

# The Westphalian–Stephanian macrofloral record from the South Wales Coalfield, UK

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(Received 6 February 2006; accepted 18 April 2006)

**Abstract** – The South Wales Coalfield has the most complete Westphalian macrofloral record anywhere on the Variscan Foreland or adjacent basins, with 135 biodiversity-meaningful morphospecies having been recognized. All of the standard macrofloral biozones of the Westphalian Stage have been recognized, although a detailed comparison with the Central Pennines Coalfields has indicated some discrepancies in the relative positions of the biozonal boundaries. Total Species Richness progressively increases through the Langsettian Substage, and then remains relatively stable through most of the Duckmantian and Bolsovian substages. There is a distinct reduction in Total Species Richness towards the top of the Bolsovian Substage, but this partially recovers in the middle Asturian Substage with the appearance of a range of marattialean ferns, and medullosalean and callistophytaleans pteridosperms. There is no evidence of any significant drop in Total Species Richness towards the top of the succession, indicating that conditions at this time were relatively stable. The change from coastal floodplain to alluvial braidplain conditions in middle Bolsovian times correlates with a marked increase in the proportion of medullosalean remains being preserved in the adpression record, reflecting an expansion of the clastic-substrate habitats.

Keywords: palaeobotany, biostratigraphy, biodiversity, Carboniferous.

## 1. Introduction

The South Wales Coalfield is one of the most important areas for Upper Carboniferous stratigraphy in Europe. It is the only part of the Variscan Foreland with a complete succession of coal-bearing Westphalian strata, much of it visible in natural outcrop (e.g. Evans *et al.* 2003). The succession yields abundant faunas and macrofloras, and was the basis of many of the pioneering studies on Upper Carboniferous macrofloral and non-marine bivalve biostratigraphy (e.g. Davies & Trueman, 1927; Dix, 1933, 1934, 1937; Dix & Trueman, 1937). Most of the marine bands now used widely for correlating these strata can be identified here (Ramsbottom *et al.* 1978), often with diverse faunas (e.g. Ramsbottom, 1952; Bloxham & Thomas, 1969). Although the coals are of relatively high rank over much of the coalfield, pollen and spores have been obtained from coals in the eastern part of the coalfield (Sullivan, 1961), and can be obtained from the clastic deposits further west (K. Higgs, pers. comm.). South Wales also has the most complete Westphalian palaeoentomological record in Britain (North, 1931; Jarzembowski, pers. comm., 2005).

At one time, South Wales was regarded as the ‘standard section’ for the Westphalian Stage in Britain (Trueman, 1933) and even Europe (Dix & Trueman, 1937; George & Wagner, 1972). However, in recent

years attention has drifted away from South Wales, as other areas in Britain (especially the Central Pennines Basin) were studied in more detail and in some cases yielded better-preserved fossils (e.g. pollen and spores). Nevertheless, South Wales remains the definitive Carboniferous succession in Britain for macrofloras, especially for those of late Westphalian and early Stephanian age.

Despite the importance of the South Wales Westphalian macrofloras, there has been no attempt at a synthesis of the data from here for over half a century. The present paper will therefore attempt to bring together all of the published records of plant macrofossils from the main part of the coalfield and to revise the taxonomy in the light of recent systematic studies. These data have then been used to prepare revised biostratigraphical range charts and, for the first time, charts showing changes in diversity of the macrofloras through the succession. This has allowed a comparison with the data from the other main area for Westphalian macrofloras in Britain, the Central Pennines Coalfields in northern England (Cleal, 2005).

The study has not included the macrofloras from the western part of the South Wales Coalfield, in Pembrokeshire. Although there are documented macrofloras from here (e.g. Goode, 1913; Jenkins, 1962; Cleal & Thomas, 1992), the succession has suffered considerable tectonic deformation, which makes detailed stratigraphical correlations difficult both within the Pembrokeshire area and with the main

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South Wales Coalfield. It was impossible, therefore, to integrate the Pembrokeshire macrofloral data with that of the main part of the coalfield at the stratigraphical resolution required by this study.

## 2. Geological background

### 2.a. Sedimentary history

The South Wales Coalfield was formed in a synclinal foreland basin between the Variscan Mountains to the south and the cratonic Wales-Brabant Massif that extended across central Wales and central England (Kelling, 1988; Gayer & Jones, 1989; Burgess & Gayer, 2000; Fig. 1). The coalfield currently covers some 500 km<sup>2</sup> (Jones, 1989), but its original extent was rather larger, due mainly to tectonic shortening of up to 60% (Jones, 1991; Gayer *et al.* 1993).

Coal-bearing deposits were formed here in two distinct phases. Between early Langsettian and middle Bolsovian times, deposition was on a coastal floodplain. The result is a sequence of alternating coals (representing periods of emergence) and mainly fine-grained clastic deposits (representing periods of flooding) (Hartley, 1993a). At least ten of the coals are persistent across the basin (Adams, 1967) and have been linked to eustatic events, Ramsbottom (1984) having regarded the coals as representing times of marine high-stand, whereas Hartley (1993a) regarded them as representing times of marine low-stand. However, neither interpretation fully took into account the relative time represented by the coals and clastic sequences (Broadhurst & France, 1986; Broadhurst, Simpson & Hardy, 1980). If the estimates by Broadhurst and his colleagues are even only approximately correct, for most of the early Westphalian times the South Wales Coalfield basin would have been covered by coal forests, and were only very briefly disrupted by flooding.

Sediment was being introduced from the north and east of the basin by high-sinuosity fluvial systems flowing from the Wales-Brabant Massif, and from

the south by low-sinuosity fluvial systems (Kelling, 1974; Jones, 1989; Hartley, 1993a,b). However, none of these sediment sources were topographically high and so the distributary channels of these river systems were smaller in scale compared with those in the contemporaneous Central Pennines Basin (e.g. Guion & Fielding, 1988) and were often deflected by relatively small-scale tectonic features (Jones, 1989).

During middle Bolsovian times, the northwards-migrating Variscan Front caused inversion and tectonic deformation of the Culm Basin in SW England (Hartley & Warr, 1990; Hartley, 1993b). This resulted in a marked increase in subsidence in South Wales due to lithospheric (thrust-sheet) loading, and a change from a coastal floodplain to an alluvial braidplain setting (Hartley, 1993a,b). Large quantities of coarse-grained immature clastic deposits were eroded off the rising Variscan Mountains to the south, and resulted in the thick sandstones now known as Pennant found throughout much of the central part of the South Wales Coalfield (Kelling, 1974, 1988; Jones, 1989; Gayer *et al.* 1993). During late Bolsovian and early Asturian times, these clastics were mainly the result of meandering and braided distributary channels, but in middle and late Asturian times the channels became straighter and the sands coarser (Jones, 1989), indicating increasing tectonic activity in the mountains to the south that were feeding the basin. Coals continued to be formed but, although some are thick and basin-wide in their distribution, most are thinner and less persistent than the lower Westphalian coals.

In very late Asturian and early Cantabrian times, there was a return to floodplain conditions in the central part of the coalfield (especially in the upper Swansea Valley), resulting in a mudstone-dominated succession with some coals (Hartley, 1993a,b). However, there is no evidence of marine influence and so these are upper delta-plain or even intramontane deposits. In the eastern part of the coalfield there are thick sandstones, but these are of different provenance to the Pennant Formation further west, and are probably a westerly extension of the Forest of Dean Pennant Formation and Halesowen Formation of the English Midlands.

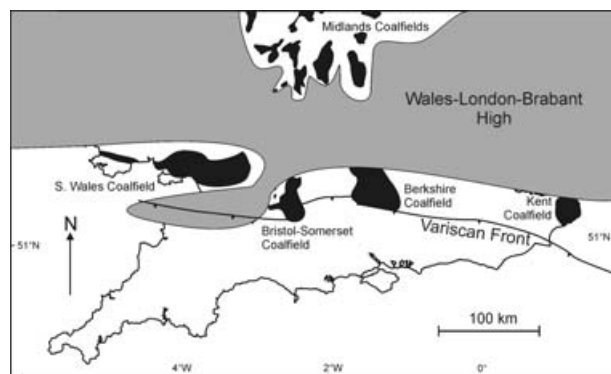


Figure 1. Geographical position of the South Wales Coalfield relative to the other main coalfields of southern Britain. Adapted from Ramsbottom *et al.* (1978) and Hartley (1993a, b).

### 2.b. Stratigraphy

This history of sedimentation is reflected in the lithostratigraphical divisions recognized (Fig. 2). The sequence is divided into three formations: the Productive Coal Formation for the lower mudstone-dominated succession, the South Wales Pennant Formation for the overlying sandstone-dominated sequence, and the Grovesend Formation for the highest mudstone-dominated sequence. Both the Productive Coal and Pennant formations are further divided into members, based on a combination of facies differences and distinctive marker horizons (Woodland, Evans &

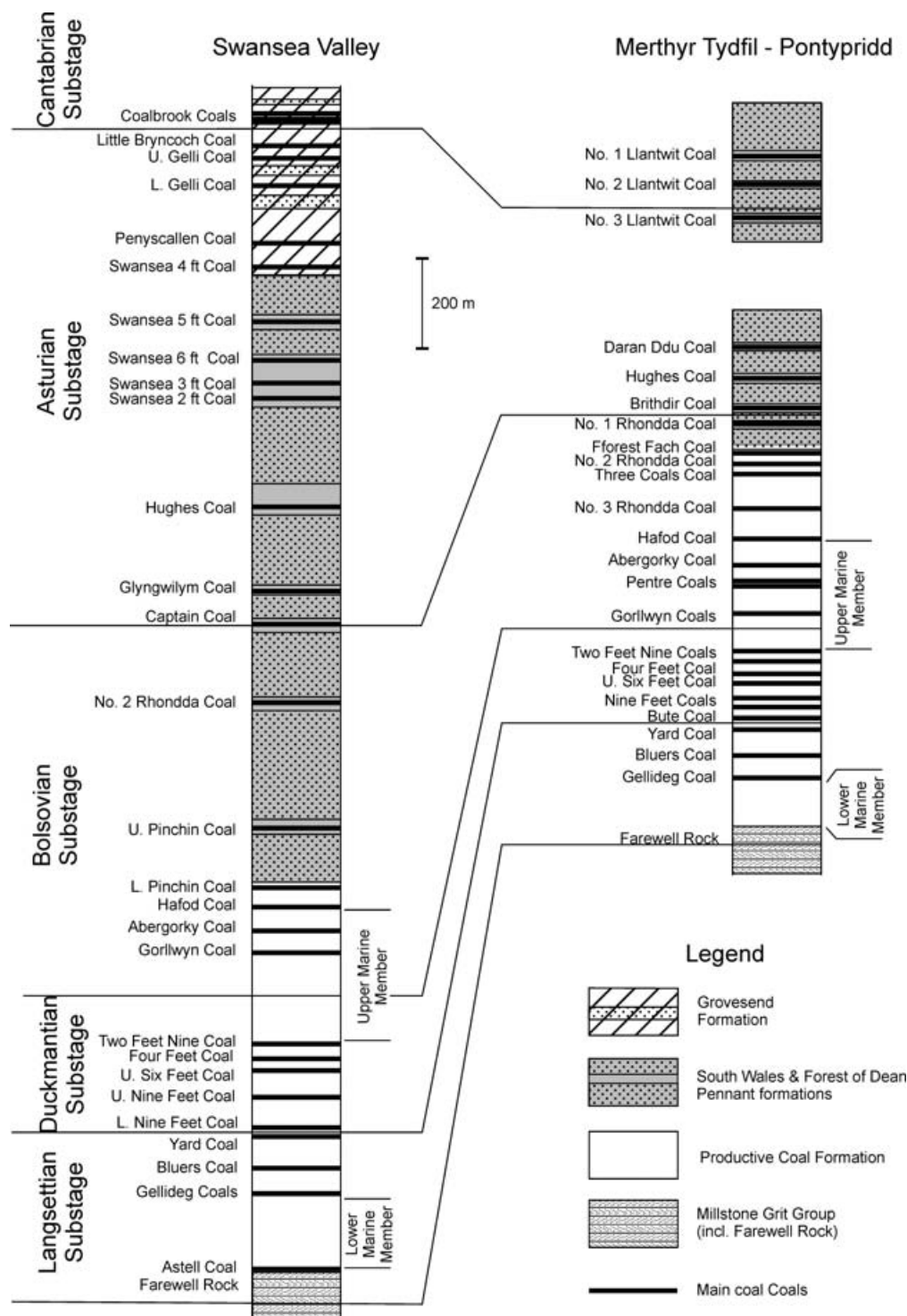


Figure 2. Summary lithostratigraphy of the South Wales Coalfield, based on successions in the Swansea Valley and Merthyr Tydfil – Pontypridd areas.

Stephens, 1957; Cleal & Thomas, 1995; Evans *et al.* 2003).

In the eastern part of the coalfield, there is a stratigraphical gap above the Hughes Beds. The overlying beds are a mainly arenaceous interval regarded by Woodland, Evans & Stephens (1957) as a lateral equivalent of the Grovesend Formation. However,

palynological evidence suggests that these beds are stratigraphically younger than most of the Grovesend Formation and correlate better with the Forest of Dean succession further east (Dimitrova, Cleal & Thomas, 2005). These will be informally referred to as the ‘Llantwit Beds’, named after the principal coal seams.

### 2.c. Coalification

The rank of the coals in the South Wales Coalfield varies from relatively high volatile caking coal (volatiles up to about 37%) in the eastern part of the coalfield to anthracite (volatiles < 8%) in the west (White, 1991). The relatively high rank of the coals was traditionally attributed to depth of burial and/or to tectonics, but Gayer *et al.* (1991) and Alderton *et al.* (2004) have instead suggested that it was due to hot fluids originating from the Variscan Mountains to the south being injected into the sediments at an early stage of lithification (these fluids may also have facilitated the extensive thrusting seen through much of the coalfield: e.g. Cole *et al.* 1990).

### 3. History of palaeobotanical studies

The South Wales Coalfield has the most complete succession of Westphalian-aged macrofloras in Europe. Despite their potential importance for understanding the history of palaeotropical vegetation of this age, there were few studies on them before the 20th century; most studies on Westphalian palaeobotany in Britain at that time were centred on northern Britain. Their presence in South Wales had been noted by Da Costa (1758) and Bevan (1858, 1860), and the eminent Austrian palaeobotanist Stur (1884, 1889), reported on a brief visit to the coalfield. Kidston (1894) attempted a synthesis of the South Wales Coalfield palaeobotany, although he did not do justice to the abundance of macrofloras from here.

The first significant contribution was by David Davies, a local colliery manager (for details of his life, see North, 1935; Thomas, 1986). He collected extensively, especially in the areas around Pontypridd and the Swansea Valley, in an attempt to identify changes in the macrofloral record that could be related to environmental change (Davies, 1920, 1921, 1929). He collaborated with Robert Kidston, who helped extensively with the identifications of the fossils, and who illustrated many of Davies's specimens in his 1923–1925 monograph (Kidston in fact died during one of his many visits to Davies's house). Perhaps his most important legacy, however, is his extensive collection of plant fossils from the South Coalfield, which is now stored at the National Museum Wales (Cardiff).

The second major contribution was by Emily Dix (for details of her life, see Burek & Cleal, 2005). Dix's interests were mainly biostratigraphical, with her main studies around the Swansea Valley (Dix, 1928, 1930, 1932, 1933, 1934, 1937). She also built up a valuable collection of fossil plants from the coalfield, which is now in the Hunterian Museum (Glasgow) and the National Museum Wales (Cardiff).

Dix's career was terminated prematurely in the late 1940s through ill health, and since then there have been few subsequent studies on the South Wales Coalfield palaeobotany. Jongmans (1940) summarized the data

then available, Thomas (1978) has described some lycophyte cones from the eastern part of the coalfield, and Cleal (1978, 1997) revised the biostratigraphy of the Pennant Formation macrofloras.

### 4. Macrofloral species inventory

A revised inventory has been collated for the plant morphospecies found in the Westphalian–Stephanian of the South Wales Coalfield, based mainly on the literature summarized in the previous section. Where possible, the nomenclature of these species has been updated using the most recent taxonomic reviews of the relevant plant groups. As with the earlier study of the Central Pennines macrofloras (Cleal, 2005), this is not a comprehensive compilation of morphotaxa in the adpression record. Since the aim is to determine diversity patterns in the original vegetation, the inventory has been restricted to morphotaxa of organs that are likely to give the closest indication of the original biological species. For most plant groups (sphenophytes, sphenophylls, ferns, pteridosperms and cordaites), foliage morphology almost certainly provides the best guide to species identification (although not necessarily to the systematic position of the species). In the ferns, this evidence can be enhanced by additional data from reproductive organs. In the cordaites, cuticle evidence would give a far more reliable indication of the original species diversity (e.g. see comments by Šimínek, 2000), but cuticles are unavailable through much of the South Wales Coalfield due to the high rank of coalification. For the lycophytes, stem/bark morphology provides the taxonomically most useful characters, although they have only been properly studied for part of the group (Thomas, 1966, 1970, 1977); *Sigillaria* in particular is in need of further revision.

A total of 135 taxa have been identified from 68 stratigraphical levels between the Farewell Rock Formation and the Llantwit and Coalbrook seams. The 108 species that occur at more than one stratigraphical level are shown in Figures 3 and 4. The remaining 27 taxa are as follows.

Immediately above Farwell Rock: *Adiantites tenellus* Kidston

Astell Seam: *Sphenopteris warei* Dix

80 feet above Farwell Rock: *Nudospermopteris hollandica* (Jongmans) Doweld

Upper Gellideg Seam: *Sphenopteris huelsenii* Gothan

25 yards below Yard Seam: *Diplothmema elegantiforme* Stur, *Pinakodendron ohmannii* Weiss

Lower Nine Feet Seam: *Karinopteris beneckeii* (Huth) Boersma

Upper Nine Feet Seam: *Lonchopteris rugosa* Brongniart, *Sphenopteris stonehousei* Kidston

Four Feet Seam: *Zeilleria hymenophylloides* Kidston, *Renaultia footneri* (Marratt) Brousmuiche, *Sphenopteris selbyensis* Kidston

Four Feet Rider Seam: *Alethopteris davreuxii* (Brongniart) Zeiller

- Abergorky Seam: *Asterophyllites grandis* (Sternberg) Geinitz  
 Hafod Rider Seam: *Lepidodendron jaraczewskii* Zeiller  
 Lower Pinchin Seam: *Rhacopteris dubia* (Lindley & Hutton) Kidston  
 No. 3 Rhondda Seam: *Margaritopteris conwayi* (Lindley & Hutton) Crookall  
 Swansea 6 ft Seam: *Diplothmema geniculatum* (Germar & Kaulfuss) Stur, *Sphenopteris seawardii* Kidston, *Sphenopteris woodwardii* Kidston  
 Swansea 4 ft Seam: *Cyclostigma cambricum* Crookall  
 Little Bryncoch Seam: *Lepidophloios macrolepidotus* Goldenberg  
 Coalbrook Coals: *Alethopteris pseudograndinioides* var. *subzeilleri* (Wagner) Zодrow & Cleal, *Odonopteris cantabrica* Wagner  
 Llantwit No. 3 Seam: *Lobopteris camertonensis* (Kidston) Wagner  
 Llantwit No. 2 Seam: *Oligocarpia gutbieri* Göppert  
 Llantwit No. 1 Seam: *Pseudomariopteris ribeyronii* (Zeiller) Danz -Corsin

## 5. Biostratigraphy

Cleal (1978) gave a detailed biostratigraphical analysis of the macrofloras from the South Wales Pennant and Grovesend formations; this will be only briefly summarized here. However, there has been no examination of the biostratigraphy of the Productive Coal Formation since the study by Dix (1934, 1937), so this will be reviewed in more detail. The boundaries between the interval zones introduced by Wagner (1984) and subsequently modified by Cleal (1991) and Cleal & Thomas (1994) provide the basis of the discussion.

### 5.a. Base of the *Neuralethopteris jongmansii* Subzone

This biohorizon occurs at about the same level as the base of the Westphalian Stage (Wagner, 1984), but identifying it on purely biostratigraphical criteria can be difficult. It coincides with the rapid expansion of the coal-forest habitats in many areas of the Variscan Foreland, and it can be difficult to determine which species are appearing simply because of this localized habitat-change. The problem is best resolved by looking at the macrofloral ranges in the few areas where there is an essentially continuous record from the upper Namurian to lower Westphalian stages, most notably in the Ruhr (Josten, 1983, 1991) and Upper Silesia (Kotasowa & Migier in Zdanowski &  akowa, 1995). By comparing the ranges in these two areas, the following morphospecies appear at or about the Namurian–Westphalian boundary in both areas: *Lyginopteris hoeninghausii*, *Neuralethopteris rectinervis*, *Alethopteris valida*, *A. decurrens*, *A. davreuxii*, *Neuropteris obliqua* and *Asterophyllites equisetiformis*. Most of these species appear in South Wales at just

above the Farewell Rock or above the Astell Seam, which are the stratigraphically lowest Westphalian macrofloras in the South Wales succession.

### 5.b. Base of the *Laveineopteris loshii* Subzone

Dix (1934) recognized a major change in the macrofloras at about the level of the Gellideg Seams (her Zone D). Wagner (1984) noted that a change occurred at about this level but did not recognize it in his biostratigraphy. Cleal (1991) subsequently recognized it as a subzone, and it was easily identified in the Central Pennines at the Better Bed Coal (Cleal, 2005). The change is most obviously marked by the appearances of the laveineopterids (*L. loshii* and *L. tenuifolia*), *Neuropteris heterophylla* and *Lobopteris miltonii*. The biohorizon also seems to correspond to a change in the floras in Nord-Pas-de-Calais at the base of the Assise de Vicoigne (Laveine, 1986), in the Ruhr at the base of the Bochum Formation (Josten, 1991, 2005), and in the middle Zależe Beds in Upper Silesia (Kotasowa & Migier in Zdanowski &  akowa, 1995).

### 5.c. Base of the *Lonchopteris rugosa* Zoness

Both Dix (1934) and Wagner (1984) recognized a zonal boundary at about the Langsettian–Duckmantian Substage boundary (Dix at a marginally higher level). However, both authors pointed out that the biohorizon is difficult to recognize in practice. Wagner (1984) noted that few species in fact appear at this level other than *Laveineopteris hollandica*; the base of the zone is instead mainly identified by the extinctions of *Lyginopteris hoeninghausii*, *Neuralethopteris schlehaniai* and *Karinopteris acuta*. *L. hoeninghausii* and *K. acuta* indeed disappear in South Wales a short distance below the Langsettian–Duckmantian boundary, but *L. hollandica* does not appear until some distance above this level. It is evident that this is a difficult zonal boundary to recognize on purely biostratigraphical criteria; neither Laveine (1986) in Nord-Pas-de-Calais, Josten (1991) in the Ruhr, nor Cleal (2005) in the Central Pennines were able to delineate it based on the macrofloras.

Cleal (1991) and Cleal & Thomas (1994) recognized a subzonal division of the *L. rugosa* Zone, based on the appearances of *Sphenophyllum majus*, *Paripteris pseudogigantea* and *Mariopteris sauveurii*. Based on the first two of these taxa, the base of the upper (*S. majus*) subzone could be located in South Wales at the level of the Upper Nine Feet Coal. However, the subzonal boundary cannot be identified in the Central Pennines, Nord-Pas-de-Calais or the Ruhr (Laveine, 1986; Josten, 1991; Cleal, 2005).

### 5.d. Base of the *Neuropteris semireticulata* Subzone

Dix (1934) placed the base of her Zone F at about the base of the Bolsovian Substage (the Cefn Coed Marine Band). It is now recognized that this level is

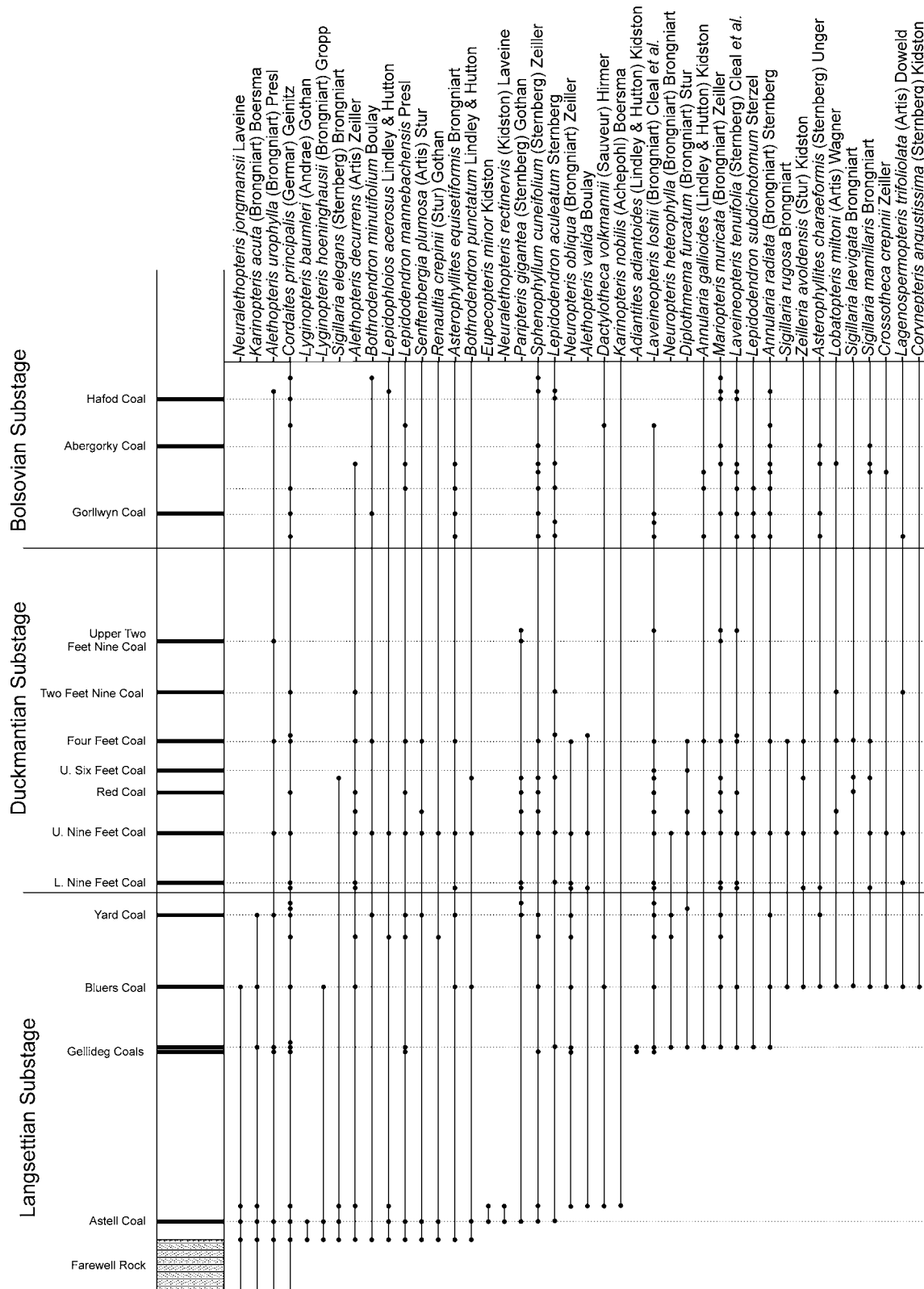


Figure 3. Macrofloral biostratigraphy of the Productive Coal Formation in the South Wales Coalfield. Legend for stratigraphical column is shown in Figure 2.

very difficult to identify based on the macrofloras alone, and Wagner (1984) instead placed a biozonal boundary at the somewhat lower level where *Mariopteris nervosa*, *Macroneuropteris scheuchzeri*, *Neudosper-*

*mopteris striata* and *Neuropteris semireticulata* appear. This level can quite clearly be recognized at the level of the Four Feet Coal in South Wales. It was also identified in the Middle Coal Measures (Stanley Main Coal) in

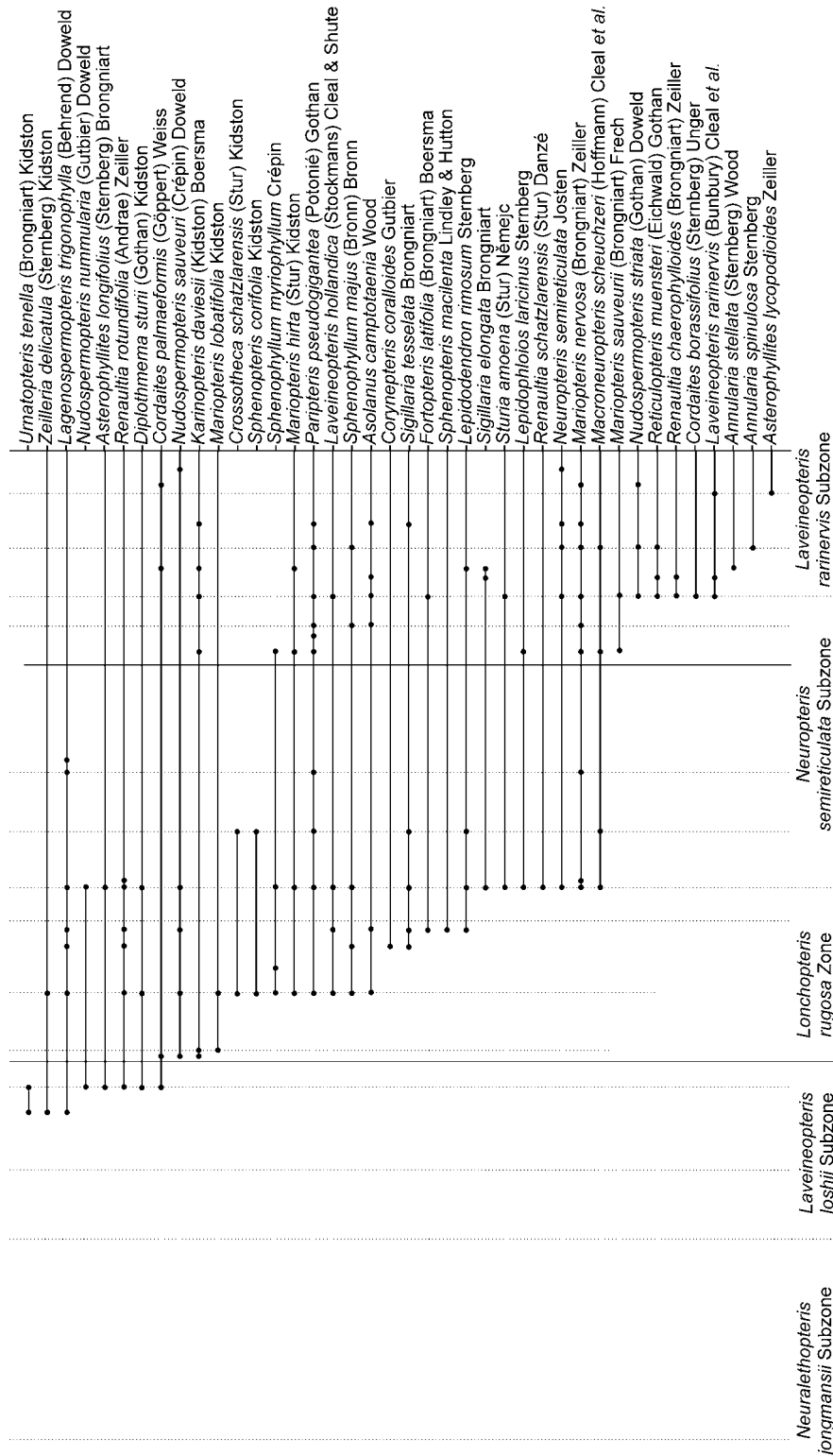


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the Central Pennines (Cleal, 2005), at the base of the Faisceau de Pouilleuse in Nord-Pas-de-Calais (Laveine, 1986), and the base of the Horst Formation in the Ruhr (Josten, 1991, 2005).

**5.e. Base of the *Laveineopteris rarinervis* Subzone**

It has been long recognized that a major change occurs in the British macrofloras in the middle

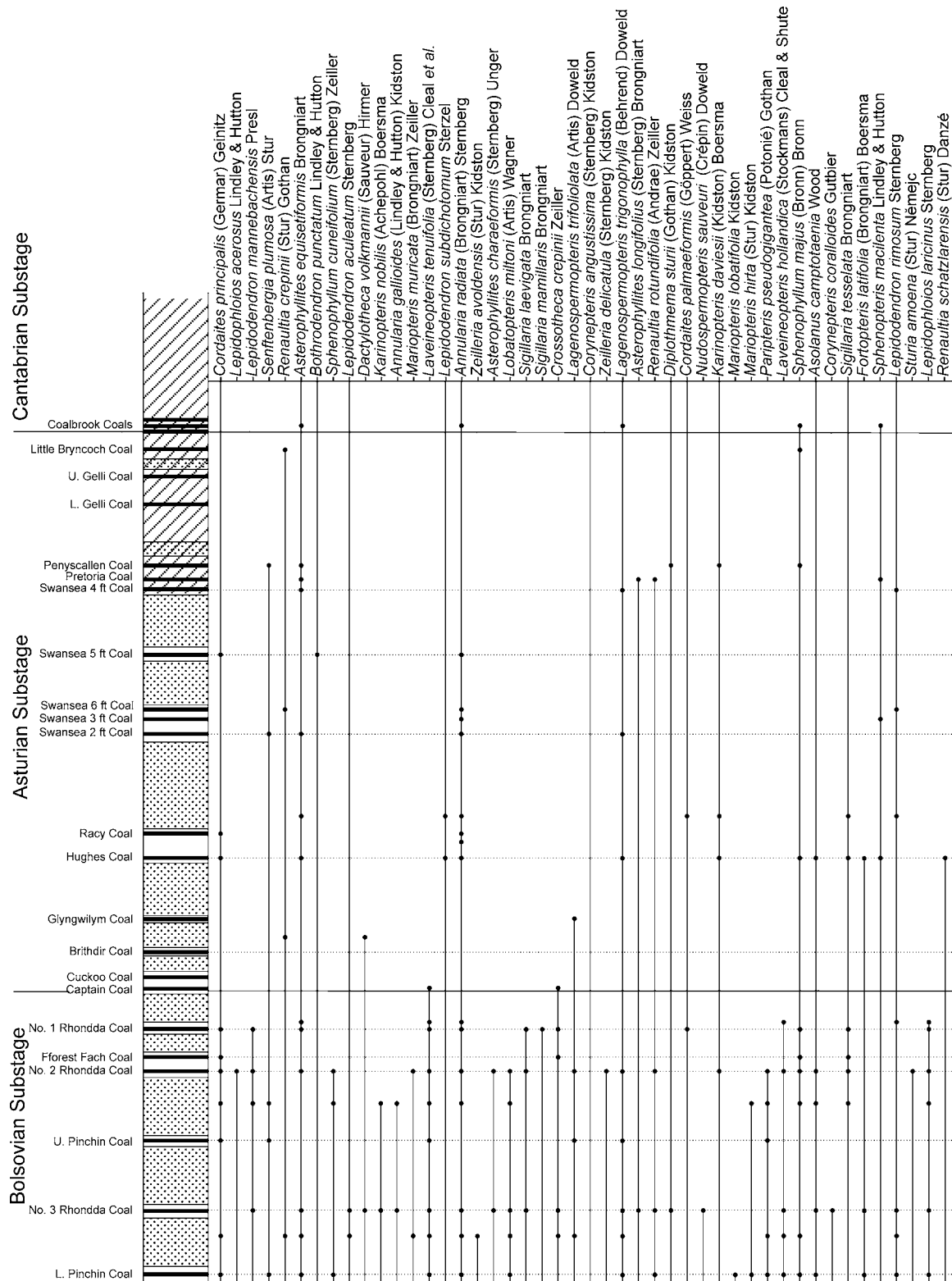


Figure 4. Macrofloral biostratigraphy of the Pennant Formation in the South Wales Coalfield. Legend for stratigraphical column is shown in Figure 2.

Bolssovian Substage of Britain, corresponding to the base of the Staffordian ‘Series’ of Kidston (1905), of Dix’s (1934) Zone G, and of the Morganian Substage of Dix & Trueman (1937). The biohorizon

was not formally incorporated into Wagner’s (1984) biozonation, although he did recognize that the change was present. In an effort to integrate the Wagner and Dix biozonations, Cleal (1991) recognized the



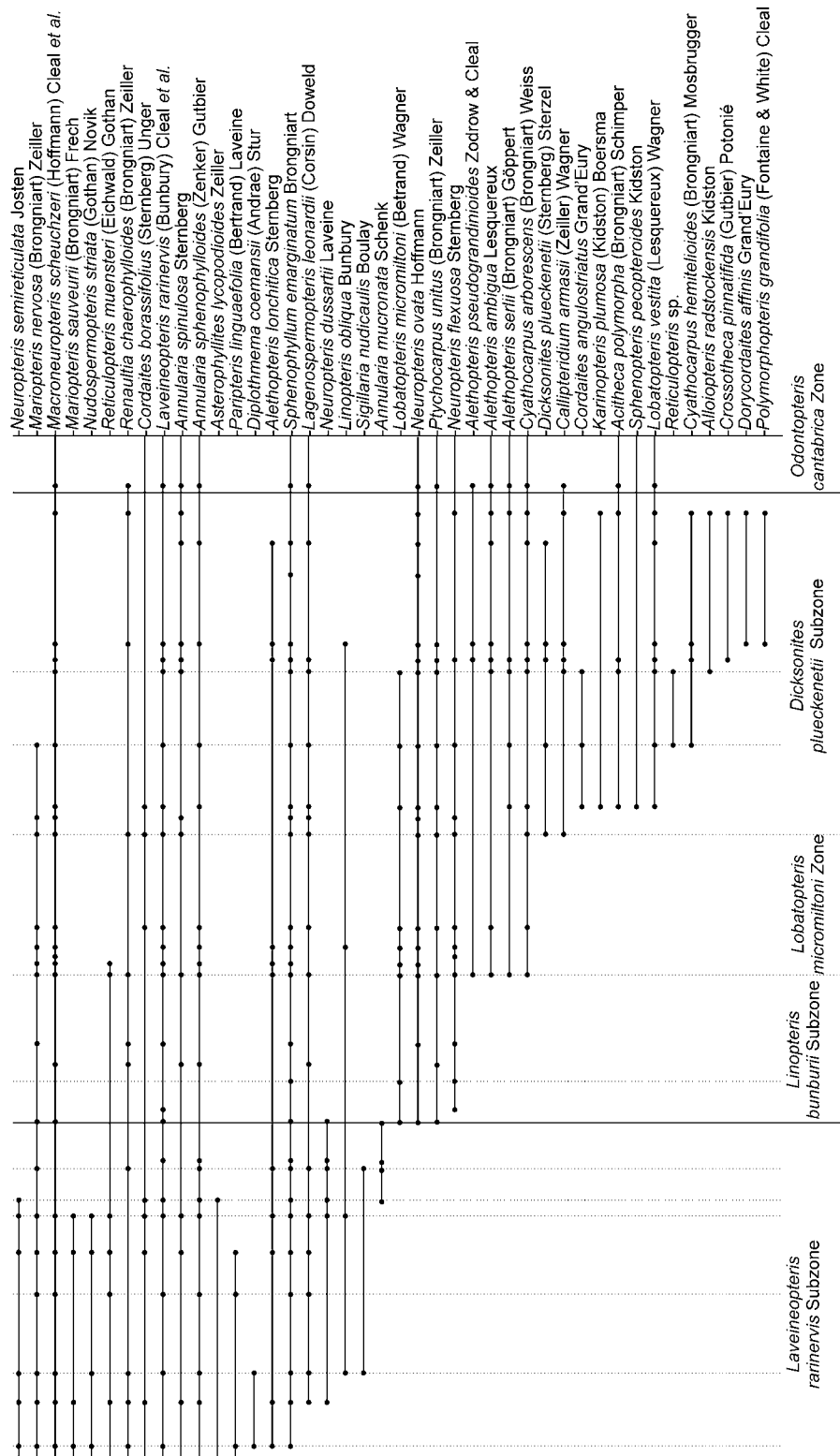


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biohorizon by dividing the *P. linguaefolia* Zone into a lower (*N. semireticulata*) and an upper (*L. rarinervis*) subzone. The level is marked by the appearances of *Laveineopteris rarinervis*, *Annularia sphenophylloides* and *Sphenophyllum emarginatum*. According to Dix

(1934), this biohorizon coincides with the base of the South Wales Pennant Formation in the Swansea area. However, based on the data presented in the present paper, the change occurs at a slightly lower level, between the Gorllwyn and Abergorky coals in the upper

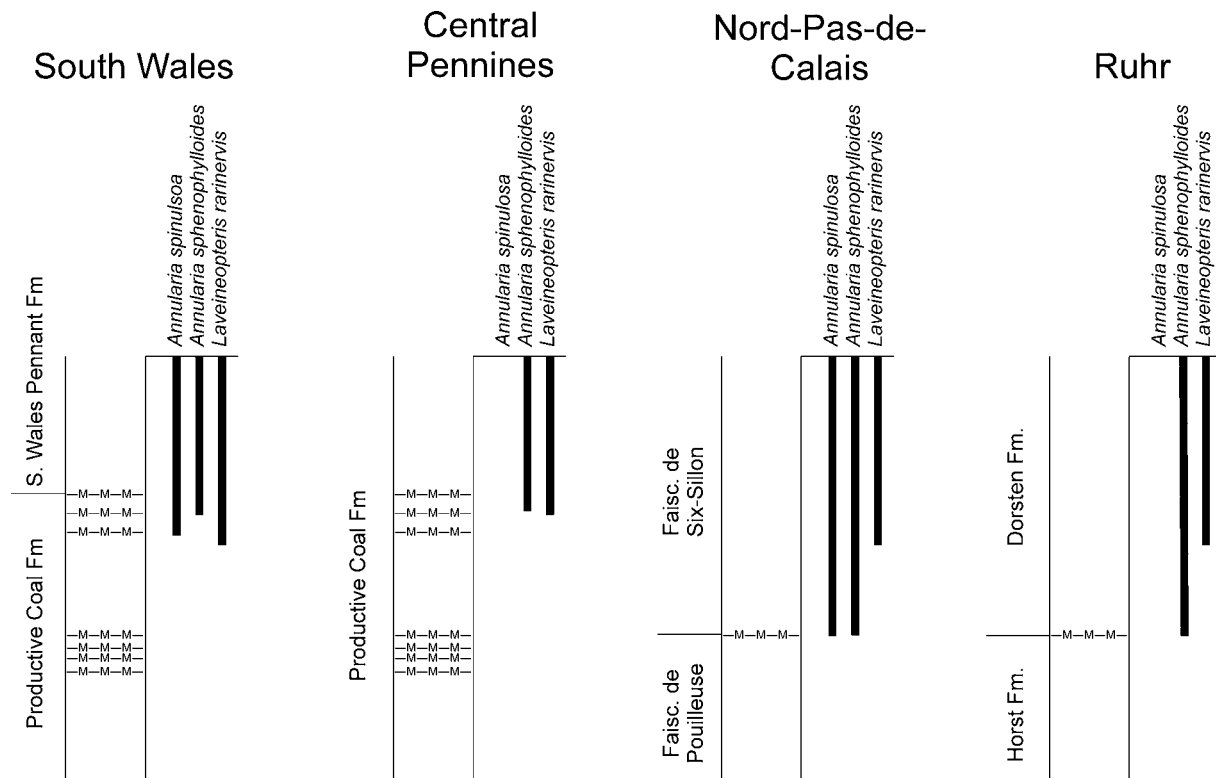


Figure 5. Stratigraphical ranges of three key macrofloral taxa in the middle Bolsovian Substage of South Wales (this paper), Central Pennines (Cleal, 2005), Nord-Pas-de-Calais (Laveine, 1986) and the Ruhr (Josten, 1991). Lithostratigraphical nomenclature for the Ruhr follows the recent revisions (Deutsche Stratigraphische Kommission, 2002). ‘M–M–’ in stratigraphical columns represents position of a marine band.

Productive Coal Formation. In the Central Pennines, a similar biohorizon occurs at about the base of the Upper Coal Measures (Cleal, 2005).

This biohorizon is less clearly delineated in continental Europe. In both the Nord-Pas-de-Calais and the Ruhr Coalfields, *L. rarinervis* appears first in the middle Bolsovian Substage, but *A. sphenophylloides* and *S. emarginatum* range down rather lower, to near the base of the Bolsovian Substage (Fig. 5). This may be a reflection of the degree of marine influence in the various areas. In all four cases, the zonal boundary seems to occur at about the same level as the highest marine band in the succession; in Britain, this is in the middle Bolsovian Substage, in continental Europe at the base of the Bolsovian Substage.

##### 5.f. Asturian and Cantabrian macrofloral biozones

Cleal (1978) identified the main macrofloral biohorizons in the Asturian and Cantabrian substages of South Wales, and little needs to be added to this: the base of the *Linopteris bunburii* Zone occurs in the upper Rhondda Beds, the base of the *Lobopteris vestita* Zone at the base of the Hughes Beds, the base of the *Dicksonites plueckenetii* Subzone in the middle Swansea Beds, and the base of the *Odontopteris cantabrica* Zone in the upper Grovesend Formation.

The most comparable successions through macrofloras of this age can be found in Cape Breton, Nova Scotia (Zodrow & Cleal, 1985), Saar-Lorraine (Cleal, 1984a) and Asturias (Wagner & Alvarez-Vázquez, 1991), where very similar biozonal sequences have been identified. However, the record is much less complete elsewhere across the Variscan Foreland. The base of the *L. bunburii* Zone can be identified in the Nord-Pas-de-Calais, at the base of the Faisceau de Du Souich (Laveine, 1986), but the stratigraphically higher biozones are absent here. None of these biozones can be identified in the main part of the Ruhr Coalfield (Josten, 1991), but *L. bunburii* and *L. vestita* Zone floras have been reported from small inliers near Osnabrück some 50 km to the northwest and from deep boreholes (Josten, Köwing & Rabitz, 1984; Josten & van Amerom, 1999). These biohorizons are also mostly absent from Upper Silesia, but *D. plueckenetii* Subzone macrofloras occur in the Libiąż Beds (Kotasowa & Migier in Zdanowski & Żakowa, 1995).

##### 5.g. Comparison with Central Pennines record

The sequence of biozones in the Productive Coal Formation in South Wales is clearly the same as the sequence seen in the Central Pennines Basin (Cleal, 2005). However, if the exact levels of the biohorizons

in the two areas are plotted against the standard succession of marine bands and non-marine bivalve 'faunal belts' (subzones) given by Ramsbottom *et al.* (1978), there are discrepancies (Fig. 6). The bases of the *N. jongmansii* and *L. loshii* subzones both occur significantly higher in South Wales, whereas the bases of the *N. semireticulata* and *L. rarinervis* subzones are significantly lower. Only the base of the *L. rugosa* Zone appears to be coincident in the two areas. However, as this latter biohorizon is very difficult to identify on purely biostratigraphical criteria and tends to be conventionally placed at the Langsettian–Duckmantian Substage boundary, this coincidence is to be expected.

It is possible that the standard succession of Ramsbottom *et al.* (1978) is at fault here and that it does not provide a sufficiently accurate scale against which to compare the macrofloral biohorizons. If the scale was only calibrated by the non-marine bivalve biostratigraphy then this might be an arguable position, but the fundamental control on the scale is the succession of marine bands that are surely isochronous (at least in a geological time-frame).

The sequence of macrofloral biozones is evidently reflecting changes in the clastic substrate vegetation that occurred in both South Wales and the Central Pennines, but at different times. Since these two areas are relatively close together, it is unlikely that the vegetation changes were purely due to climatic changes. A more likely explanation is that we are seeing vegetation changes being influenced by local edaphic factors, which in turn were the result of tectonically influenced geographical changes. This means that, although the macrofloral biostratigraphy provides a broad guide to making correlations in the lower and middle Westphalian Stage, their accuracy cannot be guaranteed. These reservations should also be borne in mind in the upper Westphalian and Stephanian stages, where macrofloras have been regarded as the most reliable biostratigraphical tool for making correlations (e.g. Wagner, 1966; Cleal, 1978, 1984a, 1997; Wagner & Alvarez-Vázquez, 1991). Unfortunately, we do not yet have a sufficiently accurate independent time-scale in these higher strata to perform the same type of detailed comparison as done here for the lower and middle Westphalian macrofloral record.

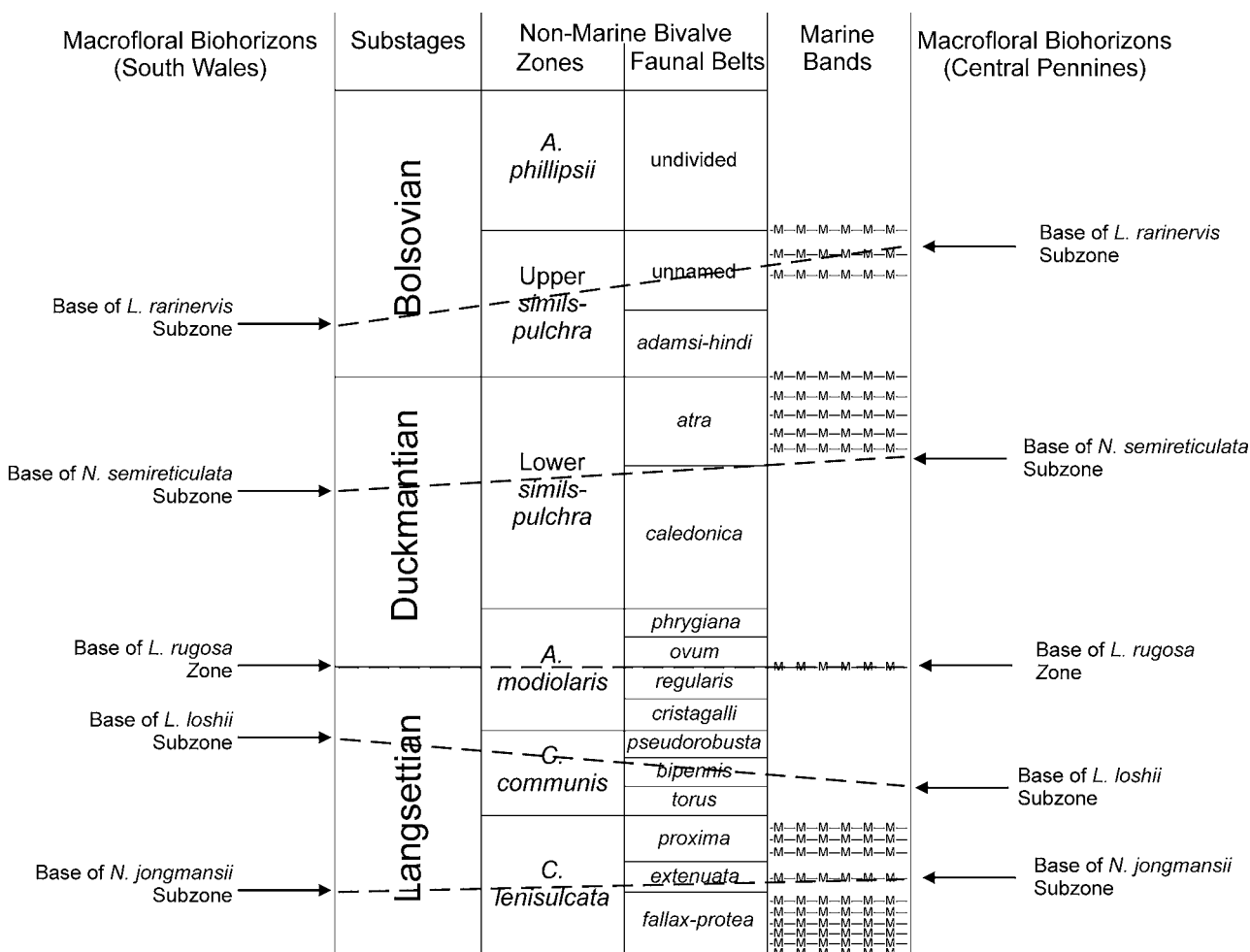


Figure 6. Relative positions of the main lower and middle Westphalian macrofloral biohorizons in the South Wales and Central Pennines Coalfields (data for the latter area in Cleal, 2005). ‘-M-M-’ in stratigraphical column represents position of a marine band.

## 6. Biodiversity changes

Studying changes in plant biodiversity is an important way of monitoring environmental change in today's terrestrial habitats (Magurran, 1988) and a similar approach should be possible for the Palaeozoic. Many of the biodiversity indices used for modern biotas, such as the Simpson and Shannon indices, are inapplicable to the macrofloral record of the coal forests. Such indices not only reflect the number of taxa present in a particular biota, but also their relative abundances. Because the adpression record of these floras consists of broken fragments of plants that were subjected to at least some transportation, it is effectively impossible to use that record to determine the abundances (either absolute or relative) of the species in terms of whole plants.

The one measure of biodiversity that is readily measurable from the fossil record is Species Richness, which is just the number of species that occur at each stratigraphical level. Experience with modern biotas has shown that simple Species Richness measures are invariably informative in monitoring environmental change (Magurran, 1988). However, even Species Richness can be difficult to assess meaningfully from the palaeontological record. Uneven sample-sizes for each stratigraphical level could potentially distort the results, but less so in the present study because of the large sample-sizes, especially in Davies's dataset (this issue will be further dealt with in the following sections). However, even where there is an extensive fossil record such as in the South Wales Coalfield, the distribution of the individual morphospecies can be very uneven, reflecting the hydrodynamics of the river system by which the plant fragments were transported and the availability of sedimentary environments suitable for their preservation. This results in a very 'noisy' signal from which it is difficult to distinguish the original biodiversity patterns from the hydrodynamic/sedimentary interference.

As the main interest of this study is to determine the broad changes in overall biodiversity, a measure analogous to the Total Generic Diversity of Raymond & Metz (1995) has been adopted, but using morphospecies instead of morphogenera (the Total Species Richness). At each sampled stratigraphical level, the Total Species Richness equals the number of species that have been reported from that level, plus the number of species whose range passes through that stratigraphical level. This undoubtedly 'smooths' the data and removes any potential evidence of small-scale biodiversity changes. However, as we are dealing with allochthonous macrofloras, much of this small-scale variation will be lost anyway through mixing during transportation.

This approach was used in an earlier study on the macrofloras of the Central Pennines Coalfields (Cleal, 2005), which revealed clear trends in the Total

Species Richness. However, these patterns could only be properly understood if the Total Species Richness values were shown separately for the major plant groups. Furthermore, they only make sense if the study is restricted to the morphospecies of that part of the plant, which is most likely to reflect the original species diversity of the group (see Section 4 where this is discussed). These same principles were therefore used to assess changes in Total Species Richness through the South Wales Coalfield succession, and so the results are directly comparable with those from the Central Pennines.

### 6.a. Total Species Richness

The pattern of change in the Total Species Richness is summarized in Figure 7. The pattern in the Langsettian Substage is remarkably similar in the two areas. Up to the Gellideg Seam in South Wales and the Better Bed Seam in the Central Pennines, Total Species Richness is 20–25. In the Central Pennines, this can be seen to be an inheritance from the Namurian Millstone Grit, where broadly similar macrofloras occur, but in South Wales the plant fossil record is virtually barren in the upper Millstone Grit.

At the Gellideg and Better Bed Seams, Total Species Richness increases to 30–40, largely due to a diversification in the herbaceous ferns and lyginopterid pteridosperms, and to a lesser extent the lycophytes and calamites. This level of diversity then remains more or less static through the middle Langsettian Substage, but towards the top of the Langsettian Substage (at about the levels of the Yard Seam in South Wales and the Parkgate Seam in Yorkshire) there is a progressive rise in Total Species Richness until it reaches values of 50–60 in the lower Duckmantian Substage. This in essence marks the full development of the 'Coal Measures Flora' in Britain.

In the Yorkshire Coalfield, a peak in the Total Species Richness occurs at the Barnsley Seam, largely due to an increased number of arborescent lycophytes, herbaceous ferns and lyginopterid pteridosperms. This has been interpreted as an essentially local event, due to unusual environmental conditions at the Barnsley Seam level (Cleal, 2005, and references therein), but it is notable that a similar but less prominent peak occurs at an approximately equivalent level (the Four Feet Seam) in South Wales.

The Four Feet Seam/Barnsley Seam excursion was short-lived, and Total Species Richness returns to 50–60 at immediately overlying horizons in both South Wales and the Central Pennines. However, from here onwards the Total Species Richness patterns in the two areas start to diverge. In the Central Pennines they decline sharply down to 35–40 from the Winter Seam, similar to the values seen in the middle Langsettian Substage. Cleal (2005) tentatively linked this fall in biodiversity to the onset of marine conditions, an influx

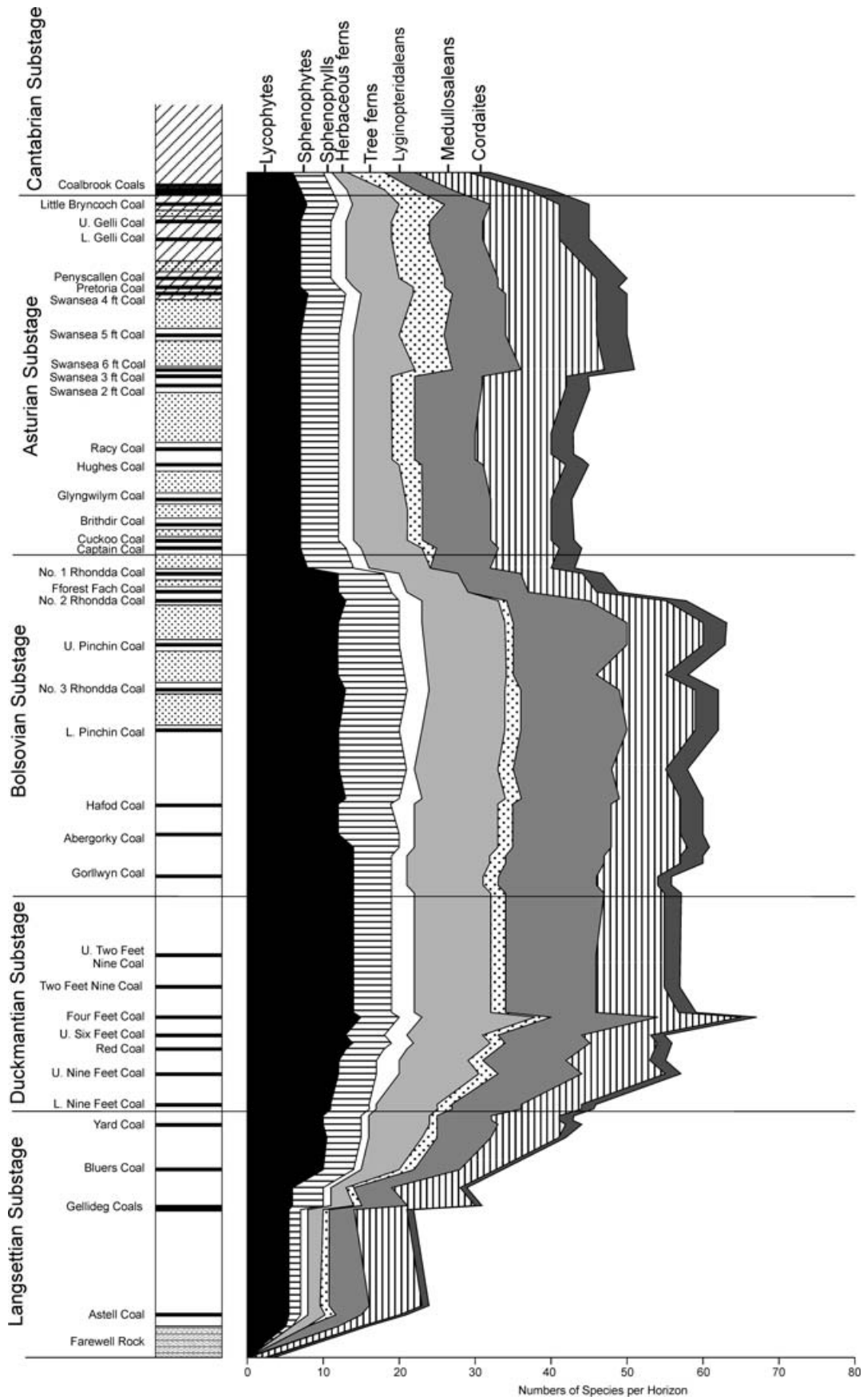


Figure 7. Macrofloral Total Species Richness through the South Wales Coalfield, based on species distributions shown in Figures 3 and 4. Legend for stratigraphical column is shown in Figure 2.

of fluvial sand, and the onset of volcanic activity in the southern part of the basin. In South Wales, however, no such fall in Total Species Richness occurs at this level, which stays at 50–65 right through to near the top of the Bolsovian Substage. From this, it is clear that the increased marine influence cannot have triggered the drop in biodiversity in the Central Pennines, as similar marine influence occurs in the contemporaneous part of the South Wales sequence. The pattern seen in the Central Pennines is therefore more likely to have been a product of the change in fluvial sedimentation patterns and the volcanic activity to the south.

These high Total Species Richness values continue in South Wales until towards the top of the Bolsovian Substage, where there is a sudden and marked drop to 40–55. This is caused by a reduction in species numbers in nearly all plant groups, but most noticeably among the lycopsids and lyginopterid pteridosperms, and to a lesser extent the ferns (both herbaceous and arborescent). The reason for the fall in Total Species Richness is at present not clear. It might have been expected that the fall would coincide with the base of the South Wales Pennant Formation, which represents both a marked increase in arenaceous sediment being introduced from the south and the final withdrawal of marine influence. However, the change in macrofloras occurs significantly above this lithostratigraphical change; the macrofloras of the lower part of the South Wales Pennant Formation (the Llynfi and most of the Rhondda beds) do not differ significantly from that of the Productive Coal Measures.

Total Species Richness partially recovers in the middle Asturian Substage, to about 50, mainly due to the appearance of new species of arborescent ferns (Marattiales) and of medullosalean pteridosperms. This is a well-documented change, which corresponds to the base of the *Lobatopteris vestita* Zone in the biostratigraphical schemes of Wagner (1984) and Cleal (1991). It represents a fundamental change in the character of the macrofloras, which start to become dominated by the remains of plants that typify the subsequent Stephanian macrofloras, notably the marattialean ferns (*Cyathocarpus*, *Acitheca*, *Ptychocarpus*), callistophytalean pteridosperms (*Dicksonites*) and alethopterid medullosaleans (*A. ambigua*, *A. pseudograndinioides*). This vegetational change, which has been recorded from several places in Europe and North America (e.g. Cleal, 1978, 1984a, 1987; Zedrow & Cleal, 1985; Wagner & Alvarez-Vázquez, 1991), coincided with Variscan tectonic activity known as the Leonian Phase (Wagner, 1966) that produced significant structural movement in the Iberian Peninsula and palaeogeographical changes in northern Europe.

This level of Total Species Richness continues up through the rest of the Asturian Substage and into the Cantabrian Substage. There is some decline in diversity at the very top of the succession, but this is probably an

artefact produced by the method of calculating the Total Species Richness values. The Total Species Richness of the stratigraphically highest levels will only include those morphospecies that actually occur there; there will not also be morphospecies that range above those levels, even though they may have been present in the original vegetation but their presence has been removed by erosion. To demonstrate this effect, the Total Species Richness values have been calculated for South Wales assuming that everything above the No. 3 Rhondda Seam had been removed by erosion (Fig. 8). This shows a similar dip in the biodiversity at the artificially truncated succession of macrofloras, similar to that seen in the actual upper part of the South Wales succession. However, it is quite different from what is seen in the Central Pennines, where the drop in Total Species Richness is much more marked and accompanied by a clear change in the compositional balance of the macrofloras. It seems likely, therefore, that the clastic substrate vegetation in South Wales was not disrupted significantly in early Cantabrian times, but that the fossil record of it has been truncated by erosion, presumably as part of the main middle to late Cantabrian Variscan uplift of the area.

#### 6.b. Rarefaction analysis

A biodiversity analysis such as described in the previous section depends in part on the sample size being sufficiently large that taxa are not being missed. One way to test for this is Rarefaction Analysis (Krebs, 1989), which takes a large sample and shows how many taxa would be present if the sample size was progressively reduced (see Wilf *et al.* 2003, for the use of this technique in Palaeogene biodiversity studies). The four largest of Davies's (1929) samples, each representing between 22 000 and 34 000 specimens, was subjected to such an analysis and the graphical results are shown in Figure 9.

The results show that the number of taxa recorded would not start to drop off significantly (loss of more than one species) until the sample size is less than about 5000–9000 specimens. Even at the extreme of the 95% confidence limit, a significant fall-off in species numbers is not seen until sample size is reduced to 15 000. From Davies's data (summarized by North, 1935) it seems that his aim was to have at least 15 000 specimens from each horizon, and this was achieved in the vast majority of cases. It can be concluded, therefore, that Davies's samples are large enough to give a reasonable representation of the Species Richness.

#### 6.c. Biomass

Davies (1920, 1921, 1929) had also attempted to determine changes in biodiversity in the South Wales coal forests, but using a rather different approach. He

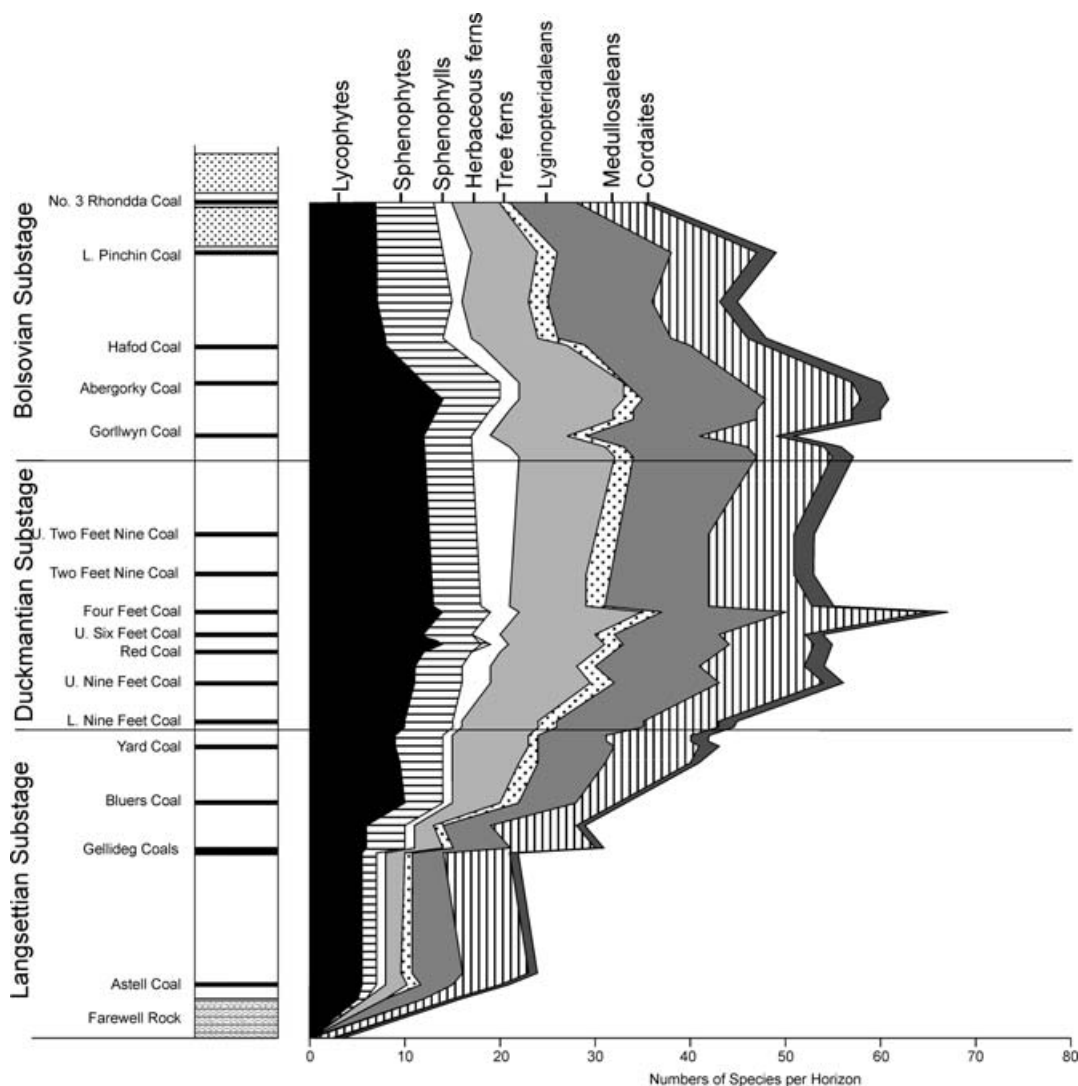


Figure 8. Hypothetical Total Species Richness pattern that would have resulted if the South Wales succession was truncated above the No. 3 Rhondda Seam. Based on species distributions shown in Figures 3 and 4. Legend for stratigraphical column is shown in Figure 2.

undertook extensive and systematic palaeontological collecting from the roof shales of successive coal seams in South Wales, from which he tried to determine statistical changes in the biotas through time. Scott (1977) analysed Davies's approach and criticized it on a number of fronts, in particular for his 'subjective' approach to counting the fossils; large and small fragments of a plant would be scored equally by Davies. Scott's criticism is undoubtedly valid in principle, but in practice the problems may not be so severe. An examination of Davies's collection in the National Museum Wales shows that there is a reasonable consistency in the size of the specimens that he recorded. Furthermore, at least some unevenness in specimen size would be compensated for by the large sample size used by Davies (from his figures, it seems that he aimed for and often achieved at least 15 000 records for each assemblage). Since Davies always gave some measure of the quantity of rock

from which his sample was derived (the figures are recorded in North's 1935 review of Davies's study), his analysis can even provide some evidence of the absolute abundances of the morphospecies, not just their relative abundances. It would seem that, despite undoubted weakness with Davies's methodology, the practical consequences for the robustness of his data should not be over-emphasized.

Scott (1977) also criticized Davies's work because of the lack of a standard sample size. In fact, this is not a problem due to the large size of Davies's samples. All of his samples from the eastern side of the coalfield, and most of those from the western side, consist of more than 1000 records. Based on the equations given by Thompson (1987), samples of 1000 records will provide species-counts within 5% of the original population values more than 99% of the time. Any variations in the size of such large samples will thus have a negligible influence on the results.

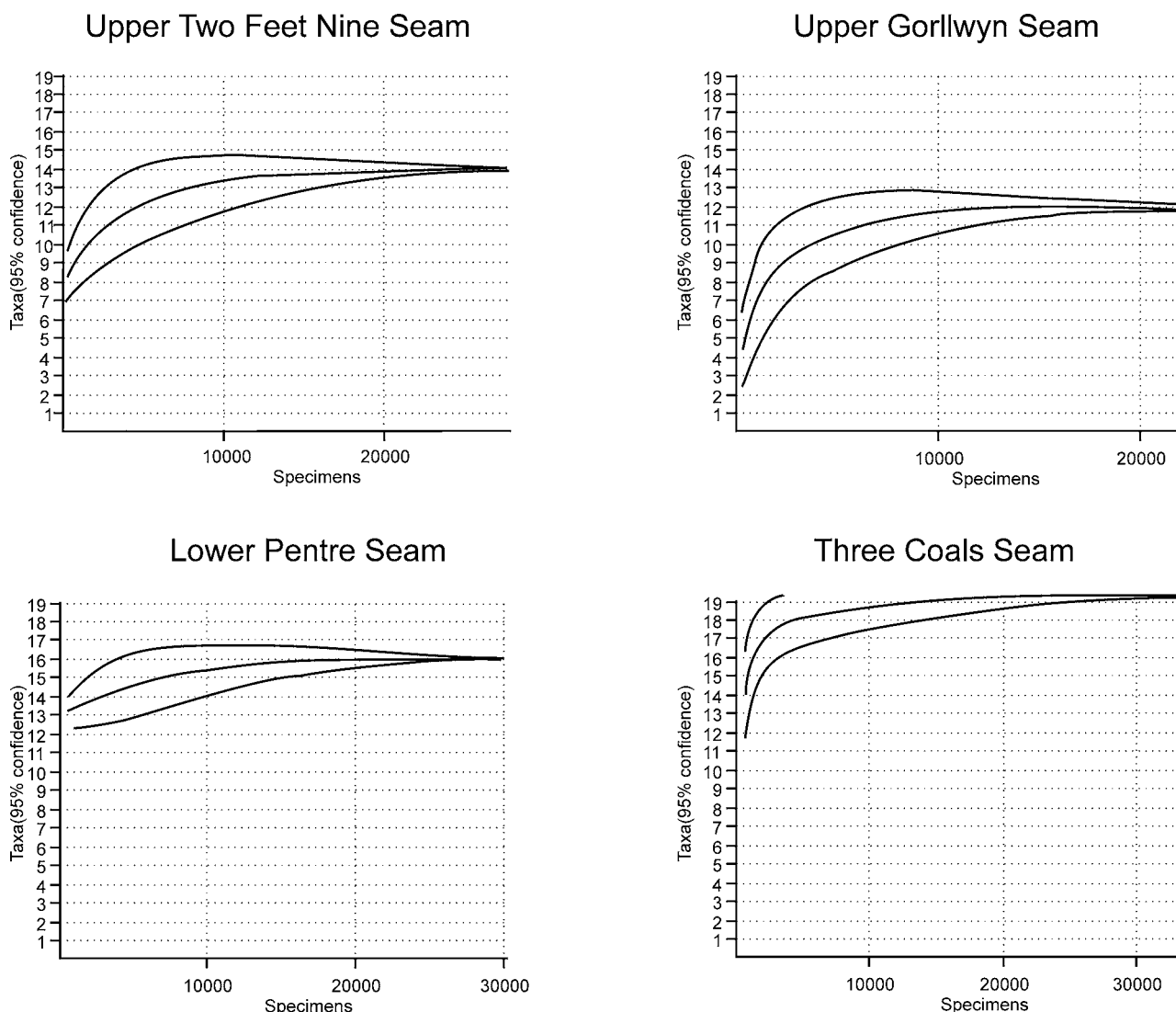


Figure 9. Rarefaction analyses of the four largest macrofloral samples from South Wales documented by Davies (1929). The analysis was performed using the PAST package (Hammer, Harper & Ryan, 2004).

However, there is undoubtedly a problem of interpreting exactly what Davies's results mean. Because this fossil record represents drifted fragments from plants of different habits (trees, lianas, scrambling plants and low herbs), the differences in the relative proportions of fossil specimens cannot be translated directly into the relative proportions of the individual organisms or even of the plant-cover. The nearest correlation may be with the relative proportions of the biomass represented by the different plant groups, although even here the correlation may not be exact. Most of the plant fragments were probably removed from the parent plant by wind during storms, which would preferentially sample tree-sized plants in the upper canopy, and plants growing in exposed locations such as river banks or lake margins. It would also preferentially sample those plants with large dissected leaves (e.g. ferns and pteridosperms) over those plants with small microphyllous leaves and small canopies

(e.g. arborescent lycophytes). Nevertheless, this is the only source of data that we have available of the relative biomass represented by the various plant groups and it cannot therefore be totally ignored.

Figure 10 shows the stratigraphical variation in the proportion of the three main plant groups recognized by Davies in the two areas that he studied: (1) the lycophytes, (2) the calamites and sphenophylls, (3) the ferns and pteridosperms, and (4) the cordaites. Two of these groups (2 and 3) are of course not meaningful in any taxonomic sense. However, one of the characteristic features of the Late Carboniferous palaeotropical wetlands is that there is a strong taxonomic partitioning between the main habitats (DiMichele, Phillips & Peppers, 1985). Davies's groups do, therefore, broadly reflect the vegetation of the main habitat-types in the coal forests: the lycophytes dominated the organic (peat) substrates (e.g. Phillips & DiMichele, 1992), the ferns and pteridosperms the



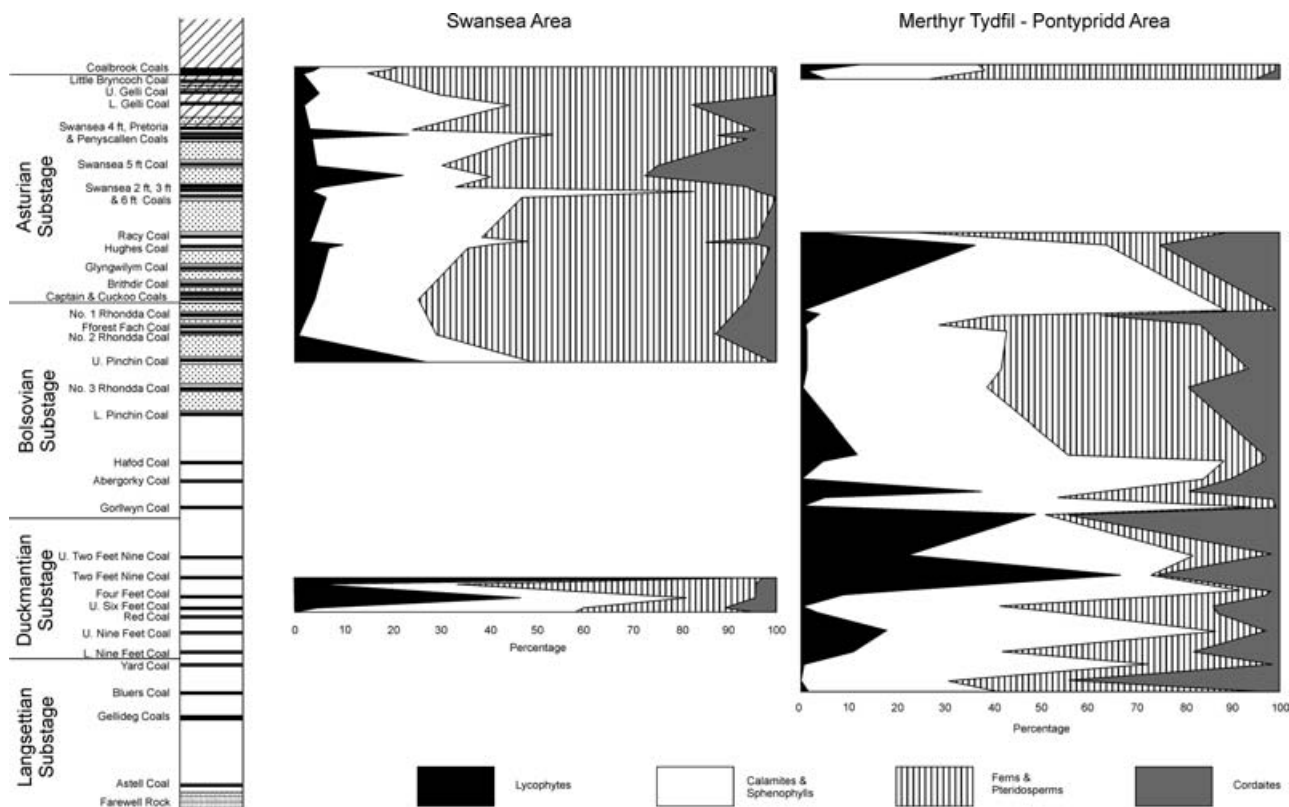


Figure 10. Stratigraphical changes in biomass of the four major plant groups recognized by Davies (1929). Data from Davies (1929) and North (1935). For legend for stratigraphical column, see Figure 2.

raised and thus somewhat drier clastic substrates (e.g. Wnuk & Pfefferkorn, 1984), and the cordaites the driest clastic substrates within the forests (e.g. Falcon-Lang, 2003). The calamites–sphenophyll complex was probably more heterogeneous in terms of ecological tolerance. The calamites mostly favoured wet clastic substrates, such as lake margins and mudflats (e.g. Gastaldo, 1992), whereas sphenophylls probably occupied open areas on the drier clastic substrates (e.g. Batenburg, 1981). However, in that part of South Wales where Davies (1929) has published a taxonomic breakdown of the broad classes that he used, the sphenophyll remains rarely represent more than 5% of the macroflora. In the following discussion, therefore, the calamites–sphenophyll complex will be taken to represent essentially vegetation of the lake margins and mudflats.

In the Langsettian and lower Duckmantian substages, there are a few levels where the fern–pteridosperm complex and even the cordaites become more abundant, suggesting that there were localized areas of slightly higher elevation within the forests. Mostly, however, calamite-dominated assemblages are most common. This suggests that between the intervals when the basin was covered by lycophyte-dominated wetlands, low-elevation mudflats were probably the dominant habitat (this agrees with the sedimentological data summarized by Hartley, 1993a). Most of Davies's

evidence for this part of the succession came from the more easterly of his two areas; although he investigated 14 horizons of this age in the Swansea area, most yielded insufficient material to give meaningful results. This agrees with my personal experience, that early Westphalian macrofloras tend to be rare in the western part of the main South Wales Coalfield.

In the upper Duckmantian and lower Bolsovian substages, the fern–pteridosperm complex remains relatively uncommon, but the lycophyte remains show a noticeable increase in abundance and the calamites a decline (again, this is only evident in the eastern area; the western area yielded no usable data for this interval). This stratigraphical interval is also characterized by several marine bands. There is evidence to suggest that the calamites could tolerate brackish conditions (Cleal & Thomas, 2004) and so the absence of calamites from this part of the South Wales succession is unlikely to be due the increased marine influence. More likely, it reflects changes in the hydrodynamics in the wetlands resulting from the elevated sea-levels, which reduced the areas of mudflats and lake margins that the calamites tended to favour.

A marked change seems to take place in the middle Bolsovian Substage, with a significant increase in the proportion of the fern–pteridosperm complex, and a corresponding decline in the proportion of lycophytes and calamites. Although the evidence from the critical

part of the succession is limited, the change seems to coincide with the appearance of predominantly alluvial braidplain conditions associated with the South Wales Pennant Formation. The resulting channel bars will have provided more extensive areas of clastic substrates, which will have favoured the fern–pteridosperm complex. There clearly were some localized mudflats, such as indicated by Davies's macrofloras from the No. 1 Rhondda Rider Seam in the eastern area, and the Swansea 3 ft and Swansea 4 ft seams in the western area, but they clearly did not dominate the South Wales Basin in the same way as they did in early Westphalian times.

There is no evidence for any significant change in the relative biomass of the four plant groups in the middle Asturian Substage, where both the biostratigraphical and Total Species Richness data suggest an important change in the vegetation (the diversification of the marattialean tree ferns, the appearance of the callistophytales, and the appearance of several widespread alethopterid medullosaleans). This suggests that, whatever caused this change in the adpression record, it only affected the vegetation growing on the clastic substrates; the general drainage patterns within the basin and overall proportions of the different habitats remained the same.

## 7. Discussion

Macrofloras have traditionally been one of the most widely used tools for stratigraphical correlation of Late Carboniferous terrestrial deposits. However, the data presented in this paper suggest that, at least in lower and middle Westphalian strata, the macrofloral biozones are reflecting vegetation changes which were being influenced by local conditions, and their reliability for detailed inter-basinal correlation must be treated with caution. The different basins may have experienced similar sequences of vegetation change, but not necessarily synchronously. We have at present no means of doing a similar check on the robustness of the upper Westphalian and Stephanian macrofloral zones for detailed correlation. This is unfortunate, as macrofloras are widely perceived to provide the most reliable tool for inter-basinal correlations of these strata (e.g. Cleal, 1984*b*, 1997; Cleal & Thomas, 1994, 1995). In the absence of an independent chronological scale, similar to the sequence of marine bands used in the lower and middle Westphalian stages, the only solution is to compare the macrofloral and palynological records, which should be ecologically independent as they tend to reflect different habitats and vegetation-types. For example, Cleal, Dimitrova & Zodrow (2003) showed that the macrofloral and palynological record near the Westphalian–Stephanian Stage boundary was similar in several different basins, suggesting that together the two biostratigraphies provided a robust means of identifying the stage boundary. However,

the ecological independence of the macrofloral and palynological records is an assumption and ideally needs to be corroborated against an independent chronological scale.

Changes in the relative biomass of the major plant groups and in the Total Species Richness through the South Wales Coalfield succession provide two different insights into the environmental changes that took place here during Westphalian times. Changes in the relative biomass of the major plant groups indicate how the mosaic of habitats changed with time across the basin. This seems to have been the result of the interaction between sea-level changes and the uplift of Variscan-generated mountains to the south. Prior to the uplift of these mountains, low-elevation habitats dominated the area, for most of the time covered by lycopphyte-dominated wetlands, but occasionally subjected to brief basin-wide flooding (Hartley, 1993*a*). During times of relatively low sea-levels, these flood-events allowed extensive calamite-dominated mudflats to develop, but during times of higher sea-levels the mudflats were less extensive. After the onset of uplift to the south, during middle Bolsovian times, the lycopphyte forests continued to dominate the area, but now they were being interrupted by influxes of coarse alluvial sediment from the rising mountains. These provided more widespread areas of clastic substrates that were somewhat drier than the early Westphalian mudflats, favouring fern–pteridosperm-dominated vegetation. There was no direct influence of marine conditions during this later phase.

In contrast, the Total Species Richness data indicate that changes were taking place within the clastic-substrate habitats. During Langsettian and early Duckmantian times, there was a progressive increase in plant biodiversity, very similar to that which has been observed in the Central Pennines Coalfields (Cleal, 2005) and presumably reflecting the progressive migration of plant species into the newly appeared wetland habitats. Unlike the Central Pennines Coalfields, where the Total Species Richness undergoes a decline, this diversity is maintained in South Wales through to late Bolsovian times. The South Wales macrofloras then undergo a drop in diversity towards the end of the Bolsovian Subage. This does not seem to be related to either the final withdrawal of marine influence across the area or the influx of coarse alluvial sediment from the south. More likely it reflects a change in climate, although it will be necessary to see if it can also be recognized in other coalfields that have a good record of macrofloras of this age (e.g. Saar-Lorraine).

The Total Species Richness increases, although not quite to the same as the Duckmantian–Bolsovian levels, due mainly to the appearance of species of marattialean ferns and of pteridosperms. This is contemporaneous with tectonic activity in southern Europe (Wagner, 1966), which also had some influence on northern European landscapes (Cleal, 1978, 1986, 1997), but

exactly how and why this caused the vegetation change is not yet clear. These relatively high Total Species Richness values continue through to the top of the South Wales Coalfield succession, the apparent drop in diversity in the stratigraphically highest beds probably being an artefact. The evidence indicates that the coal forest wetlands were continuing to flourish well into the early Stephanian Age, and that the truncation of the macrofloral record was caused by later erosion of the stratigraphical record (probably in middle to late Cantabrian times) and not due to a collapse in the wetlands habitat in early Cantabrian times.

It is evident that the changes in relative biomass of different plant groups and in Total Species Richness provide a useful index to environmental changes taking place in the palaeotropical coal forests. Measures of relative biomass are arguably the most useful for monitoring intra-basinal changes, but the practical difficulties in collecting enough samples to give statistically meaningful results will limit the extent that this can be studied; not many people have the opportunity to collect in the way that David Davies did. In practice, Total Species Richness will prove to be a more useful tool for environmental monitoring and could potentially be applied to any basin with a reasonable macrofloral record. It is important to remember that we are not measuring the biodiversity of the coal forests as a whole; the diversity of the dominant peat-substrate vegetation could only be assessed from coal-ball data (not available in South Wales) or palynology (not yet well enough understood for the accurate identification of biological species). Rather, we are measuring the diversity of the geographically limited part of the coal forests growing on the clastic-substrates. Nevertheless, it is likely that the diversity of these geographically restricted habitats will provide a far more sensitive indication of environmental change than the dominant lycophyte vegetation, where the peat-substrates significantly buffered it from all but the most severe environmental change (DiMichele, Phillips & Peppers, 1985).

**Acknowledgements.** This paper is a contribution to IGCP 469 *Late Variscan terrestrial biotas and palaeoenvironments*. The author is thankful for helpful discussions on aspects of this study with Barry Thomas and Alister Rees, and for a most helpful and constructive review of the manuscript by Dieter Uhl.

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