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Spontaneous Article

Placing the Scottish Romer's Gap tetrapods within a Tournaisian time frame

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ABSTRACT: A number of early tetrapods occur in different localities from the Ballagan Formation in Scotland. These localities are within the 12 Myr time duration of the Tournaisian so it is important to be able to place them within a chronology to better understand the evolutionary relationships of the tetrapods. Palynology is used to recognise distinct assemblages in the Norham West Mains Farm borehole and the Burnmouth coastal section which become a composite standard. The Willie's Hole tetrapods (*Koilops*, *Mesanerpeton* and *Perittodus*) come from the lower part of the Ballagan Formation with Auchenreoch Glen (*Pederpes*) somewhat higher. The oldest tetrapods are from the Harbour beds at Burnmouth with the Ross end cliffs tetrapods (*Aytonerpeton*, *Diploradus* and *Ossirarus*) the youngest assemblage. It is not possible to place the Coldstream tetrapods as the spore assemblage is low diversity. *Tantallognathus* from Tantallon is early Viséan in age. *Occidens portlocki*, an isolated partial tetrapod jaw from a historic collection in Northern Ireland, is not of Tournaisian age and hence not from within Romer's Gap, but it can be dated as Brigantian (latest Viséan) age. The other significant Romer's Gap locality from Blue Beach, Nova Scotia, Canada, is different in age span and palaeoenvironment.

KEYWORDS: Ballagan Formation, Carboniferous, palynology, spore assemblage.

It is now evident that the Tournaisian of Scotland contains the earliest and most diverse record of tetrapods through Romer's Gap, as it includes eight named species plus at least four in the process of being described. These all occur within the Ballagan Formation, an apparently monotonous sequence of fine-grained clastic sediments with distinctive dolostones (historically referred to as cementstones). Its maximum proven thickness is 520 m (Millward *et al.* 2018) and it is effectively equivalent to the Tournaisian Stage with a duration of some 12 Myr (Aretz *et al.* 2020). So, an immediate question is how to place these tetrapods within a time framework. This is particularly problematic as the Ballagan Formation is depauperate in age-diagnostic fauna that are generally limited to bivalves, ostracods, rare lingulids and orthocone nautiloids. There are pollen and spores within the Ballagan Formation, but these have commonly been regarded as similarly monotonous (Neves *et al.* 1973) with few inceptions and are represented by the single (CM) spore zone. However, significant progress was made during the TW:eed Project, with detailed description of palynological assemblages from the Norham West Mains Farm cored borehole (BGS registered borehole number NT94NW20) that penetrated almost the entirety of the Ballagan Formation. This was complemented by a parallel study of the near-vertical coastal section from Burnmouth (Smithson *et al.* 2012; Marshall *et al.* 2019) that identified a series of spore inceptions in the lower part of the sequence which could be correlated with Irish and Polish Tournaisian sections. This allowed the placement of the bases of the VI, HD and Cl 1 spore zones.

The main Tournaisian tetrapod localities (Fig. 1) are from Auchenreoch Glen, north of Dumbarton at the northwestern end of the Midland Valley of Scotland. This is where the only specimen of *Pederpes* has been found. In the Tweed Basin there are tetrapods from Willie's Hole along the Whiteadder Water, two localities on the coast section at Burnmouth, the partial jaw *Tantallognathus* from Tantallon, and the as yet undescribed tetrapods from Coldstream on the Scottish Border. To this can be added the putative Romer's Gap tetrapod *Occidens* from the historic Portlock collection in Northern Ireland.

1. Palynological processing

The palynological processing was carried out using standard methodologies with 5 g of sample roughly crushed to about a mm in size and then treated with 30 ml of 37 % HCl to remove carbonates. The samples were then decant-washed to neutral to remove any mobilised Ca^{2+} and Mg^{2+} that would subsequently precipitate as an insoluble residue when treated with hydrofluoric acid (HF). The sample was then treated with 30 ml of

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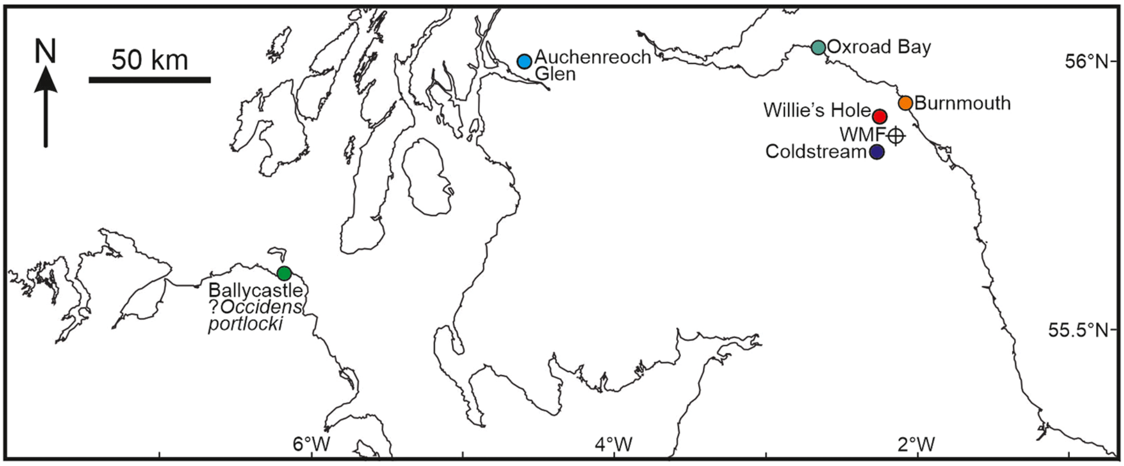

Figure 1 Map showing location of the Scottish Ballagan Formation tetrapod locations of Tournaisian age. Also shown is an inferred location at Ballycastle for the tetrapod jaw *Occidens portlocki* from Northern Ireland. Source: GMT using Python.

60 % HF to dissolve silicate minerals, followed again by decant-washing to neutral. The residue was then sieved over a 15 m mesh with the coarse fraction washed into a glass beaker, allowed to settle and the water decanted off. To this was added 60 ml of 37 % HCl and the solution was briefly boiled using a Bunsen burner. This solubilised any neoformed fluorides. Initially the organic residue is bound with the neoformed fluoride and denser than the HCl solution. As the temperature gets close to boiling, the neoformed fluorides go into solution and the organic matter floats to the top of the beaker. The contents of the beaker are then transferred into about 100 ml of water to dilute the solution sufficiently to be resieved through a 15 m nylon mesh without dissolving it. This process is far more effective in removing neoformed fluorides than any heavy liquid separation as the organic matter (post HF treatment) is intricately bound into the neoformed fluorides. Hence, the components of different density are not independent entities. The residue was then transferred onto a small 15 m sieve and flushed through with MilliQ water and pipetted in a vial. Strew slides were made by evaporating a suspension of the organic matter concentrate in MilliQ water onto 26 × 22 mm coverslips, allowed to dry overnight and then permanently mounted in Elvacite 2044™. The Elvacite was made up with analytical grade xylene so as not to have any trace benzene within the mounting medium. No oxidation (in 65 % HNO_3) was required as the spores were yellow to pale brown in colour and with negligible pyrite. Amorphous organic matter (AOM) was present in a few samples and removed by a 30 s treatment with a Sonics and Materials ultrasonic probe. This preferentially fragments the AOM that can then be removed as a fine fraction by further sieving at 15 m. The vialed residue was also top-sieved at 150 m with the coarse residue mounted to concentrate any megaspores. For selected samples, from Tantallon and Coldstream, the <150 m residue was also mounted to increase the number of spores present that would otherwise be diluted by the high phytoclast content. The Coldstream samples were dominated by the small spore *Anaplanisporites baccatus*, so the <150 m was sieved at 35 m with the 35–150 m fraction mounted in an attempt to increase the diversity of spores recovered. The slides were investigated using an Olympus BHS 313 microscope (230272) and quantitative counts made of over 200 spores on a series of mid coverslip traverses using a ×40 objective. The remainder of the slide was scanned at lower magnification (×20 objective) and any additional species recorded as out of count.

The sub gram fragment of mudstone taken from the partial tetrapod jaw *Occidens portlocki* (BGS number GSM 28498) posed a significant challenge in palynological processing. It was treated with 37 % HCl, decant-washed and then treated with 60 % HF followed by decant-washing to neutral. It was then sieved at 15 m. There was a small component of neoformed fluoride which was left in the samples as every cycle of sieving resulted in the loss of a significant proportion of the sample via processes such as surface tension creep. All the resulting thin residue was mounted in Elvacite 2044 on five 18 mm^2 coverslips. Special care was taken to avoid cross-contamination. At the time, the processing lab was not running any Carboniferous samples; those going through in the same weeks were from the Middle Devonian and Jurassic–Cretaceous boundary. It is also important to be aware that, sometimes, specimens are stabilised and repaired using powdered rock from other formations selected to match the colour of the original matrix.

2. *Pederpes finneyae*, Auchenreoch Glen

Pederpes finneyae was obtained from a single nodule at the top of the Ballagan Formation section in Auchenreoch Glen at NS 241827, 678323. It was collected in 1971 and initially identified as a fish, so it was not until it was reassigned to the tetrapods (Clack & Finney 2005) that its importance was realised. Hence, there was little attempt immediately following collection to obtain further information or material apart from the field sketch made during its discovery by Aspen (Fig. 3A in Clack & Finney, 2005). The section (Fig. 2, top) is best approached along the Garshake Road to the road end and then by following the path before cutting diagonally across the Auchenreoch Muir to the southern lip of the glen, which can then be descended northwestwards down the somewhat precipitous spur to its confluence with the Murroch Burn. The section is then accessed by climbing the waterfall that occupies the narrow cleft (formerly the Gates of Sodom (e.g., Anon 1862) and subsequently Adam's Gate (Lees 1933) but referred to as the Gates of Eden in Clack & Finney (2005)) made by the Murroch Burn as it cut down through a prominent dyke. The section was vertically logged (Fig. 3) from NS 241822, 678363 to 241827, 678323. These end points have a vertical GPS altimeter height difference of 34 m that tallies well with the 28 m of directly measured thickness but contrasts with the estimated 44 m of section in Clack & Finney (2005).

The total thickness of the Ballagan Formation in the Dumbarton area is estimated at 140 m (Paterson *et al.* 1990). Its base is transitional from the underlying sandstone of the Kinnesswood Formation and it passes vertically upwards into the Clyde Sandstone Formation. As such it represents only

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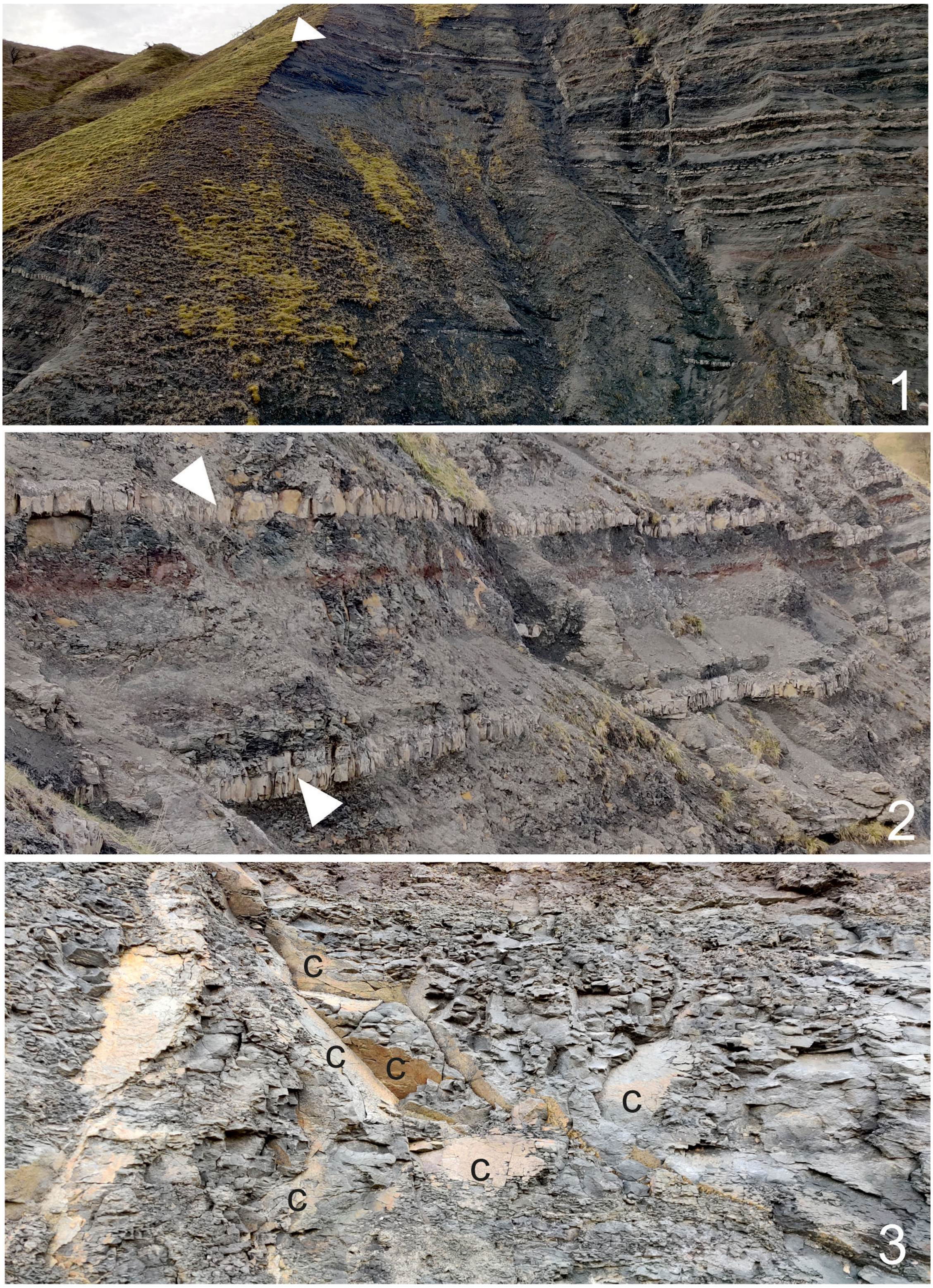

Figure 2 Location photographs of the Ballagan Formation exposure at Auchenreoch Glen, Dunbartonshire. (1) The cliff of the main exposure with the two prominent cemenstones marked. It was between these two dolostones that the nodule containing the tetrapod *Pederpes finneyae* was found. (2) Close-up of the two dolostones; note the red palaeosol in the upper part. (3) The arcuate crack sets (c) that are confined to the interval between the two prominent dolostones and together with the bleached colour confirm the interval as a vertisol. These exposures are difficult to image because of the precipitate nature of the exposure.

about 20 % of the >500 m thickness proven in the Tweed Basin (Millward *et al.* 2018). The logged section is entirely typical of the Ballagan Formation, comprising grey-coloured siltstones and mudstones interbedded with interesting dolostones that are generally 10 to 30 cm thick and which can range from continuous beds to lines of nodules. The section includes (Fig. 3, between 10–15 m) a maroon-coloured palaeosol doublet separated by four conspicuous nodule beds and gypsiferous ribs. The 2.05 m thick bed at 26.7 m (Fig. 2, middle) that included the nodule with *Pederpes* is between two conspicuously thicker continuous cementstone beds. It is mottled buff grey to red in colour and restricted within it are numerous sub-vertical inclined cracks characteristic of a vertisol palaeosol (Fig. 2, bottom). The uppermost part of the palaeosol is reddened. Vertisols are distinctive palaeosols (Kovda 2020) that represent sustained aridity under a relatively inactive climate system with

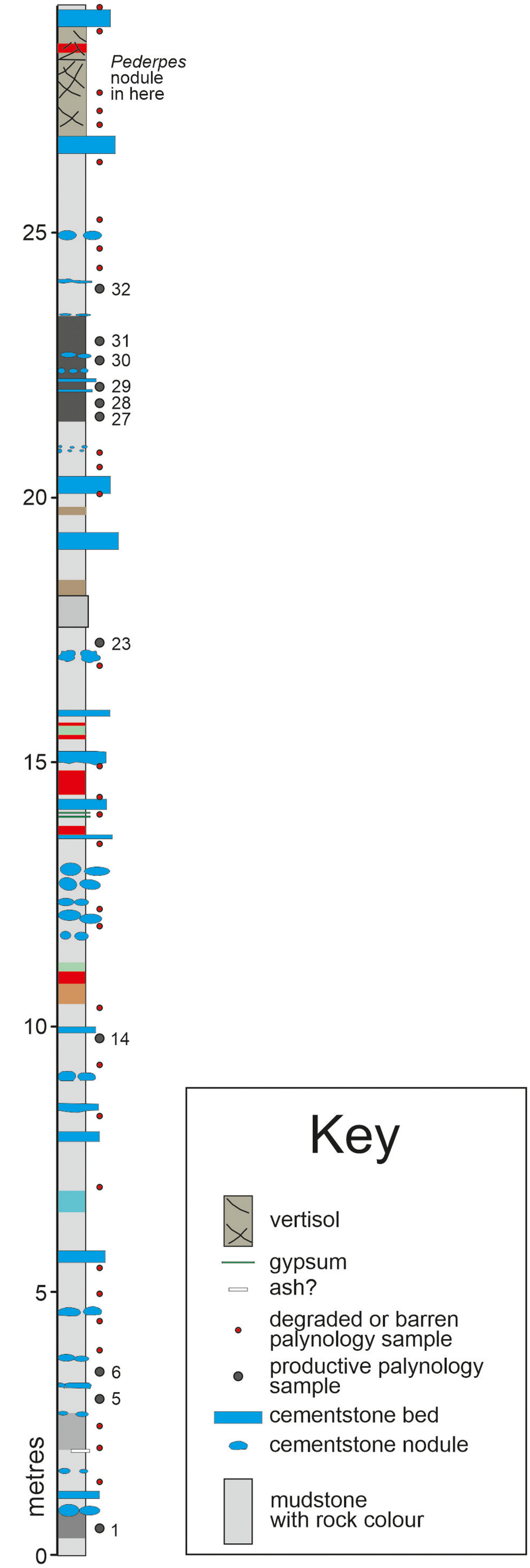

Figure 3 Logged Ballagan Formation section from Auchenreoch Glen showing location of palynological samples and position of *Pederpes*.

a low relative P/E ratio. The palaeoclimatic indicators through the logged section are all indicative of aridity apart from at 21.4 m where there is a 0.5 m thick interval of black mudstone representing an interval of wetter conditions.

The Auchenreoch Glen section contains some 33 cementstone layers in 28 m of total section giving a count of 11 dolostones per 10 m of section. This is the effective average number (Bennett *et al.* 2021) for the West Mains Farm borehole and the Burnmouth section. It shows that the section at Auchenreoch, on the northwestern side of the Midland Valley, is not obviously condensed (Millward *et al.* 2018) and represents a fraction of rather than the entire thickness of the Ballagan Formation.

Forty-one samples were collected (Fig. 3) and these were all palynologically processed. Only three samples were entirely barren, being devoid of organic matter. Of the remaining samples, 27 contained only degraded phytoclast debris and spores. It is unclear whether palynomorphs were lost from these samples through contemporaneous oxidation in the arid climates of the Ballagan Formation or from recent weathering. It is presumed to be a combination of both. The remaining 11 samples contained well-preserved spores suitable for identification, although none were from or immediately above or below the *Pederpes* level. This sporadic palynological recovery from what was a carefully selected suite of samples by an experienced collector emphasises that successful palynological recovery in the Ballagan Formation requires significant numbers of spot samples and that these must all be processed for palynomorphs.

2.1 Auchenreoch Glen palynological assemblage

The recovered palynological assemblages (Supplementary Information available at https://doi.org/10.1017/S1755691024000100) were entirely typical of the Ballagan Formation in being dominated by simple smooth and apiculate spores, including *Schopfites claviger* and *Retusotriletes incohatus.* More complex abundant spores include *Colatisporites decorus*, *Auroraspora macra* and *Anaplanisporites baccatus*. There are also a number of distinctive spores, generally present in most samples but out of count (i.e., much less than 1 %). These include *Knoxisporites* (*K. literatus* and *K. triangulatus*), *Vallatisporites* spp., *Spelaeotriletes* spp., *Velamisporites polyptycha*, *Convolutispora* (*C. major* and *C. permixta*) and *Remysporites magnificus*.

Megaspores are sporadically present in the standard palynological preparations as the isolated spines of *Setispora*. There are also isolated single and paired megaspores of *Didyomosporites scottii*. The single specimens can be identified by the presence of an adhering much smaller abortive spore (Chaloner 1958; Fig. 4, 31) which includes its own small trilete mark.

Apart from spores, the chlorophytean alga *Botryococcus* was present, and particularly abundant at the base of the black mudstone at 22 m (sample Auch-31), with this interval also containing rare specimens of *Chomotriletes* that is now known to be an euglenoid (van der Schootbrugge *et al.* 2024). No scolecodonts (the jaws of marine and marginal marine annelid worms) were found.

This assemblage from the Auchenreoch section offers the same challenge as found in all Ballagan Formation palynological assemblage in that it is apparently monotonous and with few evident inceptions. In addition, the section is in the northwestern part of the Midland Valley distant from all the detailed palynological information collected during the TW:eed Project. The lower part of the Ballagan Formation at Burnmouth contains the bases of the VI and HD spore zones. As the

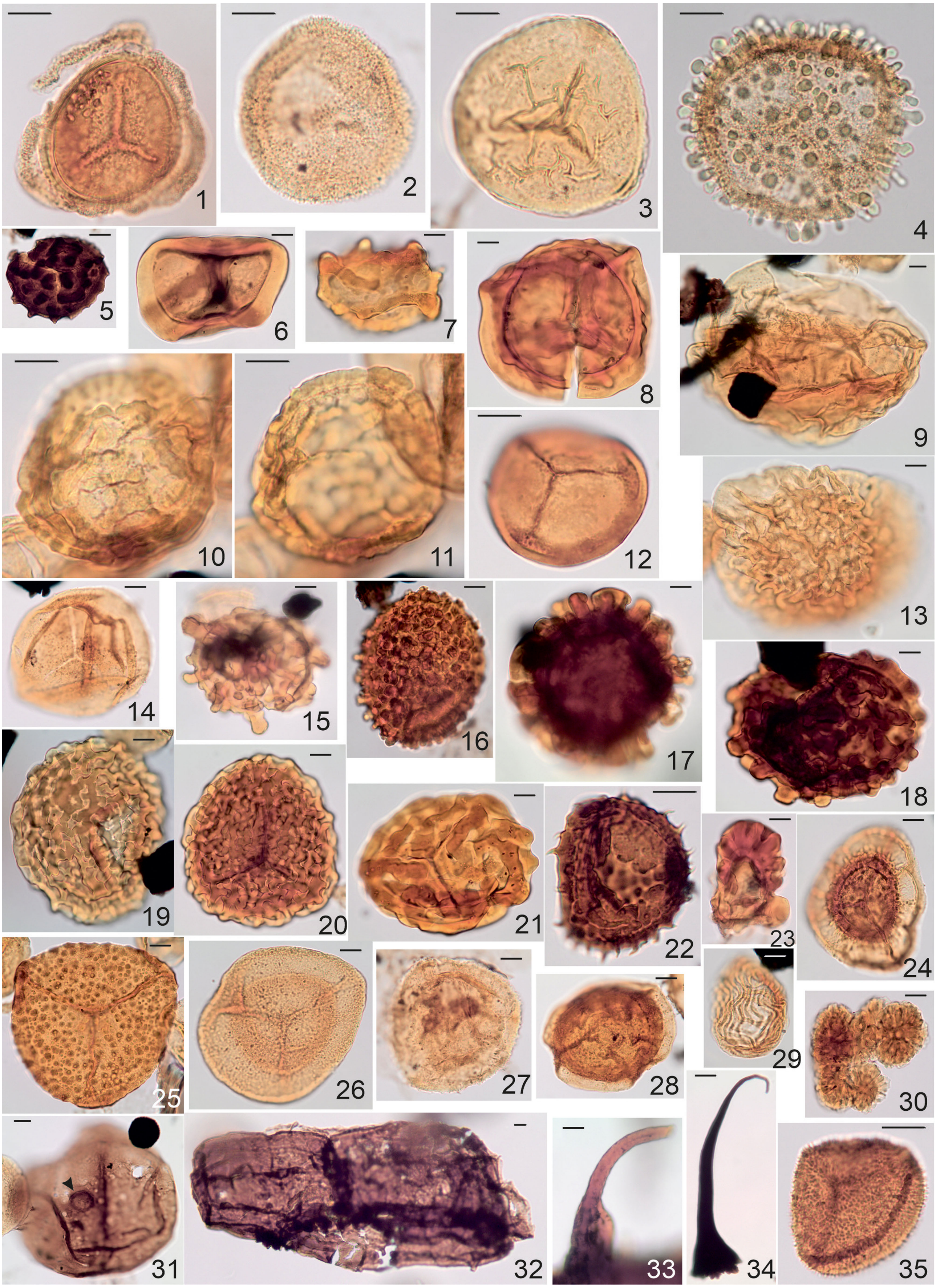

Figure 4 Illustration of important stratigraphic spores from the Ballagan Formation tetrapod localities. All figured spores are in the palynology collections of the British Geological Survey, Keyworth. Microscope co-ordinates refer to Olympus BHS-313 No. 230272 in the School of Ocean and Earth Science, University of Southampton. England Finder co-ordinates (e.g., R20-3) are also provided. Scale bars are all 10 m. **1.** *Auroraspora macra* Auch-31.2 117.7, 18.3 (J17-1). **2.** *Colatisporites decorus* Auch-31.2 131.9, 11.7 (Q31-2). **3.** *Plicatispora scolecophora* Auch-31.2 122.0, 8.2 (T21-3). **4.** *Schopfites claviger* Auch-31.2 133.0, 6.9 (V32-2). **5.** *Pustulatisporites gibberosus* Auch-23 111.7, 11.1 (Q10-4). **6.** *Knoxisporites triangulatus* Auch-31.2 109.3, 5.8 (W8-1). **7.** *Knoxisporites concentricus* oblique compression Auch-28 120.9, 6.0 (W20-1). **8.** *Knoxisporites literatus* Auch-31 132.4, 11.3 (Q32-3). **9.** *Remysporites magnificus* Auch-31 131.4, 11.9 (P31-3). **10–11.** *Prolycospora claytonii* (10 is distal focus showing verrucate sculpture,

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Auchenreoch Glen assemblages do not include these short-ranging earliest Tournaisian spores, the section is not from this lowest part of the Ballagan Formation.

In the upper part of the Ballagan Formation there are inceptions of *Curriculomonoletes orbis*, with *Monilospora mutabilis* becoming persistent. None of these occur in the Auchenreoch section, further indicating a lower, but not lowest, position within the Ballagan Formation. The presence of *Didymosporites scottii* at Auchenreoch is also significant. This megaspore is generally absent in the lower part of the Ballagan Formation but its presence in abundance above 250 m in the West Mains Farm borehole again indicates a position in the lower part of the Ballagan Formation. In sample Auch-31 there are two specimens of *Prolycospora claytonii* (Fig. 4, 10–11), which is the *in situ* spore of the seed fern *Genomosperma kidstonii* (Reeves *et al*. 2023). This is the characteristic spore within the middle part of the Ballagan Formation to the general exclusion of *Anaplanisporites baccatus* and the megaspore *Setispora* spp. The Auchenreoch Glen section thus has the assemblage of the lower *A. baccatus* acme but the inception of the spore characteristic of the overlying *Prolycospora claytonii* assemblage. So, it is placed (Fig. 5) above the inception of *Didymosporites scottii* and most likely close to the inception of *Prolycospora claytonii*.

The presence of a vertisol at the *Pederpes* level in the Auchenreoch section is also potentially significant. In the Tweed Basin these only occur (Kearsey *et al*. 2016) in the upper 300 m of the West Mains Farm Borehole. Their inception is higher in the Burnmouth coast section, but with fewer palaeosols recognisable in coastal outcrop this is interpreted as a recovery failure. So, the presence of a vertisol at Auchenreoch Glen provides additional support for its stratigraphic position. However, the distribution of Ballagan Formation vertisols in the west of the Midland Valley is poorly known. Carpenter *et al*. (2014) interpreted some palaeosols in the thin Isle of Bute succession as vertisols. Descriptions of siltstones in archive boreholes north of Glasgow and in Renfrewshire are generally grey, rather than red, implying the absence of vertisols. However, the Knocknairshill Borehole NS37SW10 [23056 67438] does contain red/red-brown siltstones (Monaghan *et al*. 2024, Fig. 10.14) in the uppermost part of the Ballagan Formation beneath the Clyde Sandstone Formation, which may include vertisols, although it is difficult to be certain.

The absence of scolecodonts indicates no marine overwash events (Kearsey *et al*. 2016; Bennett *et al*. 2017) and hence a terrestrial environment distant from any marine influence. This contrasts with the Tweed Basin sections, but is in accord with the Ballagan palaeogeography of Millward *et al*. 2018. The abundance of *Botryococcus* in the dark-coloured mudstone at 21 m indicates the presence of still, oxygenated fresh water within the system (Batten & Grenfell, 1996), presumably on an initial flooding surface at the base of the mudstone.

In the 'woodland hypothesis' (Retallack 2011, 2024), tetrapods are hypothesised to have evolved and diversified in parallel with the evolution of the first forests. It was during the Devonian that these forests stabilised the fluvial system, changing it from flashy and ephemeral to a permanent system with established meandering streams and oxbow lakes. Retallack hypothesised that it was within these early forests that tetrapods were able to occupy a diverse range of stable habitats without seasonal climate extremes. Retallack (2011, 2014) placed *Pederpes* in the very latest Tournaisian (i.e., above Romer's Gap) and environmentally coded the locality as a brackish lagoon. Clearly this compilation needs to be revised with *Pederpes* coming from the base of the middle part of the Tournaisian and preserved within a vertisol; i.e., within an environment that was characterised by sustained aridity. It is unclear how this latest Tournaisian age determination in Retallack (2011) was achieved. It might simply be that it was placed at the top of Romer's Gap on the assumption that there were no tetrapods present within the gap.

3. Willie's Hole, Whiteadder Water, Tweed Basin

This is the locality on the Whiteadder Water (NT 878547) that has yielded a prolific tetrapod fauna including *Koilops*, *Mesanerpeton* and *Perittodus* (Clack *et al*. 2016). The locality represents an isolated exposure in the river and cannot be linked to any contiguous sequence of the Ballagan Formation. The palynological assemblage comes from two samples collected from the tetrapod level. They both contain an assemblage dominated by *Anaplanisporites baccatus* together with a much lower proportion of *Colatisporites decorus*, *Auroraspora macra*, with *Schopfites claviger* being rare. *Convolutispora calignosa* is present together with *Punctatisporites* spp. and *Plicatispora scolecophora*. Megaspores are represented by both *Setispora pannosa* and *S. pseudoreticulata*. There are rare specimens of the euglenoid *Chomotriletes*.

This assemblage is dominated by the spores and megaspores of the lycopod plant *Oxroadia* (Bateman 1992; Stevens *et al*. 2010). In the absence of *Prolycospora*, *Didymosporites* and *Curriculomonoletes*, it indicates a position in the lower part of the Ballagan Formation some 100–200 m above the base of the formation. It is not possible to be more precise given the more limited assemblage.

4. Burnmouth

These data are based on the 107 productive palynological samples collected from the Burnmouth section and reported in Marshall *et al*. (2019), a contribution that focused on the position of the Devonian–Carboniferous boundary. The location of these tetrapods is known with reference to the logged stratigraphic section (Kearsey *et al*. 2016) that, when combined with the West Mains Farm borehole, makes a composite standard against which the isolated tetrapod localities can be compared.

11 is equatorial focus showing minute spines on sculptural elements) Auch-31 134.0, 18.3 (J33-2). **12.** *Retusotriletes incohatus* Auch-31.2 112.8, 18.3 (J12-1). **13.** *Velamisporites polyptycha* Auch-30 127.8, 21.2 (F27-1). **14.** *Baculatisporites fusticulus* Auch-14 135.3, 13.0 (O35-3). **15.** *Raistrickia spathulata* Auch-29 120.2, 17.1 (K19-4). **16.** *Raistrickia clavata* Auch-28 127.9, 6.1 (V27-4). **17.** *Raistrickia superba* Auch-32 127.1, 15.7 (L26-4). **18.** *Convolutispora tuberosa* Auch-23 110.1, 7.0 (V9-1). **19.** *Convolutispora caliginosa* Auch-31 122.5, 12.8 (P22-1). **20.** *Convolutispora major* Auch31.2 110.5, 7.7 (U9-2). **21.** *Convolutispora vermiformis* Auch-28 134.8, 9.3 (S34-4). **22.** *Crassispora aculeata* Auch-14 126.0, 21.1 (F25-2). **23.** *Cyrtospora cristifer* Auch-29 115.6, 9.0 (S14-4). **24.** *Radiizonates mirabilis* Auch-31.2 110.7, 16.7 (K9-4). **25.** *Grandispora echinata* Auch-31 139.3, 7.2 (U39-3). **26.** *Spelaeotriletes crustatus* Auch-29 109.8, 9.8 (S8-2). **27.** *Spelaeotriletes microspinosus* Auch-28 124.8, 22.0 (E24-1). **28.** *Indotriradites explanatus* Auch-14 118.8, 16.0 (L18-3). **29.** *Chomotriletes* sp. Auch-31 137.0, 12.7 (P37-1). **30.** *Botryococcus* sp. Auch-27 119.3, 15.2 (M18-4). **31–32.** *Didymosporites scottii* (31 is a separated single megaspore with the abortive spore preserved (arrowed) next to the monolete mark. There is a barely discernible trilete mark within the abortive spore) Auch-30 113.4, 10.1 (R12-4); (32 is the megaspore pair still preserved within its outer wall layer) Auch-29 137.7, 18.8 (H37-4). These are the spores of the fern *Stauropteris burntislandica* (Chaloner 1958). **33.** Detached spine of *Setispora* with its characteristic buttressed spine base. Coldstream-2 125.4, 10.6 (R25-1). **34.** Detached spine of *Setispora*. The simple spine base places it within *S. pseudoreticulata.* Auch-32 110.9, 10.2 (R10-3). Both *S. pannosa* and *S. pseudoreticulata* are the megaspores of the creeping lycopod *Oxroadia*. **35.** *Anaplanisporites baccatus*, the microspore of *Oxroadia* Auch-31.2 122.6, 5.0 (X22-1).

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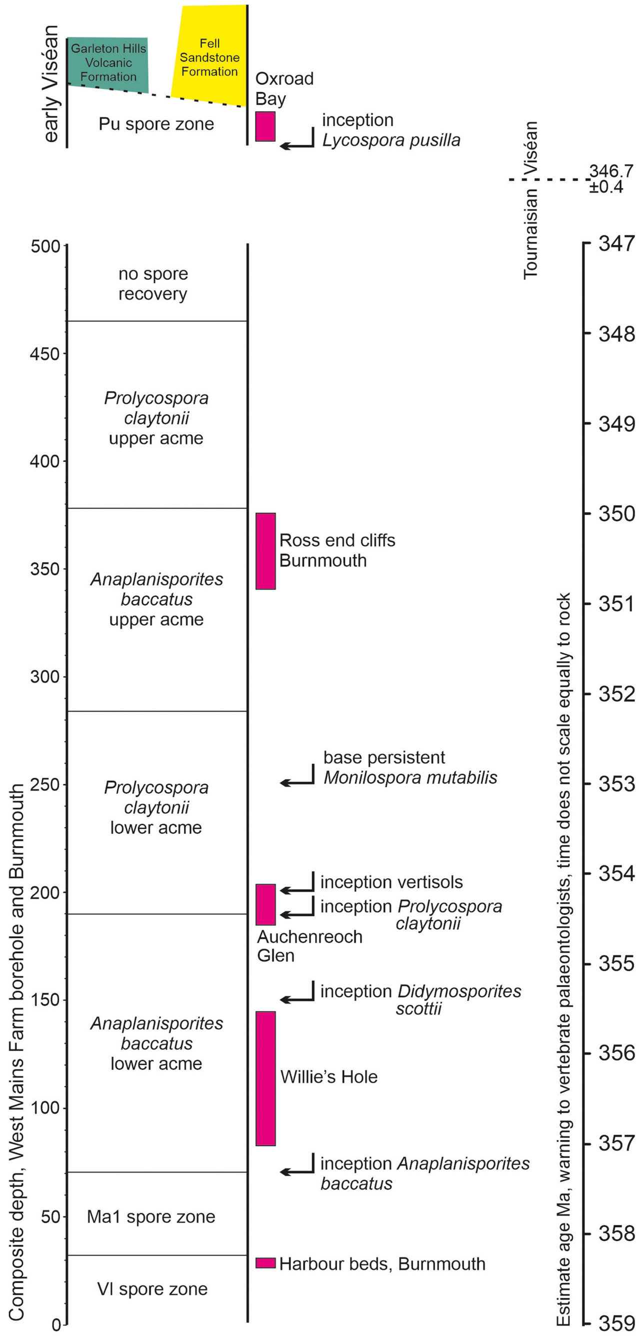

Figure 5 Tetrapod localities calibrated against a composite depth scale for the Ballagan Formation based on the Norham West Mains Farm borehole and Burnmouth outcrop section. The main palynological events are based on Reeves 2019 and Marshall *et al*. 2019. Note that the red bars showing the relative ages are error bars on the age not the age range of the tetrapods. An estimated geochronological timescale is provided scaled against the 12 Myr duration (Aretz *et al*. 2020) for the Tournaisian Stage.

Two groups of tetrapods are known from (39584 66104), the coastal sections at Burnmouth. These are as yet unnamed tetrapods from 35 m above the top of the Kinnesswood Formation (Smithson *et al*. 2012), close to the outer wall of the harbour. This is within the VI spore zone of earliest Tournaisian age.

The second group of tetrapods (*Aytonerpeton*, *Diploradus* and *Ossirarus*) is from the coastal cliffs at Ross end (9627 66054) and from 340–374 m above the base of the formation. This is within the upper interval of the Ballagan Formation rich in *Anaplanisporites baccatus*.

5. Coldstream, Northumberland

An as yet unnamed tetrapod (Smithson *et al*. 2012) was recovered from the east bank of the River Tweed, some 350 m downstream of the Coldstream Bridge (NT 852403). Its location on the east bank means the locality is just in Northumberland (England) rather than the Scottish Borders. As reported by Smithson, this is a short section (15–20 m), only visible when the water level in the river level is low. Two spot samples were provided by Tim Smithson, both originating from blocks that contain vertebrates and ostracods. Both samples were rich in AOM and with abundant framboidal pyrite. Following AOM removal by ultrasonic probe, one sample (Coldsteam-1) was dominated by pale-coloured phytoclasts including cuticular sheets and with spores. The other sample (Coldstream-2) was more typical with thicker, more opaque phytoclasts and spores (Supplementary Information).

In addition to simple and apiculate spores, both samples were dominated by *Anaplanisporites baccatus*, with Coldstream-2 containing many smaller immature specimens, frequently in tetrads and clusters. Apart from the dominance of *Anaplanisporites baccatus* the diversity is low, really only containing *Colatisporites decorus*, *Punctatisporites* spp., *Plicatisporites scolecophora* and *Convolutispora major*. Spores that are generally typical of the Ballagan Formation, such as *Retusotriletes incohatus* and *Schopfites claviger*, are rare. There is only a single specimen of *Spelaeotriletes* sp. The Coldstream-1 sample includes rare *Botryococcus*.

Given the abundance of *Anaplanisporites baccatus* it could be considered that the assemblage represents a distal sorted assemblage. However, megaspores of *A. baccatus* are not uncommon, although often fragmentary. Both *Setispora pannosa* and *S. pseudoreticulata* are present. From this, we can infer that the spores were deposited close to vegetation dominated by *Oxroadia* with the AOM and framboidal pyrite indicating a stratified water column with green sulphur bacteria promoting the formation of pyrite framboids. The >150 m fraction contains megaspores and significant large fragments of plants, again evidence for locally sourced spores. The abundance of ostracods also supports the interpretation of the palaeoenvironment as a stratified freshwater lake with oxygenated upper waters.

Given the paucity of the palynological assemblage, the age determination is problematic. Currently, it can only be placed within either of the acme of *Anaplanisporites baccatus*. None of the spores with inceptions in the upper part of the Ballagan Formation are present (e.g., *Monilospora mutabilis*), but given the low diversity it is impossible to determine if their absence results from stratigraphical position or impoverished assemblage.

6. Gin Head, Tantallon and Oxroad Bay, *Tantallognathus woodi*

Tantallognathus woodi (Chen *et al*. 2018) is from the historic Whitecross Collection, initially housed in the Burgh Museum in North Berwick and then transferred to the now National Museums Scotland. The original sampling locality and bed were identified by Stan Wood as being from Gin Head, Tantallon. The locality was revisited but the limestone lithology of the tetrapod bed that is within a volcaniclastic sequences was unsuitable for the preservation of palynomorphs. However, this same limestone bed is almost certainly present within the immediately adjacent sequence at Oxroad Bay and also represented in the uppermost 27 m of the Ballagan Formation of the Spilmersford and East Linton Boreholes. The uppermost Ballagan Formation level in these boreholes is

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from the Pu spore zone that is generally ascribed a Viséan and younger age. Immediately above the Gin Head locality is the Garleton Hills Volcanic Formation that has a recalculated (Monaghan & Parrish 2006; Monaghan *et al.* 2014) U–Pb zircon age of 343 ± 1.0 Ma and a sanidine $^{40}Ar/^{39}Ar$ age of 339.2 ± 3.9 Ma, i.e., from within the Viséan which has its base currently placed at 346.7 ± 0.4 Ma (Cohen *et al.* 2013).

In an attempt to refine and corroborate these correlations, ten samples were collected (by D. Millward) at Oxroad Bay and from the short sections as logged by Bateman & Scott (1990). Oxroad Bay is a highly protected fossil locality with anatomically preserved plants so, of necessity, excavation from the foreshore below the level of surface alteration was not possible. The Oxroad Bay locality has previously been palynologically dated (Scott *et al.* 1984) as CM zone of Tournaisian age. The palynological samples produced varied results, with a number of samples being dominated by degraded plant debris, probably a consequence of surficial alteration. However, several of the samples contained good spores, so representative assemblages could be counted from exposures B (Tantallon 2), D (Tantallon 5B) and close to C (Tantallon 3B) using the short foreshore log notation of Bateman & Scott (1990).

The palynological assemblage is a little different from that found in the lower parts of the Ballagan Formation in that the diversity is lower and simple retusoid spores from the VI recovery vegetation are relatively less abundant. In addition, more complex spores such as *Monilospora* that have inceptions within the Ballagan Formation are absent. *Anaplanisporites baccatus* is present but not dominant, which is surprising given the relative abundance of *Oxroadia* within the locality. The tree fern pollen *Prolycospora claytonii* is common. Larger spores such as *Baculatisporites fusticulus* are abundant, perhaps reflecting an ecological signal at a plant locality.

One spore more abundant at Oxroad Bay in comparison to older Ballagan Formation samples is *Radiizonates mirabilis*. This distinctive spore (Fig. 6, 2) was first described from the latest Tournaisian and earliest Viséan of Clare Island, County Mayo, Ireland (Phillips & Clayton 1980). Subsequently, it has been recorded in the somewhat older PC spore zone in addition to other CM records (Higgs *et al.* 1988).

A significant but rare component is *Lycospora*, as both *L. pusilla* and *L. noctuina* define the base of the Pu spore zone (Fig 6, 3–5). These spores are not well preserved and the cingulum appears somewhat as a fold rather than a denser ring structure. In this sense they are comparable to the cf. *L. pusilla* specimens illustrated by Stephenson *et al.* (2004) from the base of the Pu zone. There is continuing debate (Higgs *et al.* 1988; Stephenson *et al.* 2004) over whether the definition of the Pu zone should be based on the inception of *Lycospora pusilla* (the original definition of Neves & Ioannides (1974) from the Spilmersford Borehole), or when it became abundant (Owens *et al.* 1977b). This abundance of *Lycospora* spp. is a distinctive feature within many Viséan to Westphalian spore assemblages. It is also evident that this change to a spore assemblage dominated by *Lycospora pusilla* is meaningful in marking the transition to a flora dominated by large lepidodendroid trees and significantly more humid conditions. This change occurs widely across Euramerica including East Greenland (Vigran *et al.* 1999) and Spitsbergen (Lopes *et al.* 2019). In the Tweed Basin, the onset of more humid conditions is marked by a disconformity above the Ballagan Formation with the arrival of the large-scale fluvial system of the Fell Sandstone Formation.

The first appearance of *Lycospora pusilla* has also been used to palynologically identify the base of the Viséan Stage. However, it is clear that the inception of *Lycospora pusilla* is inconsistent even within Euramerica and is not a reliable indicator (Lopes *et al.* 2019) for the Tournaisian–Viséan boundary; instead, its inception indicates a position within the Viséan Stage. Hence, both the geochronological age of the Garleton Hills Volcanic Formation and the palynological assemblages for Oxroad Bay indicate that *Tantallognathus* is Viséan in age and most likely early Viséan.

7. *Occidens portlocki* from County Londonderry, Northern Ireland

The small available sample came from the partial left jaw of a tetrapod specimen illustrated in Portlock (1843) that was collected in Ireland during the memoir survey of County Londonderry and adjacent areas. The jaw was preserved in the collections of the BGS, now in Keyworth, Nottinghamshire, as GSM 28498. It was identified as *Holoptychius* and scheduled for description by Agassiz (1844–45) but was never described or figured. It was subsequently identified as a tetrapod by Clack & Ahlberg (2004), who described and formally named it (*Occidens portlocki*), and noted its resemblance to the whatcheeriids and *Crassigyrinus*. A significant issue is that the single specimen has no detailed location or geological horizon apart from a label identifying it as *Archichthys portlocki* Ag with a location of Maghera, Derry. It was supplied for palynological analysis without any context. An initial palynological report (Marshall, pers. comm. 1999) was submitted to Jenny Clack with comments on a likely age from palynological elements that included then disjunct Viséan and Namurian forms. This age did not match to the conception of the probable local geology as it was apparently younger than all of the Carboniferous present within the area. So, further palynological analyses were undertaken by Stephenson (in Clack & Ahlberg 2004) on other specimens in the same drawer as the tetrapod. This gave a CM palynological assemblage, with *Auroraspora macra* and *Schopfites claviger*, i.e., characteristic of the Ballagan Formation and of latest Tournaisian age. Within the area studied by Portlock (1843) there is a Ballagan Formation equivalent present, which is the Altagoan Formation from Draperstown. A study (Owens *et al.* 1977a) shows that the Altagoan Formation is also palynologically comparable to the Ballagan Formation, but with very rare specimens of *Lycospora pusilla* indicating, at least for the sampled level, a position in the early Viséan. This age assignment to the Tournaisian CM spore zone meant that *Occidens portlocki* became only the second tetrapod to be recognised from within Romer's Gap and in strata that were effectively contiguous to the Midland Valley of Scotland.

As the palynological report on the assemblage from the matrix of *Occidens portlocki* submitted to Jenny Clack was only preliminary, the opportunity is taken here to clarify its age in the context of our much better knowledge of Romer's Gap tetrapods. The palynological assemblage from the matrix of the jaw of *Occidens* was very thin but over 150 spores were identified and counted. These are listed in Table 1. In dealing with any potentially problematic assemblage it is important to try to find some common elements plus any preservational and thermal maturity characteristics that enable a consistent assemblage to be identified. One unusual feature of many of the spores is that they are three-dimensional (Fig 6, 6), i.e., not compressed as normal and with a common distinctive mineral damage to the exines. This is entirely consistent through preservation within a structure such as a bone, where the matrix would not undergo the normal amount of depth compaction. The most common spore is a large thick-walled species of *Punctatisporites* (*P. irrasus*). Diagnostic species include *Lycospora* (*L. noctuina* and *L. pusilla*), *Tripartites vetustus* and *Triquitrites marginatus*, *Corbulispora cancellata*, *Grumosisporites* and *Cingulizonates bialatus*. The age (Neves *et al.* 1973; Owens *et al.* 2004) is clearly Viséan or younger from the presence of *Lycospora pusilla*. *Tripartites vetustus* is present,

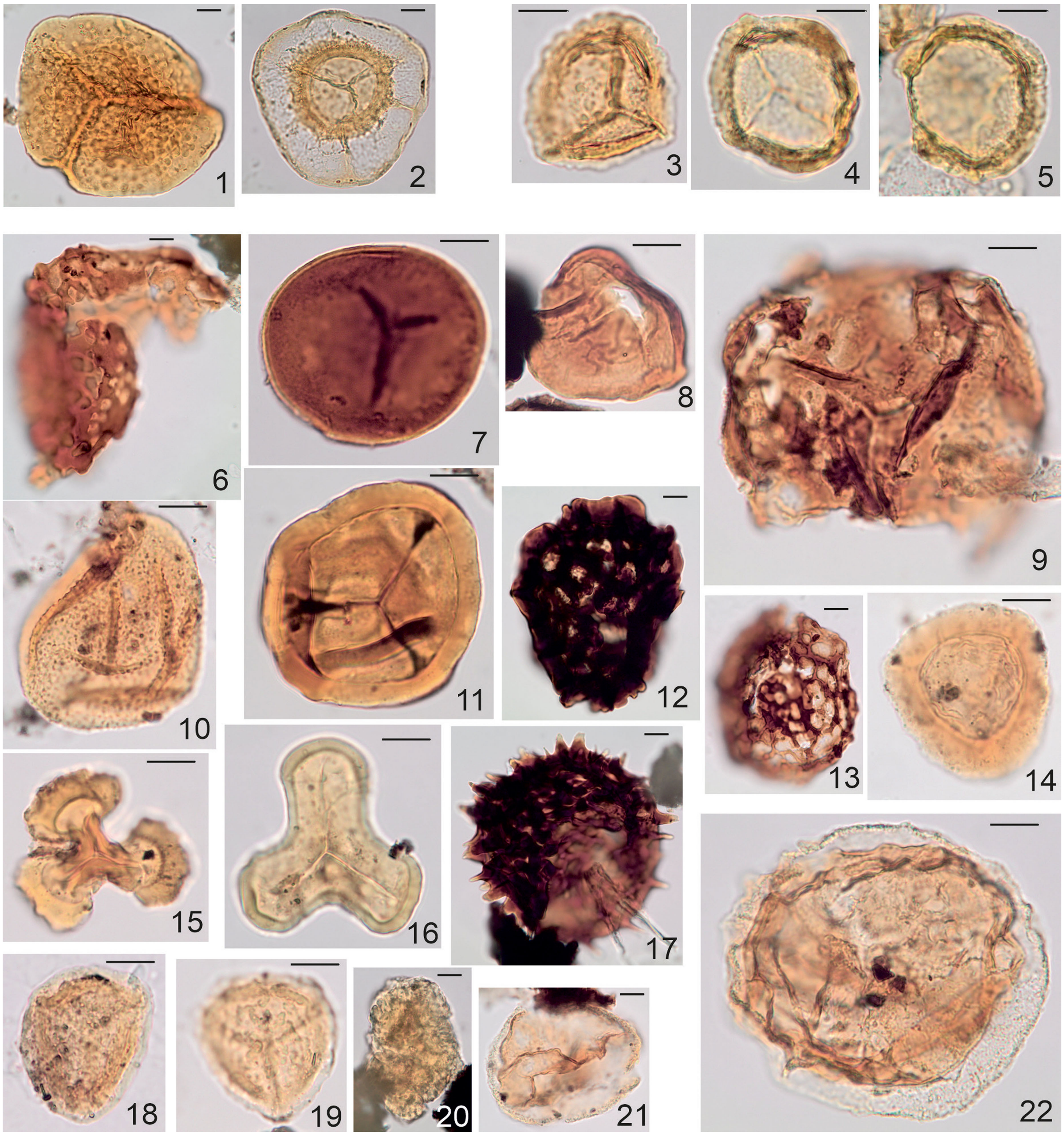

Figure 6 Illustration of important stratigraphic spores from Oxroad Bay (1–5) and the *Occidens portlocki* jaw (6–22). All figured spores are in the palynology collections of the British Geological Survey, Keyworth. All the *Occidens portlocki* slides are from BGS specimen number GSM 28498 followed by the palynological slide number, e.g., GSM 28498.2. Microscope co-ordinates refer to Olympus BHS-313 No. 230272 in the School of Ocean and Earth Science, University of Southampton. England Finder co-ordinates (e.g., R20-3) are also provided. Scale bars are all 10 m. **1.** *Spelaeotriletes pretiosus* Tantallon 5B 122.0, 17.0 (K21). **2.** *Radiizonates mirabilis* Tantallon 5B 127.7, 4.8 (X27-1). **3.** *Lycospora noctuina* Tantallon 3B 127.6, 3.9 (Y27-1). **4.** *Lycospora pusilla* Tantallon 2 131.4, 17.2 (K31-1). **5.** *Lycospora pusilla* Tantallon 2 125.1, 12.9 (O24-4). **6.** Typical *Occidens portlocki* jaw spore preservation as three-dimensional and with walls perforated by mineral growth. **7.** *Retusotriletes incohatus* GSM 28498.4 135.4, 9.5 (S35-1). **8.** *Plicatispora scolecophora* GSM 28498.1 137.2, 9.2 (S37-3). **9.** *Punctatisporites irrasus* GSM 28498.1 136.0, 10.0 (R36-3). **10.** *Cyclogranisporites commodus* GSM 28498.1 134.4, 13.8 (N34-3). **11.** *Knoxisporites literatus* GSM 28498.3 136.2, 9.5 (S36-1). **12.** *Corbulispora cancellata* GSM 28498.3 133.7, 19.7 (G33-4). **13.** *Grumosisporites* sp. GSM 28498.1 138.6, 13.1 (O38-4). **14.** *Cingulizonates bialatus* GSM 28498.3 137.7, 11.0 (Q37-4). **15.** *Tripartites vetustus* GSM 28498.3 140.8, 13.6 (O40-2). **16.** *Triquitrites marginatus* GSM 28498.1 129.0, 16.8 (K28-4). **17.** *Raistrickia corynoges* GSM 28498.3 141.0, 14.6 (N41-1). **18.** *Lycospora pusilla* GSM 28498.3 137.6, 14.0 (N37-4). **19.** *Lycospora noctuina* GSM 28498.3 135.1, 14.7 (N24-2). **20.** *Botryococcus* sp. GSM 28498.3 137.6, 12.9 (O37-4). **21.** *Colatisporites decorus* GSM 28498.1 131.2, 13.0 (N31-3). **22.** *Remysporites magnificus* GSM 28498.1 136.0, 13.5 (O35-2).

which is the zonal index for the VF spore zone but has a total range into the mid Namurian. This younger age for *Occidens* is supported by *Triquitrites marginatus*, which has an inception within the mid Viséan TC spore zone. In the now superseded Namurian spore zonation of Owens *et al.* (1977b), a spore inception within the NC zone that overlies the VF zone is *Grumosisporites rufus*. There are two specimens of *Grumosisporites* sp. within the *Occidens* spore assemblage that hints the age might be slightly younger than the VF spore zone. So, the assemblage from the matrix of *Occidens portlocki* is clearly significantly younger than the Tournaisian age preferred by Clack & Ahlberg (2004).

Within the area formally mapped and monographed by Portlock (1843) there is the thin Meenymore Formation (Fig. 7) that has been attributed to the VF spore zone (Mitchell 2004; Mitchell & Somerville 2011). The Meenymore Formation is a laterally extensive tidal flat of evaporitic facies (West *et al.* 1968) that is only 20 m thick in the Londonderry area, where it rests unconformably on the Asbian Desertmartin Limestone Formation. It is also the youngest preserved Carboniferous

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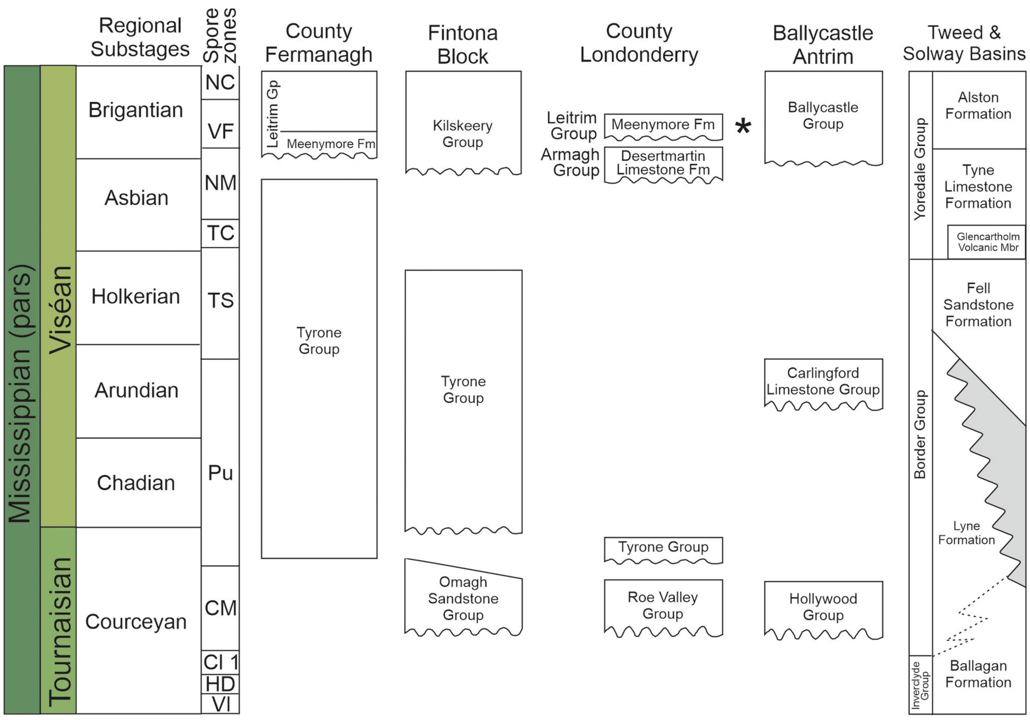

Figure 7 Stratigraphy of the Londonderry area and Northwest Carboniferous Basin of Ireland showing likely Brigantian (Viséan) stratigraphic level for the *Occipens portlocki* tetrapod jaw (*). Compiled from Mitchell & Somerville (2011), Mitchell & Owens (1990), Whitaker & Butterworth (1978), Monaghan *et al.* 2024 and Waters *et al.* (2011).

sequence in the area. In northwest Ireland (Loch Allen Basin) there has been a systematic attempt (Cózar *et al.* 2006) to identify the Asbian–Brigantian regional substage boundary by combining data from ammonoids, foraminifera, conodonts and spores. These data confirm the value of the ammonoids and foraminifera for correlation to the established international zonation and that the Meenymore Formation has its base effectively coincident with the Asbian–Brigantian boundary. The correlations of Cózar *et al.* (2006) also emphasised that the NM to VF spore zone boundary lay within the Brigantian stage, the previous correlations to the regional stages being made in sequences with largely terrestrial sediments from the Midland Valley of Scotland. There is no palynological data from the local Meenymore Formation, but the VF spore zone has also been identified in the Ballycastle area of Antrim (Whitaker & Butterworth 1978) and within the conglomeratic successions of the Fintona Block (Mitchell & Owens 1990). Limited data on Tournaisian to Namurian spore assemblages have been reported (Higgs 1984) from the Northwest Carboniferous (Loch Allen) Basin, where the Meenymore Formation is placed in the underlying NM spore zone with *Tripartites vetustus* not appearing until the Bellavally Formation. The formations in the Northwest Carboniferous Basin studied by Higgs (1984) are all much thicker (over 500 m of Brigantian Leitrim Group) than in the Londonderry area and there is direct evidence from the ammonoid zones for the attenuation of the Meenymore Formation onto depositional highs (e.g., the Lackagh Hills, Fig. 12 in Brandon & Hodson 1984). So, it is possible that only the upper part of a lithologically distinctive transgressive unit ('Meenymore' Formation) was deposited on the basement high in the Londonderry area in contrast to the Northwest Carboniferous Basin.

Table 1 Spores from the *Occipens portlocki* jaw. Taxonomic citations not in references can be found in Playford & Melo (2012) or Owens *et al.* (2004, 2010).

Apiculate spores	13
Botryococcus	2
Calamospora spp.	1
Cingulizonates bialatus	15
Colatisporites decorus	7
Convolutispora spp.	2
Corbulispora cancellata	1
Cyclogranisporites commodus	7
Grumosisporites sp.	2
Knoxisporites triangulatus	1
Lycospora noctuina	1
Lycospora pusilla	10
Plicatisporites scolecophora	3
Punctatisporites irrasus	53
Raistrickia corynoges	1
Remysporites magnificus	8
Retusotriletes incohatus	6
Retusotriletes planus	1
Tripartites vetustus	1
Triquitrites marginatus	1

This information enables us to revisit Portlock (1843) in an attempt to identify the likely locality of the specimen. It is also important to understand how the 1843 Londonderry memoir was researched and compiled (Herries Davies 1983). Portlock had a team of surveyors, some geologically trained and some not, and this staff sometimes numbered as many as 35. But by 1840, the slow progress of the truly monographic work coupled with government retrenchment saw the staff cut to four, including Portlock, who were transferred to Dublin. The intention had been to produce a series of similar memoirs for all of Ireland but the project was abandoned. Portlock was rushed to complete the memoir, which he did in January 1843, and was posted back to his regiment which was then in Corfu. In the Londonderry memoir, the fossils were collectively illustrated and described by the talented geologist and artist George Du Noyer. Examination of Plate XIII reveals that the specimen illustrated as Fig. 13a & b is both sides of the jaw of *Occidens*, to the extent that the illustration of Clack & Ahlberg (2004) shows it to be labelled XIIIB. However, it should be noted that an additional front piece to the jaw is present in the original illustration but missing from Clack & Ahlberg (2004). Hopefully, it is still present within the BGS collection and can be reunited with the other two pieces.

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Analysis of Portlock (1843) reveals numerous records of *Holoptychius*, largely scales and some teeth. *Holopytychius* is a fish that is now known to be restricted to the Devonian, becoming extinct at or immediately below the Devonian–Carboniferous boundary (Sallan & Coates 2010). These different, largely Carboniferous rhizodont teeth are placed in *Archichthys portlocki* by Jeffery (2006), with the exception of *Occidens portlocki*. Portlock (1843) lists a significant number of *Holoptychius* localities both in the systematic palaeontology, the stratigraphic compilation and the descriptions of the field sections. Although not always clear, these are often the same localities referred to in different ways. They are also not always accurate; for example, the Holywood locality is listed as being in County Antrim rather than County Down and is now a well-known site (Griffith & Wilson 1982) for *Holoptychius*. In addition, the locality information for at least one fossil in Portlock (1843, p. 464, *Megalichthys hibbertii*) was regarded as doubtful. Most of the localities are records of scales with the only teeth reported from the Moyola River and Falls of Bannagh. The latter were from mudstones (probably the Drumchoricke Siltstone Formation) of late Arundian age (Waters *et al*. 2011). The Moyola River locality is also referred to in Portlock (1843) as being Maghera and the richest fish site with *Gyracanthus* as well as *Holoptychius* teeth and scales. The locality is mapped (Geological Survey of Northern Ireland 2006) as Mormeal Member of the Altagoan Formation and of latest Tournaisian to Chadian age.

Clearly this Brigantian VF spore zone age from the palynological assemblage is at variance with the ages of the *Holoptychius* teeth reported in Portlock (1843). But nowhere in the text is there specific mention of a locality for the jaw. As noted, the cost and time overruns meant that the County Londonderry memoir project was wound down rapidly and moved to Dublin in 1840. The transferred collections (Herries Davies 1995) included some 4,824 catalogued fossils plus an additional 70 boxes of unnamed specimens. After a brief interval on other duties, Du Noyer was again assigned to the memoir project (December 1840), producing further illustrations of fossils (Hegarty 2018) until February 1842 and thereafter working casually. One clue that the specimen of *Occidens* might, in fact, be from Ballycastle (Antrim) is from Baily (1871), who noted that the Portlock Collection on display in the Royal College of Sciences, Stephen's Green, Dublin included a small number of fish specimens collected from Ballycastle, most probably from black mudstones above the Old Salt Pans (formerly the Bath Lodge) Colliery. These black mudstones (Fig. 20 in Wilson & Robbie 1966) are immediately above the Bath Lodge Coal and the youngest part of the succession in the Ballycastle Coalfield. This part of the succession is placed in the earliest Namurian (Wilson & Robbie 1966) based on marine band correlation with the Midland Valley of Scotland and Macrihanish in the Kintyre. Palynological data from the Ballycastle Coalfield (Whitaker & Butterworth 1978; Butterworth in Wilson & Robbie 1966, p. 81) includes *Rotaspora fracta* and *Tripartites vetustus*, which have inceptions in the VF spore zone or younger. Butterworth also recorded *Verrucosisporites morulatus* that Owens *et al*. (2004) used to define the Vm spore subzone to which it is restricted and is of Pendleian age, i.e., immediately post-Brigantian.

So, accepting the palynological assemblage from the *Occidens* jaw, the specimen is not from the Tournaisian but instead from the latest Viséan or younger. If it is from above the Bath Lodge Coal in the Ballycastle Coalfield then the age is early Pendleian. This locality provides a match with the palynological assemblage and there is a documented record of fossil fish from Ballycastle being within the Portlock Collection.

8. Blue Beach, Nova Scotia, Canada

The most comparable section to the Ballagan Formation that is of Tournaisian age and includes tetrapods both as skeletal material (Anderson *et al*. 2015) and footprints (Mansky & Lucas 2013; Lucas *et al*. 2022) is Blue Beach in Nova Scotia, Canada. Here, the largely disarticulated tetrapods are in the Blue Beach Member of the Horton Bluff Formation. The section at Blue Beach has been studied extensively, with detailed sedimentology (Martel & Gibling 1996) and palaeontological collections housed in the Blue Beach Museum (Mansky & Lucas 2013; bluebeachfossilmuseum.com). The Horton Bluff Formation has been studied palynologically (Utting *et al*. 1989; Utting & Giles 2004) but largely from sections other than Blue Beach. These palynological studies (Utting *et al*. 1989) show that the Blue Beach and Hurd Creek Members are all within the *Spelaeotriletes cabotii* spore zone and are of mid to late Tournaisian age, with the earliest Tournaisian represented (above a hiatus) by the largely sandstone lithologies of the Curry Brook and Harding Brook Members. These do not contain tetrapods. In addition, the Blue Beach section only includes the upper half of the exposed total thickness of the Blue Beach Member. So, although frequently portrayed as including the earliest Romer's Gap tetrapods, the Blue Beach section includes only part of the Tournaisian. Blue Beach also differs in its sedimentary environment, which is lacustrine mudstones and sandstones with a marine incursion (Mansky & Lucas 2013). These are ever wet environments and so somewhat different from the Ballagan Formation with its matrix of seasonally dry river, lagoon and marine incursions (Bennett *et al*. 2021). In addition, the palynological assemblages from Blue Beach are different in not being dominated by simple spores and *Schopfites claviger* but instead by *Spelaeotriletes* and *Vallatisporites*. Blue Beach also includes a number of horizons with *in situ* lycopod stumps (Martel & Gibling 1996; Rygel *et al*. 2006) representing a forest. Similar *in situ* lycopod roots are present in the Ballagan Formation at Burnmouth but are rather rare (Bennett *et al*. 2021). So, Blue Beach and the Ballagan Formation are only really comparable in that both contain Tournaisian tetrapods; apart from that, they are quite dissimilar in age span, palaeoenvironment and vegetation. However, these differences are valuable in that different ecosystems are being sampled and will collectively give us a much better understanding of Tournaisian tetrapods.

9. Conclusions

The five main tetrapod localities are all dated palynologically (with varying precision) and placed against a Tournaisian composite standard based on the Ballagan Formation from the Burnmouth outcrop section and the TW:eed Project Norham West Mains Farm cored borehole. Importantly, this includes the isolated tetrapod locality with *Pederpes finneyae* from Auchenreoch Glen in Dunbartonshire. The tetrapods are distributed throughout the 12 Myr represented by the Tournaisian Stage. Other non-spore or pollen palynomorphs present or absent from the palynological assemblages enable various inferences to be made as to the immediate palaeoenvironment of the tetrapod localities. *Occidens portlocki*, a tetrapod assigned to the Ballagan Formation equivalent in Northern Ireland but without locality or stratigraphic information, is reassigned using palynology to the Brigantian or younger (latest Viséan–earliest Namurian age) and possibly from the Ballycastle Coalfield. It is not a Romer's Gap tetrapod. Blue Beach in Nova Scotia is the other Tournaisian locality that contains a number of tetrapods but differs substantially from the Ballagan Formation in age span and palaeoenvironment.

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List of taxa cited

Pollen, spores and megaspores
Acanthotriletes persibus Higgs 1975
Anaplanisporites baccatus (Hoffmeister *et al.*) Smith & Butterworth 1967
Anaplanisporites centrosus Higgs *et al.* 1988
Auroraspora asperella (Kedo) Van der Zwan 1980
Auroraspora macra Sullivan 1968
Baculatisporites fusticulus Sullivan 1968
Bascaudaspora submarginatus (Playford) Higgs *et al.* 1988
Cingulizonates bialatus (Waltz) Smith & Butterworth 1967
Colatisporites decorus (Bharadwaj & Venkatachala) Williams in Neves *et al.* 1973
Colatisporites denticulatus Neville in Neves *et al.* 1973
Colatisporites pappulosus Ravn 1991
Convolutispora caliginosa Clayton & Keegan in Clayton *et al.* 1982
Convolutispora major (Kedo) Turnau 1978
Convolutispora permixta Higgs *et al.* 1988
Convolutispora tuberosa Winslow 1962
Convolutispora vermiformis Hughes & Playford 1961
Corbulispora cancellata (Waltz) Bharadwaj & Venkatachala 1961
Crassispora aculeata Neville 1968
Crassispora tychera Neves & Ioannides 1974
Cyclogranisporites commodus Playford 1964
Cyrtospora cristifer (Luber) Van der Zwan 1979
Dictyotriletes fragmentimurus Neville in Neves *et al.* 1973
Dictyotriletes trivialis Naumova in Kedo 1963
Didymosporites scottii Chaloner 1958
Discernisporites micromanifestus (Hacquebard) Sabry & Neves 1971
Endoculeosporites gradzinskii Turnau 1975
Grandispora echinata Hacquebard 1957
Indotriradites explanatus (Luber) Playford, 1990
Insculptospora confossa (Richardson) Marshall 1985
Knoxisporites concentricus (Byvscheva) Playford & McGregor 1993
Knoxisporites literatus (Waltz) Playford 1963
Knoxisporites triangulatus Higgs *et al.* 1988
Latosporites sp. A of Higgs *et al.* 1988
Lophozonotriletes concentricus (Byvscheva) Higgs *et al.* 1988
Lycospora noctuina Butterworth & Williams 1958
Lycospora pusilla (Ibrahim) Somers 1972
Monilospora mutabilis (Staplin) Clayton in Neves *et al.* 1973
Plicatispora scolecophora (Neves & Ioannides) Higgs *et al.* 1988
Prolycospora claytonii Turnau 1978
Punctatisporites irrasus Hacquebard 1957
Punctatisporites planus Hacquebard 1957
Pustulatisporites gibberosus (Hacquebard) Playford 1963
Radiizonates aligerens (Knox) Staplin & Jansonius 1964
Radiizonates mirabilis Phillips & Clayton 1980
Raistrickia clavata (Hacquebard) Playford 1964
Raistrickia corynoges Sullivan 1968
Raistrickia ponderosa Playford 1964
Raistrickia spathulata (Winslow) Higgs 1975
Raistrickia superba (Ibrahim) Schopf *et al.* 1944
Remysporites magnificus (Horst) Butterworth & Williams 1958
Retusotriletes incohatus Sullivan 1964
Retusotriletes planus Dolby & Neves 1970
Schopfites claviger (Sullivan) Higgs *et al.* 1988
Setispora pannosa (Alvin) Spinner 1982
Setispora pseudoreticulata (Butterworth & Spinner) Spinner 1982
Spelaeotriletes crustatus Higgs 1975
Spelaeotriletes microspinosus Neves & Ioannides 1974
Spelaeotriletes pretiosus (Playford) Neves & Belt 1970
Tripartites vetustus Schemel 1950
Triquitrites marginatus Hoffmeister *et al.* 1955
Velamisporites polyptychus (Neves & Ioannides) Ravn 1991
Verrucosisporites gibberosus (Hacquebard) Higgs *et al.* 1988
Verrucosporites nitidus Playford 1963
Algae
Botryococcus Kützing 1849
Chomotriletes Naumova 1937
Plants
Genomosperma kidstonii (Calder) Long 1960
Oxroadia conferta Bateman 1992
Stauropteris burntislandica P. Bertrand 1909
Tetrapods
Aytonerpeton microps Clack *et al.* 2016
Diploradus austiumensis Clack *et al.* 2016
Koilops herma Clack *et al.* 2016
Mesanerpeton woodi Smithson & Clack 2018
Occidens portlocki Clack & Ahlberg 2004
Ossirarus kierani Clack *et al.* 2016
Pederpes finneyae Clack 2002
Perittodus apsconditus Clack *et al.* 2016
Tantallognathus woodi Chen *et al.* 2018

10. Supplementary material

Supplementary material is available online at https://doi.org/10.1017/S1755691024000100.

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12. Competing interests

The authors have no competing interests.

13. References

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