GLIMPSES OF THE BOTANICAL HISTORY OF WALES

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The Ordovician through Carboniferous rocks of Wales and the Welsh Borderland (c. 250 million years) have been central to elucidating the initial phases of the colonisation of land by plants as they diversified from simple herbaceous organisms lacking leaves and roots to substantial forest trees. Spores extracted from Ordovician and younger rocks indicate that pioneering plants allied to mosses and liverworts were part of a vegetation composed of lichens and algae. Vascular plants today include ferns, horsetails, conifers and flowering plants but their earliest fossils in Silurian and Devonian rocks, although possessing all the anatomical characteristics of today's flora, had very simple architecture –essentially collections of green smooth stems and sacs of spores(e.g. *Cooksonia*),although in time branching diversified and height and reproductive capacity increased. Only one group, the clubmosses with small simple leaves, still exists, evolving into the gigantic trees that dominated Carboniferous swamps. Other members of the tropical forests included tall ferns and horsetails plus the earliest seed plants. The peat they produced was transformed into coal whose exploitation led to Wales' global influence during the Industrial Revolution.

Introduction. It was a somewhat surprising privilege to be invited to talk to the Society about my scientific research , but perhaps not inappropriate for an organisation whose name 'earliest natives' might be applicable to my fossil plants which flourished in a country that has given the global geological community the names, Cambrian, Ordovician and Silurian, to periods of time in the Palaeozoic era.

This article might be subtitled 'Plant life through the ages' and in particular those encompassing the Palaeozoic rocks of Wales and the Welsh Borderland—Offa's Dyke being no respecter of geology. The Palaeozoic was the geological era extending from the beginning of the Cambrian (c. 541 million years ago) to the end of the Permian (c. 252 million years ago) although the latter is not represented in the area [**Fig. 1**]. After this time, there are just brief glimpses of dinosaurs and the plants they ate in the Mesozoic. As regards the geological history of the planet, Wales is known globally because it is the source of the official names given to the rocks at the beginning of the Palaeozoic. These are the Cambrian, based on the Roman name for Wales, succeeded by the Ordovician and Silurian, the names of two Welsh tribes, the Ordovices (north-west to central Wales) and Silures (south-east Wales into the Welsh Borderland) also known to the Roman invaders. Indeed if we take into account the Precambrian, covering an enormous time interval then Wales would figure in the naming of over 90% of geological time! But this story begins in the Ordovician and extends into the Carboniferous. It encompasses the time when we have the first unequivocal evidence that plants lived on land, their initial diversification, the beginnings of ferns, horsetails and clubmosses, which are called free-sporing as opposed to seed plants, and the beginnings of the seed plants themselves followed by the arrival of the conifers in the late Carboniferous. Flowering plants arrived much later in the Cretaceous, but these strata are not preserved in the Principality. However Wales has a great advantage over any other part of the world in that, apart from a time of uplift and non-deposition in the mid-Devonian, its rocks extend throughout this time interval. They thus encompass pioneering phases of terrestrialisation and, even more importantly, for most of the Devonian and Carboniferous its rocks were formed on land where there was a greater chance of the preservation of terrestrial vegetation. Especially relevant to the past wealth of Wales were the peats produced by tropical forests which, following subjection to heat and pressure, were transformed into coal. Historically, specimens from the Coal Measures of north and south Wales were among the first plant fossils to be described and illustrated being included in 1699 in the first ever catalogue of fossils. This was entitled *Lithophyllacii Britannica Ichnographia* and produced by the Welsh polymath and Keeper of the Ashmolean Museum, Oxford, Edwards Lluyd.[1] Here I will concentrate on earlier phases in the colonisation of the land ranging from the Ordovician into the Lower Devonian, and end with a brief account of the forests in the Upper Carboniferous

Pioneering land vegetation. Currently, the earliest record for plant life on land is evidenced by spores recovered from mid-Ordovician strata in Argentina. Ordovician rocks in Wales are mainly volcanic, but not long after the Argentine record, similar spores were liberated (using hydrofluoric acid) from marine siltstones and mudstones exposed in the banks of the river Onny just north of Craven Arms. There are no megafossils showing the morphology of the plants that produced them, but clues for their identity come from the clustering of spores, named cryptospores, in fours (tetrads) or pairs (dyads) [**Fig.2a,b**] and the construction of the spore wall.[2] Their characters are found in liverworts today. Support for such affinity comes from molecular studies involving DNA sequencing of a wide range of plants, which indicate that the bryophytes, including mosses and liverworts, had evolved before the present day dominant group of land plants, the vascular plants or tracheophytes, which are the free-sporing and seed plants mentioned earlier. Bryophytes are described as possessing low fossilisation potential because their soft tissues are readily degraded by bacteria and fungi and so apart from their spores, where thick walls prevent drying out during dispersal by wind, they would not survive fossilisation processes. Often associated with the spores are tubes and sheets thought to derive from terrestrial fungi and provide support for the hypothesis that land surfaces were covered by association of bryophytes, algae, cyanobacteria, fungi and even lichens, associations today known as cryptogamic covers which thrive in habitats free from tracheophyte competition today such as in deserts and the Arctic

The earliest tracheophytes. Throughout the Silurian, there were gradual changes in the composition of the spore assemblages in that the tetrads and dyads were joined by single spores each showing a superficial Y or trilete mark **[Fig.2c].** This feature indicates that the spores were initiated as tetrads but that they had separated before liberation and dispersal. Today they are known to belong to free-sporing tracheophytes, but again there is no evidence of the morphology of the parent plants of the earliest examples. However later in the Silurian, they are recorded in megafossils (admittedly very small) named *Cooksonia*, the earliest examples in Wales coming from the Eppynt **[Fig.3]** and slightly later from Freshwater East, Pembrokeshire. *Cooksonia* consisted of bifurcating stems, but no leaves or roots, each stem being preserved as a film of coal terminating in a sac (sporangium) containing the trilete spores [**Fig.3**]. So how do we know that these were tracheophytes and the ancestors of almost all land plants from ferns to flowing plants? The successful conquest of the land that resulted in colonisation of a wide range of habitats and attainment of a great size was achieved by the ability of plants to maintain an internally hydrated environment regardless (within reason) of external water sources – a strategy named homoiohydry. An alternative solution (poikilohydry) is seen in bryophytes which are capable of drying out and then rehydrating to function normally. Homoiohydry in the tracheophytes was produced by acquisition of a suite of anatomical and biochemical characters – the great inventions of the land, which can be recognised in the 'simple' land plants such as ferns and clubmosses as well as the tallest of trees (e.g. *Sequoia*). Such characters include:-

i. Roots, root hairs and rhizoids for water absorption
ii. A superficial sealant (cuticle) to limit evaporation which, in order to facilitate the exchange of gases (e.g. CO_2 for photosynthesis), is accompanied by controllable turgor operated openings (stomata)
iii. Water-conducting cells (xylem composed of elongate tracheids – hence tracheophytes) to transport water from soil to aerial pats

iv. Ability to synthesise the complex aromatic polymer, lignin , to strengthen the conducting cells under tensions created when water evaporates from exposed aerial surfaces

v. Ability to synthesise the polyethylene and waxes essential for water proofing the aerial surfaces

vi. Ability to synthesise the very complex chemical, sporopollenin, which coats and seals the spores, a character shared with bryophytes

Thus in the search for the earlies t tracheophytes, the palaeobotanist investigates somewhat featureless collections of coalified stems, for anatomical evidence. *Returning to Wales.* By the early Devonian, Wales had collided with North America and parts of Europe resulting in a supercontinent named the Old Red Sandstone continent or Laurussia. Welsh Upper Silurian sediments were deposited on its southern shoreline and Lower Devonian sediments deposited on a coastal plain extending over the whole of south Wales into the Welsh Borderland. This was dissected by numerous rivers that, in flood, deposited silts and sands entombing the plants originally growing along their banks. The best preserved of the resulting fossils occur in the Old Red Sandstone rocks exposed in the Brecon Beacons and Welsh Borderland. Two localities are worthy of special mention because the fossils show excellent cellular preservation. The older is a stream section in the North Brown Clee Hill area of Shropshire where minute fossils occur in a basal Devonian (Lochkovian) mudstone and were produced when wild fire spread through litter. This charcoal marks the second oldest record of fire, the earliest being in the Upper Silurian at Ludlow, and the deposit is called a Lagerstätte or site of exceptional preservation. As is the case for spores, the rock is dissolved using hydrofluoric acid thus liberating the charcoalified fossils. These are then viewed under a high resolution microscope (scanning electron microscope) to examine surface features and then broken open to look for anatomical detail. Using such techniques we have unequivocal evidence that at least in the Lower Devonian, *Cooksonia* was a land plant, its charred stems revealing conducting cells and stomata, while its sporangia contain spores with Y marks typical of those recorded much earlier in the Silurian [**Fig.4**]. In addition, *in situ* spores with tetrad and dyad configurations similar to those recovered from Ordovician rocks have been recovered from sporangia that split into valves, a liverwort characteristic, but these minute plants have forking stems bearing stomata a combination known today only in tracheophytes. These minute plants thus might represent relicts of a 'missing link' between the earliest land colonisers and the vascular plants. The latter are represented by a number of sporangia of different shapes with spores showing a variety of surface ornament, e.g. spines, which can be linked to similar dispersed spores present in the rock here and elsewhere in rocks of similar age. Isolated charcoalified fragments also provide some insight into the nature of cryptogamic covers including the earliest records of lichens among other types of fungi. Terrestrial animal fossils have not been recorded, but there are clues to their existence in the form of coprolites (fossil faecal pellets). These contain intact spores and plant fragments leading to the inference that they were produced by millipedes consuming litter and excreting indigestible remains (detritivores), while a few containing only fungi indicate the presence of fungivores.

While demonstrating greater diversity in tracheophytes than known elsewhere in the early Devonian, it must be emphasised that consequent on their unusual type of fossilisation process they represent only one facet of land vegetation, one where plants were just a few centimetres high. Other coeval localities in the area record much larger plants – increase in height being an important vegetational change throughout the Lower Devonian. This is nicely demonstrated in plants preserved at my second locality – a personal choice because over fifty years ago, I began my palaeobotanical research at this roadside exposure on the A470 just to the north of Storey Arms in the Brecon Beacons. Here the stems are a few millimetres wide and show more complex branching patterns. The vast majority lack leaves and carried out photosynthesis via stomata and green stems. Most of the earlier plants had possessed stems with terminal sporangia, a growth condition which terminated their further growth. By contrast, most of the Brecon Beacon plants have lateral sporangia, a change in growth strategy that overcomes this architectural impediment and allows increased growth in height and reproductive capacity per stem. My favourite plant and major focus of my doctoral thesis, *Gosslingia breconensis* exemplifies this because some stems continued growing and 'overtopped' others, while sporangia were produced laterally and scattered over the aerial surfaces [**Fig. 4a**] *Gosslingia breconensis* is important because it shows another form of preservation, namely permineralisation. In this process, pyrite (iron sulphide) is precipitated in the spaces between and within cells due to the activity of bacteria while the original cell walls are eventually converted to coal. This preserves the three dimensional nature and anatomy of the stem tissues. Stems with the dimensions of matchsticks are embedded in plastic and cut into thin slices using a saw. The slices are then smoothed with carborundum and polished with diamond paste until the pyrite becomes shiny (as is appropriate for fool's gold) but the cell walls remain black [**Fig.4b**]. This provides evidence of the distribution of tissues, but the construction of cells can be examined after the pyrite [**Fig.4c,d**] has been dissolved away using concentrated nitric acid. This leaves a three dimensional skeleton of coalified walls which is ideal material for scanning electron microscopy. The ultrastructure of conducting cells can be important in determining the wider affinities of these simple plants. Thus *Gosslingia* and, from the same locality, its close relatives *Tarella* and *Deheubarthia* (note the Welsh connotations in their names) are united in possessing a type of tracheid also found in the earliest clubmosses (lycophytes). Indeed one of the oldest representatives of that group is found in the Brecon Beacons. Named *Drepanophycus*, it must have looked like a bramble in winter with arching stems and small sickle shaped leaves replacing the spines. These were the earliest leaves evolved by plants on land and were borne on a herbaceous lycophyte whose descendants some millions of years later were the giant trees of the Carboniferous, the source of the peat eventually converted to coal.

A period of major climate change. While the greening of the planet is of major interest to botanists and evolutionary biologists, its impact on the environment cannot be overestimated. Decaying plants, by introducing humus into sandy and rocky substrates, produced soils and new terrestrial habitats for animals, but arguably even more important were their effects on atmospheric composition. Today we are all aware of the dangers of increasing carbon dioxide concentration in the atmosphere that is largely due directly to man's usage of fossil fuels (coal, gas, oil). This results in increasing temperatures and the need both to cut down CO_2 emissions and to capture or draw down CO_2 from the atmosphere (carbon sequestration). Photosynthesis in plants, the most important chemical process in the world, achieves this by the production of energy-rich carbohydrate (energy comes from the sun), the basis of all food chains and webs.

At its simplest

$$CO_2 + H_2O \rightarrow CH_2O + O_2$$

carbon dioxide + water carbohydrate + oxygen

This process is reversed when the carbohydrate or its derivatives are used by both plants, animals and microbes to yield energy in the process of respiration

$$CH_2O + O_2 \rightarrow CO_2 + H_2O = \text{energy}$$

The proportions of gases in the atmosphere thus remains constant. Planting more trees can fix CO_2 into wood on the short term, and over millions of years its sequestration in peat and coal. But another process was of major significance when plants first started to live on land *viz* the chemical weathering of rock. In a series of reactions, fresh rock, such as basalt, is broken down by weak carbonic acid and the CO_2 incorporated into limestone.

At its simplest

$$CaSiO_3 + CO_2 \rightarrow CaCO_3 + SiO_2$$

rock+carbon dioxide=limestone +silica

Respiration during decay of plants in soils by bacteria and fungi produced carbon dioxide, which when dissolved in water produced carbonic acid, and this, together the carbon-containing acids secreted by the organisms, dissolved the rock. Various lines of evidence indicate that in Ordovician times, calcium dioxide concentrations in the atmosphere were as much as sixteen times higher than today and that through the Devonian there was a major decrease in carbon dioxide. Thus by Carboniferous times it had reached present day levels resulting in very cold temperatures at high latitudes and the global change from a green-house to an ice-house world. Acceleration in the mid and late Devonian was achieved by the evolution of more deeply-rooted plants such as trees with the ability to reach further supplies of fresh rock. This phase of plant evolution is not recorded in Wales, except for records of some of the earliest seeds, heralding the beginnings of gymnosperms, which were discovered during improvements to the A470 at Taffs Well, below Castell Coch.

Coal Measure forests. In the Lower Carboniferous much of Britain including north and south Wales was covered by seas resulting in the widespread deposition of limestones which were not conducive to the preservation of land plants although skeletons of calcareous algae (sea weeds) are common. However, Lower Carboniferous plants have been recorded in shales and mudstones between limestones in north Wales in the Llangollen/Prestatyn area. These include representatives of the groups such as clubmosses and horsetails that were to dominate the forests growing on the low-lying swamps in Upper Carboniferous times. Coal mines in north and south Wales revealed the existence of the plants preserved as the familiar and quite beautiful compression fossils in rocks between the coal seams. Some of the most extensive collections can be found in the National Museum Wales at Cardiff. These were largely accumulated by colliery agent, David Davies of Gilfach Goch who facilitated the collection of the plants between episodes of mining, and then carefully catalogued them before undertaking his own research on plant communities and making them available for research by others. His discoveries attracted leading palaeobotanists to visit Gilfach Goch. These included Richard Kidston, who made annual pilgrimages, and Marie Stopes, better known now for her interests in family planning.

At this time Wales was located in the tropics in a warm and wet climate, but the tropical forests contained very different types of trees from those of today. Free-sporing rather than seed plants dominated and in particular the club mosses, typified by *Lepidodendron* were of gigantic size: their trunks with familiar diamond-shaped patterning [**Fig.5a**] as long as thirty metres. On decay these plants were largely responsible for the peat that after experiencing high temperatures and pressures, became coal. Other members of the community included horse-tails (*Calamites*) as tall as fifteen metres [**Fig.5b**] and a profusion of ferns, many with bizarre branching and lacking familiar fronds, although the latter are seen in *Pecopteris*/*Psaronius* (leaves [**Fig.5c**] and trunks) on plants with growth habits similar to those in the tree fern, *Dicksonia,* today. Fern-type fronds also characterise the major group of seed plants in the forests which were predictably named the seed ferns (pteridosperms), and again different names were given to the leaves (e.g. *Neuropteris,* **Fig. 5d**) and trunks (e.g. *Medullosa*) to accommodate the reality that the plants broke up before fossilisation.

Description and reconstruction of these plants have long been preoccupations of palaeobotanists. Today there is additional interest in their ecology and distribution within the swamps and surrounding drier areas including river plains and uplands – studies that were pioneered by David Davies almost a hundred years ago. Accumulated lines of evidence are summarised in some recent, very life-like reconstructions of vegetation, produced by Annette Townsend, in close collaboration with Dr Chris Cleal and his colleagues at the National Museum [**Fig.6**], The recent discovery of casts of the bases of the trunks of plants and even their rooting systems at Brymbo Quarry near Wrexham, now displayed at a new museum nearby, provide additional and vivid insights into the actual size and distribution of the plants.

There are no Welsh rocks marking the end of the Carboniferous, but elsewhere they record an increasingly dry climate and the demise of the Coal Measures forests in the Permian, the end of the Palaeozoic. Mesozoic rocks of Wales are confined to the coastal areas of Glamorgan. They are mostly marine, with very few plant fossils including isolated conifer twigs and trunks and the occasional fern fronds, which provide very little information on the diets of the land-living dinosaurs and other terrestrial animals of the time.

References

[1] M.G. Bassett and D. Edwards, 'Fossil Plants of Wales', *Amgueddfa*,13 (1973), 2-27.

[2] D. Edwards, J.M. Morris, J.B. Richardson and P. Kenrick, ' Cryptospores and cryptophytes' reveal hidden diversity in early land floras. *New Phytologist*, 212 (2014), 212, 50-78.

[3.] D. Edwards and J.B. Richardson, 'Silurian and Lower Devonian Plant Assemblages from the Anglo-Welsh Basin: a Palaeobotanical and Palynological Synthesis ', in *The Old Red Sandstone of the Anglo-Welsh Basin,* ed. by B.J.P. Williams , R.D. Hillier and S. B. Marriott. *Geological Journal* (Special Issue), 39, 375-402.

[3] B. A. Thomas and C.J.Cleal, *The Coal Measures Forests.* (National Museum of Wales, 1993), 32 pp.

[4] C..J. Cleal and B.A. Thomas, *Plant fossils of the British Coal Measures.* (Woodbridge: Boydell Press) Fossils illustrated , volume 2. Lx+188pp, 128pls.

Legends to figures.

Figure 1. Subdivisions of the Palaeozoic era with time- line using dates produced by the United States Geological Survey in 2017 and indicating the events mentioned in the text.

Figure 2. Spores isolated from Silurian rocks. Scale bars =10μm. A and B are cryptospores, A is a dyad, B is a tetrad enclosed in an envelope. C is a trilete spore.

Figure 3. The oldest example of *Cooksonia pertoni* on mainland Britain in Upper Silurian rocks from the Eppynt, Powys. NMW 79.17G.3. Scale bar=5mm.

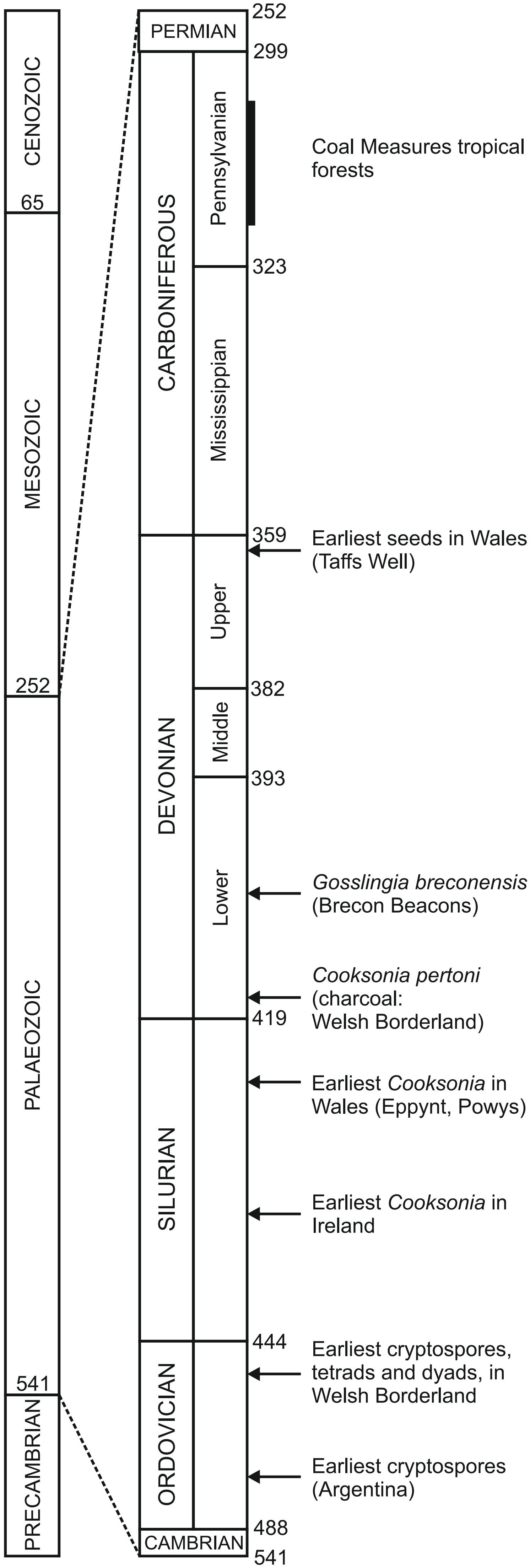
Figure 4. Charcoalified Lower Devonian *Cooksonia pertoni* from the Welsh Borderland. A, sporangium; B, spores; C,D, tracheids (C in section); E, stoma.

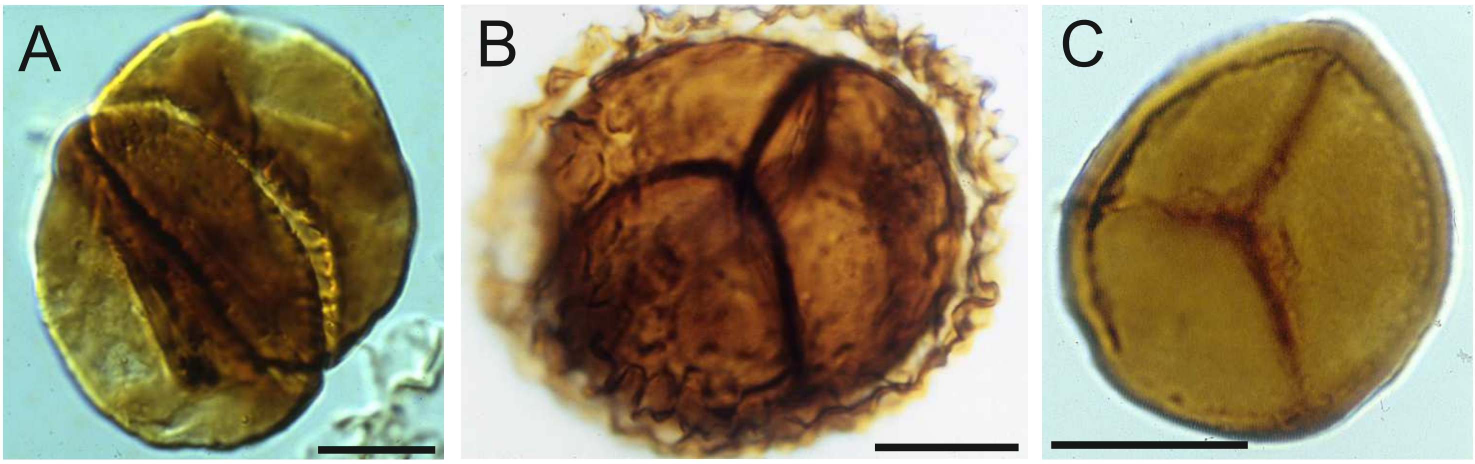
Figure 5. *Gosslingia breconensis* from the roadside quarry, near Storey Arms, Powys. A,

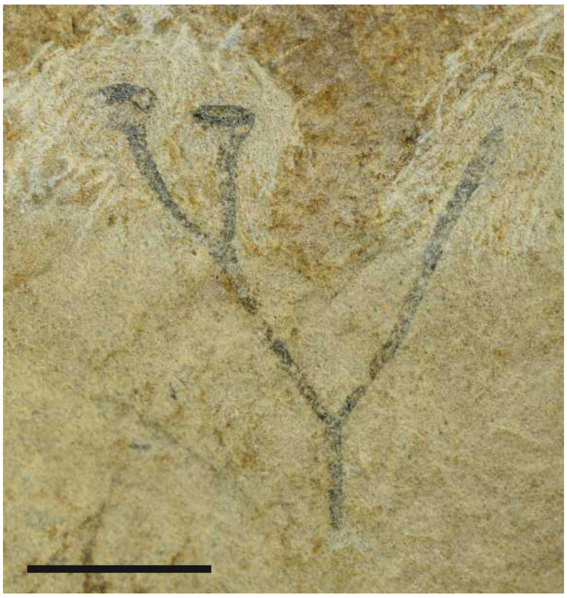
compression fossil with lateral sporangia. Scale bar = 10mm. B, transverse section through a pyritised stem with oval central conducting strand. Scale bar =100µm. C, longitudinal polished section; horizontal black bars represent tracheidal thickenings. Scale bar =10µm. D, longitudinal section in which pyrite has been partially removed revealing its crystalline nature and the projecting coalified tracheidal thickenings. Scale bar =10µm.

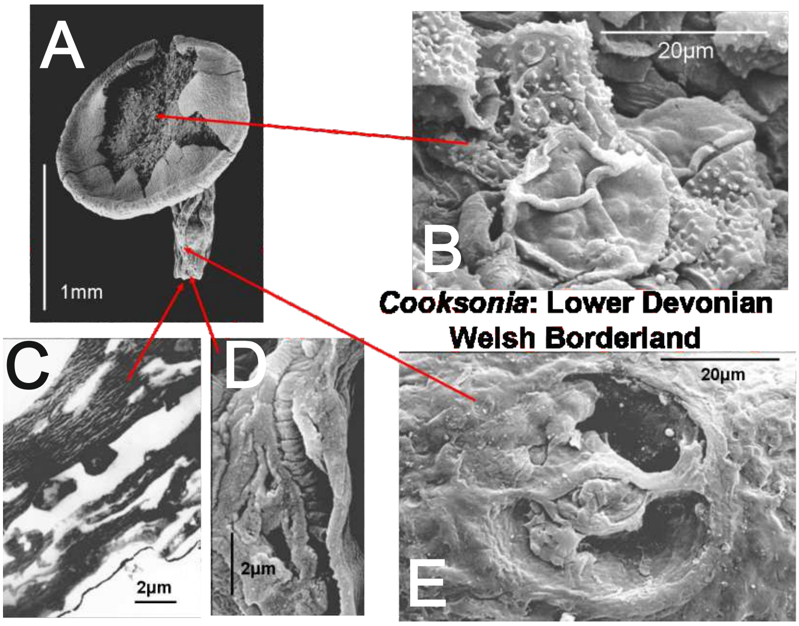
Figure 6. Coal Measure plants from South Wales .. A, *Lepidodendron* bark with remains of leaf bases. B, the fern frond, *Pecopteris*. C, leaves of the horsetail, *Calamites*, named *Annularia.* D, leaves of the seed-fern, *Neuropteris*.

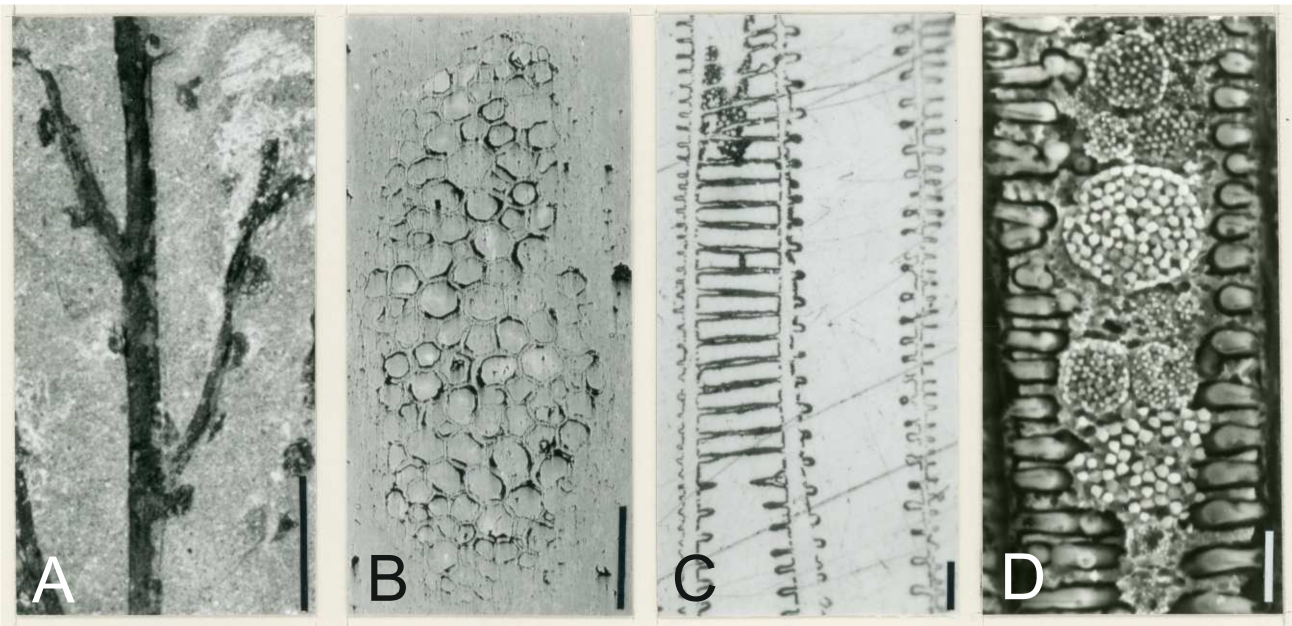
Figure 7. Reconstruction of an Upper Carboniferous forest and vegetation bordering a waterway, by Annette Townsend with permission.


CENOZOIC
65
MESOZOIC
252
PALAEOZOIC
541
PRECAMBRIAN
PERMIAN
252
299
CARBONIFEROUS
Pennsylvanian
Coal Measures tropical forests
323
Mississippian
359
Earliest seeds in Wales (Taffs Well)
DEVONIAN
Upper
382
Middle
393
Lower
Gosslingia breconensis (Brecon Beacons)
Cooksonia pertoni (charcoal: Welsh Borderland)
419
SILURIAN
Earliest *Cooksonia* in Wales (Eppynt, Powys)
Earliest *Cooksonia* in Ireland
444
ORDOVICIAN
Earliest cryptospores, tetrads and dyads, in Welsh Borderland
Earliest cryptospores (Argentina)
488
CAMBRIAN
541


A
B
C




A
1mm
B
20μm
Cooksonia: Lower Devonian
Welsh Borderland
C
2μm
D
2μm
E
20μm


A
B
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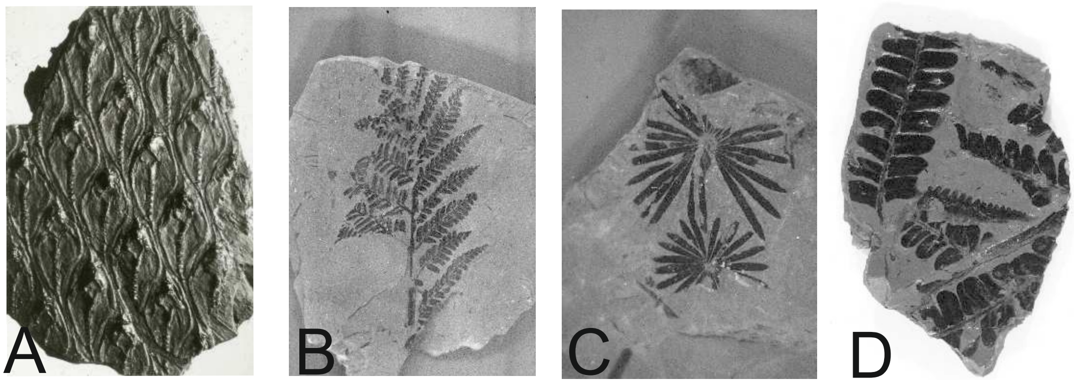
A
B
C
D


A.M.T.