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LATE PALAEOZOIC WETLAND PLANT COMMUNITIES: PALAEOECOLOGICAL, PALAEOBIOGEOGRAPHIC AND EVOLUTIONARY SIGNIFICANCE

by

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ABSTRACT

The late Palaeozoic marked the beginnings of fully established, global terrestrial ecosystems as we know them today. Large-scale provinciality of vascular plants had developed by this time, and four global phytogeographic provinces were named, superimposed on the converging Pangaean landmass: Angara (mid-high latitude north), Gondwana (mid-high latitude south), Euramerica (low latitude west) and Cathaysia (low latitude east). The low latitude provinces supported vast swathes of the famous 'coal swamp' wetland flora at this time. Delineation of these provinces has never been formally ratified due to most palaeobotanical work being on a local to regional scale, and results of this work being presumed as representative of a wide area. This thesis examines the wetland flora of the most contentious, low latitude provinces, and aims to assess the widely cited proposal of linkage and substantial interchange between Euramerica and Cathaysia. The proposal is upheld, specifically during the Stephanian (~305-300 Ma), when the well established flora in Euramerica migrated along a pathway through the tectonically complex Angara region and quickly colonised North Cathaysia, where it flourished and diversified after the extirpation of the source flora in Euramerica.

Connections between the regions at other times are also found to be highly likely, although the complexity of the tectonic backdrop, and difficulties with characterisation of highly dynamic wetland floras, lead to ultimate recommendations to analyse the floras as fully and in as wide a context as possible, and to utilise all avenues of evidence, in order to progress in uncovering their full histories.

ACKNOWLEDGEMENTS

A huge number of individuals, institutions and organisations have aided and abetted me over the course of this body of work, and so I make no apologies for the length of this section.

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No one can get very far in life without hard cash, and I have been very fortunate to secure funding not only from NERC (grant NE/F006489/1), but also a CASE partnership with the National Museum Wales, and two grants from the SYNTHESYS project (SE-TAF-4827 and BE-TAF-472) which allowed me to study Chinese fossils in the Natural History Museum (NRM), Stockholm, and the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, respectively.

My time completing this work has been immeasurably enriched by the many opportunities for me to travel nationally and internationally, visiting museum collections and key field areas. There are many people to thank for any or all of logistical, practical and academic assistance, making me feel welcome, giving up their time to help me experience the local culture, or being generally great company. I leave it to those mentioned to decide which categories they fit into. From west to east, some of these are Nick Rosenau (Southern Methodist University); Scott Elrick and John Nelson (Illinois State Geological Survey); Ian Glasspool (Field Museum); Bill DiMichele and Dan Chaney (Smithsonian Institution); Barry Thomas (Aberystwyth); Tim Ewin (formerly Bristol City Museum); Andy Chambers, Jon Clatworthy, Aruna Mistry and Andy Moss (Birmingham); Christine Thomson (BGS); Freddy Damblon (RBINS); the Czech Palaeobotany Mafia; Christian Pott, Ove Johannson, Kamlesh Khullar, Anna Lindström and Else Marie Friis (NRM); Kemal Baris (Karaelmas University); Jun Wang and Xuezhi He (Nanjing Institute of

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Andrew, Andy, Ben, Bryony, Helen, Leyla and Phil have all kept me sane, entertained me in the office and at conferences, or just been generally marvellous as appropriate. Knowing their luck...it will all be OK in the end. As long as they dodge the flying bits of trilobite.

I’m hugely grateful to all the people who have played a part in this curious journey, which has by turns been both maddening and enlightening. Many poor souls have joined me at various points, often through no fault of their own, and for that I can only commiserate. My parents, Andy N, Sophie, Tim C and Tim B all deserve a special mention for their support in many and varied ways, and for all the good times.

Special thanks go to my grandparents, as with great sadness I attempt to absolve my deep regret at omitting to mention them as such great contributors to my Masters degree. I only hoped to be able to do so while both could see this page.

So, all that’s left is a mangled cliché:

The destination would be nothing without the journey.

Onwards and upwards.

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INTRODUCTION

1.1 Late Palaeozoic wetland flora

The late Palaeozoic marked the beginnings of fully established, global terrestrial ecosystems as we know them today (DiMichele and Hook, 1992). From the Pennsylvanian (late Carboniferous) to the end of the Permian, vast areas of palaeotropical Pangaea were covered with swampy, lowland vegetation. These ecosystems have become the most heavily studied of the time due to their legacy of coal, of vital importance to the developed world since the Industrial Revolution. In recent years there has also been a growing interest in the interaction between these wetlands and climate, as a possible independent model analogous to the present day (Cleal and Thomas, 2005). While long term relative stability is evident for much of the Pennsylvanian (DiMichele et al., 2002; Willard et al., 2007), it has long been recognised that there were also times when the wetlands underwent significant changes in vegetation and areal extent, sometimes accompanied by changes in global climate (e.g. Phillips and Peppers, 1984; Gastaldo et al., 1996; Cleal and Thomas, 1999, 2005), and glacial/interglacial rhythms (e.g. DiMichele et al., 2010; Falcon-Lang, 2004).

Large-scale provinciality of vascular plants developed soon after their terrestrialisation in the Early Palaeozoic, and three phytogeographic realms became apparent (Chaloner and Creber, 1988): Angara and Gondwana covered the north and south high latitudes respectively, and Euramerica the mid latitudes, consisting largely of the swampy, wetland vegetation (Wnuk, 1996). During the late 1800s it was realised that a fourth province was in existence by the Permian (Sun and Shi, 2000), and in 1935 Halle first named it the Cathaysian flora (Figure 1.1). The high latitude floras were separated by the wide, low latitude and equatorial belt occupied by both the Euramerican and Cathaysian provinces, and so while the Angaran and Gondwanan provinces were distinctive in nature (Hilton and Cleal, 2007), there has long been a debate about the timing and extent of differentiation between the equatorial members, if indeed there was a discernable difference. Given divisions between them are often transitionary, and their precise floristic makeup, especially at their margins and in areas of complex geology, is continually under review. Support has emerged for connections between the low latitude floras into an 'Amerosinian' realm, at various times during the late Palaeozoic (e.g. Havlena, 1970; Durante, 1983; Chaloner and Creber, 1988; Laveine, 1997; Wagner, 2003; Sun, 2006; Hilton and Cleal, 2007).

Present day China is a microcosm of the late Palaeozoic floristic world, consisting of a multitude of tectonic blocks which between them manifest all four of the major phytogeographic provinces (Shen, 1995; Li and Wu, 1996). In addition, the Cathaysian flora which covered the majority of China's landmass at the time was further divided into North and South elements by the Permian, due to its occupation of different tectonic blocks and consequently different climatic regimes (Li and Wu, 1996). Ever since the tentative classification of the flora by Halle in 1935, palaeobotanists have been seeking to unravel the puzzle of Chinese late Palaeozoic floral makeup: its origin, evolution and development (e.g. Wang, 1996; Sun, 2006; Srivastava and Agnihotri, 2010). The North

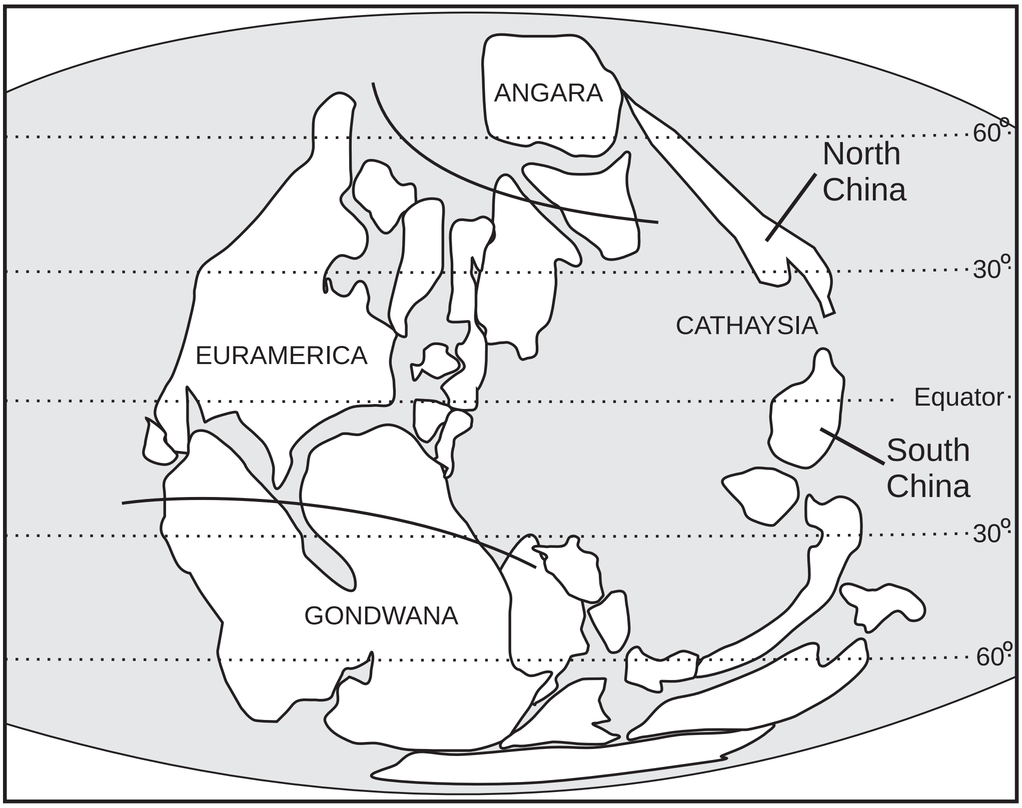

Figure 1.1: Phytogeographic provinces in the late Pennsylvanian. From Hilton and Cleal (2007), modified from Gastaldo et al. (1996).

China tectonic block sits in a strategic position in this jigsaw, containing floras spanning almost the entire extent of late Palaeozoic wetland forest existence, from the Pennsylvanian right to the end of the Permian, and adjoining the Chinese section of the Angaran phytogeographic province. This is one of the key pathways proposed as a connection with the 'mainland' of the converging Pangaea, through what is now Siberia (Laveine, 1997; Sun, 2006; Hilton and Cleal, 2007; Stevens et al., 2011). Multidisciplinary work is continuing apace to reach consensus on the complicated Late Palaeozoic history of China and the wetland forests which covered so much of it during this time. Against the backdrop of extensive tectonic movements during the amalgamation of Pangaea, and climatic changes due to glacial rhythms and the influence of the dominant wetland communities (e.g. Cleal and Thomas, 2005; Cleal et al., 2009a; DiMichele et al., 2010; Shi and Waterhouse, 2010; Koch and Frank, 2011), the late Palaeozoic was a complex and rapidly changing time.

1.2 Geological background

Sites in this thesis were selected to give an even coverage of Euramerica and North China, but especially to give a significant stratigraphic overlap between the two areas in order to trace any potential floristic connections. From west to east, these sites are Mazon Creek (USA), the Iberian Peninsula (Spain/Portugal), southwest UK (see Chapter 2), the Saint-Étienne (France) and Saar-Nahe (Franco-German border) basins, Central/West Bohemia (Czech Republic), the North Caucasus platform (European Russia), and several sites centred around North China (see Chapter 3) (Figures 1.2a-c). All of them were bound up in orogenies created by the amalgamation of Pangaea (Figures 1.2a+b). Many phases of plate movement and collision occurred overall during this process, spanning from roughly 500 Ma to 250 Ma (Matte, 1991). The majority of the areas in this thesis are in Europe, and during the tenure of the wetland ecosystems under consideration the prevalent orogeny is commonly known as the Variscan, although this is only part of the sequence of collisions which began with the Caledonian-Appalachian Orogeny commencing in the Cambrian (Krawczyk et al., 2008). These structures have also been overprinted in places by the subsequent Alpine Orogeny. An overview is given below of the geological situations of the localities, from west to east.

There is only one site included from North America, as it is outside the main focus of this study in assessing links between China and the more proximal ancient Europe. However, the terrestrial and floristic link between Europe and North America is well known (Phillips and Peppers, 1984; Wagner and Lyons, 1997; Thomas, 2007), and enough material was easily accessible from Mazon Creek to compile a comprehensive species list, which was deemed a useful comparison point to give an indication of the composition of wetland flora further west. The Mazon Creek area is found in the Illinois Basin, an intracratonic downwarped structural sag formed to the north of the Appalachian Orogeny (Bedle and van der Lee, 2006). The Appalachian Orogeny was the North American branch of the Caledonian Orogeny, active throughout Pangaean amalgamation, from the formation of Euramerica to the end of the Permian (Van Staal et al., 1998). Whilst not originating during the orogeny, associated tectonic movements reactivated the Cambrian failed rift system under the Illinois Basin, creating new accommodation space through the

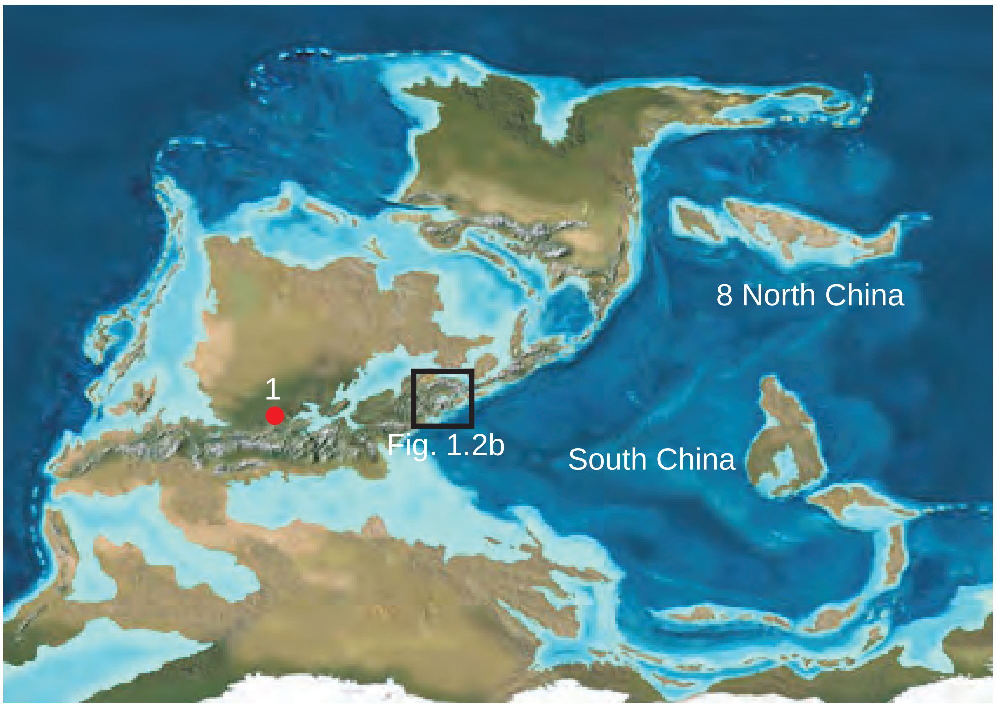

Figure 1.2a: Global late Pennsylvanian (~300 Ma) palaeogeography map showing the localities in the thesis. Mazon Creek (1) is marked with a red dot, and the approximate positions of the North (8) and South China blocks are labelled. The positions of the European localities (inset map) are shown on Figure 1.2b. Base map: Blakey (2011).

Figure 1.2b: Late Pennsylvanian (~300 Ma) palaeogeographic map showing the European localities in the thesis. For locations of Mazon Creek and North China, see Figure 1.2a. Base map: Blakey (2011).

2) Iberian Peninsula
3) UK
4) St-Étienne
5) Saar-Nahe
6) Central/West Bohemia
7) North Caucasus

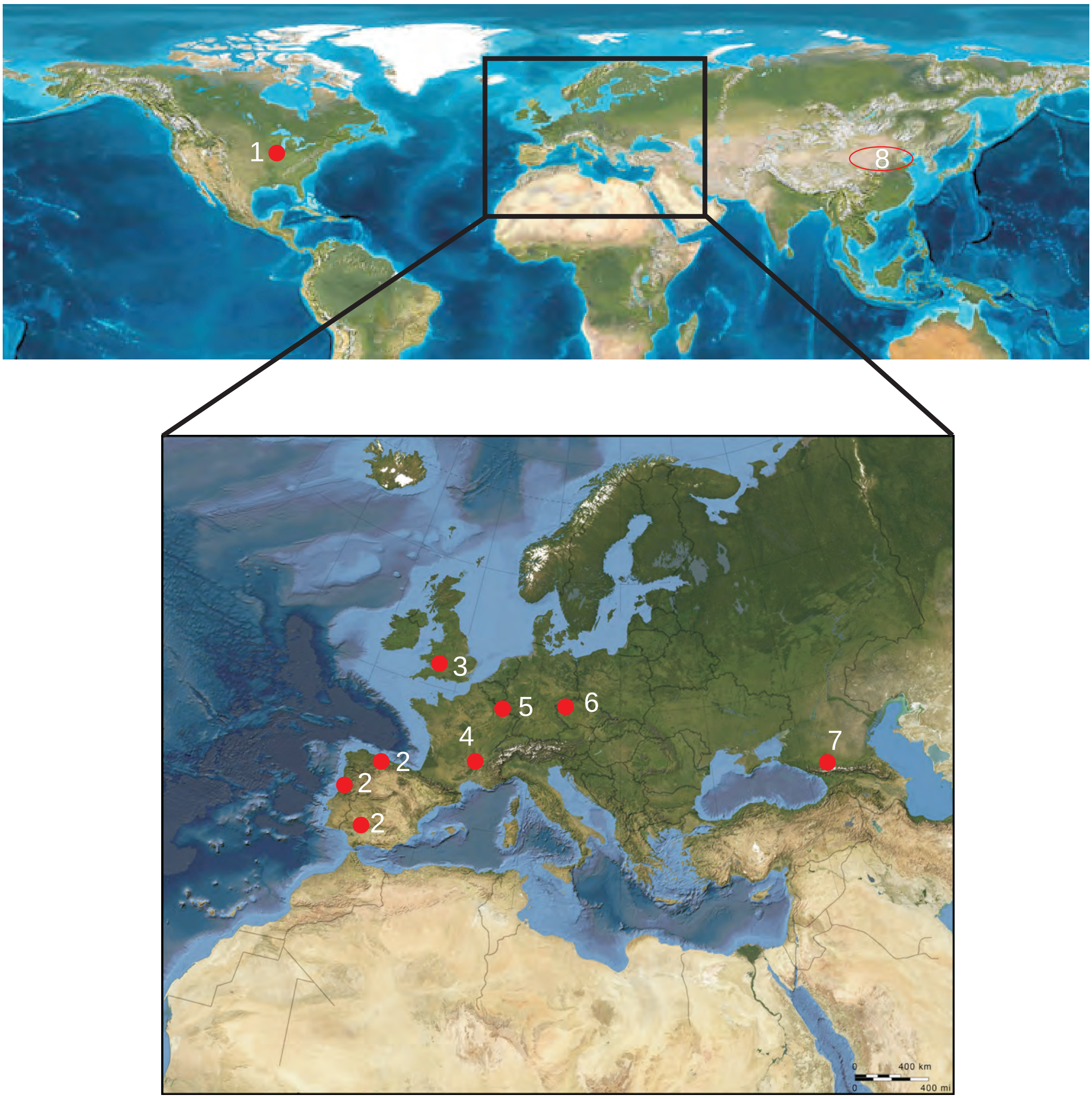

Figure 1.2c: Present day positions of the localities in the thesis. For late Pennsylvanian (~300 Ma) palaeogeographic locations see Figure 1.2a+b. Base maps: Blakey (2011).

1) Mazon Creek
2) Iberian Peninsula
3) UK
4) St-Étienne
5) Saar-Nahe
6) Central/West Bohemia
7) North Caucasus
8) North China

late Palaeozoic and exposing the south of the basin to the sea (Kolata and Nelson, 1990). Fossil localities cover a range of sites, and fossils are allochthonous and found within siderite nodules in the Francis Creek Shale. This is a succession of tidal rhythmites formed in a deltaic to marine setting (Baird et al., 1986). Fossil discoveries are informally divided into the nonmarine Braidwood biota in the northeast sites, containing the vast majority of plant material, and the brackish to marine Essex biota in the southwest areas. Mazon Creek is unusual in this study for several reasons; not only is it the only site from present day USA, it also has a strong element of marine sedimentation, and yields strongly allochthonous flora which is preserved within nodules, as opposed to closer-range compression-impression fossils as studied in all other localities.

The plant bearing coalfields of the Iberian Peninsula are mainly found on the core Iberian Massif, which was assembled during Middle Devonian-Early Permian times (Colmenero et al., 2002; Wagner, 2004). The coalfields considered in this study are from three main areas on the massif, the north, west and south, and span several complex tectonic zones. Most, if not all, are intramontane, controlled by extensive compressional strike-slip faulting (Wagner and Álvarez-Vázquez, 2010) although the northern areas show extensive marine influence and may be the remnants of a large, late-stage foreland basin (Bashforth et al., 2010).

The geology of the UK (Wales and Bristol) is given in detail in Chapter 2 (King et al., 2011). The area was a foreland basin during the Variscan Orogeny, with coal formation spanning the Moscovian stage in paralic conditions (Cleal, 2007).

The Saint-Étienne (or Loire) Basin is the largest coal bearing basin on the Massif Central, which is a large exposure of Variscides in a complex mainly consisting of metamorphosed basement rocks and granitoid intrusions, cross cut by extensive faulting. Isolated intramontane troughs, resting unconformably on the crystalline basement, collected Carboniferous-Permian continental sedimentation such as that of Saint-Étienne (McCann et al., 2008). There are three separate, contemporaneous units within the basin, whose relationships remain unclear, although it seems no thrusting was involved in their emplacement (Doubinger et al., 1995). Mattauer and Matte (1998) conclude that the basin was of pull-apart style as a result of active Variscan strike-slip faulting, rather than later stage orogenic extension.

The Saar-Nahe (or Saar-Lorraine) Basin extends across the Franco-German border, in the southwest of the latter. It is a half-graben, orientated along the southwest-northeast striking Hunsrück Boundary Fault to the north, which marks the boundary between the Rhenohercynian Zone in the north and Saxothuringian Zone to the south (Franke, 2000). Extensional reactivation of Variscan thrusts allowed fully terrestrial, limnic and extrabasinal pyroclastic fill, of thicknesses up to 10 km, spanning from the Westphalian to the Rotliegendes (=Early Permian; Henk, 1993).

The Central and Western Bohemia area in the northern Czech Republic consists of a series of basins in the northwest of the Bohemian Massif, south of the Saxothuringian Zone. Late Palaeozoic basins here were related to late stage orogenic extension, forming in horst and graben structures, alongside strike-slip faults reorganising the granitoid basement. The Massif was around 4-6° N, several hundred kilometres from the northern coast of Tethys (Opluštil and Pešek, 1998) and up to 1000 m above sea level during the late Palaeozoic (Opluštil, 2005). In the Czech area of the basin, sedimentation began at the end of the Namurian, but this study focuses on the upper Kladno Formation (Asturian-Cantabrian) through to the Linĕ Formation (Stephanian C). Sedimentation progressed from braidplain, through redbeds and fluvial/lacustrine/deltaic sequences, culminating in seasonally wet redbeds with calcretes (Cleal et al., 2009a).

The North Caucasus Basin lies at the southern edge of the Scythian Platform, which consists of Precambrian basement and highly deformed rocks of Palaeozoic and younger age. The geological history of the area is very poorly known due to a paucity of data (Saintot et al., 2006). The platform is at the eastern limit of the Variscan Orogeny, and as such is strongly overprinted by Alpine tectonics which reactivated previous movements. The North Caucasus Basin was proximal foreland in late Palaeozoic times, and shallowing marine sediments were deposited from the Namurian, progressing to conglomerates and sandstones interspersed with paralic to limnic sediment up the sequence. Volcaniclastic bands are present in the Moscovian (Tenchov, 1989).

Other areas of wetlands that had developed in the eastern Variscan area during Pennsylvanian times are the western Pontides in northern Turkey (the Zonguldak-Amasra Coalfield: Kerey et al., 1985) and the Ukraine (Donets Coalfield: Sachsenhofer et al., 2012). However, the palaeobotany of neither area has been revised in recent years, which makes any comparison of their published species lists difficult. They have not, therefore, been included in the present study.

The geology of the Chinese localities in this study is discussed in detail in Chapter 3. The Variscan Orogeny terminates at the Ural Mountains, where Siberia and Kazakhstania sutured onto the rest of Pangaea during the late Palaeozoic. East of this point, China is separated from the Euramerican sites by the Central Asian Orogenic Belt, and an assortment of terranes and orogenies accreted around the Siberian (Angaran) Craton (Şengör et al., 1993). The platform bearing Northern China was uplifted during the early stages of Pangaean formation (during Caledonian times), with paralic conditions developing by the late Palaeozoic, depositing extensive coals in cratonic basins (Liu, 1990).

There are few, if any, late Palaeozoic wetland plant-bearing localities known in the literature from the area covering present day Russia east of the Urals, and therefore this area represents a large discontinuity in the fossil plant record between Euramerica and China. The region is highly complex tectonically and is composed of the relatively small Siberian Craton to the northeast, surrounded by the Altaids, a huge accretionary belt which spans the area down to the North China block (Xiao et al., 2010). The Altaid area has been subject to extensive reorganisation and orogenesis throughout geological time, resulting in an almost undecipherable terrane history (Natal'in and Şengör, 2005). Mongolia alone consists of 44 terranes, of cratonic, metamorphic, passive margin, island arc, forearc/backarc, accretionary complex and ophiolitic types (Badarch et al., 2002).

Throughout this thesis the stages of the IUGS global chronostratigraphical divisions (Heckel and Clayton, 2006; Ogg et al., 2008) are used, alongside the substages of the Heerlen classification, as these provide the most detailed stratigraphical resolution of these basins (see Wagner, 1974). An overview of stratigraphical correlations is given in Figure 1.3, with more details given at appropriate points in the text.

1.3 Thesis aims and rationale

This thesis examines North China and the Euramerican phytogeographic province in detail to assess the similarity between their floras, and the viability of the Amerosinian realm concept. Museum inventories and monographs were examined and compiled, as in the vast majority of cases the plant fossil bearing sites in question are difficult or impossible to access at the present time, and it allowed for efficient and reliable data collection and validation of given identifications. As a result, the dataset used in this thesis is the largest and most comprehensive on these wetland floras to date, spanning Euramerica and China through their whole range, from the mid Pennsylvanian to the end of the Permian, with emphasis on southwestern UK and China.

The aims of this thesis are firstly to establish a robust procedure and methodology for collating and analysing the large volumes of data involved. This is addressed in Chapter 2, which uses the relatively small area of southwest England as a testbed. Secondly, the flora of the North China block and its surrounding areas are examined in Chapter 3, to give a detailed picture of the composition of the flora and its possible affinities further west. This feeds into Chapter 5, which analyses the whole dataset, from Euramerica and China, in order to comprehensively compare the two areas using the largest set of

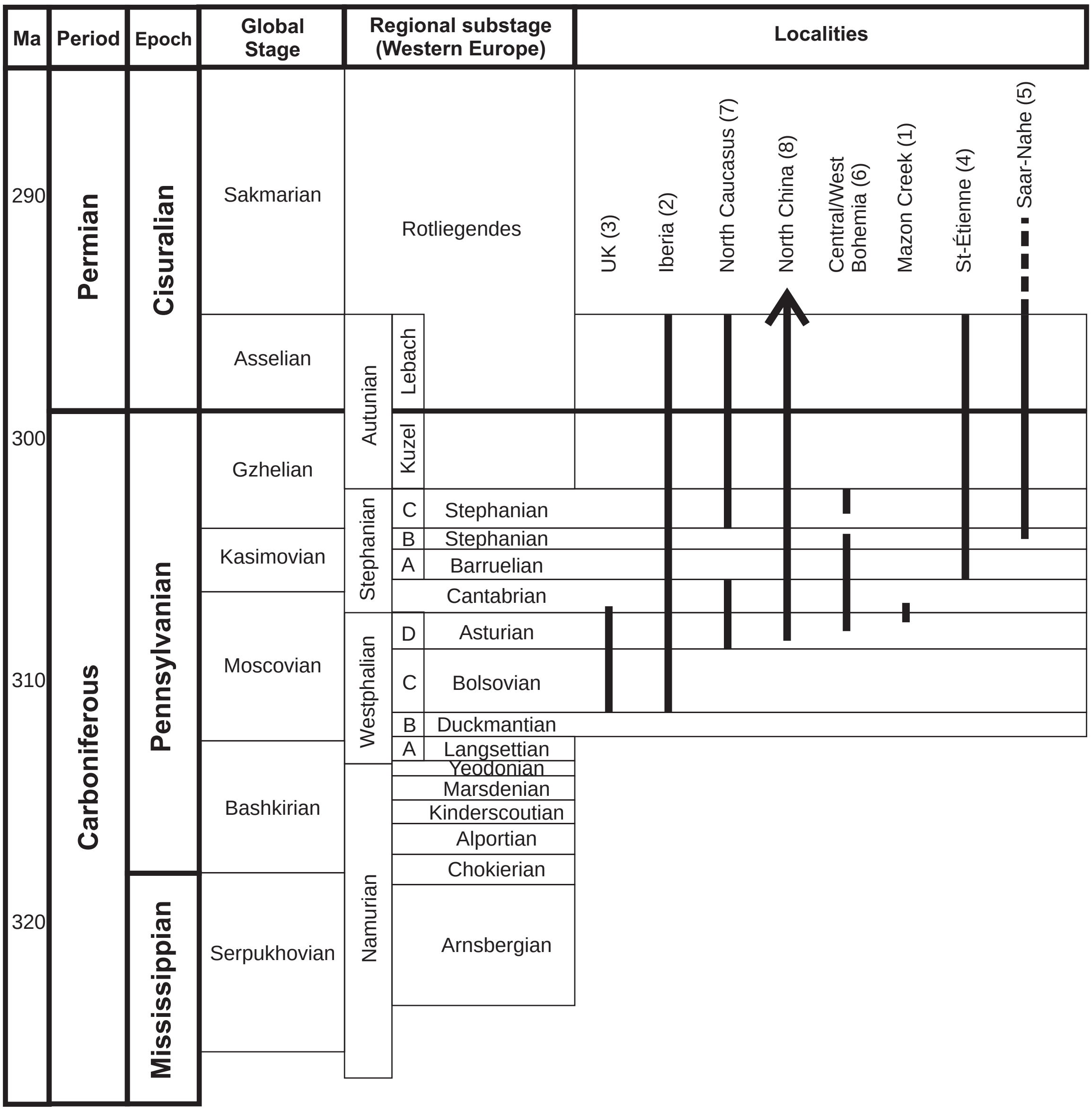

Figure 1.3: Approximate stratigraphic correlations of the sites in this thesis. Numbers in brackets correspond to those on maps in Figure 1.2a-c. Higher resolution data is given for the UK in Figure 2.2, and the full range of the Chinese data, which extends to the end of the Permian, in Figure 3.2.
Data sources: Ogg et al. (2008), Heckel and Clayton (2006), Königer et al. (2002).

macrofloral evidence thus far considered. Are these two ancient floras demonstrably similar, or did they develop more independently?

Lastly, as an augmentation to the main data-driven body of the thesis, and as a quality control function on the data inputted, several individual fossil plant species are examined in detail in Chapter 4. A multidisciplinary approach is used to assess robustness of the taxonomy and likely affinites of the plants in question, and shed some light on the significance of the taxon names used in the main database. Evidence from these species is used to support the overall findings in Chapter 5, and is also drawn upon in the conclusions (Chapter 6). Chapter 6 presents a synthesis of findings, as well as wider implications, and recommendations for future work.

-CHAPTER 2-

A METHODOLOGY FOR UTILISING LARGE, HISTORICAL DATASETS: AN EXAMPLE FROM THE UK[1]

2.1 Background

Here, two sites from the UK, covering the stratigraphic overlap with North China, provide a small-scale testbed to devise a robust methodology for analysing historical data gathered across Euramerica and China, in preparation for global analysis.

2.1.1 Historical adpression floras in Europe

One of the themes that has been investigated within wetland ecosystems is vegetation dynamics, as reflected in the macrofloral record. Most early studies focussed on plant macrofossil biostratigraphy as an aid to stratigraphical correlation (e.g. Kidston, 1905; Dix, 1934; Wagner, 1984). There were also some early attempts to use the plant macrofossils for understanding the ecology of the vegetation (e.g. Stopes, 1914; Davies, 1921; Davies, 1929; Drägert, 1964) but the taphonomy, and in particular preservational bias, of the adpression floras (a term introduced by Shute and Cleal, 1986 to replace 'compression-impression floras') has been seen to be an obstacle to such work (e.g. see discussion by Scott, 1977). More immediate success was obtained through the study of

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[1] This chapter was published in paper form as KING, S. C., CLEAL, C. J. and HILTON, J. (2011). Common ground between two British Pennsylvanian wetland floras: Using large, first-hand datasets to assess utility of historical museum collections. **Palaeogeography, Palaeoclimatology, Palaeoecology**, 308, (3-4): 405-417.

coal ball floras, which not only provided detailed anatomical evidence of the plants present, but were also remains that had suffered relatively little transportation and so reflected more closely the composition of the local vegetation (e.g. Phillips and Peppers, 1984; Phillips and Cecil, 1985; Phillips et al., 1985; Phillips and DiMichele, 1992). However, the records of coal balls across Euramerica and Cathaysia are patchy, with only North America having an extensive and well-studied coal ball record over a long stratigraphical range that is suitable for investigating the changes in taxonomic composition of the vegetation with time (Phillips, 1980; Galtier, 1997). A few other sites across the study area have isolated coal ball occurrences with variable descriptions, such as Grand Croix in the Saint-Étienne Basin (Galtier, 2008), and the Donets Basin (Snigirevskaya, 1972), and there are many incompletely reported permineralised assemblages from China (e.g. Wang et al., 2003; Seyfullah et al., 2009), but comparisons are difficult due to inconsistent documentation. Consequently, in Europe attention has returned to the plant adpression record for studying the changing floristics of the Pennsylvanian tropical plant communities, especially in terms of landscape-scale species diversities and palaeobiogeographical patterns (summarised by Cleal et al., 2009a).

A potential difficulty with such studies of the adpression floras is that they are heavily dependent on historical collections, the potential for extensive collecting of new material having become severely constrained by the general decline of coal mining, and regional mine closures. The effect of taphonomy, especially transportation of the plant fragments in the original sedimentary system in which they were deposited has been addressed by a number of authors (e.g. Gastaldo, 1985, 1987; Gastaldo et al., 1995).

Another potential problem is that of collector bias; how well does the museum collection reflect the original fossil assemblage from which it was obtained?

2.1.2 Rationale

Firstly, part of the voucher collection of plant fossils from the South Wales Coalfield, made by David Davies and now stored in the National Museum Wales, is compared against his records of the fossils systematically brought up from each underground horizon (Davies, 1929; Thomas, 1986). The question here is: how well does the voucher collection reflect the original composition of the fossil assemblage as collected on an 'almost embarrassingly large' scale (North, 1935) by Davies?

Secondly, these South Wales macrofloras are compared with floras from the nearby Bristol-Somerset Coalfield. Although there were a number of notable studies on these macrofloras during the first half of the 20th century (Crookall, 1925a, 1925b; Moore, 1937; Moore and Trueman, 1937; Moore and Trueman, 1939, 1942) none were as systematic as those undertaken by Davies in Wales. Crookall's material is still available in the Bristol City Museum and Art Gallery, but most of Moore's material appears to be lost. Additional collecting today is all but impossible as the sequences are now largely inaccessible due to Mesozoic cover (Kellaway and Welch, 1993) and urbanisation (Down and Warrington, 1971). The only parts of the Bristol-Somerset succession that have been extensively sampled recently are the Radstock and Farrington formations (e.g. Thomas and Cleal, 1994; Proctor, 1994), but even these macrofloras have never been the subject of a comprehensive monographic study to reveal a better picture of their diversity. The overall quality of the data from Bristol-Somerset can therefore be seen as relatively typical of that found in many other European and American coalfields – incomplete and accumulated with unstandardised identifications from various collectors. The second component of the study therefore, is a comparison with the atypically well constrained Welsh data.

2.1.3 Geological setting

The South Wales and Bristol-Somerset coalfields, with current areal extents of 2,300 km^2 and 870 km^2 respectively (Cleal et al., 2009a), formed during the Mississippian as part of a complex of foreland basins riding the Variscan Front to the south, and truncated by the Wales-London-Brabant High in the north (Figure 2.1). The two coalfields were part of the 'South-West Province' (*sensu* Calver, 1969) and are separated by approximately 1° longitude, or 80 km on the ground at the present time, although crustal shortening in the South Wales area alone could have been as much as 50% (Jones, 1991) and therefore may have affected their positions.

The dominant environment of the area during the mid-Moscovian was alluvial braidplain, with low- to moderate-sinuosity rivers flowing northward from the advancing Variscan Mountains (Waters and Davies, 2006). Coal formation commenced in Langsettian times. Marine influence was evident up to the mid-Bolsovian, with regular marine bands present in both coalfields (Cleal et al., 2009a) that enable reliable correlation of basins across a wide area (Waters et al., 2011). Lithostratigraphy of the later paralic basin fills is summarised in Figure 2.2. This sequence is attributable to the

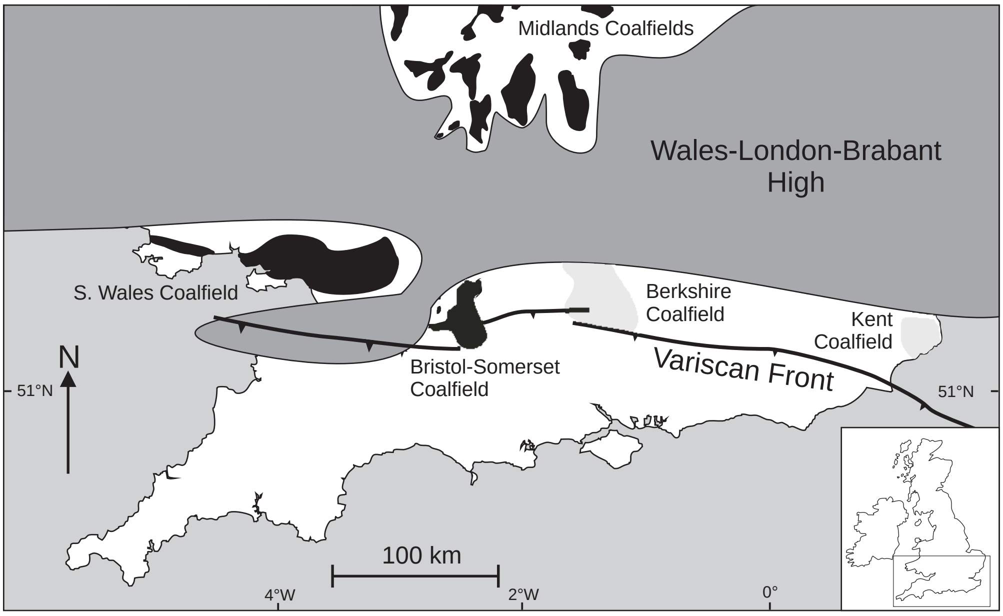


Figure 2.1: Locations of the South Wales and Bristol-Somerset Coalfields (after Cleal, 2007). The area extending to the south, separating the coalfields, is the remains of the Usk Axis (Cope et al., 1992). Exposed coalfields shown in black, concelaed coalfields in light grey, and the Wales-London-Brabant High in mid-grey.

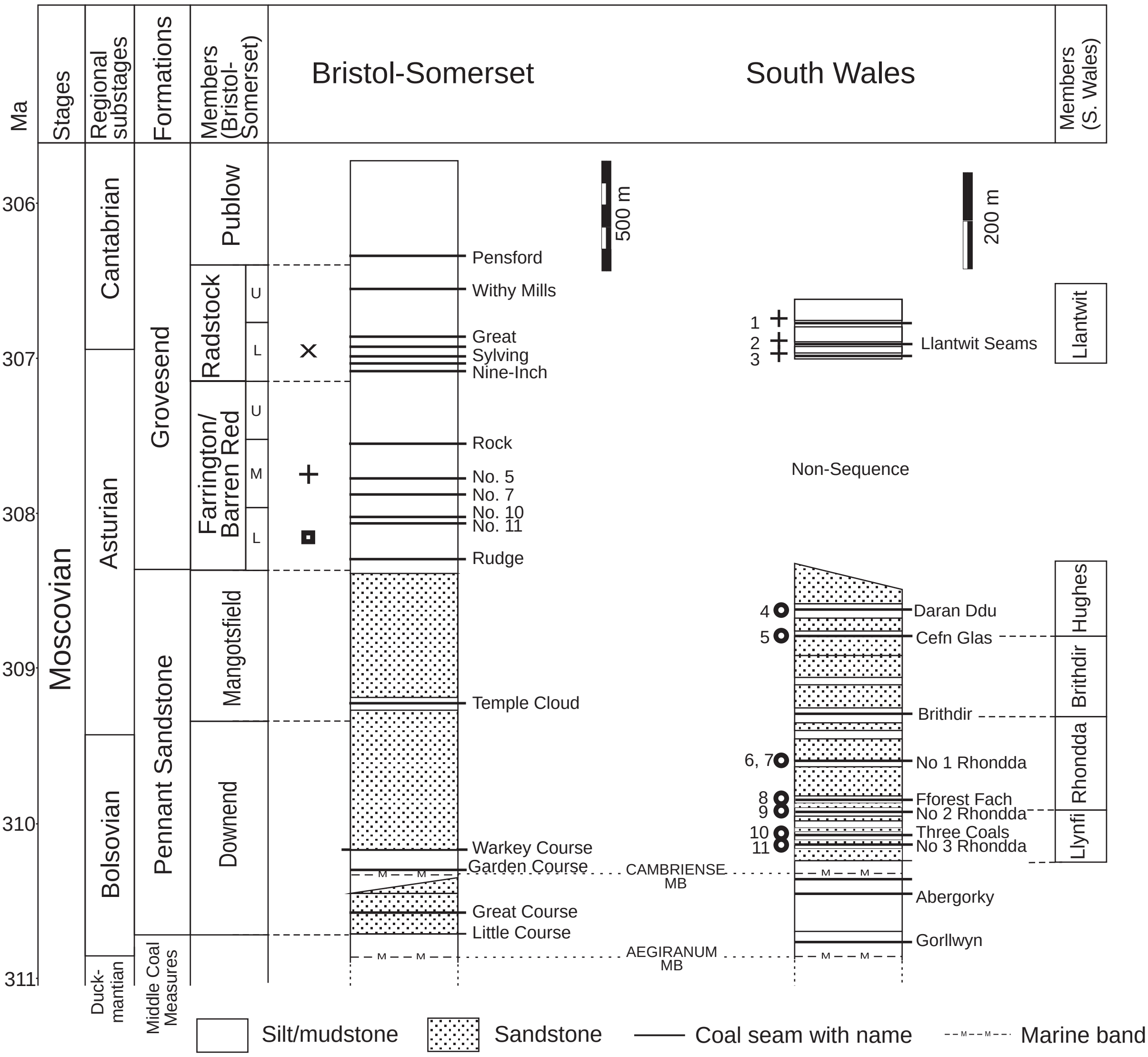


Figure 2.2: Stratigraphic placement of seams and collieries (modified from Waters and Davies, 2006; Cleal, 2007). Symbols and numbers represent groups of collieries and David Davies' (1929) coal seam numbers, respectively. For explanation of these, see Tables 2.1 and 2.2. Symbols match those of the maps in Figures 2.3 and 2.4.

proximity of the northwards prograding Variscan Front during Bolsovian times, causing uplift and change from coastal floodplain to alluvial braidplain, and depositing large quantities of coarse clastic sediment into the basins, forming the Pennant Sandstones (Kelling, 1974; Jones, 1991; Waters and Davies, 2006). In South Wales, they reach a maximum thickness of 1700 m, and 1030 m in Somerset (Cleal, 1997). As the basins filled during the Asturian, floodplain conditions returned, depositing the argillaceous, fluvio-lacustrine Grovesend Formation (Cleal, 1997, 2007), which reached 450 m thickness in the western part of the South Wales Coalfield, but up to 1400 m in Somerset (Waters and Davies, 2006). In the eastern part of the South Wales Coalfield covered in this study, however, Pennant-like facies continue up into the Cantabrian Substage, with an interval known as the Llantwit Beds containing three prominent coal seams (Dimitrova et al., 2005).

2.2 Material

2.2.1 South Wales

The material documented from South Wales is taken from Davies' (1929) publication. Davies was a local colliery manager who diligently documented all the plant fossils discovered in the roof shales above the coal seams worked in his collieries, resulting in hundreds of thousands of specimens being methodically recorded. Such was the volume of material he extracted, he was able only to publish on the eastern section of the coalfield (1921, 1929) before his death in 1931 (for an account of Davies's work see North, 1935; Thomas, 1986). However, these data are more than enough to work with;

Davies' 1929 paper documents over 200,000 specimens. What is outstanding about this collection is that Davies observed and noted all of the specimens himself irrespective of their quality and size, and systematically recorded them, applying a uniform taxonomic scheme that is elaborated in his 1929 publication. Moreover, the fossils were consistently and reliably identified at the time with the help of Robert Kidston, a well respected contemporary palaeobotanist (Thomas, 1986). As such the dataset is internally consistent. Furthermore, a subset of around 6% of the material identified is kept at the National Museum Wales, Cardiff (NMW) allowing first hand observation of the specimens, as well as an assessment of the consistency and robustness of Davies' identifications with regard to subsequent taxonomic developments.

Davies' horizons 1-11 (Figure 2.3, Table 2.1) in the upper part of the section are focussed on in this study. Davies recorded just over 110,000 specimens from these macrofloras. After systematically examining and recording the fossils in the NMW for the current study, it is apparent that the original nomenclature is remarkably robust, and that the data in this 80 year old paper can be used with confidence.

2.2.2 Bristol-Somerset area

The material from the Bristol-Somerset Coalfield was documented directly from the collections at the Bristol City Museum and Art Gallery. These collections consist of 1670 specimens from 66 localities, collected and identified at different times by different people. However, this total also includes nearly 700 identified by Kidston and Robert Crookall, Kidston's successor as chief palaeobotanist for the British Geological Survey.

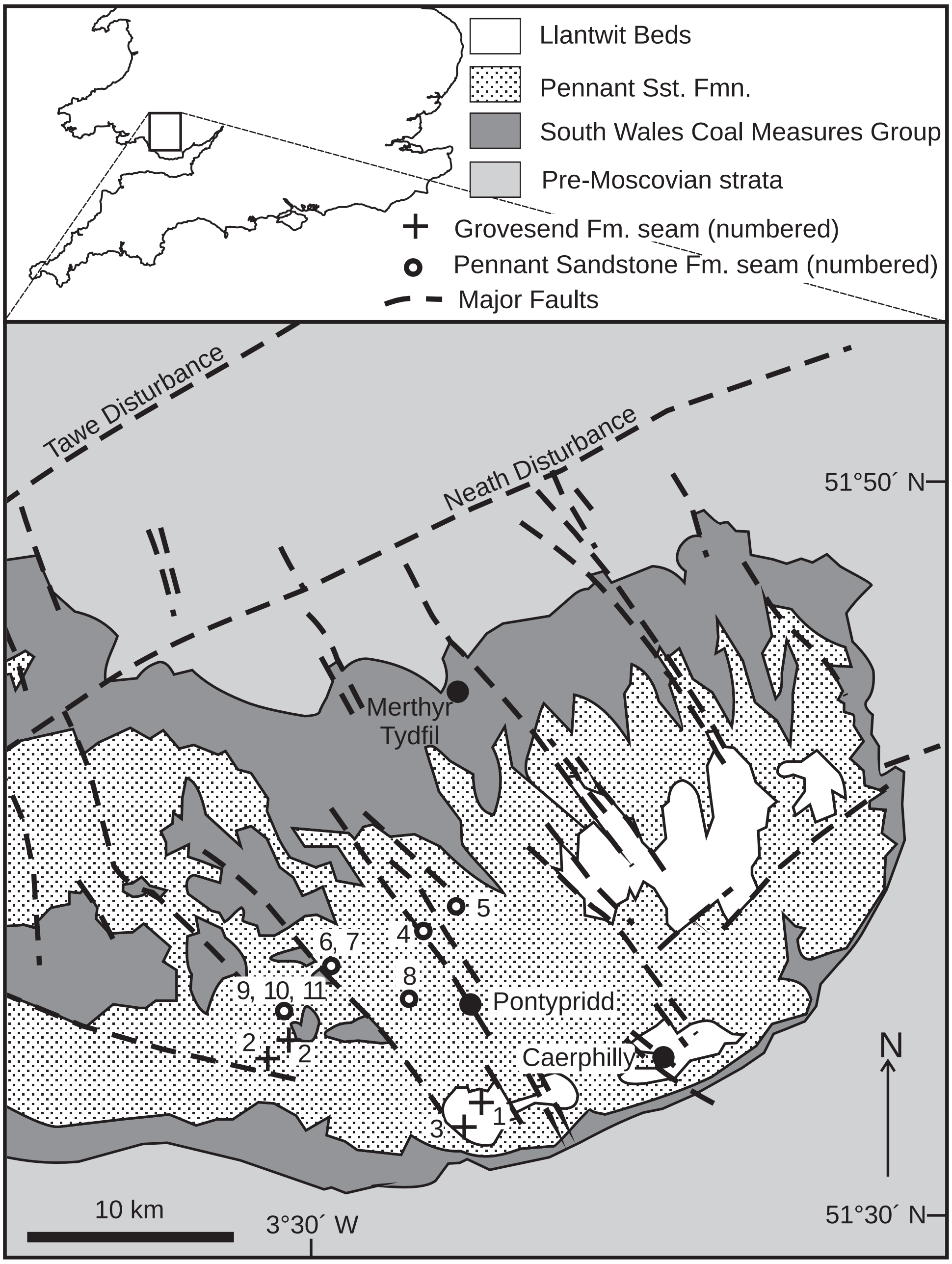


Figure 2.3: Davies' (1929) localities. Symbols match those in Figure 2.2 for cross reference. See Table 2.1 for explanation of seams.

Horizon number	Seam
1	No. 1 Llantwit Seam
2	No. 2 Llantwit Seam
3	No. 3 Llantwit Seam
4	Daran Ddu/ Penygroes Seam
5	Cefn Glas/Rec Ash Seam
6	No.1 Rhondda Rider Seam
7	No. 1 Rhondda Seam
8	Fforest Fach Seam
9	No. 2 Rhondda Seam
10	Three Coals Seam
11	No. 3 Rhondda Rider

Table 2.1: Coal seams as listed in Davies (1929). In Davies' notation, horizon 1 is youngest and 11 oldest.

Each specimen in the collections was examined and verified. After examining the raw data, localities that could not be resolved stratigraphically, and those that contained very few specimens (less than 4 in the raw dataset) were discarded. This resulted in all of the material from the Pennant Sandstone Formation being grouped, as numbers of specimens were low and the quality of preservation generally poor. However, this material was retained for analysis for comparison with the material from the Pennant Sandstone Formation in South Wales, where large numbers of specimens are recorded right through the sequence (Figure 2.2). The stratigraphic positions of three collieries (Pensford, Ludlows and Old Mills) could not be determined, but still yielded large numbers of specimens, and so were retained as valuable contributors to the dataset for the coalfield and to investigate whether their ages could be determined in relation to the other collieries. Fourteen collieries remained in the analysis (Figure 2.4), and in order to streamline overlapping stratigraphic ranges, these were grouped into three appropriate time periods based on the stratigraphic columns in Figure 2.2. These are shown in Table 2.2.

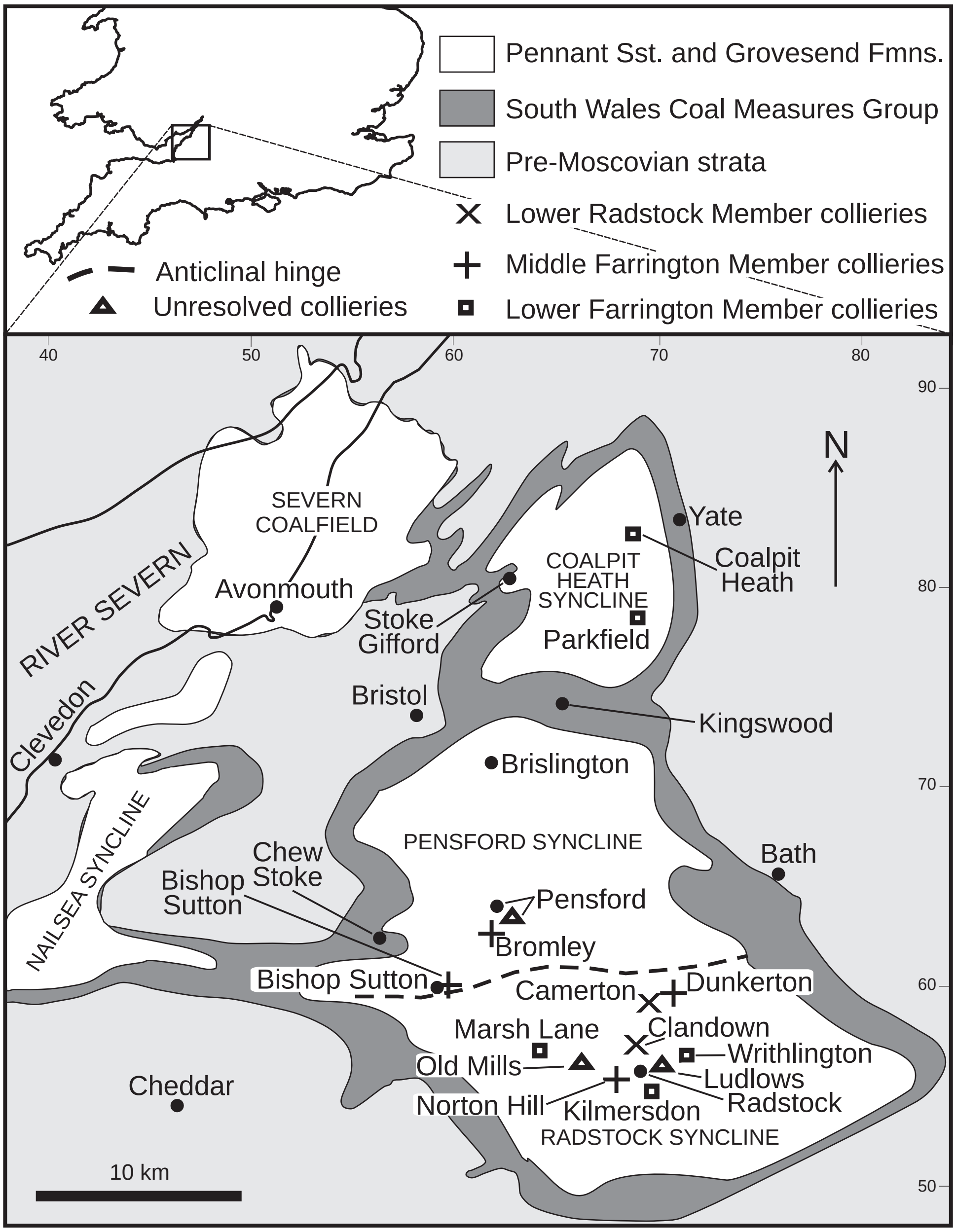


Figure 2.4: Locations of the Bristol-Somerset collieries included in the study, modified from Green (1992). Symbols match those in Figure 2.2 for cross reference.

Lower Farrington Member	Middle Farrington Member	Lower Radstock Member	Unresolved stratigraphically
Coalpit Heath	Bishop Sutton	Camerton	Pensford
Marsh Lane	Dunkerton	Clandown	Ludlows
Kilmersdon	Norton Hill		Old Mills
Parkfield	Bromley		
Writhlington			

Table 2.2: Groupings of Bristol-Somerset collieries according to stratigraphic range.

2.3 Data handling

2.3.1 Data structure

The database was built as a taxa-by-localities presence/absence matrix, with both variables derived initially from museum labelling. These were later verified, updated if necessary, and sorted manually into meaningful contemporary groupings. Ideally, absolute abundances would be best to identify changes in abundance through the sequences studied. However, when dealing with museum collections this information is simply not available, as it is impossible, in the vast majority of cases, to know the agenda of the collector and any other filters the material will have gone through before finally being placed within the museum collection. The David Davies paper (1929) is a rare exception to this, in that he documented everything he could find. Before his death, some of his material had been periodically sent to the NMW with the intent being to sort it for use as a teaching tool. A very small amount of this task was completed (North, 1935), but no records exist of what and how much. It is reasonable to assume then that the material at the NMW, mainly donated after his death, stands as a typical museum collection. As a test of the effect of filters on museum collections, the uppermost seam (the 'Llantwit No. 1') was used for comparison between the published information and the material remaining in the collections (see Section 2.4.1). Davies' original nomenclature proved remarkably robust: no new species were discovered beyond those recorded by Davies, and the species lists simply required updating to the currently accepted names. The broad plant groupings used in his paper were therefore maintainable through the NMW collections study also, with the exception of the genus *Sphenopteris* (Brongniart)

Sternberg, which was impossible to discern in some cases between fern (Filicales) or seed fern (pteridosperm) in the Davies paper. This genus makes up a very small proportion of the total (0.4%), but is separated out in the analysis nonetheless.

2.3.2 Data preparation

After data collection, the first step was to standardise the data across the different sites, to achieve analytical consistency. This largely followed the process outlined by Cleal (2007) in which the most distinctive organ of each plant group was retained for analysis, omitting other organs of the same plant groups in order to prevent repetition through organ-taxonomy; it is common for the leaves, stems, seeds, pollen organs and other organs from a single plant to have different names so rationalisation was required. For lycopsids, stems were used as the most meaningful element (following Thomas, 2007), while for all other plants, foliage was used as these have the most well developed taxonomic schemes and record the greatest diversity. Following this process, seeds, cones and root taxa were omitted. Regarding the seeds and cones, accounts of each taxon are typically based on a handful of specimens from a single site, and these are often of unknown affinity and could belong to one of several kinds of foliage preserved at the same site. Regarding roots, in many cases these are of unknown affinity, and within the lycopsids mask a diversity of stem taxa through plesiomorphy in root morphology and organisation. Following the same logic, *Rhacophyllum* Schimper was also removed following Crookall (1976) who describes this as similar to *Aphlebia* Presl, and therefore uninformative. These two ‘form-genera’ (in older parlance of the ICBN – see Bateman and

Hilton, 2009; Section 4.1.3) denote irregular, highly variable leaves found during the developmental stage in ferns, but are not species specific. *Spiropteris* Schimper (from Bristol) is a morphogenus for early developmental stages of a fern frond and so also was removed.

As a second stage, and in order to avoid repetition, taxa under open nomenclature (e.g. *Cordaites* sp.), alongside others in the same genus identified to species level, were removed; it is here concluded that the specimens referred to as 'sp.' most likely represent any of the same species as identified from the assemblage, but which are incomplete or lacking distinctive features though imperfect preservation, and hence should not be counted twice.

The next stage was updating the species list taxonomically, with specific changes listed below:

Alethopteris aquilina (Schlotheim) Goeppert and *A. pseudoaquilina* Potonié are taxonomic synonyms of *Alethopteris grandinii* (Brongniart) Goeppert, a species endemic to the Saar-Lorraine Coalfield (Cleal, 2008). The specimens from Bristol-Somerset and South Wales that were recorded under these names belong to *Alethopteris ambigua* Lesquereux, a species that tends to have more slender pinnules (Wagner, 1968).

Alethopteris lesquereuxii Wagner has been reported from both the South Wales and Bristol-Somerset Coalfields (e.g. Cleal, 1978, 1997). However, Zodrow and Cleal (1998) have shown that the pinnule morphologies that characterise *A. lesquereuxii* and *A. ambigua* represent variation within a single species, for which *A. ambigua* is the earlier published and thus legitimate name.

Pecopteris miltoni (Artis) Brongniart (sometimes referred to as *Asterotheca miltoni* (Artis) Zeiller because of the form of the attached synangia) has been reported from both South Wales and Bristol-Somerset coalfields. However, these specimens have much more slender pinnules and more tapered ultimate pinnae than the type of *P. miltoni* and belong to a quite different species (Pšenička et al., 2009). This younger species is often referred to as *Lobatopteris vestita* (Lesquereux) Wagner (e.g. Cleal, 1978, 1997) although this name is not strictly resolved, and work on it is ongoing (Pšenička et al., 2009). *Pecopteris abbreviata* Brongniart from Bristol-Somerset is another synonym of this species.

Eupecopteris camertonensis Kidston (from Bristol-Somerset) is now *Lobatopteris camertonensis* (Kidston) Wagner (Cleal, 1978).

Pecopteris polymorpha Brongniart reported from both from the Bristol-Somerset and South Wales coalfields is now normally referred to as *Acitheca polymorpha* (Brongniart) Schimper (Zodrow et al., 2006). There were also museum labels referring to '*Asterotheca polymorpha*' but this combination has never been formally published.

Pecopteris cyathea (Schlotheim) Brongniart and *Pecopteris arborescens* (Schlotheim) Brongniart have both often been referred to the fossil-genus *Asterotheca* based on the form of the synangia. Following Mosbrugger (1983), however, they are now better referred to as *Cyathocarpus cyatheus* (Schlotheim ex Brongniart) Mosbrugger and *Cyathocarpus arborescens* (Brongniart) Weiss.

Pecopteris plumosa Brongniart has synangia of the type often referred to the fossil-genera *Dactylotheca* and *Senftenbergia* (Radforth, 1938). However, as the type of the fossil-genus *Pecopteris*, this species has to be retained within that genus.

Pecopteris unita Brongniart (Bristol-Somerset) is widely referred to as *Ptychocarpus unitus* (Brongniart) Zeiller (Cleal, pers. obs., 2011), although the nomenclatural position of that fossil-genus has not been properly resolved.

Cyclopteris fimbriata Lesquereux (Bristol-Somerset and Wales) refers to the basal pinnules of *Neuropteris* Brongniart (Sternberg) species (Zodrow and Cleal, 1988; Shute and Cleal, 2002) and in the present study they were found consistently associated with pinnules of *Neuropteris ovata* Hoffmann. These *Cyclopteris* records have therefore been removed from the database.

Dictyopteris obliqua Bunbury (Bristol-Somerset) is now *Linopteris obliqua* (Bunbury) Zeiller (Zodrow et al., 2007).

Lepidodendron obovatum Sternberg (from Bristol-Somerset and Wales) is now regarded as a taxonomic synonym of *L. aculeatum* Sternberg following the work of Thomas (1970) (see also Opluštil, 2010).

Neuropteris macrophylla Brongniart and *N. scheuchzeri* Hoffman (both Bristol-Somerset) are now both referred to *Macroneuropteris* Cleal, Shute and Zodrow (Cleal and Shute, 1995).

Neuropteris rarinervis Bunbury and *N. tenuifolia* Schlotheim ex Sternberg (Bristol and Wales) are referred to the genus *Laveineopteris* Cleal, Shute and Zodrow (Cleal and Shute, 1995).

Neuropteris microphylla Brongniart (from Wales) is correctly *L. rarinervis* (Bunbury) Cleal et al. (Laveine, 1967).

Neuropteris schlehanii Stur was recorded from the Pensford Colliery in the Bristol Coalfield. However, there have been no previous verifiable records of this species above the Langsettian Substage (see analyses by Laveine, 1967; Cleal, 2005, 2008; Tenchov and Cleal, 2010). The Pensford specimens are fragmentary but the small pinnules with an angular venation resemble *Laveineopteris rarinervis* (Bunbury) Cleal, Shute and Zodrow, a species also recorded from Pensford and that is well-known from other macrofloras of similar age in southwestern Britain.

Neuropteris heterophylla (Brongniart) Sternberg is similarly known normally from much older macrofloras (e.g. Laveine, 1967; Cleal, 2005, 2008). The specimens recorded as this species from the Bromley Colliery, Bristol, have dense venation that is very similar to *Neuropteris ovata*, which is widespread and abundant in the British macrofloras of this age.

Neuropteris acutifolia Brongniart is a later taxonomic synonym of *Macroneuropteris scheuchzeri* (Brongniart) Cleal, Shute and Zodrow (Laveine, 1967) and the latter name is thus the legitimate one.

2.3.3 Data analysis

Data were analysed at species level in three different formats in order to test the robustness of any signal apparent from the dataset, and also to investigate any detrimental effects from using dated nomenclature and systematic identification: (1) ‘raw’ as collected, (2) edited with nomenclatural updates detailed above, and (3) edited with updates and single occurrences of taxa removed. The data were entered into Microsoft Excel on collection, and formatted for analysis using the freely available PAST (PAleontological STatistics software package; Hammer et al., 2001). Cluster analysis and Detrended Correspondence Analysis (DCA) were chosen in order to try and extract similarities between the groups. Cluster analysis is commonly used for comparative studies such as these (e.g. Hilton and Cleal, 2007). Cluster analysis forces data into discrete groups along relative axes by emphasising between-group differences, and therefore highlights the relationships between the formed groups. In this study Raup Crick similarity coefficients were computed as the distance metric, and the analysis was carried out using the unweighted pair-group average algorithm, as this is recommended for community studies and especially for those where sample sizes may be imbalanced (Hammer and Harper, 2006). DCA is a popular ordination technique which seeks to maintain original correspondence between localities and taxa, and is therefore well suited to presence/absence data (Cleal, 2008). In contrast to cluster analysis, it emphasises within-group similarities (Shi 1993) in a two (or more) dimensional space. All variables (Q and R) can be plotted on the same graph, and they are distributed by calculated distance. Although this method showed some evidence of compression on Axis 2 (the ‘triangle effect’ discussed in Bush and Brame, 2010), the overall results, when tested against the other major ordination method used in palaeoecological studies, NMDS (Non-parametric Multi-Dimensional Scaling), were very similar and did not affect the patterns seen. Also, DCA has the advantage that it ordinates the original data rather than a matrix of distance measures, and thus provides a better contrast to the results of cluster analyses used in this study. In subsequent analyses in this thesis, the triangle effect was stronger and it was deemed easier to interpret NMDS plots, even though the results on each plot were essentially the same.

2.4 Results

2.4.1 Comparison of voucher collection with original diversity

The order of abundances of plant groups is not vastly different between Davies' published data and the subset of material at the NMW (Figure 2.5): pteridosperms, lycopsids and sphenophytes dominate, and sphenophylls are the smallest component. Pteridosperms at 62.8% (from the collections) and 61.8% (from the paper) are the most similar in relative abundance, but after this point the percentages of the respective plant groups vary widely. The totals from the NMW show evidence of bias: an over-representation of the more minor plant groups seen in the paper, probably a conscious effort to retain a viable collection of each of the groups regardless of true abundances. While this means that each species should definitely be represented, with enough specimens to allow a degree of systematic work, it does confirm that this museum collection cannot be used for accurate species abundance studies. Different museum collections will have had different collection regimes and agendas, and therefore be subject to different biases. Where these biases cannot be adequately qualified, tested and mitigated, presence/absence matrices are the only reliable way to analyse previously collected material for floristic purposes.

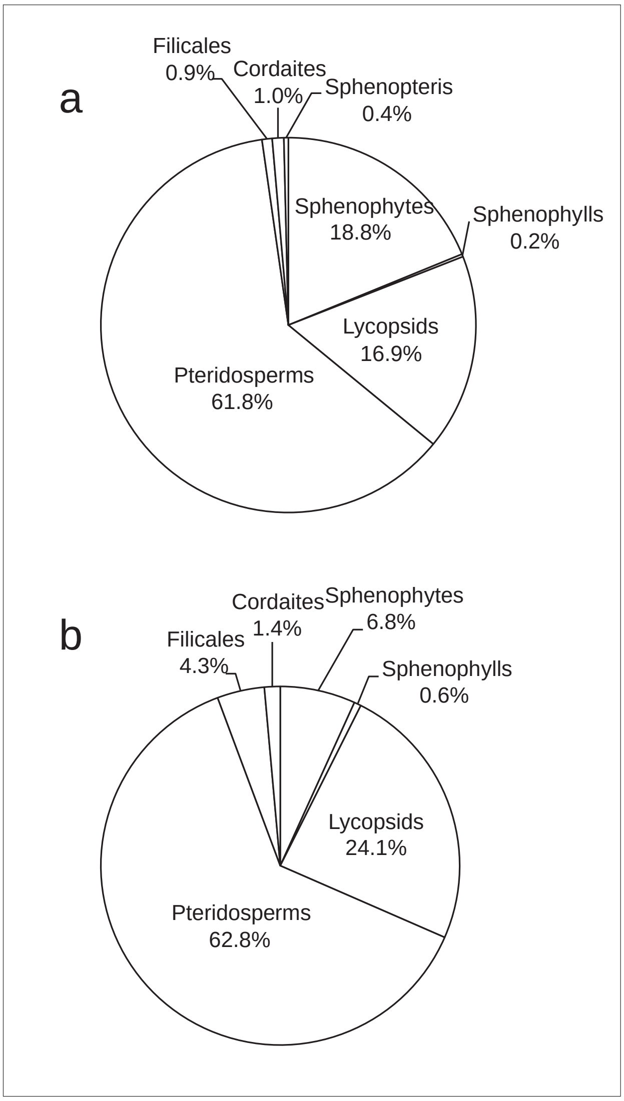


Figure 2.5: a) Davies' (1929) published data on the Llantwit No. 1 seam, comprised of over 11,000 specimens. Sphenopteris at 0.4% of the total, as documented by Davies, could be either fern or pteridosperm: unfortunately it is impossible to tell in the paper. Based on the material seen, it is most likely to be affiliated with the ferns (Filicales).
b) Data compiled from the collections at the NMW from the Llantwit No. 1 seam, comprising 634 specimens.

2.4.2 Cluster analysis

The three analyses give broadly similar topologies (Figure 2.6). The Welsh Pennant Sandstone (beds 4-11) tends to cluster together, and Llantwit Beds (1-3) for the majority, cluster together, with these being distinctly different from each other. Additionally, the contemporaneous Bristol-Somerset collieries and Welsh Llantwit beds form clusters on the same major axis in all analyses.

With the Pennant Sandstone Formation units from Wales, the clusters change position slightly between the three analyses, but the same basic patterns remain. Beds 7 and 8 either cluster together (Figures 2.6b + 2.6c) or in neighbouring groups (Figure 2.6a), and then as neighbouring groups to 6, 9 + 11 (Figures 2.6b + 2.6c), or 8 + 4 (Figure 2.6a). Bed 10 is a neighbouring group to 6 + 7, and 8 + 4 (Figure 2.6a), or an outlier (Figure 2.6b), or nested amongst (Figure 2.6c) the 6, 11 + 9, and 7 + 8 clusters. The other beds of this age from Wales (4 and 5) do tend to occupy different positions within the plots. Seam 4 is only in an unexpected position (clustered as identical to bed 8) in one analysis (Figure 2.6a). Seam 5 also changes position considerably within the analyses, although again it is most consistently placed in Figures 2.6b and 2.6c, suggesting that its cluster with the Pennant Sandstone material and Dunkerton Colliery (both from Bristol-Somerset) is relatively sound.

The Bristol-Somerset collieries retain some consistent associations across the analyses. The collieries that are stratigraphically unresolved (i.e. the precise coal seam extracted was not recorded; Pensford, Ludlows and Old Mills, triangle symbol) appear to be of Farrington Member affinity, either lower (square symbol) or middle (cross symbol),

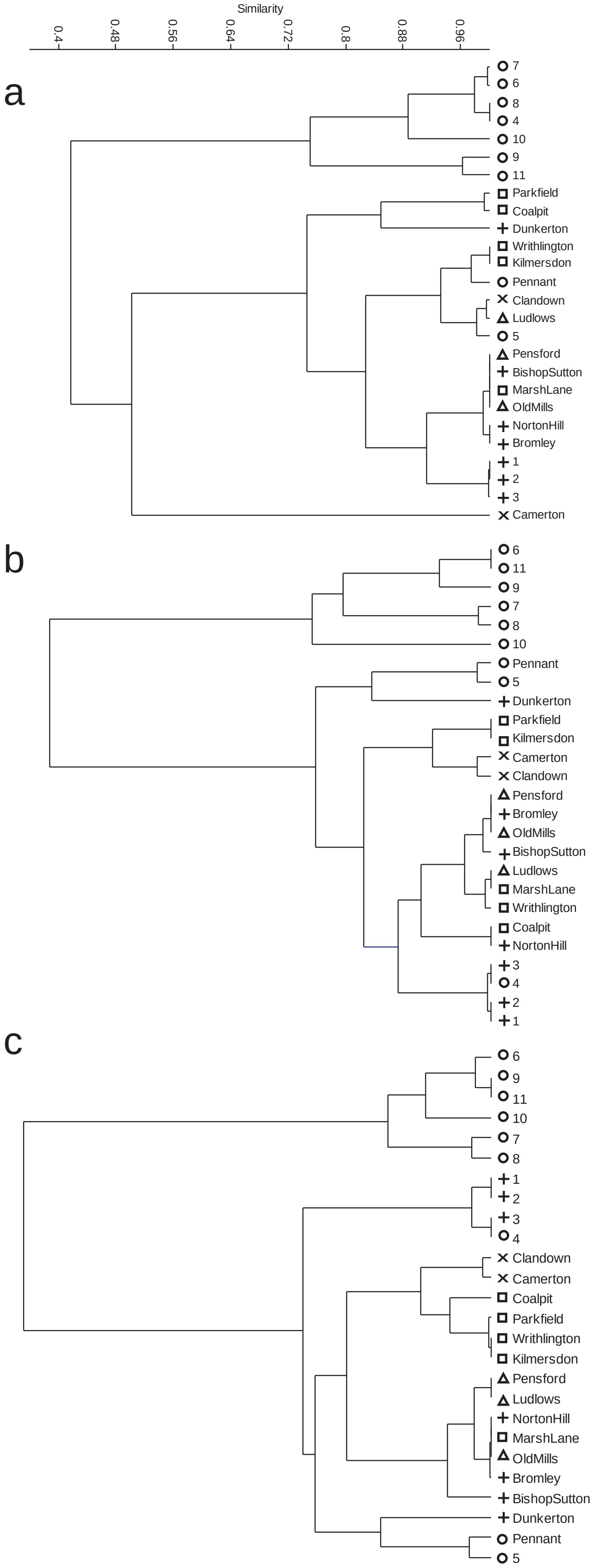


Figure 2.6: Raup Crick cluster analyses; see Tables 2.1 and 2.2 for seam names and Figure 2.2 for stratigraphic symbols.

a) Raw data,
b) Updated taxa list,
c) Updated taxa list with singletons removed.

on each analysis. The lower Farrington Member collieries are split to varying degrees on each analysis, and cluster with middle Farrington Member and mixed collieries (Figure 2.6a); or lower Radstock Member (‘x’ symbol), middle Farrington Member and unresolved collieries (Figures 2.6b and 2.6c). Again, Figures 2.6b and 2.6c are most similar in the clusters produced, although as discussed there is a degree of interspersal of the lower and middle Farrington Members. The Pennant Sandstone Formation and Dunkerton Colliery association also move around through the clusters, but again seem to be most similar to seam 5 from Wales (as in Figures 2.6b and 2.6c).

There is a stratigraphic signal carrying through all results, with Cantabrian, Asturian and Bolsovian age seams and collieries mostly clustering together, but with a few differences between analyses as discussed above. This is also due in part to the imbalance of stratigraphical ranges between the Bristol-Somerset area and South Wales. There are many more, well-sampled sites from the Pennant Sandstone Formation of South Wales than there are from the Bristol-Somerset area, and so South Wales therefore yields a larger and more continuous data sequence. The clusters and general topology are most similar between Figures 2.6b and 2.6c, suggesting that taxonomic updating is important in reflecting true relationships between plant groups and ensuring a realistic signal results from analyses. Also, removing the singleton taxa in Figure 2.6c appears to refine the patterns further, for the most part grouping those horizons of similar stratigraphical age, although not necessarily as neighbours with those either side of them. Most notably, the Welsh Llantwit Beds are moved from clustering within the Bristol-Somerset collieries, to being a neighbour to them.

2.4.3 Detrended correspondence analysis

In each plot, the Pennant Sandstone association from Wales forms a prominent association, as do the lower and middle Farrington Member collieries from Bristol-Somerset (square and cross symbols, respectively). However it is possible to make a division between data points from Bristol-Somerset and from Wales. This can be compared to the cluster analyses, which seem to be promoting stratigraphical groupings over geographical ones. The stratigraphically unresolved Bristol-Somerset collieries (triangle symbol) again could be of either lower (Figures 2.7a and 2.7b) or middle Farrington Member age (Figure 2.7b). The lower Radstock Member collieries (Camerton and Clandown, ‘x’ symbol) do not seem to have an affinity with any of the groups, and the Bristol-Somerset Pennant Sandstone Formation is also well separated, especially in Figure 2.7b. Notably, on all three plots, the middle Farrington Member and the Welsh Pennant Sandstone Formation (circle symbol) are skewed by Dunkerton Colliery and seam 5 respectively. These were also anomalous, and grouped together in the cluster analyses, reinforcing their unusual taxonomic composition.

Points from each respective stratigraphical category do form distinct groups, with relatively low separation of the constituent points. The plot using updated taxa (Figure 2.7b) again are in the closest agreement, suggesting that this is the most important step in data editing before analysis. However, removing the singly occurring taxa (Figure 2.7c) has a negligible effect on the plot arrangement in comparison to Figure 2.7b (with all taxa included), although the data spread in the individual groups is smaller. The largest data overlap is seen amongst the Bristol-Somerset collieries, and this could perhaps be expected in the light of the degree of swapping of them in the cluster analyses.

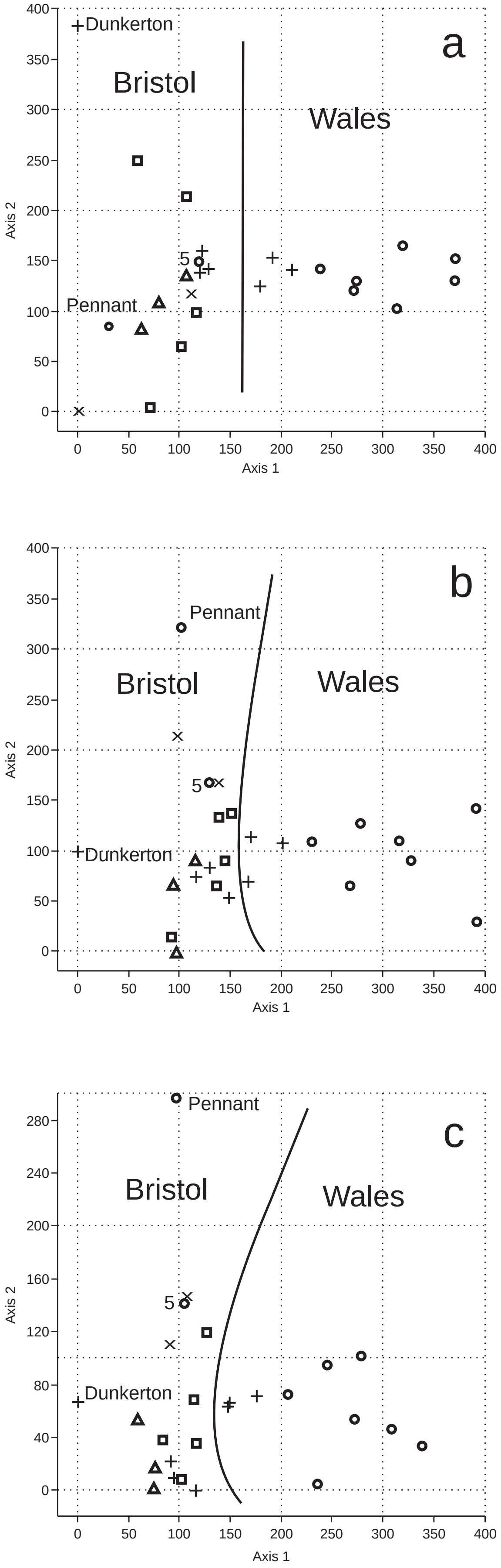


Figure 2.7: DCA plots: see Tables 2.1 and 2.2 for seam names. Figure 2.2 details stratigraphic symbols: triangle = unresolved collieries; square = lower Farrington Member; plus sign = middle Farrington Member; cross = lower Radstock Member (Bristol-Somerset). Circle = Pennant Sandstone Formation; plus sign = Llantwit Beds (Grovesend Formation) (Wales).

a) Raw data
b) Updated taxa list
c) Updated taxa list with singletons removed.

2.5 Discussion

2.5.1 Data format

Cross-referencing both forms of analysis, it would seem that the most important step in data preparation is to update taxon names. This serves to reduce synonymy and increase the precision of the species names concerned, which in turn feeds into a more accurate picture of the vegetation and the ecological information it entails. For both cluster analysis and DCA, all analyses produced similar patterns, but updated names, which consolidate and reduce the numbers of variables, do appear to strengthen signals and rearrange data points into a more logical order (either stratigraphically (e.g. Figure 2.6b) or geographically (e.g. Figure 2.7b). Taking those analyses as closer representations of ancient vegetational patterns therefore, and looking at the unedited analyses in comparison, shows the same basic patterns but with a little more noise. Inevitably there will be instances of taxa that have not been revisited for many years and will require some reclassification in the future, but it is reassuring to see that they would not necessarily obscure patterns in the data - certainly if those taxa are not core to the dataset. Clearly the underlying evolutionary and ecological affinities of these plants do have a bearing on the similarities of these subtly different facies through time and space, although interpreting these associations in the notoriously incomplete fossil record is very difficult.

Removing singleton taxa seems to refine the patterns, as seen in Figure 2.6c, although this is not necessarily borne out by Figure 2.7c. However, cluster analysis promotes separation and so is more likely to be skewed by singleton taxa. Singly occurring taxa could be either representative of rare taxa in the assemblage, or misidentified anomalies. Because of the relatively small differences between results with singleton taxa included and removed, and because the overall aim is to assess linkages of migrating communities through time, which will inherently involve new, initially marginal species, it is perhaps best to run data both with and without singleton taxa, if appropriate. The former analysis may promote linkages; and the latter may promote associations within and between datasets. Overall, in a global scale dataset, any effect singleton taxa may have may be overridden in any case, as although any database is subject to future improvement in quality and quantity, the signal generated from it at any one time is unlikely to change to a significant degree (Benton, 1999).

2.5.2 Stratigraphical signal

There are strong stratigraphical groupings through all analyses, with the Llantwit Beds data points from Wales and the Grovesend Formation data points from Bristol-Somerset clustering as sister groups, to the exclusion of the Pennant Sandstone Formation-aged beds from Wales, in cluster analysis. DCA ordination is not as striking, but does show beds of the same age ranges grouping together. Alongside the fact that many of the pairings in the cluster analyses are between beds that are not non-adjacent stratigraphically, this suggests discrete assemblages present within the lithostratigraphic members and through the Pennant Sandstone Formation, that are not necessarily evolving sequentially through them. This could be a reflection of localised heterogeneity, but also the dynamic nature of each species association as it tracked persistently present, but spatially shifting, habitat conditions in and out of the specifically sampled areas (Bashforth et al., 2011).

Three data points appear to be anomalous: Welsh seam 5, and Dunkerton Colliery and the Pennant Sandstone Formation material from Bristol-Somerset. They cluster together, separately from their respective stratigraphical and geographical sources, and skew group associations in DCA analyses. These three points share a low taxonomic richness, ranging from 3 to 7 taxa across the three input datasets for the three points. This is clearly significant as it causes the points to disengage from their predicted positions, but as the Bristol-Somerset data was compiled from a museum collection, it is only possible to investigate in detail seam 5 from Wales to attempt to explain this issue.

The resultant position of seam 5 (and the Pennant Sandstone Formation association) could simply be due to it being rather separated from all other seams stratigraphically (Figure 2.2) at lower- to mid-Asturian age, or as a transitional horizon formed in the midst of the floral turnover in exceptional conditions. Figure 2.8, compiled from Davies' (1929) species abundance tables (from these it is not clear whether *Sphenopteris* is referred to ferns or pteridosperms as this information is broken down separately) shows that seam 5 is markedly different from those either side of it. Firstly it yielded only a relatively small number of specimens in comparison to preceding and succeeding seams, perhaps continuing a transitional trend that began in seam 6. Secondly and perhaps most significantly, seam 5 contained the highest single percentage of lycopsids – 43% – in comparison to all other seams. All other seams contained up to 5% lycopsids (with the exception of seam 1, which had 15%). Also, the seams above show a

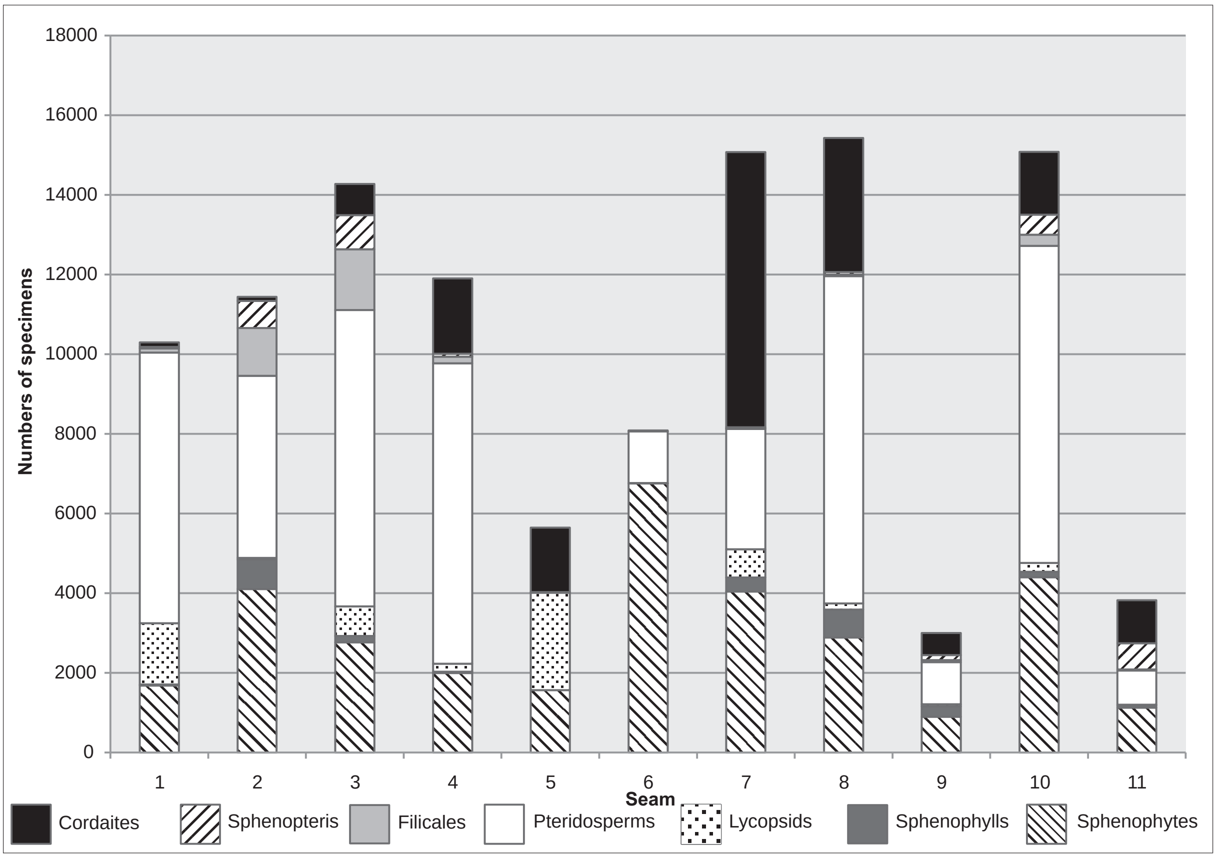


Figure 2.8: Numbers of specimens in different plant groups as recorded by Davies (1929).

change to fern and pteridosperm dominance (*Sphenopteris* is most likely fern type foliage in Davies' notation), again in keeping with the major floral turnover and mixing at this time (DiMichele and Philips, 1996). However, the reason for the elevated abundance of lycopsids in seam 5 before or at this turnover is difficult to envisage. Davies himself (1929) identified the anomaly, but merely used a rather circular argument, based on the abundance of lycopsids, to ascertain that there was a 'brief episode of wet flora' (p. 149), where 'swampy conditions prevail, with lowland of dry and damp conditions almost evenly balanced' (p. 139). A sudden relative drop in land level is implied, although there appears to be no lithological evidence for this, and no localised faulting in the area, on the current scale of mapping available (Figure 2.3). The most likely explanation is that it is a taphonomical artefact, representing a more time-averaged, localised stand of lycopsids with some washed-in clastics and other, drier adapted taxa masking the slightly different environment of this particular horizon as collected. The spatial coverage of the original sample may not have extended beyond this localised area. This highlights the importance of analysing as wide a spatial and temporal range of data as possible, to mitigate any effects from sampling or taphonomical bias over the coverage of the dataset.

2.5.3 Geographical signal

In the cluster analyses conducted, while the data points changed position to a degree, the overriding control appeared to be stratigraphic age, with geographic area as a secondary control. This suggests a generation of the swamps from the same floral stock for both basins, possibly implying a historical linkage at a critical time, and that it is reasonable to refer to the Bristol-Somerset area and South Wales as part of the overall same basin. Because the DCA plots (Figure 2.7) show the horizons within the Llantwit Beds as a separate group, it is difficult to assess the relative proportions of geographical and stratigraphical control. Figure 2.7c shows a slight overlap of the Welsh Llantwit Beds and Pennant Sandstone Formation beds, but there is also overlap of the Bristol-Somerset lower Farrington Member collieries and the Welsh Pennant aged data points.

2.5.4 Stratigraphical versus geographical influence

Cluster analysis promotes separation of groups, and therefore has highlighted the differences in flora through the stratigraphical column, with the apparent late Moscovian turnover forming a framework for this. DCA however allows the data to be viewed in ordination space, seemingly indicating geographic separation as more important. These basins in fact appear overall to be relatively stable, with a background level of evolutionary turnover accounting for subtle differences in the flora through time, and a small degree of difference due to geographical separation, presumably due to the localised, dynamic conditions promoting opportunism in the general ecological template as to which taxa specifically grew where.

2.5.5 Regional context for observed floristic changes

The difference between the macrofloras of the Pennant Sandstone, and of the Grovesend and Llantwit Beds apparent in some analyses is a manifestation of the well-known mid-Asturian vegetation change seen in western Europe and the Canadian Maritimes: in the macrofloras, it is identified as the base of Zone I in Dix (1934) and the base of the *Lobatopteris vestita* Zone in Wagner (1984), Cleal (1991) and Cleal and Thomas (1994); in the palynofloras, by a marked increase in abundance of marattialean spores such as *Thymospora obscura* (Kosanke) Wilson & Venkatachala, a biohorizon recognised as the base of the OT Zone of Clayton et al. (1977). This in turn is part of a general shift in the composition of the coal swamp vegetation, from being dominated by arborescent lycopsids to marattialean ferns, and associated with an increase in global temperatures (Gastaldo et al., 1996; Cleal and Thomas, 1999, 2005). In the original model, based mainly on evidence from the westernmost Euramerican coal swamps (the Appalachian and Interior coalfields of the USA) the turnover from lycopsid- to marattialean-dominated vegetation appeared to be abrupt at the Moscovian – Kasimovian boundary (Phillips and Peppers, 1984; Phillips et al., 1985). However, a more recent analysis has suggested that the change was diachronous, being earlier in eastern Europe (Bolsovian times), than in western Europe (late Asturian – early Cantabrian times), and then occurring in the USA (late Cantabrian times) (Cleal et al., 2009a). Moreover, in most areas the vegetation change was gradual, with a clear transitional interval of mixed lycopsid – marattialean fern vegetation. The appearance of *L. vestita* Zone macrofloras in the Grovesend and Llantwit beds represents the first development of this transitional mixed lycopsid – marattialean vegetation in the study area. However, nowhere in Britain do we see clear evidence of the fully-developed marattialean-dominated coal swamp vegetation, such as seen in the Upper Pennsylvanian of the USA.

2.6 Summary

Museum collections are becoming increasingly important in ecological and biostratigraphic studies, as computing and programming power has advanced to allow the easy input and analysis of large volumes of data, such as those from digitised collections. This study has shown that these collections, unless detailed provenance and collecting history states otherwise, cannot reliably be used for accurate species abundance studies. However, presence/absence data in these cases is usable, and can produce meaningful results.

Presence/absence matrices are an effective way to analyse floristically large and diverse plant communities, and the most consistent results are achieved by updating taxonomic nomenclature to reduce redundancy and increase validity, and then removing singly occurring taxa, which would seem to eradicate misidentified outliers. However these outliers could in some cases be valuable in recognising linkages between disparate communities. Presence/absence matrices will be used throughout this thesis in the manner detailed above.

This study has used a robust methodology for comparing plant communities, and has raised some points regarding the extension of a dataset across larger tracts of time and space. Depending on the resolution used (taxonomically, geographically and stratigraphically), localised patterns may be absorbed but should not be ignored when considering any ‘noise’ within the data.

The Bristol-Somerset and Wales seams and collieries tend to associate into Bolsovian and Asturian-Cantabrian groups. This is the development of a transitional mixed lycopsid – marattialean vegetation, in the midst of the protracted east-to-west turnover event (lycopsid- to marattialean-dominated) on the Euramerican continent around the end of the Moscovian.

The different analytical methods used highlight underlying controls on small assemblage differences, but overall there is little evidence to separate the two geographic areas. A united south-west England basin is therefore supported (Calver, 1969), and would likely fall out as such against the backdrop of a wider database; see Chapter 5. This suggests a common floral source for the two basins, probably due to a degree of linkage at some point before the Bolsovian (the oldest time period considered in this study) and perhaps even at regular intervals since that time. This is plausible given the proximity of the area to active tectonism, and the regionwide deposition of lithologies such as the Pennant Sandstones (Waters and Davies, 2006). The stability and consistency of the flora in this region supports the findings of DiMichele et al. (1996) and Willard et al. (2007), who proposed general stasis and continuity of these ecosystems through long intervals of time and space; also see Section 3.1.3.

-CHAPTER 3-

PHYTOGEOGRAPHIC CONNECTIONS OF THE NORTH CHINA BLOCK

3.1 Rationale

In order to be able to make meaningful analyses of the global dataset, it is necessary to examine the North China area in more detail. The aim is to uncover regional patterns, the implications of which will then be used to feed into the interpretation of global patterns revealed in Chapter 5.

This chapter uses statistical ordination to shed new light on the relationships, influences and interactions of the (north) Cathaysian flora as it developed on the North China block. For the first time, detailed numerical analysis is carried out on large collections of macrofloral adpressions, sourced from original museum inventories where possible, spanning three of the modern provinces which cover the majority of the ancient eastern North China tectonic block (Hebei, Shanxi and Henan), and Gansu, which serves as a snapshot of the lesser studied western section of the block.

3.1.1 Geological setting

Four major tectonic domains - each with a complex accretionary history - make up China as it is today, alongside a multitude of smaller ones. The main domains, from north to south, are the Junggar-Hinggan (part of the Angaran phytogeographic realm), Sino-

Korean-Tarim (mainly consisting of the North China block), the South China block and the Southern Xizang (Tibet)-Western Yunnan (part of Gondwana) (Figure 3.1; Li and Wu, 1996). These blocks accumulated during the amalgamation of Pangaea, and are a collage of cratons and orogens (Kusky et al., 2007). The approximate positions of the North and South China microcontinents during the Pennsylvanian can be seen in Figure 1.2a, with the remaining Angara section as found in modern China being composed of the Central Asian Orogenic Belt, which was a series of accretions of tectonic units formed over a 750Ma period (Windley et al., 2007), and the Gondwana section, which consists of a series of small islands rafted off from the northern margin of Gondwana during the late Palaeozoic (Metcalfe 2006). The Xu-Huai-Yu Subprovince was proposed by Mei et al. (1996) as a long-lived depression towards the south of the North China block. In a wider context, it is part of the Qingling-Dabie suture zone between North and South China (Kusky et al., 2007), and as such its palaeogeographical relationships are not clear cut.

The North China platform was formed in the Archaean. The basement of the present area mainly consists of the Eastern and Western blocks, which collided at 2.5 Ga, separated by the Central Orogenic Belt (Kusky et al., 2007). Following this, North China was a large, stable microcontinent through much of geological time, being covered by an epicontinental sea during the early Palaeozoic. The area was uplifted in the Ordovician, during the early stages of Pangaea amalgamation (the 'Caledonian' orogeny; Wang, 1986), resulting in nondeposition across the whole block during the Silurian and Devonian. By the Carboniferous, paralic conditions had encroached due to transgressions from the northeast and northwest, and these dominated until the end of the Permian (Liu, 1990). Coal formation began with the Pennsylvanian Benxi (Penchi in old spelling)

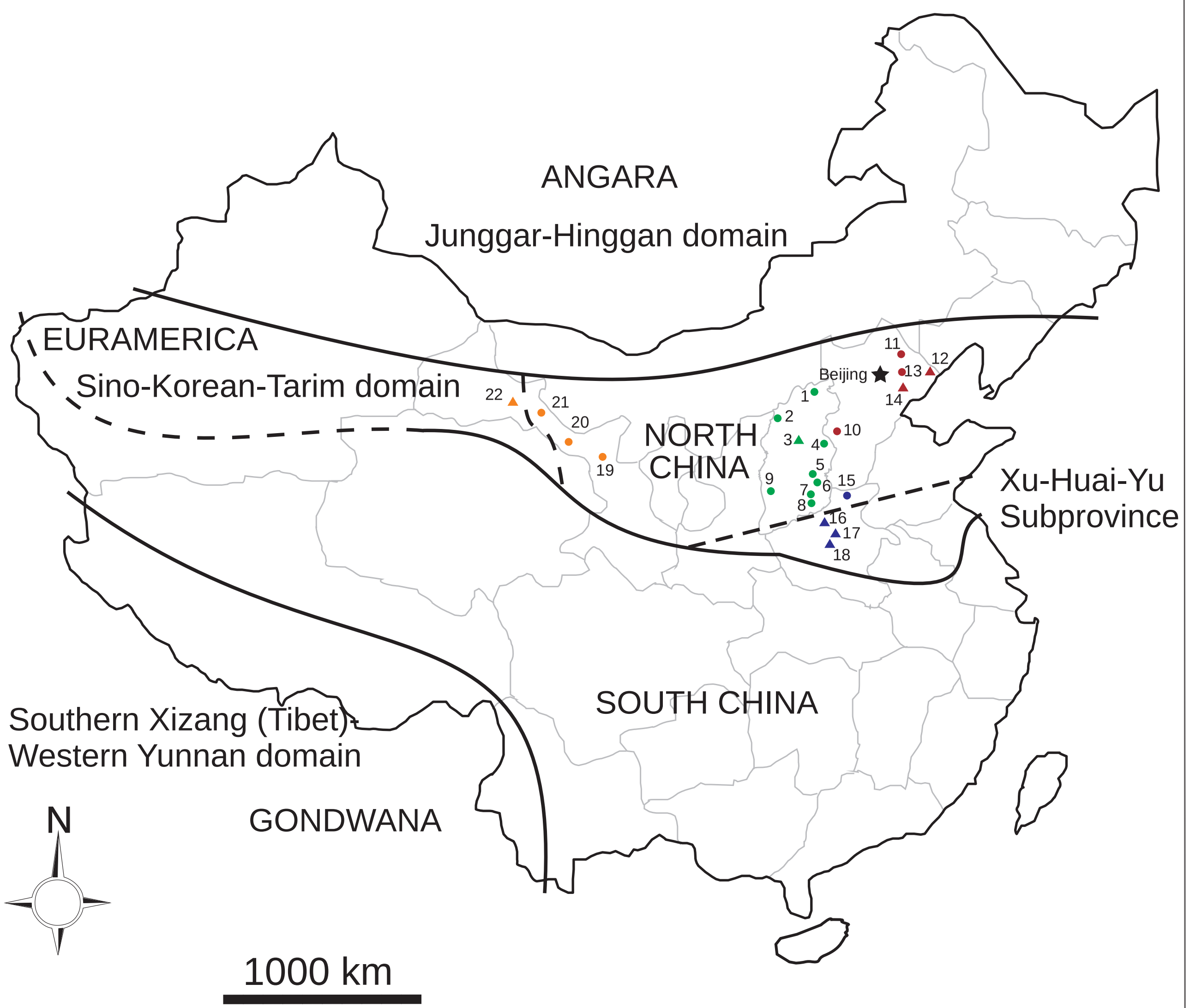


Figure 3.1: Locations of the Chinese sites in the study. Colour coding matches that on Figures 3.3-3.5.

SHANXI
1 Datong
2 Baode
3 Taiyuanfu
4 Pingding
5 Xiangyuan
6 Lucheng
7 Gaoping
8 Jincheng
9 Xiangning

GANSU
19 Wuwei
20 Minle
21 Gaotai
22 Suzhou ‘C’
22a (unmarked) Suzhou, age unknown

● Locality
▲ Locality with known age(s)

HEBEI
10 Jingxing
11 Chngde
12 Shi Men Tzai
13 Zunhua
14 Tangshan

Surrounding Tangshan are the unmarked localites of
14a Chao Ko Chwang,
14b Hung Ho,
14c Tang Chia Chwang,
14d Linsi (known ages), and
14e Majiagou (age unknown).

HENAN
15 Anyang
16 Daping
17 Yuzhou
18 Pingdingshan

Surrounding Daping are the unmarked localities of
16a Pochi,
16b Dengcao,
16c Magou (all with known ages).

Capitals on the figure are phytogeographic provinces, sentence case are tectonic domains. Locality numbers match those on Figures 3.3-3.5.

Formation towards the north of the region (Li et al., 1995), but had shifted towards the south by the Guadelupian, due to ongoing collision with the Central Asian Orogenic Belt (Junggar-Hinggan domain/Angaran realm) (Liu, 1990). Geochemical evidence shows that this event was protracted over 300-250Ma, forming the Solonker suture zone between North China and Angara (Jian et al., 2010), and marking the closure of the Palaeoasian Ocean (Kusky et al., 2007).

3.1.2 Correlation

Because of its complex history, and the sheer size of the landmasses involved, detailed stratigraphic correlation of terrestrial rocks across large areas of China has traditionally been difficult, although it has been attempted (Wu, 1995; Jin et al., 2003; Wang and Jin, 2003; Bond et al., 2010). The present study incorporates the well-studied material of Halle (1927) from Shanxi province, and high-resolution stratigraphic ranges and environmental information are given in Stevens et al. (2011). Detailed age data are not available for the remaining majority of flora in the study and therefore it is not possible to attempt in-depth biostratigraphical classification and correlation. However, it has been possible to approximate a correlation between the four study areas, as the section around Taiyuanfu, studied by Halle, has been adopted as the stratotype for the late Palaeozoic in North China, as well as the type section on which the Cathaysia flora is based (Li and Yao, 1982). Therefore, studies of the North China block at this time are often tied into Halle's lithostratigraphic framework, because his was the first to align large and detailed floristic study with stratigraphy (that of Norin, 1922). This system allows localised correlations, to time bins based on Halle's formations (Figure 3.2), but does not incorporate the diachronous nature of several of the units, or detailed lateral changes in facies and stratigraphy. Liu (1990) gives an excellent overview of the regional developments on the North China plate through the whole time period covered here, detailing the combined effects of palaeogeography, palaeoclimate and plate tectonics. The Henan area further south is slightly different, with the fluvio-deltaic Shanxi Formation contemporaneous with the marine Zhutun Formation in Henan, although there are sparse bands within it containing plant fossils (Yang, 2006). Yang warns against extrapolating Halle's formation names to the area, but nonetheless the rest of the stratigraphic sequences of the two provinces are broadly similar, with successions of fluvio-deltaic to lacustrine sediments, and the two systems have been temporally correlated in Yang's publication.

Two-thirds of the material from Gansu is derived from Bexell's collections from the Sino-Swedish expeditions in the early 1930s (Bexell, 1945), but unfortunately only 20% of this material has accompanying information tying it into Bexell's working stratigraphy, which has since been widely criticised and debated. All of this material is listed as from Zone C, which is somewhat enigmatic in age, being definitely younger than Bexell's Zones A and B (Benxi-Shanxi Formation age, and Lower-Upper Shihhotse Formation age respectively; Halle, 1937), but containing a mixture of traditionally Angaran and Cathaysian flora (Li and Yao, 1982). This suggests synchroneity rather than succession of the Angaran and Cathaysian floras, and furthermore this mixture consists of characteristic species of wide temporal and geographic ranges, further confusing the possible affinities of the flora. Durante (1992) gives an account of the evidence, and at

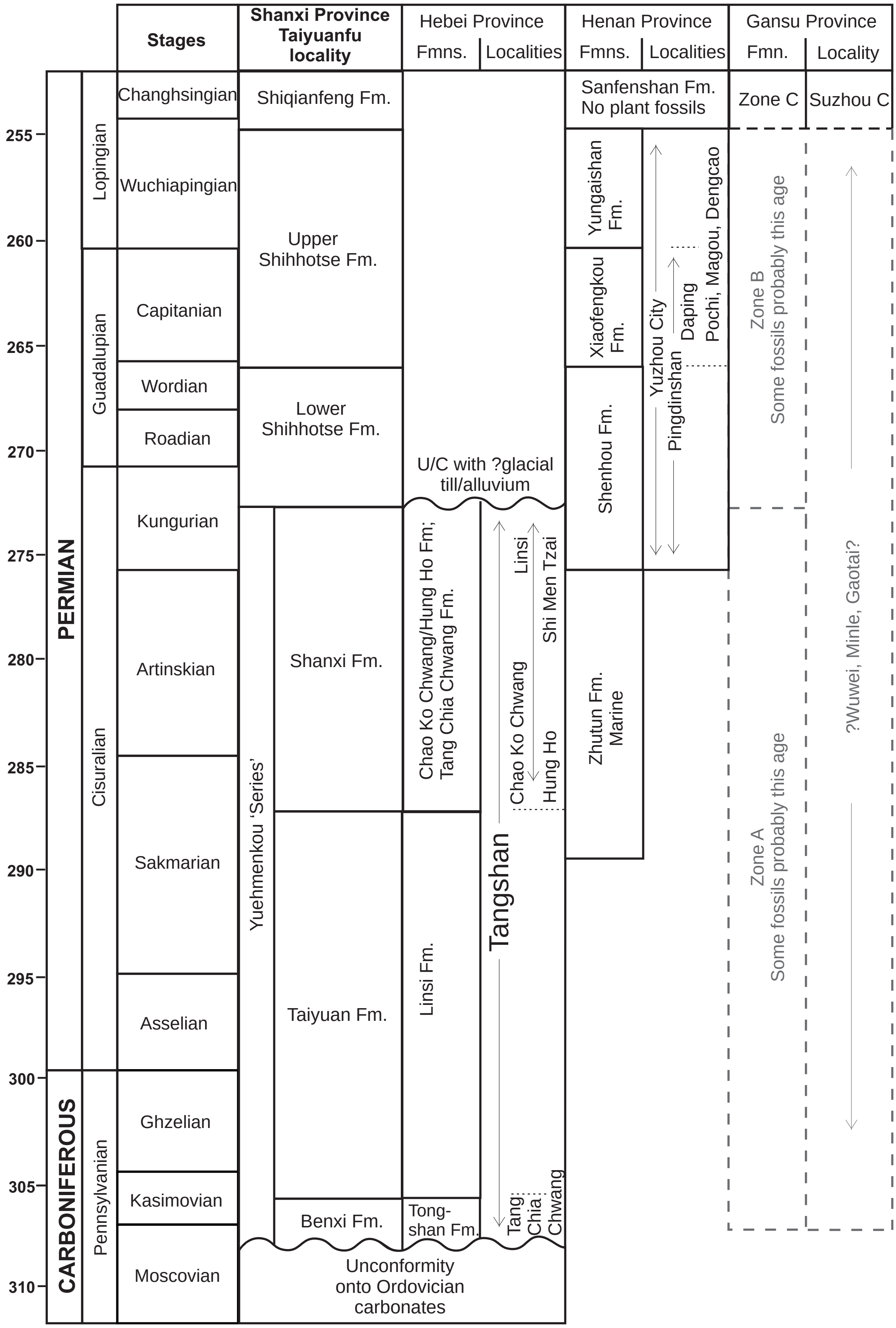


Figure 3.2: Lithostratigraphy of Shanxi province at Taiyuanfu locality (from Halle, 1927; Norin, 1922), used as the base for correlation with other provinces in the study. Additional data from Stockmans and Mathieu (1939, 1957); Yang (2006), Durante (1992), Halle (1937). Bexell's Zones in Gansu are included, but the exact provenance of much fossil material in Gansu could not be determined; see text.

this time it seems the flora of Zone C is most likely to be of latest Permian age, equivalent to Halle’s Shiqianfeng Formation (Figure 3.2), and possibly more closely related to flora on the Russian platform further west.

3.1.3 Floral migration

The overall question of this thesis, whether the palaeoequatorial wetland plant communities in Euramerica are demonstrably closely related to those in north China, encompasses a multitude of tectonic blocks across the considerable distance between these areas. Clearly, for the same taxa and communities to be found in both areas, from the same floral stock, a substantial amount of migration would be involved, across these tectonic blocks. Active migration of species is a first-stage reaction to ecosystem disturbance or upheaval, as organisms seek to track favourable habitats (DiMichele et al., 2004; Lieberman et al., 2007). This would have been in effect on a local to regional scale as communities reacted to stresses from extrinsic factors such as habitat loss and climate changes (Cleal et al., 2009a; DiMichele et al., 2010). Overall however, the wetland plant community structure was very stable over long periods of time (DiMichele et al., 2002; Willard et al., 2007), reflecting effective migration processes and widespread occurrence of stasis in the fossil record (DiMichele et al., 2004). The key to this stability, as viewed through the lens of the long-term fossil record, appears to lie in the very fact of the sheer geographic coverage of these ecosystems. Stable individual lineages were usually those which were abundant, widespread and participants in many local ecosystems (Lieberman et al., 2007). Wetland plant communities and their constituents were nested in local- to regional-scale ecosystems (DiMichele et al., 2007), and this, along with their vast overall coverage, probably served to effectively constrain species innovation over the long term through a mosaic of geographical coevolution (Eldredge et al., 2005).

While the wetland community ecosystems were for the most part conserved, they nonetheless could not fail to be affected by their global distribution across the jigsaw of tectonic blocks at different latitudes. On the scales investigated by this thesis, the two main biogeographical processes likely to become evident are vicariance (or indeed original separate evolutionary lineages) and (geo-)dispersal (Lieberman, 2005). In a broad sense, these are controlled by the presence or absence respectively, of tectonic, climatic or other barriers, to the free movement of populations across any given area. Vicariance involves the separation and isolation of species populations by a physical or environmental barrier (such as a seaway between two tectonic blocks), and subsequent divergent evolution and speciation, while dispersal is the geographic expansion of species ranges in the absence of barriers (Lieberman, 2005.)

If there are no barriers to population movement then, i.e. that there are areas of favourable habitat to be colonised, dispersal into these areas can be expected. While many of the members of these ecosystems reproduced with spores, which can be carried on the wind for great distances (Barrington, 1993), a significant proportion of the communities were seed producers, such as the pteridosperms. These relatively large structures required habitable land areas in order to migrate (Laveine et al., 1993), and would have limited the whole ecosystem to land-based dispersal. Faunal methods of floral dispersal and pollination may have been in existence by the late Palaeozoic, but would again have been limited to land (Labandeira, 1998).

If there were viable connections across from Euramerica to north China in the late Palaeozoic, these would have had to be habitable land bridges, occupying a favourable climatic belt, and with the optimum environmental conditions to support these swampy ecosystems. This would appear in analysis as a closely related and essentially unbroken continuum of wetlands across linked geographical areas. In contrast, if barriers between areas were dominant, because of the separation of tectonic plates, destruction of physical environment, or the movement of a corridor into an unfavourable climatic zone, one would expect vicariance and (allopatric) speciation, precipitating noticeable differences between analysed areas. Where repeated connection and disconnection of areas may have occurred, meaning species effectively reinvading an area, they could quickly naturalise with little negative effect on the native species, as long as there was overlap in required niche space, and there was no appreciable fitness advantage in the invader (MacDougall et al., 2009). This would have a further stabilising effect on wider scale wetland communities, as discussed above, as well as quickly overriding any divergent evolution deriving from previous disconnection, or even similar communities which were newly juxtaposed. These patterns are of course idealised; there are many filters involved in the process of studying once-living communities through preservation, collection and collation (see Section 2.4.1), and these will all have served to partially remove or conceal original patterns, requiring a degree of interpolation to reveal them.

This discussion is taken up in Section 5.1.1, concerning the palaeogeographic maps used in this thesis (Figures 1.1-1.2).

3.2 Material and methods

The methodology from Chapter 2 (King et al., 2011) was used, building a taxa-by-localities presence-absence matrix, based on original museum databases transcribed from specimen labels (Shanxi, Hebei and Gansu provinces), and monographs on the respective flora (Shanxi, Hebei, Henan). The material was chosen as having a sufficient quantity of identified/identifiable taxa for a large scale comparison of this nature, but most importantly because it was derived from expeditions by well-respected taxonomic palaeobotanists, and as such was well curated and accessible, with material and/or plates avaliable to view. Examining original material allowed the consistency and feasibility of identifications to be informally assessed, but the vast number of taxa involved meant that it was impractical to undertake a systematic review of all the material. However, taxonomic issues were shown by the methodological study (Section 2.5.1) not to have an overriding effect on results and patterns, and furthermore any possible effects from these were mitigated in this study by using material identified by prolific and historically vindicated palaeobotanists, and by analysing flora at genus (as opposed to species) level. Stratigraphic information was not available for the majority of localities, but those sites were retained nonetheless as they contained many thousands of records and could inform on geographical patterns, and provide more data surrounding those points which did have full records. It is likely that undated material is of similar provenance to that around it, as most collections are made up from only a few collectors' endeavours. Additionally, including data from different localities ensures a better coverage of data, as individual localities will have had their own taphonomic and sampling constraints, and so analysing proximal localities should mitigate this; see Section 2.5.2.

3.2.1 Shanxi

Halle's 1927 work on the Shanxi (Shansi in old spelling) flora, covered by the Taiyuanfu locality in this study, remains the most detailed and comprehensive volume on Northern Chinese floras, and this was used in conjunction with his original museum collections in the Naturhistoriska Riksmuseet (NRM) in Stockholm, consisting of 2838 specimens. The NRM collections also contain many thousands more fossils from Shanxi and other provinces, sourced from the Sino-Swedish expeditions of the 1920s and 30s, and these were incorporated into the study using the museum-created database. Many localities were difficult to ascertain on modern-day maps. They had been transcribed from original museum labels, many of which were over 90 years old, and had themselves been translated into Pinyin, and thereby lost the original Chinese subtleties in descriptive place naming which could have given more clues and detail as to exact locations. There was also no specific stratigraphic information provided with the specimens, other than variations on 'Carboniferous to Permian'. However, because of the sheer weight of data involved (3996 specimens originally before data preparation detailed below), it was decided to keep these sites in the study, in order to give a greater spread around the central and high-resolution Taiyuanfu area studied by Halle (Figure 3.1). The vast majority of the NRM collections from the ancient North China block covered Shanxi province (6834 specimens including those of Halle), with a few localities in Hebei (3844 specimens before data preparation) and one (Anyang) in Henan (1384 specimens before data preparation).

3.2.2 Hebei

Data was sourced from the monographs of Stockmans and Matthieu (1939, 1957), and again original collections were examined, at the Royal Belgian Institute of Natural Sciences (RBINS), Brussels. The original museum database for the material contained 1056 specimens. All of the material from the Stockmans and Matthieu monographs, and consequently the museum, was from Hebei, and this was expanded by almost doubling the number of localities (derived from 3844 specimens before data preparation) using the NRM collections. Because of the detailed information provided within the monographs, it was possible to locate most of the sites on modern maps (Figure 3.1), and to ascertain stratigraphic information to formation level (Figure 3.2). Stratigraphic information was not provided with the localities derived from the NRM (Majiagou, Jingxing, Zunhua, Chengde).

3.2.3 Henan

This was the only area from which original material was unavailable to view. However, the monograph of Yang (2006) represents the largest study of the flora from Henan (200 species are documented), and as a lifetime’s work it is an internally consistent and thorough volume from a leading expert in the flora there. As such it was decided to include this work to expand the coverage of the study across to the south of the North China block. Yang herself states that this flora is part of the ‘*Gigantopteris* flora’, referring to the latter phase of the Cathaysia flora as designated by Halle (1935) in the south of the North China block, and is distinct from the rest of the flora on it. All of these localities were found on modern maps, including the one (Anyang) added from the NRM (Figure 3.1), and all but Anyang have stratigraphic information to formation level (Figure 3.2).

3.2.4 Gansu

There are a total of 4199 documented identified plant remains from Gansu (Kansu in old spelling) in the catalogue of the NRM, 2838 of which sourced from Bexell’s collections from the early 1930s Sino-Swedish expedition (538 to specifically Bexell’s Zone C). As one of the largest collections known from the region, it was deemed to be of sufficient size to be comparable with that of the other included North China floras and extend the geographical and floral scope of the analysis to the west of the block. It has been determined as Angaran or mixed Angaran in affinity (Durante, 1992). Whilst Bexell’s stratigraphic field collection framework has come under criticism (Li and Yao 1982), the plant material was identified mainly by Halle (who subsequently published his 1935 and 1937 papers), and so was regarded as being reliable and consistent with that of the North China floras. In defence of Bexell, it appears that fossiliferous localities were scarce and isolated, forcing him to amalgamate several lateral areas with very specific and obscure

Chinese names in order to create a field-usable stratigraphic succession, leading to later workers’ confusion and condemnation of his techniques in laboratory based interpretations (see Appendix, Durante, 1992). Again, many of the smaller localities mentioned were difficult to locate on modern maps due to a use of older and ambiguous Pinyin Chinese for small sites on specimen labels, but they were based around four larger towns which have been used here as an approximation for the wider areas. Although there is a map present in Bexell’s (1945) publication, the locality names given in the NRM collections do not seem to be on it. Therefore, as Bexell’s material is all based around the Suzhou locality, it has been grouped with the exception of specific Zone C items, which have been split to a separate group (‘Suzhou C’). This has resulted in slightly fewer localities in Gansu compared with the other provinces (Table 3.1). While little information can be gleaned about provenance or age of the remaining third of material in the NRM collections, it was decided to retain them in the analysis because of the weight of data involved.

3.2.5 Data preparation

Preparation followed the methodology described in Chapter 2 (King et al., 2011). The floral list was edited to include only the most taxonomically meaningful organs for each group, to avoid possible biological over-representation. Reproductive structures and other morphogenera with ambiguous affinities were also removed as before. Taxa were documented at species level in original records, and these were used initially to eliminate sites with only one occurrence, as this was shown to add unnecessary noise to the analysis, and to assess the usage of ‘cf.’ nomenclature. Where both a positive, full identification was found in the compiled species lists, alongside a ‘cf.’ with exactly the same determination (either at species or genus level), these were merged. As taxa were being analysed across large tracts of land in this case, any under open nomenclature (*Genus* sp.) were only removed where a fully determined occurrence was found at the same locality, under the logic that it was likely to be the same species as that under open nomenclature, and that it would reduce overall noise within the analysis. Taxa were then consolidated up to genus level. Genera are less susceptible to misidentification, tend to be less readily reclassified, and are more likely to persist for longer time periods than individual species, providing a more realistic framework for a study such as this, which covers more than 50 Ma.

Localities were often merged, as the dataset covers a large geographical area and high resolution was not necessary. This was done based on information which could be gleaned from various sources, in an attempt to strike a balance in making each a meaningful and roughly equivalent site with regard to geographical coverage and floral analysis. Typically two sites would have very similar names in Pinyin Chinese, and upon further investigation could be shown beyond reasonable doubt to be the same locality. Several peripheral sites were also merged with proximal, larger areas when those on the periphery did not have many occurrences.

3.2.6 Data quality

Consolidating data from a range of sources can present problems, such as the accuracy of different identifiers' nomenclature, synonymy, and imbalances in data quantity and range. The data analysed in this study is summarised in Table 3.1, and shows a remarkably even number and distribution of genera across the provinces, which suggests that any of the aforementioned problems should at least be balanced across the provinces and therefore present a negligible influence.

3.2.7 Analysis

The data were again collected in MS Excel and analysed using the PAST package. Non-parametric Multi-Dimensional Scaling (NMDS) was chosen as an ordination method, as although all appropriate ordination methods available in the package highlighted the same patterns in the data, NMDS was most consistent and interpretable. Detrended correspondence (DCA) in particular was discarded as ordinations in this case showed evidence of the 'triangle effect' discussed in Bush and Brame (2010), which, while showing meaningful patterns, may have made them more difficult to interpret. The Raup Crick similarity coefficient was used as in Chapter 2 (King et al., 2011). The whole flora from all provinces was analysed together, and then flora was split into higher groups and patterns were examined to try to explain floral trends.

Province	Number of localities	Total unique genera present in province	Percentage of total number of genera (155)	Sum of genus occurrences	Percentage of total number of genus occurrences (470)	Average occurrences per locality	Average occurrences per genus
Hebei	10	60	39	127	27	13	2.1
Henan	7	51	33	90	19	13	1.8
Shanxi	9	65	42	138	29	15	2.1
Gansu	5	65	42	115	24	23	1.8

Table 3.1: Summary of the data analysed in Chapter 3.

3.3 Floristics of Northern China

An NMDS ordination of the full dataset (Figure 3.3) shows a clear division between the flora from Henan province, and that from the rest of North China. All of the provinces on the northern North China block overlap significantly, with the exception of the two outlying points from Suzhou (Gansu province). In particular, Hebei province has the largest spread of points, which appears to be a genuine signal rather than an artefact of, for example, having more occurrences (Table 3.1), a wide geographic spread (most of the localities are clustered close to Beijing; Figure 3.1) or a longer stratigraphic range: Shanxi province covers the most geological time (Figure 3.2). Nearly all of the localities from north North China fall within the range of those from Hebei province.

Clearly, the flora of central and northern North China is all more closely related to itself rather than to that further south (Henan province), closer to the border with the South China tectonic region. Therefore it appears that Hebei was an important centre for the rest of the flora on the North China microcontinent. Looking at its key position towards the northern edge of the block (Figure 3.1), it is possible that Hebei provided a gateway and a diverse ecological pool of flora encroaching from the north, most likely of Angaran or Euramerican origin. It is likely therefore that regions to the south and west of this area were heavily influenced and interspersed with Angaran flora. Henan province on the other hand appears not to be under the influence of this southern-spreading flora, plotting entirely separately. It appears that Henan may have been entirely cut off from the rest of the North China flora, within the Xu-Huai-Yu subprovince (Figure 3.1).

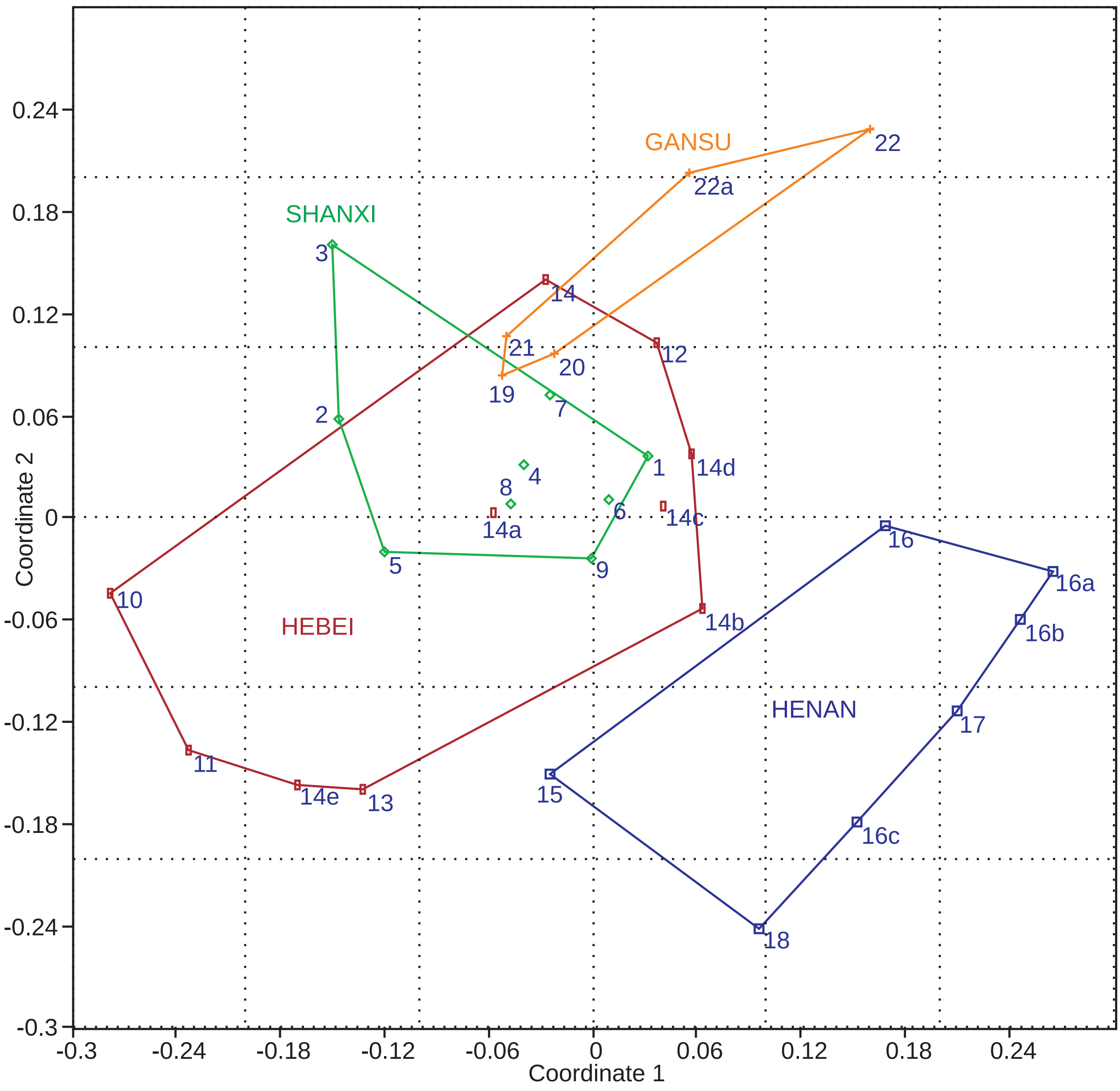


Figure 3.3: NMDS ordination of full genus list, using Raup Crick distance metric. Colours and locality numbers match those on Figure 3.1.

The spread of points from Gansu province is very interesting. Although the localities to the south of the province (Minle, Wuwei and Gaotai) plot within the area of Hebei province, the two data points from Suzhou (Suzhou/Suzhou C) are far outside this grouping. These southern localities confirm that the flora was similar across the larger Sino-Korean-Tarim domain, and may be highlighting an alternative or additional pathway along which the flora spread from the north. The positioning of the Suzhou points may be a reflection of a younger known age of the points, coupled with the phytogeographic affinities of these floras. The locality representing Bexell's Zone C ('Suzhou C') is uppermost Permian in age at the oldest, and hosts an enigmatic combination of floral elements, which can most satisfactorily be described as Subangaran (Durante, 1992). The locality 'Suzhou' is undoubtedly composed of material collected by Bexell from the area surrounding Suzhou, but the age (Zone A, B, C or D) is unknown (see Section 3.1.2, Figure 3.2). This work would suggest, as the point plots closer to the main mass of older North China points, that it is perhaps older than Zone C. Zones A and B however are correlated with the Benxi/Shanxi Formations, and the Lower-Upper Shihhotse Formations respectively (Halle, 1937) and would therefore perhaps be expected to plot closer to points of this age. The most likely explanation is some form of division across the province, whereby the Suzhou localities were under the influence of a different flora from those further south in the province. This agrees with the comments of Durante (1992) that the floras from Zone C and above were part of a transitional Subangaran zone, very different from the Cathaysian or indeed Euramerican types.

3.4 Linking flora

3.4.1 Gigantopterids

The full genus list was split into higher floral groups in order to give an idea of the kinds of plants which may have moved more readily from north to south. In practice, all groups (lycopsids, sphenophytes, sphenophylls, ferns, tingioids, pteridosperms, gigantopterids, cordaites/ginkgoids/conifers, and cycadophytes), where there was enough data to create an NMDS plot, showed highly convergent occurrences from all provinces. This indicates a migration of all groups equally within the whole ecosystem, in a like-for-like niche filling, rather than a few more hardy and readily colonising types being common to all areas. The only exception to this were the gigantopterids (Figure 3.4), which cover a much larger ordination area. Here, Henan province overlaps the provinces from further north on the North China block to a significant degree. Indeed, Henan province is far richer in gigantopterids than all the other provinces (20 occurrences of 10 genera, compared to 11 occurrences of 2 genera from all the other provinces combined; 22% of the Henan total occurrences were gigantopterids compared to 1-3% for the other provinces). Even though five of the genera in the Henan data source (Yang, 2006) were newly erected for the volume (*Hallea*, *Monogigantopteris*, *Pinnagigantonoclea*, *Pinnagigantopteris* and *Progigantonoclea*), the number of unique genera is actually fewer than in all of the other provinces (Table 3.1), and removing the gigantopterids from the analysis altogether still gives a very similar pattern to the overall provinces (Figure 3.5), showing the enduring differences between the floral makeup of the different areas. Yang (2006) acknowledged this by designating the area as part of the

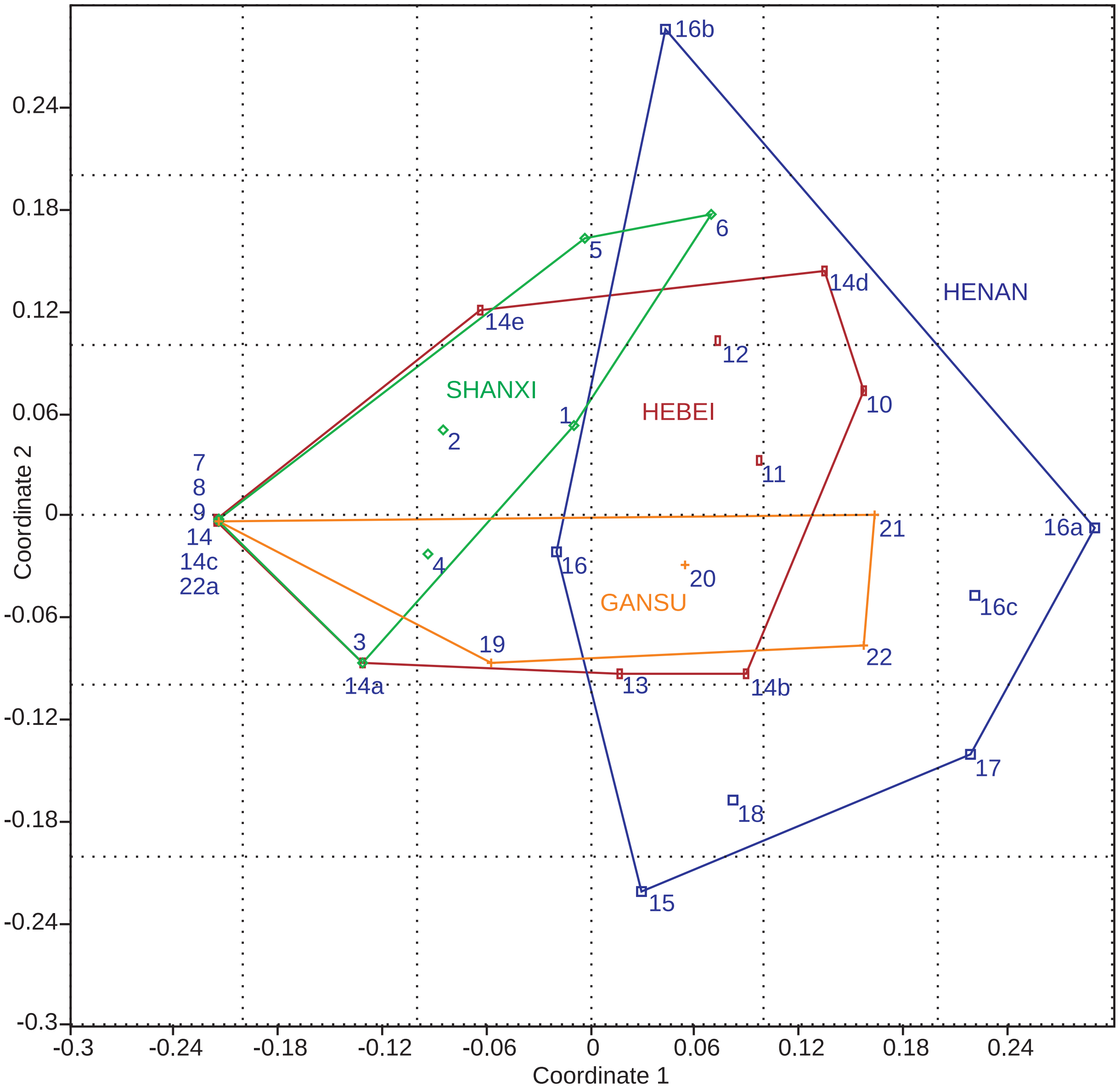


Figure 3.4: NMDS ordination of the gigantopterids only, in all provinces, using the Raup Crick distance metric. Colours and locality numbers match those on Figure 3.1.

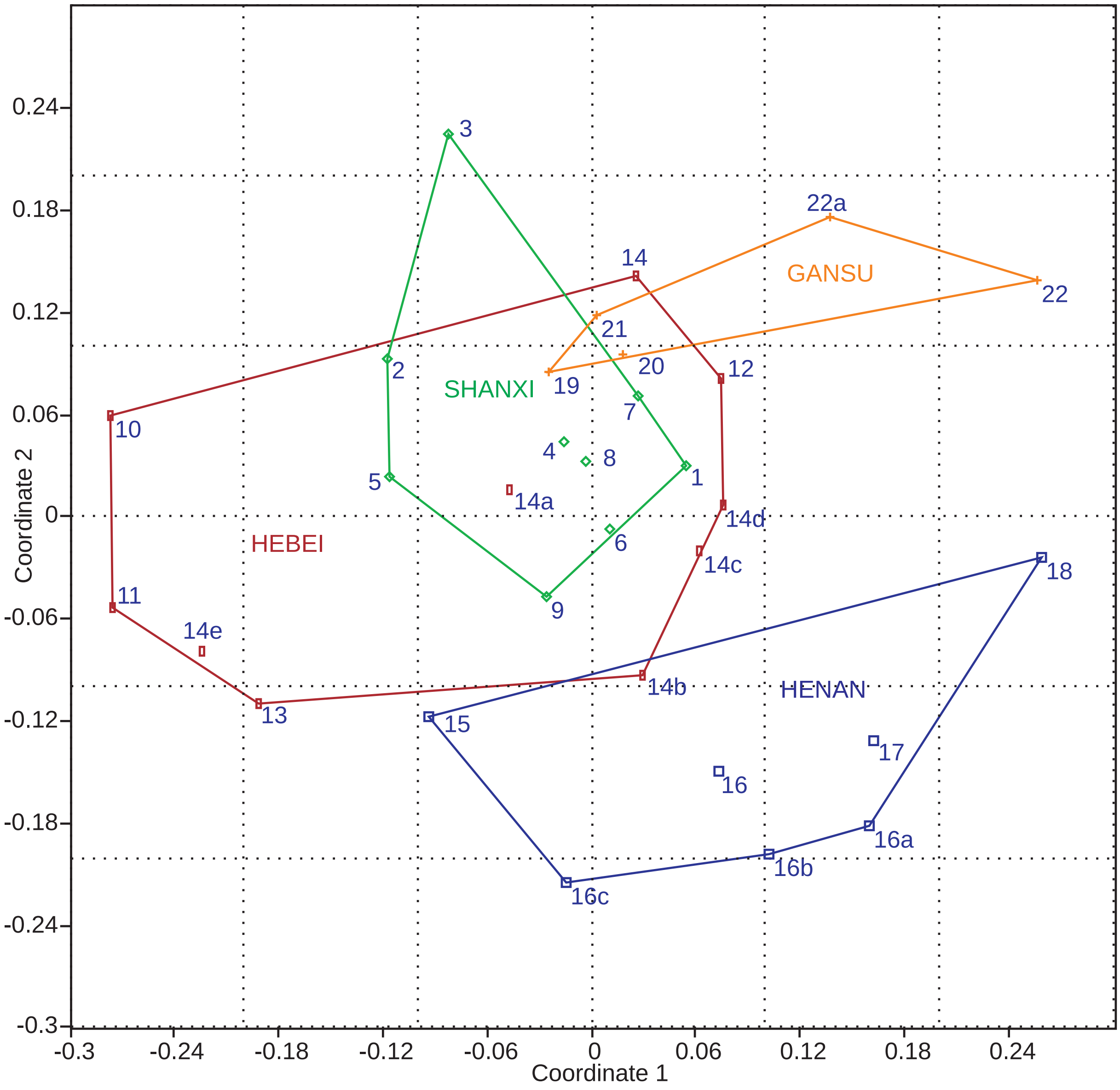


Figure 3.5: NMDS ordination of all genera except the gigantopterids, in all provinces, using the Raup Crick distance metric. Colours and locality numbers match those on Figure 3.1.

‘*Gigantopteris* flora’ of Halle, although this was still assumed to be part of the North China block. The one difference between Figure 3.5 (no gigantopterids) and the full genus plot (Figure 3.3) is a small amount of overlap with the ordination space of Hebei province, with Hung Ho locality. Interestingly, the Hung Ho data does not contain any gigantopterids, but there are enough other genera in common between the areas to create this link. Fortunately, the stratigraphic range of Hung Ho locality is known, and it is equivalent to Shanxi Formation in age. This allows the possibility of constraining the timing of connection of the two aforementioned areas; northern North China and Henan further to the south. From the data analysed here, it is possible to state that the two areas were in connection at some point in the early Kungarian, around 275 Ma (Figure 3.2). It is impossible to know the duration of the connection at this time, because it is not known how much of the upper Shanxi Formation-aged sequence is missing due to the unconformity in Hebei. The connection was long enough to allow interchange of all the major plant groups, but short enough to ensure the endemic gigantopterid species did not become cosmopolitan across North China. This implies close tectonic proximity, with migration controlled by more transient climatic or environmental factors. The flora must also have travelled through the ancient Shanxi province to make the connection, as this is roughly in between Hebei and Henan. This also implies a longer connection, because if the flora was migrating south from Hebei and had a recognisable affinity with Henan by the Kungurian, the flora in Shanxi must have been in contact with that of Henan before and after this point. The data evidencing this is clearly unavailable, either through preservational, sampling or data processing filters.

3.4.2 Individual genera

Taxa were compared across provinces to assess if any individual genera could be tracked (Figure 3.6). This method masks higher relationships, as tested by the NMDS plots above, and as such does not take into account endemic genera such as the gigantopterids in Henan because by definition they are only found in one area to genus level. Over two thirds (106) of genera were only present in one province, and so although these are clearly essential in delimiting the flora, they are uninformative in terms of determining linkages and were omitted from the diagram. This left 49 genera on Figure 3.6, which were present in two provinces or more. Hebei and Shanxi provinces can be considered together as the core of the North China block, with Gansu representing an unusual flora to the west and Henan a separate, possibly Southern Chinese, flora to the south.

There are 14 genera which cover all the provinces, including *Neuropteridium*, whose absence from Hebei province is probably an artefact of sampling or data processing procedures, given that Shanxi province is effectively in between Hebei and Henan. These genera are probably an indication of the basic components of the wetland ecosystems in Cathaysia. This could either be because they were present in all areas before connection, or because they quickly took advantage of connections and proliferated across each area. It is impossible to say which is the case, because of missing information in the province records; the sequence in Hebei is truncated by an unconformity in the Kungurian, and the age of most of the Gansu material is not known, other than the very youngest, which does not overlap with any other provinces. Either way, these genera are clearly cosmopolitan across large expanses of time and space and so are mainstays of the ecosystem, regardless of mechanism.

Figure 3.6: Occurrences of genera present in more than one province.

Nine genera cover the whole of the North China block, from Hebei to Gansu, and this is extended to 13 if those which are present in Hebei and Gansu, but not Shanxi, are included. Again, Shanxi is in between Hebei and Gansu, and so these genera would be expected to be present here but have probably been filtered out by sampling bias or data processing. Eight genera cover only Shanxi and Gansu, and these could be indicators of an influx from the west, via western Angara.

This leaves 10 genera as from central North China – Shanxi and Hebei – only. These genera are probably derived from the north, from eastern Angara, as discussed above, to become the centre of the North Cathaysia flora.

Four genera (*Asterotheca*, *Cyathocarpus*, *Nilssonia*, *Gigantonoclea*) show evidence of migrating from south to north, as they are present in Henan and one or both of Shanxi and Hebei. They may have travelled across as part of the prominent gigantopterid flora around Kungurian times, as discussed above.

This analysis is very broad, and if anything highlights the similarities between all areas of the ancient North China block evidenced in the NMDS analyses. Only a third of the genera are present in more than one province after data processing, but these are enough to produce the patterns seen in the NMDS figures. If the taxa under open or ambiguous nomenclature (e.g. *Pecopteris* vel *Asterotheca*) are merged with their apparent closest taxon (in this case either *Pecopteris* or *Asterotheca*), any differences between the provinces become even more blurred. These ambiguous taxa have been retained in the analyses because it was not possible to examine every specimen included in the dataset, and few species have been considered in a global context. This means that while the ambiguous taxa could be that to which they are compared, they could equally be a different, but perhaps related, genus entirely. This issue is discussed in detail in Chapter 4. In total, the proportion of taxa under open or ambiguous nomenclature in the whole Chinese dataset is around a third, and this is maintained across all provincial occurrences, meaning that if any patterns are skewed as a result of ambiguous taxonomy, all patterns should be affected equally. This only rises to around half when dealing with genera which are present in two provinces, which suggests that there is probably more, not less, linkage across the provinces than shown in Figure 3.6.

Overall, when the finite fossil collecting areas, amibugous taxa, and data standardisation procedures are taken into account, this analysis emphasises a core flora, in this case around a third of the total, which appears to roughly make up the cosmopolitan Cathaysian wetland ecosystem. While it is difficult to trace specific taxa and pathways under these circumstances, the patterns shown are strong and can be used to interpret a global analysis.

3.4.3 Phytogeographic implications

This study improves greatly upon previous work as it is the first to span the whole range of North Cathaysian floras in such a way. However, the data presented here is by no means exhaustive, due to the paucity of datasets available which are of comparable size, accessibility and taxonomic reliability. Coverage is sufficient to provide a hypothetical framework which can be infilled and expanded upon as more data comes to light (Figure 3.7). The main implication from this study, as has been indicated since its designation (Halle, 1935), is that the flora of the North China block is not endemically 'Cathaysian'. Although the floras in Shanxi and Hebei provinces are contemporaneous overall (Figure 3.2), there is a strong indication from this study that in fact the flora on this area of the block developed under the influence of a southwards-travelling flora from the direction of Angara, which took hold in Hebei and continued to intersperse with flora further south and to the west. The study here focusses out of necessity on the latest Carboniferous onwards, due to the unconformity at the base of the Benxi and associated Tongshan Formations, but this only serves to conceal the origins of the flora now seen in the fossil record. To be so closely related and diverse, it is possible that the wetland flora in the north of the North China block may have developed, and been able to spread freely across the Sino-Korean-Tarim domain (as shown by the points in southern Gansu province, Figure 3.1), before this time, suggesting that a pathway to Angara was open in the mid-Carboniferous or before. Chapter 5 looks at available data from the other direction, west to east, to examine this theory in more detail.

A further issue which has been highlighted is the transitionary and complex nature of the boundary zones of the main phytogeographic provinces. This is touched upon by the results from Gansu and Henan provinces. It is already apparent that the so-called Northern Cathaysian flora is probably not endemic to North China in that it had external influences from the north. Gansu province, while containing localities in the south which are of a similar floral composition to the eastern North China floras, also has the Suzhou localities, which are markedly different. Their phytogeographical affinities have long been debated (see Section 3.1.2), but this alone shows uncertainty about the position of the boundary between Angara/the Junggar-Hinggan domain, and the Sino-Korean-Tarim domain, and indeed the true identities and criteria for distinguishing either associated flora. Durante (1992) ventures that the boundary between Angara and Cathaysia was further south at the end of the Permian than it had previously been, incorporating a 'Subangara' zone (Figure 3.7), as part of a larger zone covering much of the Junggar-Hinggan domain (Durante, 1992), although its position could not be determined precisely. This analysis also does not enable a position to be pinpointed, although from the data in the study it may be suggested that there was a division between the Sino-Korean-Tarim domain and Angara (or Subangara) for the duration of the study period, or at least a time previous to the uppermost Permian in order for a distinction to be present. Unfortunately, it is not known if any of Bexell's Zones A and B aged floras, which span the range of the rest of the data, are in existence, and so contemporaneous comparisons are not possible. Therefore, the differing nature of the Zone C material in the study could simply be a consequence of evolutionary development, because it is younger than all of the other material considered.

Towards the southern border of the North China block, Henan is also clearly different from the rest of the North China flora. It is rich in gigantopterids, but the whole flora is, even exclusive of these, endemic to that area and shares few links, aside from the cosmopolitan wetland flora (Figure 3.6), to flora further north. There must have been a separation between the two regions for the majority of their respective floral developments, with the results of this study suggesting a link only around the mid-Permian, of unknown duration. The position of the localities in this study, on the edge of the proposed Xu-Huai-Yu subprovince (Mei et al., 1996), and the differing facies involved (Yang, 2006), both point to a distinct flora, which may be unique to that area. This

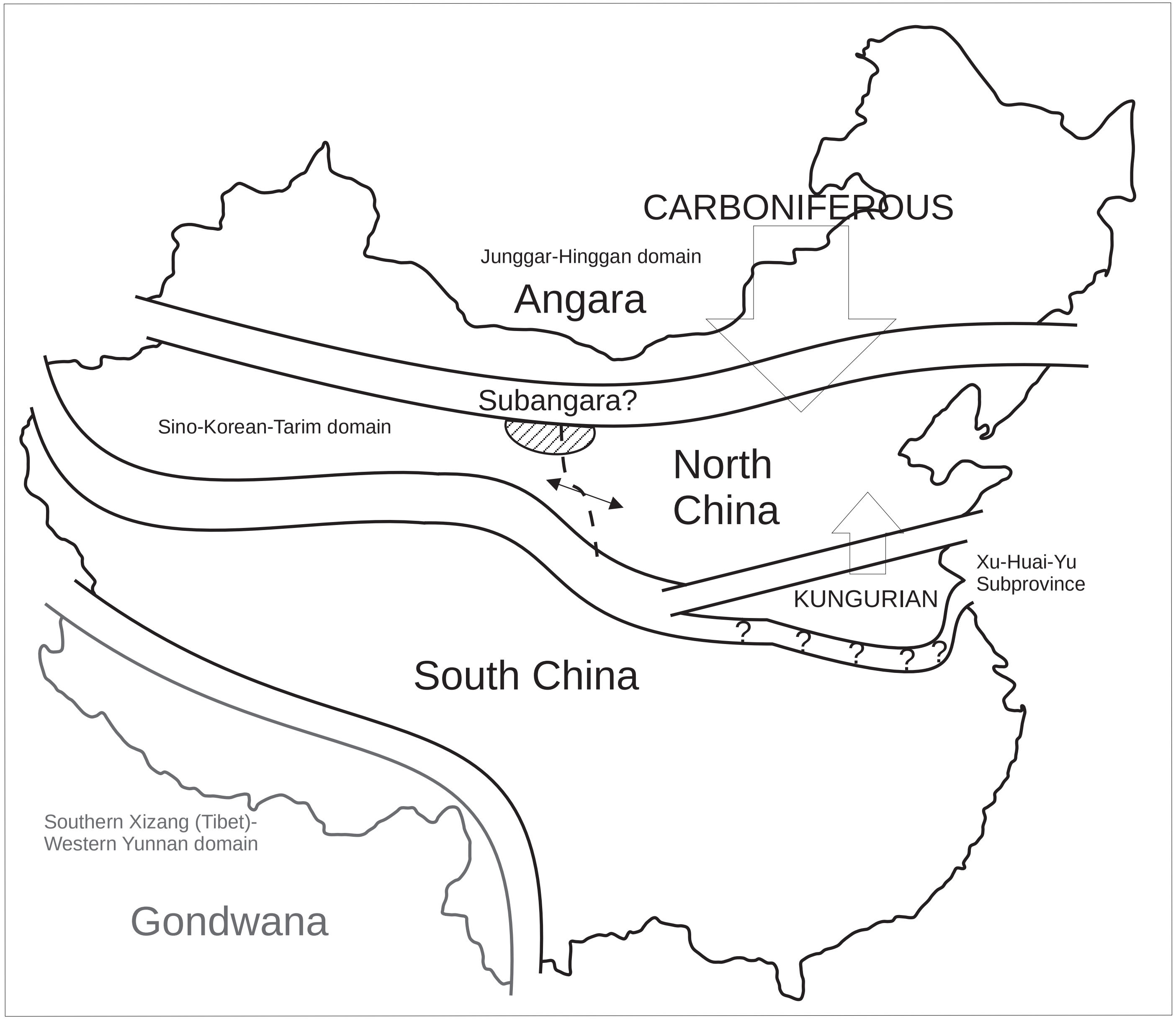


Figure 3.7: Summary model of findings in Chapter 3.

subprovince is described as a southern part of the North China block, being bounded to the south by the suture of the Sino-Korean-Tarim domain with South China (Mei et al., 1996). The flora is however clearly not derived from, nor heavily influenced by, that of North China (Figure 3.3), and therefore is more likely to have had some degree of influence from South China, introducing the possibility that the subprovince may in fact have been either a separate landmass, a northern part of South China, or somewhere in between as part of the Qingling-Dabie orogen (Kusky et al., 2007). If it was a part of South China, it also suggests a (tectonic) connection between the North and South China blocks in the Kungurian, which is later than some palaeobotanical workers have postulated (e.g. Laveine et al., 1992b), but more in line with tectonic and geochemical evidence (e.g. Mattauer et al., 1985; Li and Sun, 1999).

Whatever the true answer, it is clear that again the boundary zone between the Sino-Korean-Tarim platform and South China is complex, and that there may be a sizeable transitionary zone across it.

3.5 Discussion and context

Most often, the links between Angara and Cathaysia have become apparent after large scale monographic works have been viewed in a wider context, either contemporaneously or historically; Halle applied his extensive knowledge developed while creating his seminal work (1927) to several other collections, notably that of Bexell (1945), and he also suggested many times that the Cathaysia flora may be closely related to that in the Euramerican realm (e.g. 1935, 1937). In recent times, Halle's 1927 monograph has also been extensively used due to its clarity, coverage and depth (e.g. Wang, 2010; Seyfullah and Hilton, 2011; Stevens et al., 2011). Hilton and Cleal (2007) used data sourced from Halle's monograph in an extensive comparison with floras from across China and Euramerica, and explicitly stated a now-buried Angaran connection between the two. Other lines of evidence for a link have included the work of Laveine, who used the neuropterids and taxa therein to track the connections of Late Palaeozoic equatorial provinces, and has not just advocated linkage of all equatorial regions (including North and South China) by the early Pennsylvanian, but highlighted a two-way dispersal, proposing that the genus *Paripteris* Gothan originated in China in the Mississippian and travelled west along this corridor (Laveine, 1997). Wang (1996) provides a detailed evaluation of the evidence, proposing a Eurasian interchange whereby flora migrated and from both the north and south during the Late Permian into Angara, sourced from western Europe and southern China.

The crux of the matter is that it is becoming increasingly difficult to delineate each predetermined floral realm, and therefore comparisons can show a significant degree of overlap between realms (e.g. Sun, 2006; Srivastava and Agnihotri, 2010). All of these types of studies are of course subject to the vagaries of taxonomy, and the issue that the floras in question span vast geographic areas, meaning much work is published in relative isolation and often not in English (Chaloner and Creber, 1988; Laveine, 1997). It is clear however that in recent years increasing collaboration and re-examination of material is eroding the numbers of characteristic taxa and blurring phytogeographic boundaries. For example, genera such as *Gigantopteris*, initially believed to be characteristic of Cathaysia, were quickly found to have a much wider geographic range (Yabe, 1917), and its relatives continue to be found in North America (DiMichele et al., 2011). *Sigillaria* Brongniart has now been confirmed as a significant element of peat foming forests in Early Permian China (Wang et al., 2009), and a revision of *Yuania* Sze (Wang and Chaney, 2010) could provide another generic link between China and Euramerica.

3.6 Summary

This study presents findings which support a growing body of work proposing strong links between the Angaran and Cathaysian phytogeographic realms, in this case apparent in the mid-Carboniferous, and adds to the debate over the differences and similarities between the given realms in eastern North China. Additionally supported is the existence of a Subangaran realm, and the divided Cathaysian realm, into North and South China provinces, with fundamental differences in flora between the two. This suggests that the South China province developed an endemic flora in isolation for an extended time, at least until the mid Permian. The North Cathaysian realm appears to centre on Hebei province and include those around it (Shanxi, southern Gansu). Henan represents South Cathaysia, either fully or as a subprovince of it.

The broad approach of this study has given insight into large scale patterns, independent of taxonomic or phytogeographic presumptions. With the information currently available at this scale, it is only possible to propose a skeletal framework for the relationships and timings of connections of the flora concerned. Nevertheless, it has highlighted locations and time periods which could be crucial to these interactions and which would warrant targeted and well-constrained study in the future. In particular, this study has supported the view that Angara provided a pathway into North China, and wider evidence suggests that this pathway led back to Euramerica. Retracing this pathway could shed more light onto the migration and development of the so-called Cathaysian flora in a global context, and this is attempted in Chapter 5.

-CHAPTER 4-

LINKING TAXA OF THE EURAMERICAN AND CATHAYSIAN PHYTOGEOGRAPHIC PROVINCES

4.1 Background

4.1.1 Rationale

The assertion that the Euramerican and Cathaysian phytogeographic provinces may be related is based mainly on general compositional balance of the floras, and generic (e.g. Hilton and Cleal, 2007) and sometimes even species (e.g. Wagner, 2003) names appearing in species lists from both areas. There have been few attempts to examine this evidence in detail, aside from Laveine et al.'s (1993) work on *Paripteris* Gothan and *Linopteris* Presl, suggesting a complete connection and spread from South China through to North America by the beginning of the Namurian. This work has a wider scope than the present study, but was not put into a tectonic and floral-assemblage context. Additionally, Hilton et al. (2002) examined permineralised *Callospermarion* Eggert and Delevoryas pteridosperm ovules, linking the Early Permian Taiyuan Formation with the Pennsylvanian of Euramerica, but in the restricted coal ball forming facies. Seyfullah et al. (2009) supported these findings with further investigation on permineralised Callistophytaleans.

The aim of this chapter is firstly to augment the mainly data-driven body of the thesis, and also act as a quality control investigation of the taxonomical data inputted, by examining several individual fossil plant species in detail. A multidisciplinary approach is used, assessing robustness of the taxonomy and likely affinites of the plants in question, and illustrating the significance of the taxon names used in the main database. These findings feed into the global analyses in Chapter 5.

This chapter focuses on foliage of two groups of seed plants, the Medullosales and Cordaitales, that were widespread in Euramerica and China. The former group have been extensively used in Euramerica for biostratigraphic and palaeobiogeographic studies (e.g. Cleal, 2008; Cleal et al., 2009a). The latter group have proven more problematic, but recent developments in cuticle work (Šimůnek, 2007) are improving the situation. Selected examples, as found in the Permian Chinese collections of the NRM and RBINS, are examined in order to assess whether any species span the temporal and geographic distance between Euramerica and Cathaysia, evidencing physical links and environmental continuity between them. For the most part, the species considered here are Euramerican in erection, and documented from both regions, and this study compares specimens side-by-side to empirically assess whether the species listed in Cathaysia conform to the allocations made to Euramerican-centric species.

4.1.2 Palaeobotanical context

The Medullosales were small trees and shrubs with stems that had dissected stele. They had large compound fronds, most with a dichotomy of the primary rachis (e.g. Laveine and Belhis, 2007; Laveine, 2008). They were traditionally regarded as having large ovules carried on fronds (Halle, 1929), but recent analysis has cast doubt on this, suggesting that in at least some species the ovules attached to fertile fronds with no laminate foliage (Drinnan et al., 1990; Seyfullah and Hilton, 2009). Pollen organs were large, and produced distinctive predominantly monolete pre-pollen (*Schopfipollenites*) (Drinnan and Crane, 1994). They lived mainly on the raised levees of the swamps and rivers (Cleal and Thomas, 1994), and their range extended from Euramerica to China through the mid Carboniferous to Permian (Laveine, 1997).

The Cordaitales were also mainly trees and shrubs, but with woody stems and long, strap-like leaves. They bore compound male and female fertile structures, and saccate pollen typically of the *Florinites* type. The Cordaitales also ranged throughout Euramerica and China from the Mississipian to the Permian, and occupied a wide range of habitats, from the mires through to uplands (Taylor et al., 2009).

4.1.3 Taxonomic nomenclature

Analyses such as these lean heavily on comparisons of taxonomic names, so it is therefore important to understand what is meant by them. Taxonomic names refer to the remains of parts of plants (i.e. plant fossils) rather than to the original plants that produced those remains (fossil plants). Formal procedures, in the International Code for Botanical Nomenclature, for dealing with the multiple organs that can dissociate from a single plant, have been modified several times to try to best classify the organs (plant fossils) unambiguously, from the original organ- and form-genera, to morphogenera, to fossil taxa (Cleal and Thomas, 2010).

What a fossil taxon name refers to can vary according to how well the relevant fossils are understood. The taxon may be defined on fairly limited morphological criteria (e.g. *Stigmaria* Brongniart for rooting structures of fossil lycopsids). Or they can be defined on morphology plus some anatomical data such as from cuticles (e.g. *Neuropteris* (Brongniart) Sternberg; Cleal and Zodrow, 1989; Cleal and Shute, 1992). Or they can refer to anatomically preserved fossils where detailed cellular anatomy is known but the morphology is less understood (e.g. *Pachytesta* Brongniart; Taylor, 1965). Exactly what sorts of fossils can be included within a fossil taxon is defined, explicitly or implicitly, in the diagnosis.

Fossil taxa of a particular plant part (e.g. leaves) will often not be identical to the taxon of whole plants that produced those parts. A fossil genus of leaves, for instance, may include the leaves of a family of whole plants (Bateman and Hilton, 2009). However, the aim should always be that the hierarchy of fossil taxa should as far as possible reflect the hierarchy of taxa of the parent plants. In this study fossil taxa are of different levels, and this has had some influence on the conclusions drawn.

4.2 *Neuropteris* (Brongniart) Sternberg

Neuropteris was originally defined on the basis of pinnules which are contracted at the base, with a more or less distinct midvein, and secondary veins which curve broadly after leaving the midvein at a steep angle, bifurcate at irregular intervals and are non-anastomosed. Later work restricted the scope of *Neuropteris* to imparipinnate forms

(Wagner, 1963). Work on division of the group using frond architecture and epidermal anatomy was undertaken by Cleal et al. (1990) and Cleal and Shute (1991), incorporating a formal redescription of the group in the former. Further to the original description by Brongniart, *Neuropteris* pinnules are often partly fused to the rachis, and carry a weakly developed midvein (Cleal and Shute, 1995). Cuticular study has permitted considerable progress in delimiting neuropteroid genera and species (e.g. Barthel, 1962; Cleal and Zodrow, 1989; Cleal and Shute, 1992), and a summary table of generic features is given in Cleal and Shute (1995). *Neuropteris* fronds were attached to *Medullosa* Cotta stems (Beeler, 1983), and were at least tripinnate (Cleal and Shute, 1995). Fructification is poorly known, but may include *Whittleseya* (Wagner, 1963).

Neuropteris ovata originated in the late Moscovian (Cleal and Shute, 1995), and it comprised a wide variety of pinnule shapes and sizes, depending on their frond position. Wagner (1963) gives average proportions as length being around twice the width, at around 10-12 x 5-6 mm. However, Saltzwedel (1969) examined type material and recounted a ratio of around 1.5:1. Wagner (1963) details large, triangular, stalked pinnules in the lower part of the frond, progressing to small, rounded, broadly attached or even fused examples towards the tip. All of these pinnules are characterised by a well defined basal auricle on the basiscopic side. Saltzwedel's (1969) paper describes *Imparipteris ovata* (Hoffmann) Gothan, but this species was reassigned to *N. ovata* by Cleal and Shute (1995). The paper is a well illustrated, highly detailed treatment of pinnule morphology, giving a vein density of 45-56 veins per cm, and very variable angles of lateral veins to pinnule edge, between 30 and 90°, depending on position along the pinnule. Other sources give a venation density of 40-50 (e.g. Zodrow and Cleal, 1988).

Terminal pinnules are shown to be relatively large, elongate and subrhombic, and slightly asymmetrical, with a notch on one side resembling the position of a fused pinnule. These are also described in Zodrow and Cleal (1988), showing a much more divided form with the appearance of two pinnules fused to the base of the rhombic main apical pinnule. On the lower part of the plant, on the main rachis below the dichotomy, are attached large, fimbriate pinnules (Wagner, 1963; Zodrow and Cleal, 1988; Cleal et al., 1990).

The frond architecture of *N. ovata* was described in detail by Zodrow and Cleal (1988). Fronds were dominated by a basal dichotomy, propagated towards the end of each branch by a means of asymmetrical 'overtopping', and carried intercalated pinnae.

The cuticles of *N. ovata* are highly distinctive. Barthel (1962) was the first to illustrate them, showing the highly sinuous cell walls in the intercostal zones of the upper epidermis. The base of the pinnules carried occasional hairs with subrectangular cells in the costal zones, and irregular cells with numerous stomata in the intercostals (Cleal et al., 1999). Stomatal indices are around 25-30, and stomata are anomocytic or brachyparacytic (Cleal and Zodrow, 1989).

By far the most numerous species of *Neuropteris* in the RBINS collections is *N. pseudovata* Gothan and Sze. The diagnosis of this species is scantly qualified, Wagner (1963) commenting that it has larger and more robust pinnules than *N. ovata* and its nervation is more mixoneuroid, and Stockmans and Mathieu (1939) quote larger terminal pinnules and finer veining. Altogether, the distinction between *N. ovata* and *N. pseudovata* is not clear.

4.2.1 Morphology of Chinese specimens of *Neuropteris*

Species assigned to *Neuropteris* are abundant in collections from Shanxi, Hebei and Gansu, and the vast majority are under open nomenclature in that they are only designated as *Neuropteris* sp.. Smaller numbers of specimens from Hebei in the RBINS collections are mostly designated *N. pseudovata* Gothan and Sze, and *N. gigantea* Sternberg, *N. kaipingiana* Sze, and *N.* sp. a and b as described by Halle (1927) also feature in minor numbers across the provinces. Upon collation of the material, it became apparent that many of the specimens under open nomenclature or assigned to *N. pseudovata* can be assigned to *N. ovata* Hoffmann, as there is a range of material which demonstrates variable pinnule morphology, yields cuticle, and is large enough to show frond architecture.

All figured specimens are from Hebei province. The specimen figured on Plate I (Figure a) is the only *N. ovata* listed from Hebei in the Stockholm collections. However, it is far better preserved then the few from Gansu, and so has been figured here. It fulfils the criteria well, falling within the length-width ratio, having a constricted base and well defined basiscopic auricles on the pinnules. Two examples of typical *N. pseudovata* as assigned by Stockmans in the RBINS collections are figured on Plate I (Figures b and e). Figure b shows an ultimate pinna, and e a large fimbriate pinnule, such as is only found on the main rachis in the nueropterids of the *N. ovata* type (Zodrow and Cleal, 1988). Figures c and d show *N. pseudovata* from the Stockholm collections. Although none of these pinna specimens have a terminal pinnule, the pinnule sizes are consistent with *N. ovata*, and again all have auricles on the pinnules. Length and width measurements of pinnules all of the specimens of *N. pseudovata* in the RBINS collections were taken where possible, including vein densities, utilising a total of 35 specimens. Average length of the most basal pinnules available in the specimens was 18 mm, and width 8 mm, giving a ratio of just over 2. Vein density averaged 55. These figures are within the bounds of those given for *N. ovata*, but are towards the top end. Specimens assigned to *N. pseudovata* may indeed be larger, and manifest other features as diagnosed, but with a fossil taxon as variable as *N. ovata* it may be unnecessary to separate them.

All other specimens on Plates I-IV are under open nomenclature, and display a wide range of pinnule morphologies, mostly upon ultimate pinnae. Most display the characteristic basal auricle, and vein densities are 40-45. Several show parts of, or complete, terminal pinnules, which match the depiction in Saltzwedel's (1969) paper on *N. ovata* (Plate I, Figures g and h; Plate II, Figure e; Plate IV, Figure b). On Plate II, Figures f and g show large triangular pinnules, consistent with basal pinnules of *N. ovata* as described by Wagner (1963).

Larger specimens are figured on Plate II (Figure h), and Plate III. Figure a on Plate III shows a distal section of a penultimate pinna, with alternating lateral pinnae. The penultimate pinna terminates with an overtopping final pinna propagated to the left of the rachis. This fits with the description of the frond architecture of *N. ovata* given in Zodrow and Cleal (1988).

4.2.2 Epidermal anatomy

A large slab with several pinna yielded some cuticle from the specimen in Figure c, Plate IV. Small pieces of both the lower and upper epidermis were present, allowing positive identification to the species *N. ovata*. The upper epidermis shows the characteristic sinuous intercostal cell walls (Plate IV, Figures g and h), and the lower epidermis shows numerous stomata and several trichome bases (larger oval structures) in between the subrectangular, regular cells of the costal zones (Plate IV, Figure e). The abaxial cuticle is not so well preserved, and so it is not possible to calculate a stomatal index, but the anomocytic stomata characteristic of the emended *Neuropteris* of Cleal et al. (1990) are clearly visible in Figure f. (Compare Figure e with Figure 1 of Cleal et al., 1999 for a much better preserved example.)

4.2.3 Cuticle biochemistry

A number of previous studies have used FTIR (Fourier transform infrared) spectroscopy to explore the biochemistry of fossil plant material (e.g. Lyons et al., 1995; Zodrow and Mastalerz, 2002; Zodrow et al., 2003; Pšenička et al., 2005), and enough cuticular material was present from processing the above specimen to enable such an analysis. This was undertaken by Julian Carter, using the in-house facilities at the National Museum Wales (NMW) in Cardiff. Spectral data were captured as an accumulation of 10 scans at a resolution of 4cm^{-1}. The infrared signal was recorded in the region of 400 to 4000 cm^{-1} wavenumbers. A total of 5 spectra were collected from different fragments. The breakdown of results given by Julian appears below.

Figure 4.1 shows the full absorbance spectra typically obtained with the analysed samples. There is a broad hydroxyl peak at around 3300 cm^{-1}, with small peaks at 2926 and 2854 indicating aliphatic carbon content. In addition a number of broad bands at 1568 and 1373 cm^{-1} also dominate the spectrum. The presence of shoulders and the widths of these bands indicate a merging of bands. Spectral enhancements were then carried out using the deconvolution (Figure 4.2) functions of the Spectrum 5.0 software used to operate the spectrometer. These functions allow a more detailed evaluation of the spectral bands present which were used to support the main spectral peak assignments listed in Table 4.1. However, many chemical groups overlap with each other and given the age and chemical complexity of the samples it is not possible to accurately assign many of the enhanced peaks to a single functional group. This data suggests that a wide range of carbonyl groups, ester linkages and solid state amides are present in the samples. Fundamentally the IR spectrum itself provides a chemical fingerprint for the *N. ovata* samples analysed, in the context of their locality, facies and preservational state, and subject to their diagenetic history.

An additional comparison was made to examine chemical changes between processed samples and unprocessed samples of *N. ovata*. The results are shown in Figure 4.3. Spectral subtraction allows the differences between the two sample types to be further analysed. The two key peaks at 1640 and 1528 cm^{-1} can be assigned to the amide functional group in a solid state, ($-R-CO-NR_2$). This suggests that the processing method used affected the chemistry of the samples in this region.

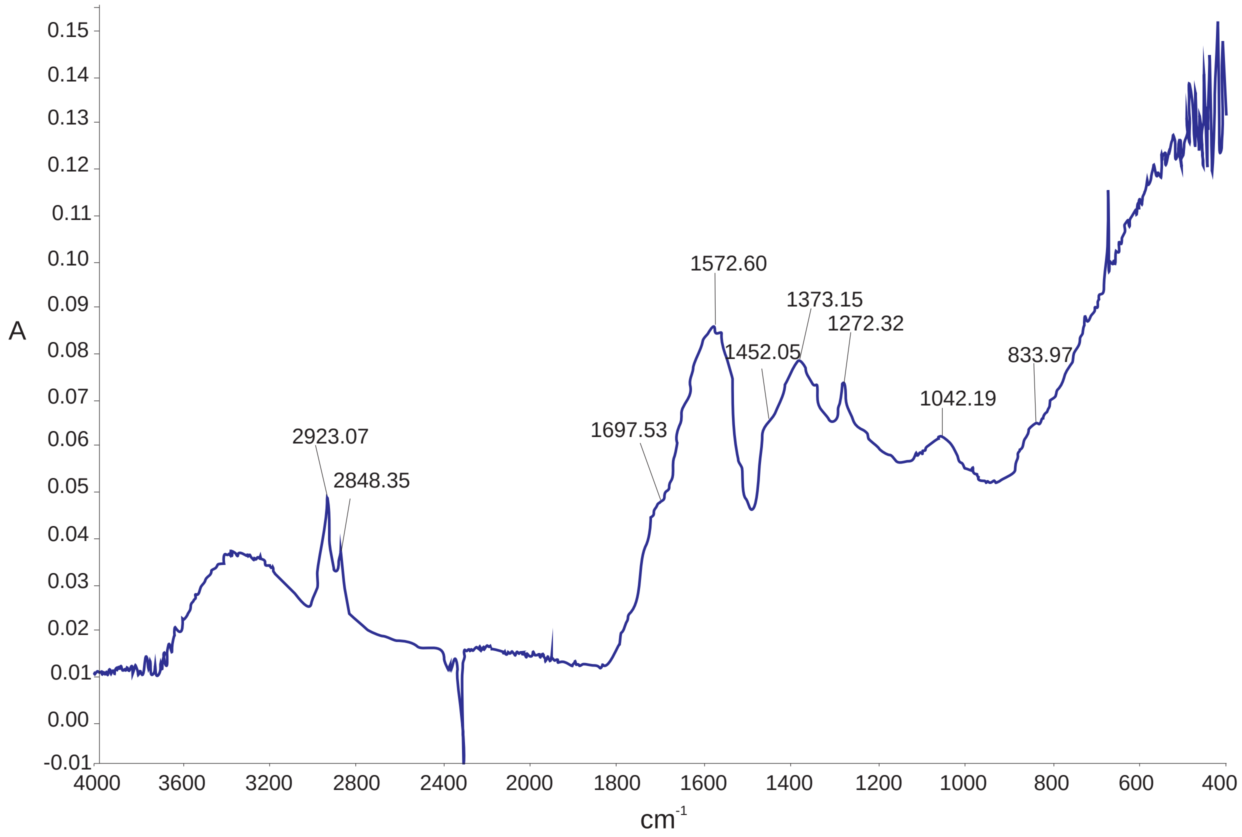


Figure 4.1: An example of the full absorbance spectrum obtained from processed *N. ovata* cuticle sample S146734, NRM collections, Majiagou, Hebei province. A is absorbance, cm^{-1} is the wave number, defined as the reciprocal of the wavelength: W=1/λ, where W=wavelength and λ= wavelength in cm.

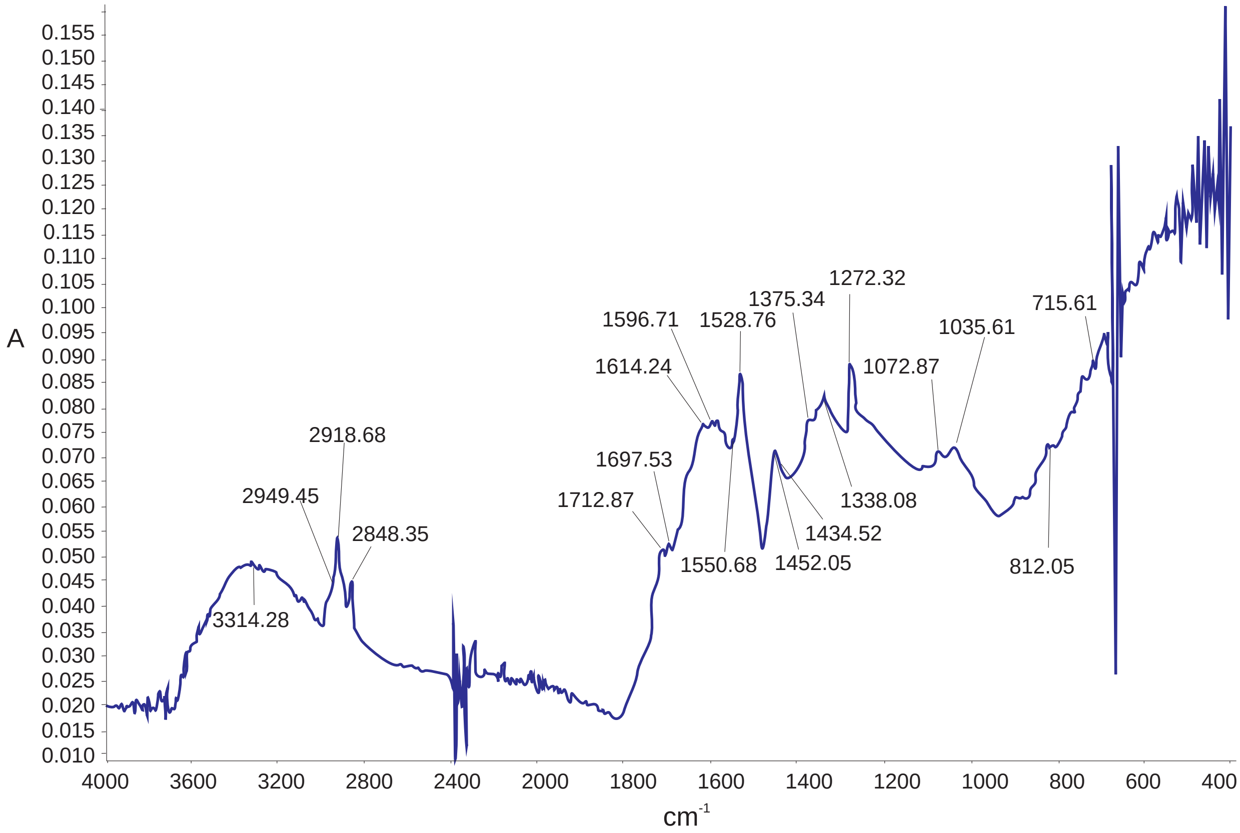


Figure 4.2: Deconvolved spectral data obtained from processed *N. ovata* cuticle sample S146734, NRM collections, Majiagou, Hebei province. A is absorbance, cm^{-1} is the wave number, defined as the reciprocal of the wavelength: W=1/λ, where W=wavelength and λ= wavelength in cm. Note: long sharp peaks at around $600cm^{-1}$ are sampling artefacts.

Chemical bond	Wavenumber assignments (cm^{-1})
OH	3300; 1417; 1345; 1275?
NH_2	1622
CH	1456
CH_3	2962; 2864
CH_2	2926; 2854
CO	e.g. 1760; 1715; 1681
$COCH_3$	1378; 1355

Table 4.1: Summary of the principle IR band assignments for the *N. ovata* cuticle analysed.

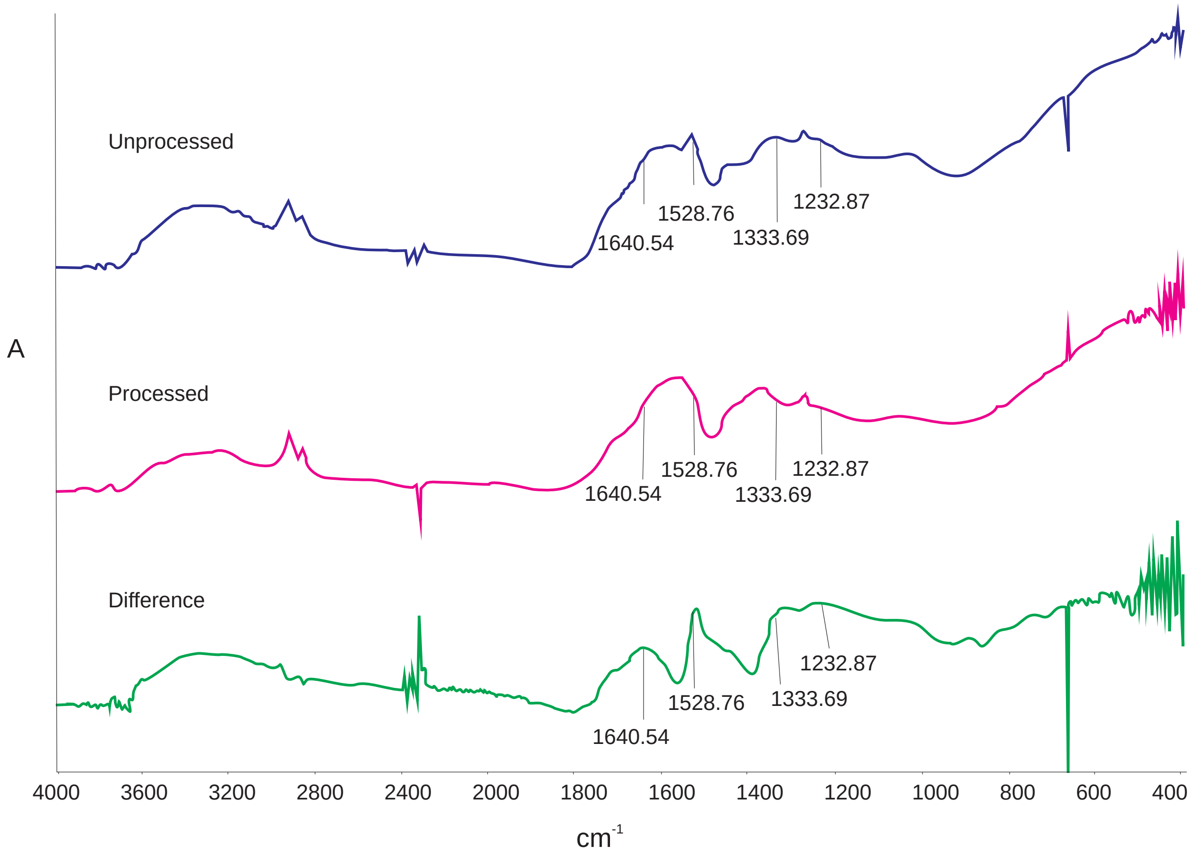


Figure 4.3: Comparison of processed and unprocessed *N. ovata* cuticle sample S146734, NRM collections, Majiagou, Hebei province.
A is absorbance, cm^{-1} is the wave number, defined as the reciprocal of the wavelength: W=1/λ, where W=wavelength and λ= wavelength in cm. Note: long sharp peaks at around $600cm^{-1}$ are sampling artefacts.

The FTIR data demonstrates that a range of organic chemical bonds are present in the sample. This includes aliphatic hydrocarbon, hydroxyl groups, carbonyl groups, and possible amide groups. The analysis in this study was limited to a few prepared fragments and does not allow detailed comparison with previous studies looking at cuticle biochemistry but does provide a chemical fingerprint for the analysed samples. FTIR analysis has shown that a range of organic molecules are present in the cuticle and the FTIR spectral data obtained is distinctive from those obtained in other studies on fossil plant remains (e.g. Lyons et al., 1995; Zodrow and Mastalerz, 2002; Zodrow et al., 2003; Pšenička et al., 2005; Cleal et al., 2009b).

4.2.4 Summary

N. ovata, in its presently delineated, highly variable fossil species form, has here been shown for the first time as unequivocally present in the Late Palaeozoic of both Europe and Cathaysia, proven with corresponding foliar forms, frond architecture, and importantly, epidermal structure.

The variable sizes and shapes of pinnules and pinna present in close association with the specimen figured in Plate IV, Figure c (Figures a, b, d), now confirmed as *N. ovata*, lend considerable weight to the overall picture of a large plant encompassing a wide range of foliage (e.g. Zodrow and Cleal, 1988).

4.3 *Alethopteris* Sternberg

During examination of collections from Shanxi, Hebei and Gansu provinces, several species of *Alethopteris* Sternberg were encountered, all of which were not known from Carboniferous Euramerica. However, in each case the material was scarce and often poorly preserved, not permitting a detailed comparison with other species within the genus *Alethopteris*. Two species were possible to examine in a little more detail, those erected by Halle in his 1927 monograph: *A. norinii* and *A. ascendens*. Again, the material was not abundant, but enough was available to determine whether these species as determined by Halle belonged to the Euramerican genus as determined by Sternberg, and could perhaps have covered both Euramerica and Cathaysia.

Alethopteris was diagnosed as a plant with large pinnate fronds, and a characteristic pinnule shape as being strongly asymmetric, fused at the base, and strongly decurrent to the basiscopic side. Pinnules are often also decurrent to the acroscopic side. Venation consists of simple, non-anastomosing lateral veins, forking at irregular intervals and joining the pinnule margins at around 90°, about a strong central midvein (Wagner, 1968). Furthermore, it has been shown by Cleal and Shute (in press) that the lateral veins towards the base of pinnules do not arise directly from the rachis, but rather from the strongly decurrent midvein, which runs closely parallel to the rachis for some time and is often obscured in this area by insufficient preservation. *Alethopteris* is a fossil genus, as it is noted that *Lonchopteris* Brongniart shows the same pinnule morphology, but anastomosing veins. It is believed, through repeated discoveries of fronds and reproductive organs in association, that *Alethopteris* carried seeds of the *Trigonocarpus*

Brongniart and *Pachytesta* Brongniart type, and synangia of the *Whittleseya* Newberry and *Dolerotheca* Halle types (Wagner, 1968). More natural classification of species can sometimes be attempted through epidermal studies, although in practice only a few such studies exist, and mainly serve to document features of established species (e.g. Barthel, 1962; Reihman and Schabilion, 1976; Zodrow and Cleal, 1998). There was no cuticle bearing material in the collections studied here and so this feature could not be used in this case. The other tool in diagnosis of pteridosperms is frond architecture, for which there was no evidence on the scale of the whole plant until Wnuk and Pfefferkorn's (1984) work, which was further developed by Laveine (1986) and Laveine et al. (1992a). However, there are no specimens showing frond architecture here, leaving pinnule morphology and venation as the key criteria.

4.3.1 *Alethopteris norinii* Halle

After initial description by Halle in 1927, this was expanded upon by him in 1929, and has more recently been reinvestigated by Seyfullah and Hilton (2009). Specimens considered here are figured on Plate V.

The pinnule shape as seen in Figure a is distinctly alethopteroid, being decurrent on both the basiscopic and acroscopic side. The pinnule midveins are strong, and appear to run parallel to the rachis for the majority of the pinnule width, giving rise to all of the secondary veins in the basiscopic part of the pinnules (Figure b). Lateral veins fork 1-3 times with no apparent pattern. But there are many more features of *A. norinii* which do not lend themselves to classification within *Alethopteris*. Most prominently, the pinnules are divided strongly asymmetrically, with the midveins shifted acroscopically and curved to meet the rachis so that they join almost in line with the acroscopic margin of the pinnule (Figure a). This feature is not found anywhere in described *Alethopteris* species (e.g. Buisine, 1961; Wagner, 1968). The midvein, while thick, is also flexuous, with lateral veins almost appearing to diverge from it rather than simply being attached, especially in the wider, entire pinnules (Figures a, b). Additionally, lateral veins reach the pinnule margins at around 40°, as opposed to the diagnosis of roughly right-angles to the margins (Wagner, 1968). Veins per cm are in the order of 27-30, which is lower than any of the morphogroups determined by Scheihing and Pfefferkorn (1980). Another feature apparently unique to *A. norinii* is the presence of small dots at regular intervals in between the lateral veins (Figure b). Indeed, this was one of the main characteristics used to define the species by Halle (1927), alongside the oblique midvein and steep secondary veins – none of which are typical alethopteroid features. The reproductive structure organically attached in Figure d was discussed at length by Halle, and decided in 1933 to be a pollen organ, probably of *Whittleseya* affinity, and therefore in keeping with a possible overall alethopteroid diagnosis. Seyfullah and Hilton (2009) discussed this enigmatic organ, concluding it to be of the *Aulacotheca* type, and that the structure of it precludes affinity with callipterids. However, Figure g shows a lobing on the basiscopic side of the pinnules, which bears a resemblance to certain forms of *Callipteridium* (Weiss) Zeiller (Laveine et al., 1977).

It is clear that this species as named by Halle is enigmatic, exhibiting a range of evidence which aligns it with several pteridosperm genera, and also unique features which set it apart from all of these groups.

4.3.2 *Alethopteris ascendens* Halle

Again, the most alethopteroid aspect of this species is the basal decurrence of the long and narrow pinnules (length being around four times the width). Including those in the Stockholm collections which have been compared to *A. ascendens*, there are two shapes of pinnule, figured on Plate VI. Halle’s specimens are very straight sided, culminating in an acroscopic apex. The *A.* cf. *ascendens* specimen (Figures f, g), plus that in Figure e, is falcate, creating a ‘swan neck’ shape. This shape is unknown amongst all other species of *Alethopteris*. Some pinnules appear to be confluent, certainly in the falcate specimens (Figures e, f, g), but the preservation in the other specimens makes it difficult to be certain. The midveins in the straight sided specimens are strong, very straight after the decurrent origin, and continue almost to the end of the pinnules. The midveins in the falcate pinnules generally appear straight, and do not always seem decurrent (Figure g), but sometimes curve slightly in order to maintain a central position along the pinnules. The defining feature of this species as diagnosed appears to be the steep secondary veining, which meets the pinnule margins at 15-20°. This is far steeper than any other species of *Alethopteris*, and alongside vein densities of around 16 per cm, is far outside the parameters stated by Scheihing and Pfefferkorn (1980).

Halle’s (1927) description is brief, due to the paucity of specimens, and he casts doubt over the allocation to *Alethopteris*, the only real evidence for it being the decurrent pinnules; but with the information available he concludes it may be placed there for the time being. This is a reasonable assessment, and the cf. specimens found elsewhere in Shanxi province may prove to be another species again, or alternatively their pinnules may have been borne on a different section of the frond. One more specimen, again of an isolated ultimate pinna, was unearthed by Stockmans and Mathieu and figured in their 1939 monograph, and further to Halle's identification of it, they opted to insert a question mark to reflect the uncertain designation of the species, but maintained that at that time *Alethopteris* was the best choice. No more specimens have come to light since these works, and therefore *A. ascendens* remains in limbo.

4.3.3 Discussion

Neither species of *Alethopteris* examined here appear to fit the genus as originally diagnosed. Their erection by Halle in 1927 predates comprehensive investigations into the genus (see Wagner, 1968), and appears to be based upon their pinnate nature and the decurrence of the pinnules and midveins, and varying degrees of pinnule confluence. While it is clear that they each represent distinct fossil species, there is much more evidence against these species being of *Alethopteris* than there is in favour. However, they also do not show enough collective features to align them to any other genera, and this is compounded by the limited amount of material, none of it bearing cuticle, and no pieces being large enough to show frond architecture. In these circumstances, the existing generic allocation is brought into doubt, but there is not enough information to furnish a revised allocation or erect a new genus. Therefore, it would be more fitting to refer to the species discussed here as aff. *Alethopteris ascendens* and aff. *Alethopteris norinii*, reflecting that the species do show some features in common with *Alethopteris*, but are not correctly placed within that genus (after Bengston, 1988).

As related above, few other well-supported *Alethopteris*-like plants were found on examination of the Chinese collections. Five others are figured in Stockmans and Mathieu (1939), of which three are new species (*A. kaipingiana*, *A. gothani* and *A. straeleni*), one is an unusual form with a taeniopterid appearance (*A. hallei* (Jongmans and Gothan)), and one is only designated as *affinis* (*A.* aff. *costei* Zeiller). Wagner and Álvarez-Vázquez (2008) acknowledge this problem, but see it as mainly one of a paucity of material, and see no reason why European *Alethopteris* species should not be found in Cathaysia. There have been no comprehensive treatments of the purported *Alethopteris* species in the Permian of Cathaysia, and so little is known of them outside the Euramerican, Carboniferous lens through which they have been viewed thus far. Laveine and Oudoire (2009) however, reference Laveine et al. (2003a: Plate 18, Figure 1) as an unequivocal specimen of *Alethopteris* from the Late Palaeozoic of northwestern China. The specimen is only 2.5 cm long and incomplete, and although the pinnule shape and venation are alethopteroid, it is scant evidence for the presence of *Alethopteris* in Cathaysia, especially as it is found so far west and could have been a part of Angara and/or Euramerica. The glaring lack of compelling evidence for *Alethopteris* in Cathaysia remains therefore, and is somewhat of a conundrum, as other pteridosperms are widely reported. The reason(s) for this are as yet unclear, as it seems unlikely to be simply a sampling issue on such a wide scale.

4.4 *Odontopteris* (Brongniart) Brongniart

The definition of *Odontopteris* is fairly simple, including foliage with pinnules connected to the rachis along their entire base, with several parallel or sub-parallel veins arising steeply from the base and bifurcating a number of times (Zodrow, 1985). The midvein is poorly developed (Zodrow and Cleal, 1988), and the veinlets which cover the pinnules arise from a single, strongly decurrent vein which runs closely parallel to the rachis (Cleal and Shute, in press). Vein density is around 18 per cm (Cleal et al., 2007). Frond architecture is similar to that of *Neuropteris*, from which it is probably a descendant (Zodrow and Cleal, 1988), although fronds were smaller and were probably borne on scrambling or lianescent plants (Cleal et al., 2007). Cuticles have been examined by several workers, and in some cases have been utilised to allocate species (e.g. Barthel, 1962, Šimůnek and Cleal, 2004). The adaxial epidermis generally consists of fairly uniform subrectangular cells, and the abaxial epidermis is differentiated into costal and intercostal zones, the former consisting of subrectangular cells, and the latter polygonal, irregular cells with numerous randomly orientated stomata (Šimůnek and Cleal, 2004). *O. subcrenulata* is a larger foliar form of the genus, with more rounded pinnule apices (Šimůnek and Cleal, 2004). Doubinger et al. (1995) described a French Stephanian-age variant (*O. subcrenulata* var. *elongata* Doubinger and Vetter) as having ultimate pinnae 8-10 cm in length, with 3-4 pairs of pinnules at 10-13 x 7-8 mm in size. Pinnules are rounded, clearly separated and decurrent at the base. Basal pinnules are strongly contracted, and pinnae terminate with a large oval pinnule. Veining is parallel.

4.4.1 Morphology of Chinese specimens of *Odontopteris*

Species of *Odontopteris* were found in Hebei, Gansu and Shanxi provinces, with by far the greater number of species being of *O. subcrenulata* (Rost) Zeiller. A few representatives of *O. orbicularis* Halle and *O. laceratifolia* Halle were found in Shanxi, but the vast majority were *O. subcrenulata*, and some of these are examined here.

The specimens examined did not yield cuticle, and were not of sufficient size to inform on larger frond makeup. The foliar morphology however (Plate VII) is highly consistent with the descriptions above, having paired, decurrent pinnules broadly attached, parallel venation and enlarged terminal pinnules. The basal pinnules are also constricted. The specimen in Figures b and c was figured by Halle (1927; Plate 34), who stated that there was no doubt about the specific identity as it was so closely matched to European specimens. There is some variation shown in the foliage, with Figure a being a larger, single pinnule attached to a rachis. The overall shape of the pinnule and the venation pattern appear to be consistent with other specimens; however it carries a strong ‘midvein’. This appears to be a contraction of the common pinna form, being reduced to a single fused pinnule, or perhaps is in effect a single ‘terminal’ pinnule as seen on other pinna. As such, it is likely to be a distal version of a terminal pinna, complete with basal constriction. Figure i is also unusual, appearing similar in form to *Neuropteris* in pinnule shape and venation. However, on closer inspection it seems to be of a distal *O. subcrenulata* pinna, the type which would have borne a specimen such as that in Figure a. This is evidenced by the pinnules in the lower right of the figure, which consist of an unmistakable rounded basal pinnule and a larger terminal pinnule of the type discussed above, about a prominent rachis. Other rachises can also be seen along the centre of pinnules to the bottom left. This specimen highlights the range of possible variation within *O. subcrenulata*, and also its close relationship with *Neuropteris*.

Having examined many specimens designated as *O. subcrenulata*, the better-preserved of which are figured on Plate VII, there is no reason to question its designation, and so this study represents renewed confirmation of its presence in Cathaysia.

4.5 *Cordaites* Unger

Cordaites is almost ubiquitous in late Palaeozoic wetland communities, and vast numbers of specimens were encountered on examination of collections of Chinese material, from Hebei, Shanxi and Gansu provinces. Henan contained the new genus *Neocordaites* Yang and Wang. Studies on anatomically preserved assemblages indicate that three species existed in the Taiyuan Formation, of which one represents a new whole plant species of *Cordaixylon* previously known from Europe and North America, while the genus *Shanxioxylon* appears to be endemic and comprises two species (Wang et al., 2003; Hilton et al., 2009).

The overwhelming majority of specimens examined here were under open nomenclature (*Cordaites* sp.), and the only specific identifications were made to either *C. principalis* (Germer) Geinitz or *C. schenkii* Halle. This reflects the fact that *Cordaites* is notoriously difficult to classify based on adpression material, as the only features the long, strap-like leaves show are fine longitudinal striations. The shape of the leaves themselves is of limited use, due to differences dependant on position on the tree, and incomplete preservation (Šimůnek and Libertín, 2006). Striations upon the leaves are representations of veins, sclerenchyma and ribs running along the leaves, which vary between leaves, with position on the leaf, side of leaf (adaxial/abaxial), and due to taphonomic factors (Halle, 1927). Therefore using patterns in the arrangement of these striations as a rudimentary identification tool is very unreliable. This statement has been reiterated since, most recently in a detailed and comprehensive study by Šimůnek (2007), in which 30 new and existing species of cordaite from the Carboniferous and Permian of the Bohemian Massif, Czech Republic, are classified into 5 morphotypes based on their cuticular features. The important cuticular feature is the stomatal complex, which remains uniform across the leaf, while cell dimensions and the number of stomatal rows per stomatiferous band vary. The power of this methodology is shown in that previously only 3-4 species were diagnosed based on venation patterns. This method then is currently the only reliable and replicable way to classify specimens of *Cordaites*. Two samples of *Cordaites* cuticle have been prepared here, one from Chao Ko Chwang, Hebei (*Cordaites* sp., Shanxi Formation=mid Permian), and one from South Wales (*C.* ‘*palmaeformis*’ (Göppert) Weiss, Llantwit No 3 seam, Grovesend Formation=mid Pennsylvanian). These are compared with Šimůnek’s monograph, the only work of its kind, in order to attempt to classify and better describe them, and investigate the ranges of such species.

4.5.1 Epidermal anatomy of South Wales cordaite

This material has been allocated to *C. palmaeformis*, but no cuticular studies of this species have been undertaken, and it is not included in Šimůnek’s monograph (2007). Moreover, as this identification would have therefore been based upon leaf shape and/or striations, this specific determination must be treated as under review.

Samples of adaxial cuticle were scarce, but an example can be seen in Plate VIII Figure b. It was not possible to discern cell structure, other than appearing to be elongate. No stomata are present, and evidence of striations on the leaf surface can be seen in the dark and light bands, although distinctions are difficult to envisage.

The abaxial cuticle (Figures c and d) is much better preserved, and differential costal and intercostal bands can clearly be seen. Lighter coloured (=thicker) veins run parallel, at around 300 µm apart, and irregularly spaced darker (=thinner) veins run in between these, again around 300 µm apart from one another. These veins are strongly suggestive of alternating vascular bundles (thicker) and sclerenchymatous bands (thinner). As with the adaxial surface, it is not possible to see individual cells along the veins. Along one side of the veins however are often prominent rows of elongated, oblong cells of a more or less uniform width (around 25 µm) and variable length (25-100 µm), which can be used to pick out the costal areas. Stomatal complexes are relatively large (around 60 x 100 µm) consisting of oval stomata flanked by two large, bloated lateral subsidiary cells and two slightly smaller polar subsidiary cells. Sometimes these polar cells are shared by a neighbouring stomatal complex. Stomata form pairs of rows in the most well-developed areas, which follow the costal bands closely. Epidermal cells are elongate, oblong in non-stomatiferous areas to oval when surrounding stomatal complexes. However, all of the intercostal areas are chaotic, with cells always orientated longitudinally, but of varying shapes and sizes. Stomata are not always present, and are not always regularly spaced, but appear to always run alongside veins. Lateral subsidiary cells are always longer and larger than the stomatal recess, and can appear oblong when very large. Polar cells range from circular, and just large enough to plug the gaps between the laterals, to almost identical in size and shape to the large laterals. A highly stylised representation of the abaxial epidermis is shown in Figure 4.4.

These characteristics place this cordaite into cuticular morphotype C, on the basis that subsidiary cells are different from ordinary cells, and the stomata are in well defined

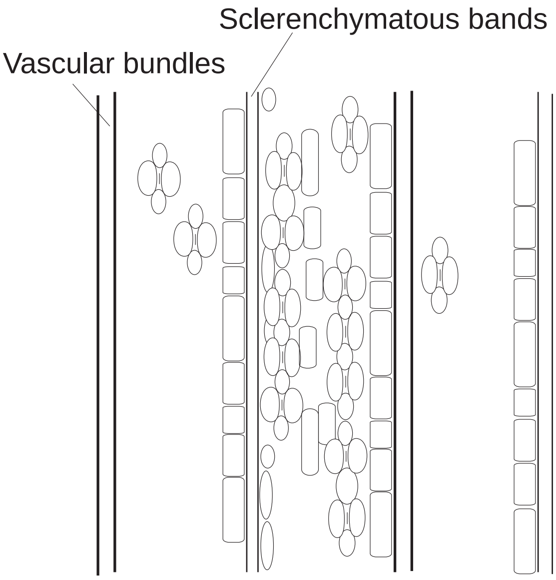


Figure 4.4: Highly stylised sketch of *Cordaites palmaeformis* cuticle from Llantwit No 3 bed, (Asturian/Cantabrian) near Llantrisant, South Wales, specimen 22.114.G2418, NMW collections, figured on Plate VIII Figures c+d. Not to scale.
Cuticle is variable so not all are cells drawn, and features do not always occur together. Generally, subsidiary cells are more oval, and can be quite bloated. Non-stomatal cells are oblong, and can be very elongate. Stomata not always present; intercostal cells can be quite chaotic.

double or multiple rows connected into stomatiferous bands. The cordaite is hypostomatic, and so of the species listed in the monograph it can only be *C. wilkischensis* Šimůnek or *C. malesicensis* Šimůnek. There are only 1-3 rows of stomata and so *C. malesicensis* should be most closely matched, but it has a stomatal crypt, which this species does not have, and furthermore it is transverse. All of the features visible on this sample are longitudinal. A wide range of cell sizes is given for both of these species and so it is unwise to use these as diagnostic. The specimen also does not match the cuticular form of *C. principalis* (Zodrow et al., 2000), or *C. schatzlerensis* Šimůnek and Libertín (Šimůnek and Libertín, 2006), and there are few other studies on European species which carry enough information for comparison (Šimůnek and Libertín, 2006). This cordaite specimen may represent a new species, or it may simply not be found in the field area covered by Šimůnek (2007). While cuticular classification of this type is in its infancy, it is difficult to assign isolated specimens to robust species, and therefore without further specimens of *C. palmaeformis* to compare, it is impossible to relinquish the allocation. Few specimens in the collections of the Llantwit No 3 seam bore any cuticle at all, and only this specimen yielded enough to survive processing and show potentially diagnostic information. Therefore, at the present time, no other material is available to test the species allocation, and so while it is not substantiated with contextual cuticle study, this specimen must remain designated *C. palmaeformis*.

4.5.2 Epidermal anatomy of Chinese cordaite

This specimen is under open nomenclature (*Cordaites* sp.). The adaxial cuticle (Plate IX, Figure d) is astomatal, with irregular slightly more strongly cutinised bands running longitudinally, suggestive of costal zones. Cells are generally oblong, 20 x 25 µm, although show some variation in patches. The abaxial cuticle (Figure c) is distinctive, although not well preserved, showing parallel single rows of stomata. The rows are around 100 µm apart, relatively strongly cutinised, and are marked out by the pale, elongate stomatal recesses. Stomatal complexes are 50 x 30 µm on average, and many appear to be wide, and oblong to rounded. Some are long and narrow. They are closely set, with a density of around 80 per mm^2, and generally two lateral and two polar cells per stoma, although some do appear to have two laterals on one side. The polar cells are often elongate, and shared by the neighbouring complex. Non stomatal cells are indistinct but are wider, polygonal, and less well organised. There are usually 3-4 across the width of the nonstomatal band. Narrow, more thickly cutinised costal bands are not in evidence on the abaxial cuticle.

These characteristics place this cordaite into Šimůnek's (2007) morphotype group B. The only hypostomatic species in the monograph is *C. idae* Šimůnek. This specimen shows many similarities to *C. idae*, but the main difference is the irregularity of both stomatal and nonstomatal cells. In addition, stomatal and nonstomatal rows in *C. idae* are variable in width (c.f. Plate 14, Figure 1, and Plate 15, Figure 1), and indeed the stomatal complexes vary in size and shape between the two. Most importantly, the stomatal recesses are uniformly square and small, relative to the subsidiary cells, and this is different from the specimen under consideration, whose stomata are elongate in shape and relatively long in comparison to the subsidiary cells.

4.5.3 Other records of cordaite cuticle from China

Wang et al. (2000) studied the cuticle of purported newly collected specimens of *C. schenkii* from the Taiyuan Formation, although as Halle's species was originally erected on macrofossil evidence, further identifications must be treated with caution. Cuticle of this species is very different from that of the specimen under consideration. '*C. schenkii*' as designated is amphistomatic, stomatal complexes are large and rounded with square to oblong stomata, and there are prominent papillous thickenings on the abaxial epidermis. Several other workers have described Chinese cordaite cuticles. Dispersed cuticle, again from the Taiyuan Formation (Wang et al., 1995), was later allocated to *C. neimengensis* Liu, Geng, Wang and Li (Liu et al., 1998). Again, this species is amphistomatic, and possesses papillae on the lower cuticle. The abaxial surface is superficially similar, especially in Liu et al. (1998), but all cells are regular and well defined, so taking this into account alongside the presence of papillae and the very regular specimens figured in Wang et al. (1995), it is clear that the specimen considered here is not an example of *C. neimengensis*. Another specimen studied by Chen (1994) was designated *C. huainanensis* Chen, but is unique amongst cordaite cuticles published so far in that it has large stomatal complexes on the adaxial epidermis only.

Sun (1991) was the first to undertake a modern study of cordaite cuticle. Sun described a new species, *C. baodeensis*, collected from the Shanxi Formation in Shanxi province. The cuticle is amphistomatic, and the abaxial epidermis consists of stomatal rows, with the complete complexes appearing almost square. There are two bloated oblong to reniform lateral subsidiary cells, and small polar cells mostly shared by adjacent stomata. Non stomatal cells are elongate and rectangular. This cuticle bears many similarities to the specimen under discussion, the main differences being the non stomatal cells and the regularity of the stomatal complexes. In *C. baodeensis*, the cells are prominent, strongly cutinised, regular and well preserved, in contrast to the cells in the specimen here, which are indistinct and polygonal. The complexes in *C. baodeensis* are of a uniform width, and always have two lateral subsidiaries, while the structures of the complexes in this specimen are more difficult to discern and more irregular, sometimes even appearing to have asymmetrical arrangements with three lateral subsidiary cells (Plate IX, Figure c). Sun compares *C. baodeensis* to *C. principalis*, but highlights the multiple rows found in that species but not in *C. baodeensis*.

4.5.4 Cuticle biochemistry of Chinese cordaite

Zodrow et al. (2000a; 2000b) have undertaken detailed studies of *C. principalis*, employing traditional epidermal examination in combination with FTIR. This has revealed that a range of cuticular morphotypes can in fact belong to the same species, based upon FTIR spectra of each type. Enough cuticular material was isolated from the specimen under consideration here to enable FTIR analysis, again performed and described by Julian Carter (Figures 4.5, 4.6).

Key features of the spectra are given in Table 4.2. In general the region 1800 – 1000 cm^{-1} represents a great abundance of C=O and C-O-R structures. The peak at 1032 cm^{-1} is also notable and can be attributed to the presence of phenolic and alcoholic C-O bonds as well as C-O-C bonds with aliphatic or aromatic carbons, as is typically found in lignite specimens (Georgakopoulos et al., 2003; Oikonomopoulos et al., 2010). This is borne out by the striking similarities between the spectra from the cordaite sample, and that of a sample of soft jet (=lignite), which was generated as a comparison (Figure 4.7).

Overall, spectra from the sample under consideration here are chemically very similar to those of *C. principalis* in Zodrow et al. (2000b, Figure 3), except for the band at 1032, which is due to the strong presence of lignin. This is often significant in modern and fossil cuticles, and survives taphonomic processes well (Zodrow et al., 2000b).

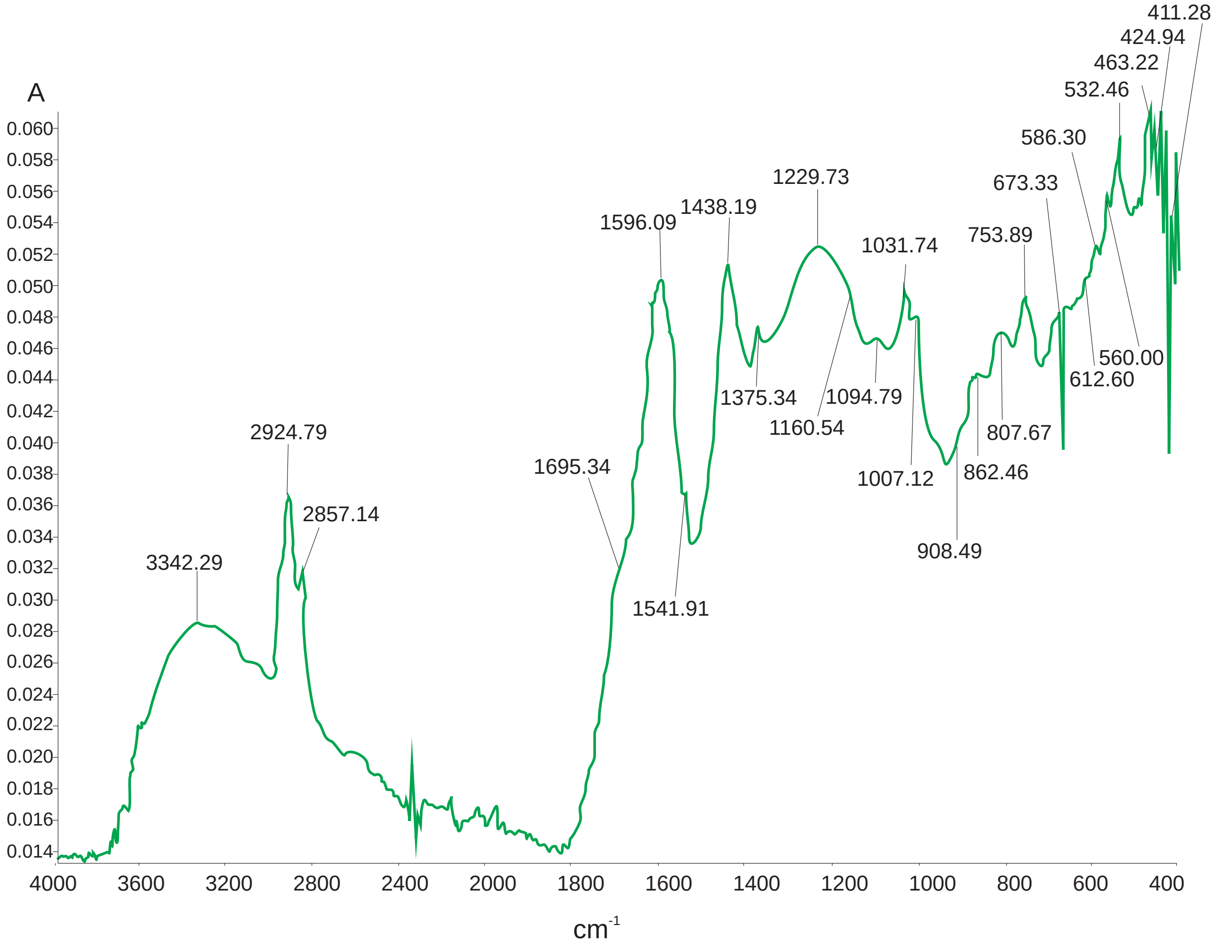


Figure 4.5: Unaltered spectral data from *Cordaites* sp., specimen number S146052-02, NRM collections, Hebei province, Chao Ko Chwang locality/Formation (Shanxi Formation age).
A is absorbance, cm^{-1} is the wave number, defined as the reciprocal of the wavelength: W=1/λ, where W=wavelength and λ= wavelength in cm.

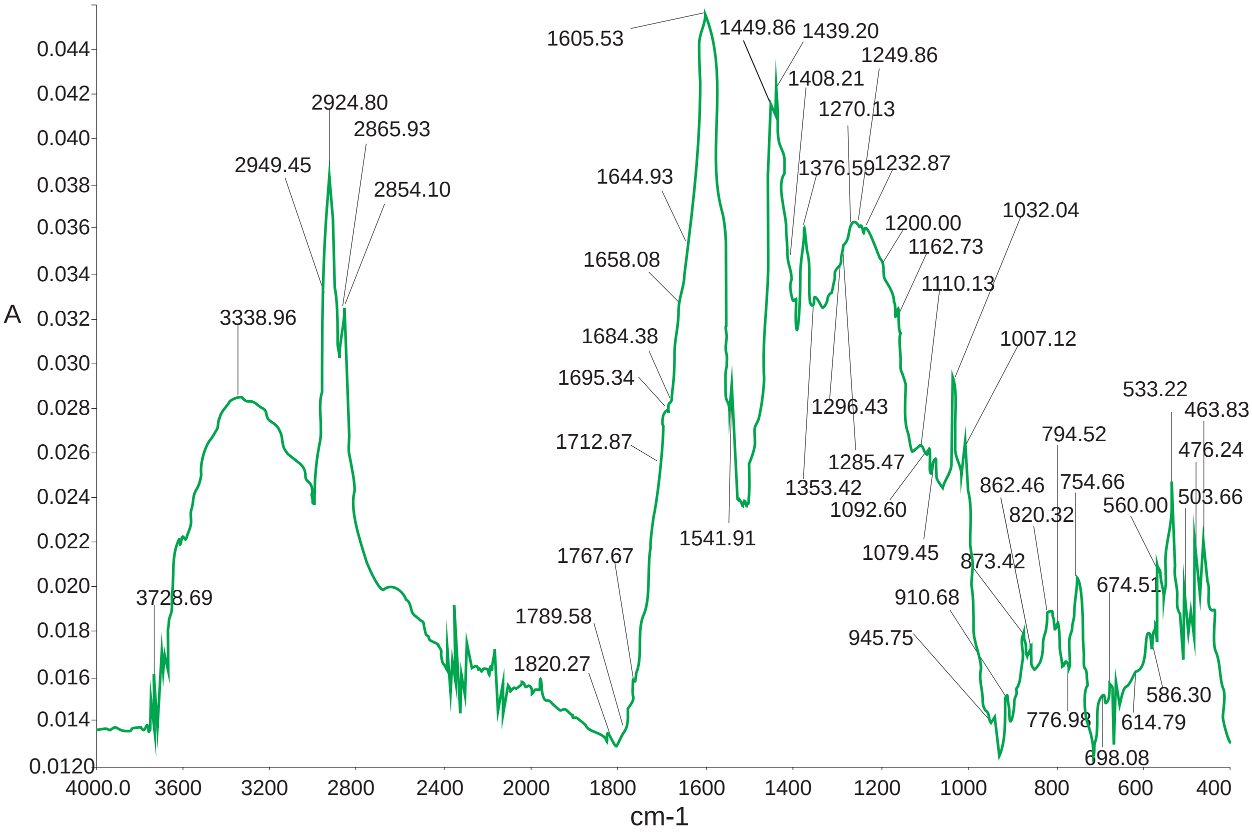


Figure 4.6: Deconvolved spectral data from *Cordaites* sp., specimen number S146052-02, NRM collections, Hebei province, Chao Ko Chwang locality/Formation (Shanxi Formation age).
A is absorbance, cm^{-1} is the wave number, defined as the reciprocal of the wavelength: W=1/λ, where W=wavelength and λ= wavelength in cm.

Feature	Appx. wavenumber assignment (cm^{-1})
Broad hydroxyl peak	3340
Aliphatic stretching region	2949 – 2854
Aliphatic bending region	1500 – 1370
Cellulose and lignin region	1300 – 1000
Aromatic out of plane region	900 – 700

Table 4.2: Key features of the spectral data for *Cordaites* sp.

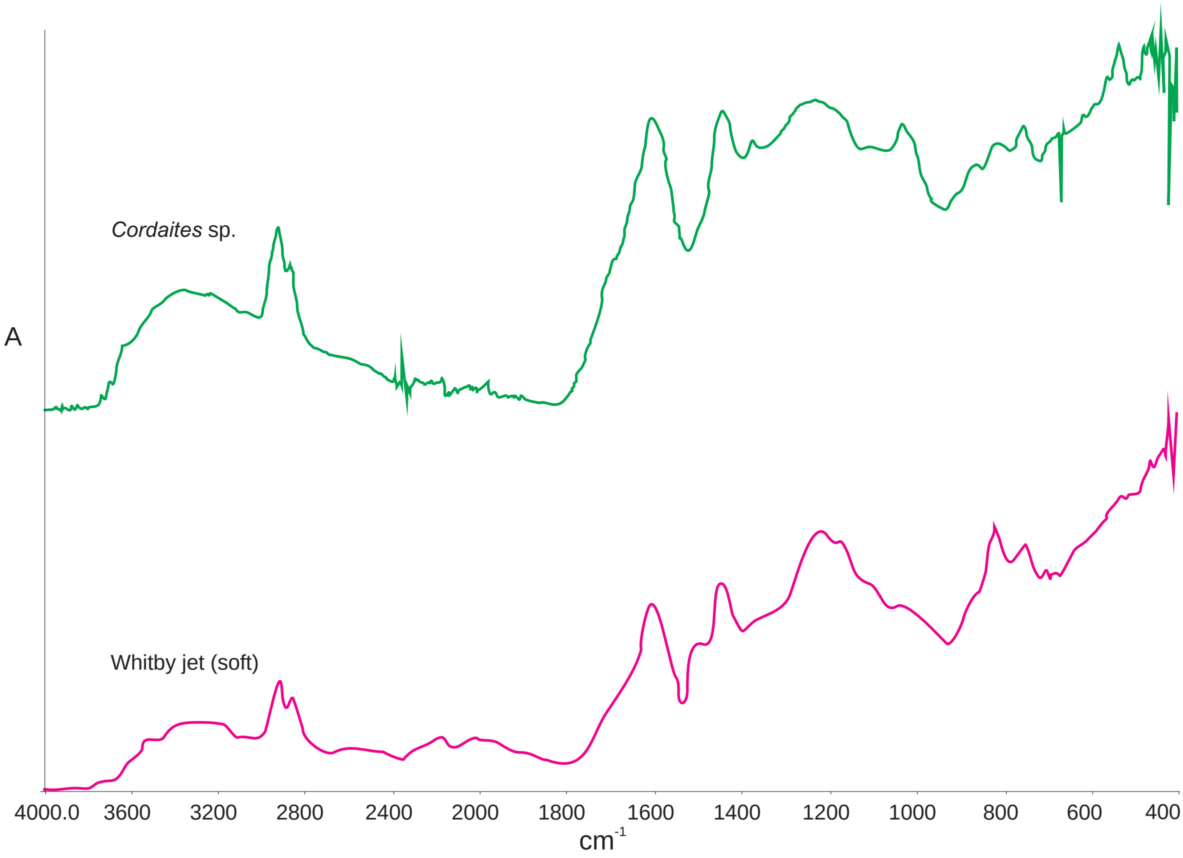


Figure 4.7: Spectral data from *Cordaites* sp., specimen number S146052-02, NRM collections, Hebei province, Chao Ko Chwang locality/Formation (Shanxi Formation age), compared with a sample of lignite (soft jet). A is absorbance, cm^{-1} is the wave number, defined as the reciprocal of the wavelength: W=1/λ, where W=wavelength and λ= wavelength in cm.

4.5.5 Discussion

It appears that the sample under consideration is most likely to belong to *C. principalis*, which does in fact confirm the previously documented occurrences of this species in China whose identifications were based upon macromorphology. The hitherto Chinese species *C. baodeensis* has a very similar epidermal form, but the chemical signature of this specimen very closely matches that of *C. principalis*. Zodrow et al. (2000b) documented a significant amount of epidermal variation within cuticles which produced identical FTIR spectra, introducing the fact that alongside the considerable variation in the pattern of veins visible on cordaite leaves in hand specimen, a range of epidermal patterns may also be seen within one species. This means that there is a distinct possibility that *C. baodeensis* is closely related to *C. principalis*, and that they may even be synonymous. Hence, cordaite taxonomy is in need of significant review, to build on the findings of both Šimůnek (2007) and Zodrow et al. (2000b) and incorporate epidermal and biochemical data into a new, replicable and easily comparable system.

4.6 Summary

This study has compared several taxa from Euramerica and Cathaysia, in order to assess their geographic and temporal scope as representatives of wider communities. A range of methods have been employed as appropriate, depending on feasibility and availability.

True *Alethopteris* was not found to be present in Cathaysia, from the limited amount of incomplete frond material deposited in the collections of the NRM and the RBINS.

Both *Neuropteris ovata* and *Odontoperis subcrenulata* were confirmed as present in Cathaysia, the former being proven unequivocally with the discovery of distinctive adaxial cuticle.

Finally, two samples of cordaite cuticle, from North China and South Wales, were examined both epidermally and biochemically (in the case of the Chinese sample) in order to attempt to ascertain their affinities. The South Wales cordaite proved inconclusive, mainly because of a paucity of comparable studies. Cleal and Shute (2007) also showed that drying of cuticle during fossilisation can significantly affect its appearance, rendering comparisons difficult depending on individual taphonomic processes. However, the addition of FTIR biochemical analysis in examination of the Chinese cordaite allowed designation to the widespread *C. principalis*, and highlighted Zodrow et al.'s (2000b) findings that as well as macroscopic venation being variable across the leaves of single cordaite species, cuticular structure can be as well. This highlights the difficulties concerning taxonomy of the cordaites, and as it stands these difficulties preclude the use of specimens, such as those examined here, as marker species for either Euramerica or Cathaysia, as it is clear that the system requires a radical overhaul. Biochemical analysis appears to be the only reliable way to determine cordaite species at this time, but more studies on microscopic specimens are needed, in order to test this theory and create a usable database with sufficient geographic and geographic range which will contextualise both epidermal (e.g. Šimůnek, 2007) and biochemical work (e.g. Zodrow et al., 2000b).

Furthermore, this database could be expanded for use as a taxonomic tool in other plant groups, incorporating isolated studies such as Cleal et al. (2009b) and the data from *Neuropteris ovata* above, and to inform on any signatures present from geographic, stratigraphic, environmental or evolutionary factors. Species could effectively be precisely identified by their unique chemical fingerprint, and tracked through space and time. More investigation is also needed into the effects of taphonomy (Zodrow et al., 2000b; Cleal and Shute, 2007) and cuticle processing methods (a discernable effect from processing is seen in the *N. ovata* spectra in Figure 4.3).

Fossil species pteridosperms *Neuropteris ovata* and *Odontopteris subcrenulata* have been confirmed as present in Cathaysia, extending their ranges from known Euramerican records considerably. *N. ovata* ranges from the Asturian (uppermost Moscovian) in Euramerica (Cleal and Shute, in press) through to the Permian - most likely at least the Artinskian, as all figured specimens which have age data attached are from the Shanxi Formation. *O. subcrenulata* ranges from the Barruelian (mid Kasimovian) (Cleal and Shute, in press) to at least the Roadian (Lower Shihhotse Formation; Halle, 1927). This gives remarkable ranges of at least 30 Ma for *N. ovata*, and at least 35 Ma for *O. subcrenulata*, and confirms a link between Cathaysia and Euramerica, whereby these species seemingly ranged unchanged across vast tracts of land on the converging Pangaean continent. This link formed possibly as early as the latest Moscovian. This supports the findings of Chapter 3, with a Carboniferous-age connection of the Angaran phytogeographic province (=Euramerican conduit) to North China. However, more resolution is needed with the fossil species under consideration here: their full temporal range in Cathaysia, in the light of results here, is not known, and would be needed in order to assess the first (and last) occurrences of them in Cathaysia, and the degree of overlap between occurrences in Cathaysia and Euramerica which may indicate a source direction and/or interchange.

These findings highlight the difference between modern, fully diagnosed whole-plants, and fossil taxa. It is highly unrealistic for one (modern) taxon to have a temporal range of over 30 Ma, as evidenced through the findings here and those of Laveine et al. (e.g. 1993; at genus level), and yet within the bounds of the fossil information available and the occasionally highly detailed analyses possible (see *N. ovata* above), all evidence points to this situation. Analytical methods will inevitably continue to improve, but will always be limited by the fossil material available, and through the filter of such vast tracts of time it is clear that we must continue to separate the majority of fossil taxa from ‘true’, self contained species for the foreseeable future.

PLATES

Plate I: *Neuropteris ovata*, *N. pseudovata*, *N.* sp.

Specimens all from Hebei province, from NRM collections unless otherwise stated. Scale bars 1 cm.

a) *N. ovata*, specimen S145945, Jingxing, age unknown.

b) *N. pseudovata*, specimen 36292 RBINS. Tangshan, Chao Ko Chwang Formation (Shanxi Formation age).

c) *N. pseudovata*, specimen S146140b, Chao Ko Chwang locality/Formation (Shanxi Formation age).

d) Enlargement of c, showing venation.

e) *N. pseudovata*, specimen 29588 RBINS. Tangshan, Chao Ko Chwang Formation (Shanxi Formation age).

f) *N.* sp., specimen S146659, Majiagou, age unknown.

g) *N.* sp., specimen S146675c, Majiagou, age unknown.

h) *N.* sp., specimen S146801, Majiagou, age unknown.

i) Enlargement of h.

PLATE I

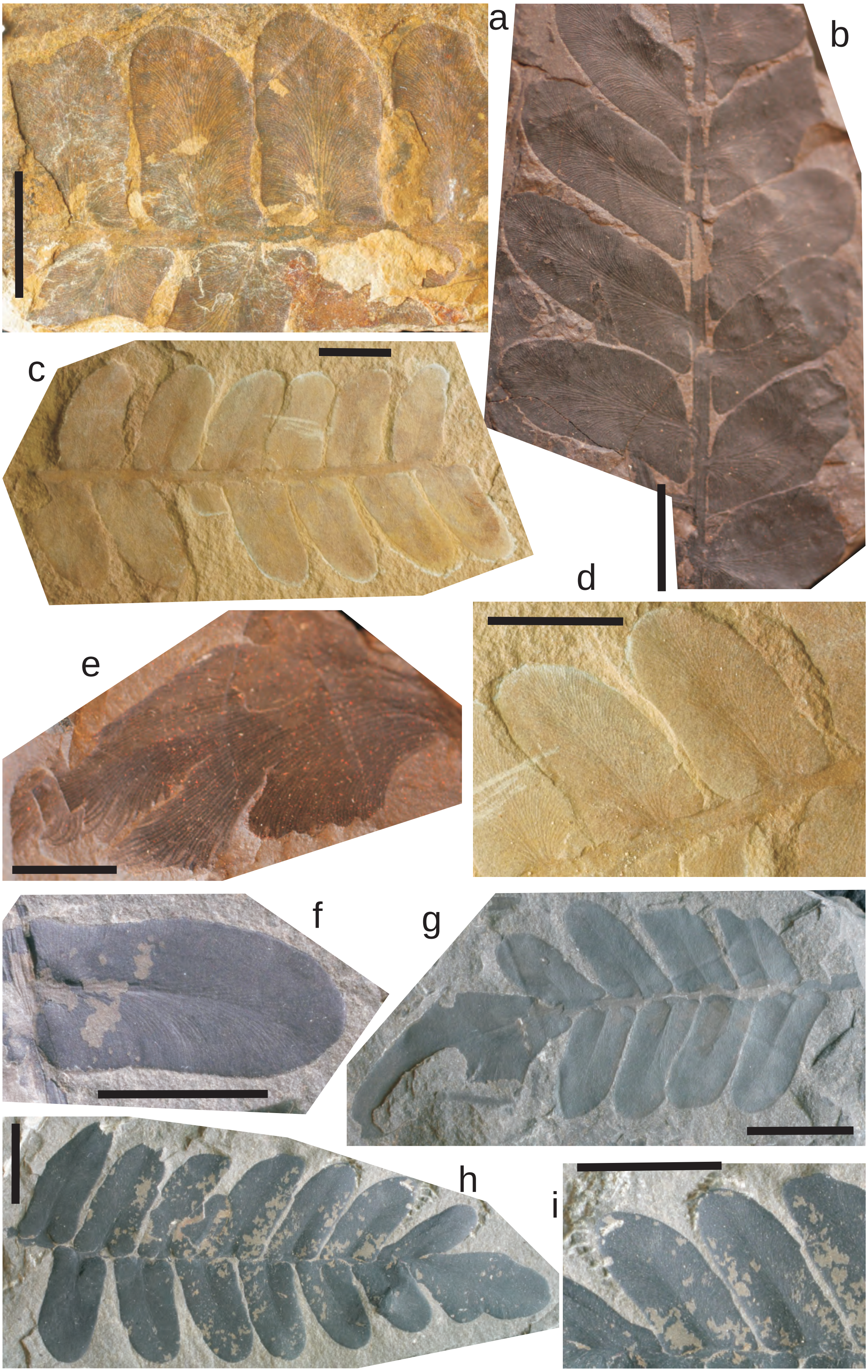


Plate II: *Neuropteris* sp.

Specimens all from Majiagou, Hebei province, from NRM collections, ages unknown, unless otherwise stated.

Scale bars 1 cm.

a) Specimen S146675b-01.
b) Enlargement of a, showing pinnule shape and venation.
c) Specimen S146677a.
d) Enlargement of c, showing venation.
e) Specimen S146742c-03.
f) Specimen S146797.
g) Enlargement of f, showing prominent basal auricle and triangular pinnule shape.
h) Specimen S146260, Luanxian=Chao Ko Chwang locality/Formation (Shanxi Formation age).

PLATE II

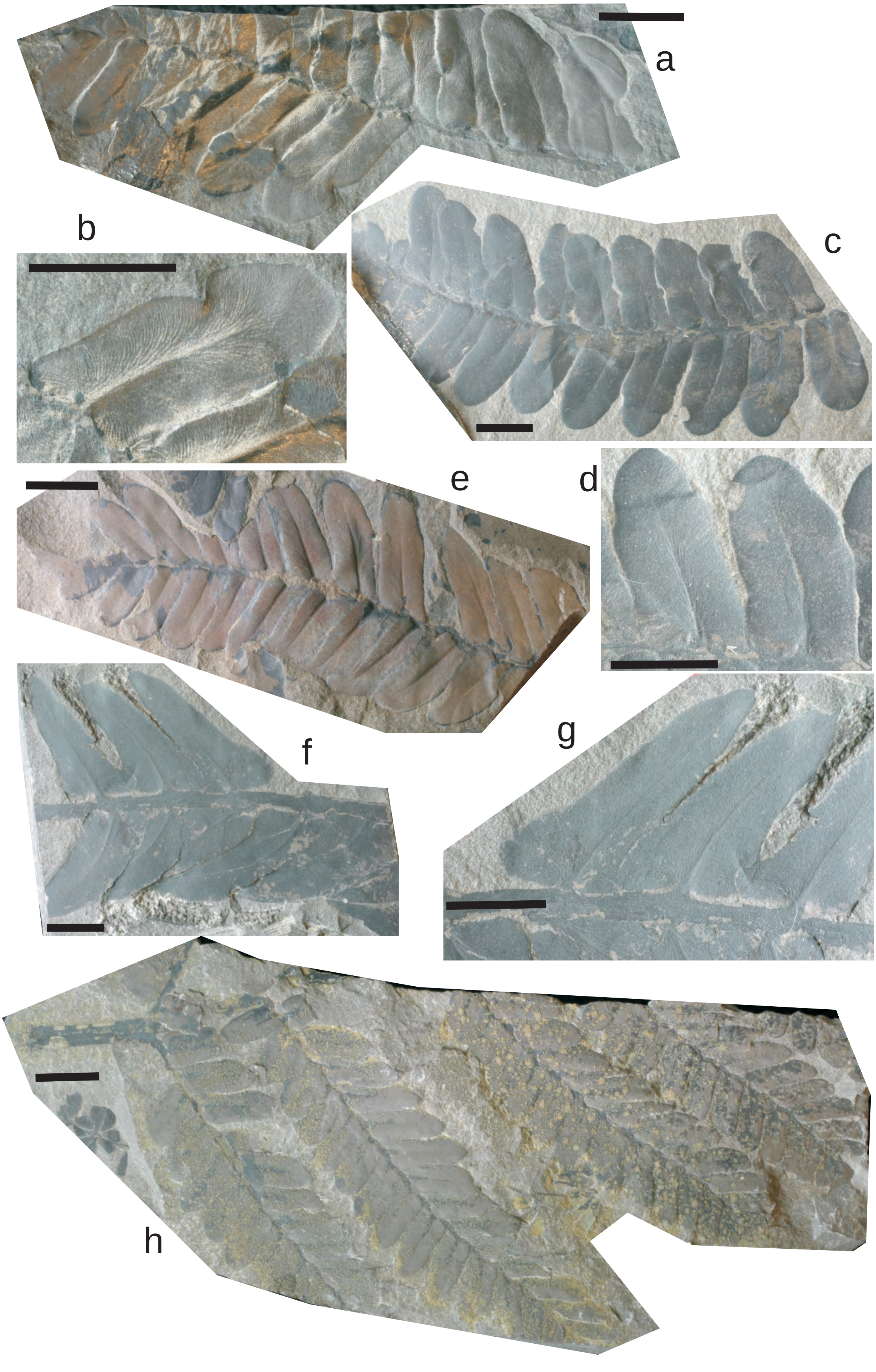


Plate III: *Neuropteris* sp.

Specimens all from Majiagou, Hebei province, from NRM collections, ages unknown.
Scale bars 1 cm.

a) Specimen S146808.
b) Specimen S146565a-03.
c) Enlargement of b.
d) Specimen S146669a-01.
e) Specimen S146812a (composite image).
f) Enlargement of e.

PLATE III

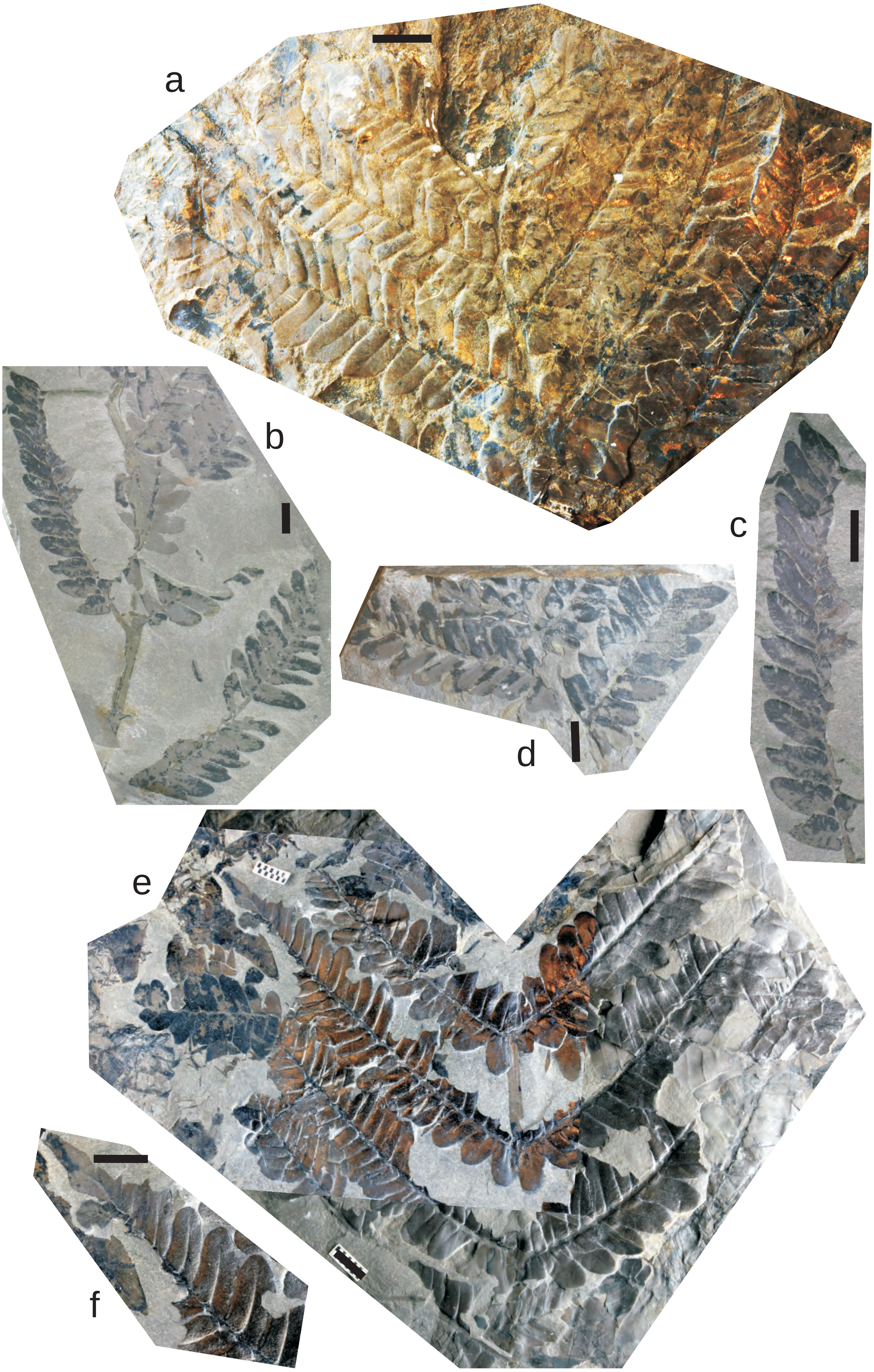


Plate IV: *Neuropteris* sp.
All specimen S146734, from Majiagou, Hebei province, from NRM collections, age unknown.
a-d: Scale bars 1 cm. Different pinna on the same slab, demonstrating variation.
e-h: Scale bars 100 microns. Cuticle samples from pinna figured in c.
e) Abaxial cuticle.
f) Abaxial cuticle. Note the trichome base (large oval) and multiple stomata.
g) Adaxial cuticle.
h) Adaxial cuticle. Note the sinuous cell walls.

PLATE IV

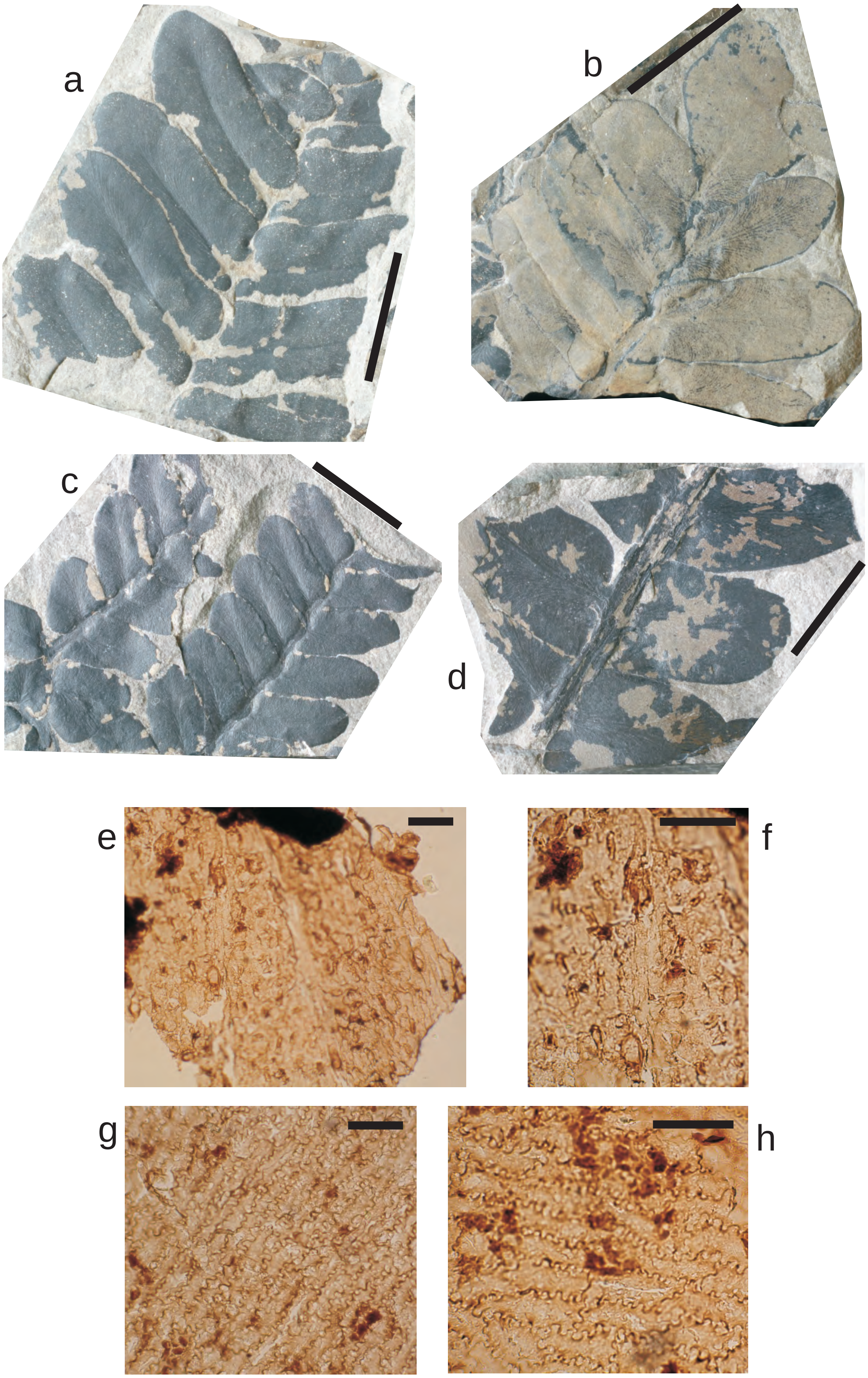


Plate V: *Alethopteris norinii*

Specimens all from Taiyuanfu area, Shanxi province, from NRM collections, from Lower Shihhotse Formation unless otherwise stated.

Scale bars 1 cm.

a) Specimen S138181.

b) Enlargement of a, showing venation and ?glands between veins.

c) Specimen S138187.

d) Specimen S138186a, from Shanxi Formation, showing a large ?seed, found in association with *A. norinii* foliage.

e) Specimen S138185.

f) Enlargement of e, showing venation.

g) Specimen S138188, showing basal pinnule lobing.

PLATE V

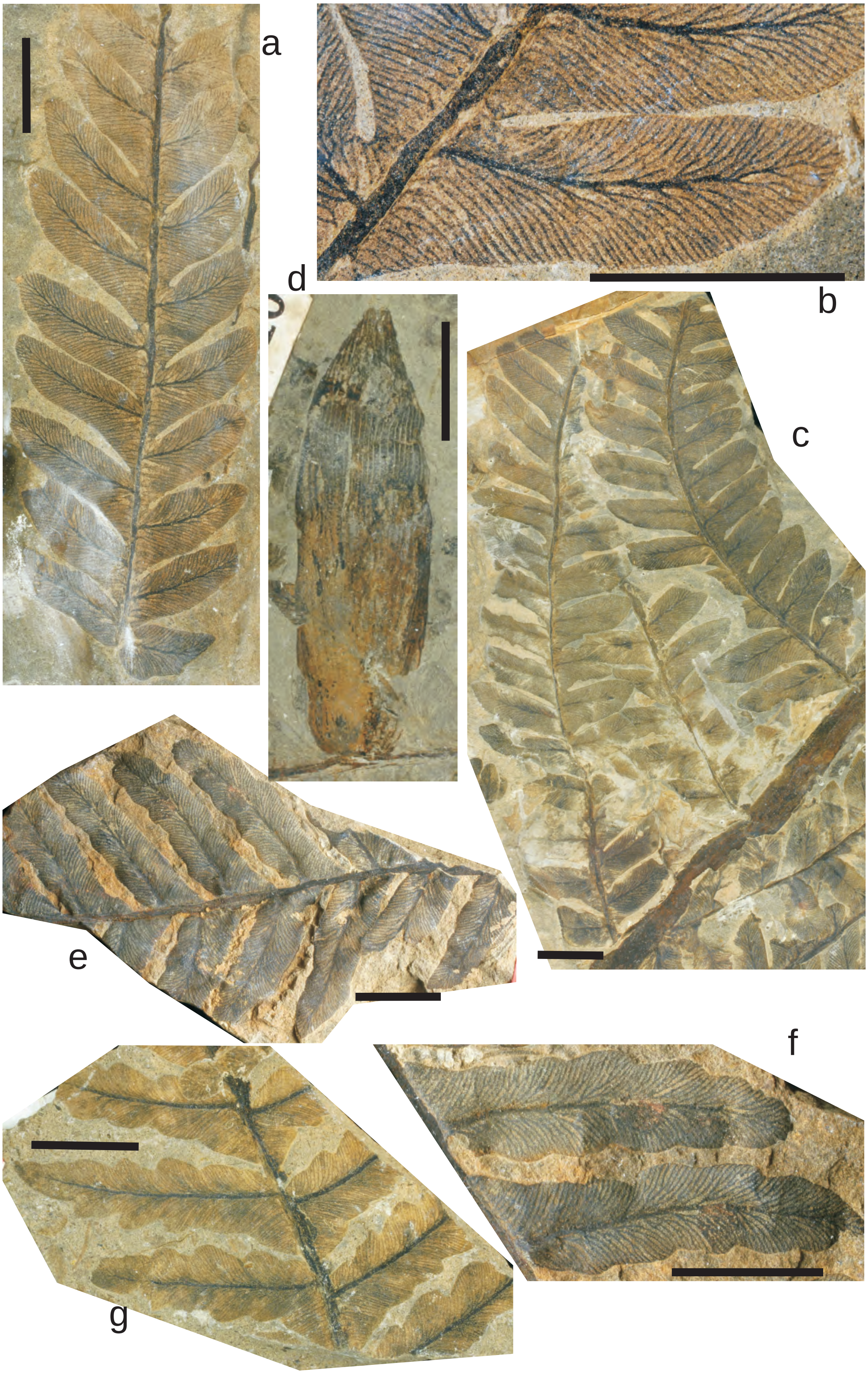


Plate VI: ***Alethopteris ascendens***
Specimens all from Shanxi province, from NRM collections.
Scale bars 1 cm.
a-d from Taiyuan area, from Lower Shihhotse Formation.
e-g from Gaoping, ages unknown.
a) Specimen S138136a.
b) Enlargement of a, showing venation.
c) Specimen S138136b.
d) Enlargement of c.
e) Specimen S143496.
f) Specimen S143521 (cf.).
g) Enlargement of f.

PLATE VI

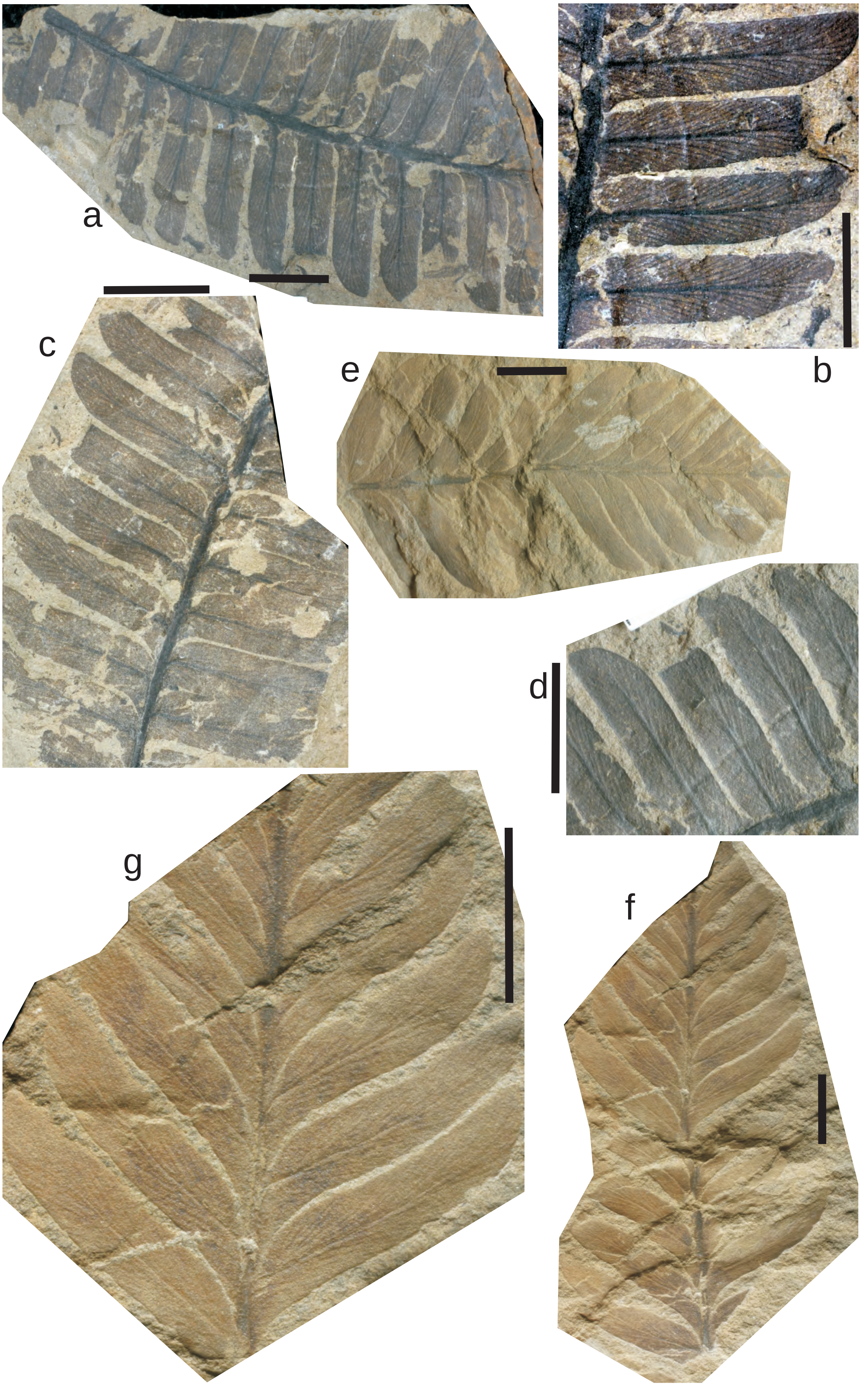


Plate VII: ***Odontopteris subcrenulata***

Specimens all from Taiyuanfu area, Shanxi province, from NRM collections, ages unknown unless otherwise stated.

Scale bars 1 cm.

a) Specimen S140120.

b) Specimen S138214, also figured by Halle (1927) Plate 34, Figure 3. From Lower Shihhotse Formation.

c) Enlargement of b.

d) Specimen S142613.

e) Enlargement of d.

f) Specimen S140119.

g) Enlargement of f.

h) Specimen S140121.

i) Specimen S140118.

PLATE VII

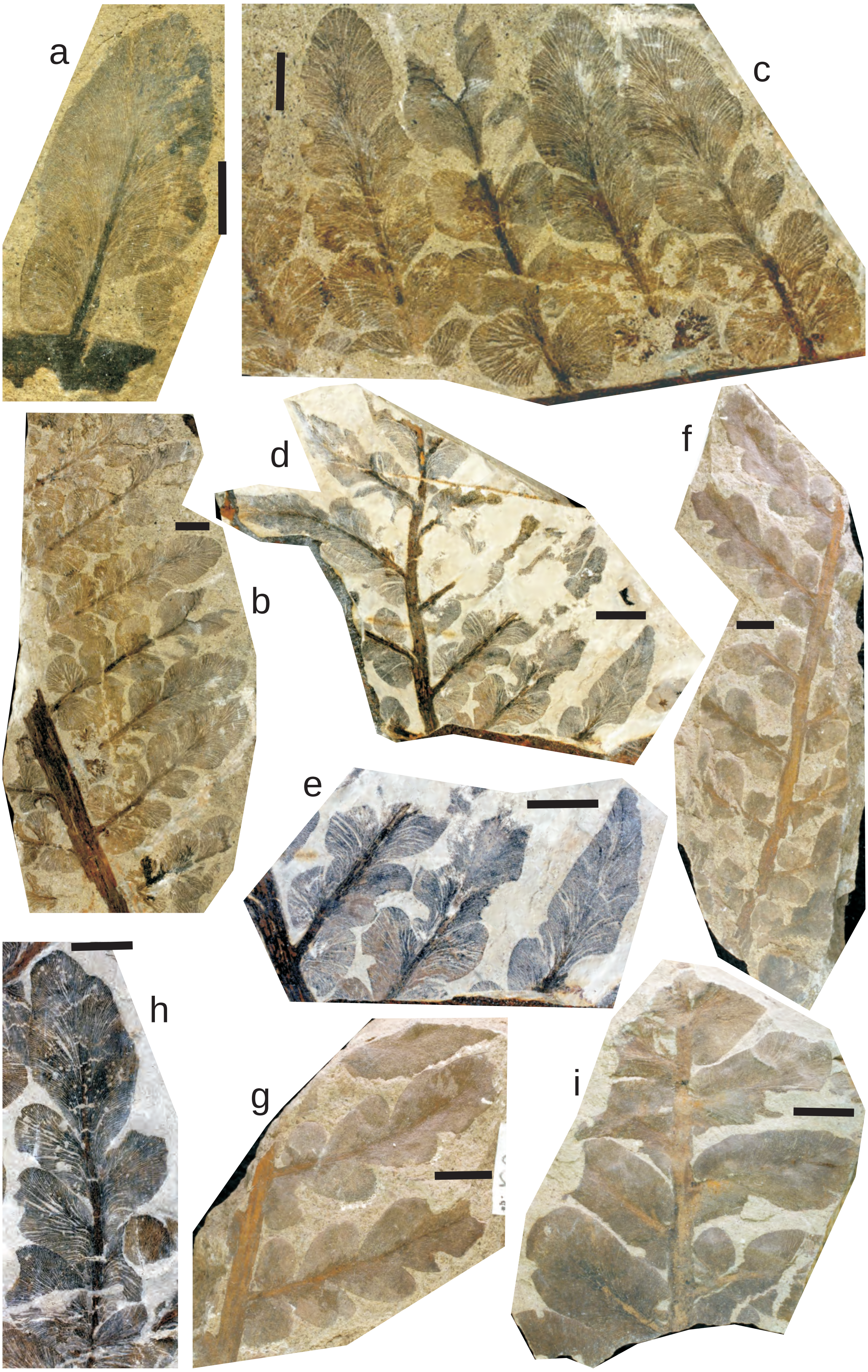


Plate VIII: *Cordaites palmaeformis,* South Wales
Specimen 22.114.G2418 from NMW collections, Llantwit No 3 bed, Grovesend Formation, Asturian/Cantabrian age, Llantrisant area.
b-d scale bar 100 microns.
a) Hand specimen. Scale bar 1cm.
b) Adaxial cuticle.
c) Abaxial cuticle.
d) Abaxial cuticle. Costal and intercostal zones are prominent, and many stomata are visible.

PLATE VIII

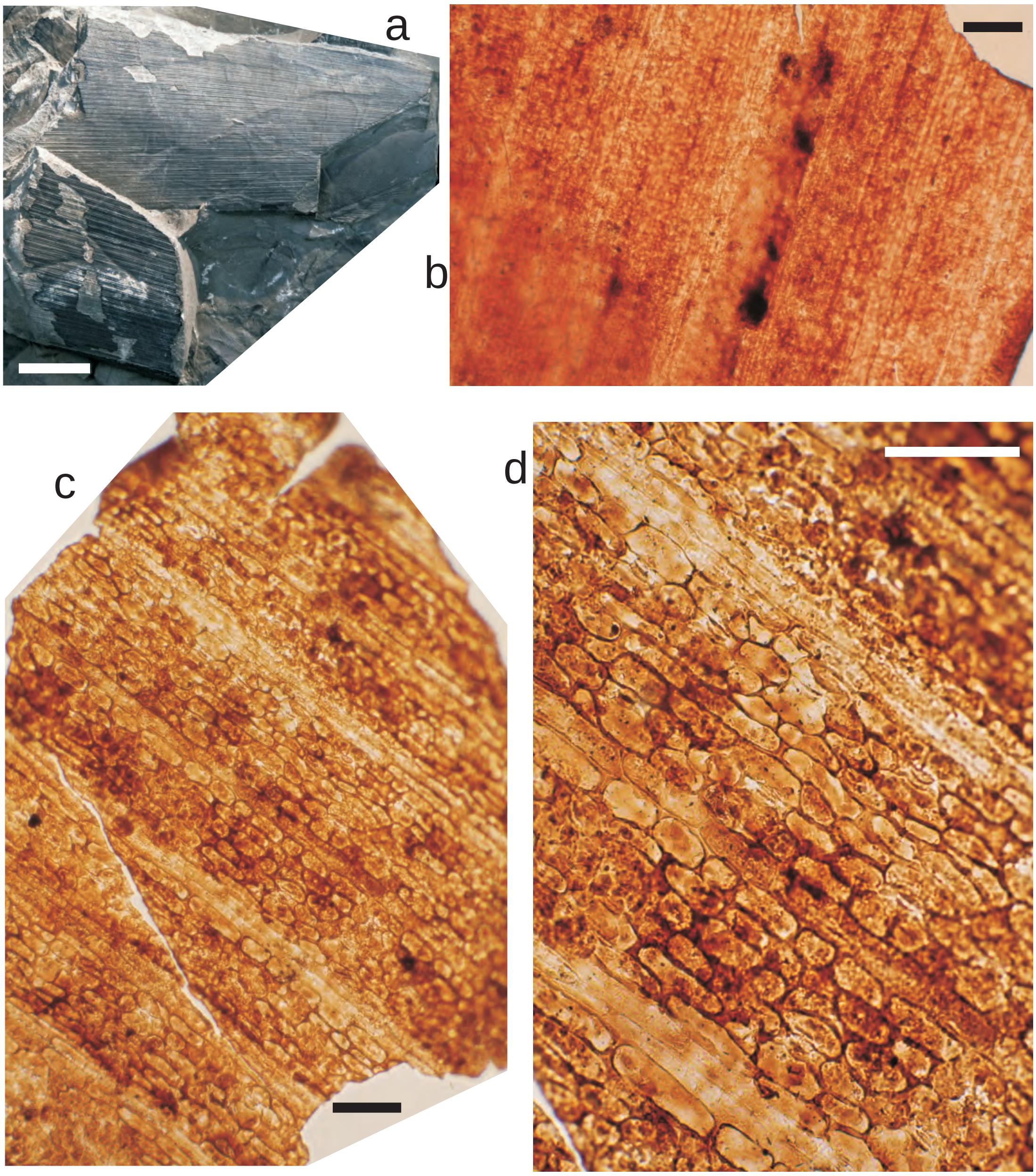


Plate IX: *Cordaites* sp., China

Specimen S146052-02 from NRM collections, Hebei province, Chao Ko Chwang locality/Formation (Shanxi Formation age).

a-b Scale bar 1 cm.

c-d Scale bar 100 microns.

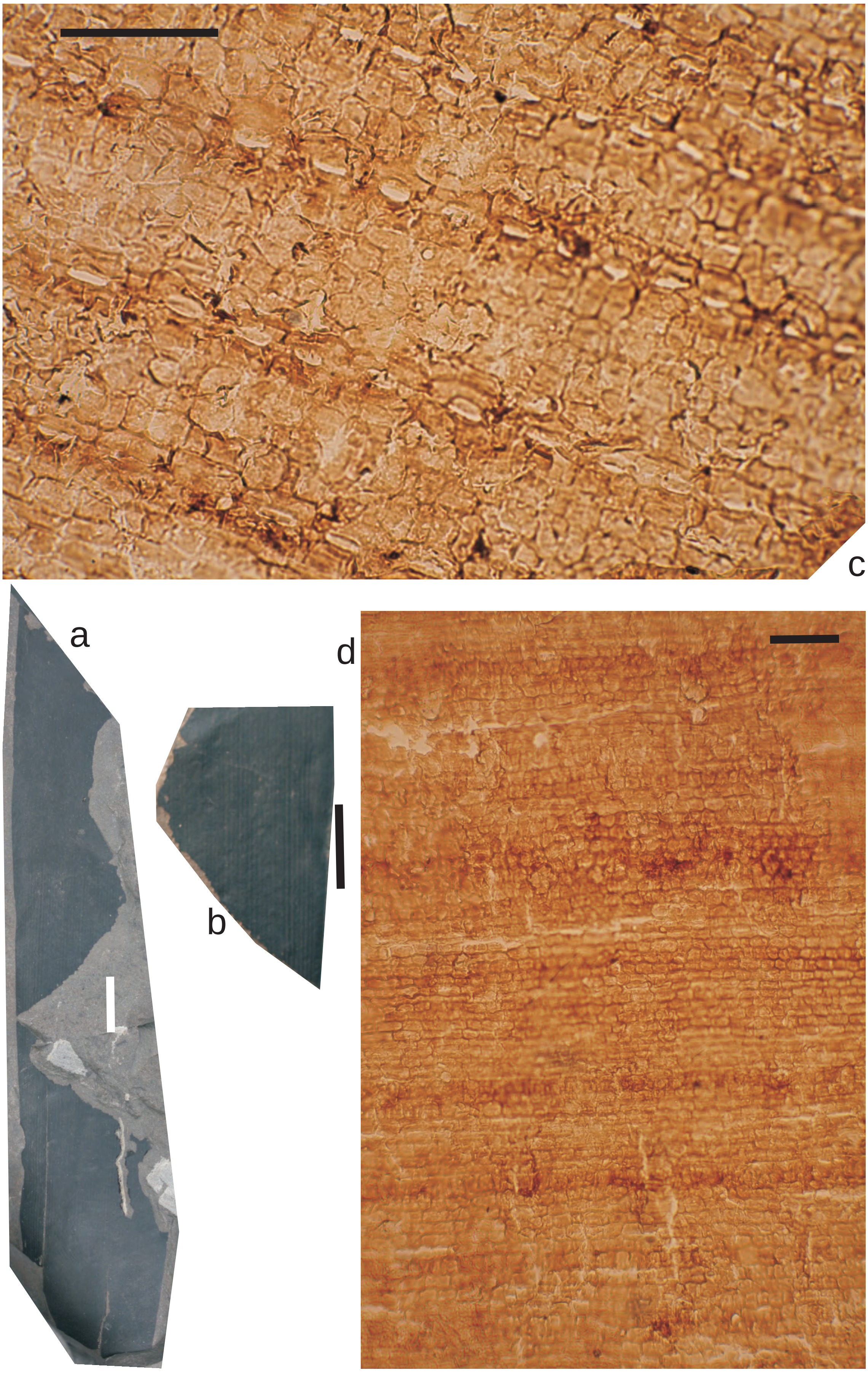
a) Hand specimen.

b) Enlargement of a.

c) Abaxial cuticle.

d) Adaxial cuticle.

PLATE IX



-CHAPTER 5-

THE RELATIONSHIP BETWEEN THE EURAMERICAN AND CATHAYSIAN PROVINCES: AN EXAMINATION USING LARGE-SCALE DATASETS

5.1 Rationale

Chapter 3 has shown that the mainly Permian wetland flora of North China was very likely to have been sourced from that of Carboniferous Angara to the west, and in turn from Euramerica. In addition, Chapter 4 has confirmed the presence of fossil taxa which span these areas, from the Carboniferous through to the Permian. This chapter now addresses the geographic gaps between these studied aspects, by gleaning the most recent species lists, where they exist, from latest Carboniferous coal basins in central and western Europe. UK sites have been discussed and analysed in Chapter 2 (King et al., 2011), and additional sites in Europe are the Iberian Peninsula (Spain/Portugal), the Saint-Étienne (France) and Saar-Nahe (Franco-German border) basins, Central/West Bohemia (Czech Republic), and the North Caucasus platform (European Russia). Mazon Creek from the USA is also included as a reference to floras further west. Flora from China were analysed in Chapter 3. Locations, geological background and correlation of all of these sites are given in Chapter 1.

The aim of this chapter is to try and trace the source of the named 'North Cathaysian' wetland flora through the stratigraphical overlap of these ecosystems between Euramerica and Cathaysia. Species lists are compared to those already studied in detail from the southwestern UK (Chapter 2) and China (Chapter 3). This is the first study to attempt such a comparison on such a large scale, and represents a new way to address a long-standing geological and palaeobotanical issue.

5.1.1 Palaeogeography

Many palaeogeographical map hypotheses for the late Palaeozoic are in existence, and the configurations of those chosen in Figures 1.1-1.2a are generally well supported using several lines of evidence (Gastaldo et al., 1996; Blakey, 2011). However, in the context of this study, these maps show a fundamental flaw. The very fact that wetland plant communities were present on the North China block, and by inference across Angara (Siberia) also, means that these two landmasses must have been positioned in far lower latitudes than depicted in these maps in order to have been within a favourable climatic belt for the wetlands to survive and prosper. The reconstructions proposed by Laveine et al. (1993), whereby the tectonic blocks from North America through central Europe, Siberia and North China are in alignment and contact about the Equator around the mid-Carboniferous, appear to be much more realistic arrangements, and as Laveine et al. state, have some geological support.

This then raises the issue of the types and causes of interchange and separation which may manifest themselves in the data from the floras of Euramerica and Cathaysia. Clearly many factors needed to be in congruence for these floras to survive, such as available, environmentally favourable habitat, and favourable climate and moisture regimes, and it would not have been possible for these communities to migrate wholesale across large bodies of water (see Section 3.1.3). Therefore, once the relevant blocks were close enough for floral migration and interchange to take place across them and across land bridges which must have formed between them, any repeated connections and disconnections on relatively short timescales would have been due to more flexible factors, such as sea level fluctuations creating temporary barriers (DiMichele et al., 2010), overprinting any patterns from the steady destruction of habitat due to the progressive amalgamation of Pangaea (Cleal et al., 2009a).

5.2 Material and methods

The UK data have been studied in depth in Chapter 2, as have the Chinese in Chapter 3, and these were reanalysed alongside the additional data sources listed above. Each was indicated as, or assumed to be, a reasonable representation of the wider area of provenance. Inevitably many of the lists have not been revisited for many years, and while the weight of the data in most cases precluded detailed examination of the lists, accompanying plates, and original material (if still in existence), the lists were subject to the processes detailed in Chapter 2. This involved standardising by removing seeds, reproductive organs, roots and stems, with the aim of only analysing material which represents discrete species so as not to over-represent taxa and groups of taxa. As before, lists were standardised at species level initially in order to allow the updating of names to currently accepted nomenclatural standards, and the merging of any taxa under open nomenclature where a fully diagnosed species of the same name was present. Single occurrences across all divisions were removed in order to streamline the data and enhance patterns (see Chapter 2). The taxonomic list was then raised to genus level to allow more meaningful comparisons across large tracts of space and time; genera will, by the very nature of containing multiple species, have a larger temporal and geographic span than individual species, and therefore will be more likely to be traceable. At all stages, data were run to check that patterns seen below were consistent and were not eroded or otherwise obscured by the data standardisation process, and this proved to be the case, indicating a very strong signal.

Stratigraphic divisions across localities, given in the source texts, were maintained where these could be correlated with more widely recognised divisions, or as an approximation to those divisions in the absence of more accurate information (Figure 5.1). This allowed as high as possible a stratigraphical resolution to be maintained, whilst also increasing the possibility of finer patterns being teased out. In most cases these divisions correspond with current global standard stages and substages, although the age of the species lists and complexities of the areas concerned means that this correspondence may not be absolute. In general, individual sources permitting, data were formatted to be stratigraphically rather than geographically compared, in order to trace floral patterns through time (Figure 5.1). Where ages were not known for the flora, from some areas in China, these data were nonetheless retained in the analyses in order to remain consistent with the analyses in Chapter 3, and to augment the number of data points for China. With localities more proximal to China, it was felt unnecessary to analyse data from lower in the sequences (e.g. Bolsovian aged) as these do not directly overlap with the Chinese data.

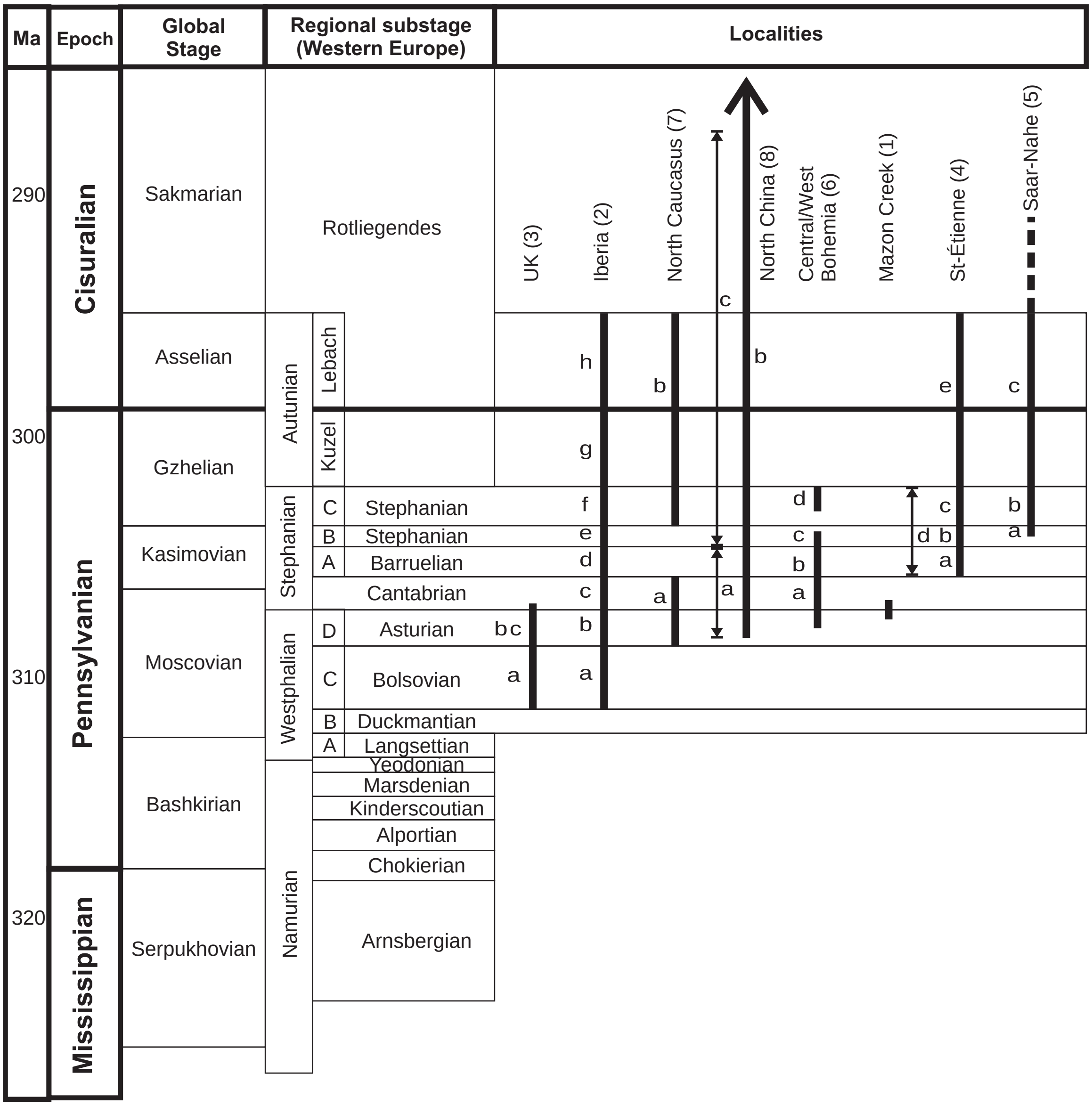


Figure 5.1: Approximate stratigraphic positions of the data points analysed from each locality. See text for sources of data.
Numbers in brackets correspond to those on maps in Figure 1.2a-c.
Letters are carried forward into NMDS analyses; see Figures 5.2 and 5.3.
For the UK, points b and c are Asturian-aged from South Wales and Bristol-Somerset respectively. See Figure 2.2 for a detailed correlation.
For China, a is the Tongshan Formation (Asturian-Barruelian age),
b is the Yuehmenkou ‘Series’ (Asturian-mid Kungurian age), and c is the Linsi Formation (Stephanian B-late Sakmarian age). For a fuller correlation of these points within the Chinese dataset, and the rest of the Chinese data points, see Figure 3.2.

Data were again analysed using the PAST package, and to visualise the results NMDS, using the Raup Crick distance metric, was again chosen in preference to DCA, as the latter showed the strong ‘triangle effect’ in the results (Bush and Brame, 2010). Although the overall patterns between the two ordination methods are undoubtedly the same, the distortion in the DCA was deemed a hindrance to interpretation of results.

5.2.1 Data sources

The UK data from Chapter 2 were split into appropriate regional substages, and the Pennant Sandstone Formation (=Bolsovian) from the Bristol Coalfield was discarded as having very few floral occurrences. This left the Grovesend Formation (=Asturian, 28 genera after data processing) of Bristol, and the Bolsovian aged seams 11-6 (23 genera), and the Asturian/Cantabrian aged upper coal seams, from 5 to 1 inclusive, from the South Wales Coalfield (23 genera) (Figure 2.2).

Most of the Chinese data from Chapter 3 were divided by the original sources according to the stratigraphic system of Halle (1927), rather than the finer resolution of global standards largely present in the European data. The Halle system was maintained as most appropriate, as although it was impossible to determine exactly where the modern stage/substage boundaries should be, it can be broadly correlated with global stratigraphic systems (Figure 3.2). Data were sorted through each province. The only section of the vast repository in the NRM (Stockholm) collections for which approximate ages are known is that studied by Halle (1927). At the time of publication, the Taiyuan and Shanxi Formations were amalgamated into the Yuehmenkou ‘Series’, with the Benxi

Formation hitherto unrecognised as the lowest section of the Taiyuan Formation. However, on examination of the flora present, both in Halle's monograph and in the NRM collections, in the whole Yuehmenkou 'Series', there were found to be only 10 unique genera after data processing as detailed above. Therefore, the constituent formations were not split out from the 'series', and the flora in the beds named by Halle as part of the Yuehmenkou 'Series' were grouped together (Figure 3.2). The Upper and Lower Shihhotse Formations remain as designated by Halle, and yield 38 genera after processing. They were combined as they are of Middle-Late Permian in age and therefore are not from the interval that overlaps with the Euramerican data. The rest of the data from the NRM collections is of unknown age as explained in Chapter 3. They are likely to be from the Lower to Upper Shihhotse Formation interval, as this is clearly where the majority of fossils were found, but this is unconfirmed and so the data have been grouped. 39 genera were present after data processing.

From Hebei province, using the collections from RBINS (Brussels) in combination with Stockmans and Mathieu (1939, 1957) as in Chapter 3, it was possible to divide the flora into the given formations, which correspond to those of Halle: Tongshan (=Benxi, 19 genera), Linsi (=Taiyuan, 17 genera), and Chao Ko Chwang/Hung Ho/Tang Chia Chwang (=Shanxi, 33 genera) formations. (Chapter 3, while using the same data, was focussed primarily on the geographical patterns within North China, and therefore it was less appropriate to disengage localities from age as several localities spanned more than one formation.) Supplementary data from the NRM, based around the localities of Majiagou, Chengde, Jingxing and Zunhua were of unknown ages, and therefore were combined, and gave a total of 17 genera.

The data from Gansu province were again sourced solely from the collections at the NRM. They were split into three divisions; Bexell's Zone C (from Suzhou locality, 31 genera), Bexell's other, unknown Zone material (also from Suzhou locality, 51 genera), and the remaining data of unknown age (from Gaotai, Minle and Wuwei localities, 25 genera). Bexell's Zone C corresponds to the uppermost Permian and this, coupled with the unknown ages of the rest of the material, means that Gansu province is included for reference alongside the rest of the Chinese data points, and also because it was implicated in Chapter 3 to be a possible secondary pathway from Euramerica to Cathayisa.

Henan province was also included for reference, and data was sourced from Yang's (2006) monograph. Although three formations are described, all floras are from the Middle-Late Permian and so not directly comparable with the overlapping Carboniferous-Permian period. Therefore the formations were merged, giving a small total of 6 genera. Data were also included from the NRM collections as in Chapter 3, from the Anyang locality which has no age information. 18 genera were present. Although floras from Henan were shown in Chapter 3 to be of a different origin from those of North China, the data is included for consistency.

Data from the Mazon Creek site in Illinois, USA were compiled from Wittry's (2006) monograph, in combination with visits to the collections of the Field Museum, Chicago, and the voucher collection at the Smithsonian, Washington DC. All the material is undergoing review by Wittry, but the species list given here is the most up to date available, comprising 25 genera. All of the Mazon material is of the same age, at around the Asturian/Cantabrian boundary, hence is included as a single data point. Attempts were made to locate other data sources of sufficient size from the USA, but this proved difficult. Focus was therefore retained on sites as close to Cathaysia as possible in order to follow up on Chapter 3 and investigate the possible source of the Cathaysian flora being within Euramerica. Mazon Creek was retained to give an indication of the relationships of North American flora to that of Europe, with the added caveat of the different preservational style of Mazon Creek (as sideritic nodules) from that of the adpression floras from Europe and Cathaysia.

Wagner and Álvarez-Vázquez (2010) provided the data from the Iberian Peninsula that is synthesised here. Data cover the whole of the peninsula, from Tournaisian through to Autunian age, but for the purposes of this study only the Bolsovian onwards was used. This gave genera numbers of 18 (Bolsovian, 4 localities), 36 (lower plus upper Asturian, 9 localities), 33 (Cantabrian, 4 localities), 29 (Barruelian, 3 localities), 38 (‘Saberian’, including upper Barruelian and some Stephanian B, 5 localities), 39 (Stephanian B, 12 localities), 38 (Stephanian C/lower Autunian, 7 localities), and 40 (mid-upper Autunian, 8 localities).

The Saint-Étienne Basin data was sourced from the comprehensive palaeobotanical monograph of Doubinger et al. (1995). There has been some subsequent revision of the stratigraphical ages of the main divisions and their floras in the basin (Wagner, 1998), and they are here divided into Barruelian (‘Stephanian A’, Rive de Gier Formation, 22 genera), Stephanian B (Gruner member, 28 genera), Stephanian C (Beaubrun and Talaudière members, 30 genera in total), and Autunian (‘Stephanian D’, Bellevue member, Couronnement stage, 28 genera in total), and Stephanian undifferentiated (26 genera).

Two data sources were used for the Saar-Nahe (Saar-Lorraine) basin in southwest Germany. Cleal (2008) covers the Ottweiler Group, and gives floras from the Stephanian B (20 genera) and C (15 genera), and Kerp and Fichter (1985) covers floras from the Rotliegendes. This conformably overlies the Ottweiler Group, but its age is disputed as the position of the Carboniferous-Permian boundary within its lower constituent (the Glan Subgroup) is not confirmed (Königer et al., 2002; Uhl et al., 2004). However, as the vast majority of flora listed in Kerp and Fichter (1985) are from the upper Rotliegendes (Nahe Subgroup), they have been combined to give one data point of Carboniferous-Permian boundary age, bearing 21 genera.

Central and West Bohemia data was compiled from Šimůnek (Table 4 in Pešek, 1994) and a later, unpublished list obtained from Šimůnek personally. This was already divided into the upper Kladno formation (Nýřany Member, 33 genera) of Asturian to Cantabrian age, and the Týnec, Slaný and Líně formations, of Barruelian ('Stephanian A', 24 genera), Stephanian B (36 genera) and Stephanian C (21 genera) ages respectively, and these groupings were maintained.

The final area under consideration is the North Caucasus. These data were sourced from Anisimova (1979), covering the upper Moscovian (12 genera), and Schegolev (1979), covering the Stephanian C and Autunian. The latter data, taken from the largest given list from the 'T1' site, were divided into 26 individual localities which did not relate to global standards, and so they were grouped together to give 18 genera.

5.3 Stratigraphic progression and relationships

Data were coloured according to stratigraphical groupings and plotted using NMDS (Figure 5.2). Most striking is the progression of the European (and American) data to the left of the plot. Data points cluster according to age, which decreases up the y-axis. The Chinese data to the right do not follow this ordering, instead having the older material on the left and the younger, if taken together, to the right. The older Chinese material plots closer to the Euramerican than the younger, indicating a surprisingly close affinity. The less ordered appearance of the Chinese data could indicate a less strong stratigraphic control, or another control altogether, but as there are fewer points of far lower resolution it is possible to place any number of interpretations on the data.

Clearly the evolutionary status of the flora as a whole, in Euramerica at least, was a strong control on floral affinity, over and above the geographical position of the particular community. This is shown especially with the clustering of the Mazon Creek point with those of a similar age in Europe, many hundreds of miles away.

There is no stratigraphic gap between the floras of Euramerica and China, but it appears the geographical gap is masking the true details of their relationship. The large geographical area of Angara is not accounted for within the fossil record studied, and so the available data are only giving the relationship between areas on either side of this discontinuity. Under these circumstances it is likely that intermediate information would fill out this relationship. In addition, the Euramerican flora covered an essentially unrestricted area across the mountains and forelands of the Variscan belt. North China however was all but isolated: even when connections to the rest of Pangaea were

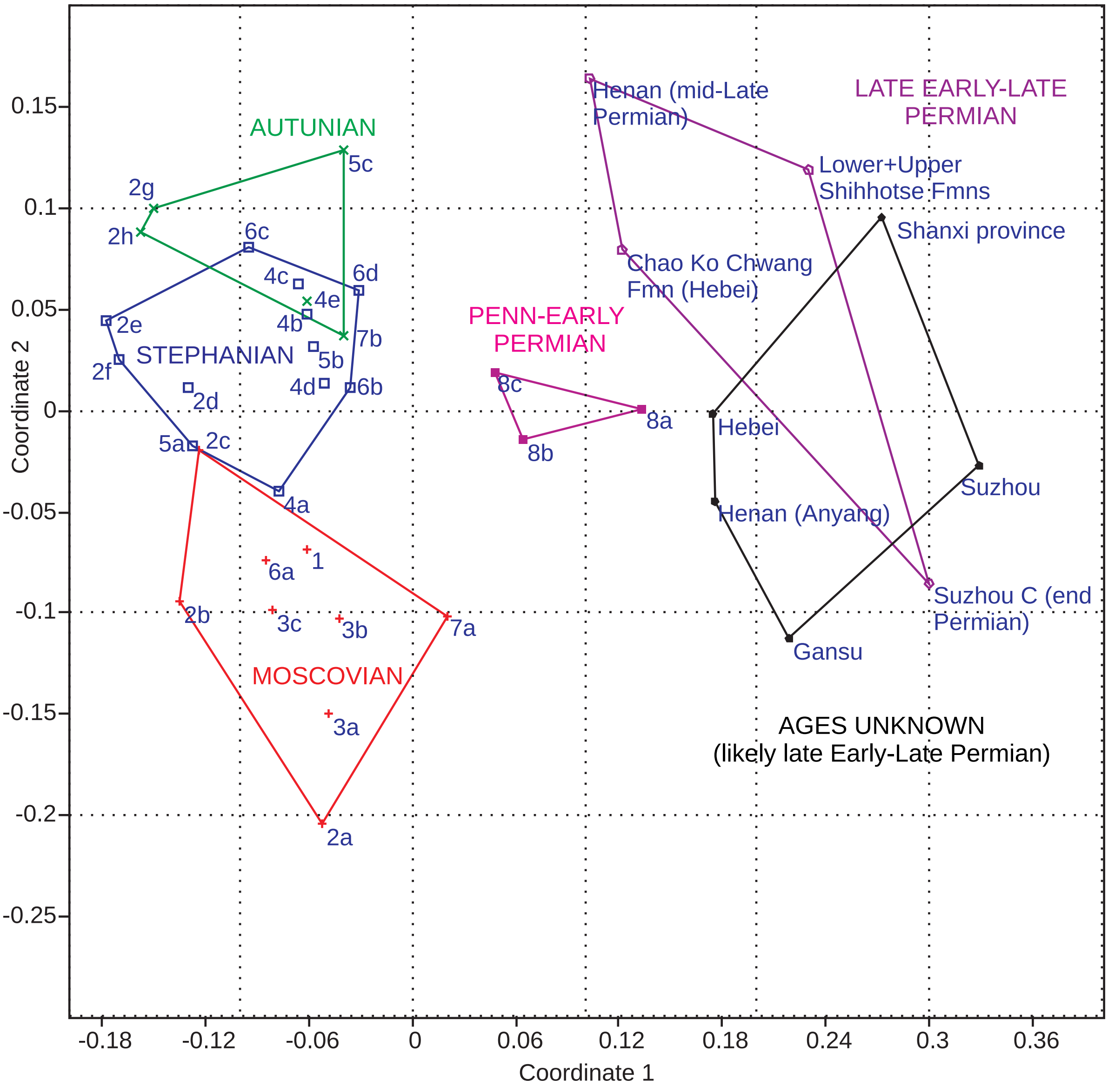


Figure 5.2: NMDS ordination of all data, coloured stratigraphically, using the Raup Crick distance metric. Numbers (=localities) and letters (=stratigraphic data bins) match those in Figure 5.1. Figure 1.2a-c show the numbered localities. Euramerican data plots to the left; Chinese to the right.
Chinese localities from later in the Permian are not coded as they do not overlap stratigraphically with Euramerican localities.

present, a whole series of Altaid terranes of varying nature formed the bridge, and furthermore, due to its discontinuous nature, it was likely to be constantly reorganising. Any land bridge would also have had to satisfy a number of criteria in order to be a conduit (see Section 3.1.3), and tectonism would have rendered long-term connection vulnerable. Interchange with Euramerica would have been entirely subject to the vagaries of this tectonically highly active region, and it is unsurprising that any direct fossil evidence of the connection has been destroyed over geological time. Therefore available Chinese flora from this time may be, or appear to be, less related to that in Euramerica, in comparison with the coherent relationships inside the Euramerican region.

Discontinuous interchange opportunities, or the subsequent erosion of the evidence of them, may also be a factor in the relatively small proportion of Chinese points which show an affinity with Euramerica. An unbroken evolutionary succession of Euramerican flora suggests repeated linkages and interchange of species to produce strongly related communities. However, it appears that connection between Cathaysia and Euramerica, from the fossils available, was only of any influential degree during the relatively short time period of the Stephanian. The oldest wetland flora known from China (within the Benxi Formation) is around this age, and is underlain by a large unconformity; the flora became regionally extinct in Euramerica shortly after the end of the Carboniferous, giving a time window of less than 10 Ma available to study today. The flora may have connected before this point and information been lost in the erosional event(s) causing the unconformity, perhaps alluded to by the proximity of the Northern Caucasian point of Asturian/Cantabrian age, although according to Liu (1990) conditions were not favourable for wetland community development in Cathaysia much before this time. Additionally, the connection may have been across a high enough latitude to only be seasonally wet (DiMichele et al., 2010), and so habitable for only part of the year. After this point, the flora in Europe was continuing a serious decline due to loss of habitat and favourable conditions (Cleal et al., 2009a), and if any further connections existed an interchange or 'reseeding' from the east would have been unlikely to take hold. This would also have broken the connection through to America, in which isolated wetland refugia may have remained (Falcon-Lang and DiMichele, 2010). In contrast, conditions were such in Cathaysia that the flora would have quickly proliferated, evolving a ubiquitous template through into the Permian, as it had done in previously in Euramerica – seen on Figure 5.2. This pattern is also suggested by the strong similarities of the North China flora in Figure 3.3. The signature of the Euramerican communities clearly persisted with the Cathaysian flora however, at least during the critical interchange period in the Stephanian.

5.4 Geographical relationships

These data provide the opportunity to examine the conclusion from Chapter 2 that, on a relatively small scale at least, stratigraphical progression (≈ plant evolution and self-regulated community stability; Eldredge et al., 2005) overrides patterns based around geographical proximity or separation. On a wider scale this does seem to also be the case. Although Figure 5.3 shows an apparent overarching progression from west (Iberia) to east (China), there is much overlap between the European (and American) localities which are along this gradient, emphasising their similarity despite varying

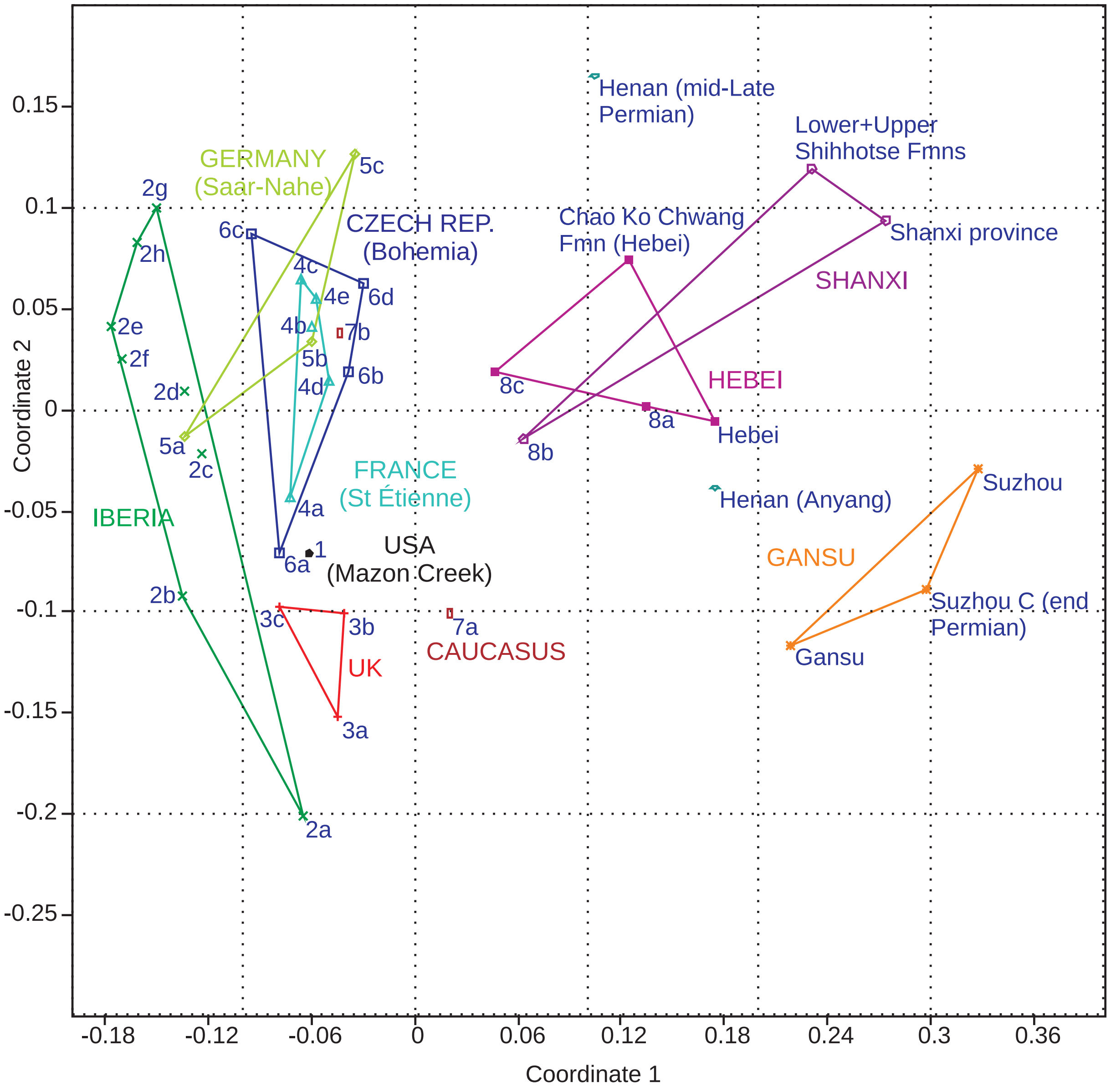


Figure 5.3: NMDS ordination of all data, coloured geographically, using the Raup Crick distance metric. Note the other North Caucasian point (7b), and that the points from Henan are separated.

degrees of geographical separation. The data in China itself is more disparate and has less stratigraphic resolution, but some geographic patterns are apparent. Hebei and Shanxi provinces overlap slightly, reflecting the close floral relationship as detailed in Chapter 3, and Gansu province is separated by some ordination distance, probably indicating its unclear relationships with other flora in this study (see Chapter 3). Henan province points are within the Chinese area, but a distance from all the other points, reflecting the differing origin of the flora from that of North China (and Euramerica).

The overlap of many geographical areas alongside strong stratigraphical progression of them, further vindicates the ability of the methodology employed (detailed in Chapter 2) to mitigate data biases between different sites and collectors, non-standardisation, and out-of-date taxonomy, and compare discrete datasets in a meaningful way. Furthermore, as the stratigraphic signal is clearly more prevalent than the geographic (Figure 5.2), even if all the datasets concerned were revisited and standardised to modern stratigraphy and nomenclature, a geographic signal, traceable across landmasses, would still be unlikely to appear. However, it is clear that the vast geographical distance between ancient Europe and China is enough to give the appearance of separating the two areas when plotted, even though there is stratigraphic overlap with some points. These overlapping points do however cluster much closer to the Euramerican data, especially when the position of the Asturian/Cantabrian aged North Caucasian data is taken into account, and so the separation is more a reflection of the fact that the majority of data from Cathaysia is much younger, and of lower resolution, than that from Euramerica, and therefore would not be expected to cluster with it. It is likely, based on evidence uncovered in this thesis, that if data were available spanning this geographic gap, the separation would become less pronounced and probably disappear into more of a continuum.

The apparent lack of logical geographic progression again highlights the complex nature of the proliferation of these ecosystems, whereby it seems to be the case that there was continual interchange and ‘reseeding’ in all directions, which replenished most areas with a common floral stock that reflected the wider evolution of the ecosystems at any given point in time (Eldredge et al., 2005; Section 3.1.3). Therefore, locating an origin for the ecosystems, and then logically tracing floral pathways, looks likely not only to be impossible, but perhaps also moot. There seems to have been so much in common over such large distances that there is a real possibility that as favourable habitats and conditions quickly took hold in the late Palaeozoic, the ecosystems colonised many locations rapidly enough that they were linked, or at least had been in contact with surrounding areas and interchanged key taxa, before they are recognised in the fossil record. Colonisation would have been straightforward as few other plants would have been able to survive in the environment (DiMichele et al., 2010).

The zenith of these almost ubiquitous wetland ecosystems, at least within the scope of the data analysed in this study, appears to be in central to eastern Europe during the latest Carboniferous to earliest Permian (Stephanian and Autunian), centred on the Czech Republic (Central/West Bohemia) where most of the data points are concentrated (Figure 5.3). It is unquestionably the time period with the most geographical overlap, as compared to the Bolsovian-Cantabrian to the bottom left of the plot, even though there may be a slight visual bias as the latter has around half the data points (Figure 5.2). This finding perhaps appears strange given the sharp decline in areal extent of these wetland ecosystems in Europe from the end of the Moscovian (Cantabrian; Cleal and Thomas, 2005), but widespread similarities between communities is not the same as dominance, and it is likely reflecting a hardy and well-established ecosystem, stable enough to withstand changing conditions and reducing habitat space. The fact that the data points in this bin cover such a wide geographical area, across the majority of Europe from southern France to Caucasia, makes it more likely to be a true signal, as opposed to a reflection of the increasingly concentrated pockets of wetland restricting diversity and promoting apparent similarity. The Stephanian was also the age in which the most influential connection was made with Cathaysia, further supporting a widespread and hardy flora, capable of colonising or overprinting local flora which were probably already present.

The Iberian data seems to be slightly separate from this, overlapping only with one other geographical area (Saar-Nahe), which perhaps reflects its western position and disparate data makeup. It does not however mark a western limit of the European flora, because Mazon Creek plots well within the realms of this data, showing that the interdispersal spread well to the west. As this study focuses on the Carboniferous-Permian boundary region of Europe, more data points from North America are needed to corroborate this, and investigate the detailed relationships of the American and European flora. In addition, earlier communities are not considered, and could shed further light on the apparent convergence of the diminishing communities through the Pennsylvanian in Europe.

5.5 Floral linkages between Euramerica and Cathaysia

5.5.1 Plant groups

General trends from older to younger and from Euramerica to Cathaysia are shown in Figure 5.4. Categories are not sequential, particularly for the Chinese data on the right, where the Tongshan Formation begins at around the Asturian (Figure 5.1), and only those data with age information attached were included. Nevertheless, it gives an indication of the development of wetland plant communities through time and space. The most obvious difference between Euramerica and China is the introduction of tingioids and increase in cycadophytes in the early stages of the latter, with the introduction of gigantopterids later in the Permian (possibly after connection with South China; see Section 3.4.1). These increases in diversity are not enough to preclude strong links between Euramerica and the Linsi Formation, slightly diminished with the Yuehmenkou 'Series' and Tongshan Formation (the Pennsylvanian-Early Permian points in Figure 5.2). The Yuehmenkou 'Series' bears neither cycadophytes nor tingioids, and so it is clear that the presence or absence of these components did not greatly affect overall floral affinity. Most other shifts in the data are due to the non sequential categories; for example Suzhou is not geographically or florally close to the Shihhotse Formations, but does follow them stratigraphically; however, because it is an unusual locality it may not be comparable to any others in the study (see Section 3.3). Other apparent anomalies in the chart are largely due to the smaller total numbers of genera from the Chinese localities, meaning that small differences cause relatively large excursions in the data plot.

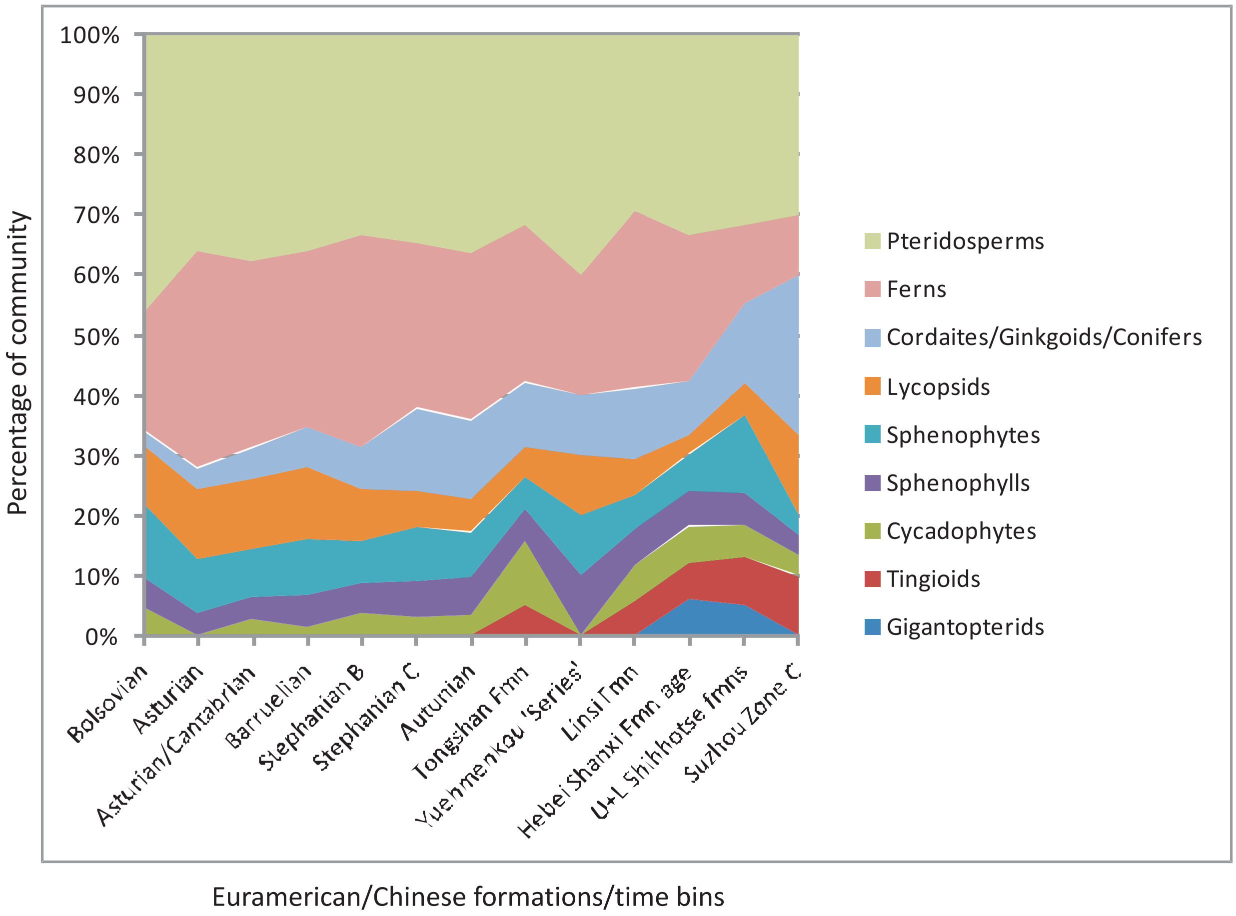


Figure 5.4: Proportions of different floral groups within each time interval. Graph has been standardised to percentages to attempt to negate any effects from differing sample sizes. Note that the intervals are not completely sequential; there is overlap between the Euramerican data on the left and the Chinese on the right, and the time bins in China are not mutually exclusive (see Figures 5.1, 3.2). Only data from China with a known age is included. Henan is not included as it has few occurrences and distorts the chart, and is not related to Euramerica.

Overall, most plant groups retain fairly constant proportions across time and space, which may be a contributing factor to the linkages apparent between Euramerica and Cathaysia. There is a decrease in the proportion of ferns across the plot, accompanied by a slight increase in cordaites, ginkgoids and conifers, and the remaining community space being taken up by the increasing diversity into China. This could be reflecting an overall drying of the climate, a shift or increase in available habitat types, or simply evolutionary diversification.

5.5.2 Genera

Figure 5.5 shows the occurrences of genera across Cathaysia and Euramerica through time. Again these bins are not sequential, but highlight floral links between the regions. In particular, as discussed above, taxa which are present in both the Stephanian of Euramerica and the Moscovian-Kungurian of China are likely to have been instrumental in the interchange and proliferation of the tropical wetland during the Stephanian. 14 genera are found in all categories: *Acitheca*, *Cyathocarpus*, *Nemejcopteris*, *Pecopteris*, *Sphenopteris*, *Alethopteris*, *Callipteridium*, *Linopteris*, *Neuropteris*, *Cordaites*, *Poacordaites*, *Annularia*, *Sphenophyllum*, and *Taeniopteris*. Most niches are represented, although the vast majority are ferns and pteridosperms. These taxa probably made up the core of the wetland flora as it spread, although this list is of course not exhaustive due to the inclusion of specific sites only, the incomplete fossil record, and the data processing procedure. This list makes up the minimum number of genera in the core of the flora; more would undoubtedly be added with more areas included, but none would

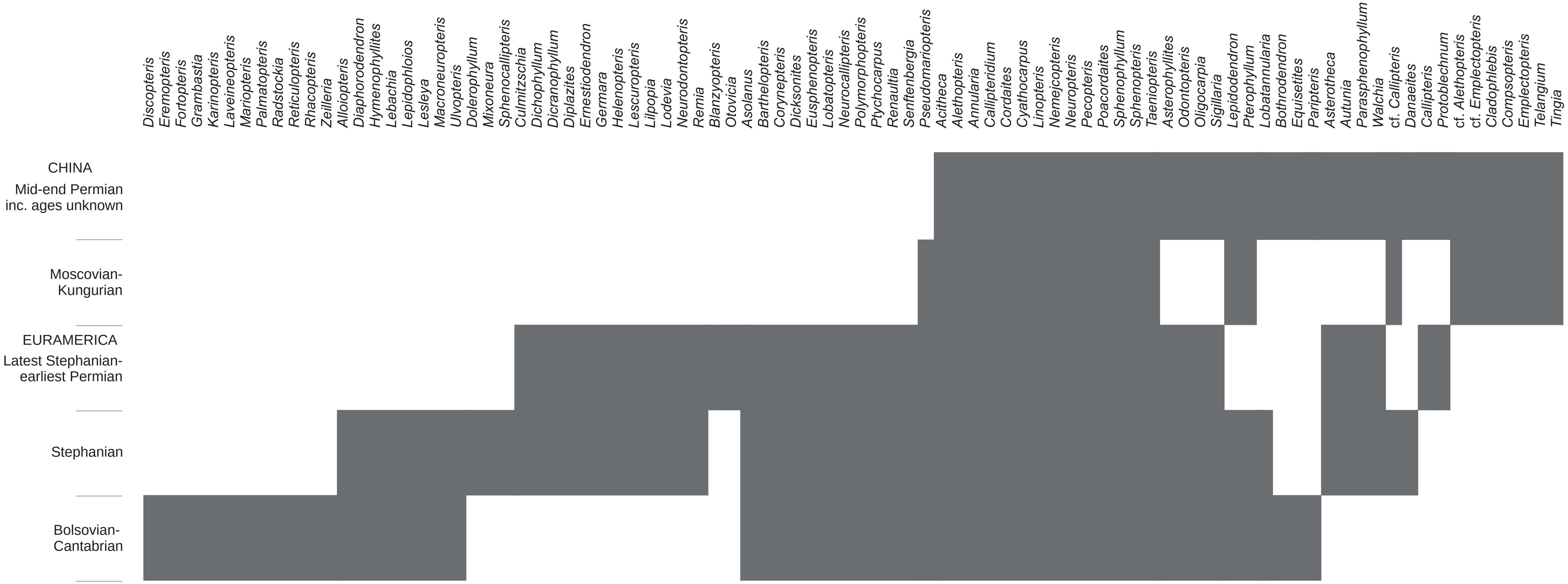


Figure 5.5: Occurrences of all genera through time and across Euramerica and China.
Note that the categories are not sequential as there is overlap between Euramerica and China.
Figure continues on the next page.

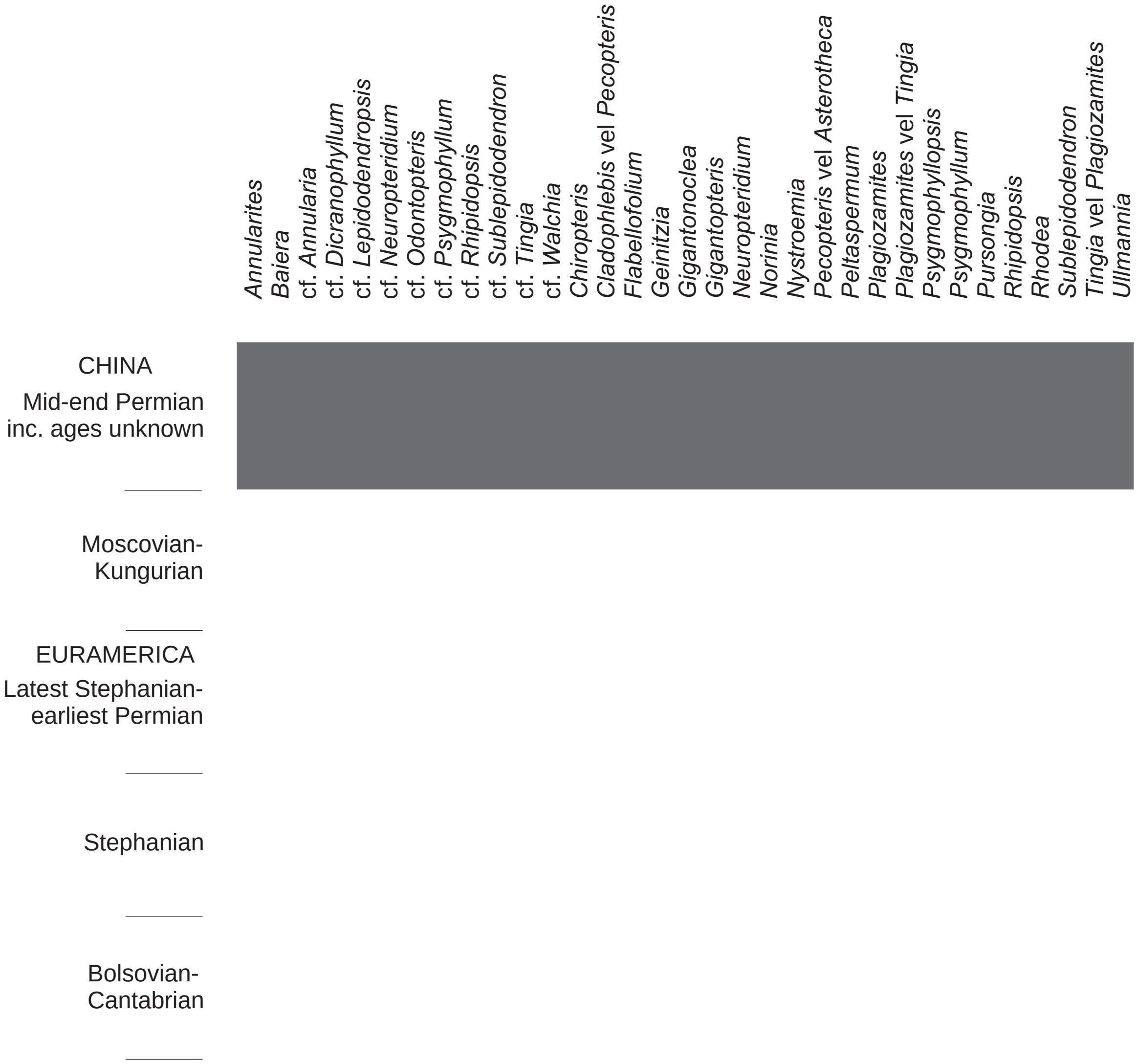


Figure 5.5 continued from previous page.

be removed. However, Section 4.3 examined the findings of '*Alethopteris*' in Cathaysia, and concluded that it was different from the Euramerican form. Unfortunately there is not enough material to redesignate the taxon, and it appears more similar to traditional *Alethopteris* than anything else and so the name was retained. Isolated situations such as these may remain within the dataset while many of the taxa have not been revisited within a global context, but the methodology employed in this analysis mitigates most taxonomical issues. In any case, *Alethopteris* as found in Cathaysia may prove to be an evolved form of that in Euramerica, or it could be convergent and therefore taxonomically indistinguishable with available material and methods. It is notable that cf. *Alethopteris* is present only in China (Figure 5.5), and the full designation of it in China (through *A. norinii* and *A. ascendens*) should strictly be designated to this group.

Floras which are found in Euramerica and China, but with a gap or gaps in occurrence, can realistically be assumed to be present throughout the range, and this covers ten more genera: *Asterophyllites*, *Equisetites*, *Lobatannularia*, *Odontopteris*, *Paripteris*, *Oligocarpia*, *Bothrodendron*, *Lepidodendron*, *Sigillaria*, and *Pterophyllum* span all categories. *Asterotheca*, *Danaeites*, *Autunia*, *Callipteris*, cf. *Callipteris*, *Protoblechnum*, *Pseudomariopteris*, *Parasphenophyllum*, and *Walchia* also span both areas, but not all time bins. These taxa could easily be present throughout the time and space under consideration, but possible reasons for their non-occurrence in various areas should not be ignored. It is likely that their absences reflect those in the fossil record, or less prominent occurrences which have been filtered out by data processing, as may be the case with *Odontopteris* which has been shown to be present in the Late Permian in China in Section 4.4, alongside other occurrences of *Odontopteris* in China of unknown Permian age. Wang et al. (2009) have also found *Sigillaria* across North China during the Pennsylvanian and Early Permian (and beyond). There could also be regional variations in taxa which, unlike *Alethopteris*, have led to differing designations across Europe and Cathaysia. The decisions as to where to place the divisions between each similar taxon in Euramerica and Cathaysia, or to combine them as a transitional range, are unlikely ever to be made, less so to develop a standardised and comparable framework, and these issues must be taken into account when interpreting data such as this. The difference between a meaningful whole plant and a fossil taxon must always be borne in mind (see Sections 4.1.3, 4.6). This is especially highlighted by findings such as that of Laveine et al. (2003b), recounting *Paripteris* from the earliest Namurian of South China, which would give a long geographic (and temporal) range across probably separated landmasses.

A final reason for absences of occurrence is that fossil collection is by necessity nearly always from a selection of pinpoints across the ancient landscape and, whilst it is hoped that findings will average out to a representative coverage, taxa may simply not have been present in that specific location during life and fossilisation, due to the diverse and constantly shifting wetland plant community habit.

Some genera do however appear relatively isolated and it is likely that they were not part of the interchange. 23 genera are found only up to the Stephanian in Euramerica; another 25 to the end of the Euramerican range. 33 genera are found only in the latest Permian of China, with seven more found through the whole Chinese range

(Figure 5.5). These floras, especially those which are present in the earliest Euramerican and latest Chinese bins, were probably not part of the floral interchange between the two areas. In Euramerica, they were probably subject to the extirpation of the flora there; in Cathaysia, they were probably filling the ecospace left by the extinct Euramerican flora, and were also new forms which evolved as the flora thrived throughout the Permian. Again, this list is representative based on the areas in this study and the parameters imposed by the data available; for example *Gigantopteris* is known from the Permian of North America (White, 1912), but clearly not in the Mazon Creek material considered here.

10 of the latest Chinese floras, and 12 overall in the exclusively Chinese material, are under open nomenclature as ‘cf.’. These have been retained in the analyses in acknowledgement that a cf. designation implies that the taxon is only provisionally allocated to that name (Bengston, 1988), and could just as easily be another genus as a form of an existing one, as in the case of *Alethopteris* in Section 4.3. This again highlights the issues when allocating taxa using criteria which may be too narrow to encompass transitional forms.

5.6 Summary

Previous chapters have examined the makeup of late Palaeozoic wetland floras using different approaches, to enable assessment of their relationships across the low latitude tropical belt encompassing Euramerica and Cathaysia. There is a small window of overlap between the first appearance of wetland communities in North China in late Moscovian times (the Benxi Formation), and the extirpation of the communities in Euramerica around the end of the Carboniferous. In this chapter, data were analysed which spanned this geographic and stratigraphic interval, in order to give the most complete evaluation of their relationships to date.

The Euramerican wetland flora in this study was very similar over huge areas of land, in both lowland (including coastal) and upland settings. It spanned foreland, montane and cratonic environments with terrestrial and paralic facies, and was apparently uninfluenced in the fossil record by the unusual taphonomic regime found at Mazon Creek. Wetland habitats were hostile and constantly shifting, favouring rapid colonisation by those resilient and fast-growing plants adapted to live there, and so evolution continued apace amongst low competition, even whilst the flora was in decline toward the end of the Carboniferous (Cleal and Thomas, 2005). The culmination of this was at the end of this period, during Stephanian and Autunian times, when the wetland flora in nearly all areas of Euramerica was virtually indistinguishable. (This point may have been reached earlier, during these ecosystems’ maximum extent in the Moscovian, but is outside the scope of this study.)

During the Stephanian, a remarkable similarity is apparent between the Euramerican and Chinese floras, strongly suggesting connection. It is unlikely that the wetland floras in North China were much developed before this connection in the Stephanian (Liu, 1990), and therefore the robust Euramerican flora would have quickly taken hold and overprinted what may have been there before (see Section 3.1.3). A range of 33 genera, notwithstanding sequential gaps in occurrence, are cosmopolitan across this time and space interval, and therefore make up the core of the flora which more than likely migrated in both directions. The temporal resolution of the Chinese data is not as fine, and therefore may be obscuring shorter-term patterns, but the Euramerican model of rapid evolution and colonisation appears to have applied, given the similarities with the flora and environment. Therefore after the extirpation of the Euramerican flora, the Chinese flora continued to evolve quickly, and diversified into new groups.

These findings support those of previous chapters, in that linkage and interchange between Euramerica and Cathaysia during the Carboniferous was extremely likely.

-CHAPTER 6-

CONCLUSIONS

6.1 Findings

This thesis has examined the affinities of the (North) Cathaysian late Palaeozoic wetland flora, and the evidence for an Amerosinian phytogeographic realm. A large dataset was assembled, through studies of museum collections and monographs, with the widest geographic and temporal range to date, covering almost the entirety of the existence of low-latitude wetland flora in the late Palaeozoic. This was analysed in part, firstly to assess the utility of such large datasets, and the best approach for gaining the most meaningful results (Chapter 2), and then to investigate the floristics of North China (Chapter 3). Finally, the whole dataset was analysed to give the best available picture of Euramerican and Cathaysian affinity (Chapter 5). In addition, individual fossil taxa were examined which potentially link the two areas (Chapter 4).

The evidence overwhelmingly supports a link and degree of interchange between the Euramerican and North Cathaysian flora, during their ~10 Ma temporal overlap, in the latest Carboniferous (Stephanian). On the North China block, the pattern of the flora is such that the northeastern area (Hebei province) appears to be a nucleus from which much of the rest of the flora on the block radiated. This implies a source for a dominating flora from the north, through the so-called Angaran phytogeographic realm. As there are no substantial published palaeobotanical records from this region to date, it is not possible to track the source of the North China flora through this area, but a comparison with well-studied Euramerican flora affirms a very strong relationship between North Cathaysia and Euramerica, lessened only by the geographic discontinuity and intermittent connections through the tectonically dynamic and fragmented Angaran (Altaid) area. The Cathaysian data are of a lower resolution than the Euramerican, but the latter suggests a model for the development and proliferation of the wetland plant communities which most likely applied in both areas. The remarkable stability of the flora over a huge area and range of terrain by the end of its existence in the earliest Permian (Autunian), suggests a well adapted, fast evolving and fast colonising community, able to proliferate widely in these hostile, swampy and ever-changing environments. Therefore, once a connection with North Cathaysia was present, by the latest in the Stephanian (although it may have been slightly earlier as there is a widespread unconformity below this in North China), the flora very quickly spread across this connection and overprinted any flora which may have been there originally, effectively extending its geographical coverage far to the east and continually interchanging with the established flora across the whole area. However, as conditions continued to change in Euramerica and the wetland flora there died out, the connection was lost and the flora continued in North Cathaysia with the pattern of fast colonisation and evolution, quickly diversifying from the core flora sourced from Euramerica, and incorporating a wider range of plant groups, perhaps also sourced from South China later in the Permian.

During, and after, the co-existence of the wetland flora in Euramerica and Cathaysia, the North Cathaysian flora may have reached as far west as Gansu, or further, or there could have been multiple pathways open intermittently between Angara and

Cathaysia. The situation to the north of Gansu province is unresolved, but may be a transitional flora ('Subangaran') between the two phytogeographic realms. Similarly, to the south of the North China block, a very different flora is represented in Henan province, which could have been part of South China, or an entirely separate block. If the former is true, a connection between North and South China is implied around the middle of the Permian (Kungurian). In either case, it is clear that the division between North and South Cathaysian floras is upheld prior to this time.

6.2 Implications and recommendations

Breaking down the elements of this thesis – using fossil taxa as indications of affinity between phytogeographic provinces – should require that both be quantifiable. Selected fossil taxa were examined in Chapter 4, to investigate the first element. When dealing with such large datasets from different sources, it is clear that as long as the taxonomical criteria are largely consistent, taxa can be regarded as valid units in a dataset (as shown by *Neuropteris ovata* and *Odontopteris subcrenulata*), even though inherently this allows potentially unrealistic geographic and temporal ranges. However, the problem of potentially transitional taxa across large areas remains (as shown by *Alethopteris ascendens* and *A. norinii*), subject to preservational problems and lack of material, and opens up the avenue of convergent evolution, especially when work such as that of Laveine et al. (1993) is taken into consideration, which proposes generic links from South China right through to western North America by the Namurian. The fact that these genera (*Paripteris* and *Linopteris*) are fossil genera, means that features which have survived in the fossil record to prescribe their classification under the same names, even though the plants were hundreds of miles apart in life, may be adaptive to the specialised wetland environment. Some convergence in wetland communities would have been likely, alongside the emergence of new, closely related taxa which filled the same niches whilst warranting a different name. In the case of this thesis however, interchange of flora from Euramerica to North Cathaysia must have been the main driver of floral affinity because the overall communities are so similar. This similarity is quantified in this thesis using given generic names, and whilst these have been updated to current standards where possible, no account has been taken of the ecology of individual genera and their possible equivalents under the same conditions, but in geographically unconnected locations. Therefore the similarities reported here are based purely on the proportions of taxa with the same given names, across vast expanses of time and space, and it has not been necessary to investigate ecological factors in depth to decipher patterns. Although these are fossil taxa, they are clearly significant and meaningful in the context of global studies such as this. The flora from Henan, low latitude and developing under much the same conditions as that in North China proper (Liu, 1990), whilst separated from it, was strikingly different from the flora there, and so there is no evidence that Northern Chinese flora would coincidentally develop such a large proportion of the same and similar fossil genera as Euramerica during the Stephanian had it been isolated from it.

In addition, potential problems with non-standard or out of date nomenclature will usually be evenly distributed through a dataset, and can be lessened by removing singly occurring species, and/or analysing taxa at genus level. With a large scale dataset, the problems are likely to be minor, especially if the contentious taxa are not a core element. In the absence of a standardised review of all taxa under consideration, the data here represents the best available approximation at the present time, and in general palaeobotanical data looks to be usable as a tool with which we can attempt to unravel past environments and geological patterns.

However, it is clear that the use of fossil taxa in delineation of individual phytogeographic realms, provinces and subprovinces can be problematic. This study empirically tests theories of similarity, in this case specifically between 'Euramerica' and '(North) Cathaysia', such as posed by Halle (e.g. 1927); Wang (1985); Cleal and Wang (2002); and Hilton and Cleal (2007), among many others, on a large scale. Results affirm that while more subjective, locally-founded theories can be a useful guide as to the character of regional flora, and present hypotheses for testing, data needs to be analysed as a whole in order that more natural affinities and divisions can be revealed in a wide context. Placing names on regions of flora can be deceptive, and ultimately confusing (Chaloner and Creber, 1988). The decision as to what constitutes a representative flora is largely arbitrary and non-standard, and often based around a relatively small area and timeframe (e.g. Sun, 1999; Wang, 2010), and furthermore is being eroded as more and more re-examination and international collaboration is taking place (e. g. Wang and Chaney, 2010). What are regarded as endemic or cosmopolitan floras from a localised viewpoint mean very little in a wider context, as taxa evolve and shift freely through time and space as avenues and niches are constantly created and destroyed (Chaloner and Lacey, 1973). This is especially true around the border regions of the given realms or provinces. In this thesis, this is demonstrated by the data from Gansu province. Predetermined as Angaran or 'Subangaran' in affinity (Durante, 1992), its position within analyses of flora from regions either side of it geographically and florally (Euramerica and Cathaysia) is by no means conclusive (Figures 5.2, 5.3), and it may or may not fit into a transitional sector. All that can be determined from the data analysed here is that the flora from northern Gansu is not aligned with Euramerica or North Cathaysia.

In this thesis, phytogeographic names have been asserted only where differences in the floras have been determined by floristic analysis, and ideally future work in this field should follow this practice. Given extents and boundaries of the regions have varied widely over the years (e.g. Chaloner and Creber, 1988), and therefore the only way to make meaningful comparisons and progress in unravelling the complex history of the wetland floras and their palaeogeographic arrangements, is to analyse the floras themselves, in context. For the time being, the concepts of realms or provinces may be used, as they are understood to convey very broad geographic and floral connotations, but with the caveat that they have little meaning in a real sense. In the future, the hope is that these realms will continue to be qualified through geological time with the addition and analysis of more data, such as has been undertaken in this study. At the other end of the scale, localised subdivisions can be useful in characterising a flora (e.g. Mei et al., 1996), but need a wider setting to show the magnitude of their digression from regional flora, and their place within it.

The establishment of an ‘Amerosinian’ realm in the literature (proposed initially by Havlena, 1970) is misleading, not because the Euramerica and North Cathaysia were not in connection, but because any connections were clearly intermittent, and in this case relatively short in duration (as seen in Figure 5.2). In Euramerica, the flora was well established long before a viable pathway through the Angaran region opened up, and the North Cathaysia flora developed so quickly after the demise of the Euramerican, that the term is not useful over geological timescales. The Euramerican and North Cathaysian floras are easily distinguished from each other over the vast majority of their temporal extent (see Figure 5.2), and so to imply that they were part of the same significant 'realm' will add to confusion. The Euramerican and North Cathaysian realms (or provinces) should be retained therefore, subject to further refinement as detailed above, but there is a need to highlight this period of connection, and that the source of the latest Carboniferous North Cathaysian flora, as found in the fossil record, was initially from Euramerica. As this thesis has been focussed on these floras from this time, emphasis should be placed on the time period (Stephanian) at which the connection has been found in this thesis, and the name 'Eurocathaysian Flora' seems appropriate here. With such a complex history, it is likely that other periods of connection will be qualified in a similar manner. Perhaps distinguishing names can be conceived to reflect their floral sources at the specific times at which the connections were made, as it is clear that the character of fast evolving wetland flora can progress quickly and will be different at any given point in time.

It is difficult to reconcile the rather abstract evidence for palaeobotanical relationships with the complex tectonic activity ongoing in the regions concerned (e.g. Chaloner and Lacey, 1973). However, Natal'in and Şengör (2005) give detailed evidence for a 'Silk Road Arc' which connected multiple tectonic blocks, from North China to the Caucasus, by the end of the Carboniferous. Clearly there are almost endless possibilities for the tectonic arrangement of the area through Angara, but in this case the biological record is corroborated with the geophysical, and this will only be further refined in future.

This thesis has focussed on the stratigraphic overlap between lowland adpression floras in North China and Euramerica, from the latest Carboniferous to earliest Permian, and found a significant relationship. However, this is only part of the story, and adpression floras are only one facet of the available fossil record. If the parameters are widened to include individual and suites of permineralised and palynological fossil taxa, as well as through to South China and North America from earlier in the Carboniferous, it is clear that connections such as found in this study may well have been made both before and after the period under consideration here (e.g. Zhu, 1995; Cleal and Wang, 2002; Hilton et al., 2002; Laveine et al., 2003; Hilton et al., 2004), and emerging studies on the less often preserved upland floras surrounding the swamps (e.g. DiMichele and Falcon-Lang, 2011; Dimitrova et al., 2011; Falcon-Lang et al., 2011) will undoubtedly refocus future study to ensure that a fuller picture of late Palaeozoic floras and their migratory and evolutionary patterns can be created. This study does not contradict any of these findings; rather, it complements them. Indeed, the found ranges of *N. ovata* and *O. subcrenulata* (Chapter 4) support such ideas. Whilst a connection and interchange of flora has been shown beyond reasonable doubt here, which may feed into later analyses of Permian (North) Cathaysian flora, it is entirely plausible that there would have been continuing connections of varying importance between Euramerica and Cathaysia, and that these have either been through areas not covered in this study, or that direct, linking evidence has been destroyed by erosion or orogenesis during the complex amalgamation of Pangaea. The unconformity underlying the Benxi/Tongshan Formations in North China may be testament to this, although it is of course impossible to postulate whether all of the factors needed for the wetland flora to flourish were in alignment before this time, and the regional uplift which caused the unconformity in the first place may have precluded the development of extensive lowlands (Liu, 1990). The wetland flora was also fast to evolve and colonise, and only a relatively short temporal or geographic separation would be enough for previously connected areas to diverge florally, masking the previous connection if direct evidence was not found.

With any geological study, it is only possible to view the end result of millions of years of geological processes, and this is further obscured by human folly in discovering, collecting, interpreting and analysing the remaining evidence. In this case, the pattern in the fossil data is strong enough to have persisted through both geological ages and human intervention, but common sense tells us that we should always seek to explore as many lines of evidence as possible when reconstructing a jigsaw puzzle as complex as the late Palaeozoic low-latitude wetland floras. This puzzle is far from completed, but all the elements are there. All that is left is to assemble them.

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APPENDIX

See enclosed CD for data analysed in Chapters 2, 3 and 5.