Ichnofauna record cryptic marine incursions onto a coastal floodplain at a key Lower Mississippian tetrapod site

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Abstract

Ichnofossils from a Lower Mississippian (Tournaisian) coastal plain succession with a rich vertebrate fauna, including early tetrapods, record repeated, short-lived marine interactions that influenced floodplain lake development and ecosystems. The ichnofauna contrasts with the more typical *Scoyenia* Ichnofacies of other Devonian-Carboniferous tetrapod sites. In the Tournaisian Ballagan Formation of the Scottish Borders, *Chondrites* is identified in 128 horizons within a 500-m succession and is associated with lesser occurrences of phycosiphoniform burrows, *Diplocraterion*, *Rhizocorallium* and *Zoophycos*?. *Chondrites* and phycosiphoniform burrows commonly occur within dolostones, interpreted as part of a saline-hypersaline lake facies association, containing a non-marine to marginal marine macrofauna of bivalves, ostracods, *Spirorbis*, *Serpula* and sarcopterygian fish. Marine scolecodonts are reported from 18 horizons of diverse lithology, four of which co-occur with *Chondrites*. The single-colonisation, single-tier, high ichnofabric index and thin beds (mean 10 cm thick) that characterise *Chondrites* horizons indicate: 1) adverse

environmental conditions; 2) rapid colonisation of the sediment; and 3) short-lived bioturbation episodes. Other ichnotaxa identified are *Monocraterion* and *Asterosoma*?, which occur exclusively within the overbank or fluvial facies associations, and are here interpreted to have lived in freshwater conditions. The *Chondrites* trace-makers are interpreted as having originated in shallow-marine waters and were transported into floodplain lakes by storm surge events, although a few examples suggest more significant transgressions. Ichnofossils are much more common than marine body fossils or scolecodonts, and thus record cryptic marine incursions that might otherwise remain unidentified. This study contributes to our understanding of the complex mosaic of environments present when terrestrial tetrapods first appeared.

Keywords: Carboniferous; *Chondrites*; ichnology; brackish; storm surge; dolostone

1. Introduction

Recent studies of Lower Mississippian sedimentary rocks from the Scottish Borders and Nova Scotia have revealed a rich vertebrate fauna of lungfish (Smithson et al., 2016) and tetrapods (Anderson et al., 2015; Clack, 2002; Smithson et al., 2012; Clack et al., 2016) within the vertebrate fossil-poor interval known as Romer's Gap. The most common animal groups in the Ballagan Formation of the Scottish Borders are bivalves, sarcopterygian fish and ostracods, which are interpreted as fresh to brackish water tolerant (Bennett et al., 2016). The ichnofaunal assemblages in these strata can elucidate the palaeoenvironment during the time when terrestrial tetrapods are first recorded (Smithson et al., 2012).

The ichnofossil record of most Devonian-Carboniferous tetrapod sites is of the *Scoyenia* Ichnofacies representing the floodplain environment (Fillmore et al., 2010; Buatois and Mángano, 2002). For example, the contemporaneous Horton Bluff Formation, of Blue Beach in Nova Scotia, Canada, has a *Scoyenia* Ichnofacies assemblage with tetrapod and invertebrate trackways and feeding traces (Mansky and Lucas, 2013). At the Middle Devonian tetrapod site of Zachelmie Quarry, Poland, lagoonal dolostones contain an impoverished *Cruziana* Ichnofacies interpreted as a marginal marine assemblage (Niedźwiedzki et al., 2014). This study reports an abundant *Chondrites* and less common phycosiphonid ichnofauna from the

Lower Mississippian Ballagan Formation of the Scottish Borders. *Chondrites* and *Phycosiphon* are reported from one other Carboniferous tetrapod locality, in a borehole through the Pennsylvanian Joggins Formation of Nova Scotia (Dafoe et al., 2011). The assemblage was only identified in core, contrasting with the prevalent *Scoyenia* Ichnofacies of the formation, and is interpreted as the result of brackish water incursions.

Chondrites and phycosiphoniform assemblages are usually reported from a range of marine settings: abyssal (Wetzel, 2010), deep marine (Buatois and Angriman, 1992), offshore (Buatois et al. 2013; Buatois and Angriman, 1992; Głuszek, 1998; Izumi, 2015), shallow/nearshore (Bjerstedt 1987; Angulo and Buatois, 2012; Pollard, 1988) and tidal flats (Hertweck et al., 2005; Wescott and Utgaard, 1987). This study is the first detailed report of ichnofauna from a Palaeozoic terrestrial tetrapod site where *Chondrites* and phycosiphoniform burrows predominate. To investigate this unusual association, ichnotaxa and ichnofacies are documented from core and field sections through the Ballagan Formation in relation to their sedimentary context and associated fauna. The implications of ichnofauna and associated scolecodonts recorded herein are discussed in terms of the extent of marine influence on a coastal floodplain which hosts the earliest terrestrial tetrapods.

2. Geological Background

The Lower Mississippian (Tournaisian) Ballagan Formation is exposed across the Midland Valley of Scotland and in the Scottish Borders. Near to Berwick-upon-Tweed it spans most of the Tournaisian and encompasses the VI to CM palynomorph zones (Fig. 1). The formation is characterised by three facies associations: 1) an overbank facies association of siltstone, sandstone and palaeosols; interbedded with 2) a saline-hypersaline lake facies association, comprising dolostone (historically and locally known as cementstone) and evaporite units. Both of these facies associations are truncated by 3) the fluvial facies association, comprising fining-upwards successions of conglomerate lags, cross-bedded sandstone and rippled siltstone (Bennett et al., 2016).

Figure 1. Location map and lithostratigraphy. The location of the Norham borehole (National Grid Reference 391589, 648135) and Burnmouth field section in the Scottish Borders are illustrated. Lithostratigraphy of the Ballagan Formation, Mississippian in the area near Berwick-upon-Tweed, adapted from Waters (2011) and Smithson *et al.* (2012). The grey unit represents an erosional surface and overlying hiatus.

Palaeosols are numerous in the Ballagan Formation and represent wetland marsh to forested landscapes (Kearsey et al., 2016). Interspersed between the palaeosols are laminated siltstones and sandy siltstones that represent floodplain lakes and pools (Bennett et al., 2016). The floodplain environment is interpreted to have been low-lying and subject to periodic desiccation and marine incursions (Andrews and Nabi, 1998; Andrews et al., 1991; Bennett et al., 2016; Kearsey et al., 2016; Scott, 1986; Stephenson et al., 2002). Evidence from flood-derived sediments, tree rings and palaeosols indicates seasonal monsoon-like heavy rainfall (Bennett et al., 2016; Falcon-Lang, 1999; Kearsey et al., 2016) in a location a few degrees south of the equator (Scotese and McKerrow, 1990). Dolostones are a key feature of the formation and are thought to have formed in brackish floodplain lakes (Andrews et al., 1991; Andrews and Nabi, 1998; Scott, 1971), and as marginal marine deposits (Belt et al., 1967), or sabkhas (Scott, 1986).

Reports of fossils from other Ballagan Formation localities in Scotland have recorded a vertebrate fauna of sarcopterygians, dipnoans, chondrichthyans, acanthodians and tetrapods (Carpenter et al., 2014; Clack, 2002; Smithson et al., 2012, 2016), shrimps (Cater et al., 1989), plants (Bateman and Scott, 1990) and palynomorphs (Stephenson et al., 2004). In a study of Ballagan Formation ostracods from the Midland Valley of Scotland, Williams et al. (2005, 2006) noted that fully marine fossils (orthocones and brachiopods) are rare in the formation. Detailed studies of the fauna of sandy siltstones from the Norham Core and Burnmouth also revealed that marine fossils are rare (Bennett et al., 2016). Sandy siltstones contain a fauna dominated by non-marine bivalves, ostracods, sarcopterygian (actinopterygian and rhizodont) fish and arthropods, with rarer occurrences of *Spirorbis*, *Serpula*, scolecodonts, tetrapods and orthocones. The fossil content of the Ballagan Formation dolostones has variously been reported as unfossiliferous apart from algae (Ghummed, 1982), impoverished apart from ostracods, bivalves and *Spirorbis* (Belt et al., 1967) and vertebrate-rich with a fauna of actinopterygians, sarcopterygians, dipnoans, chondrichthyans and acanthodians (Carpenter et al., 2014).

3. Methods and Materials

Ichnotaxa were studied from a 490-m-thick fully cored borehole at Norham West Mains Farm (the Norham Core) located about 10 km southwest of Berwick-upon-Tweed (BGS borehole NT94NW20) and a 520-m-thick coastal exposure at Burnmouth, 10 km north of Berwick-upon-Tweed (Fig. 1). The study interval covers the entire Ballagan Formation. Detailed sedimentary logging identified bioturbated intervals, and palaeontological sampling at centimetre intervals exposed further ichnofossil evidence. During borehole logging the reference half of the core was sprayed with water to better reveal trace fossils within light coloured fine-grained dolostones. Photographs of the reference half of the Norham Core were used to identify and document ichnofaunas in cross-section and bedding surfaces were examined throughout both sections. *Chondrites* are also described from standard-sized, polished thin sections of the core.

Palynological processing and analysis of 277 samples from the Norham Core and 280 samples from Burnmouth were undertaken at the University of Southampton. Only the scolecodont results are reported herein. Standard processing techniques were used on a sample size of 5 g, first treated with 30 % HCl to remove carbonates followed by decant washing and then 60 % HF to complete demineralization. After decant washing to neutral the samples were sieved at 15 μ m, placed in a glass beaker with 30 % HCl and briefly boiled to dissolve neoformed fluorides. They were then rapidly diluted and re-sieved with the residue stored in a vial. Slides were permanently mounted in Elvacite 2044. In addition to standard palynological slides, twelve palynological samples with high amounts of Amorphous Organic Matter (AOM) were re-processed to remove it. The vialled residues were treated with an ultrasonic probe for 20 seconds to fragment the AOM that was removed by further sieving at 15 μ m. Scolecodonts were identified using a compound binocular microscope.

A dual ichnofacies and ichnofabric approach (McIlroy, 2008) were used to describe bioturbated horizons on a bed-by-bed basis (Appendix 1). Ichnofossils are classified to genus level only because of the limitations of identification from core material and at the field site. At Burnmouth, the vertical dip of the beds, widespread seaweed cover and poor exposure due to tidal range meant that bioturbation is harder to identify. Indeterminate burrows include those identified in thin section only, horizontal burrows in core

(similar to *Planolites*), and those seen in the field that could not be identified. Due to these issues, only 53 % of bioturbated horizons in the Norham Core and 21 % of horizons at Burnmouth have been identified to ichnogenus level. Burrows were distinguished from roots by the lack of an internal carbon film, drab or coloured haloes and mottles or nodules (Kearsey et al., 2016).

4. Results

Within the Norham Core *Chondrites*, phycosiphoniform burrows, *Monocraterion*, *Asterosoma*?, *Zoophycos*?, *Rhizocorallium* and *Diplocraterion* occur in decreasing order of abundance (Table 1). Bioturbation is common throughout the Norham Core (288 horizons), with a lower but still significant number of similar ichnotaxa reported from Burnmouth (162 horizons). Within the Norham Core bioturbated horizons in which the burrows have been identified represent a cumulative thickness of 14.5 m (Appendix 1), just 3 % of the total 490-m-thick borehole.

Ichnotaxon diversity is low in both sections; single-colonisation and simple-tier ichnofabrics (Taylor et al., 2003) are prevalent. In the Norham Core only one ichnotaxon is present in 82 % of all identified horizons. Because of this, ichnofacies are not assigned and ichnotaxa are individually described below.

Table 1. Key features of Norham Core ichnotaxa.

Ichnotaxon	Horizons (n)	Thickness (cm)	Diameter (mm)	II	Associated Ichnotaxa
<i>Chondrites</i>	128	9.7	1-2	5	phycosiphoniform
Phycosiphoniform burrows	26	14	2	4	<i>Chondrites</i>
<i>Monocraterion</i>	15	22	5-10	2	<i>Asterosoma</i> ?
<i>Asterosoma</i> ?	10	7	10	4	<i>Monocraterion</i>
<i>Zoophycos</i> ?	3	2	0.5	3	<i>Chondrites</i> , phycosiphoniform
<i>Rhizocorallium</i>	2	11	10	3	<i>Chondrites</i>
<i>Diplocraterion</i>	1	20	10	3	<i>Chondrites</i>

Abbreviations: Horizons = the number of stratigraphic horizons in the Norham Core where this ichnotaxon has been identified; thickness = the mean thickness of the bioturbated horizon; diameter = the mean cross-sectional dimensions of an individual burrow; II = the mean ichnofabric index for each ichnotaxon, using the scheme of Droser and Bottjer (1989).

4.1. *Chondrites*

Chondrites is the most common ichnotaxon in the Norham Core (n = 128) and Burnmouth (n = 17). The traces are sub-vertical, branching and in most cases are infilled with coarser sediment than that surrounding the burrows (Figs. 2A, 5B), although examples with finer grained fills also occur. Burrows branch outwards in a dendritic pattern downwards towards the base of the burrowed horizons. The diameter of *Chondrites* in cross-section view ranges from small (0.5-1 mm diameter), to medium (1-2 mm diameter) to large (2-3 mm diameter) (Fig. 2A-C). This range in burrow diameter (0.5-3 mm) is commonly seen in burrows assigned to *Chondrites* (Izumi, 2015).

The thickness of *Chondrites* horizons ranges from 1 to 37 cm, with a mean of 10 cm and positively skewed distribution towards thin beds. Single-colonisation *Chondrites* horizons are the most common (107 of 128 horizons in the Norham Core). The mean ichnofabric index (II) of *Chondrites* is 5, the highest of all ichnotaxa (Table 1). The upper two-thirds of a *Chondrites* horizon is always extensively burrowed (BI of 5 or 6), reducing to BI 2 at the base (Fig. 3A-B).

Figure 2. Small- to large-sized *Chondrites* in core and thin section. (A) Small-size *Chondrites* traces within siltstones, mudstones and very fine sandstones, with *Modiolus* bivalves, Norham Core, 465.94 m. Black box within core photograph (A) corresponds to thin section scan and adjacent line drawing that illustrates burrow traces. (B) Medium-size *Chondrites* within siltstone and very fine sandstone, with *Naiadites* bivalves and plant fragments, Norham Core, 473.64 m. (C) Large-size *Chondrites* within siltstone and very fine sandstone underlying a dolostone, with plant fragments, Norham Core, 378.6 m.

Figure 3. Typical ichnofabric profiles of *Chondrites*, *Monocraterion*, *Asterosoma?* and phycosiphoniform burrows within the Norham Core. (A) *Chondrites* (C) phycosiphoniform burrows

(P) within a very fine grained sandstone, burrowing into grey siltstone, overlain by interbedded dolostone and siltstone, top of the bioturbated interval is at 148.75 m. (B) *Chondrites* within very fine sandstone and siltstone, pedogenically modified and rooted, top of bioturbated interval at 87.65 m. (C) *Monocraterion* (M) and *Asterosoma*? (A) within a trough-cross laminated fine to very fine sandstone, top of bioturbated interval at 397.78 m. Ichnofabric index (II) scheme is based on Droser and Bottjer (1989).

4.2. Phycosiphoniform burrows

The term phycosiphoniform is used to refer to *Phycosiphon*-like trace fossils, after 3D modelling of *Phycosiphon* in core by Bednarz and McIlroy (2009) demonstrated that the same patterns of traces can be produced by other ichnotaxa. In the Ballagan Formation phycosiphoniform burrows always co-occur with *Chondrites*, recorded in the Norham Core (n = 26) and at Burnmouth (n = 5). Phycosiphoniform burrows are on average 2 mm in diameter, sinuous, filled with a fine-grained siltstone, and in core are oblique to sub-horizontal in orientation. The dark-coloured burrow core (Figs. 3A, 8B) was easier to identify than the burrow halo (cf. Bednarz and McIlroy, 2009). After *Chondrites* they have the next highest BI of 4. The tiering of phycosiphoniform burrows in relation to co-occurring *Chondrites* is variable; in some horizons phycosiphoniform traces extend below *Chondrites* (Fig. 3A) but in others the opposite is present. Neither phycosiphoniform nor *Chondrites* traces infill other pre-existing burrows, as has been documented in marine *Phymatoderma* traces (Izumi, 2015).

4.3. *Monocraterion* and *Asterosoma*?

Monocraterion is documented from 14 horizons in the Norham Core and 3 at Burnmouth. Traces are sub-vertical, 5-10 mm in diameter, extend from 1 to 10 cm in depth and are commonly infilled with spreite, with a funnel shape at the top of the burrow with a laminated sediment fill (Fig. 3C). *Monocraterion* has the lowest ichnofabric index (average II 2) of any ichnotaxon in the formation (Table 1), leaving well-preserved

sedimentary structures such as cross-lamination (Fig. 3C). *Monocraterion* co-occurs with *Asterosoma*? in three horizons in the Norham Core and two at Burnmouth, occupying the upper tier relative to *Asterosoma*. Recent work examining the morphological range of vertical burrows with funnel-shaped apertures have assigned many species of *Monocraterion* to the genus *Laevicyclus* (Buatois et al., 2016; Knaust, 2015). Also, the funnel shaped opening is superficially similar to that of *Rosselia* (Campbell et al., 2016). The rarity of specimens in the Ballagan Formation precludes a re-assignment to another ichnogenus or a confident interpretation of the trace maker (bivalves or polychaetes).

Asterosoma? is recorded from 11 horizons in the Norham Core and 3 at Burnmouth. The characteristic radial arrangement of horizontal burrows is not observed and bedding-plane views of identified specimens are absent. Instead, *Asterosoma* is identified in cross-section by a densely spaced fabric of oblique to sub-vertical 1-cm-diameter traces, infilled with fine-grained sediment with spreiten, some of which have a concentric pattern. The burrows have a complex shape, 5-10 cm in height that has an average BI of 4. Clearly circular burrow shapes are not seen in cross-section and the assignment to *Asterosoma* remains tentative.

4.4. Rare Ichnotaxa

Zoophycos? is identified in the Norham Core (n = 3) and Burnmouth (n = 2), always associated with *Chondrites* and phycosiphoniform burrows (Table 1). Burrows are sub-horizontal to curved, sinuous and have a fine-grained infill of dark siltstone with spreiten. In most cases several sub-horizontal traces occur within a rock thickness of 2-3 cm. This ichnotaxon has not been seen on bedding surfaces and the assignment to *Zoophycos* remains tentative.

Diplocraterion, identified in the Norham Core (n = 1) and at Burnmouth (n = 3). Burrows are approximately 10 mm in diameter, U-shaped and contain spreiten (Fig. 5C). On bedding-plane surfaces at Burnmouth small sand-rich circles at either end of the U-shaped burrow are present, representing a sand-rich

burrow infill. In the core the assignment is tentative; sub-vertical burrows with spreiten are present, but the U-shape is not preserved.

Rhizocorallium is tentatively identified from two horizons in the Norham Core, associated with *Chondrites*. Burrows are approximately 10 mm in diameter, sub-horizontal and contain spreiten.

Bivalve burrows are identified within one sandy siltstone bed at Burnmouth and are sub-vertical, approximately 10 mm in diameter and 2-3 cm in length. They are likely to have been produced by the semi-infaunal bivalve *Modiolus* that is common in the Ballagan Formation (Bennett et al., 2016).

4.5. Scolecodonts

Fifty-eight scolecodont specimens are reported from 17 samples in the Norham Core and one sample from Burnmouth (Appendix 2). Scolecodont specimens were not taxonomically identified but display a varied morphology (Fig. 4). The number of specimens per sample is generally low, although in one sample 23 specimens were identified (Appendix 2). In general, the scolecodont-bearing palynological samples also have a high Amorphous Organic Matter (AOM) content. Scolecodonts are associated with *Chondrites* in four out of eighteen horizons, with indeterminate bioturbation in another four horizons, and occur in a range of lithologies (Appendix 2).

Figure 4. Scolecodonts. Photomicrographs of scolecodonts recorded from the Norham Core. (A) 93.38 m; (B, H-I) 148.71 m; (C-E) 231.57 m; (F) 368.83 m; (G) 253.41 m; (J-K) 367.64 m; (L) 501.18 m. Scale bars 20 μ m length.

5. Bioturbation in a sedimentary context

An example of the relationship between the fluvial facies association, the saline-hypersaline facies association and bioturbation is illustrated in Figure 5A, where inclined layers within a fluvial channel body are truncated by an overlying a set of planar siltstone and dolostone beds. *Chondrites* burrows originate from the dolostone and extend into the underlying siltstone and sandstone beds. This relationship has been identified at Burnmouth at one other location (108 m stratigraphic height), but is not identified in core where

the lateral context cannot be observed. Most of dolostone beds at Burnmouth do not have observable erosional surfaces at their base and appear to be conformable with underlying siltstone or sandstone units.

Figure 5. Bioturbation in relation to sedimentary facies at Burnmouth. (A) Photograph showing an example of a possible marine transgression event, at 120-123 m; note that the dip of the beds is nearly vertical. On the right is an illustration of the same section, beds are younger to the right (arrowed). Inclined layers within a channel body (fluvial facies association) are truncated against an overlying dolostone bed (saline-hypersaline lake facies association). The dolostone contains a coquina (concentrated shell deposit) of *Naiadites* and *Modiolus* bivalves, gastropods, ostracods, *Serpula* and fish fragments. *Chondrites* originates from the dolostone and extends into underlying plant-rich siltstones that form the top of the channel-fill. (B) *Chondrites* viewed in a cross-section through a

dolostone bed on the foreshore that was polished by wave action, at 275.5 m. (C) Bedding-plane view of *Diplocraterion* within a fine-grained cross-bedded sandstone, fallen block from approximately 373.8 m section height.

The lithological association of the *Chondrites* burrows is diverse, encompassing siltstone, sandstone and dolostone (Fig. 6A, B). In the Norham Core 70 % of *Chondrites* horizons either occur within a dolostone bed or in sedimentary rocks directly underlying a dolostone and 75 % are within the saline-hypersaline lake facies association (Fig. 6B; Appendix 1). *Chondrites* is not present in dolostone beds containing gypsum or anhydrite (Fig. 6A). The thickness of bioturbated horizons, *Chondrites* burrow diameter and ichnofabric index are independent of lithology. *Chondrites* occurrences are associated with *Paraparchites* ostracods, rhizodont and actinopterygian fish and the bivalves *Naiadites* and *Modiolus* (Fig. 7; Appendix 1). Rarer faunal associations are arthropod cuticle, orthocone fragments, *Spirorbis*, *Serpula*, gastropods, and *Schizodus* and *Phestia* bivalves.

Figure 6. Ichnofossil distribution in the Norham Core in a sedimentary context. (A) This section of the Norham Core (450-480 m) is the most densely bioturbated part of the cored succession. There is a close correspondence between bioturbation and the occurrence of dolostones. Facies Associations: S = Saline-Hypersaline Lake; O = Overbank; F = Fluvial. (B) Lithological associations of the four most common ichnotaxa (pie charts) and occurrence percentage in each facies association.

Monocraterion and *Asterosoma?* exclusively occur within fine- to very fine-grained sandstone and siltstone units that vary in thickness from tens of centimetres to several metres and are part of the fluvial or overbank facies association (Fig. 6B). *Monocraterion* typically occurs in the upper part of sandstone units, above the transition from cross-bedding into cross-lamination where there is very fine sand grainsize and high (up to 50 %) silt component. These units contain plant and actinopterygian fish fragments. In three horizons at Burnmouth and in the Norham Core, *Asterosoma?* occurs within fine-grained sandstones of the overbank facies association. The context of these thin sandstones is variable, for example they can occur between dolostones (Fig. 6A), above palaeosols or within thick units of laminated grey siltstone. Eight out of eleven occurrences of *Asterosoma?* in the Norham Core are within fluvial sandstones. The position of *Asterosoma?* within fluvial units is variable: burrows can be at the top of the unit, near the top, in the middle or at the base.

Bioturbated horizons are distributed throughout the Burnmouth and Norham Core sections (Fig. 7) although there are fewer burrows within thick sandstone units. In the Norham Core intervals with a high frequency of bioturbated horizons (greater than 10 per 10 metre interval) are located at 110 m, 180 m, 230 m, 270 m, 320 m, 330 m, 460 m, 470 m and 490 m (Fig. 7). There is an association between the frequency of bioturbation and the occurrence of dolostone beds and marine macrofauna; this is especially clear between 450-480 m at the base of the Norham Core (Figs. 6A, 7). The presence of scolecodonts in the Norham Core mostly, but not always, corresponds to a high frequency of bioturbation (Fig. 7). At Burnmouth a high frequency of bioturbated horizons is only recorded at 180 and 100 m (Fig. 7).

Figure 7. Stratigraphical occurrence of all ichnotaxa and ichnofabrics within the Norham Core and at Burnmouth. Yellow beds on the sedimentary log indicate the fluvial facies association. Bioturbation is common throughout the succession, apart from in thick fluvial facies association successions. A refers to a detailed log of this section of the Norham Core illustrated in Figure 6. Stacked bioturbation horizons (starred) refer to successions with more than two stacked bioturbated horizons, examples of which are shown in Figure 8. ‘Marine’ fauna are euryhaline to marginal marine groups and comprise: *Spirorbis*, *Serpula*, orthocones, robust bivalves (*Schizodus*, *Sanguinolites*), brachiopods, shrimps and gastropods (Bennett et al., 2016). Bivalves are the number of all bivalve-bearing horizons per 10 metres, with assemblages numerically dominated by *Naiadites* and *Modiolus* representing non-marine conditions (Bennett et al., 2016). Scolecodonts are reported in this study (see Appendix 2), with the number of scolecodonts present per palynological slide in the Norham Core recorded as horizontal bars. Abbreviations: Phycosiph. = phycosiphoniform burrows, *Monocrater.* = *Monocraterion.*; *Rhizocorall.* = *Rhizocorallium*; *Diplocrater.* = *Diplocraterion.*

Unidentified (indeterminate) burrows are still important when examining the sedimentological context of ichnofossils because they give a good indication of bioturbation frequency throughout the formation (Fig. 7). In the Norham Core there is a good correspondence between high frequency intervals of *Chondrites* and indeterminate burrows, whereas at Burnmouth this relationship is not as pronounced, largely because of the lower number of ichnotaxa identified.

Stacked successions with more than two horizons of bioturbation are identified at 11 levels in the Norham Core and occur within intervals of peak bioturbation frequency (Fig. 7). The thickest of these contains seven *Chondrites* horizons within a thickness of 1.2 metres (Fig. 8A). An example of a thinner stacked unit comprises two *Chondrites* and phycosiphoniform horizons (Fig. 8B). In all cases, burrows are either within dolostone beds or originate at their base. The bioturbated dolostone units are composed of

321 interbedded siltstone, sandstone and micritic dolomite, ranging in thickness from a few centimetres to tens
322 of centimetres (Fig. 8). These stacked sequences clearly demonstrate the important relationship between
323 dolostones and *Chondrites*.

Figure 8. Examples of two stacked bioturbation sequences. (A) Seven stacked bioturbated horizons in a dolostone sequence, with common *Chondrites* (C) and some phycosiphoniform burrows (P) associated with a fauna of *Serpula*, ostracods, bivalves and fish fragments, Norham Core, 237.4-238.7 m. Burrows are within or originate from the base of dolostone beds. (B) Two stacked bioturbated horizons originating from dolostone beds, with *Chondrites* and phycosiphoniform burrows associated with plant and fish fragments, ostracods and *Naiadites* bivalves, Norham Core, 184-184.45 m.

6. Discussion

The typical ichnofacies that would be expected in the Ballagan Formation palaeoenvironments of floodplains, river channels and coastal lakes are the *Scoyenia*, *Skolithos* and *Mermia* Ichnofacies respectively (Buatois and Mángano, 2004), all of which are absent. The lack of a freshwater lacustrine ichnofauna may be because of poor preservation, a shortage of fresh bedding-plane surfaces in the field succession, overprinting by *Chondrites*, or its true absence. The typical shallow marine ichnofacies of *Skolithos* and *Cruziana* are also absent, although *Chondrites* and *Rhizocorallium* are members of the latter (Seilacher, 1967). As such, it is difficult to classify the ichnofaunal assemblages into either a typical marine or continental ichnofacies. *Chondrites* and *Phycosiphon* are indicator species of normal marine salinities or periods of heightened salinity within brackish water environments (Buatois et al., 2005). *Chondrites* is recorded in association with Carboniferous marine faunas nearby in east Fife (Chisholm, 1968). In the Carboniferous *Zoophycos* is typically found in shallow marine to offshore deposits (Bhattacharya and Bhattacharya, 2007; Miller, 1991). *Rhizocorallium*, thought to be produced by marine polychaetes, commonly occur in the *Cruziana* Ichnofacies shallow-marine environment, although they are also present in marginal marine settings in the Carboniferous (Knaust, 2013). *Zoophycos* and *Rhizocorallium* have both been recorded in marine Carboniferous facies in Fife (Chisholm, 1968). On balance, the typical association of *Chondrites* with marine faunas in other Carboniferous successions and its abundance in the Ballagan

Formation suggest the observed ichnofaunal assemblages are marine in origin, but do not occur here in a normal marine environment.

Chondrites and *Phycosiphon* are produced as a result of deposit-feeding on the sediment (Simpson, 1956; Wetzel, 2010). *Chondrites* trace-makers have been variously attributed to annelids, sipunculoid worms, chemosymbiotic bivalves, nematodes, crustaceans and sea pens (see references within Głuszek, 1998). In the shallow marine environment, it has been observed that *Chondrites* traces are produced by polychaete worms (Hertweck et al., 2007). We rule out bivalves as the trace-maker and favour polychaete worms, because there is no association between *Chondrites* burrows and bivalve macrofossils in the Norham Core. The organisms responsible for *Chondrites* and phycosiphoniform burrows likely thrived through deposit feeding on fine-grained sediment rich in predominantly terrestrial organic matter that was common in this floodplain environment and is preserved directly underlying the dolostone beds (Figs. 5, 8). Abundant *Chondrites* has been attributed to the presence of organic matter rich marine sediments (Vossler and Pemberton, 1988).

The *Monocraterion* and *Asterosoma*-producing organisms occur in fluvial sandstone facies, so were likely adapted to survive in sandy substrates subjected to rapid rates of deposition. An impoverished *Skolithos* lacustrine ichnofacies (Buatois and Mángano, 2004) is superficially similar to the ichnofacies fabric of the *Monocraterion* and *Asterosoma*? ichnofossil association, however, these ichnotaxa usually occur within marine sandstones in the geological record; examples include tide-dominated deltas (McIlroy, 2004), shallow-marine sandstones (Angulo and Buatois, 2012; Gowland and Riding, 1991) and sandstones interpreted as storm-deposits in lagoons (Goldring et al., 1998). However, *Monocraterion* is present in association exclusively with non-marine body fossil faunas in east Fife (Chisholm, 1968). The occurrence of *Monocraterion* and *Asterosoma*? within fluvial sandstones, and more commonly within overbank sediments in the present study demonstrates that periodic marine influx onto the floodplain occurred. The mechanism of this marine influx is discussed below. The position of *Asterosoma*? within the fluvial sandstones of the Norham Core is random; it doesn't occur at a specific level within the successions, such as at the top. There

is no evidence to suggest that the Ballagan Formation sandstones are deltaic rather than fluvial: Bennett et al. (2016) described them as fining-upwards successions up to 36-m-thick, with a conglomerate lag at the base, overlain by cross-bedded sandstones, then fine, rippled silt-rich sandstone. The ripples are unidirectional and do not show evidence of any tidal indicators such as mud-drapes. Scott (1986) interpreted the sandstones as meandering systems because of the presence of lateral accretion surfaces. The overbank facies association sandstones that host *Monocraterion* and *Asterosoma*? are thin-bedded or lenticular units that are interpreted as deposited in overbank flood events (Bennett et al., 2016) or during crevasse splays (Stephenson et al., 2002).

Although traditionally a component of the marine *Skolithos* Ichnofacies, *Diplocraterion* has been recorded from Cretaceous non-marine floodplain lakes (Kim and Paik, 1997) and Silurian aeolian-fluvial sandstones (McNamara, 2014; Trewin and McNamara, 1994). In the Carboniferous of Fife it is present in sediments interpreted as representing a range of salinities (Chisholm, 1968). Scolecodonts are the jaws of marine Eunicida and Phyllodocida polychaetes (Parry et al., 2014).

The palaeoenvironment and mechanism for ichnofaunal development of the Ballagan Formation is summarised in Figure 9, illustrating how sediment deposition occurred in a coastal floodplain that experienced the periodic input of marine waters. The trace-maker responsible for *Chondrites* lived in lakes alongside faunas that are interpreted as freshwater to brackish (*Naiadites*, *Modiolus*, actinopterygian fish and ostracods) and marine to euryhaline (orthocones, *Spirorbis*, *Serpula*, gastropods, scolecodonts and *Schizodus* bivalves) (Bennett et al., 2016). Marine faunas and ichnotaxa occurring in these floodplain lakes originated from events supplying marine waters, whereas freshwater to brackish animals may have been native to pre-existing freshwater floodplain lakes and river systems. The largely monospecific occurrence of *Chondrites* and the shallow burrowing depths indicate that habitable lake conditions may have been so short-lived as to limit other burrowers. Evidence of hypersalinity, desiccation and pedogenesis (Kearsey et al., 2016; Scott, 1986) supports this interpretation. However, as *Chondrites* is not found in association with gypsum- and anhydrite-bearing dolostones, the trace-maker did not survive where lakes were strongly evaporitic.

Figure 9. Palaeoenvironment of ichnotaxa in the Norham Core. The environment is a coastal floodplain, briefly inundated by marine waters during periodic storm events. Ichnofossils occur in all three facies associations representing river channels, overbank deposits and saline-hypersaline lakes.

Low diversity ichnoassemblages are typical of low salinity or brackish waters in marginal marine or brackish environments (Miller, 1984; Mángano and Buatois, 2004). Monospecific *Chondrites* assemblages (Bromley and Ekdale, 1984; De Gibert and Ekdale, 1999; Etter, 1995) and *Phycosiphon* within turbidites (Carvalho et al., 2005) have also been interpreted as indicators of anoxia. In marine mudstone successions with alternations between anoxic, dysoxic and oxic environments, *Chondrites* is commonly the first colonizer of the substrate after an anoxic event, suggesting some tolerance of dysoxic conditions (e.g. in the Lias of England: Moghadam and Paul, 2000). However, there is no other evidence for anoxic conditions in the Ballagan Formation and *Chondrites* is also common in well-oxygenated environments (Hertweck et al., 2005, 2007). The presence of AOM within 12 samples indicates the degradation of organic material during anoxic conditions within the sediment occurred (Pacton et al., 2011), although the AOM could subsequently

have been transported from a marine environment onto the floodplain. Further work needs to be done to investigate how storm-surge events may have influenced sediment oxygen conditions within the coastal lakes. The mostly monospecific occurrence of *Chondrites* may also be related to a tolerance for unusual environmental conditions. *Chondrites* and *Phycosiphon* are typical of harder substrates, but have also been reported from soft, clay-rich substrates (Taylor et al., 2003) and *Chondrites* is one of the first colonisers of soft substrates (Ming, 2004). In modern dolomite-precipitating saline lakes ‘soupy’ soft substrates are typical (De Deckker and Last, 1988). It must also be considered that this low diversity could be a taphonomic artefact, representing deep tier *Chondrites* burrows which may have re-worked any evidence of shallow burrows from other ichnotaxa.

Fully marine sedimentary rocks such as the marine limestones of the Scottish Middle to Upper Mississippian (Browne et al., 1999) are absent in the Ballagan Formation. However, the input of marine waters into floodplain lakes provide a mechanism for the development of extensive dolostone beds that are a feature of the formation (Andrews et al., 1991; Andrews and Nabi, 1998; Scott, 1971). The primary mechanism of marine incursion is unlikely to have been significant marine transgressions that established a broad marine shelf across a previously subaerial coastal plain because diverse stenohaline macrofossils, microfossils or ichnofossils are absent (Scott, 1986). Even where fluvial deposits are truncated against an overlying dolostone bed, interpreted as erosion (ravinement) associated with establishing a lake, monospecific *Chondrites* is the only associated ichnotaxa (Fig. 5). The Ballagan Formation does not contain any sedimentological evidence of tidal incursions onto a floodplain (Bennett et al., 2016) such as inclined heterolithic stratification associated with *Skolithos* and *Cruziana* Ichnofacies (Rebata et al., 2006). Lagoonal indicators, such as stromatolites and thrombolites, which occur in Famennian dolostones in Belgium (Thorez et al., 2006) are absent.

Short-lived inundation of coastal floodplains by marine waters is more likely to relate to storm surges. Today, some of the largest hurricanes result in storm surges advancing 480 river kilometres upstream (e.g. Hurricane Issac: US Army Corps of Engineers, 2013; Liu et al., 2014). A modern example of inundation and

sediment transport is the inland storm surge deposit on the Louisiana coast resulting from Hurricane Rita. The 0.5 metre deposit comprises two layers: a lower fine sand and mud layer, a few centimetres thick with abundant foraminifera, that extends at least 500 metres inland and is overlain by a much less extensive (100-150 metres) 30-40 cm thick cross-bedded fine sand with rare foraminifera (Williams, 2009). The mud layer is analogous to Ballagan Formation dolostone beds, whereas the cross-bedded sand layer is more difficult to identify. Other examples include storm deposits along the western coastline of Florida (Goodbred and Hine, 1995), where 3 m high surge waters inundated the coastal plain and travelled greater than 6 km inland along the Waccasassa River. Deposits associated with this surge were, found up to 2 cm thick in the marsh interiors and several hundred metres from the river banks with thicker (12 cm) deposits on river levees (Goodbred and Hine, 1995). As marine waters also travelled up the river itself during these events, this could explain the occurrence of *Asterosoma*?, a marine ichnotaxon, within the fluvial sandstones of the Ballagan Formation. In the Phillipines, overwash sediments deposited in a typhoon in 2013 comprise 1-8 cm thick sand beds with foraminifera, extending up to 1.7 km inland (Pilarczyk et al., 2016). Storm-transported sediment deposited into coastal saline lakes is also sand-rich and contains foraminifera (e.g. Park et al., 2009).

Rare marine to marginal marine fossils (orthocones, scolecodonts, *Serpula*, bivalves, ostracods, *Spirorbis* and sarcopterygian fish) are associated with the *Chondrites* in the Ballagan Formation but foraminifera, so typical of modern storm deposits on coastal plains (Pilarczyk et al., 2014) have not been identified in the sections studied here. Rare (3) micro-foraminiferal linings were recorded from the Ballagan Formation at the Heads of Ayr section in Scotland (Stephenson et al. 2002). Tournaisian foraminifera are known from the Namur-Dinant Basin in Belgium although the environmental conditions (e.g. depth of seaway) were considered to have been less favourable for foraminifera than those later in the Visean (Poty et al., 2006). In the Ballagan Formation of central Scotland, marine influence from sea water flooding of coastal floodplains during storm events has also been evoked (Stephenson et al., 2004; Williams et al., 2005) but the associated sedimentary deposits were not identified.

The ichnofossil character of modern storm deposits is understudied and, interestingly, few of the studies referred to comment on any associated burrowers or bioturbation. Goodbred and Hine (1995) noted that the identification of older storm deposits preserved in the Waccasassa marshes is not possible because the sediments are homogeneous and are subject to bioturbation throughout the year. Despite this, stacked sequences of *Chondrites* in association with dolostone beds can be reasonably interpreted to represent repeated storm events. Storm surges would result in variable, fluctuating salinities and environments. It is not surprising that only a few burrowing organisms could survive under these adverse conditions, representing a low diversity infauna populated by the most opportunistic species.

In reviews of freshwater lacustrine ichnodiversity trends, Miller et al. (2002) and Miller and Labandeira (2002) noted that there was limited bioturbation in these environments before the Jurassic, as a benthic infauna of burrowing insects had not yet evolved. On the other hand, it could be argued that the low-diversity ichnoassemblage is a sample bias due to the analysis of core. While many ichnotaxa could not be identified, in particular horizontal traces, other studies indicate that core does not significantly restrict ichnofossil identification. For example, well-preserved and diverse ichnological assemblages are recorded from core in the marine and non-marine Carboniferous of Fife (Chisholm, 1968, 1970) and in the Late Devonian-Carboniferous Bakken Formation of Saskatchewan, Canada (Angulo and Buatois, 2012). An important result of the present study is that *Chondrites*-dominated bioturbation horizons are far more abundant than horizons with marine macrofossils or scolecodonts (Fig. 7). This could be because trace fossils are more easily preserved than macrofossils, because they produce high-volume sedimentary structures relative to their size, and thus have a higher preservation bias. Polychaete trace-makers are smaller, lighter and more readily transported by marine water incursions than macrofossils. The observation that there are 128 *Chondrites* horizons plus another nine un-bioturbated scolecodont horizons in the Norham Core suggests that there are many cryptic marine-influenced horizons. In addition, the high frequency of indeterminate bioturbation throughout the succession (with a frequency distribution matching that of *Chondrites*: Fig. 7) implies that perhaps yet greater numbers of marine-influenced horizons are present.

In the Ballagan Formation the trace-makers were aquatic and are interpreted as of marine origin but must have been adapted to living in an unusual saline lake environment. Although palaeosols (Kearsey et al., 2016) and tetrapods with terrestrial features (Smithson et al., 2012) have been recorded from the Ballagan Formation, tetrapod and arthropod trackways have not been reported to date. The lack of trackways can be attributed to a paucity of fresh bedding surfaces at Burnmouth and their seaweed cover, compared with the rapidly eroding coastal cliffs at other tetrapod sites such as Blue Beach which provide fresh bedding surfaces (Mansky and Lucas, 2013). In addition, the study of core material has allowed the identification of very small *Chondrites* traces that are hard to identify in field section. This is an unusual record of mostly monospecific *Chondrites* from a restricted marine-influenced non-marine setting. Future work to compare the Joggins Formation *Chondrites* and *Phycosiphon* assemblage (Dafoe et al., 2011) with that of the Ballagan Formation would be important to understand the palaeoenvironmental constraints on this unusual ichnoassemblage. Clack et al. (2016) discuss how the range of different environments present in the Ballagan Formation may have influenced the evolution of the many derived and primitive forms of tetrapods present. Whereas all tetrapods from the Ballagan Formation discovered to date are associated with floodplain palaeosols and temporary lakes (Clack et al., 2016), the ichnofaunal and scolecodont evidence presented herein indicates that the environment that was subject to marine incursions, predominantly through storm surges and through rarer marine transgressions. Future studies are needed to investigate how the diverse habitats and floodplain environments (Bennett et al., 2016; Kearsey et al., 2016) of the Lower Mississippian Ballagan Formation may have played a role in tetrapod recovery after the end-Devonian extinction event (Kaiser et al., 2016).

7. Conclusions

More than 100 horizons of monospecific *Chondrites* are recorded from the Mississippian Ballagan Formation of the Scottish Borders, from borehole and field samples. *Chondrites* rarely occurs in association with phycosiphoniform burrows, *Monocraterion*, *Asterosoma*?, *Zoophycos*? and *Rhizocorallium*. This is one of the most detailed records of *Chondrites* documented from an environment where lakes periodically

affected by marine incursions existed on a coastal plain. Lithology controls the ichnological assemblages: *Monocraterion* and *Asterosoma*? occur within cross-bedded sandstone or rippled siltstone of the fluvial or overbank facies association. *Chondrites* and associated ichnotaxa mostly occur in dolostones or in sedimentary rocks directly underlying them, and are sometimes associated with rare scolecodonts. The ichnofabric of the Ballagan Formation represents short-lived but rapid colonisation of the sediment by opportunistic organisms transported from shallow marine environments during storm events. Burrowing mostly took place in coastal lakes but also in river and floodplain overbank environments. The low diversity of ichnotaxa indicates that normal marine conditions were never sustained and the environment was too hostile for most marine burrowing organisms to successfully exploit. *Chondrites* may have been adapted to cope with the soft sediment and disturbance during transport.

Ichnofossils of a marine origin (*Chondrites*, phycosiphoniform burrows, *Zoophycos* and *Rhizocorallium*) are much more common than marine body fossils or scolecodonts in the Ballagan Formation. As such, ichnofossils are a good indicator of cryptic, short-lived marine incursions, especially in complex coastal to alluvial environments. The examination of borehole material as opposed to field sections aids the identification of these burrows in fine-grained lithologies, especially small *Chondrites* burrows, but biases against horizontal traces such as trackways. The ichnofaunal and scolecodont evidence presented in this study highlights that the coastal floodplain in which terrestrial tetrapods diversified after the end-Devonian mass extinction was subject to periodic storm surges and rare marine transgressions.

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References

- Andrews, J.E. and Nabi, G. 1998. Palaeoclimatic significance of calcretes in the Dinantian of the Cockburnspath Outlier (East Lothian-North Berwickshire). *Scottish Journal of Geology* 34, 153-164.
- Andrews, J.E., Turner, M.S., Nabi, G. and Spiro, B. 1991. The anatomy of an early Dinantian terraced floodplain: palaeo-environment and early diagenesis. *Sedimentology* 38, 271-287.
- Anderson, J.S., Smithson, T., Mansky, C.F., Meyer, T. and Clack, J. 2015. A Diverse Tetrapod Fauna at the Base of 'Romer's Gap'. *PLoS ONE* 10, 1-27, doi:10.1371/journal.pone.0125446.
- Angulo, S. and Buatois, L.A. 2012. Ichnology of a Late Devonian–Early Carboniferous low-energy seaway: The Bakken Formation of subsurface Saskatchewan, Canada: Assessing paleoenvironmental controls and biotic responses. *Palaeogeography, Palaeoclimatology, Palaeoecology* 315, 46-60.
- Bateman, R.M. and Scott, A.C. 1990. A reappraisal of the Dinantian floras at Oxroad Bay, East Lothian, Scotland. 2. Volcanicity, palaeoenvironments and palaeoecology. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 81, 161-194.
- Bednarz, M. and McIlroy, D. 2009. Three-dimensional reconstruction of “phycosiphoniform” burrows: implications for identification of trace fossils in core. *Palaeontologia Electronica* 12, 12.3.
- Belt, E.S., Freshney, E.C. and Read, W.A. 1967. Sedimentology of Carboniferous dolostone facies, British Isles and Eastern Canada. *The Journal of Geology* 75, 711-721.

- Bennett, C.E., Kearsley, T., Davies, S.J., Millward, D. Clack, J.A., Smithson, T.R. and Marshall, J.E.A. 2016. Early Mississippian sandy siltstones deposited in seasonal flooding episodes preserve rare non-marine fossils. *Sedimentology* 63, 1677-1700.
- Bhattacharya, B. and Bhattacharya, H.N. 2007. Implications of trace fossil assemblages from late Paleozoic glaciomarine Talchir Formation, Raniganj basin, India. *Gondwana Research* 12, 509-524.
- Bjerstedt, T.W. 1987. Latest Devonian-Earliest Mississippian Nearshore Trace-Fossil Assemblages from West Virginia, Pennsylvania, and Maryland. *Journal of Paleontology* 61, 865-889.
- Bromley, R.G. and Ekdale, A.A. 1984. *Chondrites*: a trace fossil indicator of anoxia in sediments. *Science* 224, 872-874.
- Browne, M.A.E., Dean, M.T., Hall, I.H.S., McAdam, A.D., Monro, S.K. and Chisholm, J.I. 1999. A lithostratigraphical framework for the Carboniferous rocks of the Midland Valley of Scotland: British Geological Survey Research Report RR/99/07.
- Buatois, L.A. and Angriman, A.O.L. 1992. The ichnology of a submarine braided channel complex: the Whisky Bay Formation, Cretaceous of James Ross Island, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 94, 119-140.
- Buatois, L.A. and Mángano, M.G. 2002. Trace fossils from Carboniferous floodplain deposits in western Argentina: implications for ichnofacies models of continental environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 183, 71-86.
- Buatois, L.A. and Mángano, M.G. 2004. Animal-substrate interactions in freshwater environments: applications of ichnology in facies and sequence stratigraphic analysis of fluvio-lacustrine successions. *Geological Society, London, Special Publications* 228, 311-333.

- Buatois, L.A., Angulo, S. and Mángano, M.G. 2013. Onshore expansion of benthic communities after the Late Devonian mass extinction. *Lethaia* 46, 251-261.
- Buatois, L. A., Gingras, M. K., Maceachern, J., Mángano, M. G., Zonneveld, J. P., Pemberton, S. G., Netto, R. G. and Martin, A. 2005. Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaaios* 20, 321-347.
- Buatois, L.A., Wisshak, M., Wilson, M.A. and Mángano, M.G. 2016. Categories of architectural designs in trace fossils: A measure of ichnodisparity. *Earth-Science Reviews*.
<http://dx.doi.org/10.1016/j.earscirev.2016.08.009>.
- Campbell, S.G., Botterill, S.E., Gingras, M.K. and MacEachern, J.A. 2016. Event sedimentation, deposition rate, and paleoenvironment using crowded *Rosselia* assemblages of the Bluesky Formation, Alberta, Canada. *Journal of Sedimentary Research* 86, 380-393.
- Carpenter, D.K., Falcon-Lang, H.J., Benton, M.J, and Henderson, E. 2014. Carboniferous (Tournaisian) fish assemblages from the Isle of Bute, Scotland: systematics and palaeoecology. *Palaeontology* 57, 1215-1240.
- Carvalho, I.D.S., Fernandes, A.C.S., Andreis, R.R., Paciullo, F.V.P., Ribeiro, A. and Trouw, R.A.J. 2005. The Ichnofossils of the Triassic Hope Bay Formation, Trinity Peninsula Group, Antarctic Peninsula. *Ichnos* 12, 191-200.
- Cater, J.M.L., Briggs, D.E.G. and Clarkson, E.N.K., 1989. Shrimp-bearing sedimentary successions in the Lower Carboniferous (Dinantian) Dolostone and Oil Shale groups of northern Britain. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 80, 5-15.
- Chisholm, J.I. 1968. Trace fossils from the Geological Survey boreholes in east Fife, 1963-4. *Bulletin of the Geological Survey of Great Britain* 28, 103-119.

- Chisholm, J.I. 1970. Lower Carboniferous trace fossils from the Geological Survey boreholes in west Fife (1965-6). *Bulletin of the Geological Survey of Great Britain* 31, 19-35.
- Clack, J.A. 2002. An early tetrapod from 'Romer's Gap'. *Nature* 418, 72-76.
- Clack, J.A., Bennett, C.E., Carpenter, D.K., Davies, S.J., Fraser, N.N., Kearsey, T.I., Marshall, J.E.A., Millward, D., Otoo, B.K.A., Reeves, E.J., Ross, A.J., Ruta, M., Smithson, K.Z., Smithson, T.R. and Walsh, S.A. 2016. Phylogenetic and Environmental Context of a Tournaisian Tetrapod Fauna. *Nature Ecology and Evolution* doi:10.1038/s41559-016-0002.
- Dafoe, L.T., Stimson, M. and Gibling, M.R., 2011. One more piece to the puzzle: new developments in the trace fossil record from the Pennsylvanian Joggins Formation. *Atlantic Geology* 47, p17. Abstract of the 37th Annual Colloquium and Annual General Meeting of the Atlantic Geoscience Society.
- De Deckker, P. and Last, W.M. 1988. Modern dolomite deposition in continental, saline lakes, western Victoria, Australia. *Geology* 16, 29-32.
- De Gibert, J.M. and Ekdale, A.A. 1999. Trace fossil assemblages reflecting stressed environments in the Middle Jurassic Carmel Seaway of central Utah. *Journal of Paleontology* 73, 711-720.
- Droser, M. L., and Bottjer, D. J. 1989. Ichnofabric of sandstones deposited in high-energy nearshore environments: measurement and utilization. *Palaios* 598-604.
- Etter, W. 1995. Benthic diversity patterns in oxygenation gradients: an example from the Middle Jurassic of Switzerland. *Lethaia* 28, 259-270.
- Falcon-Lang, H.J. 1999. The early Carboniferous (Courceyan-Arundian) monsoonal climate of the British Isles: evidence from growth rings in fossil woods. *Geological Magazine* 136, 177-187.

- 622 Fillmore, D.L., Lucas, S.G. and Simpson, E.L., 2010. Invertebrate trace fossils in semi-arid to arid braided-
623 ephemeral-river deposits of the Mississippian middle member of the Mauch Chunk Formation, eastern
624 Pennsylvania, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292, 222-244.
- 625 Ghummed, M.A. 1982. Petrology and geochemistry of the carbonates, Ballagan Formation, N.W. Midland
626 Valley, Scotland. Ph.D. thesis, University of Glasgow.
- 627 Głuszek, A. 1998. Trace fossils from Late Carboniferous storm deposits, Upper Silesia Coal Basin, Poland.
628 *Acta Palaeontologica Polonica* 43, 517-546.
- 629 Goldring, R., Astin, T.R., Marshall, J.E.A., Gabbott, S. and Jenkins, C.D. 1998. Towards an integrated study
630 of the depositional environment of the Bencliff Grit (Upper Jurassic) of Dorset. In: Underhill, J. R.
631 (ed.) Development, Evolution and Petroleum Geology of the Wessex Basin. *Geological Society*,
632 London, *Special Publications* 133, 355-372.
- 633 Goodbred, S.L. and Hine, A.C. 1995. Coastal storm deposition: Salt-marsh response to a severe extratropical
634 storm, March 1993, west-central Florida. *Geology* 23, 679-682.
- 635 Gowland, S. and Riding, J.B. 1991. Stratigraphy, sedimentology and palaeontology of the Scarborough
636 Formation (Middle Jurassic) at Hundale Point, North Yorkshire. *Proceedings of the Yorkshire*
637 *Geological Society* 48, 375-392.
- 638 Gray, J. 1988. Evolution of the freshwater ecosystem: the fossil record. *Palaeogeography*,
639 *Palaeoclimatology, Palaeoecology* 62, 1-214.
- 640 Greig, D.C. 1988. Geology of the Eyemouth district. Memoir of the British Geological Survey, Sheet 34.
- 641 Hertweck, G., Wehrmann, A. and Liebezeit, G. 2007. Bioturbation structures of polychaetes in modern
642 shallow marine environments and their analogues to *Chondrites* group traces. *Palaeogeography*,
643 *Palaeoclimatology, Palaeoecology* 245, 382-389.

- Hertweck, G., Wehrmann, A., Liebezeit, G. and Steffens, M. 2005. Ichnofabric zonation in modern tidal flats: palaeoenvironmental and palaeotrophic implications. *Senckenbergiana Maritima* 35, 189-201.
- Izumi, K. 2015. Composite *Phymatoderma* from Neogene deep-marine deposits in Japan: Implications for Phanerozoic benthic interactions between burrows and the trace-makers of *Chondrites* and *Phycosiphon*. *Acta Palaeontologica Polonica* 60, 1009-1020.
- Kaiser, S.I., Aretz, M. and Becker, R.T. 2016. The global Hangenberg Crisis (Devonian–Carboniferous transition): review of a first-order mass extinction, in Becker, R.T., Königshof, P. and Brett, C.E., eds., Devonian Climate, Sea Level and Evolutionary Events: Geological Society, London, Special Publications 423, 387-437.
- Kearsey, T., Bennett, C.E., Millward, D., Davies, S.J., Gowing, C.J.B., Kemp, S., Leng, M.J., Marshall, J.E.A. and Browne, M.A.E. 2016. The terrestrial landscapes of tetrapod evolution in earliest Carboniferous seasonal wetlands of the Ballagan Formation in S.E. Scotland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 457, 52-69.
- Kim, J.Y. and Paik, I.S., 1997. Nonmarine *Diplocraterion luniforme* (Blanckenhorn 1916) from the Hasandong Formation (Cretaceous) of the Jinju area, Korea. *Ichnos* 5, 131-138.
- Knaust, D. 2013. The ichnogenus *Rhizocorallium*: classification, trace makers, palaeoenvironments and evolution. *Earth-Science Reviews* 126, 1-47.
- Knaust, D. 2015. Siphonichnidae (new ichnofamily) attributed to the burrowing activity of bivalves: Ichnotaxonomy, behaviour and palaeoenvironmental implications. *Earth-Science Reviews* 150, 497-519.
- Liu, K.B., McCloskey, T.A., Bianchette, T.A., Keller, G., Lam, N.S., Cable, J.E. and Arriola, J., 2014. Hurricane Isaac storm surge deposition in a coastal wetland along Lake Pontchartrain, southern Louisiana. *Journal of Coastal Research* 70, 266-271.

- Mángano, M.G. and Buatois, L.A. 2004. Ichnology of Carboniferous tide-influenced environments and tidal flat variability in the North American Midcontinent. *Geological Society, London, Special Publications* 228, 157-178.
- Mansky, C.F. and Lucas, S.G. 2013. Romer's Gap revisited: continental assemblages and ichno-assemblages from the basal Carboniferous of Blue Beach, Nova Scotia, Canada. In: Lucas, S.G., DiMichele, W.A., Barrick, J.E., Schneider, J.W., Speilmann, J.A., editors. *The Carboniferous-Permian Transition*. Albuquerque: New Mexico Museum of Natural History and Science, Bulletin 60, 244–273.
- McIlroy, D. 2004. Ichnofabrics and sedimentary facies of a tide-dominated delta: Jurassic Ile Formation of Kristin Field, Haltenbanken, offshore Mid-Norway. In: McIlroy, D. (ed.) *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*. *Geological Society, London, Special Publications* 228, 237-272.
- McIlroy, D. 2008. Ichnological analysis: The common ground between ichnofacies workers and ichnofabric analysts. *Palaeogeography, Palaeoclimatology, Palaeoecology* 270, 332-338.
- McNamara, K.J. 2014. Early Paleozoic colonisation of the land—evidence from the Tumblagooda Sandstone, Southern Carnarvon Basin, Western Australia. *Journal of the Royal Society of Western Australia* 97, 111-132.
- Miller, M.F. 1984. Distribution of Biogenic Structures in Paleozoic Nonmarine and Marine-Margin Sequences: An Actualistic Model. *Journal of Paleontology* 58, 550-570.
- Miller, M.F. 1991. Morphology and paleoenvironmental distribution of Paleozoic *Spirophyton* and *Zoophycos*: implications for the *Zoophycos* ichnofacies. *Palaios* 6, 410-425.
- Miller, M.F. and Labandeira, C.C. 2002. Slow crawl across the salinity divide: delayed colonization of freshwater ecosystems by invertebrates. *GSA today* 12, 4-10.

- 689 Miller, M.F., McDowell, T., Smail, S.E., Shyr, Y. and Kemp, N.R. 2002. Hardly used habitats: dearth and
690 distribution of burrowing in Paleozoic and Mesozoic stream and lake deposits. *Geology* 30, 527-530.
- 691 Ming, G.Y. 2004. Facies characteristics and tiering distributions of *Chondrites*. *Acta Palaeontologica Sinica*
692 1, 1-8.
- 693 Moghadam, H.V. and Paul, C.R.C. 2000. Trace fossils of the Jurassic, Blue Lias, Lyme Regis, Southern
694 England. *Ichnos* 7, 283-306.
- 695 Niedźwiedzki, G., Narkiewicz, M. and Szrek, P. 2014. Middle Devonian invertebrate trace fossils from the
696 marginal marine carbonates of the Zachemie tetrapod tracksite, Holy Cross Mountains, Poland.
697 *Bulletin of Geosciences* 89, 593-606.
- 698 Pacton, M., Gorin, G.E. and Vasconcelos, C. 2011. Amorphous organic matter - Experimental data on
699 formation and the role of microbes. *Review of Palaeobotany and Palynology* 166, 253-267.
- 700 Park, L.E., Siewers, F.D., Metzger, T. and Sipahioglu, S. 2009. After the hurricane hits: recovery and
701 response to large storm events in a saline lake, San Salvador Island, Bahamas. *Quaternary*
702 *International* 195, 98-105.
- 703 Parry, L., Tanner, A. and Vinther, J. 2014. The origin of annelids. *Palaeontology* 57, 1091-1103.
- 704 Pilarczyk, J.E., Dura, T., Horton, B.P., Engelhart, S.E., Kemp, A.C. and Sawai, Y. 2014. Microfossils from
705 coastal environments as indicators of paleo-earthquakes, tsunamis and storms. *Palaeogeography,*
706 *Palaeoclimatology, Palaeoecology* 413, 144-157.
- 707 Pilarczyk, J.E., Horton, B.P., Soria, J.L.A., Switzer, A.D., Siringan, F., Fritz, H.M., Khan, N.S., Ildefonso,
708 S., Doctor, A.A. and Garcia, M.L. 2016. Micropaleontology of the 2013 Typhoon Haiyan overwash
709 sediments from the Leyte Gulf, Philippines. *Sedimentary Geology* 339, 104-114.
- 710 Pollard, J.E. 1988. Trace fossils in coal-bearing sequences. *Journal of the Geological Society* 145, 339-350.

- Poty, E., Devuyst, F.X. and Hance, L. 2006. Upper Devonian and Mississippian foraminiferal and rugose coral zonations of Belgium and northern France: a tool for Eurasian correlations. *Geological Magazine* 143, 829-857.
- Rebata, L.A., Räsänen, M.E., Gingras, M.K., Vieira, V., Barberi, M. and Irion, G. 2006. Sedimentology and ichnology of tide-influenced Late Miocene successions in western Amazonia: The gradational transition between the Pebas and Nauta formations. *Journal of South American Earth Sciences* 21, 96-119.
- Scotese, C.R. and McKerrow, W.S. 1990. Revised world maps and introduction. *Geological Society of London, Memoir* 12, 1-21.
- Scott, W.B. 1971. The sedimentology of the dolostone group in the Tweed basin: Burnmouth and the Merse of Berwick. Ph.D. thesis, Sunderland Polytechnic.
- Scott, W.B. 1986. Nodular carbonates in the Lower Carboniferous, Dolostone Group of the Tweed Embayment, Berwickshire: evidence for a former sulphate evaporite facies. *Scottish Journal of Geology* 22, 325-345.
- Seilacher, A. 1967. Bathymetry of trace fossils. *Marine Geology* 5, 413-428.
- Simpson, S. 1956. On the trace-fossil Chondrites. *Quarterly Journal of the Geological Society* 112, 475-499.
- Smithson, T.R., Richards, K.R. and Clack, J.A. 2016. Lungfish diversity in Romer's Gap: reaction to the end-Devonian extinction. *Palaeontology* 59, 29-44.
- Smithson, T.R., Wood, S.P., Marshall, J.E.A. and Clack, J.A. 2012. Earliest Carboniferous tetrapod and arthropod faunas from Scotland populate Romer's Gap. *PNAS* 109, 4532-4537.

- Stephenson, M.H., Williams, M., Monaghan, A.A., Arkley, S. and Smith, R.A. 2002. Biostratigraphy and palaeoenvironments of the Ballagan Formation (Lower Carboniferous) in Ayrshire. *Scottish Journal of Geology* 38, 93-111.
- Stephenson, M.H., Williams, M., Leng, M.J. and Monaghan, A.A. 2004. Aquatic plant microfossils of probable non-vascular origin from the Ballagan Formation (Lower Carboniferous), Midland Valley, Scotland. *Proceedings of the Yorkshire Geological Society* 55, 145-158.
- Taylor, A., Goldring, R. and Gowland, S. 2003. Analysis and application of ichnofabrics. *Earth-Science Reviews* 60, 227-259.
- Thorez, J., Dreesen, R. and Streel, M. 2006. Fammenian. *Geologica Belgica* 9, 27-45.
- Trewin, N.H. and McNamara, K.J. 1994. Arthropods invade the land: trace fossils and palaeoenvironments of the Tumblagooda Sandstone (? late Silurian) of Kalbarri, Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 85, 177-210.
- US Army Corps of Engineers. 2013. Hurricane Isaac with and without 2012 100-year HSDRRS evaluation, Final Report. 230 pp.
- Vossler, S.M. and Pemberton, S.G. 1988. Superabundant *Chondrites*: a response to storm buried organic material? *Lethaia* 21, 94-94.
- Waters, C.N. 2011. A revised correlation of Carboniferous rocks in the British Isles. *Geological Society, London, Special Report* 26, pp190.
- Wescott, W.A. and Utgaard, J.E. 1987. An Upper Mississippian Trace-Fossil Assemblage from the Tar Springs Sandstone, Southern Illinois. *Journal of Paleontology* 61, 231-241.
- Wetzel, A., 2010. Deep-sea ichnology: observations in modern sediments to interpret fossil counterparts. *Acta Geologica Polonica* 60, 125-138.

- 753 Williams, H.F.L. 2009. Stratigraphy, Sedimentology, and Microfossil Content of Hurricane Rita Storm
754 Surge Deposits in Southwest Louisiana. *Journal of Coastal Research* 25, 1041 – 1051.
- 755 Williams, M., Stephenson, M.H., Wilkinson, I.P., Leng, M.L. and Miller, C.G. 2005. Early Carboniferous
756 (Late Tournaisian-Early Viséan) ostracods from the Ballagan Formation, central Scotland, UK.
757 *Journal of Micropalaeontology* 24, 77-94.
- 758 Williams, M., Leng, M. L., Stephenson, M. H., Andrews, J. E., Wilkinson, I. P., Siveter, D. J., Horne, D. J.
759 and Vannier, J. M. C. 2006. Evidence that Early Carboniferous ostracods colonised coastal flood plain
760 brackish water environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 230, 299-318.