BIOGENIC SEDIMENTARY STRUCTURES PRODUCED BY WORMS IN SOUPY, SOFT MUDS: OBSERVATIONS FROM THE CHATTANOOGA SHALE (UPPER DEVONIAN) AND EXPERIMENTS

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ABSTRACT

Abundant trace fossils occur within rhythmically interbedded black and gray shales of the Chattanooga Shale (Upper Devonian) in central Tennessee. Burrows cross the boundaries between layers and tend to obscure the contacts between alternate layers. Infills of individual burrows often display an array of complex, convoluted features, apparently due to mixing of soft to soupy black and gray muds.

Assuming that the burrowers were elongate worm-like organisms, experiments were made to study the relationships between the general morphology of burrowers (simple worms, worms with appendages, etc.), sediment viscosity, and textural features. Rubber bait worms were pulled through superimposed layers of plaster in a first set of experiments. Comparable experiments were then conducted with earthworms. The resulting textures were studied by sawing the hardened plaster blocks perpendicular and horizontal to bedding. The explored viscosities ranged from that of heavy motor oil to that of lithium grease (at 25°C).

The study shows that (1) convolute textures observed in plaster experiments closely resemble those seen in Chattanooga Shale burrows; (2) the degree of convolution increases as the vicosity of the substrate decreases; (3) the length of the worm determines the extent of mixing between layers; (4) mixing patterns produced by smooth worms and worms with appendages, although similar, contrast in detail; (5) earth worms and bait worms produce generally similar structures, but show certain differences due to contrasting styles of locomotion (peristalsis vs. unidirectional pull). "Virtual" compaction and decompaction of digital images shows close resemblance between experimentally produced structures and burrow textures from the Chattanooga Shale, suggesting that the latter were indeed produced by worm-like animals that moved through semi-fluid muds.

INTRODUCTION AND STATEMENT OF PURPOSE

Descriptions of bioturbation go back to the early 19th century (Brongniart 1823; Darwin 1838), although systematic ichnology did not start until about a century later (Richter 1927). Seilacher's (1953) behavioral approach to the classification of trace fossils, as well as the actualistic studies of the "Wilhelmshaven School" (Schäfer 1956, 1962; Reineck et al. 1967; Reineck et al. 1968; Häntzschel 1962), provided a conceptual and observational basis for a steadily expanding number of trace-fossil studies in modern and ancient sediments (see, e.g., Frey 1975; Bromley 1996). The integrated study of modern deep-sea and shelf sediments in the Deep Sea Drilling Project provided new insights into the relationship between environmental conditions and trace fossils, and led to the development of the concepts of ichnofabrics and bioturbation textures (Griggs et al., 1969; Ekdale 1977; Larson and Rhoads 1983; Bromley and Ekdale 1986; Easthouse and Driese 1988; Bottjer and Droser 1991; Savrda and Bottjer 1994; Wetzel 1991).

Trace-fossil studies of shales (Byers 1972, 1982; Griffith 1978; Miller 1979, 1982; Cluff 1980; Jordan 1980, 1985; Pratt et al. 1986; Savrda and Bottjer 1986; Bezys and Risk 1990; Wignall 1991; Schieber 1994a; Hasenmüller 1993; Wetzel and Uchman 1998) are vastly outnumbered by investigations of bioturbation in sandstones and carbonates, probably because compaction and generally small burrow sizes make the visualization of burrow morphologies a very challenging and time-consuming task. Also, even in cases where select burrow types were studied in detail (e.g., Seilacher 1978; Jordan 1985), the explanations of the mechanisms that produced particular burrow features are often somewhat general (Bromley 1996).

The burrows that we discuss in this paper superficially resemble either *Planolites* or *Palaeophycus* (Pemberton and Frey 1982), but differ in detail. They are characterized by (a) internal textures that resemble marble cake (swirls), and/or (b) elliptical rings (mantles) of either dark or light colored shale. These textures are collectively referred to as "mantle and swirl" traces in the rest of this paper.

Burrows of a "halo"-like appearance that resemble the "mantle and swirl" type traces in the Chattanooga Shale have previously been described in the literature (e.g., Donahue 1971; Byers 1982; Bromley 1996; Jordan 1985), and were assumed to form (1) by precipitation of diagenetic minerals, such as for example pyrite, next to the burrow (Donahue 1971; Byers 1973; Ekdale 1977; Wetzel 1987); (2) by selective ingestion of certain particles (Beyers 1973); or (3) by burrow stabilization with slime and/or fecal pellets (e.g., Bromley 1996). Petrographic and textural observations, however, indicate that none of these three scenarios applies to the Chattanooga Shale (see below). Thus, although a halo burrow explanation was our initial working hypothesis for the "mantle and swirl" traces of the Chattanooga Shale, we felt that we had to look for alternative explanations. To find this alternative and to evaluate its significance for the interpretation of shale successions was the primary purpose of this study.

Because the observed marbled textures were suggestive of fluid mixing, we designed experiments to test that hypothesis. Solid rubber bait worms were pulled through a liquid substrate in a first set of experiments, and in a second set of experiments live earthworms moved through the same type of substrate. By comparing experimental and actual trace fossils, we were able to examine the relationships between the firmness and/or water content of the substrate, the morphology of the trace maker, and the textural features of these traces.

Our study strongly suggests that the "mantle and swirl" traces in the Chattanooga Shale were produced by worm-like organisms that moved through very soft soupy

Figure 1: Overview map of the southeastern US. Study area in Tennessee is marked with stipple pattern south and east of Nashville.

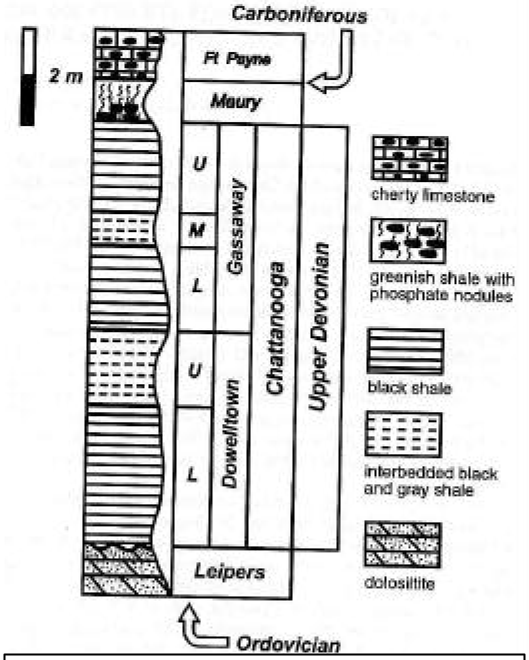

Figure 2: Generalized stratigraphic section and weathering profile of the Chattanooga Shale in central Tennessee. At the base, the Chattanooga Shale is separated by an angular unconformity from older Ordovician strata (Leipers Formation), and at the top it is unconformably overlain by the Carboniferous/Mississippian Maury Formation and Fort Payne Chert.

muds. Although the Chattanooga Shale contains other burrows that postdate the liquid-substrate burrows discussed in this paper (e.g., *Planolites*, *Teichichnus*, and *Chondrites*), these will not be discussed in this contribution. The complete trace-fossil assemblage of the Chattanooga Shale and its paleoecologic implications will be described and discussed in forthcoming publications.

GEOLOGIC SETTING

The Chattanooga Shale is the distal part of a thick clastic wedge that accumulated during the Late Devonian in the Appalachian Basin and on the adjacent North American craton. Although it has long been assumed that these black shales accumulated beneath the dysaerobic-anaerobic boundary of a deep stratified water column (e.g., Byers 1977; Potter et al. 1982), recently uncovered evidence, such as hummocky cross-stratified siltstone/sandstone beds, mud tempestites, lag deposits, and erosion surfaces, suggest a shallow-water depositional setting for these sediments (Schieber 1994a, 1994b, 1994c). In the study area in central Tennessee (Fig. 1), approximately 9-10 m of Chattanooga Shale are found above a basal unconformity (Fig. 2), and the succession is subdivided into the (lower) Dowelltown and (upper) Gassaway Members (Conant and Swanson, 1961). Preliminary conodont data suggest that the Chattanooga Shale in that area spans the time interval from the lower/middle Frasnian to the uppermost Famennian (Ettensohn et al. 1989; Jeff Over, personal communication). Schieber (1994a) observed widespread bioturbation in the Dowelltown Member (Schieber 1994a), suggesting that anoxic conditions were not a prerequisite for black shale deposition.

OBSERVATIONS ON MODE OF BURROWING AND EXPERIMENTS

In the upper part of the Dowelltown Member (Fig. 2), alternating black and gray shale layers (1-10 cm thick) facilitate the observation of biogenic structures. Burrows that traverse layers of contrasting color are in many instances filled with shale of the opposing color (Fig. 3) and are thus easily recognized. Subhorizontal and slightly meandering tubes (now compacted) are conspicuous (Fig. 3). Their most significant textural features are (1) swirl-like mixtures of black and gray shale (Fig. 4), and (2) mantle-like elliptical structures that consist of oppositely colored shale (Figs. 4, 16). The swirl patterns resemble textures that are produced when viscous fluids of contrasting color are stirred together (e.g. oil and honey, dark and light dough in marble cake), suggesting that they reflect mixing of fluid muds. Because both textural features were probably produced in a semi-liquid substrate, we refer to them not as burrows, but chose to call them collectively “mantle and swirl” traces.

Petrographic examination shows that gray ellipses are of the same composition as gray shale layers (mainly clays and quartz silt), and that black ellipses are of the same composition as black shale layers (clay, quartz silt, and up to 20% organic matter). Excepting clays, the most common diagenetic mineral in these shales is disseminated pyrite that occurs as single crystals (a few microns in diameter) or as framboids (0.1-0.4 mm). The pyrite abundance in black or gray “mantles” is the same as in black and gray shale beds, respectively.

The above observation suggests that these ellipses cannot be considered diagenetic "halos" (Donahue 1971; Ekdale 1977). Similarly, the absence of fecal pellets in ellipses as well as of wall-parallel aligned clays suggests that burrow stabilization with fecal pellets or slime (Bromley 1996) does not provide a viable explanation for the observed elliptical features. Finally, the compositional equivalence between gray and black ellipses and gray and black shale layers, respectively, strongly suggests that the constituent materials of these ellipses are directly derived from either gray or black shale layers, and did not form as a consequence of selective ingestion of certain particles (Byers 1973). Whereas above observations essentially rule out a halo burrow origin for our ellipses (see introduction), the

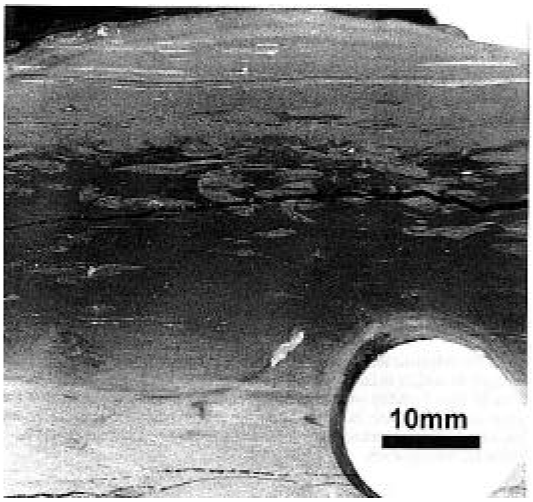

Figure 3: Cut and polished sample from the Dowelltown Member of the Chattanooga Shale, showing alternating black and gray shale beds. The gray beds are more intensely bioturbated to homogenized, and the most visible burrows are those that are filled with black mud. Burrows in black shale beds are filled with gray shale. Coin is 18 mm in diameter.

recognition of compositional equivalence with like-colored shale layers clearly points towards a fluid mixing origin.

In our experiments we attempted to simulate the movement of worms in fluid muds. The important variables that we investigated were: substrate firmness (viscosity) and worm morphology, followed by type and speed of movement. While it may seem simple to obtain realistic data for most of these parameters from observations of modern environments, there is unfortunately a scarcity of precise observational data. This reflects the fact that so many of the factors that determine the state of modern marine substrates (benthic population, water content, erodability, rate of sediment transport, etc.) are complexly interrelated, and that there are many practical difficulties to be overcome before these problems can be investigated (e.g., Hall 1994). There is no question, however, that the described type of animal/sediment interaction could very profitably be approached from a physics or engineering point of view once the necessary data are available. At present, however, we can only offer a qualitative approach to the problem of worms moving through fluid muds.

Experiments with Rubber Bait Worms

In these experiments various rubber bait worms (Fig. 5) were pulled through two horizontal layers (6 cm thick) of liquid plaster of Paris. The bottom layer was colored with a dark dye, and the worms were attached to strings that ran through a series of loops at the bottom of the plaster container. For the experiment, the worms were (1) pulled downwards through the white top layer, (2) across the boundary with the colored layer, and (3) once they had cleared the loops they were pulled upwards across the color boundary again (Fig. 6).

Of course, in real life a worm pushes its way through the sediment rather than being pulled. We felt, however, that moving the worms through the plaster was the key parameter, rather than attempting to exactly mimic the worm's locomotion. Also, because the strings were of much smaller diameter (0.2 mm) than the worms, their interaction with the plaster was negligible, relative to the effect of the worm. The velocity at which the worms were pulled ranged from 6 cm/s to 25 cm/s, so that we could assess the impact of velocity on the resulting structures.

Figure 4: Polished slab of black shale bed from the Dowelltown Member, showing abundant "mantle and swirl" type bioturbation features (arrows). White arrows point to features that show predominantly the "mantle" character, and gray arrows point to features that display well developed "swirl" characteristics.

When the worms traversed the layer boundary, they dragged some plaster of contrasting color across (Fig. 6). Eight to twelve different worms were used in each run, and points of entry and exit were recorded for each worm. The viscosity of plaster mixtures varies with the initial water/plaster ratio and the time that has elapsed since the preparation of the mixture. We used this property of plaster to simulate low-viscosity vs. high-viscosity substrates. Because the setting of plaster accelerates towards the end of the process, the experiments were carried out early, before the onset of the rapid increase in viscosity.

Water/plaster volume ratios of 2 parts water to 3 parts plaster (2W:3P) and 3 parts water to 2 parts plaster (3W:2P) were used, and the best time for conducting the "worm pulling" experiment was found to be 5 minutes after mixing of the plaster. Pulling all worms through the plaster took an additional 8 to 12 seconds. At the five-minute mark, 2W:3P mixtures had the viscosity of lithium grease, and 3W:2P mixtures had the viscosity of heavy motor oil at room temperature (similar to the viscosity of buttermilk or undiluted latex paint).

The ability to examine sedimentary features shortly after the experiment is a main advantage of using plaster for these simulations. A drawback is the viscosity increase in the course of the experiment, and the possibility that this may lead to sedimentary features that are unlikely to form in a clay/water mixture. Through carefully adhering to certain mixing ratios, and through conducting the worm movement always at the same time after combining plaster and water, we tried to minimize this problem.

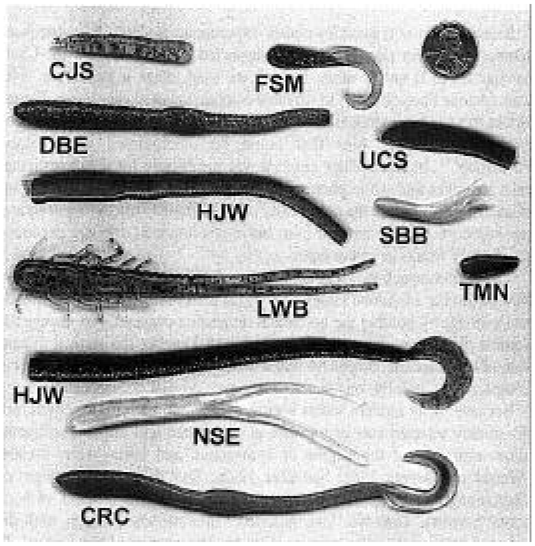

Figure 5: The various rubber bait worms used in our experiments. The rubber worms are solid and the three-letter identifiers are those used elsewhere in the paper. Coin for scale (18 mm diameter).

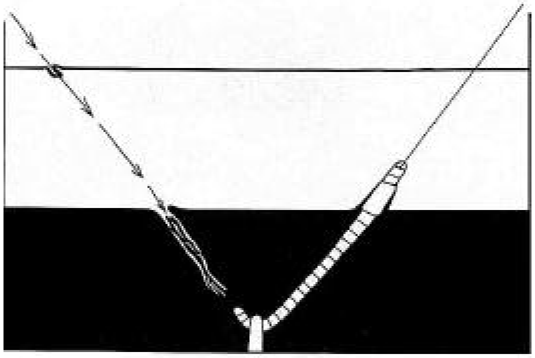

Figure 6: Schematic drawing that shows how rubber bait worms were moved through the plaster layers. Note the colored mud that adheres to the worm and is dragged into the white plaster layer, and how “mantle and swirl” traces form behind the moving worm.

Experiments with Earthworms

Because pulling the worms is a departure from reality, we found it advisable to repeat our experiments with live worms. We chose earthworms because they are readily available. Although we cannot expect them to behave exactly like marine worms, our main objective was to examine the sedimentary features that are produced when a self-propelled worm-like organism moves through a semi-liquid substrate. Because earthworms tend to escape upwards from water-saturated soils after heavy rainfall, we assumed that they would try to move upwards when covered with plaster. In the experiments, earthworms were placed at the base of a layer of colored plaster (6 cm thick), which in turn was immediately covered with a layer of white plaster. Water/plaster ratios and timing were the same as in previous experiments. The worms moved upwards, crossed the boundary between the plaster layers (Fig. 7), and dragged colored plaster upwards into the white layer. From the time it took the worms to reach the surface of the plaster we estimate that they moved at speeds between 1 and 10 cm/s.

Comparing Experiments with Actual Rocks via Manipulation of Digital Images

Because burrow features in plaster experiments undergo no subsequent compaction, direct comparison with suspected fossil analogs in the Chattanooga Shale is not possible. Instead, we used image manipulation software (Adobe Photoshop™) to simulate compaction of plaster traces. Plaster blocks were cut perpendicular to bedding, and placed on a scanner to produce digital image files that could be manipulated with Adobe Photoshop™. In cases where contrast was insufficient for direct scanning, enlarged black-and-white photographs of the cut surface were scanned instead. To fully capture the complexity of bioturbation structures a scanning resolution of 300 dpi worked best, but a resolution of 100 dpi produced satisfactory results in many cases.

"Virtual compaction" was achieved as follows: (1) select image menu from menu bar of Adobe Photoshop™; (2) select image size submenu; (3) resize image by holding the horizontal dimension constant, and change the vertical dimension. For example, reducing to 2 inches the vertical dimension of an image that originally was 4 inches tall corresponds to 50 percent compaction. Similarly, one can also achieve "virtual decompaction".

Because many modern worm burrows show circular cross sections, appropriately selected cuts of burrows in compacted and lithified sediments allow estimates of the degree of compaction and initial water content (Wetzel and Aigner 1986; Seilacher 1992). To "decompact" images of Chattanooga Shale we searched for perpendicular cross sections of horizontal burrows. Then we "decompacted" in a stepwise fashion, until the selected burrows became circular (Fig. 8).

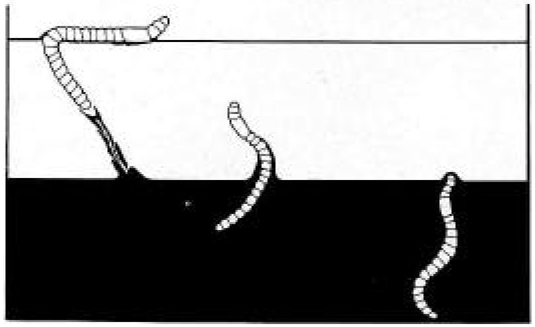

Figure 7: Schematic drawing that shows how earthworms moved through the plaster layers. In contrast to the experiments with the rubber bait worms, the earthworms cross the layer boundary only once, as they endeavor to move upwards out of the water-saturated substrate. Note again how the colored mud adheres to the worms and is dragged into the white plaster layer, and how “mantle and swirl” traces form behind the moving worm.

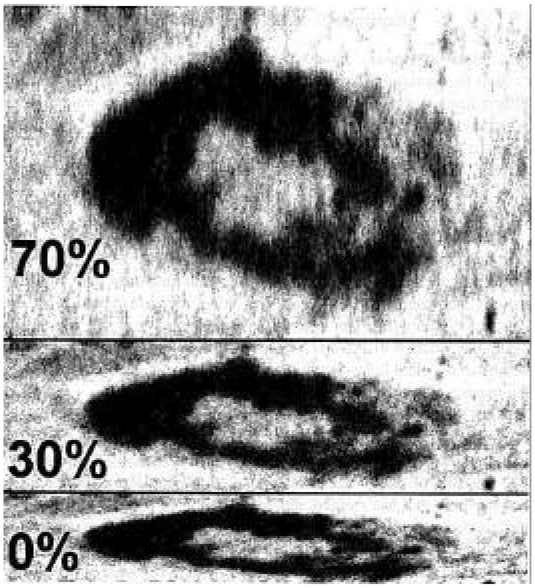

Figure 8: “Virtual decompaction" of elliptical “mantle”-type trace from the Chattanooga Shale. The polished slab of shale (bottom image) was assumed to have 0% water content and porosity. Decompaction was done in 5% increments until the trace (perpendicular cut) assumed a more or less circular outline at 70% “virtual” porosity. Original plaster images are 11 mm wide. This trace is very similar to the experimentally produced structure in Figure 9. The fuzziness of the “mantle” edges in the top image are an artifact that resulted from “virtual” decompaction of a magnified trace (pixels are pulled apart along the vertical axis).

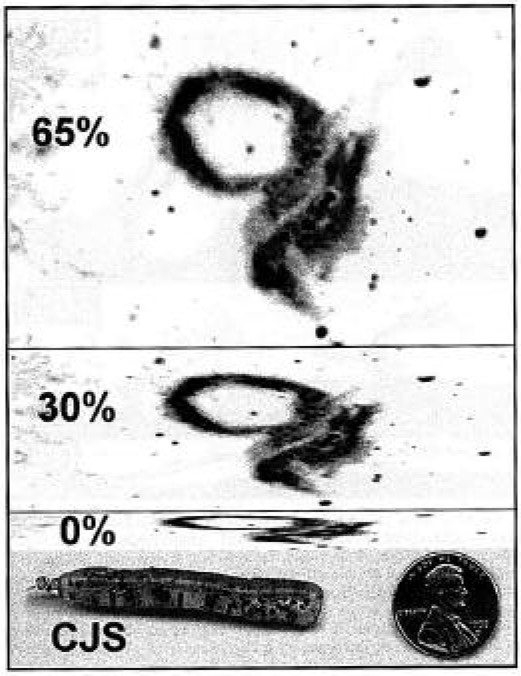

Figure 9: Dark “mantle”-type trace in white plaster and "virtual compaction". The top image is the original scan of a plaster slice. The original plaster image is 18 mm wide, and the inner diameter of the dark mantle is 4 mm. The assumption is that the initial water content of the mud is 65%, and then the vertical dimension is progressively shortened to simulate decreasing water content and porosity. The original outline of the “mantle”-type trace is circular, and when 0% porosity is reached the trace strongly resembles elliptical “mantle”-type traces in the Chattanooga Shale (Fig. 4). This trace was produced by a short and round rubber bait worm labeled CJS (see also Figure 5). Note that the worm is reduced in size relative to the plaster images. The coin that serves as a scale for the rubber worm is 18 mm in diameter.

The change of the vertical dimension of the image is a measure of the amount of “virtual decompaction" and of the initial water content (or porosity) of the rock. Analogously, images of plaster slabs underwent stepwise "virtual compaction", until circular burrow fills were flattened to the same degree observed in the Chattanooga Shale. At that point of “compaction”, the plaster images were assumed to be analogous to a shale with essentially zero water content and porosity.

RESULTS

That structures that were essentially identical to “mantle and swirl” traces from the Chattanooga Shale formed in both sets of experiments is our most significant result. For example, Figure 9 shows that "virtual compaction" of "mantle"-like structures produced with rubber bait worms yields features that look identical to elliptical “mantle” traces in the Chattanooga Shale (Figs. 4, 16). When “mantle” traces in the Chattanooga Shale are “decompacted” they look identical to circular structures in the plaster experiments (Figs. 8, 9, 10).

Swirl-like features (Figs. 11, 12) were readily produced in both sets of experiments. Just as in real rocks (Fig. 4), they are irregular and show a large range of outward morphologies (Fig. 4). Internally, however, they always have a marble-cake-like texture (Fig. 4). Although a range of velocities was explored in the experiments with rubber bait worms, no appreciable change in structures was observed.

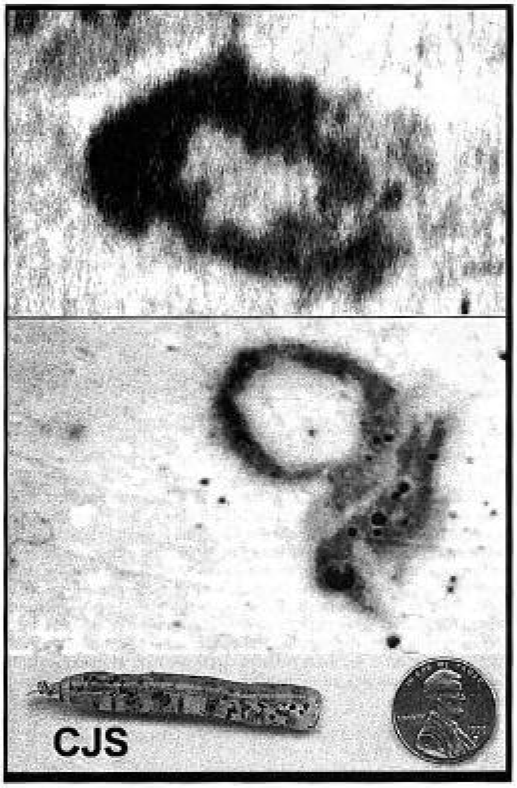

Figure 10: Direct comparison of a decompacted “mantle”-type trace from the Chattanooga Shale (top image, see also Figure 8, image 11 mm wide) with a “mantle”-type trace produced by rubber bait worm CJS in a plaster experiment (middle image, see also Figure 9, image 18 mm wide). The fuzzy edges of the margins of the decompacted “mantle” trace (upper image) are an artifact produced by the “stretching” of the image. Bottom image shows worm CJS. Note that the worm is reduced in size relative to the plaster images. The coin that serves as a scale for the rubber worm is 18 mm in diameter.

The more complex, swirl-like structures were typically produced in water-rich plaster mixtures (consistency of heavy motor oil). The “mantle”-like features were usually observed in stiffer mixtures (consistency of lithium grease). Serial sectioning of plaster blocks shows that the following happened (Figs. 6, 7):

(a) Colored plaster was dragged across the layer boundary as a tubular sheet because of friction against the worm surface, leading to "mantle"-like features.

(b) As the worms moved farther into the next layer this tubular sheet was breached in places to allow the surrounding sediment to fill the interior portions. In this way central portions of these “tubes” tend to be of opposite color and may show "swirl"-like structures.

(c) Plaster was “sucked in” behind the moving worm, leading to "swirl"-like features.

Simple worms (without legs, fins, or tails) produced the most regular and circular structures (Fig. 13),

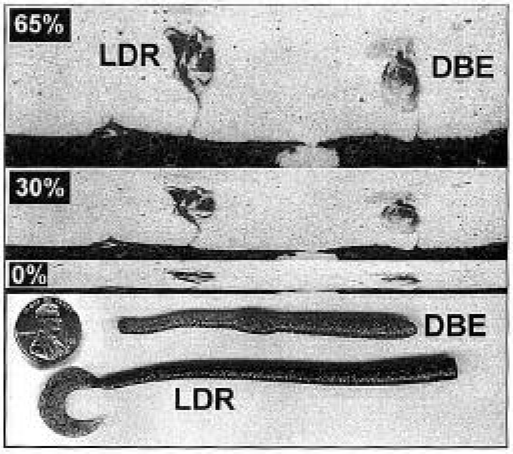

Figure 11: "Swirl"-like features produced in plaster of latex-paint-like consistency by rubber bait worms DBE (long and round) and LDR (long with fin). The original plaster image is 66 mm wide. The "swirl"-like feature on the right (white layer, top image) is more rounded and regular and was produced by the long, smooth, and round worm DBE. The "swirl"-like feature on the left (white layer, top image) is more irregular and was produced by the finned worm LDR. The bottom image shows worms DBE and LDR. Note that the worms are reduced in size relative to the plaster images. The coin that serves as a scale for the rubber worm is 18 mm in diameter. "Virtual compaction" (from 65 to 0% porosity) shows the changing appearance of these traces with decreasing porosity. Had these structures been produced in an actual muddy sediment, the traces produced by the two types of worms would be essentially indistinguishable after compaction.

whereas appendages resulted in more irregular outlines (Fig. 14) and infills (Fig. 11) in the same experimental run. Worm length determines the extent of mixing between layers. When long worms (e.g., worms marked as DBE and HJW in Figure 5) were pulled across the color boundary, "mantle and swirl" features extended for a much larger distance into the next layer than was the case for short worms (e.g., CJS, TMN, UCS).

Although textural features produced in the rubber bait worm and earthworm experiments were overall the same, the mode of locomotion is nonetheless reflected in the appearance of the traces. In the case of simple forward motion (rubber bait worms) there is no significant variation in burrow diameter. The peristaltic motion of earthworms, on the other hand, can lead to burrows with significant diameter variations (Fig. 15).

"Virtual decompaction" of shales to the point where elliptical burrows became circular (Fig. 16) indicates initial water contents of 65 to 75 percent. "Decompaction" also shows that burrows that are subhorizontal in the compacted rock were originally subvertical to quite steeply inclined (Fig. 16).

DISCUSSION

Although the experiments only approximate the processes that actually formed the "mantle and swirl" traces, three considerations indicate that our experiments have a direct bearing on their origin.

(1) Different locomotion styles between rubber bait worms (pulled, uniform speed) and earthworms (peristalsis) could invalidate comparison of structures. During a peristaltic motion cycle, the shear stress between earthworm and sediment more complex swirl patterns, no significant differences were recognized between those of earthworms and rubber bait worms (Figs. 9, 11, 12, 14, 15). The main difference is that earthworm traces show longitudinal variations in width (Fig. 15) due to peristaltic changes of worm diameter. As long as we have motion through the sediment, differences in locomotion style seem not to cause fundamental differences in trace characteristics. Schäfer (1956) reached similar conclusions from bioturbation experiments in sandy sediments.

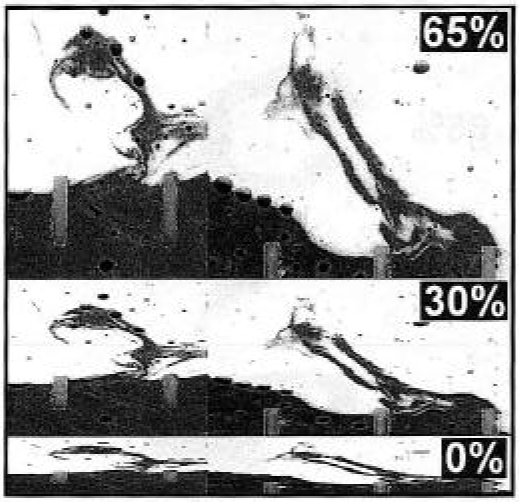

Figure 12: "Swirl"-like features produced by earthworms in plaster with the consistency of latex paint. Shows various "swirl" features produced by fluid mixing of dark and white plaster (top image). The swirl feature on the right (top image) is a partial longitudinal cut of an earthworm trace. It shows an outer layer of dark plaster that would appear as a dark "mantle" in a perpendicular section, and an internal fill that variably consists of white plaster or swirled white/dark plaster. It also shows breaches through which white plaster entered and filled the tubular sheet of dark plaster. The original plaster images are 96 mm wide. "Virtual compaction" (from 65% to 0% porosity) also shows that these features become increasingly alike as compaction proceeds, and closely resemble those observed in the Chattanooga Shale (Fig. 4).

(2) Could the velocities in the experiments with rubber bait worms (6-25 cm/s) be too high for a realistic evaluation of "mantle and swirl" structures? Although data on the actual speed of worm locomotion are very sparse (Clark 1976; Banse and Hobson 1974; Barr and Smith 1979; Martinez 1996), these velocities are on the same order of magnitude as exhibited by actual marine worms. For example, *Ophiodromus*, a worm approximately 2 cm long, can move at speeds of 2 cm/s over mud surfaces, and swims at speeds of 4-6 cm/s (Merz, personal communication). Longer worms should be able to move several times faster. Because bait worm experiments show that from 6 to 25 cm/s there is no appreciable change in sedimentary features, the structures produced by earthworms at the low end of the velocity spectrum (1-10 cm/s) should also be considered realistic analogs.

Because velocity and locomotion style do not seem to affect the developing sedimentary features, it is possible that mud density was an important factor. At a water content of 75 percent, the bulk density of the sediment (assuming a clay/water mixture) would be about 1.4 g/cm^3. This sediment would have a comparatively high viscosity, and at the envisioned

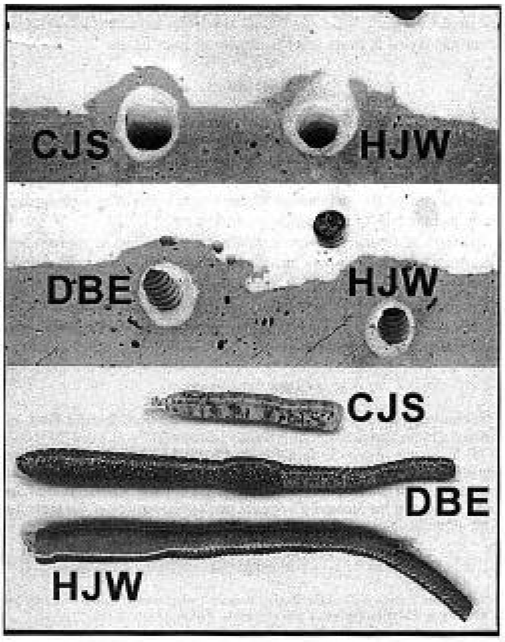

Figure 13: White "mantle"-type traces in dark plaster. These traces were produced at comparatively large viscosities (like that of lithium grease), and the worms accidentally became detached from the fishing line and got stuck in the hardening plaster. The traces are in essence a tube-like sheet of white plaster that adhered to the worms and was dragged downwards into the colored plaster. Had the worms not become stuck, the central portion would be filled with either dark plaster or a swirl-like mixture of white and dark plaster. Traces were produced by three different types of short and long round worms (CJS and HJW/DBE, respectively). The original plaster images are 54 mm wide. Notice in the upper plaster image that the "mantle" produced by worm HJW is thicker than the one produced by the shorter worm CJS. This indicates that longer worms produce thicker "mantles", in accordance with boundary-layer theory (see discussion). Note that the worms are reduced in size relative to the plaster images (refer to Figure 5 for actual size).

speeds of worm motion, the Reynolds number should be so low as to ensure a prevalence of laminar flow. Also, in high-concentration suspensions such as the envisioned soupy sediment there is considerable dampening of turbulence (McCave and Jones 1988).

(3) Finally, as the traces of worms with appendages (legs, fins, tails) show, the morphology of the trace maker also influences the resulting trace. In experiments with layered sandy sediments, Schäfer (1956) likewise observed that burrowers with appendages produce more complex and irregular structures. Yet, although worms with appendages did produce more irregular traces (Figs. 11, 14) when compared to traces produced by smooth worms (Fig. 13), the basic features (mantles and swirls) still formed. "Mantle and swirl" traces from the Chattanooga Shale (Figs. 4, 8) do more closely resemble the traces produced by smooth worms (Figs. 9, 10, 13), suggesting that simple worms or comparable organisms produced them.

That "mantle"-like features were more commonly produced at higher viscosities (lithium grease), and swirl-like features at lower viscosities (heavy motor oil), is consistent with a fluid mixing model. "Swirls" reflect mixing and eddy formation at lower viscosities, whereas "mantles" result from laminar flow (tubular sheets of mud) along the moving worm at higher viscosities. Boundary-layer theory (Schlichting 1960) predicts that at a given speed and viscosity, the thickness of the boundary layer around a moving object is proportional to the square root of its length. This agrees well with the observation that "mantles" produced by long worms are thicker (Fig. 13) and extend much farther across layer boundaries than those produced by short worms. Viscosity, rather than locomotion type, speed, and details of organism morphology, seems to determine formation and extent of "mantle"- or "swirl"-like features.

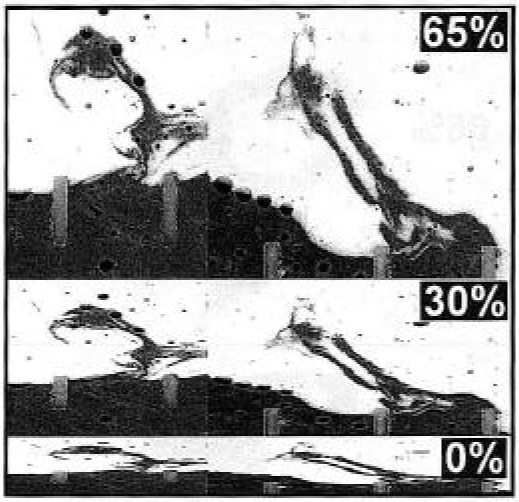

Figure 14: "Swirl"-like features produced in plaster with the consistency of latex paint by rubber bait worm LWB (long with legs and tail; right image, refer to Figure 5 for actual size). Note the irregular outline and high degree of convolution in this trace, which is attributable to the appendages of the worm. As in Figure 9, "virtual compaction" (from 65 to 0% porosity) shows the changing appearance of this trace with decreasing porosity. The original plaster images are 24 mm wide.

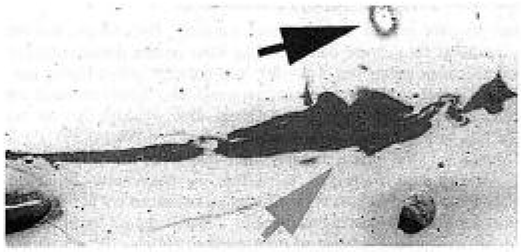

Figure 15: Features produced by earthworms in plaster. In the central portion of the picture is a horizontally oriented earthworm trace (gray arrow) that shows how peristalsis affects burrow diameter. The worm was moving from left to right, the consistency was that of latex paint, and we see the development of "swirl"-like features. The dark circle in the top right half of the picture (black arrow) is a "mantle"-type burrow produced by another worm that crossed this volume of plaster a little later when it had reached the viscosity of lithium grease. The hole in the bottom right half of the picture is due to a worm that got stuck and then decayed. Decay processes produced the fuzzy gray halo in the plaster adjacent to the worm. The original plaster image is 120 mm wide.

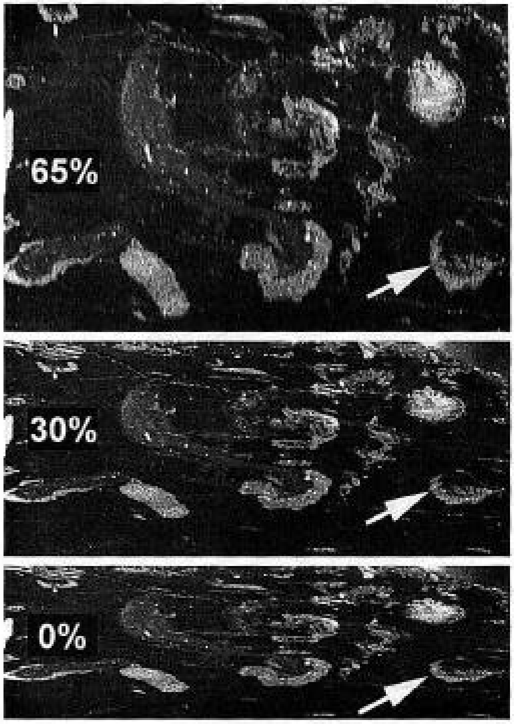

Figure 16: "Virtual decompaction" of a slab of Chattanooga Shale cut perpendicular to bedding (image of actual rock at 0%, bottom image). The elliptical trace in the lower right corner of the bottom image (arrow) becomes circular once the image is stretched to simulate a porosity or water content of 65%. Thus, we assume that the initial water content or porosity of the sediment was close to 65%. Note "mantle"-type burrows that are cut at various angles, and that subhorizontal burrows were originally probably quite steeply inclined. Images are 45 mm wide.

The close match between traces produced in bait worm and earth worm experiments (Figs. 9, 11, 12, 13, 14, 15) and those found in the Chattanooga Shale (Figs. 4, 8, 16) is probably the most compelling argument that the latter were produced by worms or worm-like organisms that moved through a sediment of soupy consistency. A 70 percent water content and soupy character are also indicated by "virtual" decompaction.

In modern sediments, eddy-like features and indistinct and diffuse outlines that are produced by organisms that move through soupy substrates have been described as biodeformational structures (e.g., Wetzel 1991). Although they have diffuse rather than sharp outlines, they may be modern analogs to "mantle and swirl" traces observed in this study. What type of outline/margin we see may well depend on the viscosity of the substrate and the color contrast between mixed sediments. For example, had our experiments been carried out at a higher water content (lower viscosity), more vigorous mixing would probably have produced diffuse burrow margins. A small or absent color contrast would have further obscured the boundary between trace and host sediment. Thus, although they are not identical to biodeformational structures as described (Wetzel 1991), our "mantle and swirl" traces probably still belong in that category.

Although there is a general resemblance, our experiments suggest that "mantle and swirl" traces in the Chattanooga Shale do not fit the definitions for *Planolites* (active backfilling by a mobile deposit feeder) or *Palaeophycus* (passive infilling of open dwelling burrow) (Pemberton and Frey 1982). *Planolites* and *Palaeophycus* both require a substrate that is firm enough to allow preservation of sharp and distinct burrow outlines. "Virtual decompaction", however, indicates a large initial water content and soupground conditions (Ekdale et al. 1984). Because of the clear color contrast between burrow fill and host sediment, "mantle and swirl" traces from the Chattanooga Shale are easily mistaken for firmground burrows of the *Planolites* and *Palaeophycus* type. A cursory examination of photos in the trace-fossil literature shows possible candidates for "swirl and halo" type traces in other formations (Ekdale 1977; Cluff 1980; Bromley 1996), and makes it appear likely that comparable traces have been misidentified or misinterpreted in many previous studies of trace fossils.

CONCLUSIONS

"Mantle and swirl" traces in the Chattanooga Shale formed when worms or worm-like organisms moved through a liquid to semi-liquid substrate, and can be considered biodeformational structures. How "mantle and swirl" traces develop in detail is influenced by the consistency of the substrate (viscosity), the morphology of the worms (smooth or with appendages), and the type of locomotion (peristalsis etc.).

Although of similar appearance, *Planolites*, *Palaeophycus*, or halo burrows form in firmer substrate than "mantle and swirl" traces. To mistake them for "mantle and swirl" traces causes erroneous assessments of environmental and substrate conditions. "Mantle and swirl" traces are in all likelihood widespread in the sedimentary record, and were probably misidentified in many previous studies.

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REFERENCES

Banse, K., and Hobson, K.D., 1974, Benthic errantiate polychaetes of British Columbia and Washington:, Fisheries Research Board of Canada, Bulletin 185, p. 1-111.

Barr, D., and Smith, B.P., 1979, The contribution of setal blades to effective swimming in the aquatic mite *Limnochares americana* (*Acari: Prostigmata:Limnocharidae*): Zoological Journal of the Linnean Society, v. 65, p. 55-69.

Bottjer, D.J. and Droser, M.L., 1991, Ichnofabric and basin analysis: Palaios, v. 6, p. 199-205.

Brongniart, A., 1823, Observations sur les Fucoides: Société de l'Histoire Naturelle, Paris, Memoires, v. 1, p. 301-320.

Bromley, R.G., 1996, Trace fossils; Biology and Taphonomy, 2nd Edition: London, Unwin Hyman Ltd, 280 p.

Bromley, R.G., and Ekdale, A.A., 1986, Composite ichnofabrics and tiering of burrow: Geological Magazine, v. 123, p. 59-65.

Byers, C.W., 1972, Analysis of paleoenvironments in Devonian black shale by means of biogenic structures (abstract): Geological Society of America, Abstracts with Programs, v.4/7, 464 p.

Byers, C.W., 1973, Biogenic structures of black shale paleoenvironments [unpublished Ph.D. dissertation], New Haven, Connecticut, Yale University, 131 p.

Byers, C.W., 1977, Biofacies patterns in euxinic basins: a general model: Society of Economic Paleontologists and Mineralogists, Special Publication 25, p. 5-17.

Byers, C.W., 1982, Geological significance of biogenic sedimentary structures, *in* McCall, P.R., and Tevesz, M.J.S., eds., Animal-Sediment relations; the biogenic Alteration of Sediments: New York, Plenum Press, p. 221-256.

Bezys, R.K., and Risk, M.J., 1990, The Long Rapids Formation; an Upper Devonian black shale in the Moose River basin, northern Ontario: Canadian Journal of Earth Sciences, v. 27, p. 291-305.

Clark, R.B., 1976, Undulatory swimming in polychaetes. *in* Davis, P.S. ed., Perspectives in Experimental Biology, Proceedings of the Fiftieth Anniversary Meeting of the Society for Experimental Biology, Volume 1, Zoology: New York, Pergamon Press, p. 437-446.

Cluff, R.M., 1980, Paleoenvironment of the New Albany Shale group (Devonian-Misissippian) of Illinois: Journal of Sedimentary Petrology, v, 5, p. 767-780.

Conant, L.C., and Swanson, V.E., 1961, Chattanooga Shale and related rocks of central Tennessee and nearby areas: U.S. Geological Survey, Professional Paper 357, 91 p.

Darwin, C., 1838, On the formation of the mould: Geological Society of London, Proceedings, v. 2, p. 574-576.

Donahue, J., 1971, Burrow morphologies in north-central Pacific sediments: Marine Geology, v. 11, p. 1-7.

Easthouse, K.A., and Driese, S.G., 1988, Paleobathymetry of a Silurian shelf system; application of proximality trends and trace-fossil distributions: Palaios, v. 3, p. 473-486.

Ekdale, A.A., 1977, Abyssal trace fossils in worldwide Deep Sea Drilling Project cores, *in* Crimes, T.P., and Harper, J.C. eds., Trace Fossils 2: Geological Journal Special Issue No. 9., Proceedings of an International Symposium held in Sidney, Australia, 23, 24 August 1976 as part of the 25th International Geological Congress, p. 163-182.

Ekdale, A.A., Bromley, R.G., and Pemberton, S.G., 1984, Ichnology ; Trace Fossils in Sedimentology and Stratigraphy: SEPM, Short Course 15, 316 p.

Ettensohn, F.R., Goodman, P.T., Norby, R., and Shaw, T.H., 1989, Stratigraphy and biostratigraphy of the Devonian-Mississippian black shales in west-central Kentucky and adjacent parts of Indiana and Tennessee: 1988 Eastern Oil Shale Symposium, Proceedings Volume, University of Kentucky, Institute for Mining and Minerals Research, p. 237-245.

Frey, R.W., 1975, The Study of Trace Fossils; A Synthesis of Principles, Problems, and Procedures in Ichnology: New York, Springer-Verlag, 562 p.

Griffith, C., 1978, Depositional environment of the New Albany Shale (Upper Devonian) in North-central Kentucky (abstract): Geological Society of America, Abstracts with Programs, v.10/6, p. 255.

Griggs, G.B., Carey, A.G., and Kulm, L.D., 1969, Deep-sea sedimentation and sediment-fauna interaction in Cascadia Channel and Cascadia Abyssal Plain: Deep-Sea Research, v. 16, p. 157-170.

Häntzschel, W. 1962, Trace fossils and problematica, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part W: Geological Society of America and University of Kansas Press, p. W177-W245.

Hasenmüller, N.R., 1993, New Albany Shale (Devonian and Mississippian) of the Illinois Basin, *in* Roen, J.B. and Kepferle, R.C. eds., Petroleum Geology of the Devonian and Mississippian Black Shale of Eastern North America: U.S. Geological Survey Bulletin 1909, p. C1-C19.

Jordan, D.W., 1980, Trace fossils and stratigraphy of Devonian black shale in Eastern-central Kentucky: American Association of Petroleum Geologists Bulletin, v. 64, p. 729-730.

Jordan, D.W., 1985, Trace fossils and depositional environments of Upper Devonian black shales, East-central Kentucky, U.S.A., *in* Curran, H.A. ed., Biogenic structures: Their Use in Interpreting Depositional Environments: SEPM, Special Publication 35, p. 279-298.

Larson, D.W., and Rhoads, D.C., 1983, The evolution of infaunal communities and sedimentary fabrics, *in* Tevesz, M.J.S., and McCall, P.L., eds., Biotic Interactions in Recent and Fossil Benthic Communities: New York, Plenum Press, p. 627-648.

Martinez, M.M., 1996, Issues for aquatic pedestrian locomotion: American Zoologist, v. 36, p. 619-627.

McCave, I.N., and Jones, P.N., 1988, Deposition of ungraded muds from high-density non-turbulent turbidity currents: Nature, v. 333, p. 250-252.

Miller, M.F., and Rehmer, J., 1979, Trace fossils in interpretation of sharp boundaries: an example from the Devonian of New York (abstract): Geological Society of America, Abstracts with Programs, v.11/1, p. 45.

Miller, M.F., 1982, Biogenic structures as indicators of oxygen availability during deposition of the Chattanooga Shale and Maury shales (Devonian-Mississippian), central Tennessee (abstract): Geological Society of America, Abstracts with Programs, v.14/7, p. 566.

Pemberton, S.G., and Frey, R.W., 1982, Trace fossil nomenclature and the *Planolites- Paleophycus* dilemma: Journal of Paleontology, v. 56, p. 843-881.

Potter, P.E., Maynard, J.B. and Pryor, W.A., 1982, Appalachian gas bearing Devonian shales: Statements and discussions: Oil and Gas Journal, v. 80, p. 290-318.

Pratt, L.M., Claypool, G.E., and Kink, J.D., 1986, Geochemical imprint of depositional conditions of organic matter in laminated-bioturbated interbeds from fine grained marine sequences: Marine Geology. v. 70, p. 67-84.

Pryor, W.A., 1975, Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments: Geological Society of America, Bulletin, v. 86, p. 1244-1254.

Reineck, H.-E., Gutmann, W.F., and Hertweck, G., 1967, Das Schlickgebiet südlich Helgoland als Beispiel rezenter Schelfablagerungen: Senckenbergiana Lethaia, v. 48, p. 219-275.

Reineck, H.-E., Dörjes, J., Gadow, S., and Hertweck, G., 1968, Sedimentologie, Faunenzonierung und Faziesabfolge vor der Ostküste der inneren Deutschen Bucht: Senckenbergiana Lethaia, v. 49, p. 261-309.

Richter, R., 1927, Die fossilen Fährten und Bauten der Würmer, ein Überblick über ihre biologischen Grundformen und deren geologische Bedeutung: Paläontologische Zeitschrift, v. 9, p. 193-240.

Savrda, C.E., and Bottjer, D.J., 1986, Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters: Geology, v. 14, p. 3-6.

Savrda, C.E., and Bottjer, D.J., 1994, Ichnofossils and ichnofabrics in rhythmically bedded pelagic/hemi-pelagic carbonates; recognition and evaluation of benthic redox and scour cycles, *in* de Boer, P.L., and Smith, D.G., eds., Orbital Forcing and Cyclic Sequences: International Association of Sedimentologists, Special Publication 19, p. 195-210.

Schäfer, W., 1956, Wirkung der Benthos-Organismen auf den jungen Schichtverband: Senckenbergiana Lethaia, v. 37, p. 183-263.

Schäfer, W., 1962, Aktuo-Paläontologie nach Studien in der Nordsee: Frankfurt, Kramer, 666 p.

Schieber, J., 1992, Observations suggestive of persistent bottom currents and episodic high energy events during deposition of the Chattanooga Shale, Devonian of central Tennessee: implications for probable water depth and sediment condition (abstract): Geological Society of America, Abstracts with Programs, v. 24/7, p. 351-352.

Schieber, J., 1994a, Evidence for high-energy events and shallow-water deposition in the Chattanooga Shale, Devonian, central Tennessee, USA: Sedimentary Geology. v. 93, p. 193-208.

Schieber, J., 1994b, Paleoflow patterns and macroscopic sedimentary features in the Late Devonian Chattanooga Shale of Tennessee: Differences between the Appalachian Basin and the American Craton, *in* Embry, A.F., Beauchamp, B., and Glass, D.J., eds., Pangea: Global Environments and Resources: Canadian Society of Petroleum Geologists, Memoir 17, p. 763-772.

Schieber, J., 1994c, Reflection of deep vs shallow water deposition by small scale sedimentary features and microfabrics of the Chattanooga Shale in Tennessee, *in* Embry, A.F., Beauchamp, B., and Glass, D.J., eds., Pangea: Global Environments and Resources: Canadian Society of Petroleum Geologists, Memoir 17, p. 773-784.

Schlichting, H., 1960, Boundary Layer Theory: New York, McGraw Hill, 647 p.

Seilacher, A., 1953, Über die Methoden der Palichnologie: 1. Studien zur Palichnologie: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 96, pp 421-452.

Seilacher, A., 1978, Use of trace fossil assemblages for recognizing depositional environments, *in* Basan, B., ed., Trace Fossil Concepts: SEPM Short Course 5, p. 167-180.

Seilacher, A. 1992, Quo vadis ichnology, *in* Maples, C.G., and West, R.R., eds., Trace Fossils: The Paleontological Society, Short Courses in Paleontology No. 5, 240 p.

Wetzel, A., 1987, Ichnofabrics in Eocene to Maestrichtian sediments from Deep Sea Drilling Project Site 605, off the New Jersey coast, *in* van Hinte, J.E., Wise, S.W., et al., eds., Initial Reports of the Deep Sea Drilling Project, vol. XCII, Washington, D.C., U.S. Government Printing Office, p. 825-835.

Wetzel, A., 1991, Ecologic interpretation of deep-sea trace fossil communities: Palaeontology, Palaeoclimatology, Palaeoecology, v. 85, p. 47-69.

Wetzel, A., and Aigner, T., 1986, Stratigraphic completeness: tiered trace fossils provide a measuring stick: Geology, v. 14, p. 234-237.

Wetzel, A., and Uchman, A., 1997, Biogenic sedimentary structures in mudstones - an overview, *in* Schieber, J., Zimmerle, W., and Sethi, P., eds., Shales and Mudstones, volume 1, Basin Studies, Sedimentology, and Paleontology: Stuttgart, Schweizerbart'sche Verlagsbuchhandlung, p. 351-369.

Wignall, P.B., 1991, Dysaerobic trace fossils and ichnofabrics in the Upper Jurassic Kimmeridge Clay of southern England: Palaios, v. 6, p. 264-270.