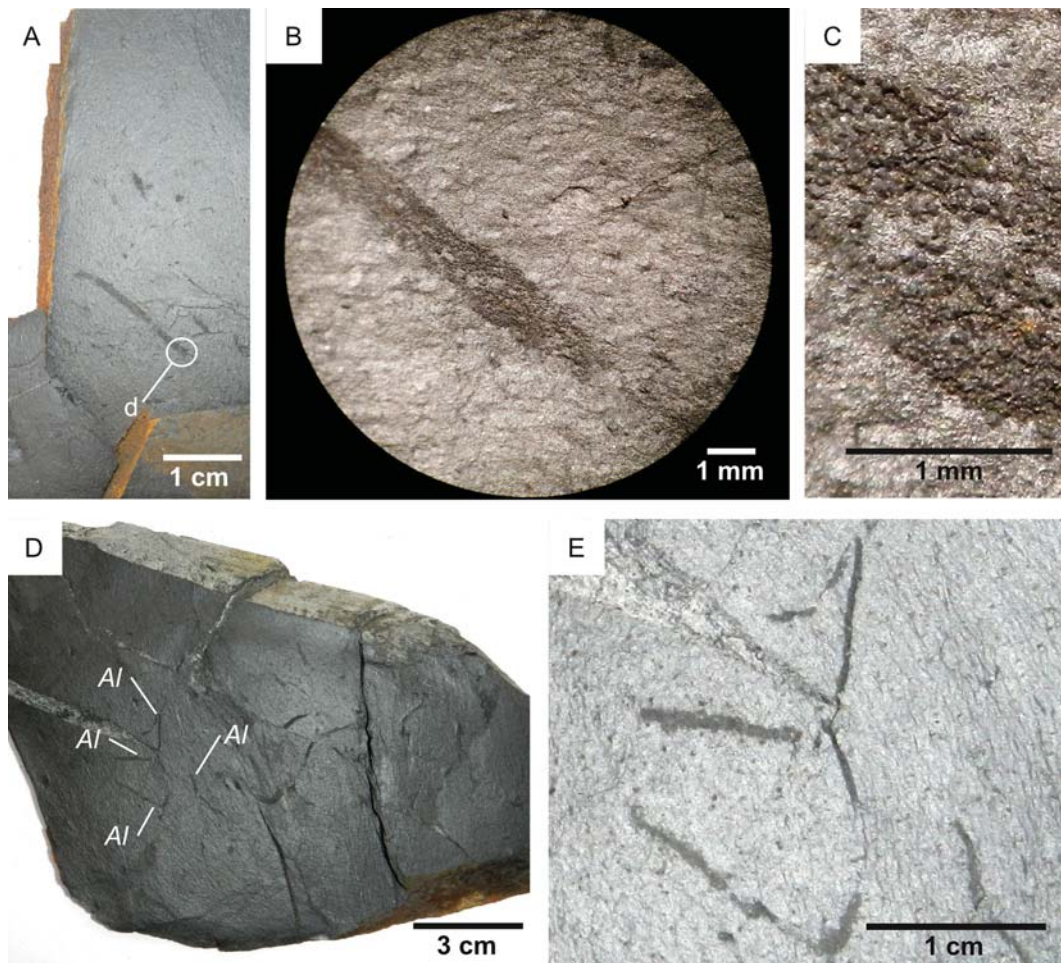


Fig. 8. *Alcyonidiopsis*. A. *Alcyonidiopsis* with rectilinear configuration. The circle (d) shows the area magnified in B. Sample GMX#23. B. *Alcyonidiopsis*, photographed at the stereoscopic microscope (bedding plane view). C. Detail of B showing the pellet fill. D. Four specimens of *Alcyonidiopsis* (Al) within sample GMX#25. E. Detail of the four specimens highlighted in D. It is problematic to ascertain whether the four specimens pertain to a single branched burrow system or not. Note the faintly granular texture, which results from the pellet-rich fill.

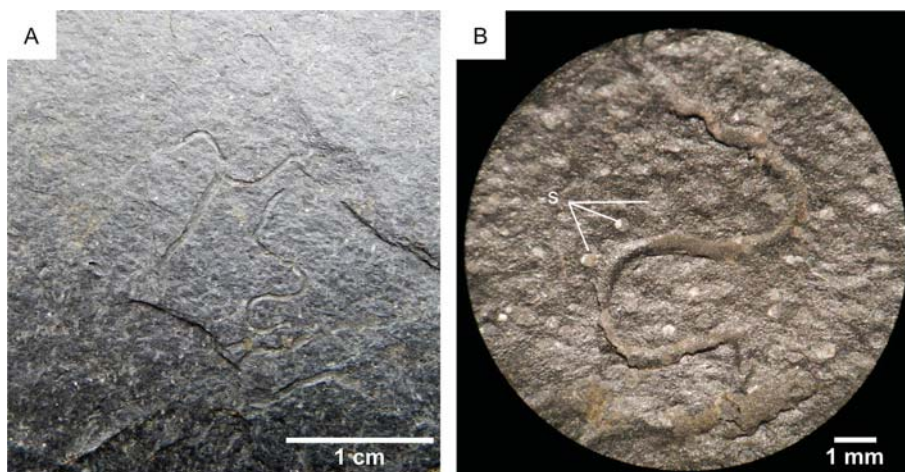


Fig. 9. *Cochlichnus*. A. Specimens are concave because the fill is not preserved. Sample GMX#12, B. detail of A showing the meandering course of the trace and associated spherules (s). Image recorded at the stereoscopic microscope (bedding plane view).

the Genna Muxerru Formation. The trace is preserved in full relief. Burrow width ranges from 1 to 7 mm. Average width is 3.7 mm ($n = 9$).

Associated structures: The trace is frequently associated with spherules and prismatic microstructures. *Planolites* (large morphotype) is associated with *Alcyonidiopsis* and *Planolites* (rough morphotype).

Remarks: Elongate, carbonaceous vermiform structures are difficult to interpret in black shales because they may represent body fossils of soft-bodied animals (e.g. Conway Morris and Robison, 1986), body fossils of algae (e.g. Haines, 2000) or trace fossils. The here described structures do not show anatomical features proper of worm-like

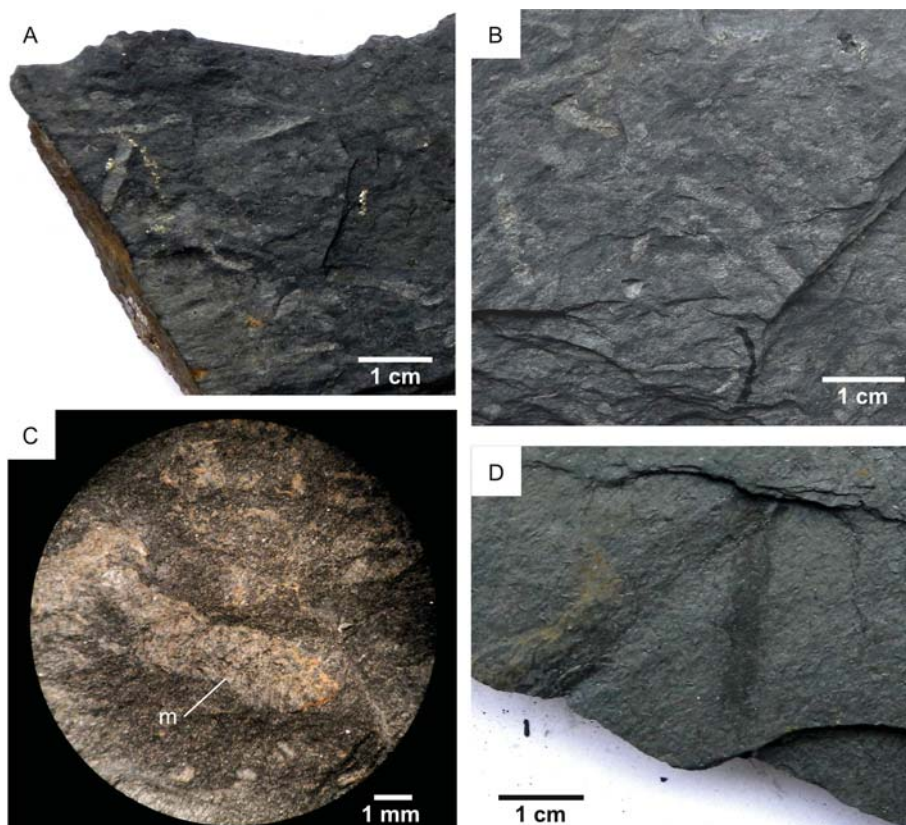


Fig. 10. Large chondritids. A. *Phymatoderma*, sample GMX#11. B. close-up of sample GMX#11 showing branched burrows. C. stereoscopic microscope image of GMX#11 showing meniscate packets. Arrow points to a meniscate packet (m). Bedding plane view. D. dark-filled chondritid (*Phymatoderma* or *Chondrites*; sample GMX#22).

animals, which have been previously reported from black shale deposits (e.g. proboscis, setal bundles, sclerites, annulations, cuticular surface structure; Steiner et al., 2005; Johnston et al., 2009). It should be however noted that anatomical features may be not observed in fossils of extensively decayed soft-bodied animals (e.g. Conway Morris and Robinson, 1986). Morphology and preservation style of the studied structures is partly compatible with those of fossil sponges preserved in black shale facies (e.g. Botting and Butterfield, 2005; Wu et al., 2005). However, the studied specimens do not show any unquestionable evidence that falsifies the trace fossil hypothesis and that reveals a sponge nature (spiculae or related fabrics, vasiform shape, osculum; see Botting and Butterfield, 2005; Wu et al., 2005; Carrera and Ortega, 2009).

In addition, the host sediment is deformed by the structures, which is plausibly explained as the result of burrowing activity. A trace fossil origin is also suggested by the oblique orientation of the structures with respect to the lamination (see Fig. 11A). In fact, sedimentological features of the Genna Muxerru Formation (fine-grained, laminated black shales) point to a hydrodynamically quiet environment where elongate organic remains would have been deposited in parallel to the seafloor. This idea is confirmed by the orientation of graptolites of the Genna Muxerru Formation, which is parallel to the lamination. In sum, the characteristics of the here described structures are more compatible with trace fossils than with body fossils.

Because the carbonaceous fill contrasts with the host rock, the trace is here interpreted as the result of deposit-feeding. According to this interpretation, the tracemaker backfilled its burrow with sediment that has been ingested and processed (ingestion-and-excretion backfilling; sensu Baucon et al., 2014). This fits with the interpretation of *Planolites* as the feeding trace of a deposit feeder (Pemberton and Frey, 1982; Keighley and Pickerill, 1995). Bioglyphs and absence of lining indicate that the sediment was moderately cohesive at the time of tracemaking (Ekdale and de Gibert, 2010). *Planolites* is a typical environment-crossing ichnotaxon (Pemberton and Frey, 1982; Keighley and Pickerill, 1995) and has been reported from oxic (Baucon and Neto de Carvalho,

2016) to dysoxic (Boyer et al., 2014) settings.

Septa-like structures are interpreted as post-diagenetic features resulting from tectonic stretching of burrows. According to this interpretation, stress would have broken and extended burrows, leaving open spaces within which minerals crystallized. In other words, the burrows with septa-like structures are ichnological analogues of the so-called ‘boudinaged belemnites’ and similar broken and extended belemnites (e.g., fig. 3.1 in Fossen, 2016). Raman spectroscopy reveals that these structures consist of quartz.

5.5. *Planolites* (rough morphotype)

Description: Straight, unlined, horizontal to oblique structures preserved in full relief (Fig. 14). Carbonaceous fill, contrasting in texture with the host rock. Margins are characteristically rough. Burrow width ranges from 3 to 10 mm. Average width: 5 mm ($n = 7$).

Associated structures: The trace is frequently associated with spherules and prismatic microstructures, as well as with ‘Small chondritid’ and *Cochlichnus*.

Remarks: The here described structure resembles the *Oikobesalon*-like fossils reported from the Afon Gam black shales (Fig. 4j in Botting et al., 2015). *Oikobesalon* is common in the Silurian (Thomas and Smith, 1998) and it has been initially interpreted as worm body fossil and successively as a soft sediment burrow with a thin organic lining (Thomas and Smith, 1998; Vinn and Toom, 2014). However, the absence of lining allows to distinguish the here studied structure from *Oikobesalon* and attribute it to the ichnogenus *Planolites*. This morphotype differs from *Planolites* (large morphotype) for having larger size and rough margins. However, these features may be not only the product of animal behaviour, but also the result of taphonomic processes interacting with a burrow resembling the previously described *Planolites* (large morphotype). Sharp walls and absence of lining suggest that the trace was produced in a moderately cohesive substrate.

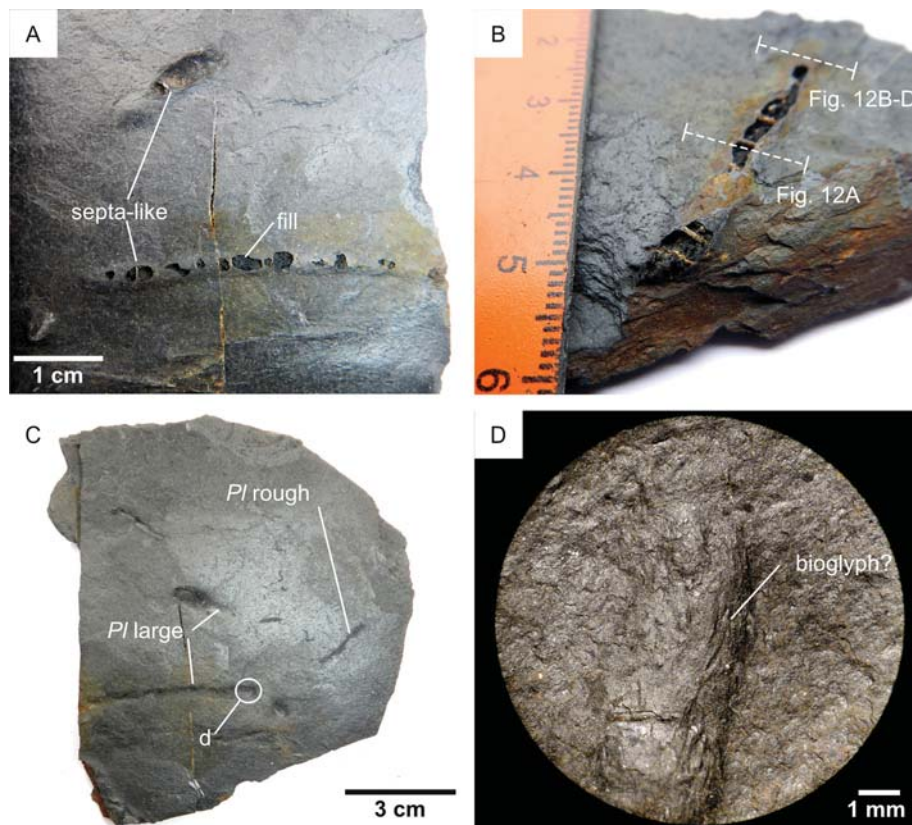


Fig. 11. *Planolites* (large morphotype). A. two specimens of *Planolites* showing septa-like structures and carbonaceous fill. Sample GMX#2. B. *Planolites* with carbonaceous fill and septa-like structures. Scale in mm (smaller ticks), numbers refer to cm. Dashed lines show location of the sections of Fig. 12B-E. Sample #GMX1. C. *Planolites* (PI), large and rough morphotype. Large morphotype is concave. The circle labelled with 'd' shows the magnified area presented in D. Sample GMX#15, that is the counterpart of GMX#2 in Fig. 13A. D. Detail of A showing possible bioglyphs. Burrow is preserved as concave relief. Stereoscopic microscope image, bedding plane view.

5.6. 'Small chondritid'

Description: dichotomously branched network consisting of sub-horizontal tunnels with constant diameter (Fig. 15). A maximum of 2 branching orders are observed. Fill is carbonaceous and contrasts to the host rock. Fill is massive, although some specimens apparently suggest a faint pelletal infill (Fig. 15D). Wall is unlined, burrow margin is smooth. Full relief preservation. The trace is frequently associated with spherules, which are present in the host rock but not in the burrow fill. Burrow width is constant and less than 1 mm. Tunnel length is approximately 1.6 cm.

Associated structures: spherules, *Alcyonidiopsis*.

Remarks: The here described structure presents morphological and textural features (dichotomous branching, constant width, textural contrast with the host rock) shared among chondritid trace fossils and algae. Because of this resemblance, branched trace fossils, and especially chondritids, have been frequently mistaken for algae (Neto de Carvalho et al., 2016a; Baucon et al., 2020). Converse cases are also reported, i.e. trace fossils being reinterpreted as algae (e.g. Haines, 2000). It is particularly difficult to distinguish between plant and trace fossils in dark-coloured shales. For instance, carbonaceous films on bedding surfaces of dark grey shales have been first attributed to the ichnogenus *Helminthoidichnites*, and then assigned to algae (Oehler and Oehler, 1976).

The Genna Muxerru structures resemble the 'common branching alga' reported from the Afon Gam black shales (fig. 3 of Botting et al., 2015). However, the here describe structures often present a faint pelletal infill and always lack self cross-cutting branches, for which reason it is here interpreted as a trace fossil.

The studied trace pertains to chondritids (Knaust, 2017). It shows many of the features of *Chondrites*, including those that distinguish it from the morphologically similar *Phymatoderma*: tunnels of constant diameter, well-defined walls and no self-cross cutting (Aalto and Miller, 1999; Seilacher, 2007; Izumi, 2012). Although size is rejected as an

ichnotaxobase (Bertling et al., 2006), small burrow size is also compatible with *Chondrites* (Izumi, 2012). However, it should be noted that the faintly visible pellets (Fig. 10D) are consistent with the ichnogenus *Phymatoderma*, whereas *Chondrites* does not show pellets (Aalto and Miller, 1999; Seilacher, 2007; Izumi, 2012).

The texture of the burrow fill suggests that the tracemaker ingested sediment and then backfilled tunnels by excreting processed sediment organized in pellet-like elements ('ingestion-and-excretion backfilling' sensu Baucon et al., 2014). Self-avoiding branching is interpreted as the result of systematic deposit-feeding.

Monogenic or low-diversity assemblages with *Chondrites* are typically referred to dysoxic environments (Bromley and Ekdale, 1984; Bromley, 1996; Buatois and Mángano, 2011). In fact, the tracemakers of *Chondrites* appear to be capable of colonizing environments characterized by oxygen levels well below levels needed for the survival of other animals (Savrda and Bottjer, 1986). *Phymatoderma* is also interpreted as a dysoxia-related trace (Izumi, 2012). Both *Chondrites* and *Phymatoderma* are interpreted as the work of vermiform deposit-feeding animals (Rodríguez-Tovar and Uchman, 2004; Izumi, 2012). Seilacher (1990) and Fu (1991) also suggested that chemosymbiotic bivalves produced *Chondrites* to provide sulfur-oxidizing symbionts with the chemical reductants they required for metabolism.

6. Discussion

6.1. Palaeoenvironment of the bioturbated black shales

This section delineates a palaeoenvironmental reconstitution by considering the major environmental parameters that control the distribution of bioturbators (Bromley, 1996; Buatois and Mángano, 2011). However, before interpreting the palaeoenvironment based on the available data, it is important to carry out a taphonomic analysis of body and trace fossils. Specifically, it is central to assess the fidelity of the studied fossil assemblage, that is, establishing how closely the

Genna Muxerru black shales preserve evidence for past life. In fact, the lack of fossils other than graptolites and burrows may reflect (1) ecological factors, i.e. graptolites and tracemakers would have been the major macroscopic lifeforms of the studied ecosystem, or (2) preservational factors, i.e. post-depositional processes would have obliterated evidence for other organisms.

Data show that metamorphism is unlikely to have obliterated shelly fossils. Metamorphism can modify and obliterate all incorporated remains and features like sedimentary structures and body fossils (Maletz, 2017). However, metamorphism is unlikely to have obliterated shelly fossils in the studied unit because of its low-grade. In fact, in the external zone of the Variscan chain of Sardinia, illite crystallinity ranges between 0.26 and 0.45, with a cluster of values from 0.32 to 0.38 (Eltrudis et al., 1995; Franceschelli and Puxeddu, 2006; Funedda and Oggiano, 2009). These values are comprised in metamorphic anchizone (Eltrudis et al., 1995; Franceschelli and Puxeddu, 2006; Funedda and Oggiano, 2009), that is, a transitional zone of incipient metamorphism between diagenesis and low-grade metamorphism (Merriman and Frey, 1999).

Results show no evidence of dissolution of eventual shelly fauna. In general terms, high organic content in sediment increases the drive for microbially mediated decay and acidity, thus favouring dissolution of calcareous shelly fossils (Cherns and Wright, 2009). Dissolution has been cited as the cause for the lack of calcareous fossils in several black shale units (Schovsbo, 2001). For instance, in the Afon Gam Lagerstätte skeletal calcium carbonate is normally dissolved, being occasionally found as recrystallized material in the most robust trilobite exoskeletons, and at some horizons in originally aragonitic shells (Botting et al., 2015). The preservation style of the Afon Gam trace fossils resembles that of the Genna Muxerru ones (e.g. Fig. 4d in Botting et al., 2015), thus suggesting similar taphonomic pathways. Nevertheless, there is no evidence of re-precipitated calcium carbonate in the Genna Muxerru Formation. Carbonate re-precipitation is also cited for the Burgess Shale, where carbonate carrying capacity of porewaters was reduced as sulfate reduction proceeded, and carbonate was re-precipitated in pore spaces and as cement linings on calcitic fossils prior to final lithification and compaction (Gaines et al., 2005). Such evidence is completely lacking from the Genna Muxerru Formation, which shows no carbonate and poor evidence of sulfur compounds. In the Burgess Shale shelly fossils can be preserved as carbonaceous films (Martí Mus, 2014), but such evidence has never been observed in the Genna Muxerru Formation. Syndepositional dissolution of calcium carbonate can be excluded for the studied black shales. In more general terms, syndepositional dissolution of calcium carbonate manifests as dissolution features, early cementation, and loss of aragonitic faunas (Cherns and Wright, 2009). None of these features is documented from the Genna Muxerru Formation. Post-lithification dissolution of a fossil can leave a mould, which may remain as a void or may be subsequently filled by cement to create a natural cast (Nichols, 2009). None of these post-lithification features have been observed in the Genna Muxerru Formation, either at the macroscopic or the microscopic scale. Therefore, there is no evidence indicating *syn*- or post-depositional dissolution of eventual shelly fauna. For this reason, we hypothesize that the Genna Muxerru ecosystem was dominated by soft-bodied animals, whereas dysoxic conditions prevented colonization of the seafloor by other organisms. This scenario fits with the ecological structure of modern low-oxygen settings. For instance, the oxygen minimum zone on the Oman margin is dominated by a dense soft-bodied assemblage (polychaetes, sponids, cirratulids, paraonids and ampharetids), whereas molluscs and most crustaceans are common only below the oxygen minimum zone (Levin et al., 2000).

Taphonomy of trace fossils indicates that burrows were actively filled in a steady depositional regime. In fact, trace fossils are preserved in full-relief, which is typical of steady deposition (Bromley, 1996). Sharp lithological contrasts are lacking in the studied unit, but even in these settings trace fossils may be preserved because of constructional

differences in compaction, grain orientation and organic content of fill and walls (Bromley, 1996). Most of the studied ichnotaxa are actively pellet-filled, which implies differences in texture, grain orientation and organic content between the burrows and the matrix. SEM-EDS analyses demonstrate that textural differences are accompanied by chemical ones, i.e. the trace fills are richer in Mg and Fe than the host rock (Fig. 7). The studied burrows reflect selective uptake of organic-rich particulate matter. Many burrows of the Genna Muxerru Formation have a carbonaceous aspect, suggesting a richer content in organic matter with respect to the host sediment. Colour differences between burrows and the host rock may be explained by the presence of different mineral phases in the burrow fill, but observations at the petrographic microscope do not show such evidence. SEM-EDS analyses demonstrate that the trace fills are richer in Mg and Fe than the host rock (Fig. 7C), whereas TiO₂ rods are present both in the fill and the host rock. A higher carbon content in the burrow fill than in the host rock may sound controversial, especially for deposit-feeding burrows. In fact, deposit-feeding tracemakers ingest sediment and extract organic contents from it during digestion. Consequently, one might expect that excreted material would be poorer in organic carbon than the ingested sediment, not richer, as it is instead shown by the studied trace fossils. This paradox is explained by analogy with the modern polychaete *Heteromastus filiformis*. Neira and Höpner (1994) show that the content of organic carbon in fresh pellets of *H. filiformis* is 2.4-fold higher than in the feeding zone sediment. This phenomenon is interpreted as the result of selective uptake of organic-rich particulate matter (Wild et al., 2005). *Heteromastus filiformis* feeds on carbon sources stored in anoxic and sulfidic sediments, using detritus, benthic algae and bacteria as food source (Clough and Lopez, 1993; Wild et al., 2005). However, the carbon retention efficiencies of *H. filiformis* are very low (4% for detritus; Clough and Lopez, 1993). This may be due to the refractory character of the ingested food and explains the high organic content of the pellets (Wild et al., 2005). Based on the analogy with these modern polychaetes, we interpret the carbonaceous aspect of the studied fossil burrows as the result of selective uptake of organic-rich particulate matter. Following Bromley (1996), the aforementioned textural and chemical differences plausibly initiated localized diagenesis that enhanced the visibility of the trace fossils in the Genna Muxerru Formation (Fig. 16).

We searched for pyrite and its typical alteration products (sulfates, iron oxides and iron hydroxides) using SEM-EDS analyses, SEM observations and petrographic microscope observations. Result show no evidence of pyrite and its alteration products in the studied samples, except for the subordinate presence of iron hydroxides in some burrow linings (Fig. 12).

6.1.1. Oxygenation

The bioturbated black shales of the Genna Muxerru Formation place together two apparently contrasting concepts: (1) metazoans rely on oxygen for metabolism (Diaz and Rosenberg, 1995) and (2) black shales deposited in low oxygen conditions (Werne et al., 2002). There is, therefore, a fundamental question about the Genna Muxerru Formation: what were the oxygen levels of the Genna Muxerru palaeoenvironment? Answering this question is challenging because it would be tautological using just ichnological evidence, as manifested by existing ichnofossil models of palaeoxygenation (Savrdá and Bottjer, 1986; Ekdale and Mason, 1988; Leszczyński, 1991; Martin, 2004; Savrdá, 2007). This is further complicated by the fact that anoxia is not necessary for black shale deposition (Bednarz and McIlroy, 2015; Smith et al., 2019). For these reasons, we used a combination of body fossil paleoecology, taphonomy and sedimentology to assess oxygenation.

Several ecological models point to low-oxygen conditions. According to the actualistic research of Rhoads and Morse (1971), faunal diversity declines sharply as oxygen levels fall below 0.5–1.0 ml/l until a zero point is reached at the anaerobic-dysaerobic boundary (see also Allison et al., 1995; Doyle, 1996). This principle is supported by a

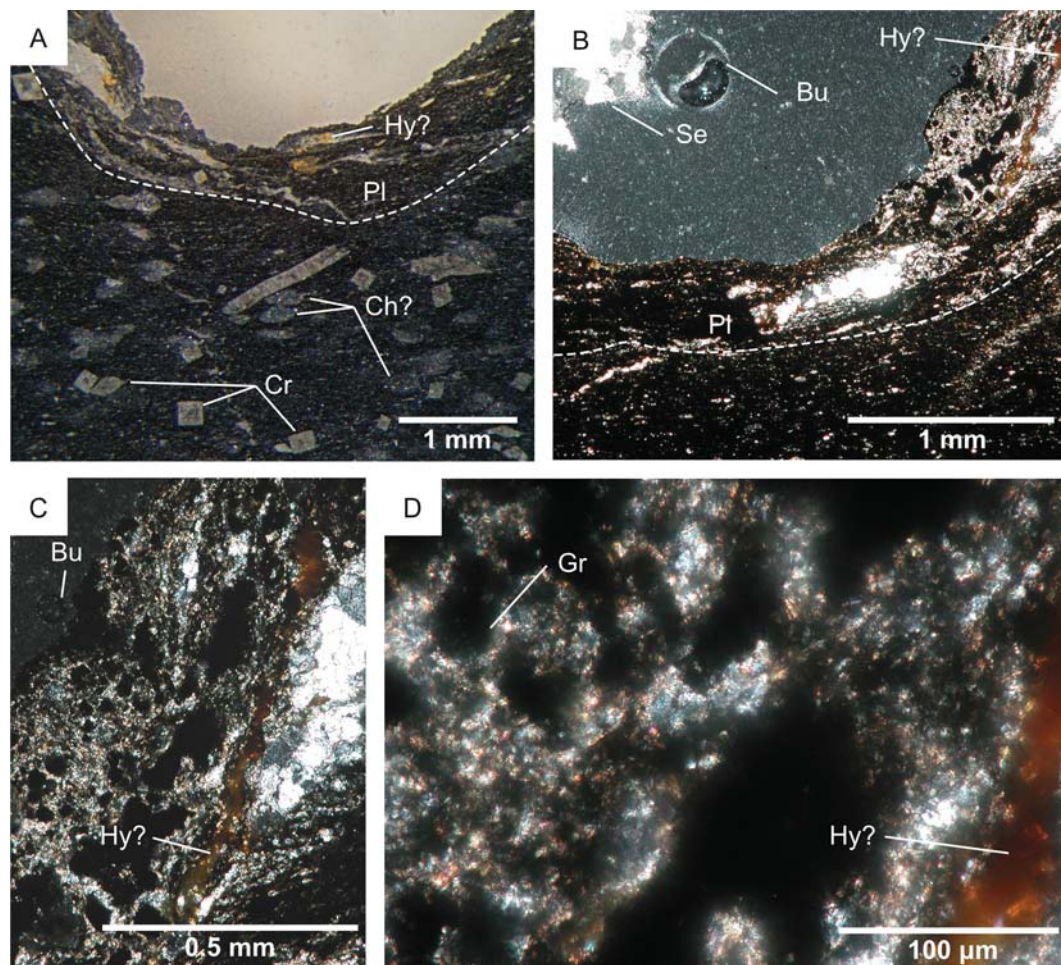


Fig. 12. Thin sections of *Planolites* (large morphotype) in reflected (A) and transmitted (B-D) light. Sample GMX#1. Location of thin sections is shown in Fig. 11. A. Ichnofabric associated to *Planolites* (large morphotype). Thin section photographed at the stereoscopic microscope, crossed nicols. Dashed line delimits the wall of *Planolites* (Pl). Hy?: possible iron hydroxides; Ch?: possible *Chondrites*; Cr: hydromorphic crystals. B. *Planolites* in thin section. Dashed line delimits the wall of *Planolites* (Pl). Crossed nicols. Se: Septa-like structure consisting of quartz. Bu: air bubble. C. Organization of the burrow fill. Detail of B. Crossed nicols. Bu: air bubble; Hy?: possible iron hydroxides. D. Microfabric of the burrow fill. Detail of C. Crossed nicols. Gr: organic-rich grain; Hy?: possible iron hydroxides.

great body of data from modern low-oxygen environments (Allison et al., 1995; Tyson and Pearson, 1991). In the Genna Muxerru Formation, the diversity of shelled benthos is zero, thus suggesting a low-oxygen environment according to the model of Rhoads and Morse (1971). The ichnofauna of the Genna Muxerru Formation presents a moderate-low diversity, thus being coherent with a low-oxygen setting. It should be however highlighted that, as Buatois and Mángano (2011) noted, the relationship between biodiversity and ichnodiversity is not linear.

Besides diversity, Rhoads and Morse (1971) noted that calcareous-shelled taxa disappear at low oxygen values, so that soft-bodied animals are the commonest benthonic organisms below 1.0 ml O₂/l (see also Doyle, 1996). This is clearly the case of the Genna Muxerru Formation, which preserve abundant trace fossils produced by soft-bodied organisms but no shelly benthos.

Further models corroborate the low-oxygen interpretation for the black shales of the Genna Muxerru Formation. The observation of Rhoads and Morse (1971) is supported by Byers (1977) who defined a dysaerobic biofacies as “calcareous epifauna lacking, but sediment bioturbated due to the activities of resistant fauna”. This clearly fits with the Genna Muxerru Formation, which preserves no shelly taxa but abundant soft-bodied trace fossils. It should be noted that Allison et al. (1995) considered Byers' position oversimplified because shelly taxa, and particularly echinoderms, can be abundant in modern low-oxygen settings. This does not change the interpretation of the Genna Muxerru

Formation because no shelly taxa are documented from it.

Wignall and Hallam (1991) proposed five oxygen-restricted biofacies (ORB), which are defined by the number of species and sediment fabric. The Genna Muxerru Formation presents mixed features from ORBs 1–3: laminated sediment, presence of nektonic species, absence of nektobenthic species and absence of benthos (with the exception of soft-bodied tracemakers). The Genna Muxerru Formation lacks praecardiacean bivalve genera (e.g. *Cardiola*; *Dualina*) which are characteristic of ORB 3 and 4 in the Silurian (Allison et al., 1995). The similarity with ORBs 1–3 points to low-oxygen conditions for the Genna Muxerru Formation, since ORBs 1–2 correspond to anaerobic conditions and ORB3 to dysaerobic ones (Allison et al., 1995).

Low-oxygen conditions are also suggested by the model of Štorch (1998), who distinguished three depth–/nutrient-related graptolite sub-faunas in the Early Silurian of peri-Gondwanan Europe. The graptolite fauna of the Genna Muxerru Formation fits with Štorch's “hemipelagic anoxic black shales” fauna, which is characterized by no non-graptolite body fossils, high diversity and abundance of graptolites, including dimorphograptid ones.

Low-oxygen conditions are also supported by indirect geochemical proxies. Pyrite is by far the most abundant authigenic mineral formed under anoxic conditions and it is used to indicate oxygenation through the degree of pyritization (DOP) index (Allison et al., 1995). In the Genna Muxerru Formation, there is neither marcasite nor pyrite present. This suggests that either the environment was fully oxygenated, or

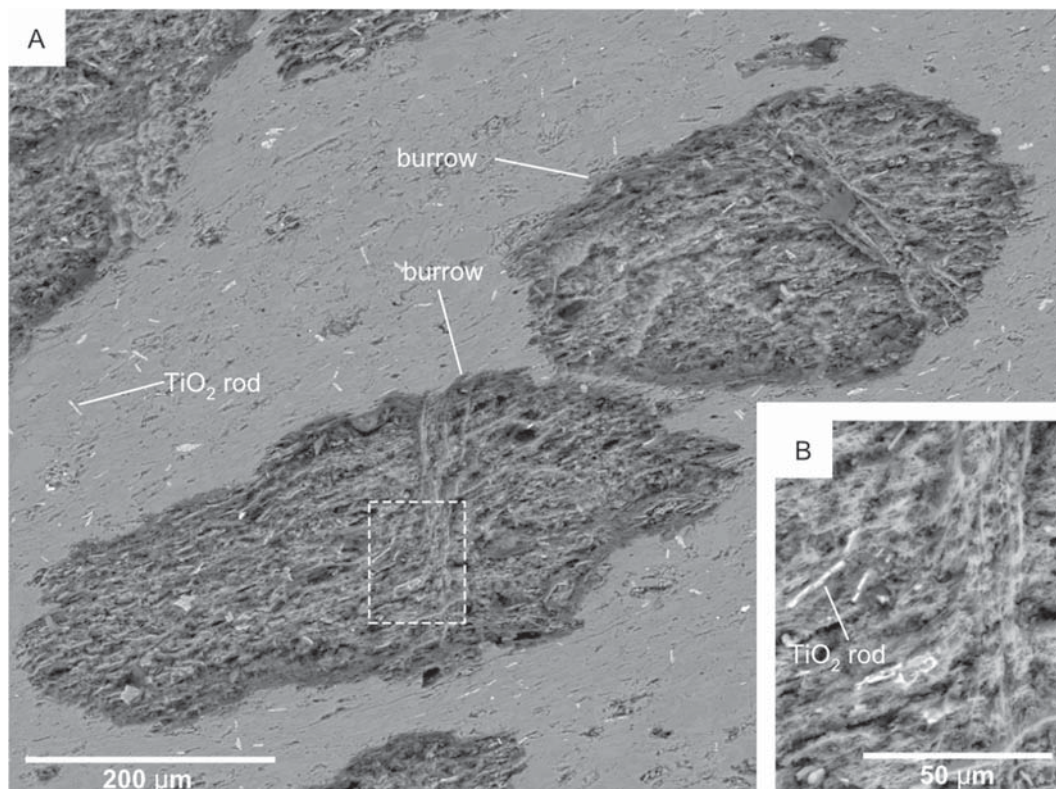


Fig. 13. SEM BSE observations of the burrow fill of *Planolites* (large morphotype). Sample GMX#1. A. The little white rods are TiO_2 . Dashed rectangle corresponds to the area magnified in B. B. Detail of A showing texture and TiO_2 rods.

the chemical conditions necessary for iron sulfide precipitation were absent. The occurrence of a high total organic carbon content (TOC) in sediments is often taken to indicate low oxygen conditions (Allison et al., 1995). TOC can be estimated by considering shale colour because all colour in shales is ultimately controlled by the amount of organic matter present (Potter et al., 1980). According to diagrams relating rock colour and organic carbon (Fig. 1.25 in Potter et al., 1980; fig. 15 in Sandberg and Gutschick, 1984), the black shales of the Genna Muxerru Formation contain at least 1% organic carbon. This result supports the low-oxygen hypothesis for the Genna Muxerru Formation. On the whole, these observations point to low-oxygen conditions, from dysoxic to suboxic ones.

Low-oxygen conditions are also supported by the ichnological characteristics of Genna Muxerru Formation. Persistently small burrow diameters are best associated with reduced salinity or low-oxygen stress (Gingras et al., 2011). Monogeneric or low-diversity assemblages with *Chondrites* are related to oxygen-depleted settings (Bromley and Ekdale, 1984; Bromley, 1996; Buatois and Mángano, 2011). Fodinichnia is the dominant ethology, which indicates anoxic interstitial waters and at least dysoxic bottom waters (Ekdale and Mason, 1988). However, most

of our studied traces are backfilled, hence the problem in this interpretation is explaining how organisms maintained a connection with the oxygenated bottom-water. A possibility is retractive backfilling or, alternatively, that organisms were adapted to such low oxygen conditions. According to the Ekdale and Mason (1988) model, if both interstitial and bottom waters are at least dysoxic, pascichnia would have been dominant (see also Buatois and Mángano, 2011).

The model of Savrda and Bottjer (1986) places more emphasis on the pore-water oxygenation, although it does not rule out the role of bottom waters and substrate consistency in controlling tiering. The synthesis of this model is illustrated through a hypothetical oxygenation gradient in which diversity, size and penetration depth diminishes with diminishing oxygen (Savrda and Bottjer, 1986, 1989; Savrda, 1992). At the high-oxygen end of the gradient, large traces and a well-developed tiering structure, while at the lower end, just above the anaerobic threshold, only small, shallow-tier traces (e.g. *Chondrites*) are present (Savrda and Bottjer, 1986; Neto de Carvalho and Baucon, 2016). The latter, low-oxygen case fits with the Genna Muxerru ichnoassociation.

The hypothesis of a dysoxic water column is consistent with modern

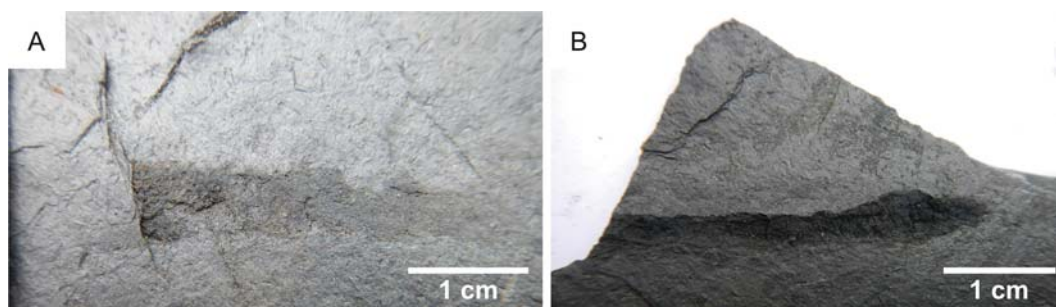


Fig. 14. *Planolites* (rough morphotype). A, GMX#17 B, GMX#18.

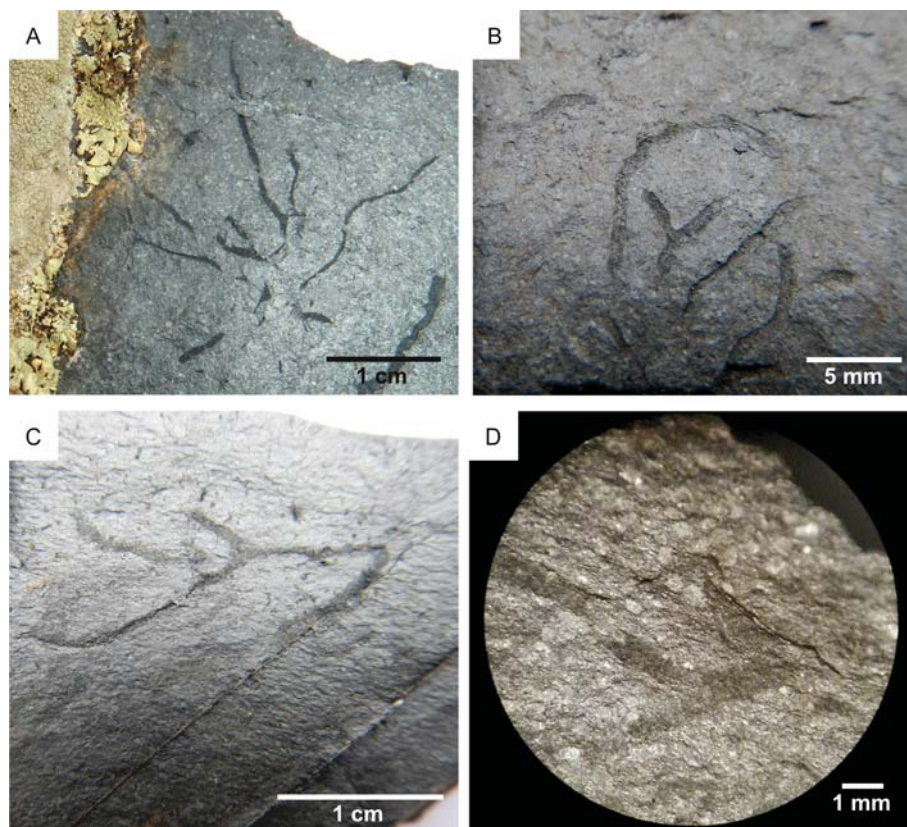


Fig. 15. ‘Small chondritid’. A. Specimen showing radial distribution of tunnels, sample GMX#10. B. Dichotomously branched tunnels (GMX#7). C. Specimen showing two branching orders (GMX#6). D. Stereoscopic image of GMX#6 showing very small pellets in the burrow fill. Bedding plane view.

oxygen minimum zones (OMZs), that are O_2 -deficient layers in the ocean water column (Paulmier and Ruiz-Pino, 2009). Observations on modern environments show that, where OMZs extend to the seafloor, the benthic fauna is adapted to dissolved concentrations as low as 0.1 ml of O_2/l (Diaz and Rosenberg, 2008). This is only apparently contrasting with the finding that the traditional definition to designate waters as hypoxic (2 ml O_2/l) is below the sublethal and lethal thresholds for a large number of animals (Vaquer-Sunyer and Duarte, 2008). In fact, response to oxygen depletion is often species-specific, with several organisms adapted to low oxygen concentrations (Diaz and Rosenberg, 1995). For instance, bioturbation by symbiont-bearing burrowing oligochaetes has been documented within a nearly anoxic basin (0.02–0.03 ml O_2/l H_2O) on the Peru margin (305 m of depth) (Levin et al., 2003). Sampling of open-ocean OMZ benthos suggests a strong lower-boundary effect, with high densities of hypoxia-tolerant faunas aggregating in the lower parts of OMZs (Levin et al., 2009). The bioturbated black shales in this study are consistent with this OMZ scenario, although further studies are required to confirm (or disprove) this hypothesis.

6.1.2. Salinity

The bioturbated black shales deposited under normal marine salinities. Highly diverse ichnofossil suites record optimal ecological conditions, whereas low-diversity suites suggest environmental stress (Gingras et al., 2011). Consequently, the low diversity of the Genna Muxerru Formation is likely to represent a stressed environment. Similar information is provided by the small size of burrows. Small burrows are associated with chemical stress, which is typically associated with substantial departures from marine salinities or lowered dissolved oxygen concentrations (sensu Gingras et al., 2011). Lowered dissolved oxygen is supported by the aforementioned sedimentological and ichnological observations. The presence of graptolites and of the marine

ichnotaxon *Phymatoderma* point to normal marine salinities.

6.1.3. Substrate and hydrodynamics

The tracemakers of the Genna Muxerru Formation colonized a low-hydrodynamics environment characterized by stiff mud and, in shallower tiers, water-saturated soupgrounds. The presence of a lining is commonly (but not exclusively) related to the presence of shifting substrates in the depositional locale (Gingras et al., 2011; Crippa et al., 2018). Consequently, the predominance of unlined burrows, together with the presence of bioglyphs, point to moderately stiff mud. This interpretation is supported by the bioturbation style. In muds, traces can be produced by “sediment swimmers” in soupy substrates or “tunnel builders” in firmer sediments (Schieber, 2003). The pelletal infill observed in many traces of the Genna Muxerru Formation is more compatible with tunnel builders than sediment swimmers, the latter of which characteristically produce mantle-and-swirl structures (Lobza and Schieber, 1999) that have been not documented in the studied outcrop. It should be noted, however, that *Cochlichnus* is a shallow-tier trace that is typical of soft- to soupground conditions (Buatois and Mángano, 2011). As such, the shallow-tier sediments of the Genna Muxerru Formation are interpreted as water-saturated soupgrounds, whereas deeper tiers were likely stiffer.

Low-hydrodynamics ichnofaunas are dominated by horizontal traces and have a relatively higher diversity compared to high-hydrodynamics ones; on the other hand, high-energy ichnofaunas are characterized by vertical burrows and low-diversity suites (Buatois and Mángano, 2011). The ichnofauna of the Genna Muxerru Formation shows the typical characteristics of low-hydrodynamics ichnofaunas.

6.1.4. Food supply and sedimentation rate

Data suggest that the Genna Muxerru palaeoenvironment was characterized by steady sedimentation and high food supply. The

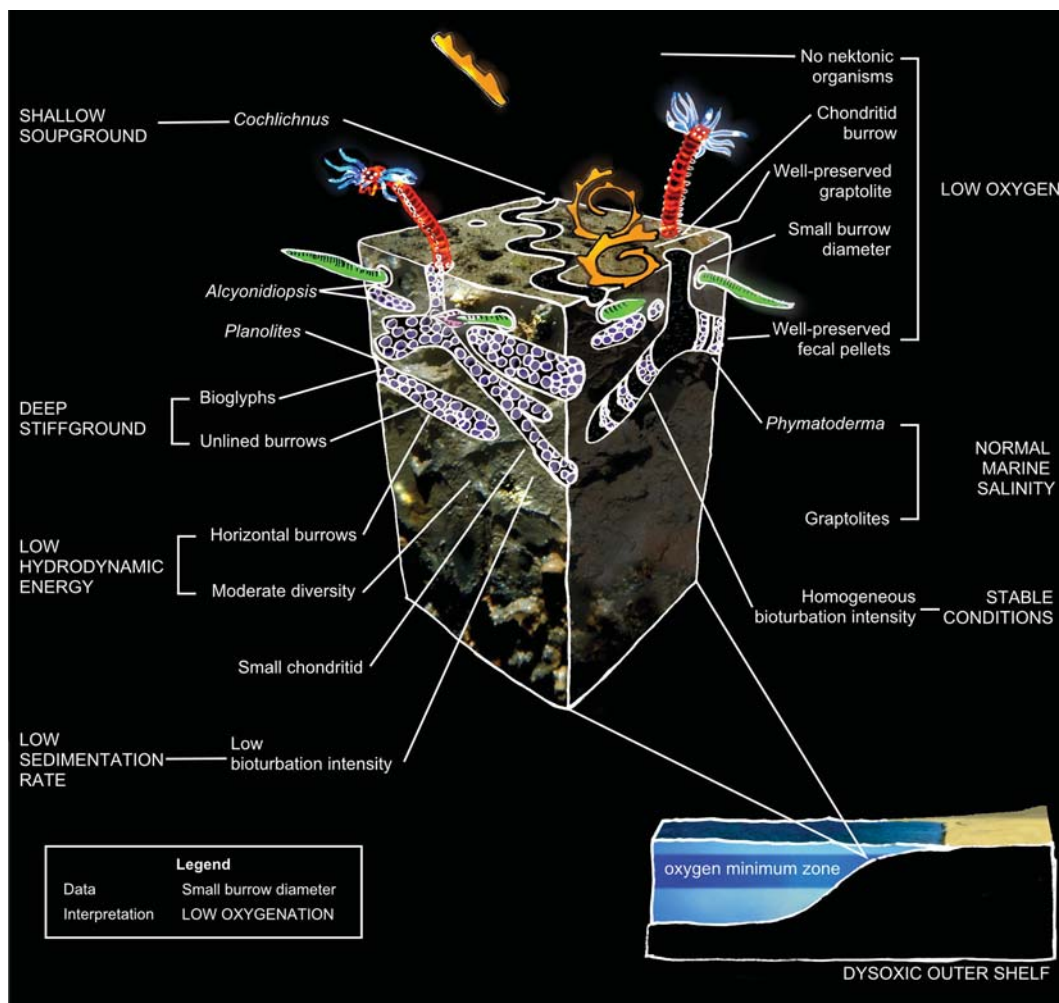


Fig. 16. Ichnological model of the Genna Muxerru Formation.

Genna Muxerru ichnofauna meets most criteria for high amounts of food supply (Wetzel and Uchman, 1998; Buatois and Mángano, 2011): (1) dark-coloured sediments; (2) complete bioturbation; (3) high density of shallow-tier ichnofossils; (4) rarity or absence of graphoglyptids; (5) deep tiers totally bioturbated by feeding systems connected with the surface. Specifically, the studied ichnofauna completely meets criterion 1 (it is hosted in black shales), 3 (it presents shallow-tier ichnofossils such as *Alcyonidiopsis* and *Planolites*), and 4 (no graphoglyptids are found). Criteria 2 and 5 are not completely met, although occasionally high bioturbation intensities are observed, as well as the presence of feeding systems connected with the surface (*Phymatoderma*). Ichnological evidence reflects the interplay between sedimentation, erosion and bioturbation (Buatois and Mángano, 2011). Neoichnological experiments show that low levels of bioturbation correlate with elevated levels of sedimentation and/or low densities of bioturbators (Gingras et al., 2008). The predominantly low bioturbation intensity of the studied outcrop is likely to reflect one of these aspects.

The homogeneous distribution of bioturbation is compatible with steady sedimentation rates. This is supported by physical sedimentary structures, which comprise lamination but no evidence for event deposition. Faults and soil cover preclude the possibility of exactly measuring the vertical extent of the Genna Muxerru Formation. For this reason, it is not possible to estimate the average deposition rate based on the biozones of the Genna Muxerru Formation.

6.1.5. Depth

Sedimentological evidence does not provide unequivocal answers

about bathymetry. In fact, sedimentation of organic-rich muds occurs within a wide depth range, from shallow (< 30 m) to deep marine environments (Smith et al., 2019). The presence of lydites (i.e., black cherts) in the lower part of the Genna Muxerru Formation (Gnoli et al., 1990) does not provide an exhaustive answer to the question of depth. Siliceous ooze is a typical deep-sea sediment, but biogenic siliceous sediments occur both in deep and shallow water depositional environments (Hesse, 1989; Racki and Cordey, 2000). It should be noted, however, that biogenic cherts mostly withdrew from peritidal settings to shelves and basins in the Early to Middle Ordovician (Kidder and Tomescu, 2016).

Body fossils of the Genna Muxerru Formation correspond to the sub-fauna of “typical hemipelagic black shales”, which are characterized by few non-graptolite fossils and moderately to highly diverse graptolite assemblages (Štorch, 1998). According to Štorch (1998), this sub-fauna corresponds to the deep shelf to upper slope environments (deeper than 100 m). Because of their diversity, graptolite faunas of SW Sardinia correspond to deeper settings (Štorch, 1998). This interpretation is supported by the presence of *Phymatoderma*, which occurs mostly in outer shelf or deeper environments (Uchman and Gaździcki, 2010).

6.1.6. Physicochemical variability

Oxygenation changes explain the observed fine-scale variations in bioturbation intensity. The outcrop characteristics prevent a thorough understanding of the distribution of burrowed media, which is a sensitive indicator of the physicochemical variability (both spatially and temporally) in a depositional setting (Gingras et al., 2011). In fact,

faults and soil cover preclude the possibility of following bioturbation along a stratigraphic log. This is certainly a severe limitation, but qualitative estimates can be done on the basis of the exposed bedsets and the regional distribution of bioturbated media.

Results indicate fine-scale variations in physicochemical conditions. Different metrical bedsets of the Genna Muxerru Formation generally display the same low (BPBI 2) bioturbation intensity. This suggests that, at the metrical scale, bioturbation is homogeneously distributed and, therefore, it indicates the persistence of low-oxygen conditions in time and space. At finer scales, bioturbation is sporadically heterogeneous, thus indicating variability in physicochemical conditions at a fine spatiotemporal scale. For example, an intensely bioturbated horizon (BPBI 3–4) with *Phymatoderma* (Fig. 10A) overlies horizons with lower bioturbation intensities.

The studied site is the only locality where trace fossils are found in the Genna Muxerru Formation, either in the type locality or in other areas of SW Sardinia, thus suggesting a stratigraphically (and/or spatially) abrupt transition from bioturbated to unbioturbated black shales. This transition from bioturbated to unbioturbated black shales requires an explanation. Following previous works (Savrda, 2007; Buatois and Mángano, 2011; Gingras et al., 2011), changes in four parameters may explain the observed changes in bioturbation intensity: (1) substrate attributes, (2) hydrodynamics, (3) depositional rate and (4) oxygenation. First, substrate controls can be excluded because the lithofacies of bioturbated deposits is virtually the same as that of unbioturbated black shales. Second, black shale deposition may have occurred in settings that were periodically influenced by significant current activity (Egenhoff and Fishman, 2013), hence a plausible hypothesis is that significant changes in hydrodynamics controlled bioturbation intensity. However, graptolite rhabdosomes of the Genna Muxerru Formation show no evidence of preferential orientation, therefore the depositional environment is likely to have been hydrodynamically quiet. Random orientation of graptolites is confirmed by previous studies (Ferretti et al., 2009). Third, biostratigraphical resolution does not permit a test of the hypothesis of changes in depositional rate.

Finally, oxygenation changes are the most obvious process accounting for the observed variation in bioturbation intensity. Observations on modern oxygen minimum zones show that relatively slight changes in dissolved oxygen allow the transition from bioturbated to unbioturbated sediments. For instance, Levin et al. (2009) described a transition from unbioturbated (completely laminated) to fully bioturbated sediments with an oxygen increase of only 0.10 ml/l, taking place over a 300 m depth range. Based on this evidence, the observed changes in bioturbation intensity can reflect similarly small variations in oxygenation.

6.1.7. Depositional environment and control processes

The aforementioned environmental parameters indicate that the bioturbated black shales deposited in an outer shelf environment with persisting depletion in oxygen, low hydrodynamics and moderately stiff muddy substrate. After elucidating the depositional environment, the crucial question is what processes did control the deposition of organic-rich muds in the Genna Muxerru Formation. Two traditional end-member models explain the organic enrichment observed in black shales (Werne et al., 2002): the preservation model (Demaison and Moore, 1980) and the productivity model (Pederson and Calvert, 1990). In the preservation model, anoxic conditions derived from stratified water column favouring preservation of organic matter. By contrast, in the productivity model, high concentrations of organic matter result from high primary productivity (Werne et al., 2002).

The productivity model fits with the larger ecological picture proposed for the lower Silurian of peri-Gondwana. In fact, high productivity has been proposed as the trigger of the widespread peri-Gondwanan dysoxia during Llandovery and Wenlock times (Štorch, 1998). This hypothesis links the extensive distribution of graptolite-rich black shales to low-oxygen conditions, which were in turn triggered by

high productivity. According to Štorch (1998), high productivity resulted from the influx of nutrients washed down from the continent and it was maintained by a cool south-subpolar circum-Gondwanan current. It should be noted that the productivity hypothesis does not exclude water column anoxia, which is indeed suggested by the absence of nekton in the Genna Muxerru Formation. Oxygen depletion is not only a Silurian phenomenon, but it is widespread in modern oceans (Levin, 2003) and is expected to increase (Vaquer-Sunyer and Duarte, 2008). For this reason, the Genna Muxerru Formation can represent a useful model to predict future changes in benthic ecosystems.

6.2. Infaunal ecology of black shales: How to survive in a near-anoxic world?

This section aims to delineate the characteristics (body plan, identity, and lifestyle) that allowed tracemakers to survive the harsh conditions of the Genna Muxerru Formation. These aspects are important to elucidate because the Genna Muxerru Formation represents a model to understand the faunal response to low oxygen conditions, which are expected to increase in the future as a result of the combined effects of coastal eutrophication and global warming (Vaquer-Sunyer and Duarte, 2008). This case study also demonstrates that fine-scale observations, including microscopic ones, are key to investigate infaunal ecology of black shales. Bioturbation in black shales is occasionally reported, and it may be commoner than expected (Williams and Rickards, 1984; Schieber, 2003; Izumi, 2012; Neto de Carvalho et al., 2016). In fact, visibility of black shale traces is low because of the relatively low textural contrast with the host rock (e.g. “black on black traces” of Schieber, 2003).

The body plan of the Genna Muxerru tracemakers was predominantly vermiform, whereas a precise taxonomic identification of the tracemakers is precluded. However, the burrows of the Genna Muxerru Formation can be grouped according to their bioprint, i.e. the characters that allow recognition of the maker (Rindsberg and Kopaska-Merkel, 2005). *Alcyonidiopsis* has a distinctive bioprint that is shared with the *Cochlichnus* and ‘*Small chondritid*’ of the Genna Muxerru Formation. These traces are therefore likely the burrows of the same (or similar) vermiform animals. *Planolites* (large morphotype) may share its bioprint with *Planolites* (rough morphotype), whereas *Phymatoderma* does not present common elements with other traces.

The characteristics of the Genna Muxerru ichnofauna (moderate to low bioturbation intensity, relatively low diversity, shallow tier, and small size) fit with the existing ichnological models for reconstructing the degree of paleooxygenation (Savrda and Bottjer, 1986; Ekdale and Mason, 1988; Leszczyński, 1991; Martin, 2004; Savrda, 2007). All of them agree that the density of bioturbation, trace fossil diversity, maximum penetration and burrow size tend to decrease with decreasing oxygen (Savrda and Bottjer, 1986; Buatois and Mángano, 2011).

In the Genna Muxerru Formation a pellet-backfilling sediment-feeding lifestyle dominates. The dominance of sediment feeders is explained by the fact that low-oxygen conditions promote organic carbon burial in marine sediments (Koho et al., 2013), which constitute a food source for sediment feeders. This is also supported by neoichnological observations, showing that low-oxygen substrates favour intense bioturbation by deposit-feeding tracemakers, provided that the water column is sufficiently oxygenated (Baucon and Felletti, 2013a, 2013b). Enhanced preservation of organic matter in low-oxygen settings has been proposed by several authors (Werne et al., 2002). For instance, the high total organic contents within sediments of Peruvian oxygen minimum zones have been explained by enhanced preservation (Böning et al., 2004). However, according to Calvert (1987), the preferential preservation of organic matter under low oxygen conditions is considered to be of secondary importance in governing the accumulation of carbon. Accordingly, the primary processes which determine the organic content of sediments are the supply of organic matter (controlled

by primary productivity) and the bulk sedimentation rate (Calvert, 1987). In addition, low oxygen environments favour the proliferation of sulfate reductive bacteria, which in turn could be excellent food resources for deposit feeders (Luo et al., 2016).

Data from other low-oxygen environments, both fossil and modern, support the idea of sediment feeding (deposit-and detritus-feeding) as a dominant strategy in low-oxygen settings. In fact, dysaerobic fossil associations characteristically include ichnofossils reflecting detritus and deposit feeding, as well as chemosymbiotic strategies (Savrdá and Bottjer, 1989; Buatois and Mángano, 2011; Mángano, 2011). The burrows of the modern spionid polychaete *Paraprionospio pinnata*, implementing both suspension and deposit feeding, have been observed in conditions of severe hypoxia (Sturdivant et al., 2012). Levin et al. (2009) suggest that under modern exaerobic conditions the dominating lifestyle is that of large, mobile detritivores residing in permanent burrows.

Burrows of the Genna Muxerru Formation are commonly filled by pellets, and the same phenomenon is documented from other low oxygen palaeoenvironments. Examples include *Phycodes canalensis* and *Tomaculum problematicum* from the Ordovician black slates of Canelas (Neto De Carvalho et al., 2016b); *Phymatoderma granulata* from the Jurassic Posidonia Shale (Izumi, 2012). The commonality of pellet-filled burrows in black shales is explained by two hypotheses. The first hypothesis is preservational. It is well established that low-oxygen conditions are beneficial to the preservation of organic matter, including that of faecal matter (Koho et al., 2013; Luo et al., 2016). Consequently, the abundance of pellet-filled ichnofossils from low-oxygen settings may reflect the favourable preservation of faecal pellets in low-oxygen environments. As Uchman (1999) observed, it is likely that numerous traces were previously filled with faecal pellets, which however failed to be preserved. The second hypothesis is behavioural. Pellet-backfilled burrows may be common in low-oxygen environments because they provide an adaptive advantage to their producers. For instance, tracemakers could store pellets to use them as a bacteria-enriched resource during times of food shortage (Bromley, 1991; Izumi, 2012; García-Ramos et al., 2014; Kotake, 2014; Löwemark, 2015). This may involve chemosymbiotic strategies (Izumi, 2012; García-Ramos et al., 2014). Following the interpretation of *Chondrites* by Fu (1991), the *Chondrites*-like burrow ('*Small chondritid*'; Fig. 15) of the Genna Muxerru Formation may indicate chemosymbiotic strategies (see also Baucon et al., 2020). Nevertheless, the probable presence of pellets within the '*Small chondritid*' is more compatible with a pellet-filling, sediment-feeding behaviour.

7. Conclusions

A new black shale ichnosite hosts small trace fossils produced by sediment-feeders. The black shales of the studied site appear featureless at the macroscopic scale, whereas fine-scale observations reveal an abundant and well-preserved ichnofauna. This suggests that bioturbation in black shales may be commoner than expected and that an observation bias may have precluded documentation of black shale ichnofaunas at a global scale. This agrees with previous works on organic-rich mudstones. Consequently, this study encourages the development of image enhancement techniques to better appreciate bioturbation in black shales. The poor visibility of the Genna Muxerru Formation raises problems concerning ethological and ichnotaxonomical interpretation of black shale traces. In fact, the pellets filling the Genna Muxerru traces are submillimetric and poorly visible, therefore they raise the problem of how to deal with similar traces in ethological and ichnotaxonomical analysis.

In addition, the Genna Muxerru structures raise the problem of how to distinguish between trace and body fossils in black shales. Fossil algae and trace fossils share morphological and preservational characteristics, for these reasons the interpretation of the Genna Muxerru structures has been particularly challenging. In this regard, the

presence of pelletal infill makes the ichnological interpretation more plausible. We highlight the need of a specific study on how to distinguish trace fossils from fossil algae in black shales, even because this is fundamental for sound palaeoenvironmental interpretations.

Integration of sedimentology, ichnology and body fossil palaeontology reveals the depositional environment of the bioturbated black shales of the Genna Muxerru Formation. The bioturbated black shales were deposited in outer shelf (or deeper) settings with severe depletion in oxygen in both bottom- and porewaters (up to 0.1 ml of O₂/l). The environment was hydrodynamically quiet. The seafloor consisted of moderately stiff muds that provided a high food supply for bioturbators. These extreme conditions persisted throughout the deposition of the bioturbated horizon and, possibly, a slight depletion in oxygen produced the successive disappearance of bioturbators. A pellet-filling sediment feeding lifestyle dominated the low-oxygen muds of the Genna Muxerru Formation. This can reflect a preservational or behavioural control. Further neoichnological studies of low oxygen environments are required to understand why pellet-filled burrows are so common in oxygen-depleted settings.

The aforementioned ecological scenario was probably part of a larger picture, that is, the widespread peri-Gondwanan dysoxia of Llandovery and Wenlock times. Oxygen depletion is not only a Silurian phenomenon, but it is widespread in modern oceans, and is expected to increase. The results of this study, therefore, encourage more studies on peri-Gondwanan ichnofaunas of Silurian times. Trace fossils are primarily the product of behaviour, i.e. different organisms can produce the same trace if behaving similarly. This property allows a direct comparison between modern and fossil ichnofaunas, for which recent studies on Silurian peri-gondwanan ichnofaunas can help to predict the benthos response to the current expansion of low-oxygen seafloors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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