Small is beautiful:

new investigations into Lower Devonian plant mesofossils and their *in situ* spores

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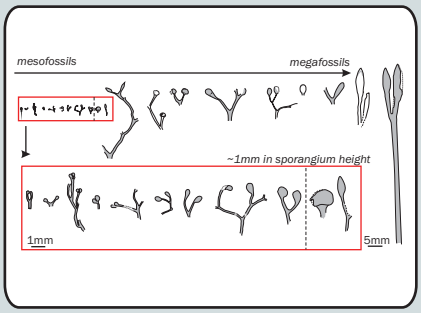
Introduction

- The Ordovician to Early Devonian was a time of great 'experimentation' by vegetation to conquer the land, a period from which the major lineages of plants we know today diversified.
- It is likely that several attempts at phototerrestrialisation were made: several groups may have adapted novel innovations for survival on land, but most became extinct, followed by the diversification of more successful lineages.
- Basal vascular plants emerged during the Early Silurian: the earliest megafossil record is from the Wenlock[1], although trilete spores, thought to have derived from tracheophytes, have been found from the Late Ordovician[2]. These basal plants continued to diversify into the Late Silurian and Early Devonian (see rhyniophytoid images on right).
- Cryptospores are also a major component of the dispersed spore record, found back to the Mid Ordovician[3], with evidence of rare cryptospore-producers from the Late Ordovician[4]. Little is known regarding these plants due to their poor preservation in the rock record.

Typical rhyniophytoids of the Early Devonian

Mesofossils

- A second component of Early Devonian vegetation has been discovered; a group of minute naked branching axes with terminal sporangia of variable morphologies (see figure on right).
- An assemblage of these mesofossils from a quarry near Brecon, Wales, show complex branching of the subtending axes, and hence can be considered a separate group from the larger rhyniophytes.
- However fossils from this locality are predominately coalified compressions, and little anatomical detail has been preserved.
- Similar mesofossils from a locality in Shropshire[5] are exceptionally preserved via charcoalification (see below), with anatomical detail and *in situ* spores, including cryptospores.
- This assemblage is currently being investigated with the following questions.



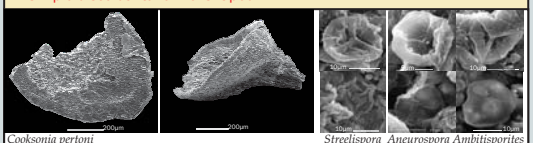
1. How diverse are these minute plants?

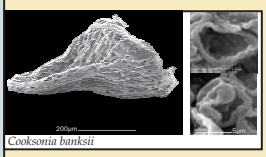
- Sporangial morphology is highly diverse: from discoidal, funnel-shaped, bivalved reniform, oval, elongate to birfurcating (see boxes 1 to 6); and therefore represent several genera.
- Dehiscence mechanisms are also variable, from:
  - disintegration of the sporangial wall or cuticle (*Cooksonia* and cooksonioid sporangia);
  - splitting marginally into two equal valves (*Resilitheca* and *Sporathylacium*);
  - longitudinal splitting into two equal valves (*Salopella*);
  - dehiscence associated with twisting; (*Tortilicaulis*)
  - valvate dehiscence (into 3 or more valves).

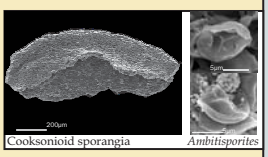
2. Are their *in situ* spores recognised taxa from the dispersed spore record?

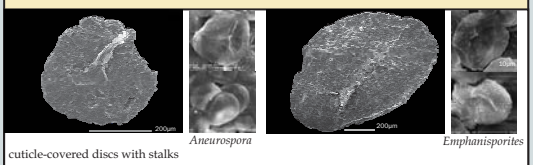
- Both trilete and cryptospore taxa have been found within these fossils.
- Some taxa have been described from the dispersed spore record (e.g. *Streelispora newportensis, Cymbohilates horridus, Ambitisporites*) , while others are new (including a new species of *Aneurospora*).
- The *in situ* spores also reveal cryptic diversity: one plant species may produce spores from different taxa (e.g. *Cooksonia pertoni* can contain *Aneurospora, Streelispora or Ambitisporites*).
- The same spore taxa can be known from several different plant species; this is one of the main challenges of linking the *in situ* spores with the dispersed spore record.

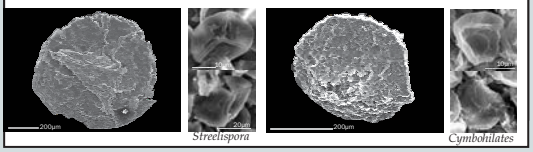
1. Simple discoidal to funnel-shaped



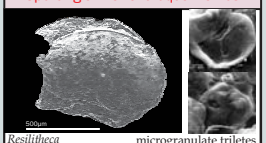


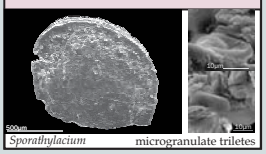




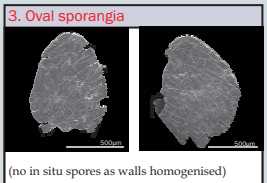


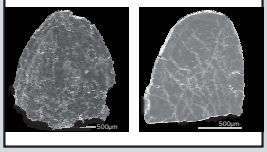
2. Sporangia with two equal valves



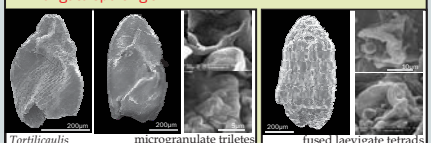


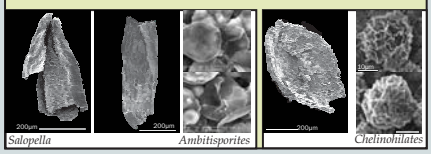
3. Oval sporangia



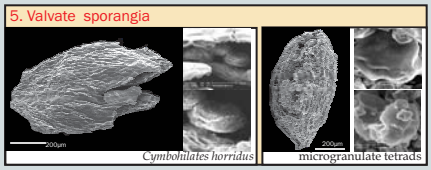


4. Elongate sporangia

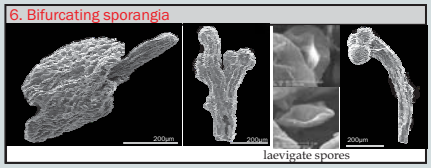




5. Valvate sporangia

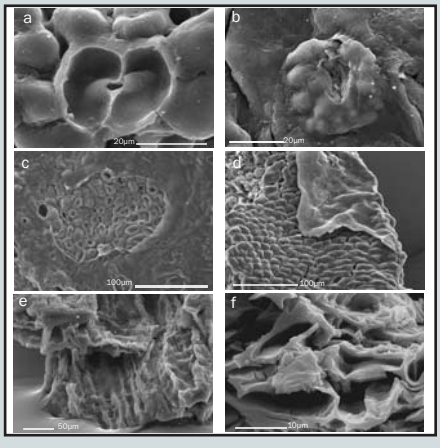


6. Bifurcating sporangia



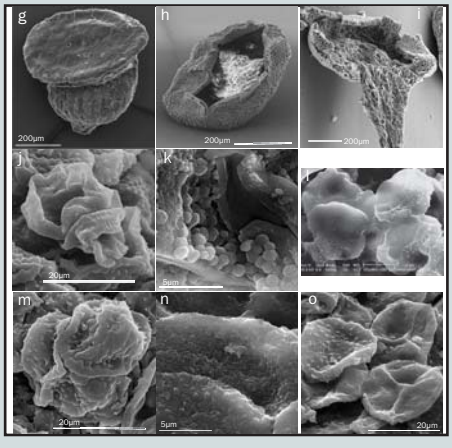
3. Were these mesofossils adapted to life on land?

- Evidence to suggest that these mesofossils were adapted to life on land include:
  - stomata (a and b);
  - cuticular coverings (c and d);
  - water - conducting cells in the axial parts (e and f).
- There is some debate as to whether the sub-aerial axial parts of these plants were of sufficient diameter to support all the functions required for survival on the land, in particular photosynthesis[6]. It has been suggested that these minute plants may have been gametophyte-dependant[6], although there is no fossil evidence to suggest this.



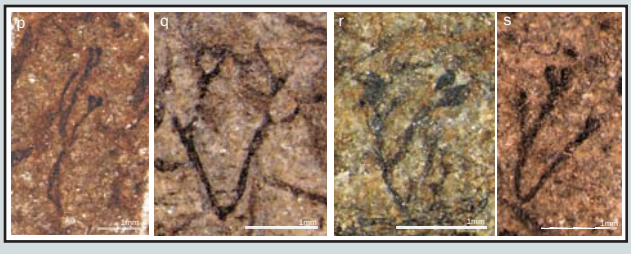
4. Can ontogenic or developmental stages be recognised?

- The difference stages of sporangial maturity have been observed, from:
  - immature, pre-dehiscence sporangia (g);
  - sporangia during active dehiscence (h);
  - and post-dehiscence, empty sporangia (i).
- Spore development has also been recognised, from:
  - immature spores (j), associated with tapetal residue (k);
  - enveloped spores, particularly tetrads (l);
  - loose to parting tetrads/dyads (m), sometimes covered with disintegrating envelopes / peripheral layers (n);
  - loose monads/hilates (o).



5. What are the possible affinities of these mesofossils?

- Despite having very well preserved sporangial anatomy, this assemblage of mesofossils only have short lengths of subtending axes, and therefore branching habit cannot be determined.
- From this assemblage alone, without the knowledge of the branching habit, it has not previously been possible to distinguish these mesofossils as a separate group to the larger rhyniophytes e.g. *Cooksonia hemispherica, Uskiella* etc. It is possible that these mesofossils represent just the tips of larger plants.
- A second assemblage of mesofossils from the Brecon Beacons, preserved as coalified compressions, include specimens with longer lengths of subtending axes (see p to s). Some specimens have subtending axes that are complexly branched (at least pseudomonopodial branching has been observed), and therefore more complex than the simple dichotomous branching of the rhyniophytes. This suggests that a separate group of turf-sized vegetation was living alongside the larger rhyniophytes.
- The presence of *in situ* trilete spores and tracheids in some specimens confirm that they are early embryophytes e.g. *Cooksonia pertoni.* However the presence of *in situ* cryptospores is more charactertistic of bryophytes.
- However, complex branching suggests that this group are not bryophytes *senso stricto*, as extant bryophytes have unbranching axes.
- These mesofossils may represent stem-group embryophytes with bryophytic characteristics, and may represent several lineages that later failed to diversify, but from which the larger rhyniophytes evolved. A similar assemblage is known from Ludlow, of Late Silurian age[5], and therefore this group may have evolved prior to the Late Silurian from gametophyte-dependant unbranching bryophytes, the presence for which has been inferred from the cryptospore record.



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