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Spore assemblages from the Lower Devonian 'Lower Old Red Sandstone' deposits of the Northern Highlands of Scotland: the Berriedale Outlier

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ABSTRACT: Assemblages of well-preserved dispersed spores have been recovered from the 'Lower Old Red Sandstone' deposits of the Berriedale Outlier in the Northern Highlands of Scotland. They belong to the *annulatus–sextantii* Spore Assemblage Biozone (AS SAB), in the spore zonation of Richardson & McGregor (1986), indicating an Early Devonian Emsian (but not earliest Emsian or latest Emsian) age. Comparison with the spore zonation of Streel *et al*. (1987) suggests they may be confined to the *annulatus–bellatulus* Oppel Zone (AB OZ), further constraining the age to early Emsian. This new biostratigraphical datum provides an age constraint for the onset of 'Lower Old Red Sandstone' sedimentation in the Orcadian Basin and, in particular, northwest of the Great Glen Fault System on the Northern Highlands. In the Orcadian Basin, there is a gap between 'Lower Old Red Sandstone' and 'Middle Old Red Sandstone' sedimentation, represented by either unconformity or disconformity, which appears to be variable in duration. In the Berriedale Outlier, it is estimated to represent up to 16 million years, but with an unknown thickness of 'Lower Old Red Sandstone' sequence removed at the unconformity. However, this basin-wide unconformity/disconformity is likely due to minor, local rather than large-scale, regional tectonism, and the evidence suggests little, if any, syn-depositional strike-slip movement along the Great Glen Fault System during Devonian 'Old Red Sandstone' deposition. The described spore assemblage is the most diverse AS SAB/AB OZ assemblage described from the British Isles. However, compared to contemporary spore assemblages from elsewhere on the Old Red Sandstone continent, the Scottish material is rather depauperate, with certain key taxa absent. This probably reflects subtle ecological effects, with the Scottish material representing restricted floras of the inland intermontaine basins.

KEY WORDS: Early land plants, Emsian, Great Glen Fault System, Ousdale Mudstone Formation

This article is the first to describe in detail and illustrate spore assemblages recovered from the 'Lower Old Red Sandstone' 'Basement Beds' of the Berriedale, or Ousdale–Badbea, Outlier of the Northern Highlands of Scotland. It represents a further contribution to a series of papers describing dispersed spore assemblages from Upper Silurian–Lower Devonian 'Lower Old Red Sandstone' deposits of Scotland (Wellman 1993a, b, 1994, 2006, 2010; Wellman & Richardson 1993, 1996; Lavender & Wellman 2002). The aim is to: (i) biostratigraphically age date and stratigraphically correlate these deposits; (ii) use this information to improve understanding of the complex geological relationships of the 'Lower Old Red Sandstone' deposits of this region (particularly regarding their relationship to the assembly of the Old Red Sandstone continent); and (iii) shed light on the palaeoenvironments and biotas of these deposits.

1. Geological setting

The Devonian 'Old Red Sandstone' deposits of the Orcadian Basin straddle the Great Glen Fault System and, as such, outcrop on both the Northern Highlands to the northwest and the Grampian Highlands to the southeast. This laterally and vertically extensive sequence rests unconformably on an ancient landscape consisting largely of Moine schists. Over most of the area, there is a thin basal unit (originally termed the 'Basement Group' or 'Barren Group') that is generally considered to be 'Lower Old Red Sandstone' of Early Devonian age. The 'Basement Group' is overlain by 'Middle Old Red Sandstone deposits' of Mid Devonian age. The contact is either unconformable (e.g., the Berriedale Outlier) or disconformable (e.g. the Sarclet Outlier). The 'Basement Group' of the Northern Highlands north of the Great Glen Fault System consists of a series of discrete outcrops (Fig. 1):

(i) the Sarclet Outlier of the Sarclet Dome;
(ii) the "northern Lower Old Red Sandstone" (*sensu* Trewin & Thirlwall 2002), outcropping 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;
(iii) the Badbea Basin (Berriedale, or Ousdale–Badbea, Outlier), located north of the Helmsdale Granite (Dec 1992);
(iv) the Golspie Basin (Brora Outlier), located south of the Helmsdale Granite (Dec 1992);
(v) the Meall Odhar or Crask Outlier;
(vi) the Strath Rannoch Outlier;
(vii) Struie–Strathpeffer;
(viii) the Den Siltstone Formation (Fletcher *et al*. 1996); and
(ix) the Mealfuarvonie Outlier (Mykura & Owens 1983).

The 'Lower Old Red Sandstone' deposits of the Badbea Basin (*sensu* Dec 1992) are often referred to as the Berriedale,

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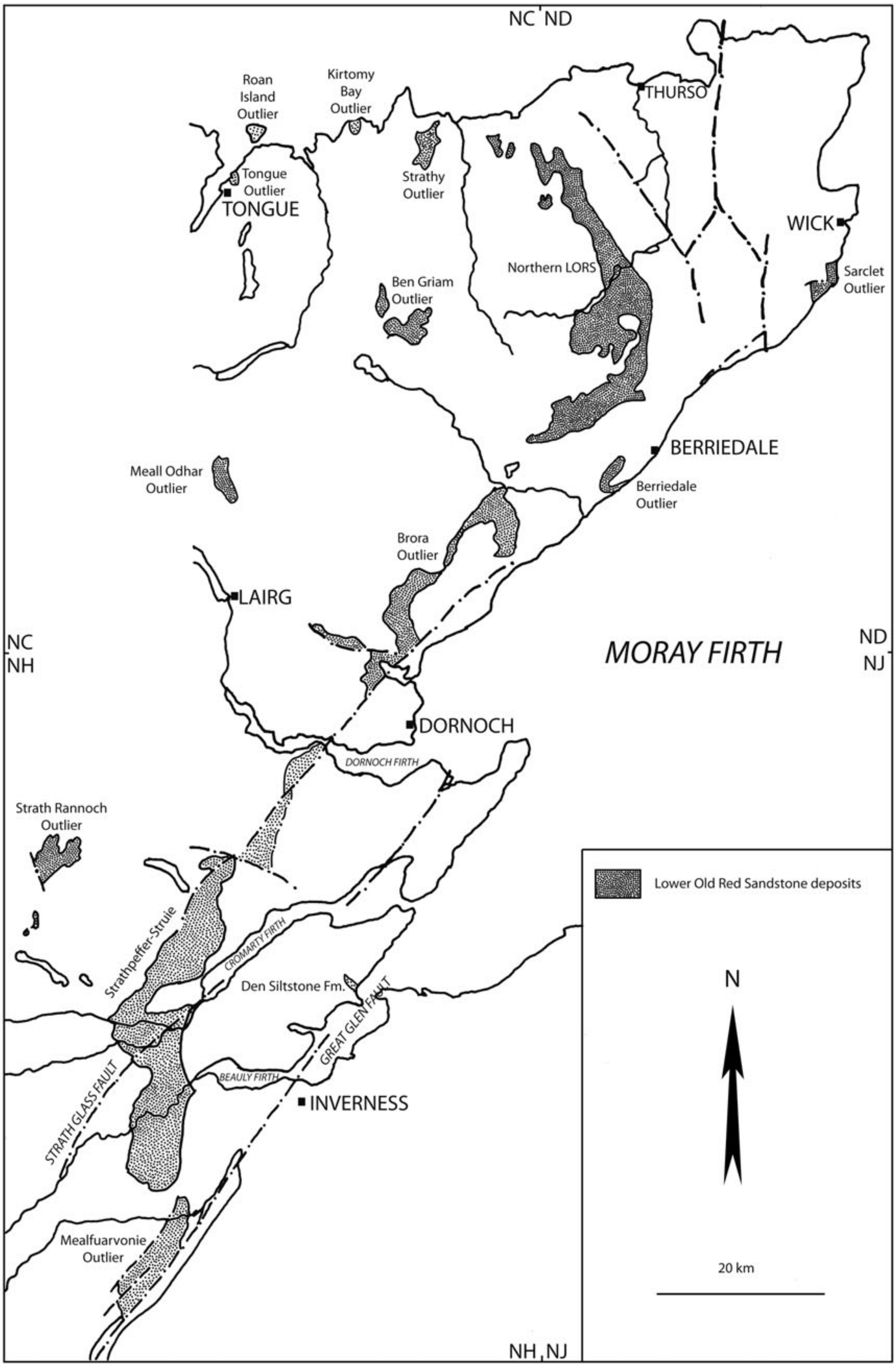

Figure 1 Map of the eastern part of the Northern Highlands of Scotland, showing the distribution of Lower Devonian 'Lower Old Red Sandstone' deposits.

or Ousdale-Badbea, Outlier. They are mapped on the British Geological Survey 1:50 000 Series Scotland Sheets 109 and 110. The geology of these deposits is described in the associated *Memoirs of the Geological Survey of Scotland* (Crampton & Carruthers 1914; Read 1931). More recently, the geology of the deposits has been considered by Westoll (1977), Friend & Williams (1978), Dec (1992), Trewin (1993, 2009a) and Trewin & Thirlwall (2002) (Figs 2 & 3).

The Berriedale Outlier is separated from the main strip of "northern Lower Old Red Sandstone" (*sensu* Trewin &

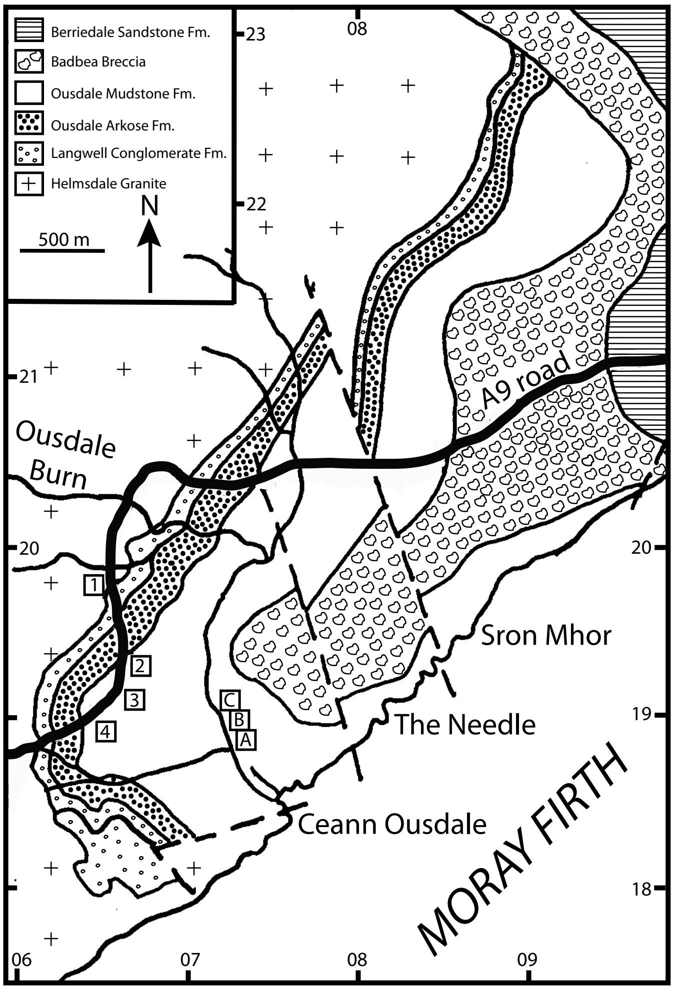

Figure 2 Geological map of the Berriedale Outlier, illustrating the location of sampled exposures. The numbers 1–4 refer to roadcut and roadside quarry localities in Trewin (1993; 2009a) and the letters A–C refer to exposures in Ousdale Burn (see Table 2).

Thirlwall (2002), see (ii) above) by a narrow gap across the Scaraben–Newport ridge of basement rocks. The 'Lower Old Red Sandstone' deposits lie on an irregular surface consisting of the Helmsdale Granite, which is intruded into the Moine schists. Basal deposits consist of a regolith of Helmsdale Granite and fossil screes that are overlain by red-brown indurated sandstones. The thin impersistent basal conglomerate is called the Langwell Conglomerate Formation. It passes laterally into the Ousdale Arkose Formation. These are in turn overlain by the Ousdale Mudstone Formation, which consists predominantly of brownish siltstones (but with some thin green and grey layers) with some sandier layers. The 'Lower Old Red Sandstone' sequence is unconformably overlain by the 'Middle Old Red Sandstone' Badbea Breccio–Conglomerate Member. The sequence is interpreted as a low energy floodplain deposit, with drainage to the northeast, interrupted by occasional sheet-wash deposits of very local origin (Friend & Williams 1978; Trewin 1993, 2009a).

The Ousdale Mudstone Formation has yielded scales of the fish *Porolepis* (Collins & Donovan 1977), plant fragments ("*Psilophyton*") and nematophytes (*Pachytheca)* (Collins & Donovan 1977), dispersed spore assemblages (Richardson 1967; Collins & Donovan 1977) and trace fossils (Trewin 1993, 2009a). Together, these fossils remains have been interpreted to suggest an age high in the Early Devonian (Westoll 1977; Friend & Williams 1978; Trewin 1993, 2009a).

2. Palynology

2.1. Previous palynological investigation

Richardson (1967) reported relatively poorly preserved and highly coalified spore assemblages recovered from the Ousdale "mudstones" of the Basement Group of Berriedale. He noted that the assemblage consisted entirely of azonate spores that in the most part could be assigned to *Retusotriletes*, ?*Apiculiretusispora* and *Emphanisporites* (*rotatus* type). Richardson (1967) suggested that the spore assemblage was most likely of Early Devonian age. Subsequently, Collins & Donovan (1977) reported on a moderately well preserved but slightly coalified spore assemblage recovered from the Ousdale Mudstones from road cuttings on the A9. They listed the species present and their relative abundance (Table 1). They suggested an early Emsian age based on the spores.

2.2. Methods

During the course of two fieldtrips, 18 siltstone horizons were sampled from throughout the 'Lower Old Red Sandstone' sequence of the outlier (Table 2). They were processed using standard palynological techniques: HF-HCl-HF acid maceration followed by heavy liquid separation using zinc chloride. Recovered organic residues were sieved using a 20 µm mesh, oxidised for varying periods of time using Schultz solution, and strew mounted for light microscope analysis. Of the 18

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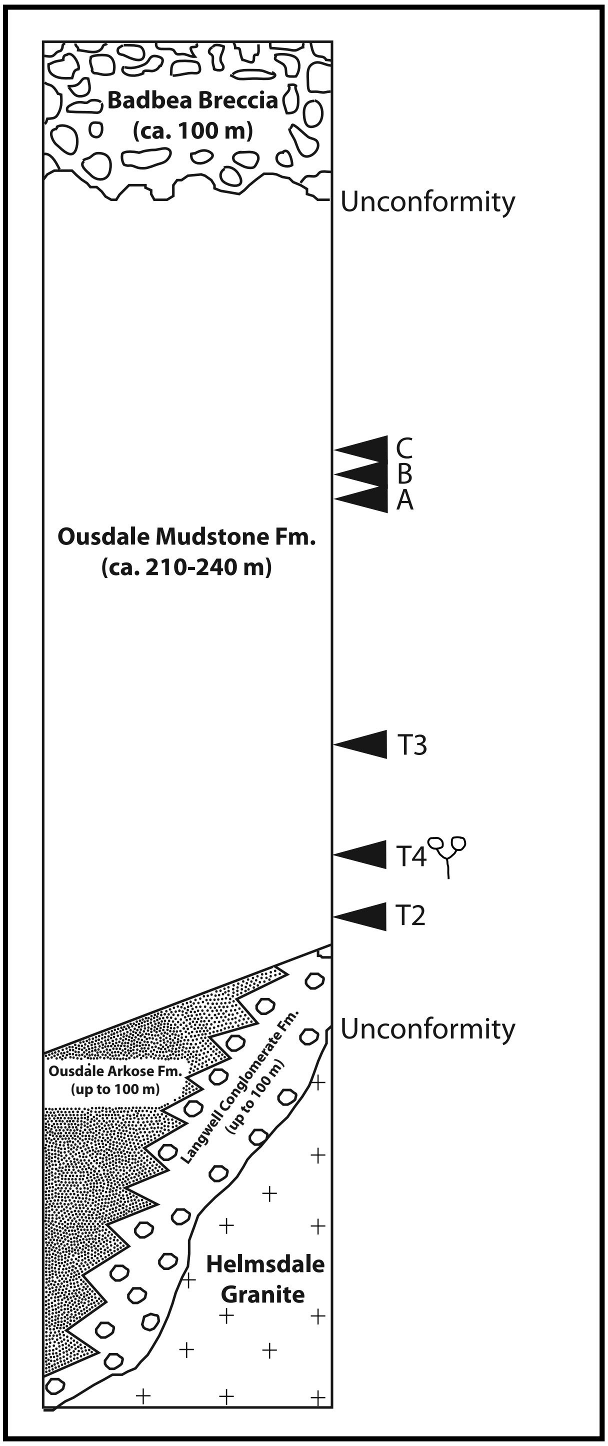

Figure 3 Stratigraphical succession in the Berriedale Outlier. The approximate position of productive palynological samples was calculated based on strike/dip information and measured distances using British Geological Survey 1:50,000 Series Scotland Sheets 109 and 110. T2–T4 refer to roadcut and roadside quarry localities in Trewin (1993; 2009a) and A–C refer to exposures in Ousdale Burn. Productive samples are: T4 (AOU7, BOU4, BOU5); T3 (BOU3); A (BOU6, BOU7, BOU8); B (BOU9); C (BOU10, BOU11) (see Table 2). The location of plant remains discovered at locality T4 is indicated by the sketch of a Lower Devonian fossil plant.

samples, ten were productive and all came from the Ousdale Mudstone Formation. The assemblages are rich in palynomorphs that are of good to excellent preservation and moderate thermal maturity (Thermal Alteration Index 3- to 3 from the chart provided in Traverse 2007). Oxidation with Schultz solution (a maximum of 30 minutes was required) cleared the spores to a workable translucent dark orange–pale brown colour. All materials (samples, residues, slides) are housed in the collections of the Centre for Palynology of the University of Sheffield.

Table 1 Spore taxa and their abundance reported by Collins & Donovan (1977). P = Present (<1 %); C = Common (1–10 %); A = Abundant (>10 %).

Ambitisporites sp.	C
Anaplanisporites spp.	P
Apiculatisporis sp.	C
Apiculiretusispora spp.	A
Aurorospora cf. *minuta* Richardson	P
Calamospora spp.	A
Camptozonotriletes cf. *aliquantus* Allen	P
Cyclogranisporites spp.	A
Dibolisporites sp.	P
Dictyotriletes spp.	P
Emphanisporites annulatus McGregor	P
E. macgregori Schultz	P
E. rotatus McGregor	C
Lophozonotriletes sp.	P
Punctatisporites spp.	C
Retusotriletes spp.	A
Verrucosisporites cf *polygonalis* Lanninger	C
Unidentified tripapillate spore	P

2.3. Description of spore assemblages

All of the productive samples essentially yield an identical palynomorph assemblage (see Table 1; Figs 4–6). They contain only dispersed spores and palynodebris. The dispersed spores are dominated by laevigate retusoid spores (*Retusotriletes* spp.) (Fig. 4a, b) and apiculate retusoid spores, with a sloughing extra-exosporal layer that bears the ornament (*Apiculiretusispora* spp.) (Fig. 4c–e). Many of the *Retusotriletes* have thickenings (triangular or annular) associated with the trilete mark and extra-exosporal material adhering to them (Fig. 4a, b). Similarly, some of the *Apiculiretusispora* have a triangular thickening associated with the trilete mark (Fig. 4d, e). Other apiculate retusoid spores have a biform sculpture (*Dibolisporites* spp., including *D. ardchoircii, D. echinaceus* and *D. eifeliensis*) (Fig. 4f–k). The genus *Dictyotriletes* is notably under-represented, with only very rare examples (e.g., Fig. 5c). Laevigate crassitate (*Ambitisporites* spp.) (Fig. 4b) and patinate (*Archaeozonotriletes chulus*) (Fig. 6g, h) spores are relatively uncommon. Ornamented crassitate forms are present, including apiculate forms (*Aneurospora* sp. A) (Fig. 5d, e), verrucate forms (*Verrucosisporites polygonalis*) (Fig. 6k) and foveolate forms placed with *Brochotriletes* spp. (Fig. 6a–c, j), including *B. bellatulus* (Fig. 6b, c). Ornamented patinate forms are extremely rare (e.g., *Cymbosporites* spp.) (Fig. 6i, j). The highly distinctive spore *Amicosporites streelii* (Fig. 6d) is identified. Spores with proximal radial ribbing are rare, but present in all samples, and include examples of *E. annulatus, E. erraticus, E. rotatus, E. schultzii* and *E. zavallatus*? (Fig. 5f, i–n). Zonate spores are present and include *Camptozonotriletes caperatus* (Fig. 6p), a new species of *Samarisporites* (Fig. 6l, m) and a solitary possible example of *Breconisporites* (Fig. 6o). Very rare cryptospores are present and are represented by the laevigate hilate spores (*Laevolancis divellomedium*) (Fig. 6q) and the permanent tetrad *Tetrahedraletes medinensis* (Fig. 6n). A complete list of identified spore taxa is provided in Table 3.

2.4. Age determination

The described spore assemblages are correlated with the *Emphanisporites annulatus*–*Camarozonotriletes sextantii* Spore Assemblage Biozone (AS SAB) of Richardson & McGregor (1986),

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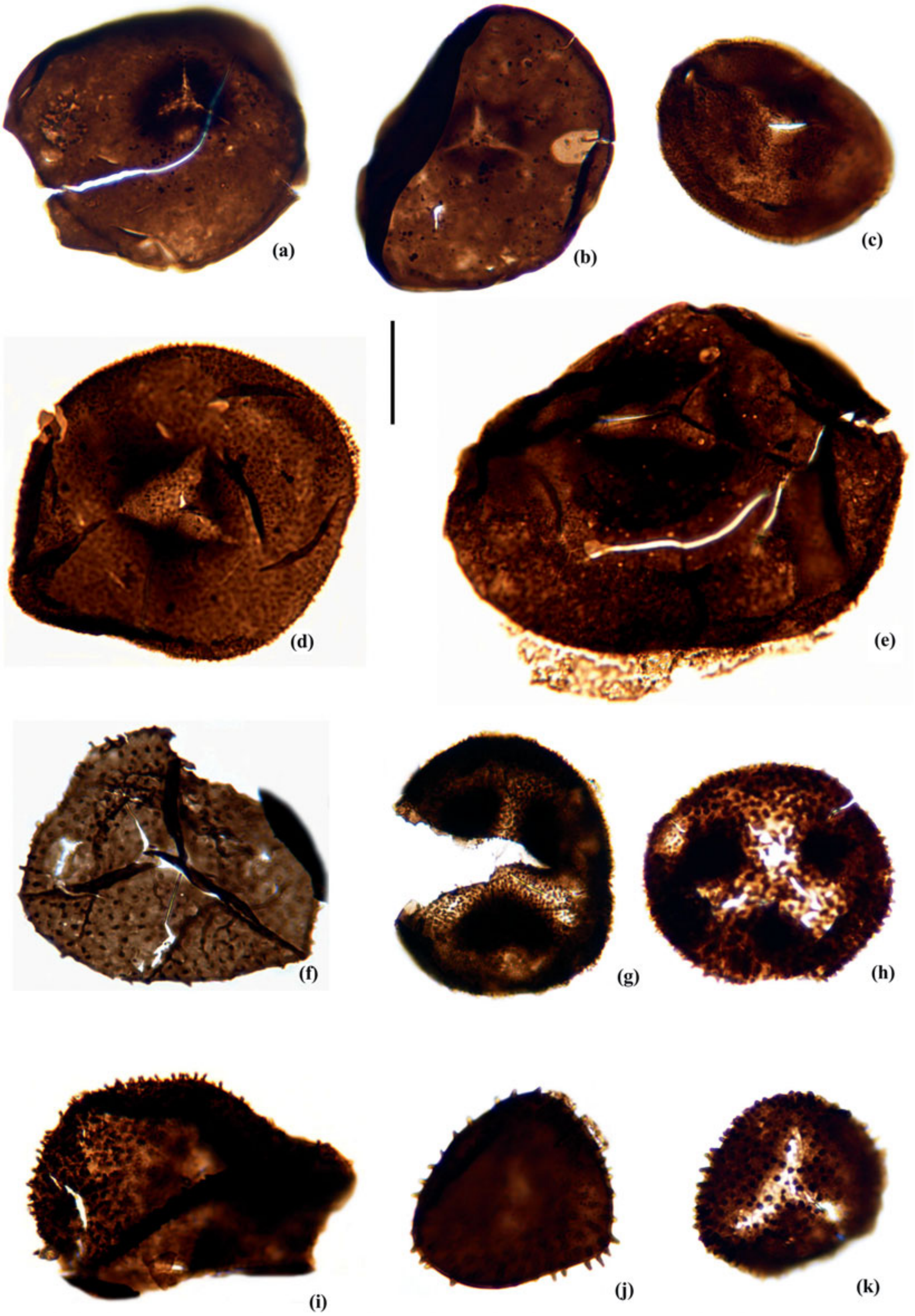

Figure 4 Light microscope images of dispersed spores from the Ousdale Mudstone Formation of the Berriedale Outlier: (a) *Retusotriletes* cf. *triangulatus* (Streel) Streel, 1967, slide BOU3/1, E.F. No. (H28/1); (b) *Retusotriletes rotundus* (Streel) Streel, 1967, slide BOU3/1, E.F. No. (J44); (c) *Apiculiretusispora plicata* (Allen) Streel, 1967, slide BOU3/1, E.F. No. (J24/1); (d) *Apiculiretusispora brandtii* Streel, 1967, slide BOU9/1, E.F. No. (D47/4); (e) *Apiculiretusispora brandtii* Streel, 1967, slide BOU11/1, E.F. No. (J50/3); (f) *Dibolisporites eifeliensis* (Lanninger) McGregor, 1973, slide BOU3/1, E.F. No. (T46/2); (g) *Dibolisporites ardchoircii* Wellman & Richardson, 1996, slide BOU3/1, E.F. No. (F44); (h) *Dibolisporites* cf. *ardchoircii* Wellman & Richardson, 1996, slide BOU4/1, E.F. No. (H55/1). Note that this specimen has some sculptural elements that are spatulate; (i) *Dibolisporites echinaceous* (Eisenack) Richardson, 1965, slide BOU10/1, E.F. No. (T26); (j) *Dibolisporites eifeliensis* (Lanninger) McGregor, 1973, slide AOU7/4, E.F. No. (J38/1); (k) *Dibolisporites eifeliensis* (Lanninger) McGregor, 1973, slide AOU7/2, E.F. No. (R50/1). Scale bar = 20 μm.

based on the presence of one of the nominal species (*E. annulatus*) and the general characteristics of the assemblage in terms of morphotypes present and their general abundances. The preceding and succeeding zones are precluded by, amongst other observations, the presence of *E. annulatus* and the absence of spores with grapnel-tipped spines, respectively. The age of the AS Spore Assemblage Biozone is Early Devonian Emsian (but not earliest Emsian nor latest Emsian). In the spore zonation

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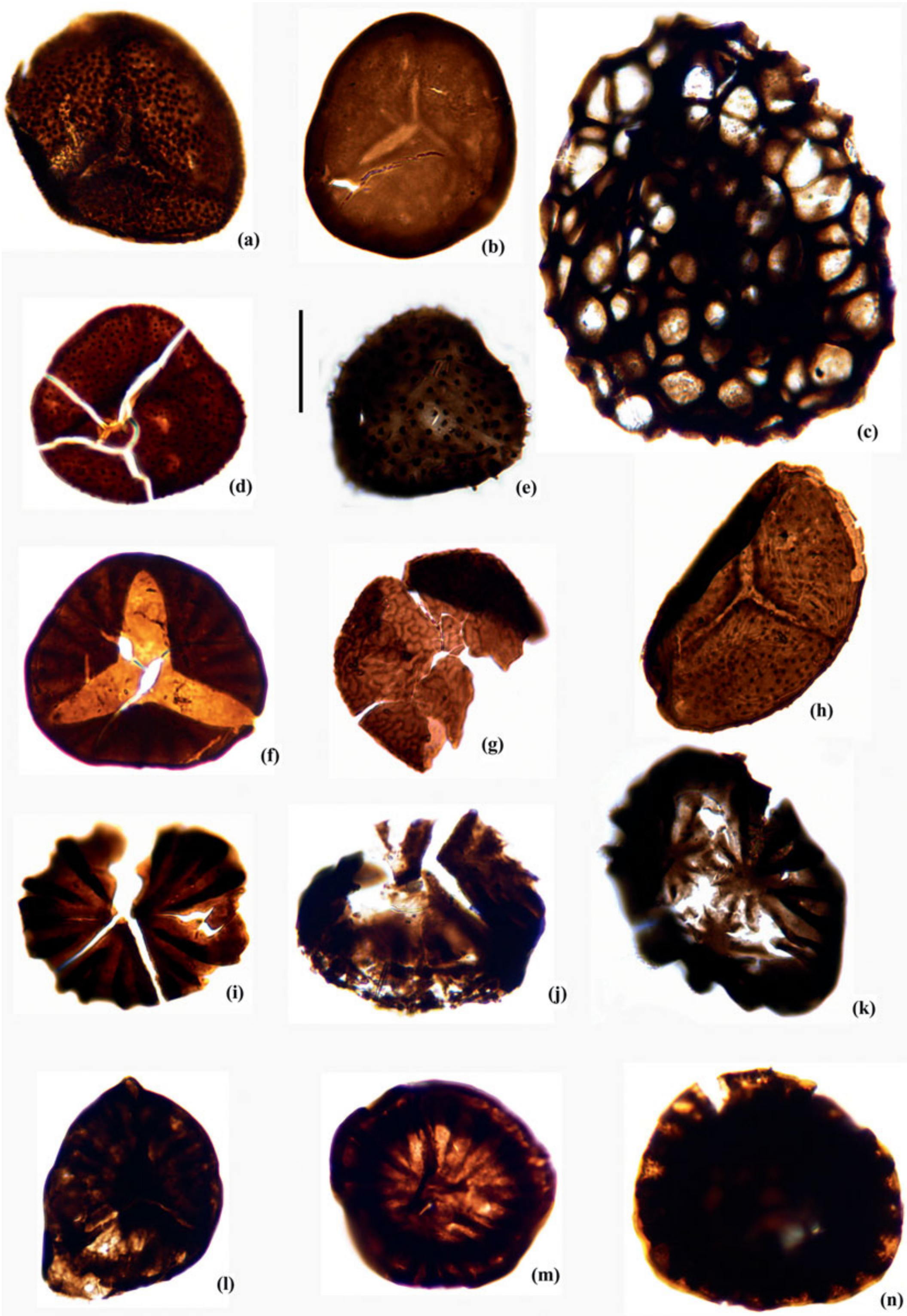

Figure 5 Light microscope images of dispersed spores from the Ousdale Mudstone Formation of the Berriedale Outlier: (a) *Dibolisporites* sp., slide BOU11/1, E.F. No. (F35/2); (b) *Ambitisporites* sp., slide BOU8/1, E.F. No. (M29); (c) ?spore of *Dictyotriletes*-type, slide BOU9/1, E.F. No. (G48/4); (d) *Aneurospora* sp. A, slide BOU11/1, E.F. No. (G40); (e) *Aneurospora* sp. A, slide BOU3/1, E.F. No. (Q46/1); (f) *Emphanisporites rotatus* McGregor, 1961, slide BOU7/1, E.F. No. (N26); (g) spore with distinctive reticulate ornament, slide BOU4/1, E.F. No. (E25); (h) spore with ornament of distinctive proximal striae and distal coni, slide BOU8/1, E.F. No. (Q42); (i) *Emphanisporites rotatus* McGregor, 1961 (*robustus*-type), slide BOU9/1, E.F. No. (S42); (j) *Emphanisporites zavallatus*? Richardson *et al*., 1982, slide BOU3/1, E.F. No. (M24); (k) *Emphanisporites schultzii* McGregor, 1973, slide BOU3/1, E.F. No. (V39/1); (l) *Emphanisporites annulatus* McGregor, 1961, slide AOU7/3, E.F. No. (K45); (m) *Emphanisporites erraticus* (Eisenack) McGregor, 1961, slide BOU3/1, E.F. No. (Q23); (n) *Emphanisporites annulatus* McGregor, 1961, slide BOU10/1, E.F. No. (K49/2). Scale bar = 20 µm.

scheme of Streel *et al.* (1987), the AS Spore Assemblage Biozone is equivalent to the *annulatus–bellatulus* and *foveolatus–dubia* Oppel Zones (AB OZ and FD OZ). Both nominal species of the AB OZ are present: *E. annulatus* and *B. bellatulus*. Neither of the nominal or other characteristic species of the FD Oppel Zone is present. Thus, the spore assemblage may belong to the AB OZ, constraining the age to early Emsian. However, one must be cautious when applying the Ardennes–Rhenish scheme

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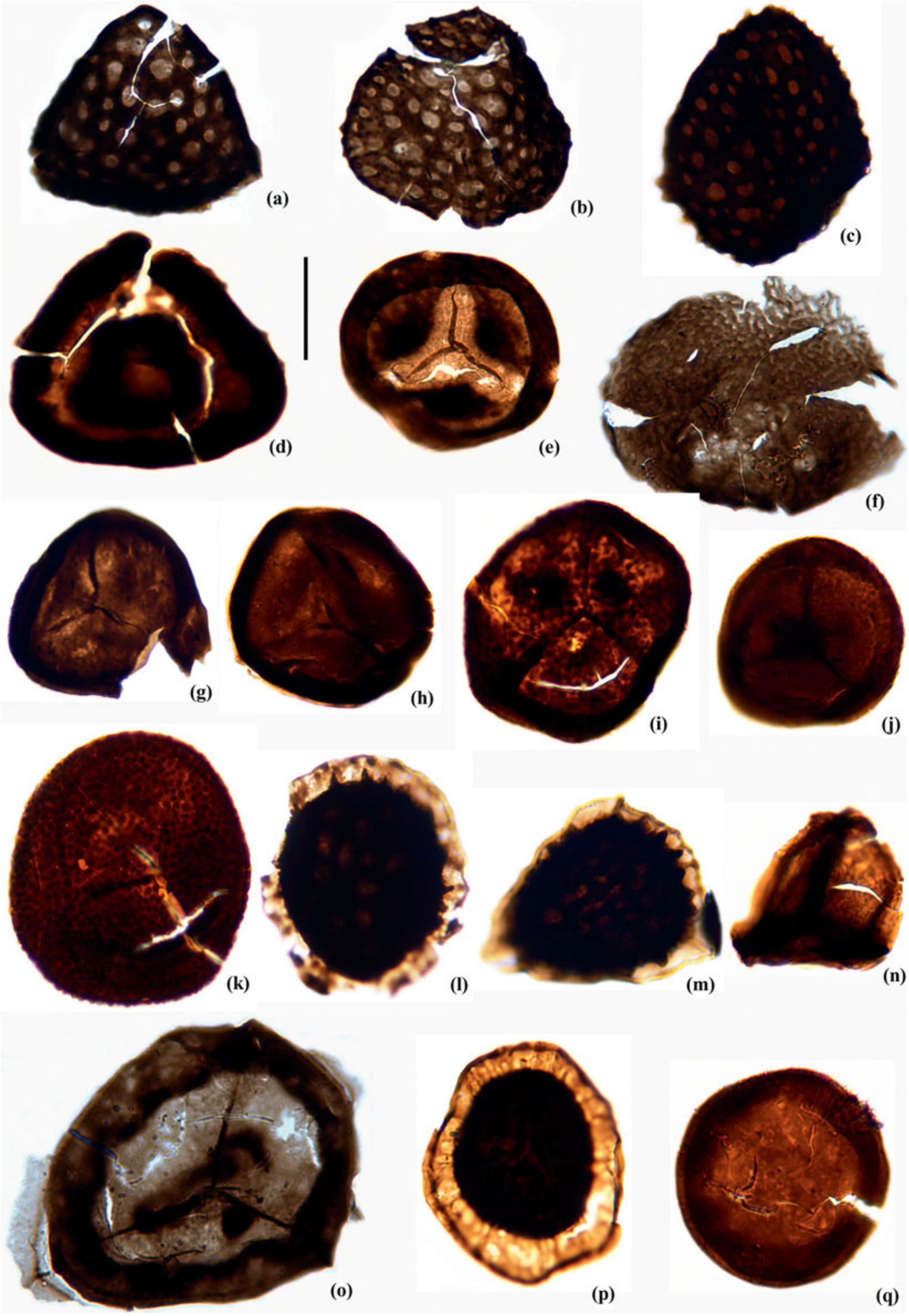

Figure 6 Light microscope images of dispersed spores from the Ousdale Mudstone Formation of the Berriedale Outlier: (a) *Brochotriletes foveolatus*? Naumova, 1953, slide BOU3/1, E.F. No. (F51/3); (b) *Brochotriletes bellatulus* Steemans, 1989, slide BOU3/1, E.F. No. (G39); (c) *Brochotriletes bellatulus* Steemans, 1989, slide BOU3/1, E.F. No. (T46/2); (d) *Amicosporites streelii* Steemans, 1989, slide BOU5/1, E.F. No. (Q40/1); (e) distinctive patinate spore, slide BOU9/1, E.F. No. (G47); (f) *Brochotriletes rarus* Arkangelskaya, 1978, slide BOU3/1, E.F. No. (D47); (g) *Archaeozonotriletes chulus* (Cramer) Richardson & Lister, 1969, slide BOU3/1, E.F. No. (N51/3); (h) *Archaeozonotriletes chulus* (Cramer) Richardson & Lister, 1969, slide BOU9/1, E.F. No. (F32); (i) *Cymbosporites* sp., slide BOU6/1, E.F. No. (L33); (j) *Cymbosporites* sp., slide BOU7/1, E.F. No. (R49); (k) *Verrucosisporites polygonalis* Lanninger, 1968. Note that there is considerable integradation between two characters in the Scottish population of this species: verrucae vary from rounded to polygonal and structure varies from retusoid to crassitate. Slide BOU8/1, E.F. No. (L26); (l) *Samarisporites* sp. A, slide AOU7/3, E.F. No. (J44/2); (m) *Samarisporites* sp. A. This new taxon has a laevigate zona but the distal surface below the inner body has an ornament of spines around the margin that merge to form a reticulum over the inner body. Slide AOU7/3, E.F. No. (X28); (n) *Tetrahedraletes medinensis* (Strother & Traverse 1979 emend. Wellman & Richardson 1993), slide BOU9/1, E.F. No. (C35/1); (o) *Breconisporites* sp., slide BOU3/1, E.F. No. (C32/4); (p) *Camptozonotriletes caperatus* McGregor, 1973, slide BOU5/1, E.F. No. (T28/2); (q) *Laevolancis divellomedium* (Chibrikova) Burgess & Richardson, 1991, slide BOU11/1, E.F. No. (H33). Scale bar = 20 µm.

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Table 2 Details of samples (listed in approximate stratigraphical order from oldest to youngest); see Figs 2–3. B = barren; P = productive.

SAMPLE	LOCALITY	GRID REF.	PALY
AOU4	East face New Quarry on A9. Locality 2 of Trewin (1993)	ND06594/19555	B
AOU5	Northeast face New Quarry on A9. Locality 2 of Trewin (1993)	ND06594/19555	B
BOU1	East face New Quarry on A9. Locality 2 of Trewin (1993)	ND06594/19555	B
BOU2	West face New Quarry on A9. Locality 2 of Trewin (1993)	ND06594/19555	B
AOU6	Southern end of major roadcut on west side of A9. Locality 4 of Trewin (1993)	ND062/190	B
AOU7	50 m from southern end of major roadcut on west side of A9. Locality 4 of Trewin (1993)	ND062/190	P
AOU7/BOU4	Centre of major roadcut on west side of A9. Locality 4 of Trewin (1993)	ND062/190	P
BOU5	Southern end of major roadcut on west side of A9. Locality 4 of Trewin (1993)	ND062/190	P
AOU1	Roadcut on west side of A9. Locality 3 of Trewin (1993)	ND06676/19243	B
AOU2	Roadcut on west side of A9. Locality 3 of Trewin (1993)	ND06676/19243	B
AOU3	Old Quarry on west side of A9. Locality 3 of Trewin (1993)	ND06676/19243	B
BOU3	Roadcut on west side of A9. Locality 3 of Trewin (1993)	ND06706/19297	P
BOU6	Ousdale Burn. 1 cm siltstone lense	ND07355/18817	P
BOU7	Ousdale Burn. 20 cm mudchip conglomerate	ND07355/18817	P
BOU8	Ousdale Burn. 20 cm mudchip conglomerate	ND07355/18817	P
BOU9	Ousdale Burn. Laminated shale	ND07250/18903	P
BOU10	Ousdale Burn. Prominent siltstone	ND07197/19120	P
BOU11	Ousdale Burn. Prominent siltstone	ND07197/19120	P

to the 'Lower Old Red Sandstone' of Scotland because: (i) there is a large distance between northern Scotland and the Ardennes–Rhenish region; (ii) the two regions represent different facies (intermontaine basin versus coastal plain); and (iii) many of the taxa present in the diverse spore assemblages of the coastal plain deposits of the Ardennes-–Rhenish region are not present in the depauperate spore assemblages of the inland intermontane deposits of Scotland (see below).

2.5. Palynofacies analysis and palaeoenvironmental interpretation

The palynomorph assemblages contain only land-derived forms. These consist predominantly of disarticulated plant parts (cuticles, including some with stomata, and conducting tissues) and spores derived from the plants. There are also rare fungal hyphae, rare banded tubes similar to those produced by nematophytes, and a single fragment interpreted as the organic remnants of a fish scale. The nature of the palynomorph assemblages suggests accumulation in a non-marine environment. This strongly supports previous interpretations of these deposits, based on sedimentological observations, as accumulating in typical 'Lower Old Red Sandstone' terrestrial fluviatile–lacustrine floodplain environments (e.g., Trewin 1993, 2009a).

3. Geological implications

Understanding the Caledonian Orogeny and determining how and when the various Scottish terranes were emplaced are long standing problems (e.g. Trewin & Thirlwall 2002). The new biostratigraphical information suggests that the age of the 'Basement Group' of the Berriedale Outlier is Early Devonian Emsian (but not earliest Emsian nor latest Emsian), with an early Emsian age most likely. This has a number of implications relevant to these debates.

The Caledonian Orogeny involved the closing of the Iapetus Ocean and collision between Avalonia, Laurentia and Baltica. During closure, there was basement thrusting, uplift and exhumation due to deep weathering. Closure was oblique, with significant sinistral strike-slip movement along a number of NE-trending faults, including the Great Glen Fault System (e.g., McClay *et al.* 1986; Norton *et al.* 1987). During the Late Silurian–Early Devonian 'Lower Old Red Sandstone', facies deposits began to be deposited on the southeast margin of the newly-created Old Red Sandstone continent. Modern theories regarding Devonian sedimentation in the Orcadian Basin revolve around three main models (summarised in Trewin 2009b): (i) sedimentation was controlled by extensional collapse of the Caledonian crust and occurred in half-grabens, with unconformities resulting from footwall uplift (e.g. Norton *et al.* 1987); (ii) strike-slip was important, with extension occurring in transtensional basins, with sediment deriving from erosion of transpressional highs (e.g., Trewin 1989); (iii) a combination of the above, with extensional collapse superimposed on compressional structures relating to earlier strike-slip (e.g., Underhill & Brodie 1993).

The new early Emsian (ca. 403–407 Ma) age provides a constraint for the commencement of sedimentation in the Orcadian basin and, in particular, on the Northern Highlands to the northwest of the Great Glen Fault System. The Helmsdale Granite has been dated as ca. 420 Ma (Pidgeon & Aftalion 1978). Thus, the new age constraint indicates a long period of ca. 15 million years for granite weathering on the post-Caledonian land surface (based on ages provided in Gradstein *et al.* 2012). Trewin (2009b) estimates that at least 3 km of rock was weathered, unroofing the Helmsdale Granite and Moine metamorphics. Mendum & Noble (2010) estimate ca. 12–15 km of uplift, with exhumation rates of between 2 and 4 mm per annum, based on dating of events associated with the Rosemarkie Inlier. Interestingly, there are no 'Lower Old Red Sandstone' deposits identified as older than early Emsian associated with the Orcadian Basin, although beyond the Orcadian Basin on the Grampian Highlands there are 'Lower Old Red Sandstone' deposits of Pragian–?earliest Emsian age in the Rhynie Outlier (Wellman 2006), of Lochkovian age at Glen Coe (Wellman 1994) and of latest Silurian–earliest Devonian age at Lorne (Wellman & Richardson 1996). These older deposits probably represent an early onset of 'Lower Old Red Sandstone' sedimentation on the post-Caledonian land surface, and it is possible that somewhere in the Orcadian Basin, volcanic collapse structures and half-grabens preserving pre-Emsian deposits are concealed by overstep.

The new age also suggests that in the Berriedale Outlier, the unconformity between 'Lower Old Red Sandstone' (early Emsian) and 'Middle Old Red Sandstone' (late Eifelian) deposits

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Table 3 Identified spore taxa and their occurrence

TAXON [ILLUSTRATION]	BOU3	AOU7 BOU4	BOU5	BOU6	BOU7	BOU8	BOU9	BOU10	BOU11
Retusotriletes cf. *rotundus* (Streel) Streel, 1967 [Fig. 4b]	X	X	–	–	–	X	–	–	–
Retusotriletes cf. *triangulatus* (Streel) Streel, 1967 [Fig. 4a]	X	X	X	X	X	X	X	X	X
Retusotriletes spp.	X	X	X	X	X	X	X	X	X
Apiculiretusispora brandtii Streel, 1967 [Fig. 4d–e]	X	X	–	X	X	–	X	X	X
Apiculiterusispora plicata (Allen) Streel, 1967 [Fig. 4c]	X	X	–	–	–	–	–	X	–
Apiculiretusispora spp.	X	X	X	X	X	X	X	X	X
Dibolisporites ardchoircii Wellman & Richardson, 1996 [Fig. 4g–h]	X	X	X	X	–	–	X	–	–
Dibolisporites echinaceous (Eisenack) Richardson, 1965 [Fig. 4f, i]	X	X	X	–	X	X	X	X	–
Dibolisporites eifeliensis (Lanninger) McGregor, 1973 [Fig. 4j–k]	X	X	X	–	–	–	–	X	X
Dibolisporites spp. [Fig. 5a]	X	X	X	–	X	X	X	X	X
Dictyotriletes spp. [Fig. 5c]	–	–	–	–	–	–	X	X	–
Ambitisporites spp. [Fig. 5b]	X	X	–	–	–	X	X	X	–
Aneurospora sp. A [Fig. 5d–e]	X	–	X	X	X	–	X	–	X
Emphanisporites annulatus McGregor, 1961 [Fig. 5l, n]	–	?	–	–	–	–	–	X	?
Emphanisporites erraticus (Eisenack) McGregor, 1961 [Fig. 5m]	X	–	–	–	–	–	–	–	–
Emphanisporites rotatus McGregor, 1961 [Fig. 5f, i]	X	X	–	X	X	–	X	X	X
Emphanisporites schultzii McGregor, 1973 [Fig. 5k]	?	–	–	–	–	–	–	–	–
Emphanisporites zavallatus Richardson *et al.*, 1982 [Fig. 5j]	?	–	–	–	–	–	–	–	–
Brochotriletes bellatulus Steemans, 1989 [Fig. 6b–c]	X	X	–	–	–	–	–	–	–
Brochotriletes foveolatus? Naumova, 1953 [Fig. 6a]	X	–	?	–	–	–	–	X	–
Brochotriletes rarus Arkhangelskaya, 1978 [Fig. 6f]	X	–	–	–	–	–	–	–	–
Amicosporites streelii Steemans, 1989 [Fig. 6d]	–	–	X	–	–	–	X	–	X
Verrucosisporites polygonalis Lanninger,1968 [Fig. 6k]	–	X	X	X	X	X	X	–	X
Archaeozonotriletes chulus (Cramer) Richardson & Lister, 1969 [Fig. 6g–h]	X	X	–	–	–	–	X	X	X
Cymbosporites spp. [Fig. 6i–j]	–	–	–	X	X	–	–	–	–
Breconisporites spp. [Fig. 6o]	X	–	–	–	–	–	–	–	–
Camptozonotriletes caperatus McGregor, 1973 [Fig. 6p]	–	X	X	X	–	–	X	X	X
Samarisporites sp. A [Fig. 6l–m]	–	–	–	X	–	–	–	–	–
Zonate spp.	–	X	–	X	–	X	–	–	–
Laevolancis divellomedium (Chibrikova) Burgess & Richardson, 1991 [Fig. 6q]	–	X	–	–	–	–	–	–	X
Tetrahedraletes medinensis Strother & Traverse, 1979 emend Wellman & Richardson, 1993 [Fig. 6n]	–	–	–	–	–	–	X	–	–

represents an estimated 16 million years in duration. Presumably, however, an unknown thickness of 'Lower Old Red Sandstone' sequence could have been removed during this time. Thus, the basin-wide 'Lower Old Red Sandstone'/'Middle Old Red Sandstone' unconformities/disconformities are likely variable in duration and are almost certainly due to minor, local rather than large-scale, regional tectonism. However, Mendum & Noble (2010) suggest that deformation in 'Lower Old Red Sandstone' deposits on the Northern Highlands (e.g., at Struie) may have resulted from a Mid Devonian Acadian event.

The juxtapositioning of Orcadian Basin deposits across the Great Glen Fault System suggests that there was little-or-no syn-depositional strike-slip movement along this fault during Devonian 'Old Red Sandstone' deposition (Rogers *et al.* 1989; Marshall & Hewett 2003). Rogers *et al.* (1989) suggest that the early history of the Great Glen Fault System included late Caledonian sinistral motion, but that this had ceased by the late Emsian and the fault system was not active transcurrently during 'Old Red Sandstone' deposition. The new age date provided herein helps refine the dating of movement.

Adjacent offshore 'Lower Old Red Sandstone' deposits are only present southeast of the Great Glen Fault System (Marshall & Hewett 2003). These accumulated in extensional half-graben systems and are genetically related to onshore deposits of the Grampian Highlands, such as those of the Turriff Basin (Richards 1985; Sweet 1985). These deposits are highly interesting because they are surprisingly thick (in excess of 1000 m in thickness in boreholes 12/27-1, 12-27-2 and 12/29-2). Marshall & Hewitt (2003) suggest that different dynamics in different half-graben systems were responsible for such significant variation in thickness of 'Lower Old Red Sandstone' deposits in the Orcadian Basin.

4. Palaeobotanical implications

Coeval spore assemblages are known from elsewhere in Scotland and adjacent areas: (i) the Midland Valley deposits of the Strathmore Basin (Richardson 1967; Ford 1971; Wellman 2010); (ii) the lowland floodplain deposits of southern England (Chaloner 1963; Richardson & Rasul 1978a, b), although these are probably slightly younger and equate to the FD OZ of mid Emsian age of the spore zonation of Streel *et al*. (1987); (iii) the coastal plain deposits of the Ardennes–Rhenish region (Streel *et al.* 1987). Although all three locations share many common spore taxa, indicating similarities in the flora, both the Scottish and southern English assemblages appear rather depauperate compared to those from the Ardennes–Rhenish region, and indeed from other localities on the Old Red Sandstone continent such as Gaspé, eastern Canada (McGregor 1973, 1977). AS SAB/AB OZ spore assemblages from both the Ardennes–Rhenish region and Gaspé yield in the region of 50 taxa. As discussed by Richardson & Rasul (1978b), these differences most likely reflect ecological, or perhaps facies, effects.

The absence from Scotland of several well-known and distinctive species is interesting in that it suggests that these plants may not have inhabited the inland uplands. Notable absences are *Acinosporites lindlarensis* and *Camarozonotriletes sextantii*. *Acinosporites lindlarensis* is the spore of the lycopsid *Leclercqia* (Richardson *et al.* 1993; Wellman *et al.* 2009) and *C. sextantii* is the microspore of the unclassified, probably heterosporous plant, *Chaleuria* (Andrews *et al*. 1974; McGregor & Camfield 1976). However, *C. sextantii* is known to have patchy distribution (see discussion in Richardson & McGregor 1986, pp 13–14).

Deposits belonging to the AS SAB/AB OZ from Scotland, southern England and the Ardennes–Rhenish region have all yielded plant megafossils. At present, the Scottish flora is limited to the zosterophyll *Sawdonia ornata* and lycopsid *Drepanophycus spinaeformis* (Rayner 1983, 1984), and the southern English flora to the zosterophyll *S. ornata* and trimerophyte *Dawsonites arcuatus* (Chaloner *et al*. 1978). It is evident that the Ardennes–Rhenish plant assemblages are much more diverse (e.g. Kräusel & Weyland 1930; Stockmans 1939; Leclercq 1942; Schweitzer 1983; Fairon-Demaret 1985; Gerrienne 1993) and include rhyniophytes, zosterophylls (including the possible barinophyte *Krithodeophyton*), lycopsids, trimerophytes and a possible sphenopsid (*Estinnophyton*) and cladoxyle (*Foozia*). To some extent, this almost certainly reflects collector bias, with the Ardennes–Rhenish region extremely well exposed and highly researched, and the southern English sequences only exposed in the subsurface. However, the Scottish deposits are reasonably well explored (e.g., Henderson 1932; Lang 1932; Rayner 1983, 1984) and it does seem likely that the floras of the intermontaine basins of Scotland were less diverse than those from the floodplains. Nonetheless, in this respect the lack of diversity of both spores and plant megafossils in southern English floodplain deposits is puzzling. It is noteworthy that spore assemblages from all of these regions are dominated by *Retusotriletes* spp. and *Apiculiretusispora* spp. that were most likely produced in the main by various zosterophylls, lycopsids and trimerophytes. However, many distinctive spore morphotypes are still of unknown affinity, suggesting that plant megafossil diversity is not entirely reflective of the regional floras as a whole.

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