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# Styles of behavioral complexity recorded by selected trace fossils

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## Abstract

At least four styles of complex behavior are recorded in trace fossils: (1) Intricate, programmed behavior that is recorded in complex trace fossils, such as *Spirophyton* and *Zoophycos*. (2) Behavior that is complex in consisting of multiple simple behaviors performed by a single organism, as indicated by one trace fossil merging into another (compound trace fossils). (3) Behavior in which an animal constructs both complex and simple structures, as demonstrated by direct connection between the two structures. (4) Two scales of complex behavior reflected in multiple specimens of one trace fossil arranged in a pattern to produce a distinctive, larger-scale structure. Until recently complex trace fossils (e.g. *Zoophycos*) alone have served as proxies for complex behavior. Recognition and reconstruction of diverse modes of behavioral complexity allow more biological information to be gleaned from the trace fossil record.

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## 1. Introduction

Complex behavior of ancient organisms is interpreted most commonly from complex trace fossils. These are large, intricate or complicated structures that are considered to represent a life-long domicile or project (e.g. [Ekdale et al., 1984](#); [Bromley, 1996](#); [W. Miller and D'Alberty, 2001](#)). Complex trace fossils typically have been considered to reflect complex behavior, which is specialized for a narrow range of environmental con-

ditions (e.g. [Seilacher, 1967, 1977, 1978](#); [Crimes, 1975](#)).

Because of the utility of complex trace fossils as paleoenvironmental indicators, the wealth of biological information encoded in them has been under-explored and under-appreciated (e.g. [W. Miller, 1998, 2002](#)). Recent work on complex trace fossils has expanded to reveal that complex behavior is recorded in compound trace fossils as well as in complex trace fossils. According to [Pickerill \(1994, p. 23\)](#), 'The most common type of compound specimens comprise intergradational forms in which one ichnotaxon passes gradually or directly into another, in most situations probably reflecting different behavioral activity

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of the same producing organism'. Recognition of compound trace fossils allows the full spectrum of a producer's behavioral options to be evaluated. Some studies suggest that the ranges of animal behavior are much broader than would be reconstructed if the intergradational character of the superficially unconnected trace fossils was not appreciated (M. Miller, 1991; M. Miller and Collinson, 1994; W. Miller, 2001).

This paper delineates styles of complex behavior based on interpretation of both complex and compound trace fossils. Four types of complex behavior are discussed from Devonian marine margin and shallow marine deposits of New York, Pennsylvanian deltaic deposits of Tennessee, Permian and Triassic fluvial deposits of the Central Transantarctic Mountains, Antarctica, and Ordovician marine limestones of Tennessee. The identification of diverse styles of behavioral complexity allows much greater appreciation of the range of behavior of infaunal animals.

## 2. Styles of behavioral complexity

### 2.1. Style A: one animal – one type of complex behavior – one complex trace fossil

This style of complex behavior is the most commonly recognized style. It is characterized by a complex trace fossil produced by a single type of animal, presumably over much of the animal's lifetime. An example of behavior Style A is recorded by *Spirophyton*, in its occurrence in the marine margin and estuarine deposits of the Devonian Catskill delta in eastern New York State (M. Miller and Woodrow, 1991).

*Spirophyton* consists of whorls of spreite around an axial shaft (Fig. 1A). Specimens occurring in profusion on one bedding plane show little variation in size or morphology, although both clockwise and counter-clockwise spiraling occur. In longitudinal section the arrangement of the whorls around the axial tunnel is consistent and unchanging (Fig. 1B). The exact mode of formation is not known, although it is clear that the animal incorporated sand from an overlying layer into the spreite, and the complexity and uniform-

ity of the structure reflect highly programmed and elaborate behavior. However, the occurrence of scattered laminae that resemble individual whorls suggests that the producing animal did not complete all structures it started (M. Miller, 1991), testifying that even this animal's behavior was not completely restricted to a single program.

One might predict that such specialized behavior as recorded by *Spirophyton* would be particularly advantageous in stable environments with predictable supplies of resources and that trace producers would be K-selected. In contrast, the environmental distribution of *Spirophyton* in these Devonian marine-margin deposits and its patterns of abundance indicate that the producer was an r-selected opportunist (M. Miller and Johnson, 1981). This demonstrates that ecological opportunists can be behavioral specialists, and it argues against the seemingly reasonable coupling of ecological and behavioral specialization.

### 2.2. Style B: one animal – multiple simple behaviors – several simple trace fossils

In behavior Style B, the animal engages in multiple simple types of behavior, and the complexity of the resultant trace fossil arises from the collection or range of behavior rather than from a single behavior. Style B behavior is recorded as discrete, superficially unconnected ichnofossils. It is recognized only when forms transitional between two ichnotaxa or specimens that change from one ichnotaxon to another are found.

Behavior Style B results in compound trace fossils (Pickerill, 1994), examples of which are well documented in the literature. Specimens of the resting trace *Rusophycus* have been found to merge into the crawling trace *Cruziana* and the trackway *Diplichnites*; they all are interpreted as produced by trilobites variably hiding in or moving through or across the sediment (Crimes, 1970). The knobby walled boxworks, mazes, and/or shafts of *Ophiomorpha nodosa* have been observed to merge into spreiten structures, *Thalassinoides* (morphologically similar to *O. nodosa*, but unpeletted), *Spongiomorpha* (similar to *Thalassinoides*, but with external ridges or scratch

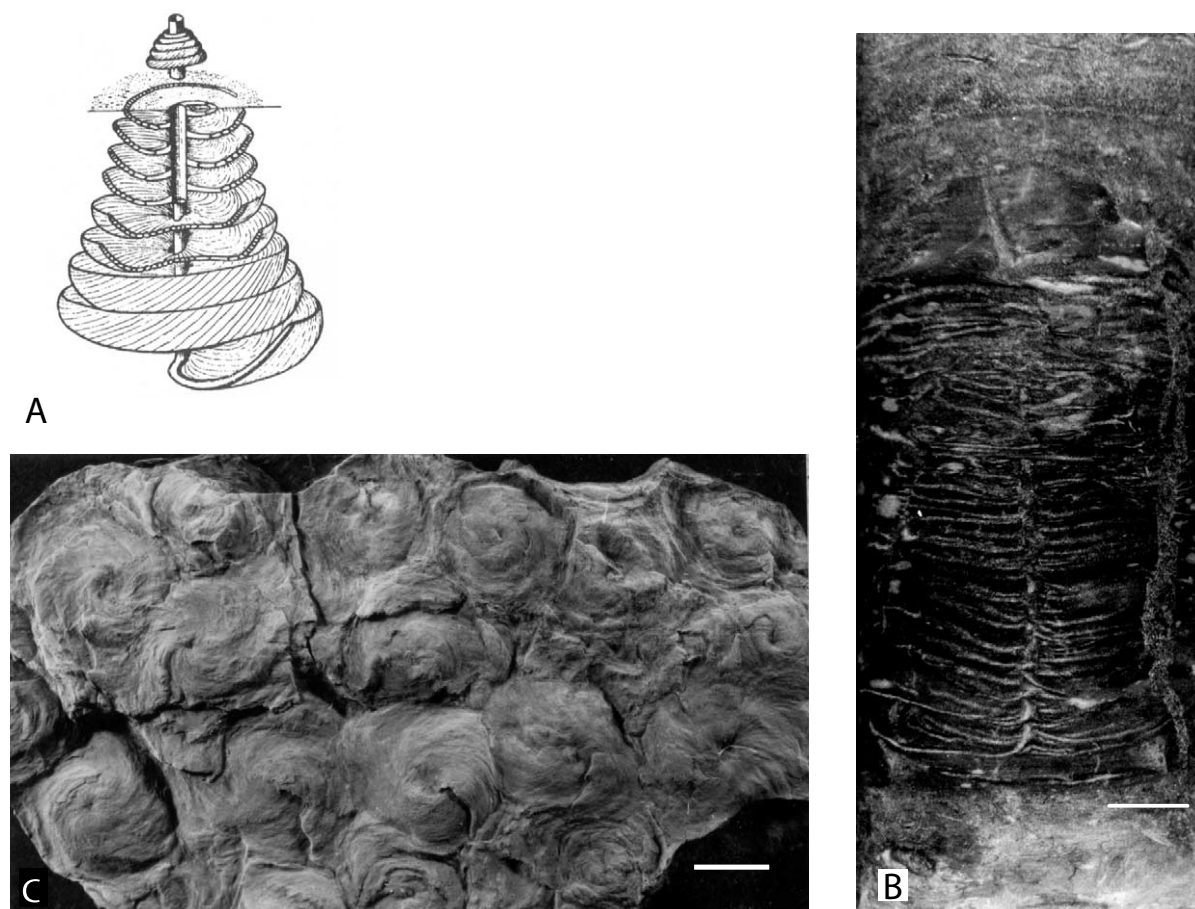


Fig. 1. (A) Reconstruction of *Spirophyton* from Hantzschel (1975). Note lamina (spreite) wound around central axis. (B) Longitudinal section of *Spirophyton* in core, showing lamina and axial tunnel filled with light-colored very fine-grained sandstone that the producer piped down from the overlying sand layer. Devonian, Schoharie Valley, New York. Bar = 1 cm. (For information of *Spirophyton* and *Zoophycos* illustrated, see M. Miller and Johnson, 1981; M. Miller, 1991; M. Miller and Woodrow, 1991.) (C) *Spirophyton* on underside of bed. Note similarity of specimens in size and morphology. Devonian, Schoharie Valley, New York. Bar = 1 cm.

marks), and *Gyrolithes* (vertically spiraled burrows) (Hester and Pryor, 1972; Bromley and Frey, 1974; Bromley, 1996).

With a few exceptions (e.g. Ekdale and Bromley, 2001), compound structures have been discussed in the context of the preservation issues and ichnotaxonomic problems that they present rather than with the goal of elucidating the behaviors recorded (e.g. Pickerill, 1994; Bromley, 1996). The change from (pelleted) *Ophiomorpha nodosa* to (unpelleted) *Thalassinoides* commonly is interpreted to reflect a change from unstable

to more cohesive substrate conditions (Frey et al., 1978). Change from *O. nodosa* to unpelleted burrows has been documented within specimens from (Miocene) tidal channel margin deposits recording no identifiable change in environmental conditions or substrate stability; here the variation in trace characteristics was attributed to behavioral plasticity of the trace-producing thalassinid shrimp (M. Miller and Curran, 2001).

Care must be taken to distinguish compound trace fossils from composite trace fossils discussed by Pickerill (1994). In contrast to compound

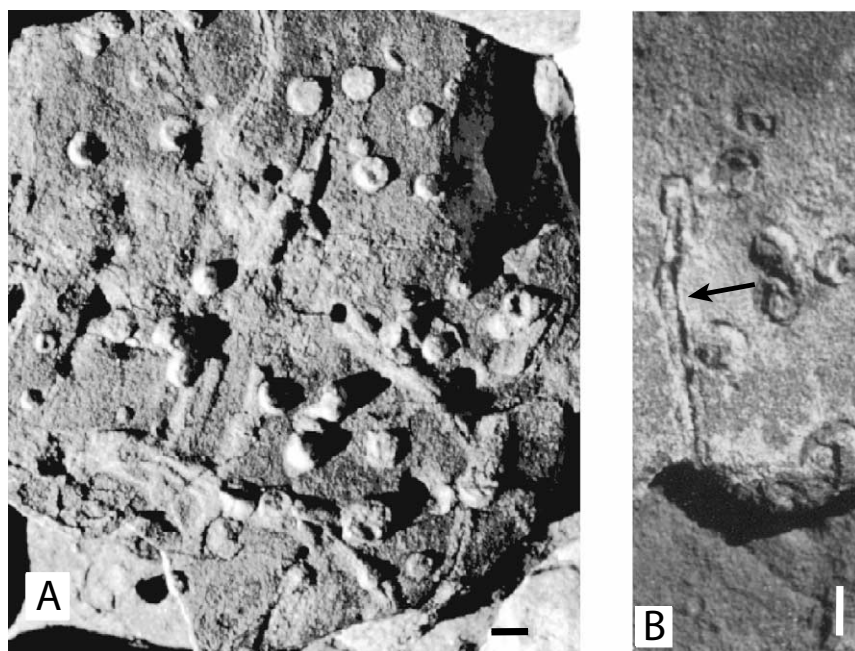


Fig. 2. (A) Intersecting specimens of *Skolithos* and *Palaeophycus* on upper bedding surface (field photo). Although these specimens are simply cross-cutting occurrences of specimens merging from one ichnogenus to another in these Permian and Triassic fluvial sandstones, although rare, indicate a common producer of four types of trace fossils (*Skolithos*, *Palaeophycus*, *Cruziana*, chevron burrows). Fremouw Formation, Beardmore Glacier area, Central Transantarctic Mountains. Bar = 1 cm. (B) *Skolithos* merging into *Cruziana*, demonstrating that both trace fossils were produced by the same animal (field photo). Buckley Formation (Permian), Beardmore Glacier area, Central Transantarctic Mountains. Bar = 1 cm.

traces, which are the work of a single trace producer, composite traces are cross-cutting traces recording the work of unrelated producers, possibly inhabiting the same substrate ecospace at different times.

Significant paleobiologic information has been gleaned from compound trace fossils that occur in fluvial channel sandstones of the Permian Buckley Formation and Triassic Fremouw Formation in the Central Transantarctic Mountains, Antarctica (M. Miller and Collinson, 1994; M. Miller, 2000). Four trace fossils, *Skolithos*, *Palaeophycus*, *Cruziana*, and chevron burrows, are common on upper bedding planes of large-scale trough cross-bedded sandstones and less common on vertical surfaces. *Skolithos* and *Palaeophycus* are most abundant (Fig. 2). Although some of the specimens clearly are cross-cutting (Fig. 2A), two lines of evidence indicate that in these fluvial sandstones all four of the trace fossils were produced by a single type of animal: (1) numerous specimens were found that

change from one trace into another (Fig. 2B), and (2) diameters (widths) and distribution of diameters are nearly the same for all ichnotaxa (M. Miller and Collinson, 1994, fig. 2A; figs. 5 and 6; M. Miller, 2000, fig. 2A; fig. 4).

The behaviors represented by the four trace fossils are simple: vertical burrowing (*Skolithos*), horizontal tunneling at different depths beneath the sediment–water interface (*Palaeophycus*, *Cruziana*), and basically horizontal movement with some vertical motion above and below the bedding plane (chevron traces). However, the overall behavior recorded is complicated as evidenced both by the diversity of component behaviors and by the necessity for a mechanism to trigger change from one behavioral option to another. All of the traces occur in medium- to coarse-grained channel-fill sandstones and there is no evidence either that animal behavior was controlled by substrate characteristics or that the different traces reflect a single behavior that is

recorded in different ways in substrates of different consistencies.

Some ichnologists have rejected the notion that an organism would produce both *Skolithos* and *Palaeophycus* or *Planolites*, reasoning that no animal would switch from suspension feeding to deposit feeding. However, recent work on modern thalassinid shrimp that burrow in marine sediments has demonstrated that individual species derive nutrition from more than one feeding mode and suggests that deposit feeding and suspension feeding can grade into one another (Nickell and Atkinson, 1995; Nickell et al., 1998; Stamhuis et al., 1998). This trophic flexibility is consistent with the observed plasticity in burrowing behavior of modern thalassinids (Rowden and Jones, 1995; Bishop and Bishop, 1992), with difficulty in linking burrow architecture to feeding mode of modern thalassinids (Griffis and Suchanek, 1991; Rowden and Jones, 1995), and with diversity of behaviors recorded in compound trace fossils produced by ancient thalassinids (e.g. *Ophiomorpha*, *Thalassinoides*, see above).

Similarly, the change from *Skolithos* to *Palaeophycus* and *Cruziana* recorded in Permian and Triassic fluvial channel sandstones can not be interpreted reliably as reflecting change from suspension feeding to deposit feeding. Categories in classifications of trophic relations of aquatic insects (abundant freshwater infaunal animals) are more diverse than the suspension and deposit feeding styles that dominate the marine benthos (e.g. Cummins, 1979, table 4C), probably reflecting the smaller-scale heterogeneity and the greater importance of locally derived plant debris in freshwater, particularly riverine systems. Compared to those of marine animals, the feeding and burrowing behavior and burrow morphology of benthic infaunal freshwater animals are poorly known. An exception is that of the ephemeropteran *Hexagenia*. *Hexagenia* constructs broadly U-shaped burrow networks with branching horizontal and vertical components in as little as 3 days (Charbonneau et al., 1997). Presence of setae on the mandibular tusks of *Hexagenia* indicates that it is a filter feeder (Bae and McCafferty, 1995). Although rapid burrowing followed by burrow abandonment is considered by ichnologists to be

characteristic of deposit feeders, the freshwater filter feeding mayfly *Hexagenia* also demonstrates this behavior. Trophic interpretation of these ancient freshwater aquatic trace fossils is further complicated by the facts that many modern insects that burrow in river channel sands are predators rather than deposit or suspension feeders (e.g. Ward, 1992; Westfall, 1979), and that tubedwelling in some freshwater animals may be more related to predator avoidance than to food gathering (Brennan and McLachlan, 1979).

Recognition of these four types of trace fossils as produced by a single producer was facilitated by extraordinary exposure of bedding planes containing the traces in the Beardmore Glacier area. I estimate that less than 0.5% of specimens merge from one ichnotaxon into another. If this percentage is typical for specimens of compound trace fossils, it implies that compound trace fossils will be recognized only given extensive exposure or abundant trace fossils, or some combination thereof.

In this case, recognition of the complex behavior of one animal producing compound trace fossils allowed additional biologically significant information to be gleaned from the trace fossils. The producer of the four traces was the dominant infaunal animal in both the Permian and the Triassic stream bottoms. Its dominance during both periods demonstrates that it was not affected by the Permian extinction (M. Miller, 2000). Although limited, this ichnologic evidence provides some of the only information available about the effect of the extinction on freshwater aquatic communities.

### 2.3. *Style C: one animal – simple+complex behavior – simple+complex trace fossils*

The key to complex behavior Style C is variability, from complicated behavior resulting in complex (and variable) trace fossils to simple behavior recorded by simple (but variable) trace fossils. Complex behavior Style C is under-recorded in the literature. Geologists and ichnologists have tended to emphasize the most striking example, to illustrate the perfect specimen, and to ignore other specimens that are not complete, not well pre-

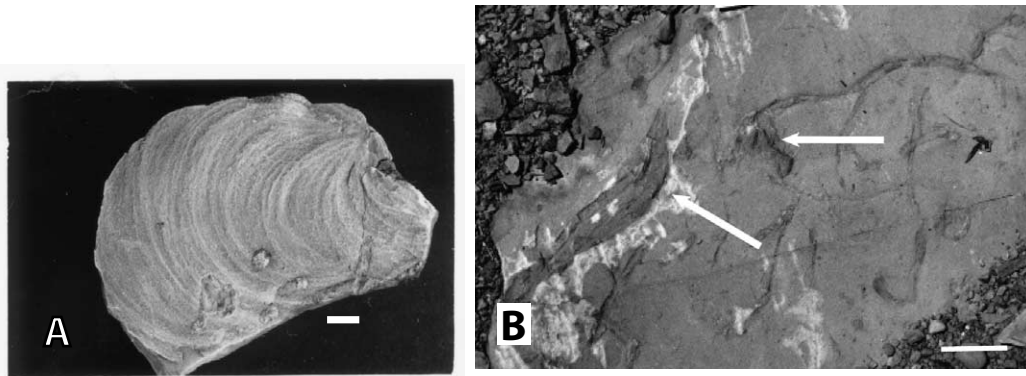


Fig. 3. *Zoophycos* and meniscate burrows in Devonian marine storm deposits, east-central New York. (A) *Zoophycos* with lamellae tightly curved. Bar = 1 cm. (B) *Zoophycos* on upper bedding surface (field photo). Top arrow points to very loosely curved lamellae. Lower arrow points to spreite that connects to horizontal meniscate burrow. Bar = 4 cm.

served, or not like the typical (e.g. perfect, complex) form, although this practice is changing (see W. Miller and D'Alberto, 2001; Bromley, 2001). In so doing, the full range of behavior represented by the trace fossils is not identified. For example, in the 1800s when James Hall collected *Zoophycos* (then called *Taonurus caudi-galli*) from the Devonian of New York, he selected large, impressively regular specimens, which now are housed in the New York State Museum. Not represented were equally abundant and highly variable specimens, which are discussed and illustrated herein and in M. Miller (1991).

*Zoophycos* is abundant in fine-grained sandstones and siltstones deposited near storm wave base in the marine portion of the Catskill deltaic complex (Devonian) of New York State. Most specimens are parts of larger structures whose architecture is unknown, but they are sufficiently complete to reflect, at least partly, the range of variation. Some spreite have well defined marginal tubes, but others do not; some are lobate, but most are not; and some spreite extend outward and downward from a single point, whereas others extend upward from two marginal tubes (M. Miller, 1991, fig. 6). The tightness of coiling of lamellae within the spreite laminae is particularly variable (Fig. 3). At one end of the continuum are the tightly curved lamellae of a 'classic' Devonian *Zoophycos* (Fig. 3A). At the other end of the continuum are lamellae that are barely

curved (Fig. 3B) and in fact they appear to grade into a horizontal meniscate burrow (perhaps *Taenidium*). A second observation is that meniscate burrows can be traced laterally into the spreite of *Zoophycos* (Fig. 3B). This illustrates that the producer of the complex *Zoophycos* spreiten structure also produced very simple meniscate burrows, and thus it was capable of both simple and complex behavior.

The range of variation of behavior recorded by *Zoophycos* in Pennsylvanian deltaic deposits in the northern Cumberland Plateau of Tennessee is even greater than that recorded by the shallow marine *Zoophycos* in New York. Here the *Zoophycos* producers burrowed in quartz-rich sands deposited in interdistributary bays by crevasse splays. The light-colored sandstones are overlain by black shale (bay deposits). Because the *Zoophycos* producers filled their burrows with dark mud that contrasts with the light-colored sandstone matrix (Fig. 4), the burrow morphology, and thus the producer's activity, is easily reconstructed.

The overall biogenic structure is three dimensional, with laminae extending outward from a central axis, and the structure varies both in its overall architecture and in the smaller-scale laminae. In some specimens the *Zoophycos* is well organized, with a vertical central axis and relatively evenly spaced laminae (Fig. 4A). In other cases the structure is poorly defined, with the axial

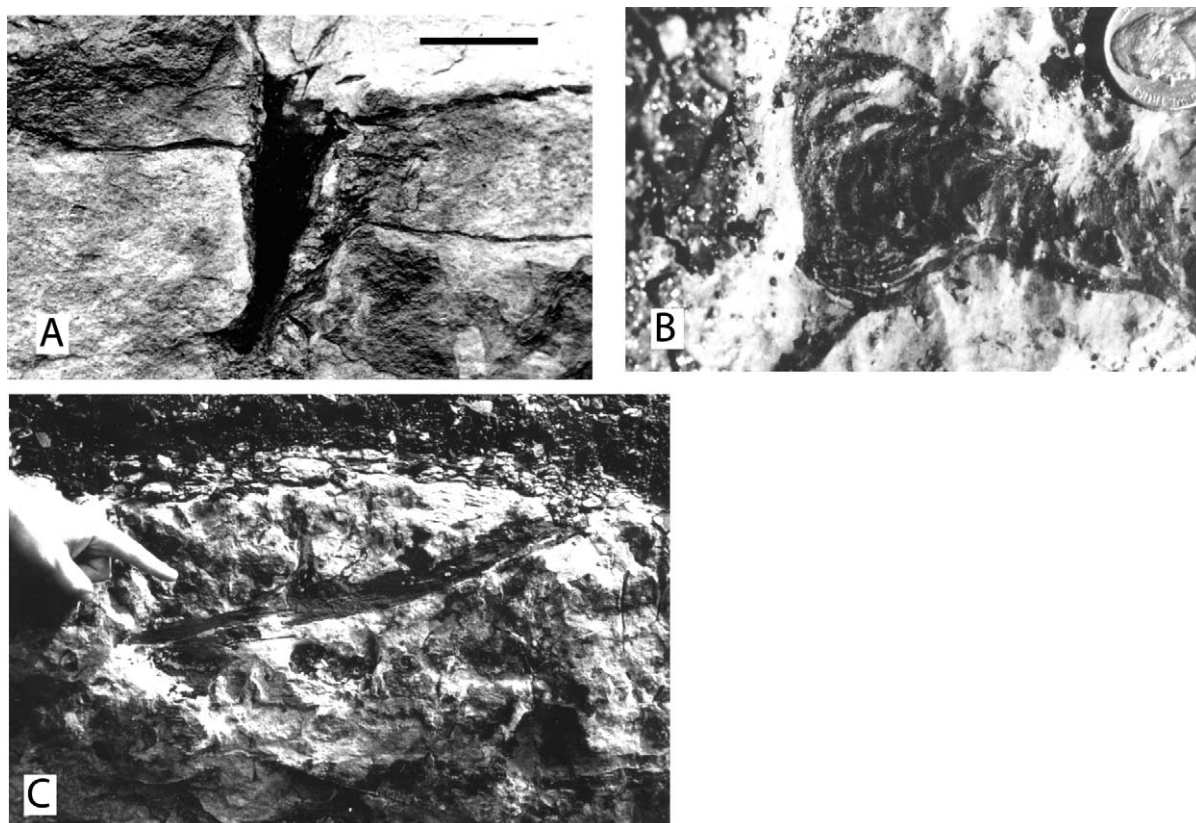


Fig. 4. *Zoophycos* in Pennsylvanian deltaic deposits (Crooked Fork Group), northern Cumberland Plateau, eastern Tennessee (field photos). The producer burrowed in quartz-rich crevasse-splay sands, piping the overlying dark mud downward. (A) Vertical section showing well defined axial tunnel from which laminae extend outward at regular intervals. Bar=5 cm. (B) Lamina on upper bedding plane showing regular lamellae. Coin is 2 cm in diameter. (C) Obliquely oriented axial plane of *Zoophycos* with laminae produced by chaotic, unprogrammed behavior of *Zoophycos* producer.

structure oriented obliquely and laminae coming off at various orientations (Fig. 4B). On a smaller scale, some laminae are small, well defined, and horizontally oriented and thus form clear spreite on bedding planes (Fig. 4C). Other laminae merge into meniscate burrows of diverse orientations. These grade into chaotic bioturbate textures defined by swirls of dark material from the overlying shale into the sandstone (Fig. 4B).

The variations in biogenic structures reflect behavioral plasticity on the part of the producer. It clearly was capable of highly programmed behavior on both a large scale (Fig. 4A) and a small scale (Fig. 4C). However, it also produced large structures at different orientations, from which it did not make evenly spaced, horizontally oriented

incursions; at times it apparently introduced mud from above into the sand as it moved in no apparent pattern (Fig. 4B).

The key to behavior Style C is that the programmed behavior, resulting in the clear examples of the complex trace fossil *Zoophycos*, was just one of the behavioral options, which also included simple movement through the sediment and construction of meniscate burrows of various orientations. Variable behavior of the producing animal has also been interpreted for younger (Jurassic and Cretaceous) *Zoophycos* (W. Miller and D'Alberto, 2001; Olivero, 2001). As in behavior Style B, the complex behavior must have included some mechanism for triggering change in behavior.

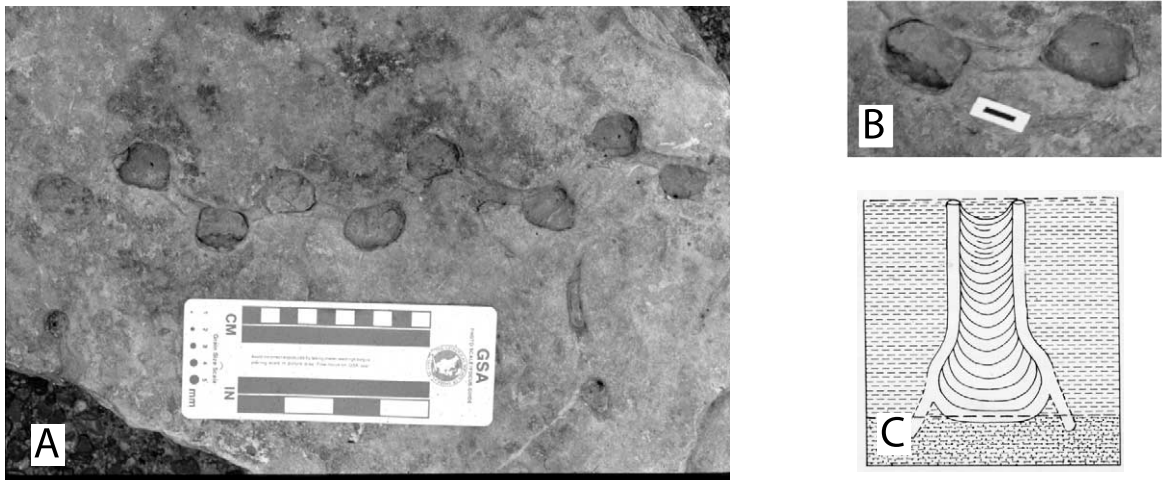


Fig. 5. (A) Zig-zag series of pits on upper bedding plane, Middle Ordovician limestone (Lebanon Limestone), Central Tennessee. Pits are connected by grooves. (B) Close-up of two pits and connecting groove. Sectioning shows no spreite between pits. Bar = 1 cm. (C) Reconstruction of *Diplocraterion* (*Corophioides*) *biclavata* from Osgood (1970, text-fig. 9) recorded as dumb-bell like structures on upper bedding surfaces, the location of which is indicated in the diagram by a dashed line. In the Tennessee specimen, the base of the U-shaped spreite is connected to the deeper sides of the U, which form the pits. The pits in the zig-zag pattern are interpreted to have been connected by U-shaped spreite, as reconstructed for single specimens by Osgood.

#### 2.4. Style D: one animal – invariant behavior on two scales – hierarchy of trace fossils in single structure

Behavior Style D involves two (or more) scales of invariant behavior that result in complex trace fossils whose components are interpreted as composed of numerous specimens of a smaller-scale trace fossil. Style D behavior is inferred from the single specimen of a newly discovered, unnamed trace fossil that occurs on the upper bedding surface of the slab of Middle Ordovician limestone (Lebanon Limestone) of central Tennessee. The large-scale structure consists of a zig-zag line of pits (Fig. 5A). The pits are connected by grooves (Fig. 5A,B) that appeared somewhat like the upper surfaces of a vertical spreite, presumably hung between two marginal tubes. The pits were assumed to be the upper terminations of the marginal tubes.

In this scenario, the biogenic structure was interpreted initially as consisting of a series of *Diplocraterion*, each specimen sharing its marginal tube with adjacent specimens. However, no spreiten were observed when vertical cuts were made through the grooves, precluding the inferred

mode of formation by an animal burrowing downward from the bedding surface to produce multiple overlapping *Diplocraterion* in a zig-zag pattern. If the pits on this upper bedding surface actually represented the bottoms of U-shaped burrows and the grooves the lowest level of the spreite, no part of the spreite would be present beneath the upper surface. Similar pit and groove structures preserved on upper bedding planes of Ordovician limestone in Ohio were interpreted as produced by this process, and the traces were included in the ichnospecies *Diplocraterion* (*Corophioides*) *biclavata* (Osgood, 1970, text-fig. 9, see Fig. 5C; Fürsich, 1974). The groove does not intersect the pits in the Osgood reconstruction as it does in the Tennessee specimen, probably because the marginal tube flares outward at the base of the Ohio specimens, but does not in the Tennessee specimen (Fig. 4C). Osgood (1970) did not report the zig-zag arrangement of pits observed in the Tennessee specimen. D. (C.) *biclavata* records only formation of a spreite between arms of a U-shaped tube.

The current interpretation is that this trace fossil records a hierarchy of behavior: the repeated formation of spreiten between consecutive U-



shaped burrows, and the addition of branches of the burrows to form an overall zig-zag pattern. It is not clear whether the specimen found records the work of one animal successively producing all the observed spreiten or several evenly spaced and consistently oriented individuals each producing a single spreite. In either case the inferred behavior is complex and invariant on both small and large scales. However, the range of variation in trace morphology and thus in behavior may increase if, and when, more specimens are found.

### 3. Discussion

What constitutes complex behavior? Whereas complex behavior previously was restricted to the behavior recorded in complicated, invariant trace fossils, it is now clear that this highly programmed behavior is but one style of complex behavior. Some animals are capable of multiple simple behaviors, each recorded by a single trace fossil, between which they can switch back and forth, and the resulting compound trace fossils directly reflect complex behavior. Recognition of these multiple behaviors raises the question of what initiates the change from one behavior to another. Unless the switches are random and chaotic, there must be some mechanism for controlling behavior. This is true no matter what the change in behavior is in response to (e.g. change in substrate stability or in chemical environment). The existence of a triggering mechanism in itself implies complex behavior.

Evaluation of the examples of different styles of complex behavior presented herein demonstrates that programmed behavior that produces complicated trace fossils commonly is not obligate. In the case of shallow-water Paleozoic *Zoophycos* in rocks of both Devonian and Pennsylvanian age, the *Zoophycos* producer exercised a number of other behavioral options, none of which was as programmed and as complex as that resulting in *Zoophycos*, including at least one that seems to have resulted more in generalized disruption than in the formation of discrete trace fossils. Why is the highly programmed behavior used under some circumstances but not others?

Although the answer is not known, the question itself demonstrates the complexity of the behavior involved.

The identification of diverse styles of complex behavior recorded in trace fossils in rocks deposited in fluvial, marine-margin, and storm-dominated environments indicates that behavioral complexity was environmentally widespread, even occurring in settings that can be characterized as unstable and unpredictable. Coupling of behavioral complexity with behavioral and ecological specialization is unfounded in the light of these occurrences and others (e.g. *Paleodictyon* in non-marine deposits; Pickerill, 1990).

Recognition of diverse styles of complex behavior requires ichnologists to ask new questions. Instead of ‘How many and what discrete trace fossils are at this outcrop?’, the question becomes ‘How was (were) the animal(s) that made this trace fossil behaving? What is the range of variation and what does it mean?’ The emphasis is placed on deciphering the style, abundance, and meaning of seemingly aberrant specimens and how they relate to the more idiomorphic specimens. Evaluating the full range of burrowing behavior recorded requires good exposure with many specimens, as well as tenacity to search for compound trace fossils and transitional forms.

Documenting the full spectrum of behavior represented by trace fossils pays off in the biological information uncovered. For example, recognition of complex behavior Style B (compound trace fossils with multiple simple traces produced by one animal) allowed the abundance of the producer in Permian and Triassic fluvial deposits to be determined and its response to the end-Permian events to be assessed. More fundamentally, extracting the most behavioral information possible from biogenic structures will maximize our understanding of how ancient animals lived and responded to their environment.

### 4. Conclusions

Trace fossils contain a wealth of behavioral information that can be used to reconstruct the trace producers’ ways of life. Maximum biological

information is obtained by reconstructing the full range of a trace producer's behavior. This involves searching for connections between seemingly disparate trace fossils to identify compound trace fossils and the range of behavior they record, as well as evaluating the less-than-perfect specimens that reflect variation in behavior. This approach led to delineation of four different styles of complex behavior recorded in Paleozoic trace fossils, several of which would not be recognized if complex trace fossils alone were used as proxies for complex behavior. Complex behavior is recorded in (a) morphologically complicated, relatively invariant structures such as *Spirophyton*; (b) compound trace fossils that individually reflect simple behavior but collectively indicate complex behavior including mechanisms for controlling behavior; (c) variations in complex structures (e.g. *Zoophycos*) that show that the producer had both complicated and simple behavioral options; and (d) larger-scale structures comprised of regularly arranged, smaller trace fossils, implying a hierarchy of producing behaviors. More styles of behavioral complexity probably will be recognized as ichnologists continue to focus on reconstructing the full range of behavior reflected by trace fossils.

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