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RESEARCH PAPER

Burrows without a trace—How meioturbation affects rock fabrics and leaves a record of meiobenthos activity in shales and mudstones

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Abstract

Understanding fine-grained sediment accumulation is critical for developing robust geologic models and inferring environmental conditions. Here we report on processes that produce compositional layering at the mm and sub-mm scale, with gradational rather than sharp layer boundaries. Sometimes described as fuzzy laminae, this feature occurs in modern muds that accumulate under oxygen-stressed conditions, caused by meiofauna (tiny organisms; benthic foraminifera, polychaetes, nematodes, etc.) that disrupts the original fabric. In the rock record, fuzzy laminae are common in shales that accumulated under presumed oxygen-stressed conditions. Like their presumed modern analogs, ancient examples contain remains of benthic foraminifera and other small benthic organisms that were the likely agents of fabric disruption. As preserved lamination is considered indicative of bottom water anoxia in ancient shales, we need to better understand the cause of fuzzy lamination, because such insights have the potential to allow much refined assessments of the depositional history of laminated organic-rich shales. In experiments, nematode activity blurred the originally sharp contacts between successive sediment layers with contrasting composition. Although nematode activity produces tiny temporary traces aside of blurring of primary fabric, the former have minimal preservation potential due to compaction of the water-rich substrate. Experimental fabrics compare well to those observed in a wide range of ancient black shales, suggesting common meiofaunal activity in the latter. Our findings imply that the details of lamination (fuzzy vs. sharp) in ancient shales are not necessarily controlled by bottom water oxygenation, but instead result from the interplay between sedimentation rates and bottom current activity.

Keywords Meioturbation · Black shales · Suboxic · Anoxia · Banding · Meiofauna

Introduction

Bioturbation is an important cause for fabric disruption in sediments and affects porosity, permeability, diagenetic processes, and mechanical properties of the final deposit (Pemberton and Gingras 2005; Hovikoski et al. 2008; Aplin and Macquaker 2011; Lemiski et al. 2011; Bednarz and McIlroy 2012; Hart et al. 2013). Prior studies of bioturbation in mudstones have focused on macroscopically visible traces, with an emphasis on event sedimentation and identification of particular burrow associations and burrow successions, aimed at deriving information about substrate conditions and oxygen availability in pore spaces and bottom waters (Byers 1977; Jordan 1985; Savrda and Bottjer 1986, 1989; Cuomo and Rhoads 1987; Ekdale and Mason 1988; Cuomo and Bartholomew 1991; Savrda and Ozalas 1993; Lobza and Schieber 1999; Schieber 2003; Löwemark et al. 2006; Boyer and Droser 2011; Bednarz and McIlroy 2012). With regard to bottom water oxygenation levels, four categories are commonly considered for modern environments and corresponding biofacies, respectively (Tyson and Pearson 1991), namely oxic (8.0–2.0 ml/l O_2) and aerobic, dysoxic (2.0–0.2 ml/l O_2) and dysaerobic, suboxic (0.2–0.0 ml/l O_2) and quasi-anaerobic, and anoxic (0.0 ml/l O_2, H_2S) or anaerobic. In the rock record, aerobic sediments are characterized by the activity of shelly and vermiform macrofauna and clearly visible burrows; dysaerobic sediments largely reflect the activity of smaller vermiforms (polychaetes, nematodes); quasi-anearobic sediments record the activities of an

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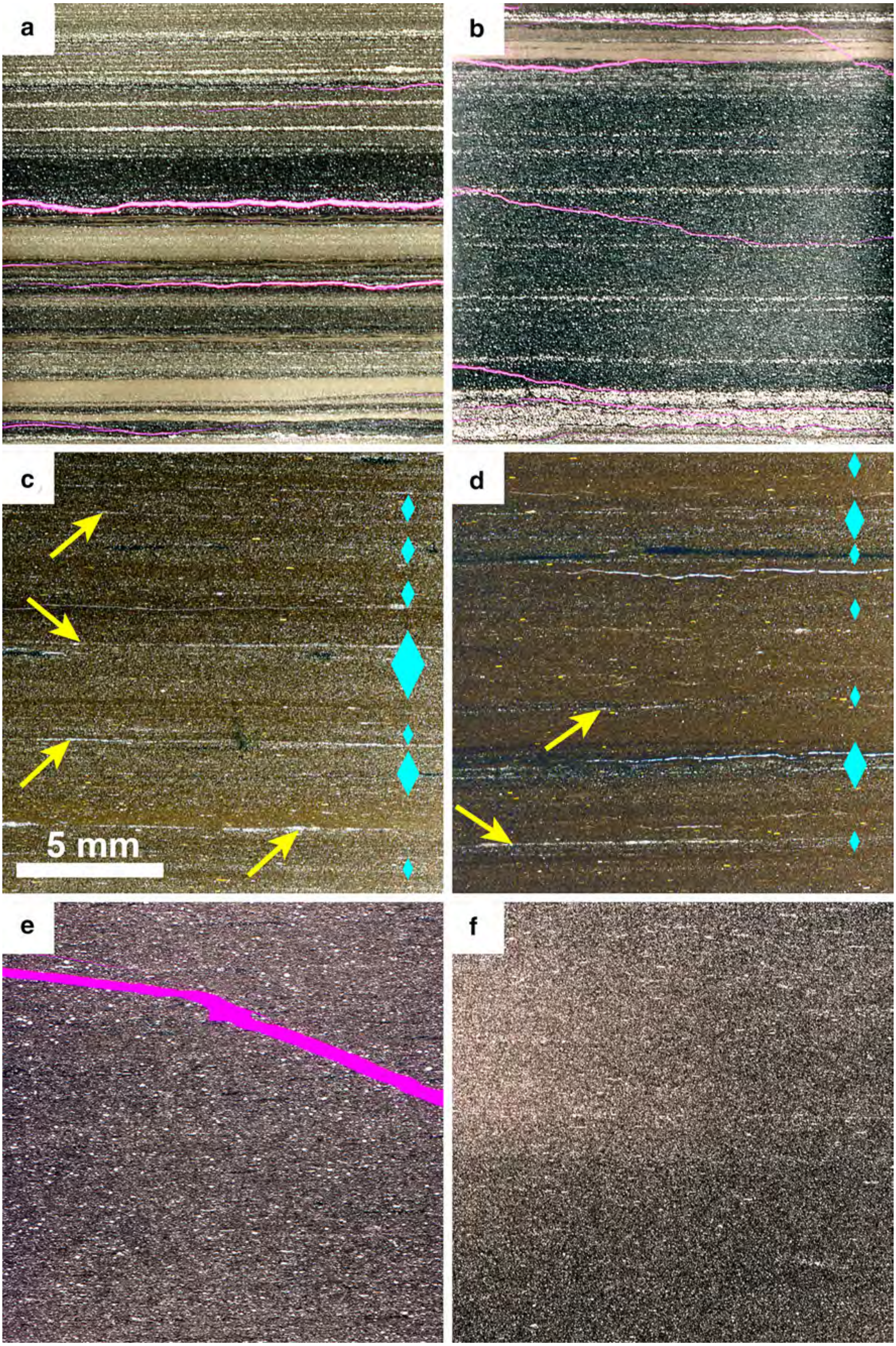
a
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5 mm

◂**Fig. 1** Comparing shales with true primary lamination to shales where various levels of meiofaunal modification may have degraded or even erased primary laminae. **a**, **b** Photomicrographs of shale laminae in theMesoproterozoic Velkerri Formation of Australia. Given the age of these rocks, the laminae are considered primary. They have the appearance of bottom current produced laminae seen in flume experiments, reflecting a continuum of flocculation, bedload transport, and coarse silt segregation (Yawar and Schieber 2017). **c**, **d** Photomicrographs of the Late Devonian New Albany Shale (Indiana, USA). These rocks are commonly described as laminated, but their "lamination" differs substantially from that seen in Precambrian shales. Although there are some laminae that appear reasonably well defined (yellow arrows), there are also zones (or "bands") where a silt-enriched interval passes gradually into under- and over-lying clay-rich intervals (blue lozenges). **e**, **f** The "worst case" scenario, complete homogenization. Samples from the Devonian Muskva Shale, British Columbia, Canada (**e**), and the Late Devonian Chattanooga Shale of Tennessee, USA

impoverished community of very small vermiforms (polychaetes, nematodes) and benthic foraminifera; and anaerobic sediments have not been disrupted by benthic organisms (Bernhard and Reimers 1991; Savrda and Bottjer 1991; Tyson and Pearson 1991; Bernhard et al. 1997).

In the context of this paper, macrobioturbation is understood as clearly visible traces produced by macrofauna, i.e., fauna > 1 mm in diameter (Giere 2009). In shales, common ichnogenera in this category include *Chondrites, Zoophycos, Planolites, Teichichnus, Thalassinoides, Phycosiphon, Spirophyton, Scolicia, Nereites, Palaeophycus, Lophoctenium,* and *Trichichnus* (Savrda and Bottjer 1991; Savrda and Ozalas 1993; Wetzel and Uchman 1998, 2012).

The ubiquity of meiobenthos in marine muds has long been known to marine biologists (Mare 1942; Higgins and Thiel 1988), and there is a growing recognition of concomitant meiofaunal fabric disruption in modern muds (Cullen 1973; Riemann and Schrage 1978; Pike et al. 2001; Bernhard et al. 2003; Löhr and Kennedy 2014). However, how meiofaunal activity can be detected in fully compacted and lithified ancient mudstones and shales is an unresolved issue (Egenhoff and Fishman 2013; Schieber 2014; Schieber et al. 2021). Meiofauna are benthic invertebrates that are loosely defined by size (pass through a 1-mm mesh sieve and are retained by a 45-micron sieve), include organisms such as nematodes, copepods, ostracods, and foraminifera (Giere 2009), and occur in a wide variety of surface substrates and sedimentary environments. Nematodes are considered the dominant sediment infauna on the basis of abundance and biomass (Riemann and Schrage 1978; Reichelt 1991; Giere 2009). In modern marine settings, nematodes are most abundant in the uppermost centimeters of the substrate with distribution governed by concentrations of dissolved oxygen and organic matter (OM) (Neira et al. 2001; Giere 2009). Generally, as dissolved oxygen decreases downwards in the sediment, so does the abundance of nematodes. Nematodes tend to be most abundant in the uppermost few cm's of the sediment column where the abundance of metabolizable OM is highest (Giere 2009). In modern deep sea sediments, the concentration of nematodes in the uppermost 5 cm can be as large as 500 individuals per cm^3 (Shirayama and Kojima 1994; Guilini et al. 2011). In the modern suboxic to dysoxic bottom waters of the central Santa Barbara Basin, meiofaunal abundance at a depth of 0–1 cm can be as high as ~ 80 individuals per cm^3 (Pike et al. 2001). Modern marine nematodes create a closely spaced network of sinusoidal burrows (Cullen 1973; Jensen 1996; Pike et al. 2001), as well as vertical sinuous tubes (Neira et al. 2001). Bioturbation by meiofauna (such as nematodes) in modern muds is subtle in terms of ready visibility, but nonetheless has significant impact on sediment fabrics, nutrient fluxes, and sediment chemistry (Cullen 1973; Riemann and Schrage 1978; Reichelt 1991; Aller and Aller 1992; Jensen 1996; Pike et al. 2001; Giere 2009).

Because it is becoming increasingly evident that many organic-rich shales were not deposited under persistent anoxic conditions (Macquaker et al. 1998; McCollum 1988; Schieber 2003, 2009, 2011; Boyer et al. 2011; Trabucho-Alexandre et al. 2012; Wilson and Schieber 2015; Liu et al. 2019; Smith et al. 2019), criteria that allow us to detect benthic life at the cusp of anoxia in ancient muds are essential for more realistic and sophisticated assessments of paleo-oxygenation. On the modern seafloor, meiobenthos thrives under suboxic to dysoxic bottom water conditions, owing to the absence of competing or predatory macrofauna (Levin et al. 1991; Savrda and Bottjer 1991). Given that the nematode body fossil record dates back to 400 Ma, and may extent to ~ 470 Ma (Baliński et al. 2013) or even 550 Ma (Parry et al. 2017) via possible burrow evidence, it is rather plausible that nematodes and other meiobenthos were a common component of the muds that eventually became ancient black shale successions. Current methodologies for assessing past benthic activity (Smith and Schafer 1984; Droser and Bottjer 1993) do not address this aspect of benthic life, and are in need of augmentation to allow inclusion and assessment of meiofaunal activity.

The effects of meiofaunal activity have been well documented in sandy sediments, where meiofauna acts to blur the primary sedimentary fabric (Howard and Frey 1975; Pemberton et al. 2008). Pemberton et al. (2008) used the term cryptobioturbation to collectively describe the "obscuring" effect of meiobenthos, and noted that it leaves no discrete trace in the sediment and that originally sharp laminae now have fuzzy boundaries due to grain displacement. In shales, the term cryptobioturbation has been applied to a range of phenomena attributed to benthic organisms, such as compacted fecal pellet strings produced by polychaete worms (Cuomo and Rhoads 1987; Cuomo and Bartholomew 1991), false silt laminae created from segregation or reorientation of grains (Schieber 1999), as well as faintly visible burrows due to lacking color contrast between host rock and burrow fill (Schieber 2003), and disruption of primary laminae

(Sageman 1985, 1989; Savrda and Bottjer 1991). Closely allied (if not identical) with this outlook on subtle bioturbation features in mudstones is the term bio-deformational structures (sensu Schäfer 1956; Wetzel and Uchman 1998). In multiple studies of black shale units, primary physcial laminae (Fig. 1a, b) have been contrasted with apparently degraded primary laminae (Fig. 1b, c). The latter have been ascribed to cryptobioturbation in a general sense (e.g. O'Brien 1987; Schieber 1999, 2003; Leonowicz 2015; Wilson and Schieber 2015; Boulesteix et al. 2019; Woo et al. 2021), with "crypto" denoting a "challenge of identification" regardless of the actual size of the causative organism.

Whereas degraded laminae as seen in Fig. 1c and d may be considered merely "troublesome", we also find in condensed black shales cm- and even dm-thick intervals that look so uniform and featureless (Fig. 1e, f) that one is hard pressed to interpret them in terms of any known depositional processes. Given the fact that these rocks accumulated very slowly and can have organic carbon contents upwards of 10 wt.%, one would reasonably expect them to be well laminated. Instead, the best word one can find to describe them is a headache-inducing "homogeneous". The observations made in the course of this study suggest that the combined influences of net sedimentation rate, bottom current activity, and oxygen limitation produce a continuum of black shale fabrics that range from perfectly laminated to fully homogenized, and that "reading" these fabrics in the broader context of the stratigraphic succession can be highly informative.

Neoichnological experimentation produces traces and burrows under controlled conditions that can serve as analogs that help us to understand presumed biogenic textures in the rock record (Lobza and Schieber 1999; Fairchild and Hasiotis 2011; Retrum et al. 2011). Whereas burrowing by meiofauna in modern fine-grained sediments is well documented (Cullen 1973; Riemann and Schrage 1978; Savrda et al. 1984; Reichelt 1991; Zobrist and Coull 1992; Jensen 1996; Neira et al. 2001; Pike et al. 2001; Giere 2009; Löhr and Kennedy 2014), how a record of such activity might be preserved in ancient mudstones is poorly understood and provided the motivation for the experiments described here. In these experiments we used nematodes to produce "fabric blurring" and "fuzzy laminae" that resemble those observed in Phanerozoic shale successions (Fig. 1c, d). Because of the ephemeral nature and low preservation potential of nematode burrows (Cuomo and Rhoads 1987; Pike et al. 2001; Löhr and Kennedy 2014; Schieber 2014), the focus of our experiments was not to document a specific burrowing style or burrow morphology, but rather on the cumulative effect of meiofaunal activity on sedimentary fabrics and textures. On the basis of detailed observations made in these experiments we were able to observe how nematodes produced gradational layer boundaries and fuzzy laminae, and relate this style of lamina degradation to observations made on modern sediments (Schäfer 1956; Savrda et al. 1984). We propose the terms "meioturbation" or "meioturbated" to describe this kind of "diffused" layering that presents as "fuzzy" laminae, blurred contacts, and compositional "banding" in ancient mudstones (Wilson and Schieber 2015).

Methods

Neoichnological experiments were conducted in small aquaria and 1000 mL glass cylinders. In order to explore the potential influence of salinity on developing fabrics, room temperature (~ 20 °C) experiments were conducted in freshwater as well as at marine salinity (3.5% salt content), although the majority of the experiments were conducted with freshwater because it extended the life of the nematodes used in the experiments. The sediment was industrial grade kaolinite and illite, as well as naturally occurring mud from salt marshes near Savannah, Georgia, USA. The latter was sieved to grain sizes < 63 µm, 63–150 µm, 150–350 µm, and 500–1000 µm. The finest fraction (dark, organic-rich mud) contained naturally occurring meiofauna. To make layers and layer boundaries easier to observe, colored chalk was added to some clay layers for better contrast with underlying or overlying layers. Clay was mixed with water in a blender for ~ 10 min to break up aggregates before spreading it evenly across the tank/cylinder surface and allowing it to settle until the water was clear (approximately 1–2 days). Initial water contents in volume percent were determined for the clay layers immediately before nematode addition. The thickness of clay layers was measured multiple times in the course of a given experiment.

Anguillula silusiae, a nematode commonly used as fish food, was used in the experiments (Fig. 2) because cultures are readily obtained from biological supply stores and easy to propagate. Slender and vermiform in shape, *Anguillula silusiae* may reach 2 mm in length and 0.05 mm in width. It was used as a proxy for marine mud nematodes because its body shape and burrow morphology resembles those of its marine counterparts (Cullen 1973).

Fig. 2 Photomicrograph of the nematode *Anguillula silusiae* used in experiments

The abundance of nematodes added to an experiment was estimated as follows: a 1 cm long swipe with a Q-tip collects approximately 350 nematodes from the nematode film along the lower wall of the culture tank. Thus, as long as the total "swipe length" (in cm) is known, the number of nematods can be estimated. The density of *Anguillula silusiae* added to an experiment was then calculated by dividing the estimated number of collected specimens by the surface area of the clay layer and under assumption that most nematodes would populate the uppermost cm of the sediment layer. The thus achieved specimen density was equivalent to the nematode density in the central Santa Barbara Basin (Pike et al. 2001) which was reported as ~ 80 nematodes per cm^3 at a depth of 0–1 cm below the sediment surface. Variables in the experiments included different grain sizes, sediment composition, organic content, and thickness of layers. Once nematodes were added, the experiments extended for about 1–2 days.

Digital camera still photographs, high definition video, time-lapse photography, and core sampling of water-saturated sediments were utilized to capture fabric disruption during experiments. The core samples were stabilized with a water–acetone–epoxy exchange method (Schimmelmann et al. 2018) that produced a Spurr-resin impregnated core with a diameter of ~ 1 cm (Lotter and Lemcke 1999). Sample cores were sectioned and argon ion-milled for scanning electron microscope (SEM) observation (Schieber 2013; Schieber et al. 2016). High-resolution plan view and cross sectional images of the experiments were taken at the beginning, during, and at the end of each experiment (Fig. 3).

To evaluate what the experimental muds might look like in the rock record, the images were virtually compacted with image processing software (Adobe Photoshop™) to simulate the compaction induced loss of water (Fig. 4; Lobza and Schieber 1999), which in modern surface muds of the Santa Barbara Basin can be as high as 95% by volume (Schimmelmann et al. 1990). It should be noted that virtual compaction only works when the sediments in question are muds. It cannot replicate the compaction of framework supported or heterogeneous sediments, such as interlayered sand and mud.

Results

Textures of nematode burrows in natural muds

In some experiments, organic-rich mud with natural meiofauna from Savannah, Georgia, was used as one of the layers, and SEM images of the Spurr-embedded and ion milled core samples show the impact of meiofauna on the mud-fabric (Fig. 4).

Closer examination of the dark layer in Fig. 4 showed more textural detail that can be attributed to nematode burrows and also shows that large portions of the matrix do not show diagnostic features of nematode burrows (Fig. 5). The latter observation, combined with the likelihood that compaction will render burrows unrecognizable (Schieber 2014) does not bode well for recognizing nematode burrows in ancient mudstones.

A similar clotted-mottled background fabric is also dominant in Fig. 6, where several rounded features stand out as likely cross-sections of nematode tunnels. These tunnel cross sections appear to be stabilized by some cohesion-providing substance, most plausibly mucus that is excreted abundantly by nematodes as they pass through the mud matrix (Moens et al. 2005; Schratzberger et al. 2019).

In view of the high water content (in excess of 85 vol%) of the mud shown in Figs. 4, 5, and 6, the sharp contrast between tunnels and adjacent sediment matrix (Fig. 5b) suggests that something inside the tunnels kept the tunnels from collapsing or from being infilled with matrix. In consideration of likely mucus stabilized wall linings and concentric alignment of clay particles (Fig. 6), this contrast (Fig. 5b) and the lack of tunnel collapse is best explained with tunnels that are filled with mucus that was left behind by nematodes moving through the sediment (Moens et al. 2005).

Burrow density of macrofauna vs. meiofauna

Natural muds used in this project contained a wide range of infaunal organisms, but with regard to trace makers there were various polychaete worms of up to 5 cm length, and mm-scale nematodes. Though the macroburrows produced by the polychaetes are readily visible along the aquarium wall (Fig. 7b), they only affect a comparatively small volume of sediment when compared to the burrowing activity of the much more abundant nematodes (Fig. 7c). Macroburrowers may move substantial volumes of sediment, as illustrated by the fecal mound in Fig. 7b, but they only disrupt layering at a cm-scale spacing, whereas nematodes pervasively intercept layer boundaries at the sub-mm scale. Any single nematode may move or displace only a small number of sediment particles, but their cumulative effect is to persistently mix sediment at layer boundaries and to fully disrupt the internal fabric of primary layers at a length scale of 10s to 100s of micrometers.

Particle dispersal by nematode burrowing

Experiments where thin layers of sand grains were placed on top of the mud surface vividly illustrate the effectiveness of nematodes to disperse particles and "diffuse" them away from their original location (Fig. 8). The same holds true for dispersal of coarse silt grains and smaller particles, but it is more difficult to see without added effort (resin embedding, polishing, and SEM imaging). In less than 2 days about 75% the sand layer in Fig. 8a had been diffused into the

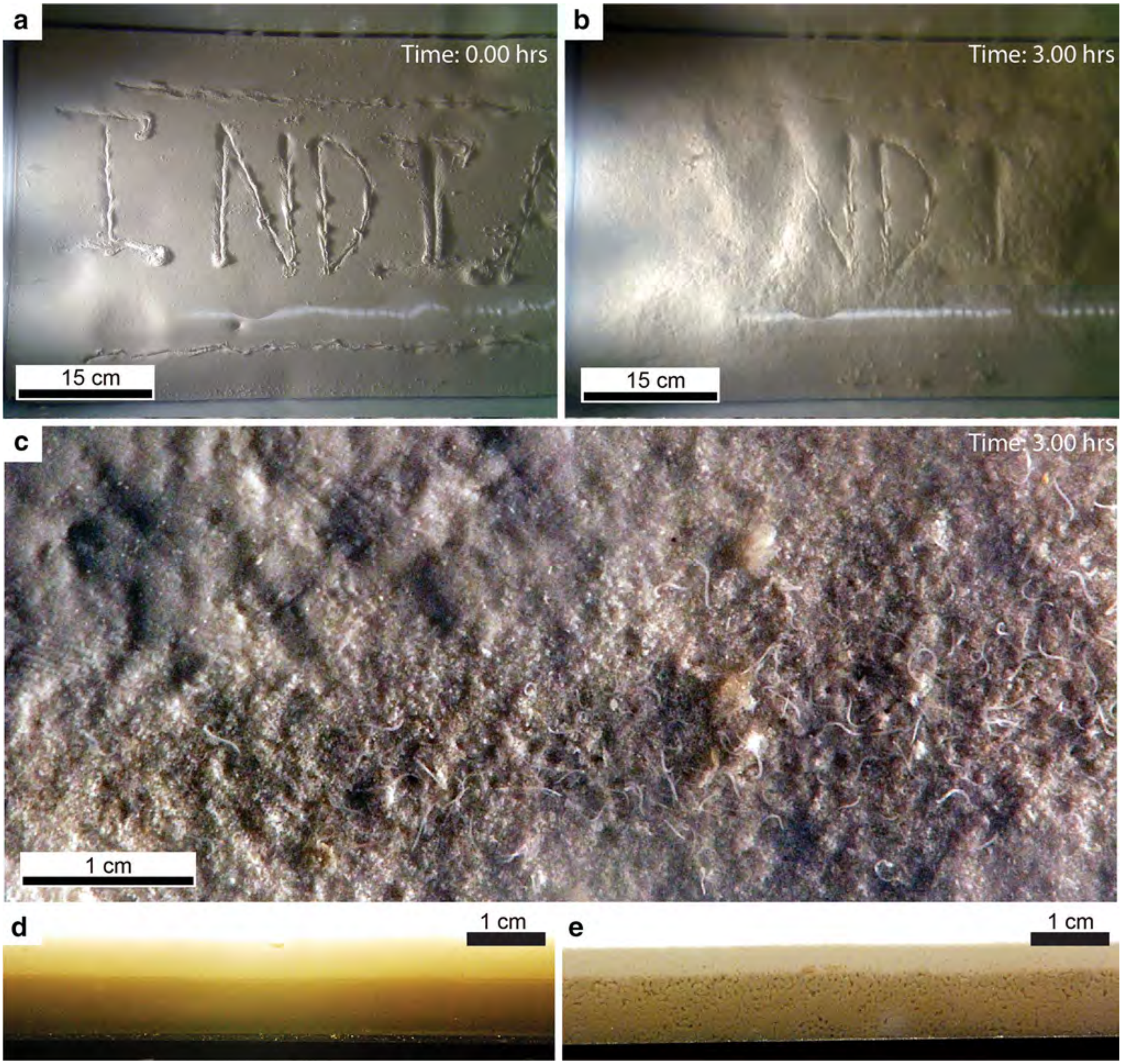

Fig. 3 Representative images from the first experiment. **a** Plan view image of the sediment surface (kaolinite) with "INDIANA" carved into sediment. **b** Same surface 3 h after adding nematodes to the lower left corner of the aquarium. Note the decreasing clarity of the "INDIANA" outline from right to left. **c** Close-up image of the surface showing nematodes burrowing into the kaolinite layer. **d** Cross-sectional image of the experiment before addition of nematodes with sharp boundary between the lower (illite) and upper (kaolinite) clay layer. **e** Cross-sectional image 3 h after adding nematodes. Note the open network of nematode burrows and onset of fuzziness at the boundary between the clay layers

underlying mud layer (Fig. 8b), an indication that even layers with a marked compositional contrast to the prevailing mud matrix can become "invisible" very quickly.

Blending and erasing layer boundaries

Multiple experiments were conducted to simulate the impact of meiofaunal disruption on primary fabrics. During clay addition to experiment tanks, most of the clay settled to the bottom over the course of several hours, and sharp and straight layer boundaries developed (Fig. 3d). The water content of freshly settled clays can exceed 90 vol.% initially, and once nematodes are added they cause partial collapse of this very fragile initial fabric (Fig. 9). The collapse causes layer thickness to be reduced by 40–50%, and the water content drops to about 85 vol.% (Fig. 9c), comparable to the water

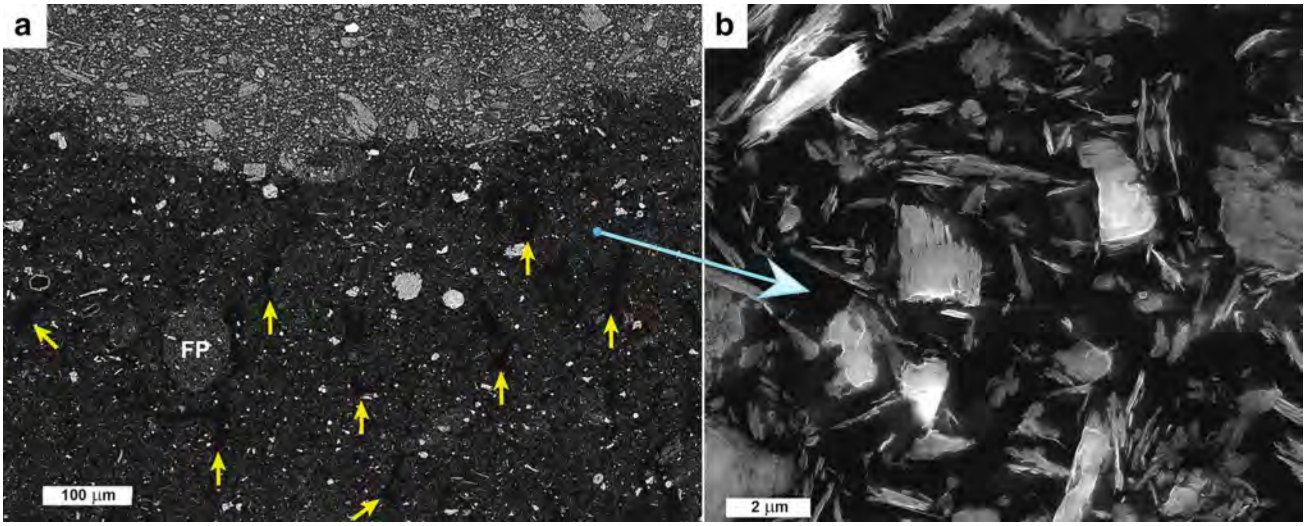

Fig. 4 **a** SEM backscatter image of epoxy-embedded organic-rich mud (dark layer) overlain by a silt layer (light layer). Yellow arrows point to epoxy-filled worm traces due to nematodes. FP marks a fecal pellet from a larger organism. **b** A detailed view of the matrix of the dark layer that shows a cardhouse structure of clay particles. The dark areas, now epoxy, were originally filled with pore fluids, and attest to a high initial water content

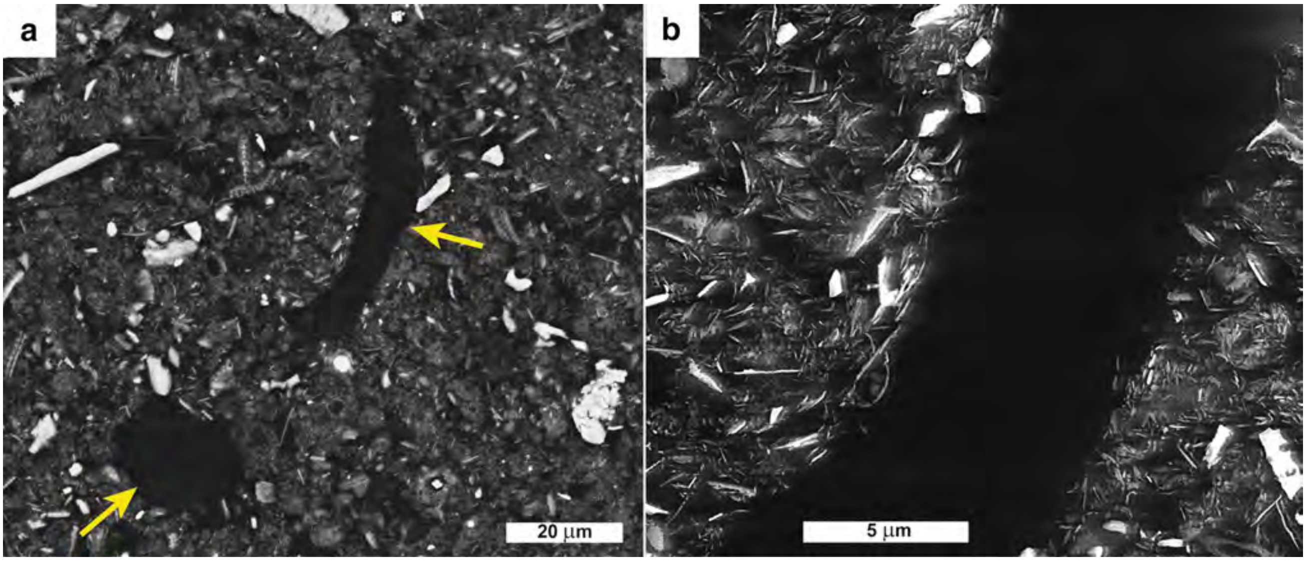

Fig. 5 **a** SEM backscatter image of ion-milled modern mud (Savannah, Georgia) with circular and elongate holes (yellow arrows) in a water-dominated clotted-mottled matrix. The holes are most likely tunnels produced by nematodes. **b** A closeup of the elongate hole in A (SEM image, secondary electron mode) that shows sharp boundaries between the opening and the surrounding matrix

content of surficial muds on the modern seabed (Schieber 2011).

Whereas initially the nematodes literally swam through the very water-rich substrate, within half an hour their disruptive activity typically became apparent (Fig. 9b), within a day substantial homogenization had taken place (Fig. 9c), and an intricate, dense burrow network had developed in the uppermost centimeters (Fig. 10). Maximum observed penetration depth of nematode burrow networks was 5 cm.

Whereas in experiments with clay layers significant blending of layer boundaries and layer diffusion occurred typically within half an hour of nematode addition, when layers of quartz sand (150–350 µm grain size) were included (Fig. 8), it required at least one hour to produce noticeable meioturbation fabrics. Apparently, displacement of sand grains was impeded because particle diameters greatly exceeded the diameter of the organisms (Fig. 2). After approximately an hour however, depending

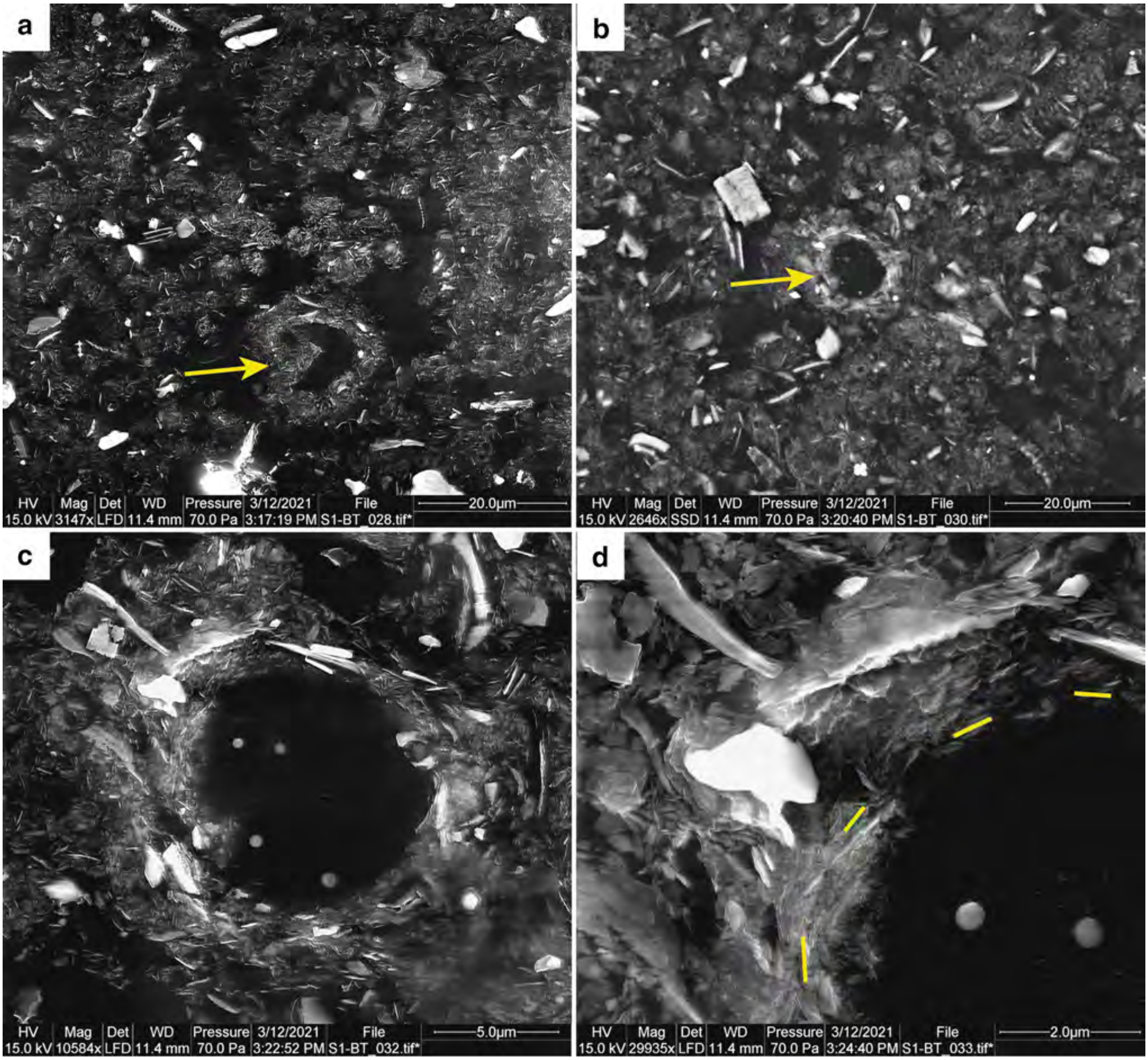

Fig. 6 **a**, **b** SEM images (backscatter mode) of nematode inhabited natural muds with round openings (yellow arrows) that are likely cross-sections of nematode tunnels. In both (**a**) and (**b**), the tunnels appear surrounded by a lining of sediment particles, and in (**a**) this liner appears partially compressed vertically. (c, d) higher magnification images of the tunnel in (b) (secondary electron mode). Platy clay particles show a preferred tangential orientation (yellow dashes) relative to the tunnel margin

on grain size and thickness of sand layers, nematode burrows and blurring of clay layer boundaries became visible below the sand layer. Burrowing activities moved sand grains into the sediment above or below by ~ 3 mm or less.

The observed difference in “diffusibility” of sand vs. clay is illustrated in Fig. 11, a four layer system with all layers below 63 µm in grain size. Unlike in Fig. 9, where disruption of sand layers led to a mottled fabric where the sand layers used to be, when all layers are in the mudstone size range, smoother gradients and less mottling is observed (Fig. 11). An accelerating factor for layer diffusion in Fig. 11 was the use of about twice the normal nematode load.

Simulation of water expulsion and compaction through virtual compaction (vertical shortening of images) does make layers and layer boundaries that were originally gradational and fuzzy look better defined (sharper) at the hand specimen scale, but the gradations are still visible because of high contrast images. However, if the various layers would merely differ in color by shades of gray, as is the norm for many carbonaceous shales in the rock record, it is relatable how such rocks could be called laminated on casual

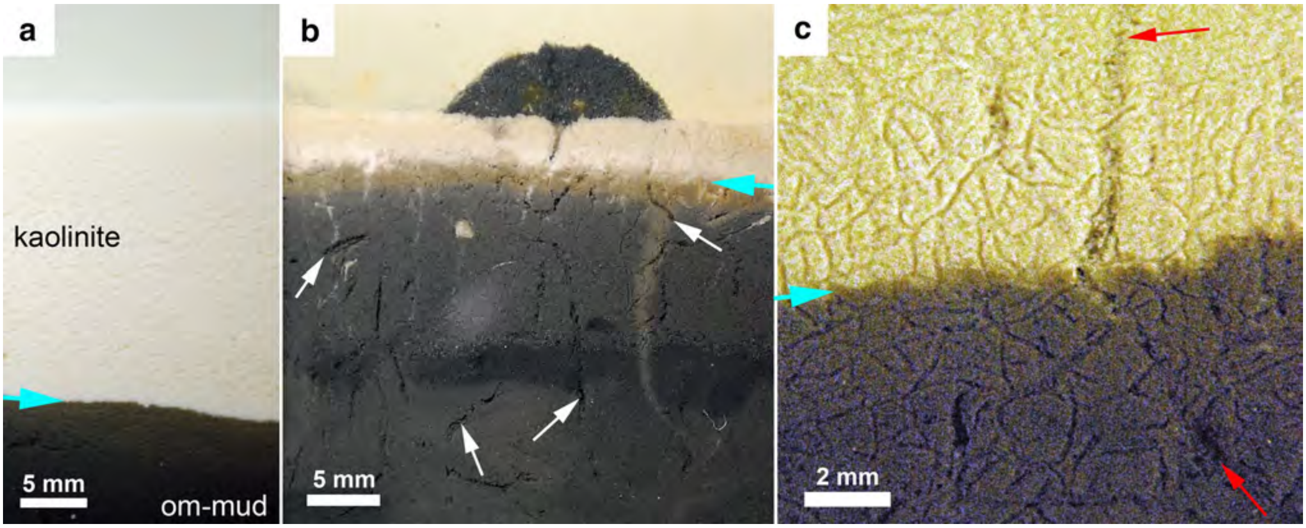

Fig. 7 **a** Organic-rich mud (om-mud) overlain by freshly deposited kaolinite. The image was taken immediately after deposition of kaolinite, and the blue arrow points to a sharp boundary between the two layers. **b** Twelve days later polychaete worms have traversed the sediment, produced a network of macroburrows (white arrows), and built a fecal mound on top of the kaolinite layer. **c** Nine more days and the volume of sediment between macroburrows (red arrows) is covered with a dense meshwork of nematode trails. The blue arrows in (**b**) and (**c**) point to a boundary between the organic-rich mud and kaolinite that clearly has lost its original sharpness

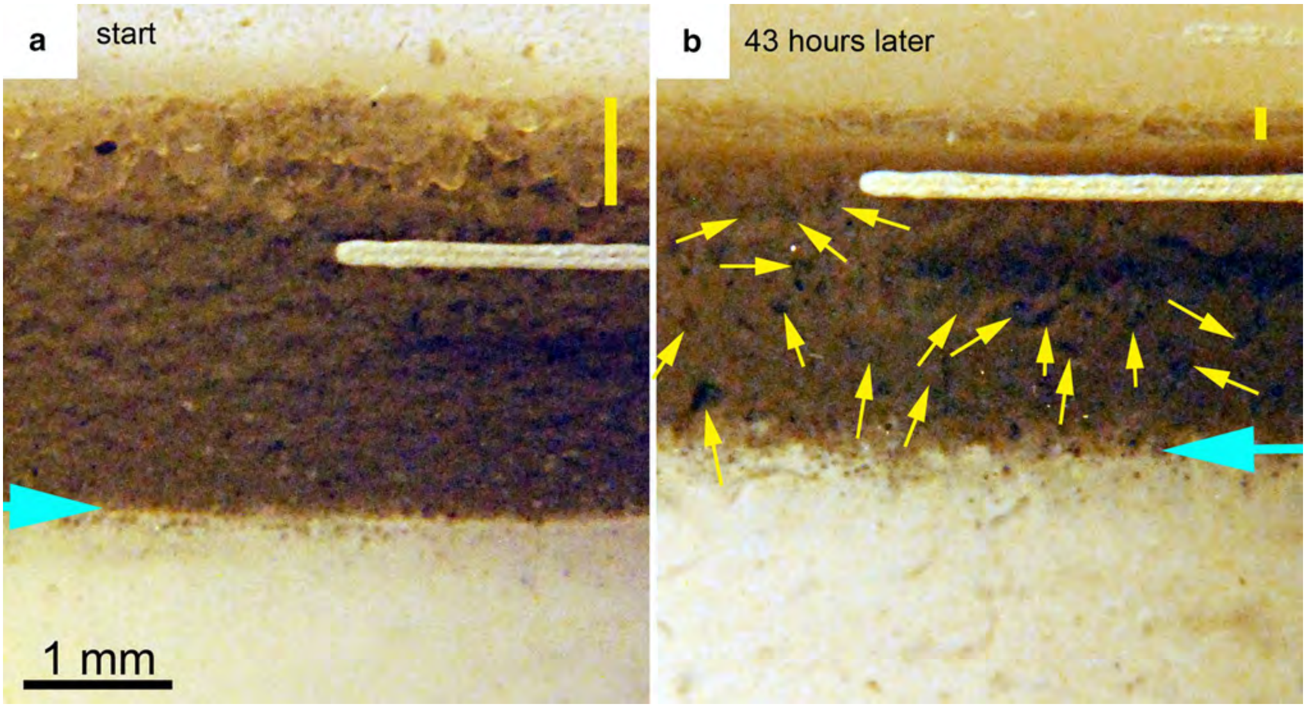

Fig. 8 **a** A sand layer (yellow bar) deposited on top of layered mud deposit. **b** The same layer 43 h later. Most of the sand grains (yellow arrows) have been mixed into the underlying mud via nematode agitation of the mud fabric. Only a thin surface layer of sand grains remains (yellow bar). The blue arrow in both images points to the boundary between a basal kaolinite layer (white) and an overlying organic-rich mud (brown). At the start of the experiment (**a**) this contact is still rather sharp, but mixing at the boundary (**b**) results in a "fuzzy" contact

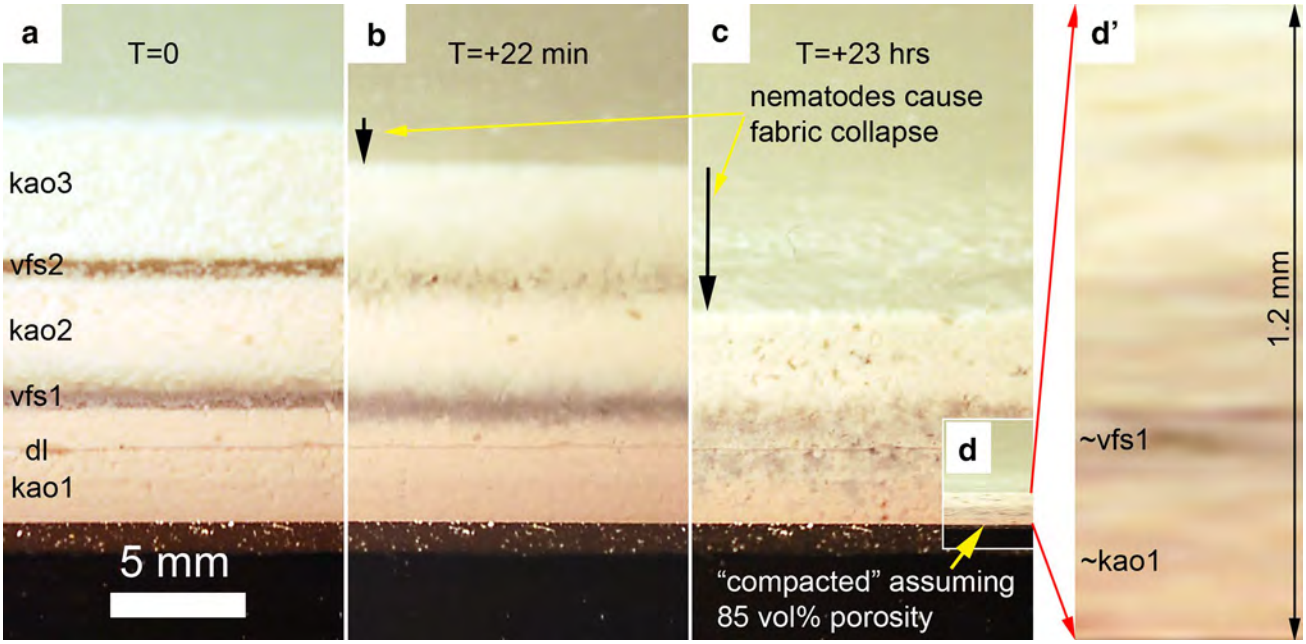

Fig. 9 Impact of nematode addition to a 5-layer mud deposit (kao = kaolinite; vfs = very fine sand; dl = "dirt line", an artifact/stain on the inside of the aquarium wall). **a** Deposit before addition of nematodes. Note sharp layer boundaries. **b** Appearance after 22 min of nematode activity. Layer blurring is better developed in shallower parts of the deposit because nematode activity decreases downwards. **c** A day later the original layers are no longer discernible. **d** The same image as in (**c**), but vertically shortened by 85% to simulate full dewatering and compaction. **d'** The sediment layer from (**d**), enlarged to better see internal texture. The location of the former kao1 layer is marked by a pinkish hue (contains a red pigment), the approximate location of the former vfs1 layer is marked by dark mottles, and the uppermost 3 layers have been completely mixed

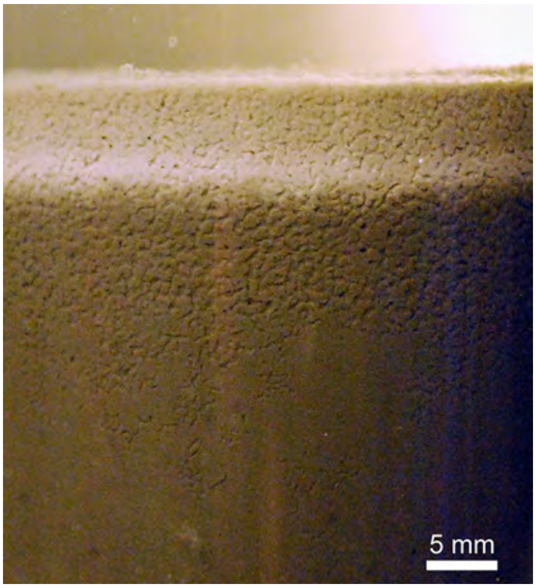

Fig. 10 Intricate nematode burrow network, 36 h after nematode addition. Initially sharp layer boundaries have blurred. Burrow activity was most intense in the uppermost 17 mm, and becomes sporadic below that depth. There was no obvious production of fecal pellets, and thus the fabric is largely attributed to burrowing activity

inspection and without the benefit of a detailed/magnified look at the layer margins.

Detailed petrographic examination of various organic-rich black shale units (i.e., Maquoketa Formation, Wufeng-Longmaxi Shale, New Albany Shale, Huron Shale, Geneseo Shale, Eagle Ford Shale) suggests that the type of fabric disruption observed in our experiments is pervasive in many of these shales, and may in some intervals affect up to 100% of the sediment volume. Given that in modern examples of oxygen limited marine muds meiofaunal mixing of the surface sediment is well developed (Bernhard and Reimers 1991; Bernhard et al. 1997, 2003; Pike et al. 2001), and considering that meiobenthos still needs some oxygen to survive (Bernhard and Reimers 1991; Bernhard et al. 2003), our experimental textures and their ancient counterparts strongly suggest that many ancient black shales were not deposited under anoxic bottom waters.

Meiofaunal fabric disruption in modern low-oxygen settings

The modern muds of the central Santa Barbara Basin are known for their well-developed marine varves (Schimmelmann et al. 2016), annual couplets of terrigenous (winter) and organic-rich (summer) sediment inputs that

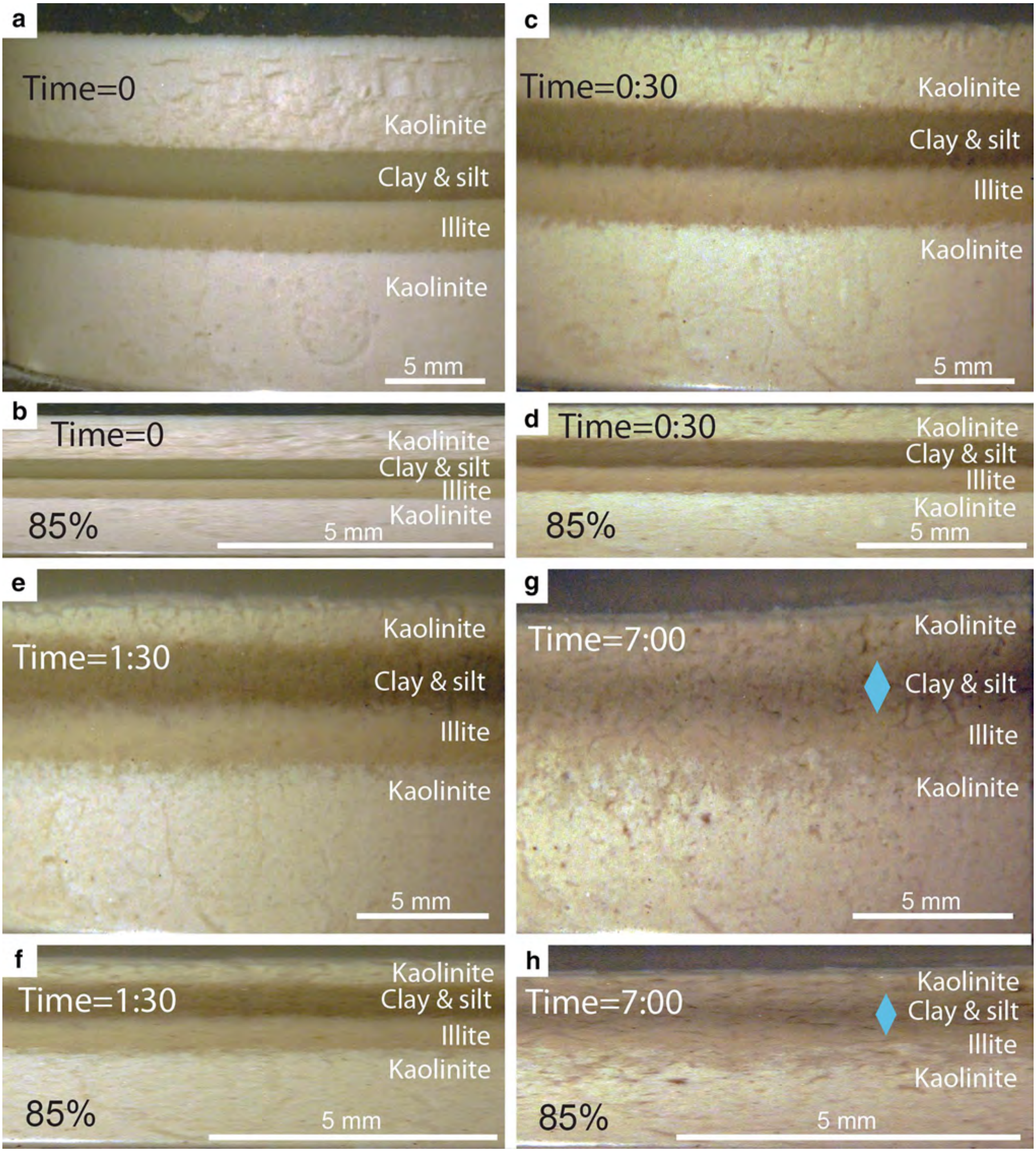

Fig. 11 Example of disruption of layer contacts over a 7-h period with a high density of nematodes (~ 137 nematodes/cm^3). **a** Image of sharp and straight sediment contacts before addition of nematodes. Layers are in ascending order kaolinite, illite, clay and silt (< 63 µm), and kaolinite. **b** A virtually compacted (rock record) view of the layering in (**a**), under assumption of 85 vol.% initial water content. **c** Layer contacts after 30 min of nematode activity. Burrows are visible and contacts are becoming irregular and blurry. **d** A virtually compacted (rock record) view of the layering in (**c**), under assumption of 85 vol.% initial water content. **e** Layer contacts after 1.5 h of nematode activity. Burrows are visible and contacts are becoming more irregular and blurry when compared to (**c**). **f** A virtually compacted (rock record) view of the layering in (**e**), under assumption of 85 vol.% initial water content. **g** Layer contacts after 7 h of nematode activity. Burrows are visible and layer boundaries are gradational and blurry. **h** A virtually compacted (rock record) view of the layering in (**g**), under assumption of 85 vol.% initial water content. The originally well-defined clay-silt layer has through mixing changed into a compositional "band" (blue-lozenges), not unlike those seen in ancient rocks (Fig. 1c, d). Note variability of scale bars with respect to "compacted" sub-figures (**b**), (**d**), (**f**), and (**h**) (enlarged to show compacted layer fabrics more clearly)

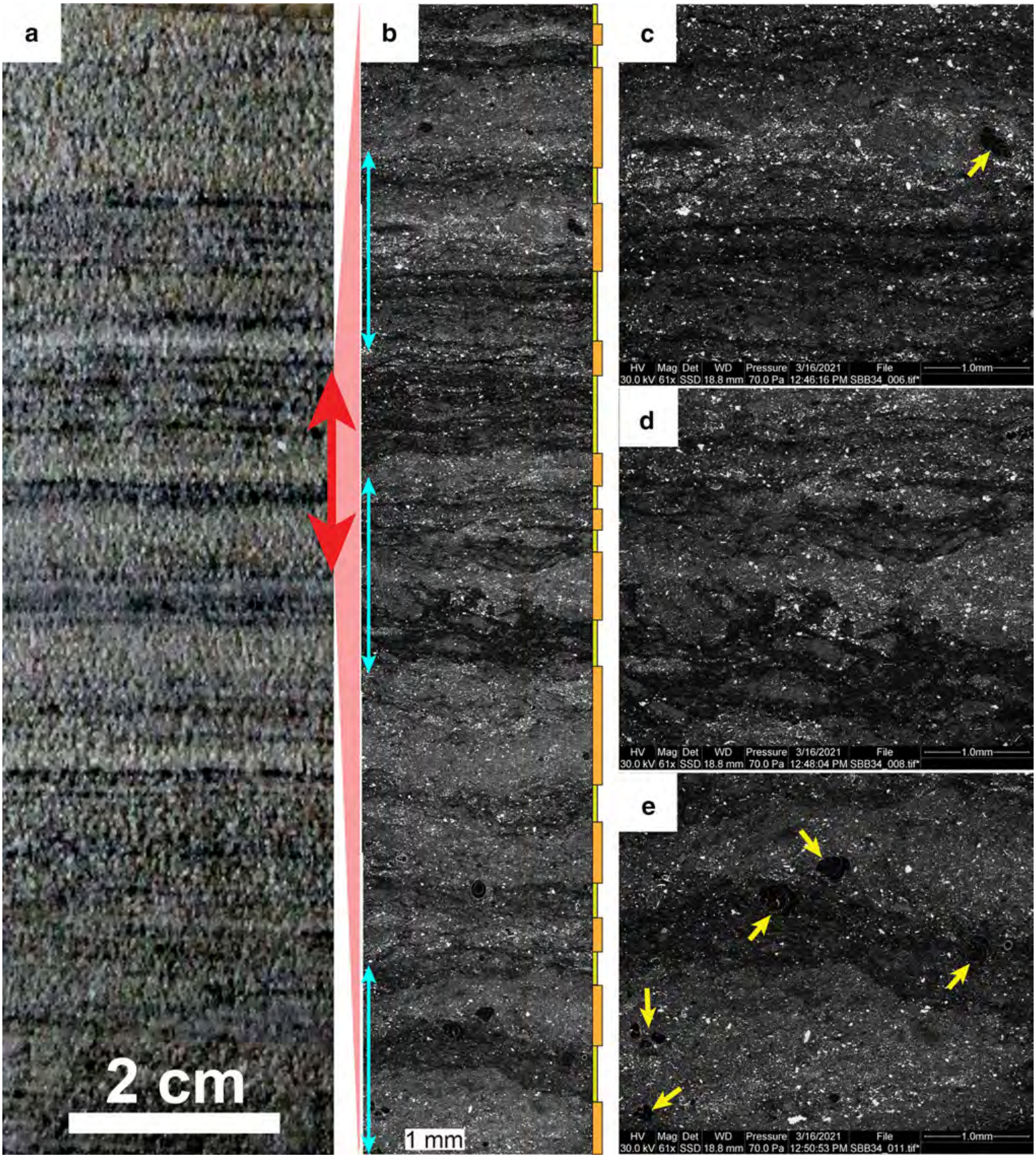

Fig. 12 Images from the laminated muds of the central Santa Barbara Basin. **a** Photo of lamination in a kasten core, the sediment is soft and water saturated and was scraped clean with a knife. **b** SEM mosaic of a traverse through a polished Spurr-resin embedded sample of this core. **c**–**e** are enlarged portions of (**b**) that show details of the sediment fabric (vertical extent and location of these images is indicated with blue double arrows). The sediment contains large benthic foraminifera (yellow arrows)

are preserved as clearly visible laminae (Fig. 12a) due to the exclusion of macrobenthos by severe oxygen limitation in the bottom waters (Bograd et al. 2002). These sediments contain eukaryotic meiobenthos, including benthic foraminifera (Fig. 12c, e) and nematodes, that affects fabric integrity (Bernhard and Reimers 1991; Pike et al.

2001). We examined resin embedded and polished samples of these sediments under the SEM (Fig. 12b–e) to serve as a real world textural counterpart to the fabric disruption observed in our experiments.

Considering that what we see in Fig. 12a are wet water-rich sediments, the laminae look quite parallel and regular. One can imagine that after compaction and lithification such a rock would pass as well laminated without question, and to interpret its depositional environment as stagnant and anoxic would not be considered controversial. Yet, when epoxy stabilized samples are examined under the SEM (Fig. 12b), it is obvious that these laminae have undergone considerable post-depositional modification. From studies of the microfauna within these sediments (Bernhard and Reimers 1991; Bernhard et al. 2003) we know that the surface muds of the central Santa Barbara Basin contain an abundance of eukaryotic micro-organisms (meiofauna) that have adapted to live in at times very low oxygen conditions, and move through the uppermost mm's to cm's of the substrate in the search for food (Pike et al. 2001). In the process, they make tiny burrows, mix sediment along layer boundaries, and destroy the original sharp boundaries of land-derived clastic layers (Schimmelmann et al. 2016). Thus, even though at first these laminae may appear rather pristine (Fig. 12a), recognizing the meiofaunal overprint (Fig. 12b) precludes us to interpret them as evidence for anoxic bottom waters. Oxygen monitoring in the Santa Barbara Basin (Bograd et al. 2002) suggests that suboxic conditions are the norm, excluding macroburrowers, and allowing meiobenthos to colonize and disturb surficial muds.

One could argue that once compacted and lithified, the laminae should show much better definition and may thus be misinterpreted as an indicator of a seabed devoid of motile benthic live, a likely outcome as long as these laminae are looked at only in hand specimens and with the help of a hand lens. If a polished thin section were made of such a rock and examined under the SEM, could we still recognize the damage done by meiobenthos? Virtual compaction of Fig. 12b, an SEM image that shows very clearly the disruption caused by meiobenthos, under assumption of an original water content of 85 vol.%, shows that the disrupted and "diffused" nature of laminae should still be readily observable in a good quality polished section (Fig. 13).

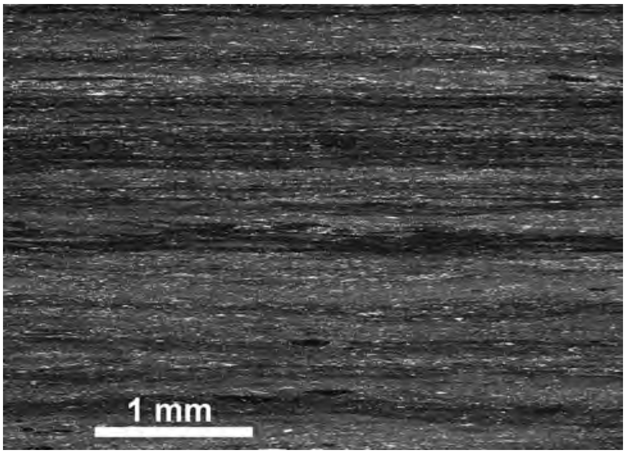

Fig. 13 A view of Fig. 12b after changing the vertical dimension to 15% of the original thickness, simulating expulsion of 85 vol.% water during compaction. Although laminae appear more laterally continuous when compared with Fig. 12b, they lack sharp boundaries and diffuse layer boundaries are still in evidence

The rock record perspective

Having confirmed with experiments and modern analogs that nematodes and by extension meiobenthos are capable of damaging and destroying primary mud layering, the next step in further exploring this phenomenon is to examine how widespread it might be in the Phanerozoic rock record, and also to develop a methodology for detecting and visualizing it. To this end we surveyed the large collection of shale samples curated by the Indiana University Shale Research Lab (IUSRL), a collection that spans materials from Archean to recent in age. Doing so showed that meioturbation is a ubiquitous textural element in ancient shale and mudstone successions. The list of examples illustrated below is by no means exhaustive, but is intended to give an appreciation of the various ways in which meioturbation manifests itself in the rock record.

At this juncture it is probably appropriate to clearly define what we mean by "bands" and "compositional banding" in the context of this paper and our general work on shale fabrics (Schieber 1999; Wilson and Schieber 2014, 2015). Figure 14 illustrates primary physical laminae, their simulated progressive degradation by meiofauna, and associated terminology, such as fuzzy margins, fuzzy laminae, and compositional bands. With respect to rock record examples, recognition of compositional "bands" (Figs. 1, 14 and 15) is a very useful criterion for the identification of meiobenthic degradation of primary shale fabrics.

Maquoketa Formation

The Maquoketa Formation is Ordovician in age and was deposited in the Illinois Basin (Gray 1972). In drill core, well-defined as well as fuzzy silt-rich bands are observed (Fig. 15a). In thin section, the diffuse nature of these bands contrasts clearly with primary layers of current deposited silt (Fig. 15). At higher magnification (Fig. 15d, e) the fuzzy-gradational nature of these bands is unmistakable. Had these layers/bands been primary silt layers, compaction would have served to enhance the sharpness of the mud-silt contacts, and resulted in fabrics like seen in Fig. 1a and b.

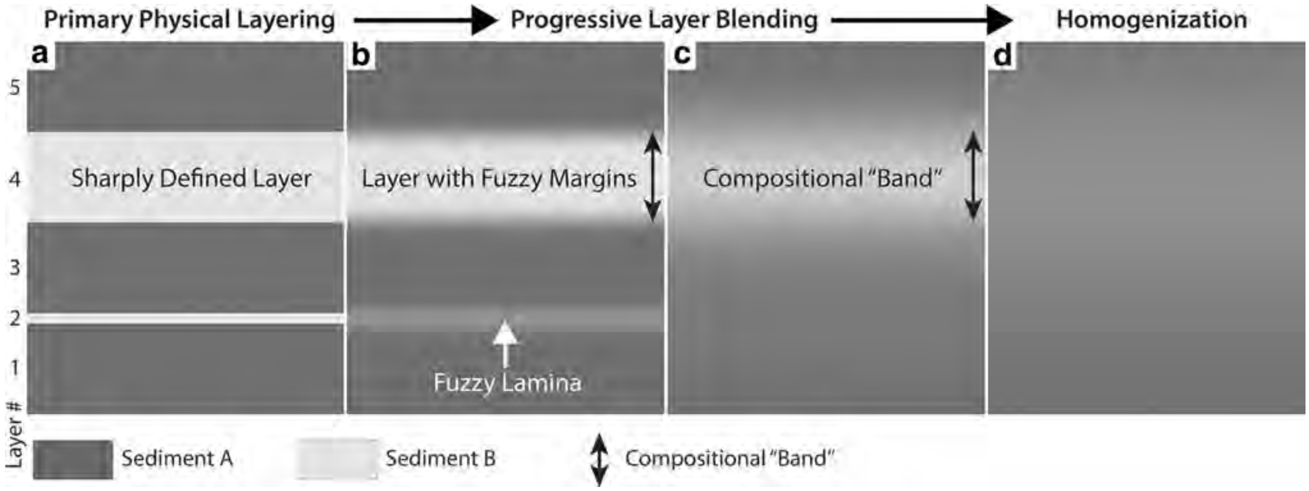

Fig. 14 A defintion sketch that illustrates the origin and nature of "fuzzy" layers/laminae and "compositional bands" and the textural continuum (**A**–**D**) from pristine layering to complete meiofaunal homogenization. **A** Layered sediment with five sharply defined layers of alternating composition (Sediment A and B, e.g. silt layers vs. clay rich layers). **B** The "Gaussian Blur" filter of Photoshop™ has been applied to image A, simulating sediment blending by meiofauna. Layer 2 has been transformed into a "fuzzy lamina", and layer 4 has developed fuzzy-gradational margins. Because it is dominated by sediment B, it can also be called a "compositional band" (marked by black double arrow). **C** Shows the effects of additional blurring/blending. Layer 4 has now wide blended margins and forms what we consider a typical "compositional band". It still is dominated by sediment B, and as such stands out from underlying and overlying layers that are dominated by sediment A. Because layer 4 is thick enough it is still visible, in spite of blurred boundaries, whereas the thinner layer 2 has been assimilated and is no longer discernible. **D** Additional blurring results in a homogenized looking sediment

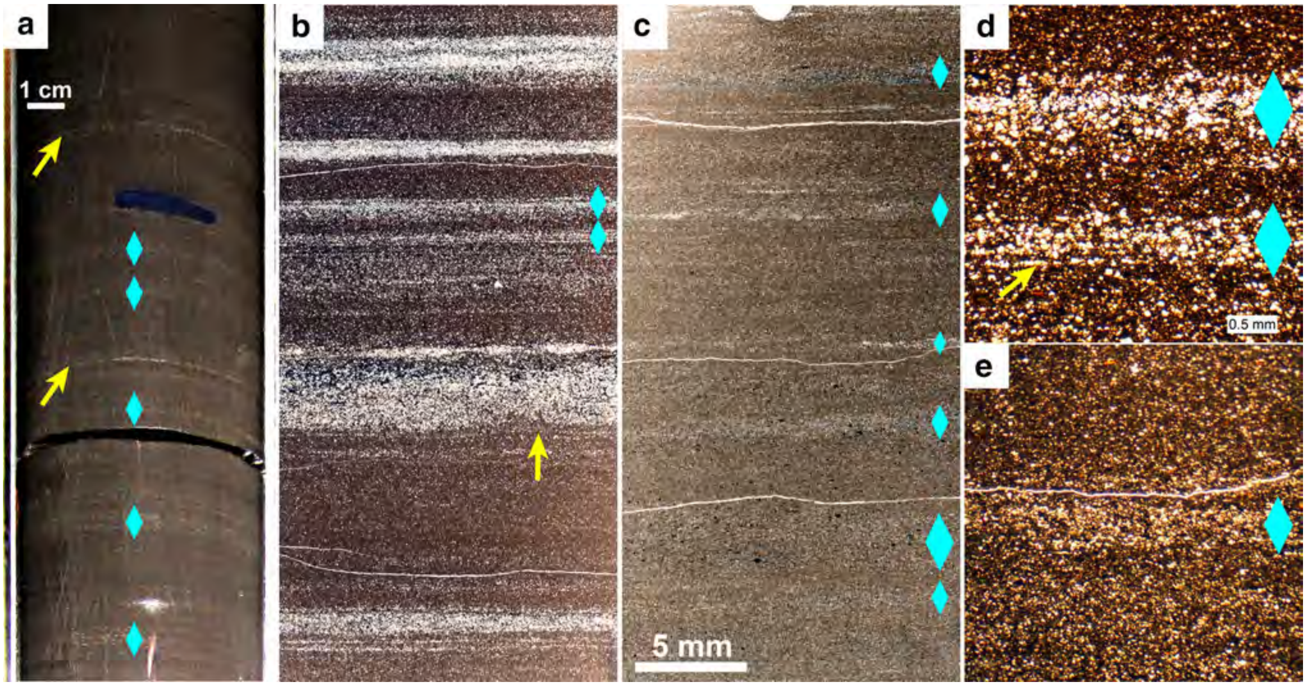

Fig. 15 Compositional bands and fuzzy laminae at multiple scales in the Ordovician Maquoketa Formation (subsurface of Indiana). **a** Photo of drill core showing primary laminae (yellow arrows) as well as compositional bands (blue lozenges). **b** Thin section with primary silt laminae that can show disruption by burrowers (yellow arrow) as well as diffused laminae (blue lozenges). Same scale as (**c**). **c** Thin section with mostly diffuse compositional bands (blue lozenges). **d** Magnified view of diffused laminae from (**b**) (blue lozenges). Note that primary laminae are still partially preserved (yellow arrow). **e** Magnified view of compositional band in (**c**) (blue lozenge). Same scale as (**d**)

Wufeng-Longmaxi Shale succession

The Wufeng-Longmaxi Shale succession of Sichuan/China is Ordovician to Silurian in age, and its black shales have been interpreted as deposited under largely anoxic bottom waters (e.g. Yan et al. 2012). However, recognition of ubiquitous banded shale fabrics (Fig. 16), tentatively attributed to meiofaunal reworking (Li et al. 2017), indicate that the depositional setting was likely oxygen limited, but not entirely devoid of oxygen. The range of lamina fabrics in the Wufeng-Longmaxi succession (Fig. 16) can be interpreted in terms of either increasing bottom water oxygenation (more meiofaunal activity) or in terms of decreasing net sedimentation rate from left to right (Fig. 16) that allows meiobenthos more time to homogenize the sediment.

Geneseo Shale

Deposition of the Middle Devonian Geneseo Shale occurred in the northern Appalachian Basin and reflects very distal sedimentation in a broad epicontinental seaway (Wilson and Schieber 2015; Smith et al. 2019). Meioturbation is very common in the Geneseo, as is the presence of benthic fecal pellets, benthic foraminifera (agglutinated), and ostracods. Compositional banding is well developed (Fig. 17).

Fig. 17 Compositional banding in a piece of drill core from the Middle Devonian Geneseo Shale. Yellow arrows point to compositional bands with fuzzy-gradational boundaries

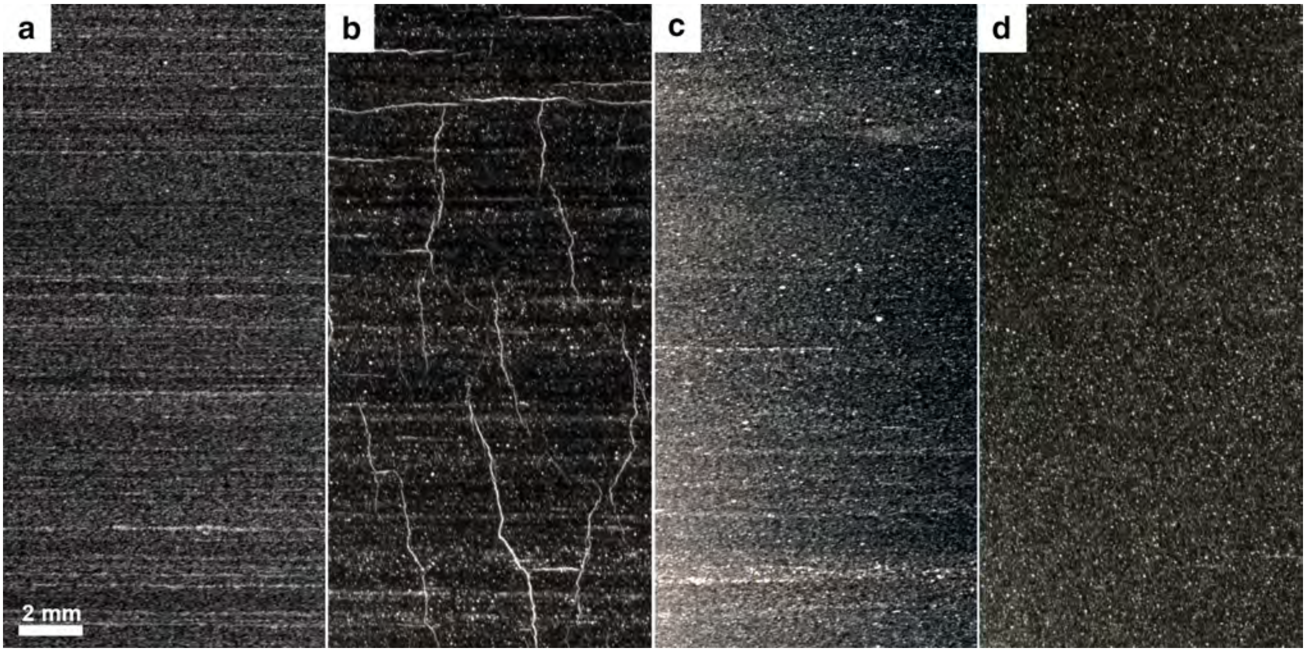

Fig. 16 A range of fabric categories in the Ordovician to Silurian age Wufeng-Longmaxi succession probably reflects increasing levels of meioturbation from left to right. **a** Well developed primary lamination, probably recording frequent bottom current activity (Schieber et al 2007; Schieber 2011, 2016; Yawar and Schieber, 2017) that inhibits meiofauna. **b** Well developed compositional banding, fuzzy layer boundaries due to meioturbation. **c** Compositional bands are broader and quite faint. Meioturbation has broadened and reduced the number of still visible bands. **d** Meioturbation has succeeded to produce a fully homogenized fabric

New Albany Shale

Deposition of the Middle to Late Devonian New Albany Shale occurred within the Illinois Basin (Cluff 1980; Buschbach, and Kolata 1990; Kolata and Nelson 1990). The core sample in Fig. 18a shows alternating bands of brown to brownish-gray shale that become less distinct moving up section. Similar lithofacies have been shown by Cluff (1980: Figs. 7, 8) and were described as thinly to thickly laminated mudstones. The bottom and top boundaries of these layers tend to be irregular and what appears as "layers" in core specimen (Fig. 18a) typically has fuzzy-gradational boundaries to adjacent layers (Fig. 18b) and give it a banded appearance.

Huron Shale

The Huron Shale is a Late Devonian black shale unit deposited in the Appalachian Basin (Provo et al. 1978), and has long been interpreted as the result of distal accumulation in a deep anoxic basin (Ettensohn 1992; Kepferle 1993). More recent sedimentologic (Schieber and Lazar 2004) and geochemical studies (Rimmer et al. 2004), however, suggest a depositional setting that was oxygen limited rather than truly anoxic. Samples and thin sections of the Huron Shale show that although primary laminae may be preserved in places, more typically the presumed primary laminae are compositional bands (Fig. 19). Petrographic examination shows compositional bands and gradational layer boundaries, as well as evidence for meiobenthos (Fig. 19e, f).

Eagle Ford Shale

The Cenomanian–Turonian Eagle Ford Shale of Texas (Donovan and Staerker 2010) is a well-studied shale succession. Physical, biogenic, and chemical data indicate that the Eagle Ford Shale accumulated in depositional sub-environments with significant variations in primary biogenic production, bottom-energy and oxygen levels, and sediment accumulation modes and rates (Schieber et al. 2016). Sediment was delivered as organo-mineralic aggregates (Syvitski 1991), fecal pellets, and floccules by traction transport (Schieber et al. 2007), sediment gravity flows, and suspension settling (benthic and pelagic).

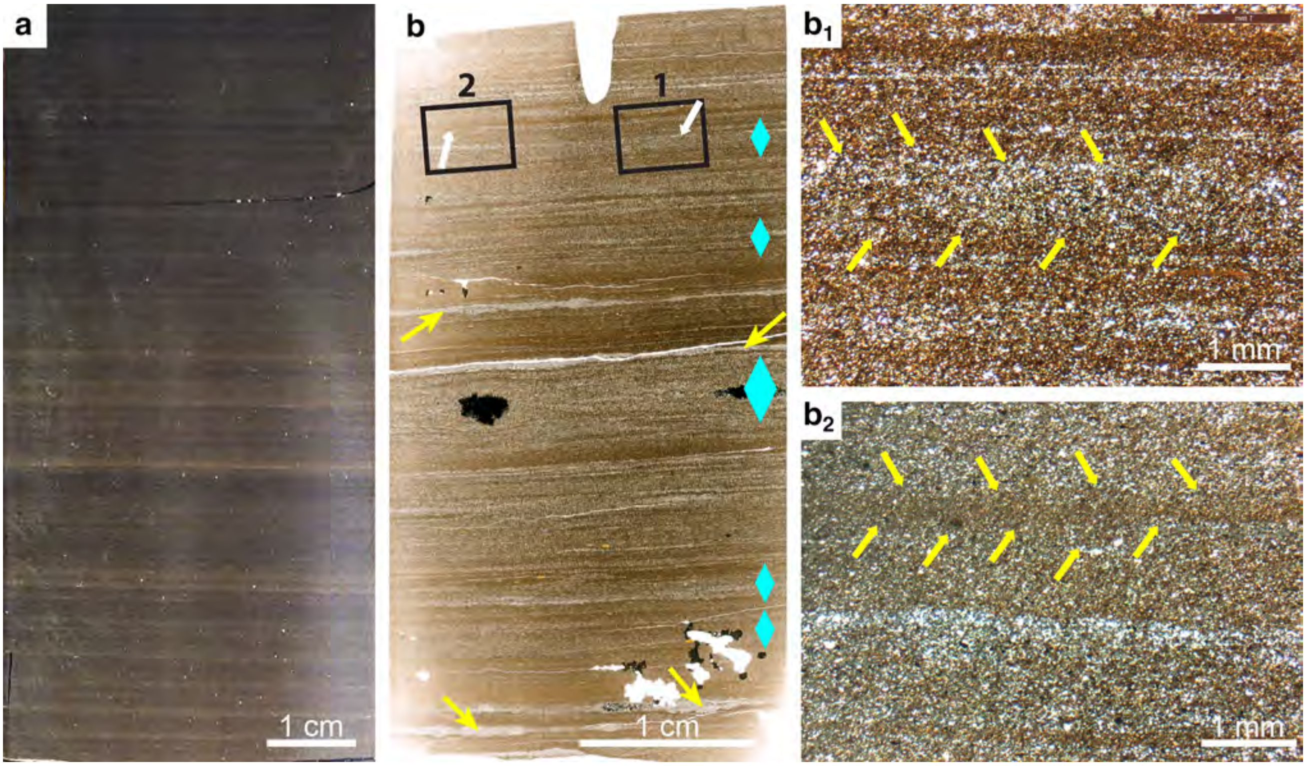

Fig. 18 Varying degrees of meioturbation in the Middle to Late Devonian New Albany Shale. **a** Drill core sample that shows layering but generally lacks sharp layer boundaries and instead appears "banded". **b** A thin section of this rock that shows more clearly that whereas there are thin layers that are well defined and presumed primary (yellow arrows) most of the layers are not as well defined and have lower silt content than the primary layers. Several of the poorly defined layers show fuzzy transitional "contacts" (blue lozenges). (**b1 and b2**) Detail views from (**b**) (box 1 and box 2) that show the gradational fuzzy boundaries (yellow arrows) of select silt-enriched layers (or bands)

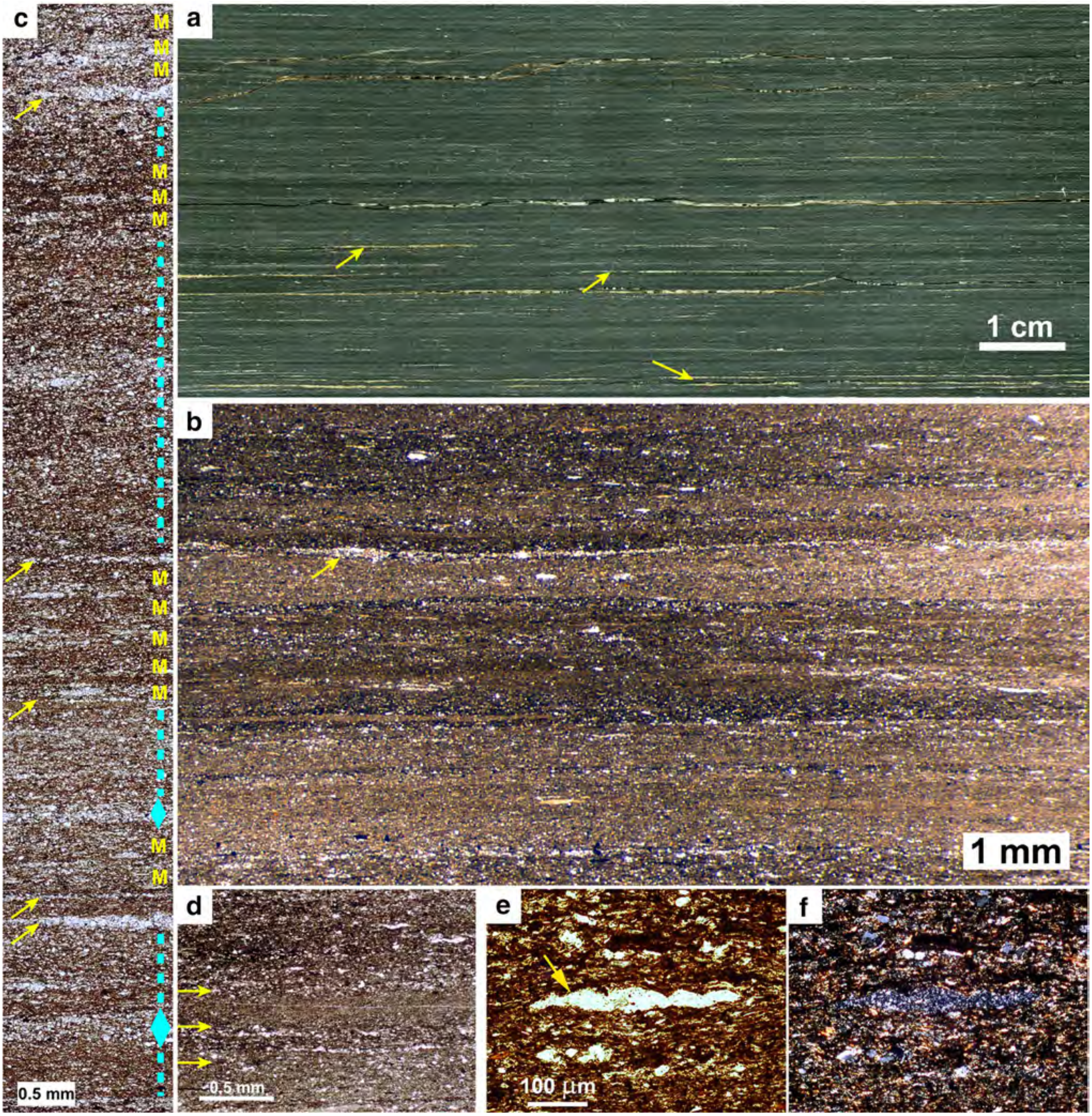

Fig. 19 Observations on samples from the Lower Huron Shale of Ohio. **a** Polished sample shows the general paucity of primary laminae (laminae marked by yellow arrows) and the overall banded appearance of the rock. **b** Thin section photomicrograph that shows compositional bands and a small erosional scour (yellow arrows) that signifies activity of strong bottom currents. **c** A vertical traverse across a thin section that shows some variably preserved primary laminae (yellow arrows), compositional bands with diffuse boundaries (blue lozenges), homogenized intervals (dashed blue lines), and mottled intervals (M) due to burrowing. **d** Closeup of successive layers with diffuse boundaries (yellow arrows). **e**, **f** A compacted agglutinated foraminifera (meiobenthos) in transmitted (**e**) and cross-polarized light (**f**)

Benthic energy levels were capable of transporting sand-sized grains as suggested by scour surfaces, wave, current, and combined-flow ripples, graded beds, and fossil and pyrite lags. Paleo-redox conditions in the bottom-water column were frequently dysoxic with the potential for intermittent anoxic and oxic intervals (Schieber et al. 2016). The latter range of oxygenation scenarios is reflected in the gradient of meioturbation in Fig. 20.

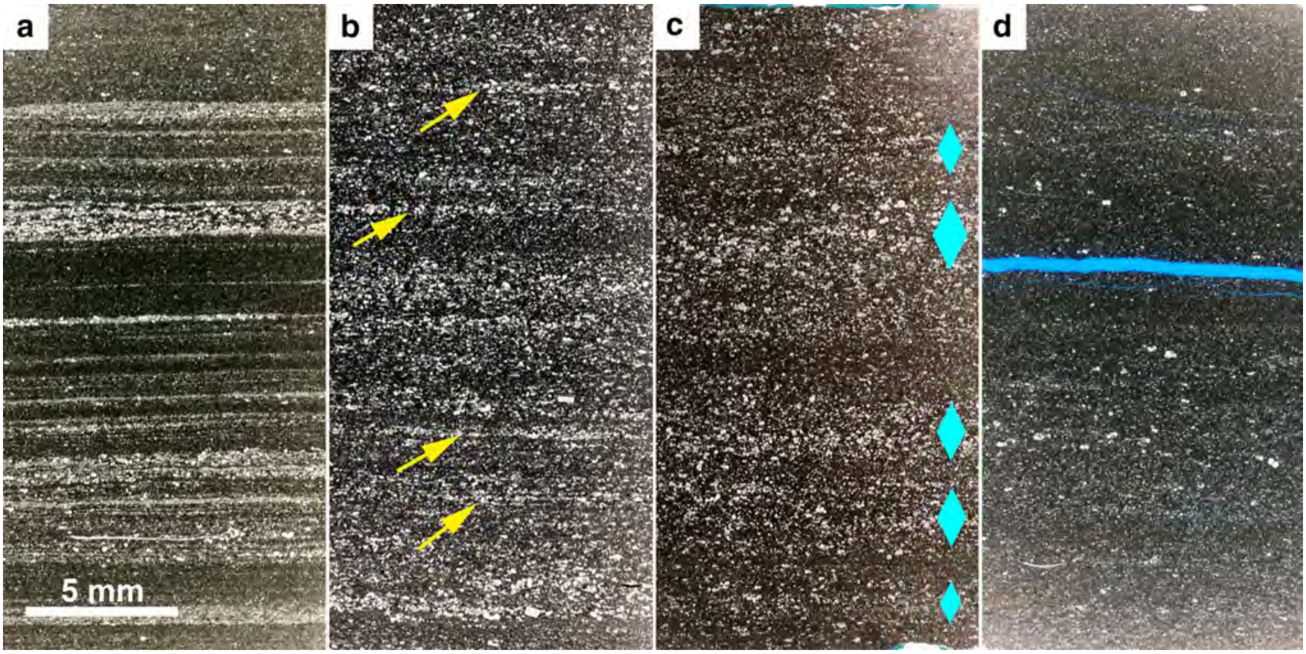

Fig. 20 A continuum of fabric categories in the Cenomanian–Turonian Eagle Ford Formation, reflecting (**a**) dominantly physical sedimentation processes, (**b**) meioturbation with remnants of primary fabric (yellow arrows) and onset of banding, (**c**) complete destruction of primary layering and fully developed meioturbation-induced banding, and finally (**d**) a fully homogenized fabric. The well-developed primary lamination (**a**), probably records frequent bottom current activity (Schieber et al 2007; Schieber 2011, 2016; Yawar and Schieber 2017) that inhibits meiofauna or overprints its homogenizing tendencies. Compositional banding and fuzzy layer boundaries due to meioturbation broaden as the activity of meiobenthos intensifies with increasing oxygen supply and leads to fully homogenized fabric if there is enough oxygen or enough time for homogenization

Rocks like shown in Fig. 20a are described as laminated calcareous shale in the literature (Donovan and Staerker 2010), but the degraded fabrics (Fig. 20b–d) typically have not been captured descriptively. Yet, they carry important clues to the level and dynamics of paleo-oxygenation.

Each of above examples shows characteristics that parallel criteria given by Pemberton et al. (2008) to identify cryptobioturbation in sandstone units, such as the absence of discrete traces, small potential burrowers (< 2 mm), and fuzzy laminae lacking sharp top–bottom contacts. Fuzzy margins are due to particle displacement, but there is no visible displacement of sediment layers as would be seen in the presence of macroburrows. In hand specimens, individual laminae are planar, parallel, and lack macrobioturbation or other discrete traces. Close inspection with a hand lens shows compositional bands with wavy and fuzzy lower and upper boundaries. Typically layer boundaries are not associated with erosional surfaces.

For comparison of above examples to our neoichnology experiments, the images of experiments were digitally compressed along the vertical dimension to simulate water loss that would occur due to compaction (Lobza and Schieber 1999). Although this procedure improves layer definition (Figs. 7, 8, 9, 10, 11), close up inspection of enlarged images shows nonetheless that the layer boundaries are still irregular and fuzzy.

Discussion

Identification of non-bioturbated laminated shales

Campbell (1967) defined laminae as the thinnest sub-units of a sedimentary deposit. In shales, one of the most commonly used descriptors is “finely laminated”, referring to sub-mm to mm-thin repeated layers that are generally uniform in composition and have sharp boundaries (Campbell 1967). In previous decades, it was common practice to interpret laminated shales as the outcome of slow settling of particles out of the water column in an anoxic environment that prevented bioturbation (e.g., Byers 1977; Ettensohn et al. 1988; Wignall 1994). However, presumed primary laminae like those seen in various ancient black shales (Figs. 1, 15, 16, 20) are not readily reproduced in laboratory experiments. Instead, laboratory loading of muddy sediments with gravity settled thin layers of silt or sand tends to produce irregular beds because of the high water content of underlying muds (Schieber 2011). In contrast, when deposition from moving muddy suspensions is studied in flume experiments, nice parallel laminae are par for the course (Schieber et al. 2007; Yawar and Schieber 2017). In these experiments (flow velocity 15–25 cm/sec at 5 cm effective flow depth) laminae are produced as bedload transported mud floccules and coarse silt form current ripples that migrate over the bed, leave behind a thin veneer of sediment, and over time produce a bed that consists of interspersed mud and silt laminae (Yawar and Schieber 2017). Other details observed in these experiments, such as low-angle downlapping laminae, have been found a common element in many ancient laminated mudstones, confirming that sediment-carrying bottom currents are a dominant lamina-forming process in black shale deposition (Schieber 2011, 2016).

For the purpose of this paper, non-bioturbated laminae are considered continuous parallel layers with sharp basal and top contacts, which in ancient deposits may locally include low-angle inclined and convergent laminae (Schieber 2011, 2016). In the experiments described here (Figs. 3, 7, 8, 9, 11), the primary laminae are continuous with sharp basal and top contacts.

There is also the issue of how meioturbation as defined here might aid the search for earliest animal-sediment interactions in Ediacaran-age strata. Parry et al. (2017) report what appears to be full-relief preservation of nematode burrows in late Ediacaran siltstones as the to date oldest meiofaunal burrows the in the rock record, and application of the criteria developed in this paper may help to further expand the deep time range of meiofaunal benthos.

Preservation potential of meiofaunal burrowing activity

Once meioturbation as illustrated in our experiments is accepted as a viable mechanism for fabric modification in muds, it is rather difficult to not find it in Phanerozoic organic-rich mudstones (Figs. 15, 16, 17, 18, 19, 20). Combined with the recognition that well-preserved primary lamination in these shales is more likely an expression of bottom current activity (Schieber et al 2007; Yawar and Schieber 2017), the "imperfect" fuzzy laminae and compositional "bands" that are the other common lamina style in Phanerozoic black shales strongly suggest that bottom water anoxia were much rarer than commonly appreciated, and are not the often presumed (Byers 1977; Ettensohn et al. 1988; Wignall 1994) key factor for their formation.

In our experiments, the disruptive activity of nematodes became apparent within half an hour of their addition to the sediment (Fig. 9b), and substantial homogenization took place within the first 24 h. In that context one may wonder under what conditions laminae actually have a chance of preservation in the rock record. High sedimentation rates could potentially enhance the preservation potential of laminae, but in the case of more distal and slowly accumulating successions (such as our rock record examples) this is not an option. Our experiments were conducted under well oxygenated conditions, but as oxygen supply is scaled down, meiofaunal density as well as activity can be expected to be reduced significantly (Bernard and Reimers 1991; Bernard et al. 1997).

Modern carbonaceous muds that are described as thinly laminated, such as those of the central Santa Barbara Basin, accumulate under suboxic conditions at comparatively high net sedimentation rates (~ 1 mm/year on a water free basis; Schimmelmann et al. 2006) and still support enough meiobenthos to allow lamina degradation to be visible and likely transmitted to the rock record (Figs. 12, 13). In the Santa Barbara Basin evidence of meiofaunal burrowing activities has been reported from the deepest portions of the basin, and as well as from sediments collected from the more oxygenated basin slope (Savrda et al. 1984; Behl 1995; Pike et al. 2001). Under conditions of similar oxygenation levels as encountered in the Santa Barbara Basin, but at net sedimentation rates typical for distal black shales (~ 0.01 mm/year or less, Schieber 1998), meioturbation can be expected to completely homogenize the fabric, such as shown in Figs. 1e, f; 15d, 18c, 19d. Published mention of possible meiofaunal burrowing in the geological record is rather sparse, owing to the small size of the organisms, severe compaction of water-rich muds, and a lack of grain size contrast in the substrate (Elliott 1984; Sageman 1985, 1989; Cuomo and Rhoads 1987; Savrda and Bottjer 1991; Pemberton et al. 2008). In sandy substrates meiofaunal organisms are of similar size as the host sediment, thus precluding the likelihood of visible burrows (Giere 2009). As shown in our experiments, in fine-grained substrates the potential for creation of meiofaunal burrow structures is greatly enhanced, but the high water content of the sediment renders them rather fragile structures with very low preservation potential (Cullen 1973; Riemann and Schrage 1978; Cuomo and Rhoads 1987; Nehring et al. 1990). Under favorable circumstances, such as high sedimentation rates, relict open burrows have been identified in Holocene muds of the Palmer Deep of Antarctica and the Santa Barbara Basin (Pike et al. 2001) and in Pliocene Mediterranean sapropels (Löhr and Kennedy 2014). Brodie and Kemp (1995) observed aggregate structures in Holocene laminated sediments offshore Peru that they interpreted as meiofauna-induced grain redistribution at the sediment–water interface. Elliott (1984) suggested that the trace fossil *Cochlichnus kochi* (less than 1 mm in diameter), observed in well-laminated Westphalian mudstones, was likely produced by animals with a hydrostatic skeleton (such as nematodes) in watery near-surface muds. In the deep time rock record, what has been described as subtle, incomplete laminations, has by some people been tentatively attributed to meiofaunal activity (Sageman 1985, 1989; Savrda and Bottjer 1991; Wilson and Schieber 2015). In our experiments particle displacement by nematodes was in the mm-range and open burrows were not filled with overlying sediment and so fragile that they were easily destroyed with a slight shake of the tank. Overall, meiofaunal burrows are unlikely to be preserved, unless supported by some kind of cohesive matrix or a rigid grain fabric (e.g., Pike et al. 2001).

In experiments where both macrofauna and meiofauna occupied the sediment, the more visible burrows were produced by macro-organisms, but the meiofaunal burrows were much more abundant and pervasively affected the sediment volume (Fig. 7). Thus, if one sees macroburrows or related biodeformational structures (in high water-content sediments, Wetzel and Uchman 1998; Lobza and Schieber 1999) in ancient mudstones, it is probably safe to assume that meiobenthos had a substantial role in homogenizing the sediment adjacent to these more obvious signs of benthic life.

Indirect evidence for the former activity of meiobenthos can also come from the identification of fecal pellets (Cuomo and Bartholomew 1991). Cuomo and Rhoads (1987) proposed that small worms can produce fecal pellets that, when compacted, can give the appearance of pelleted lamination, and agglutination of sediment particles in mucus lined burrow walls might be another proxy of meiobenthic sediment processing (Riemann and Schrage 1978; Nehring et al. 1990; Riemann and Helmke 2002). SEM examination of ion milled sections from our experiments did not show identifiable remains of fecal pellets, suggesting low preservation potential overall.

Previous studies noted that bioturbation by meiofauna causes the gradual destruction of larger (mm to cm scale) surficial and vertical features in sediments (Cullen 1973; Zobrist and Coull 1992). Our experiments expand on this theme by demonstrating that meiobenthos as a rule blurs layer boundaries and may erase layers completely if given enough time, in agreement with observations by Brodie and Kemp (1995) from offshore Peru. Rather than generating burrows that can be recognized in the rock record, meioturbation fuels short range particle diffusion that results in stratiform compositional zones or bands with gradational margins or even complete homogenization. Upon compaction, thin bands may easily be mistaken for primary lamination. Our experiments suggest that one of the simplest ways to identify potential meiofaunal activity in organic-rich sediments is the observation of compositional bands with gradational/fuzzy margins instead of clearly defined laminae. In association with banding, homogeneous appearing sediment intervals were likely deposited so slow that meiofaunal mixing could go to completion, or alternatively under somewhat improved oxygenation that supported higher meiofaunal population densities.

Implications for paleoenvironmental interpretations

Making a distinction between true primary laminae and banding is important for several reasons. Because this distinction has not been made in past studies, many black shale successions were interpreted to have been devoid of benthic fauna due to anoxic or even euxinic bottom waters. Yet, considering “bands” as a product of meiobenthos invalidates that simplistic assumption and requires us to look closer, so as not to miss evidence for meiofaunal activity. Because meiobenthic organisms are all eukaryotes, they need at least some oxygen to be able to survive (Bernhard and Reimers 1991; Bernhard et al. 1997), and that in turn implies that the bottom waters could not have been anoxic. Modern meiobenthos can endure brief interludes (a few months) of anoxic bottom waters (Bernhard and Reimers 1991; Bernhard et al. 2003), but in the long term some oxygen is required if they are to persist on the seafloor.

The lack of macrobioturbation in meioturbated sediments illustrated above (Figs. 12, 13, 15, 16, 17, 18, 19, 20) implies that oxygen levels were too low to support larger organisms, but at what oxygen level these are excluded can be debated. Whereas it is customary to think of macroburrowers to be viable under dysoxic (2.0–0.2 ml/l O_2) conditions (Savrda and Bottjer 1991; Tyson and Pearson 1991), data from the modern Texas shelf show that reduced oxygen levels that are still in the oxic range (3–4 ml/l) and lie well above suboxic levels, already have a dramatic impact on the health of infaunal communities and cause severe reductions in the ichnological character of sediments (Dashtgard et al. 2015). A parallel study on Cretaceous mudstones from Canada indicates that meiofauna thrives and remineralizes OM regardless of absence or presence of macroburrowers (Dashtgard et al. 2015). Thus, absence or paucity of macrobioturbation should not automatically be equated with suboxic conditions. Nonetheless, in view of how rapidly nematodes homogenize the sediment under oxic conditions (Figs. 9, 10), the observation of preserved compositional bands in many ancient black shales suggests that the suboxic setting of the Santa Barbara Basin, resulting in substantially slower rates of meioturbation, may be an appropriate modern analog for many ancient black shales.

Meiofaunal interaction with the sediment can affect sediment stability and fabric by collapsing delicate particle frameworks, binding particles through mucus secretions, and enhance diffusion from overlying waters into the sediment (Platt and Warwick 1980; Reichelt 1991; Aller and Aller 1992). Our experiments show that the nematodes induced fabric collapse of water-rich layers, and in tiny increments (but persistently) mixed and relocated sediment particles over short distances. Open burrows are common, likely because of stabilization by mucus linings (Cullen 1973; Riemann and Schrage 1978; Riemann and Helmke 2002), although they are easily destroyed by slight disturbances. Mucus-stabilized mud fabrics in modern sediments also appear to be rather fragile (Riemann and Schrage 1978) and are in addition subject to bacterial degradation of the mucus matrix (Moens et al. 2005). Thus, the stabilizing effect of mucus secretions may be of a decidedly ephemeral nature. For all these reasons, finding and documenting meiofaunal burrows within modern muds is challenging and at a minimum quite labor intensive (Nehring et al. 1990; Pike et al. 2001), a situation that is further complicated by compaction when ancient equivalents are considered.

Augmenting trace fossil based models for paleo-oxygenation

Trace fossil models for fine-grained substrates typically focus on the size, abundance, tiering, ethological category, and cross-cutting relationships of macroscopic trace fossils to determine relative oxygen concentrations in pore spaces and bottom waters (Byers 1977; Bromley and Ekdale 1984; Savrda and Bottjer 1986; Ekdale and Mason 1988). However, there appears to be a need for better understanding what observations can inform us about bioturbation under low oxygen conditions. Observations of modern seafloor sediments have documented for some time the presence of small infaunal organisms at low oxygen levels (Thompson et al. 1985; Savrda and Bottjer 1991; Levin et al. 2003), with the latter authors reporting oligochaetes in waters with oxygen concentrations as low as 0.02–0.03 ml O_2 l^{-1} H_2O. Cuomo and Rhoads (1987) related lab experiments with small polychaetes to the thin section scale fabrics (compacted fecal pellets) of Devonian black shales and questioned the prevailing assumption of anoxic bottom waters. Savrda and Bottjer (1991) defined muds lacking macrobentos and with slightly disrupted laminae as quasi-anaerobic (<0.1 ml O_2 l^{-1} H_2O).

Yet, in spite of the overwhelming evidence for meiofaunal activity in modern low oxygen environments, this likely aspect of ancient benthic life usually is not part of the ichnological assessments of ancient rocks. If there is not at least some visible lamina disruption, there is at present little guidance for the identification of meiofaunal cryptobioturbation in mudstones and shales, and the whole issue is simply ignored for the lack of diagnostic criteria. We hope that our experiments can convince that fuzzy laminae, layer blending, and compositional bands are a direct consequence of meiobenthos interacting with water-rich surface muds. Accepting this insight should make it easier to recognize the former presence of meiobenthos in muddy substrates and help to improve paleoenvironmental assessments of organic-rich mudstones and black shales.

Conclusions

Neoichnology experiments with nematodes provide empirical evidence that meiofaunal burrowing in fine-grained substrates induces short-range grain displacement that leads to blurring of layer contacts and to a banded fabric. Whereas nematodes do produce an initial burrowed fabric, the water-rich nature of the substrate (compaction) and microbial consumption of their mucus secretions (particle cohesion) ensure that these burrows do not leave a record of any permanence. Manipulation of images of experimental muds (virtual compaction) to visualize their post-compaction state shows that the blurry and irregular boundaries persist through compaction, although they may appear somewhat sharper and straighter. The banded fabric we created in experiments compares well with banded shale fabrics observed in multiple ancient examples of carbonaceous mudstones and indicates that many supposedly laminated black shales in the rock record may very well not bear witness to ancient anoxia and oceanic anoxic events. In the absence of macrobioturbation, banding and fuzzy laminae indicate the continued presence of small metazoans and dissolved oxygen at the seafloor. Oxygen may have been low, but the bottom waters were not anoxic. We propose the terms “meioturbation” or “meioturbated” to collectively describe “fuzzy” laminae, blurred contacts, and compositional “banding” in ancient mudstones. Meioturbation represents a continuum of fabric disruption that starts at the “low” end with disruption of primary laminae and then progresses through increasingly broad compositional bands with fuzzy-gradational margins to a fully homogenized fabric at the “high” end. How far meioturbation progresses in a given instance depends on net sedimentation rates (limits depth and intensity), bottom current activity (competes for fabric dominance), and bottom water oxygenation (controls intensity of meiofaunal activity).

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