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Pennsylvanian (Carboniferous) biotas and palaeoenvironments

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Westphalian–Stephanian macrofloras of the southern Pennines Basin, UK[2]

(Figs 1–4; Tabs 1–4)

Abstract. The southern part of the Pennines Basin (Warwickshire, South Staffordshire and Wyre Forest coalfields) has a condensed succession of middle Langsettian to upper Asturian or lower Cantabrian strata. The Langsettian–Duckmantian part of the succession is in a grey coal-bearing facies, in which many coal seams have become vertically accreted, and in which macrofloras of the *Laveineopteris loshii* Subzone, *Lonchopteris rugosa* Zone and *Neuropteris semireticulata* Subzone can be recognised. Species composition and Total Species Richness diversity curves compare well with those from the Central Pennines Basin to the north, suggesting that they represent an essentially unified area of vegetation. Red beds of the Etruria Formation appear in the lower Bolsovian Substage (stratigraphically lower in the marginal southernmost part of the basin). The Etruria Formation macrofloras are not abundant, but where they do occur are not significantly less species-rich than in the contemporaneous grey coal-bearing sequence in the Central Pennines. The Etruria Formation macrofloras belong to the *N. semireticulata* Subzone, and there is no evidence of the overlying *Laveineopters rarinervis* Subzone that would indicate a late Bolsovian age. The grey, mainly arenaceous Halesowen Formation unconformably overlies the Etruria Formation, and yields low-diversity macrofloras that probably indicate the late Asturian *Dicksonites plueckenetii* Subzone. The succeeding red-beds of the Salop Formation yield even lower diversity macrofloras, but there is some evidence that they may belong to the Cantabrian *O. cantabrica* Zone. A comparison of these new data with the evidence from the Central Pennines helps confirm the robustness of Total Species Richness as a proxy for environmental change in Late Carboniferous palaeotropical coal-bearing sequences.

Key words: Carboniferous, palaeobotany, biostratigraphy, diversity-analysis.

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INTRODUCTION

The Pennsylvanian (Late Carboniferous) aged Pennines Basin in central and northern England has an extensively-collected macroflora, especially in the early and middle Westphalian aged coal-bearing part of the succession. A recent study investigated the biostratigraphy of these macrofloras and demonstrated clear changes in species diversity through the stratigraphical sequence (Cleal, 2005). That study focused on the central part of the basin in the Yorkshire, Lancashire and North Staffordshire coalfields, where the stratigraphically-thickest successions can be seen. However, the more condensed successions in the southern part of the basin, notably the Warwickshire, South Staffordshire and Wyre Forest coalfields have also yielded important macrofloras of this age.

Most of our palaeobotanical knowledge of these southern Pennines Basin coalfields comes from a series of papers by Kidston (1888, 1891, 1914; *in* Kidston *et al.*, 1917), and his extensively-illustrated monographs published towards the end of his life and posthumously (Kidston, 1923–1925; Crookall, 1955–1976). Also at about this time, Arber (1914, 1916) was publishing illustrated accounts of these floras. Dix (1935, 1941) started to investigate the stratigraphy and palaeobotany of these coalfields, but her work was unfortunately terminated by the Second World War and her subsequent illness (Burek & Cleal, 2005). Much of the published data was critically collated by Jongmans (1940), which provides a valuable starting-point for assessing the historical records. Most recently, the late Westphalian and early Stephanian palaeobotany of these coalfields was investigated by Besly & Cleal (1997) although detailed species lists have yet to be published.

The present paper reviews the published macrofloral data from the southern Pennines Basin. The resulting data are then used to assess the biostratigraphical and biodiversity patterns in these coalfields, which will then be compared with the patterns reported in the central part of the basin (Cleal, 2005). If the observed patterns are essentially comparable, then both areas may be regarded as part of the same vegetational system and the biostratigraphical distributions from the two areas may be legitimately combined. The new data will also provide a means of testing whether the observed changes in species diversity through the succession in the central Pennines Basin reflects a real change in the vegetation, or is merely an edge-effect induced by the analytical method used. In particular, is there any significant difference in the observed fall in species diversity towards the top of the grey coal-bearing strata in the upper Duckmantian and lower Bolsovian Substages? Finally, the paper will present some of the detailed palaeobotanical records on which the Besly & Cleal (1997) study was partly based.

There are other coalfields south of the central Pennines Basin area, which have yielded plant fossils, notably the Coalbrookdale, Shrewsbury, Denbigh and Flint coalfields. However, published evidence of the palaeobotany from these coalfields is limited and rarely accompanied by illustrations of the fossils, and so is difficult to assess (e.g. Arber, 1914; Wood, 1936). These areas have not therefore been included in the present study.

GEOLOGICAL SETTING

The area being dealt with in this paper represents the part of the Pennines Basin that laps onto the Wales-London-Brabant High (Fig. 1). The exposed coalfields occur in what were embayments along the northern edge of the High, formed by approximately N–S oriented faults, and these divided this part of the basin into distinct sub-basins (Fulton & Williams, 1988; Waters *et al.*, 1994). Nevertheless, the successions in the areas under consideration are all essentially similar, even to the extent that individual coals can be correlated.

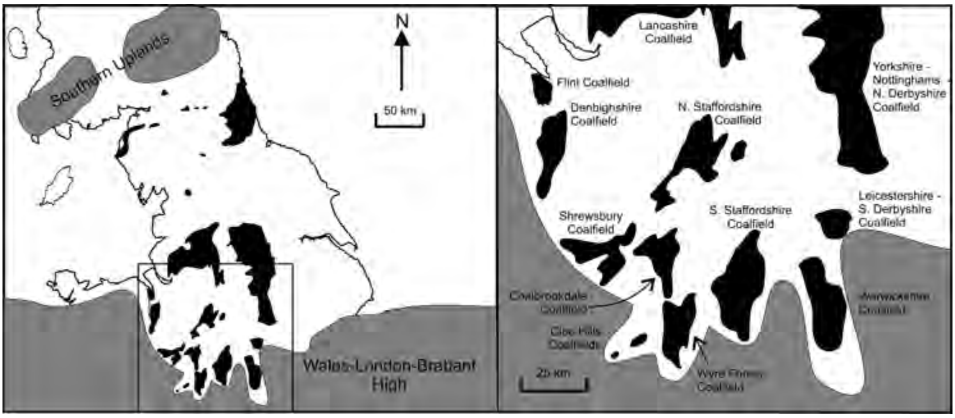

Fig. 1. Central and northern England showing the location of the coalfields dealt with in this paper

The sequences are characterised by a rapid southwards attenuation as they lap onto the Wales-London-Brabant High. The most recently published detailed stratigraphical data for the South Staffordshire and Warwickshire Coalfields (Bridge *et al.*, 1998; Powell *et al.*, 2000a) indicate that the succession thins by over 60% over a distance of about 10 km, but that most of the loss is in the clastic part of the succession; the coal seams only reduce in thickness by about 30%. As a consequence, many of the coals coalesce vertically, the best example being the Thick Seam (also known as the Highley Brooch Coal in the Wyre Forest and the Great Coal in the Clee Hills – Whitehead & Pocock, 1947), which in the southern South Staffordshire Coalfield is a 12 m thick more-or-less coherent seam, but northwards separates into at least seven separate seams (e.g. Cope & Jones, 1970).

The Upper Carboniferous succession of the area under consideration is broadly divided into a grey coal-bearing Pennines Coal Measures Group, and a mainly barren, varicoloured Warwickshire Group (Tab. 1). In the northern parts of these coalfields, the Pennines Coal Measures Group extends down to the Subcrenatum Marine Band at the base of the Westphalian Stage. However, most of the data dealt with in this paper originated from the southernmost part of the basin, and here the stratigraphically lowest Westphalian beds are middle Langsettian in age (upper *C. robusta* Zone in the standard British non-marine bivalve zonation of Ramsbottom

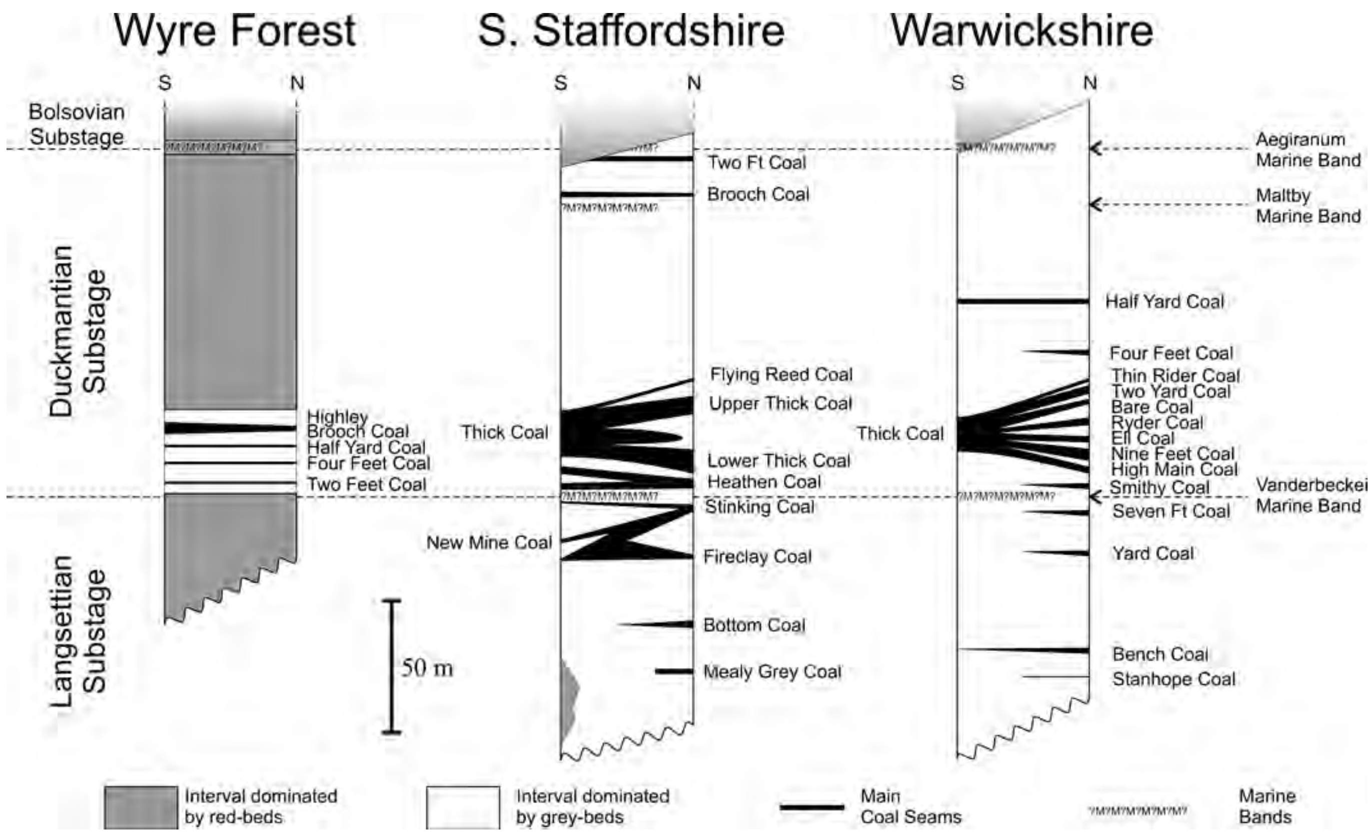

Fig. 2. Generalised lithostratigraphy of the Wyre Forest, South Staffordshire and Warwickshire Coalfields, showing relative positions of principal coals. Each column shows the southwards coalescing of the coal seams, as the successions lap on to the Wales-Brabant-High. Marine bands are named according to the standard classification of Ramsbottom *et al.* (1978). Note that in the southern Pennines Basin, the Maltby Marine Band only occurs in the South Staffordshire Coalfield

Table 1

General lithostratigraphical scheme for the Westphalian and lower Stephanian successions in the three main coalfields dealt with in this paper. Adapted from Ramsbottom *et al.* (1978) and Powell *et al.* 2000b)

Group	Formation	Members (Thickness)		
		Wyke Forest	S. Staffordshire	Warwickshire
Warwick-shire Group	Salop Formation (lower part)	GAP	GAP	Allesley Mbr (140 m)
				Keresley Mbr (197-306 m)
			Enville Mbr (100-247 m)	Whiteacre Mbr (280-357 m)
		Alveley Mbr (45 m)	Alveley Mbr (152-247 m)	
	Halesowen Formation	Undivided (≤200 m)	Dark Slade Mbr (40-90 m)	Undivided (70-127 m)
			Unnamed mbr (35-60 m)	
	Etruria Formation	Undivided (90 m)	Undivided (50-100 m)	Undivided (70-90 m)
Pennines Coal Measures Group	Productive Coal Formation	'Sweet Coals' (30 m)	Middle Coal Measures (100 m)	Middle Coal Measures (90 m)
		'red beds' (30-50 m)	Lower Coal Measures (120 m)	Lower Coal Measures (120 m)

et al., 1978). The Pennines Coal Measures Group then mostly extends continuously upwards to near the top of the Duckmantian Substage. The sedimentology of these strata indicates deposition in an upper delta plain broadly similar to that seen in the central part of the Pennines Basin (Fulton & Williams, 1988).

The coal-bearing grey beds are diachronously overlain by the Warwickshire Group. The stratigraphically-lowest part of the Warwickshire Group consists of red-beds of the Etruria Formation (Besly & Turner, 1983; Besly, 1988; Glover *et al.*, 1993). The sedimentology of these beds does not differ substantially from that of the underlying grey coal-bearing strata, and the red colouration appears to have been secondary, as a result of a lower water table. Red beds similar to Etruria Formation also occur at stratigraphically-lower levels, especially in the South Staffordshire Coalfield, but only in a very narrow band a few hundred metres wide near the Wales-London-Brabant High. Biostratigraphical control on the Etruria Formation is extremely limited, but it is widely assumed to extend up into the upper Bolsovian Substage.

Above the Etruria Formation there appears to be a non-sequence, although field-evidence is limited due to poor exposure. However, the overlying Halesowen Formation has yielded macrofloras indicative of a late Asturian or possibly early Cantabrian age (Besly & Cleal, 1997). These arenaceous beds, probably a lateral equivalent of the Forest of Dean Pennant Formation (Cleal, 1986), probably represent southerly-derived alluvial deposits eroding from the advancing Variscan Mountains to the south. They are heterogeneous in character, mostly coarse-grained, but with very occasional thin coals. There have been no detailed sedimentolgical investigations of these beds, but they are likely to have been formed in unstable, relatively high-energy environments, where coal forest habitats could only develop ephemerally.

The Halesowen Formation is then succeeded by more red beds, known as the Salop Formation (Powell *et al.*, 2000b), representing northerly-derived alluvial deposits formed under more arid conditions (Besly, 1988). Powell *et al.* (2000b) have divided this formation into a number of members according to distinctive facies (partly summarised in Table 1). Plant fossils occur mainly in the lower part of the formation, notably the Alveley Member.

MACROFLORAL SPECIES INVENTORY

As in the previous studies on the macrofloras of the central Pennines (Cleal, 2005) and South Wales (Cleal, 2007), the present paper does not provide a complete inventory of all plant morphospecies from the southern Pennines Basin. Since the aim of the study is to determine changes in plant biodiversity through the succession, the lists are restricted to those morphotaxa that are likely to give the best indication of the original species biodiversity. For the arborescent lycophytes, the stem morphotaxa are regarded as being providing the closest reflection of original species diversity (B. A. Thomas, pers. comm.). For the other groups, the morphotaxa of foliage are probably the most reliable.

Productive Coal Formation

A total of 87 species have been identified from the grey coal-bearing parts of the succession in the three coalfields. Of these, 60 have been identified from more than one stratigraphical level and are shown on the range chart (Fig. 3). The other 29 species are listed below according to the stratigraphical level where they occur:

Fireclay Coal: *Lepidodendron acutum* Presl;

Bench Coal: *Corynepteris coralloides* Gutbier;

New Mine Coal: *Sigillaria cordigera* Zeiller, *S. nodosa* Lindley & Hutton, *S. punctirugosa* Kidst.;

Stinking Coal: *Renaultia chaerophylloides* (Brongn.) Zeiller;

White Ironstone: *Sphenopteris deltiformis* Kidst.;

Thick Coal: *Asolanus camptotaenia* Wood, *Sigillaria davreuxii* Brongn., *S. decorata* Weiss, *S. nudicaulis* Boulay, *S. reticulata* Lesq., *Oligocarpia brongniartii* Stur, *Nudospermopteris nummularia* (Gutbier) Doweld;

Coseley 10 ft Ironstone: *Asterophyllites charaeformis* (Sternb.) Unger, *Equisetites hemingwayii* Kidst., *Cosleya glomerata* Kidst., *Sphenopteris rutaefolia* Gutbier, *S. souichii* Zeiller, *S. stonehousei* Kidst., *S. truncata* Kidst., *Corynepteris similis* (Sternb.) Kidst., *Crossotheca hughesiana* Kidst., *Eusphenopteris grandis* (Keller) van Amerom;

6 ft (= c. 2 m) above Brooch Coal: *Zeilleria hymenophylloides* Kidst., *Palaeopteridium reussii* (Ettingshausen) Kidst., *Dicranophyllum anglicum* Kidst.

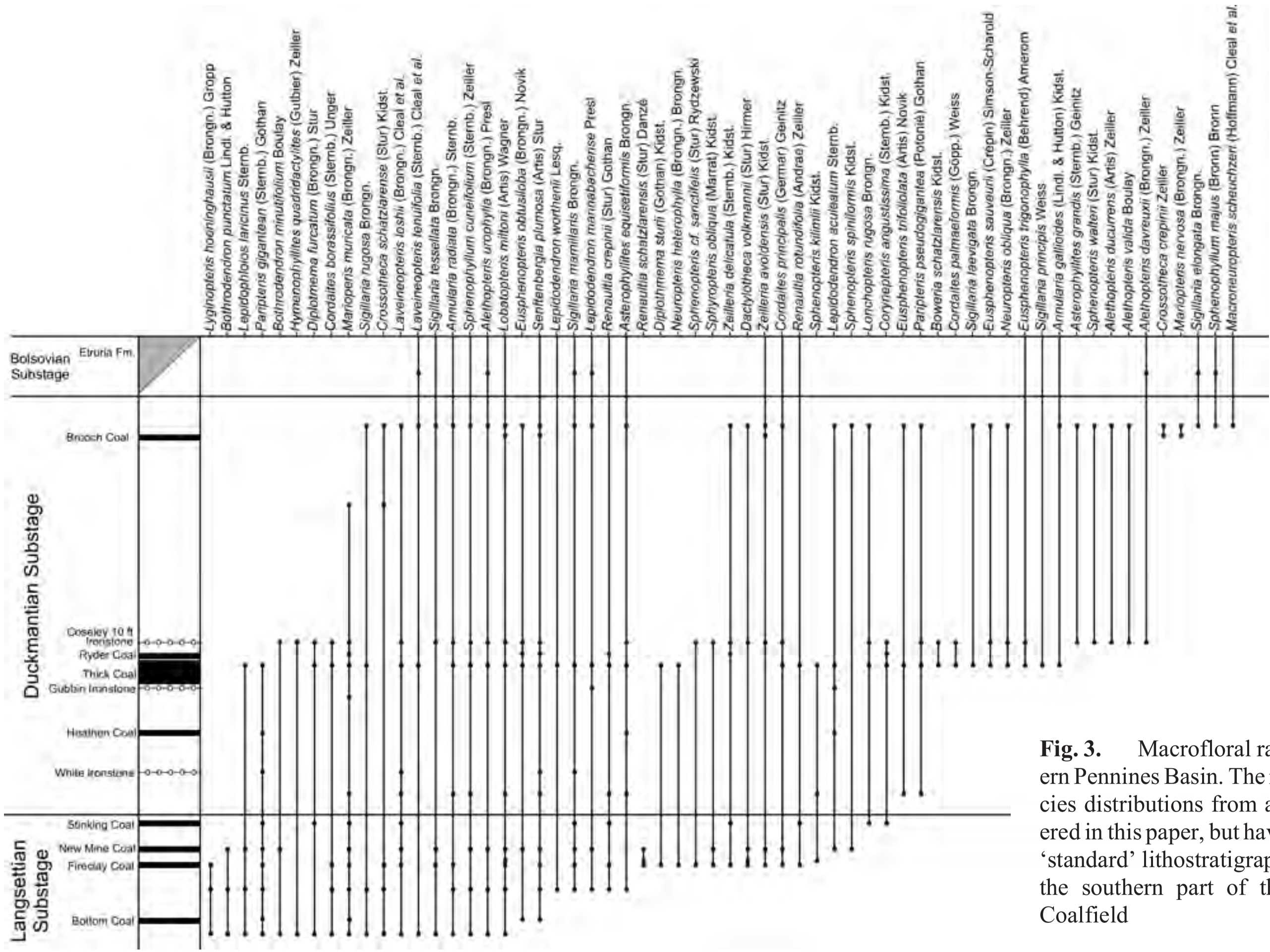

Fig. 3. Macrofloral range chart for the southern Pennines Basin. The ranges are based on species distributions from all three coalfields covered in this paper, but have been plotted against a 'standard' lithostratigraphical column, based on the southern part of the South Staffordshire Coalfield

Etruria Formation

The Etruria Formation is largely barren of plant fossils, the most notable discovery in recent years being of anatomically-preserved conifer remains in the South Staffordshire Coalfield (Galtier *et al.*, 1992). This paucity of plant fossils is largely put down to the low preservation-potential of these red-beds, the plant remains having rapidly oxidized after burial. However, this cannot be the total explanation, as there are records of 27 morphospecies of plant adpressions from the Etruria Formation, most notably by Arber (1916) (summarized in Tab. 2).

Halesowen Formation

The author, in a Natural Environment Research Council (NERC) project done in conjunction with B. M. Besly (University of Keele), has reviewed the distribution of plant macrofossils in this interval. Some of the lithostratigraphical conclusions of this work have been published (Besly & Cleal, 1997) and the detailed palaeobotanical records will be published as a Technical Report of the British Geological Survey. Table 3 summarises the palaeobotanical identifications that resulted from this study, which included only ten taxa identified to the rank of species, and a further five generic identifications.

Salop Formation

As part of the same project mentioned in the previous section, the author has also reviewed the available evidence from the Salop Formation. The only macrofloral evidence of any note was found in the Claverley Borehole in the Wyre Forest, at a depth of 267 m (corresponding to a level low in the Alveley Member) where the following taxa were identified: *Neuropteris ovata* Hoffmann, *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.*, ?*Odontopteris cantabrica* Wagner, *Laveineopteris rarinervis* (Bunbury) Cleal *et al.*

Slightly lower in the same borehole (261 m), still in the Aveley Member there is a specimen of conifer twig identified by Florin (in a note accompanying the specimen) as *Culmitzschia parvifolia*, associated with some fragments of *Neuropteris ovata* and *Laveineopteris rarinervis*. Conifer fragments were also seen at a depth of 344 m in the Birch Tree Farm Borehole in the Warwickshire Coalfield (Whitacre Member of the Salop Formation).

COMPARISON WITH CENTRAL PENNINES MACROFLORAS

A comparison with the macrofloral inventory for the central Pennines (Cleal, 2005) shows a good agreement. Table 4 gives the Jaccard Coefficients (i.e. the proportion of species that are in common between the two areas) for the whole assemblages, and for the major plant groups. Between a third and a half of all of the species occur in both areas, which may not seem that high. However, the detailed breakdown between plant groups shows that much of the apparent endemism between the two areas is due to the lycophytes and the sphenopteroid ferns, both of

Table 2

Distribution of macrofloral morphospecies within the Etruria Formation of the southern Pennines Basin. All localities are in the South Staffordshire Coalfield unless otherwise marked

	134 m above Thick Coal	178 m above Thick Coal	224 m above Thick Coal	Upper 100 m of 'Old Hill Marls'	'Within 200 yds above 4ft Coal' (Titterstone Clee)	Four Ashes (659 m)
Lepidodendron mannabachense	+		+			
Lepidodendron worthenii	+					
Lepidophloios acerosus			+			
Sigillaria elongata	+					
Sigillaria mamillaris	+					
Sigillaria principis			+			
Sigillaria tessellata			+			
Annularia galioides		+	+			
Annularia radiata			+			
Asterophyllites equisetiformis		+	+			
Sphenophyllum cuneifolium		+	+			
Sphenophyllum majus			+			
Sphenophyllum myriophyllum			+			
Renaultia crepinii			+			
Renaultia rotundifolia				+	+	
Sphenopteris kayii			+			
Zeilleria avoldensis			+			
Lobatopteris miltoni			+	+		
Senftenbergia plumosa			+			
Eusphenopteris obtusiloba	+	+				
Alethopteris davreuxii	+		+			
Alethopteris lonchitica	+		+			
Macroneuropteris scheuchzeri						+
Laveineopteris jongmansii			+			
Laveineopteris tenuifolia	+					
Laveineopteris loshii		+				
Cordaites principalis			+			

which tend to be of low abundance and therefore particularly vulnerable to sampling problems. Among those species that only occur in one or other of the two areas being compared, very few are truly endemic, i.e. they are known to occur in areas other than the Pennines Basin. Of the more abundant groups, notably the

Table 3

Distribution of macrofloral morphospecies within the Halesowen Formation of the southern Pennines Basin. Each column represents a macroflora from a single borehole at a defined stratigraphical depth. The figure given at the head of each column is the depth below ground level

	Saredon Hill Borehole[1] (depth 224 m)	Calf Helath Borehole[1] (depth 382 m)	Claverley Borehole[2] (depth 460 m)	Four Ashes Borehole[1] depth 629 m)	Birch Tree Farm Borehole[3](depth 597 m)	Alveley No. 1 Borehole[2] (depth 223 m)	Birch Tree Farm Borehole[3] (depth 546 m)	Calf Heath Borehole[1] (depth 325 m)	Allotment No. 1 Borehole[1] (depth 248 m)	Whittington Heath Borehole[1] (depth 248 m)	Claverley Borehole[2] (depth 389 m)	Claverley Borehole[2] (depth 349 m)	Moat Farm Borehole[1] (depth 246 m)
Lepidodendron sp.			+					+	+				
Lepidophloios sp.												+	
Asterophyllites equisetiformis											+		
Annularia sp.											+		
Sphenophyllum sp.												+	
Lobatopteris vestita							+		+			+	
Cyathocarpus arborescens									+			+	+
Oligocarpia gutbieri					+								
Eusphenopteris trigonophylla				+									
Alethopteris ambigua			+									+	
Alethopteris serlii											+		
Neuropteris ovata											+		
Macroneuropteris scheuchzeri	+	+				+	+		+	+	+		
Laveineopteris rarinervis			+	+									
Cordaites sp.				+							+		+

[1]South Staffordshire; [2]Wyre Forest; [3]Warwickshire

sphenophytes, tree-ferns and medullosaleans, over half of species occur in both areas, and in many cases between two-thirds and three-quarters are in common. From this, it seems reasonable to conclude that the southern Pennines and central Pennines areas formed a relatively coherent floristic unit during early and middle Westphalian times.

Table 4

Jaccard Coefficients showing level of similarity of the macrofloras of the central and southern Pennines Basin. Data for the central Pennines from Cleal (2005)

	Middle-Upper Langsettian Substage	Lower-Middle Duckmantian Substage	Upper Duckmantian Substage	Lower Bolsovian Substage
Other lycophytes	0.38	0.36	0.33	0.33
Sigillarians	0.18	0.33	0.57	0.60
Sphenophytes	0.20	0.57	0.67	0.60
Sphenophylls	0.33	0.40	0.67	0.67
Sphenopteroid ferns	0.32	0.34	0.21	0.00
Tree ferns	0.67	1.00	1.00	1.00
Lyginopteridaleans	0.43	0.56	0.45	0.00
Medullosaleans	0.40	0.75	0.73	1.00
Cordaites	1.00	0.75	0.33	0.50
TOTAL	0.36	0.46	0.49	0.36

Of particular interest is the Jaccard Coefficients for the lower Bolsovian Substage. Here we are comparing grey-beds of the Productive Coal Formation in the central Pennines with red-beds of the Etruria Formation in the southern Pennines. It might be expected that the different facies might have had a significant impact on the comparison, but in fact it does not. For most plant groups, there is in fact a greater similarity in the macrofloras than is seen in stratigraphically-lower levels where both areas are in the grey Productive Coal Formation. Only the sphenopteroid-ferns and lyginopteridaleans show significant differences, due to the virtually absence of these groups from the Etruria Formation of the southern Pennines. As pointed out by Besly & Turner (1983), the reddening of the Etruria Formation does not reflect an increase in aridification of the area, but rather oxidation due to lowered water-tables and improved drainage. This undoubted had an effect on taphonomy and preservation of the plant debris, and probably explains the apparent low-diversity of the sphenopteroid ferns, which mostly had delicate fronds that were particularly vulnerable to poor preservation. For the other plant groups, however, the effect of this secondary reddening was limited.

BIOSTRATIGRAPHY

The following analysis is based on the biostratigraphical scheme developed by Wagner (1984) and subsequently modified by Cleal (1991) and Cleal & Thomas (1994).

The lower part of the succession up to the Stinking Coal and equivalent horizons clearly belongs to the *Lyginopteris hoeninghausii* Zone, notably through the presence of the eponymous morphospecies. There is no evidence of the lower of the two subunits of the zone (*Neuralethopteris jongmansii* Subzone), as *Laveineopteris loshii*, *L. tenuifolia* and *Lobatopteris miltoni* all range down to the lowest level from which there is macrofloral evidence (the Bottom Coal). This is compatible with the non-marine bivalve evidence, as the Bottom Coal yields a '*pseudorobusta*' fauna (Ramsbottom *et al.*, 1978), making it homotaxial with the Crow Coal in Yorkshire, which is well above the base of the *L. loshii* Subzone in that sequence.

The base of the *Lonchopteris rugosa* Zone is nominally placed at the base of the Vanderbeckei Marine Band, although the macrofloral change there is not strong. This is compatible with the evidence from the southern Pennines Basin, as just below this level *Lyginopteris hoeninghausii* disappears, and *Lonchopteris rugosa* and *Renaultia rotundifolia* appear; also, just above this level, *Paripteris pseudogigantea* appears.

A subzonal division of the *L. rugosa* Zone was suggested by Cleal (1991) and Cleal & Thomas (1994), but it could not be identified in the central Pennines Basin succession (Cleal, 2005) nor can it in the southern part of the basin. The next apparent major change in the southern Pennines Basin succession is at about the level of the Thick Coal and the Coseley 10 ft Ironstone. However, the taxa that appear here are often found at lower horizons in other coalfields and it is likely that this biostratigraphical change in the southern Pennines Basin reflects uneven collecting at these different stratigraphical levels.

The next major biozonal boundary in the standard scheme is the base of the *Paripteris linguaefolia* Zone, marked mainly by the appearance of taxa such as *Macroneuropteris scheuchzeri* and *Mariopteris nervosa*. This can be recognised in the southern Pennines Basin at about the level of the Brooch Seam. This is again compatible with the evidence from the central Pennines Basin (Cleal, 2005), where this biohorizon occurs at the Stanley Main Seam; the roof shales of both the Stanley Main and Brooch Coals have yielded non-marine bivalves of the '*atra*' fauna of the upper Lower *Similis-Pulchra* Zone (Ramsbottom *et al.*, 1974).

The *P. linguaefolia* Zone is currently divided into a lower *Neuropteris semireticulata* Subzone and an upper *Laveineopteris rarinervis* Subzone. The boundary between the subzones was identified in the central Pennines at about the Shafton Coal (Cleal, 2005), but it cannot be recognised in the southern Pennines Basin. If it were to occur here, it would be expected to be in the red-beds of the Etruria Formation, which might bias the distribution of the index taxa for the boundary. On the other hand, the number of taxa recorded from the Etruria Formation in the southern Pennines Basin is not that less than that reported from the contemporaneous grey-measures in the central Pennines, suggesting that the absence of *L. rarinervis* Subzone floras is biostratigraphically significant.

The macrofloras of the Halesowen Formation are of low diversity, but the sporadic presence of *Alethopteris ambigua*, *A. serlii, Cyathocarpus arborescens*, and especially of *Lobatopteris vestita* indicate that they are not stratigraphically lower than the *Dicksonites plueckenetii* Subzone of the *L. vestita* Zone. The Salop Formation has yielded even less macrofloral evidence, although the possible presence of *Odontopteris cantabrica* tends to indicate the zone of that name. A superficial reading of the data might therefore suggest that the lower half to two-thirds of the Halesowen Formation is lower *L. vestita* Zone, the upper third to a half of the formation upper *L. vestita* Zone (this based on the detailed distribution of *L. vestita* within the formation) and the Salop Formation is *O. cantabrica* Zone and maybe higher. However, the macrofloras are so rare in these beds that a safer interpretation would probably be that the Halesowen Formation is all within the *D. plueckenetii* Subzone, and just possibly the Salop Formation may extend into the Stephanian *O. cantabrica* Zone.

DIVERSITY ANALYSIS

Following a similar approach to that used in the central Pennines (Cleal, 2005) and South Wales (Cleal, 2007), the Total Species Richness of the macrofloras through the southern Pennines Basin sequences have been calculated and plotted (Fig. 4). There is clearly a broad similarity in the pattern of changes observed here compared to the central Pennines, with a peak in the middle Duckmantian Substage, but there are also a number of differences that deserve some comment.

The diversity at the lowest level for which we have data in the southern Pennines Basin (the Bottom Coal) is about half that found at homotaxial levels in the central Pennines (such as the Crow Coal based on non-marine bivalve data – Ramsbottom *et al.*, 1974). This is probably a combination of relatively poor sampling and an edge-effect induced by the analytical method used (for a similar effect at the top of the South Wales Coalfield succession, see Cleal, 2007). The apparent low diversity at the Bottom Coal is due to small numbers of sphenopteroid fern species, which tend to be rare and can be under-represented in all but the best-sampled macrofloras. It is notable that diversity in the southern Pennines Basin has increased to levels comparable with homotaxial levels in the central Pennines by the Fireclay Coal.

Whilst these new data confirm that edge-effect has to be taken into account when interpreting the ends of Total Species Richness curves, they cannot provide the whole explanation for the observed low-diversity macrofloras in the lower Langsettian part of the central Pennines succession (Cleal, 2005). The Yorkshire macrofloras remain consistently low in diversity over several stratigraphical levels in the lower Langsettian Substage, before increasing sharply at the Better Bed Coal; this is in contrast to the southern Pennines Basin where the diversity increases immediately above the Bottom Coal. The evidence clearly supports the view that the clastic substrate vegetation in earliest Langsettian times was truly low-diversity, presumably reflecting relatively unfavourable conditions in these habitats.

As in the central Pennines, Total Species Richness values of about 40 per macroflora have been reached by the upper Langsettian Substage, and continue through to the upper Duckmantian Substage; this represents the 'fully-developed' Coal Measures macrofloras of the British literature (e.g., Kidston, 1923–1925; Crookall, 1955–1976). As in both the central Pennines and South Wales, there is a brief but marked increase in diversity in the middle Duckmantian Substage, at a level in the non-marine bivalve lower Lower *Similis-Pulchra* Zone ('caledonica'

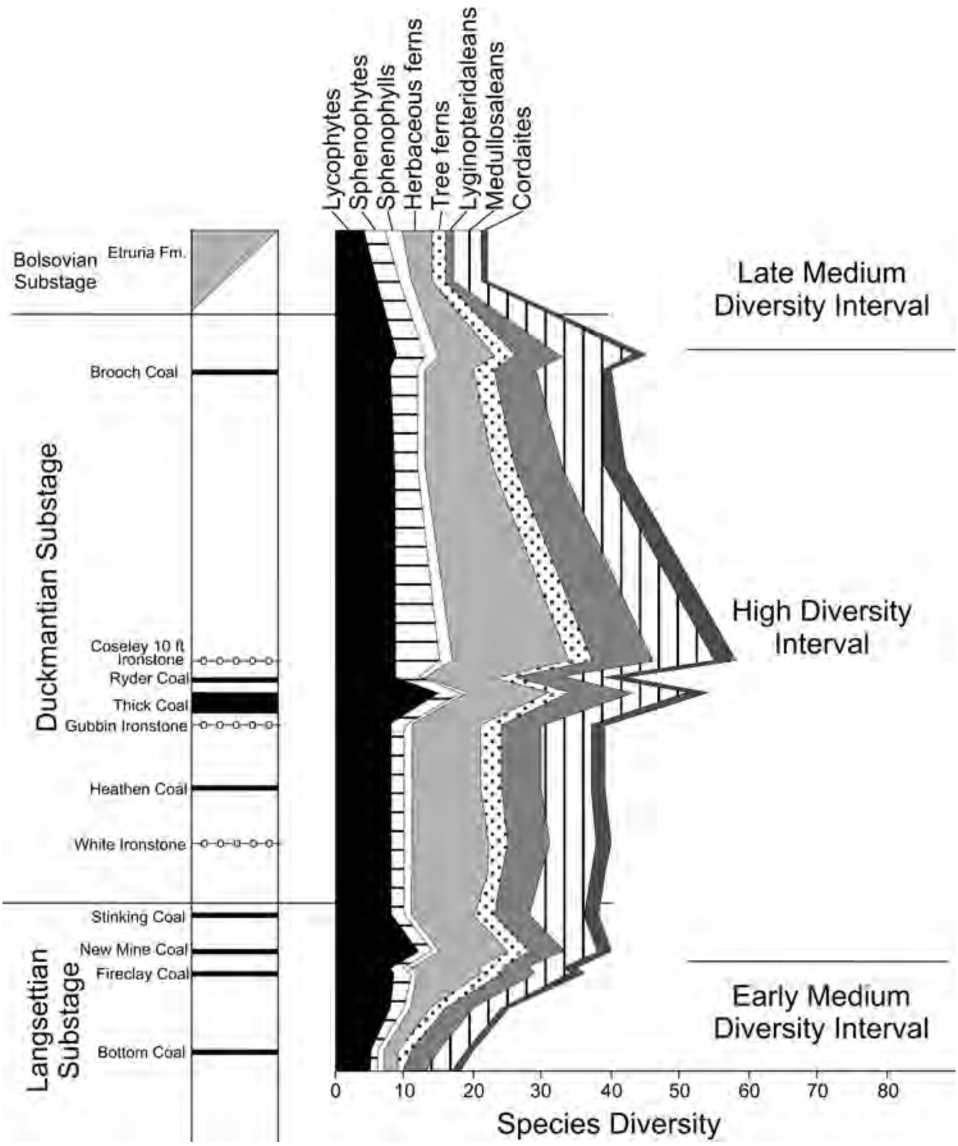

Fig. 4. Total Species Richness curves for the main plant groups in the southern Pennines Basin, based on the range chart in Fig. 3. The three diversity intervals shown on the right-side of the figure are equivalent to the intervals identified in the Central Pennines Basin by Cleal (2005)

faunal belt *sensu* Ramsbottom *et al.*, 1974). If viewed in isolation, these peaks might be dismissed as merely due to uneven sampling, but their presence in three different areas suggests otherwise. Furthermore, the peaks are not evident in all plant groups, as would be expected if it were merely a sampling effect. In the central Pennines and South Wales, the peak is only significant in species of lycophyte, sphenopteroid fern and lyginopteridalean pteridosperms. In the southern Pennines, the situation is slightly more complex, with higher numbers of lycophyte species at the Thick Seam, higher numbers of sphenopteroid fern species at the Coseley 10 ft Ironstone, and higher numbers of lyginopteridalean pteridosperms in both floras. Nevertheless, the southern Pennines data still seem to corroborate a real and clear increase in plant diversity in the vegetation represented in the macrofloral record during middle Duckmantian times.

There is an apparent fall in Total Species Richness after the Brooch Coal in the upper Duckmantian of the southern Pennines. This coincides with the onset of red-beds of the Etruria Formation but, as pointed out earlier, this probably did not have a significant effect on the original vegetation at least of the clastic substrates; the reddening of the Etruria Formation was due to improved drainage of the area rather than aridification (Besly & Turner, 1983). Whilst this has had an undoubted effect on taphonomy and preservation of the plant debris, and thus of the abundance of plant fossils in the sequence, the effect on the original vegetation was probably less marked. There is little difference in the Total Species Richness in the Etruria Formation macrofloras compared with homotaxial levels within the central Pennines (e.g., that associated with the Shafton Coal). There is also no evidence in the southern Pennines of a major change in the balance of plant groups within the macrofloras, such as observed towards the very top of the central Pennines Coal Measures Formation. The diversity changes observed above the Brooch Coal in the southern Pennines may thus be correlated with the comparable changes observed in the uppermost Duckmantian part of the central Pennines (the Late Medium Diversity Interval *sensu* Cleal, 2005), and may reflect regional or even climatic changes taking place at this time.

There is no significant difference in species diversity between the Halesowen Formation of the southern Pennines and central Pennines Basin, both of which appear to be much less diverse than at homotaxial levels in South Wales (Cleal, in press). However the scarcity of macrofloras anywhere within the Halesowen Formation makes it impossible to draw any meaningful conclusions from species richness values.

CONCLUSIONS

The macrofloral evidence supports the view that the Pennines Basin as a whole represented a coherent floristic unit during early and middle Westphalian times, at least for the clastic-substrate vegetation. The composition of the vegetation was broadly similar, especially for the more abundant plant groups, and there are broadly similar changes in species diversity in the two areas. The onset of red-bed formation in the southern part of the basin in early Bolsovian times caused enhanced substrate oxidation and macrofloras are less widely found here. Where they do occur in these red-beds, however, they do not differ significantly in composition or species diversity compared with the contemporaneous grey-beds of the central part of the basin.

The evidence from the southern part of the basin also supports the view that the low-diversity macrofloras observed in the basal Langsettian and upper Bolsovian parts of the Central Pennines succession is not just due to edge-effect. The late Namurian and earliest Westphalian vegetation of the Pennines Basin was truly of low-diversity, presumably reflecting relatively unfavourable conditions on the clastic substrates during the transition from marine to terrestrial environments. Similarly, the observed drop in macrofloral diversity during late Bolsovian times reflects declining diversity in the parent vegetation, probably due to the progressive drying-out of the environment.

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