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Exceptional Preservation and Substrate Evolution in Early Paleozoic Marine Shelfal Environments

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Exceptional Preservation and Substrate Evolution in Early Paleozoic Marine Shelfal
Environments

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Geological Sciences

by

Lidya Grace Tarhan

December 2013

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firmgrounds: evidence for predation and implications for Palaeozoic substrate evolution in *Rusophycus* burrows from the Silurian of New York" (*Lethaia*, 2012, v. 45, p. 329-341). The co-author Mary L. Droser listed in that publication directed and supervised the research which forms the basis for this dissertation. The co-author Sören Jensen provided field assistance, technical expertise and thoughtful discussion.

ABSTRACT OF THE DISSERTATION

Exceptional Preservation and Substrate Evolution in Early Paleozoic Marine Shelfal
Environments

by

Lidya Grace Tarhan

Doctor of Philosophy, Graduate Program in Geological Sciences
University of California, Riverside, December 2013
Dr. Mary L. Droser, Chairperson

The radiation of burrowing metazoans in the early Phanerozoic is commonly assumed to
have dramatically altered the properties of marine sediment. The advent of biogenically-
mediated sediment mixing, by profoundly impacting nutrient burial fluxes, organic
carbon remineralization, seafloor oxygenation and sediment ecology, likely instigated
Phanerozoic biogeochemical cycling. However, the timing of the development of mixed
seafloor sediment has, historically, not been well constrained. Mixing has commonly
been assumed, in the absence of data, to occur at the Precambrian–Cambrian boundary
with the appearance of the index fossil and three-dimensional burrow *Treptichnus pedum*
(the "Cambrian substrate revolution" or "agronomic revolution"). Likewise, instances of
exceptional preservation—preservation of near-surface structures of high taphonomic
fidelity, including bioglyphic detail—have previously been anecdotally reported from
lower Paleozoic trace fossil assemblages worldwide. However, it has hitherto been
unknown to what extent this exceptional preservation characterizes the lower Paleozoic
record as a whole.

Herein I present new ichnological, stratigraphic and taphonomic data suggesting that, although significant developments in infaunalization— paleobiologically complex animal–substrate interactions, particularly burrow construction—occurred during the early Paleozoic, mixing remained suppressed throughout this interval. I demonstrate that shelfal sediment in the earliest Cambrian was essentially unmixed and that, even as late as the middle Ordovician—over 75 million years after the Precambrian–Cambrian transition and well after the appearance and diversification of supposedly deposit-feeding trilobites, seafloor shelfal sediment remained largely unmixed on a global scale. Moreover, lower Paleozoic heterolithic shelfal successions are also characterized by widespread exceptional preservation of shallow-tier ichnological assemblages and bioglyphic structures, implying formation and preservation in a cohesive, i.e. unmixed substrate. Bed-sole assemblages are preserved through syndepositional casting rather than intrastratally. Well-mixed intervals are typically of limited spatial extent; macro-scale depositional fabrics are largely undisrupted. These findings challenge the current assumption that mixing occurred with the first appearance of three-dimensional burrows and that early Paleozoic infauna were efficient sediment mixers. The protracted development of the mixed layer holds important implications for exceptional preservation in both the trace and body fossil records, for the structure of lower Paleozoic benthic ecosystems, and for the advent and development of modern-style biogeochemical cycling.

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INTRODUCTION

Substrate Evolution and the Precambrian-Cambrian Transition

A profound radiation in the morphological and ecological complexity of life occurred during the Cambrian Period (542–488 million years ago). Prior to the Cambrian, the seafloor was populated largely by soft-bodied and stationary organisms living atop or very shallowly within microbially-bound sediments (e.g. Gehling, 1999; Gehling and Droser, 2009). However, following dramatic increases in animal abundance, diversity, biomineralization and mobility in the Cambrian—an interval of unprecedented macrofaunal innovation commonly known as the "Cambrian Explosion" (e.g. Sepkoski, 1981; Erwin et al., 2011)—life on the seafloor became much more complex, both at the organismal and the ecosystem level.

The diversification of burrowing marine bilaterian animals and the onset of sediment mixing, an event commonly referred to as the "Cambrian substrate revolution" (Bottjer et al., 2000) or "agronomic revolution" (Seilacher and Pflüger, 1994) is considered to have played a major role in this transformation. The radiation of burrowing animals, the development of the infaunal (within seafloor sediments) lifestyle—common among marine invertebrates today, which utilize it as a source of nutrition, protection and site of ambush—and colonization of this previously unexplored niche profoundly altered the ecological structure of seafloor communities (e.g. Rhoads and Young, 1970; Thayer, 1979).

The development of three-dimensional burrowing, following the appearance of *Treptichnus pedum*—the earliest complex, three-dimensional burrow (e.g. Narbonne et al., 1987; Landing, 1994; Droser et al., 1999)—in the earliest Cambrian is commonly invoked as the primary causative agent for the transformation of the microbial mat-sealed seafloor ("matgrounds") and largely immobile organisms of the Proterozoic to the thoroughly burrowed seafloor sediments ("mixgrounds") and active infauna of the Phanerozoic (Seilacher and Pflüger, 1994), as well as for a wide range of contemporaneous geochemical and taphonomic phenomena, such as declines in microbialite abundance and diversity, significant changes in nutrient fluxes, seafloor oxygenation and ocean chemistry, the disappearance of the Ediacara Fauna and Ediacaran-style preservation, changes in the stratigraphic character of event bedding and the loss of Burgess Shale-type preservation (e.g. Awramik, 1971; Brasier, 1990; Sepkoski et al., 1991; Allison and Briggs, 1993a, b; Gaines and Droser, 2002; Canfield and Farquhar, 2009). The initiation of infaunal sediment mixing, moreover, profoundly impacted the development of Phanerozoic biogeochemical cycles. Foremost, sediment mixing likely dramatically altered bioessential nutrient fluxes and the cycling of redox-sensitive elements by increasing seafloor porosity and oxygenation (e.g. Brasier, 1990; Canfield and Farquhar, 2009). However, neither the timing of the development of infaunal sediment mixing nor the varying impact of an emergent mobile infauna across different seafloor environments are well constrained. Constraining the pace of mixed layer development—and thus the role of burrowing animals as ecosystem engineers—is

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an essential prerequisite to tracking the establishment of modern biogeochemical cycling

and Phanerozoic-style seafloor communities across both time and space.

The ecological and geochemical character of the modern seafloor is strongly influenced

by the nature and depth of the mixed layer—the zone of sediment homogenized by

burrowing animals, which today extends 3–10 cm below the sediment-water interface

(Ekdale et al., 1984). The modern mixed layer consists of sediment of 'soupy' or

flocculent consistency, high water content and low shear strength. The mixed layer is

densely populated by infaunal meiofauna and macrofauna and heavily exploited by both

infauna and epifauna (benthic organisms living on top of the seafloor surface) for its high

nutritional content. The mixed layer and its associated infaunal communities are not,

however, well represented in the stratigraphic record; due to continual homogenizing

activity by burrowing infauna and resulting low sediment shear strength, burrows

collapse once they are vacated and resuspension of mixed layer sediments is common

(Ekdale et al., 1984; Davis, 1993). The fossil record, therefore, is heavily skewed toward

the transition and historical layers – the deeper zones of sediment in which the burrows of

deep-burrowing (maintaining open burrows of up to 2.5 m depth in modern seafloor

environments), 'elite tier' fauna are preserved (Pemberton et al., 1976; Ekdale et al.,

1984; Bromley, 1996).

The trace fossil record—burrows, tracks and trails preserved in the geologic record—

provides our best window into the record of early animal behavior and seafloor

colonization. Unlike body fossils, trace fossils are not actual remains, but rather directly record the behavior of an organism and seafloor substrate conditions at the time of the structure's formation, and thus capture morphological, functional, ecological and environmental information otherwise inaccessible from the body fossil record alone (e.g. Frey and Seilacher, 1980). Burrows, tracks and trails that are made close to the sediment-water interface (shallow-tier trace fossils) are rarely preserved today because they are typically re-burrowed by other organisms; the majority of the Phanerozoic stratigraphic record is characterized by infaunally reworked sediments and complex (three-dimensional) fabrics ("ichnofabrics") (e.g. Bromley and Ekdale, 1986).

There is some evidence that the trace fossil record of the lowermost Paleozoic, however, is distinct from the majority of the Phanerozoic (Droser et al., 2002a). The exceptionally high fidelity of preservation of surficially produced and shallow-tier (mm- to cm-scale depth) traces like *Treptichnus* and the trilobite-produced *Rusophycus* burrows and *Cruziana* furrows commonly found in lower Paleozoic successions indicate a cohesive substrate and limited sediment mixing (Droser et al., 2002a). Bioturbation at the Precambrian-Cambrian transition and in the earliest Cambrian appears to have been very shallow, relative to modern seafloor sediments, with traces commonly penetrating no more than a couple centimeters' depth into the sediment (Droser et al., 2002a). The exceptions, such as *Skolithos* and *Arenicolites*, common in early Cambrian and younger near-shore, high-energy sands (e.g. Sepkoski et al., 1991) are attributed to dwelling rather than deposit-feeding structures (Thayer, 1979; Thayer, 1983; Droser et al., 2002b).

However, dwelling burrows would have merely locally increased advection of bottom-waters into the sediment (Aller, 1982; Droser et al., 2002a, b), rather than mediating physical or chemical homogenization. The exceptional preservation of shallow (mm- to cm-scale) traces like *Gyrolithes*, *Treptichnus* and *Rusophycus* and surficial biogenic structures such as the scratch circle Kullingia and tool marks reported from certain lower Cambrian deposits, as well as 'floating' preservation of open burrows suggest that, in earliest Cambrian sediments, the mixed layer was locally very poorly developed, extending no more than a couple centimeters' depth (Droser et al., 2002a). The crisp preservation of these shallow-tier structures may represent a critical 'Goldilocks' temporal interval in the record of infaunalization: some level of infaunal activity is clearly necessary to create these structures. However, too much infaunal activity will lead to their destruction and sediment homogenization; upon reaching a certain threshold, infaunal activity becomes 'self-erasing.' Therefore, the available evidence suggests that the shallow-tier trace fossil record of the lower Paleozoic may be a preservational anomaly, representing a brief temporal window of precariously balanced infaunal development, and one ideally suited to the study of seafloor ecology and taphonomy during the early stages in the diversification of metazoan life.

Certain workers (e.g. Droser et al., 2004; Jensen et al., 2005) have suggested that limited bioturbation and thus mixed layer development may have, in earliest Paleozoic marine settings of fine-grained siliciclastic lithologies, allowed a cohesive substrate to form at or within centimeters of the sediment-water interface. A cohesive substrate or firmground,

by sharply casting and preserving the imprint of metazoan activity (as well as of abiogenic sedimentological processes), may have greatly enhanced the preservation of shallow-tier and surficial structures in the earliest Paleozoic (Droser et al., 2002a). Firmgrounds offer an explanation for the exceptionally preserved shallow-tier trace fossils and surficial sedimentary structures observed in lower Paleozoic normal marine strata (Crimes, 1975; Jensen et al., 1997; Jensen et al., 2002a, b; Droser et al., 2002a, b, 2004). However, the mechanisms responsible for the anomalous capture of these structures are debated; it is unclear whether early Paleozoic firmgrounds were due solely to mechanical sedimentary properties (Crimes, 1975; Goldring, 1995) or if their formation required an organic "bioglue" coating of sediment grains (Seilacher, 2008). Further, non-actualistic preservational conditions may also have contributed to exceptional trace fossil preservation. For instance, benthic silica or carbonate precipitation may have been more common and rapid in the early Paleozoic (e.g. Maliva et al., 1989; Sepkoski et al., 1991; Gaines et al., 2012b).

Likewise, whether "exceptional" trace fossil preservation was the exception or the rule for early Paleozoic marine environments and what relationship exceptional preservation may bear to mixed layer development have long remained unresolved. Detailed and systematic studies tracking the distribution of shallow-tier trace fossils in lower Paleozoic strata have largely been lacking or confined to the scale of individual samples and assemblages, limiting their applicability to the detection of broad-scale temporal and environmental trends. Previous efforts have also tended to focus upon the advent of

infaunal colonization, rather than to the development of sediment mixing or have been confined to the upper Neoproterozoic and lowermost Cambrian (McIlroy and Logan, 1999; Droser et al., 2002a, b; Droser et al., 2004; Jensen et al., 2005). Protracted mixed layer development has been documented in carbonate strata of the western USA (Droser and Bottjer, 1988; Droser and Bottjer, 1989), but comparable studies documenting trends in siliciclastic strata, coupled exploration of the relationship between exceptional preservation and mixing, and examination of these data at an inter-regional or global scale have hitherto been lacking.

The Mechanical Properties of Sediments

The cohesiveness of a substrate is greatly influenced by the innate physical properties of its constituent sedimentary particles. Both the production and the preservation of traces are directly related to a substrate's bearing capacity and this in turn is dependent upon sediment cohesion, internal angle of friction, density and water content (Crimes, 1975). Since the cohesion and internal angle of friction of sediments are directly related to grain size, fine-grained sediments (silts and muds) are naturally more cohesive than some coarser sediments (Crimes, 1975). Therefore, as demonstrated by Hjulström (1935), fine-grained sediments are more resistant to erosion than coarser-grained sediments; likewise, currents depositing even coarse sand will not be strong enough to erode silt or mud (Hjulström, 1935; Crimes, 1975). The natural cohesiveness of fine-grained sediments is enhanced by decreased water content and increased consolidation (Postma, 1967; Crimes, 1975). Over-consolidation of fine-grain sediments, accomplished either through

exhumation of previously buried material (Richards, 1967), slow accumulation rate, early cementation or drainage into underlying porous sands (Crimes, 1975) will also augment natural sedimentary cohesiveness. Other textural properties besides grain size also play a role in sediment cohesiveness. For instance, particles with high angularity and low sphericity can be packed much more tightly than highly rounded and spherical particles and are thus associated with lower pore space volume (Giere, 2009).

Therefore, especially in settings characterized by heterolithic bedding, the mechanical properties of fine-grained sediments, which are most likely to foster the formation of traces with fine-scale anatomical (bioglyphic) detail, are also those most likely to resist current-mediated erosion (Crimes, 1975). The circumstances responsible for heterolithic bedding (e.g. background deposition of fine-grained material alternating with 'event' sedimentation of sandy distal tempestites or turbidites), are also likely to promote the preservation of surficial and shallow structures formed in silty or muddy sediments; overlying sands will cast rather than erode underlying mud while subsequent mud deposition will protect underlying layers from current exhumation (cf. Crimes, 1975). Thus environments characterized by both heterolithic deposition and relatively high sedimentation rates might be expected to provide the optimal facies for initial preservation and subsequent recognition of bioglyphic shallow-tier structures.

Modern Ecology of Firm Sediments

Bioturbating organisms have been long considered important ecosystem engineers (e.g. Meysman et al., 2006; Herringshaw et al., 2010). Infaunal activity has been documented to significantly alter the stability and cohesiveness of modern marine and estuarine sediments. Rhoads and Young (1970), for instance, found that high densities of deposit feeders colonizing muddy subtidal sediments at Buzzards Bay, Massachusetts not only excluded suspension-feeding populations but were also responsible for intensive reworking, fluidization and resuspension of the uppermost substrate. Rhoads and Boyer (1982) calculated that, in normal shallow marine environments, the top 10cm of sediment are thoroughly homogenized on monthly to yearly timescales. Similarly, Davis (1993) reported that deposit-feeding bivalves were responsible for sediment resuspension at rates as high as 20 mg/min/individual, as well as promoting the physical resuspension of destabilized sediments. Even in the absence of macrofauna, meiofauna may still efficiently homogenize or "cryptobioturbate" sediments (Howard and Frey, 1975), obliterating macro-sedimentary structures on surprisingly short (weekly) timescales (Cullen, 1973).

Likewise, decreased infaunal activity, either natural or induced, has been demonstrated to increase seafloor stability. Yingst and Rhoads (1978), after documenting seasonal variations in the benthic ecology of Long Island Sound, concluded that periods of increased seafloor stability (i.e. experimentally-determined decreases in seafloor erodibility [Rhoads et al., 1978]) coincided with decreased abundances of micro-, meio-

and macro-fauna, in conjunction with decreased sediment water content. Similarly, de Dedeckere et al. (2001) found that the addition of pesticides to sediment plots in the Humber Estuary (UK) resulted, in four days, in notable (48% and 34%, respectively) declines in macro- and meiofaunal abundances, an 8% decrease in sediment water content and a 300% increase in sediment stability (i.e. critical erosion threshold). Therefore, the activity of bioturbating metazoans may have a significant impact upon the cohesiveness of marine and estuarine sediments; in the absence of infauna, mixing largely ceases and the substrate at the sediment-water interface becomes firm.

These observational and experimental data have indicated that the modern seafloor may, temporarily, readily 'revert' to what we might envision as a more 'nascent' form, characterized by benthic physical, biological and chemical processes unmediated or with limited modification by infauna. If firmgrounds can, under exceptional circumstances, form at the modern sediment-water interface, it seems parsimonious to conclude that firmgrounds may have been present, perhaps even prevalent, in early Paleozoic marine settings prior to the development of significant levels of sediment mixing.

The Importance of Facies

Ichnological and ichnofabric analyses are dependent not only on the occurrence and preservation of ichnological structures, but also on our ability to recognize them in the rock record. Unless preferential diagenesis enhances biological or chemical differences (e.g. tracemaker sorting of organic matter) or mediates late-stage pore-fluid

remobilization (e.g. Berger et al., 1979), intra-stratal trace fossils are notoriously difficult to recognize (e.g. Baldwin, 1977). This difficulty is compounded in massive or large- (meter-) scale bedding. Conversely, bed-junction preservation and thinly bedded strata maximize the visibility and thus utility of trace fossils (e.g. Crimes et al., 1975). In the field, trace fossils are most easily discerned in facies characterized by heterolithic lithologies, particularly thinly (mm- to dm-scale) bedded and thinly interbedded muddy, silty and sandy material. Therefore, for practical reasons, any attempt to discern temporally and spatially widespread biological patterns by means of systematic ichnofabric analysis is best confined to facies characterized by fine-scale lithological heterogeneity. However, selection of this particular lithological package is not necessarily restrictive, because these heterolithic facies represent a broad array of continental-margin settings, ranging across environments as varied as tidal flats, estuaries, subaqueous deltas and storm-dominated shelves (e.g. Miall, 1986; Walker, 1986). Therefore, since the regular alternation of mud- and sand-depositing processes, resulting in fine-scale heterolithic packages (e.g. flaser or lenticular bedding) is not truly diagnostic of any one depositional setting but common to many, study of ichnological assemblages contained by these facies permits comparison of biological and taphonomic trends across a wide range of marine environments. However, since particular environmental or biologically-restrictive factors are likely to play a major role in the preservation of such trends (e.g. settings characterized by very low sedimentation rates may artificially appear more thoroughly bioturbated than settings characterized by high sedimentation rates; conversely, especially high sedimentation rates may increase the biotic stress of certain

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environments, thus limiting the extent of substrate colonization), rigorous study of facies

assemblages and careful environmental interpretation is essential.

Scope of This Work

In this dissertation I will investigate the lower Paleozoic history of infaunal sediment

mixing and the impact of infaunalization upon the ecological, geochemical and

sedimentological character of substrates in marine shelfal settings. The following

chapters pursue questions of the timing and pace of mixed layer development, temporal

trends in exception preservation of shallow-tier trace fossils, the relationship between

sediment mixing and exceptional preservation and the importance of infaunal ecology for

mixed layer development. Infaunal organisms are significant ecosystem engineers in both

modern and ancient seafloor settings. Elucidation of the temporal and spatial dynamics of

infaunalization therefore holds the potential to dramatically impact our understanding of

the evolution of seafloor communities and processes.

CHAPTER 1: WIDESPREAD DELAYED MIXING IN EARLY TO MIDDLE CAMBRIAN MARINE SHELFAL SETTINGS

Abstract

The radiation of burrowing metazoans in the early Phanerozoic dramatically altered the properties of marine sediment, an event commonly referred to as the "Cambrian substrate revolution" or "agronomic revolution." The advent of infaunalization, and especially biogenically-mediated sediment mixing, profoundly impacted the development of Phanerozoic biogeochemical cycling, including nutrient fluxes, organic carbon burial, seafloor oxygenation and sediment ecology. However, the timing of the development of mixed seafloor sediment has, historically, not been well constrained. Mixing has been assumed, in the absence of data, to occur at the Precambrian–Cambrian boundary with the appearance of the index fossil and three-dimensional burrow *Treptichnus pedum*. Herein I present new ichnological, stratigraphic and taphonomic data suggesting that, although significant developments in infaunalization—paleobiologically complex animal–substrate interactions, particularly burrow construction—occurred during the early and middle Cambrian, mixing remained suppressed throughout this interval. I demonstrate that shelfal sediment in the earliest Cambrian was essentially unmixed. Moreover, my findings indicate that even as late as the middle Cambrian—30 million years after the Precambrian–Cambrian transition and well after the appearance of supposedly deposit-feeding trilobites—seafloor shelfal sediment remained largely unmixed on a global scale. These findings challenge the current assumption that mixing

occurred with the first appearance of three-dimensional burrows and hold important

implications for the advent and development of modern-style biogeochemical cycling.

Introduction

The physical and chemical mixing of sediment, known as bioturbation, by burrowing

(infaunal) animals plays a critical role in modern marine biogeochemical cycling.

Infaunal churning, particularly by bilaterian macrofauna, is responsible for heightened

nutrient recycling—including the reoxidation of buried reduced compounds—and the

deep and widespread oxidation of seafloor sediment in the modern ocean (Aller, 1982,

1984, 1994). The activity of burrowing animals also significantly impacts substrate

consistency and thus the character of benthic communities (Rhoads and Young, 1970;

Thayer, 1979, 1983). The modern seafloor and the majority of the Phanerozoic

stratigraphic record are characterized by biogenically reworked, well-churned sediment

(Bromley and Ekdale, 1986). In contrast, the lack of widespread or penetrative burrowing

in Neoproterozoic strata, along with an abundant and diverse record of organic surface

textures, suggests that the Ediacaran seafloor was commonly microbially sealed and

populated by a fauna of limited mobility (Gehling, 1999; Seilacher, 1999; Jensen, 2003;

Jensen et al., 2005; Gehling and Droser, 2009).

The ecological and geochemical character of the modern seafloor is strongly influenced

by the nature and depth of the mixed layer—the zone of biogenically homogenized

sediment, which today extends 3–10 cm below the sediment-water interface (Ekdale et

al., 1984). The modern mixed layer consists of sediment of 'soupy' or flocculent consistency, high water content and low shear strength. The mixed layer is densely populated by infaunal meiofauna and macrofauna and heavily exploited by both infauna and epifauna for its high nutritional content. The mixed layer and its associated infaunal communities are not, however, represented in the stratigraphic record; due to continual homogenizing activity by burrowing infauna and resulting low sediment shear strength, burrows collapse once they are vacated (Ekdale et al., 1984). The trace fossil record, therefore, is heavily skewed toward the transition and historical layers—the deeper zones of sediment in which the burrows of deep-burrowing (maintaining open burrows of up to 2.5 m depth in modern seafloor environments), 'elite tier' fauna are preserved (Pemberton et al., 1976; Ekdale et al., 1984; Bromley, 1996).

The geologic timing of the development of the mixed layer has not been well constrained. It has long been assumed, without evidence beyond the appearance of the index fossil and three-dimensional burrow *Treptichnus pedum* and the disappearance of widespread matground structures, that mixgrounds appeared during an "agronomic revolution" or "Cambrian substrate revolution" at the Precambrian–Cambrian boundary (Seilacher and Pflüger, 1994; Bottjer et al., 2000). Although several workers have suggested that the development of sediment mixing may have been a more gradual process or have documented protracted increases in local stratigraphic successions (e.g. Droser and Bottjer, 1988; McIlroy and Logan, 1999; Droser et al., 2002b), the 'Precambrian–Cambrian boundary model' has remained the classic and most widely cited view (e.g.

Rydell et al., 2001; Pawlowska et al., 2013). Moreover, there is a conspicuous paucity of data constraining how rapidly the global (inter-basinal and inter-continental) development of an appreciable mixed layer, typical of modern seafloor sediment, followed the evolution of infaunal metazoans. And although certain authors, such as Droser et al. (2002a, b), Jensen et al. (2005) and McIlroy and Logan (1999) have described earliest Cambrian advances in infaunalization, systematic documentation of trends in sediment mixing, made from a jointly ichnological and sedimentological perspective, and consideration of post-lower Cambrian strata have largely been lacking.

Constraining the timing of this transformation in seafloor substrate is, however, essential, given that bioturbation has long been considered the cause of a plethora of geochemical, ecological and taphonomic phenomena, including changes in nutrient fluxes, seafloor oxygenation and ocean chemistry; declines in the diversity and abundance of microbialites; the disappearance of the Ediacara Biota, Ediacara-style preservation and matgrounds; changes in lipid biomarker preservation; changes in the stratigraphic character of event bedding and the decline of Burgess Shale-type preservation (Awramik, 1971; Brasier, 1990; Sepkoski et al., 1991; Allison and Briggs, 1993; McIlroy and Logan, 1999; Orr et al., 2003; Callow and Brasier, 2009; Canfield and Farquhar, 2009; Brasier et al., 2011; Pawlowska et al., 2013).

Previous work (Droser et al., 2002a, b; Jensen, 2003; Jensen et al., 2005) has documented that burrowing in the latest Ediacaran, at the Precambrian–Cambrian transition and in the

earliest Cambrian (Terreneuvian Epoch) was shallow (≤ 2 cm depth). The exceptions,

such as *Skolithos* and *Arenicolites*, common in early Cambrian and younger nearshore,

sandy, high-energy environments (e.g. Sepkoski et al., 1991) attained much greater

depths. However, these structures, which have been attributed to dwelling rather than

deposit-feeding organisms (Thayer, 1979; Droser et al., 2002b), would have merely

statically increased advection of bottom-waters into the sediment on a very localized

scale (Aller, 1982; Droser et al., 2002a, b), rather than mediating physical or chemical

homogenization. Therefore, even densely colonized 'pipe rock' does not represent well-

mixed sediment. In contrast, it would be expected that with the appearance of trilobites—

mobile, benthic organisms long considered to be largely deposit feeders and thus

sediment mixers (Seilacher, 1985, 2007)—in the latest early Cambrian, the mixed layer

should have become well developed in open marine, oxygenated environments. This

study represents the first systematic test of this prediction.

Assessment of Mixed Layer Development

Geologic Setting

Data were collected from lowermost Cambrian through lower middle Cambrian

successions across the Great Basin (USA), in southern Spain and in Newfoundland (Fig.

1). Shallow marine siliciclastic deposits were targeted because siliciclastic sediment and

strata represent the vast majority of both the modern seafloor and the stratigraphic record,

respectively (e.g. Bluth and Kump, 1991), and generally contain better preserved and

more abundant trace fossils. Shallow marine environments, long considered to be both

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modern diversity 'hotspots' and cradles of early seafloor diversity (Jablonski et al.,

1983), would be the expected locus of the earliest and most dynamic changes in seafloor

communities and thus sediment mixing. Additionally, emphasis was placed upon

lithologic heterogeneity—thinly (mm- to dm-scale) bedded and interbedded mudstone,

siltstone and sandstone—in order to maximize resolution of mixing trends (see "The

Importance of Facies").

The lower Cambrian Wood Canyon and lower to middle Cambrian Pioche (and

correlative Bright Angel Shale) formations (Great Basin) and the lower Cambrian

Torreárboles Sandstone (Spain) are characterized by thinly bedded, fine-grained

heterolithic lithologies (Palmer, 1971; Gozalo et al., 2003). They are interpreted, on the

basis of facies, fauna and paleogeographic reconstructions, to have been deposited under

shallow, oxygenated marine waters. Data from the lowermost Cambrian Chapel Island

Formation—a well-exposed succession of thinly bedded heterolithic strata, which

contains the GSSP for the Precambrian–Cambrian boundary (Myrow and Hiscott, 1993;

Droser et al., 2002a, b; Droser et al., 2004)—were also collected. These were used as a

baseline to track the development of infaunal mixing recorded in lower and middle

Cambrian successions.

Criteria

Over 450 meters of section (Figs. 2-6), comprising over 24,300 discrete beds, were

examined, and data were collected 1) as average data for meter-scale intervals and 2)

from individual discrete beds, according to the criteria outlined below, to determine the extent of biogenic sediment mixing in typical Laurentian and Gondwanan early to middle Cambrian marine shelfal environments.

In order to address this issue, we examined the Cambrian rock record according to six criteria: 1) bedding thickness; 2) fabric disruption; 3) depth of bioturbation; 4) bioglyphic preservation; 5) the paleobiological and paleoecological complexity of trace fossil assemblages and 6) surficially produced physical sedimentary structures. Although these metrics are related, they are independent indicators of substrate consistency and the extent to which seafloor sediment was mixed. Assessment of mixing intensity is a difficult procedure even in modern seafloor sediment, let alone the stratigraphic record. Mixing intensity reflects a delicate interplay between environmental, ecological and preservational conditions; variation in any of these facies parameters may strongly impact perception of mixing intensity and thus evolutionary interpretations. However, in contrast to secondary proxies, such as body fossil and geochemical records, the shallowly emplaced trace fossil record represents the only direct record of infaunal mixing, and as such it provides an independent and semi-quantitative record of substrate development. This uniquely multipronged approach was employed in order to maximize the range of infaunal mixing data that could be collected and assessed. Collection of these data was often challenging; data pertaining to each individual criterion was not always available over each stratigraphic interval. Despite this, examination of the resulting suite of proxy

data provided the most thorough and complete approximation possible of infaunal mixing intensity.

1) *Bedding thickness*: The thickness of beds separated by clear bed junctions indicates the maximum depth to which bioturbation penetrated without having disrupted the coherency of individual beds. Bed junctions will be erased by intensive and deep burrowing; sediment deposited as thin event beds will be homogenized and merged into thicker beds (cf. Sepkoski et al., 1991). In contrast, thin event beds preserved in a stratigraphic succession imply relatively reduced infaunal reworking intensities. Bedding thickness was assessed on the individual bed scale (absolute thickness, measured for each individual, discrete bed) over representative, 50 cm- or 100 cm-thick 'microstratigraphic sections.' Additionally, bedding thickness was assessed on the package scale (approximate thickness of beds, demarcated as mm-scale [1–10 mm], cm-scale [1–10 cm], dm-scale [1–10 dm] or m-scale [≥1 m], determined for individual facies packages over each one-meter stratigraphic interval) for each stratigraphic section (tens to hundreds of meters).

2) *Fabric disruption*: Biogenic fabric disruption constitutes another parameter for measurement of the extent to which burrowing organisms have disrupted the stratigraphic expression of original physical fabrics. The Ichnofabric Index (ii) of Droser and Bottjer (1986) schematically demarcates the level of infaunal disruption of sedimentary fabrics into six indices, ranging from ii 1 (laminated) to

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ii 6 (completely homogenized). The Ichnofabric Index provides a useful and efficient metric for both field (particularly where stratigraphic exposure is greater than bedding-plane exposure) and laboratory assessment of infaunal mixing intensity. Ichnofabric Index was measured throughout field exposures, wherever possible, as well as for selected hand samples, which were collected at regular intervals, cut, polished and scanned. For each hand sample, maximum Ichnofabric Index (irrespective of scale) and average ('whole-rock') Ichnofabric Index were measured.

3) *Depth of bioturbation*: The depth of discrete burrows indicates the maximum depth of the zone of infaunal activity (i.e., the infaunal 'habitable zone'). This, in turn, provides information concerning the morphological ability of animals to penetrate the substrate. Moreover, where contact with the ancient sediment-water interface can be clearly determined, maximum burrow depth provides an upper estimate for the maximum depth to which the mixed layer may have been developed. Maximum burrow depth was noted, wherever possible, over each stratigraphic interval.

4) *Bioglyphic preservation*: The quality of preservation of shallowly emplaced trace fossils is a direct metric of substrate consistency; soupy, well-mixed sediment will not capture the same level of detail as a firm and undisturbed substrate. The preservation of bioglyphs—finely-preserved burrow ornamentation or other organismal "fingerprints" such as scratch marks (Ekdale and de Gibert, 2010)—is a particularly useful indicator of exceptional preservation and thus a firm (i.e.

unmixed) substrate at the depth of emplacement. When coupled with data documenting depth of bioturbation, trace fossil preservation in general, and bioglyphic preservation in particular, can provide information on substrate conditions at a reliably estimated distance from the ancient sediment-water interface. The presence or absence of bioglyphic preservation was noted throughout all measured stratigraphic successions.

5) *Paleobiological and paleoecological complexity*: The morphological and assemblage-level complexity of shallowly emplaced trace fossils, including trace fossil size, density, diversity and taphonomy are important metrics of the extent and character of substrate colonization. The preservation of open burrows, such as *Treptichnus*, *Gyrolithes*, *Monocraterion*, *Arenicolites* or *Diplocraterion* (e.g., Alpert, 1974; Droser et al., 1999; Jensen et al., 2000; Droser et al., 2002b; Vannier et al., 2010) indicates that shallow sediment was cohesive and unmixed, whereas truncated burrows and infill by foreign material suggest high levels and multiple generations of substrate colonization and sediment mobilization (Bromley and Ekdale, 1986). Additionally, the Bedding Plane Bioturbation Index (BPBI) of Miller and Smail (1997), which demarcates burrowed bed surfaces according to the density of surface coverage and disruption (from BPBI 1 [0% disruption] to BPBI 5 [60–100% disruption]), was used to characterize the extent of infaunal colonization of bedding plane exposures. Cross-cutting and consistent tiering relationships were further used to quantify maximum depth of bioturbation (Bromley and Ekdale, 1986; Wetzel and Aigner, 1986).

6) *Surficially produced physical sedimentary structures*: Like surficially and shallowly produced trace fossils, surficially produced physical sedimentary structures, such as tool marks and other sharp erosional features are particularly informative metrics of substrate consistency and the depth of sediment mixing (e.g. Elliott, 1965). Sedimentologists have long noted that delicately sculpted tool and flute marks could not have been formed in either "quasi-liquid" or "quasi-solid" sediment; "hydroplastic" or cohesive sediment is required for their formation and preservation (Elliott, 1965). Well-preserved and fine-scale tool marks are therefore especially suggestive of cohesive (unmixed) sediment at the sediment-water interface. Tool marks and similar features were noted as "absent," "present/rare," "common" or "abundant" for all available basal bedding plane exposures.

The Importance of Facies

Stratigraphic sections (Figs. 2–6) were selected on the basis of thickness (10 m- to 100 m-scale), exposure and continuity. Heterolithic successions were selected because biogenic structures preserved in such successions can be easily discerned, and thus patterns of infaunalization can be tracked on a much more detailed scale than in homogeneous lithologies (e.g. Crimes, 1975). Examination of the shallow-tier trace fossil record in heterolithic facies permits constraint of conditions at the ancient sediment-water interface and at shallow sediment depths. Moreover, heterolithic siliciclastic sediment and strata represent a broad range of marine and continental margin settings (Miall, 1986;

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Walker, 1986; Boggs, 2006); they comprise well-represented facies in both modern environments and the stratigraphic record. Sedimentation rate and other environmental and biologically-restrictive factors are likely to play a major role in the preservation of such records. For instance, settings characterized by very low sedimentation rates may artificially appear more thoroughly bioturbated than settings characterized by high sedimentation rates; conversely, especially high sedimentation rates may increase the biotic stress of certain environments, thus limiting the extent of substrate colonization. Rigorous study of facies assemblages and careful environmental interpretation is essential in order to distinguish inter-facies variability from temporal developments in mixing intensity. Successions characterized by similar (heterolithic) facies packages were consistently selected in order to minimize inter-facies biases.

Results

Bedding Fabric and Depth of Bioturbation in Heterolithic Facies

Each stratigraphic succession was examined according to the criteria outlined above, in order to evaluate the extent to which early to middle Cambrian marine shelfal sediment was mixed by bioturbating infauna:

1) *Bedding thickness*: Individual beds were observed to be coherent, preserved on the mm- to cm-scale and separated by well-defined junctions. Bed contacts are typically planar or rippled, and lack evidence for significant erosional exhumation (e.g., deep scouring, abundant rip-ups or intraclasts, and truncated trace fossils are uncommon). Mean macrostratigraphic bed thickness (recorded on the scale of

individual packages over each 1 m interval in a stratigraphic succession) is on the mm to cm scale (Fig. 7); mean microstratigraphic bed thickness (recorded on the scale of individual beds) is 1.2 cm (Fig. 8).

2) *Fabric disruption*: In spite of the very common high density of trace fossil assemblages along bedding planes (see below), slabbed specimens collected at regular stratigraphic intervals reveal that ichnofabrics (measured by Ichnofabric Index [ii], the extent of infaunal disturbance of physical sedimentary fabric, with ii 1 denoting laminated and ii 6 completely homogenized strata [Droser and Bottjer, 1986]) are poorly developed (Figs. 9K–O). The most disrupted intervals are characterized by a maximum ichnofabric index (ii) of 3 and an average ii of 2, but are commonly confined to very limited (mm- to cm-) spatial scales; average 'whole-rock' ichnofabrics rarely exceed ii 2 (Fig. 10), and both 'whole-rock' values and 'partial rock' zones of ii 1 are common. Moreover, ichnofabrics are typically dominated by sub-mm- to mm-scale 'microburrows' cast on the base of sub-mm- to mm-scale laminae without, or with only minor, disruption to the overall laminated fabric of the rock (Fig. 9M, lower arrow). Infilled burrows occurring within beds cast rather than penetrate individual laminae and other internal sedimentary horizons (Figs. 9L–M).

3) *Depth of bioturbation*: Maximum burrow depth is typically on the mm scale. Even the deepest observed burrows never exceed 3 cm in depth.

Ichnology, Paleoecology and Taphonomy of Heterolithic Facies

Ichnofabric observations were supplemented with bedding plane data concerning organismal paleobiological and paleoecological complexity, the extent and type of infaunalization, and preservational conditions:

4) *Trace fossil assemblage complexity*: Despite extremely low average bed thickness and low levels of sediment mixing, dense (e.g. BPBI 4–5 of Miller and Smail, 1997) trace fossil assemblages (comprised of individuals of mm- to cm-scale diameter and relief) occur along both basal- and upper-bed surfaces (Figs. 9C–D, F, H). Burrows are preserved as infilled casts along bed bases (e.g. Figs. 9I, L), rather than penetrating through beds.

5) *Quality of preservation*: Structures are typically very sharply and delicately preserved. Even where trace fossil density approaches the highest levels of bedding plane bioturbation indices, assemblages are characterized by discrete trace fossils rather than mixed fabrics (e.g. Fig. 9H). Shallowly emplaced and surficial trace fossils occur abundantly and are commonly characterized by bioglyphic (anatomically explicit) preservation, including scratch marks, appendage imprints, burrow wall ornamentation and sharp wall margins (Figs. 9A–E, G–H, J).

6) *Surficially produced sedimentary structures*: Additionally, delicately preserved surficial erosional sedimentary structures, such as tool marks, are common (Fig. 9D). Where tool marks occur, they occur in great density and on the mm scale.

Implications for Cambrian Biogeochemical Cycling and Ecology

The conjunction of dense trace fossil assemblages along bedding planes and poorly developed ichnofabrics indicates that although significant increases in infaunal motility had occurred by the middle Cambrian, marine shelfal sediment remained, at this time, largely unmixed. The consistently high quality of preservation of shallow-tier biogenic and physical sedimentary structures indicates that the substrate directly adjacent to the sediment-water interface was, even as late as the early middle Cambrian—30 million years after the Precambrian–Cambrian boundary—cohesive and poorly mixed. The common occurrence of thin and coherent beds, and the predominance of non-disruptive, meiofauna-scale microburrowing or cryptobioturbation suggest that bioturbation was both limited in extent and shallow in depth. These findings from Laurentian and Gondwanan lower to middle Cambrian siliciclastic strata are further supported by previous studies of lowermost Cambrian units from Avalonia, Baltica and Australia, as well as the carbonate record of the Great Basin (Droser et al., 2002a, b; Droser and Bottjer, 1988); the records of five paleocontinents suggest that the development of infaunal mixing was a drawn-out process and did not occur at the Precambrian–Cambrian boundary, nor even 30 million years later.

Intriguingly, none of the measured criteria appear to vary systematically with time. For example, some of the deepest burrowing (≤ 3 cm depth) was recorded from the lower Cambrian Wood Canyon Formation, whereas certain facies of the lower middle Cambrian Pioche Formation are characterized by sparse and sub-millimetric burrowing,

reminiscent of the lowermost Cambrian Chapel Island Formation. This lack of temporal variability, combined with the consistently low levels of bioturbation observed in each unit independently, suggests that variations in infaunal mixing were strongly dependent on facies but that, across most marine shelfal environments, mixed layer development was suppressed throughout the early Cambrian.

This widespread exceptional preservation of shallowly emplaced biogenic and physical sedimentary structures, atypical of the majority of the Phanerozoic record, indicates that a global taphonomic window, linked to anomalous seafloor conditions, was active in the early Paleozoic. Contrary to previous assumptions concerning the timing of mixed layer development (e.g. Seilacher and Pflüger, 1994), and in spite of the development of a mobile benthic fauna—particularly trilobites, which represented a well-established component of the marine benthos by about 20 myrs after the start of the Cambrian— seafloor sediment was still largely unmixed, at least as late as the early middle Cambrian. Trilobites are commonly assumed to have been largely infaunal deposit-feeders, although this interpretation is controversial (e.g. Seilacher, 1970, 1985, 2007; Goldring, 1985). The findings of this study would suggest that, in spite of the abundance of trilobites and trilobite-attributed trace fossils in lower and middle Cambrian successions, trilobites did not contribute significantly to sediment mixing at this time. The synchroneity of poorly developed sediment mixing and prominent advances in animal body plans is not, however, as jarring a contradiction as it may initially seem; significant ecological and ethological developments continued to appear through the later Cambrian and the

Ordovician Radiation (e.g. Budd and Jensen, 2000). Therefore, although animals developed the morphological machinery to colonize the infaunal realm during the terminal Ediacaran and the Cambrian Explosion, it is possible that more sophisticated means of sediment processing, such as deposit feeding, had not yet been extensively developed by the early middle Cambrian (Butterfield and Jensen, 2001). *Treptichnus pedum*, for example, although a three-dimensional burrow system, probably represents a dwelling structure and the *T. pedum* tracemaker most likely fed at the sediment-water interface rather than at depth (Jensen, 1997; Dzik, 2005; Vannier et al., 2010). Therefore, these organisms, along with other early Cambrian infauna burrowing surficially or in the shallow substrata, would have likely had only a minor impact upon sediment chemistry and mixed layer development. Interestingly, the peak of Burgess Shale-type (BST) preservation occurs during this period of poorly developed shelfal bioturbation (Gaines et al., 2012a). Suppressed mixing may have played a role not only in the anomalous trace fossil preservation that is characteristic of the Cambrian, but also in the exceptional preservation of the body fossil record, notably BST deposits in non-restricted shelfal settings, characteristic of this interval.

My evidence for protracted sediment mixing and oxidation may help resolve debate concerning the evolution of the global sulfur cycle. Canfield and Farquhar (2009) proposed that fundamental differences between Proterozoic and Phanerozoic fractions of sulfur buried in the reduced versus the oxidized form ($f_{sulfide}$) are likely linked to bioturbation. A gradual shift in $f_{sulfide}$ in the earliest Phanerozoic may have been caused

by bioturbation-mediated increases in benthic pyrite oxidation rates and thus sulfate

burial (Canfield and Farquhar, 2009). My observations directly support this model by

providing evidence for protracted sediment mixing (and thus protracted sediment

ventilation) through the early Phanerozoic. These findings question alternative

interpretations of the sulfur mass balance (e.g. Halevy et al., 2012) that do not invoke

progressive sediment ventilation. More broadly, my findings provide support for the view

(Jensen et al., 1998; Gill et al., 2011) that, rather than following in the wake of dramatic

geochemical and ecological transformation at the Precambrian–Phanerozoic boundary,

Cambrian ecosystems and environments represent a unique system transitional between

that of the Precambrian and that of the later Phanerozoic.

Conclusions

The development of well-mixed sediment has long been assumed to occur at the

Precambrian–Cambrian boundary and in the earliest Cambrian, in conjunction with the

appearance of the first three-dimensional burrow system, *Treptichnus pedum*. Subsequent

studies of earliest Cambrian geochemical, ecological and taphonomic phenomena have

sought an explanation in the appearance of infaunally churned sediment and, in so doing,

have propagated this assumption. However, the results of this study indicate that, in spite

of concurrent advances in infaunalization, not only was sediment mixing poorly

developed in earliest Cambrian marine shelfal settings, but even 30 million years later,

infaunal mixing remained suppressed. These findings bear significantly upon our

understanding of Cambrian paleobiology, paleoecology, ocean and sediment biogeochemistry and taphonomy.

1) Infaunal mixing was globally suppressed across a wide range of early and middle Cambrian marine and marginal marine seafloor settings. However, variability in mixing intensity within the heterolithic packages examined suggests that apparent trends in mixed layer development may be strongly associated with particular facies, indicating that the role of local environmental factors needs to be carefully considered in the reconstruction of global records.

2) This apparent stasis in mixed layer development continued through the early middle Cambrian and therefore appears to have been unaffected by not only notable developments in infaunalization—the paleobiological complexity of animal-substrate interactions and burrow construction—but also the appearance and widespread diversification of trilobites, a clade commonly assumed to consist largely of infaunal deposit feeders. However, the lack of evidence for infaunal mixing (in spite of the abundance of trilobite- and arthropod-produced burrows documented in the studied successions) suggests that Cambrian trilobites, in fact, did not contribute significantly to infaunal mixing, lending support to previous studies suggesting that trilobites were characterized by a wide range of life modes and feeding ecologies. Moreover, the conjunction of densely-burrowed beddings planes with a paucity of well-mixed horizons may indicate that mobile deposit feeding, which is employed by many of the most effective bioturbators of the

modern seafloor, was not yet a well-developed feeding strategy at this interval of time.

3) The lower to middle Cambrian stratigraphic record is characterized by an anomalous preponderance of exceptionally preserved soft-bodied biotas and surficial and shallowly emplaced trace fossil assemblages. A lack of intensive infaunal mixing may have allowed anomalous substrate conditions and thus a taphonomic window favoring exceptional preservation of both body and trace fossil assemblages to develop.

4) Delayed sediment mixing provides support for geochemical models favoring protracted sediment ventilation and secular variation in the sediment and oceanographic cycling of important biogeochemical compounds such as sulfate through the early Phanerozoic.

Figures

Figure 1. Lower–middle Cambrian study localities. Areas of study (marked by stars) include the Great Basin, western USA (see inset map; from west to east: Salt Spring Hills, CA [Wood Canyon Fm.]; Frenchman Mountain, NV [Pioche Fm.]; Pioche Mining District, NV [Pioche Fm.]; House Range, UT [Pioche Fm.]); Newfoundland, Canada (Fortune Head [Chapel Island Fm.]) and southern Spain (Guadajira [Torreárboles Sandstone]).

Figure 2. Stratigraphic profile of the Chapel Island Formation (Fortune Head, Newfoundland, Canada). Macrostratigraphic (meter-scale) record of sedimentological and paleontological features, with microstratigraphic (bed-scale) inset of meters 10-11. Dashed lines indicate points of correlation between sections. Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c, coarse-grained sand; cgl, conglomeratic-sized particles (granule, pebble, cobble).
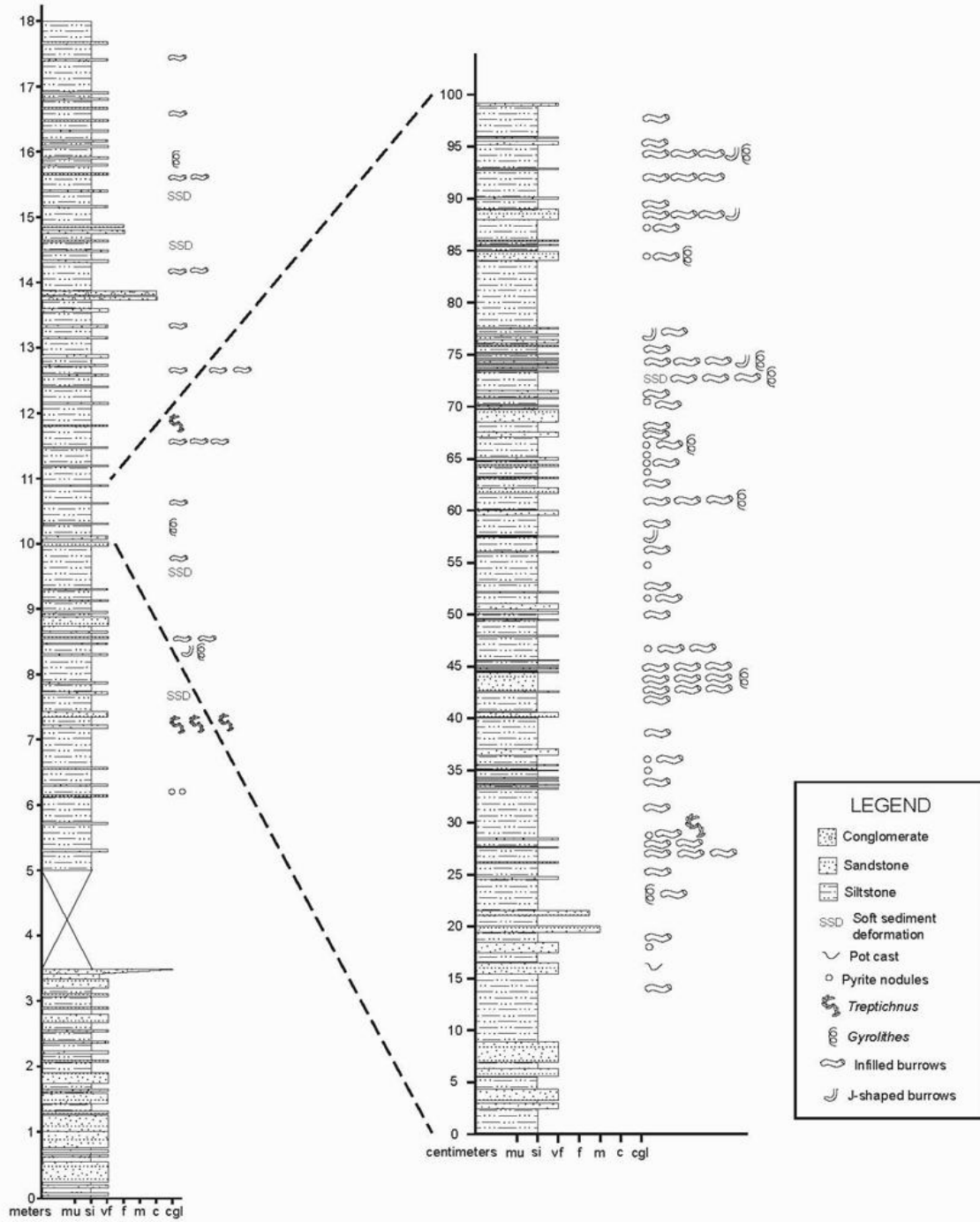
Figure 3. Stratigraphic profile of the Torreárboles Sandstone (Guadajira, Spain). Macrostratigraphic (meter-scale) record of sedimentological and paleontological features. Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c, coarse-grained sand.

Figure 4. Stratigraphic profile of the Pioche Formation (Frenchman Mountain, Nevada, USA). Macrostratigraphic (meter-scale) and microstratigraphic (bed-scale) record of sedimentological and paleontological features. A: Macrostratigraphic section with B: microstratigraphic inset of meters 4.5-5. C: Second macrostratigraphic section, < 1 km to north of section depicted in A. Dashed lines indicate points of correlation between sections. Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c, coarse-grained sand.

LEGEND

Sandstone   Trilobite sclerites

Sandy siltstone   Infilled burrows

Siltstone   Horizontal furrows

Symmetrical ripples   Plugs

Low-angle lamination   Delicate trace fossils

Tool marks   Scratch marks

Kinneyia   Rusophycus

Non-disarticulated trilobites

A meters   mu si vf f m c

B centimeters   mu si vf f m c

C meters   mu si vf f m c
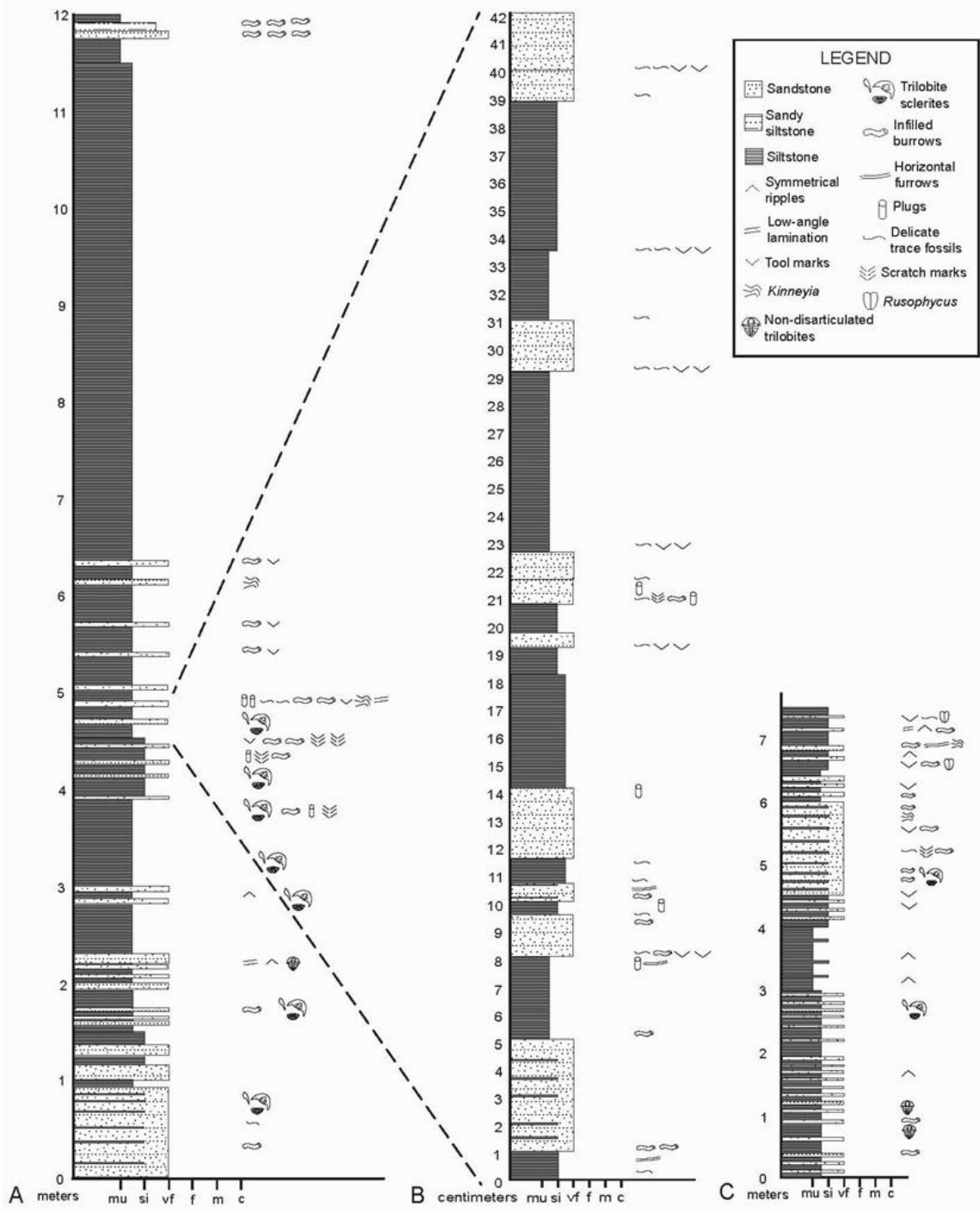
Figure 5. Stratigraphic profile of the Pioche Formation (House Range, Utah, USA). Macrostratigraphic (meter-scale) record of sedimentological and paleontological features. A: Macrostratigraphic section measured at the mouth of Marjum Canyon, House Range. B: Second macrostratigraphic section, < 1 km to east of section depicted in A. Dashed lines indicate points of correlation between sections. Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c, coarse-grained sand; cgl/carb, conglomeratic-sized particles (granule, pebble, cobble) or carbonate.
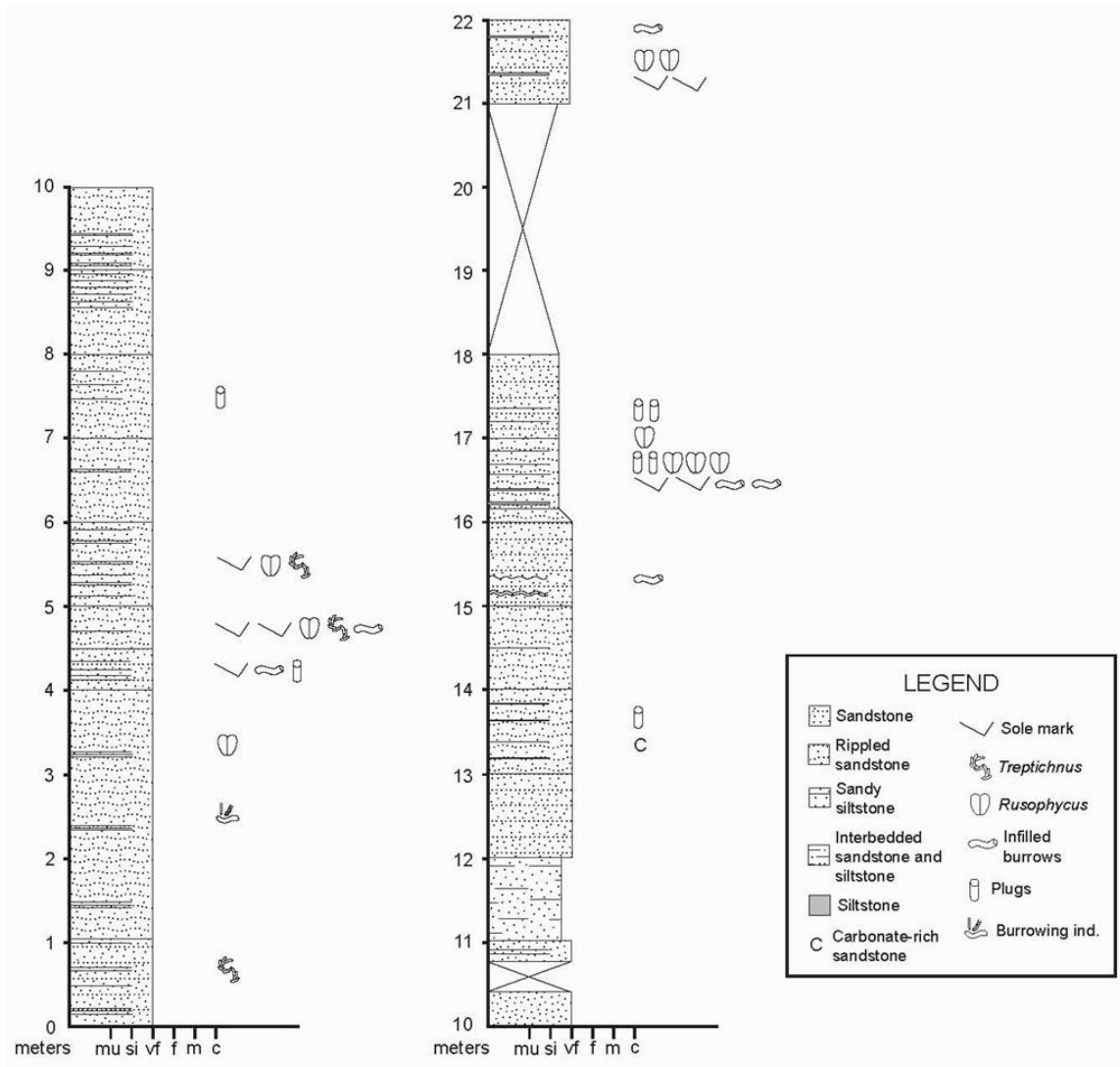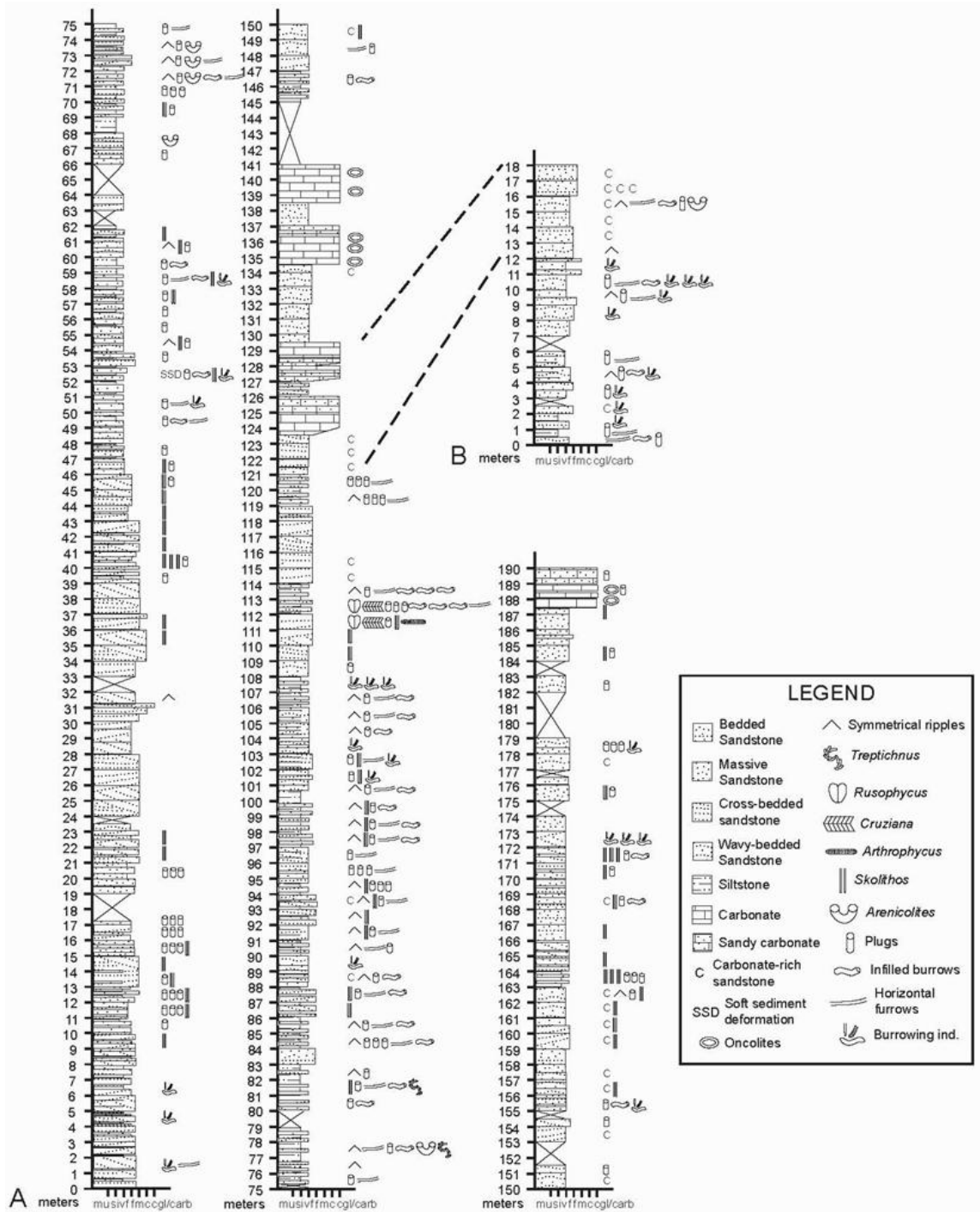
Figure 6. Stratigraphic profile of the Pioche Formation (Pioche Mining District, Nevada, USA). Macrostratigraphic (meter-scale) and microstratigraphic (bed-scale) record of sedimentological and paleontological features. A: Macrostratigraphic section measured east of Comet Mine, Highland Range. B: Microstratigraphic inset of meters 2.5-3. C: Microstratigraphic inset of meters 28.5-29.5. D: Microstratigraphic inset of meters 54-55. Dashed lines indicate points of correlation between sections. Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c/carb, coarse-grained sand or carbonate; cgl, conglomeratic-sized particles (granule, pebble, cobble).

LEGEND

Sandstone	Carbonate	Non-disarticulated trilobites
Cross-bedded sandstone	Sandy carbonate	Trilobite sclerites
Siltstone	Nodular carbonate	*Treptichnus*
Muddy siltstone	Clastic carbonate	*Rusophycus*
Shale	Bioclastic carbonate	*Cruziana*
Low-angle lamination	C Carbonate-rich sandstone	*Rhizocorallium*
Symmetrical ripples	Oncolites	Plugs
		Horizontal furrows
		Vertical piping
		Infilled burrows
		Burrowing ind.
		Delicate trace fossils

A meters mu si vf f m c/carb

B centimeters mu si vf f m c cgl

C centimeters mu si vf f m c cgl

D centimeters mu si vf f m c cgl

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Figure 7. Macrostratigraphic bed thickness. Thickness of discrete beds (demarcated as mm-scale, mm–cm-scale, cm-scale, cm–dm -scale or dm-scale), determined for lithological packages over each 1 m stratigraphic interval in a 'macrostratigraphic' (10 m- to 100 m-scale) section. Data from Fortune Head, Newfoundland (Chapel Island Fm.); Guadajira, Spain (Torreárboles Sandstone); Pioche Mining District, Nevada, USA (Pioche Formation); Frenchman Mountain, Nevada, USA (Pioche Formation) and Marjum Canyon, Utah, USA (Pioche Formation).
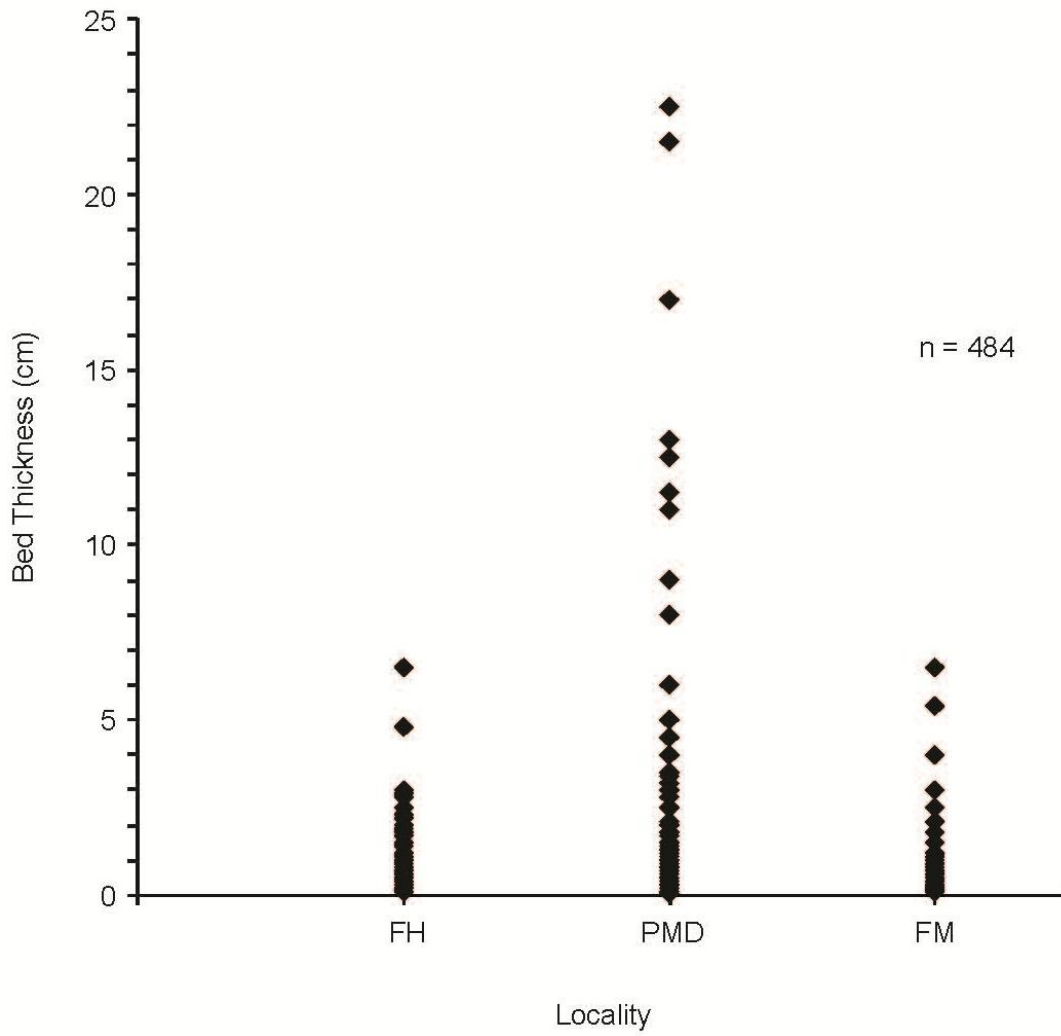
Figure 8. Microstratigraphic bed thickness. Thickness of discrete beds, measured for each successive individual bed over facies-representative 50 cm- or 100-cm 'microstratigraphic' sections. FH, Fortune Head (Chapel Island Fm.); PMD, Pioche Mining District (Pioche Fm.); FM, Frenchman Mountain (Pioche Fm.).

Figure 9. Dense, exceptionally preserved trace fossil assemblages coupled with limited sediment mixing. A: Compound *Rusophycus*, of probable trilobite origin, characterized by exceptionally preserved scratch marks (hyporelief). UCR-WC-SSH-001, Upper Mbr., Wood Canyon Fm. (Salt Spring Hills, lower Cambrian). B: *Gyrolithes* specimen characterized by multiple (> 5) sand-infilled whorls within a siltstone matrix. Field photograph. Chapel Island Fm. (Fortune Head, lower Cambrian). C: Dense trace fossil assemblage (BPBI 4) characterized by scratch mark preservation (see arrows; hyporelief). UCR-P-PMD-001. Pioche Fm. (Pioche Mining District, middle Cambrian). D: Crisply preserved surficial and shallowly-emplaced assemblage, including ornamented burrow walls and sub-millimetric- to millimetric-scale tool marks and scratch marks (see arrows; hyporelief). UCR-P-FM-001. Pioche Fm. (Frenchman Mountain, lower to middle Cambrian). E: *Rusophycus* characterized by bioglyphic scratch mark preservation, in spite of coarse-grained matrix (hyporelief). UCR-WC-SSH-002. Upper Mbr., Wood Canyon Fm. (Salt Spring Hills, lower Cambrian). F: Dense assemblage of millimetric-scale, intergradational *Rusophycus* and *Cruziana*, cast on rippled sandstone bed base (hyporelief). UEX-T-GUAD-001. Upper Mbr., Torreárboles Sandstone (Guadajira, lower Cambrian). G: Arthropod-produced *Dimorphichnus* characterized by bioglyphic preservation of second-order (multi-appendage) scratch marks (epirelief). Field photograph. Chapel Island Fm. (Fortune Head, lower Cambrian). H: Dense (BPBI 4) assemblage of millimetric-scale, intergradational *Rusophycus* and *Cruziana* (hyporelief). UCR-P-MC-001. Pioche Fm. (House Range, middle Cambrian). I: Millimetric, sand-infilled cast treptichnid burrows (see arrow) and 'floating' pot casts within siltstone matrix, reflecting bypass sedimentation. Field photograph. Chapel Island Fm. (Fortune Head, lower Cambrian). J: Crisply preserved sand-infilled radiating treptichnid burrow complex within siltstone matrix (hyporelief). UEX-T-GUAD-002. Upper Mbr., Torreárboles Sandstone (Guadajira, lower Cambrian). K: Slabbed section characterized by strong low-angle lamination and unmixed fabric (ii 1). Vertical features are due to late-stage cracking and fluid flow. UCR-P-FM-002. Pioche Fm. (Frenchman Mountain, lower to middle Cambrian). L: Slabbed section characterized by strongly laminated fabric, sub-millimetric microburrowing and rare millimetric-scale burrows (see arrow) (ii 2) cast on the base of individual laminae. UCR-P-FM-003. Pioche Fm. (Frenchman Mountain, lower to middle Cambrian). M: Slabbed section characterized by bioglyphic preservation of millimetric-scale backfill burrows (upper arrows) and sub-millimetric- and millimetric-scale cast (lower arrow) and 'floating' burrows (ii 2-3). UEX-T-GUAD-003. Upper Mbr., Torreárboles Sandstone (Guadajira, lower Cambrian). N: Slabbed section characterized by laminated fabric and microburrows (see arrow) and sparse millimetric-scale burrows cast on the base of individual laminae (ii 2). UCR-P-FM-004. Pioche Fm. (Frenchman Mountain, lower to middle Cambrian). O: Slabbed section characterized by strongly laminated fabric, cross-cut by rare u-burrows (see arrow) and 'floating' full-relief burrows (ii 2). UCR-P-PMD-002. Pioche Fm. (Pioche Mining District, middle Cambrian). Scale bars denote 1 cm. UEX-T-GUAD-001, UEX-T-GUAD-002 and UEX-T-GUAD-003 are reposited in the collections of the Área de Paleontología, Universidad de Extremadura; all other specimens are reposited in the Invertebrate Paleontology collection of the University of California, Riverside.
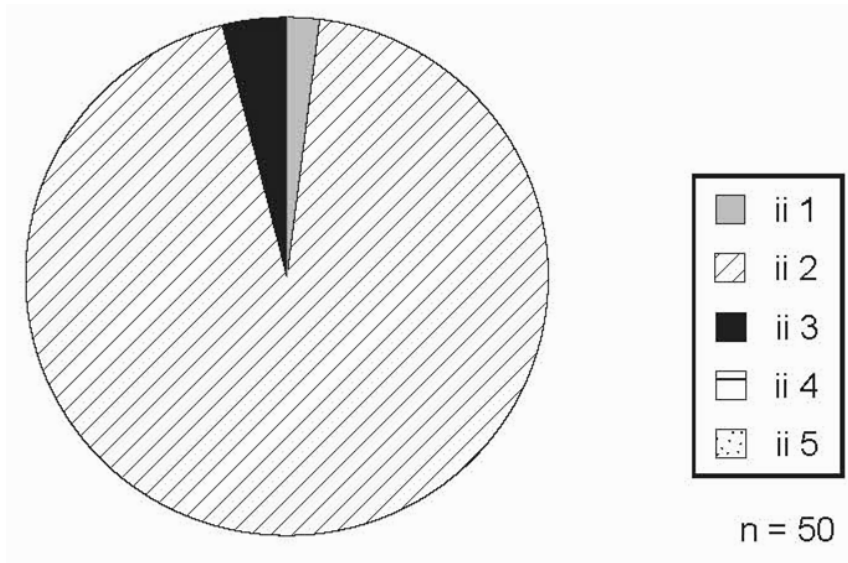
Figure 10. Average ichnofabric index (ii). Values reflect mean ('whole-rock')
ichnofabric indices, as measured from cut, polished and scanned hand samples, collected
in situ from measured stratigraphic sections (Figs. 2–6). Data from Fortune Head,
Newfoundland (Chapel Island Fm.); Guadajira, Spain (Torreárboles Sandstone); Salt
Spring Hills, California, USA (Wood Canyon Fm.), Pioche Mining District, Nevada,
USA (Pioche Formation); Frenchman Mountain, Nevada, USA (Pioche Formation) and
Marjum Canyon, Utah, USA (Pioche Formation).

CHAPTER 2: EXCEPTIONAL TRACE FOSSIL PRESERVATION AND MIXED LAYER DEVELOPMENT IN CAMBRO-ORDOVICIAN SILICICLASTIC STRATA

Abstract

Instances of exceptional preservation—preservation of near-surface structures of high taphonomic fidelity, including bioglyphic detail—have been previously reported from Cambro-Ordovician trace fossil assemblages worldwide. However, it has hitherto been unknown to what extent this exceptional preservation characterizes the Cambro-Ordovician record as a whole. Herein we present ichnological, sedimentological and taphonomic data collected from the Bell Island Group (Beach Formation) and Wabana Group (Powers Steps Formation, Scotia Formation, Grebes Nest Point Formation) of Canada and the Bynguano Formation of Australia, units selected as representative of Cambro-Ordovician marine shelfal settings. Additionally, data from outgroup (both lower and higher energy) facies were collected from the Barrancos Formation of Spain, the Juniata Formation of the eastern United States and the Pacoota Sandstone of Australia in order to assess the role of depositional environment in Cambro-Ordovician infaunal colonization and exceptional preservation. The Bynguano, Beach, Powers Steps, Scotia and Grebes Nest Point formations are characterized by widespread exceptional preservation of shallow-tier ichnological assemblages and bioglyphic structures, implying formation and preservation in a cohesive substrate. In spite of the common density and complexity of trace fossil assemblages, ichnofabric is (and thus infaunal mixing was) only poorly to moderately well developed. Trace fossils are preserved as discrete structures both along bedding planes and in cross-section. Well-mixed intervals are

typically of limited spatial extent and composed of millimeter-scale structures resulting in limited disruption of macro-scale depositional fabrics. Bed-sole assemblages are cast onto the bases of thin (millimeter- to centimeter-scale) sandstone horizons or beds rather than penetrating through beds. Comparison with outgroup facies both confirms the limited extent of biogenic mixing across a range of Cambro-Ordovician marine settings and highlights the significance of heterolithic facies for exceptional preservation and recognition of shallow-tier assemblages.

Substrate Evolution and the Precambrian–Cambrian Transition

Prevailing evidence suggests that a major biological and chemical transition occurred across the Precambrian–Cambrian boundary. This transition, which was followed, over the next tens of millions of years, by dramatic increases in metazoan diversity, abundance, biomineralization and mobility (e.g. Sepkoski, 1981; Erwin et al., 2011), sparked the period of unprecedented macrofaunal innovation commonly known as the Cambrian Explosion, recorded in a plethora of lower to middle Cambrian Lagerstätten. Specifically, the radiation of a mobile, sediment-mixing benthic fauna is commonly invoked as the causative agent for a wide range of contemporaneous ecological, geochemical and taphonomic phenomena, including declines in microbialite abundance and diversity, significant changes in nutrient fluxes, seafloor oxygenation and ocean chemistry; the disappearance of the Ediacara Biota, Ediacara-style preservation and matgrounds; changes in biomarker taphonomy; changes in the stratigraphic character of event bedding and the loss of Burgess Shale-type preservation (e.g. Awramik, 1971;

Brasier, 1990; Sepkoski et al., 1991; Allison and Briggs, 1993a,b; McIlroy and Logan, 1999; Gaines and Droser, 2002; Canfield and Farquhar, 2009; Pawlowska et al., 2013). The advent of infaunalization by triploblastic metazoans, as marked by the appearance of *Treptichnus pedum* and complex, three-dimensional burrowing (e.g. Narbonne et al., 1987; Landing, 1994; Droser et al., 1999), is considered to have mediated the transformation of the sediment-water interface from the microbial mat-bound surfaces of the Proterozoic to the deep zone of chemically and physically homogenized sediments—known as the mixed layer—of the Phanerozoic (Seilacher and Pflüger, 1994; Bottjer et al., 2000). However, the timing of this "agronomic revolution" (Seilacher and Pflüger, 1994) or "Cambrian substrate revolution" (Bottjer et al., 2000) remains poorly resolved; it is not clear how rapidly the advent of an appreciable mixed layer followed the disappearance of matgrounds, nor how rapidly the mixed layer reached thicknesses typical of modern siliciclastic seafloor sediment. The timing of mixed layer development, in turn, bears directly on our understanding of the development of Phanerozoic biogeochemical cycling (e.g. seafloor oxygenation and the establishment of modern redox potential discontinuities) and Phanerozoic-style seafloor communities, as well as shedding light on the role of metazoans as ecosystem engineers.

Exceptional Preservation in the Lower Paleozoic Stratigraphic Record

The Cambro-Ordovician stratigraphic record is characterized by exceptional preservation of not only the body fossil record, but also of shallow-tier (near-surface) trace fossils (e.g. Osgood, 1970; Droser et al., 2002a, b). Modern marine sediments are notably

characterized by a well-developed (i.e. thoroughly homogenized) mixed layer commonly extending to depths in excess of 5–10 cm, passing into a much deeper transition layer of heterogeneous mixing, and the absence of a shallow-tier record (e.g. Berger et al., 1979; Ekdale et al., 1984; Bromley, 1996). Siliciclastic strata of Cambro-Ordovician age, in contrast, are commonly characterized by well-preserved shallow-tier and surficial trace fossils; i.e. structures formed at (and open to) and extending very shallowly below the sediment-water interface and containing bioglyphic (anatomical) detail (e.g. Droser et al., 2002a). This is particularly true for lowermost Cambrian strata; for instance, the ichnofabric of Member 2 of the Chapel Island Formation (containing the GSSP for the Precambrian–Cambrian boundary and immediately overlying strata) is dominated by well-preserved examples of such shallow-tier (surface to near-surface) forms as *Treptichnus*, *Gyrolithes*, *Teichichnus*, *Rusophycus*, *Monomorphichnus* and *Planolites*, all of which were presumably open at the sediment-water interface (Droser et al., 2002b). Although the mode of formation of *Rusophycus*, *Cruziana* and related forms remains controversial (e.g. Crimes, 1975; Baldwin, 1977; Seilacher, 1985; Goldring, 1985), rheotactic alignment and association with undisturbed primary sedimentary structures strongly indicate a surficial or open furrow origin in many instances (Osgood, 1970; Crimes, 1975; Baldwin, 1977; Tarhan et al., 2012). These shallow structures are further characterized by bioglyphic preservation of anatomical detail; burrows are commonly sharp-walled and ornamented; individual scratch marks are readily discernible in arthropod burrows and trackways (e.g. Osgood, 1970; Jensen, 1997).

Lowermost Paleozoic strata are further characterized by exceptionally (crisply and bioglyphically) preserved non-ichnological surficial sedimentary structures, such as the passively produced biogenic sedimentary structure Kullingia. Once considered a chondrophore hydrozoan (e.g. Narbonne et al., 1991) and subsequently re-interpreted as a "scratch circle," the concentric rings imparted in the sediment by current-induced rotation of a tethered organism (Jensen et al., 2002b), Kullingia is characteristic of Ediacaran through Ordovician marine siliciclastic strata but rare in younger sequences. Likewise, tool marks and other sharp bed-sole erosional features—which require "hydroplastic" or cohesive sediments to form and be preserved (Elliott, 1965)—appear to be an especially common feature of Cambro-Ordovician shelfal, heterolithic successions.

Preservation of this level of detail so close to the sediment-water interface is anactualistic (Ekdale et al., 1984). This style of preservation, moreover, appears to be almost entirely confined to the lowermost Paleozoic. Since the shallow infaunal life mode is undoubtedly still present and morphologically similar burrows are being formed today, the temporal discontinuity of the shallow-tier trace fossil record is most likely due to changing substrate-related—and thus taphonomic, rather than first-order ecological or biological—circumstances.

The temporal distinctiveness of this exceptional preservation has, historically, been often overlooked. However, in a series of studies published over the past decade, Droser and others (Droser et al., 2002a; Droser et al., 2004; Jensen et al., 2005) have suggested that,

in earliest Paleozoic marine settings of fine-grained siliciclastic lithologies, bioturbation and thus mixed layer development may have been limited, allowing a cohesive substrate to form at or within centimeters of the sediment-water interface. A cohesive substrate or firmground, by sharply casting and preserving the imprint of metazoan activity (as well as of abiogenic sedimentological processes), may have greatly enhanced the preservation of shallow-tier and surficial structures in the earliest Paleozoic (the "Firmground Hypothesis;" Droser et al., 2002a). Firmgrounds offer an explanation for the exceptionally preserved shallow-tier trace fossils and surficial sedimentary structures commonly observed in lowermost Cambrian normal marine successions (Crimes, 1975; Jensen et al., 1997; Jensen et al., 2002a; Droser et al., 2002a, b, 2004). However, the mechanisms responsible for the formation and anomalous capture of shallow-tier structures such as *Rusophycus* remain contentious. Certain workers have suggested that microbial mats may have provided a cohesive template for bioglyph preservation (e.g. Buatois and Mángano, 2010; Harazim et al., 2013). However, the lack of direct and widespread association between microbially-induced sedimentary structures and exceptionally-preserved shallow-tier traces suggests that this cohesiveness was not due to microbial binding. Others have suggested that lower Paleozoic firmground preservation may have been due solely to the mechanical properties of fine-grained sediments (Crimes, 1975; Goldring, 1995), an assertion supported by modern and experimental studies suggesting that, in the absence of infaunal disruption, fine-grained sediments undergo drastic decreases in porosity and increases in critical erosion threshold (e.g. de Deckere et al., 2001). Thus, prior to the advent of a well-developed mixed layer, fine-

grained siliciclastic sediments may have been anactualistically cohesive, even without the aid of organic binding agents. Alternatively, organic binding may have augmented this mechanical cohesiveness; the formation and preservation of shallow-tier bioglyphic structures may have required an organic "bioglue" coating of sediment grains (Seilacher, 2008). The crisp preservation of these shallow-tier structures represents a critical 'Goldilocks' interval in the development of infaunalization: 'too little' infaunal activity will not result in the production of biogenic structures or fabrics. However, 'too much' infaunal activity will lead to their destruction and sediment homogenization; upon reaching a certain threshold of intensity, infaunal activity becomes 'self-erasing.' Some 'just right' level of infaunal activity is necessary to create and preserve these structures. Therefore, the shallow-tier trace fossil record of the lower Paleozoic is a taphonomic anomaly, representing a brief temporal window of precariously balanced infaunal development, and one ideally suited to the study of seafloor ecology and taphonomy.

However, the broader applicability of the "Firmground Hypothesis" is still untested; it is unclear how prevalent firmgrounds may have been across space and time. Detailed and systematic studies tracking the distribution of shallow-tier trace fossils in lower Paleozoic strata have largely been lacking; previous studies have been confined to the uppermost Neoproterozoic and lowermost Cambrian (Droser et al., 2002a, b; Droser et al., 2004; Jensen et al., 2005) or lower to middle Cambrian (see Chapter 1, herein). Although well-preserved *Rusophycus* and other shallow-tier trace fossils have been previously recorded from lower to middle Paleozoic units, these earlier studies have largely been confined to

the scale of individual samples and assemblages, limiting their applicability to the detection of broad-scale temporal and environmental trends. This study, in contrast, presents trace fossil, sedimentological and taphonomic data systematically collected throughout thick, stratigraphically continuous packages, thus bringing new light to the temporal and environmental distribution of exceptionally preserved Cambro-Ordovician trace fossil assemblages.

Geological Setting and Methods

Data were collected from several Cambro-Ordovician successions worldwide (Fig. 11) in order to assess the temporal distribution of exceptionally preserved trace fossil assemblages and address the possibility of paleoenvironmental and paleogeographic disparity. Shallow marine siliciclastic deposits were targeted because siliciclastics represent a major component of both the modern seafloor and the stratigraphic record and because the vast majority of documented exceptionally preserved shallow-tier trace fossil assemblages occur in siliciclastic units. Moreover, lithologically heterogeneous units were selected for practical reasons, as lithological heterogeneity greatly enhances the frequency of bed-junction preservation and thus the likelihood that infaunal mixing and trace fossil taphonomy can be assessed and temporal and environmental patterns construed (cf. Crimes, 1975). Stratigraphic units were selected for study on the basis of age, exposure and lithological heterogeneity. Moreover, only strata interpreted, on the basis of facies relationships and fauna, to have been deposited under well-mixed marine waters were included in this study. The Cambro-Ordovician Bell Island and Wabana

groups of Bell Island, Newfoundland, Canada consist of a thick (1000 m-scale), well-exposed succession of siliciclastic, thin-bedded, heterolithic strata, interpreted to have been deposited in a shallow marine to shelfal setting (Ranger et al., 1984). In particular, the thinly interbedded mudstones, siltstones and sandstones of the Beach Formation (Bell Island Group) and Powers Steps, Scotia and Grebes Nest Point formations (Wabana Group), of probable Tremadocian-Arenigian age (Ranger et al., 1984), contain prolific and exceptionally preserved trace fossil assemblages (Fillion and Pickerill, 1990).

The Cambro-Ordovician (Tremadocian?) Bynguano Formation of the Mootwingee area of New South Wales, Australia likewise consists of thinly bedded (cm- to m-scale) quartzose sandstones interbedded with mudstones and siltstones, interpreted to have been deposited in a shallow marine environment (Droser et al., 1994). The Bynguano Formation contains diverse, architecturally complex and well-preserved trace fossil assemblages, notably the anomalous capture of both 'pre-depositional' and 'post-depositional' assemblages associated with individual bedding planes.

Cambro-Ordovician data collected from Australia and Avalonia were supplemented by observations from Gondwanan (Iberian Peninsula) and Laurentian (Appalachian Basin) outgroup successions (interpreted to have been deposited under lower- and higher-energy conditions, respectively). The Barrancos Formation of southwestern Spain and Portugal consists of thinly bedded (mm- to cm-scale) mudstones, siltstones and very fine-grained sandstones and is interpreted to represent a bathyal-abyssal 'flysch'-style succession

(Robardet and Gutiérrez Marco, 2004) of, on the basis of acritarch and graptolite

biostratigraphy, late Arenigian-early Oretanian age. The upper Ordovician (Ashgillian)

Juniata Formation of the Appalachian Basin consists largely of channelized, immature,

very fine- to coarse-grained litharenitic sandstones, interpreted to represent a marginal

marine to deltaic setting (Cotter, 1982; Freile and Baldwin, 1988). Both the Barrancos

and Juniata formations contain well-documented and diverse trace fossil assemblages

(Robardet and Gutiérrez Marco, 2004; Freile and Baldwin, 1988) and provide important

facies end-members for this study of Cambro-Ordovician trends in trace fossil

taphonomy, ecological complexity and mixed layer development.

In order to assess the extent of exceptionally preserved shallow-tier trace fossil

assemblages, we examined these Cambro-Ordovician successions according to six

criteria: 1) bedding thickness; 2) fabric disruption; 3) bioglyphic preservation; 4)

surficially produced physical sedimentary structures; 5) the paleobiological and

paleoecological complexity of trace fossil assemblages and 6) depth of bioturbation.

Although these metrics are related, they provide non-dependent indicators of substrate

consistency, the extent to which seafloor sediments were mixed and thus benthic

taphonomy.

The thickness of beds separated by clear bed junctions indicates the maximum depth to

which bioturbation penetrated without disrupting the coherency of individual beds.

Biogenic fabric disruption (quantified by means of the Ichnofabric Index [Droser and

Bottjer, 1986]), which measures the extent to which burrowing organisms have disrupted the stratigraphic expression of physical depositional fabrics, provides another parameter for mixing intensity. Ichnofabric Index was determined both in the field and by slabbing, polishing and scanning facies-representative collected specimens. The taphonomic fidelity (quality of preservation) of shallow-tier trace fossil assemblages was employed as a direct metric of substrate consistency; soupy, well-mixed sediments will not capture anywhere near the same level of detail as a firm (unmixed) substrate. The exceptional preservation of bioglyphs—finely-preserved burrow ornamentation or other organismal "fingerprints" such as arthropod scratch marks—are particularly useful indicators of cohesive sediments at the depth of emplacement (Ekdale and de Gibert, 2010). Physical sedimentary structures formed at the paleo-sediment-water interface, such as tool marks and other sharp bed-sole erosional features are also, like shallow-tier ichnofossils, informative metrics of substrate consistency (e.g. Elliott, 1965). The morphological and assemblage-level complexity of shallowly emplaced trace fossils, including trace fossil size, density, diversity and taphonomy was used to evaluate the extent and character of substrate colonization. The presence or absence of individual taxa was recorded on the scale of individual bedding planes and through sections and formations. If present, taxa were characterized as "abundant," "common" or "rare" according to how frequently they were observed, e.g. present on each bedding plane and often multiple occurrences per bedding plane ("abundant"); multiple occurrences within 5 m ("common"); or < 5 occurrences per section ("rare"). Open burrows, such as *Treptichnus*, *Gyrolithes* (lower Paleozoic examples of which may be distinct from post-Paleozoic examples; Netto et al.,

2007) *Arenicolites* and *Diplocraterion* (e.g. Alpert, 1974; Droser et al., 1999; Jensen et al., 2000; Droser et al., 2002b; Vannier et al., 2010) were used to estimate depth of bioturbation and mixed layer depth; well-preserved open burrows were considered to indicate shallow mixing, whereas truncated burrows and infill by foreign material suggest multiple generations of substrate colonization and sediment mobilization and thus higher mixing intensity (Bromley and Ekdale, 1986). Cross-cutting and consistent tiering relationships were further used to quantify the maximum depth of bioturbation (Bromley and Ekdale, 1986; Wetzel and Aigner, 1986). Both bed thicknesses and trace fossil dimensions were characterized according to metric 'scale': "mm-scale" (1–10 mm), "cm-scale" (1–10 cm; i.e. the range of values between 10 mm and 1 dm) or "dm-scale" (1–10 dm). Specimens are reposited in the invertebrate paleontology collection of the Department of Earth Sciences, University of California, Riverside (UCR).

Sedimentology and Ichnology

Strata of the Bell Island and Wabana groups (Figs. 12–14) and the Bynguano Formation (Fig. 15) were examined according to the criteria outlined above in order to track the distribution of exceptionally preserved trace fossil assemblages and to assess the relationship between trace fossil taphonomy and the intensity of biogenic sediment mixing. Stratigraphic analyses were performed on both the meter- and the bed-scale. Bed-scale 'microstratigraphic' sections were selected from facies-representative intervals on the basis of exposure. The sedimentological, ichnological and taphonomic character of bedding plane surfaces was documented.

Individual beds were observed to be coherent and commonly thin; bed-by-bed analysis of microstratigraphic sections (Figs. 12–14) through representative facies of the Bell Island and Wabana groups yielded a mean bed thickness of 3.30 cm. Junctions between beds are well defined, ranging from planar to wavy or rippled. Small-scale (mm- to cm-scale length, sub-mm to mm-scale width) tool marks are commonly observed along bedding planes of the Bell Island and Wabana groups and are especially common in the Powers Steps Formation (Wabana Group). Evidence for strong or frequent erosion (rip-ups, scoured bed bases, truncation of burrows) is lacking and evidence for even moderate-scale erosion is uncommon in the Bell Island and Wabana groups; evidence for erosion is rare to common in the Bynguano Formation. The physical fabric of beds is commonly characterized by prominent laminations, ranging from parallel to low-angle (up to 30–40° but typically lower) cross-laminations. Stratigraphic successions are predominantly composed of beds of very fine- to fine-grained sand (with laminae defined by sub-millimetric mudstone horizons or drapes) occurring as planar horizons or lobes, interbedded with mudstone or siltstone beds containing millimetric sand lenses, stringers or laminae. Soft sediment deformation is not uncommonly observed in sandy intervals, suggesting, in conjunction with cross-laminated horizons and a general lack of trace fossil compaction, that deposition of sand-rich intervals occurred fairly rapidly. The above lithological and sedimentological data indicate a shallow marine origin, ranging from nearshore or deltaic to shelfal.

Bedding planes of the Bell Island and Wabana groups and the Bynguano Formation are characterized by dense and diverse trace fossil assemblages (Figs. 16–18). The Beach Formation (Bell Island Group) was observed to contain abundant *Arenicolites*, *Bergaueria*, *Cruziana*, *Gyrolithes*, *Palaeophycus*, *Planolites*, *Rusophycus*, *Teichichnus*, *Treptichnus* and arthropod scratch marks; *Cruziana*, *Gyrolithes* and *Rusophycus* are especially dominant as both individual occurrences and components of bedding plane assemblages (e.g. Fig. 18B). The Powers Steps and Scotia formations (Wabana Group) are similarly populated by abundant *Arenicolites*, *Arthraria*, *Cochlichnus*, *Cruziana*, *Gyrolithes*, *Monomorphichnus*, *Palaeophycus*, *Phycodes*, *Planolites*, *Rusophycus*, *Teichichnus*, *Treptichnus*, *Trichophycus*, arthropod scratch marks and 'scribbling traces' (cf. Fillion and Pickerill, 1990); *Arthraria*, *Cruziana*, *Rusophycus*, *Teichichnus* and *Trichophycus* are especially common components of bedding plane assemblages (e.g. Figs. 16A–B, 17A). The Grebes Nest Point Formation (Wabana Group) contains a similar assemblage of trace fossils, with especially abundant *Trichophycus* (e.g. Fig. 16G) and secondarily abundant *Arthraria*, *Rusophycus* and *Teichichnus*. The Bynguano Formation contains extremely dense monotaxic assemblages of *Rusophycus* (e.g. Fig. 16D), as well as more diverse assemblages populated by *Arenicolites*, *Monocraterion*, *Skolithos*, *Thalassinoides* and *Trichichnus*. Trace fossil assemblages are commonly dense; examples of bedding planes characterized by the highest indices of bedding plane bioturbation are common (e.g. indices 4–5 of Miller and Smail [1997] are not uncommon and beds of indices 3–4 occur abundantly). Multiple generations of sediment colonization are commonly observed (Fig. 18), for instance exceptionally well-preserved *Cruziana* are

cross-cut by equally well-preserved treptichnids and other small, sequentially excavated burrows and pipes (e.g. Figs. 18A, B, F). Individual trace fossils—in particular individuals of *Cruziana*, *Rusophycus* and *Trichophycus*—of cm-scale diameters and lengths commonly occur throughout the study intervals; burrows of up to 10 cm diameter and up to 12 cm length were observed.

In spite of the high density of trace fossil assemblages found in these Cambro-Ordovician strata, biogenic sediment mixing is poorly developed (Figs. 19–20). Rare and spatially limited portions of beds and successions attain Ichnofabric Index (ii) values of 5 (denoting the densest levels of biogenic disruption of physical fabric possible without completely homogenizing bed fabric) (Fig. 19D). However, average (mean) ii values for each formation consistently ranged between ii 2 and ii 3 (Beach Formation: ii 3; Powers Steps Formation: ii 2; Grebes Nest Point Formation: ii 2; Bynguano Formation: ii 3). Intervals of low ii (ii 1–2) are common throughout the strata examined. Moreover, both low and higher ii values are commonly characterized by 'microburrowing' or cryptobioturbation (cf. Howard and Frey, 1975)—disruption caused by meiofauna-scale burrowing, occurring on a spatially limited (sub-mm- to mm-scale) scale (e.g. Fig. 19C). Cryptobioturbation, in particular, but also smaller-scale (mm- to cm-scale) macroburrowing, occurs commonly in intimate spatial association with undisrupted physical sedimentary fabrics, particularly laminated intervals (e.g. Figs. 19A, C, E; Fig. 20H). In these cases, burrows are delicately cast on the bases of beds or individual sandy laminae within beds or occur as 'floating' sand-infilled endorelief (full relief) structures

within a muddy matrix (Figs. 19A, C, E). Burrows are nearly universally observed to be cast rather than penetrative; burrows occurring along the bases of beds or internal horizons are overlain by undisrupted laminae (Figs. 19C, 20). With the exception of post-depositional assemblages of the Bynguano Formation (which consist primarily of U-burrows and pipes such as *Arenicolites* and *Skolithos*), burrow depths of greater than 5 cm were not observed.

Trace Fossil Taphonomy

The vast majority of the trace fossil assemblages observed in the Bell Island and Wabana groups and the Bynguano Formation contain elements characterized by extremely high taphonomic fidelity. Assemblages consist of crisply preserved, high relief structures with diameters ranging from the sub-millimetric to the upper end of the centimetric scale in diameter (Figs. 16–18, 20). Trace fossils occur much more commonly in contact with each other than in isolation and assemblages may approach the highest indices of bedding-plane bioturbation (e.g. indices 4–5 of Miller and Smail [1997]) (Fig. 18). Yet in spite of the abundant occurrence of dense bedding-plane trace fossil assemblages, individual traces occur as discrete, crisply preserved structures. Multiple generations and tiers of biogenic structures are preserved in immediate spatial association at very high fidelity and without evidence of compaction, suggesting that fossil structures currently in contact were also in contact at the time of formation. Even complex, delicate and three-dimensional structures, such as multi-whorled *Gyrolithes* are preserved intact and undeformed.

Strikingly, trace fossils are characterized by bioglyphic preservation – the capture of fine-scale anatomical (rather than merely structural) detail. *Rusophycus* and *Cruziana* from all units studied are commonly characterized by both endopodal and exopodal scratch marks (Figs. 17A, 18A–B, E–F); *Trichophycus* burrows of all sizes are characterized by parallel and radiating scratch marks of sub-millimetric diameter (Figs. 16A, E, G). *Palaeophycus* and other cylindrical burrows are commonly characterized by transverse markings or other wall ornamentation (e.g. Fig. 16B). Isolated scratch marks are common and characterized by the same crispness of preservation (Fig. 17). This bioglyphic preservation extends to non-biogenic surficially produced sedimentary structures such as tool marks. Very fine-scale tool marks (sub-mm-scale diameters, mm-scale lengths) occur in sharp demarcation from and relatively high relief above bedding planes and are not associated with penetrative intrastratal fabrics (Figs. 20A–B, E–F).

Other Cambro-Ordovician Facies

Additional Cambro-Ordovician sections, characterized by facies packages distinct from those of the Bell Island and Wabana groups and Bynguano Formation were examined in order to constrain the role of environmental variability in exceptional trace fossil preservation and mixed layer development. Accordingly, the Juniata Formation of the Appalachian Basin, the Pacoota Sandstone of the Northern Territories, Australia and the Barrancos Formation of southwestern Spain and Portugal were selected as higher-energy,

nearshore to marginal marine (Juniata, Pacoota) and lower-energy, offshore (Barrancos) outgroups.

The Juniata Formation

The upper Ordovician (Ashgillian [approximately upper Katian–lower Hirnantian]) Juniata Formation, which crops out across the Appalachian Basin, eastern United States, was examined at Waggoner's Gap, near Carlisle, Pennsylvania. At this locality, the Juniata Formation consists largely of medium to thick (upper cm- to upper dm-scale) beds of maroon red, medium-grained litharenite, interbedded with minor thinner (cm-scale) beds of silt or very fine-grained sandstone. Litharenite beds are both texturally and compositionally immature; particles are subangular and horizons of irregularly-shaped mud chips are common, as are horizons of coarse-, very coarse- and granule-sized material. Beds are strongly trough cross-laminated (Fig. 21H) and both bed tops and bases are commonly wavy. This facies package has led to dispute regarding the probable paleoenvironment of the Juniata Formation as either fluvial or shallow marine (Cotter, 1982; Freile and Baldwin, 1988).The features we observed (e.g. interbedding of silty and coarser-grained beds, particle immaturity and evidence of high-energy flow) are consistent with a marginal marine, fluvially sourced, delta-front setting.

Two types of trace fossil assemblage are preserved in the Juniata Formation: 1) Assemblage Type A consists of low to moderately dense assemblages of *Skolithos*, which occur endogenically and are visible in cross-section (Fig. 21H). 2) Assemblage Type B

consists of moderate to high density assemblages of trace fossils occurring on bed bases
(Fig. 21G). Type A assemblages occur rarely in the Juniata Formation but are common
where they occur. Individual *Skolithos* pipes of up to 8 cm in depth and 0.5 cm in
diameter were observed. *Skolithos* openings were only rarely observed along bedding
planes; burrows commonly originate from muddy horizons or laminae within cross-
bedded litharenites and cut through underlying laminae. Type B assemblages are
common along the bases of beds throughout the exposed Juniata Formation and consist
most prominently of positive-relief infilled burrows, including *Rusophycus*, *Arthrophycus*
and *Lockeia*. Burrows are up to 7 cm in length and 1.5 cm in diameter; discrete traces as
small as < 0.5 cm in diameter are also observed. Type B assemblages are commonly
poorly preserved and largely lack bioglyphic detail. However, well-preserved Type B
assemblages, consisting of sequentially produced or intergradational mm- to lower cm-
scale *Rusophycus* and *Cruziana* or crisply preserved high-relief *Lockeia* are not
uncommon (Figs. 21D, G). Assessment of ichnofabric was challenging due to the lack of
lithological heterogeneity; however, where conditions permitted accurate measurement, ii
values were determined to be consistently low (ii 1–2).

The Barrancos Formation

Outcrops of the lower–middle Ordovician (upper Arenigian–lower Oretanian
[approximately Dapingian–Darriwilian]) Barrancos Formation of the southwestern
Iberian Peninsula were examined near Encinasola, Spain. The exposed upper portion of
the Barrancos Formation consists of very thin (sub-mm- to mm-scale) beds of mudstone

and siltstone with rare thin beds of very fine-grained sandstone. Beds are well-laminated with planar junctions, with rare low-amplitude wavy bedforms also observed. Sedimentary structures are rare and consist largely of frondescent marks preserved as casts on bed bases. The sedimentological and lithological features we observed are consistent with previous interpretations (e.g. Robardet and Gutiérrez Marco, 2004) for a low-energy, sub-storm wavebase flysch setting with occasional, higher-energy incursions of coarser-grained material.

Low-diversity, low- to moderate-density trace fossil assemblages were commonly observed along bedding planes of the Barrancos Formation (Figs. 21A–C). Small and large 'scribbling' curvilinear traces of mm- to cm-scale diameter and cm- to dm-scale length were most common. Well-preserved (though non-bioglyphic) and high-relief bilobed traces of rusophyciform morphology (though lacking transverse markings) occur as both isolated individuals and sequential 'scribbles' or circling forms (Figs. 21A, C). Rare but crisply preserved *Chondrites* and *Nereites* were also observed. Intra-bed fabrics are strongly laminated with consistently low ii values (ii 1–2). Fabric-disruptive biogenic structures are limited to rare endogenic (full-relief) 'floating' silt- and sand-infilled burrows of mm-scale depths and diameters. Also present are rare sub-mm to mm-scale microburrows cast on the base of individual sandy and silty laminae within a predominantly muddy matrix.

The Pacoota Sandstone

The Cambro-Ordovician Pacoota Sandstone was examined near Ellery Creek in the Northern Territories, Australia. At this locality, the Pacoota Sandstone crops out as decimeter-scale sandstone packages comprising parallel- and cross-stratified centimeter-scale sandstone event beds (Figs. 21E–F). *Skolithos* and *Diplocraterion* burrows pipe down from the tops of many of these sandstone beds and amalgamation horizons but are not so dense as to obliterate bedding (Fig. 21F). Dense assemblages of *Rusophycus* occur on the bases of bedding planes (Figs. 16C, 21E). Similar to those preserved in the Bynguano Formation, Pacoota *Rusophycus* do not penetrate but rather are cast by the overlying sandstone. They are also characterized by exceptional, bioglyphic preservation, including high relief structures and scratch marks preserved in spite of high assemblage density and multi-generational contact. *Rusophycus* were presumably formed in thin silt interbeds and subsequently cast by sand. Bed-junction preservation, coupled with the lack of preserved counterparts or interbeds, indicates that these silty interbeds were likely destroyed, post-casting, by weathering and compaction. These beds represent deposition in a high-energy, nearshore setting at or below fair-weather wavebase.

Discussion

The Cambro-Ordovician shelfal successions surveyed (Bynguano, Beach, Powers Steps, Scotia and Grebes Nest Point formations) are characterized by exceptional and extensive preservation of shallow-tier, bioglyphic trace fossil assemblages. This exceptional preservation, which encompasses the capture of discrete and undeformed structures even

where assemblages are extremely dense and multigenerational contact is common, high integrity of morphologically and spatially complex structures, a lack of compaction, the crisp preservation of sub-millimetric biogenic and abiogenic structures and the bioglyphic capture of anatomical detail such as scratch marks and burrow wall ornamentation, necessitates that these structures formed in a cohesive substrate.

When combined with sedimentological and ichnological indicators, this exceptional preservation suggests that a cohesive substrate was situated within centimeters of the sediment-water interface. The presence of abundant trace fossils of shallow depth interpreted, on the basis of burrow morphology and functional and ethological reconstructions, to have been formed as structures open at the sediment-water-interface, such as *Treptichnus*, *Teichichnus* or *Gyrolithes* (e.g. Vannier et al., 2010), suggests that the horizon along which these structures were preserved was situated very near to the paleo-sediment-water interface. Moreover, the presence of clear and largely undisrupted physical sedimentary structures, such as planar and cross-laminae, observed within the infill of structures such as *Rusophycus* or *Cruziana*, is strongly indicative of an open furrow origin for these structures as well as capture of an extremely shallow tier. Surficially produced sedimentary structures such as tool marks, which are a common occurrence in the Bell Island and Wabana groups, are indicative of a firm substrate in contact with the overlying water column.

The paucity of high ichnofabric indices, the preponderance of low- to mid-range ii values and the general limitation of higher ii values to either spatially confined zones of macrofaunal disruption or horizons of non-disruptive, meiofaunal cryptobioturbation indicate that even as late as the Ordovician, mixing intensity remained low in marine shelfal settings. It is unlikely that water-column oxygen limitation was responsible for this suppressed mixing, as 1) the majority of the examined units appear to have been deposited within wavebase and thus within the zone of oceanographic mixing; and 2) suppressed infaunal mixing was consistently observed across a range of facies, basins and continents. An underdeveloped mixed layer may, however, have played a substantial role in the widespread preservation of the shallow-tier and surficial structures preserved in these units. The limited extent of fabric perturbation—particularly the lack of efficiently destructive chemical and physical churning effected by 'bulldozing' invertebrates such as modern holothurians (e.g. Thayer, 1979)—may have permitted the naturally cohesive properties of fine-grained sediments (Crimes, 1975; de Deckere et al., 2001; Droser et al., 2002a) to have had a disproportionate (i.e. anactualistic) impact upon substrate consistency and thus benthic taphonomic fidelity.

Erosion undoubtedly occurred at intervals during the depositional history of these units and, in cases in which surficially produced 'firmground' structures are preserved, may have been responsible for the prior removal of a shallow mixed layer and exhumation of the underlying cohesive substrate. For instance, although certain ichnological assemblages in the Bynguano contain evidence of pre-depositional substrate colonization

resulting in dense *Rusophycus*-dominated horizons, other assemblages lack evidence of pre-depositional substrate perturbation and contain independent sedimentological evidence of exhumation, such as scouring and uneven bed topography (Droser et al., 1994). However, in most of the examined units, sedimentological or ichnological evidence for significant erosion (e.g. sharp and irregular bed junctions, rip-ups, washed-out or truncated burrows) was only rarely observed. Moreover, high-relief trace fossils, suggesting cohesive substrate conditions, were commonly observed in conjunction with surficial or shallow-tier structures, indicative of very near proximity to the paleo-sediment-water interface. The majority of the fossiliferous assemblages examined in this study can thus be presumed to have been shallowly produced under cohesive substrate conditions. Therefore, although the sediment-water interface itself may have been characterized by mixed sediments, a cohesive substrate must have existed within centimeters or perhaps even millimeters of the sediment-water interface, such that fine-scale erosion of a shallow mixed layer would have resulted in exhumation, colonization and preservation of this horizon.

These data also shed light upon long-standing debate concerning the formation (particularly the horizon of origin) of structures such as *Rusophycus* and exceptional preservation in general. Certain workers (e.g. Seilacher, 1955, 1970, 1985; Goldring, 1985), seeking an explanation for the bioglyphic preservation of *Rusophycus* and related structures at lithologic interfaces, have interpreted these structures as either intrastratal in origin or as palimpsest undertracks. Others (e.g. Osgood, 1970; Crimes, 1975; Baldwin,

1977; Tarhan et al., 2012), however, indicating instances of rheotaxis and preservation of primary sedimentary structures within burrow infill, have suggested a surficial origin for these traces. My observations favor the latter interpretation. Burrows are only rarely observed to be washed out or truncated; they are preserved with high taphonomic fidelity. Moreover, burrows occur as casts rather than penetrative structures; they occur most commonly as discrete structures at the bases of beds or individual laminae and contain undisrupted primary physical sedimentary fabrics. They are also overlain by undisrupted laminae, further indicating that burrows preserved along bed bases were not sourced from bed tops or intrastratally. Likewise, the crisp and minute preservation of sub-millimetric structures like tool marks (of definitive surficial origin) or isolated or burrow-associated scratch marks and the absence of intrastratal deformation structures suggesting penetration through the overlying bed are not consistent with undertrack preservation. There are of course examples of bed-top origin and intrastratal perturbation associated with more complex, three-dimensional burrow systems preserved within these units. However, the vast majority of bed sole trace fossil assemblages observed in these units cannot be demonstrated to be either intrastratal or penetrative (bed-top) in origin but rather are morphologically and taphonomically consistent with a pre-depositional origin and syn-depositional casting.

Comparison of shallow marine, shelfal successions with those of other settings both reinforces the pattern of limited mixing observed in the Bell Island and Wabana groups and the Bynguano Formation and emphasizes that shelfal settings were likely at the

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forefront of increasing seafloor colonization. Neither the higher-energy Juniata Formation (maximum: ii 2; ii 1 common) and Pacoota Sandstone nor the lower-energy Barrancos Formation (maximum: ii 2; ii 1 common) is characterized by mixed layer development comparable to that observed in the Bell Island and Wabana groups and the Bynguano Formation. The Juniata Formation and Pacoota Sandstone display striking similarities to the Bynguano Formation in the concurrence of pre-depositional (Type B) bed sole assemblages and post-depositional (Type A) assemblages of epifaunal and intrastratal origin. Intriguingly, although the preservational quality observed in each formation is higher than expected and commonly bioglyphic, differences in relief suggest that *Rusophycus* assemblages of the otherwise similar but higher-energy Pacoota Sandstone may have experienced less erosion than those of the Bynguano Formation. Although indifferently to poorly preserved Type B assemblages are not uncommon in the Juniata Formation, crisply preserved Type B assemblages, consisting of millimetric-scale trace fossils preserved along the bases of strongly cross-bedded medium-grained sandstone beds characterized by size-specific horizons of coarse-grained material, are also present. This suggests that the same preservational process observed in shelfal units—the casting of delicate structures along bed bases—also occurred in much more proximal and high-energy settings of this time period.

The quality of preservation observed in the Juniata, Pacoota and Barrancos, although in instances unexpectedly high, is, however, not comparable to the preservation characteristic of shelfal sections, further emphasizing the importance of facies—

particularly of lithological heterogeneity—in the exceptional preservation of shallow-tier

structures. Ichnological and ichnofabric analyses are dependent not only on the

occurrence and preservation of ichnological structures, but also on our ability to

recognize them in the rock record. This difficulty is greatly compounded in cases of

lithological homogeneity. Conversely, bed-junction preservation and thinly bedded strata

maximize the visibility and thus utility of trace fossils (e.g. Crimes et al., 1975). In the

field, trace fossils are most easily discerned in facies characterized by heterolithic

lithologies, particularly thinly (mm- to dm-scale) bedded and thinly interbedded muddy,

silty and sandy material. Therefore, for practical reasons, any attempt to discern

temporally and spatially widespread biological patterns by means of systematic

ichnofabric analysis is best confined, particularly in the field, to facies characterized by

fine-scale lithological heterogeneity. However, sedimentation rate or other environmental

or biologically-restrictive factors are likely to play a major role in the preservation of

such trends. For instance, settings characterized by very low sedimentation rates (with the

extreme endmember of hiatal surfaces) may artificially, through (biological-scale) time-

averaging, appear more thoroughly bioturbated than settings characterized by high

sedimentation rates. Conversely, especially high sedimentation rates—such as those

responsible for the deposition of the Juniata Formation—may increase the biotic stress of

certain environments, thus limiting the extent of substrate colonization. Thus rigorous

study of facies assemblages is essential to ensure that only units of comparable

depositional environment are used to establish setting-specific trends as a baseline for the

interpretation of paleobiological and paleoecological patterns.

Conclusions

A range of Cambro-Ordovician units interpreted to have been deposited in marine shelfal settings was examined to determine the nature and extent of exceptionally preserved trace fossil assemblages. The Bynguano, Beach, Powers Steps, Scotia and Grebes Nest Point formations were found to be characterized by widespread exceptional preservation of shallow-tier ichnological assemblages, necessitating formation in a cohesive substrate. Biogenic sediment mixing was determined to be poorly developed; well-mixed intervals were of limited spatial extent and the majority of bed-sole structures were observed to be cast rather than penetrative or intrastratal. Comparison with outgroup facies, represented by the Juniata and Barrancos formations, and the Pacoota Sandstone, confirms the limited extent of mixing across Cambro-Ordovician marine environments and emphasizes the importance of lithologically heterogeneous facies to the taphonomic fidelity of shallow-tier assemblages and bioglyphic preservation.

Figures

Figure 11. Cambro-Ordovician study localities. Areas of study include central Pennsylvania, Appalachian Basin, eastern USA (Waggoner's Gap [Juniata Fm]); Bell Island, Newfoundland, Canada (The Beach, [Beach Fm.], Grebes Nest Point [Powers Steps Fm., Scotia Fm., Grebes Nest Point Fm.], Upper Grebes Nest Point [Powers Steps Fm., Scotia Fm.]); southwestern Iberian Peninsula, Spain (Encinasola [Barrancos Fm.]); New South Wales, Australia (Mootwingee [Bynguano Fm.]); and Northern Territories, Australia (Ellery Creek [Pacoota Sandstone]).

Figure 12. Stratigraphic profile of the Beach Formation (The Beach, Bell Island, Newfoundland, Canada). Macrostratigraphic (meter-scale) record of sedimentological and paleontological features, with microstratigraphic (bed-scale) inset of meters 2–3. Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c, coarse-grained sand; cgl, conglomeratic-sized particles (granule, pebble, cobble).

Figure 13. Stratigraphic profile of the Powers Steps Formation (Upper Grebes Nest Point, Bell Island, Newfoundland, Canada). Macrostratigraphic (meter-scale) record of sedimentological and paleontological features, with microstratigraphic (bed-scale) inset of meters 8–9. Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c, coarse-grained sand; cgl, conglomeratic-sized particles (granule, pebble, cobble).
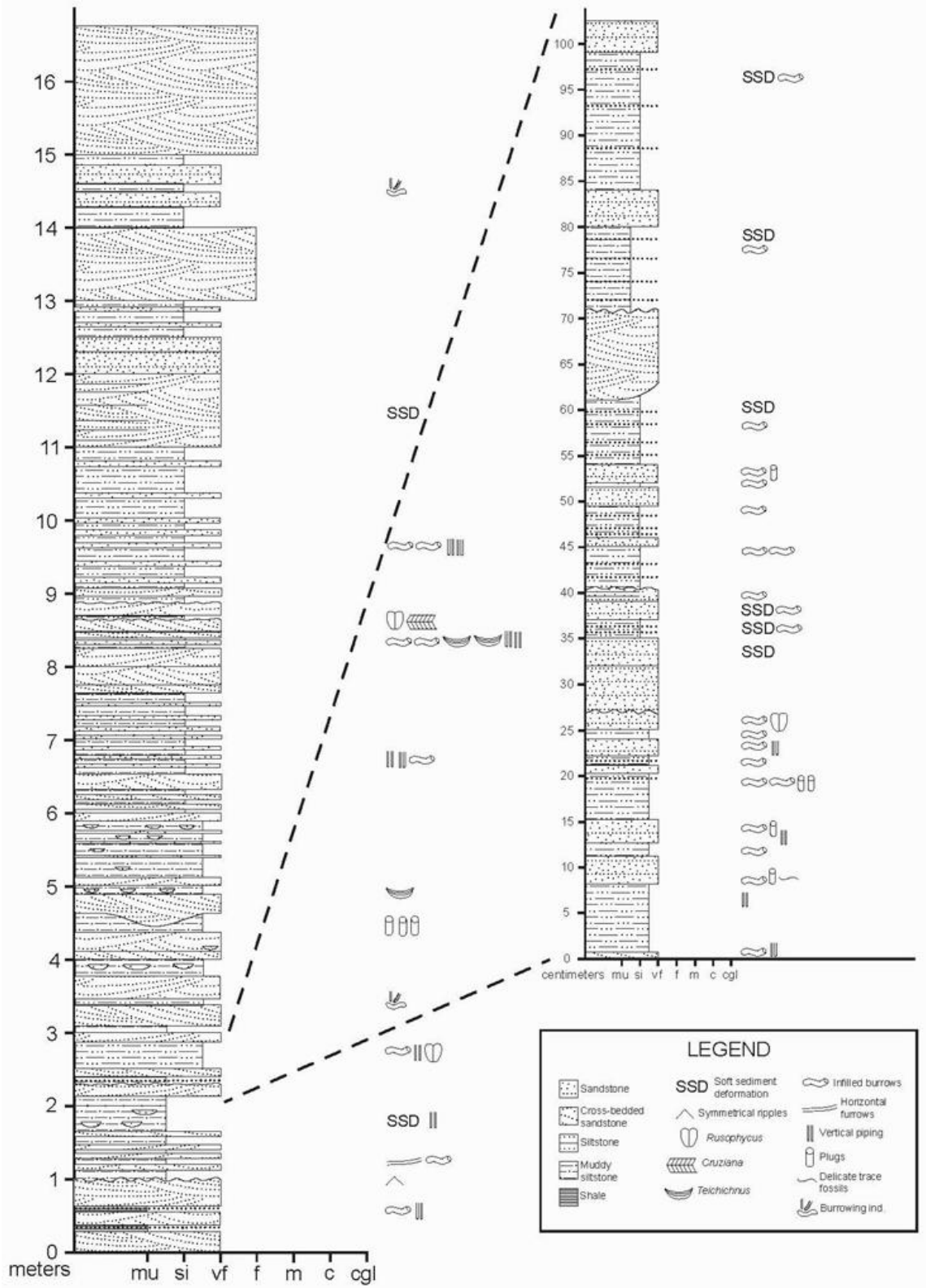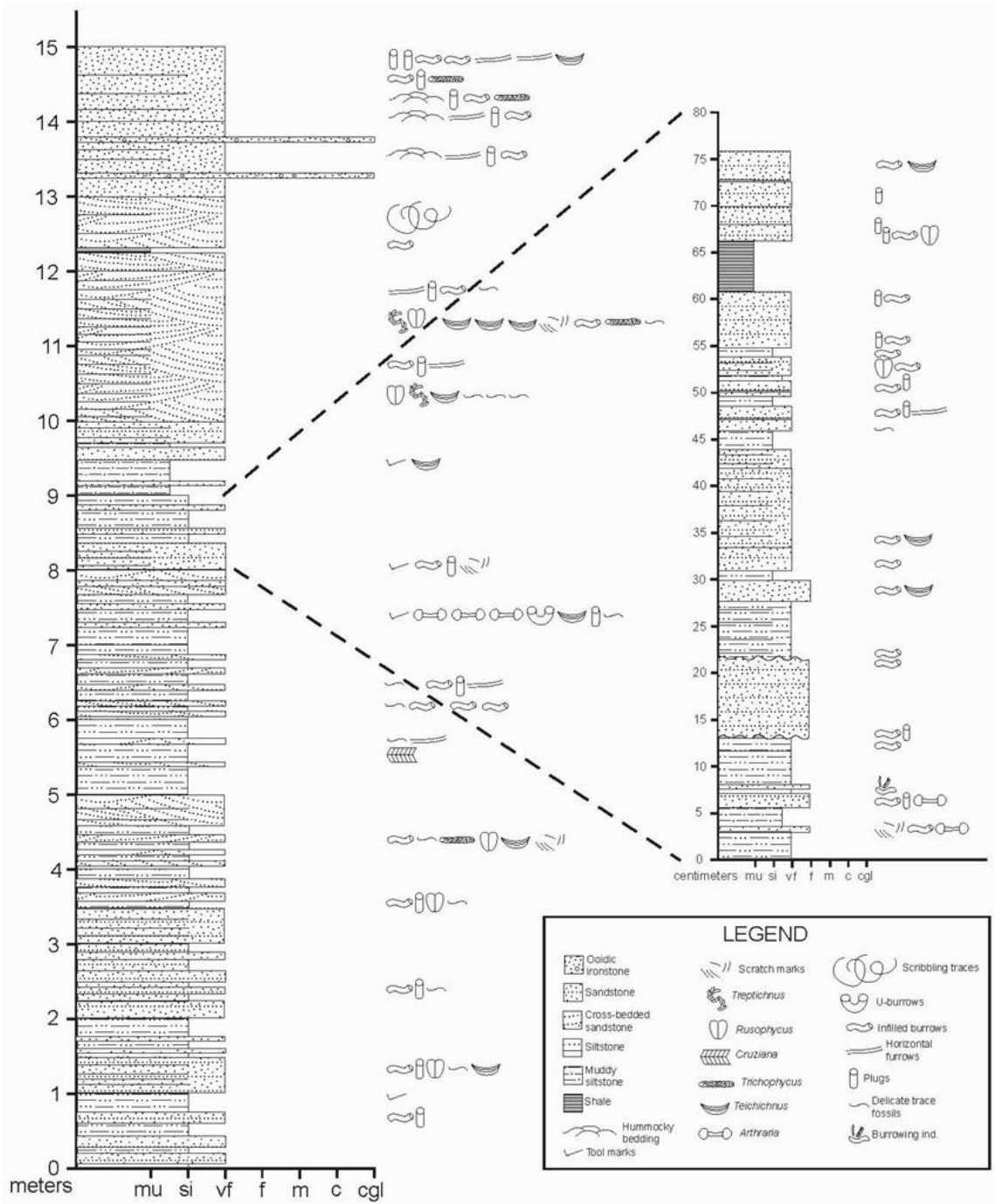
Figure 14. Stratigraphic profile of the Grebes Nest Point Formation (Grebes Nest Point, Bell Island, Newfoundland, Canada). Macrostratigraphic (meter-scale) record of sedimentological and paleontological features, with microstratigraphic (bed-scale) inset of meters 1–2. Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c, coarse-grained sand; cgl, conglomeratic-sized particles (granule, pebble, cobble).
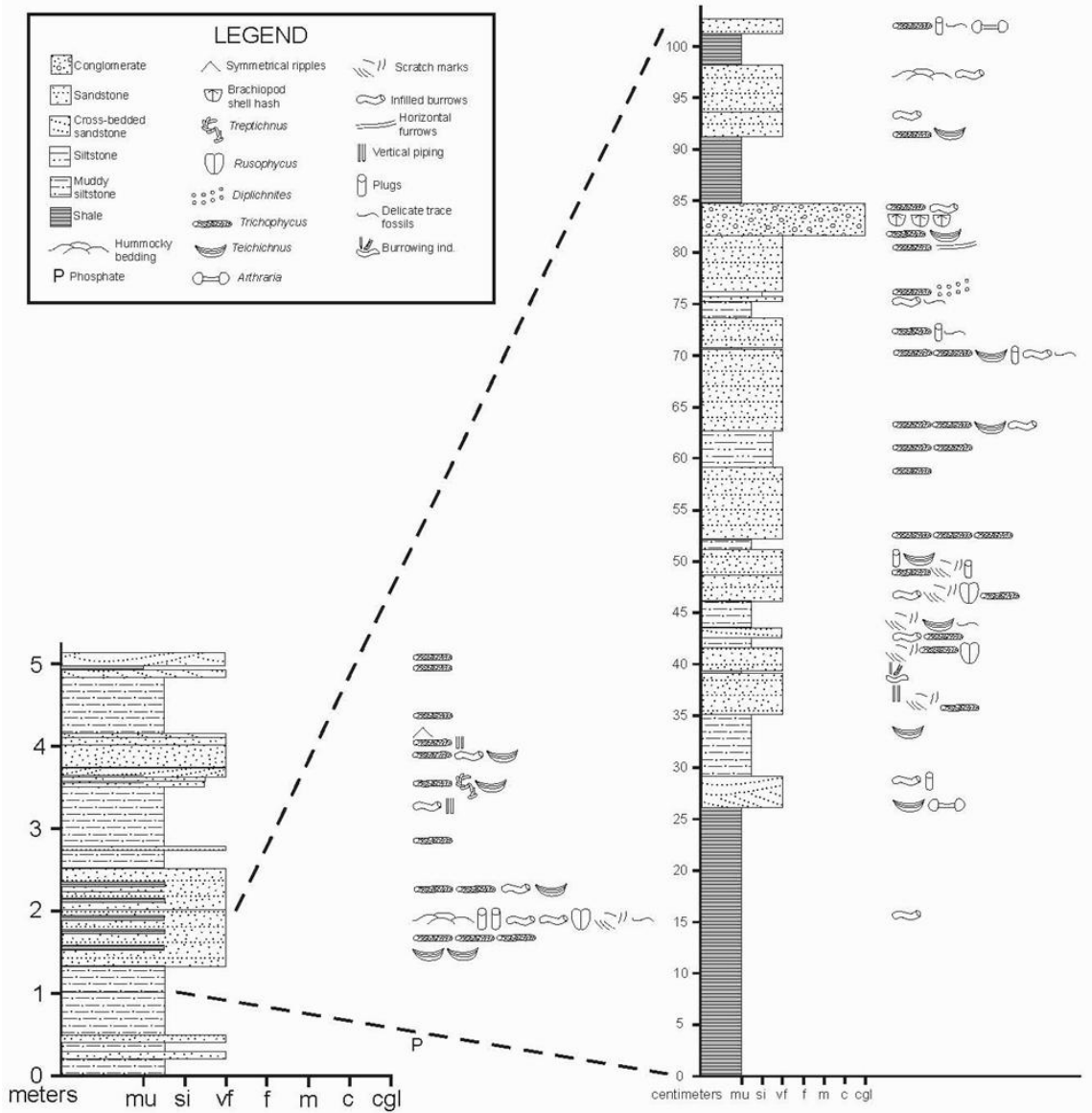
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Figure 15. Stratigraphic profile of the Bynguano Formation (Mootwingee, New South Wales, Australia). Along a single horizon, one sedimentological or paleontological symbol denotes that the feature is 'present,' two symbols denote that the feature is 'common' and three that it is 'abundant.' Grain sizes: mu, mud; si, silt; vf, very fine-grained sand; f, fine-grained sand; m, medium-grained sand; c, coarse-grained sand.

Figure 16. Exceptionally preserved Cambro-Ordovician shallow-tier trace fossil assemblages. A: Field photograph. Assemblage includes *Arthraria*, *Trichophycus*, *Teichichnus* and *Lockeia*. Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. B: UCR 11133/1. *Palaeophycus* and *Teichichnus*. Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. C: Field photograph. *Rusophycus*. Pacoota Sandstone, Ellery Creek, Northern Territory, Australia. Hyporelief. Australian one dollar coin (diameter approximately 2.5 cm) for scale. D: Field photograph. *Rusophycus and Skolithos*. Bynguano Fm., Mootwingee, New South Wales, Australia. Hyporelief. Length of pocket knife is 8.2 cm. E: UCR 11132/3. *Trichophycus*. Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. F: UCR 11132/3. *Palaeophycus*, with obliquely meniscate or 'corkscrew' structures. Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. G: UCR 11134/1. *Trichophycus*. From 1.49 m in Fig. 14. Grebes Nest Point Fm., Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. Scale bars: A–B, E–G = 1 cm.
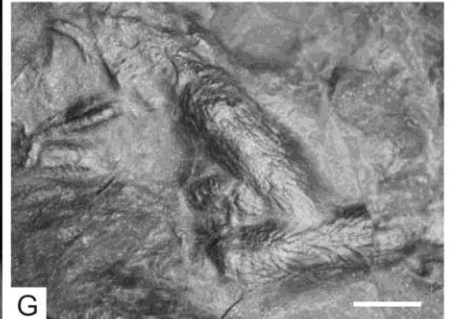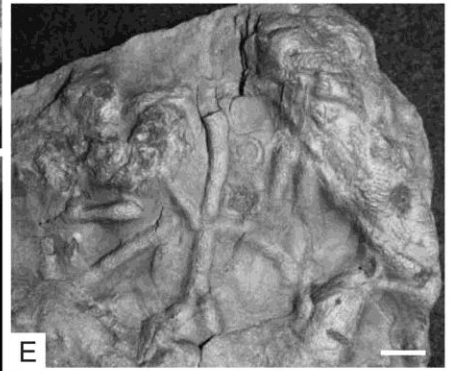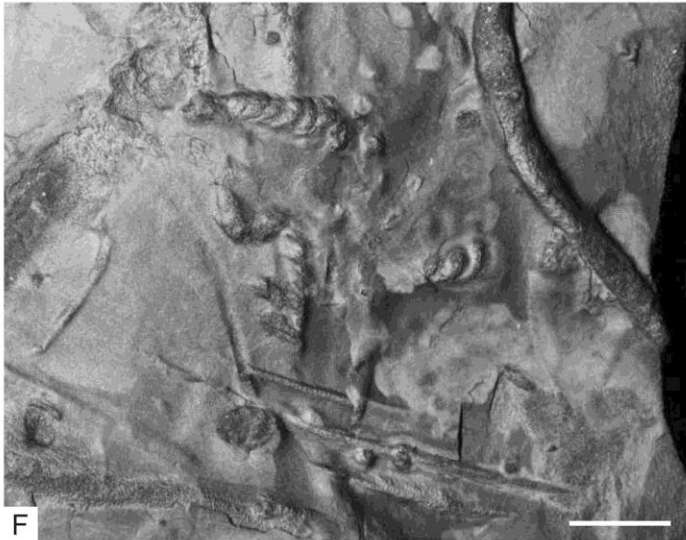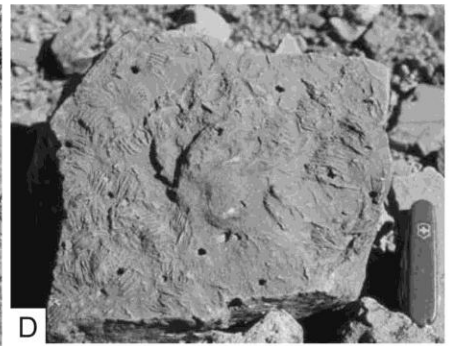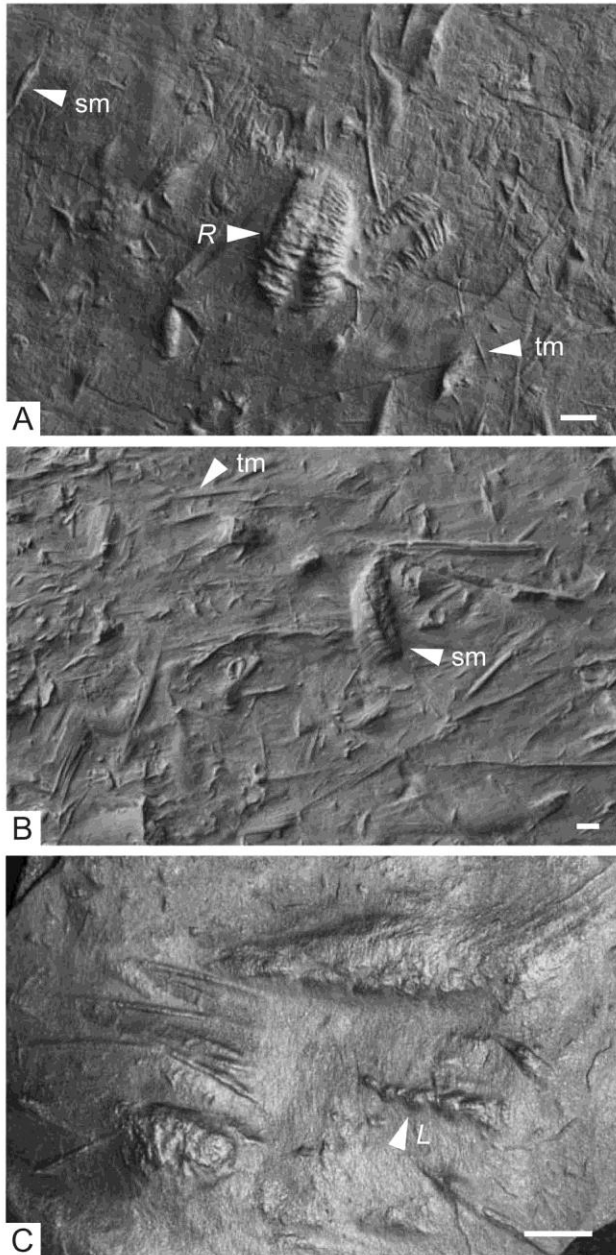
Figure 17. Bioglyphic preservation of biogenic and abiogenic sedimentary structures of the Powers Steps Fm. A: Field photograph. Exceptionally preserved *Rusophycus*, scratch marks and tool marks. Hyporelief. B: Field photograph. Surface characterized by dense assemblage of arthropodal scratch marks, including scratch marks produced by multiple podites, and tool marks. Hyporelief. C: UCR 11132/5. Crisply preserved scratch marks, tool marks and sequential *Lockeia*. Hyporelief. All specimens from the Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Scale bar = 1 cm. *R*, *Rusophycus*; *L*, *Lockeia*; sm, scratch marks; tm, tool marks.

Figure 18. Exceptional preservation of dense bedding plane assemblages. A: Field photograph. Dense assemblage of shallow-tier trace fossils, including prominent *Cruziana* characterized by high relief and bioglyphic preservation of scratch marks. Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. B: UCR 11135/2. Bioglyphically preserved *Cruziana*. Note that crisp preservation of *Cruziana* is undisturbed by subsequent generations of infaunal activity (see arrow). Beach Fm., The Beach, Bell Island, Newfoundland. Hyporelief. C: UCR 11135/1. Moderately dense to dense assemblage dominated by treptichnids and *Palaeophycus*. Note lack of deformation in numerous instances of sequential burrow production and multi-generational contact (see arrows). Beach Fm., The Beach, Bell Island, Newfoundland. Hyporelief. D: UCR 11132/2. Assemblage characterized by overlapping but non-deforming multiple generations of shallow-tier structures. Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. E: Field photograph. Dense bedding plane fabric dominated by sand-infilled *Treptichnus*, *Cruziana* and *Rusophycus* (see arrow) within a silty matrix. Note crisp preservation of overlapping *Treptichnus*, as well as bioglyphic preservation (although some of the highest relief casts have broken off) of *Cruziana* and *Rusophycus*. Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. F: Field photograph. Dense bedding plane assemblage with bioglyphic preservation of *Cruziana* (see arrow). Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. Hyporelief. Scale bar = 1 cm.

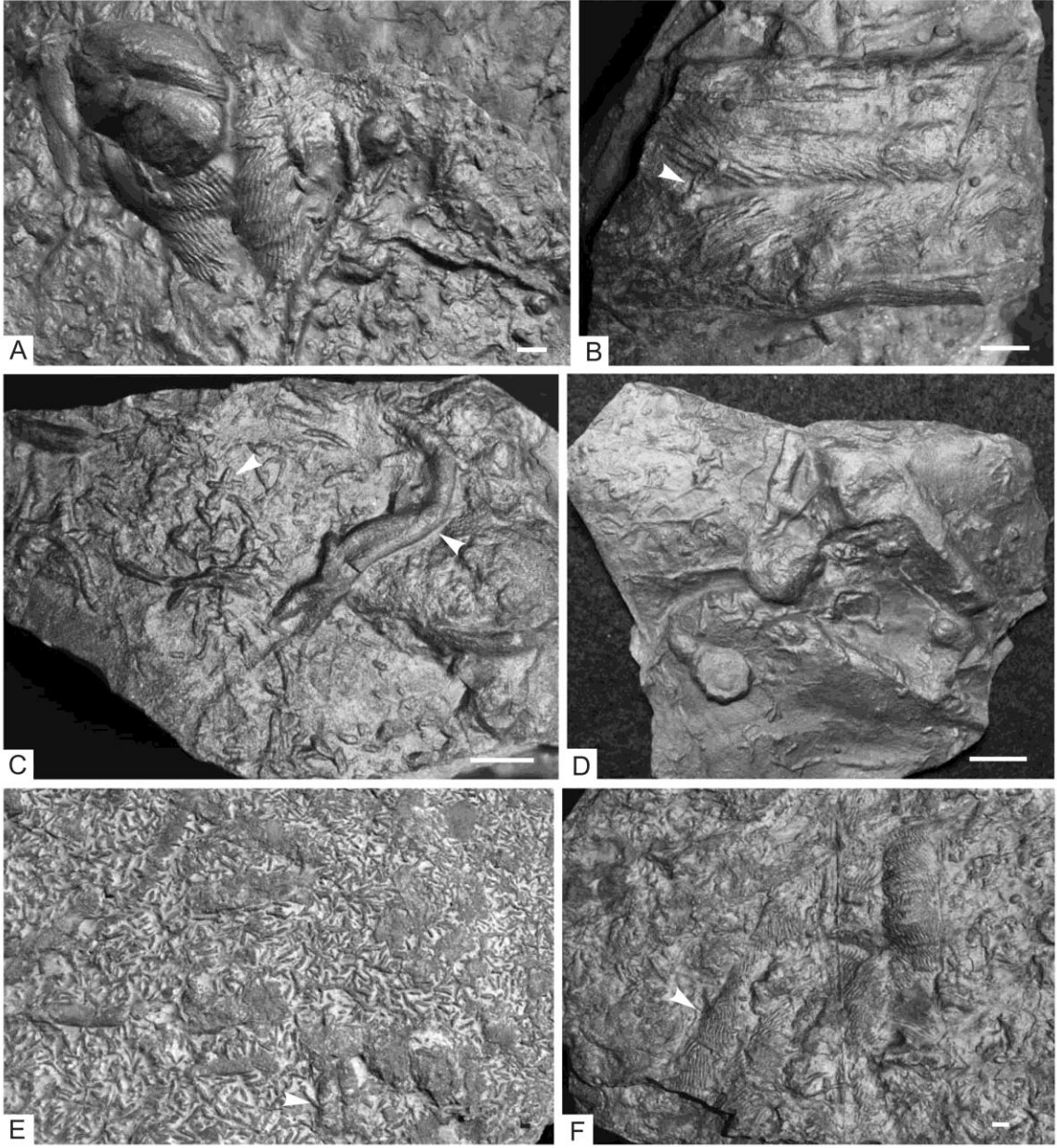**Figure 19**. Ichnofabrics of the Bell Island and Wabana groups. A: UCR 11132/4. Specimen characterized by heterogeneous ichnofabrics; crisply preserved *Teichichnus* (see white arrow) at slab base is overlain by intensely burrowed (ii 4) zone (lower black arrow) comprising mm-scale burrows, which is overlain in turn by a strongly laminated and largely undisturbed (ii 1–2) fabric (upper black arrow). Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. B: UCR 11134/1. Specimen characterized by strongly cross-laminated fabric. The infill of the *Trichophycus* burrow at bottom right (see arrow) is moderately disturbed by micro-scale structures (ii 3); however, the encasing macroburrow is structurally intact, as is the fabric of the overlying laminae (ii 1–2). Grebes Nest Point Fm., Grebes Nest Point, Bell Island, Newfoundland. C: UCR 11135/3. Specimen (from 2.35 m, Fig. 12) characterized by undisrupted (lower arrow) to moderately disrupted (ii 3, upper arrow) ichnofabric. Note that zones of disruption largely consist of mm-scale burrows and that macro-scale fabric remains intact. Beach Fm., The Beach, Bell Island, Newfoundland. D: UCR 11136/2. Specimen characterized by both moderate (ii 3) and intense (ii 5) zones of disruption. In the intensely burrowed zone at slab base (arrow), characterized by *Planolites* ichnofabric, physical (depositional) fabric has been obscured (although bedding orientation is still discernible), yet ichnofabric remains clear and crisply preserved, rather than homogenized. In overlying region of moderate disruption, laminated depositional fabric is still visible. Beach Fm., The Beach, Bell Island, Newfoundland. E: UCR 11136/1. Specimen characterized by cryptobioturbation (sub-mm-scale) and small-scale (mm-scale) macroburrowing. Even in zones of high disturbance (ii 4), structures do not penetrate or disturb laminated intervals; burrows occur most abundantly as casts on the base of individual laminae or as 'floating' sandstone-infilled structures within the siltstone matrix. Beach Fm., The Beach, Bell Island, Newfoundland. Scale = 1 cm.
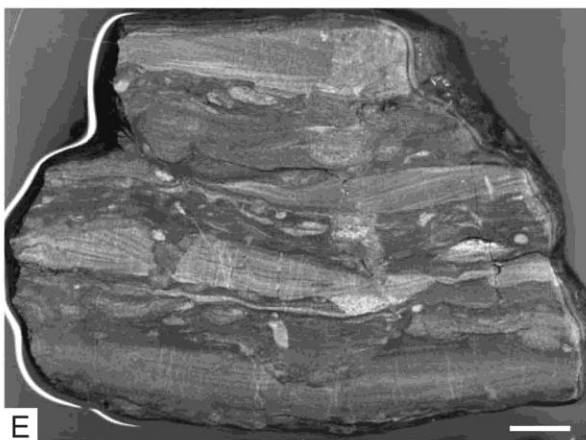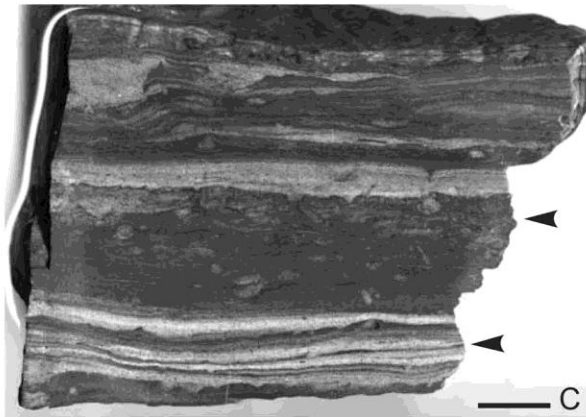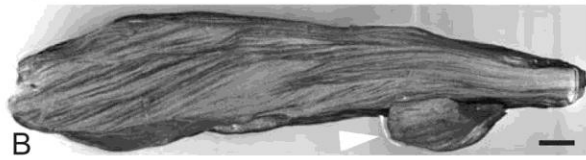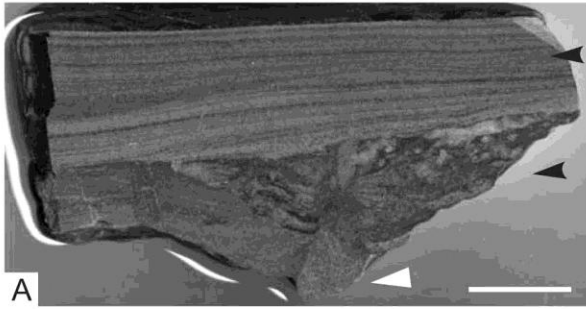
Figure 20. Relationship between bedding plane assemblage density and preservation and ichnofabric development. A–B: UCR 11132/1. A: Crisply preserved, moderately dense bedding plane assemblage of shallow-tier trace fossils and physical sedimentary structures. Hyporelief. B: Poorly developed ichnofabric (ii 2). Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. C–D: UCR 11133/1. C: Bedding plane assemblage characterized by moderately high density, bioglyphic preservation of surface ornamentation and high relief *Palaeophycus* and *Teichichnus* specimens. Hyporelief. D: Strongly laminated fabric (ii 2) characterized by sparse and spatially limited zones of moderate reworking (ii 3). Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. E–F: UCR 11132/5. E: Bioglyphic preservation, notably of scratch marks. Hyporelief. F: Fabric characterized by low-angle cross-lamination and little to no biogenic disruption (ii 1–2). Powers Steps Fm., Upper Grebes Nest Point, Bell Island, Newfoundland. G–H: UCR 11135/2. G: Bioglyphic preservation of large *Cruziana* coupled with crisp preservation of subsequently formed burrows and pipes. Hyporelief. H: Largely undisrupted fabric. Macroburrowing is limited to a couple vertical pipes and sparse mm-scale sand-infilled burrows 'floating' within the silty matrix or cast onto the base of sandy laminae. The *Cruziana* infill (arrow) is characterized by the zone of greatest disruption and consists of sub-mm-scale cryptobioturbation (ii 3). However, vestigial laminae are still visible in this infill and the overlying bed is strongly laminated in fabric. Beach Fm., The Beach, Bell Island, Newfoundland. Scale = 1 cm. Arrows in A, C, E and G denote line of cut to produce slabbed sections shown in B, D, F and H, respectively. Specimens B, D, F and H are oriented with bed top at top of frame and bed base at bottom of frame.
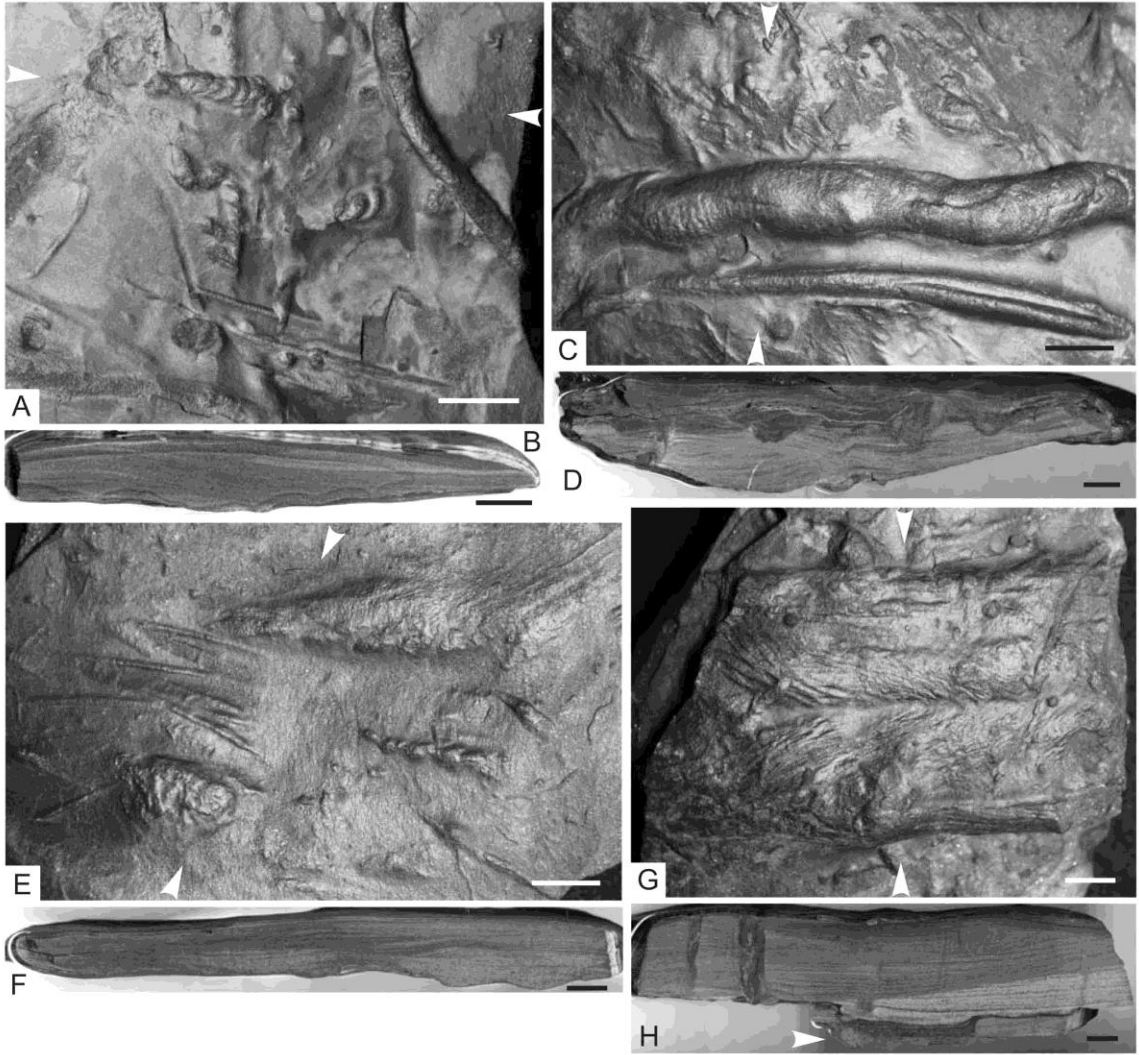
Figure 21. Field photographs of additional Cambro-Ordovician units and facies. A–C: Barrancos Formation, Encinasola, Spain. D, G–H: Juniata Formation, Carlisle, Pennsylvania. E–F: Pacoota Sandstone, Ellery Creek, Northern Territory. A: 'Scribbling' bilobed traces. Hyporelief. B: Frondescent marks, horizontal furrows and shallow-relief burrows. Epirelief. C: *Rusophycus*. D: Millimeter-scale, high-relief *Rusophycus* or *Isopodichnus*. Hyporelief. E: Dense assemblages of high-relief *Rusophycus* (see arrow), characterized by bioglyphic preservation of scratch marks, cast along bed bases. Hyporelief. F: Beds additionally characterized by *Skolithos* and *Diplocraterion* internal fabric formed by burrows piped in from the tops of beds and amalgamation horizons (upper arrow; lower arrow denotes *Rusophycus* assemblage). G: Moderate- to high-density bedding plane assemblages consisting largely of infilled burrows and *Lockeia* (see arrow). Hyporelief. H: Fabric characterized by prominent cross-lamination and non-fabric-destructive *Skolithos*. Scale: A–F, H = 1 cm; G: 10 cm field scale bar, each increment represents 1 cm.
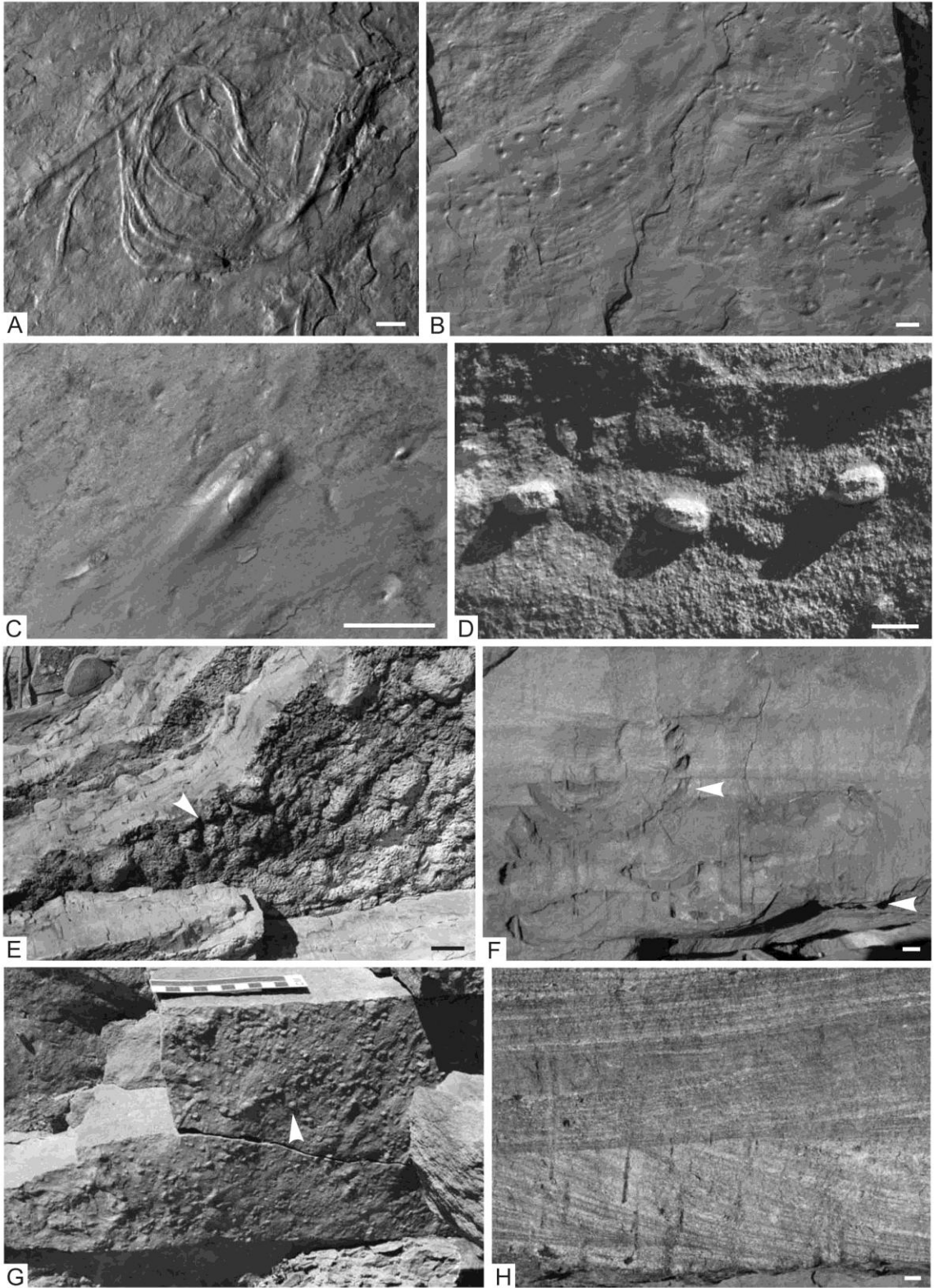
CHAPTER 3: FURROWS AND FIRMGROUNDS: EVIDENCE FOR PREDATION AND IMPLICATIONS FOR PALEOZOIC SUBSTRATE EVOLUTION IN *RUSOPHYCUS* HUNTING BURROWS FROM THE SILURIAN OF EAST-CENTRAL NEW YORK

Abstract

The Silurian-aged Herkimer Formation of east-central New York contains abundant exceptionally preserved composite *Rusophycus-Teichichnus* burrows. We suggest that the most likely interpretation of these composite trace fossils is as structures formed by trilobites entering the sediment in search of prey. Parallel alignment of the paired traces, asymmetrical configuration of the *Teichichnus* along the longitudinal axis of the associated *Rusophycus*, depth correlation and deformation of the *Teichichnus* all suggest that this relationship was predatory. In addition, sectioned material indicates that these *Rusophycus* may have been open at the sediment-water interface, while the crisp preservation of both *Rusophycus* and *Teichichnus*, along with the preservation of such delicate morphological details as scratch marks, suggests that the sediment must have been relatively firm at the time the traces were formed. The formation and preservation of *Rusophycus* in cohesive sediments located very close to the sediment-water interface hold important implications for the manner in which we consider Paleozoic substrates and their temporal and spatial evolution. Moreover, these findings demonstrate that the morphology and taphonomy of ichnological associations may, in the context of sedimentological relationships, prove a powerful proxy for tracking substrate conditions through both space and time.

Introduction

Trilobites are among the earliest well-known candidates for macrophagous predators (e.g.

Whittington, 1975, 1980, 1997; Briggs and Whittington, 1985; Fortey and Owens, 1999;

Hughes, 2001; Babcock, 2003; Vannier and Chen, 2005). Direct testimony of trilobite

predatory activity is found in trace fossils where trilobite traces are found in particular

association with trace fossils of infaunal prey. These types of composite trace fossil (see

Pickerill and Narbonne, 1995) have been referred to as "hunting burrows." Reports of

such associations are rare (Table 1) and, not surprisingly, the interpretation of these

associations has been a matter of discussion, not least because of the possibility of chance

associations or inverse temporal relations (see Brandt et al., 1995; Rydell et al., 2001;

Neto de Carvalho, 2006; Brandt, 2008).

Furthermore, the preservation of these associations likely required exceptional

taphonomic circumstances. The stratigraphic record of the lowermost Paleozoic is

renowned for its unparalleled ichnological record—the crisp preservation of trace fossils

formed at or near the sediment-water interface (e.g. Droser et al., 2002a; Osgood, 1970).

Both Crimes (1975) and Goldring (1995) have suggested that cohesive substrates may

facilitate the preservation of shallow-tier ichnofossils and bioglyphs. However, the large-

scale operation of this taphonomic phenomenon and its confinement to the early

Cambrian have gone largely unquestioned and, until recently, unexplained. Droser and

others (e.g. Droser et al., 2004) have proposed that firmgrounds, consisting of fine-

grained (silt-sized) sediments of low water content, were widespread in early Cambrian

normal marine shelfal settings (Droser et al., 2002a; Droser et al., 2004; Jensen et al., 2005). In the absence of an extensive mixed layer, these silts may have formed a cohesive substrate within centimeters of the sediment-water interface, able to sharply retain the imprint of biogenic activity. Firmgrounds offer an explanation for the exceptional quality of preservation observed in trace fossils and sedimentary structures occurring in lower Paleozoic siliciclastic strata.

The purpose of this paper is to describe a rich deposit of hunting burrows from the Silurian-aged Herkimer Formation of New York. A unique *Rusophycus-Palaeophycus* composite specimen from the Herkimer Formation had previously been figured by Hall (1852) and discussed in the context of hunting burrows by Osgood and Drennen (1975). Here we discuss the case for a predatory origin of the Herkimer Formation composite trace fossils and examine the sedimentology and morphology of these features with the objective of using these *Rusophycus* as indicators of substrate conditions.

Material and Methods

Material for this study was collected from a single bed in the Joslin Hill Member of the Herkimer Formation near Clinton, New York. The collection locality is situated in a quarry adjacent to Sherman Brook (UTM 18T 470018E, 4766226N), downstream from the bridge on Dawes Avenue (Section 33 of Gillette, 1947; Station 3 of Muskatt, 1972 and Locality 4 of Osgood and Drennen, 1975) (Fig. 22). The face of the quarry forms a nearly vertical wall, limiting collection to six confined areas. To avoid extensive damage

to the outcrop, only material that could be easily extracted was collected. All extractable material from this horizon was collected, regardless of fossil content, in total comprising 0.48 m^2 (Table 2, Fig. 23). Samples were collected at several localities along a nearly straight line, spanning about 13 m laterally. Material frequently occurred in loose pieces; no effort was made to establish original horizontal orientation within the source horizon.

Sedimentological characteristics of the composite trace fossil-bearing bed were examined, specimen morphology was described, measured and photographed and taphonomic variability noted for each specimen. In addition, seven specimens (five composite *Rusophycus-Teichichnus* and two individual *Rusophycus*) were sectioned to permit lithological and sedimentological characterization of burrow infill material. Specimens are reposited in the invertebrate paleontology collection of the Department of Earth Sciences, University of California, Riverside (UCR).

Geological Setting

The Herkimer Formation is a thin (18–22 m), dominantly siliciclastic unit of median Wenlockian age, forming part of Sequence 5 of the Silurian Appalachian foreland basin (Osgood and Drennen, 1975; Brett et al., 1990). The Joslin Hill Member is composed of interbedded shale and fine- to medium-grained dolomitic sandstones with a siliciclastic:carbonate bulk composition ranging from 1:1 to 1:3 (Osgood and Drennen, 1975). The interval included in this study consists of mm-cm scale mudstones packages, punctuated by cm-scale sandstone event beds, arranged in a general shallowing-upward

sequence (Figs. 24–25). Sedimentary structures consist primarily of symmetrical ripples and locally abundant tool marks (Osgood and Drennen, 1975; this study). Low-angle cross-lamination is observed in the upper portion of the section (Fig. 24). Although the Joslin Hill Member as a whole has been interpreted to represent a high-energy, near-shore shallow marine environment (Zenger, 1971; Muskatt, 1972), the predominance of mud and erosive sedimentary structures at this locality are more typically referred (e.g. Walker, 1986) to a shallow shelfal (between normal and storm wave-base) environment.

Trace Fossils

Trace fossils are present in variable abundances and grades of preservation throughout the section. One bed in particular, occurring at 1.6 m within the measured section (Fig. 24), is notably characterized by dense and well-preserved composite *Rusophycus-Teichichnus* (Figs. 25B-D). These composite traces are preserved on the base of a 1–4 cm thick layer of poorly-sorted sandstone (Figs. 25B-D). Sand grains range from sub-angular to sub-rounded and are medium- to coarse-grained. This sandstone is capped sharply by a dark gray siltstone with sparse sub-rounded coarse quartz grains (Figs. 24, 25B–D). The top surface is of variable, uneven relief and largely devoid of sedimentary or ichnological structures, although sectioning reveals cross-bedding and biogenic piping through the sandy infill of certain individuals. The base of the sandstone is underlain by a recessive dark gray muddy siltstone (Figs. 24, 25B–D), which thinly coats the hyporelief surface of the sandstone bed, suggesting that it was into this muddy lithology that the burrowers delved.

Trace fossils include numerous *Rusophycus*, *Cruziana* and *Diplichnites* of variable

orientation, size, morphology and extent, all preserved in positive (convex) hyporelief

(Figs. 26A–H, 27). Several examples of the peculiar dumbbell-shaped trace fossil,

Arthraria antiquata Billings, 1872 (Fig. 26I), also occur on this bedding surface.

Specimens also appear to occupy the morphological gradient between the three

supposedly behavioral endmembers of *Rusophycus*, *Cruziana* and *Diplichnites* (see

Seilacher, 1970; Osgood and Drennen, 1975). In several examples, gradation between

morphologically disparate specimens suggests a common origin (Figs. 26C, H); i.e. a

single tracemaker that engaged in multiple trace-making behaviors or at least displayed

highly variable interaction with the substrate in a spatially and temporally limited setting.

This ichnoassemblage is dominated by *Rusophycus*, ranging from 3 to 10 cm in length

and from 2 to over 5 cm in width and typically characterized by sharp and steeply-angled

margins (Figs. 25B–D, 26A–F). Many of these are characterized by coarse transverse

ridges (formed through posteriorly-directed digging motions by the appendages of the

putative trilobite tracemaker), a pronounced median furrow and, commonly, lateral ridges

and can thus be further classified as *Rusophycus biloba* (e.g. Fig. 26A). Additionally,

these *Rusophycus* are characterized by high relief (approximately 0.5–3 cm depth; Figs.

26D–F). Smaller, shallower (approximately 0.2–0.5 cm depth), more rounded forms with

fainter yet still distinctly preserved transverse ridges (Figs. 26B–C) are also common and

are tentatively assigned to *Rusophycus pudicus*, based on similarity to material previously described from the Herkimer Formation by Osgood and Drennen (1975).

The *Rusophycus biloba* are also prominently associated with vertical and horizontal traces characterized by a broad U-shaped profile and wall-like structure (Figs. 26J–L). In spite of the apparent lack of spreiten in sectioned material, possibly due to the coarseness of fill, this general morphology suggests that these are *Teichichnus* burrows (see Brett [1983] for comparable material from the laterally correlative Rochester Shale). Moreover, evidence for retrusive spreiten is seen along the base of some specimens, due to either intersecting spreiten lamellae or their partial weathering. Although *Rusophycus* and *Teichichnus* burrows commonly occur in relative isolation (i.e. within centimeters of one another but not in direct contact; 5 complete examples of *Rusophycus biloba* without association, 9 unassociated *Teichichnus*) on the same bedding surface, we also commonly find, in direct spatial association, *Rusophycus* superimposed upon *Teichichnus* (20 examples of association) (Fig. 27). These latter associations are characterized by strongly parallel orientation of the length axes of the two ichnofossils and abrupt truncation of the *Teichichnus*. Moreover, in such pairings the *Teichichnus* is typically in contact with only one lobe of the *Rusophycus* (e.g. Fig. 27F), which does not extend to the base of the former. Furthermore, some *Teichichnus* were deformed by penetrating scratch-marks during the production of associated *Rusophycus* (Figs. 27E–F). Those *Teichichnus* occurring with *Rusophycus* consistently appear to have been formed more deeply (i.e. higher convex relief) than those occurring in isolation. Additionally, there are five

occurrences of *Rusophycus* associated with the vertical portion of a cylindrical trace fossil (Fig. 27G). Like the *Teichichnus*, these traces are also positioned off-center relative to the bilobate *Rusophycus* (see Table 2 for a summary of trace associations).

Interpretation of Trace Fossil Associations

We suggest that the most likely interpretation of these composite trace fossils is as structures formed by trilobites entering the sediment in search of prey. The associations show many similarities to material from the Lower Cambrian Mickwitzia sandstone (Bergström, 1973; Jensen, 1990, 1997). That the trilobite did not dig down to the base of the retrusive *Teichichnus* (e.g. Figs. 27C–D) suggests that the trilobite's object was the inhabitant of the burrow, which would have occupied only the uppermost portion of the cumulative retrusive structure, not the burrow itself. It has been suggested that macrophagous trilobites may have been necrophagous as well as predatory (Fortey and Owens, 1999, Neto de Carvalho, 2006). However, the positioning of the trilobite parallel but off-center to the *Teichichnus* may have facilitated handling of live prey (Jensen, 1990) although, unlike the Mickwitzia material, the Herkimer *Rusophycus* are not characterized by asymmetrical lobe depth (i.e. greater depth of the lobe in contact with the *Teichichnus*). Instances of deformation (i.e. scratching) of the *Teichichnus* by the associated *Rusophycus* (Figs. 27E–F), observed in conjunction with parallel, asymmetrical alignment, provide compelling evidence of directed, controlled behavior on the part of the trilobitic tracemaker. Vertical cylindrical burrows associated with *Rusophycus* (e.g. Fig. 27G) and other, more sinuous, shallower-relief horizontal

cylindrical burrows may represent a different teichichnid morphology, a different spatial association with *Rusophycus* or a different type of trace altogether.

The absence of deep *Teichichnus* except in association with *Rusophycus* merits further consideration. This depth restriction may be taphonomically mediated; in cases of association the presence of the *Rusophycus* may have increased the preservation potential of the *Teichichnus* by providing a buttress. Without this buttress, the *Teichichnus* would most likely have broken off from the overlying sand bed during compaction.

Three alternative interpretations of these composite trace fossils must be considered:

1) *Chance occurrence in time and space*: the two traces may intersect by contemporaneous chance or even through compactional telescoping of tiers. However, close examination of certain composite specimens (Figs. 27E–F) reveals deformation of the *Teichichnus* by the *Rusophycus*, indicating a primary (i.e. not an artefact of compaction) spatial and temporal association. Moreover, the consistent commonality in place, independent of the density of substrate perturbation (Fig. 23), and, in particular, the strongly parallel orientation of the two traces suggests that chance associations are highly unlikely for the Herkimer Formation material. Likewise, there is no apparent difference in the quality or style of preservation of the *Rusophycus* and *Teichichnus*, which suggests that the two were not only preserved through

similar taphonomic processes, but also formed during a narrow interval of time.

2) *Reverse temporal order*: the worm burrow may have been constructed subsequent to the formation of the arthropod burrow. In a study of Lower Cambrian material from Sweden, Rydell et al. (2001) concluded, upon examination of the point of contact, that the majority of worm burrows post-dated associated arthropod burrows. However, in the Herkimer material, instances of deformation of the *Teichichnus* by associated *Rusophycus* indicate that formation of the former must have preceded that of the latter. Also, the lack of a continuous or lengthy association between composite individuals suggests that the *Teichichnus* tracemaker was not exploiting the *Rusophycus* fabric for purposes of deposit feeding or locomotion (see Neto de Carvalho, 2006).

3) *The trilobite may have been digging into a biogenic sedimentary structure for reasons other than predation, such as necrophagy* (see Neto de Carvalho, 2006 for further discussion). However, as discussed above, the parallel but asymmetrical configuration of *Teichichnus* along one lobe of associated *Rusophycus* may have facilitated the handling of live prey by the *Rusophycus* tracemaker. An active (or opportunistic) hunting interpretation for the Herkimer material is therefore more likely than a scavenging one.

The producers of the Herkimer Formation *Rusophycus biloba* are reasonably well-constrained; Osgood and Drennen (1975) detailed several morphotypes of Herkimer Formation *R. biloba* and assigned them to *Trimerus delphinocephalus* and *Dalmanites limulurus*. Burrows of the former can be recognized on the basis of general outline and a consistent length:width ratio (2.3:1). Burrows of *Dalmanites limulurus* differ in overall proportions and on the presence of structures interpreted as casts of genal and pygidial spines. These features are also present in most of the *Rusophycus biloba* described above. Moreover, *Trimerus delphinocephalus* and *Dalmanites limulurus* both belong to trilobite groups that, based on morphological features, have been suggested to have had a predatory mode of life (Fortey and Owens, 1999). The identity of the *Teichichnus* tracemaker is too uncertain to warrant speculation.

Nature of the Substrate

The subject of the mode of formation of *Rusophycus* and *Cruziana* has historically inspired much controversy. Certain workers (e.g. Seilacher, 1955, 1970, 1985; Goldring, 1985) have posited an intrastratal origin for *Rusophycus* and *Cruziana*, whereas others (e.g. Osgood, 1970; Crimes, 1975; Baldwin, 1977) have countered that rheotaxis and association with undisturbed primary sedimentary structures indicate a surficial origin for these traces. Sectioned material from the Herkimer Formation suggests that some *Rusophycus* may have been open at the sediment-water interface.

Slabbed specimens reveal undisrupted planar or cross-bedded laminae within the sandy infill (Figs. 28A–B), indicating that sand sedimentation post-dated formation of the burrow (Baldwin, 1977; Droser et al., 1994). These *Rusophycus*, therefore, were either constructed as open burrows at the sediment-water interface or were later exposed and infilled. In contrast, if the *Rusophycus* tracemaker had been moving intrastratally, any original sedimentary structures would have been disrupted. Likewise, since it is very unlikely that the sandy event beds casting the *Rusophycus* would have been featureless when deposited (e.g. Walker, 1986), seemingly massive *Rusophycus* may be most parsimoniously interpreted as biogenically homogenized.

Certain *Rusophycus* specimens are characterized by a sandy basal infill (Fig. 28A), the morphology of which, although unlaminated, once again indicates a surficial origin. This coating is thicker at the base of the burrow and thinner along the slopes, demonstrating dip-dependent slope stability and suggestive of passive infill. In other cases (Figs. 28C–D), however, the sandy infill appears, apart from faint vestigial grading and diagenetic color banding, to be largely uniform (i.e. homogeneous) in texture. This homogeneity is most likely not primary, as discussed above. Rather, biogenically-mediated homogenization (i.e. thorough bioturbation) of the sediment seems indicated. It is unclear, in these examples, whether a single continuous event, pulsed sediment influx or temporally disparate sedimentation events are responsible for the burrow infill. It is also unresolved whether homogenization occurred before, during or after the formation of *Rusophycus*. However, the presence of primary laminae in morphologically similar

Rusophycus, as well as small undisturbed burrows piping down from sands overlying the infill of certain *Rusophycus* (Fig. 28B) suggests that homogenization post-dated formation of *Rusophycus*.

Since, as demonstrated by Crimes (1975) and Goldring (1995), it is not possible to cast delicate ichnological structures in a coarse lithology without a cohesive substrate, the relatively crisp preservation of both *Rusophycus* and *Teichichnus* suggests that the sediment must have been firm at the time the traces were formed. Moreover, both sedimentological (discussed above) and morphological evidence indicates that at least some *Rusophycus* were open at the sediment-water interface. Whether they were originally formed as open burrows or were formed intrastratally and subsequently exposed, eroded and filled in is a question requiring careful consideration. The coarseness of the overlying sediment, as well as the presence of erosional structures in the Joslin Hill Member (Fig. 24; Osgood and Drennen, 1975), suggests that some erosion may have occurred. Presumably, mixgrounds would have been more developed in the Silurian than the Cambrian; firm sediments may not have occurred directly at the sediment-water interface and the overlying veneer of mixed sediment may have been more prone to erosion (Droser et al., 2002a). But the mixed layer may still have been fairly shallow; firm sediments may have occurred at only a few centimeters' depth. Additionally, the depth of many of these *Rusophycus* is remarkable; that they were originally significantly deeper and subsequently eroded to their present depth is improbable, i.e. that the traces were not substantially eroded seems to be the most parsimonious explanation in keeping

with their unusual depth. Moreover, the exquisite preservation of such delicate morphological details as scratch marks, in conjunction with well-preserved *Cruziana* and *Diplichnites* (Figs. 26C, G–H) on these surfaces, traces traditionally attributed to organisms moving along or at a shallow depth beneath the sediment-water interface (e.g. Crimes, 1970; Seilacher, 1970; Crimes, 1975; Baldwin, 1977; Goldring, 1985), indicates not only a firm substrate, but a shallow one. Therefore, although it may be impossible for us to precisely constrain how much erosion occurred, it seems most parsimonious to conclude that the Herkimer *Rusophycus* were formed at or very near to the sediment-water interface and did not experience significant erosion.

Discussion

Considerable caution is needed in the interpretation of composite *Rusophycus-Teichichnus*, especially when such interpretations are based upon individual associations. However, the *Rusophycus* of the Herkimer Formation provide compelling evidence that these *Rusophycus-Teichichnus* associations are not of a fortuitous nature, but rather resulted directly from predatory activity. The parallel alignment of *Rusophycus* with *Teichichnus*, *Rusophycus*-mediated deformation of associated *Teichichnus* and the termination of many of these *Teichichnus* at points in contact with associated *Rusophycus* suggest a predatory interaction. Although "predatory" composite traces of this sort are rare, this scarcity is perhaps not surprising. Predatory trilobites would presumably have been opportunistic feeders and not all may have actively searched for infaunal prey. A likely method of trilobite food-search may have been shallow furrowing by means of

lowering the head-shield into the sediment to stir up prey, much like modern limulids (Whittington, 1980, 1997). Candidate trace fossils for this behavior have been reported from the Lower Cambrian of Sweden (Jensen, 1997, p. 99, fig. 66) and the Ordovician of Canada (Rudkin et al., 2003). However, this activity would have required uncompacted sediment and therefore would have likely possessed a low preservation potential. The scarcity of "predatory" trilobite traces may therefore be taphonomically mediated.

The formation and preservation of *Rusophycus* in firm sediments located very close to the sediment-water interface hold profound implications for the manner in which we consider Paleozoic substrates and their temporal and spatial evolution. Moreover, the preservation of shallow-tier trace fossils and delicate morphological structures as late as the Silurian, when the size, complexity and extent of burrowing was well advanced from the record of the lowermost Cambrian, is cause for further consideration and may provide some indication that firmgrounds were indeed the norm and not the exception in Lower Paleozoic shelfal siliciclastic sediments.

Figures
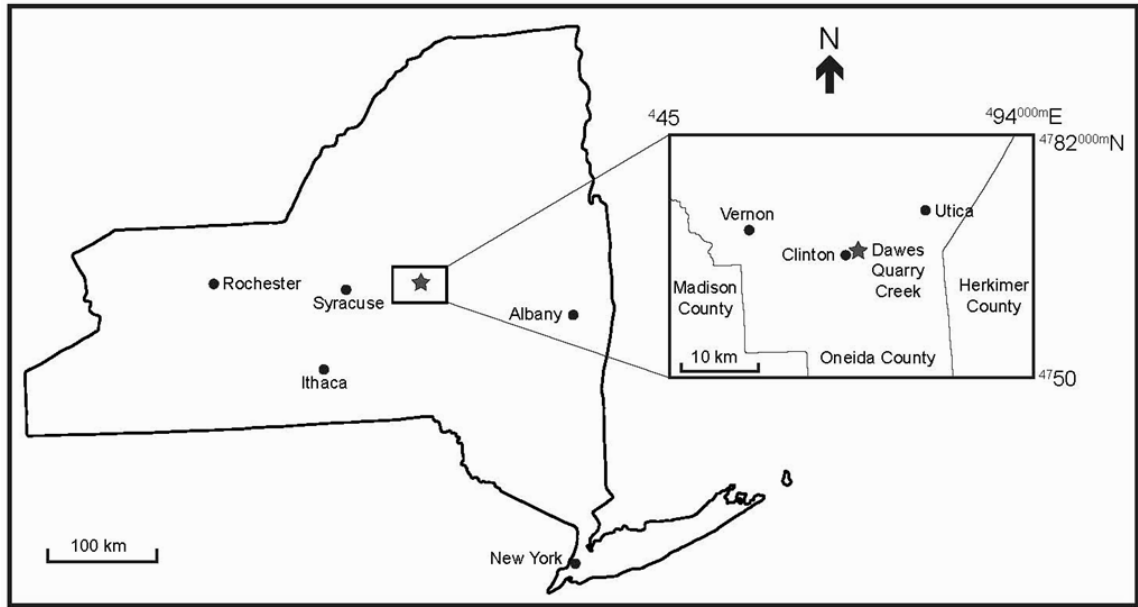
Figure 22. General geography of New York, with inset of Oneida County. Location of study area marked by asterisk.

Figure 23. Sketches of all collected material. Roman numerals refer to the laterally equivalent localities from which material was collected; all material was collected from the same stratigraphic horizon. Light gray shading represents *Rusophycus* specimens; dark gray shading represents *Teichichnus* specimens. Circled numbers denote depth (height of each specimen above base of bed), in mm. Hyporelief. Scale = x0.2.
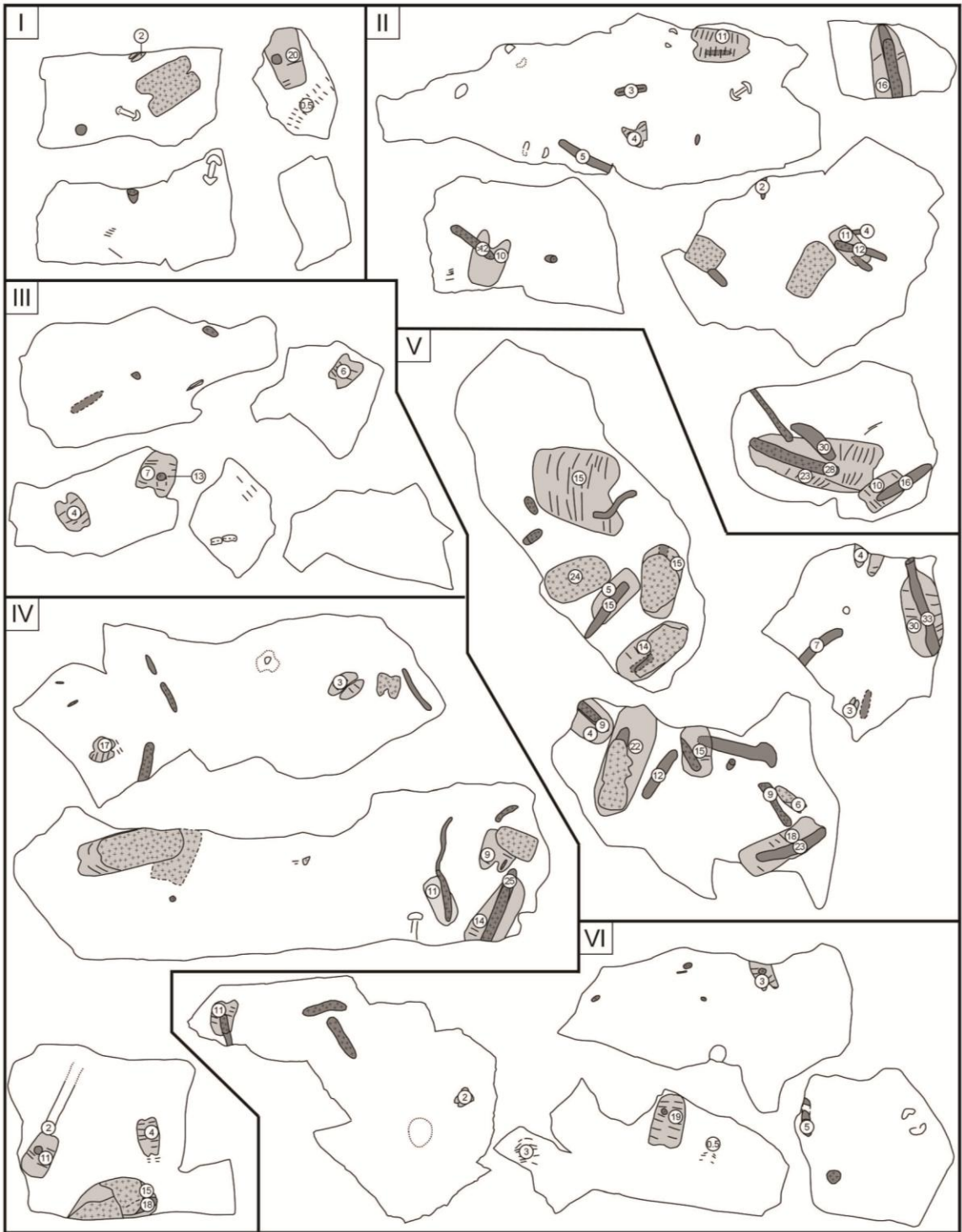
Figure 24. Stratigraphic log of the Herkimer Formation at Dawes Creek Quarry. Although *Rusophycus* is common throughout this interval, *Rusophycus-Teichichnus* hunting burrows occur along only one horizon (see arrow at 160 cm). Where multiples of the same symbol are present next to a single stratigraphic horizon, one symbol conveys that the trace fossil is present, two that it is common and three that it is abundant. Grain size scale: md = mud, st = silt, vf = very fine-grained sand, f = fine-grained sand, m = medium-grained sand and c = coarse-grained sand.
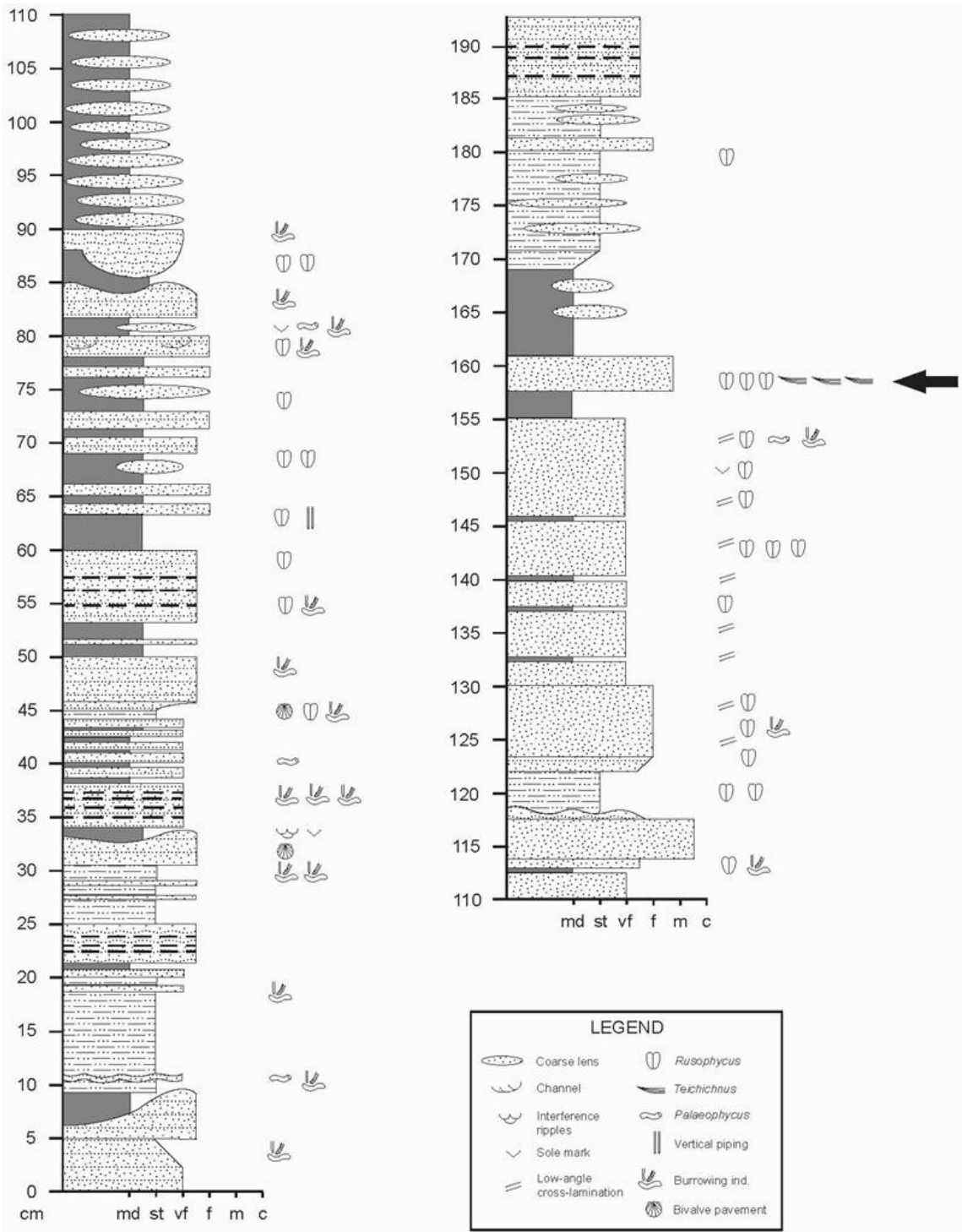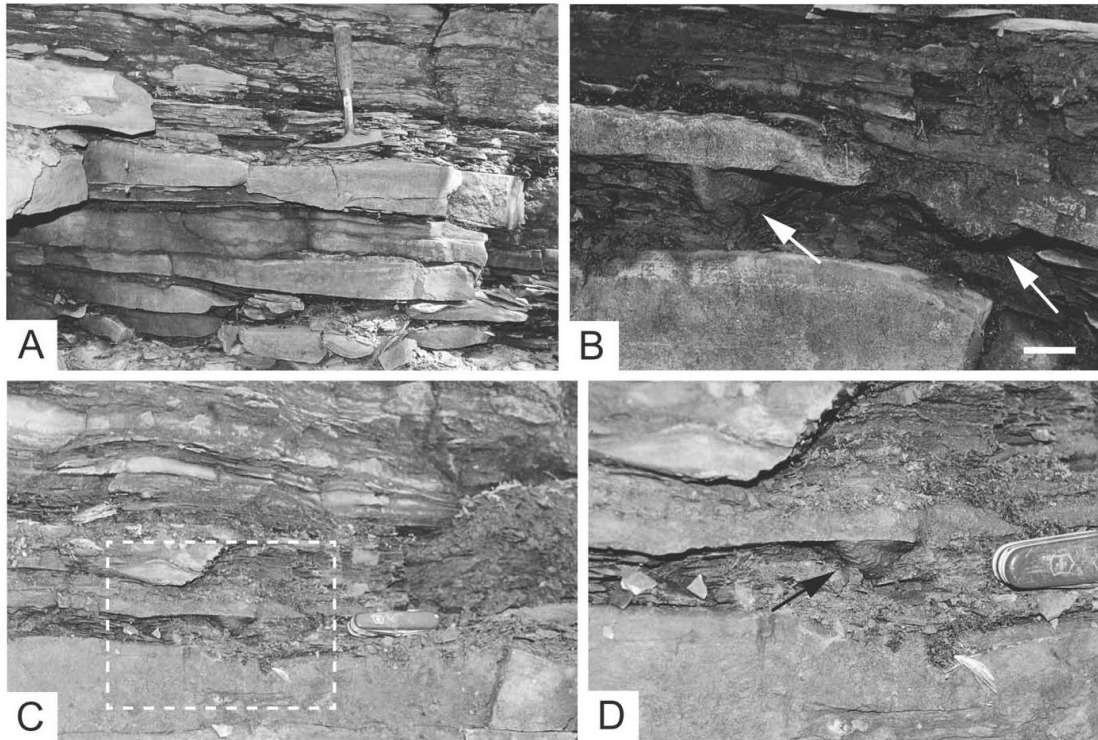
Figure 25. Lithology of the Joslin Hill Member, Herkimer Formation. A: At the study locality, the Joslin Hill Member consists of thinly interbedded shales, siltstones and fine- to medium-grained dolomitic sandstones. Field photograph, rock hammer for scale. B–D: Dense assemblages of well-preserved composite *Rusophycus-Teichichnus* (B: white arrows, D: black arrow) characterize the base of a 1–4 cm thick, poorly-sorted, medium- to coarse-grained sandstone. B: Field photograph, scale = 2 cm. C: Field photograph, width of Swiss army knife is approximately 1.8 cm (across center of insignia). D: Detail of specimen figured in C, field photograph.

Figure 26. Trace fossils of the Joslin Hill Member, Herkimer Formation. A: *Rusophycus biloba*, UCR 11070/7. B–C: *Rusophycus pudicus*, UCR 11070/65, 11070/28. Note smaller cruzianaform *Rusophycus* cross-cutting larger specimen in bottom right of C. D–F: Composite *Rusophycus-Teichichnus*. D–E: UCR 11070/45. F: UCR 11070/21. Note unusually high relief characteristic of *Rusophycus* from this locality. G: *Diplichnites isp*., UCR 11070/5. H: Specimen characterized by both rusophyciform and cruzianaform morphology, UCR 11070/42. I: *Arthraria antiquata*, UCR 11070/3. J–L: Representative examples of *Teichichnus* morphology, UCR 11070/53, 11070/11, 11070/12. All specimens preserved in hyporelief. Scale = 2 cm.
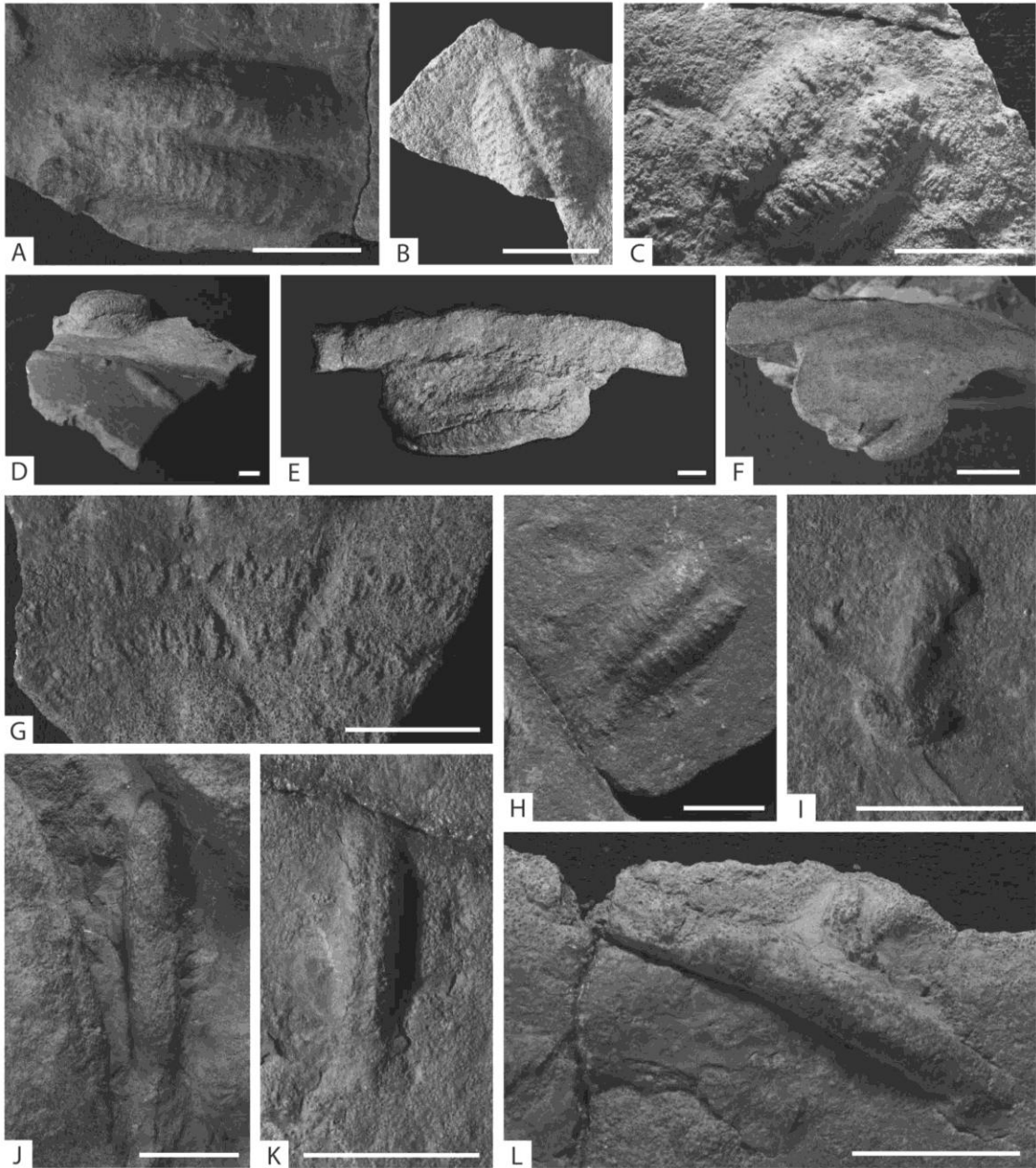
Figure 27. *Rusophycus* hunting burrows of the Joslin Hill Member, Herkimer Formation. A-B: Specimens displaying characteristic longitudinal alignment, asymmetrical placement and abrupt termination of *Teichichnus* with respect to associated *Rusophycus*. A: UCR 11070/56-60. B: UCR 11070/38-41. C–D: Specimens displaying bioglyphic preservation of transverse morphological features. Note that *Rusophycus* are deepest where in contact with *Teichichnus*. *Rusophycus* are also never observed to penetrate the deepest portion of associated *Teichichnus*. C: UCR 11070/45. D: UCR 11070/56. E–F: Compound *Rusophycus-Teichichnus* characterized by strong longitudinal alignment, prominent asymmetrical placement of *Teichichnus* with respect to transverse plane of *Rusophycus* and abrupt termination of *Teichichnus*. Specimen figured in bottom right of E (detail in F) displays *Teichichnus* deformed by cross-cutting *Rusophycus* scratch marks. E: UCR 11070/21-22. F: UCR 11070/22. G: *Rusophycus* associated with cylindrical, vertically-oriented worm burrow. Note asymmetrical placement of worm burrow with respect to bilobate *Rusophycus*. UCR 11070/66. H: Deep curvilinear or sequential *Rusophycus* associated with multiple *Teichichnus* specimens, UCR 11070/17. All specimens preserved in hyporelief. Scale = 2 cm.
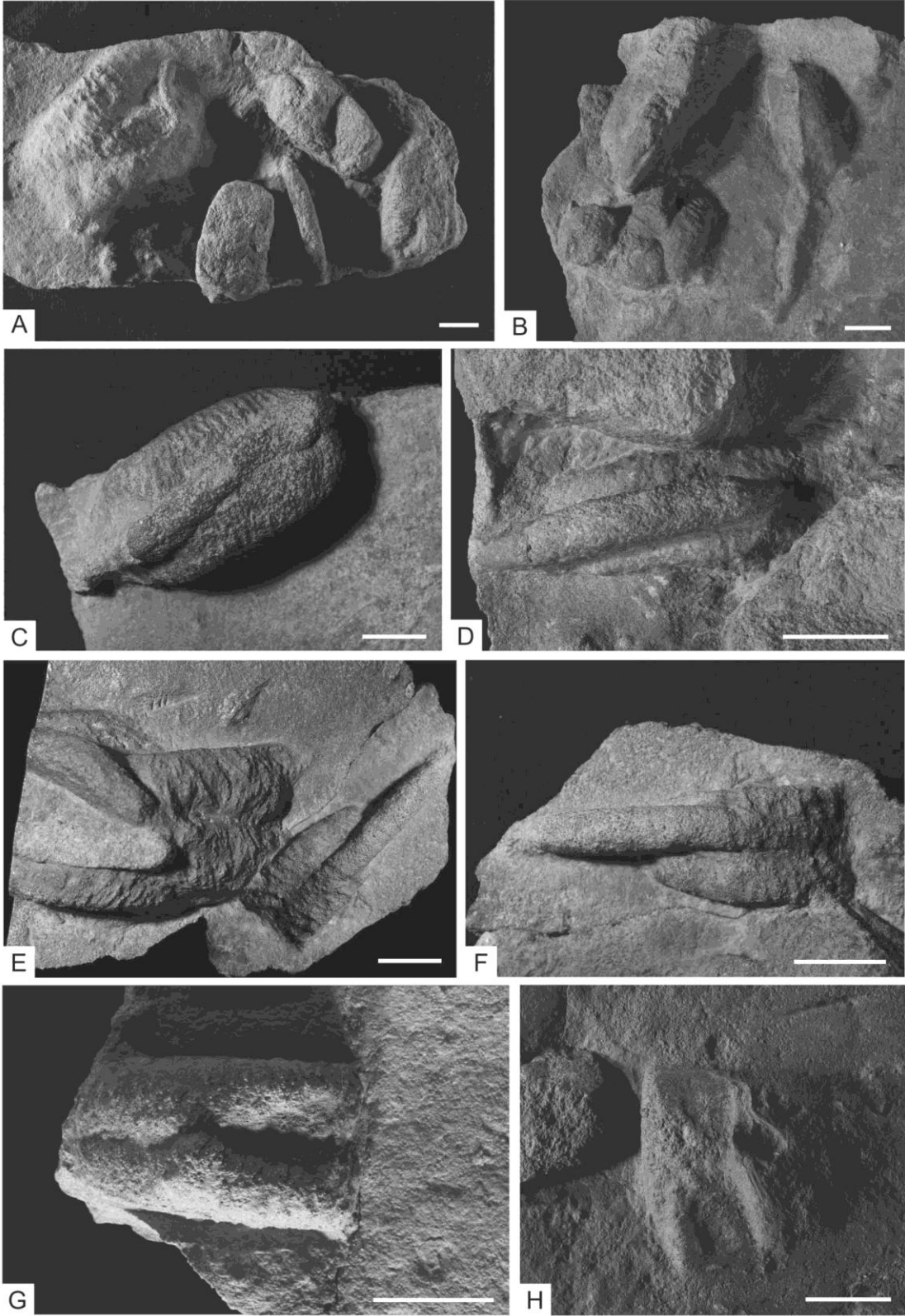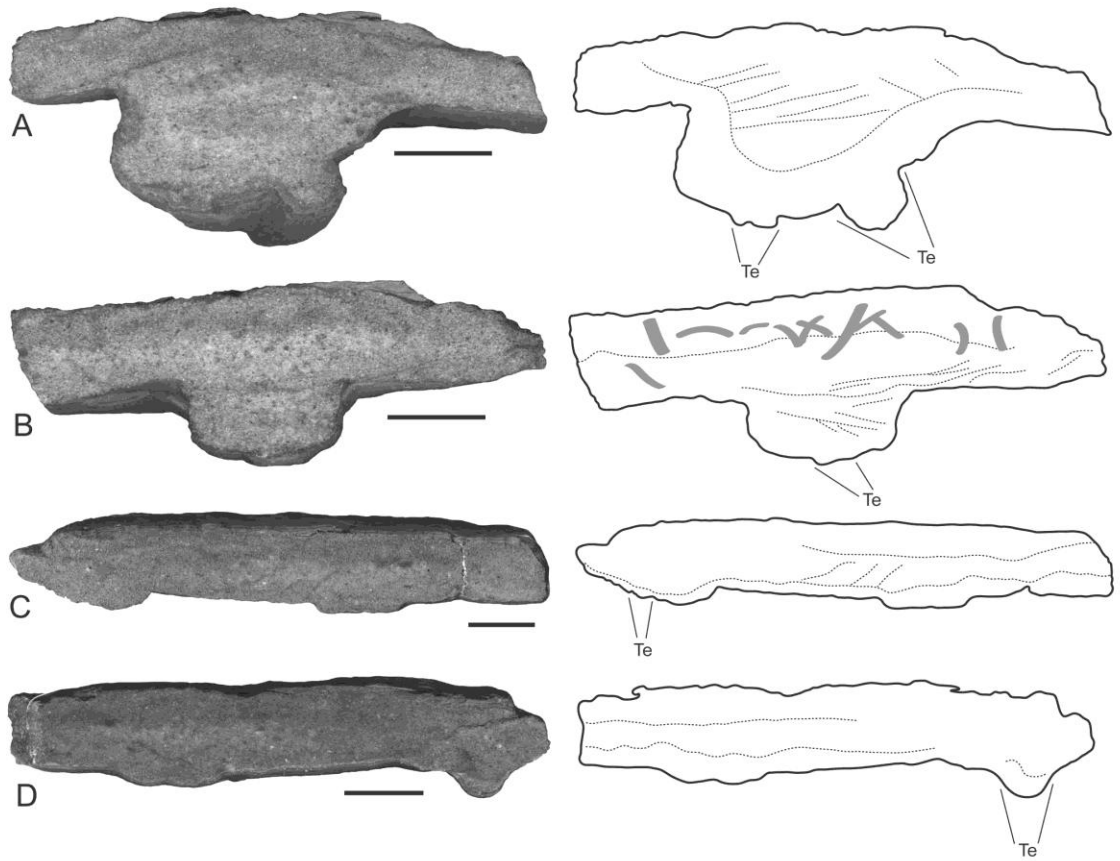
Figure 28. Cut and polished material from the Joslin Hill Member, Herkimer Formation reveals that portions of *Rusophycus* infill retain primary sedimentary structures. A: Composite *Rusophycus-Teichichnus* filled with sand of varying thickness—thicker at the base of the burrow and thinner along burrow margins. This sandy coating is overlain by weakly cross-stratified medium-grained sand. UCR 11070/21. B: Composite *Rusophycus-Teichichnus* infill characterized by cross-stratified sands at burrow base, overlain by biogenically-piped sand laminae, UCR 11070/20. C–D: Part and counterpart of slab containing two *Rusophycus* specimens. Specimen to left of frame in C corresponds to specimen to right of frame in D and is a composite trace; specimen to right of frame in C, corresponding to specimen to left of frame in D, represents an individual *Rusophycus pudicus*. Burrow infill is characterized by diagenetically-accentuated layered sand and slight, possibly vestigial grading. C: UCR 11070/29-1, 11070/28-1. D: UCR 11070/28-2, 11070/29-2. "Te" notes limits of associated *Teichichnus*. All specimens preserved in hyporelief. Scale = 2 cm.

Stratigraphy	Geography	Rusophycid	Worm Burrow	Association	Publication
L. Dev.	Rhineland, Germany	*C .dispar*, homalonotid trilobite	"worm trace"	D(2)	Wenndorf, 1990
U. Sil.	New York, USA	*R. biloba*, *Trimerus, Dalmanites*	*Palaeophycus, Teichichnus*	D	Hall, 1852; Osgood and Drennen, 1975; this paper
U. Ord.	Ohio and Kentucky, USA	*R. carleyi, R. pudicum, Isotelus, Flexicalymene*	*Palaeophycus*	B	English and Babcock, 2007
U. Ord.	Ohio, USA	*R. carleyi, Isotelus*	*Palaeophycus*	A	Brandt et al., 1995
L.-M. Ord.	Penha Garcia, Portugal	*C. rugosa*	*Palaeophycus*	D	Delgado, 1886; Neto de Carvalho et al., 1998, 2006
L. Ord.	Newfoundland, Canada	*R. leiferikssoni*	*Gyrolithes, Planolites*	B/D	Fillion and Pickerill, 1990
M.-U. Cam.	New Brunswick, Canada	*R. isp.*	*Helminthopsis*	C	Pickerill and Blissett, 1999
M. Cam.	Öland, Sweden	*C. irregularis*	*Teichichnus*	B/D	Martinsson, 1965
M. Cam.	Montana, USA	"trilobite trail"	"annelid trail"	B	Walcott, 1918
L. Cam.	Västergötland, Sweden	*R. dispar, C. rusoformis,* olenellacean trilobite	*Teichichnus, Palaeophycus*	D	Bergström, 1973; Jensen, 1990, 1997
L. Cam.	Yunnan, China	*R. isp.*	"worm trace"	B(2)	Weber and Zhu, 2004
L. Cam.	Sonora, Mexico	*R. multilineatus*	*Planolites*	A	McMenamin, 2003
L. Cam.	Salt Range, Pakistan	*C. cf. irregularis*	"infilled burrow"	C	Seilacher, 1955

Table 1. Literature compilation of documented cases of rusophycid (*Rusophycus* and rusophyciform *Cruziana*) hunting burrows. "Association" refers to degree of association between components of composite trace fossils: A: Single 'composite' specimen with no particular association. B: Multiple 'composite' specimens with no particular association. C: Single composite specimen with particular association. D: Multiple composite specimens with particular association. B or D followed by (2) indicates that only two specimens have been documented. Multiple degrees of association (e.g. B/D) indicate that the published material was insufficiently specific to permit further classification.

	I	II	III	IV	V	VI	I-VI
area, cm^2	381	1078	458	1155	837	870	4779
Rusophycus biloba/*Teichichnus* "hunting" association	0	6	0	4	9	1	20
Rusophycus biloba/vertical tube "hunting" association	1	0	1	1	0	2	5
Other association	0	1	0	0	0	0	1
R. biloba not in association	1	2	1	7	3	0	14
of which incomplete	1	1	0	4	3	0	9
Teichichnus not in association	0	2	(1)	2	2(3)	3	9(11)
Rusophycus pudicus/ *Rusophycus isp.*	1	0	3	0	1	2	7
Cruziana/*Diplichnites*	1	0	2	2	0	1	6
Arthraria antiquata	2	4(5)	0	1	0	1	8(9)
distance, m	1.2	4	5.5	1.2	1.2		13.1

Table 2. Trace fossil associations of collected material, Joslin Hill Member, Herkimer Formation. Roman numerals refer to laterally equivalent localities along producing horizon.

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CONCLUSIONS

Bioturbation is a critically important process in modern seafloor environments. Infaunal sediment mixing profoundly impacts the physical, chemical, biological and ecological structure of seafloor substrates. By extension, bioturbation shapes the composition and complexity of ancient living eukaryotic communities, the taphonomic processes responsible for their preservation in the fossil record and the chemical composition of seawater. In that light, an understanding of the evolution of infauna as ecosystem engineers and of mixing as a major engineering process is essential to reconstruction of the evolutionary history of benthic eukaryotic life and environments.

The early Paleozoic was one of the most dynamic intervals in life history, associated with not only unprecedented biotic innovation but also high turnover rates at both the organismal and community levels. The onset of significant levels of bioturbation would have dramatically changed the nature of the early Paleozoic seafloor. The lower Paleozoic trace fossil record is thus a valuable metric for tracking evolutionary changes in the ethology and functional morphology of burrowing organisms, as well as the character of seafloor substrates and their associated benthic ecosystems.

The development of well-mixed sediment has long been assumed to have occurred at the Precambrian–Cambrian boundary and in the earliest Cambrian, in conjunction with the appearance of the first three-dimensional burrow systems. This assumption has become engrained in the literature; the onset of extensive bioturbation has been evoked as a

trigger for a myriad of late Neoproterozoic and earliest Cambrian geochemical, ecological and taphonomic phenomena. However, the results of this study, drawn from marine shelfal successions of four paleocontinents, indicate that, in spite of contemporaneous advances in infaunalization, not only was sediment mixing poorly developed in earliest Cambrian marine shelfal settings, but even in the middle Ordovician, 75 million years later, infaunal mixing remained suppressed. Therefore, it is likely that many of the late Neoproterozoic and earliest Cambrian phenomena that have historically been blamed upon the advent of infaunal mixing, such as declines in microbialite abundance and diversity and the disappearance of the Ediacara Biota, have been misattributed.

Mixed layer development appears to have been relatively unaffected by notable early Paleozoic developments in infaunalization. The densely colonized bedding plane horizons characteristic of many lower Paleozoic heterolithic successions indicate that significant increases in infaunal motility had occurred by the middle Ordovician. However, biogenic sediment mixing remained poorly developed: beds are commonly thin and coherent; ichnofabrics consist predominantly of non-disruptive, meiofauna-scale cryptobioturbation or small-scale macroburrowing; well-mixed intervals are of limited spatial extent and shallow depth; trace fossils are commonly preserved as discrete, bioglyphic, high-relief structures; and the majority of bed-sole structures were formed through syndepositional casting rather than through intrastratal or penetrative burrowing.

The consistently high quality of preservation of shallow-tier biogenic and physical sedimentary structures throughout these lower Paleozoic successions indicates that the substrate directly adjacent to the sediment-water interface was, even as late as the middle Ordovician—over 75 million years after the Precambrian–Cambrian boundary—cohesive and poorly mixed. The exceptional fidelity of the lower Paleozoic shallow-tier trace fossil record suggests that anactualistic substrate conditions were responsible for the operation of a taphonomic window, and one which remained open until at least the mid-Ordovician.

The appearance and widespread diversification of trilobites, a clade commonly assumed to consist largely of infaunal deposit feeders, does not appear to have significantly impacted mixed layer development. The abundance of trilobite- and arthropod-produced burrows preserved in conjunction with a lack of evidence for well-developed sediment mixing in the examined lower Cambrian to middle Silurian successions suggests that early Paleozoic trilobites did not, in fact, contribute significantly to infaunal mixing.

The preservation of composite *Rusophycus-Teichichnus* burrows in the Wenlockian Herkimer Formation provides a compelling example of the variable feeding ethology and substrate interactions of benthic trilobites. The parallel alignment of *Rusophycus* with *Teichichnus*, *Rusophycus*-mediated deformation of associated *Teichichnus* and the termination of many of these *Teichichnus* at points in contact with associated *Rusophycus* suggest a predatory interaction. These findings, along with other instances of trilobite 'hunting burrows,' are in agreement with previous studies of the trilobite body fossil

record which suggest that certain trilobites were particularly well-adapted to the capture of live prey and ingestion of large food particles. Moreover, the conjunction of dense *Rusophycus* and *Cruziana* and trilobite body fossil assemblages with a paucity of well-mixed horizons or even well-mixed *Rusophycus* and *Cruziana* infill suggests that many trilobites and other burrowing arthropods were apparently not efficient bioturbators. Therefore, although trilobites have historically been classified as mobile deposit feeders, the trilobite clade likely encompassed a wide range of life modes and feeding ethologies. Moreover, mobile deposit feeding, which is employed by many of the most effective bioturbators of the modern seafloor, was likely not yet a well-developed feeding strategy in the early Paleozoic.

Lastly, delayed sediment mixing provides support for geochemical models favoring protracted (rather than constant) sediment ventilation and associated secular variation in the sediment and oceanographic cycling of important redox-sensitive and bioessential compounds such as sulfate through the early Phanerozoic. In this light, the record of infaunal mixing may help to resolve current debate concerning the factors controlling the evolution of the global sulfur cycle. Protracted sediment mixing may also be linked to the anomalous preponderance of exceptionally preserved soft-bodied biotas and shallow-tier trace fossil assemblages characteristic of the lower Paleozoic stratigraphic record. A lack of intensive infaunal mixing may have fostered anactualistic substrate and thus taphonomic conditions uniquely suited to the preservation of both body and trace fossil assemblages. Lower Paleozoic ecosystems and environments appear to represent a unique

system, associated with dynamic ecological and chemical transformations, transitional

between that of the Precambrian and the later Phanerozoic.

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