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Paleobiology of the Climactichnites Trackmaker: An Enigmatic Late Cambrian Animal Known Only from Trace Fossils

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PALEOBIOLOGY OF THE *CLIMACTICHNITES* TRACKMAKER: AN ENIGMATIC LATE CAMBRIAN ANIMAL KNOWN ONLY FROM TRACE FOSSILS

A Thesis Presented

by

PATRICK RYAN GETTY

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ABSTRACT

PALEOBIOLOGY OF THE *CLIMACTICHNITES* TRACKMAKER: AN ENIGMATIC LATE CAMBRIAN ANIMAL KNOWN ONLY FROM TRACE FOSSILS

MAY 2007

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Based on a thorough examination of museum and field *Climactichnites* specimens, two species of this trace, which is restricted to North America, are recognized, each representing a unique behavioral variant. *C. wilsoni* represents surface-produced trackways, whereas *C. youngi* is re-erected for subsurface burrows. Burrowing behavior is supported by the presence of *C. youngi* within beds, the orientation of burrows inclined to bedding, and the presence of distinct burrow fills. Burrows are distinguished from surface traces by characteristics including the absence of lateral ridges and the presence of mm-sized striations superimposed on the trace. Burrowing behavior was previously unknown and represents a new behavior for the animal. A new ichnospecies, *Musculopodus sedentarius*, is erected for sedentary impressions of the animal. In the future *Musculopodus* may be expanded to include the resting traces of other soft-bodied animals known from fossils.

Analysis of *Climactichnites* indicates that the trackmaker was elongate, bilaterally symmetric, dorsoventrally flattened, and soft-footed. These characteristics are consistent with the trackmaker being a primitive mollusk or mollusk-like animal. Unlike other Neoproterozoic and Cambrain mollusks, such as *Matthevia*, *Wiwaxia*, and

Odontogryphus, the *Climactichnites* trackmaker could reach considerable size. At up to 29 cm wide and possibly 67 cm long, it was one of the largest animals of its time.

During locomotion, the animal generated muscular waves along the sole of its foot, which was extended and clamped into the substrate. Contraction of pedal muscles then pulled the body forward. This method of locomotion is similar to that employed by some gastropods, including *Bullia* and *Polinices*, which make *Climactichnites*-like trackways in exposed intertidal settings today. However, these modern trackways are not preserved because they are eroded by wind, waves, flood tides and subsequent bioturbation, as experiments confirm. Abundant microbial sedimentary structures associated with Cambrian occurrences suggests that microbial binding may have mediated the preservation of *Climactichnites*.

Two lines of evidence suggest that the *Climactichnites* trackmaker may have been one of the first animals to venture onto land: the co-occurrence of subaerially-produced sedimentary structures, such as adhesion structures and raindrop impressions, and trackways with variable preservation quality along their length.

PREFACE

Climactichnites is a unique fossil trackway that has generated endless controversy since it was found in 1859. Over 20 professional papers have been published on C*limactichnites* and yet no consensus exists as to what type of animal made the trackway and how it was made. Indeed, some researchers have even called into question the identification of *Climactichnites* as a trace fossil. The reason for such disparate hypotheses about the origins of this enigmatic fossil is its morphology. No other fossil is known to have ripple-like bars and furrows bound by lateral ridges. Additionally, despite the occurrence of similar trackways in modern intertidal environments, most workers have not explored the link between the fossil and its modern analogues.

The purpose of the present study was to examine *Climactichnites* both in the field and in museums in an attempt to answer the basic questions of "what was the trackmaker?" and "how did it make the trackway?" that have vexed the paleontological community for so long. This study took advantage of a greatly expanded knowledge base about Late Cambrian environments in which the trackmaker lived, which aided in the development of new interpretations about the fossil. For example, since the last study of *Climactichnites* was published in 1993, a whole body of knowledge has developed about the influence of microbial mats on Neoproterozoic and late Cambrian siliciclastic sediments. With this knowledge in hand, sedimentary structures have been identified in *Climactichnites*-bearing deposits, and even on the same beds, that indicate that microbial mats may have flourished in the same areas that the trackmaker traversed. The presence of these mats may have aided in the preservation of *Climactichnites* and, with the disappearance of widespread mat-bound surfaces by the early Ordovician, may also explain why *Climactichnites* is unique in the fossil record.

The present study was also greatly aided by neoichnological experimentation with modern gastropods, a practice that has not been used widely in the analysis of *Climactichnites* in recent years. This type of research allowed certain hypotheses to be tested that had hitherto remained speculative. For example, the question of how such a fossil could have been preserved in wave- and tidally-influenced environments was a matter of conjecture. The analysis of modern gastropods and their mucus-bound trackways allowed the hypothesis that mucus secreted by the foot of the *Climactichnites* animal preserved the fossil (Yochelson & Fedonkin 1993) to be tested and rejected.

Every known occurrence of *Climactichnites* was examined, with special emphasis placed on the Krukowski Quarry in Mosinee, Wisconsin. This quarry has by far the largest number of *Climactichnites* exposures in one locality, with 19 exposed beds preserving the trackway. Additionally, the Krukowski Quarry is flanked by numerous smaller quarries in which *Climactichnites* is found. With quarrying operations continuing throughout the timeframe of this study, new specimens were discovered each field season, thus adding greatly to the number of specimens available for study. Additional fieldwork was conducted at *Climactichnites*-bearing localities in Missouri, New York, Quebec, and Ontario.

The results of this research project are presented in two chapters, each of which will be submitted to a different journal for publication. The first chapter deals with the taxonomy of *Climactichnites*. Over the course of this study it became apparent that the trackmaker engaged in burrowing behavior, which has not been reported before for the animal. Because the burrows are morphologically distinct from surface-produced trackways it was necessary to give the burrows a distinct name and to define explicitly the differences between the two types of traces. Further, it was necessary to erect a new ichnogenus (a generic name for a trace fossil) for resting traces of the trackmaker, which are often found independently of the trackway or burrow. The taxonomy chapter will be submitted to the *Journal of Paleontology*.

The second chapter deals with the paleobiology of the trackmaker and will be submitted to the journal *Lethaia*. This chapter addresses the fundamental questions about *Climactichnites* discussed earlier, but it also addresses much more. For example, the large amount of data that was collected permits discussion about the possible growth habits of the trackmaker, a topic that was not previously considered because of the limited nature of most previous studies. Additionally, new lines of evidence about the quality of preservation of the trackway are presented that can help constrain whether or not the trackmaker made subaerial excursions.

It is important to note here that this study was part of a collaborative work between my advisor and me. However, I conducted the lion's share of data collection and analysis, with notable exceptions including the collection of data at the Miller Museum of Queens University, Royal Ontario Museum, and University of Missouri being done by Whitey Hagadorn. Dr. Hagadorn also examined localities, such as the Minke quarry in Wisconsin and Big Springs State Park in Missouri, which I was unable to visit, and took the photographs used in figures 5G, 9C, 15F and 25. Dr. Hagadorn also collected portions of the data included in Appendix 1 and Table 3 and figures 11, 15B, 15C, and 16. Numerous students at Amherst College, including Jed Bernstein, Megan

Dickoff, Charlie Hoxie, Ariel Morales, Kate Raddock, Lydia Tarhan, Zalmi Yawar, and Anna York assisted in collecting data in the field. The data that they collected was integral to composing the graphs in figures 11, 12, and 14, as well as the sketch maps in figures 21 and 22. Lydia Tarhan conducted an in-depth study of the surface at 9.13 m up section in the Krukowski quarry (PRI-100-9.13), and I have relied on the results of her work when discussing *Climactichnites* specimens from that surface. Numerous other collaborators, including Jeff Chiarenzelli, Dan Damrow, Al Donaldson, Bob Dott, Mark Erickson, Dave Franzi, Bill Gillingham, Pierre Groulx, Rob MacNaughton, and Bruce Stinchcomb aided in locating *Climactichnites*-bearing field localities, and Dan Damrow, Pierre Groulx, and Bruce Stinchcomb helped collect specimens as well as permitted examination of specimens from their private collections.

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LIST OF ABBREVIATIONS

Museums and Localities:

American Museum of Natural History (AMNH)

Amherst College Museum of Natural History (ACM and ACM UC)

Geological Survey of Canada, Ottawa, Ontario (GSC)

Miller Museum, Queens University (MMQ)

Minna Anthony Common Nature Center, Wellesley Island, NY (WINC)

New York State Museum, Albany, New York (NYSM)

Parc archeologique de la Pointe du Buisson, Melocheville, Quebec (JF)

Peabody Museum, Yale University (YPM)

Quebec, specimens owned by Pierre Groulx (QUE-PH)

Quebec, specimens from Les Carrieres du Charm Quarry (PRI-102)

Redpath Museum, McGill University (RM)

Royal Ontario Museum, Toronto (ROM)

Science Museum of Minnesota, Saint Paul (SMM)

Smithsonian Institution, Washington D.C. (NMNH)

Springfield Science Museum, Springfield, MA (SSM)

University of Wisconsin at Madison (UW)

University of Missouri at Rolla (UMR)

Other abbreviations used in the text:

Wisconsin, specimens owned by Daniel Damrow (WI-DF)

Wisconsin, Krukowski Quarry (PRI-100; numerical designation after 100 indicates the horizon from which the discussed specimen comes)

Wisconsin, Nemke Quarry (PRI-101; numerical designation after

101 indicates the horizon from which the discussed specimen comes)

Other trace fossils:

Arenicolites (Ar)

Diplichnites (D)

Diplopodichnus (Di)

Indeterminate arthropod (IA)

Planolites (Pl)

Protichnites (Pr)

CHAPTER I

INTRODUCTION

The ichnogenus *Climactichnites* was erected in 1860 by William Logan to encompass unusual trackways consisting of two parallel ridges, between which are undulating bars and furrows (Fig. 1). Since then, our understanding of trace fossil taphonomy and microbially influenced siliciclastic environments has changed substantially (Hagadorn & Bottjer 1999; McIlroy & Logan 1999) and new *Climactichnites* morphotypes have been identified (Yochelson & Fedonkin 1993; Getty & Hagadorn 2005, 2006). These morphotypes result from variation in trackmaker behavior and morphology as well as sediment consistency and taphonomy. These new morphotypes permit more constrained interpretations of the trackmaker's behavior and morphology, and require re-examination and revision of the systematics of *Climactichnites*-related trace fossils.

Climactichnites only occurs in Late Cambrian sandstones of North America. Specimens occur in three generalized regions including Wisconsin (Elk Mound Group, which includes the Mt. Simon Sandstone and Wonewoc Formation), Missouri (Lamotte Sandstone and Gunter Sandstone member of the Gasconade Formation) and the St. Lawrence-Lake Champlain regions of Ontario, Quebec, and New York. *Climactichnites* is found in upper portions of the Potsdam Group, including the Nepean Sandstone of Ontario, Cairnside Formation of Quebec, and Keesville member of the Potsdam Formation in New York (Yochelson & Fedonkin 1993; Getty & Hagadorn 2005, 2006; Fig. 2, Table 1). These units represent a range of marine, aeolian, and fluvial environments; however, *Climactichnites* is restricted to shallow tide and wave influenced marine environments (Houseknecht & Ethridge 1978; Driese *et al.* 1981; Yesberger 1982; Wolf & Dalrymple 1984, 1985; Dott *et al.* 1986; Bjerstedt & Erickson 1989; Yochelson & Fedonkin 1993; Runkel *et al.* 1998). Sedimentary structures associated with some *Climactichnites* trackways, including raindrop impressions, adhesion structures, and polygonal desiccation cracks, suggest that the *Climactichnites* trackmaker may have traversed tidal flats under subaerial as well as subaqueous conditions, making the trackmaker, along with euthycarcinoid-like arthropods, among the first terrestrial pioneers (MacNaughton *et al.* 2002, 2003; Hoxie & Hagadorn 2005).

Because *Climactichnites* is limited stratigraphically and geographically to the Late Cambrian of North America, and because no similar trace fossils are known from the Phanerozoic, contradictory hypotheses about the morphology, locomotion, and identity of the animal have been proposed. Nearly a century and a half after the fossil was first described no consensus exists as to what type of organism made the trail (see an historical account in Yochelson & Fedonkin 1993). Yochelson and Fedonkin (1993) suggested that the trail resulted from feeding activity of an unknown phylum of animals with anterior and lateral muscular flaps. However, it is unlikely that the trackmaker had lateral flaps because the trackway does not disturb sedimentary structures adjacent to the trail (e.g. Malz 1968, fig. 1), which would have occurred if the animal were pulling sand in towards the body with these flaps (see below). Damrow *et al.* (2001) proposed that *Climactichnites* represents siphonophore-like zooplankton that washed ashore, but the depth of many trackways indicates that the fossil was produced within the sediment by plowing activity of an animal. Further, *Climactichnites* never exhibits folding, twisting, tearing, or transport, which would be expected in at least some examples if the fossil were that of a long, strap-like organism. In contrast, other soft-bodied organisms, such as jellyfish, that were washed ashore in *Climactichnites*-bearing deposits exhibit all of these features (Hagadorn *et al.* 2002; Hagadorn and Belt in press). Evidence presented in this paper supports the hypothesis of Seilacher-Drexler and Seilacher (1999), who proposed that *Climactichnites* was made by a mollusk or mollusk-like animal.

A variety of modern gastropods, including *Polinices*, *Littorina*, *Hydrobia*, and *Bullia* produce *Climactichnites*-like trackways with lateral ridges and transverse bars when crawling about on subaerially exposed intertidal sand flats (Raymond 1922; Abel 1935; Häntzschel 1938; Gräff 1956; Brown 1971; Schäfer 1972; Trueman & Brown 1976; Knox & Miller 1985; Fig. 3). The method of locomotion inferred for the *Climactichnites* trackmaker is similar to that employed by *Bullia* and *Polinices*, which extend the flexible anterior part of the foot and then clamp it down on the sediment to obtain purchase during trackmaking (Trueman & Brown 1976; Knox & Miller 1985). The similarity between these modern trackways and *Climactichnites* suggests that gastropods are the most appropriate modern analogue for the *Climactichnites* trackmaker and that the preservation and paleoecological role of *Climactichnites*, rather than its morphology, are its most unique characteristics.

In order to develop a better understanding of trackmaker morphology, locomotion, and behavior, as well as to better constrain the paleoenvironment in which the trackway was produced and preserved, an extensive field study of *Climactichnites* was conducted. Both previously published and new track localities were examined, with special emphasis being placed on the Krukowski Stone Quarry in Mosinee, WI, from which thousands of trackways were excavated during quarrying operations. Additionally, all known museum specimens were examined. Finally, modeling experiments were conducted in which modern gastropods produced *Climactichnites*-like trackways to test hypotheses about how the fossil was preserved (Getty & Hagadorn 2006, this study).

Some *Climactichnites* were produced as burrows, rather than as surface trails, and the name *C. youngi* is re-erected to encompass them. *C. youngi* has a morphology distinct from surface traces, including a lack of lateral ridges and the presence of commonly bifurcate transverse bars and fine striations superimposed on transverse bars and furrows. The recognition of *C. youngi* as a burrow sheds new light onto the biology and ecology of the trackmaker, suggesting that the animal was not a short-term visitor of intertidal sand flats that was occasionally stranded when the tide receded (Burling 1917), but probably inhabited the intertidal zone, including the moist subsurface, on a more permanent basis.

A new genus, *Musculopodus*, is erected to encompass body impressions of the *Climactichnites* trackmaker. This is necessary because body impressions represent trace morphology distinct from the trackway and burrow and were produced by a different behavior: body impressions are representative of the trackmaker's foot while it was stationary, whereas trackways and burrows represent locomotion on or below the surface. Additionally, many body impressions are not directly associated with a trackway and as such do not fit within the definition of *Climactichnites*. Finally, the erection of the new genus permits the naming of other ovoid body impressions from the fossil record that until now have remained unnamed (Gehling 1996; Seilacher 1997; Ivantsov & Malakovskaya, 2002; Fedonkin, 2003).

CHAPTER II

SYSTEMATIC PALEONTOLOGY

Repositories.—Specimens are housed at the American Museum of Natural History (AMNH), Amherst College Museum of Natural History (ACM and ACM UC), Geological Survey of Canada, Ottawa, Ontario (GSC), Miller Museum, Queens University (MMQ), Minna Anthony Common Nature Center, Wellesley Island, NY (WINC), New York State Museum, Albany, New York (NYSM), Parc archeologique de la Pointe du Buisson, Melocheville, Quebec (JF), Peabody Museum, Yale University (YPM), Redpath Museum, McGill University (RM), Royal Ontario Museum, Toronto (ROM), Science Museum of Minnesota, Saint Paul (SMM), Smithsonian Institution, Washington D.C. (NMNH), Springfield Science Museum, Springfield, MA (SSM), University of Missouri at Rolla (UMR), University of Wisconsin at Madison (UW).

Morphological terminology.—The terms lateral ridge, transverse bar, furrow, and medial ridge are adopted from Yochelson and Fedonkin (1993). However, we use the terms “resting trace” and “body impression” rather than “oval impression” because the new term more accurately reflects the origin of the trace as the impression of the animal while at rest.

Ichnogenus *Climactichnites* Logan 1860

Type species.—*Climactichnites wilsoni* Logan 1860

Included species.—*Climactichnites youngi* Todd 1882

Emended diagnosis.—A trackway or burrow consisting of undulating bars and furrows oriented at an angle to the direction of travel.

Description.— Transverse bars straight-, sinusoidal-, zipper-, V-, U-, or arch-shaped. Straight bars can be perpendicular to or at an angle to the direction of travel; V- and U-shaped bars usually open in the direction of travel, with a few exceptions. In burrows, and rarely surface traces, the transverse bars often exhibit tuning fork bifurcations. Medial ridge occasionally present within the trackway; can be straight, ovoid, sinusoidal, or irregularly shaped.

Occurrence.— Quartz arenites in Wisconsin (Elk Mound Group), Missouri (Lamotte and Gunter Sandstones), Quebec, Ontario, and New York (Potsdam Group).

Discussion.—Previous diagnoses included the presence of ridges bounding the trackway; however, *Climactichnites* specimens often lack lateral ridges as a result of taphonomy (Fig. 4A, 4B) or of infaunal burrowing behavior (Fig. 4C). Because burrows never have lateral ridges, it is necessary to exclude the ridges as a defining characeristic of the ichnogenus. As a result, two ichnospecies of *Climactichnites* are recognized: *C. wilsoni* for epifaunal trackways in which lateral ridges were produced, and *C. youngi*, in which lateral ridges are absent due to burrowing within the substrate. Trackways in which lateral ridges are absent due to taphonomic processes, such as when lateral ridges remain within the cast of the trackway or are washed away before preservation (Fig. 4A, 4B), are referred to *C. wilsoni*.

Climactichnites has been used twice as the name for traces found outside of North America. *C. mathieui* Sun (1924) was erected for a trackway collected from the Lower Cambrian Manto Shale in Luanchou, China; it was removed from *Climactichnites* by Yochelson and Fedonkin (1993) because the species lacked lateral ridges. *C. youngi*, a burrow, lacks lateral ridges; therefore, the absence of this characteristic alone can not be used to justify removing *C. mathieui* from the ichnogenus. However, *C. mathieui* was preserved as a cast on the sole of an overlying bed and thus the original trace was produced on the bed surface, like *C. wilsoni*. Thus, this trace is unlike surface-produced *C. wilsoni* in lacking lateral ridges (see below). The trackway in question is much smaller (3.5 mm) than even the smallest *Climactichnites* found in North America (1.4 cm) and is found in Lower Cambrian marine shales rather than Upper Cambrian sandstones, as are all North American examples. Thus I remove *C. mathieui* from *Climactichnites* based on morphology, size, geographic, and stratigraphic distribution.

De *et al.* (1994) reported *Climactichnites* from the Early Cambrian Tal Formation of India. This trace is also very narrow (4 mm) and is found in siltstones exhibiting desiccation cracks. Interestingly, Tiwari and Parcha (2006) did not report *Climactichnites* in their study of trace fossils from the Tal Formation, but did list eight other ichnotaxa, six of which are thought to have been made by arthropods. Many of these ichnotaxa have similar widths to the purported material of *Climactichnites* described by De *et al.* (1994) and thus it is possible that the specimen described by De *et al.* (1994) is a preservational variant of the taxa described by Tiwari and Parcha (2006).

As with *C. mathieui*, I remove the traces described by De *et al.* (1994) from *Climactichnites* because of differences in morphology, size, geographic, and stratigraphic distribution. Both *C. mathieui* and the trace described by De *et al.* (1994) likely belong to another ichnogenus having v- or stitch-shaped structures, such as *Gyrochorte*.

Climactichnites wilsoni Logan 1860

Figures 1, 4A, 4B, 5

Climactichnites wilsoni LOGAN 1860, p. 279-295, figs. 1-5; DAWSON 1890, p. 595-618, fig 4.

Climactichnites fosteri TODD 1882, p. 277, pl. 1.

Climactichnites wilsoni WOODWORTH 1903, p. 959-966, fig. 1, pl. A and B; WALCOTT 1912 (in part), p. 259-261, pl. 40, fig. 2, non pl. 40, fig. 1; BURLING 1917, p. 390-397, figs. 4, 5; ABEL 1935, p. 242-249, figs. 214, 215; YOCHELSON AND FEDONKIN 1993 (in part), p. 1-74, frontispiece, figs. 1, 3-5, 7, 8, 10-14, 16, 17-24, 28, 35-43, 45-50, 52, 53-56, non 15, 16, 20, 25-27, 29-34, 44, 51.

Emended diagnosis.—A trackway consisting of lateral ridges between which are undulating transverse bars and furrows.

Description.— Lateral ridges straight, crenulated, or packeted. Transverse bars straight, sinusoidal, V- or U-, zipper-, or double arch-shaped. Straight bars can be perpendicular or at a high angle to the direction of travel; V- and U-shaped bars usually open in the direction of travel, with a few exceptions. Bars occasionally exhibit bifurcation. Intercalcated half-bars may occur. Sub-millimeter wide ovate striations are known only from one specimen on a surface that may have been microbially-bound; they are superimposed on transverse bars and furrows (MacNaughton *et al.* 2003). Medial ridge, which may be straight, ovoid, sinusoidal, or irregularly shaped, occasionally present within the trackway.

Material examined.—ACM 68/1, ACM 68/2, ACM 68/3, ACM UC 232, ACM UC 235, ACM UC 236, ACM UC 242, AMNH 51449, GSC 6299, JF 16 FC, JF 18 FC, MMQ 2380, MMQ 2381, NMNH 532847, NMNH 532849, NMNH 532851, NMNH 532852, NYSM E-3436, NYSM 6, NYSM unnumbered, RM 206837, RM 206840, RM 206841, RM 206843, ROM 22171, SMM-P- 76.21.1 (III-IV), SMM-P- 76.21.1 (39 pieces), SSM 2006/20-1, SSM 2006/20-2, SSM 2006/20-3, SSM 2006/20-4, SSM 2006/20-5, UMR 7283, UW 4019, UW 4020, UW 4021, WINC unnumbered, YPM 150696, YPM 150698, YPM 150699, YPM 150700, YPM 150701, YPM 174721, YPM 174722, YPM 203860, YPM 203874.

Other material examined.—Hundreds of additional trackways were examined in the field (Fig. 2, Table 1).

Discussion.—The trackway's morphology is quite variable due to the complex interactions between the animal and the substrate over which it moved (Fig. 5E). Individual trackways often exhibit multiple transverse bar morphotypes over their length (Fig. 5F) as a result of slightly different foot placement during locomotion, which was dependent on behavior and/or sediment consistency. Plowing activity produced lateral ridges as the animal displaced sediment from in front of the body to the side as it moved across the surface. Crenulated lateral ridges appear only in trackways with low vertical relief (e.g., Fig. 5A, 5C) whereas straight ridges generally occur in trackways with greater relief (Fig. 1, 5B, 5D). Packeted lateral ridges (Fig. 5G) are rare and appear to have been generated by the animal as it moved over a cohesive surface; as the animal moved forward, the cohesion caused the sediment to fold like a like a rug when one drags a foot across it (MacNaughton *et al.* 2003).

Climactichnites youngi Todd 1882

Figures 4C, 6, 7, 8

Climactichnites youngi TODD 1882, p. 276-281, pl.1; DAWSON 1890, p. 595-618; WALCOTT 1912 (in part), p. 259-261, pl. 38, fig. 1, pl. 39, figs. 1, 2, pl. 40, fig. 1; BURLING 1917, p. 390-397, figs. 2, 3; ABEL 1935, p. 242-249, figs. 216; YOCHELSON AND FEDONKIN 1993 (in part), p. 1-74, figs. 15, 16, 31, 32, 44, 51.

Emended diagnosis.—Burrows occurring within beds (may be inclined to and crosscut bedding) or at bed interfaces, consisting of undulating bars and furrows which are often oriented at a high angle to the direction of travel. Lateral ridges absent.

Description.— Transverse bars straight, sinusoidal, V-, U-, or stitch-shaped. Straight bars can be perpendicular or at an angle to the direction of travel; V- and U-shaped bars most often open in the direction of travel. Bars often exhibit bifurcation (Fig. 6B, 6C) and sometimes have backwards-pointing lateral extensions (Fig. 8D). Sub-millimeter- to millimeter-sized linear grooves may be superimposed on the transverse bars and furrows, and are oriented parallel or subparallel to the long axis of the trackway

(Fig. 8C); ovoid striations may also be superimposed atop transverse bars and furrows (Fig. 6C, 6D). The fossil may be composed of a discrete burrow fill (Fig. 7) or may be preserved as a trace on an exposed surface (when excavated; Fig. 8). When present, the burrow fill is elliptical in cross-section, and is thickest in the middle and tapers towards the edges (Fig. 7C).

Types. —Neotypes NMNH 58544, NMNH 58545, NMNH 58546, NMNH 58547 (Fig. 6).

Other Material examined.— ACM UC 237, ACM UC 238, JF 05 FC (Fig. 6, 7).

Discussion.— Several characteristics of *C. youngi* suggest that it was produced as a burrow: 1) it may appear at bedding interfaces as discrete burrow fills, 2) it may be inclined to and crosscut bedding, 3) it may be found within beds when thick beds are split, 4) it is often loaded, deformed, and stretched, and 5) it is never directly associated with surface-produced sedimentary structures such as ripples and raindrop impressions.

C. youngi was erected by Todd (1882) in part to include trackways without lateral ridges. Unfortunately, the type specimens were lost and were not available to Yochelson and Fedonkin when they revised the ichnogenus in 1993. Consequently, these authors examined other slabs to determine the validity of the ichnospecies and, upon examination of trackways on a slab at Amherst College (ACM 68/1), concluded that *C. youngi* should be synonymized with *C. wilsoni* based on their interpretation that lateral ridges were present only intermittently on some of the trackways. Yochelson and Fedonklin (1993) suggested that the presence and absence of lateral ridges was likely the result of variation in sediment consistency and individual trackmaker behavior. There are some cases in which *C. wilsoni* lacks lateral ridges; for example, in some part-counterpart specimens the lateral ridges adhere to the overlying bed (Fig. 4A, 4B), giving the impression that the original trackway lacked ridges. However, even in cases in which *C. wilsoni* lacks lateral ridges it is often possible to determine that they are surface traces because they are associated with raindrops or other surface-produced sedimentary structures (Fig. 4A, 4B). In contrast, *C. youngi* is the result of a fundamentally different locomotive behavior (burrowing) and lacks lateral ridges. The lateral ridges are absent because the body was completely encapsulated by sand and thus sediment was unable to accumulate at the sides of the animal. Therefore, the re-erection of *C. youngi* is warranted.

Other Paleozoic burrows, such as *Plagiogmus* and *Psammichnites*, have transverse bars and therefore share some morphological characteristics with *C. youngi* (Seilacher 1995; McIlroy & Heys 1997). However, *Plagiogmus* is a structurally complex burrow with a bilobed upper surface expression that has not been seen thus far in *C. youngi*. The burrow fill in *Plagiogmus* is quite unlike that of the surrounding rock: it has laminations oriented at 20° to horizontal and is enriched in clay minerals (McIlroy & Heys 1997). *C. youngi* have been found that consist of a burrow fill but they have not been examined petrographically to determine if laminae are present or to quantify any possible difference in lithology to the host rock.

The morphology and lithology of *Plagiogmus* led McIlroy and Heys (1997) to suggest that the burrower fed by sucking up organic-rich detritus from the sea floor by using a snorkel that protruded through the overlying sediment up to the sediment-water interface. The consumed material was then excreted into the burrow where it formed the burrow fill. This feeding strategy is quite different than the one proposed for the *Climactichnites* trackmaker (see below). Transverse bars in *Plagiogmus* are thought to have formed at the posterior of the animal (McIlroy & Heys 1997), whereas in *Climactichnites* the position of transverse bars at the front of body impressions indicate that the bars were produced by a locomotory organ located at the front of the body (see below).

Musculopodus new ichnogenus

Figure 9

Type species.—*Musculopodus sedentarius* by monotypy

Diagnosis.—Ovoid to elongate impressions that are relatively flat in cross-section. Impression is shallow relative to its linear dimensions. In soft substrates, largest dimensions of impression are oriented approximately parallel to bedding.

Etymology.—Latin, *musculus*, muscle, for the muscular foot that likely made this trace.

Occurrence.— Cambrian intertidal to subtidal quartz sandstones in Wisconsin (Elk Mound Group), Missouri (Lamotte and Gunter Sandstones), Quebec, Ontario, and New York (Potsdam Group).

Discussion.— When *Musculopodus* appears with *Climactichnites* the two can be considered a compound trace fossil (Pickerill 1994). However, numerous examples of isolated body impressions occur in New York, Quebec, and Wisconsin. For example, of the 25 *Musculopodus* prints illustrated by Clarke (1905, plate 3), 19 are associated with trackways but six are not. Isolated *Musculopodus* are found on *Climactichnites*-bearing surfaces such as NYSM unnumbered (e.g., Yochelson & Fedonkin 1993, figs. 25 and 27) and ACM 68/2. Other ovate body impressions have been reported in coeval Laurentain sandstones and in Ediacaran deposits (Gehling 1996; Seilacher 1997; Ivantsov & Malakhovskaya, 2002; Stinchcomb personal communication, 2005; Murray Gingras, personal communication, 2006) and merit inclusion within *Musculpodus*.

Musculopodus sedentarius new ichnospecies

Diagnosis.—Elongate to ovoid body impressions. Length to width ratio between 1.9 and 2.7 to 1. Impressions are shallow relative to their linear dimensions. When produced in soft substrates, largest dimensions of impressions are oriented parallel or subparallel to bedding.

Description.— Impressions may be associated with *C. wilsoni* (Fig. 9A, 9B) or *C. youngi* (Fig. 6D, 9D, 9E) or may be isolated (Fig. 9C). Lateral ridges of sediment may be present at the edges of impressions on bed surfaces (Fig. 9B). The anterior portion of the impression (see discussion below for determining the orientation of isolated body impressions), when present, may have subtriangular and anteriorly directed projections whereas the rear of the impression is generally rounded (Fig. 9A). The interior of the impression is typically smooth but may have transverse bars at its anterior end (Fig. 9B) or along its sides (Fig. 9E, 9F) and/or ovoid lineations superimposed on top of it (Fig. 6C, 6D, 9E, F). One specimen (Fig. 9E, F) has a ruffled to wavy margin surrounding an ovate, raised and striated region.

The impression is not always complete. In some cases where *Climactichnites* is associated with *Musculopodus*, the anterior portion of the impression is missing (Fig. 6D, 9D). Portions of isolated impressions may be missing as well (Fig. 9C).

Etymology.—Latin, *sedentarius*, sedentary, for the presumed habit of the animal during production of the trace.

Types.— NYSM unnumbered-1-1 and NYSM unnumbered-1-2.

Other material examined.— ACM 68/2, ACM UC 239, JF 20 FC , NMNH 58544

Occurrence.— Cambrian quartz arenites in Wisconsin (Elk Mound Group), Missouri (Lamotte and Gunter Sandstones), Quebec (Napean Formation), Ontario (Napean Formation), and New York (Potsdam Sandstone).

Discussion. —Orientation of *M. sedentarius* may be determined when the impression is associated with *Climactichnites*, because all known trackways and burrows extend away from the sedentary impression (Clark & Usher 1948; Yochelson & Fedonkin 1993; this study). When found in isolation it is difficult to determine orientation, but orientation may be inferred based on the shape of the margins of the impression. The ovate terminations of some incomplete impressions (e.g., Fig. 9C) may represent the posterior of the body because it is the posterior of the complete specimens that is typically round. The criteria for determining the orientation of isolated, partial specimens outlined above is only valid for those specimens found in deposits in which *Climactichnites* has been found. New criteria may be needed for additional species as they are added to the ichnogenus.

The amount of morphological detail is variable in *M. sedentarius* and is likely the result of where the impression was produced. Impressions found on bedding planes and associated with *C. wilsoni* only show gross morphological detail and are for the most part smooth on the inside (e.g., Fig. 9A, 9C). In contrast, *M. sedentarius* that were produced below the surface and are associated with *C. youngi* show millimeter to sub-millimeter striations (Fig. 6D, 9D) or ruffles (Fig. 9E), as do *C. youngi*. The production of *C. youngi* and associated *M. sedentarius* below the surface permanently protected these traces from erosion and permitted fine morphological details, which are the result of interactions of the (mucus-producing?) foot and substrate, to be preserved.

CHAPTER III

PALEOBIOLOGY OF THE *CLIMACTICHNITES* TRACKMAKER

Methods

Thousands of trackways were examined in the field and hundreds more in museum collections. From this large sample, two hundred ninety-six well-preserved trackways (including lateral ridges, transverse bars, and furrows) were examined in detail, with as many as twelve measurements being recorded from each trackway. Quantitative measurements (Fig. 10) included inner and outer track width, transverse bar height and wavelength, and lateral ridge height. Qualitative track observations include lateral ridge shape, transverse bar completeness, transverse bar shape, transverse bar cross-sectional shape, presence or absence of intercalcated bars, presence or absence of a medial ridge, and cross cutting relationships with sedimentary structures and other trace fossils. Hundreds of additional trackways were examined in the field for only a few of these parameters because of poor preservation. Topographic profiles of trackways were generated by placing a carpenter's contour gauge over the trackway; the resulting profile was then traced onto paper for study. Finally, maximum length, maximum width, and maximum depth were measured from body impressions.

Some trackways were serially sectioned both longitudinally and perpendicular to the long axis of the trackway to look for disrupted bedding. Slab thicknesses ranged between 4.4 and 13.6 mm. These trackways were examined visually and with Xradiography. X-ray imaging was conducted at the University of Massachusetts Health Services and slabs were exposed at 60kv and 5 mA.

Experimental trackways were produced by the gastropod *Viviparus intertextus*, which were collected from local ponds and placed in a plastic container measuring 65 x 46 x 8 cm. The container was partly filled with medium- to coarse-grained sand (Table 2), which was sculpted into a hill and valley with a slope of 8º. The topography permitted the snails to rest in pooled water so that they would not dehydrate from prolonged periods of subaerial track production (*V. intertextus* is normally aquatic; however, the snails did move subaerially). After the trackways were produced the snails were removed from the apparatus and the trackways were allowed to remain exposed for approximately 40 minutes to 1 hour. Then the tank was filled with water to simulate incoming tides. The effects of the simulated tides on the *V. intertextus* trackways were then recorded.

Museum specimens were examined at 15 institutions, whose abbreviations can be found in the "List of Abbreviations" section above. Field specimens were examined in New York, Quebec, Ontario, Wisconsin, and Missouri (Fig. 2; Table 1).

Paleoenvironmental Context

Climactichnites is restricted to fine- to coarse-grained Late Cambrian marginal marine sandstones of North America (Fig. 11), including the Elk Mound Group of Wisconsin, the Potsdam Group of New York, Quebec, and Ontario, and Lamotte and Gunter Sandstones of Missouri (Logan 1860; Todd 1882; Hall 1889; Walcott 1912; Summerson 1951; Stinchcomb 1997; Fig. 2). These formations are of mixed terrestrial and marine origin, with marine deposits recording intertidal and shallow subtidal facies (Selleck 1975; Houseknecht & Ethridge 1978; Dott *et al.* 1986; Runkel *et al.* 1998).

During the Late Cambrian the Laurentian craton straddled the equator, with present day Canada to the east of what is now the United States (Dott & Batten 1981). Most of the United States was submerged beneath an epeiric sea while Canada and Greenland had considerable topographic highs. Portions of Missouri formed a peninsula that extended southeast to northwest from a north-south-running shoreline that roughly paralleled the present day boundaries between the United States and Canada. Wisconsin and the St. Lawrence lowlands of New York, Quebec, and Ontario were oriented along the north-south trending shoreline at this time.

The sea was very shallow, with an estimated depth of no more than 100 m and a slope of about 0.1 m/km (Byers & Dott 1995; Runkel *et al.* 1998). Palmer (1971) proposed three marine depositional environments that graded into each other as the water gradually deepened to the west (the current continental United States): an inner detrital belt consisting of siliciclastic sediments, a middle detrital belt in which carbonates were deposited, and an outer detrital belt where fine-grained sediments were deposited. The sea provided considerable moisture to the continent and Dott *et al.* (1986) proposed that, during the deposition of the Mt. Simon sandstone in Wisconsin (the lowermost unit in the Elk Mound Group), the climate was humid due to the inferred location of the area near the equator and along a tropical trade-winds belt. Houseknecht (1975) proposed that the climate in Missouri during the deposition of the Lamotte was also humid due to the intensely weathered nature of feldspar grains in the sandstone. He also noted the presence of laterally extensive longitudinal bar deposits in the braided fluvial facies, which indicate a constant source of water. It seems plausible that a humid climate also prevailed in the New York-Quebec-Ontario region.

In spite of the humid climate, the terrestrial realm was probably devoid of vegetation at this time, permitting sand seas to develop over large portions of the Laurentian continent (Horodyski & Knauth 1994; Eriksson *et al.* 1998; Prave 2002). Thus, detritus was relatively unhindered in its transport to the sea and large quantities of sand were moved via wind and water from the continent and deposited in nearshore environments. Extensive microbial mats existed in portions of the intertidal zone as is evidenced by numerous sedimentary structures found in these environments, including sand chips, sand roll-ups, exfoliating sand laminae, old elephant skin, domal build-ups, and patchy ripples (Hilowle *et al.* 2000; Donaldson & Chiarenzelli 2004; York *et al.* 2005; Getty & Hagadorn 2006; Hagadorn & Belt in press). *Climactichnites* occasionally occurs with domal build-ups on erosionally resistant surfaces. It has been suggested that biofilms may have mediated the preservation of the trackways and may have served as a food source for the trackmaker (Seilacher 1997; York *et al.* 2005; Getty & Hagadorn 2006).

Beds on which *Climactichnites* is found exhibit numerous sedimentary structures suggesting that the animal inhabited an intertidal environment. For example, in the Lamotte Sandstone, Summerson (1951) described a *Climactichnites*-bearing slab exhibiting cross-bedding, whereas a slab described by Stinchcomb (1997) exhibits ripples, poorly defined cross-beds, and small channels in cross section. Slabs built into a gate at the entrance to Columbia Park, in Park Hills, MO exhibit small trackways imprinted on round crested ripples. More recently, Hagadorn and Belt (in press) identified small zones of emergent tidal flat facies preserving polygonal desiccation cracks, flat-topped ladder-back ripples, adhesion structures, and oscillation ripples in the Potsdam Sandstone in the Au Sable area of northeast New York that bound beds preserving *Climactichnites*. In Wisconsin, *Climactichnites* is found in beds that preserve sedimentary structures, such as polygonal desiccation cracks, gas escape structures, and raindrop imprints that indicate intermittent subaerial exposure for the beds on which the animal crawled (see below). Thus the trackmaker inhabited a shallow marine environment that was intermittently subjected to subaerial exposure.

What did the *Climactichnites* trackmaker look like?

Body impressions of the trackmaker, which indicate the shape of the animal at rest, are roughly bilaterally symmetric and elongate and have a semicircular posterior (Fig. 9, 12A, 12B, 15A). Laterally, the sides of the body were roughly parallel to each other unless the animal was contracting or expanding the foot. While at rest the animal often extended one side of its anterior margin as a broad flap that tapered distally (e.g. Yochelson & Fedonkin 1993, figs. 20 & 26). The ventral portion of the anterior of the animal was capable of being extended in many ways, as can be determined from the wide variety of irregularly shaped partial transverse bars at the beginning of trackways (Fig. 15A). Had the foot been more rigid the morphology of the resultant transverse bars would be more conservative; that is, there would be fewer bar types (Woodworth 1903). Fine striations produced at the rear of the animal that are superimposed over the transverse bars and furrows indicate that, unlike the front of the foot, the rear of the animal retained a constant arcuate shape during locomotion (Fig. 6D, 12B). It is unclear how the ovate striations, as well as the linear striations (Figs. 6D, 6.E) that appear on some of the infaunal burrows were produced. If in fact the trackmaker was a stem-group mollusk (see below) it is possible that linear striations were produced by a series of sclerites on the dorsal and lateral parts of the body.

The animal was dorsoventrally flattened based on evidence from both burrows and surface trackways. For example, on slab JF 05 FC, a burrow 11.4 cm wide has a vertical thickness of only 1.5 cm, or approximately 13% of the track width (Fig. 12C). Although this burrow likely underwent compression during diagenesis, it demonstrates that the animal was at least 1.5 cm tall. More accurate estimates of the trackmaker's height cannot be determined without observing crosscutting relationships of intrastratal trackways with overlying sedimentary structures. Large animals must have been at least 2-3 cm tall because trackways excavated by the animal to this depth do not have sediment collapsing back into the trackway from above; that is, they are not burrows. Most of the sediment was excavated to the side and piled into lateral ridges. One trackway at PRI-

100-8.22 is 20 cm wide and 2.5 cm deep (Fig. 12D). If the trace were produced as a burrow, sediment displaced by the animal would have refilled the space left by the burrower. However, this is not the case, as sediment was piled to the sides of the trackmaker into tall lateral ridges, indicating that the trace was made on the surface. The ridges are unusually large: they are up to 6 cm wide and 0.5 cm high. In comparison, other, shallower (~0.5 cm deep) trackways of similar width occur on this surface and have lateral ridges up to 3 cm wide and 0.5 cm high (Fig. 12D). The depth of the trackway, 2.5 cm (or about 13% of the trackway width), is a minimum estimate of this trackmaker's height. Thus, data from both trackways and burrows suggest that the *Climactichnites* animal was relatively squat, with a height roughly 10-15% of its width.

The ventral surface of the animal was muscular and flexible. Individual trackways appear uniformly wide but upon closer inspection nearly all trackways are slightly variable in width; some vary considerably in width over short distances. Thus the sole of the foot was capable of lateral expansion and contraction. For example, a trackway only 34 cm long on slab T-302 from PRI-100 decreases in width from 8.7 to 7.3 cm along its length (Fig. 12E). Additionally, on RM 206837 a trackway decreases in width from 17.1 to 15.5 cm (Yochelson & Fedonkin 1993, figs. 48 & 55) in a distance of only 12.3 cm, which is less than the inferred body length of 36 cm (determined from length to width ratios calculated from body impressions; see below).

The variation in transverse bar morphology within trackways also indicates that the sole of the foot of the *Climactichnites* trackmaker was flexible (Todd 1882; Burling 1917; Yochelson & Fedonkin 1993; this study); a stiff foot would have been able to produce one or at most a few of the wide variety of bar morphologies seen in individual trackways (Woodworth 1903). Yochelson and Fedonkin (1993) noted that the symmetric, V-shaped bars that are depicted in many illustrations are rare. Often, the bars are asymmetric in shape, with one side of the V much longer than the other; the sides are usually offset slightly at the V's apex (Fig. 12 E, 12F). Additional bar morphotypes include straight bars (both at an angle and perpendicular to lateral ridges), U- or arch-shaped bars, stitched bars, and sinusoidal bars (Todd 1882; Burling 1917; this study). In a few cases bars point in the direction of travel, but this is very rare. More typically, the V- and U-shaped bars open up in the direction of travel (Clark & Usher 1948). The transverse bar shape within a trackway can change with a single advance of the foot (Fig. 12F), and individual trackways often exhibit multiple bar morphologies along their lengths. Offset V's and the insertion of partial transverse bars indicate that the animal was capable of alternate left-right motions of the body (Todd 1882). Bar bifurcation occurs as well, usually in association with intrastratal trackways (Figure 12G), further illustrating the pliability of the foot.

Additional evidence for the soft-bodied nature of the foot of the *Climactichnites* trackmaker comes from turning trackways. Within these trackways the posterior end of the trackmaker's foot does not swing outside portions of the trackway made by the anterior of the foot (Yochelson & Fedonkin 1993). This indicates that the trackmaker could flex its foot tightly to the side and contrasts with the trackways of hard-shelled arthropods, such as limulids, whose telson swings to the side of the legs during tight turns, leaving a tail drag outside the trackway (e.g., Malz 1964, figs. 12 and 15; Barthel *et al.*, 1990, figs. 5.5 and 7.35).

Morphological features of *Climactichnites*, such as the smoothness of the trackway and the fine striations, suggest that the trackmaker may have had mucus-secreting glands and/or a ciliated foot. Experiments with *V. intertextus* (Getty & Hagadorn 2006) showed that the mucus secretions produced by the snails smoothed the sediment over which they crawled, a feature that is common in *Climactichnites* (Yochelson & Fedonkin 1990, 1993). The fine striations, such as those on NMNH 58544, 58545, and 532848, could also have been made by mucus secretions in which sand was entrained. Longitudinal striations were originally interpreted as drag marks produced by bristles along the ventral surface of the animal (Todd 1882; Walcott 1912; Burling 1917). Yochelson and Fedonkin (1993), however, suggested that the striations were the result of cilia brushing sand forward as the animal fed on microbes within the sediment. It is also possible that the striations result from the mucus band being corrugated by beating cilia as it was shed off of the rear of the animal.

Based on the presence of a purple stain on the lateral ridges and transverse bars of trackways from Battersea, Ontario (MMQ 2380 and 2381), Yochelson and Fedonkin (1990, 1993) proposed that the *Climactichnites*-trackmaker produced copious amounts of mucus during locomotion. The stain was interpreted as the degradation byproduct of the mucus. However, the stain appears on other parts of the slab and in these areas is unassociated with trackways. It is unlikely that the animal would have secreted large amounts of mucus to cover these surfaces and it is therefore unclear if the stain in fact represents the byproduct of mucus or an inorganic diagenetic process.

There is no evidence indicating the presence of a ventrally oriented mouth, as was proposed by Yochelson and Fedonkin (1993) based on circular structures on some slabs.

The structure on NMNH 532847 (Yochelson & Fedonkin 1993, fig. 34) is not associated with a resting trace or a trackway and cannot be confidently interpreted as having been made by the *Climactichnites* animal. Rather, the concentric rings of sediment are on a rough, slightly ripple marked surface between trackways and are similar to a collapsed sand volcano. Water-saturated sand probably flowed onto the surface in successive pulses, creating the concentric circles. The presence of other sand volcanoes on this surface, and on horizons at locality PRI-100 supports this interpretation. Yochelson and Fedonkin (1993) also suggested that the mouth produced circular structures within trackways on AMNH 51449 and MPM 28389; however, circular structures also occur outside of the trackways on these surfaces, suggesting that the structures may have been made by sedimentary processes acting over the whole surface.

Neither is there evidence for lateral flaps of musculature, which Yochelson and Fedonkin (1993) suggested were responsible for the production of lateral ridges. Had muscular flaps pulled sediment in towards the animal to produce the lateral ridges, any sedimentary structures to the sides of the animal would be disrupted. However, this is not the case. On slabs where trackways crosscut sedimentary structures, including other trackways, the boundary between the structures is sharp (e.g. Malz 1968, fig. 1; Fig. 1). Lateral ridges were generated by sediment that was pushed outward and laterally as the animal moved forward. This interpretation is supported by observations made from cross sectional profiles of trackways of uneven depth, in which the deeper side of the trackway had taller lateral ridges than the shallow side (Fig. 13A, 13B). A preliminary plot of trackway depth vs. lateral ridge height (Fig. 13C) also shows a slight increase in lateral ridge height as trackway depth increases, also suggesting that sediment was excavated from in front of and beneath the animal to produce the ridges.

Did the trackmaker grow allometrically?

There is evidence to suggest that the animal may have grown allometrically. Examination of 181 trackways of different sizes demonstrates that large trackways are not simply larger versions of small trackways; the proportions of trackway features change as the trackway increases in width. Relative to trackway width, the wavelength between transverse bars is much greater in small trackways than it is in large trackways (Fig. 14A-C). As trackways increase in width the wavelength increases at a much slower rate (Fig. 14D). It is possible that during growth the pedal musculature grew more slowly than the rest of the body.

What type of animal was the trackmaker?

Yochelson and Fedonkin (1993) rejected the possibility that arthropods, worms, and mollusks could have produced *Climactichnites* and instead suggested that the trackmaker was a member of a completely extinct phylum of animals with lateral flaps used in locomotion. The presence of lateral flaps was inferred from the regularly spaced crenulations seen in some trackways. New observations indicate that the animal did not have lateral flaps and that the lateral ridges are mounds of sediment pushed out from around the muscular foot of the animal. Additionally, crenulations may be seen in the lateral ridges of modern gastropod trackways (e.g. Brown 1971, fig. 1). In fact, there are no characteristics that can be inferred for the *Climactichnites* trackmaker that would indicate a completely unique morphology deserving of a new phylum. We are left with an elongate, bilaterally symmetric, dorsoventrally flattened animal with a soft, muscular foot.

The characteristics listed above are common in extant gastropods and are found in Ediacaran and Cambrian soft-bodied mollusks or mollusk-like animals (Runnegar *et al.* 1979; Conway Morris 1985; Conway Morris & Peel 1990; Fedonkin & Waggoner 1997; Vinther & Nielsen 2005; Stinchcomb & Angeli 2002; Caron *et al.* 2006; Conway Morris & Caron 2007). Among these, *Kimberella* and *Odontogriphus* reached the widths of small- to medium-sized *Climactichnites* trackways and had a similar body shape (Fedonkin & Waggoner 1997; Caron *et al.* 2006). It is possible that a large, related form evolved to inhabit marginal marine sand flats during the Late Cambrian and produced *Climactichnites*.

Additional evidence supporting a molluscan trackmaker comes from extant gastropods, many of which produce *Climactichnites*-like trackways (Fig. 3). *Bullia digitalis, Bullia rhodostoma*, *Hydrobia ulvae*, *Littorina littorea*, *Lunatia heros* and *Polinices duplicatus*, which live in intertidal settings, produce trackways with lateral ridges and transverse bars (Raymond 1922; Abel 1935; Häntzschel 1938; Gräff 1956; Brown 1971; Schäfer 1972; Trueman & Brown 1976; Knox & Miller 1985). These animals produce lateral ridges by displacing sand with their muscular foot; both Abel (1935) and Brown (1971) figured crenulated lateral ridges in *Bullia* trackways.

The mechanisms by which these gastropods produce the transverse bars, however, are poorly understood. According to Raymond (1922), *L. littorea* produces transverse bars by bulldozing sediment in front of the foot as it advances forward, thus building a ridge over which the body then moves. In contrast, Schäfer (1972) suggested that *L. littorea* produces transverse bars as the shell and visceral mass of the animal are suddenly pulled forward over the advancing foot. The additional weight of the shell on top of the foot depresses it into the substrate before it is extended again, creating depressions at regular intervals. *L. heros* and *H. ulvae* trackways also contain transverse bars, but it is unknown how they are produced (Raymond 1922; Schäfer 1972). Neither author indicated how the transverse bars were formed. The gastropods *B. digitalis*, *B. rhodostoma*, and *P. duplicatus* produce transverse bars and furrows by extending the foot, which then anchors to the substrate while the animal is pulled forward by the contraction of pedal musculature (Brown 1971; Trueman & Brown 1976; Knox & Miller 1985). Thus these gastropods produce trackways in a manner similar to that inferred for the *Climactichnites* trackmaker (see below).

How big was the animal?

Because the inner width of trackways corresponds closely with the width of body impressions, trackways of relatively constant width may be used as a proxy for the body size of the trackmaker (Fig. 15A). In addition, because there is a rough correlation of length to width of body impressions, with an average length to width ratio of approximately 2.3 to 1 (Fig. 15B), it is possible to estimate how long the trackmaker's body was. Figure 6C shows the inner widths of 296 *C. wilsoni*, and thus offers a rough indication of the size of the animals that made the trackways. The widths fall into an approximately normal distribution with most trackways between 2 and 18 cm wide. The smallest trackway, on SSM 2006/20-1 (Fig. 6C), is only 1.4 cm wide, suggesting a body length of 3.2 cm. The largest trackway, on JF 16 FC, has a variable width from 23 cm to 29 cm and the animal was possibly as long as 53 to 67 cm (Fig. 15C, 15D). No other Cambrian or Neoproterozoic trace fossils reach this size (but see Baldwin 1977). The size of this trackway indicates that rarely the *Climactichnites* trackmaker attained much larger sizes than previously thought.

The range in size for *C. youngi*, which represents the burrowing habit of the trackmaker, is also quite large. The smallest trackways are around 1.8 cm wide whereas the largest are 15 cm wide or more (Fig. 16), and yield body lengths of 4.1 to 34.5 cm. Comparison of the size ranges for *C. wilsoni* and *C. youngi* might suggest that infaunal burrowers were smaller than epifaunal ones. However, due to the variability in width, overlapping nature of some of these trackways, and lack of bounding ridges, it is more difficult to determine the size of animals from burrows. Additionally, some *C. youngi* are incomplete or highly irregular (e.g. Fig. 15E), with some having fine backwards-oriented striations at the sides of the burrow.

There are very few small *C. wilsoni*; only 16 trackways are less than 3 cm wide. Small trackways are occasionally found individually among much larger trackways (Fig. 15F), but two bedding planes, PRI-100-6.5 and PRI-101 from Wisconsin exhibit large numbers of trackways of small individuals, as do loose slabs from New York and Quebec (Fig. 15G). Conspicuously, large trackways are absent from these surfaces.

Grain sizes for 61 distinct bedding planes and slabs containing large *C. wilsoni* (> 6 cm width) and 8 beds containing small- to medium-sized *C. wilsoni* were examined. Twenty-six of the beds, over 80%, with large *Climactichnites* consisted of coarse or medium sand and twenty-three beds, less than 20%, had a dominant lithology of fine sand. In contrast, five beds (63%) containing small- to medium-sized trackways were composed of medium sand and three beds (~37%) consisted of fine sand; none of the beds had a considerable quantity of coarse sand (Fig. 11). Thus, it appears that large trackmakers were not restricted to beds of certain grain sizes, but that small trackmakers were. It is evident that small trackmakers inhabited the same beds as large individuals (Fig. 15F); therefore it is unlikely that the restriction of small trackways to beds of fine and medium sand represents an actual habitat restriction or taphonomic bias. Rather, it is likely that sediment grain size played a considerable role in the generation of *Climactichnites*, with small animals being unable to produce trackways in coarse sand, even though they may have inhabited coarse-grained beds. This hypothesis is supported by observations made by Brown (1971), who noted that small individuals of the gastropod *Bullia rhodostoma* produced trackways in fine sand but had considerable difficulty producing trackways in coarse sand. In contrast, larger *B. rhodostoma* were not hindered by grain size during trackway production.

Another variable that probably influenced the production of *Climactichnites*, and therefore the size distribution of trackways, was the relative water content of the sand. Sand is more cohesive, and thus more difficult to sculpt, when it has minor amounts of interstitial liquid, such as water (Hornbaker *et al.* 1997; Tegzes *et al.* 1999, 2003; Schiffer 2005). When saturated, water lubricates the grains and allows them to flow past one another (Tegzes *et al.* 1999, 2003). Small animals, therefore, would be more likely to produce trackways in the sand as water content increased. Presumably, larger individuals would have been less hindered by the water content of the sand. Thus, if the animal moved about on exposed, partly dry tidal flats (see below) it is more likely that large animals would have produced trackways while small animals would not.

As a consequence of the variables outlined above, the number of small trackways in Figure 14 probably reflects the relative abundance of individuals that were able to produce trackways more than it reflects the relative abundance of small individuals in populations of *Climactichnites* trackmakers. In contrast, the number of large trackways is probably more reflective of the size distribution of the number of individuals of that size in actual populations.

Although grain size and sediment saturation clearly influenced the distribution of small *Climactichnites*, this mechanism is insufficient to completely explain the selective distribution of larger trackways. Some bedding planes that preserve *Climactichnites* only show slight variation in trackway width (Fig. 17). Thus, medium-sized trackways appear with medium-sized trackways and large trackways appear with other large trackways (e.g. Figs. 12A, 15G, 20A, 22). It is possible that populations of the trackmaker at any given locality were size and/or age dependent, thus accounting for the small variation in width. Alternatively, populations may have been sexually dimorphic, with the sexes inhabiting different areas. Yet other possibilities are that the same animal or only a few animals may have produced multiple trackways on the same surface or that these surfaces were exposed to some type of environmental gradient that may have restricted the size range of animals that inhabited the locality.

How did the animal move?

Locomotion of the *Climactichnites* trackmaker must be inferred from a combination of features observed in numerous specimens. The position of transverse bars at the front of *Musculopodus* body impressions indicates that locomotion was initiated at the front end of the trackmaker's body (Figs. 12A, 12B, 15A). The anterior portion of the foot advanced forward, possibly through contraction of a hydrostatic skeleton, and dug into the sand to obtain purchase. Clamping the foot into the sand generated furrows. After the foot clamped onto the sand, contraction of the foot pulled the body forward. Transverse bars were produced as sediment was compressed between the anterior part of the foot and the advancing body. Muscular contractions may have moved posteriorly over the entire foot based on lightly impressed, partial bars along the lateral margins on several body impressions, or these structures may have been made by the lateral margins of the body independently of locomotive contractions (Fig. 12A). The rear of the animal glided over the transverse bars, sculpting them into a dune-like shape (Yochelson & Fedonkin 1993) with a steep slope directed anteriorly and a shallow slope toward the rear (Fig. 10, inset). Often, before locomotion commenced one half of the foot was extended and the side opposite it was advanced in multiple steps until it "caught up" with the extended side, thus producing half bars next to the extended portion of the resting trace (Fig. 15A). Once the trailing side caught up, locomotion commenced. Half-bars were also inserted on one side of the trackway when that side of the animal lagged behind the other side; by taking partial steps that produced partial bars the trailing portion of the foot caught up with the opposite side. Most often, the animal extended sides of the body in an alternating fashion; while one side of the foot was in motion the other was clamped onto the substrate.

The locomotive process presented here is similar to that inferred by Yochelson and Fedonkin (1993, fig. 57), except that the animal did not have lateral flaps. Two strides (defined as the movements that produce a single complete set of transverse bars) of the trackmaker are illustrated in Figure 18, beginning with the animal at rest (Fig. 18A), with the right anterior of the foot extended. The animal subsequently extended the left half of the anterior of the foot until it was next to the right side (Fig. 18B), and clamped it onto the surface, producing a partial transverse bar. The left portion of the foot was extended again until it reached beyond the right side (Fig. 18C), and again clamped into the substrate. After the left side of the foot had fully extended and obtained purchase in the sand, the right side of the foot was advanced and then clamped into the sand next to the left side to complete the first stride (Fig. 18D). Thus, a complete transverse bar was produced. The second stride, resulting in a second full transverse bar, was completed by alternately extending the left side of the foot (Fig. 18E), which then clamped into the substrate, and then the right side (Fig. 18F).

Each transverse bar shape reveals how the foot was emplaced at the time contraction occurred. Contraction could be monotaxic, meaning that the entire front of the animal was advanced as a unit, or ditaxic, indicating that the animal moved by alternately extending the left and right sides (e.g. Fig. 18). Monotaxic locomotion is indicated by single arched, straight, crescentic, U-shaped, and some V-shaped bars, whereas ditaxic locomotion is indicated by double-arched, multi-crescentic, some V-shaped, zipper-shaped, sinusoidal, and half bars (Fig. 5). Multiple bar morphologies could be produced in short distances, indicating that foot morphology could be rapidly changed (Fig. 12F). Partial bars on the sides of the trackway separated by undisturbed areas might indicate that only the lateral edges of the foot were used, or might indicate that sediment consistency was not conducive to bar formation or preservation (Yochelson & Fedonkin 1993, fig. 52). However, the latter seems unlikely over such short distances. Because some trackways narrow and end just after the bars become incomplete (Yochelson & Fedonkin 1993, fig. 54) it is possible that the animal may have subsequently engaged in a different behavior that altered the morphology of the trackway.

Most trackways meander slightly (e.g. Summerson 1951, fig. 1) whereas a few show abrupt turns (Clark & Usher 1948). Of 28 turning trackways examined in this study (e.g. Fig. 15D, 19A, 19B, 19D), in 26 trackways the transverse bars on the outside of the turn have a greater wavelength than the transverse bars on the inside of the turn (Table 3), suggesting that when the trackmaker made turns it often extended the side of the foot on the outside of the turn more than the side of the foot that was turning. The portion of the foot on the turning side advanced only slightly and the transverse bars on the turning side were positioned close together. When the animal turned tighter the wavelength between transverse bars on the outside of the turn increased correspondingly. Greater extension on the opposite side of the turn coincides with the slightly longer distance that the outer portion of the foot had to travel while the animal turned.

Lateral ridge height and trackway width also vary during turns. Lateral ridges on the outside of turning trackways are sometimes taller than those on the inside of the turn because the animal dug in more on the outside of the turn (Fig. 13A, 19A). For example, as an animal made a 90° turn to the right on UW 4019, it held the right side in place while the left side of the body turned; the entire body narrowed around the turn (Fig. 19B). The large trackway on JF 16 FC shows the opposite trend; the trackway widened as the animal executed a hairpin turn with an internal radius of only 6.5 cm (Fig. 15D).

In some cases where the animal traversed a surface perpendicular to sharp-crested oscillation ripples, the animal modified the ripples into transverse bars. The animal also used the transverse bars of previously made trackways in making its own tracks (Fig. 19C). In one spectacular example of a turning animal crossing an oscillation ripple marked surface, an animal that produced a trackway on NYSM unnumbered greatly extended the foot on the outside of the turn in order to anchor the foot onto the ripples (Fig. 19D). Thus, the animal selectively used sedimentary structures to aid in locomotion.

The *Climactichnites* animal burrowed below the surface, creating *C. youngi* trails with morphology distinct from surface trackways (Figs. 6, 7, 8, 12B, 12G, 15E, 20). Subsurface trails lack lateral ridges and the transverse bars show considerable morphological variability: the transverse bars often bifurcate and have lateral extensions pointing to the rear that decrease significantly in wavelength and amplitude (Fig. 15E, upper left portion of trace). Despite the lack of lateral ridges, the trackways show distinct boundaries, which are smoother than the surrounding matrix (Figs. 12G, 15E). Burrows may have a more irregular outline than surface traces (e.g. Fig. 15E), suggesting that, when burrowing beneath the sediment surface, the animal often increased and decreased the width of the foot in irregular intervals.

What did the animal eat?

The reinterpretation of the supposed mouth impressions and lateral ridges as outlined above suggests that the animal must have employed another feeding mechanism than the one proposed by Yochelson and Fedonkin (1993). Seilacher-Drexler and Seilacher (1999) hypothesized that *Climactichnites* was made by an epibenthic mollusk that grazed on microbial mats. In their view, the presence of the mollusk feeding trace *Radulichnus* in deposits of similar age in Saudi Arabia suggested that similar animals could have been responsible for both *Radulichnus* and *Climactichnites*. In addition, body impressions similar to *Musculopodus* (the impression left by the *Climactichnites* trackmaker when at rest) have been found associated with *Radulichnus* in Neoproterozoic deposits of Australia and Russia (Gehling 1996; Seilacher 1997; Fedonkin 2003). If *Climactichnites* were made by a mollusk, then the animal would have had a radula; however *Radulichnus* has not been found associated with *Climactichnites*.

It is possible that some trackways may represent grazing behavior. For example, on PRI-100-6.5 (Fig. 21), the trackways are of similar width (~6.0-6.6 cm) and appear to show the same looping pattern: the animal(s) first traversed the substrate, which is covered with domal sand build-ups (a.k.a. sand stromatolites), at approximately 70-75°. The trackmaker(s) then took a sharp turn to their right and proceeded at about 110°. One animal clearly looped to the left and continued at 290°; the other trackmaker may have turned to the left too, but the portion where the turn would be is covered. The second trackway appears to then traverse the slab at 290°, as the first trackway does. The similar size and pattern of locomotion of these two trackways suggests that the same animal might have made them. Alternatively, similarly sized individuals could have made them. Regardless of whether these trackways represent one or two animals, their complex, yet similar directional pattern suggests some sort of systematic behavior, and their presence on a surface covered with suspect-microbial structures suggests that the animal(s) could have been grazing on microbial mats.

Elsewhere, trackways have been observed following the ripple troughs. For example, at PRI-100-9.54 (Fig. 22), 23 of 62 trackways are found exclusively within troughs and segments of 29 others are within the troughs. Only 10 trackways on this surface cross ripples without moving in the troughs. The preferred direction of travel by the animals through the troughs of the ripples may be the result of the animals feeding on material that was growing in or was deposited within the troughs.

Rarely, medial ridges occur within trackways (e.g. Logan 1860, figs. 1, 3, 4, 5; Fig. 23). Yochelson and Fedonkin (1993) proposed that the ridges were the remnants of fecal strands that the animal excreted as it grazed. If the medial ridge is a fecal strand then the animal must have consumed large quantities of sand along with its food. However, other researchers have suggested different origins for the ridge. For example, Woodworth (1903) suggested that the ridge was formed by a fold on the bottom of the animal’s foot.

To test the hypothesis that the medial ridge represents a fecal strand we serially sectioned a ridge-bearing *Climactichnites* perpendicular and parallel to the long axis of the trace (Fig. 23). This ridge was selected for study because it had a tight sinusoidal shape (Fig. 23A), was clearly distinct from the transverse bars, and was from a part-counterpart specimen in which the layer that buried the trackway was also preserved. When viewed in cross section the trackway cuts through a laminated bed; however, the medial ridge lacks the well-developed laminations that are present immediately below it (Fig. 23B, 23C). The ridge is less compact than and contains slightly smaller grains than the underlying laminated bed. Like the upper portions of the laminated bed, the ridge has higher concentrations of mud, hematite, and limonite. The ridge is not enriched in organic matter.

Some of the observed features are consistent with the hypothesis that this medial ridge is a fecal strand. For example, the sinuous shape of the ridge is consistent with a coherent string of material being excreted. Additionally, if the ridge were the result of an inward fold on the sole of the animal's foot one would expect laminations to be present, but in a deformed state. However, laminae are absent and the sediment appears to represent a homogenized mixture of grains in adjacent laminae. It is difficult to explain the mixing of sediment, the lack of laminae, and the sinusoidal shape of the ridge as the result of a sulcus on the sole of the foot. It is also possible that the medial ridge in question is the lateral ridge of one trackway that is partly superimposed on top of another trackway, as is the case in some other trackways (e.g. Fig. 19C). However, this explanation does not easily account for the distinctive shape of the studied ridge, and no other trackways that may have interfered with it are preserved.

Many animals that graze algae or eat organic detritus consume sand and silt from the uppermost layers of the bed on which they are feeding (Schäfer 1972). Thus it is possible to envision, based on evidence from ACM-UC 233, a large slug-like animal grazing on a mud-draped sandy layer and excreting a mud- and sand-laden fecal strand.

However, evidence for such an origin is still equivocal. For example, one must wonder why, if a grazing animal produced the surface traces, medial ridges are so rare. The preservation of other fecal-pellet-like structures in the same deposits as *Climactichnites* and the preponderance of microbial binding in *Climactichnites*-bearing deposits argues against widespread taphonomic removal of medial ridges from trackways. Further sectioning of trackways with medial ridges is needed to refine or falsify the fecal strand hypothesis.

Did the trackmaker make subaerial excursions?

Climactichnites is often found on beds preserving sedimentary structures such as adhesion warts, foam marks, polygonal desiccation cracks, and raindrop imprints, indicating that the substrates upon which the animal tread were intermittently subaerially exposed (MacNaughton *et al.* 2003). At PRI-100 the *Climactichnites* animal moved in and out of tidal channels, and in some cases crossed over channel levees, characterized by polygonal mud cracks (MacNaughton *et al.* 2003). However, the co-occurrence of the trackway and these sedimentary structures is not definitive evidence that the trackmaker made subaerial excursions. Where desiccation cracks are present they often crosscut the trackway, indicating that the cracks formed after track production. Thus it is possible that the trackways were produced subaqueously and that the tide went out after the trackway was formed. Similarly, some trackways were produced in wind-dominated settings, such as QUE-PH-101, in which wind-blown sand adhered to previously made trackways (Fig. 24). Although one other surface has been found with *Climactichnites* associated with adhesion structures (PRI-100-7.82) no trackways have been found that crosscut adhesion structures to date. Such crosscutting relationships are critical for constraining possible evidence of subaerial exposure.

Raindrop impressions might provide more conclusive evidence for subaerial track formation because it is possible for an animal to produce a trackway during a shower. This would produce a trackway that both crosscuts and is crosscut by raindrop impressions, thus suggesting that the trackway was produced during or between rain events. For example, at PRI-100-9.13 both *Climactichnites* and raindrop impressions are preserved (Fig. 25). The trackways are crosscut by the raindrop impressions, indicating that the surface was rained on after track formation, which may have been under water. Alternatively, the trackways may have been produced subaerially before the shower. In any case, the evidence for subaerial track making on this surface is equivocal.

Another line of evidence that could indicate that the trackmaker made subaerial excursions is the preservation of the trackway. Knox and Miller (1985) demonstrated that the preservation quality of *Polinices duplicatus* trackways made in sand varied depending on whether the trackway was produced subaerially or subaqueously. Under subaerial conditions, *P. duplicatus* produced *Climactichnites*-like trackways that had well-defined lateral ridges and transverse bars and furrows. However, when *P. duplicatus* trackways were produced in wet, less compact sediment the lateral ridges and transverse bars were faint. Under water the animal burrowed and produced a trackway whose sides collapsed due to the high water content of the sand, producing a trace with a v-shaped cross section. The varying track morphotypes reflect trails made in sediments of variable sediment consistency (Knox & Miller 1985). It is possible that some well-preserved *Climactichnites* trackways were produced under subaerial conditions and that the preservation quality of the fossil is at least in part due to production either subaerially or subaqueously. For example, *Climactichnites* moving out of channels on PRI-100-10.45 have variable morphologies (Fig. 26). At the bottom of the channel no trackways are visible, but about halfway up the channel trackways with well-pronounced straight lateral ridges were observed. These trackways do not exhibit transverse bars and furrows. However, toward the top of the channel some of the trackways exhibit transverse bars and furrows. The variable track morphology suggests that the sediment had different degrees of saturation; one possible interpretation is that animals were moving out of a submerged channel onto a subaerially exposed portion of the channel. Another possibility is that the animal may have been buoyed up more by deeper water at the bottom of the channel, thus not producing trackways.

Inter- and intra-specific relationships

Climactichnites is often the only trace fossil found on beds on which it occurs (Table 4). Of the 77 discrete bed surfaces and museum specimens analyzed, only 19 had additional trace fossils on them. In cases in which *Climactichnites* does occur with other traces, these are primarily arthropod trackways such as *Diplichnites* and *Protichnites*; however, *Arenicolites*, *Diplopodichnus*, *Planolites*, and indeterminate arthropod trackways also occur on some surfaces (Table 4). There is no direct evidence of interaction between the *Climactichnites* trackmaker and other trackmakers; most often one trackway is superimposed on the other, indicating that they were made at different times. This is particularly true of *Arenicolites*, which often punctures traces on underlying beds (Bjerstedt & Erickson 1989; Hagadorn & Belt in press). The paucity of other trace fossils on *Climactichnites*-bearing beds suggests that the trackmaker was one of the few animals of its time to be adapted to the extremes of the upper intertidal zone, where physical conditions such as ultraviolet light, temperature, salinity, water saturation, and oxygen concentration vary considerably (Yochelson & Fedonkin 1993).

C. wilsoni can occur as an isolated trackway or in abundance on bedding planes. Surface disruption, characterized by bedding plane bioturbation indices of Miller and Smail (1997), ranges from very low (Figs. 21, 25), to high (Figs. 15G, 24). When *Climactichnites* is abundant on bedding planes they may have a common direction of travel. For example, on PRI-100-9.54 trackways run through the troughs of high-amplitude, high-wavelength ripple marks, both parallel and antiparallel to each other (Fig. 22, see discussion above). Thus, these animals were selectively choosing the troughs through which to move.

C. youngi also can occur in large numbers within beds (e.g. Fig. 20). The occurrence of these traces within beds indicates that the trackmaker was capable of burrowing with its body completely buried within the sediment. The bifurcation of bars and their change in wavelength and amplitude laterally in some trackways implies that the method of locomotion may have varied somewhat from that inferred from surface trails; for example, the lateral edges of the foot may have made much shorter steps than more medial portions of the foot, thus leading to the short wavelength and amplitude bar striations seen in some trackways (Fig. 8.4).

How was the trackway preserved?

It is possible that the *Climactichnites* trackmaker produced copious amounts of mucus during locomotion and that the mucus led to preservation of the trackway (Yochelson & Fedonkin 1990, 1993). However, in modern intertidal deposits mucus-laden epifaunal gastropod trackways similar to *C. wilsoni* are rarely, if ever, preserved because of obliteration by wave and current action. To test the hypothesis that mucus is sufficient to preserve epifaunal, mucus-bound trackways, a series of experiments was undertaken with the gastropod *Viviparus intertextus* in an experimental tank (Getty & Hagadorn 2006). *V. intertextus*, on rare occasions, produced trackways with lateral ridges, transverse bars, and furrows (Fig. 27A), which were formed by the animal pressing its shell into the sand, presumably in an attempt to burrow. Although this method of transverse bar production is different from that inferred for the *Climactichnites* trackmaker, it posed no problem for this experiment, which was intended only to determine how mucus-bound trackways with transverse bars and furrows are preserved. After some time the animal would move a short distance and begin pressing its shell into the sediment again. As the foot moved over the transverse bars and furrows it deposited a mucus band over them. Experiments were conducted with these trackways in which the apparatus was filled slowly with water poured from a beaker. Water was poured from the other side of the tank to prevent the stream of water from directly touching the trackway; thus the disturbance from the water was limited to minute oscillatory waves generated as the water reflected off the side of the tank. Even these waves were enough to disrupt the sand around the trackway and thereby undermine it. Additionally, the mucus floated to the surface of the water and as a consequence did not provide any protection for the trackway (Fig. 27B). These experimental observations suggest that mucus secretions are not enough to preserve trackways. In light of the problems preserving gastropod trackways bound by mucus in similar environments, it is unlikely that mucus played a major role in preserving *Climactichnites*.

The presence of epifaunal arthropod, annelid, and other invertebrate trackways on the same surfaces as *Climactichnites* (e.g. Summerson 1951; Yochelson & Fedonkin 1993, fig. 55; Table 4) further weakens the mucus preservation hypothesis. Because these traces are not bound by mucus and occur on surfaces composed of loose sand, they should have been washed away. There are two possible reasons that the arthropod trackways were preserved: they are undertracks or the surface on which they were impressed was cohesive enough to resist erosion due to tidal cycles. Goldring and Seilacher (1971) demonstrated that telson drags only occur on or very close to the surface on which trackways are produced; therefore, the presence of continuous telson or abdominal drag marks in trackways such as *Protichnites* on the same surfaces as *Climactichnites* suggest that these trackways are true trackways rather than underprints. It appears that at least in some cases entire surfaces on which *Climactichnites* and other traces were impressed have been preserved. For example, the type slab at the Geological Survey of Canada (GSC 6299) and a large slab at the Redpath Museum (RM 206837), both of which are from Perth, Ontario, preserve large *Diplichnites* and *Protichnites* (e.g. Yochelson & Fedonkin 1993, figs. 18 & 55). Additionally, some surfaces preserve sedimentary structures, such as raindrop impressions, that are not usually preserved in sand (Fig. 25). It follows then that these surfaces were cohesive enough to resist erosion.

A striking example of the cohesive nature of some of the beds appears at PRI-100-9.54, where numerous channel foresets and bottomsets, consisting of medium to very coarse sand, overly a *Climactichnites*-bearing surface consisting of fine to medium sand (Fig. 22). Had the surface not been cohesive, the trackways would have been scoured away by the flowing water that produced the channels.

There are numerous reasons that such surfaces can be cohesive. Surface tension produced by liquids, such as water, provides considerable cohesion between grains of sand (Hornbaker *et al.* 1997; Tegzes *et al.* 1999, 2003; Schiffer 2005). However, the ability of water to provide cohesion to sand diminishes as grain size increases (R. H. Dott, Jr., personal communication), and many *Climactichnites*-bearing beds consist of medium- and coarse-grained sand (Fig. 10), in which aqueous cohesion is less capable of holding the grains together. Furthermore, as the amount of interstitial water increases the cohesive properties imparted by water decrease; in saturated sand water acts as a lubricant, thus allowing the grains to slip past each other (Tegzes *et al.* 1999, 2003). Trackways under water would have been made in sand with a high degree of water content, thus limiting their preservation potential unless the water was very calm. Additionally, incoming tides would have increased water content of subaerially exposed tidal flat sands and any trackways on these surfaces would be subject to a decreased preservation potential when flooded. Because the observed distribution of *Climactichnites* is grain size dependent, it is likely that surface cohesion was a more important factor for the preservation of small trackways, which are found in fine-grained sand, than for larger trackways.

Clay within the sand also could have imparted cohesive properties to the beds due to the Van der Waals forces between the particles (Craig 2004). However, mudstones and shale are rare in the Potsdam Group (Wiesnet 1961; Lewis 1971) and its equivalents in Wisconsin and Missouri (Runkel *et al.* 1998; Ojakangas 1963) and only one bed in the Carrieres du Charm quarry and three beds in the Krukowski and Nemke quarries had trackways preserved on muddy surfaces. It has been suggested by some authors that the lack of clay is due to strong winds carrying the material out to sea (e.g. Dalrymple *et al.* 1985), or that these materials were carried in suspension across the shelf and deposited in shallow areas only when permanent currents were weak (Pettijohn *et al.* 1973; Runkel *et al.* 1998). Consequently, it is unlikely that clay aided in the preservation of many trackways except for those with which clay and the trackways co-occur directly (e.g. Fig. 28).

Surface cohesiveness also could have been increased by the presence of biofilms or microbial mats covering the trace-fossil-bearing beds. Numerous microbial sedimentary structures have been found in the units that contain *Climactichnites*, including domal build-ups (i.e. sand stromatolites), sand chips, sand curls, exfoliating sand laminae, patchy ripples, “Astropolithon”, broached ripples, and elephant skin (Hilowle *et al.* 2000; Donaldson & Chiarenzelli 2004; York *et. al* 2005; Getty & Hagadorn 2006; Hagadorn & Belt in press). Some of these structures occur on the same beds as *Climactichnites*. For example, trackways crosscut and are crosscut by sand stromatolites on PRI-100-6.35 (Fig. 21), suggesting that these trackways were produced on a microbially-bound surface and that the mat continued to grow after the trackways were made. Thus, the mat may have directly aided in the preservation of these trackways.

Although none of the processes outlined above can explain the preservation of all *C. wilsoni*, it is likely that each played a role in preserving some of the traces, and that these processes could have worked together to preserve many of the surfaces in question.

Preservation of *Climactichnites youngi* was mediated by their production below the surface; sediment shed off of the back of the trackmaker immediately filled in the void left as the animal burrowed, allowing for fine structures such as striations to be preserved (Fig. 20B). This is similar to the preservation of other Cambrian infaunal burrows with transverse bars, such as *Plagiogmus* and *Psammichnites* (Seilacher 1995; McIlroy & Heys 1997, and references therein).

CHAPTER IV

DISCUSSION AND CONCLUSIONS

Discussion

Since its discovery in 1859, *Climactichnites* has been subject to continued debate due to its unique morphological characteristics among fossil trackways; thus numerous contradictory hypotheses have been proposed concerning the identity of the trackmaker. Some have suggested that the trackmaker was a member of a completely extinct phylum of soft-bodied animals (Yochelson & Fedonkin 1993) that inhabited Late Cambrian, marginal marine, siliciclastic environments along the shore of the Laurentian craton. These authors suggested that the unique morphology of the trackway reflected a distinct and novel body plan that evolved in response to the selective pressure of inhabiting this harsh environment. When the environments inhabited by the *Climactichnites* trackmaker changed at the close of the Cambrian the animal became extinct. However, my sedimentologic, taphonomic, paleoenvironmental, and paleoecologic analyses do not support this interpretation. A more parsimonious framework for interpreting *Climactichnites* and its trackmaker is to examine modern gastropods that produce *Climactichnites*-like trackways and to evaluate the preservation potential of Cambrian mollusk trackways in an evolutionary paleoecological context.

The features inferred for the trackmaker as outlined in this paper are consistent with a molluskan trackmaker, a conclusion that is supported by body fossil evidence of similarly shaped mollusks from the Ediacaran and Cambrian. It is possible that soft-bodied mollusks or a mollusk-like animal was able to inhabit sand flats during the Late Cambrian. Further support for this hypothesis is the fact that modern gastropods inhabiting similar environments make *Climactichnites*-like trackways.

Because gastropods produce similar trackway morphologies, the most unique feature of *Climactichnites* is not its morphology, but its preservation. Given the long fossil record of soft-footed mollusks (Fedonkin & Waggoner 1997), why is *Climactichnites* preserved in the Late Cambrian, while similar trackways produced by gastropods are absent from the fossil record throughout the remainder of the Phanerozoic? This question implies that there is something unique about the Late Cambrian. During this time microbial mats still predominated in areas where significant vertical burrowing was minimal (Hagadorn & Belt in press). It is possible that the trackmaker inhabited one of these environments, for a well-developed *Skolithos* ichnofacies, dominated by vertical burrows, is not observed in association with *Climactichnites* at any of the 25 studied localities. Additionally, some *Climactichnites*-bearing surfaces preserve microbially-produced sedimentary structures, suggesting that the preservation of epifaunal trackways may have been mediated by microbes. Consequently, the absence of *Climactichnites* after the Cambrian may not be the result of the extinction of the trackmaker or of a particular locomotory behavior, but of the lack of a suitable microbially-bound and poorly bioturbated substrate in which to preserve the trackway during later times.

Conclusions

The *Climactichnites* trackmaker was an elongate, bilaterally symmetric, dorsoventrally flattened, soft-footed animal with a muscular anterior used during locomotion. Most trackmakers were between 1.4 and 18 cm wide and 3.2 to 41 cm long, and evidence suggests that the body was about 13% as tall as wide. One exceptionally large trackway measures as much as 29 cm wide, corresponding to an animal 67 cm long. The ventral surface of the animal may have had glands that secreted mucus during track formation, and the dorsal surface may have been naked or may have borne sclerites.

The trackmaker was likely a mollusk or mollusk-like animal that inhabited sandy intertidal to subtidal environments. The animal could move epifaunally and infaunally, producing trackways like those in Fig. 29. Infaunal burrows can be identified by the presence of fine striations and tapering and bifurcating transverse bars, which are rarely, if ever, preserved on surface trackways. Additionally, subsurface burrows do not have lateral ridges. The trackmaker may have made some trackways under subaerial conditions; if the *Climactichnites* trackmaker was indeed a mollusk and made subaerial excursions then mollusks may have been among the first terrestrial pioneers, along with arthropods (MacNaughton *et al.* 2002).

Locomotion on the surface resulted from manipulation of the soft foot in a manner similar to that that employed by extant gastropods such as *Bullia* and *Polinices*. Transverse bars in *Climactichnites* were generated as the animal clamped its foot onto the substrate, while the lateral ridges resulted from the foot plowing sediment to the side as the animal moved forward.

Climactichnites is also notable because it is one of the only trace fossils to go "extinct". The unique morphology of the trackway and its sudden disappearance from the fossil record has been viewed as the result of the radiation of a unique group of animals that subsequently went extinct. However, the present evidence suggests that *Climactichnites* trackways were likely as common as the intertidal mollusks that made them, and their disappearance from the fossil record is largely tied to the loss of environmental conditions suitable for the preservation of horizontal trace fossils in such settings.

TABLE 1. *Climactichnites* field localities.

Region	**Locality**	**Coordinates or reference**	**Taxa Present**
Wisconsin	Abandoned Quarry	N44º42.739' W89º30.343'	*C.w.*
	Black River Falls	Yochelson and Fedonkin (1993)	*C.w.*
	Central Wisconsin Stone	N44º42.873' W89º31.011'	*C.w.*
	Chippewa River, 2 sites	Yochelson and Fedonkin (1993)	*C.w.*
	Irma	N45º21.088' W89º39.335'	*C.w.*
	Krukowski Quarry	N44º42.755' W89º30.786'	*C.w., C.y., M.s.*
	Lemonweir River quarries	Todd (1882)	*C.y.*
	Mauston	Yochelson and Fedonkin (1993)	*C.w.*
	Minke Quarry	N44º42.295' W89º31.394'	*C.w.*
	Nemke Quarry	N44º41.709' W89º32.110'	*C.w.*
	Pointe Quarry	N44º42.500' W89º30.092'	*C.w.*
	Quarry in Marshfield	N44º36.937' W90º13.280'	*C.w.*
Missouri	Big Spring State Park	N36º56.837' W90º59.431'	*C.w.*
	Black River Stone Quarry	N36º58.369' W90º36.617'	*C.w., M.s.*
	Columbia Park	N37º50.516' W90º59.431'	*C.w.*
	Fredericktown	N37º34.626' W90º24.331'	*C.w.*
	Ste. Genevieve	N37º50.760' W90º13.920'	*C.w.*
	Williamsville	N36º58.393' W90º32.988'	*C.w.*
New York	Au Sable Chasm	N44º31.387' W73º27.585'	*C.w.*
	Bidwell Crossing	N44º55.452' W73º26.640'	*C.w.*
	Hammond	N44º25.471' W75º46.563'	*C.w.*
	Gadway SS pavement	N44º58.689' W73º44.847'	*C.w., C.y.*
	Mooers	N44º57.549' W73º34.759'	*C.w., M.s.*
	Port Henry	Hall (1889)	*C.w.*
	Wellesley Island	N44º18.382' W76º02.005'	*C.w.*

Quebec	Carriere Dolomite Quarry	N45º18.747' W73º55.998'	*C.w.*
	Les Carrieres du Charm	N45º02.575' W73º46.374'	*C.w., C.y.*
	Melochville	N45º18.965 ' W73º55.110'	*C.w.*
	Réserve Ecol. du Pin-Ridge	N45º06.576' W73º52.871'	*C.w.*
	Rogier's Farm	N45º19.337' W73º54.788'	*C.w.*
	covered by water		
	St. Hermas	N45º36.894' W74º12.453'	*C.w.*
Ontario	Battersea	N44º26.264' W76º22.670'	*C.w.*
	Perth	Logan (1860); no longer exists	*C.w.*

TABLE 2. Sediment composition for experiments.

Grain Size (Φ)	Percent Composition
≥ 4	3.4
3-4	9.8
2-3	33.2
1-2	31.8
0-1	14.2
¯1-0	5.4
≤¯1	2.2

TABLE 3. Bar wavelength (λ) on turning trackways. Measurements taken on left and right sides of 28 curving *Climactichnites*. In 26 of the trackways λ increases on the outside of the curve, corresponding to the longer distance the portion of the foot on the outside of a curve had to travel.

Specimen	**Track**	**Turn**	**Left λ**	**Right λ**	**comments**
ACM 68/2	1	right	2.4	2.4	
ACM 68/2	2	left	1.1-1.3	1.6-2.2	
ACM 68/2	3	right	2.3	1.6	
ACM 68/2	4	right	3.0	2.6	
ACM 68/3		left	2.4-3.9	2.7-3.8	No correlation
ACM UC 235		left	1.9-2.4	2.3-2.9	
NMNH 532849	2	left	1.0	2.2	
NYSM unnumbered	1	right	not measured	not measured	greater outside
NYSM unnumbered	2	left	1.5-2.0	2.5-3.0	
NYSM E-3436	2	right	2.3	1.3	
NYSM E-3436	3	left	0.9	1.5	
NY-WI	1	left	0.6	1.2	
NY-WI	4	right	0.9-1.5	0.8-1.2	
SMM P.76.21.1	T-1-1	right	1.8-2.2	2.3-3.6	greater outside
ACM UC 235		left	1.9-2.4	2.3-2.9	
WI-DF-2		right	2.2	1.1	

WI-DF-80		left	1.2	2.5
WI-DF-104	1	left	0.9	1.8
WI-KQ-499	2	right	not measured	not measured
WI-KQ-500	2	right	2.3	1.9
WI-KQ-500	5	left	0.9	1.3
WI-KQ-501	1	right	2.1	1.5
WI-KQ-501	2	left	not measured	not measured
YPM 150696		left	2.1	2.3
YPM 150698		left	1.3	2.0
YPM 150700		right	3.5	2.4
YPM 174721		right	2.4	3.1
St. Hermas, Quebec		left	2.3-3.1	2.6-3.4

TABLE 4. Trace fossils associated with *Climactichnites*. See p. xvii for abbreviations.

Surface/Slab	**Formation**	**Associated Trace Fossils**
ACM 68/2	Potsdam Group?	Pl
AMNH 51449	Potsdam Group	D
GSC 6299	Nepean Fm	Pr
MO-CP-1-2	Gunter Ss member	Pr
NMNH 532847	Cairnside Fm	IA
NYSM no #	Potsdam Group	D
QUE-BE-7	Cairnside Fm	D, Pl
SSM 2006/20-4	Cairnside Fm	IA
SSM 2006/20-5	Cairnside Fmn	IA
WI-DF-94	Elk Mound Group	Di, Pr
WI-DF-104	Elk Mound Group	Pr
WI-DF-112	Elk Mound Group	Pr
WI-DF-200	Elk Mound Group	D
PRI-100-6.3	Elk Mound Group	IA
PRI-100-9.13	Elk Mound Group	Di
PRI-101-1	Elk Mound Group	Pl
RM 206837	Nepean Fm	Pr, Ar
UMR 7283	Lamotte Ss	Pr

Figure 1. ACM 68/01. Photograph (A) and interpretive drawing (B) of ACM 68/1, of the upper surface of a slab of medium-grained sandstone from New Lisbon, Wisconsin (probably Mt. Simon Formation). The slab preserves oscillation ripple marks overprinted by *Climactichnites*. The trackways are bound by lateral ridges between which are undulating transverse bars and furrows. The depth of the trackways indicates that the animals were moving at approximately the same depth as the ripple troughs. The sharp boundaries between trackways and ripple marks indicates that sediment was not pulled inward by lateral flaps to form the lateral ridges; rather, sediment was plowed from in front of the animal to the sides. Approximate order of track formation indicated by numbers and direction travel indicated with arrowheads. Scale bar is 15 cm.

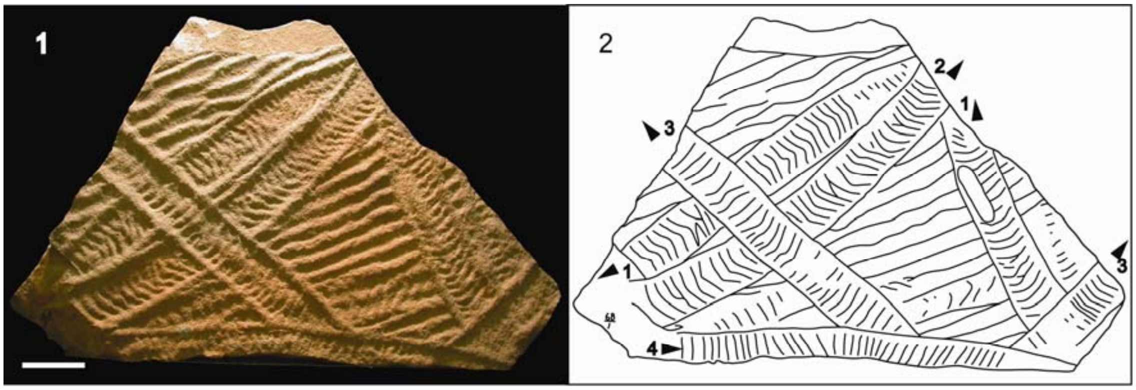


Figure 1.

Figure 2. Locality maps and stratigraphic context of formations. (A) Outline drawings of Wisconsin (WI), Missouri (MO), and the St. Lawrence lowlands regions of New York (NY), Quebec (QUE), and Ontario (ONT), showing late-Cambrian sandstones in yellow. *Climactichnites*-bearing field localities are indicated by red circles. (B) stratigraphic correlation between the three regions. Figures modified from Hagadorn et al. (2002) and Hagadorn & Belt (in press). A drafted by J.W. Hagadorn, W. Chen, and J. Collette.

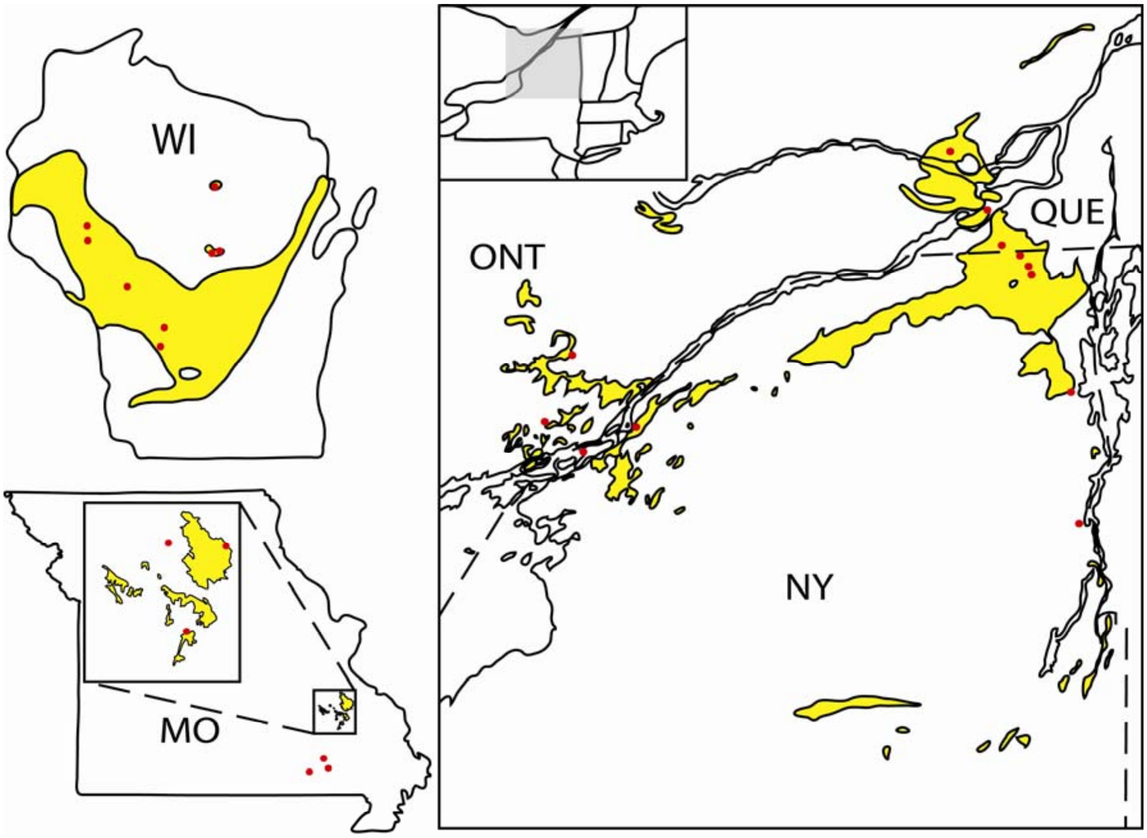


Figure 2.

Figure 3. Modern gastropod trackways. Note the pronounced lateral ridges (**lr**) and the transverse bars (**tb**). (A) shows trackways produced by *Littorina littorea* and was modified from Graff (1956), (B-C) show trackways produced by *Bullia digitalis* and were modified from Abel (1935), and (D) shows trackways produced by *Polinices duplicatus* and was modified from Knox and Miller (1985). The illustration and photographs are used with permission from Schweizerbarte, Elsevier, and Society of Sedimentary Geology (SEPM) respectively. No scale was provided with the originals of (A-C); however, Raymond (1922) noted *Littorina* trails up to 1.4 cm wide with transverse bars. *Bullia digitalis* reaches 6 cm long (Branch et al., 1994) and the foot may expand to approximately 70% of the shell length (C. L. Griffiths, personal communication), for a maximum width of 4.2 cm.

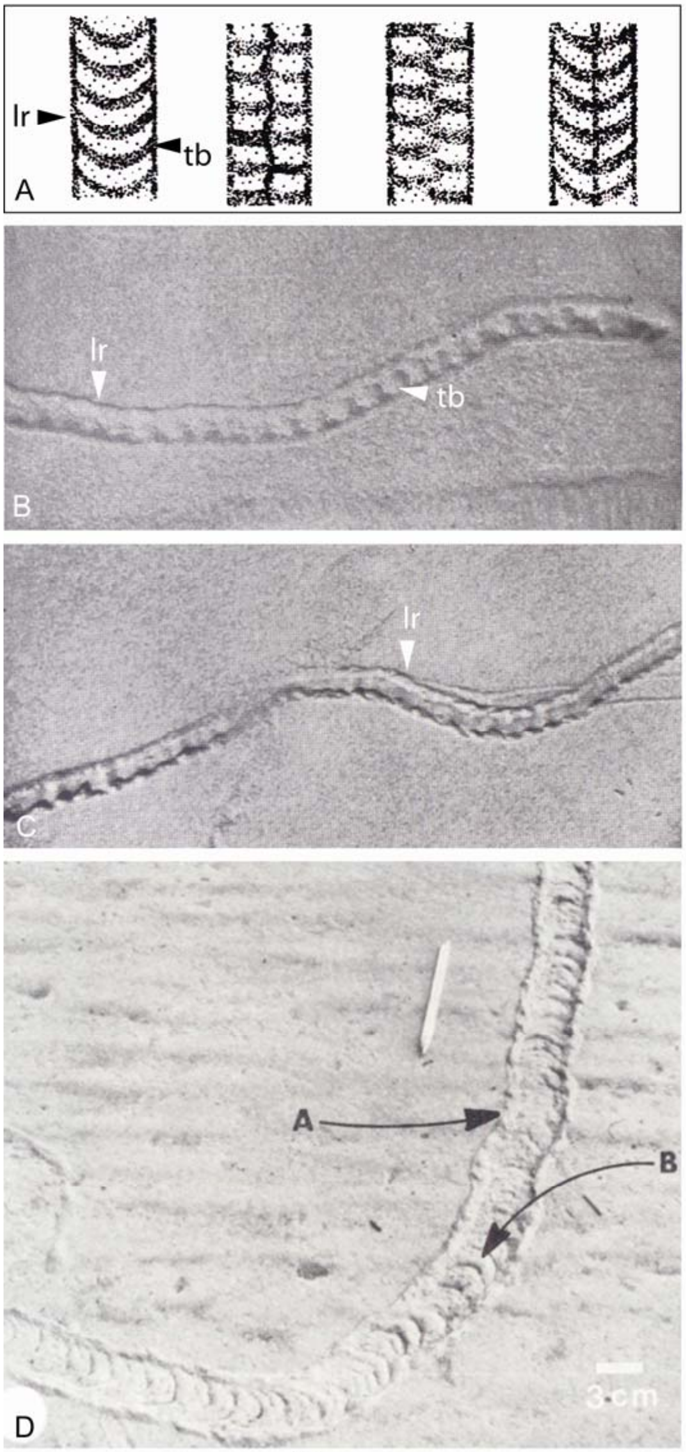


Figure 3.

Figure 4. Trackways and burrows lacking lateral ridges. (A) RM 206840 and (B) RM 206841, part and counterpart slabs preserving *C. wilsoni* as an original trackway on a bed top and natural cast from the overlying bed sole, respectively. The slabs are aligned such that the cast (B) would fit perfectly on top of the mold (A) if it were flipped over and moved to the left. The mold appears to lack lateral ridges, especially towards the upper right of the specimen. However, inspection of the natural cast reveals that lateral ridges were present when the trackway was produced. When the beds split, the lateral ridges cleaved off and were retained in the natural cast (arrowed and labeled **lr**). Toward the bottom of RM 206841, portions of the transverse bars can be seen adhering to the overlying slab (arrowed and labeled **tb**). Note also the pustular texture to the upper right of the slab in (A). Sedimentary structures such as these are never found in association with *C. youngi*, such as this part-counterpart specimen from PRI-100 (C), which lacks lateral ridges because it was produced as an infaunal burrow. Scale is 10 cm.

Figure 4.

Figure 5. Morphological variability in *Climactichnites wilsoni*. All surfaces except (F) are bed tops. (A), YPM 150698, exhibiting crenulated lateral ridges and v-shaped transverse bars. (B), part of SMM-P 76.21.1, the trackway has straight, continuous lateral ridges and v-shaped transverse bars that are alternately asymmetric (one limb of the v shorter than the other) on the right (towards the bottom of the slab) and then on the left (towards the top). (C), part of SSM 2006/20-1, a plaster reproduction of a trackway made from its natural cast showing a zipper-like pattern to the transverse bars and crenulated lateral ridges. At only 1.37 cm wide, this is the narrowest *C. wilsoni* trackway known. (D), part of ACM UC 232 showing a trackway with straight lateral ridges and straight transverse bars, which are oriented perpendicular to the direction of travel. (E), SMM-P 76.21.1 (III-IV), note the trackway oriented perpendicular to the long axis of the slab, which has straight transverse bars oriented at an angle to the direction of travel. Numerous trackways that overprint each other are oriented roughly perpendicular to the trackway with straight bars; these trackways are only partially impressed. (F), Part of ACM UC 240, a slab preserving the sole of an overlying bed and *C. wilsoni* as natural casts. The well-preserved trackway shows both v-shaped bars (to the right) and u-shaped bars (to the left). (G), Part of ACM UC 244 preserving a trackway on a raindrop- and sand ball-bearing surface exhibiting a straight lateral ridge on the left and a packeted lateral ridge on the right (arrowed). The packets are elongate and point in towards the direction of travel. Silicone rubber molds of this trackway are preserved as ACM UC 241. All scale bars are 5 cm.

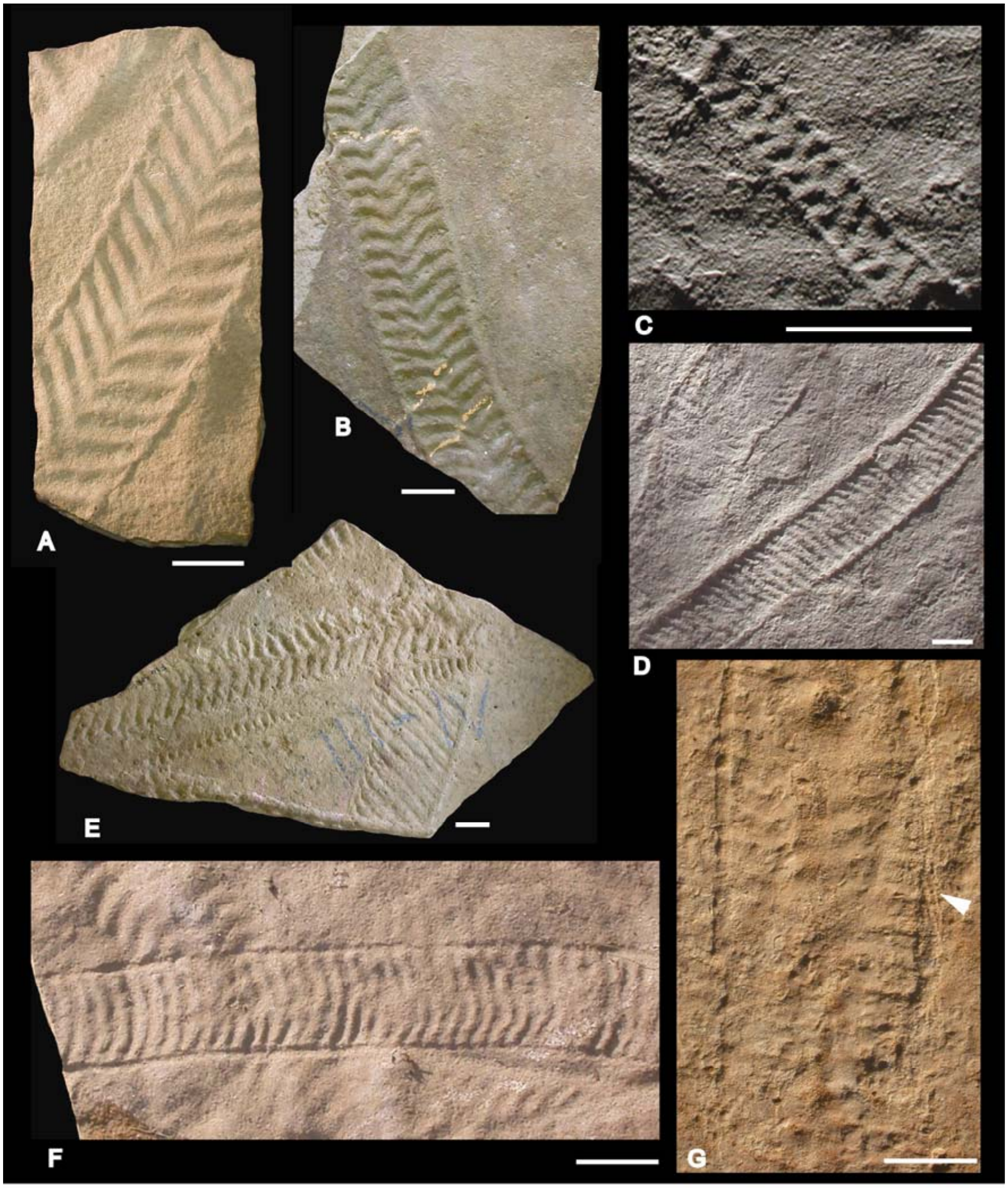


Figure 5.

Figure 6. *Climactichnites youngi* neotypes. (A), Obverse and (B), reverse of NMNH 58547, showing multiple generations of burrow production. One trackway is preserved on the top of the slab (A) whereas two are preserved on the bottom (B). In (B), one trackway traverses right to left across the slab and consists of sinuous, bifurcating bars and furrows. Stratigraphically above this trackway (but visible due to spalling of the lower layer in a lowercase R-shaped pattern) is an even more irregularly shaped burrow with only partial bars visible, over which are superimposed numerous striations (arrowhead indicates the location of this trackway). (C), NMNH 58546, showing bar bifurcations characteristic of the burrow. Partial burrows may be seen on the upper left portion of the slab. (D), NMNH 58544 (counterpart is Fig. 9D), this burrow begins from a *Musculopodus* imprint, over which are superimposed ovate striae (**os**). The animal that produced this burrow started from rest below the surface and moved from right to left across the slab. (E), NMNH 58545, note the fine longitudinal (**ls**) and ovate striations superimposed on the transverse bars (see arrowheads). Lateral ridges were not formed in any of these specimens. Also note the irregular surface lateral to the traces in all specimens, which corresponds to fracturing of the rock within the bed itself rather than at a bedding plane. Scale bars are 5 cm.

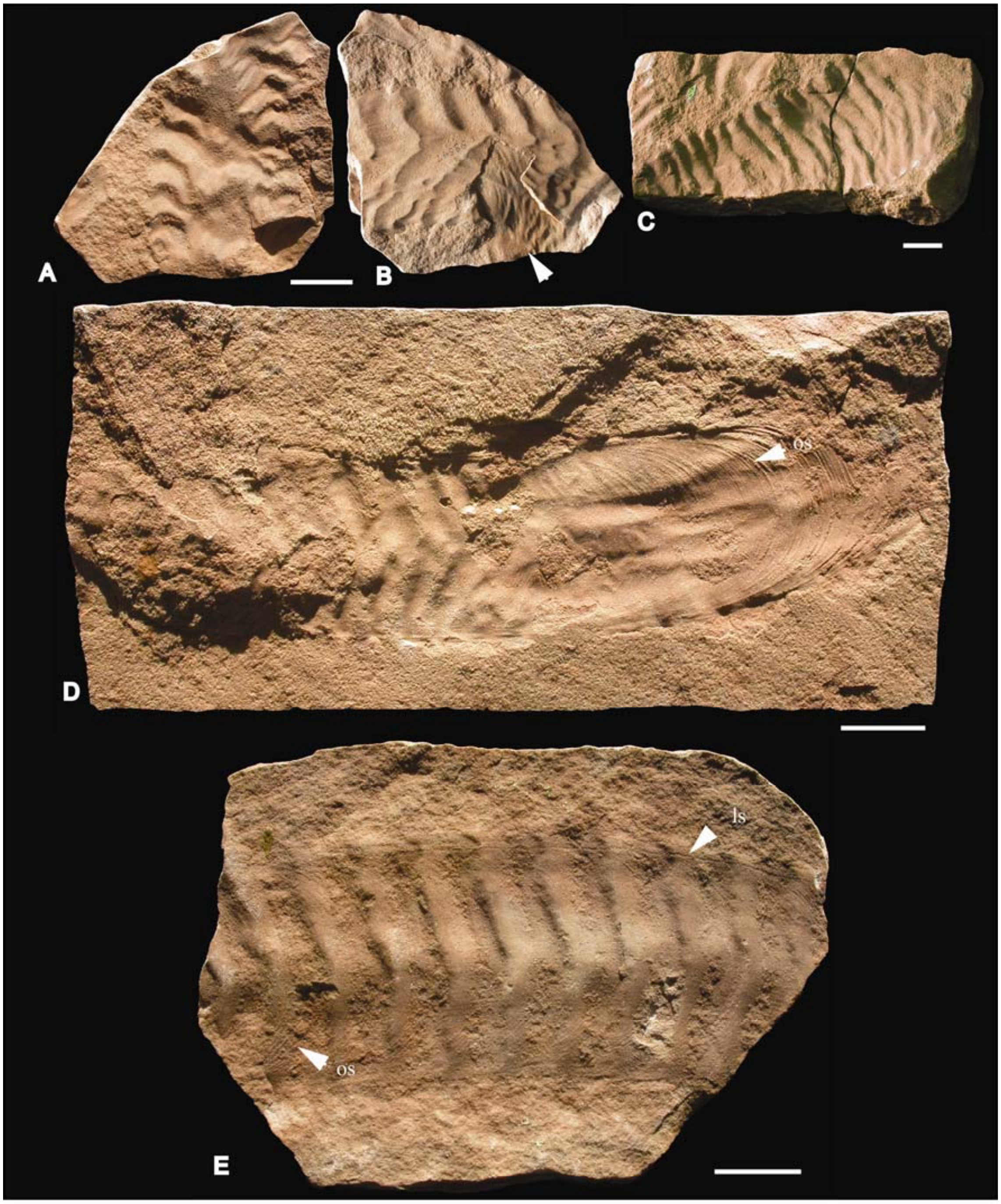


Figure 6.

Figure 7. *C. youngi* from Les Carrieres du Charm Quarry. (A), JF 05 FC, a large float block quarried from the St. Lawrence Seaway, seen in oblique view. The surface shown is the sole of a sandy bed deposited atop a mixed mud and sand bed. The animals that produced the burrows traversed the interface between the two beds before significant drying generated desiccation cracks in the underlying muddy layer; the burrows are crosscut by the desiccation cracks, which are preserved as sand casts. The burrows appear as discrete fills consisting of sand and mud that are spalling off of the block; one such burrow, indicated by a square in (A), is seen in close-up in (B), and in cross-section in (C). The arrow in (B) indicates the direction of view that produces image (C). These burrows have u-shaped transverse bars exhibiting bifurcation. Scale is 20 cm.

Figure 7.

Figure 8. ACM UC 237 and 238. (A), ACM UC 237, lower portion of a large block that when split in half, produced a completely burrowed surface. These burrows are preserved in convex epirelief and concave hyporelief. Note the wavy appearance of the bars in these burrows. (B), ACM UC 238, the overlying portion of the block, preserving the casts of these burrows. (C), A close-up of one of the burrows showing numerous linear grooves (indicated by arrowhead) etched into the transverse bars (possibly by part of the animal's body?). (D), A burrow exhibiting backwards-oriented striations (indicated by arrowhead) lateral to the transverse bars. The white line traces one of the bars from the middle of the burrow to its lateral edge, and follows a backwards-oriented striation connected to the bar. Such striations are common in *C. youngi*. Pencil, approximately 14 cm long, in 1 and 2, and coin, diameter 24.26 mm in 3 and 4 for scale.

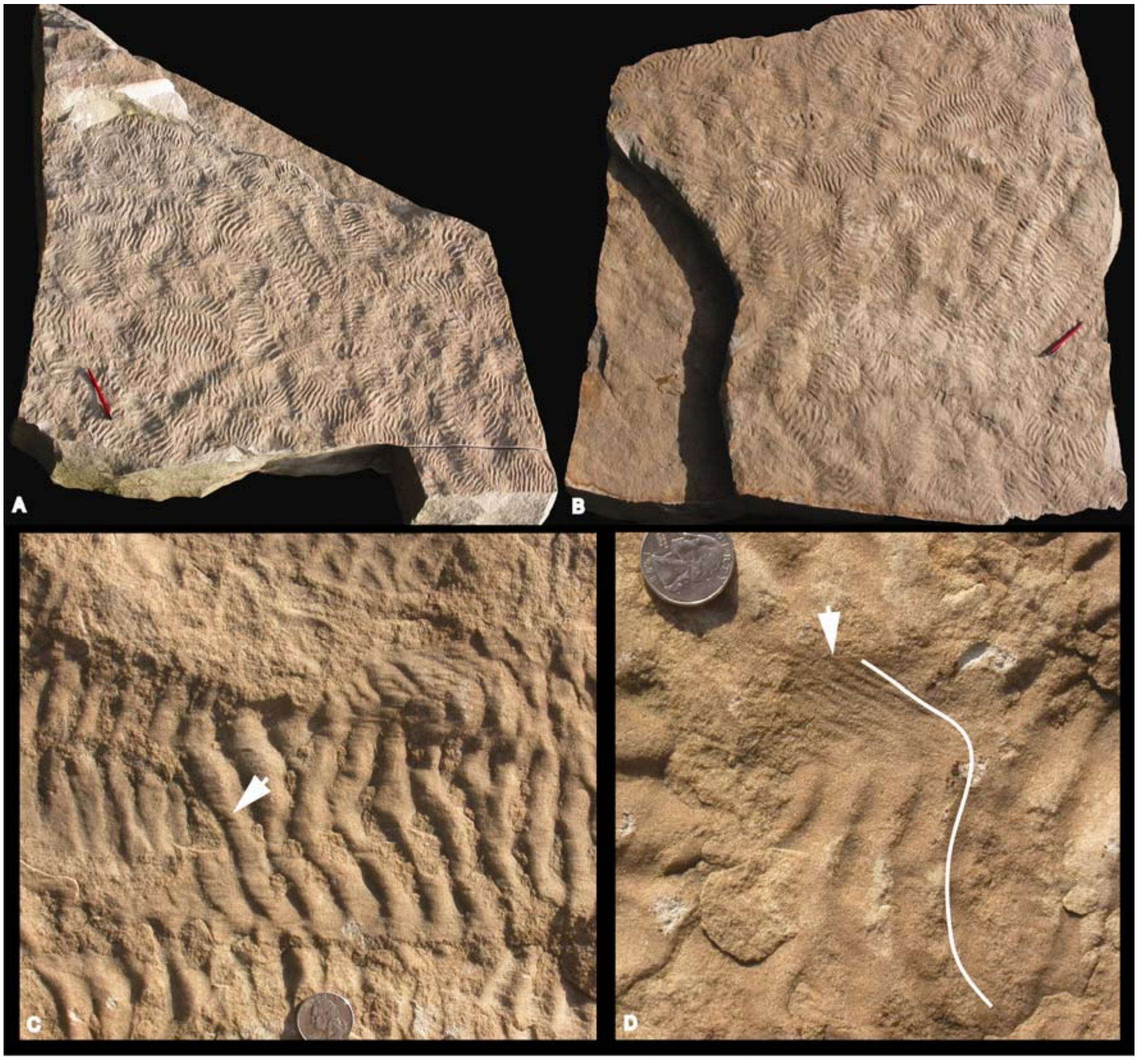


Figure 8.

Figure 9. M*usculopodus sedentarius* new ichnogenus and ichnospecies. (A), NYSM-unnumbered-1-1 and NYSM-unnumbered-1-2, type specimens. NYSM-unnumbered-1, on the left, is an isolated *M. sedentarius* specimen, whereas NYSM-unnumbered-1-2, second trace from the right, has the beginning of a trackway at its anterior end. Both exhibit triangular projections (**ap**) at the anterior end of the trace. (B), A portion of ACM 68/2, showing a partial *M. sedentarius* merging into *C. wilsoni*. Note that the initial transverse bars on the left side are subparallel to the long axis of the trace and extend backwards into the body impression, whose anterior margin is marked by a dashed line. The bounding lateral ridges are clearly visible in this surface-produced trace. (C), Close-up of JF 20 FC showing an isolated, partial *M. sedentarius* preserved as a natural cast. The presumed anterior portion of the body did not impress into the sediment. The surface on which this trace was made consisted of sandy mud that produced desiccation cracks, which are preserved as casts, upon drying (cf. Fig. 7). A smaller *M. sedentarius* (not figured) of similar morphology is also preserved on the slab. (D), NMNH 58544 (counterpart to the slab shown in Fig. 6C), showing ovate striations (**os**) superimposed along its length by the rear of the animal. This body impression, attached to a *C. youngi* burrow, lacks bounding ridges and was produced infaunally. (E), Close-up of ACM UC 239 showing another infaunally generated body impression leading into a partial *C. youngi* (**tw**), and (F), interpretative drawing of the same. This impression, like other infaunal traces, shows more detail than surface traces. Partial transverse bars (**ptb**) and fine-scale folds (**fsf**) can be seen within the impression. All scales are 10 cm.

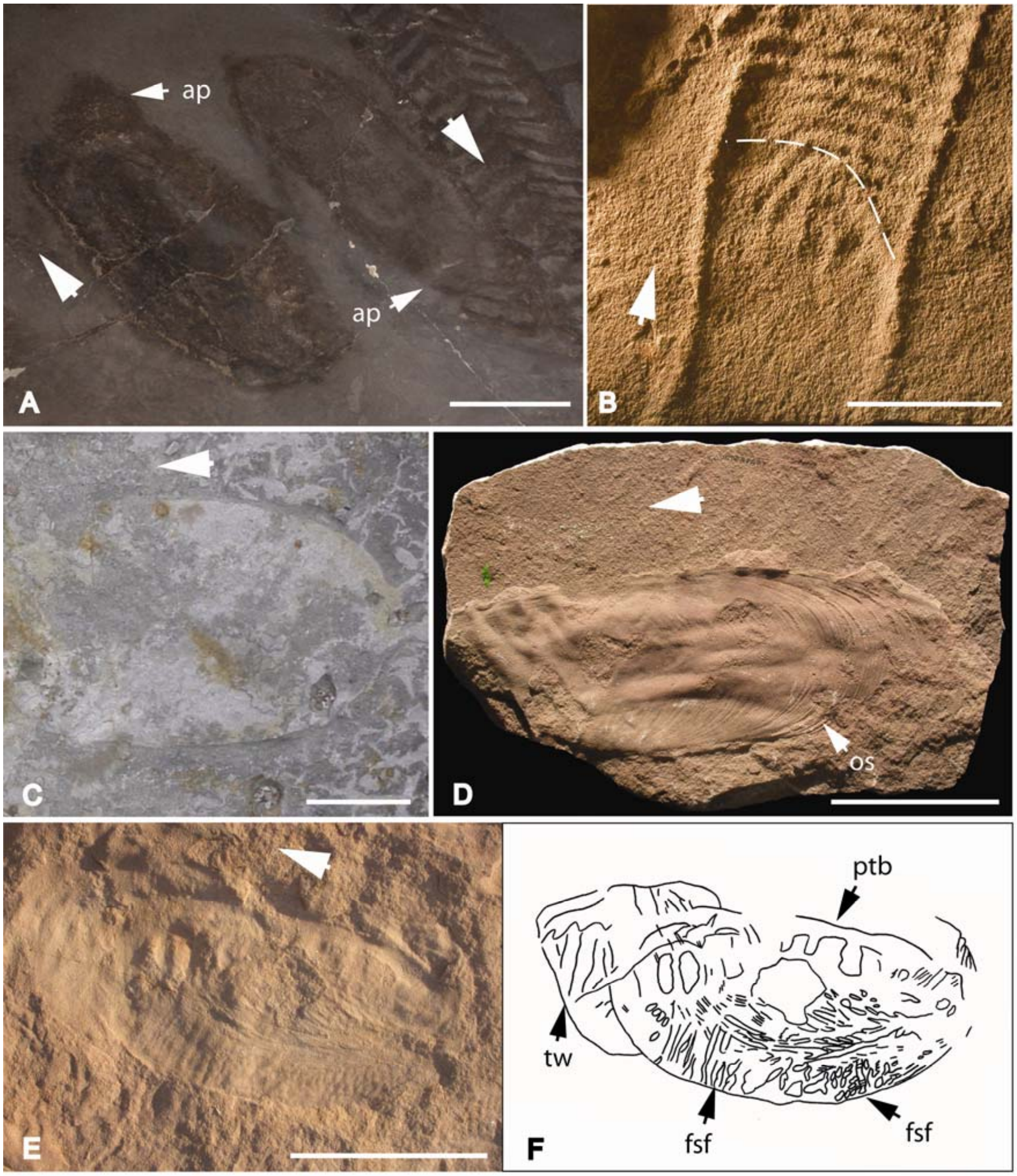


Figure 9.

Figure 10. Quantitative measurements taken from trackways. YPM 150696, a “typical” epifaunal trackway with lateral ridges (**LR**), transverse bars (**B**), and furrows (**F**). In this specimen the ridges are crenulated. Other lateral ridge morphotypes are described by Getty & Hagadorn (in review). Quantitative measurements taken from trackways include inner width (**I**), outer width (**O**), wavelength between bars (**W**), and lateral ridge height (**H**). **W** was measured from the crests of transverse bars (see inset), or, in the case of natural casts, between the “crests” of inverted troughs. **H** was measured from the top of the ridge to a line connecting the bottom of the trackway and the surrounding surface (**Y-Y’**). Transverse bar height (not labeled) was measured from the bottom of the furrows (**F**) to the top of the bar. Direction of travel is from upper right to lower left.

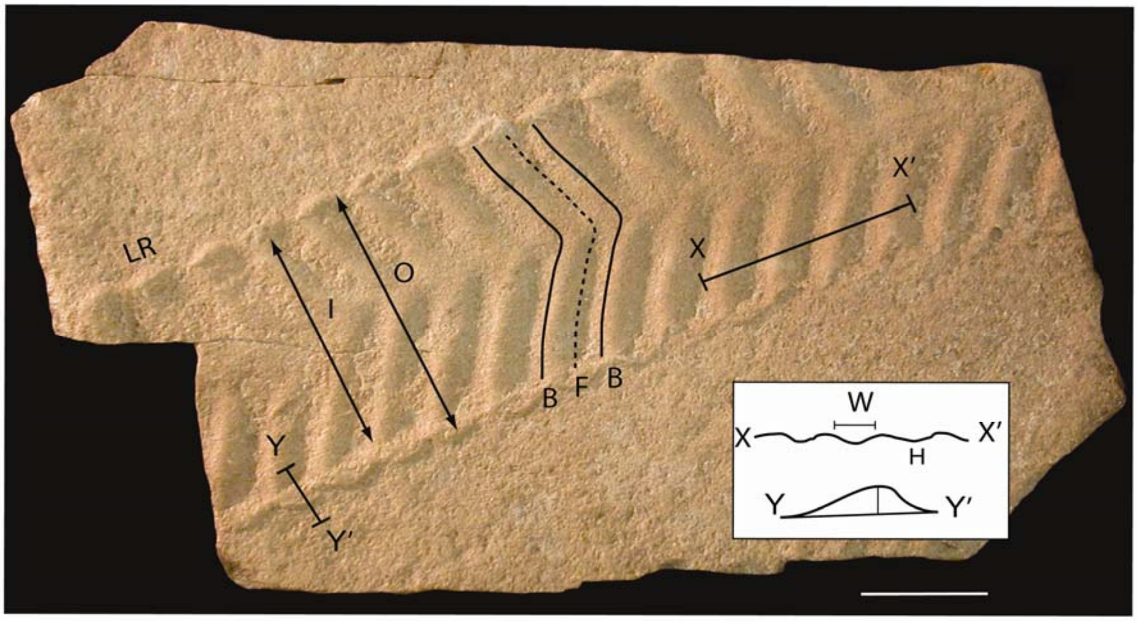


Figure 10.

Figure 11. Distribution of trackways based on grain size. Phi 1, coarse sand; 2, medium sand; and 3, fine sand. Large trackways (> 6 cm) are relatively unrestricted by grain size whereas small trackways (< 6 cm) occur mostly in fine and medium sand.

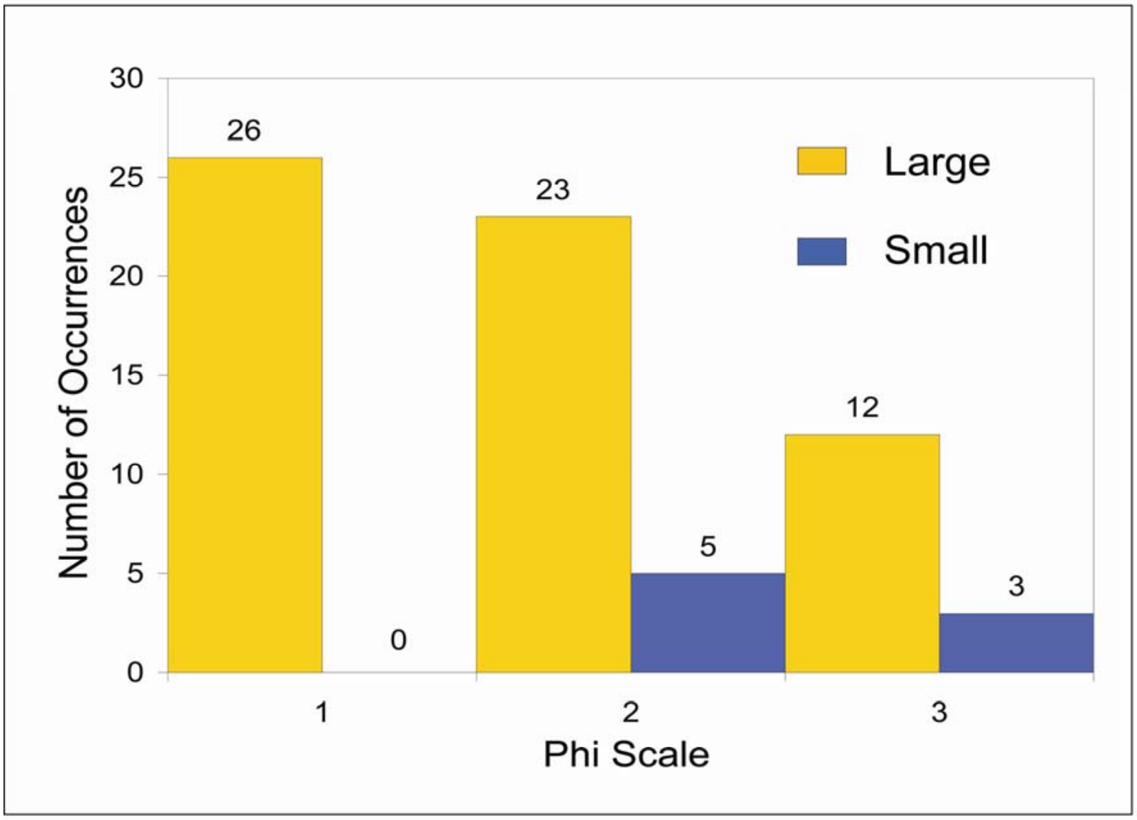

30
25
20
15
10
5
0
Number of Occurrences
26
0
23
5
12
3
Large
Small
1
2
3
Phi Scale

Figure 11.

Figure 12. Morphological characteristics inferred for the trackmaker. *Musculopodus* (=body impressions, labeled **bi**), such as those on NYSM-unnumbered-1 (A) indicate that the animal was elongate, ovoid, and bilaterally symmetric. Each impression connects with a trackway. The fine arcuate striations in NMNH 58544 (B) indicate that the rear of the animal maintained a constant oval shape during locomotion; these striations may have been produced by sand entrained in a mucus band produced by the trackmaker. *C. youngi* burrows, such as JF 05 FC (C) are much thinner than wide, and together with deep trackways, such as the tightly looping one in the center of the field photograph (D), from PRI-100 indicate that the animal was dorsoventrally flattened. Note the shallower trackway on the upper right of the photo; the animal that made it avoided entering the deeper trackway. Slab is offset by a joint at upper right. Some *C. wilsoni*, such as the one on T-302 (E), from PRI-100, change width considerably over short distances, indicating that the ventral surface of the animal's foot lacked a rigid skeleton. The intercalcated half bars (F; the first 7 bars are numbered; the half bars are 3 and 5) in a trackway on SSM 2006/20-1, from PRI 102, and the bifurcation of bars, as in a burrow on NMNH 532848 (G) further illustrate the flexibility of the foot. Note in (G) the rapid change in transverse bar shape as the animal moved from left to right. The first two bars are V-shaped, the next is an intercalcated half bar, which is in turn followed by a straight bar angled to the direction of travel. The next bar is a wedge-shaped half bar inserted opposite to the first half bar. Then, the bars become v-shaped again. Also note the smooth texture of the burrow in (G) relative to the surrounding matrix. Scales are 5 cm.

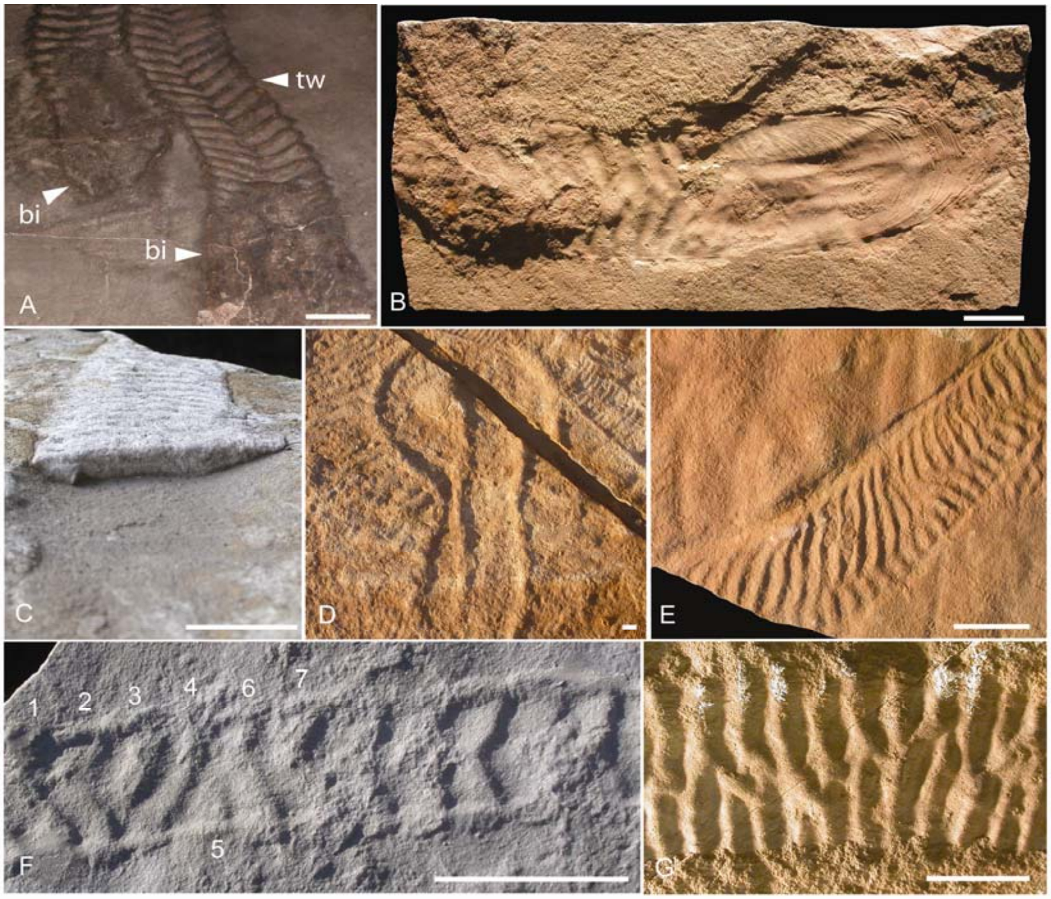


Figure 12.

Figure 13. Relationship of ridge height to trackway depth. The relationship suggests that lateral ridges resulted from the plowing of sediment out from under the animal as it moved. When seen in cross sectional profile, trackways of unequal depth, such as those in (A), have higher lateral ridges (indicated by arrowheads) on the deeper side of the trackway. Plot of pilot data (B) shows a similar correlation between lateral ridge height and trackway depth as that seen in the profiles, although not as pronounced. The correlation may not be strong due to the small sample size and also because *Climactichnites* on different surfaces may have undergone different weathering and erosional processes, such as the intensity of wind or water currents washing away sediment, that may have affected lateral ridge height. The data set is small because the original trackway height (or depth) measurement included both the height of the lateral ridge and depth of the trackway. Thus, the original measurement had to be modified before it could be applied to specimens, which was not done until late in this study. Consequently, only those specimens at Amherst College could be usedThe upper profile in (A) is taken from the curving trackway is seen in detail in Fig. 11A and the lower profile is taken from a trackway on the surface seen in Fig. 17. These profiles are not at the same scale.

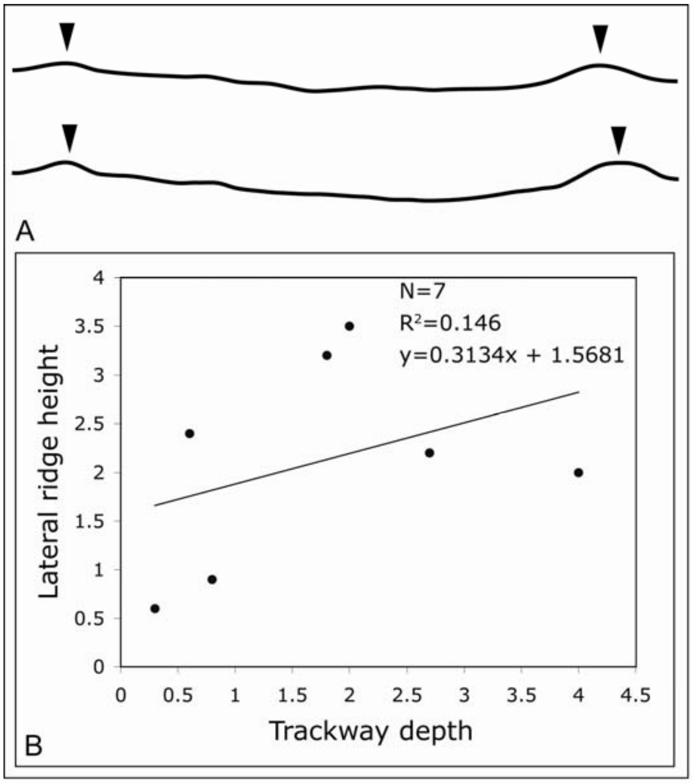

A
B
N=7
R²=0.146
y=0.3134x + 1.5681
Lateral ridge height
Trackway depth
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5

Figure 13.

Figure 14. Variability due to size. Line drawings of YPM 150696 (A), and the narrow trackway on SSM 2006/20-1 (B) drawn to the same scale (5 cm). Lateral ridges and transverse bars are in white, while furrows are colored black. When a portion of SSM 2006/20-1 is expanded to the same width as YPM 150696 (C), it becomes apparent that the wavelength is much greater in the narrow trackway, indicating that the wavelength between transverse bars does not increase at the same rate as the width of trackways. The scatter diagram (D), which plots maximum width and maximum wavelength for 181 trackways for which both the inner width and the bar wavelength could be measured, shows that wavelength increases at about one fifth the rate of track width.

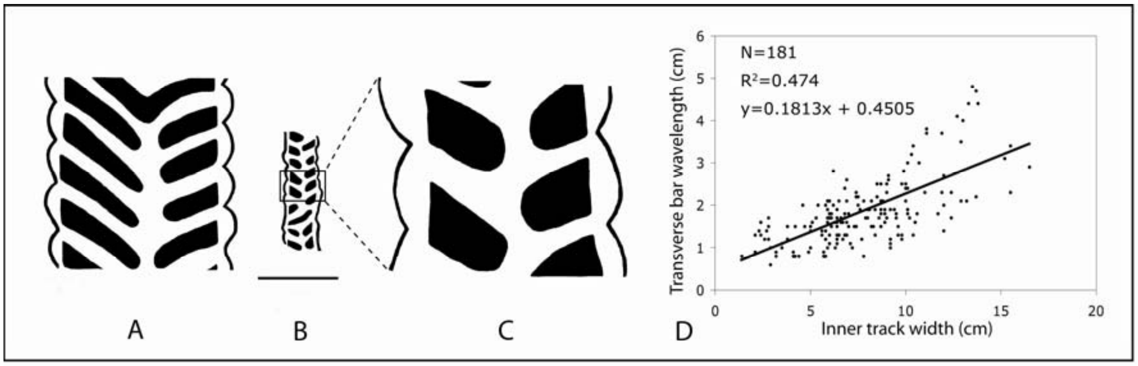

A
B
C
D
N=181
R²=0.474
y=0.1813x + 0.4505
Transverse bar wavelength (cm)
Inner track width (cm)
0
1
2
3
4
5
6
0
5
10
15
20

Figure 14.

Figure 15. Width and size distribution of trackways. In (A) the body impression leading into a trackway on ACM 68/2 illustrates the continuity in width often exhibited between resting and crawling traces. Thus it is possible to estimate body width from trackways without body impressions, provided that the trackway does not change considerably in width. The plot in (B) shows the length and width of 25 body impressions (solid circles), with an average length to width indicated by an open circle; the ratio is ~2.3:1. The histogram in (C) shows the width of 296 trackways for which inner width could be measured, and thus shows the inferred width of the trackmakers. Most trackways are between ~2 and 18 cm wide. The trackway on JF 16 FC (D), is currently the largest trackway known, and can be seen to the far right of the histogram in (C). ACM UC 234 (E) is a highly irregular infaunal burrow and illustrates the difficulty sometimes encountered when trying to determine the size of the animal based on subsurface traces. The trackway is oriented with its long axis extending from the lower left to the upper right. Note the frilly margin extending from the lateral margin of the burrow at upper left and that the burrow is partly buried at lower right. Compare the frilly margin with the lower right portion of Fig. 12B. The small trackway in (F), indicated by arrows, is exceptional in that the animal crosses a surface with abundant larger trackways, whereas most surfaces exhibit trackways of only one size range, as in the unnumbered slab from WINC (G). Scales in A and G are 5 cm, in E and F 10 cm, and the head of the hammer in D is X cm long. Arrows in (A) and (D) indicate the direction of locomotion.

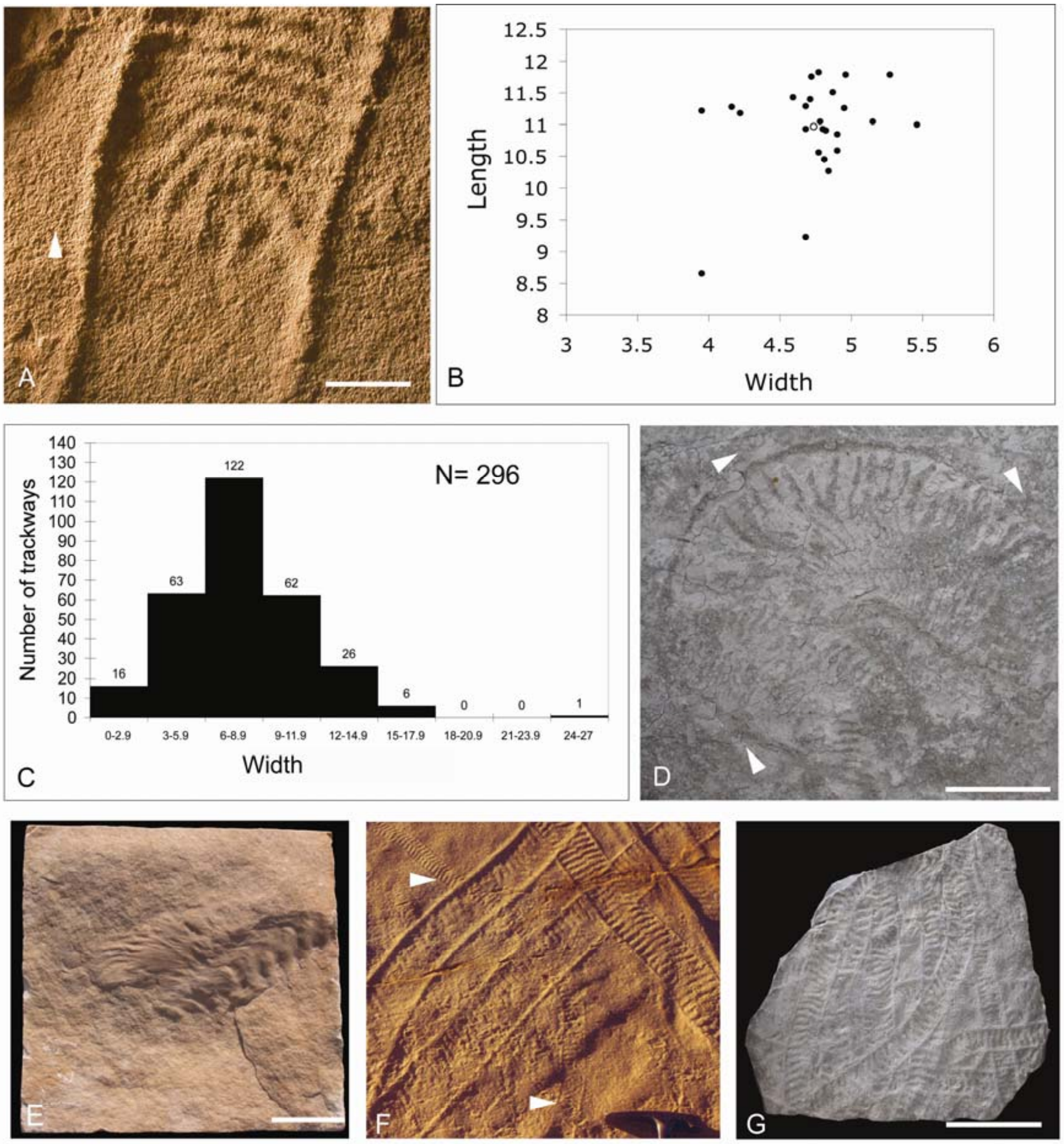

A
B
12.5
12
11.5
11
10.5
10
9.5
9
8.5
8
Length
3
3.5
4
4.5
5
5.5
6
Width
C
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
Number of trackways
N= 296
16
63
122
62
26
6
0
0
1
0-2.9
3-5.9
6-8.9
9-11.9
12-14.9
15-17.9
18-20.9
21-23.9
24-27
Width
D
E
F
G

Figure 15.

Figure 16. Width distribution for *C. youngi*. Measured specimens are from 1.8 to 10.6 cm wide.

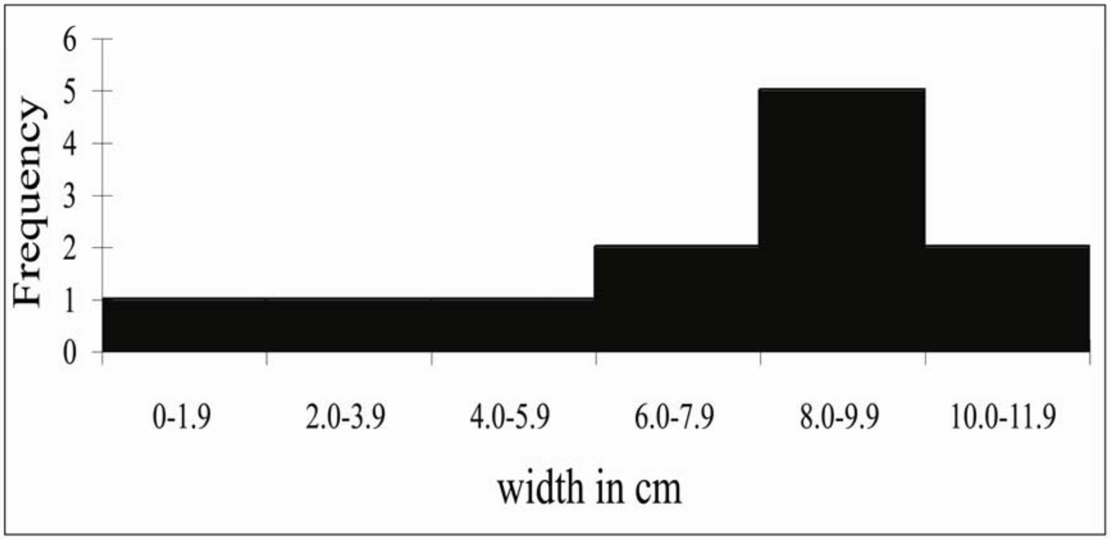
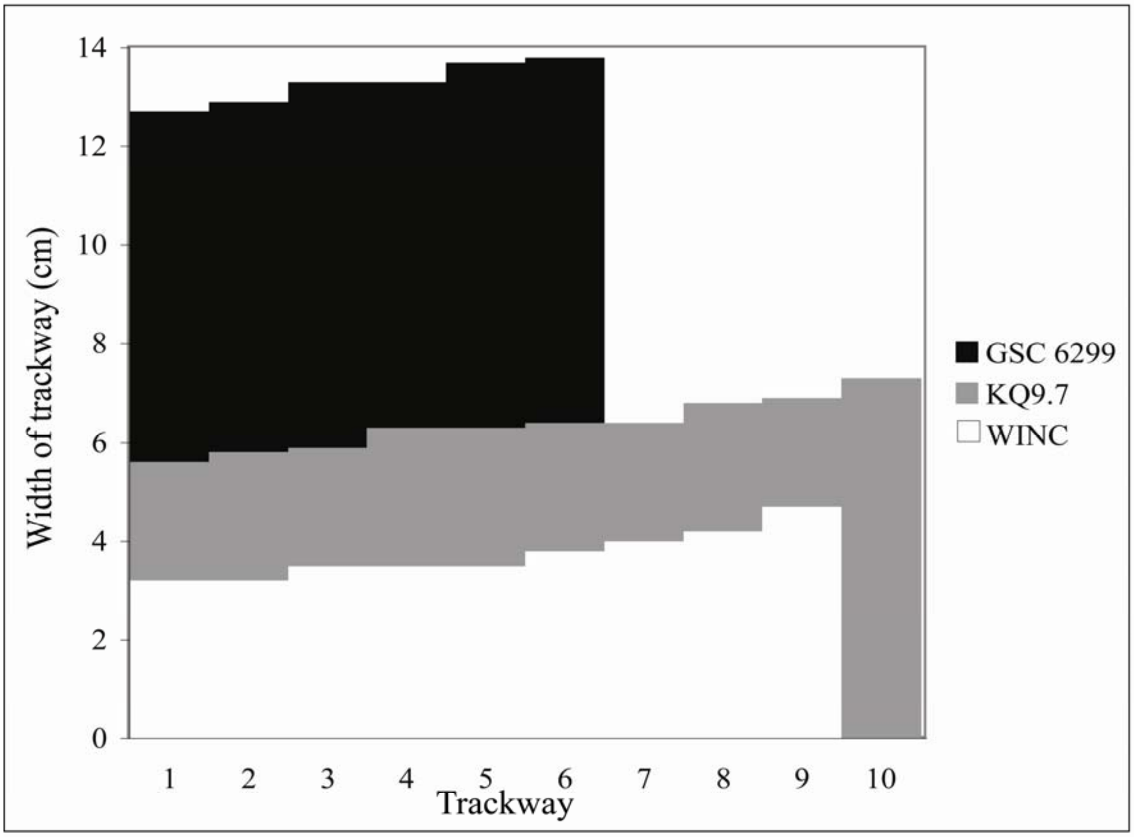

Frequency
6
5
4
3
2
1
0
0-1.9
2.0-3.9
4.0-5.9
6.0-7.9
8.0-9.9
10.0-11.9
width in cm

Figure 16.

Figure 17. Surfaces exhibiting limited size variability. The type slab, GSC 6299, from the Nepean Formation of Perth, Ontario, has large trackways ranging from 12.7 to 13.8 cm in width. In contrast, a slab at WINC, from the Potsdam Group of northwestern New York, bears trackways from 3.2 to 4.7 cm wide, and an *in situ* surface at the Krukowski quarry (PRI 100) bears trackways from 5.6 to 7.3 cm long.



14
12
10
8
6
4
2
0
Width of trackway (cm)
1
2
3
4
5
6
7
8
9
10
Trackway
■ GSC 6299
■ KQ9.7
□ WINC

Figure 17.

Figure 18. Locomotion of the *Climactichnites* trackmaker. Two complete strides are shown. Thick black lines within the outline of the body indicate transverse bars and ovate striations produced at the rear of the animal may be seen behind the body as thin black lines. Lateral ridges are omitted for clarity. See text for details of foot movement.

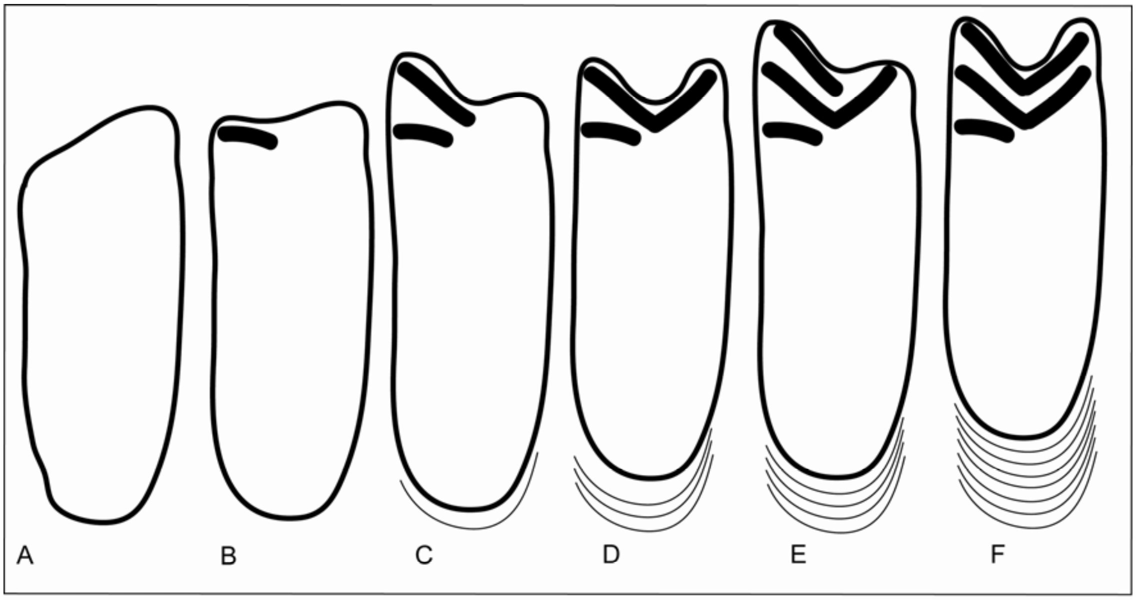


Figure 18.

Figure 19. Turning mechanisms. While turning, the animal often extended the side of the foot on the outside of the turn more than the side on the inside of the turn (A & B). In (A), ACM UC 232, the animal moved from left to right and made a right turn down the page; the wavelength between bars reaches over 2X as long on the left side of the turn as on the right (0.9 cm vs. 2.2 cm). In (B), UW 4019, the animal moved from right to left and took a 90° right turn up the page. Although the transverse bars are not visible on the outside of the turn, it is clear that the animal would have to have come to a near-complete stop on the right while the left side of the body turned. Two trackways are recorded on (C), a portion of SMM P 76.21.1, one on top of the other. The transverse bars of the overlying trackway were emplaced on the tops of the transverse bars of the underlying trackway. The animal presumably selected the transverse bars of the underlying trackway as anchor points during locomotion. As one trackmaker on NYSM-unnumbered-2 (D) made its turn to the left (the surface is a cast so the turn is opposite to what it appears in the photo) on a sharp-crested ripple-marked surface the portion of the body on the outside of the turn anchored on the crests of the ripples. Thus the animal selectively used sedimentary structures during locomotion. Arrowheads indicate direction of locomotion. Scale is 5 cm.

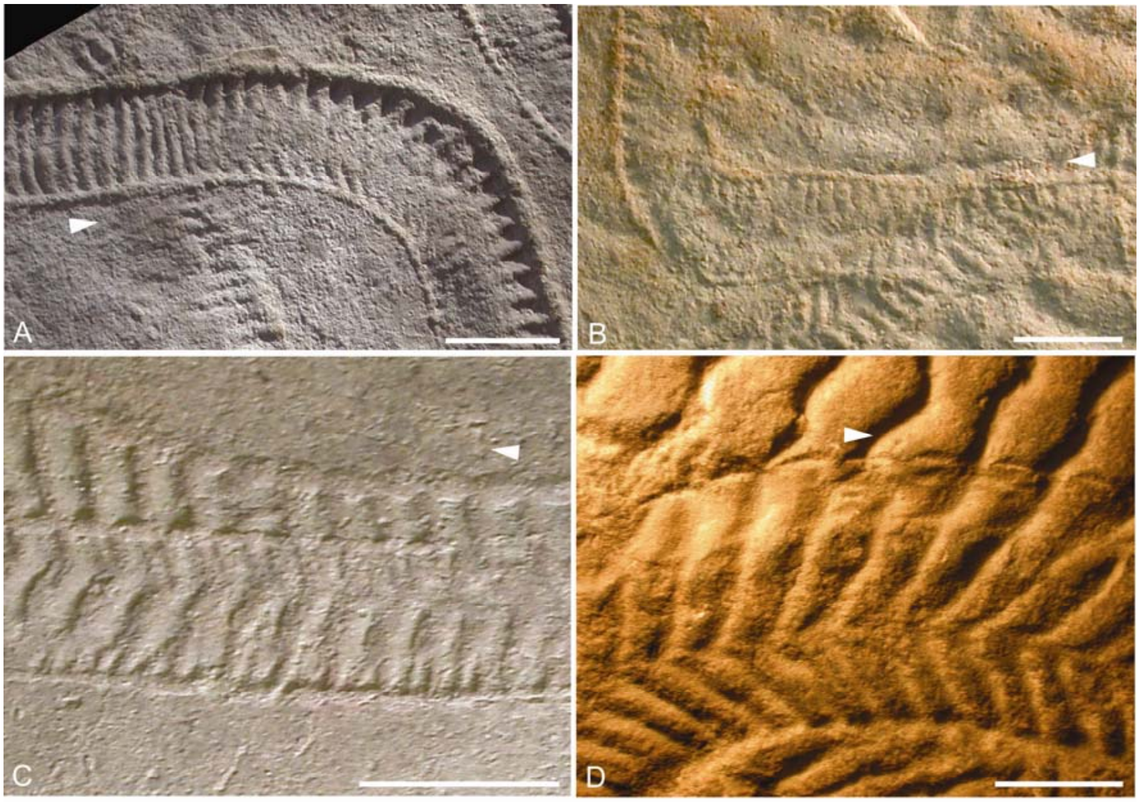


Figure 19.

Figure 20. *C. youngi*. Photograph of the lower portion of a large block from PRI-100 (A). When the block was split in half, this completely burrowed surface became visible. (B) is a close-up photograph of one of the trackways showing some of the characteristics common in burrows, including the lack of lateral ridges, bifurcating transverse bars, and fine striations superimposed on the bars. The pencil in (A) is ~14 cm long and the scale in (B) is 5 cm.

Figure 20.

Figure 21. Possible grazing surfaces. Sketch map of PRI-100-6.35. This bed preserves numerous domal structures, indicated by colored ovals, that are interpreted as microbial in origin. Two trackways on the surface follow the same looping pattern, possibly representing feeding. The large gray area is part of an overlying bed. See text for details. Drafted by W. Chen.

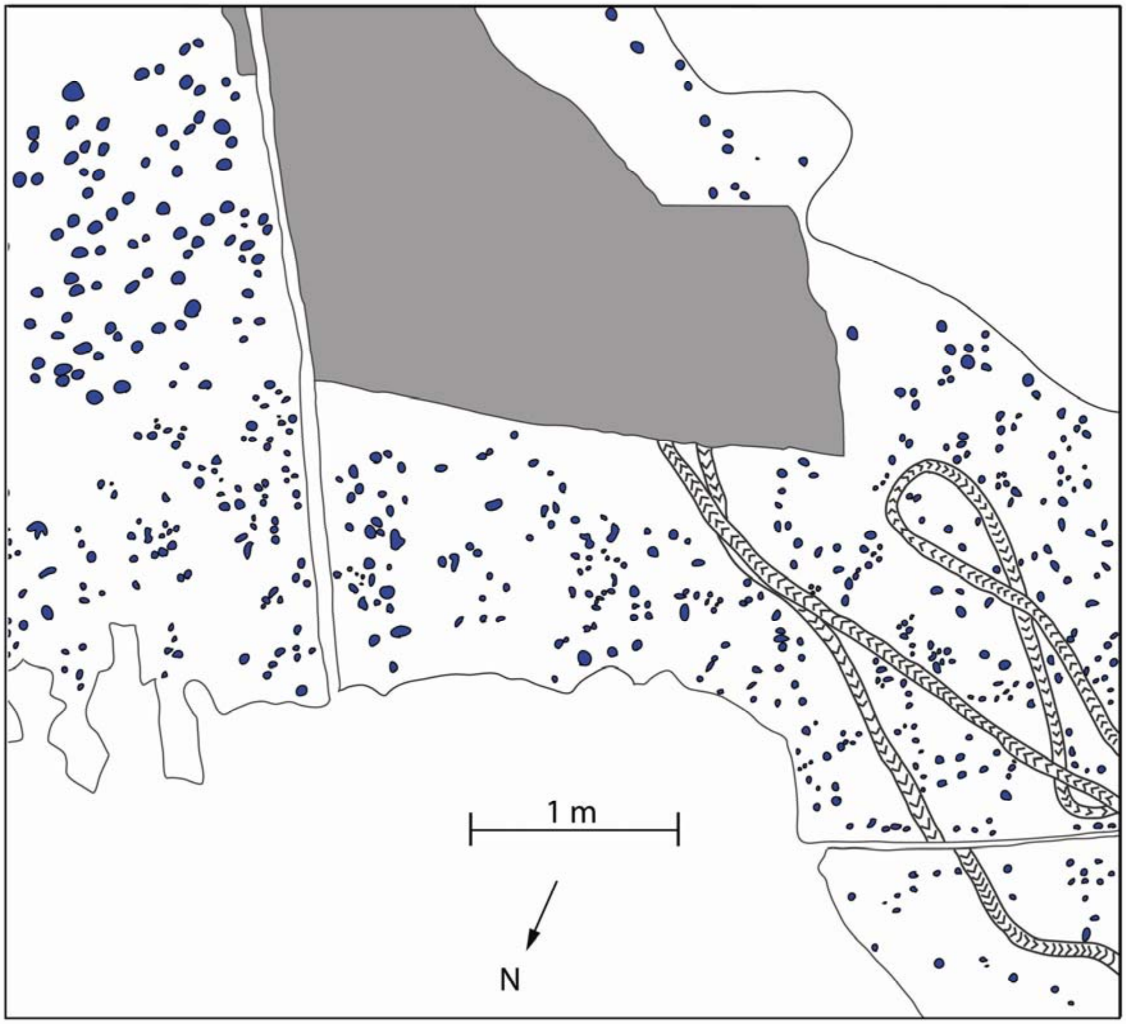


Figure 21.

Figure 22. *Climactichnites* moving through ripple troughs. A rippled, fine- to medium-grained sandstone layer at PRI-100-9.54 preserves numerous *Climactichnites* moving through the troughs of ripples. Note also the numerous channels, composed of medium- to very coarse-grained sandstone, above the rippled and bioturbated surface. These channels do not erode the ripples or trackways, suggesting that the rippled surface was cohesive at the time channel scouring occurred. The lack of clays and evaporite minerals in the rippled bed suggest that cohesion must have been achieved by some other means, perhaps by microbial mats. Drafted by W. Chen.

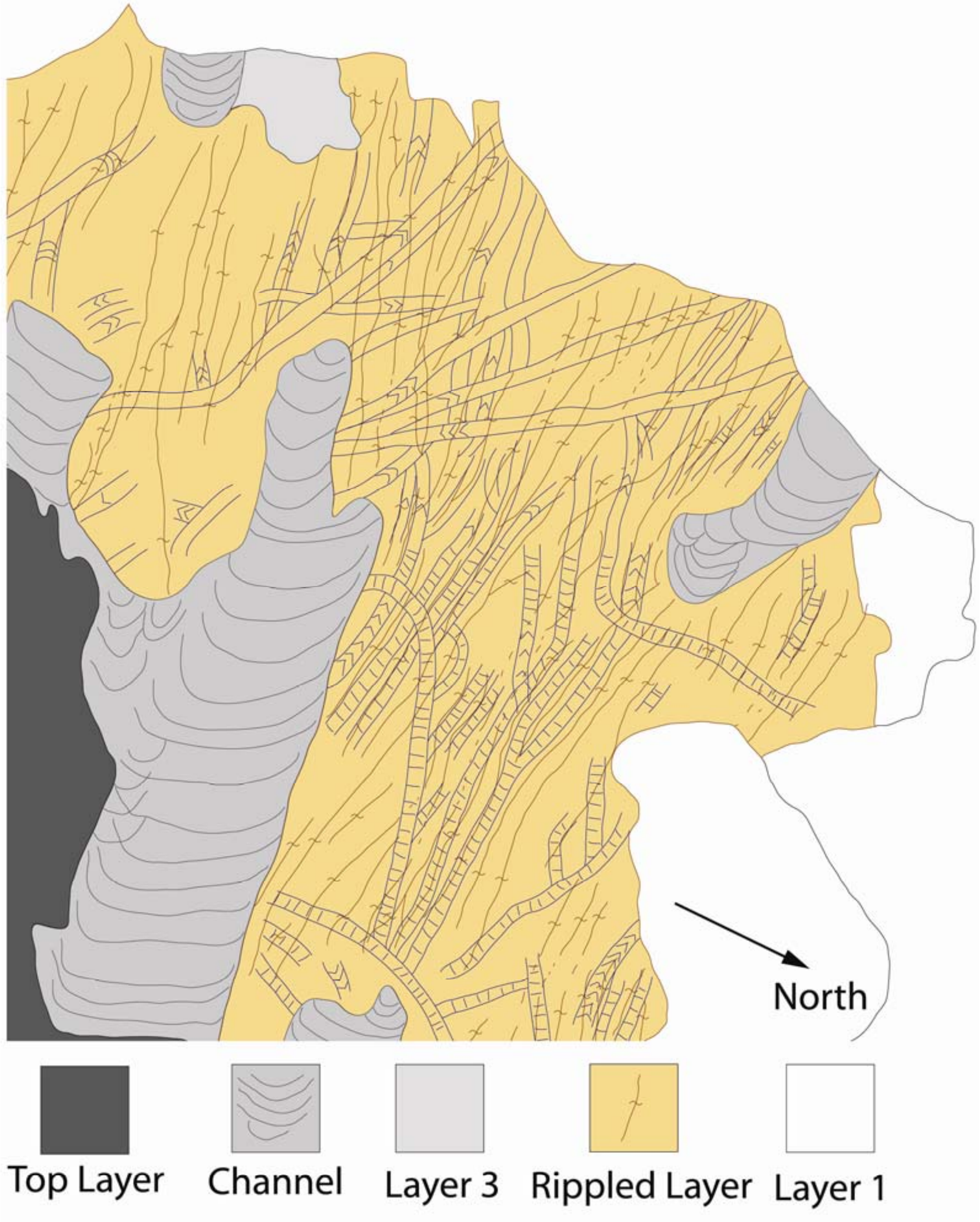


Figure 22.

Figure 23. A possible fecal strand (**mr**) within ACM UC 233. (A) is a plan view of the trackway showing the tightly folded nature of the median ridge (indicated by the large arrowhead). This trackway has a lateral ridge (**lr**) on the left side, but not the right. The area between the two lines represents one of the sections that was cut from the slab for analysis. The small arrowhead next to the lower line indicates the side of the section viewed in (B) and (C). (B) is a photograph of part of the cross section in visible light and (C) is an X-radiograph of the same. Note the conspicuous absence of laminations within the medial ridge in both the light and X-ray photos. Also note the dark black color of the ridge in (B), due to concentrated mud, compared to the adjacent sediment. Thin mud laminae are interspersed throughout the slab, including on the track surface, and appear black in (B) and white in (C). Scale is 5 cm.

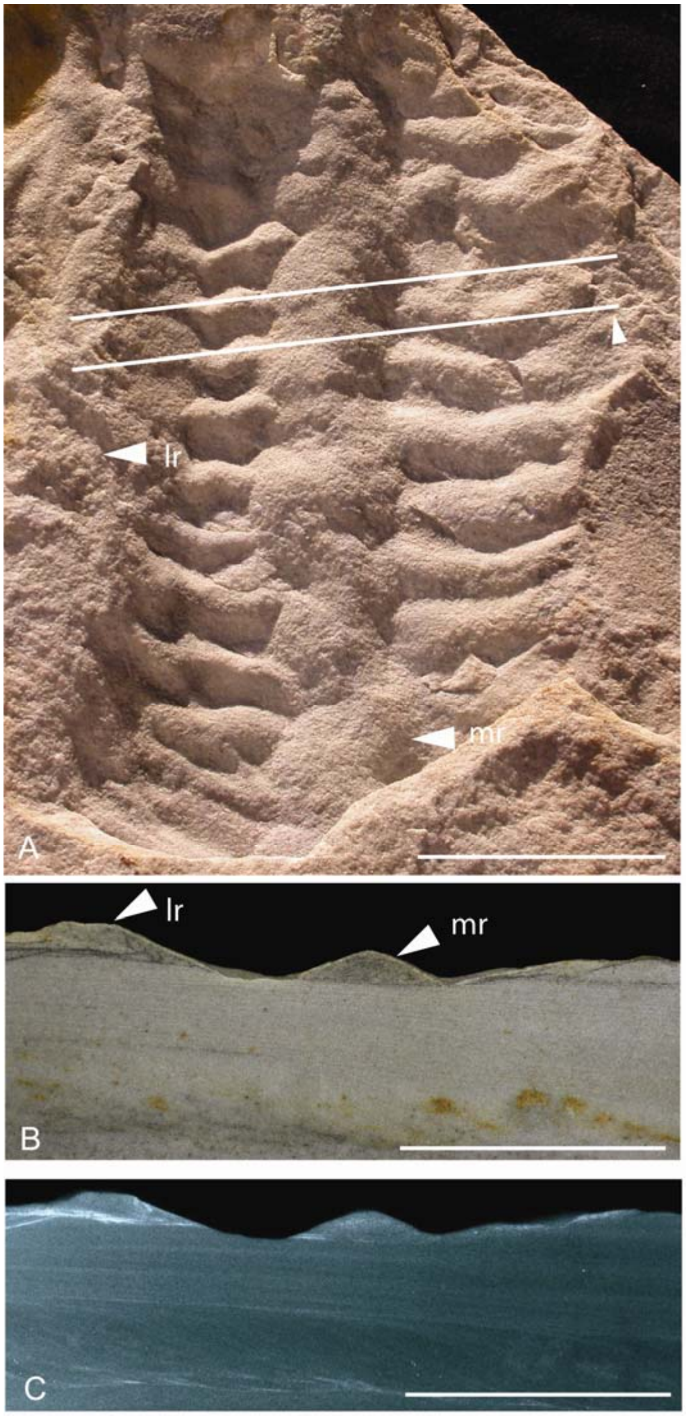


Figure 23.

Figure 24. Adhesion structures atop trackways. Field photograph of adhesion structures superimposed on a *Climactichnites*-bearing surface. (A) is an overview of a slab found as float at locality PRI-102. The box marks the boundaries of the close-up viewed in (B). The adhesion structures, which are produced subaerially by wind-blown sand, are superimposed on the trackways. It is unclear whether the trackways were produced subaqueously and then the water drained away from the surface to allow the adhesion structures to form or if the trackways formed subaerially. Coin in (A) is 19 mm wide.

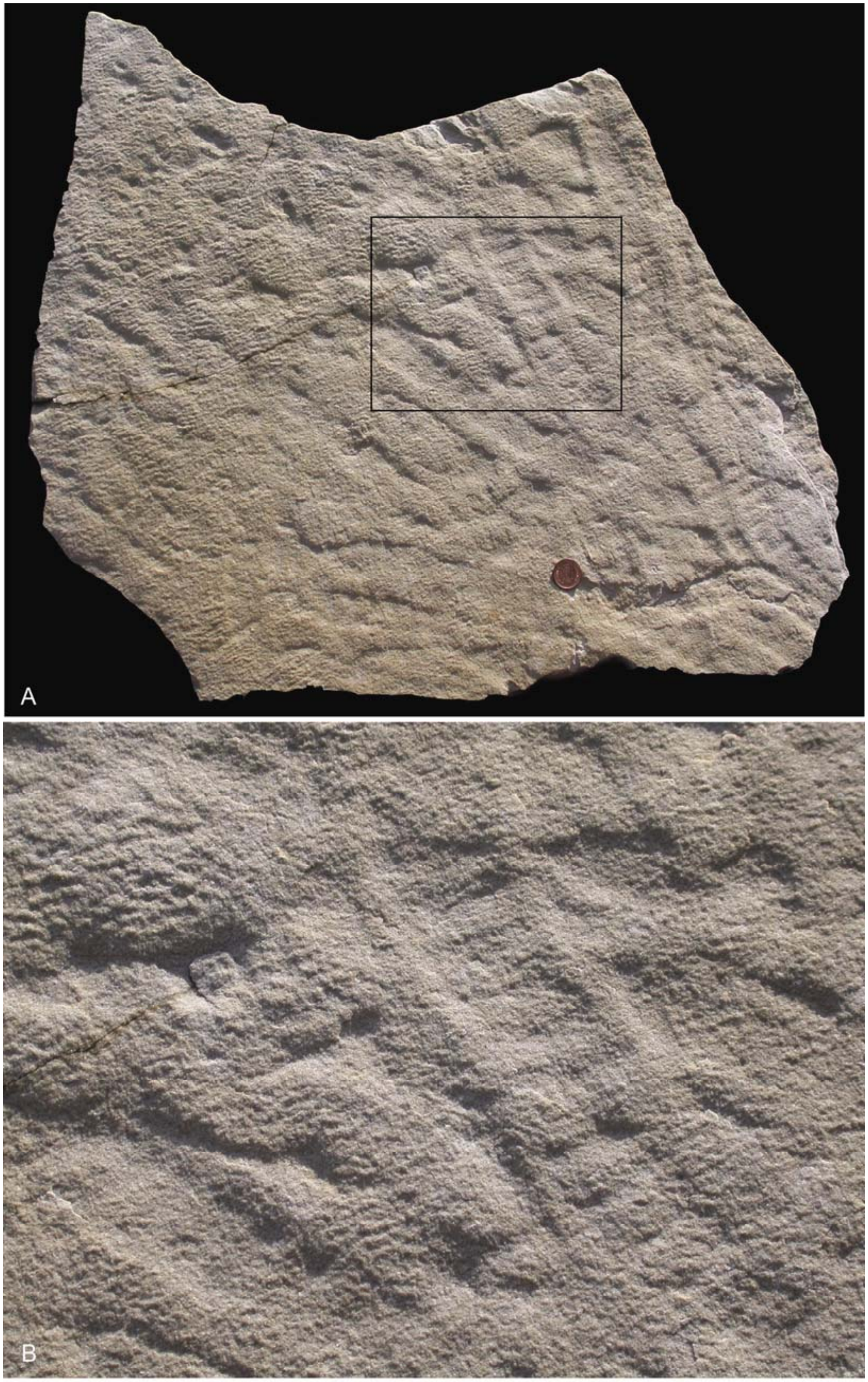


Figure 24.

Figure 25. Raindrop impressions atop trackways. Field photograph of *C. wilsoni* on a surface preserving raindrops at PRI-100-9.13. The raindrop craters are shown close-up in the right inset. However, all of the craters observed crosscut the trackways (left inset), indicating that the shower occurred after the trackway was produced. Thus, evidence for subaerial excursions by the trackmaker is equivocal on this surface. Scale is indicated by a ruler marked in both inches and centimeters and by a Swiss army knife 8.3 cm long.

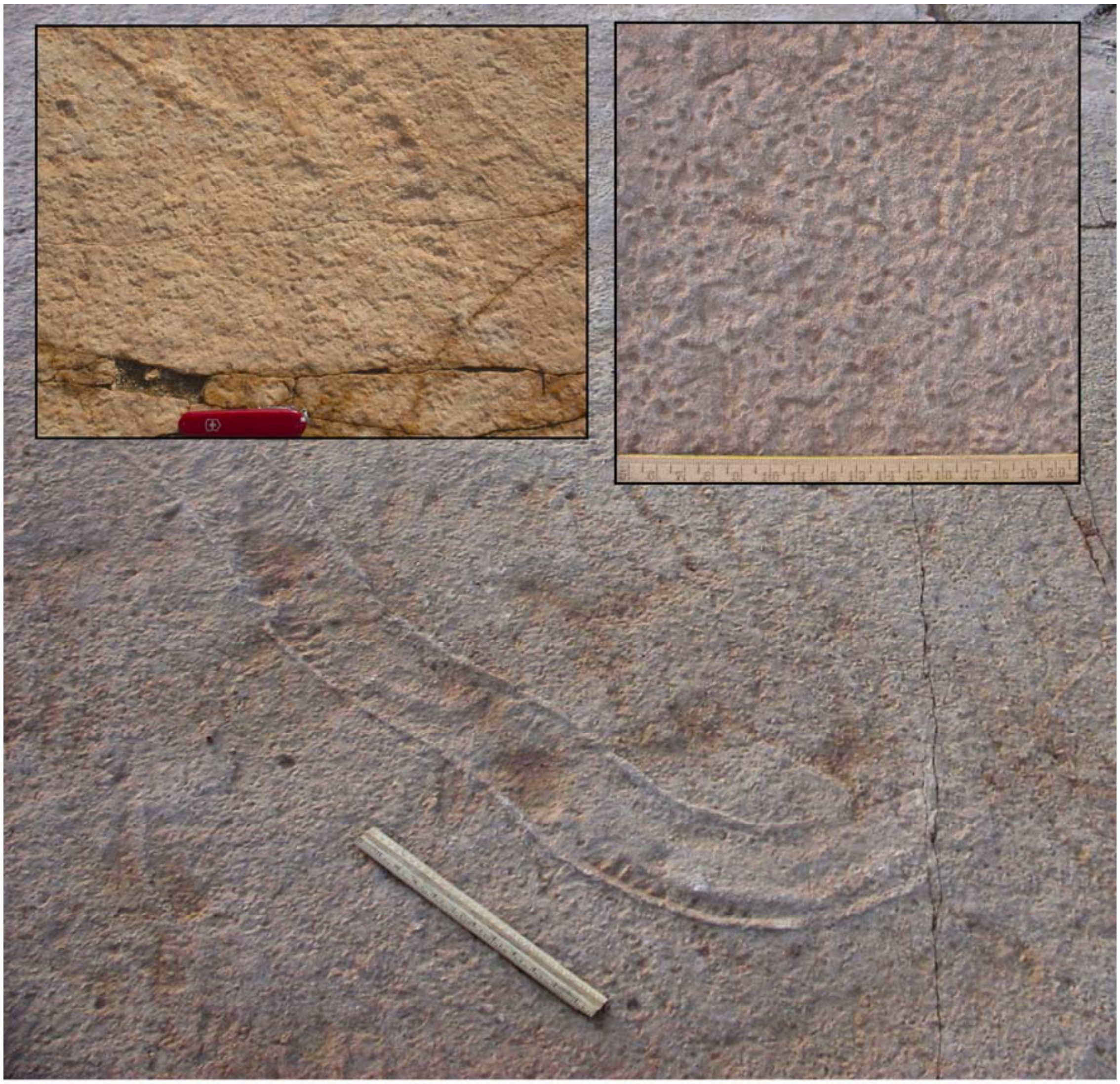


Figure 25.

Figure 26. Trackways within tidal channels. Field photograph of *C. wilsoni* in a tidal channel at PRI-100. The deep part of the channel is at the bottom of the photograph and the channel progressively shallows up the page; the tidal levee begins at the rubble pile at the top of the photograph. The preservational quality of the trackways varies with the depth of the channel. Toward the channel bottom no trackways are visible, but about halfway up the channel trackways consisting of lateral ridges are present. At the top of the channel trackways with transverse bars are visible (indicated by arrowheads). The inset at the upper left of the figure is an enlargement of the leftmost arrowed trackway. Variable *Climactichnites* morphology may offer additional evidence for subaerial excursions made by the trackmaker because preservation of the trackway is dependent on the amount of water in the sediment. In this case it is inferred that the channel was only partly full when the trackways were made and that saturated sand at the bottom of the channel did not preserve trackways, or that they were eroded. However, as the degree of saturation decreased upslope on the channel sides, the sediment was firmer and was able to preserve trackways. Tape measure is extended to 1 m.

Figure 26.

Figure 27. Experiment with gastropod trackways. *Climactichnites*-like trackways produced by *Viviparus intertextus* in a sand-filled tank. (A) Shows a trackway consisting of transverse bars and furrows, bound intermittently with lateral ridges, produced subaerially on wet sand. (B) Shows the same trackway as the tank is being filled with water. The large horizontal arrowhead points to the mucus band that draped the trackway; note that it is beginning to float on top of the water. The smaller vertical arrowhead points to the water level at the time the photograph was taken. This experiment suggests that mucus may not have been sufficient to preserve *Climactichnites*. Pencil in (A) is 6 mm wide and scale bar in (B) is 2 cm.

Figure 27.

Figure 28. Clay-rich *Climactichnites*-bearing slab, ACM-UC 243. Found as float at PRI-103, this slab shows a greenish colored clay, which may have played a role in the preservation of the trackways. Scale is 5 cm.

Figure 28.

Figure 29. Reconstruction of trackmakers. Here they are shown in a partially filled channel. The trackways become more clearly defined as the animal exits the water and begins subaerial trackmaking. Eyes are stylized and only included to indicate the anterior of the animal. The arthropod trackways *Diplichnites* and *Protichnites* are also visible. Sketch by PRG.

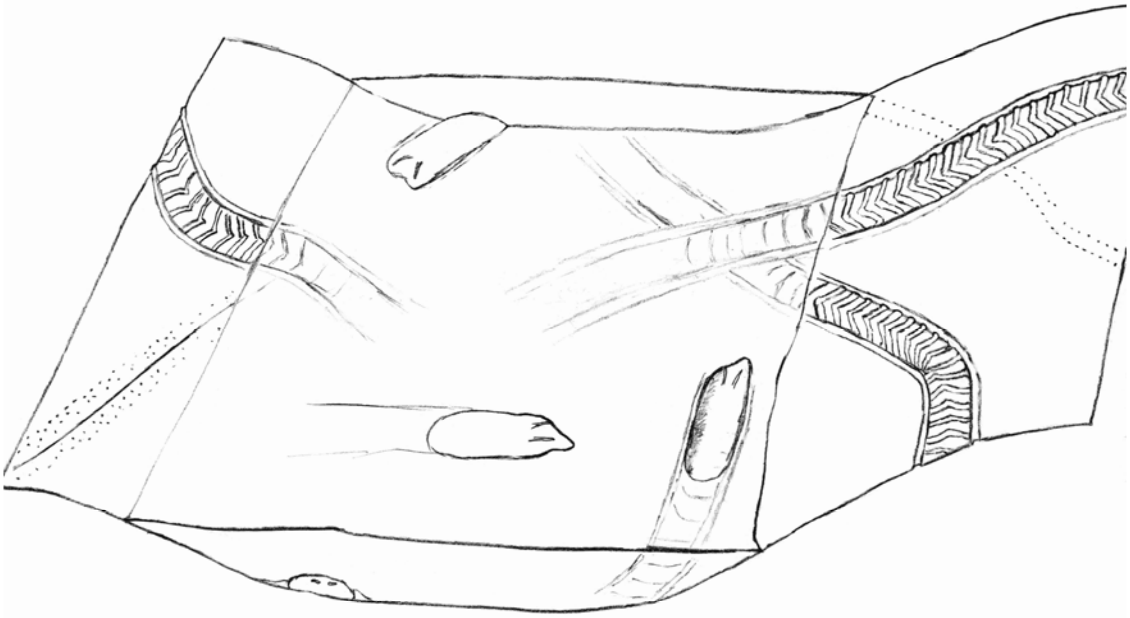


Figure 29.

APPENDIX A

TRANSVERSE BAR WAVELENGTH (RIGHT) TO INNER WIDTH (LEFT) FOR 181 TRACKWAYS.

DATA USED IN FIG. 14. MEASUREMENTS IN CM.

8.9	1.8
8.6	1.7
9.6	1.5
9.4	1.9
8.5	2.2
8.9	1.9
10.0	2.4
9.2	1.9
10.0	2.1
10.4	1.3
12.0	2.7
15.2	3.1
7.8	0.8
5.0	1.5
7.7	1.2
9.8	1.2
10.0	2.5
12.0	2.0
11.9	2.3
9.9	2.8
15.5	2.3
12.9	2.1
7.5	2.0
8.4	1.9
7.4	1.5
8.0	1.9
8.7	1.5
8.7	2.1
8.1	1.9
8.7	1.9
7.9	1.7
8.4	1.9
7.9	1.7
8.2	1.5
6.3	1.6
6.3	1.0
6.9	1.3
5.9	1.6
6.8	1.3
6.4	1.7

6.4	1.6
5.6	1.3
5.8	1.4
9.2	1.1
9.2	1.0
9.6	1.3
9.5	1.8
8.0	1.7
6.6	1.7
6.4	1.5
5.0	1.4
5.1	1.6
6.1	1.8
6.8	1.7
9.0	1.7
10.6	1.8
10.2	1.7
8.9	1.6
13.2	2.1
9.8	1.3
7.6	1.9
9.2	1.2
4.6	2.0
6.4	1.9
6.2	2.0
4.7	1.5
9.5	1.7
5.4	2.0
8.5	2.5
7.8	2.1
2.9	1.0
12.4	1.7
6.1	1.5
5.8	2.0
6.5	2.1
6.6	1.6
5.9	1.0
5.8	0.8
6.0	1.7
6.4	1.3
6.4	1.1
6.0	1.3
5.7	0.9
5.7	0.8
6.4	1.2
6.3	1.6
6.0	1.1
7.1	1.1
4.1	0.8
6.9	1.6

7.3	1.5
5.9	2.1
6.9	2.6
11.1	3.8
11	2.3
13.0	4.0
11.9	3.7
10.3	3.2
11.1	3.7
10.7	3.0
16.5	2.9
2.8	1.5
2.6	1.2
2.3	1.4
12.0	1.4
4.2	1.5
3.2	0.9
3.8	1.2
3.5	1.1
3.5	1.0
4.7	1.5
5.8	1.2
15.5	3.4
13.0	4.0
9.1	2.6
2.8	1.7
2.9	0.6
3.2	0.8
4.1	0.9
2.1	0.9
4.2	0.8
4.4	0.8
13.7	2.2
6.0	1.8
10.5	1.6
10.1	3.0
7.2	1.0
5.3	1.7
6.8	1.8
9.0	2.3
5.6	1.4
6.2	2.8
7.0	1.5
5.9	1.7
6.1	1.7
6.0	2.1
7.5	2.2
7.4	1.5
8.7	1.8
8.7	2.5

9.0	2.5
6.8	2.4
7.4	2.3
9.1	2.7
10.4	3.4
10.1	1.9
10.1	2.4
5.9	1.9
8.2	2.1
6.9	2.1
6.1	1.5
7.0	1.8
6.7	1.2
8.3	1.5
6.7	1.6
8.2	2.1
8.0	1.9
8.4	1.3
2.7	1.4
2.4	1.6
1.4	0.8
2.8	1.2
3.8	1.5
2.4	1.3
2.1	1.3
11.7	1.8
4.9	0.9
6.0	1.1
5.0	1.0
12.4	2.3
10.1	1.8
9.8	2.5
8.8	2.1
7.4	2.2
6.5	1.3
13.7	4.7
13.3	4.4
12.9	3.5
12.7	4.1
13.8	4.4
13.5	4.8

APPENDIX B

MUSCULOPODUS SEDENTARIUS LENGTH (LEFT) AND WIDTH (RIGHT).

MEASUREMENTS ARE IN CM.

4.95	11.26
3.95	8.65
3.95	11.22
4.96	11.79
4.78	11.05
4.16	11.28
4.87	11.51
4.68	10.93
4.72	11.76
4.22	11.18
4.84	10.27
4.81	10.45
4.90	10.59
5.46	11.00
4.77	11.83
4.68	11.29
4.90	10.85
5.15	11.05
4.77	10.56
4.80	10.93
5.27	11.79
4.68	9.23
4.59	11.43
4.71	11.40
4.82	10.91

APPENDIX C

MEASUREMENTS OF INNER WIDTH (IN CM) OF *CLIMACTICHNITES* FOR FIG. 15C.

1.4
2.1
2.1
2.2
2.3
2.4
2.4
2.5
2.6
2.7
2.8
2.8
2.8
2.9
2.9
3.0
3.0
3.1
3.1
3.2
3.2
3.2
3.5
3.5
3.5
3.6
3.7
3.8
3.8
3.8
3.9
4.0
4.0
4.0
4.1
4.1
4.1
4.2
4.2
4.2
4.2
4.4
4.5
4.6
4.7
4.7
4.8
4.9
4.9
5.0
5.0
5.0
5.0
5.1
5.1
5.1
5.1
5.3
5.3
5.4
5.4
5.4
5.5
5.5
5.5
5.6
5.6
5.6
5.6
5.7
5.7
5.8
5.8
5.8
5.9
5.9
5.9
5.9
5.9
6.0
6.0
6.0
6.0
6.0
6.0
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6.0
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6.2
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6.3
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6.4
6.4
6.5
6.5
6.5
6.5
6.6
6.6
6.6
6.7
6.7
6.7
6.8
6.8
6.8
6.8
6.8
6.9
6.9
6.9
6.9
7.0

7.0
7.0
7.1
7.1
7.1
7.2
7.2
7.3
7.3
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7.4
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7.4
7.4
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8.0
8.0
8.0
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8.5
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10.0
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10.2
10.2
10.3
10.4
10.4
10.4
10.5
10.6
10.6
10.6
10.6
10.6
10.7
10.7
11
11.1
11.1
11.4
11.6
11.7
11.9
11.9
11.9
11.9
12.0
12.0
12.0
12.2
12.4
12.4
12.6
12.7
12.7
12.7
12.9
12.9
13.0
13.0
13.2
13.3
13.3

13.3	13.8	15.5
13.5	14.0	16.8
13.6	14.0	17.0
13.7	15.2	25.0
13.7	15.5	
13.8	15.5	

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