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Unusual biota and palynofacies of a Lower Devonian intermontane basin saline lake–playa mudflat ecosystem

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Abstract: The Strathpeffer–Struie Lower Devonian LORS (Lower Old Red Sandstone) deposits of the Northern Highlands of Scotland contain the decidedly unusual ‘foetid beds’. These are interpreted as being deposited in a highly saline sulphate lake and associated playa mudflat, which developed in an intermontane basin in the Caledonian Mountains of Laurussia. Palynological analysis was undertaken to investigate the biota and environments of deposition of these deposits. The sediments of the saline lake and associated playa mudflat reveal highly unusual palynofacies dominated by cyanobacterial, fungal and algal remains. Presumably the high salinity lacustrine conditions excluded grazing invertebrates and fish, enabling microbial mats and stromatolites to flourish, as is the case in modern

high-altitude highly saline sulphate lakes. Dispersed spore assemblages recovered from the sequence are equated to the D–E Spore Assemblage Biozone/AP Opper Zone (Pro Interval Zone) and suggest a latest Emsian age. The spore assemblages are depauperate compared with those from coeval lowland deposits from Laurussia, suggesting that the vegetation represents a restricted, partially endemic, upland flora. In the palynological samples, rare examples of the terrestrial fauna of the basin are represented by dispersed arthropod cuticle, including the earliest example of a scorpion pectinal tooth with peg sensilla.

Key words: Scotland, Emsian, spore, early land plants, microbial mat, stromatolite.

THE Strathpeffer–Struie outcrop of the Northern Highlands of Scotland preserves a remarkable sequence of Lower Devonian LORS (Lower Old Red Sandstone) deposits (Fig. 1). They accumulated in a back-tilted basin (Dingwall–Strathpeffer Basin) that developed in a strike-slip zone between the Northern Highlands and Grampian Highlands terranes (Clarke & Parnell 1999). The basin infilled with typical LORS terrestrial-fluviatile-lacustrine sediments, but also includes unusual saline lake and associated playa mudflat deposits. The latter consist of foetid bituminous and calcareous shales with thin limestones. The famous ‘sulphur waters’ of Strathpeffer’s Victorian spa are produced by groundwater percolating through these beds. In this paper I describe the palynofacies of the unusual sedimentary sequence of this basin, utilize the dispersed spore assemblages to age constrain and correlate the beds, and reconstruct the flora and fauna of the basin.

GEOLOGICAL SETTING

The Devonian ORS deposits of the Orcadian Basin straddle the Great Glen Fault System and as such crop

out on both the Northern Highlands to the northwest and the Grampian Highlands to the southeast. These deposits accumulated in the Caledonian Mountains, situated on southeast Laurussia at *c.* 30°S, in the arid-semiarid climate belt (Torsvik & Cocks 2017). The laterally and vertically extensive ORS deposits rest unconformably on an ancient landscape consisting largely of Moine Schists. Over most of the area there is a thin basal sedimentary unit (originally termed the ‘Basement Group’ or ‘Barren Group’) that is generally considered to be LORS of Early Devonian age. The Basement Group is overlain by MORS of Middle Devonian age. The contact is either unconformable (e.g. Berriedale Outlier) or disconformable (e.g. Sarclet Outlier). The Basement Group of the Northern Highlands north of the Great Glen Fault System forms a series of discrete outcrops (Fig. 1):

1. The Sarclet Outlier of the Sarclet Dome.
2. The ‘northern Lower Old Red Sandstone’ (*sensu* Trewin & Thirlwall 2002) cropping out in a strip from Braemore northwards to Shurrery, and including the smaller Strathy, Ben Griam, Kirtomy, Roan Island and Tongue Outliers to the west of this.

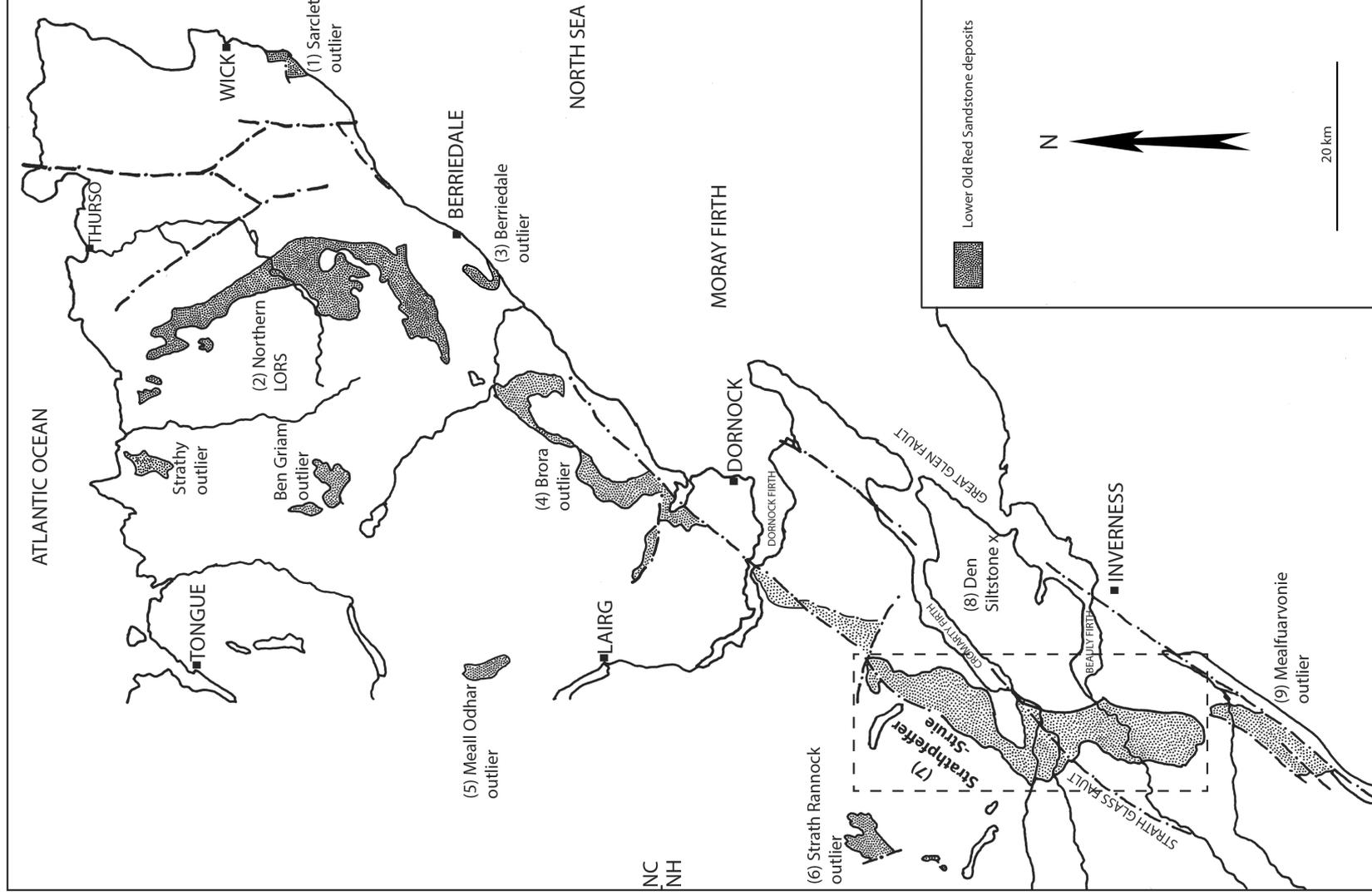


FIG. 1. Map of the eastern part of the Northern Highlands of Scotland, showing the distribution of Lower Devonian LORS (Lower Old Red Sandstone) deposits. The Strathpeffer–Struie outcrop is enclosed in the dashed box. 1, Sarclet Outlier of the Sarclet Dome; 2, ‘northern Lower Old Red Sandstone’ (*sensu* Trewin & Thirlwall 2002) cropping out in a strip from Braemore northwards to Shurrery, and including the smaller Strathy, Ben Griam, Kirtomy, Roan Island and Tongue Outliers to the west of this; 3, Berriedale Outlier (Badbea Basin or Ousdale–Badbea Outlier) located north of the Helmsdale Granite (Wellman 2015); 4, Brora Outlier (Golspie Basin) located south of the Helmsdale Granite (Dec 1992); 5, Meall Odhar or Crask Outlier; 6, the Strath Rannoch Outlier; 7, Strathpeffer–Struie deposits of the Dingwall–Strathpeffer Basin (this paper); 8, Den Siltstone Formation (Fletcher *et al.* 1996); 9, Mealfuarvonie Outlier (Mykura & Owens 1983).

3. The Berriedale Outlier (Badbea Basin or Ousdale–Badbea Outlier) located north of the Helmsdale Granite (Wellman 2015).
4. The Brora Outlier (Golspie Basin) located south of the Helmsdale Granite (Dec 1992).
5. The Meall Odhar or Crask Outlier.
6. The Strath Rannoch Outlier.
7. The Strathpeffer–Struie deposits of the Dingwall–Strathpeffer Basin (this paper).
8. The Den Siltstone Formation (Fletcher *et al.* 1996).
9. The Mealfuarvonie Outlier (Mykura & Owens 1983).

The LORS deposits of the Strathpeffer–Struie outcrop are mapped on the British Geological Survey 1:50 000 Series Scotland Sheet 83, 93 and 94. The geology of these deposits is described in the associated Memoirs of the Geological Survey of Scotland (Horne & Hinxman 1914 (sheet 83); Peach *et al.* 1912 (sheet 93) and Horne 1923 (sheets 84 and 94)). More recently the geology of the deposits has been considered by Westoll (1977), Friend & Williams (1978), Parnell (1985a, 1985b), Clarke & Parnell (1999), Trewin & Thirlwall (2002) and Marshall (2024). It is noteworthy that subsurface Lower Devonian sequences in excess of 1 km in thickness are present offshore in the Moray Firth (Marshall & Hewett 2003). These occur in a series of half-grabens that are located to the south of the Great Glen Fault.

The Strathpeffer–Struie outcrop forms a southwest–northeast-oriented strip *c.* 55 km long and up to 8 km wide (Figs 1–3). To the west it unconformably overlies or is faulted against Proterozoic metasediments (Moine Schists). To the east it is unconformably overlain or is faulted against Middle Devonian MORS deposits. The sedimentary sequence in the basin has been variously subdivided and named over the years (summarized in Table 1). Most recently these deposits have been mapped by the British Geological Survey as the Sarclet Sandstone Group (Ousdale Arkose Formation (including Mealfuarvie Sandstone Member) and Braemore Mudstone Formation). However, this coarser regional stratigraphical nomenclature loses some important detail. In this paper we use the stratigraphical terminology of Clarke &

Parnell (1999) and include their nomenclature for the different facies developed (Tables 1, 2; Figs 1–3).

The basin is dominated by a lacustrine system (Fig. 4). A basal breccia represents talus scree and alluvial fan deposits (Facies 1–3 of the Torr Achilty Fm.). A perennial, highly saline, sulphate lake developed and is represented by Facies 6a of the Strathpeffer Fm. with Facies 6b of the same formation developed at the margins of the lake as marginal lacustrine mudflats. These merge into playa mudflats (Facies 5 of the Moy Formation) that merge into distal fluvial plain deposits (Facies 4 of the Moy Fm.).

Of particular interest are the ‘foetid beds’, which smell of hydrogen sulphide when freshly split. Groundwater percolating through these produces the ‘sulphur waters’ that made Strathpeffer famous as a Victorian spa town. The ‘foetid beds’ contain dolomitized stromatolite and algal mat structures that developed in the saline lake. Kerogenous laminae are also present that probably represent microbial mats. Evaporites, preserved as gypsum (and possibly anhydrite) pseudomorphs and diagenetic quartz nodules, are interpreted as developing due to evaporative concentration of the saline lake (Parnell 1985a). Parnell (1985a) suggested that the presence of pyrite is likely to reflect sulphate reduction during diagenesis.

Richardson (1967) briefly reported on spore assemblages recovered from the Basement Group ‘olive shales’ at Strathpeffer. He noted that the assemblages were poor, but not carbonized, and contained ‘robust ribbed *Emphanisporites*’, *E. ?annulatus* and ‘well-developed zonate-pseudosaccate spores’. He compared them with other spore assemblages from Scotland and noted that they were closest to those from the Strathmore Beds, although the zonate-pseudosaccate spores were more abundant and showed greater variety in the Strathpeffer assemblages, and the presence of smooth ?pseudosaccate forms suggested a slightly younger age. At this early stage in the study of Early Devonian dispersed spores, with few independently age-dated records, age constraint was imprecise and Richardson suggested that the Basement Group assemblages of the Strathpeffer area were probably Early Devonian in age. Subsequently, Richardson &

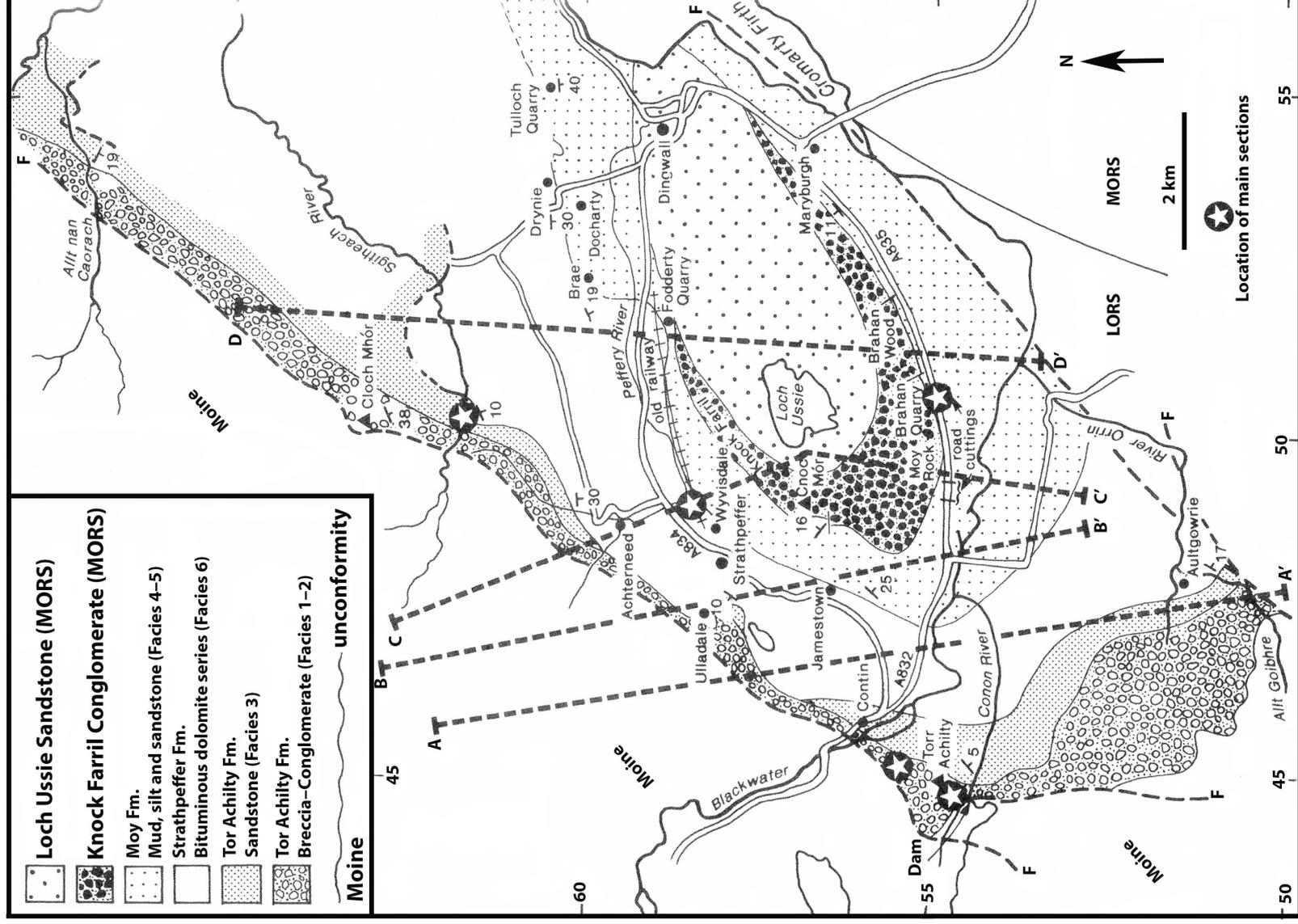


FIG. 2. Geological map showing localities in part of the Strathpeffer–Struie outcrop. The positions of cross-sections shown in Figure 3 are marked by the dashed lines. Modified from Clarke & Parnell (1999) with permission. *Abbreviations:* LORS, Lower Old Red Sandstone; MORS, Middle Old Red Sandstone.

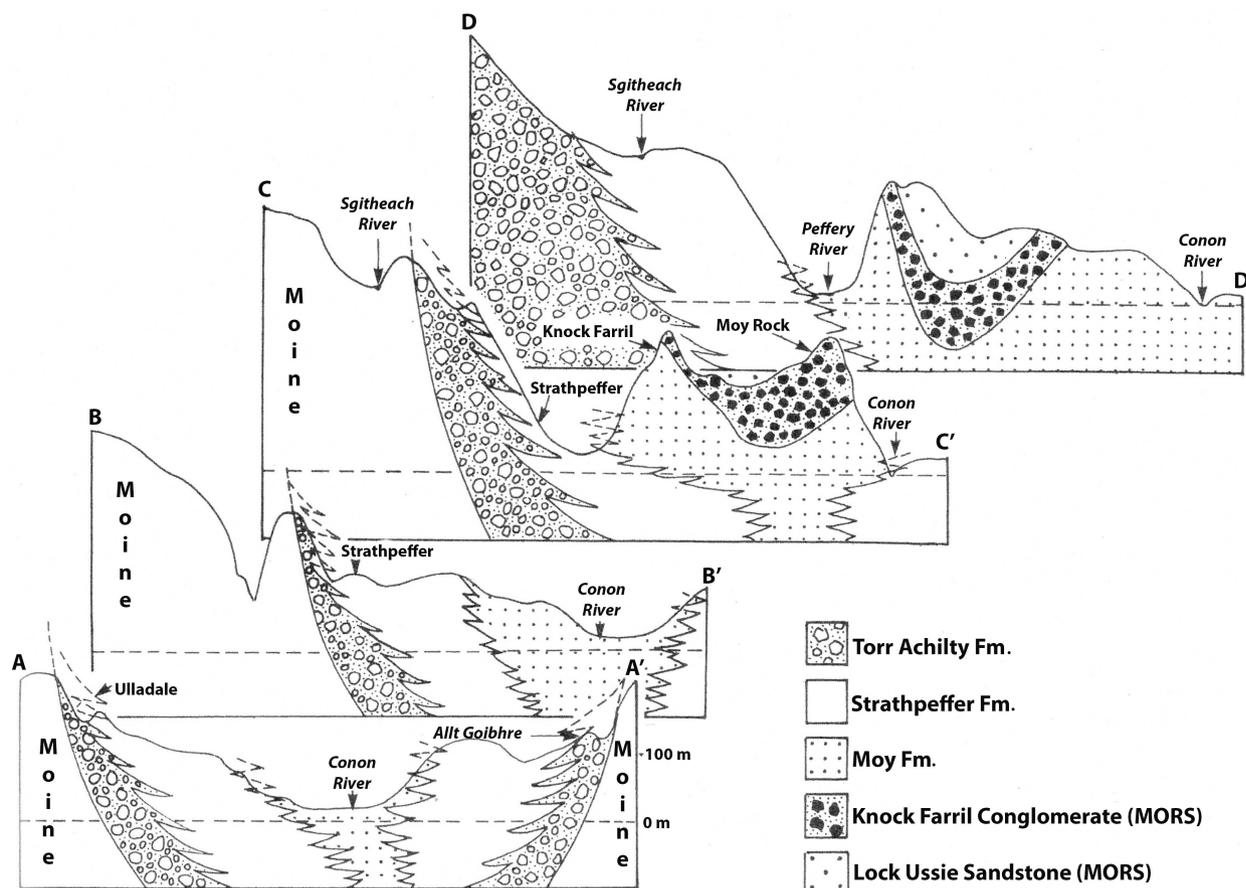


FIG. 3. Cross-sections through the Strathpeffer–Struie outcrop showing the distribution of geological formations and numbered facies. The locations of the cross-sections are marked in Figure 2. Modified from Clarke & Parnell (1999) with permission. *Abbreviation:* MORS, Middle Old Red Sandstone.

TABLE 1. Stratigraphical nomenclature for the sequence of the Strathpeffer–Struie Basin.

Horne & Hinxman (1914)	Johnstone & Mykura (1989)	Clarke & Parnell (1999)
5. Red shales passing upwards into sandstone (c. 600 ft)	Strathpeffer Group: Red Shales and Sandstones (200 m)	Moy Fm. (>200 m) (Facies 4–5)
4. Olive shales with shaly foetid limestone (c. 280 ft)	Strathpeffer Group: Olive Shales (85 m)	Strathpeffer Fm. (>250 m) (Facies 6)
3. Foetid bituminous calcareous shales and thin limestones (the Spa beds) (c. 100 ft)	Strathpeffer Group: Spa Beds (30 m)	“
2. Olive shales and foetid calcareous bands (the Ord beds) (800–1000 ft)	Strathpeffer Group: Ord Beds (250–300 m)	“
1. Red and yellow sandstones and conglomerates (basement group)	Kilmorack Group: Basal Conglomerate and Breccia	Torr Achilty Fm. (>245 m) (Facies 1–3)

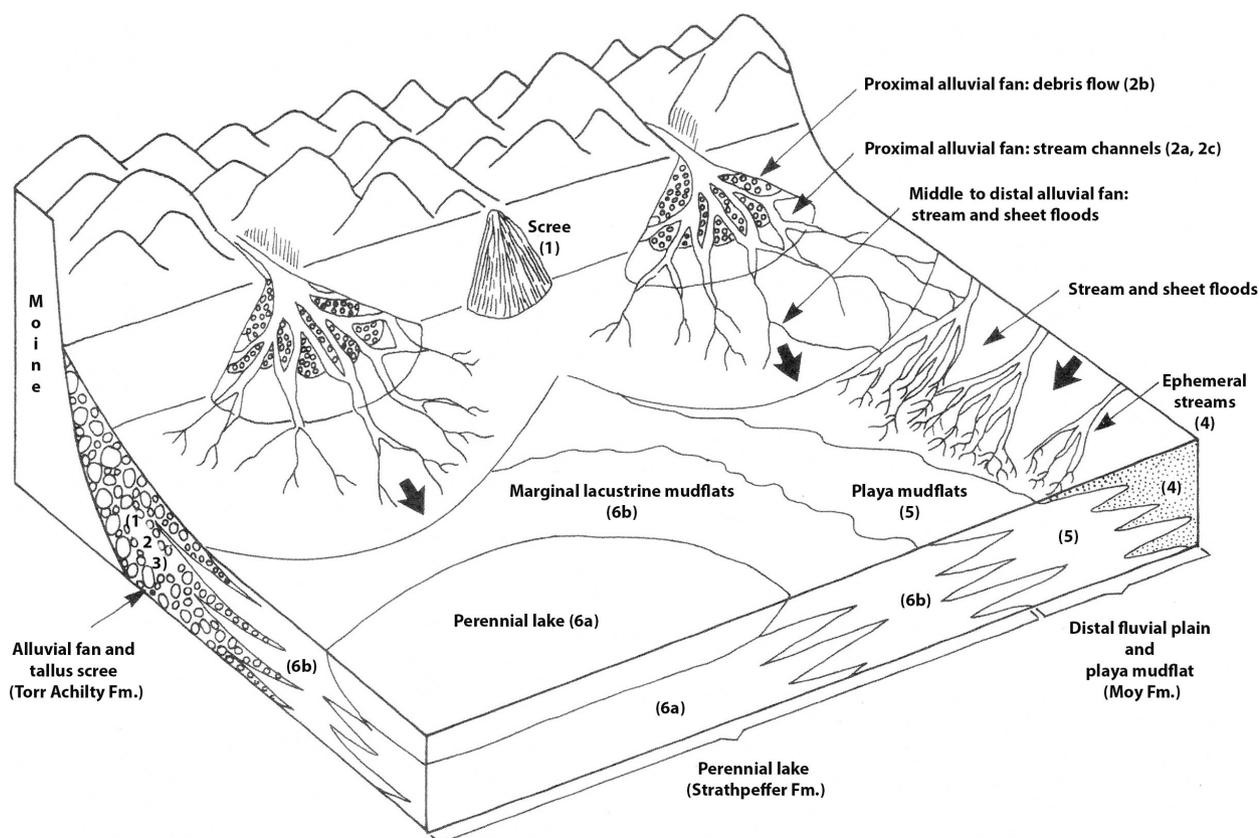
Note that Johnstone & Mykura (1989) used a separate stratigraphical terminology (the Struie Group) for the sediments in the north of the basin.

Rasul (1978) noted that the assemblages were almost identical to those from the Strathmore Group of the Midland Valley (Table 3) that were therein dated as Emsian (probably middle Emsian).

Macrofossils are extremely rare in the sequence. From Allt Goibhre (Appendix A), where there is exposure in the river south of the bridge and in the road cutting immediately west of the bridge, dark grey shales and fine

TABLE 2. Facies developed in the Strathpeffer–Struie Basin (after Clarke & Parnell 1999).

Formation	Environment	Facies	Palaeoenvironment
Torr Achilty Fm.	Talus scree and alluvial fan	(1) Breccia	Localized scree deposits
Torr Achilty Fm.	Talus scree and alluvial fan	(2a) Clast-supported conglomerate	Localized grain flow deposits
Torr Achilty Fm.	Talus scree and alluvial fan	(2b) Matrix-supported conglomerate	Streamflood and stream channel deposits
Torr Achilty Fm.	Talus scree and alluvial fan	(2c) Pebbly sandstones	Debris flow deposits
Torr Achilty Fm.	Talus scree and alluvial fan	(3) Micaceous sandstones and siltstones	Streamflood and overbank sheetflood deposits
Moy Fm.	Playa mudflats and distal fluvial plain	(4) Buff and red sandstones	Channelled streamflood and unconfined sheetflood
Moy Fm.	Playa mudflats and distal fluvial plain	(5) Red and grey mudstones	Sheetflood and settle-out from playa lakes
Strathpeffer Fm.	Perennial lacustrine	(6a) Interlaminated bituminous dolomitic series	Perennial saline lake and rare subaerial exposure
Strathpeffer Fm.	Perennial lacustrine	(6b) Interbedded bituminous dolomitic series	Sheetflood and settle-out at lake margins

**FIG. 4.** Model of the Lower Old Red Sandstone palaeoenvironments of the Dingwall–Strathpeffer Basin showing the distribution of numbered facies. Modified from Clarke & Parnell (1999) with permission.

sandstones (Torr Achilty Fm. Facies 3) have yielded a clam shrimp (reported as *Estheria* sp.) and a solitary fish fragment (Mykura 1978). Dunlop *et al.* (2023) described a scorpion fragment (Fig. 5A) recovered during

palynological analysis from Wyvisdale (Appendix A: Sample CSP1) where there is an excellent exposure of interdigitating sediments belonging to Facies 6b (interbedded bituminous dolomitic series) and Facies 5 (red and grey

TABLE 3. Previously reported dispersed spore assemblages from the LORS of Scotland.

Terrane	Locality/stratigraphy	Age [Ma] (spore zone)	References
SMVOS (W–E)	Midland Valley Silurian inliers	Early Wenlock [430–433] (CN Zone)	Wellman & Richardson (1993) Wellman (2024)
SMVOS (W–E)	Greywacke Conglomerate	Lochkovian [414–418] (MN Zone)	Wellman (2024)
NMVOS (W)	Arran	Early–middle Emsian [400–410] (AS Zone)	Wellman (2010)
NMVOS (W)	Portencross Beds	Lochkovian [414–418] (MN Zone)	Wellman (1993a)
NMVOS (E)	Stonehaven Group	Late Wenlock [427–430] (BV Zone)	Marshall (1991) Wellman (1993b) Lavender & Wellman (2002) Wellman <i>et al.</i> (2023)
NMVOS (E)	Arbuthnott Group	Lochkovian [414–418] (MN Zone)	Richardson <i>et al.</i> (1984) Lavender & Wellman (2002)
NMVOS (W–E)	Strathmore Group	Early–middle Emsian [400–410] (AS Zone)	Richardson (1967) Richardson <i>et al.</i> (1984)
GHOS (W)	Lorne	Earliest Lochkovian [418–420] (pre-Mn Zone)	Marshall (1991) Wellman & Richardson (1996)
GHOS (W)	Glencoe	Lochkovian [414–418] (MN Zone)	Wellman (1994)
GHOS (E)	Rhynie	Late Pragian to ?earliest Emsian [410–413] (PE Zone)	Wellman (2006)
NHOS	Mealfuarvonie inlier	Late Emsian to ?earliest Eifelian [393–400]	Mykura & Owens (1983)
NHOS	Strathpeffer–Struie outcrop	Latest Emsian [393–400] (DE Zone)	Richardson (1967) This paper
NHOS	Berriedale Outlier	Early–middle Emsian [400–410] (AS Zone)	Collins & Donovan (1977) Wellman (2015)

E, east; GHOS, Grampian Highlands of Scotland; LORS, Lower Old Red Sandstone; NHOS, Northern Highlands of Scotland; NMVOS, Northern Midland Valley of Scotland; SMVOS, Southern Midland Valley of Scotland; W, west. Numerical age dates are based on the International Commission on Stratigraphy International Chronostratigraphic Chart (v2024-12; Cohen *et al.* 2013).

mudstones) in the Strathpeffer and Moy fms (Clarke & Parnell 1999).

MATERIAL & METHOD

During the course of six fieldtrips 60 samples were collected from throughout the LORS sequence of the outlier (Appendix A). In addition, a single sample of a now inaccessible exposure was donated by John Parnell. The samples were processed using standard palynological techniques: HCl–HF acid maceration followed by heavy liquid separation using zinc chloride. Recovered organic residues were sieved using a 20 µm mesh, strew mounted onto glass coverslips, and attached to a glass slide using epoxy resin. A single slide of unoxidized residue was prepared for palynofacies analysis using a light microscope. The remainder of the organic residue was oxidized for 10–20 min using Schultz solution, to remove excess amorphous organic

matter (AOM) and pyrite and lighten the palynomorphs. Several slides of oxidized residue were prepared for light microscope analysis of the spore content. The palynological preparations were extremely variable, often displaying unusual palynofacies, as described below (see also Appendix A). When present, dispersed spores are of thermal alteration index 3– to 3 (based on the colour chart provided in Traverse 2007). Low thermal maturity is suggested based on the recovery of molecular biomarkers from the Strathpeffer sequence (Akinsanpe *et al.* 2024). All materials (samples, residues, slides) are housed in the collections of the Centre for Palynology of the University of Sheffield.

RESULTS: PALYNOFACIES

The nature of the palynological preparations (palynofacies) for each of the main formations/facies is described in the following account with sample details provided in Appendix A.



FIG. 5. Palynodebris from the Strathpeffer sequence. A, scorpion pectinal tooth with peg sensilla; slide CSP1/3; England Finder (EF) G49/2. B, banded tube; slide BAS3/2; EF O35. C, laevigate tube; slide CSP2/3; EF W40/4. D, banded tube; slide CSP2/2; EF M39/2. E, banded tube; slide CSP2/4; EF K35. F, fragment of *Prototaxites* sp.; slide BAS3/2; EF U47/3. G, bundle of filaments; slide 12SCOT07K; EF K45/1. H, fungal hypha; slide CSP1/4; EF J31/3. I, filament spirally arranged; sample CSP1(k); EF L42/1. J, spore preserved as a 'ghost' that is highly degraded and covered in pyrite crystals; slide AAG4/1; EF R30/2. K, filament associated with clump of amorphous organic matter (AOM); slide 12SCOT07(k); EF M28. L, sphaeromorph with surface spot; slide: CSP1/3; EF L39/2. M, sphaeromorph with surface spot; slide CSP2/3; EF K44. N, branching filament associated with a clump of AOM; slide CSP1(k); EF L42. O, clump of AOM infested with pyrite; slide 12SCOT07(k); EF U36. P, clump of AOM run through by parallel-arranged filaments; slide CSP1(k); EF P39/4. Scale bar represents: 150 μm (A); 120 μm (B–F, K); 60 μm (G, L, M); 30 μm (H–K, N, P); 20 μm (O).

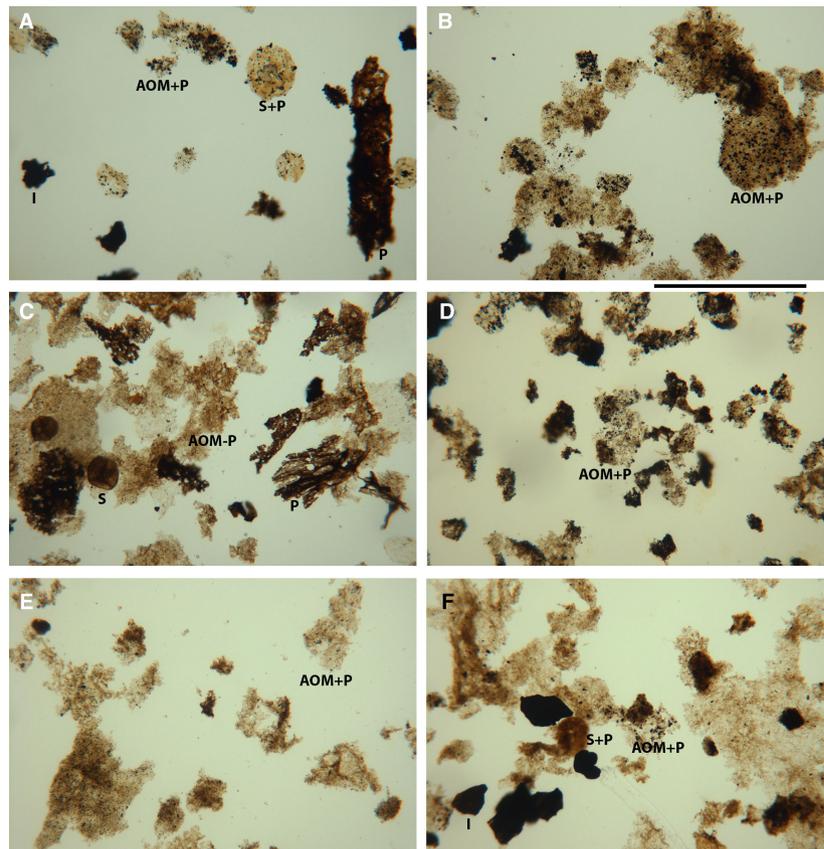


FIG. 6. Palynofacies and palynodebris from the Strathpeffer sequence. All images taken using a blue filter. See text for a description of the palynofacies. Phytodebris labels are placed directly below the relevant fragment: AOM + P, amorphous organic matter infested with pyrite; AOM-P, amorphous organic matter without pyrite; I, inertinite; P, phytodebris; S, spore; S + P, spore infested with pyrite. A, sample AAG5(k) from Facies 1–2 of the Tor Achilty Fm. at Aigas Dam. B, sample 14SCO07(k) from Facies 3 of the Tor Achilty Fm. at Allt Goibhre. C, sample CSP2(k) from Facies 5 of the Strathpeffer/Moy fms at Wyvisdale. D, sample JP1(k) from Facies 6 of the Strathpeffer Fm. at Strathpeffer village. E, sample ASP4(k) from Facies 6 of the Strathpeffer Fm. near Strathpeffer Golf Course. F, sample 12SCO07(k) from Facies 6 of the Strathpeffer Fm. at Strath Sgitheach. Scale bar represents 220 μm .

Torr Achilty Fm. Facies 1–3

Facies 1–2 conglomerates and breccias contain very little finer grained lithologies suitable for palynological analysis. However, samples were collected from a lens of sandy siltstones. They are dominated by AOM infested with pyrite with occasional inertinite fragments

(Fig. 6A). Spores and phytodebris are present in some samples. The spores are highly degraded and washed out ('ghosts'), infested with pyrite and unidentifiable (Fig. 5J). Facies 3 was collected at the Allt Goibre and River Orrin river sections. The palynofacies is identical to that described above for Facies 1–2 (Fig. 6B).

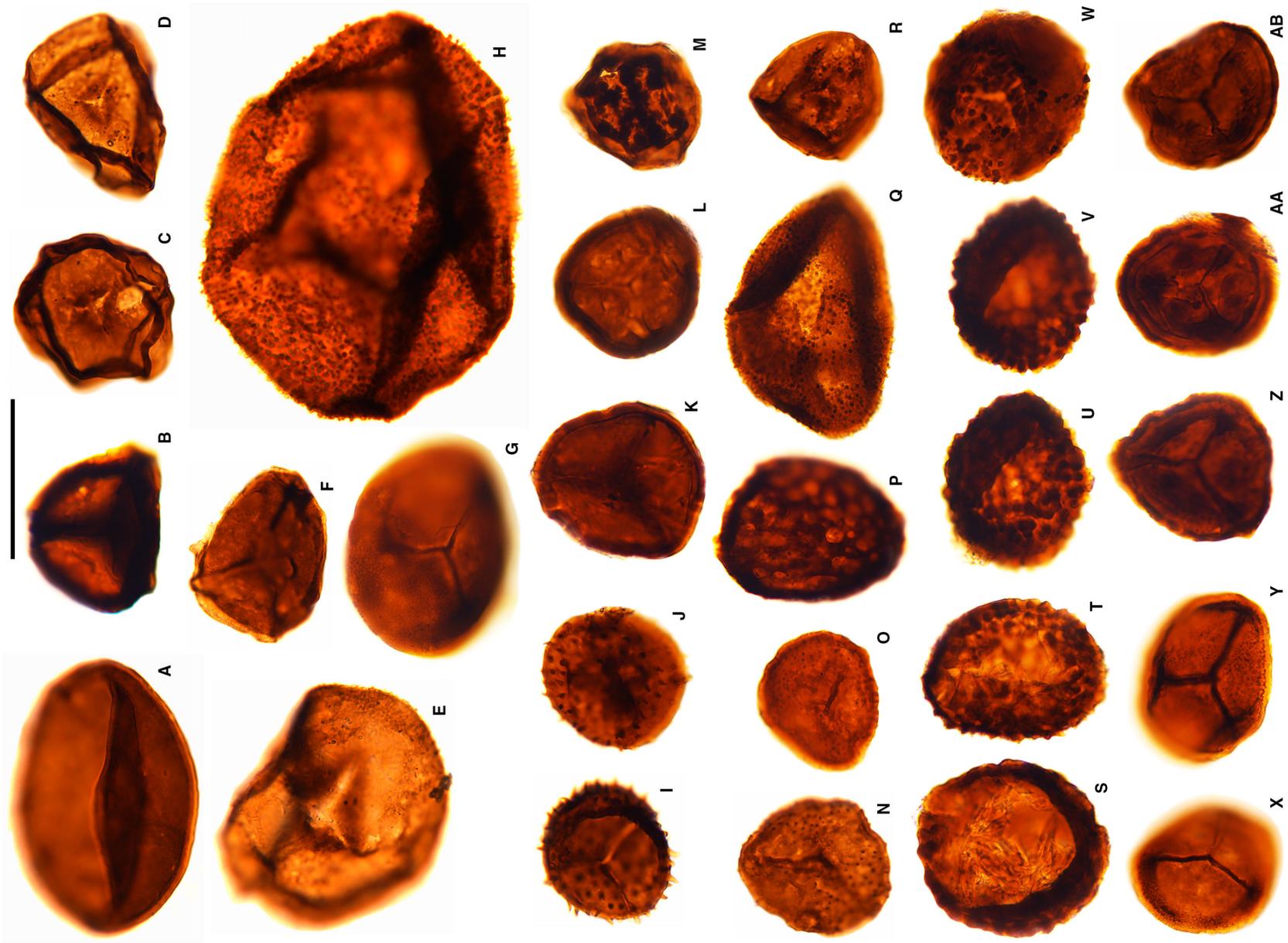


FIG. 7. Dispersed spores from the Moy Fm. A, *Latosporites* sp. (simple, laevigate monolet spore); slide CSP1.2; England Finder (EF) M36. B, *Tetraedraletes medinensis* (cryptospore permanent tetrad); slide CSP1.3; EF O41. C, *Retusotriletes rotundus*; slide CSP1.3; EF L34/1/2. D, *Retusotriletes triangulatus*; slide CSP2.2; EF P40/1/3. E, *Apiculiretusispora brandtii*; slide: CSP2.3; EF L43. F, *Apiculiretusispora plicata*; slide: CSP2.4; EF P45/2. G, *Apiculiretusispora gaspiensis*; slide CSP1.2; EF S32. H, *Dibolisporites echinaceus* (Eisenack) Richardson 1965; slide CSP2.2; EF N29/2/4. I, *Dibolisporites eifeliensis*; slide CSP2.4; EF C43. J, *Dibolisporites eifeliensis*; slide CSP1.2; EF W36. K, *Ambitisporites* sp.; slide CSP1.4; EF D30. L, *Archaeozonotriletes chulus* (Cramer) Richardson & Lister 1969; slide CSP1.3; EF V31/4. M, cf. *Amicosporites* sp. A; FSP1.2; EF E41/2. N, *Aneurospora* sp. A; slide CSP1.3; EF J34/1. O, *Aneurospora* sp. A; slide CSP1.4; EF G41/1. P, *Brochotriletes foveolatus*; slide CSP2.3; EF N47/3. Q, *Verrucosporites* cf. *Polygonalis*; slide CSP2.2; EF J37.2. R, *Verruciretusispora dubia*; slide CSP2.3; EF M46/2. S, *Chelinospora* sp. A; slide CSP1.2; EF D33.1. T, *Chelinospora* sp. A; slide CSP1.2; EF Z39/1. U–V, *Chelinospora* sp. A (different focal planes of the same specimen); slide CSP2.2; EF R42.1. W, *Verrucosporites* sp.; slide CSP1.3; EF Y42. X, *Cymbosporites* sp. A; slide CSP1.2; EF S43/1. Y, *Cymbosporites* sp. A; slide CSP1.3; EF X47. Z, cf. *Amicosporites* sp. B; slide CSP1.2; EF H30. AA, cf. *Amicosporites* sp. B; slide CSP1.3; EF S51/3. AB, cf. *Amicosporites* sp. B; slide CSP2.3; EF R50/4. Scale bar represents 20 μm .

Moy Fm. Facies 4–5

Facies 4–5 are usually too coarse (sandstones) or too oxidized (red mudstones–siltstones) to yield palynomorphs. However, rarely, unoxidized mudstones–siltstones of Facies 5 are encountered. Some of these samples are dominated by well-preserved spores and phytodebris (Fig. 6C). Others also contain additional AOM with pyrite content varying from low to high (Fig. 5O). The phytodebris includes a variety of tubular structures, cuticle-like sheets and arthropod cuticle (Fig. 5A). The tubular structures include laevigate tubes (Fig. 5C), banded tubes (Fig. 5B, D, E) and fungal hyphae (Fig. 5H). The tubular structures often occur in monospecific wefts (Fig. 5G) or a mixed association that probably represent *Prototaxites* (Fig. 5F). In the main these tubular structures probably represent nematophytes and fungi.

Strathpeffer Fm. Facies 6a & 6b

The bituminous dolomitic series (both Facies 6a interlaminated and 6b interbedded) was collected from a number of localities. A sample of black mudstone (Facies 6a) from behind the pump house (sample JP1) contained a huge quantity of AOM infested with pyrite and nothing else (Fig. 6D). Parnell (1985b) recorded total organic content levels of up to 2.48%. The samples of interlaminated and interbedded dolomite from the River Orrin, adjacent to the golf course and Strath Sgitheach (Fig. 6E–F) are dominated by AOM infested with pyrite (Fig. 5O) but often also contain inertinite and rare spores that are highly degraded and washed out ('ghosts'), infested with pyrite and unidentifiable (Fig. 5J). Fragments of microbial mat are represented by AOM associated with filaments that probably represent cyanobacteria (Fig. 5I, K, P). Often these cyanobacterial filaments are parallel-aligned (Fig. 5P). In one case the filament appears to be coiled (Fig. 5I). Branching tubular structures associated by AOM

are wider and are considered to be fungal hyphae (Fig. 5N).

Struie Beds

Samples from further north from the Struie Beds are variable and are usually either dominated by pyrite-infested AOM or inertinite and lacking spores and phytodebris. However, two samples, from the Alness River and Allt Muigh-Bhlairaidh, contained inertinite and well preserved spores and phytodebris (Appendix A).

RESULTS: DISPERSED SPORE ASSEMBLAGES

Workable spore assemblages were recovered from only four of the 61 samples collected. Two of these assemblages are from the Moy Fm. (Facies 5) at Wyvisdale and two are from further north, at the Alness River and Allt Muigh-Bhlairaidh (Appendix A). They all essentially contain the same spore assemblage. Table 4 lists the taxa reported and these are shown in Figures 7 and 8. Many of the other palynological samples contain spores but they are usually too degraded to identify confidently.

The Strathpeffer spore assemblage can be equated with the *douglstownense–eurypterota* Spore Assemblage Biozone (DE SAB) of Richardson & McGregor (1986), indicating a late Emsian to earliest Eifelian age. Both of the nominal species are present (*Grandispora douglstownensis* and *Ancyrospora eurypterota*), and eight out of the 14 characteristic species (Table 4). These include spores with grapnel-tipped processes (*Ancyrospora* and *Hystricosporites*), a diversity of large, apiculate and spinose, zonate-pseudosaccate spores and the persistence of species such as *Dibolisporites echinaceus* and *Verruciretusispora dubia*. A number of long-ranging spores characteristic of the preceding *annulatus–sextantii* SAB, such as

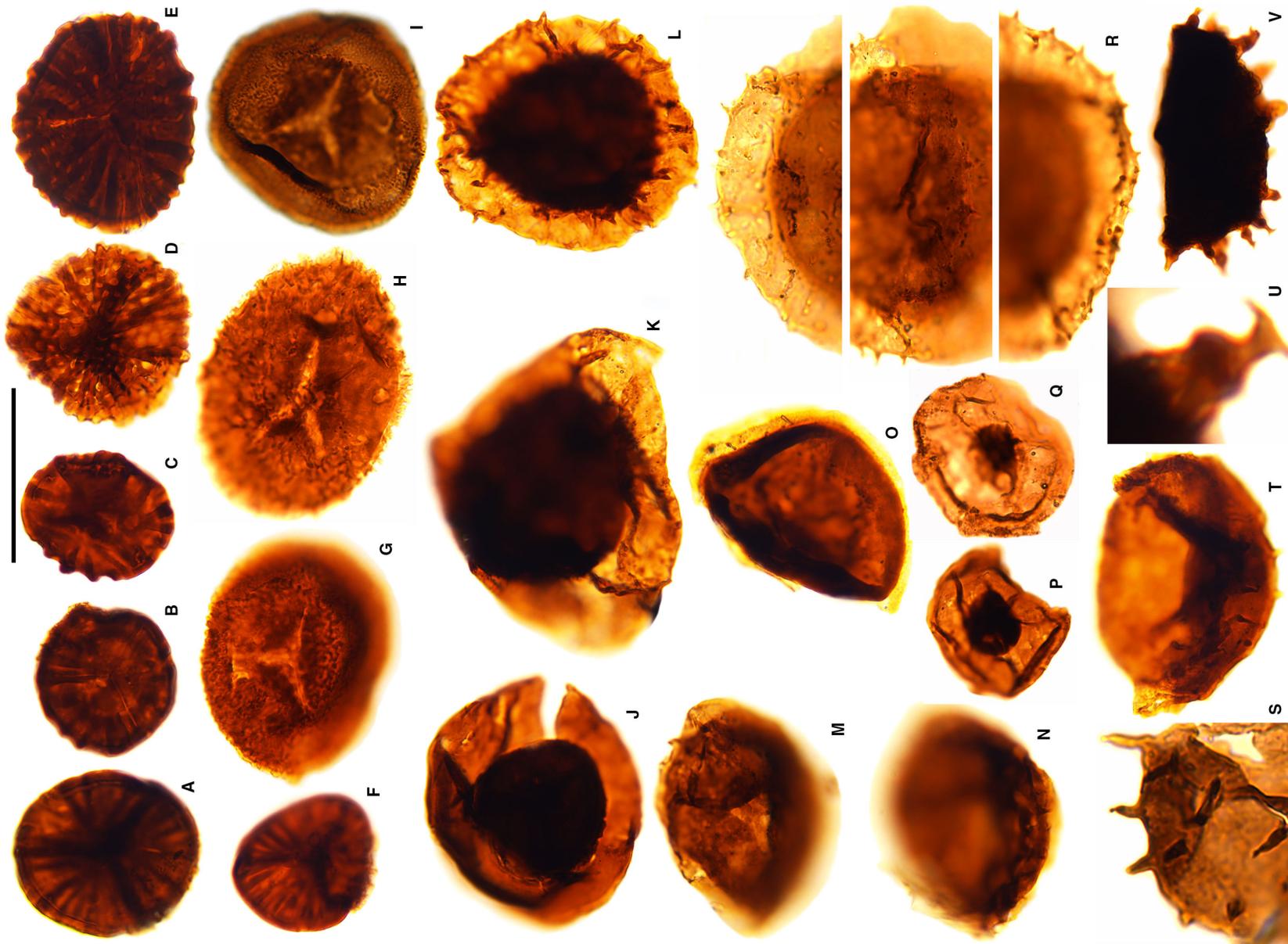


FIG. 8. Dispersed spores and other palynomorphs from the Moy Fm. A, *Emphanisporites rotatus*; slide CSP1.2; England Finder (EF) G38. B, *Emphanisporites annulatus*; slide CSP2.2; EF P41. C, *Emphanisporites erraticus*; slide CSP1.3; EF H46. D, *Emphanisporites foveolatus*; slide CSP2.2; EF V28/3. E, *Emphanisporites foveolatus*; slide CSP1.2; E N29/2. F, *Emphanisporites mcgregorii*; slide BAS3.2; EF R30/2. G, *Acinosporites lindlarensis*; slide CSP2.4; EF J45/2. H, *Acinosporites lindlarensis*; slide CSP2.4; EF H37. I, *Acinosporites apiculatus*; slide CSP1.4; EF U41/2. J, laevigate zonate spore; slide: CSP2.3; EF J46/2. K, *Calyptosporites proteus*; slide CSP2.2; EF R39. L, *Grandispora douglastownensis*; slide CSP1.4; EF O49. M–N, *Samarisporites inusitatus* (different focal planes of the same specimen); slide CSP2.3; EF N39/1. O, *Rhabdosporites minutus*; slide CSP2.3; EF O49/1. P, sphaeromorph with spot; slide CSP2.3; EF K44. Q, sphaeromorph with spot; slide CSP1.3; EF L39/2. R, *Ancyrospora eurypterota* (composite of three images of the same specimen); slide CSP2.3; EF J37. S, *Hystricosporites microancyreus* (close up of ornament on a broken specimen); slide CSP2.4; EF J31/3. T, *Hystricosporites microancyreus*; slide CSP2.4; EF M32. U–V, *Ancyrospora eurypterota* (specimen in lateral compression with proximal surface missing; U is a close up of the ornament); slide CSP2.3; EF N48. Scale bar represents 20 μm except in S (22 μm) and U (10 μm).

Emphanisporites annulatus, persist into the Strathpeffer spore assemblage.

In terms of the spore zonation scheme of Streel *et al.* (1987) the Strathpeffer assemblage can be placed with the Pro Interval Zone of the AP Opper Zone, again indicating a latest Emsian to earliest Eifelian age. Designation to this zone is based on the presence of *Calyptosporites proteus*, *Acinosporites apiculatus* and the first appearance of spores with grapnel-tipped processes. Once again, certain spores characteristic of preceding zones are present, such as *Emphanisporites foveolatus* and *Rhabdosporites minutus*.

A latest Emsian age seems probable based on the absence of spores characteristic of the Eifelian. For example, *Ancyrospora nettersheimensis* and *Calyptospora velatus* that feature in the zonal scheme of Streel *et al.* (1987) are not present. Riegel (1982) provided a range chart of stratigraphically significant spores that he identified at the Emsian–Eifelian boundary in the type Eifel region, and none of the spores that made their inception in the Eifelian are reported from the Strathpeffer assemblage.

DISCUSSION

The interpretation reported herein suggests that the Strathpeffer–Struie spore assemblages are of a slightly younger age than proposed by Richardson (1967) and Richardson & Rasul (1978), and belong with the D–E Spore Assemblage Biozone. These are the first D–E spore assemblages reported from Scotland (summarized in Table 3). It is becoming clear that the Basement Group of the Orcadian Basin, that unconformably overlies the Moine, is of slightly different ages in different places (Table 3). This has implications regarding a staggered onset of ORS facies sedimentation in northeast Scotland and hence implications for tectonic models for the region (e.g. Law *et al.* 2025).

In terms of palaeoenvironment, the palynofacies analysis supports interpretation as a shallow, highly saline,

sulphate lake and associated playa mudflat in a restricted intermontane basin. Potential modern analogues include high-altitude lakes in the Andes and Tibetan Plateau (Risacher & Fritz 2009; Zheng & Liu 2009). It is difficult to determine the altitude of the Scottish Caledonian Mountains towards the end of the Emsian, although Barker *et al.* (2000) suggested, based on analysis of meteoric fluid veining, that the north Norwegian Caledonides had a topography in excess of 5 km in the Lower Devonian. It is clear that microbial mats and stromatolites thrived in the Strathpeffer–Struie lake and on the associated playa, presumably in the absence of grazing organisms (be they invertebrates or fish). Note that the solitary fish fossil recovered from the sequence is from Facies 3 (stream-flood and overbank sheetflood deposits) and was probably a fluvial form washed in during a flood. The microbial mats are preserved as kerogenous laminae in certain facies (Table 2) and are recovered as AOM in the palynological assemblages (Fig. 5P). The latter often contain filaments interpreted as cyanobacterial remains and fungal hyphae (Fig. 5). The presence of planktonic algae in the lake is indicated by the recovery of algal cysts (Fig. 5L–M). Interestingly biomarker studies by Akin-sanpe *et al.* (2024) suggested that a significant proportion of the lake primary productivity was in the form of halophilic archaea. The harsh aquatic and terrestrial environments were not entirely devoid of animal life, as evidenced by the presence of arthropod cuticles, including those from terrestrial scorpions, and clam shrimps (reported as *Estheria* sp.). Extant clam shrimps commonly inhabit modern playas in addition to fresh water habitats.

The presence of abundant pyrite, in rock specimens collected in the field and in palynological preparations, is noteworthy (Fig. 5J, O). This could indicate a perennial lake that was deep and stratified with anoxic bottom waters that precipitated pyrite. However, the presence of microbial mats indicates a lake depth shallower than the photic zone, and the limited lateral extent of the basin also suggests a lake of small dimensions. Alternatively, the pyrite may have formed at the sediment–water interface

TABLE 4. Reported spore taxa with a key to illustrations herein.

Taxon	Illustration
<i>Tetraedraletes medinensis</i> Strother & Traverse emend Wellman & Richardson 1993	Figure 7B
<i>Latosporites</i> sp.	Figure 7A
<i>Retusotrilletes triangulatus</i> (Streel) Streel 1967	Figure 7D
<i>Retusotrilletes rotundus</i> (Streel) Streel 1967	Figure 7C
<i>Retusotrilletes</i> spp.	
<i>Apiculiretusispora brandtii</i> Streel 1964	Figure 7E
<i>Apiculiretusispora gaspiensis</i> McGregor 1973	Figure 7G
<i>Apiculiretusispora plicata</i> (Allen) Streel 1967	Figure 7F
<i>Dibolisporites echinaceus</i> (Eisenack) Richardson 1965	Figure 7H
<i>Dibolisporites eifeliensis</i> (Lanninger) McGregor 1973	Figure 7I, J
<i>Ambitisporites</i> spp.	Figure 7K
<i>Aneurospora</i> sp. A	Figure 7N, O
<i>Brochotrilletes foveolatus</i> Naumova 1953	Figure 7P
<i>Emphanisporites annulatus</i> McGregor 1961	Figure 8B
<i>Emphanisporites erraticus</i> (Eisenack) McGregor 1961	Figure 8C
<i>Emphanisporites foveolatus</i> Schultz 1968	Figure 8D, E
<i>Emphanisporites mcgregorii</i> Cramer 1966	Figure 8F
<i>Emphanisporites rotatus</i> McGregor 1961	Figure 8A
<i>Verruciretusispora dubia</i> (Eisenack) Richardson & Rasul 1978	Figure 7R
<i>Verrucosporites polygonalis</i> Lanninger 1968	Figure 7Q
<i>Verrucosporites</i> sp.	Figure 7W
cf. <i>Amicosporites</i> sp. A	Figure 7M
cf. <i>Amicosporites</i> sp. B	Figure 7Z–AB
<i>Archaeozonotrilletes chulus</i> (Cramer) Richardson & Lister 1969	Figure 7L
<i>Chelinospora</i> sp. A	Figure 7S–V
<i>Cymbosporites</i> sp. A	Figure 7X, Y
<i>Acinosporites apiculatus</i> (Streel) Streel 1967	Figure 8I
<i>Acinosporites lindlarensis</i> Riegel 1968	Figure 8G, H
<i>Ancyrospora eurypteroata</i> Riegel 1973	Figure 8R, U, V
<i>Calyptosporites proteus</i> (Naumova) Allen 1965	Figure 8K
<i>Grandispora douglstownensis</i> McGregor 1973	Figure 8L
Zonate laevigate spore	Figure 8J
<i>Hystricosporites microancyreus</i> Riegel 1973	Figure 8S, T
<i>Rhabdosporites minutus</i> Tiwari & Schaarschmidt 1975	Figure 8O
<i>Samarisporites inusitatus</i> Allen 1965	Figure 8M, N

in a shallow perennial–ephemeral lake. Saline sulphate-rich water at the lake–sediment interface (free water above the interface and/or interstitial water just below) can interact with sulphate-reducing bacteria.

Consequently reduced sulphate and ferric oxides can react to form pyrite, H₂S and CH₄ (Hardie *et al.* 1978). Such an interpretation is supported by the presence of gypsum pseudomorphs associated with pyrite as discussed by Parnell (1985a) and Clarke & Parnell (1999).

Beyond the saline lake and associated playa mudflat, it is evident based on the presence of dispersed spores, that the basin harboured a significant vegetation. Dispersed spore assemblages from coeval deposits from elsewhere on the ORS continent have been described from north-eastern USA and eastern Canada (McGregor 1973, 1977; Andrews *et al.* 1977; Wellman 2018), the Ardenne–Rhenish region (Riegel 1973, 1982; Streel *et al.* 1981) and Poland (Turnau 1974, 1986; Filipiak 2011; Filipiak *et al.* 2022). The Strathpeffer spore assemblage is depauperate compared with these, with fewer taxa and certain key elements missing (e.g. spores with grapnel-tipped spines such as *Ancyrospora eurypteroata* Riegel 1973, *Ancyrospora keddoae* (Riegel) Turnau 1974, *Ancyrospora loganii* McGregor 1973 and *Hystricosporites* cf. *H. corystus* Richardson 1962 *sensu* Riegel 1973). There are also spores that have not previously been described (e.g. the two species of *Amicosporites*) or are rare elsewhere (e.g. *Emphanisporites foveolatus* that is unusually abundant in the assemblages described herein). These differences probably reflect the fact that the Strathpeffer assemblage is from an inland, upland intermontane basin, with a depauperate and partially endemic flora, whereas the other assemblages are from lowland basins relatively close to the Laurussian shoreline, which presumably harboured a more diverse vegetation.

The presence of tubular structures interpreted as nematophyte in origin is interesting. Banded tubes are rarely reported from post-Pragian strata (Wellman & Ball 2021). However, the nematophyte *Prototaxites* is known to have extended into the Late Devonian (Honegger *et al.* 2017), and fragments of this enigmatic organism are found in the Strathpeffer dispersed spore assemblages. Here they co-occur with other fragments of cuticle and conducting tissues that clearly derive from embryophytic land plants.

CONCLUSIONS

1. Dispersed spore assemblages indicate that the deposits of the Dingwall–Strathpeffer Basin are of late Emsian age (c. 394 Ma).
2. Palynofacies analysis supports deposition in a back-tilted basin associated with a highly saline sulphate lake and associated playa mudflat.
3. Dispersed spore assemblages indicate that the surrounding upland vegetation was restricted and to a certain extent endemic.

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REFERENCES

- Akinsanpe, T. O., Bowden, S. A. and Parnell, J. 2024. Molecular and mineral biomarker record of terrestrialisation in the Rhy-
nie chert. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **640**, 112101.
- Allen, K. C. 1965. Lower and Middle Devonian spores of North
and Central Vestspitsbergen. *Palaeontology*, **8**, 687–748.
- Andrews, H. N., Kasper, A. E., Forbes, W. H., Gensel, P. G. and
Chaloner, W. G. 1977. Early Devonian flora of the Trout Val-
ley Formation of northern Maine. *Review of Palaeobotany and
Palynology*, **23**, 255–285.
- Barker, A. J., Bennett, D. G., Boyce, A. J. and Fallick, A. E. 2000.
Retgression by deep infiltration of meteoric fluids into
thrust zones during late-orogenic rapid deroofing. *Journal of
Metamorphic Geology*, **18**, 307–318.
- Clarke, P. and Parnell, J. 1999. Facies analysis of a back-tilted
lacustrine basin in a strike-slip zone, Lower Devonian, Scotland.
Palaeogeography Palaeoclimatology Palaeoecology, **151**, 167–190.
- Cohen, K. M., Finney, S. C., Gibbard, P. L. and Fan, J.-X. 2013.
The ICS international chronostratigraphic chart. *Episodes*, **36**,
199–204.
- Collins, A. G. and Donovan, R. N. 1977. The age of two Old
Red Sandstone sequences in southern Caithness. *Scottish Jour-
nal of Geology*, **13**, 53–57.
- Cramer, F. H. 1966. Palynology of Silurian and Devonian rocks
in Northwest Spain. *Boletín del Instituto Geológico y Minero de
España*, **77**, 223–286.
- Dec, T. 1992. Textural characteristics and interpretation of
second-cycle, debris-flow-dominated alluvial fans (Devonian
of northern Scotland). *Sedimentary Geology*, **77**, 269–296.
- Dunlop, J. A., Wellman, C. H., Prendini, L. and Shear, W. A.
2023. A pectinal tooth with peg sensilla from an Early Devo-
nian scorpion. *Journal of Arachnology*, **51**, 255–257.
- Filipiak, P. 2011. Palynology of the Lower and Middle Devonian
deposits in southern and central Poland. *Review of Palaeo-
botany and Palynology*, **166**, 213–252.
- Filipiak, P., Kenrick, P., Wawrzyniak, Z., Kondas, M. and
Strullu-Derrien, C. 2022. Plants and palynomorphs from the
Lower Devonian (upper Emsian) of the Holy Cross Mountains,
Poland. *Review of Palaeobotany and Palynology*, **302**, 104666.
- Fletcher, T. P., Auton, C. A., Highton, A. J., Merritt, J. W.,
Roberston, S. and Rollin, K. E. 1996. *Geology of the Fortrose
and eastern Inverness district, Scotland. Sheet 84W (S)*. Mem-
oirs of the British Geological Survey.
- Friend, P. F. and Williams, B. P. J. 1978. *A field guide to selected
areas of the Devonian of Scotland, the Welsh Borderland and
South Wales. International Symposium on the Devonian System
(PADS 78)*. The Palaeontological Association.
- Hardie, L. A., Smoot, J. P. and Eugster, H. P. 1978. Saline lakes
and their deposits: a sedimentological approach. 7–41. In Mat-
ter, A. and Tucker, M. E. (eds) *Modern and ancient lake sedi-
ments*. Special Publication of the International Association of
Sedimentology 2.
- Honegger, R., Edwards, D., Axe, L. and Strullu-Derrien, C.
2017. Fertile *Prototaxites taiti*: a basal ascomyte with inopercu-
late, polysporous asci lacking croziers. *Philosophical Transac-
tions of the Royal Society B*, **373**, 20170146.
- Horne, J. 1923. *The geology of the Lower Findhorn and Lower
Strath Nairn including part of the Black Isle near Fortrose
(explanation of sheet 84 and part of 94)*. Memoirs of the Geo-
logical Survey of Scotland.
- Horne, J. and Hinxman, L. W. 1914. *The geology of the country
round Beaulieu and Inverness: Including a part of the Black Isle
(explanation of sheet 83)*. Memoirs of the Geological Survey of
Scotland.
- Johnstone, G. S. and Mykura, W. 1989. *British regional geology:
The Northern Highlands of Scotland*, Fourth edition. HM Sta-
tionery Office, London.
- Lanninger, E. P. 1968. Sporen-Gesellschaften aus dem Ems der
SW-Eifel. *Palaeontographica, Abteilung B*, **122**, 95–170.
- Lavender, K. and 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.
- Law, R. D., Thigpen, J. R., Mako, C. A., Kylander-Clark, A.,
Caddick, M. J., Moore, L. R., Becker, C., Holdsworth, R. E.,
Strachan, R. A. and Leslie, A. G. 2025. The timing and signifi-
cance of mid-crustal shearing and exhumation of
amphibolite-facies rocks along the Great Glen Fault Zone,
Scotland. *Journal of the Geological Society*, **182**, jgs2024-264.
- 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. 2024. Old Red Sandstone: continental sedi-
mentation on the eroding Caledonian orogen. 259–292. In
Smith, M. and Strachan, R. (eds) *The geology of Scotland*, Fifth
edition. Geological Society, London.
- Marshall, J. E. A. and Hewett, A. J. 2003. Devonian. 65–81. In
Evans, D., Graham, C., Armour, A. and Bathurst, P. (eds) *The
millennium atlas: Petroleum geology of the central and northern
North Sea*. Geological Society, London.
- McGregor, D. C. 1961. Spores with proximal radial pattern from
the Devonian of Canada. *Geological Survey of Canada Bulletin*,
76, 1–11.
- McGregor, D. C. 1973. Lower and Middle Devonian spores of
eastern Gaspé, Canada. I. Systematics. *Palaeontographica Abtei-
lung B*, **142**, 1–77.
- McGregor, D. C. 1977. Lower and Middle Devonian spores of
eastern Gaspé, Canada. II. Biostratigraphy. *Palaeontographica
Abteilung B*, **163**, 111–142.
- Mykura, W. 1978. South-Western Moray Firth. 27–37. In Friend,
P. F. and Williams, B. P. J. (eds) *A field guide to selected*

- outcrop areas of the Devonian of Scotland, *The Welsh Borderland and South Wales. International Symposium on the Devonian System (PADS 78)*. Palaeontological Association.
- Mykura, W. and Owens, B. 1983. The Old Red Sandstone of the Mealfuarvonie Outlier, west of Loch Ness, Inverness-shire. *Institute of Geological Sciences Report*, **83/7**, 1–17.
- Naumova, S. N. 1953. Spore–pollen assemblages of the Upper Devonian of the Russian Platform and their stratigraphic significance. *Transactions of the Institute of Geological Sciences, Academy of Sciences of the USSR*, **143** (geological series no. (60), 1–203. [in Russian]
- Parnell, J. 1985a. Evidence for evaporates in the ORS of northern Scotland: replaced gypsum horizons in Easter Ross. *Scottish Journal of Geology*, **21**, 377–380.
- Parnell, J. 1985b. Hydrocarbon source rocks, reservoir rocks and migration in the Orcadian Basin. *Scottish Journal of Geology*, **21**, 321–335.
- Peach, B. N., Gunn, W., Clough, C. T., Hinxman, L. W., Crampton, C. B. and Anderson, E. M. 1912. *The geology of Ben Wyvis, Carn Chuinneag, Inchbae and the surrounding country, including Garve, Evanton, Atness and Kincardine (explanation of sheet 93)*. Memoirs of the Geological Survey of Scotland.
- Richardson, J. B. 1962. Spores with bifurcate processes from the Middle Old Red Sandstone of Scotland. *Palaeontology*, **5**, 171–194.
- Richardson, J. B. 1965. Middle Old Red Sandstone spore assemblages from the Orcadian basin, north-east Scotland. *Palaeontology*, **7**, 559–605.
- Richardson, J. B. 1967. Some British Lower Devonian spore assemblages and their stratigraphic significance. *Review of Palaeobotany and Palynology*, **1**, 111–129.
- Richardson, J. B. and Lister, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology*, **12**, 201–252.
- Richardson, J. B. and McGregor, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geological Survey of Canada Bulletin*, **364**, 1–79.
- Richardson, J. B. and Rasul, S. M. 1978. Palynological evidence for the age and provenance of the Lower Old Red Sandstone from the Appley Barn Borehole, Witney, Oxfordshire. *Proceedings of the Geologists' Association*, **90**, 27–42.
- Richardson, J. B., Ford, J. H. and Parker, F. 1984. Miospores, correlation and age of some Scottish Lower Old Red Sandstone sediments from the Strathmore region (Fife and Angus). *Journal of Micropalaeontology*, **3**, 109–124.
- Riegel, W. 1968. Die Mitteldevon-flora von Lindlar (Rheinland). 2. Sporae dispersae. *Palaeontographica, Abteilung B*, **123**, 76–96.
- Riegel, W. 1973. Sporenformen aus den Heisdorf-, Launch- und Nohn-Schichten (Emsium und Eifelium) der Eifel, Rheinland. *Palaeontographica Abteilung B*, **142**, 78–104.
- Riegel, W. 1982. Palynological aspects of the Lower/Middle Devonian transition in the Eifel region. *Courier Forschungsinstitut Senckenberg*, **55**, 279–292.
- Risacher, F. and Fritz, B. 2009. Origin of salts and brine evolution of Bolivian and Chilean salars. *Aquatic Geochemistry*, **15**, 123–157.
- Schultz, G. 1968. Eine unterdevonische Mikroflora aus den Kletter Schichten der Eifel (Rheinisches Schiefergebirge). *Palaeontographica, Abteilung B*, **123**, 4–42.
- Streel, M. 1964. Une association de spores du Givétien inférieur de la Vesdre, à Goé (Belgique). *Annales de la Société Géologique de Belgique*, **87**, 1–30.
- Streel, M. 1967. Associations de spores du Dévonien inférieur belge et leur signification stratigraphique. *Annales de la Société Géologique de Belgique*, **90**, 11–53.
- Streel, M., Fairon-Demaret, M., Otazo-Bozo, N. and Steemans, P. 1981. Etudes stratigraphiques des spores du Devonien Inférieur au bord sud du synclinorium de Dinant (Belgique) et leurs applications. *Annales de la Société Géologique de Belgique*, **104**, 173–191.
- Streel, M., Higgs, K., Loboziak, S., Riegel, W. and Steemans, P. 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenn-Rhenish region. *Review of Palaeobotany and Palynology*, **50**, 211–229.
- Tiwari, R. S. and Schaarschmidt, F. 1975. Palynological studies in the Lower and Middle Devonian of the Prum Syncline, Eifel (Germany). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **534**, 1–129.
- Torsvik, T. H. and Cocks, L. R. M. 2017. *Earth history and palaeogeography*. Cambridge University Press.
- Traverse, A. 2007. *Paleopalynology*, Second edition. Springer.
- Trewin, N. H. and Thirlwall, M. F. 2002. Old Red Sandstone. 213–249. In Trewin, N. H. (ed.) *The geology of Scotland*, Fourth edition. Geological Society, London.
- Turnau, E. 1974. Microflora from core samples of some Palaeozoic sediments from beneath the flysch Carpathians (Bielsko-Wadowice area, southern Poland). *Annales de la Société Géologique de Pologne*, **44**, 143–169.
- Turnau, E. 1986. Lower to Middle Devonian spores from the vicinity of Pionki (Central Poland). *Review of Palaeobotany and Palynology*, **46**, 311–354.
- Wellman, C. H. 1993a. A Lower Devonian sporomorph assemblage from the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **84**, 117–136.
- Wellman, C. H. 1993b. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven Group, Scotland. *Journal of Micropalaeontology*, **12**, 47–66.
- Wellman, C. H. 1994. Palynology of the “Lower Old Red Sandstone” at Glen Coe, Scotland. *Geological Magazine*, **131**, 563–566.
- Wellman, C. H. 2006. Spore assemblages from the Lower Devonian “Lower Old Red Sandstone” of the Rhynie outlier, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **97**, 167–211.
- Wellman, C. H. 2010. Spore assemblages from the Lower Devonian ‘Lower Old Red Sandstone’ deposits of Arran, Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **100**, 391–397.
- Wellman, C. H. 2015. Spore assemblages from the Lower Devonian ‘Lower Old Red Sandstone’ deposits of the Northern Highlands of Scotland: the Berriedale Outlier. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **105**, 227–238.

- Wellman, C. H. 2018. The classic Lower Devonian plant-bearing deposits of northern New Brunswick, eastern Canada: dispersed spore taxonomy and biostratigraphy. *Review of Palaeobotany and Palynology*, **249**, 24–49.
- Wellman, C. H. 2024. Spore assemblages from the Silurian–Lower Devonian ‘Lower Old Red Sandstone’ deposits of the Lanark basin of the Midland Valley of Scotland. *Fossil Imprint*, **80**, 9–18.
- Wellman, C. H. and Ball, A. C. 2021. Early land plant phytodebris. 309–320. In Marret, F., O’Keefe, J., Osterloff, P., Pound, M. and Shumilovskikh, L. (eds) *Applications of non-pollen palynomorphs: From palaeoenvironmental reconstruction to biostratigraphy*. Geological Society, London, Special Publications 511.
- Wellman, C. H. and Richardson, J. B. 1993. Terrestrial plant microfossils from Silurian inliers of the Midland Valley of Scotland. *Palaeontology*, **36**, 155–193.
- Wellman, C. H. and Richardson, J. B. 1996. Sporomorph assemblages from the “Lower Old Red Sandstone” at Lorne, Scotland. *Special Papers in Palaeontology*, **55**, 41–101.
- Wellman, C. H., Lopes, G., McKellar, Z. and Hartley, A. 2023. Age of the basal ‘Lower Old Red Sandstone’ Stonehaven Group of Scotland: the oldest reported air-breathing land animal is Silurian (late Wenlock) in age. *Journal of the Geological Society*, **181**, jgs2023-138.
- Westoll, T. S. 1977. Northern Britain. 66–93. In House, M. R., Richardson, J. B., Chaloner, W. G., Allen, J. R. L., Holland, C. H. and Westoll, T. S. (eds) *A correlation of Devonian rocks of the British Isles*. Geological Society, London, Special Report 7.
- Zheng, M. P. and Liu, X. F. 2009. Hydrochemistry of salt lakes of the Qinghai-Tibet Plateau, China. *Aquatic Geochemistry*, **15**, 293–320.
- AAG1 (98CW061) [Dominated by AOM infested with pyrite. Spores and phytodebris common but highly degraded, pyrite infested and unidentifiable.]
- AAG2 (98CW0G) [Dominated by AOM infested with pyrite and inertinite. No palynomorphs present.]
- AAG3 (98CW048) [Dominated by AOM infested with pyrite. Rare spores present but highly degraded, pyrite infested and unidentifiable.]
- AAG4 (98CW016) [Dominated by spores and phytodebris with a moderate amount of AOM infested with pyrite. Spores and phytodebris highly degraded, pyrite infested and unidentifiable.]
- AAG5 (98CW062) [Dominated by AOM infested with pyrite with rare inertinite. Spores and phytodebris common but highly degraded, pyrite infested and unidentifiable.]

Allt Goibhre NH2480/8508 (exposure in river south of bridge and in the road cutting immediately west of bridge)

The river yields a continuous section with a coarse basal conglomerate (Torr Achilty Fm. Facies 1–2) overlain by dark grey shales and fine sandstones (Torr Achilty Fm. Facies 3). The latter have yielded the clam shrimp ‘*Estheria* sp.’ and in the road cutting above the bridge a solitary fish fragment (Mykura 1978). All of the samples collected were from Facies 3.

BSP6 (99CW061) Barren

BSP7 (00CW016) Barren

BSP8 (00CW017) Barren

14SCO05 (14CW006) [Dominated by AOM infested with pyrite. Rare spores and phytodebris present but highly degraded, pyrite infested and unidentifiable.]

14SCO06 (14CW007) [Dominated by AOM infested with pyrite. Rare spores and phytodebris present but highly degraded, pyrite infested and unidentifiable.]

14SCO07 (14CW008) [Dominated by AOM infested with pyrite. Rare spores and phytodebris present but highly degraded, pyrite infested and unidentifiable.]

River Orrin NH2476/8516 (exposure in River Orrin at Falls of Orrin)

The river yields a near continuous section with a coarse basal conglomerate-breccia (Torr Achilty Fm. Facies 1–2) overlain by dark grey fine sandstones (Torr Achilty Fm. Facies 3) overlain by the bituminous dolomitic series (Strathpeffer Fm. Facies 6) (Clarke & Parnell 1999). Both samples are from Facies 6.

BSP9 (99CW74) Barren

14SCO08 (14CW009) [Dominated by AOM infested with pyrite. Rare spores and phytodebris present but highly degraded, pyrite infested and unidentifiable.]

River Conon Power Station in Torr Achilty area NH2447/8546

There are only conglomerates, breccias and sandstones exposed in this vicinity belonging to Facies 1–2:

APPENDIX A

Details of exposures, sampling and palynological results from Strathpeffer–Alness–Struie (S to N) (Figs 1–3). Samples marked with an asterisk and in bold were palynologically logged.

A833 roadcuts

Only conglomerates-breccias are exposed in this vicinity belonging to Facies 1–2: breccia-conglomerate (Torr Achilty Fm.). No samples suitable for palynological analysis.

A831-River Beaully roadcuts

There are predominantly conglomerates-breccias exposed in this vicinity belonging to Facies 1–2: breccia-conglomerate (Torr Achilty Fm.). No samples suitable for palynological analysis.

Aigas Dam, River Beaully NH2474/8436 (east bank of River Beaully just north of the bridge/power station)

Samples were collected from a sandy siltstone layer in the conglomerates-breccias belonging to Facies 1–2: breccia-conglomerate (Torr Achilty Fm.) that overlie the highly irregular Moine Schist/LORS unconformity (Mykura 1978).

breccia-conglomerate and Facies 3: sandstone of the Torr Achilty Fm. (Clarke & Parnell 1999). No samples collected.

A835 roadcuts between Marybank turnoff and Brahan Quarries

The exposed rock consists entirely of red sandstones belonging to Facies 4–5: mudstone, sandstone and siltstone of the Moy Fm. (Clarke & Parnell 1999). No samples collected.

Ditch in N–S road to the west of the Railway Station NH2488/8580

Small exposure of Facies 6: bituminous dolomitic series (Strathpeffer Fm.).

- BSP2 (99CW050) Barren
- BSP3a (99CW060) Barren
- BSP3b (00CW014) Barren
- BSP4 (00CW015) Barren
- BSP5 (99CW073) Barren

Wyvisdale NH2492/8587 to NH2493/8584

Excellent exposure of interdigitating sediments belonging to Facies 6b: interbedded bituminous dolomitic series and Facies 5: red and grey mudstones (Strathpeffer and Moy fms) (Clarke & Parnell 1999). All samples are from the mudstones of Facies 5.

***CSP1 (00CW061) [Dominated by abundant and well preserved spores and phytodebris.]**

***CSP2 (00CW052) [Dominated by AOM with abundant and well preserved spores and phytodebris.]**

CSP3 (00CW062) [Dominated by AOM with some pyrite with moderately abundant poorly preserved unidentifiable spores and phytodebris.]

CSP4 (00CW063) [Dominated by AOM infested with pyrite with rare poorly preserved unidentifiable spores and phytodebris.]

CSP5 (00CW064) Barren.

CSP6 (00CW053) [Entirely inertinite]

CSP7 (00CW065) Barren.

14SCO09 (14CW010) – 14SCO15 (14CW016) Barren.

Fodderty Quarry NH2517/8588

Overgrown with poorly exposed red sandstones and siltstones belonging to Facies 4–5: mudstone, sandstone and siltstone (Moy Fm.) (Clarke & Parnell 1999). No samples collected.

Strathpeffer Village behind pump house and adjacent areas NH2483/8581

Reported exposures in the ‘Spa Beds’ (PADS 1978) that are no longer accessible, although two float samples were collected. The ‘Spa Beds’ were incorporated into Facies 6: bituminous dolomitic series (Strathpeffer Fm.) by Clarke & Parnell (1999). A previously collected sample was supplied by John Parnell.

14SCO16 (14CW017) Barren

14SCO17 (14CW018) Barren

JP1 (14CW005) [Dominated by pyrite-infested AOM.]

Strathpeffer Golf Course and adjacent areas NH2479/8585 (PADS 1978 locality 22)

Numerous exposures (including small quarries) in the Ord Beds that are now included in Facies 6: bituminous dolomitic series (Strathpeffer Fm.)

ASP1 (98CW017) [Dominated by pyrite-infested AOM.]

ASP2 (98CW049) [Dominated by pyrite-infested AOM.]

ASP3 (98CWF) [Dominated by pyrite-infested AOM.]

ASP4 (98CW068) [Dominated by pyrite-infested AOM with rare spores and phytodebris that are poorly preserved, pyrite infested and unidentifiable.]

ASP5 (98CW069) [Dominated by abundant AOM with rare poorly preserved unidentifiable palynomorphs.]

BSP1 (00CW013) Barren

14SCO18 (14CW019) [Dominated by pyrite-infested AOM.]

14SCO19 (14CW020) [Dominated by pyrite-infested AOM.]

14SCO20 (14CW021) [Dominated by pyrite-infested AOM.]

Strath Sgitheach

Section through Facies 1–2: breccia-conglomerate and Facies 3: sandstone (Torr Achilty Fm.) and Facies 6: bituminous dolomitic series (Strathpeffer Fm.) (Clarke & Parnell 1999). All of the collected samples are from Facies 6.

CSP8 (00CW050) [Dominated by pyrite-infested AOM with subsidiary inertinite and abundant spores and phytodebris that are highly degraded, pyrite infested and unidentifiable.]

12SCO04 (12CW031) [Dominated by pyrite-infested AOM with rare inertinite and rare spores and phytodebris that are highly degraded, pyrite infested and unidentifiable.]

12SCO05 (12CW032) [Dominated by pyrite infested AOM with rare inertinite and rare spores and phytodebris that are highly degraded, pyrite infested and unidentifiable.]

12SCO06 (12CW033) [Dominated by AOM but with rare spores and phytodebris that are poorly preserved and unidentifiable.]

*12SCO07 (12CW034) [Dominated by pyrite-infested AOM and abundant inertinite with abundant spores and phytodebris that are moderately well preserved.]

12SCO08 (12CW035) [Dominated by inertinite with rare spores and phytodebris that are poorly preserved and unidentifiable.]

12SCO09 (12CW036) [Dominated by AOM with rare poorly preserved spores and phytodebris that are unidentifiable.]

Allt nan Caafack-Glen Glass road between NH2542/8695

The exposures in Glen Glass and adjacent roads were examined. These strata are mapped by the BGS as Ousdale Arkose Fm. and Braemore Mudstone Fm.

14SCO21 (14CW022) [Dominated by pyrite-infested AOM.]

14SCO22 (14CW023) [Dominated by dense, dark AOM.]

Alness River and adjacent Boath road and Ardross road

Exposures in the Alness River and adjacent Boath and Ardross roads were examined. These strata are mapped by the BGS as Ousdale Arkose Fm. and Braemore Mudstone Fm.

*CSP9 (00CW055) [Sparse inertinite and well preserved spores and phytodebris.]

CSP10 (00CW066) Barren.

Upper reaches of Strath Rory

Exposures in the upper reaches of Strath Rory were examined. These strata are mapped by the BGS as Ousdale Arkose Fm. and Braemore Mudstone Fm. No lithologies suitable for sampling were discovered.

Allt Muigh-Bhlaraidh NH661/823

Described by Mykura (1978). Mapped by the BGS as the Braemore Mudstone Fm.

BAS1 (10CW082) Barren

BAS2 (10CW083) [Dominated by pyrite-infested AOM and inertinite.]

***BAS3 (10CW084) [Dominated by inertinite and well preserved spores and phytodebris.]**

12SCO10 (12CW037) [Dominated by inertinite.]

12SCO11 (12CW038) [Dominated by AOM and inertinite with very rare poorly preserved spores and phytodebris.]

12SCO12 (12CW039) [Dominated by inertinite.]

12SCO13 (12CW040) [Dominated by inertinite.]