ICHNOLOGICAL ASSESSMENT OF DEPOSITIONAL ENVIRONMENTS FROM ICEHOUSE AND GREENHOUSE GLOBAL CLIMATES IN POLAR AND NEAR-EQUATORIAL POSITIONS

By

Adam M. Jackson

Submitted to the graduate degree program in Geology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Chairperson Dr. Michael Blum

Co-Advisor Dr. Jon Smith

Dr. Jennifer Roberts

Dr. Paul Selden

Dr. Christopher Beard

Date Defended: <<insert date>>

The Dissertation Committee for Adam M. Jackson

certifies that this is the approved version of the following dissertation:

ICHNOLOGICAL ASSESSMENT OF DEPOSITIONAL ENVIRONMENTS FROM ICEHOUSE AND GREENHOUSE GLOBAL CLIMATES IN POLAR AND NEAR-EQUATORIAL POSITIONS

Chairperson Dr. Michael Blum

Co-Advisor Dr. Jon Smith

Date approved: 04/16/2020

ABSTRACT

This dissertation uses ichnological assessment to reevaluate depositional environments and the physicochemical controls on benthic organisms. I am assessing environments from icehouse and greenhouse global climates, and from polar and near-equatorial positions. This comparison originates from recent trends in the literature which suggested that the physicochemical controls on bioturbation are significantly different between climatic regimes and latitudinal positions. We identified these major controls from the high-latitude Permian Mackellar Fm, the mid-latitude Cretaceous Dakota Group, and the mid-latitude Cretaceous Greenhorn and Niobrara formations. In addition to interpretation of physicochemical controls, each chapter explores an application of ichnology: reevaluation of depositional environments (Mackellar Fm), identification of biogenic modification of porosity and permeability (Dakota Group), description of bioturbation trends through Oceanic Anoxic Event (OAE) strata (Greenhorn and Niobrara Fms), and the use of bioturbation intensity and ichnocoenoses to identify Milankovitch cyclicity (Greenhorn and Niobrara Fms).

The Mackellar Fm was previously interpreted to had been deposited in a lacustrine system, but this study refutes this interpretation based on the identification of ichnogenera that only known from marine systems. Mackellar Fm ichnogenera have diminutive morphotypes, shallow penetration, low individual bed and high overall ichnodiversity and are interpreted as a short-lived benthic community that was stressed by freshwater input and high sedimentation rates in a river-dominated deltaic to fully marine system. The study on the Dakota Group assessed physicochemical parameters at the time of deposition using ichnocoenoses and ichnofacies to reinterpret depositional histories, reevaluate sequence stratigraphic models, and evaluate the influence of bioturbation porosity and permeability in these formations. Dakota Group depositional environments are interpreted as: fluvial to deltaic (Lytle Fm), paralic to nearshore (Plainview Fm), distal to proximal shoreface (Glencairn Fm), and continental to offshore marine depositional environments (Muddy Fm). Lastly, analysis of Greenhorn and Niobrara fm ichnology identified a high diversity with abundant bioturbation throughout oxic and OAE intervals. I interpreted that the anoxic events were not long-term events but a period of dysoxic conditions with punctuated periods of anoxia. Additionally, based on observed cyclic patterns in ichnocoenoses and bioturbation, identified harmonic cycles that match Milankovitch cyclicity (eccentricity, obliquity, and precession).

ACKNOWLEDGEMENTS

I am deeply indebted to my father, who passed during this dissertation, for instilling me with a love for scientific inquiry. This dissertation took on a greater meaning in the later years, while I worked to become as critical and fair-minded as he was.

I thank my committee who watched me fall, helped pick me up, and guided my academic growth.

Without the support of IBGS, not only would I had learned less while at KU, but I have never improved my ability to recognize and appreciate constructive criticisms and help my writing become better focused. I need to specifically thank Dr. Brian Platt and Dr. Amanda Falk for being guide posts for my Ph.D. Derek Raisennan and Dr. James Golab for being great friends and office/lab mates. Matt Jones, Bob Rader, Sean Fischer, Alexa Goers, and Sean Hammersburg for their friendship and help with many of my grants, and manuscripts during IBGS. Outside of IBGS, I have to thank some members of the Lindley basement general population: Hannah Wasserman- my weekend basement buddy; Danielle Wooding- who let me mentor and guide some of her geological interests and was a great field assistant; and Logan Byers- who always has a well thought out and deep scientific query ready to go; and those others that have heard me talk, rant, or simply suggest that we do science.

For the Dakota Group Study, Chapter 4, I am indebted to Cindy and Barry Smith, members of the Cañon City fossil club, they opened up their community and house to me during my trips to Cañon City. The Dakota Group project seemed to had been cursed from the onset with fire, theft, road closures, and other fun; however, Cindy has been available to help though it

all as field support when I am out there or providing local information to help me judge when to be or not to be there.

Without the financial support of NSF (OPP 0944282 to STH), KU Department of Geology, KU Geology donor named grants (Dan Merriam Outstanding Student Research Award, Ray P. Walters Scholarship, Joseph M. Paterson Scholarship, Roscoe G. Jackson II Field Research Scholarship), The Kansas Interdisciplinary Carbonates Consortium, the Paleontological Society Rodney M. Feldman Award, The Geological Society of America Student Research Grant, and The American Association of Petroleum Geologists Raymond C. Moore Memorial Grant, this dissertation would not had been possible. I would also like to thank the KU Department of Geology again for providing two teaching positions during the 2015–2016 academic year. The opportunity to teach stratigraphy reawakened a downtrodden love of geology. My last semester, living in Lawrence, I had the great opportunity to teach History of the Earth and take an online course to the next level and integrate social and multimedia presentation from the students into a unique social learning experience.

Special recognition is for Dr. Larry Martin, who was on my committee until his passing. Meetings with Larry were always lighthearted, but got to the point of what needed to occur. He will always be remembered by me for his perspective on the Antarctica chapter of this dissertation and the US presence on Antarctica.

Finally, I must acknowledge the support from my family throughout this chapter of my life, and especially the support of my wife, Christa. Without them, I would not have made it.

Cheers.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

The purpose of this dissertation is to identify and characterize the physicochemical controls that influence trace fossils, and compare these during icehouse and greenhouse global climates and between high and low latitudes. This was achieved through three studies: 1) the high-latitude icehouse-climate Lower Permian Mackellar Formation (Fm), Central Transantarctic Mountains, Beardmore Glacier Region, Antarctica; 2) the low-latitude greenhouse climate Upper Cretaceous Greenhorn and Niobrara fms of the AMOCO Rebecca K. Bounds #1 Well core from Greeley County, Kansas; and 3) the low-latitude greenhouse climate Cretaceous Dakota Group from the Skyline Drive Outcrop in Cañon City, Colorado. The Mackellar Fm records a complex deltaic to basinal system that deposited sediments into a marine basin during the initial melt of the Permian Antarctic icecap. The other two projects provide deltaic and distal shoreface (the Dakota Group) out to basinal (the Greenhorn and Niobrara fms) environments of deposition (EOD) of the Western Interior Seaway (WIS) during the late-Early to early-Late Cretaceous.

Ichnofossils, trace fossils, preserve the behavioral responses of organisms to the physical, chemical and biological conditions that occurred during their lifespan; with the potential of some ichnofossils (burrow networks, i.e., *Thalassinoides*) being occupied by multiple organisms through time (Bromley, 1996). In the case of marine organisms, common physicochemical controls on behavior include sedimentation rates, depositional energy, oxygenation, medium (substrate), nutrients, salinity, hydrology, and turbidity (Hasiotis and Platt, 2012). The preserved record of these behaviors, trace fossils, can be used to interpret and identify the dominate controls at the time of the trace fossils creation and that of the co-occurring ecological community via ichnocoenoses (Wetzel, 1991). The goals each project were similar—to identify ichnogenera present, characterize ichnocoenoses, interpret ichnofacies, and interpret and describe the physicochemical parameters at the time of deposition—although each study varied in its particular scope or emphasis.

The second chapter revaluates the interpretations for the EOD of the Mackellar Fm from glacial lake to inland sea (Miller and Isbell, 2010). This study identifies 30 ichnogenera from Turnabout Ridge and Buckley Island, Beardmore Glacier Region, Antarctica. These trace fossils are grouped into six reoccurring ichnocoenoses, which are generally characteristic of epi- and endobenthic worms, arthropods and gastropods. The trace fossils identified are nearly all diminutive in morphology and exhibit shallow penetration depths. Of the trace fossils, none are exclusive to freshwater environments, 20 are found in fresh, brackish, and marine systems, and the remaining 10 are only known from marine environments. Sedimentologically, the Mackellar Fm consists of strata consistent with prodelta, delta front, and subaqueous terminal distributary channel deposits (Flaig et al., 2016). The diminutive morphotypes, shallow penetration, low individual bed and high overall ichnodiversity are interpreted as, and consistent with modern examples of short-lived benthic communities stressed by high-freshwater input and high sedimentation rates in a river-dominated deltaic to fully marine system.

Chapter three is a reevaluation and refinement of previous EOD interpretations for the Greenhorn and Niobrara fms, which were deposited during fully marine conditions on the eastern side of the WIS basin during the Late Cretaceous. Additionally, based on observed cyclic patterns in ichnocoenoses and bioturbation, these attributes were statistically tested for harmonic cycles that correlate with Milankovitch cyclicity (eccentricity, obliquity, and precession). Seventeen ichnogenera were described from these formations, and six nearly identical ichnocoenoses were identified for each formation. Ichnocoenoses and ichnofabric index (ii) (the semiquantitative proxy for bioturbation) were tested for orbital harmonics using multitaper methods, evolutive harmonic analysis, and average spectral misfit following the methods of Sageman et al. (1998), and Meyers et al. (2012). Harmonic frequencies that match Milankovitch were identified in both formations, the four members tested, from both ichnocoenoses and ii data. Eccentricity and obliquity-scale harmonics were identified in both ichnocoenoses and ii in all members, with the obliquity harmonic being less strong than the eccentricity signal. The precessional harmonic signal was weakly identified across both formations, but not as persistently as the obliquity or eccentricity signals. Across both formations ichnocoenoses identify a more abundant and stronger precessional scale signal than ii. Previous studies suggested that bioturbation could reduce or obliterate orbital scale signals (Cramer et al., 2003). This study shows, however, that this assumption is broadly incorrect and that ichnological records can be used as proxies with-or-without other common proxies (∂^{13}C, % $CaCO_3$) to identify harmonic cyclities and signals in ancient strata and modern deposits. The Greenhorn and Niobrara fms also recorded two global anoxic events, Oceanic Anoxic Events (OAE) 2 and 3. Previous studies have interpreted these anoxic zones to contain little to no benthic activity. This study identifies high ichnodiversity and abundant bioturbation in these intervals, and suggests that the anoxic events are more accurately characterized as dysoxic and punctuated by brief periods of anoxia.

Chapter four on the Dakota Group outcrops in Cañon City, CO, is designed to complement Chapter 3 by providing a Cretaceous WIS deltaic to paralic EOD comparison with the basinal interpretations of the Greenhorn and Niobrara fms. Previous studies have focused on sedimentology and petroleum potential of the Dakota Group (e.g., Weimer and Land 1978; Gustason and Kauffman 1985). Many of these studies have noted the presence of trace fossils, but none have addressed their vertical distribution or provided ichnotaxonomic descriptions (e.g., Altschuld 1980; Gustason and Kauffman 1985). The Dakota Group in the Cañon City area is divided into the Lytle, Plainview, Glencairn and Muddy formations (e.g., Holbrook and Ethridge 1996). This chapter assesses physicochemical parameters at the time of deposition using ichnocoenoses and ichnofacies to reinterpret EOD and depositional histories, reevaluate sequence stratigraphic models, identify vertical heterogeneity in EOD, and evaluate the influence of bioturbation porosity and permeability in these formations (e.g., Jackson et al. 2016). Integrating the ichnology and sedimentology for each Dakota Group formation resulted in the following EOD interpretations: fluvial (Lytle Fm), deltaic to paralic (Plainview Fm), offshore to shoreface (Glencairn Fm), and fluvial to offshore marine depositional environments (Muddy Fm). The 31 ichnogenera identified constitute seven ichnocoenoses that comprise the Scoyenia, Skolithos, and proximal to distal Cruziana ichnofacies. Throughout the Dakota Group, generally, highly bioturbated strata correlate with higher permeability and lower porosity. By integrating ichnological methods (ichnotaxonomy, characterization of ichnocoenoses, and ichnofacies identification) with sedimentology, this study presents a revised depositional model for the Plainview and Muddy fms, as well as a reinterpreted sequence stratigraphic framework for the Dakota Group in the Cañon City area.

The final chapter reviews the major findings of each of the previous chapters and synthesizes a large conclusion on the comparisons between icehouse and greenhouse conditions; high and low latitude environmental effects on the ichnogenera identified; and interpreted physicochemical controls at the time of deposition. Previous studies suggest that physicochemical controls on marine ichnogenera are different during icehouse and greenhouse global climates (e.g., Goldring et al. 2004), and that high and low latitudinal setting have different physicochemical controls (e.g., Quiroz et al. 2010). This dissertation identified similar ichnocoenoses and ichnofacies between the Permian icehouse high-latitude Mackellar Fm and the Cretaceous greenhouse low-latitude Dakota, Greenhorn, and Niobrara fms. In addition to these results, the application of ichnological records as secondary proxies for orbital cyclicity identification in the Western Interior Seaway is novel; furthermore, the preservation of an ichnological signal throughout the OAE 2 and OAE 3 strata indicates that benthic conditions were not wholly anoxic as previously interpreted. Applications of methods and results from this dissertation can be used to further refine physicochemical interpretations of marine strata using ichnology, as well as refining cyclostratigraphic studies with additional ichnological proxies.

REFERENCES

ALTSCHULD, K.R., 1980. Stratigraphy and depositional environments of the Dakota Group. Cañon City area, Colorado: MS thesis, Colorado School Mines, Golden.

BROMLEY, R.G., 1996. Trace Fossils: Biology, Taphonomy and Applications: Chapman and Hall, London, 361 p.

CRAMER, B.S., WRIGHT, J.D., KENT, D.V., AND AUBRY, M.P., 2003, Orbital climate forcing of δ13C excursions in the late Paleocene–early Eocene (chrons C24n–C25n): Paleoceanography, v. 18, doi:10.1029/2003PA000909.

FLAIG, P.P., HASIOTIS, S.T., AND JACKSON, A.M., 2016. An Early Permian, paleopolar, postglacial, river-dominated deltaic succession in the Mackellar–Fairchild formations at Turnabout Ridge, Central Transantarctic Mountains, Antarctica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, p. 241–265.

GOLDRING, R., CADÉE, G.C., D'ALESSANDRO, A., DE GIBERT, J.M., JENKINS, R. AND POLLARD, J.E., 2004. Climatic control of trace fossil distribution in the marine realm: Geological Society, London, Special Publications, v. 228, p. 77–92.

GUSTASON, E., AND KAUFFMAN, E., 1985, The Dakota Group and the Kiowa-Skull Creek Cyclothem on the Cañon City-Pueblo area, Colorado: SEPM Guidebook No. 4, p. 72–89.

HASIOTIS, S.T., AND PLATT, B.F., 2012, Exploring the sedimentary, pedogenic, and hydrologic factors that control the occurrence and role of bioturbation in soil formation and horizonation in continental deposits: An integrative approach: The Sedimentary Record, v. 10, p. 4–9.

HOLBROOK, J.M., AND ETHRIDGE, F.G., 1996, Sequence stratigraphy of the Dakota Group and equivalents from northcentral Colorado to northeastern New Mexico: downdip variations in sequence anatomy: Geologic Excursions to the Rocky Mountains and Beyond, 1996 GSA Guidebook, Colorado Geological Survey Special Publication 44. 44 p.

JACKSON, A.M., HASIOTIS, S.T., AND FLAIG, P.P., 2016, Ichnology of a Paleopolar, River-Dominated, Shallow Marine Deltaic Succession in the Mackellar Sea: The Mackellar Formation (Lower Permian), Central Transantarctic Mountains, Antarctica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, p. 266–291.

MEYERS, S.R., SAGEMAN, B.B. AND ARTHUR, M.A., 2012, Obliquity forcing of organic matter accumulation during Oceanic Anoxic Event 2: Paleoceanography, v. 27, PA3212.

MILLER, M.F., AND ISBELL, J.L., 2010. Reconstruction of a high-latitude, post-glacial lake: Mackellar Formation (Permian), Transantarctic Mountains, in: LÓPEZ-GAMUNDÍ, O.R., AND BUATOIS, L.A., eds., Late Paleozoic Glacial Events and Postglacial Transgressions in Gondwana. GSA Special Paper 468, Boulder, p.193–207.

QUIROZ, L.I., BUATOIS, L.A., MÁNGANO, M.G., JARAMILLO, C.A. AND SANTIAGO, N., 2010. Is the trace fossil *Macaronichnus* an indicator of temperate to cold waters? Exploring the paradox of its occurrence in tropical coasts: Geology, v. 38, p.651–654.

SAGEMAN, B.B., RICH, J., ARTHUR, M.A., DEAN, W.E., SAVRDA, C.E., AND BRALOWER, T.J., 1998, Multiple Milankovitch cycles in the Bridge Creek Limestone (Cenomanian-Turonian), Western Interior Basin, *in* Dean, W.E., and Arthur, M.A., (eds), Stratigraphy and Paleoenvironments of the Cretaceous Western Interior Seaway, USA: Concepts in Sedimentology and Paleontology, vol. 6, Society for Sedimentary Geology, Tulsa, OK, p. 153–171.

WEIMER, R.J., AND LAND, C.B., 1978, Field guide to Dakota Group (Cretaceous) stratigraphy Golden-Morrison area, Colorado: The Mountain Geologist, v. 9, p. 241–267.

WETZEL, A., 1991. Ecologic interpretation of deep-sea trace fossil communities: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 85, p. 47–69.

CHAPTER 2: ICHNOLOGY OF A PALEOPOLAR, RIVER-DOMINATED, SHALLOW MARINE DELTAIC SUCCESSION IN THE MACKELLAR SEA: THE MACKELLAR FORMATION (LOWER PERMIAN), CENTRAL TRANSANTARCTIC MOUNTAINS, ANTARCTICA

Published as:

Jackson, A.M., Hasiotis, S.T., and Flaig, P.P., 2016, Ichnology of a Paleopolar, river-dominated, shallow marine deltaic succession in the Mackellar Sea: The Mackellar Formation (lower Permian), Central Transantarctic Mountains, Antarctica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, p. 266–291.

ABSTRACT

The Lower Permian Mackellar Formation in the Beardmore Glacier Area of the Central Transantarctic Mountains, Antarctica, was deposited between 80 and 85°S paleolatitude. Previous studies suggest that Mackellar Formation strata were deposited in either a large glacial lake or inland sea. Our study identified 30 ichnogenera from Turnabout Ridge and Buckley Island of which: 1) none are exclusively freshwater forms; 2) 20 ichnogenera are found in freshwater, brackish, and marine settings; and 3) 10 ichnogenera are exclusively found in marine settings. Combining ichnologic evidence with sedimentologic observations suggests that the Mackellar Formation was deposited in a river-dominated delta in a fully marine to brackish-marine setting. Trace-fossil associations are grouped into the *Arenicolites-Phycodes, Lingulichnus, Arenicolites*-*Planolites, Kouphichnium, Phycodes*-*Teichichnus*-*Arenicolites*, and *Planolites*-*Teichichnus*-*Phycodes* ichnocoenoses of a mixed Skolithos–Cruziana ichnofacies.

These associations are characteristic of epi- and endobenthic worms, arthropods, and mollusks, with the vast majority of the traces being diminutive in diameter and length, and exhibit shallow (≤ 10 mm) penetration depths. These ichnocoenoses occur in paleoenvironments that include the prodelta, distal to proximal delta front including mouth bars, and subaqueous terminal distributary channels. The diminutive morphology, shallow penetration depth, low bed ichnodiversity, high overall ichnodiversity, and sedimentologic characteristics are indicative of benthic organisms in a marine deltaic environment with short-lived communities composed of small-bodied organisms stressed by high freshwater input and high sedimentation rates.

1. Introduction

Previous interpretations of the Lower Permian Mackellar Formation (Fm) depositional environments include subaqueous channel systems, levees, and turbidites fed by braided streams entering a regionally extensive lake (Miller and Isbell, 2010) or a shallow inland sea (Miller and Frisch, 1986; Miller and Collinson, 1994; Miller and Isbell, 2010). Salinity interpretations have varied between freshwater (Miller and Frisch, 1986; Miller et al., 1991; Collinson et al., 1994), brackish water (Miller and Frisch, 1986; Miller et al., 1991; Collinson et al., 1994), and full marine conditions (Collinson et al., 1994). The variability of the interpretation for Mackellar Fm environments of deposition and salinities is, in part, due to a lack of both body fossils and detailed ichnotaxonomic study of component trace fossils in areas free of strata altered by contact metamorphism. This study focuses on Mackellar Fm outcrops in the Beardmore Glacier area at Turnabout Ridge and Buckley Island that contain relatively well-preserved trace-fossil assemblages.

The purpose of this study is to interpret environments of deposition for the Mackellar Fm using an integrative approach of ichnology and sedimentology to test the hypothesis that the Mackellar Fm was deposited in a regionally extensive postglacial lake. Our objectives in the Mackellar Fm are to: 1) describe the ichnogenera at Turnabout Ridge and Buckley Island; 2) identify ichnocoenoses; 3) assign ichnofacies; and 4) interpret the physicochemical controls of the depositional environments that determined the occurrence and distribution of ichnocoenoses and ichnofacies. Characterizing the Mackellar Fm depositional environments and their physicochemical parameters has implications for the type of basin the Mackellar Fm was deposited in and the subsequent evolution of the basin during Permian deglaciation and further transition from an icehouse to greenhouse climate in Antarctica.

1.1. Geological Setting and Study Area

The Beacon Supergroup is within the Central Transantarctic Mountains, a mountain range that extends across Antarctica from the Waddell Sea to Northern Victoria Land (Fig. 1; Barrett et al., 1986). The Beardmore Glacier area contains a thick (up to 4 km), relatively complete succession of the Beacon Supergroup (Collinson et al., 1994). Within the Beacon Supergroup, the Upper Carboniferous to Lower Jurassic Victoria Group represents the majority of the exposed strata. Our study focuses on Lower Permian strata. The oldest Permian strata in the Beardmore Glacier area, the Pagoda Fm, is composed of subglacial diamictites and proximal and distal glaciomarine deposits (Isbell et al., 2003, 2008). The Mackellar Fm is found above a gradational contact with these glacial deposits. Named by Grindley (1963), the Mackellar Fm is a regionally extensive, 60–150-m-thick succession composed primarily of shale and fine-grained sandstone (Young and Ryburn, 1968; Collinson et al., 1994). No body fossils have been found in the Mackellar Fm; however, trace fossils have been identified previously but were not studied in detail (Miller et al., 1991; Miller and Collinson, 1994; Miller and Isbell, 2010).

The melting of Gondwanan ice sheets during the early Permian produced rising sea levels that flooded low-lying continental areas across the paleo-Pacific Antarctic coast (e.g., Leblanc-Smith and Eriksson, 1979; Barrett et al., 1986; Domack, 1988; Isbell et al., 2008; Koch and Isbell, 2013). The Permian–Triassic portion of the Victoria Group, deposited during and after the melting of Permo-Carboniferous ice sheets, records the icehouse to greenhouse transition in the Beardmore Glacier area (Miller and Smail 1996; Collinson, 1997; Rees et al., 2002; Miller and Isbell, 2010). Delayed crustal rebound during the retreat of the Permian ice sheet was the driving force behind the formation of an elongate intercratonic basin, which ultimately evolved into a retroarc foreland basin (Elliott, 1975). This transitional basin (> 3,000 km long) was flooded by what was initially interpreted as the Mackellar Sea (Elliot, 1975).

Early Jurassic emplacement of the Ferrar Large Igneous Province produced isolated successions of the Victoria Group preserved between Jurassic sills and dikes, and has modified their original physical and stratigraphic alignment (Elliott, 2013). Some of the least disrupted and metamorphosed sections, however, are located in the Beardmore Glacier area, where the strata remain nearly horizontal (Miller and Collinson, 1994). The metamorphic effects of Ferrar emplacement on the Victoria Group are reported as moderate (Ballance and Waiters, 2002). These effects potentially hampered previous ichnological studies (e.g., Miller and Collinson, 1994; Wildermuth et al., 2012) as the recrystallization of sandstone and mudstone matrix can decrease trace fossil fidelity (e.g., Powell, 2003).

This study focuses on samples collected from the Mackellar Fm at Turnabout Ridge and Buckley Island (Fig. 1, 2A, B). The modern latitude of the Turnabout Ridge and Buckley Island outcrop belts are similar to the early Permian paleolatitudinal position (~80–85°S, Powell and Li, 1994; Miller and Isbell, 2010). Turnabout Ridge (coordinates: S 83.24°, E 162.90°) is located in the Mount Rabot 1:250,000 Antarctica Reconnaissance Series Quadrangle near Bowden Névé at the confluence of the Linehan and Lowery Glaciers (Fig. 2A). Buckley Island (coordinates: S 85.01°, E 164.10°) is located in the Buckley Island 1:250,000 Antarctica Reconnaissance Series Quadrangle along the Beardmore Glacier (Fig. 2B).

Previous Mackellar Fm interpretations have regarded the absence of body fossils (e.g., *Eurydesma* fauna) as a critical issue with the interpretation of depositional environments. The Weaver and Polestar formations, thought to be contemporaneous to the Mackellar Fm (Minshew, 1967; Runnegar and Campbell, 1976; Bradshaw et al., 1984; Lopez-Gamundi, 1989; Collinson et al., 1994), contain the marine trace fossils *Paleodictyon* (Weaver Formation; Collinson et al., 1994) and *Phycodes* (Polestar Formation; Miller and Collinson, 1994). Previously identified trace fossils in the Mackellar Fm include *Cochlichnus, Cruziana, Isopodichnus* (*=Diplichnites*), *Diplopodichnus, Mermia carickensis* (= *Gordia carickensis;* Netto et al., 2012), *?Orbiculichnus*, *Palaeophycus* or *Planolites*, and *Treptichnus* (Miller et al., 1991; Miller and Collinson, 1994; Briggs et al., 2010; Miller and Isbell, 2010). These trace fossils have not been systematically analyzed for their ichnotaxonomic positions.

2. Materials and Methods

A total of 675 samples, consisting of slabs and individual specimens, were collected for ichnological study from Turnabout Ridge and Buckley Island during the 2010–2011 austral Antarctic field season. A representative succession of the Mackellar Fm–Fairchild Fm was measured at Turnabout Ridge and a stratigraphic column with detailed descriptions of grain size, lithology, contacts, sedimentary structures, and relative locations of trace fossils was produced (Fig. 3; modified from Flaig et al., 2016). Ichnological samples from Turnabout Ridge and Buckley Island are held in the IchnoBioGeoSciences (IBGS) Collections, Department of Geology, The University of Kansas, Lawrence, Kansas, USA.

Trace-fossil identification was made to ichnospecies level when appropriate. Trackway measurements were made following the procedures of Trewin (1994), Braddy (2001), and Minter et al. (2007). Burrow architectural and surficial morphologies were described following the procedures of Hasiotis and Mitchell (1993) and Bromley (1996) and compared to those in the literature. As trace fossils are found on bedding planes, each sample was considered its own ichnocoenoses—reoccurring, lithologically associated, trace-fossil associations representing a community that was active in the same environment at the same time—and grouped into six common ichnocoenoses (cf. Pemberton et al., 2005). Trace-fossil abundance and diversity is qualified relatively, (i.e. ≥ 5 ichnogenera per sample is high, whereas ≤ 2 ichnogenera is low diversity).

3. Results

3.1 Ichnology

3.1.1 *Arenicolites* Salter, 1857

Arenicolites isp. (Fig. 4A)

Description: Paired (1–3 mm diameter), concave and/or convex epirelief, funnel-shaped, round to ovoid apertures perpendicular to bedding. Where bedding crosses through paired tubes, matrix between them is visible. Apertures are commonly 2 mm apart (measured between nearest edge of shafts), with rare examples up to 10 mm apart.

Remarks: *Arenicolites* has been interpreted as the U-shaped burrow of a suspension-feeding organism, such as a worm (Häntzschel, 1975). Burrow depth was unable to be determined as no example was found in complete lateral view. *Arenicolites* has been reported from a wide variety of environments since the Cambrian, including marine, brackish water, fluvial, lacustrine, and eolian (e.g., Bromley and Asgaard, 1979; Eager et al., 1985; Hasiotis, 2002, 2012).

3.1.2 *Bergaueria* Prantal, 1945

Bergaueria isp. *cf. B. perata* Prantal, 1945 (Fig. 4B)

Description: Cylindrical to semihemispherical, unornamented, slightly ridged, thinly lined to unlined, convex hyporelief, vertical to obliquely vertical protrusion with undifferentiated fill. Apical end of the burrow is narrower than opening, and may taper slightly to a subrounded termination. The majority of *Bergaueria* are ≤ 5 mm in diameter, with a single collected example (11SHTRMK-215) up to 26.05 mm.

Remarks: *Bergaueria* is commonly interpreted as a resting or dwelling trace of an anemone. They are marine to brackish marine type trace fossil from the Ediacaran to recent (i.e., Pemberton et al., 1988; Uchman 1998; Hasiotis, 2012; James et al., 2014).

3.1.3 *Chondrites* von Sternberg, 1833

Chondrites isp. (Fig. 4C)

Description: Horizontal to gently inclined, concave or convex epirelief, dendritic downward to horizontally branching burrow network originating from a central node. Branching pattern is irregular in angle. Nodes (remnant of the central shaft) average 0.3 mm in diameter, with branch diameters of 0.1–0.2 mm and lengths ≤ 7 mm. Branches are circular to elliptical in cross section.

Remarks: Where present, the *Chondrites* tunnels are often abundant, although the central node, is not well preserved. *Chondrites* is interpreted as a feeding burrow, and are typical of low-oxygen environments, and can be found in lagoonal mudstones, shelfal sandstones, to deep-sea mudstones from the Cambrian to recent (e.g., Fürsich, 1974; Bromley and Ekdale, 1984; Crimes, 1987; Hasiotis, 2012).

3.1.4 *Circulichnus* Vialov, 1971

Circulichnus montanus Vialov, 1971 (Fig. 4D)

Description: Smooth to slightly rough, distinct ellipsoid trail preserved in concave or convex epirelief on fine-grained sandstone with mudstone interbeds. Trails are 0.1–0.3 mm wide. Trace fossil outer diameter up to 16 mm, with common diameters between 5–6 mm.

Remarks: *Circulichnus* occur on low-angled to planar cross-bedded sandstones, and have been identified from Cambrian to recent, from marine and continental environments (e.g., Fillion and Pickerill, 1990; Davies et al., 2010).

3.1.5 *Cochlichnus* Hitchcock, 1895

Cochlichnus isp. (Fig. 4E)

Description: Continuous, near sinusoidal, regularly meandering trail at the surface or as near-surface burrows. Trails are smooth and preserved in concave epirelief. Trail width varies from 0.2–3 mm, with trails ≤ 118 mm long. Amplitudes of sinusoidal meander can vary along the trail; for example, 11SHTRMK-28, amplitude reduced by ~50% in each cycle, from 16.32 mm to 9.28 mm, along a 118-mm-long trail.

Remarks: *Cochlichnus* commonly occurs with other traces attributed to vermiform organisms (e.g., *Gordia*, *Planolites*). *Cochlichnus* tends to be found on the leeward side of ripples. *Cochlichnus* has been identified from Ediacaran to recent, and from continental to deep marine settings (e.g., Hasiotis and Bown, 1992; Crimes 1992; Buatois and Mángano, 1993; Hasiotis, 2002; 2012).

3.1.6 *Conichnus* Männil, 1966

Conichnus conicus Männil, 1966 (Fig. 4F)

Description: Unlined, perpendicular to bedding, convex hyporelief or concave epirelief, shallow, cone-shaped burrow. The wider opening distally tapers to a narrow apex. Infill, when present, is massive and the same composition as the surrounding matrix. Burrow depth is < 2 mm, with upper diameters ≤ 6 mm.

Remarks: *Conichnus* tends to occur in clusters. *Conichnus* is typical of marine environments, and found from the Cambrian to recent (e.g., Männil, 1966; Schroder, 1982; Hiscott et al., 1984).

3.1.7 *Crossopodia* McCoy, 1851

Crossopodia isp. (Fig. 5A)

Description: Meandering to straight, concave epirelief or convex hyporelief trail, with or without a central furrow, with feathered to smooth external ridges. Trails from 1–8 mm wide, and ≤ 65 mm long.

Remarks: Characteristic of high-energy marine environments, *Crossopodia* has been identified from the Cambrian to recent (e.g., Hattin and Frey, 1969; Uchman and Pervesler, 2006). Previous studies proposed a vermiform tracemaker (e.g., Seilacher and Seilacher (1994), whereas Uchman and Pervesler (2006) suggested arthropod tracemakers based on neoichnological studies.

3.1.8 *Cruziana* d'Orbigny, 1842

Cruziana isp. (Fig. 5B)

Description: Trails or the floor of shallow burrows preserved as long, bilobate furrows with poorly to well-preserved internal herringbone-like lineations on the trail walls. Outer edges of the trails may preserve striations or grooves perpendicular to the trail. Trails are preserved most often in concave epirelief; commonly 1–3 mm wide and up to 70 mm long.

Remarks: Interpreted as a surficial to burrowing trail of an arthropod (Seilacher, 1962). *Cruziana* is known from the Cambrian to Triassic from shallow marine to continental deposits (e.g., Zonneveld et al., 2002; Hasiotis, 2012).

3.1.9 *Cylindrichnus* Howard, 1966

Cylindrichnus isp. (Fig. 5C)

Description: Concentrically laminated, vertical to subvertical, concave to convex epirelief burrow, 3–5 mm in diameter. The concentric laminations weather out obliquely.

Remarks: The orientation of *Cylindrichnus* grades between horizontal to vertical based on the depositional energy—the higher the energy, the more *Cylindrichnus* is inclined to vertical (Goldring, 1996; Howard, 1966; Frey, 1990). *Cylindrichnus* ranges from the Cambrian to recent in marine settings (Landing, 1989; Goldring, 1996; Aguirre et al., 2010; Belaústegui et al 2012).

3.1.10 *Diplichnites* Dawson, 1873

Diplichnites isp. *cf* isp C of Fillion and Pickerill, 1990 (Fig. 5D)

Description: Trackway consisting of concave epirelief, circular to tapered external tracks of staggered symmetry. Tapered external tracks oriented near perpendicular to the trackway midline. Trackway width is ≤ 20 mm, and average track diameter of 0.5 mm. Track repeat distance 1–15 mm with staggered symmetry, with overall trackway lengths up to 150 mm.

Remarks: A majority of the tracks identified are not the typical linear scratches characteristic of *Diplichnites*; however, they are shallow depressions attributed to the leg tips during locomotion (e.g., Minter et al., 2007). *Diplichnites* is interpreted as a locomotion trace of an unknown arthropod, and has been identified from continental and marine deposits from the Cambrian to recent (e.g., Fillion and Pickerill, 1990; MacNaughton et al., 2002; Hasiotis, 2012).

3.1.11 *Diplocraterion* Torell, 1870

Diplocraterion isp. (Fig. 5E)

Description: Concave or convex epirelief cross sections of paired burrow apertures, perpendicular to bedding, with unidirectional protrusive spreiten. Spreiten are preserved in relief, discernible from burrow wall and shaft infill. Specimens were only seen in plan view and crossing bedding planes. Shaft diameters of 0.7–1.3 mm and apertures or shafts are ≤ 6 mm apart with spreiten thicknesses between 1 and 2 mm.

Remarks: The spreiten of *Diplocraterion* are interpreted as the response of the organism to changes in surface sedimentation or erosion rates, and/or organismal growth (Fürsich and Hurst, 1974). *Diplocraterion* is found in deposits from the Cambrian to recent from shallow to deep marine environments (e.g., Fürsich and Hurst, 1974; Mason and Christie, 1985; Cornish, 1986; Hasiotis, 2012).

3.1.12 *Gordia* Emmons, 1844

Gordia marina Emmons, 1844 (Fig. 5F)

Description: Long, smooth, bent to winding to looping, nonbranching, concave epirelief trails. Trails consistent in diameter across the length of the trace, and often contain at least one full loop. Trail widths average 1 mm, with overall lengths of 8–76 mm. The loop crossing is level with the rest of the trail.

Remarks: *Gordia* is often found on the crests of ripples, on the stoss side, or transitioning from the ripple crest down the stoss side. The tracemakers were likely vermiform and grazing for food (e.g., Ksiżkiewicz, 1977). *Gordia* ranges from the Ediacaran to the recent occurs in fluvial, lacustrine, lagoonal, deltaic, shallow marine, and deep marine deposits (e.g., e.g., Radcliffe and Fagerstrom, 1980; Seilacher et al., 2005; Hasiotis, 2012).

3.1.13 *Gyrolithes* de Saporta, 1884

?*Gyrolithes*. (Fig. 6A)

Description: A single vertical trending dextral half-whorl spiral burrow, preserved in concave epirelief, with two interior menisci (11SHTRMK-87). Horizontal trail is 1.65 mm wide and 7.8 mm long leading to the spiral. The spiral length is 9.77 mm, with a consistent width of 1.33 mm to where it descends under the upper horizontal trail, outside loop diameter is 3.4 mm.

Remarks: The menisci interior walls are similar to *T. serpentinum*, however, the spiral pattern is consistent with *Gyrolithes*. Tracemaker interpretations range from crustaceans to vermiform organisms (e.g., Bromley and Frey, 1974), and occur in marine environments from the Cambrian to recent (e.g., Heer, 1865; Gernant, 1972; Crimes, 1987; Hasiotis, 2012).

3.1.14 *Kouphichnium* Nopcsa 1923

Kouphichnium isp. (Fig. 6B)

Description: Concave epirelief, ≤ 0.1 mm deep, parallel to near parallel, alternating to paired, lineations, bifid tracks, and occasional oval to round pits. Trackways are straight to slightly curved, 28–42 mm wide, and generally continue for overall lengths ≤ 200 mm. Bifid tracks are the most common component of the trackways.

Remarks: *Kouphichnium* isp. is found on fine- to very fine-grained sandstone beds with mudstone interbeds across ripple crests. *Kouphichnium* have been identified from marine and freshwater environments (e.g., Hasiotis, 2002, 2004, 2008), and have been found from the Ordovician to the recent (e.g., Hasiotis, 2002; Rudkin et al., 2008).

3.1.15 *Lingulichnus* Hakes, 1976

Lingulichnus verticalis Hakes, 1976 (Fig. 6C)

Description: Elliptically compressed ovoid to lenticular, vertical, concentrically filled burrows. Burrow apertures are up to 1 mm wide and 6 mm long. Apertures occasionally have a ridge creating a lip.

Remarks: *Lingulichnus* ranges from the Cambrian to recent and is generally found in shallow marine to brackish conditions, but has been identified from deep shelf environments (e.g., Pickerill, 1973; Pemberton and Kobluk, 1978; Zonneveld et al., 2007). Lingulid brachiopods are most often found in salinity-stressed environments and can be used as an indicator of brackish conditions (Hamman and Lum, 1977; Emig, 1997; Zonneveld et al., 2007).

3.1.16 *Lockeia* James, 1879

Lockeia silliquaria James, 1879 (Fig. 6D)

Description: Convex hyporelief, almond- to oval-shaped burrows. Burrows are 1–2 mm wide and up to 7 mm long. Apex of burrow may be sharp or rounded, depending on if a central ridge is present with smooth to rugose walls. Proximal and distal edges taper sharply or gently.

Remarks: *Lockeia* is interpreted as a resting or dwelling trace of bivalve-like organisms and have been found from the Ediacaran to recent (i.e., Osgood 1970; Häntzschel, 1975; Seilacher and Seilacher, 1994; McMenamin, 1996). *Lockeia* is found in freshwater and marine environments (e.g., Häntzschel, 1975; Hakes, 1976; Hasiotis, 2002, 2004, 2008).

3.1.17 *Margaritichnus* Bandel, 1973

Margaritichnus reptilis Bandel, 1973 (Fig. 6E)

Description: Unornamented, convex hyporelief, series of compressed to slightly compressed, spherical to semispherical structures arranged in an en echelon pattern of hemispherical to spherical structures. Overall sphere sizes of up to 3.84 mm diameter and burrow up to 28 mm long.

Remarks: *Margaritichnus* has been identified from marine and fluvial meandering river deposits, and been interpreted to represent dwelling or feeding traces created by vermiform or bivalve-like organisms (e.g., Bandel, 1967; Seilacher, 1990; Garvey and Hasiotis, 2008). *Margaritichnus* has been identified from the Ediacaran through the Holocene (Bandel, 1967; Glaessner, 1969; Narbonne, 1984).

3.1.18 *Palaeophycus* Hall, 1847

Palaeophycus tubularis Miller 1889 (Fig. 7A)

Description: Convex hyporelief, cylindrical to near-cylindrical, subhorizontal to horizontal, smooth, lined burrow. Burrows are unbranched with a similar to slightly coarser fill than matrix. Burrow widths from 1.5–3 mm, and lengths mostly from 3–9 mm, but up to 24 mm.

Remarks: Preserved lining is not common in collected samples; but its presence is apparent by the separation of the trace fossil from the matrix. *Palaeophycus* is identified in deposits from Ediacaran to recent, and are found in freshwater and marine environments (e.g., Osgood, 1970; Garvey and Hasiotis, 2008).

3.1.19 *Parataenidium* Buckman, 2001

Parataenidium mullaghmorensis Buckman, 2001 (Fig. 7B)

Description: Horizontal, convex epirelief or hyporelief, burrows consisting of a series of irregularly subspherical, imbricated sediment packages. Burrow width varies from 0.5–3 mm, with burrow length up to 56 mm.

Remarks: *Parataenidium* is interpreted as being produced by two distinct behaviors attributed to the upper and lower portions of the burrows—where the upper portion is more meniscate from feeding and the lower portion is produced from locomotion (Uchman and Gaździcki, 2006). *Parataenidium* has been identified from the Carboniferous to the Paleogene (Eocene) in marine environments (Buckman, 2001; Uchman and Gaździcki, 2006).

3.1.20 *Phycodes* Richter, 1850

3.1.20.1 *Phycodes* isp. (Fig. 7C)

Description: Cylindrical to subcylindrical, subhorizontal, distally enlarged and deepened burrows with poorly formed spreiten, and rare branching. Burrows vary from 0.2–10 mm wide and 1–73 mm long.

Remarks: Incipient *Phycodes* with rare single branching. The limited branching with antecedent occasional side grooves suggests that these could be *P. antecedens* (Webby, 1970). *Phycodes* has been identified in marine environments from the Cambrian to recent (e.g., Crimes, 1987; Hasiotis, 2012).

3.1.20.2 *Phycodes ungulates* Fillion and Pickerill, 1990 (Fig. 7D)

Description: Convex hyporelief of a cylindrical to subcylindrical burrow with multiple branches that radiate from a point and are shorter than the originating burrow. Branches are often wider than the original. Burrows vary from 1–7 mm wide and 3–22 mm long.

Remarks: *Phycodes ungulates* is found on low angle cross-bedded sandstones with fill similar to the matrix. *Phycodes ungulates* is interpreted as characteristic of offshore marine deposits and is known from the Ordovician (Fillion and Pickerill, 1990).

3.1.20.3 *Phycodes curvipalmatum* Pollard, 1981 (Fig. 7E)

Description: Cylindrical to subcylindrical, horizontal, concave hyporelief, burrows 1–7 mm wide and 3–22 mm long, and are commonly curved and branched in a palmate form.

Remarks: *Phycodes curvipalmatum* occurs on the soles of fine-grained sandstone beds. Burrows often are not found near other *P. curvipalmatum*, but near other *Phycodes*. *Phycodes curvipalmatum* has previously been described in marine deposits from the Triassic of England and Germany (Pollard, 1981).

3.1.20.4 *Phycodes templus* Hans and Pickerill, 1994 (Fig. 7F)

Description: Concave hyporelief, cylindrical to subcylindrical burrow with multiple, repeated (≥2) horizontally splayed burrows originating from a single point. Burrow bundles are 0.1–5 mm wide, with primary individual burrows ≤ 24 mm long, and burrow splays of ≤ 5 mm long and < 5 mm wide.

Remarks: *Phycodes templus* has previously been identified in Devonian marine rocks (Hans and Pickerill, 1994). Similar to the other Mackellar Fm *Phycodes*, *P. templus* occurs in fine-grained sandstones with low-angle crossbeds.

3.1.20.5 *Phycodes reniforme* Hofmann 1979 (Fig. 8A)

Description: A cylindrical to subcylindrical, convex hyporelief, horizontal burrow with spreiten that originate from a single point and may overprint each other. The first burrow is from 0.5–2 mm wide with splays up to 8 mm wide, with overall length of the burrow system ≤ 39 mm.

Remarks: *Phycodes reniforme* occurs with *Phycodes* isp., *Planolites*, and *Teichichnus*. This ichnospecies was previously only known from Ordovician marine strata (Hofmann, 1979).

3.1.20.6 *Phycodes palmatus* Hall, 1852 (Fig. 8B)

Description: A multibranched, convex hyporelief, cylindrical to subcylindrical burrow with thick rounded branches originating from a single point. At the origination point the branches become homogenous because of overprinting. Branches are 2–5 mm wide, and ≤ 28 mm long.

Remarks: The branching pattern of *P. palmatus* is most similar to *P. curvipalmatum*, but at a larger scale. *Phycodes palmatus* has been found in marine strata from the Cambrian to Paleogene (Jensen and Grant, 1998; Miller, 2001).

3.1.21 *Planolites* Nicholson, 1873

Planolites isp. (Fig. 8C)

Description: Unornamented, unlined, cylindrical to subcylindrical, horizontal to subhorizontal, straight to gently curved burrows in convex hyporelief. Undifferentiated infill is commonly finer than the matrix. Burrows are 0.5–4 mm in diameter and ≤ 53 mm long.

Remarks: Burrows occur along bedding planes, often on the stoss side of ripples. Known from Ediacaran–recent (e.g., Pemberton and Frey, 1982; Hasiotis 2012), and is interpreted as grazing burrow in marine sediment (e.g., Pemberton and Frey, 1982). *Planolites* is also known from continental environments (e.g., Hasiotis, 2002, 2004, 2008; Collette et al., 2011; Chakraborty et al., 2013).

3.1.22 *Protovirgularia* McCoy, 1850

Protovirgularia isp. (Fig. 8D)

Description: Horizontal to subhorizontal, convex to concave epirelief burrows composed of triangular-, almond-, or occlupanid-shaped (Fig. 8D arrow) segments when viewed in cross section. The basal portions in convex hyporelief appear keeled to cylindrical with a ridged to ribbed exterior. Burrows are from 2–5 mm wide and ≤ 101 mm long.

Remarks: Commonly interpreted as lateral adjustment of bivalves (e.g., Seilacher and Seilacher, 1994). *Protovirgularia* has been identified from marine environments from the Ordovician to recent (Seilacher, 1994).

3.1.23 *Rusophycus* Hall, 1852

Rusophycus isp. (Fig. 8E)

Description: Small bilobate, coffee-bean-shaped, laterally striated and centrally furrowed depressions as convex hyporelief. Lobes are generally parallel, but can diverge at one end. Highly variable in size: 1–11.48 mm wide and 2–13 mm long. Larger specimens have better preserved lobe striations.

Remarks: *Rusophycus* ranges from the Cambrian–recent, and is found in marine and lacustrine environments (e.g., Bromley and Asgaard, 1979; Garvey and Hasiotis, 2008; O'Brien et al., 2009; Hasiotis, 2012).

3.1.24 *Sagittichnus* Seilacher, 1953

Sagittichnus lincki Seilacher, 1953 (Fig. 8F)

Description: Teardrop-, arrowhead-, or rice-grain-shaped burrows as convex epirelief. The wider end is rounded, whereas the thinner end tapers to a point. Traces from 0.7–3 mm wide, and 1–5 mm long. Overall axis is dominantly straight, but can be slightly curved.

Remarks: *Sagittichnus* has been reported from freshwater to brackish environments from the Cambrian–recent (e.g., Garvey and Hasiotis, 2008). Previous studies have interpreted *Sagittichnus* as a resting trace of ostracodes or conchostracans (e.g., Retrum et al., 2011).

3.1.25 *Scolicia* de Quatrefages, 1849

Scolicia isp. (Fig. 9A)

Description: Meandering, concave epirelief or convex hyporelief, bilobed trail with a faint median furrow or groove. Specimens are 1.5–3.5 mm wide and ≤ 47 mm long.

Remarks: *Scolicia* are a common marine environmental indicator and have been used to note environments with low oxygen or brackish water from the Cambrian–recent (e.g., Häntzschel, 1975; Bromley et al., 1995; Hasiotis, 2012). They are, however, also found in freshwater aquatic environments (e.g., Hasiotis, 2002, 2004, 2008; Bohacs et al., 2007).

3.1.26 *Skolithos* Haldemann, 1840

Skolithos isp. (Fig. 9B)

Description: Vertical to subvertical, straight to slightly curved, unlined burrows, with fill consistent with the matrix. Burrows are 1–3 mm in diameter and ≤ 10 mm long.

Remarks: Only specimens that penetrated the collected slabs were identified at *Skolithos*. *Skolithos* are comparatively rare in the Mackellar Fm. Burrow depths were constrained by the slab thickness. *Skolithos* occurs from the Ediacaran–recent (e.g., Alpert, 1975; Fillion and Pickerill, 1990; Pemberton et al., 2001; Hasiotis, 2012).

3.1.27 *Taenidium* Heer*,* 1877

Taenidium serpentinum Herr, 1877 (Fig. 9C)

Description: Straight to slightly meandering, convex epi- or hyporelief, horizontal to subhorizontal, unlined, unbranching meniscate backfilled burrow. Burrow lengths are up to 50 mm, with widths from 1–4 mm, and menisci packages ≤ 2 mm thick.

Remarks: This study follows Smith et al. (2008) for the taxonomic placement of the Mackellar Fm morphotype. *Taenidium* occur on very fine-grained sandstone with mudstone interbeds. *Taenidium* is known from the Cambrian–recent and is found in marine depositional environments (e.g., Savrda et al., 2000; Hasiotis, 2012).

3.1.28 *Teichichnus* Seilacher, 1955

Teichichnus rectus Seilacher, 1955 (Fig. 9D–E)

Description: Abundant, convex hyporelief and full relief, horizontal to gently inclined burrows with spreiten. Tunnel diameters between 2–7 mm, with burrows ≤ 35 mm long and overall depth ≤ 14.21 mm. Spreiten are 0.3–1 mm thick and retrusive. Individual burrows may occur near each other, but do not originate from the same point.

Remarks: *Teichichnus* exhibits the greatest penetration depth of all ichnogenera identified from the Mackellar Fm. One sample—11SHTRMK-211—extends to a depth is 14.21 mm. *Teichichnus* is a marine environment indicator that spans from the Cambrian–recent (e.g., Seilacher, 1955; Pemberton et al., 2001; Hasiotis, 2012), and are interpreted to be produced by opportunistic deposit feeders that flourish in dysoxic, high sedimentation rates, or other salinity stressed systems (e.g., Chisholm, 1970; Ekdale and Mason, 1988; Pemberton et al., 2001).

3.1.29 *Treptichnus* Miller, 1889

?*Treptichnus pollardi* Buatois and Mángano, 1993 (Fig. 9F)

Description: Horizontal to subhorizontal, cylindrical to subcylindrical, convex hyporelief burrow consisting of regular to near-regular length segments offset from the previous segment. Burrows are 0.25–4 mm wide and ≤ 84 mm long with burrow segments ≤ 1.5 mm.

Remarks: The Mackellar Fm *Treptichnus* are consistent with *T. pollardi*, except for the absence of nodes at the ends of each segment. *Treptichnus* has been identified in rocks from the Cambrian–recent in freshwater and marine systems, and is interpreted as being produced by a deposit-feeding behavior, where the successive segments are abandoned as the organism moved forward (e.g., Häntzschel, 1975; Maples and Archer, 1987; Rindsberg and Kopaska-Merkel, 2005; Netto et al., 2009; Hasiotis, 2012).

3.1.30 *Undichna* Anderson, 1976

Undichna isp. cf *britannica* Higgs, 1988 (Fig. 10)

Description: Three asymmetric, low-amplitude, near sinusoidal intertwined out-of-phase trails. The outer trails are 180º offset, symmetric, discontinuous trails that have a near-sinusoidal form and cross the central trail. The outer trails becomes less pronounced and dissipates as it crosses the central trail, while the next high amplitude discontinuous trail begins and then increases to the full depth after crossing, completing about half of the overall sinusoidal form. The central trail is 1.24 mm wide and 127.99 mm long, whereas the outer trail is ≤ 1.62 mm wide and each length is ≤ 49.48 mm long.

Remarks: *Undichna* has been found in both freshwater and marine systems, although a majority of samples are from lacustrine deposits (e.g., Anderson, 1970; Gilbert et al., 1999; Minter and Brady, 2006; Garvey and Hasiotis, 2008; Hasiotis et al., 2012).

3.2 Sedimentology

The Mackellar Fm–Fairchild Fm interval at Turnabout Ridge and Buckley Island expose an overall coarsening-upward succession of interbedded sandstone, siltstone, and shale at both localities, becoming increasingly sand rich up section (Flaig et al., 2016). The Mackellar Fm at Turnabout Ridge is ~ 90 m thick (Flaig et al., 2016). At Turnabout Ridge the Mackellar Fm gradationally overlies glaciomarine deposits of the Pagoda Fm (Koch and Isbell, 2013) and is overlain by braid plains of the Fairchild Fm (Elliot 1975, 2013). The Mackellar Fm–Fairchild Fm succession at Buckley Island preserves similar depositional environments as those at Turnabout Ridge. Results indicate that Mackellar Fm strata at Turnabout Ridge comprise six facies, five of which contain trace fossils (Fig. 11, Table 4; Flaig et al., 2016). Two facies (Facies 6 and 7 of Flaig et al., 2016) compose the bulk of the overlaying braided stream deposits of the Fairchild Fm.

Facies 1 is structureless- to current-ripple laminated shale and siltstone which contains abundant trace fossils, including *Arenicolites*, *Cruziana*, *Kouphichnium*, *Phycodes*, and *Rusophycus*. Facies 2 and 3 are symmetrical cross-laminated sandstone (wave-rippled sandstone) with similar trace fossils to facies 1, with the addition of *Circulichnus*, *Gordia*, and *Protovirgularia*. Facies 4 is climbing ripple cross-laminated sandstone with abundant *Planolites* and *Phycodes*. Facies 5 is low-angle, planar-laminated sandstone with rare bioturbation, often only *Planolites*. Facies 6 is unbioturbated trough cross-stratified sandstone and facies 7 is stuctureless to rippled mudstone. Soft-sediment-deformation and dewatering structures can be found commonly in facies 1–5. These facies are further grouped into four facies associations (Table 5). The Mackellar Fm contains three of the four facies associations. Facies Association 1 represents the distal delta front and prodelta, whereas facies association 2 represents subaqueous terminal distributary channels and levees. Facies Association 3 represents proximal delta front, and facies association 4 represents braided channels and floodplains.

4. Discussion

Thirty ichnogenera are identified in the Mackellar Fm at Turnabout Ridge and Buckley Island. Previous studies identified seven ichnogenera in the Mackellar Fm at Buckley Island and several other localities in the Beardmore Glacier area. Previous trace-fossil identifications were likely difficult to constrain because of metamorphic alternation by nearby Ferrar Dolerite intrusions (i.e., Miller and Collinson, 1994; Miller and Isbell, 2010; Wildermuth et al., 2012). Metamorphic effects can lead to a loss in morphologic fidelity and the grouping of several different traces fossils into one group (Bucher, 1953). The Mackellar Fm at Turnabout Ridge appears to have been less altered than at many other sites, likely because of the relative lack of large dolerite dikes that intrude the Mackellar Fm elsewhere (USGS Buckley Island, Mount Rabot Maps; D.H. Elliott, 2014, personal communication). Samples of the Mackellar Fm from Buckley Island show a higher influence of contact metamorphism (mica and garnet growth) from Ferrar intrusions compared those from Turnabout Ridge.

4.1 Ichnocoenoses and Ichnofacies

The 30 ichnogenera identified in this study (Table 1, 3) are grouped into six reoccurring ichnocoenoses (Fig. 13, Table 2) found in generally thinly bedded, fine-grained sandstones with or without thin mudstone interbeds. The highest ichnodiversity occurs in the *Phycodes-Teichichnus-Planolites* ichnocoenoses, which can contain up to 12 of the 30 identified ichnogenera (see Fig. 12). The lowest diversity is found in both the *Arenicolites-Phycodes* and *Lingulichnus* ichnocoenoses. Most of the trace fossils identified do not form major, commonly reoccurring component of the any ichnocoenosis (i.e. ?*Gyrolithies*).

The distinction of *Arenicolites-Planolites* and *Arenicolites-Phycodes* ichnocoenoses, beyond presence of the secondary trace, is based on the interpreted ethological difference between *Planolites* and *Phycodes*. Both *Planolites* and *Phycodes* are deposit-feeding morphotypes; *Phycodes* is attributed to near-sessile, deposit-feeding behavior where an organism feeds out from a primary tunnel, or a series of tunnels, and then moves on to feed in another location (Seilacher, 1955), whereas *Planolites* is attributed to a continuously mobile deposit feeder (Pemberton and Frey, 1982). The *Arenicolites-Phycodes* ichnocoenoses is interpreted to be a more stable environment in which the *Phycodes* tracemaker has time to selectively mine for food. The *Lingulichnus* ichnocoenoses is nearly monospecific, occurring only with rare *Phycodes* in thinly bedded fine-grained sandstone with mudstone interbeds with oscillation-rippled surfaces. These sediments are interpreted to been deposited in the proximal to distal delta front where the sediment-water interface is wave reworked. The environments in the delta front are consistent with previously interpreted positions for linguilid brachiopods in salinity-stressed,brackish-water environments (Hamman and Lum, 1977; Emig, 1997; Zonneveld et al., 2007).

The *Kouphichnium* ichnocoenoses is found in thinly bedded, wave-rippled sandstones characteristic of bar forms along the delta front in the Mackellar Fm delta complex. Often occurring with *Kouphichnium* are such shallow-water trails and trackway trace fossils as *Circulichnus*, *Gordia*, *Cruziana*, and *Diplichnites*. The abundance of small trails and trackways compared to near absence of burrows, suggests that the environment was dynamic where organisms could occupy the bar forms temporarily before the next depositional event which precluded more complicated burrowing behaviors. *Phycodes-Teichichnus-Arenicolites* and *Planolites-Teichichnus-Phycodes* ichnocoenoses are the most diverse, with later having the highest overall diversity. Both of these ichnocoenoses occur in similar sedimentary packages, thinly bedded sandstones with thin mudstone interbeds, from similar interpreted environments—distal delta front to prodelta. The differentiation of these ichnocoenoses is that the *Planolites-Teichichnus-Phycodes* ichnocoenoses tend to occur in more distal to prodelta deposits where the environment is more stable. In this more stable environment, a greater abundance of organisms could have time between freshets (Flaig et al, 2016) to create burrow systems with higher complexity (i.e., *Protovirgularia*, *Taenidium* and *Treptichnus*).

The basal Mackellar Fm contains the highest diversity *Planolites*-*Teichichnus*-*Phycodes* and the *Arenicolites-Phycodes* ichnocoenoses. The lower Mackellar Fm depositional environment is interpreted as being the most stable, such that a higher diversity of behaviors including higher complexity deposit feeding structures. The absence of large, high-energy, sediment-flow deposits supports this lower energy depositional environment interpretation. The middle Mackellar Fm contains the five out of six of the ichnocoenoses, with the higher diversity *Planolites*-*Teichichnus*-*Phycodes* and *Planolites*-*Teichichnus*-*Arenicolites* ichnocoenoses in the lower middle section grading through the *Arenicolites*-*Phycodes* to the *Arenicolites*-*Planolites* ichnocoenoses. Although the middle section contains the most ichnocoenoses the diversity is reduced compared to the lower unit. The middle section consists predominantly of interbedded fine-grained sandstones and mudstones, with terminal distributary channels containing climbing ripples, wave ripples, and rare trough cross-bedding. These deposits indicate a higher energy environment and the associated trace fossils confirm this with *Phycodes* and *Taenidium* occurring in the interbedded sandstones, whereas the channel levees have *Conichnus*, *Kouphichnium*, and *Skolithos*.

The upper Mackellar Fm has relatively lower diversity, with only the *Lingulichnus*, *Arenicolites-Phycodes*, and *Kouphichnium* ichnocoenoses. The terminal distributary channels composed of climbing and oscillation rippled, cross-laminated sandstones contain primarily surface trails and trackways. The absence of abundant deposit-feeding traces and a shift to a majority of trails, such as *Cruziana*, *Gordia*, and *Kouphichnium*, suggests that the dynamic environment is not stable enough for long-term colonization. The changes in ichnocoenoses follows the sedimentologic changes within each section of the Mackellar Fm, where the highest relative diversity within each section is at the base and transitions upward to a lower diversity group with the increasing interpreted depositional energy and environment of deposition.

The Mackellar Fm trace fossils are consistent with those identified in previous studies on brackish water ichnology and fit in an impoverished Skolithos–Cruziana ichnofacies (i.e., Gilbert and Ekdale, 1999; Bann et al., 2004; Chakraborty, and Bhattacharya, 2005). Coates and MacEachern (2005) outline the key ichnological characteristics for river-dominated deltas derived from the Dunvegan Fm, Allomember E, from the Western Interior Seaway. A common ichnological component of their facies and that of numerous other river-dominated delta studies, are the presences of *Ophiomorpha*, *Rhizocorallium*, *Rosselia, and Zoophycos* (e.g. Gingras et al., 1998; Coates and MacEachern, 2005). These trace fossils have not been identified in the Mackellar Fm, which, based on the sedimentological and ichnological data, fit the river-dominated deltaic system criteria (Flaig et al. 2016). Coates and MacEachern (2005) describe how those trace fossils are part of a suite, which represent opportunistic colonization of the river turbidite and tempestite deposits. *Ophiomorpha*, in particular, is created as the organism colonizes the media during the waning or following calm periods of deposition, which is interpreted to take a minimum of 3.5 months (Buck, 1987; Pollard et al., 1993).

The absence of such higher complexity burrows as *Ophiomorpha* and *Rhizocorallium*, or beds with fully marine-sized examples of the trace fossils identified within the Mackellar Fm, suggest that deposition was not irregular enough to support event colonization and/or stable enough for the development of large complex trace fossils produced by marine organisms; the high freshwater and sediment inputs from the melting glaciers kept the tracemakers of the

Mackellar delta complex in a near-constant environmentally stressed condition rather than in normal marine salinity conditions. The upward trend of reduction in trace-fossil diversity and change from ichnocoenoses that are biased with deposit-feeding behaviors to filter-feeding and trackway-creating behaviors suggests a transition from a Cruziana to a Skolithos ichnofacies with the uppermost unit being unstable for colonization. The variation in trace-fossil presences and the associated ichnocoenoses (i.e., *Arenicolites* occurring from the base to the top) indicate a mixed Skolithos–Cruziana ichnofacies for the Mackellar Fm.

4.2 Paleoenvironmental Interpretations

Prior reconstructions of the depositional environment of the Mackellar Fm have varied (lake or inland sea—open or restricted), therefore, reinterpretation of paleosalinity for the Mackellar Fm deposits is critical. In spite of being unable to identify the precise paleosalinity directly from trace fossils, relative paleosalinity can be interpreted by comparisons with neoichnologic studies (e.g., Dorjes and Howard, 1975; Seilacher, 1986; Fu and Werner, 2000; Gingras et al., 2002). For example, Seilacher (1986) and Fu and Werner (2000) studied modern analogues to constrain the ancient salinity tolerance for *Scolicia* to polyhaline and euhaline conditions (Fig. 14; e.g., Venice System for Salinity, 1959).

Organism behaviors, and thus trace fossils, are controlled by many physicochemical parameters, including sedimentation rate, depositional energy, oxygenation, media, salinity, nutrient supply, turbidity, temperature and hydrology, among others (Fig. 15A; e.g., Bottjer and Ausich 1986; Leszczynski, 1991; Hasiotis and Platt, 2012). Sedimentation rate, depositional energy, and oxygenation are the predominant controls of trace fossils in the marine environment (e.g., Hasiotis and Platt, 2012). In modern brackish water settings, salinity becomes a major control with the increase of freshwater input (e.g., Remane 1934; Attrill, and Rundle 2002; Zettler et al., 2007; Uwadiae, 2009; Denisenko, 2010; Whitfield et al., 2012). Similarly, a major physicochemical control shift occurs in river-dominated deltaic environments with greater influence coming from the high sedimentation rate and freshwater input (e.g., Gingras et al., 1998; Coates and MacEachern, 1999; Bann et al., 2004; MacEachern et al. 2005). In river-dominated, marine deltaic environments, fluvial systems deliver sediment-laden freshwater to the marine basin and typically produce hyperpycnal density flows that travel along the benthic surface (i.e., Bhattacharya and MacEachern, 2009) alternating with background sedimentation from hypopycnal plumes (Bhattacharya and MacEachern, 2009; Flaig et al., 2016). In these types of environments with reoccurring but temporary high-sedimentation events, ichnocoenoses will consist of fewer suspension-feeding types and a greater abundance of deposit-feeding structures (e.g., Bromley and Ekdale, 1986; Bann et al., 2004; MacEachern et al., 2005; Dafoe, 2009). The Mackellar Fm ichnocoenoses do show a trend for greater abundances of deposit-feeding structures in the lower Mackellar Fm, where the high-sedimentation events were less often or less intense than what deposited the middle and upper Mackellar Fm.

4.2.1 A Lacustrine vs. Brackish-Marine Paleoenvironment for the Mackellar Formation

Miller and Isbell (2010) listed five criteria for their interpretation of the Mackellar Fm as lacustrine in origin: 1) limited ichnodiversity of low-complexity morphotypes; 2) similar freshwater trace fossils to those found in the Upper Permian Buckley Fm; 3) the Mackellar Fm shale has high carbon/sulfur (C/S) ratios; 4) contains no marine-type trace fossils; and 5) has no marine-type organism body fossils.

This study provides updated and/or alternative explanations for these points used to reinterpret the Mackellar Fm depositional environments. 1) Our more recent field investigation builds upon their previous work and added an additional 22 ichnogenera, such that the new total count is more akin to marine paleoenvironments (e.g., Seilacher, 1977, MacEachern and Gingras, 2007). 2) The paleoenvironmental distribution of the new list of ichnotaxa contain no freshwater-restricted trace fossils, 20 facies breaking ichnotaxa, and 10 ichnotaxa from exclusively marine settings, suggesting a transitional marine setting (e.g. MacEachern and Gingras, 2007). 3) Berner and Raiswell (1984) state that C/S ratios should not be used for samples with < 1% organic C, whereas Miller and Isbell (2010, table 3, p. 201) did record a mean of 0.61% TOC in their Mackellar Fm samples, indicating that their interpretations are likely less reliable due to a ≤ 1% organic C. 4) Trace fossils of lacustrine environments are typically of lower diversity and do not reflect similar diversity, distribution, burrowing depths as do trace fossils in marine settings (e.g., Hasiotis, 2004, 2008; Hasiotis et al., 2012). 5) Although this study also found no marine body fossils, their absence is not evidence of a lacustrine environment.

Brackish waters along marine coastlines are often caused by an influx of freshwater from fluvial systems, which drive reoccurring turbidite-like underflows on the delta front and induce fluctuating salinities, producing ecologically stressed systems (e.g., McMahon and Russel-Hunter, 1978; Lopez, 1988; Sibly and Calow, 1989; Sibly et al., 2000; Kimmerer, 2002; Pillai and Diwan, 2002). Under these stressed conditions, the brackish water system diversity and ichnodiversity is lower than in fully marine or freshwater systems (see Fig. 14; Remane, 1934;

McLusky, 1989; Pickerill and Brenchley, 1991; Attrill, 2002; Zettler et al., 2007; Denisenko, 2010; Whitfield et al., 2012).

The diagnostic ichnologic criteria for brackish water environments are: 1) low diversity when compared to fully marine systems; 2) ichnocoenoses dominated by marine trace fossils; 3) ichnocoenoses characterizing a mixed-Skolithos–Cruziana ichnofacies; 4) a higher abundance of burrows than surface trails; 5) low complexity trace fossils; 6) monospecific ichnocoenoses with a few dominant trace fossils; and 7) small morphotypes (Sanders et al., 1965; Hakes, 1976, 1985; Beynon and Pemberton, 1992; Pemberton and Wightman, 1992; Pemberton et al., 1992; Ranger and Pemberton, 1992; Pemberton and MacEachern, 1997; Buatois et al, 1999; Gingras et al., 1999; Netto and Rossetti, 2003; MacEachern and Gingras, 2007). The mixed salinity system ichnofacies that Pemberton and Wightman (1992) identified includes the marine indicator of *Teichichnus* as a key indicator of brackish water systems. The ichnology of brackish water systems suggests a majority of lower salinity tolerant marine organisms, rather than an equal mixture of freshwater and marine organisms. The interpreted salinity for the Turnabout Ridge and Buckley Island areas, based on the absence of freshwater-restricted trace fossils and relative percentages of facies breakers to marine trace fossils is ~12 ‰, or mid-mesohaline conditions, when compared to the Remaine diagram (Fig. 14). The Mackellar Fm salinity could have become lower during freshet pulses, but not over the length of time that is represented by the Mackellar Fm.

Brackish water organisms have been described as being typically smaller and diminutive, compared to their counterparts in fully marine-water systems, and their trace fossils reflect this size difference as well (i.e. Mackellar *Lockeia* are ≤ 2mm wide, whereas other Permian examples are ≥ 20 mm wide, Paranjape et al., 2013)(e.g., Beynon and Pemberton, 1992; Pemberton and

Wightman, 1992; Ranger and Pemberton, 1992; Gingras et al., 1999). The sizes of the Mackellar Fm trace fossils at Turnabout Ridge and Buckley Island (nearly all ≤ 5 mm in diameter) likely reflect the size of the original tracemakers (i.e., Kowalewski and Demko, 1996; Kowalewski et al., 1998). Thus, the Mackellar Fm trace fossils likely represent small-bodied organisms adapted to the brackish water conditions associated with the large amounts of freshwater input (or freshets; see Flaig et al., 2016). Key marine environmental indicator trace fossils from the Mackellar Fm are: *Diplocraterion* which is found in from shallow to deep marine environments (e.g., Mason and Christie, 1985); *Lingulichnus* which is found in brackish-water conditions (e.g., Pemberton and Kobluk, 1978; Zonneveld et al., 2007); *Margaritichnus*, which occurs in other Permian marine Gondwanan basins (Skwarko and Seilacher, 1993); *Scolicia*, whose rare occurrence suggests that the system was not fully marine or it would be more abundant (e.g., Fu and Werner, 2000); and *Teichichnus*, which has been used to separate the freshwater and marine dominated portions of deltas (e.g., Seilacher, 1955; Pemberton and Wightman, 1992; Hasiotis et al., 2013). Mackellar Fm ichnogenera, ichnocoenoses, burrow sizes, penetration depths, and formational and bed ichnodiversity trends at Turnabout Ridge and Buckley Island are consistent with those expected for a deltaic–brackish water marine setting (Fig. 15B).

4.2.2 A River-Dominated Deltaic Environment

In the Beardmore Glacier area, the Mackellar Fm has been previously interpreted as a turbidite channel and levee complex fed by braided streams of the Fairchild Fm, along with shallow paleoshoreline successions off the flank of these channel systems (Miller and Collinson, 1994; Miller and Isbell, 2010). The Mackellar Fm facies at Turnabout Ridge (Table 4) combine to record deposition on the subaqueous portions of a river-dominated delta with environments that include subaqueous terminal distributaries, the proximal to distal delta front, and prodelta (Fig. 16; Flaig et al., 2016) with the overlying Fairchild Fm recording deposition in braided streams and on associated floodplains. Strata at Buckley Island, which contains similar facies in similar stratigraphic positions, may have been deposited in shallower nearshore paleoenvironments (Miller and Isbell, 2010) further from the major river. This is in contrast to sedimentation in a more axial position relative to a sediment source and delta at Turnabout Ridge (Flaig et al., 2016).

4.2.3 High Latitude Implications

The paleopolar position of the Lower Permian Mackellar Fm is interpreted to not have a direct control on the trace fossils present; however, the near-glacial melt outflow position of the study area did influence the physicochemical parameters during deposition and, thus the trace fossil assemblages (e.g., Virtasalo et al., 2006). This interpretation is in agreement with previous studies on other Permian Gondwanan basins (Turner et al., 1981; Nogueira and Netto, 2001; Gandini et al., 2007). Studies on the Ecca Group of the Karoo Basin in South Africa and Rio do Sul and upper Mafra fms from the Paraná basin in southern Brazil have identified impoverished Skolithos–Cruziana ichnofacies in sediments deposited in fjords or basins outward of melting glaciers (Hobday and Tavener-Smith, 1975; Netto and Goso, 1998; Balisteri and Netto, 2002; Balistieri et al., 2003; Netto et al., 2007; Buatois et al., 2010). During the late Paleozoic other inland postglacial basins contain fluvial to lacustrine environments and *Mermia*-type ichnologic suites (Buatois et al., 2010). The glacial melt discharges affected downstream areas and created a range of freshwater-dominated basins from fully freshwater lakes to freshwater-dominated fjords, to freshet-influenced marine systems (Buatois et al., 2006; Flaig et al., 2016). The sedimentological and ichnological characteristics of these ancient freshwater-influenced marine systems are similar to the freshwater gradients identified in core from the Baltic Sea (e.g., Virtasalo et al., 2006), which is proposed as an analog for the Mackellar Fm (Barrett et al., 1986; Collinson and Miller, 1991). The Mackellar Fm represents a near-continuous, high-sediment and high-freshwater discharge system that that created an environment suitable to a limited number of tracemakers in more proximal settings, while the more distal settings were more stable and could allow for a greater diversity of tracemakers, or at least behaviors.

5. Conclusion

This study integrated ichnology and sedimentology to identify Mackellar Fm depositional environments as part of a freshwater-stressed, high-sedimentation, river-dominated marine deltaic system. The ichnology indicates a marine to brackish-water environment for the Mackellar Fm based on: 1) the presence of exclusively marine trace fossils; 2) the absence of exclusively continental trace fossils; 3) a pronounced reduction in trace-fossil size and penetration depth compared to normal marine systems; and 4) the overall high ichnodiversity with low individual bed ichnodiversity. Mackellar Fm ichnocoenoses are consistent with the three main physicochemical controls of sedimentation rate, salinity, and depositional energy and represents a mixed Skolithos–Cruziana ichnofacies. This study falsified the hypothesis that the Mackellar Fm was deposited in a lacustrine system, and showed that the Mackellar Fm at Turnabout Ridge and Buckley Island was deposited into a freshwater-stressed, high-sediment-accumulation marine environment—the Mackellar Sea—and reinterprets the glaciolacustrine interpretation as a transitional marine environment fed by high-freshwater, high-sediment-discharge from glacial-meltwater-fed rivers. Although body fossils have not been found, the 30 ichnogenera and the six ichnocoenoses described are indicators of a stressed marine system. The Mackellar Fm does not contain a high-latitude ichnological signature; however, the combination of ichnocoenoses with glaciomarine deposits produced by high freshwater and sediment inputs from glacially fed river systems suggests a strong association with high latitudinal settings.

Our revised interpretation is more parsimonious with the depositional model of the Antarctic Interior Seaway filling an eperic seaway in an intercratonic basin, where the fully marine Weaver, Discovery Ridge, and Polestar fms were deposited. Including the Mackellar Fm with these other formations extends the marine extent of the seaway across the Ellsworth, Pensacola, and Transantarctic mountains to the Beardmore Glacier area. As the Antarctic Interior Sea, and thus, the Mackellar Sea retreated, the Mackellar sediments were overlain by the braided fluvial systems of the Fairchild Fm, filling remaining accommodation in the basin. Additional research is necessary at other outcrops along the Central Transantarctic Mountains to locate areas where the brackish water environments in the Mackellar Fm are observed to transition from fully marine conditions in the more distal parts of the basin to freshwater environments in the most proximal areas.

6.0 Acknowledgements

Thanks to J. Isbell and D. Elliott for critical discussions regarding the geology of the Transantarctic Mountains. Thanks also to M. Miller for discussions on Beacon Supergroup ichnology. NSF OPP/ANT 0944282 to Dr. S.T. Hasiotis provided funding for this research. Thanks to the New York Air National Guard, Ken Borak Air, Petroleum Helicopters International, and the support staff at McMurdo Station and CTAM Camp for field assistance. We thank reviewers William Miller III, an anonymous reviewer, and managing guest editor Paul McCarthy for comments and edits that improved the manuscript. We also thank the **I**chno**B**io**G**eo**S**ciences Research Group for ichnological discussions; and the Polar Geospatial Center for image preparation. This work is part of the Ph.D. dissertation of A.M.J., who thanks his wife for support.

7.0 References

AGUIRRE, J., DE GIBERT, J.M., AND PUGA-BERNABÉU, A., 2010, Proximal–distal ichnofabric changes in a siliciclastic shelf, Early Pliocene, Guadalquivir Basin, southwest Spain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 291, p. 328–337.

ALLEN, G.P., AND CHAMBERS, J.L.C., 1998, Sedimentation in the modern and Miocene Mahakam delta: Indonesian Petroleum Association Guidebook, 236p.

ALPERT, S.P., 1975, *Planolites* and *Skolithos* from the Upper Precambrian–Lower Cambrian, White-Inyo Mountains, California: Journal of Paleontology, v. 49, p. 508–521.

ATTRILL, M.J., AND RUNDLE, S.D., 2002, Ecotone or ecocline: ecological boundaries in estuaries. Estuarine: Coastal and Shelf Science, v. 55, p. 929–936.

BALISTERI, P.R.M.N., AND NETTO, R.G, 2002, A *Glossifungites* suite in deposits of the Itararé Group (Upper Carboniferous–Lower Permian of Paraná Basin) at Mafra region, north of

Santa Catarina State, Brazil: Ichnotaxonomy, and paleoecological and stratigraphical contraints: Acta Geologica Leopoldensia, v.55, p. 91–106.

BALISTIERI, P., NETTO, R.G., VERDE, M., AND GOSO, C.A.A., 2003, Comparison between two trace fossil assemblages recorded in Upper Carboniferous–Lower Permian deposits from the Paraná Basin (Rio do Sul Formation, Brazil and San Gregorio Formation, Uruguay), Third Latin American Sedimentological Congress, Belém Brazil: Abstracts, p, 172.

BALLANCE, P.F., AND WAITERS, W.A., 2002, Hydrothermal alteration, contact metamorphism, and authigenesis in Ferrar Supergroup and Beacon Supergroup rocks, Carapace Nunatak, Allan Hills, and Coombs Hills, Victoria Land, Antarctica: New Zealand Journal of Geology and Geophysics v. 45, p. 71–84.

BANDEL, K., 1967, Trace fossils from two upper Pennsylvanian Sandstones in Kansas: Paleontological Contributions to the University of Kansas v. 18, p. 1–13.

BANDEL, K., 1973, A new name for the ichnogenus *Cylindrichnus* Bandel, 1967: Journal of Paleontology, v. 47, p. 1002–1002.

BANN, K.L., FIELDING, C.R., MACEACHERN, J.A., AND TYE, S.C., 2004, Differentiation of estuarine and offshore marine deposits using integrated ichnology and sedimentology: Permian Pebbley Beach Formation, Sydney Basin, Australia, *in* McIlroy, D. (ed.), The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis: Geological Society of London, Special Publication 228, p. 179–211.

BARRETT, P.J., ELLIOT, D.H., AND LINDSAY, J.F., 1986, The Beacon Supergroup (Devonian–Triassic) and Ferrar Group (Jurassic) in the Beardmore Glacier Area, Antarctica, *in* Turner, M.D. and Splettstoesser, J.F (eds.), Geology in the central transantarctic mountains: Antarctic Research Series, AGU, Washington, DC, 36, p. 339–428.

BELAÚSTEGUI, Z., DE GIBERT, J.M., DOMÈNECH, R., MUÑIZ, F., AND MARTINELL, J., 2012, Clavate borings in a Miocene cetacean skeleton from Tarragona (NE Spain) and the fossil record of marine bone bioerosion: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 323, p. 68–74.

BERNER, R.A., AND RAISWELL, R., 1984, C/S method for distinguishing freshwater from marine rocks: Geology, v. 12, p. 365–368.

BEYNON, B.M., AND PEMBERTON, S.G., 1992, Ichnological signature of a brackish water deposit and example from the lower Cretaceous Grand Rapids Formation, Cold Lake oil sands area, Alberta, *in* Pemberton S.G. (ed.), Applications of Ichnology to Petroleum Exploration: SEPM Core Workshop Notes 17, p. 199–221.

BHATTACHARYA, J.P., AND MACEACHERN, J.A., 2009, Hyperpycnal rivers and prodeltaic shelves in the Cretaceous seaway of North America: Journal of Sedimentary Research, v. 79, p. 184–209.

BOHACS, K.M., HASIOTIS, S.T., AND DEMKO, T.M., 2007, Continental ichnofossils of the Green River and Wasatch Formations, Eocene, Wyoming: a preliminary survey, proposed relation to lake-basin type, and application to integrated paleo-environmental interpretation: The Mountain Geologist, v. 44, p. 79-108

BOTTJER, D.J., AND AUSICH, W.I., 1986, Phanerozoic development of tiering in soft substrata suspension-feeding communities: Paleobiology, v. 12, p. 400–420.

BRADDY, S.J., 2001, Trackways-arthropod locomotion, in: Briggs, D.E.G., and Crowther, P.R., (Eds.): Palaeobiology II, Blackwell Science, London, pp. 389–393.

BRADSHAW, M.A., NEWMAN, J., AND AITCHISON, J.C., 1984, Preliminary geological results of the 1983–84 Ohio Range expedition: New Zealand Antarctic Record, v. 5, p. 1–17.

BRIGGS, D.E., MILLER, M.F., ISBELL, J.L., AND SIDOR, C.A., 2010, Permo-Triassic arthropod trace fossils from the Beardmore Glacier area, central Transantarctic Mountains, Antarctica: Antarctic Science, v. 22, p. 185–192.

BROMLEY, R., AND ASGAARD, U., 1979, Triassic freshwater ichnocoenoses from Carlsberg Fjord, east Greenland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 28, p. 39–80.

BROMLEY, R.G., AND EKDALE, A.A., 1984, *Chondrites*: a trace fossil indicator of anoxia in sediments: Science, v. 224, p. 872–874.

BROMLEY, R.G., AND EKDALE, A.A., 1986, Composite ichnofabrics and tiering of burrows: Geological Magazine, v. 123, p. 59–65.

BROMLEY, R.G., AND FREY, R.W., 1974, Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*: Bulletin of the Geological Society of Denmark, v. 23, p. 311–335.

BROMLEY, R.G., JENSEN, M., AND ASGAARD, U., 1995, Spatangoid echinoids: deep-tier trace fossils and chemosymbiosis: Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen, v. 195, p. 25–35.

BROMLEY, R.G., 1996, Trace fossils: biology, taphonomy and applications: Chapman and Hall, London, 361 pp.

BUATOIS, L.A., AND MÁNGANO, M.G., 1993, Trace fossils from a Carboniferous turbiditic lake: implications for the recognition of additional nonmarine ichnofacies: Ichnos, v. 2, p. 237–258.

BUATOIS, L.A., MÁNGANO, G., AND CARR, T.R., 1999, Sedimentology and ichnology of Paleozoic estuarine and shoreface reservoirs, Morrow Sandstone, Lower Pennsylvanian of

Southwest Kansas, USA. Kansas Geological Survey: Current Research in Earth Sciences Bulletin, v. 243, p. 1–35.

Buatois, L.A., Netto, R.G., and Mángano, M.G., 2010, Ichnology of late Paleozoic postglacial transgressive deposits in Gondwana: Reconstructing salinity conditions in coastal ecosystems affected by strong meltwater discharge, *in* López-Gamundi, O.R., and Buatois, L.A., (eds.), Late Paleozoic Glacial Events and Postglacial Transgressions in Gondwana: GSA Special Publication, v. 468, p. 149–173.

Bucher, W.H., 1953, Fossils in metamorphic rocks: a review: Geological Society of America Bulletin, v. 64, p. 275–300.

Buck, S.G., 1987, Facies and sedimentary structures of the Folkestone beds (Lower Greensand, Early Cretaceous) and equivalent strata in southern England: Ph.D. Dissertation, University of Reading, UK. 758 p.

Buckman, J.O., 2001, *Parataenidium*, a new *taenidium*-like ichnogenus from the carboniferous of Ireland: Ichnos, v. 8, p. 83–97.

Chakraborty, A., and Bhattacharya, H. N., 2005, Ichnology of a Late Paleozoic (Permo-Carboniferous) glaciomarine deltaic environment, Talchir Formation, Saharjuri Basin, India: Ichnos, v. 12, p. 31–45.

Chakraborty, A.T., Hasiotis, S.T., Ghosh, B., and Bhattacharya, H.N., 2013, Fluvial trace fossils in the Middle Siwalik (Sarmatian-Pontian) of Darjeeling Himalayas, India: Journal of Earth System Science, v. 122, p. 1023–1033.

Chisholm, J.I., 1970, *Teichichnus* and related trace-fossils in the Lower Carboniferous at St. Monance, Scotland: Bulletin of the Geological Survey of Great Britain, v. 32, p. 21–51.

COATES, L., AND MACEACHERN, J.A., 1999, The ichnological signature of wave- and river dominated deltas: Dunvegan and Basal Belly River formations, West-Central Alberta, *in* Wrathall, B., Johnston, G., Arts, A., Rozsw, L., Zonneveld, J.-P., Arcuri, D., McLellan, S. (eds.), Digging Deeper, Finding a Better Bottom Line: Canadian Society of Petroleum Geologists and Petroleum Society, Core Conference, p. 99–114C.

COATES, L., MACEACHERN, J.A., 2007, The ichnological signatures of river- and wave dominated delta complexes: differentiating deltaic and non-deltaic shallow marine successions, Lower Cretaceous Viking Formation and Upper Cretaceous Dunvegan Formation, west-central Alberta, *in* MacEachern, J.A., Bann, L.K., Gingras, M.K., Pemberton, S.G. (eds.): Applied ichnology. SEPM, Short Course Notes 52, p. 227–254.

COLLETTE, J.H., GETTY, P.R., AND HAGADORN, J.W., 2011, Insights into an Early Jurassic dinosaur habitat: ichnofacies and enigmatic structures from the Portland Formation, Hoover Quarry, Massachusetts, USA: Atlantic Geology, v. 47, p. 81–98.

COLLINSON, J.W., 1997, Paleoclimate of Permo–Triassic Antarctica, in: Ricci, C.A. (Ed.), The Antarctic Region: Geological Evolution and Processes: Terra Antarctica Publication, Siena Italy. pp. 1028–1034.

COLLINSON, J.W., AND MILLER, M.F., 1991, Comparison of Lower Permian post-glacial black shale sequences in the Ellsworth and Transantarctic Mountains, Antarctica, *in* Ulbrich, H., and Rocha-Campos, A.C., (eds), Gondwana Seven Proceedings: Instituto de Geociecias de Universidad de Sâo Paulo, Sâo Paulo, p. 217–231.

COLLINSON, J.W., ISBELL, J.L., ELLIOT, D.H., MILLER, M.F., MILLER, J.M., AND VEEVERS, J.J., 1994, Permian-Triassic Transantarctic Basin: Geological Society of America Memoirs, v. 184, p. 173–222.

CORNISH, F.G., 1986, The trace-fossil *Diplocraterion*; evidence of animal-sediment interactions in Cambrian tidal deposits: PALAIOS, v. 1, p. 478–491.

CRIMES, T.P., 1987, Trace fossils and correlation of late Precambrian and early Cambrian strata: Geological Magazine, v. 124, p. 97–119.

CRIMES, T. P., 1992, The record of trace fossils across the Proterozoic-Cambrian boundary: Origin and Early Evolution of the Metazoa, 10, pp.177.

DAVIES, N.S., RYGEL, M.C., AND GIBLING, M.R., 2010, Marine influence in the Upper Ordovician Juniata Formation (Potters Mills, Pennsylvania): Implications for the history of life on land: PALAIOS, v. 25, p. 527–539.

DAFOE, L.T., 2009, Ichnological assemblages of wave-influenced and mixed river-and wave influenced deltaic deposits in the Viking Formation, Alberta, Canada: SEPM Short Course Notes, v. 52, p. 291–306.

DAWSON, J.W., 1873, Impressions and footprints of aquatic animals and imitative markings, on Carboniferous rocks: American Journal of Science, v. 105, p. 16–24.

DENISENKO, N.V., 2010, The description and prediction of benthic biodiversity in high arctic and freshwater-dominated marine areas: The southern Onega Bay (the White Sea): Marine Pollution Bulletin, v. 61, p. 224–233.

DOMACK, E.W., 1988, Biogenic facies in the Antarctic glaciomarine environment: basis for a polar glaciomarine summary: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 63, p. 357–372.

DÖRJES, J., AND HOWARD, J.D., 1975, Estuaries of the Georgia coast, USA: Sedimentology and biology. IV. Fluvial-marine transition indicators in an estuarine environment, Ogeechee River-Ossabaw Sound: Senckenbergiana Maritima, v. 7, p. 137–179.

EAGER, R.M.C., BAINES, J.G., COLLINSON, J.D., HARDY, P.G., OKOLO, S.A., AND POLLARD, J.E., 1985, Trace fossil assemblages and their occurrence in Silesian (Mid-Carboniferous) deltaic sediments of the Central Pennine basin England, *in* Curran, H.A (ed.), Biogenic structures: Their use in interpreting depositional environments: SEPM special volume 35, p. 99–149.

EKDALE, A.A., AND MASON, T.R., 1988, Characteristic trace-fossil associations in oxygen-poor sedimentary environments: Geology, v. 16, p. 720–723.

ELLIOTT, D.H., 1975, Gondwana basins of Antarctica, in: Campbell, K.S.W., (Ed.): Gondwana Geology. Australia National University Press, Canberra, pp. 493–536.

ELLIOTT, D.H., 2013, The geological and tectonic evolution o the transantarctic mountains: a review, *in* Hambrey, M.J., Barker, P.F., Barrett, P.J., Davies, B., Smellie, J.L., and Tranter, M. (eds): Antarctic Paleoenvironments and Earth-surface Processes. Geological Society, London, Special Publications 381, London, p. 7–35.

EMIG, C.C., 1997, Biogeography of inarticulated brachiopods: in Kaesler, R.L., (Ed.), Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised) v.1: Geological Society of America and Paleontological Institute, Boulder and Lawrence, p. 497–502.

EMMONS, E., 1844, The Taconic System: based on observations in New York, Massachusetts, Maine, Vermont and Rhode Island: Caroll and Cook, Albany, 68 p.

FILLION, D., AND PICKERILL, R.K., 1990, Ichnology of the Upper Cambrian? to Lower Ordovician Bell Island and Wabana groups of eastern Newfoundland, Canada: Canadian Society of Petroleum Geologists, v. 7, p. 1–119.

FLAIG P.P., HASIOTIS, S.T., AND JACKSON, A.M., 2014, A paleopolar deltaic succession from the Early Permian of Antarctica: Delta front hyperpycnites and shelf channels at the Mackellar-

Fairchild transition, Turnabout Ridge, Central Transantarctic Mountains: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, p. 241–265.

FREY, R.W., 1990, Trace fossils and hummocky cross-stratification, Upper Cretaceous of Utah: PALAIOS, v. 5, p. 203–218.

FU, S., AND WERNER, F., 2000, Distribution, ecology and taphonomy of the organism trace, *Scolicia*, in northeast Atlantic deep-sea sediments: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 156, p 289–300.

FÜRSICH, F.T., AND HURST, J.M., 1974, Environmental factors determining the distribution of brachiopods: Paleontology, v. 17, p. 879–900.

GANDINI, R., NETTO, R.G., AND SOUZA, P.A., 2007, Paleoicnologia e a palinologia dos ritmitos do Groupo Itararé na pedreira de Águas Claras (Santa Catarina, Brazil): Gaea, v. 3, p. 47–59.

GARVEY, J.M., AND HASIOTIS, S.T., 2008, An ichnofossil assemblage from the Lower Carboniferous Snowy Plains Formation, Mansfield Basin, Australia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 258, p. 257–276.

GERNANT, R.E., 1972, The paleoenvironmental significance of *Gyrolithes* (lebensspur): Journal of Paleontology, v. 46, p. 735–741

GIBERT, J.M. DE, AND EKDALE, A.A., 1999, Trace fossil assemblages reflecting stressed environments in the Middle Jurassic Carmel Seaway of central Utah: Journal of Paleontology, v. 73, p. 711–720.

GIBERT, J.M. DE, BUATOIS, L.A., FREGENAL-MARTÍNEZ, M.A., GABRIELA MANGANO, M., ORTEGA, F., POYATO-ARIZA, F.J., AND WENZ, S., 1999, The fish trace fossil *Undichna* from the Cretaceous of Spain: Paleontology, v. 42, p. 409–427.

GINGRAS, M.K., MACEACHERN, J.A., AND PEMBERTON, S.G., 1998, A comparative analysis of the ichnology of wave- and river-dominated allomembers of the Upper Cretaceous Dunvegan Formation: Bulletin of Canadian Petroleum Geology, v. 46, p. 51–73.

GINGRAS, M.K., PEMBERTON, S.G., SAUNDERS, T.D.A., AND CLIFTON, H.E., 1999, The ichnology of modern and Pleistocene brackish-water deposits at Willapa Bay, Washington: variability in estuarine settings: PALAIOS, v. 14, p. 352–374.

GINGRAS, M.K., RASANEN, M.E., PEMBERTON, S.G., AND ROMERO, L.P., 2002, Ichnology and sedimentology reveal depositional characteristics of bay-margin parasequences in the Miocene Amazonian foreland basin: Journal of Sedimentary Research, v. 72, p. 871–883.

GLAESSNER, M.F., 1969, Trace fossils from the Precambrian and basal Cambrian: Lethaia, v. 2, p. 369–393.

GRINDLEY, G.W., 1963, The geology of the Queen Alexandra Range, Beardmore Glacier, Ross Dependency, Antarctica, with notes on the correlation of Gondwana sequences: New Zealand Journal of Geology and Geophysics, v. 6, p. 307–347.

GOLDRING, R., 1966, The sedimentological significance of concentrically laminated burrows from Lower Cretaceous Ca-bentonites, Oxfordshire: Journal of the Geological Society, v. 153, p. 255–263.

HAKES, W.G., 1976, Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas: The University of Kansas Paleontological Contributions, v. 63, p. 1-46.

HAKES, W.G., 1985, Trace fossils from brackish-marine shales, Upper Pennsylvanian of Kansas, U.S.A., in: Curran, H.A. (Ed.), Biogenic Structures–Their Use in Interpreting Depositional

Environments: Society of Economic Paleontologists and Mineralogists, Special Publication 35, Tulsa, pp. 21–35.

HALDEMAN, S.S., 1840, Supplement to number one—A monograph of the Limniades, or fresh-water univalve shells of North America— containing descriptions of apparently new animals in different classes, and the names and characters of the subgenera in Paludina and Anculosa. J. Dobson, Philadelphia.

HALL, J., 1852, Palaeontology of New York (Vol. II). C. Van Benthuysen, Albany, New York, 350 pp.

HAMMEN, C.S., AND LUM, S.C., 1977, Salinity tolerance and pedical regeneration of Lingula: Journal of Paleontology, v. 51, p. 548–551.

HAN, Y., AND PICKERILL, R.K., 1994, Taxonomic reassessment of *Protovirgularia* M'Coy 1850 with new examples from the Paleozoic of New Brunswick, eastern Canada: Ichnos, v. 3, p. 203–212.

HÄNTZSCHEL, W., 1975, Treatise on invertebrate paleontology. Miscellanea. Trace Fossils and Problematica. Part W. Supplement 1. C. Teichert, L. McCormick, R. B. Williams, and R. C. Moore (Eds.): Geological Society of America. 269p.

HASIOTIS, S.T., 2002, Continental ichnology: using terrestrial and freshwater trace fossils for environmental and climatic interpretations: SEPM Short Course 51. 132 p.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., 2008, Reply to the Comments by Bromley et al., of the paper "Reconnaissance of the Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis: Sedimentary Geology, v. 208, p. 61–68.

HASIOTIS, S.T., 2012, A brief overview of the diversity and patterns in bioturbation preserved in the Cambrian–Ordovician carbonate and siliciclastic deposits of Laurentia, *in* Derby, J.R., Fritz, R.D., Longacre, S.A., Morgan, W.A., and Sternbach, C.S., (eds.), The Great American Carbonate Bank: The Geology and Economic Resources of the Cambrian-Ordovician Sauk Megasequence of Laurentia: AAPG Memoir 98, p. 113–125.

HASIOTIS, S.T., AND BOWN, T.M. 1992, Invertebrate trace fossils: the backbone of continental ichnology, in: C.G. Maples, R.R. West (Eds.): Trace Fossils. Short Courses in Paleontology No. 5, pp. 64–104.

HASIOTIS, S.T., AND MITCHELL, C.E., 1993, A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures: Ichnos, v. 2, p. 291–314.

HASIOTIS, S.T., AND PLATT, B.F., 2012, Exploring the sedimentary, pedogenic, and hydrologic factors that control the occurrence and role of bioturbation in soil formation and horizonation in continental deposits: an integrative approach: The Sedimentary Record, v. 10, p. 4–9.

HASIOTIS, S.T., MCPHERSON, J.G., AND REILLY, M.R.W., 2013, Using ichnofossils to reconstruct the depositional history of sedimentary successions in alluvial, coastal-plain, and deltaic settings. IPTC 2013: International Petroleum Technology Conference.

HASIOTIS, S.T., PLATT, B.F., REILLY, M., AMOS, K., LANG, S., KENNEDY, D., TODD, J.A., AND ELLINOR MICHEL, E., 2012, Actualistic studies of the spatial and temporal distribution of terrestrial and aquatic organism traces in continental environments to differentiate lacustrine from fluvial, eolian, and marine deposits in the geologic record, *in* Bagans, O.W., Bartov, Y., Bohacs, K., and Nummedal, D., (eds.): AAPG memoir 95, p. 433–489.

HATTIN, D.E., AND FREY, R.W., 1969, Facies relations of *Crossopodia* sp., a trace fossil from the Upper Cretaceous of Kansas, Iowa, and Oklahoma: Journal of Paleontology, v. 43, p. 1435–1440.

HEER, O., 1865, Die Urwelt der Schweiz: Friedrich Schulthess, Zurich, 622 p.

HEER, O., 1877, Flora fossils helvetiae. Die vorweltliche Flora der Schweiz. J. Würster and Co, 182 pp

HERRIED, B., 2012, Central Transantarctic Mountains (ANT REF-MS2006-001) [map]. 1:1,000,000. PGC Transantarctic Mountains Series. Saint Paul, MN: Polar Geospatial Center.

HIGGS, R., 1988, Fish trails from the Upper Carboniferous of south-west England: Palaeontology, v. 31, p. 255–272.

HITCHCOCK, E., 1858, Ichnology of New England. A report on the sandstone of the Connecticut Valley, especially its footprints. Boston, 220p.

HISCOTT, R.N., JAMES, N.P., AND PEMBERTON, S.G., 1984, Sedimentology and ichnology of the Lower Cambrian Bradore Formation, coastal Labrador: fluvial to shallow-marine transgressive sequence: Bulletin of Canadian Petroleum Geology, v. 32, p. 11–26.

HOBDAY, D.K., AND TAVENER-SMITH, R., 1975, Trace fossils in the Ecca of northern Natal and their palaeoenvironmental significance: Palaeontologica Africana, v. 18, p. 47–52.

HOFMAN, H.J., 1979, Chazy (middle Ordovician) trace fossils in the Ottawa-St. Lawrence Lowlands: Bulletin of the Geological Survey of Canada, v. 321, p. 27–59.

HOWARD, J.D., 1966, Characteristic trace fossils in Upper Cretaceous sandstones of the Book Cliffs and Wasatch Plateau: Utah Geological and Mineral Survey Bulletin, v. 80, p. 35–53.

ISBELL, J.L., LENAKER, P.A., ASKIN, R.A., MILLER, M.F., AND BABCOCK, L.E., 2003, Reevaluation of the timing and extent of late Paleozoic glaciation in Gondwana: Role of the Transantarctic Mountains: Geology, v. 31, p. 977–980.

ISBELL, J.L., KOCH, Z.J., SZABLEWSKI, G.M., AND LENAKER, P.A., 2008, Permian glacigenic deposits in the Transantarctic Mountains, Antarctica, *in* Fielding, C.R., Frank, T.D., and Isbell, J.L., (eds.), Resolving the Late Paleozoic Ice Age in Time and Space: Geological Society of America Special Paper 441, p. 59–70.

JAMES, P., 1879, Descriptions of new species of fossils and remarks on some others from the Lower and Upper Silurian rocks of Ohio: The Paleontologist, v. 3, p. 17–24.

JAMES, N.P., SEIBEL, M.J., DALRYMPLE, R.W., BESSON, D., AND PARIZE, O., 2014, Warm-temperate, marine, carbonate sedimentation in an Early Miocene, tide-influenced, incised valley; Provence, south-east France: Sedimentology, v. 61, p. 497–534.

JENSEN, S., AND GRANT, S.W., 1998, Trace fossils from the Dividalen Group, northern Sweden: implications for Early Cambrian biostratigraphy of Baltica: Norsk Geologisk Tidsskrift, v.78, p. 305–317.

KIMMERER, W.J., 2002, Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages?: Marine Ecology Progress Series, v. 243, p. 39–55.

KOCH, Z.J., AND ISBELL, J.L., 2013, Processes and products of grounding-line fans from the Permian Pagoda Formation, Antarctica: Insight into glacigenic conditions in polar Gondwana: Gondwana Research, v. 24, p. 161–172.

KOWALEWSKI, M., AND DEMKO, T. M., 1996, Trace fossils and population paleoecology: comparative analysis of size-frequency distributions derived from burrows: Lethaia, v. 29, p. 113–124.

KOWALEWSKI, M., DULAI, A., AND FÜRSICH F. T., 1998, A fossil record full of holes: The Phanerozoic history of drilling predation: Geology, v. 26, p. 1091–1094.

KSIAZCAKIEWICZ, M., 1977, Trace fossils in the Flysch of the Polish Carpathians: Palaeontol. Polonia, v. 36, p. 1–208.

LANDING, E., 1989, The Placentian Series: appearance of the oldest skeletonized faunas in southern Newfoundland: Journal of Paleontology, v. 63, p. 739–769.

LEBLANC-SMITH, G., AND ERIKSSON, K.A., 1979, A fluvioglacial and glaciolacustrine deltaic depositional model for Permo-Carboniferous coals of the northeastern Karoo Basin, South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 27, p. 67–84.

LESZCZYŃSKI, S., 1991, Oxygen-related controls on predepositional ichnofacies in turbidites, Guipuzcoan Flysch (Albian-lower Eocene), northern Spain: PALAIOS, v. 6, p. 271–280.

LOPEZ, G.R., 1988, Comparative ecology of the macrofauna of freshwater and marine muds: Limnology and Oceanography 33, v. 4, p. 946–962.

LOPEZ-GAMUNDI, O.R., 1989, Postglacial transgressions in Late Paleozoic basins of western Argentina: A record of glacioeustatic sea level rise: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 71, p. 257–270.

MACEACHERN, J.A., BANN, K.L., BHATTACHARYA, J.P., AND HOWELL, C.D., 2005, Ichnology of deltas, *in* Giosan, L., and Bhattacharya, J.P. (eds.), River Deltas: Concepts, Models, and Examples: SEPM Special Publication 83, Tulsa, p. 49–85.

MACEACHERN, J.A., AND GINGRAS, M.K., 2007, Recognition of brackish-water trace fossil suites in the Cretaceous Western Interior Seaway of Alberta, Canada, *in* Bromley, R.G., Buatois, L.A., Mángano, M.G., Genise, J.F., and Melchor, R.N. (eds.), Sediment-Organism Interactions: a Multifaceted Ichnology: SEPM Special Publication 89, Tulsa, p. 149–194.

MACNAUGHTON, R.B., COLE, J.M., DALRYMPLE, R.W., BRADDY, S.J., BRIGGS, D.E., AND LUKIE, T.D., 2002, First steps on land: Arthropod trackways in Cambrian-Ordovician eolian sandstone, southeastern Ontario, Canada: Geology, v. 30, p. 391–394.

MÄNNIL, R., 1966, O vertikalnykh norkakh zaryvaniya v Ordovikskikh izvestnyakakh Pribaltiki, *in* Hecker, R.F. (ed.), Organizm i sreda v geologischeskom proshlom. Akademiya Nauk SSSR: Paleontologicheskij Institut, p. 200–207.

MAPLES, C.G., AND ARCHER, A.W., 1987, Redescription of early Pennsylvanian trace-fossil holotypes from the nonmarine Hindostan Whetstone beds of Indiana: Journal of Paleontology, v. 61, p. 890–897.

MASON, T.R., AND CHRISTIE, A.D.M., 1986, Palaeoevironmental significance of ichnogenus *Diplocraterion* Torell from the Permian Vryheid formation of the Karoo Supergroup, South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 52, p. 249–265.

MCCOY, F., 1850, On some genera and species of Silurian Radiata in the collection of the University of Cambridge: Annales and Magazine of Natural History, v. 6, p. 270–290.

MCCOY, F., 1851, On some new Protozoic annulate: Annual Magazine of Natural History, v. 2, p. 394–396.

MCLUSKY, D.S., 1989, The estuarine ecosystem, second ed. Blackie, Glasgow, 215 pp.

MCMAHON, R.F., AND RUSSELL-HUNTER, W.D., 1978, Respiratory responses to low oxygen stress in marine littoral and sublittoral snails: Physiological Zoology, v. 51, p. 408–424.

MCMENAMIN, M.A., 1996, Ediacaran biota from Sonora, Mexico: Proceedings of the National Academy of Sciences, v. 93, p. 4990–4993.

MILLER, M.F., AND FRISCH, R.S., 1986, Depositional setting of the (Permian)Mackellar Formation, Beardmore Glacier Area: Antarctic Journal of the US , v. 5, p. 37–38.

MILLER, M.F., COLLINSON, J.W., AND FRISCH, R.S., 1991, Depositional setting and history of a Permian port-glacial shale, Mackellar Formation, Beardmore Glacier area, Antarctica, *in* Ulbrich, H., and Rocha-Campos, A.C., (eds.), Gondwana Seven Proceedings, Instituto de Geociecias de Universidad de Sâo Paulo, Sâo Paulo, p. 201–215.

MILLER, M.F., AND COLLINSON, J.W., 1994, Late Paleozoic post-glacial inland sea filled by fine-grained turbidites: Mackellar Formation, Central Transantarctic Mountains, *in* Deynoux, M., Miller, J.M.G., Domack, E.W., Eyles, N., Fairchild, I.J., and Young, G.M. (eds.), Earth's Glacial Record. Cambridge University Press, Cambridge. p. 215–233.

MILLER, M.F., AND SMAIL, S.E., 1996, Permian and Triassic biogenic structures, Shackleton Glacier and Mount Weaver areas, Transantarctic Mountains: Antarctic Journal of the US, v. 31, p. 5–7.

MILLER, M.F., AND ISBELL, J.L., 2010, Reconstruction of a high-latitude, post-glacial lake: Mackellar formation (Permian), Transantarctic Mountains, *in* López-Gamundí, O.R., and Buatois, L.A. (eds.), Late Paleozoic Glacial Events and Postglacial Transgressions in Gondwana: GSA Special Paper 468, Boulder, p.193–207.

MILLER, S.A., 1889, North American Geology and Paleontology. Western Methodist Book Concern, Cincinnati, 664 p.

MILLER, W., III, 2001, *Thalassinoides-Phycodes* compound burrow systems in Paleocene deep-water limestone, Southern Alps of Italy: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 170, p. 149–156.

MINSHEW, V.W., 1967, Geology of the Scott glacier and Wisconsin range areas, central transantarctic mountains, Antarctica. Unpublished Ph.D. dissertation, The Ohio State University, Columbus Ohio, 268p.

MINTER, N.J., BRADDY, S.J., DAVIS, R.B., 2007, Between a rock and a hard place: arthropod trackways and ichnotaxonomy: Lethaia, v. 40, p. 365–375.

MINTER, N.J., AND BRADDY, S.J., 2006, The fish and amphibian swimming traces *Undichna* and *Lunichnium*, with examples from the Lower Permian of New Mexico, USA: Paleontology, v. 49, p. 1123–1142.

NARBONNE, G.M., 1984, Trace fossils in Upper Silurian tidal flat to basin slope carbonates of Arctic Canada: Journal of Paleontology, v. 58, p. 398–415.

NETTO, R.G., AND ROSSETTI, D.F., 2003, Ichnology and salinity fluctuations: a case study in the Early Miocene (Lower Barreiras Succession) of São Luís Basin, Maranhão, Brazil: Revista Brasileira de Paleontologia, v. 6, p. 5-18.

NETTO, R.G., BALISTIERI, P.R., LAVINA, E.L., AND SILVEIRA, D.M., 2009, Ichnological signatures of shallow freshwater lakes in the glacial Itararé Group (Mafra Formation), Upper Carboniferous–Lower Permian of Paraná Basin, S Brazil): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 272, p. 240–255.

NETTO, R.G., BENNER, J.S., BUATOIS, L.A., UCHMAN, A., MÁNGANO, M.G., RIDGE, J.C.,

KAZAKAUSKAS, V. AND GAIGALAS, A., 2012, Glacial environments, *in* Knaust, D. & Bromley R.G. (eds.), Trace fossils as indicators of sedimentary environments. Elsevier: Developments in Sedimentology, v. 64, p. 297–336.

NETTO, R.G., AND GOSO, C.A.A., 1998, Icnología de la Formación San Gregorio (Pérmico Inferior), en el area de los Cerros Guazunambí, Cuenca Norte, Uruguaya: Actas Congreso Uruguayo de Geologia, Punta del Este, Uruguay, v. 1, p. 188–189.

NETTO, R.G., BUATOIS, L.A., MÁNGANO, M.G., AND BALISTIERI, P., 2007, *Gyrolithes* as a multipurpose burrow: an ethologic approach: Revista Brasileira de Paleontologia, v. 10, p. 157–168.

NICHOLSON, H.A., 1873, Contributions to the errant annelides of the older Palaeozoic rocks: Royal Society of London Proceedings, v. 21, p. 288–290.

NOGUEIRA, M.S., AND NETTO, R.G., 2001, Icnofauna da Formação Rio do Sul (Groupo Itararé, Permiano da bacia do Paraná) na Pedreira Itaú-Itauna, Santa Catarina, Brazil: Acta Geologica Leopoldensia, v. 52, p. 397–406.

NOPCSA, F., 1923, Die familien der reptilian: Fortschritte der Geologie und Palaëontologie, v. 2, p. 1–210.

O'BRIEN, L.J., BRADDY, S.J., AND RADLEY, J.D., 2009, A new arthropod resting trace and associated suite of trace fossils from the Lower Jurassic of Warwickshire, England: Paleontology, v. 52, p. 1099–1112.

ORBIGNY, A., de, 1842, Voyage dans l'Amerique meridionale 3, 188p.

OSGOOD, R.G., 1970, Trace fossils of the Cincinnati area: Palaeontographica Americana, v. 6, p. 281–439.

PARANJAPE, A.R., KULKARNI, K.G., AND GURAV, S.S., 2013, Significance of Lockeia and associated trace fossils from the Bada Bagh Member, Jaisalmer Formation, Rajasthan: Journal of Earth System Sciences, v. 122, p. 1359–1371.

PEMBERTON, S.G., AND KOBLUK, D.R., 1978, Oldest known brachiopod burrow: the Lower Cambrian of Labrador: Canadian Journal of Earth Sciences, v. 15, p. 1385–1389.

PEMBERTON, S.G., AND FREY, R.W., 1982, Trace fossil nomenclature and the *Planolites–Palaeophycus* dilemma: Journal of Paleontology, v. 56, p. 843–881.

PEMBERTON, S.G., FREY, R.W., AND BROMLEY, R.G., 1988, The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils: Canadian Journal of Earth Sciences, v. 25, p. 866–892.

PEMBERTON, S.G., AND MACEACHERN, J.A., 1997, The ichnological signature of storm deposits—The use of trace fossils in event stratigraphy, *in* Brett, C.E., and Baird, G.C. (eds.), Paleontological Events—Stratigraphic, Ecological, and Evolutionary Implications, Columbia University Press, New York, p. 73–109.

PEMBERTON, S.G., REINSON, G.E., AND MACEACHERN, J.A., 1992, Comparative ichnological analysis of Late Albian estuarine valley-fill and shelf-shoreface deposits, Crystal Viking Field, Alberta, *in* Pemberton, S.G. (ed.), Applications of Ichnology to Petroleum Exploration—A Core Workshop, Core Workshop 17, Society of Economic Paleontologists and Mineralogists, Tulsa, p. 291–317.

PEMBERTON, S.G., SPILA, M., PULHAM, A.J., SAUNDERS, T., MACEACHERN, J.A., ROBBINS, D., AND SINCLAIR, I. K., 2001, Ichnology and sedimentology of shallow to marginal marine systems: Ben Nevis and Avalon reservoirs, Jeanne d'Arc Basin. Geological Association of Canada Short Course Notes 15, 343 pp.

PEMBERTON, S.G., AND WIGHTMAN, D.M., 1992, Ichnological characteristics of brackish water deposits, *in* Pemberton, S.G. (ed.), Applications of Ichnology to Petroleum Exploration—A Core Workshop, Core Workshop 17, Society of Economic Paleontologists and Mineralogists, Tulsa, p. 141–167.

PICKERILL, R.K., 1973, *Lingulasma tenuigranulata*-palaeoecology of a large Ordovician linguloid that lived within a strophomenid-trilobite Community: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 13, p. 143–156.

PICKERILL, R.K., AND BRENCHLEY, P.J., 1991, Benthic macrofossils as paleoenvironmental indicators in marine siliciclastic facies: Geoscience Canada, v. 18, p. 119–138.

PILLAI, B.R., AND DIWAN, A.D., 2002, Effects of acute salinity stress on oxygen consumption and ammonia excretion rates of the marine shrimp *Metapenaeus monoceros*: Journal of Crustacean Biology, v. 22, p. 45–52.

POLLARD, J.E. 1981, A comparison between the Triassic trace fossils of Cheshire and South Germany: Palaeontology, v. 24, p. 555–588.

POLLARD, J.E., GOLDRING, R., AND BUCK, S.G., 1993, Ichnofabrics containing *Ophiomorpha*: significance in shallow-water facies interpretation: Journal of the Geological Society, v. 150, p. 149–164.

POWELL, C.MCA., LI, Z.X., 1994, Reconstruction of the Panthalassan margin of Gondwanaland, *in* Veevers, J.J., Powell, C.McA. (eds.), Permian–Triassic Pangean basins and foldbelts along the Panthalassan margin of Gondwanaland, GSA Memoir 184, GSA, Denver, p. 5–9.

POWELL, W., 2003, Greenschist-facies metamorphism of the Burgess Shale and its implications for models of fossil formation and preservation: Canadian Journal of Earth Sciences, v. 40, p. 13–25.

Prantl, F., 1945, Dvē záhadné zkameneēliny (stopy) z vrstev chrustenickÿch-dδ2, Rozpravy II: Tridy české Akademie, v. 55, p. 3–8.

Quatrefages, M.A., de, 1849, Note sur la Scolicia prisca (A. De Q.) annélide fossile de la craie: Ann. Sci. Nat. Zool., v. 12, p. 265–266.

Ranger, M.J., and Pemberton, S.G., 1992, The sedimentology and ichnology of estuarine point bars in the McMurray Formation of the Athabasca Oil Sands Deposit, northeastern Alberta, Canada, *in* Pemberton, S.G., (ed.), Applications of ichnology to petroleum exploration—A core workshop, Society of Economic Paleontologists and Mineralogists Core Workshop 17, Tulsa, p. 401–421.

Ratcliffe, B.C., and Fagerstrom, J.A., 1980, Invertebrate lebensspuren of Holocene floodplains: their morphology, origin and paleoecological significance: Journal of Paleontology, v. 54, p. 614–630.

Rees, P.M., Ziegler, A.M., Gibbs, M.T., Kutzbach, J.E., Behling, P.J., Rowley, D.B., 2002, Permian phytogeographic patterns and climate data/model comparisons: The Journal of Geology, v. 110, p. 1–31.

Remane, A., 1934, Die brackwasserfauna. Verhandlungen der Deutschen Zoologischen: Gesellschaft, v. 36, p. 34–74.

Retrum, J.B., Hasiotis, S.T., and Kaesler, R.L., 2011, Neoichnological experiments with the freshwater ostracode *Heterocypris incongruens*: Implications for reconstructing aquatic settings: PALAIOS, v. 26, p. 509–518.

Richter, R., 1850, Aus der thüringischen grauwacke. Deutsche Geologische Gesellschaft: Zeitschrift, v.2, p. 198–206.

RINDSBERG, A.K., AND KOPASKA-MERKEL, D.C., 2005, *Treptichnus* and *Arenicolites* from the Steven C. Minkin Paleozoic Footprint site (Langsettian, Alabama, USA). Pennsylvanian Footprints in the Black Warrior Basin of Alabama: Alabama Paleontological Society Monograph v. 1, p. 121–141.

RUDKIN, D. M., YOUNG, G. A., AND NOWLAN, G. S., 2008, The oldest horseshoe crab: A new Xiphosurid from Late Ordovician Konservat-Lagerstätten Deposits, Manitoba, Canada: Palaeontology, v. 51, p. 1–9.

RUNNEGAR, B., AND CAMPBELL, K.S.W., 1976, Late Palaeozoic faunas of Australia: Earth-Science Reviews, v. 12, p. 235–257.

SALTER, J.W., 1857, On annellide burrows and surface markings from the Cambrian rocks of the Longmynd: Journal of the Geological Society of London, v. 13, p. 199–206.

SANDERS, H.L., MANGELSDORF, P.C., AND HAMPSON, G.R., 1965, Salinity and faunal distribution in the Pocasset River, Massachusetts: Limnology and Oceanography, v. 10, p. 216–229.

SAPORTA, G. de, 1884, Les organismes problématiques des anciennes mers. Paris, Masson, 102 p.

SAVRDA, C.E., BLANTON-HOOKS, A.D., COLLIER, J.W., DRAKE, R.A., GRAVES, R.L., HALL, A.G., NELSON, A.I., SLONE, J.C., WILLIAMS, D.D. AND WOOD, H.A., 2000, *Taenidium* and associated ichnofossils in fluvial deposits, Cretaceous Tuscaloosa Formation, eastern Alabama, southeastern USA: Ichnos, v. 7, p. 227–242.

SCHRODER, C.H., 1982, Trace fossils of the Oconee Group and basal Barnwell Group of east-central Georgia: Georgia Geological Survey Bulletin 88. 138p.

SEILACHER, A., 1953, Studien zur palichnologie. I. uber die methoden der palichnologie: Neues Jahrb Geologie Palaontologie Abhandlungen, v. 96, v. 421–452.

SEILACHER, A., 1955, Spuren und Lebensweise der Trilobiten. Abhandlungen der Akademie der wissenschaften und der Literatur, Mainz: methermatisch-naturwissenschaftliche Klasse Jahrgang, p. 342–372.

SEILACHER, A., 1962, Paleontological studies on turbidite sedimentation and erosion: Journal of Geology, v. 70, p. 227–234.

SEILACHER, A., 1977, Evolution of trace fossil communities: Developments in Palaeontology and Stratigraphy, v. 5, p. 359–376.

SEILACHER, A., 1986, Evolution of behaviour as expressed in marine trace fossils, *in* Nitecki, M.H., and Kitchell, J.A., (eds.), Evolution of Animal Behaviour. Oxford University Press, New York, p. 67–87.

SEILACHER, A., 1990, Paleozoic trace fossils, *in* Said, R., (ed.), The Geology of Egypt, A.A. Balkema Publishers, Netherlands, p. 649–670.

SEILACHER, A., 1994, How valid is *Cruziana* stratigraphy?: Geologische Rundschau, v. 83, p. 752–758.

SEILACHER, A., BUATOIS, L.A., AND MANGANO, G.M., 2005, Trace fossils in the Ediacaran–Cambrian transition: behavioral diversification, ecological turnover and environmental shift: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 227, p. 323–356.

SEILACHER, A.T., AND SEILACHER, E., 1994, Bivalvian trace fossils: a lesson from actuopaleontology: Courier Forschungsinstitut Senckenberg, v. 169, p. 5–15.

SKWARKO, S.K., AND SEILACHER, A., 1993, Trace fossils and problematica. Geological Survey of Western Australia: Bulletin, v. 136, p. 390–403.

SIBLY, R.M., AND CALOW, P., 1989, A life-cycle theory of responses to stress: Biological Journal of the Linnean Society, v. 37, p. 101–116.

SIBLY, R.M., WILLIAMS, T.D., AND JONES, M.B., 2000, How environmental stress affects density dependence and carrying capacity in a marine copepod: Journal of Applied Ecology, v. 37, p. 388–397.

SMITH, J.J., HASIOTIS, S.T., KRAUS, M.J., AND WOODY, D.T., 2008, *Naktodemasis bowni*: New ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and paleoenvironmental implications, Paleogene Willwood Formation, Bighorn Basin, Wyoming: Journal of Paleontology, v. 82, p. 267–278.

STERNBERG, K.M., VON, 1833, Versuch einer geognostisch-botanischen: Darstellung der Flora der Vorwelt, v. 1, p. 1–80.

TREWIN, N.H., 1994, A draft system for the identification and description of arthropod trackways: Palaeontology, v. 37, p. 811– 823.

TURNER, B.R., STANISTREET, I.G., AND WHATELEY, M.K.G., 1981, Trace fossil and palaeoenvironments in the Ecca Group of the Nongoma Graben, northern Zululand, South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 36, p. 113–123.

TORELL, O., 1870, Petrificata suecana formatioanis Cambricae. Lunds. Univ. Arsskr. 6. Avdel, v. 2, p. 1–14.

UCHMAN, A., 1998, Taxonomy and ethology of flysch trace fossils: a revision of the Marian Książkiewicz collection and studies of complementary material: Annales Societatis Geologorum Poloniae, v. 68, p. 105–218.

UCHMAN, A., AND GAŹDZICKI, A., 2006, New trace fossils from the La Meseta Formation (Eocene) of Seymour Island, Antarctica: Polish Polar Research, v. 27, p. 153–170.

UCHMAN, A., AND PERVESLER, P., 2006, Surface lebensspuren produced by amphipods and isopods (crustaceans) from the Isonzo delta tidal flat, Italy: PALAIOS, v. 21, p. 384–390.

UWADIAE, R.E., 2009, Response of benthic macroinvertebrate community to salinity gradient in a sandwiched coastal lagoon: Science Report and Opinion, v. 1, p. 45–55.

Venice System, 1959, Symposium on the classification of brackish waters, Venice, April 8–14, 1958: Archivio di Oceanografia e Limnologia, v. 11, p. 1–248.

VIALOV, O.S., 1971, The rare Mesozoic problematica from the Pamir and Caucasus: Paleontologicheskiy Sbornik, v. 7, p. 85–93.

VIRTASALO, J.J., KOTILAINEN, A.T., AND GINGRAS, M.K., 2006, Trace fossils as indicators of environmental change in Holocene sediments of the Archipelago Sea, northern Baltic Sea: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 240, p. 453–467.

WEBBY, B.D., 1970, Late Precambrian trace fossils from new south wales: Lethaia, v. 3, p. 79–109.

WHITFIELD, A.K., ELLIOTT, M., BASSET, A., BLABER, S.J.M., AND WEST, R.J., 2012, Paradigms in estuarine ecology–a review of the Remane diagram with a suggested revised model for estuaries. Estuarine: Coastal and Shelf Science, v. 97, p. 78–90.

WILDERMUTH, S.C., HASIOTIS, S.T., MILLER, M.F., ISBELL, J. L., AND BABCOCK, L.E., 2012, A diverse high-latitude ichnofauna from the Permian Pagoda and Mackellar formations (Beacon Supergroup), Shackleton Glacier area, Central Transantarctic Mountains, Antarctica: Geological Society of America Abstracts with Programs, v. 44, p. 90.

YOUNG, D.J., AND RYBURN, R.J., 1968, The geology of Buckley and Darwin islands, Beardmore Glacier, Ross Dependency, Antarctica: New Zealand Journal of Geology and Geophysics, v. 11, p. 922–929.

ZETTLER, M.L., SCHIEDEK, D., BOBERTZ, B., 2007, Benthic biodiversity indices versus salinity gradient in the southern Baltic Sea: Marine Pollution Bulletin, v. 55, p. 258–270.

ZONNEVELD, J.P., PEMBERTON, S.G., SAUNDERS, T.D.A., AND PICKERILL, R.K., 2002, Large, robust *Cruziana* from the Middle Triassic of northeastern British Columbia: Ethologic, biostratigraphic and paleobiologic significance: PALAIOS, v. 17, p. 435–448.

ZONNEVELD, J.P., BEATTY, T.W., AND PEMBERTON, S.G., 2007, Lingulid brachiopods and the trace fossil *Lingulichnus* from the Triassic of Western Canada: implications for faunal recovery after the end-Permian mass extinction: PALAIOS v. 22, p. 74–97.

TABLES

Table 1. Thirty ichnogenera collected from the Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier Area, Antarctica.

Environments of Deposition	**Trace Fossils**
Marine	*Bergaueria, Chondrites, Crossopodia, Cylindrichnus, ?Gyrolithes, Lingulichnus, Margaritichnus, Parataenidium, Phycodes, Teichichnus*
Facies Breakers (*Marine, and/or Brackish, and/or Freshwater*)	*Arenicolites, Circulichnus, Cochlichnus, Conichnus, Cruziana, Diplichnites, Diplocraterion, Gordia, Kouphichnium, Lockeia, Palaeophycus, Planolites, Protovirgularia, Rusophycus, Sagittichnus, Scolicia, Skolithos, Taenidium, Treptichnus, Undichna*
Freshwater	N/A

Table 2. Ichnocoenoses identified in the Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier Area, Antarctica.

Ichnocoenoses	**Key Component Trace Fossils**	**Lithofacies**	**Environments of Deposition**
1- *Arenicolites-Planolites*	*Arenicolites*, *Planolites, and rare Diplocraterion*	Thinly bedded fine-grained sandstone with thin mudstone interbeds in F 1, 2, 5	Proximal to distal delta front; FA 2–3
2- *Lingulichnus*	*Lingulichnus*	Thinly bedded fine-grained sandstone with mudstone interbeds in F 1, 3	Proximal to distal delta front with subaqueous splays; FA 2–3
3- *Arenicolites-Phycodes*	*Arenicolites* with rare *Phycodes*	Thinly bedded sandstone with mudstone interbeds in F 1, 2	Delta front with subaqueous splays to prodelta; FA 1–2
4- *Kouphichnium*	*Circulichnus*, *Cruziana, Diplichnites, Gordia, Kouphichnium*, *Planolites*, *Rusophycus*	Bedded sandstone in F 2, 3	Barforms at submarine channels; FA 2–3
5- *Phycodes-Teichichnus-Arenicolites*	*Arenicolites*, *Conichnus*, *Phycodes*, *Sagittichnus*, *Skolithos*, *Teichichnus*	Thinly bedded sandstone with mudstone interbeds in F 1, 2	Distal delta front with subaqueous splays; FA 1–2
6- *Planolites-Teichichnus-Phycodes*	*Bergaueria, Chondrites, Lockeia, Palaeophycus, Phycodes, Planolites*, *Protovirgularia, Sagittichnus, Taenidium, Teichichnus*, *Treptichnus*	Thinly bedded sandstone with mudstone interbeds in F 1, 2	Distal delta front to prodelta; FA 1, 3

Table 3. Potential tracemakers, potential behaviors, and environments of deposition in which they are found at Turnabout Ridge and Buckley Island, Beardmore Glacier Area, Antarctica.

Trace Fossil	**Potential Tracemaker**	**Potential Behavior**	**Environment of Deposition**
Arenicolites	Polychaete worm	Dwelling, suspension feeding	Submarine channels and levees to prodelta
Bergaueria	Sea anemone	Dwelling, resting	Delta front to prodelta
Chondrites	Vermiform organism	Deposit feeding	Delta front to prodelta
Circulichnus	Vermiform organism	Grazing trail	Submarine channels and levees
Cochlichnus	Neamatode, vermiform organism	Locomotion	Submarine channels and levees to delta front
Conichnus	Anemone or clam	Dwelling, suspension feeding	Delta front
Crossopodia	Polychaete worm	Locomotion	Delta front
Cruziana	Arthropod	Locomotion	Submarine channels and levees to prodelta
Cylindrichnus	Vermiform organism	Dwelling, feeding	Delta front
Diplichnites	Arthropod	Locomotion	Submarine channels and levees to delta front
Diplocraterion	Vermiform organism	Dwelling, suspension feeding	Delta front
Gordia	Neamatode, vermiform organism	Grazing trail	Submarine channels and levees
?*Gyrolithes*	Polychaete worm or arthropod	Dwelling burrow	Delta front
Kouphichnium	Limulid	Locomotion	Submarine channels and levees
Lingulichnus	Linguilid brachiopod	Dwelling, feeding	Delta front
Lockeia	Clam	Resting, feeding trace	Delta front to prodelta
Margaritichnus	Vermiform organism	Feeding, dwelling, or	Delta front
Palaeophycus	Vermiform organism	Dwelling, locomotion	Delta front to prodelta
Parataenidium	Vermiform organism	Feeding, dwelling, locomotion	Delta front
Phycodes	Vermiform organism	Feeding	Submarine channels and levees to prodelta
Planolites	Polychaete worm	Feeding, locomotion	Submarine channels and levees to prodelta
Protovirgularia	Clam or arthropod	Dwelling and feeding	Delta front to prodelta
Rusophycus	arthropod	Resting trace	Submarine channels and levees to prodelta
Sagittichnus	Bivalve or ostracod	Resting, feeding trace	Delta front to prodelta
Scolicia	Gastropod, echinoderm	Locomotion or feeding	Delta front to prodelta
Skolithos	Vermiform organisms, arthropod	Dwelling, suspension feeding, predation	Submarine channels and levees to prodelta
Taenidium	Vermiform organism	Deposit feeding	Delta front to prodelta
Teichichnus	Vermiform organism	Dwelling and deposit feeding burrow	Delta front to prodelta
Treptichnus	Vermiform organism, arthropod	Dwelling and deposit feeding	Delta front to prodelta
Undichna	Fish	Locomotion	Delta Front to Prodelta

Table 4. Sedimentary facies and associated sedimentary attributes for the Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier Area, Antarctica.

Facies	**Sedimentary Attributes**
1	Current-rippled to structureless shale and siltstone
2	Oscillation rippled fine sandstone
3	Current rippled to planar-laminated fine sandstone
4	Cross laminated sandstone with climbing ripples
5	Planar-laminated sandstone
6	Trough cross-bedded sandstone
7	Structureless to ripple cross-laminated mudstone

Table 5. Sedimentary facies associations, their key features, and component sedimentary facies for the Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier Area, Antarctica.

Mackellar Fm Facies Association	**Facies**	**Key Features**
1 Distal Delta Front and Prodelta	F 1–3	Sub-meter beds of F 2 & 3 within F1 shales
2 Subaqueous Terminal Distributary Channels and Levees	F 1–4, 6	Channels eroded into F 1–3 and Levees made up of F 4 & 5
3 Proximal Delta Front	F 1–6	F 1–3 with abundant planar-laminated F 5 and cross-stratified F 4 with climbing ripples.

FIGURES

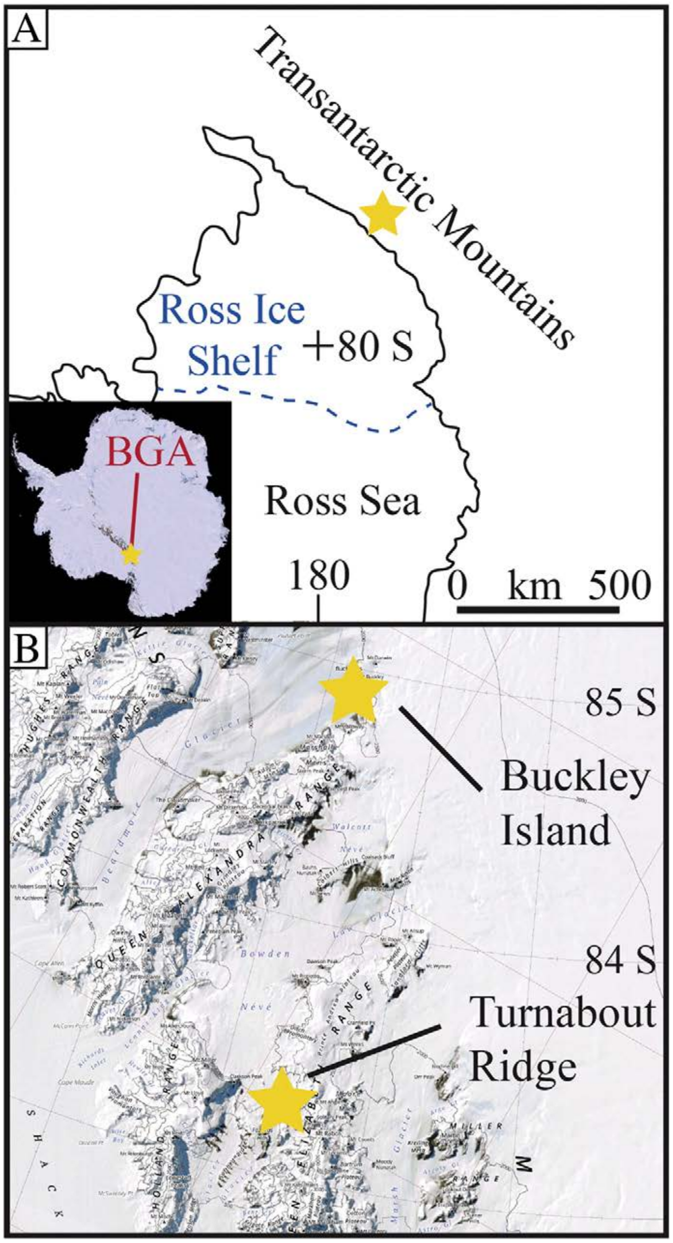
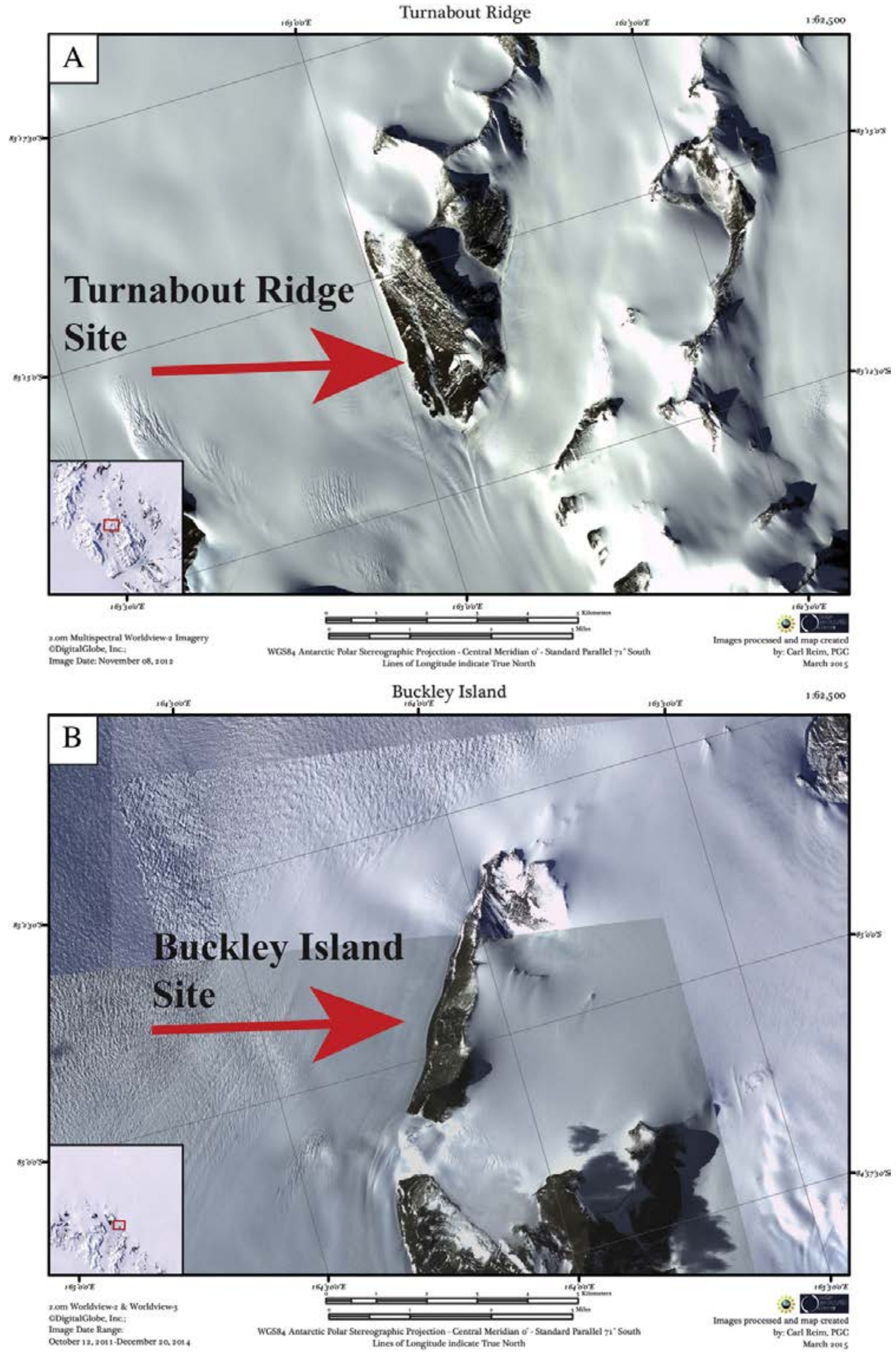


Figure 1. Location for Turnabout Ridge and Buckley Island in the Beardmore Glacier Area, Central Transantarctic Mountains. Landsat image mosaic of Antarctica, 2007; and general location map for the Transantarctic Mountains, modified from Collinson et al. (1994); and modified from 1:1,000,000 Central Transantarctic Mountains McMurdo Dry Valleys to Wisconsin Range, Polar Geospatial Center, 2012.



2.0m Multispectral Worldview-2 Imagery
©DigitalGlobe, Inc.;
Image Date: November 08, 2012

WGS84 Antarctic Polar Stereographic Projection - Central Meridian 0° - Standard Parallel 71° South
Lines of Longitude indicate True North

Images processed and map created
by: Carl Reim, PGC
March 2015

2.0m Worldview-2 & Worldview-3
©DigitalGlobe, Inc.;
Image Date Range:
October 12, 2011-December 20, 2014

WGS84 Antarctic Polar Stereographic Projection - Central Meridian 0° - Standard Parallel 71° South
Lines of Longitude indicate True North

Images processed and map created
by: Carl Reim, PGC
March 2015

Figure 2. Composite satellite imagery of both locations: A) Turnabout Ridge, and B) Buckley Island, Beardmore Glacier Area, images prepared by the Polar Geospatial Center, 2014.

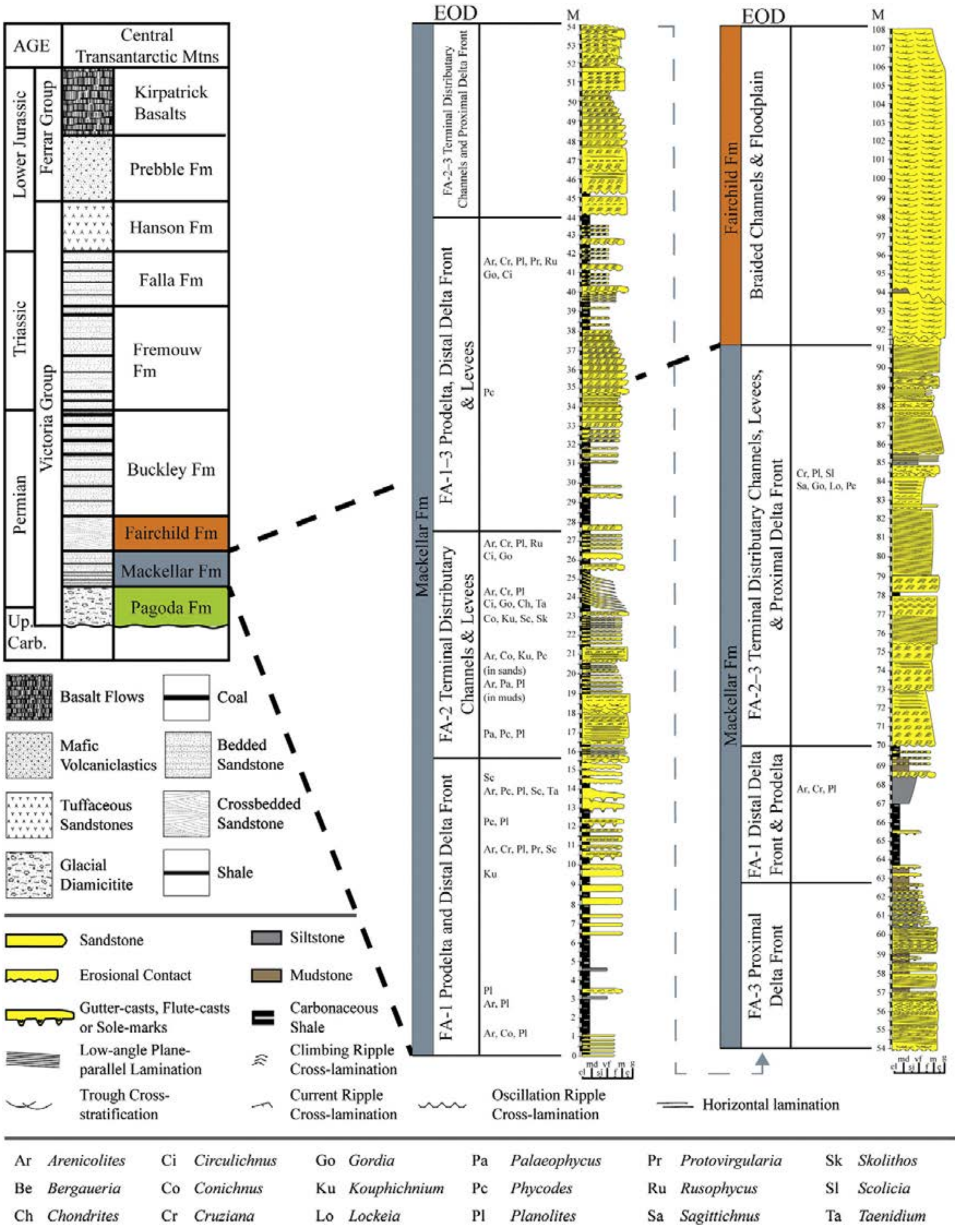


Figure 3. General stratigraphic columns for the Victoria and Ferrar groups in the Beardmore Glacier Area and measured section at Turnabout Ridge, with interpreted environments of deposition and ichnological data. Modified from Elsner (2010), and Flaig et al. (2016).

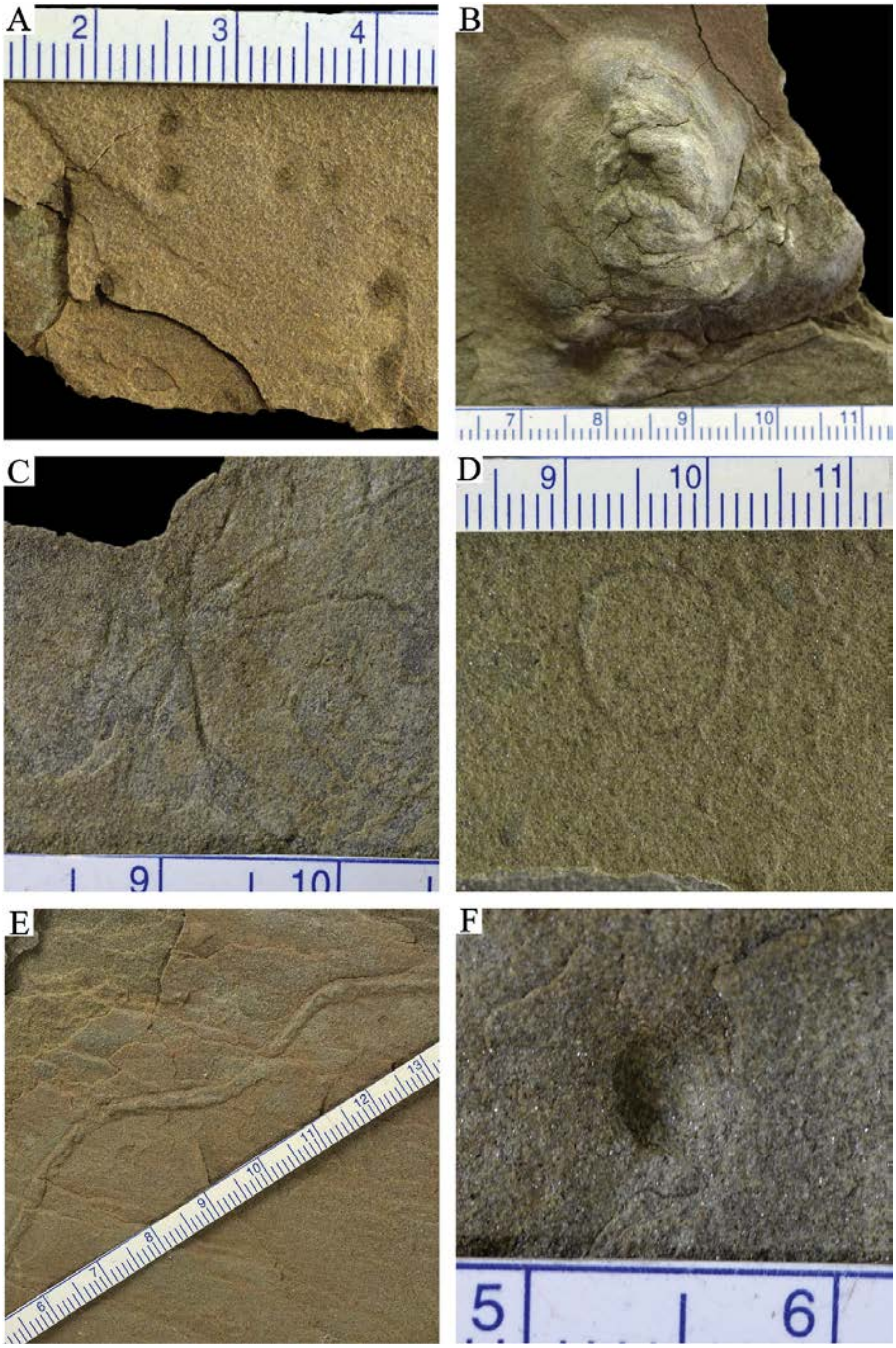


Figure 4. Ichnotaxa identified from the lower Permian Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier area. A) *Arenicolites* (11SHTRMK-40). B) *Bergaueria* isp. *cf*. *B. perata* (11SHTRMK-215). C) *Chondrites* (11SHTRMK-197). D) *Circulichnus montanus* (11SHTRMK-8). E) *Cochlichnus* (11SHTRMK-28). F) *Conichnus conicus* (11SHTRMK-61). All scales in cm.

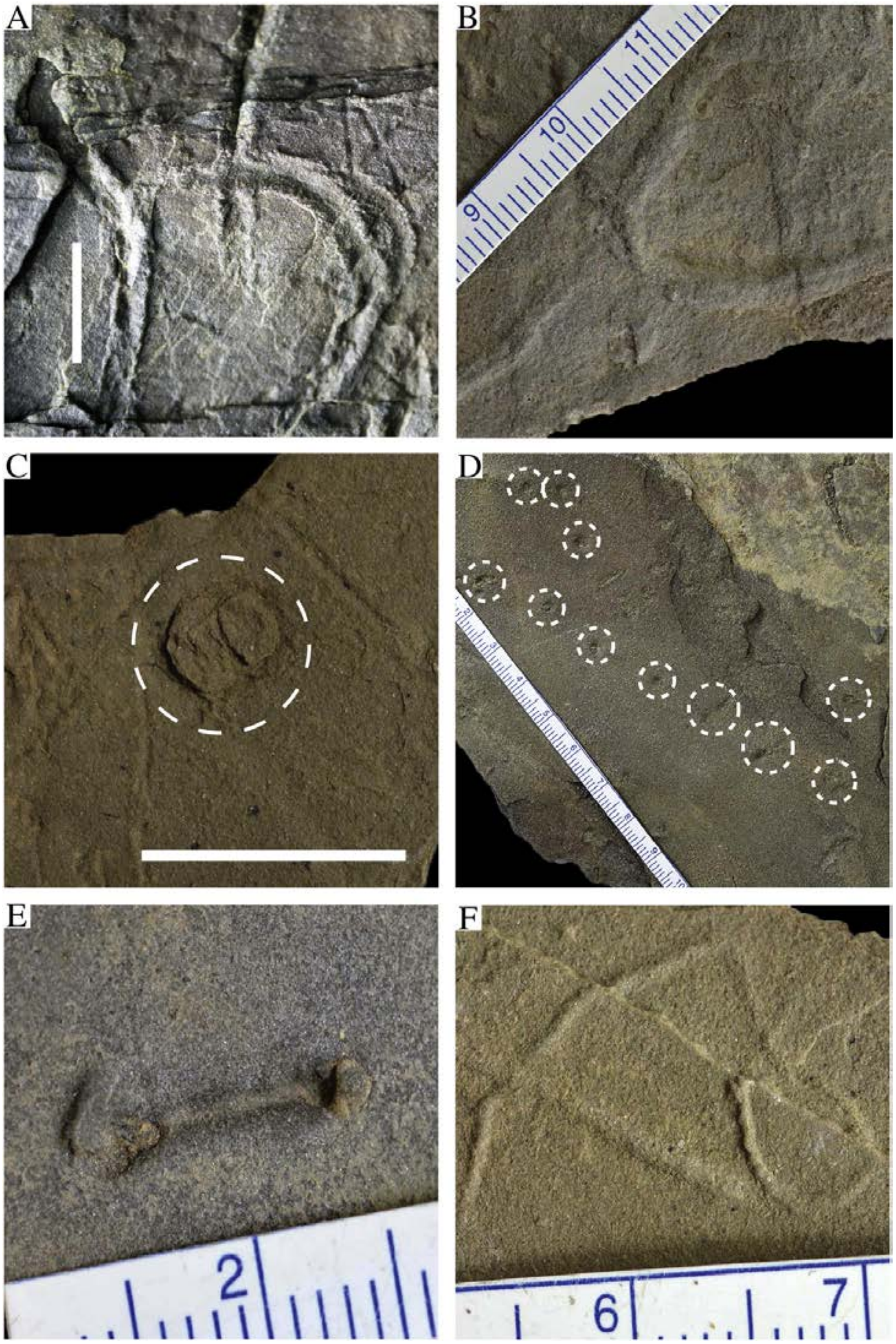


Figure 5. Ichnotaxa identified from the lower Permian Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier area. A) *Crossopodia* (11SHTRMK-210). B) *Cruziana* (11SHBIMK-239). C) *Cylindrichnus* (11SHBIMK-446). D) *Diplichnites* (11SHTRMK-206). E) *Diplocraterion* (11SHTRMK-87). F) *Gordia marina* (11SHBIMK-405). All scales in cm.

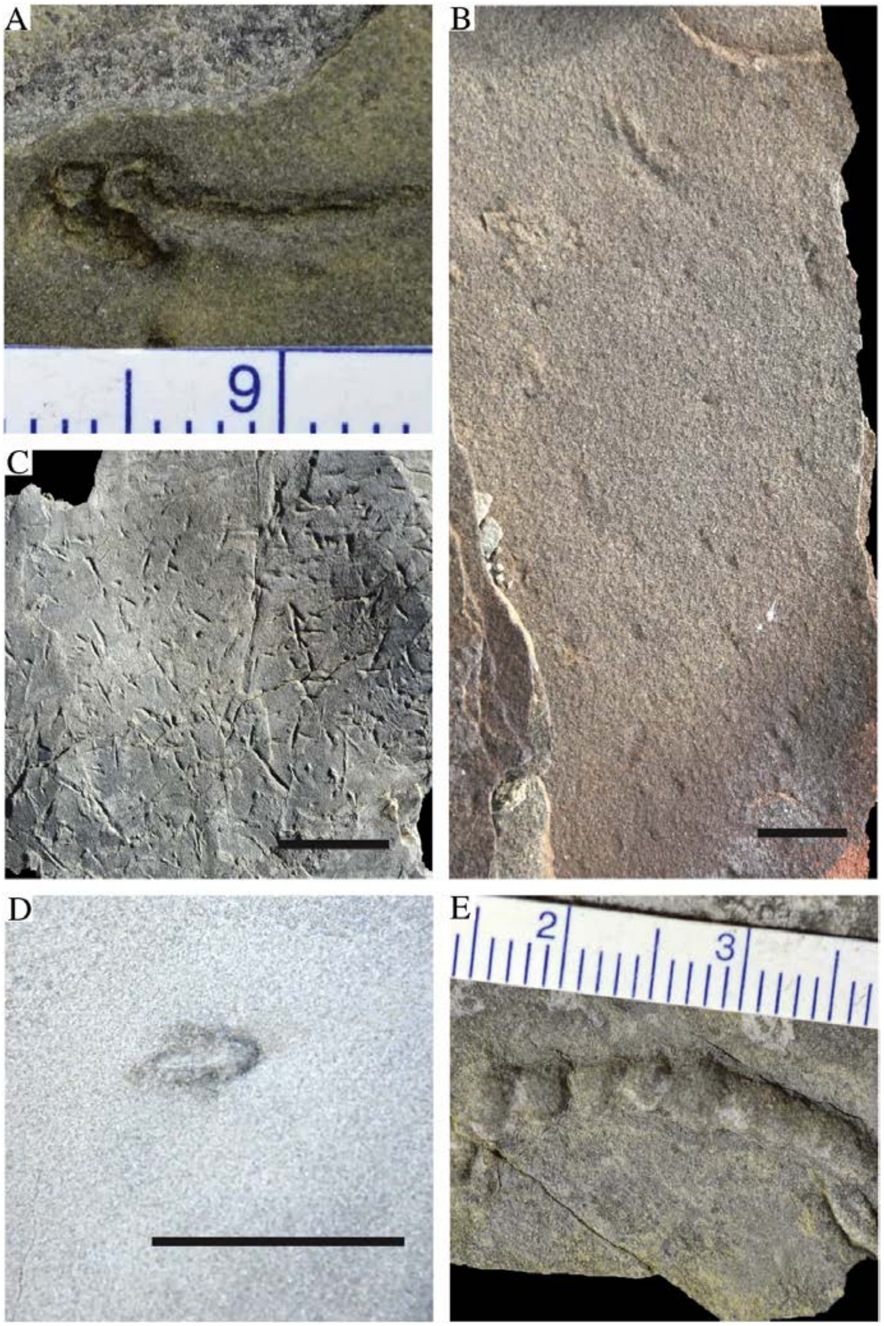


Figure 6. Ichnotaxa identified from the lower Permian Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier area. A) *cf. Gyrolithes* (11SHTRMK-8). B) *Kouphichnium* (Field Photograph); scale bar 30 mm. C) *Lingulichnus verticalis* (Field Photograph); scale bar 30 mm. D) *Lockeia silliquaria* (Field Photograph); scale bar 15 mm. E) *Margaritichnus reptilis* (11SHTRMK-144). All scales in cm.

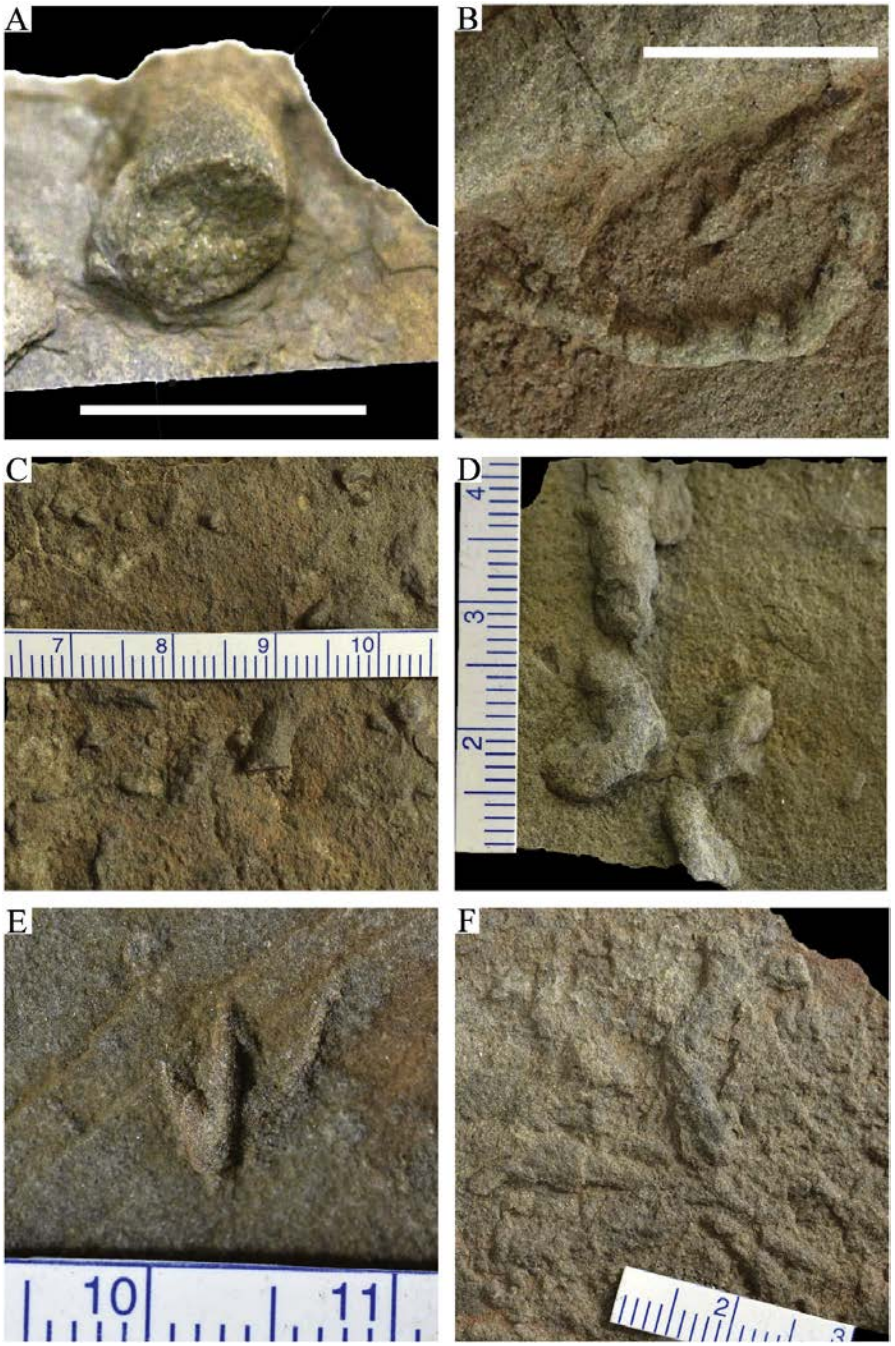


Figure 7. Ichnotaxa identified from the lower Permian Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier area. A) *Palaeophycus tubularis* (11SHBIMK-287). B) *Parataenidium mullaghmorensis* (11SHBIMK-241). C) *Phycodes* (11SHBIMK-255). D) *Phycodes ungulates* (11SHTRMK-8). E) *Phycodes curvipalmatum* (11SHTRMK-48). F) *Phycodes templus* (11SHBIMK-195); scale bar 10 mm. All scales in cm.

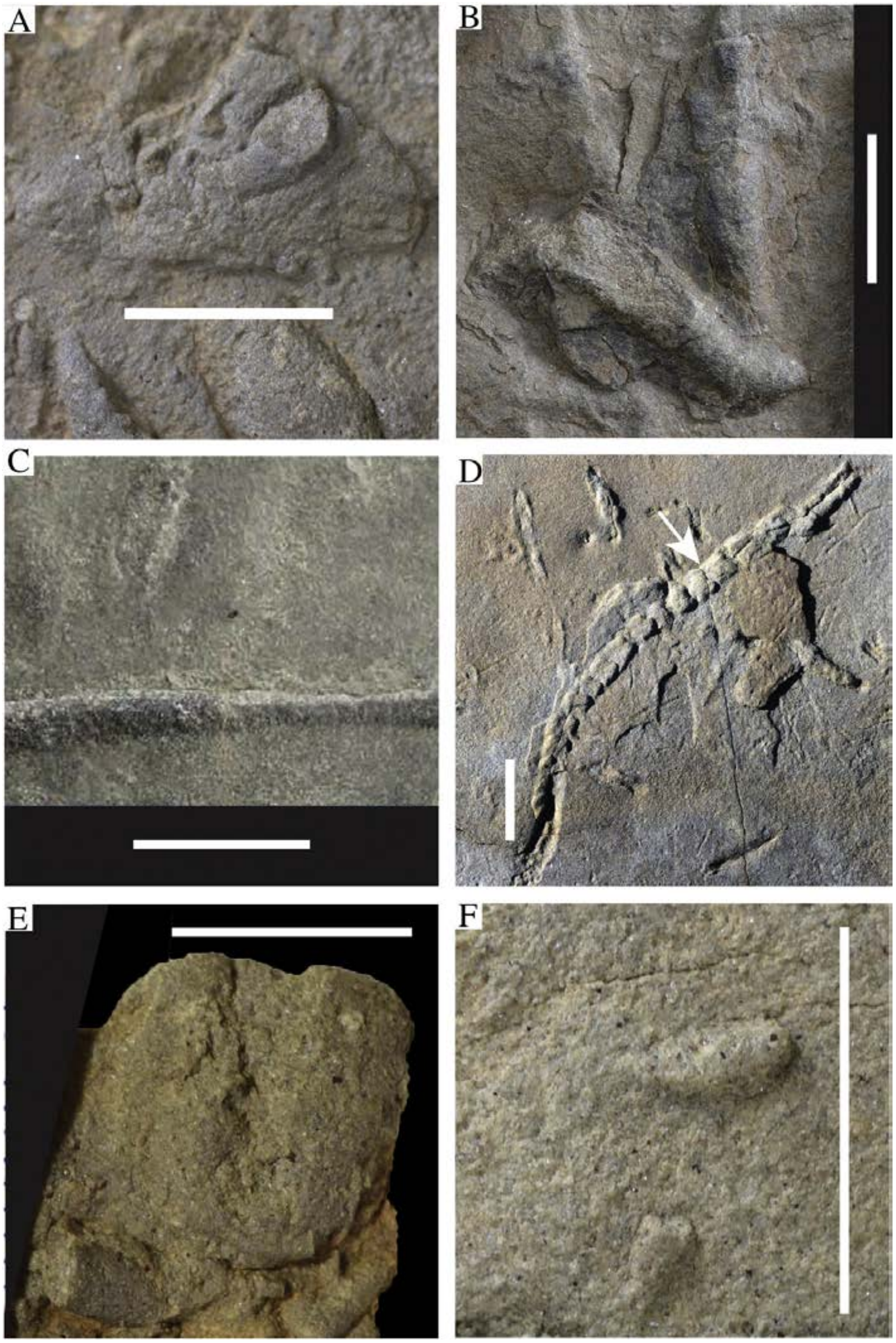


Figure 8. Ichnotaxa identified from the lower Permian Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier area. A) *Phycodes reniforme* (11SHBIMK-37). B) *Phycodes palmatus* (11SHBIMK-322). C) *Planolites* (11SHTRMK-143). D) *Protovirgularia* (Field Photograph); scale bar 30 mm. E) *Rusophycus* (11SHBIMK-262). F) *Sagittichnus lincki* (11SHBIMK-78). All scales in cm.

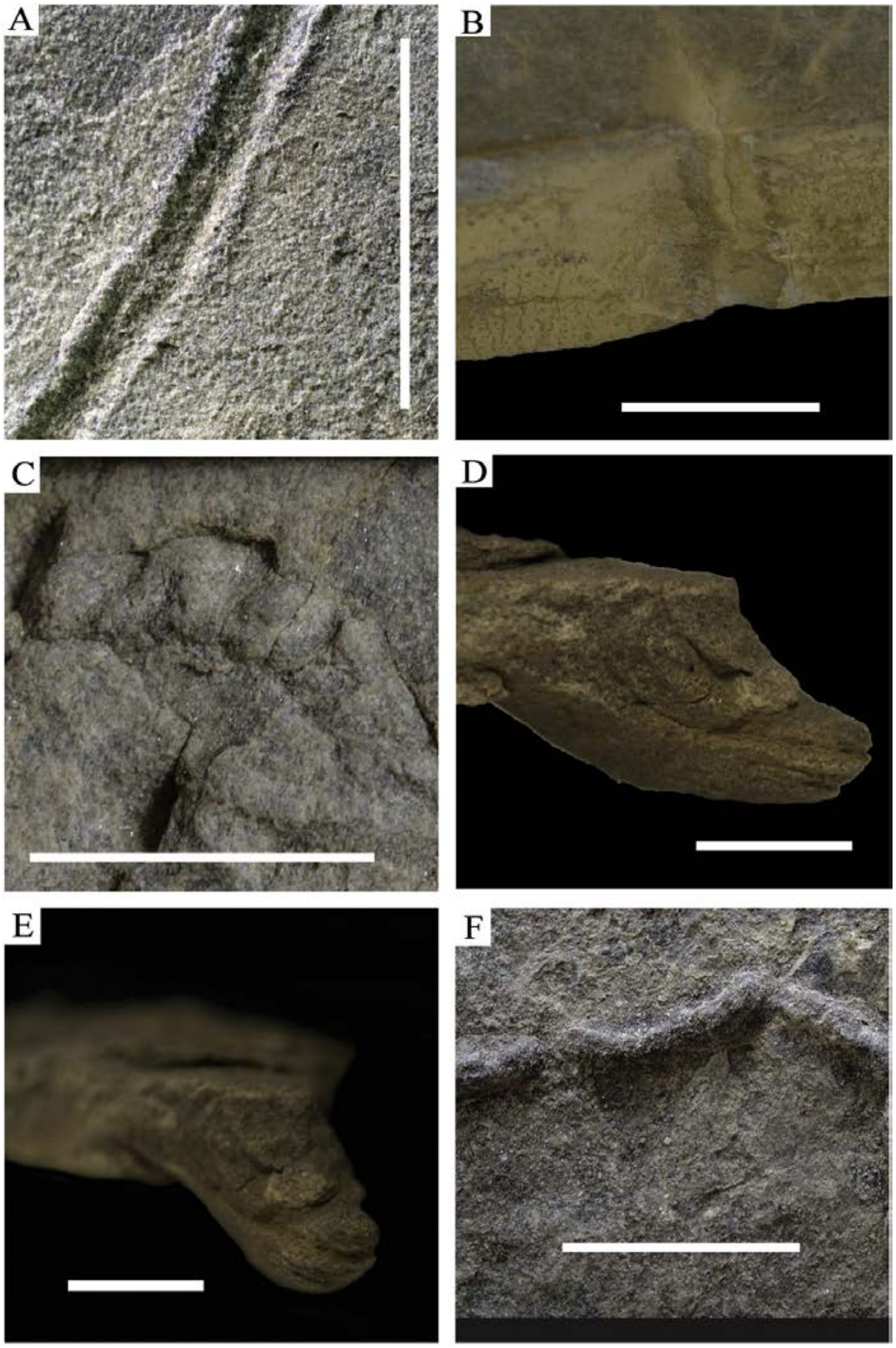


Figure 9. Ichnotaxa identified from the lower Permian Mackellar Formation at Turnabout Ridge and Buckley Island, Beardmore Glacier area. A) *Scolicia* (11SHBIMK-37). B) *Skolithos*, lateral view; scale bar is 10 mm (11SKBIMK-448). C) *Taenidium serpentinum* (11SHTRMK-61). D–E) *Teichichnus rectus* (11SHBIMK-211); lower scale bar in cm. F) *Treptichnus* isp. *cf pollardi* (11SHTRMK-96). All scales in cm.

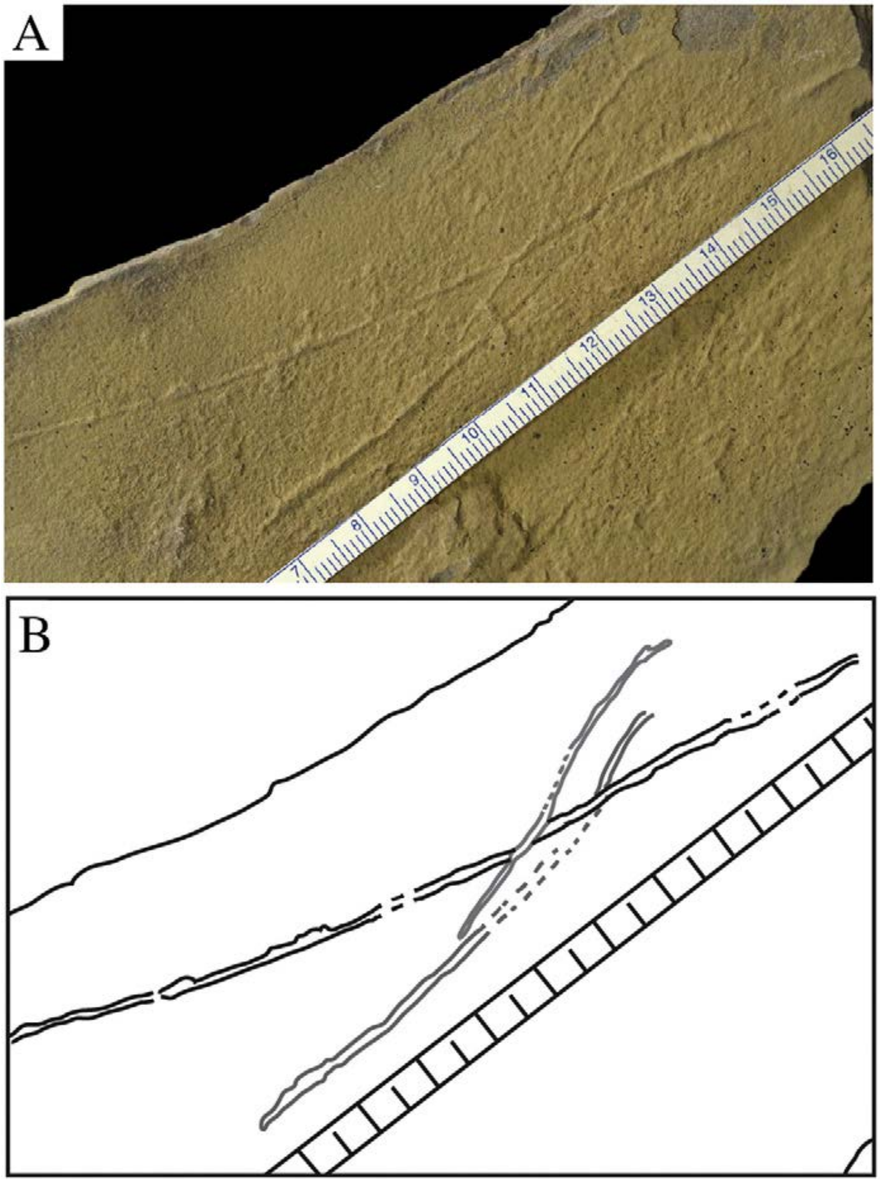


Figure 10. Photographs and line drawing of *Undichna isp. cf britannica* (11SHBIMK-102) identified from the lower Permian Mackellar Formation at Turnabout Ridge, Beardmore Glacier area. All scales in cm

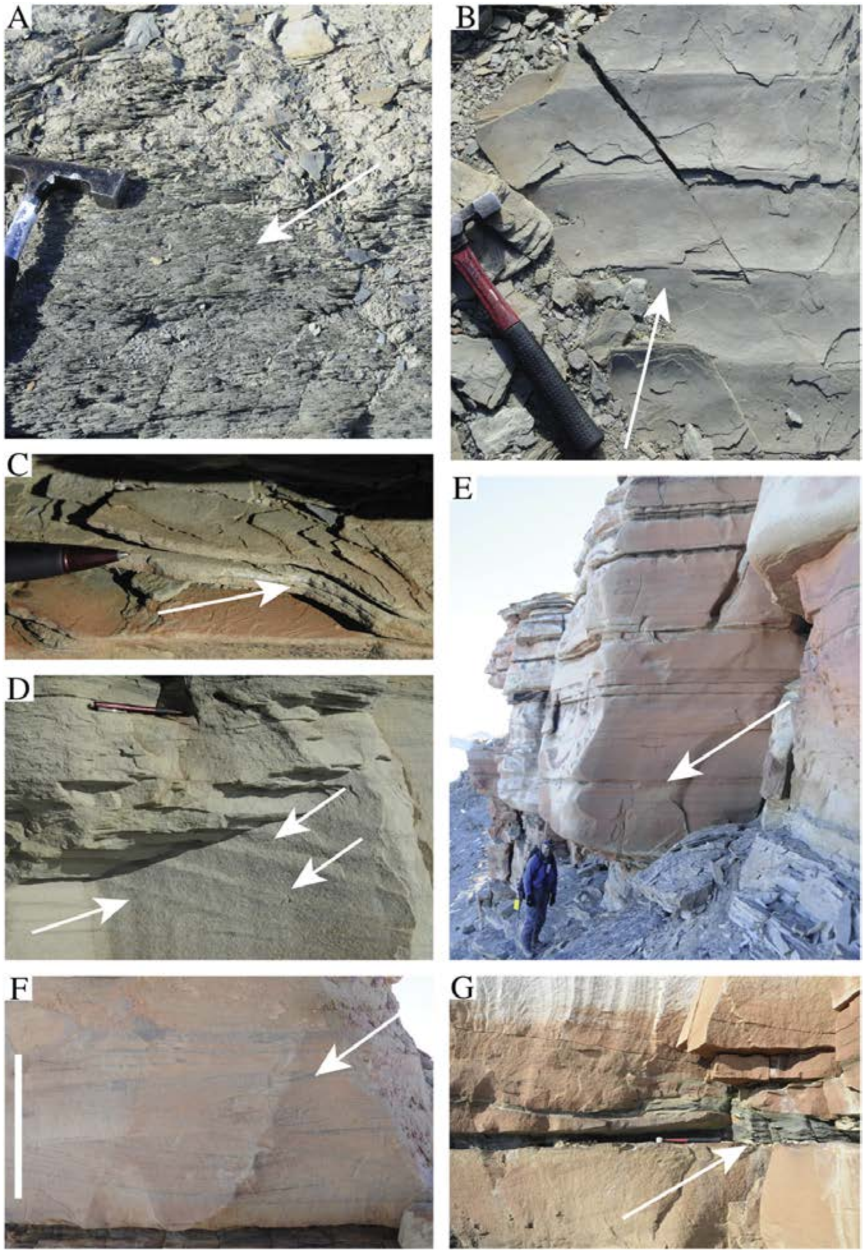


Figure 11. Sedimentary facies at Turnabout Ridge, Beardmore Glacier area. A) Facies 1- Massive to current rippled shale and siltstone. B) Facies 2- Symmetrical cross ripple-laminated sandstone. C) Facies 3- Current rippled cross-laminated to planar-laminated sandstone. D) Facies 4- Climbing ripple cross-laminated sandstone. E) Facies 5- Planar laminated sandstone. F) Facies 6- Trough cross stratified sandstone. G) Facies 7- Structureless to ripple cross-laminated mudstone. Hammers are 35 cm in length, F scale bar is 1 meter.

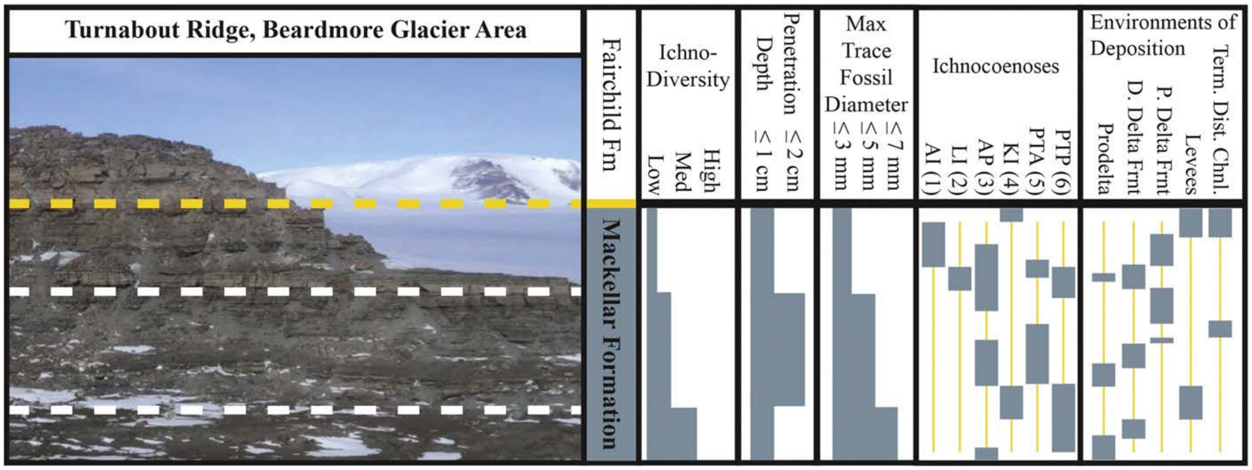


Figure 12. Trends in ichnodiversity, penetration depth, and maximum trace fossil diameters with distribution of ichnocoenoses and environments of deposition at Turnabout Ridge, Beardmore Glacier area.

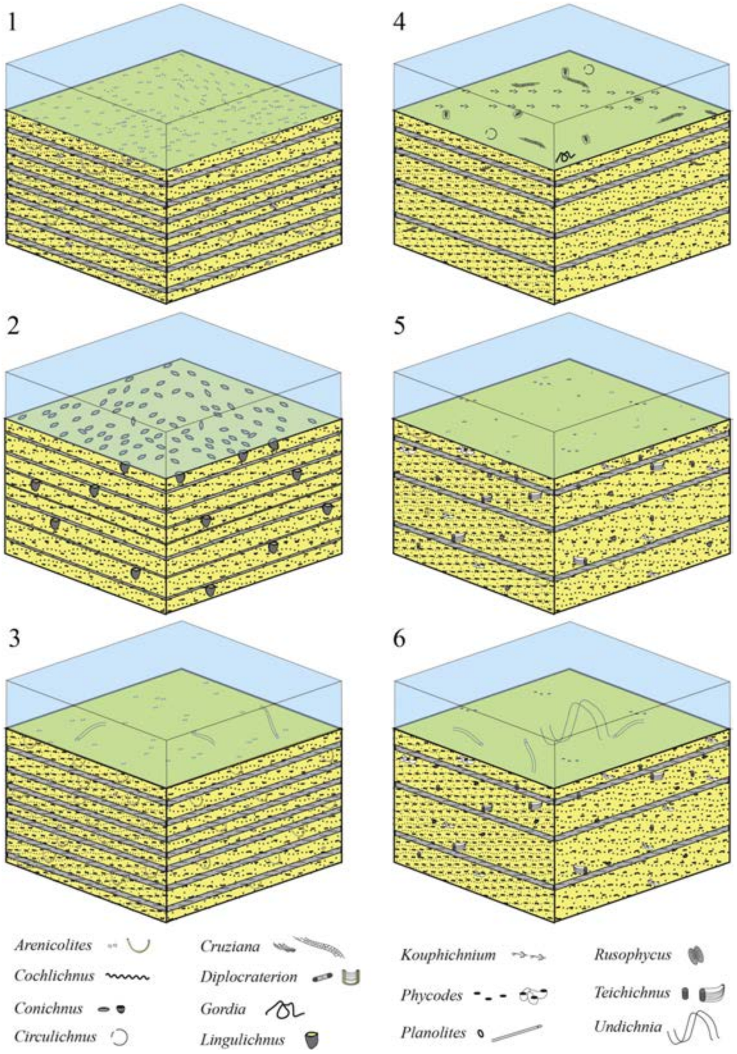


Figure 13. Box diagrams for each of the six ichnocoenoses from the Mackellar Formation at Turnabout Ridge and Buckley Island. 1) The *Arenicolites-Phycodes* ichnocoenoses found in thinly bedded, fine-grained sandstones with thin mudstone interbeds, interpreted as proximal to distal delta front environments. 2) *Lingulichnus* ichnocoenoses found in thinly bedded fine-grained sandstones with mudstone interbeds, interpreted as proximal to distal delta front with subaqueous splays. 3) *Arenicolites*-*Planolites* ichnocoenoses found in thinly bedded, fine-grained sandstones with mudstone interbeds, interpreted as delta front with subaqueous splays to prodelta environments. 4) *Kouphichnium* ichnocoenoses found in bedded sandstones, interpreted as barforms along submarine channels. 5) *Phycodes*-*Teichichnus*-*Arenicolites* ichnocoenoses found in thinly bedded sandstones with thin mudstone interbeds, interpreted as distal delta front with subaqueous splays to prodelta. 6) *Planolites*-*Teichichnus*-*Phycodes* ichnocoenoses found in thinly bedded sandstones with thin mudstone interbeds, interpreted as distal delta front with subaqueous splays to prodelta.

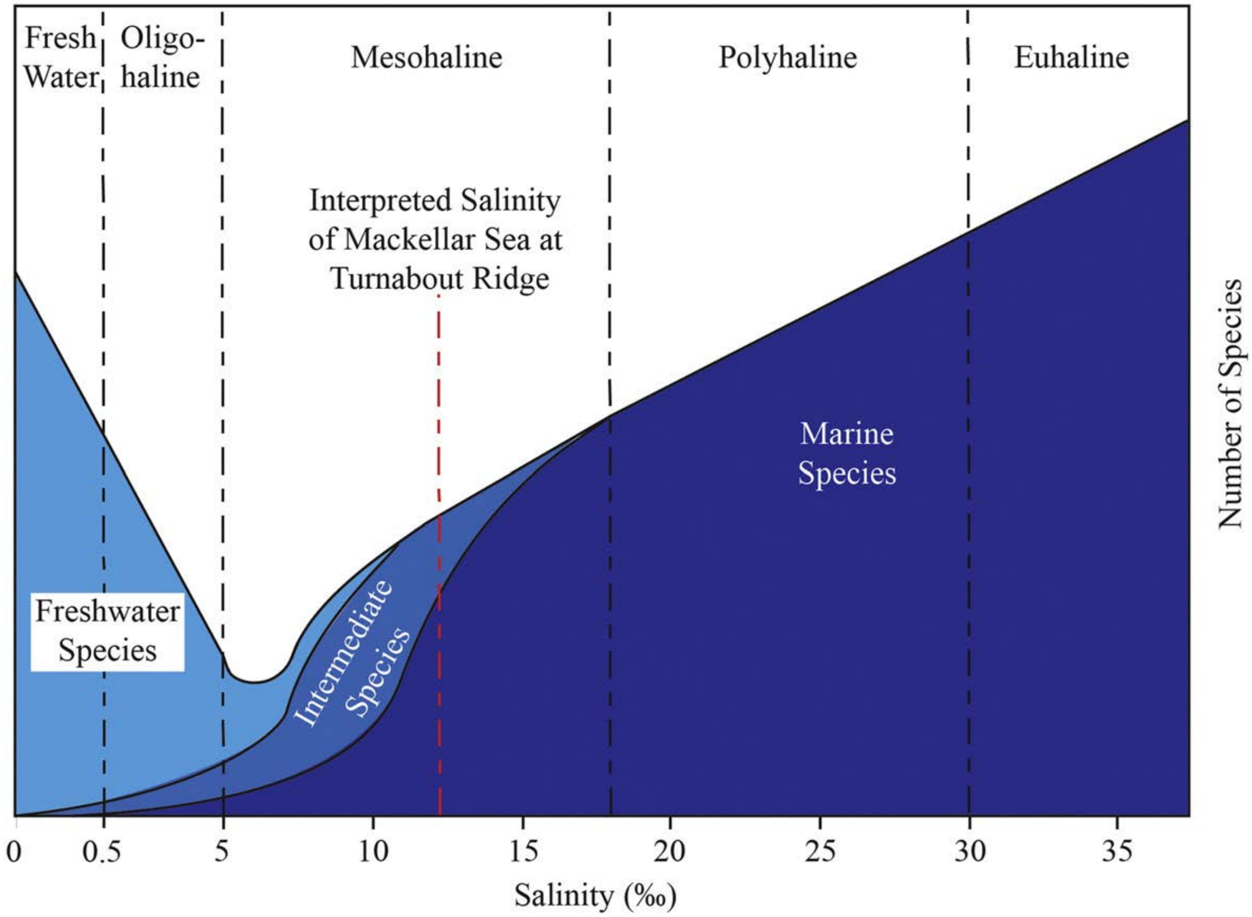


Figure 14. Relative number of species related to the Venice System salinity ‰. Red dashed line is interpreted salinity for the Mackellar Formation at Turnabout Ridge based on the percentages of fully marine to facies breaking ichnogenera identified. Modified from Remane (1943).

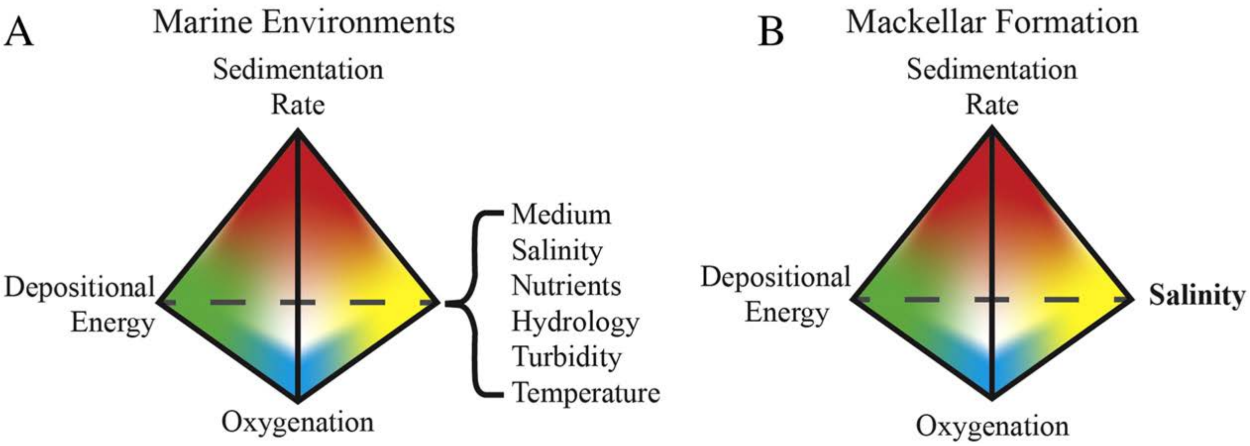


Figure 15. Major physicochemical controls on organismal behavior and resulting trace fossils. A) Established general physicochemical controls on organismal behavior for marine environments. B) Interpreted physicochemical controls for the Mackellar Formation based on trace fossils at Turnabout Ridge and Buckley Island. Modified from Hasiotis and Platt (2012).

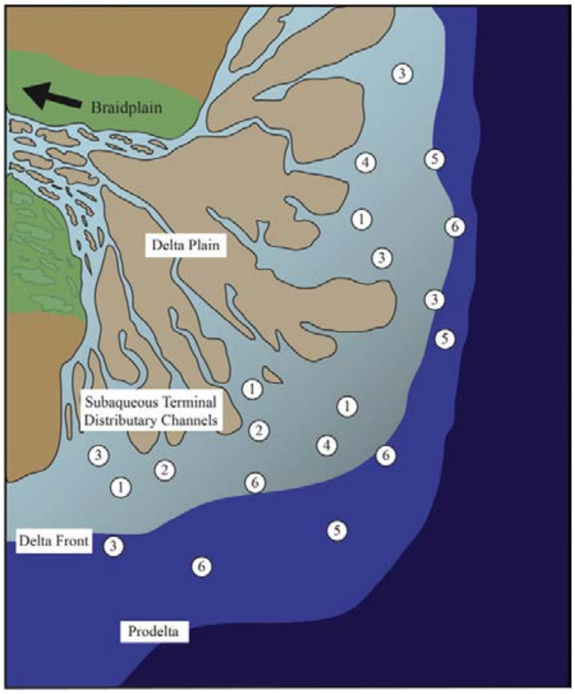


Figure 16. Interpreted positions for the six Mackellar Formation ichnocoenoses across the river-dominated shallow marine deltaic system based on stratigraphic positions of samples. Modified from Allen and Chambers (1998).

CHAPTER 3: ICHNOLOGICAL SIGNALS OF LIFE DURING OAEs AND MILANKOVITCH CYCLICITY DURING THE LATE CRETACEOUS: A REFINED ICHNOLOGICAL ASSESSMENT OF THE UPPER CRETACEOUS GREENHORN AND NIOBRARA FORMATIONS

Currently in preparation as:

JACKSON, A.M., HASIOTIS, S.T., AND SMITH, J.J., Ichnological signals of life during OAEs and Milankovitch cyclicity during the late Cretaceous: a refined ichnological assessment of the Upper Cretaceous Greenhorn and Niobrara formations, Journal of Sedimentary Research.

ABSTRACT

Ichnological analysis of Upper Cretaceous Greenhorn and Niobrara fms in the AMOCO Rebecca K. Bounds #1 Well core from Greeley County, Kansas, reveals 60% and 65% of strata deposited during OAE 2 and OAE 3, respectively, contain relatively high ichnodiversities and moderate to high bioturbation intensities. These findings suggest that the oceanic anoxic events were not wholly anoxic, but rather more accurately characterized as dysoxic to oxic and punctuated by periods of anoxia. Benthic oxygenation, sedimentation rate, and media type are the primary influences on ichnocoenosis within each lithofacies within each formation. Limestone lithofacies contain the Cruziana Ichnofacies, whereas argillaceous limestone lithofacies contain of the Zoophycos Ichnofacies and marlstone lithofacies record the Nereites Ichnofacies.

The Ichnocoenosis and bioturbation intensity patterns within the Greenhorn and Niobrara formations were tested as secondary proxies for the identification of Milankovitch cyclicity.

Vertical changes in both ichnocoenoses and bioturbation intensity contained precession, obliquity, and eccentricity signals. Less burrowed strata retained the highest number of identified cyclicities and highly bioturbated strata producing only obliquity signals. This ichnologic study shows that: 1) OAE 2 and OAE 3 strata were not entirely anoxic in the Western Interior Seaway based on the diversity, and distribution of identified ichnogenera in the Bounds core; 2) bioturbation may not completely remove sedimentary features that record orbital signals; and 3) sedimentary patterns of bioturbation intensity or ichnocoenoses may be used as a secondary proxy to identify Milankovitch-scale harmonic cyclicities.

INTRODUCTION

The Greenhorn and Niobrara formations are well known for containing strata deposited in the Western Interior Seaway (WIS) during Oceanic Anoxic Events (OAE) 2 and 3 (Arthur and Schlanger 1979; Dean and Arthur 1998a). In addition, the limestone and marlstone facies of these formations have been the focus of studies detecting Milankovitch-scale orbital cyclicities (Meyers et al., 2012). Relatively few studies have described the presence of bioturbation within sediments interpreted to had been deposited in anoxic conditions. Sediments deposited during OAEs are commonly described as being unbioturbated; however, recent studies in Europe have described OAE 2-containing-strata with high bioturbation intensity (e.g., Uchman et al. 2013a). Identification and characterization of bioturbation intensity, and the ichnogenera present within previously interpreted anoxic strata, may provide information on the relative duration and intensity of the anoxic events and other physicochemical conditions at the time of deposition.

Cyclostratigraphy has commonly focused on unbioturbated strata, as the original sedimentary layers, and any biogenic constituents (e.g., foraminifera) are not homogenized through the sedimentary unit. Studies have identified Milankovitch cyclicity as a control on glacial (e.g., Santarelli et al. 1998; Hepp et al. 2006), clastic (e.g., Sethi and Leithold 1994; Lamy et al. 1998), and carbonate (e.g., Sageman et al. 1998) environments by influencing climatic and oceanographic processes (McLeod et al. 2001). Various primary proxies (i.e., attributes being tested) can be used to identify Milankovitch cycles within a basin and across the globe (Table 1). Re-evaluation of depositional physicochemical conditions through analysis of ichnocoenoses and bioturbation intensity has implications for understanding how bioturbation may preserve orbital cyclicity signals (e.g., Gordon 1975; Poore et al. 2012; Rodríguez-Tovar 2014).

Proxies used in cyclostratigraphic studies can be categorized as either *primary* or *secondary* in their response to orbital signals (Meyers et al. 2008). Primary proxies, such as temperature and circulation patterns, are the direct response of the climate system to Milankovitch-forced changes in insolation. Secondary proxies, such as sedimentation rates and benthic oxygenation, represent changes in depositional systems in response to the primary climate forcing. For example, a primary proxy for obliquity would be chemostratigraphic variations in $\delta^{18}O$ from ice cores recording cyclical changes in global temperature (Erb et al. 2018). Lower global temperatures may result in an increase in the stratigraphic frequency of tillite and other glacially derived deposits and would be considered secondary proxies for obliquity. Common primary proxies used to identify Milankovitch cycles in the WIS include stratigraphic variations in $\delta^{13}C$ and $\%CaCO_3$ (Table 1). Bioturbation is a secondary proxy, as it records the responses of organisms (behavior) to environmental physicochemical controls (Table 2; Meyers et al. 2008; Hasiotis and Platt 2012).

Bioturbation inherently disrupts original sedimentary features (e.g., Gingras et al., 2015); however, sediments deposited into or during anoxic regions or events are often described as unbioturbated (e.g., Schieber 2003). Ichnocoenoses record the behavior of a benthic community, whereas bioturbation intensity records the good (high BI) or poor (low BI) physicochemical conditions (i.e., nutrient input, sedimentation rate, oxygenation) during and after deposition (Bromley, 1996). Both ichnocoenoses and bioturbation intensity record organismal responses to the environment (e.g., Droser and Bottjer 1986; Ekdale 1988; Savrda 1995; Twitchett 1999). Conditions with nutrient input, low depositional energy, low sedimentation rates, and a well-oxygenated benthos may record multiple generations of bioturbation that homogenize sediment. Conditions with low nutrient input, high depositional energies, high sedimentation rates, and/or an anoxic benthos record little to no bioturbation that result in laminated sediments (e.g., Ekdale et al. 1984b; Savrda and Bottjer 1986; Wheatcroft 1990; Smith et al. 1993).

The purpose of this study is to use ichnological and statistical analyses to reinterpret depositional conditions during OAE events in the Greenhorn and Niobrara fms and to also test if orbital-cyclicity signatures can be detected in stratigraphic variations of ichnocoenoses—trace-fossil associations that record the behaviors of the benthic community—and bioturbation intensity. To accomplish this, we examined the AMOCO Rebecca K. Bounds #1 Well core (i.e., Bounds core) to: 1) describe the ichnogenera; 2) interpret the environments of deposition; 3) identify ichnocoenoses; 4) characterize the bioturbation intensity; 5) evaluate physicochemical controls on biota at time of deposition; 6) assign ichnofacies; and 7) statistically analyze the stratigraphic frequency of ichnocoenoses and bioturbation intensity for harmonic signals that are consistent with known cycles.

BACKGROUND

Greenhorn Formation

Deposited into the WIS during the Cenomanian–Turonian (Fig. 1), the Greenhorn Fm is composed of the Lincoln Limestone, Hartland Shale, and the Bridge Creek Limestone members (mbrs), in ascending order (Fig. 2A; Hattin 1985). In Kansas, Greenhorn Fm strata crop out from north central Kansas to the border with Colorado (Fig. 2B) and are predominantly marlstone lithofacies with sparse calcarenite and bentonite. The Bridge Creek Limestone and Lincoln Limestone mbrs contain rhythmically bedded cycles of marlstone and limestone (e.g., Gilbert 1895; Hattin 1971; Sageman and Johnson 1985; Martin and Shimida 2008). Previous studies suggest ≤ 1.5 cm/ky sedimentation rate for the Bridge Creek Limestone and Lincoln Limestone mbrs and ≤ 3 cm/ky sedimentation rate for the Hartland Shale Mbr based on bentonite ages and interpreted orbital cyclicity using isotope stratigraphy (Ma et al. 2014).

Niobrara Formation

The Niobrara Fm, deposited in the WIS during the Turonian–Campanian (see Fig. 1), is composed of the Fort Hays Limestone and Smoky Hill Chalk mbrs (Miller 1958; see Fig. 2A). Previous studies divided the Smoky Hill Chalk Mbr into seven informal units (Scott and Cobban 1964; Hattin 1982); however, only the basal five units were collected in the Bounds core (Savrda 1998b). The Niobrara Fm in western Kansas (Fig. 2B) is dominated by white to grey limestone lithofacies in the Fort Hays Limestone Mbr, and grey to black marlstone lithofacies in the Smoky Hill Chalk Mbr. Decimeter-scale limestone to marlstone cycles are present in both members; limestone is more prevalent in the Fort Hays Limestone Mbr cycles, whereas marlstone is the dominant lithology in the Smoky Hill Chalk Mbr cycles (Savrda 1998b). Sedimentation rates in the Niobrara Fm have been interpreted to vary between 1–1.5 cm/ky, with rates of up to 2.5 cm/ky occurring in the marlstone lithofacies (Locklair and Sageman 2008).

Oceanic Anoxic Events

The Greenhorn and Niobrara fms record periods of global OAEs characterized by low to zero faunal diversity recorded, and positive $\delta^{13}C$ excursions (Schlanger and Jenkyns 1976; Arthur et al. 1988; Arthur and Sageman 1994; Leckie et al. 2002; Wagreich et al. 2011). OAE strata primarily occur as black shale (Schlanger and Jenkyns 1976). Three OAEs occurred during the Cretaceous, with OAE 1 (Aptian–Albian) and OAE 2 (Cenomanian–Turonian) reflecting the peak greenhouse climates, and OAE 3 deposited during the transition to a waning greenhouse regime through the Coniacian–Campanian (Jenkyns 2003; Friedrich et al. 2012). The extent of each OAE is variable, with OAE 1 occurring globally, OAE 2 being nearly global, and OAE 3 generally restricted to the North Atlantic and shallow basins (i.e., WIS) (Arthur and Schlanger 1979; Wagner et al. 2004; Wagreich 2012).

Of the three OAEs, OAE 2 had the greatest effect on the WIS (Arthur et al. 1987; Erba and Premoli-Silva 2004). OAE 2 occurred during the latest Cenomanian to earliest Turonian maximum Greenhorn Transgression (Arthur et al. 1987). The Bridge Creek Limestone Mbr of the Greenhorn Fm was deposited during OAE 2, and has been studied extensively for refining the timing of OAE 2 (e.g., Sageman et al. 1997, 2006; Meyers et al. 2001, 2012; Ma et al. 2014). The most distinguishing characteristic of OAE 2 is a pronounced positive $\delta^{13}C$ excursion near the Cenomanian-Turonian boundary (Schlanger et al. 1987); however, other attributes include biotic turnover (Leckie et al. 2002) and anoxia (Arthur and Schlanger 1979). In the Polish Outer Carpathians, the effects of OAE 2 on bioturbation (ichnocoenoses and bioturbation intensity) were interpreted to have resulted from fluctuations of benthic oxygenation and sediment consistency (Uchman et al. 2008, 2013a).

The Santonian–lower Campanian OAE 3 is the least pervasive OAE to occur in the Cretaceous WIS, and is characterized by a less positive excursion of $\delta^{13}C$ than either OAE 1 or OAE 2 (Arthur and Schlanger 1979). The depositional areas affected by OAE 3 tend to be biased to portions of basins where upwelling may have occurred (Rey et al. 2004). The comparatively limited stratigraphic record of OAE 3 has led some researchers to suggest that it was not a global event (Wagreich 2009, 2012; Locklair et al. 2011; Lowery 2015; Tessin et al. 2015).

Cyclicity in the Greenhorn and Niobrara Formations

G.K. Gilbert (1895) first described the cyclic sedimentary pattern between marlstone and limestone lithofacies in the Greenhorn and Niobrara fms. Later studies attribute the sedimentary cycles to local or regional oceanographic processes (e.g., climate fluctuations, tectonics, and surface-water fertility; e.g., La Ferriere et al. 1987; Watkins 1989). Milankovitch cyclicity has been studied using sediment thicknesses (e.g., Kauffman and Caldwell 1993; Elder et al. 1994), sediment chemistry percentages ($CaCO_3$, e.g., Dean and Arthur 1998b), stable isotopes (e.g., Sageman et al. 1997, 1998; Meyers et al. 2012; Ma et al. 2014), and foraminiferal communities (e.g., Coccioni and Galeotti 1993). The use of ichnology in astrochronologic studies, however, has been comparatively rare (e.g., Kuhnt et al. 2005; Rodríguez-Tovar et al. 2009b; Uchman et al. 2013b Rodríguez-Tovar 2014).

In general, bioturbation is a postdepositional or destructive process, which can modify recorded cyclicities (e.g., Benninger et al. 1979; Hutson 1980; Schiffelbein 1984; Wheatcroft 1990; Trauth et al. 1997; Anderson 2001; Leuschner et al. 2002; Savrda 2008).

Cyclostratigraphic studies outside North America that include bioturbation tend to focus on OAE 2 (i.e., Kuhnt et al. 2005; Rodríguez-Tovar et al. 2009b; Uchman et al. 2013b). These studies on OAE-2-containing strata identified *Chondrites*, *Planolites*, *Thalassinoides*, and *Zoophycos* in similar depositional environment to the Greenhorn and Niobrara fms (Rodríguez-Tovar et al. 2009a, 2009b; Rodríguez-Tovar and Uchman 2011; Uchman et al. 2013a, 2013b).

MATERIALS AND METHODS

The Lincoln Limestone and Bridge Creek Limestone mbrs of the Greenhorn Fm and the Smoky Hill Chalk and Fort Hays Limestone mbrs of the Niobrara Fm were studied in 73.3 m (31 m of Greenhorn; 42.3 m of Niobrara) of the AMOCO Bounds core (API 15-071-20446) to identify trace fossils, ichnocoenoses, bioturbation intensity, and lithology at the mm scale. Scientists at AMOCO collected core of the entire Greenhorn Fm, but did not collect the upper two informal units of the Niobrara Fm (upper limestone and upper shale units of the Smoky Hill Chalk Mbr) to use in regional correlations (Dean and Arthur 1998a). The Greenhorn Fm core is 99.8% complete, whereas the Niobrara Fm is 99.5% complete for the cored interval, both with additional minor loss from sampling by earlier studies (e.g., Dean and Arthur 1998a; Sageman et al. 1998) and rare in-box mixing (i.e., loss of stratigraphic continuity). Due to use restrictions, the Bounds core could not be broken along bedding planes to examine fresh surfaces. Core surfaces were examined under dry and wet conditions using 10x, 14x, and 20x Bausch and Lomb® Hastings triplet hand lenses. Surfaces were photographed using a Nikon model D3100 with a Nikkor 40 mm 1:2.8G Micro lens.

Ichnological Methods

This study builds on the methods of Savrda (1998a, 1998b), who identified ichnogenera and ichnocoenoses in the Bounds core and related the types and abundances to relative levels of benthic oxygenation. In this study, trace fossils were measured and identified to ichnogeneric level following Bromley (1996) and Pemberton et al. (2001). Trace fossils were measured with General Tools® #147 digital calipers with accuracy to 0.0254 mm. Cryptobioturbation was identified based on the serial repetition of broken laminite layers or zones with mottling, or haloed zones (sensu Pemberton et al. 2008). Ichnocoenoses were erected following Pemberton et al. (2001) as trace-fossil associations. Ichnocoenoses were named for the most abundant ichnogenera in each association. For each formation, the respective ichnocoenoses were identified and labeled from 1–n in order of their interpreted increasing benthic oxygenation. There is no additional meaning for ichnocoenoses labels of 1–n beyond a numerical delineation. Ichnocoenosis 2 is not twice the diversity, or abundance of ichnocoenosis 1. Interpreted physicochemical conditions at or during deposition and bioturbation were interpreted based on literature (e.g., Pemberton et al., 2001; Hasiotis and Platt, 2012). Ichnofacies were determined by the identified ichnogenera, characterized ichnocoenoses, and interpreted physicochemical parameters (e.g., Seilacher 1977).

This studies interpretation of physicochemical parameters from trace fossils is based on the accretive work of much of the ichnological community (e.g., Seilacher 1977; Ekdale et al., 1984a; Savrda and Bottjer 1986; Bromley 1996) (Table 2). Well oxygenated environments are commonly characterized by large trace fossil sizes (i.e., diameter) (e.g., Bromley 1975), and increasing abundance/ intensity of trace fossils/bioturbation (e.g., Ekdale and Mason 1988). Dysoxic environments generally contain low ichnodiversities (e.g., Savrda and Bottjer 1986), smaller burrow sizes and limited burrowing depth or intensity (e.g., Bromley and Ekdale 1984).

Hasiotis and Platt (2012) refined the method for characterizing the primary physicochemical controls on bioturbation and this study uses their tetrahedron approach to characterizing the Greenhorn and Niobrara fms depositional conditions.

Bioturbation intensity was semiquantitatively measured using ichnofabric indices (ii) following the methods of Droser and Bottjer (1986): ii1 = 0% bioturbated, ii2 = 0–10% bioturbated, ii3 = 10–40% bioturbated, ii4 = 40–60% bioturbated, ii5 = 60–100% bioturbated, ii6 >100% bioturbated. Zones without ichnocoenoses data (i.e., missing strata, or no bioturbation) were placed into Ichnocoenosis 0. Trace fossil abundance, ichnocoenoses, ii, and lithologies were integrated to interpret benthic physicochemical parameters during and after deposition. This study used a modified version of the oxygenation scheme of Tyson and Peterson (1991) to interpret benthic oxygenation from ichnocoenoses and ii: oxic (> 2.0 ml/l O_2), upper dysoxic (2.0–1.0 ml/l O_2), lower dysoxic (1.0–0.5 ml/l O_2), and anoxic (≤0.5 ml/l O_2) (Table 3).

Statistical Evaluation for Cyclicity

Examinations of ichnocoenoses and bioturbation intensities in both formations for cyclical patterns was conducted using the Astrochron package (Meyers 2014) developed for the R statistical software (R Core Team 2015; 3.2.2, Fire Safety). Employed analyses included a multitaper method (MTM), evolutive harmonic analysis (EHA), and average spectral misfit analysis (ASM) (Meyers and Sageman 2007; Meyers et al. 2012). MTM separates the target spectra from noise and refines the number of spectral peaks within the dataset to those with a >90% confidence in the harmonic F–test (Sageman et al. 1998; Meyers et al. 2008). The resulting data from the MTM test was then processed using EHA to identify spectral-peak amplitudes and probabilities in a range of tested cycles per meter (c/m) (Meyers et al. 2012).

ASM then compares the targeted orbital spectra (Table 4; Laskar et al. 2011; Waltham 2015) and spectral peaks in the EHA data with potential sedimentation rates using a sequentially shifting data window (Meyers and Sageman 2007; Meyers et al. 2012). The target orbital spectra are based on those identified in previous studies on the Greenhorn (Savrda and Bottjer 1994; Sageman et al. 1998, 2006; Savrda 1998a) and Niobrara fms (Dean and Arthur 1998b; Locklair and Sageman 2008; Sageman et al. 2014) from the Bounds core (Laskar et al. 2011, and refined by Waltham 2015). For the Greenhorn and Niobrara fms, four Milankovitch cycles are needed to accept the identification of Milankovitch Cycles in the Cretaceous following the guidelines of Waltham (2015). ASM was used with a Nyquist frequency of 50 (based on the sampling interval), the standard Raleigh frequency of 0.1245274, and the target orbital spectra to test for harmonic spectra in the distribution of ichnocoenoses and bioturbation intensity (Table 4). Greenhorn Fm data were tested with sedimentation rates between 0.96–5.85 cm/ka (Ma et al. 2014), and Niobrara Fm data were tested with sedimentation rates between 0.75–4.6 cm/ka (Locklair and Sageman 2008). Based on the previously identified depositional rates, a vertical resolution of 1 cm has a minimum duration for each cm of strata of 0.04 ky for the Greenhorn Fm, and 1.34 ky/cm for the Niobrara Fm using the accumulation rates of Ma et al. 2014 and Locklair and Sageman 2008. Ideal Milankovitch-scale harmonic scales (in cycles per meter) were identified using the minimum accumulation rates as determined by Ma et a., 20014 and Sageman 2008.

RESULTS

Ichnology

Seventeen ichnogenera were identified in the Greenhorn and Niobrara fms (Table 5; Figs. 3–7). The Niobrara Fm contains four ichnogenera not found in the Greenhorn Fm: *Diplocraterion*, *Ophiomorpha*, *Schaubcylindrichnus*, and *Trichichnus*. *Arenicolites* and *Trichichnus* occur only once in either formation, whereas *Chondrites*, *Helminthopsis*, *Thalassinoides*, and *Zoophycos* are abundant in both formations. In the Greenhorn Fm, six of the seven ichnogenera found by Hattin (1971) and all five identified by Savrda (1998a) were identified in this study. Seven of the 10 trace fossils seen by Frey (1970, 1972), and all six identified by Savrda (1998b) in the Niobrara Fm.

Ichnocoenoses

Six ichnocoenoses were identified in each formation: Greenhorn Fm ichnocoenoses (GFI) 1–6 and Niobrara Fm ichnocoenoses (NFI) 1–6 (Table 6; Figs. 8–9). Due to no identified bioturbation or an absence of core material, 24% of the Greenhorn Fm and 13.3% of the Niobrara Fm were interpreted as containing no ichnocoenoses. Ichnocoenoses are similar between both formations; however, each formations ichnocoenoses are exclusive to itself and used to interpret the unique physicochemical parameters at deposition with that ichnocoenoses present.

Greenhorn Ichnocoenoses.—GFI 1 is the most abundant ichnocoenosis in both the Lincoln Limestone and Bridge Creek Limestone mbrs (Table 6 Fig. 8A). The abundance of cryptobioturbation mostly is within the laminated marlstone lithofacies. In laminated strata, zones with cryptobioturbation potentially indicate graphoglyptid trace fossils (e.g., *Cosmorhaphe*, *Paleodictyon*, *Spirorhaphe*; Wetzel 1984). GFI 2 is composed of *Chondrites*, *Planolites*, and rare *Teichichnus* (Fig. 8B). GFI 2 occurs in 3% of the formation and commonly is manifest as 1–3 individual traces in an interval. All three ichnogenera in GFI 2 are < 5 mm in diameter; however, the vertical extent of *Teichichnus* may exceed 5 mm. GFI 3, 10% of the fm, contains *Planolites*, *Teichichnus*, and rare *Zoophycos* in marlstone and argillaceous limestone lithofacies (Fig. 8C). GFI 4 contains *Palaeophycus*, *Planolites*, *Teichichnus*, and *Zoophycos*, and is 3.2% of the Greenhorn Fm (Fig. 8D). GFI 4 occurs mostly in argillaceous limestone and limestone lithofacies of the Bridge Creek Limestone Mbr, with only four occurrences in the Lincoln Limestone Mbr. Strata assigned to GFI 5 comprise 7% of the formation and only occur in the limestone lithofacies of the Bridge Creek Limestone Mbr (Fig. 8E). These strata are some of the most highly bioturbated (ii5–6). This ichnocoenosis includes *Palaeophycus*, *Planolites*, *Teichichnus*, *Thalassinoides*, and *Zoophycos*, and tends to occur in the middle and bottom of the Bridge Creek Limestone Mbr. GFI 6 is the least abundant ichnocoenosis in the Greenhorn Fm (Fig. 8F). This ichnocoenosis is similar to GFI 5; however, *Zoophycos* is absent, and *Chondrites* and *Helminthopsis* are present. Strata of GFI 6 tend to occur at the upper transitions of limestone beds, as the pass up into marlstone lithofacies.

Niobrara Ichnocoenoses.—NFI 1 is characterized by cryptobioturbation and makes up 9.9% of the formation. NFI 1 is identical to GFI 1 in lithofacies and ichnogenera (Fig. 9A). Strata of NFI 2 consist of *Chondrites*, cryptobioturbation, *Helminthopsis,* and *Zoophycos* in marlstone lithofacies (Fig. 9B). Additionally, NFI 2 contains the only observed occurrence of *Trichichnus* in the Niobrara Fm. NFI 2 is not abundant (4%) in the Fort Hays Limestone Mbr; however, it is prevalent (31%) in the Smoky Hill Chalk Mbr. NFI 3 contains *Chondrites*, *Helminthopsis*, *Planolites*, *Teichichnus*, and *Zoophycos*, and is the most abundant ichnocoenosis in the formation (20.1%) (Fig. 9C). NFI 3 has the highest ichnodiversity in the Niobrara Fm and occurs near many of the lithological transitions from marlstone to limestone. NFI 4 (Fig. 9D) includes abundant *Teichichnus* and *Zoophycos* with occasional *Asterosoma* and *Rosselia*. NFI 4 records the transition from the marlstone-dominated lithofacies to the limestone lithofacies. Strata with NFI 5 are heavily bioturbated with *Planolites*, *Teichichnus*, and *Zoophycos* (Fig. 9E). In NFI 5, the abundant *Teichichnus* and *Zoophycos* have nearly (ii5–6) homogenized the lithofacies in which they occur. NFI 6, which makes up nearly 15% of Niobrara Fm strata, is dominated by *Thalassinoides* in the limestone lithofacies (Fig. 9F). This ichnocoenosis also includes *Planolites* and *Teichichnus*, with accessory *Zoophycos*. These strata are highly bioturbated (ii5–6), and commonly are mottled by piping into the underlying argillaceous limestone to marlstone lithofacies. NFI 4–6 can contain secondary *Chondrites* that appear to have exploited the original bioturbated zone after further deposition.

Bioturbation Intensity.— Limestone and argillaceous limestone lithofacies are highly bioturbated (ii3–6), whereas calcareous mudstone and marlstone lithofacies are unbioturbated to partially bioturbated (ii1–3) (Figs. 10A, 11A). 15% of the Lincoln Limestone and Bridge Creek Limestone mbrs of the Greenhorn Fm are unbioturbated (ii1) (Fig 10A). The overlying Niobrara Fm differs in that 32% are unbioturbated (ii1), predominantly in the OAE3 section (Fig. 11A).

Ichnofacies.—Both formations contain strata assigned to the Cruziana, Zoophycos, and Nereites ichnofacies (Table 6). Marlstone and calcarenite lithofacies, which include GFI 1 and NFI 1, are interpreted to represent the Nereites Ichnofacies. The characterization of the Nereites Ichnofacies is based on the absence of identifiable trace fossils, nearly continuous laminations and rare-lamina disrupting cryptobioturbation (e.g., Ekdale et al. 1984b; Savrda et al. 1998; Pemberton et al. 2008).

Argillaceous limestone lithofacies with *Chondrites*, *Planolites*, *Teichichnus*, and *Zoophycos* (GFI 3–4; NFI 3–5) are consistent with the Zoophycos Ichnofacies (e.g., Ekdale and Mason 1988; Goldring 1993). The increasing carbonate sediment percentage (versus marlstone) in the strata assigned to this ichnofacies indicates that carbonate depositional rates were faster than clastic input (Locklair and Sageman 2008). Limestone lithofacies with abundant *Thalassinoides. Planolites*, and *Teichichnus* record ichnocoenoses that are a mix of dominichia and fodinichnia (GFI 4–5; NFI 4–5) and represent the Cruziana Ichnofacies (e.g., Frey and Howard 1982; Wetzel 2008). These strata contain the highest ichnodiversity and bioturbation intensity.

Cyclicity

Harmonic signals matching orbital spectra were identified in both ichnocoenoses and bioturbation intensities for the Bridge Creek Limestone Mbr of the Greenhorn Fm and Fort Hays Limestone and Smoky Hill Chalk mbrs of the Niobrara Fm (Tables 7–9). Milankovitch cyclicities were identified for each formation, based on the sedimentation rates determined in ASM within the controls of rates determined by Locklair and Sageman (2008) and Ma et al. (2014).

Greenhorn Cyclicity.— The Lincoln Limestone Mbr and much of the Bridge Creek Limestone Mbr had multiple fitting sedimentation rates that included the minimum sedimentation rate of 0.96 cm/ky (Table 7). Ichnofabric Index identified multiple precessional, obliquity, and eccentricity harmonics (Table 8; Fig. 10A,C,). Similarly, ichnocoenoses in the Lincoln Limestone Mbr logged precessional, obliquity, and a non-continuous eccentricity signal (Fig. 10B,D,). Harmonic signatures in ii and ichnocoenoses were not identified across the entire Lincoln Limestone Mbr of the Greenhorn Fm, as there was not enough bioturbation and/or variability in bioturbation in the upper and lower 1.5 m to statistically identify for an orbital signature in the section (Figs. 10E,F).

The Bridge Creek Limestone Mbr contains both ii and ichnocoenoses harmonics that match all three orbital parameters (Fig. 10C,D). The precessional ii signal varies throughout, with multiple signals showing high probability (≥ 80%) (Fig. 10C). An obliquity signal is strong (~70% probability) in the ii from the base of the unit to ~20 m; however, a strong eccentricity signal was not identified in the ii, except for the upper 3 m (Table 8). Seven signals with frequencies > 6.1 c/m—those with periods < 13 ky—were identified (Fig. 10C).

All three Milankovitch cyclicities are identified in the ichnocoenoses of the Bridge Creek Limestone Mbr (Fig 10D). Three ideal precessional signals are identified (Table 7, 9). The obliquity signal is strongest near 2.8 c/m, whereas the dominant eccentricity signal has a frequency of 0.9 c/m (Fig 10D). Ichnocoenoses in the Bridge Creek Limestone Mbr identify additional subprecessional frequencies (> 6.1 c/m), which are similar to the frequencies produced from the ii in the Bridge Creek Limestone and Lincoln Limestone mbrs.

Niobrara Cyclicity.—The upper part of Fort Hays Limestone and middle part of the Smoky Hill Chalk mbrs show the highest strength and diversity of signals in the Niobrara Fm (Fig. 11, Table 7, 10). The middle part of the Fort Hays Limestone and lower part of the Smoky Hill Chalk mbrs also show strong signal but not equally for both ii and ichnocoenoses. The upper

Smoky Hill Chalk and lower Fort Hays mbrs are the most variable between ii and ichnocoenoses, where ii identifies a lower diversity of strong frequencies than the ichnocoenoses.

The basal Fort Hays Limestone Mbr records harmonics that match all three Milankovitch cycles (Fig. 11C,F). The strongest signals in the Fort Hays Limestone Mbr are 0.65–0.85 c/m eccentricity frequency for both ii and ichnocoenoses (Fig. 11C,F). Similarly, both proxies contain obliquity signals at 2.15 c/m. Ichnocoenoses have a stronger obliquity signal in the basal 5 m, and both ii and ichnocoenoses lose signal strength between 10–15 m from the base. Overall, the bioturbation intensity and ichnocoenoses present differ in precessional and higher frequency cycles (Fig 11C,F). The Fort Hays Limestone ii contains no ideal precessional cycles (see Table 11). Similarly, the Fort Hays Limestone ichnocoenoses have no ideal precessional signal in the lower 10 m, but two in the upper 10 m (3.85, and 4.5 c/m). The Smoky Hill Chalk Mbr does not record precessional signals as strongly as the Fort Hays Limestone Mbr (Fig 11C,D,E,F). The Smoky Hill Chalk ichnocoenoses also have a robust ideal obliquity signal (2.15 c/m). The three precessional signals of the Smoky Hill Chalk Mbr ii and ichnocoenoses are relatively weak (50% ≤ X ≤ 70% probability) or absent.

OAE 2 and OAE 3 Cyclicity.—There is no clear difference in background sedimentation rates (1.3 cm/ky average) or identified harmonic frequencies in the ii or ichnocoenoses for the OAE 2 section (2.8–6.35 m) versus the entirety of the Bridge Creek Limestone Mbr (Fig. 12). The three orbital signals are identified in the ichnocoenoses and ii of the OAE 2 strata. A strong eccentricity signal was not identified in ii; however, it did indicate a strong precessional signal in the lower part and obliquity signal throughout (Fig. 12B). Ichnocoenoses data contained strong but non-continuous signals of precession, obliquity, and eccentricity (Fig. 12C). The Smoky Hill

Chalk Mbr (OAE 3 strata) does not record strong eccentricity- or precessional-scale harmonic signals akin to the underlying Fort Hays Limestone Mbr (see Fig. 11).

DISCUSSION

This study identifies bioturbation across and through Oceanic Anoxic Events (OAEs), indicating that these events were not anoxic for their duration. Bioturbation within OAE 2 and OAE 3 strata indicates temporary periods of dysoxic to oxic conditions allowing for colonization and bioturbation of these sediments. The bioturbation throughout OAE deposits within the Bridge Creek Limestone and Smoky Hill Chalk mbrs disagrees with previous assertions and prevailing acceptance of wholly anoxic conditions during these events and in black shales in general (i.e., Arthur and Sageman, 1994; Cluff 1980). The abundance and variation of bioturbation within OAE zones and throughout the Greenhorn and Niobrara fms, further allowed for the identification of cyclostratigraphic trends in the vertical distribution of ichnocoenoses and bioturbation intensity (ii).

Ichnocoenoses

The Greenhorn and Niobrara fms contain strata that range from unbioturbated to highly bioturbated, with six ichnocoenoses identified within both formations. Both formations include ichnocoenoses that characterize dysoxic to oxic conditions, in addition to the anoxic-interpreted unbioturbated strata.

Greenhorn Fm Ichnocoenoses.—GFI 1 records a phase of benthic oxygenated conditions with limited surface or shallow endobenthic activity (following Seilacher 1977; Ekdale et al. 1984a) during periods of unfavorable conditions (e.g., Ekdale and Mason 1988; Martin 2004;

Dashtgard et al. 2015). GFI 2 records a longer period of oxygenated conditions in marlstone depositional time than GFI 1. The presence of *Chondrites* and *Planolites* in GFI 2 suggest that benthic oxygen conditions were in the lower dysoxic zone (Bromley and Ekdale 1984; Ekdale and Mason 1988; Savrda 1998a).

The ichnogenera of GFI 3 indicate that benthic oxygenation ranges from lower to mixed lower and upper dysoxic conditions (Savrda and Bottjer 1986, 1989a; Ekdale and Lewis 1991). The complex spreiten trace fossil, *Zoophycos,* also is interpreted to characterize greater stability of the seafloor (Miller 1991; Richiano 2015). GFI 3 contains an ichnological suite nearly identical to GFI 4, with the exception of *Palaeophycus* in GFI 4. The addition of *Palaeophycus*––interpreted as praedichnia and dominichia—indicates that the endobenthic oxygenation and environmental stability is greater than interpreted in GFI 1–3 (Pemberton and Frey 1984; Uchman and Tchoumatchenco 2003).

GFI 5 records an oxic benthic environment, based on the appearance of *Thalassinoides* in limestone with *Palaeophycus*, *Planolites*, and *Zoophycos* (Bromley and Frey 1974; Ekdale 1992). *Thalassinoides* is the trace fossil with largest diameter (up to 22 mm) in these strata, and represents either the appearance of the largest tracemaker or increased benthic stability (sedimentation or oxygenation) such that existing tracemakers could grow larger and construct large burrow networks (Linström 1979; Savrda 1998a). Sediment mixing and piping into the underlying sediments by *Teichichnus* and *Zoophycos* in GFI 5 indicate that organisms exploited nutrients in the underlying sediment deeper than previous ichnocoenoses (Ekdale and Mason 1988; Kotake 1989; Baas et al. 1998). Strata that contain GFI 6 also record a less oxygenated depositional environment than GFI 5, based on the appearance of rare, shallow *Chondrites* and *Helminthopsis* (e.g., Gong and Droser 2001). Ichnogeneric variability in GFI 6 suggest a shift from *Thalassinoides*-dominated dominichia to fodinichnia-dominated behaviors where selective mining occurs as sediment becomes more argillaceous.

Niobrara Fm. Ichnocoenoses.—NFI 1 is nearly identical to GFI 1, and both likely represent similar periods of lower dysoxic to near anoxic conditions favorable to low oxygen-tolerant organisms (e.g., Uchman 2003). NFI 2 strata record periods when benthic conditions were appropriate for limited colonization by fodinichnia—*Chondrites*, *Helminthopsis*, and *Zoophycos*. The relatively low ichnodiversity, low abundance of ichnogenera, and absence of pervasively disrupted sedimentary layers reinforces that the benthic environment was in the lower dysoxic range (e.g., Savrda 1998b; Gingras et al. 2011).

NFI 3 and NFI 4 consist of higher ichnodiversity (≥8 ichnogenera) and better bioturbated (ii3–5) marlstone to argillaceous limestone strata than NFI 1 and NFI 2. Ichnogenera of NFI 3 (i.e., *Chondrites*, *Helminthopsis*, *Planolites*, *Teichichnus*, and *Zoophycos*) represents an increase in diversity of fodinichnia. NFI 4 is similar to NFI 3; however, NFI 4 does not have *Chondrites* and *Helminthopsis*, and has added fodinichnia of *Asterosoma* and *Rosselia* and the dominichia-praedichnia *Palaeophycus*. An increase in ethological diversity is consistent with benthic stability and well-oxygenated conditions (e.g., Crimes and Droser 1992; Gingras et al. 2011). Associations of *Planolites*, *Teichichnus,* and *Zoophycos*, among *Asterosoma*, *Palaeophycus*, and *Rosselia*, are commonly are found in the Cruziana and Zoophycos ichnofacies (Frey and Howard 1982; Ekdale and Mason 1988; MacEachern et al. 1999).

Both NFI 5 and NFI 6 consist of lower ichnodiversity, but record periods of the highest interpreted benthic oxygenation (Savrda 1998b). NFI 5, dominated by *Planolites* and *Teichichnus*, records a continued increase and/or an increase in the duration of benthic oxygenation relative to NFI 1–4, such that the organisms burrowed and reworked sediments to ii5–6 (e.g., Savrda and Bottjer 1986; Savrda 1998b). *Teichichnus* are interpreted as fodinichnia and are characteristic of the dysoxic to oxic benthic oxygenation (e.g., Loughlin and Hillier 2010). NFI 5 sediments likely were deposited in near oxic conditions that allowed tracemakers to pipe lime-mud into deeper sediments while burrowing for nutrients, based on pervasive *Planolites* and *Teichichnus* and high ii. NFI 6 contains larger *Planolites* and *Teichichnus* co-occuring with *Thalassinoides* in highly bioturbated (average ii5–6) limestone strata and is the only Niobrara Fm ichnocoenosis with *Thalassinoides* (Fig. 9F). NFI 6 likely represents the most oxic conditions in the Niobrara Fm, and likely the most stable benthic conditions. .

Ichnofacies

Both formations contain the Nereites, Zoophycos and Cruziana, ichnofacies. The most abundant is the Nereites Ichnofacies, which occurs in GFI 1 and NFI 1. These unbioturbated to cryptobioturbated strata occur in zones that were deposited under dysoxic to anoxic conditions. The abundance of Nereites Ichnofacies strata in OAE 2 and OAE 3 zones are 32% and 18%, respectively. This is consistent with previous interpretations of laminated marlstone lithofacies that contain GFI 1 and NFI 1 and represent times when tracemakers were influenced by high sedimentation rate or lower dysoxic to anoxic benthic oxygenation as the primary physicochemical controls (Savrda 1998a, 1998b).

Zoophycos Ichnofacies are found in GFI 2, GFI 3, NFI 2, and NFI 3 (see Table 6). Strata containing the Zoophycos Ichnofacies were likely deposited during lower to upper dysoxic benthic conditions. Argillaceous limestone to limestone lithofacies that contain GFI and NFI 4–6, are interpreted to represent the Cruziana ichnofacies, and record the highest ichnodiversity and bioturbation intensities. In general, strata with elevated carbonate content include trace-fossils with larger diameters and increasing bioturbation intensity. Compared to the other ichnofacies, the higher ichnodiversity and larger burrow diameters indicate that the depositional environment was more oxygenated than during times where other ichnofacies were present.

Controls on Trace Fossils and Ichnofacies

Organism behaviors and the resulting trace fossils are influenced by multiple physicochemical controls (Fig. 13A) (e.g., Hasiotis and Platt 2012, and references therein). Many studies have sought to identify the primary physicochemical controls and how their fluctuations influence benthic biota and trace fossils (see Table 2). The general three primary controls in marine environments have been identified as sedimentation rate, depositional energy, and oxygenation (Hasiotis and Platt 2012). The fourth primary physicochemical control varies (i.e., nutrient input, medium, salinity, hydrology, turbidity) between depositional environments and conditions (e.g. Hasiotis and Platt 2012).

Previous studies of the Greenhorn and Niobrara fms attributed changes in ichnocoenoses to fluctuations in benthic oxygenation (Savrda and Bottjer 1986; Savrda 1998a, 1998b). This study also interprets the primary control to be benthic oxygenation based on the ichnogenera present and bioturbation intensities (Fig. 13B). Of the 17 ichnogenera described, *Chondrites*, *Helminthopsis*, and *Zoophycos* are common in dysoxic environments, whereas *Asterosoma*, *Rhizocorallium, Teichichnus,* and *Thalassinoides* are common in oxic conditions (e.g., Savrda and Bottjer 1986; Ekdale and Mason 1988; Uchman et al. 2013b). This study identifies media as the fourth physicochemical control based on the trends of higher ii, deeper burrow penetration depth, and increasing ichnodiversity that follow lithofacies changes from marlstone to limestone (e.g., Weimer 1970; Savrda 1998a, 1998b; Locklair and Sageman 2008). The Lincoln Limestone Mbr and upper half of the Bridge Creek Limestone Mbr, both within the Greenhorn Fm, consist of marlstone to argillaceous limestone lithofacies that are mostly unburrowed (see Fig. 8, 10 A). These lithofacies record episodes of anoxic to dysoxic benthic conditions, whereas the lower part of the Bridge Creek Limestone with GFI 2–6 and ii2–6 in limestone lithofacies record periods of relatively higher benthic oxygenation. In the Niobrara Fm (see Fig. 9, 11A), unburrowed to burrowed (ii1–3) marlstone lithofacies of the Smoky Hill Chalk Mbr record periods of lower dysoxic to anoxic benthic oxygenation (NFI 1–3). Moderately to well-bioturbated (ii3–6), argillaceous limestone and limestone lithofacies of the Fort Hays Limestone Mbr are consistent with upper dysoxic to fully oxic benthic conditions (NFI 4–6) (Savrda 1998b).

Ichnological record of OAE 2 and OAE 3

Strata deposited during each OAE show varying amounts of ichnodiversity and bioturbation intensity, indicating that both periods were not continuously anoxic throughout. The OAE 2 interval has a greater abundance, diversity, and bioturbation intensity than OAE 3.

OAE 2.—Strata for OAE 2 record a diverse assemblage of trace fossils (GFI 1–6) and range of bioturbation (ii1–6), suggesting that this event was not wholly anoxic in this region of the WIS (Fig. 10A,B). Strata deposited during interpreted anoxic conditions represent 41% of the OAE 2 interval, with the reminder interpreted as deposited during lower dysoxic (26%) and upper dysoxic to oxic (33%) conditions, based on the bioturbation intensities and ichnocoenoses present. Critically, this presence of bioturbated strata indicates that nearly 60% of the OAE 2 strata in this area of WIS were deposited during dysoxic to oxic conditions, and rather than in anoxic settings.

Changes in ichnodiversity, morphological size, and benthic oxygenation have been identified in European OAE 2 intervals (i.e., Rodríguez-Tovar et al. 2009b; Rodríguez-Tovar and Uchman 2011; Uchman et al. 2013b). Each of those studies identified a pre-OAE 2 level of bioturbation, and followed by a decrease in ichnodiversity and tiering (i.e., penetration depth) up section into the OAE 2 strata, where unbioturbated to sparsely bioturbated strata occur with punctuated periods of dysoxic to oxic conditions identified by increased ichnodiversity and bioturbation. In OAE 2 strata of the Bedic Flysch Basin (SE Spain), Rodríguez-Tovar and Uchman (2011) identified *Chondrites* and *Trichichnus* in dysoxic shale and rare *Planolites* and *Thalassinoides* in colonization surfaces on sandy turbidites. Approximately 2,000 km away, in the Bohemian Basin, Uchman et al. (2008) identified bioturbated Cretaceous OAE 2 strata in the Barnasiówka area and interpreted the strata to be deposited under dysoxic conditions, which constituted ~ 45% of the OAE 2 zone. In the same basin, Uchman et al. (2013a) interpreted the oxic benthic conditions during OAE 2 deposition of strata in the Sztolnia area (Polish Outer Carpathians). They characterized a repeated, high-ichnodiversity Zoophycos Ichnofacies for 93% of OAE 2 strata. Variation of ichnologic responses to OAE 2 in different basins (i.e., WIS vs. Bedic Flysch vs. Bohemian basins) likely are due to different oceanographic controls (i.e., mixing depths, water-mass differences, water depth; Erbacher et al. 2001; Bowman and Bralower 2005; Pearce et al. 2009).

OAE 3.—The wholly OAE 3 containing Smoky Hill Chalk Mbr has less bioturbation (ii) and lower diversity of trace fossil than the underlying Fort Hays Limestone Mbr; however the abundance and distribution of bioturbation indicates that OAE3 was not completely anoxic. This member contains low-diversity ichnocoenoses and low bioturbation intensities throughout.

Dysoxic to oxic conditions were dominant (77% of the member), with 76% occurring during interpreted dysoxic periods and 1% deposited during oxic intervals. The relatively common occurrence of *Planolites*, *Teichichnus*, and *Zoophycos* throughout the OAE 3 zone corroborates the hypothesis that this period was not continuously anoxic (cf. Wagreich 2009, 2012; Locklair et al. 2011). The abundance of bioturbation in these strata indictes that OAE 3 was less anoxic in the WIS than previously interpreted.

Bioturbation in Cyclicity

Bioturbation is not directly controlled by Milankovitch Cycles; these orbital cycles influence the Earth's climate. The resulting climatic fluctuations (e.g., glacial to interglacial periods), again, do not directly influence bioturbation as their scales are orders of magnitude greater than organismal lifespans. The local to regional fluctuations in relative sea-level and oceanographic processes that change in the different climatic regimes are the processes that affect the physicochemical controls on bioturbation (e.g., Hasiotis and Platt 2012). These nesting variations from orbital dynamics through global climatic shift, and then the local physicochemical conditions, sets-up a hierarchy of orbital to climatic to regional oceanographic processes. Organisms that exist on/in the seafloor at any one time, only react to their local conditions; as such, a singular trace fossil or a bioturbated bed cannot record orbital cyclities. Variation in presence and strength (i.e., probability) of Milankovitch cyclicities does not correlate directly with presence or absence of high bioturbation intensities or diverse ichnocoenoses (see Fig. 10–12).

Trace fossils are morphologically and behaviorally conservative (Seilacher, 1977), and the changes in trace fossil assemblages with time, within a similar depositional environment, can be used to identify larger-scale physicochemical changes through depositional time. Du Vivier et al. (2014) identified pulses of oceanic water from small-scale transgressions that moved oxygenated, pre-Atlantic waters into the WIS during OAE 2. These oceanic pulses, or similar events, may directly influence higher amounts of bioturbation and ichnodiversity observed in the OAE intervals of the Greenhorn and Niobrara fms. Any trace fossils presence, or a single bioturbation intensity does not identify orbital signals, it is the alternation or variation of trace fossil characteristics (ichnocoenoses, bioturbation intensity of a series of endobenthic fauna and their communities) that record local physicochemical condition changes, and identify orbital cycles.

Strata that contain high variability in ii or ichnocoenoses are interpreted to show one to all three Milankovitch cycles. In the Bridge Creek Limestone Mbr, the basal 10 m have abundant ii3–6 fluctuations that exhibit strong obliquity and weaker precessional signals (Fig. 10C). The lower portion of this section contains OAE 2 strata where ii variations display additional precessional signals. The Niobrara Fm does not contain strata with a similar amount and intensity of ii variability. There is a lower diversity of Milankovitch signals identified from ichnocoenoses data where fluctuations between ichnocoenoses are observed. In both ichnocoenoses and ii, zones of small-scale changes of ii or ichnocoenoses generally show the greatest diversity of signals (Figs. 10–11). This trend is most clear in the Greenhorn Fm where the upper half of the Bridge Creek Mbr contains all three major signals in both the low variation ii and ichnocoenoses data (Fig. 10C,D). Ichnocoenoses of the upper part of Fort Hays Mbr show a similar trend (Fig. 11).

The Milankovitch cycles of the Greenhorn and Niobrara fms include up to three eccentricities, three obliquities, and five precessional signals in total (Tables 9–10). By convention, however, short eccentricity and precession have four commonly accepted component cycles and obliquity has one (see Table 4). Multiple eccentricity and processionals are expected; however, identification of three obliquity signals was not (i.e., 24–25 m, Bridge creek Limestone ichnocoenoses; see Table 4 Fig. 10D). At any one point, 4 or 5 eccentricity or precessional harmonics are not identified, but 4–5 different frequencies can be identified across the formation. Signal strength was gradational between cycles where dual obliquity signals occurred (e.g., 5–15 m level in Fig. 10C). From the Bridge Creek Limestone Mbr, this study identifies E1–2, E4, O, and P1–4, whereas Sageman et al. (1998) identified O2, O1, P2, and P1 cyclicities (see Table 11). Sageman et al. (1998) identified approximately 4 eccentricity, 4–5 obliquity, and 3–10 precessional signals in each 5-m interval in the Bridge Creek Limestone Mbr. They identified O2, P2, and P1 cyclicities in ichnocoenoses, and O2, O1, P2, and P1 cycles in burrow-diameter data.

Cycles identified from ii and ichnocoenoses are generally similar (e.g., Figure 9, Fort Hays Limestone Mbr 17–21 m) in that strata that contain high diversity ichnocoenoses (i.e., GFI 4–6, NFI 4–6) are highly bioturbated (ii4–6), and the converse trend (low diversity with low bioturbation intensities) is also generally true. These related proxies show similar cycles, although ii does not identify as many cycles compared to ichnocoenoses (Tables 10, 11). This difference in interpreted cyclicities is not due to the physicochemical controls at the time of deposition directly; rather higher bioturbation intensities lead to homogenization of previous burrowed intervals and sedimentary structures. Whereas, strata with higher ichnodiversities and less well bioturbated strata preserve the greater cycle diversity due to less homogenization of sedimentary structures.

Ideal precessional signals are preserved in the top and bottom of the Bridge Creek Mbr, with near-precessional signals throughout. Ichnocoenoses signals are the least similar between 8–12 m where one strong obliquity to precessional signal is dominant; whereas the Sageman et al. (1998) results contain abundant precessional signals in related strata. The ii cyclicities, which did not have an equivalent test by Sageman et al. (1998), identified E1, E4, obliquity, and P3 signals (see Table 13; Fig. 10). Comparing ideal cycle frequencies (Table 8) and identified cycles (Table 9, 11) indicate that bioturbation modifies the sedimentologic record such that the identified frequencies do not match the expected frequencies; however, benthic oxygenation was not prolonged enough to homogenize the sediments and remove all potential sedimentologic character.

Cyclostratigraphic studies on these formations (Ma et al., 2014; Locklair and Sageman, 2008) have proposed sedimentation rates to be between 0.75–5.85 cm/ka, this study using those as min/max controls found best-fit rates of 0.9–2 cm/ka. Using these ranges, the duration of anoxia for zones with no bioturbation could be up to 30 ky for sections of 30 cm in thickness. In contrast, most individual bioturbated zones do not exceed 10 cm in thickness; however, this does not likely equate to the potential sedimentation time of 11 ky (using an average 1.1 cm/ka) as endobenthic foraminifera have been shown to move up to 3 cm/hr (Geslin et al 2004). Changes in orbital cyclicity do not directly translate into the presence or intensity of bioturbation. The effect of orbital position on climate is the driving force on glacial changes and resulting climatic influences on sea level and sedimentation changes and their respective benthic conditions, and thusly a biotic response is not to the orbital changes, but to the resulting physicochemical changes (Du Vivier et al. 2014).

Orbital driven physicochemical changes are not on the scale of an organismal lifespan, but become resolvable on the community scale; where climatic condition changes can affect regional to local benthic oxygenation or sedimentation rates. Within the Bounds Core Greenhorn fm, a majority of GFI 5 are often followed up-section by GFI 6; thus, suggesting a shift from a well-oxygenated condition in the GFI5 zone to the dysoxic low-diversity and low-II GFI6 zone above. These paired ichnocoenoses occur over 6–10 cm or potential 8–11 ky; however, that depositional timeframe does not adequately describe the organismal timespan to create bioturbation of cm/hr. Based on the factor of time differences between sedimentation rates and lifespan of the endobenthic community, this study indicates that the periods of oxygenation allowed for benthic occupation and occasional deep bioturbation through OAE events; but, were not of a sufficient duration to allow the endobenthic community to fully homogenize the sediments during their existence.

CONCLUSIONS

This study identified 17 ichnogenera from the Greenhorn and Niobrara fms of the AMOCO Rebecca K. Bounds #1 Well core, and described six ichnocoenoses for each formation. Trace fossils and ichnocoenoses occur throughout the two formations, including strata that contain the duration of OAE 2 and OAE 3 events. The abundance of interspersed bioturbated beds within OAE 2 and OAE 3 strata (60% and 65%, by thickness of the Greenhorn and Niobrara fms respectively) with similar ichnodiversity and bioturbation intensity to pre-OAE strata is inconsistent the hypothesis of continuous anoxic conditions across and within the seafloor. We interpret both formations as having benthic oxygenation for the primary physicochemical control of the benthic trace-making biota. Variations in benthic oxygenation with sedimentation rate and media type are the factors that influenced which ichnocoenosis was present in each lithofacies. Generally, limestone strata in both formations include the Cruziana Ichnofacies, whereas argillaceous limestone to marlstone strata are representative of the Zoophycos Ichnofacies and marlstone strata contain the Nereites Ichnofacies.

Harmonics consistent with Milankovitch cyclicities were determined from the sedimentary patterns of bioturbation intensity (i.e., ii) and ichnocoenoses. Analysis of ichnocoenoses data patterns produced all three major orbital cycles, with the greater ichnodiversity ichnocoenoses producing all three cycles and the lower diversity ichnocoenoses commonly not producing precessional signals. Bioturbation intensity also produced all three Milankovitch cycles. Low ii strata produced the highest number of cycles, whereas high ii strata identified produced only one signal in any interval, commonly obliquity.

Vertical variation in both ichnocoenoses and ii produced multiple harmonic signals suggesting that all scales of these harmonic signals have an effect on the physicochemical controls across multiple temporal scales. Periods of limited variability suggest a stable benthos, whereas high variability strata suggest dynamic changes in benthic conditions. This study found a greater abundance and a longer duration of orbital cyclicities preserved in sedimentary patterns defined by bioturbation, than cycles identified using isotopes in previous studies on correlated strata. Furthermore, this study shows the presence, and abundance, of bioturbation through commonly considered anoxic OAE strata. As cyclicity in the sedimentary record has been well noted since G.K. Gilbert, we have shown that ichnological characteristics provide another proxy to use in the identification and correlation of astronomical cycles.

ACKNOWLEDGEMENTS

We thank Dave Laflen (retired) from the KGS for assistance with the Bounds core. We recognize the Kansas Interdisciplinary Carbonates Consortium for funding portions of this research. We thank Dr. Gene Rankey, and the **I**chno**B**io**G**eo**S**ciences Research Group for discussions of an earlier manuscript version.

REFERENCES

ANDERSON, D.M., 2001, Attenuation of millennial-scale events by bioturbation in marine sediments: Paleoceanography, v. 16, p. 352–357.

ARTHUR, M.A., DEAN, W.E., AND PRATT, L.M., 1988, Geochemical and climatic effects of increased marine organic carbon burial at the Cenomanian/Turonian boundary: Nature, v. 335, p. 714–717.

ARTHUR, M.A., AND SAGEMAN, B.B., 1994, Marine black shales: Depositional mechanisms and environments of ancient deposits: Annual Review of Earth and Planetary Sciences, v. 22, p. 499–551.

ARTHUR, M.A., AND SCHLANGER, S.O., 1979, Cretaceous "oceanic anoxic events" as causal factors in development of reef-reservoired giant oil fields: American Association of Petroleum Geologists Bulletin, v. 63, p. 870–885.

ARTHUR, M.A., SCHLANGER, S.O., AND JENKYNS, H.C., 1987, The Cenomanian-Turonian Ocean Anoxic Event II. Palaeoceanographic controls on organic-matter production and preservation, *in* Brooks, J., and Fleet, A., eds., Marine Petroleum Source Rocks: Geological Society of London Special Publication 26, p. 401–420.

BAAS, J.H., SCHÖNFELD, J., AND ZAHN, R., 1998, Mid-depth oxygen drawdown during Heinrich events: evidence from benthic foraminiferal community structure, trace-fossil tiering, and benthic $\delta^{13}C$ at the Portuguese Margin: Marine Geology, v. 152, p. 25–55.

BASAN, P.B., and SCOTT, R.W., 1979, Morphology of Rhizocorallium and associated traces from the lower Cretaceous Purgatoire Formation, Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 28, p. 5–23.

BENNINGER, L.K., ALLER, R.C., COCHRAN, J.K., AND TUREKIAN, K.K., 1979, Effects of biological sediment mixing on the 210 Pb chronology and trace metal distribution in a Long Island Sound sediment core: Earth and Planetary Science Letters, v. 43, p. 241–259.

BLAKEY, R., 2014, Colorado Plateau Geosystems, Arizona, USA.

BOWMAN, A.R., AND BRALOWER, T.J., 2005, Paleoceanographic significance of high-resolution carbon isotope records across the Cenomanian–Turonian boundary in the Western Interior and New Jersey coastal plain USA: Marine Geology, v. 217, p. 305–321.

BROMLEY, R.G., 1975, Trace fossils at omission surfaces, *in* Frey, R.W., ed., The study of trace fossils, p. 399–428.

BROMLEY, R.G., 1996, Trace fossils. Biology, Taphonomy and Application: Chapman and Hall, London, 361 p.

BROMLEY, R.G., AND EKDALE, A.A.,1984, *Chondrites*: a trace fossil indicator of anoxia in sediments: Science, v. 224, p. 872–874.

BROMLEY, R.G., AND FREY, R.W., 1974, Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*: Bulletin of the Geological Society of Denmark, v. 23, p. 311–335.

CLUFF, R.M., 1980, Paleoenvironment of the New Albany Shale Group (Devonian-Mississippian) of Illinois: *Journal of Sedimentary Research*, v.50, p. 767–780.

COCCIONI, R., AND GALEOTTI, S., 1993, Orbitally induced cycles in benthonic foraminiferal morphogroups and trophic structure distribution patterns from the Late Albian "Amadeus Segment" (Central Italy): Journal of Micropalaeontology, v. 12, p. 227–239.

CRIMES, T.P. 1975, The stratigraphical significance of trace fossils, *in* Frey, R.W., ed., The study of trace fossils, p. 109–130.

CRIMES, P.T., AND DROSER, M.L., 1992, Trace fossils and bioturbation: the other fossil record: Annual Review of Ecology and Systematics, v. 23, p. 339–360.

DASHTGARD, S.E., GINGRAS, M.K., and PEMBERTON, S.G., 2008, Grain-size controls on the occurrence of bioturbation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 257, p. 224–243.

DASHTGARD, S.E., SNEDDEN, J.W., AND MACEACHERN, J.A., 2015, Unbioturbated sediments on a muddy shelf: Hypoxia or simply reduced oxygen saturation?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 425, p. 128–138.

DEAN, W.E., AND ARTHUR, M.A., eds., 1998a, Stratigraphy and paleoenvironments of the Cretaceous Western Interior Seaway, USA: SEPM, Concepts in Sedimentology and Paleontology, no. 6, 255 p.

DEAN, W.E., AND ARTHUR, M.A., 1998b, Cretaceous Western Interior Seaway drilling project: an overview, *in* Dean, W.E., and Arthur, M.A., eds., Stratigraphy and paleoenvironments of the Cretaceous Western Interior Seaway, USA: SEPM, Concepts in Sedimentology and Paleontology, no. 6, p. 1–10.

DE GILBERT, J.M., EKDALE, A.A., 2002, Ichnology of a restricted epicontinental sea, Arapien Shale, Middle Jurassic, Utah, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 183, p. 275–286.

DE VLEESCHOUWER, D., DA SILVA, A.C., BOULVAIN, F., CRUCIFIX, F., and CLAEYS, P., 2012, Precessional and half-precessional climate forcing of Mid-Devonian monsoon-like dynamics: Climate of the Past, v. 8, p. 337–351.

DROSER, M.L., AND BOTTJER, D.J., 1986, A semiquantitative field classification of ichnofabric: Journal of Sedimentary Research, v. 56, p. 558–559.

DU VIVIER, A. D., SELBY, D., SAGEMAN, B. B., JARVIS, I., GRÖCKE, D. R., AND VOIGHT, S., 2014, Marine ^{187}Os/^{188}Os isotope stratigraphy reveals the interaction of volcanism and ocean circulation during Oceanic Anoxic Event 2: Earth and Planetary Science Letters, v. 389, p. 23–33.

EKDALE, A.A., 1992, Muckraking and mudslinging: the joys of deposit feeding, *in* MAPLES, C.G., AND WEST, R.R., eds., Trace Fossils: Paleontological Society Short Course 5, p. 145–171.

EKDALE, A.A., BROMLEY, R.G., PEMBERTON, S.G., 1984a, Ichnology: The use of trace fossils in sedimentology and stratigraphy: Society of Economic Paleontologists and Mineralogists, Tulsa, 371 pp.

EKDALE, A.A., AND LEWIS, D.W., 1991, The New Zealand *Zoophycos* revisited: morphology, ethology, and paleoecology: Ichnos, v. 1, p. 183–194.

EKDALE, A.A., AND MASON, T.R., 1988, Characteristic trace-fossil associations in oxygen-poor sedimentary environments: Geology, v. 16, p. 720–723.

EKDALE, A.A., MULLER, L.N., AND NOVAK, M.T., 1984b, Quantitative ichnology of modern pelagic deposits in the abyssal Atlantic: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 45, p. 189–223.

ELDER, W.P., GUSTASON, E.R., AND SAGEMAN, B.B., 1994, Correlation of basinal carbonate cycles to nearshore parasequences in the Late Cretaceous Greenhorn seaway, Western Interior U.S.A.: Geological Society of America Bulletin, v. 106, p. 892–902.

ERB, M. P., JACKSON, C. S., BROCCOLI, A. J., LEA, D. W., VALDES, P. J., CRUCIFIX, M., AND DINEZIO, P. N., 2018, Model evidence for a seasonal bias in Antarctic ice cores: Nature Communications, v. 9, no. 1, p. 1361.

ERBA, E. AND PREMOLI-SILVA, I., 1994, Orbitally driven cycles in trace-fossil distribution from the Piobbico Core (Late Albian, Central Italy), *in* de Boer, P.L., and Smith, D.G., eds., Orbital Forcing and Cyclic Sequences: Blackwell Publishing Ltd., Oxford, UK. p. 211–225.

ERBACHER, J., HUBER, B.T., NORRIS, R.D., AND MARKEY, M., 2001, Increased thermohaline stratification as a possible cause for an ocean anoxic event in the Cretaceous period: Nature, v. 409, p. 325–327.

FREY, R.W., 1970, Trace fossils of Fort Hays Limestone Member of Niobrara Chalk (Upper Cretaceous), west-central Kansas: University of Kansas Paleontological Contributions, Art. 53 (Cretaceous 2), 41 p.

FREY, R.W., 1972, Paleoecology and depositional environment of Fort Hays Limestone Member, Niobrara Chalk (Upper Cretaceous), west-central Kansas: University of Kansas Paleontological Contributions, Art. 58 (Cretaceous 3). 72 p.

FREY, R.W., AND HOWARD, J.D., 1982, Trace fossils from the upper Cretaceous of the Western Interior: potential criteria for facies models: The Mountain Geologist, v. 19, p. 1–10.

FRIEDRICH, O., NORRIS, R.D., AND ERBACHER, J., 2012, Evolution of middle to Late Cretaceous oceans – A 55 my record of Earth's temperature and carbon cycle: Geology, v. 40, p. 107–110.

GESLIN, E., HEINZ, P., AND HEMBLEBEN, C., 2004, Behaviour of *Bathysiphon* sp. and *Siphonammina bertholdii* under controlled oxygen conditions in laboratory: implications for bioturbation phenomenon, in: BUBIK M., AND KAMINSKI M.A., eds, Proceedings of the Sixth International Workshop on Agglutinated Foraminifera. Grzybowski Foundation Special Publication 8, p. 105–118.

GILBERT, G.K., 1895, Sedimentary measurement of Cretaceous time: The Journal of Geology, v. 3, p. 121–127.

GINGRAS, M.K., MACEACHERN, J.A., AND DASHTGARD, S.E., 2011, Process ichnology and the elucidation of physico-chemical stress: Sedimentary Geology, v. 237, p. 115–134.

GINGRAS, M.K., MACEACHERN, J.A., and DASHTGARD, S.E., 2012, The potential of trace fossils as tidal indicators in bays and estuaries: Sedimentary Geology, v. 279, p. 97–106.

GINGRAS, M.K., PEMBERTON, S.G., and SMITH, M., 2015, Bioturbation: reworking sediments for better or worse: Oilfield Review v.26, p. 46–58.

GOLDRING, R., 1993, Ichnofacies and facies interpretation: PALAIOS, v. 8, p. 403–405.

GONG, Y., AND DROSER, M.L., 2001, Periodic anoxic shelf in the Early-Middle Ordovician transition: ichnosedimentologic evidence from west-central Utah, USA: Science in China Series D: Earth Sciences, v. 44, p. 979–989.

GORDON, W.A., 1975, Physical controls in marine biotic distribution in the Jurassic Period. in: ROSS, C.A., ed, Paleogeographic provinces and provinciality: Society of Economic Paleontologists and Mineralogists, Special Publication 21, p. 136–147.

HASIOTIS, S.T., AND PLATT, B.F., 2012, Exploring the sedimentary, pedogenic, and hydrologic factors that control the occurrence and role of bioturbation in soil formation and horizonation in continental deposits: An integrative approach: The Sedimentary Record, v. 10, p. 4–9.

HATTIN, D.E., 1971, Widespread, synchronously deposited, burrow-mottled limestone beds in Greenhorn Limestone (Upper Cretaceous) of Kansas and southeastern Colorado: American Association of Petroleum Geologists Bulletin., v. 55, p. 412–431.

HATTIN, D.E., 1982, Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (upper Cretaceous) of the type area, western Kansas: Kansas Geological Survey Bulletin 225, 108 p.

HATTIN, D.E., 1985, Distribution and significance of widespread, time-parallel pelagic limestone beds in the Greenhorn Limestone (Upper Cretaceous) of the Central Great Plains and Southern Rocky Mountains, *in* Pratt, L.M., Kauffman, E.G., and Zelt F.B., eds., Fine-Grained Deposits and Biofacies of the Cretaceous Western Interior Seaway: Evidence of Cyclic Sedimentary Processes: SEPM Field Trip Guidebook No. 4, p. 28–37.

HAUCK, T.E., DASHTGARD, S.E., PEMBERTON, S.G., and GINGRAS, M.K., 2009, Brackish-water ichnological trends in a microtidal barrier island–embayment system, Kouchibouguac National Park, New Brunswick, Canada: Palaios v. 24, p. 478–496.

HEARD, T.G., PICKERING, K.T., and CLARK, J.D., 2014, Ichnofabric characterization of a deep-marine clastic system: a subsurface study of the Middle Eocene Ainsa System, Spanish Pyrenees: Sedimentology, v. 61, p. 1298–1331.

HEPP, D.A., MÖRZ, T., AND GRÜTZNER, J., 2006, Pliocene glacial cyclicity in a deep-sea sediment drift (Antarctic Peninsula Pacific Margin): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 231, p. 181–198.

HOWARD, J.D., Sedimentology and trace fossils, 1978, Sedimentology and trace fossils. *in* Basan, P.B., ed., Trace fossil concepts, SEPM Short Course 5, p. 13–47.

HOWARD, J.D., and FREY., R.W., 1973, Characteristic physical and biogenic sedimentary structures in Georgia estuaries: AAPG Bulletin, v. 57, p. 1169–1184.

HOVIKOSKI, J, LEMISKI, R., GINGRAS, M., PEMBERTON, S.G., and MACEACHERN, J.A., 2008, Ichnology and sedimentology of a mud-dominated deltaic coast: Upper Cretaceous Alderson Member (Lea Park Fm), western Canada: Journal of Sedimentary Research, v. 78, p. 803–824.

HUTSON, W.H., 1980, Bioturbation of deep-sea sediments: Oxygen isotopes and stratigraphic uncertainty: Geology, v. 8, p. 127–130.

IZUMI, K., 2013, Geochemical composition of fecal pellets as an indicator of deposit-feeding strategies in the trace fossil *P hymatoderma*: Lethaia, v. 46, p. 496–507.

JACKSON, A.M., HASIOTIS, S.T., and FLAIG, P.P., 2016, Ichnology of a paleopolar, river-dominated, shallow marine deltaic succession in the Mackellar Sea: the Mackellar Formation (Lower Permian), central Transantarctic Mountains, Antarctica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, p. 266–291.

JENKYNS, H.C., 2003, Evidence for rapid climate change in the Mesozoic–Palaeogene greenhouse world: Philosophical Transactions of the Royal Society, v. 361, p. 1885–1916.

KOTAKE, N., 1989, Paleoecology of the *Zoophycos* producers: Lethaia, v. 22, p. 327–341.

KOTLARCZYK, J., and UCHMAN, A., 2012, Integrated ichnology and ichthyology of the Oligocene Menilite Formation, Skole and Subsilesian nappes, Polish Carpathians: A proxy to oxygenation history: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 331 p. 104–118.

KORUS, J.T., and FIELDING, C.R., 2015, Enhanced bioturbation on the down-drift flank of a Turonian asymmetrical delta: Implications for seaway circulation, river nutrients and facies models: Sedimentology, v. 62, p. 1899–1922.

KUHNT, W., LUDERER, F., NEDERBRAGT, S., THUROW, J. AND WAGNER, T., 2005, Orbital-scale record of the late Cenomanian–Turonian oceanic anoxic event (OAE-2) in the Tarfaya Basin (Morocco): International Journal of Earth Sciences, v. 94, p. 147–159.

LA FERRIERE, A.P., HATTIN, D.E., AND ARCHER, A.W., 1987, Effects of climate, tectonics, and sea-level changes on rhythmic bedding patterns in the Niobrara Formation (Upper Cretaceous), US Western Interior: Geology, v. 15, p. 233–236.

LAMY, F., HEBBELN, D. AND WEFER, G., 1998, Late Quaternary precessional cycles of terrigenous sediment input off the Norte Chico, Chile (27.5 S) and palaeoclimatic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 141, p. 233–251.

LASKAR, J., FIENGA, A., GASTINEAU, M. AND MANCHE, H., 2011, La2010: a new orbital solution for the long-term motion of the Earth: Astronomy and Astrophysics, v. 532, p. A89.

LAURIN, J., ČECH, S., ULIČNÝ, D., ŠTAFFEN, Z., and SVOBODOVÁ, M., 2014, Astrochronology of the Late Turonian: implications for the behavior of the carbon cycle at the demise of peak greenhouse: Earth and Planetary Science Letters, v. 394, p. 254–269.

LECKIE, R.M., BRALOWER, T.J., AND CASHMAN, R., 2002, Oceanic anoxic events and plankton evolution: biotic response to tectonic forcing during the mid-Cretaceous: Paleoceanography, v. 17, p. 623–642.

LEONOWICZ, P., 2015, Ichnofabrics of shallow-marine mudstone, the result of changing environmental conditions: an example from the Middle Jurassic ore-bearing clay from southern Poland: Facies, v. 61, p. 1-21.

LEUSCHNER, D.C., SIROCKO, F., GROOTES, P.M., AND ERLENKEUSER, H., 2002, Possible influence of *Zoophycos* bioturbation on radiocarbon dating and environmental interpretation: Marine Micropaleontology, v. 461, p. 111–126.

LEVIN, L.A., 2003, Oxygen minimum zone Benthos: Adaptation and community response to hypoxia: Oceanography and Marine Biology, v. 41, p. 1–45.

LOCKLAIR, R.E., AND SAGEMAN, B.B., 2008, Cyclostratigraphy of the Upper Cretaceous Niobrara Formation, western interior, USA: a Coniacian–Santonian orbital timescale: Earth and Planetary Science Letters. v. 269, p. 540–553.

LOCKLAIR, R.E, SAGEMAN, B.B., AND LERMAN, A., 2011, Marine carbon burial flux and the carbon isotope record of Late Cretaceous (Coniacian–Santonian) Oceanic Anoxic Event III: Sedimentary Geology, v. 235, p. 38–49.

LOUGHLIN, N.J., AND HILLIER, R.D., 2010, Early Cambrian *Teichichnus*-dominated ichnofabrics and palaeoenvironmental analysis of the Caerfai Group, Southwest Wales, UK: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 297, p. 239–251.

LOWERY, C.M., 2015, Oceanographic controls on the expression of Cretaceous oceanic anoxic events in the Western Interior Sea: Unpublished PhD Dissertation. University of Massachusetts, Amherst, 165 p.

MA, C., MEYERS, S.R., SAGEMAN, B.B., SINGER, B.S., AND JICHA, B.R., 2014, Testing the astronomical time scale for Oceanic Anoxic Event 2, and its extension into Cenomanian strata of the Western Interior Basin (USA): Geological Society of America Bulletin, v. 126, p. 974–989.

MACEACHERN, J.A., STELCK, C.R., AND PEMBERTON, S.G., 1999, Marine and marginal marine mudstone deposition: paleoenvironmental interpretations based on the integration of ichnology, palynology and foraminiferal paleoecology, *in* Bergman, K.M., and Snedden, J.W., eds., Isolated Shallow Marine Sand Bodies: Sequence Stratigraphic and Sedimentologic Interpretation: SEPM, Special Publication 64, p. 205–225.

MARTIN, D.J., AND SHIMADA, K., 2008, Lithostratigraphy and depositional environment of the Lincoln Limestone Member of the Greenhorn Limestone (Upper Cretaceous) in Russell County, Kansas, with special reference to the basal beds: Transactions of the Kansas Academy of Science, v. 111, p. 79–92.

MARTIN, K.D., 2004, A re-evaluation of the relationship between trace fossils and dysoxia: Geological Society of London, Special Publications, v. 228, p. 141–156.

MERRIAM, D.F., 1963, The Geologic History of Kansas: Kansas Geological Survey Bulletin 162. 317 p.

MEYERS, S.R., 2014, astrochron: An R Package for Astrochronology. http://cran.r-project.org/package=astrochron

MEYERS, S.R., AND SAGEMAN, B.B., 2007, Quantification of deep-time orbital forcing by average spectral misfit: American Journal of Science, v. 307, p. 773–792.

MEYERS, S.R., SAGEMAN, B.B. AND ARTHUR, M.A., 2012, Obliquity forcing of organic matter accumulation during Oceanic Anoxic Event 2: Paleoceanography, v. 27, PA3212.

MEYERS, S.R., SAGEMAN, B.B., HINNOV, L.A., 2001, Integrated quantitative stratigraphy of the Cenomanian-Turonian Bridge Creek Limestone Member using evolutive harmonic analysis and stratigraphic modeling: Journal of Sedimentary Research, v. 71, p. 627–643.

MEYERS, S.R., SAGEMAN, B.B., AND PAGANI, M., 2008, Resolving Milankovitch: Consideration of signal and noise: American Journal of Science, v. 308, p. 770–786.

MIERAS, B.L., SAGEMAN, B.B., and KAUFFMAN, E.G., 1993, Trace fossil distribution patterns in Cretaceous facies of the Western Interior Basin, North America: Geological Association of Canada Special Paper, v. 39, p. 585–620.

MILLER, H.W., JR., 1958, Stratigraphic and paleontologic studies of the Niobrara Formation (Cretaceous) in Kansas: Unpublished Ph.D. dissertation, The University of Kansas., Lawrence, 181 p.

MILLER, M.F., 1991, Morphology and paleoenvironmental distribution of Paleozoic *Spirophyton* and *Zoophycos*: implications for the Zoophycos ichnofacies: PALAIOS, v. 6, p. 410–425.

MITCHELL, J.M., 1976, An overview of climatic variability and its causal mechanisms: Quaternary Research, v. 6, p. 481–493.

MOLINIE, A.J., OGG, J.G., 1992. Milankovitch cycles in Upper Jurassic and Lower Cretaceous radiolarites of the equatorial Pacific: spectral analysis and sedimentation rate curves, *in* Larson, R.L., Lancelot, Y., et al. eds., Proc. Ocean Drilling Program, Sci. Res., v. 129, p. 529–547.

PEARCE, M.A., JARVIS, I., AND TOCHER, B.A., 2009, The Cenomanian–Turonian boundary event, OAE 2 and palaeoenvironmental change in epicontinental seas: New insights from the dinocyst and geochemical records: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 280, p. 207–234.

PEMBERTON, S.G. AND FREY R.W., 1984, Ichnology of storm-influenced shallow marine sequence: Cardium Formation (Upper Cretaceous) at Seebe, Alberta, *in* Stott, D.F., and Glass, D.J., eds., The Mesozoic of Middle North America: Canadian Society of Petroleum Geologists Memoir No. 9, p. 281–304.

PEMBERTON, S.G., MACEACHERN, J.A., GINGRAS, M.K., AND SAUNDERS, T.D., 2008, Biogenic chaos: Cryptobioturbation and the work of sedimentologically friendly organisms: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 270, p. 273–279.

PEMBERTON, S.G., SPILA, M., PULHAM, A.J., SAUNDERS, T., MACEACHERN, J.A., ROBBINS, D., AND SINCLAIR, I.K., 2001, Ichnology and sedimentology of shallow to marginal marine systems: Ben Nevis and Avalon Reservoirs, Jeanne d'Arc Basin: Geological Association of Canada Short Course Notes 15, 343 p.

POORE, A.G., CAMPBELL, A.H., COLEMAN, R.A., EDGAR, G.J., JORMALAINEN, V., REYNOLDS, P.L., SOTKA, E.E., STACHOWICZ, J.J., TAYLOR, R.B., VANDERKLIFT, M.A. AND EMMETT-DUFFY, J., 2012, Global patterns in the impact of marine herbivores on benthic primary producers: Ecology letters, v. 15, p. 912–922.

R Core Team, 2015, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. R 3.2.2 Fire Safety.

REY, O., SIMO, J.A., AND LORENTE, M.A., 2004, A record of long-and short-term environmental and climatic change during OAE 3: La Luna Formation, Late Cretaceous (Santonian–early Campanian), Venezuela: Sedimentary Geology, v. 170, p. 85–105.

RHOADS, D.C., and MORSE, J.W., 1971, Evolutionary and ecologic significance of oxygen-deficient marine basins: Lethaia v. 4, p. 413–428.

RICHIANO, S., 2015, Environmental factors affecting the development of the Zoophycos ichnofacies in the Lower Cretaceous Río Mayer Formation (Austral Basin, Patagonia): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 439, p. 17–26.

RODRÍGUEZ-TOVAR, F.J., 2014, Orbital climate cycles in the fossil record: From semidiurnal to million-year biotic responses: Annual Review of Earth and Planetary Sciences, v. 42, p. 69–102.

RODRÍGUEZ-TOVAR, F.J., AND UCHMAN, A., 2011, Ichnological data as a useful tool for deep-sea environmental characterization: a brief overview and an application to recognition of small-scale oxygenation changes during the Cenomanian-Turonian anoxic event: Geo-Marine Letters, v. 31, p. 525–536.

RODRÍGUEZ-TOVAR, F.J., UCHMAN, A., AND MARTÍN-ALGARRA, A., 2009a, Oceanic Anoxic Event at the Cenomanian-Turonian boundary interval (OAE 2): ichnological approach from the Betic Cordillera, southern Spain: Lethaia, v. 42, p. 407–417.

RODRÍGUEZ-TOVAR, F.J., UCHMAN, A., MARTÍN-ALGARRA, A., AND O'DOGHERTY, L., 2009b, Nutrient spatial variation during intrabasinal upwelling at the Cenomanian-Turonian oceanic anoxic event in the westernmost Tethys: an ichnological and facies approach: Sedimentary Geology, v. 215, p. 83–93.

SAGEMAN, B.B., AND JOHNSON, C.C., 1985, Stratigraphy and paleobiology of the Lincoln Limestone Member, Greenhorn Limestone, Rock Canyon Anticline, Colorado, *in* PRATT, L.M., KAUFFMAN, E.G., ZELT, F.B., eds., Fine-Grained Deposits and Biofacies of the Cretaceous Western Interior Seaway: Evidence of Cyclic Sedimentary Processes: Society of Economic Paleontologists and Mineralogists, Tulsa, OK, p. 100–109.

SAGEMAN, B.B., MEYERS, S.R., AND ARTHUR, M.A., 2006, Orbital time scale and new C-isotope record for Cenomanian-Turonian boundary stratotype: Geology, v. 34, p. 125–128.

SAGEMAN, B.B., RICH, J., ARTHUR, M.A., BIRCHFIELD, G.E., AND DEAN, W.E., 1997, Evidence for Milankovitch periodicities in Cenomanian-Turonian lithologic and geochemical cycles, Western Interior USA: Journal of Sedimentary Research, v. 67, p. 286–302.

SAGEMAN, B.B., RICH, J., ARTHUR, M.A., DEAN, W.E., SAVRDA, C.E., AND BRALOWER, T.J., 1998, Multiple Milankovitch cycles in the Bridge Creek Limestone (Cenomanian-Turonian), Western Interior Basin, *in* Dean, W.E., and Arthur, M.A., eds, Stratigraphy and Paleoenvironments of the Cretaceous Western Interior Seaway, USA: SEPM Concepts in Sedimentology and Paleontology, v. 6, p. 153–171.

SAGEMAN, B.B., SINGER, B.S., MEYERS, S.R., SIEWERT, S.E., WALASZCZYK, I., CONDON,D.J., JICHA, B.R., OBRADOVICH, J.D., AND SAWYER, D.A., 2014, Integrating 40Ar/39Ar, U-Pb, and astronomical clocks in the Cretaceous Niobrara Formation, Western Interior Basin, USA: Geological Society of America Bulletin, v. 126, p. 956–973.

SANTARELLI, A., BRINKHUIS, H., HILGEN, F.J., LOURENS, L.J., VERSTEEGH, G.J.M., AND VISSCHER, H., 1998, Orbital signatures in a Late Miocene dinoflagellate record from Crete (Greece): Marine Micropaleontology, v. 33, p. 273–297.

SAVRDA, C.E., 1995, Ichnologic applications in paleoceanographic, paleoclimatic, and sea-level studies: PALAIOS, v. 10, p. 565–577.

SAVRDA, C.E., 1998a, Ichnology of the Bridge Creek Limestone: evidence for temporal and spatial variations in paleo-oxygenation in the Western Interior Seaway, *In* Dean, W.E. and Arthur, M.A., eds., Stratigraphy and Paleoenvironments of the Western Interior Seaway, USA: SEPM Concepts in Sedimentology and Paleontology, no. 6, p. 127–136

SAVRDA, C.E., 1998b, Ichnocoenoses in the Niobrara Formation: Implications for Benthic Oxygenation Histories, *in* Dean, W.E., and Arthur, M.A., eds., Stratigraphy and Paleoenvironments of the Western Interior Seaway, USA: SEPM Concepts in Sedimentology and Paleontology, no. 6, p. 137–151.

SAVRDA, C.E., 2008, *Zoophycos*, Systematic stratigraphic leaking, and lamella stratigraphy, *in* Harries, P.J., ed., High-Resolution Approaches in Stratigraphic Paleontology: Springer Press, Amsterdam, p. 129–148.

SAVRDA, C.E., AND BOTTJER, D.J., 1986, Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters: Geology, v. 14, p. 3–6.

SAVRDA, C.E., AND BOTTJER, D.J., 1989a, Anatomy and implications of bioturbated beds in black shale sequences: Examples from the Jurassic Posidonienschiefer (southern Germany): PALAIOS, v. 4, p. 330–342.

SAVRDA, C.E., AND BOTTJER, D.J., 1989b, Trace-fossil model for reconstructing oxygenation histories of ancient marine bottom waters: application to Upper Cretaceous Niobrara Formation, Colorado: Palaeogeography. Palaeoclimatology. Palaeoecology., v. 74, p. 49–74.

SAVRDA, C.E., AND BOTTJER, D.J., 1994, Ichnofossils and ichnofabrics in rhythmically bedded pelagic/hemi-pelagic carbonates: recognition and evaluation of benthic redox and scour cycles, *in* Deboer, P., and Smith, D., eds., Orbital Forcing and Cyclic Sequences: International Association of Sedimentologists, Special Publication 19, p. 195–210.

SAVRDA, C.E., LOCKLAIR, R.E., HALL, J.K., SADLER, M.T., SMITH, M.W., AND WARREN, J.D., 1998, Ichnofabrics, ichnocoenoses, and ichnofacies implications of an upper cretaceous tidal-inlet sequence (Eutaw formation, central Alabama): Ichnos, v. 6, p. 53–74.

SCHIFFELBEIN, P., 1984, Effect of benthic mixing on the information content of deep-sea stratigraphic signals: Nature, v. 311, p. 651–653.

SCHIEBER, J., 2003, Simple gifts and buried treasures—implications of finding bioturbation and erosion surfaces in black shales: The Sedimentary Record v.1, p. 4–8.

SCHLANGER, S.O., AND JENKYNS, H.C., 1976, Cretaceous anoxic events: Causes and consequences: Netherlands Journal of Geosciences, v. 55, p. 179–184.

SCHLANGER, S.O., ARTHUR, M.A., JENKYNS, H.C., AND SCHOLLE, P.A., 1987, The Cenomanian–Turonian oceanic anoxic event I. Stratigraphy and distribution of organic carbon–rich beds and the marine δ13C excursion, *in* Brooks, J., and Fleet, A.J., eds., Marine Petroleum Source Rocks: Geological Society of London Special Publication 26, p. 371–399.

SCOTT, G.R., AND COBBAN, W.A., 1964, Stratigraphy of the Niobrara Formation at Pueblo, Colorado: U.S. Geological Survey Professional Paper 454-L, 30 p.

SCOTT, R.W., FRANKS, P.C., EVETTS, M.J., BERGEN, J.A., AND STEIN, J.A., 1998, Timing of mid-Cretaceous relative sea level changes in the western interior: Amoco No. 1 Bounds core, *in* Dean, W.E., and Arthur, M.A., eds., Stratigraphy and Paleoenvironments of the Cretaceous

Western Interior Seaway, USA: SEPM Concepts in Sedimentology and Paleontology 6, p. 11–34.

SEILACHER, A., 1967, Bathymetry of trace fossils: Marine geology v. 5, p. 413–428.

SEILACHER, A., 1977, Evolution of trace fossil communities, *in* Hallam, A., ed., Patterns of Evolution as Illustrated by the Fossil Record: Developments in Paleontology and Stratigraphy, no. 4, p. 359–376.

SEILACHER, A., 1978, Use of trace fossil assemblages for recognizing depositional environments, *in* Basan, P.B. ed., Trace Fossil Concepts: SEPM Short Course, v. 5, p. 167–181.

SETHI, P.S., AND LEITHOLD, E.L., 1994, Climatic cyclicity and terrigenous sediment influx to the early Turonian Greenhorn Sea, southern Utah: Journal of Sedimentary Research, v. 64, p. 26–39.

SMITH, C.R., POPE, R.H., DEMASTER, D.J., AND MAGAARD, L., 1993, Age-dependent mixing of deep-sea sediments: Geochimica et Cosmochimica Acta, v. 57, p. 1473–1488.

STOTT, L., POULSEN, C., LUND, S., and THUNELL, R., 2002, Super ENSO and global climate oscillations at millennial time scales: Science, v. 5579, p. 222–226.

TESSIN, A., HENDY, I., SHELDON, N., AND SAGEMAN, B., 2015, Redox-controlled preservation of organic matter during OAE 3 within the Western Interior Seaway: Paleoceanography, v. 30, p. 702–717.

TRAUTH, M.H., SARNTHEIN, M., AND ARNOLD, M., 1997, Bioturbational mixing depth and carbon flux at the seafloor: Paleoceanography, v. 12, p. 517–526.

TWITCHETT, R.J., 1999, Palaeoenvironments and faunal recovery after the end-Permian mass extinction: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 154, p. 27–37.

TYSON, R.V., AND PEARSON, T.H., 1991, Modern and ancient continental shelf anoxia: an overview: Geological Society, London, Special Publications, v. 58, p. 1–24.

UCHMAN, A., 2003, Trends in diversity, frequency and complexity of graphoglyptid trace fossils: evolutionary and palaeoenvironmental aspects: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 123–142.

UCHMAN, A., BĄK, K., AND RODRÍGUEZ-TOVAR, F.J., 2008, Ichnological record of deep-sea palaeoenvironmental changes around the Oceanic Anoxic Event 2 (Cenomanian–Turonian boundary): an example from the Barnasiówka section, Polish Outer Carpathians: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 262, p. 61–71.

UCHMAN, A., RODRÍGUEZ-TOVAR, F.J., MACHANIEC, E., AND KĘDZIERSKI, M., 2013a, Ichnological characteristics of Late Cretaceous hemipelagic and pelagic sediments in a submarine high around the OAE-2 event: A case from the Rybie section, Polish Carpathians: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 370, p. 222–231.

UCHMAN, A., RODRÍGUEZ-TOVAR, F. J., AND OSZCZYPKO, N., 2013b, Exceptionally favourable life conditions for macrobenthos during the Late Cenomanian OAE 2 event: Ichnological record from the Bonarelli Level in the Grajcarek Unit, Polish Carpathian: Cretaceous Research, v. 46, p. 1–10.

UCHMAN, A., AND TCHOUMATCHENCO, P., 2003, A mixed assemblage of deep-sea and shelf trace fossils from the Lower Cretaceous Valanginian Kamchia Formation in the Troyan region, central Fore-Balkan, Bulgaria: Annales Societatis Geologorum Poloniae, v. 73, p. 27–34.

UCHMAN, A., and WETZEL, A., 2011, Deep-sea ichnology: the relationships between depositional environment and endobenthic organisms, *in* Hüneke, H., Mulder, T., eds., Deep-Sea Sediments: Developments in Sedimentology, v. 63. p. 517–556.

UCHMAN A., AND WETZEL A., 2012, Deep-sea fans, *in*, Knaust D., and Bromley R., eds., Trace Fossils as indicators of Sedimentary Environments, Development in Sedimentology: Elsevier, 64, 643–671.

VAN KREVELD, S.M, . SARNTHEIN, H., ERLENKEUSER, P., GROOTES, S., JUNG, M., NADEAU, J., PFLAUMANN, U., and VOELKER, A., 2000, Potential links between surging ice sheets, circulation changes, and the Dansgaard-Oeschger cycles in the Irminger Sea 60–18 kyr: Paleoceanography, v. 15, p. 425–442.

VIRTASALO, J.J., LEIPE, T., MOROS, M., and KOTILAINEN, AT., 2011, Physicochemical and biological influences on sedimentary-fabric formation in a salinity and oxygen-restricted semi-enclosed sea: Gotland Deep, Baltic Sea: Sedimentology, v. 58, p. 352–375.

WAGNER, T., SINNINGHE-DAMSTE, J. S., HOFMANN, P., AND BECKMANN, B., 2004, Euxinia and primary production in Late Cretaceous equatorial Atlantic surface waters fostered orbitally driven formation of marine black shales: Paloceanography, v. 19, PA3009.

WAGREICH M., 2009, Coniacian‑Santonian oceanic red beds and their links to Oceanic Anoxic Event 3, *in* HU, X., WANG, C., SCOTT, R.W., WAGREICH, M., AND LANSA, L., eds., Cretaceous Oceanic Red Beds: Stratigraphy, Composition, Origins, and Paleoceanographic and Paleoclimatic Significance: Society for Sedimentary Geology Special Publication 91, p. 235–242.

WAGREICH, M., 2012, OAE 3 regional Atlantic organic carbon burial during the Coniacian–Santonian: Climate of the Past, v. 8, p. 1447–1455.

WAGREICH, M., HU, X., AND SAGEMAN, B., 2011, Causes of oxic–anoxic changes in Cretaceous marine environments and their implications for Earth systems—An introduction: Sedimentary Geology, v. 235, p. 1–4.

WALTHAM, D., 2015, Milankovitch period uncertainties and their impact on cyclostratigraphy: Journal of Sedimentary Research, v. 85, p. 990–998.

WATKINS, D.K., 1989, Nannoplankton productivity fluctuations and rhythmically-bedded pelagic carbonates of the Greenhorn Limestone (Upper Cretaceous): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 74, p. 75–86.

WEIMER, R.J., 1970, Rate of deltaic sedimentation and intrabasin deformation, Upper Cretaceous of the Rocky Mountain region, *in* Morgan, J.P., ed., Deltaic Sedimentation, Modern and Ancient: Society of Economic Paleontologists and Mineralogists Special Paper No. 15, p. 270–292.

WETZEL, A., 1984, Bioturbation in deep-sea fine-grained sediments: influence of sediment texture, turbidite frequency and rates of environmental change: Geological Society, London, Special Publications, v. 15, p. 595–608.

WETZEL, A., 2008, Recent bioturbation in the deep South China Sea: a uniformitarian ichnologic approach: PALAIOS, v. 23, p. 601–615.

WETZEL, A., 2015, Burrows storing an otherwise lost sedimentary record: Ichnology: Papers from ICHNIA III: Geological Association of Canada, v. 9, p. 211–224.

WETZEL, A., and AIGNER, T., 1986, Stratigraphic completeness: Tiered trace fossils provide a measuring stick: Geology, v. 14, p. 234–237.

WHEATCROFT, R.A., 1990, Preservation potential of sedimentary event layers: Geology, v. 18, p. 843–845.

WHEATCROFT, R.A., and DRAKE, D.E., 2003, Post-depositional alteration and preservation of sedimentary event layers on continental margins, I. The role of episodic sedimentation: Marine Geology, v. 199, p. 123–137.

TABLES

***TABLE 1**—Primary proxies and where they have been used to identify orbital cyclicities.*

Primary Proxy	**Location**	**Cyclicity identified**	**Example Reference**
%Organic Carbon	Western Interior Seaway	Obliquity, Precession	SAGEMAN ET AL. 1998
% $CaCO_3$	Western Interior Seaway	Eccentricity, Obliquity, Precession	SAGEMAN ET AL. 1998
Nannofossil Abundance %	Western Interior Seaway	Eccentricity, Obliquity, Precession	SAGEMAN ET AL. 1998
Radiolarite	IOPD Site 800 Legg 129, Pacific Ocean	Eccentricity	MOLINIE AND OGG 1992
$\delta^{18}O$	Irminger Sea Core, Greenland	Dansgaard-Oeschger (~1.5 kyr)	VAN KREVLED ET AL. 2000
Mg/Ca paleothermometry	Core MD98-2181, off-shore Indonesia	10 ky interstatial Super-ENSO	STOTT ET AL. 2002
Organic Carbon Weight %	Proto North-Atlantic Transect	Obliquity	MEYERS ET AL. 2012
Magnetic Susceptibility	Devonian Dinant Synclinorium	Precession, Half-Precession	DE VLEESCHOUWER ET AL. 2012
$\delta^{13}C_{carb}$	BCH-1 Core, Bohemian Cretaceous Basin, central Europe	Obliquity	LAURIN ET AL. 2014
Intensity of Bioturbation	Asina Basin, Spain	Eccentricity, Obliquity	HEARD ET AL. 2008
Bioturbation Presence-Absence	South China Sea	Eccentricity, Obliquity, Precession	RODRÍGUEZ-TOVAR ET AL. 2011
Bioturbation Density	Umbrian–Marchean Basin, Italy	Eccentricity, Obliquity	ERBA AND PRIMOLI-SILVA 1994
Maximum Burrow Diameter	Western Interior Seaway	Obliquity, Precession	SAGEMAN ET AL. 1998
Oxygen-Related Ichnocoenoses	Western Interior Seaway	Obliquity, Precession	SAGEMAN ET AL. 1998

TABLE 2—Physicochemical parameters and their relative influence on bioturbation.

Potential Environmental Influence		**Bioturbation effects or affect on sediments**	**Selected References**
Sedimentation Rate	Increase	Temporary large (>10 cm) sedimentation events may reduce bioturbation, increase fugichnia, and lead to preservation of event sedimentation; smaller increases may not significantly affect the burrowing populations	Howard 1972; Wheatcroft and Drake 2003; Wetzel 2015
	Decrease	Bioturbation will homogenize sediments and may increase tiering and burrow penetration	Howard 1972; Wetzel 1984; Anderson 2001
Benthic Oxygenation	Increase	An increase from low O_2 produces larger traces and deeper tiering	Bromley 1975; Ekdale and Mason 1988; Kotlarczyk and Uchman 2012
	Decrease	Reduction in ichnodiversity, tiering, and size	Rhoads and Morse 1971; Savrda and Bottjer 1986; Levin 2003
Media Size (Grain Size)	Increase	Decrease in intensity of bioturbation	Seilacher 1967; Crimes 1975; Dashtgard et al. 2008
	Decrease	Increasing burrow intensity and diversity, unless sediments become thixotropic	Howard and Frey 1973; Bromley 1996; Hovikoski, et al. 2008
Salinity	Increase	Decrease in ichnodiversity, intensity, and tiering	Seilacher 1977; de Gilbert and Ekdale 2002; Virtasalo et al. 2011
	Decrease	Change in ichnodiversity to polyhaline conditions, then reduction of ichnodiversity, burrowing intensity and tiering in meso- and oligohaline settings	Seilacher 1978; Hauck et al. 2009; Jackson et al. 2016
Depositional Energy	Increase	Reduction in complexity and transition to filter feeding strategies from deposit feeding	Seilacher 1978; Pemberton and Frey 1984; Mieras et al., 1993
	Decrease	Increase in trace-fossil complexity and deposit-feeding burrow behaviors: fodinichnia, pascichnia, and agrichnia	Seilacher 1978;Uchman and Wetzel 2011; Gingras et al. 2012
Nutrient Input	Increase	Increase of bioturbation intensity, tiering, and depth	Wetzel and Aigner 1986; Izumi 2013; Korus and Fielding 2015
	Decrease	Reduction in bioturbation intensity, depth, tiering; increase in trace-fossil complexity	Basan and Scott 1979; de Gilbert and Ekdale 2002; Leonowicz 2015

T**ABLE **3—*Benthic oxygenation system used in this study (modified from Savrda 1998a).*

Oxygen ml/l	**Savrda and Bottjer (1987)**	**Tyson and Pearson (1991)**	**This Study**
8.0 – 2.0	Aerobic	Oxic	Oxic
2.0 – 1.0	Dysaerobic	Moderate Dysoxic	Upper Dysoxic
1.0 – 0.5	Exaerobic	Severe to Extreme Dysoxic	Lower Dysoxic
0.5 – 0	Anaerobic	Suboxic to Anoxic	Anoxic

***TABLE 4**—Evolutive harmonic analysis target spectra (modified from Waltham 2015).*

Periods (kyr)	**Tested Periods (kyr)**	**Interpreted cyclicity driver**
405.6 ± 2.4	405.6	Long Eccentricity
130.8 ± 2.9	130.8	Short Eccentricity
123.9 ± 2.6	123.9	Short Eccentricity
98.9 ± 1.5	98.9	Short Eccentricity
94.9 ± 1.4	94.9	Short Eccentricity
40.977 ± 0.086	40.98	Obliquity
23.678377 ± 0.000013	23.68	Climate Precession
22.3722 ± 0.0074	22.37	Climate Precession
19.103 ± 0.056	19.10	Climate Precession
18.950 ± 0.055	18.95	Climate Precession

***TABLE 5**—Descriptions of ichnogenera in the Greenhorn and Niobrara fms of the Rebecca K. Bounds #1 Well core and their associated lithofacies and formations.*

Ichnogenera	Description	Lithofacies	Formation
Arenicolites	U-shaped burrow with paired shaft rugose shaft texture; 2-mm separation between from 2–6 mm in diameter	Limestone	Greenhorn
Asterosoma	Horizontal, concentrically laminated, alternating lithologies; burrow 4.26–11.11 mm in diameter, average 7.6 mm	Limestone, Argillaceous Limestone	Both
Chondrites	Cylindrical to semicylindrical downward branching burrows that occur in clusters with different fill material than the surrounding matrix; burrows from 0.14–2.78 mm in diameter, average 1.4 mm	Marlstone, Argillaceous Limestone, Limestone	Both
Cosmorhaphe	Small meandering burrow system with lighter halo surrounding burrow fill; 0.86–7.91 mm in diameter, average of 2.98 mm	Limestone	Both
Diplocraterion	Vertical burrow, dumbbell-shaped in cross-section, internal spreiten visible with multiple shafts on one side; 23.7 mm to outside of shafts, 35 mm wide at middle of spreiten, 5 mm shaft diameter	Limestone	Niobrara
Helminthopsis	Abundant small burrows with darker fill than surrounding matrix, appear as commas and dashes; 0.31–0.7 mm in diameter, average 0.52 mm	Marlstone	Both
Ophiomorpha	Horizontal to subhorizontal burrow with pelleted lining, one example with pellets of 1 mm diameter and burrow diameter of 5 mm	Argillaceous Limestone	Niobrara
Palaeophycus	Subhorizontal to subvertical lined burrows with similar fill to the surrounding matrix; 1.53–3.9	Limestone, Argillaceous Limestone	Both

	mm in diameter, average 2.64 mm		
Planolites	Horizontal to subhorizontal burrows with different fill than surrounding matrix, cylindrical to subcylindrical in cross section; 1.86–7.2 mm in diameter, average of 3.77 mm	Limestone, Argillaceous Limestone, Calcareous Mudstone, Marlstone	Both
Rhizocorallium	Paired horizontal to obliquely horizontal shafts with spreiten; 4.8 mm in diameter, 8 mm separation, 30.5 mm overall width	Limestone, Argillaceous Limestone	Both
Rosselia	Vertically oriented cylindrical burrow with bulbous upper portion and thinner cylindrical shaft below, bulb contains concentric layers, can show a repeat of the smaller cylindrical base extending up from a lower bulb; lower part 4.37 mm in diameter, bulb up to 26.39 mm.	Argillaceous Limestone	Both
Schaubcylindrichnus	Bundle of possibly joined calcareous walled tubular burrows; burrow diameter ≤ 7.9 mm	Marlstone to Argillaceous Limestone	Niobrara
Taenidium	Unlined unbranching horizontal to subhorizontal burrow with meniscate backfill; 1.89–6.67 mm in diameter , average 3.72 mm	Argillaceous Limestone to Limestone	Both
Teichichnus	Vertical to subvertical spreiten, both intrusive and retrusive spreiten were present; 2.39–8.97 mm in diameter, average 5.97 mm	Limestone, Argillaceous Limestone, Calcareous Mudstone, Marlstone	Both
Thalassinoides	Unlined cylindrical boxwork burrownetwork, with horizontal and vertical branching; 2.41–23.2 mm in diameter, average 9.56 mm	Limestone, Argillaceous Limestone,	Both
Trichichnus	Downward penetrating pyritized burrow; shaft 1 mm wide, total burrow length up to 10.6 mm	Limestone	Niobrara

Zoophycos	Vertical, subvertical, to dominantly horizontal spreiten, curved to chevron internal spreiten; 2.45–7.62 mm in diameter, average 5.5 mm	Limestone, Argillaceous Limestone, Marlstone, Calcareous Mudstone	Both

***TABLE 6*—Ichnocoenoses, ichnofacies, and associated lithofacies for the Greenhorn and Niobrara fms of the Amoco Rebecca K. Bounds #1 Well core. Trace fossils in alphabetical order.*

Ichnocoenoses	**Greenhorn Formation**	**Niobrara Formation**	**Ichnofacies**
1 – Cryptoturbation	Cryptobioturbation in marlstone and calcarenite facies	Cryptobioturbation in marlstone facies	Nereites
2 - Chondrites	*Chondrites*, *Planolites*, and *Teichichnus* in marlstone facies	*Chondrites*, *Helminthopsis*, cryptobioturbation with accessory *Trichichnus*, and *Zoophycos* in marlstone facies	Zoophycos
3 – Planolites-Teichichnus-Zoophycos	*Planolites*, *Teichichnus*, and rare *Zoophycos* in marlstone and argillaceous marlstone facies	*Chondrites*, *Helminthopsis*, *Planolites*, *Teichichnus*, *Zoophycos* and accessory cryptobioturbation in marlstone to argillaceous limestone facies	
4 – Planolites-Palaeophycus	*Palaeophycus*, *Planolites*, *Teichichnus*, and *Zoophycos* in argillaceous limestone and limestone facies	*Planolites*, *Teichichnus*, *Zoophycos*, and accessory *Asterosoma*, *Palaeophycus*, *Rosselia* in argillaceous limestone to limestone facies	Cruziana
5 –Teichichnus-Planolites	*Palaeophycus*, *Planolites*, *Teichichnus*, *Thalassinoides*, and secondary *Zoophycos* in limestone facies	*Planolites*, *Teichichnus*, and secondary *Zoophycos* in argillaceous limestone to limestone facies	
6 - Thalassinoides	Large *Asterosoma*, *Planolites*, *Teichichnus*, *Thalassinoides*, and accessory *Chondrites* and *Helminthopsis* in limestone facies	*Large Planolites*, *Teichichnus*, *Thalassinoides*, and *Zoophycos* in limestone facies	

***TABLE 7**—Average-spectral-misfit-derived orbital frequencies for ichnological data within the Greenhorn and Niobrara fms. Frequency ranges set dashed vertical lines in figures 10–12.*

Interpreted Cyclicity Driver	Set Cycle Period (kyr)	Greenhorn Frequency (c/m)	Niobrara Frequency (c/m)	Frequency range (c/m)
Long Eccentricity	405.6	0.28	0.21	Greenhorn: 0–1.5 Niobrara: 0–1
Short Eccentricity	130.8	0.88	0.67	
Short Eccentricity	123.9	0.93	0.70	
Short Eccentricity	98.9	1.16	0.88	
Short Eccentricity	94.9	1.21	0.92	
Obliquity	40.98	2.80	2.13	Greenhorn: 1.5–3 Niobrara: 1–2.5
Climate Precession	23.68	4.85	3.68	Greenhorn: 3–6 Niobrara: 2.5–5
Climate Precession	22.37	5.13	3.89	
Climate Precession	19.1	6.01	4.56	
Climate Precession	18.95	6.06	4.60	

***TABLE 8**—Observed cyclicities in the Greenhorn Fm with ≥ 80% probability for each orbital proxy.*

Formation	**Member**	**Proxy**	**Interval (m)**	**Eccentricity Scale**	**Obliquity Scale**	**Precession Scale**
				Frequency (cycles per meter)		
Greenhorn	Bridge Creek Limestone	Ichnocoenoses	20–25	0.35, 0.5, **0.85**	1.75, 2.5, 2.65	3, 3.25, 3.5, 4.35, **5.15**, **6**
			15–20	0.5, 0.65, 0.75, **1.15**	1.65, 1.75, 1.85, 2.25, 2.65, **2.75**	
			10–15	0.35, 0.5, **0.85**, 1, **1.15**	1.75, 2.35, 2.5, **2.75**	3
			5–10	0.35, **0.85**, **1.15**, **1.25**	1.85, 2.35, 2.5, **2.85**	3.25, 3.5, 3.65, 3.85, 4.25
			0–5	0.35, 0.65, **1.15**	1.5, 1.65, 1.8, 2.35, 2.5, **2.85**	3.35, 3.5, 4.25, **4.75**, 5, 5.35
		Ichnofabric Index	20–25	0.5, 1.35	2.75	3, 3.15, 3.25, 4, 5
			15–20	0.35, 0.6, **1.25**	1.6, 1.75, 1.8, 2, 2.25, **2.85**	3, 3.6, 3.8, 4.15, 4.5, **5.15**
			10–15	0.35, **0.8**, 1.35	2.15, 2.35, 2.65, **2.8**	3.15, 3.85
			5–10		1.35, 1.85, 2.35	
			0–5	0.5, 0.75, 1, **1.15**, 1.35	1.66, 2.25, 2.5, **2.85**	3.25, 3.6, 4.15, 4.6
	Lincoln Limestone	Ichnofabric Index	0–5	0.4, 0.7, **0.9**, 1.45	2	3.15, 3.7, 4.6, 5.25
		Ichnocoenoses	0–5	0.75, **0.95**, 1.3	1.85, 2.25	3.63, 4.65, 5.25

TABLE 9*—Observed cyclicities in the Niobrara Fm with ≥ 80% probability for each orbital proxy..*

Formation	**Member**	**Proxy**	**Interval (m)**	**Eccentricity**	**Obliquity**	**Precession**
				Frequency (cycles per meter)		
Niobrara	Smoky Hill Chalk	Ichnocoenoses	15+	0.5, **0.75**, 1, 1.25, 1.5, 1.65		
			10–15	0.5, **0.75**, 1, 1.25, 1.5, 1.65	2, **2.15**, 2.75	
			5–10	0.5, **0.65**, **0.75**, 1, 1.25, 1.5	2, 2.75	
			0–5	0.35, 0.5, **0.85**, 1, 1.5, 1.85	2, 2.5, 3	
		Ichnofabric Index	15+	0.35, **0.65**, **0.75**, 1, 1.15, 1.25, 1.35, 1.5, 1.65, 1.75, 1.85	2	
			10–15	0.35, 0.5, **0.85**, 1, 1.15, 1.25, 1.5	2.75, 2.85	
			5–10	0.5, **0.75**, **0.85**, 1, 1.15, 1.25, 1.35, 1.5		
			0–5	0.35, 0.5, **0.65**, **0.85**, 1, 1.15, 1.5	2.25, 3	
	Fort Hays Limestone	Ichnocoenoses	15+	0.35, 0.5, **0.75**, 1, 1.15, 1.5, 1.75	2, 2.25, 2.5, 3, 3.5	4.15, **4.5**, 5.15
			10–15	0.5, **0.65**, **0.75**, **0.85**, 1, 1.35	3	**3.85**, 4.25, 4.75, 5.25
			5–10	0.35, 0.5, **0.85**, 1, 1.15, 1.25, 1.35, 1.75	2.5, 2.75, 3, 3.15, 3.25	4.25, 4.75, 5.25
			0–5	1, 1,65, 1,85	2, **2.15**	
		Ichnofabric Index	15+	0.35, 0.5, **0.65**, 1, 1.15, 1.25, 1.75	2, 2.25, 2.35, 2.5, 3.65, 3.75	
			10–15	**0.65**, **0.75**, **0.85**, 1, 1.15, 1.25, 1.75, 1.85	2.5	
			5–10	0.35, **0.75**, **0.85**, 1.25, 1.75, 1.85	2.25, 2.65	
			0–5	**0.65**, **0.85**, 1.75	2.35, 2.75, 3.5	4.15

Table 10*—Ideal and identified frequencies (cycles/meter; c/m) for each Milankovitch cycle in the Greenhorn and Niobrara fms.*

Interpreted Cyclicity Driver	**Cycle Period (kyr) (from Waltham 2015)**	**Ideal Greenhorn Frequency (c/m)**	**Identified Greenhorn Frequency(s) (c/m)**	**Ideal Niobrara Frequency (c/m)**	**Identified Niobrara Frequency(s) (c/m)**
Long Eccentricity	405.6	0.28	–	0.21	–
Short Eccentricity (E4)	130.8	0.88	0.8, 0.85	0.67	0.65
Short Eccentricity (E3)	123.9	0.93	0.9, 0.95	0.70	0.75
Short Eccentricity (E2)	98.9	1.16	1.15	0.88	0.85
Short Eccentricity (E1)	94.9	1.21	1.25	0.92	–
Obliquity	40.98	2.80	2.75, 2.85	2.13	2.15
Climate Precession (P4)	23.68	4.85	4.75	3.68	–
Climate Precession (P3)	22.37	5.13	5.15	3.89	3.85
Climate Precession (P2)	19.1	6.01	6	4.56	4.5
Climate Precession (P1)	18.95	6.06	6	4.60	–

***Table 11**—Comparison of cyclicities identified by Sageman et al. (1998) and this study. X = Cyclicity identified by Sageman et al. 1998 using Maximum Burrow Diameter (MBD) and Oxygen Related Ichnocoenoses (ORI) in the Bridge Creek Limestone; G = Identified cyclicities in this study from the Greenhorn Fm; N = Identified cyclicities in this study from the Niobrara Fm.*

Interpreted Cyclicity Driver	Set Cycle Period (kyr)	Sageman et al. (1998) MBD	Sageman et al. (1998) ORI	This study ii	This study ichnocoenoses
Long Eccentricity	405.6			–	–
Short Eccentricity (E4)	130.8			G, N	G, N
Short Eccentricity (E3)	123.9			G, N	G, N
Short Eccentricity (E2)	98.9			G, N	G, N
Short Eccentricity (E1)	94.9			G	G
Obliquity (O2)	~ 53	X	X		
Obliquity (O)	40.98			G	G, N
Obliquity (O1)	~ 32	X			
Climate Precession (P4)	23.68				G
Climate Precession (P3)	22.37			G	N
Climate Precession (P2)	19.1	X	X		G, N
Climate Precession (P1)	18.95	X	X		G

FIGURES

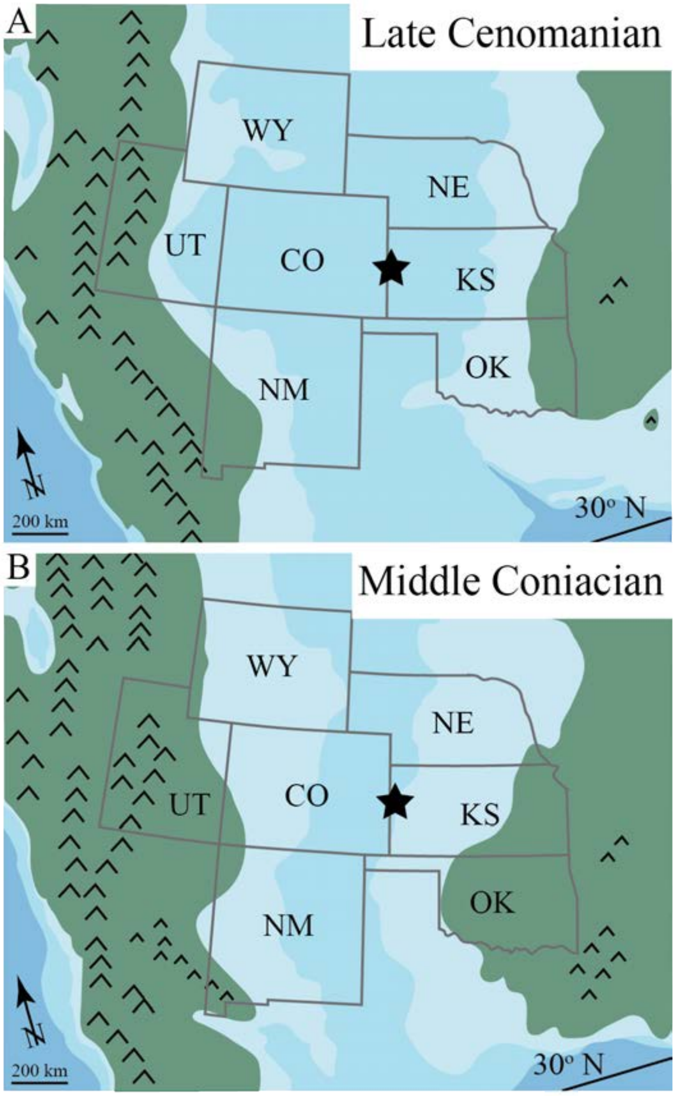


Figure 1—Paleogeographic maps of the Western Interior Seaway with location of AMOCO Rebecca K. Bounds #1 well (stars). A) Late Cenomanian. B) Middle Coniacian (modified from Blakey 2014).

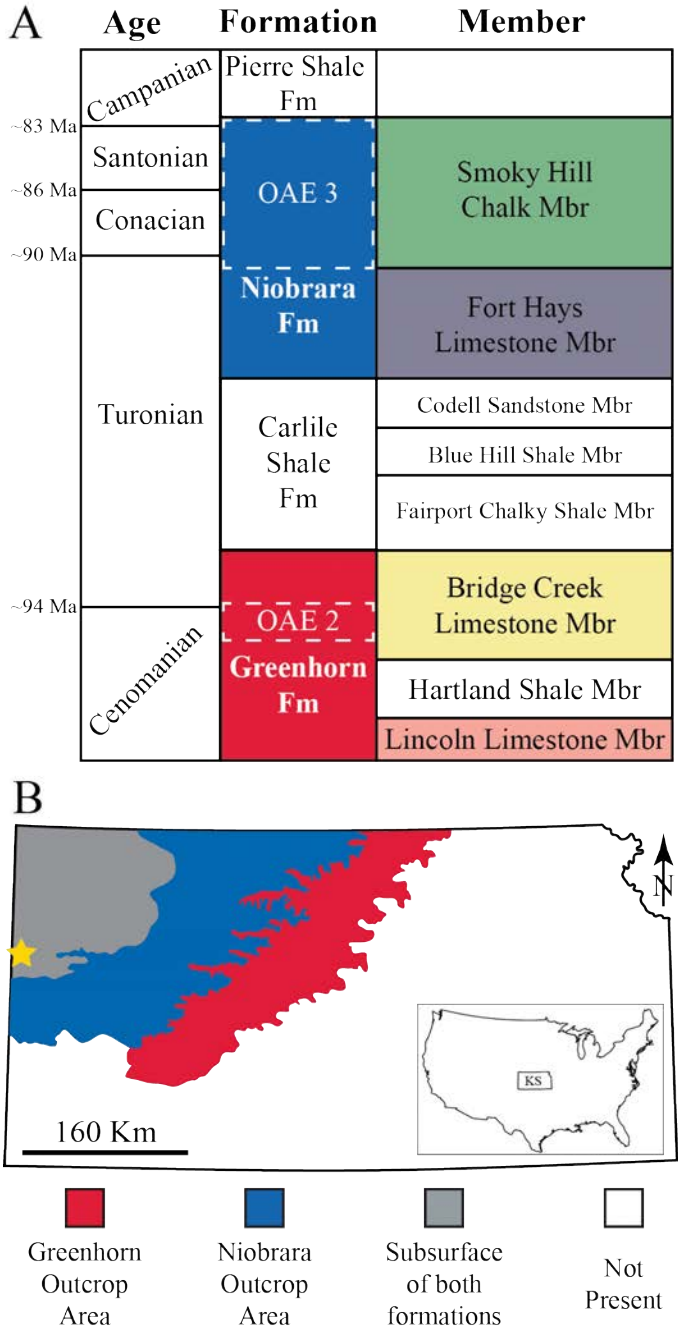


FIGURE 2—A) Stratigraphic column of the Upper Cretaceous formations, members, ages, and interpreted duration of OAE 2 and OAE 3 used in this study. B) Outcrop map of Greenhorn and Niobrara fms in Kansas. Star is location of AMOCO Rebecca K. Bounds #1 well (modified from Merriam 1963).

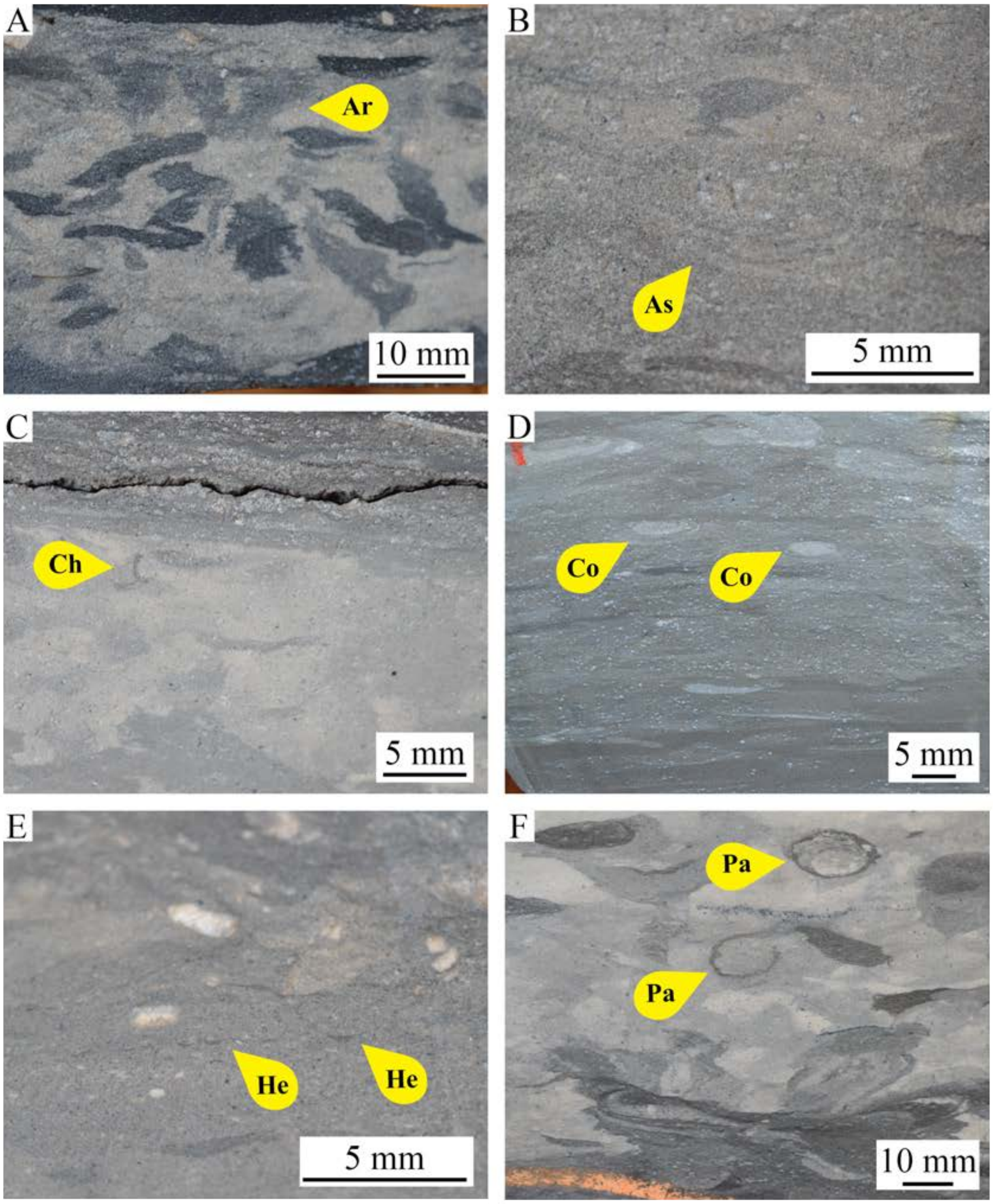


FIGURE 3—Ichnogenera in the Greenhorn Fm of the Bounds core. A) *Arenicolites* (Ar). B) *Asterosoma* (As). C) *Chondrites* (Ch). D) *Cosmorhaphe* (Co). E) *Helminthopsis* (He). F) *Palaeophycus* (Pa).

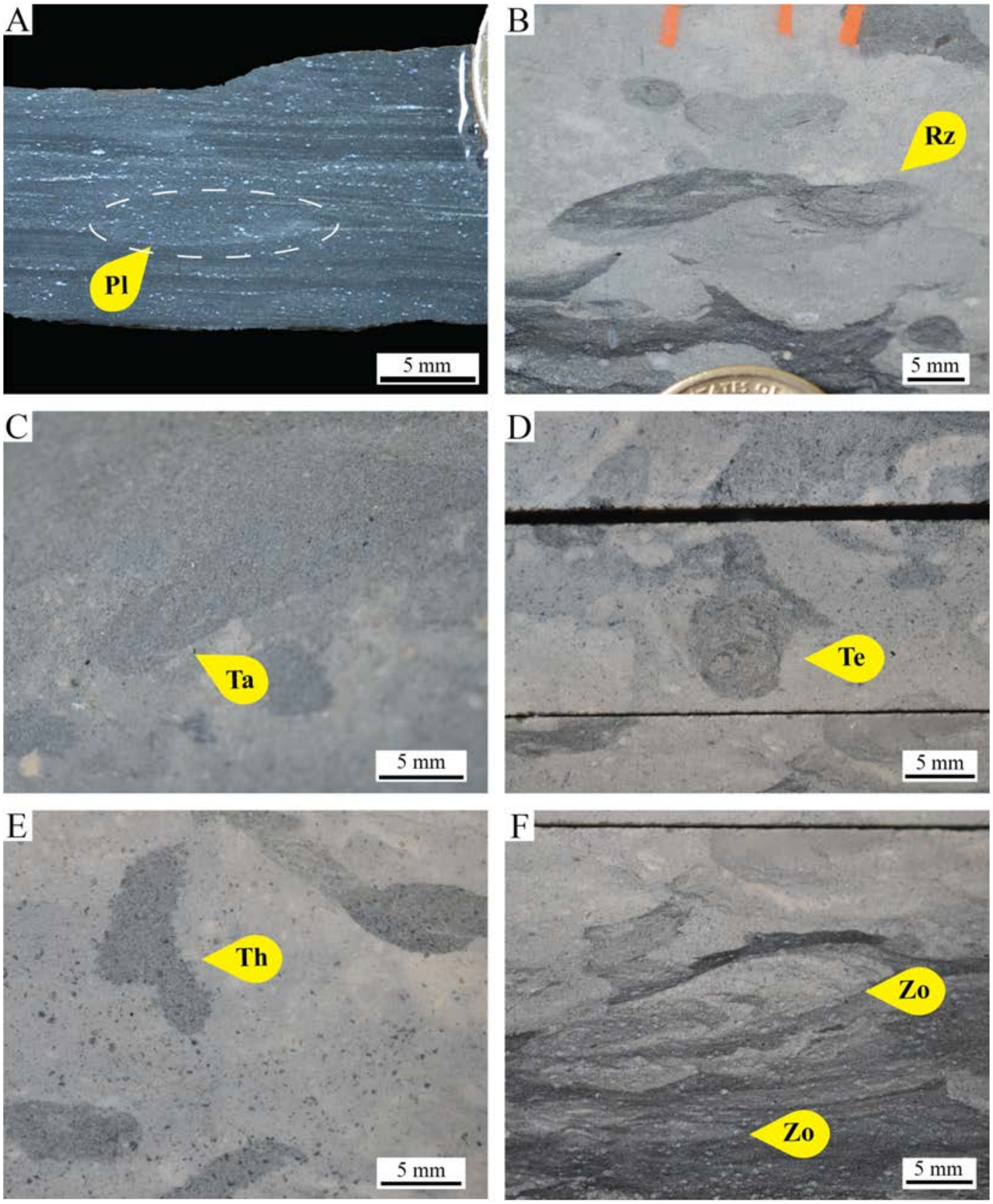


FIGURE 4—Ichnogenera in the Greenhorn Fm of the Bounds core. A) *Planolites* (Pl). B) *Rhizocorallium* (Rh). C) *Taenidium* (Ta). D) *Teichichnus* (Te). E) *Thalassinoides* (Th). F) *Zoophycos* (Zo).

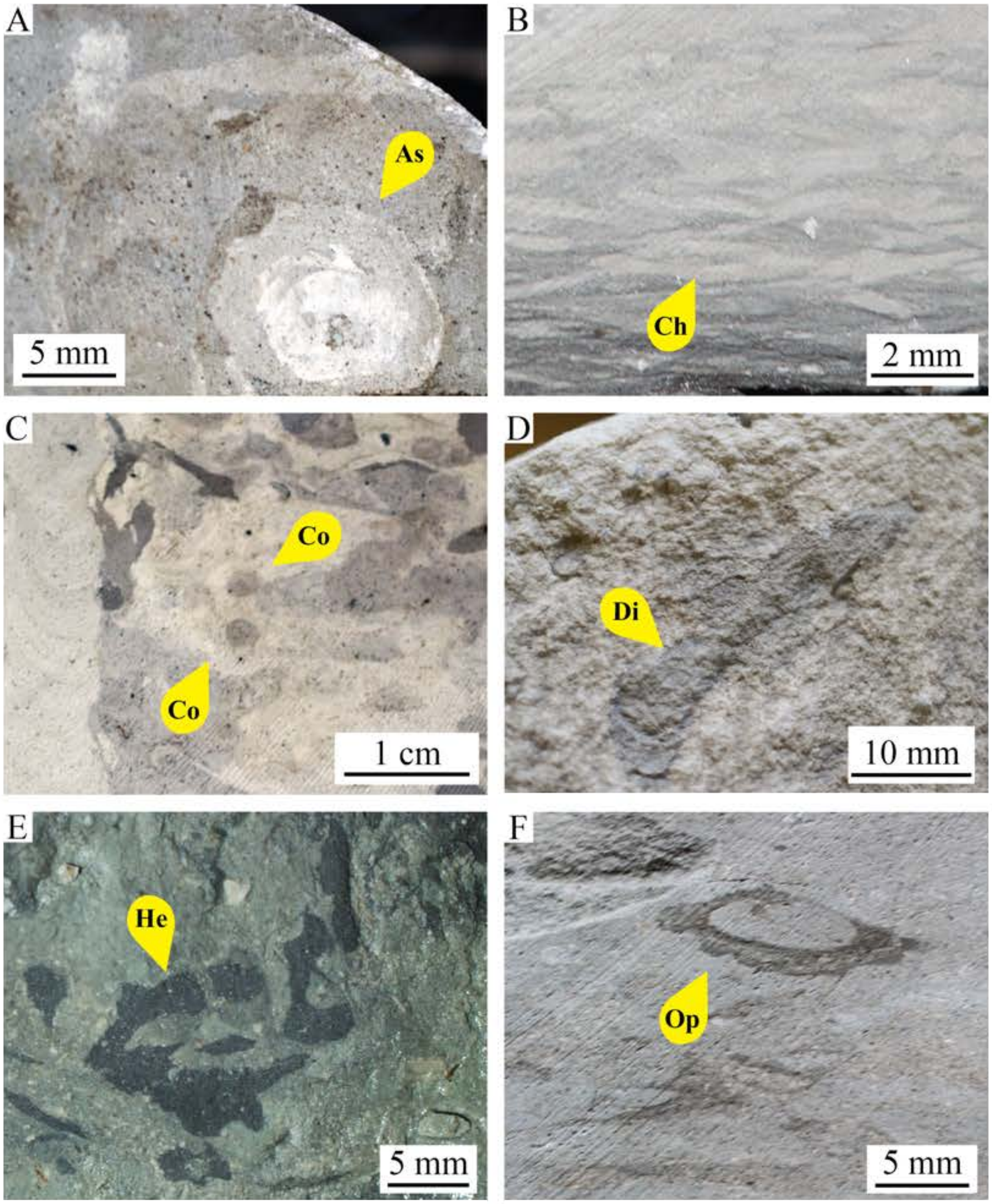


FIGURE 5—Ichnogenera in the Niobrara Fm of the Bounds core. A) *Asterosoma* (As). B) *Chondrites* (Ch). C) *Cosmorhaphe* (Co). D) *Diplocraterion* (Di). E) *Helminthopsis* (He). F) *Ophiomorpha* (Op).

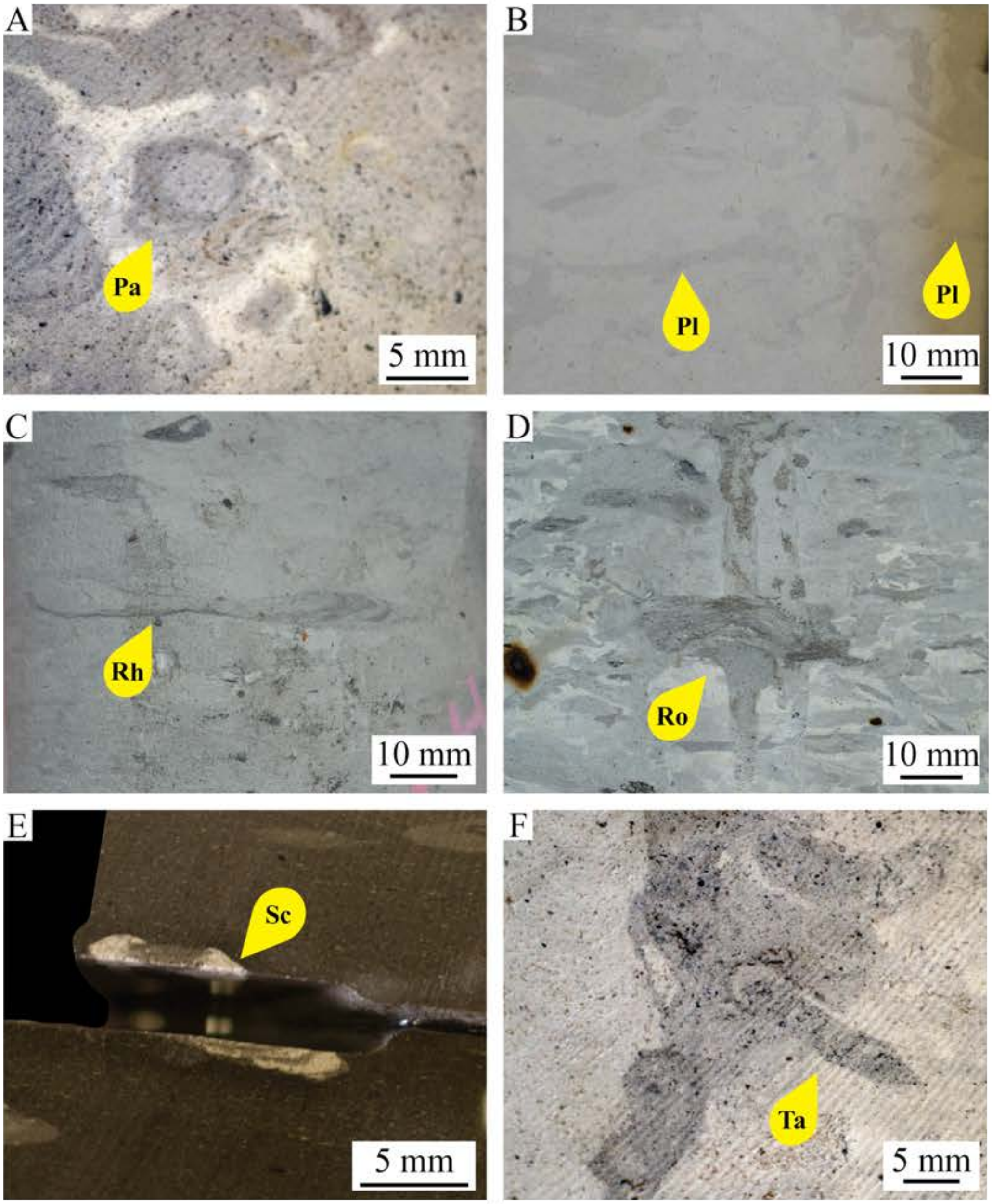


FIGURE 6—Ichnogenera in the Niobrara Fm of the Bounds core. A) *Palaeophycus* (Pa). B) *Planolites* (Pl). C) *Rhizocorallium* (Rh). D) *Rosselia* (Ro). E) *Schaubcylindrichnus* (Sc). F) *Taenidium* (Ta).

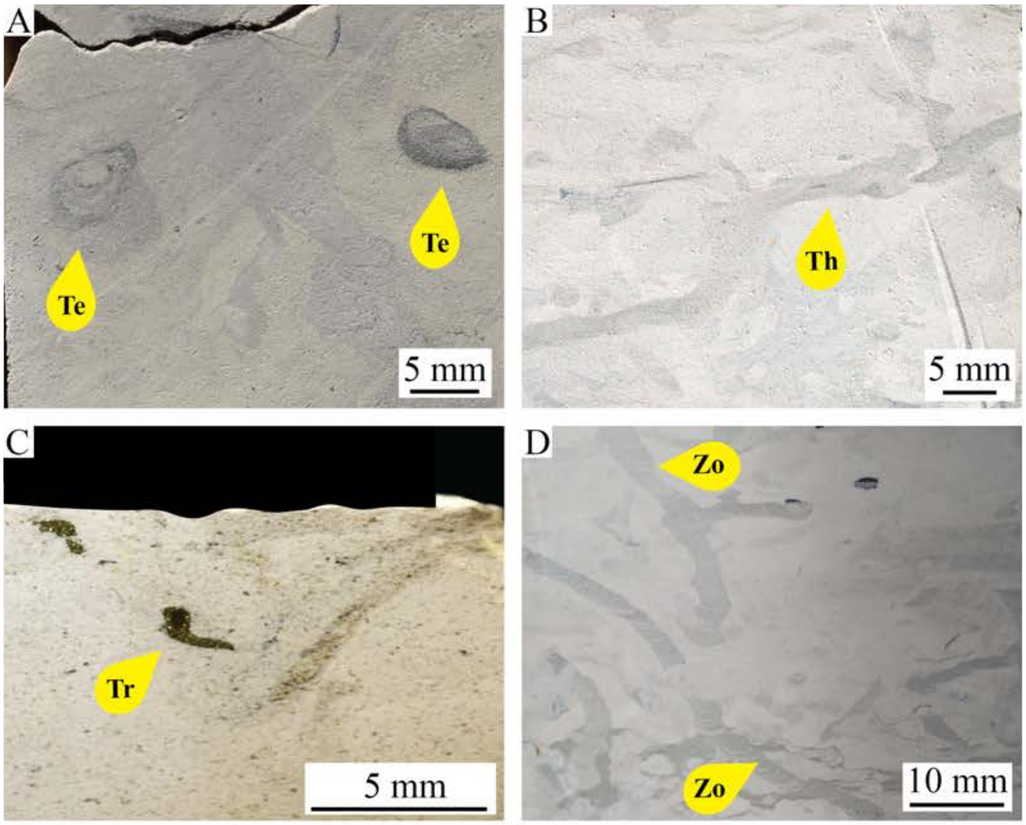


FIGURE 7—Ichnogenera in the Niobrara Fm of the Bounds core. A) *Teichichnus* (Te). B) *Thalassinoides* (Th). C) *Trichichnus* (Tr). D) *Zoophycos* (Zo).

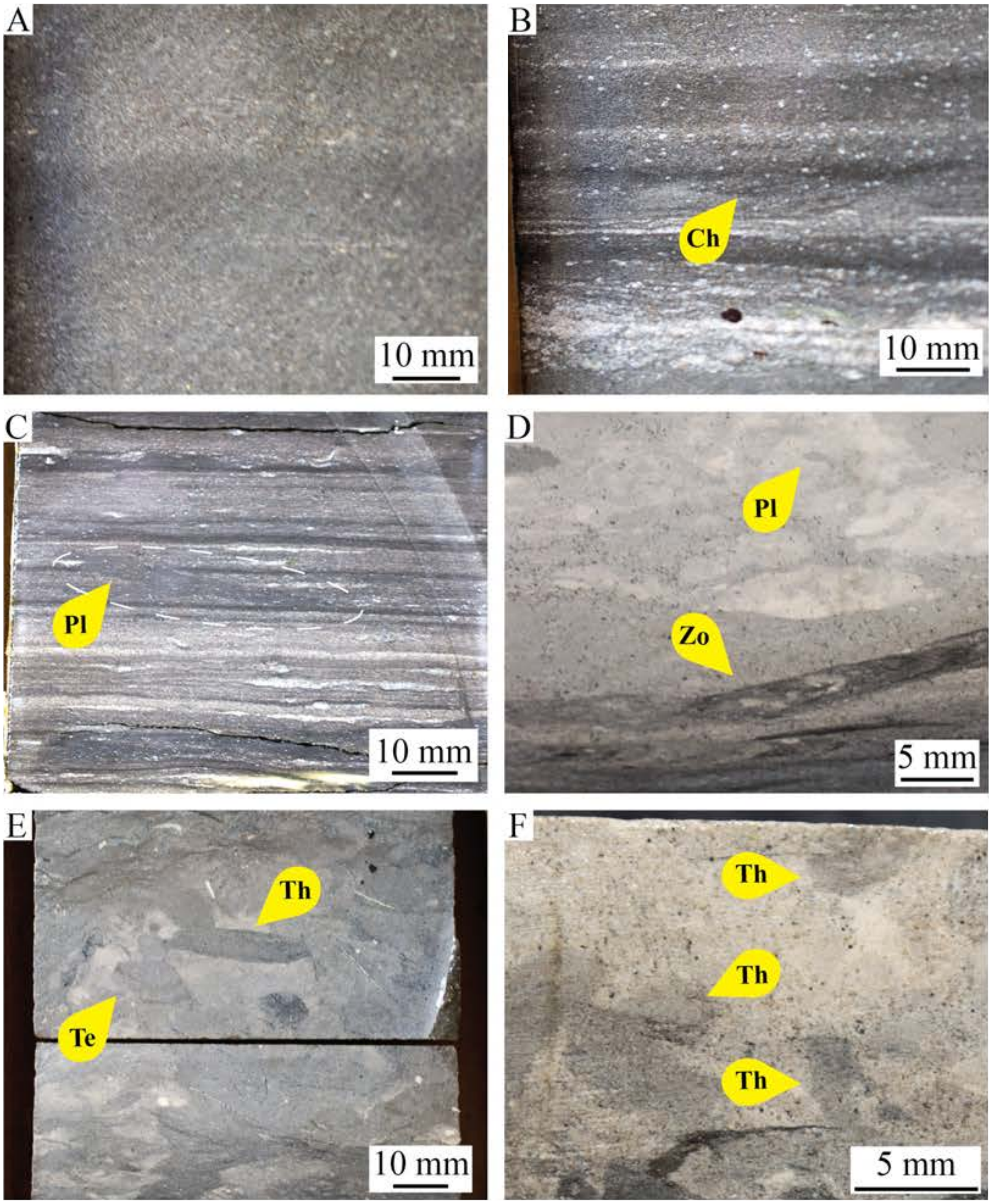


FIGURE 8—Greenhorn Fm Ichnocoenoses in the Bounds core. A) GFI 1 with cryptobioturbation in calcarenite and laminated marlstone. B) GFI 2 with *Chondrites* (Ch) in marlstone. C) GFI 3 with *Planolites* (Pl) in marlstone to argillaceous limestone. D) GFI 4 with *Planolites* (Pl) and *Zoophycos* (Zo) in argillaceous limestone. E) GFI 5 with *Thalassinoides* (Th) and *Teichichnus* (Te) as GFI 4 in limestone lithofacies. F) GFI 6 highly bioturbated (ii5–6) limestone with *Thalassinoides* (Th).

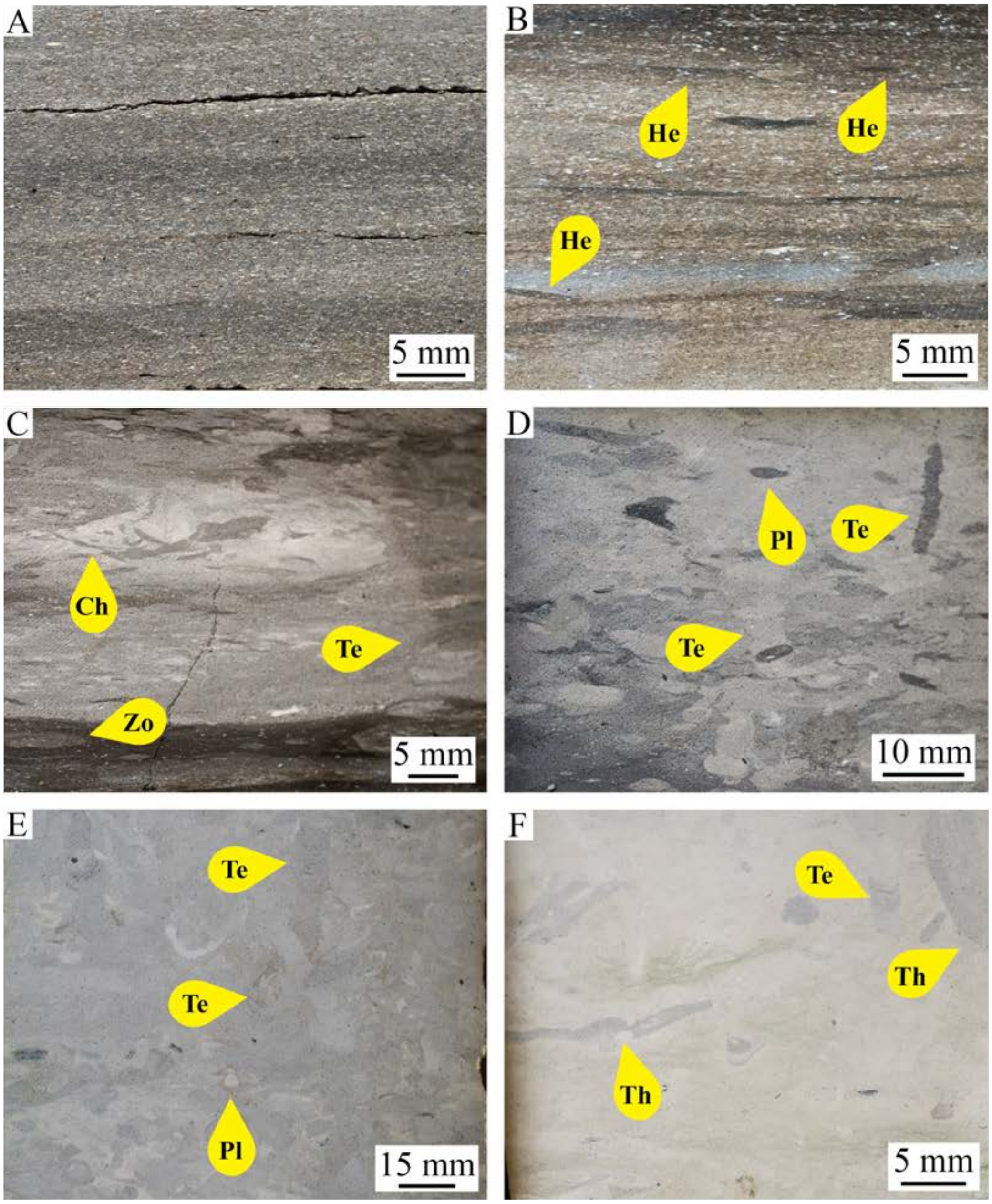


FIGURE 9—Niobrara Fm Ichnocoenoses in the Bounds core. A) NFI 1 with cryptobioturbation in marlstone lithofacies. B) NFI 2 with *Helminthopsis* (He) and cryptobioturbation in marlstone lithofacies. C) NFI 3 with similar ichnogenera as NFI 2, plus *Teichichnus* (Te) and *Zoophycos* (Zo) in argillaceous limestone lithofacies. D) NFI 4 with *Planolites* (Pl), *Teichichnus* (Te) in argillaceous limestone to limestone lithofacies. E) NFI 5 with dominantly *Planolites* (Pl) and *Teichichnus* (Te) in moderately well to highly bioturbated (ii4–5) limestone lithofacies. F) NFI 6 with *Teichichnus* (Te) and *Thalassinoides* (Th) in highly bioturbated (ii5–6) limestone lithofacies.

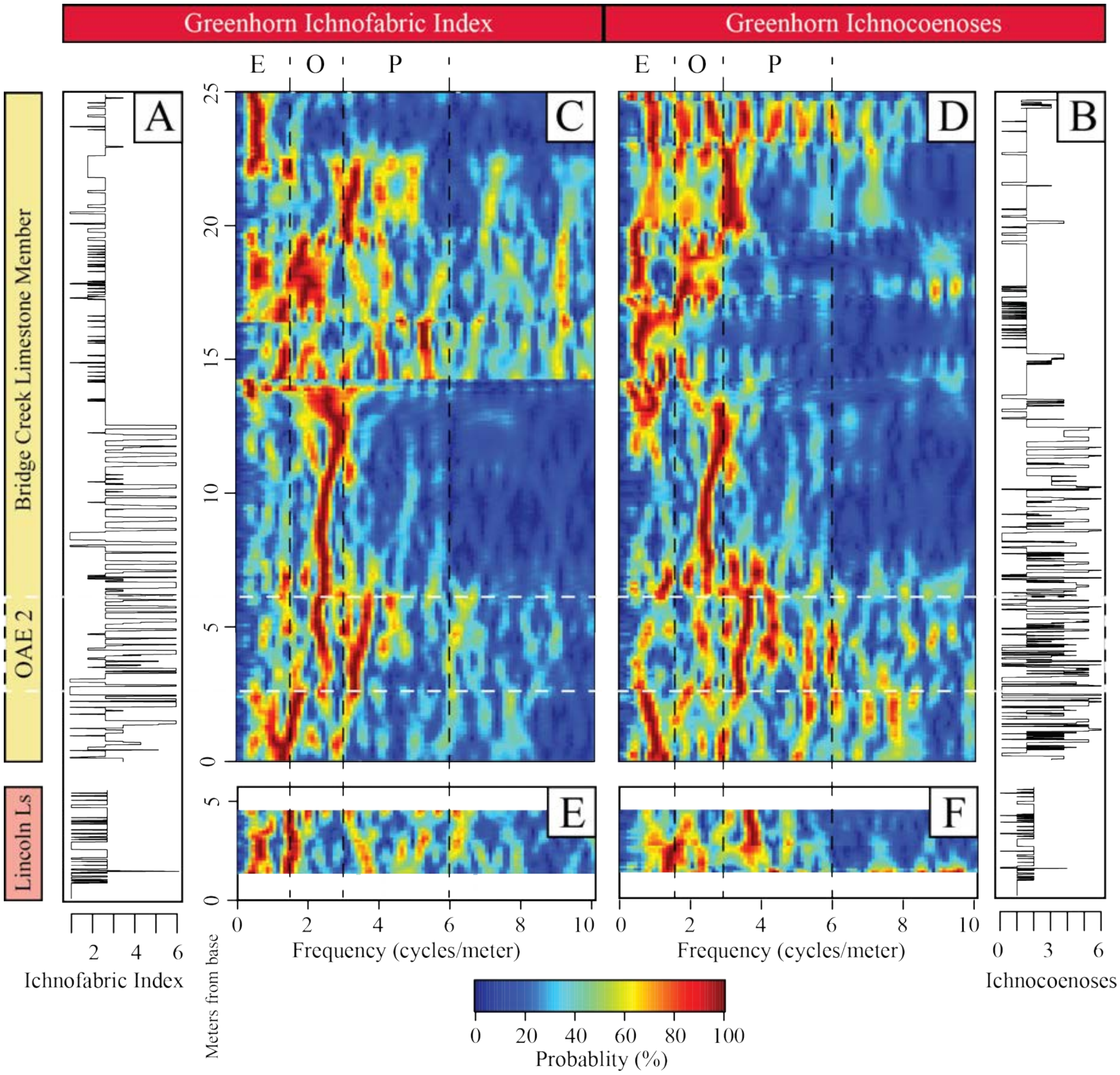


FIGURE 10—Spectral identification of cyclicities for the Greenhorn Fm, see text for discussion. A) Ichnofabric index (ii) distribution, unbioturbated strata (ii1) on the left to completely bioturbated strata on the right (ii6). B) Ichnocoenoses distribution, with ichnocoenosis 1 on the left to ichnocoenosis 6 on the right. C) Evolutive harmonic analysis (EHA) of ii data for the Bridge Creek Limestone Mbr; The X-axis is the harmonic frequency of astronomical cycles per meter of strata, and the Y-axis is position in the formation, the presence of a colored blob indicates a signal of that datatype (ii or ichnocoenosis) containing at frequency at that position, the color of the blob denotes the probability of that signal being significant, Eccentricity (E), Obliquity (O), and Precessional (P) frequency ranges are identified by the black dashed lines. D) EHA of ichnocoenoses data for the Bridge Creek Limestone Mbr. E) EHA of ii data for the Lincoln Limestone Mbr. F) EHA of ichnocoenoses data for the Lincoln Limestone Mbr.

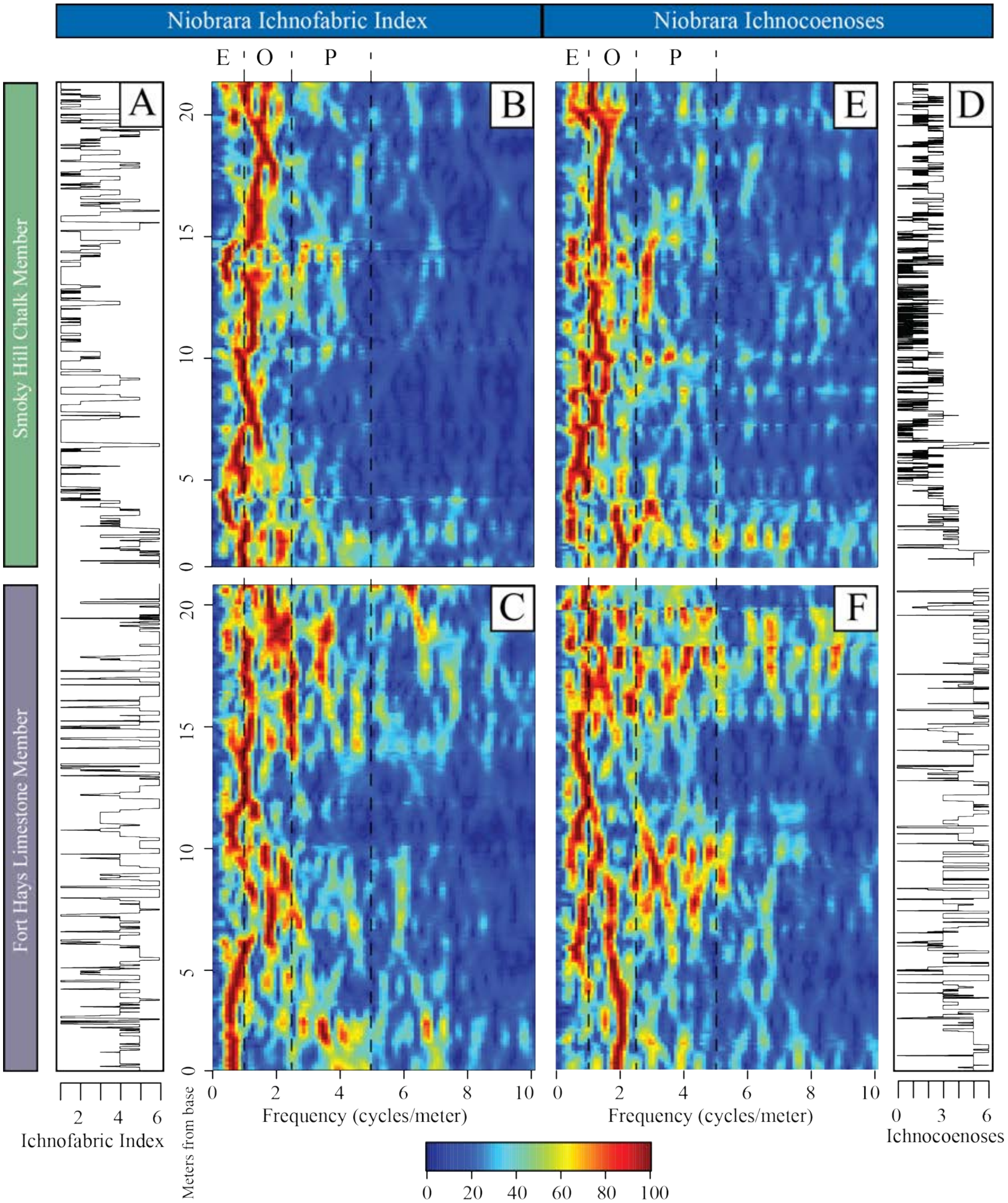


FIGURE 11—Spectral identification of cyclicities for the Niobrara Fm. A) Ichnofabric index (ii) distribution. D) Ichnocoenoses distribution. B) Evolutive harmonic analysis (EHA) of ii data for the Smoky Hill Chalk Mbr. E) EHA of ichnocoenoses data for the Smoky Hill Chalk Mbr. C) EHA of ii data for the Fort Hays Limestone Mbr. F) EHA of ichnocoenoses data for the Fort Hays Limestone Mbr.

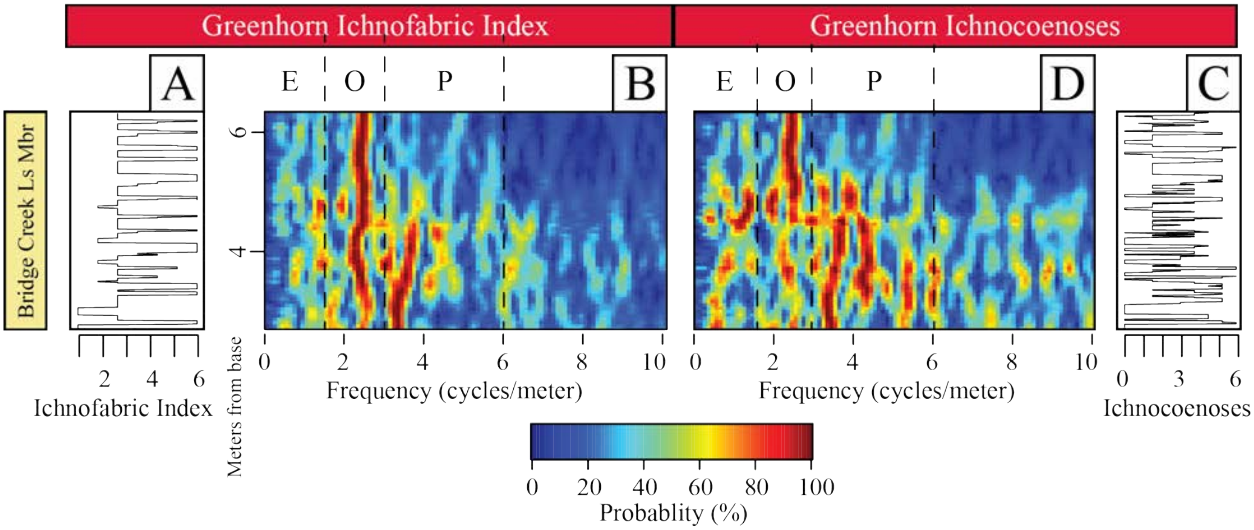


FIGURE 12— Spectral identification of cyclicities for the OAE 2. A) Ichnofabric index (ii) distribution. C) Ichnocoenoses distribution. B) Evolutive harmonic analysis (EHA) of ii data for the Bridge Creek Limestone Mbr in the OAE 2 range. D) EHA of ichnocoenoses data for the Bridge Creek Limestone Mbr in the OAE 2 range. Figure is 2X vertical exaggeration compared to Fig. 11.

CHAPTER 4: ICHNOLOGICAL ASSESSMENT OF DEPOSITIONAL ENVIRONMENTS IN THE CRETACEOUS DAKOTA GROUP, CAÑON CITY, COLORADO

Currently in preparation as:

JACKSON, A.M., HASIOTIS, S.T., AND SMITH, J.J., Ichnological assessment of depositional environments in the Cretaceous Dakota Group, Cañon City, Colorado, PALAIOS.

ABSTRACT

The Cretaceous Dakota Group of Colorado (CO) is well studied sedimentologically; however, the ichnology has not been fully integrated into the groups' analyses. This study of Dakota Group in the Cañon City, CO, area examines the: (1) vertical distribution of lithofacies and trace fossils; (2) influence of bioturbation on porosity and permeability; and (3) vertical changes in trace fossil assemblages to infer variations in local physicochemical parameters at the time of deposition. Thirty-one invertebrate ichnogenera were identified from fluvial (Lytle Fm), lower shoreface (Plainview Fm), offshore to shoreface (Glencairn Fm), and continental to offshore marine deposits (Muddy Fm) of the Dakota Group. Seven ichnocoenoses identified are consistent with the Scoyenia, Skolithos, and Cruziana ichnofacies. Within parasequences of the Glencairn Fm, burrow diameter generally increases within each parasequence; conversely, ichnodiversity generally decreases up section. Overall, ichnodiversity is the greatest in the Glencairn Fm and lowest in the Lytle Fm. Bioturbation in the Dakota Group both increased and decreased porosity and permeability depending on bioturbation intensity and lithofacies. Strata with high bioturbation generally occur with lower porosity and higher permeability. Vertical trends in burrow diameter and abundance indicate that the media primarily controls the distribution of some ichnogenera, whereas others are controlled by oxygenation or salinity.

INTRODUCTION

The Dakota Group of Colorado (CO) (Fig. 1, 2) is a time-transgressive unit of interbedded sandstone, mudstone, and shale deposited in the Western Interior Seaway (WIS) of North America (Gustason and Kauffman 1985). The geographically widespread Dakota Group extends from Utah to Iowa and from Idaho to New Mexico and further with time-equivalent strata (e.g., Tainter 1984; Higley et al. 1995). The Dakota Group in the Cañon City area (Fig. 3) records a complex history of shifting depositional environments on the western edge of the WIS (Kaufmann 1977). These strata represent fluvial to shelf environments with multiple parasequence and sequence boundaries (e.g., Altschuld 1980; Odien 1997). Studies on the Dakota Group have primarily focused on sedimentology, stratigraphic relationships and environments of deposition (e.g., Hart 2015; Lockley et al. 2016; Walaszczyk and Cobban 2016). The Dakota Group is a well-known, resource-bearing unit in eastern Colorado, and has been an active resource play since 1923 (Arps and Roberts 1958; Pruit and Coffin 1978).

Few studies have examined the Dakota Groups' invertebrate ichnology beyond its inclusion in the sedimentological fabric, use in identification between freshwater and marine depositional environments, or ichnofacies (e.g., Altschuld 1980; Gustason and Kauffman 1985, Odien 1997). The application of ichnology to characterizing depositional facies and stratigraphic interpretations has become a key tool in better understanding petroleum-resource plays and flow behavior in groundwater aquifers (e.g., Pemberton and Wightman 1992; Pemberton et al. 2001; Cunningham and Sukop, 2012; Gingras et al. 2012; Golab et al. 2017b). Trace fossils are major modifiers of primary sedimentary fabrics (e.g., Droser and Bottjer 1986) and can change permeability and porosity by orders of magnitude (e.g., Gingras et al. 1999, 2002, 2012; Golab et al., 2017a). Core and outcrop studies have characterized how trace fossils can both increase or decrease lateral and vertical connectivity (e.g., Pemberton and Gingras 2005; Cunningham and Sukop, 2012; Gingras et al. 2012; Golab et al. 2017a,b).

Due to the varied previous environmental interpretations of the Dakota Group, the purpose of this study is to apply an integrated sedimentological and ichnological approach to further refine environments of deposition in the Cretaceous Dakota Group and to access the role of bioturbation on the sedimentary pore characteristics (permeability and porosity) of its various subunits. This study characterized the: (1) trace fossils; (2) ichnocoenoses; (3) ichnofacies; (4) vertical trends in ichnodiversity, trace fossil size, and bioturbation; and (5) physicochemical controls on trace fossil distribution. We identified 31 invertebrate trace fossil genera that were assembled into seven distinct ichnocoenoses, indicating continental to marine depositional environments, and grouped with three previously established ichnofacies (Scoyenia, Skolithos, and Cruziana). In Dakota Group strata, the influence of trace fossils on pore characteristics varies based on the lithofacies and bioturbation intensity. Trace fossil size and distribution also changes with lithofacies associations and interpreted physicochemical controls related to the depositional environment

Geologic Setting

Initially described in Nebraska by Meek and Hayden (1861), the Cretaceous Dakota Group can be traced to the CO Front Range, where it is differentiated into multiple formations (fms) and members (mbrs). While the lexicon of these named sedimentary units has varied, particularly in the Cañon City area, we follow the nomenclature of Gustason and Kauffman (1985). The Lytle, Plainview, Glencairn, and Muddy fms were deposited into the developing Sevier foreland basin and along the western margin of the WIS. Simultaneous basinal subsidence and global sea-level rise, coupled with a varied coastline, lead to a variety of EOD and interpretations along the Front Range (e.g., Waage 1953; Dyman et al. 1994).

The basal Lytle Fm is widely recognizable along the Front Range by its trough cross-bedded sandstone strata with pebble lags (e.g., Waage 1953) (see Fig. 2A). Interpreted as an erosional valley-fill deposit cut into the underlying Morrison Fm, the Lytle Fm can range up to 20-m thick (Odien 1998). The upper contact with the Plainview Fm is erosional across the Front Range (Odien 1997).

The Plainview Fm contains two informal members in the Cañon City area that preserve sediments deposited into valleys incised into the underlying Lytle Fm (Weimer et al. 1990). The lower member consists of muddy to heterolithic strata, including a sandstone bed with ≥ 50 ankylosaur tracks and one theropod track (Kurtz et al. 2001). Sandstone beds immediately above the dinosaur tracks contain abundant fossil plant material and impressions of branches and logs (see Fig. 2A; Gustason and Kauffman 1985; Kurtz et al. 2001). The upper member is dominated by highly bioturbated to homogenized sandstone (Altschuld 1980, Odien 1997). This study follows Waage (1953) and Odien (1997) for the Plainview-Glencairn fm contact placement above this member at the base of the Glencairn ~ 30-cm-thick conglomerate bed.

The Glencairn Fm, also known as the Skull Creek Fm (e.g., Mateer 1987; Holbrook and Dunbar 1992), is interpreted to overlie a transgressive surface of erosion marked by a basal conglomerate bed, which is traceable across most of the Front Range (Odien 1997). Previous interpretations identified 3–4 coarsening upward successions (Fig. 4; Altschuld 1980; Gustason and Kauffman 1985; Odien 1997). Deposited near the peak of the Kiowa-Skull Creek transgression, each parasequence varies from 2–8 m thick (Gustason and Kauffman 1985). Some parasequences contain hummocky cross-stratified (HCS) beds ≤ 10 cm thick (Altschuld 1980;

Gustason and Kauffman 1985; Odien 1997). These studies also noted bioturbation increasing from the basal mudstone upward into the upper sandstone, often homogenizing primary sedimentary structures in each parasequence.

The Muddy Fm (known as the J Sandstone in subsurface; Weimer and Sonnenberg 1989) erosionally cuts the uppermost parasequence of the Glencairn Fm, (Dolson and Weimer 1992). The Muddy Fm is subdivided into the Lower Channel Sandstone Mbr (LCSM) and the Upper Transitional Mbr (UTM; see Fig. 2C–D). The basal LCSM consists of trough cross-bedded sandstone that grades upward into ripple cross-bedded sandstone. The upper portion of the LCSM consists of trough cross-bedded sandstones that grade into heterolithic strata with abundant bioturbation (Altschuld 1980). The overlying UTM contains interbedded sandstone and shale, increasing in shale content to the Mowry/Graneros Fm contact (Gustason and Kauffman 1985; Odien 1997). Previous studies vary on the interpreted contact between the Muddy and Graneros fms (Burtner and Warner 1984, Gustason and Kauffman 1985, Odien 1997).

Sequence Stratigraphic Interpretations

The Dakota Group has been placed into multiple sequence stratigraphic models based on outcrop and well logs (e.g., Gustason and Kauffman 1985; Weimer and Sonnenberg 1989; Dyman et al. 1994). Most studies agree on the placement of the three sequence boundaries within the group, but differ on the placements of parasequences (Fig. 4; Altschuld 1980, Weimer 1983; Gustason and Kauffman 1985; Odien 1997). The sequence boundary (SB) 1 of Weimer (1983) is the base of the Lytle Fm and can be traced across the Front Range. The contact between the Lytle-Plainview fms represents the SB-2 unconformity (Weimer 1983; Holbrook and Ethridge 1996).

Disagreements exist regarding the boundary between the Plainview and Glencairn fms, and their sequence stratigraphic positions (Fig. 4). Altschuld (1980) and Odien (1997) interpret the ~ 30-cm-thick pebble conglomerate as a deposit resting on a transgressive surface of erosion (TSE), which is also the Plainview-Glencairn fm contact. Long (1966) and Gustason and Kauffman (1985) argue that the contact between the Plainview-Glencairn fms is ~ 4 m lower, where their interpreted estuarine and delta-plain deposits of the Plainview Fm transition into progradational marine sandstones.

With the exception of the basal conglomerate, the Glencairn Fm comprises a series of stacked, upward coarsening parasequences that record the Skull Creek transgression through a series of small, relative sea-level rises and progradational shorelines (Gustason and Kauffman 1985; Holbrook and Ethridge 1996; Odien 1997). The contact between the Glencairn-Muddy fms—SB 3 (Fig. 4)—is a scour surface that cuts into the Glencairn Fm (Gustason and Kauffman 1985). Within the Muddy Fm, the contact between the Lower Channel Sandstone and Upper Transitional mbrs has been interpreted as a ravinement surface (Gustason and Kauffman 1985; Odien 1997).

Ichnology of the Dakota Group

Ichnological studies of the Dakota Group are rare and mainly concentrate on the dinosaur trackways in the Front Range (e.g., Kurtz et al. 2001; Lockley et al. 2014). Previous studies did not focus on the interpretations and implications of the ichnofossils or their assemblages (ichnocoenoses) beyond Seilacherian ichnofacies (e.g., Waage and Eicher 1960, Mackenzie 1965; Gustason and Kauffman 1985; Odien 1997). Fewer than five trace fossils have been described in most papers on these strata (e.g., Mackenzie 1965; Chamberlain 1976; Basan and

Scott 1979; Wescot 1979; Kauffman 1984). Mackenzie (1963) and Weimer (1971) utilized trace fossils to separate estuarine to marine strata from continental strata.

MATERIALS AND METHODS

This study documents the types and distribution of trace fossils within a composite stratigraphic section of the Dakota Group along the Skyline Drive Hogback in Cañon City, CO, (Fig. 2) with additional ichnological data within the Muddy Fm collected from nearby Slot Canyon (Fig. 5). Each formation was described for its lithofacies and trace fossils (following Compton 1985). Trace fossils from all Dakota Group formations were identified to ichnogeneric level based on architectural and surficial morphology and fill (following Hasiotis and Mitchell 1993; Bromley 1996), and compared with previous published descriptions. Nearly 2000 trace fossils were measured for width(s), length(s), diameter(s), and penetration depth to identify trends. Measurements were made with a General Tools® #147 digital caliper (± 0.0254 mm accuracy). Plainview Fm dinosaurian trace fossils were not measured or described ichnotaxonomically (See Kurtz et al. 2001, for dinosaur track discussion). Bioturbation intensity was semiquantatively measured to identify trends across and between the fms using the ichnofabric index (ii) of Droser and Bottjer (1986) in 10-cm intervals. Glencairn Fm parasequence 4 (GP4) was selected for analysis of the lateral and vertical distribution of trace fossils in outcrop (Fig. 5), and had a minimum of 150 trace fossils measured per traceable bed or bedset (total of 1403). Sandstone to shale ratios were also calculated for GP4, where 1 is 100% sand, and 0 is 100% shale to identify any trace fossil changes with lithofacies ratios.

Ichnocoenoses were characterized based on reoccurring trace-fossil associations (following Bromley 1996; Pemberton et al. 2001). Ichnofacies—reoccurring trace-fossil assemblages found in a similar lithofacies—were defined and used to interpret the EOD of each unit, in conjunction with the sedimentology (e.g., Seilacher 1967). Changes in ichnodiversity and variation in trace-fossil distribution, size, and tiering depth were used to interpret the physicochemical conditions (e.g., benthic oxygenation, salinity changes) at the time of deposition (following Hasiotis and Platt 2012).

Thirty-seven thin sections with blue epoxy were made from stratigraphically representative hand samples to identify grain size, grain composition, and to describe sedimentary fabric with respect to the morphology, infill, and porosity of trace fossils (following Bouma 1969; Frey 1975). Thin-section porosity was estimated visually using jPOR process in NIH ImageJ (Grove and Jerram 2011; Rasband 2015). Permeability at the Skyline Drive outcrop (Lytle to Muddy fms section) was measured using a New England Research TinyPerm II portable air permeameter with a calibrated permeability range from 0.10 D–10 Darcys. Measurements were taken at 10-cm intervals when possible, and duplicated and averaged for each location (e.g., Goss and Vlotnik 2007).

Measurements of trace fossils and outcrop porosity and permeability were statistically tested to analyze variation among and between ichnogenera from the four formations using R3.2.3 Wooden Christmas Tree (R Core Team 2015). Standard descriptive statistics were used to analyze morphological variation of trace-fossil attributes (e.g., minimum, maximum, mode, and average of length, width, and diameter[s]). The percentile for widths or diameters was identified, and ichnogenera-specific cross-plots were made to compare the size percentile and width ratio to identify morphological trends (after Bromley and Hanken 1991).

RESULTS

Lithofacies

The Dakota Group in the study area consists of 6 primary lithofacies ranging from Mudstones to course sandstones with two gravel conglomerate beds (Table 1, Fig. 6). The lithofacies identified in this study are relatively consistent laterally in exposures along Skyline drive, though the distribution of similar facies in the rest of the Front Range is more variable (e.g., Odien 1997). At Skyline Drive the most abundant facies is Facies 3, with Facies 6 being the least abundant. Within the upper Plainview and Glencairn fms Facies 4 is the primary lithofacies, consisting of much the of the upper Plainview Fm and the upper halves to two-thirds of each Glencairn Fm parasequence.

Ichnology

Thirty-one invertebrate ichnogenera were identified from marine and continental depositional environments in the Dakota Group (Table 2, Fig. 7–12). The lowest ichnodiversity was in the Lytle Fm where only two ichnogenera and rhizoliths were observed. The overlying Plainview Fm contained nine ichnogenera, including the ankylosaur and theropod tracks (Kurtz et al. 2001). The Glencairn Fm contained the greatest ichnodiversity with 26 distinct ichnogenera.

Nine ichnogenera have a consistent vertical abundance distribution through Glencairn Fm parasequence 4 (*Arenicolites*, *Bergaueria*, *Chondrites*, *Cochlichnus*, *Palaeophycus*, *Phycodes*, *Skolithos*, *Teichichnus*, and *Treptichnus*), and of these only four (*Phycodes*, *Skolithos*, *Teichichnus*, and *Treptichnus*) have one bed in which their abundance increases greatly (e.g., *Skolithos* in bedset 4; Fig. 13. The abundance of identified *Planolites* varies thought the parasequence, with the greatest occurrences in bedsets with lower sandstone to shale ratios.

Thalassinoides was the most abundant trace fossil identified, with a maximum of 198 measured in bedset 6. The abundance of *Thalassinoides* increases to this bedset as the sandstone to shale ratio increases to the middle of parasequence 4, with abundance decreasing further up section. This decrease in abundance is likely due to higher bioturbation intensities (ii6) in the upper strata, which greatly reduces the number of discernable, individual trace fossils.

Size within and among ichnogenera varies throughout the Dakota Group based on 1,790 measurements (Fig. 14). The greatest variation in trace-fossil size occurs in *Asthenopodichnium*, *Fuersichnus*, *Lockeia*, and *Thalassinoides*, whereas *Arenicolites*, *Diplocraterion*, and *Helminthopsis* vary the least. Within GP4, the parasequence that was the focus of the morphometric study, overall ichnogeneric size (n=1403) varies with stratigraphic position (Figs. 13, 14). Eight Dakota Group ichnogenera exceeded 25 mm in diameter (or width) (*Asthenopodichnium*, *Diplocraterion*, *Fuersichnus*, *Lockeia*, *Ophiomorpha*, *Planolites*, *Teichichnus*, and *Thalassinoides*) (Fig. 14). *Helminthopsis* is the most morphologically conservative, whereas *Thalassinoides* has the greatest variability in size. Twenty-three of the 31 identified trace fossils occur within GP4; whereas 17 of the 23 trace fossils identified in the Glencairn Fm have more than one occurrence in GP4. Nine ichnogenera decrease in size from shale to sandstone strata, whereas seven increase in size and only one (*Helminthopsis*) has no trend (Fig. 13).

Ichnocoenoses

The 31 ichnogenera identified within the Dakota Group comprise 7 distinct and recurring assemblages or ichnocoenoses which vary in stratigraphic frequency amongst the different formations (Table 3, 4). The lower member of the Plainview Fm contains the Fuersichnus

Ichnocoenoses, whereas the upper member preserves the Thalassinoides Ichnocoenosis. Parasequences within the Glencairn Fm contain the Helminthopsis-Phycodes Ichnocoenosis at their base, which are overlain with Thalassinoides Ichnocoenosis and then Ophiomorpha-Thalassinoides Ichnocoenosis in the uppermost portion. The LCSM of the Muddy Fm contains no ichnocoenoses. The UTM dominantly contains the Diplocraterion Ichnocoenosis, but also has sparse occurrences of *Planolites* and *Skolithos* in highly bioturbated fine- to medium-grained sandstone. Also within the UTM, thinly bedded sandstones with mud interbeds (Facies 4) contain the Planolites-Phycodes Ichnocoenosis.

Rhizolith Ichnocoenosis

Description.—This ichnocoenosis consists of rhizoliths and a single occurrence of *Skolithos*. The rhizoliths are only found on the uppermost surface of the Lytle Fm, and do not penetrate deeply (≤ 4 cm) or extend laterally more than 3 cm. The rhizoliths are a rusty red hue and taper down to their tip with few side rootlets observed.

Interpretation.—The presence of rhizoliths indicates subaerial exposure and colonization of bars within the Lytle braided river system (e.g., Bown 1982; Smith et al., 2008). The limited abundance, one colonized surface, and coarseness of the facies suggests that the area of deposition that is now the Skyline Drive exposure was not subaerially exposed for a long enough time for colonization and was generally in higher energy position of the river system.

Fuersichnus Ichnocoenosis

Description.—This ichnocoenosis consists of common *Fuersichnus, Lockeia,* and *Planolites. Fuersichnus* and *Lockeia* occur in plant-debris-filled sandy beds, whereas *Lockeia* are abundant in muddier sediments. This ichnocoenoses also contains the dinosaurian trackway. Overall, strata with the Fuersichnus Ichnocoenosis are highly bioturbated (ii4–6), with large amounts of plant debris included within the facies.

Interpretation.—This ichnocoenosis characterizes the initial continental to marine environment transitional position in the Dakota Group. Strata containing this ichnocoenosis record a shallow freshwater environment with abundant plant debris, including branches with *Asthenopodichnium* (Freshwater-only mayfly borings), and *Lockeia* (fresh to marine clam traces) The fluvially sourced *Asthenopodichnium* bored branches, and the *Fuersichnus* bored wood was deposited record a variable depositional environment at the intersection of the shoreline and a further from the river depositional axis portion where *Lockeia* are pervasive as they continue up section into marine upper Plainview Fm (e.g., Lucas et al. 2015; Moran et al. 2010). The presence of the dinosaur trackways in strata surrounded by this ichnocoenosis supports a paralic interpretation of these beds (Kurtz et al. 2001).

Thalassinoides Ichnocoenosis

Description.—Occurring in the upper Plainview, Glencairn, and Muddy fms, the Thalassinoides Ichnocoenoses generally consists of *Diplocraterion, Skolithos, Teichichnus*, and *Thalassinoides* in well- to highly bioturbated (ii4–6) sandstone strata (Facies 2–4). *Thalassinoides* box works can become so extensive that beds become entirely homogenized. *Rhizocorallium* is a major component of this ichnocoenosis in the Glencairn Fm.

Interpretation.—The Thalassinoides ichnocoenosis represents a highly stable environment where the burrowing organisms can develop complex box-work burrow networks. The occurrences of *Rhizocorallium* in the Glencairn and Muddy fms also suggest further stabilization of the depositional environment, allowing the serial exploitation of nutrient-rich areas on a larger scale (e.g. Basan and Scott 1979). In the uppermost Plainview Fm and upper portions of each Glencairn Fm parasequence are dominated by this ichnocoenoses and are nearly monospecific and are often highly bioturbated to homogenized (ii5–6).

Helminthopsis-Phycodes Ichnocoenosis

Description.—The Helminthopsis-Phycodes Ichnocoenosis primarily contains *Helminthopsis Phycodes*, *Planolites*, and *Treptichnus* in the basal mudstones of each Glencairn parasequence, and occurs in the upper mudstones in the Upper Transitional Member of the Muddy Fm (Facies 5 & 6). *Phycodes*, *Planolites*, and *Treptichnus* tend to occur in heterolithic strata where the mudstone transition into the overlying sandstones, whereas *Chondrites* and *Helminthopsis* occur in the laminated mudstone strata.

Interpretation.—This ichnocoenoses occurs in fine-grained mudstone strata deposited in the most distal environments in the Dakota Group. In the Glencairn fm this ichnocoenosis fits prodelta to distal delta front deposits in the mudstone to mudstone with sandstone interbed zones. (Jackson et al., 2016). Trace fossil sizes are not diminutive, nor are there monotypic trace fossil suits, suggesting that the trace-making organisms were not environmentally stressed (Jackson et al. 2016).

Ophiomorpha-Thalassinoides Ichnocoenosis

Description.—Consisting of *Ophiomorpha, Planolites*, *Thalassinoides*, and *Teichichnus*, this ichnocoenosis occurs in the middle to upper beds of the Glencairn Fm parasequence. The co-occurrence of *Thalassinoides* and *Ophiomorpha* varies, with more *Ophiomorpha* in the basal muddier sections and more *Thalassinoides* in upper sandier strata.

Interpretation.—This association records a shallow nearshore, where the benthic medium was not as stable and/or dewatered as the Thalassinoides Ichnocoenosis strata (Facies 3). (e.g., Frey et al. 1978; Seilacher 1978; Taylor and Gawthorpe 1993; Gani et al., 2008). The *Ophiomorpha* in the muddier strata indicated initial colonization of the area, then as sedimentation transitions to increased sand composition, the burrow integrity increases to allow for *Thalassinoides* to be developed. *Planolites* and *Teichichnus* occur in all facies, however their abundance decreases with the increasing abundance of *Thalassinoides*.

Diplocraterion Ichnocoenosis

Description.—This near-monospecific ichnocoenosis consists of *Diplocraterion* with rare occurrences of other ichnogenera. The moderately to well-bioturbated (ii3–5) strata with this ichnocoenosis are predominately medium-grained sandstones that occur on top of highly bioturbated Thalassinoides Ichnocoenosis beds. The Diplocraterion ichnocoenosis occurs in the upper sandstone bed in series of mudstone strata with sandstone beds (Facies 3 & 4). The two occurrences of this ichnocoenosis are followed by mudstone deposition (F-6) that contains the Helminthopsis-Phycodes Ichnocoenosis.

Interpretation.—The Diplocraterion ichnocoenosis is distinct in its abundance and density of the *Diplocraterion*. These occur in rippled sandstone beds and indicate a position with higher energy development of ripples where the *Diplocraterion* organisms can adjust to the shifting surfaces while filter feeding (Martin et al. 2016). The primary occurrence of this ichnocoenosis marks the transition between nearshore to the distal shoreface environments in the UTM, as the overlying facies are mudstone dominated distal shoreface trace fossils.

Planolites-Phycodes Ichnocoenosis

Description.— This ichnocoenosis is commonly found in laminated to alternating sandstone and mudstone bedsets (38–41 m in Fig 5), (Facies 2, 4, & 5). This ichnocoenosis ichnogenera (including: *Planolites, Phycodes, Taenidium,* and *Treptichnus*) are attributed to mostly surface and subsurface feeders, are commonly found in shallow conditions in brackish, and marine systems (e.g., Pemberton and Wightman 1992; Hauck et al 2009; Jackson et al., 2016).

Interpretation.— Occurring in the transitional zone of the Lower Channel Sandstone to the Upper Transitional Mbrs of the Muddy Fm, the Planolites-Phycodes Ichnocoenosis records a paralic to marine transition, based on the absence of rhizoliths from the underlying Fuersichnus ichnocoenosis (identified by a single *Paleobuprestis* in the LSCM) and the rapid transition to overlying Thalassinoides ichnocoenosis in the UTM. The trace fossils in this ichnocoenosis do not have the monotypic trace fossil dominated beds, nor are the trace fossils diminutive as would be expected with a salinity stressed brackish system (Jackson et al. 2016), suggesting a marine dominated system.

Bioturbation Intensity

Bioturbation intensity is high (ii4–6) over much of the Dakota Group in the study area, with the lowest intensities in the fluvial strata of the Lytle Fm and the Lower Channel Sandstone Mbr of the Muddy Fm (see Fig. 15C). Similarly, the mudstones of the Glencairn Fm and Upper

Transitional Mbr of the Muddy Fm are not highly (ii1–3) bioturbated. The majority of mudstone strata record ii1–2, whereas sandstone strata of the Plainview and Glencairn fms and Upper Transitional Mbr of the Muddy Fm are highly bioturbated with ii4–6. Generally, bioturbation intensity in the Dakota Group increases up section within each formation (see Fig. 15C). Within the Glencairn Fm, each parasequence increases in bioturbation intensity upwards (ii1–6), with parasequences 3–5 more highly bioturbated than parasequences 1–2. The Plainview and Muddy fms both increase in bioturbation up section, with the Plainview Fm increasing rapidly, and the Muddy Fm increasing from the Lower Channel Sandstone (ii1) through the transitional zone (ii1–3) and into the Upper Transitional Member (ii 2–5) before decreasing from ii5 to ii2 into the transition to the Granerous Fm.

Porosity and Permeability

Dakota Group porosity varies from 0.8% in the Glencairn Fm to 17.8% in the Muddy Fm. Within the Lytle and Plainview fms, porosity decreases up section. Porosity trends in the Glencairn Fm increase up section in parasequences (PS) 1 and 5, but decreases in PS 2 and 4; PS 3 shows a decrease followed by an increase in porosity. The LCSM of the Muddy Fm appears to show a slight decrease in porosity up section, while the UTM shows a general decrease in porosity. Porosity increased or decreased in burrows compared to the surrounding matrix in the Muddy Fm. In sandstone with mud matrix between grains, burrows commonly increased porosity (see Fig. 16A). Strata with higher intergranular porosity contained burrows with lower porosity than the surrounding matrix (see Fig. 16B–F).

Permeability is highly variable, ranging from 0.13–29.82 D in the Dakota Group, with an average permeability for each formation between 4–5 D (see Fig. 15). Within the Lytle Fm, the average pebble conglomerate permeability is lower than the coarse sandstone average (0.65 vs 13 D), with a formational average of 5.62 D. The Plainview Fm has the lowest permeability with 0.13 D at 20 cm above the Lytle-Plainview Fm contact, and a lower average permeability (4.72 D) than the underlying Lytle Fm. Generally, the upper Plainview Fm fluctuates between 0.13–15 D, with two highly bioturbated intervals with ~13 and ~14 D at ~6 and ~5 m, respectively. The Glencairn Fm has the greatest variable permeability of the Dakota Group measured in this study (Fig. 15B). The highest permeabilities occur in moderately- to well-bioturbated (ii3–4), slightly muddy sandstones in parasequences 1–3. The more highly bioturbated parasequences 4 and 5, and the upper 2 meters of parasequence 3 record lower permeabilities than the lower portion of the formation. The three highest permeabilities of the Glencairn Fm occur in muddy sandstones of parasequence 3 at ~17, ~19, and 20 m. Permeability decreases up section within the Lower Channel Sandstone Mbr, and increases up section within the Upper Transitional Mbr until the transition (i.e., last 2 m) with the overlying Graneros Fm. The maximum permeability within the Muddy Fm occurs in sandstone at ~ 46 m.

DISCUSSION

Ichnology

Trace fossils of the Dakota Group are generally similar between formations and members with similar lithofacies and depositional environments. The Lytle Fm, lower Plainview Fm, and Lower Channel Sandstone Mbr of the Muddy Fm all record continental deposystems and have similar ichnogenera. Similarly, paralic to lower shoreface strata of the upper Plainview and Glencairn fms and Upper Transitional Member of the Muddy Fm have similar ichnogenera and ichnocoenoses. Trace fossils within the five parasequences of Glencairn Fm show nearly the same diversity, distribution, and ichnocoenoses (Table 4).

Despite the similarities in ichnofossil diversity and distribution in the Dakota Group, trace fossil size distribution can be highly variable. The large variation in *Asthenopodichnium* is likely due to many of the individual borings consolidating into a larger feature that was then preserved, and not mayfly borings up to 5 cm in width. Different traces fossils show different size patterns, including sigmoidal patterns. The variation in *Thalassinoides* and similar traces is likely due to longer-term environmental stability during which the burrow networks were continuously occupied and expanded the tracemakers over an extended period of time (Lewis and Ekdale, 1992; Löwemark et al., 2016). In previous studies Alberch et al. (1979) identified that ontogenetic growth can create a sigmoidal distribution patterns in the population. *Thalassinoides* and *Ophiomorpha* show a sigmodal growth pattern, while the rest of the measured trace fossils are nearly liner in the width by width-percentile cross-plots and a few (i.e., *Phycodes* and *Arenicolites*) appear to plateau at a size. This plateau suggests the maximum size of the organisms that made those trace fossils in Skyline Drive region and that depositional time.

Ichnofacies

The Dakota Group contains four ichnofacies across the Lytle, Plainview, Glencairn, and Muddy fms (Table 3). Each ichnocoenosis is characteristic of a depositional environment and a set of physicochemical parameters and used to identify the associated ichnofacies. Using ichnofacies and their vertical trends, the stacking patterns of depositional environments and changing physicochemical conditions can be identified (e.g. Giannetti and Monaco 2015).

Scoyenia Ichnofacies.—All continental strata (Lytle, and Muddy formations) in the Dakota Group are interpreted as recording the Scoyenia Ichnofacies. This ichnofacies consists of the Dinosaur trackway, Fuersichnus, and Rhizolith ichnocoenoses, which occur in the Lytle and lower Plainview fms and the Lower Channel Sandstone Mbr of the Muddy Fm. These ichnocoenoses record the variable conditions in fluvial (including continental with the Lytle Rhizoliths) to paralic environments in continental and coastal plain environments (e.g., Bromley and Asgaard 1991; Hasiotis 2004, 2008; Hasiotis et al. 2007). Facies containing this ichnofacies are predominately sandstone with the only mudstone beds occurring in the lower Plainview Fm.

Skolithos Ichnofacies.—The Skolithos Ichnofacies was only identified in the strata that contain the transition between the Lower Channel Sandstone and Upper Transitional Mbrs of the Muddy Fm. The Planolites-Phycodes or Diplocraterion ichnocoenoses are not the archetypical associations of Skolithos ichnofacies ichnogenera, however, they record the variable conditions in these strata (Beynon and Pemberton 1992; Gingras et al. 2002; Jackson et al. 2016). Similar ichnocoenoses have described in a distal Skolithos Ichnofacies, which often grade into the Cruziana Ichnofacies (MacEachern et al., 2009).

Cruziana Ichnofacies.—The majority of marine strata in the Dakota Group are consistent with the Cruziana Ichnofacies. This ichnofacies occur in strata with Facies 2–5 and Facies associations 2 & 3 that grade from distal mudstone facies to heterolithic facies to proximal sandstone facies. The proximal portion of the Cruziana Ichnofacies occur in the upper Plainview Fm, middle and upper portions of the Glencairn Fm parasequences, and in the lower portion of the Upper Transitional Member of the Muddy Fm. These strata contain the Ophiomorpha-Thalassinoides and Thalassinoides ichnocoenoses, which are consistent with higher energy conditions (e.g., MacEachern et al. 1999). These ichnocoenoses contain an abundance of domichnia, fodinichnia, praedichnia, and cubichnia, such as *Bergaueria, Palaeophycus,* and *Thalassinoides*. The vertical succession from Phycodes, Treptichnus, through to Thalassinoides and the Ophiomorpha-Thalassinoides ichnocoenoses in the Glencairn Fm represents a transition from distal to proximal Cruziana Ichnofacies. Mudstone strata with the Helminthopsis-Phycodes Ichnocoenosis are assigned to and represent the most distal expression of the Cruziana Ichnofacies (after MacEachern et al. 2005, 2012), and occur in the base of parasequences in the Glencairn Fm, and in Muddy Fm mudstone. The abundance of ichnogenera, primarily *Helminthopsis*, with *Phycodes* and *Planolites* follow the expected dominance of deposit-feeding and grazing behaviors in calm, relatively deeper marine environments (Gingras et al. 1998; MacEachern et al. 1999, 2009). The mudstones of Glencairn parasequences 3 and 4 contain thin (≤ 10 cm thick, and 2–3 m long) HCS beds within the distal Cruziana ichnofacies, no trace fossils were noted within these beds to compare to other event deposit ichnological studies (i.e., Pemberton et al., 1997).

Facies Associations

Five facies associations (FAs) were identified within the Dakota Group (Table 5). In sum they represent a transition in the Dakota Groups from the braided channel of the Lytle Fm to the shelfal thin-bedded shales of the Muddy Fm. The component trace fossils for each facies association are key in the interpretation of the physicochemical conditions during deposition and the interpretation of their deposystems.

FA-1: Braided Channels.—This channel facies association is typified by the trough cross-bedded Lytle Fm (F1) and the majority of the Lower Channel Sandstone Mbr of the Muddy Fm. The LCSM also contains minor mudstone beds indicative of overbank deposits. The upper surface of the Lytle also contains rhizoliths, indicating subaerial exposure and colonization of the channel sands (Kraus and Hasiotis, 2006). The rare woody debris imprints with *Asthenopodichnium* (Lytle Fm) and *Paleobuprestis* (LCSM of the Muddy Fm) show the paleo-transportation and internment of branches that had been bored by insects (Moran et al., 2010)

FA-2: Paralic to Shallow Marine.—This shallow freshwater to marine facies association consists of Facies 2 overlain by Facies 3 and records the transition from a freshwater system to a marine system primarily based on the component trace fossils. The freshwater paralic facies are Facies 2—tabular muddy silt to fine-grained sandstone.. This facies includes the dinosaur trackways, *Asthenopodichnium*, and *Lockeia*. The absence of ripple laminations, with low bioturbation (ii1–3) indicated a relatively calm depositional environment (*Arenicolites*, and *Lockeia* – filter feeding associated trace fossils) with occasional input of fluvially transported plant debris. The average grainsize coarsens and ripples marks are preserved in the overlying Facies 3 component of FA-2. This transition is marked by the appearance of *Teredolites* indicating that wood was transported from a marine environment before deposition. Upsection from the *Teredolites* are the marine trace fossils of *Ophiomorpha* that then grades into *Thalassinoides* up section with high bioturbation (ii4–6) that overprints primary sedimentary structures.

FA-3: Middle to Lower Shoreface.—Facies 4 and 5 comprise the third facies association. These facies and their respective trace fossils represent suspension to deposit feeding marine organisms in a shoreface position where ripples can be formed, but calm enough for the organisms to move through the sediments feeding without significant disturbance (MacEachern and Pemberton, 1992). Facies 5 strata with the unrippled mudstones and rippled sand interbeds indicate a lower shoreface position with the fine-grained deposition and deposit feeding *Helminthopsis*, whereas, the rippled sandstone interbeds indicate pulses of higher energy deposits and contain *Phycodes* and *Planolites*. The rippled sandstone with mud interbeds of Facies 4 are interpreted as a middle shoreface or delta front, where waves can affect the sands to develop strong ripples, and shorter periods of calm for the mud interbeds. The *Thalassinoides* box-works are well developed in this FA and indicate relatively longer periods of environmental stability (Gingras et al. 2004).

FA-4: Offshore Marine.—Consisting of Facies 6, this facies association is representative of distal shoreface to shelfal conditions. The thinly laminated shales are lightly bioturbated (ii1–2) with a low diversity of trace fossils (e.g., *Arenicolites* and *Helminthopsis*) and consistent with shelfal systems (Pemberton et al., 2001) or prodelta environments (Flaig et al., 2016; Jackson et al., 2016). Additionally, the presences of fine sandstone interbeds or lenses indicates likely storm system transportation and resultant deposition onto the otherwise low energy shelf (Reinson, 1984). The lower and middle portions of the UTM, composed of mostly Facies 4 and 5 grades up section into the FA-4. This transition appears conformable and records the transition of shore from below wave-base to below storm weather wave base.

Physicochemical Controls on Trace Fossils

Identification of physicochemical controls on organisms is critical for understanding the environment at the time of deposition and during the biotic occupation of those sediments (Fig. 17; Hasiotis and Platt 2012). Marine and continental depositional environments are interpreted to have different primary physicochemical controls (Fig. 17A–B). For the Dakota Group, four sets of primary physicochemical controls are interpreted to be dominant (Fig. 17C–F) that can be used to characterize continental strata (Facies Association 1, Fig. 17C), Transitional (Facies Association 2, Fig 17D), and marine strata (Facies Associations 3 and 4, Fig. 17EF).

The Lytle Fm and Lower Channel Sandstone Mbr of the Muddy Fm record identical continental physicochemical controls (Fig 17C). In both, the groundwater profile is the fourth major control. Groundwater profile is identified as the major control based on that plants only colonized the upper surfaces and produce rhizoliths within the high-energy (trough cross bedded with pebble conglomeratic lags) fluvial environment (e.g., Kraus and Hasiotis 2006). The Lower Chanel Sandstone Mbr records an erosive event, and then contains trough-cross-bedded to unidirectional-climbing-rippled indicating that the hydrological transition (due to base level control) is controlling the facies that are preserved (e.g., Harmes et al. 1982; Weissmann et al. 2015).

Occurring solely in the Plainview Fm, Facies Association 2 records the shift between continental and marine physicochemical environments and controls in the Dakota Group as it transitional from Paralic to shallow marine depositional conditions. Ichnogenera in this transitional zone are interpreted to have been controlled by sedimentation rate, depositional energy, oxygenation, and salinity (Fig. 17D; e.g., Archer and Maples 1984). The FA-2 trace fossils record the change from the freshwater Fuersichnus to the marine Thalassinoides ichnocoenoses with the change in salinity as the delineation of the environments. The burrowing patterns shift from burrows that occur, on transported and deposited, branches in freshwater environments (*Asthenopodichnium*) in muddy fine sand to *Ophiomorpha* in muddy fine sand, finally capping in a rippled fine sandstone with *Thalassinoides*. This transition indicates that with a relative sea-level rise, the salinity shifts from fresh to marine, and the depositional energy and sedimentation rate increases through the Thalassinoides ichnocoenoses (e.g., Crimes 1975; Gingras et al. 2004).

The Glencairn Fm and Upper Transitional Mbr of the Muddy Fm contain Facies Association 3 and thus record marine environments with similar ichnological communities (ichnocoenoses), ichnofacies (Cruziana), and represent similar primary physicochemical parameters (Fig. 17E). This facies association shows variation in media and depositional energy, in that the basal mudstone beds are not rippled, but have rippled sandstones, whereas the upper beds are rippled sandstone with mudstone interbeds indicating a shift in depositional energy. The repeated alternation of ichnocoenoses (Helminthopsis-Phycodes to Thalassinoides) and facies (F-5 to F-4), is interpreted to record the Cruziana ichnofacies in a distal (mudstone dominated) to proximal (sandstone dominated) position (Pemberton et al., 1992). The Glencairn Fm ichnocoenoses repeat from a basal Helminthopsis-Phycodes through Ophiomorpha-Thalassinoides ichnocoenoses, to an upper Thalassinoides ichnocoenosis multiple times. These repeated changes are interpreted to record a series of sea-level rises and later progradation, which changes the depositional medium, and depositional energy, (e.g., Zonneveld et al. 2001; Gingras et al. 2002).

Facies Association 4 strata, occurring only in the Upper Transitional Member of the Muddy Fm, records the distal Cruziana ichnofacies and consists almost entirely of Facies 6, a thinly bedded shale. Within FA-4 the relatively consistent F-6 strata and its ichnological constituents (e.g., Helminthopsis, Phycodes, and event beds with Diplocraterion) indicate a consistent benthic oxygenation regime, sedimentation rate, and depositional energy, with nutrients interpreted as the fourth point of the physicochemical tetrahedron based on the trace fossil community being primarily deposit feeders (Pemberton et al., 2001) (Fig. 17F)

Sequence Stratigraphy

Three major Cretaceous unconformities (K0–2), two major transgressive surfaces—one of which is a transgressive surface of erosion (TSE, following Allen and Posmontier 1993)—and five Glencairn Fm parasequences have been identified based on lithofacies, ichnocoenoses, and ichnofacies in this study (see Fig. 5C). The overall trend of transgression for the Dakota Group, with smaller transgressive pulses within the Plainview, Glencairn, and Muddy fms agrees with previous studies (e.g., Waage 1953; Altschuld 1980; Gustason and Kauffman 1985; Odien 1997). The major differences between this and previous studies is the interpreted TSE placement of the Plainview-Glencairn fm contact (i.e., Gustason and Kauffman 1985) and the number of Glencairn Fm parasequences (i.e., Odien 1997).

Relative sea level fell after Plainview Fm deposition, creating an erosive surface, which was then transgressed over during the beginning of the Skull Creek Transgression (e.g., Cattaneo and Steel 2003). The placement of Plainview-Glencairn fm contact TSE is based on the identification the basal Glencairn Fm pebble conglomerate, which has filled in a previous scour into a Plainview Fm *Thalassinoides* bed, and then overlain by shelfal mudstones. Previous studies place the contact ~4 m further down section into the Plainview Fm at the continental to marine trace fossil change (Gustason and Kauffman 1985). The Glencairn Fm five parasequences were identified based on repeated coarsening upward lithofacies that record distal to proximal Cruziana ichnofacies (e.g. Pemberton and MacEachern 1995). Within each successive parasequence, they consist of thicker more highly bioturbated proximal Cruziana Ichnofacies sandstone beds (F-4) up section. The Muddy Fm records a complex series of relative sea-level changes. The fluvial system that deposited the lower Channel Sandstone Mbr eroded into the Glencairn Fm before the start of the Greenhorn Transgression, with shoreface and delta facies (e.g., Gustason and Kauffman 1985; Odien 1997).

Ichnological Effects on Hydrocarbon Systems

Each formation of the Dakota Group has been explored for resources, described both as conventional and unconventional petroleum systems, along the Front Range (Higley and Cox 2007). Fluid flow through a single trace fossil is of a lower volume than in fractures; but trace fossils are more abundant in most reservoir facies (e.g., Gingras et al. 1999, 2012; Golab et al. 2017a); thus, the abundance of bioturbation is critical to characterize, understand, and model for reservoir facies. Variation of bioturbation intensity influences conductivity more than the presence of any one burrow (Gingras et al. 1999; Golab et al. 2017b). La Croix et al. (2012) showed, via modeling, that continuous flow pathways are developed through the bioturbated regions when strata are 20–30% bioturbated. The Muddy Fm along Skyline Drive Hogback, records an increasing bioturbation intensity (ii1–5) with a decreasing permeability from a high of 20 D down to 5 D. In these strata, the changes in bioturbation intensity and permeability do not correlate with the changes in porosity.

Dakota Group strata record increases and decreases in porosity and/or permeability depending on the relationship between bioturbation intensity, formation, and lithofacies. In general, the more highly bioturbated strata have lower porosities than low to unbioturbated strata (see Fig. 15). The greatest porosity was found in the Muddy Fm, near the Lower Channel Sandstone Mbr and Upper Transitional Mbr contact, with the second highest porosities in the lower Lytle Fm, both of which are effectively unbioturbated. Porosity generally decreases through the Lytle, Plainview, and Glencairn fms, but increases from the fifth Glencairn parasequence through the Lower Channel Sandstone Mbr. Porosity exhibits a decreasing trend in the Upper Transitional Mbr but increases over the last 3 m of section. Porosity tends to decrease with higher bioturbation intensities. This trend is most clear in the Lytle to Glencairn fms, where lower porosity occurs at near identical positions to strata with ii4–6. Similarly, in the Upper Transitional Mbr, the increase from ii3 to ii5 trends with a drop-in porosity from ~18–5 % (Fig. 15). Within the Glencairn Fm, the strata with the highest bioturbation intensity also have the highest permeability. Highly bioturbated strata (ii5–6) can increase permeability up to 300% (10 D to 30 D) within lower and middle sections of each Glencairn Fm parasequences (Fig. 15). These high permeabilities occur in *Thalassinoides*-ichnocoenoses dominated sandstones. The higher permeabilities in the bioturbated sandstone of Glencairn Fm agree with other studies elsewhere that identified high permeability in strata with abundant trace fossils (e.g., Gingras et al. 1999, La Croix et al. 2012, Baniak et al. 2015; Hsieh et al. 2015; Golab et al., 2017a,b).

CONCLUSION

This study identified 31 ichnogenera from continental and marine strata in the Cretaceous Dakota Group at the Skyline Drive Hogback, in Cañon City, CO. Seven ichnocoenoses—two from continental depositional environments and five from marine depositional environments—are characteristic of three ichnofacies (Scoyenia, Skolithos, and Cruziana ichnofacies). Ichnodiversity varies throughout the Dakota Group: lowest in the Lytle Fm, and highest in the Glencairn Fm. The progradational parasequence set of the Glencairn Fm records a general increase in trace fossil size and bioturbation intensity, and a reduction in ichnodiversity up section as the sandstone:shale ratio increases. Trace fossils affect permeability and porosity of Dakota Group strata differently based on the lithofacies and bioturbation intensity. Where bioturbation intensity is highest, strata generally record higher permeabilities and lower porosity values. Trace fossils in the well- to highly bioturbated (ii4–6) sandstones of the Glencairn and

Muddy fms could be hydrocarbons flow conduits in these resource-rich formations. This study confirmed a fifth parasequence within the Glencairn Fm, based on the ichnology and vertical successions of ichnofacies, and reaffirms the position of the Plainview Fm-Glencairn Fm contact in this area.

ACKNOWLEDGEMENTS

We thank D. Woodring, C. & B. Smith, M. Smeins, and C. Jackson for assistance in the field. Additional thanks to Royal Gorge Outfitters for property access. We recognize The Geological Society of America, Paleontological Society (Rodney M Feldman Award), and American Association of Petroleum Geologists (Raymond C. Moore Memorial Grant) for student research grants to A.M.J. We also recognize KU Geology for summer support and facility use in Cañon City, CO, to A.M.J. Thanks to the IBGS Research group for comments on an earlier version of this manuscript.

REFERENCES

ALBERCH, P., GOULD, S.J., OSTER, G.F., AND WAKE, D.B., 1979, Size and shape in ontogeny and phylogeny, Paleobiology, v. 5, p. 296–317.

ALTSCHULD, K.R., 1980, Stratigraphy and depositional environments of the Dakota Group. Canon City area, Colorado: MS thesis, Colorado School Mines, Golden.

ALLEN, G.P., AND POSAMENTIER, H.W., 1993, Sequence stratigraphy and facies model of an incised valley fill: The Gironde estuary, France: Journal of Sedimentary Petrology, v. 63, p. 378–391.

ARCHER, A.W. AND MAPLES, C.G., 1984, Trace-fossil distribution across a marine-to-nonmarine gradient in the Pennsylvanian of southwestern Indiana. Journal of Paleontology, v. 58, p.448–466.

ARPS, J.J. AND ROBERTS, T.G., 1958, Economics of drilling for Cretaceous oil on east flank of Denver-Julesburg basin: AAPG Bulletin, v. 42, p. 2549–2566.

BANIAK, G.M., GINGRAS, M.K., BURNS, B.A. AND PEMBERTON, S.G., 2015, Petrophysical Characterization of Bioturbated Sandstone Reservoir Facies in the Upper Jurassic Ula Formation, Norwegian North Sea, Europe: Journal of Sedimentary Research, v. 85, p. 62–81.

BASAN, P., AND SCOTT, R., 1979, Morphology of Rhizocorallium and associated traces from the Lower Cretaceous Purgatoire Formation. Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 28, p. 5–23.

BEYNON, B.M., AND PEMBERTON, S.G., 1992, Ichnological signature of a brackish water deposit: an example from the Lower Cretaceous Grand Rapids Formation, Cold Lake oil sands area, Alberta, in PEMBERTON, S.G., (ed.), Applications of Ichnology to Petroleum Exploration: SEPM Core Workshop Notes 17, p. 199–221.

BJERSTEDT, T.W., 1988, Multivariate analyses of trace fossil distribution from an Early Mississippian oxygen-deficient basin, central Appalachians. PALAIOS, v. 3. p. 53–68.

BOWN, T.M., 1982, Ichnofossils and rhizoliths of the nearshore fluvial Jebel Qatrani Formation (Oligocene), Fayum Province, Egypt: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 40, p. 255–309.

BOUMA, H.A. 1969, Methods for the Study of Sedimentary Structures. Kringer, Huntington, NY. 458 pages

BROMLEY, R.G, 1996, Trace Fossils: Biology, Taphonomy and Applications. Chapman & Hall, London, 361 pp.

BROMLEY, R.G. AND ASGAARD, U., 1991, Ichnofacies: a mixture of taphofacies and biofacies: Lethaia, v. 24, p. 153–163.

BROMLEY, R.G. AND HANKEN, N.M., 1991, The growth vector in trace fossils: examples from the Lower Cambrian of Norway: Ichnos, v. 1, p. 261–276.

BURTNER, R.L., AND WARNER, M.A., 1984, Hydrocarbon generation in Lower Cretaceous Mowry and Skull Creek Shales of the Northern Rocky Mountain area, in WOODWARD, JANE, MEISSNER, F.F., AND CLAYTON, J.L., (eds.), Hydrocarbon source rocks of the Greater Rocky Mountain Region: Rocky Mountain Association of Geologists, p. 449–467.

CATTANEO, A. AND STEEL, R.J., 2003, Transgressive deposits: a review of their variability. Earth-Science Reviews, v. 62, p. 187–228.

CHAMBERLAIN, C., 1976, Field Guide to the trace fossils of the Cretaceous Dakota Hogback along Alameda Avenue, west of Denver Colorado: in EPIS, R., AND WEIMER, R., (eds.), Studies in Colorado field geology: Professional Contributions of Colorado School of Mines, v. 8, p. 242–250.

COMPTON, R.R., 1985, Geology in the Field. Wiley, New York.

CRIMES, T.P., 1975, The production and preservation of trilobite resting and furrowing traces: Lethaia, v. 8, p. 35–48.

CUNNINGHAM, K.J. AND SUKOP, M.C., 2012, Megaporosity and Permeability of Thalassinoides-Dominated Ichnofabrics in the Cretaceous Karst-Carbonate Edwards-Trinity Aquifer System, Texas: U.S. Geological Survey Open-File Report 2012-1021, 4 p.

DASHTGARD, S.E., 2011, Linking invertebrate burrow distributions (neoichnology) to physicochemical stresses on a sandy tidal flat: implications for the rock record: Sedimentology, v. 58, p. 1303–1325.

DASHTGARD, S.E. AND GINGRAS, M.K., 2012, Marine invertebrate neoichnology. Trace fossils as indicators of sedimentary environments: Developments in Sedimentology, v. 64, p. 273–295.

DOLSON, J.C., AND WEIMER, R.J., 1992, Examples of unconformities of related systems tracts, Cretaceous through Precambrian strata, Front Range (Colorado) and Wyoming, in FLORES, R.M., (ed.), Field Trip Guidebook, Mesozoic of the Western Interior, SEPM (Society for Sedimentary Geology) 1992 Theme Meeting, p. 55–74.

DROSER, M.L., AND BOTTJER, D.J., 1986, A semiquantitative field classification of ichnofabric: Journal of Sedimentary Research, v. 56, p. 558–559.

DYMAN, T.S., MEREWETHER, E.A., MOLENAAR, C.M., COBBAN, W.A., OBRADOVICH, J.C., WEIMER, R. J., AND BRYANT, W.A., 1994, Stratigraphic transects for Cretaceous rocks, Rocky Mountains and Great Plains regions, in CAPUTO, M.V., PETERSON, J.A., AND FRANCZYK, K.J., (eds.), Mesozoic systems of the Rocky Mountain region, U.S.A.: Denver, Colorado, SEPM, Rocky Mountain Section, p. 365–392.

EASTHOUSE, K.A. AND DRIESE, S.G., 1988, Paleobathymetry of a Silurian shelf system: application of proximality trends and trace-fossil distributions: PALAIOS, v. 3. p.473–486.

ELLIOTT, R.E., 1984, September. An interpretation of the trace fossil Cochlichnus kochi (Ludwig) from the East Pennine Coalfield of Britain, in, Proceedings of the Yorkshire Geological and Polytechnic Society, Geological Society of London, v. 45, p. 183–187).

FLAIG, P.P., HASIOTIS, S.T., AND JACKSON, A.M., 2016, An Early Permian, paleopolar, postglacial, river-dominated deltaic succession in the Mackellar–Fairchild formations at Turnabout Ridge, Central Transantarctic Mountains, Antarctica. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, p. 241–265.

FREY, R. 1975, The realm of ichnology: its strengths and limitations. In: FREY, R. (ed.) The Study of Trace Fossils. Springer-Verlag, Berlin, p. 18–38.

FREY, R.W., HOWARD, J.D. AND PRYOR, W.A., 1978, *Ophiomorpha*: its morphologic, taxonomic, and environmental significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 23, p. 199–229.

GANI, M.R., BHATTACHARYA, J.P., AND MACEACHERN, J.A., 2008, Using ichnology to determine the relative influence of waves, storms, tides, and rivers in deltaic deposits: Examples from Cretaceous Western Interior seaway, U.S.A., in MACEACHERN, J.A., BANN, K.L., GINGRAS, M.K., AND PEMBERTON, S.G., (eds.), Applied ichnology: SEPM Short Course Notes 52, p. 209–225.

GIANNETTI, A. AND MONACO, P., 2015, Definition of sequences through ichnocoenoses and taphofacies: An example from the Sácaras Formation (early Cretaceous, eastern Spain): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 438, p. 70–80.

GINGRAS, M.K., BANIAK, G., GORDON, J., HOVIKOSKI, J., KONHAUSER, K.O., LA CROIX, A., LEMISKI, R., MENDOZA, C., PEMBERTON, S.G., POLO, C. AND ZONNEVELD, J.P., 2012, Porosity and permeability in bioturbated sediments. Trace Fossils as Indicators of Sedimentary Environments: Developments in Sedimentology, v. 64, p.837–868.

GINGRAS, M.K., MACEACHERN, J.A. AND DASHTGARD, S.E., 2011, Process ichnology and the elucidation of physico-chemical stress: Sedimentary Geology, v. 237, p. 115–134.

GINGRAS, M.K., MACEACHERN, J.A. AND PEMBERTON, S.G., 1998, A comparative analysis of the ichnology of wave-and river-dominated allomembers of the Upper Cretaceous Dunvegan Formation: Bulletin of Canadian Petroleum Geology, v. 46, p. 51–73.

GINGRAS, M.K., MACEACHERN, J.A. AND PICKERILL, R.K., 2004, Modern perspectives on the Teredolites ichnofacies: observations from Willapa Bay, Washington: PALAIOS, v. 19, p. 79–88.

GINGRAS, M.K., PEMBERTON, S.G., MENDOZA, C.A., AND HENK, F., 1999, Assessing the anisotropic permeability of *Glossifungites* surfaces: Petroleum Geoscience, v. 5, p. 349–357.

GINGRAS, M.K., RASANEN, M.E., PEMBERTON, S.G. AND ROMERO, L.P., 2002, Ichnology and sedimentology reveal depositional characteristics of bay-margin parasequences in the Miocene Amazonian foreland basin: Journal of Sedimentary Research, v. 72, p. 871–883.

GOLAB, J. A., SMITH, J. J., CLARK, A. K., AND BLOME, C. D., 2017a, Effects of *Thalassinoides* ichnofabrics on the petrophysical properties of the Lower Cretaceous Lower Glen Rose Limestone, Middle Trinity Aquifer, Northern Bexar County, Texas: Sedimentary Geology, v. 351, p. 1-10.

GOLAB, J. A., SMITH, J. J., CLARK, A. K., AND MORRIS, R. R., 2017b, Bioturbation-influenced fluid pathways within a carbonate platform system: The Lower Cretaceous (Aptian-Albian) Glen Rose Limestone: Palaeogeography Palaeoclimatology Palaeoecology, v. 465, p. 138-155.

GOSS, D. AND ZLOTNIK, V.A., 2007, Air permeameter investigation of surficial dune structures in the Nebraska Sand Hills: American Association of Petroleum Geologists Bulletin, v. 91, p. 645–652.

GROVE, C. AND JERRAM, D.A., 2011, jPOR: An ImageJ macro to quantify total optical porosity from blue-stained thin sections: Computers & Geosciences, v. 37, p. 1850–1859.

GUSTASON, E., AND KAUFFMAN, E., 1985, The Dakota Group and the Kiowa-Skull Creek Cyclothem on the Cañon City-Pueblo area, Colorado: SEPM Guidebook No. 4, p. 72–89.

HART, B.S., 2015, The Greenhorn Cyclothem of the Cretaceous Western Interior Seaway: Lithology Trends, Stacking Patterns, Log Signatures, and Application to the Eagle Ford of West Texas: Gulf Coast Association of Geological Societies Transactions, v. 65, p. 155–174.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, 177–268.

HASIOTIS, S.T., 2008, Reply to the Comments by Bromley et al., of the paper “Reconnaissance of the Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses” by Stephen T. Hasiotis: Sedimentary Geology, v. 208, 61–68.

HASIOTIS, S.T. AND MITCHELL, C.E., 1993, A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo-and neo-ichnological evidence, and the identification of their burrowing signatures: Ichnos, v. 2, p. 291–314.

HASIOTIS, S.T., KRAUS, M.J., AND DEMKO. T.M., 2007, Climate controls on continental trace fossils, in MILLER, W., III, (ed.), Trace Fossils—Concepts, Problems, Prospects: Elsevier, Amsterdam, p. 172–195.

HASIOTIS, S.T. AND PLATT, B.F., 2012, Exploring the sedimentary, pedogenic, and hydrologic factors that control the occurrence and role of bioturbation in soil formation and horizonation in continental deposits: An integrative approach. The Sedimentary Record, v. 10, p. 4–9.

HAUCK, T.E., DASHTGARD, S.E., PEMBERTON, S.G. AND GINGRAS, M.K., 2009, Brackish-water ichnological trends in a microtidal barrier island–embayment system, Kouchibouguac National Park, New Brunswick, Canada: PALAIOS, v. 24, p. 478–496.

Higley, D.K., and Cox, D.O., 2007, Oil and gas exploration and development along the Front Range in the Denver Basin of Colorado, Nebraska, and Wyoming, in, Higley, D.K. (ed.), Petroleum systems and assessment of undiscovered oil and gas in the Denver Basin Province, Colorado, Kansas, Nebraska, South Dakota, and Wyoming—USGS Province 39: U.S. Geological Survey Digital Data Series DDS–69–P, 41 p.

HIGLEY, D.K., POLLASTRO, R.M., AND CLAYTON, J.L., 1995, Denver Basin Province (039), in GAUTIER, D.L., DOLTON, G.L., TAKAHASHI, K.I., AND VARNES, K.L., ed., 1995, National Assessment of United States oil and gas resources; Results, methodology, and supporting data: U.S. Geological Survey Digital Data Series DDS-30, Release 2, one CD-ROM.

HOLBROOK, J.M. AND DUNBAR, R.W., 1992, Depositional history of Lower Cretaceous strata in northeastern New Mexico: Implications for regional tectonics and depositional sequences: Geological Society of America Bulletin, v. 104, p. 802–813.

HOLBROOK, J.M., AND ETHRIDGE, F.G., 1996, Sequence stratigraphy of the Dakota Group and equivalents from northcentral Colorado to northeastern New Mexico: downdip variations in sequence anatomy: Geologic Excursions to the Rocky Mountains and Beyond, 1996 GSA Guidebook, Colorado Geological Survey Special Publication 44. 44 p.

HSIEH, A.I., ALLEN, D.M. AND MACEACHERN, J.A., 2015, Statistical modeling of biogenically enhanced permeability in tight reservoir rock: Marine and Petroleum Geology, v. 65, p. 114–125.

JACKSON, A.M., HASIOTIS, S.T., AND FLAIG, P.P., 2016, Ichnology of a Paleopolar, River-Dominated, Shallow Marine Deltaic Succession in the Mackellar Sea: The Mackellar Formation (Lower Permian), Central Transantarctic Mountains, Antarctica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, p. 266–291.

KAUFFMAN, E.G., 1984, Paleobiogeography and evolutionary response dynamic in the Cretaceous Western Interior Seaway of North America, in WESTERMAN G., (ed.) Jurassic-Cretaceous biochronology and paleogeography if North America: GAC, SP27, p. 297–335.

KIRSCHBAUM, M.A., AND SCHENK, CJ., 2011, Sedimentology and reservoir heterogeneity of a valley-fill deposit-a field guide to the Dakota Sandstone of the San Rafael Swell, Utah. U.S. Geological Survey Scientific Investigations Report: 2010-5222, 36 pp.

KRAUS, M.J. AND HASIOTIS, S.T., 2006, Significance of different modes of rhizolith preservation to interpreting paleoenvironmental and paleohydrologic settings: examples from Paleogene paleosols, Bighorn Basin, Wyoming, USA: Journal of Sedimentary Research, v. 76, p. 633–646.

KURTZ, W.J., LOCKLEY, M.G. AND ENGARD, D.J., 2001, Dinosaur Tracks in the Plainview Formation, Dakota Group (Cretaceous, Albian) near Canon City, Colorado: A Preliminary Report on Another "Dinosaur Ridge": Mountain Geologist, v. 38, p. 155-164.

LA CROIX, A.D., GINGRAS, M.K., DASHTGARD, S.E., PEMBERTON, S.G., 2012, Computer modeling bioturbation: the creation of porous and permeable fluid-flow pathways: American Association of Petroleum Geologists Bulletin. v. 96, p. 545–556.

LEWIS, D.W., AND EKDALE, A.A., 1992, Composite ichnofabric of a mid-Tertiary unconformity on a pelagic limestone, Palaios, v. 7, p. 222–235.

LOCKLEY, M.G., CART, K., MARTIN, J.., PRUNTY, R.., HOUCK, K.., HUPS, K.., LIM, J., KIM, K.S., GIERLINSKI, G., AND MILNER, A., 2014, A bonanza of new tetrapod tracksites from the Cretaceous Dakota Group, western Colorado: implications for paleoecology: New Mexico Museum of Natural History and Science Bulletin, v. 62, p. 393–409.

LOCKLEY, M.G., MCCREA, R.T., BUCKLEY, L.G., LIM, J.D., MATTHEWS, N.A., BREITHAUPT, B.H., HOUCK, K.J., GIERLIŃSKI, G.D., SURMIK, D., KIM, K.S. AND XING, L., 2016, Theropod courtship: large scale physical evidence of display arenas and avian-like scrape ceremony behaviour by Cretaceous dinosaurs: Scientific reports 6, p.18952-18952.

LONG, C.S., JR.,1966, Basal Cretaceous strata, southeastern Colorado: unpublished Ph. D. thesis, Univ. of Colorado. 479 p.

LÖWEMARK, L., ZHENG, Y.C., DAS, S., YEH, C.P., AND CHEN, T.T., 2016, A peculiar reworking of Ophiomorpha shafts in the Miocene Nangang Formation, Taiwan, Geodinamica acta, v. 28, p. 71–85.

LUCAS, S.G., SULLIVAN, R.M., AND ROBINSON R.F., 2015, The Trace Fossil *Asthenopodichnium* from the Upper Cretaceous of the San Juan Basin, New Mexico, in, SULLIVAN, R.M. AND LUCAS, S.G., (eds.), Fossil Record 4. New Mexico Museum of Natural History and Science Bulletin 67. p. 217–220.

MACEACHERN, J.A., BANN, K.L., PEMBERTON, S.G., AND GINGRAS, M.K., 2005, The ichnofacies paradigm: high-resolution paleoenvironmental interpretation of the rock record, in MACEACHERN, J.A., BANN, K.L., GINGRAS, M.K., PEMBERTON, S.G., (eds.), Applied Ichnology. SEPM Short course, 52, p. 1–33.

MacEachern, J.A., and Pemberton, S.G., 1992, Ichnological aspects of Cretaceous shoreface successions and shoreface variability in the Western Interior Seaway of North America, in Pemberton, S.G., ed., Applications of Ichnology to Petroleum Exploration, A Core Workshop: SEPM, Core Workshop, 17, p. 57–84.

MacEachern, J.A., Pemberton, S.G., Bann, K.L., and Gingras, M.K., 2007, Departures from the archetypal ichnofacies: effective recognition of environmental stress in the rock record, in MacEachern, J.A., Bann, K.L., Gingras, M.K., and Pemberton, S.G., (eds.), Applied Ichnology: SEPM, Short Course Notes 52, p. 65–93.

MacEachern, J.A., Stelck, C.R., and Pemberton, S.G., 1999, Marine and marginal marine mudstone deposition: paleoenvironmental interpretations based on the integration of ichnology, palynology and foraminiferal paleoecology, in Bergman, K.M., and Snedden, J.W., (eds.), Isolated Shallow Marine Sand Bodies: Sequence Stratigraphic and Sedimentologic Interpretation: SEPM, Special Publication 64, p. 205–225

MacEachern, J.A., Bann, K.L., Pemberton, S.G., and Gingras, M.K., 2009, The ichnofacies paradigm: high-resolution paleoenvironmental interpretation of the rock record. in MacEachern, J.A., Bann, K.L., Gingras, M.K., and Pemberton, S.G., (eds.), Applied Ichnology: SEPM, Short Course Notes 52, p 27–64.

MacEachern, J.A., Bann, K.L., Gingras, M.K., Zonneveld, J.P., Dashtgard, S.E. and Pemberton, S.G., 2012, The ichnofacies paradigm. Trace fossils as indicators of sedimentary environments. Developments in Sedimentology 64, p. 103–138.

MacKenzie, D., 1965, Depositional Environments of Muddy Sandstone, Western Denver Basin, Colorado: AAPG Bulletin, v. 49, p. 186–206.

MARTIN, A.J., BLAIR, M., DATTILO, B.F., HOWALD, S., AND FARLOW, J.O., 2016, The ups and downs of Diplocraterion in the Glen Rose Formation (Lower Cretaceous), Dinosaur Valley State Park, Texas (USA), Geodinamica Acta, v. 28, p. 101–119.

MATEER, N.J., 1987, The Dakota Group of northeastern New Mexico and southern Colorado. In Northeastern New Mexico: New Mexico Geological Society guidebook, 38th Field Conference, Northeastern New Mexico, p. 223–236.

MEEK, F.B., AND F.V. HAYDEN, 1861, Descriptions of new Lower Silurian (Primordial), Jurassic, Cretaceous, and Tertiary fossils, collected in Nebraska Territory, with some remarks on the rocks from which they were obtained: Proceedings Academy Natural Philadelphia, p. 415–447.

MORAN, K., HILBERT-WOLF, H.L., GOLDER, K., MALENDA, H.F., SMITH, C.J., STORM, L.P., SIMPSON, E.L., WIZEVICH, M.C. AND TINDALL, S.E., 2010, Attributes of the wood-boring trace fossil Asthenopodichnium in the Late Cretaceous Wahweap Formation, Utah, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 297, p. 662–669.

ODIEN, R., 1997, The Dakota Group of South-Central Colorado. Controls on Stratigraphy Sedimentation and Ichnology, Volume I, Boston University, Boston, Massachusetts, 377 p.

ODIEN, R.J., 1998, The Morrison Formation Dakota Group Contact along the northeastern flank of the Wet Mountains, Colorado: Evidence for a reinterpretation of Lytle Formation thickness: The Mountain Geologist, v. 35, p. 1–14.

PEMBERTON, S.G. AND GINGRAS, M.K., 2005, Classification and characterizations of biogenically enhanced permeability. AAPG bulletin, v. 89, p. 1493–1517.

PEMBERTON, S.G., AND MACEACHERN, J.A., 1995, The sequence stratigraphic significance of trace fossils: examples from the Cretaceous foreland basin of Alberta, Canada. in VAN

WAGONER, J.C., AND BERTRAM, G.T., (eds.), Sequence stratigraphy of foreland basin deposits; outcrop and subsurface examples from the Cretaceous of North America. American Association of Petroleum Geologists Memoir 64, p. 429–475.

PEMBERTON, S.G., MACEACHERN, J.A., AND BRETT, C.E., 1997, The ichnological signature of storm deposits: the use of trace fossils in event stratigraphy. Paleontological Events. Stratigraphic, ecological and evolutionary implications. Columbia University Press, New York, p. 73–109.

PEMBERTON, S., SPILA, M., PULHAM, A., SAUNDERS, T., MACEACHERN, J., ROBBINS, D., AND SINCLAIR, I., 2001, Ichnology and Sedimentology of Shallow to Marginal Marine Systems: Ben Nevis and Avalon Reservoirs, Jeanne d'Arc Basin, GAC, Short Course Notes, 15, 343 p.

PEMBERTON, S.G., VAN WAGONER, J.C., AND WACH, G.D., 1992, Ichnofacies of a wave-dominated shoreline, in PEMBERTON, S.G., (ed.), Applications of Ichnology to Petroleum Exploration, , SEPM Core Workshop 17, p. 339–382.

PEMBERTON, S.G. AND WIGHTMAN, D.M., 1992, Ichnological characteristics of brackish water deposits, in PEMBERTON, S.G., (ed.), Applications of Ichnology to Petroleum Exploration, , SEPM Core Workshop 17, p. 141–167.

PRUIT, J.D., and COFFIN, P.E., 1978, Energy resources of the Denver Basin. Denver: Rocky Mountain Association of Geologists, 272 pp.

R CORE TEAM, 2015, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. R 3.2.2 Fire Safety.

RASBAND, W.S., 2015, ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997–2015.

REINSON, G.E., 1984, Barrier-island and associated strand-plain systems, in WALKER, R.G., (ed.), Facies Models, second edition: p. 119–140. Geoscience Canada, Geological Association of Canada.

RODRÍGUEZ-TOVAR, F.J., UCHMAN, A., PAYROS, A., ORUE-ETXEBARRIA, X., APELLANIZ, E. AND MOLINA, E., 2010, Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 285, p. 50–65.

SEILACHER, A., 1967, Bathymetry of trace fossils, Marine Geology, v. 5, p. 413–428.

SEILACHER, A., 1978, Use of trace fossil assemblages for recognizing depositional environments, in BASAN, P.B. (ed.), Trace Fossil Concepts, SEPM Short Course 5, p. 167–181.

SMITH, J. J., HASIOTIS, S. T., KRAUS, M. J., AND WOODY, D. T., 2008, Relationship of floodplain ichnocoenoses to paleopedology, paleohydrology, and paleoclimate in the Willwood Formation, Wyoming, during the Paleocene-Eocene Thermal Maximum: PALAIOS, v. 23, no. 10, p. 683-699.

TAINTER, P.A., 1984, Stratigraphic and paleostructural controls on hydrocarbon migration in Cretaceous D and J sandstones of the Denver Basin, in WOODWARD, J.F., MEISSNER, F.F., AND CLAYTON, J.L., (eds.), Hydrocarbon source rocks of the greater Rocky Mountain region: Rocky Mountain Association of Geologists, p. 339–354.

TAYLOR, A.M. AND GAWTHORPE, R.L., 1993, Application of sequence stratigraphy and trace fossil analysis to reservoir description: examples from the Jurassic of the North Sea. In Geological Society, London: Petroleum Geology Conference series, v.4, p. 317–335.

WAAGE. K., 1953, Refractory clay deposits of south-central Colorado US Geological Survey Bulletin 993, 104 p.

WAAGE, K., AND EICHER, D.L., 1960, Dakota Group in northern Front Range area: Guide to the Geology of Colorado; Rocky Mountain Association of Geologists, p. 230–237.

WALASZCZYK, I., AND COBBAN, W.A., 2016, Inoceramid bivalves and biostratigraphy of the upper Albian and lower Cenomanian of the United States Western Interior Basin: Cretaceous Research, v. 59, p. 30–68.

WEIMER, R.J., 1971, Stratigraphy and Petroleum Potential of Dakota Group (Cretaceous), Western Denver Basin, Colorado: AAPG Bulletin, v. 55, p. 544–544.

WEIMER, R.J., 1983, Relation of unconformities, tectonics and sea level changes, Cretaceous of the Denver basin and adjacent areas, in REYNOLDS, M.W., DOLLY, E.D. (eds.), Mesozoic Paleogeography of West-Central United States, Rocky Mountain Section SEPM, pp. 359–376.

WEIMER, R.J. AND SONNENBERG, S.A., 1989, Sequence stratigraphic analysis of Muddy (J) sandstone reservoir, Wattenberg field, Denver basin, Colorado, in COALSON, E., (ed.), Sandstone reservoirs: Denver, Colorado: Rocky Mountain Association of Geologists, p.197–220.

WEIMER, R.J., DOLSON, J.C., ETHRIDGE, F.G., AND WARME, J., 1990, 2-Day Geology Field Trip, Sequence Stratigraphy-Lower K, Fort Collins, Boulder, Morrison Area: Rocky Mountain Association of Geologists, 130 p.

WEISSMANN, G.S., HARTLEY, A.J., SCUDERI, L.A., NICHOLS, G.J., OWEN, A., WRIGHT, S., FELICIA, A.L., HOLLAND, F. AND ANAYA, F.M.L., 2015, Fluvial geomorphic elements in modern sedimentary basins and their potential preservation in the rock record: A review: Geomorphology, v. 250, p. 187–219.

WESCOT, W., 1979, Lower Dakota Group depositional environments and stratigraphic evolution: Colorado Front Range, Larimer County, Colorado, in ETHRIE, F., (ed.), Field Guide northern Front Range and northwest Denver Basin, Colorado: Rocky Mountain Section, GSA, p. 57–85.

YOUNG, R.G. 1960, Dakota Group of Colorado Plateau: AAPG Bulletin, v. 44, p. 156–194.

ZONNEVELD, J.P., GINGRAS, M.K. AND PEMBERTON, S.G., 2001, Trace fossil assemblages in a Middle Triassic mixed siliciclastic-carbonate marginal marine depositional system, British Columbia. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 166, p. 249–276.

TABLES

***TABLE 1**—Facies identified in the Dakota Group.*

Lithofacies	1	2	3	4	5	6
	Trough cross-stratified sandstone	Tabular muddy silt to fine sand	Ripple cross-laminated to massive medium to very-fine sand	Ripple cross-laminated fine sand with mudstone lenses	Silty mudstone with rippled fine to very fine-sandstone lenses	Thin-bedded shale
Formation(s)	Lytle Fm, Muddy Fm	Plainview Fm, Glencairn Fm, Muddy Fm	Plainview Fm, Glencairn Fm, Muddy Fm	Glencairn Fm, Muddy Fm	Glencairn Fm, Muddy Fm	Plainview Fm, Glencairn Fm, Muddy Fm
II	1–2	2–3	3–6	4–5	3–4	1–2
Common Trace Fossils	*Paleobuprestis*, *Skolithos*, rhizoliths	Dinosaur tracks, *Asthenopodichnium*, *Fuersichnus*, rhizoliths	*Ophiomorpha*, *Teredolites*, *Thalassinoides*	*Ophiomorpha*, *Planolites*, *Thalassinoides*	*Chondrites*, *Helminthopsis*, *Phycodes*, *Planolites*, *Treptichnus*	*Chondrites*, *Planolites*, *Skolithos*
Avg. Air Perm (D)	5.62	4.92	4.53	3.46	2.93	<1
Thickness (cm)	20–170	18–50	11–430	8–83	13–51	2–42
Lithology	White to light rusty tan, erosional base and is composed of trough cross-bedded, coarse- to medium-grained sandstone that may have a pebble lag in the base of the basal troughs. Trough cross-beds in the Lytle Fm are coarser grained than those in the lower channel sandstone member of the Muddy Fm	Black to dark grey, silt that quickly coarsens upward to orange-tan fine-grained sand within one meter; discrete beds of muddier or sandier silts	Buff to light orange, the symmetrically rippled, sandstone contains some lithic fragments and impressions of woody debris. Dominant facies for much of the Plainview and the upper portions of each Glencairn Fm parasequences	Buff to rusty tan, symmetrically rippled, fine-grained sandstone with light to dark grey mud drapes or interbedded with thin (< 1 cm) mud beds	Light grey to black mudstone with interbedded buff to rusty rippled sandstone lenses	Black to grey highly laminated fissile shale with buff very fine- to fine-grained sandstone interbeds; are discontinuous bentonite beds

***Table 2**— Dakota Group trace fossil ichnotaxonomy.*

Ichnogenera	Stratigraphic Occurrence	Description	Interpreted Behavior
Arenicolites	Glencairn and Muddy fms	U-shaped burrow with paired vertical shafts; ≤ 9 mm separation between shaft ends; shaft varies from 1.1–8.4 mm in diameter	Dwelling, Suspension feeding
Asthenopodichnium	Lytle and Plainview fms	Oblong borings into fossil xylic media; 1.26–7.07 mm long, and ≤ 52 mm wide	Dwelling, Reproduction
Aulichnites	Muddy Fm	Trail with two convex ridges separated by a median furrow; ≤ 189 mm long and 20 mm wide	Feeding, Locomotion
Bergaueria	Glencairn Fm	Cylindrical depressions (inverted mounds in epirelief) with smooth walls and rounded base; 1.5–11.3 mm deep, 1.4–13.5 mm wide	Dwelling, Resting
Chondrites	Plainview and Glencairn and Muddy fms	Dendritic downward to semihorizontal branching burrow systems; 0.1–1.93 mm wide, 0.1 to 22.85 mm long	Deposit feeding
Cochlichnus	Glencairn and Muddy fms	Small sinuous horizontal trace; 0.99–5.42 mm wide, 3.78–22.83 mm long	Locomotion
Conichnus	Glencairn and Muddy fms	Vertically orientated cone-shaped burrow; 1.2–5.6 mm diameter, ≤ 5 mm deep	Dwelling, Suspension feeding
Cruziana	Glencairn Fm	Elongate, bilobate furrows with medial ridges (concave epirelief), some furrows are striated; 1.3–10.9 mm wide and ≤ 30 mm long	Locomotion
Cylindrichnus	Plainview Fm	Wide U-shaped vertical to subvertical, convex epirelief burrow; 3.35–6.2 mm wide ≤ 93 mm long	Dwelling, Feeding
Diplocraterion	Plain and Glencairn and Muddy fms	Vertical, U-shaped burrow with spreiten; dumbbell shape in cross section; 1.8–34.12 mm wide, ≤ 77 mm shaft separation	Dwelling, Suspension feeding
Fuersichnus	Plainview Fm	U-shaped burrows comprised of convex spreiten; 18.26–69.22 mm wide, ≤ 23 mm long	Deposit feeding
Gyrolithes	Glencairn Fm	Downward dextral coiling helical burrow; 0.51 cm burrow diameter, 8.2 cm helical diameter	Dwelling

Haplotichnus	Glencairn Fm	Simple straight to curved trail that often includes nonregular near-sinusoidal meanders; 1 mm wide, 22.9 mm long	Locomotion
Helminthopsis	Glencairn and Muddy fms	Unbranched, meandering, horizontal burrows or trails that do not touch or crosscut; 0.2–0.9 mm wide, ≤ 5 mm long	Feeding
Lockeia	Plainview Fm	Generally smooth almond- to ovoid-shaped oblong burrows preserved in convex hyporelief; 18.22–55.1 mm wide, ≤ 35 mm long	Resting, Feeding
Monomorphichnus	Glencairn Fm	Series of straight ridges, may be paired; 20.8 mm wide, 31.82 mm long, each ridge is ≤ 1 mm wide	Locomotion
Ophiomorpha	Plainview and Glencairn fms	Vertical and horizontal cylindrical burrows with ovoid pellet lining; 9.84–125.4 mm long, ≤ 37 mm wide	Dwelling, Suspension feeding
Palaeophycus	Glencairn Fm	Horizontal unbranched, lined, cylindrical burrows; fill identical to surrounding rock; walls may or may not be striated; 6.75–183.4 mm long, ≤ 12 mm wide	Dwelling, Locomotion
Paleobuprestis	Muddy Fm	Channels in xylic media; generally straight and do not intersect; may end in chambers; 6.2–16.2 wide; length indeterminant	Dwelling
Phycodes	Plainview and Glencairn and Muddy fms	Bundled series horizontal burrows originating from a central point. 2.4-36.37 mm long, ≤ 17 mm wide	Feeding
Planolites	Plainview and Glencairn and Muddy fms	Straight to slightly curved, horizontal to bedding, unlined, unbranched cylindrical or subcylindrical burrows with different fill than surrounding matrix; 0.06–154.01 mm long, ≤ 78.2 mm wide	Feeding, Locomotion
Rhizocorallium	Glencairn	Horizontal to near horizontal U-shaped tubes with spreiten, usually parallel to oblique to bedding; 37 mm long, 10.1 mm wide, and 3.1 mm diameter tunnel	Dwelling, Deposit feeding
Rhizolith	Lytle and Plainview fms	Downward tapering filamentous structures that range in diameter from 0.82–8.17 mm	Plant Root
Rusophycus	Glencairn Fm	Bilobate structure, lobes are parallel; ≤ 9 mm long, ≤ 5 mm wide	Resting

Skolithos	All fms	Straight vertical to slightly inclined cylindrical tube burrows; 0.48–10.9 mm in diameter, ≤ 47 mm long	Dwelling, Suspension feeding
Taenidium	Glencairn Fm	Unlined unbranching horizontal to subhorizontal burrow with meniscate backfill; 14.1–77.6 mm long, ≤ 13 mm wide	Deposit feeding
Teichichnus	Plainview and Glencairn and Muddy fms	Vertical series of horizontally stacked burrows with spreiten; 6.96–77.65 mm long, 0.82–30.9 mm wide, ≤ 17 mm diameter	Dwelling, Deposit feeding
Teredolites	Plainview Fm	Clustered club to flask-shaped tubes in Xylic medium; 2.5–7.5 mm in diameter, ≤ 3 mm long	Dwelling, Suspension feeding
Thalassinoides	Plainview and Glencairn and Muddy fms	3D boxwork of cylindrical burrows interconnected by vertical shafts; 2.9–225.7 mm long, ≤ 45 mm wide	Dwelling, Suspension feeding
Treptichnus	Plainview and Glencairn and Muddy fms	Shallow, U-shaped segments connected in a zigzag to irregular pattern, 3.4–79.4 mm long, ≤ 16 mm wide	Dwelling, Deposit feeding
Zoophycos	Glencairn Fm	Helical patterns of spreiten in circular to lobate shapes ≤ 134 mm long, ≤ 45 mm wide, and shaft diameter ≤ 4 mm	Dwelling, Deposit feeding

***TABLE 3**—Ichnocoenoses and Ichnofacies of the Dakota Group and their associated formations.*

Dominant Trace Fossils	**Ichnocoenosis**	**Ichnofacies**	**Formation(s)**
Rhizoliths*, minor Skolithos*	Rhizolith	Scoyenia	Lytle Fm; lower Plainview Fm; LCSM of the Muddy Fm
Dinosaur tracks, *Lockeia, Fuersichnus*, and *Planolites*	Fuersichnus		
Planolites, Phycodes, Cochlichnus, Conichnus, Taenidium, and *Treptichnus*	Planolites-Phycodes	Skolithos	Transition between LCSM and UTM of the Muddy Fm
Diplocraterion, Skolithos, Teichichnus, and *Thalassinoides*	Thalassinoides	Cruziana (proximal)	upper Plainview Fm; Glencairn Fm; UTM of the Muddy Fm
Ophiomorpha, Planolites, *Thalassinoides*, *Teichichnus*	Ophiomorpha-Thalassinoides		
Diplocraterion	Diplocraterion		
Chondrites, *Helminthopsis Phycodes*, *Planolites*, and *Treptichnus*	Helminthopsis-Phycodes	Cruziana (distal)	Glencairn Fm; UTM of the Muddy Fm

Table 4—Trace fossils and Ichnocoenoses by bedset in the fourth Glencairn Fm parasequence and sandstone:shale ratios for each bedset; dominant ichnogenera are bolded.

Glencairn Bed Set	Average Thickness (cm)	Trace Fossils	Facies	Ichnocoenoses	Sandstone: Shale ratio
1	135	***Chondrites***, *Circulichnus, Conichnus, Cruziana*, ***Helminthopsis***, ***Phycodes***, ***Planolites***, *Teichichnus, Treptichnus*	5	Helminthopsis-Phycodes	0
2	34	*Bergaueria, Cochlichnus, Cruziana, Diplocraterion, Phycodes*, ***Planolites***, *Skolithos, Taenidium, Teichichnus*, ***Thalassinoides***	4	Thalassinoides	0.25
3–4	16	*Ophiomorpha, Planolites, Skolithos*, ***Thalassinoides***	5	Thalassinoides	0.5
5–6	16	*Arenicolites, Chondrites, Cochlichnus, Conichnus, Cruziana, Diplocraterion, Ophiomorpha, Palaeophycus*, ***Phycodes, Planolites***, *Rhizocorallium, Rusophycus, Skolithos, Taenidium, Teichichnus*, ***Thalassinoides***, *Treptichnus*	4	Thalassinoides	0.75
7	17	***Ophiomorpha***, *Planolites*, ***Thalassinoides***	5	Ophiomorpha-Thalassinoides	1
8	26	*Chondrites, Ophiomorpha, Phycodes, Planolites, Teichichnus*, ***Thalassinoides***	4	Thalassinoides	0.75
9-10	15	*Cochlichnus, Monomorphichnus*, ***Ophiomorpha***, *Palaeophycus, Phycodes*, ***Planolites***, *Skolithos, Teichichnus*, ***Thalassinoides***, *Treptichnus*	5	Ophiomorpha-Thalassinoides	1
11	33	*Bergaueria, Arenicolites, Chondrites, Palaeophycus, Planolites, Skolithos*, ***Thalassinoides***	4	Thalassinoides	0.5
12	14	*Palaeophycus, Planolites, Skolithos, Teichichnus*, ***Thalassinoides***	4	Thalassinoides	1
13	28	*Arenicolites, Chondrites, Cochlichnus, Ophiomorpha, Palaeophycus, Phycodes*, ***Planolites***, *Skolithos, Teichichnus*, ***Thalassinoides***, *Treptichnus*	4/5	Thalassinoides	1

***Table 5**—Lithofacies associations of the Dakota Group.*

Lithofacies Associations	**Lithofacies**	**Common Component Trace Fossils**
1 *Braided Channels*	F-1, Trough cross-stratified sandstone	Rare Rhizoliths, *Asthenopodichnium*, *Paleobuprestis*
2 Paralic to Shallow Marine	F-2 Tabular upward coarsening muddy silt to fine sand; F-3 Ripple cross-laminated to massive medium to very fine sand	*Asthenopodichnium, Lockeia, Teredolites Ophiomorpha, Thalassinoides*
3 *Middle to Lower Shoreface*	F-4 Ripple cross-laminated fine sand with mudstone lenses; F-5 Silty mudstone with fine to very fine-sand lenses	*Helminthopsis, Phycodes, Planolites, Thalassinoides*
4 *Offshore Marine*	F-6 Thin-bedded shale	*Arenicolites, Helminthopsis*

FIGURES

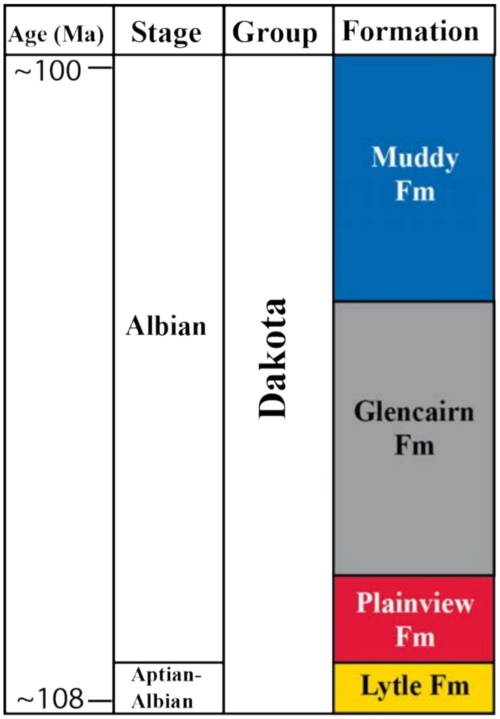


FIGURE 1—General stratigraphic column of the Dakota Group within the Cañon City Embayment, approximate ages from Gustason and Kauffman (1985).

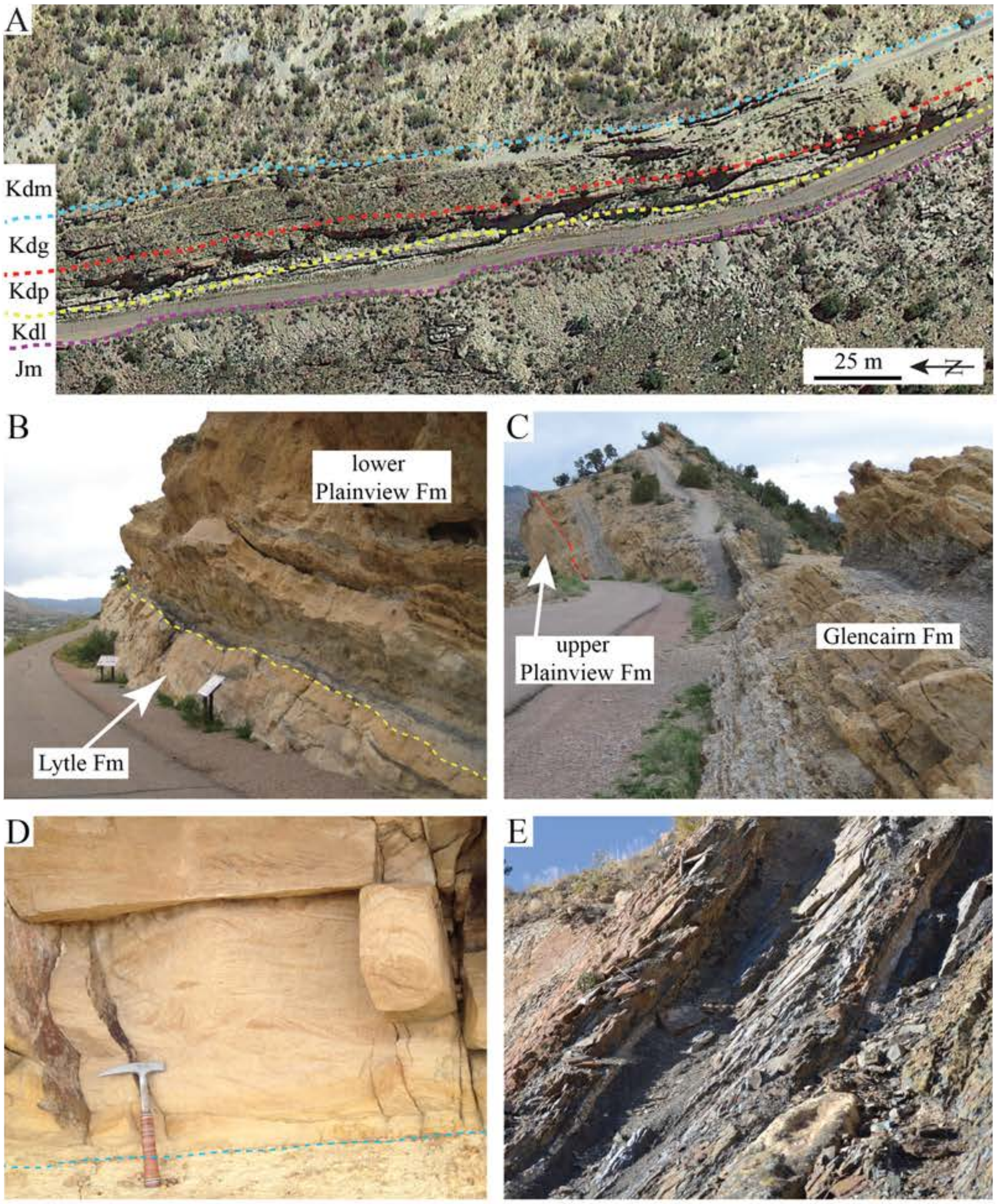


FIGURE 2—A) Outcrop of Dakota Group (Kd) formations unconformably overlying the Jurassic Morrison Formation (Jm) along Skyline Drive at approximately 38° 27'50.15" N; 105° 15' 9.09" W; Kdl = Lytle Fm; Kdp = Plainview Fm; Kdg = Glencairn Fm; Kdm = Muddy Fm; Dashed lines identity boundaries between formations. B) Lytle and lower Plainview formations. C) Upper Plainview and Glencairn formations. D) Characteristic trough cross-bedded sandstone of the lower Channel Sandstone Member of the Muddy Formation. E) Interbedded shale and sandstone of the Upper Transitional Member of the Muddy Formation. Rock hammer 33 cm long.

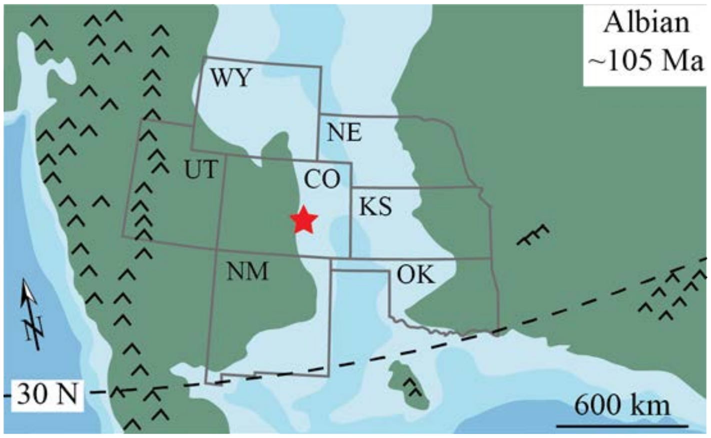


FIGURE 3—Late Albian (~105 Ma) paleogeographic map of the Western Interior Seaway; red star is study location. Modified from Blakey 2014.

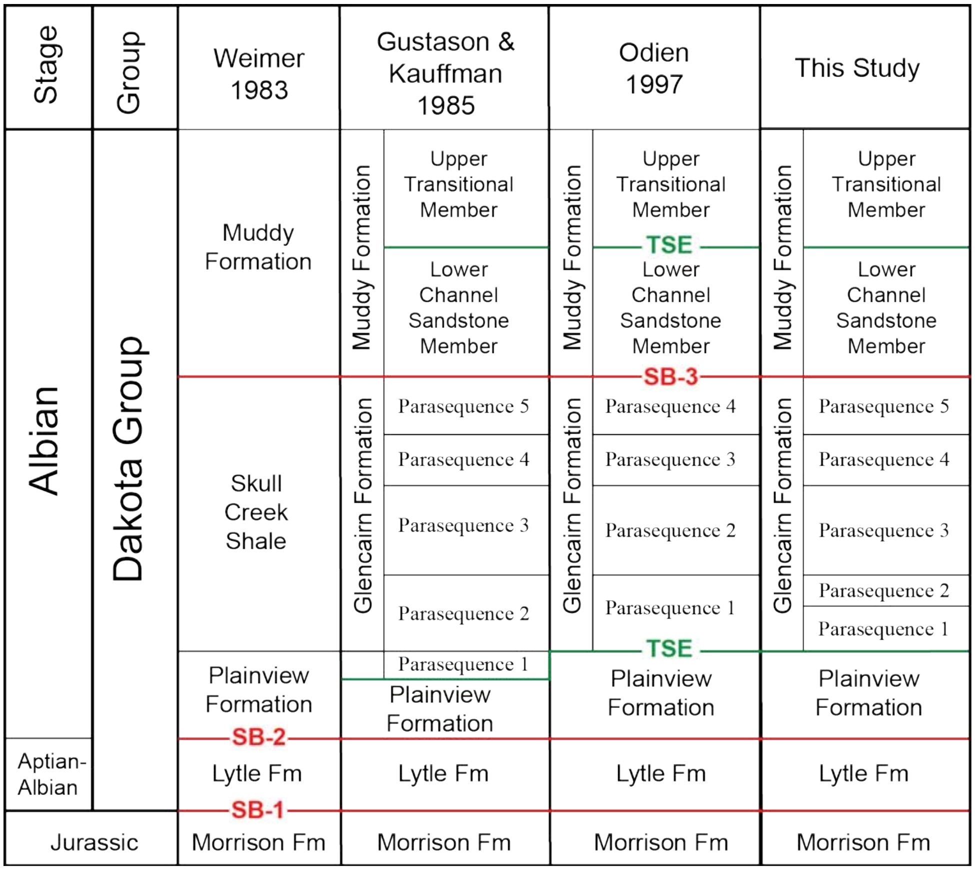


FIGURE 4—Sequence stratigraphic interpretations for the Dakota Group along the Front Range from Weimer (1983), Gustason and Kauffman (1985), Odien (1997), and this study. Transgressive Surface of Erosions (TSE), Sequence Boundary (SB), Parasequence (PS). The TSE demarcating the Plainview-Glencairn fms contact marks the Skull Creek transgression. The intra-Muddy Fm TSE marks the Greenhorn transgression.

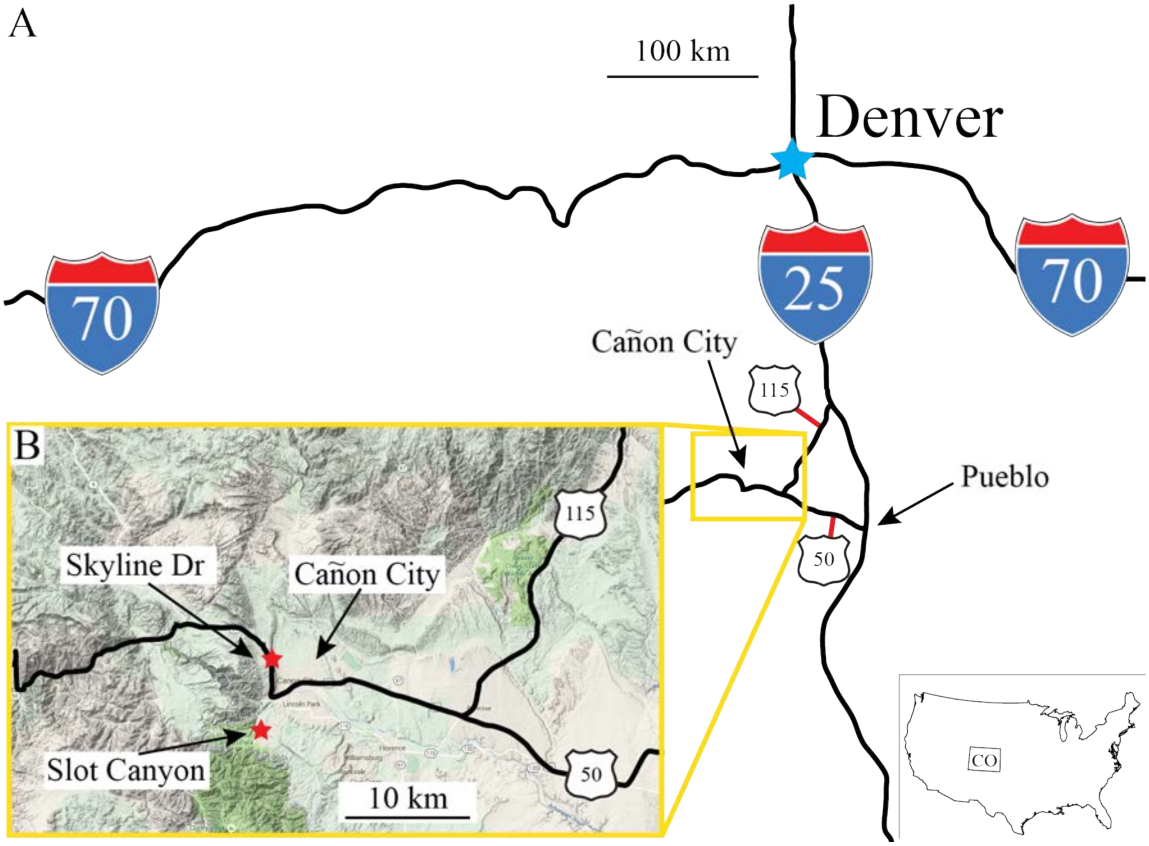


FIGURE 5—Map of Denver–Pueblo–Cañon City, CO, region and field sites in Cañon City area. A) Denver area regional map including major highways. B) Inset map of Cañon City area with field locations highlighted by red stars. Maps modified from Google Earth.

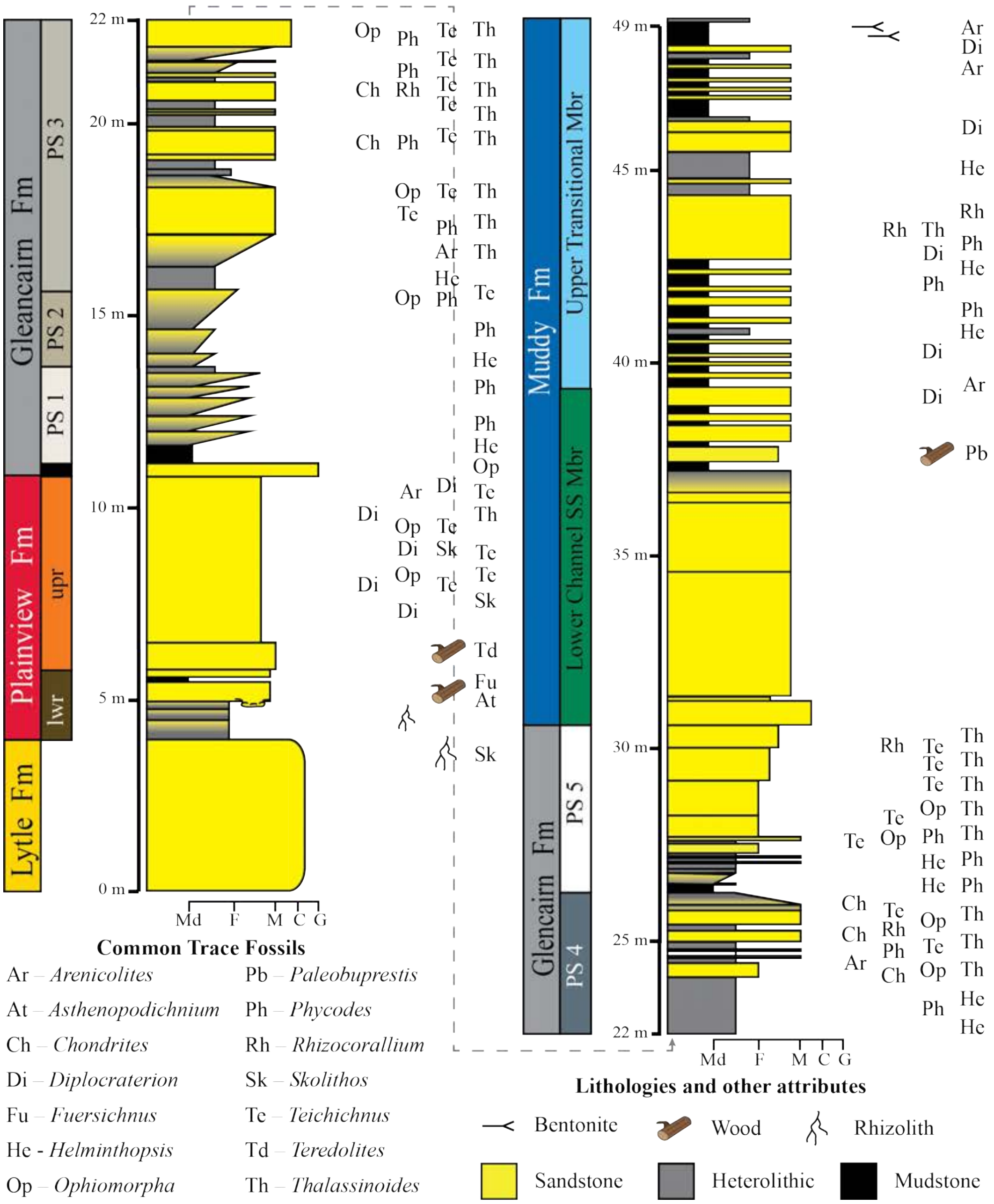


Figure 6—Stratigraphic column of the Dakota Group along the Skyline Drive Hogback with lithologies, common trace fossils, and other attributes.

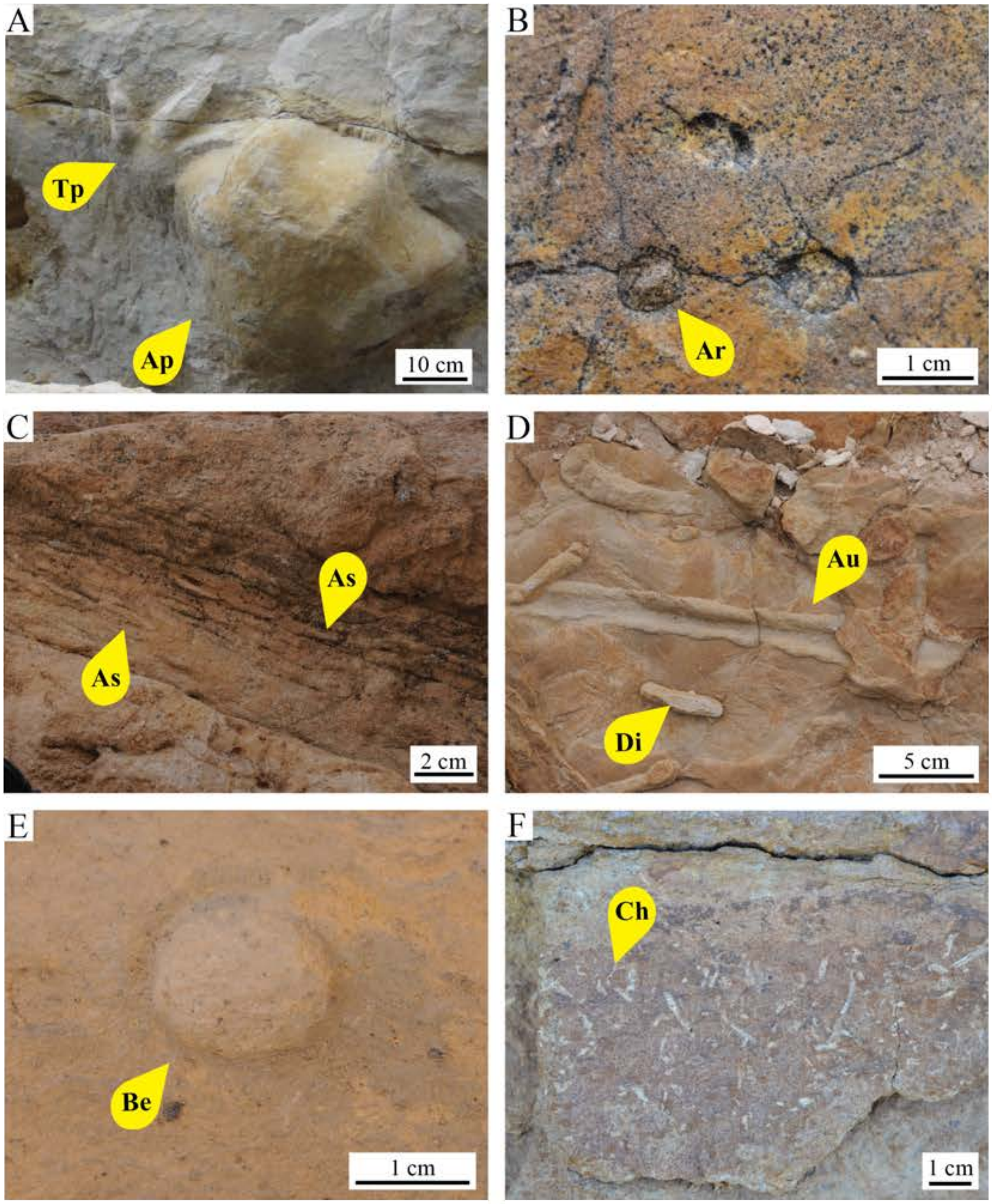


FIGURE 7—Trace fossils of the Dakota Group. A) *Apulosauripus* (ankylosaur print) (*Ap*). B) *Arenicolites* (Ar). C) *Asthenopodichnium* (As). D) *Aulichnites* (Au) and *Diplocraterion* (Di). E) *Bergaueria* (Be). F) *Chondrites* (Ch).

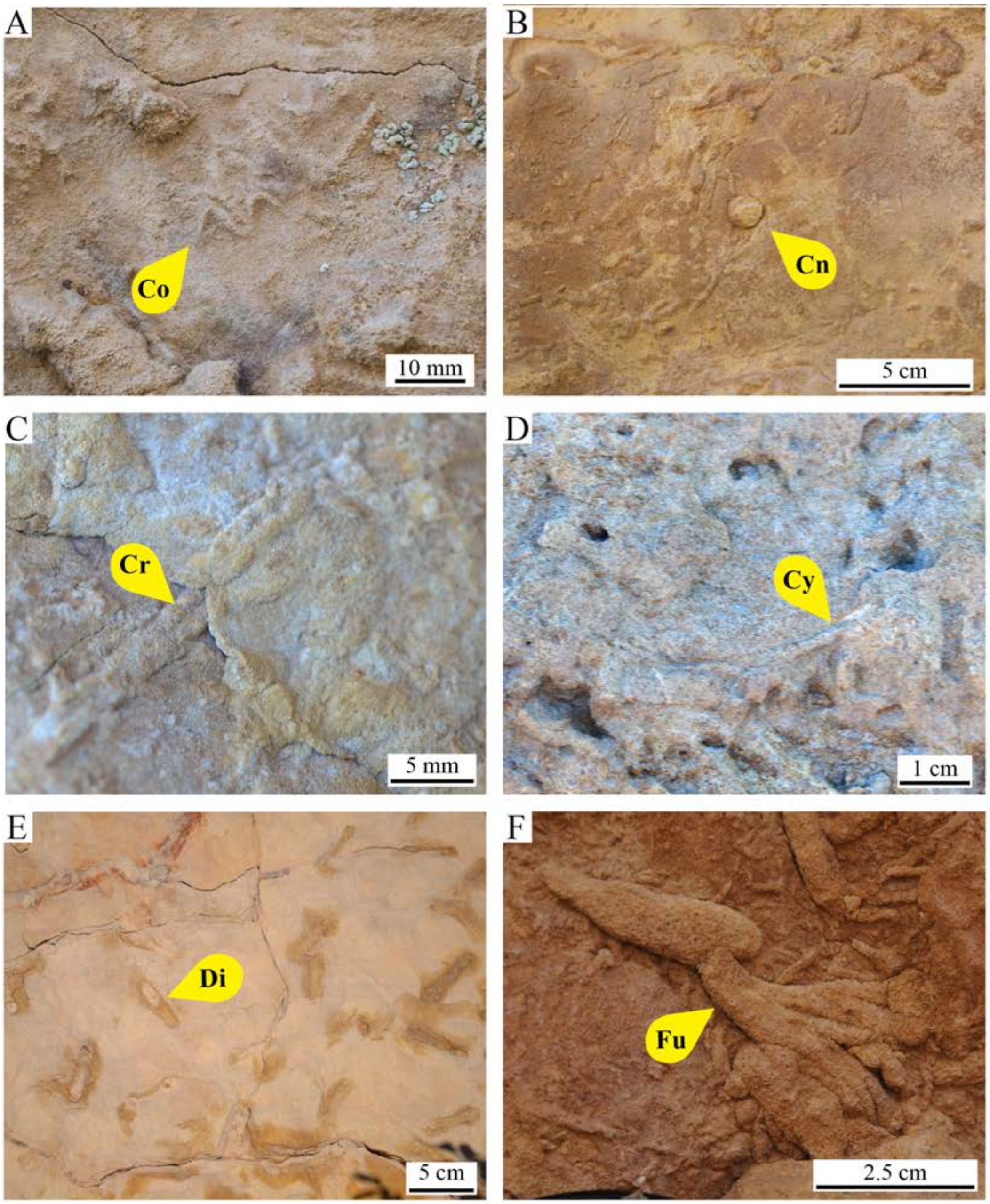


FIGURE 8— Trace fossils of the Dakota Group continued. A) *Cochlichnus* (Co). B) *Conichnus* (Cn). C) *Cruziana* (Cr). D) *Cylindrichnus* (Cy). E) *Diplocraterion* (Di). A) *Fuersichnus* (Fu).

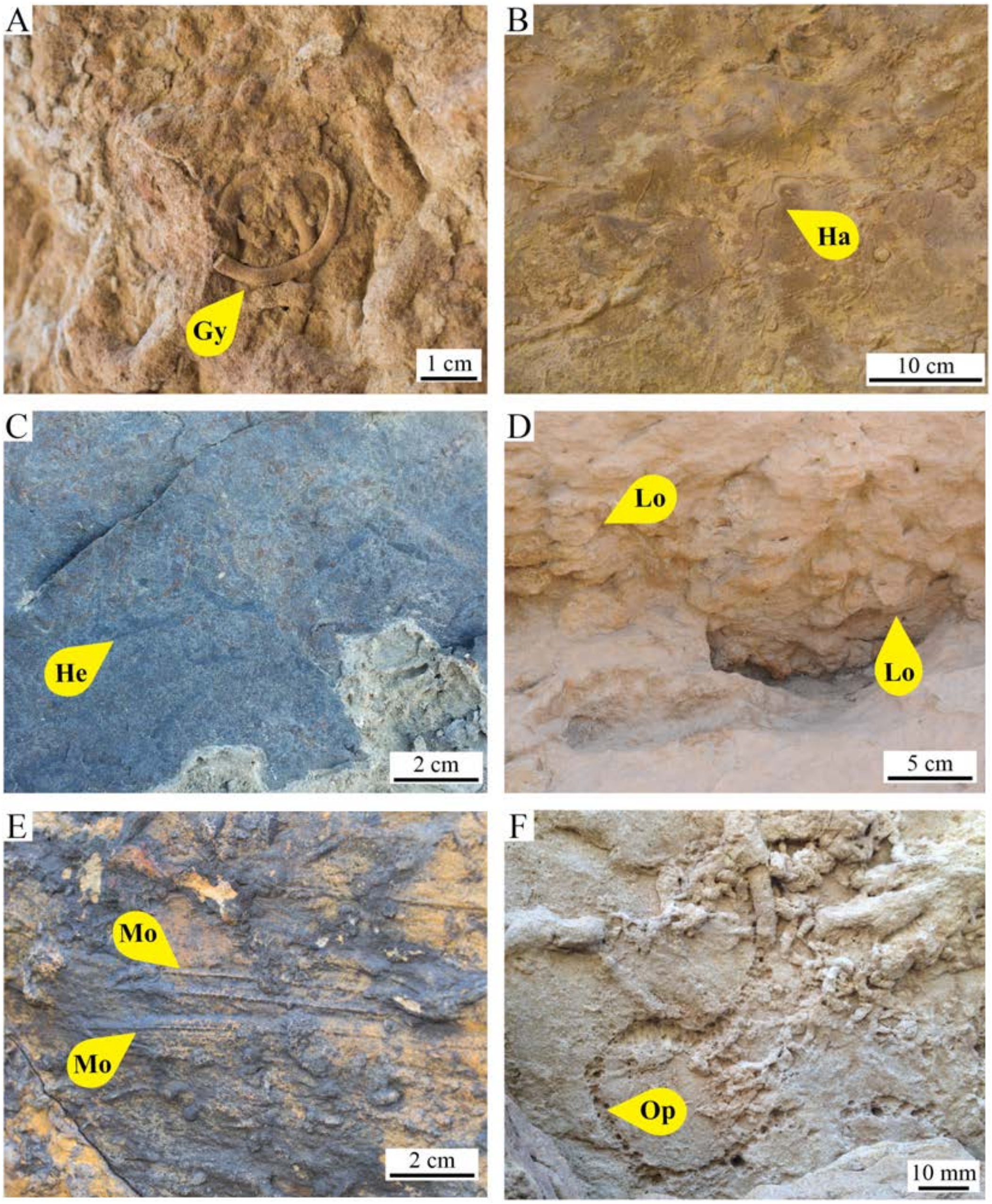


FIGURE 9— Trace fossils of the Dakota Group continued. A) *Gyrolithes* (Gy). B) *Haplotichnus* (Ha). C) *Helminthopsis* (He). D) *Lockeia* (Lo). E) *Monomorphichnus* (Mo). F) *Ophiomorpha* (Op).

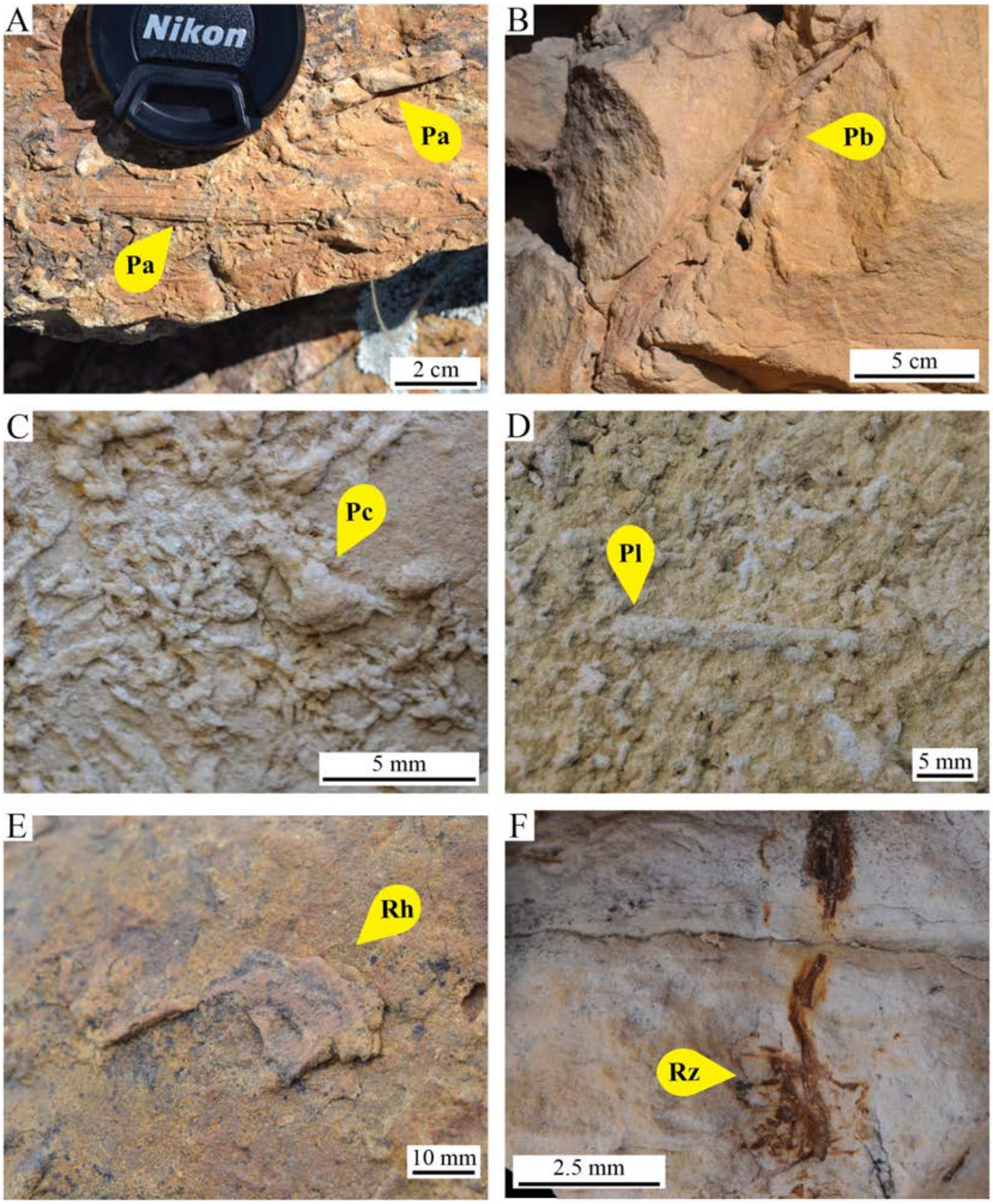


FIGURE 10— Trace fossils of the Dakota Group continued. A) *Palaeophycus* (Pa). B) *Paleobuprestis* (Pb). C) *Phycodes* (Pb). D) *Planolites* (Pl). E) *Rhizocorallium* (Rh). F) Rhizolith (Rz).

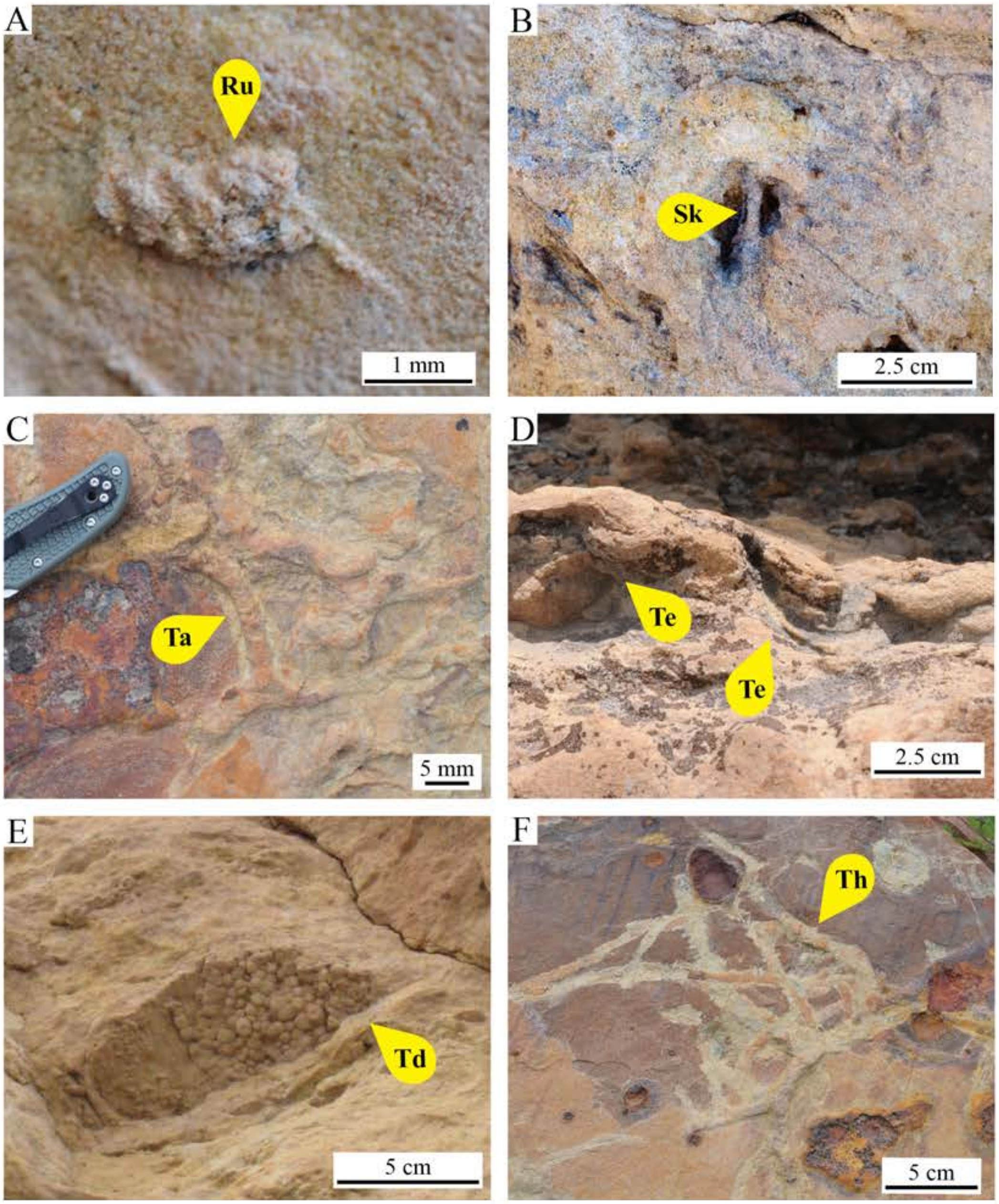


FIGURE 11— Trace fossils of the Dakota Group continued. A) *Rusophycus* (Ru). B) *Skolithos* (Sk). C) *Taenidium* (Ta). D) *Teichichnus* (Te). E) *Teredolites* (Tr). F) *Thalassinoides* (Th).

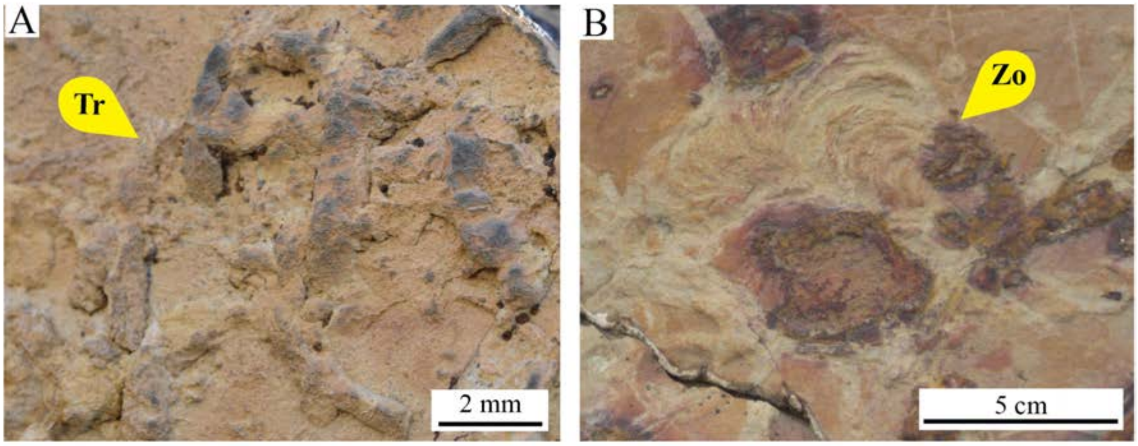


FIGURE 12— Trace fossils of the Dakota Group continued. A) *Treptichnus* (Tr). B) *Zoophycos* (Zo).

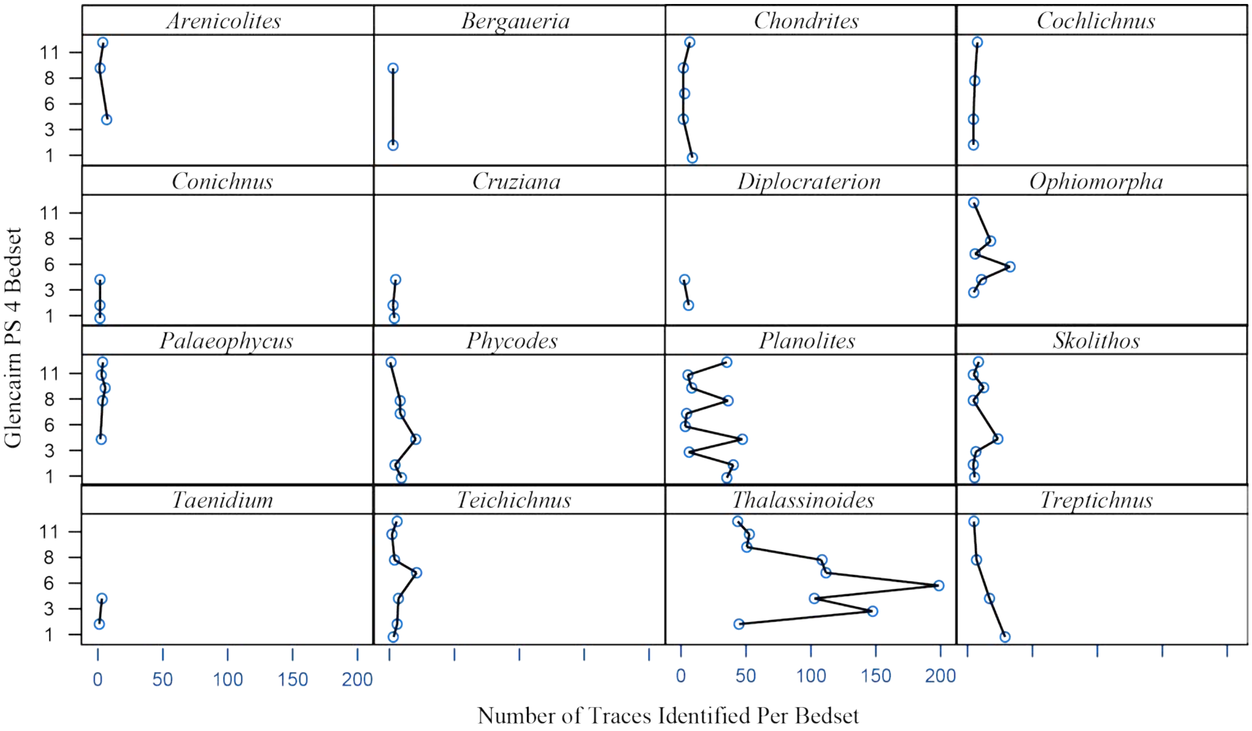


FIGURE 13—Cross-plots of vertical distribution of trace-fossil abundance per bedset for each ichnogenera.

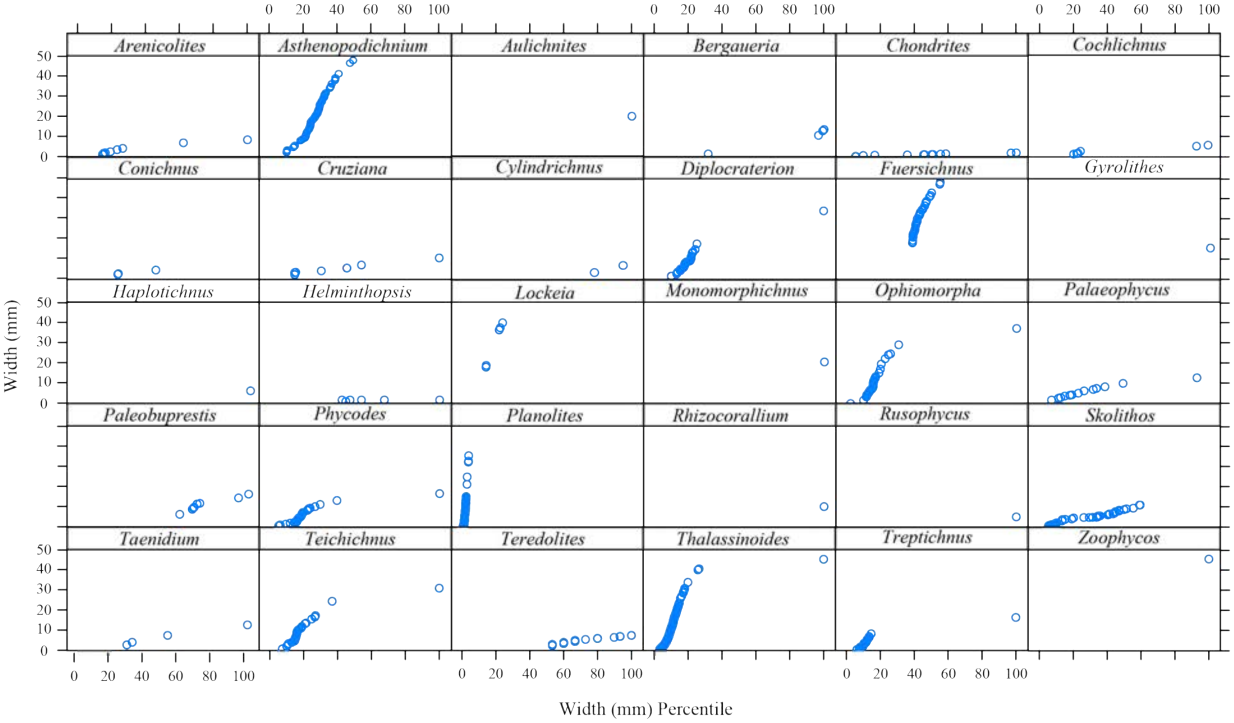


FIGURE 14—Cross-plot of trace-fossil diameters (or widths depending on trace fossil) versus percentile for invertebrate ichnogenera.

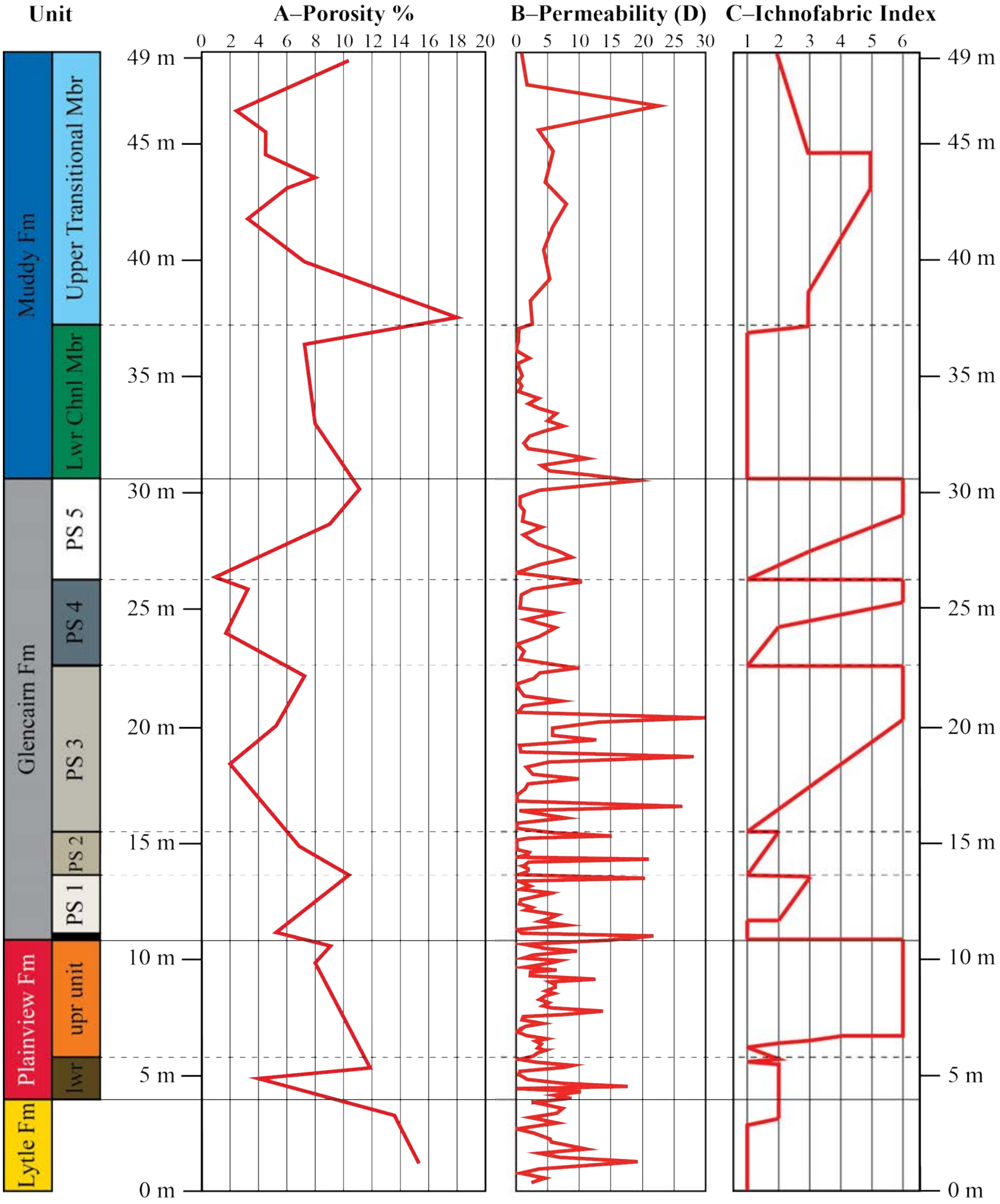


FIGURE 15—Trends in Porosity, Permeability, and Bioturbation Intensity (ii) for the Dakota Group. A) Percent porosity determined by thin section analysis. B) Permeability (D) of the Dakota Group. C) Bioturbation intensity (ii) of the Dakota Group.

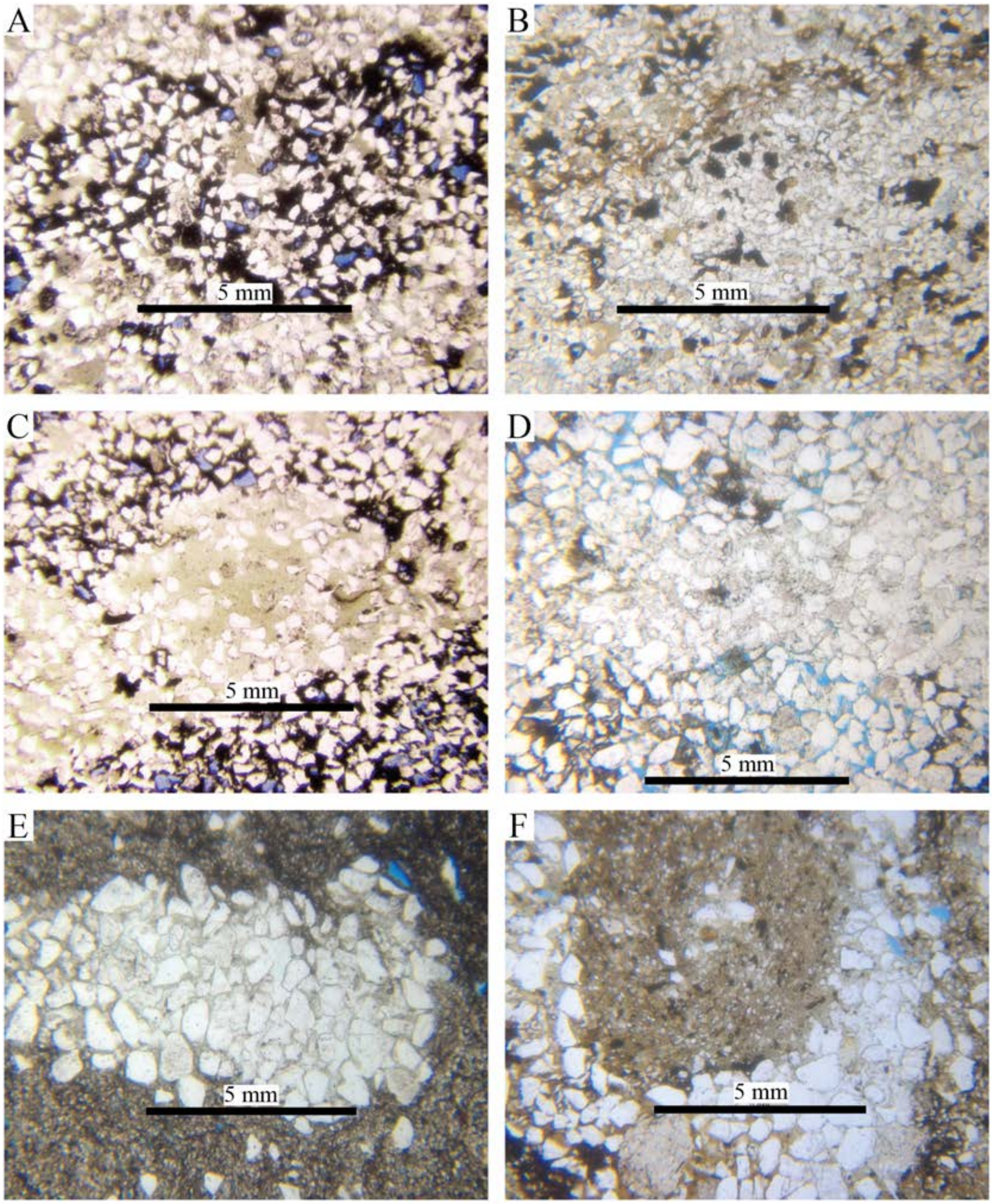


FIGURE 16—Thin section photomicrographs of trace fossils from the Dakota Group. A) Mud-lined *Palaeophycus* with higher porosity than surrounding matrix (Slide 17, Glencairn Fm). B) Infilled *Palaeophycus* with less porosity than surrounding matrix (Slide 28, Muddy Fm). C) Burrow infilled by string of fecal pellets (Slide 17, Glencairn Fm). D) Unlined *Planolites* burrow with lower porosity than surrounding matrix (Slide 12, Plainview Fm). E) Sand packages of *Taenidium* in mudstone strata (Slide 31, Muddy Fm). F) Mud-filled, sand-lined *Palaeophycus* in mud matrix (Slide 30, Muddy Fm).

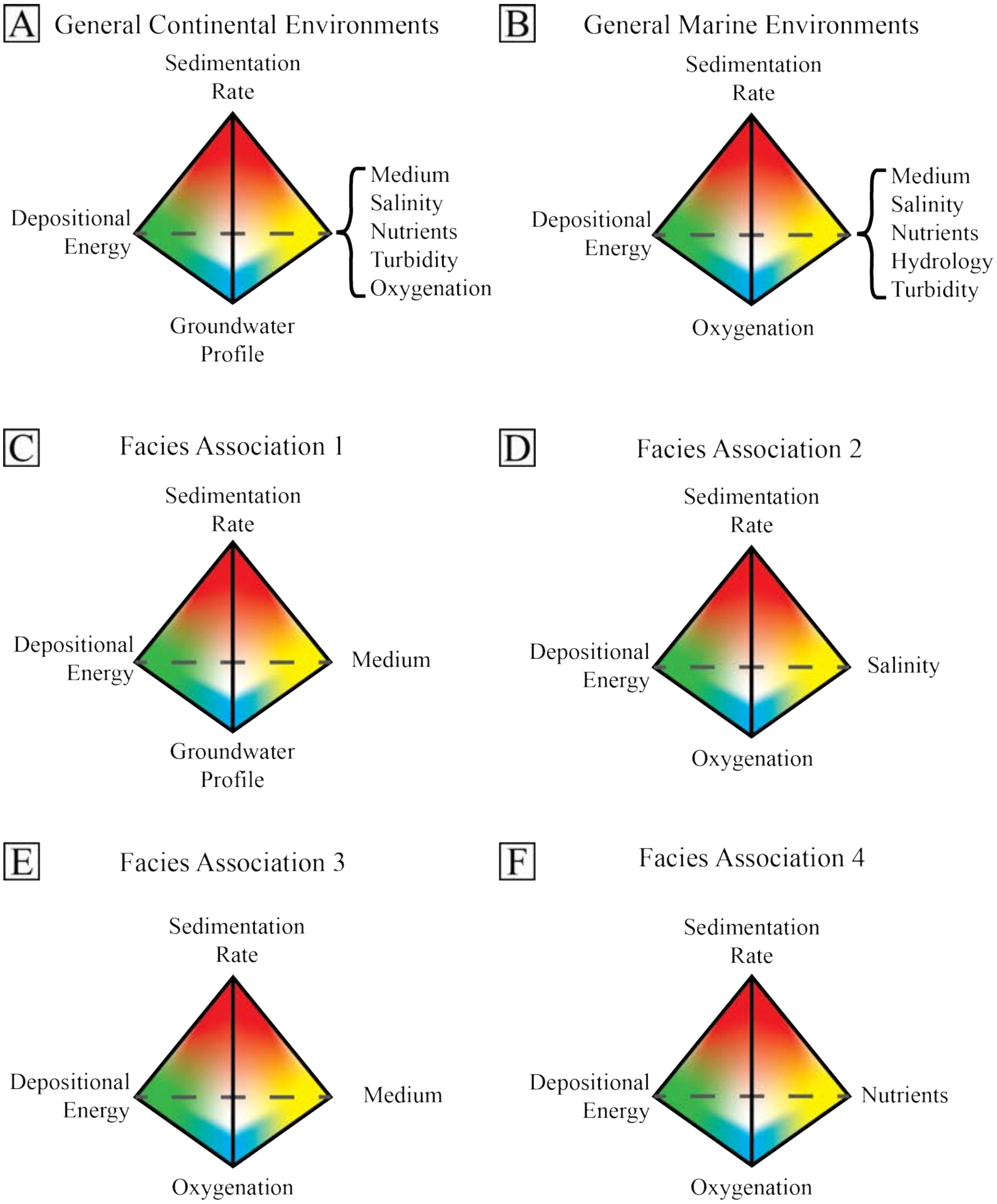


FIGURE 17—Tetrahedrons of primary physicochemical parameters that influence organism behaviors. A) Physicochemical parameters for continental environments. B) Physicochemical parameters for marine environments. C) Interpreted dominant physicochemical parameters for Facies Association 1 (the Lytle Fm and the Lower Channel Sandstone Mbr, Muddy Fm). D) Interpreted dominant physicochemical parameters for Facies Association 2 (in the Plainview and Glencairn fms). E) Interpreted dominant physicochemical parameters for Facies Association 3 in the Glencairn and Muddy fms. F) Interpreted dominant physicochemical parameters for Facies Association 4 in the Upper Transitional Mbr of the Muddy Fm (modified from Hasiotis and Platt 2012).

CHAPTER 5: CONCLUSION

The previous three chapters represent a multi-temporal and cross–latitudinal approach to identifying the physicochemical parameters at the time of deposition thru the integrative study of ichnology. The purpose of this chapter is the combine the key findings of this dissertation into a clear comparison and discussion of the variability in bioturbation-controlling factors. This final chapter also reviews the major findings of each of the previous chapters and synthesizes a large conclusion on the comparisons between; icehouse and greenhouse conditions; high and low latitude environmental effects on the ichnogenera identified; and interpreted physicochemical controls at the time of deposition. Previous studies suggest that physicochemical controls on marine ichnogenera are different during icehouse and greenhouse global climates (e.g., Goldring et al. 2004), and that high and low latitudinal setting have different physicochemical controls (e.g., Quiroz et al. 2010). The Dakota and Mackellar fms record the most similar depositional environments of nearshore deltaic to distal shoreface systems, compared to the Greenhorn and Niobrara fms offshore basinal conditions.

The Mackellar Formation

This study integrated ichnology and sedimentology to identify Mackellar Fm depositional environments as part of a freshwater-stressed, high-sedimentation, river-dominated marine deltaic system. The ichnology indicates a marine to brackish-water environment for the Mackellar Fm based on: 1) the presence of exclusively marine trace fossils; 2) the absence of exclusively continental trace fossils; 3) a pronounced reduction in trace-fossil size and penetration depth compared to normal marine systems; and 4) the overall high ichnodiversity with low individual bed ichnodiversity. Mackellar Fm ichnocoenoses are consistent with the three main physicochemical controls of sedimentation rate, salinity, and depositional energy and represents a mixed Skolithos–Cruziana ichnofacies. This study failed to accept the hypothesis that the Mackellar Fm was deposited in a lacustrine system, and showed that the Mackellar Fm at Turnabout Ridge and Buckley Island was deposited into a freshwater-stressed, high-sediment-accumulation marine environment—the Mackellar Sea—and reinterprets the glaciolacustrine interpretation as a transitional marine environment fed by high-freshwater, high-sediment-discharge from glacial-meltwater-fed rivers. Although body fossils were not found, the 30 ichnogenera and the six ichnocoenoses described are indicators of a stressed marine system. The Mackellar Fm does not contain a high-latitude ichnological signature; however, the combination of ichnocoenoses with glaciomarine deposits produced by high freshwater and sediment inputs from glacially fed river systems suggests a strong association with high latitudinal settings.

Our revised interpretation is more parsimonious with the depositional model of the Antarctic Interior Seaway filling an eperic seaway in an intercratonic basin, where the fully marine Weaver, Discovery Ridge, and Polestar fms were deposited. Including the Mackellar Fm with these other formations extends the marine extent of the seaway across the Ellsworth, Pensacola, and Transantarctic mountains to the Beardmore Glacier area. As the Antarctic Interior Sea, and thus, the Mackellar Sea retreated, the Mackellar sediments were overlain during by the braided fluvial systems of the Fairchild Fm, filling remaining accommodation in the basin. Additional research is necessary at other outcrops along the Central Transantarctic Mountains to locate areas where the brackish water environments in the Mackellar Fm are observed to transition from fully marine conditions in the more distal parts of the basin to freshwater environments in the most proximal areas.

The Greenhorn and Niobrara formations

This study identified 17 ichnogenera from the Greenhorn and Niobrara fms of the AMOCO Rebecca K. Bounds #1 Well core, and described six ichnocoenoses for each formation as secondary proxies that record orbital perturbations in environmental conditions. We interpret both formations as having benthic oxygenation for the primary physicochemical control and sedimentation rate, media type, and nutrient input as secondary controls, based on variations in ichnocoenoses and bioturbation intensity. Variations in benthic oxygenation and sedimentation rate are the factors that influence which ichnocoenosis was present in each lithofacies. Generally, limestone strata in both formations are consistent with the Cruziana Ichnofacies, whereas argillaceous limestone to marlstone strata are representative of the Zoophycos Ichnofacies and marlstone strata reflect the Nereites Ichnofacies. The abundance of interspersed bioturbated beds within Oceanic Anoxic Event (OAE) 2 and OAE 3 strata (60% and 65%, respectively) with similar ichnodiversity and bioturbation intensity to pre-OAE strata falsifies the hypothesis of continuous anoxic conditions across and within the seafloor.

Using EHA, the distribution of ii and ichnocoenoses preserve harmonics consistent with Milankovitch cyclicities. Ichnocoenoses data records all three major orbital cycles, with the higher ichnocoenoses recording all three cycles and the lower ichnocoenoses commonly not identifying precessional signals. Bioturbation intensity (i.e., ii) also identified all three Milankovitch cycles. Low ii strata record the highest diversity of cycles, whereas high ii strata identified only one signal in an interval, often obliquity. Oscillations in both secondary proxies tested and their relative distributions of variability identify multiple harmonic signals, and these changes record the physicochemical parameters during deposition. Periods of limited variability are indicative of a stable benthos, whereas high variability strata suggest dynamic shifts in benthic conditions. The trend for high ichnocoenoses recording more cycles is likely due to the better benthic conditions and greater stability of the environment during deposition of those sediments. ASM of ii and ichnocoenoses identified average sedimentation rates for Greenhorn Fm as 1.148 cm/kyr, and 0.889 cm/kyr for the Niobrara Fm, which are within previous estimated values based on oxygen isotopes and other primary proxies. Comparisons with previous studies on correlated strata identify a greater abundance and longer duration of identified orbital cyclicities preserved in bioturbation data.

Bioturbation intensities within OAE 2 strata (60% bioturbated) reflect strong obliquity and moderate precessional signals, whereas ichnocoenoses record partial obliquity and precessional signals. Both bioturbation intensities and ichnocoenoses record strong obliquity and weak eccentricity and precessional harmonics in OAE 3 strata. The ichnological record of OAE 2 and OAE 3 in the WIS agrees with studies from European basins, temporary oxic conditions allowed colonization and bioturbation of the benthos. The abundance of bioturbation in OAE 3 strata (~65% bioturbated) strengthens the current hypothesis that OAE 3 was not continuous global event, but maybe a series of smaller temporary events. Such primary proxies as $\delta^{13}C$, $\delta^{18}O$, and %CaCO3 in unbioturbated strata provide clear orbital cyclicities. In highly bioturbated strata, bioturbation records the physicochemical controls and cyclic harmonics. The secondary proxies of ichnocoenoses and ii identified harmonics consistent with all three Milankovitch signals (eccentricity, obliquity, and precession). Cyclostratigraphic results using ichnocoenoses may vary based on how individual researchers identify and characterize an ichnocoenosis. Where there are sampling restrictions, absence of primary proxy data, and/or time restrictions, bioturbation may be an ideal secondary proxy to conduct cyclostratigraphic studies.

The Dakota Group

This study identified 31 ichnogenera from continental and marine strata in the Dakota Group at the Skyline Drive Hogback, in Cañon City, CO. Seven ichnocoenoses, two from continental depositional environments and five from marine depositional environments are characteristic of three ichnofacies (Scoyenia, Skolithos, and Cruziana ichnofacies). The Dakota Group is interpreted to record fluvial (Lytle Fm), a freshwater to marine transition (Plainview Fm), offshore to shoreface (Glencairn Fm), and continental to offshore marine depositional environments (Muddy Fm). Ichnodiversity varies throughout the Dakota Group, with the lowest in the Lytle Fm, and highest ichnodiversity in the Glencairn Fm. The progradational parasequence set of the Glencairn Fm records a general increase in trace fossil size and bioturbation intensity, and a reduction in ichnodiversity up section as the sandstone:shale ratio increases. Trace fossils effect permeability and porosity of Dakota Group strata differently based on the lithofacies and bioturbation intensity. Where bioturbation intensity is highest, strata generally record higher permeabilities and lower porosity values. Trace fossils in the well to highly bioturbated (ii4–6) sandstones of the Glencairn and Muddy fms could be hydrocarbons flow conduits in these resource-rich formations. Based on the ichnology and vertical successions of interpreted depositional environments, this study refined the fifth parasequence within the Glencairn Fm, and reaffirms the position of the Plainview Fm-Glencairn Fm contact in this area.

Physicochemical Controls on Trace Fossils

Through this dissertation, continental and marine strata have been characterized and each depositional environment interpreted based on their sedimentology and ichnological composition. Environments of deposition have spanned from fluvial to deltaic and basinal settings. In each of these continental and marine environments, the primary physicochemical parameters are different, and similar depositional setting can vary in their controls (Fig. 1 see Hasiotis and Platt 2012 for discussion). The diversity of depositional settings is highest in the Dakota Group, and lowest in the Bounds Core Greenhorn and Niobrara fms.

Continental strata only occur in the Lytle, Plainview, and Lower Channel Sandstone Mbr of the Muddy Fm. In the Lytle and Lower Channel Sandstone Mbr of the Muddy Fm the fluvial strata are trough cross-bedded and are indicative of a braded river system (Gustafson and Kauffman 1985). Strata containing these depositional environments are dominantly controlled by sedimentation rate, depositional energy, medium, and hydrology (Fig. 1B). The lower Plainview Fm records a transgression from the Lytle Fm and the resulting freshwater environment with *Apulosauripus* (dinosaur tracks), *Asthenopodichnium* and rhizoliths (Fig 1C).

Deltaic depositional environments can occur in continental and marine systems depending on location and vary in dominant influences (i.e., tidal, river, waves) (Bhattacharya 2006). Deltaic depositional environments compose the Mackellar Fm, and a section of the Upper Transitional Member of the Muddy Fm. The Mackellar Fm strata at Turnabout Ridge record deposition on the subaqueous portions of a river-dominated delta with environments that include subaqueous terminal distributaries, the proximal to distal delta front, and prodelta. The Mackellar fm is interpreted as river dominated based on the sedimentary characteristics (such as compensational stacked subaqueous terminal distributary channels, and hyperpycnites and hypopycnal plume deposits) and the key ichnological aspects of diminutive trace fossil morphologies and marine-only-type ichnofauna (i.e., *Teichichnus*) (Flaig et al. 2016). The pro-deltaic strata of the Muddy Fm, record sandstone event deposits that are characteristic of river pulse events, in an otherwise wave-dominated system (Ben-Awuah and Padmanabhan 2014). In dynamic deltaic depositional environments sedimentation rate, depositional energy, oxygenation, and salinity are the major controls (Fig. 1D, E).

Marginal marine EODs were only identified in the Dakota Group. These strata are consistent with the Skolithos and Cruziana Ichnofacies that record the highest ichnodiversity described in this dissertation. The upper Plainview and Glencairn fms are often highly bioturbated (ii5–6) and contain up to 24 ichnogenera. The Glencairn Fm records five progradational parasequences that contain shelfal to nearshore strata that record distal to proximal Cruziana Ichnofacies; whereas the Plainview Fm only contains the proximal Cruziana Ichnofacies. Trace fossils in these strata are interpreted to had been controlled by sedimentation rate, depositional energy, hydrology, and salinity for the Plainview (FA 2) (Fig. 1C), with medium as the changing variable for the Glencairn FA3 (Fig. 1D). The interpretation of these physicochemical controls are consistent with previous studies on the Bluesky and McMurray formations among many others (e.g., Botterill, et al. 2015; Shchepetkina, et al., 2016).

Offshore marine depositional environments were identified in the Muddy, Greenhorn, and Niobrara fm strata. Within these formations, oxygenation is identified as a major control; although, more so in Greenhorn and Niobrara fm strata than the Muddy Fm (Fig. 1D,F). For the Greenhorn and Niobrara fms, benthic oxygen has long been considered a major physicochemical control due to the presences of OAE 2 and OAE 3 in these strata (Savrda 1998a; Meyers 2006). Across the WIS and European basins the identification of bioturbation within OAE 2 and OAE 3 strata shows that temporary periods of dysoxic to oxic conditions allowed for colonization and bioturbation of these strata (e.g., Sageman et al. 1998; Uchman et al. 2013b; this dissertation). The distal shoreface to shelfal depositional environments Muddy Fm are not controlled by oxygenation, as the Greenhorn and Niobrara fms, but by fining upward sedimentological changes (media) that change nutrient input (nutrient control) that occur during the greenhorn transgression and relative sea-level rise that occurred during deposition (Fig. 1F; Rodriguez-Tovar et al. 2010). The interpreted physicochemical controls for all the marine strata studied are quite similar, in spite of their occurrences in different global climates and paleolatitudes.

Conclusion

This dissertation identified similar ichnocoenoses and ichnofacies between the Permian icehouse high-latitude Mackellar Fm and the Cretaceous greenhouse low-latitude Dakota, Greenhorn, and Niobrara fms. Each of the studies in this dissertation have characterized the environment of deposition and major controlling physicochemical parameters for each formation, member, or unit studied. Across the formations studied, the physicochemical controls are generally similar (i.e. Oxygen in the Upper Transitional Mbr of the Muddy Fm, Glencairn, Mackellar, Greenhorn and Niobrara fms; Fig. 1D–F). Physicochemical controls differ between these formations, not based on the global climate at the time of deposition, but their local oceanographic and depositional processes.

Additionally, this study proposes and shows how high-resolution ichnological data can be integrated into cyclostratigraphic studies as a secondary proxy for the identification of Milankovitch-scale harmonics. The ability to use ichnological data for cyclostratigraphy is based on how the organisms react to the physicochemical conditions at the time of deposition, and how those conditions are controlled by the predominant oceanographic processes, and climate at that time; which is further influenced by the earths orbital parameters. Further studies will hopefully begin to test this method in additional cretaceous basins, and for identification and comparison of cyclicities between strata deposited during different global climatic conditions.

REFERENCES

BEN-AWUAH, J. AND PADMANABHAN, E., 2014, Impact of Bioturbation on Reservoir Quality: A Case Study of Biogenically Reduced Permeabilities of Reservoir Sandstones of the Baram Delta, Sarawak, Malaysia: Journal of Applied Sciences, v. 14, p. 3312–3317.

BHATTACHARYA, J.P., 2006, Deltas, *in* Posamentier, H.W., and Walker, R.G., (eds.), Facies models revisited: Tulsa, Oklahoma, SEPM (Society for Sedimentary Geology) Special Publication 84, p. 237–292.

BOTTERILL, S.E., CAMPBELL, S.G., PEMBERTON, S.G. AND GINGRAS, M.K., 2015, Process ichnological analysis of the Lower Cretaceous Bluesky Formation, Alberta: Bulletin of Canadian Petroleum Geology, v. 63, p. 123–142.

FLAIG, P.P., HASIOTIS, S.T. AND JACKSON, A.M., 2016, An Early Permian, paleopolar, postglacial, river-dominated deltaic succession in the Mackellar–Fairchild formations at Turnabout Ridge, Central Transantarctic Mountains, Antarctica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, pp.241–265.

GUSTASON, E., AND KAUFFMAN, E., 1985, The Dakota Group and the Kiowa-Skull Creek Cyclothem on the Cañon City-Pueblo area, Colorado: SEPM Guidebook No. 4, p. 72–89.

HASIOTIS, S.T. AND PLATT, B.F., 2012, Exploring the sedimentary, pedogenic, and hydrologic factors that control the occurrence and role of bioturbation in soil formation and horizonation in continental deposits: An integrative approach: The Sedimentary Record, v. 10, p. 4–9.

MEYERS, P.A., 2006, Paleoceanographic and paleoclimatic similarities between Mediterranean sapropels and Cretaceous black shales: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 235, p. 305–320.

RODRÍGUEZ-TOVAR, F.J., UCHMAN, A., PAYROS, A., ORUE-ETXEBARRIA, X., APELLANIZ, E. AND MOLINA, E., 2010, Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 285, p. 50–65.

SAVRDA, C.E., 1998, Ichnology of the Bridge Creek Limestone: evidence for temporal and spatial variations in paleo-oxygenation in the Western Interior Seaway, in Dean, W.E. and Arthur, M.A., eds., Stratigraphy and Paleoenvironments of the Western Interior Seaway, USA: SEPM Concepts in Sedimentology and Paleontology, no. 6, p. 127–136

SHCHEPETKINA, A., GINGRAS, M.K., PEMBERTON, S.G. AND MACEACHERN, J.A., 2016. What does the ichnological content of the Middle McMurray Formation tell us?: Bulletin of Canadian Petroleum Geology, v. 64, p. 24-46.

FIGURE

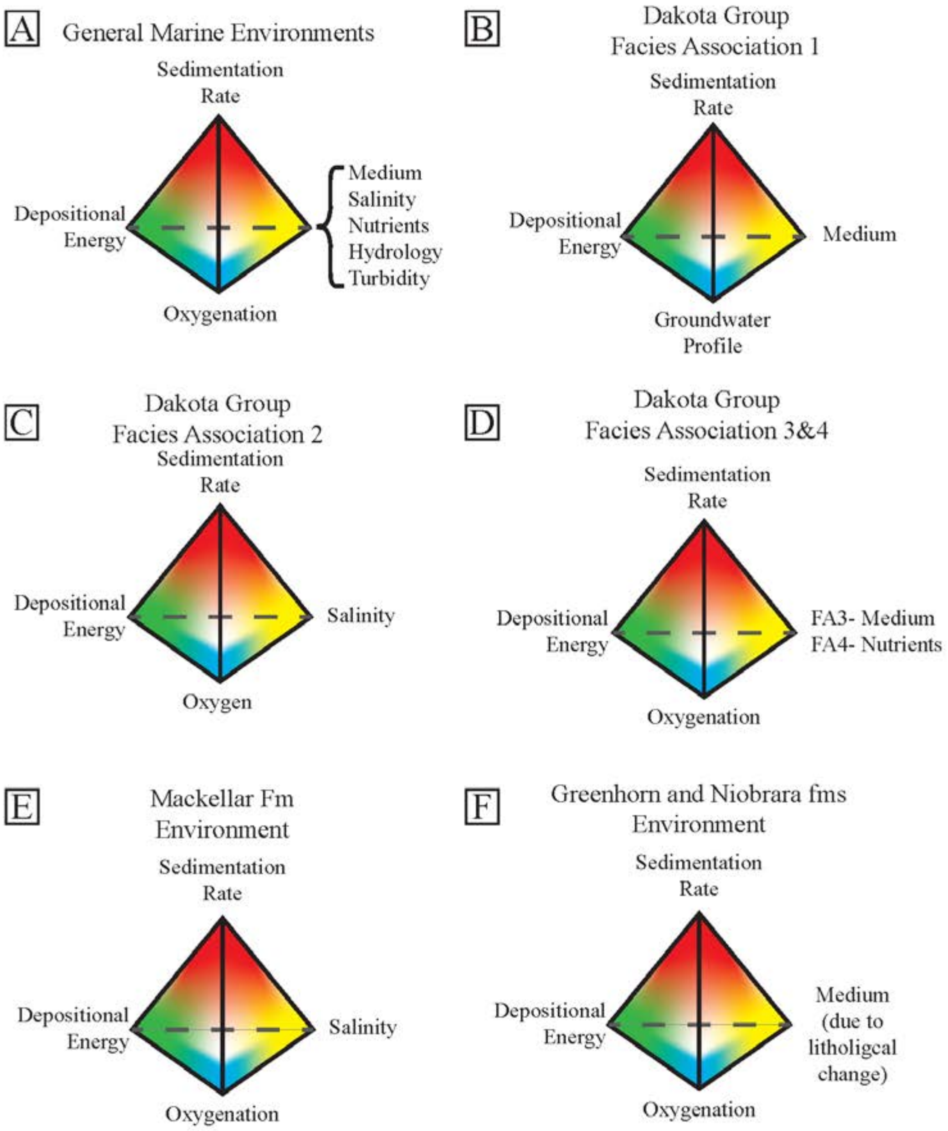


FIGURE 1—Tetrahedrons of interpreted primary physicochemical parameters that influenced organism behaviors. A) Physicochemical parameters for general marine depositional environments. B) Interpreted dominant physicochemical parameters for the Dakota Group Facies Association 1 (Lytle Fm and the Lower Channel Sandstone Mbr of the Muddy Fm). C) Interpreted dominant physicochemical parameters for the Dakota Group Facies Association 2 (Plainview Fm). D) Interpreted dominant physicochemical parameters for the Dakota Group Facies Association 3 and 4 (Glencairn Fm and Upper Transitional Mbr of the Muddy Fm). E) Interpreted dominant physicochemical parameters for the Mackellar Formation. F) Interpreted dominant physicochemical parameters for the Greenhorn and Niobrara fms; (modified from Hasiotis and Platt 2012).