University of Alberta

Ichnology of the upper Toad and lower Liard formations, northeastern British Columbia: implications for infaunal recovery after the Permian-Triassic mass extinction

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science

Department of Earth and Atmospheric Sciences

Spring, 2012
Edmonton, Alberta

This thesis is dedicated to my parents, Toyoshi and Itsuko: for their love and support, I am eternally grateful.

ABSTRACT

The Middle Triassic upper Toad and lower Liard formations at Williston Lake in northwestern British Columbia contain a suite of highly diverse ichnofossils. The environmental distribution of the ichnofossils is wide, ranging from marine offshore to upper shoreface. Compared with the Lower Triassic ichnofossils in northeastern British Columbia, ichnofossils in the Toad-Liard interval are larger and contain more complicated tiering relationships. Despite this difference, offshore sediments in the Middle Triassic include less diverse ichnofossils with simple tiering relationships. Therefore, except in offshore environments, the bottom water condition in the Middle Triassic was healthy and habitable, unlike the Lower Triassic. Moreover, the Middle Triassic ichnology in the studied interval suggests that marine ichnofacies models are applicable other than offshore ichnofossils. This implies that recovery after the end-Permian extinction was environmentally and faunally incomplete in the Middle Triassic of the study area. Ichnology, therefore, is useful for studies of post-extinction recovery.

ACKNOWLEDGEMENTS

I would like to express my gratitude to many people for their role in the completion of my M.Sc. First of all, to both of my supervisors, Murray Gingras and John-Paul Zonneveld, who led me to the road of research and taught me how to walk the road. They supported the growth of my ideas and gave me guidance in the scientific research community. I am truly indebted and thankful to you both for the opportunity to become a part of the scientific community. Likewise, I would not have become a geologist without their goodwill, thoughtfulness, and insight. George Pemberton, you were my first introduction to the world of ichnology and sparked the flame I carried throughout my geological journey. No matter how many times I say thank you, it will never be enough. I am truly grateful.

I also would like to thank the members of Ichnology Research Group (IRG). Without them, I would lost be in the forest of science. First, to Luck McHugh, Chelsea Fefchak, Greg Baniak, and Jenna Philips, who helped me collect data and kept me entertained during fieldwork. Without their help, fieldwork wouldn't have been as interesting as it was. I thank Ryan King for for answering my countless questions, and for editing my long, dreary manuscript. Thanks to Greg Baniak, who argued with me about the manuscript and challenged my content and edits, for which I am thankful (now). To the other members of IRG, with whom I have argued about geological wonders and scientific thoughts, your presence has always encouraged me and brought a level of richness to my learning experience.

In addition to these scientific minds, I need to acknowledge a friend: Taku Yamanaka. You were the rock outside the world of geological science. Without your friendship, I would have lost my grip on sanity, buried in an avalanche of research, data, and manuscript writing. To you and to all my friends who took my mind off things and reminded me to enjoy life, I am thankful.

I also thank the Natural Sciences and Engineering Research Council of Canada for their generous financial support to John-Paul Zonneveld's grant.

Finally, I would like to express enormous gratitude to my wife, Ayumi Hyodo, who has loved, helped, and supported me these many years. Your presence and love were my energy. Without you to share them, the road, the journey, and the accomplishments of the M.Sc. would be empty. I love you.

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Sedimentology and stratigraphy

Fm	Formation	HCS	Hummocky cross-stratification
Mbr	Member	SCS	Swaley cross-stratification
L	Lower	TCS	Trough cross-stratification
U	Upper	OS	Offshore
Jr	Jurassic	OT	Offshore transition
Pm	Permian	LSF	Lower shoreface
FS	Flooding surface	USF	Upper shoreface
MFS	Maximum flooding surface	Sls	Siltstone
SWB	Storm wave base	Ss	Sandstone
FWWB	Fair-weather wave base	mya	million years ago

Ichnofossil abundance

a	abundant	p	present
c	common	r	rare

Ichnofossil associations

PS	*Phycosiphon-Scalarituba* association
CST	*Cruziana-Spongeliomorpha-Thalassinoides* association
DP	*Diplocraterion-Palaeophycus* association
SP	*Skolithos-Palaeophycus* association

Ichnogenus

An	*Anconichnus*	Pa	*Palaeophycus*
Ar	*Arenicolites*	Ph	*Phycodes*
At	*Asteriacites*	Py	*Phycosiphon*
As	*Asterosoma*	Pl	*Planolites*
Be	*Bergaueria*	Rh	*Rhizocorallium*
Co	*Conichnus*	Ro	*Rosselia*
Cr	*Cruziana*	Ru	*Rusophycus*
Cy	*Cylindrichnus*	Sc	*Scalarituba*
Di	*Diplocraterion*	Sl	*Scolicia*
Gc	*Gyrochorte*	Si	*Siphonichnus*
Gy	*Gyrolithes*	Sk	*Skolithos*
He	*Helminthoida*	Sp	*Spongeliomorpha*
Hl	*Helminthopsis*	Te	*Teichichnus*
Li	*Lingulichnus*	Th	*Thalassinoides*
Lk	*Lockeia*	Tp	*Treptichnus*
Mc	*Monocraterion*	Un	*Undichna*
Mm	*Monomorphichnus*		

Cardinal direction

NW	Northwest	NE	northeast

Symbols

▤	shale/ laminated siltstone
▤	Sitly sandstone
▤	hummocky cross-stratified sandstone
░	massive sandstone
░	calcareous sandstone
░	swelay cross-stratified sandstone
▦	brachiopod bioclastic limestone
▦	encrinite (crinoid bioclastic)
▦	bioclastic limestone

CHAPTER 1

INTRODUCTION

Atypically abundant ichnofossil assemblages occur in the Middle Triassic of northeastern British Columbia (e.g., Zonneveld et al., 1997; Zonneveld, 1999, 2008). These trace fossil associations comprise an invaluable dataset that provides insight into marine diversity and faunal distribution during a poorly understood interval in earth history. Although considerable attention has been given in recent years to lower Triassic trace and body fossil associations and their relationship to faunal recovery after the terminal Permian mass extinction (Twitchett and Wignall, 1996; Pruss and Bottjer, 2004; Fraizer and Bottjer, 2005; Beatty et al., 2008; Bottjer et al., 2008; Mata and Woods, 2008; Mata and Bottjer, 2010; Zonneveld et al., 2010), minimal attention has been given to the Middle Triassic (Zonneveld et al., 1997, 2001, 2007; Zonneveld and Greene, 2010; Greene et al., 2011). This interval is integral to discussions of extinction recovery since many prior studies have indicated that extinction recovery was delayed until the end of the Lower Triassic (Twitchett, 1999; Erwin, 2001; Twitchett and Barras, 2004). Analyses of Middle Triassic faunal trace and body fossil associations provide the only concrete evidence regarding the health of Middle Triassic ecosystems and thus are the most appropriate test of post-extinction faunal recovery.

This study provides an assessment of Middle Triassic trace fossil assemblages in a study area located on the northwestern margin of Pangea in a mid paleolatitudinal setting. Diverse and abundant ichnofossil assemblages within the study area provide evidence that Middle Triassic environments had become more hospitable than those of the Early Triassic. The analyses of these ichnofaunas provided herein contribute substantively to the understanding of environmental and faunal conditions, and to the timing of post-extinction marine faunal recovery after the end-Permian mass extinction.

PREVIOUS WORK

Triassic strata occur extensively in outcrop and the subsurface of western Canada (Barss et al., 1964). The Triassic rocks in western Canada were first recognized by Selwyn in 1875 on the Peace River (Selwyn, 1877). F. H. McLearn conducted the first detailed paleontological investigations of Triassic outcrops in western Canada (McLearn, 1918, 1921, 1930; Tozer, 1984). His work established the initial biostratigraphic framework for the Triassic of western Canada (McLearn, 1918, 1921, 1930, 1940, 1941, 1945, 1947; McLearn and Kindle, 1950). McLearn's works, along with his extensive ammonoid and bivalve collections, have become the foundation for subsequent research (Tozer, 1967, 1984, 1994; Orchard and Tozer, 1997). Tozer (1967, 1984, 1994) summarized the Triassic biostratigraphy of western Canada. Orchard and Tozer (1997) utilized conodonts for Triassic biostratigraphy, providing further improvement of Triassic biochronology in western Canada. The stratigraphy of Triassic strata in the Peace River area was investigated by the Geological Survey of Canada in the 1960s and 1970s and summarized in a series of memoirs, bulletins and field guides (Irish, 1965; Gibson, 1971, 1974). Paleontological investigations in the area have focused primarily on taxa used for biostratigraphic purposes, including bivalves, ammonoids and conodonts (McLearn, 1940, 1941, 1947; Tozer, 1967; 1984; Orchard and Tozer, 1997). The inter-calibrated ammonoid-conodont zonation developed by Orchard and Tozer (1997) has been particularly useful in developing a precise, regional biostratigraphy and establishing a global Triassic biostratigraphic framework.

Trace fossils have been used as a practical tool in analyzing the environmental models of sedimentary deposits for about five decades. Seminal work on the grouping of ichnotaxa within recurrent environmentally related assemblages (i.e., ichnofacies) was carried out by Adolf Seilacher in the 1950s and 1960s (Seilacher, 1953, 1964). Recent studies have established that an integrated approach using the principles of sedimentology, stratigraphy and paleontology (including ichnology) is the most robust approach for detailed reconstruction of depositional environments (Osgood, 1970; Miller, 1984; Saunders, 1988; Pemberton and MacEachern, 1995; Gingras et al., 1998).

The upper Toad and lower Liard formations of northeastern British Columbia are Middle Triassic (Ladinian) in age (Fig. 1-1) (Orchard and Tozer, 1997; Zonneveld, 1999). Both formations are fossiliferous, yielding abundant body fossils and trace fossils (Zonneveld et al., 1997; Zonneveld, 1999, 2001, 2008). Despite the high abundance and diversity of trace fossils in these strata, early studies reported minimal ichnological data, and focused instead on physical sedimentological characteristics and stratigraphic correlation (Gibson, 1971, 1974). More recently, several ichnological studies have been completed on trace fossils from the Toad and Liard formations; however, these have focused on specific taxa or environmental settings rather than encompassing the ichnological totality of the units (Zonneveld et al., 1997; Zonneveld, 2001; Zonneveld et al., 2001, 2002; Zonneveld and Pemberton, 2003; Zonneveld et al., 2007; Greene et al., 2011). Numerous issues remain unresolved for the Middle Triassic strata of western Canada. These include complete ichnological treatment of the Toad and lower Liard formations and assessment of the depositional environment and ecological environment during deposition of the Toad and Liard formations. This study seeks to fill these knowledge gaps by providing a detailed analysis of trace fossils, as well as associated physical sedimentological characteristics, in the upper Toad and lower Liard formations.

THE END-PERMIAN MASS EXTINCTION AND TRIASSIC ICHNOLOGY

Five major mass extinctions have been recognized in the history of Earth: 1) end-Ordovician; 2) Late Devonian; 3) end-Permian; 4) end-Triassic; and 5) end-Cretaceous. Biodiversity of marine faunas decreased during these mass extinctions and increased afterward, in so-called faunal recovery intervals. The end-Permian is recognized as the most severe of these extinctions, resulting in the demise of 90 - 96 % of skeletonized marine species, and approximately 83 % of marine genera (Raup, 1977; Sepkoski, 1989; Erwin, 1993; Benton, 1995). The recovery of fauna after the end-Permian mass extinction took place during Triassic (Sepkoski, 1981). Triassic culminated with another of the five major biotic perturbations (Raup, 1977).

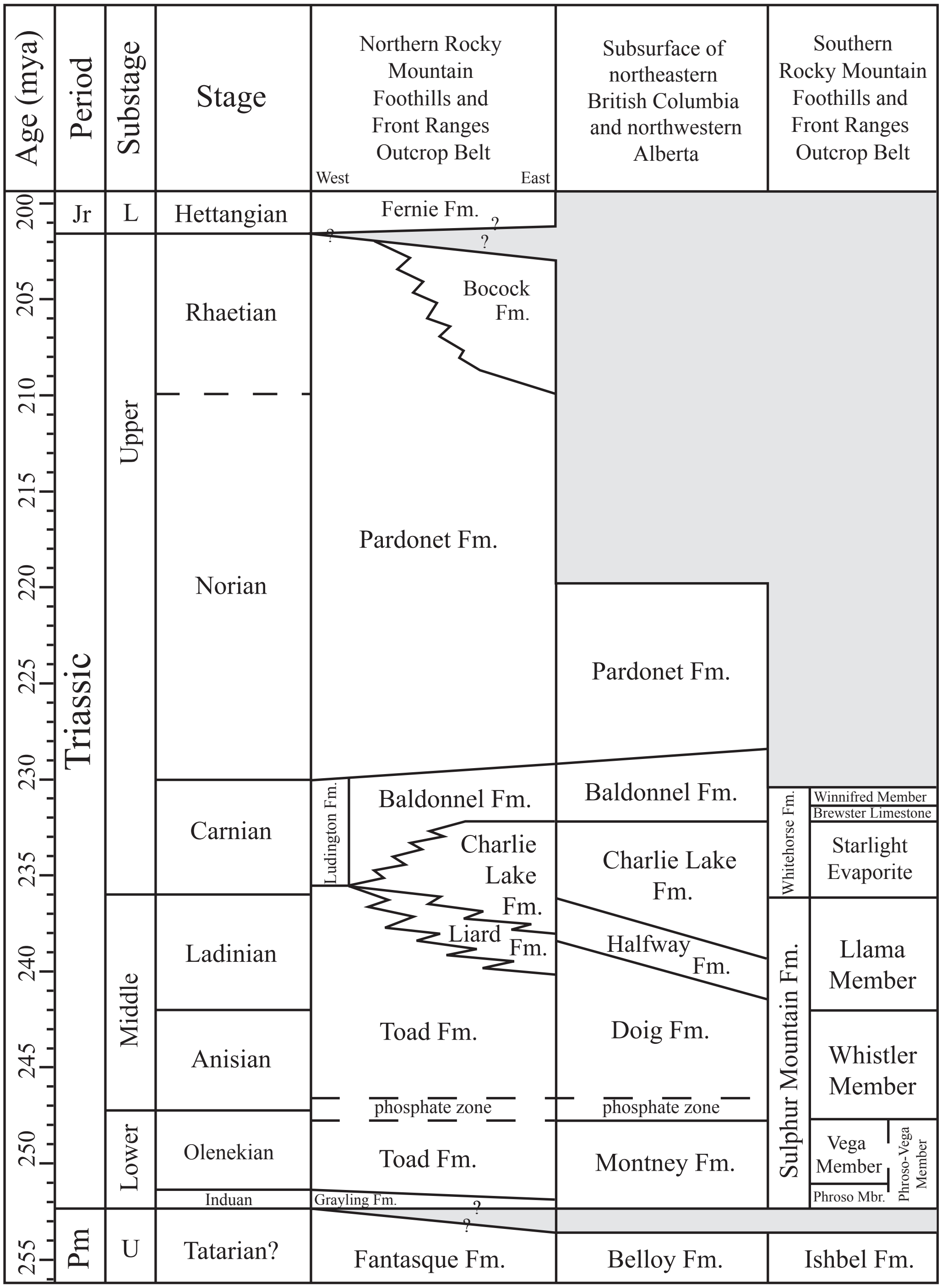

FIGURE 1-1—Triassic stratigraphic nomenclature, subsurface and outcrop in northeastern British Columbia, northwestern Alberta and Rocky Mountains (after Zonneveld, 1999, 2008; Orchard and Zonneveld, 2009; Mundi et al., 2010; Hüsing et al., 2011). Grey indicates strata missing by unconformity. Pm = Permian, Jr = Jurassic, L = lower, U = upper, Fm. = Formation, Mbr. = Member, mya = million years ago.

Sepkoski (1981) suggested that Phanerozoic marine animals can be divided into three faunas in geologic history: Cambrian fauna, Paleozoic fauna and Mesozoic-Cenozoic ("modern") fauna. Sepkoski (1984) provided the diversification model of marine animals, which has been summarized in the following. In the model (Fig. 1-2), the end-Permian extinction lowered all three faunas into 7 % of their original diversity (Sepkoski, 1984). This extinction affected the Paleozoic fauna more severely than more recently evolved ("modern") fauna (Fig. 1-2) (Sepkoski, 1984). Afterward, in the Early Triassic, both the remaining Paleozoic and "modern" faunas began rebounding rapidly (Sepkoski, 1984); the rate of the Paleozoic fauna recovery was as rapid as the "modern" fauna (Fig. 1-2). Subsequently, the end-Triassic mass extinction reduced the diversity of the Paleozoic fauna to slightly lower than that after the end-Permian mass extinction although the total faunal diversity in the early Jurassic was higher than that in the early Triassic (Sepkoski, 1984; Greene et al., 2011). After the end-Triassic mass extinction, Paleozoic fauna rebounded but started to decrease in diversity, whereas the modern fauna rebounded rapidly (Sepkoski, 1984). Consequently, the end-Permian and end-Triassic mass extinctions influenced both the turnover of dominant fauna after the end-Permian extinction, and the biological diversity patterns of the Mesozoic (Sepkoski, 1981; 1984). The Triassic is the key to understanding how the Paleozoic fauna declined and was subsequently replaced by the "modern" fauna.

Several studies showed the influence of the end-Permian extinction on the ichnological record from United States, Italy, and Canada (Twitchett and Wignall, 1996; Twitchett, 1999; Pruss et al., 2004; Pruss and Bottjer, 2004; Beatty et al., 2008). These studies recognized overall reduction of trace fossil size and diversity in the Early Triassic ichnofaunas. Although there are several studies on the impact of the end-Permian mass extinction on burrowing fauna, few studies have been conducted on how the turnover of dominant fauna after the end-Permian extinction influenced the characteristics of Triassic trace fossils (e.g., Zonneveld et al., 2002; Zonneveld and Pemberton, 2003; Zonneveld et al., 2007). Middle Triassic strata in western Canada include highly diverse and abundant

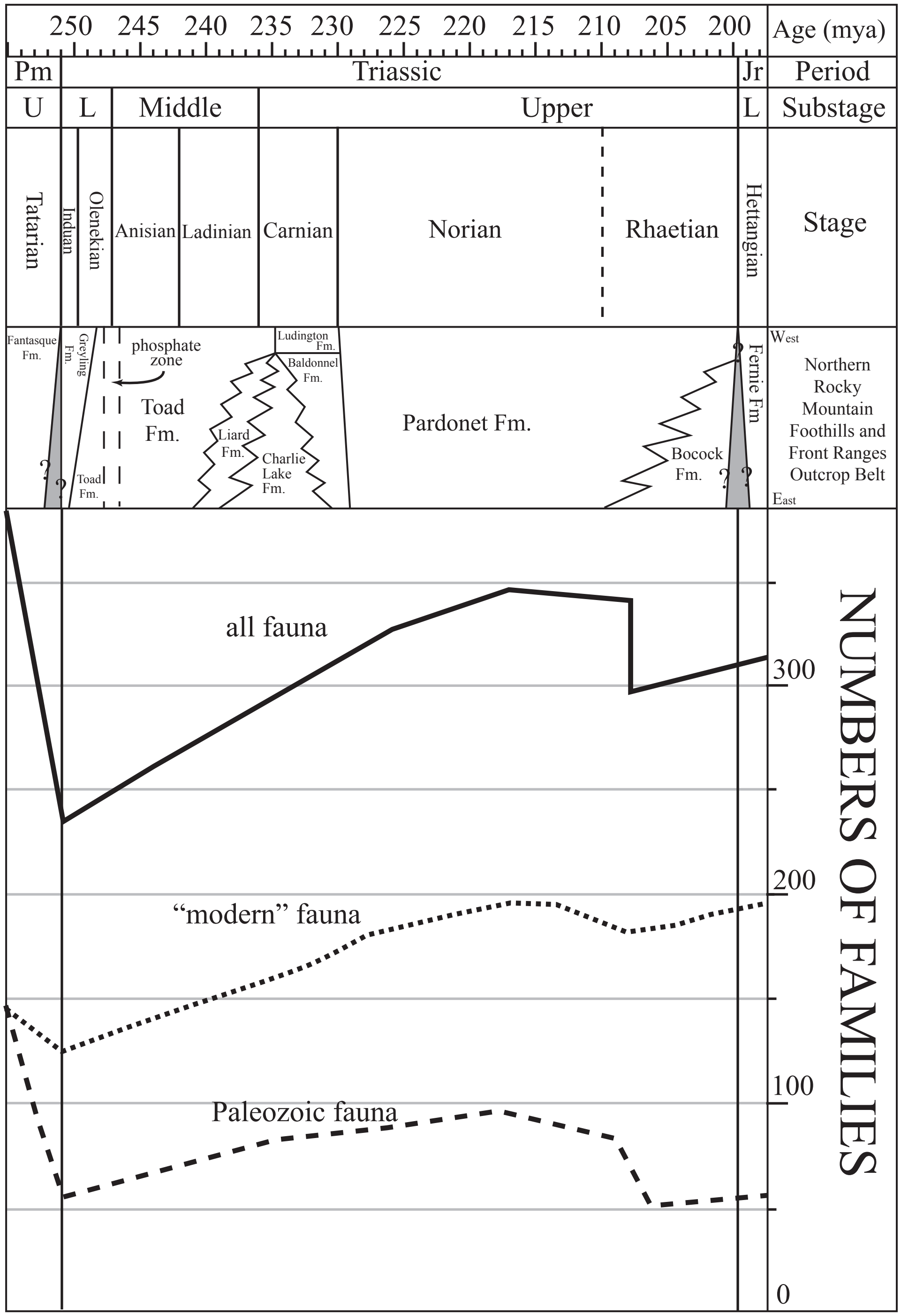

FIGURE 1-2—Triassic stratigraphy of the study area and numbers of families during Triassic (after Sepkoski, 1984; Zonneveld, 1999, 2008; Mundi et al., 2010; Hüsing et al., 2011). Grey indicates missing strata by unconformity. In the graph, a thick solid line indicates all fauna, a short-dashed line indicates Mesozoic-Cenozoic ("modern") fauna, and a long-dashed line indicates Paleozoic fauna. Pm = Permian, Jr = Jurassic, U = upper. L = lower, Fm = Formation, Mbr = Member, mya = million years ago.

trace fossil assemblages (Zonneveld, 1999, 2008). It is uncertain why Middle Triassic benthic ecology in western Canada established highly diverse ichnofossil assemblages. This study seeks to elucidate the ecology of this succession using a detailed analysis of ichnology in the Williston Lake area of northeastern British Columbia.

This study has three main objectives: 1) to describe and interpret the trace fossils of the upper Toad and lower Liard formations as a whole; 2) to discuss environmental and ecological implications of the aftermath of the end-Permian extinction from trace fossils; and 3) to contribute ichnofossil analyses to an understanding of ichnofaunas during post-extinction faunal recovery.

STUDY AREA

This thesis focuses on the Williston Lake area, which is located in northeastern British Columbia. Four outcrop sections (Brown Hill, Folded Hill, Beattie Ledge and Aylard Creek) along Williston Lake were chosen for this study (Fig. 1-3). Data from the upper Toad and lower Liard formations at the studied outcrops were collected through detailed ichnological analyses associated with subordinate sedimentological analyses of mainly ichnofossil-bearing rocks. Ichnological analysis included identifying ichnotaxa, measuring trace size and relative abundance, and defining an association of ichnofossils and their patterns. Sedimentological analysis concentrated mainly on characteristics (e.g., grain size and type, sorting, bed thickness and grading, the nature of bedding contacts, physical sedimentary structures) of host rocks of observed ichnofossils. These host rock characteristics were compared with previous studies (Zonneveld et al., 1997; Zonneveld, 1999; Zonneveld et al., 2001, 2002; Zonneveld, 2008). Ichnological data was incorporated with sedimentology to understand and interpret environmental settings of ichnofossils within the upper Toad and lower Liard formations. Collected ichnological data were qualitatively and semi-quantitatively assessed in order to discuss implications of ichnofossils.

OUTLINE

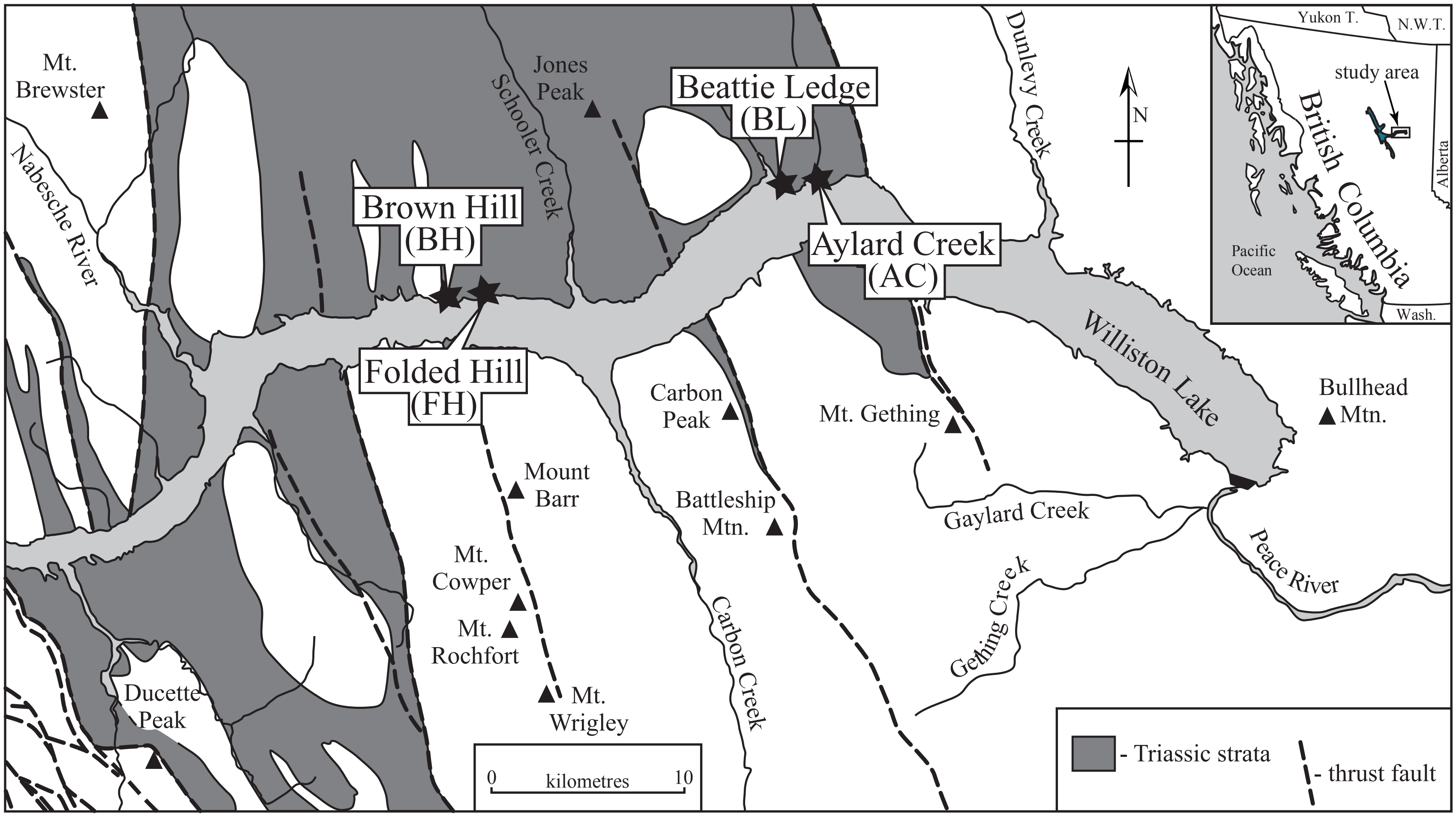

FIGURE 1-3—Location map of the study area (after Zonneveld, 2008). Four outcrop locations along the Peace Reach of Williston Lake are denoted.

Chapter 2 establishes associations of ichnofossils from the upper Toad and lower Liard formations of four outcrops based on ichnology, ichnotaxa contents, sedimentological characteristics of host rocks, and interpreted depositional environment. Implications of depositional environments are speculated from these ichnofossil associations, and the environmental implications of ichnofossils are discussed.

Chapter 3 describes observed ichnotaxa from the study interval. Interpretations of each ichnotaxon and defined ichnofossil associations are utilized to evaluate applicability of the ichnofacies models to the study interval. Ethological implications of the studied succession are discussed. Influences of post-extinction recovery on ichnofossils are argued on the basis of applicability of ichnofacies and ethological implications of ichnofossils.

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CHAPTER 2

MIDDLE TRIASSIC SHALLOW MARINE ICHNOLOGY OF WESTERN CANADA WITHIN SILICICLASTIC SEDIMENTS AND IMPLICATIONS OF POST-EXTINCTION RECOVERY

INTRODUCTION

The end of the Permian Period experienced the greatest mass extinction event in Earth's history (Raup, 1977; Raup and Sepkoski, 1982; Sepkoski, 1989; Erwin, 1993; Benton, 1995). Amongst skeletonized marine taxa, this mass extinction resulted in the elimination of over 90% of marine species and over 80% of marine genera (Raup, 1977; Erwin, 1993; Benton, 1995). Although the contributing causes for this extinction remain the focus of considerable debate, it is now well established that global, shallow-water anoxia played a seminal role (e.g., Hallam, 1991; Wignall and Hallam, 1992; Twitchett and Wignall, 1996; Hays et al., 2007). Globally pervasive shallow water anoxia developed during the Late Permian and remained widely distributed throughout the Early Triassic (Wignall and Hallam, 1992; Twitchett and Wignall, 1996).

The Early Triassic has been considered by some authors to be an interval of recovery (or radiation) after the extinction (Sepkoski, 1981, 1984). However, it has been shown by many recent practitioners that the recovery was delayed by several million years (e.g., Knoll et al., 1996; Twitchett, 1999). By the Middle Triassic, large-scale amelioration of adverse environmental conditions had been inferred from the Triassic beds of northern Italy and western United States with radiations of marine taxa (i.e., conodonts and mollusks) (Twitchett and Wignall, 1996; Twitchett, 1999; Twitchett and Barras, 2004; Bottjer et al., 2008). The Triassic recovery was relatively short-lived in that another biotic crisis quickly followed (Sepkoski, 1981, 1984).

Paleontological analyses of marine fossils have shown that major extinction events were followed by intervals of faunal rebound that resulted in major shifts in the dominant fauna (Sepkoski, 1981, 1984). Sepkoski (1981) suggested that marine animals throughout geological history be sub-divided into three related groupings or ‘faunas’: the ‘Cambrian fauna’, ‘Paleozoic fauna’, and ‘Mesozoic-Cenozoic (“modern”) fauna’. The Cambrian fauna is dominated by trilobites with polychaetes, monoplacophorans, inarticulate brachiopods, and abundant hyolithids (Sepkoski, 1981). The Paleozoic fauna is dominated by articulate brachiopods, crinoids, ostracodes, cephalopods and anthozoans, with lesser abundances of stenolaemates, gastropods, stelleroids and bivalves. The “modern” fauna consists mainly of gastropods and bivalves associated with lesser bony fish, malacostracans, and echinoids (Sepkoski, 1981).

The end of the Permian demarcates the boundary between dominance of the Paleozoic and “modern” fauna, however there is some overlap (Sepkoski, 1981, 1984). During the later Early Triassic (Olenekian) and Middle Triassic, diversity of elements characteristic of both the Paleozoic and “modern” faunas started rebounding rapidly (Sepkoski, 1984; Greene et al., 2011). However, by the late Triassic, the “modern” fauna diversified more rapidly than the Paleozoic fauna, and the “modern” fauna became dominant (Sepkoski, 1984). At the end-Triassic mass extinction, the diversity of the Paleozoic fauna decreased more severely than the diversity of the “modern” fauna (Sepkoski, 1981, 1984).

After the end-Triassic mass extinction, the Paleozoic fauna initially expanded rapidly but subsequently diminished (Sepkoski, 1981, 1984). The diversity of the Paleozoic fauna during the Mesozoic and Cenozoic interval never re-attained pre-Triassic levels of diversity (Sepkoski, 1981, 1984). In contrast, the “modern” fauna rebounded rapidly in the Early Jurassic and radiated through the later Mesozoic and Cenozoic (Sepkoski, 1984). Consequently, both the end-Permian and end-Triassic mass extinctions played important roles in the post-Permian turnover of dominant faunas and the pattern of diversity during the Mesozoic (Sepkoski, 1984). The Triassic Period comprises a transitional interval between periods of faunal dominance (Sepkoski, 1984; Fraiser and Bottjer, 2007; Greene et al., 2011). It is, therefore, critical to study Triassic fossils in order to understand both the pattern of marine faunal recovery and the factors that led to the shift from Paleozoic style faunas to the “modern” fauna.

The paleontology of the end-Permian extinction has been well studied, revealing the rapid disappearance of many pre-extinction organisms and the gradual appearance of new taxa (Raup, 1977; Sepkoski, 1989; Erwin, 1993; Benton, 1995). As a result of this faunal turnover, ichnofaunal characteristics, including the composition and variety of ichnofossils and the environmental distribution of individual traces, were strongly affected as well (e.g., Zonneveld, 2011). However, ichnological studies through the Permian–Triassic extinction and recovery interval are much fewer than paleontological studies (Twitchett and Wignall, 1996; Twitchett, 1999; Beatty et al., 2008; Zonneveld et al., 2010b). Recent analyses have demonstrated a reduction in trace fossil size and a drop in ichnodiversity in the Early Triassic, similar to that recorded for body fossils (Hayami, 1997; Zonneveld et al., 2010a, 2010c). Twitchett and Wignall (1996) reported that some Lazarus taxa had not reappeared in the latest Lower Triassic in northern Italy. However, few studies on Middle Triassic ichnofossils are available (Knaust, 2004; Rodríguez-Tovar et al., 2007; Mørk and Bromley, 2008; Rodriguez-Tovar and Perez-Valera, 2008).

Unlike body fossil analyses, ichnological studies provide clear *in situ* insight into depositional stresses such as oxygenation, temperature, salinity, and sedimentation rate, among many others (e.g., Gingras et al., 2007). Given these capabilities, a better understanding of ichnological characteristics is required of post-end-Permian studies to understand ecosystems from different views.

The present study focuses on shallow marine (proximal offshore, offshore transition and shoreface) trace fossils preserved in northeastern British Columbia, Canada. The focus is on discussing the ichnological attributes preserved with the sediments and their implications for the ecology of Middle Triassic benthic communities.

Middle Triassic Stratigraphy

Triassic strata in western Canada occur within the Rocky Mountain Front

Ranges and Foothills and subsurface as a westward-thickening package of marine and marginal marine sediments (Barss et al, 1964). The Peace River-Williston Lake area was a major depocentre during the Triassic (Gibson and Edwards, 1990). There are three nomenclatural systems for Triassic rocks in Alberta, and British Columbia (Fig. 2-1): two outcrop nomenclatures (northern and southern Rocky Mountain Front Ranges and Foothills, separated by the Pine River in British Columbia), and one for the subsurface of Alberta and British Columbia. The study area occurs in the northern outcrop area (Fig.2-2). The Triassic formations from base to top in the study area consist of the Grayling, Toad, Liard, Charlie Lake, Baldonnel (and laterally equivalent Ludington) and Pardonet formations (Gibson and Edwards, 1990; Edwards et al., 1994; Zonneveld, 2008; Fig. 2-3).

The study interval consists of the interfingering upper Toad Formation and lower Liard Formation. The Toad Formation was first described by Kindle (1944) in northeastern British Columbia. At its type area, the Toad Formation consists of fissile, dark grey, brown, and black silty shale to siltstone, thinly bedded calcareous siltstone, massive sandy siltstone, and dark silty limestone lenses (Kindle, 1944, 1946). Throughout British Columbia, the Toad Formation ranges in age from Lower Triassic (Induan) through Middle Triassic (Anisian-Ladinian) (Tozer, 1994; Orchard and Tozer, 1997). The upper Toad Formation consists of dark grey, fissile, dolomitic to calcareous siltstone, silty limestone and dolostone, and very fine- to fine-grained sandstone (Gibson, 1971, 1975; Zonneveld, 1999, 2008). The proportion of sandstone to siltstone increases towards the top of the Toad Formation (Zonneveld, 1999).

Kindle (1946) first defined a 180 m succession of calcareous sandstone and sandy limestone above the Toad Formation as the Liard Formation in the area of the Toad and Liard rivers, in northernmost British Columbia. The Liard Formation of the study area generally consists of very fine- to fine-grained (and rarely medium-grained) sandstone and bioclastic packstone and grainstone (Zonneveld, 2008). The Liard Formation is primarily Middle Triassic (Anisian-Ladinian) in age (Tozer, 1994; Orchard and Tozer, 1997) although recent

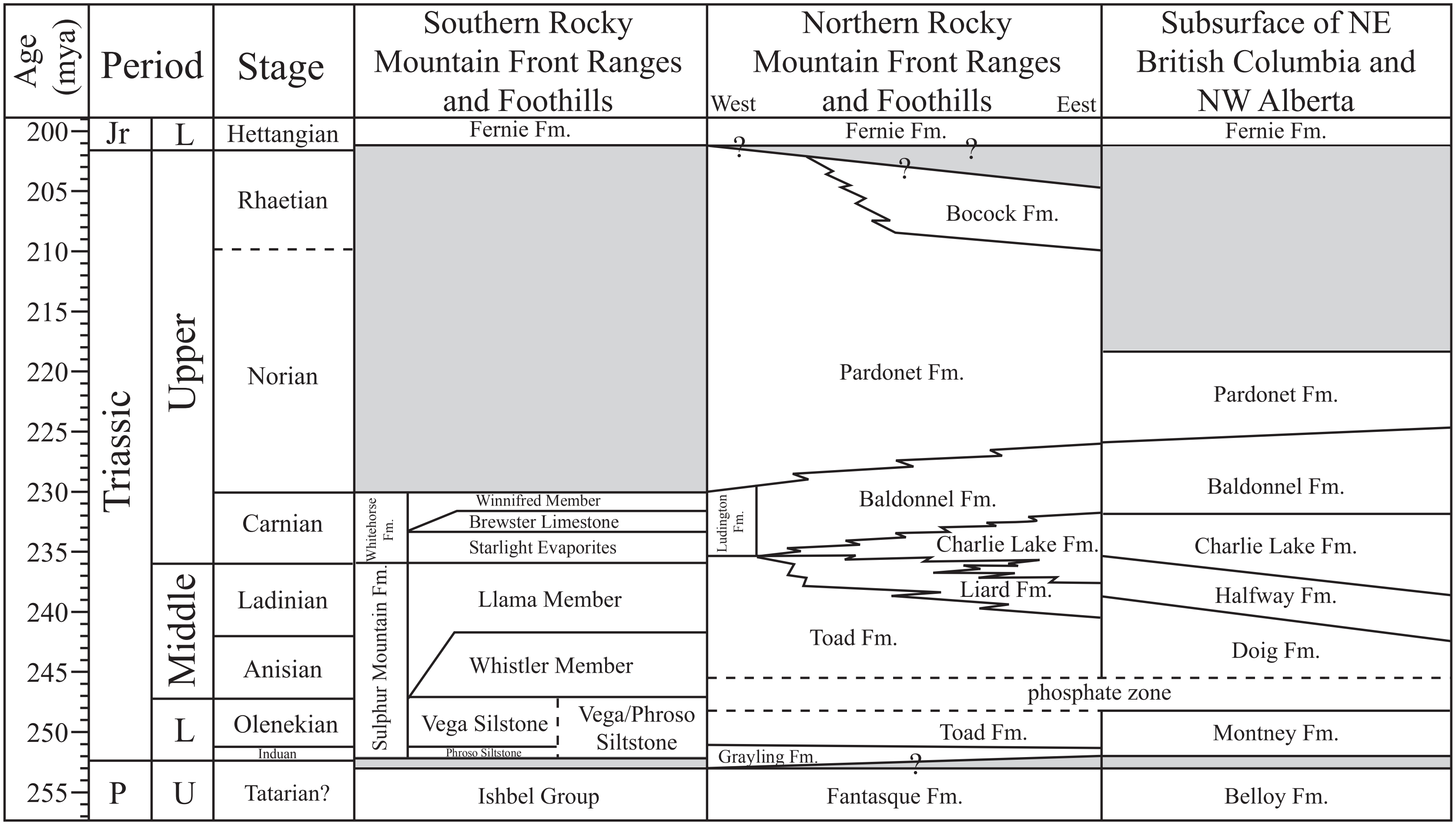

FIGURE 2-1—Triassic nomenclatures of western Canada (after Edwards et al., 1994; Zonneveld, 2008; Mundi et al., 2010; Hüsing et al., 2011). Grey spaces indicate lack of beds. P = Permian, U = upper, Jr = Jurassic, L = lower. Fm = Formation, mya = milion years ago, NE = Northeastern, NW = Northwestern.

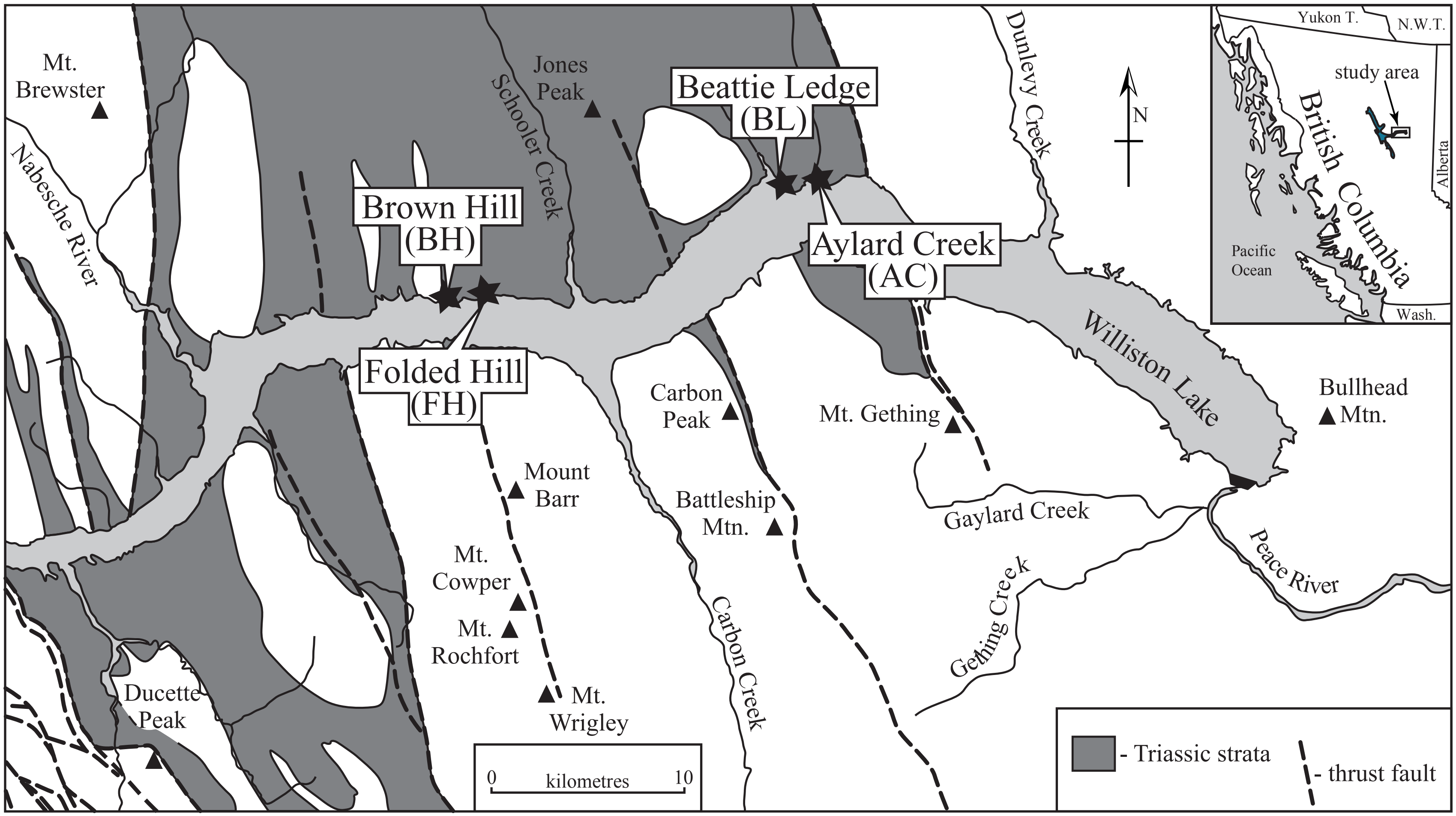

FIGURE 2-2—Location map of the study area (after Zonneveld, 2008). Four outcrop locations along the Peace Reach of Williston Lake are denoted.

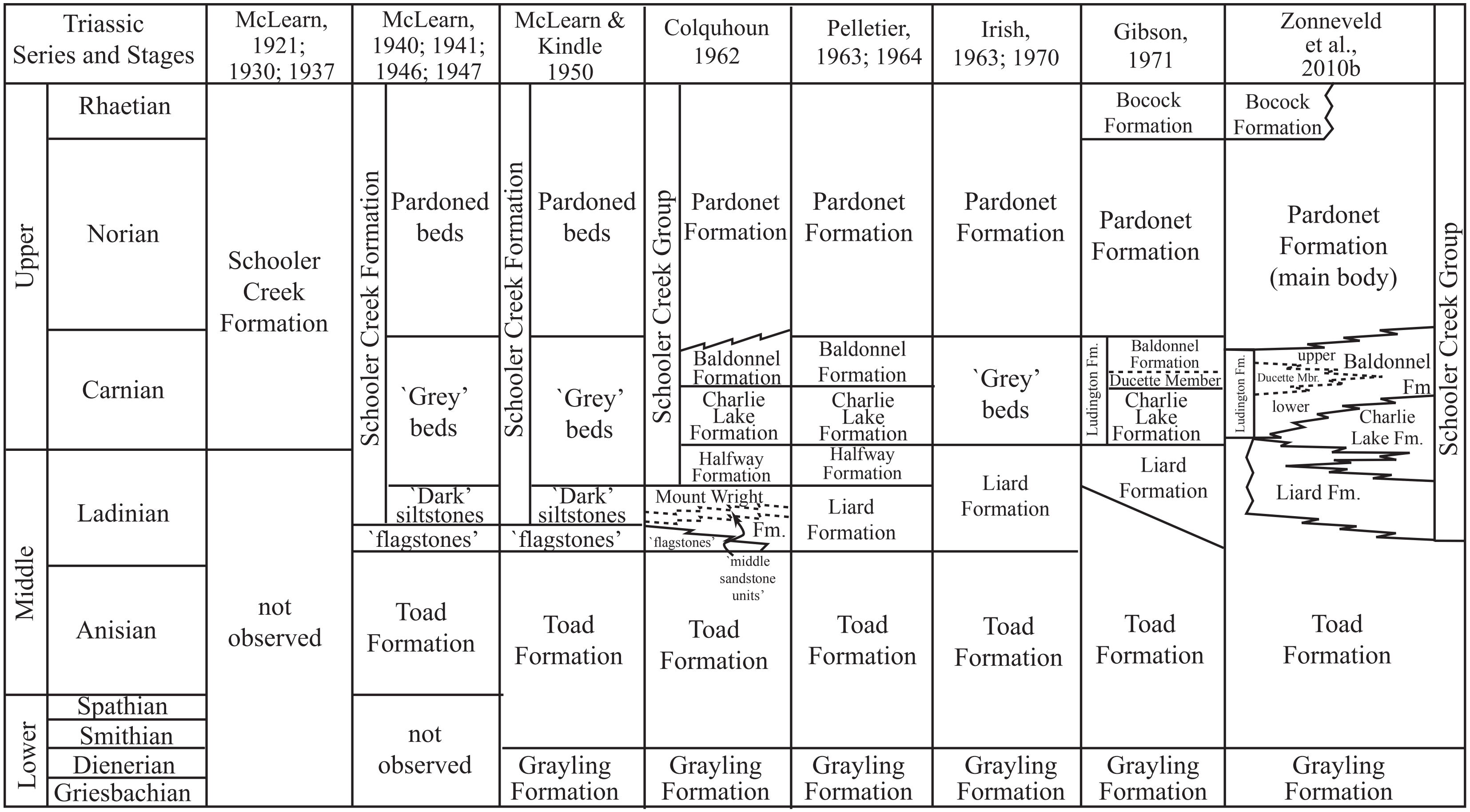

FIGURE 2-3—Evolution of Triassic nomanclature in the Peace River -Williston Lake area (after Zonneveld 2008).

revisions to Triassic stages (Loriga-Broglio et al., 1999) has reallocated the uppermost Liard Formation to the lowermost Upper Triassic (Lower Carnian). The present study interval consists of heterolithic siltstone and sandy siltstone beds, very fine to medium-grained sandstone, and bioclastic packstone and grainstone. The age of the study interval has been established based on biochronology of ammonoids and conodonts, correlation between outcrop sections, stratigraphic positioning of lithostratigraphic units and outcrop gamma scans, and is limited to the Ladinian (Tozer, 1994; Orchard and Tozer, 1997; Zonneveld, 1999, 2008). Both the upper Toad and lower Liard formations are fossiliferous, yielding abundant body fossils such as brachiopods, ammonoids, bivalves, gastropods, crinoids, echinoids, ophiuroids, decapods, crustaceans, and vertebrate fragments, in addition to diverse trace fossils (Zonneveld et al., 1997; Zonneveld, 1999, 2001, 2008).

Study Area

The study area is located in northeastern British Columbia, Canada, along the Peace Reach of Williston Lake in the Muskwa Range area of the Rocky Mountain Front Ranges and Foothills (Fig 2-2). During the Triassic, the study area was situated along the northwestern margin of Pangaea at ~30°N (Habicht, 1979; Wilson et al., 1991).

The Peace River region was an area of considerable tectonic activity throughout much of the history of the Western Canada Sedimentary Basin (O'Connell, 1994) and indeed comprises the main depocentre of Triassic strata in the Western Canada Sedimentary Basin (Gibson and Edwards, 1990). Although this area was a topographic high (Peace River Arch) during much of the Paleozoic, it collapsed during the Carboniferous and remained a major embayment and depocentre throughout the Triassic (O'Connell, 1994).

Analyses of aeolian sandstone units in the Charlie Lake Formation suggest dominant paleo-wind direction from the northeast (Arnold, 1994). The climate was likely arid, as indicated by evaporative minerals and solution collapse breccias in marginal marine strata of the Middle to Upper Triassic Charlie Lake

Formation, which interfingers with the Toad and Liard formations in the study area (Zonneveld et al., 1997, 2001). Physical sedimentary structures indicate that the paleo-shoreline during deposition of the shallow marine Liard Formation was oriented overall northwest-southeast (Pelletier, 1965). The shoreline occurred in a high-energy setting with strong longshore currents likely generated from the north (Pelletier, 1965; Zonneveld et al., 1997). Despite suggestions of minimal affect of tectonism on the Triassic deposition in western Canada (Gibson and Barclay, 1989), more recent studies have illustrated the affects of syndepositional tectonism on Middle Triassic strata in western Canada (Wittenberg, 1992; 1993; Evoy and Moslow, 1995; Caplan and Moslow, 1997; Evoy, 1997). In summary, the Middle Triassic of Alberta and British Columbia was deposited in shallow marine to terrestrial environments under arid, somewhat tectonically active conditions with longshore currents from the northwest and dominant winds from the northeast.

Methods and datasets

The study area is characterized by both excellent bedding plane and vertical exposures. This study focuses on the ichnology and sedimentology of four main outcrop sections through the upper Toad and lower Liard formations: Brown Hill, Folded Hill, Beatty Ledge and Aylard Creek (Figs. 2-2). The thickness of the study interval varies between localities. Depositional environments within the study interval range from offshore through offshore transition, lower shoreface and upper shoreface to intertidal and supratidal (Zonneveld et al., 1997; Zonneveld, 1999; Zonneveld et al., 2001; 2008). However, not all depositional environments are present at each location. Each outcrop exhibits an overall coarsening upward trend composed of numerous smaller scale coarsening-upward and/or shallowing-upwards successions.

Ichnological observations in this study included ichnotaxonomy, size measurements, relative abundance, diversity, and the composition and distribution of ichnofossils in different environments. Physical sedimentological data (i.e., lithology, bed thickness, physical structures, body fossil content) were collected, and collated with facies analyses completed in previous studies (Zonneveld et al., 1997; Zonneveld, 1999, 2001; Zonneveld et al., 2001, 2002; Zonneveld, 2008). The observed Facies of this study are listed (Table 2-1). Sedimentological analysis concentrated mainly on grain size, grading, descriptions of bedding contacts and identification of primary physical sedimentary structures in association with ichnological descriptions. The stratigraphy of the four outcrops is represented in Fig. 2-4, 2-5, 2-6 and 2-7.

All ichnotaxa identified within the study interval are listed in Table 2-2. Sizes of burrows are provided where possible. For vertical forms length indicates burrow depth. Both burrow width and length include lining thickness. Bioturbation intensity was observed on bedding cross-section with ichnofabric indices (Droser and Bottjer, 1986) and/or bedding-plane bioturbation indices (Miller and Smail, 1997) except for beds with poorly preserved cross-sectional and/or bedding plane surfaces.

During colonization process, settlement of organisms is dependent upon accessibility to an ecospace and previous residents of the ecospace (e.g., Brenchley, 1982; Commito, 1982). As colonization takes place, faunas naturally distribute in clumps (e.g., Lloyd, 1967; Sasaki, 1997). Moreover, previously formed trace fossils can be destroyed by newer ones or during digenesis (e.g., Goldring, 1965; Austin and Bottjer, 1982; Bromley, 1996). These aspects made establishments of statistical parameters of ichnofossil distribution and abundance difficult and incomplete. Consequently, absolute numbers of ichnofossils or each ichnotaxon are not statistically useable without interpretation. Thus, qualitative terminology is applied in this study. Classifications are as follows: 1) rare (less than 5 specimens), 2) present (5 - 30 specimens), 3) common (31 - 50 specimens), 4) abundant (> 50 specimens) out of the overall study interval. All the abundant ichnotaxa occur at all four outcrop sites, commonly at multiple levels. Relative abundances presented in Table 2-2 apply for the overall study interval. Ichnofossil associations were identified based on recurrent associations of co-occurring ichnotaxa within sedimentologically similar beds.

TABLE 2-1—Facies of the upper Toad and lower Liard formations in the Williston Lake area, northeastern British Columbia (after Zonneveld et al., 1997; Zonneveld, 1999; Zonneveld et al., 2001; Zonneveld, 2008). An = *Anconichnus*, Ar = *Arenicolites,* At = *Asteriacites,* As = *Asterosoma*, Be = *Bergaueria*, Co = *Conichnus*, Cr = *Cruziana*, Cy = *Cylindrichnus*, Di = *Diplocraterion*, Gc = *Gyrochorte*, Gy = *Gyrolithis*, He = *Helminthoidia*, Hl = *Helminthopsis*, Li = *Lingulichnus*, Lk = *Lockeia*, Mc = *Monocraterion*, Mm = *Monomorphichnus*, Pa = *Palaeophycus*, Ph = *Phycodes*, Py = *Phycosiphon*, Pl = *Planolites*, Rh = *Rhizocorallium*, Ro = *Rosselia*, Ru = *Rusophycus*, Sc = *Scalarituba*, Sl = *Scolicia*, Si = *Siphonichnus*, Sk = *Skolithos*, Sp = *Spongeliomorpha*, Te = *Teichichnus*, Th = *Thalassinoides*, Tp = *Treptichnus,* Un = *Undichna,* PST = pellet-stuffed trace, ES = escape structure.

FACIES	LITHOLOGY	PHYSICAL SEDIMENTARY STRUCTURES	BIOGENIC STRUCTURES	FOSSILS	DEPOSITIONAL ENVIRONMENT
A1	Laminated Black Shale	Plane parallel laminae, rare silt and sand laminations, rare carbonate and/or phosphate concretions	None Observed	None observed	Distal Shelf/Slope
A2	Laminated Black silty shale	Plane parallel laminae, discontinuous normally graded sand/silt laminae, rare HCS and current ripple laminae	An, He, Hl, Py, Pl, Sc, Th	*Lingularia*, rare fish and ammonoids	Distal Shelf/Slope
B	Interlaminated HCS Siltstone and sandstone	Plane parallel laminae, flow ripples, HCS, rare oscillation ripples	An, Ar, As, Cr, Cy, Di, Gc, Gy, He, Hl, Li, Lk, Mc, Mm, Pa, Ph, Py, Pl, Ro, Ru, Sc, Sl, Sp, Te, Th, Tp, Un, ES	whole lingulids, bones, bioclastic hash layers	Offshore / Shoreface Transition
C	HCS sandstone (very fine)	Amalgamated HCS beds, planar bedding, current and oscillation ripples	An, Ar, At, As, Be, Co, Cr, Cy, Di, Lk, Mc, Pa, Pl, Rh, Ro, Sl, Si, Sk, Sp, Te, Th, Tp, Un, PST, ES	lingulide brachiopods, bivalves, fish, britlte stars.	Lower Shoreface
D	Calcareous sandstone (very fine to fine)	Predominantly TCS, rare HCS (SCS?), rare oscillation ripples	Ar, Op, Pa, Pl, Sk, Rh, Sk, PST	scattered brachiopod and echinoderm debris	Distal Upper Shoreface

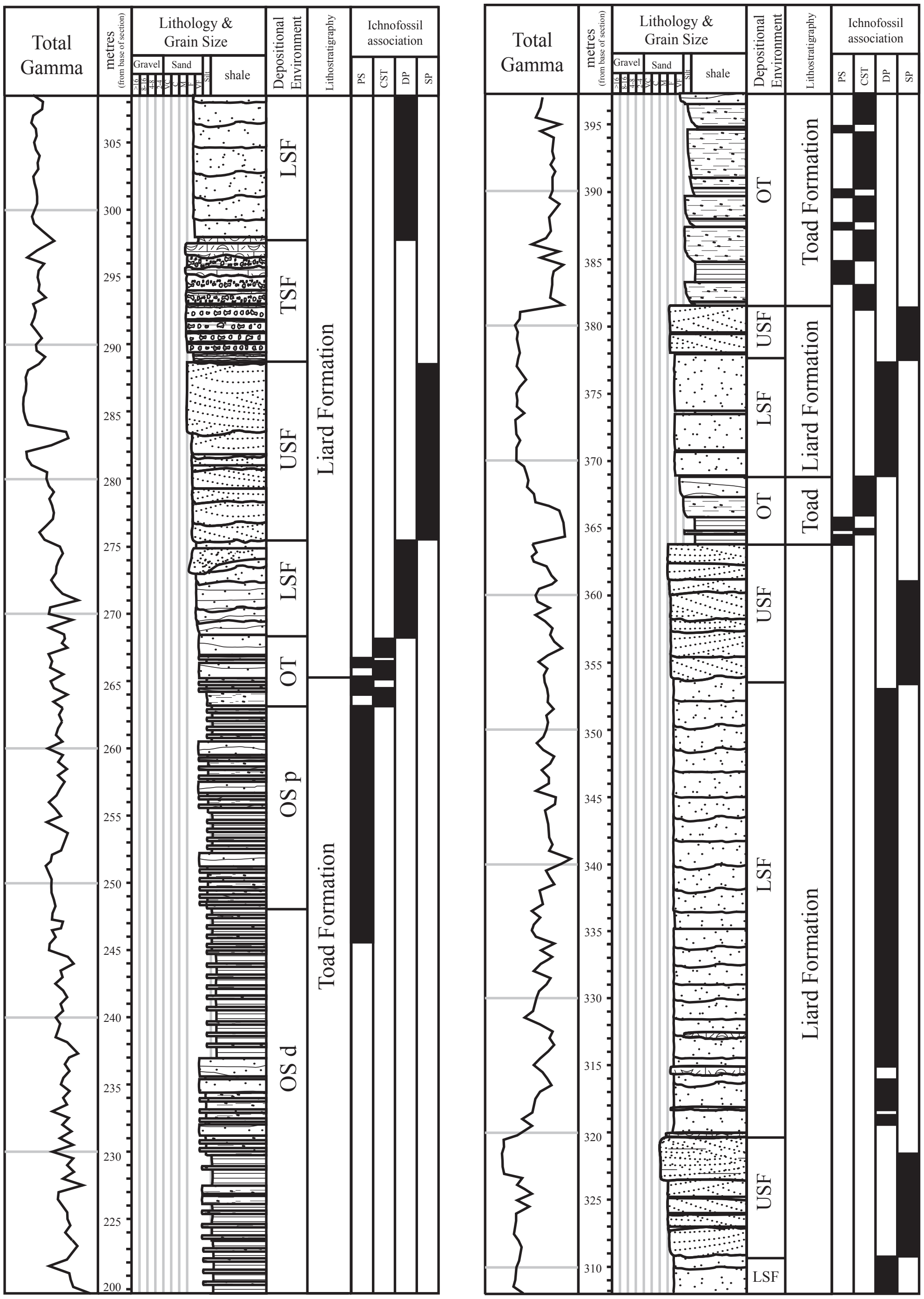

FIGURE 2-4—Stratigraphy of the study interval at Brown Hill with containing ichnofossil associations (after Zonneveld, 2008). OS d = distal offshore; OS p = proximal offshore; OT = offshore transition; LST = lower shoreface; USF = upper shoreface; TSF = transgressive shoreface; PS =*Phycosiphon*-*Scalarituba* association; CST = *Cruziana*-*Spongeliomorpha*-*Thalassinoides* association; DP = *Diplocraterion*-*Palaeophycus* association; SP = *Skolithos*-*Palaeophycus* association.

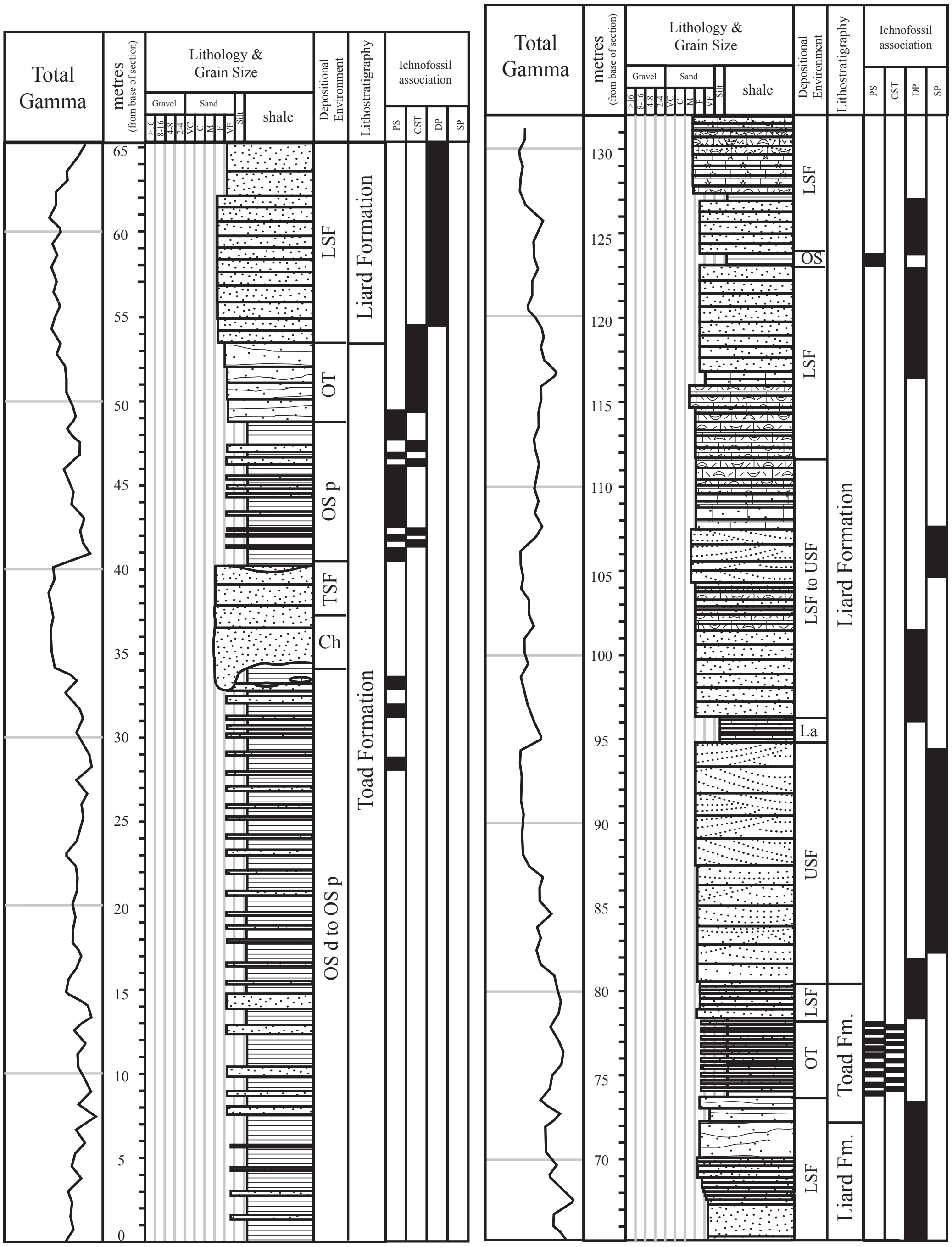

FIGURE 2-5—Stratigraphy of the study interval at Folded Hill (after Zonneveld, 2008). OS d =distal offshore; OS p = proximal offshore; OT = offshore transition; LST = lower shoreface; USF = upper shoreface; TSF = transgressive shoreface; Ch = Channel, La = Lagoonal; PS = *Phycosiphon-Scalarituba* association; CST = *Cruziana-Spongeliomorpha-Thalassinoides* association; DP = *Diplocraterion-Palaeophycus* association; SP = *Skolithos-Palaeophycus* association; Fm. = Formation.

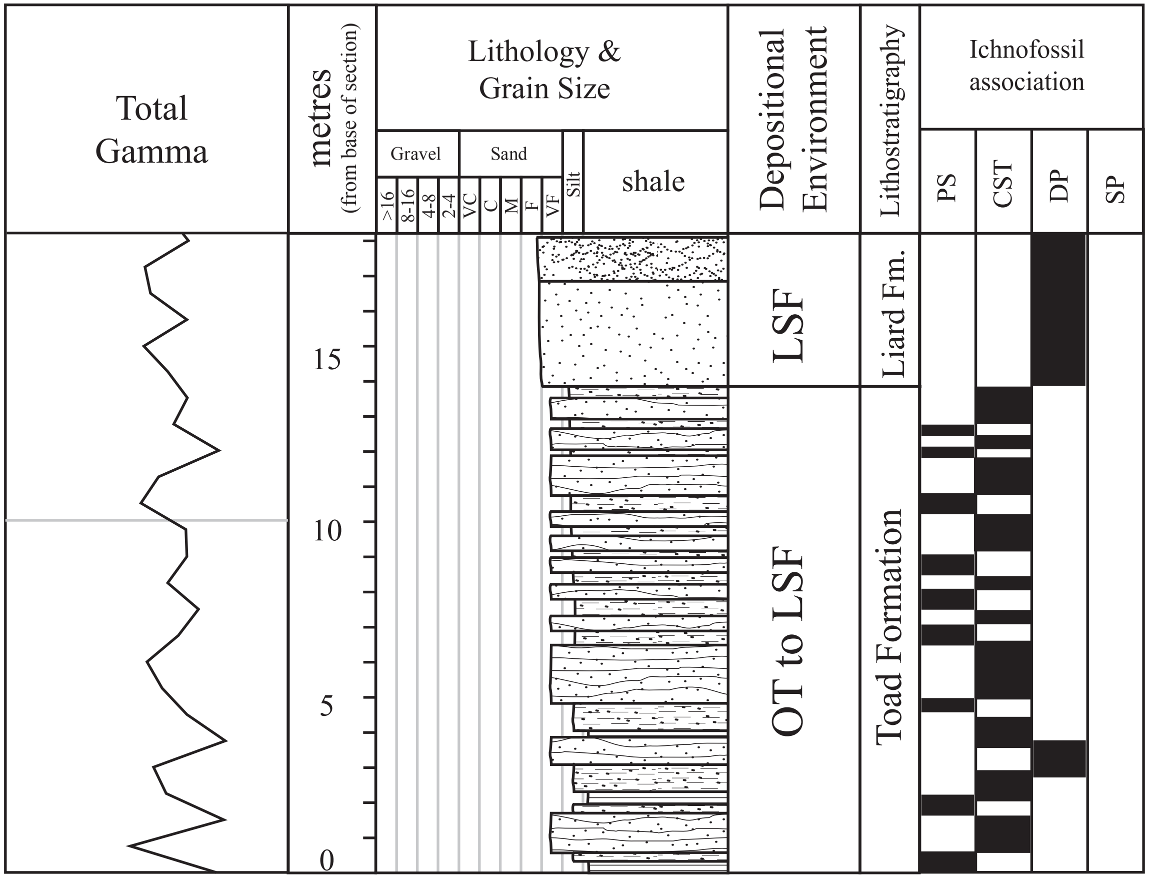

FIGURE 2-6—Stratigraphy of the study interval at Beatty Ledge (after Zonneveld, 2008). OT = offshore transition; LST = lower shoreface; PS = *Phycosiphon-Scalarituba* association; CST = *Cruziana-Spongeliomorpha-Thalassinoides* association; DP = *Diplocraterion-Palaeophycus* association; SP = *Skolithos-Palaeophycus* association; Fm. = Formation.

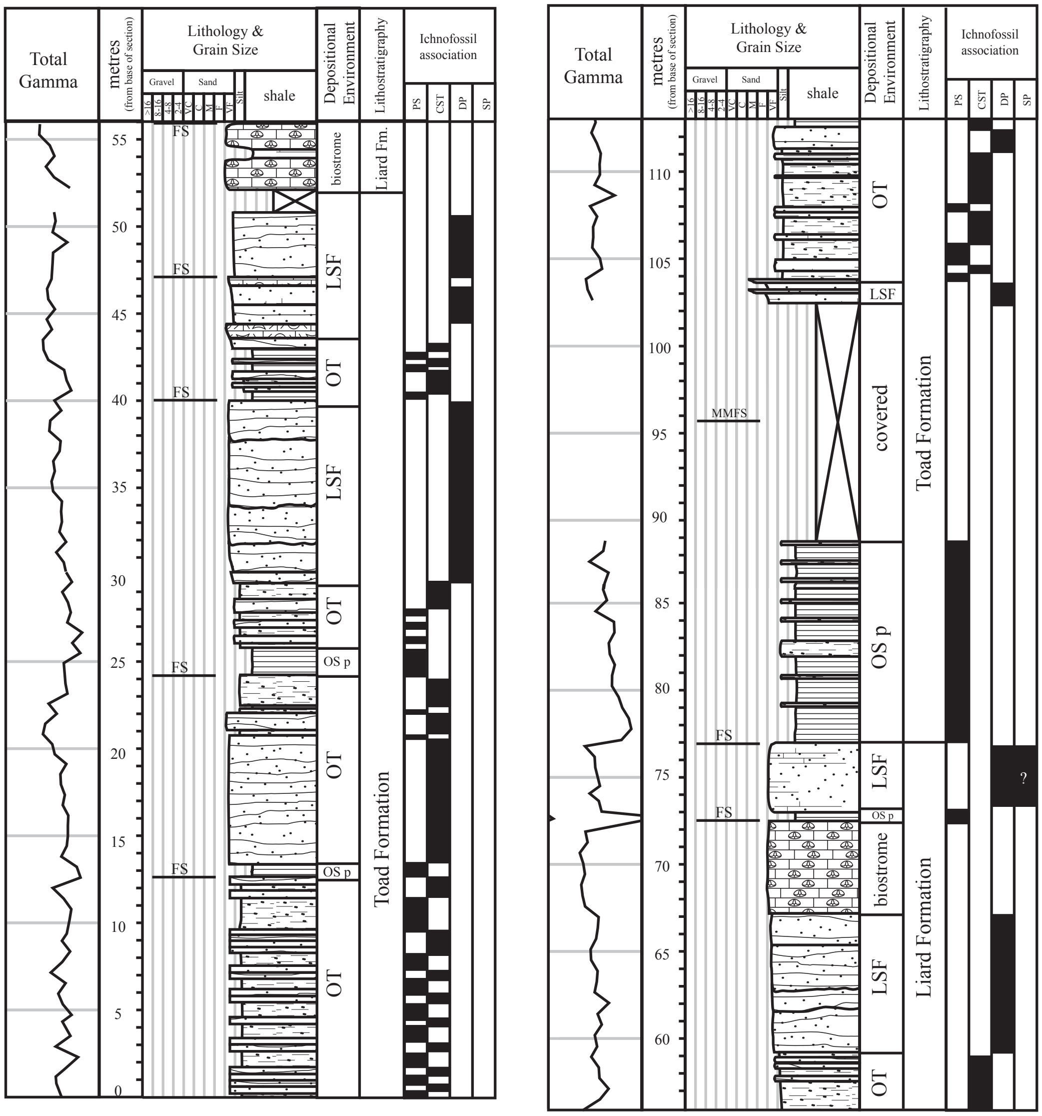

FIGURE 2-7—Stratigraphy of the study interval at Aylard Creek (after Zonneveld, 2008). OS p = proximal offshore; OT = offshore transition; LST = lower shoreface; USF = upper shoreface; PS = *Phycosiphon*-*Scalarituba* association; CST = *Cruziana*-*Spongeliomorpha*-*Thalassinoides* association; DP = *Diplocraterion*-*Palaeophycus* association; SP = *Skolithos*-*Palaeophycus* association; FS = flooding surface, MMFS = maximum flooding surface; Fm. = Formation.

TABLE 2-2—Ichnotaxonomy of the upper Toad and lower Liard formations at focused outcrops along Williston Lake, in northeastern British Columbia. Widths of spriten-bearing U-shaped burrows (i.e., *Diplocraterion* and *Rhizocorallium*) are shaft to shaft widths. Relative abundance is of in the overall study interval. OS = offshore, OT(sts) = silstone beds of offshore transition, OT(ss) = sandstone beds of offshore transition, LSF = lower shoreface, USF = upper shoreface.

ichnotaxon	**burrow width**	**burrow length**	**relative abundance**	**behaviour**	**Depositional environment**					**inferred tracemaker**
					OS	OT (sts)	OT (ss)	LSF	USF	
Anconichnus	<1 mm	unknown	common	grazing	x	x	x	x		vemiforms (Goldring et al., 1991)
Arenicolites	N/A	N/A	present	dwelling				x	x	arthropods (Hakes, 1976)
Asteriacites	10-50 mm	unknown	present	resting				x		asteroids or ophiuroids (Häntzschel, 1975; Mikuláš, 1990)
Asterosoma	10-50 mm	unknown	?abundant	feeding			x	x		vemiforms (Chamberlain, 1971)
Bergaueria	5 mm	unknown	rare	resting / dwelling				x		sea anemones (Pemberton et al., 1988)
Conichnus	2-5 mm	10 mm	rare	dwelling					x	sea anemones (Frey and Howard, 1981)
Cruziana	8-100 mm	~<400 mm	abundant	dwelling			x	x		arthropods (Zonneveld et al., 2002)
Cylindrichnus	5-20 mm	80 mm	present	dwelling			x	x		vermiforms (Frey and Howard, 1985)
Diplocraterion	12-120 mm	<100 mm	abundant	dwelling			x	x	x	polychaetes or arthropods (Fürsich, 1974b; Bromley, 1996)
Gyrochorte	6-10 mm	~100 mm	present	crawling				x	x	gastropod and vermiform (Heinberg, 1973)
Gyrolithis	5-25 mm	unknown	rare	dwelling					x	vermiform or arthropods (Powell, 1977, Wetzel, et al, 2007)
Helminthoidia	<1 mm	unknown	present	grazing	x	x				vermiforms (Bjerstedt, 1987)
Helminthopsis	<1 mm	unknown	present	grazing	x	x				vermiforms (Bjerstedt, 1987)
Lingulichnus	<20 mm	unknown	present	dwelling / feeding			x			lingulides (Hakes, 1976)
Lockeia	7-10 mm	~10 mm	present	resting			x	x		bivalves (Nara, 2003)
Monocraterion	5-10 mm	unknown	rare	dwelling / feeding			x	x		polychaetes (Bjerstedt, 1988)
Monomorphichnus	<1 mm	30-40 mm	present	crawling			x			arthropods (Mikuláš, 1995)

TABLE 2-2—Ichnotaxonomy continued. OS = offshore, OT(sts) = siltstone beds of offshore transition, OT(ss) = sandstone beds of offshore transition, LSF = lower shoreface, USF = upper shoreface.

ichnotaxon	burrow width	burrow length	relative abundance	behaviour	Depositional environment					inferred tracemaker
					OS	OT (fw)	OT (sw)	LSF	USF	
Ophiomorpha	5- 10 mm	N/A	rare?	dwelling					x	crustacean (Frey et al., 1978)
Palaeophycus	5-20 mm	unknown	abundant	dwelling			x	x	x	polychaete (Pemberton and Frey, 1982)
Phycodes	10-30 mm	unknown	rare	feeding / dwelling			x			vemiforms (Han and Pickerill, 1994)
Phycosiphon	<1 mm	unknown	common	grazing	x	x				vemiforms (Chamberlain, 1971)
Planolites	2-15 mm	<15 mm	abundant	feeding / dwelling	x	x	x	x	x	polychaetes (Pemberton and Frey, 1982)
Rhizocorallium	10-60 mm	unknown	common	feeding / dwelling				x	x	polychaetes (Fürsich, 1974a)
Rosselia	10-25 mm	>20 mm	common	feeding / dwelling			x	x		polychaetes (Nara, 1995)
Rusophycus	10-25 mm	~ 20 mm	present	resting			x			arthropods (Crimes, 1975)
Scalarituba	1-5 mm	>20 mm	common	grazing	x	x				vermiforms (Conkin and Conkin, 1968)
Scolicia	5-8 mm	unknown	present	feeding			x	x		echinoids or gastropods (Häntzschel, 1975; Bromley and Ekdale, 1986)
Siphonichnus	10 mm	100 mm	present	resting / dwelling			x			bivalves (Pearson and Gingras, 2006)
Skolithos	2-5 mm	40 mm	common	dwelling			?x	x	x	polychaete or phoronid (Pemberton and Frey, 1984)
Spongeliomopha	10-60 mm	~<150 mm	common	dwelling			x	x		arthropod (Metz, 1993)
Teichichnus	2-10 mm	~<30 mm	present	dwelling / feeding			x	x		vermiforms (Frey and Howard, 1985)
Thalassinoides	10-50 mm	unknown	abundant	dwelling / feeding	x	x	x	x		arthropods (Howard and Frey, 1984)
Treptichnus	2-5 mm	unknown	rare	feeding / resting			x	x		vermiforms (Seilacher and Hemleben, 1966)
Undichna	2 mm	unknown	rare	swimming			x	x		fish (Anderson, 1976; Gibert, 2001)
pellet-stuffed trace	0.5-2 mm	~50 mm	present	?dwelling / feeding				x	x	?ophiuroids (J-P. Zonneveld, personal communication, 2011)
Escape trace (*fugichnia*)	5-10 mm	10-50 mm	present	escaping			x	x		?arthropod, ?vermiform

Previous Ichnological Work

Studies of Triassic ichnofossils in western Canada are relatively recent (i.e., Zonneveld et al., 1997, 2001, 2002; Zonneveld, 1999) although the presence of ichnofossils in these strata has been known for several decades (Gibson, 1971). This is because Triassic field research in western Canada focused initially on biostratigraphy (McLearn, 1921, 1940, 1945, 1946; Tozer, 1967, 1994) and later on the lithostratigraphical framework (Gibson, 1971, 1974, 1975). Recent studies have noted that the Middle Triassic strata contain highly abundant and diverse trace fossil assemblages (Gibson, 1971; Zonneveld et al., 1997; Zonneveld, 1999; Zonneveld et al., 2001; Zonneveld, 2002, 2008). However, these studies were limited to brief surveys of trace fossil assemblages (i.e., Zonneveld et al., 1997; Zonneveld, 1999), which focused on specific settings (i.e., Zonneveld et al., 1997, 2001) or specific ichnotaxa (i.e., Zonneveld et al., 2002; Zonneveld and Pemberton, 2003; Zonneveld et al., 2007). Neither systematic comparison of ichnofossil diversity nor detailed discussion of these extraordinarily diverse trace fossil assemblages has been attempted.

RESULTS AND INTERPRETATIONS

The Toad-Liard trace fossil associations

A total of 36 ichnotaxa were recognized from the overall study interval. These ichnofossils occur as assemblages within beds. Ichnofossil assemblages show similar characteristics (e.g., containing ichnotaxa, relative abundances of ichnotaxa) within sedimentologically similar beds and are called ichnofossil associations herein this study. These Ichnofossil associations are interpreted to represent specific depositional environments and faunas. Descriptions and interpretations of four ichnofossil associations are following. Letter after the each ichnotaxon indicates its relative abundance; (a) is abundant; (c) is common; (p) is present; and (r) is rare within the ichnofossil associations. Detailed descriptions of each ichnotaxon and evaluations of these associations as ichnofacies are mentioned in chapter three.

Phycosiphon-Scalarituba ichnofossil association

Description

Observed in all outcrop sections included in this study, the *Phycosiphon-Scalarituba* (PS) ichnofossil association consists of *Anconichnus* (a)*, Helminthoida* (p)*, Helminthopsis* (c), *Phycosiphon* (a), *Planolites* (p), *Scalarituba* (a), and *Thalassinoides* (r). Some specimens of *Anconichnus*, *Helminthoida*, *Helminthopsis* and *Phycosiphon* were difficult or impossible to be differentiated within some beds due to preservation conditions and similar appearances.

This ichnofossil association occurs within heterolithic dark grey, sandy to muddy siltstone beds, and very fine- to fine-grained sandstone beds (Facies A). These beds are mainly interpreted as proximal offshore deposits (Zonneveld, et al., 1997; Zonneveld, 1999, 2008). These beds often include soft sediment deformation, micro faults, and convolute bedding. At Aylard Creek, the basal several decametres of the study interval includes relatively large-scale convolute bedding. Amongst other lines of evidence, this soft sediment deformation may indicate the presence of prodeltaic successions (Zonneveld, 2008). Towards the tops of most individual occurrences, the siltstone beds become sandier and are interbedded with thicker, very fine-grained, hummocky cross-stratified (HCS) sandstone. Thick, heterolithic muddy siltstone and HCS sandstone beds (Facies B) are interpreted to have been deposited in an offshore transition environment (Zonneveld, 1999, 2008). Muddy siltstone beds represent fair-weather sediments and HCS sandstone beds represent storm weather sediments in the offshore transition (Harms et al., 1975). Ichnofossils occur more commonly within siltstone beds of Facies B than Facies A. Facies A occurs mainly in the lower part of the study interval except for at Aylard Creek. Overall, Facies A contains fewer numbers of ichnofossils than siltstone beds of Facies B and, in several examples, completely lack trace fossils. Proximal offshore deposits (Facies A) in the upper part of the Aylard Creek section are more intensely bioturbated than offshore deposits elsewhere in the studied outcrops. The ratio of ichnotaxa present is relatively consistent between outcrop sections.

Ichnotaxa within this ichnofossil association are dominated by horizontal to slightly oblique forms and thus were generally easily observed on bedding plane exposures (Fig. 2-8). *Thalassinoides* and *Planolites* were identified in both horizontal and cross-sectional profile. Specimens of *Thalassinoides* were limited in occurrence to thicker (~2 to 5 cm) siltstone and sandstone beds. Although most *Thalassinoides* occurred as horizontal tubes, rare vertical shafts were also observed. Large (>10 mm wide) *Thalassinoides* are rare. Most ichnotaxa in the PS association are diminutive (Fig. 2-8). The burrow width of *Anconichnus*, *Helminthoida*, *Helminthopsis* and *Phycosiphon* was generally below 1 mm. *Scalarituba* and *Planolites* ranges from 2 mm to 8 mm wide. The *Thalassinoides* are comparably large (up to 15 mm wide). Many specimens of *Scalarituba* and *Planolites* exhibited branching. The abundance of *Planolites* and *Thalassinoides* increases upwards at all locations. *Phycosiphon*, *Anconichnus*, *Scalarituba*, *Helminthoida*/*Helminthopsis*, and *Planolites* commonly occur together on the same bedding planes, forming assemblages. However, overlapping burrows of different ichnotaxa were rarely observed. Only a few specimens of *Scalarituba* display crosscutting relationships with *Phycosiphon*, *Anconichnus*, *Helminthoida*, and/or *Helminthopsis*. Such overlapping relationships occur at all of outcrop locations in this study. *Thalassinoides* rarely occurs with other ichnotaxa within this association. Few specimens of *Thalassinoides* occur together with *Anconichnus* and *Planolites* at Aylard Creek.

The bioturbation intensity of beds that contain the PS association is variable, ranging from bedding-plane bioturbation indices of 1 to 3, and ichnofabric indices of 1 to 3. Part of Facies A contains no bioturbation, equal to bedding-plane bioturbation and ichnofabric indices of 1. Overall bioturbation intensity within these shale and siltstone beds reaches the highest levels at Aylard Creek (bedding-plane bioturbation indices of 3). Ichnofabric index of 3 is formed by abundant *Anconichnus*, *Planolites*, and rare *Thalassinoides* at Aylard Creek. The tier of burrows of this association is very shallow, less than 5 cm below sediment-water interfaces. Most traces only occur on bedding-plane surfaces. Overprinting of earlier burrows is generally absent within this association. Tiering relationships of the PS association is very simple with deep-tiered burrows absent

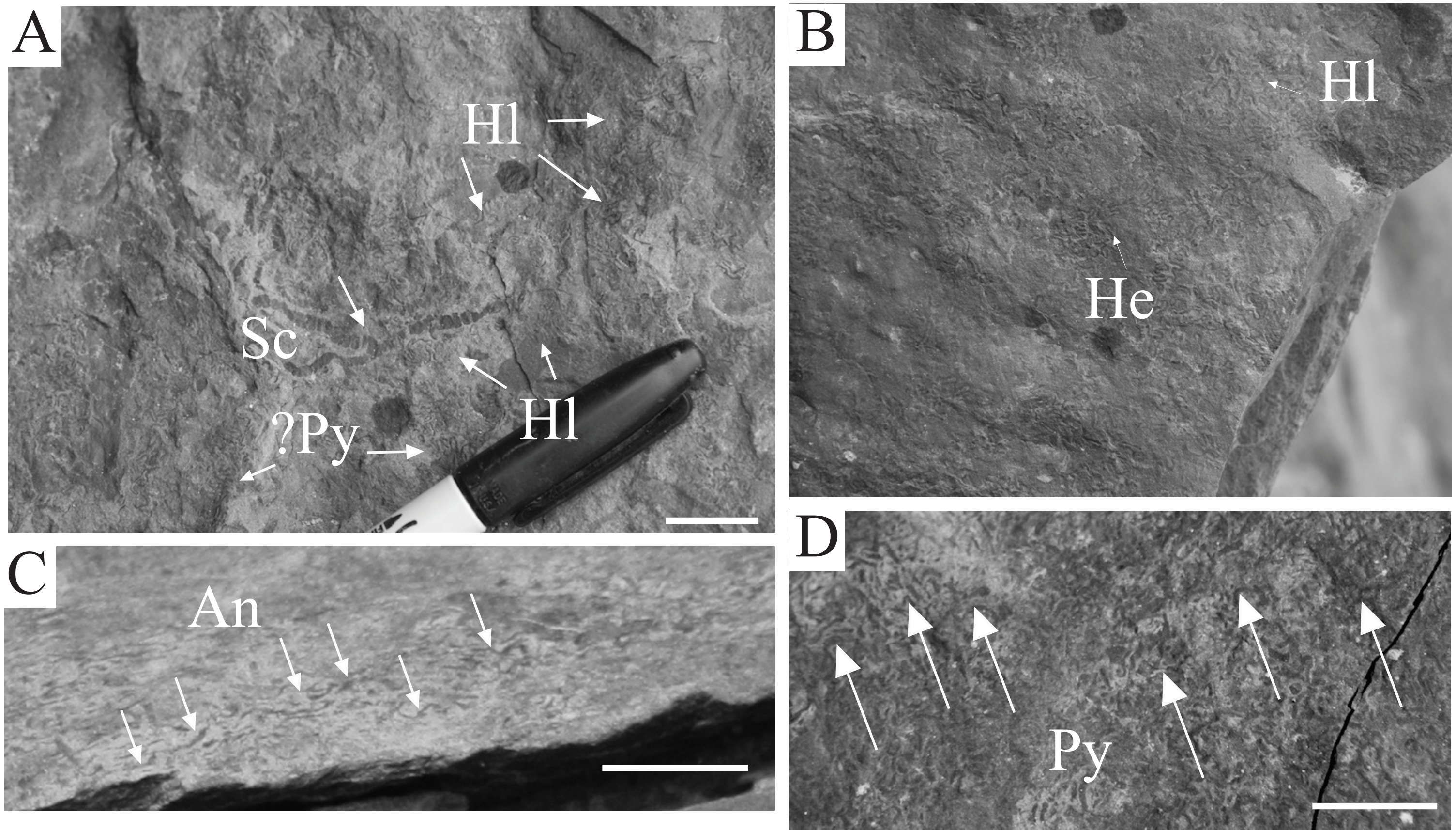

FIGURE 2-8—Photos of the *Phycosiphon*-*Scalarituba* association within sandy siltstone of Facies B at Aylard Creek. (A) Very thin black lines (Hl, and ?Py) and thicker, aligned semicircles (Sc) on one surface. (B) Dence colonization of *Helminthoida* and *Helminthopsis*on on bedding. (C) Multiple specimens of *Anconichnus* on a bedding cross-section. (D) Dence bioturbation of *Phycosiphon* on bedding plane. Scale bar = 1 cm. An = *Anconichnus*, He = *Helminthoida*, Hl = *Helminthopsis*, Py = *Phycosiphon*, Sc = *Scalarituba*.

in this association.

Interpretation

The *Phycosiphon*-*Scalarituba* (PS) association includes characteristics of the *Zoophycos* Ichnofacies (*sensu* MacEachern et al., 2007a). *Helminthopsis*, *Phycosiphon* and *Planolites* are commonly dominant ichnotaxa in the *Zoophycos* Ichnofacies (MacEachern et al., 2007a). As well, sedimentological and environmental characteristics of Toad Formation outcrop characterized by the PS association are similar to those reported from examples of the *Zoophycos* Ichnofacies described elsewhere (i.e., MacEachern et al., 2007a). However, *Zoophycos* and *Chondrites*, which are commonly dominant elements of the *Zoophycos* Ichnofacies in some successions, are absent in this association.

Despite the high level of complexity and depth of tiering of many examples of the *Zoophycos* Ichnofacies (i.e., MacEachern et al., 2007a, 2007c), overall tiering of the PS association in the study area is both simple and quite shallow. Further discussions of this phenomenon are provided in chapter three.

Anconichnus, *Helminthoida*, *Helminthopsis, Phycosiphon* and *Scalarituba* are all interpreted to be grazing/deposit-feeding structures (Conkin and Conkin, 1968; Bjerstedt, 1987; Wetzel and Bromley, 1994). *Planolites* is the deposit feeding trace fossil of worm-like organisms (e.g., polychaetes) or crustaceans (Pemberton and Frey, 1982). *Thalassinoides* within the Toad and Liard formations are most likely the fodinichnia/domichnia of decapod crustaceans (Zonneveld et al., 2002; Amati et al., 2004). Horizontal grazing behavior is a strongly predominant ethologic mode in the PS association, likely reflecting abundant organic detritus both at the sediment water interface as well as buried within the upper few centimetres of the sediment. Abundant grazing structures, few scour surfaces and thin hummocky cross-stratified sandstone beds indicate deposition near storm wave base (Harms et al., 1975). Simple and shallow tiering of the PS association probably indicates a lack of tracemakers that were able to burrow deeply.

Although the PS association occurs in both Facies A and part of Facies B, the environmental interpretation differs slightly. Facies A includes beds with (Facies A1) and without ichnofossils (Facies A2). The main differences are the presence of ichnofossils and frequency of preservation of physical structures (i.e., soft sediment deformation, convolute-bedding, and micro-faults). Such differences indicate that Facies A1 was deposited relatively rapidly, resulting in highly stressful conditions due to high sedimentation rates and possibly other factors (e.g., low-oxygen content) which may have prevented the occurrences of trace constructors (e.g., Savrda and Bottjer, 1989; Martin, 2004). In contrast, the paucity or absence of soft-sedimentation deformation, micro-faults, and convolute-bedding within Facies A2 implies relatively low sedimentation rates. Additionally comparably abundant ichnofossils within Facies A2 may indicate sufficient oxygen and nutrients in bottom waters, and within the upper few centimetres of the substrate. Within the siltstone beds of Facies B, individual abundances of ichnofossils are slightly higher than those in Facies A2. Facies B was probably deposited under favorable condition for tracemakers of the PS association. Such conditions likely indicate an abundant supply of nutrients, slow rates of sedimentation and high oxygen content, both in the water column and adjacent sediment.

Cruziana-Spongeliomorpha-Thalassinoides ichnofossil association

Description

The *Cruziana*-*Spongeliomorpha*-*Thalassinoides* (CST) ichnofossil association is exceptionally diverse, consisting of *Anconichnus* (a), *Arenicolites* (r), *Asterosoma* (p), "*Corophioides*" (r), *Cruziana* (a), *Cylindrichnus* (c), *Diplocraterion* (a), *Gyrochorte* (p), *Gyrolithes* (p), *Lingulichnus* (c), *Lockeia* (p), *Monocraterion* (r), *Monomorphichnus* (r), *Palaeophycus* (c), *Phycodes* (r), *Phycosiphon* (p), *Planolites* (a), *Rosselia* (p), *Rusophycus* (p), *Scolicia* (p), *Spongeliomorpha* (a), *Teichichnus* (c), *Thalassinoides* (a), *Treptichnus* (r), *Undichna* (r) and escape traces (p). Locally abundant accumulations of fecal pellets are common as well. The CST association is present at all localities in the study area.

The CST association occurs within very fine-grained, hummocky cross-stratified (HCS) sandstone beds interbedded with sandy siltstone beds (parts of Facies B). Most ichnofossils occur within the top 10 cm of HCS sandstone beds of Facies B. The interbedded HCS sandstone and sandy siltstone are interpreted as offshore transition deposits (Zonneveld et al., 1997; Zonneveld, 1999, 2008). The HCS sandstone beds commonly occur interbedded with muddy siltstone interbeds that contain ichnofossils of the *Phycosiphon*-*Scalarituba* association. In heterolithic intervals the proportion of sandstone to siltstone or muddy siltstone beds is variable, however, neither lithology was observed to exceed 2 m in thickness. In the upper part of the Brown Hill section, heterolithic interbeds with very fine-grained sandstone and shale/siltstone successions occur as a series of coarsening upward successions associated with an increase in the proportion of sandstones (Zonneveld, 1999, 2008). Similar trends were also noted at other localities.

Dominant ichnotaxa, *Thalassinoides*, *Cruziana* and *Spongeliomorpha* (Fig. 2-9A, B), occur horizontally on the top surfaces of sandstone beds as mainly concave (and rarely convex) downward impressions with a few other ichnotaxa. They commonly occur in variably complex branching networks. These three forms commonly create compound forms with each other and thus are interpreted to have been constructed by a common tracemaker. Fecal pellets are commonly preserved on bedding planes adjacent to these ichnotaxa and occur in parts of the burrow fill as well. Many specimens of these three ichnogenera produce composite forms with *Anconichnus* and/or possible *Phycosiphon* (Fig. 2-9D). Rarely, specimens of *Palaeophycus* exhibit a crosscutting relationship with *Cruziana*, *Thalassinoides*, or *Spongeliomorpha*. Specimens of *Cruziana* and *Spongeliomorpha* are similar in size to *Thalassinoides*, generally ranging from around 10 to 70 mm wide. At Beatty Ledge, multiple specimens of *Cruziana* reach sizes well over 100 mm wide and more than 40 cm long. Although few specimens of *Thalassinoides* occur in the PS association, this ichnotaxon is much more abundant in the CST association and are quite large (20 to 70 mm wide). Additionally, specimens of *Thalassinoides* in the CST association occur more

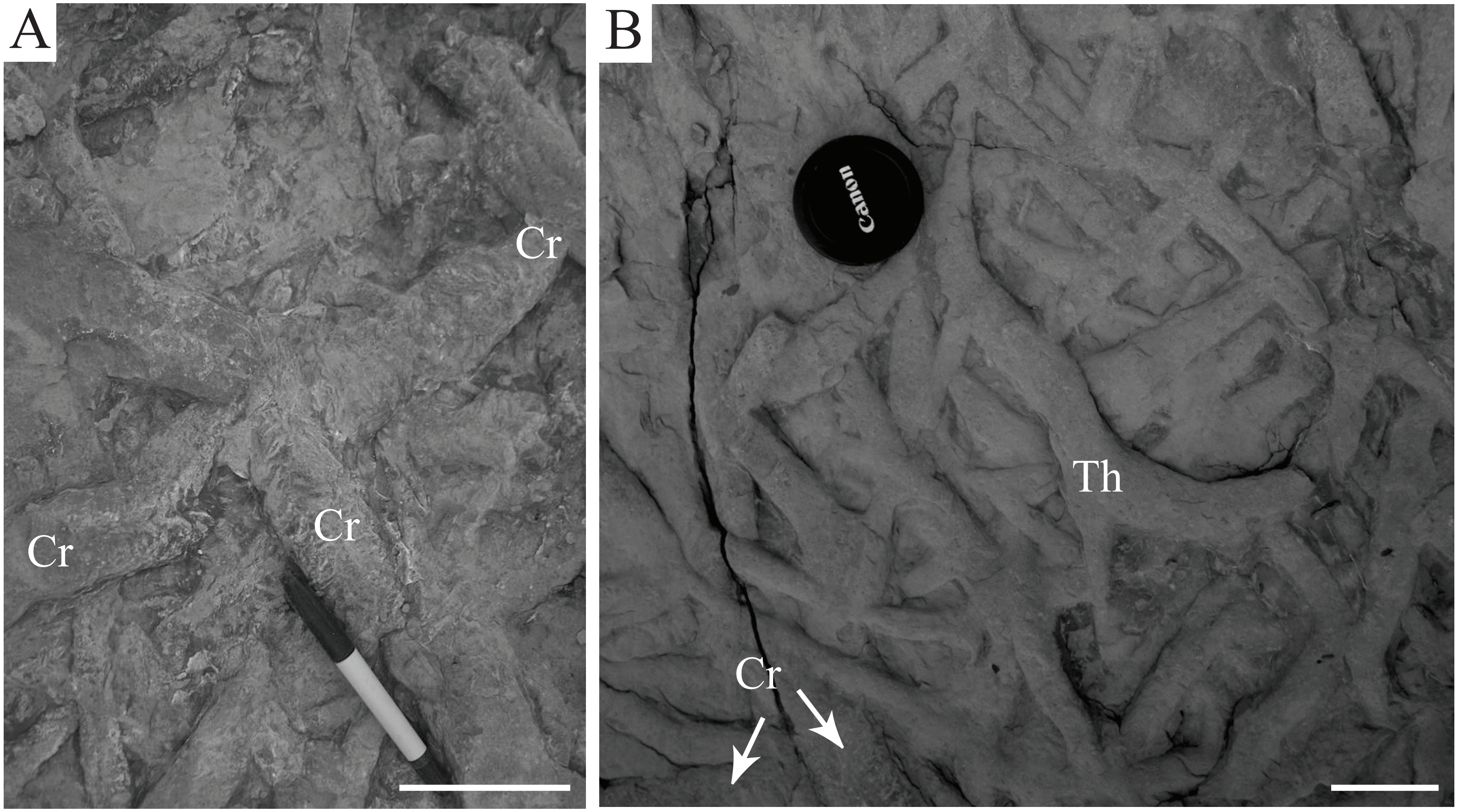

FIGURE 2-9—Photos of trace fossils XVPhotos of the CST association within very fine-grained sandstone of Facies B. (A) Dense occurrence of *Cruziana,* possibly branching at Beatty Ledge. (B) Networking structures of *Thalassinoides* with fewer *Cruziana* at Beatty Ledge. Scale bar = 5 cm. An = *Anconichnus*, Cr = *Cruziana*, Py = *Phycosiphon*, Sp = *Spongeliomorpha*,

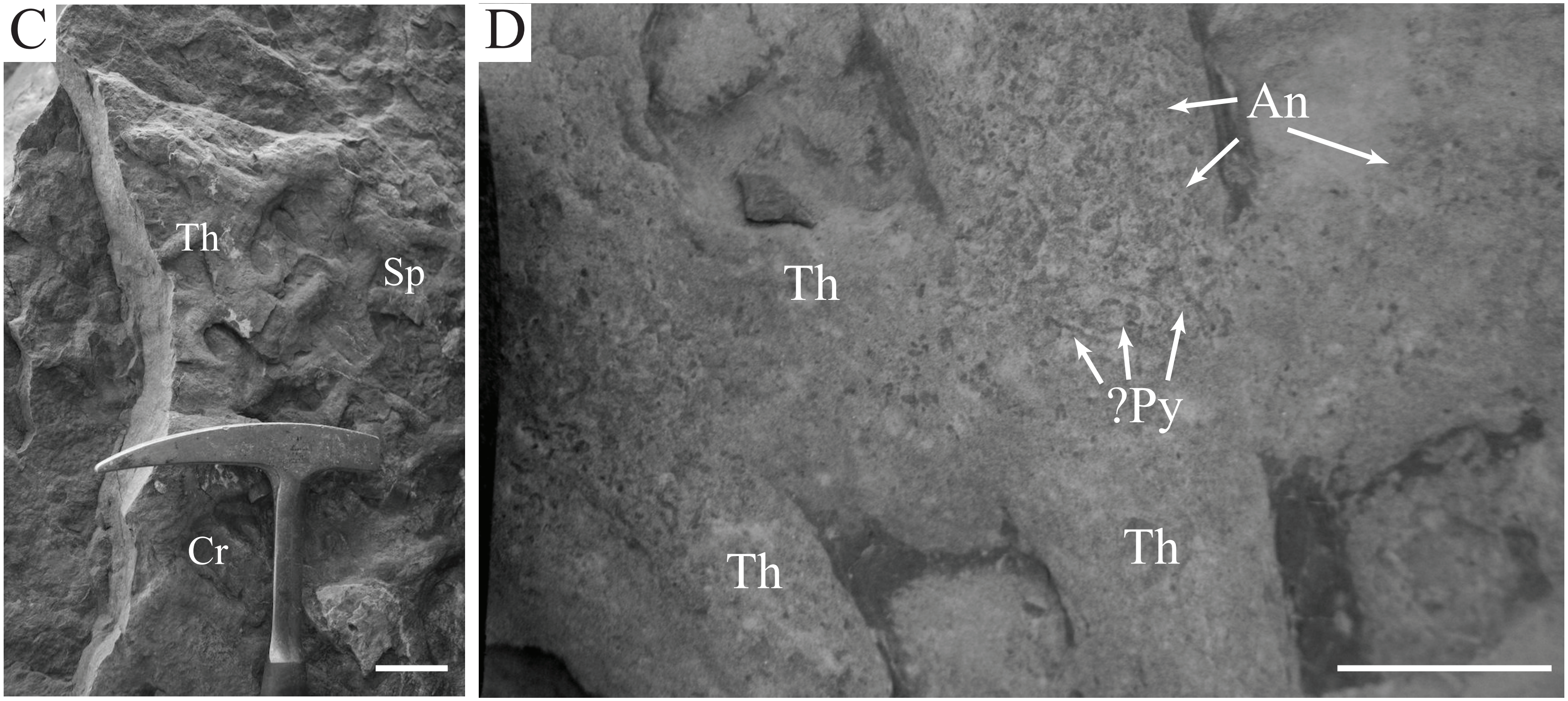

FIGURE 2-9—Photos of the CST association continued. (C) Possible composite form of *Spongeliomorpha-Thalassinoides* at Aylard Creek. A specimen of *Cruziana* occurs separately. Scale bar = 5 cm. (D) Compound ichnofossils of *Anconichnus* and/or possible *Phycosiphon*, and *Thalassinoides* occur at Beatty Ledge. Scale bar = 1 cm. An = *Anconichnus*, Cr = *Cruziana*, Py = *Phycosiphon*, Th = *Thalassinoides*.

frequently as vertical and networking structures more than those within the PS association. On the same bedding surfaces as these three ichnotaxa, scratch marks are regularly observed as concave downward impressions. The size of scratch marks is around 1 to 5 mm wide and up to 15 mm long. As well, *Rusophycus* and *Monomorphichnus* often occur associated with *Cruziana*, *Thalassinoides*, and *Spongeliomorpha* and are interpreted to have been made by similar constructors. Relatively rare specimens of *Gyrochorte* also occur with *Cruziana*, *Thalassinoides* and *Spongeliomorpha*.

Less abundant ichnotaxa in the CST association often occur in vertical forms, such as *Diplocraterion*, *Monocraterion*, *Lingulichnus*, *Lockeia*, *Rosselia* and *Siphonichnus*. Although these vertical burrows are relatively diverse in terms of ichnotaxonomy, total abundances of these vertical traces are not as high as the arthropod-constructed traces (*Cruziana*, *Spongeliomorpha* and *Thalassinoides*) discussed above. Only *Diplocraterion* and *Lingulichnus* exhibit high abundance in the CST association among vertical burrows. *Lingulichnus* were locally abundant (at Brown Hill) in this association, but were not evenly distributed. They typically occur, commonly in high abundances, within sharp-based hummocky cross-stratified sandstone beds (Zonneveld and Greene, 2010). The *Lingulichnus* tend to occur in patches of approximately equal-sized traces. These traces occur in association with abundant *in situ* lingulides as well as lingulide specimens on bedding planes.

Despite its high abundance, no completely preserved specimens (i.e., aperature to base) of *Diplocraterion* were observed. At all studied locations, multiple surfaces characterized by dense, nearly monotypic *Diplocraterion* assemblages occur, sometimes with a few associated specimens of *Palaeophycus* (Fig. 2-10). Within the study interval *Diplocraterion* exhibit wide size variance. Specimens that occurred at dense *Diplocraterion*-surfaces consist mainly of smaller specimens, ranging from 20 to 50 mm in width (Fig. 2-10). In contrast, in the middle of the Aylard Creek succession, large specimens, oriented at up to ~ 20° from vertical, are up to 120 mm in width. A single large specimen, reminiscent of the defunct ichnogenus *Corophioides* (see Fürsich, 1974b), was

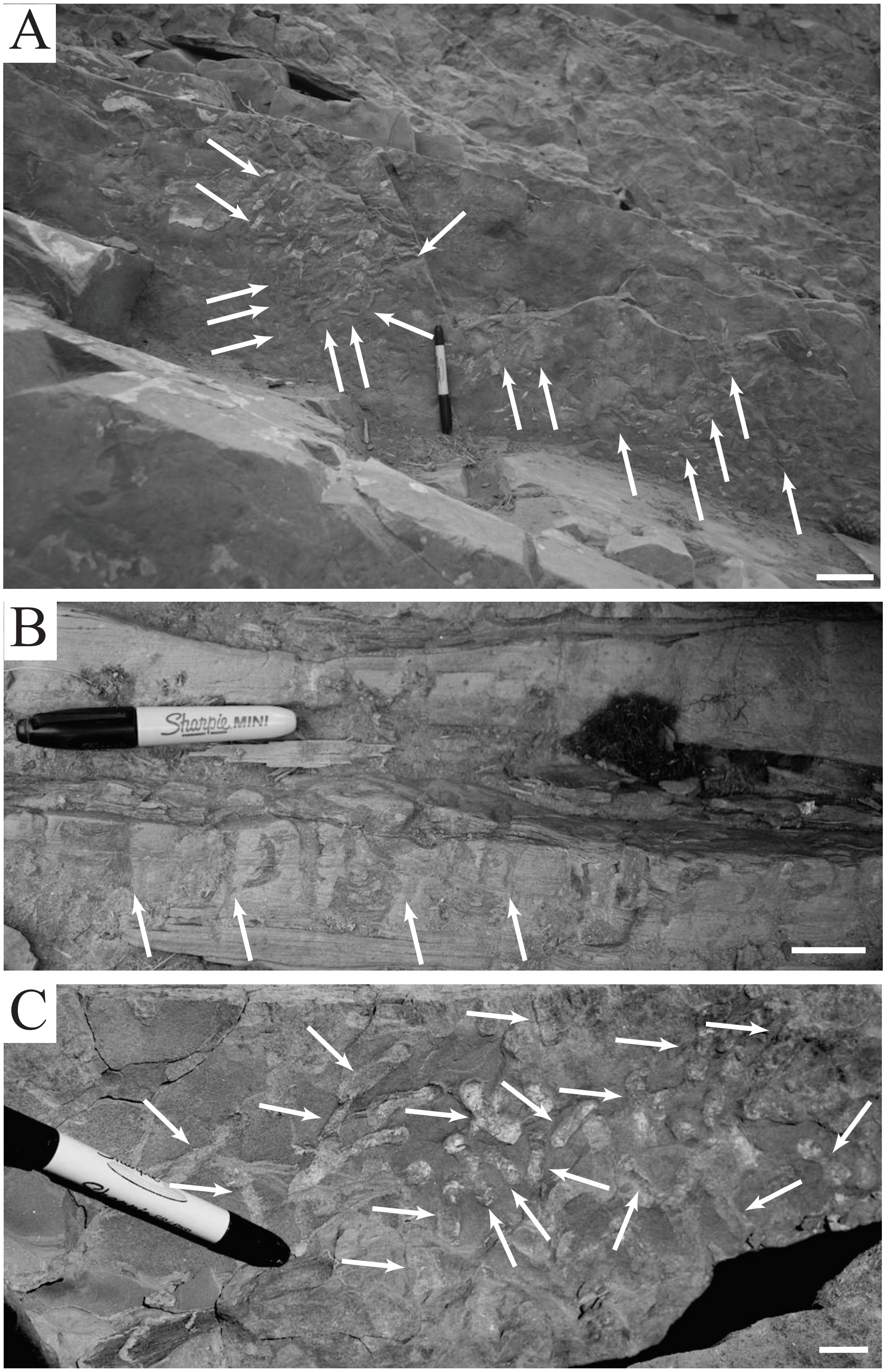

FIGURE 2-10—Multiple specimens of *Diplocraterion* colonize surfaces of the CST association. (A) Relatively small specimens of *Diplocraterion* dominating a surface at Brown Hill. (B) Cross-sectional view of *Diplocraterion* surface. (C) A small area (plan view) occupied by multiple specimens of *Diplocraterion*. Scale bar = 5 cm (A), 1cm (B, and C).

260 mm in width with causative tubes 30 mm in width at Aylard Creek. Most specimens of *Diplocraterion* in this association consist of top-cut-off traces dominated by protrusive spreiten. Other vertical burrows, such as *Rosselia* and *Cylindrichnus* are present, but in lower abundances than horizontal traces. Specimens of *Lockeia* are relatively rare, but do occur with high density in a few beds. Escape traces are commonly observed in this association.

Bedding-plane bioturbation indices range from 3 to 4, and ichnofabric indices are usually 2 and rarely 3 within HCS sandstone beds of Facies B. Within the CST association, overall ichnofossil diversity is high. Individual abundances vary from high to low depending on the ichnotaxon. *Thalassinoides* and *Spongeliomorpha* probably represent medium- to deep-tiered burrows. *Cruziana* and *Diplocraterion* are medium-tiered. Others (e.g., *Planolites*, *Rusophycus* and *Gyrochorte*) are shallow-tierer or surface structure. Despite a wide variety of tiering types, tiering relationships in this association are relatively simple. Composite forms probably indicate a type of overprinting of earlier traces.

Interpretation

The *Cruziana*-*Spongeliomorpha*-*Thalassinoides* (CST) association contains many elements in common with the archetypal *Cruziana* Ichnofacies (MacEachern et al., 2007a, 2007c). The depositional environment of beds characterized by the CST association has been interpreted as offshore transition, between fair weather base and storm-wave base (Zonneveld, 1999, Zonneveld et al., 2002; Zonneveld, 2008). Storm-generated beds predominate, consistent with an open coastal setting (Zonneveld et al., 1997; Zonneveld 1999, 2008). This environmental setting is typical of the archetypal *Cruziana* Ichnofacies (MacEachern et al., 2007a). However, previous studies have removed cyclic heterolithic beds of storm-generated sandstone and fair-weather shale and siltstone from Seilacher's original ichnofacies framework and placed them into ichnofossil assemblages that develop in stressed conditions (e.g., high sedimentation rate, and low oxygen contents) (MacEachern et al., 2007a, 2007b). Such ichnofossil assemblages within storm generated event beds and fair-weather siltstone beds are also described as mixed *Skolithos*-*Cruziana* ichnofacies due to their characteristics (MacEachern et al., 2007b).

Dominantly horizontal ichnotaxa such as *Thalassinoides*, *Cruziana*, and *Spongeliomorpha* are classified as fodinichnia or domichnia (Häntzschel, 1975; Howard and Frey, 1984; Metz, 1993; Zonneveld et al., 2002). Their inferred tracemakers are probably arthropods (likely decapods) (Howard and Frey, 1984; Metz, 1993; Zonneveld et al., 2002, 2010bc). Another important ichnotaxon, *Diplocraterion,* is commonly interpreted as a dwelling burrow of suspension feeders, such as polychaetes and crustaceans (Fürsich, 1974b; Bromley, 1996). Several ichnotaxa are interpreted as grazing structures (e.g., *Anconichnus* and *Phycosiphon*), deposit-feeding burrows (e.g., *Asterosoma* and *Scolicia*), and burrows of detritus feeders (e.g., *Rosselia*) (Chamberlain, 1971; Wetzel and Bromley, 1994; Nara, 1995). *Rusophycus*, *Monomorphichnus,* and random scratch marks are common in this association, representing repichnia or cubichnia by arthropods (Mikuláš, 1990, 1995; Zonneveld et al., 2002). The presence of these resting and crawling traces implies activities of crustaceans at the sediment-water interface (Mikuláš, 1995; Zonneveld et al., 2002). Rare *Undichna* are interpreted as the swimming traces of fish (Anderson, 1976; Gibert, 2001).

The abundant ichnofossils of the CST ichnofossil association indicate the presence of a highly complex benthic community with diverse organisms. The trace fossils in this association represent the activities of a wide variety of possible tracemakers, including vermiform organisms, arthropods, molluscs, and fish. Such diverse tracemakers imply an abundant food supply and well-oxygenated water. Compound forms of *Cruziana*/*Thalassinoides*/*Spongeliomorpha* are indicative of slight behavioral plasticity change during the formations of burrows. Grazing traces of this association (*Anconichnus*/*Phycosiphon*) tend to occur as composite ichnofossils with *Cruziana*/*Thalassinoides*/*Spongeliomorpha*. These kinds of composite forms suggest *Cruziana*/*Thalassinoides*/*Spongeliomorpha* occurred first (Pickerill and Narbonne, 1995; Bromley, 1996). Thus, all the tracemakers may not have been constructed simultaneously. Overall, the beds within the CST ichnofossil association were deposited within an environment that was highly hospitable to many types of benthic and infaunal organisms, likely owing to high oxygen content and excellent food resources.

Diplocraterion-Palaeophycus ichnofossil association

Description

The *Diplocraterion-Palaeophycus* (DP) association contains the most diverse suite of ichnofossils in the study interval. It consists of *Anconichnus* (r), *Arenicolites* (p)*, Asteriacites* (p), *Asterosoma* (a), *Bergaueria* (r), *Conichnus* (r) *Cruziana* (p), *Cylindrichnus* (c), *Diplocraterion* (a), *Lingulichnus* (c), *Lockeia* (p), *Monocraterion* (r), *Palaeophycus* (a), *Phycodes* (r), *Planolites* (c), *Rhizocorallium* (c), *Rosselia* (var. *R. rotatus*) (a), *Siphonichnus* (c), *Skolithos* (p), *Spongeliomorpha* (p), *Teichichnus* (p), *Thalassinoides* (p)*, Treptichnus* (r), *Undichna* (r), pellet-stuffed traces (p), and escape structure (c). Escape traces are more abundant in the DP association than in the CST association. The DP association is present at all localities.

The DP association occurs within amalgamated, very fine-grained hummocky cross-stratified (HCS) sandstone beds (Facies C). The units that include the DP association were previously interpreted as lower shoreface sediments (Zonneveld et al., 1997; Zonneveld, 1999, 2008). Amalgamated HCS sandstone beds characterized by the DP association also include disarticulated echinoid elements, crinoid ossicles, bivalves, brachiopod shells and locally articulated ophiuroids (Zonneveld et al., 1997; Zonneveld, 1999, 2008) (Zonneveld et al., 1997; Zonneveld, 1999, 2008). The succession at Aylard Creek is very well-exposed along bedding planes and thus more ichnotaxa were observed on bedding planes than in vertical section.

The most abundant ichnofossils of the DP association are *Diplocraterion* and *Palaeophycus* (Fig. 2-11). Specimens of *Diplocraterion* within this association dominantly display protrusive spreiten, which indicate sedimentation rather than erosion when the tracemakers of *Diplocraterion* were alive and adjusting upwards (Fig. 1; Goldring, 1964). Burrow width of *Diplocraterion* ranges from 50 to 120 mm. Most specimens of *Diplocraterion* are not completely

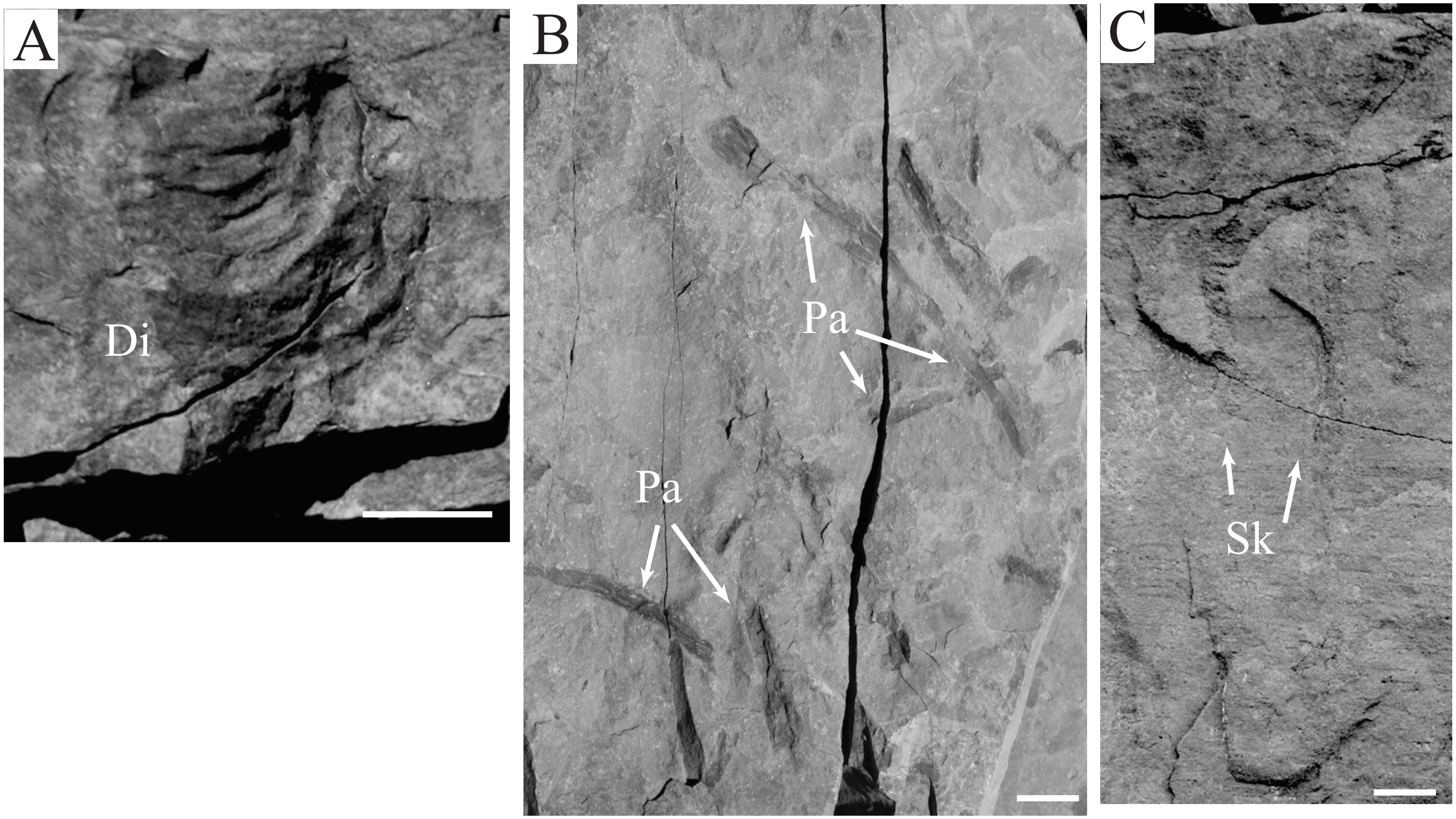

FIGURE 2-11—Trace fossils of the *Diplocraterion*-*Palaeophycus* association within Facies C. (A) Relatively small *Diplocraterion* within very-fine grained sandstone at Brown Hill. (B) Horizontal *Palaeophycus* overlapping each other at Aylard Creek. (C) Vertical borrows of *Skolithos* at Folded Hill. Scale bar = 1 cm. Di = *Diplocraterion*, Pa = *Palaeophycus*, Sk = *Skolithos*.

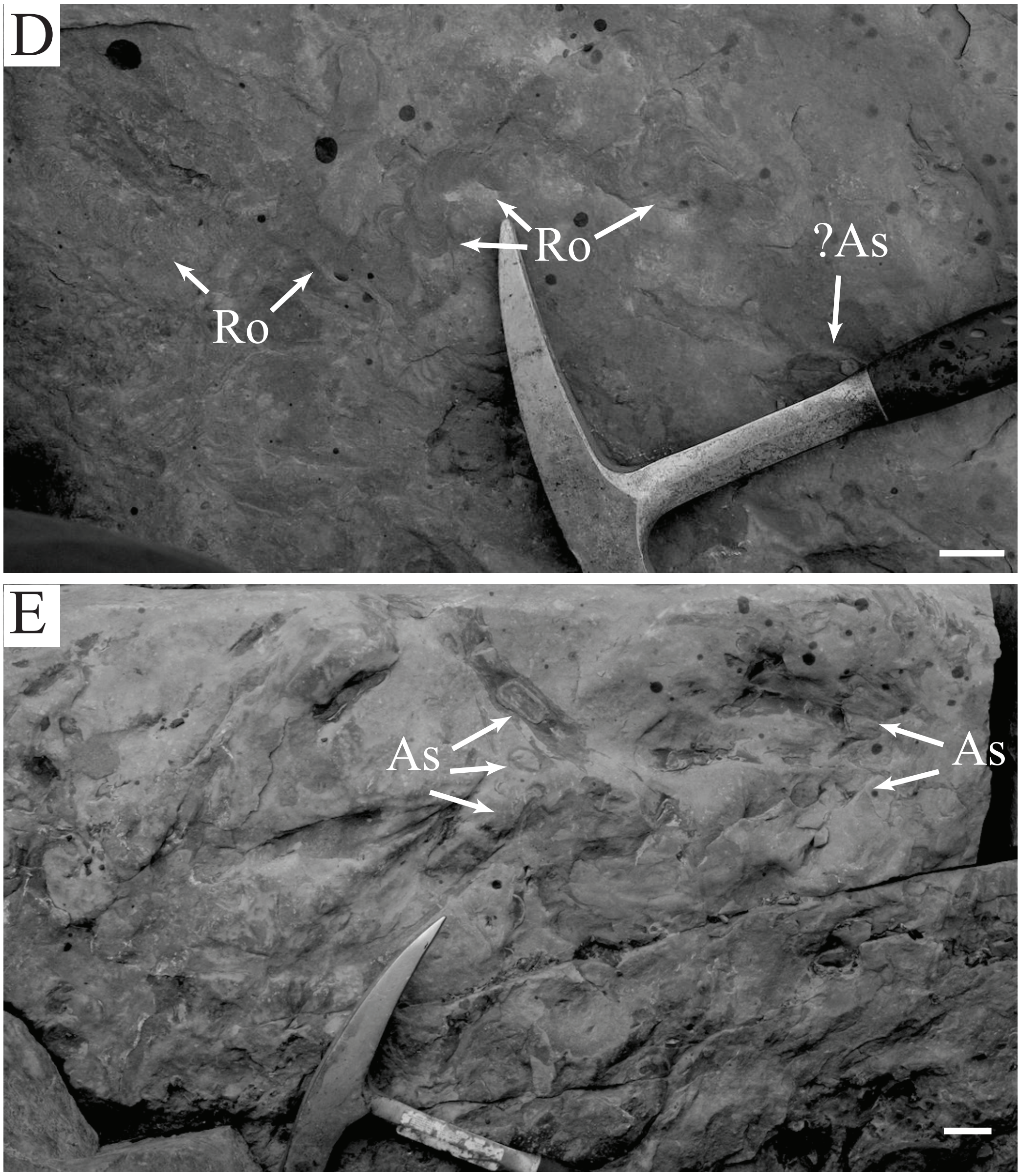

FIGURE 2-11—Trace fossils of the *Diplocraterion*-*Palaeophycus* association continued. (D) Recurring crescent-shape structure, *Rosselia rotatus* on a surface of Facies C at Aylard Creek. (E) A plan view of subhorizontal to horizontal samples of *Asterosoma*, which densely occur within amalgamated hummocky cross-stratified sandstone at Aylard Creek. Scale bar = 1 cm. Ro = *Rosselia*, As = *Asterosoma*.

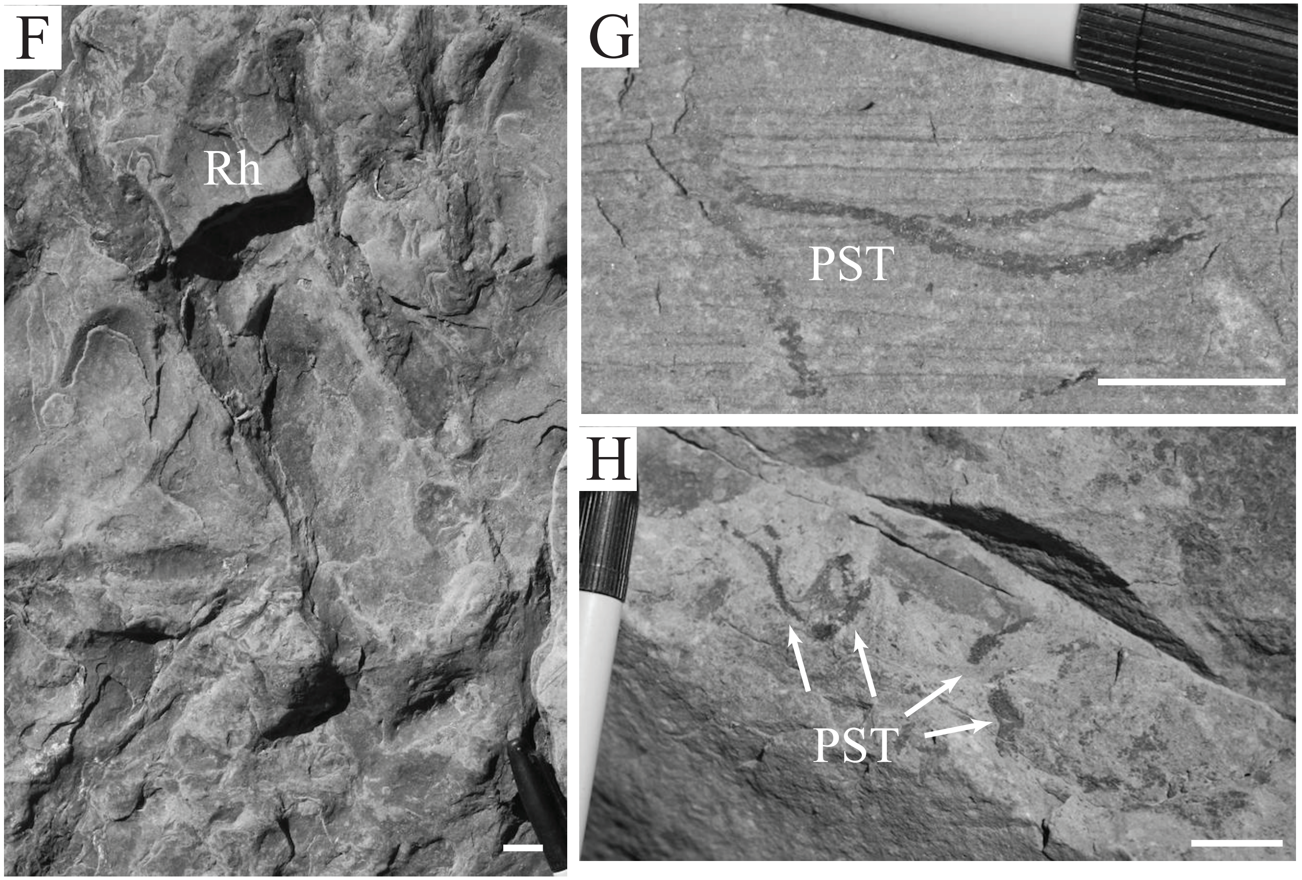

FIGURE 2-11—Trace fossils of the *Diplocraterion-Palaeophycus* association continued. (F) Large *Rhizocorallium* within amalgamated hummocky sandstone at Aylard Creek. (G) Vertical pellet stuffed traces at Aylard Creek. (H) Another pellet stuffed trace at Aylard Creek, oriented perpendicular to bedding. Ophiuroid body fossils occur nearby the specimens. Scale bar = 1 cm. Rh = *Rhizocorallium*, PST = pellet-stuffed trace.

preserved from top opening to bottoms. Some specimens only preserve spreite at the bottom of *Diplocraterion* burrows. These indicate erosion occurred after post-sedimentation adjustment of *Diplocraterion* animals (Goldring, 1964). Some *Diplocraterion* commonly occurs together with other ichnotaxa such as *Palaeophycus*, *Rosselia*, *Skolithos*, and escape traces. Horizontal to subhorizontal *Palaeophycus* occur at all outcrop locations, and range from 5 to 20 mm in width.

In addition to the two most abundant ichnotaxa (*Diplocraterion* and *Palaeophycus*), the DP association contains a higher portion of relatively complicated forms of trace fossils, such as *Asterosoma*, *Rosselia* and *Cylindrichnus*. These were observed in both bedding plane exposure and in cross section. However, more abundant individuals of *Asterosoma* and *Rosselia* are distinguished on bedding plane exposure. At Aylard Creek, multiple surfaces are densely bioturbated by *Asterosoma*, *Rosselia* and possibly *Cylindrichnus* (Fig. 2-11D, E). These dense occurrences of *Asterosoma* and *Rosselia* make separations of individual specimens difficult and they may even transform from one to another, producing compound specimen. Furthermore, horizontal specimens on these surfaces may overlap each other and multiple specimens of *Skolithos* cross cut *Asterosoma* and possible *Cylindrichnus* on these densely packed surfaces.

Amalgamated HCS sandstone beds contain *Thalassinoides*, *Cruziana* and *Spongeliomorpha*, but in much lower abundance than the CST association. Unnamed pellet-stuffed traces are also common within these beds, associated with abundant randomly oriented pellets (Fig. 2-11G, H). They often occur within the same beds as ophiuroid fossils. Escape traces are common within this ichnofossil association and ranges 5 to 15 mm wide. At Aylard Creek, escape traces occur within the same beds as large (~120 mm wide) protrusive spreite-bearing *Diplocraterion*.

Bedding-plane bioturbation indices of this assemblage range from 2 to 3 except for intensely bioturbated surfaces by *Asterosoma* and *Rosselia* at Aylard Creek. The bedding-plane bioturbation indices of the *Asterosoma*-*Rosselia* surfaces are 4. Despite the high diversity of present ichnotaxa in this association, total intensity is, with the exception of certain beds, relatively low. Overall, tiering relationships of this association are relatively simple, but exhibit more complex relationships than other associations in the study interval. Nonetheless, overprinting of earlier traces by later burrowers is not commonly observed in vertical sections, however *Palaeophycus* commonly overlaps on other ichnofossils on bedding planes. Also on the *Asterosoma*/*Rosselia* surfaces, multiple specimens of *Asterosoma* overlap on other *Asterosoma*, *Rosselia*, *Cylindrichnus* and possible *Rhizocorallium*.

Interpretation

Many of the trace fossils present in this association (e.g., *Arenicolites, Cylindrichnus*, *Diplocraterion*, *Lockeia*, *Palaeophycus*, *Rosselia*, *Skolithos*, *Siphonichnus*, and *Thalassinoides*) are interpreted as dwelling structures (e.g., Fürsich, 1974b; Häntzschel, 1975; Hakes, 1976; Pemberton and Frey, 1982; Frey and Howard, 1985; Pearson and Gingras, 2006). *Lockeia* is interpreted as resting traces (Häntzschel, 1975; Nara, 2003). Inferred tracemakers of dwelling structures in this interval are mostly arthropods, vermiforms and bivalves, possibly suspension feeding animal (e.g., *Diplocraterion*, *Palaeophycus*, *Siphonichnus* and *Skolithos*) (Fürsich and Wendt, 1977; Pemberton and Frey, 1982, 1984; Pearson and Gingras, 2006). Fewer burrows are interpreted as feeding traces of deposit feeders (e.g., *Asterosoma* and *Rosselia*) (Chamberlain, 1971; Nara, 1995). An ichnotaxon interpreted as a grazing trace, *Anconichnus* (Bromley, 1996) is found, but its relative abundance, and the diversity of these forms, is very low compared to other behavioral types.

This association shows similarities with the distal *Skolithos* ichnofacies (MacEachern et al., 2007a). Ichnotaxa in the DP association are interpreted to represent colonization by dwelling structures (likely by suspension feeders) with less abundant deposit feeding and fewer grazing structures. Such an ethological mixture (abundant dwelling structures, less abundant deposit feeding burrows, and subordinate grazing traces) is similar to the distal *Skolithos* Ichnofacies (MacEachern, et al., 2007a). These dwelling are mainly vertical with minor horizontal structures, resembling the *Skolithos* Ichnofacies, as well (MacEachern et al., 2007a). Sedimentologically, this association occurs within amalgamated HCS sandstone beds, which represent lower shoreface and is consistent with common substrate preferences of the *Skolithos* Ichnofacies (MacEachern et al., 2007a). Deposit feeding burrows (including *Asterosoma* and *Rosselia*) are locally abundant, showing similarity with the *Cruziana* Ichnofacies rather than *Skolithos* Ichnofacies. Additionally, the high diversity is atypical of the *Skolithos* Ichnofacies. To conclude, the DP association probably includes the mixed characteristics of both the *Skolithos* and *Cruziana* ichnofacies. Most characteristics of this association, such as dominant vertical trace fossils, abundant burrows of suspension feeders, and substrate types are analogous to the characteristics of distal portion of the *Skolithos* Ichnofacies (MacEachern et al., 2007a). More so, the overall deep-tiered burrows more commonly occur within lower shoreface deposits rather than within offshore and offshore transition deposits. This indicates higher wave energy stresses in shoreface, which led tracemakers to burrow deeply to protect their burrows (Pemberton et al., 1992; Bromley, 1996).

Skolithos-Palaeophycus ichnofossil association

Description

The *Skolithos-Palaeophycus* (SP) association consists of *Arenicolites* (p), *Ophiomorpha* (p), *Palaeophycus* (c), *Planolites* (p), *Rhizocorallium* (p), *Skolithos* (c) and pellet-stuffed traces. This association is present only at Brown Hill and Folded Hill. Fewer specimens of *Palaeophycus* are present in the *Skolithos-Palaeophycus* ichnofossil association than in the *Diplocraterion-Palaeophycus* (DP) association.

This ichnofossil association occurs within trough cross-stratified very fine- to medium-grained, calcareous sandstone beds, associated with ripple cross beds or rare hummocky cross-stratification. Packages of these calcareous sandstones (Facies D) conformably overlie amalgamated hummocky cross-stratified (HCS) sandstone beds (Facies C). Many packages of calcareous sandstone beds are sharply overlain by siltstone beds of Facies A or B, which are interpreted as marine flooding surfaces (Zonneveld et al., 1997; Zonneveld, 2008).

Vertical burrows (e.g., *Skolithos*, and *Arenicolites*) are common and abundant within this association. Except for *Palaeophycus*, horizontal ichnotaxa, such as *Planolites* and *Rhizocorallium,* are fewer and in low abundance. Specimens of *Skolithos* are relatively abundant and range from 2 - 5 mm wide. The width of *Palaeophycus* burrows ranges from 2 - 8 mm. Within Facies D occur units that contain surfaces with pronounced iron oxide staining and are commonly occupied with moderate numbers of trace fossils cross-cutting the background sediment. Only *Ophiomorpha* is present on these surfaces, and it is absent within all other beds.

Compare to the DP and *Cruziana*-*Spongeliomorpha*-*Thalassinoides* associations, the SP association includes the least diverse ichnotaxa. Overall bioturbation intensity and abundance of trace fossils is remarkably low compared to other trace fossil associations. Bedding-plane bioturbation indices are 2 and ichnofabric indices are 2. Tiering relationships of this association are simple and exhibit no overprinting of burrows by newer burrows. Shallow- to medium-tiered burrows are predominant, up to 2 - 6 cm below the sediment-water interfaces.

Interpretation

A main component of the *Skolithos*-*Palaeophycus* association is the vertical shafts of *Skolithos* and *Diplocraterion* and the horizontal to sub-horizontal orientation of *Palaeophycus*. These aforementioned trace fossils, in addition to *Arenicolites,* are interpreted as dwelling burrows of suspension feeders, such as vermiforms and arthropods (Fürsich, 1974a; Hakes, 1976; Pemberton and Frey, 1982; Bromley, 1996). *Palaeophycus* has also been interpreted as the dwelling structure of predaceous polychaetes (Pemberton and Frey, 1982). *Ophiomorpha* burrows are generally interpreted as the dwelling burrows of decapod crustaceans (Frey et al., 1978).

Ichnotaxa present within this assemblage exhibit strong similarity with the archetypal *Skolithos* Ichnofacies (MacEachern et al., 2007a). The presence of wave ripples on bedding planes and trough cross stratification are common physical sedimentary structures for sediments associated with the *Skolithos* Ichnofacies (MacEachern et al., 2007a, 2007c). Likewise, the depositional environment of the strata with the SP association is distal upper shoreface, which is the most common interpreted depositional setting for the occurrence of the *Skolithos* Ichnofacies (Pemberton, et al., 1992; MacEachern et al., 2007a). Low ichnofossil abundance and low diversity of this association is also identical to the characteristics of the *Skolithos* Ichnofacies (Pemberton, et al., 1992; MacEachern et al., 2007a). Overall, an environment of the SP association was relatively stress-full with continuous wave activity, resulting in low intensity and diversity of trace fossils, as well as vertical burrows and simple tiering relationship (Pemberton, et al., 1992; MacEachern et al., 2007a). Frequent water movements supplied sufficient food and optimized the environments for dwelling suspension feeding animals to thrive (e.g., Ekdale, 1985; Bottjer and Ausich, 1986; Bromley, 1996).

DISCUSSION

Distribution and diversity of ichnofossils

The ichnofossils in this study occur within depositional environments ranging from proximal offshore through distal upper shoreface. Four marine ichnofossil associations are recognized in the study interval: (i) *Phycosiphon-Scalarituba* (PS) association; (ii) *Cruziana-Spongeliomorpha-Thalassinoides* (CST) association; (iii) *Diplocraterion-Palaeophycus* (DP) association; and (iv) *Skolithos-Palaeophycus* (SP) association. To date, the only Triassic ichnofaunas described in detail from western Canada are Middle Triassic (Ladinian) trace fossils from the study area, and Lower Triassic (Induan) ichnofaunas from the Montney Formation (Zonneveld et al., 2010a, 2010c). Figure 2-12 illustrates ichnotaxonomic diversity through Middle Triassic shallow marine environments in the study area and compared their trends with those from lower Triassic succession in Alberta and British Columbia.

The proximal offshore successions have low overall ichnodiversity (total

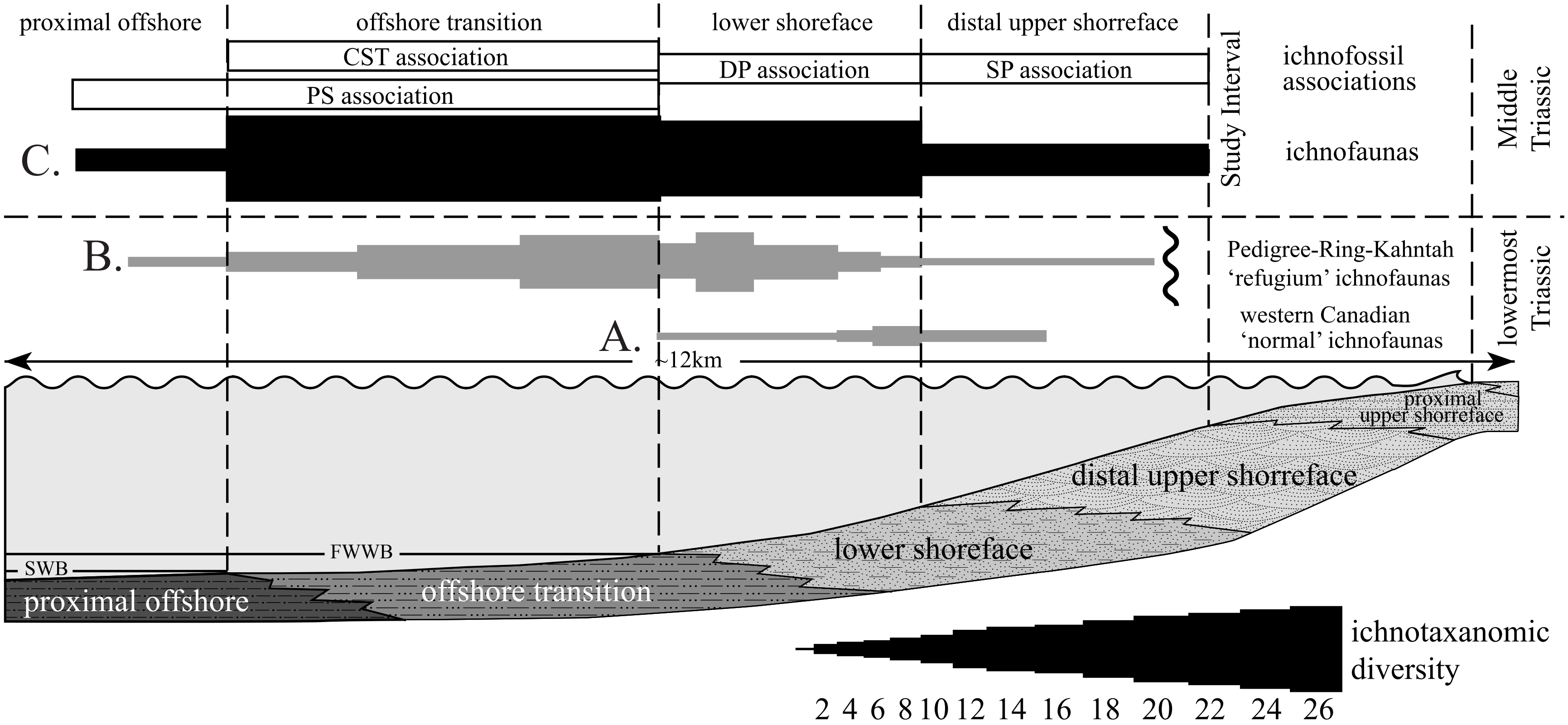

FIGURE 2-12—Ichnofaunas distribution trends in the Triassic of western Canada. Environmental distribution of ichnofossil association is also illustrated here. A: Lowermost Triassic shallow marine ichnofaunas in western Canada (Beatty et al., 2008). B: A refugium in the Ring-Kahntah-Pedigree area of Alberta and British Columbia (after Zonneveld et al., 2010c). C: The upper Toad and lower Liard ichnofossil assemblages in the study interval. PS = *Phycosiphon-Scalarituba*, CST = *Cruziana-Spongeliomorpha-Thalassinoides,* DP = *Diplocraterion-Palaeophycus,* SP = *Skolithos-Palaeophycus,* FWWB = approximate fair-weather wave base, SWB = approximate storm wave base.

of 7 ichnotaxa). Storm-generated beds, although deposited in a bathymetrically similar setting, have a much higher ichnodiversity (25 ichnotaxa). This suggests that environmental conditions in proximal offshore and offshore transition successions were not conducive to a wide variety of behaviours. Further work is needed to ascertain what stressor prevented additional taxa from colonizing this setting; however, several lines of evidence, including the presence of abundant pyrite framboids in finer grained lithologies, suggests that dysoxic conditions prevailed in shallow shelf areas below fair-weather wave base (FWWB) (e.g., Raiswell et al., 1988; Canfield et al., 1996). This is similar to the situation observed within lowermost Triassic (Induan) succession in the Montney Formation on the Alberta-British Columbia border in the Pedigree- Ring-Kahntah area (Zonneveld et al., 2010a, 2010c).

High ichnodiversity in storm-generated event beds and low ichnodiversity in background 'host' strata suggests that many of these forms are storm-transported, opportunistic colonizers (*sensu* Pemberton and MacEachern, 1997). These assemblages are interpreted to exemplify the "doomed pioneer" hypothesis (*sensu* Grimm and Föllmi, 1990) in which event beds emplaced in oxygen deficient settings are colonized by organisms transported basinward with the sediment. These taxa survived for a short while in oxygen-enriched sediments of the event beds but either perished as oxygen levels within the event beds diminished to background conditions, or alternatively, failed to reproduce in these high-stress settings (Grimm and Föllmi, 1990, 1994; Föllmi and Grimm, 1990; Pemberton and MacEachern, 1997).

Lower shoreface deposits of amalgamated HCS sandstone beds include 26 ichnotaxa, higher than any other environmental setting in the study area. This diversity, both in ichnotaxonomy as well as ethological groupings, underscores that Middle Triassic shoreface environments in the study area were well-oxygenated (Savrda and Bottjer, 1989), with sufficient food resources to support a diverse infaunal and epifaunal community. The distal upper shoreface contains significantly less forms (10 ichnotaxa). Lower ichnodiversity in the shoreface and foreshore is typical of many modern and ancient successions, and likely reflects the inherently higher wave stress that characterizes these settings (i.e., MacEachern et al., 2007b; Beatty et al., 2008).

Previous investigations of Middle Triassic depositional successions in the study area (e.g., Zonneveld, 1999, 2001; Zonneveld et al., 2001) provided brief synopses of the ichnotaxonomic composition of the Toad and Liard formations, however these studies were focused on the physical sedimentology of the study interval and do not provide details on the ichnofaunal relationships and detailed descriptions of the ichnofaunas were not attempted. Exceptionally diverse suites of ichnofossils reported from Lower Triassic strata of the Pedigree, Ring and Kahntah areas in British Columbia and Alberta were interpreted to represent environmental refugia within which marine invertebrates were sheltered from the worst effects of extinction-related environmental stressors (Zonneveld et al., 2010a, 2010c). Refugia represent an anomalous situation during the Induan (Zonneveld et al., 2010a, 2010c) and indeed most lowermost Triassic trace fossil assemblages, in western Canada as well as elsewhere in the world, are characterized by very low diversity (i.e., Twitchett and Wignall, 1996; Beatty et al., 2008).

Lower Triassic ichnofossils from the Alberta-British Columbia refugia successions occur within storm-generated beds and/or relatively shallow, proximal lower to distal upper shoreface, whereas ichnofossils are absent from other environments (Beatty et al., 2008; Zonneveld et al., 2010c). In contrast, ichnofossils in the Middle Triassic study interval occur from proximal offshore through upper shoreface environments. The ichnofossils reach highest diversity in distal lower shoreface and offshore transition settings. This broad distribution and shift in peak ichnotaxonomic diversity in depositional environment between the Lower Triassic to Middle Triassic suggest that the Early Triassic shelf successions that suffered from anoxia/dysoxia (Zonneveld et al., 2010c) and concomitant vacant ecospace had become inhabitable by the Middle Triassic (i.e., a broader extent of the shelf became habitable). The fact that ichnodiversity remained low in proximal offshore settings indicates that dissolved oxygen levels remained low below storm wave base. Thus, although environmental conditions clearly had recovered between the Lower Triassic and Middle Triassic, adverse conditions apparently continued in distal shelf (proximal offshore) settings. Further study is needed to clarify whether uninhabitable conditions continued from the Lower Triassic or, rather, were temporally and geographically restricted to the Ladinian of the study interval.

Trends in trace sizes

Traces within the study interval are, overall, larger than those that occur in Lower Triassic successions in western Canada. The width ranges of six ichnotaxa, common in both Lower and Middle Triassic successions, are presented in Figure 2-13. Both the largest and smallest specimens of *Planolites* and *Palaeophycus* within the study interval are slightly larger than those that occur within Lower Triassic strata in western Canada (Fig. 2-13). *Cruziana* in the study interval varies in width, from ~10 to more than 100 mm (Fig. 2-13). The widths of *Thalassinoides* and *Spongeliomorpha* are very similar*,* ranging from 10 to 70 mm (Fig. 2-13) since both trace fossils were probably constructed by the same or very similar tracemakers. All decapod-burrows are larger than those of the Lower Triassic successions. Specimens of *Diplocraterion* range from 20 to 120 mm wide. Although the smallest *Diplocraterion* of the Middle Triassic is smaller than the largest *Diplocraterion* of the Lower Triassic, maximum width of *Diplocraterion* of the study intervals are much wider than Lower Triassic specimens. Likewise, *Rhizocorallium* in the study interval ranges up to 80 mm in width, far larger than Lower Triassic specimens.

Despite the wide range, the size distribution of *Cruziana* and *Diplocraterion* specimens is bimodal (Fig. 2-13). One population of *Cruziana* is in the 10 to 30 mm width range and the other is in the 70 to 100 mm range, possibly indicating two distinct types of tracemakers. Smaller specimens of *Diplocraterion* occur in dense, monospecific surfaces, ranging from ~20 to 40 mm in width. Specimens that occur in less dense assemblages, and those that occur as scattered specimens in more ichnologically diverse beds range from 80 to 120 mm wide. Although all *Diplocraterion* in the study area are assigned to *D.*

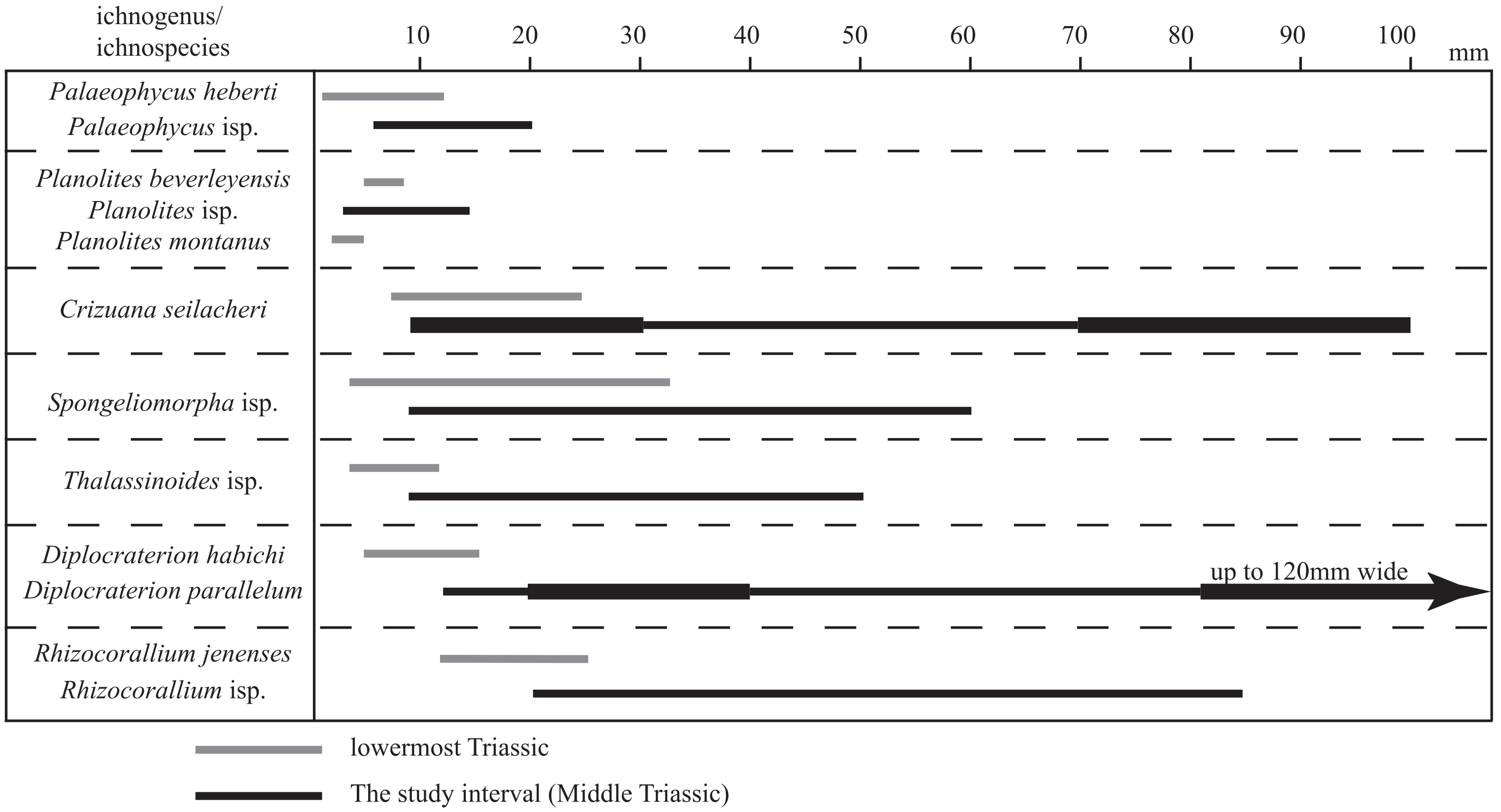

FIGURE 2-13—Trace fossil widths from Triassic of northeastern British Columbia. Grey lines represent traces measured from the lowermost Triassic (Induan / Griesbachian), Montony Formation in the Pedgree-Ring-Kahntah area (Zonneveld et al., 2010c). Black lines indicate traces from the Middle Triassic (Ladinian) upper Toad and lower Liard fromations in the study area along Williston Lake. Thickened parts of lines indicate higher numbers of specimens within those range.

parallelum, the smaller population is similar in size to *D. habichi* observed in Lower Triassic successions (Zonneveld et al., 2010c). Although this may represent size differences within a single species of tracemaker, the bimodal size distribution makes it likely that at least two different taxa, which belong to the same or different lineages, are responsible for constructing each of these ichnogenera. Amati et al. (2004) reported on chimaerastacid lobsters from the upper Liard Formation. These arthropods lived infaunally and are possible tracemakers of both *Diplocraterion* and *Cruziana* (and probably of *Spongeliomorpha* and *Thalassinoides* as well) (Zonneveld et al., 2002). Recent fieldwork has revealed that although most of these arthropods were small (2 - 6 cm from front of cephalothorax to end of abdomen), larger arthropods (up to 22 cm) also occurred (J-P. Zonneveld, personal communication, 2011). Coincidentally large *Cruziana* are absent from the Lower Triassic and appear during the Middle Triassic in beds that occur just below the arthropod fossil beds.

Previous studies have noted that Early Triassic ichnofaunas exhibit a Lilliput effect wherein post-extinction ichnotaxa are characterized by extraordinarily small sizes (Hayami, 1997; Twitchett and Wignall, 1996; Twitchett and Barras, 2004; Twitchett, 2007; MacNaughton and Zonneveld, 2010; Zonneveld et al., 2010c). The Lilliput effect has been interpreted to have resulted from globally stressed conditions due to low levels of dissolved oxygen in marine water (Wignall and Hallam, 1992; Twitchett and Wignall, 1996). Despite insufficient ichnofossil data from the uppermost Permian of western Canada to assess Paleozoic trace fossil sizes, the relatively small trace sizes within Lower Triassic successions of western Canada has also been attributed to the Lilliput effect (Zonneveld et al., 2010c). It is also suggested that the Lilliput effect diminished in the Olenekian in western Canada (Zonneveld et al., 2010a). In contrast, the ichnofossils of the study intervals are considerably larger than identical ichnotaxa of the Lower Triassic. The larger burrow sizes of the Middle Triassic ichnofossil assemblage of the study interval indicate that whatever adverse conditions prompted the Lilliput effect in the Lower Triassic were no longer in play (or were at least less prevalent) in the Middle Triassic.

Tiering trends

In the study interval, overall tiering is generally simple and shallow to deep in depth (i.e., 2 to 10 cm deep sediment-water interfaces and rare overprinting of older burrows by newer ones). Ichnotaxa within the study interval exhibit a variety of burrow depths and some ichnotaxa (e.g., *Thalassinoides* and *Spongeliomorpha*) are relatively deep-tiered. However, most traces are shallow- to medium-tier burrows (e.g., *Anconichnus*, *Arenicolites*, *Diplocraterion*, *Phycosiphon*, *Planolites*, and *Cruziana*). Despite such variable tiering, tiering relationships in the study interval are generally simple. As mentioned above, the simple tiering relationship within Facies D is due to upper shoreface settings with high-energy stress (Pemberton et al., 1992; MacEachern, 2007a). Only within lower shoreface successions were locally complex tiering relationships observed within the study interval.

Bromley and Ekdale (1986) showed relationships between burrow depth and ichnofabric due to taphonomic reasons (e.g., preservation potential). The deeper structures that dominate the ichnofabric and sediments with high ichnofabric indices tend to be solely bioturbated by deep-tiered burrows (Bromley, 1996). The ichnofabric indices of the study interval are low, mostly 2 and rarely 3 within limited beds of Facies C. Only a limited number of lower shoreface successions at Aylard Creek show ichnofabric indices of 4. This highest observed ichnofabric index consists of shallow to medium-tier structures (i.e., *Diplocraterion*, *Skolithos*, *Planolites*, *Palaeophycus*, *Asterosoma*, and *Anconichnus*). *Palaeophycus* and *Asterosoma* are more abundant within the beds and *Palaeophycus* tends to overlap other burrows like *Asterosoma*. A few specimens of *Asterosoma* also overlap each other or *Cylindrichnus* specimens. Although tiering patterns are locally complex in the lower shoreface interval, they are simple, compared to complex tiering relationships of previous studies of non-recovery periods (e.g., Locklair and Savrda, 1998).

Within offshore transition beds, tiering is observed to be simple despite the occurrence of various tier types. Deep-tiered burrows of *Thalassinoides* and

Spongeliomorpha have few interactions with shallow- to medium burrows, except for with *Cruziana* and *Anconichnus*. Composite forms with these ichnotaxa and *Anconichnus* implies that *Anconichnus* were produced after *Cruziana, Thalassinoides* and *Spongeliomorpha* (Pickerill and Narbonne, 1995; Bromley, 1996). A few specimens of *Planolites* overlap on *Cruziana* and *Spongeliomorpha*. A wide variety of tiering types, despite relatively simple tiering relationship, indicate relatively slow biogenic activities by a wide range of ichnofossil constructors within hospitable and healthy environments (e.g., Bromley, 1996).

In the study area, *Zoophycos* and *Chondrites*, which exhibit deep tiering in muddy substrata, are completely absent from the study interval, despite widespread preservation of lithologies and environments identical to those in which these traces normally occur. Zonneveld et al. (2010c) discussed the absence of *Chondrites* and *Zoophycos* in Lower Triassic successions. Although tolerant of dysoxic conditions, the *Chondrites* tracemeakers were not tolerant of complete anoxia (Savrda and Bottjor, 1989). Thus, the absence of *Chondrites* in the Lower Triassic may result from prolonged anoxic conditions in offshore successions of northwestern Pangaea/northwestern Panthalassa (Zonneveld et al., 2010c). Its continued absence in the Middle Triassic indicates that tracemakers of *Chondrites* had not yet recolonized the offshore of northwestern Pangaea.

Absence of *Zoophycos* and *Chondrites* probably indicate that Paleozoic tracemakers of these two ichnotaxa disappeared in western Canada during the end-Permian mass extinction event and post-Paleozoic tracemakers of these two ichnotaxa had not yet appeared by the Middle Triassic in the study area. In addition to the absence of specific tracemakers, benthic environments below wave base of the study interval were probably inimical to deep burrowers. Storm-generated sandstone beds of the offshore transition include a few deep burrows, but tiering relationships remained simple. Likewise, some lower shoreface beds contain deep burrows, but relatively simple tiering patterns were maintained. As previously mentioned, sediments that were deposited below fair-weather wave base (FWWB) occasionally include possible evidence of dysoxic conditions (i.e., pyrite framboids) (e.g., Raiswell et al., 1988; Canfield et al., 1996). These beds also contain surface grazing and shallow-tier structures with subordinate shallow-tiered burrows. Hence, conditions below FWWB in the study interval were suitable for shallow burrowers and grazers, but were probably not suitable for deep burrowers. Since wave activity increases the amount of oxygen dissolved in marine water in modern settings (Chanson and Cummings, 1994), conditions above FWWB in the Middle Triassic were likely well-oxygenated. Water above FWWB was continuously mixed with atmospheric oxygen. Pore waters in shallow sediments were also oxygenated due to frequent wave activity. Although some tracemakers can bypass oxidized water from sediment-water interfaces, oxygenation of sediment pore water is generally necessary for deep-tiered burrowers (Ekdale and Manson, 1988). Despite the stress of rapid sedimentation and high wave energy, recurring wave mixing supplied oxygen and nutrients, which maintained habitable conditions in the lower shoreface. Rapid recolonization occurred after sedimentation events, which is inferred by high ichnofabric indices and complex tiering-patterns. It is likely that similar conditions prevailed during storms above storm-wave base, as is indicated from relatively deep-tiered burrows within storm-generated beds below FWWB. However high ichnofabric indices and complex tiering relationships of lower shoreface beds were only locally observed, possibly indicating that the lower shoreface did not provide adequate amounts of food and oxygen in all areas to enable complex tiering relationships.

Implications of the diverse ichnofossils

Zonneveld et al. (2010c) reported abundant ichnofossil assemblages from the lowermost Triassic Montney Formation in the Pedigree-Ring-Kahntah River area. These ichnofossil assemblages were interpreted to represent environmental refugia, areas in which the crisis-causing environmental stressors were muted and thus marine invertebrates were less affected (Zonneveld et al., 2010c). The Pedigree-Ring-Kahntah ichnofaunas stand in stark contrast to other Early Triassic ichnofaunas in their high level of ichnodiversity and locally high ichnofabric indices. Total ichnofossil diversity of the Lower Triassic Pedigree-Ring-Kahntah

River is similar to that of the study interval. Similar to the Lower Triassic successions, the Toad-Liard assemblages also include many ichnotaxa that were common during the Paleozoic, such as *Cruziana*, *Rusophycus* and *Monomorphichnus*. As well, trace fossils interpreted to have been produced by arthropods (e.g., *Cruziana*, *Rusophycus*, *Diplocraterion*, and *Rhizocorallium*) are common within the study interval.

Despite the similarities between the present study interval and the Pedigree-Ring-Kahntah River ichnofossil assemblages, other aspects differ strongly. The dominant type of inferred tracemakers in the Toad-Liard succession are vermiform organisms. As discussed above, the Toad-Liard succession contains significantly larger traces than those in the Lower Triassic. Additionally, a wide variety of other tracemakers are interpreted to have produced the ichnofossils within both study intervals, including arthropods, echinoderms, sea anemones, bivalves, gastropods, brachiopods and fish (Table 2-1). This diversity of probable tracemakers implies high biological diversity. The Toad-Liard ichnofossil diversity, the overall abundance of traces in the study interval, and the robust sizes of the traces indicate that environmental stresses associated with the end-Permian extinction were no longer affecting infaunal and epifaunal organisms above storm wave base. It is also likely that geographic proximity to environmental refugia played a role in sourcing the taxa that migrated into the study area when conditions were ameliorated.

The global biological diversity of marine organisms during the Middle Triassic is considered to be lowest of any geological time period (Sepkoski, 1981, 1984). The end-Permian is marked by a pronounced reduction in the biological diversity of skeletonized marine taxa (e.g., Sepkoski, 1981). The perturbation was followed by an overall slow increase in total faunal diversity throughout the Triassic (Sepkoski, 1981, 1984, Alroy et al., 2008). Previous studies of skeletonized marine taxa have illustrated that the global diversity of Triassic marine faunas never attained the pre-Permian-Triassic extinction levels although relatively high numbers of new genera and families appeared during the Middle and Upper Triassic (Sepkoski, 1981, 1984, Alroy et al., 2008). The present study contains a broad variety of ichnotaxa indicating a relatively wide variety of tracemakers, probably reflecting the appearance of new taxa. Diverse ichnofossils in the study interval infer amelioration of environmental conditions. Nevertheless, overall simple tiering patterns may indicate that the benthic environments of the Middle Triassic were not completely suitable for the Middle Triassic benthic fauna. High ichnofossil diversity in the study interval likely reflects an increase in the behavioral innovation of a large number of species. Ethological characteristics and interpretations of the study interval are discussed in chapter three.

During the Early Triassic, many shallow marine benthic successions remained vacated or were scarcely populated due to shallow marine anoxia (Wignall and Hallam, 1992). However, surface water was probably oxic due to dissolution of oxygen into water by wave activity at the atmosphere-water interface (Chanson and Cummings, 1994). Beatty et al. (2008) suggested that storm-mixing of oxygen into the water column played a major role during the Early Triassic by allowing a shallow marine habitable zone to develop in areas where the shelf and shoreface profile were optimal. The habitable zone of the Lower Triassic in western Canada occurred between fair-weather and storm wave bases thus restricting shallow marine habitation to a very narrow belt (Beatty et al., 2008). In contrast, the broader environmental distribution of ichnofossils in the study interval indicates that a more extensive area of upper shoreface through proximal offshore environments were available for colonization. However, tiering trends imply sub-environments below fair-weather wave base likely remained stressed by low oxygen levels.

Ichnofossil communities in the study interval imply recovery of benthic environments in the study area after the end-Permian extinction. A broad range of environments from proximal offshore to distal upper shoreface became habitable in Middle Triassic. However, proximal offshore sediments include evidence of low oxygen levels. This probably indicates that the Middle Triassic shallow marine environment in northwestern Pangaea had yet completely recovered. Global comparisons of Middle Triassic ichnofossil assemblages are necessary to enhance understanding of global recovery patterns and clarify the timing of full recovery of benthic environments after the end-Permian mass extinction event.

CONCLUSION

Middle Triassic (Ladinian) strata in the Williston Lake area contain highly diverse trace fossil assemblages. Four ichnofossil associations within the study intervals were recognized based on ichnofossil content and sedimentological characteristics. The environmental distribution of trace fossils ranges from offshore to upper shoreface. Thirty-six ichnotaxa were observed in these successions. Traces exhibit a wide range of sizes, however, most ichnotaxa exhibit an increase in width compared to those within the Lower Triassic of western Canada. Shallow tiering characterizes the study interval with relatively deep-tiered burrows also occurring within lower shoreface beds. Tiering relationships are simple except for a few lower shoreface beds.

The *Phycosiphon*-*Scalarituba* (PS) ichnofossil association consists of 7 ichnotaxa within heterolithic beds of shale and sandy siltstone and thin muddy siltstone beds that are interpreted to have been deposited below fair-weather wave base. Ichnofossil intensity is zero to moderate: both ichnofabric and bedding-plane indices of 1 to 3. The present trace fossils are interpreted as grazing and deposit feeding structures. Shallow-tier structures and grazing traces exhibit simple tiering relationships. This association is similar to the *Zoophycos* Ichnofacies.

The *Cruziana-Spongeliomorpha-Thalassinoides* (CST) association contains 25 ichnotaxa and is dominated by horizontal to subhorizontal traces within storm-generated hummocky cross-stratified (HCS) sandstone beds that interbed with sandy siltstone characterized by the PS association. Composite and compound forms are common. Bioturbation intensity is moderate, with ichnofabric indices of 2 to 3, and bedding-plane bioturbation indices of 3 to 4. Behavioral interpretation of this assemblage is a mixture of dwelling structures of suspension feeders and deposit feeders as well as crawling, resting, and grazing structures. Shallow-tier structures emplaced at the sediment-water interface are dominant and rare deep-tiered burrows occur. This association is similar to the archetypal *Cruziana* Ichnofacies.

The *Diplocraterion-Palaeophycus* association, containing 26 ichnotaxa, is the most diverse trace fossil association in the study area. Main components of this association include *Diplocraterion* and *Palaeophycus*. Vertical burrows and horizontal burrows are present in nearly equal numbers. This assemblage occurs within amalgamated HCS sandstone beds, interpreted as lower shoreface deposits. Overall diversity is high, but individual abundances are relatively low. Bioturbation intensity is generally moderate to low, with ichnofabric indices of 2 to 3 and bedding-plane bioturbation indices of 2 to 3, but locally with ichnofabric and bedding-plane bioturbation indices of 4. A wide variety of ethological types of ichnofossils occur (e.g., domiciles of suspension feeders, deposit feeding burrows, burrows of passive carnivores, grazing burrows, resting burrows and crawling traces). This trace fossil association is similar to the distal *Skolithos* Ichnofacies.

The *Skolithos*-*Palaeophycus* association contains 10 ichnotaxa, including *Diplocraterion*, *Skolithos*, *Palaeophycus* and *Rhizocorallium*. This association occurs at only two outcrop locations within trough cross-stratified, fine-grained, calcareous sandstone beds, which are interpreted as distal upper shoreface deposits. Bioturbation intensity in this association is low in the study interval. Ichnofabric indices and bedding-plane bioturbation indices are both 2. The ichnotaxa are dominantly domichnia of suspension feeders. This association is analogous to the archetypal *Skolithos* Ichnofacies.

Broader environmental distributions of ichnofossils within the study interval indicates that shallow marine environments during the Middle Triassic Ladinian were habitable due to sufficient oxygen and nutrient content unlike comparable succession in the Lower Triassic of western Canada. High ichnofossil diversity and a wide variety of implied tracemakers probably indicates high local biological diversity despite relatively low global biological diversity during the Triassic reported elsewhere.

Burrow sizes of specific ichnotaxa within the study interval are much larger than those of the Lower Triassic of western Canada. Despite the lack of size comparison with identical ichnotaxa in Permian beds, the overall size of the Middle Triassic traces is up to 10 times larger with broader range of burrow size. Thus, the Lower Triassic Lilliput effect had disappeared by the Ladinian in western Canada, probably implying environmental recovery in proximal marine environments.

Overall tiering relationships within the study interval are simple and tiers are shallow to rarely deep (more than 10 cm). However, relatively deep-tiered burrows are generally absent within sediment below fair-weather wave base and tiering relationships are locally complex within lower shoreface beds. Hence it is suggested that bottom water and/or sediment pore water below fair-weather wave base was oxygenated, but not fully suitable for deep burrowing behaviours and/or organisms. Recurring wave activity supplied enough oxygen and nutrients above fair-weather wave base, producing relatively complex tiering relationships locally and deep-tiered burrows.

Ichnofossils of the study interval indicate that shallow marine environmental conditions were ameliorated after prolonged bottom water anoxia during the Lower Triassic. High diversity, large burrow size, broader size range, and wider environmental distributions of ichnofossils imply that biological diversity of the Ladinian of the study area was probably high. Overall relatively simple tiering relationships and absence of deep-tiered burrows in offshore implies that environmental stresses (e.g., low-oxygen level) may have been present.

In summary, Middle Triassic infaunal communities in shallow marine environments of the study area were diverse and back to ‘normal’ (i.e., back to pre-extinction levels). Nevertheless, organism recovery was not complete and depressed oxygen conditions likely continued below fair-weather wave base.

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CHAPTER 3

POST-EXTINCTION RECOVERY AND ETHOLOGICAL IMPLICATION OF SHALLOW MARINE ICHNOFOSSILS OF WESTERN CANADA

INTRODUCTION

The end-Permian mass extinction was the most severe mass extinction in Earth history (e.g., Raup, 1977; Raup and Sepkoski, 1982; Erwin, 1993). Although the direct cause of this strong perturbation is not completely understood, it has been suggested that global shallow-water anoxia (e.g., Wignall and Hallam, 1992; Wignall, 2007), as well as oceanic acidification (e.g., Knoll et al., 1996; Montenegro et al., 2011) resulted in a drop in the number of biological families at the end of the Permian). As a result of the disappearance of taxa during mass extinctions, and the concomitant creation of available ecospace, biotic diversification commonly occurs after environmental recovery (Sepkoski, 1981, 1984; Fraiser and Bottjer, 2007).

It is postulated that during recovery periods, the extinction of dominant faunas allows lesser faunas to dominate (e.g., Sepkoski, 1981, 1984). Since trace fossils preserve an *in situ* record of organismal behaviour (Gingras et al., 2007), they can be utilized as a dataset to examine changes in infaunal diversity over time. The constructors of individual ichnogenera may differ before extinctions and during the post-extinction recovery interval (e.g., Zonneveld et al., 2002; Zonneveld, 2008). As an example, *Cruziana*, which has been inferred to be the product of trilobite locomotion, occurs mainly within Paleozoic marine strata (e.g., Seilacher, 1964; Häntzschel, 1975). Specimens of *Cruziana*, however, are present in Lower and Middle Triassic marine beds in western Canada (including the study area) (e.g., Zonneveld et al., 2002; MacNaughton and Zonneveld, 2010; Zonneveld et al., 2010a, 2010b). The complete elimination of trilobites at (or possibly prior to) the end-Permian mass extinction indicates that the tracemakers of the Triassic *Cruziana* were not trilobites (Zonneveld et al., 2002). Instead, it has been proposed that these *Cruziana* likely reflect the activities of other marine arthropods, possibly decapods or isopods (Zonneveld et al., 2002, 2010b). Like this example, mass extinctions should have a profound effect on ichnology, including the composition of ichnofacies, the environmental distribution of individual ichnotaxa and the appearance or disappearance of specific ichnotaxa.

Ichnofacies and Post-Extinction Recovery

Ichnofacies were first introduced for recurrent associations of ichnofossils, with relationship to both sedimentary facies and depositional environment through the Phanerozoic on a global scale (Seilacher, 1964). Subsequently, ichnofacies were applied at smaller scales, such as individual rock units (e.g., Hayward, 1976). Although their early usage was primarily as bathymetric indicators (e.g., Farrow, 1966; Sellwood, 1971), ichnofacies are now known to be controlled by other factors in addition to water depth, such as substrate texture, level of energy, food type and availability, water turbidity, water salinity, and other stresses (e.g., Crimes, 1973; Bromley and Ekdale, 1984; Pemberton and Frey, 1984a; Savrda and Bottjer, 1989; Frey et al., 1990; Dashtgard et al., 2008). Due to the fact that ichnofacies are controlled by various environmental factors, ichnofacies analyses provide datasets for high-resolution interpretation of depositional environments (e.g., Pemberton and Frey, 1984a; Savrda and Bottjer, 1989; MacEachern et al., 2007a, 2007c).

Ichnofacies are identified and classified based on substrate type and depositional environment (marine or continental). There are marine softground ichnofacies (e.g., *Psilonichnus*, *Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites* ichnofacies), firmground ichnofacies (e.g., *Glossifungites* Ichnofacies), hardground ichnofacies (e.g., *Trypanites* Ichnofacies), and woodground ichnofacies (e.g., *Teredolites* Ichnofacies) as well as continental ichnofacies (e.g., *Scoyenia*, *Mermia*, and *Coprinisphaera* ichnofacies) (MacEachern et al., 2007a, 2007c). Walther's Law (Middleton, 1973) is applicable to ichnofacies (MacEachern et al., 2007a). Thus, a conformable vertical succession of ichnofacies also represents lateral adjacency of environments (e.g., MacEachern et al., 2007a, 2007c). In many cases, if there is no unconformity, ichnofacies that represent adjacent environments grade into each other (MacEachern et al., 2007a).

Although the basic underpinnings of individual ichnofacies hold true, regardless of temporal occurrence, minimal attention has been given to assessing how these models may vary from the norm during intervals of unusual environmental stress. Despite the fact that Seilacher's early studies included Triassic trace fossils in order to establish ichnofacies (Seilacher, 1964), the applicability of the ichnofacies framework to a recovery period following a mass extinction has not been tested. Moreover, ichnological analyses of the recovery interval after the end-Permian extinction are limited. Early Triassic examples from the United States and Italy identified seminal characteristics of survivor faunas including overall reductions in trace fossil size and ichnofaunal diversity (Twitchett and Wignall, 1996; Twitchett, 1999; Pruss et al., 2004; Pruss and Bottjer, 2004). Early Triassic examples from northeastern British Columbia have shown that a narrow 'habitable zone' occurred in the lower shoreface to offshore transition, wherein ichnogeneric diversity was anomalously high although ichnofossil sizes were generally quite small (Beatty et al., 2008; Zonneveld et al., 2010a, 2010b).

In contrast with Lower Triassic ichnofossil studies, analyses of Middle Triassic ichnology are even rarer (e.g., Knaust, 2007; Rodríguez-Tovar et al., 2007; Mørk and Bromley, 2008; Rodríguez-Tovar and Pérez-Valera, 2008). The Middle Triassic is generally thought to be a post-recovery period (e.g., Erwin, 2001). So that Middle Triassic strata ought to exhibit different characteristics of ichnofossils and/or ichnofacies than those described from recovering Early Triassic successions. For this reason, the Middle Triassic is a particularly important period for paleoecological analyses. This chapter describes in detail all ichnotaxa identified from the Middle Triassic upper Toad and lower Liard formations at Williston Lake in northeastern British Columbia (Fig. 3-1). Ichnofossil associations (defined in chapter two) are compared with ichnofacies to test applicability of ichnofacies models to the study interval. Comparison of the

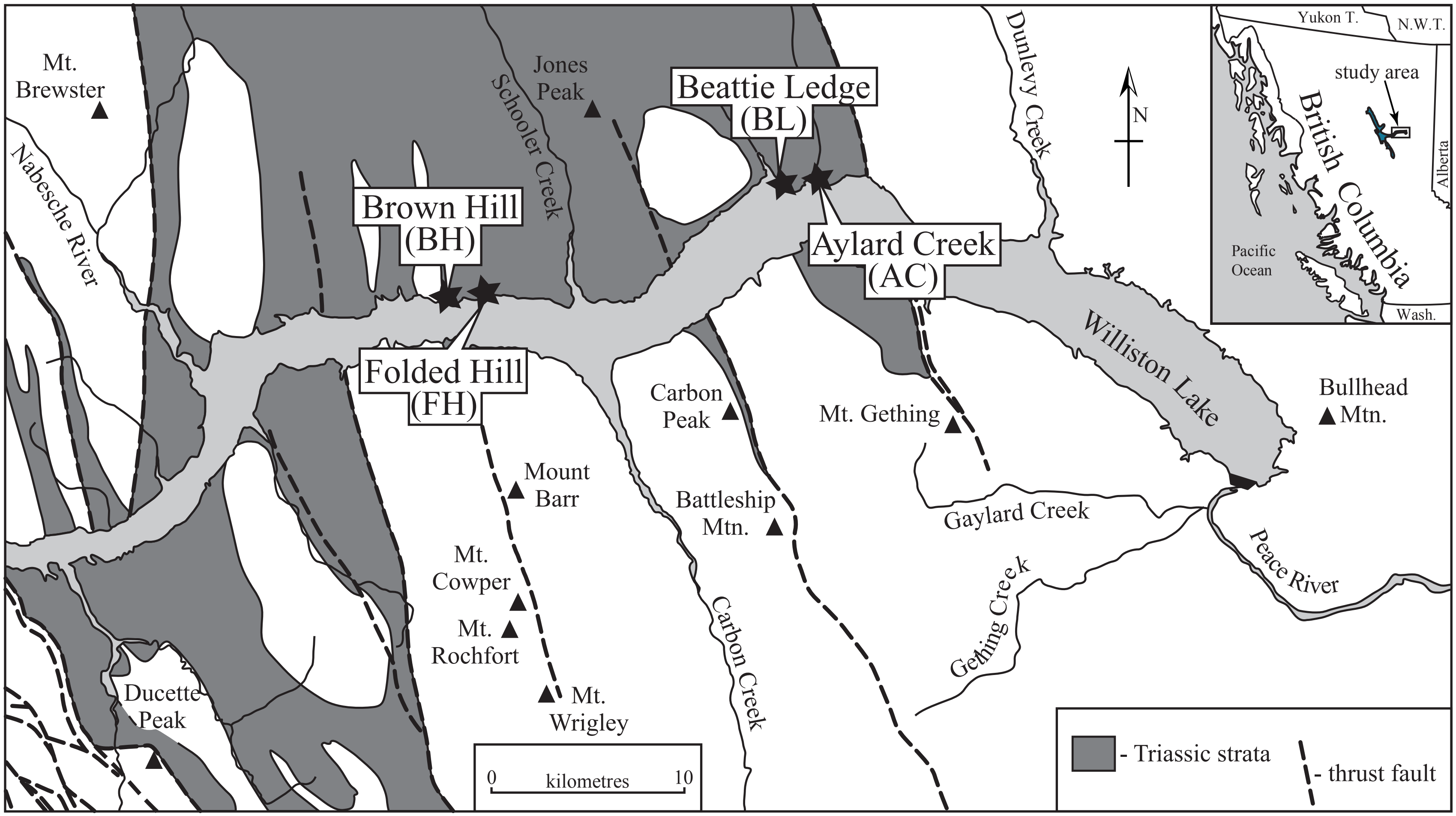

FIGURE 3-1—Location map of the study area (after Zonneveld, 2008). Four outcrop locations along the Peace Reach of Williston Lake are denoted.

Williston ichnofossil associations with traditional ichnofacies provides a method with which post-extinction ecological recovery can be assessed.

Datasets and Methods

In this study, the ichnology of four outcrop sections (Fig. 3-2) in the upper Toad and lower Liard formations is described (see chapter two for stratigraphy). Ichnological analysis of the intervals of interest was conducted by identifying ichnotaxa, measuring trace fossil sizes, interpreting ethology and interpreting possible tracemakers. Ichnofossil associations summarized in chapter two are utilized to compare against ichnofacies and to discuss the ethological implications of the Middle Triassic ichnofossil associations in the study intervals. Characteristics of ichnofacies are summarized from MacEachern et al. (2007a, 2007b, 2007c).

All the ichnotaxa observed in the study intervals are listed by outcrop section in Tables 3-1 through 3-4. The size of traces is provided where possible. Trace fossil lengths represent trace depth of vertical forms. Both trace width and length include lining thickness. Distributions of faunas are generally patchy in their nature (e.g., Lloyd, 1967; Sasaki, 1997), and settlements of taxa is controlled by accessible ecospace and occurring taxa in the ecospace (e.g., Brenchley, 1982; Commito, 1982). In case of trace fossils, overprintings or destructions of old trace fossils by newer ones can occur (e.g., Goldring, 1965; Austin and Bottjer, 1982; Bromley, 1996). These aspects made establishments of statistical parameters of ichnofossil distribution and abundance difficult and incomplete. Consequently, absolute numbers of ichnofossils or each ichnotaxon are not statistically useable without interpretation. the abundance of each ichnotaxon herein is reported qualitatively. Qualitative categories for relative abundance of ichnotaxon per outcrop are as follows: 1) rare (1-3 specimens), 2) present (4-15 specimens), 3) abundant (>15 specimens). In many cases, each ichnogenus shows different relative abundances depending on sediment type and a depositional environment.

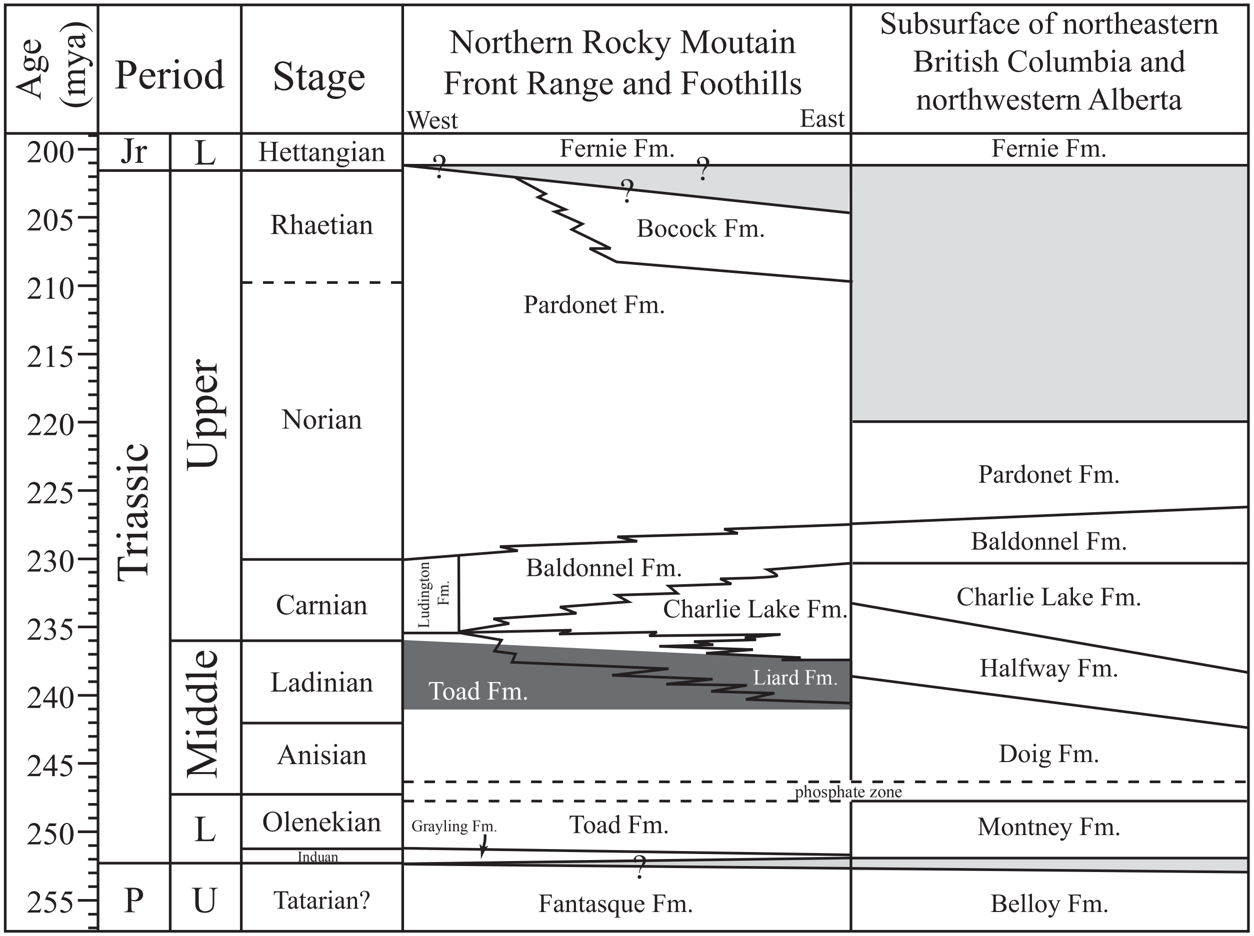

FIGURE 3-2—Triassic nomenclatures of western Canada (after Edwards et al., 1994; Zonneveld, 2008; Mundi et al., 2010; Hüsing et al., 2011). Light grey indicates lack of beds. The dark grey denotes the approximate study interval. P = Permian, Jr = Jurassic, Up = upper, L = lower, Fm. = Formation, mya = million years ago.

TABLE 3-1—List of trace fossils within the study interval at Brown Hill. White indicate no trace. Light grey indicate rare (1-3 specimens). Light dark grey indicate present (4-10 specimens). Dark grey indicate common (10-15 specimens). Black indicate abundant (>15 specimens). PS = *Phycosiphon-Scalarituba* association; CST = *Cruziana-Spongeliomorpha-Thalassinoides* association; DP = *Diplocraterion-Palaeophycus* association; SP = *Skolithos-Palaeophycus* association.

ichnotaxon	**burrow width**	**burrow length**	**behaviour**	**ichnofossil association**				**inferred tracemaker**
				PS	CST	DP	SP	
Anconichnus	<1 mm	unknown	grazing	█	▒	░		vemiforms (Goldring et al., 1991)
Arenicolites	N/A	N/A	dwelling			░	░	arthropods (Hakes, 1976)
Asteriacites	10-50 mm	unknown	resting			▒		asteroids or ophiuroids (Häntzschel, 1975; Mikuláš, 1990)
Asterosoma	10-50 mm	unknown	feeding		░	▓		vemiforms (Chamberlain, 1971)
Conichnus	2-5 mm	10 mm	dwelling				░	sea anemones (Frey and Howard, 1981)
Cruziana	10-20 mm	<10 mm	dwelling		░			arthropods (Zonneveld et al., 2002)
Cylindrichnus	5-20 mm	80 mm	dwelling		░	▒		vermiforms (Frey and Howard, 1985)
Diplocraterion	12-120mm	<100 mm	dwelling		█	▓		polychaetes or arthropods (Fürsich, 1974b; Häntzschel, 1975)
Gyrochorte	6-10 mm	>100 mm	crawling		░			gastropod and vermiform (Heinberg, 1973)
Helminthoidia	<1 mm	unknown	grazing	▓				vermiforms (Bjerstedt, 1987)
Helminthopsis	<1 mm	unknown	grazing	▓				vermiforms (Bjerstedt, 1987)
Lingulichnus	<20 mm	unknown	dwelling / feeding		▓	▒		lingulides (Hakes, 1976)
Lockeia	7-10 mm	~10 mm	resting		▓	▓		bivalves (Nara, 2003)
Monocraterion	5-10 mm	unknown	dwelling / feeding		░	░		polychaetes (Bjerstedt, 1988)
Monomorphichnus	<1 mm	30-40 mm	crawling		░			arthropods (Mikuláš, 1995)
Ophiomorpha	5- 10 mm	N/A	dwelling				█	arthropods (Frey et al., 1978)
Palaeophycus	5-20 mm	unknown	dwelling		▒	█	█	polychaete (Pemberton and Frey, 1982)
Phycosiphon	<1 mm	unknown	grazing	█	░			vemiforms (Chamberlain, 1971)
Planolites	2-15 mm	<15 mm	feeding / dwelling	█	█	▓	░	polychaetes (Pemberton and Frey, 1982)
Rhizocorallium	10-60 mm	unknown	dwelling / feeding			▒	▒	polychaetes (Fürsich, 1974a)
Rosselia	10-25 mm	>20 mm	feeding / dwelling		░	▒		polychaetes (Nara, 1995)
Rusophycus	10-25 mm	15 mm	resting		▒			arthropods (Crimes, 1975)
Scalarituba	1-5 mm	>2 mm	grazing	█				vermiforms (Conkin and Conkin, 1968)
Scolicia	5-8 mm	unknown	feeding		▒			echinoids or gastropods (Häntzschel, 1975; Bromley and Ekdale, 1986)
Siphonichnus	10 mm	100 mm	resting / dwelling			▒		bivalves (Pearson and Gingras, 2006)
Skolithos	2-5 mm	40 mm	dwelling			█	▓	polychaete or phoronid (Pemberton and Frey, 1984)
Spongelimopha	10-60 mm	~<150 mm	dwelling		▓	░		arthropod (Metz, 1993)
Teichichnus	2-10 mm	~<30 mm	dwelling / feeding		▒	▒		vermiforms (Frey and Howard, 1985)
Thalassinoides	10-50 mm	unknown	dwelling / feeding	█	█	▒		arthropods (Howard and Frey, 1984)
Pellet-filled trace	0.5-2 mm	~50 mm	?dwelling / feeding			▒	░	?ophiuroids (J-P. Zonneveld, personal communication, 2011)
Escape trace (*fugichnia*)	5-10 mm	10-50 mm	escaping		▒	▒		?arthropod, ?vermiform

TABLE 3-2—List of trace fossils within the study interval at Folded Hill. White indicate absence. Light grey indicate rare (1-3 specimens). Light dark grey indicate present (4-10 specimens). Dark grey indicate common (10-15 specimens). Black indicate abundant (>15 specimens). PS = *Phycosiphon-Scalarituba* association; CST = *Cruziana-Spongeliomorpha-Thalassinoides* association; DP = *Diplocraterion-Palaeophycus* association; SP = *Skolithos-Palaeophycus* association.

ichnotaxon	burrow width	burrow length	behaviour	ichnofossil association				inferred tracemaker
				PS	CST	DP	SP	
Anconichnus	<1 mm	unknown	grazing	█	▓	░		vemiforms (Goldring et al., 1991)
Asterosoma	10-50 mm	unknown	feeding		▓	▓		vemiforms (Chamberlain, 1971)
Cruziana	10-20 mm	<10 mm	dwelling		░	░		arthropods (Zonneveld et al., 2002)
Cylindrichnus	5-20 mm	80 mm	dwelling		▒	▒		vermiforms (Frey and Howard, 1985)
Diplocraterion	12-120 mm	<100 mm	dwelling		█	█		polychaetes or arthropods (Fürsich, 1974b; Häntzschel, 1975)
Gyrochorte	6-10 mm	>100 mm	crawling		░			gastropod and vermiform (Heinberg, 1973)
Helminthoidia	<1 mm	unknown	grazing	█				vermiforms (Bjerstedt, 1987)
Helminthopsis	<1 mm	unknown	grazing	█				vermiforms (Bjerstedt, 1987)
Lingulichnus	<20 mm	unknown	dwelling / feeding		▒	▒		lingulides (Hakes, 1976)
Monomorphichnus	<1 mm	30-40 mm	crawling		░			arthropods (Mikuláš, 1995)
Ophiomorpha	5- 10 mm	N/A	dwelling				░	arthropods (Frey et al., 1978)
Palaeophycus	5-20 mm	unknown	dwelling		▒	█	▓	polychaete (Pemberton and Frey, 1982)
Phycosiphon	<1 mm	unknown	grazing	█	░			vemiforms (Chamberlain, 1971)
Planolites	2-15 mm	<15 mm	feeding / dwelling	█	█	▓	░	polychaetes (Pemberton and Frey, 1982)
Rhizocorallium	10-60 mm	unknown	dwelling / feeding			▒	▒	polychaetes (Fürsich, 1974a)
Rusophycus	10-25 mm	15 mm	resting		▒			arthropods (Crimes, 1975)
Scalarituba	1-5 mm	>2 mm	grazing	█				vermiforms (Conkin and Conkin, 1968)
Scolicia	5-8 mm	unknown	feeding		▒			echinoids or gastropods (Häntzschel, 1975; Bromley and Ekdale, 1986)
Skolithos	2-5 mm	40 mm	dwelling			▓	▓	polychaete or phoronid (Pemberton and Frey, 1984)
Spongelimopha	10-60 mm	~<150 mm	dwelling		▓	░		polychaete or phoronid (Pemberton and Frey, 1984)
Teichichnus	2-10 mm	~<30 mm	dwelling / feeding			▒		arthropod (Metz, 1993)
Thalassinoides	10-50 mm	unknown	dwelling / feeding	█	█	▒		vermiforms (Frey and Howard, 1985)
Undichna	2 mm	unknown	swimming		░	░		fish (Anderson, 1976)
Pellet-filled trace	0.5-2 mm	~50 mm	?dwelling feeding			▒	▒	?ophiuroids (J-P. Zonneveld, personal communication, 2011)
Escape trace (*fugichnia*)	5-10 mm	10-50 mm	escaping		▒	▓		?arthropod, ?vermiform

TABLE 3-3—List of trace fossils within the study interval at Beatty Ledge. White indicate no trace. Light grey indicate rare (1-3 specimens). Light dark grey indicate present (4-10 specimens). Dark grey indicate common (10-15 specimens). Black indicate abundant (>15 specimens). PS = *Phycosiphon-Scalarituba* association; CST = *Cruziana-Spongeliomorpha-Thalassinoides* association; DP = *Diplocraterion-Palaeophycus* association.

ichnotaxon	**burrow width**	**burrow length**	**behaviour**	**ichnofossil association**			**inferred tracemaker**
				PS	CST	DP	
Anconichnus	<1 mm	unknown	grazing	█	▓	░	vemiforms (Goldring et al., 1991)
Arenicolites	N/A	N/A	dwelling			▒	arthropods (Hakes, 1976)
Asteriacites	10-50 mm	unknown	resting		░	░	asteroids or ophiuroids (Häntzschel, 1975; Mikuláš, 1990)
Asterosoma	10-50 mm	unknown	feeding		▒	▒	vemiforms (Chamberlain, 1971)
Cruziana	10-20 mm	<10 mm	dwelling		▓	░	arthropods (Zonneveld et al., 2002)
Diplocraterion	12-120mm	<100 mm	dwelling		▒	▓	polychaetes or arthropods (Fürsich, 1974b; Häntzschel, 1975)
Helminthoidia	<1 mm	unknown	grazing	▒			vermiforms (Bjerstedt, 1987)
Helminthopsis	<1 mm	unknown	grazing	▒			vermiforms (Bjerstedt, 1987)
Lingulichnus	<20 mm	unknown	dwelling / feeding		▒	▒	lingulides (Hakes, 1976)
Lockeia	7-10 mm	~10 mm	resting		▒	▒	bivalves (Nara, 2003)
Palaeophycus	5-20 mm	unknown	dwelling		▒	█	polychaete (Pemberton and Frey, 1982)
Phycosiphon	<1 mm	unknown	grazing	█	▒		vemiforms (Chamberlain, 1971)
Planolites	2-15 mm	<15 mm	feeding / dwelling	█	█	▒	polychaetes (Pemberton and Frey, 1982)
Rhizocorallium	10-60 mm	unknown	dwelling / feeding			▒	polychaetes (Fürsich, 1974a)
Rusophycus	~10 mm	15 mm	resting		▒		arthropods (Crimes, 1975)
Scalarituba	1-5 mm	>2 mm	grazing	█			vermiforms (Conkin and Conkin, 1968)
Scolicia	5-8 mm	unknown	feeding		▒		echinoids or gastropods (Häntzschel, 1975; Bromley and Ekdale, 1986)
Skolithos	2-5 mm	40 mm	dwelling			▒	polychaete or phoronid (Pemberton and Frey, 1984)
Spongelimopha	10-60 mm	~<150 mm	dwelling		▒	░	arthropod (Metz, 1993)
Teichichnus	2-10 mm	~<30 mm	dwelling / feeding		▒	▒	vermiforms (Seilacher and Hemleben, 1966)
Thalassinoides	10-50 mm	unknown	dwelling / feeding	█	█	▒	arthropods (Howard and Frey, 1984)
Treptichnus	2-5 mm	unknown	feeding / resting		░	░	vermiforms (Zonneveld et al., 2010)
Pellet-filled trace	0.5-2 mm	~50 mm	?dwelling / feeding			▒	?ophiuroids (J-P. Zonneveld, personal communication, 2011)
Escape trace (*fugichnia*)	5-10 mm	10-50 mm	escaping		▒	▒	?arthropod, ?vermiform

TABLE 3-4—List of trace fossils within the study interval at Aylard Creek. White indicate absence. Light grey indicate rare (1-3 specimens). Light dark grey indicate present (4-10 specimens). Dark grey indicate common (10-15 specimens). Black indicate abundant (>15 specimens). PS = *Phycosiphon-Scalarituba* association; CST = *Cruziana-Spongeliomorpha-Thalassinoides* association; DP = *Diplocraterion-Palaeophycus* association.

ichnotaxon	burrow width	burrow length	behaviour	ichnofossil association			inferred tracemaker
				PS	CST	DP	
Anconichnus	<1 mm	unknown	grazing	█	▓	▒	vemiforms (Goldring et al., 1991)
Arenicolites	N/A	N/A	dwelling			▒	arthropods (Hakes, 1976)
Asteriacites	10-50 mm	unknown	resting		░	░	asteroids or ophiuroids (Häntzschel, 1975; Mikuláš, 1990)
Asterosoma	10-50 mm	unknown	feeding		░	▓	vemiforms (Chamberlain, 1971)
Bergaueria	50 mm	unknown	resting / dwelling			░	sea anemones (Pemberton et al., 1988)
Cruziana	10-20 mm	<10 mm	dwelling		▒	░	arthropods (Zonneveld et al., 2002)
Cylindrichnus	5-20 mm	80 mm	dwelling		░	▓	vermiforms (Frey and Howard, 1985)
Diplocraterion	12-120 mm	<100 mm	dwelling		█	▓	polychaetes or arthropods (Fürsich, 1974b; Häntzschel, 1975)
Gyrochorte	6-10 mm	>100 mm	crawling		░		gastropod and vermiform (Heinberg, 1973)
Gyrolithes	5-25 mm	unknown	dwelling		▒		vermiforms or arthropods (Powell, 1977; Wetzel et al., 2007)
Helminthoidia	<1 mm	unknown	grazing	▓			vermiforms (Bjerstedt, 1987)
Helminthopsis	<1 mm	unknown	grazing	▓			vermiforms (Bjerstedt, 1987)
Lingulichnus	<20 mm	unknown	dwelling / feeding		▒	▒	lingulides (Hakes, 1976)
Lockeia	7-10 mm	~10 mm	resting		▒	▒	bivalves (Nara, 2003)
Monomorphichnus	<1 mm	30-40 mm	crawling		░		arthropods (Mikuláš, 1995)
Palaeophycus	5-20 mm	unknown	dwelling		▒	█	polychaete (Pemberton and Frey, 1982)
Phycodes	3mm	unknown	feeding / dwelling		░		vermiforms (Han and Pickerill, 1994)
Phycosiphon	<1 mm	unknown	grazing	█	▒		vemiforms (Chamberlain, 1971)
Planolites	2-15 mm	<15 mm	feeding / dwelling	█	█	▒	polychaetes (Pemberton and Frey, 1982)
Rhizocorallium	10-60 mm	unknown	dwelling / feeding			▨	polychaetes (Fürsich, 1974a)
Rosselia	10-25 mm	>20 mm	feeding / dwelling			▓	polychaetes (Nara, 1995)
Rusophycus	~10 mm	15 mm	resting		▨		arthropods (Crimes, 1975)
Scalarituba	1-5 mm	>2 mm	grazing	█			vermiforms (Conkin and Conkin, 1968)
Scolicia	5-8 mm	unknown	feeding		▨	░	echinoids or gastropods (Häntzschel, 1975; Bromley and Ekdale, 1986)
Skolithos	2-5 mm	40 mm	dwelling			▨	polychaete or phoronid (Pemberton and Frey, 1984)
Spongelimopha	10-60 mm	~<150 mm	dwelling		▓	▒	arthropod (Metz, 1993)
Teichichnus	2-10 mm	~<30 mm	dwelling / feeding			▒	vermiforms (Frey and Howard, 1985)
Thalassinoides	10-50 mm	unknown	dwelling / feeding	█	█	▨	arthropods (Howard and Frey, 1984)
Treptichnus	2-5 mm	unknown	feeding / resting		░	░	vermiforms (Seilacher and Hemleben, 1966)
Pellet-filled trace	0.5-2 mm	~50 mm	?dwelling / feeding			▒	?ophiuroids (J-P. Zonneveld, personal communication, 2011)
Escape trace (*fugichnia*)	5-10 mm	10-50 mm	escaping		▒	▨	?arthropod, ?vermiform

ICHNOTAXONOMY

Ichnofossils Observed within the Study Interval

Ichnotaxa described and interpreted here are listed alphabetically. Detailed descriptions of ichnofossil associations are provided in chapter two.

Anconichnus Kern, 1978

Anconichnus is a small, sinuous to meandering burrow (Kern, 1978; Goldring et al., 1991; Wertz and Bromley, 1994). It is three-dimensionally oriented within sediments unlike *Helminthoida*, *Helminthopsis* and *Phycosiphon*, which are limited to bedding-plane occurrences. Grey halos surround dark black cores on cross-sectional view of this trace (Kern, 1978; Goldring, 1991). *Anconichnus* is interpreted to represent the grazing behavior of diminutive vermiform organisms (Goldring et al., 1991; Bromley, 1996). The burrow is very small (less than 1 mm), and is common within very fine-grained sandstone, sandy siltstone, and muddy siltstone beds at all locations (chapter two; Table 3-1 through 3-4). The trace commonly occurs within the infill of *Cruziana*, *Thalassinoides*, and *Spongeliomorpha* burrows (as composite ichnofossils), mainly within very fine- to fine- grained sandstone beds (Fig. 3-3A, B). *Anconichnus* commonly occurs associated with *Scalarituba*, *Planolites*, *Phycosiphon*, *Helminthoida*, and *Helminthopsis* in siltstone beds. Within some beds, specimens of *Anconichnus* are very difficult to distinguish from *Phycosiphon*, *Helminthoida*, and *Helminthopsis* due to similar appearance and size of these traces, as well as the poor preservation of trace fossils at outcrop.

Arenicolites Salter, 1857

Arenicolites is an unlined vertical, U-shaped tube without spreite (Chamberlain, 1971; Pickerill et al., 1984; Bjerstedt, 1988). It is interpreted to be a burrow constructed by worms or crustaceans (Goldring, 1962; Hakes, 1976; Häntzschel, 1975; Bromley, 1996). In the study interval, this trace occurs within fine-grained sandstone beds, interpreted as lower shoreface at Beatty Ledge and

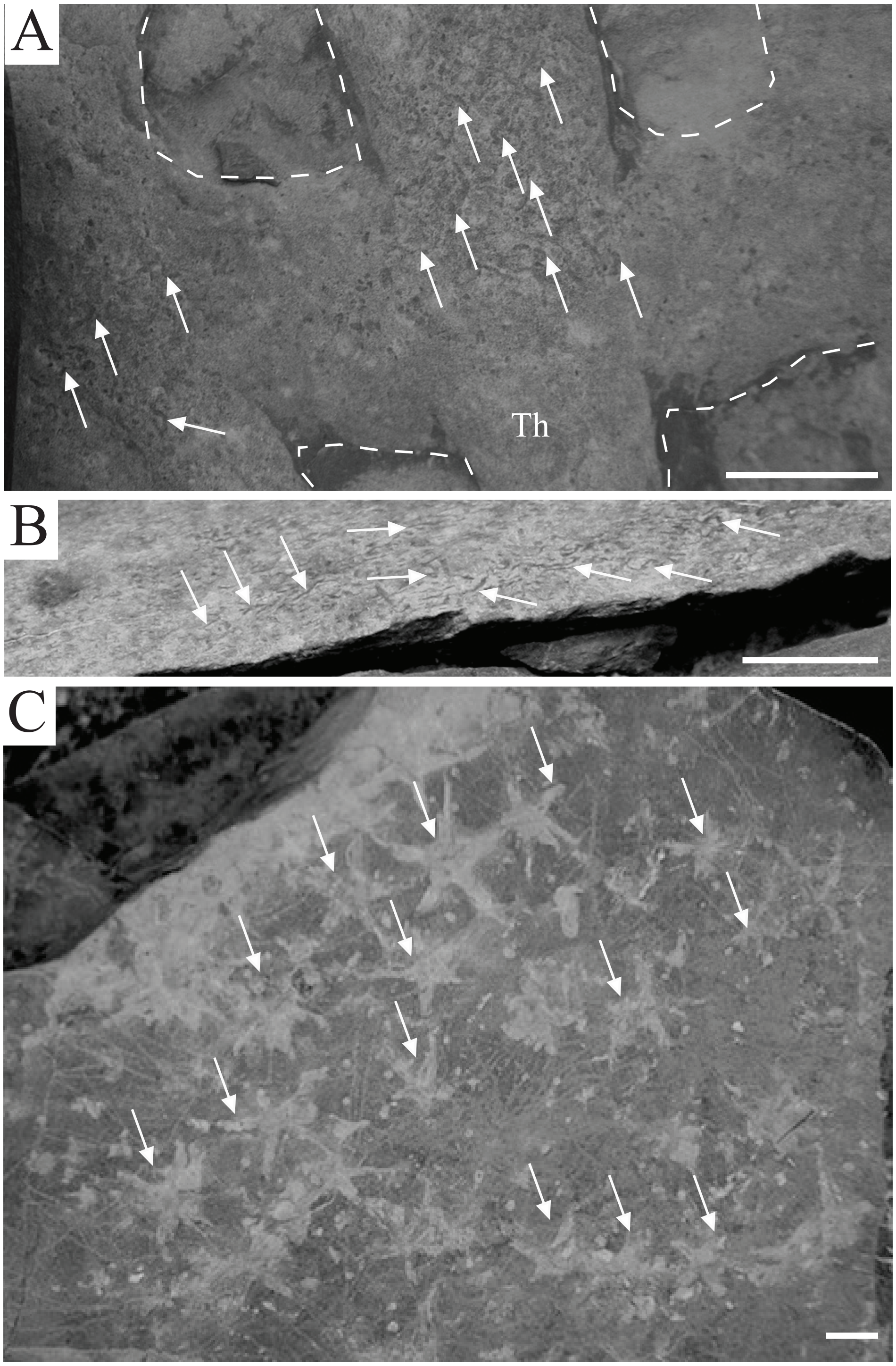

FIGURE 3-3—Photos of trace fossils I. (A) Dark black structures of *Anconichnus* (arrowed) occur within *Thalassinoides* (Th) burrow (outlined with dashed lines) in very fine-grained sandstone (Facies B) at Beatty Ledge. (B) *Anconichnus* (arrowed) occur within offshore transition sandy siltstone at Aylard Creek. (C) Multiple specimens of star-shaped *Asteriacites* occur within a fallen slab (fine-grained sandstone beds) at Brown Hill. Scale bar = 1 cm (A and C), 0.5 cm (B).

Aylard Creek, and lower to upper shoreface sediments at Brown Hill. At these outcrop locations *Arenicolites* typically occurs in isolation of other ichnotaxa. The width of tubes ranges from 5 to 15 mm (Table 3-1, 3-3, and 3-4).

Asteriacites Schlotheim, 1820

Asteriacites is a star-shaped structure and is oriented parallel to bedding (Häntzschel, 1975; Mángano et al, 1999). The trace is interpreted as resting traces of asteroids or ophiuroids (Häntzschel, 1975; Mikuláš, 1990). In the study interval, the trace occurs in hummocky cross-stratified (HCS) sandstone beds of the lower shoreface and offshore transition zones at Aylard Creek and Beattie Ledge. In addition to these, *Asteriacites* occurs in very fine-grained sandstone beds of a fallen slab at Brown Hill (Table 3-4), seen as a concave-downward impression. The surface of the slab contains multiple specimens of *Asteriacites* associated with *Skolithos* (Fig. 3-3C). Within the study area *Asteriacites* is no more than 5 cm wide. All specimens of *Asteriacites* from the study interval have long slender arms and are likely attributable to ophiuroids (brittle stars) rather than true starfish (asteroids) (J-P. Zonneveld, personal communication, 2011). Note that these fossils are common in some sandstone beds in the study interval (Zonneveld, 1999, 2008).

Asterosoma Otto, 1854

Asterosoma is a roughly star-shaped, systematic burrow, consisting of vertical tubes and radially spreading tubes to the sides (Chamberlain, 1971; Häntzschel, 1975). The lateral tubes are bulb shaped with relatively thick linings, and show alternatingly concentric sand and mud laminae, surrounding central tubes (Bromley and Uchman, 2003; Carmona et al., 2008). These burrows are interpreted as the dwelling structures of deposit feeding worm-like organisms (Chamberlain, 1971). In the study interval, the trace occurs in hummocky cross-stratified (HCS), very fine-grained sandstones, interpreted as the offshore transition and lower shoreface environment in all the studied sections. The lateral tubes of *Asterosoma* are 1 to 5 cm wide. Lower shoreface sediments at Aylard

Creek contain dense packages of *Asterosoma*-*Rosselia* beds (see chapter two) (Fig. 3-4A, B) (Table 3-4). On the plan view of these beds, some specimens of *Asterosoma* horizontally change into *Cylindrichnus*-like, and rarely into *Rosselia*-like burrows.

Bergaueria Prantl, 1946

Bergaueria is a plug-shaped, vertically-oriented burrow (Pemberton et al., 1988). The lower end is rounded, and the diameter of the trace is nearly equal to, or up to twice, the depth (Häntzschel, 1975; Pemberton et al., 1988). The base sometimes includes a central depression with, or without, radial ridges (Pemberton et al., 1988). *Bergaueria* is interpreted as the resting trace of a sea anemone (Alpert, 1973; Pemberton et al., 1988). In the study interval, this trace generally occurs in isolation within amalgamated hummocky cross-stratified sandstone beds (Facies C) (see Table 2-1) at Aylard Creek. It is approximately 5 cm wide in the study interval.

Conichnus Myannil, 1966

Conichnus is a conical or cone-shaped structure, oriented perpendicular to bedding (Häntzschel, 1975; Pemberton et al., 1988). Trace width narrows downward to the bottom (Häntzschel, 1975; Pemberton et al., 1988). Trace diameter is generally approximately half of its depth (Pemberton et al., 1988). A small protrusion may occur at its bottom (Pemberton et al., 1988). The trace is interpreted as a dwelling burrow of a sea anemone (Frey and Howard, 1981; Pemberton et al., 1988). In the study interval, a few of *Conichnus* occur together in isolation from other trace fossils within lower shoreface sediments at Brown Hill (Table 3-1). The trace size ranges from 2 to 5 mm wide.

Cruziana d'Orbigny, 1842

Cruziana is a horizontal, bilobate track or burrow with regular striations or scratch marks on its basal surface that are generally oriented perpendicular or oblique to the long axis of the burrow (Häntzschel, 1975). These burrows are

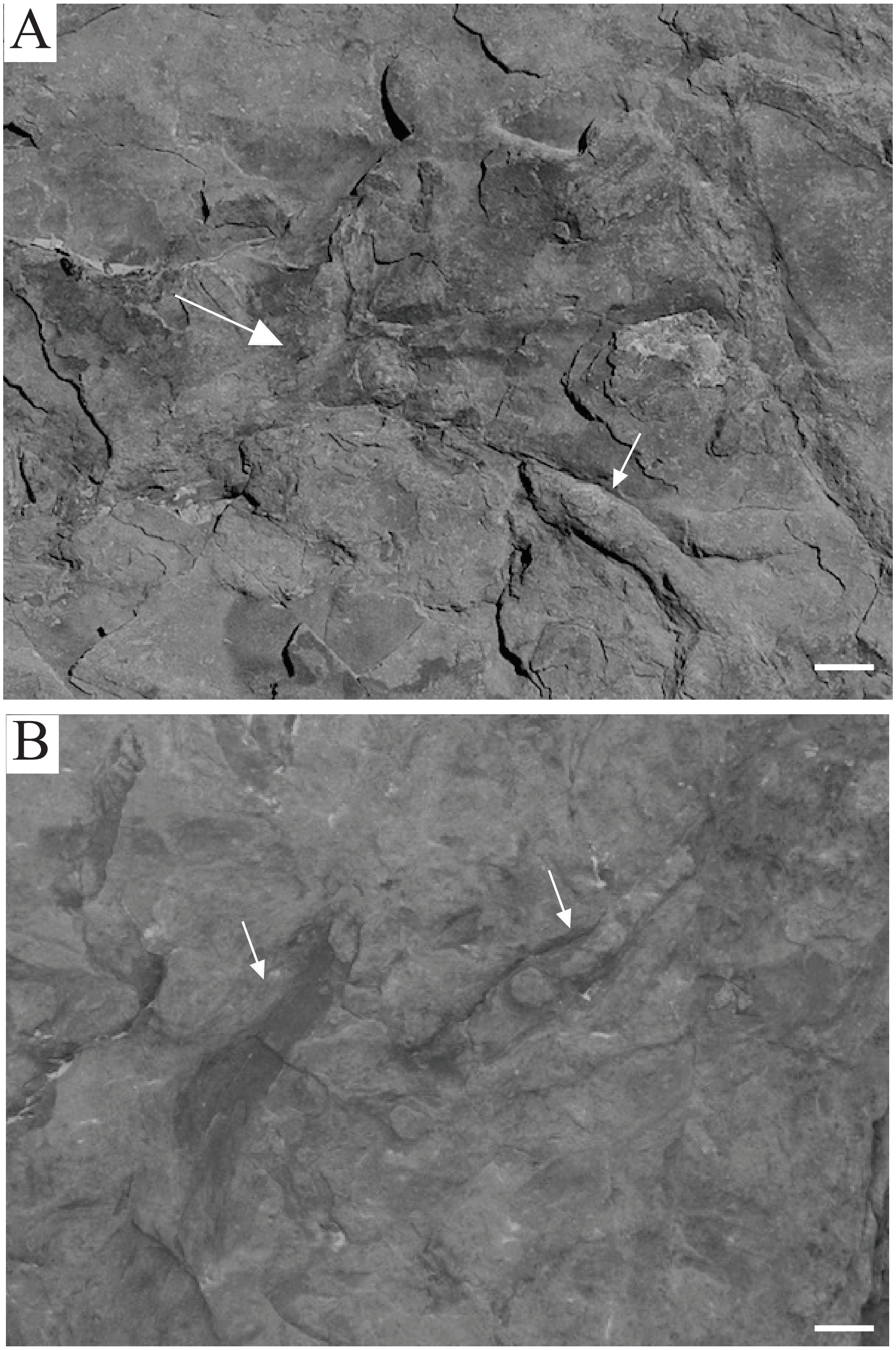

FIGURE 3-4—Photos of trace fossils II. (A) A roughly star-shaped structure (large arrow) of *Asterosoma* occur in very fine-grained sandstone of lower shoreface beds at Aylard Creek with a spreading "arm" (small arrow) (B) Piece of spreading arms of *Asterosoma* (arrows) in the same sediments as (A) at Aylard Creek. Scale bar = 1 cm.

interpreted as crawling traces or deposit feeding structures constructed by arthropods, such as trilobites and decapod crustaceans (Seilacher, 1964; Häntzschel, 1975; Zonneveld et al., 2002). *Cruziana* occurs as both surficial furrows as well as intrastratal burrows (Crimes, 1975; Goldring, 1985). Only intrastratal burrows were noted in the study area. In the study interval, the trace mainly occurs on the tops of hummocky cross-stratified sandstone beds in heterolithic interstratified sandstone, siltstone and silty shale successions (Facies B and rarely Facies C) at all locations (Fig. 3-5) (Table 3-1 through 3-4). *Cruziana* occasionally occurs as a network burrow. Specimens at Beatty Ledge are relatively large, reaching over 10 cm wide and 100 cm long (Fig. 3-5C).

Cylindrichnus Howard, 1966

Cylindrichnus consists of a long, slender tube surrounded by concentric layers of sand and mud or silt (Häntzschel, 1975; Howard and Frey, 1984; Frey and Howard, 1985). It is cylindrical to subconical and has a vertical to subvertical orientation (Häntzschel, 1975). The basal length of the burrow sometimes deviates to the side and becomes near-parallel to bedding (Frey and Howard, 1985). This burrow is interpreted as the dwelling / suspension feeding burrow of a vermiform organism (Häntzschel, 1975; Frey and Howard, 1985). Within the study interval, the burrow occurs in hummocky cross-stratified sandstone beds of Facies B and C at Brown Hill, Folded Hill and Aylard Creek (see chapter two). Multiple specimens of this trace occur relatively abundantly at Aylard Creek, and they are commonly associated with abundant *Asterosoma*, and *Rosselia*. This burrow is 5 to 20 cm wide (Fig. 3-6A).

Diplocraterion Torell, 1870

Diplocraterion is a U-shaped burrow, oriented perpendicular to bedding (Fürsich, 1974b; Häntzschel, 1975; Šimo and Olšavský, 2007). Plan view of the trace shows paired openings. Unlike *Arenicolites*, the burrow has spreite in between and/or beneath, the two limbs (Fürsich, 1974b; Häntzschel, 1975). Cross sectional view of tubes is generally circular to semicircular (Häntzschel, 1975;

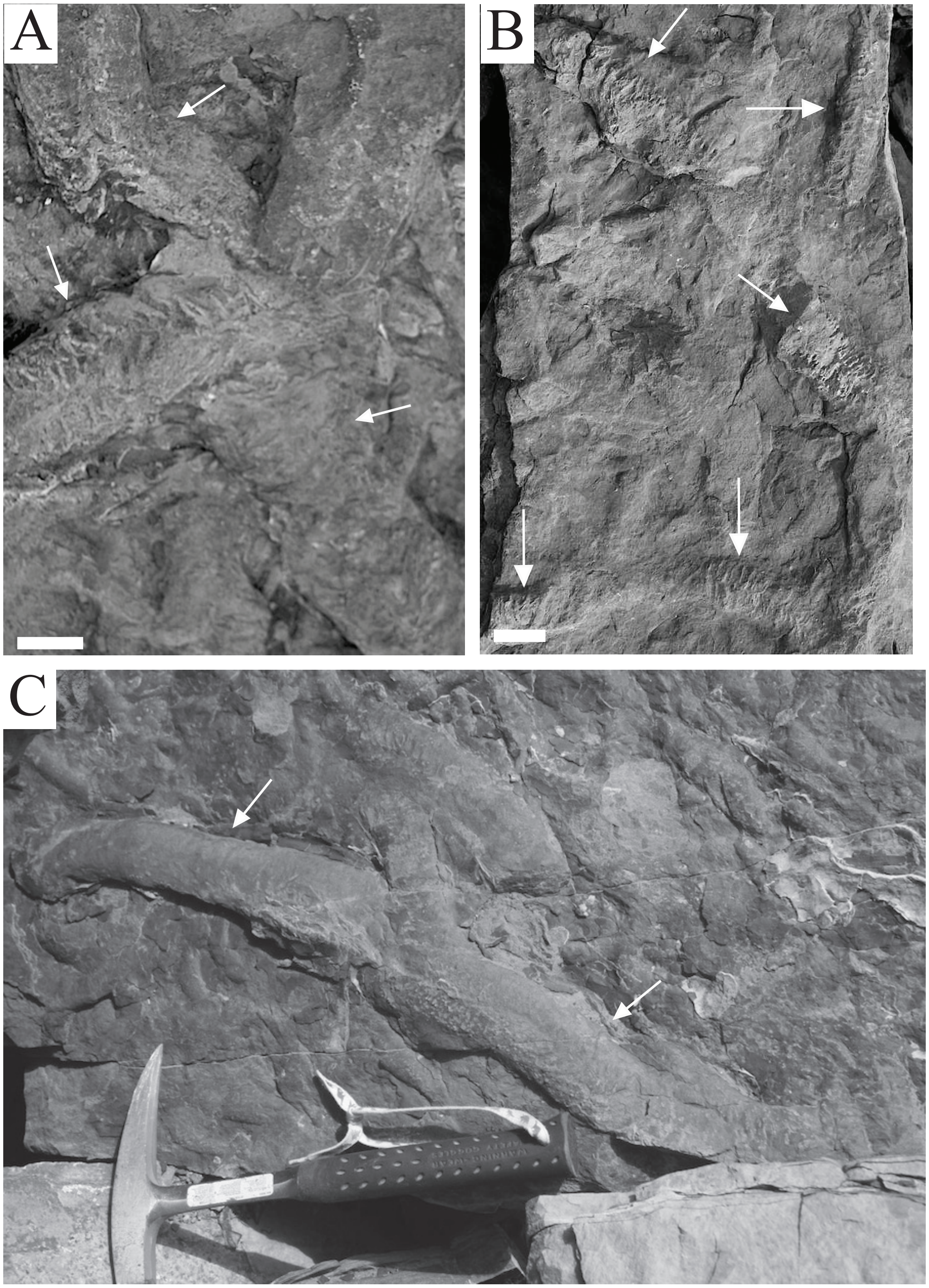

FIGURE 3-5—Photos of trace fossils III. (A) Overlapping or branching *Cruziana* specimens occur in very fine-grained sandstone at Beatty Ledge. (B) *Cruziana* are present in a fallen slab of very fine-grained sandstone (Facies B or C) at Aylard Creek. (C) A large, long specimen of *Cruziana* is present in offshore transition beds at Beatty Ledge. The length of the hammer is about 30 cm. Scale bar (A and B) = 1 cm.

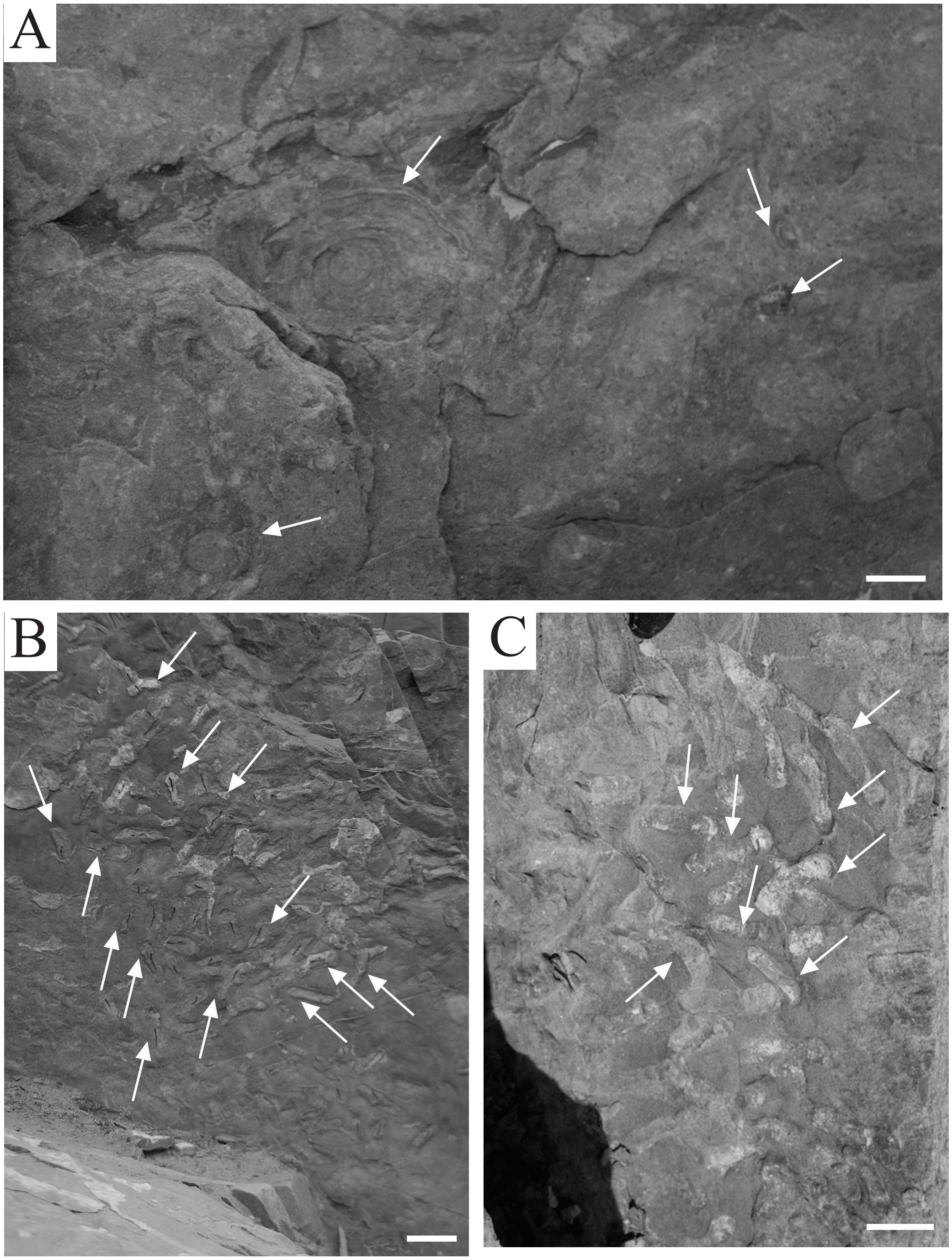

FIGURE 3-6—Photos of trace fossils IV. (A) Specimens of *Cylindrichnus* (arrowed) are seened on bedding plane in fine-grained sandstone of lower shoreface beds at Aylard Creek. (B) Multiple specimens of *Diplocraterion* densely occur in very fine-grained sandstone at Brown Hill. (C) Dense occurrence of *Diplocraterion* is also present in very fine-grained sandstone of offshore transition at Folded Hill. Scale bar = 1 cm (A and C), 2cm (B).

Šimo and Olšavský, 2007). The burrow is interpreted as dwelling structures of vermiforms, such as polychaetes (Fürsich, 1974b) or arthropods (Bromley, 1996). In the study interval, the burrow is ubiquitous within hummocky cross-stratified sandstone beds, interpreted as offshore transition sediments at all outcrop locations. The trace densely colonizes multiple surfaces of offshore transition sandstone beds (see chapter two) (Fig. 3-6B, C). On these bedding plane surfaces, *Diplocraterion* occurs as dumb-bell-like shapes or elongated rectangles with rounded edges (Fig. 3-6B, C). Fewer specimens of *Diplocraterion* are also present within amalgamated hummocky cross-stratified sandstone beds (Facies C) at all localities. The size distribution of this ichnogenus is bimodal (see chapter two); Specimens within the offshore transition are smaller (~ 1 to 4 cm) than those within lower shoreface deposits (~ 6 to 12 cm) (Fig. 3-7A, B, C). Of note, the specimens of this trace fossil present in the Aylard Creek lower shoreface successions were particularly large (Fig. 3-7B).

Gyrochorte Heer, 1865

Gyrochorte is a straight to meandering track, oriented parallel to bedding (Heinberg, 1973; Häntzschel, 1975, Powell, 1992). *Gyrochorte* occurs on bedding planes as a convex downward ridge with medial groove and a concave-downward groove with no medial ridge (Häntzschel, 1975; Powell, 1992). *Gyrochorte* is interpreted as the crawling track of gastropods or vermiforms (Heinberg, 1973; Heinberg and Birkelund, 1984). In the study interval, the trace occurs rarely on the tops of HCS sandstone beds of Facies B at Brown Hill, Folded Hill and Aylard Creek, associated with *Cruziana*, *Thalassinoides*, and *Planolites* (Fig. 3-7D). The trace size is 0.6 to 1 cm wide.

Gyrolithes Saporta, 1884

Gyrolithes is a coil-shaped burrow, oriented perpendicular to bedding (Bromley and Frey, 1974; Häntzschel, 1975). The trace loosely coils, with the coil narrowing downwards (Häntzschel, 1975). The burrow is interpreted as the dwelling burrow of suspension feeders, including shrimps and worms (Bromley

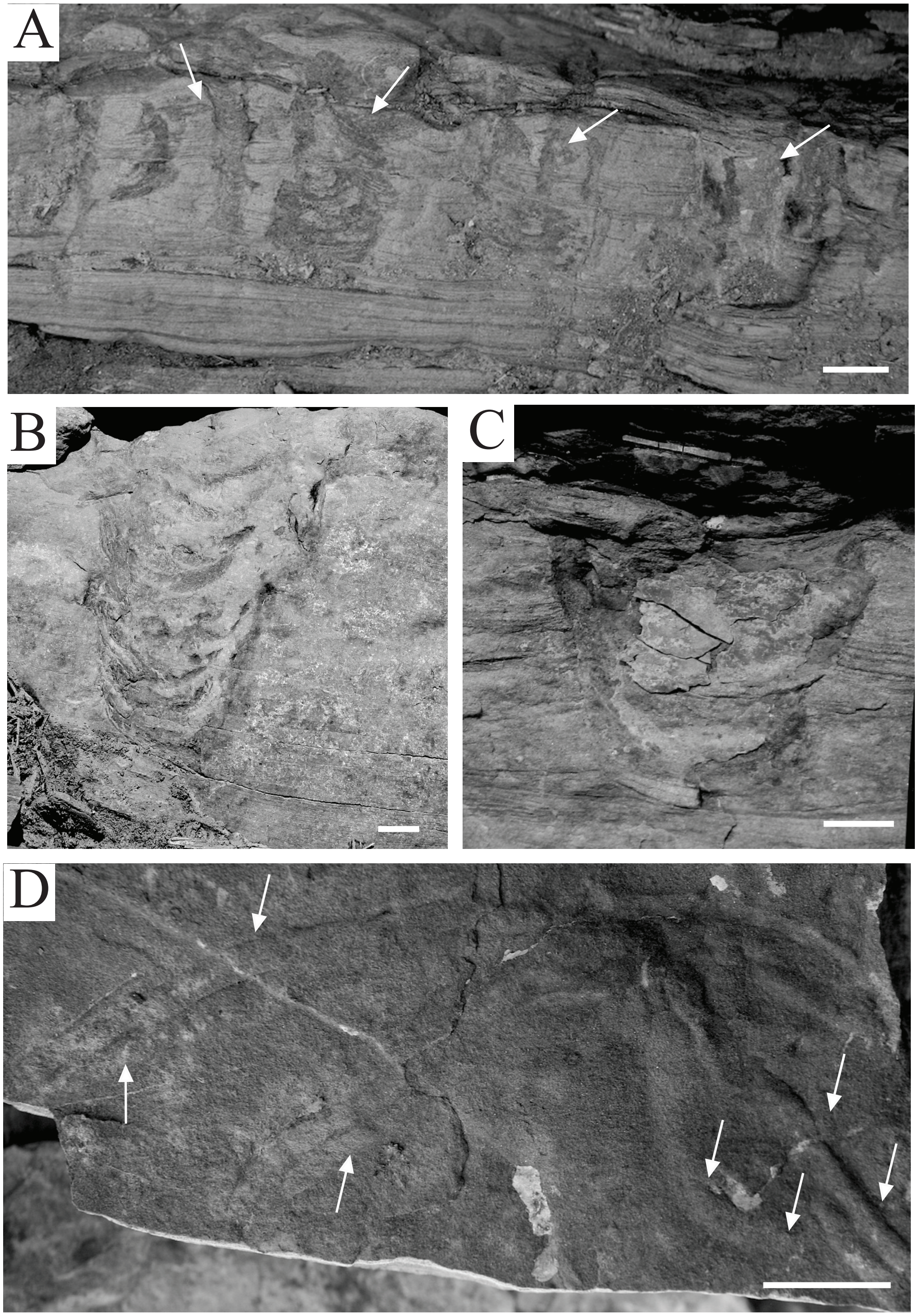

FIGURE 3-7—Photos of trace fossils V. (A) Specimens of *Diplocraterion* (arrowed) occur in fine-grained sandstone of offshore transition beds at Brown Hill. (B) A large *Diplocraterion* occurs in lower shoreface sandstone at Aylard Creek. (C) *Diplocraterion* within lower shoreface at Folded Hill. (D) Specimens of *Gyrochorte* are observed on a bedding plane of Facies B at Folded Hill. Scale bar = 1 cm.

and Frey, 1974; Powell, 1977; Dworschak and Rodrigues, 1997; Wetzel et al., 2007). In the study interval, the burrow varies its size (5 to over 25 mm). Only a few specimens of *Gyrolithes* occur in offshore transition sediments at Aylard Creek (Table 3-4). It occurs in isolation from other observed ichnotaxa.

Helminthoida Schafhäutl, 1851

This trace is a complex meandering trace along the bedding plane (Häntzschel, 1975; Crimes and Crossley, 1991; Uchman, 1991). Unlike *Phycosiphon*, spreite never develop in between the meandering trail (Häntzschel, 1975; Crimes and Crossley, 1991). The width of the trace is approximately 1 to 10 mm (Häntzschel, 1975; Crimes and Crossley, 1991). The trace is interpreted as the grazing structure of vermiforms (Ekdale, 1985; Bjerstedt, 1987; Ekdale and Lewis, 1991). In the study interval, the trace occurs within muddy siltstone of offshore or offshore transition sediments at all localities, and is associated with *Anconichnus*, *Scalarituba*, *Planolites*, *Helminthopsis*, and *Phycosiphon* (Fig.3-8A). *Helminthoida* in the study interval is up to 1 mm wide.

Helminthopsis Herr, 1877

Helminthopsis is an irregularly meandering trace on bedding planes (Chamberlain, 1971; Bjerstedt, 1987, 1988). The trace size is similar to that of *Helminthoida* (Häntzschel, 1975). However, the meandering pattern of *Helminthopsis* is irregular and random, rather than regular / systematic like that exemplified by *Helminthoida* (Häntzschel, 1975). The trace is interpreted as grazing structures produced by vermiforms (Bjerstedt, 1987). In the study interval, the trace occurs commonly within muddy siltstone beds (Facies A2 and parts of Facies B), associated with *Anconichnus*, *Scalarituba*, *Planolites*, *Helminthoida*, and *Phycosiphon* (Fig.3-8B). The trace is very thin, less than 0.5 cm wide. Some specimens of *Helminthopsis* are very hard to separate from *Helminthoida*, and *Phycosiphon*, due to similar appearance and preservation conditions of the host rock.

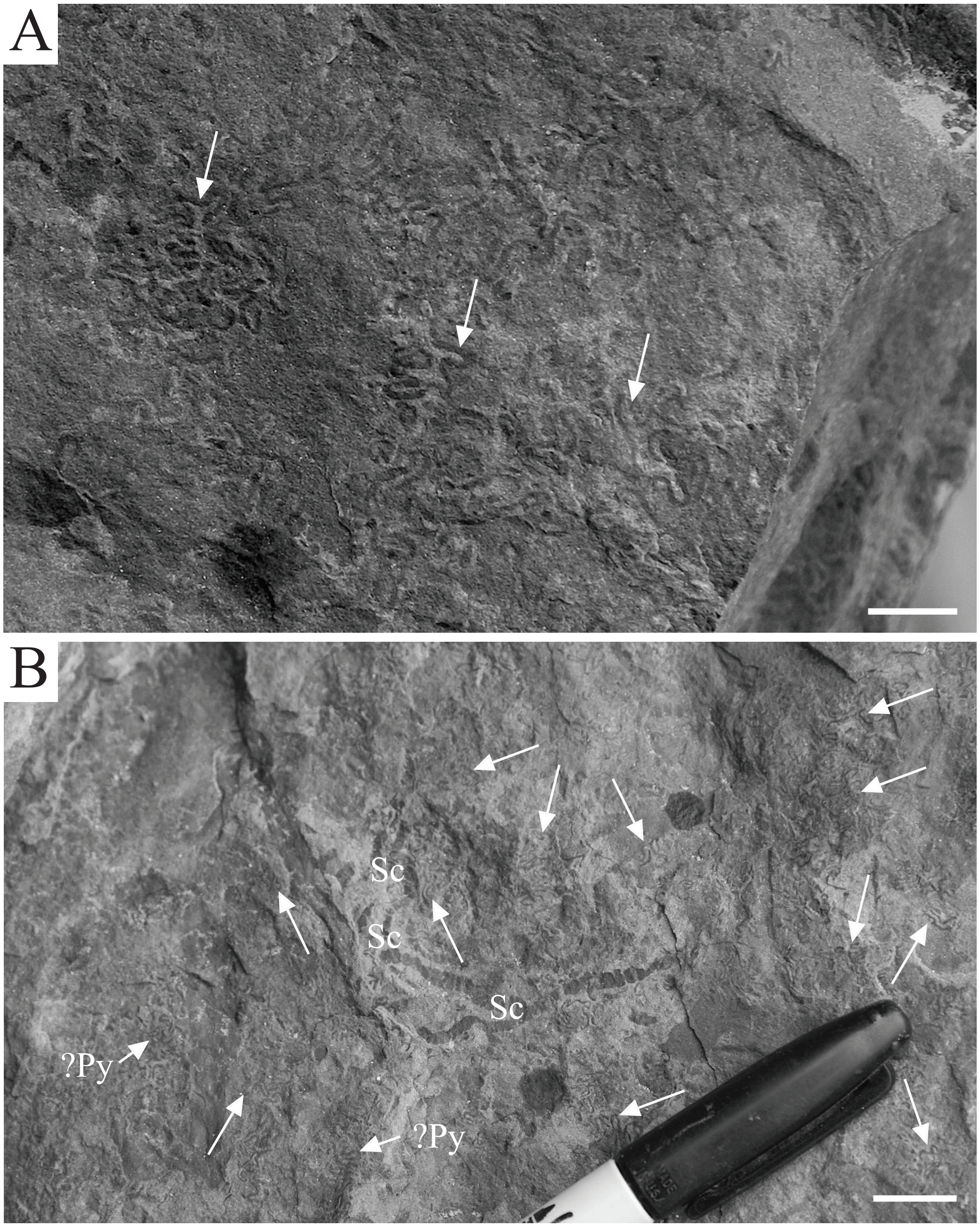

FIGURE 3-8—Photos of trace fossils VI. (A) Multiple specimens of *Helminthoida* occur in offshore transition siltstone at Aylard Creek. (B) Possible specimens of *Helminthopsis* associated with *Scalarituba* (Sc) and possible *Phycosiphon* (?Py) occur within offshore transition siltstone at Aylard Creek. Scale bar = 1 cm.

Lingulichnus Hakes, 1976

Lingulichnus is a cylindrical structure, oriented perpendicular, sub-perpendicular or oblique to bedding (Hakes, 1976; Zonneveld and Pemberton, 2003). In cross-sectional view, *Lingulichnus* appears similar to the shape of an eye (oval with pointed ends) (Zonneveld and Pemberton, 2003). The trace is straight to slightly sinuous or sometimes J- to U-shaped (Zonneveld and Pemberton, 2003). Some specimens of the trace have concentric laminae or spreite (Zonneveld and Pemberton, 2003). The trace is interpreted as the dwelling structure of lingulide brachiopods (Hakes, 1976; Szmuc et al., 1976, 1977; Zonneveld and Pemberton, 2003, Zonneveld et al., 2007; Zonneveld and Greene, 2010). Several specimens were noted at Brown Hill in which the preserved shell of the trace maker remains (Zonneveld and Greene, 2010). In the study interval, the trace is relatively abundant in the offshore transition at Brown Hill but occurs in both offshore transition and lower shoreface successions at all other outcrop localities (Zonneveld and Greene, 2010). *Lingulichnus* commonly occurs with *Planolites* and *Diplocraterion*. The trace is up to 2 cm in width.

Lockeia James, 1879

Lockeia is a small teardrop-shaped or almond-shaped structure in convex hyporelief (Häntzschel, 1975; Nara, 2003). The trace is asymmetrical in horizontal profile, with a rounded end and a pointy end and thus is easily differentiated from *Lingulichnus* (Häntzschel, 1975; Nara, 2003). *Lockeia* is interpreted as the resting trace of an infaunal bivalve (Häntzschel, 1975; Ekdale and Bromley, 2001; Nara, 2003). In the study interval, the trace occurs within very fine-grained sandstone beds, interpreted as lower shoreface and offshore transition of all localities (Fig. 3-9A). The size of *Lockeia* is 0.7 to 1 cm wide. Specimens of *Lockeia* commonly occur together in isolation from other trace fossils in the study interval (Table 3-1 through 3-4).

Monocraterion Torell, 1870

Monocraterion is a trumpet-shaped trace, oriented perpendicular to the

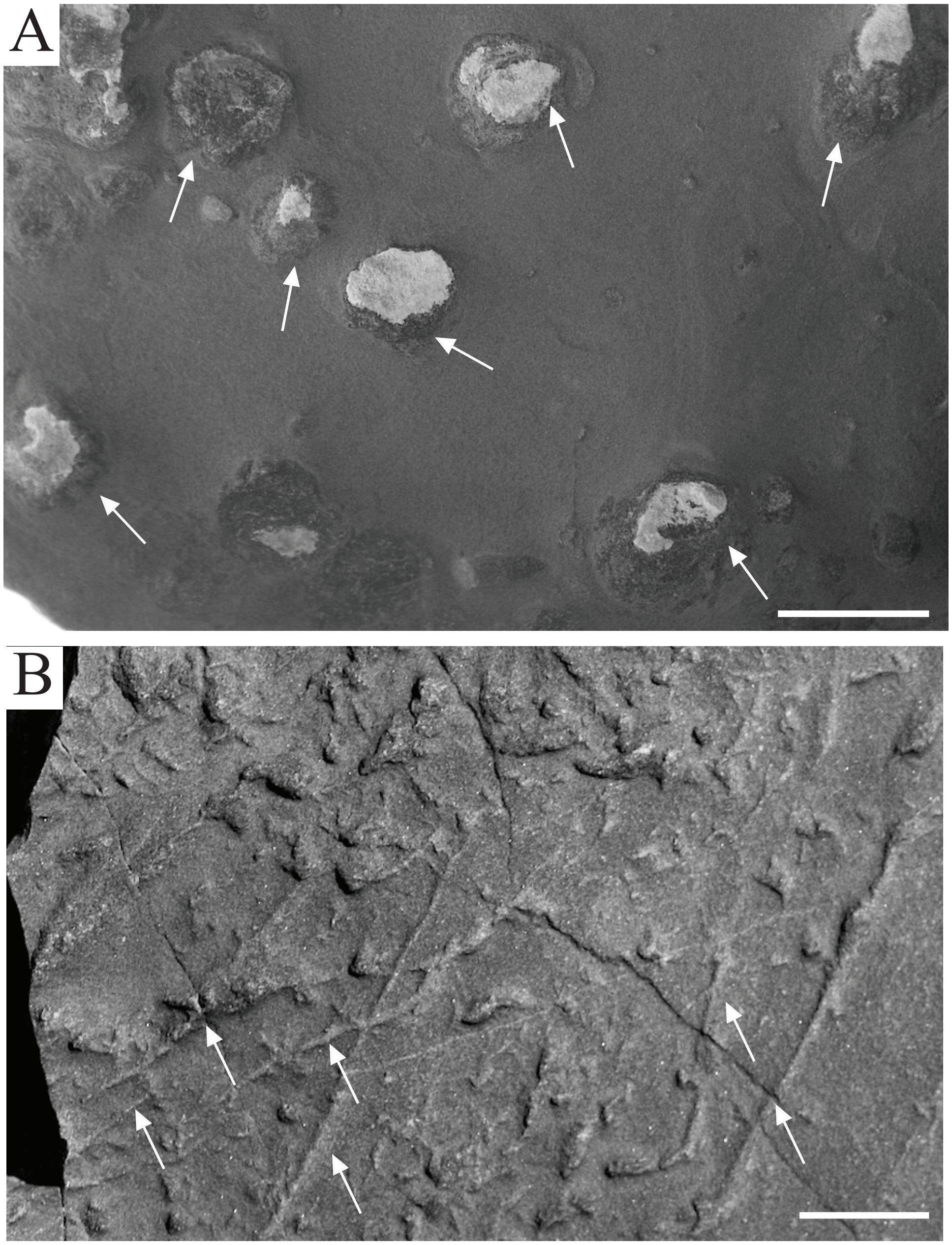

FIGURE 3-9—Photos of trace fossils VII. (A) Specimens of *Lockeia* (arrowed) occupy in lower shoreface sandstone beds at Folded Hill. (B) *Monomorphichnus* occurs associated with scratch marks in offshore transition sandstone at Folded Hill. Scale bar = 1 cm.

bedding plane (Hallam and Swett, 1966; Häntzschel, 1975; Bjerstedt, 1988). Like a trumpet, the opening to the sediment-water interface is wider than the rest of the burrow (Häntzschel, 1975; Bjerstedt, 1988). The trace is straight or slightly curved (Häntzschel, 1975). *Monocraterion* is interpreted as the dwelling burrow of suspension feeding animals, such as worms (Hallam and Swett, 1966; Häntzschel, 1975; Bjerstedt, 1988). In the study interval, the trace is limited to hummocky cross-stratified sandstone beds at Brown Hill, interpreted as offshore transition and lower shoreface depositional environments. The trace size is 0.5 to 1 cm wide. A few specimens of *Monocraterion* commonly occur together in isolation from other traces.

Monomorphichnus Crimes, 1970

Monomorphichnus is a series of straight or slightly curved hypichnial ridges and/or epichnial grooves on bedding planes (Häntzschel, 1975; Mikuláš, 1995). In many cases, the ridges occur in pairs, with one ridge thicker than the other (Häntzschel, 1975). The trace fossil may be continuous laterally over several tens of centimetres (Crimes, 1970; Häntzschel, 1975). The trace is interpreted as the locomotion structure of arthropods (Crimes, 1970; Mikuláš, 1995). In the study interval, the trace occurs on the upper surface of hummocky cross-stratified sandstone beds associated with the offshore transition deposits at Brown Hill, Folded Hill, and Aylard Creek (Fig. 3-9B). The width of each ridge is very thin, less than 0.1 cm. However, overall size (as a series of ridges) it reaches up to 1 cm. This trace commonly occurs in association with *Cruziana*, *Spongeliomorpha*, and *Rusophycus*.

Ophiomorpha Lundgren, 1891

Ophiomorpha is a pellet-walled, cylindrical burrow (Frey and Howard, 1985). Orientation of *Ophiomorpha* is highly variable, including horizontal, subhorizontal, subvertical, and vertical orientations (Bromley and Frey, 1974; Häntzschel, 1975; Frey and Howard, 1985). The burrow occasionally branches (Bromley and Frey, 1974; Frey et al., 1978; Frey and Howard, 1985). In some cases it occurs as a network structure, similar to *Thalassinoides* (Bromley, 1996). The burrow is interpreted as the dwelling burrow of arthropods, such as crustaceans (Frey et al., 1978; Frey and Howard, 1985). In the study interval, the trace is observed below ravinement surfaces at Brown Hill and Folded Hill, visible as a burrow oriented perpendicular to bedding, with an oval or circular cross-section and thick walls (~3 mm) (Fig. 3-10A, B). Their occurrence beneath ravinement surfaces is interpreted as a function of their construction in upper shoreface sandstone beds that have been subsequently exhumed. In the study interval, the burrow width is 0.5 to 1 cm wide, and solely occurs on the interpreted ravinement surfaces (Zonneveld, 1999, 2008).

Palaeophycus Hall, 1847

Palaeophycus is a thin, generally mud-lined trace, oriented parallel to bedding (Pemberton and Frey, 1982; Howard and Frey, 1984). The trace can be branched or unbranched (Pemberton and Frey, 1982; Frey and Howard, 1985). In cross-section, the trace is oval to circular (Pemberton and Frey, 1982; Howard and Frey, 1984; Frey and Howard, 1985). The burrow filling of the trace is usually the same sediment as the host rock (Pemberton and Frey, 1982). The trace is interpreted as the dwelling structures of passive carnivorous polychaetes (Pemberton and Frey, 1982; Vossler and Pemberton, 1989). In the study interval, the burrow is extremely common within very fine- to fine-grained sandstone beds, interpreted as lower and upper shoreface sediments (Fig. 3-10C through E). Some specimens also occur within sandstone beds of the offshore transition (Table 3-1 through 3-4). The trace size is generally 1 cm wide and it commonly occurs with *Diplocraterion* and unnamed pellet-stuffed traces.

Phycodes Richter, 1850

Phycodes is a bundled structure with a broom-like pattern (Häntzschel, 1975; Bjerstedt, 1988). The burrow consists of horizontal tubes that are bundled on one side and spread radially outwards on the other side (Häntzschel, 1975). The trace is interpreted as the deposit-feeding structure of worm-like organisms

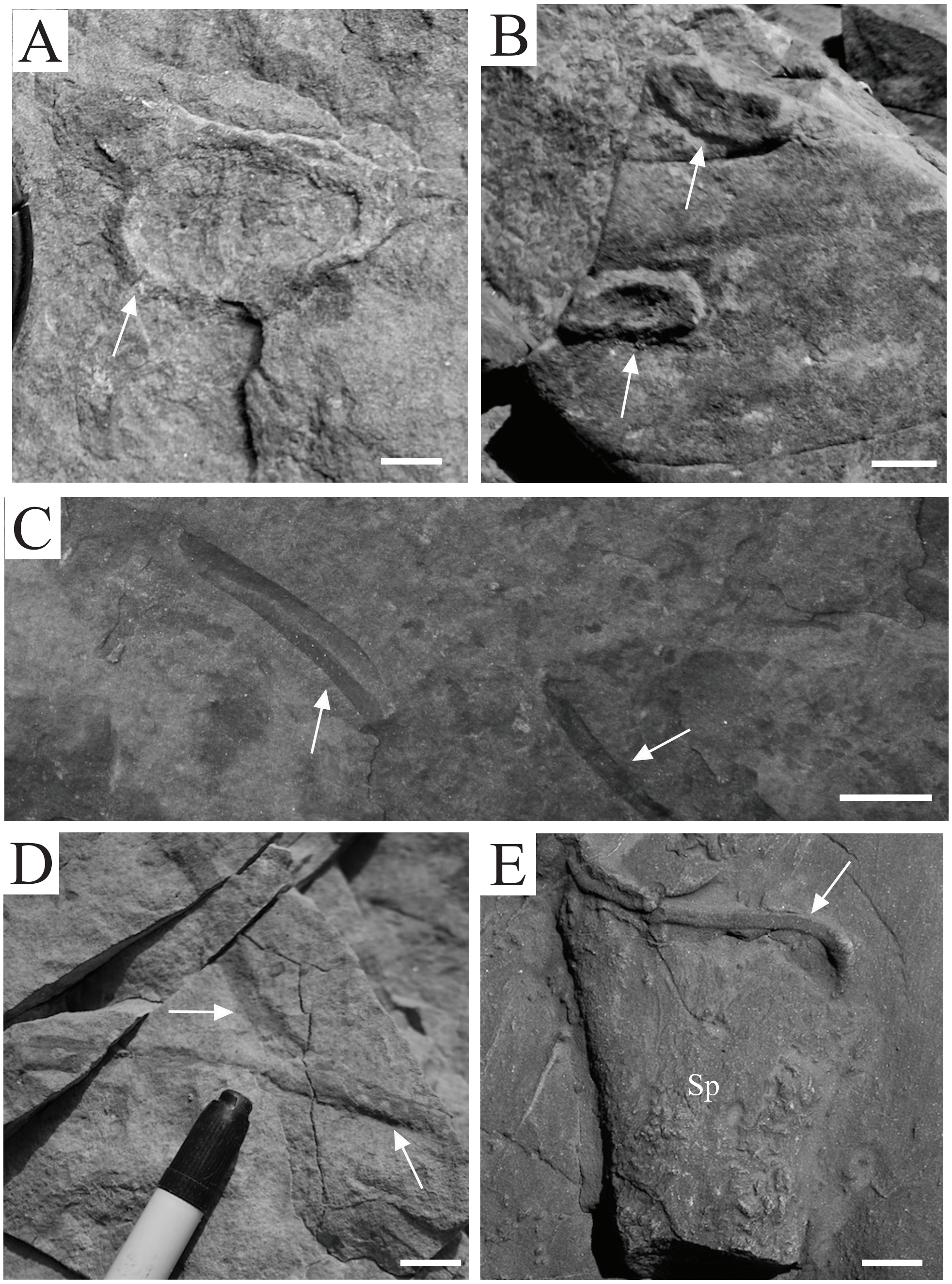

FIGURE 3-10—Photos of trace fossils VIII. (A) A specimens of *Ophiomorpha* occurs in upper shoreface sandstone beds at Folded Hill. (B) Thick-walled *Ophiomorpha* occur in upper shoreface at Brown Hill section. (C) Horizontal *Palaeophycus* occur in lower shoreface sandstone at Aylard Creek. (D) *Palaeophycus* specimens exhibit overlapping relationships on bedding plane in upper shoreface sediments at Brow Hill. (E) A specimen of *Palaeophycus* (arrowed) overlaps on *Spongeliomorpha* (Sp) in Facies B of Folded Hill. Scale bar = 1 cm.

(Häntzschel, 1975; Han and Pickerill, 1994). In the study interval, the trace is rare, occurring solely in isolated beds interpreted as lower shoreface at Aylard Creek (Fig. 3-11A). *Asterosoma*, *Rosselia* and *Cylindrichnus* are associated with the trace within these beds. The burrow width of the narrow end is approximately 1 cm and the wider end is 3 cm.

Phycosiphon Fischer-Ooster, 1858

Phycosiphon is an irregularly meandering, black trace, generally oriented parallel to bedding (Chamberlain, 1971; Häntzschel, 1975; Wetzel and Bromley, 1994). In cross-section, the trace is cylindrical to sub-cylindrical and very commonly preserved as a U-shaped to sinuous structure in the horizontal bedding profile (Häntzschel, 1975). The burrow sometimes exhibits spreite (Häntzschel, 1975; Bjerstedt, 1988; Wetzel and Bromley, 1994). The burrow is interpreted as the grazing structures constructed by worm or worm-like organisms (Chamberlain, 1971). In the study interval, the trace is common within muddy siltstone and hummocky cross-stratified sandstone beds at all localities (Fig. 3-11B). Commonly associated ichnotaxa are *Anconichnus*, *Scalarituba*, *Planolites*, *Helminthoida*, *Helminthopsis*, and *Thalassinoides*. The trace width is very small (< 0.5 mm). Some specimens are difficult to differentiate from *Anconichnus*, *Helminthoida*, and *Helminthopsis* because of similar burrow size and appearance (Fig. 3-11C).

Planolites Nicholson, 1873

The trace is a cylindrical to subcylindrical structure, oriented in a horizontal to inclined position (Pemberton and Frey, 1982; Bjerstedt, 1988). Branching is common (Pemberton and Frey, 1982; Bjerstedt, 1988). The burrow is straight to slightly curved (Pemberton and Frey, 1982; Bromley and Uchman, 2003). The burrow is interpreted to be a result from deposit-feeding activities of mobile animals, such as infaunal polychaetes or other worm-like organisms (Chamberlain, 1971; Pemberton and Frey, 1982). In the study interval, the trace occurs within a wide range of host rock types, from sandy siltstone beds to fine-

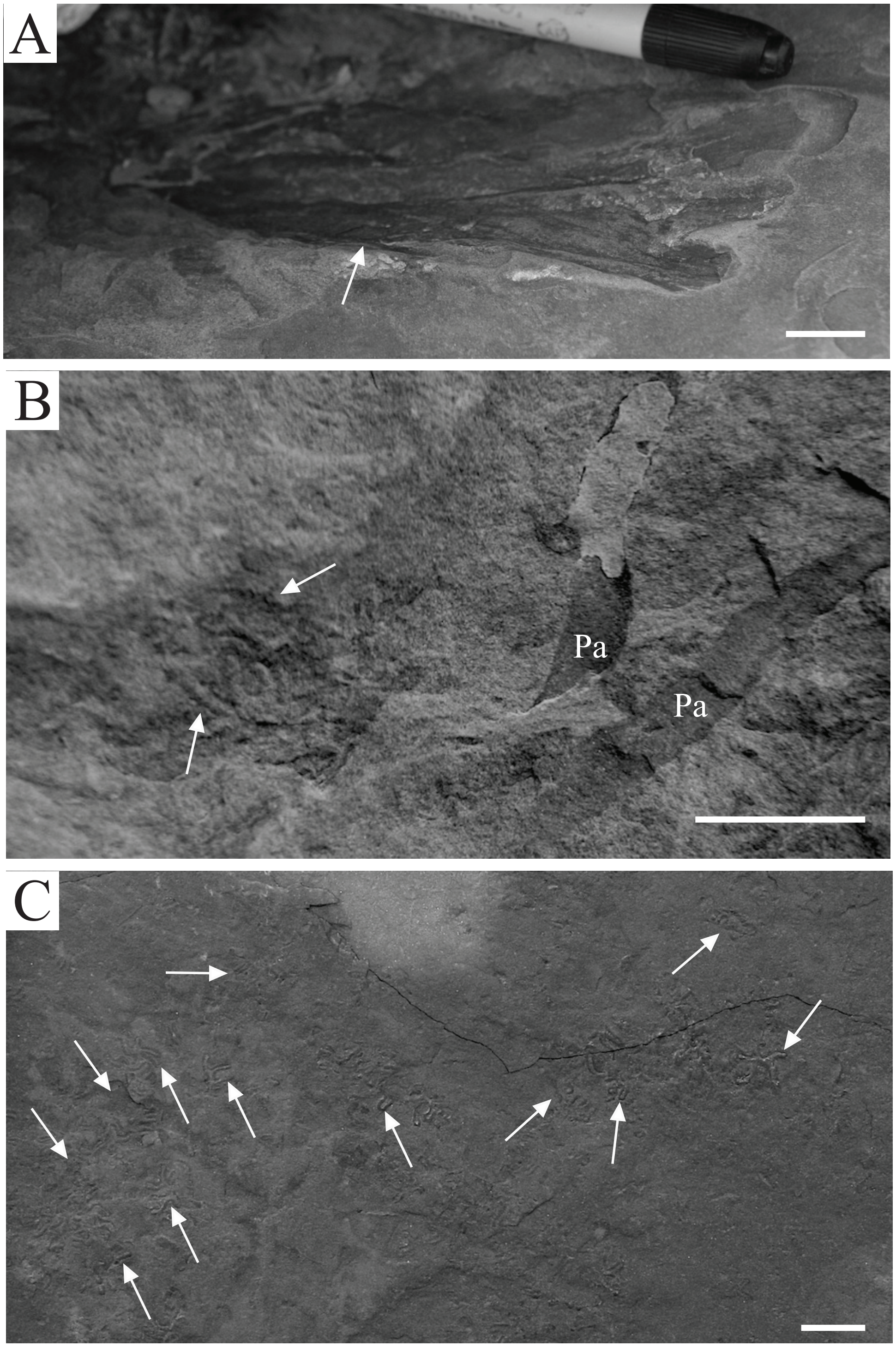

FIGURE 3-11—Photos of trace fossils IX. (A) A specimens of possible *Phycodes* occurs in lower shoreface sandstone beds at Aylard Creek. (B) offshore transition sandstone beds at Brown Hill contain *Phycosiphon* (arrows) associated with *Palaeophycus* (Pa). (C) Possible *Phycosiphon* occur in offshore siltstone at Aylard Creek. In that sediment, *Phycosiphon* is similar to *Helminthopsis* and *Helminthoida*. So sometimes, it is hard to separate them. Scale bar = 1 cm.

grained sandstone beds (Fig. 3-12A, B). The trace occurs at all localities, and is associated with *Diplocraterion*, *Scalarituba*, *Helminthopsis*, *Phycosiphon*, and *Thalassinoides* (Tables 3-1 through 3-4). The trace size is commonly 0.5 to 1.5 cm wide.

Rhizocorallium Zenker, 1836

Rhizocorallium is a U-shaped burrow, oriented horizontal or oblique to bedding (Fürsich, 1974a; Häntzschel, 1975; Bjerstedt, 1987). Spreite are well-developed between the limbs of the U (Fürsich, 1974a; Bjerstedt, 1987). The trace is interpreted as a feeding burrow of deposit-feeders (Häntzschel, 1975; Rodríguez-Tovar and Pérez-Valera, 2008) or a dwelling burrow of suspension-feeders (Fürsich, 1974a; Häntzschel, 1975), such as crustaceans (Fürsich, 1974a; Rodríguez-Tovar and Pérez-Valera, 2008). In the study interval, the trace occurs within hummocky cross-stratified sandstone beds of lower shoreface successions at all locations, and less commonly occurs within fine-grained sandstone beds, interpreted as upper shoreface sediments at Folded Hill (Fig. 3-12C, Table 3-1 through 3-4). *Rhizocorallium* is 1 to 6 cm and commonly occurs with *Asterosoma*, and *Cylindrichnus*.

Rosselia Dahmer, 1937

Rosselia socialis Dahmer, 1937

Rosselia socialis is a funnel shaped bulb with central shaft, oriented perpendicular or inclined to the bedding planes (Chamberlain, 1971; Bjerstedt, 1988). The funnel shape opens upward (Bjerstedt, 1988; Nara, 1995, 1997). The trace is interpreted as the deposit-feeding burrows of polychaetes or the dwelling structures of suspension feeding polychaetes (Chamberlain, 1971; Häntzschel, 1975; Nara, 1995). In the study interval, the trace occurs rarely within hummocky cross-stratified (HCS) sandstone beds of the offshore transition and lower shoreface at Brown Hill, in isolation from other ichnotaxa.

An unusual form of *Rosselia*, similar to *Rosselia rotatus* described by McCarthy (1979), occurs at Aylard Creek. This trace is different from *Rosselia*

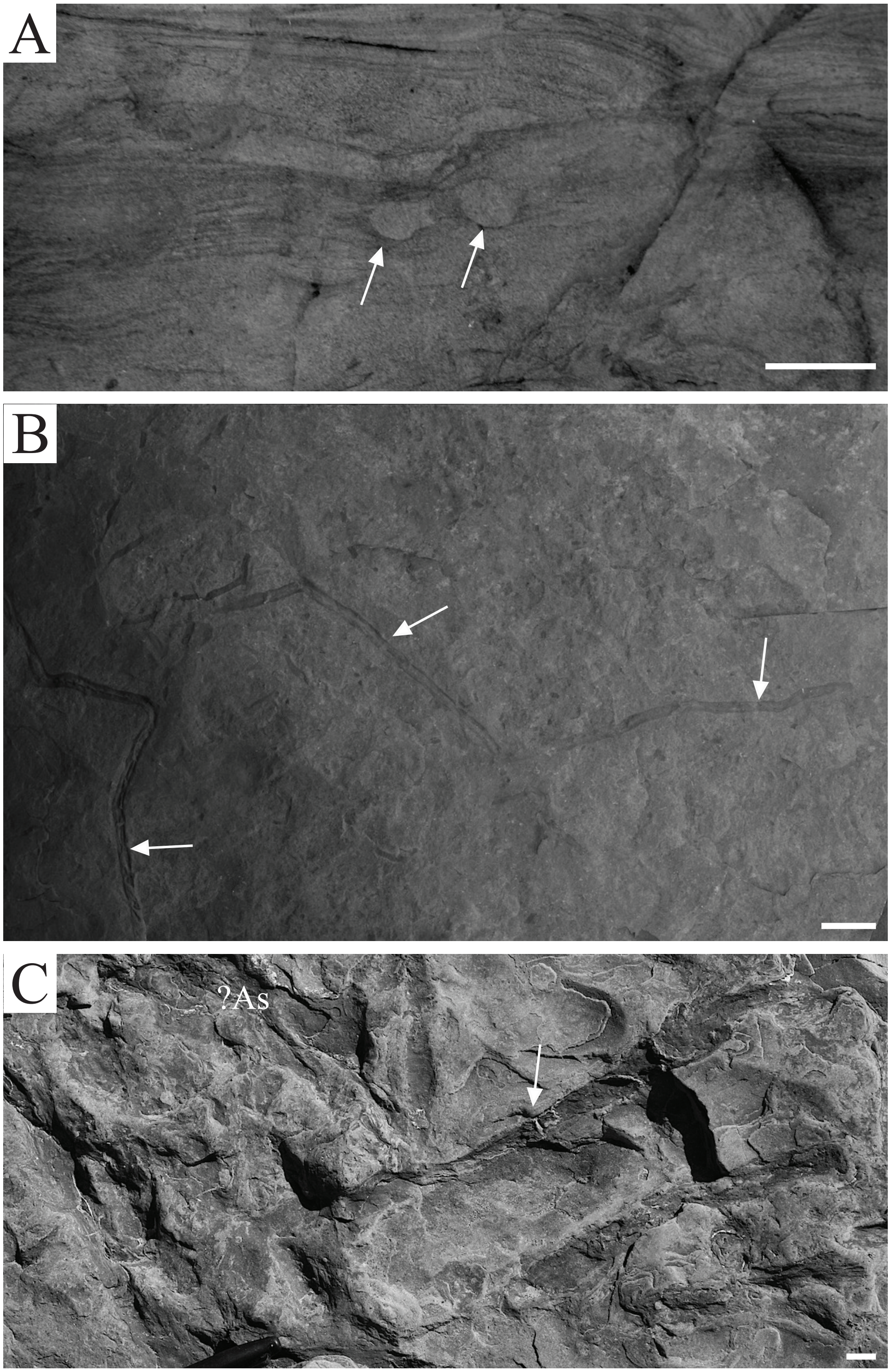

FIGURE 3-12—Photos of trace fossils X. (A) Cross-sectional view of *Planolites* in offshore transition sediments at Brown Hill. (B) Numbers of *Planolites* occur on bedding plane in offshore siltstone beds at Aylard Creek associated with very thin black lines of *Helminthopsis* and *Phycosiphon*. (C) A specimen of *Rhizocorallium* occurs in lower shoreface sandstones at Aylard Creek associated with possible *Asterosoma* (As). Scale bar = 1 cm.

socialis in the orientation of the burrow tube and the presence of spreite that indicate that the bulb migrated laterally on sea floor (McCarthy, 1979; Zonneveld, 2008). In the study interval, the burrow is represented by aligned crescent-shaped structures in plan view of the HCS sandstone beds deposited in the lower shoreface (Fig. 3-13A, B, C). It occurs with *Asterosoma*, and *Cylindrichnus*. The trace is approximately 1.5 cm wide, and laterally traceable for more than 10 cm.

Rusophycus Hall, 1852

Rusophycus is a, short, bilobate structure with striae or scratch marks on each lobe (Bromley and Asgaard, 1979; Pickerill et al., 1984). The trace crudely resembles the shape of paired coffee beans (Häntzschel, 1975). It generally occurs as convex-downward impressions on the soles of sandstone beds (Bjerstedt, 1988). The trace is interpreted as the resting structure of trilobites, or other types of arthropods (Seilacher, 1955; Crimes, 1975; Bergström, 1976; Zonneveld et al., 2002). In the study area, the trace occurs at all locations at the top of hummocky cross-stratified sandstone beds of the offshore transition zone (Fig. 3-14A). *Rusophycus* is about 1 to 2.5 cm wide and commonly occur with *Cruziana*, *Spongeliomorpha*, *Thalassinoides*, and *Palaeophycus*.

Scalarituba Weller, 1899

Scalarituba is a thin, subcylindrical, sinuous burrow, oriented parallel or oblique to bedding (Häntzschel, 1975; Bjerstedt, 1987). Burrows are sometimes branched (Bjerstedt, 1987). The burrow is characterized by "Scalariform" ridges (Häntzschel, 1975; Bjerstedt, 1988). "Scalariform" ridges occur with gaps of a few millimeters and each ridge is semicircular, oval or chevron shaped (Chamberlain, 1971; Häntzschel, 1975; Bjerstedt, 1987, 1988). *Scalarituba* represents a burrow formed through deposit-feeding activities by vermiform taxa (Conkin and Conkin, 1968; Bjerstedt, 1987). In the study interval, the burrow commonly occurs in siltstone and mudstone beds of the offshore and the offshore transition at all outcrop locations (Fig. 3-14B, C) (Table 3-1 through 3-4). It commonly occurs in association with *Phycosiphon*, *Helminthopsis* or

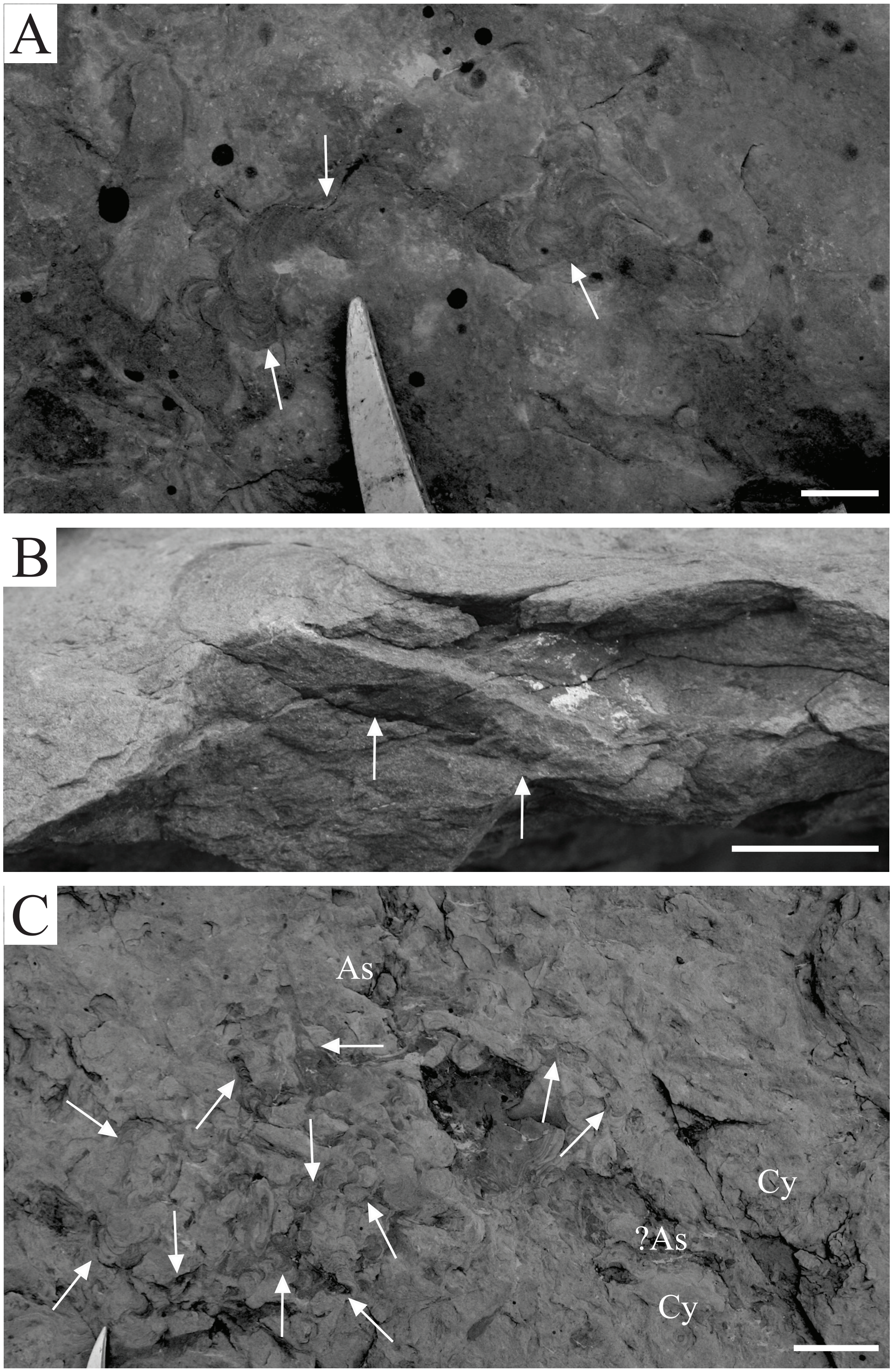

FIGURE 3-13—Photos of trace fossils XI. Very fine- to fine-grained sandstone beds at Aylard Creek contain *Asterosoma*, *Rosselia rotatus*, and *Cylindrichnus* in high abundance. (A) Aligned crescent-shaped structures represent *R. rotatus*. (B) Cross-sectional view of a bed shows inclined orientation of *R. rotatus*. (C) Multiple specimens of *R. rotatus* occur associated with *Asterosoma* (As), and *Cylindrichnus* (Cy). Scale bar = 1 cm (A and B), 5 cm (C).

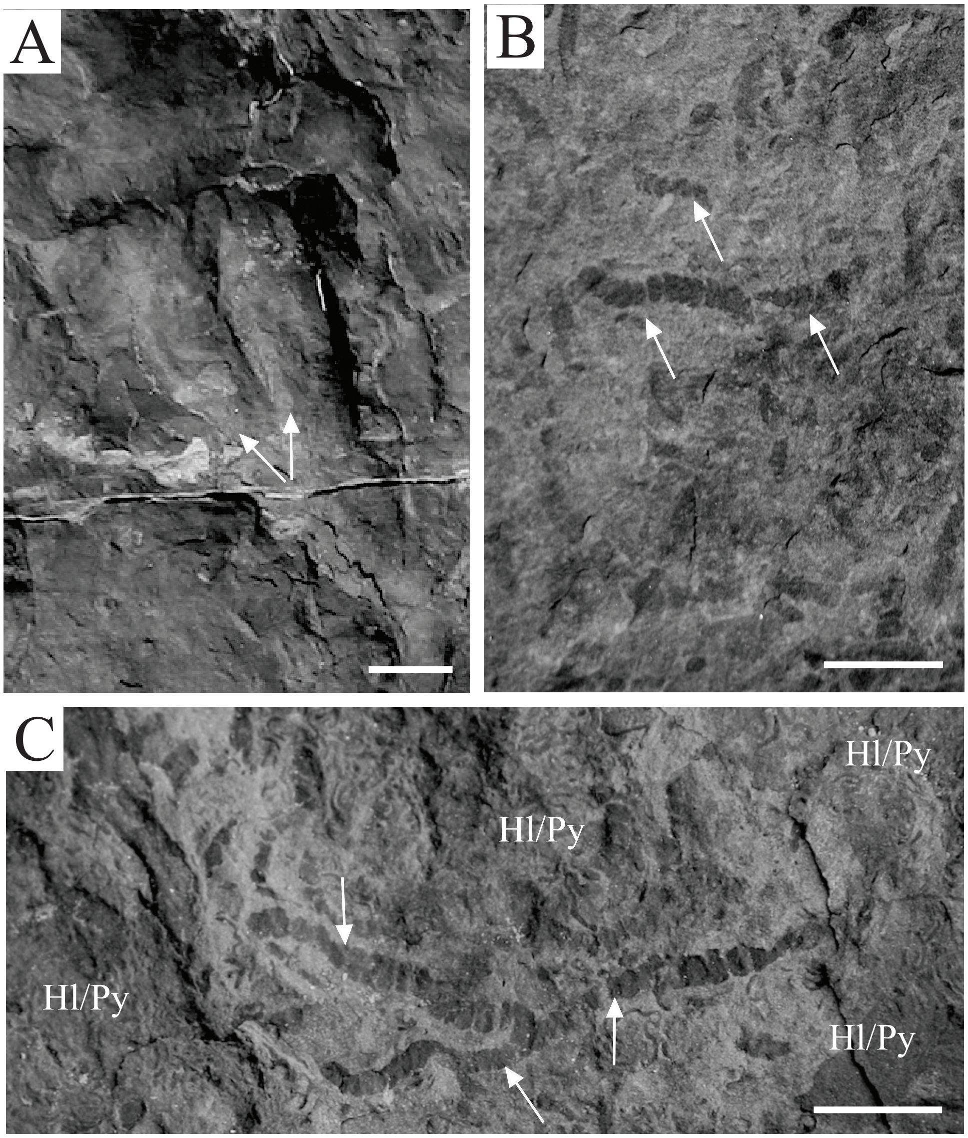

FIGURE 3-14—Photos of trace fossils XII. (A) A specimen of *Rusophycus* occurs in offshore transition sandstone bed at Beatty Ledge. (B) Multiple specimens of *Scalarituba* occupy siltstone beds of offshore or offshore transition at Beatty Ledge. (C) A specimens of *Scalarituba* is brunched in siltstone of offshore transition sediments at Aylard Creek, associated with very thin, black traces of *Helminthopsis* (Hl) or *Phycosiphon* (Py). Scale bar = 1 cm.

Helminthoida.

Scolicia Quatrefages, 1849

Scolicia is a bilaterally symmetrical trail or burrow, oriented parallel to bedding (Häntzschel, 1975; Bjerstedt, 1988). The trace is long and has a band-like morphology with possible sculptures (i.e., ridges and grooves) depending on the methods of burrowing and the types of constructing organisms (Häntzschel, 1975; Bjerstedt, 1988). The trail commonly occurs in surface epirelief (Bjerstedt, 1988). The internal burrow type is a full relief, band-like, tri-lobate structure, which is traceable great distance (>20 cm) (Häntzschel, 1975; Bjerstedt, 1988). The trace is interpreted as the trails or a lateral burrow of echinoids or gastropods (Häntzschel, 1975; Bromley and Ekdale, 1986). In the study interval, the trace is preserved in concave hyporelief in the offshore transition sediments at all localities. Rare specimens of *Scolicia* occur in lower shoreface sediments at Aylard Creek, associated with *Planolites* and *Palaeophycus* (Table 3-1 through 3-4). The trace size is 0.5 to 0.8 cm wide.

Siphonichnus Stanistreet, 1980

Siphonichnus consists of concave-downward protrusive and/or concave-upward retrusive traces with either one or two long central tubes (Stanistreet et al., 1980; Carmona et al., 2008). This trace is oriented vertically (perpendicular to bedding) (Carmona et al., 2008). It is interpreted to be a dwelling burrow produced by bivalves (Stanistreet et al., 1980; Pearson and Gingras, 2006; Zonneveld, 2008). In the study area, the trace occurs primarily at Brown Hill within fine-grained sandstone beds of the lower shoreface (Table 3-1). It occurs in isolation from other ichnotaxa and is approximately 1 cm wide.

Skolithos Haldemann, 1840

Skolithos is an unlined, or very thinly lined, slender, vertically-oriented burrow (Hallam and Swett, 1966; Bjerstedt, 1988). *Skolithos* is comprised of a simple shaft that is circular in horizontal profile (Hallam and Swett, 1966;

Häntzschel, 1975). The trace is straight, to slightly sinuous, and is unbranched (Frey and Howard, 1985). It is interpreted as the dwelling burrow of suspension feeding vermiforms (Pemberton and Frey, 1984b). In the study interval, the trace occurs at all locations, and is found mainly in amalgamated hummocky cross-stratified (HCS) sandstone beds, interpreted as lower shoreface, and fine-grained sandstone beds, interpreted as upper shoreface sediments (Fig. 3-15A, B). It commonly occurs with *Diplocraterion* and *Skolithos*. The burrow is generally thin, ranging 0.2 to 0.5 cm in width.

Spongeliomorpha Saporta, 1887

Spongeliomorpha is an unlined, elongated tube, oriented parallel to bedding (Häntzschel, 1975; Metz, 1993). The trace is commonly branched and may occur in moderately complex networks with vertical shafts (D'Alessandro and Bromley, 1995). Unlike *Cruziana*, the striae or scratch marks of *Spongeliomorpha* are irregularly and randomly oriented (Metz, 1993). The striae differentiate this ichnogenus from *Thalassinoides* (Häntzschel, 1975; Metz, 1993). The trace is interpreted as an arthropod dwelling burrow with clear scratch-marked burrow walls (Häntzschel, 1975; D'Alessandro and Bromley, 1995). In the study interval, the trace occurs at all localities and is a cylindrical tube structure mainly on the upper surface of hummocky cross-stratified (HCS) sandstone beds, which are interpreted as offshore transition sediments. It occurs in association with *Cruziana*, *Palaeophycus*, and *Thalassinoides* (Fig. 3-15C, D). A few specimens of this trace laterally change into non-striated *Thalassinoides* as compound forms. Rare specimens of *Spongeliomorpha* also occur within HCS sandstone of lower shoreface sediments at Aylard Creek. The trace size ranges 1 to 6 cm wide.

Teichichnus Seilacher, 1955

Teichichnus is a horizontal to oblique, band-like structure with spreite (Häntzschel, 1975; Bjerstedt, 1988). The spreite are either retrusive or protrusive with various angles (Häntzschel, 1975; Pickerill et al., 1984). It is rarely branched

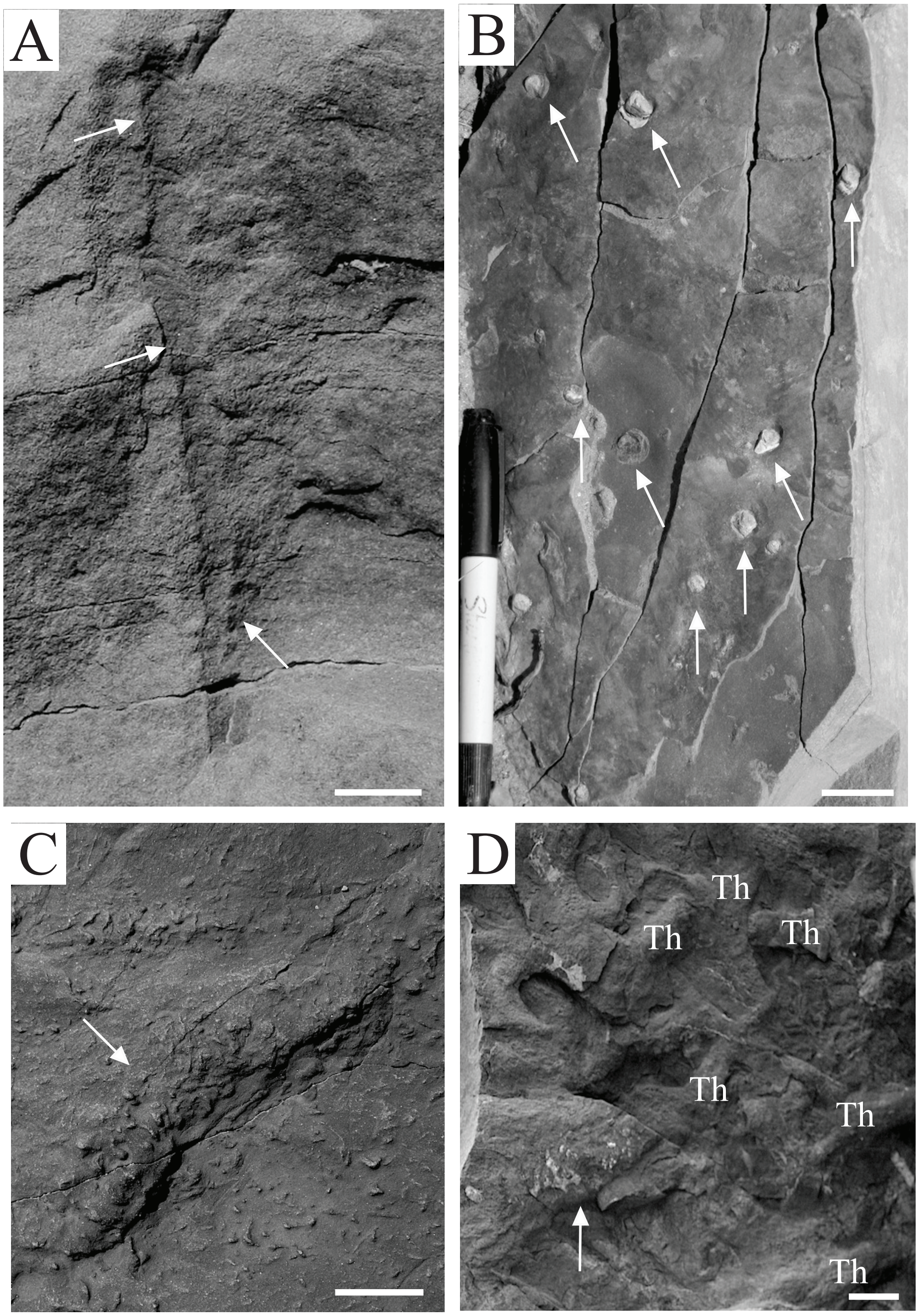

FIGURE 3-15—Photos of trace fossils XIII. (A) Vertical section of *Skolithos* was observed in lower shoreface fine-grained sandstone bed at Aylard Creek. (B) Multiple openings of *Skolithos* are present in upper shoreface sandstone at Folded Hill. (C) A specimen of *Spongeliomorpha* occurs in a sandstone bed of offshore transition at Folded Hill. (D) A specimen of *Spongeliomorpha* is associated with networking *Thalassinoides* (Th) in sandstone beds of offshore transition at Aylard Creek. Scale bar = 1 cm (A), 2 cm (B, C and D).

(Häntzschel, 1975). The trace is interpreted as a dwelling burrow of deposit-feeders such as arthropods and vermiforms (Chamberlain, 1977; Pickerill et al., 1984; Frey and Howard, 1985). In the study interval, the burrow occurs mainly within very fine-grained sandstone beds of lower shoreface sediments at all outcrops and less commonly occurs within hummocky cross-stratified sandstone beds of offshore transition sediments at Brown Hill (Table 3-1 through 3-4). Only retrusive spreite are observed in the study area. This trace is 0.2 to 1 cm wide and commonly occurs with *Diplocraterion* and *Palaeophycus*.

Thalassinoides Ehrenberg, 1944

Thalassinoides is a cylindrical to sub-cylindrical burrow (Howard and Frey, 1984). It occurs as a three-dimensional branching system connected to the surface by vertical shafts (Howard and Frey, 1984; Rodríguez-Tovar and Uchman, 2004). Unlike *Cruziana* or *Spongeliomorpha*, striae are not present (Howard and Frey, 1984). *Thalassinoides* is interpreted as the dwelling burrow of a decapod crustacean (Häntzschel, 1975; Howard and Frey, 1984). In the study interval, these burrows occur at all locations and are found in a relatively wide range of sediments, which are interpreted as offshore (Facies A), offshore transition (Facies B), and lower shoreface deposits (Facies C) (Fig. 3-16). *Thalassinoides* most commonly occurs as tubular structures on the tops of hummocky cross-stratified sandstone beds of Facies B and C. It is often associated with *Spongeliomorpha* and locally with *Cruziana* in these sediments (see chapter two). In contrast to specimens that occur within Facies B and C, specimens of this trace that occur with *Planolites* within Facies A are exclusively small, about 15 mm wide.

Treptichnus Miller, 1889

Treptichnus is a straight to curved series of short structures, alternating to the right and left, showing a zigzag pattern (Häntzschel, 1975; Archer and Maple, 1984; Maples and Archer, 1987). Sections are regular in length, with a vertical or oblique shaft connecting to the sediment-water interface at section junctions

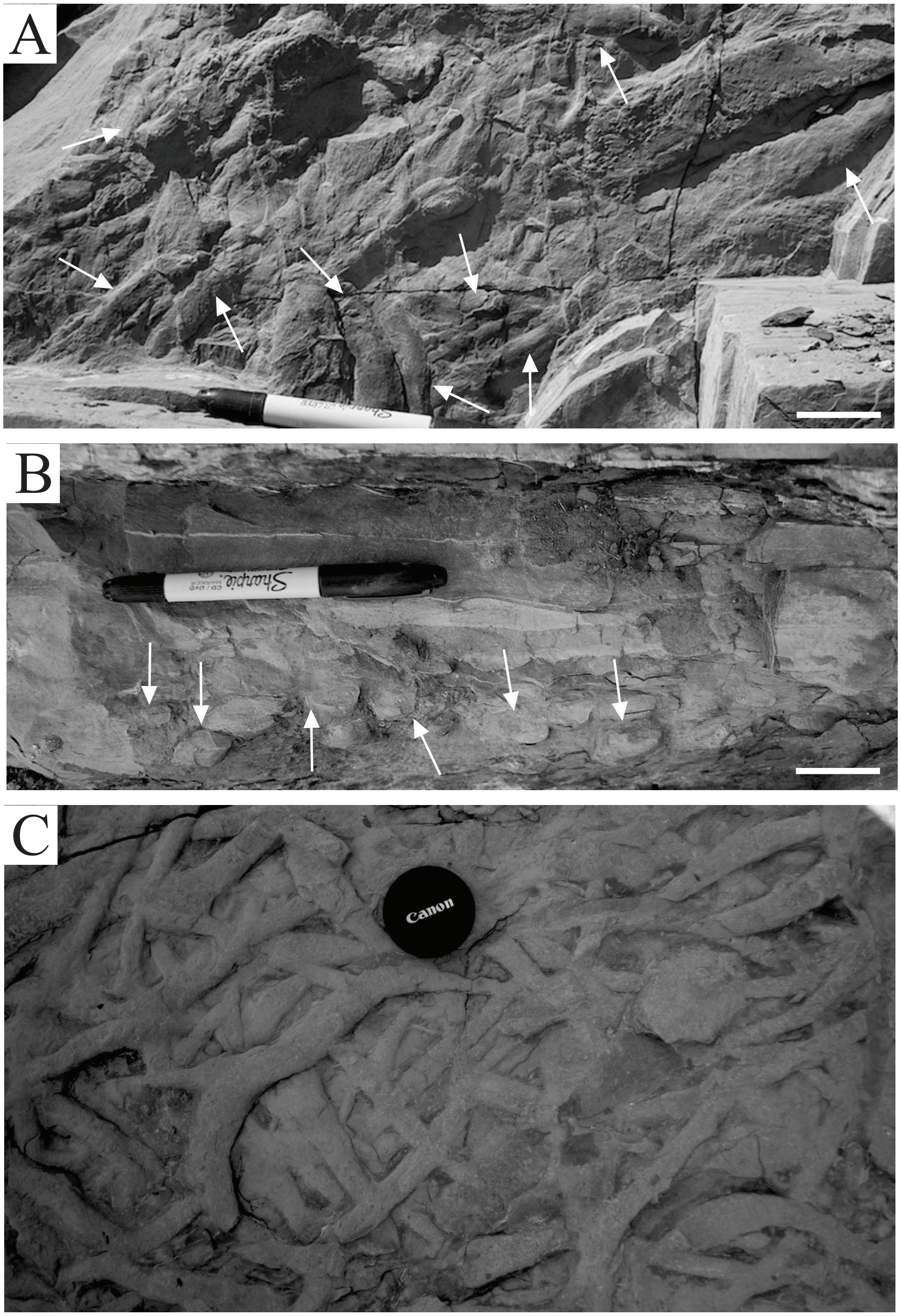

FIGURE 3-16—Photos of trace fossils XIV. (A) Horizontal *Thalassinoides* occur at the bottom of thin siltstone of offshore transition sediments, concaving into sandstone beds at Brown Hill. (B) Semicircular shape of *Thalassinoides* on cross-sectional view of a bed at Folded Hill within offshore sandstone beds. (C) Specimens of *Thalassinoides* at Beatty Ledge exhibit a complex network structure in a sandstone bed of offshore transition sediments. Scale bar = 1 cm (A and B). Lens cap diameter = 6 cm.

(Häntzschel, 1975; Archer and Maple, 1984). The trace is interpreted as a feeding structure of infaunal polychaetes (Seilacher and Hemleben, 1966; Häntzschel, 1975). In the study area, the trace occurs in isolation from other trace fossils, and is limited to very fine-grained sandstone beds, interpreted as offshore transition and lower shoreface, at Beatty Ledge and Aylard Creek. The trace size is approximately 5 mm wide.

Undichna Anderson, 1976

This trace is a set of incised, regularly sinuous grooves on bedding planes (Anderson, 1976; Gibert, 2001). These grooves are long and the sinuosity maintains a consistent wavelength and height (Anderson, 1976; Gibert, 2001). The waving grooves are intertwined with each other. The trace is interpreted as the structures created by the fins of fish (Anderson, 1976; Gibert, 2001). In the study area, the trace has only been observed in sandstone beds of shoreface sediments at Folded Hill. It occurs in isolation from other trace fossils. The size of grooves is very thin, around 2 mm wide.

Unnamed pellet-stuffed trace

This trace is thin, straight to sinuous and completely stuffed with pellets. The trace is oriented horizontal, oblique to sub-vertical, and vertical. In the study interval, the burrow commonly occurs in sandstone beds of lower shoreface and upper shoreface sediments at all localities (see chapter two) (Fig. 3-17A, B). Width of this trace is relatively small (up to 5 mm wide). This trace is commonly associated with *Palaeophycus*. Individual pellets are longitudinally about 1 mm in size. Pellets are randomly oriented. Since this trace often occurs within the same bed as ophiuroid fossils, ophiuroids may be the constructors of this trace (J-P. Zonneveld, personal communication, 2011).

Escape structure (*fugichnia*)

These structures consist of roughly aligned disturbances of laminae (Frey and Seilacher, 1980; Bromley, 1996). The structure is oriented vertical to

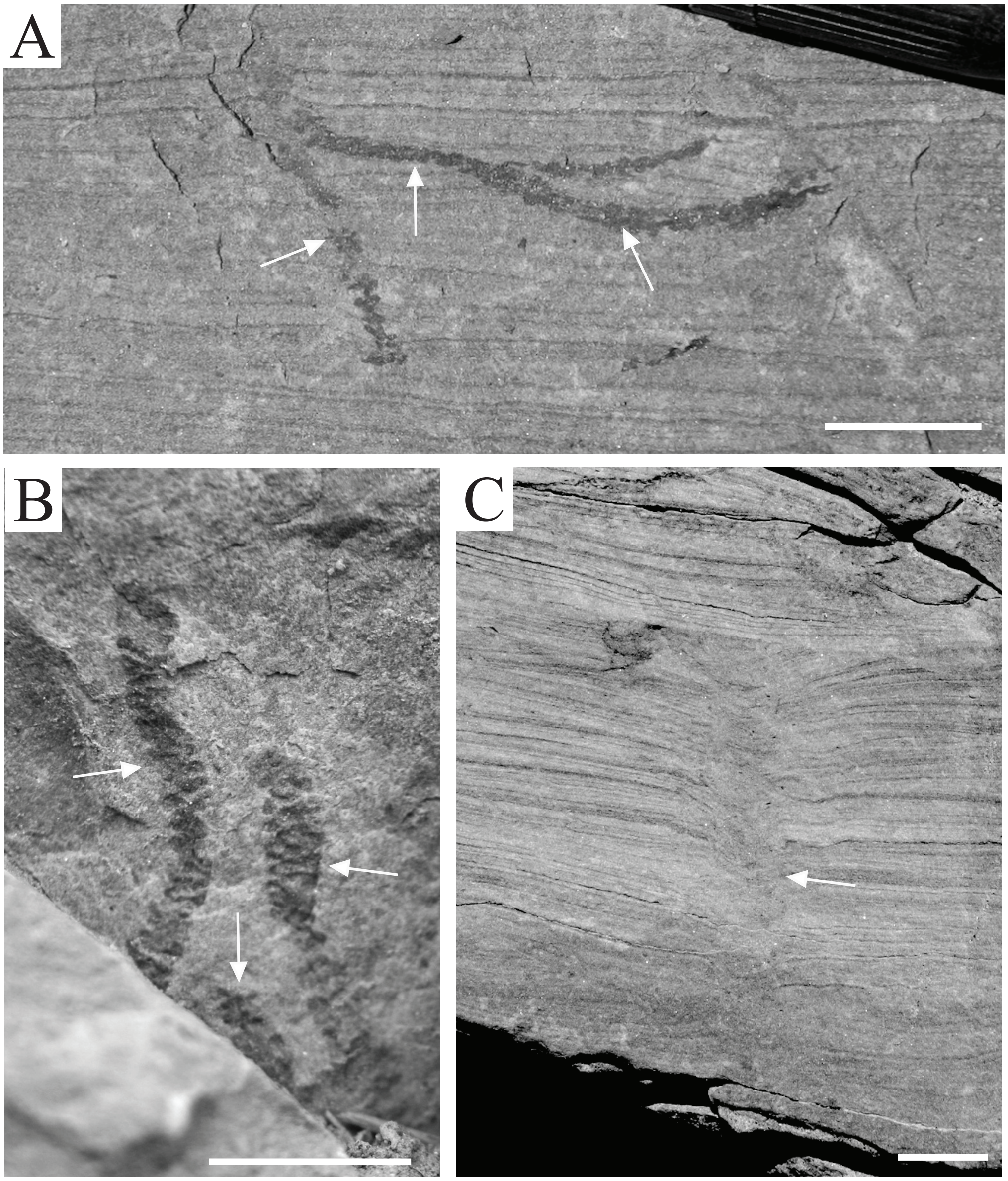

FIGURE 3-17—Photos of trace fossils XV. (A) A vertical specimen of pellet stuffed burrow that exhibits brunching structure (may not be a true brunching) is observed Facies C at Aylard Creek. It orients vertical to subvertical to laminae (B) Multiple unnamed pellet stuffed burrows are horizontally oriented on bedding plane of fine-grained sandstone of upper shoreface at Brown Hill. (C) An escape structure occurs in very fine-grained sandstone of lower shoreface at Aylard Creek. Scale bar = 1 cm.

subvertical, and can be straight to slightly curved (Häntzschel, 1975; Bromley, 1996). It represents the escaping activity of mobile organisms after rapid deposition (Häntzschel, 1975; Bromley, 1996). In the study interval, the trace occurs in hummocky cross-stratified sandstone beds of the offshore transition and lower shoreface at all outcrops (Fig. 3-17C). It commonly occurs with *Diplocraterion*. The trace fossil size ranges 0.5 to 1 cm.

DISCUSSION

Middle Triassic Ichnofacies of Western Canada

Ichnofossils within the study interval occur in recurring ichnofossil associations that typically correspond to sedimentologically similar beds, and thus are inferred to have occurred in identical depositional environments (see chapter two). Four ichnofossil associations (*Phycosiphon-Scalarituba*, *Cruziana-Spongeliomorpha-Thalassinoides*, *Diplocraterion-Palaeophycus*, and *Skolithos-Palaeophycus*) were defined and described in detail in chapter two (Table 3-5). Each ichnofossil association includes similarities with individual ichnofacies of the traditional ichnofacies models.

The *Phycosiphon-Scalarituba* (PS) ichnofossil association exhibits many characteristics of the *Zoophycos* Ichnofacies as summarized in MacEachern et al. (2007a). These include 1) low diversity and high abundance of ichnofossils; 2) dominant ethological modes are grazing and deposit-feeding structures; and 3) dominance of horizontal burrows. In contrast with many other examples of the *Zoophycos* Ichnofacies, deep-tier burrows such as *Chondrites* and *Zoophycos* are absent in the PS ichnofossil association.

Lack of deep-tier burrows is likely indicative of low oxygen levels (e.g., Bromley and Ekdale, 1984; Savrda and Bottjer, 1989). Martin (2004) summarized ichnological characteristics under reduced oxygen conditions. Under low oxygen levels, trace fossils exhibit less diversity, size reduction, and decreased depth of tiering (Bromley and Ekdale, 1984; Savrda and Bottjer, 1989, 1991; Martin 2004).

TABLE 3-5—List of defined ichnofossil associations in the study interval. Lithology, depositional environment and occurring ichnotaxa of each association is denoted. HCS = hummocky cross-stratified.

Ichnofossil association	Lithology	Depositional environment	Occurring Ichnotaxa
Phycosiphon-Scalarituba	Laminated black silty shale (Facies A2), and sandy siltstone of Facies B	proximal offshore and offshore transition (fair-weather sedimnets)	*Anconichnus, Helminthoida, Helminthopsis, Phycosiphon, Planolites, Scalarituba, Thalassinoides*
Cruziana-Spongeliomorpha-Thalassinoides	Thin HCS sandstone of Facies B	offshore transition (storm-generated sediments)	*Anconichnus, Arenicolites, Asterosoma, Cruziana, Cylindrichnus, Diplocraterion, Gyrochorte, Gyrolithes, Lingulichnus, Lockeia, Monocraterion, Monomorphichnus, Palaeophycus, Phycodes, Phycosiphon, Planolites, Rosselia, Rusophycus, Scolicia, Spongeliomorpha, Teichichnus, Thalassinoides, Treptichnus, Undichna,* escape structure
Diplocraterion-Palaephycus	Amalgamated very fine-grained HCS sandstone (Facies C)	lower shoreface	*Anconichnus, Arenicolites, Asteriacites, Asterosoma, Bergaueria, Conichnus, Cruziana, Cylindrichnus, Diplocraterion, Lingulichnus, Lockeia, Monocraterion, Palaeophycus, Planolites, Rhizocorallium, Rosselia rotatus, Scolicia Siphonichnus, Skolithos, Spongeliomorpha, Teichichnus, Thalassinoides, Treptichnus, Undichna,* pellet-stuffed traces, escape structure
Skolithos-Palaephycus	Very fine- to fine-grained calcareous sandstone (Facies D)	distal upper shoreface	*Arenicolites, Ophiomorpha, Palaeophycus, Planolites, Rhizocorallium, Skolithos,* pellet-stuffed traces

These characteristics are consistent with those observed for the PS ichnofossil association. Despite the fact that the *Zoophycos* Ichnofacies is considered to represent lower oxygen levels in organic-rich, quiescent settings, below the zone of dominant wave reworking (Frey and Seilacher, 1980; Pemberton et al., 1992), significant characteristics of the *Zoophycos* Ichnofacies (i.e., presence of deep-tiering burrows) (e.g., MacEachern et al., 2007a, 2007c) are absent in the PS association. Additionally, as noted in chapter two, pyrite framboids, which are possible evidence of low oxygen levels (e.g., Raiswell et al., 1988; Canfield et al., 1996; Wignall and Newton, 1998), occur within the beds that contain the PS association. Thus, the PS association probably occurred in environments with lower levels of oxygen (i.e., moderately dysoxic although clearly not anoxic) rather than in the well-oxygenated conditions at characterize most other examples of the *Zoophycos* Ichnofacies.

The *Cruziana*-*Spongeliomorpha*-*Thalassinoides* (CST) ichnofossil association shares similarities with the archetypal *Cruziana* Ichnofacies (MacEachern et al., 2007a). These similarities are 1) mixture of horizontal, inclined and U-shaped vertical burrows; 2) mixture of dominant deposit-feeding burrows, and subdominant dwelling, grazing, crawling, and resting traces; and 3) high ichnofossil diversity and individual abundances. In addition to these similarities, the CST ichnofossil association consists of ichnofossils with a wide variety of tiering depth, such as deep-tier burrows (e.g., *Spongeliomorpha* and *Thalassinoides*), moderate-tier burrows (e.g., *Diplocraterion*, *Cruziana*, and *Lingulichnus*) and shallow-tier burrows (e.g., *Planolites* and *Palaeophycus*). This wide variety is also analogous to the *Cruziana* Ichnofacies (MacEachern et al., 2007a, 2007c). Thus, the CST ichnofossil association represents the *Cruziana* Ichnofacies, summarized in MacEachern et al. (2007a, 2007c).

The *Diplocraterion*-*Palaeophycus* (DP) ichnofossil association resembles the distal *Skolithos* Ichnofacies (MacEachern et al., 2007a) in the following two ways: 1) vertical and U-shaped traces are dominant, and 2) traces consist mainly of dwelling burrows of suspension feeders, domiciles of passive carnivores with subordinate deposit feeding structures, and lesser resting and grazing burrows

(MacEachern et al., 2007a, 2007c). A relatively wide variety of ethological types within the DP association probably resulted from admixture of elements of both the *Skolithos* and *Cruziana* ichnofacies. The ethologies represented within the DP association (i.e., dominant vertical, dwelling burrows of suspension feeders and subordinate deposit-feeding structures) suggest that the DP association is more closely allied with the *Skolithos* Ichnofacies. Thus, the DP association is interpreted to represent the distal *Skolithos* Ichnofacies despite its high diversity.

The *Skolithos-Palaeophycus* (SP) ichnofossil association is similar to the archetypal *Skolithos* Ichnofacies that was summarized by MacEachern et al. (2007a). Similarities are 1) predominantly vertical traces, 2) dominantly suspension feeders and passive carnivores domichnia ethological types, and 3) low overall ichnodiversity. Furthermore, the SP association is consistent with inferred depositional settings of the *Skolithos* Ichnofacies (upper shoreface; i.e., Pemberton and MacEachern, 1992; MacEachern et al., 2007a).

Each of the above-defined ichnofossil associations exhibits many similarities with archetypal marine soft-bottom ichnofacies. Most importantly, the ethological characteristics of each compared ichnofossil association and ichnofacies are consistent. This indicates that existing shallow marine ichnofacies models are indeed applicable to the study interval.

Despite the existing marine ichnofacies models being overall applicable to the study interval, the PS ichnofossil association and the *Zoophycos* Ichnofacies exhibit distinct dissimilarities, for example the presence of deep-tier burrows. As discussed above, these dissimilarities are probably a result of low levels of oxygen in offshore settings. Since ichnofacies models were established from ichnofossil data derived dominantly from ‘equilibrium’ (i.e., non-recovery) intervals (e.g., Ordovician, Devonian, Jurassic and Cretaceous), dissimilarity between the PS ichnofossil association and the *Zoophycos* ichnofacies may imply that either stressed environmental conditions persisted into the Middle Triassic or that infaunal recovery occurred very slowly. Regardless, it is apparent that endobenthic marine conditions in the study interval differed from those characteristic of non-recovery intervals.

Effect of the P-T Mass Extinction on Ethological Distribution

Ichnofossils in the upper Toad-lower Liard succession at Williston Lake represent a broad variety of ethological types: permanent dwelling burrows of suspension feeders and passive carnivores, deposit-feeding and grazing structures, resting traces, and trails / trackways representing mobile epifauna. The possible tracemakers include a diverse variety of forms such as arthropods, vermiform organisms (e.g., annelids, hemichordates, nematodes, and polychaetes), echinoderms, bivalves, brachiopods, gastropods, actinarians (anemones), and fish. The wide variety of behaviours and tracemakers suggests relatively high biodiversity in the study area during the Middle Triassic.

Several ichnotaxa in the study interval are globally limited to Triassic and older sediments; *Cruziana* and *Rusophycus* are absent throughout most of the world in post-Permian sediments (Häntzschel, 1975) and commonly occur in Paleozoic sediments (Crimes, 1975). *Cruziana* and *Rusophycus* are generally interpreted to represent the locomotory activities of trilobites in Paleozoic sediments (e.g., Crimes, 1975; Häntzschel, 1975; Bergström, 1976). Despite the extinction of trilobites after the end-Permian mass extinction, *Cruziana* and *Rusophycus* have been observed in Lower and Middle Triassic succession in several areas of northeastern British Columbia, and Alberta (Zonneveld et al., 1997; Zonneveld, 1999; Zonneveld et al., 2002, 2010b). Tracemakers of *Cruziana* and *Rusophycus* in the study interval were likely either isopods or decapod crustaceans (Zonneveld et al., 2002, 2010b). Likewise, *Monomorphichnus*, which elsewhere occurs solely in Paleozoic sediments, is interpreted to be the result of the activity of trilobites and other crustaceans (Crimes, 1970; Mikuláš, 1995). This trace fossil is also present in the study interval, and has also been observed in Lower Triassic successions in western Canada (Zonneveld et al., 2010b). Similar to *Cruziana* and *Rusophycus*, arthropods are likely constructors of *Monomorphichnus* in the study interval, due to their morphology, as well as their similar size and associated occurrences with *Cruziana* and *Rusophycus* (Zonneveld et al., 2010b). It is apparent that, in the aftermath of the extinction, and concomitant loss of Paleozoic arthropod forms, new arthropod taxa utilized similar behavioral strategies to those used by their predecessors whilst occupying similar depositional settings (Zonneveld et al., 2002, 2010b).

In contrast to the unusual presence of *Cruziana* and associated ichnotaxa, *Zoophycos*, which widely occurs in deep to shallow marine sediments of a broad-age range (from Paleozoic to Tertiary) (e.g., Seilacher, 1964; Häntzschel, 1975; Bromley and Ekdale, 1986; Bjerstedt, 1988; Kotake, 1994), is absent in the study interval. *Zoophycos* is absent worldwide in Early to Middle Triassic successions and its reappearance was delayed until the Middle Triassic (Knaust, 2004). When it did reappear, it initially shows up in the German Tethys region (Knaust, 2004). Previous studies noted that the *Zoophycos* animals were widely adapted in most ecological preferences, including water depth, substrate preference, food resources, and paleo-oxygen levels (Pemberton et al., 1992; MacEachern et al., 2007a). The global absence of *Zoophycos* in lower Triassic successions implies that, despite the high tolerance of the organisms that create *Zoophycos* to a variety of stresses, the *Zoophycos* tracemaker was relegated to a few restricted refugia after the end-Permian mass extinction. Ongoing marine anoxia/dysoxia in offshore settings may have prevented reappearance of *Zoophycos* by the Middle Triassic on the eastern Panthalassa coast.

Many ichnotaxa (e.g., *Asteriacites*, *Bergaueria*, *Conichnus*, *Gyrolithes* and *Monocraterion*) occur in low abundances and are restricted to specific beds or outcrops in the study area. One possible reason for this is that these ichnotaxa are surface traces (i.e. relatively shallow structures) and occur in lower shoreface settings where wave-energy is high and preservation of fair-weather physical and biogenic sedimentary structures is low. In the lower shoreface, frequent storm waves destroyed surface and shallowly penetrating structures. Consequently, ichnotaxa that occur preferentially in the lower shoreface are preserved only in rare circumstances (Bromley, 1996; MacEachern et al., 2007a).

A few ichnotaxa (*Diplocraterion*, *Thalassinoides*, *Planolites* and *Palaeophycus*) commonly occur in multiple beds and outcrops within the study interval. These ichnotaxa are also present in a wide range of depositional environments, similar to facies-crossing ichnotaxa (MacEachern et al., 2007a). Possible tracemakers of these ichnotaxa include both arthropods and vermiforms (Fürsich, 1974b; Häntzschel, 1975; Pemberton and Frey, 1984a). These tracemakers were probably adapted to broad ranges of water-depth, nutrient content, oxygen, and energy levels in the Middle Triassic. These characteristics and high abundance correspond to r-selected (opportunistic) animals (Pianka, 1970; Bromley, 1996; Reznick et al., 2002). Opportunistic taxa are likely early colonizers, both after small scale, common events (i.e., storms), as well as large-scale rare events (i.e., biotic perturbations and extinctions).

Storm-generated beds with high ichnodiversity interbedded with low-diversity fair-weather beds in the study interval suggest that opportunistic pioneers were transported by storms (Facies B of chapter two; Pemberton, et al., 1992; Pemberton and MacEachern, 1997). The small trace size, low trace fossil diversity, and low intensity of the Lower Triassic are indicative of an opportunistic trace fossil community (Beatty et al., 2008; Zonneveld et al., 2010b). Despite some opportunistic characteristics, trace-making faunas in the study interval also show equilibrium characteristics such as larger trace size and higher diversity ichnofossil communities than those of equivalent Lower Triassic successions in western Canada (see chapter two; Beatty et al., 2008; Zonneveld et al., 2010b). Thus, overall, ichnofaunas in the study interval exhibit characteristics that fit somewhere between true equilibrium and opportunistic / recovery successions.

Despite high overall ichnofossil diversity, the ethological implications of ichnofossils from the study interval, as well as the environmental distribution of these trace fossils, suggests that Middle Triassic endobenthic faunas in western Canada were emplaced under ongoing recovery conditions. The distribution of infauna supports the inference that low-levels of oxygen persisted in proximal offshore (and deeper) settings, and thus neither the environment, nor the resident faunas, had re-attained equilibrium (pre-extinction) levels.

Post-Extinction Recovery and the Toad-Liard Ichnofossils

Post-extinction recovery patterns record a complex mixture of surviving taxa, expansion of opportunistic taxa, innovation and diversification of new species, and eventual reappearance of the Lazarus taxa (Erwin, 1998). Previous studies have shown that the end-Permian mass extinction had wide-reaching ecological and evolutionary effects (Erwin, 1993, 1994; Solé et al., 2002). It has also been suggested that taxonomic changes after mass extinction intervals occurred nonsimultaneously with ecological changes (Droser et al., 2000; McGhee, et al., 2004; Greene et al., 2011).

During the initial post-end-Permian extinction recovery, most Early Triassic successions world-wide were characterized by low-diversity assemblages of opportunistic forms (Schubert and Bottjer, 1995; Twitchett and Wignall, 1996; Twitchett, 1999; Erwin, 2001; Pruss and Bottjer, 2004; Fraiser and Bottjer, 2005; Pruss et al., 2005; Twitchett et al., 2005; Fraiser and Bottjer, 2007; Fraiser, 2010). Exceptions occur in isolated Lower Triassic refugia successions of western Canada, which, although characterized by small burrow size, exhibit exceptionally high ichnofossil diversity (Beatty et al., 2008; Zonneveld et al., 2010a, 2010b, Zonneveld, 2011).

During the recovery period, biotic speciation resulted in abundant new taxa (Erwin, 1998; Twitchett, 1999; Erwin, 2001). These new organisms may have had different ethological characteristics from previously existing organisms. As a result, ichnology before biotic crisis in a certain environmental setting may be different from that after biotic crisis in the same environmental setting. Thus, the innovations of new lineages may have resulted in the appearance of completely new ichnotaxa or, alternatively, the introduction of previously absent ichnotaxa to given environments. Alternatively, new organisms may occupy vacated ecospace and produce biogenic structures similar (or identical) to structures once made by very different organisms (Zonneveld et al., 2010a).

Erwin (2001) indicated that Lazarus taxa commonly reappeared around the latest Early to Middle Triassic. The reappearance of Lazarus taxa increased biodiversity and, concomitantly, increased ichnofossil diversity (e.g., Twitchett and Wignall, 1996; Twitchett, 1999). Total ichnofossil diversity increased overall through the recovery interval (e.g., Twitchett and Wignall, 1996; Twitchett, 1999; Twitchett and Barras, 2004; Mata and Woods, 2008; Mata and Bottjer, 2010). Reappearance of certain ichnotaxa (e.g. Spathian *Rhizocorallium* in western Italy, and Middle Triassic *Thalassinoides* in western United States) played a role on the ichnofossil diversification, and these taxa were probably Lazarus ichnotaxa at each location (Schubert and Bottjer, 1995; Twitchett and Wignall, 1996; Twitchett, 1999; Twitchett and Barras, 2004). Within the study interval, several ichnotaxa, such as *Siphonichnus,* have not been reported from northwestern Pangaean successions and thus may fit the definition of Lazarus taxa, at least in a local sense. Occurrence of possible Lazarus taxa likely implies that the post-extinction recovery was locally in progress during Middle Triassic.

The characteristics of ichnofossils in the study interval imply that infaunal ecosystems had not yet re-attained equilibrium population dynamics by the Middle Triassic in western Canada. It is postulated that shallow marine (shelf) bottom water anoxia persisted from the beginning of the Triassic well into the Middle Triassic. During the Lower Triassic, diverse populations were restricted to isolated refugia within the ‘habitable zone’ (i.e., shallow intervals of wave-mixing *sensu* Beatty et al., 2008). During the Middle Triassic, shallow marine (offshore transition and shoreface zones) became fully habitable, however the proximal offshore remained inimical to most complex organisms. As bottom marine environments started to mend, previously abandoned ecosystems (i.e., distal lower shoreface, offshore transition and proximal offshore) started to be re-colonized. Early colonizers were probably opportunistic and thus, were characterized by high tolerance to stress, an ability to utilize a variety of food types, low diversity and high abundances (i.e., Pianka 1970; Bromley, 1996; Reznick et al., 2002). When survivor taxa and their offshoots colonized ecospace vacated by the extinction event, it is presumed that intraspecies behaviours diversified and, concomitantly ichnofossil diversity increased. Ichnological similarities between recovery ichnofaunas and pre-extinction equilibrium ichnofaunas reflects both survivorship of key ichnotaxa as well as behavioural convergence and re-invention of ethological answers to ecological problems by new faunal elements (i.e., new taxa constructing burrows similar to those constructed by other taxa prior to the extinction; Zonneveld et al., 2010a). Pioneer ichnofossils in these ecosystems exhibit ethological similarities to existing ichnofacies models (i.e., the CST association and the archetypal *Cruziana* Ichnofacies, the DP association and the distal *Skolithos* Ichnofacies, the SP association and the archetypal *Skolithos* Ichnofacies).

Ichnological analyses of Middle Triassic shallow marine successions are limited to only a few localities worldwide, including Canada (discussed herein and in Zonneveld, 1999, 2008), Germany (Knaust, 2007), Spain (Rodríguez-Tovar et al., 2007; Rodríguez-Tovar and Pérez-Valera, 2008), and Svalbard (Mørk and Bromley, 2008). Unlike the study interval, these studies exhibit relatively low ichnofossil diversity, ranging from 3 to 9 ichnotaxa (Knaust, 2007; Rodríguez-Tovar et al., 2007; Mørk and Bromley, 2008; Rodríguez-Tovar and Pérez-Valera, 2008). Outside of Canada, all of these Middle Triassic examples were deposited in carbonate platform settings, thus differing strongly from the depositional conditions of this study interval. Considerable work is needed to establish global patterns of Middle Triassic shallow marine trace fossil assemblages. Significantly, those in east Pangaean successions are of low diversity. Although trace fossil assemblages in the study area are, overall, quite diverse, they are restricted to shallow marine (offshore transition and shoreface) depositional settings. More distal settings contain few, if any, trace fossils, indicating that environmental conditions in distal shelf and deeper settings remained inimical to life.

CONCLUSION

The upper Toad and lower Liard Formations in western Canada record ecosystems that occurred approximately 14 - 24 million years after the end-Permian mass extinction. Oceanic acidity and global marine anoxia contributed to the elimination of large numbers of taxa. These conditions prevailed through the lower Triassic and may have continued into the Middle Triassic. The subsequent recovery interval saw the introduction of new taxa and a shift in dominant shallow marine taxa. The consequences on taxonomic composition likely had a profound affect on ichnological parameters as well, including the disappearance of some ichnotaxa, the appearance of others and a shift in tracemakers of identical or near identical ichnotaxa after the end-Permian mass extinction. Thus, some characteristics of ichnofacies in Triassic successions are expected to differ from other intervals although it is expected that the fundamental characteristics will remain the same

Overall the Toad-Liard study interval contains 36 ichnotaxa: 31 ichnotaxa at Brown Hill, 26 ichnotaxa at Folded Hill, 24 ichnotaxa at Beatty Ledge, and 32 ichnotaxa at Aylard Creek. Some ichnotaxa (e.g., *Diplocraterion*, *Thalassinoides*, *Planolites*, and *Palaeophycus*) are abundant and broadly distributed; others (e.g., *Gyrolithes*, *Ophiomorpha*, and *Siphonichnus*) are limited to a few outcrop or specific horizons.

Despite considerable dissimilarities between the ichnofossil associations defined in this study and previously established ichnofacies models, sufficient similarities indicate that the ichnofacies paradigm is applicable to the study interval. The differences in ichnofossil composition suggest that Middle Triassic recovery faunas differed from those that occurred in other intervals. Environmental stresses, such as low oxygen levels and acidic ocean waters were likely present in the study interval, especially below fair-weather wave base, during the Middle Triassic.

The study interval includes several holdover Paleozoic ichnotaxa, such as *Cruziana*, *Rusophycus*, and *Monomorphichnus*, which have been interpreted to most likely represent locomotion of trilobites in Paleozoic sediments. The presence of these ichnotaxa in the study interval, despite the extinction of trilobites at the end-Permian mass extinction, makes ichnology in the study interval unique. Therefore, other types of arthropods, such as isopods or decapods, likely constructed these ichnotaxa. They are interpreted to reflect evolutionary convergence in the functional morphology of marine arthropods.

Within the study area, the abundance of each ichnotaxon varies, depending on depositional environments and the distribution of facies at each outcrop section. Rare ichnotaxa suggest low preservation potential or paucity of certain tracemakers. Arthropods and vermiforms are the inferred tracemakers of many ichnotaxa in this study interval. These groups are adapted to a wide range of depositional environments and include some of the earliest post-extinction colonizers.

During the post-extinction recovery interval, new taxa appear and those that vanished locally subsequently reappeared. The appearance of these taxa increased biotic diversity, which is reflected in the increased diversity of trace fossils (preserved behaviour) within shallow marine successions. High ichnofossil diversity in the study interval provides evidence of increasingly healthy shallow marine ecosystems. Ichnological parameters of the study interval provide evidence that the Middle Triassic of western Canada records an interval of ongoing biotic and environmental recovery after the end-Permian mass extinction.

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CHAPTER 4

CONCLUSION

This thesis investigated ichnology of the upper Toad and lower Liard formations in northeastern British Columbia in order to understand post-extinction (endobenthic) ecology. The primary focus of this study revolved around two aspects of ichnological examination. The first involved constructing detailed trends of ichnofossil characteristics and distributions in order to evaluate the applicability of ichnofacies to post-extinction intervals. Secondly, the environmental and ethological implications of the upper Toad-lower Liard ichnology were used to examine the effect of the end-Permian mass extinction on studied successions.

ICHNOLOGY

The upper Toad and lower Liard formations in the Williston Lake area contain a wide variety of trace fossils (36 ichnotaxa). Environmental distributions of the trace fossils range from offshore to distal upper shoreface. Ichnotaxonomic diversity reaches a maximum in the offshore transition zones (28 ichnotaxa) and slightly less ichnotaxa (25 ichnotaxa) in the lower shoreface sediments. Conversely, diversity is found to be the lowest in the offshore and upper shoreface, with only seven ichnotaxa. Four ichnofossil associations (*Phycosiphon-Scalarituba*, *Cruziana-Spongeliomorpha-Thalassinoides*, *Diplocraterion-Palaeophycus*, and *Skolithos-Palaeophycus* ichnofossil associations) are established from the studied intervals on the basis of ichnology, host rock sedimentology and depositional environment.

The *Phycosiphon-Scalarituba* (PS) ichnofossil association occurs in muddy and sandy siltstones representing an offshore/offshore transition setting. PS association is characterized by low diversity and relatively high individual abundances. The ichnofossils of this association are interpreted as grazing structures (e.g., *Helminthopsis*, and *Phycosiphon*) and deposit feeding structures (e.g., *Planolites*, and *Thalassinoides*) of vermiforms (Häntzschel, 1975; Pemberton and Frey, 1982; Bromley, 1996).

The *Cruziana-Spongeliomorpha-Thalassinoides* (CST) association occurs within thin hummocky cross-stratified sandstones that are interbedded with muddy siltstones and represent storm-deposits in offshore transition setting. Ethological interpretation of constituent ichnofossils (e.g., *Anconichnus*, *Cruziana*, *Planolites*, *Diplocraterion*, and *Rusophycus*) indicate that they are mainly deposit-feeding burrows and subordinate dwelling, resting, crawling and grazing structures by various tracemakers (e.g., Häntzschel, 1975; Pemberton and Frey, 1982; Bromley, 1996).

The *Diplocraterion-Palaeophycus* (DP) association occurs within amalgamated hummocky cross-stratified sandstone beds within the lower shoreface setting. Vertical dwelling burrows of suspension feeders (e.g., *Diplocraterion* and *Lockeia*) dominate with subordinate deposit-feeding burrows (e.g., *Rhizocorallium* and *Thalassinoides*) (e.g., Häntzschel, 1975; Pemberton and Frey, 1982). Numbers of ichnotaxa within lower shoreface beds are as high as within offshore sediments, reaching 26 ichnotaxa. Possible trace makers vary, such as vermiforms, arthropods, echinoids, bivalves and gastropods.

The *Skolithos-Palaeophycus* (SP) ichnofossil association occurs within upper shoreface fine-grained sandstone beds. Trace fossil diversity is low with only nine ichnotaxa, and individual intensity is also low. Vertical domiciles of suspension feeders (e.g., Arenicolites and *Skolithos*) dominate the sediments (e.g., Pemberton and Frey, 1982, 1984).

Except for the PS association, the presented ichnofossil associations listed above share strong similarities with the archetypical ichnofacies summarized by (MacEachern et al., 2007): the CST association with the archetypal *Cruziana* Ichnofacies, the DP association with the distal *Skolithos* Ichnofacies, and the SP association with the archetypal *Skolithos* Ichnofacies. Thus, these associations are probably representative of corresponding ichnofacies. Dissimilarity of the PS association and the ichnofacies models from MacEachern, et al. (2007) likely indicate that unique endobenthic faunas and slightly stressed offshore environments (i.e., low-levels of oxygen in an offshore setting).

IMPLICATIONS OF ICHNOFOSSILS AND POST EXTINCTION RECOVERY

Relative to the Lower Triassic strata of western Canada (Zonneveld et al., 2010), the upper Toad and lower Liard ichnofossils of the Middle Triassic displays the following differences: increases in trace fossil diversity, trace fossil size, tiering depth, and complexity of the tiering pattern. These changes were probably caused by broad size variations of the tracemakers, and high rate of trace-producing activities as a result of sufficient oxygen and nutrients. These suggest that the Middle Triassic of the study area had minimal affects from end-Permian mass extinction, unlike the Lower Triassic strata with low diversity and small size of ichnofossils (Zonneveld, et al., 2010). Large-sized trace fossils (more than 5 cm in diameter) and deep tiering burrows were absent in offshore sediments. This is feasibly a result of the retention influences of the end-Permian extinction (i.e., low-levels of oxygen).

A wide variety of possible tracemakers probably indicates high biodiversity. Possible tracemakers of many ichnotaxa (e.g., *Diplocraterion*, *Thalassinoides*, *Planolites*, and *Palaeophycus*) are vemiforms and arthropods, implying dominance of these taxa in the ecosystem. It is also likely that either an environmental setting was more suited for these taxa or post-extinction recovery of these taxa was more rapid than for other taxa. These taxa may have been opportunistic.

The upper Toad and lower Liard ichnology implies that post-extinction recovery had not yet been completed in the Middle Triassic. High ichnofossil diversity was probably caused by the reappearance of Lazarus taxa and appearance of new taxa. Opportunism of early colonizers to previously abandoned sites might have also caused behavioral innovation, and a following wide variety of ichnotaxa. In these ways, faunal recovery can be recorded in ichnofossils. Thus, ichnology, incorporated with sedimentology and paleontology, provide understandings of a post-extinction faunal recovery.

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