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# Ichnology of the Winnipeg Formation, southeast Saskatchewan: a glimpse into the marine infaunal ecology of the Great Ordovician Biodiversification Event

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# LETHAIA



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The ichnology of the Middle Ordovician Winnipeg Formation has been analysed based on the study of cores from five wells drilled in southeast Saskatchewan (Canada). Six sedimentary facies, ranging from upper shoreface to lower offshore settings in a shallow-marine environment, have been characterized. Ichnological attributes are consistent with those in currently proposed models for shallow-marine wave-dominated settings, but ichnodiversity is lower than in post-Palaeozoic settings. Low ichnodiversity in the Winnipeg Formation most likely reflects evolutionary factors rather than environmental controls. Interestingly, low-energy, distal deposits of the Winnipeg Formation display intense degree of bioturbation, reflecting a well-developed mixed layer and underscoring the importance of the Great Ordovician Biodiversification Event in terms of sediment mixing.  $\Box$  *Great Ordovician Biodiversity, ichnology, shallow-marine environments, tiering, Winnipeg Formation.* 

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The Great Ordovician Biodiversification Event (GOBE) was associated with a remarkable increase in global biodiversity in connection with the rise of the Palaeozoic Evolutionary Fauna (Sepkoski 1995, 1997; Miller 1997; Servais & Harper 2018). These changes were expressed in the benthos by the appearance of more complex tiering structures, particularly with respect to epifaunal tiering (Servais *et al.* 2008, 2010). In addition to a diversification in deposit feeders, detritus feeders, suspension feeders and grazers in the benthos, suspension feeders and predators diversified in the water column, leading to a revolution in oceanic trophic webs (Bambach 1983; Sheehan 2001; Servais *et al.* 2008, 2010).

The ichnological expression of these fundamental changes in the benthos has been explored in several studies (Mángano & Droser 2004; Buatois *et al.* 2016a; Mángano *et al.* 2016). However, there are still few studies analysing the nature of tiering structures as a result of the GOBE and the impact of these changes in sediment mixing, to establish comparisons with the post-Palaeozoic world, which essentially shows the appearance of the modern benthos

that emerged from the Mesozoic Marine Revolution. In addition, it has been shown that global ichnodiversity increased through the Phanerozoic, with evolutionary radiations in marine ecosystems intimately linked with accelerated rates in trace-fossil diversification at ichnogenus level (Buatois & Mángano 2016). These issues are of interest not only for palaeobiologists and evolutionary palaeoecologists, but also potentially for sedimentary geologists interested in using ichnological data in palaeoenvironmental reconstructions in order to avoid the risk of uncritically extrapolating trace-fossil models based on post-Palaeozoic data to the Palaeozoic world.

The Middle Ordovician Winnipeg Formation of subsurface Saskatchewan (Canada) records transgression in open-marine environments over the North American Craton (Kreis 2004) (Fig. 1). This unit is ideally suited for evaluating the nature of bioturbation during the GOBE because it consists of sedimentary facies encompassing sub-environments ranging from the upper shoreface to the lower offshore along a wave-dominated depositional profile (Dorador *et al.* 2014). In addition, the overall transgressive scenario provided with colonization windows that were sufficiently long to allow the establishment of climax communities (Dorador *et al.* 2014). The main aims of this study were to (1) document the Winnipeg Formation ichnofauna within its palaeoenvironmental context; (2) compare ichnodiversity levels in this unit with those that typically characterize similar environments in the Mesozoic and Cenozoic; and (3) document tiering structure and sediment mixing along the depositional profile.

## Geological setting

The Middle Ordovician Winnipeg Formation occurs in subsurface of Saskatchewan and Manitoba in Canada, and Montana, North Dakota, Wyoming and South Dakota in United States, as well as in a few outcrops along the shores and some islands of Lake Winnipeg in Manitoba (Macauley 1952; Stocker 1956; Oberg 1966; Sweet 1982; Ferguson *et al.* 2007) (Fig. 1). This formation records transgressive deposition in the Willinston Basin (Norford *et al.* 1994; Ferguson *et al.* 2007). It is unconformably underlain by the Middle Cambrian to Lower Ordovician Deadwood Formation in most of the Williston Basin in Saskatchewan (Fig. 2) and directly by the Precambrian basement in the eastern area of Saskatchewan and Manitoba (LeFever 1996). The Upper Ordovician Yeoman Formation overlies unconformably the Winnipeg Formation in southeast Saskatchewan, being the lower interval of a thick succession of carbonates and evaporates (Big Horn Group), ranging in age from Late Ordovician to Early Silurian (Kendall 1976; Norford *et al.* 1994; Holmden 2009).

The Winnipeg Formation has been traditionally considered as Middle Ordovician based on its fauna, mainly conodonts (e.g. Macauley 1952; Oberg 1966; Sweet 1982; Norford et al. 1994; Kreis 2004; Ferguson et al. 2007). It has been divided into three members, which from bottom to top, are as follows: Black Island, Icebox and Roughlock members (Carlson 1960; Carlson & Thompson 1987). The Black Island Member is mainly characterized by bioturbated quartzose sandstone and scarce dark shale (Kreis 2004), and has been interpreted as a recording a wide variety of depositional environments, including fluvial, aeolian, coastal, shoreface and storm shelf (Kessler 1991). The Icebox Member is mostly composed of greenish grey bioturbated shale and mudstone. This member mostly records deposition in distal marine environments, including shelf settings



Fig. 1. Location of the studied cores (1-5) in southeast Saskatchewan (Canada). [Colour figure can be viewed at wileyonlinelibrary.com]



*Fig. 2.* Precambrian to Ordovician stratigraphy in southeast Saskatchewan (modified from Norford *et al.* 1994 and Saskatchewan Ministry of the Economy, 2013). [Colour figure can be viewed at wileyonlinelibrary.com]

(Kessler 1991). The Roughlock Member is dominated by calcareous shale, being locally restricted, and has not been recognized in the study area. The cores studied correspond to the sandstone-dominated Black Island Member, with only a few metres of the Icebox Member being present (Fig. 2).

## Methods

Cores from five wells were studied, all of them housed at the Saskatchewan Subsurface Geological Laboratory in Regina: (1) University of Regina (50°24.6'N, 104°35.4'W); (2) Nal Chapleau Lake (50°12.6'N, 103°34.8'W); (3) CPEC et al. Hartaven (49°47.4'N, 103°7.2'W); (4) Longview et al. Midale (49°30.6'N, 103°23.4'W); and (5) Shell Workman (49°3.6'N, 101°44.4'W) (Fig. 1). All wells are located in southeastern Saskatchewan (Fig. 1) and approximately recover 90 m of the Winnipeg Formation. Although cores are not continuous and a stratigraphical correlation between cores is uncertain due to the complex architecture of this formation (Potter 2006), they provide a representative sample of the sedimentary facies of the Winnipeg Formation. Cores were slabbed, described and interpreted following standard practice in facies analysis, as well as integrating ichnological data.

Ichnotaxa were classified at ichnospecies level wherever possible. Ichnotaxonomic identifications are based on observations in cross-sectional views and only occasionally are horizontal surfaces available for examination. Biogenic structures cannot be observed in three-dimension in core, adding a level of uncertainty to trace-fossil identification. However, morphological features (e.g. burrow fill, wall structure, form in cross-section) provide key evidence to support ichnotaxonomic assignments. Current procedures for identification of trace fossils in core have been established in detail elsewhere (e.g. Bromley 1990, 1996; Pemberton et al. 1992; Gerard & Bromley 2008; Knaust 2017).

The degree of bioturbation was determined using the Bioturbation Index (BI) proposed by Reineck (1963) and later adapted by Taylor & Goldring (1993), with differentiation of seven degrees from 0 (no bioturbation) to 6 (completely bioturbated).

# Winnipeg Formation ichnofauna

The Winnipeg Formation is characterized by an ichnofauna of moderate diversity consisting of ten ich-Arenicolites isp., notaxa: Asterosoma isp., Diplocraterion parallelum, Palaeophycus tubularis, Phycosiphon incertum, Planolites beverlevensis, Siphonichnus eccaensis, Skolithos linearis, Teichichnus rectus and Thalassinoides isp. (Fig. 3), illustrating the Skolithos and Cruziana ichnofacies. The main ichnotaxa present is as follows:

#### Arenicolites isp.

Consisting of U-shaped, lined vertical burrows lacking spreiten (Fig. 3A). Depth is 3.0–6.0 cm and diameter is 0.5–0.8 cm. It is considered a dwelling burrow probably produced by a suspension-feeding polychaete (Ekdale & Lewis 1991), although detritus-feeding has been documented in modern Ushaped burrows as well (Bromley 1996). *Arenicolites* is common in settings affected by rapid sedimentation, such as shorefaces and delta fronts, among



Fig. 3. Ichnotaxa recognized across the studied cores. A, Ar, Arenolites isp. B, As, Asterosoma isp. C, Di, Diplocraterion parallelum. D, Pa, Palaeophycus tubularis. E, Ph, Phycosiphon incertum. F, Pl, Planolites beverleyensis. G, Si, Siphonichnus eccaensis. H, Sk, Skolithos linearis. I, Te, Teichichnus rectus. J, Th, Thalassinoides isp. Scale bar 1 cm. [Colour figure can be viewed at wileyonlinelibrary.com]

others (e.g. Howard & Frey 1975; Bromley & Asgaard 1979; Ekdale & Lewis 1991).

#### Asterosoma isp

This ichnotaxon appears as zones of disturbed sediment exhibiting a concentric fill surrounding a central tube, representing the cross-section of the branches of a radial structure (Fig. 3B). Diameter is 0.5–1.5 cm. *Asterosoma* is interpreted as a feeding structure of a worm-shaped, vermiform organism (Chamberlain 1971; Vossler & Pemberton 1989; Pemberton *et al.* 2001; Seilacher 2007) and is commonly found in fully marine environments, ranging from shoreface to offshore (Farrow 1966; Frey & Howard 1970; Vossler & Pemberton 1989).

#### Diplocraterion parallelum

This consists of U-shaped vertical burrows with spreiten between both arms (Fig. 3C). Depth is 5.0– 7.0 cm and width is 2.1–3.5 cm. *Diplocraterion parallelum* is interpreted as a dwelling burrow probably produced by suspension-feeding polychaetes or crustaceans (Goldring 1964; Fürsich 1974; Gradzinski & Uchman 1994; Gingras *et al.* 1999). *Diplocraterion* commonly occurs in relatively high-energy settings, such as shorefaces, tidal flats and sub-tidal sandbodies, but also in a variety of marginal-marine and deep-water environments (e.g. Goldring 1964; Cornish 1986; Olivero *et al.* 2010; Carmona & Ponce 2011; Rodríguez-Tovar & Pérez-Valera 2013; Zhang *et al.* 2017a) and, less commonly, in continental environments (e.g. Zhang *et al.* 1998).

#### Palaeophycus tubularis

This ichnotaxon occurs as cross-sections of cylindrical, lined, horizontal burrows having an infill identical to the host rock (Fig. 3D). Diameter is 0.5– 1.2 cm. It is considered the dwelling burrow of suspension-feeding or predator polychaetes and is a facies-crossing ichnotaxon known in almost all sedimentary environments, including both marine and non-marine (Pemberton & Frey 1982; Mángano *et al.* 2002).

#### Phycosiphon incertum

This ichnotaxon is observed as small, dark, contorted burrows surrounded by a poorly defined light halo (Fig. 3E). Diameter is 0.2–0.5 cm. *Phycosiphon* is considered a fodinichnial structure produced by deposit feeders, commonly in low-energy areas of marine environments (Wetzel & Bromley 1994; Pervesler & Uchman 2007; Angulo & Buatois 2012; Rodríguez-Tovar *et al.* 2014).

#### Planolites beverleyensis

This consists of cross-sections of unlined, cylindrical sub-horizontal burrows, having an infill different to the host rock (Fig. 3F). Diameter is 0.4–0.7 cm and length is 0.6–1.4 cm. *Planolites beverleyensis* is interpreted as a feeding burrow of a worm-like deposit feeder and considered as a facies-crossing ichnotaxon produced in a wide variety of settings (Pemberton & Frey 1982; Mángano *et al.* 2002).

#### Siphonichnus eccaensis

This consists of vertical to sub-vertical cylindrical burrows having associated concave downward laminae (Fig. 3G). Diameter is 0.7 cm and length is 3.8–10.0 cm. *Siphonichnus eccaensisis* is produced by filter-feeder bivalves in response to sedimentation and erosion in areas where there is an alternation of sediment accumulation and erosive periods, such as deltas, estuarine bays or shorefaces (Stanistreet *et al.* 1980; MacEachern *et al.* 2005; Angulo & Buatois 2012; Dashtgard & Gingras 2012; Zonneveld *et al.* 2012).

#### Skolithos linearis

This structure occurs as vertical and sub-vertical lined burrows having an infill identical to the host rock (Fig. 3H). Diameter is 0.6–1.4 cm and length is 5.0–13.0 cm. In places, they are present in high densities forming characteristic piperock (e.g. Hallam & Sweet 1966; Droser 1991; Desjardins *et al.* 2010). This dwelling structure is produced by suspension feeders, probably polychaetes or phoronids, which colonize sediments that are rapidly deposited (e.g. during a storm) or in areas with actively migrating bedforms (Pemberton & Frey 1984; Vossler & Pemberton 1988; Fillion & Pickerill 1990).

#### Teichichnus rectus

This consists of horizontal burrows displaying a vertical spreiten (Fig. 3I). Diameter is 0.6–1.2 cm and height is 1.5–3.8 cm. *Teichichnus rectus* is a feeding structure produced by a worm-like organism or arthropods that migrates vertically (e.g. Knaust 2017). This ichnotaxon is present in a wide variety of marine environments, including lower shoreface, offshore, deltaic, estuarine and deep marine (e.g. Howard & Frey 1984; Beynon & Pemberton 1992; Pemberton *et al.* 1992; Corner & Fjalstad 1993; Buckman 1996; Pemberton *et al.* 2001).

#### Thalassinoides isp

It appears as sub-circular (0.5–4.0 cm diameter) cross-sections of sub-horizontal branching burrows, although branching is typically not seen in core expression (Fig. 3J). *Thalassinoides* is interpreted as a feeding structure. Post-Palaeozoic examples are produced by decapod crustaceans, but other tracemakers have been suggested for Palaeozoic examples (Myrow 1995; Carmona *et al.* 2004; Zhang *et al.* 2017b). *Thalassinoides* is a facies-crossing ichnotaxon, commonly found in oxygenated marine environments and soft and firm sediments (Ekdale *et al.* 1984; Schlirf 2000; Rodríguez-Tovar *et al.* 2008).

# Palaeoenvironmental distribution of trace fossils

Integration of sedimentological and ichnological evidence allows characterization of six facies (Table 1; Figs 4, 5), described and interpreted elsewhere (Dorador et al. 2014). These facies record deposition in a shallow-marine wave-influenced environment. encompassing upper, middle and lower shoreface, upper and lower offshore, and transgressive deposits. We follow previous environmental schemes and consider the shoreface as the area between the low tide and the fair-weather wave base and the offshore as located below the fair-weather wave base, but above storm wave base (e.g. MacEachern et al. 1999; Buatois & Mángano 2011). These deposits show marked differences in terms of hydrodynamic energy levels along the classic depositional profile of a wave-influenced platform (Pemberton et al. 1992; Pemberton et al. 2001, 2012; Buatois & Mángano 2011).

Upper shoreface deposits (Facies A) are represented by unbioturbated massive or trough to planar cross-bedded sandstone. These deposits were formed under high-energy conditions, dominantly by dune migration due to multi-directional currents, preventing the establishment of a benthic community (Howard 1972; MacEachern & Pemberton 1992).

Middle shoreface deposits (Facies B) consist of planar cross-bedded, and wave ripple cross- and parallel-laminated medium-grained sandstone, containing Arenicolites isp., Diplocraterion parallelum, Palaeophycus tubularis, Planolites beverleyensis, Siphonichnus eccaensis, Skolithos linearis and Thalassinoides isp.; Skolithos piperock occurs locally. BI is 1–4. The middle shoreface is characterized by

Table 1. Summary of the	sedimentary facies identified in Winni	peg Formation (based on Dorador et al. 2014	).	
Facies	Sedimentology	Ichnology	Depositional conditions	Environmental setting
A: Unbioturbated, cross-bedded, coarse- to medium-grained sandstone	White to grey, coarse- to medium- grained sandstone, with discrete 20- to 40-cm-thick beds. Structureless appearance and local presence of trough and planar cross-bedding	Absence of bioturbation (BI = 0)	High-energy conditions, inducing an inhospitable environment at the seafloor and precluding the establishment of a benthic community	Upper shoreface This area is commonly dominated by multi-directional current flows that generate dunes (Clifton 2006) whose migration prevents infaunal colonization (Howard 1972) MacEachern & Dombortory 1000)
B: Poorly bioturbated, cross- and parallel- laminated medium- grained sandstone	Light to dark grey medium- grained sandstone forming 15- to 30-cm-thick beds Local planar cross-bedding, wave ripples, cross- and parallel lamination and iron nodules	Ichnoassemblage comparatively of low to moderate diversity, including Arenicolites, Diplocraterion, Palaeophycus, Planolites, Siphonichnus, Skolithos and Thalassinoides, being dominant the vertical structures. Degree of bioturbation commonly low (BI = 1– 2) except in some discrete intervals (BI = 4) with a high abundance of	Presence of lamination and dominance of vertical structures of suspension feeders indicate high energy, abundance of suspension particles and good oxygenation	Fernorion 1272) Middle shoreface Area dominated by storms and high energy (MacEachern & Pemberton 1992). However, pipe rocks reveal short time periods without sedimentation when the colonization windows allow bioturbation of dume deposits (e.g. Desjardins <i>et al.</i> 2010)
C: Variably bioturbated, medium- to fine- grained sandstone	Light grey medium- to fine- grained sandstone, in 10- to 20- cm-thick layers and subordinated dark grey mudstone General absence of sedimentary structures, other than local presence of low-angle cross- lamination	vertical burtows (pipe rocks) Ichnoassemblage relatively diverse with ten identified ichnotaxa (Arenicolites, Asterosoma, Diplocraterion, Palaeophycus, Phycosiphon, Planolites, Siphonichnus, Skolithos, Teichichnus and Thalassinoides), being dominant horizontal structures of deposit feeders. Variable bioturbation index, ranging from 2 to 5, with dominance of intensely bioturbated intervals where discrete trace fossils cannot be clearly differentiated	Low-energy setting close to the fair- weather wave base. Variable energy determined by the storm frequency and intensity, controlling bioturbation (MacEachern & Pemberton 1992; Buatois & Mángano 2011). Sparsely bioturbated intervals dominated by structures of opportunistic organisms reflecting short colonization windows during times of relatively high energy. Longer low energy periods during fair- weather times represented by intensely bioturbated intervals and dominance of horizontal structures of deposit feeders	Lower shoreface Variable energy determined by storm influence (MacEachern & Pemberton 1992)
D: Intensely bioturbated, fine- grained muddy sandstone and mudstone	Dark grey and very fine- to fine- grained muddy sandstone and mudstone in 12- to 31-cm-thick individual layers. Mudstone dominant over sandstone	Intense bioturbation is abundant (BI = 4 -5), but just six ichnotaxa present (Asterosoma, Palaeophycus, Phycosiphon, Planolites, Teichichnus and Thalassinoides) typically superimposed on a mottled background. Horizontal dwelling or feeding structures of deposit/detritus feeders clearly dominant	I watcharter of removement of 1992 Low- to moderate-energy setting allowing colonization by macrobenthic tracemakers under favourable environmental conditions (MacEachern & Pemberton 1992)	Upper offshore

(continued)

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Facies	Sedimentology	Ichnology	Depositional conditions	Environmental setting
E: Fully bioturbated sandy mudstone	Dark grey mudstone in 4- to 5- cm-thick layers. Appearance is mostly massive, locally with very thin, very fine-grained sandstone laminae	Deposits completely bioturbated (BI = 6); discrete trace fossils cannot be identified	Very-low-energy setting dominated by suspension fall out under favourable conditions, allowing intense bioturbation. Bioturbation mainly concentrated in the uppermost centimetres on the sediment, destroying any sedimentary structure and causing total sediment mixing	Lower offshore
F: Moderately bioturbated, medium- to fine-grained sandstone	Light grey, poorly sorted, medium- to very fine-grained sandstone, with low-angle cross- lamination and iron nodules, forming 18- to 30-cm-thick beds. These beds are stacked forming fining-upward intervals, in some cases capped by mudstone layers	Seven ichnotaxa were identified ( <i>Arenicolites</i> , <i>Diplocraterion</i> , <i>Palaeophycus</i> , <i>Planolites</i> , <i>Skolithos</i> , <i>Teichichnus</i> and <i>Thalassinoides</i> ). Variable degree of bioturbation (BI = 2 -4) according to dominance of vertical burrows (BI = 2) or horizontal structures (BI = 3-4), the latter being more common	Well-oxygenated shallow-marine setting that reflects transgressive conditions. Intense bioturbation, erosive bases and very poor sorting suggest several punctuated transgression and wave ravinement	Transgressive deposits

high-energy conditions and dune and ripple migration in the area where waves initially break (Clifton 2006).

Lower shoreface deposits (Facies C) are characterized by medium- to fine-grained muddy sandstone, locally with low-angle cross-lamination. Arenicolites isp., Asterosoma isp., Diplocraterion parallelum, Palaeophycus tubularis, Phycosiphon incertum, Planolites beverleyensis, Siphonichnus eccaensis, Skolithos linearis, Teichichnus rectus and Thalassinoides isp. are present. Horizontal structures of deposit feeders are clearly dominant, and degree of bioturbation varies from low (BI = 2) in some intervals to commonly high (BI = 5). Lower shoreface reflects variable energy conditions, determined by storm intensity and frequency (MacEachern & Pemberton 1992). Sparsely bioturbated intervals, dominated by vertical structures of suspension feeders produced by opportunistic organisms, reflect short colonization windows during relatively high-energy conditions. On the other hand, intensely bioturbated intervals dominated by horizontal structures of deposit feeders were formed during low-energy periods (MacEachern & Pemberton 1992; Buatois & Mángano 2011).

Upper offshore deposits (Facies D) are represented mostly by mudstone and subordinate fine- to very fine-grained muddy sandstone. *Asterosoma* isp., *Palaeophycus tubularis, Phycosiphon incertum, Planolites beverleyensis, Teichichnus rectus* and *Thalassinoides* isp. are present. Deposits are intensely bioturbated (BI = 4–5) with discrete trace fossils overprinted on a non-distinct mottled background. Dwelling or feeding structures of deposit/detritus feeders are clearly dominant. Upper offshore deposits reflect low- to moderate-energy conditions, supporting colonization of tracemakers (MacEachern & Pemberton 1992).

Lower offshore deposits (Facies E) are characterized by mudstone locally with very thin, very finegrained sandstone laminae. These intervals are completely bioturbated (BI = 6), and discrete trace fossils cannot be identified. Lower offshore deposits illustrate very-low-energy conditions and sedimentation by suspension fall out, allowing colonization of infaunal organisms in the uppermost centimetres of the sediment and resulting in complete sediment reworking and erasing of any primary sedimentary structure (MacEachern & Pemberton 1992).

Transgressive deposits (Facies F) consist of medium- to very fine-grained sandstone stacked forming fining-upward intervals in some cases capped by mudstone layers. They contain *Arenicolites* isp., *Diplocraterion parallelum*, *Palaeophycus tubularis*, *Planolites beverleyensis*, *Skolithos linearis*, *Teichichnus rectus* and *Thalassinoides* isp. Degree of bioturbation

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Dorador et al.



Fig. 4. Schematic distribution of sedimentary facies and associated trace fossils along the depositional profile: Ar, Arenicolites isp.; As, Asterosoma isp.; Di, Diplocraterion parallelum; Pa, Palaeophycus tubularis; Ph, Phycosiphon incertum; Pl, Planolites beverleyensis; Sk, Skolithos linearis; Te, Teichichnus rectus; Th, Thalassinoides isp. Scale bar 1 cm. [Colour figure can be viewed at wileyonlinelibrary.com]

is typically moderate (BI = 2-4). These deposits were formed in a well-oxygenated shallow-marine setting undergoing transgression. These deposits suggest punctuated transgression due to wave ravinement (Cattaneo & Steel 2003).

#### Ichnodiversity levels

The Winnipeg Formation ichnofauna displays the typical features of trace-fossil assemblages from weakly storm-affected shallow-marine areas (MacEachern & Pemberton 1992; Buatois 8 Mángano 2011; Pemberton et al. 2012). However, ichnodiversity levels are lower than expected considering the most commonly used models for shallowmarine environments (Buatois & Mángano 2011; Pemberton et al. 2012), with only ten ichnotaxa identified in the Winnipeg Formation. Ichnodiversity levels in the Winnipeg Formation should be framed within a broader context. Therefore, several ichnological studies from shallow-marine deposits have been compiled ranging from the Ordovician to the Cretaceous (Tables 2, S1). Comparison with younger units shows a general trend towards an increase in total ichnodiversity levels. However, in order to more accurately compare ichnodiversity levels and to frame the Winnipeg ichnofauna into a broader evolutionary context, alpha ichnodiversity has been considered for each of the environmental subdivisions of the depositional gradient (Table 2). Alpha ichnodiversity reflects the number of ichnotaxa that can be identified within a specific community, therefore providing information about ecological complexity of particular communities (Buatois & Mángano 2011, 2013; Mángano & Buatois 2014). Alpha ichnodiversity levels from the Winnipeg Formation, from upper shoreface to lower offshore, are consistent with those observed in other Palaeozoic units, but lower that those ones from the Mesozoic, particularly Jurassic and Cretaceous units. This is clearly reflected by upper offshore deposits containing only six ichnotaxa, which is very low compared with typical post-Palaeozoic levels (Table 2).

The overall low alpha ichnodiversity displayed by the Winnipeg ichnofauna underscores the need for calibrating trace-fossil models through geological time (e.g. Buatois *et al.* 2005). Ichnodiversity levels that may be taken as indicative of stress factors (e.g. brackish water, oxygen depletion) in post-Palaeozoic settings may be the norm for older shallow-marine ichnofaunas.

#### Tiering structure

Infaunal communities live vertically zoned with respect to the sediment-water interface due to

#### LETHAIA 52 (2019)

![](_page_8_Figure_2.jpeg)

*Fig.* 5. Sedimentological logs of the studied cores illustrating lithology, sedimentary structures, trace fossils, bioturbation index and sedimentary facies (from A to F). Well depth is indicated at the top and bottom of each core.

variation of physical, chemical and biological factors (Ausich & Bottjer 1982; Bromley 1990, 1996; Mángano & Buatois 2014). This vertical distribution is referred as tiering and suggests that organisms located in the same tier exploit resources in the same way (see Buatois & Mángano 2011 for a more detailed explanation). According to this vertical zonation, Bromley (1990, 1996) proposed the ichnoguild concept based on bauplan, food source and use of space, providing information about ecospace utilization by the benthos.

The Winnipeg Formation displays relatively simple tiering structures (Fig. 6). The uppermost centimetres of the sediment were characterized by the presence of a completely bioturbated mixed layer, as can be inferred by the mottled background clearly identified in offshore facies. This indistinct mottling is overprinted by the shallowtier trace fossils *Planolites beverleyensis*, *Phycosiphon incertum*, *Asterosoma* isp. and *Palaeophycus tubularis*. In turn, these are cross-cut by midtier ichnotaxa, namely *Teichichnus rectus* and *Thalassinoides* isp.; and the deep-tier ichnotaxa *Skolithos linearis*, *Arenicolites* isp., *Diplocraterion parallelum* and *Siphonichnus eccaensis*. Six ichnoguilds have been identified in this multitiering community (Fig. 6).

Planolites *ichnoguild.* – Characterized by transitory, shallow-tier, deposit-feeder structures produced by vermiform organisms. This ichnoguild is composed of *Planolites beverleyensis* and *Phycosiphon incertum*, but the latter is not present in the most proximal facies.

Asterosoma *ichnoguild.* – This monospecific ichnoguild is composed of stationary, shallow-tier, depositfeeder burrows produced by worm-like organisms.

Palaeophycus *ichnoguild.* – Semipermanent, shallow-tier, suspension feeder or predator structures produced by vagile vermiform organisms. *Palaeophycus tubularis* is the single element in this ichnoguild.

Teichichnus *ichnoguild.* – Defined by vagile, midtier, deposit-feeder structures. This is a monospecific ichnoguild represented by *Teichichnus rectus*.

Thalassinoides *ichnoguild*. – This ichnoguild is composed of stationary, mid-tier, deposit-feeder

			Shore	ace		1.50	Offshor	6					
		References	Uppei	· Middle	Lower	Uttshore Transition	Upper	Middle	Lower	Max.	Av.	Total	Comments
Mesozoic	Cretaceous	Howard & Frey (1984)	8	11	11		6	51	5	11	∞	16	Middle and lower offshore intensively
		Frey & Howard (1990)		10	12		10	D.	2	12	8	16	bioturbated but discrete trace tossils are rare Lower offshore deposits are thoroughly
		MacEachern &	4	16	23		17		10	23	14	27	DIOLUEDAIED DUI UISCIELE LEACE JOSSIIS AFE FAFE
		Pemberton (1992) Pemberton <i>et al</i> (1992)	¢	9	14		14		ſ	14	¢	ر ار	
		Reid & Pemberton (2007)	1	15	16		16		14	16	15	22	Deltaic influence
		Hansen & MacEachern		8	11		8	13		13	10	16	Deltaic influence (asymmetric delta)
	Jurassic	Martin & Pollard (1996)	4	3	Ŋ	11	3		4	11	Ŋ	15	
		Joseph et al. (2012)	8	20	11	25	22		11	25	16	30	Depositional setting inferred in the present study
		Baniak et al. (2014)	~ ~	9 (	υ u		L 0		9 0		u n	15	Depositional setting inferred in the present study
		Fürsich <i>et al.</i> (2018)	13 4	4	n		n		لا	13 م	C	14 13	Storm deposit. Only upper shoreface recognized
	Triassic	Zonneveld <i>et al.</i> (2001)	3	4	6	9				6	9	11	Mixed siliciclastic carbonate marginal-marine
		Zonneveld <i>et al.</i> (2004)	0		Ŋ	11				11	ŝ	12	depositional system
		Zonneveld et al. (2010)	1		14	3	17		1	14		25	Offshore and offshore transition inferred in the
Dalaeozoic	Dermian	Rann & Fielding (2004)	ø	L	10	10	1		σ	10	13	70	present study
I alacuzulu	I CITIII di I	Bann et al (2004)	0		15	18	12		ر د د	12	<u>, 1</u>	+7 00	
	Carboniferous	Gluszek (1998)			18	0	1		3	18	2	18	Storm deposit. Only lower shoreface to upper
		Buntais at al (2002)	ç	10	13	~	6			13	y	17	offshore recognized
		Bhattacharya & Bhattacharya & Bhattacharya	1	2	<u>.</u>	۲	10		1	10	0 0	10	
		(2007)		,		,							
	Devonian	Bradshaw (2010)	0	9	10	0	0		,	10	4	16	
		Angulo & Buatois (2012)		1	4	D	90		_	9 u	4 ;	9 1	
		Da Suva et ul. (2012) Sharafi et al. (2014)		را د	4		0			01 4	14	10	
		Zhang & Zhao (2015)	~	2	4		Ŋ		5	• ∞	9	13	
		Fan & Gong (2016)		1	2	9	6			6	5	12	
	Silurian	Sedorko <i>et al.</i> (2017)			16					16		16	Only lower shoreface to offshore transition
	Ordovician	Mángano <i>et al.</i> (2005)			1	9	12		1	12	Ŋ	13	le distinction between middle and lower
		de Gibert <i>et al.</i> (2011) Winnineg Fm (nresent	C	6 1	10		9			7	s v	9 01	shoreface
		paper)	0				)			0	0	0	

LETHAIA 52 (2019)

![](_page_10_Picture_2.jpeg)

*Fig.* 6. Schematic diagram of tiering structure and ichnoguilds from Winnipeg Formation. [Colour figure can be viewed at wileyonline-library.com]

burrows. *Thalassinoides* isp. is the only constituent ichnotaxa of this ichnoguild.

Skolithos *ichnoguild.* – Characterized by permanent structures, deep-tier, suspension-feeder organisms. This ichnoguild is composed of *Skolithos linearis*, *Arenicolites* isp., *Diplocraterion* isp. and *Siphonichnus eccaensis*.

These ichnoguilds are linked to fluctuations in environmental controls and show a clear distribution along the depositional setting profile from proximal to more distal areas (Fig. 7). Accordingly, the ichnoguild characterized by deep-tier dwelling structures of suspension feeders (Skolithos ichnoguild) occurs in shoreface environments affected by continuously agitated waters, whereas ichnoguilds dominated by shallow- to mid-tier feeding structures of deposit feeders (e.g. Teichichnus ichnoguild) tend to be abundant in low-energy offshore deposits. In the more distal deposits, the discrete structures identified may overprint a bioturbated background, revealing emplacement in the transition zone located below a well-developed mixed layer. Overall, offshore deposits typically show a higher degree of bioturbation (Fig. 7).

## **Evolutionary implications**

The overall ichnodiversity in the Winnipeg Formation is lower than the one that characterizes archetypal expressions of the *Cruziana* Ichnofacies. In addition, tiering structures is less complex and, with the exception of the *Skolithos* ichnoguild and the *Planolites* ichnoguild, all the other ones are monospecific. Depauperate expressions of the *Cruziana* Ichnofacies are commonly related to stressed conditions, as occurs in marginal-marine settings affected by rapid salinity fluctuations (e.g. MacEachern & Pemberton 1994; MacEachern et al. 2005; Carmona et al. 2009; Sarkar et al. 2009). However, similar ichnodiversity levels to those recorded in the studied deposits are also observed in other early Palaeozoic trace-fossil assemblages (e.g. Mángano et al. 2005). Moreover, impoverished trace-fossil assemblages due to stressed conditions are characterized not only by lower ichnodiversity than that of the corresponding archetypal ichnofacies, but also by a less intensity of bioturbation and uneven distribution of biogenic structures in contrast to the more uniform and intense bioturbation of fully marine environments (MacEachern et al. 2005). However, the Winnipeg Formation is for the most part characterized by relatively uniform high degrees of bioturbation (BI = 4-5), making this scenario inconsistent with a stressed setting.

Although global ichnodiversity shows a continuous increase through the Ordovician as result of the GOBE, ichnodiversity levels remained lower than in post-Palaeozoic settings (Mángano & Droser 2004; Buatois & Mángano 2011, 2016; Buatois et al. 2016a; Mángano et al. 2016). The relatively low ichnodiversity levels of the Winnipeg Formation are interpreted as reflecting evolutionary rather than environmental constrains. Therefore, alpha ichnodiversity in wavedominated to wave-influenced shallow-marine environments seems to display similar trends to those identified for global ichnodiversity (Buatois & Mángano 2016). This fact would explain the differences between ichnodiversity levels of the Middle Ordovician Winnipeg Formation and those from post-Palaeozoic units.

Notably, the highest ichnodiversity per ichnoguild occurs in the nearshore *Skolithos* ichnoguild, comprising *Arenicolites* isp., *Diplocraterion parallelum* and *Skolithos linearis* produced by worm-like organisms and *Siphonichnus eccaensis* by bivalves. These are the common structures in Palaeozoic foreshore to middle shoreface deposits of wave-dominated shallow-

![](_page_11_Figure_2.jpeg)

*Fig. 7.* Trace-fossil distribution (grouped by ichnoguilds) from upper shoreface to lower offshore facies. [Colour figure can be viewed at wileyonlinelibrary.com]

marine systems, characterized by well-oxygenated and high-energy conditions (Droser 1991; Mángano *et al.* 2005, 2016; Desjardins *et al.* 2010). However, in similar environments of the Mesozoic and Cenozoic, deposits are characterized by structures produced by crustaceans, such as *Ophiomorpha* or *Thalassinoides*, underscoring a change in the dominant infauna (Mángano *et al.* 2016). This replacement has been explained due to radiation of decapods crustaceans during the Mesozoic (e.g. Carmona *et al.* 2004; Buatois *et al.* 2016b; Mángano *et al.* 2016).

Our study underscores the importance of carefully evaluating the evolutionary context when using ichnological models for Palaeozoic strata. Trace-fossil models used to characterize shallow-marine settings are mostly based on the study of post-Palaeozoic deposits, but these settings present a higher ichnodiversity and were not dominated by the same tracemaker community and thus, the ichnological content is different. This may result in misinterpretations of Palaeozoic ichnofaunas.

# Sediment mixing and benthic activity

The topic of sediment mixing and the timing of the establishment of the mixed layer during the early

Palaeozoic has attracted considerable attention in recent years (e.g. McIlroy & Logan 1999; Droser et al. 2002, 2004; Buatois & Mángano 2011; Mángano et al. 2013; Mángano & Buatois 2014, 2016, 2017; Tarhan & Droser 2014; Tarhan et al. 2015; Gougeon et al. 2018). Lower Palaeozoic shallow-marine deposits in places display evidence of firm conditions close or at the sediment surface, as indicated by the occurrence of unlined open burrows in mudstone, presence of bioglyphs and scratch trace fossils, detailed preservation of tiny structures, preservational bias in favour of very shallow-tier structures and absence of well-developed mottled textures (Droser et al. 2002, 2004; Dornbos et al. 2004; Jensen et al. 2005; Mángano et al. 2013; Tarhan & Droser 2014). The existence of widespread firmgrounds is also supported by the presence of helicoplacoid echinoderms living as sediment stickers and edrioasteroids living unattached on the seafloor (Bottjer et al. 2000; Dornbos 2006; Kloss et al. 2015). Also, lower Cambrian ichnofaunas are commonly associated with microbially induced sedimentary structures, suggestive of microbial stabilization of substrates (Dornbos et al. 2004; Buatois et al. 2014). These different lines of evidence have been regarded as indicative of the virtual absence of a mixed layer early in the Phanerozoic (Droser et al. 2002, 2004; Dornbos et al. 2004; Jensen et al. 2005;

Dornbos 2006; Mángano *et al.* 2013; Tarhan & Droser 2014; Kloss *et al.* 2015).

The mixed layer consists of the uppermost centimetres of the sediment which are intensely bioturbated by the activity of the shallowest tier producers in a soupy substrate (Teal *et al.* 2010). The presence of the mixed layer favours sediment oxygenation and consequently nutrient recycling, having a marked impact in the distribution of organic matter (e.g. Adámek & Maršálek 2013; Metzger *et al.* 2014). The timing of appearance of the mixed layer in the geological record is still debatable (e.g. Zhang *et al.* 2017b). Although originally regarded as first occurring in the Ordovician (e.g. Droser *et al.* 2002), it has been recently proposed that marine sediment mixing was limited through all the early Palaeozoic, first taking place during the late Silurian (Tarhan *et al.* 2015).

The Winnipeg Formation provides an excellent opportunity to assess sediment mixing along the depositional profile during the GOBE. In particular, the lower energy deposits formed below fair-weather wave base are intensely bioturbated. Lower offshore deposits are thoroughly bioturbated and no evidence of the primary fabric is preserved. Moreover, lower shoreface and upper offshore deposits are characterized by a mottled background overprinted by discrete trace fossils. This mottling has been elsewhere interpreted as a consequence of the high bioturbation of organisms in soupy sediments corresponding to the mixed layer (e.g. Rodríguez-Tovar & Dorador 2014). Therefore, it is suggested that given the appropriate environmental conditions (i.e. low energy, oxygenated bottom and interstitial waters, continuous colonization windows), there is ample evidence of a well-developed mixed layer in these Middle Ordovician strata. Intense bioturbation in low-energy, fair-weather fully marine deposits have been recently documented in Upper Ordovician carbonates of the Willinston Basin (Zheng et al. 2018).

## Conclusions

An ichnological study of the Middle Ordovician Winnipeg Formation was performed in different cores from southeast Saskatchewan. Ten ichnotaxa were characterized belonging to the *Skolithos* and *Cruziana* Ichnofacies. Lithology, sedimentary structures and ichnological features reveal deposition in a shallow-marine setting, from upper shoreface to lower offshore, under variable energy conditions.

In spite of an overall agreement with the traditionally proposed ichnofacies models for wavedominated shallow-marine environments, anomalously low alpha ichnodiversity levels are recorded in each sub-environment along the depositional profile. Considering that the most common models are based on Mesozoic deposits, low ichnodiversity levels from Winnipeg Formation can be explained by evolutionary trends. This fact underscores the importance of assessing evolutionary factors when applying ichnological models to the study of Palaeozoic deposits to avoid misinterpretations.

Tiering reveals a relatively simple infaunal community. Six ichnoguilds have been identified. The common presence of a mottled background points the existence of intense bioturbation in the uppermost centimetres of the sediment. This fact suggests the presence of a well-developed mixed layer at the time of the GOBE.

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LETHAIA 52 (2019)

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## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Detailed list of ichnotaxa characterized bysubenvironment in every study considered inTable 2.