Proceedings of the Geologists' Association 128 (2017) 815–828

Contents lists available at ScienceDirect

Proceedings of the Geologists' Association

journal homepage: www.elsevier.com/locate/pgeola

Archetypally Siluro-Devonian ichnofauna in the Cowie Formation, Scotland: implications for the myriapod fossil record and Highland Boundary Fault Movement

Anthony P. Shillito*, Neil S. Davies

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, United Kingdom

ARTICLE INFO

Article history:
Received 2 March 2017
Received in revised form 4 August 2017
Accepted 7 August 2017
Available online 6 September 2017

Keywords:
Silurian
Devonian
Non-marine
Fluvial
Taenidium
Arenicolites

ABSTRACT

The Cowie Formation of the Stonehaven Group is the lithostratigraphically oldest unit of the Old Red Sandstone in Scotland. A reliable determination of the formation's age has implications for the arthropod fossil record (as it contains the world's oldest known fossils of air-breathing myriapoda), the unit's burial history, and constraints on the timing of the movement of the regionally significant Highland Boundary Fault. Previous studies, utilising different dating techniques, have provided conflicting ages for the unit: middle Silurian (late Wenlock), based on palynomorph biostratigraphy; or Early Devonian (Lochkovian–Pragian), from U-Pb dating of tuffs. Here we report a previously undescribed non-marine trace fossil assemblage that has implications for the age of the Cowie Formation when it is compared with other Siluro-Devonian formations worldwide. The trace fossil assemblage is a low diversity ichnofauna of *Arenicolites* isp., *Taenidium barretti* and rare comma-shaped impressions, in addition to sporadic bioturbated layers and sedimentary surface textures of a possible microbial origin. The low ichnodiversity reflects continental (alluvial) deposition during the earlier stages of the global terrestrialization of arthropods. However, the Cowie Formation ichnofauna is more diverse than that from other continental deposits of middle Silurian age, and shares greater similarity with worldwide Pridoli to Devonian-aged ichnofaunas. Here we consider the ichnofauna against two competing hypotheses: (1) that the Cowie Formation records the oldest known non-marine ichnofauna of vertical and back-filled meniscate burrows globally; or (2) that the Cowie Formation is 5–20 Ma younger than is presently documented. Comparing the ichnofauna with contemporaneous deposits worldwide, and considering other unresolved geological issues with the presently-documented age, circumstantial evidence strongly favours the latter hypothesis. Here we suggest that the palynologically-dated strata of the Cowie Formation (inland exposures) represent an older, unrelated, and presently un-named formation, and that the more extensively-exposed fossil-bearing strata were deposited within a narrow stratigraphic window during the early Lochkovian.

1. Introduction

The Cowie Formation of the Stonehaven Group consists of c. 730 m of siliciclastic sedimentary strata and minor volcanic horizons that crop out in coastal and inland exposures around Stonehaven, Aberdeenshire, in the Northern Midland Valley (Fig. 1). It is a key unit for understanding of the terrestrialization of life, by virtue of part of the unit (the Cowie Harbour Siltstone Member) hosting the oldest known body fossils with direct evidence for air-breathing (the spiracle-bearing myriapod *Pneumodesmus newmani*) (Wilson and Anderson, 2004), in addition to a range of other arthropod and fish fossils such as the enigmatic *Dictyocaris* and several agnathan taxa (Campbell, 1911, 1912, 1913).

As the basal unit of the Old Red Sandstone in the Midland Valley, the age of Cowie Formation is also crucial to the understanding of the movement history of the Highland Boundary Fault. Various authors have taken the age of rocks bounding the Highland Boundary Fault to place constraints on intervals of displacement (Bluck, 2002; Tanner, 2008; Hartley and Leleu, 2015).

The palaeobiological and tectonic implications of the formation are presently understood on the basis that the unit is late Wenlock in age (Lavender and Wellman, 2002), but recent U-Pb dating of ash bands within the formation suggests that it may in fact be

---

* Corresponding author.
E-mail address: as2195@cam.ac.uk (A.P. Shillito).

http://dx.doi.org/10.1016/j.pgeola.2017.08.002
0016-7878/

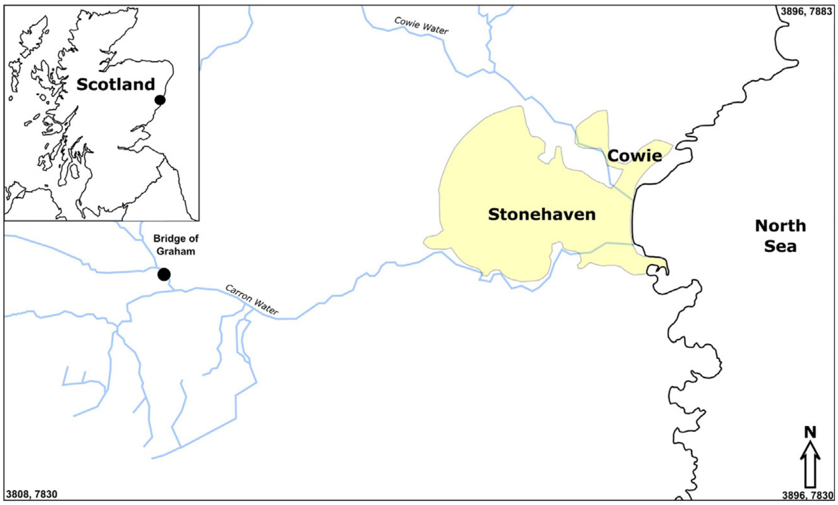

Fig. 1. Location of the area of study. The Cowie Formation crops out in the area around Stonehaven, in the north-east of the Midland Valley of Scotland.

Early Devonian (Suarez et al., 2017). The Wenlock age is determined from palynomorphs retrieved from the inland exposures of the formation at Carron Water (Bridge of Graham) [NO 825853] and Carron Wood [NO 807848] (Marshall, 1991; Wellman, 1993; Lavender and Wellman, 2002). However, the inland outcrop is poorly exposed in comparison to coastal exposures north of Stonehaven, from which most interpretations of sedimentary facies, and all macrofossil samples, are known. In the coastal exposures, samples from the Cowie Formation have not thus far yielded biostratigraphically-useful microfossils (Wellman, pers. comm.).

In this paper we describe a previously unrecorded terrestrial ichnofauna from the coastal exposures, between Cowie and Ruthery Head, within strata that constitute the Castle of Cowie Member (which lies stratigraphically below the Cowie Harbour Siltstone Member) (Fig. 2). The ichnofauna is dominated by a low complexity, low diversity assemblage of *Taenidium* and *Arenicolites*: an archetypal infaunal ichnological signature of Siluro-Devonian (used here to mean Pridoli and Lochkovian) continental sedimentary facies in other worldwide locations, deposited after the initial terrestrialization of arthropods but prior to a Devonian radiation of continental ichnodiversity (Buatois et al., 1998; Minter et al., 2017). Given the discrepant nature of the Cowie Formation ichnofauna with respect to other mid-Silurian examples, we consider the plausibility and implications of two competing hypotheses: (1) that the Cowie Formation contains the oldest record, worldwide, of infaunal back-filled and U-shaped burrows in a non-marine environment; or (2) that the coastal exposures of the Cowie Formation are earliest Devonian in age, and distinct from the well-dated inland exposures.

This paper presents evidence that favours the hypothesis that the trace fossil-bearing coastal exposures are (a) younger than presently mapped, and (b) represent a distinct fault-bounded stratigraphic unit to the palynomorph-dated inland outcrop presently mapped as Cowie Formation.

2. Geological setting

The c. 1.6–2.0 km-thick Stonehaven Group records the onset of Old Red Sandstone deposition in the northern Midland Valley. It sits unconformably on top of Ordovician rocks of the Highland Border Complex, and disconformably below the poorly-dated Old

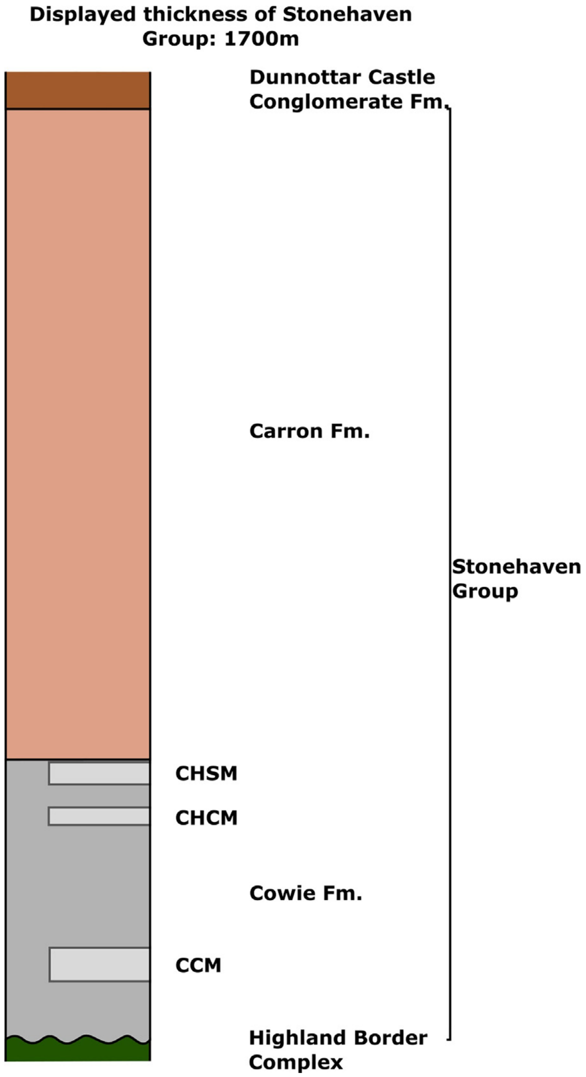

Fig. 2. Stratigraphic column for the Stonehaven Group, illustrating the unconformable relationship with the underlying Highland Border Complex, and conformable relationship with the overlying Dunnottar Castle Conglomerate Formation, of the Dunnottar-Crawton Group (after British Geological Survey, 1999). CCM – Castle of Cowie Member; sandstone, sandy siltstone and siltstone. CHCM – Cowie Harbour Conglomerate Member; conglomerate, sandstone and volcaniclastics. CHSM – Cowie Harbour Siltstone Member; siltstone, sandstone and a fish bed.

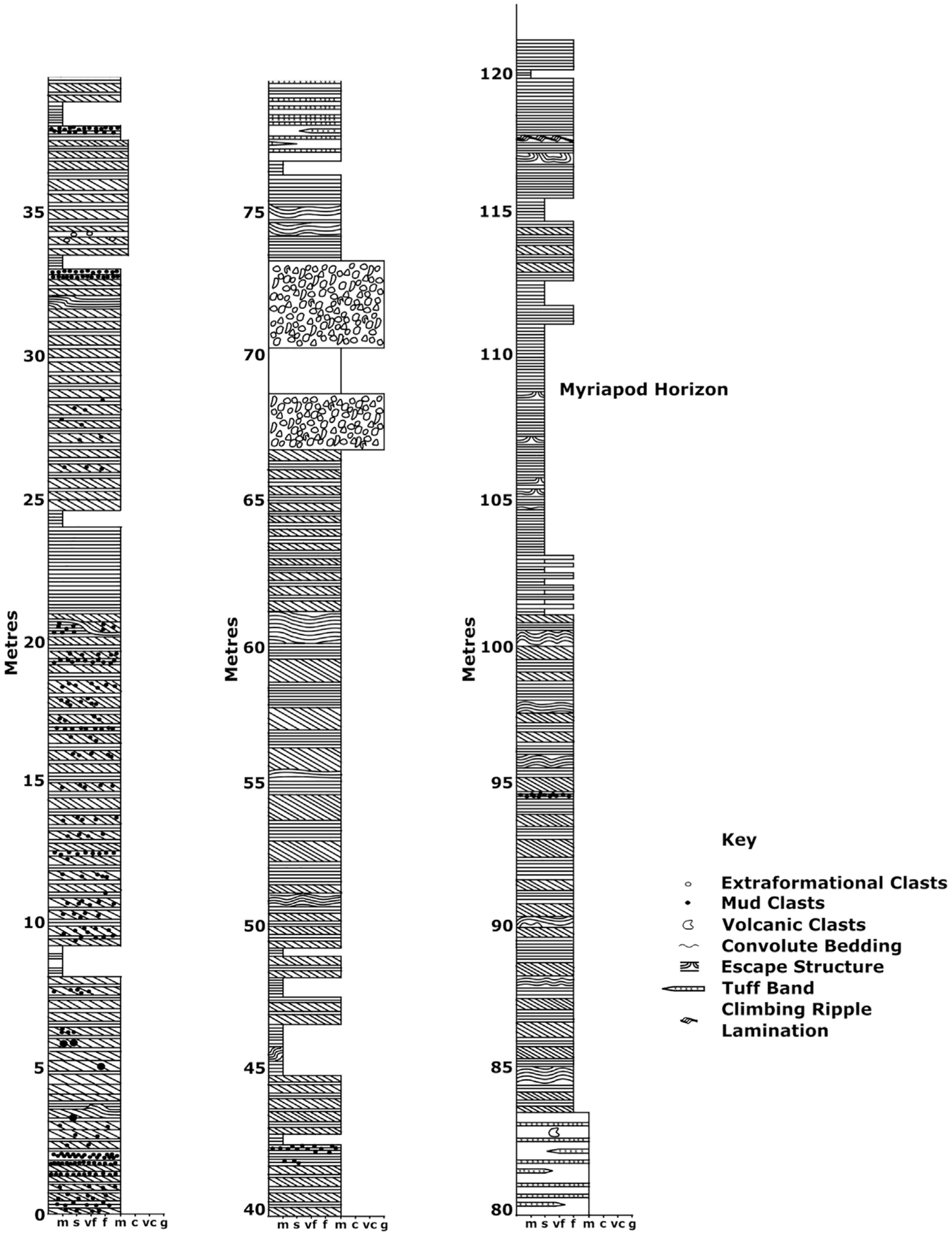

Fig. 3. Stratigraphic log of the Cowie Formation exposed in Cowie Harbour. The log covers a thickness of approximately 120 m of exposure on the foreshore, from undifferentiated Cowie Formation to Cowie Harbour Siltstone Member at the top of the section. A horizon from where myriapod body fossils have previously been collected is marked.

Red Sandstone conglomerates and sandstones of the Dunnottar-Crawton Group (Browne et al., 2002).

The group is bounded to the north by the Highland Boundary Fault, a major structural lineament that extends NE-SW across central Scotland and largely separates the Dalradian rocks of the Grampian Highlands from Old Red Sandstone of the Midland Valley. The fault is thought to have been reactivated multiple times, with a significant but unknown net displacement (Bluck, 2002).

The Stonehaven Group is subdivided into two formations: the lower Cowie Formation and the upper (860–1260 m-thick) Carron Formation. Both formations are dominated by cross-bedded arkosic sandstones, with subordinate siltstones and mudstones, and minor volcanogenic conglomerates and tuff bands (Browne et al., 2002). This study concentrates on the Cowie Formation, cropping out along the coast north of Stonehaven as cliff exposures and low gradient coastal rock platforms, with bedding that dips near-vertical and youngs to the south-east (such that outcrops of the youngest strata visible can be studied only at low tide). In these outcrops, the Cowie Formation sits unconformably on top of Ordovician rocks of the Highland Boundary Complex to the north-east, but elsewhere its thickness is attenuated by the Highland Boundary Fault (Carroll, 1995), abutting against Precambrian metasedimentary rocks. Inland exposures of the formation are restricted to small, discontinuous stream and railway cuttings in the vicinity of Carron Wood [NO 807848] and Carron Water (Bridge of Graham) [NO 825853].

The Cowie Formation contains three named members: the Castle of Cowie Member (CCM), Cowie Harbour Conglomerate Member (CHCM), and Cowie Harbour Siltstone member (CHSM) (Fig. 2), along with stratigraphically-undifferentiated strata and several informal 'members' (e.g. Purple Sandstone 'Member', Brown and Grey Sandstone 'Member') (British Geological Survey, 1999). The Castle of Cowie Member crops out between NO 880868 and NO 883871 (British Ordnance Survey National Grid References), as interbedded sandstone, sandy siltstone and siltstone. The Cowie Harbour Conglomerate Member is exposed in Cowie Harbour between NO 877863 and NO 880866, and contains volcaniclastic conglomerate bands interbedded with sandstone. The macrofossil-yielding Cowie Harbour Siltstone Member (previously known as the *Dictyocaris* Member (Carroll, 1995; Browne et al., 2002)) is also exposed in Cowie Harbour between NO 877863 and NO 880866, and is composed of interbedded sandstones and siltstones.

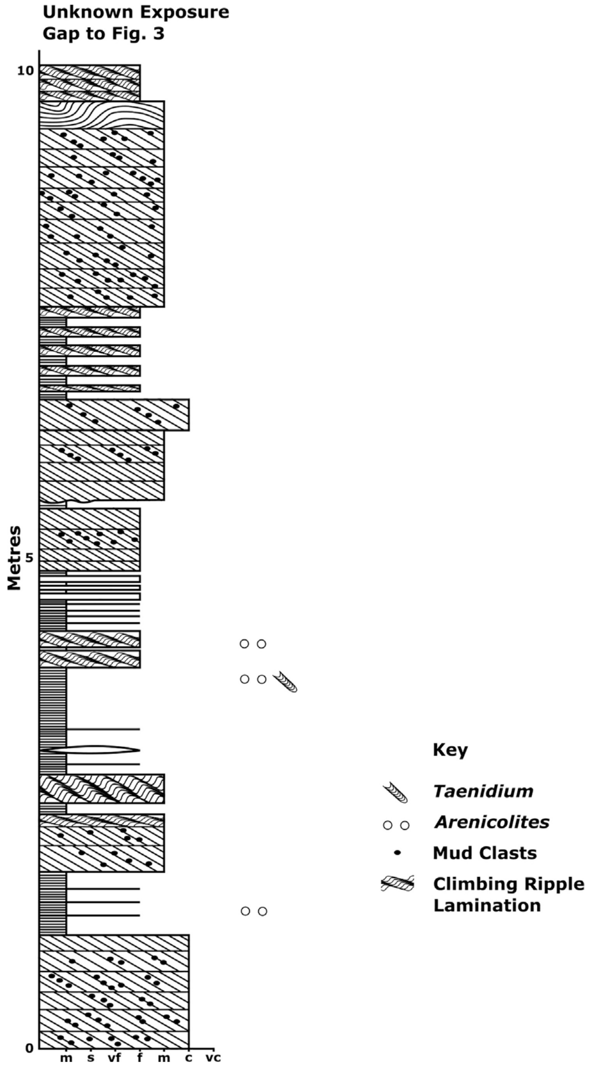

Fig. 4. Stratigraphic log of part of the Castle of Cowie Member where trace fossils are observed, exposed in cliffs to the north side of Cowie Harbour. The log covers a continuous section approximately 10 m thick. Due to gaps in exposure and structural complexities associated with the proximity to the Highland Boundary Fault this can not be exactly correlated with the stratigraphic section detailed in Fig. 3, but is known to have occurred stratigraphically lower.

3. Sedimentary environments of the Cowie Formation

3.1. Undifferentiated Cowie Formation

The majority of the Cowie Formation is not assigned to a member, as it is lithologically indistinguishable and occurs intermittently throughout the stratigraphy between the named members (British Geological Survey, 1999). The undifferentiated Cowie Formation is predominantly comprised of cross-bedded, medium-grained arkosic sandstone, with frequent planar bedded layers and occasional mudstones (Fig. 3). Cross-bedding indicates a dominant palaeoflow towards the west (Hartley and Leleu, 2015). Intraformational rip up clasts are commonly incorporated into the cross-bedded sandstones, and infrequent layers are almost entirely composed of mud chips, with subordinate clasts of calcrete. The cross-bedded sandstones of the Cowie Formation are interpreted as having a fluvial origin, with the finer, planar beds corresponding to overbank deposits and incorporation of intraformational clasts attesting to overbank reworking.

3.2. Castle of Cowie Member

This member crops out in the cliffs to the north of Cowie Harbour. The member is comprised of fine- to coarse-grained arkosic sandstone, typically cross-bedded with mud chips and reworked calcrete, and finely laminated mudstone bands up to 1 m thick (Fig. 4). Occasional heterolithic beds up to 1 m thick are observed, with climbing ripples in the sandier beds. As with the undifferentiated Cowie Formation, the Castle of Cowie Member is of alluvial origin, with a combination of fluvial and overbank deposits. This member yields the bulk of the ichnofauna described below, in both sandstone and mudstone layers.

3.3. Cowie Harbour Conglomerate Member

This member contains alternating layers of volcaniclastic conglomerate and massive sandstone, observed between 67 m and 73 m on the log in Fig. 3. The conglomerate is matrix supported, and clasts are clearly compositionally different to the sandstone making up the rest of the formation. Further evidence of volcanic activity occurs further up the section, with frequent layers of tuff between 77 m and 83 m on Fig. 3. Occasional large volcanic clasts occur between the bands of tuff.

3.4. Cowie Harbour Siltstone Member

This member marks the top of the exposed Cowie Formation in the coastal Cowie Harbour section (Fig. 3 100 m upwards), and crops out at the seaward end of coastal platform exposures. This member, aside from the recorded fossil fish and arthropod fauna, consists of laminated siltstones exhibiting frequent small scale convolute bedding and water escape structures. It is likely that some of these structures are the result of bioturbation (Fig. 6C). Both subaerial (*Pneumodesmus newmani*, Wilson and Anderson, 2004) and subaqueous (Campbell, 1913) fossil fauna are known from the section, suggesting that deposition was subaqueous, but intermittently emergent. The dominance of fine sediment and lack of cross-bedding or mud chips argue against tractional deposition and suggest deposition in low energy, possibly lacustrine, standing water.

A non-marine depositional environment for all of the constituent members of the Cowie Formation is attested to by a suite of

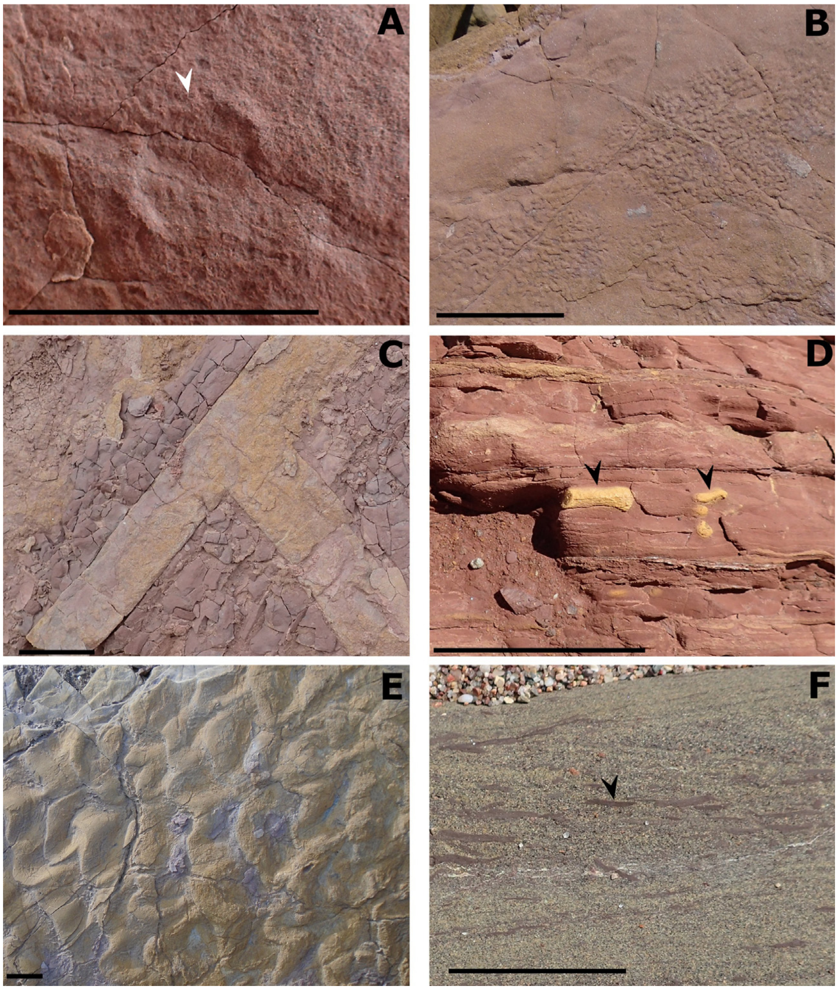

Fig. 5. Sedimentary structures observed in the Castle of Cowie Member on the Cowie foreshore. A — individual raindrop impression, with characteristic raised rim. B — small scale adhesion structures showing consistent directionality, suggesting an abiotic origin. Under the scheme proposed by Davies et al. (2016) these are classified as A. Mud chips, often thin and elongate in form. C — large, complete desiccation cracks. These cracks occur in association with *Taenidium* and *Arenicolites*. D — small pieces of calcrete (arrowed), suggesting periods of subaerial exposure for the overlying substrate during its formation. E — asymmetric ripples. F — thin, elongate mud clasts. Clasts appear to be reworked floodplain deposits in a sandstone matrix. Preferential alignment suggests unidirectional flow. A scale bar 10 mm, B–F scale bar 50 mm.

sedimentary structures and surface textures including raindrop impressions, adhesion marks, desiccation cracks and calcrete — all formed during intervals of substrate exposure and sedimentary stasis (Fig. 5). These and other sedimentary structures are fully described in Table 1, with details of their dimensions, frequency and origin.

The variable quality of exposure places limitations on sedimentological and ichnological field observations. The Castle of Cowie Member is well-exposed in both vertical section and as bedding planes, while the Cowie Harbour Conglomerate Member and Cowie Harbour Siltstone Member are observable only in vertical sections (where a wave-cut platform has developed perpendicular to the steep bedding), are accessible only at low tide, and are extensively covered with algae and barnacles. As such, while the observed ichnofauna from the Castle of Cowie Member appears more abundant than the younger members, this likely reflects outcrop constraints rather than a primary signature.

4. Ichnological and biogenic structures of the Cowie Formation

In addition to the well-known body fossils, the sedimentary strata of the Cowie Formation yield previously-unreported indirect evidence of life in the form of identifiable ichnotaxa, problematic traces, bioturbated horizons and putative microbial structures, described below. All of the surface traces occur within strata that bear primary sedimentary structures indicative of a subaerial environment (adhesion marks, desiccation cracks, raindrop impressions; Fig. 6), suggesting that the trace makers interacted with sedimentary substrates during intervals of sedimentary stasis in a non-marine environment (Davies et al., 2017).

4.1. Arenicolites Salter, 1857

Abundant paired burrows, with no evidence of spreite, are observed in plan view on several bedding planes of the Castle of Cowie Member. The burrow shafts have a narrow diameter (2–3 mm) and each paired aperture is separated by 10–29 mm. No internal structure can be observed, and the burrow infill is typically fine sand, similar to the host sediment. Burrows are readily recognisable due to differential weathering. The traces can be diagnosed as *Arenicolites*, despite lack of 3D exposure, due to their pairing, and the absence of sediment disturbance between the burrow apertures.

Elsewhere in the global rock record, *Arenicolites* is reported from the Cambrian (Mángano and Buatois, 2016) until the present day (Virtasalo et al., 2011), but absent in non-marine strata until

Table 1
Descriptions of sedimentary structures observed in the Cowie Formation. Table details any association of features with trace fossils, dimensions of structures, abundance in the coastal Cowie Formation, classification based on biotic or abiotic formation, and a description of means of formation.

Feature	Associated trace fossils	Median dimensions	Coverage	Classification	Formation
Raindrop impressions	*Arenicolites* and *Taenidium*	5 mm (diameter)	Rare	Abiotic	Individual or multiple precipitation events
Mud clasts		20 mm × 2 mm (length × height)	Widely very abundant	Abiotic	Rip up clasts from flooding events
Calcrete		15 mm × 5 mm × 5 mm (length × width × height)	Widely very frequent	Abiotic	Slow precipitation subterraneously whilst surface is subaerially exposed
Convolute bedding	Possible indistinct bioturbation	70 mm × 45 mm (width × depth)	Locally abundant (only CHSM)	Abiotic or produced by macrofauna	Soft sediment deformation, either abiotic or formed by bioturbation.
Complete desiccation cracks	*Arenicolites* and *Taenidium*	40 mm (width)	Infrequent	Abiotic	Progressively developed during an interval of drying
Partial desiccation cracks		1 mm × 10 mm (width × max length)	Rare	Abiotic or microbial	Progressively developed during an interval of drying. Total shrinkage insufficient to separate surface into individual plates
Adhesion marks		4 mm (width)	Rare	Abiotic	Punctuated episodes of accretion arising from aeolian transport of sediment over a damp substrate
Asymmetric ripple marks		65 mm (wavelength)	Locally abundant	Abiotic	Unidirectional flow over a substrate causing ordering of sedimentary particles into bedforms.
Climbing ripple marks		20 mm × 10 mm (wavelength × height)	Widely abundant	Abiotic	Unidirectional flow over a substrate causing ordering of sedimentary particles into bedforms, accompanied by a high sedimentation rate.
Wrinkle marks		<1 mm (width)	Rare	Abiotic or microbial	Developed due to accretion of small amounts sediment on a substrate due to abiotic or biotic processes

the Pridoli (Morrissey et al., 2012a, 2012b). The tracemaker is typically interpreted as being a vermiform organism (Häntzschel, 1975).

4.2. Taenidium Heer, 1877

4.2.1. T. barretti Bradshaw, 1981

Taenidum barretti comprises unlined, sub-cylindrical, sub-vertical, backfilled structures with burrow depths of 45–70 mm, and burrow widths of 10–32 mm, present within the Castle of Cowie Member (Fig. 6C). Examples occur in isolation or in association with *Arenicolites*. Some specimens exhibit mud flecks within the burrow when viewed in horizontal cross section. Menisci are tightly packed in the specimens within which they can be clearly observed. The specimens are assigned specifically to *T. barretti* as the infilling material is organised as heterogeneous, thinly segmented, arcuate menisci (Keighley and Pickerill, 1994).

It is likely that these traces were produced by burrowing arthropods, and a range of potential tracemaker taxa is known from the overlying Cowie Harbour Siltstone Member (Campbell, 1913). Examples of *T. barretti* are sparsely distributed through the section, with fewer examples than of *Arenicolites*. Elsewhere in the global rock record, *Taenidium* is reported from the lower Cambrian (Stachacz, 2012) until the present day (D'Alessandro et al., 1993), but is only found in non-marine strata from the Late Silurian onwards (Fig. 7).

4.3. "Comma-shaped" impressions

Problematic traces with a circular "body" and curved "tail" tapering to a point (i.e., "comma-shaped") can be observed on some bedding planes of the Castle of Cowie Member. In two specimens, the tail appears to exhibit a meniscate pattern, concave towards the body of the trace. The diameters of the body of the traces are 2–3 mm, and the total length of each trace is 6–12 mm.

It is not possible to confidently diagnose whether the "comma-shaped" impressions represent burrows with a main shaft and evidence of migration, or individual tracks with "splash marks" behind footfalls. If the traces are burrows, they resemble migrating J-tubes (such as *Teichichnus*, *Dictyodora*, *Paradictyodora*). However, unlike these ichnotaxa the traces taper sharply and have very limited lateral extent at the surface. "Splash marks" are a common feature of several invertebrate track ichnotaxa, such as *Koupichnium* (Seilacher, 2007), recording slipping of sediment behind a footfall, displaced by the animal as it walked across the substrate. However, such splash marks lack the internal structure seen in some of the Cowie specimens.

The apparent presence of meniscate structures in the tails of some traces indicates that a burrow origin is more probable, with a back-filling trace maker similar to *Taenidium*.

4.4. Undifferentiated bioturbation

The upper part of the Cowie Formation (Cowie Harbour Siltstone Member) is devoid of identifiable trace fossils, despite it hosting the millipede fossil-bearing horizon. In part this may be due to the lack of bedding plane outcrop and poor exposure within vertically-dipping, intertidally-exposed strata. However, the disturbance of sedimentary laminae in some beds is evidence of bioturbation in this member (Fig. 6).

4.5. Possible microbial sedimentary surface textures

Possible microbial signatures are observed in the Castle of Cowie Member, where some bedding planes exhibit either wrinkle marks or partial, sinuous desiccation cracks (Fig. 6). The means of formation of these structures is ambiguous: while they may record microbial colonization of substrates during quiescent sedimentary intervals, solely abiotic origins cannot be ruled out (Davies et al., 2016). Following Davies et al. (2016), these structures are assigned an 'ab' classification, as confident diagnosis of their origin is

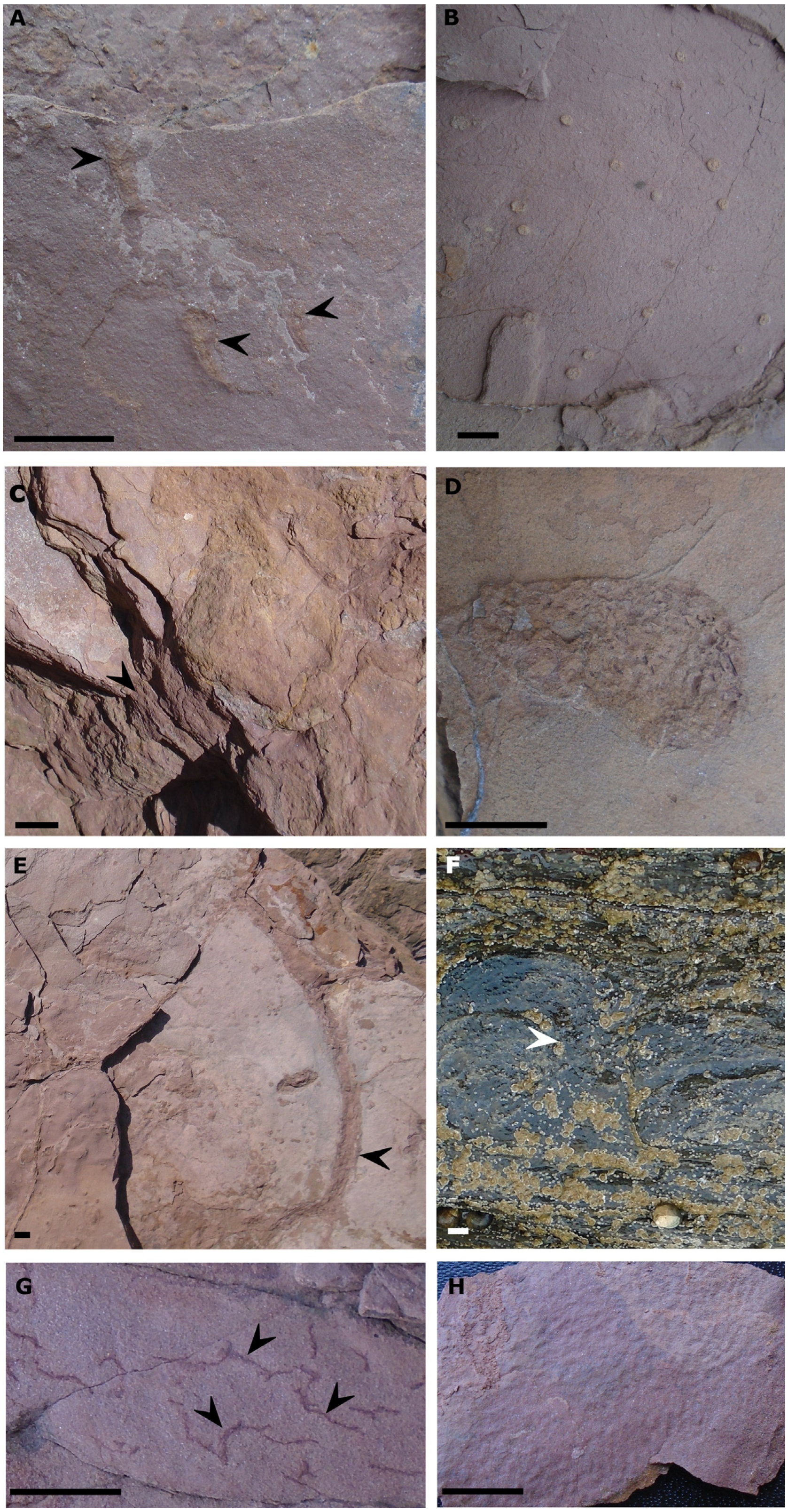

Fig. 6. Trace fossils observed in the Castle of Cowie Member and Cowie Harbour Siltstone Member. A — "comma-shaped" burrows (arrowed) observed in plan view on a bedding plane. Burrows occur in same horizon as *Arenicolites*. B — multiple *Arenicolites* traces observed in plan view on a bedding plane. C — *Taenidium barretti* viewed from above and in cross section. D — a burrow infilled with mud chips (likely *Taenidium*). E — meniscate burrow and Arenicolites viewed from above, in association with desiccation cracks (arrowed). F — convolute bedding in the Cowie Harbour Siltstone Member, likely due to bioturbation. G — discontinuous, meandering desiccation cracks, possibly due to microbial binding of sediment. H — wrinkle marks, formed on a very small scale and showing no evidence of preferential directionality. Possibly formed under microbial influence. Scale bar 10 mm.

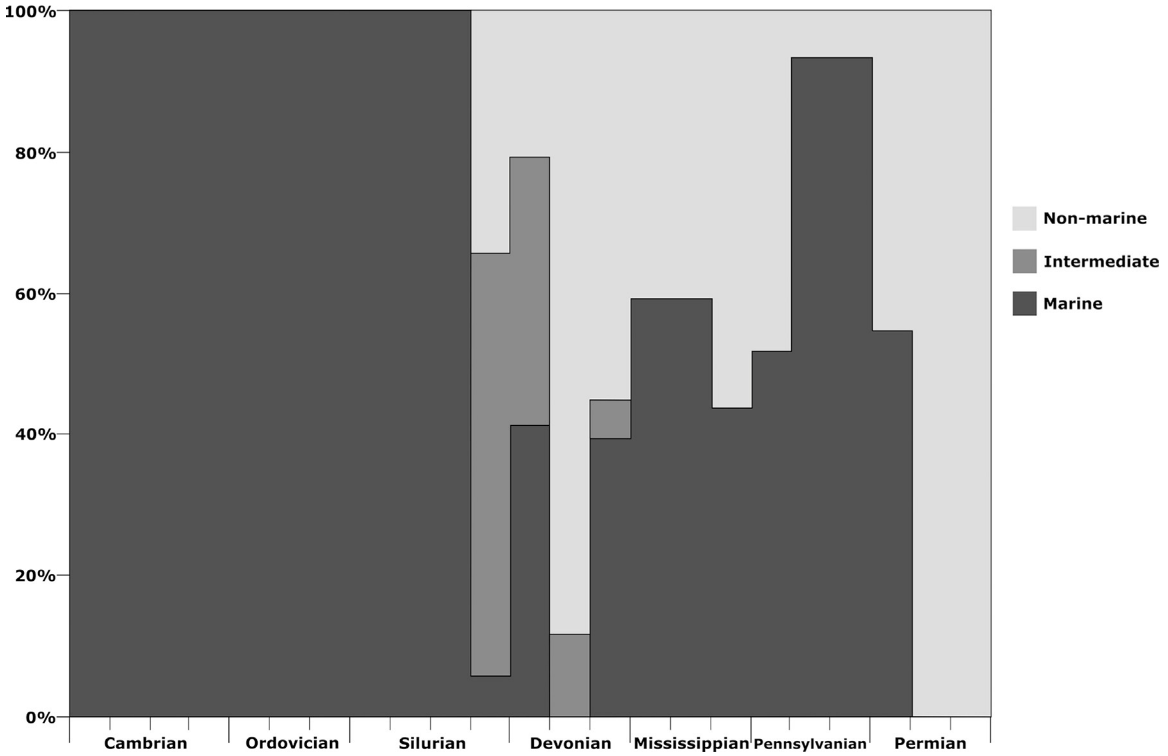

Fig. 7. A histogram illustrating the appearances of meniscate burrows in the rock record from the start of the Cambrian until the end Permian. *Scoyenia* is not included in the analysis. Graph shows percentage of reported occurrences from an epoch in marine, intermediate and non-marine settings based on classifications made in previous literature. Intermediate settings are those which occur in the region of both terrestrial and marine influence. In all other locations meniscate burrows are reported worldwide they are not know outside of the marine realm until the Pridoli. Histogram compiled from data held in the following references: Abassi (2007),Aceñolaza and Buatois (1993), Baucon et al. (2015), Benton (1982), Bjerstedt (1988), Bradshaw (2010), Bridge et al. (1986), Bruck et al. (1985), Chamberlain (1971), Crimes et al. (1992), Crowley et al. (2009), D'Alessandro and Bromley (1987), Donovon and Lewis (2008), Draganits et al. (2001), Fan and Gong (2016), Fillmore et al. (2010), Friend and Williams (2000), Gand et al. (1997), Germs (1972), Goldring and Pollard (1995), Graham and Pollard (1982), Hakes (1976), Han and Pickerill (1994), Häntzschel (1975), Hunter and Lomas (2003), Knaust (2004), Kulkarni and Borkar (2014), Kumpulainen et al. (2006), Maples and Archer (1987), Maples and Suttner (1990), Martino (1989), Mikulas (1993), Minter et al. (2007), Morrissey and Braddy (2004), Narbonne (1984), O'Sullivan et al. (1986), Pearson (1992), Pickerill (1991), Pickerill (1992), Pickerill et al. (1987), Pickerill et al. (1984), Prescott et al. (2014), Qi et al. (2012), Savoy (1992), Smith (1993), Stephenson and Gould (1995), Tanoli and Pickerill (1989), Thomas and Smith (1998), Tunbridge (1984) and Weber and Braddy (2004).

problematic. However, possible microbial sedimentary structures have also been reported from other Old Red Sandstone formations in Wales and Norway (Davies et al., 2006; Marriott et al., 2013), some of which closely resemble the Cowie Formation wrinkle marks.

5. Discussion of Silurian trace fossils

Sedimentological signatures in the Cowie Formation attest to its non-marine deposition, and their close association with certain traces (*Taenidium barretti*, *Arenicolites*) suggest that these traces were formed in subaerially-exposed substrates. Were these rocks of Silurian age as previously proposed, the traces may have global significance, as contemporaneous strata worldwide contain evidence for the progressive colonization of non-marine environments during this period (Minter et al., 2016, 2017), and terrestrial ichnofossil assemblages from the middle Silurian are scarce. From an ichnostratigraphic standpoint two possibilities exist: (1) that the Cowie Formation contains the oldest record, worldwide, of infaunal back-filled and U-shaped burrows in a non-marine environment; or (2) that the coastal exposures of the Cowie Formation early Devonian in age, in agreement with dating of the tuffs (Suarez et al., 2017), and distinct from the well-dated inland exposures.

We emphasise that the second hypothesis is favoured due to three lines of circumstantial evidence: (1) the unlikelihood of one succession revealing the advent of multiple different ethological innovations; (2) the absence of trace fossils in Wenlock continental strata worldwide; (3) the similarities of the ichnofauna to other Scottish Siluro-Devonian sites.

With a middle Silurian age, both U-shaped and meniscate burrows would pre-date other continental examples worldwide by 5–10 Ma (Minter et al., 2016). The co-occurrence of the globally first instances of two distinct ethological styles of trace fossil warrants closer inspection, particularly as elsewhere in the global stratigraphic record, the first instances of these traces occur in multiple different intertidal and continental successions worldwide, within a very narrow time range of 3 Ma.

The geologic record of meniscate burrows extends from the lower Cambrian (Stachacz, 2012) until the present day (D'Alessandro et al., 1993, with non-marine forms becoming most prevalent from the Late Devonian onwards (Fig. 7). Outside of the Stonehaven Group, the Old Red Sandstone of Anglo-Welsh Basin contains the oldest recorded example of fully terrestrial meniscate burrows in the global rock record (Morrissey et al., 2012a, 2012b), in rocks of Pridoli age (Allen and Williams, 1981; Barclay et al., 2015). Meniscate burrows reported from the mid-Silurian Grampians Group of Western Australia probably formed in a fully marine setting (George, 1994; *contra* Gouramanis et al., 2003). Elsewhere they are reported in Late Silurian-Early Devonian deposits from transitional continental-marine settings in the Ringerike Group of Norway, Tumblagooda Sandstone of Western Australia, and Mereenie Sandstone of the Northern Territory, Australia (Trewin and McNamara, 1994; Davies et al., 2006 Gouramanis and McLoughlin, 2016).

Using individual ichnotaxa as 'ichnostratigraphic' markers is inadvisable. Beyond ichnogeneric level it is often extremely challenging to distinguish between trace fossils, as morphological differences are often subtle and the quality of specimens highly variable (Egenhoff et al., 2007). However, the bulk ichnofauna of a succession may be more indicative of age as it indirectly records the suite of organisms and ethological styles active in the depositional environment.

During an interval of evolutionary innovation (such as the colonization of non-marine environments), such an approach may be particularly valuable. Illustrating this, Fig. 7 shows the ranges of four meniscate burrow ichnogenera from the Lower-Middle Palaeozoic (*Taenidium*, *Beaconites*, *Ancorichnus*, *Muensteria*), suggesting that the presence of meniscate burrows in the terrestrial realm during the mid-Silurian is highly anomalous, and in disagreement with the global trend.

If the Cowie Formation were late Wenlock in age (Marshall, 1991; Lavender and Wellman, 2002), the bulk ichnofauna is more complex than any others known worldwide (Minter et al., 2016); though it should be noted that few middle Silurian non-marine formations are known globally. A later Early Devonian age appears more likely from this evidence, in keeping with the global norm, and being a more parsimonious explanation for the similarity of the Cowie ichnofauna with other Siluro-Devonian strata of Scotland: U-shaped and back-filled burrows are known from the Early Devonian Crovie Group of Turriff, 60 km NNW of Cowie (Trewin, 2002) (Fig. 7).

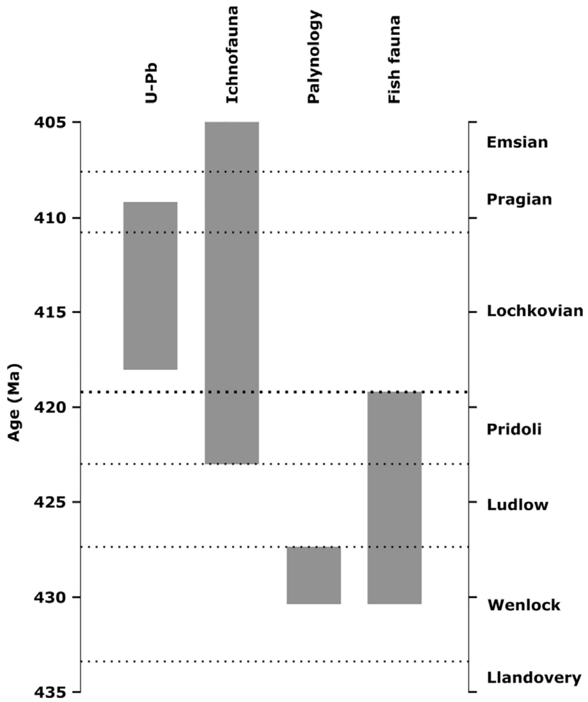

Fig. 8. A comparison of predicted ages for the Cowie Formation based on U-Pb dating of tuffs, palynology of exposures at Bridge of Graham, the ichnofaunal assemblage of the Cowie foreshore, and fish and arthropod fossils from the Cowie Harbour Siltstone Member. The greatest degree of overlap occurs in the Pridoli-Lochkovian.

6. The age of the Cowie Formation

6.1. Geological evidence

The age of the Cowie Formation is problematic as different means of dating have produced mutually exclusive results (Fig. 8). U-Pb dating of tuff bands within the coastal exposures of the Cowie Harbour Siltstone Member suggests a Lochkovian–Pragian age (Suarez et al., 2017), palynological samples at the Bridge of Graham suggests a late Wenlock age (Lavender and Wellman, 2002), the endemic fish fauna from the Cowie Harbour Siltstone Member suggests a Pridoli age (later revised to 'Wenlock–Pridoli' to account for the palynological age (Dineley, 1999a)), and the ichnofauna described herein suggests a Pridoli-Early Devonian age.

Considering all of these ages alongside one another, the greatest overlap occurs in the Pridoli-Lochkovian. Within this interval however, there are still some difficulties in reconciling the Lochkovian U-Pb age of the tuffs and the Pridolian age of the vertebrate fauna. The Cowie fish fauna is dominantly agnathan (Dineley, 1999a), whereas other Lochkovian strata within the Midland Valley (the Dundee Formation of the Arbuthnott Group) contain gnathostome-rich assemblages (Dineley, 1999b) (both also contain cephalaspids (Campbell, 1912; Dineley, 1999b)). The Dundee Formation is lithostratigraphically higher in the Midland Valley Old Red Sandstone succession than the Cowie Formation (British Geological Survey, 1999), and an explanation for the discrepant faunas may lie in the coarseness of the named stratigraphic stages at the Siluro-Devonian boundary. The Lochkovian epoch spans an interval of 8.4 Ma; a greater duration than the 8.2 Ma of the preceding Ludlow and Pridoli epochs combined. A plausible explanation for the discrepant fish fauna may be that the Dundee Formation was deposited in the late Lochkovian, while the Cowie Formation was deposited millions of years earlier in the early Lochkovian. Combined with the recognition that 'Pridolian' fish fauna could be reasonably expected to have a range that marginally extended into the earliest Devonian, this hypothesis can be used to explain the discrepant fish faunas in light of the fact that U-Pb dating has shown a Lochkovian age (Suarez et al., 2017). Such a scenario implies that the true age is near the oldest ages bracketed within the range recognised by Suarez et al. (2017).

The agnathan fish fauna of the Cowie Formation provides further circumstantial evidence of an earliest Devonian age when compared with other Old Red Sandstone successions. The Cowie fish fauna is generally considered similar to that of the Ringerike Group of Norway, which was deposited near the Silurian-Devonian boundary (Davies et al., 2005). In that unit, a diverse fish fauna has yielded possible ages from Llandovery to Lochkovian, with no overlap between known stratigraphic ranges of some assemblages (explained by localized reworking of fish debris; Davies et al., 2005). The Ringerike Group exhibits a similarly depauperate ichnofauna in its fully alluvial strata (Davies et al., 2006) (though better exposure of coastal/marine-influenced strata in the group mean that 16 ichnogenera in total are known from the unit). The similarities in fish fauna and ichnofossils between the Cowie Formation and the Ringerike Group are circumstantial evidence of a similar age, providing more support that the Cowie Formation is earliest Lochkovian.

As the bulk of geological evidence (ichnology, fish fauna, U-Pb dates) thus points to an earliest Devonian age for the Cowie Formation, the previously accepted Wenlock age, obtained from palynostratigraphy (Marshall, 1991; Lavender and Wellman, 2002), appears anomalous. This age was determined based on dated palynomorphs recovered from inland exposures at Bridge of Graham (Marshall, 1991; Lavender and Wellman, 2002), but can be accounted for by considering the inland outcrop as a discrete, unrelated formation to the true Cowie Formation at the coast.

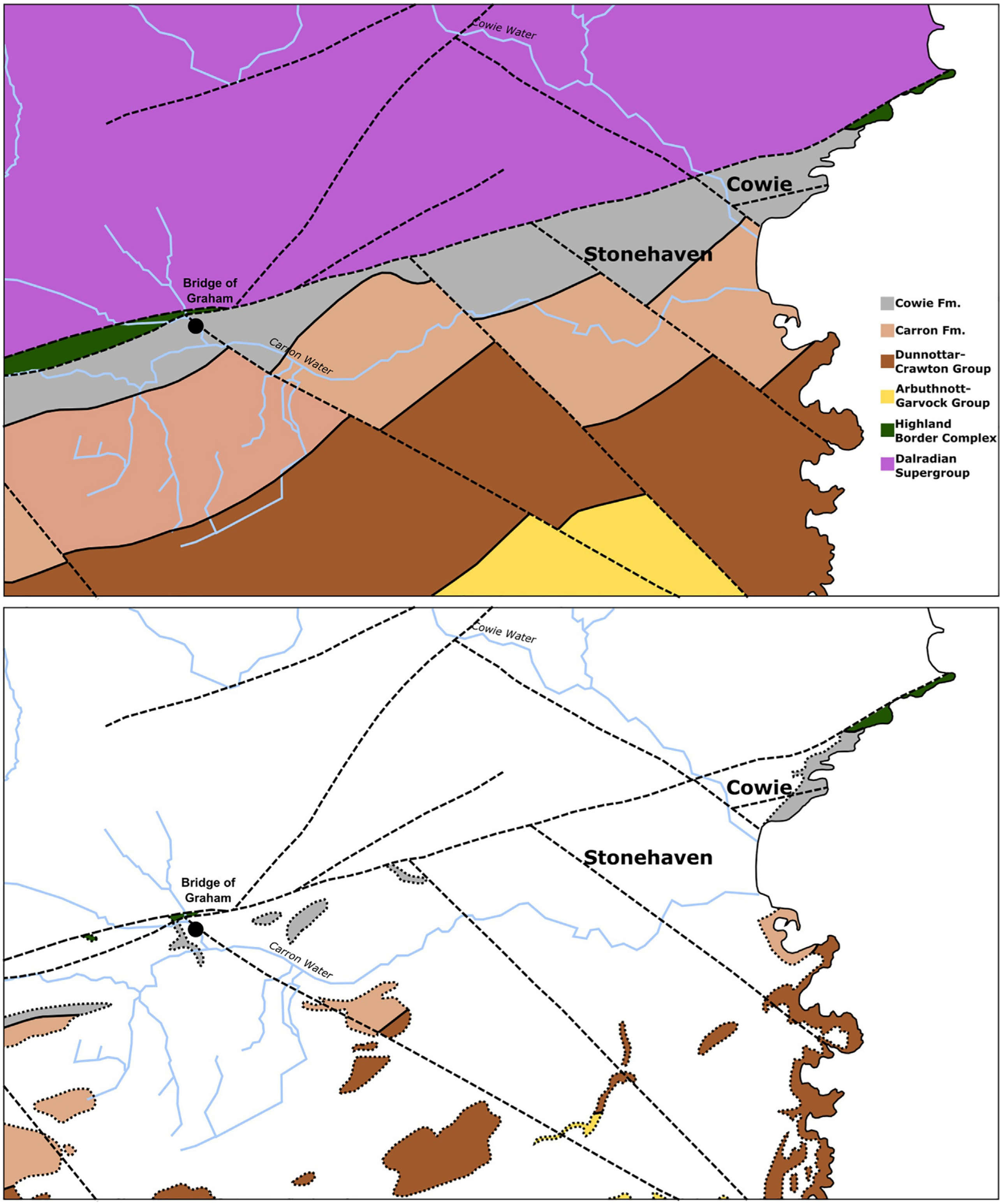

Fig. 9. A – geological map of the area of study. The Cowie Formation is mapped as a continuous unit from the coast for 12 km inland. B – exposure map of the geology south of the Highland Boundary Fault between the coast and Carron Wood. There is very little exposure of any of the Lower Old Red Sandstone away from the coastal cliffs. As there are complex fault slivers associated with the Highland Boundary Fault in the area it is possible that the exposures at Carron Wood and Bridge of Graham have also been brought in as unrelated faulted blocks.

Presently the Stonehaven Group is lithostratigraphically mapped as a contiguous unit that extends inland for 12 km from the coastal exposures (British Geological Survey, 1999) (Fig. 9A). However, there is no contiguous inland exposure and no borehole data exists to confirm the interpreted genetic link between the two exposure areas (British Geological Survey, 2017) (Fig. 9B). The palynologically-dated Bridge of Graham outcrop is of only limited extent and poorly exposed (Fig. 10). It consists of interbedded sandstones and

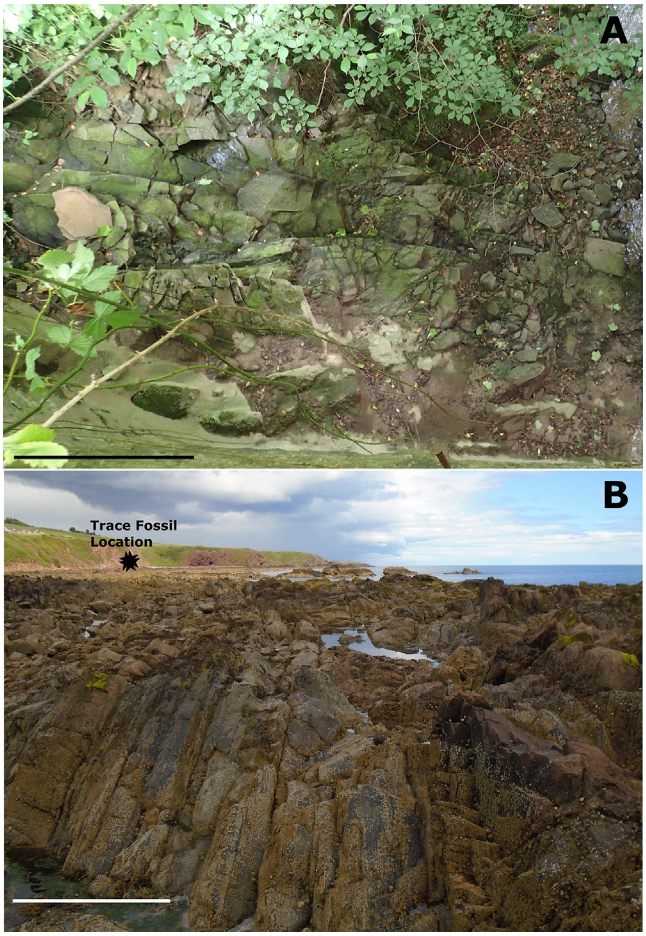

Fig. 10. A — the outcrop that is exposed at the Bridge of Graham, along Carron Water. This outcrop is the location from which palynological samples used to date the Cowie Formation were collected (Marshall, 1991). Scale bar 1 m. B — coastal exposure of the Cowie Formation, viewed looking towards Castle of Cowie Member in cliffs from the Cowie Harbour Siltstone Member. This exposure is significantly more extensive than that observed inland.

mudstones that lack the oxidised red colour that typifies many of the coastally-exposed Cowie Formation strata. Thus, other than proximity and a similar grain-size, there is little evidence to conclusively state that this exposure is correlative with the coastal outcrop, and there are no shared sedimentological, ichnological, palaeontological or biostratigraphic characteristics between the exposures. Given that both the inland and coastal outcrops of presently-defined Cowie Formation abut against the Highland Boundary Fault, it is regarded most likely that the inland exposures record outcrops of a discrete, older, and previously unidentified “Bridge of Graham Formation”, brought up as fault-bounded slivers along the fault zone. Analogous slivers of Highland Border Complex are present locally (Fig. 9A). This possibility retains a Wenlock age for the oldest Old Red Sandstone in Scotland, but recognises that this is a poorly-exposed formation cropping out only near Bridge of Graham, with limited scope for study, and older and discrete from the true, Lochkovian Cowie Formation at the coast. This stratigraphic explanation reconciles the conflicting evidence from the ichnofauna, palynomorphs, fish fauna, and U-Pb dates in the region.

6.2. Implications of a Lochkovian age for the Cowie Formation

A Lochkovian age for the Cowie Formation has implications for, and additional support from, palaeontology, tectonics, provenance and burial history at a regional and global scale.

The fossil fauna of the Cowie Formation was previously thought to contain the oldest myriapods known from the body fossil record, described in the Cowie Harbour Siltstone Member (Wilson and Anderson, 2004; Shear and Edgecombe, 2010). All specimens are likely diplopods; amongst them the oldest definitively air breathing myriapod *Pneumodesmus newmani* and the explicit diplopod *Cowiedesmus eroticopodus*.

Non-marine myriapods now known to be older than those of the Cowie Formation have been described from two locations of Silurian age. The myriapod now recognised as the oldest terrestrial specimen, *Casiogrammus ichthyeros*, was described from the Wenlock Fish Bed Formation of the Hagshaw Hills Inlier, Scotland (Wilson, 2005). Unlike examples of *P. newmani* however, *C. ichthyeros* does not exhibit spiracles, and evidence for non-marine origin relies on its association with a fully non-marine

Table 2
Interpretations and Implications for movement on the Highland Boundary Fault and the source of the Old Red Sandstone in the Midland Valley from previous work on the area.

Interpretation (Highland Boundary Fault Movement)	Author	Implications of Lochkovian Cowie Formation
Any strike-slip movement on the Highland Boundary Fault must have occurred before the Wenlock, as there is no evidence for large-scale sinistral strike-slip movement on the Highland Boundary Fault in the late Silurian to Early Devonian.	Hartley and Leleu (2015)	A younger age moves the onset of restrictions placed upon the movement of the Highland Boundary Fault (based on no syn-depositional strike-slip movement), to the Early Devonian.
A proto-Highland Boundary Fault occupied the present line of the fault, was covered by Lower Old Red Sandstone sediments, began to be active again during the sedimentation, and developed during Acadian deformation as a reverse fault. There is irrefutable evidence for restricting post-Early Devonian lateral movement on the Highland Boundary Fault to a few tens of kilometres.	Tanner (2008)	A Lochkovian age is compatible with movement occurring on the Highland Boundary Fault during deposition of the Lower Old Red Sandstone.
Thrust and strike-slip convergence of the Dalradian onto the Midland Valley occurred in Wenlock-Devonian times.	Bluck (2002)	Bluck considers movement on the Highland Boundary Fault to have occurred through any period in which the Cowie Formation has been thought to have been deposited.
Interpretation (Source of Midland Valley Old Red Sandstone)		
Scandian deformation is responsible for relief to the east of the Midland Valley Basin and sourcing the Cowie and overlying formations.	Hartley and Leleu (2015)	A younger Cowie Formation places its deposition 6–9 Ma after the cessation of Scandian deformation (435–425 Ma). Whilst a westerly flow direction agrees with a source in the region of Scandian deformation, it is unlikely related to the deformation event itself, and may be related to later uplift (Oliver et al., 2008).
During the Silurian and Early Devonian sources were mainly within the Midland Valley, and mature, recycled sediments were mixed with volcanic clasts.	Bluck (2000, 2010)	Sources within the Midland Valley (such as the Highland Border Complex and volcanics) are compatible with a younger Cowie Formation; as such sources were available in the Lochkovian as well as the Wenlock.

palynomorph assemblage (Wellman, 1993). The second example comes from the Ludfordian Downton Castle Sandstone Formation at the Ludford Lane locality in Shropshire, England, where fractured legs of *Crussolum* spp. are found along with specimens of *Eoarthropleura ludfordensis*, none of which exhibit spiracles (Shear and Selden, 1995; Shear et al., 1998). These specimens are interpreted as being non-marine due to comparison with younger species from the Devonian (Shear and Selden, 1995), but the sediments in which they are found are of marine origin (Loydell and Frýda, 2011).

Other than in *P. newmani*, the oldest occurrence of spiracles in myriapods globally dates from the Lower Carboniferous (Visean) of Scotland (Shear, 1993). Whilst a Lochkovian age for the Cowie Formation would thus not change the date of the first appearance of non-marine myriapods, it would mean that the oldest direct evidence for definitively air-breathing forms date from strata 9–12 Ma younger than previously thought.

A Lochkovian age for the Cowie Formation also has tectonic implications; (1) for the duration in which the Highland Boundary Fault was active, and (2) for the provenance of the eastern Midland Valley Old Red Sandstone. A number of authors have provided differing views on the Early Palaeozoic history of the Highland Boundary Fault (Bluck, 2000, 2002, 2010; Tanner, 2008; Hartley and Leleu, 2015). In Table 2, the authors summarize the implications of a Lochkovian age for the Cowie Formation based on several such interpretations.

Both Bluck (2000) and Tanner (2008) present the view that strike-slip movement of the Highland Boundary Fault was limited after the Early Devonian due to the Lintrathen ignimbrite, correlated across the fault (Paterson and Harris, 1969) and constraining lateral movement to a few tens of kilometres (Trench and Haughton, 1990). However, both consider movement on the fault during deposition of the Lower Old Red Sandstone to be plausible. Taking this view, a younger age for the Cowie Formation does not have any implications for Silurian displacement of the Highland Boundary Fault.

The westward palaeoflow exhibited by cross-stratified fluvial sandstones in the Cowie Formation supports a source to the north east, the region in which the Scandian deformation event was occurring (Hartley and Leleu, 2015). However, as the Cowie Formation appears early Lochkovian age, it post-dates Scandian deformation by 6–9 Ma, but could indicate a source area during later uplift to the east (related to granite intrusions occurring from mid-Wenlock to Emsian; Oliver et al., 2008). The majority of such uplift is thought to have occurred between 410–405 Ma, and to have provided the sediment source for the Dunnottar, Crawton and Arbuthnott groups that overlie the Stonehaven Group. A Lochkovian age for the Cowie Formation raises the possibility that the Stonehaven Group shared a source area with the younger strata above it. The volcanogenic conglomerate and tuff bands of the Cowie Harbour Conglomerate Member in the coastal section must correspond to local periods of volcanism, presently only known to have occurred in the Midland Valley from Pridoli to Pragian times (Thirlwall, 1988).

Marshall et al. (1994) performed a vitrinite reflectivity study on rocks thought to belong to the Cowie Formation, along with others from the Old Red Sandstone of the Midland Valley and found low values that suggested a burial depth (5 km) at odds with the measured stratigraphic thickness of the Lower Old Red Sandstone along the coast (9 km of Carron Formation, and Dunnottar and Crawton groups). Marshall et al. (1994) reconciled this by suggesting that the Cowie Formation originally underlaid a thinner succession, in a separate basin to that in which the presently overlying sandstones accumulated. However, Marshall et al.'s (1994) samples came from the inland exposures, so this burial depth is not enigmatic when this is considered to be a discrete, fault-adjacent unit from the coastal exposures. The two-formation scenario proposed here removes the problem of having to reconcile the vitrinite reflectance data with the coastal Cowie Formation having been buried to a depth appropriate to the cumulative thickness of the overlying strata.

Removing the tenuous lithostratigraphic correlation between the palynomorph-bearing inland and palynomorph-barren coastal exposures of the Cowie Formation, as presently mapped, thus resolves a number of geological quandaries in the region; explaining the disparity between ages of the inland and coastal exposures, bringing the age of the spiracle-bearing myriapods closer to that of other worldwide examples, and providing an alternative resolution for contradictory issues surrounding the timing of movement of the Highland Boundary Fault.

7. Conclusions

A previously unrecorded ichnofauna, with archetypal Siluro-Devonian constituent trace fossils, is reported from non-marine strata of the Cowie Formation and supports the recently described Lochkovian age for coastal exposures of the formation. The presence of meniscate burrows in terrestrial settings is unknown elsewhere worldwide prior to the Pridoli, and uncommon before the Devonian. A late Wenlock age for the palynomorph-bearing inland exposures can be accommodated if it is considered that these exposures reflect a completely different stratigraphic unit to the Lochkovian coastal exposures.

The younger age for these Old Red Sandstone deposits pushes forward the age of the earliest known conclusively air breathing myriapod *Pneumodesmus newmani* by 9–12 Ma and removes constraints on interpreting strike-slip movement of the Highland Boundary Fault during the Wenlock and Ludlow (Hartley and Leleu, 2015). A Lochkovian age for the Cowie Formation has no direct implications for fault displacement. Whilst palaeocurrent data confirm that the source of sediment for the Cowie Formation was located to the north east, a Lochkovian age implies the same granitic uplifted source as overlying strata, rather than a Scandian source area. Further support for the coastal and inland exposures being unrelated exists in published vitrinite reflectance data: if the coastal exposures are a different unit, this removes the need to invoke special circumstances to account for an apparently lesser burial depth than is reflected by the preserved overlying stratigraphic pile.

These conclusions illustrate the potential of bulk ichnofauna as potential age indicators during intervals of evolutionary innovation, particularly when viewed amongst other lines of geological evidence. When applied conservatively, ichnostratigraphy in this manner can provide insights where biostratigraphic markers are lacking.

Acknowledgements

The authors thank Nigel Woodcock for helpful discussion concerning the Highland Boundary Fault. APS was supported by the Natural Environment Research Council [grant number NE/L002507/1].

References

Abassi, N., 2007. Shallow marine trace fossils from Upper Devonian sediments of the Kuh-E Zard, Zefreh Area, Central Iran. Iranian Journal of Science & Technology, Transaction A 31, 23–33.

Aceñolaza, F.G., Buatois, L.A., 1993. Nonmarine perigondwanic trace fossils from the late Paleozoic of Argentina. Ichnos 2, 183–201.

Allen, J.R.L., Williams, B.P.J., 1981. Sedimentology and stratigraphy of the Townsend Tuff Bed (Lower Old Red Sandstone) in South Wales and the Welsh Borders. Journal of the Geological Society, London 138, 15–29.

Barclay, W.J., Davies, J.R., Hiller, R.D., Waters, R.A., 2015. Lithostratigraphy of the Old Red Sandstone successions of the Anglo-Welsh Basin. British Geological Survey Research Report, RR/14/02. 96 pp.

Baucon, A., Venturini, C., de Carvalho, C.N., Felletti, F., Muttoni, G., 2015. Behaviors mapped by new geographies: ichnonetwork analysis of the Val Dolce Formation (lower Permian; Italy-Austria). Geosphere 11, 744–776.

Benton, M.J., 1982. *Dictyodora* and associated trace fossils from the Palaeozoic of Thuringia. Lethaia 15, 115–132.

Bjerstedt, T.W., 1988. Multivariate analyses of trace fossil distribution from an early Mississippian oxygen-deficient basin, Central Appalachians. Palaios 3, 53–68.

Bluck, B.J., 2000. Old Red Sandstone basins and alluvial systems of Midland Scotland. In: Friend, P.F., Williams, B.P.J. (Eds.), New Perspectives on the Old Red Sandstone, 180. Special Publications, Geological Society London, pp. 417–437.

Bluck, B.J., 2002. The Midland Valley terrane, In: Trewin, N. (Ed.), Geology of Scotland. 4th edn Geological Society, London, pp. 149–166.

Bluck, B.J., 2010. The Highland Boundary Fault and the Highland Border Complex. Scottish Journal of Geology 46, 113–124.

Bradshaw, M.A., 1981. Paleoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (lower Beacon Supergroup), Antarctica. New Zealand Journal of Geology and Geophysics 24, 615–652.

Bradshaw, M.A., 2010. Devonian trace fossils of the Horlick Formation, Ohio Range, Antarctica: systematic description and palaeoenvironmental interpretation. Ichnos 17, 58–114.

Bridge, J.S., Gordon, E.A., Titus, R.C., 1986. Non-marine bivalves and associated burrows in the Catskill magnafacies (Upper Devonian) of New York State. Palaeogeography, Palaeoclimatology, Palaeoecology 55, 65–77.

British Geological Survey, 1999. Stonehaven, Scotland Sheet 67, Solid and Drift Geology, 1:50,000. British Geological Survey, Keyworth, Nottingham.

British Geological Survey, 2017. Borehole Scans. . http://mapapps.bgs.ac.uk/geologyofbritain/home.html.

Browne, M.A.E., Smith, R.A., Aitkin, A.M., 2002. Stratigraphical framework for the Devonian (Old Red Sandstone) rocks of Scotland south of a line from Fort William to Aberdeen. British Geological Survey Research Report RR/01/04. 67 pp.

Bruck, P.M., Forbes, W.H., Nance, D., Pickerill, R.K., 1985. Beaconites antarcticus in the (?Middle) Late Devonian McAras Brook Formation, Cape George, Nova Scotia. Maritime Sediments and Atlantic Geology 21, 87–96.

Buatois, L.A., Mangano, M.G., Genise, J.F., Taylor, T.N., 1998. The ichnologic record of the continental invertebrate invasion; evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity. Palaios 13, 217–240.

Campbell, R., 1911. Preliminary note on the geology of south-eastern Kincardineshire. Geological Magazine 8, 63–69.

Campbell, R., 1912. Cambrian, Downtonian and Lower Old Red Sandstone rocks near Stonehaven. Proceedings of the Geologists' Association 23 (291–294), 297–298.

Campbell, R., 1913. The geology of northeastern Kincardineshire. Transactions of the Royal Society, Edinburgh 48, 1–37.

Carroll, S., 1995. Geology of the Stonehaven district. British Geological Survey Technical Report WA/94/19, 4–6.

Chamberlain, C.K., 1971. Morphology and ethology of trace fossils from the Ouachita Mountains, Southeast Oklahoma. Journal of Palaeontology 45, 212–246.

Crimes, T.R., Garcia Hidalgo, J.F., Poire, D.G., 1992. Trace fossils from arenig flysch sediments of eire and their bearing on the early colonisation of the deep seas. Ichnos 2, 61–77.

Crowley, S.F., Higgs, K.T., Piper, J.D.A., Morrissey, L.B., 2009. Age of the Peel Sandstone Group, Isle of Man. Geological Journal 44, 57–78.

D'Alessandro, A., Bromley, R.G., 1987. Meniscate trace fossils and the *Muensteria-Taenidium* problem. Palaeontology 30, 743–763.

D'Alessandro, A., Bromley, R.G., Loiacono, F., 1993. Marine and nonmarine trace fossils and plant roots in a regressional setting (Pleistocene, Italy). Rivista Italiana Di Paleontologia E Stratigrafia 98, 495–521.

Davies, N.S., Turner, P., Sansom, I.J., 2005. A revised stratigraphy for the Ringerike Group (Upper Silurian, Oslo Region). Norwegian Journal of Geology 85, 193–201.

Davies, N.S., Sansom, I.J., Turner, P., 2006. Trace fossils and paleoenvironments of a late Silurian Marginal-Marine/Alluvial System: the Ringerike Group (Lower Old Red Sandstone), Oslo Region, Norway. Palaios 21, 46–62.

Davies, N.S., Liu, A.G., Gibling, M.R., Miller, R.F., 2016. Resolving MISS conceptions and misconceptions: a geological approach to sedimentary surface textures generated by microbial and abiotic processes. Earth Science Reviews 154, 210–246.

Dineley, D.L., 1999a. Silurian fossil fishes sites of Scotland. In: Dineley, D.L., Metcalf, S.J. (Eds.), Fossil fishes of Great Britain. Joint Nature Conservation Committee, Peterborough, pp. 31–62.

Dineley, D.L., 1999b. Early Devonian fossil fishes sites of Scotland. In: Dineley, D.L., Metcalf, S.J. (Eds.), Fossil fishes of Great Britain. Joint Nature Conservation Committee, Peterborough, pp. 145–165.

Donovon, S.K., Lewis, D.N., 2008. A conundrum from the Llandovery (Lower Silurian) of Devil's Dingle, Shropshire. Proceedings of the Yorkshire Geological Society 57, 75-78.

Draganits, E., Braddy, S.J., Briggs, D.E.G., 2001. A Gondwanan Coastal Arthropod Ichnofauna from the Muth Formation (Lower Devonian, Northern India): paleoenvironment and Tracemaker Behavior. Palaios 16, 126–147.

Egenhoff, S.O., Weber, B., Lehnert, O., Maletz, J., 2007. Biostratigraphic precision of the Cruziana rugosa group: a study from the Ordovician succession of southern and central Bolivia. Geological Magazine 144, 289–303.

Fan, R., Gong, Y., 2016. Ichnological constraints of palaeoenvironmental and palaeoclimatological features of the middle Palaeozoic Palaeo-Asian Ocean, evidence from the western Junggar, NW China. Palaeogeography, Palaeoclimatology, Palaeoecology 459, 209–228.

Fillmore, D.L., Lucas, S.G., Simpson, E.L., 2010. Invertebrate trace fossils in semi-arid to arid braided-ephemeral-river deposits of the Mississippian middle member of the Mauch Chunk Formation eastern Pennsylvania, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 292, 222–244.

Friend, P.F., Williams, B.P.J. (Eds.), 2000. New Perspectives on the Old Red Sandstone. Special Publications, Geological Society London, pp. 180.

Gand, G., Kerp, H., Parsons, C., Martinez-Garcia, E., 1997. Palaeoenvironmental and stratigraphic aspects of animal traces and plant remains in Spanish Permian red beds (Pefia Sagra Cantabrian Mountains, Spain). GEOBIOS 30, 295–318.

George, A.D., 1994. Tidal sedimentation in part of the Late Silurian Grampians Basin, southeastern Australia. Journal of Sedimentary Research B64, 311–325.

Germs, G.J.B., 1972. Trace Fossils from the Nama Group: South-West Africa. Journal of Palaeontology 46, 864–870.

Goldring, F., Pollard, J.E., 1995. A re-evaluation of Ophiomorpha burrows in the Wealden Group (Lower Cretaceous) of southern England. Cretaceous Research 16, 665–680.

Gouramanis, C., McLoughlin, S., 2016. Siluro-Devonian trace fossils from the Mereenie Sandstone, Kings Canyon, Watarrka National Park, Amadeus Basin, Northern Territory, Australia. Alcheringa: An Australasian Journal of Palaeontology 40, 118–128.

Gouramanis, C., Webb, J.A., Warren, A.A., 2003. Fluviodeltaic sedimentology and ichnology of part of the Silurian Grampians Group, western Victoria. Australian Journal of Earth Sciences 50, 811–825.

Graham, J.R., Pollard, J.E., 1982. Occurrence of the trace fossil Beaconites antarcticus in the Lower Carboniferous fluviatile rocks of County Mayo Ireland. Palaeogeography, Palaeoclimatology, Palaeoecology 38, 257–268.

Hakes, W.G., 1976. Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, Northeast Kansas. University of Kansas Palaeontological Contributions 63, 1–11.

Han, Y., Pickerill, R.K., 1994. Palichnology of the Lower Devonian Wapske Formation, Perth-And over-Mount Carleton region, northwestern New Brunswick, eastern Canada. Atlantic Geology 30, 217–245.

Häntzschel, W., 1975. Treatise on Invertebrate Palaeontology: Miscellanea, Supplement 1. Part W. Geological Society of America.

Hartley, A.J., Leleu, S., 2015. Sedimentological constraints on the late Silurian history of the Highland Boundary Fault, Scotland: implications for Midland Valley Basin development. Journal of the Geological Society 172, 213–217.

Heer, O., 1877. Flora Fossilis Helvetiae: Die vorweltliche flora der Schweiz. J. Wurster & co. 182 pp.

Hunter, M.A., Lomas, S.A., 2003. Reconstructing the Siluro-Devonian coastline of Gondwana: insights from the sedimentology of the Port Stephens Formation, Falkland Islands Journal of the Geological Society. London 160, 459–476.

Keighley, D.G., Pickerill, R.K., 1994. The ichnogenus Beaconites and its distinction from Ancorichnus and Taenidium. Palaeontology 37, 305–337.

Knaust, D., 2004. Cambro-Ordovician trace fossils from the SW-Norwegian Caledonides. Geological Journal 39, 1–24.

Kulkarni, K.G., Borkar, V.D., 2014. Ichnofauna from the Harbans Bed of the Badhaura Formation (Sterlitmakian), Rajasthan, India. Journal of Earth System Science 123, 421–432.

Kumpulainen, R.A., Uchman, A., Woldehaimanot, B., Kreuser, T., Ghirmay, S., 2006. Trace fossil evidence from the Adigrat Sandstone for an Ordovician glaciation in Eritrea, NE Africa. Journal of African Earth Sciences 45, 408–420.

Lavender, K., Wellman, C.H., 2002. Lower Devonian spore assemblages from the Arbuthnott Group at Canterland Den in the Midland Valley of Scotland. Review of Palaeobotany and Palynology 118, 157–180.

Loydell, D.K., Frýda, J.I.Ø.Í., 2011. At what stratigraphical level is the mid Ludfordian (Ludlow Silurian) positive carbon isotope excursion in the type Ludlow area, Shropshire, England. Bulletin of Geosciences 86, 197–208.

Mángano, M.G., Buatois, L.A., 2016. The Cambrian explosion. In: Mángano, M.G., Buatois, L.A. (Eds.), The Trace-Fossil Record of Major Evolutionary Events Volume 1: Precambrian and Paleozoic. Springer International Publishing, Dordrecht, pp. 73–126.

Maples, C.G., Archer, A.W., 1987. Redescription of early Pennsylvanian trace-fossil holotypes from the Nonmarine Hindostan Whetstone Beds of Indiana. Journal of Palaeontology 61, 890–897.

Maples, C.G., Suttner, L.J., 1990. Trace fossils and marine-nonmarine cyclicity in the Fountain Formation (Pennsylvanian: Morrowan/Atokan) near Manitou Springs, Colorado. Journal of Palaeontology 64, 859–880.

Marriott, S.B., Hillier, R.D., Morrissey, L.B., 2013. Enigmatic sedimentary structures in the Lower Old Red Sandstone, south Wales, UK: possible microbial influence on surface processes and early terrestrial food webs. Geological Magazine 150, 396–411.

Marshall, J.E.A., 1991. Palynology of the Stonehaven Group, Scotland: evidence for a Mid Silurian age and its geological implications. Geological Magazine 128, 283–286.

Marshall, J.E.A., Haughton, P.D.W., Hillier, S.J., 1994. Vitrinite reflectivity and the structure and burial history of the Old Red Sandstone of the Midland Valley of Scotland. Journal of the Geological Society, London 151, 425–438.

Martino, R.L., 1989. Trace Fossils from marginal marine facies of the Kanawha Formation (Middle Pennsylvanian), West Virginia. Journal of Palaeontology 63, 389–403.

Mikulas, R., 1993. New information on trace fossils of the Early Ordovician of Prague Basin (Barrandian area, Czech Republic). Journal of the Czech Geological Society 38, 171–182.

Minter, N.J., Krainer, K., Lucas, S.G., Braddy, S.J., Hunt, A.P., 2007. Palaeoecology of an Early Permian playa lake trace fossil assemblage from Castle Peak Texas, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 246, 390–423.

Minter, N.J., Buatois, L.A., Mángano, M.G., Davies, N.S., Gibling, M.R., Labanderia, C., 2016. The establishment of Continental ecosystems. In: Mángano, M.G., Buatois, L.A. (Eds.), The Trace-Fossil Record of Major Evolutionary Events Volume 1: Precambrian and Paleozoic. Springer International Publishing, Dordrecht, pp. 205–324.

Minter, N.J., Buatois, L.A., Mangano, M.G., Davies, N.S., Gibling, M.R., MacNaughton, R.B., Labandeira, C.C., 2017. Early bursts of diversification defined the faunal colonization of land. Nature Ecology and Evolution 1, 0175.

Morrissey, L.B., Braddy, S.J., 2004. Terrestrial trace fossils from the Lower Old Red Sandstone southwest Wales. Geological Journal 39, 315–336.

Morrissey, L.B., Hillier, R.D., Marriott, S.B., 2012a. Late Silurian and Early Devonian terrestrialisation: Ichnological insights from the Lower Old Red Sandstone of the Anglo-Welsh Basin U.K. Palaeogeography, Palaeoclimatology, Palaeoecology 337–338, 194–215.

Morrissey, L.B., Braddy, S.J., Dodd, C., Higgs, K.T., Williams, B.P.J., 2012b. Trace fossils and palaeoenvironments of the Middle Devonian Caherbla Group, Dingle Peninsula, southwest Ireland. Geological Journal 47, 1–29.

Narbonne, G.M., 1984. Trace fossils in Upper Silurian Tidal Flat to Basin Slope Carbonates of Arctic Canada. Journal of Palaeontology 58, 398–415.

Oliver, G.J.H., Wilde, S.A., Wan, Y., 2008. Geochronology and geodynamics of Scottish granitoids from the late Neoproterozoic break-up of Rodinia to Palaeozoic collision. Journal of the Geological Society, London 165, 661–674.

O'Sullivan, M.J., Cooper, M.A., MacCarthy, A.J., Forbes, W.H., 1986. The palaeoenvironment and deformation of Beaconites-like burrows in the Old Red Sandstone at Gortnabinna, SW Ireland. Journal of the Geological Society, London 143, 897–906.

Paterson, I.B., Harris, A.L., 1969. Lower Old Red Sandstone Ignimbrites from Dunkeld, Perthshire. Institute of Geological Sciences Report 69/7.

Pearson, P.N., 1992. Walking traces of the giant myriapod Arthropleura from the Strathclyde Group (Lower Carboniferous) of Fife. Scottish Journal of Geology 28, 127–133.

Pickerill, R.K., 1991. The trace fossil Neonereites multiserialis Pickerill and Harland, 1988 from the Devonian Wapske Formation, northwest New Brunswick. Atlantic Geology 27, 119–126.

Pickerill, R.K., 1992. Carboniferous nonmarine invertebrate ichnocoenoses from southern New Brunswick eastern Canada. Ichnos 2, 21–35.

Pickerill, R.K., Fyffe, L.R., Forbes, W.H., 1987. Late Ordovician-Early Silurian trace fossils from the Matapedia Group Tobique River, western New Brunswick, Canada. Maritime Sediments and Atlantic Geology 23, 77–88.

Pickerill, R.K., Romano, M., Melendez, B., 1984. Arenig trace fossils from the Salamanca area western Spain. Geological Journal 19, 249–269.

Prescott, Z.M., Stimson, M.R., Dafoe, L.T., Gibling, M.R., Macrae, R.A., Calder, J.H., Hebert, B.L., 2014. Microbial mats and ichnofauna of a fluvial-tidal channel in the Lower Pennsylvanian Joggins Formation, Canada. Palaios 29, 624–645.

Qi, Y., Wang, M., Zheng, W., Li, D., 2012. Calcite Cements in Burrows and Their Influence on Reservoir Property of the Donghe Sandstone, Tarim Basin, China. Journal of Earth Science 23, 129–141.

Salter, J.W., 1857. On annelide-burrows and surface-markings from the Cambrian rocks of the Longmynd, No. 2. Quarterly Journal of the Geological Society of London 13, 199–206.

Savoy, L.E., 1992. Environmental record of Devonian-Mississippian carbonate and low-oxygen facies transitions, southernmost Canadian Rocky Mountains and northwesternmost Montana. Geological Society of America Bulletin 104, 1412–1432.

Seilacher, A., 2007. Trace fossil analysis. Springer Science & Business Media.

Shear, W.A., 1993. Myriapodous arthropods from the Viséan of East Kirkton, West Lothian, Scotland. Earth and Environmental Science Transactions of The Royal Society of Edinburgh 84, 309–316.

Shear, W., Selden, P., 1995. Eoarthropleura (Arthropoda, Arthropleurida) from the Silurian of Britain and the Devonian of North America. Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen 196, 347–376.

Shear, W.A., Edgecombe, G.D., 2010. The geological record and phylogeny of the Myriapoda. Arthropod Structure and Development 39, 174–190.

Shear, W.A., Jeram, A.J., Selden, P., 1998. Centiped legs (Arthropoda, Chilopoda, Scutigeromorpha) from the Silurian and Devonian of Britain and the Devonian of North America. American Museum Novitates 3231.

Smith, R.M.H., 1993. Sedimentology and ichnology of floodplain paleosurfaces in the Beaufort Group (Late Permian) Karoo Sequence, South Africa. Palaios 8, 339–357.

Stachacz, M., 2012. Ichnology of Czarna Shale Formation (Cambrian, Holy Cross Mountains, Poland). Annales Societatis Geologorum Poloniae 82, 105–120.

Stephenson, D., Gould, D., 1995. British Regional Geology: the Grampian Highlands, 4th edition HMSO for the British Geological Survey, London.

Suarez, S.E., Brookfield, M.E., Catlos, E.J., Stöckli, D.F., 2017. A U-Pb zircon age constraint on the oldest-recorded air-breathing land animal. PLoS One 12, e0179262.

Tanner, G., 2008. Tectonic significance of the Highland Boundary Fault, Scotland. Journal of the Geological Society, London 165, 915–921.

Tanoli, S.K., Pickerill, R.K., 1989. Cambrian shelf deposits of the King Square Formation, Saint John Group, southern New Brunswick. Atlantic Geology 25, 129–141.

Thirlwall, M.F., 1988. Geochronology of Late Caledonian magmatism in northern Britain. Journal of the Geological Society, London 145, 951–967.

Thomas, A.T., Smith, M.P., 1998. Terebellid polychaete burrows from the lower Palaeozoic. Palaeontology 41, 317–333.

Trench, A., Haughton, P.D., 1990. Palaeomagnetic and geochemical evaluation of a terrane-linking ignimbrite: evidence for the relative position of the Grampian and Midland Valley terranes in late Silurian time. Geological Magazine 127, 241–257.

Trewin, N.H. (Ed.), 2002. The Geology of Scotland. The Geological Society, London.

Trewin, N.H., 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.

Tunbridge, I.P., 1984. Facies model for a sandy ephemeral stream and clay playa complex; the Middle Devonian Trentishoe Formation of North Devon, U.K. Sedimentology 31, 697–715.

Virtasalo, J.J., Bonsdorff, E., Moros, M., Kabel, K., Kotilainen, A.T., Ryabchuk, D., Kallonen, A., Hamalainen, K., 2011. Ichnological trends along an open-water transect across a large marginal-marine epicontinental basin, the modern Baltic Sea. Sedimentary Geology 241, 40–51.

Weber, B., Braddy, S.J., 2004. A marginal marine ichnofauna from the Blaiklock Glacier Group (?Lower Ordovician) of the Shackleton Range, Antarctica. Transactions of the Royal Society of Edinburgh: Earth Sciences 94, 1–20.

Wellman, C.H., 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven Group, Scotland. Journal of Micropalaeontology 12, 47–66.

Wilson, H.M., 2005. Zosterogrammida, a new order of millipedes from the Middle Silurian of Scotland and the Upper Carboniferous of Euramerica. Palaeontology 48, 1101–1110.

Wilson, H.M., Anderson, L.I., 2004. Morphology and Taxonomy of Paleozoic Millipedes (Diplopoda: Chilognatha: Archipolypoda) from Scotland. Journal of Palaeontology 78, 169–184.