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Behavioral Paleoecology of Lower Cambrian Deposit Foragers: Reinterpreting Looping and Meandering Traces using Optimal Foraging Theory and Quantitative Analysis

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BEHAVIORAL PALEOECOLOGY OF LOWER CAMBRIAN DEPOSIT FORAGERS: REINTERPRETING LOOPING AND MEANDERING TRACES USING OPTIMAL FORAGING THEORY AND QUANTITATIVE ANALYSIS

By

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ABSTRACT

The early Cambrian was a period of transition during which the seafloor environment was changing from a microbial-mat-dominated environment to a bioturbation-dominated environment. The result was a patchy landscape of variable food resources for foraging burrowers to exploit. Looping trace fossils, such *Psammichnites gigas* and *Taphrhelminthopsis nelsoni*, appear in strata worldwide during this transitional period, and the ecological niche they filled is a subject of debate among ichnologists. The objectives of this study are (1) to determine the foraging strategies preserved by looping traces through the application of optimal foraging theory and quantitative analysis, and (2) use those results to determine the relationships between paleoenvironmental conditions, neurological complexity, and foraging behavior. These data are used to test three hypotheses for the purpose of looping behavior preserved in Cambrian trace fossils: (1) looping is inefficient active feeding behavior, (2) looping is search behavior, and (3) looping is an optimal foraging strategy in environments with densely packed and high quality patches.

In order to explore how the distribution and quality of food patches influence foraging behavior, I apply optimality models, such as marginal value theorem, from contemporary animal behavior theory to looping and meandering trace fossils. I use fractal dimension analysis and goniograms as quantitative analysis methods for quantifying trace fossils, in order to compare the foraging strategies preserved in looping and meandering traces, and also to test the possible relationship between trace fossil patterns and environmental conditions.

Results suggest that the *P. gigas* tracemaker utilized looping as search behavior. I conclude that the tracemaker used chemoklinotaxis or chemotropotaxis to find an external attractant from a food patch, while the *T. nelsoni* tracemaker used looping as an optimal foraging strategy.

Cambrian tracemakers used looping as an optimal foraging strategy in an environment with densely packed, high-quality food patches, while those that used a meandering foraging pathway did so in widely dispersed, low-quality food patches. Fractal dimension analysis and the succession of shorter to longer foraging pathways may be used as a proxy for patch quality and density in a given environment. Environmental quality, rather than neurological complexity, is the primary driver for complex trace morphology.

ACKNOWLEDGEMENTS

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TABLE OF CONTENTS

LIST OF FIGURES

1. INTRODUCTION

The early Cambrian (Terreneuvian epoch and Cambrian epoch 2) records a time when metazoans began to radiate into the diverse biota that is typical of the Paleozoic seafloor. As burrowing niches expanded, the preservation of complex behavior as trace fossils also diversified. Each of these unique types of trace fossils records a specific behavior that demonstrates how ancient organisms lived through activities such as domicile construction, locomotion, and foraging. Within the foraging group of trace fossils, there is a record of a wide variety of feeding strategies employed by Cambrian bilaterians. One group of foraging traces that I focus on in this study is the group that displays looping patterns, such as the ichnofossils *Taphrhelminthopsis nelsoni* (Fig. 1) and *Psammichnites gigas* (Fig. 2). These looping traces occur in Cambrian strata worldwide and they play an important role in understanding the evolution of foraging behavior in early invertebrates (Crimes and Anderson, 1985; Crimes and Fedonkin, 1994; Seilacher and Gamez-Vintaned, 1995; Seilacher et al., 2005; McIlroy and Heys, 1997; Seilacher, 1997; Álvaro and Vizcaïno, 1999; Hagadorn et. al., 2000; Jensen et. al., 2002; Jensen, 2003; Miller et. al., 2009; Wang et. al., 2009; Collette et. al., 2010; Gingras et. al., 2011;

Figure 1 - Specimen of the looping trace Taphrhelminthopsis nelsoni in the Wood Canyon Formation in the Salt Spring hills, San Bernardino County, California. Scale is 50 cm long, divided into decimeters.

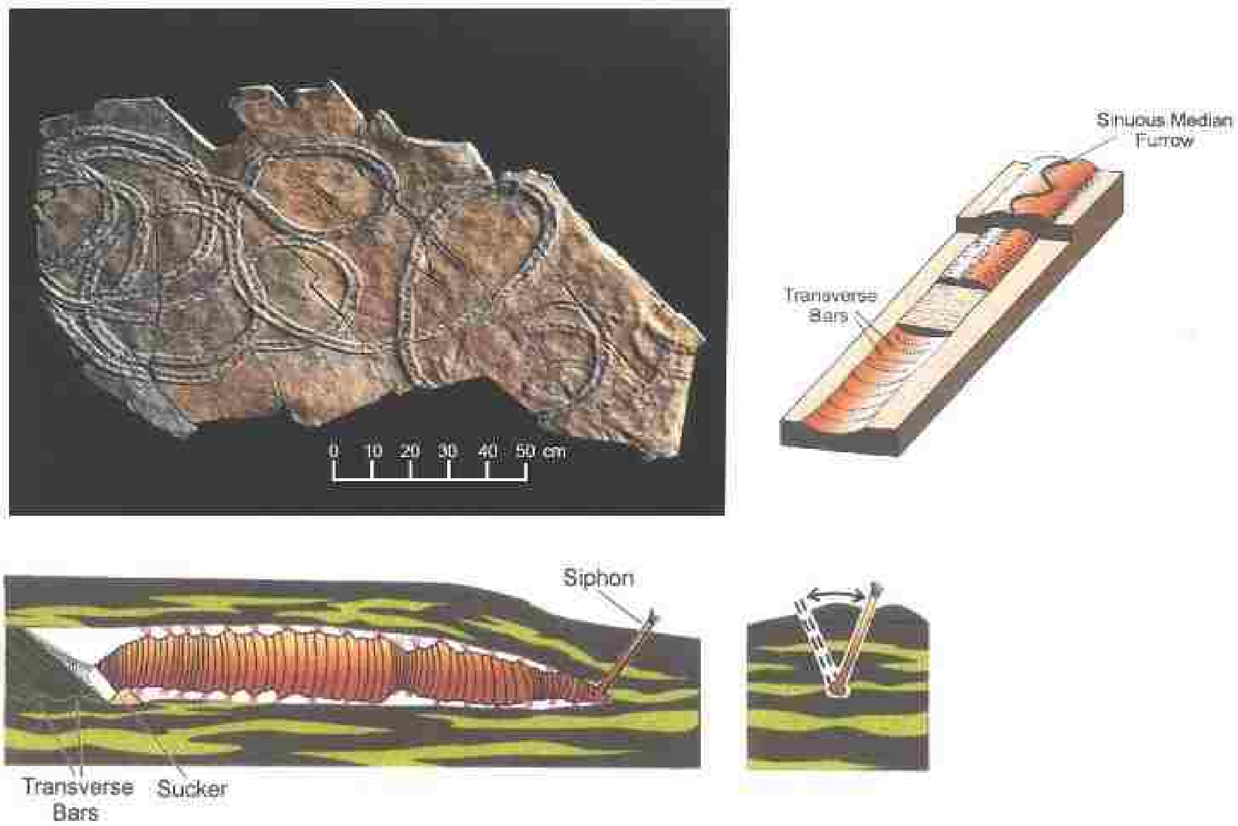


Figure 2 – Photo of Psammichnites gigas specimen from central Spain with preservational tiers and schematic of a possible body plan of the tracemaker. Photo from Seilacher (1997); illustrations from Rowland (unpublished).

Singh, 2011). I document the looping and meandering traces chosen for this study in Appendix A, and their biostratigraphic relationship to one another is illustrated in Figure 3.

Looping trace fossils have traditionally been interpreted as recording an inefficient foraging strategy, in which looping tracemakers inefficiently crossed their own foraging pathways as a result of primitive neurology that limited their foraging capabilities (Seilacher, 1997). Seilacher (2007) interpreted meandering trace fossils as foraging more efficiently by avoiding areas they had already exploited. In this study, I use the principles of contemporary

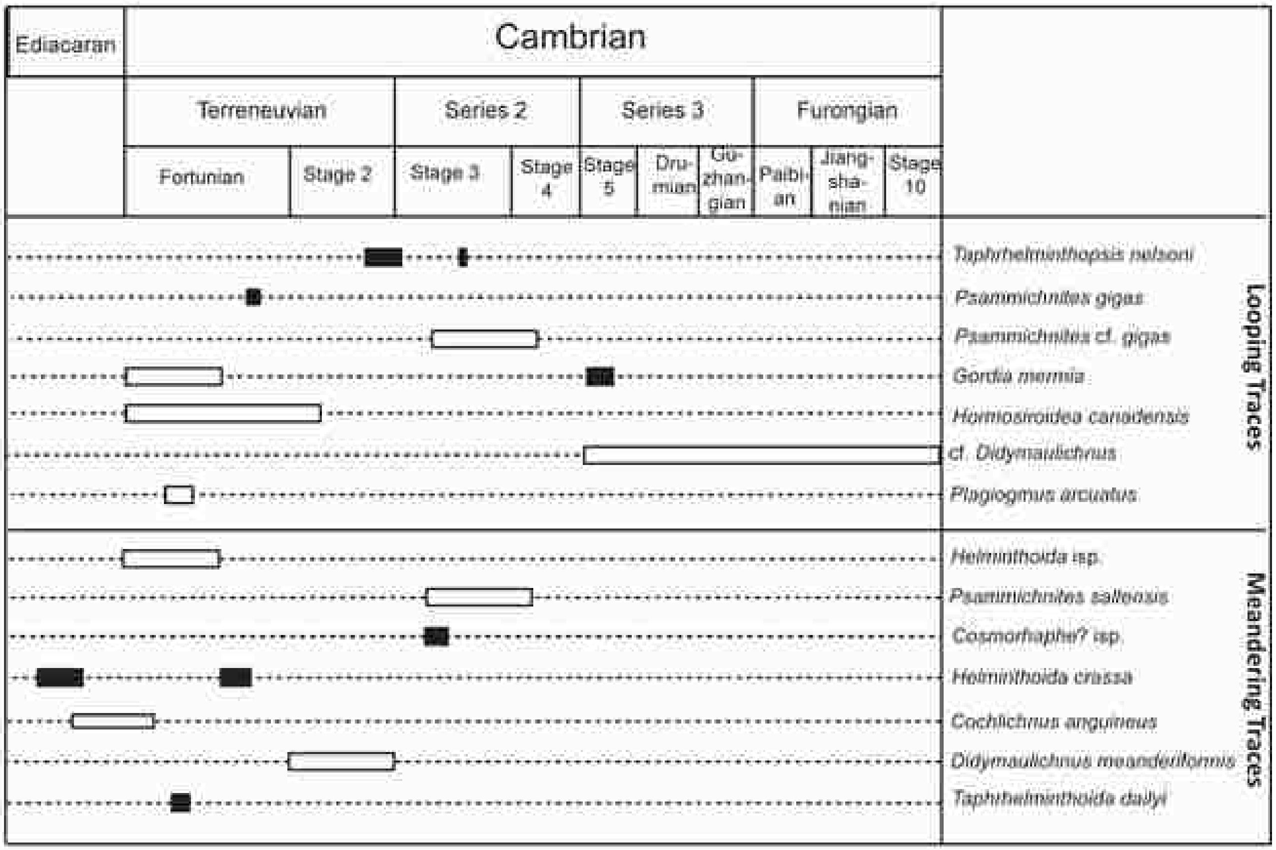


Figure 3 - Biostratigraphic ranges for trace fossils used for quantitative analysis. Black bars represent trace fossils that can be sourced to a single member within a formation, while white bars represent trace fossils that can only be sourced to a formation or time period (Crimes and Anderson, 1985, Hofmann and Patel, 1989; Crimes and Fedonkin, 1994; McIlroy and Heys, 1997; Hagadorn et. al., 2000; Seilacher et. al., 2005; Gamez Vintaned et. a., 2006; Babcock and Peng, 2007; Leonov, 2007; Wang et. al., 2009; Collette et. al., 2010; Adams et. al., 2011; Palacios et. al., 2011; Buatois and Mangano, 2012; Aparicio Gonzalez et. al., 2014).

animal ethology to reinterpret the behavior of looping trace fossils. In sections 2 and 3, I provide a primer on looping behavior in modern animals, and I show that looping may be an optimal foraging strategy under certain environmental conditions. Section 4 provides the evolutionary context for looping trace fossils by discussing the environmental conditions in which looping traces occur, and the geologic setting in which they occur. This will set the framework for reinterpreting looping trace fossils.

In section 5, I propose three hypotheses for reinterpreting looping traces. Hypothesis 1 posits that looping is an ancestral trait that developed as a spatially inefficient intermediary step toward more efficient, tightly meandering, foraging paths (Seilacher, 1997). Hypothesis 2 posits that looping traces are recording search behavior that represents a directed response to a chemical stimulus from some attractant (Rowland, 2006). Finally, hypothesis 3 posits that looping is an optimal foraging strategy that is adaptive for nutrient-rich environments, such as early Cambrian microbial matgrounds, in which many of them occur. These hypotheses divide the interpretation of looping behavior into two possible foraging categories: searching and active feeding. Examples of these two categories in living animals are presented in sections 2 and 3.

In section 6, I test these hypotheses using quantitative analysis to compare looping and meandering traces beyond qualitative descriptions. I use two means of quantitative analysis to test the three hypotheses listed above: goniograms, which measure angular deviation per unit length along a trace, and fractal dimension analysis, which measures how completely a pattern fills a given area. Goniograms, introduced by Hofmann (1990), can be used to measure randomness recorded in an organism’s foraging path. I use fractal dimension analysis, modified from Lehane and Ekdale (2013), to measure the spatial efficiency of a foraging pathway. I employ these quantitative means of analysis to evaluate looping behavior as searching and active feeding, in order to favor one hypothesis over another. Additionally, I contribute to a growing database of quantitative trace-fossil data that can be used in future studies.

2. LOOPING BEHAVIOR IN LIVING ANIMALS AS A SEARCH STRATEGY

Among extant species, looping during locomotion is a highly conserved search behavior that occurs in even the simplest of organisms, even at the sub-organism level. Sperm cells use chemokinesis, a non-directed response to a chemical stimulus, in their search for egg cells to fertilize (Eisenbach, 1999). Bacteria, such as *Escherichia coli*, also use chemokinesis while moving toward a source of external stimulus. The non-directed response of kinesis means that the rate of movement changes or the rate of turning increases as the concentration of the attractant signal increases, so that the probability of reaching the attractant increases. This means that the intensity of looping increases as the seeker gets closer to its destination; actors rely on probability to reach their target (Benhamou and Bovet, 1992). Chemokinesis in these examples is merely a reactionary movement that requires no decision making or memory. It is an effective search behavior for cellular organisms which do not have the capacity to act beyond simple reactions to stimuli.

Many higher-level organisms use chemotaxis, a directed response to a chemical stimulus. This means that the organism makes an intentional, non-random movement toward an attractant. Chemotaxis can be divided into two categories based on the organism’s sensory receptors: chemoklinotaxis and chemotropotaxis (Gomez-Marin and Louis, 2012). Klinotaxis is a directed response using a single sensory receptor, while tropotaxis involves the use of multiple sensory receptors. Examples of sensory receptors used in tropotaxis are paired appendages: ears, antennae, barbels, etc. Multiple receptors allow the organism to pinpoint the direction to an attractant by comparing signals from different receptors. In the case of tropotaxis, the comparison can happen instantaneously and the direction to the attractant can accurately be determined at any moment in time. Organisms generally can move straight toward the attractant.

Klinotaxis, on the other hand, uses only a single sensory receptor to find an attractant. The organism must sample the environment in multiple iterations to find the attractant. Klinotaxis, therefore, requires the use of memory, as the samples must be compared in a delayed manner (Gomez-Marin and Louis, 2012). In the case of klinotaxis, it is more common for an organism to wander in search of the attractant rather than moving straight toward it.

To illustrate the difference, imagine searching for a buzzing alarm clock in a dark room. The direction from which the sound is coming is easily determined, and anywhere you are in the room you can orient in the specific direction of the sound. The brain can instantly compare the signals going to each ear and respond accordingly. Now imagine the same dark room but with a scent attractant instead of a sound. Since only one sensory receptor (the nose) is in play, multiple samples must be taken in order to find the source. The samples will differ depending on the orientation of the scent gradient. The scent direction with the greatest intensity will be the direction toward which you will move. The strength of each sample must be committed to memory in order to compare one sample with previous and subsequent samples. If you were to compare your movements toward the sound and scent sources, you would find significantly more "wandering" in the case of the scent attractant because of the use of klinotaxis rather than tropotaxis. The scent example in humans is actually not one hundred percent klinotaxis, but rather a mild form of tropotaxis due to a slight differential (5-10%) in the signal between the left and right nostril (Gomez-Marin and Louis, 2012). However, the low differential makes it one of the closest forms of klinotaxis that humans can experience.

Among extant animals, there are several examples in which looping has been experimentally shown to be an adaptive search behavior. For example, a study involving the nematode *Caenorhabditis elegans* found that as the gradient of an attractant fades, nematodes will make “pirouettes” in order to reorient themselves perpendicular to the gradient of the chemical attractant (Pierce-Shimomura et. al., 1999). However, this is an example of chemokinesis because pirouettes increase in frequency as the nematodes reach the attractant. The straight pathway exiting each pirouette is in the general direction of the attractant because the pirouettes permit the nematodes to stay on the correct course toward the attractant. Several different looping patterns are created by *C. elegans,* including some paths that double back en route to the attractant (Pierce-Shimomura et. al., 1999) (Fig. 4). Some of the paths resemble the patterns recorded in looping trace fossils.

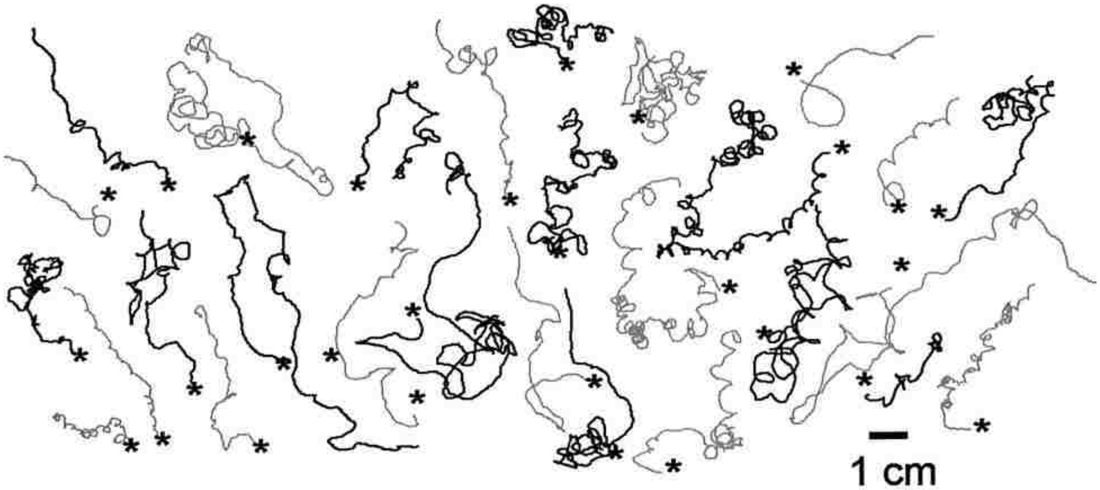


Figure 4 - Tracks of 28 individual nematodes moving toward an attractant indicated by an asterisk symbol. From Pierce-Shimomura et. al. (1999).

The larvae of the fruit fly *Drosophila melanogaster* demonstrate chemoklinotaxis in their search behavior. This organism samples its environment by laterally moving its head back and forth. Sensory receptors located in the head primarily use olfaction to find an attractant, but photoreception and temperature are also used (Gomez-Marin et. al., 2011). Because this method relies on comparing sequentially received signals, organisms using this method must utilize some form of memory in order for the strategy to be successful.

Organisms that are normally tropotactic have also been shown to use klinotaxis if one of their paired receptors is experimentally incapacitated. Biologists performed an experiment on bullhead fish in which they removed their barbels on one side of their head and cauterized a nare on the same side. The swim path of the fish toward a food source included several loops, with the terminal loop exit oriented toward the attractant (Fig. 5) (Bardach et. al., 1967). Another experiment involved the water bug *Notonecta undulata*, which is attracted to light sources. When one of a water bug’s eyes was blackened with asphalt, it looped toward the light (Clark, 1928). Such examples show that, even when tropotaxis is the primarily method used for seeking an attractant, some animals can use klinotaxis as a backup navigational strategy.

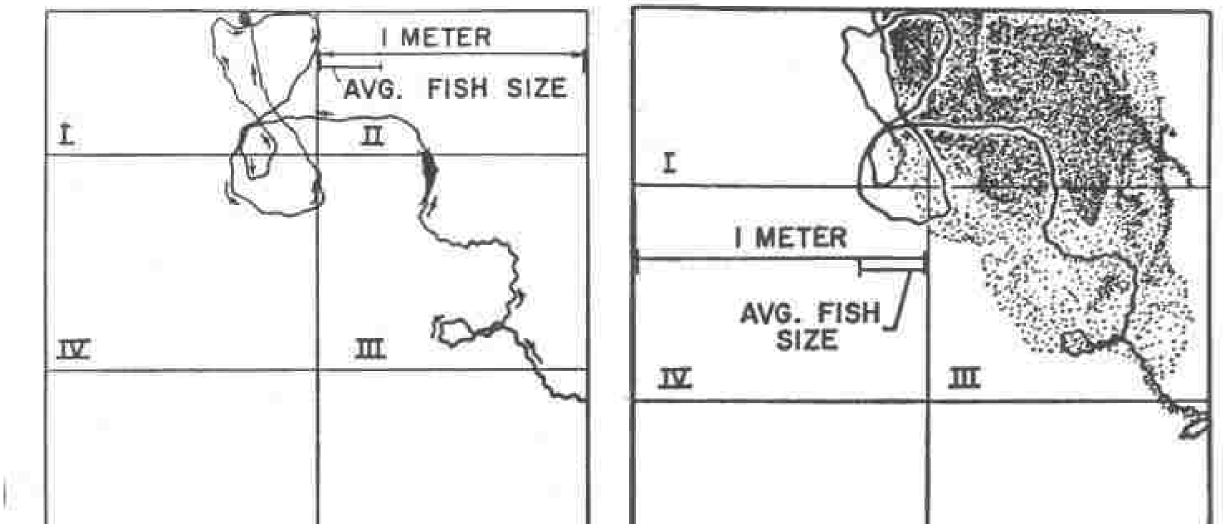


Figure 5 - Induced klinotaxis in a bullhead fish via cauterization of barbels and nares on one side of head. From Bardach et. al. (1967).

Looping traces may be the purposeful path an animal takes in its search for an attractant stimulus, such as a food patch. Three possible mechanisms could be involved in the creation of a looping search path. The organism could have utilized chemoklinotaxis, using a single sensory receptor, in search of a chemical attractant (Hagadorn, 2000; Rowland, 2006). Alternatively, it may use chemoklinokinesis, involving the use of a single sensory receptor, to travel in a non-directed path in search of an attractant. This is accomplished by making biased random walks, meaning that the loop exit direction should be in the general direction of an attractant; the result is that the animal loops more frequently as it moves closer to the source. Finally, it could have used chemotropotaxis, in which it used multiple sensory receptors to perceive a chemical gradient and move toward an attractant. As the signal fades, the organism must reorient itself in all three methods until it senses a stronger signal, just as in the examples discussed above. As a result of each of these three navigational strategies, the organism will inevitably create a looping pathway as it seeks the attractant.

3. LOOPING AND MEANDERING BEHAVIOR IN THE CONTEXT OF OPTIMAL FORAGING THEORY

In this section, I apply conceptual models from optimal foraging theory to scenarios that are comparable to the environmental conditions in which looping traces occur, in order to ascertain whether the traditional view of looping traces is in congruence with modern ecological principles. These models are based on the assumption that natural selection favors organisms that optimize their foraging strategies. Ideas from optimal foraging theory, such as patch choice model and marginal value theorem, are powerful tools for predicting how animals will forage in a given environment (Charnov, 1976). The Ediacaran-Cambrian transition provides an interesting example of diverse and complex behaviors emerging from increased environmental heterogeneity. In this study, I aim to provide a conceptual framework for future modelling that can unite the principles of modern animal behavior with ichnology. There is a need to bridge the gap between these two fields so that ichnologists are not relying on outdated biological concepts to interpret trace fossils (Plotnick, 2012).

Optimal foraging theory is based on the principle that natural selection will favor animals that are able to maximize their fitness through foraging in a way that will maximize their net energy intake while minimizing their time and energy spent foraging (Charnov and Orians, 1973). Conceptual mathematical models have been created to predict how an animal will forage based on this idea. These models have been refined over the years by experimental data and real world observations so that they are a powerful tool in predicting how animals will forage in a variety of situations (Charnov and Orians, 1973). A foraging strategy does not need to be spatially efficient to be considered an optimal strategy; there may be other factors at work such as environmental variation. Foragers are expected to exploit food patches in a way that maximizes their fitness. Foraging strategies recorded in trace fossils can therefore be interpreted using conceptual models from optimal foraging theory. In this section, I present conceptual models from marginal value theorem using hypothetical environments, so that the resulting generalizations can be applied to the early Cambrian environments in which the traces in this study are found.

Marginal value theorem (MVT) is an optimality model that balances resource intake, foraging time within a patch, and travel time between patches (Fig. 6) **(**Charnov, 1976). The graph in Figure 6 illustrates this concept: The X axis represents foraging time, in which the negative side is time spent not foraging, or travelling between patches, the positive side is time spent foraging within a patch, and the Y axis represents cumulative resource intake. This model assumes that the environment contains nutrients concentrated in patches, with areas between the patches that are either devoid of food or that contain sub-optimal quantities that are energy inefficient for foragers. Within each patch, the animal acquires fewer resources the longer it stays in a patch, resulting in diminishing returns. The curve in Figure 6 represents the diminishing resource intake by the animal per unit of time spent in the patch. MVT also assumes that if there are patches with differing qualities, they are randomly distributed in the environment (Charnov and Orians, 1973). The sloping line in Figure 6 represents the average energy intake rate across all patches in an environment. An animal will deplete the resources within a patch until the instantaneous intake rate within a patch reaches the average intake rate. If the rate of energy intake within a patch is lower than the average, the animal will leave that patch because at that point, it is more efficient to find a new patch than to remain in a diminished patch. If a new patch is suboptimal, meaning the energy intake rate within that patch is beneath the average intake rate, then the forager will not exploit that patch.

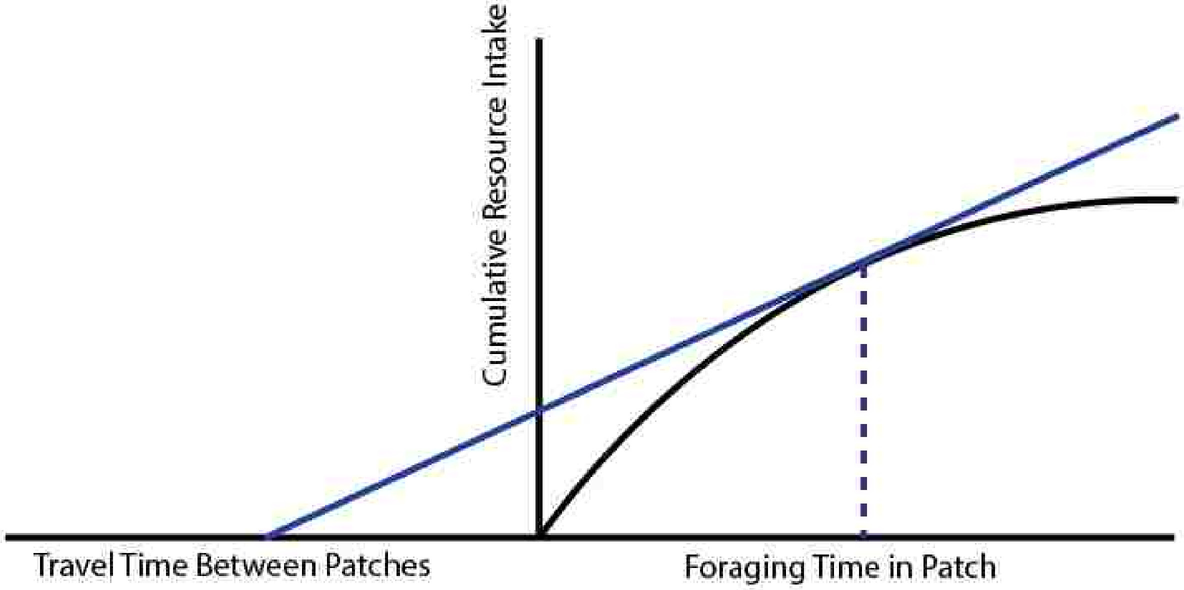


Figure 6 – Marginal value theorem balances the relationship between travel time, resource intake, and foraging time. Modified after Charnov (1976). The X axis is foraging time, in which the negative side represents time not foraging, or travel time between patches, and the positive side represents time actively foraging within a patch. The curve represents the cumulative resource intake over time, in which the forager experience diminishing returns of energy intake over time. The blue line represents the average intake rate across all patches in an environment. The point where the line is tangent to the intake curve represents the optimal foraging time within a patch.

I present two hypothetical scenarios to illustrate how patch quality and travel time between patches affect foraging behavior. The first scenario is illustrated in Figure 7, which represents a hypothetical environment in which travel time between patches is negligible, but the quality of patches is variable. Travel time is made negligible by removing the negative portion of the X axis from the graph (cf. Fig. 6), and variability in patch quality is represented by adding another diminishing-returns curve for a higher quality patch. Curve A represents food intake per unit of time in high-quality patches, while curve B represents food intake per unit of time in low-quality patches. For this scenario, these patches are randomly distributed in an environment, as

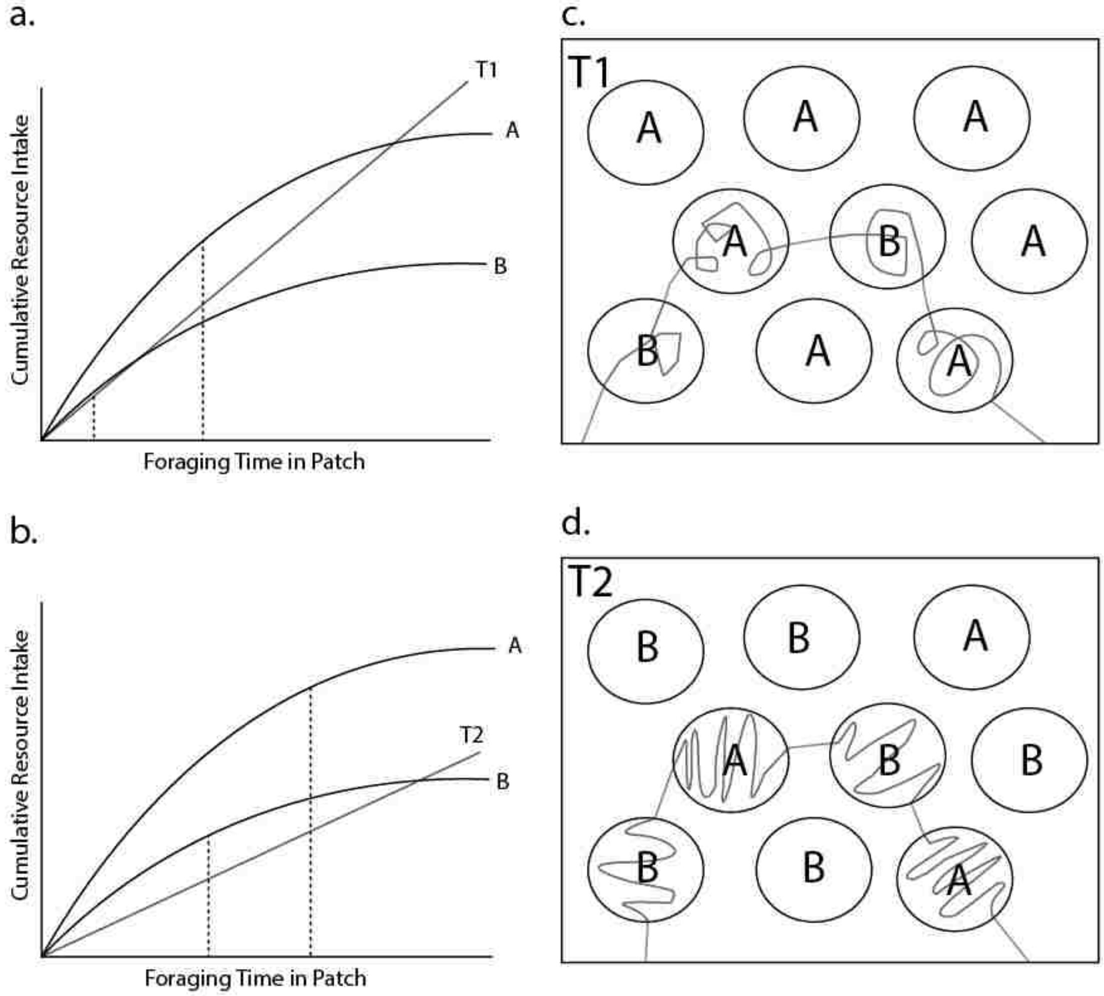


Figure 7 – Graphs and illustrations that show the application of marginal value theorem at two time intervals where travel time is negligible. Dotted lines show where a line parallel to the average energy intake line is tangent on patch curves A and B. The environments are titled according to their average intake rate lines, T1 and T2. Adapted from Charnov and Orians (1973).

(a) Time interval in which high quality patch A occurs in higher proportion to lower quality patch B. Line T1 represents the average energy intake rate where patch-type A occurs in higher proportion to patch-type B.

(b) Time interval in which high quality patch A occurs in lower proportion to lower quality patch B. Line T2 represents the average energy intake rate where patch-type A occurs in lower proportion to patch-type B.

(c, d) Schematic illustrating the environments represented by 4a and 4b. A possible foraging pathway is shown in each environment. Looping is favored in T1 and meandering is favored in T2.

shown in Figures 7c and 7d. Lines T1 and T2 in Figures 7a and 7b represent the average energy intake of the environment represented by the graph. Figure 7a represents an environment in which high-quality patches are more abundant than low-quality patches, and Figure 7b represents an environment in which low-quality patches are more abundant than high-quality patches. This is illustrated by line T1 having a greater slope than line T2.

As a forager encounters a food patch, it will exploit the resources within that patch as long as its rate of intake is equal to or greater than the average rate (represented by lines T1 and T2 in Figs. 7a and 7b). In other words, the X axis coordinate of the point on each curve where a line parallel to T1 or T2 is tangent is the foraging time in that patch, represented by a dotted line. Per Figure 7a, an animal will spend more time foraging in patch-type A than in patch-type B. Figure 7b is the same as Figure 7a, except that the average intake rate, represented by line T2, is lower. The lower-quality patch-type B occurs in a higher proportion in the Figure 7b environment than in the Figure 7a environment. The trend is similar to the previous situation in that foragers will still spend more time in a higher quality patch, but foraging time increases for all patch qualities as average patch quality decreases in the environment.

The scenario presented above treated travel time between patches as negligible. Now, in order to examine the effect of the density of the distribution of patches, I consider environments in which all of the patches are equal in quality but variable in their proximity to one another. Figure 8 illustrates two environments with different patch distributions. In this scenario, distance between patches governs the average intake rate, as shown by lines D1 and D2 in Figure 8a. Line D1 represents the average energy intake rate in an environment in which patches are close together, and line D2 represents the average energy intake rate in an environment in which patches are father apart. In this model, the point on the diminishing-returns curve that is tangent

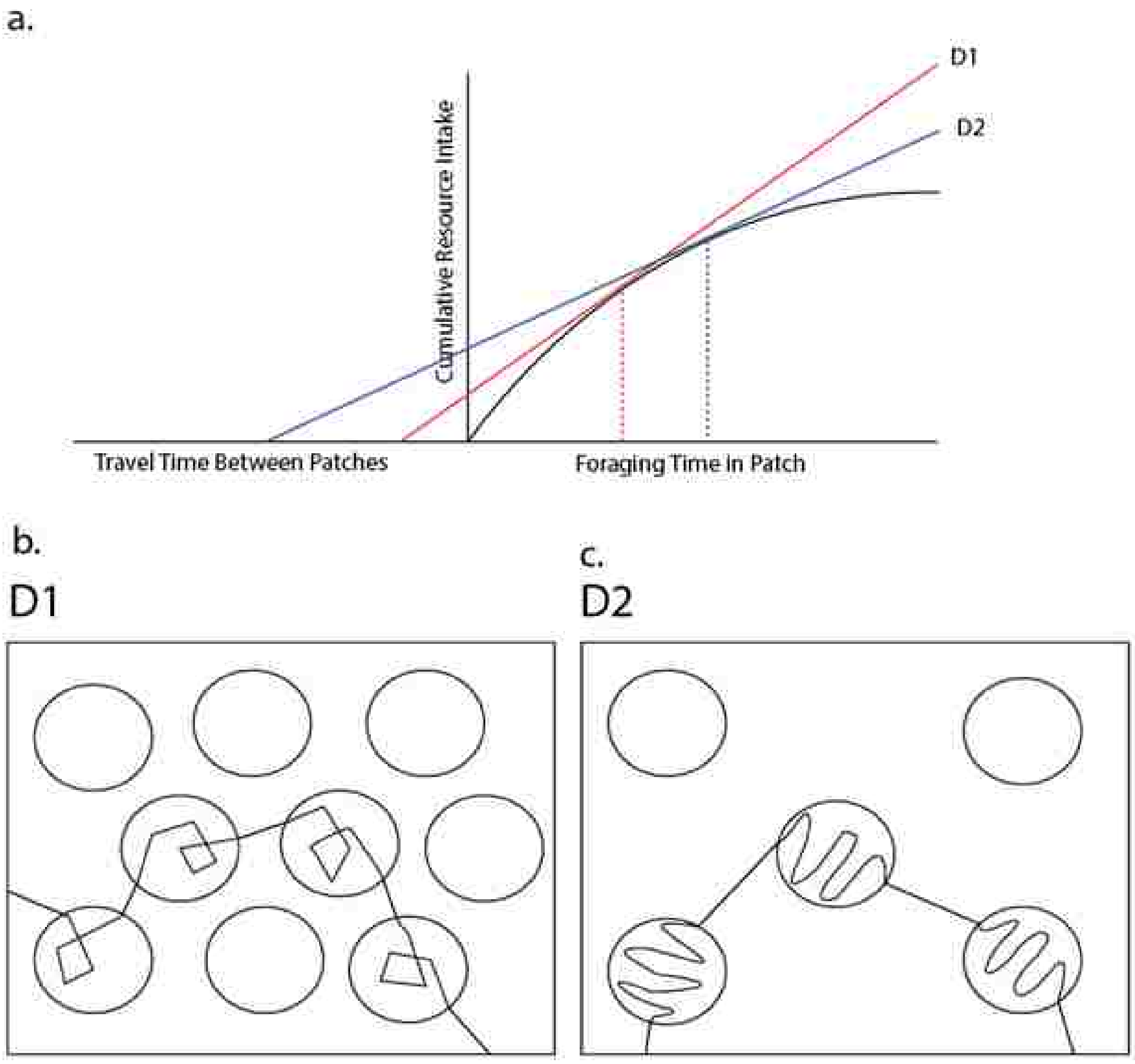


Figure 8 – Application of marginal value theorem with two ideal environments that differ by patch density. The environments are titled according to their average energy intake lines, D1 and D2. Adapted from Charnov and Orians (1973).

(a) Environment D1 contains patches that are close together and environment D2 contains patches that are farther apart, as indicated by the point where each line intersects the X axis. Travel time is fixed for each line and the line is drawn so that it is tangent to the resource intake curve for a given patch, with the tangent point representing the optimal foraging time within a patch, indicated by the vertical dashed lines.

(b, c) Illustrations of environments represented by lines D1 and D2 in 6a. D1 is an environment where patches are sparsely distributed; meandering paths are favored. D2 is an environment where patches are closely distributed; looping paths are favored.

to D1 or D2 represents the time spent foraging in each patch as a function of travel time between patches. According to this model, when patches are densely packed together, shorter foraging bouts are favored. Conversely, when patches are farther apart, longer foraging bouts are favored.

These two scenarios can be synthesized into a single graph (Fig. 9) that represents an environment in which average patch quality decreases and patches become more dispersed over time. Average intake line T1 represents an environment in which patches are densely packed and average patch quality is high, and line T2 represents an environment in which patches are farther apart and average patch quality is low. Overall, foragers will spend more time in T2-type environment patches than in T1-type environments. As a result, longer foraging pathways are expected in T2 environments, while shorter foraging pathways are expected in T1 environments. In section 5, I will return to this model and apply it to looping trace fossils as a possible optimal foraging strategy.

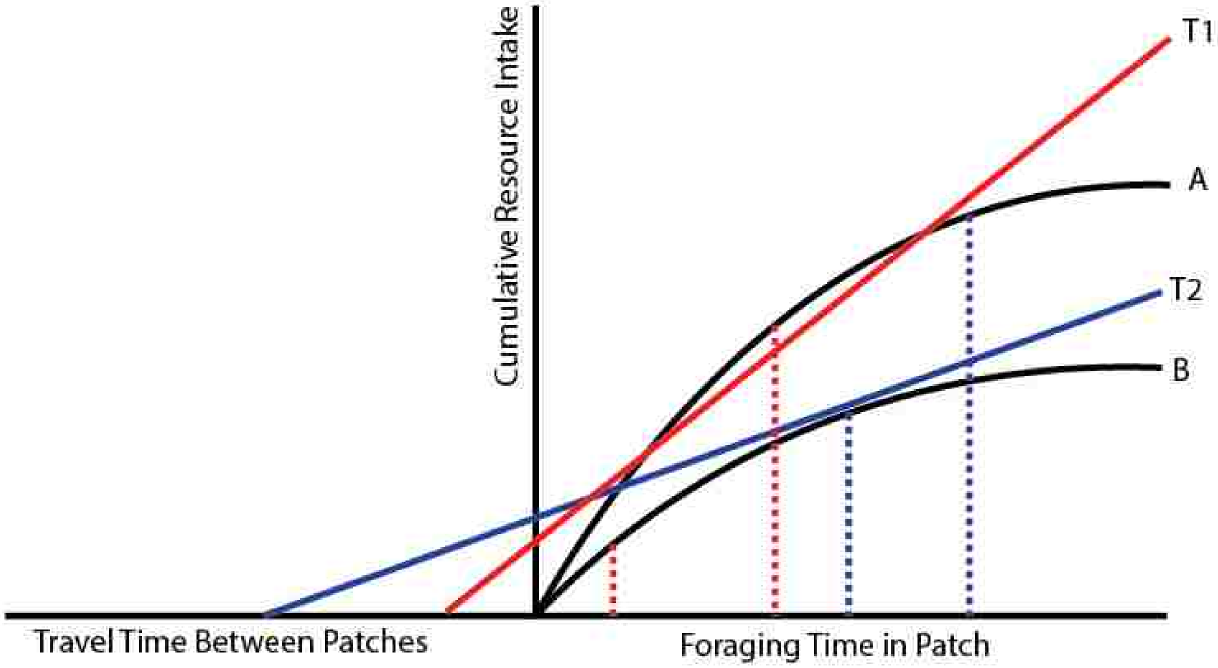


Figure 9 - A synthesis of the two ideas presented in the patch quality scenario (Fig. X) and the patch density scenario (Fig. X). Curve A represents high quality patches and curve B represents low quality patches. Line T1 represents an environment with higher average quality patches (high ratio of patch type A to B) that are closely spaced together, and line T2 represents an environment with lower average quality patches (low ratio of patch type A to B) that are sparsely distributed. Vertical dashed lines represent the optimal foraging time, which is the point where a line that is parallel to the same color line is tangent to patch curve A or B. Adapted from Charnov and Orians (1973).

4. EVOLUTIONARY CONTEXT OF LOOPING TRACE FOSSILS

The Terreneuvian and lower Series 2 epochs of the Cambrian, the time interval in which most of the trace fossils in this study occur, was a transitional time in environment and evolution in newly formed Laurentia, one of the continental remnants of the rifted supercontinent Rodinia. In this study I use “early Cambrian” to collectively refer to the Terreneuvian and Series 2 epochs. During the Ediacaran, the sea floor was dominated by microbial mats. Natural selection favored animals that could maximize their fitness by occupying adaptive niches within this biomat-rich environment. Heterotrophs that lived in this environment grazed on top or beneath the biomats, or had evolved the ability to anchor or encrust themselves on the biomats and filter feed (Seilacher, 1999; Bottjer et al, 2000; Droser et. al., 2002; Carbone and Narbonne, 2014). These biomats also influenced the composition of the underlying sediment. The sediments were mostly anoxic due to the lack of bioturbation, as nearly all the benthic ecological niches were at the sediment-water interface. The level of atmospheric oxygen was also very low in the early Cambrian (Seilacher, 1999).

During the early Cambrian, deep sediment bioturbators such as brachiopods, mollusks, and arthropods became prevalent and began to break up the biomats and bring oxygen from the water column into the sediment through sediment mixing (Fig. 10). The result was a heterogeneous environment that required the evolution of new foraging strategies that were strongly dependent on local conditions, similar to what is seen on the modern sea floor. The transitional environment of the early Cambrian, as seen in the middle ternary diagram of Figure 10, was the type of environment that contains the trace fossils that are the subject of this study.

The change seen in the environment is reflected in the increase in trace fossil diversity. Because of the change to a heterogeneous environment, specialized foraging strategies that were

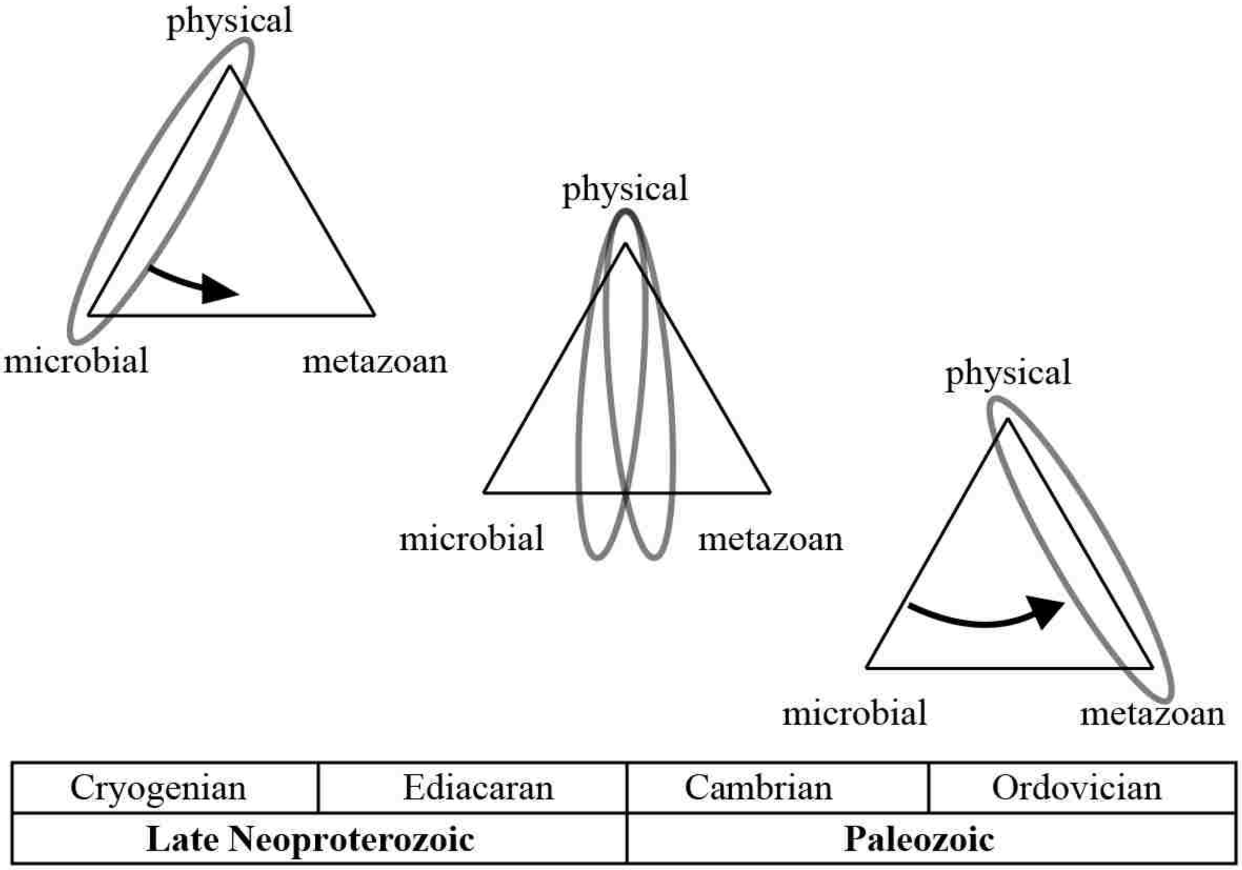


Figure 10 - Ternary diagram illustrating the change in biogenic influence in siliciclastic sediments through the Ediacaran-Cambrain transition. Adapted from Hagadorn and Bottjer (1999).

adapted to microenvironments began to evolve. The main variables relevant to this study that differentiated these microenvironments were availability and quality of food. This is also when looping traces begin to appear in the fossil record. Looping traces occur in strata worldwide in the Terreneuvian and Series 2 epochs (Seilacher, 1997), but none of the looping traces in this study appear before the early Cambrian. Their ubiquity in the early Cambrian indicates that they represent a foraging strategy favored by natural selection under certain circumstances. Traces with varying degrees of meander also first appear in the early Cambrian. The relationships that these traces have with variable microenvironments are discussed later in this thesis.

The standard interpretation of these various types of traces is that the looping and less ordered traces represent an ancestral or less derived foraging strategy (Ekdale and Lamond, 2003). According to this interpretation, traces with tight meanders and increased degrees of meandering represent a more derived behavioral trait (Fig. 11). This interpretation assumes that Cambrian environments were homogeneous, and that the most significant variable influencing burrow morphology was neurological complexity. In this study I argue that Cambrian marine environments were in fact quite variable and that the variety of foraging traces record different strategies of maximizing foraging efficiency in different environmental conditions.

The interpretation that some Cambrian trace fossils record foraging strategies that are more complex than others assumes that the neurology of Cambrian invertebrates became more and more complex throughout the Cambrian and beyond. However, recent research of fossils in Lagerstätten in China suggests that the arthropod brain had already advanced to near present-day conditions in the Cambrian. Cambrian decapod-like fossils from China contain exceptionally preserved brain structures, and these structures are remarkably similar to those of modern arthropods (Edgecombe et. al., 2015). Additionally, an anomalocarid fossil from the Chengjiang Lagerstätte in southwest China contains brain structures that resemble those of modern onychophoran velvet worms (Cong et. al., 2014). These fossils may be used as representatives of Cambrian biota, especially those with a soft body and poor preservational potential such as annelids and shell-less gastropods. For the purposes of this study, I adopt the view that the brains of many bilaterian invertebrate clades had already developed sufficient complexity to affect

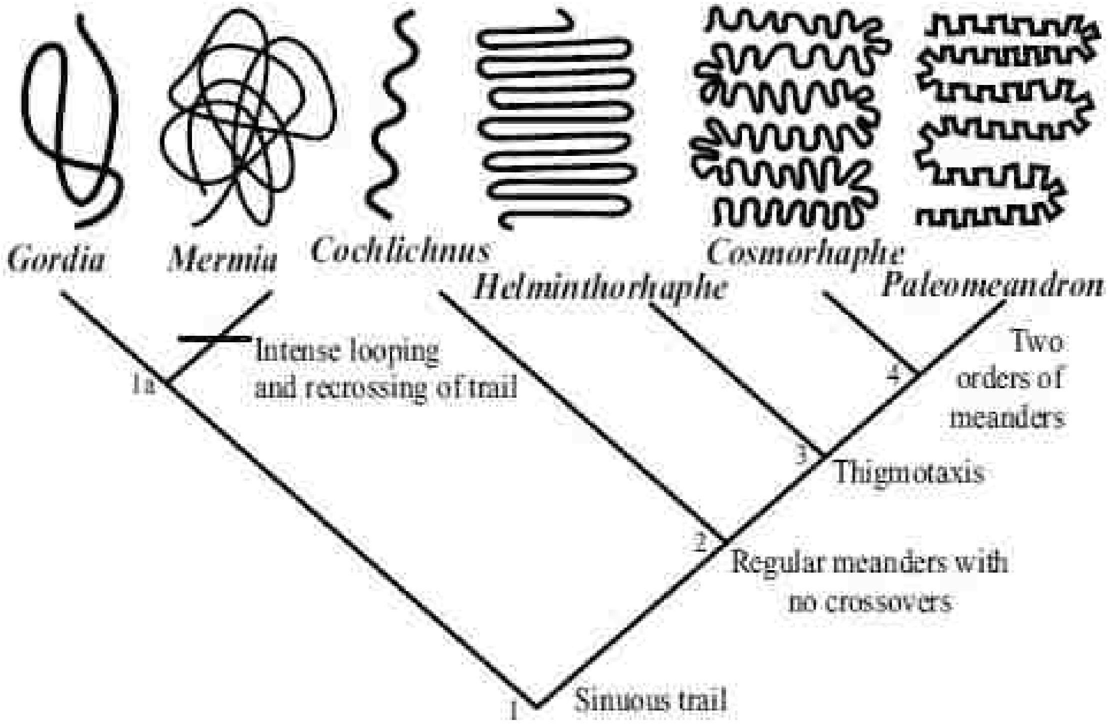


Figure 11 - Cladogram showing a hypothesized phylogenetic relationship among looping and meandering ichnotaxa. From Ekdale and Lamond (2003).

complex behavior early in the Cambrian. Increasingly complex Cambrian trace fossils, therefore, may not represent increasing neurological complexity, but rather behavioral adaptations to increasing environmental complexity and heterogeneity.

5. GEOLOGIC SETTING FOR *TAPHRHELMINTHOPSIS NELSONI*

The field localities for this study are located in the Salt Spring Hills and the White-Inyo Mountains of southeastern California, and the Montezuma Range of Esmeralda County, Nevada. The Wood Canyon Formation is the focus for the Salt Spring Hills area, the Campito Formation is the focus for the Montezuma Range area, and the Poleta Formation is the focus for the White-Inyo Mountains area. Specimens were documented in the field for this study in the Wood Canyon Formation and the Campito Formation, while images of the Poleta Formation specimens are taken from Hagadorn et. al. (2000). The Campito Formation contains the meandering trace *Cosmorhaphe*? isp. (Fig. 12), which is used as local meandering trace for comparison to *T. nelsoni*.

Figure 12 – Cosmorhaphe? isp. from the Campito Formation in the Montezuma Range, Esmeralda County, Nevada. This image was produced using photogrammetry. Paper markers are used for photogrammetry software recognition. Ruler for scale is 30 cm.

The stratigraphic relationships of the three units is shown in Figure 13. The *T. nelsoni* samples from the White-Inyo Mountains come from the middle member of the Poleta Formation in an area called the “Poleta Folds” (Hagadorn et. al., 2000). The Campito Formation occurs stratigraphically below the Poleta Formation, and the Wood Canyon Formation is roughly correlative with the lower member of the Campito Formation. The meandering trace from the

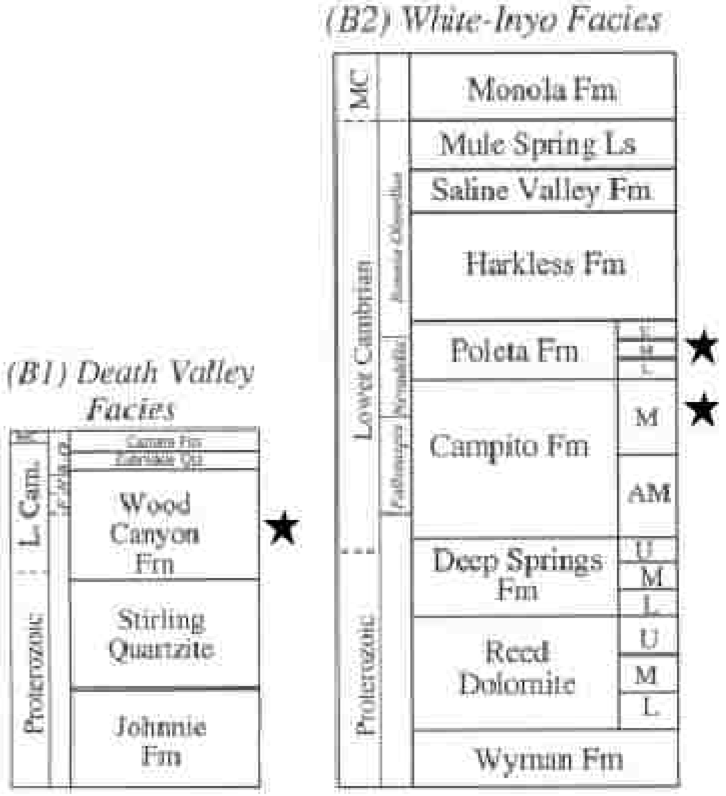


Figure 13 – Stratigraphic relationship of the strata in which T. nelsoni and Cosmorhaphe? isp. occur indicated by a star (modified from Hagadorn and Bottjer, 1999)

upper member of the Campito Formation is older than the *T. nelsoni* samples from the White-Inyo Mountains but younger than the *T. nelsoni* samples from the Salt Spring Hills region. The Campito Formation and the Wood Canyon Formation form the basal units at the base of the Cambrian (Hagadorn and Bottjer, 1999).

The Wood Canyon Formation in the Salt Spring Hills consists of cross-bedded fine-grained quartz sandstone with some sandy siltstone interbeds. The sandstone has a brown to purple color and is very dense. The bedding surfaces are highly fractured to the point where continuous trace fossil exposures are rare, however small isolated blocks of self-crossing *T.*

nelsoni occur in some areas (Fig. 1). Fortunately, in many cases there is still enough of the trace preserved to be identifiable. There are also abundant wrinkle structures present at the Salt Spring Hills locality (Fig. 14). The Wood Canyon Formation exposures in the Salt Spring Hills are Terreneuvian in age. This is constrained by occurrences of *Treptichnus pedum*, which defines the base of the Terreneuvian, and the absence of trilobite body fossils, which defines the base of Series 2.

Figure 14 – “Kinneyia”-type wrinkle structures, inferred to be the remnant of a microbial mat, in the Wood Canyon Formation in the Salt Spring Hills. A burrow is preserved among the wrinkles, likely by a grazer.

The Campito Formation in the Montezuma Range consists of thinly laminated beds of silty mudstone. The mudstone is brown to tan in color; it contains many small burrow segments that resemble the unnamed meandering trace in size and color, but not shape. This unit also contains abundant olenellid trilobites.

The Poleta Formation in the “Poleta Folds” region of the White-Inyo Mountains is similar in lithology to the Wood Canyon Formation. It consists of 20-to-40-centimeter-thick sandstone units with thin, fine-grained sandstone interbeds (Hagadorn et. al., 2000). The *T. nelsoni* specimens are located on top of the massive sandstone beds.

“Kinneyia”-type wrinkle structures (Porada et. al., 2008) are common in the Wood Canyon Formation in the Salt Spring Hills (Fig. 14). These are sedimentary structures that occur on the surfaces of bedding planes. These structures exhibit irregular troughs and crests, dissimilar to ripples. The troughs are rounded and approximately 1 to 2 millimeters in depth, while the crests are level with the bedding surface. Each trough and each crest is approximately 2-3 millimeters wide. Occasionally burrows can be seen within wrinkle structures, such as in Figure 14.

Wrinkle structures have been interpreted by Noffke et. al. (2001) to be related to the presence of microbial mats, thus these structures are a type of microbially induced sedimentary structures (MISS). The presence of MISS in the Wood Canyon Formation, along with burrows, suggests that the paleoenvironment preserved in that unit represents a transitional environment from the microbial mat-dominated environments of the Ediacaran to the bioturbation-dominated environments starting in the Cambrian. Wrinkle structures have been described in both the Wood Canyon Formation and Poleta Formation sections (Hagadorn and Bottjer, 1999), so for the purpose of this study I hypothesize that *T. nelsoni* occurs in a transitional environment.

6. HYPOTHESES FOR INTERPRETING LOOPING TRACES

In this section I present three competing hypotheses for the occurrence of looping behavior among early Cambrian burrowers. In section 6, I will use quantitative methods to test these hypotheses.

Hypothesis 1: Inefficient Wandering

According to this hypothesis, looping is an inefficient foraging method that is attributed to an ancestral behavioral trait that later evolved into more efficient meandering foraging patterns. Herein, efficiency in foraging is defined as a burrowing pattern covering the greatest area using the shortest burrow length. Looping patterns leave a lot of unexploited sediment, and self-crossing paths result in redundancy that wastes time and energy. Seilacher (1997) proposed that *Psammichnites gigas* was representative of an organism actively feeding while burrowing beneath the surface. He suggested that the meandering median furrow represents a siphon-like appendage that acquired food by sweeping back and forth across the sediment surface in a vacuum-like manner, illustrated in Figure 2. This back-and-forth sweeping siphon was a way for the organism to compensate for its inefficient looping. However, natural selection favors animals that have the most efficient foraging method, so the idea that an animal can evolve to be inefficient is at odds with modern biological principles (Pyke, 1984).

Seilacher (1997) interpreted the *P. gigas* tracemaker to have been a primitive animal with limited neurological capacity, such that it was unable to forage in more spatially efficient meandering pathways because meandering is “more difficult to program.” This interpretation treats the tracemaker’s brain as being a simple computer program that caused the animal to react to its environment in a constant and methodical manner. Plotnick (2012) challenged the idea that the brains of early foragers were “closed programs” with limited repertoires of simple commands governing locomotive patterns. This idea is part of an obsolete biological principle that the brains of organisms are hardwired to respond to stimuli according to a set of computer-program-like rules (Plotnick, 2012). Cognitive abilities, such as learning and memory, are highly conserved behaviors that are present in nearly any animal with a nervous system, even simple organisms such as the nematode *C. elegans* (Ardiel and Rankin, 2010; Dukas, 2009). Experience plays a key role in animal foraging behavior, and the strict computer program model proposed by Seilacher (1997) does not allow for learning to change behaviors. The reality is that behavior is plastic in most animals, which allows acclimatization to dynamic environments. Animals may have a behavioral baseline for using a certain set of foraging strategies such as meandering, but natural selection will favor animals that use information from their environment to change their behavior. Using pre-programmed commands for foraging without taking the environment into consideration is not a feasible strategy that can persist through natural selection.

There are several scenarios in which Seilacher's inefficient wandering hypothesis for *P. gigas* can still be feasible with a few adjustments. However, within each scenario, the trace should not be interpreted as recording inefficient behavior. First, it could be a randomly generated behavior that is adaptive for an environment in which there were sufficient nutrients just above the water-sediment interface for the animal to sweep its siphon back and forth to acquire nutrients from the sediment surface. In this scenario, the organism may not have required a meandering pattern because it was not deriving its food from the sediment in which it was bulldozing. The looping could simply be the result of random walks. While random walks are usually attributed to search behavior, they could also be a component of an active feeding strategy, given the above scenario.

Hofmann (1990) explored random walks using a computer simulation. In that study, he simulated an organism making pathways that went straight, left, or right with a maximum angular deviation (Fig. 15). When the maximum angular deviation is kept low in these simulations, around 20 degrees, several looping patterns were observed that resemble actual looping trace fossils. If the tracemaker was in an environment in which this random-walk strategy was adaptive, then it is possible that a strategy like this could be prevalent enough to be preserved in the fossil record. However, the *P. gigas* trace in this study does not have the erratic, jagged pattern of Hofmann's simulation. Additionally, burrowing beneath the sediment to gather food from the surface, as *P. gigas* is inferred to have done, is much more energy intensive than simply grazing on top of the surface sediments.

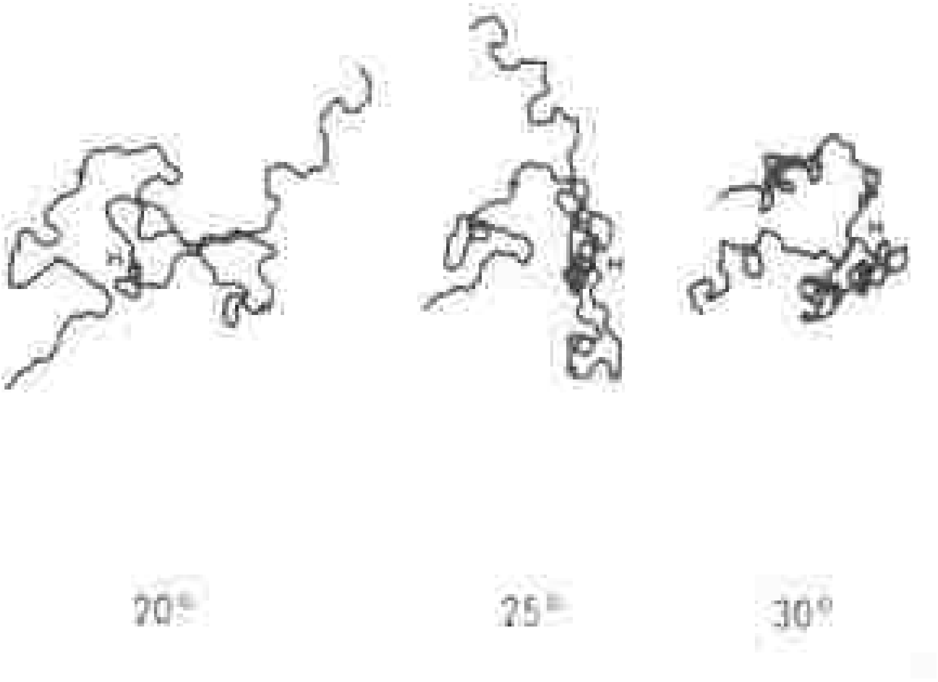


Figure 15 - Simulated random patterns that have the option of going straight or turning left or right at a given angle. From Hofmann (1990).

The second scenario that could explain the energy intensive looping of *Psammichnites* and similar traces is that it represents antipredator behavior. The presence of predatory anomalocarids and healing scars on trilobites indicates that predation was a significant environmental pressure on animals in the early Cambrian (Alpert and Moore, 1975; Chen et. al., 1994). Feeding while concealed beneath the surface would have been an adaptive strategy for increasing the fitness of prey organisms. Therefore, a costlier foraging strategy would persist through natural selection if there is enough selective pressure from predation risk. Additionally, looping could have been the tracemaker's strategy for unpredictability to avoid predators. Unpredictability is a common antipredator behavior in modern arthropods (Dean, 1993; Domenici et. al., 2008). Meandering is a highly predictable pattern, and any discerning predator could pluck a meandering forager from the sediment. Looping is more unpredictable than meandering, and the use of random walks would further contribute to the unpredictability. This hypothesis can be applied to other looping traces that maintain a connection to the surface, such as the median furrow in *T. nelsoni*.

Hypothesis 2: Search Behavior

The search strategy that produced the looping path preserved in *P. gigas* may have been either chemoklinotaxis or chemoklinokinesis (as discussed in section 2). The meandering median furrow in the trace could be the path of a rhinophore-like appendage used to receive chemical signals from a food source. The presence of only a single furrow suggests that the organism was using a single sensory receptor. In the case of klinotaxis, the loop exits should be oriented in the general direction of an attractant; for klinokinesis, the organism would display increased looping behavior as it got closer to an attractant. At first glance, the highly erratic looping seen in the *P. gigas* illustrated in Figure 2 suggests that chemoklinokinesis was being used. However, this is true only if the *P. gigas* traces on this slab represent only a single pathway rather than several different pathways. If several different pathways are represented in the *P. gigas* sample of Figure 2, then chemoklinotaxis is a better representation of the search strategy. Due to the incompleteness of the *P. gigas* sample, it is not possible to distinguish between multiple different pathways and a single pathway.

While *T. nelsoni* does not have a meandering furrow, there is a median furrow present (Fig. 1). This suggests that the tracemaker may have used a strategy similar to the *P. gigas* tracemaker, but without the need for a meandering rhinophore-like appendage. However, *T. nelsoni* is a less convoluted trace than *P. gigas*, displaying fewer loops per trace. In this case, the tracemaker may have used taxis rather than kinesis – kinesis-oriented pathways in general contain more loops because kinesis is linked to increased activity. An example that illustrates this concept well is evident in samples of *Cruziana semiplicata* (Fig. 16) (Seilacher, 1997). While multiple traces may be preserved on the bedding plane, the intense frequency of looping that is clearly seen within the trace. *T. nelsoni* does not contain looping frequency that is comparable to *C. semiplicata* or *P. gigas*, so kinesis can be ruled out in favor of taxis as a search strategy. Without any morphological features indicating that the tracemaker used only a single sensory receptor, it is not possible to conclude whether the tracemaker used klinotaxis or tropotaxis.

Figure 16 – Illustration of Cruziana semiplicata, which records the search behavior of a Cambrian trilobite. From Seilacher (2007).

If the organism was truly using klinotaxis or tropotaxis, the loop exits should be oriented in the general direction of an attractant. However, the lack of continuous burrow exposures creates difficulties in determining whether each loop exit has the same direction. The first problem is that the attribution of a complex of burrows on a single bedding plane to a single organism is not possible when the burrows are not continuous. Multiple loops could be separate burrows made by different animals. This is an issue in the *C. semiplicata*, cf. *Didymaulichnus*, *P. arcuatus*, and *P. gigas* specimens used in this study; because many of the burrows are not connected, they may not belong to the same individual. The second problem is determining movement direction. Seilacher (2007) suggests that looping burrows crossed over, not under, themselves. If a looping trace is well preserved, such as *P. gigas* (Fig. 2), then Seilacher's logic can be applied to determine loop termination direction. In the case of *T. nelsoni* burrows, there is not a clear indicator of which part of the burrow is crossing over because bilobate structures are preserved in both crossing burrows (cf. Fig. 1). Thus, it is in some cases impossible to determine the direction that the animal was burrowing, and in turn, the loop exit direction. To resolve this, both movement directions should be taken into consideration with each trace. Fortunately, this is not an obstacle in this study because loop exit direction is not used in quantitative analysis.

Hypothesis 3: Optimal Foraging

This hypothesis refers back to section 2, where I discussed the marginal value theorem and how it applies to three hypothetical scenarios: 1) two environments with differing proportions of patch quality, 2) two environments with differing travel time between patches, and 3) two environments with both differing proportions of patch quality and differing travel time between patches. These scenarios are applied to the early Cambrian environment to predict how foragers will behave in differing environments.

Figure 7 illustrates the first scenario where T1 represents an environment with mostly high quality patches, and T2 represents an environment with mostly low quality patches. The early Cambrian is represented by T1 and middle Cambrian and beyond is represented by T2. In the early Cambrian, microbial mats were beginning to be broken up by bioturbation, so the environment would have consisted primarily of patches similar in quality to low-quality patch-type A, represented by diminishing-returns curve A in Figures 7a and 7b. As microbial mats were broken up and nutrients were less concentrated in the sediment, patches would have become more like low-quality patch-type B, represented by diminishing-returns curve B in Figures 7a and 7b, which would have decreased the overall average intake rate across all patches. Different foraging strategies would have become more adaptive as patch quality decreased across the seafloor.

Looping traces are generally shorter than meandering traces and therefore represent shorter foraging bouts. Shorter foraging bouts are adaptive in environments dominated by higher quality patches. Therefore, as patch quality decreased, meandering strategies should have been favored over shorter foraging patterns such as looping, as illustrated in Figures 7c and 7d. The opposite also holds true: when higher quality patches, such as microbial mats or sediments containing microbial mat material, are dominant, shorter foraging patterns like looping should be favored over meandering patterns.

Figure 8 illustrates the second scenario in which D1 represents densely packed patches, like those in the early Cambrian, and D2 represents sparsely distributed patches, like those in Cambrian Series 3 and beyond. Applying this model to the evolution of foraging traces in the Cambrian, food patches would become increasingly farther apart as bioturbation broke up microbial mats. Therefore, we can hypothesize that in the early Cambrian, shorter foraging traces such as looping were favored due to the presence of densely packed patches. However, advancing forward through the Cambrian, longer foraging traces such as meandering ones were favored because patches became more widely dispersed. In fact, the tightness and complexity of meandering pathways (cf. Fig. 11) should have increased as patch density decreased. With respect to meandering traces, short traces are predicted to transition into loosely meandering traces, in turn transitioning to tightly meandering traces. This hypothesized succession in the morphology of meandering traces is beyond the scope of this study.

Both of the scenarios illustrated in Figures 7 and 8 use idealized models that do not represent realistic conditions in the early Cambrian. Neither patch quality nor travel time between patches is likely to have been negligible, so I will apply the two scenarios in tandem to better represent reality. This is illustrated in Figure 9, in which T1 represents an environment with high-quality, closely-spaced patches, and T2 represents an environment with low-quality, sparsely-distributed patches. Foragers will spend more time in patches in a T2 environment than they will a T1 environment. I hypothesize that patch quality and patch density both decrease through the Cambrian, based on evidence that microbial mats were broken up by bioturbation because of the agronomic revolution (Bottjer, et. al., 2000). Shorter foraging patterns should have been favored in the early Cambrian, with foraging patterns becoming longer as microbial matgrounds and their detritus disappeared from the sea floor sediments.

This hypothesis challenges the previously held view that meandering foraging behavior is more derived than looping foraging behavior. The cladogram in Figure 11 represents the notion that looping is an ancestral trait, and that progressively more complex meandering traces represent more advanced strategies. However, instead of behavioral complexity evolving, what actually may have happened is that behavior evolved in response to environment changes rather than due to advancements in neurological complexity. The fact that preserved arthropod brains found in the Cambrian resemble modern arthropod brains supports the idea that foraging strategy changes were not linked to increased neurological complexity, but rather to environmental changes.

7. QUANTITATIVE ANALYSIS – METHODS AND RESULTS

In this section, I use two means of quantitative analysis, goniograms and fractal dimension analysis, to provide numerical data to test the hypotheses in the previous section.

Goniogram Methods

Goniograms are measurements of angular deviation along a path at predetermined intervals (Fig. 17) **(**Hofmann, 1990). They are useful for quantitative analysis of a given path, and for testing for randomness of a given path. Because the looping trace fossils in this study are generally continuous and do not have any branching pathways, goniogram analysis is a useful tool for determining whether a foraging pathway records random or deliberate movements. Goniograms also show whether there is a preferred direction of movement along a trace, and they can be used to compare looping traces with those that do not loop. Data from Rowland (unpublished) and Hagadorn (2000) are compiled alongside goniograms created for this study.

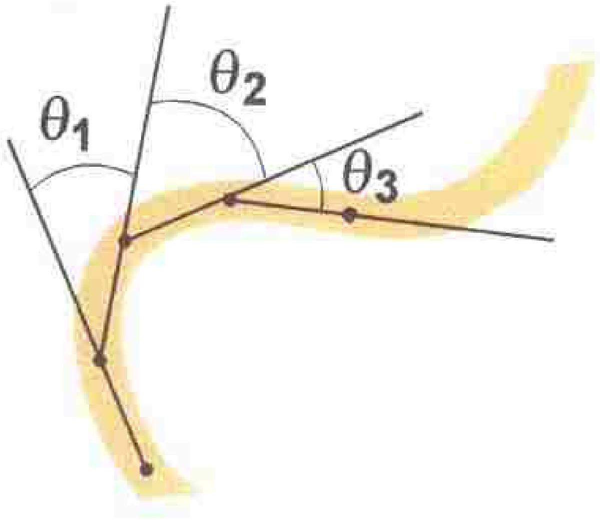


Figure 17 – Goniograms measure angular deviation per unit length. The angle is measured as positive or negative based on dextral or sinistral deviation. All of the angles shown are positive, assuming the tracemaker was moving toward the upper right. After Hofmann (1990).

Fractal Dimension Analysis Methods

The fractal dimension method used in this study is based on Lehane and Ekdale's (2013) graphoglyptid study and Le Comber et. al.'s (2002) study of modern mole-rat burrows. Fractal dimension is a value that quantifies how completely a pattern fills a given space. The calculated fractal dimension is a number between 1 and 2; the higher the number, the more completely the pattern fills a defined space. Fractal dimension is a scaleless measure of pattern complexity, which is very useful for trace fossils because many traces have similar shapes and patterns, but their sizes may vary immensely.

In this study, I use the box-counting method of calculating fractal dimension (D_{box}). This method places a fixed box-width grid over a pattern, and the number of boxes containing the pattern is counted (Lehane and Ekdale, 2014). Progressively smaller X/2 box-width grids are overlain on the pattern and boxes are counted again. Two values are recorded: N is the number of boxes that cover the pattern, and r is the magnification, or the inverse of box size. For each iteration, log(N) is plotted on the Y axis and log(r) on the X axis. An exponential curve is then estimated to fit the plotted empirical curve. Solving for D_{box} in the equation for the fitted exponential curve results in the following equation:

$$D_{box} = \frac{\log(N)}{\log(r)}$$

I used the free software Fractalyse to calculate the fractal dimension of each trace fossil specimen. The specimens used for calculating fractal dimension came from multiple sources, including field observations and the published literature.

Trace Fossils used for Quantitative Analysis

The main trace fossils studied occur in the southwestern United States (*T. nelsoni*) and central Spain (*P. gigas*). In order to have a sufficiently large sample size for meaningful quantitative analysis, I have also selected trace fossils from the ichnology literature from early Cambrian strata in eastern Canada, northwestern Argentina, northern Russia, and south China (Emmons, 1884; Crimes and Anderson, 1985; Crimes and Fedonkin, 1994; Seilacher et. al., 2005; Wang et. al., 2009; Mángano and Buatois, 2012). For the purposes of this study I have selected traces that are mostly continuous, and that are long enough to display patterns of looping and meandering. Published photographs documenting traces were used only if they were clear enough to allow me to trace a continuous path. If a published study contained an interpretive drawing of a complete trace fossil, the drawing was used rather than the photograph. Illustrations of traces used in this study can be found in Appendix A. These traces are compiled in a biostratigraphic chart in Figure 3.

The looping trace *Taphrhelminthopsis nelsoni* occurs in the Poleta Formation (Hagadorn et. al., 2000) in Inyo County, California, and also in the Wood Canyon Formation in San Bernardino County, California (Fig. 1). I used field specimens of *Taphrhelminthopsis nelsoni* from the Salt Spring Hills near Death Valley, as well as specimens figured by Hagadorn et. al. (2000). For analyses of the looping trace *Psammichnites gigas*, I used specimens from central Spain and northwest Argentina figured by Seilacher (1997) and Seilacher et. al. (2005) (Fig. 2). A meandering trace, tentatively named *Cosmorhaphe*? isp., from the Campito Formation (Fig. 12) is used to compare different foraging strategies of early Cambrian organisms. I performed the same quantitative analysis on this meandering trace as I did on the looping traces to quantitatively compare foraging strategies.

Taphrhelminthopsis nelsoni is a bilobate burrow approximately 3 to 4 centimeters in width (Fig. 1). The lobes are convex on the surface of the bedding plane. A burrow-parallel straight furrow runs between the two lobes. The burrow is continuous with no branching paths. A cross-section of a burrow, cut with a rock saw, revealed that the median furrow goes down into the burrow at a diagonal angle (Fig. 18). There is no ornamentation, such as backfill, associated with this specimen. The burrow fill is the same color and grain size as the surrounding sediment. A key characteristic of *T. nelsoni* that is most pertinent to this study is that it is typically self-crossing, or looping (Fig. 1).

Figure 18 - Cross-sectional view of T. nelsoni. The median furrow can be seen extending approximately 2 cm into the burrow at a steep angle. Hand lens for scale.

The type specimen of *T. nelsoni*, housed in the invertebrate paleontology collections of the Los Angeles County Natural History Museum, originated in the Poleta Formation of the White-Inyo Mountains in eastern California. I compared specimens from the Salt Spring Hills with the type specimen, and I determined that they belong to the same ichnospecies.

Gordia mermia (Appendix A, Fig. A1j) from the Terreneuvian Chapel Island Formation in eastern Canada is a looping trace with abundant cross-overs. It is a smooth trace which lacks ornamentation. The trace is approximately 2-3 mm wide (Crimes and Anderson, 1985).

Gordia mermia (App. A, Fig. A1j, A1k) from the Cambrian Series 3 Kaili Formation in south China is similar in appearance to the *G. mermia* in eastern Canada. However, the Kaili Formation specimen appears within body fossils of soft-bodied organisms. Wang et. al. (2009) suggested that the *G. mermia* tracemaker was feeding on the tissue of the soft-bodied organism.

cf. *Didymaulichnus* (App. A, Fig. A1n) is a bilobate trace from Series 3 and Furongian units of the Potsdam Group in Quebec (Collette et al., 2010). The cf. *Didymaulichnus* trace chosen for this study does not exhibit self-crossing, but it is the longest trace in its set and occurs within the same bedding as fragments of cf. *Didymaulichnus* that do cross themselves. Collete et. al. (2010) interpreted this trace fossil to belong to the arthropod *Mictomerus melochevillensis* because body fossils of this species are found at several terminations of cf. *Didymaulichnus*.

Plagiogmus arcuatus (App. A, Fig. A1o) is a bilobed looping trace from the Terreneuvian units of the Arumbera Sandstone in central Australia (McIlroy and Heys, 1997). This unornamented trace crosses itself frequently. McIlroy and Heys (1997) show that in cross section, the self-crossing path goes either above or below the original path, however, they do not interpret whether the tracemaker is crossing over or crossing under. We can use Seilacher's (2007) logic to interpret that the tracemaker always crossed over.

Hormosiroidea canadensis (App. A, Fig. A1m) is a looping trace that consists of a series of steep burrows that occur as “semi-circular knobs” (Crimes and Anderson, 1985). This trace occurs in the Terreneuvian Bayview Formation of southeastern Newfoundland, Canada. It probably represents a different foraging strategy than simple deposit feeding, but looping is a recurring component of its foraging pathway.

I have not yet designated an ichnogenus or ichnospecies to the meandering trace fossil from the Cambrian Series 2 Campito Formation in the Montezuma Range, Esmeralda County, Nevada (Fig. 12). I am tentatively calling it *Cosmorhaphe*? isp. based on the morphology of its presumably second-order meanders. This trace has a meandering pattern that forms a wide U-shape, as if the organism was turning around as it meandered. The burrow is 2 to 3 centimeters wide. The burrow fill is lighter in color than the surrounding sediment, and it contains no internal structures. In cross section, the meandering trace is approximately 1 millimeter in depth, and there is no structure apparent in the cross-sectional view.

I used two specimens of *Helminthoida crassa* (App. A, Figs. A2a, A2e), and one of *Helminthoida* isp. (App. A, Fig. A2c) in this study. *Helminthoida.* isp. and one of the *H. crassa* specimens are from the Terreneuvian Chapel Island Formation in Newfoundland, Canada. The other *H. crassa* specimen is from the Ediacaran Ust Pinega Formation in the Zimny Coast of White Sea, Russia (Crimes and Fedonkin, 1994). These traces contain tight meanders and do not contain any significant ornamentation.

Taphrhelminthoida dailyi (App. A, Fig. A2b) of the Terreneuvian Ratcliffe Brooke Formation in New Brunswick, Canada, is a bilobed trace with regular sinusoidal meanders (Hofmann and Patel, 1989). A straight median furrow bisects the trace. This trace does not contain any ornamentation.

Didymaulichnus meanderiformis (App. A, Fig. A2d) is a bilobed meandering trace that occurs in the Upper Kessyuse Formation of Siberia (Crimes and Fedonkin, 1994). This trace occurs in shallow water deposits at the Ediacaran-Cambrian boundary, but Crimes and Fedonkin (1994) do not specify in which part of the Upper Kessyune Formation *D. meanderiformis* occurs.

Cochlichnus anguineus (App. A, Figs. A2g, A2h) is a loosely meandering trace from the Ediacaran-Cambrian Puncoviscana Formation of Argentina (Buatois and Mángano, 2012). Buatois and Mángano (2012) do not specify in which part of the Puncoviscana Formation *C. anguineus* occurs. This trace occurs in deep marine strata. There is no ornamentation associated with this trace.

Psammichnites saltensis (App. A, Figs. A2i, A2j) is a regularly meandering bilobed trace that occurs in the Cambrian Series 2 Guachos Formation of Argentina (Seilacher et. al., 2005). This trace is unique in that each meander includes a sharp V-shaped kink.

Goniogram – Results and Conclusions

I constructed goniograms for the three meandering traces that are most complete (App. A, Figs. A2b, A2d, A2f). Negative angular values indicate movement to the left, and positive angular values indicate movement to the right. The goniograms are displayed in Appendix B. The regularity with which the goniograms switch from positive to negative values is a diagnostic characteristic of meandering traces. Goniograms of meandering traces also commonly have obtuse angular deviations at the end of each path as the trace turns toward the opposite direction.

Goniograms for seven looping traces are displayed in Appendix B, created by Rowland (unpublished) and Hagadorn et. al. (2000). These goniograms display less regularity in changing direction than do the meandering traces; instead they show a preference for turning in a single direction for a while, and then switching directions. The deviation angle is also generally lower than angles seen in the goniograms of meandering traces.

Goniograms can be used to characterize angular deviation patterns in trace fossils. Meandering traces are characterized by periodicity in which the goniogram switches between positive and negative deviation at regular intervals. Goniograms of meandering traces also display higher positive and negative deviation angles than those of looping traces. If meandering traces are non-random, methodical patterns, then goniograms can assist in quantitatively characterizing them and comparing them with other trace fossil patterns.

Goniograms of looping traces are quite different than those of meandering traces. There is no periodicity in looping traces; rather, there is a seemingly random crossing of the zero axis. There are also longer intervals of exclusively negative or exclusively positive turns, instead of periodic switching between the two. Traces that loop tend to display a preferred direction of turning, which is evident in goniograms that stay negative or positive for a long duration. There are a few examples of meander-like behavior shown in traces in the Poleta Formation reported by Hagadorn et. al. (2000), but those may be attributable to the tracemakers performing random walks in their foraging pathways. Additionally, a series of angular deviations that are close to zero could represent the tracemaker traveling to a food patch. That interpretation is compatible with the search behavior hypothesis. Hagadorn et. al. (2000) suggested that the distribution of *T. nelsoni* looping traces is patchy, and that they tend to occur in localized environments with sparse exploitation of intermediary areas. This reinforces the idea that nutrients occurred in concentrated patches in early Cambrian shallow-marine environments. The pattern of near-zero angles followed by intervals of high angular deviation seen in the goniograms supports this inference.

The *P. gigas* goniograms (App. B, Fig. B4) display sustained preferences for positive and negative deviations. The goniogram in blue shows a strong preference for positive angular deviation for nearly its entire length. This strong preference suggests that the tracemaker was not travelling directly to an area, but rather searching for a signal of an attractant. This is also supported by the two loop terminations facing in roughly the same direction. I interpret the characteristics of this trace to indicate that the tracemaker used looping to reorient itself toward an attractant. The goniogram in red shows an initial preference for negative angular deviation; about halfway through it switches preference to positive angular deviation. This suggests that the tracemaker acquired the signal of an attractant and that it turned around in order to track the increasing strength of the attractant signal. As with the former example, the loop terminations are in the same direction, indicating that the attractant was in that direction.

Fractal Dimension Analysis – Results and Conclusions

The fractal dimension values of the ten meandering traces range from 1.213 to 1.589, with an average of 1.479 and a standard deviation of 0.013 (Table 1). All but one of the traces have correlation coefficients greater than 0.98. The lowest was *Cosmorhaphe*? isp. at 0.87, which is not low enough to significantly impact the data. The outliers in this dataset are the two *C. anguineus* traces with fractal dimension values of 1.264 and 1.213. These low values are likely due to this ichnospecies displaying the loosest meander pattern out of the ten traces chosen for this study. Removing these two increases the average to 1.54.

The fractal dimension values of the fifteen looping traces range from 1.273 to 1.69, with an average of 1.424 and a standard deviation of 0.11 (Table 2). All fifteen traces have correlation coefficients of at least 0.91. There is no apparent correlation between the number of loops within a trace and fractal dimension value.

Table 1 - Fractal dimension values for looping traces.

Trace	Ichnospecies	Location	Geologic Unit	Age	Dbox	Corr. Coef.
A	*Helminthoida crassa*	Newfoundland	Chapel Island Formation	Terreneuvian	1.536	0.988589
B	*Taphrhelminthoida dailyi*	New Brunswick	Ratcliffe Brook Formation	Terreneuvian	1.548	0.998327
C	*Helminthoida* isp.	Newfoundland	Chapel Island Formation	Terreneuvian	1.546	0.993646
D	*Didymaulichnus meanderiformis*	Siberia	Upper Kessyune Formation	Terreneuvian	1.589	0.989539
E	*Helminthoida crassa*	White Sea, Russia	Ust Pinega Formation	Ediacaran	1.565	0.982396
F	Unnamed	Southern California	Campito Formation	Terreneuvian	1.461	0.870594
G	*Cochlichnus anguineus*	Argentina	Puncoviscana Formation	Ediacaran-Terreneuvian	1.264	0.982
H	*Cochlichnus anguineus*	Argentina	Puncoviscana Formation	Ediacaran-Terreneuvian	1.213	0.988
I	*Psammichnites saltensis*	Argentina	Guachos Formation	Series 2	1.577	0.985
J	*Psammichnites saltensis*	Argentina	Guachos Formation	Series 2	1.494	0.996

Table 2 - Fractal dimension values for meandering traces.

Trace	Ichnospecies	Location	Geologic Unit	Age	Dbox	Corr. Coef.
A	*Taphrhelminthopsis nelsoni*	Southern California	Poleta Formation	Series 2	1.274	0.982382
B	*Taphrhelminthopsis nelsoni*	Southern California	Poleta Formation	Series 2	1.273	0.973965
C	*Taphrhelminthopsis nelsoni*	Southern California	Poleta Formation	Series 2	1.444	0.993121
D	*Taphrhelminthopsis nelsoni*	Southern California	Poleta Formation	Series 2	1.361	0.95957
E	*Taphrhelminthopsis nelsoni*	Southern California	Poleta Formation	Series 2	1.388	0.978203
F	*Psammichnites gigas*	Central Spain	unknown, Cambrian SS	Terreneuvian-Tommotian	1.336	0.983267
G	*Psammichnites gigas*	Central Spain	unknown, Cambrian SS	Terreneuvian-Tommotian	1.389	0.988293
H	*Taphrhelminthopsis nelsoni*	Salt Spring Hills	Wood Canyon Fm	Terreneuvian	1.473	0.93
I	*Psammichnites* cf. *gigas*	NW Argentina	Guachos Formation	Series 2	1.41	0.926
J	*Gordia marina*	South China	Kaili Biota	Series 3	1.597	0.986
K	*Gordia marina*	South China	Kaili Biota	Series 3	1.33	0.997
L	*Gordia marina*	Newfoundland	Chapel Island Formation	Terreneuvian	1.426	0.985
M	*Hormosiroidea canadensis*	Newfoundland	Bayview Formation	Series 3	1.487	0.969
N	*cf. Didymaulichnus isp.*	Quebec	Potsdam Group	Terreneuvian	1.484	0.91352
O	*Plagiogmus arcuatus*	central Australia	Arumbera Sandstone	Terreneuvian	1.69	0.967

The results of the fractal dimension analysis show that most of the meandering traces fall within a narrow range of values. In contrast, the looping traces vary by nearly an order of magnitude more than the meandering traces, as evident in their standard deviations. Because of this, I do not recommend using only fractal dimension analysis to diagnose the function of a looping trace fossil. While meandering traces generally have higher fractal dimension values than do looping traces, the difference is not as much as would be expected if meandering traces are more spatially efficient than looping traces.

Based solely on these data, looping traces are shown to be less spatially efficient than meandering traces. If we assume that the tracemaker relied solely on internal programming, and did not forage optimally, then the spatial inefficiency results can be used to support the inefficient active feeding hypothesis for looping Cambrian tracemakers. However, animals show an ability to learn, and the ones that are able to make decisions based on changes in their environment and forage optimally are favored by natural selection. Moreover, looping ichnogenera have been described in Cambrian strata worldwide (Crimes and Anderson, 1985;

Crimes and Fedonkin, 1994; Seilacher and Gamez-Vintaned, 1995; Seilacher et al., 2005; McIlroy and Heys, 1997; Seilacher, 1997; Álvaro and Vizcaïno, 1999; Hagadorn et. al., 2000; Jensen et. al., 2002; Jensen, 2003; Miller et. al., 2009; Wang et. al., 2009; Collette et. al., 2010; Gingras et. al., 2011; Singh, 2011), so looping behavior cannot have been the result of a unique, local, evolutionary circumstance.

Fractal dimension analysis can have applications for situations in which tracemakers used optimal foraging strategies. It can quantitatively characterize foraging pathways, in order to interpret the environmental conditions under which a trace was made. Lower fractal dimension values represent environments with higher quality and more densely distributed food patches, while higher fractal dimension values represent the opposite. Spatial efficiency is more useful for determining the type of environment in which the trace occurred than for interpreting the neurological complexities of the tracemaker. However, this method should only be used if there is supporting evidence for environmental conditions, such as microbially induced sedimentary structures.

8. DISCUSSION

The models derived from optimal foraging theory applied to early Cambrian trace fossils suggest that environmental conditions rather than expanding neurological complexity were the driving factors influencing trace morphology. Neurological data from well preserved specimens in China (Cong et. al., 2014) suggest that the arthropod brain had evolved complexity similar to living arthropods in the early Cambrian. There may not have been significant changes in neurological complexity since the Cambrian to account for the increase in complexity of foraging behavior. Instead, as the quality and density of nutrients in the substrate decreased, as a result of microbial mats becoming sparsely distributed, foraging strategies adapted and behaviors developed that were better suited to the changing environment.

Assuming that trace morphology is linked to patch quality and density, the complexity of a trace can potentially be used as a proxy for the environmental conditions in a given stratigraphic unit. For example, the strata of the Wood Canyon Formation in the Salt Spring Hills, where looping traces are abundant, can be interpreted to be a nutrient-rich environment with high quality and densely packed food patches. This is supported by the abundance of wrinkle structures (Fig. 14). Using the same reasoning, the presence of meandering traces suggests an environment with lower quality food patches. Furthermore, the tightness of meandering traces is predicted to be negatively correlated with patch quality and density. As patch quality and patch density decrease, meandering traces are expected to be tighter, more curved, and in some cases contain second order meanders. The cladogram in Figure 11 can thus have an alternative interpretation, with each trace representing a foraging strategy optimal for a particular suite of environmental conditions. Higher quality environments are home to the traces on the left, *Gordia* and *Mermia*, with environmental conditions becoming progressively lower in quality to the right.

To further test this idea, time periods in which microbial mats became prevalent again should be explored for a behavioral succession similar to the succession seen in the Cambrian. Looping may not be present, but the trend of shorter pathways transitioning to longer pathways should persist. Post-mass extinction successions may be good areas to look for these trends. For example, after the end-Permian mass extinction, wrinkle structures appear in many localities (Pruss et. al., 2004; Pruss et. al., 2006). Further research should explore these strata to see if they contain a succession of trace fossils with the trends predicted in this study.

If these trends are associated with the emergence and subsequent decline of microbial mats, then looping traces may be a potential environmental marker for significant events that change the makeup of the seafloor environment, such as the Cambrian radiation and mass extinction events. Looping traces have been recorded worldwide in lower Cambrian strata, so their presence could have use in biostratigraphy as a marker for the lower Cambrian. Looping and self-crossing are also easily identifiable features, if large enough bedding plane exposures are available.

The weakness of the optimal foraging hypothesis is that it relies heavily on assumptions about the environmental quality recorded in the geologic record, with little evidence to back up the assumptions. The ideas presented in the hypothesis have roots in modern animal behavior principles; it is important for ichnologists to employ modern biology in the study of trace fossils. The logic behind the hypothesis makes sense within the context of the early Cambrian transitional environment, however more evidence is needed to fully support it. With that caveat, non-ornamented looping traces, such as *T. nelsoni*, that occur in the same bedding surfaces as wrinkle structures should be interpreted in light of optimal foraging strategy, based on the logic presented in this study. In the absence of wrinkle structures or any other proxies for environmental conditions, it is not possible to fully support optimal foraging as an interpretation. Another example in which environmental conditions are preserved is in the case of looping *Gordia mermia* in the Kaili Biota of South China (App. A, Figs. A1j, A1k) (Wang et. al., 2009). In this example, *G. mermia* occurs only within soft-bodied animal fossils. The interpretation is that the tracemaker was feeding on the remains of the soft-bodied animal. The tracemaker did not employ a meandering foraging pathway in this example, but rather used looping and disorderly pathways in this presumed "high quality patch." Rare examples such as this help illustrate how optimal foraging pathways are not always spatially efficient.

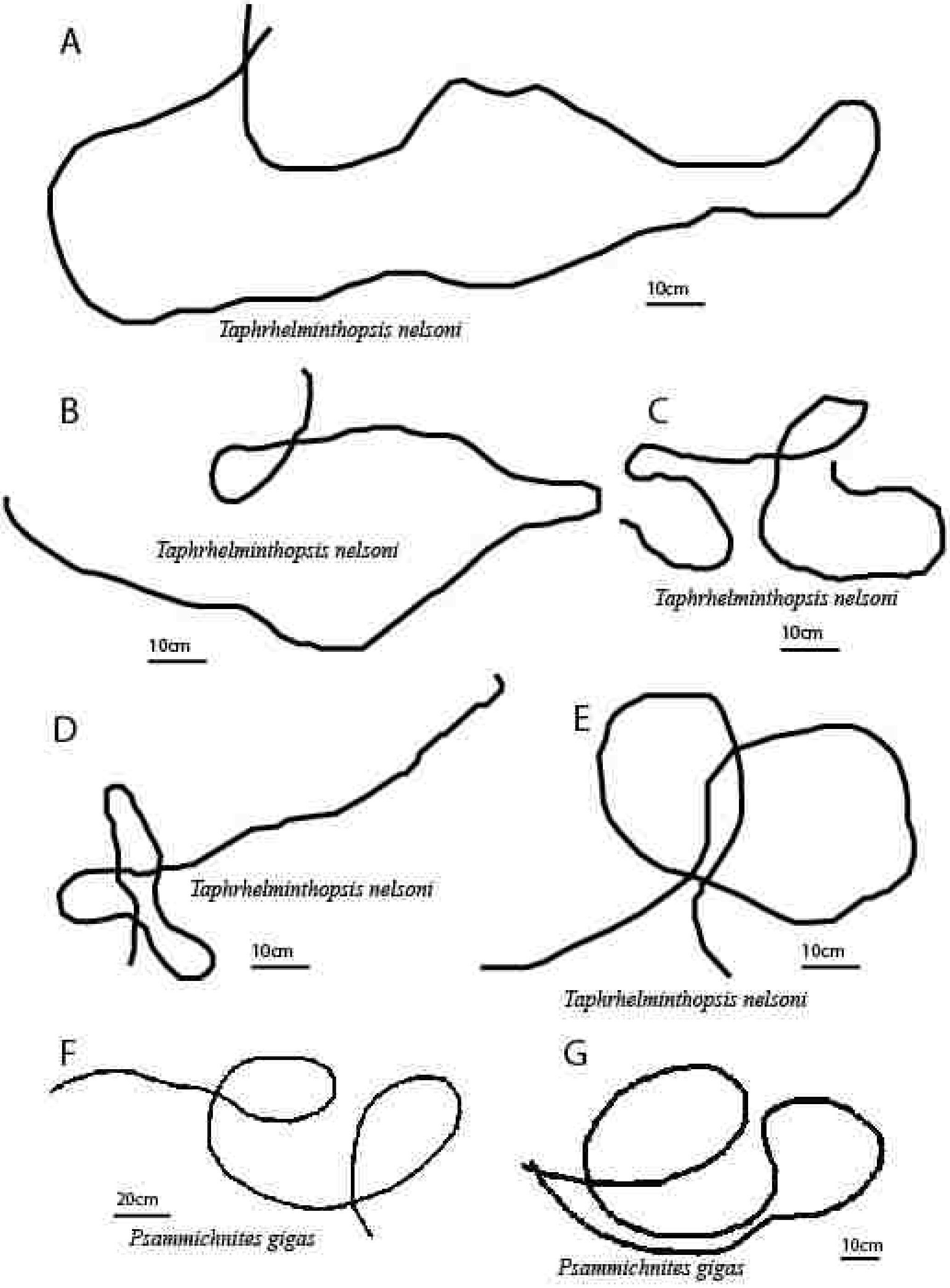
However, looping traces with ornamentation that indicate another behavior, as in *P. gigas*, need an interpretation that accounts for said ornamentation. The meandering median furrow in *P. gigas* indicates that the animal was using an appendage for an additional purpose. Because the rhythmic meandering pattern record in *P. gigas* resembles the motions of modern klinotactic animals, I infer that *P. gigas* records a search behavior; the tracemaker was seeking an attractant, rather than actively feeding. Looping was a conserved navigational strategy in early bilaterians that had applications in any behavior that required locomotion. The *T. nelsoni* tracemaker used looping for active foraging, while the *P. gigas* tracemaker used looping to search for an attractant, such as a food source or possibly seeking the pheromones of a potential mate.

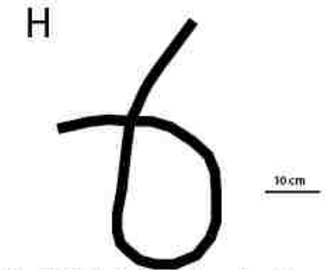
Until recently, outdated ideas have been used to interpret behavior recorded in trace fossils, and this has led to interpretations that are contrary to elementary concepts such as natural selection. Adhering to modern ideas may require a reevaluation of the ethological categories so that proper foraging concepts can be integrated into interpreting trace fossils. Modern ecological principles should be incorporated into ichnology. The classic interpretation of early tracemakers as robotically searching the sediment for food should be cast aside in favor of a more modern view of tracemakers as animals that can learn and adapt based on experience (Plotnick, 2012). Natural selection favors animals that maximize their fitness through learning and adapting. In this study, I do not use the traditional behavioral taxonomy of Seilacher (1967), with categories such as pascichnia, fodinichnia, and agrichnia. I use instead a more contemporary behavioral classification. Seilacher's classic terms can be combined into a single all-encompassing category: foraging traces. Seilacher's terms are still useful in differentiating specific foraging strategies for substrate feeders, but they should not be used as a way to interpret the efficiency of an organism. Each of Seilacher's categories characterizes a specific strategy that is used in an environment favorable for that foraging method.

The changing environment of the early Cambrian stimulated the evolution of many different foraging strategies in response to changes in sediment nutrient quality and distribution. Specifically, looping and meandering strategies preserved in trace fossils reflect animals being favored by natural selection for their ability to optimally forage in changing environments. The strategy preserved in looping trace fossils may be a search behavior, in which the animal was seeking a new food patch, or it may be an optimal active-feeding strategy in an environment where patch quality and density was high. Quantitative analysis methods such as fractal dimension analysis and goniograms assist in characterizing trace fossils with different foraging strategies, as well as providing quantitative data for interpreting paleoenvironmental conditions. This methodology provides a way to look at the evolution of animal behavior during the Ediacaran-Cambrian transition and expand our understanding of what causes behavior to change over time. Environmental change, rather than evolving neurological complexity, is the primary driver for behavioral changes over time.

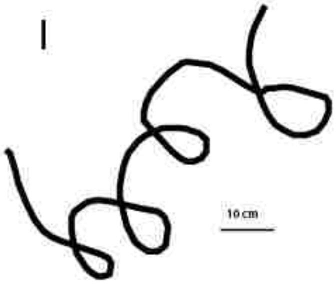
APPENDIX A – ILLUSTRATIONS OF LOOPING AND MEANDERING TRACES USED FOR QUANTITATIVE ANALYSIS

Figure A1 - Looping Trace Fossils

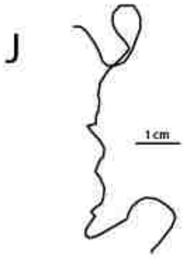




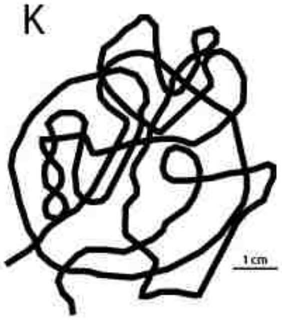
Taphrhelminthopsis nelsoni



Psammichnites cf. *gigas*

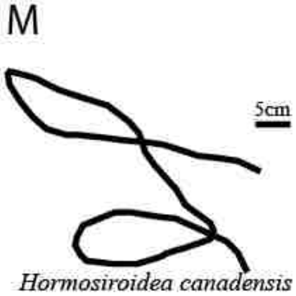


Gordia mermia

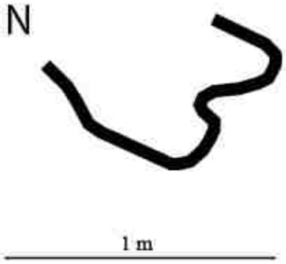


Gordia mermia

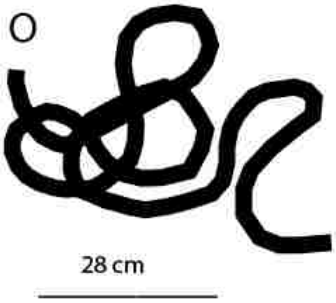
Gordia mermia



Hormosiroidea canadensis

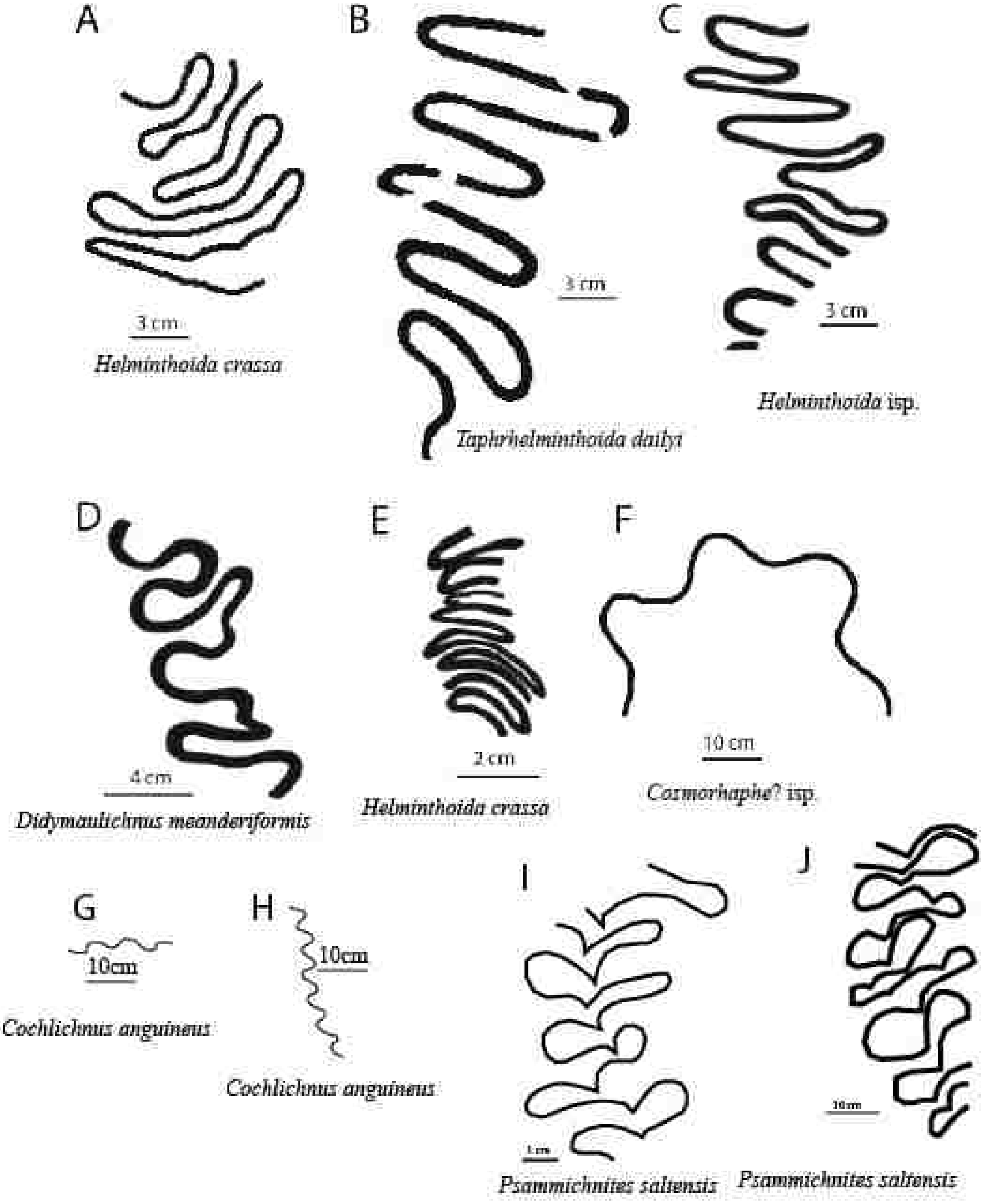


cf. *Didymaulichnus* isp.



Plagiogmus arcuatus

Figure A2 - Meandering Trace Fossils



APPENDIX B - GONIOGRAMS

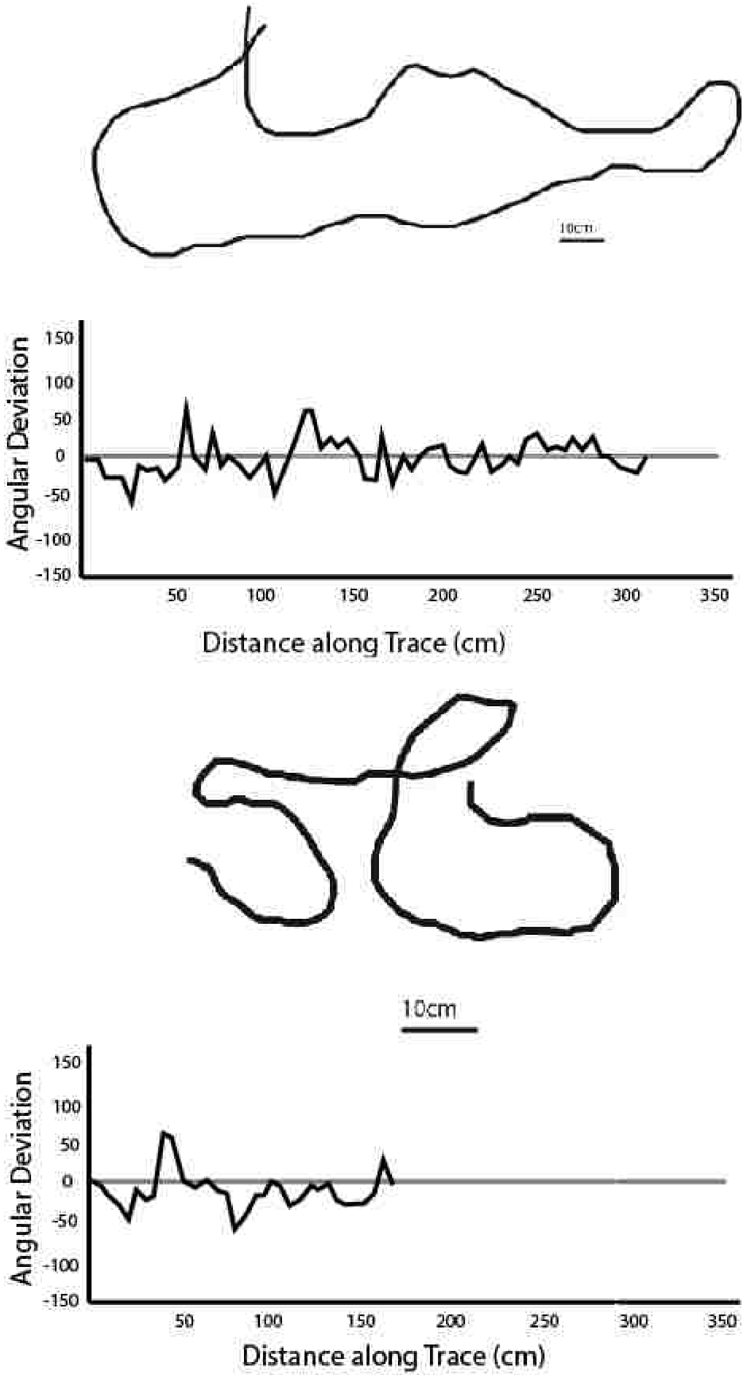


Figure B1 – Goniograms for Taphrhelminthopsis nelsoni (modified from Hagadorn et. al., 2000)

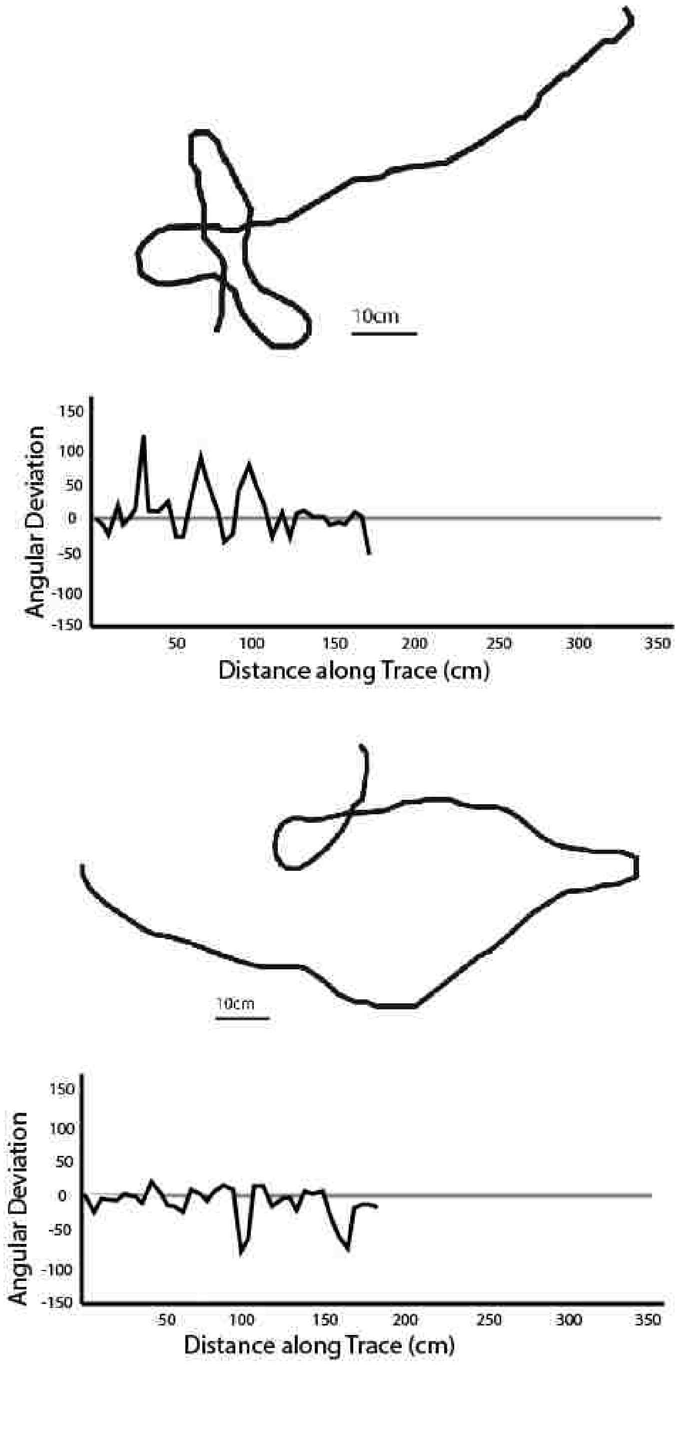


Figure B2 – Goniograms for Taphrhelminthopsis nelsoni (modified from Hagadorn et. al., 2000)

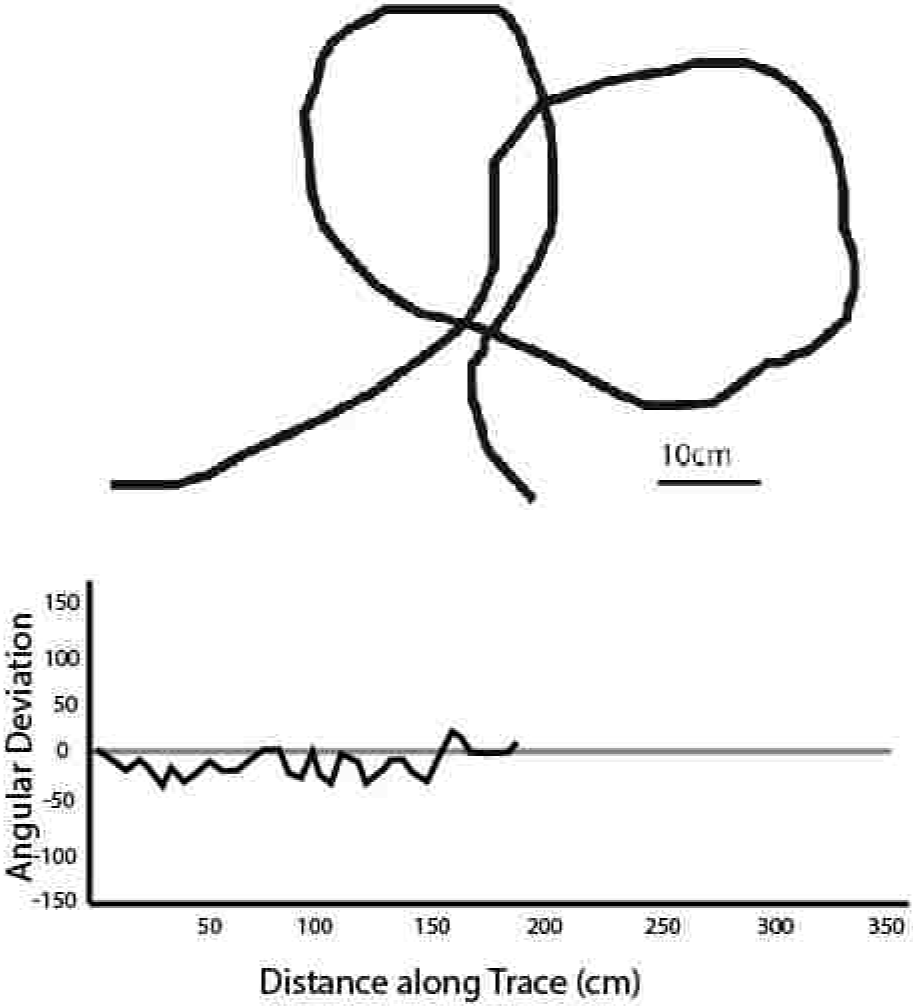


Figure B3 – Goniogram for Taphrhelminthopsis nelsoni (modified from Hagadorn et. al., 2000)

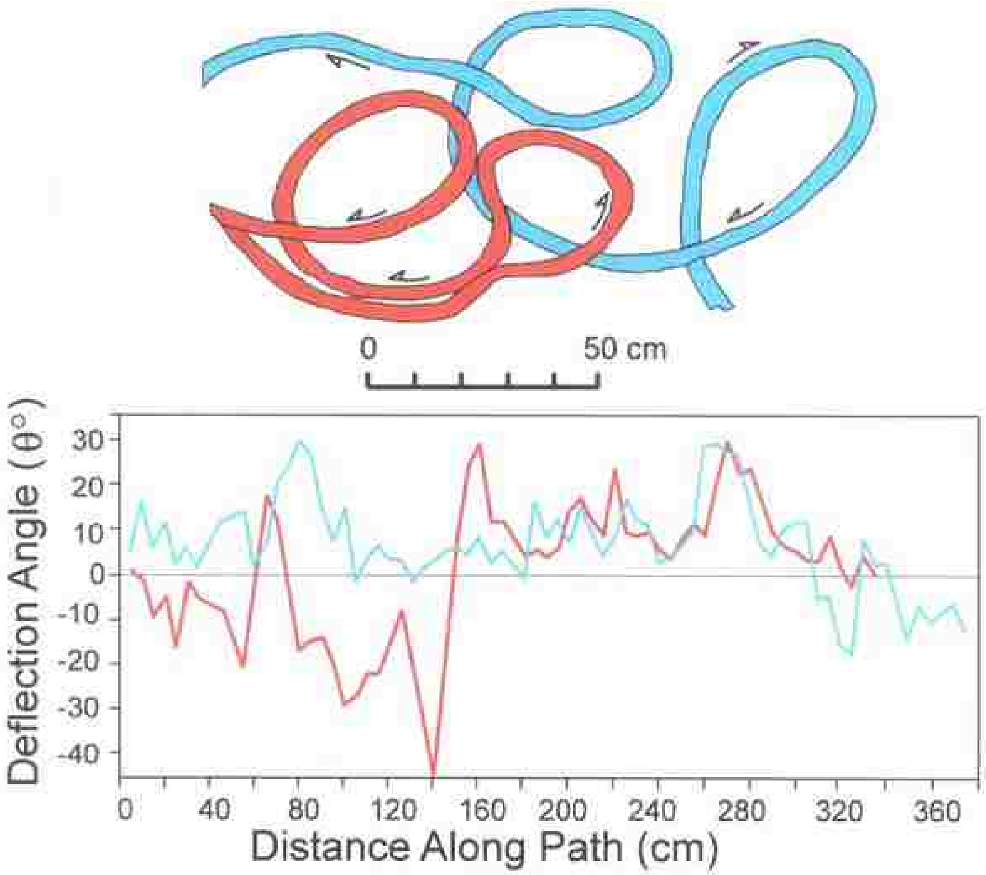


Figure B4 - Goniograms for *Psammichnites gigas* from Rowland (unpublished).

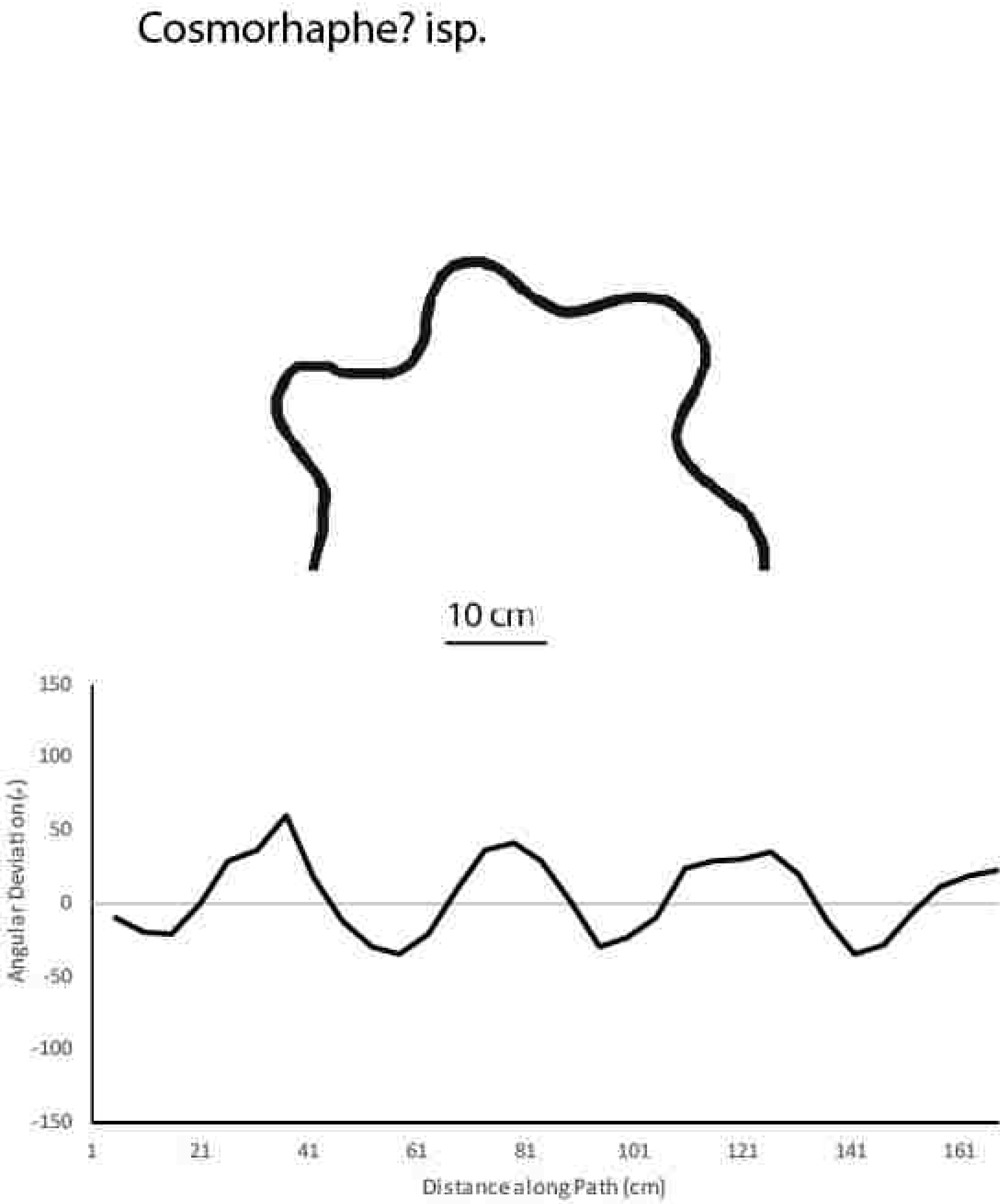


Figure B5 – Goniogram for Cosmorhaphe? isp.

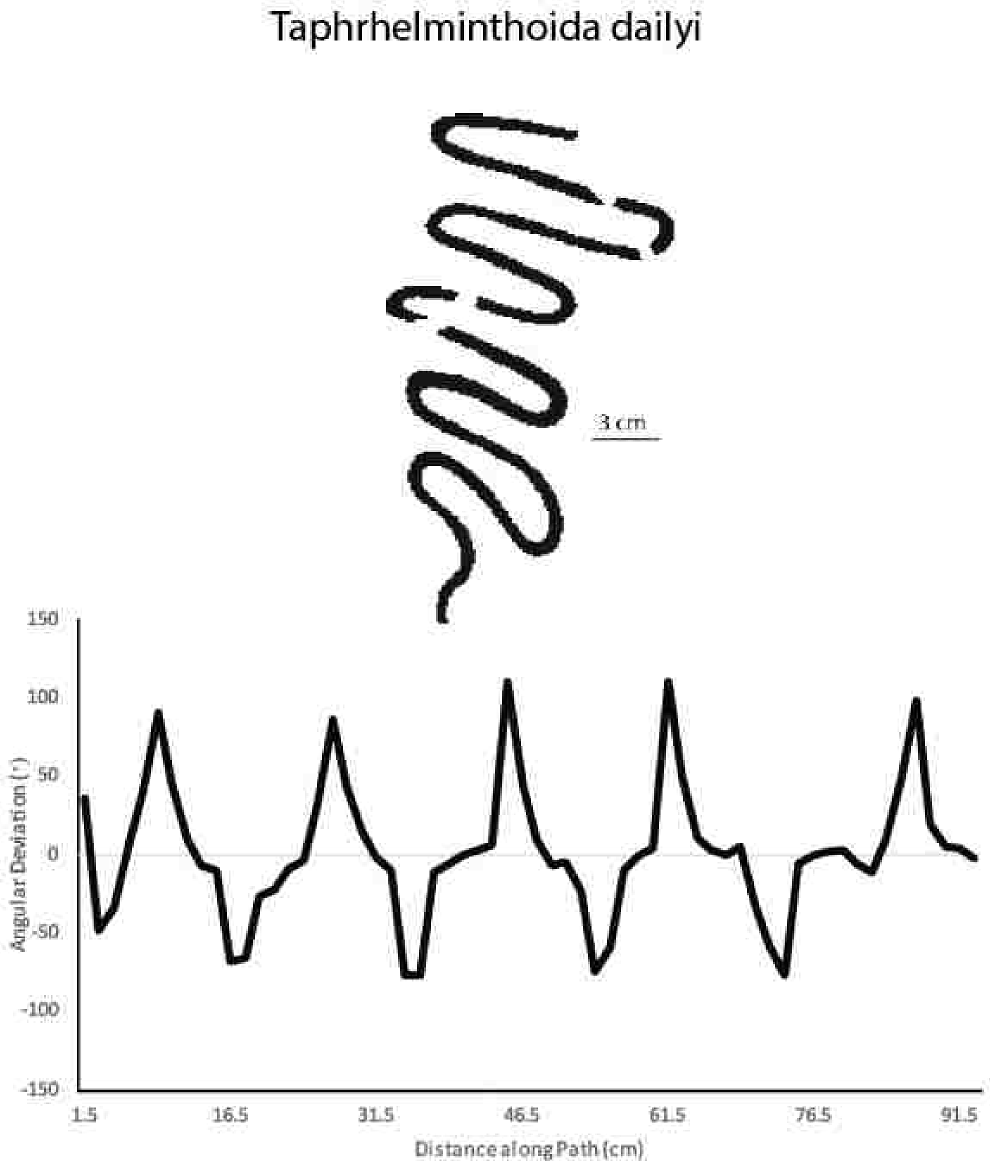


Figure B6 – Goniogram for Taphrhelminthoida dailyi

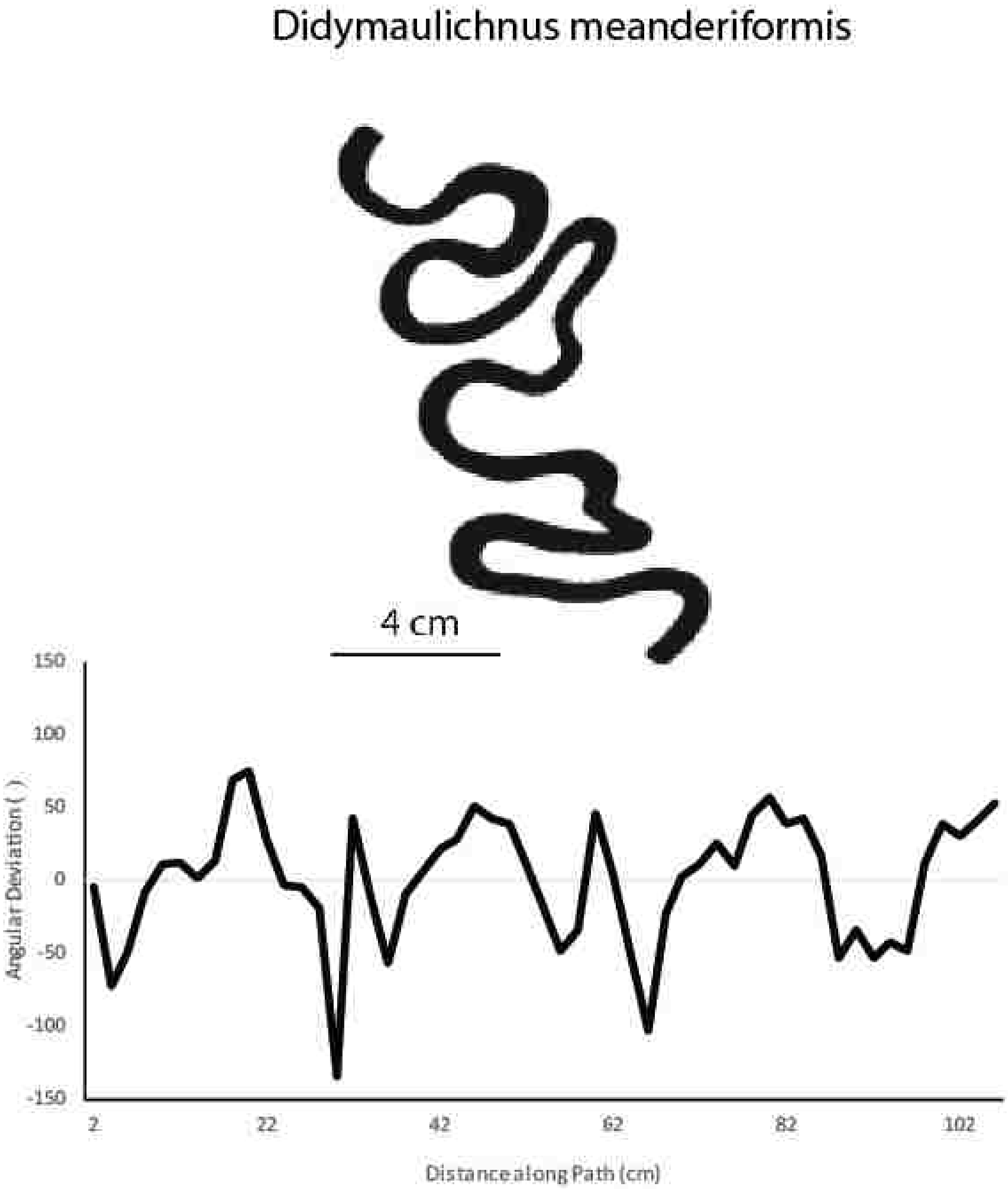


Figure B7 – Goniogram for *Didymaulichnus meanderiformis*

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Research Interests

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Physical Geology, Historical Geology

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Undergraduate Teaching/Grading Assistant 8/2012 to 5/2014
Petrology, Paleobiology, Geology of the National Parks

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