Lowermost Cambrian Ichnofabrics from the Chapel Island Formation, Newfoundland: Implications for Cambrian Substrates

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Bioturbation long has been 'blamed' for eliminating late Proterozoic-style sedimentary structures and fabrics. While the presence of diverse and complex burrows in lowermost Cambrian strata is indisputable, analysis of Precambrian–Cambrian successions in southeast Newfoundland demonstrate that this burrowing style did not produce typical Phanerozoic-style ichnofabrics.

Three hundred meters of the siltstone/sandstone facies of member 2 of the Chapel Island Formation were examined in the area of the Precambrian–Cambrian boundary stratotype. Gyrolithes, Planolites, *and* Skolithos *occur as sand infills ubiquitously throughout siltstone beds, most commonly without direct contact with an overlying sandstone bed, as if "floating" in the siltstone. In contrast,* Treptichnus pedum *occurs as sand infills adhering onto the base of thin sandstone beds that have different grain size and texture than the burrow infills. Both of these burrow types represent a style of preservation in which the burrows are unattached to an overlying bed of the casting sediment. These styles of preservation occur frequently in the* Treptichnus pedum *Zone and continue into the* Rusophycus avalonensis *Zone in spite of an increase in trace fossil diversity. The sandstone beds are bioturbated only very rarely. The resultant fabric produced by floating and, in particular, adhering burrows in these shallow marine deposits appears to be characteristic of many Lower Cambrian rocks. Silt layers appear to have been firm enough to have supported open burrows, likely as a result of a negligible mixed layer. This line of reasoning would predict that preservation of this type would be uncommon in younger strata deposited in open marine settings.*

INTRODUCTION

An increase in trace fossil diversity and complexity through the terminal Proterozoic–Cambrian interval has long been recognized (Crimes, 1987). Because workers have known that there was a major shift in the nature of bioturbation between the late Proterozoic through the Early Cambrian, bioturbation has been "blamed" for a number of changes during this transition. These include the: (1) decline of stromatolites (Garrett, 1970), (2) decline of microbial mat structures (Gehling, 1999, 2000), (3) loss of Ediacaran fossils, (4) advent of Burgess Shale-type preservation (Butterfield, 1995), and (5) increased nutrient cycling (e.g., Brasier, 1990; McIlroy and Logan, 1999). The specific role that bioturbation played in producing any of these changes during the Precambrian–Cambrian radiation is not understood, and indeed, the distribution of discrete trace fossils alone cannot be utilized to resolve these issues. It is the disruption and mixing of the sediment that is critical to understanding possible links with changing taphonomic conditions and the destruction of mat surfaces, as well as potential links with nutrient recycling. The Early Cambrian is a time of transition to Phanerozoic trace fossils and ichnofabrics (e.g., Bottjer et al., 2000). Typical Phanerozoic ichnofabrics are characterized by either thorough or complete bioturbation producing complex ichnofabrics (e.g., Bromley and Ekdale, 1986) or, as are particularly common in storm deposits, by a series of basal erosion surfaces or sharp bases overlain by laminated strata grading up into bioturbated strata. The latter is commonly referred to as "lam-scram." The burrows reflect piping down into the storm-deposited sediment. The details of the transition from Neoproterozoic surface or near-surface trace fossils to this style of three-dimensional bioturbation—other than simply the development of more bioturbation and increased depth of bioturbation—have not been explored. Yet, these issues are critical to understanding the early history of metazoans and the development of the infaunal biological benthic boundary layer. The necessary first steps are to understand the nature of trace fossil preservation during the terminal Proterozoic–Early Cambrian and how ichnofabrics of this age were formed. Understanding how this record may differ from that of later times is critical to the accurate evaluation of the effects of the initiation of these early styles of bioturbation.

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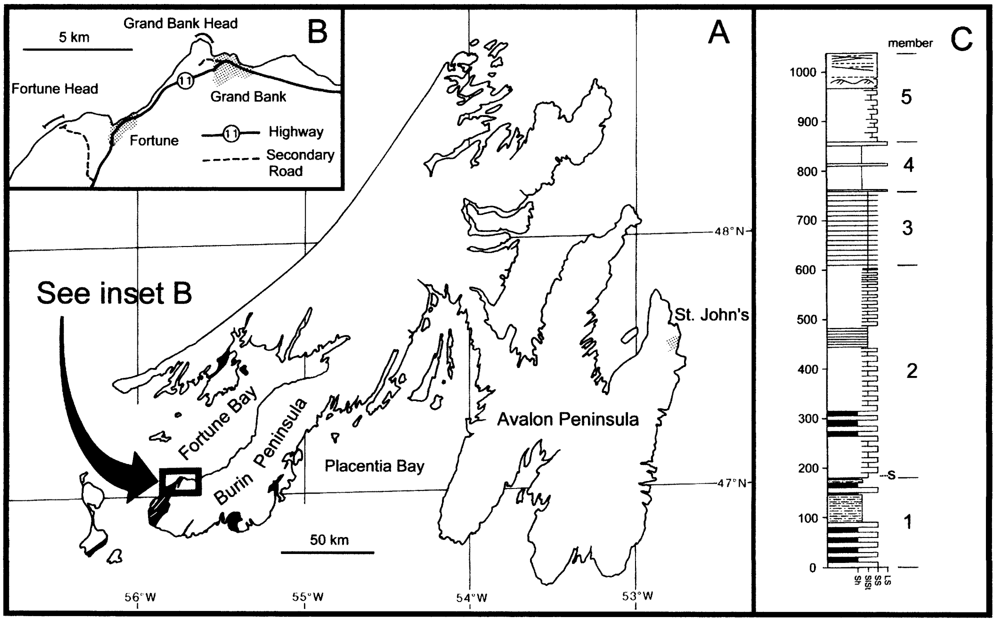

FIGURE 1—Locality map for the present study and stratigraphic column of the Chapel Island Formation. Modified from Myrow and Hiscott (1991, 1993). (A) Location of field area at Fortune and Grand Bank. Outcrop distribution of the Chapel Island Formation shown in black. (B) Location of outcrops of member 2 of the Chapel Island Formation marked by black bars. (C) Simplified stratigraphic column of the Chapel Island Formation. Sh = shale, SiSt = siltstone, SS = sandstone, LS = limestone.

To address this issue, the Precambrian–Cambrian boundary succession on the Burin Peninsula of Newfoundland was examined because it offers a thick succession through lowermost Cambrian deposits. It contains the Precambrian–Cambrian global boundary stratotype (Narbonne et al., 1987; Landing, 1994) and records a succession of terrigenous clastic strata that are well constrained sedimentologically and stratigraphically (Myrow, 1987; Landing et al., 1988; Myrow and Hiscott, 1993). These strata consist of a succession of thin- to medium-bedded tempestites and muddy siltstone. The thick and well-exposed section offers excellent opportunity for thorough examination of discrete trace fossils and ichnofabrics in this paleogeographic setting.

LOCATION AND GEOLOGIC SETTING

The Chapel Island Formation at Fortune Head is exposed on the southwest tip of the Burin Peninsula of southeastern Newfoundland (Fig. 1). The Global Stratotype Section and Point (GSSP) is at a horizon marking the top of the *Harlaniella podolica* (ichnofossil) Zone and the base of the *Treptichnus pedum* (ichnofossil) Zone (Narbonne et al., 1987). The ichnofossil zones spanning the boundary correspond to assemblages first described by Crimes (1987) from terminal Proterozoic–Cambrian successions around the globe. The GSSP is positioned at what was considered the first occurrence of *Treptichnus pedum*, 2.4 m above the base of member 2 in the Chapel Island Formation (Narbonne et al., 1987). Since then, specimens of *T. pedum* have been recorded 3.11 and 4.4 m below the GSSP (Gehling et al., 2001).

This section was chosen for the remarkably thick succession of siliciclastic strata (~1000 m) comprising the Chapel Island Formation that spans the Proterozoic–Cambrian boundary, and ranges through the "*Ladatheca*" *cylindrica* and *Watsonella crosbyi* small shelly fossil-assemblage zones (Narbonne et al., 1987; Landing et al., 1988; Landing and Westrop, 1997). The Chapel Island Formation conformably overlies the terrestrial to paralic deposits of the Rencontre Formation (Smith and Hiscott, 1984).

Detailed logs were made of sections at Fortune Head and an additional section at Grand Bank Head (7 km north of Fortune Head; Fig. 1), based on and keyed into the labeled measured sections of Myrow (1987), Myrow et al. (1988), and Landing et al. (1988). Working at centimeter scale, ichnofabrics and the associated trace fossil taxa were described in relation to the sedimentary facies.

SEDIMENTARY FACIES

The Chapel Island Formation is divided into five members (Fig. 1; Bengtson and Fletcher, 1983; Narbonne et al., 1987). Myrow and others (Myrow, 1987; Myrow et al., 1988; Myrow and Hiscott, 1993) have described the sedimentology. The lowest member contains red-and-green sandstone and shale deposited in tidal flat and shallow subtidal environments, and darker green/gray siltstone and black shale deposited in semi-restricted shoreline environments. Member 2 consists primarily of interbedded green siltstone and thinly laminated to medium-bedded, very fine- to medium-grained sandstone deposited in a storm-influenced deltaic setting (Figs. 2, 3). The third member is a thinly laminated siltstone unit with carbonate nodules that represents deposition in a mid- to outer-shelf setting, predominantly below storm-wave base. Member 4 consists of red and green mudstone with minor limestone, whereas member 5 is a coarsening-upward suc-

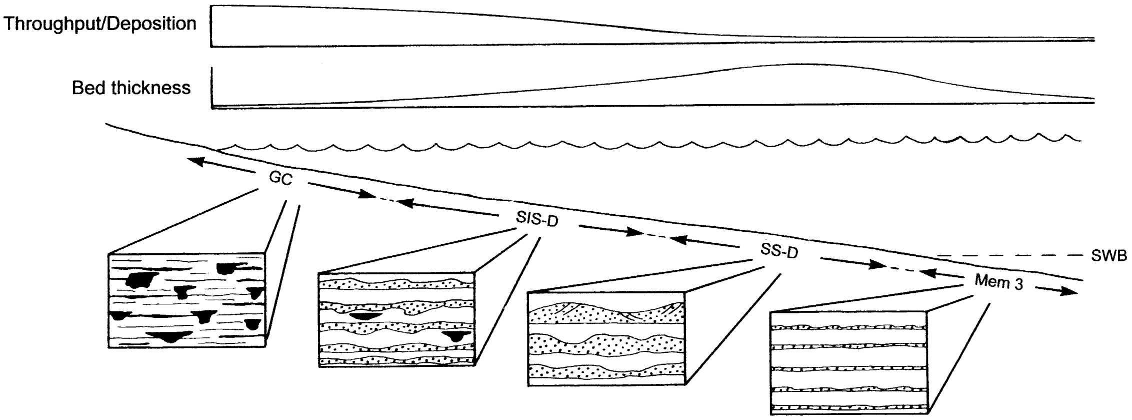

FIGURE 2—Tempestite bypass model proposed by Myrow (1992) for member 2. See text for details. GC, SIS-D, and SS-D indicate Gutter Cast, Siltstone-Dominated, and Sandstone-Dominated facies, respectively, of member 2. Figure modified from Myrow (1992).

cession of storm- and wave-dominated sandstone and siltstone.

This paper focuses on member 2, which is over 400 meters thick, contains the Precambrian–Cambrian boundary, and includes the Lower Cambrian *Treptichnus pedum* and *Rusophycus avalonensis* Zones. Because only 2.4 meters of Precambrian strata are included in member 2, this paper is concerned almost entirely with the lowermost Cambrian record.

Myrow (1987, 1992a) has described three facies from this member: (1) the Gutter Cast Facies, characterized by muddy siltstone with well-preserved thin laminae to very thin sandstone beds and abundant pot casts and gutter casts; (2) the Siltstone-Dominated Facies consisting of laminated siltstone with 30–50% laminae to medium beds of sandstone and few, if any, erosional structures; and (3) the Sandstone-Dominated Facies of similar lithology and character, but with thicker sandstone beds (hummocky cross-stratified, in part) and a higher sandstone percentage.

All facies show a strong influence of storm processes (Myrow et al., 1988; Myrow, 1992a). Thin-to medium sandstone beds record deposition under the influence of waning flows with initial offshore-directed currents followed by wave oscillations. Flat pebble conglomerate beds represent erosion and transport of siltstone and rounded shale rip-up clasts. Hummocky cross-stratification occurs on a variety of scales. Finally, gutter casts and pot casts (in particular in the Gutter Cast Facies; Myrow et al., 1988; Myrow, 1992a) record localized erosion by storm-generated flows. Details of gutter-cast and pot-cast formation are described in Myrow (1992b).

Myrow (1987, 1992a) proposed a model for storm sedimentation (Fig. 2) in which the Gutter Cast Facies occupies the shallow subtidal zone. This is an area dominated by sediment bypass or throughput across which high-velocity, sediment-laden flows erode deep, narrow scours (gutters) into a muddy cohesive substrate. Very little sand is deposited outside of these scours; most of the sediment bypasses the shallow subtidal zone and is deposited in deeper water where, due to flow deceleration, erosion of the sea floor ceases and continuous beds of more even thickness are deposited (Siltstone-Dominated Facies). Farther from shore, bed thickness reaches a maximum (Sandstone-Dominated Facies) and hummocky cross-stratification is abundant. More distally, below storm wave base, bed thickness decreases further. These distal deposits are represented by the thinly-laminated siltstone of member 3 (see Myrow et al., 1988, for description).

ICHNOFABRIC

Trace fossils from member 2 of the Chapel Island Formation have been described by Crimes and Anderson (1985), Narbonne et al. (1987), Narbonne and Myrow (1988), Myrow et al. (1988), and Gehling et al. (2001). McIlroy and Logan (1999) measured ichnofabric indices and did a very broad study of the entire Lower Cambrian of southeastern Newfoundland. For the purpose of this paper, a few principal ichnogenera that were most important for the production of ichnofabrics were recognized (Fig. 4). Several of these ichnogenera are likely intergradational (Fig. 4). Burrows typically are preserved with remarkably sharp boundaries. Rare arthropod traces, *Monomorphichnus* and *Rusophycus*, are also present in the *R. avalonensis* Zone, and are preserved similarly in exquisite detail.

In both the *Treptichnus pedum* and *Rusophycus avalonensis* Zones and within all three facies, the ichnofabric is developed nearly always within siltstone. Sandstone beds remain largely unbioturbated through this interval (but see below). With few exceptions, the ichnofabric consists of a lithological contrast between the coarser sandier material of the trace fossil and the surrounding siltstone (Figs. 4, 5). The contrast between the material filling the traces and the surrounding matrix is too large to be explained as a remnant from material sorted from the siltstone during feeding. Rather, the dominant means of preservation was by gravitationally induced, passive filling of coarser sediment into open burrows. In most instances, the source for the burrow fill is no longer present and the burrows are preserved in two manners: (1) floating forms completely engulfed in siltstone, and (2) adhering forms attached to the bases of sandstone beds as a result of amalgamation. In these cases, the casting bed subsequently was winnowed away or, in the cases of sediment bypass, never deposited above the burrow at all. Additionally, the shallower parts of some burrows were eroded, producing incomplete burrow casts. Comparable styles of unattached bur-

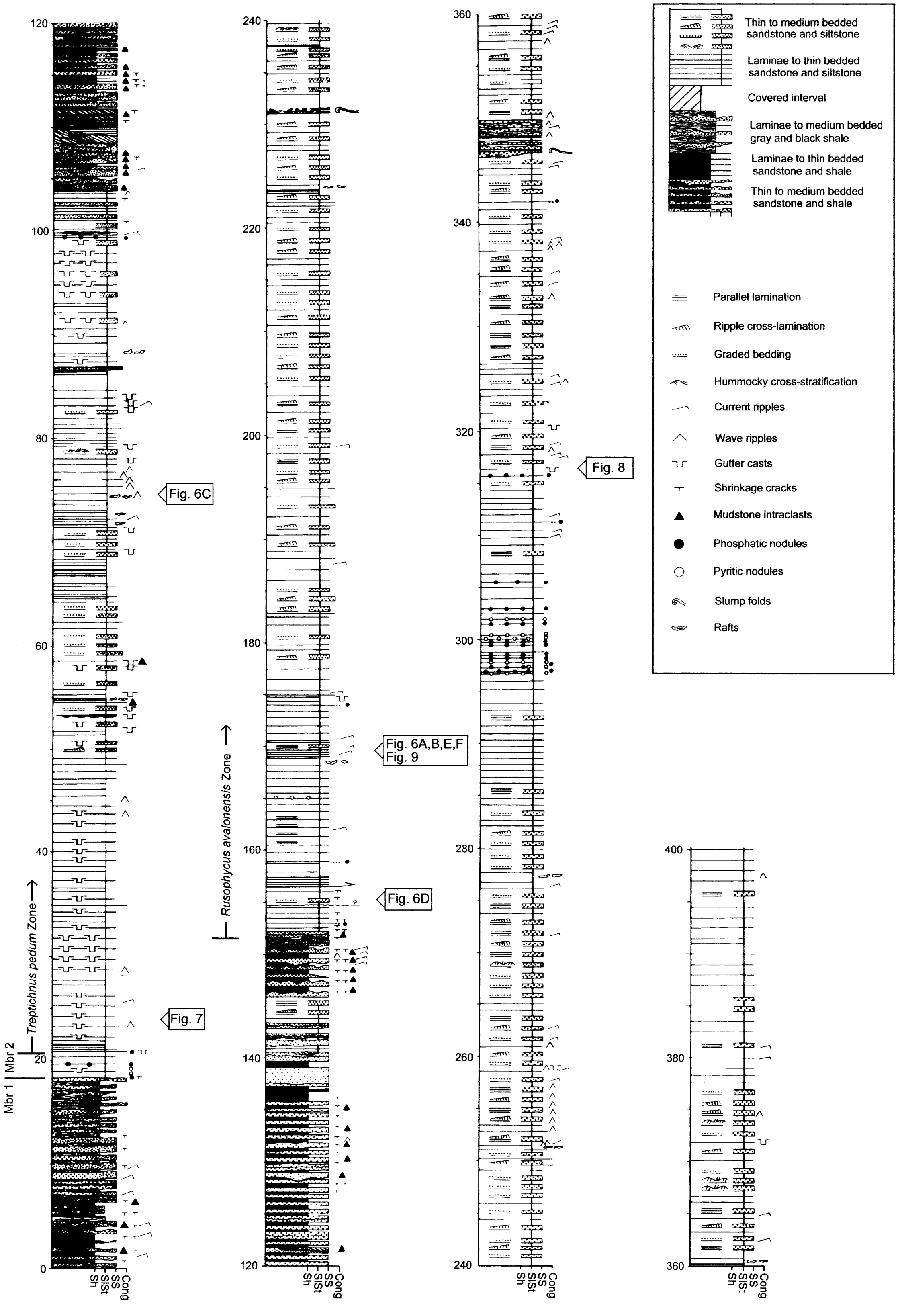

FIGURE 3—Stratigraphic section for member 2 at Fortune, showing major sedimentological features and range of *Treptichnus pedum* and *Rusophycus avalonensis* Zones. Boxes enclosing figure numbers refer to stratigraphic position of material figured in this paper. Section based on Myrow and Hiscott (1991, fig. 3). Note: Figures 6A, B, E, F and Fig. 9 are from the Grand Bank Locality and are tied in to the Fortune Section at approximately 170 meters based on sedimentological and stratigraphic evidence.

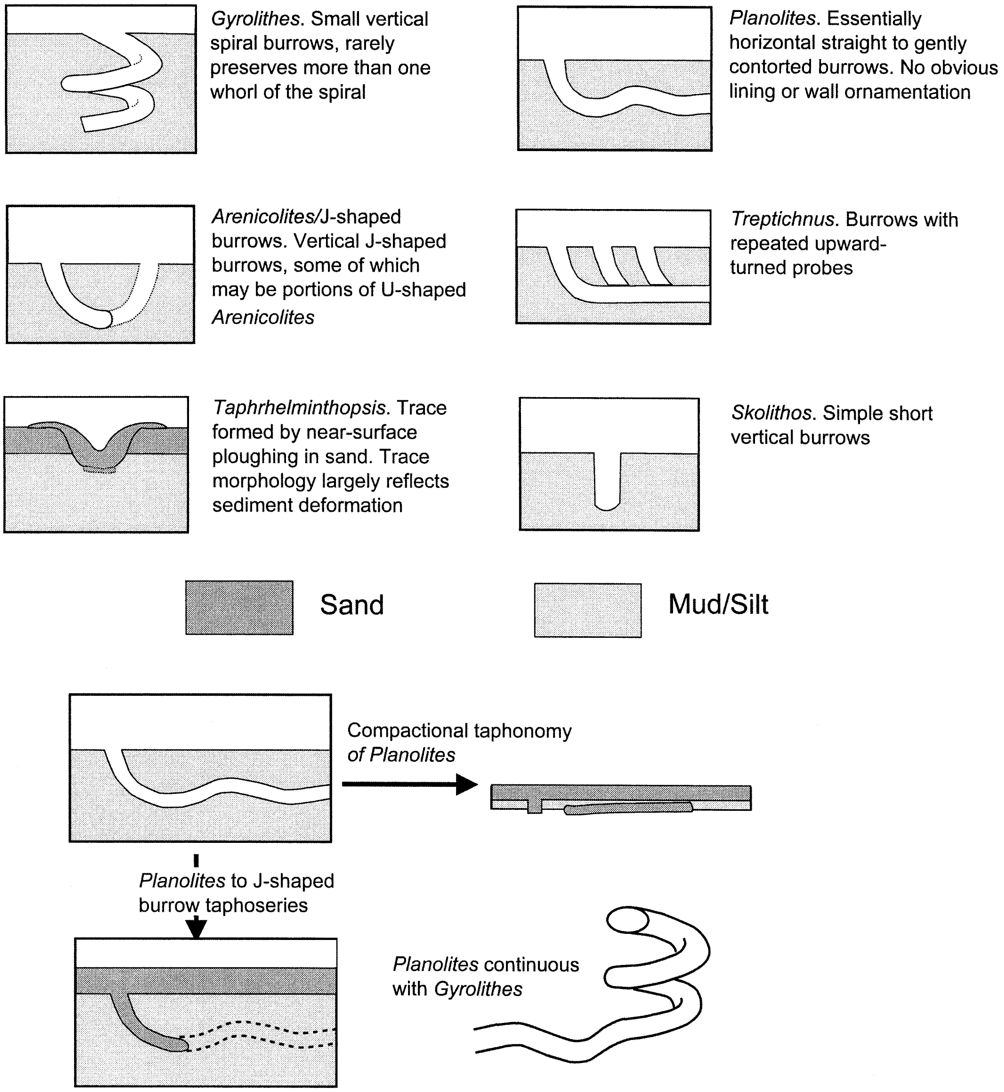

FIGURE 4—Schematic depictions of principle ichnofabric forming trace fossils in Chapel Island Formation member 2. Also shown are selected taphonomic relations of these ichnotaxa. The use of *Taphrhelminthopsis* probably should be abandoned for these Cambrian forms (e.g., Seilacher-Drexler and Seilacher, 1999) but is maintained for the purpose of this paper as it provides better continuity with previous work on the Chapel Island Formation.

row preservation were discussed by Simpson (1957). Figure 5 provides a scheme of preservational histories. In this paper, attached burrows are defined as those that are piping down into the underlying sediment but remain in contact with their casting medium.

The ichnofabric of both zones is dominated by *Planolites*, *Gyrolithes*, and to a lesser extent, J-shaped and simple U-shaped burrows. Burrow diameters are generally millimeter scale, with rare specimens of *Planolites* reaching diameters of 7 mm. Preserved depth of bioturbation is generally less than a centimeter and rarely up to 3 cm. Typically, these traces occur as isolated bodies of sandstone in siltstone (Figs. 6C, F, 7). Where a vertical trace is followed into contact with an overlying sandstone bed (i.e., adhering burrow preservation), closer examination generally reveals that there is a difference in sediment character (Fig. 8) and often an extremely thin lamina of siltstone at the contact (Fig. 6F). Only in very rare cases are burrows attached to a bed that provided the source of the burrow fill (Fig. 7).

A typical slab from the Siltstone Dominated Facies (Fig. 7) shows repeated 1-to-4 mm-thick layers with sharp bases and coarser-grained basal divisions that rapidly grade to siltstone. Boundaries between the layers are sharp; some disturbance from bioturbation is seen only in a 5-mm-thick interval near the center of the slab. Minor erosion of the seafloor is evident from the sharp tops of the beds and from local down-cutting. The depth of the erosion is difficult to evaluate. The problem of truncation by erosion is discussed below. In many places, the siltstone contains virtually uninterrupted very fine sandstone laminae (cf. Myrow, 1992a), which makes it unlikely that there was major bioturbation that did not preserve.

In the Gutter-Cast Facies, trace fossils rarely are preserved on the sides of gutter casts. The burrows show fluting, suggesting that these were open burrows that were

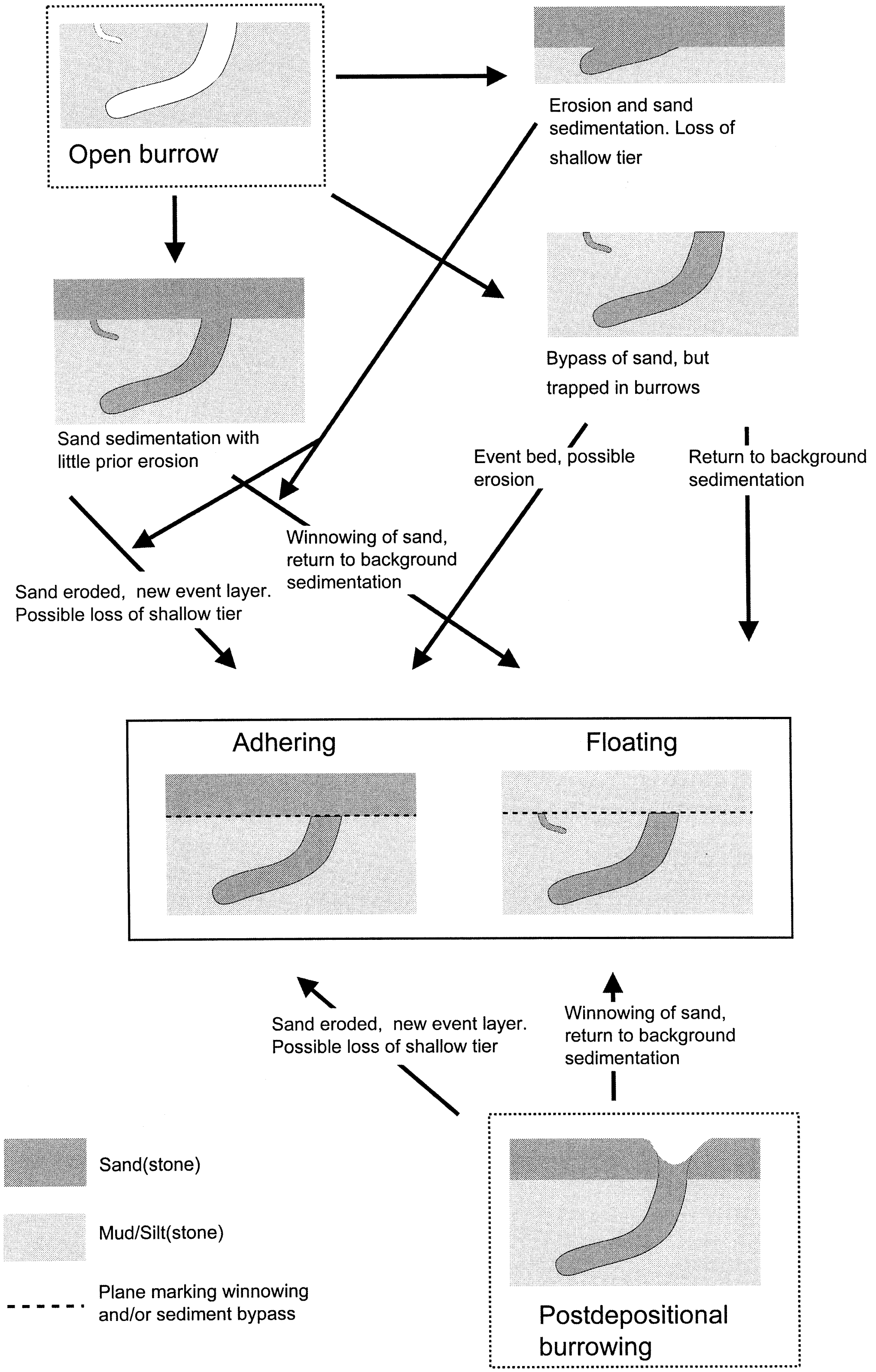

FIGURE 5—Possible pathways for the formation of unattached preservation of trace fossils in Chapel Island Formation member 2.

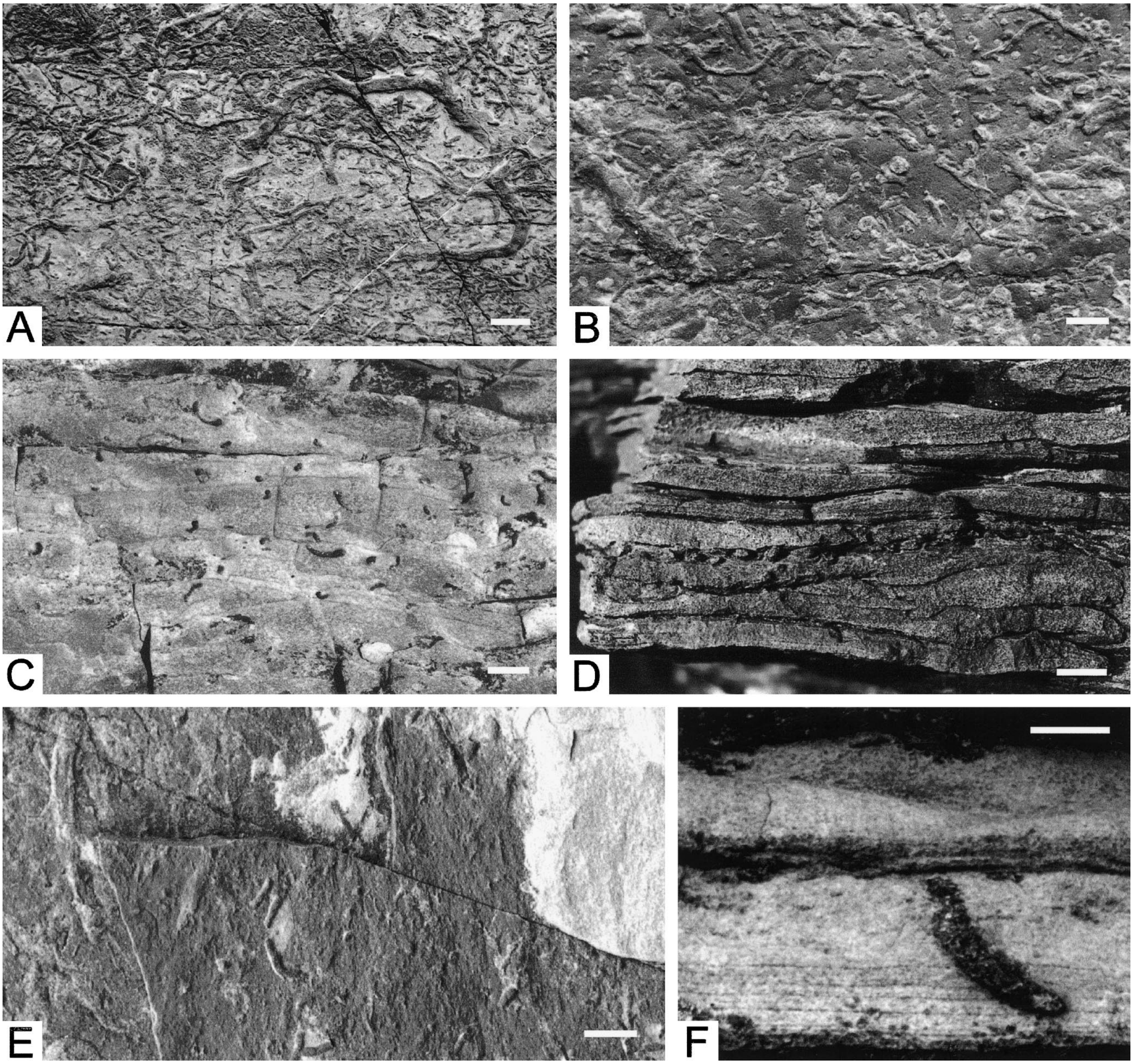

FIGURE 6—Field photographs of ichnofabrics of Chapel Island Formation member 2. See Figure 3 for stratigraphic position. (A) Sole of sandstone bed showing numerous trace fossils, dominated by *Planolites*. Large trace may be sole preservation of a *Taphrhelminthopsis*. Grand Bank Head, *Rusophycus avalonensis* Zone. Scale bar is 30 mm. (B) Close-up of bed surface from the same level and locality as A, showing compactional taphonomy of *Planolites* and a rare example of an intact U-shaped *Planolites* (upper left portion). Scale bar is 10 mm. (C) Specimens of *Gyrolithes* occurring in floating preservation. View is oblique cross-section. Fortune Head, *Treptichnus pedum* Zone. Scale bar is 10 mm. (D) Interval with thin sandstone beds. Note siltstone horizon with abundant sand-filled burrows. Upper part of member 2A at Fortune Head, *Rusophycus avalonensis* Zone. Scale bar is 10 mm. (E) Base view showing two sandstone beds and two siltstone beds. The upper bed (right) shows relatively rare trace fossils as does the adjacent siltstone. The lower sandstone bed has a greater diversity of trace fossils as does the lower siltstone. Grand Bank Head, *Rusophycus avalonensis* Zone. Scale bar is 10 mm. (F) Curved burrow possibly representing portion of an *Arenicolites* or *Planolites*. Note laminated undisturbed sediment. Grand Bank Head, *Rusophycus avalonensis* Zone. Scale bar is 5 mm.

exhumed and partly filled by sand at the time of gutter formation. Exhumed burrows from the profile of surrounding sediment, cast by the sand on the sides of the gutter fill, are confined to the top 1-to-1.5 cm of gutter casts, confirming that burrows were restricted to a shallow tier. The absence of burrow casts in the lower parts of profiles of gutter casts, up to 10 cm deep, suggests that burrowing was not only shallow, but also initiated at discrete surfaces.

In strata of the *Rusophycus avalonensis* Zone, bioturbation is rare within the sandstone beds and only a few examples preserve evidence that animals dug vertically through a bed (Fig. 9). Disruption caused by horizontal plowing by the progenitor of *Taphrhelminthopsis* did occur (Fig. 9), but it was never so intense as to cause extensive mixing (Narbonne et al., 1987; fig. 6F). A representative slab from a sandier part of the siltstone facies within this

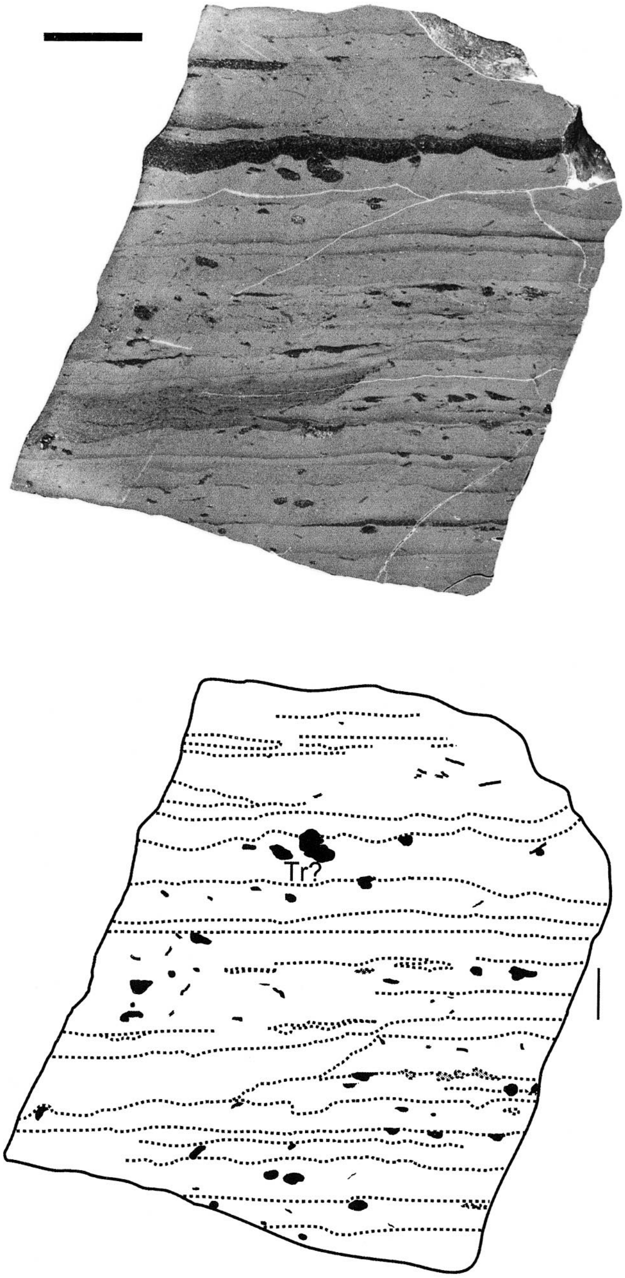

FIGURE 7—Ichnofabric from gutter cast facies of the Chapel Island Formation, near the base of member 2 at Fortune Head, *Treptichnus pedum* Zone. Schematic tracing depicts main bed contacts and trace fossils (shown in black). Siltstone dominated slab showing evidence of repeated sediment by-pass manifested by thin remnants of sandstone beds. In most of the slab, there is no obvious source for the sand that fill trace fossils. Vertical bar next to schematic tracing marks interval with higher sediment mixing. A possible *Treptichnus* is seen in the upper portion (marked Tr?). In this case, the source of the burrow fill is preserved. Scale bar is 10 mm.

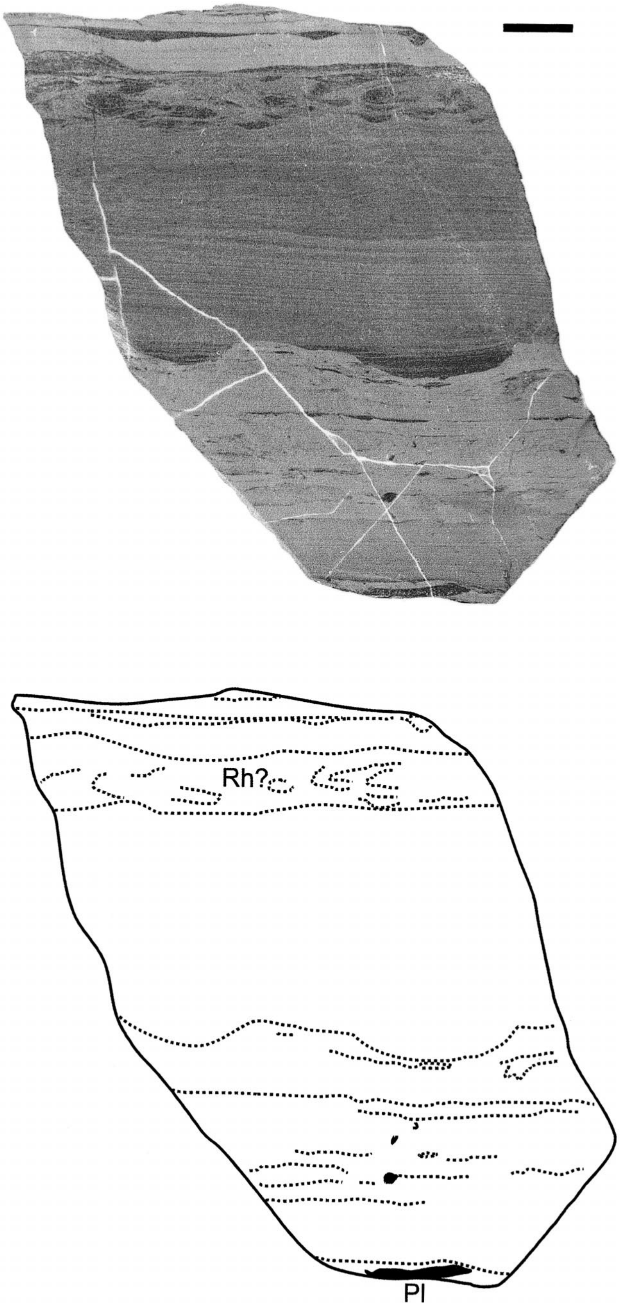

FIGURE 8—Polished section and schematic tracing of slab with a distinctive, horizontally laminated sandstone with small-scale scouring at the base. The preserved top of the bed is disrupted by what appear to be horizontal spreite, probably *Rhizocorallium* (marked Rh?). Lower siltier portion of slab has little sign of bioturbation. Near base of slab is a *Planolites* in adhering preservation (marked Pl). The fill of the *Planolites* is distinctly different from the bed to which it is adhered. Fortune Head, *Rusophycus avalonensis* Zone. Scale bar is 10 mm.

zone shows little disturbance of lamination overall. A narrow zone of sandstone, about 3 mm thick, shows irregular fabric apparently representing bioturbation (Fig. 9).

Treptichnus pedum appears to be restricted largely to the sandier portions of the Siltstone Dominated Facies where it occurs as adhered burrows. In neither the *T. pedum* nor *Rusophycus avalonensis* Zones are there examples of this trace fossil extending up into an overlying sandstone layer, although there are rare examples of treptichnid burrows with probes impinging downwards into the top of sandstone beds.

A large number of sub-horizontal, burrow “fragments” are abundant particularly in the transitions from silt-

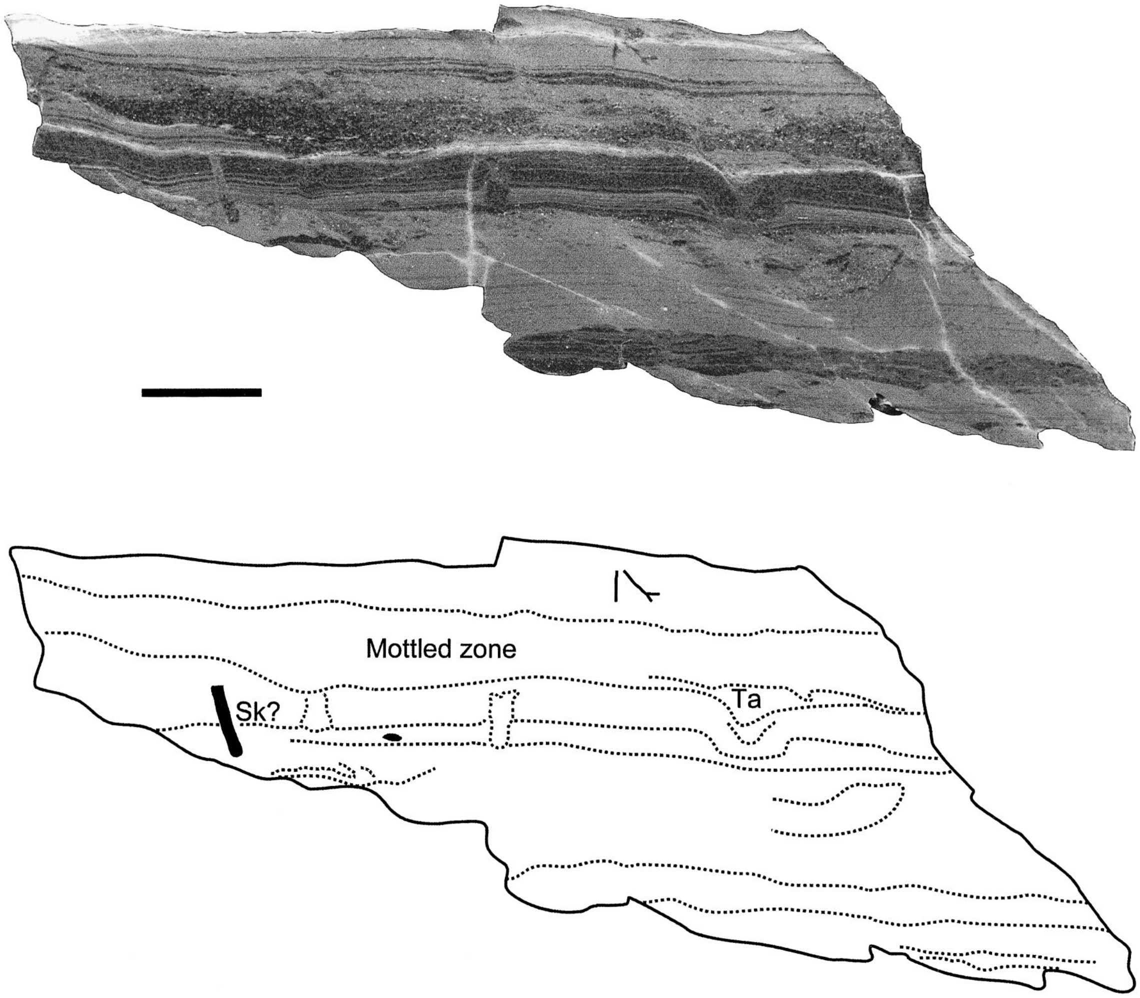

FIGURE 9—Polished section and schematic tracing of ichnofabric from siltstone facies of the Chapel Island Formation, Grand Bank Head, *Rusophycus avalonensis* Zone. Sandier portion in upper part of figure shows an example of disruption caused by *Taphrhelminthopsis* (marked Ta). Bed just overlying this trace shows sign of more intense mixing. An inclined vertical burrow, possibly *Skolithos* (marked Sk?) penetrates a sandstone. Scale bar is 10 mm.

stone-dominated to sandstone-dominated facies in the *Rusophycus avalonensis* Zone. As observed in the field and viewed in cross-section, these give the appearance of being remnants of strongly bioturbated sandstone beds. However, on closer examination, the sandstone burrows are surrounded by siltstone. It is not clear if these represent intense reworking of a sandstone bed, or if these beds formed by repeated trapping of bypassed sand in open burrows. However, there are abundant thin (mm to less than 1 cm) sandstone beds with well-exposed laminae that are not bioturbated at all. Bases of other beds contain relatively abundant trace fossils (Fig. 6A, B). Close inspection reveals that, for the most part, these were not simply infilled by the overlying sandstone bed, but represent unattached burrows.

DISCUSSION

Nature of Ichnofabric

Sepkoski (1982) made a general comparison between the inferred influence of the infauna on Cambrian and post-Cambrian Paleozoic tempestite deposits. Based on Upper Cambrian strata in the western USA, he suggested that Cambrian infauna were of rather limited size and burrowed only to a limited depth in the sediment. Thus, beds largely escaped reworking, and oxygen piping through open burrows did not reach deep into the sediment. Where intense bioturbation was observed, it rarely reached deeper than about 5 mm into the beds. Although it is well known that there was an increase in trace fossil diversity and complexity through the terminal Proterozoic–Cambrian interval, there has been little additional detailed evidence on the nature of early ichnofabrics. The general role of bioturbation in changing sediment character has been emphasized repeatedly (e.g., McIlroy and Logan, 1999). However, too little attention has been paid to the nature of the early infaunal influence on sediment properties, including fabric, geotechnical strength, porosity, and grain-size. In particular, there is a very important distinction between observing discrete trace fossils and inferring from them the intensity of bioturbation. For example, the presence of *Taphrhelminthopsis* on the same beds as Ediacara-type fossils in the Uratanna Formation (Jensen et al., 1998) does not necessary indicate that these beds have "intense ichnofabrics" as was suggested by McIlroy and Logan (1999). This is because; (1) the trace fossils are rare; (2) intense bioturbation would eliminate the preservation of discrete surface trace fossils; and (3) the bed, itself, is not bioturbated as viewed in cross-section except where a *Taphrhelminthopsis* occurs.

The results presented herein substantiate that the levels of bioturbation were low, but also reveal some details concerning the nature of early ichnofabrics at the stratotype. As discussed above, the styles of preservation suggest that the ichnofabrics largely consist of passively-filled, open burrows or, in some cases, perhaps, represent material falling in behind the burrower (cf. Fig. 5). In the *Treptichnus pedum Zone*, no burrows have been found that indicate backfill, evidence of sorting, or fecal material. *Teichichnus*, simple vertical spreite burrows that reflect vertical burrow adjustment, first appear in member 2B (Landing et al., 1988, fig. 23). Horizontal spreite burrows, probably *Rhizocorallium*, were found high in member 2A within the *Rusophycus avalonensis* Zone (Fig. 8) in the present study.

No general conclusion can be made concerning the ethology of the organisms that created these open burrows. *Planolites* often is interpreted as a combined feeding and/or locomotion trace (Pemberton and Frey, 1982; Keighley and Pickerill, 1995). Identification of this trace often has to be based on fragmentary specimens. Specimens have been found that were drawn-out U-shaped forms (Fig. 6B), which may represent permanent or semi-permanent dwelling burrows. *Treptichnus pedum* often has been interpreted as formed by deposit feeders, and, while this remains a possibility, alternative interpretations need be considered, including the possibility that these represent dwelling burrows for sediment-surface feeders (cf. Jensen, 1997). The ethological interpretation of the vertical spiral burrow *Gyrolithes* is similarly problematic. This type of trace is produced by a wide range of marine invertebrates for a wide range of purposes (Jensen, 1997; Dworschak and Rodrigues, 1997). The mode of *Gyrolithes* fill and examples of specimens continuous with *Planolites* (Fig. 4) is consistent with a dwelling burrow. Therefore, most of the ichnofabric-forming trace fossils of member 2 of the Chapel Island Formation may have been dwelling burrows. The low levels of bioturbation could be a reflection of a fauna with limited infaunal mobility. *Taphrhelminthopsis*, nevertheless, is one of the few trace fossils made by organisms that disturbed sand in the earliest Cambrian. As such, it is the only trace close in character to those made by the bulldozing organisms in younger Phanerozoic deposits. These *Taphrhelminthopsis* extend no more than a few centimeters (rarely more than 1 cm) into the rock and only cover a small fraction of the sediment surface area in question. Seilacher-Drexler and Seilacher (1999) suggested that these types of traces were made by an animal that kept in contact with the sediment surface by means of a snorkel, the length of which would limit the depth of emplacement of the animal in the sediment. While it is not possible to deduce if this was the morphology of the producer of *Taphrhelminthopsis* in the Chapel Island Formation, these traces formed very close to, if not on top of, the sediment surface. Therefore, the earliest Cambrian version of bull-dozing, which occurred only rarely, barely affected the upper few centimeters of a sand bed. In addition, these early bulldozers were of moderate size. Several studies suggest that (other things being equal) animal size (cross-section) rather than density may be of greater importance for effectiveness of bioturbation (e.g., Sandnes et al., 2000).

Preservation of Ichnofabric

In discussing the type of ichnofabric seen in member 2 of the Chapel Island Formation, it is important to consider the role of depositional environment on the formation of ichnofabric. These lithologies were deposited during a transition from tectonically-active, small linear pull-apart basins (Rencontre Formation) to more extensive, open marine environments associated with sea-level rise and onlap of older volcaniclastic units to the east during the Early Cambrian (Hutchinson, 1962; Anderson, 1981; Hiscott, 1982; Smith and Hiscott, 1984; Landing et al., 1988). Cambrian and Ordovician deposits accumulated in linear marine basins affected by repeated epeirogenic movements (Hutchinson, 1962; Landing, 1992, 1996).

Member 2 represents a subtidal, storm-influenced deltaic setting (Myrow and Hiscott, 1991; Myrow, 1992a,b). Normally, some erosion of the sea floor and a loss of primary sedimentological and trace fossil information might be expected from this type of depositional environment (e.g., Goldring, 1964). Similarly, the effect of bioturbation generally will be less intense in settings of rapid sedimentation. There is evidence that rates of sedimentation were high in this deltaic setting, including abundant penecontemporaneous gravity-flow structures (Myrow and Hiscott, 1991). Therefore, one may wonder: how faithful is the record of animal infaunal activity preserved in member 2 of the Chapel Island Formation? This question can be broken down into two parts: (1) was there bioturbation that presently is not readily visible in the siltstone, and (2) was there bioturbation in parts of the sediment that is not now preserved?

As discussed above, in many places, the siltstone contains uninterrupted fine sandstone laminae (cf. Myrow, 1992a), which makes it unlikely that there was major bioturbation that did not preserve. This still leaves the possibility of exclusively horizontal bioturbation, which may leave a negligible ichnofabric in vertical section (Droser et al., 1999). However, evidence for this, such as small-scale disruption of laminae, is not observed. Fine-scale stratigraphic completeness is more difficult to evaluate. However, a number of factors suggest that shallow tiers are preserved. The primary evidence for this is that *Treptichnus pedum* likely represents a shallow tier. The probes have been interpreted as having been open to the sediment surface (Seilacher, 1955). The vertical extent of the probes was a few centimeters at most. This form is very rare in the Gutter Cast Facies. It is tempting to suggest that its rarity here indicates deeper erosion, although there is no independent evidence to confirm this. That said, the location and nature of trace fossil preservation on gutter casts, as discussed above, indicates that bioturbation occurred at shallow depths. Although there is evidence of sea-floor erosion in member 2, this is not universal. Extensive examination revealed negligible evidence for a mixed layer in the *Treptichnus pedum* Zone and relatively scarce evidence in the *Rusophycus avalonensis* Zone. The preservation of what seem to be shallow-tier trace fossils suggests that a mixed layer, where developed, had a depth of a few millimeters.

Substrate Consistency

In recent years, there has been a growing body of evidence that terminal Proterozoic sediment surfaces were bound by microbial mats to a far greater extent than what would be typical of most of the Phanerozoic (e.g., Seilacher and Pflüger, 1994; Gehling, 1999). These mats appear to have had a significant role in bedding-plane preservation of Ediacara-type fossils (Gehling, 1999), and it has been suggested that these mats structured early metazoan communities (Seilacher, 1999; Bottjer et al., 2000). Sedimentary structures of suspected microbial connection, such as wrinkle marks, are common in Cambrian rocks (Hagadorn and Bottjer, 1997). The elephant-skin texture widely found on bed soles with Ediacara-type preservation in the terminal Proterozoic, and thought to reflect mat topography, appear to be rare in the Cambrian. Metazoan grazing of sediment surfaces is unlikely by itself to destroy surface mats (cf. Farmer, 1992). The advent of infaunal mixing, particularly by larger animals, was probably a significant factor in the reduction of microbial surface mats and depletion of the interstitial organic component of fine sediment. Increased sediment mixing led to expansion of microbial activity into the sediment (e.g., Seilacher and Pflüger, 1994). Indeed, certain Cambrian shallow-water trace fossils have been suggested to reflect a response to sediment with an enhanced microbial content, including such shallow infaunal traces with meandering or circling patterns as *Taphrhelminthopsis* (e.g., Hagadorn et al., 2000).

The siltstone-sandstone succession of member 2 of the Chapel Island Formation shows no typical mat-related structures or signals, such as wrinkle marks, peetee structures, elephant skin texture, or pyrite-rich horizons. However, the nature of trace fossil preservation and ichnofabric suggests that the sediment was indeed firm. Evidence for this includes: (1) preservation of shallow tiers, (2) limited evidence of any mixed layer (see below), (3) trace fossil preservation on gutter casts that imply open burrow systems, and (4) sharp detail of trace fossils and delicate scratching of *Monomorphichnus* and *Rusophycus*.

The bypass environment of the Chapel Island Formation is not necessarily typical of the Lower Cambrian. However, owing to conditions in this setting, it is possible to detect the ubiquity of open burrows in the siltstone that otherwise would go undetected. The evidence for firm Cambrian substrates is not unique to this part of the Chapel Island Formation. In particular, exquisitely preserved *Rusophycus* and *Treptichnus* have been described from Cambrian–Lower Ordovician deposits worldwide (e.g., Crimes, 1975; Walter et al., 1989; Droser et al., 1994; Orlowski and Zylinska, 1996). This suggests that Early Cambrian mud and silt substrates, on the whole, were relatively firm and that through the terminal Proterozoic, Cambrian, and into the Early Ordovician, firm substrates in siliciclastic sediment were not uncommon. The importance of organic material in binding sediment is indisputable, but Cambrian substrates also likely would have been firm because of low levels of bioturbation. This is because bioturbation creates a more open sediment fabric leading to increased porosity and water content (e.g., Rhoads, 1970; Rhoads and Young, 1970). This effect is most pronounced in sediment of clay-silt grade; in a sandy substrate there may be no effect or even increased compaction as a result of bioturbation (Lee and Swartz, 1980). Rhoads and Young (1970) found that burrowed mud experienced a more than fivefold increase in sediment resuspension by volume than nonburrowed mud. Low levels of bioturbation would lead to more rapid dewatering and compaction of sediment and greater resistance to erosion.

The relative firmness of the mud also could explain the great abundance of unattached burrows. Hallam (1975) opined that floating and adhering styles of burrow preservation are probably rare. In the lower Chapel Island Formation, however, this type of preservation is common as a result of the bypass environment and firm substrates. This type of preservation, particularly adhered burrows, is common also in the Lower Cambrian of the Mickwitzia sandstone, Sweden (Jensen, 1997, e.g., fig. 41A), the Lükati Formation, Estonia (author's unpublished observations), the Wood Canyon Formation, western USA (Droser et al., 2001), and in the Cambro-Ordovician Bynguano Formation, New South Wales (Droser et al., 1994).

If the above argument concerning the importance of bioturbation to the consistency of silty sediment is correct, it follows that this type of preservation should become less common as the extent of bioturbation increases and, in particular, lead to a lessening in the preservation of shallow tiers in shallow marine environments. Thus, earliest Cambrian siltstone may have better preserved shallow tiers than those of typical deposits of later Phanerozoic strata and, hence, provide a relatively reliable record of the activity of early infauna. On the other hand, this type of preservation could be expected in later stressed settings with limited bioturbation. The nature of standard trace fossil descriptions in the literature makes it difficult to compile a detailed comparison with younger strata. Thus, further work is needed to test this prediction.

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