The Paleoecology of Vegetation on Pennsylvanian Basin Margins

by

Arden Roy Bashforth

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Research Supervisors: ________________

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For Julie, who endured this

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ABSTRACT

Most paleobotanical studies involving Pennsylvanian vegetation have focused on communities that inhabited mires and associated clastic substrates in poorly drained basinal lowlands. In contrast, this thesis provides a paleoecological evaluation of riparian floras on basin margins and inland settings. Such landscapes were characterized by steep gradients and high-energy regimes due to their proximity to uplands, and the prevalence of coarse-grained sediment enhanced soil drainage and hindered peat accumulation.

To help resolve the full spectrum of vegetation cover in tropical Euramerica, megafloral assemblages were documented from strata that accumulated on disturbance-prone fluvial tracts within or adjacent to Pennsylvanian mountain belts. Taphonomic indicators and multivariate analyses reveal that riparian vegetation comprised a collage of monospecific to low-diversity communities, with patchiness occurring at local and regional scales. Habitat partitioning saw plant clades organized along ecological gradients controlled by the drainage and stability of substrates. In the Tynemouth Creek Formation (Lower Pennsylvanian, Cumberland Basin, New Brunswick), which records deposition on a fluvial megafan under strongly seasonal conditions, gigantic cordaitalean forests dominated the landscape, particularly alongside ephemeral channels. Floodplains were largely dry and degraded, although pteridosperms, ferns, and lycopsids persisted around poorly drained depressions. On the Nýřany Member braided-river plain (Middle Pennsylvanian, Central and Western Bohemian Basin, Czech Republic), raised channel margins supported long-lived site-occupiers, such as cordaitaleans and pteridosperms. Pioneering vegetation comprising fast-growing, opportunistic taxa, particularly ferns and sphenopsids, was common on wetter, shifting substrates of frequently flooded abandoned channels, low-lying floodplains, and lake margins. In La Magdalena Coalfield (Late Pennsylvanian, Spain), pteridosperms dominated marginal wetlands adjacent to steep basin margins. Opportunistic ferns were abundant in or adjacent to frequently disturbed braided channel belts, whereas communities on interfluve wetlands distant from channel influence comprised pteridosperm patches enclosed in a fern-dominated matrix.

In the South Bar Formation (Middle Pennsylvanian, Sydney Coalfield), sandstone successions comprising flood deposits are capped by log accumulations, many of which are overlain by abandoned channel mudstones. It is proposed that flood sediment buildup and log jam development prompted avulsion and channel abandonment, thus providing some of the earliest evidence for the effects of large woody debris on fluvial systems.

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This degree would never have been completed without the help and encouragement of numerous people, to whom I extend my most sincere gratitude. In their own way, my parents brought me up right. By example, they instilled me with the capacity to work hard, to be persistent, and to take pride in a job well done, all assets that proved invaluable to getting this thesis finished.

I owe so much to my wife Julie Qvistgaard, who provided me with just the right mix of emotional support, encouragement, and tough love to see this degree to fruition. I appreciate the personal sacrifices she made, particularly for bearing the brunt of the financial burden over the last few years without making me feel guilty about it. She certainly kept her end of the 'for better or worse' vow, for which I am grateful.

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I also would like to express my appreciation to Howard Falcon-Lang, who was the initial brains and ringmaster behind this project and stuck with it until it bore fruit. In particular, I thank him for applying his uncanny organizational skills to rough drafts of thesis chapters. I also thank Rob Fensome and John Calder, the other members of my supervisorial committee, for their advice. In particular, I appreciate Rob's intense and detailed editorial comments on chapters. I regret that I was not able to benefit from their guidance as much as I would have liked, but we can blame the Atlantic Ocean for that.

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Finally, I offer my gratitude to those involved along the way in helping with logistical details, such as fieldwork, arranging accommodation, or access to museum collections. In the Czech Republic, I appreciate the friendship and aid of the 'Czech Carboniferous Mafia'. In particular, I express my sincerest thanks to Stanislav Opluštil, who willingly shared his knowledge of the local geology, and gave me so much of his precious time. In Spain, Roberto Wagner was the supreme guide during introductions to the local geology, and was always candid but kind when deviant interpretations needed a nudge back in the right direction. In Nova Scotia, Erwin Zodrow made time for me to examine his fossil collections, and provided valuable paleobotanical advice and literature. And in New Brunswick, Randy Miller is thanked for spending time in the field with me. It was so reassuring to have a friend on those lonely and occasionally frightful shores.

CHAPTER 1: INTRODUCTION

1.1. OVERVIEW

Peat-forming vegetation covered vast tracts of paleoequatorial lowland during the Pennsylvanian (299 to 323 Ma), and these so-called ‘Coal Forests’ (Fig. 1) have come to symbolize this important stage of Earth history. Inhabited by bizarre plants with few modern analogues, the ‘Coal Forests’ have captivated the imagination of scientists for two centuries, with the result that they are among the best-understood ecosystems of the past (DiMichele & Phillips, 1994). The amount of attention devoted to these unique biomes clearly corresponds to the economic importance of coal reserves resulting from

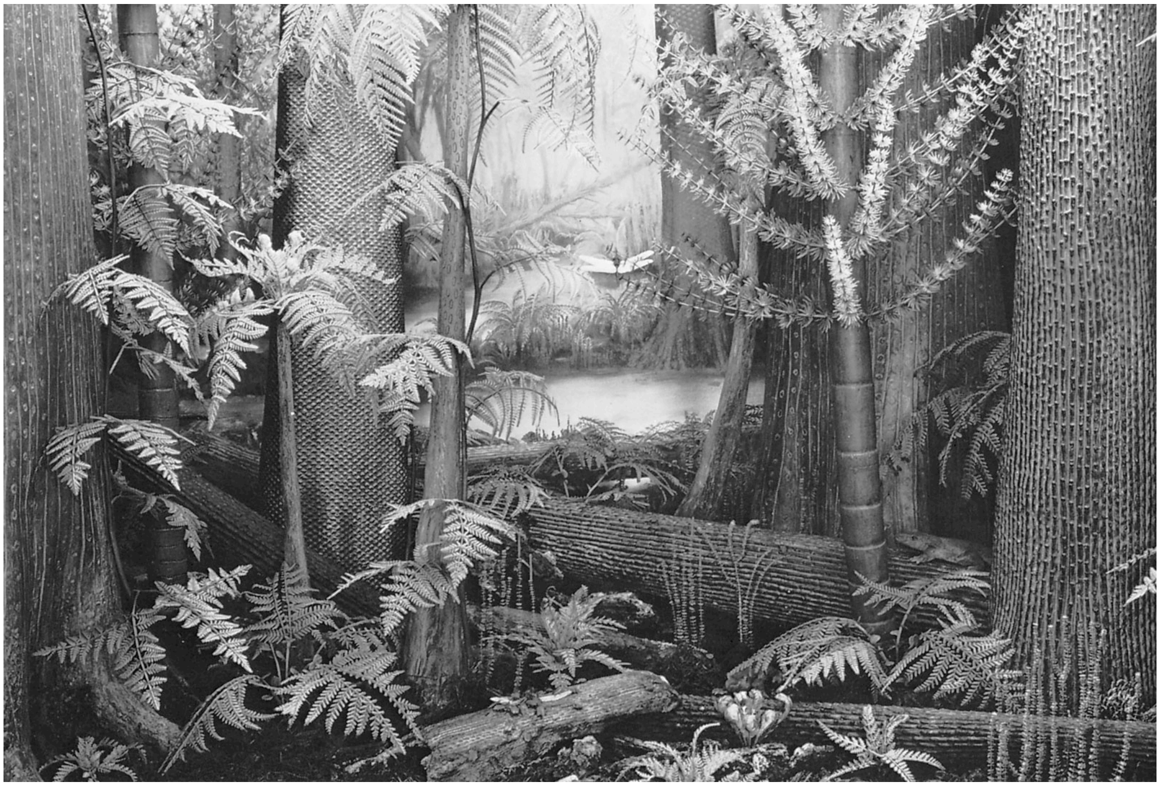


Figure 1. Classic reconstruction of a Pennsylvanian ‘Coal Forest’ in a diorama at the American Museum of Natural History, New York.

their formation, and to the enhanced preservation potential of plant debris in wet or waterlogged substrates (Behrensmeyer et al., 2000; DiMichele & Gastaldo, 2008; Gastaldo & Demko, in press).

Although some Pennsylvanian mires attained enormous sizes (Greb et al., 2003), their initiation and persistence required the coincidence of various geologic, climatic, and edaphic conditions (Calder, 1994; Calder & Gibling, 1994; Cecil, 1990; Cecil & Dulong, 2003; Gibling et al., 2004; Gastaldo, 2010). Even when such requisites were met, widespread peat accumulation may have been relatively short-lived due to high-frequency climate rhythms linked to orbital cycles (Falcon-Lang, 2004a; Falcon-Lang et al., 2009; DiMichele et al., 2009a, 2010). Global compilations that show the distribution of coal deposits superimposed on paleogeographic maps indicate that, even at the acme of development under ideal climatic conditions in the Middle Pennsylvanian (306 to 312 Ma; Cleal & Thomas, 2005), the 'Coal Forests' and associated communities on poorly drained clastic substrates occupied only a fraction of the landscape (Fig. 2). Most land surfaces had depositional environments or drainage conditions unfavorable to peat accumulation, or were elevated regions that experienced net erosion. Although distinct vegetational biomes thrived in these largely non-peat-forming environments, either in relatively better-drained settings on basin margins or elevated uplands or in basinal lowlands during times of increased seasonality, the paleoecology of these communities is poorly known because they had low preservation potential (Behrensmeyer et al., 2000; DiMichele et al., 2008, 2010). The manifestation of this taphonomic megabias is a paradox that continues to perplex Carboniferous paleobotany—much is known about peat-forming and associated clastic wetland vegetation in poorly drained basinal

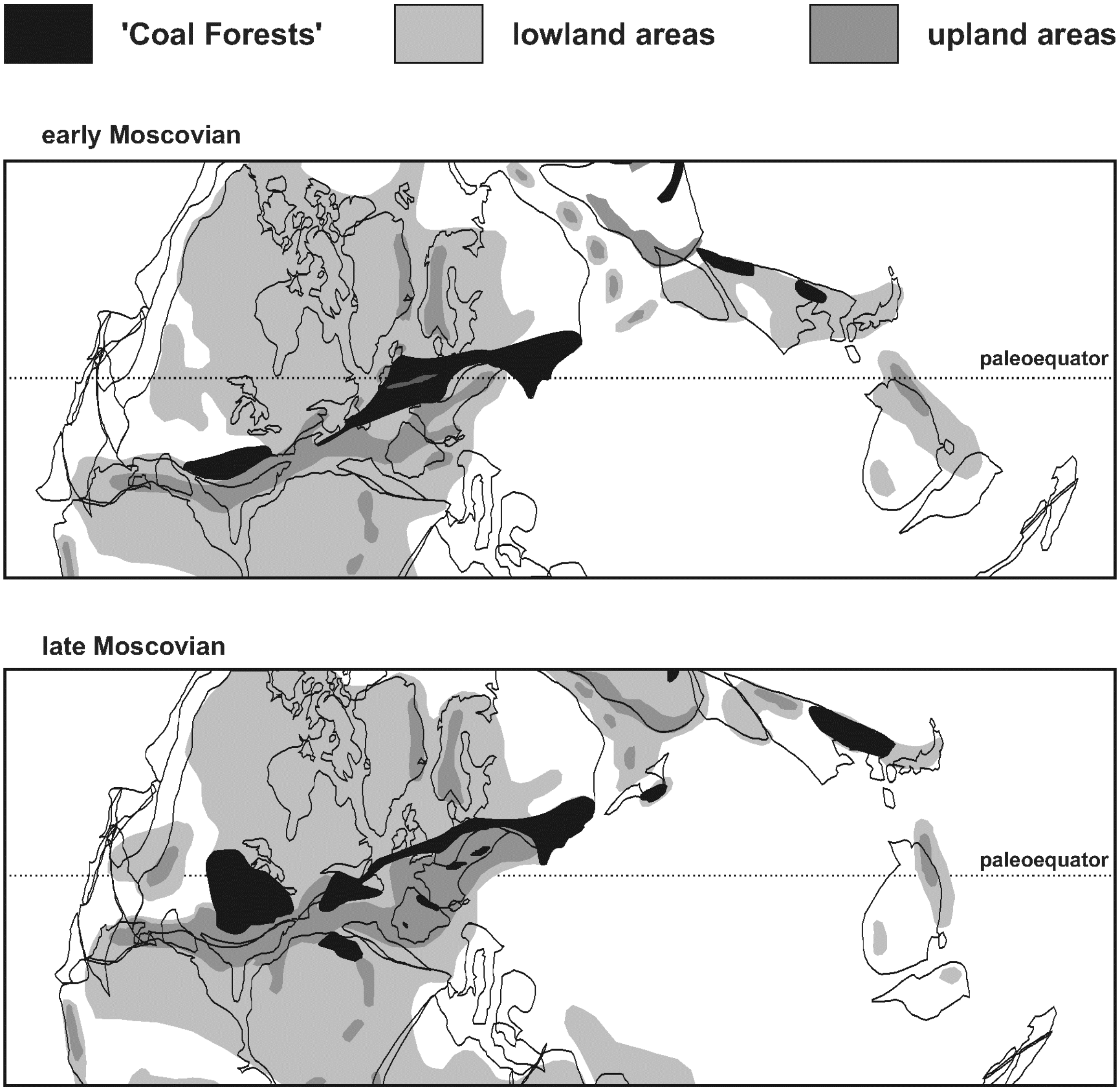


Figure 2. Paleogeographic maps showing distribution of ‘Coal Forests’, lowland regions, and upland regions at two time slices during the Middle Pennsylvanian. Although the early to late Moscovian represents the acme of development of peat-forming habitats, they only comprise a fraction of terrestrial landscapes. Modified from Cleal & Thomas (2005, fig. 4), with base maps adapted from Scotese (2001).

lowlands, which probably only existed in temporally and spatially narrow windows, and little is known about floras adapted to lower soil moisture regimes, which prevailed over larger areas and for longer intervals.

Clarifying the paleoecology of non-peat-forming vegetation that thrived outside the confines of basinal lowlands during the Pennsylvanian has important consequences for modeling Paleozoic ecosystems. As the terrestrialization and landward expansion of plants progressed through the Ordovician to Devonian, soil formation intensified due to root/substrate interactions, and increased density and penetration depth of roots limited erosion and facilitated landscape stabilization (Algeo et al., 1995; Algeo & Scheckler, 1998). Erosional and depositional processes in the alluvial realm became increasingly contemporary near the Silurian-Devonian boundary (Davies & Gibling, 2010a, b), and the linkage between biological and physical systems may have been quite 'modern' by the Carboniferous due to increased vegetation stature, complexity, and tolerance to moisture deficiency. Furthermore, the colonization of terrestrial surfaces contributed to a drawdown of paleoatmospheric CO_2 and a concomitant rise in O_2 owing to amplified silicate weathering, photosynthesis, and burial of organic carbon, ultimately leading to episodic global icehouse conditions during the Carboniferous and Permian (Berner, 2003). However, the role of vegetation in modeling late Paleozoic atmospheric compositions is largely limited to the volumes of organic carbon removed from the carbon cycle in coals (Berner & Raiswell, 1983; Berner, 2001), and does not account for the presence of plants on non-peat-forming substrates characterized by better drainage. Also important to consider is that moisture deficient habitats, especially those outside the confines of Carboniferous basinal lowlands, may have been the primary locus of morphological innovations responsible for the evolution of new plant taxa, most of which were members of seed-plant clades (DiMichele & Aronson, 1992). Their prior adaptation to drier substrates allowed them to move into basinal lowlands in the late Carboniferous and Permian, where they replaced the earlier peat-forming biomes when the water table lowered due to climatic drying (DiMichele et al., 2006a) or increased sediment input during the assembly of Pangea (Kerp, 1996; Cleal & Thomas, 2005; Cleal et al., 2009).

1.2. PRESENT RESEARCH

1.2.1. Initial Objectives: The Elusive 'Upland Floras'

When this project was conceived, the aim was to determine the paleoecology of a poorly understood group of Pennsylvanian plants known under various guises, including 'upland floras' (used hereafter), 'extrabasinal floras', 'hinterland floras', 'The Mesophytic Flora', and 'Flözfern' (reviewed by Mapes & Gastaldo, 1986; Gastaldo, 1996; Falcon-Lang, 2004b; DiMichele et al., 2008, 2010). This biome was dominated by mesic to xeric taxa, particularly gymnosperms such as walchian conifers, cordaitaleans, and derived pteridosperms (DiMichele & Aronson, 1992), and has been linked by most researchers to well-drained soils inferred to have existed well above sea level and/or outside the confines of depositional basins (DiMichele et al., 2010). Assuming this conjecture to be valid, megafloral assemblages were investigated from numerous Pennsylvanian successions throughout Euramerica, all of which were deposited in high-energy environments adjacent to elevated basin margins (e.g., alluvial fans, braided rivers). The rationale for targeting these environs was straightforward—if 'upland floras' existed in the hinterlands, their remains should have been transported downstream and occasionally preserved in proximal settings along basin margins.

The following lithostratigraphic units were examined (in ascending stratigraphic order; Figs. 3, 4): (i) the Tynemouth Creek Formation (upper Lower Pennsylvanian), Cumberland Basin, New Brunswick, Canada; (ii) the South Bar Formation (middle Middle Pennsylvanian), Sydney Coalfield, Nova Scotia, Canada; (iii) the Nýřany Member (upper Middle Pennsylvanian), Central and Western Bohemian Basin, Czech Republic; and (iv) undivided strata (middle Upper Pennsylvanian) in La Magdalena Coalfield, Spain.

Immediately after data collection commenced, it was clear that plant remains found in basin-margin strata simply comprise a subset of the species pool known from contemporaneous basinal lowland habitats. The weird and wonderful ‘upland floras’ identified elsewhere were virtually absent in the study areas. In fact, of the ≈35000 foliar fragments identified during the project, only a handful could be confidently assigned to an ‘upland flora’ taxon. Thus, although this unique biome surely existed in elevated habitats, it is clear that its remains were rarely transported to basin margin or basinal lowland settings.

DiMichele et al. (2010) made the crucial observation that ‘upland floras’ are exclusively known from deposits *within* basins. Quantitative analyses undertaken during this project clearly indicate that their remains were not readily transported from extrabasinal habitats. So how did ‘upland floras’ come to be preserved in basinal lowlands? DiMichele et al. (2006a, 2008, 2009a, 2010) surmised that ‘upland floras’ are indicators of soil moisture deficits, and could have occurred anywhere that climate

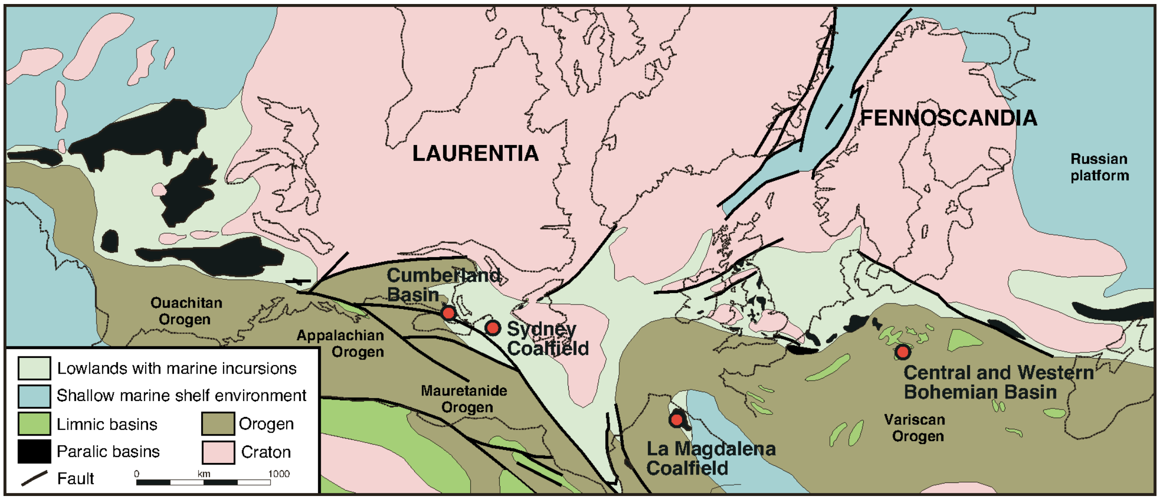


Figure 3. Paleogeographic map of tropical Euramerica at the end of the Westphalian (late Middle Pennsylvanian, late Moscovian), showing location of four basins/coalfields examined. Modified from Opluštil (2004).

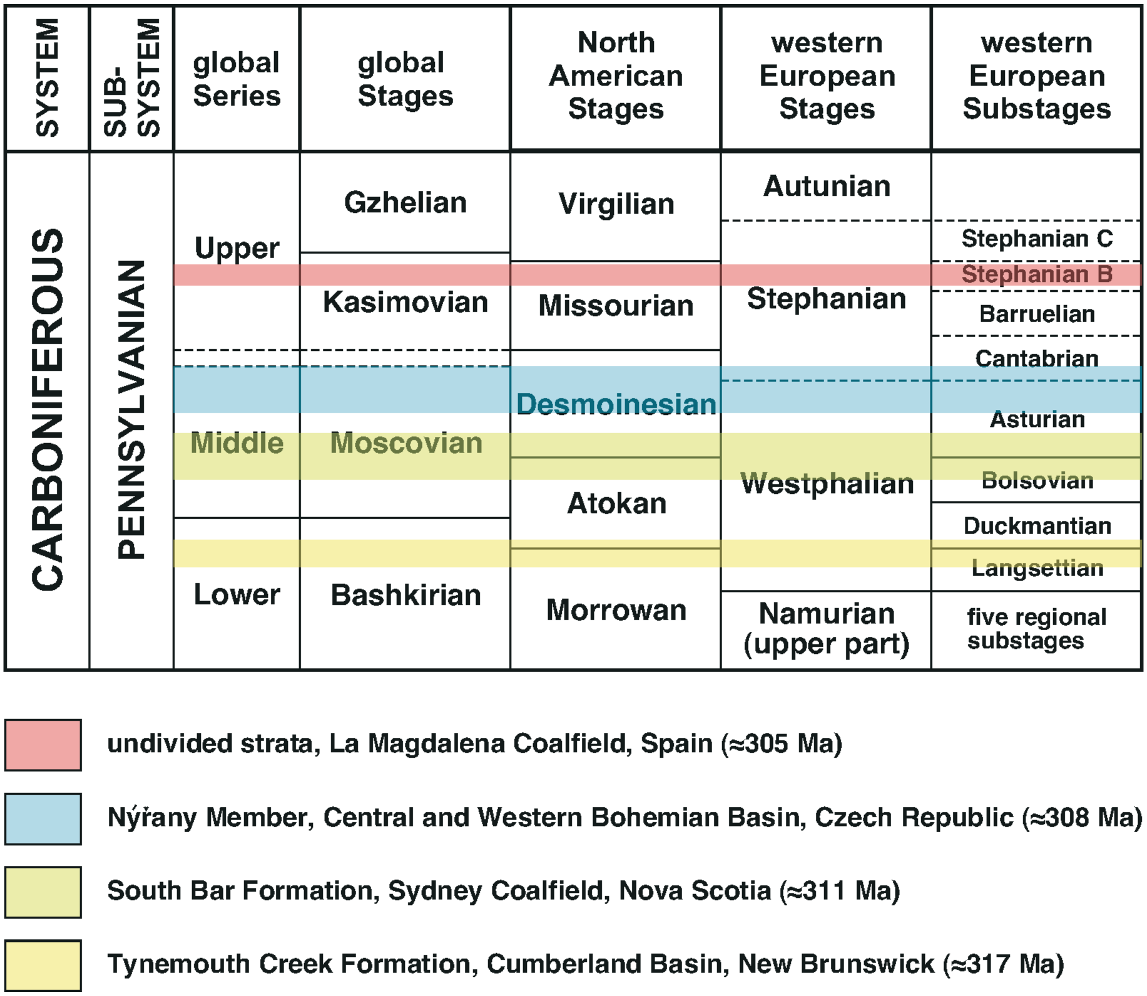


Figure 4. Chart showing ratified global series and stage subdivision of the Pennsylvanian, with approximate equivalency of North American stages and western European stages and substages. Dashed lines indicate uncertainty of boundary levels and/or correlation with global stages. Approximate intervals of successions studied in four basins/coalfields indicated. Chart modified from Heckel & Clayton (2006), with ages approximated from Davydov et al. (2010).

created such conditions. Accordingly, although mesic and xeric plants probably existed in extrabasinal settings during the Pennsylvanian, they also occupied basinal lowlands during seasonally drier climatic excursions.

1.2.2. Modified Objectives: Non-peat-forming Floras along Basin Margins

Although the search for ‘upland floras’ was decidedly unsuccessful, a large, census-sampled data set was compiled for megafloral assemblages preserved in largely non-peat-forming, basin-margin environments. Over the course of the project, 43779 megafloral specimens were collected, the majority of which could be identified to the specific or generic level, from Lower to Upper Pennsylvanian basin-margin strata dispersed over a large part of paleoequatorial Euramerica. Recognizing the significance of this large data set, the project objectives shifted to a paleoecological evaluation of Pennsylvanian vegetation that inhabited high-energy environments along basin margins, where high surface gradients and the proximity of relief or mountainous terrain may have influenced the composition, structure, and distribution of plant communities. In contrast, most previous paleoecological studies from this interval have focused on areas of low relief, low elevation, and low surface gradients, particularly in basinal lowlands where mires and associated wet clastic substrates were prevalent.

Megafloral assemblages associated with high-energy environments tend to be fragmentary and poorly preserved, and thus have received less attention from Carboniferous paleobotanists, who have traditionally been drawn to the large and well-preserved specimens typical of basinal lowland strata. Focusing on plant remains from basin-margin strata was a challenging exercise, but in my view, has ultimately resulted in a more encompassing perspective on Pennsylvanian vegetative biomes. By carefully linking quantitative analyses with depositional environments and taphonomic indicators, the project has resulted in a detailed understanding of the relationships between plant communities and their environment in non-peat-forming, basin-margin settings.

This research project comprised four primary objectives, which were accomplished to varying degrees and merge at several levels:

1. To determine the paleoecology of Pennsylvanian vegetation on basin margins, characterized by high-energy environments and minimal peat accumulation.
2. To evaluate changes in these communities through the Pennsylvanian.
3. To compare them with contemporaneous floras in basinal lowlands, characterized by low-energy environments and significant peat accumulation.
4. To ascertain when forests became sufficiently dense and tall to affect fluvial systems, and to determine the influence that large woody debris had on Pennsylvanian rivers.

These topics were addressed in three peer-reviewed papers, each of which forms a chapter in this thesis and were in various stages of the publication process when the thesis was submitted. Each chapter represents an essentially unmodified version of the peer-reviewed papers. A formal explanation of my contribution to each and a summary of their publication status are provided in Section 1.3 and Appendix 1. I co-authored the three papers, and contributed a substantial portion of the writing and research involved in their production. Section 1.3.5 contains information on additional paleoecological data that were collected during this study, but which were excluded from the thesis due to time constraints. Section 1.3.6 provides a summary of papers (in various phases of completion) that I co-authored or worked on during this project, but that lie outside the scope of the thesis objectives.

1.3. CHAPTERS AND CONTRIBUTIONS

1.3.1. Chapter 2

Chapter 2 is entitled *Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nýřany Member, Central and Western Bohemian Basin, Czech Republic)*, by Arden R. Bashforth, Jana Drábková, Stanislav Opluštil, Martin R. Gibling, and Howard J. Falcon-Lang. The paper was accepted by Review of Palaeobotany and Palynology in July of 2010, after peer-review by William DiMichele and an anonymous reviewer. A revised manuscript will be submitted in early September 2010.

This manuscript represents the product of a reconnaissance (2005) and two subsequent field seasons (2006, 2007) in the Czech Republic, during which new and historical (institution-based) megafloral collections were quantified from fine-grained intercalations in braided-river plain deposits of the upper Middle Pennsylvanian Nýřany Member of the Central and Western Bohemian Basin. A total of 20263 plant fragments were quantified in 41 quadrats, of which 12404 were identifiable. In addition to providing a paleoecological model for disturbance-prone and largely non-peat-forming settings in an intramontane basin, the study delved into modern ecological theory for lotic ecosystems to explain the distribution of various plant clades on the Pennsylvanian braided-river plain. With the exception of palynological analyses by J. Drábková

(Tables 7 and 8) and the segregation of fossiliferous, fine-grained strata into a comprehensive facies model by M.R. Gibling (Table 1), I wrote the manuscript and conducted the fieldwork and background research upon which the paper is based. Stanislav Opluštil contributed to fieldwork, and provided guidance on potential localities, repositories of historical collections, and background literature. The suggestions of H.J. Falcon-Lang were instrumental to the manuscript's organization.

1.3.2. Chapter 3

Chapter 3 is entitled *Vegetation heterogeneity on a Late Pennsylvanian braidplain draining the Variscan Mountains, La Magdalena Coalfield, northwestern Spain*, by Arden R. Bashforth, Howard J. Falcon-Lang, and Martin R. Gibling. The paper was peer-reviewed by William DiMichele and Robert Gastaldo, and published in the 15 June 2010 issue of Palaeogeography, Palaeoclimatology, Palaeoecology (v. 292, issue 3–4, pp. 367–390).

This manuscript represents the product of a reconnaissance (2006), with assistance from Roberto Wagner, and subsequent field season (2007) in northwestern Spain, during which megafloral assemblages were quantified from numerous facies in middle Late Pennsylvanian braided-river plain deposits preserved in La Magdalena Coalfield. A total of 12553 plant fragments in 93 quadrats were counted. In addition to providing a new paleoenvironmental interpretation for the basin fill and improving knowledge of Late Pennsylvanian tropical ecosystems in marginal settings, the findings demonstrate how the spatial structure of ancient plant communities can be reconstructed from multiple quadrats sampling a vertical succession. I wrote large parts of the manuscript and conducted all quantitative analyses, whereas M.R. Gibling was responsible for describing and interpreting depositional environments in the basin fill and placing the coalfield in tectonic and paleogeographic context. Quadrat data collection and specimen identification were undertaken by myself and H.J. Falcon-Lang, who suggested additional analyses and provided the manuscript with a more coherent organization.

1.3.3. Chapter 4

Chapter 4 is entitled *Log jams and flood sediment buildup caused channel avulsion in the Pennsylvanian of Atlantic Canada*, by Martin R. Gibling, Arden R. Bashforth, Howard J. Falcon-Lang, Jonathan P. Allen, and Christopher R. Fielding. The paper was peer-reviewed by Mike Leeder, Greg Nadon, and James Pizzuto, and published in the March 2010 issue of the Journal of Sedimentary Research (v. 80, issue 3, pp. 268–287).

At several levels in the South Bar Formation, sandstone successions showing evidence of rapid deposition at high-flow-stage are overlain by tangled accumulations of logs and coal intraclasts, above which fine-grained strata are sometimes developed. In an idea conceived during field discussions, M.R. Gibling proposed and championed a mechanism to explain these successions. During major floods, sediment-choked channels undercut banks of gravelly sand capped by mud and forested peat, widened the channels, and toppled riparian vegetation. Resulting log jams may have caused substantial channel blockage, thereby promoting avulsion and channel abandonment. These log jams are among the oldest known examples of large woody debris affecting channel dynamics, and the chapter discusses when arborescent plants might have begun to influence fluvial systems due to increased tree size and forest density through the Devonian and

Carboniferous. I contributed stand-alone sections to the manuscript, as well as parts that M.R. Gibling revised and incorporated with the rest of the text. Specifically, I was responsible for collecting size and composition data for log jam accumulations, summarizing the habit and paleoecological preferences of plant groups represented, calculating the original height of trees in the log jams, and offering an explanation for the absence of identifiable plant remains in abandoned channel deposits. Howard J. Falcon-Lang contributed to the Discussion, particularly a section on early vegetation history relevant to the emergence of log jams. Given that J.P. Allen and C.R. Fielding were working simultaneously on flood deposits in the South Bar Formation, some of their results were incorporated.

1.3.4. Chapter 5

Chapter 5 draws together concepts from the body of work brought together in this thesis, and addresses implications of the research for recognizing broad trends in floristic patterns and the influence early plants had on their ecosystems. To begin with, a synthesis summarizes what is currently known about the paleoecology of vegetation that occupied largely non-peat-forming habitats during the Pennsylvanian, with a focus on temporal changes in plant communities from basin-margin settings. The crucial role that plants played in the evolution of early landscapes is discussed, as is the inherent role of vegetational heterogeneity to terrestrial plant communities. The discussion also delves into the debate about the composition and distribution of ‘upland’ versus that of ‘lowland’ floras on Pennsylvanian landscapes, and provides a preliminary classification of plant biomes that existed during this important interval of Earth history.

1.3.5. Paleoecological Work Not Included as Chapters in this Thesis

Due to time constraints, some paleoecological data gathered during this project were not fully analyzed and thus will not be presented in this thesis. However, it is anticipated that the results will form a component of future papers that I will co-author.

1.3.5.1. Paleoecological Model for Vegetation on a Dry Fluvial Megafan, Tynemouth Creek Formation

Megafloral assemblages were quantified from the upper Lower Pennsylvanian Tynemouth Creek Formation in New Brunswick, previously interpreted as the deposits of a prograding alluvial fan shed from the margin of the Cumberland Basin (Plint & van de Poll, 1982). Based on new sedimentological analyses conducted by M.R. Gibling, the succession is reinterpreted as the product of a fluvial megafan laid down under subhumid to semi-arid climatic conditions (Falcon-Lang et al., 2010). Narrow fixed-channels that contained ephemeral flow characterized the dryland alluvial setting, and although floodplains were largely dry and partly indurated, shallow ponds were locally present. Megafloral assemblages are common, and represent riparian vegetation that occupied channel banks and overbank habitats.

I quantified 5360 plant fragments from 32 discrete fossiliferous units (40 quadrats) through the succession, from both grey and red strata. All assemblages are dominated by *Cordaites* (leaves of cordaitalean trees), although the poorly preserved remains of medullosalean pteridosperms, ferns, and sphenopsids are more common in grey beds. Detailed fossil identifications and quantitative analyses of megafloral assemblages are not yet complete, but some general inferences are included in Chapter 5. Building on the preliminary study of Falcon-Lang (2006a), a paleoecological model will be constructed for riparian vegetation on a Lower Pennsylvanian fluvial megafan deposited in a subhumid to semi-arid climate.

1.3.5.2. Paleoecological Model for Wetland Vegetation in South Bar and Waddens Cove Formations

The middle Middle Pennsylvanian South Bar Formation forms part of the succession in the Sydney Coalfield in Nova Scotia, and accumulated on a braided-river plain adjacent to elevated uplands (Rust et al., 1987; Rust & Gibling, 1990a). Partly coeval deposits of the Waddens Cove Formation are attributed to anastomosing rivers incised into floodplains, some of which were well drained (Rust et al., 1987; Gibling & Rust, 1990). Coal seams are largely thin, impure, and discontinuous in both units, although large coal intraclasts (formerly rafted peat) and logs attributed to peat-forming vegetation abound in channel deposits of the South Bar Formation, indicating that mires were common but mostly eroded (Gibling et al., 2010; see Section 1.3.3 and Chapter 4).

Despite targeted searches, overbank deposits in these units are essentially devoid of identifiable plant remains. Megafloral assemblages (excluding logs) were only found in fine-grained strata above coal seams (i.e., 'roof shales'). I quantified 4545 plant fragments (21 quadrats) from 'roof shales' above the McAulay, Shoemaker, and Mullins seams (South Bar Formation) and Tracy Seam (Waddens Cove Formation). All assemblages are dominated by pteridosperm or cordaitalean foliage. Grab samples of coal from each seam were collected for palynological analysis, done by T.Kh. Dimitrova (Sofia, Bulgaria). Detailed fossil identifications and quantitative analyses of megafloral assemblages are not yet complete, but some general inferences from the research are included in Chapter 5. In the future, integration of megafloral and palynological data will result in a model for wetland vegetation on Middle Pennsylvanian braided- and meandering-river plains, and biostratigraphic analysis will help constrain the age of the South Bar and Waddens Cove formations.

1.3.6. Work Outside the Thesis Scope

1.3.6.1. Sphenophyll Reconstruction

A paper entitled *Partial reconstruction and palaeoecology of* Sphenophyllum costae *(Middle Pennsylvanian, Nova Scotia, Canada)*, by Arden R. Bashforth and Erwin L. Zodrow, was written during the PhD project. The manuscript was peer-reviewed by Milan Libertín and an anonymous reviewer, and published in the December 2007 issue of the Bulletin of Geosciences (v. 82, no. 4, pp. 365–382).

Building on initial descriptions, measurements, and photographs by E.L. Zodrow, I did further morphological analyses, rewrote the entire manuscript, and developed arguabley the most life-like reconstruction of a sphenophyll to date (Fig. 5).

1.3.6.2. Middle Pennsylvanian Mire Buried by Volcanic Ash

During the 2006 field season in the Czech Republic, I briefly helped colleagues excavate *in situ* plant remains from a tuff overlying a Middle Pennsylvanian coal seam in the Radnice Member (Kladno Formation; Fig. 6). Volcanic ash covered the forested mire in a geological instant (T^0 deposit), thereby preserving the peat-forming ecosystem in extraordinary detail. I was a co-author in the paper entitled *A Middle Pennsylvanian (Bolsovian) peat-forming forest preserved* in situ *in volcanic ash of the Whetstone Horizon* in the Radnice Basin, Czech Republic, by Stanislav Opluštil, Josef Pšenička,

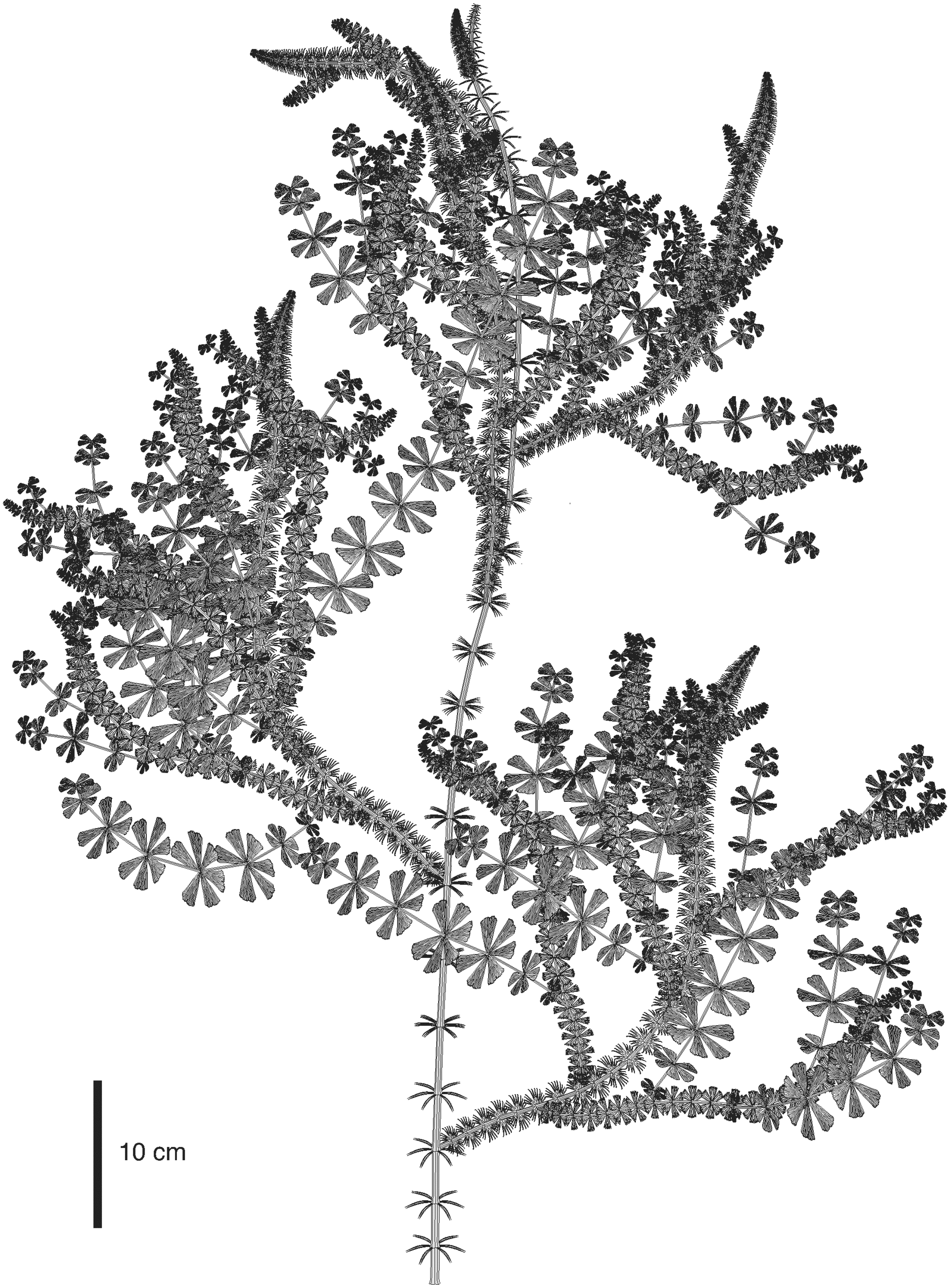


Figure 5. Reconstruction of *Sphenophyllum costae*. From Bashforth & Zodrow (2007, fig. 10).

Milan Libertín, Arden R. Bashforth, Zbyněk Šimůnek, Jana Drábková, Jiřina Dašková. The paper was peer-reviewed by William DiMichele and Robert Gastaldo, and published in the June 2009 issue of the Review of Palaeobotany and Palynology (v. 155, issue 3–4, pp. 234–274). Initially, I was to edit the 'English', but my role expanded to writing several stand-alone sections and fortifying paleoecological interpretations.

1.3.6.3. Description and Taxonomy of Callipteridium rubescens

While in the Czech Republic in 2005, well preserved specimens of *Callipteridium rubescens*—a poorly known medullosalean pteridosperm originally described from the Czech Republic—were documented from the Rozdělov locality of the Nýřany Member (Section 2.5.4). Realizing *C. rubescens* may be an earlier synonym of *Callipteridium jongmansii* (Němejc, 1936a), a biostratigraphically important species described from France and more frequently noted in the literature, I embarked on a morphometric study to determine if the two taxa are indeed conspecific. Preliminary morphometric analyses indicate that they are synonymous (Bashforth, 2007). Zbyněk Šimůnek (Prague, Czech Republic) is currently examining cuticles of both species, based in part on fragments from type material of *C. jongmansii* I obtained on a visit to Lille, France. Initial results of the cuticular investigation suggest that *C. rubescens* and *C. jongmansii* are separate species. Thus, we either have a single species with variable cuticles (a notion that I favor), or two species with identical foliar morphologies and biostratigraphic ranges (a scenario that seems to me unlikely). Large parts of this paper have been written, but further morphometric and cuticular analyses are needed. The preliminary title is *Reaffirming the synonymy of* Callipteridium rubescens *and* Callipteridium jongmansii*: a* *biostratigraphically important Middle to Upper Pennsylvanian pteridosperm from Euramerica*, by Arden R. Bashforth, Zbyněk Šimůnek, and Stanislav Opluštil, and the manuscript will be submitted to the Journal of Systematic Palaeontology.

1.3.6.4. Arthropleura *Body Impression*

Randall Miller (Saint John, Canada) discovered an interesting fossil in the Tynemouth Creek Formation, New Brunswick (see Section 1.3.5.1) during joint fieldwork in 2008. The specimen appears to be an impression of an arthropleurid, a large millipede-like terrestrial arthropod, together with tetrapod tracks. The paper entitled *A putative* Arthropleura *body impression in the Lower Pennsylvanian Tynemouth Creek Formation, New Brunswick, Canada*, by Randall F. Miller, Arden R. Bashforth, Howard J. Falcon-Lang, and Martin R. Gibling, was submitted to PALAIOS in July 2009. Unfortunately, it was rejected after peer-review by three anonymous reviewers. My role was to provide preliminary biostratigraphic information based on megafloral species, along with general editorial comments.

1.3.6.5. Angiospermous Features in Jurassic Wood from Greenland

I was asked to edit the 'English' of a manuscript describing an unusual Early to Middle Jurassic wood taxon from Jameson Land, Eastern Greenland, which shows many morphological features typical of angiosperms. Based on my editing, I was invited to be a co-author in the paper entitled Ecpagloxylon mathiesenii *gen. nov. et sp. nov., a Jurassic wood from Greenland with several primitive angiosperm features*, by Marc Philippe, Gilles Cuny, and Arden R. Bashforth. The paper was peer-reviewed by Ronny

Rößler, and published in the July 2010 issue of Plant Systematics and Evolution (v. 287, number 3–4, pp. 153–165). Although it was not possible to confirm the angiosperm affinity of *Ecpagloxylon*, in the paper we suggest that, if a Jurassic angiosperm existed, it might well have had similar wood.

1.3.6.6. Tetrapod Trackways

During joint fieldwork in 2008, Howard J. Falcon-Lang discovered numerous tetrapod trackways in the Tynemouth Creek Formation, New Brunswick (see Section 1.3.5.1). The resulting paper entitled *Diverse tetrapod trackways in the Lower Pennsylvanian Tynemouth Creek Formation, near St. Martins, southern New Brunswick, Canada*, by Howard J. Falcon-Lang, Martin R. Gibling, Randall F. Miller, Michael J. Benton, and Arden R. Bashforth, will be published in the 1 October issue of Palaeogeography, Palaeoclimatology, Palaeoecology (v. 296, issue 1–2, pp. 1–13). It was peer-reviewed by Jenny Clack and an anonymous reviewer. Results of the study suggest that early amniotes (tetropods that lay terrestrially adapted eggs) were well adapted to dryland settings by the Early Pennsylvanian. My role in the study was to provide biostratigraphic resolution to the trackways based on megafloral assemblages, along with photographs of some of the most abundant plant fossil species.

CHAPTER 2: LANDSCAPE GRADIENTS AND PATCHINESS IN RIPARIAN VEGETATION ON A MIDDLE PENNSYLVANIAN BRAIDED-RIVER PLAIN PRONE TO FLOOD DISTURBANCE (NÝŘANY MEMBER, CENTRAL AND WESTERN BOHEMIAN BASIN, CZECH REPUBLIC)

Arden R. Bashforth, Jana Drábková, Stanislav Opluštil, Martin R. Gibling,

and Howard J. Falcon-Lang

2.1. ABSTRACT

The spatial heterogeneity and community ecology is reconstructed for riparian vegetation preserved in fluvial deposits of the late Asturian to middle(?) Cantabrian Nýřany Member, Central and Western Bohemian Basin, Czech Republic. Channel sandstone and conglomerate dominate at the four localities studied, but fine-grained intercalations, representing abandoned channels, floodplains, and shallow lakes, yielded rich megafloral and palynological assemblages. Sedimentological evidence indicates that high-energy flow characterized a braided-river plain prone to avulsion and flooding. Taphonomic observations and multivariate analysis of 41 quadrats containing mostly (par)autochthonous megafloral assemblages reveal that riparian vegetation comprised a collage of monospecific to low-diversity communities, with patchiness prevalent at local and regional scales. The vertical arrangement of megafloral assemblages provides evidence for ecological succession at some sites, with pioneering sphenopsid-dominated seres being replaced by marattialean tree ferns and then medullosalean pteridosperms as ponded waters shallowed and exposure increased. At other sites, the composition and

structure of megafloral assemblages remains unchanged through short stratigraphic intervals, indicating short-term persistence and resilience of communities. Non-metric multi-dimensional scaling exposes habitat partitioning between different plant groups, which were organized along ecological gradients controlled by the drainage and stability of substrates. Well-drained and stable channel margins supported long-lived site-occupiers, such as cordaitaleans and monospecific stands of medullosalean pteridosperms. Application of the Patch Dynamics Concept, which predicts patterns of community recovery after disturbance, indicates that these species assemblages were 'dominance-controlled' (i.e., contained one or more K-selected species that were competitively superior to all others). Pioneering vegetation comprising fast-growing, opportunistic taxa, particularly ferns and sphenopsids, was most common on wetter, shifting substrates of frequently flooded abandoned channels, low-lying floodplains, and lake margins. In these 'founder-controlled' communities, several r-selected species had similar competitive abilities. Ferns, sphenopsids, and various lycopsids dominated swamps, marshes, and ephemeral mires on distal floodplains. The heterogeneous distribution of riparian plants is consistent with that of modern, disturbance-dominated fluvial environments, although species richness was much lower in the Middle Pennsylvanian. A review of floristic patterns in latest Middle Pennsylvanian clastic vegetation of Euramerica confirms that arborescent ferns proliferated across non-peat-forming wetlands during the late Asturian, although medullosalean pteridosperms remained the most important component of most communities. The Nýřany Member seems to be an exception, as pteridosperm relative abundance may have declined dramatically at a level coincident with the fern radiation.

2.2. INTRODUCTION

Vegetation in modern ecosystems is patchy over a wide spectrum of spatial and temporal scales, largely due to natural disturbances that include abiotic (e.g., fire, windthrow, flooding, landslides, drought) and biotic (e.g., insect/fungal outbreaks, herbivory, senescence) processes (Delcourt et al., 1983; White, 1979; White & Pickett, 1985). The response of ecosystems to the cumulative effects of recurring natural disturbances is the main tenet of the Patch Dynamics Concept (Pickett & White, 1985; Townsend, 1989), which predicts changes in the organization and structure of communities through time and space.

Riparian zones are an interface between terrestrial and aquatic realms, and thus are one of the most complex ecological systems on Earth (Gregory et al., 1991; Naiman et al., 2000). As used in this paper, a riparian zone encompasses a river channel and those parts of the surrounding landscape where vegetation can be influenced by elevated watertables or flooding, even if very infrequently (i.e., *sensu* Naiman & Décamps, 1997). Recurring flooding maintains the physical heterogeneity of the drainage network (Swanson et al., 1988), and repeated habitat destruction or disturbance followed by recovery ensures that riparian communities are equally heterogeneous (Osterkamp & Hupp, 1984; Harris, 1987; Rot et al., 2000). The compositional and successional variability of the vegetative mosaic results in high diversity (Salo et al., 1986; Pollock et al., 1998), and facilitates the coexistence of plants with disparate life history strategies (Denslow, 1985; Naiman & Décamps, 1997).

The earliest land plant communities undoubtedly were heterogeneous and influenced by natural disturbances, and there is clear paleobotanical evidence for patchiness and ecological gradients in Early Devonian terrestrial ecosystems (e.g., Elick et al., 1998; Griffing et al., 2000; Hotton et al., 2001; Cressler et al., 2010). Landscape-scale gradients have been well documented in Pennsylvanian mires, with the distribution of taxa dependent on the complex interplay between edaphic conditions and their physiological requirements and reproductive strategies (DiMichele & Phillips, 1994, 1996a, 2002; Phillips & DiMichele, 1992; DiMichele et al., 2006b, 2007). Although such gradients are apparent at broad scales, peat-forming vegetation also was heterogeneous at local scales due to disturbances, soil conditions, and forest tiering (DiMichele & Nelson, 1989; Gastaldo et al., 2004; DiMichele et al., 2009b; Libertín et al., 2009a; Opluštil et al., 2009a, b).

Such patterns are not as well constrained for wetland communities occupying clastic substrates (e.g., swamps, floodplains) associated with extensive mires in the lowlands of paralic basins (Scott, 1977, 1978, 1979; Gastaldo, 1987; Calder et al., 2006). Even less is known about the composition and distribution of vegetation in basin-margin settings (e.g., alluvial fans, high-energy fluvial systems) where peat accumulation was restricted. Broad landscape-scale gradients have been inferred for such disturbance-dominated regimes (Iwaniw, 1985; Bashforth, 2005; Martín-Closas & Galtier, 2005; Falcon-Lang, 2006a; Martín-Closas & Martínez-Roig, 2007; Charbonnier et al., 2008; Libertín et al., 2009b), and Bashforth et al. (2010; Chapter 3) provided a glimpse into the local-scale heterogeneity in riparian plant communities in these high-energy environments.

To improve knowledge of the ecology of riparian vegetation in basin-margin settings, we present a study of the upper Middle Pennsylvanian (upper Moscovian)

Nýřany Member, which accumulated in the heart of the Variscan Mountains in the Central and Western Bohemian Basin (CWB) of the Czech Republic. We examined four localities where sandstone and conglomerate predominates, fine-grained facies are rare but rich in plant remains, and coal seams are absent or thin and clastic-rich. Together these features indicate a braided-river plain characterized by high-energy flow conditions and frequent flooding. The sedimentology and megafloral assemblages at each locality are documented in detail for the first time, and a representative suite of species is illustrated. By integrating sedimentologic and taphonomic observations with quantitative megafloral and palynological analyses, we interpret the spatial and temporal distribution of riparian vegetation in this disturbance-dominated regime. Along with evidence for ecological succession and persistence, we identify broad ecological gradients and local- and regional-scale heterogeneity. The reconstructed landscape is compared with riparian communities in modern fluvial environments, and with the Patch Dynamics Concept to determine the structure and organization of the vegetation. Changes in floristic patterns in latest Middle Pennsylvanian vegetation that occupied clastic substrates of Euramerica are also assessed.

In this paper, we use the terminology of Greb et al. (2006) to differentiate the various types of vegetated wetlands characterized by wet or waterlogged soil conditions: *marshes* are dominated by herbaceous, emergent plants rooted in mineral substrates; *swamps* are forested wetlands on mineral substrates; and *mires* have peat substrates, which are dominated by trees (*forested mires*) or herbaceous and/or shrubby plants (*non-forested mires*).

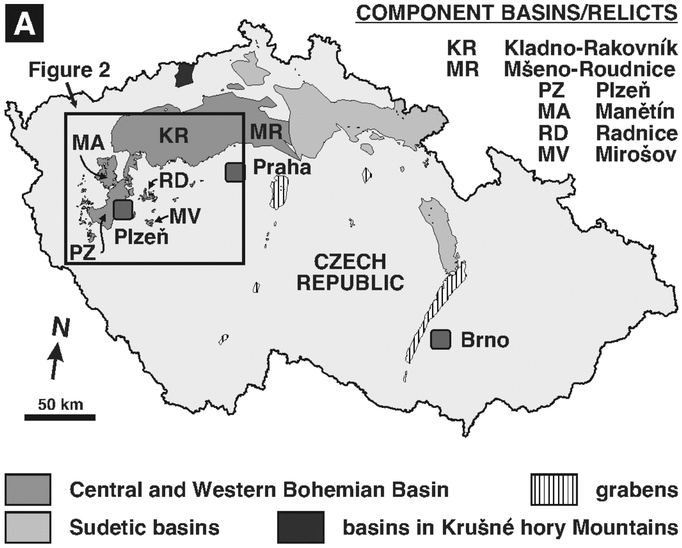
2.3. GEOLOGICAL SETTING

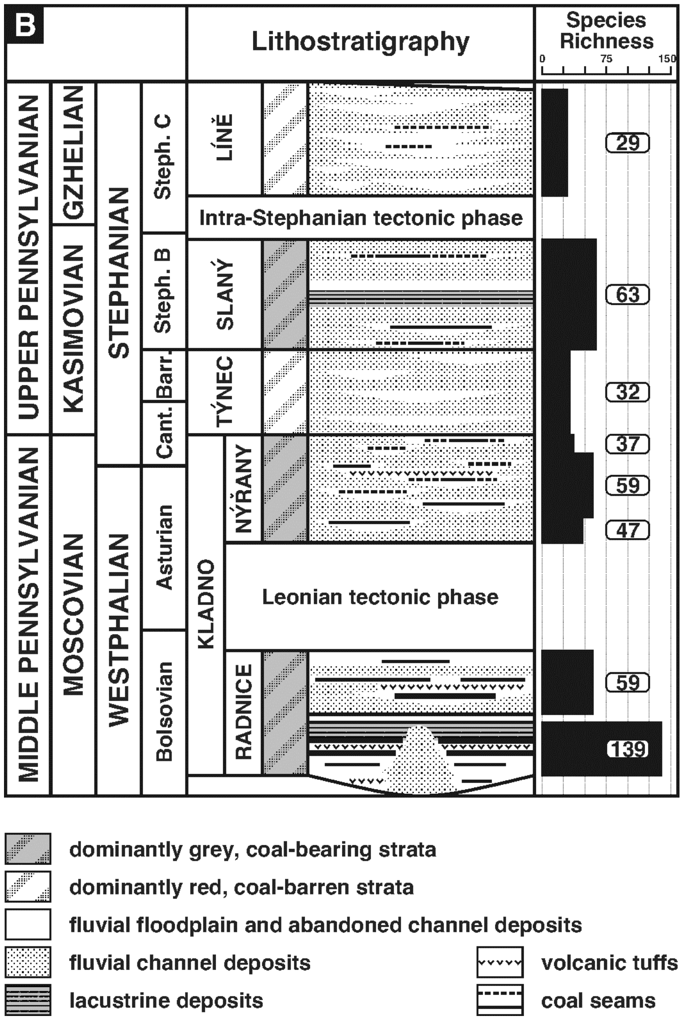
2.3.1. Central and Western Bohemian Basin

The CWB is one of several intramontane basins that developed atop the Bohemian Massif due to collapse and concomitant strike-slip and wrench faulting during the Variscan Orogeny (Fig. 6A; Pašek & Urban, 1990; Pešek, 1994, 2004; Opluštil & Pešek, 1998). It filled with terrestrial sediment during the late Paleozoic, and comprised a single, large depocentre during later stages of development (Havlena, 1977). Uplift and subsequent denudation led to a complex of larger basins surrounded by small erosional relicts that share common lithostratigraphic packages. Up to 1400 m of Middle to Upper Pennsylvanian (Moscovian to Gzhelian) strata are assigned to the Kladno, Týnec, Slaný, and Líně formations (Fig. 6B; Weithofer, 1896, 1902; Havlena & Pešek, 1980; Pešek, 1994). The alternation between mainly grey, coal-bearing and mainly red, coal-barren formations has been interpreted to record deposition under different climatic regimes (Holub et al., 1975; Opluštil & Pešek, 1998; Opluštil & Cleal, 2007), although changes in floodplain drainage and tectonics undoubtedly played a prominent role (Opluštil, 2004).

During the Middle Pennsylvanian, the CWB was situated in the midst of the Variscan Mountains, ≈400 km south of the North Variscan Foreland Basin and >1000 km north of the Paleotethys Ocean (Scotese & McKerrow, 1990; Zeigler, 1990). Paleomagnetic data indicate a paleolatitude of 4 to 6° N (Krs & Pruner, 1995). Drainage was northwestward to the North Variscan Foreland Basin via the Zwickau Coalfield in Saxony, and southwestward to the Naab Basin in Bavaria (Opluštil, 2005a). Despite its location in the heart of the Variscan Mountains, the original paleoelevation of the CWB is uncertain. Opluštil (2005a) inferred a paleoelevation of ≈1000 m based on the presumed

Figure 6. A. Distribution of upper Paleozoic basins in Czech Republic, and components of Central and Western Bohemian Basin. From Pešek (1994, fig. 1) and Pešek et al. (1998, appendix 15). B. Stratigraphy and megafloral species richness through Central and Western Bohemian Basin. Members not differentiated for Slaný Formation. Species richness values do not include new taxa identified herein. Modified from Opluštil & Cleal (2007, fig. 6).


A
COMPONENT BASINS/RELICTS
KR Kladno-Rakovník
MR Mšeno-Roudnice
PZ Plzeň
MA Manětín
RD Radnice
MV Mirošov
Figure 2
MA
KR
MR
RD
MV
Plzeň
PZ
Praha
CZECH REPUBLIC
Brno
N
50 km
Central and Western Bohemian Basin
Sudetic basins
grabens
basins in Krušné hory Mountains


B
Lithostratigraphy
Species Richness
0
75
150
UPPER PENNSYLVANIAN
MIDDLE PENNSYLVANIAN
GZHELIAN
KASIMOVIAN
MOSCOVIAN
STEPHANIAN
WESTPHALIAN
Steph. C
Steph. B
Barr.
Cant.
Asturian
Bolsovian
LÍNĚ
Intra-Stephanian tectonic phase
SLANÝ
TÝNEC
NÝŘANY
KLADNO
Leonian tectonic phase
RADNICE
29
63
32
37
59
47
59
139
dominantly grey, coal-bearing strata
dominantly red, coal-barren strata
fluvial floodplain and abandoned channel deposits
fluvial channel deposits
lacustrine deposits
volcanic tuffs
coal seams

length and gradient of the northwestward drainage system. However, the species pool is comparable to that known from coeval paralic basins, where the vegetation grew at or near sea level. Nonetheless, the absence of evidence for marine or brackish incursions in the basin fill, along with the highly variable topography of the basin floor (Opluštil, 2005a), is consistent with a minimal paleoelevation of a few hundred metres. Accordingly, very steep margins and a fairly low-elevation floor may have characterized the CWB.

2.3.2. Nýřany Member

The Nýřany Member is the uppermost unit of the Kladno Formation (Fig. 6B), and reaches a thickness of ≈450 m in the Kladno-Rakovník Basin (Fig. 1A; Pešek, 1994). Strata accumulated on a broad alluvial plain that blanketed an incompletely peneplained plateau punctuated by low ridges of emergent Neoproterozoic and lower Paleozoic basement, with deposition gradually encroaching northeastward through time (Pešek, 1994, 2003, 2004; Opluštil & Pešek, 1998). Most detritus was supplied from granitoid sources to the south and southeast (Kukal, 1984; Fig. 7), and overall drainage was northward.

2.3.2.1. Depositional Environments

The depositional settings of the alluvial plain on which the Nýřany Member was deposited are, for the most part, poorly constrained due to limited exposure. Nonetheless, Opluštil & Pešek (1998, fig. 6) and Pešek et al. (1998, appendix 35) provided a rough guide to regional lithological changes in the unit, which they divided into four

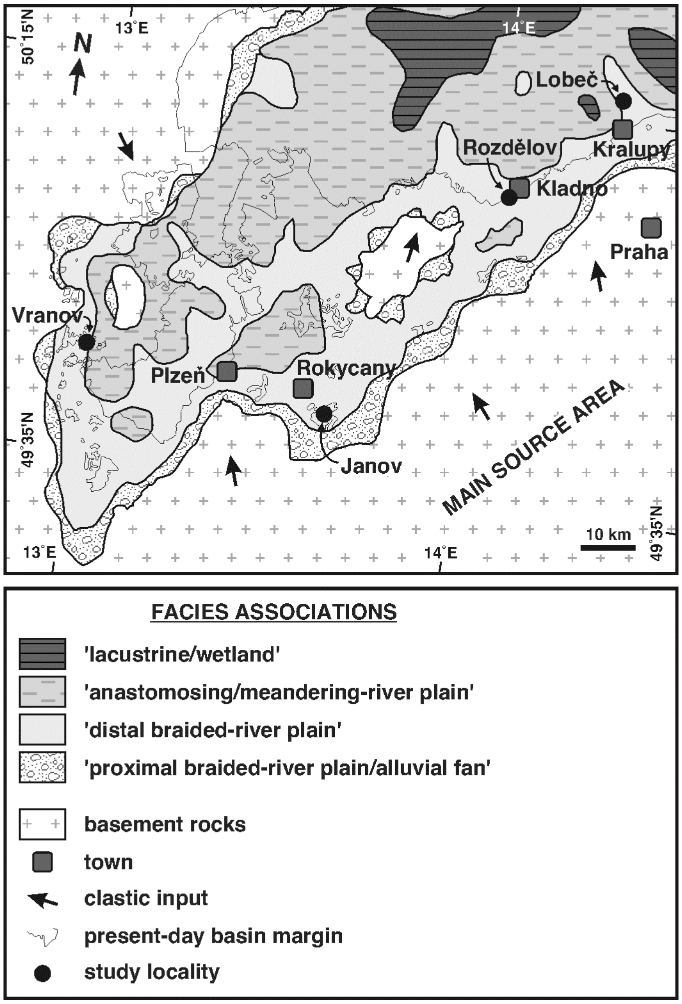


Figure 7. Original paleogeographic extent of Nýřany Member in Central and Western Bohemian Basin, divided into four facies associations on broad alluvial plain. Segregation of facies associations based on proportion of ‘coarse’ strata (medium- to very coarse-grained sandstone and conglomerate) in borehole cores (see Section 2.3.2.1 for details). Several facies associations may be present at any given place, but distribution is based on that which dominates. Accordingly, the Janov locality is shown as part of the ‘distal braided-river plain’ facies association, although the basal Mirošov Horizon belongs to the ‘proximal braided-river plain/alluvial fan’ facies association. See inset in Figure 6 for position. After Pešek et al. (1998, appendix 35), with clastic input directions from Opluštil et al. (2005, fig. 2).

lithological groupings. Their distribution (Fig. 7) is primarily based on the proportion of 'coarse' (=medium- to very coarse-grained sandstone and conglomerate) versus 'fine' strata in >1000 borehole cores over the CWB, supplemented by sedimentological data from scattered outcrops. Although detailed borehole analyses are needed to produce a more comprehensive facies model, the four lithological groupings have herein been adopted as facies associations and given preliminary names based on their dominant depositional environments.

2.3.2.1.1. 'Proximal Braided-river Plain/Alluvial Fan' Facies Association.

Known as the 'Mirošov Horizon' (Fig. 8), Opluštil & Pešek (1998) included this association in their 'colluvium, alluvial fan, fan delta' lithological grouping. It is the coarsest component of the Nýřany Member, and comprises a basal layer of 'coarse' strata with lesser colluvium and breccia that unconformably overlies the Radnice Member or basement rocks. Although principally known from borehole cores, the unit is exposed in the Mirošov Relict (Section 2.5.1), and is inferred to have rimmed the basin margin and elevated ridges. We interpret most of the Mirošov Horizon as proximal braided fluvial deposits rather than alluvial fan remnants, but the unit is clearly different from the relatively finer and more widespread 'distal braided-river plain' facies association.

A discrete, fan-shaped package of varicolored mudstone with sporadic sandstone intercalations at the base of the Plzeň Basin (the 'Komberk Horizon') has been interpreted as an alluvial fan (Pešek, 1968). This unit has been correlated with the Mirošov Horizon on paleobotanical and lithological grounds (Šetlík, 1968a; Havlena & Pešek, 1980).

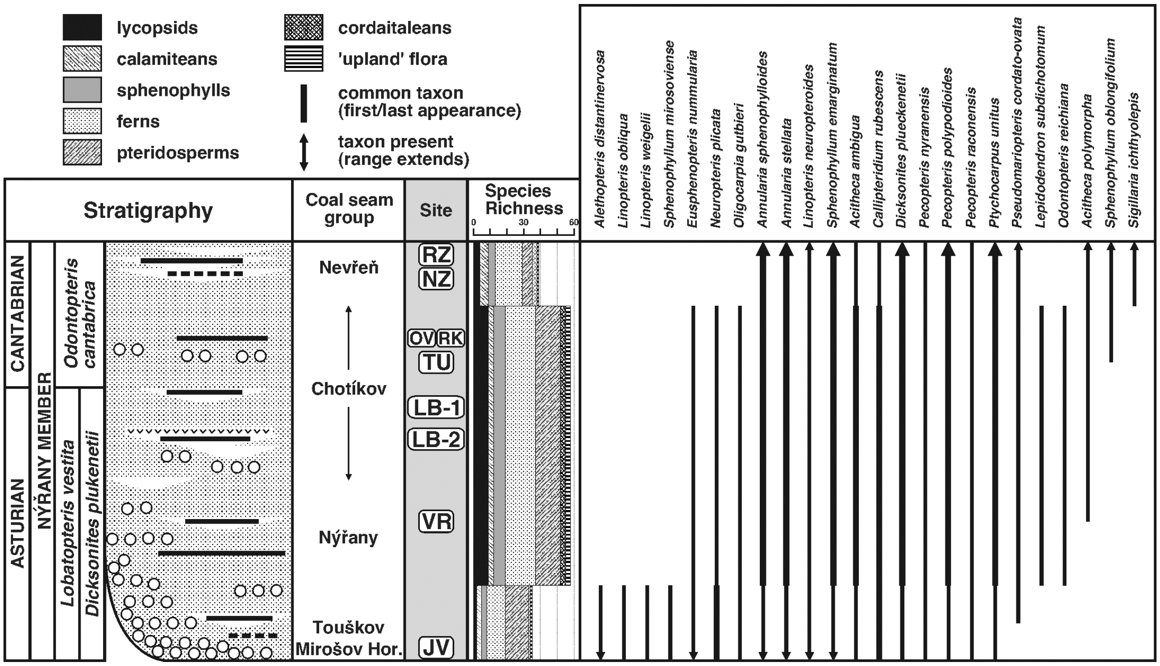


Figure 8. Stratigraphic context of Nýřany Member, indicating proposed correlation with biozonation of Cleal & Thomas (1994), vertical position of coal seam groups and studied localities/sites, ranges of important taxa, and species richness (segregated by plant group) based on all biological taxa listed in Pešek (2004, table 2). 'Upland' flora comprises *Lesleya* sp., *Pterophyllum* sp., and *Rhacopteris* spp. Abbreviations: Janov locality (JV); Vranov locality (VR); Lobeč cliff base site (LB-2); Lobeč cliff top site (LB-1); railway tunnel site (TU); gully site (RK); Olovnice site (OV); Nelahozeves site (NZ); Rozdělov locality (RZ). See Figure 6 for legend showing lithology symbols; white circles represent conglomerate. The Komberk Horizon (not shown) correlates with the Mirošov Horizon and Touškov group of coal seams. Note that the range of *Acitheca polymorpha* now extended down to Roof Nýřany Seam (VR), and the first appearance of *Sphenophyllum oblongifolium* is at the railway tunnel site (TU). Modified from Opluštil & Cleal (2007, fig. 11).

2.3.2.1.2 'Distal Braided-River Plain' Facies Association

Opluštil & Pešek (1998) included this association in their 'alluvial plain dominated by channel conglomerate and sandstone' lithological grouping. It comprises ≥80% 'coarse' strata, with subordinate fine-grained intercalations and rare coal seams that are clastic-rich, thin, and laterally discontinuous. Opluštil et al. (2005) provided a detailed facies model for the coarse-grained component of this association based on outcrops in the Plzeň and Kladno-Rakovník basins. They concluded that strata accumulated on braided-river plains that changed in dynamics through time, with high-energy, low-sinuosity, laterally migrating systems replaced by lower energy, higher sinuosity, vertically aggrading systems. Associated fine-grained rocks (Section 2.3.2.2) represent abandoned channels, floodplains, shallow lakes, swamps, and marshes, and coal seams record short-lived mires. The association is most common in western Bohemia (e.g., Plzeň Basin).

2.3.2.1.3. 'Anastomosing/Meandering-River Plain' Facies Association

Opluštil & Pešek (1998) included this association in their 'alluvial plain with ephemeral lakes' lithological grouping. It comprises 30 to 80% 'coarse' strata, and fine-grained sediment is lithologically similar to that of the 'distal braided-river plain'. However, clastic wetland facies are better developed and coal seams are thicker and more laterally extensive, indicating a lower energy regime favorable to prolonged peat accumulation. Subordinate sandstone and lesser conglomerate facies may represent anastomosing or meandering river deposits. This association is known only from borehole cores, and is most common in central Bohemia (e.g., Kladno-Rakovník Basin), particularly in areas distant from basin margins and with higher subsidence rates.

2.3.2.1.4. 'Lacustrine/Wetland' Facies Association

Opluštil & Pešek (1998) included this association in their 'alluvial plain dominated by lakes' lithological grouping. It is lithologically similar to the 'anastomosing/meandering-river plain' facies association, but comprises ≤30% 'coarse' strata and contains little conglomerate. Much of the fine-grained strata may be lacustrine, although this requires confirmation. This association is only known from borehole cores, and dominates central and eastern parts of the CWB (e.g., eastern Kladno-Rakovník and Mšeno-Roudnice basins), corresponding to areas with the highest subsidence rates and most restricted clastic input.

2.3.2.2. Facies Model for Fossiliferous, Fine-Grained Strata on Braided-river Plain

Opluštil et al. (2005) produced a detailed interpretation of the coarse-grained component of the 'distal braided-river plain' facies association, but a lack of exposure precluded fuller development of a facies model for associated fine-grained strata. To fill this void, we provide a preliminary classification of these deposits (Table 1), specifically focusing on depositional settings in which well-preserved plant remains were recovered during this study. We propose that two types of avulsion, operating on different spatial and temporal scales, resulted in depositional environments suitable for the preservation of identifiable megafloral assemblages. In most cases, facies demarcation is challenging

Features	Abandoned Channel		Floodplain	Shallow lake
	Mainstem	Minor		
Geometry	lensoid in cross-section, sheet-like in longitudinal section (channel form)		sheet-like	
Thickness	matches that of mainstem active channels	matches that of minor active channels; thin, fine-grained fills may cap mainstem channels mainly filled with coarse-grained sediment	typically thick	
Width	matches that of mainstem active channels; decametres to hectometres	matches that of minor active channels; metres to decametres	typically hectometres to kilometres	
Lithology	laminated or thinly interbedded mudstone and siltstone; sandstone beds common if periodically flooded by active channels		very variable; typically mudstone, with some coarse-grained beds due to flooding or avulsion	laminated mudstone, with coarse-grained beds at margins
Paleosols (rooting)	poorly developed but common, especially at top of fill	poorly developed and rare	well developed and common	well developed at margins
Coal seams	rare in upper parts but laterally restricted		common and may be laterally extensive	may be laterally extensive along margins
Source of megafloral assemblages	(par)autochthounous remains from vegetation that occupied aggrading channel-floor substrates and channel flanks; some allochthonous remains from distant sources	(par)autochthonous remains from vegetation that occupied channel flanks; some allochthonous remains from distant sources	(par)autochthonous remains from vegetation that occupied numerous subenvironments, including mires, swamps, marshes, and margins of small ponds and floodplain channels	(par)autochthonous remains from vegetation that occupied lake margins
Preservation of megafloral assemblages	excellent due to rapid burial, slightly acidic waters, reducing conditions, limited rhizoturbation, and/or minor fluctuations in water table		poor due to common rhizoturbation and/or persistent fluctuations in water table, leading to microbial degradation and oxidation; excellent in small ponds and floodplain channels	excellent due to rapid burial, slightly acidic waters, reducing conditions, limited rhizoturbation, and/or minor fluctuations in water table
Localities/sites	VR, RZ	JV, LB-1, TU	LB-2, LB-3, LB-4, RK, OV	VR, NZ

Table 1. Characteristics of fossiliferous, fine-grained facies on Nýřany Member braided-river plain.

because facies show only subtle differences, and because informative laterally extensive outcrops are rare.

During local avulsion (Fig. 9), flow relocation within a braided channel belt resulted in abandonment of one or more mainstem and minor channels. Abandoned channel dimensions match those of the parent channel, although some units that resembleabandoned minor channels may instead represent a thin, fine-grained cap of a mainstem channel largely filled by coarse-grained sediment. The proximity of active flow resulted in frequent incursions of sediment-laden floodwaters, resulting in rare coal seams that are thin and laterally restricted. Rooted paleosols are poorly developed but common in some abandoned mainstem channels.

Studies of modern analogues indicate that abandoned channel sediments can entomb well-preserved megafloral assemblages, with most plant parts derived from channel-flanking vegetation (Gastaldo, 1989; Gastaldo et al., 1989a). Although stagnant or sluggish ponded waters are relatively shallow, their high organic content leads to anoxic or slightly acidic conditions unfavorable to detritivorous, burrowing invertebrates. Furthermore, high sedimentation rates result in rapid burial of plant remains, thus moving them to an anoxic geochemical setting where microbial decay is minimized (Gastaldo, 1994).

Extensive floodplains developed during regional avulsion (Fig. 9), when the flow system transferred to a more distant part of the braided-river plain. After abandonment, exposure may have partially reduced microtopographic relief on the sand and gravel surface. Mudstone-dominated wetland deposits accumulated atop this surface, which may have been partly indurated. Mires, swamps, marshes, and shallow lakes probably

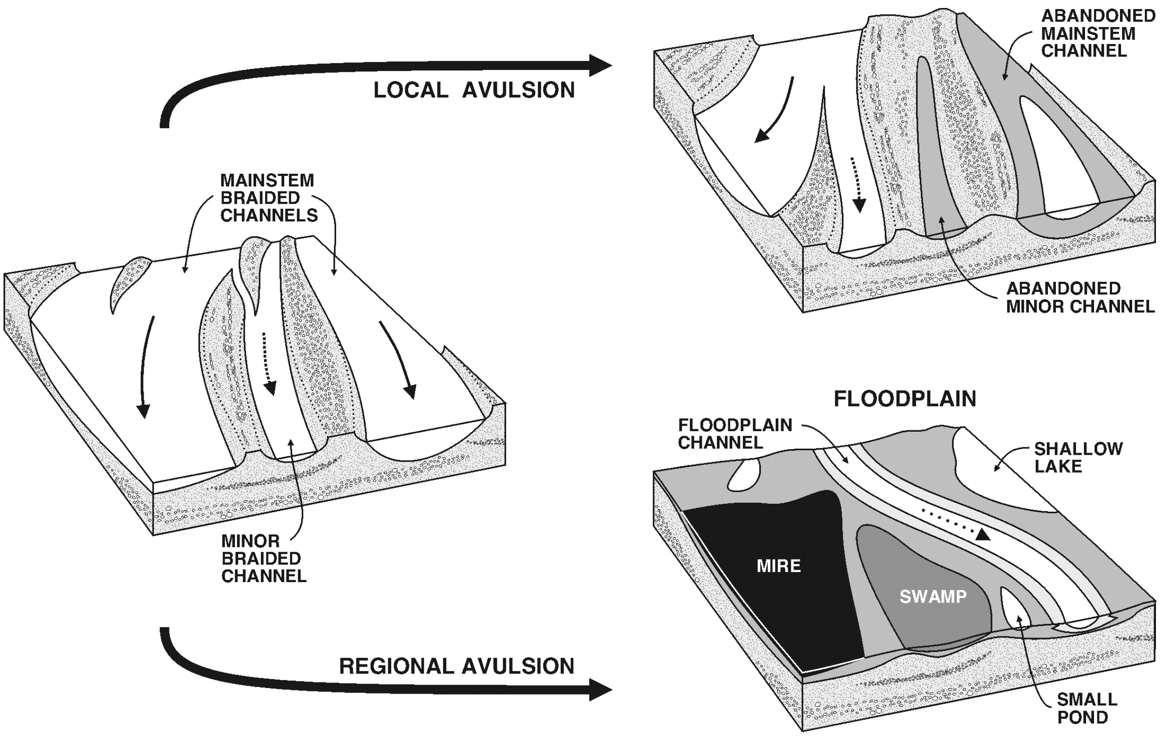


Figure 9. Schematic block diagrams showing the range of depositional environments resulting from local versus regional avulsion on the Nýřany Member braided-river plain. Megafloral assemblages were collected from fine-grained facies representing abandoned mainstem and minor channels, floodplain channels, small floodplain ponds, and shallow lakes. Only palynological assemblages were collected from swamp, marsh, and mire deposits. See Table 1 for details on segregation of fine-grained, fossiliferous facies, and Section 2.3.2.2 for their potential for preserving megafloral remains.

formed in microtopographic lows, and narrow floodplain channels transected wetlands containing numerous small ponds. Rooted paleosols are well developed and common, attesting to colonization by dense stands of vegetation, and coal seams are thin but laterally extensive.

Forest floor litters on modern floodplains have a low preservation potential, particularly in (para)tropical settings (Burnham, 1989; Gastaldo, 1989; Gastaldo et al., 1989a). Leaves and other non-woody canopy organs suffer rapid degradation due to catabolic processes, microbial decay, and detritivory (Ferguson, 1985; Gastaldo, 1994; Gastaldo & Staub, 1999). Leaves buried during minor flood events suffer a similar fate due to pervasive rhizoturbation and watertable fluctuations that introduce oxygenated meteoric waters to the shallow subsurface. However, well-preserved megafloral assemblages derived from floodplain communities can be entombed when high sedimentation rates result in rapid burial, particularly during anomalous flood events, or if plant remains are deposited in anoxic and/or slightly acidic waters. On the Nýřany Member braided-river plain, the remnants of shallow lakes, small ponds, and floodplain channels contain well-preserved megafloral assemblages, indicating that the regional water table level generally was high (DiMichele & Gastaldo, 2008; Gastaldo & Demko, in press).

2.3.2.3. Climate

The late Middle Pennsylvanian was characterized by fluctuating ice volumes at high latitudes, with attendant changes in sea level, climate, and vegetational biomes in paleoequatorial regions (Frakes et al., 1992; Fielding et al., 2008a, b; Pfefferkorn et al., 2008; Falcon-Lang et al., 2009; DiMichele et al., 1996, 2009a, 2010; Falcon-Lang & DiMichele, 2010; Dolby et al., in press). Although the effects of these glacial-interglacial intervals are pronounced in paralic basins, recognition of cyclical changes in climatic conditions is extremely difficult in coeval paleoequatorial intramontane basins that were unaffected by marine incursions. For the Nýřany Member, establishing a paleoclimatic framework is further confounded by the fact that outcrops are limited, small, and widely scattered. As such, at the resolution of the present study, it has not yet been possible to disentangle the effects of regional climatic shifts from other allocyclic or autocyclic factors operating during deposition on the Nýřany Member braided-river plain.

The thick successions of coarse-grained siliciclastic strata in the Nýřany Member point to highly seasonal rainfall (Cecil, 1990; Cecil & Dulong, 2003), together with steep stream gradients and the proximity of elevated source rocks. Seasonal precipitation results in increased sediment yield because vegetation cover is less dense, leading to increased erosion and runoff during intense rainfalls (Hooke, 2000). Although uncommon, varicolored fine-grained rocks characterized by high chroma colors are present at several levels, features that reflect the oxidation of well-drained sediment in a seasonal climatic regime.

Despite sedimentological evidence for largely seasonal precipitation, at least 20 coal seams and numerous rooted horizons are scattered through the Nýřany Member, recording the development of rheotrophic mires, swamps, and marshes under persistently wet or waterlogged soil conditions. Most coal seams are a few tens of centimetres thick, and economic seams 1 to 2 m thick occur only sporadically. The fact that coal seams tend to be concentrated within short stratigraphic intervals (Fig. 8, see below) suggests that the accumulation and preservation of peat may have occurred when precipitation was less seasonal (Cecil, 1990; Cecil & Dulong, 2003). However, even the thickest seams are not widespread, indicating that mire distribution was partly controlled by differential subsidence, clastic input, and paleotopography (Opluštil, 2005b). It is also plausible that some mires developed in groundwater recharge zones in front of alluvial fans (cf. Calder, 1993, 1994). However, in the 'proximal braided-river plain/alluvial fan' and 'distal braided-river plain' facies associations—the deposits examined in this study—coal seams are very rare, clastic-rich, thin, and of limited lateral extent (i.e., uneconomic). Mainly autocyclic processes may have controlled the distribution of these ephemeral mires.

2.3.2.4. Coal Seam Groups

Pešek (1994) divided the coal seams into four stratigraphic groups (Fig. 8). The basal Touškov group correlates with the Mirošov and Komberk horizons, and the thickest and most economically important Nýřany group is largely confined to the Plzeň Basin. The Chotíkov group incorporates all seams between the Nýřany and Nevřeň groups, and the latter lies immediately below the overlying Týnec Formation.

2.3.2.5. Megafloral Assemblages, Biostratigraphy, and Age

Plant remains from the Nýřany Member are poorly studied in comparison with the underlying Radnice Member, and documented species richness is greater in the latter, probably due to more intensive coal exploitation (Fig. 6B; Šimůnek, 2004; Opluštil & Cleal, 2007). Šetlík (1968a, 1977) and Šimůnek (1994, 2004, 2008) provided the best-illustrated megafloral reviews, and Pešek (2004, tables 2 to 4) showed the distribution of plant and palynomorph species through the unit. Šetlík (1968a, 1977, 1980) recognized at least three informal megafloral intervals that he correlated with different coal seam groups (Fig. 8; Table 2).

Application of the biostratigraphic scheme established for Pennsylvanian megafloras (Wagner, 1984; Cleal, 1991; Cleal & Thomas, 1994) indicates a late Asturian to middle(?) Cantabrian age for the Nýřany Member. *Dicksonites plukenetii* is rare in the Mirošov Horizon (Pešek, 2004), but its presence indicates that the base of the unit belongs in the late Asturian *Dicksonites plukenetii* Subbiozone (*Lobatopteris vestita* Biozone; Fig. 8). The Asturian/Cantabrian boundary is difficult to pinpoint (Cleal et al., 2003), but *Sphenophyllum oblongifolium* abounds in strata equivalent to the upper part of the Chotíkov group of seams, suggesting that the base of the Cantabrian *Odontopteris cantabrica* Biozone lies just below this level. It is not clear how these megafloral biozones relate to the global subdivisions of the Carboniferous System (Davydov et al., 2004, 2010; Heckel & Clayton, 2006), though correlation is most likely with the late Moscovian, at a position just below the Middle to Upper Pennsylvanian boundary in North America (Fig. 6; Heckel, 2008). Comparison with age constraints provided by Davydov et al. (2010, fig. 2) suggests that the Nýřany Member accumulated over ≈2.0 Ma, beginning at around 309 Ma.

2.4. DATA COLLECTION: MATERIALS AND METHODS

2.4.1. Localities and Sites

The paleoecology of riparian plant communities is described based on quantitative analyses of fossiliferous, fine-grained facies that developed due to local and regional

Megafloral interval	**Age**	**Correlative coal seam group(s)**	**Important species**
'young' assemblage	early to middle(?) Cantabrian	Nevřeň	*Sphenophyllum oblongifolium*, *Sigillaria ichthyolepis*
'typical' assemblage	late Asturian to early Cantabrian	Nýřany, Chotíkov	*Annularia stellata, Annularia sphenophylloides*, *Sphenophyllum emarginatum*, *Pecopteris polypodioides*, *Ptychocarpus unitus*, *Dicksonites plukenetii*
'Mirošov-type' assemblage	late Asturian	Touškov; Mirošov and Komberk horizons	*Neuropteris plicata*, *Linopteris obliqua*, *Linopteris weigelii*, *Sphenophyllum mirosoviense*, holdovers from Radnice Member

Table 2. Informal megafloral intervals through Nýřany Member (Šetlík, 1968a, 1977, 1980).

avulsion on the braided-river plain (Table 1; Fig. 9). Four localities were studied. In ascending stratigraphic order, these are the Janov, Vranov, Lobeč, and Rozdělov localities (Fig. 7; Table 3). The Janov and Lobeč localities are subdivided into a number of sites (Table 3) that range from tens of metres to several kilometres apart, each of which is described separately. (Hereafter, when referring to a feature at one or more localities, and at one or more sites comprising a locality, we use the term 'locality/site'). The Rozdělov locality is currently inaccessible, and several sites at the Lobeč locality are no longer exposed. Sandstone and conglomerate dominates at each locality, but rich and well-preserved megafloral and palynological assemblages occur in associated thin and laterally discontinuous, fine-grained intercalations. Strata at the Janov locality belong to the 'proximal braided-river plain/alluvial fan' facies association, and all other localities to the 'distal braided-river plain' facies association.

2.4.2. Megafloral Assemblages

2.4.2.1. Collections

Quantitative data were obtained from two types of megafloral collection, for which full repository information is given in Tables 3 and 4. At exposed localities/sites, the first author identified discrete fossiliferous horizons ('units' in Table 3), from which 'new collections' were made in 2006 and 2007. 'Historical collections' from now inaccessible or unexposed localities/sites were also examined. Specifically, these include collections made by the third author from the Rozdělov locality (1976 to 1991), and those made by several workers from sites at the Lobeč locality in the mid-20th century (Table 4). For these latter assemblages, we determined facies context based on photographs and/or

Locality	**Site**	**Unit(s)**	**Census quadrats (megaflora)**[a]	**Supplementary quadrats (megaflora)**	**Palynology (miospores)**	**Palynology (megaspores)**
Rozdělov		'coarse' (sandy siltstone)		RZ-1C[b]		
		'fine' (mudstone and muddy siltstone)		RZ-1F[b]	PAL-19	PAL-19
Lobeč	Nelahozeves			NZ-1[c]		
	Olovnice			OV-1[c]		
	Gully			RK-1.1, 1.2[c]		
	Railway tunnel			TU-1.1 to 1.5[c]		
	Top of Lobeč cliff	'light' (buff sandstone)	LB-1.1L, 1.2L	LB-1.3L[c]		
		'dark' (grey mudstone and siltstone)	LB-1.1D to 1.5D	LB-1.6D to 1.11D[c]		
	Base of Lobeč cliff ('cave')	F			PAL-10	PAL-10
		E			PAL-11	PAL-11
		D			PAL-12	
		B	LB-2.1 to 2.3	LB-2.4, 2.5[c]	PAL-15	
	Lateral equivalent to 'cave' (LB-3)				PAL-13B	PAL-13B
	Lateral equivalent to 'cave' (LB-4)					PAL-14
Vranov		Section 1 (upper)	VR-3			
		Section 1 (middle)	VR-2		PAL-18	PAL-18
		Section 1 (lower)	VR-1.1, 1.2		PAL-17	
Janov	'Caves'	C (outside southern 'cave')	JV-2			
		A (outside southern 'cave')	JV-1.1 to 1.3			
		A, B (inside southern 'cave')	JV-3.1, 3.2		PAL-7	PAL-7
	Outdoor theatre		JV-4			

Table 3. Relationship between localities, sites, units, census quadrats, supplementary quadrats, and palynological samples. Note repository information as it relates to illustrated specimens in Plates I to III. (a) Collected by first author (2006 to 2007); reposited at West Bohemian Museum, Plzeň [denoted (WBM) in Plates]. (b) Collected by third author (1976 to 1991); reposited at Charles University, Prague [denoted (CU) in Plates]. (c) See Table 4 for collector details; reposited at Czech Geological Survey offsite facility, Lužná [denoted (CGS) in Plates].

Site	Quadrat(s)	Box	Collected and/or identified by
Base of Lobeč cliff ('cave') (LB-2)	LB-2.4	951	Šetlík *in* Vejlupek (1970)
	LB-2.5	802	
Top of Lobeč cliff (LB-1)	LB-1.6D, 1.7D	501	Obrhel (1960); Vejlupek (1970)
	LB-1.8D, 1.9D	745	
	LB-1.10D, 1.11D	736	
	LB-1.3L	501	
Olovnice (OV)	OV-1	962	Němejc (1947b)
Railway tunnel (TU)	TU-1.1, 1.2	725	Obrhel (1960); Vejlupek (1970)
	TU-1.3	745	
	TU-1.4, 1.5	747	
Gully (RK)	RK-1.1	962	Němejc (1947b); Němejc et al. (1950); Šetlík (1951, 1968b); Obrhel (1957, 1960)
	RK-1.2	723	
Nelehozeves (NZ)	NZ-1	839	Šetlík (1968b); Vejlupek (1970)

Table 4. Supplementary quadrats from historical collections from unexposed sites at Lobeč locality. Boxes stored at offsite facility of Czech Geological Survey (Lužná).

stratigraphic logs made at the time of recovery, along with the sedimentology of fossiliferous slabs. The use of new and historical collections was necessary because outcrops of the Nýřany Member are now rare, and to rely on new collections from exposed sections would have limited the study.

2.4.2.2. Quadrats

Megafloral assemblages were quantified using a variant of the quadrat technique employed by Iwaniw (1985). The benefit of a census approach is that dominance-diversity characteristics are recorded for standardized units of area. Data were obtained in two different ways for 41 quadrats.

'Census quadrats' (n = 21; Table 3) were obtained from new collections, which were removed from outcrops and quantified onsite. Because bedding planes are rarely exposed, fossiliferous horizons were excavated until enough slabs were collected to fill a 50 x 50 cm (0.25 m^2) quadrat. All slabs in a quadrat contained at least one fossil fragment, and were collected from as thin an interval as possible to avoid mixing of assemblages with different taphonomic histories. Replicates were done for especially fossil-rich beds. The state of fragmentation and pertinent taphonomic information was recorded. In each quadrat, every plant fragment was counted as a single individual. Most remains could be identified to the fossil species level (*sensu* Cleal & Thomas, 2010), although poorly preserved examples or those lacking diagnostic features were recorded at the fossil genus or higher rank. Comminuted plant debris was recorded as recommended by Iwaniw (1985; see below). A small representative collection was made to verify field identifications.

‘Supplementary quadrats’ (n = 20; Table 3) were obtained from historical collections. Plant fossil assemblages from the unexposed Lobeč sites (Table 4) were randomly divided into 18 quadrats, such that the number of specimens in each approximated that of a 0.25 m^2 quadrat. Specimens from the inaccessible Rozdělov locality were divided into two quadrats based on lithology (Table 3). Thereafter, quantification was identical with the aforementioned method. Historical collections were not census-sampled, and thus contain some collector bias because emphasis was placed on large specimens and rare or biostratigraphically significant taxa. Consequently, the relative abundances of dominant taxa are not entirely representative of the original taphocoenoses, although the quadrats provide insight into overall species diversity (especially among rare taxa). While cognizant of these weaknesses, data from historical collections were included in our survey because they provide a more complete view of species richness in the Nýřany Member.

2.4.2.3. Abundance Matrix and Fossil Taxa

A total of 20263 plant fragments were counted in the 41 quadrats, but a large proportion consists of comminuted plant debris (4492 or 22.2%) and axes of unknown affinity (3367 or 16.6%). Although these data can provide information about the taphonomic history of a plant assemblage (Iwaniw, 1985), they offer little insight into the biological diversity of the original plant communities. There remain 12404 identifiable specimens, with individual quadrats containing 43 to 845 specimens (mean = 303). Prior to analyses, all fossil taxa were condensed into true biological taxa using the methods of Gastaldo et al. (2004a) and Bashforth et al. (2010; Chapter 3), resulting in an abundance matrix that more accurately reflects the true biological composition of the sample population. For example, records of *Hexagonocarpus* were grouped with *Linopteris* (Laveine et al., 1993; Zodrow et al., 2007), whereas sphenophyll axes were grouped with *Sphenophyllum*, their respective parent plants. In quadrats where a fossil taxon could belong to multiple parent plants, its abundance was proportionately redistributed between all potential parent plants. For example, records of *Calamites* were proportionately divided between *Asterophyllites* and *Annularia* based on the relative abundances of these biological taxa in the quadrat. Through this process, 27 biological genera containing 46 biological species were recognized (Table 5). The redistributed abundance matrix, from which all subsequent analyses were performed, is provided in Table 6.

Most specimens were identified at the species level, although some are left in open nomenclature at the genus level. As the purpose of this investigation is to compare the composition of fossil assemblages from various localities, nomenclatural consistency is vital. Thus, even for contentious taxa that could not be identified with certainty, we ensured that they were grouped in an internally consistent way. Several biological taxa recovered are new to the Nýřany Member, and supplement the fossil species list of Pešek (2004, table 2). Although descriptions and taxonomic revisions are outside the scope of this manuscript, Table 5 lists pertinent references that contain detailed descriptions or illustrations of all taxa identified. Plates I to III illustrate examples of abundant or significant taxa.

Plate I. 1. “*Lepidodendron*” *subdichotomum*, LB-2, Box 802 (CGS), X3. 2. *Annularia* “*spicata*”, NZ-1, Box 839 (CGS), X3. 3. *Sphenophyllum mirosoviense*, JV-3, F12469 (WBM), X2. 4. *Annularia carinata*, RZ-1 (CU), X1. 5. *Alloiopteris erosa*, TU-1, Box 725 (CGS), X2. 6. *Sphenophyllum oblongifolium*, RZ-1 (CU), X2. 7. *Sphenophyllum emarginatum*, RZ-1 (CU), X2. 8. *Cyathocarpus* sp. A, OV-1, Box 962 (CGS), X2. 9. *Lobatopteris* sp. B, LB-1, Box 736 (CGS), X2. 10. *Pecopteris* sp. G, RZ-1 (CU), X2. 11. *Lobatopteris* sp. A, RK-1, Box 962 (CGS), X2. 12. *Ptychocarpus unitus*, LB-1, Box 501 (CGS), X2.

[NOTE THAT, DUE TO DIFFERENCES IN FORMAT, ALL MAGNIFICATIONS ARE 82.9% OF THAT STATED IN PLATE CAPTION]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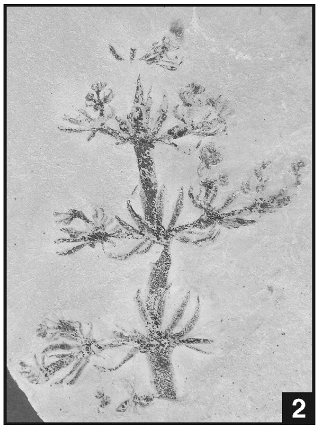
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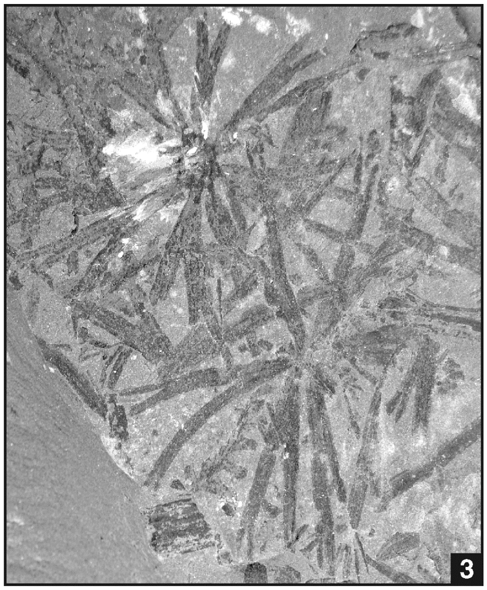
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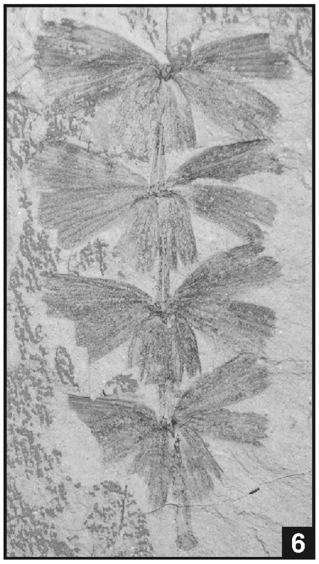
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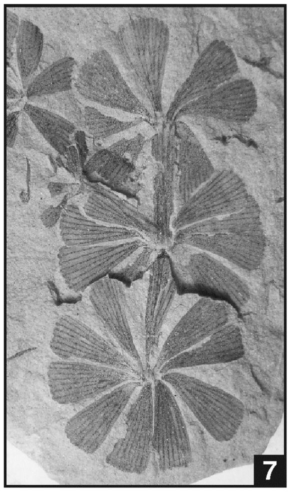
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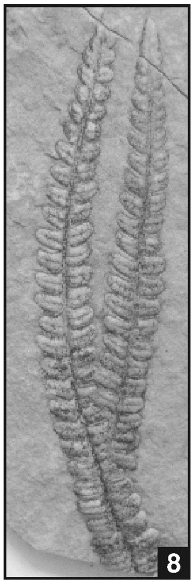
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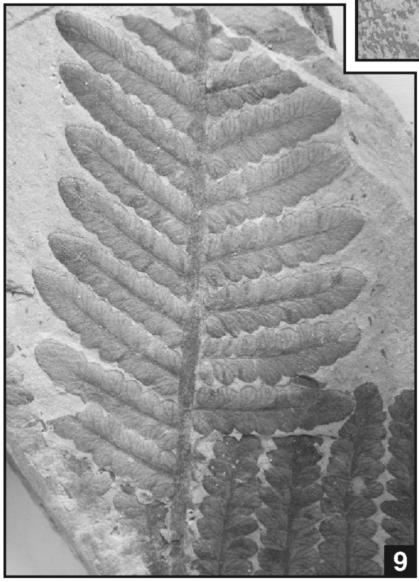
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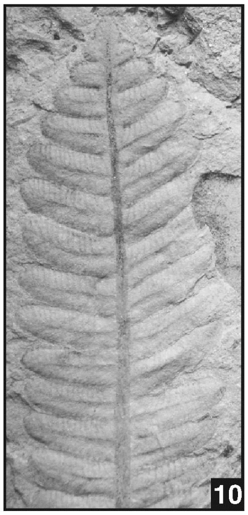
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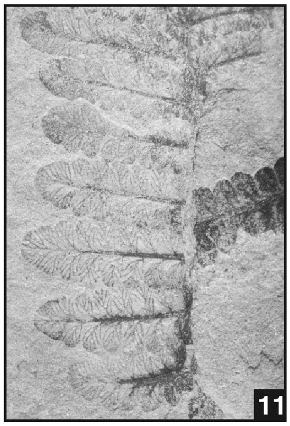
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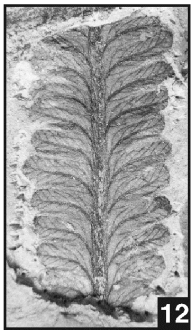
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Plate II. 1. *Acitheca* sp. A, RZ-1 (CU), X2. 2. *Pseudomariopteris cordato-ovata*, RK-1, Box 723 (CGS), X2. 3. *Acitheca polymorpha*, VR-2, F12471 (WBM), X2. 4. "*Alethopteris*" *kettneri*, RZ-1 (CU), X2. 5. *Pecopteris raconensis*, RZ-1 (CU), X2. 6. *Pecopteris* sp. F, RZ-1 (CU), X2. 7. *Callipteridium rubescens*, RZ-1 (CU), X2. 8. *Linopteris neuropteroides*, RZ-1 (CU), X2. 9. *Oligocarpia gutbieri*, TU-1, Box 745 (CGS), X2. 10. *Eusphenopteris nummularia*, LB-1, Box 736 (CGS), X2. 11. *Linopteris palentina*, LB-1, Box 745 (CGS), X2. 12. *Linopteris obliqua*, JV-4, F12470 (WBM), X2. 13. *Odontopteris reichiana*, RZ-1 (CU), X2. 14. *Neurocallipteris planchardii*, RZ-1 (CU), X2.

[NOTE THAT, DUE TO DIFFERENCES IN FORMAT, ALL MAGNIFICATIONS ARE 82.9% OF THAT STATED IN PLATE CAPTION]


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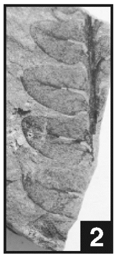
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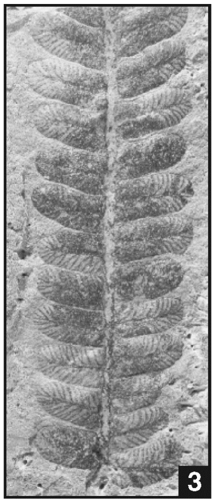
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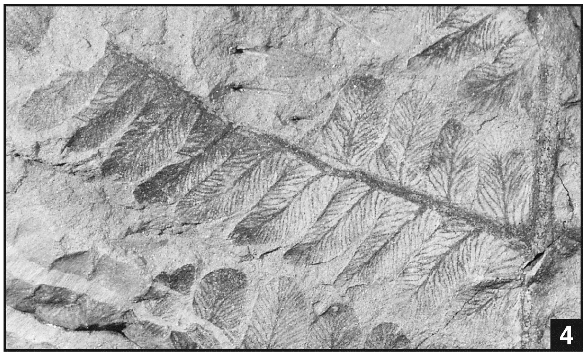
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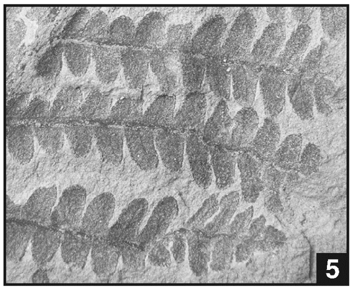
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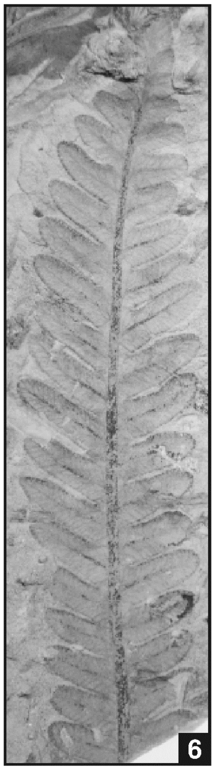
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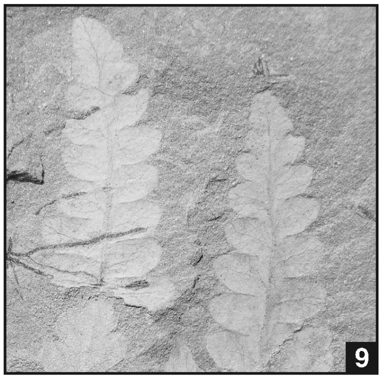
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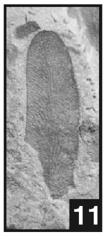
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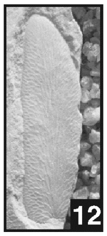
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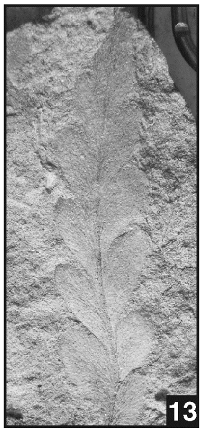
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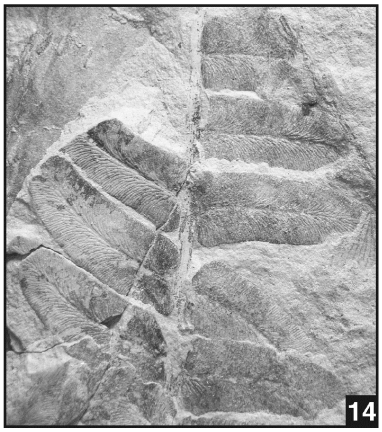
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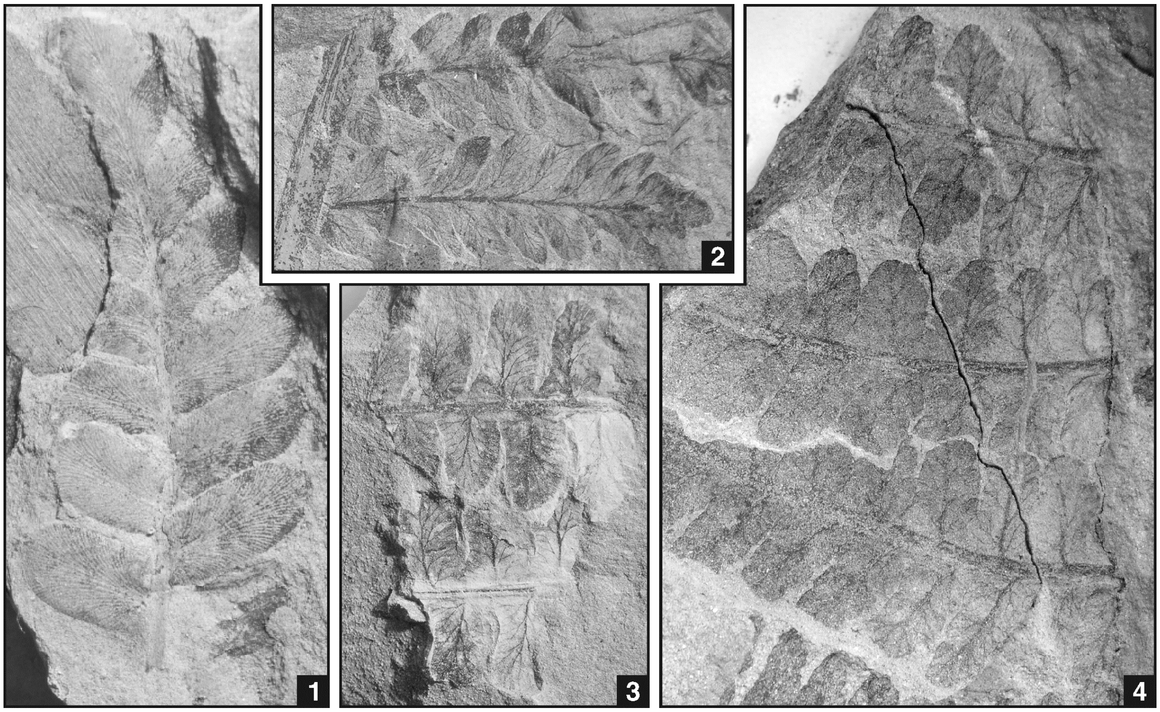


Plate III. 1. *Neuropteris plicata*, LB-1, Box 723 (CGS), X2. 2. *Sphenopteris ovalis*, RZ-1 (CU), X2. 3. *Dicksonites sterzelii*, TU-1, Box 747 (CGS), X2. 4. *Dicksonites plukenetii*, RZ-1 (CU), X2.

[NOTE THAT, DUE TO DIFFERENCES IN FORMAT, ALL MAGNIFICATIONS ARE 82.9% OF THAT STATED IN PLATE CAPTION]

2.4.3. Palynological Assemblages

Palynological assemblages were obtained from all four localities. Palynology provides complementary insights into the composition of plant communities because palynomorphs (spores and pollen) have a high dispersive potential, and thus are derived from a broader spectrum of the regional vegetation. Furthermore, plants shed far more palynomorphs than megafloral remains, increasing the likelihood that rare taxa are represented. Nonetheless, the interpretation of palynological assemblages can be difficult because the frequency and abundance of spore and pollen production differs markedly among taxa (Willard, 1993).

Twenty palynology samples were processed for miospores and megaspores. All were collected from the same clastic beds that yielded quadrats, with the exception of PAL-11, which was taken from a coal seam. Organic matter was isolated from 50 to 100 g samples using hydrochloric (35%) and hydrofluoric (38%) acids. Some residues were macerated in nitric acid (0.5 to 8 hours) and lightened in potassium hydroxide. Five slides were made from each sample, with residues mounted in glycerine jelly. Where possible, quantification was based on a point count of 200 miospores per sample. In addition, megaspores were retrieved from samples using a sieve with 200 μm mesh. All miospore slides and megaspores are stored at the Czech Geological Survey in Prague under accession numbers 1132 to 1151.

Most samples contained meager and poorly preserved assemblages due to natural oxidation, decay, and/or mechanical degradation during transport. Nonetheless, nine samples contained enough miospores to permit point counts, and seven samples contained megaspores (Table 3). Some palynomorphs were identified at the fossil species level, although poor preservation meant that most could only be confidently assigned to fossil genera. In recent years, a major focus of the Czech paleobotanical community has been the study of *in situ* spores isolated from fertile organs of Carboniferous plants, some of which involve taxa from the Nýřany Member (e.g., Bek, 1998; Bek & Opluštil, 1998, 2004; Bek et al., 2001, 2008; Pšenička, 2005; Zodrow et al., 2006). Based on these and other studies (Ravn, 1986; Balme, 1995; Rothwell & Mapes, 2001), the majority of miospores (Table 7) and megaspores (Table 8) could be placed into the plant clade, or even plant family, that produced them following the approach of Dimitrova et al. (2005) and Dimitrova & Cleal (2007).

2.5. LOCALITY DESCRIPTIONS

2.5.1. Janov Locality

The Mirošov Relict (Figs 6, 10A) is situated near the southern margin of the area originally covered by the Nýřany Member (Fig. 7). It contains a 140 to 160 m thick sandstone-dominated succession, with three to five coal seams of the Nýřany group located 25 to 45 m above the basement (Figs 8, 10B; Purkyně, 1904; Němejc, 1930, 1938; Čepek, 1951; Kalibová-Kaiserová, 1982; Pešek, 2003). Below this, the Mirošov Horizon comprises 10 to 20 m of conglomerate and sandstone that unconformably overlie basement rocks. These strata, which represent proximal braided fluvial deposits, are equivalent to the Touškov group of coals according to Pešek (1994; Fig. 8). Thin, fine-grained intercalations yield abundant plant fossils, parochially termed the ‘Mirošov-type’ assemblage (Němejc, 1938; Šetlík, 1968a, 1969, 1977; Table 2). Megafloral assemblages were analyzed in two historical sandstone quarries (Fig. 10C; Pešek, 2003). The main

PLANT GROUP	PLANT FAMILY	MEGASPORE FOSSL TAXON	PAL-10 LB-2	PAL-11 LB-2	PAL-13B LB-3	PAL-14 LB-4	PAL-7 JV-3	PAL-18 VR-2	PAL-19 RZ-1F
Lycopsids	Selaginellaceae	*Bentzisporites* sp. cf. *B. bentzii*	0	0	0	0	3	0	2
	Selaginellaceae	*Triangulatisporites* sp. A	0	0	0	0	8	0	0
	Selaginellaceae	*Triangulatisporites* sp. B	0	0	0	2	0	0	0
	Diaphorodendraceae	*Cystosporites diabolicus*	0	50	5	0	2	4	0
Calamiteans		*Calamospora* sp.	0	0	0	0	0	5	0
Pteridosperms	Medullosales	*Schopfipollenites ellipsoides*	3	0	2	32	12	0	2

Table 8. Absolute abundances of megaspore fossil taxa, segregated by plant group (and family, where possible).

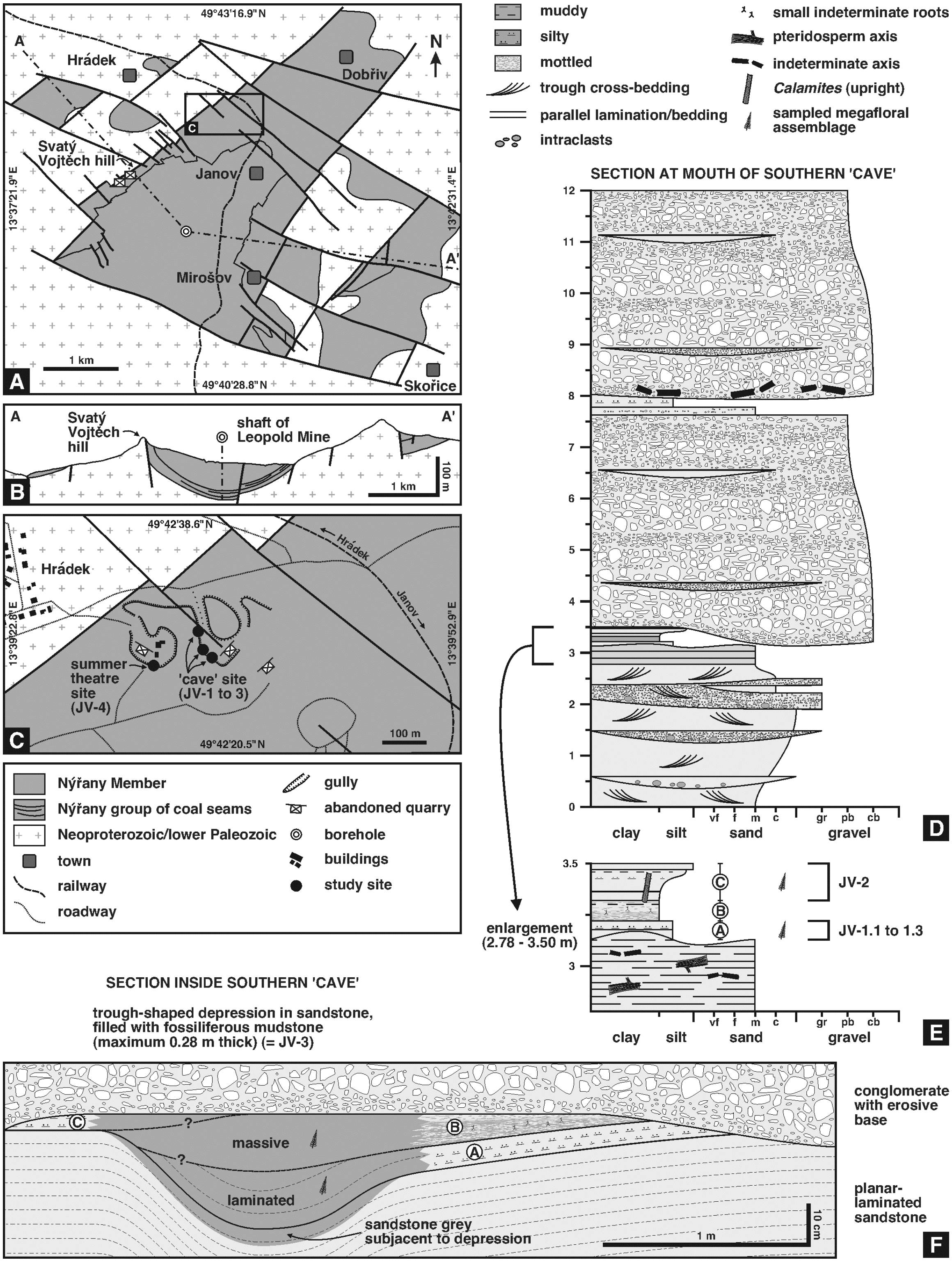
site (JV-1 to 3) comprises three 'caves' (southern, middle, and northern 'caves'), and the other site (JV-4) is now an outdoor theatre ≈130 m to the west.

2.5.1.1. 'Caves' Site (JV-1 to 3)

2.5.1.1.1. Sedimentology

The basal 3.2 m of the section at the southern 'cave' (Fig. 10C, D) consists of trough cross-bedded sandstone with scours filled by granules, pebbles, and intraclasts, and planar-laminated sandstone containing recurved pteridosperm branches (Fig. 10E). Above this, rich and well-preserved megafloral assemblages are found in a 0.7 m thick package of laminated mudstone and siltstone, which coarsens upward and comprisesthree discrete fossiliferous beds (Fig. 10E; Table 3). Unit A is 50 to 90 mm thick and consists of buff, interlaminated mudstone and siltstone. The overlying mudstone bed (Unit B) is 30 to 100 mm thick, exhibits dark grey to buff mottling, and contains scattered roots of unknown affinity. Unit C is 140 to 180 mm thick and primarily comprises poorly laminated to massive, buff mudstone that coarsens upward to reddish muddy siltstone near the erosive contact with the overlying conglomerate. Inside the southern 'cave', these three beds comprise a trough-shaped depression filled with medium grey, laminated and massive mudstone (Fig. 10F). Units A and B seemingly pinch out between the southern and middle 'caves'. However, Unit C can be traced ≈70 m northward to the middle and northern 'caves' (Fig. 10C), although it is eroded in places and largely unfossiliferous. The overlying succession comprises 8.5 m of poorly sorted, crudely stratified, clast-supported pebble and cobble conglomerate with subrounded to subangular clasts. Unidentifiable plant axes are scattered along the base of the upper

Figure 10. A. Geology of Mirošov Relict. Plan view outline of uppermost seam of Nýřany group of coal seams shown. B. Cross-section showing profile view of relict. The Mirošov Horizon comprises the basal 10 to 20 m of the succession. C. Position of ‘cave’ (JV-1 to 3) and summer theatre (JV-4) sites (Janov locality) in Mirošov Horizon along basin margin, situated in historical quarries between Hrádek and Janov. D. Stratigraphic section from mouth of southern ‘cave’. E. Enlargement of fossiliferous interval (2.78 to 3.50 m of above section), showing position of census quadrats (JV-1 and 2) and Units A to C above sandstone containing pteridosperm axes. Units A and B corresponds to abandoned minor channel facies, and Unit C to shallow lake facies. F. Schematic illustration of fossiliferous mudstone-filled depression yielding quadrat JV-3 (from Units A and B) from inside southern ‘cave’. Compare position of Units A to C with those outside ‘cave’ in E. Note that vertical and horizontal scales differ. A and B modified from Čepek (1951, pl. 4).


49°43'16.9"N
A
Hrádek
Dobřiv
N
c
Svatý Vojtěch hill
Janov
13°37'21.9"E
13°42'31.4"E
A'
Mirošov
1 km
Skořice
49°40'28.8"N
A
Svatý Vojtěch hill
shaft of Leopold Mine
A'
100 m
1 km
B
49°42'38.6"N
Hrádek
Janov
Hrádek
13°39'22.8"E
13°39'52.9"E
summer theatre site (JV-4)
'cave' site (JV-1 to 3)
100 m
49°42'20.5"N
C
Nýřany Member
Nýřany group of coal seams
Neoproterozoic/lower Paleozoic
town
railway
roadway
gully
abandoned quarry
borehole
buildings
study site
muddy
silty
mottled
trough cross-bedding
parallel lamination/bedding
intraclasts
small indeterminate roots
pteridosperm axis
indeterminate axis
Calamites (upright)
sampled megafloral assemblage
SECTION AT MOUTH OF SOUTHERN 'CAVE'
12
11
10
9
8
7
6
5
4
3
2
1
0
vf f m c
gr pb cb
clay silt sand gravel
D
3.5
3
C
B
A
JV-2
JV-1.1 to 1.3
enlargement (2.78 - 3.50 m)
vf f m c
gr pb cb
clay silt sand gravel
E
SECTION INSIDE SOUTHERN 'CAVE'
trough-shaped depression in sandstone, filled with fossiliferous mudstone (maximum 0.28 m thick) (= JV-3)
C
?
B
massive
?
A
laminated
sandstone grey subjacent to depression
10 cm
1 m
conglomerate with erosive base
planar-laminated sandstone
F

conglomerate (Fig. 10D). Paleocurrent data are scarce, but the orientation of troughs in the cross-bedded sandstone and long axes of plant stems in the conglomerates (025° to 115°, mean = 076°, n = 6), along with the southward dip of imbricated clasts, suggests northeastward paleoflow. The outcrop is thus oriented approximately normal to paleoflow.

Units A and B of the thin, fine-grained interval are attributed to a minor abandoned channel (Table 1; Fig. 9), with parallel lamination (Unit A) implying deposition from suspension in shallow water. The mottled and rooted horizon (Unit B), which represents a poorly developed paleosol, indicates colonization by vegetation once the ponded waters had shallowed, although the unrooted mudstone-filled depression inside the southern 'cave' suggests that stagnant or sluggish water persisted locally. Abandonment likely resulted from local avulsion, although the absence of sandstone in the abandoned channel fill implies minimal input from active channels. The lateral extent (>70 m) of Unit C suggests deposition in a shallow lake (Table 1; Fig. 9) that developed as active channels became more distal. The overlying conglomerate records a return to active fluvial conditions. The striking shift from a sandbed to gravelbed river system may reflect a sudden gradient change due to tectonic uplift, or may be related to increased seasonality and erosion of the source terrain. Frequent avulsion through floodplains, reactivation of abandoned channels, and/or bank undercutting explains the abundance of intraclasts and plant axes in the active channel deposits.

2.5.1.1.2. Megafloral Assemblages

Five quadrats were obtained from the abandoned minor channel deposits. Three replicates (JV-1.1 to 1.3) from Unit A outside the southern 'cave' (Fig. 5E) have nearly identical compositions, being dominated by isolated pinnules of *Linopteris neuropteroides* (94.4 to 95.2%; Pl. II, Fig. 8) with rare *Cordaites*, *Annularia carinata* (Pl. I, Fig. 4), and *Sphenophyllum mirosoviense* (Pl. I, Fig. 3). Two replicates (JV-3.1 and 3.2) from Units A and B inside the southern 'cave' (Fig. 5F) are also dominated by isolated pinnules and striate axes of *L. neuropteroides* (54.6 to 71.0%), but large, articulated fragments of *S. mirosoviense* are more common (14.9 to 17.1%).

Articulated whorls, isolated leaves, and branches of *Annularia carinata* dominate (76.0%) the quadrat (JV-2) from the shallow lake facies (Unit C; Fig. 10E). *Sphenophyllum mirosoviense* is subordinate (16.4%), *Cordaites* and *Linopteris neuropteroides* are rare, and a few subvertical *Calamites* are preserved.

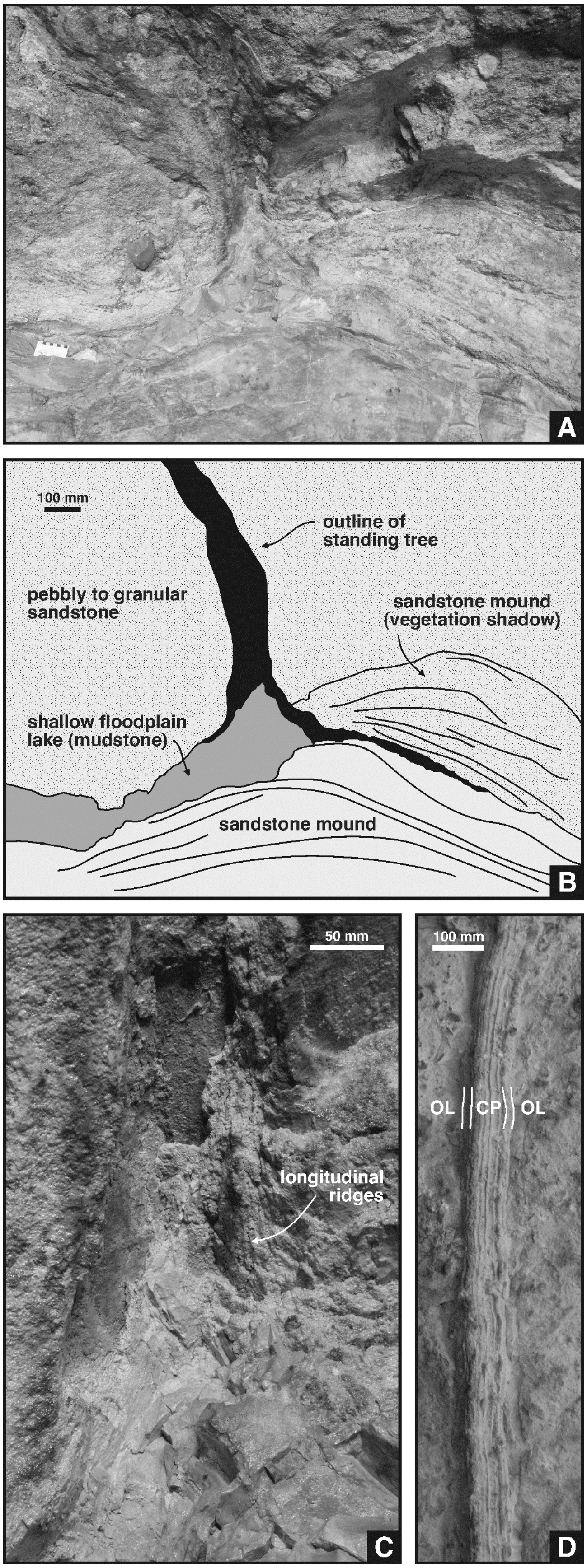
A tree of uncertain affinity is preserved in growth position on the back wall of the northern 'cave' (Figs 10C, 11A to C). There is no evidence of a vertical taproot, although some lateral roots are present. The basal flare and general outline are similar to those of cordaitalean trees (Falcon-Lang & Bashforth, 2004, 2005; Falcon-Lang, 2005, 2006a), but there is no septate pith (*Artisia*). The tree may be a pteridosperm, but this is speculative. Although basal parts of the trunk are filled with mudstone attributed to a shallow floodplain lake (= Unit C), the tree is rooted atop an underlying sandstone hummock. A sandstone mound containing steeply dipping laminae flanks and overlies the lateral roots of the tree, the upper part of which is entombed in sandstone and oriented at 055°. These observations suggest that the living plant was growing alongside an active braided channel and drowned in the ensuing lake after avulsion. When an active channel tract reavulsed over the floodplain, the standing tree temporarily obstructed flow, resulting in a vegetation shadow (*sensu* Rygel et al., 2004), until finally being bent over and buried by northeastward-flowing channels.

Two other axes of unknown affinity are preserved on the ceiling of the northern ‘cave’, positioned at the contact between the shallow lake facies and overlying conglomerate (Fig. 11D). Both are oriented at 120°. Continuous longitudinal ridges characterize their central part, which is enveloped by a thick outer layer. The stems resemble calamitean axes (Eggert, 1962), but nodes are absent. A southeastward-flowing channel probably flattened these plants, but their original habitat is unknown because they were uprooted.

2.5.1.1.3. Palynology

Abandoned channel mudstone from inside the southern ‘cave’ yielded miospores and megaspores (PAL-7; Table 3). Spores from numerous fern families dominate the miospore assemblage (42.0%), and those of marattialean ferns are most common (24.0%; Table 7). Sphenophyll spores are subordinate (21.6%), and those of calamiteans and several lycopsid families are less common. Most pollen grains belong to cordaitaleans, whereas those of conifers and pteridosperms are rare. Medullosalean pteridosperms and herbaceous lycopsids are well represented in the megaspore assemblage (Table 8).

Figure 11. Axes of uncertain affinity in northern ‘cave’, Janov locality. A. Photograph of tree rooted on sandstone hummock but filled with mudstone of shallow lake on back wall of ‘cave’. Upright trunk is 120 mm wide just above basal flare. Scale bar increments are centimetres. B. Schematic illustration clarifying features in A. Note remnants of lateral roots. C. Close-up from near base of tree in A and B, showing impressions of longitudinal ridges, possibly on outside of central stele. D. Uprooted axis (≈2.5 m long, tapering from 100 to 60 mm wide) lying on ceiling of ‘cave’ at contact between shallow lake mudstone and overlying conglomerate. Central part (CP; pith cast?) characterized by well-preserved and continuous longitudinal ridges, enveloped by a ≈10 mm wide outer layer (OL; xylem and cortex?). An associated axis (≈1.2 m long and 90 mm wide) has an outer layer ≈20 mm wide with no central part remaining.


A
100 mm
outline of standing tree
pebbly to granular sandstone
sandstone mound (vegetation shadow)
shallow floodplain lake (mudstone)
sandstone mound
B
50 mm
longitudinal ridges
C
100 mm
OL
CP
OL
D

2.5.1.2. Summer Theatre Site (JV-4)

On the southern quarry wall (Fig. 10C), a sliver of well- laminated, buff silty mudstone rests atop trough cross-bedded sandstone and is truncated above and laterally by conglomerate. The lithology of the mudstone is similar to, and its stratigraphic position identical to, that of Unit A at the ‘cave’ site, suggesting that it is an erosional remnant of the same abandoned minor channel. Assuming a northeastward paleoflow, as determined at the ‘cave’ site, these strata represent the upstream correlative of the abandoned channel. The megafloral assemblage (JV-4) is co-dominated by leaves and axes of *Sphenophyllum mirosoviense* (35.4%) and *Cordaites* (33.9%), whereas isolated pinnules of *Linopteris obliqua* (Pl. II, Fig. 12) are less common (15.0%). The taphocoenosis is relatively diverse but very fragmentary, suggesting a largely allochthonous origin with elements of several communities mixed during transport.

Species lists in Němejc (1938) point to this quarry as the source of the syntypes of *Neuropteris plicata* (Pl. III, Fig. 1), which Sternberg (1825, 1833) described based on material from the loosely constrained area of “Mireschow” (=Mirošov). Slab lithology (buff silty mudstone) and preservation mode (decarbonized adpressions) of a large collection of type material at the National Museum (Prague) is identical to that of Unit A at the ‘cave’ site, suggesting derivation from laterally correlative abandoned minor channel deposits. Ultimate and penultimate pinnae fragments of *N. plicata* dominate all slabs, along with recurved pteridosperm axes. This assemblage clearly originated beneath a monospecific patch of *N. plicata*, based on the close association of foliar and axial components of the same species and the near absence of other taxa. Surprisingly, this species is absent in all census quadrats from the Janov locality.

2.5.2. Vranov Locality

The Vranov Relict (Fig. 12A) is an erosional remnant near the southwestern margin of the Plzeň Basin (Fig. 6A; Pešek, 1960, 2003), and developed along the western margin of the area originally covered by the Nýřany Member (Fig. 7). Small depressions between ridges of basement contain ≈55 m of strata dominated by sandstone and conglomerate laid down on a distal braided-river plain. A single coal seam (divided by clastic partings into benches) lies 8 to 15 m below the surface in a graben on the west side of the relict. Megafloral and palynological assemblages correlate with the Nýřany group of coals, particularly the Roof Nýřany seam (Fig. 8; Němejc, 1936b; Pešek, 1960, 2003; Kalibová-Kaiserová, 1979, 1982). Strata exposed in three short sections (Fig. 12B, C) are positioned about halfway between the basement and coal seam. Megafloral assemblages were quantified from Section 1.

2.5.2.1. Sedimentology

Sections 2 and 3 (Fig. 12C) are unfossiliferous and dominated by conglomerate with minor sandstone, whereas Section 1 comprises a 3.5 m thick fining upward succession of interbedded siltstone and sandstone. Only comminuted plant debris was found in the basal 1.2 m, but planar-laminated interbeds of siltstone and sandstone in the middle 1.3 m contain rich megafloral assemblages. This interval is characterized by upright *Calamites*, finely rugose axes of unknown affinity, and large indeterminate roots that are smooth and curve outward at their base. In the upper 1.0 m, plant remains are poorly preserved and axes are generally prostrate. Granules and pebbles in the

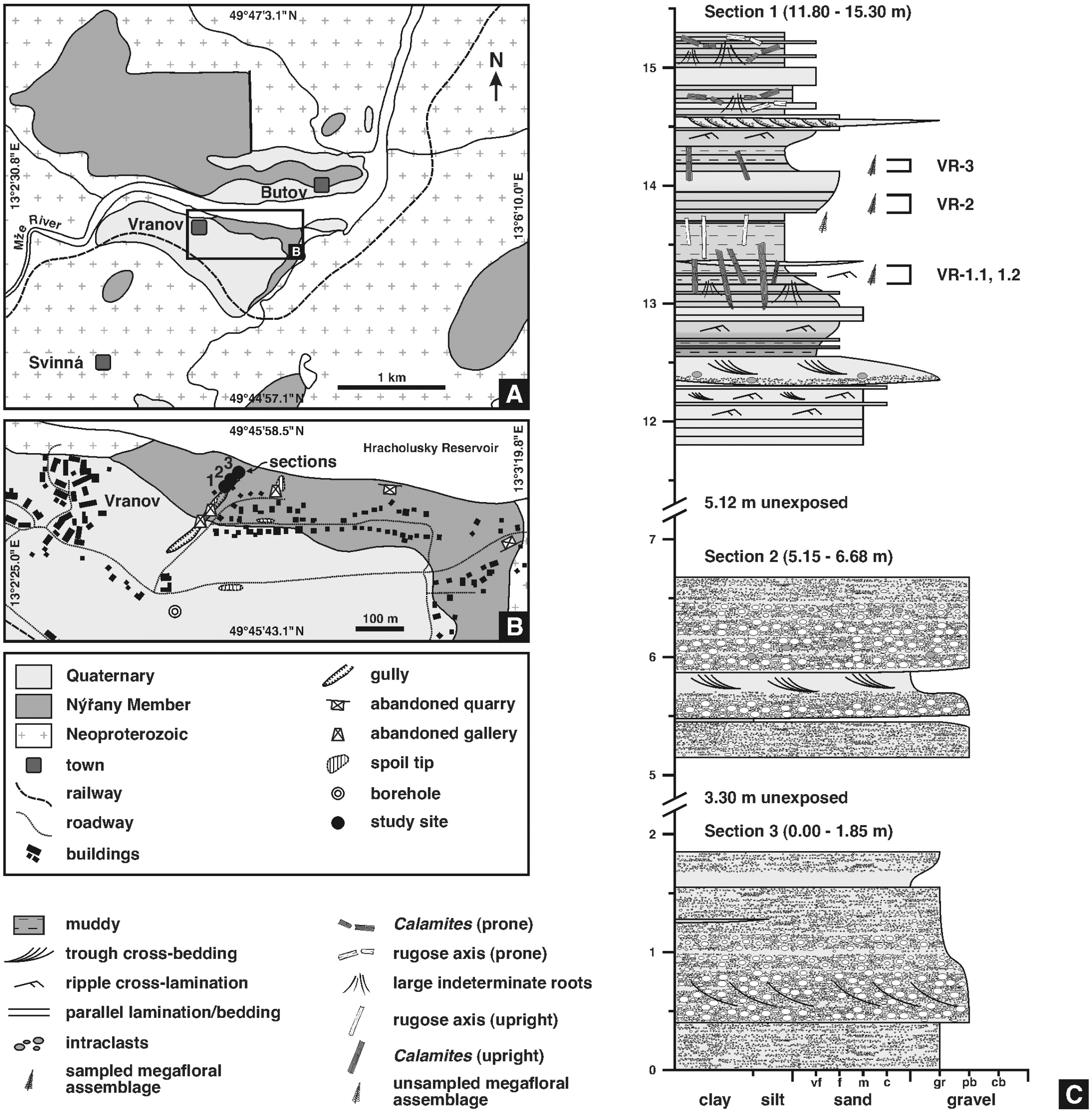


Figure 12. A. Geology of Vranov Relict. B. Position of Sections 1 to 3 of Vranov locality, exposed along banks of a narrow, vegetated gully, situated just west of area of summer cottages east of Vranov. Coal seam was mined along gully, and further to east and south. C. Stratigraphy of Sections 1 to 3, showing position of census quadrats (VR-1 to 3) collected from abandoned mainstem channel facies. A and B modified from Pešek (1960, fig. 3).

overburden immediately above the exposure imply that conglomerate and sandstone overlie Section 1.

Interbedded sandstone and siltstone in Section 1 record the gradual abandonment of a mainstem channel (Table 1; Fig. 9) based on the thickness and upward fining of the succession, and its stratigraphic position between conglomerate and sandstone attributed to active braided channels. The abundance of sandstone interbeds, which reflect periodic incursions of sediment-laden floodwaters, points to the proximity of active systems, and implies that abandonment was due to local avulsion. Parallel-laminated siltstone interbeds indicate deposition from suspension in ponded waters. Upright axes and roots tend to originate in sandstone interbeds, indicating that sand influxes caused rapid shallowing and provided a substrate favorable to colonization.

2.5.2.2. Megafloral Assemblages

Five quadrats were sampled from the abandoned mainstem channel facies (Fig. 12C). Replicates from the lowest interval (VR-1.1 and 1.2) are compositionally similar, being dominated (71.2 to 76.7%) by ferns [*Pecopteris raconensis* (Pl. II, Fig. 5), *Lobatopteris* sp. A (Pl. I, Fig. 11), *Acitheca polymorpha* (Pl. II, Fig. 3)] with lesser sphenopsids (20.9 to 28.8%, particularly *Annularia carinata*; Pl. I, Fig. 4). Upright *Calamites* are abundant but rooted in the subjacent sandstone. VR-2 comprises a nearly monospecific assemblage of *A. polymorpha* (91.8%). Indeterminate roots and subvertical finely rugose axes of unknown affinity are common just below the fossiliferous horizon. In VR-3, ferns dominate (69.3%, particularly *Lobatopteris* sp. A), *Sphenophyllum emarginatum* (Pl. I, Fig. 7) is common (17.7%), and cordaitaleans and pteridosperms are rare. Upright *Calamites* are present but rooted in the underlying sandstone. The prevalence of a single fern species in VR-2 and VR-3 suggests that these taphocoenoses are (par)autochthonous, whereas the presence of several fern species in VR-1 may indicate slightly more transport.

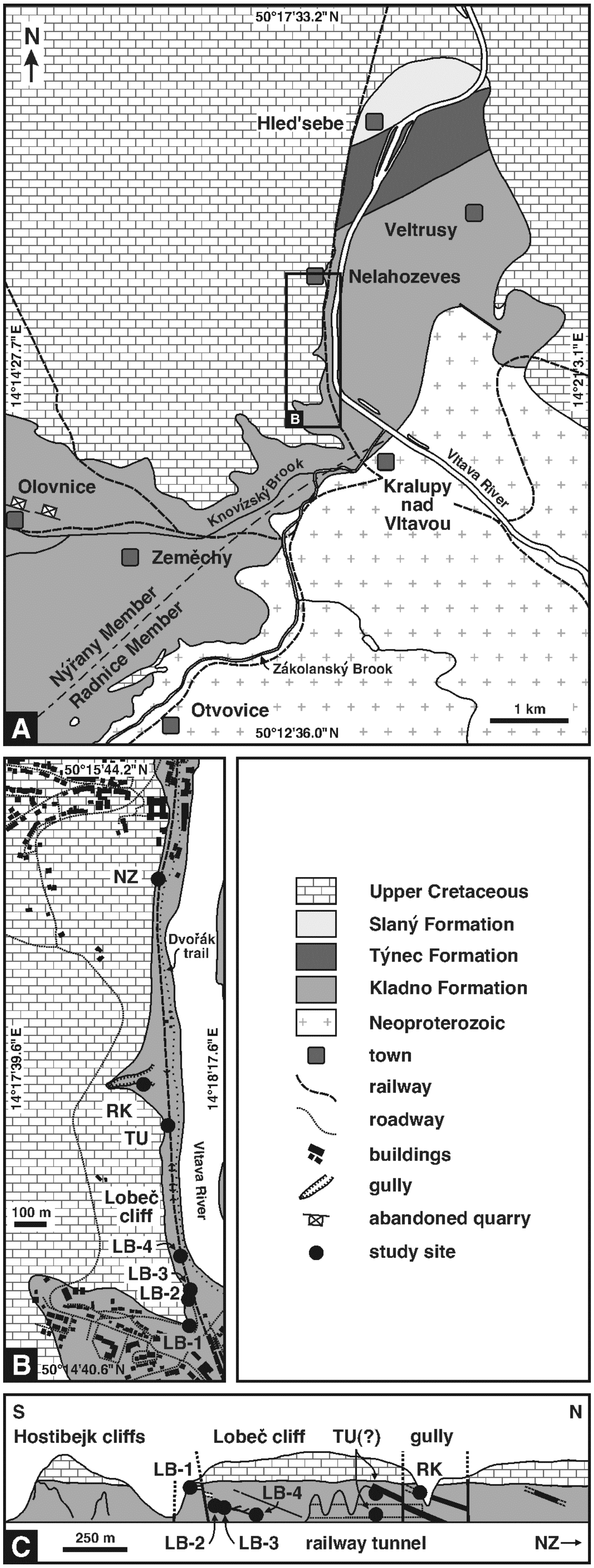
2.5.2.3. Palynology

Spores of various fern families dominate (47.5 to 55.8%, particularly marattialeans and gleicheniaceans) miospore samples (PAL-17 and 18; Tables 3, 7), sphenophyll spores are subordinate (18.4 to 19.0%), and those of calamiteans and lycopsids are uncommon to rare. Most pollen grains belong to cordaitaleans, whereas those of conifers and pteridosperms are rare. Calamiteans and arborescent lycopsids are well represented in the megaspore assemblage (PAL-18; Tables 3, 8). A coal sample processed by Kalibová-Kaiserová (1979) from overlying strata yielded a similar assemblage, which she considered indicative of poorly drained settings.

2.5.3. Lobeč Locality

The Lobeč locality (Fig. 13) comprises eight sites situated along the southern margin of the CWB, west of the informal boundary between the Kladno-Rakovník and Mšeno-Rounice basins (Fig. 6A; Stárková et al., 1994; Holub, 1997). Although Upper Cretaceous strata blanket the region, a 200 to 300 m thick (Vejlupek, 1970, fig. 2) succession of the Nýřany Member crops out along a ≈1.7 km long cliff section on the eastern bank of the Vltava River (Fig. 13B, C). The section, hereafter referred to as Lobeč cliff, is dominated by sandstone and conglomerate deposited on a distal braided-

Figure 13. A. Geology along southeastern margin of Kladno-Rakovík Basin. Boundary between Radnice and Nýřany members approximate and based on Němejc (1947b). Olovnice site (OV) of Lobeč locality situated in historical quarry near Olovnice, ≈4.1 km southwest of southern edge of Lobeč cliff. B. Position of seven sites of Lobeč locality along Lobeč cliff exposed along railway between Kralupy nad Vltavou and Nelahozeves. Position of railway tunnel (TU), gully (RK), and Nelahozeves (NZ) sites approximate and based on Obrhel (1960) and Vejlupek (1970) and labels accompanying historical collections. C. Schematic profile of Hostibejk and Lobeč cliffs, showing position of coal seams (thick black lines) and sites. Cliff buttresses shown near Hostibejk and railway tunnel sections. Note great vertical exaggeration. A and B modified from Vejlupek (1970, fig. 1), and C modified from Obrhel (1960, fig. 3).


A
N
50°17'33.2"N
50°12'36.0"N
14°14'27.7"E
14°21'3.1"E
Hled'sebe
Veltrusy
Nelahozeves
B
Olovnice
Knovízský Brook
Kralupy nad Vltavou
Vltava River
Zeměchy
Nýřany Member
Radnice Member
Zákolanský Brook
Otvovice
1 km
B
50°15'44.2"N
50°14'40.6"N
14°17'39.6"E
14°18'17.6"E
NZ
Dvořák trail
RK
TU
Vltava River
Lobeč cliff
100 m
LB-4
LB-3
LB-2
LB-1
Upper Cretaceous
Slaný Formation
Týnec Formation
Kladno Formation
Neoproterozoic
town
railway
roadway
buildings
gully
abandoned quarry
study site
C
S
N
Hostibejk cliffs
Lobeč cliff
TU(?)
gully
LB-1
RK
LB-4
250 m
LB-2
LB-3
railway tunnel
NZ→

river plain (Opluštil et al., 2005). The middle and upper parts of the Nýřany Member are exposed, and dip gently northward to be overlain by the Týnec Formation (Fig. 13A). Thin coal seams exploited in historical mines between Lobeč and Nelahozeves correlate with the Chotíkov group of coals (Fig. 8; Pešek, 1994).

Megafloral assemblages were studied at seven sites along Lobeč cliff. Four sites remain exposed (LB-1 to 4), and three (TU, RK, NZ) are represented by historical collections (Tables 3, 4). An abandoned quarry near Olovnice (Fig. 13A) also yielded a historical collection (OV).

2.5.3.1. Sites at Base of Lobeč Cliff (LB-2 to 4)

A thin, fine-grained interval underlies a prominent internal boundary surface along the southern part of the cliff base (Vejlupek, 1970). The erosional surface extends >250 m, and Opluštil et al. (2005) noted differences in fluvial architecture and flow conditions across the boundary. Obrhel (1960) considered strata beneath the surface as equivalent to the Mělník group of coals (Jelenice Member, Slaný Formation; Fig. 6B), although megafloral and palynological evidence confirms assignment to the Nýřany Member (Šetlík and Kaiserová, respectively, *in* Vejlupek, 1970).

At the southern edge of Lobeč cliff, the fine-grained interval is ≈7 m above ground level and contains a small 'cave' resulting from local coal exploitation (LB-2; Figs 13B, C, 14A; Vejlupek, 1970, pl. 2, fig. 1). Here, ≤1.7 m of predominantly fine-grained strata are sandwiched between thick sandstone and conglomerate successions. Palynology samples were taken from laterally correlative strata ≈30 m (LB-3) and ≈140 m (LB-4) north of LB-2.

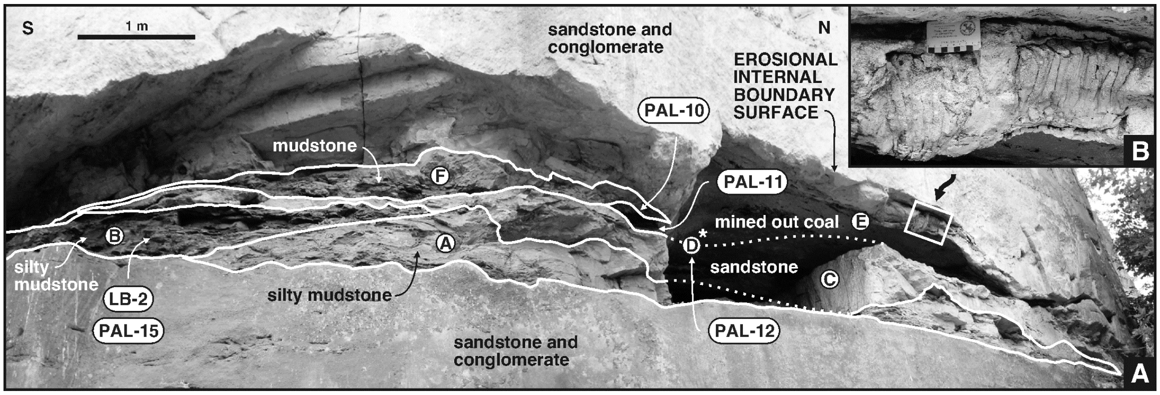


Figure 14. A. Photograph of Lobeč cliff base site (LB-2) of Lobeč locality, showing Units A to F in floodplain facies sandwiched between thick sandstone and conglomerate successions. Base of upper sandstone represents erosional internal boundary surface. Shown are units from which census and supplementary quadrats (LB-2) and palynology samples (PAL-10 to 12, 15) were taken. The 'cave' was accessed by climbing a ladder placed on the roof of a small building adjacent to the cliff – we caution that entry is exceptionally difficult and dangerous! B. Upright tree fern axes rooted near top of coal seam and preserved at base of overlying sandstone.

2.5.3.1.1. Sedimentology

There are six discrete units at LB-2 (Table 3; Fig. 14A). Unit A is a ≤0.5 m thick, laminated, unfossiliferous, light grey silty mudstone that is blocky and has abundant slickensides in places. Unit B is a ≤0.4 m thick lens of poorly laminated, dark grey mudstone containing a rich megafloral assemblage, along with slickensides and abundant stigmarian rhizomorphs. Unit C is a lens of light grey, very coarse-grained sandstone that contains abundant intraclasts, and has an erosive base and irregular thickness (≤0.6 m). Exposed only inside the 'cave', Unit D is a sliver (≤0.2 m thick) of medium grey, rubbly mudstone that contains stringers of granular sandstone. Unit E is a ≤1.0 m thick coal seam that is brown in color and contains numerous clastic partings, particularly in its upper part. It has a variable thickness and only extends ≈4.4 m laterally. Overlying and/or interfingering with the coal seam is a ≤0.4 m thick, blocky, unfossiliferous, light grey mudstone (Unit F) that is thickest where the coal seam is absent. Remnants of upright axes (Fig. 14B) are rooted near the top of the coal seam and preserved at the base of the overlying sandstone, which forms the prominent erosive internal boundary surface. The axes are attributed to tree ferns on the basis of the rounded longitudinal ridges along their exterior surfaces, which may represent sediment-filled adventitious roots of the basal root mantle (cf. Morgan, 1959).

Below the boundary surface to the north (Fig. 13B, C), LB-3 comprises a 0.2 m thick, laminated, medium grey siltstone. At LB-4, a 0.1 m thick lens of well-laminated, dark grey siltstone grades laterally into planar-laminated, fine- to medium-grained sandstone.

Opluštil et al. (2005) interpreted the Lobeč cliff section as the deposits of a braided-river plain characterized by vertically aggrading channels of moderate sinuosity. The planar and laterally extensive body of fine-grained strata between the thick channel successions is interpreted as the remnants of a floodplain, and the abrupt change from channel to floodplain accumulation records regional avulsion (Table 1; Fig. 9). Floodplain fines accrued above a sharp and irregular surface of sand and gravel, which may have been partly indurated. Marked lithological contrasts between individual fine-grained units point to deposition in various wetland settings, and evidence for paleosol development indicates prolonged intervals of exposure with minimal sediment accumulation. The generally poor preservation of megafloral assemblages and presence of a coal seam supports a floodplain origin.

The abundance of pedogenic slickensides in Unit A indicates that it is an immature vertisol, a soil type that contains >30% expandable clays and develops under seasonally variable conditions (Wilding & Tessier, 1988; Driese & Ober, 2005). The lensoid form of Unit B suggests that it represents a narrow floodplain channel, and well-preserved megafloral remains in its mudstone fill imply burial under anoxic conditions, probably in stagnant or sluggish waters. Stigmarian rhizomorphs and pedogenic slickensides indicate colonization and vertisol development after infilling. Unit C records the avulsion of a small channel through the floodplain, although floodplain deposition soon resumed in the form of mudstone (Unit D) and peat (Unit E). The mire may have preferentially developed atop the relatively stable and less compactable sandstone (Unit C; cf. Tibert & Gibling, 1999), and interfingered with, and/or was overlain by, mudstone (Unit F). The brown color of the coal reflects exposure and weathering of the peat. The abundance of clastic partings in upper parts of the coal seam attests to increasingly frequent incursions of nutrient-rich floodwaters. The coal seam was probably more laterally extensive, particularly to the south. Its irregular dimensions could be attributed to syn- and post-depositional erosion, although the tortured appearance of the coal seam may reflect soft-sediment deformation and post-burial plastic flow under load. Sandstone and conglomerate above the internal boundary surface record the erosive reavulsion of braided channels over the floodplain.

Laterally equivalent floodplain deposits at LB-3 are similar to the immature vertisol (Unit A) at LB-2. In contrast, the well-laminated siltstone and associated planar-laminated sandstone at LB-4 have no equivalent at LB-2. These strata may represent a narrow floodplain channel, with the siltstone deposited by suspension in sluggish waters.

2.5.3.1.2. Megafloral Assemblages

Five replicates were collected from Unit B (Fig. 14A; Tables 3, 4). Census quadrats (LB-2.1 to 2.3) have similar compositions, being dominated by "*Lepidodendron*" *subdichotomum* (Pl. I, Fig. 1) organs (79.9 to 88.7%, mostly *Cyperites bicarinatus* leaves), with uncommon *Cordaites* (6.5 to 11.6%) and foliage and axes of *Sphenophyllum emarginatum* (4.2 to 9.7%; Pl. I, Fig. 7). Supplementary quadrats (LB-2.4, 2.5) also contain abundant "*L.*" *subdichotomum*, but include several species that are rare or absent in the census quadrats [e.g., *Annularia carinata* (Pl. I, Fig. 4), *Lobatopteris* sp. B (Pl. I, Fig. 9), *Ptychocarpus unitus* (Pl. I, Fig. 12), *Dicksonites plukenetii* (Pl. III, Fig. 4)].

These quadrats combine two distinct taphocoenoses. The primary taphocoenosis is relatively diverse and dominated by sphenopsids and ferns with lesser cordaitaleans and pteridosperms. Plant remains are fragmentary and associated with abundant comminuted debris, and are interpreted as a parautochthonous to allochthonous assemblage derived from various communities. The secondary taphocoenosis is almost exclusively the remains of "*Lepidodendron*" *subdichotomum*, including canopy elements (leaves, axes, cones) and stigmarian rhizomorphs. This autochthonous assemblage records the litter beneath a swamp community that colonized the mud-filled floodplain channel. Rhizoturbation and pedogenic slickensides fragmented the entombed primary taphocoenosis.

2.5.3.1.3. Palynology

Four samples (PAL-10 to 12, 15) were collected from four beds at LB-2 (Tables 3, 7, 8). PAL-15 (Unit B) contains a diverse palynological spectrum that suggests substantial mixing of plant communities, supporting the interpretation that taphocoenoses in the floodplain channel have variable taphonomic histories. Fern spores derived from numerous families dominate, but cordaitalean and pteridosperm pollen and spores of arborescent lycopsids (primarily lepidocarpaceans), sphenophylls, and calamiteans are present. In the mudstone (PAL-12, Unit D) beneath the coal seam, sphenophyll spores dominate, cordaitalean pollen and fern spores are subordinate, and herbaceous lycopsid spores are rare but conspicuous, implying open marshy conditions. In the coal seam (PAL-11, Unit E), fern spores dominate (particularly marattialean tree ferns) and those of lepidocarpacean and diaphorodendracean lycopsids are subordinate, indicative of a forested mire. *Cystosporites diabolicus*, a megaspore shed by the diaphorodendracean "*Lepidodendron*" *subdichotomum* (unpublished data), is exceptionally abundant in the coal. Sphenophyll spores dominate, fern spores (especially gleicheniacean) are subordinate, and lepidocarpean spores are present in marsh deposits (PAL-10, Unit F) that interfinger with the coal seam. The megaspore assemblage yielded rare medullosalean pteridosperm pollen.

The paleosol at LB-3 (PAL-13B) is dominated by miospores of a lepidocarpacean lycopsid, together with subordinate fern spores. Megaspores derived from "*Lepidodendron*" *subdichotomum* and medullosalean pteridosperm pollen are rare. In contrast, medullosalean pollen is abundant in floodplain channel deposits (PAL-14) at LB-4.

2.5.3.2. Site at Top of Lobeč Cliff (LB-1)

Obrhel (1960) collected plant fossils from a fine-grained interval at the top of Lobeč cliff, on the promontory at its southeastern edge (Fig. 13B, C). The fossiliferous beds are disconformably overlain by Upper Cretaceous rocks, and are separated from LB-2 by ≈24 m of sandstone and conglomerate (Opluštil et al., 2005). Numerous elliptical hollows (molds <1.0 m wide), representing the remnants of large trees, are a conspicuous feature of these coarse-grained strata. Obrhel (1960) assigned the succession to the Malesice Member (Slaný Formation; Fig. 6B), but the megafloral assemblage is typical of the Nýřany Member (Šimůnek, 2004; Opluštil et al., 2005).

2.5.3.2.1. Sedimentology

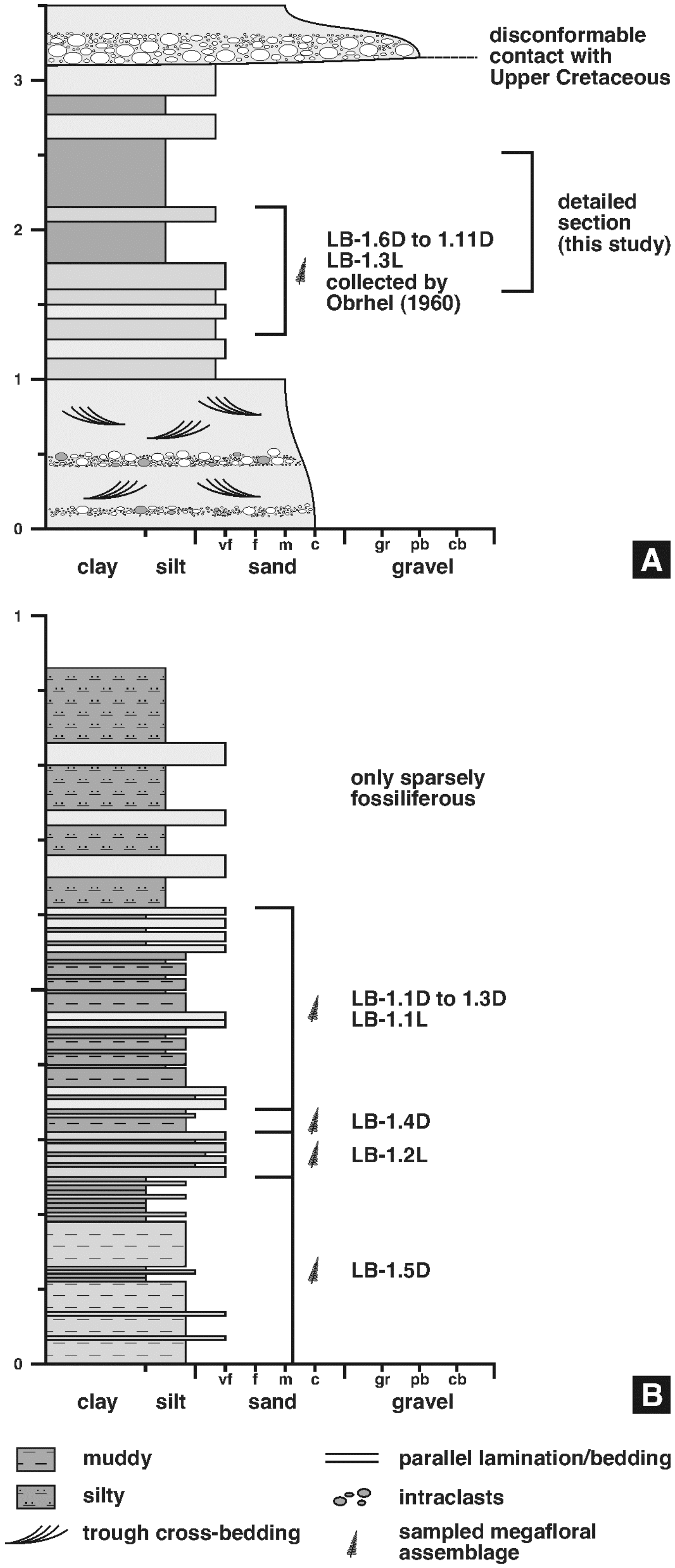
The fossiliferous horizon (Fig. 15A) is a 2.2 m thick and <20 m wide lens that rests on trough and tabular cross-bedded sandstone and conglomerate containing abundant intraclasts (Obrhel, 1960; Opluštil et al., 2005). The lens comprises thin interbeds of medium to dark grey mudstone or siltstone alternating with buff, very fine-grained sandstone. Darker beds are well laminated and very fossiliferous, whereas sandstone beds are sparsely fossiliferous and either massive or exhibit poorly preserved ripple cross-lamination. Upright stems are absent and indeterminate roots are rare.

The fossiliferous lens is interpreted as the fill of an abandoned minor channel resulting from local avulsion (Table 1; Fig. 9). Light-colored sandstone interbeds accumulated during initial stages of flooding, with massive units recording rapid deposition and ripple cross-laminated units produced by low-energy, unidirectional currents. Lamination in dark-colored interbeds, together with the random orientation of fossils on bedding planes, indicates deposition of suspended sediment and plant debris in shallow ponded waters as flooding waned. The paucity of roots and absence of autochthonous axes imply rare colonization of the abandoned channel. Abundant intraclasts in associated sandstone and conglomerate attest to frequent avulsion through floodplains or reactivation of abandoned channels.

2.5.3.2.2. Megafloral Assemblages

Seven census and seven supplementary quadrats were quantified from LB-1. During excavation of the new collection, and prior to quadrat analysis, ‘dark’ (grey mudstone and siltstone) and ‘light’ (buff sandstone) slabs were separated (Table 3) to

Figure 15. Stratigraphic section through abandoned minor channel facies at Lobeč cliff top site (LB-1) of Lobeč locality. A. Section based on “profile 1” of Obrhel (1960, p. 21). Historical collection of Obrhel (1960) derived from ≈0.8 m thick interval, whereas new collection taken from partly overlapping 0.9 m thick interval. Accounting for overlap, 1.2 m of strata sampled. B. Detailed stratigraphic section, showing distribution of ‘light’ (buff sandstone) and ‘dark’ (grey mudstone and siltstone) units from which census quadrats taken.


disconformable contact with Upper Cretaceous
detailed section (this study)
LB-1.6D to 1.11D
LB-1.3L
collected by Obrhel (1960)
3
2
1
0
vf
f
m
c
gr
pb
cb
clay
silt
sand
gravel
A
1
0
only sparsely fossiliferous
LB-1.1D to 1.3D
LB-1.1L
LB-1.4D
LB-1.2L
LB-1.5D
vf
f
m
c
gr
pb
cb
clay
silt
sand
gravel
B
muddy
silty
trough cross-bedding
parallel lamination/bedding
intraclasts
sampled megafloral assemblage

determine whether their taphocoenoses showed compositional differences. There are five 'dark' (LB-1.1D to 1.5D) and two 'light' (LB-1.1L and 1.2L) census replicates from the new collection (Fig. 15B), together with one 'light' (LB-1.3L) and six 'dark' (LB-1.6D to 1.11D) supplementary replicates from the historical collection (Fig. 15A; Table 4).

The five 'dark' census replicates are dominated by *Cordaites* (85.4 to 96.8%), whereas frond fragments of *Lobatopteris* sp. B (0.7 to 11.4%; Pl. I, Fig. 9) and *Eusphenopteris nummularia* (0.0 to 3.6%; Pl. II, Fig. 10) and whorls of *Annularia carinata* (0.0 to 5.1%; Pl. I, Fig. 4) are uncommon to absent. The six 'dark' supplementary replicates also contain abundant *Cordaites*, but have higher proportions of *Lobatopteris* sp. B and include several species that are very rare to absent in the census quadrats [e.g., *Annularia sphenophylloides*, *Sphenophyllum emarginatum* (Pl. I, Fig. 7), *Ptychocarpus unitus* (Pl. I, Fig. 12), *Callipteridium rubescens* (Pl. II, Fig. 7), *Linopteris neuropteroides* (Pl. II, Fig. 8), *Linopteris palentina* (Pl. II, Fig. 11), *Neuropteris plicata* (Pl. III, Fig. 1), *Neurocallipteris planchardii* (Pl. II, Fig. 14)]. The three most characteristic taxa (*Cordaites*, *Lobatopteris* sp. B, *E. nummularia*) are the least fragmented – most *Cordaites* leaves were entire before excavation, whereas large penultimate fronds of *Lobatopteris* sp. B and *E. nummularia* are common. We speculate that these three taxa are (par)autochthonous and derived from local sources, whereas rarer and more fragmentary species may be allochthonous. Megafloral assemblages in the three 'light' quadrats are more fragmentary, less diverse, and have different relative abundances, although *Cordaites* and *Lobatopteris* sp. B are still the dominant elements.

We expected that 'light' and 'dark' beds would contain disparate taphocoenoses, as the former presumably record higher energy flow conditions that sampled a broader spectrum of communities across the landscape. However, a chi-square test on the relative abundance distributions of the nine taxa in the census quadrats indicates no statistically significant compositional differences [$\chi^2 = 3.74$, df = 6, *MC p(same)* = 0.88]. Thus, plant fossils from both lithologies were derived from the same communities.

Although tree-stem molds are a characteristic feature of the sandstone and conglomerate all along Lobeč cliff, their exposure is best in the section below LB-1. The inner surface of the hollows is smooth to ropy, similar to that attributed to large cordaitalean trees (see Falcon-Lang & Bashforth, 2005, fig. 6). Referral to this group is supported by the abundance of *Cordaites* in the abandoned minor channel facies. Application of Niklas's (1994) empirically derived biomechanical relationship between trunk diameter and tree height for 'woody' plants indicates a maximum buckling height of ≤38.9 m for the cordaitalean trees (assuming diameters of ≤1.0 m).

2.5.3.3. Railway Tunnel Site (TU)

This site is situated ≈170 m south of the northernmost railway tunnel between Lobeč and Nelahozeves, either near the tunnel base or on the slope of Lobeč cliff (Fig. 13B, C). Obrhel (1960) included these strata in the upper Ledce Member (Slaný Formation; Fig. 6B), but plant remains clearly belong to the Nýřany Member. Fossiliferous slabs are light grey to buff, and range from silty mudstone to siltstone that is either blocky or moderately laminated. Such subtle lithological differences imply interbedding, and we speculate that specimens were collected from an abandoned minor channel deposit resulting from local avulsion (Table 1; Fig. 9).

2.5.3.3.1. Megafloral Assemblages

Five supplementary quadrats (TU-1.1 to 1.5; Tables 3, 4) from the historical collection yield five main species. Large articulate portions of *Sphenophyllum oblongifolium* dominate (36.3 to 72.0%; Pl. I, Fig. 6), whereas *Alloiopteris erosa* (8.5 to 23.0%; Pl. I, Fig. 5), *Dicksonites sterzelii* (9.3 to 24.6%; Pl. III, Fig. 3), *Pecopteris* sp. G (3.2 to 19.4%; Pl. I, Fig. 10), and *Oligocarpia gutbieri* (5.9 to 15.2%; Pl. II, Fig. 9) are characteristic elements. Frond fragments are relatively large (penultimate and antepenultimate pinnae are common), and many petioles are preserved. The consistent association of all five taxa, despite probable derivation from several interbeds, suggests that the assemblage is (par)autochthonous and faithfully records an original plant community. Co-occurring axes and foliage of the same parent plants, and the paucity of comminuted plant debris, support this interpretation.

2.5.3.4. Gully Site (RK)

A small gully ≈800 m north of the southern edge of Lobeč cliff contains the overgrown remnants of a 19th-century coal mine (Fig. 13B, C). Fine-grained strata associated with a thin coal seam were formerly assigned to the Kounov group of coals (Kounov Member, Slaný Formation, Fig. 6B; Němejc, 1947b; Němejc et al., 1950; Šetlík, 1951; Obrhel, 1957), specifically with the Upper Kounov seam (Obrhel, 1960). However, the strata were reassigned to the Nýřany Member on paleobotanical and stratigraphical grounds (Šetlík, 1968b; Vejlupek, 1970; Stárková et al., 1994; Holub, 1997), and were included in the Chotíkov group of coals by Pešek (1994; Fig. 8). Upper

Cretaceous conglomerate containing coal clasts disconformably overlies the succession (Obrhel, 1960).

2.5.3.4.1. Sedimentology

Obrhel (1960) logged a ≈4.5 m section on the southern side of the gully (Fig. 16). The basal part comprises interbeds of sandstone and brownish grey, laminated mudstone containing rich megafloral assemblages. Plant adpressions are poorly preserved in the upper part, which consists of varicolored beds with mottling and hematite(?) concretions. Stigmarian rhizomorphs are common throughout the succession, particularly in the ‘seat earth’ beneath the coal seam where indeterminate roots and coal stringers abound.

The succession is interpreted as floodplain deposits that accumulated under variable drainage conditions after regional avulsion (Table 1; Fig. 9). Basal sandstone units were laid down on proximal floodplains, and overlying mudstone represents distal floodplain deposits. Mottled, varicolored units indicate well-drained, oxidizing conditions and seasonal precipitation, whereas lamination in the brownish grey, fossiliferous units suggests accumulation in shallow floodplain ponds in microtopographic lows. Abundant stigmarian rhizomorphs and mottling (possibly associated with roots) indicates that the entire floodplain was vegetated, regardless of drainage conditions. The ‘seat earth’ beneath the thin coal seam records swamp development followed by peat accumulation in an ephemeral mire.

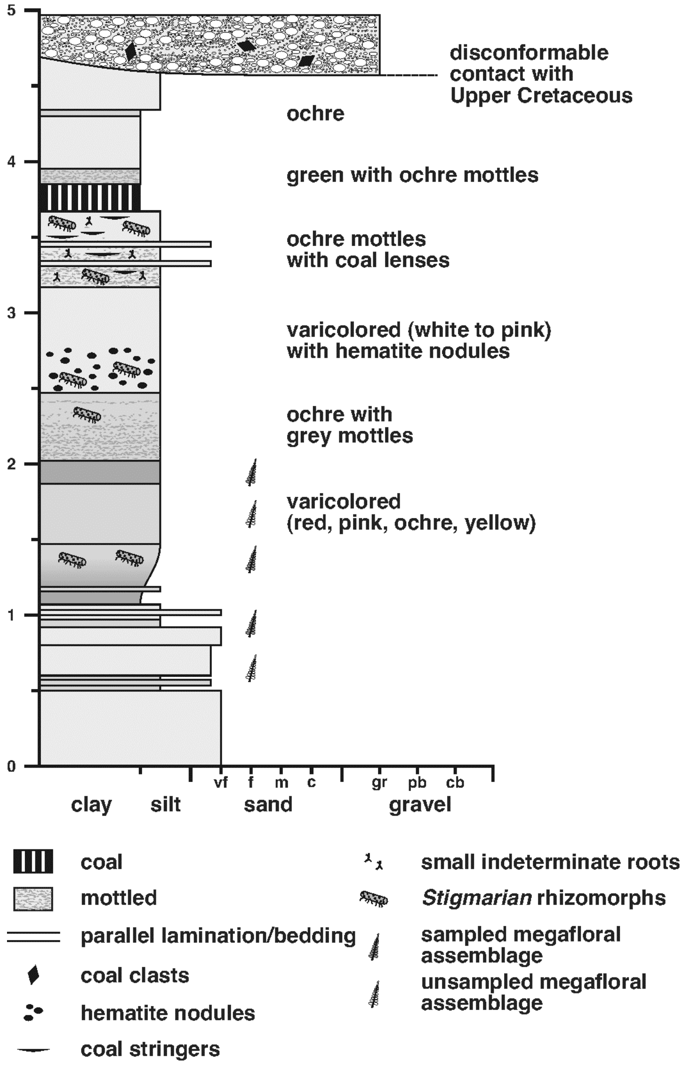


Figure 16. Stratigraphic section through floodplain facies at gully site (RK) of Lobeč locality, based on "profile 3" of Obrhel (1960, p. 25). Historical collection derived from three discrete beds near base.

2.5.3.4.2. Megafloral Assemblages

Slab lithology in the historical collections indicates derivation from floodplain pond deposits near the section base (Fig. 16). In the two supplementary replicates (RK-1.1 and 1.2; Tables 3, 4), fronds of *Lobatopteris* sp. A (52.3 to 69.3%; Pl. I, Fig. 11) dominate, and *Cordaites* (21.9 to 22.3%) and isolated *Linopteris neuropteroides* pinnules (3.1 to 10.1%; Pl. II, Fig. 8) are subordinate. Rare and biostratigraphically significant taxa include *Ptychocarpus unitus* (Šetlík, 1951; Pl. I, Fig. 12), cf. *Blanzyopteris* sp. (Šetlík, 1951, as *Neuropteris crenulata*), *Callipteridium rubescens* (Němejc et al., 1950, as *Pecopteridium costei*; Pl. II, Fig. 7), *Neuropteris plicata* (Pl. III, Fig. 1), *Odontopteris reichiana* (Němejc, 1947b, as *Odontopteris obtusiloba*; Pl. II, Fig. 13), *Dicksonites plukenetii* (Šetlík, 1968b; Pl. III, Fig. 4), and *Pseudomariopteris cordato-ovata* (Němejc et al., 1950, as *Diplotmena ribeironi*; Pl. II, Fig. 2).

Obrhel (1960) recorded similar assemblages (with *Lobatopteris* sp. A dominance and lesser *Cordaites*) in three discrete fossiliferous beds spread through 1.1 m of strata (Fig. 16), suggesting that the taphocoenoses are largely (par)autochthonous and reflect the true composition of communities in the vicinity. Although autochthonous stigmarian rhizomorphs are present in the collections and dispersed through the section, lycopsid foliage and axes are absent. This suggests that lycopsid-dominated communities colonized the floodplain after burial of the (par)autochthonous assemblages.

2.5.3.5. Olovnice Site (OV):

Němejc (1947b) collected plant fossils from several places near Olovnice (Fig. 13A). Unfortunately, the provenance of the historical collection is uncertain because none of his species lists clearly match taxa found in the assemblage. A label with the specimens indicates that the source is an abandoned quarry just north or south of Olovnice. According to Němejc (1947b, p. 411), the quarries are correlative, and expose a thin, coaly horizon near the top of a "rather big", fossiliferous, fine-grained interval that is sandwiched between thick sandstone successions. Strata were ascribed to the Kounov group of coals (Kounov Member, Slaný Formation; Fig. 6B) and correlated with the gully site (RK; Fig. 8; Němejc, 1947b; Obrhel, 1960). However, the megafloral assemblage clearly belongs to the Nýřany Member.

Němejc (1947b) did not specify the thickness of the fine-grained interval, but his wording alludes to a substantial accumulation. Furthermore, he recorded comparable stratigraphic sections and megafloral assemblages to the east and west of Olovnice, implying lateral continuity over >5.5 km. Accordingly, we speculate that the fine-grained package records floodplain deposition after regional avulsion (Table 1; Fig. 9). The coaly unit either represents a swamp or mire. Slabs in the historical collection are greyish brown silty mudstone, and their moderate fissility suggests deposition in shallow floodplain ponds.

2.5.3.5.1. Megafloral Assemblage

The supplementary quadrat (OV-1; Tables 3, 4) is co-dominated by *Lobatopteris* sp. A (37.6%; Pl. I, Fig. 11), *Sphenophyllum emarginatum* (33.5%; Pl. I, Fig. 7), and *Cyathocarpus* sp. A (25.7%; Pl. I, Fig. 8). Sphenophyll remains are poorly preserved, and almost all were referred to *S. emarginatum* (after Němejc, 1947b). However, *Sphenophyllum oblongifolium* (Pl. I, Fig. 6) was recorded and likely is underrepresented.

Many sphenophyll axes crosscut bedding, indicating rapid burial of standing vegetation. This fact, combined with low species richness, suggests that the assemblage is (par)autochthonous and faithfully records a low-diversity community.

2.5.3.6. Nelahozeves Site (NZ)

This unexposed site is situated along the railway ≈650 m north of the gully site (RK; Fig. 13B, C), and comprises a fossiliferous, fine-grained unit overlying a thin coal seam (Vejlupek, 1970). Šetlík (1968b) considered the megafloral assemblage representative of the upper Nýřany Member. We concur and suggest correlation with the Nevřeň group of coals (Fig. 8), although Holub (1997) cautioned that it could be younger.

2.5.3.6.1. Sedimentology

Based on the description and photograph of Vejlupek (1970, pl. 2, fig. 2), a thin paleosol comprising mudstone with roots and coal stringers sits directly atop sandstone. Above this is a ≤350 mm thick coal seam that contains a 100 mm thick mudstone parting, followed by a thin, light grey to buff bed of moderately laminated, fossiliferous mudstone and silty mudstone with abundant roots, upright *Calamites*, and a conchostracan (clam shrimp) valve. Erosion during emplacement of the overlying sandstone removed most of the coal seam (now only ≈6.0 m wide) and fossiliferous unit.

The fine-grained strata are interpreted to record floodplain development after regional avulsion (Table 1; Fig. 9). Soil formation in muds that accumulated atop channel sands indicates prolonged exposure with minimal sediment accrual. A mire developed on the floodplain once conditions were conducive to peat accumulation, and the coal seam thickness indicates that the mire was once more laterally extensive. The mudstone parting records an incursion of sediment-laden floodwaters over the mire. ‘Growth lines’ on the conchostracan valve (labeled as *Leaia* in the specimen tray) suggests referral to the spinicaudatans, which are reliable indicators of freshwater conditions from the Westphalian onwards (Vannier et al., 2003). Specifically, *Leaia* is indicative of freshwater assemblages (Weller, 1957; Williams, 1960), implying that the laminated mudstone above the coal seam records development of a shallow lake that drowned the mire. Roots and upright *Calamites* in the lacustrine unit suggest that plant remains represent a post-mire community.

2.5.3.6.2. Megafloral Assemblage

Foliage, axes, and fructifications of *Annularia* “*spicata*” (Pl. I, Fig. 2) dominate (87.9%) the supplementary quadrat (NZ-1; Tables 3, 4). *Lobatopteris* sp. A (Pl. I, Fig. 11) fronds and foliage and axes of *Sphenophyllum emarginatum* (Pl. I, Fig. 7) and *Sphenophyllum oblongifolium* (Pl. I, Fig. 6) are uncommon. Some remains show evidence of microbial and/or mechanical degradation (cf. Spicer, 1981), and comminuted plant debris is abundant. Common upright *Calamites* represent the vertical shoots of the *A.* “*spicata*” plant. The dominance of organs attributable to a whole-plant taxon implies that much of the assemblage records the litter beneath a monospecific grove of *A.* “*spicata*”. Less common taxa may be parautochthonous, and comminuted debris may be allochthonous.

2.5.4. Rozdělov Locality

The Rozdělov locality (Fig. 17) is situated ≈600 m north of the southern margin of the CWB (Fig. 6A), on the fringe of the area originally covered by the Nýřany Member (Fig. 7). The strata dip gently northward, and largely comprise sandstone and conglomerate deposited on a distal braided-river plain. Rich megafloral assemblages, which correlate with the Nevřeň group of seams (Fig. 8; Pešek, 1994), were recovered from an inaccessible sand(stone) quarry south of Rozdělov.

2.5.4.1. Sedimentology

Lower parts of the quarry wall comprise >6.0 m of trough and tabular cross-bedded sandstone with minor conglomerate and rare coaly lenses. Above this is a 0.7 to 1.3 m thick interval comprising dark to light grey and buff interbeds of mudstone and siltstone containing rich megafloral assemblages (Fig. 18). Planar-laminated beds are most common in lower parts, whereas massive beds become more abundant and the degree of rooting intensifies upward. The fossiliferous interval is laterally continuous over the ≈100 m wide quarry face, but is split by sandstone and locally thickens into lenticular bodies. Sparsely fossiliferous interbeds of ferruginous siltstone and sandstone containing abundant roots punctuate and gradually overlie the plant fossil-bearing unit.

Coaly lenses in the cross-bedded sandstone and conglomerate may record accumulation of allochthonous plant matter along braided channel bases. Fine-grained beds are interpreted to record the infilling of an abandoned mainstem channel with an irregular base (Table 1; Fig. 9). Sandstone lenses that punctuate the fossiliferous interval attest to the proximity of active channels and imply local avulsion. Parallel laminae and

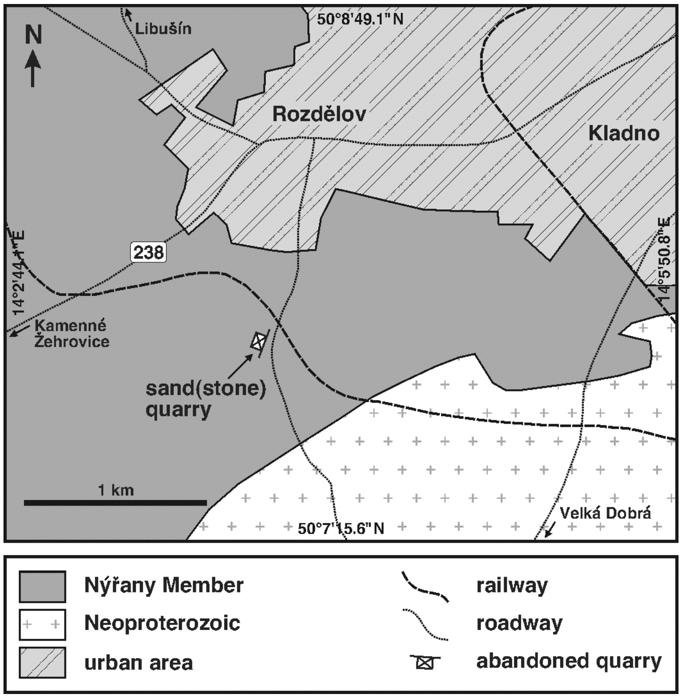


Figure 17. Geology along southern margin of Kladno-Rakovník Basin in vicinity of Rozdělov (suburb of Kladno), where inaccessible sand(stone) quarry comprises Rozdělov locality. Position of basin margin after Opluštil (2005a, fig. 1C).

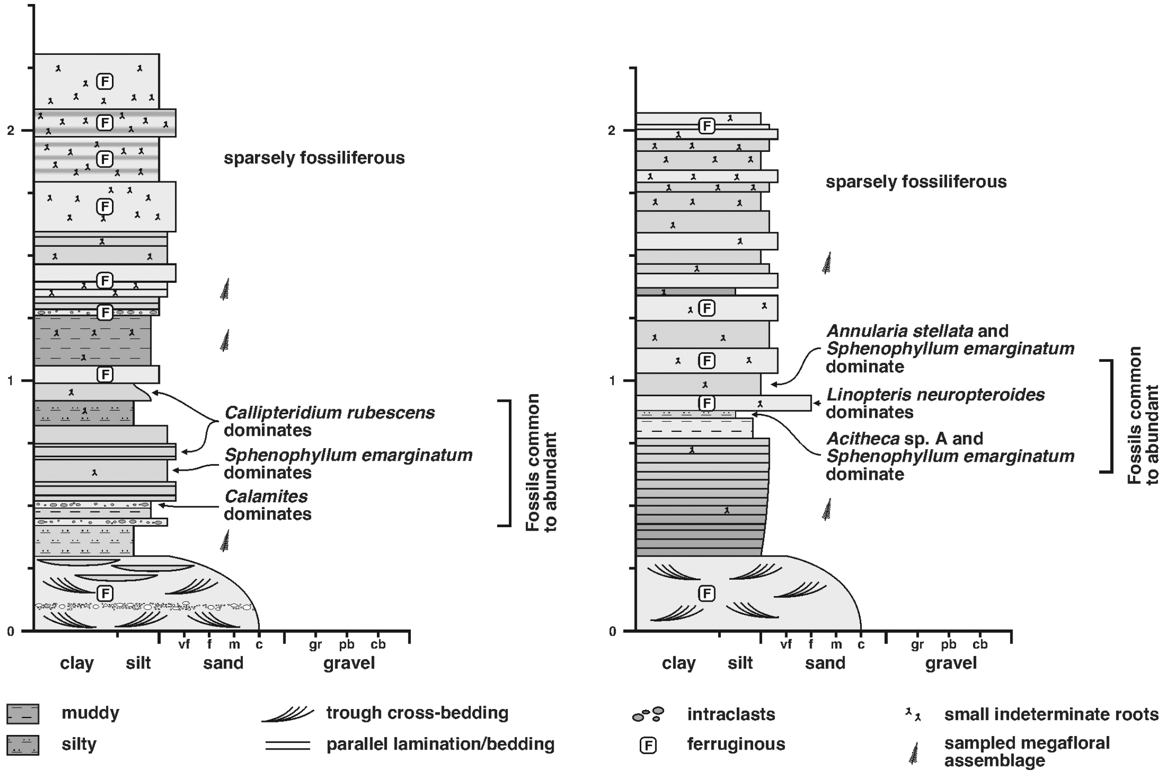


Figure 18. Stratigraphic sections through abandoned mainstem channel facies in upper part of sand(stone) quarry wall at Rozdělov locality. Reddish, ferruginous units increasingly common upwards. Slabs differentiated into a 'fine' (RZ-1F, mudstone and muddy siltstone) and a 'coarse' (RZ-1C, sandy siltstone) supplementary quadrat.

the paucity of roots in basal abandoned channel beds indicate deposition in ponded waters too deep to be colonized. The upward increase in massive beds, which record deposition from sediment-laden floodwaters, and rooting intensity indicate gradual shallowing. Overlying ferruginous strata accumulated under subaerial, oxidizing conditions in late stages of infilling.

2.5.4.2. Megafloral Assemblages

Years of collecting (Table 3) have yielded a diverse and well-preserved megafloral assemblage comprising 30 fossil taxa belonging to 26 biological species. Most specimens were collected from two thicker lenses that fill depressions ≈40 m apart along the abandoned channel base (Fig. 18). During collection, species distribution was recorded semi-quantitatively (i.e., abundant, common, rare, or exceptional) in each bed. However, specimens were thereafter amalgamated into a single collection, and in this study the entire assemblage is treated as a single taphocoenosis.

The amalgamated historical collection is co-dominated by pteridosperms (36.1%), ferns (34.1%), and sphenopsids (29.4%). Cordaitaleans are exceptionally rare and lycopsids are absent, although *Cordaites* is greatly underrepresented and one stigmarian rhizomorph was seen in outcrop. Most abundant among the pteridosperms are medullosaleans, such as *Linopteris neuropteroides* (10.2%; Pl. II, Fig. 8), *Callipteridium rubescens* (8.4%; Pl. II, Fig. 7), *Neuropteris plicata* (8.4%; Pl. III, Fig. 1), and *Neurocallipteris planchardii* (5.0%; Pl. II, Fig. 14). Rare pteridosperms include "*Alethopteris*" *kettneri* (Pl. II, Fig. 4), *Odontopteris reichiana* (Pl. II, Fig. 13), *Dicksonites plukenetii* (Pl. III, Fig. 4), and *Eusphenopteris scribanii*. Several fern families are represented, although the marattialean tree ferns *Acitheca* sp. A (17.0%; Pl. II, Fig. 1), *Pecopteris* sp. G (6.7%; Pl. I, Fig. 10), and *Pecopteris* sp. F (5.4%; Pl. II, Fig. 6) are most abundant. The main sphenopsids are *Annularia carinata* (13.0%; Pl. I, Fig. 4) and *Sphenophyllum emarginatum* (11.4%; Pl. I, Fig. 7), whereas *Sphenophyllum oblongifolium* (4.3%; Pl. I, Fig. 6) is less common.

The most abundant taxa are widely dispersed through the abandoned channel fill, although their distribution is laterally and vertically variable. In many cases, several organs of a single biological species dominate thick laminae or thin beds, whereas two or three taxa co-occur in other thin horizons (Fig. 18). These monospecific and very low-diversity taphocoenoses are interpreted as (par)autochthonous, recording the rapid burial of *bona fide* communities, an interpretation supported by the large size of specimens and the absence of evidence for mechanical or microbial degradation. Lower to middle parts of the abandoned channel fill, coinciding with a slight grain-size increase, invariably yield the richest assemblages, whereas plant remains are rare or absent in the finest strata just above the underlying sandstone. Sphenopsids are most common in lower parts of fossiliferous intervals, whereas ferns and pteridosperms increase in abundance upwards (Fig. 18).

To elucidate the original distribution and composition of communities, slabs were segregated into a ‘fine’ (RZ-1F, mudstone and muddy siltstone) and a ‘coarse’ (RZ-1C, sandy siltstone) supplementary quadrat (Table 3). The quadrats share many species, but there are important proportional differences among plant clades. Fern relative abundance is slightly higher in ‘fine’ than in ‘coarse’ strata (36.9 vs. 25.6%, respectively), but sphenopsids are more common in the ‘fine’ quadrat (33.4 vs. 17.3%) and pteridosperms are more plentiful in the 'coarse' quadrat (57.1 vs. 29.2%). A chi-square test confirms that differences are statistically significant [$\chi^2 = 17.16$, df = 3, *MC p(same)* = 0.0004]. Comparison at the species level also reveals statistically significant differences [$\chi^2 = 50.84$, df = 20, *MC p(same)* <0.0001]. *Sphenophyllum emarginatum*, *Sphenophyllum oblongifolium*, *Pecopteris* sp. F, and *Pecopteris* sp. G are 4.7 to 2.0 times more abundant in 'fine' strata, whereas *Neuropteris plicata*, *Callipteridium rubescens*, "*Alethopteris*" *kettneri*, and *Dicksonites plukenetii* are 8.4 to 2.9 times more abundant in 'coarse' strata. This suggests that, although taxa were drawn from a common species pool, the taphocoenosis records the mixing of two broad (though not mutually exclusive) communities – one dominated by sphenopsids and the other by pteridosperms, with ferns important in both.

2.5.4.3. Palynology

A sample (PAL-19) from 'fine' strata is dominated by spores of numerous fern families (Table 7), reflecting the array of ferns in the megafloral assemblage. Cordaitalean and pteridosperm pollen is relatively abundant, and sphenopsid spores are underrepresented. Rare lycopsid spores are mostly derived from herbaceous forms. The meager megaspore assemblage (Table 8) contains palynomorphs from herbaceous lycopsids and medullosalean pteridosperms.

2.6. SPATIAL DISTRIBUTION OF VEGETATION

2.6.1. Local-scale Patchiness

Dominance-diversity patterns in individual megafloral assemblages exemplify the prevalence of local-scale patchiness on the braided-river plain. A single biological species has a relative abundance of ≥80% in 15 of 41 quadrats (36.6%), ≥50% in 28 quadrats (68.3%), and ≥40% in 34 quadrats (82.9%). Furthermore, only in one quadrat (RZ-1F) does the dominant taxon have a relative abundance of <20%. This implies that most patches were virtually monospecific or had very low diversities.

Empirical observations support this concept. At Janov, two distinct megafloral assemblages (JV-1 and 2; Fig. 10E) were retrieved from abandoned minor channel and shallow lake deposits in an interval only 0.7 m thick. Both taphocoenoses contain the same taxa, indicating derivation from a small species pool, but the proportions of individual species differ radically in the superposed beds. *Linopteris neuropteroides* dominates the lower bed (Unit A, abandoned channel), which suggests sampling of an essentially monospecific stand of this medullosalean pteridosperm. Organization of this group into monospecific clumps is confirmed by the dominance of *Neuropteris plicata* in laterally equivalent beds. In contrast, the upper bed (Unit C, shallow lake) contains a low-diversity assemblage dominated by the sphenopsids *Annularia carinata* and *Sphenophyllum mirosoviense*. Similarly, shallow lacustrine strata at Nelahozeves are characterized by an essentially monospecific stand of *Annularia* "*spicata*". Comparable patterns are seen at Vranov, where 1.0 m of an abandoned mainstem channel entombs three unique megafloral assemblages (Fig. 12C), each characterized by one marattialean tree fern species: *Pecopteris raconensis* (VR-1), *Acitheca polymorpha* (VR-2), and

Lobatopteris sp. A (VR-3). Lithologies are nearly identical at each level, implying that compositional disparities are unrelated to differing substrate conditions. Finally, at Rozdělov, mass occurrences of one or two species (e.g., *A. carinata*, *Sphenophyllum emarginatum*, *Acitheca* sp. A, *L. neuropteroides*, *Callipteridium rubescens*) occur along discrete laminae or thin beds (Fig. 18), indicating burial of monospecific or very low-diversity patches. These observations provide evidence for local-scale heterogeneity on the braided-river plain, with the sphenopsids, marattialean ferns, and medullosalean pteridosperms organized into a mosaic of small patches dominated by one or a few species.

2.6.2. Evidence for Persistence and Resilience

Pimm (1984, p. 322) defined persistence as “the time a variable lasts before it is changed to a new value”, and resilience as “how fast the variables return towards their equilibrium following a perturbation”. From a paleobotanical perspective, a megafloral assemblage that retains its compositional or structural attributes through a succession of strata could be considered persistent, and one that quickly returns to its pre-disturbance dominance-diversity state could be considered resilient (DiMichele & Phillips, 1996a). Although evidence is indirect, we observed subtle signs of these phenomena at several sites at the Lobeč locality. At the top of Lobeč cliff, a 1.2 m thick package of abandoned minor channel deposits (Fig. 15A) yielded 14 quadrats characterized by the consistent association of *Cordaites*, *Lobatopteris* sp. B, and *Eusphenopteris nummularia*. This implies continuous input from a low-diversity community that persisted nearby as the abandoned channel filled. In the same facies at the railway tunnel site, five species

(*Sphenophyllum oblongifolium*, *Alloiopteris erosa*, *Dicksonites sterzelii*, *Pecopteris* sp. G, *Oligocarpia gutbieri*) recur in five quadrats. Axes and foliage of each species are preserved, indicating rapid burial and limited transport of remains, and the invariable association of the five taxa in successive interbeds implies persistence and resilience of the community despite repeated disturbance. Finally, at the gully site, *Lobatopteris* sp. A dominates and *Cordaites* is subordinate in three discrete beds that punctuate a 1.1 m thick floodplain interval (Fig. 16). The megafloral assemblages were recovered from pond deposits, whereas associated floodplain deposits are largely unfossiliferous and were well drained. Thus, although microelevation and drainage conditions were variable, the same low-diversity community reestablished itself during wetter phases. These observations provide further evidence for short-term, local-scale persistence of communities that exhibited resilience to disturbances and changing substrate conditions.

2.6.3. Successional Patterns

Connell & Slatyer (1977, p. 1119) defined succession as "…changes observed in an ecological community following a perturbation that opens up a relatively large space". After disturbance and exposure of a new substrate, a continuum of seres establishes as the ecosystem advances towards a hypothetical 'climax community' or 'steady state'. We speculate that the vertical arrangement of megafloral assemblages provides insight into compositional changes during succession. In abandoned mainstem channel deposits at Rozdělov (Fig. 18), statistical analyses and qualitative observations indicate that sphenopsids appeared once ponded waters shallowed sufficiently for colonization. Marattialean ferns arose as sediment accrued and exposure increased, and medullosalean pteridosperms became increasingly prevalent as channels filled and grain size increased. This pattern is incomplete elsewhere, but evidence clearly indicates that sphenopsids were the first clade to appear on shallowly submerged or newly exposed substrates. For example, marattialean ferns are the most abundant group in abandoned mainstem channel deposits at Vranov (Fig. 12C), but sphenopsids are most common low in the succession. Shallow lacustrine deposits at Nelahozeves and Janov (Fig. 10E) are also dominated by sphenopsids, suggesting that habitat conditions along shallow lake margins were analogous to the ponded waters of abandoned channels.

2.6.4. Regional-scale Patchiness

Each locality/site yielded a unique suite of species, with megafloral assemblages typified by a single taxon or the consistent association of two to five dominant taxa. This is exemplified by the fact that only five of 46 biological species (10.9%) occur at 6 or more localities/sites (Table 5). Even though cosmopolitan, none of these taxa are a major component (≥20.0%) at more than one locale. Furthermore, many taxa are extremely abundant at one locality/site, but rare or absent elsewhere (Table 5). These observations imply landscape-scale heterogeneity in the metacommunity occupying the braided-river plain.

To explore this pattern, we analyzed the 41 (census and supplementary) quadrats using non-metric multi-dimensional scaling (NMDS; Kruskal, 1964; Taguchi & Oono, 2005), a type of unconstrained ordination that allows multivariate data sets to be visualized in n-dimensional space, revealing trends or groupings. The analysis was performed using the absolute abundance matrix comprising 46 biological species (supplementary file), with quadrats grouped into nine localities/sites (all Janov quadrats combined). As recommended by Ludwig & Reynolds (1988), the chord distance measure was used because it normalizes away absolute abundance values. This is preferred because the population is dominated by only a few species, and important information from rarer taxa could be obscured by the abundances of these principal elements (Hammer & Harper, 2006). The ordination was run in two dimensions using PAST (v. 1.86b; Hammer et al., 2001).

The NMDS ordination plot (Fig. 19) demonstrates that quadrats from each group cluster tightly in multivariate space, and a PERMANOVA analysis (Anderson, 2001) indicates statistically significant differences between groups [$F = 14.33$, $p(same) < 0.0001$]. Likewise, pairwise PERMANOVAs between all pairs of groups in a post-hoc test indicate that most localities/sites differ significantly [$p(same) \leq 0.05$]. In other words, compositional dissimilarities between groups are greater than those within groups. There are two exceptions. The post-hoc test indicates that the Rozdělov locality and gully site are compositionally similar [$p(same) = 0.33$] due to the mutual presence of *Linopteris neuropteroides*, *Annularia carinata*, and *Sphenophyllum emarginatum*, and probably because both contain the rare pteridosperms *Callipteridium rubescens*, *Neuropteris plicata*, *Odontopteris reichiana*, and *Dicksonites plukenetii*. Likewise, the Vranov locality and gully site are somewhat similar [$p(same) = 0.19$] because they share *Lobatopteris* sp. A, *S. emarginatum*, *A. carinata*, *C. rubescens*, and *Pseudomariopteris cordato-ovata*.

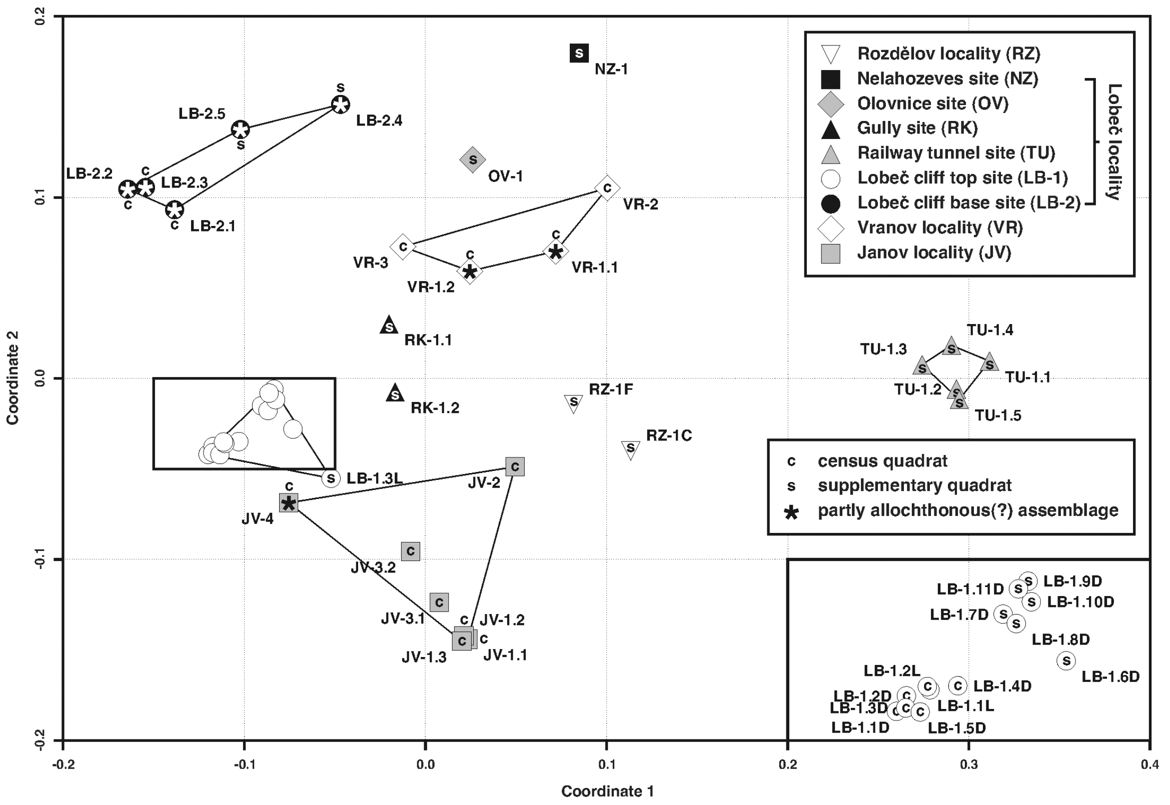


Figure 19. Two-dimensional ordination plot after non-metric multidimensional scaling of 41 census (c) and supplementary (s) quadrats separated into nine localities/sites. Computed from absolute abundance matrix (Table 6) comprising 46 biological species using chord distance measure. Tight cluster of data points enlarged in inset. Quadrats containing a significant proportion of presumed allochthonous components denoted (*).

The ordination also permits assessment of the effect of sampling method on data quality. Although census and supplementary quadrats (new and historical collections, respectively) were used for the Lobeč cliff top and cliff base sites (Fig. 19), quadrats from each site plot in discrete clusters in multivariate space. Thus, despite differences in the proportional abundances of taxa in new and historical collections, the composition of megafloral assemblages at each site is sufficiently unique to override differences in collection protocol.

Given the distance between localities (27 to 108 km apart; Fig. 7), and between sites yielding megafloral assemblages at the Lobeč locality (83 m to 4.5 km apart; Fig. 13), these results indicate that riparian communities were patchy at a regional scale. For the most part, the heterogeneity cannot be explained by biostratigraphic changes, as most taxa are present through all or most of the Nýřany Member (Fig. 8; Pešek, 2004, table 2). Exceptions include *Sphenophyllum mirosoviense* and *Linopteris obliqua*, which go extinct above the Mirošov Horizon, and *Sphenophyllum oblongifolium*, which appears near the base of the Cantabrian. Disparate taphonomic histories may be partly responsible, but most megafloral assemblages are interpreted as (par)autochthonous and representative of true communities. Accordingly, we conclude that the compositional uniqueness of each locality/site reflects the fact that a heterogeneous mosaic of vegetation blanketed the braided-river plain.

2.6.5. Ecological Gradients

The distribution of vegetation over a landscape records interactions between substrate conditions and the physiological requirements and reproductive strategies of different taxa (DiMichele & Phillips, 1996a; DiMichele et al., 1996a, 2002). A second NMDS analysis was used to assess whether ecological gradients were recognizable among the main plant groups. Quadrats were categorized by depositional facies: abandoned minor channels (25), abandoned mainstem channels (6), floodplains (8), and shallow lakes (2). Absolute abundance data (supplementary file) were segregated into eight plant groupings (lycopsids, calamiteans, sphenophylls, marattialean tree ferns, ‘other’ ferns, medullosalean pteridosperms, ‘other’ pteridosperms, cordaitaleans).

The NMDS ordination plot (Fig. 20) shows that the four depositional environments are distinguishable in multivariate space based on their plant fossil content, although quadrats from most facies are arranged in loose clusters. With the exception of five quadrats from the railway tunnel site (TU), abandoned minor channel deposits are widely dispersed over the lower left quadrant, whereas abandoned mainstem channels concentrate in a central position. The floodplain facies is scattered over the lower right quadrant, and shallow lake deposits plot close together in the upper centre. Despite the overlap of data points from the abandoned minor channel, abandoned mainstem channel, and floodplain facies, a PERMANOVA analysis indicates statistically significant differences between all environments [$F = 5.12$, $p(same) < 0.0001$], and pairwise PERMANOVAs between all pairs of groups in a post-hoc test confirms that all facies have significantly different megafloral compositions [$p(same) \leq 0.04$]. The ordination plot thus implies strong habitat partitioning among plant clades, presumably reflecting

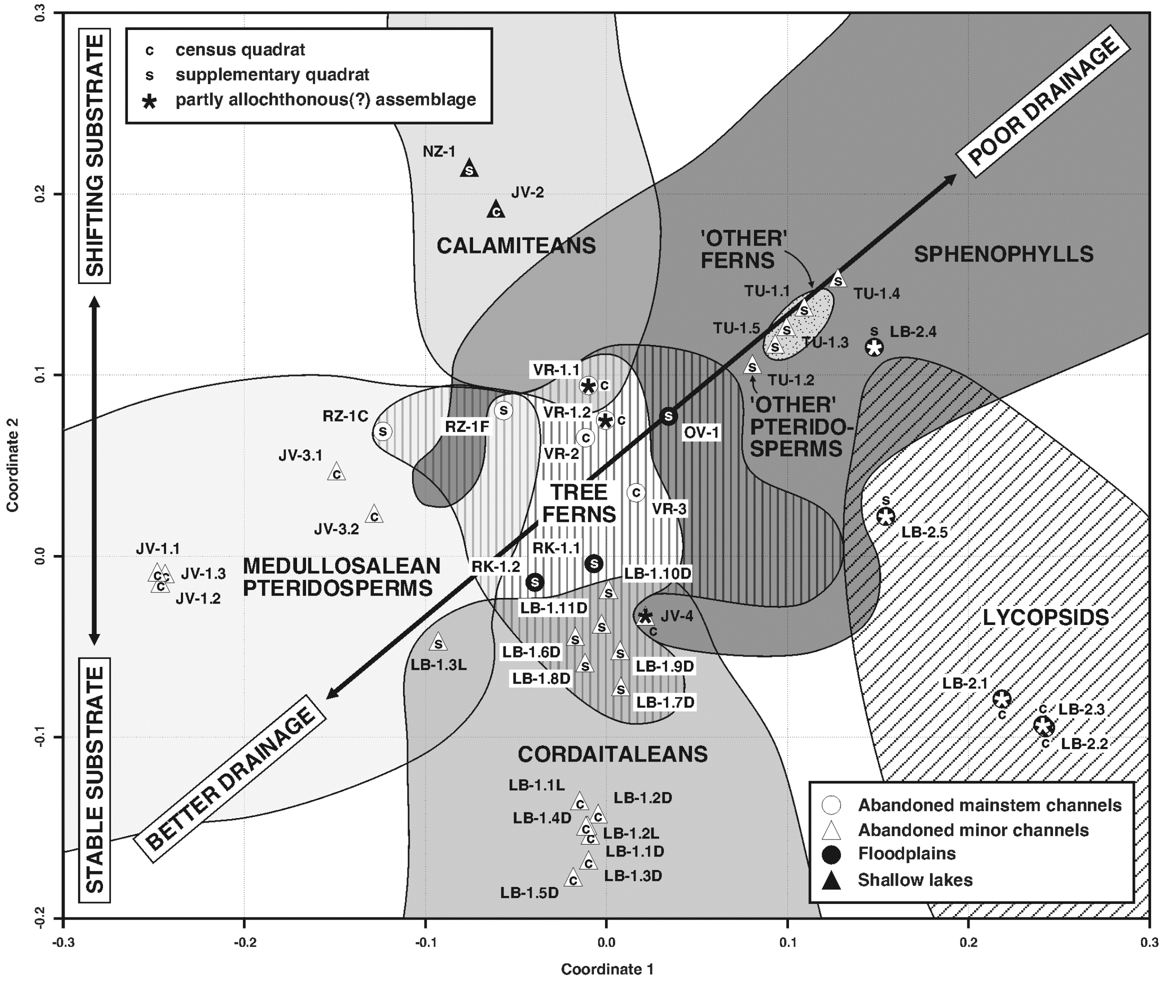


Figure 20. Two-dimensional ordination plot after non-metric multidimensional scaling of 41 census (c) and supplementary (s) quadrats segregated by depositional facies: abandoned mainstem channels, abandoned minor channels, floodplains, shallow lakes. Computed from absolute abundance matrix (Table 6) comprising eight plant groups: lycopsids, sphenophylls, calamiteans, 'other' ferns, arborescent ferns, medullosalean pteridosperms, 'other' pteridosperms, and cordaitaleans. Quadrats containing a significant proportion of presumed allochthonous components denoted (*). Relative abundance contour lines (≥25%) shown for each plant group. Note broad ecological gradients related to substrate stability and drainage, with position of each plant group representing interplay between substrate conditions and life history strategies.

their biological and reproductive constraints in concert with the various landforms available for colonization.

Two methods were used to improve clarity on the segregation and distribution of plant groups on the braided-river plain. First, contour lines were drawn delineating zones where each clade has a relative abundance of ≥25% (Fig. 20). The lycopsids, cordaitaleans, medullosalean pteridosperms, calamiteans, and sphenophylls form prominent end-members. The ‘other’ ferns occupy a small zone inside the area of sphenophyll dominance, and only one quadrat contains ≥25% ‘other’ pteridosperms. Significantly, there is almost no overlap between the five end-members, signifying strong habitat partitioning (cf. DiMichele & Phillips, 1996a). In contrast, dominance of the marattialean tree ferns in the centre, where they overlap with all end-members except the lycopsids, suggests that they were more cosmopolitan and occupied numerous habitats.

Second, when the life history strategies of the plant groups are considered, they appear to be arranged along two broad ecological gradients demarcating differences in substrate conditions (Fig. 20). Along Coordinate 2, there is a change from ‘K-selected’ taxa (site-occupiers) at the bottom to ‘r-selected taxa’ (opportunists and/or pioneering communities) at the top, corresponding to a decrease in substrate stability (and increase in disturbance frequency) from bottom to top. Furthermore, if the plot is divided diagonally into an upper right and lower left sector (i.e., by a line perpendicular to the proposed drainage gradient), the upper right sector almost exclusively contains spore-producing taxa that required wet or waterlogged substrates to reproduce, whereas the lower left sector is dominated by gymnosperms capable of occupying better-drained substrates.

Thus, a broad decrease in drainage conditions is evident from the lower left to upper right. The marattialean tree ferns are spread over the boundary between sectors.

Medullosalean pteridosperms were architecturally complex, bore large seeds, and had a low reproductive output, all characters of slow-growing colonizers or site-occupiers that reproduced infrequently or over extended intervals (DiMichele & Phillips, 1994; Dimitrova et al., 2005; DiMichele et al., 2006b). They preferred undisturbed habitats (Bashforth et al., 2010; Chapter 3), consistent with their position on the plot in the domain of better-drained, stable substrates. Cordaitaleans were slow-growing gymnosperms with dense wood (DiMichele & Phillips, 1994, 1996a), and the fact that some forms inhabiting clastic substrates attained enormous heights (Falcon-Lang & Bashforth, 2004, 2005) implies growth on relatively stable sediment. We speculate that communities dominated by medullosalean pteridosperms and/or cordaitaleans were as close to a 'steady state community' as existed on the braided-river plain. Using the categorization of modern plants based on their functional adaptations to disturbances (Table 9), these gymnosperms could be classified as 'resisters'.

Placement of the calamiteans in the upper middle of the plot agrees with their opportunistic growth strategy and ability to form clonal, regenerative groves on frequently disturbed, rapidly aggrading sediment (Scott, 1978, 1979; Gastaldo, 1992; Pfefferkorn et al., 2001; Calder et al., 2006). Such characteristics are typical of 'endurers'. The sphenophylls, 'other' ferns, and 'other' pteridosperms plot in the field of poorly drained, shifting substrates, consistent with the fact that these groups comprise opportunistic groundcover elements (Batenburg, 1977, 1981; DiMichele & Phillips, 2002; Phillips & Galtier, 2005; DiMichele et al. 2006b; Libertín et al., 2009a) that formed

Category	Functional adaptations to disturbances	Comparable Carboniferous plant group(s)
Invader	produces large numbers of wind- and water-dispersed propagules that colonize newly exposed substrates after disturbance	sphenophylls, 'other' ferns, marattialean tree ferns, 'other' pteridosperms
Endurer	stems and/or roots resprout after breakage or burial by floods	sphenophylls, calamiteans, marattialean tree ferns
Resister	withstands prolonged but seasonal flooding	medullosalean pteridosperms, cordaitaleans
Avoider	lacks adaptations to severe habitat destruction during flooding; low survival of individuals germinating in unfavorable habitats	lycopsids

Table 9. Classification of modern plants based on their functional adaptations to disturbances, and comparable Carboniferous plant group(s). Modified from Naiman & Décamps (1997) and Agee (1993).

pioneering communities on newly exposed substrates after disturbance. All of these plant groups could be termed ‘invaders’, although the sphenophylls might also qualify as ‘endurers’.

The lycopsids preferred waterlogged soils, and although they could not withstand severe habitat destruction (DiMichele & Phillips, 1985, 1994; Phillips & DiMichele, 1992), polycarpic forms could tolerate minor disturbances (Calder et al., 2006). The lycopsids are considered ‘avoiders’, in agreement with their centroid on the lower right of the plot. Arborescent ferns were ‘cheaply’ constructed, grew rapidly, produced copious spores, and could regenerate through burial events, all of which point to an opportunistic lifestyle with wide dispersal potential and colonization of disturbed habitats (Willard, 1993; DiMichele & Phillips, 1994, 2002; Baker & DiMichele, 1997; Falcon-Lang, 2006b; Bashforth et al., 2010; Chapter 3). These are the characteristics of ‘invaders’ and ‘endurers’. The marattialean ferns apparently formed seres in secondary stages of succession (Section 2.6.3), and thus probably colonized slightly more stable substrates already occupied by pioneering species, which may explain their central position on the plot.

2.7. PALEOECOLOGICAL RECONSTRUCTION

The Nýřany Member braided-river plain clearly was inhabited by a myriad of communities, and a detailed picture (Fig. 21) of the vegetation emerges when taphonomic and sedimentologic observations are combined with quantitative analyses of quadrat data. Multivariate analyses indicate that a collage of low-diversity communities was spread over the landscape (Fig. 19), with patchiness occurring at various spatial scales, and

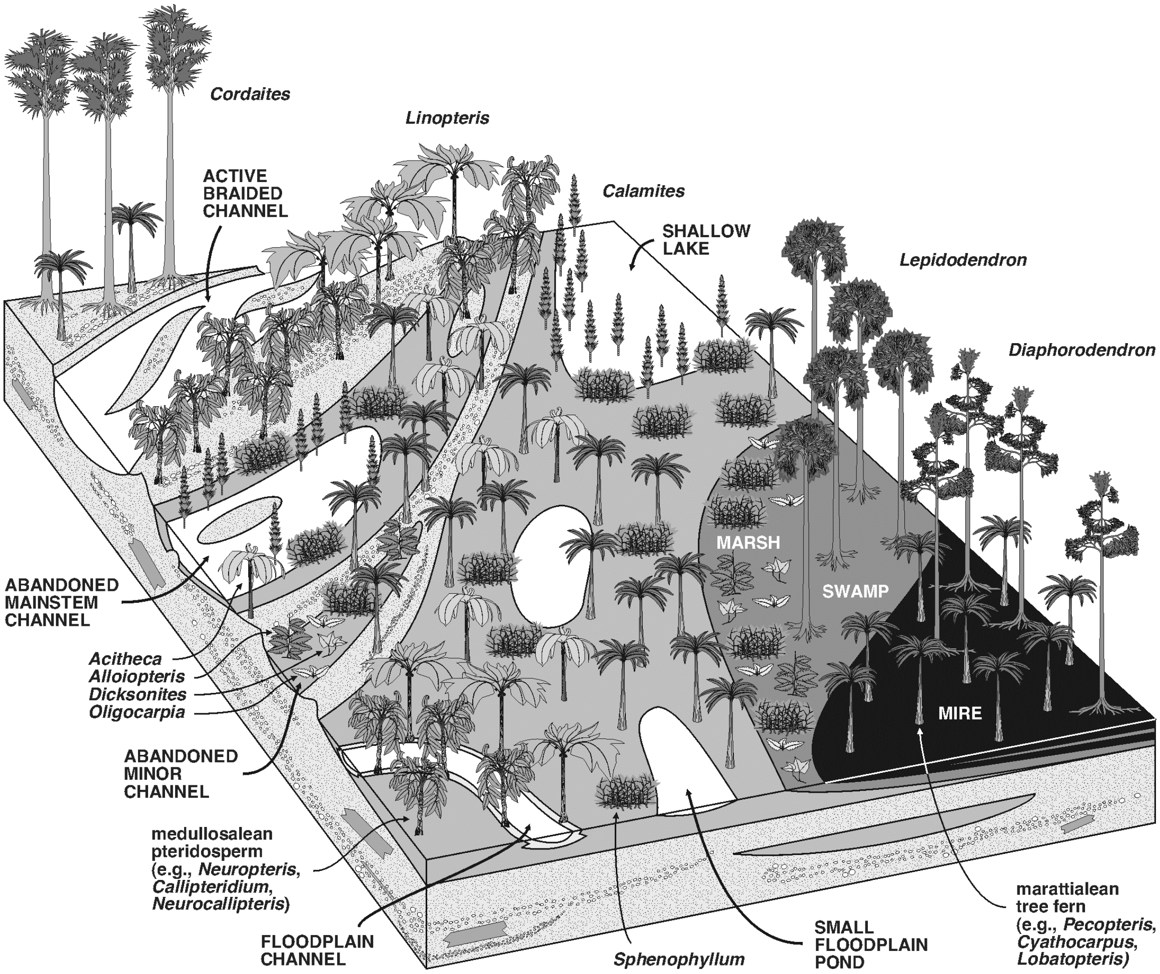


Figure 21. Interpreted distribution of riparian vegetation on reconstructed Nýřany Member braided-river plain. Landforms resulting from local and regional avulsion shown together, a scenario unlikely to have occurred in nature. No vertical or lateral scales implied.

provide compelling evidence for habitat partitioning among different clades and even families (Fig. 20). We recognize unique plant communities in three main depositional environments: (i) active channel margins; (ii) abandoned channels; and (iii) floodplains. The latter setting is further subdivided into: (iv) floodplain channels; (v) swamps, marshes, and mires; and (vi) shallow lakes. However, as landforms are in a state of flux in fluvial systems, a continuum exists among these settings and the vegetation they supported. For example, plants fringing an active channel will persist long after abandonment, and will continue to supply litter to the abandoned channel. In addition, channel avulsion through a floodplain will result in the sudden juxtaposition of floodplain communities against an active channel. Where possible, the proposed reconstruction takes these dynamics into account.

2.7.1. Active Channel Margins

Large woody debris in active channels is primarily derived from riparian vegetation that collapses due to bank undercutting or bar erosion during major flood events, lateral migration, or avulsion (Scheihing & Pfefferkorn, 1984; Murphy & Koski, 1989; Spicer, 1989; Latterell & Naiman, 2007). Accordingly, we interpret the molds of large logs scattered through channel deposits along Lobeč cliff as the remnants of tall cordaitalean trees that occupied the flanks of active braided channels, a scenario documented elsewhere in Pennsylvanian fluvial strata adjacent to uplands (Falcon-Lang & Scott, 2000; Bashforth, 2005; Falcon-Lang & Bashforth, 2004, 2005; Falcon-Lang, 2006a; Gibling et al., 2010; Chapter 4). The deep vertical taproot or wide lateral rootplate of the cordaitaleans facilitated growth in unconsolidated but stable sands and gravels (Falcon-

Lang & Bashforth, 2004, 2005), and although channel flanks were frequently overtopped, the sediment coarseness resulted in rapid drainage when water levels dropped (Naiman & Décamps, 1997).

That tall cordaitaleans rimmed active channels is supported by the composition of megafloral assemblages at Lobeč (LB-1), where the remains of a low-diversity community were shed into an abandoned minor channel (Fig. 15). The absence of upright axes and rarity of roots in the strata imply that foliage was largely derived from vegetation on channel margins. The taphocoenosis is dominated by *Cordaites*, which typically are entire and show no evidence of mechanical or biological degradation, suggesting direct input to ponded waters after abscission. The marattialean tree fern *Lobatopteris* sp. B likely formed a scattered low canopy (Morgan, 1959; DiMichele & Phillips, 2002) where gaps let in more light, and the lyginopteridalean *Eusphenopteris nummularia* either crept along the forest floor or was lianescent (Shadle & Stidd, 1975; Laveine, 1993; DiMichele et al., 2006b).

Evidence from Janov indicates that active channel margins also supported stands of medullosalean pteridosperms. Channel sandstones contain abundant recurved pteridosperm axes (Fig. 10E), presumably derived from channel-flanking vegetation that toppled during bank erosion. *Linopteris neuropteroides* pinnules, which dominate in overlying abandoned minor channel deposits (Unit A), probably were stripped from the same plants after they fell over. An upright tree of possible pteridosperm affinity rooted atop a sandstone mound (Fig.11A to C) supports the interpretation that medullosalean pteridosperms inhabited raised and better-drained substrates along channel margins. Monospecific clumps of *L. neuropteroides* or *Neuropteris plicata* likely comprised low but dense canopies (Laveine & Brousmiche, 1985; Zodrow & Cleal, 1988; Laveine et al., 1993; Zodrow et al., 2007).

2.7.2. Abandoned Channels

Frequent inundation by floodwaters ensured that abandoned channels were dynamic environments. Not surprisingly, megafloral assemblages are characterized by pioneering communities or opportunistic vegetation capable of enduring repeated disturbances and sediment aggradation. Progressive shallowing and eventual exposure lead to a succession of seres, with early stage sphenopsids supplanted by a secondary stage of fern dominance.

2.7.2.1. Abandoned Mainstem Channels

At Vranov, shallowing after flood-induced sand incursions permitted colonization of an abandoned mainstem channel (Fig. 12C) by a spatially and temporally heterogeneous array of marattialean tree-fern-dominated communities. *Pecopteris raconensis*, *Lobatopteris* sp. A, and *Acitheca polymorpha* formed a low canopy above subarborescent *Calamites* (Hirmer, 1927; Barthel, 1980; Daviero & Lecoustre, 2000) bearing *Annularia carinata* foliage in JV-1, an essentially monospecific stand of *A. polymorpha* (Zodrow et al., 2006) colonized JV-2, and *Lobatopteris* sp. A stood above a thicket of *Sphenophyllum emarginatum* (Batenburg, 1977, 1981) in JV-3.

At Rozdělov (Fig. 18), *Annularia carinata* and *Sphenophyllum emarginatum* established in shallow waters along the margin of an abandoned mainstem channel. With increased exposure, a low canopy of marattialean ferns (*Acitheca* sp. A, *Pecopteris* spp.) rose above the sphenopsids. Thereafter, communities dominated by medullosalean pteridosperms (*Linopteris neuropteroides*, *Callipteridium rubescens*, *Neuropteris plicata*, *Neurocallipteris planchardii*) or co-dominated by pteridosperms and ferns, both with low canopies, became prominent. They may have occupied better-drained and relatively stable substrates, such as mounds in the abandoned channel or raised banks along its flanks.

2.7.2.2. Abandoned Minor Channels

At the railway tunnel site, a (par)autochthonous assemblage dominated by low-stature vegetation provides insight into marsh-like communities that colonized abandoned minor channels. The marattialean fern *Pecopteris* sp. G formed a low and sparse canopy above a dense carpet of groundcover species, including thickets of *Sphenophyllum oblongifolium* (Galtier & Daviero, 1999), the rampant zygopterid fern *Alloiopteris erosa* (Galtier, 2004; Phillips & Galtier, 2005), the rhizomatous gleicheniacean fern *Oligocarpia gutbieri* (Stevens & Hilton, 1999), and the scrambling or climbing, callistophytalean pteridosperm *Dicksonites sterzelii* (Rothwell, 1981; Galtier & Béthoux, 2002; Krings et al., 2003; DiMichele et al., 2006b). This pioneering community probably colonized newly exposed sediment in the abandoned channel (rather than channel margins), with abscission and/or burial during flooding, rather than wind transport (cf. Scheihing, 1980), accounting for the abundance of groundcover taxa.

2.7.3. Floodplains

Differences in microelevation and drainage conditions resulted in the heterogeneous distribution of floodplain vegetation. Palynological spectra, along with multivariate analysis of megafloral assemblages (Fig. 20), indicate that various ferns and sphenopsids dominated most clastic substrates. At the gully site (Fig. 16), the marattialean fern *Lobatopteris* sp. A may have formed nearly monospecific stands that persisted on damp soils adjacent to shallow floodplain ponds. Associated cordaitalean foliage was probably derived from trees growing alongside channel margins. In contrast, at Olovnice, the tree ferns *Cyathocarpus* sp. A and *Lobatopteris* sp. A coexisted as a low canopy above thickets of *Sphenophyllum emarginatum* and *Sphenophyllum oblongifolium*.

2.7.3.1. Floodplain Channels

Although pteridosperms are rare in megafloral assemblages from floodplain strata, palynological evidence indicates that they occupied slightly elevated, better-drained areas. At Lobeč (LB-4), medullosalean pollen is exceptionally abundant in floodplain channel deposits, suggesting that the parent plants formed monospecific stands along the raised margins of narrow sluggish channels traversing floodplains.

2.7.3.2. Swamps, Marshes, and Mires

Waterlogged soils in topographically low-lying parts of floodplains supported vegetation adapted to swamps, marshes, and ephemeral mires. The virtual absence of lycopsid remains in abandoned channel deposits implies that the group was centered in swamps and forested mires, consistent with their paleoecological preferences (Phillips & DiMichele, 1992; DiMichele & Phillips, 1994). This is confirmed by palynology, which shows that sphenophylls and various fern families also were prominent.

Palynological and megafloral assemblages from Lobeč (LB-2) provide insight into the composition of swamp, marsh, and mire vegetation. Sphenophyll spores dominate marsh deposits (Units D and F; Fig. 14A), indicating rather open conditions, with a dense swath of groundcover plants punctuated by scattered herbaceous and arborescent lycopsids and marattialean tree ferns. DiMichele et al. (1979) documented comparable low-stature communities in broadly coeval non-forested mires in the USA. In contrast, the abundance of "*Lepidodendron*" *subdichotomum* remains in Unit B implies that swamps were dominated by arborescent lycopsids with few understory or groundcover plants. The spore assemblage from the coal seam (Unit E) indicates that mires were forested and dominated by marattialean tree ferns that formed a low canopy below emergent, arborescent lycopsids. Autochthonous stems above the coal seam (Fig. 14B), which contains numerous clastic partings near the top, attest to the prevalence of marattialean ferns in terminal nutrient-rich phases of mire development.

Palynological data from Lobeč (LB-2 and 3) also provide evidence for habitat partitioning among the arborescent lycopsids. Palynomorphs in the coal seam at LB-2 (Unit E; Fig. 14A) indicate that the diaphorodendrid "*Lepidodendron*" *subdichotomum* (producing *Cappasporites* miospores and *Cystosporites diabolicus* megaspores) was far more abundant than *Lycospora*-producing lepidodendrids in forested mires, particularly considering the fact that diaphorodendrids are greatly underrepresented in palynological assemblages due to their low but extended reproductive output (DiMichele & Phillips, 1985; Phillips & DiMichele, 1992; Willard, 1993). In contrast, clastic sediments yielded more lepidodendrid than diaphorodendrid spores. These observations corroborate the paleoecological amplitudes interpreted for these lycopsids, which have diaphorodendrids centered in mires and lepidodendrids preferring nutrient-enriched settings (DiMichele & Phillips, 1994).

2.7.3.3. Shallow Lakes

Shallow lake margins were dominated by sphenopsids, particularly by calamiteans. In lacustrine strata at Janov (Unit C; Fig. 10E), subarborescent *Calamites* bearing *Annularia carinata* foliage stood above a thicket-forming groundcover of *Sphenophyllum mirosoviense*. Similarly, an essentially monospecific stand of *Annularia* "*spicata*" colonized lake margins at Nelahozeves.

2.8. TEMPORAL CHANGES IN COMMUNITY COMPOSITION

The relative abundances of the eight main plant groups were compiled for the nine localities/sites (Fig. 22) to look for changes in community composition on the Nýřany Member braided-river plain over its ≈2.0 Ma duration. Direct comparison is challenging because megafloral assemblages are neither isotaphonomic nor derived from equivalent taphofacies (*sensu* Behrensmeyer et al., 2000). Furthermore, local- and regional-scale vegetation patchiness had a significant impact on assemblage composition. Consequently, it is difficult to distinguish evolutionary trends from ecological noise. Despite these biases in the dataset, broad floristic patterns may be evident because biostratigraphic changes are minimal through the Nýřany Member, all megafloral assemblages were derived from communities that inhabited disturbance-prone clastic substrates, and most taphocoenoses are interpreted as (par)autochthonous.

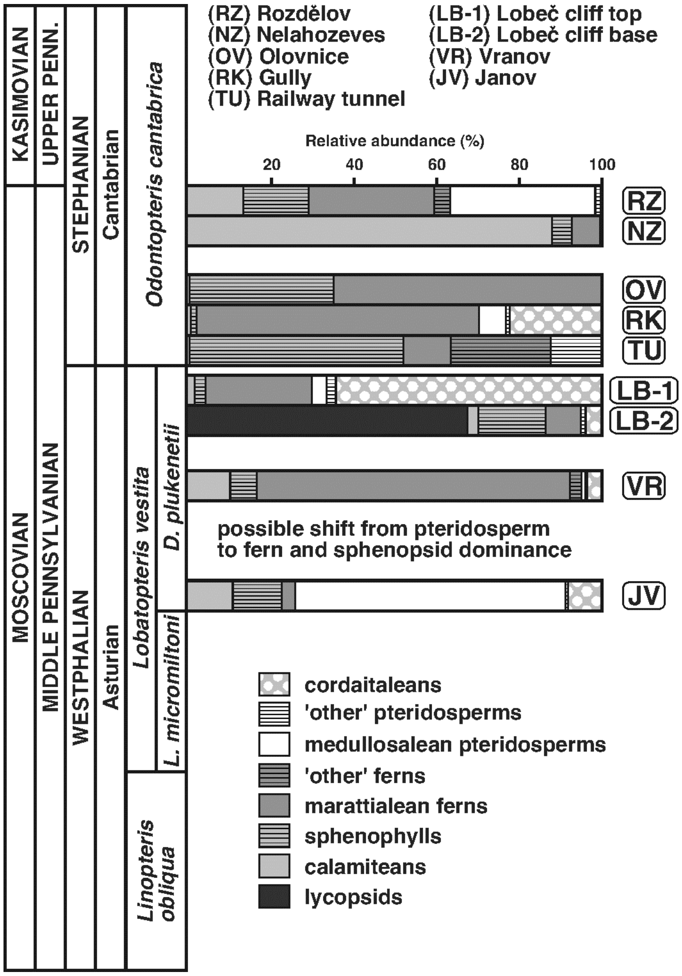


Figure 22. Relative abundances of eight plant groups at nine localities/sites. Note speculative shift from medullosalean pteridosperm dominance to fern and/or sphenopsid dominance in late Asturian (early to middle *Dicksonites plukenetii* Subbiozone).

The ferns, particularly arborescent forms, are most prominent, and either dominate (VR, RK, OV) or co-dominate with the sphenophylls (TU) or sphenopsids and medullosalean pteridosperms (RZ). A single group dominates at other localities/sites: calamiteans at NZ, lycopsids at LB-2, medullosalean pteridosperms at JV, and cordaitaleans at LB-1. Despite compositional disparities, the relative abundance of medullosalean pteridosperms seems to decline sharply above the Mirošov Horizon (JV), after which ferns and sphenopsids dominate or co-dominate at all but two localities/sites (LB-2 and LB-1). Provisionally, the evidence thus suggests a broad shift in community composition in the late Asturian (early to middle *Dicksonites plukenetii* Subbiozone), with medullosalean pteridosperms being replaced by fern- and/or sphenopsid-dominated communities that persisted into the middle(?) Cantabrian. The changeover presumably coincides with an increase in habitats favored by ferns and sphenopsids, such as floodplains and abandoned channels. This is consistent with temporal changes in the fluvial system identified by Opluštil et al. (2005), which imply a reduction in flow energy and grain size and an increase in sinuosity and proportion of fine-grained facies.

Šimůnek (2004) and Opluštil & Cleal (2007) documented changes in species richness through the CWB, and noted that the middle Nýřany Member was more diverse than upper and lower parts (Fig. 6). They concluded that changes largely reflect a sampling bias due to preferential exploitation of coals of the Nýřany and Chotíkov groups, a result confirmed by reanalysis of species richness using the macrofloral species list of Pešek (2004, table 2; Fig. 8). Ferns are more diverse above the Mirošov Horizon (Touškov coal seam group), corresponding with their increase in relative abundance (Fig. 22). In contrast, pteridosperm diversity remains high up to the top of the Chotíkov coal seam group, well above their speculative decline in relative abundance. The general trend of increased diversity and relative abundance of ferns, at the expense of pteridosperms, continues into the Týnec Formation (Opluštil & Cleal, 2007).

2.9. DISCUSSION

2.9.1. Comparison with Riparian Vegetation in Modern Fluvial Environments

The distribution of riparian vegetation is complex in modern fluvial environments, reflecting the dynamics of lotic ecosystems. Habitable landforms and geomorphic surfaces constantly change due to ongoing fluvial and ecological processes (Swanson et al., 1988), resulting in a patchy mosaic of plant communities of variable composition and at different successional stages (Gregory et al., 1991; Naiman et al. 2000). Physical heterogeneity of the drainage network is maintained by flood-induced disturbances operating at various temporal and spatial scales (Osterkamp & Hupp, 1984; Pollock et al., 1998; Rot et al., 2000), and intermittent habitat destruction or disruption and recovery renders riparian communities equally heterogeneous (White, 1979; Harris, 1987). As a result, vegetation has a high degree of structural and compositional diversity, which is sustained by the spatial heterogeneity of microhabitats and landforms, local climate variations related to elevation changes or substrate conditions, lateral migration of rivers, and by the frequency, magnitude, duration, and spatial distribution of flooding (Gregory et al., 1991; Barrat-Segretain & Amoros, 1996; Pollack et al., 1998; Naiman et al., 2000; Rot et al., 2000). Consequently, a myriad of species with different reproductive strategies and physiological requirements, or different seral communities, coexist in proximity (Denslow, 1985, Naiman & Décamps, 1997).

Gregory et al. (1991) distinguished two types of ‘reach’ in fluvial environments. ‘Constrained reaches’ have a single, straight channel confined to a narrow valley by adjacent slopes. During floods, the stream channel is relatively fixed in a narrow floodplain, resulting in fewer habitable geomorphic surfaces. In contrast, braided channels, extensive floodplains, and broad riparian zones characterize ‘unconstrained reaches’, which contain numerous geomorphic surfaces due to widespread and frequent flooding. As expected, plant communities have a heterogeneous distribution and comprise patches of various ages.

From a sedimentological perspective, the Nýřany Member braided-river plain clearly accumulated in unconstrained reaches. Strata were laid down on an incompletely peneplained plateau punctuated by sporadic topographic highs, and braided channels were prone to lateral migration rather than confined to narrow paleovalleys between bedrock ridges. Floodplain strata are rarely preserved, but the prevalence of intraformational clasts in channel deposits and the abundance and diversity of palynomorphs derived from waterlogged habitats point to the prior existence of broad floodplains. Consistent with unconstrained reaches, floodplains resulting from regional avulsion contained numerous landforms, including floodplain channels, swamps, mires, and shallow lakes in low-lying areas, and oxidized sediment in well-drained areas. Together with abandoned channels that developed after local avulsion, an ever-changing mosaic of habitats was available for colonization.

Statistical and taphonomic analyses show that the Nýřany Member braided-river plain was blanketed by a patchwork of low-diversity plant communities at various scales, and that habitats were partitioned among major plant groups. These observations are consistent with the distribution of riparian vegetation in modern, disturbance-dominated lotic ecosystems. Characteristic species assemblages occupy different geomorphic surfaces (e.g., active channel margins, abandoned channels, floodplains), and community distribution is controlled by the frequency and intensity of flooding over those surfaces (Osterkamp & Hupp, 1984; Harris, 1987; Rot et al., 2000). In addition, microelevation differences on landforms impact the frequency and spacing of disturbances and the distribution of communities they support (Pollock et al., 1998). The heterogeneity of riparian vegetation on the dynamic Nýřany Member braided-river plain was undoubtedly controlled by these basic factors.

Modern fluvial environments in tropical regions are renowned for their high diversity (Godoy et al., 1999), particularly in reaches with high habitat complexity (Salo et al., 1986). In contrast, our data indicate that comparable Middle Pennsylvanian settings supported a mosaic of monospecific and low-diversity communities, a fundamental difference that warrants discussion. The scale of investigation is of utmost importance; modern ecosystems can have low diversity at small scales, but high diversity at landscape scales (Reed et al., 1993; Pollock et al., 1998; Godoy et al., 1999). Likewise, the low-diversity taphocoenoses we observed were undoubtedly derived from higher diversity community associations, a point emphasized by the number of taxa in palynological assemblages but absent in megafloral assemblages. Taphonomy surely played a significant role, with biostratinomic and diagenetic processes ensuring that only a fraction of the original vegetation was preserved. Furthermore, the angiosperms, which dominate most modern plant biomes, had yet to arrive on the scene. However, despite such preservational and evolutionary megabiases, we maintain that a patchwork of low-diversity stands characterized Middle Pennsylvanian disturbance-dominated regimes in paleoequatorial regions, representing a radical departure from modern riparian communities in the tropics. Wing & DiMichele (1995) noted similar features in late Paleozoic and early Cenozoic wetland vegetation in basinal lowlands. They suggested that low diversity was inherent to wetlands, and reflected geologically early colonization and ecological 'saturation' in terms of the number of taxa capable of coexisting under such difficult edaphic conditions.

2.9.2. Comparison with the Patch Dynamics Concept

The Patch Dynamics Concept strives to explain the effects of disturbance on the structure and dynamics of communities (Pickett & White, 1985). Townsend (1989) applied the theory to fluvial ecosystems, and produced a habitat template (Fig. 23) relating diversity and differences in community structure to spatial variation (i.e., microhabitat heterogeneity) and temporal variation (i.e., disturbance frequency). Our reconstruction of the braided-river plain vegetation and position of the main plant groups (Figs 20, 21) is compared with this model to clarify the structure and organization of the riparian communities.

We have argued that the Nýřany Member braided-river plain was a dynamic environment characterized by frequent flooding and an ever-changing medley of habitable microhabitats. These features correspond to high spatial and intermediate temporal variation on the habitat template (Fig. 23). According to Townsend (1989), intermediate levels of disturbance, combined with significant microhabitat heterogeneity, produce high-diversity communities, either resulting from a mosaic of patches at different

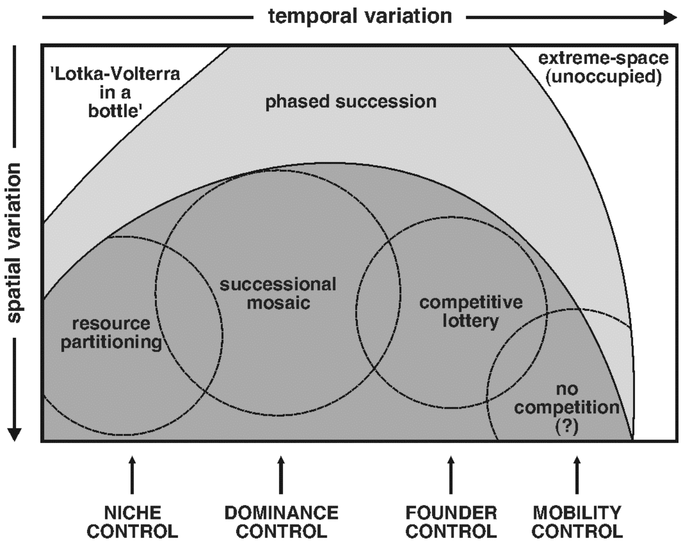


Figure 23. Schematic illustration of Patch Dynamics Concept, demonstrating how spatial variation (microhabitat heterogeneity) and temporal variation (disturbance frequency) relate to diversity and affect community structure. Darker shading represents greater species richness. Competitive exclusion in homogenous, unchanging environments results in extremely low species richness (‘Lotka-Volterra in a bottle’), but an increase in spatial variation and resource partitioning allows more species to coexist in ‘niche-controlled’ communities. At intermediate levels of temporal variation and increased microhabitat heterogeneity, high diversity may result from a mosaic of patches at different successional stages (‘dominance-control’) or a competitive lottery (‘founder control’). In a continuously changing landscape, ‘mobility-controlled’ communities contain itinerant organisms moving between habitable locales (not applicable to vegetation, which is sedentary). An intermediate level of temporal variation in a homogeneous environment is characterized by lower diversity in communities controlled by ‘phased succession’. Settings faced with unrelenting disturbances may be unoccupied (‘extreme-space’). After Townsend (1989, fig 1).

successional stages (‘dominance-control’) or a competitive lottery (‘founder-control’). ‘Dominance-controlled’ communities contain one or more species that are strongly competitively superior to all others, particularly (K-selected) species that can tolerate low resource levels, and that can reach maturity in the presence of earlier (r-selected) species that they eventually outcompete (i.e., seres). Where habitat destruction or disruption is more frequent, ‘founder-controlled’ communities comprise fast-growing opportunistic (r-selected) taxa with similar competitive abilities. The suite of taxa in the pre- and post-disturbance communities may differ due to a ‘competitive lottery’ during recovery (Sale, 1977; Cheson & Warner, 1981; Barrat-Segretain & Amoros, 1996).

Intuitively, the magnitude, frequency, and duration of flooding diminish laterally away from active channels, and at increasing elevation above the channel surface (Osterkamp & Hupp, 1984; Harris, 1987; Gregory et al., 1991; Rot et al., 2000). It follows that abandoned channels and low-lying floodplains on the braided-river plain were inundated more often and for longer intervals than elevated floodplains or raised channel banks. The patch dynamics model predicts that more diverse communities comprising fast-growing, opportunistic (r-selected) species inhabit disturbance-prone landforms (abandoned channels, low-lying floodplains), whereas more stable landforms (raised channel banks, well-drained floodplains) support less diverse communities dominated by K-selected species. When compared with the ecological gradients identified by multivariate analysis (Fig. 20), these premises support our interpretations on the spatial arrangement of the plant groups (Fig. 21). Opportunistic and primarily spore-producing taxa, which plot in the domain of unstable and wetter substrates, are more abundant in frequently disturbed locales, particularly in abandoned channels and low-lying floodplains. These pioneering communities could be termed ‘founder-controlled’ (Fig. 23), and the persistence of flood-induced habitat destruction or disruption probably lead to frequent turnover that maintained their heterogeneous distribution and diversity. In comparison, the slow-growing gymnosperms, which plot in the domain of stable and better-drained substrates, dominated on raised active channel banks and alongside floodplain channels where habitat perturbations were less frequent. These monospecific or low-diversity communities may have been ‘dominance-controlled’ (Fig. 23). Patterns of vegetational succession observed in abandoned channel fills, from sphenopsid- to fern- to pteridosperm-dominated communities, presumably reflected decreasing flood frequency and increasingly drier and more stable substrates (Bornette & Amoros, 1996). Although modern ‘founder-’ and ‘dominance-controlled’ riparian communities have high diversity, their Middle Pennsylvanian counterparts were typified by a mosaic of low diversity stands.

2.9.3. Changing Floristic Patterns through the Latest Middle Pennsylvanian

Increased drying through the latest Middle Pennsylvanian presaged a major climatic shift at the Middle to Late Pennsylvanian (Moscovian-Kasimovian) boundary (Phillips & Peppers, 1984; Frakes et al., 1992; Gastaldo et al., 1996; Fielding et al., 2008a, b). Mirroring these climatic changes, tree ferns became increasingly abundant in mires after the middle Asturian, and at the Middle to Late Pennsylvanian boundary, replaced lycopsids as the dominant peat-forming vegetation over parts of the tropics (Phillips et al., 1974, 1985; DiMichele & Phillips, 1996a, b; Pfefferkorn et al., 2008; DiMichele et al., 2009a). The changeover was thought to be broadly synchronous over Euramerica, although it is evident that other factors played a significant role in the timing, or even the existence, of this reorganization event (Cleal & Thomas, 2005; Dimitrova & Cleal, 2007; Opluštil & Cleal, 2007; Cleal et al., 2009).

Vegetation on clastic substrates also experienced changing dominance-diversity patterns during the latest Middle Pennsylvanian. Pfefferkorn & Thomson (1982) analyzed adpression assemblages from Pennsylvanian strata of Euramerica, and recognized a prominent middle Asturian shift in community composition. Pteridosperms and sphenopsids dominated below this level, and marattialean tree ferns became more prevalent in the late Asturian. They concluded that clastic wetland and mire vegetation responded similarly to climatic drying, but that a pronounced rise in arborescent fern abundance occurred earlier on clastic soils.

Cleal (2007) compiled the relative abundance data of Davies (1929) and North (1935) for Asturian and early Cantabrian megafloral assemblages in the South Wales Coalfield, UK. Pteridosperm and fern remains dominate, but floristic changes are masked because both plant groups were combined in the early studies. Scrutiny of the original data set (e.g., Davies, 1929, chart 2) indicates that pteridosperms comprise almost all of the ‘fern-pteridosperm complex’ (Dimitrova et al., 2005), and that marattialean tree ferns only became noticeable in the late Asturian when several new fern and pteridosperm species appeared according to species richness data (Cleal, 2007). Pteridosperms are the most diverse group in impoverished megafloral assemblages in upper Asturian to lower Cantabrian strata of the Pennines Basin, UK (Cleal, 2005, 2008a), and in contemporaneous deposits in the Upper Silesian Basin, Poland (Opluštil & Cleal, 2007). In the Czech part of the Intrasudetic Basin, low-diversity characterizes the late Asturian, and fern and pteridosperm diversity increases in the middle Cantabrian (Šimůnek, 2004; Opluštil & Cleal, 2007). Finally, Uhl & Cleal (2010) documented increased species richness in arborescent tree ferns, sphenophylls, and various pteridosperms in late Asturian strata of the Saarland Coalfield, Germany.

This brief review corroborates the conclusions of Pfefferkorn & Thomson (1982) that Euramerican clastic wetland communities experienced a prominent floristic shift during the middle to late Asturian. Relative abundance and/or species richness data indicate that arborescent ferns proliferated at a level corresponding to the base of the *Lobatopteris vestita* Biozone or the *Dicksonites plukenetii* Subbiozone (Cleal, 2007), consistent with the speculative changeover observed in the Nýřany Member (Figs 8, 22). In most basins, however, fern expansion was not at the expense of the pteridosperms, which remain the most abundant and diverse group in most latest Middle Pennsylvanian megafloral assemblages. The Nýřany Member may be a notable exception, as pteridosperm relative abundance seems to decline dramatically at a level coincident with the fern radiation (Fig. 22). The disparity may be related to the intramontane position of the CWB, or to the fact that taphocoenoses studied represent communities adapted to a high-energy, disturbance-prone environment.

2.10. CONCLUSIONS

The braided-river plain of the late Asturian to middle(?) Cantabrian Nýřany Member was a dynamic environment, with frequent flooding, combined with local and regional avulsion, resulting in an ever-changing mosaic of habitable landforms. As in modern fluvial systems, riparian vegetation had a heterogeneous distribution that reflected life in a disturbance-prone setting, and patchiness occurred at a variety of scales. Most communities comprised monospecific or low-diversity stands, a fundamental departure from the high diversity characteristic of modern lotic ecosystems. The spatial organization of communities was a response to the complex interplay between substrate conditions and the life history strategies of various plant groups. Pioneering, 'founder-controlled' communities comprising opportunistic species were most common in flood-prone abandoned channels and low-lying floodplains, whereas 'dominance-controlled' communities containing slow-growing site-occupiers preferred raised, stable banks fringing active channels.

2.11. ACKNOWLEDGMENTS

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CHAPTER 3: VEGETATION HETEROGENEITY ON A LATE PENNSYLVANIAN BRAIDED-RIVER PLAIN DRAINING THE VARISCAN MOUNTAINS, LA MAGDALENA COALFIELD, NORTHWESTERN SPAIN

Arden R. Bashforth, Howard J. Falcon-Lang, and Martin R. Gibling

3.1. ABSTRACT

The spatial heterogeneity and community ecology is reconstructed for Late Pennsylvanian (Stephanian B *sensu lato*) vegetation preserved in La Magdalena Coalfield, northwestern Spain. The ≈1500 m thick basin-fill accumulated rapidly along the margin of the Variscan Mountains, and the principal sedimentary facies comprise the deposits of large braided streams that dissected extensive wetlands containing large lakes. Quadrat analysis of 93 mostly (par)autochthonous megafloral assemblages indicates that pteridosperms and ferns dominated communities, with three taxa (*Pecopteris* spp., *Callipteridium pteridium*, and *Neuropteris ovata*) accounting for ≈58% of all plant remains. Sphenopsids and lycopsids were less common but widespread, and cordaitaleans were rare. At the local scale, laterally exposed bedding planes reveal that communities comprised a complex and heterogeneous mosaic of species. At the landscape scale, ecological gradients are evident from multivariate analyses of quadrats in a facies context. Pteridosperms dominated marginal wetlands adjacent to steep basin margins. A greater proportion of ferns occurred in or adjacent to braided channel belts, consistent with their opportunistic growth and prolific reproductive capacity, characteristics advantageous in frequently disturbed habitats. In interfluve wetlands

distant from channel influence, communities consisted of low-diversity or monospecific patches of slow-growing pteridosperms enclosed in a fern-dominated matrix. Pteridosperms in interfluve wetlands were arranged along an environmental gradient: *Alethopteris* and *Pseudomariopteris* preferred more disturbed sites, *Neuropteris*, *Linopteris*, and *Odontopteris* occupied more stable settings, and *Callipteridium* was cosmopolitan. Ephemeral wetland swamps were dominated by tree ferns with lesser *Sigillaria*, and *Omphalophloios* was a major constituent in long-lived rheotrophic mires that resulted in thick coal seams. In addition to improving knowledge of Late Pennsylvanian tropical ecosystems in marginal settings, the findings demonstrate how the spatial structure of ancient plant communities can be reconstructed from multiple quadrats sampling a vertical succession.

3.2. INTRODUCTION

Peat-forming tropical rainforests that spanned the Pennsylvanian equator are one of the best-understood ecosystems in the fossil record. These 'Coal Forests' are portrayed in museum dioramas the world over, and have become an icon for this interval of Earth history. However, despite the fact that some mires covered enormous areas (Greb et al., 2003) and re-occurred throughout the Pennsylvanian (318 to 299 Ma), global compilations of coal deposits show that Coal Forests occupied only a fraction of terrestrial landscapes (e.g., Cleal & Thomas, 2005, fig. 4). The majority of land surfaces either comprised depositional environments unfavorable to peat accumulation, or were elevated regions that experienced net erosion. Even in coastal wetlands where widespread mires did periodically develop, their tenure was relatively short-lived due to the effects of high-frequency climate rhythms on a 10^5 year-scale linked to orbital cycles (Falcon-Lang, 2004a; Falcon-Lang et al., 2009).

In comparison with Early to Middle Pennsylvanian (Bashkirian to Moscovian) tropical ecosystems, Late Pennsylvanian (Kasimovian to Gzhelian) plant communities are poorly resolved (Willard et al., 2007). This is significant because there was a major reorganization in wetland vegetation near the Middle to Late Pennsylvanian boundary, with tree ferns replacing lycopsids as the dominant peat-forming clade over parts of tropical Pangea (Phillips et al., 1974, 1985; DiMichele & Phillips, 1996a; DiMichele et al., 2001). Current debate is centered on whether this changeover was broadly coincident with a major climate shift (Phillips & Peppers, 1984; DiMichele et al., 2009a), or if reorganization was diachronous and related to regional tectonism and increased sediment production (Cleal & Thomas, 2005).

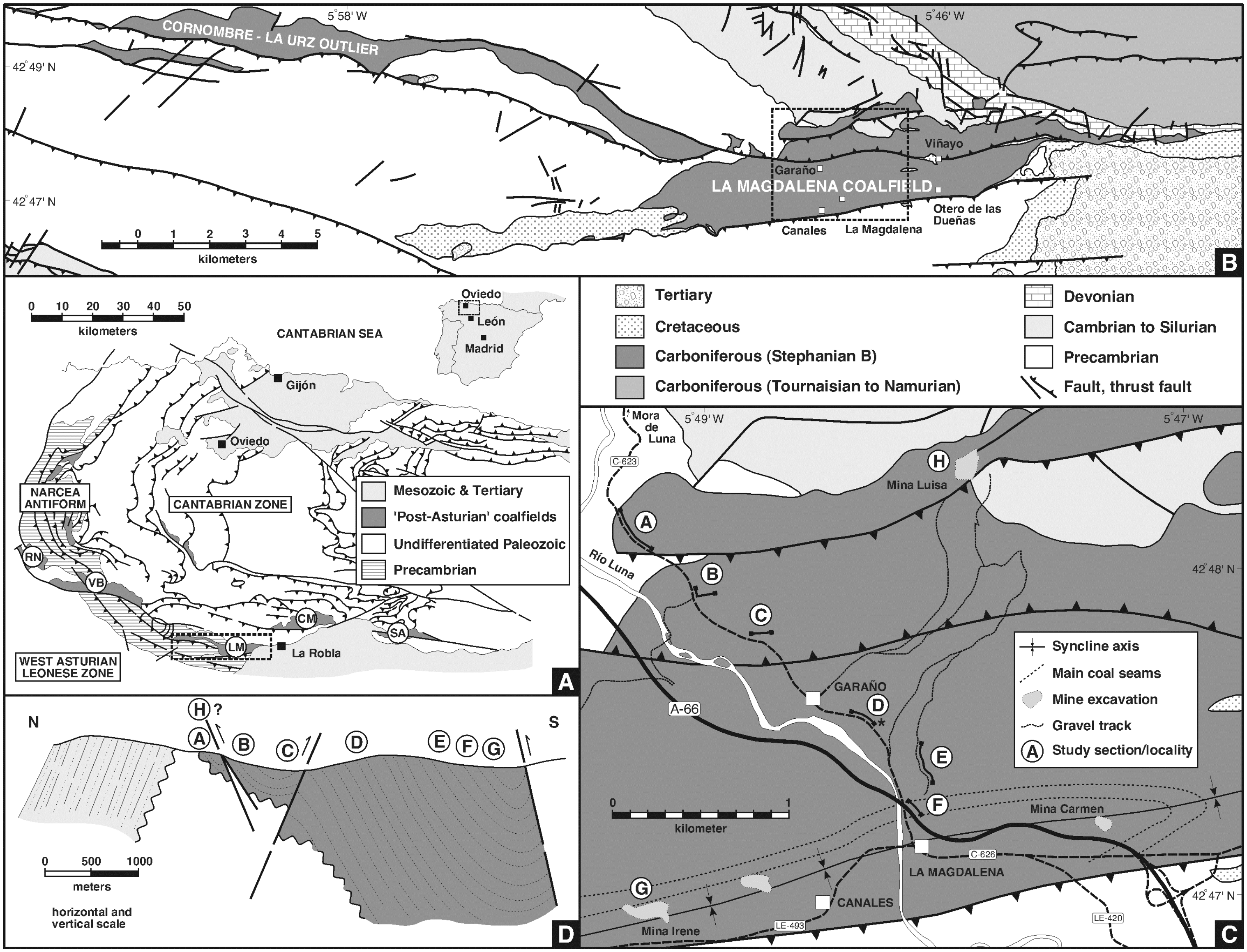
This paper presents a paleoecological study of the Late Pennsylvanian (middle to late Kasimovian, ≈305 Ma) La Magdalena Coalfield of northwestern Spain, which was situated in the foothills of the Variscan Mountains. This work improves understanding of the Pennsylvanian tropical biome in two key ways. First, it sheds light on poorly known plant communities that occupied marginal parts of basins (e.g., Iwaniw, 1985; Bashforth, 2005; Falcon-Lang, 2006a), which were characterized by high-energy environments and negligible peat accumulation. Second, the study helps to constrain the nature of ecosystems that followed the Middle to Late Pennsylvanian reorganization event. Furthermore, by using a quantitative quadrat approach based on collections at tens of stratigraphic intervals, the study captures the spatial heterogeneity and landscape gradients in these communities. Such phenomena are usually only discernible when plants were buried instantly (T^0 assemblages; e.g., Gastaldo et al., 2004a, b; DiMichele et al., 2007; Libertín et al., 2009a; Opluštil et al., 2009a). Thus, the method offers a new way to reconstruct the structure of ancient vegetation using quantitative studies of plant assemblages in vertical succession.

3.3. GEOLOGICAL SETTING

La Magdalena Coalfield is situated on the southern flank of the Cantabrian Mountains in north-central León province, northwestern Spain. It is one of several coalfields in the region that contain middle to upper Stephanian (middle Kasimovian to Gzhelian) strata unconformably overlying rocks assembled during the Variscan Orogeny (Fig. 24A; Martínez-García, 1990; Ábalos et al., 2002; Colmenero et al., 2002). These coalfields originated following a middle Barruelian (lower Kasimovian) tectonic event termed the 'Asturian Phase' (*sensu* Wagner, 1966). They roughly parallel the arcuate trend of Variscan structures, and contain successions that become progressively younger westward.

The disjunct nature of the coalfields led to their interpretation as isolated intramontane basins (e.g., Heward, 1978a; Colmenero et al., 1996, 2002; Ábalos et al., 2002). However, they are more likely tectonic and erosional remnants of a large, 'post-Asturian' foreland basin that drained northwards and eastwards toward the western end of the Paleotethys Ocean (R.H. Wagner, unpublished data), with strata diachronously onlapping basement rocks due to progressive basin expansion (Evers, 1967; Wagner, 1970; Wagner & Winkler Prins, 1985). This scenario is supported by the occurrence of rare horizons with brackish faunas in the Sabero, Ciñera-Matallana, and La Magdalena

Figure 24. Geological context of La Magdalena Coalfield. A. Ibero-Amorican arc in northwestern Spain, indicating position of Cantabrian Zone, Narcea Antiform, and West Asturian-Leonese Zone. Tectonic and erosional remnants of 'post-Asturian' foreland basin containing upper Stephanian deposits include (from east to west) Sabero (SA), Ciñera-Matallana (CM), La Magdalena (LM), Villablino (VB), and Rengos (RN) coalfields. Modified from Pérez-Estaún et al. (1988). B. Geological setting of La Magdalena Coalfield and Cornombre-La Urz outlier. After Leyva et al. (1984) and Martín Parra et al. (1989), with modifications based on Pulgar et al. (1999). C. Detailed map of study area in La Magdalena Coalfield, showing location of sections studied. D. Schematic cross-section across La Magdalena Coalfield, from north to south, indicating approximate stratigraphic position of sections studied. After Leyva et al. (1984), with modifications based on Pulgar et al. (1999).

5°58' W
5°46' W
CORNOMBRE - LA URZ OUTLIER
42°49' N
42°47' N
LA MAGDALENA COALFIELD
Viñayo
Garaño
Otero de las Dueñas
Canales
La Magdalena
0 1 2 3 4 5
kilometers
B
Tertiary
Cretaceous
Carboniferous (Stephanian B)
Carboniferous (Tournaisian to Namurian)
Devonian
Cambrian to Silurian
Precambrian
Fault, thrust fault
0 10 20 30 40 50
kilometers
CANTABRIAN SEA
Oviedo
León
Madrid
Gijón
Oviedo
NARCEA ANTIFORM
CANTABRIAN ZONE
Mesozoic & Tertiary
'Post-Asturian' coalfields
Undifferentiated Paleozoic
Precambrian
RN
VB
CM
SA
LM
La Robla
WEST ASTURIAN LEONESE ZONE
A
Mora de Luna
5°49' W
5°47' W
C-623
H
Mina Luisa
A
Río Luna
B
C
42°48' N
Syncline axis
Main coal seams
Mine excavation
Gravel track
A Study section/locality
GARAÑO
D
A-66
E
F
0 1
kilometer
Mina Carmen
C-626
LA MAGDALENA
G
CANALES
42°47' N
LE-420
LE-493
Mina Irene
C
N
S
H ?
A
B
C
D
E
F
G
0 500 1000
meters
horizontal and vertical scale
D

coalfields (Fig. 24A), implying periodic marine connections (Eagar & Weir, 1971; Knight, 1971; Iwaniw & Knight, 1981; Eagar, 1985), and by the diverse and cosmopolitan nature of megafloral species shared among the coalfields, which Wagner (1970, 1971a) considered indicative of paralic basins. Nonetheless, lithostratigraphic correlation between adjacent coalfields is challenging (Wagner & Artieda, 1970; Knight *in* Wagner, 1971b; Knight, 1974; Knight, 1983b), particularly since deposition took place along the flanks of a mountain belt with substantial topography. Thus, some of the coalfields may have been partly separated by intervening highs and elevated above sea level by a few tens or hundreds of meters.

La Magdalena Coalfield covers an area of ≈33 km^2 and extends 31.8 km in an east–west orientation, but is only 2.9 km wide at its broadest extent north of La Magdalena village (Fig. 24B, C). The origin of the coalfield is uncertain. Ábalos et al. (2002) concluded that it is an isolated intramontane basin that resulted from localized deformation along a deep, vertical fault, whereas Heward & Reading (1980) considered it to be a pull-apart basin related to strike-slip faulting. An alternative hypothesis is that it developed in proximal parts of the 'post-Asturian' foreland basin, with strata gradually filling paleorelief along the mountain front (R.H. Wagner, unpublished data). A distant marine connection is implied by thin intervals containing brackish bivalves high in the basin-fill (Heward, 1978a; Eagar, 1985).

The coalfield is subdivided into an eastern part, the focus of this study (La Robla 129/13–8 map sheet; Leyva et al., 1984), and a western part comprising the Cornombre-La Urz outlier (Riello 128/12–8 map sheet; Martín Parra et al., 1989; Fig. 24B). In La Magdalena Coalfield, basin-fill rests with angular unconformity atop lower Paleozoic strata of the Cantabrian Zone in the east and Precambrian strata of the Narcea Antiform in the west (Fig. 24A, B; Colmenero et al., 2002). It is bound by a steeply dipping thrust fault to the south (Fig. 24D; Leyva et al., 1984), and strata are folded into a syncline whose east-west axis lies close to the southern faulted margin (Fig. 24C, D). Rotation and local overturning of the succession occurred during the late Stephanian (R.H. Wagner, unpublished data) and/or Alpine Orogeny (Alonso et al., 1996, fig. 5, section V–V′; Pulgar et al., 1999). The basin-fill is ≈1500 m thick (Heward, 1978a, b), although minor thrust faults on the northern flank may repeat lowermost parts of the succession (Wagner, 1970; Leyva et al., 1984).

3.4. BIOSTRATIGRAPHY AND AGE

Determining the age of La Magdalena Coalfield and its correlation with the IUGS timescale (Davydov et al., 2004, 2010; Heckel & Clayton, 2006) is challenging because stratigraphic subdivision of the middle and late Stephanian is in a state of flux (Wagner, 1998; Wagner & Martínez-García, 1998, p. 103). To précis, proposals are underway to divide the Stephanian B Substage, as defined by IUGS, into two units (Fig. 25). The older unit would correlate with strata in the Carmaux Basin of the French Massif Central, and would be designated as the ‘Saberian substage’, equivalent to the *Alethopteris zeilleri* Biozone of Wagner (1984; unpublished data). The younger unit would represent the Stephanian B Substage (*sensu stricto*) as originally conceptualized in the St. Étienne Basin of the Massif Central, and would be equivalent to the *Sphenophyllum angustifolium* Biozone.

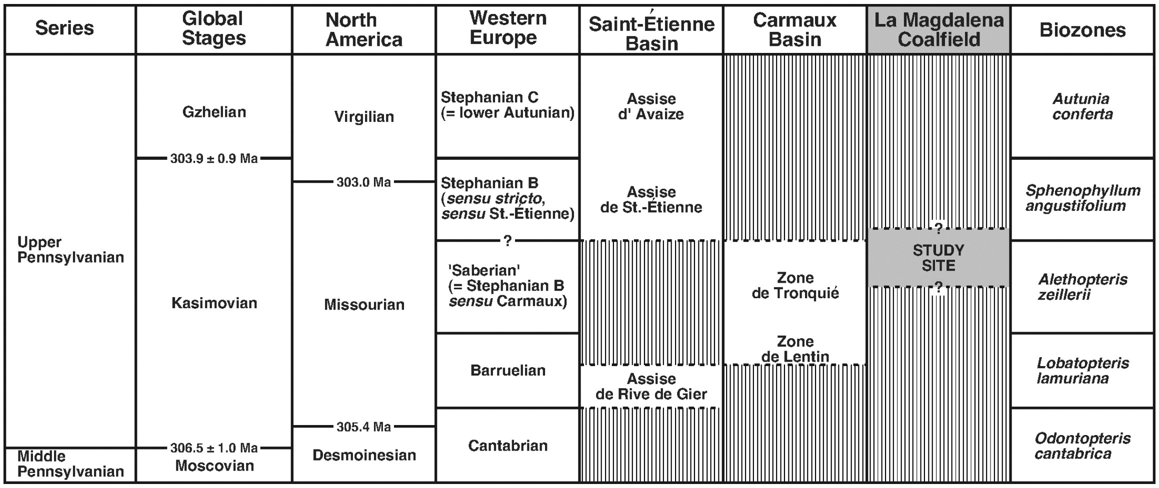


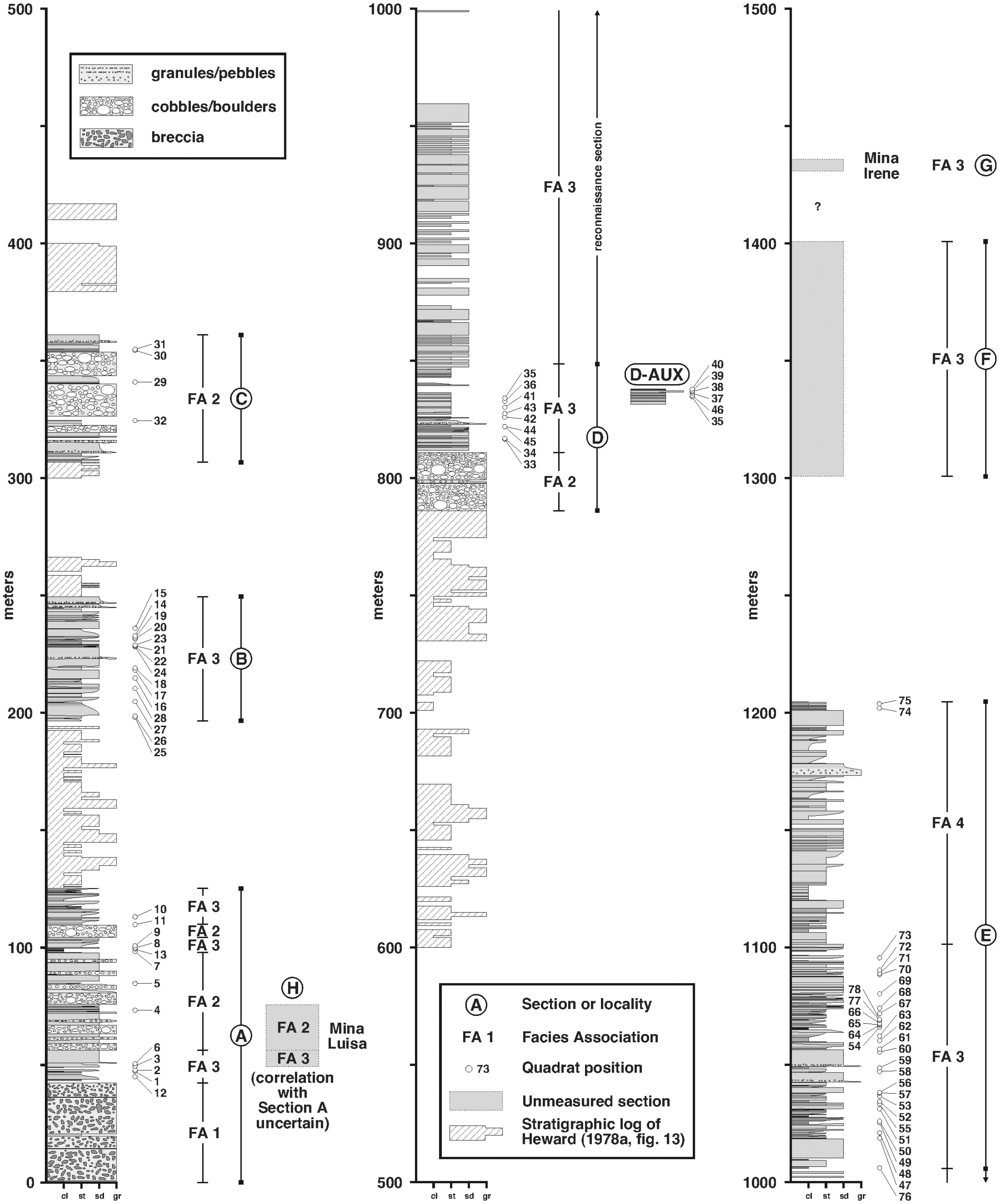
Figure 25. Correlation between global series and stages, North American and western European substages, strata of Saint-Étienne and Carmaux basins (Massif Central, France) and La Magdalena Coalfield, and megafloral biozones. Chart after Wagner (1998), position of global series and stages after Heckel and Clayton (2006) and Heckel (2008), and absolute ages after Davydov et al. (2004) and Heckel (2008). Stratigraphic interval in La Magdalena Coalfield after Castro (2005b). Vertical scale not uniform.

Within this stratigraphic context, Castro (2005b) assigned most of the basin-fill of La Magdalena Coalfield to the 'Saberian' based on megafloral assemblages, although upper parts may correspond to the lowest Stephanian B (Fig. 25). This interval encompasses the middle *Alethopteris zeilleri* to lowermost *Sphenophyllum angustifolium* biozones. Megafloral assemblages characteristic of the middle and upper *A. zeilleri* Biozone occur in the lower half of the Ottweiler Group in the Saar-Lorraine Coalfield (Cleal, 2008b). Tonstein 0 in the Wahlschied Seam (Dilsburger Formation) near the bottom of this unit has a radiometric age of 304.2±0.6 Ma (Davydov et al., 2004), and extrapolation of this tie-point using megafloral biozones implies that La Magdalena Coalfield is of middle to late Kasimovian age in IUGS nomenclature (Fig. 25). Both biostratigraphic and radiometric data allow <1 Ma for the interval encompassing the middle *A. zeilleri* to lower *S. angustifolium* biozones (Cleal, 2008b), inferring very rapid accumulation of strata in La Magdalena Coalfield. This assertion is supported by the fact that the most abundant taxa are present throughout the basin-fill (Castro, 2005b), with little evidence for evolutionary change in the flora.

3.5. DEPOSITIONAL FACIES

Sedimentary facies were analyzed to provide depositional context to the megafloral assemblages studied. We focused on an oblique transverse section through the coalfield, exposed along Highway C–623 (Fig. 24C). Six stratigraphic sections (A to E, plus the short auxiliary Section D-AUX), comprising ≈33% of the ≈1500 m thick basin-fill, were measured at cm-scale and tied to the reference section of Heward (1978a, fig. 13; Fig. 26). In addition, a m-scale reconnaissance section was measured between Sections D and

Figure 26. Stratigraphic log through La Magdalena Coalfield, showing the vertical distribution of Sections A to E (measured at cm-scale), unmeasured localities (F to H), Facies Associations (FA 1 to 4), and quadrats (MG-1 to 78). Gaps in log partially filled by log of Heward (1978a, fig. 13), after correlation with our sections. Top of basin-fill may lie ≈100 m above Mina Irene. The reconnaissance section between Sections D and E measured at m-scale, and is approximate. See Figure 24 for position of study sections and localities.


granules/pebbles
cobbles/boulders
breccia
meters
cl st sd gr
FA 1
FA 2
FA 3
FA 2
FA 3
FA 2
FA 3
FA 2
A
B
C
H
FA 2
FA 3
Mina Luisa
(correlation with Section A uncertain)
D
D-AUX
reconnaissance section
Section or locality
Facies Association
Quadrat position
Unmeasured section
Stratigraphic log of Heward (1978a, fig. 13)
FA 4
E
F
G
Mina Irene
?

E, and an inaccessible (but visible) road cut (Section F) and quarry walls in two inactive opencast coalmines (Sections G and H) were examined but not measured. Four facies associations (FA 1 to FA 4) containing 13 depositional facies were identified (Table 10). Characteristics of the dominant facies associations (FA 2 and FA 3) are illustrated in Figure 27, but the complete set of 1:100 scale logs are available as Appendix 3.

3.5.1. Facies Association 1 (FA 1): Debris Flow Deposits

3.5.1.1. Observations

This association, seen at the base of Section A, is restricted to the lowermost ≈3% of the basin-fill (42.4 m thick; Figs. 24C, 26; Table 10). It comprises red, stacked breccia units (DFB facies) that rest with angular unconformity atop reddened Precambrian metasediments, the source of virtually all clasts. The deposits fill bedrock paleovalleys hundreds of meters wide and a few tens of meters deep on the unconformity surface (Heward, 1978a). Breccia units are 0.4 to 6.0 m thick (mean = 2.4 m, n = 17), contain angular phyllite and sandstone pebbles and cobbles with isolated boulders up to 2.2 m in diameter, and may be weakly stratified. They are clast-supported and comprise poorly sorted, randomly oriented fragments in a matrix of red sandstone or mudstone. Most units are sheet-like, but some infill north–south oriented scours. Units either coarsen upward with outsized clasts on top, or fine upward to red siltstone lenses, some of which are conchoidally weathered. Plant fossils are absent.

3.5.1.2 Interpretation

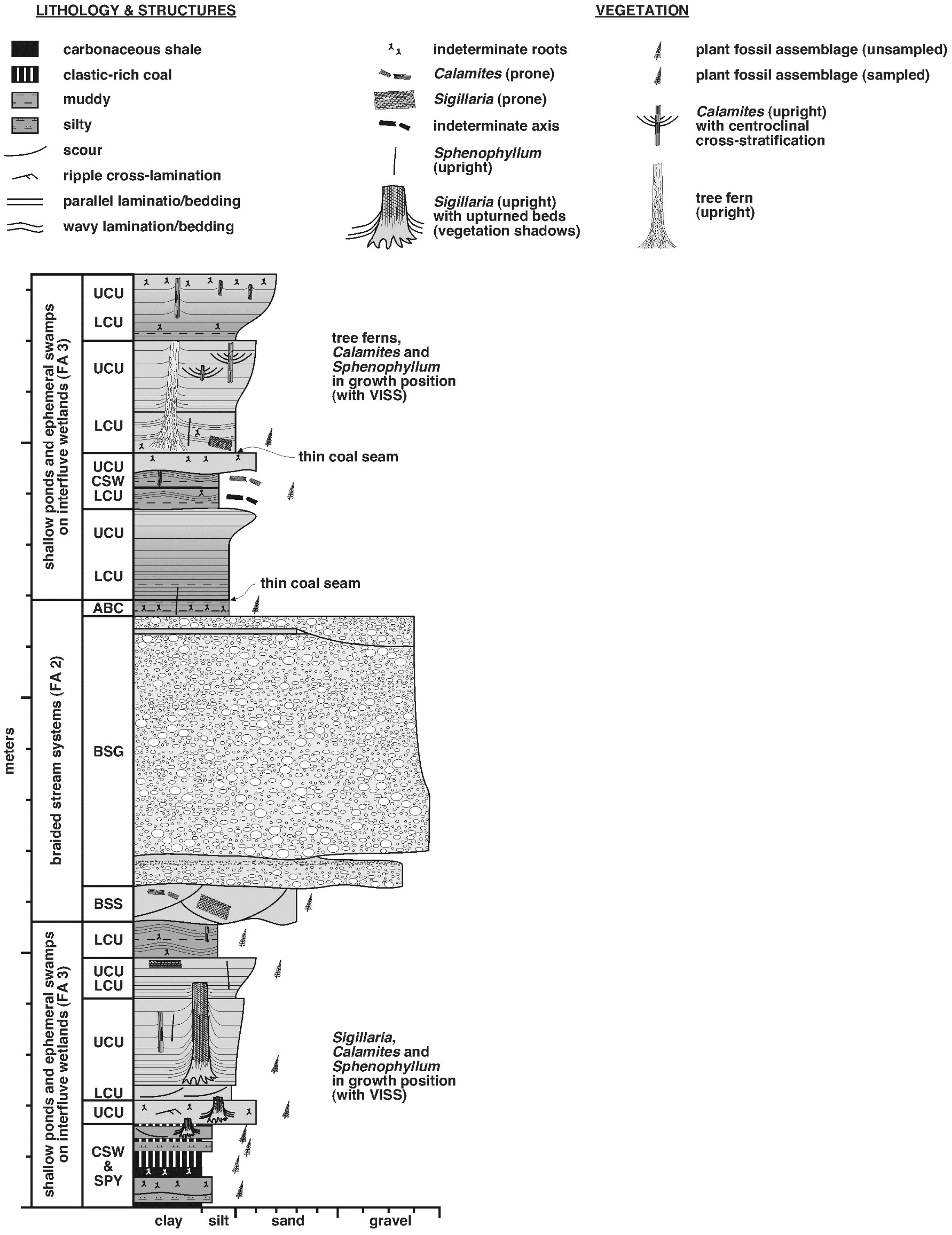
The upward fining of some units, the intimate association of clasts and matrix, and the presence of outsized clasts on top of some beds indicate that framework particles and finer components were emplaced together as debris flows (Fisher, 1971). It is unlikely that they represent scree and colluvial debris (Heward, 1978a) because openwork or cemented beds are absent. The poor sorting and lack of preferred grain orientation also argues against deposition by stream flow mechanisms (Blair & McPherson, 1994a). Hence, the breccias (DFB facies) are interpreted as debris flow deposits that filled bedrock valleys with locally derived material. Scours may be primary depositional features or formed by secondary processes, such as water traversing shallow channels atop the breccia pile (Blair & McPherson, 1994b). The red color reflects that of the bedrock source. Precambrian basement is reddened to depths of 15 m in the Cornombre-La Urz outlier (van den Bosch, 1969; Fig. 24B), implying that a long interval of weathering predated emplacement of debris flow deposits.

3.5.2. Facies Association 2 (FA 2): Braided Channel Belt

3.5.2.1. Observations

This association is restricted to the lower half of the succession (Sections A, C, D; Figs. 24C, 26), and makes up ≈12% of the basin-fill (≈173 m aggregate thickness; Table 10). It comprises stacked, composite units of conglomerate and sandstone, intercalated with thin, fine-grained intervals (Fig. 27). Individual composite units are 1.5 to 22.2 m thick, but vertical stacking has resulted in intervals 5.6 to 47.2 m thick that either fine

Figure 27. Representative stratigraphic section through braided channel belt (FA 2) and interfluve wetland (FA 3) deposits (98.0 to 116.3 m above base of section). These two facies associations comprise ≈90% of the basin-fill. Upright axes, although abundant in this section, are rare in the succession. See Table 10 for abbreviations of depositional facies.


LITHOLOGY & STRUCTURES
carbonaceous shale
clastic-rich coal
muddy
silty
scour
ripple cross-lamination
parallel laminatio/bedding
wavy lamination/bedding
indeterminate roots
Calamites (prone)
Sigillaria (prone)
indeterminate axis
Sphenophyllum (upright)
Sigillaria (upright) with upturned beds (vegetation shadows)
VEGETATION
plant fossil assemblage (unsampled)
plant fossil assemblage (sampled)
Calamites (upright) with centroclinal cross-stratification
tree fern (upright)
meters
shallow ponds and ephemeral swamps on interfluve wetlands (FA 3)
braided stream systems (FA 2)
shallow ponds and ephemeral swamps on interfluve wetlands (FA 3)
UCU
LCU
UCU
LCU
UCU
CSW
LCU
UCU
LCU
ABC
BSG
BSS
LCU
UCU
LCU
UCU
LCU
UCU
CSW & SPY
tree ferns, Calamites and Sphenophyllum in growth position (with VISS)
thin coal seam
thin coal seam
Sigillaria, Calamites and Sphenophyllum in growth position (with VISS)
clay
silt
sand
gravel

(Section A) or coarsen upward (Sections C, D) slightly (cf. Heward, 1978b). These imposing bodies are sheet-like and traceable laterally for hundreds of meters.

Composite units commence with a sandstone sheet (0.9 to 5.5 m thick) containing abundant scours with lesser trough or planar cross-bedding and ripple cross-lamination (BSS facies). Plant fossils are rare and poorly preserved, and comprise allochthonous axes of *Sigillaria*, *Calamites*, and pteridosperms. One upright, punctate pteridosperm axis was observed. Stacked sheets of clast-supported conglomerate (BSG facies) abruptly overlie the sandstone beds. The conglomerates (0.4 to 13.7 m thick) have planar or shallowly erosive bases, and contain rare and poorly preserved *Sigillaria* and *Calamites*. Clasts comprise well-rounded quartzite in a sandstone matrix, and although most units have a uniform clast size (pebbles, cobbles, or boulders), the coarsest beds are poorly sorted and structureless (Sections C, D). Packages may fine or coarsen upward slightly, but their tops invariably terminate abruptly; thin siltstones and carbonaceous shales may rest on this surface (ABC facies).

Heward (1978a) reported paleoflow trends to the north and northwest based on clast imbrication in several conglomerates, consistent with our limited measurements (vector mean 013°, n = 7). At Section H in the lower part of the succession (Figs. 24C, 26), northward paleoflow is evident in conglomerate sheets that contain imbricated clasts and large-scale, low-angle cross-beds with planar to slightly concave low-angle foresets up to 5 m high.

Thin packages of fine-grained strata (0.3 to 4.2 m thick) intercalate with the composite units of conglomerate and sandstone. The intervals are dominated by sandstone with planar bases, but individual beds may coarsen upward from siltstone or mudstone (LCU facies)—or from carbonaceous shale or a thin, clastic-rich coal seam (CSW facies)—to scoured and/or ripple cross-laminated sandstone (UCU facies). Megafloral assemblages abound in the LCU and UCU facies, which typify and are better developed in FA 3 (Section 4.3).

3.5.2.2. Interpretation

The composite units of sandstone and conglomerate are attributed to braided sandbed (BSS facies) and gravelbed (BSG facies) rivers. Low in the basin-fill (Sections A, H; Figs. 24C, 26), stacked cross-sets in conglomerate formed in downstream and laterally accreting gravel bars, and abundant channel forms, scours, clast-supported texture, moderate sorting, and clast imbrication imply relatively organized flow. Indistinct fining- or coarsening-upward trends suggest rapid deposition, whereas the abrupt capping of conglomerates by thin, fine-grained units records sudden waning of flow and/or channel abandonment (ABC facies). The basal sandstone sheet of composite units, heralding subsequent gravel deposition, indicates that bedload entered the basin in pulses, with sand outpacing gravel. The coarser, poorly sorted, and structureless conglomerates (Sections C, D) may represent hyperconcentrated flows deposited during major river floods (Smith, 1986; Pascucci et al., 2006), although some could be debris flow deposits. The main drainage direction apparently was northwards.

Intercalated, fine-grained packages are interpreted as the deposits of isolated pond-fills (LCU and UCU facies) between braided channels, abandoned braided channels, and thin floodplain sheets. The scarcity of such facies, which characterize FA 3, indicates that large, high-energy, braided channels dominated the landscape, with flanking floodplains restricted to isolated pockets. The punctuation of fine-grained deposits by conglomerates indicates recurring, sudden episodes of coarse clastic input to the basin.

3.5.3. Facies Association 3 (FA 3): Marginal and Interfluve Wetlands

3.5.3.1. Observations

This association (Sections A, B, D, D-AUX, E; Figs. 24C, 26) makes up ≈78% of the basin-fill (≈1170 m aggregate thickness; Table 10). The dominant motif is lensoid, coarsening-upward units, 0.2 to 4.9 m thick (mean = 0.9 m, n = 128) and less than a few tens of meters wide, that contain rich megafloral assemblages. Lenses commence as carbonaceous shale or mudstone (LCU facies) overlain by siltstone or sandstone with poorly preserved trough cross-bedding, ripple cross-lamination, wavy lamination, and/or soft-sediment deformation (UCU facies). Stacked coarsening-upward units locally entomb upright plant axes that can be associated with vegetation-induced sedimentary structures (VISS, cf. Rygel et al., 2004; Fig. 27). Most autochthonous vegetation is rooted near the base of lenses, and includes abundant *Calamites*, *Sigillaria*, and sphenophylls; marattialean tree ferns and pteridosperms are rare. Unit tops exhibit rooting, scour fills, or structureless siltstone with conchoidal weathering.

Coarsening-upward units are commonly grouped into composite units reaching 11.0 m thick; these units coarsen upward as the individual components thicken and coarsen. Carbonaceous shales and/or thin, clastic-rich coal seams (CSW facies), which are genetically similar, are developed atop some composite units. These organic horizons are only meters to a few tens of meters wide, and very thin: carbonaceous shales are 10 to 200 mm thick (mean = 50 mm, median = 25 mm, n = 34) and coal seams are 5 to 300 mm thick (mean = 70 mm, median = 30 mm, n = 38). Although unidentifiable roots are present beneath some organic horizons, stigmarian rhizomorphs are rare. The clastic-rich coal seams are locally split by mudstone or siltstone partings that contain rich megafloral assemblages (SPY facies). Thin coal seams prevail in the basin-fill, but the number of inactive opencast coalmines in the coalfield indicates that more extensive, dm- to m-scale coal seams (RTM facies) are present, especially near the syncline axis along the southern basin margin. A seat earth underlying a worked out coal seam in Mina Irene (Section G; Figs. 24C, 26) exposes abundant swollen bases of *Omphalophloios* and less common stigmarian rhizomorphs.

Sandstone channel bodies (DSC facies) that are 1.5 to 16.0 m thick (mean = 4.3 m, n = 30) and fine upward from a sharp, slightly erosive base are a common feature of FA 3. No channel bodies are completely exposed, but they appear to be relatively narrow with a low width:thickness ratio. The thickest show multiple stories separated by erosion surfaces or mudstone beds. Channel bases may have granular to pebbly lags, and some contain abundant and large allochthonous axes of varying affinity. Scour-based lenses of structureless sandstone characterize channels, and poorly preserved trough or planar cross-bedding, low-angle plane beds, ripple cross-lamination, and/or soft-sediment deformation are occasionally preserved. Limited cross-beds indicate a westward paleoflow (vector mean of 273°, n = 5), similar to those measured by Heward (1978a). The upper fill of some channel bodies comprises interbedded sandstone and siltstone exhibiting parallel, wavy, or ripple cross-lamination (ADC facies). Autochthonous *Calamites* axes are rare, but megafloral assemblages are common. Some units are capped by rooted paleosols (rarely containing stigmarian rhizomorphs) overlain by carbonaceous shale or thin, clastic-rich coal seams.

An uncommon component of FA 3 is small sandstone bodies (0.7 to 2.1 m thick) that have sharp, slightly erosive bases, contain scours and ripple cross-lamination, and fine upward to rooted siltstone (FPC facies). Some contain rich megafloral assemblages, and an upright pteridosperm trunk is entombed in one example. These units typify the 8.4 m thick interval between the breccias of FA 1 and the lowest braided river deposits of FA 2 (Fig. 26).

3.5.3.2. Interpretation

The prevalence of coarsening-upward cycles (LCU and UCU facies) suggests that the filling of small, shallow bodies of standing water was the prevailing depositional activity. Autocyclic processes may have initiated ponding, perhaps in conjunction with periodic co-seismic events that caused subsidence, thereby maintaining a high water table (Gastaldo et al., 2004b; Gastaldo & Demko, in press). Ponds repeatedly filled to subaerial conditions, or at least to depths shallow enough for vegetation to become rooted. The abundance of VISS associated with standing trees indicates that river-generated floods frequently invaded interfluve wetlands. Thicker composite units provide evidence for deeper standing water, which progressively shallowed due to periodic inputs and progradation of coarser detritus from pond margins.

Sandstone channel bodies (DSC facies) are attributed to distributary channels discharging into wetlands based on their relatively low aspect ratio, largely structureless appearance, and the presence of superimposed stories with scoured bases (Gibling, 2006).

However, some may be part of through-flowing drainage systems, possibly of anastomosing pattern (cf. Makaske et al., 2002). Sandstone and siltstone interbeds at the top of some distributary bodies (ADC facies) represent abandoned channel fills, with sand deposited during relatively higher energy events. Small, fining-upward sandstone bodies with slightly erosive bases (FPC facies) represent narrow, shallow floodplain channels (Gibling, 2006) that drained wetlands. These channels are abundant and exclusively found in an 8.4 m thick interval above the breccias of FA 1. Because these wetland deposits are distinct from those higher in the succession, they are hereafter termed ‘marginal wetlands’.

Thin, gleyed paleosols at the top of coarsening-upward cycles and sandstone channel bodies show few indications of prolonged soil formation. Thin, small lenses of carbonaceous shale and clastic-rich coal (CSW facies) are interpreted as the remnants of ephemeral swamps that developed in topographic lows due to autocyclic processes. These organic horizons probably represent thin O-horizons that capped poorly developed paleosols, rather than true histosols (i.e., mires). Mudstone or siltstone partings that split swamp deposits (SPY facies) record the breaching or overtopping of channel banks during major flood events, with splays smothering vegetation and causing temporary cessation of organic accumulation. Laterally extensive, dm- to m-scale coal seams (RTM facies) are interpreted as having formed in rheotrophic (planar) mires characterized by prolonged peat accumulation. Although one thick coal seam was observed in marginal wetland deposits near the succession base (Mina Luisa, Section H; Figs. 24C, 26), most are confined to the upper part of the basin-fill, rather than scattered throughout it, implying that their distribution was controlled by allocyclic processes. The mires may have formed in a humid climate with little to no seasonality (Cecil, 1990; Cecil & Dulong, 2003), although increased accommodation due to subsidence (Pashin, 1998) or inland ponding of freshwater during marine transgression (Kosters & Suter, 1993) may have played roles in their distribution. The mire in Mina Luisa (Section H) may have preferentially developed above the stable, less compactable pile of breccia of FA 1 (Tibert & Gibling, 1999).

3.5.4. Facies Association 4 (FA 4): Large Lakes

3.5.4.1. Observations

This association is only found in the upper half of the succession (Section E; Figs. 24C, 26), and makes up ≈7% of the basin-fill (≈103 m aggregate thickness; Table 10). It is characterized by coarsening-upward units (LAC facies) that are better-stratified and thicker (1.8 to 15.6 m; mean = 4.1 m, n = 10) than those of FA 3. Units commence with platy, buff mudstone or siltstone, and bed thicknesses increase as the units coarsen upward into planar-bedded siltstone or sandstone exhibiting ripple cross-lamination and/or scours. Basal parts of some units contain organic mudstone horizons and briefly fine upward before the coarsening-upward trend sets in. Coarser grained caps have abrupt tops, and in places, equally abrupt bases. In comparison with similar beds in FA 3, paleosols are absent, evidence of rooting is exceedingly rare, and comminuted plant debris is sparse. Depauperate megafloral assemblages accompanied by upright sphenophyll axes were only encountered at one level. Heward (1978a, fig. 2) recorded thin 'brackish marine horizons' in this facies, based on the presence of the brackish bivalves *Curvirimula*, *Euestheria*, and *Anthraconaia* (Eagar, 1985).

Sandstone channel bodies (DSC facies) that are 3.1 to 6.9 m thick (mean 5.0 m, n = 5) locally fill cuts into these beds. Some appear lensoid, with a relatively low width:thickness ratio that is confirmed by aerial photographs. Channel-fills fine upward and generally are structureless, although poorly preserved scours are rare.

3.5.4.2. Interpretation

Thick intervals of platy mudstone indicate prolonged subaqueous conditions, and the thickness of coarsening-upward units (LAC facies) attests to the filling of extensive bodies of standing water too deep for vegetation to colonize (i.e., lakes; Heward, 1978a). Ripple cross-lamination and scours in upper parts of coarsening-upward units imply modest flow intensity, and the sharply based caps of some cycles may represent discrete belts of coarser shoreline deposits. Fining-upward followed by coarsening-upward trends suggest gradual rather than sudden deepening, allowing for a transition from shallow- to deep-water lacustrine facies. The prevalent buff coloration points to predominantly oxygenated water. Rare horizons containing brackish bivalves indicate sporadic connection to marine conditions, and may be the inland manifestation of distant marine transgressions. Channel bodies (DSC facies) are interpreted as the product of distributary channels that fed into a lake. Their fills generally are much coarser than topmost parts of associated coarsening-upward units, implying formation during relative shallowing when detritus was transported out across the lake.

3.5.5. Climate

In the modern tropics, peat accumulation and sediment supply are closely linked to the amount and seasonality of rainfall (Cecil, 1990; Cecil & Dulong, 2003). Siliciclastic sediment supply is highest when the degree of seasonality is at a maximum, and the ideal conditions for the formation and preservation of low-ash peat, as a precursor to economic coal, occur in humid and perhumid climates where a dense vegetation cover minimizes erosion (Cecil et al., 1985; Hooke, 2000). Applying this model to La Magdalena Coalfield, the combination of high stream gradient and strongly seasonal rainfall, evident from the episodic nature of drainages, may account for the deposition of a thick siliciclastic succession in <1 Ma. At the top of the basin-fill, a shift to wetter, less seasonal conditions may have resulted in decreased sediment input and the development of rheotrophic mires, probably in concert with other allocyclic controls.

There is, however, little empirical evidence in the coalfield to support the notion of strong seasonality. The succession contains no redbeds, with the exception of the basal breccias (FA 1), which reflect a reddened bedrock source rather than better-drained conditions. Furthermore, paleosols are poorly developed and invariably gleyed, indicative of saturated soils (Driese & Ober, 2005) in a uniformly poorly drained environment, promoting the preservation of buried plant remains (DiMichele & Gastaldo, 2008; Gastaldo & Demko, in press). Vertisols, which develop under seasonally variable conditions (Wilding & Tessier, 1988; Driese & Ober, 2005), are conspicuously absent. The degree of seasonality and general climate of La Magdalena Coalfield remains an open question.

3.5.6. Synopsis of Basin-fill

Earliest stages of sedimentation in La Magdalena Coalfield comprise debris flow deposits of breccia (FA 1) that blanketed an incised and deeply weathered bedrock surface. These involved small drainage systems that transported clasts from steep slopes forming the basin margin. The pronounced shift in sedimentation style and clast type between breccias of FA 1 and the quartzite conglomerate sheets of FA 2 near the base of Section A indicates the development of drainage systems with much larger catchments, probably linked to through-flowing systems. The change may have been triggered by ongoing subsidence, which captured major north-flowing rivers in a broad basin or valley system.

Composite units of conglomerate and sandstone (FA 2) are interpreted as braided gravelbed and sandbed rivers that were deposited by steam flows, hyperconcentrated flows, and possibly debris flows. These rivers carried torrential influxes of coarse detritus from upland catchments. Although such large rivers might have disgorged into an internal intramontane basin, it is more probable that they drained to a marine coastline that lay to the north or east, an interpretation supported by the occurrence of thin brackish intervals high in the basin-fill. Despite sporadic marine connections, the depocenter probably was elevated above mean sea level for most of its duration, and mountain ridges may have partly separated La Magdalena from adjacent, coeval coalfields. The dominance of paleorelief-filling breccia and conglomerate in the Cornombre-La Urz outlier (Martín Parra et al., 1989) may provide evidence for such a barrier to the west.

The overwhelming dominance of interfluve wetland deposits (FA 3) implies that braided rivers traversed large expanses of wetland fed by a distributary channel network.

Westward paleoflow (Heward, 1978a; this study) is problematic if marine conditions lay to the north or east, but post-depositional rotation of the basin margin and basin-fill during Variscan and Alpine events may be responsible for the disparity, along with the variable orientations of original drainage networks. Regardless, westward paleoflow implies that some distributary channels were orthogonal to the main drainage direction of the braided system. The prevalence of wetland (FA 3) and deep lake deposits (FA 4) suggests that subsidence was sufficiently rapid to maintain a high water table, which may have masked evidence for high sedimentation under strongly seasonal conditions. Deep lake deposits in the upper part of the succession point to increased subsidence and/or decreased sediment supply. A return to wetland facies in the topmost strata (Sections F, G), where economic coals abound, may reflect decreased seasonality or inland ponding of freshwater during marine transgression.

This sedimentological model for the La Magdalena Coalfield (Fig. 28) contrasts with earlier studies (Heward, 1978a, b; Leyva et al., 1984; Colmenero et al., 1996) that interpreted the succession as the product of large alluvial fans. These authors were no doubt heavily influenced by the impressive nature of the coarse sheets of conglomerate and basin-margin breccias in the lower half of the basin-fill. However, the aggregate thickness of the breccia (FA 1) and coarse conglomerate sheets (FA 2) is only ≈216 m according to our measurements and those of Heward (1978a, fig. 13), representing just ≈14% of the total basin-fill. Indeed, the conglomerates in FA 2 may represent local fans that entered the basin at mountain exit points, perhaps contributing to nearby axial river systems. However, an alluvial fan attribution for thick sections of sandstone, mudstone, and coal (FA 3) that form the bulk of the succession (≈78%) is more problematic. These

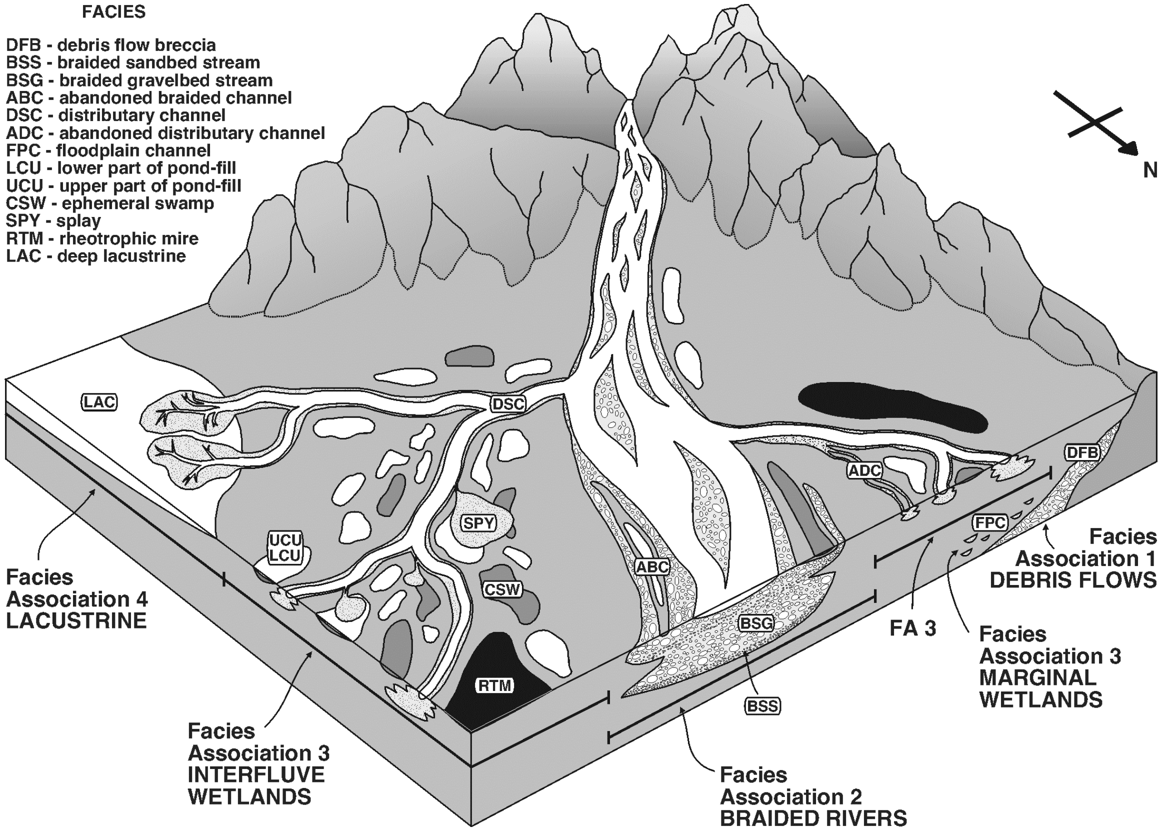


Figure 28. Paleoenvironmental reconstruction illustrating the 13 depositional facies and 4 facies associations in La Magdalena Coalfield. See Table 10 for depositional facies. No spatial scale implied.

strata are attributed to wetlands traversed by distributary or through-flowing fluvial systems that, although fed by local high-gradient streams, were not themselves part of alluvial fan systems.

A possible modern facies analogue, albeit in the north temperate zone with a continental climate, is the Columbia River, British Columbia, which traverses a deep, 1.5 km wide valley linked to tectonic lineaments in the Canadian Cordillera. The basin floor is an extensive wetland with anastomosing rivers, shallow lakes, mires, crevasse splays, and log jams (Makaske et al., 2002). Alluvial fans build out across the valley from steep tributary rivers, generating wedges of coarse detritus that locally span the valley, constrict axial drainage, and extend downstream in river channels. Another possible analogue is drainage systems of West Timor, Indonesia, which is situated in the tropical zone and has a dry subhumid climate. Braided rivers with steep gradients originate in high mountainous catchments, and drain directly to the coast (Cecil et al., 2003). Cobbles and pebbles dominate bedload, and sediment discharge is largely restricted to torrential flows during the short rainy season.

3.6. COMPOSITION OF MEGAFLORAL ASSEMBLAGES

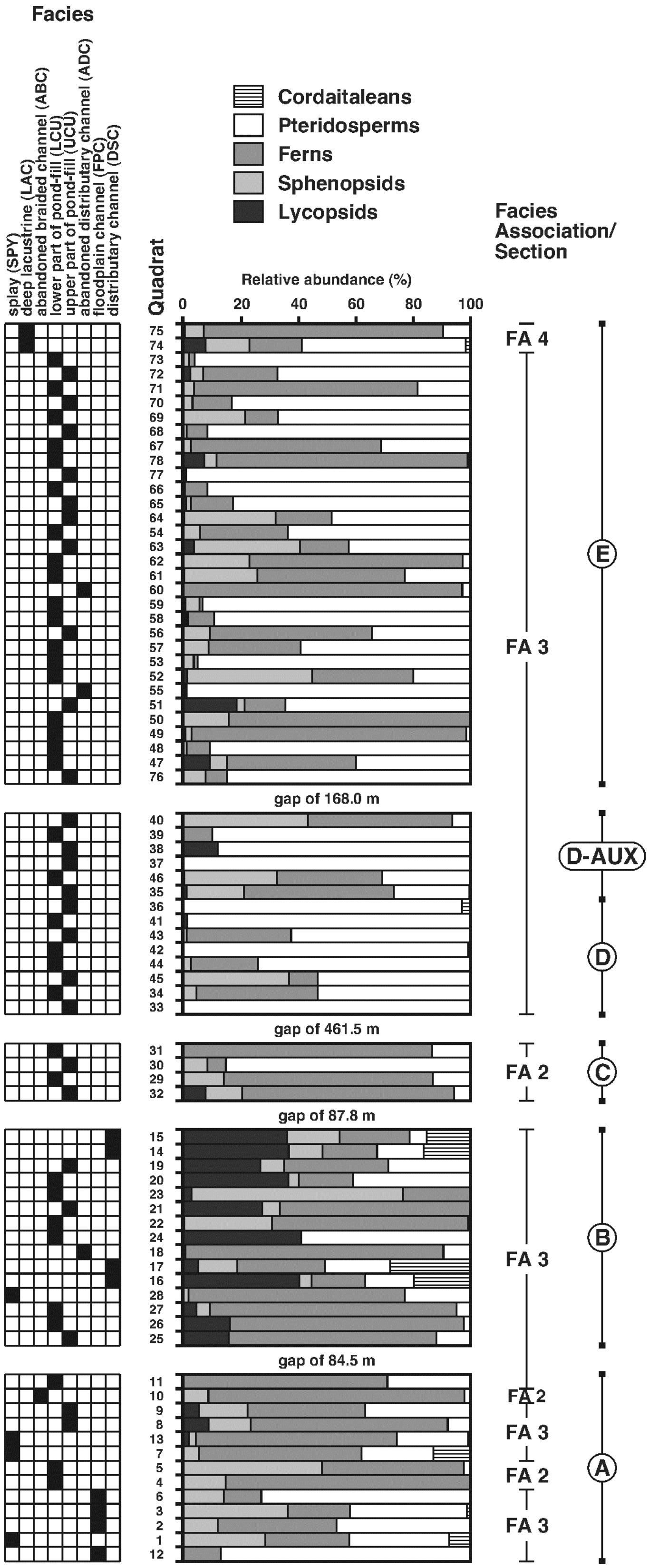
Castro (2005a, b) described the megafloral species of La Magdalena Coalfield, and gave a detailed historical account of previous stratigraphical and paleobotanical studies. In contrast, this paper aims to elucidate the spatial structure and ecology of these plant communities.

3.6.1. Quadrat Data Collection

The composition of megafloral assemblages was recorded using a variant of the quadrat technique of Iwaniw (1985). Because bedding planes are rarely exposed, fossiliferous horizons were taken apart until enough slabs were collected to fill a 50 x 50 cm (0.25 m^2) quadrat. (The DSC facies was an exception, for which each quadrat had an area of ≈2.5 m^2; Table 10). All slabs in a quadrat contained at least one fossil fragment, and were collected from as thin an interval as possible to avoid mixing of assemblages with different taphonomic histories. Most sample horizons were 50 to 200 mm thick, and all comprised a single facies. The state of fragmentation and pertinent taphonomic information were recorded.

In total, 78 fossiliferous units (MG-1 through MG-78; Fig. 26) were analyzed, with 93 quadrats sampled due to replicates made along-strike at nine horizons (Table 10). The meterage of each quadrat was recorded on the cm-scale stratigraphic log, and nine depositional facies were sampled (Table 10). In each quadrat, every plant fragment was identified based on the taxonomy of Castro (2005a, b) and counted as a single individual. Most remains could be identified to fossil species level, although poorly preserved examples or those lacking diagnostic features were recorded at the fossil genus rank. A small representative collection was made to verify field identifications. A total of 12553 plant fragments were counted, with quadrats containing 11 to 406 specimens (mean = 135). Figure 29 shows the composition of all quadrats arranged in stratigraphic order, with plants segregated into the five major clades (lycopsids, sphenopsids, ferns, pteridosperms, cordaitaleans).

Figure 29. Vertical changes in proportional distribution of five main plant clades (lycopsids, sphenopsids, ferns, pteridosperms, cordaitaleans) through La Magdalena Coalfield. Depositional facies (see Table 10) denoted for each quadrat.


Facies
splay (SPY)
deep lacustrine (LAC)
abandoned braided channel (ABC)
lower part of pond-fill (LCU)
upper part of pond-fill (UCU)
abandoned distributary channel (ADC)
floodplain channel (FPC)
distributary channel (DSC)
Quadrat
Cordaitaleans
Pteridosperms
Ferns
Sphenopsids
Lycopsids
Relative abundance (%)
0 20 40 60 80 100
75 74 73 72 71 70 69 68 67 78 77 66 65 64 54 63 62 61 60 59 58 56 57 53 52 55 51 50 49 48 47 76
gap of 168.0 m
40 39 38 37 46 35 36 41 43 42 44 45 34 33
gap of 461.5 m
31 30 29 32
gap of 87.8 m
15 14 19 20 23 21 22 24 18 17 16 28 27 26 25
gap of 84.5 m
11 10 9 8 13 7 5 4 6 3 2 1 12
Facies Association/ Section
FA 4
FA 3
FA 2
FA 3
FA 2
FA 3
FA 2
FA 3
E
D-AUX
D
C
B
A

The benefit of the census approach used is that dominance-diversity characteristics were recorded for standardized units of area, equivalent to 0.25 m^2 of bedding plane. It is acknowledged that the method used could overestimate the relative abundances of easily disaggregated and/or profuse organs (e.g., pinnate fern-like leaves versus lycopsid branches). However, this bias was largely offset by the fact that foliar fragments—produced in abundance by all plant clades and affected by comparable taphonomic processes—comprised 70.9% (n = 8896) of the sample population, 95.5% (n = 8501) of which were ≤100 mm.

3.6.2. Data Matrices and General Dominance-diversity Characteristics

Of the 84 fossil taxa recorded (Table 11), 80 could either be assigned to fossil species (n = 55) or fossil genera (n = 25) level (9381 or 74.7% of specimens), and 81 could be assigned to one of the five plant groups (9400 or 74.9%). Striate and punctate axes formed almost all of the remaining three fossil taxa (2932 or 23.4%, and 219 or 1.7%, respectively), with two seeds of unknown affinity comprising the third fossil taxon. Prior to analyses, all fossil taxa were condensed into true biological taxa using the method of Gastaldo et al. (2004a), resulting in an abundance matrix that more accurately reflects the true paleobiological composition of the sample population. For example (Table 12), records of *Sigillariostrobus* and *Syringodendron* were grouped with *Sigillaria*, whereas *Artisia* and *Cordaicladus* were grouped with *Cordaites*, their respective parent plants. In quadrats where a fossil taxa could belong to multiple parent plants, its abundance was proportionately redistributed between all potential parent plants. For example, records of *Calamites* were proportionately divided between

Plant group	**Number of specimens (*n*)**
LYCOPSIDS	**[558]**
Fossil species	
Asolanus camptotaenia	4
“*Lepidodendron*” *dissitum*	12
Lepidostrobophyllum majus	2
Sigillaria rugosa	30
Stigmaria ficoides	4
Fossil genera	
Cyperites sp.	400
Lepidostrobus sp.	1
Sigillaria sp.	62
Sigillariostrobus sp.	15
Syringodendron sp.	9
Assignable to group	
Decorticated lycopsid axes	19
SPHENOPSIDS	**[1341]**
Fossil species	
Annularia mucronata	58
Annularia sphenophylloides	266
Annularia stellata	270
Asterophyllites equisetiformis	134
Calamites sp. cf. *C. brongniartii*	1
Parasphenophyllum crenulatum	3
Sphenophyllum alatifolium	32
Sphenophyllum incisum	35
Sphenophyllum longifolium	2
Sphenophyllum oblongifolium	103
Fossil genera	
Annularia sp.	25
Calamites sp.	182
Macrostachys sp.	4
Sphenophyllum sp.	131
Sphenophyllum axes	95
FERNS	**[3031]**
Fossil species	
Danaeites emersonii	1
Diplazites longifolius	99
Lobatopteris corsinii	4
Lobatopteris viannae	14
Nemejcopteris feminaeformis	380
Oligocarpia gutbierii	73
Oligocarpia leptophylla	58
Pecopteris ameromii	197
Pecopteris apicalis	35
Pecopteris arborescens	213
Pecopteris candolleana	112
Pecopteris sp. cf. *P. longiphylla*	22
Pecopteris daubreei	9
Pecopteris densifolia	15
Pecopteris jongmansii	9
Pecopteris melendezii	9
Pecopteris monyi	10
Polymorphopteris magdalenae	64
Polymorphopteris polymorpha	243
Senftenbergia elaverica	36
Senftenbergia grunerii	11
Sphenopteris fayolii	2
Sphenopteris magdalenae	9
Sphenopteris mathetii	1
Sphenopteris rossica	9
Fossil genera	
Lobatopteris sp.	8
Oligocarpia sp.	2
Pecopteris sp.	1279
Polymorphopteris sp.	63
Senftenbergia sp.	1
Sphenopteris sp.	35
Caulopteris sp.	7
Megaphyton sp.	1
PTERIDOSPERMS	**[4434]**
Fossil species	
Alethopteris bohemica	60
Alethopteris zeillerii	84
Callipteridium pteridium	1668
Dicksonites plukenetii	77
Eusphenopteris rotundiloba	9
Eusphenopteris talensii	1
Lescuropteris genuina	1
Linopteris gangamopteroides	1
Linopteris neuropteroides	382
Mixoneura wagnerii	57
Neuropteris obtusa	108
Neuropteris ovata	1396
Odontopteris brardii	190
Pseudomariopteris busquetii	24
Pseudomariopteris cordato-ovata	284
Fossil genera	
Cyclopteris sp.	43
Hexagonocarpus sp.	37
Trigonocarpus sp.	9
Petioles of *Callipteridium*	3
CORDAITALEANS	**[36]**
Fossil genera	
Artisia sp.	6
Cordaicladus sp.	1
Cordaites sp.	29
UNCERTAIN AFFINITY	**[3153]**
Punctate axes	219
Striate axes	2932
Small seeds	2
TOTAL	**12553**

Table 11. List of 84 fossil taxa recorded in La Magdalena Coalfield, segregated by clade.

Non-biological fossil taxon	**Biological genera to which reassigned**
Striate axes	*Pecopteris*, *Callipteridium*, *Neuropteris*, *Polymorphopteris*, *Nemejcopteris*, *Linopteris*, *Pseudomariopteris*, *Odontopteris*, *Alethopteris*, *Diplazites*, *Oligocarpia*, *Dicksonites*, *Sphenopteris*, *Mixoneura*, *Senftenbergia*, *Lobatopteris*, *Eusphenopteris*, *Danaeites*, *Lescuropteris*
Punctate axes	
Cyperites	*Sigillaria*, *Lepidodendron*
Calamites	*Annularia*, *Asterophyllites*
Sphenophyll axes	*Sphenophyllum*, *Parasphenophyllum*
Cyclopteris	*Callipteridium*, *Neuropteris*, *Odontopteris*
Hexagonocarpus	*Linopteris*
Decorticated lycopsid axes	*Sigillaria*, *Lepidodendron*, *Asolanus*
Sigillariostrobus	*Sigillaria*
Trigonocarpus	*Callipteridium*, *Neuropteris*, *Odontopteris*, *Alethopteris*, *Mixoneura*
Syringodendron	*Sigillaria*
Caulopteris	*Pecopteris*, *Polymorphopteris*
Artisia	*Cordaites*
Macrostachya	*Annularia*, *Asterophyllites*
Stigmaria or *Stigmariopsis*	*Sigillaria*
Petioles of *Callipteridium*	*Callipteridium*
Lepidostrobophyllum	*Lepidodendron*
Small seeds	*Callipteridium*, *Neuropteris*, *Pseudomariopteris*, *Odontopteris*, *Alethopteris*, *Eusphenopteris*
Lepidostrobus	*Lepidodendron*
Cordaicladus	*Cordaites*

Table 12. List of non-biological fossil taxa in La Magdalena Coalfield, and biological genera to which they were proportionately allocated prior to analyses.

Asterophyllites and *Annularia*, based on the relative abundance of these biological genera in the quadrat. Only 1.41% of specimens could not be redistributed—for example, if *Calamites* were present in a quadrat but *Asterophyllites* and *Annularia* were absent—and this material was excluded in all subsequent analyses. Through this process, 27 biological genera containing at least 52 biological species were recognized. The redistributed abundance matrix (comprising 27 biological genera), from which all subsequent analyses were performed, is provided as Table 13. The raw abundance matrix is given in Table 14.

When the 27 biological genera are ranked by relative abundance (Table 15), *Pecopteris*, *Callipteridium* and *Neuropteris* comprise 57.6% of the assemblage, after which there is a sharp decline in the contribution of other genera (i.e., data are strongly right-skewed). Condensing the abundance data into plant groups indicates that pteridosperms (49.0%) and ferns (35.2%) are dominant, whereas sphenopsids (10.7%) and lycopsids (4.4%) are poorly represented and the cordaitaleans (0.6%) rare (Table 16). However, when species diversity is analyzed, ferns are richest (25 of 52 species or 48.1%), pteridosperms (28.8%) and sphenopsids (17.3%) less rich, and lycopsids (5.8%) least represented. (Cordaitaleans are not included as they are represented by one biological genus, *Cordaites*). This analysis shows that pteridosperms, while more abundant in absolute numbers and biomass, have a relatively lower diversity than the more species-rich ferns.

3.6.3. Comparison with Analyses of Castro (2005b)

Castro (2005b, table 2) recorded 140 fossil taxa based on a collection of 10530 plant fragments. When proportionately redistributed, the population contains 40 biological genera and 90 biological species (Tables 15, 16). Although more diverse than our assemblage, the 13 biological genera not encountered in our study account for just 0.74% of Castro's population (Table 15). Thus, it is not surprising that our sampling did not capture these rare elements.

Castro's data set reveals a similar pattern of vegetation composition to our own when the relative abundance distributions are compared (Table 15). *Pecopteris* and *Callipteridium* are the dominant biological genera in both sets, and when the rankings are split into the top five, top 10, and top 15 genera, the majority is common to each grouping (4 of 5, 7 of 10, 13 of 15). Nonetheless, some discrepancies exist. *Sigillaria* has a markedly higher relative abundance in our data set (4.2%, sixth rank) than it does in Castro's (0.4%, 20th rank). This presumably reflects the fact that lycopsid leaves (*Cyperites*) were counted in this study, almost all of which were allotted to *Sigillaria* (Table 12), whereas Castro did not make such an assignment. Castro also noted a much higher proportion of *Sphenophyllum* (8.4%, third rank) than we did (3.2%, 20th rank).

Our three most abundant biological genera (*Pecopteris*, *Callipteridium*, *Neuropteris*), which account for 57.6% of our sample population, comprise only 38.3% of Castro's, whereas some the rarest taxa in our data set are more abundant in her assemblage. Thus, although both data sets are strongly right-skewed, Castro's distributions are more evenly spread among taxa (Fig. 30). The difference is likely related to collection protocols. As Castro's was a taxonomic study, rare taxa probably

Table 15. Ranked relative abundances of biological genera in La Magdalena Coalfield (plus non-biological taxa that could not be reallocated), comparing sample populations from this study ($N = 12553$) and Castro (2005b, table 2, $N = 10530$). ([a]) Unique to sample population.

This study		**Castro (2005b)**	
Biological genera	**Relative abundance (%)**	**Biological genera**	**Relative abundance (%)**
Pecopteris	22.19	*Pecopteris*	20.28
Callipteridium	18.93	*Callipteridium*	10.66
Neuropteris	16.43	*Sphenophyllum*	8.43
Annularia	5.91	*Neuropteris*	7.38
Polymorphopteris	4.32	*Annularia*	7.3
Sigillaria	4.18	*Polymorphopteris*	5.46
Nemejcopteris	3.89	*Odontopteris*	5.11
Linopteris	3.81	*Alethopteris*	4.69
Pseudomariopteris	3.6	*Pseudomariopteris*	4.66
Sphenophyllum	3.15	*Asterophyllites*	4.64
Odontopteris	2.55	*Nemejcopteris*	3.86
Alethopteris	1.73	*Sphenopteris*	3.46
Diplazites	1.44	*Linopteris*	2.57
Oligocarpia	1.4	*Mixoneura*	2.55
Asterophyllites	1.19	*Diplazites*	2.34
Dicksonites	0.85	*Oligocarpia*	1.79
Sphenopteris	0.75	*Dicksonites*	1.47
Mixoneura	0.67	*Senftenbergia*	1.09
Senftenbergia	0.56	*Lobatopteris*	0.4
Cordaites	0.29	*Sigillaria*	0.37
Lobatopteris	0.28	*Parasphenophyllum*	0.18
Lepidodendron	0.15	*Neurocallipteris*[a]	0.18
Eusphenopteris	0.13	*Taeniopteris*[a]	0.18
Asolanus	0.11	*Lepidodendron*	0.16
Parasphenophyllum	0.04	*Cordaites*	0.14
Danaeites	0.01	*Eusphenopteris*	0.14
Lescuropteris	0.01	*Danaeites*	0.07
Non-biological genera		*Lescuropteris*	0.07
Woody axes in DSC facies*	0.96	*Dicranophyllum*[a]	0.07
Calamites	0.38	*Ulvopteris*[a]	0.07
Caulopteris[a]	0.06	*Remia*[a]	0.05
Megaphyton[a]	0.01	*Omphalophloios*(?)[a]	0.05
Total	99.98	*Renaultia*[a]	0.03
		Barthelopteris[a]	0.02
		Helenopteris[a]	0.02
		Desmopteris[a]	0.02
		Alloiopteris[a]	0.02
		Spiropteris[a]	0.02
		Asolanus	0.01
		Selaginella[a]	0.01
		Total	100.02

	This study			
Plant group	**Relative abundance (%)**	**Relative generic diversity (%)[b]**	**Relative specific diversity (%)**	**Biological genera (species)**
Lycopsids	4.44	11.11	5.77	3 (3)
Sphenopsids	10.68	14.81	17.31	4[c] (9)
Ferns	35.23[a]	33.33	48.08	9[d] (25)
Pteridosperms	49.03[a]	37.04	28.85	10 (15)
Cordaitaleans	0.60[a]	3.70	-	1 (-)
Total	**99.98**	**99.99**	**100.01**	**27 (52)**

	Castro (2005b)[e]			
Plant group	**Relative abundance (%)**	**Relative generic diversity (%)**	**Relative specific diversity (%)**	**Biological genera (species)**
Lycopsids	0.60	13.89	5.81	5 (5)
Sphenopsids	20.63	11.11	10.46	4 (9)
Ferns	38.98	36.11	60.46	13 (52)
Pteridosperms	39.65	36.11	23.26	13 (20)
Cordaitaleans	0.14	2.78	-	1 (-)
Total	**100**	**100**	**99.99**	**36 (86)**

Table 16. Relative abundances of five plant groups in La Magdalena Coalfield, comparing sample populations from this study and Castro (2005b, table 2). (a) Values include 1/3 of woody axes from DSC facies (i.e., 0.32% each; see Table 15). (b) Values ignore woody axes from DSC facies. (c) Does not include *Calamites*. (d) Does not include *Caulopteris* or *Megaphyton*. (e) To remain consistent with Castro (2005b), *Taeniopteris*, *Dicranophyllum*, *Ulvopteris*, and *Desmopteris* removed from data set (combining for only 0.34% of sample population) because group affinity uncertain.

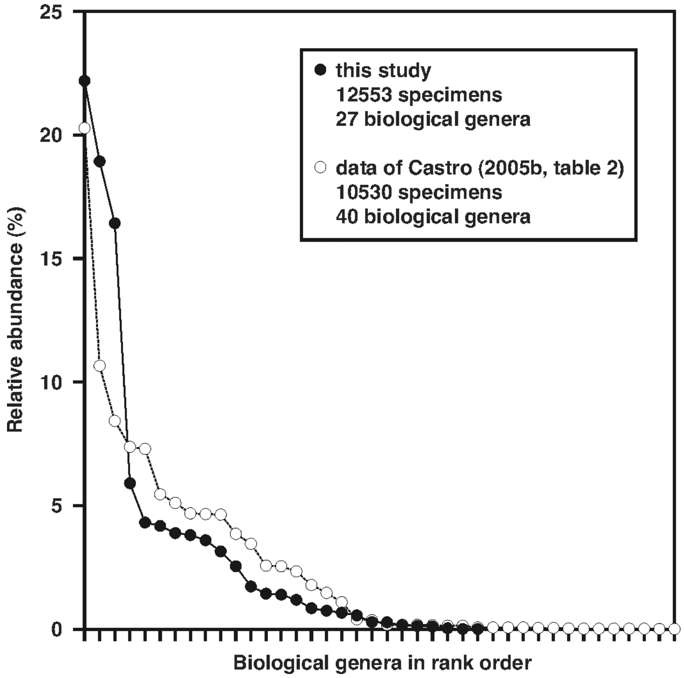


Figure 30. Relative abundance distribution curves, with biological genera arranged in rank order, comparing sample populations in this study and Castro (2005b, table 2). The latter overestimates the abundance of rare taxa and underestimates the abundance of common taxa.

were preferentially collected. In contrast, everything was recorded in this study as a consequence of census sampling. Another difference is that 41.8% of Castro's specimens were derived from spoil tips in former coalmines (i.e., 'roof shales' of rheotrophic mires; Sectors 2 and 5 of fig. 22), whereas mine reclamation precluded our access to this facies. Therefore, although Castro's data provide a more complete record of species richness in La Magdalena Coalfield, it is a less reliable predictor of the biodiversity and paleoecology of the vegetation throughout the coalfield because it is biased towards rare taxa and contains a disproportionate number of specimens from one facies.

3.7. LOCAL-SCALE VEGETATIONAL HETEROGENEITY

Having established the general dominance-diversity characteristics of the sample population, the taphonomy and relative abundances of plant fossils were analyzed in a facies context to determine the composition and spatial heterogeneity of communities at a local scale.

3.7.1. Provenance and Preservation of Plant Remains in Modern Wetlands

Empirical observations indicate that most canopy litter in modern (para)tropical wetland forests is derived from trees growing within a ≈0.1 Ha area (Burnham, 1993). Thus, fossilized parautochthonous megafloral assemblages in wetland deposits represent 'ecological snapshots' of communities that lived in the vicinity, providing an estimate of relative abundances in the source vegetation (Wing & DiMichele, 1995; DiMichele & Gastaldo, 2008). However, leaves and other non-woody canopy organs decay very rapidly if exposed on the forest floor, particularly in (para)tropical environments

(Ferguson, 1985; Gastaldo, 1994; Gastaldo & Staub, 1999). This removes the potential bias of taphonomic time-averaging (Wing & DiMichele, 1995), but it means that plant remains will only be preserved if rapidly buried and moved to an anoxic geochemical setting where microbial decay is minimized.

Studies of modern analogues indicate that abandoned channels can entomb well-preserved plant remains, with most litter derived from channel-flanking vegetation (Gastaldo, 1989; Gastaldo et al., 1989a). Although stagnant or sluggish ponded waters are relatively shallow, their high organic content leads to anoxic or slightly acidic conditions unfavorable to detritivorous, burrowing invertebrates. In contrast, plant remains have a low preservation potential on exposed floodplains (Burnham, 1989; Gastaldo, 1989; Gastaldo et al., 1989a). Preservation occurs only if high sedimentation rates result in rapid burial, such as during anomalous flood events, or if plant remains are deposited in anoxic and/or slightly acidic waters of small ponds or floodplain channels. A persistently high regional water table promotes the preservation of megafloral detritus and upright axes once buried (Gastaldo et al., 2004b; Gastaldo & Demko, in press).

3.7.2. Taphonomy of Quadrats

Qualitative indicators were used to characterize the taphonomy of the 93 quadrats. Three of four facies associations, and eight of 13 facies, were sampled (Tables 10, 17). The majority of quadrats (n = 71) were obtained from coarsening-upward units that record the filling of small ponds (LCU and UCU facies), which were prevalent in interfluve wetlands (FA 3) and uncommon in braided channel belts (FA 2). As a generalization, fossils in the finer grained LCU facies (n = 36) were deposited in relatively deeper water in the middle of ponds. This facies frequently overlies

Table 17. Summary of data collected, biodiversity indices, and relative abundances of main plant groups in eight depositional facies containing megafloral assemblages in La Magdalena Coalfield. Values presented as 'minimum [weighted mean] maximum', with mean values weighted on number of specimens in each quadrat. ([a]) Each quadrat ≈2.5 m^2. ([b]) 22.00 m^2 without DSC facies. S = number of biological species in quadrat; $H = -\sum p_i \ln p_i$, where $p_i = n_i/N$ (proportion of i^{th} species), n_i (number of observations of i^{th} species), and N (number of observations of all species); and $J = H/\ln S$.

Facies	ABC	DSC	ADC	FPC	LCU	UCU	SPY	LAC	Totals/weighted means
Specimens (*N*)	146	240	413	408	5870	4488	521	467	**12553**
Quadrats	1	5	3	6	36	35	5	2	**93**
Mean *N*/quadrat	146	48	138	68	163	128	104	234	**135**
Total bedding plane area sampled (m^2)	0.25	≈12.50[a]	0.75	1.5	9	8.75	1.25	0.5	**34.5[b]**
Species richness (*S*)	[9]	4 [7] 9	5 [6] 8	7 [8] 10	2 [11] 20	1 [9] 16	6 [12] 15	14 [15] 16	**1 [10] 20**
Shannon-Wiener diversity index (*H*)	[1.51]	1.01 [1.20] 1.75	0.50 [0.82] 1.18	1.08 [1.62] 1.94	0.08 [1.48] 2.50	0.00 [1.40] 2.27	1.31 [1.79] 2.21	2.23 [2.27] 2.30	**0.00 [1.47] 2.50**
Pielou's equitability (*J*)	[0.69]	0.56 [0.64] 0.98	0.31 [0.44] 0.61	0.56 [0.77] 0.93	0.12 [0.62] 0.98	0.00 [0.61] 0.91	0.62 [0.74] 0.82	0.83 [0.83] 0.84	**0.00 [0.63] 0.98**
Lycopsids (%)	absent	5.4 [33.8] 44.7	0.0 [0.5] 0.9	absent	0.0 [4.0] 43.8	0.0 [4.9] 44.4	0.0 (0.6) 2.3	0.7 [3.4] 7.9	**0.0 [4.4] 44.7**
Sphenopsids (%)	[8.9]	2.4 [8.8] 18.2	0.0 [0.5] 1.0	0.0 [27.0] 38.5	0.0 [10.9] 75.4	0.0 [10.5] 48.4	0.0 [7.3] 28.7	6.6 [9.8] 15.2	**0.0 [10.7] 75.4**
Ferns (%)	[88.9]	18.4 [20.8] 30.6	0.0 [45.2] 97.2	7.9 [20.8] 52.8	0.0 [36.1] 95.6	0.0 [27.7] 85.0	29.3 [63.6] 92.0	18.2 [58.6] 83.3	**0.0 [35.2] 97.2**
Pteridosperms (%)	[2.2]	6.1 [17.1] 22.5	2.8 [53.8] 98.6	16.5 [51.5] 86.8	0.0 [49.0] 99.1	0.0 [56.6] 100.0	4.6 [25.6] 51.4	9.4 [27.4] 57.0	**0.0 [49.0] 100.0**
Cordaitaleans (%)	absent	15.2 [19.6] 27.9	absent	0.0 [0.7] 1.9	0.0 [0.0] 0.9	0.0 [0.2] 3.0	0.0 [2.9] 13.0	0.0 [0.6] 1.7	**0.0 [0.6] 27.9**

carbonaceous shales or thin, clastic-rich coal seams (CSW facies), and drowning of ephemeral swamp vegetation may have resulted in shallow but anoxic and/or slightly acidic waters that promoted preservation. Most megafloral assemblages are interpreted as parautochthonous, sampling vegetation from the pond perimeter (<100 m transport distance). In contrast, fossils in the coarser grained UCU facies (n = 35) were deposited in shallower water as sediment aggraded and filled the ponds. Rapid burial promoted preservation, and megafloral assemblages are interpreted as near-autochthonous, recording vegetation growing on exposed substrates around ponds that were essentially filled (meters to tens of meters transport distance). The preservation of upright axes in coarsening-upward units indicates that water table levels remained high after burial.

Most other facies probably also contain parautochthonous megafloral assemblages. Those from abandoned channel deposits (ABC and ADC facies, n = 4) are locally associated with upright vegetation and rooted layers, suggesting derivation from vegetation that colonized exposed channel banks. During storm events, flood deposits may have rapidly buried plant remains that blew into pooled waters. Similar processes probably preserved taphocoenoses in narrow floodplain channels (FPC facies, n = 6) on marginal wetlands, with channel-flanking vegetation the source of most litter. Plant remains in splay deposits (SPY facies, n = 5), which temporarily disturbed ephemeral swamp communities, either fell from tree canopies or represent rapidly buried groundcover elements.

In contrast, large logs in the distributary channels (DSC facies, n = 5) are clearly allochthonous, having been transported in the thalweg of channels, as are fragmentary megafloral assemblages from deep lake deposits (LAC facies, n = 2). In both facies, plant remains represent a mixture of fragments removed from various communities. They are therefore of limited use for paleoecological reconstruction, and are only used in the following analyses to support findings based on the 86 (par)autochthonous assemblages.

3.7.3. Community Structure

The 86 (par)autochthonous quadrats are assumed to be isotaphonomic and a faithful representation of a local patch of vegetation (≈0.1 Ha; cf. Burnham, 1993). For each quadrat, several diversity indices were calculated (Table 17) to measure the distribution of biological species in each patch. The indices, combined with qualitative and quantitative inspection of taxonomic data, reveal important insights into the local-scale (sub-hectare) spatial heterogeneity of the vegetation. A particularly informative analysis was to plot the Shannon-Wiener diversity index (H) against the relative abundance of the dominant plant group in the 86 (par)autochthonous quadrats (Fig. 31). Pteridosperms and ferns dominate in 42 (48.8%) and 40 (46.5%) quadrats, respectively, whereas sphenopsids dominate in 4 quadrats (4.6%). Lycopsids and cordaitaleans, where they occur, are always subordinate.

In pteridosperm-dominated quadrats, relative abundance values for pteridosperms range from 34.6 to 100.0% (weighted mean = 77.5%). These quadrats show a range of diversity values ($H = 0.00$ to 2.22), but in comparison with quadrats dominated by ferns or sphenopsids, pteridosperm-dominated assemblages generally have lower diversity (weighted mean = 1.22; ferns = 1.75; sphenopsids = 1.60). Furthermore, pteridosperm relative abundance shows large negative correlation ($r = -0.76$) with H (Fig. 31),

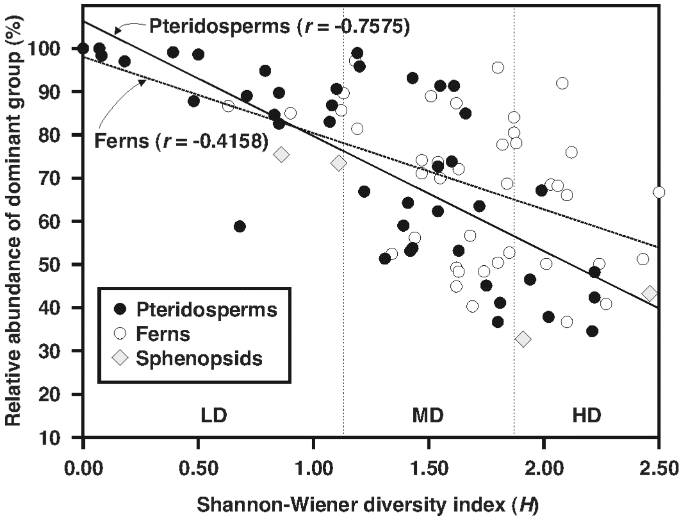


Figure 31. Scatterplot showing relative abundance of dominant plant group in 86 (par)autochthonous quadrats versus Shannon-Wiener diversity index (*H*). Linear correlation coefficients (*r*) given for pteridosperms and ferns. Low diversity (LD): 0.00 to 1.13 (< 25th percentile); medium diversity (MD): 1.13 to 1.87; high diversity (HD): 1.87 to 2.50 (> 75th percentile).

indicating that pteridosperms mostly grew in low-diversity or even monospecific communities. This interpretation is supported by the fact that half (n = 21) of the pteridosperm-dominated quadrats contain >80% pteridosperms. Of these quadrats, 11 are dominated by a single species making up >75% of the sample, whereas the other 10 are co-dominated by two or more pteridosperms. The most common taxa forming monospecific assemblages are *Neuropteris ovata*, *Callipteridium pteridium*, and *Linopteris neuropteroides*, and details for seven quadrats containing the lowest diversity assemblages ($H \leq 0.50$) are given in Table 18. Pteridosperms are also the primary component of medium- and high-diversity quadrats, but these assemblages may record taphonomic mixing of several communities.

In fern-dominated assemblages (Fig. 31), fern relative abundance ranges from 36.7 to 97.2% (weighted mean = 68.8%). Quadrats have a wide range of diversity values (H = 0.63 to 2.50), but they are generally higher (weighted mean = 1.75) than those of pteridosperm-dominated samples. This inference is confirmed by medium negative correlation between fern relative abundance and H (r = -0.42). Twelve quadrats contain >80% ferns, but only one (MG-31) is dominated by a single species (*Pecopteris arborescens*) making up >75% of the sample. This indicates that ferns did not form the kind of monospecific assemblages that pteridosperms did. Instead, most low diversity quadrats are dominated or co-dominated by one or more species of *Pecopteris* or *Polymorphopteris*, although *Nemejcopteris feminaeformis*, *Diplazites longifolius*, and *Oligocarpia gutbieri* are locally abundant.

In sphenopsid-dominated assemblages (Fig. 31), sphenopsid relative abundance ranges from 32.7 to 75.4% (weighted mean = 55.8%), and diversity values are variable

(*H* = 0.86 to 2.46, weighted mean = 1.60). The small number of sphenopsid-dominated quadrats implies that the group was most common in mixed plant communities. Nevertheless, the sphenopsids are widespread, with *Annularia* and *Sphenophyllum* occurring in 51 and 54 quadrats, respectively; only *Pecopteris* (79 quadrats) and *Callipteridium* (59 quadrats) occur more frequently. Likewise, sigillarian lycopsids are never locally dominant, but their remains occur in 46 quadrats. Consequently, it is concluded that the sphenopsids and lycopsids were a subordinate but widespread component of the vegetation in the coalfield. In contrast, cordaitaleans had a limited distribution, being present in only 15 quadrats, and their very low absolute abundance in the sample population confirms that they were rare even when present.

3.7.4. Evidence for Spatial Heterogeneity and Ecological Persistence

The dominance-diversity patterns discussed above provide indirect support for spatial heterogeneity of the vegetation. Specifically, the results imply that small, low-diversity patches of pteridosperms were interspersed in a fern-dominated matrix, together with subordinate but widespread sphenopsids and lycopsids. To provide more conclusive evidence for patchiness, particularly among the pteridosperms, some key, very low-diversity assemblages (Table 18) were examined in detail. Furthermore, patch size was estimated by looking at replicates taken along-strike on single bedding planes.

On one especially informative bedding plane, a quadrat (MG-36; 0.25 m^2) was obtained from Section D along Highway C–623 (Fig. 26), and a large (2.5 m high x 11.0 m wide; 27.5 m^2) exposure of the same surface was examined but not quantified in Section D-AUX, ≈8 m along strike. The remains of *Neuropteris ovata* dominated the

Quadrat	Meterage (m)	Facies	N	H	Redistributed relative abundances of biological taxa
MG-37	836.1	UCU	287	0.00	*Linopteris neuropteroides* (100.0 %)
MG-33	816.5	UCU	101	0.07	*Neuropteris ovata* (98.6 %); *Dicksonites plukenetii* (1.4 %)
MG-41	830.1	LCU	299	0.08	*Neuropteris ovata* (98.3 %); *Sigillaria* sp. (1.7 %)
MG-36	832.7	UCU	168	0.18	*Neuropteris ovata* (96.3 %); *Cordaites* sp. (3.0 %); *Linopteris neuropteroides* (0.8 %)
MG-42	826.0	LCU	114	0.39	*Callipteridium pteridium* (88.6 %); *Neuropteris ovata* (10.6 %); *Cordaites* sp. (0.9 %)
MG-55	1033.5	ADC	213	0.50	*Neuropteris ovata* (85.3 %); *Callipteridium pteridium* (12.7 %); *Sigillaria* sp. (0.9 %); *Linopteris neuropteroides* (0.6 %); *Calamites* sp. (0.5 %)

Table 18. Details of six quadrats containing very low-diversity megafloral assemblages ($H \leq 0.50$). Meterage is vertical distance above base of basin-fill (see Figs. 26, 29 for position). N is number of counts in quadrat; H is Shannon-Wiener diversity index.

quadrat (Table 18), and were exclusively present on the surface of the large exposure, which also contained pteridosperm roots and several large, striate axes with recurved branches similar to those attributed to *N. ovata* (Laveine & Brousmiche, 1985; Zodrow & Cleal, 1988). This assemblage clearly originated beneath a monospecific patch of *N. ovata*, based on the association of foliar and axial components of the same species and the absence of litter from other taxa. Assuming continuity of vegetation cover between the large bedding plane and quadrat along the highway (≈8 m), the monospecific stand had a minimum diameter of 19.5 m. In addition, when a small area on the large bedding plane (Section D-AUX) was excavated, successive laminae continued to contain only *N. ovata* to a depth of ≈200 mm below the surface. This attests to ecological persistence of the pteridosperm-dominated communities. This pattern of persistence was evident at all sites listed in Table 18, particularly at MG-55, where *N. ovata* was dominant through >700 mm of interbedded sandstone and siltstone.

On another exposed bedding plane, three replicates (MG-35.1 to 35.3; 0.75 m^2) were obtained from Section D (Fig. 26), and two replicates (MG-35.4, 35.5; 0.50 m^2) from Section D-AUX ≈14 m along strike (Fig. 32). The surface was unexposed in the intervening area. Individual quadrats contain seven to 11 biological species, and 14 species are present in all five replicates combined. However, only five taxa are common to all five quadrats (*Neuropteris ovata*, *Pecopteris* spp., *Polymorphopteris polymorpha*, *Asterophyllites equisetiformis*, and *Sphenophyllum* spp.). The ferns are dominant or co-dominant in all quadrats, suggesting that a fern-dominated community was the main contributor to the taphocoenosis. However, fern and sphenopsid relative abundances increase towards the northeast, concomitant with a marked reduction in *Neuropteris*

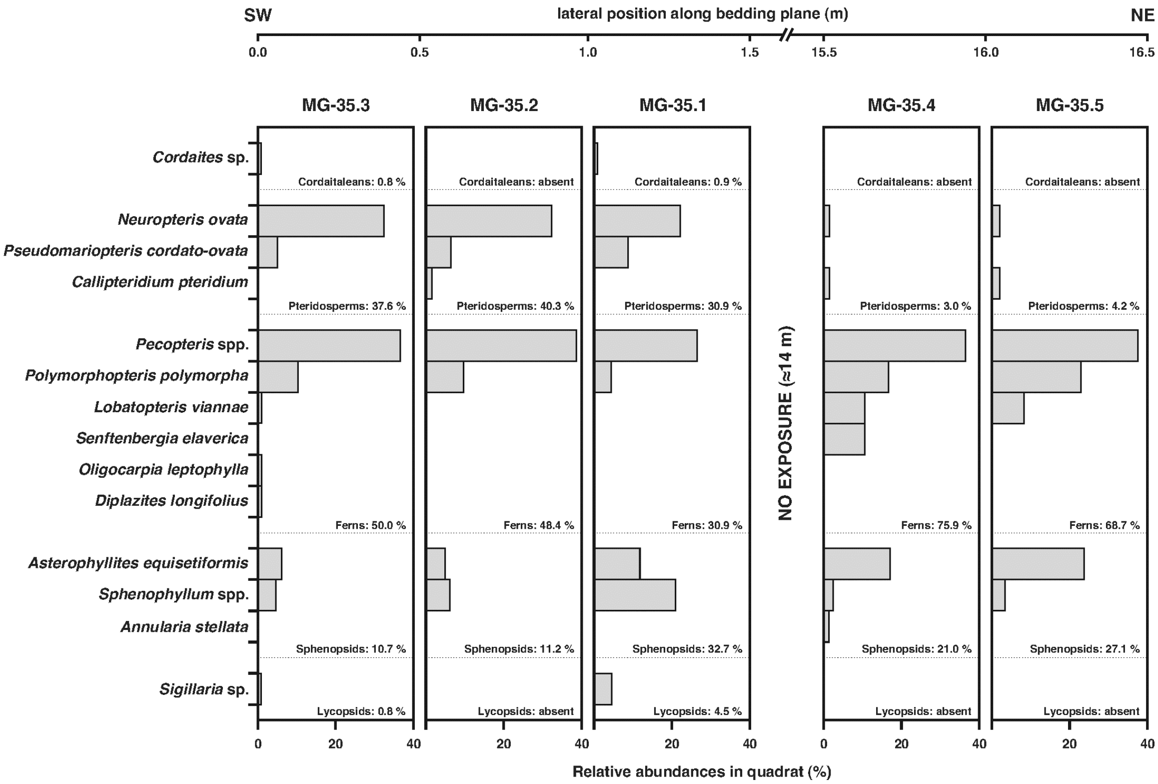


Figure 32. Schematic diagram showing relative abundances of biological taxa in five replicates taken along single bedding plane (MG-35) in Section D and laterally correlative Section D-AUX (at 834.0 m above base of succession).

ovata and *Pseudomariopteris cordato-ovata*. These observations again imply that a clump of pteridosperms (dominated by *N. ovata*) existed in a more continuous belt of fern-dominated vegetation. Assuming minimal transport of pteridosperms from their growth site, and given that *N. ovata* occurs in all five replicates, the radius of the pteridosperm-dominated patch would have been >15 m.

3.8. LANDSCAPE-SCALE ECOLOGICAL GRADIENTS

Examination of megafloral assemblages at individual horizons sheds important light on the local structure and patchiness of vegetation. However, where there is limited exposure along single bedding planes, it is difficult to determine lateral compositional changes and landscape-scale gradients. Nonetheless, when assemblages are analyzed in a facies context, a large number of quadrats sampling a variety of depositional environments in a vertical succession can be used to infer large-scale temporal and spatial vegetation patterns.

3.8.1. Multivariate Analysis of Quadrats (NMDS)

To determine if landscape-scale ecological gradients existed in the data set, the 86 (par)autochthonous quadrats were analyzed using non-metric multi-dimensional scaling (NMDS), a type of unconstrained ordination that allows multivariate data sets to be visualized in n-dimensional space, revealing trends or groupings. Prior to analyses, once-occurring biological genera (*Danaeites*, *Lescuropteris*) and non-biological fossil genera (*Calamites*, *Caulopteris*, *Megaphyton*) were removed from the redistributed abundance matrix (Table 13). Quadrats were divided into four groups (Table 10), each comprising a unique depositional setting when viewed from a basin-scale context: (i) marginal wetland deposits (FA 3, n = 7) overlying debris flow breccias (FA 1) at the base of the succession; (ii) braided channel belt deposits (FA 2, n = 8); (iii) interfluve wetland deposits (FA 3, n = 5) occurring ≤5 vertical meters from FA 2, inferred to be wetlands directly adjacent to braided channels; and (iv) interfluve wetland deposits (FA 3, n = 66) occurring >5 vertical meters from FA 2, inferred to be wetlands distant from braided channels. Under the assumption that all vegetation types coexisted on the landscape, group comparison allowed two key questions to be addressed: (i) did wetland communities adjacent to basin-margin slopes differ from those in more distal positions; and (ii) did occupying a disturbance-prone setting adjacent to major braided channel belts influence community composition? The chord distance measure was used, which normalizes away absolute abundance values (Ludwig & Reynolds, 1988). This is preferred because the population is dominated by a few genera, and important information from rarer genera could be obscured under the variation in abundance of these dominant elements (Hammer & Harper, 2006). The ordination was run in two dimensions using PAST (v. 1.86b; Hammer et al., 2001).

The NMDS ordination plot (Fig. 33A) demonstrates that quadrats from marginal wetlands, braided channel belts, and interfluve wetlands adjacent to braided channels form tight clusters, although each group overlaps the widely scattered point cloud produced by quadrats of interfluve wetlands distant from braided channels. A PERMANOVA analysis indicates statistically significant differences between the four groups [$F = 2.89$, *p(same)* = 0.0001]. However, quadrats from braided channel belts and interfluve wetlands adjacent to braided channels clearly intergrade, and pairwise

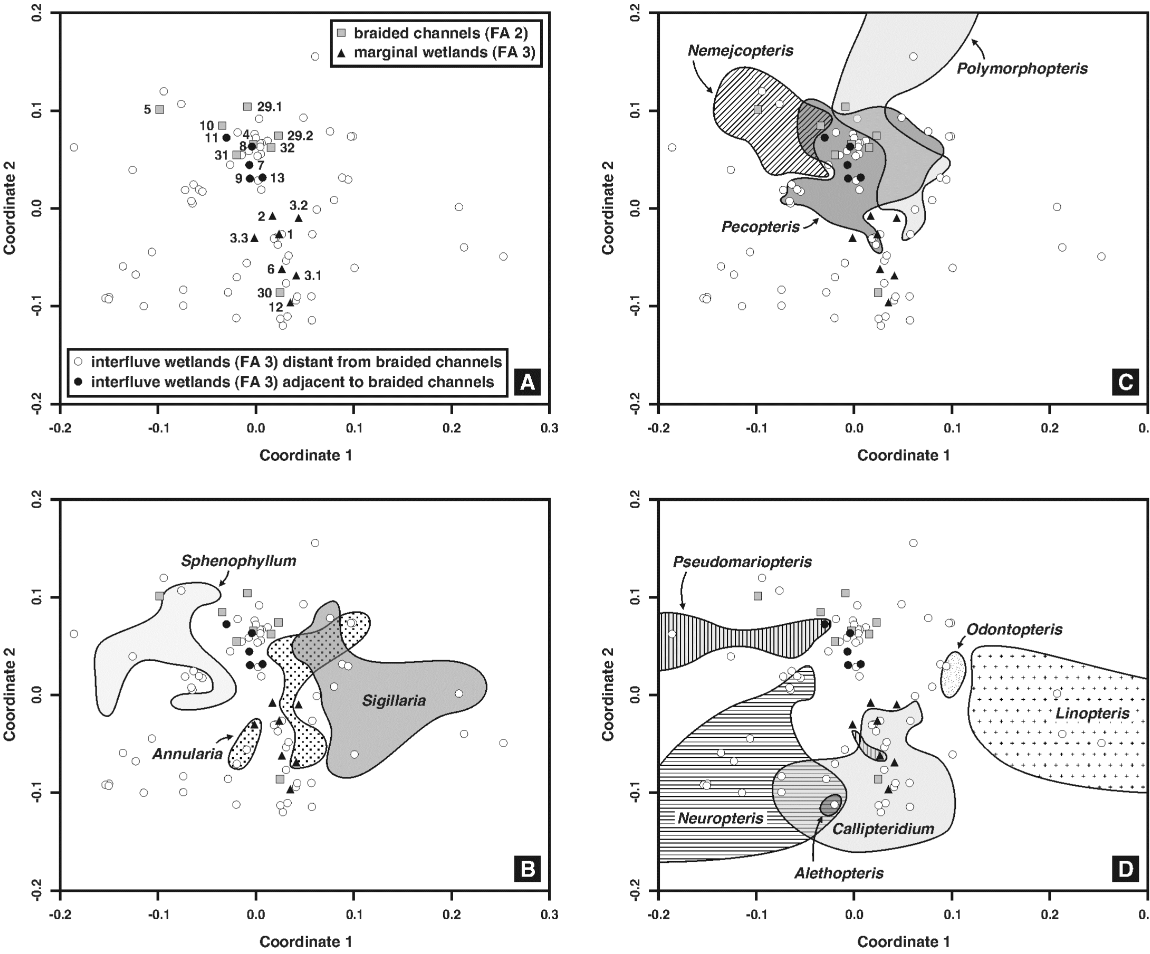


Figure 33. A. Two-dimensional ordination plot after non-metric multi-dimensional scaling (NMDS) of 86 (par)autochthonous quadrats separated into four groups: (i) marginal wetland deposits (FA 3, n = 7) overlying debris flow breccias (FA 1); (ii) braided channel belt deposits (FA 2, n = 8); (iii) interfluve wetland deposits (FA 3, n = 5) vertically adjacent (≤5 m) to FA 2; and (iv) interfluve wetland deposits (FA 3, n = 66) vertically distant (>5 m) to FA 2. Computed from redistributed absolute abundance matrix (Table 13) comprising 25 biological genera and using chord distance measure. B. Relative abundance contour lines (≥25%) for sphenopsids (*Annularia*, *Sphenophyllum*) and the lycopsid *Sigillaria*. C. Relative abundance contour lines for ferns (*Pecopteris*, *Polymorphopteris*, *Nemejcopteris*). D. Relative abundance contour lines for pteridosperms (*Callipteridium*, *Alethopteris*, *Pseudomariopteris*, *Neuropteris*, *Linopteris*, *Odontopteris*).

PERMANOVAs between all pairs of groups in a post-hoc test indicate that the two groups can not be differentiated in multivariate space [*p(same)* = 0.25], confirming the outcome of visual examination. To help clarify the distribution of plants on the braided-river plain, contour lines were drawn on the ordination plot delineating zones where the most abundant biological genera have a relative abundance of ≥25% (lycopsids and sphenopsids: Fig. 33B; ferns: Fig. 33C; pteridosperms: Fig. 33D).

3.8.1.1. Marginal Wetlands (FA 3)

Abundance data from individual quadrats indicate that marginal wetlands differ from interfluve wetlands higher in the succession because: (i) *Callipteridium*, *Annularia*, *Alethopteris*, and *Pseudomariopteris* are more abundant; (ii) *Pecopteris* is less abundant and *Polymorphopteris* is absent; (iii) *Neuropteris* and *Linopteris* are rare and *Odontopteris* is absent; and (iv) lycopsids are absent. Pteridosperms dominate or co-dominate with sphenopsids and/or ferns in all but one quadrat (MG-3.2).

Multivariate analysis confirms most of these observations. *Callipteridium* forms an important component in all seven quadrats, which explains why data points lie within or on the periphery of its abundance contour, far from the centroids of the rare pteridosperms *Neuropteris* and *Linopteris* (Fig. 33D). Quadrats co-dominated by sphenopsids (particularly *Annularia*; Fig. 33B) and ferns (*Pecopteris*; Fig. 33C) plot closer to the center of the point cloud. Based on these observations, it is concluded that marginal wetlands adjacent to steep, basin-margin slopes were dominated by pteridosperms (particularly *Callipteridium*, with lesser *Alethopteris* and *Pseudomariopteris*), with subordinate ferns and sphenopsids.

3.8.1.2. Braided Channel Belts (FA 2)

Braided channel deposits are characterized by fern dominance, which explains their tight clustering in the upper middle of the ordination plot (Fig. 33C). They are either dominated by *Pecopteris* (MG-4, 31, 32), or co-dominated by *Pecopteris* and *Polymorphopteris* (MG-29.1, 29.2) or *Pecopteris* and *Nemejcopteris* (MG-5, 10). Sphenopsids, particularly *Sphenophyllum*, *Annularia*, and *Asterophyllites*, are locally important (Fig. 33B). MG-30 deviates from this pattern, being dominated by *Callipteridium* (Fig. 33D), indicating that pteridosperms were not entirely excluded from disturbed channel belts.

3.8.1.3. Interfluve Wetlands (FA 3) Adjacent to Braided Channels

Like the braided channel belt, interfluve wetland deposits laid down adjacent to braided channels are fern-dominated, which is why the groups overlap in multivariate space (Fig. 33A). In this transitional and disturbance-prone setting, *Pecopteris* is the most abundant fern, which explains why all five quadrats lie within its abundance contour (Fig. 33C), together with significant *Nemejcopteris* (Fig. 33C) and *Pseudomariopteris* (Fig. 33D) in MG-11. *Callipteridium* has atypically low proportions, whereas *Alethopteris* is more abundant than usual. However, the presence of both biological genera in the lowermost quadrats (MG-7, 9, 13) is responsible for pulling them downwards on the plot (Fig. 33D).

3.8.1.4. Interfluve Wetlands (FA 3) Distant from Braided Channels

Of the 66 quadrats from interfluve wetlands that accumulated far from braided channel influence, inferred to comprise relatively undisturbed habitats, pteridosperms (n = 35) or ferns (n = 27) dominate in most, whereas sphenopsid dominance is rare (n = 4). Of the pteridosperms, *Callipteridium* remains an important component of many assemblages (Fig. 33D). However, a crucial observation is that *Neuropteris* dominates or co-dominates in many quadrats, and that *Linopteris* and *Odontopteris* are important at scattered localities (Fig. 33D); these biological genera are conspicuously absent or rare in the other three depositional settings. In addition, there is a marked reduction in *Alethopteris* and *Pseudomariopteris*, although both are locally abundant. Regarding the ferns (Fig. 33C), *Pecopteris* remains the most important genus, but *Polymorphopteris* and *Oligocarpia* dominate or co-dominate in some samples. In addition, *Nemejcopteris* is less abundant here than in the braided channel belt. Sphenopsids (*Annularia*, *Sphenophyllum*) and lycopsids (*Sigillaria*) are widespread but rarely dominant (Fig. 33B), although the latter is much more common here than elsewhere.

3.8.2. Summary of Ecological Gradients

The NMDS analysis reveals clear ecological gradients in La Magdalena Coalfield. On the whole, marginal wetlands were dominated by pteridosperms. Fern-dominated communities characterized disturbance-prone braided channel belts and interfluve wetlands close to braided rivers. A mixture of pteridosperm- and fern-dominated communities existed in the interfluve wetlands distant from the influence braided rivers. Furthermore, the analysis demonstrates vegetational gradients among the pteridosperms.

Neuropteris, *Linopteris*, and *Odontopteris* apparently preferred distal, less disturbed interfluve wetlands, whereas *Alethopteris* and *Pseudomariopteris* were more common in frequently disturbed areas closer to braided rivers. *Callipteridium* was more cosmopolitan and occupied both settings.

3.9. PALEOECOLOGICAL SYNTHESIS

Drawing together results from Sections 3.5 to 3.8, a detailed paleoecological synthesis emerges for Late Pennsylvanian vegetation of La Magdalena Coalfield. Discrete communities are recognized in four main depositional environments: (i) marginal wetlands adjacent to basin margins; (ii) braided channel belts; (iii) interfluve wetlands; and (iv) lake shorelines.

3.9.1. Communities on Marginal Wetlands (FA 3)

The vegetation of marginal wetlands, which developed along the basin margin, differed from that of interfluve wetlands (FA 3) higher in the succession. In particular, marginal wetlands were dominated by the pteridosperm *Callipteridium*, with lesser *Alethopteris* and *Pseudomariopteris*, whereas *Neuropteris* and *Linopteris* were rare to absent. Sphenopsids (especially *Annularia*) and ferns (*Pecopteris*) were subordinate, and lycopsids were absent. The differences may imply that these communities were in a state of flux, possibly transitional from vegetation that colonized inactive parts of associated debris flow breccias (FA 1), or even the steep slopes of the basin margin itself. Based on previous whole-plant reconstructions, marginal wetland communities comprised a low canopy of the medullosalean pteridosperms *Callipteridium* (Laveine et al., 1977) and

Alethopteris (Laveine, 1986; Zodrow, 2007), along with scattered occurrences of the marattialean tree fern *Pecopteris* (Morgan, 1959; Willard & Phillips, 1993; DiMichele & Phillips, 2002). The understory consisted of sub-arborescent *Calamites* with *Annularia* foliage, and the callistophytalean pteridosperm *Pseudomariopteris* either occurred as groundcover or a liana (Krings & Kerp, 2000).

Conchoidally weathered siltstones in the breccia pile (FA 1) may record weak rooting, but the source vegetation is unknown. Nonetheless, the lowest margin wetland quadrat (MG-12) lies just 1.6 m above the breccia pile (Fig. 26), indicating that marginal wetlands and breccias probably were spatially juxtaposed in places. MG-12 is dominated by pteridosperms (86.8%), particularly *Callipteridium* (71.0%), and it is plausible that the latter occupied inactive surfaces of debris flow deposits. In addition, a large *Dicranophyllum gallicum* specimen was discovered at an isolated outcrop (not quantified), situated upslope from Highway C–623 but in strata correlative with marginal wetland deposits of Section A (Figs. 24C, 26), lying just 4.5 m above Precambrian basement. *Dicranophyllum* may be an early conifer (Barthel, 1977) that formed a component of 'upland' vegetation in well-drained habitats (Barthel et al., 1998; Wagner, 2005), and comprised densely spaced, slender, unbranched stems up to 3 m high (Barthel et al., 1998; Barthel & Noll, 1999). Castro (2005a, b) also recorded this species, but only from Mina Luisa (Section H; Figs. 24C, 26) next to the basin margin. These observations suggest that *Dicranophyllum* may have been part of plant communities on basin-margin slopes.

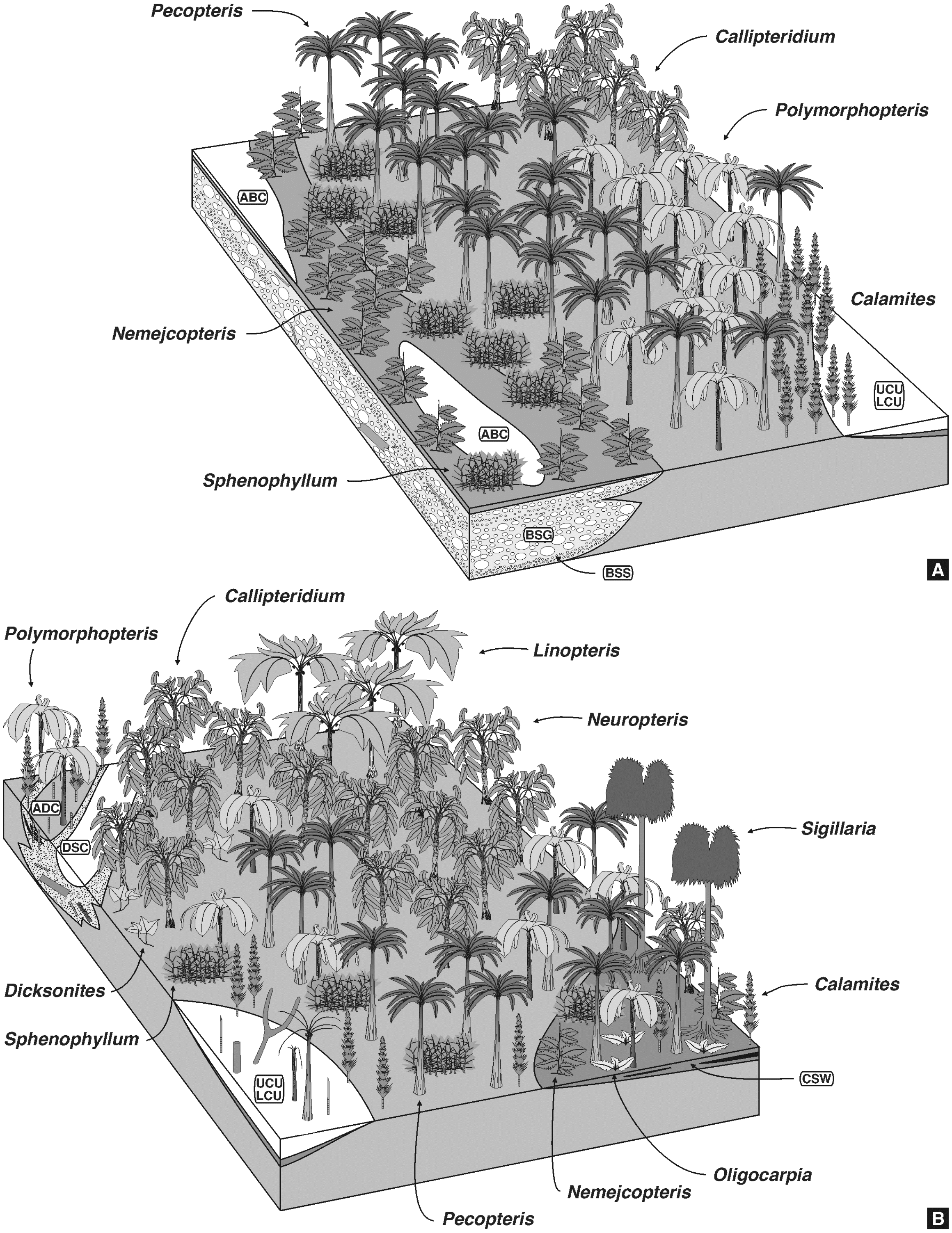
Ephemeral swamps (CSW facies) were common in marginal wetlands, but the absence of lycopsid remains indicates that another plant clade dominated this facies. An upright pteridosperm was observed in a floodplain channel (FPC facies), but it was rooted in a subjacent swamp deposit. Thus, it is possible that ephemeral swamps, like all other habitats on the marginal wetlands, were dominated by pteridosperms.

3.9.2. Communities in Braided Channel Belts (FA 2)

The NMDS analysis (Fig. 33) indicates that ferns dominated braided channel belts (Fig. 34A), particularly the arborescent marattialeans *Pecopteris* and *Polymorphopteris* (Zodrow et al., 2006) and the low-stature zygopterid *Nemejcopteris*, which crept along the forest floor (Barthel, 1968; Phillips & Galtier, 2005). Sphenopsids were locally abundant, especially sub-arborescent calamiteans bearing *Annularia* foliage and thicket-forming sphenophylls (Batenburg, 1977, 1981; Galtier & Daviero, 1999; Bashforth & Zodrow, 2007). Arborescent medullosalean pteridosperms such as *Callipteridium* had a sporadic distribution.

The prevalence of ferns and sphenopsids is not surprising in such a dynamic, disturbance-prone environment. The tree ferns were ‘cheaply’ constructed, grew rapidly, and produced large quantities of spores, consistent with an opportunistic life history and the potential for wide dispersal and prompt colonization of disturbed habitats (Willard 1993; DiMichele & Phillips 1994, 2002; Baker & DiMichele, 1997). Furthermore, they could regenerate through repeated burial events (Falcon-Lang, 2006b). Similarly, the sphenopsids, particularly calamiteans, formed clonal, regenerative groves on unstable, rapidly aggrading substrates (Gastaldo, 1992; Pfefferkorn et al., 2001). In contrast, the medullosalean pteridosperms were architecturally complex, bore large seeds, and had a comparatively low reproductive output, all characters of long-lived site-occupiers that

Figure 34. Reconstruction of plant communities on braided-river plain of La Magdalena Coalfield. A. Vegetation adjacent to braided channel belt (FA 2). Low-stature *Nemejcopteris* and *Sphenophyllum* occupy newly exposed substrates of an abandoned braided channel (ABC facies), and form the groundcover of a stand of marattialean tree ferns (*Pecopteris*) on the channel flanks. *Polymorphopteris* only partly mixes with the larger *Pecopteris* stand. A *Calamites* grove surrounds a shallow pond (LCU and UCU facies), and a monospecific clump of the medullosalean *Callipteridium* is situated more distant from the channel and pond. B. Vegetation on interfluve wetlands (FA 3). In the upper left, *Calamites* and the marattialean tree fern *Polymorphopteris* inhabit newly exposed substrates of an abandoned distributary channel (ADC facies). On the opposite bank of the distributary channel (DSC facies), a low-diversity, pteridosperm-dominated community comprises a low canopy of *Callipteridium* above a groundcover of *Dicksonites*. Monospecific patches of *Linopteris* and *Neuropteris* form distant from channel influence. In the lower right, the canopy of an ephemeral swamp (CSW facies) community comprises abundant tree ferns (*Pecopteris*, *Polymorphopteris*) and lesser pteridosperms, whereas the groundcover contains *Oligocarpia*, *Nemejcopteris*, and *Sphenophyllum*; the arborescent lycopsid *Sigillaria* forms scattered emergents. In the lower left, a mixture of tree ferns and sphenopsids occupies the margin of a shallow pond (LCU and UCU facies) that contains the drowned vegetation of a preexisting ephemeral swamp.


Pecopteris
Callipteridium
Polymorphopteris
ABC
Calamites
Nemejcopteris
UCU
LCU
ABC
Sphenophyllum
BSG
BSS
A
Callipteridium
Polymorphopteris
Linopteris
Neuropteris
ADC
DSC
Sigillaria
Dicksonites
Sphenophyllum
Calamites
UCU
LCU
CSW
Oligocarpia
Nemejcopteris
Pecopteris
B

reproduced infrequently or over extended intervals (DiMichele et al., 2006b). Hence, occupying a disturbance-prone setting would have conferred a paleoecological disadvantage on the pteridosperms, which may explain their rarity. Ephemeral swamps (CSW facies) were rare and rheotrophic mires (RTM facies) absent in the braided channel belt. This may reflect high levels of disturbance, with frequent incursions of sediment inhibiting sustained organic accumulation.

Braided channel deposits (BSS and BSG facies) contain rare allochthonous axes of *Sigillaria* and *Calamites*, along with pteridosperm branches. No tree ferns were recognized, but their non-woody stems may have suffered rapid mechanical degradation under the prevailing high-energy flow conditions. Large woody debris in fluvial channels is primarily derived from channel-flanking vegetation that toppled due to bank undercutting or bar erosion (Scheihing & Pfefferkorn, 1984; Latterell & Naiman, 2007), and the presence of an upright pteridosperm axis in the BSS facies confirms that some axes have a local origin. However, as lycopsid canopy organs are rare in quadrats from the braided channel belt, the *Sigillaria* trunks may have entered channels when they avulsed through interfluve wetlands (Gastaldo & Degges, 2007; Gibling et al., 2010).

3.9.3. Communities on Interfluve Wetlands (FA 3)

The large number of quadrats, combined with taphonomic observations, permits a detailed reconstruction of the composition and distribution of vegetation on interfluve wetlands (Fig. 34B). A heterogeneous mosaic of communities existed, reflecting the range of depositional environments present. Non-peat-forming vegetation dominated, but organic accumulation occurred in ephemeral swamps and rheotrophic mires.

3.9.3.1. Ephemeral Swamp Communities

Several lines of evidence shed light on the vegetation of ephemeral swamps, which developed in small depressions and are recorded by thin lenses of carbonaceous shale and clastic-rich coal (CSW facies). Unfortunately, 10 palynology samples from the facies were barren. Roots are common beneath the organic accumulations (O-horizons?), although the affinity of most is unknown and stigmarian rhizomorphs are rare. Coarsening-upward units (LCU and UCU facies) that overlie swamp deposits record the drowning of swamp vegetation (Fig. 34B), and upright axes entombed in pond-fills, but rooted in the swamps, include common *Sigillaria*, along with rare marattialean tree ferns and sphenophylls. In addition, (par)autochthonous megafloral assemblages from pond-fills may represent canopy organs of swamp-inhabiting plants. Either ferns (especially *Pecopteris* with lesser *Nemejcopteris*) or pteridosperms (*Callipteridium* or *Neuropteris*) dominate these taphocoenoses (n = 17), but sphenopsids are locally important (*Annularia* and lesser *Sphenophyllum*) and lycopsids are rare (*Sigillaria* or '*Lepidodendron*').

(Par)autochthonous megafloral assemblages preserved in splays (SPY facies), which temporarily interrupted organic accumulation, may comprise ephemeral swamp vegetation. Flood sediments may have buried groundcover elements, whereas canopy organs may have been torn from arborescent plants by concomitant strong winds. Ferns (particularly *Pecopteris*, with lesser *Diplazites*, *Oligocarpia*, or *Senftenbergia*) or pteridosperms (*Callipteridium* with lesser *Alethopteris*) dominate these taphocoenoses (n = 5; Table 17), although sphenopsids (*Annularia*) are locally important. Lycopsid remains are rare, but an upright *Sigillaria* stump, rooted in an ephemeral swamp deposit, is entombed in one splay. *Cordaites* are also rare, but more common in this facies than any other (Table 17).

In summary, ephemeral swamp communities were either dominated by marattialean tree ferns (particularly *Pecopteris*), together with some understory and groundcover forms, or by medullosalean pteridosperms (particularly *Callipteridium*). Sphenopsids with sub-arborescent and groundcover habits were locally abundant. Arborescent lycopsids (particularly *Sigillaria*), which would have emerged tens of meters above the canopy (Phillips & DiMichele, 1992), were surprisingly rare, although they likely were more common in swamps than in non-peat-forming habitats on interfluve wetlands.

3.9.3.2. Rheotrophic Mire Communities

During intervals when humid climatic conditions prevailed, prolonged peat accumulation resulted in extensive rheotrophic mires, preserved as dm- to m-scale coal seams (RTM facies). Mine reclamation precluded quantitative sampling of this facies, although an exposed ‘seat earth’ at Mina Irene (Section G; Fig. 24C) provides insight into the composition of mire vegetation. Two types of rooting structure occur on this paleosol surface. Most common are swollen, circular (non-stigmarian) rooting structures attributed to *Omphalophloios*, a small-stature, arborescent lycopsid (Wagner, 1989; Brousmiche-Delcambre et al., 1995; Wagner et al., 2003) with an opportunistic or colonizing life history (DiMichele & Phillips, 1994). Less common are stigmarian rhizomorphs of arborescent sigillarians and/or lepidodendroids. Additional impressions include common prone axes of *Sigillaria*, *Asolanus*, and decorticated lycopsids, along with lesser *Calamites* and uncommon pteridosperm and/or fern petioles. These (par)autochthonous axes indicate that various arborescent lycopsids formed an important component of rheotrophic mires, at least initially. Sphenopsids, tree ferns, and pteridosperms were undoubtedly important in some phases of mire development, although they may have been more common in ephemeral swamps.

3.9.3.3. Non-peat-forming Communities

The interfluve wetlands were dominated by non-peat-forming vegetation, the composition and distribution of which is well constrained by abundant (par)autochthonous megafloral assemblages in pond-fills (LCU and UCU facies, n = 64) and abandoned distributary channel deposits (ADC facies, n = 3). NMDS analysis (Fig. 33) demonstrates that ecological gradients existed on interfluve wetlands, with fern-dominated communities adjacent to disturbance-prone braided channel belts, and a mixture of pteridosperm and fern dominance further from channel influence. In addition, vegetational gradients were present among the pteridosperms, with *Callipteridium*, *Pseudomariopteris*, and *Alethopteris* favoring wetlands fringing braided channel belts, and *Callipteridium*, *Neuropteris*, *Linopteris*, and *Odontopteris* more common in undisturbed settings distant from braided rivers. Of the ferns, the marattialeans *Pecopteris* and *Polymorphopteris* were most abundant, whereas the sphenopsids (particularly *Annularia* and *Sphenophyllum*) and lycopsids (*Sigillaria*) were widespread but rarely dominated communities. Dominance-diversity characteristics of megafloral assemblages (Fig. 31), together with along-strike compositional changes on bedding planes (Fig. 32), imply that non-peat-forming communities were heterogeneous and comprised large swathes of ferns that enclosed monospecific or low-diversity patches of persistent pteridosperms (Table 18).

In fern-dominated communities (Fig. 34B), *Pecopteris* formed a dense but low canopy above an understory of *Polymorphopteris*, *Sphenopteris*, and *Calamites*. A range of taxa blanketed the forest floor, particularly thicket-forming sphenophylls and the small-stature ferns *Nemejcopteris* and *Oligocarpia* (Stevens & Hilton, 2009). Groundcover presumably formed in canopy gaps, possibly sustained by recurring disturbance. Monospecific or low-diversity patches of medullosalean pteridosperms (Fig. 34B), comprising *Callipteridium*, *Alethopteris*, *Neuropteris* (Laveine & Brousmiche, 1985; Zodrow & Cleal, 1988) and/or *Linopteris* (Laveine et al., 1993; Zodrow et al., 2007), would have had canopy and understory heights similar to those of the surrounding fern-dominated communities. Groundcover included the fern *Diplazites*, along with the scrambling or climbing callistophytalean pteridosperms *Pseudomariopteris* and *Dicksonites* (Rothwell, 1981; Galtier & Béthoux, 2002; DiMichele et al., 2006b) and the medullosalean pteridosperm *Odontopteris* (Šimůnek & Cleal, 2004; Krings et al., 2006). Again, groundcover and lianescent taxa probably thrived in canopy gaps. The arborescent lycopsid *Sigillaria* and tall cordaitalean trees (e.g., Falcon-Lang & Bashforth, 2004, 2005) probably had a sporadic distribution, and would have towered tens of meters above the dense canopy of arborescent ferns or pteridosperms.

Scours and soft-sediment deformation in distributary channels (DSC facies) that traversed interfluve wetlands probably represent cryptic VISS, indicating that plants grew along channel margins. Upright *Calamites* axes were found near the top of some channel-fills, particularly in abandoned distributary channel deposits (ADC facies).

Large pinnae of marattialean tree ferns (*Pecopteris* or *Polymorphopteris*) and medullosalean pteridosperms (*Neuropteris*) were recovered from this facies, and their limited disarticulation implies growth in or adjacent to abandoned channels (Fig. 34B; DiMichele et al., 2005, 2006b).

3.9.4. Communities Associated with Deep Lakes (FA 4)

Thick coarsening-upward units that record the filling of deep lakes (LAC facies), and intermittent distributary channels (DSC facies) feeding the lakes, are nearly devoid of plant remains. In fact, only two quadrats were obtained from ≈100 m of strata. In modern lacustrine environments, plant litter tends to be blown into lakes from surrounding vegetation (Spicer, 1981, 1989; Ferguson, 1985), and most is deposited only tens of meters from shore (Rau, 1976; Spicer, 1981). Hence, the two allochthonous assemblages may partly comprise shoreline vegetation. Rare roots of unknown affinity at the top of some coarsening-upward units, together with upright sphenophyll axes, confirm that shorelines were locally colonized.

Ferns dominate one of the quadrats (MG-75), and pteridosperms dominate the other (MG-74), but a mixture of plant clades is present in both. Accordingly, this facies has the highest biodiversity and evenness indices (Table 17). In addition, plant remains are highly fragmented. These observations imply significant transport and mixing of organs derived from several communities. Thus, although some vegetation was probably derived from shoreline communities, particularly the sphenophylls, most identifiable remains probably represent part of the suspended load of distributary channels debouching into the lakes.

3.10. RECONSTRUCTING LANDSCAPES FROM QUADRATS SAMPLING A VERTICAL SUCCESSION

This study shows how the spatial structure and ecological gradients in ancient plant communities can be reconstructed from multiple quadrats sampling a vertical succession of strata. To date, such insights have only been resolved for vegetation buried in a geological instant (a T^0 assemblage), thereby fixing plant relationships in time and space. Several mechanisms can produce a T^0 assemblage, such as sudden inundation of a landscape after an earthquake or channel breaching, or burial by volcanic ash. Gastaldo et al. (2004a, b) quantified compositional changes in the 'roof shale' above a drowned Lower Pennsylvanian mire in Alabama, and documented local-scale heterogeneity in the peat-forming forest. DiMichele et al. (2007) similarly analyzed material above a Middle Pennsylvanian mire in Illinois. Because their study involved a much larger area, they were able to recognize that local-scale heterogeneity was overprinted by landscape-scale ecological gradients. Libertín et al. (2009a) and Opluštil et al. (2009a) documented Middle Pennsylvanian mires buried by volcanic ash in the Czech Republic, and were able to describe forest tiering, synecological relationships, and successional patterns of the peat-forming vegetation in extraordinary detail.

Although plant communities in La Magdalena Coalfield could not be reconstructed at the resolution offered by a T^0 assemblage, local-scale heterogeneity and landscape-scale ecological gradients could be recognized. Although T^0 assemblages represent a precise 'snapshot' of the vegetation in an area at an instant of geological time, the method described in this study provides a series of broader depictions of the vegetative landscape as it changes through time. Therefore, this study demonstrates that a quantitative quadrat approach, together with careful qualitative observations and multivariate statistical analyses, can be used to reconstruct community ecology from a vertical succession of strata.

3.11. CONCLUSIONS

La Magdalena Coalfield was situated in the proximal reaches of a large foreland basin on the western end of the Paleotethys Ocean, and contains the remnants of a Late Pennsylvanian braided-river plain draining the adjacent Variscan Mountains. The ≈1500 m thick basin fill can be divided into four facies associations: (i) debris flow breccias shed from steep slopes along the basin margin; (ii) high-energy gravelbed and sandbed rivers forming a braided channel belt; (iii) marginal wetlands next to the basin margin and interfluve wetlands in more distal positions; and (iv) large, deep lakes.

Quantification of megafloral assemblages in 93 quadrats indicates that pteridosperms and ferns dominated the vegetation, sphenopsids and lycopsids were less common but widespread, and cordaitaleans were rare. Multivariate analysis of 86 (par)autochthonous quadrats in a facies context reveals landscape-scale ecological gradients. Pteridosperms dominated marginal wetlands, and ferns dominated braided channel belts and disturbance-prone interfluve wetlands near channels. Low-diversity or monospecific clumps of pteridosperms enclosed in a more continuous belt of fern-dominated vegetation characterized interfluve wetlands further from channel influence. The distribution of plant clades was related to the complex interplay between edaphic conditions and their life history strategies, and the vegetation responded to disturbance in patterns similar to those found in modern landscapes.

This study demonstrates how both local-scale vegetation heterogeneity and landscape-scale ecological gradients can be inferred from analysis of multiple quadrats sampling a vertical succession, so long as the sedimentary context is well constrained. It therefore offers a new approach to reconstructing the paleoecology of ancient vegetated landscapes.

3.12. ACKNOWLEDGMENTS

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CHAPTER 4: LOG JAMS AND FLOOD SEDIMENT BUILDUP CAUSED CHANNEL ABANDONMENT AND AVULSION IN THE PENNSYLVANIAN OF ATLANTIC CANADA

Martin R. Gibling, Arden R. Bashforth, Howard J. Falcon-Lang, Jonathan P. Allen, and Christopher R. Fielding

4.1. ABSTRACT

Accumulations of logs and flood sediment frequently block modern channels and may trigger avulsion, but these effects are difficult to demonstrate for the ancient record. Braided-fluvial channels in the Pennsylvanian South Bar Formation of Atlantic Canada contain sandstone successions up to 6 m thick of sigmoidal cross-beds, plane beds, and antidunes, deposited rapidly at high-flow-stage. These strata are commonly capped by accumulations up to 2.5 m thick of flattened, coalified logs and coal intraclasts (originally peat fragments), many of which are overlain by mudstone laid down in abandoned channels. The logs include lycopsids, calamiteans, tree ferns, pteridosperms and cordaitaleans, inferred to have grown on inactive braided tracts near the channels. A compaction estimate suggests that one log accumulation was originally more than four times its present thickness. Most accumulations are interpreted as stable 'transport log jams' formed during floods, although some may have been 'unstable jams' stranded on bars during peak-flow recession. Associated with the logs are extrabasinal gravel, mudstone and coal intraclasts, which suggest that floods in sediment-choked channels undercut banks of gravelly sand capped by mud and forested peat, widened the channels,

and toppled riparian vegetation. An estimated blockage ratio of 8% for one accumulation (ratio of the cross-sectional areas of the log jam and host channel) is close to the 10% value considered to cause substantial blockage in some modern rivers. In two instances, a radical change in paleoflow between pre- and post-abandonment channels is consistent with an interpretation that log jams and flood sediment buildup promoted channel-belt avulsion. Although large trees had evolved by Middle to Late Devonian times, it is unlikely that riparian plants occurred in stands that were sufficiently dense to exert a major influence on river dynamics until the Pennsylvanian. Thus, we report some of the earliest evidence for the effects of woody debris on ancient fluvial systems.

4.2. INTRODUCTION

Avulsion is the process by which flow is diverted from an established river channel into a newly incised or a pre-existing channel, and is a fundamental aspect of river dynamics (Slingerland & Smith, 2004). In local avulsions where cutoff and diversion takes place within a channel belt, the new channel rejoins the parent channel downstream (Heller & Paola, 1996). In regional avulsions, a new channel is established on a distant part of the floodplain. Avulsions may be full, with all the flow diverted from the parent channel, or partial, with only a portion of the flow transferred. Where flow in the abandoned reach is greatly reduced, fine-grained sediment accumulates within the former channel.

Where a potential course has a gradient steeper than that of the existing channel, a particular flood may promote avulsion of a system that is near an avulsion threshold (Jones & Schumm, 1999). Alternatively, avulsion may be triggered by events unrelated to the channel gradient, including a change in bed geometry or discharge that reduces the channel's capacity to transport flow. Triggers may involve factors external to the channel system, including fault activity, sea-level rise, or an increase in flood peak discharge, and factors intrinsic to the system, including sediment influx, breakout along animal pathways, and blockage by ice jams, plant growth, log jams, and beaver dams (Jones & Schumm, 1999; Makaske et al., 2002; Slingerland & Smith, 2004). The Holocene history of avulsion in the Rhine-Meuse Delta demonstrates the importance of both external and intrinsic factors (Stouthamer & Berendsen, 2007).

In the ancient record, the appearance and termination of a channel body in a stratigraphic succession implies that channel abandonment and avulsion has taken place, but the trigger mechanism can seldom be identified. Consequently, studies of the ancient record have frequently sought to explain channel behavior by recourse to external factors such as tectonics and sea-level change, for which there may be evidence from broader geological considerations.

We present here unusually clear evidence that intrinsic effects repeatedly caused channel abandonment and avulsion during deposition of the South Bar Formation, a Middle Pennsylvanian braided-river succession in Atlantic Canada. Earlier studies of the formation noted plane beds and antidunes, attributed to deposition during high-flow stage, along with thick beds of logs mixed with sediment (Rust & Gibling, 1990a, b; Fielding, 2006). During a recent re-examination of key sections, it became apparent that many high-flow-stage strata and log accumulations are overlain by mudstone beds deposited in abandoned channels, raising the possibility that rapid flood aggradation and log jams contributed to channel abandonment and avulsion. Although logs are common in ancient channel deposits, the only detailed interpretation of a log jam in the stratigraphic record to date is that of Gastaldo & Degges (2007) from the Lower Pennsylvanian of Alabama. We discuss criteria for identifying log jams in the South Bar Formation based on comparison with modern occurrences, estimate the original thickness of one log accumulation based on a compaction protocol, and consider when log jams might first have become common as large plants evolved.

4.3. SOUTH BAR FORMATION

The South Bar Formation of Middle Pennsylvanian age (Bolsovian to Asturian, or Moscovian; Zodrow & Cleal, 1998) lies within the Sydney Basin of Nova Scotia (Fig. 35A). The formation is up to about 1 km thick and fills a series of bedrock valleys cut into Mississippian formations, the two most prominent valleys running from Kempt Head to Cape Dauphin and along Sydney Harbour (Fig. 35B). Paleoflow is predominantly northeastward, sub-parallel to the valleys (Fig. 35C) and is more uniform in the uppermost parts of the formation, at which level the valleys were largely filled to yield a broad fluvial plain. The formation is faulted against Precambrian rocks at Cape Dauphin, where a basal layer of cobble to boulder conglomerate has clasts up to 230 mm in diameter, and at Bateston where pebbly sandstone beds are present. The relatively coarse-grained particles suggest that the faulted strata lay near the original basin margin. We conducted detailed studies in the type section at South Bar on the east side of Sydney Harbour, and at Cape Dauphin and Bateson (Fig. 35C, D).

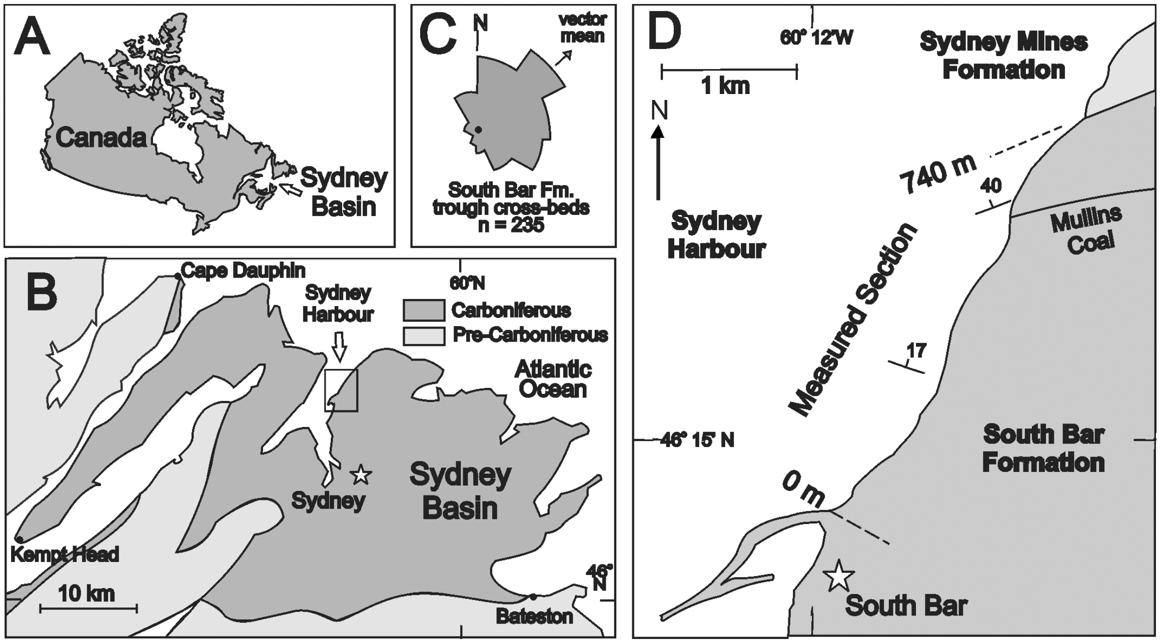


Figure 35. The South Bar Formation in the Sydney Basin of Atlantic Canada. A, B. Location of Sydney Basin (from Rust & Gibling, 1990a). C. Paleoflow data from Gibling et al. (1992); dot marks centre of rose. D. Measured type section of the formation.

4.3.1. General Description

At South Bar (Fig. 35D), 740 m of strata are almost completely exposed. Rust & Gibling (1990a) designated the basal 105 m as the Pebbly Sandstone Facies Assemblage, and the remainder as the Sandstone Facies Assemblage. The strata consist mainly of stacked, erosionally based successions of trough cross-bedded and plane-bedded sandstone deposited in fluvial channels, with some planar cross-sets and ripple cross-laminated beds. Extrabasinal clasts are composed principally of quartzite, granitoids, schist and vein quartz, with local reworked siderite nodules, and are present as rare conglomerate beds, lags on erosional surfaces, and isolated particles, declining in abundance up-section. The largest clast recorded was 80 mm in diameter, and most are 5 to 40 mm in diameter. Mudstone comprises less than 10% of the measured section, mainly as lenses up to 5 m thick with their tops eroded beneath overlying channel-sandstone beds. Most mudstone units are laminated and represent the fills of abandoned channels, but some mudstone units are slump blocks emplaced at channel bases.

Organic material is prominent in the formation. Thin and discontinuous coals, generally decimeters thick, are present locally, but the Mullins Coal at the 430 m level (Fig. 35D) is 2.1 m thick and extends for 15 km along strike. Thirty-eight sandstone beds contain fragments of banded, vitrinite-rich coal up to 300 mm thick and 3.5 m long, which represent the eroded remnants of peats; they are hereafter referred to as “coal intraclasts” but we emphasize that they were in the form of peat at the time of deposition. Within sandstones, abundant logs are up to 900 mm wide and 3.2 m long, and comminuted, millimeter-scale plant debris is common on bed surfaces. Prominent accumulations of logs and coal intraclasts are locally as much as 2.5 m thick. Erect trees and roots are rare. The mudstone beds are largely devoid of identifiable plant matter.

4.3.2. High-flow-stage Deposits

Of particular note within the channel deposits is the abundance of sedimentary structures attributed by Fielding (2006) to the Upper Flow Regime architectural element and referred to here as high-flow-stage (HFS) deposits. These include (i) humpback and sigmoidal cross-beds formed at the dune/plane bed transition; (ii) plane beds with primary current lineation, representing the upper plane bed phase; and (iii) flat to low-angle laminae and convex-upward bedforms, representing deposition at the plane bed/antidune transition and within the antidune stability field (Rust & Gibling, 1990b; Fielding, 2006).

Within the lower 300 m of the measured section at South Bar, channel deposits are characterized predominantly by trough cross-stratification and associated low-flow-stage structures. The upper 440 m is characterized by the appearance and marked increase of HFS deposits such that, in the upper 200 m, channel deposits are largely composed of HFS deposits with modest amounts of low-flow-stage deposits. The preservation of these features implies rapid aggradation and flow deceleration during highly variable discharge events that precluded reworking into lower flow-stage bedforms (Fielding, 2006). According to Fielding et al. (2009), this fluvial style is characteristic of strongly seasonal subhumid tropical and sub-tropical settings.

4.3.3. Channel Dimensions

Width and depth estimates of South Bar channels are needed in order to evaluate how effective sediment buildup and log accumulations may have been in blocking channels. Depth estimates are based on four independent approaches: cross-bed thickness; thickness of cross-bed cosets and HFS accumulations; thickness of fining-up cycles; and decompacted thickness of mudstone in abandoned channel fills.

Based on flume experiments, Bridge & Tye (2000) and Leclair & Bridge (2001) provided equations that utilize the distribution of cross-bed thickness to estimate the original dune height, which scales broadly with formative flow depth. Combining numerous channel fills in the Sandstone Facies Association, the mean thickness of 113 cross-beds is 0.38 m, and standard deviation divided by the mean is 0.683, within the preferred range of 0.88 ± 0.3 suggested by Bridge (2003) as an initial test for the applicability of the method. The mean cross-bed thickness equates to a mean dune height of 1.13 m. Using average values of 6 to 10 for the ratio of flow depth to mean dune height (Bridge & Tye, 2000), the formative flow depth for many South Bar channels would have been in the range of 6.8 m to 11.3 m.

Cosets of trough cross-beds range from 1 to 4 m thick (Rust & Gibling, 1990a). These cosets provide only a minimum estimate of flow depth because most are bounded by erosional surfaces and represent only part of the channel fill. The maximum observed thickness of HFS deposits without intervening erosion surfaces is 6 m.

Fourteen channel-fill successions are considered relatively complete. They rest on a prominent erosional surface cut into mudstone or sandstone, and fine upward into mudstone. The successions range from 2.2 to 8.3 m in thickness, averaging 5.1 m.

However, basal surfaces cut into sandstone may not be channel bases in every case, and mudstone caps are truncated. Thus, the thickness range provides a minimum estimate of channel depth.

The thickness of mudstone within abandoned channels is up to 5 m for laminated fills and 6 m in one instance where an inclined, slumped fill is preserved. Using X-ray diffraction analysis to determine the clay proportion and applying a compaction ratio, Rust & Gibling (1990a) estimated that the 6 m mudstone was originally 8 m thick. This is a minimum channel-depth estimate because, as discussed below, many channels were partially filled by substantial sand accumulation prior to abandonment and mud accumulation.

In summary, cross-bed analysis suggests channel depths in the range of 6.8 to 11.3 m, and the other three methods suggest minimum depths for some channels of 6 m, 8.3 m, and 8 m, respectively. We infer that many channels were originally at least 7 m deep, and some may have been 10 m deep or more.

Channel width is not known. Some mudstone units are less than 10 m wide, but others can be traced for at least 30 m along depositional strike, as far as outcrop extends. Modern alluvial channels with 7 to 10 m bankfull depth are commonly about 140 to 200 m wide based on a modal width:depth ratio of 20 (Church & Rood, 1983; Gibling, 2006).

4.3.4. Facies Models

The formation was interpreted by Rust & Gibling (1990a) as a braided-river deposit with relatively deep channels confined by banks of mud and peat that had built up on inactive fluvial tracts. Trough cross-bedded channel fills predominate in the basal 300 m of the formation at South Bar, where planar cross-sets indicative of braid bars (macroforms) are present locally. Higher in the South Bar section, channel fills comprise about 35% trough cross-beds and 65% HFS deposits. The presence of stacked, erosionally based sandstone units, with numerous instances of radical paleoflow differences above and below erosion surfaces, suggests that the channels repeatedly avulsed, eroding the vegetated and peat-covered tracts.

Miall (1996) presented models for braided sandbed rivers, and the South Bar bedform assemblages match in part his deep perennial and high-energy braided groups. However, vegetation is not part of most facies models. Vegetated islands are present in the sandy braided Platte River in Nebraska, where they probably form by the gradual abandonment of multi-thread channels. Vegetated tracts have been especially well described from gravelly braided rivers in western Canada. In the Donjek River, Williams & Rust (1969) recognized four levels from the modern channel system to vegetated islands, with higher levels showing progressively less frequent inundation and more vegetation. Numerous reaches of the Bella Coola River, a wandering gravelbed river, have several sinuous channels that split around vegetated islands and medial bars (Church, 1983; Desloges & Church, 1987). These multichannel reaches show progressive erosion of cutbanks opposite the islands and bars, toppling mature trees. Bar migration reduces channel flow in some threads, causing avulsion and generating fine-grained abandonment fills, and woody debris on bar heads, riffles and channel entrances diverts flow, causes widening of smaller channels, and promotes avulsion.

The presence of agglutinated foraminifera with restricted-marine affinity in association with the Mullins Coal suggests that the braided system fed directly into the ocean, and that the Mullins was a coastal peat formed during transgression (Tibert & Gibling, 1999). Coal intraclasts at other levels are up to 300 mm thick, and the original peat was probably considerably thicker than this, based on compactional estimates (see later text). Based on this understanding and a modern peat accumulation rate of about 1 mm/year (McCabe, 1984), the fragments imply centuries to a few millennia of accumulation. Such durations match the avulsion periodicity of Rhine-Meuse Delta channels (Stouthamer & Berendsen, 2007), and we infer that South Bar peat formation reflects intrinsic processes of channel abandonment and avulsion. However, some coal intraclasts may represent transgressive coastal peats, eroded after rivers reoccupied and incised the area during sea-level highstand and falling stage.

Vertisol-like paleosols are present in the uppermost South Bar Formation (Gibling et al., 2004), and are abundant in the coeval Waddens Cove Formation. Modern paleosols of this type form where precipitation is strongly seasonal, under a range of climatic settings from humid to semi-arid (Driese et al., 2005). The abundance of HFS deposits in the formation also supports a strongly seasonal climate (Fielding et al., 2009).

4.4. STRATIGRAPHIC SUCCESSIONS

Figures 36 to 39 represent sandstone, mudstone, and log accumulations between the 310 and 640 m levels of the measured South Bar section recorded in figure 2 of Rust & Gibling (1990a), within the Sandstone Facies Assemblage. Paleoflow arrows variously represent trough cross-beds and ripple cross-lamination, and are oriented with respect to north being at the top of the page. The strata are visible in low cliffs, but limited bedding-plane exposure precludes a full analysis of paleoflow and log orientation.

Paleoflow is also difficult to assess for coarse-grained, plane-bedded sandstone beds, in which primary current lineation is poorly developed, and for convex-up bedforms. Of four types of succession identified (Table 19), the first three types are common and the fourth is rare.

4.4.1. Type 1. Flood Sediment and Mudstone

Type 1 successions contain thick HFS strata and mudstone but lack log accumulations. In Figure 36, pebbly trough cross-bedded sandstone at 406 m is overlain by 2.5 m of lineated plane beds without erosional breaks, passing upward into 2 m of beds that exhibit convex-upward stratification, indicating deposition as a sediment mound. The overlying mudstone (409 to 411 m) fills an abandoned channel, and laps against the sloping, slightly incised surface of the mound. The mudstone has a locally disrupted fabric, indicating some slumping during channel filling. Apart from a few logs in the basal cross-beds and some comminuted plant fragments, organic accumulations are lacking. Paleoflow in the overlying channel body is nearly opposite to that below, showing 175^{o} divergence (arrows at left).

We infer that a channel at least 5.5 m deep rapidly accumulated HFS beds during a single episode of sedimentation under high-flow-stage conditions. Sand buildup was followed by channel abandonment and mud accumulation. The radical change in paleoflow direction suggests that the channel belt avulsed to a distant part of the floodplain (regional avulsion). By the time the channel belt was reestablished in the area, pre-existing channels were largely filled and not available for reoccupation, resulting in incision of a new channel with a different orientation.

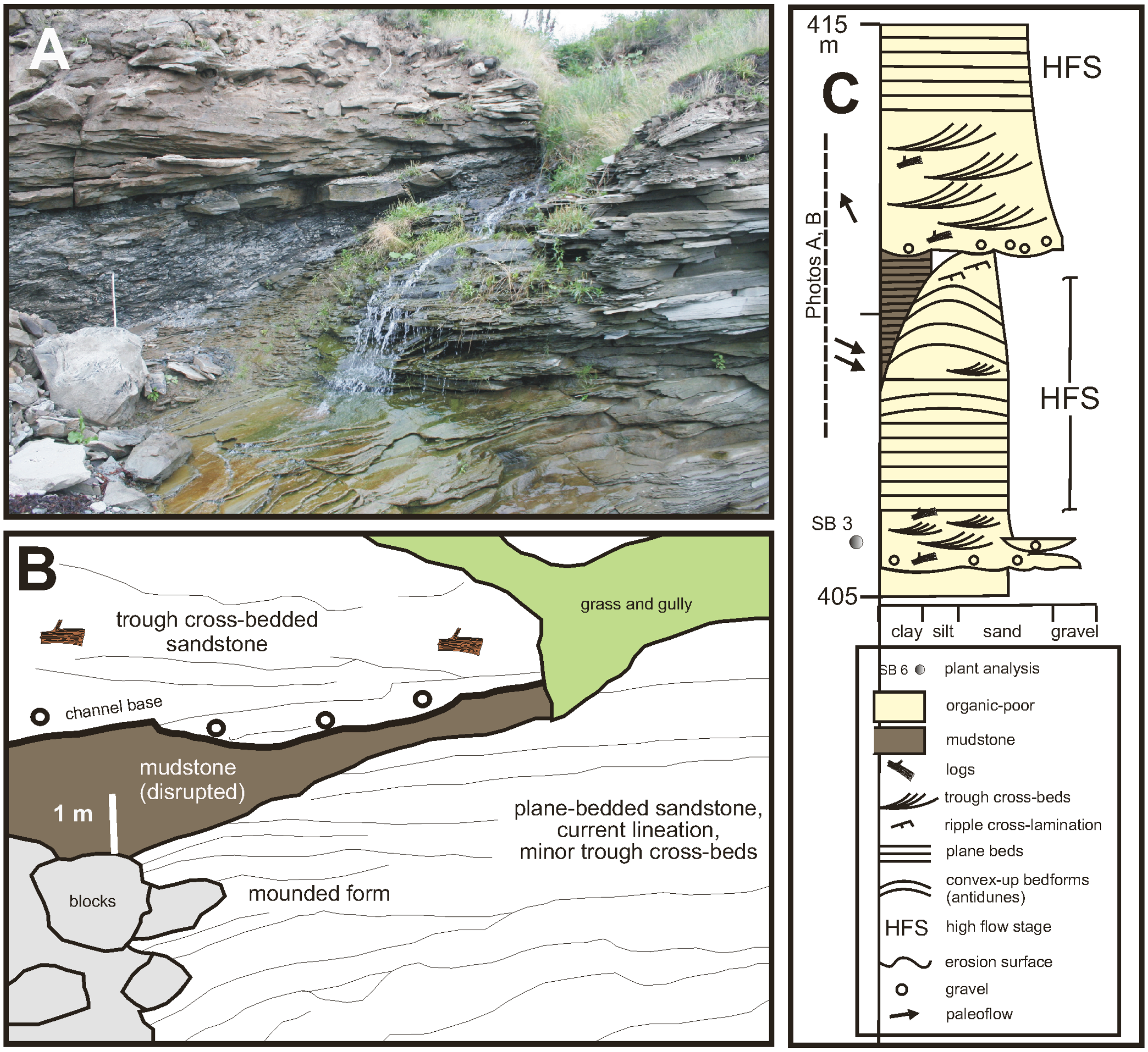


Figure 36. Type 1 succession. Photo of outcrop (A), line drawing (B), and visual log (C) show plane-bedded sandstone with mounded form, overlain by abandoned-channel mudstone. Dispersed logs are found in the topmost channel sandstone, with only finely comminuted plant material in the sandstone below the mudstone. Note the radical difference in paleoflow for sandstones below and above the mudstone (arrows at left-hand side of C). Succession at 405 to 415 m of South Bar section (Rust & Gibling, 1990a, fig. 2).

Type of Succession	Coarse Sediment	Mudstone	Organic Material	Meterage (Figures)	Interpretation
1) Flood Sediment and Mudstone	HFS deposits (plane beds, sigmoidal cross-beds, antidunes), locally mounded. LFS deposits present (trough cross-beds, ripple cross-lamination)	Cap coarse successions, up to 2.5 m thick	Isolated logs and sparse comminuted material.	410 m (2) 484 m (5B)	Rapid accumulation of flood sediment filled channels, leading to abandonment and avulsion.
2) Flood Sediment, Logs, and Mudstone	HFS deposits predominant; LFS deposits present locally	Cap coarse successions, up to 6 m thick. Mudstone clasts with logs.	Abundant logs (2.5 m layers). Isolated logs in sandstone.	316 m (3) 610 m (5C) 633 m (5D)	Flood sediment substantially filled channels, reducing cross-sectional area. Emplacement of log jams promoted bank erosion and channel abandonment.
3) Flood Sediment and Logs	HFS and LFS deposits	Mudstone clasts with logs.	Abundant logs and coal intraclasts (3.5 m layers and mounds). Isolated logs in sandstone.	350 m (5A) 588, 593 m (4) 605 m (5C) 627 m (5D)	Flood sediment and log jams caused channel abandonment, but mudstone and peat intraclasts are the only remaining evidence of abandonment.
4) Mudstone and Logs	Thin sheets of pebbly sandstone	Interbedded with mudstone	Abundant logs and coal intraclasts (1.0 m layers).	487 m (5B)	Flood sediment and logs were deposited in an abandoned channel, but the flood event did not lead to reoccupation.

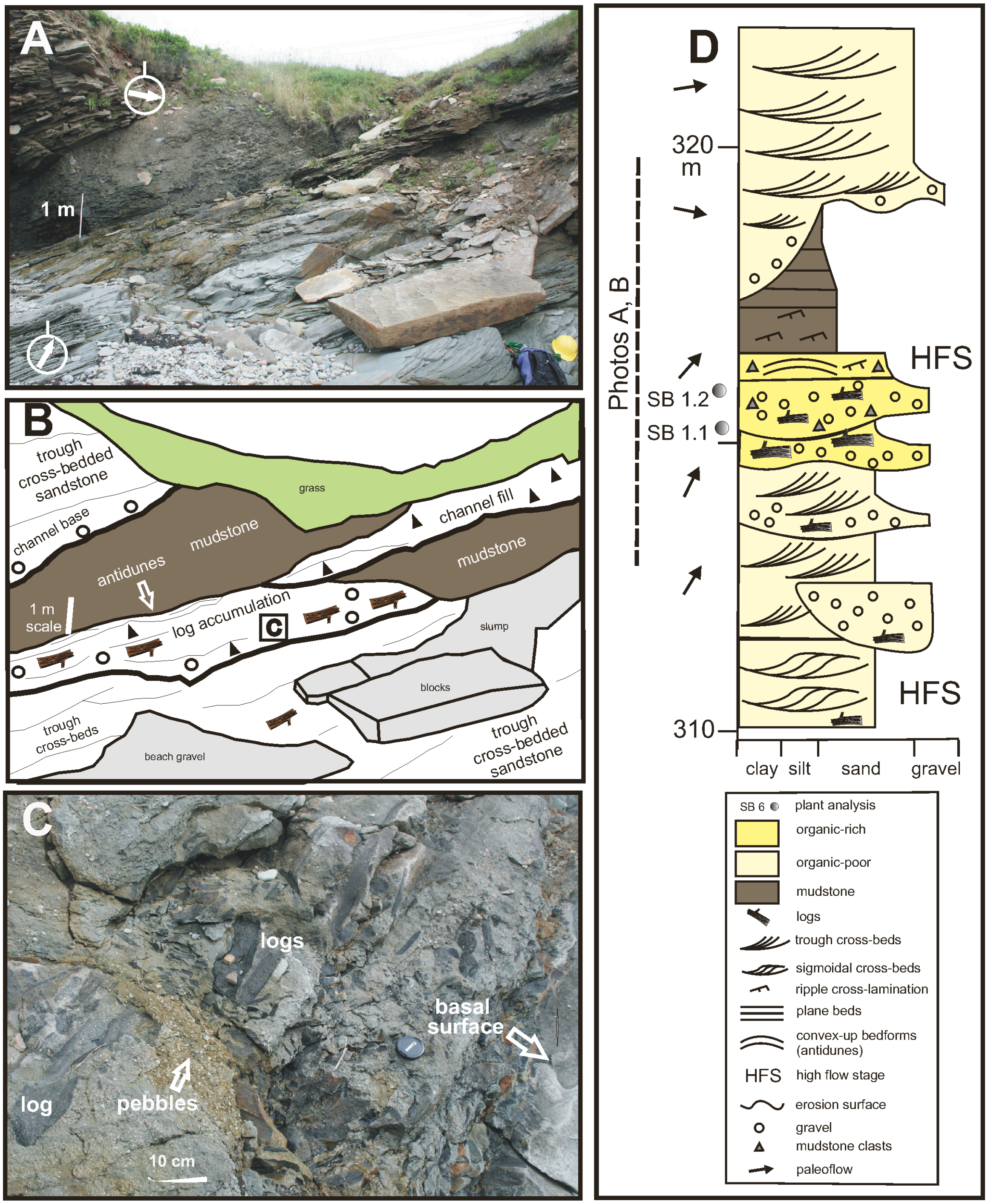
Table 19. Types of succession that include flood sediment, log accumulations, and mudstone, South Bar Formation. High-flow-stage (HFS) and low-flow-stage (LFS) deposits.

4.4.2. Type 2. Flood Sediment, Logs, and Mudstone

Type 2 successions comprise both flood sediment and logs with a mudstone cap. In the 310 to 315 m interval of Figure 37, channel deposits comprise medium-grained, trough and sigmoidal cross-stratified sandstone beds with pebbly lenses and northward paleoflow. Resting on an erosional surface at the 315 m level is a log accumulation 1.8 m thick with a matrix of medium-grained sandstone, with subordinate pebbles and mudstone clasts (Fig. 37C). The accumulation extends for 20 m along depositional strike, as far as outcrop is visible. The largest logs are up to 300 mm wide and 1 m long, with a slight degree of preferred orientation near-normal to the paleoflow. A thin sandstone sheet with antidunes 0.2 m high caps the log accumulation. In the adjacent cliff (right-hand side of Fig. 37A, B), a shallow channel fill 1.5 m thick cuts the log-bearing bed, and contains a thin mudstone overlain by sandstone with abundant mudstone clasts. The overlying thick mudstone commences with ripple cross-laminated beds, passing up into laminated beds. Resting erosionally on the mudstone is trough cross-bedded channel sandstone, which shows eastward paleoflow (about 70^{o} difference from the sandstone beds below).

We infer that a channel accumulated sediment largely under low-flow-stage conditions. Logs and pebbles accumulated in the final stages of filling, during which bank erosion generated mud clasts. Deposition terminated with antidunes formed under HFS conditions in very shallow water (cf. Langford & Bracken, 1987). Mud accumulated in a shallow channel bordering the log accumulation, but the channel was later reoccupied with erosion of the mud and, probably, adjacent muddy banks. The parent channel was then abandoned, but received some initial flow. Subsequently, a new

Figure 37. Type 2 succession. Photo of outcrop (A), line drawing (B), photo of logs (C) and visual log (D) of log accumulation with extrabasinal pebbles. The accumulation rests on trough cross-bedded sandstone and is overlain by an abandoned-channel mudstone (left-hand side of A and B). At the right-hand side of A and B, the log accumulation abuts against a mudstone lens cut by a small channel fill rich in mudstone clasts. In A, circles (north at top) contain arrows that show paleoflow directions derived from trough cross-beds; paleoflow is directed into the cliff for channel deposits below the mudstone (northeast), and to the right for channel deposits above (east). C. Illustrates plant fragments in pebbly log accumulation at location marked “C” in B; the accumulation is cut through obliquely at this location, with the top surface at top left and the basal surface at lower right. Succession at 310 to 322 m of South Bar section (Rust & Gibling, 1990a, fig. 2).


A
1 m
B
trough cross-bedded sandstone
channel base
grass
mudstone
antidunes
channel fill
mudstone
1 m scale
log accumulation
C
slump
blocks
trough cross-beds
beach gravel
trough cross-bedded sandstone
C
logs
basal surface
log
pebbles
10 cm
D
320 m
Photos A, B
HFS
SB 1.2
SB 1.1
HFS
310
clay
silt
sand
gravel
SB 6
plant analysis
organic-rich
organic-poor
mudstone
logs
trough cross-beds
sigmoidal cross-beds
ripple cross-lamination
plane beds
convex-up bedforms (antidunes)
HFS
high flow stage
erosion surface
gravel
mudstone clasts
paleoflow

channel was emplaced at a high angle to the earlier channel orientation, suggesting that the earlier channel abandonment was accompanied by avulsion to a distant part of the floodplain.

It is possible that the erosional surface at the base of the log accumulation (315 m level) represents a new channel base where logs and pebbles were concentrated, rather than erosion within a largely filled channel. The medium-grained sandstone matrix of the log accumulation is similar to the grain size of the underlying sandstones. If the accumulation represents a channel base, the channel would have been abandoned shortly after its formation. However, our preference is for deposition high in the channel, in view of evidence set out in the next paragraphs.

In the 627 to 632 m interval of Figure 39D, channel deposits consist of four stacked, erosionally based units of coarse-grained sandstone with low-angle lamination, humpback cross-stratification, and convex-up bedforms (antidunes). The succession is capped by 2 m of logs with pebbles, mudstone clasts, and thin beds of fine-grained sandstone with antidunes (632 to 634 m interval), below a 5 m mudstone.

The mixture of gravel and logs in the 632 to 634 m interval might normally suggest deposition at a channel base. However, a channel-top position for these strata is inferred in view of the fine grain size of the associated sandstone beds (fine-grained sand), in contrast with the coarse-grained sandstone of the four stacked units below. If so, the pebbles in this interval may have originated from bank erosion of adjacent channel deposits, rather than being traction deposits at a channel base. Flows at a high level in the channel may have been unable to transport the pebbles away or bring in coarser sand.

We infer that the channel accumulated flood sediment with logs at the top of the deposit, prior to channel abandonment.

4.4.3. Type 3. Flood Sediment and Logs

Type 3 successions comprise interbedded flood sediment and logs, but lack mudstone. In Figure 38, three superimposed channel deposits are each 5 m thick or more, with prominent erosional channel bases (Fig. 38E) overlain by sandstone. The sandstone beds are very coarse- to medium-grained and consist mainly of HFS deposits of lineated plane beds, sigmoidal cross-beds, and convex-up structures, with minor trough cross-beds and ripple cross-lamination. Capping the lower two channel deposits are accumulations up to 3.5 m thick that variously include coal intraclasts (Fig. 38A) and logs (Fig. 38B to D). The organic materials have a matrix of fine- to medium-grained sandstone and are associated with pebbles and thin units of sigmoidal cross-beds. At the 589 m level (Figs. 4C, D), a bed 1.2 m thick consists entirely of densely packed plant fragments in a matrix of fine- to medium-grained sandstone. The grain size of the matrix is considerably finer than that of the HFS sandstone beds below and above. The topmost channel deposit (594 m and above) comprises 6 m of very coarse- to coarse-grained sandstone, fining upward slightly (only the basal part is shown in Fig. 38E); bedforms are plane beds and sigmoidal cross-beds, with no erosional breaks.

We infer that channels repeatedly accumulated flood sediment deposited largely under HFS conditions, with large volumes of organic material laid down on top of the flood deposits. Mudstone clasts are lacking, but coal intraclasts indicate that vegetated tracts were eroded. As with the Type 2 deposits of Figure 39D, a channel-top position is

Figure 38. Type 3 succession. A. Coal intraclasts and sigmoidal cross-beds, with paleoflow into the outcrop (northeast). B. Large lycopsid fragments in log accumulation. C, D. Cross-section and surface view of 1.2 m accumulation of plant fragments. Plant accumulation is denoted as SB 5.1, and was used to estimate compaction ratio (see text). E. Visual column, with locations of photos indicated. Succession at 585 to 597 m of South Bar section (Rust & Gibling, 1990a, fig. 2).

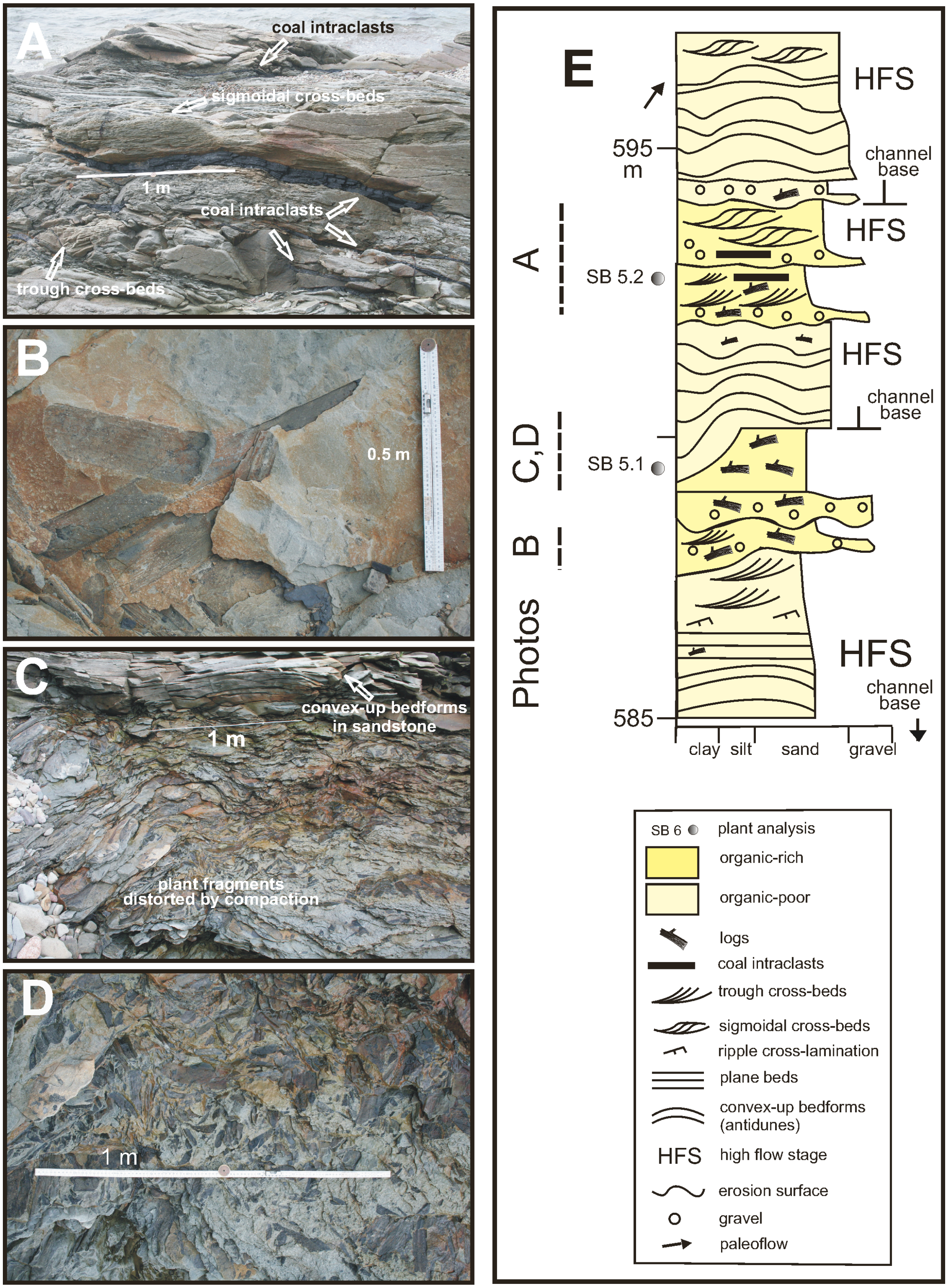
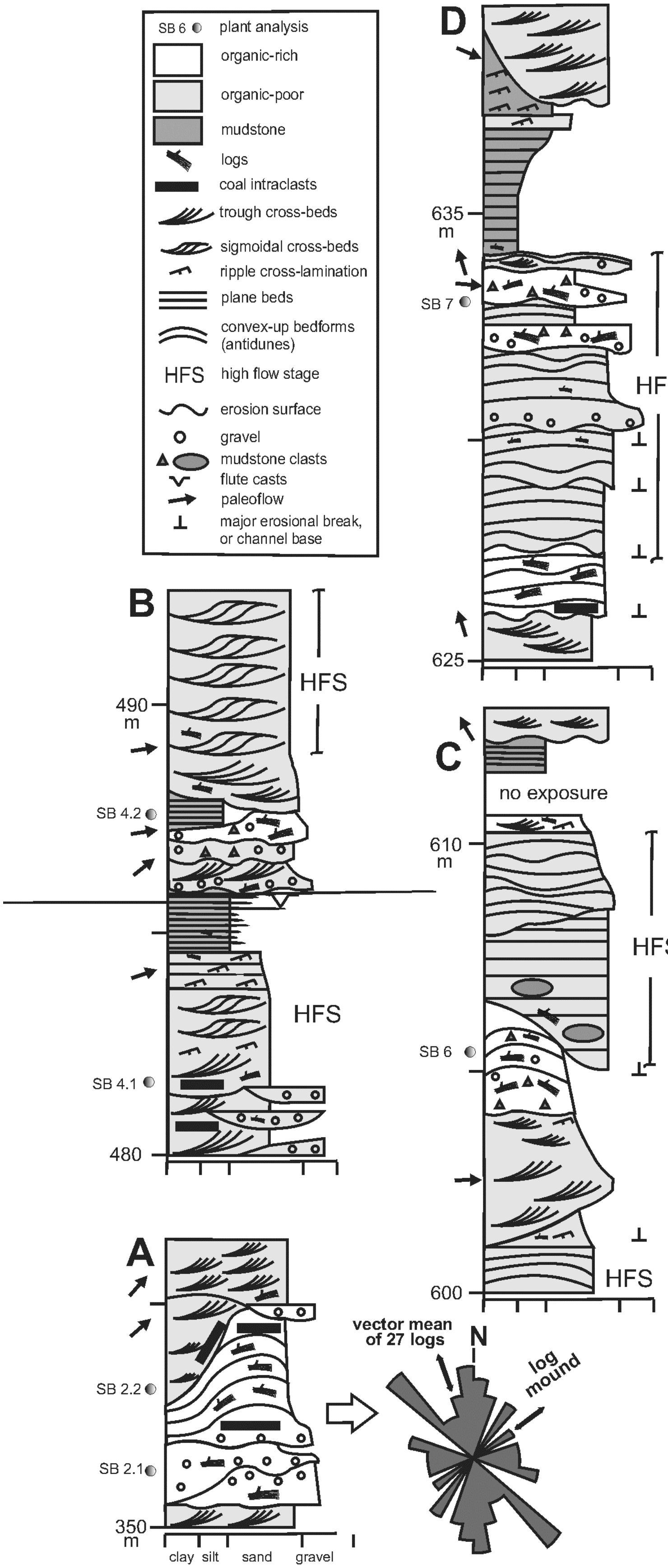

A
coal intraclasts
sigmoidal cross-beds
1 m
coal intraclasts
trough cross-beds
B
0.5 m
C
convex-up bedforms
in sandstone
1 m
plant fragments
distorted by compaction
D
1 m
E
HFS
595
m
channel
base
HFS
SB 5.2
HFS
channel
base
SB 5.1
HFS
channel
base
585
clay silt sand gravel
Photos
A
C,D
B
SB 6 plant analysis
organic-rich
organic-poor
logs
coal intraclasts
trough cross-beds
sigmoidal cross-beds
ripple cross-lamination
plane beds
convex-up bedforms
(antidunes)
HFS high flow stage
erosion surface
gravel
paleoflow

Figure 39. Measured sections (A to D) of additional log-bearing successions in the South Bar Formation, Sydney Harbour.


SB 6 ◐ plant analysis
organic-rich
organic-poor
mudstone
logs
coal intraclasts
trough cross-beds
sigmoidal cross-beds
ripple cross-lamination
plane beds
convex-up bedforms (antidunes)
HFS high flow stage
erosion surface
gravel
mudstone clasts
flute casts
paleoflow
major erosional break, or channel base
D
635 m
625
SB 7
HFS
C
no exposure
610 m
600
SB 6
HFS
HFS
B
490 m
480
SB 4.2
SB 4.1
HFS
HFS
A
350 m
SB 2.2
SB 2.1
clay
silt
sand
gravel
vector mean of 27 logs
N
log mound

inferred for the log- and pebble-bearing beds in view of their fine matrix (fine- to medium-grained sand), in contrast with the relative coarseness of the HFS deposits (very coarse- to medium-grained sand).

Figure 39C illustrates superimposed erosionally-based channel deposits, with the bases of two channels marked on the figure. The deposits above the 601 m level are capped by a 2.5 m accumulation of logs, pebbles and mudstone clasts with convex-upward stratification, indicating a depositional mound. The overlying channel fill occupies a former depression adjoining the mound, and large mudstone clasts (up to 1.5 m long) suggest that banks nearby or upstream had undergone substantial erosion. Although no mudstone layers are preserved at this level, the presence of mudstone clasts suggests that the earlier channel had been abandoned prior to reoccupation and deposition of the later channel deposit.

In Figure 39A, a prominent accumulation of logs, coal intraclasts, and pebbles lies within channel-sandstone beds and exhibits convex-upward stratification, indicating a depositional mound. The accumulation commences with gravelly layers on an erosion surface, with coal intraclasts at the base. The mound is 2.5 m thick and linear, extending at least 15 m parallel to the paleoflow direction of the associated sandstone beds. Logs and coal intraclasts up to 1.3 m long are prominent on the mound crest, which is slightly eroded. Logs >50 mm wide lie near-normal to oblique to the mound orientation (rose diagram at right of Fig. 39A). The presence of coal intraclasts suggests that banks nearby or upstream had undergone erosion.

4.4.4. Type 4. Mudstone and Logs

Type 4 successions represent thin log accumulations within mudstone. In Figure 39B, the mudstone fill of an abandoned channel (484.5 to 486 m interval) is eroded below a thin pebbly layer containing mudstone clasts, with flute casts on the basal surface of the layer. Logs and coal intraclasts are stacked on the top surface of this layer, with some of the largest logs oriented normal to paleoflow. A thin mudstone above is overlain by channel deposits with sigmoidal cross-beds (Fig. 40). Paleoflow was similar for the two sets of channel deposits and for the pebbly layer. We infer that a flood entered and eroded an abandoned channel but failed to convert the channel into an active reach. The log accumulation may have contributed to the renewed abandonment of the channel.

4.5. PLANT ASSEMBLAGES

Log accumulations represent portions of tree trunks or canopy branches, or wide petioles of large leaves. No identifiable foliage or seeds were observed, and roots and standing trees were noted at only two localities within the sandstone-dominated successions, apart from roots below and above the Mullins Coal. The logs are parautochthonous or allochthonous (*sensu* Gastaldo et al., 1995) within channels, having been transported an unknown distance from their site of growth. To constrain their provenance, the taxonomic composition and size distribution of axes were studied for 19 log accumulations at South Bar, Bateston, and Cape Dauphin, the latter two areas near the basin margin (Fig. 35B). A total of 1058 plant axes were counted, with 27 to 96 logs (mean of 56) in each accumulation.

Figure 40. Sigmoidal cross-beds in a Type 4 succession, 492 m level of Figure 39B. Topsets curve over into foresets, with paleoflow to the right.

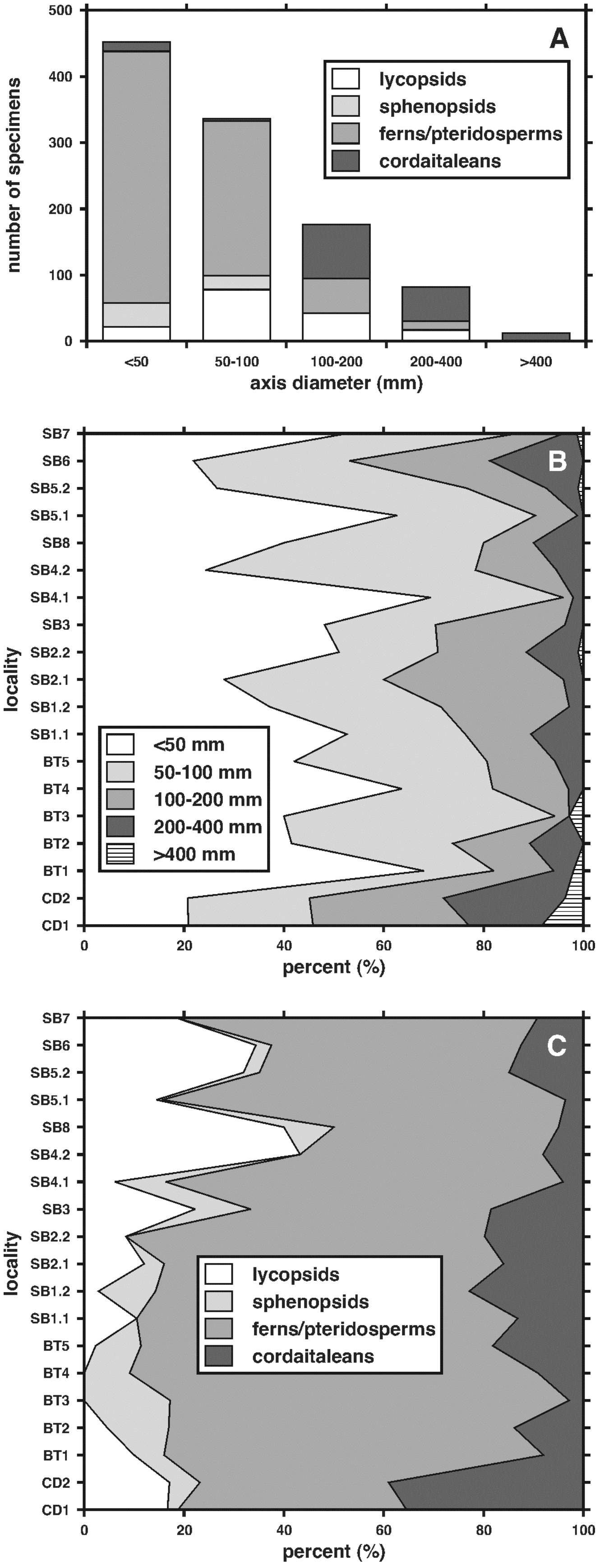
Logs are generally poorly preserved and commonly decorticated, although many have retained organic matter. Ten morphotypes were identified based on anatomical characters and preservational state, and were assigned to lycopsids, sphenopsids, tree ferns, pteridosperms, or cordaitaleans with varying degrees of confidence (Fig. 41A, C). Most logs are flattened, but some sandstone-cast axes and those permineralized by carbonate show less compaction. For some cordaitalean logs, both wood and internal pith has been permineralized, resulting in anatomically preserved petrifactions. Logs were assigned to one of five size bins (<50 mm, 50 to 100 mm, 100 to 200 mm, 200 to 400 mm, >400 mm) based on their maximum preserved width. The log accumulations vary in size distribution through the formation (Fig. 41A, B). Fragments <100 mm wide form the bulk of the material in all but the two lowermost accumulations at Cape Dauphin.

4.5.1. Plant Groups

Arborescent lycopsid logs are mainly 50 to 200 mm in diameter (Fig. 41A), suggestive of branches and/or small trunks, and the longest is 1.25 m long. *Sigillaria* is common, and lepidodendroids are also present. Arborescent lycopsids had a pole-like architecture, and in many forms a reproductive crown of branches arose just prior to death (Phillips & DiMichele, 1992; DiMichele & Phillips, 1994). These plants grew rapidly to attain heights of 40 m, and were supported by a thick rind of decay-resistant, wood-like periderm.

The only sphenopsid encountered is *Calamites*, a woody plant typified by jointed, aerial shoots that reached subtree to tree heights (Hirmer, 1927; Barthel, 1980). The hollow pith of these plants commonly filled with sediment, and most *Calamites* counted

Figure 41. Plant fragments in 19 log accumulations in the South Bar Formation (12 from South Bar type section, SB; five from Bateston, BT; and two from Cape Dauphin, CD; Fig. 35B). A. Size distribution of 1058 plant axes (logs) for five plant groups. B. Change in log diameter through the formation. Samples are shown in stratigraphic order, but the scale does not correspond directly to meterage. C. Change in log composition through the formation.


A
number of specimens
0
100
200
300
400
500
<50
50-100
100-200
200-400
>400
axis diameter (mm)
lycopsids
sphenopsids
ferns/pteridosperms
cordaitaleans
B
locality
SB7
SB6
SB5.2
SB5.1
SB8
SB4.2
SB4.1
SB3
SB2.2
SB2.1
SB1.2
SB1.1
BT5
BT4
BT3
BT2
BT1
CD2
CD1
<50 mm
50-100 mm
100-200 mm
200-400 mm
>400 mm
0
20
40
60
80
100
percent (%)
C
locality
SB7
SB6
SB5.2
SB5.1
SB8
SB4.2
SB4.1
SB3
SB2.2
SB2.1
SB1.2
SB1.1
BT5
BT4
BT3
BT2
BT1
CD2
CD1
lycopsids
sphenopsids
ferns/pteridosperms
cordaitaleans
0
20
40
60
80
100
percent (%)

are preserved as pith casts. All are less than 100 mm in diameter (Fig. 41A), and less than 0.7 m long.

Tree ferns and pteridosperms are represented by adpressed fragments of narrow, defoliated frond petioles. In the absence of associated foliage, it is difficult to differentiate between the two groups, and they have accordingly been grouped together. These organs generally are less than 100 mm in diameter (Fig. 41A), and the longest specimen is 1.6 m. Trunk remains of these two groups are also present, but have few diagnostic characters and are difficult to identify. Some tree fern trunks have *Megaphyton*-type petiole scars, whereas other axes show recurved branches suggestive of medullosalean pteridosperms. Tree ferns, up to 10 m high, had a "cheaply" constructed stem (Baker & DiMichele, 1997) supported by a thick mantle of adventitious roots, and were topped by a crown of pinnate fronds several meters long (DiMichele & Phillips, 2002). Medullosalean pteridosperms, up to 5 to 10 m high, consisted of a robust, monoaxial stem supported by centrally located wedges of wood, and were topped by a crown of large, seed-bearing pinnate fronds (DiMichele et al., 2006b).

Cordaitalean remains are mainly flattened trunk adpressions, 100 to 400 mm in diameter (Fig. 41A), although one specimen is 900 mm wide and 3.2 m long. Their identity is confirmed by the local occurrence of sandstone- or carbonate-filled pith casts of *Artisia*-type, less than 50 mm in diameter. Locally present are anatomically preserved trunks permineralized with carbonate and showing pycnoxylic wood of *Dadoxylon*-type. These axes range from less than 100 mm to more than 500 mm in diameter, suggesting that both trunks and branches were encountered. They reach a length of 5 m. The cordaitaleans were comparatively slow growing and long-lived gymnosperms (DiMichele

& Phillips, 1994) with wood structurally similar to that of extant araucarian conifers. Cordaitaleans dwelling in mires (peat-forming wetlands) were small trees or scramblers, whereas those occupying clastic substrates achieved heights of 50 m (Falcon-Lang & Bashforth, 2004, 2005).

4.5.2. Plant Habitats

The bulk of plant remains in modern channels that traverse lowland floodplains is derived from local riparian sources (Thorne, 1982; Scheihing & Pfefferkorn, 1984; Murphy & Koski, 1989; Spicer, 1989). The South Bar accumulations are probably the remnants of vegetation that grew in mires and associated clastic substrates adjacent to the channels, and the abundance of coal intraclasts supports this interpretation. Arborescent lycopsids growing in mires typically were smaller than those occupying clastic substrates (DiMichele & Phillips, 1994), and the relatively small diameter of lycopsid trunks (Fig. 41A) suggests partial derivation from peat-forming habitats. Most identifiable lycopsid trunks belong to *Sigillaria*, a genus that preferred wet clastic substrates alongside channels or peripheral to mires (Gastaldo, 1987; Phillips & DiMichele, 1992; DiMichele & Phillips, 1994). Sigillarians are also known from swamps that experienced frequent incursions of nutrient-rich floodwaters (DiMichele & Nelson, 1989), in accord with the setting of the South Bar Formation. Furthermore, an *in situ* lycopsid root (*Stigmaria*) was observed in a sandstone bed at Bateston, indicating that lycopsids colonized channel flanks or even sandy bedforms within the channels. Furthermore, lycopsids are prominent higher in the formation (Fig. 41C), increasing at about the level where paleoflow data suggest a bedrock valley gave way to an alluvial plain more favorable to peat accumulation. If plant matter entering the fluvial system was derived from mires, it follows that the lycopsids—centered in such habitats—would become increasingly abundant.

Calamites were adapted to shifting and rapidly aggrading landscapes (Scott, 1978; Gastaldo, 1987, 1992; Pfefferkorn et al., 2001)—the norm in this depositional regime—but was less common in mires. The surprisingly low abundance of these plants (Fig. 41C) supports a mire derivation for much of the vegetation.

Cordaitaleans living in peat-forming habitats generally were smaller than those occupying clastic substrates (DiMichele & Phillips, 1994). The large size of most cordaitalean remains suggests an origin along the channel flanks, rather than in the mires. Permineralized cordaitalean logs are rare at South Bar but are conspicuous at Bateston and Cape Dauphin (Fig. 41B) and at Kempt Head, close to the basin margins. Trees in these occurrences probably came from riparian zones along high-energy streams at the basin margins or in uplands outside the basin confines (Falcon-Lang & Scott, 2000; Falcon-Lang & Bashforth, 2004, 2005).

4.5.3. Reconstruction of Tree Sizes in Log Accumulations

The logs are visible in vertical sections and on small areas of bed surfaces where they extend into the outcrops. Thus, their width or diameter can be determined, but the length of most fragments is not known. Niklas (1994) developed equations for the allometric relationship between diameter and tree height for several extant plant groups, including “woody” and “non-woody” forms. Cordaitaleans were woody and, although lycopsid axes had little true wood, their thick bark (periderm) was wood-like (DiMichele

& Phillips, 1994). Thus, as noted by Niklas, it is reasonable to estimate the original tree height of cordaitaleans and lycopsids in the log accumulations using the equation:

$$\log_{10}H = 1.59 + 0.39(\log_{10}D) - 0.18(\log_{10}D)^2$$

where H = predicted fossil plant height, and D = known stem diameter (all measurements in m). Although not explicitly stated by Niklas (1994), the equations probably assume diameter at breast height (DBH) above any basal flare. Unfortunately, the logs could have been positioned anywhere along the living tree trunk, and only a maximum width (equivalent to the original diameter) could be measured. The estimated heights (Table 20) are rough approximations but, given the upward taper in tree trunks, can be considered minimum values.

The largest cordaitalean fragment at South Bar was 900 mm wide and >3.2 m long (in SB 7; Fig. 39D), corresponding to a trunk at least 37.3 m long. Cordaitalean widths generally range from 100 to 400 mm. Although some may have been branches, those that represent trunks would correspond to trees 10 to 25 m high. Based on a similar approach, Middle Pennsylvanian cordaitaleans from Newfoundland were estimated as up to 48 m tall (Falcon-Lang & Bashforth, 2004). Most lycopsid fragments range from 50 to 200 mm in diameter. Many smaller fragments were probably branches, but some at least would have come from trees 6 to 17 m tall, with a maximum of 29 m. Thus, many of the logs represent trunk fragments from large trees, and some may be much longer than evident from the limited exposure.

Log diameter or width (mm)	**Estimated tree height (m)**
50	6.0
100	10.5
200	17
400	25.5
500	28.6

Table 20. Estimate of tree height using diameter of uncompacted log or width of compressed log, based on equation of Niklas (1994). See text for equation and explanation.

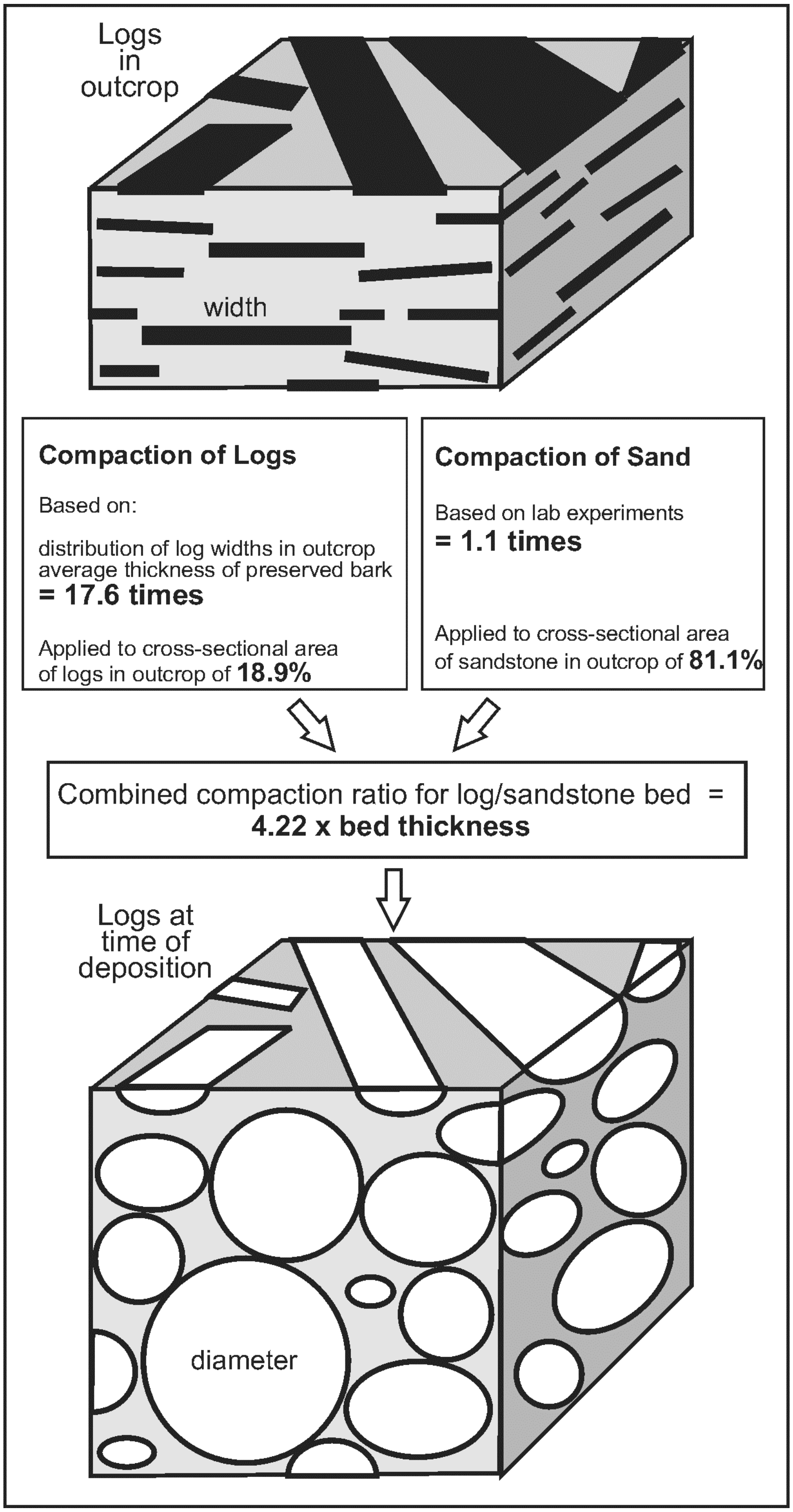
4.6. COMPACTION OF LOG ACCUMULATIONS

No single published value can be used to estimate the amount of compaction experienced by the log accumulations during burial and lithification. The original accumulations comprised a suite of logs with a range of diameters, enclosed in sand (lower part of Fig. 42). Sand compacts to about 90% of its original volume by improved packing, yielding a compaction ratio of 1.1 (Ethridge & Schumm, 1978). Although the internal anatomy of the logs would have varied, the preserved width of a flattened axis approximates the original stem diameter (Walton, 1936; Rex & Chaloner, 1983; upper part of Fig. 42). The degree of compaction is closely related to the log diameter. For example, logs of 500 mm and 100 mm diameter will both compact down to a thin sheet of coalified bark, but the 500 mm log will have experienced a much greater volume reduction, and compaction estimates must take this into account.

To estimate compaction, we selected accumulation SB 5.1, which is exposed in a near-vertical rock face with enough of the bedding planes visible nearby to measure the widths of numerous flattened logs. There is no evident preferred orientation of fragments (Fig. 38C, D). In the field, 83 logs were measured and assigned to bins based on width ranges, as noted above. The midpoint of bin width was used in calculation (Table 21). For each bin, the number of logs in this size range was multiplied by the bin midpoint width (average width) in millimeters, and the products were added to yield a value of 4375 mm—the aggregate original thickness of the 83 logs (Table 21).

The preserved thickness of coalified bark for the log accumulations is difficult to estimate. Each accumulation contains several plant groups (Fig. 41C), each with a different anatomical structure and original bark thickness. Additionally, bark thickness

Figure 42. Method for estimation of compaction ratio for log accumulations (see text). The compaction process is illustrated by comparing the lower diagram (logs at the time of deposition) with the upper diagram (logs in outcrop): the original diameter and present width of the logs are similar, but compaction has greatly reduced their thickness. A compaction estimate must take account of the differing effects of compaction on framework woody debris and sandy matrix, as well as the original range of log diameters (approximated by the present width of the fragments in outcrop). Results are for log jam SB 5.1 (Fig. 37C, D, E).



Compaction of Logs

Based on:

distribution of log widths in outcrop
average thickness of preserved bark
= 17.6 times

Applied to cross-sectional area
of logs in outcrop of **18.9%**

Compaction of Sand

Based on lab experiments
= 1.1 times

Applied to cross-sectional area
of sandstone in outcrop of **81.1%**

Combined compaction ratio for log/sandstone bed =
4.22 x bed thickness

A. No. of Logs	**B. Average width (mm)***	**C. Aggregate original thickness (A x B, in mm)**[1]	**D. Present thickness of individual logs (mm)**[2]	**E. Aggregate present thickness (A x D, in mm)**
52	25	1300	3	156
23	75	1725	3	69
7	150	1050	3	21
1	300	300	3	3
	Total	4375		249
Compaction Ratio for Organics			4375 / 249 = 17.6	
Compaction Ratio for Sand[3]			1.1	
Log Bed Components	**Volume Percent**[4]	**Compaction Ratio**	**Volume Percent x Compaction Ratio**	
Organics	18.9 / 100	17.6	3.33	
Sand	81.1 / 100	1.1	0.89	
Compaction Ratio for Log Bed			**4.22**	

Table 21. Compaction estimate for log-bearing bed SB 5.1, South Bar section. (1) measured in outcrop, with width of compressed logs approximately equivalent to their original diameter; (2) estimated from measurements of a set of Sydney Basin fossils; (3) from Ethridge & Schumm (1978); (4) obtained by point counting of traced image; see text for a fuller explanation.

increases with size of fragments, and different proportions of plant groups are present in each bin size. Fragments would have experienced varied degrees of decay, abrasion and decortication before, during, and after transport. Actual measurement of specimens is difficult, with coalified bark varying in thickness around the stem, especially where bark is corrugated. For a set of Sydney Basin specimens, we estimate that preserved coalified bark is about 0.5 mm thick for ferns and pteridosperms, 1 mm thick for sphenopsids, 3 mm thick for lycopsids, and 6 mm thick for cordaitaleans. These values would be doubled for compressed logs. A suite of 21 logs 8 mm to 190 mm wide that included representatives of all groups averaged 1.6 mm in bark thickness, or 3.2 mm for a compressed log. Using an estimate of 3 mm for each log, the 83 logs have an aggregate thickness of 249 mm, and the compaction ratio for the organic component of SB 5.1 is 4375 mm divided by 249 mm, or 17.6 (Table 21; Fig. 42).

The log and sand compaction ratios were applied according to their proportions in the bed. These proportions were estimated visually using a high-resolution photograph of a 1.0 m by 1.1 m area of the near-vertical rock face. The image was imported into a graphics software package, and individual plant fragments were traced precisely. A grid was placed over the tracing, and 1000 grid intersections were classified as plant or sand. Plant material comprises 18.9% of the imaged area; because some fragments were imaged obliquely due to distortion of the stratification, this value is probably a slight overestimate. The value seems low, but is reasonable for what originally would have been a loose stack of logs. Applying log and sand compaction ratios to proportions of 18.9% plant material and 81.1% sand in the log accumulation, the estimated compaction ratio for the total bed is 4.22 (Table 21). Currently 1.2 m thick, the bed would originally have been 5 m thick, a considerable bulking up.

The value for SB 5.1 is probably among the highest for any log jam in the formation because the accumulation lacks pebbles and mudstone clasts, and because all the fragments are compacted, whereas a small proportion of fragments in other accumulations are sediment-filled. Nevertheless, the original thickness of some South Bar log accumulations would have matched the depth of smaller channels.

Our compaction protocol may provide a conservative estimate. Logs with a low proportion of woody material may have been crushed by the weight of overlying logs and wet sand, reducing the original bulk. Additionally, many accumulations may originally have been composed largely of logs, and infiltrated sediment may not have displaced all the water and air during shallow burial; if water or air pockets remained in the log stack, estimates based on sandstone and organic percentages would underestimate the degree of compaction.

Coal intraclasts form a small proportion of most organic accumulations, but are prominent locally. The most appropriate compaction ratio for assessing the peat-to-coal transition, as well as the timing of compaction, remains debatable (Ryer & Langer, 1980; Nadon, 1998; Rajchl & Uličný, 2005; van Asselen et al., 2009), especially as estimates for Mesozoic and Cenozoic coals may not apply to Paleozoic coals due to differences in peat-forming vegetation. However, at the time of deposition as peat fragments, the intraclasts were probably considerably thicker than at present, possibly several times thicker.

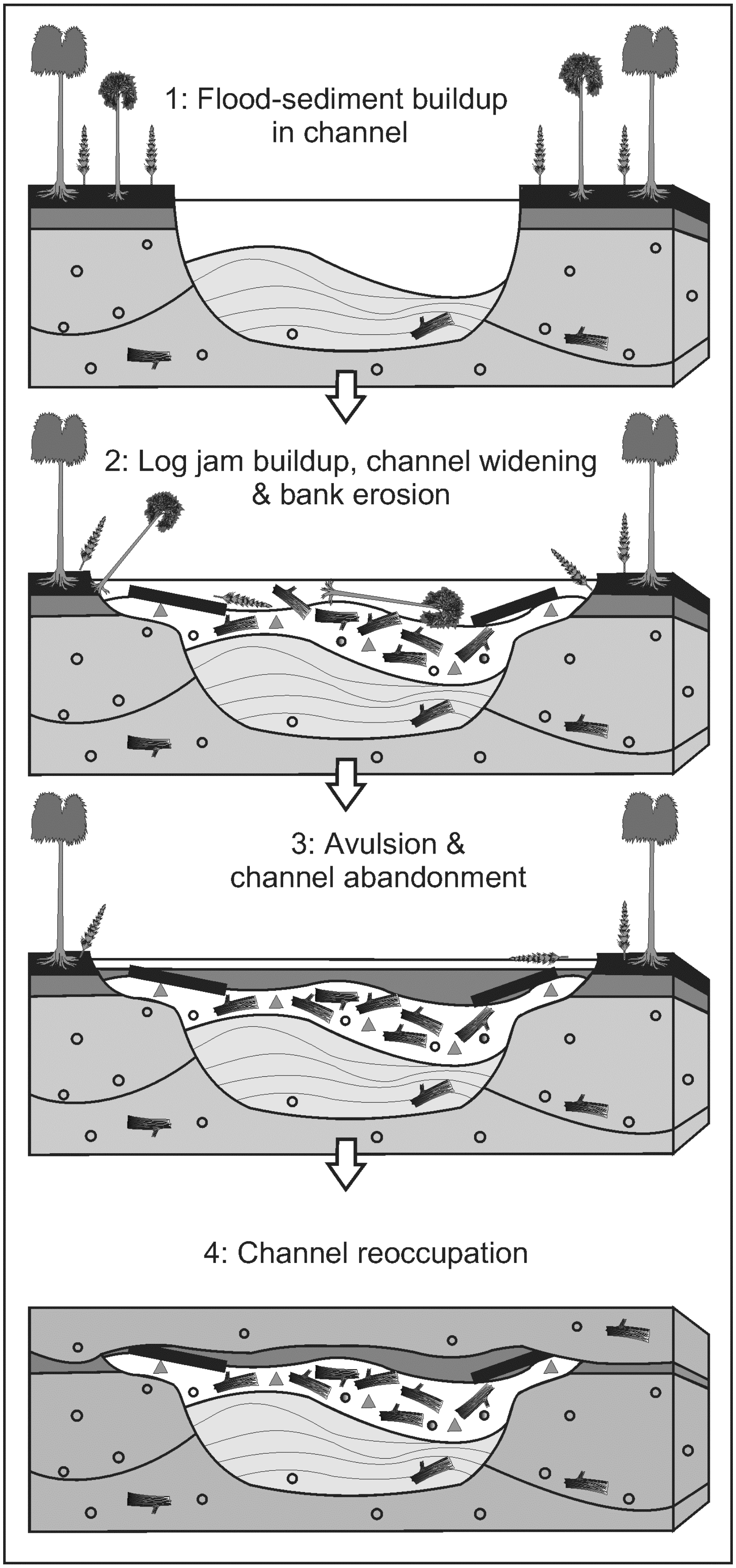
4.7. INTERPRETATION

4.7.1. Evidence that Flood-sediment Aggradation and Log Accumulations Triggered Avulsion

Mudstone beds at South Bar mark periods of channel abandonment. Pre- and post-abandonment channels generally show similar paleoflow directions (Fig. 39B), and later channels appear mainly to have reoccupied previous courses. This suggests that most examples of channel abandonment represent local events, probably including relocation of flow to other channel threads within the braided South Bar system. However, in several cases (Figs. 36, 37, 39D), the post-abandonment channel shows a radical shift in paleoflow direction. This suggests that the channel belt avulsed to a distant part of the fluvial plain and returned to its former site after the inactive tract had become an even surface.

Stratigraphic evidence suggests that both rapid sediment aggradation and organic accumulation contributed to channel abandonment and avulsion. At numerous levels, mudstone beds are underlain by HFS sediment, by organic accumulations, or both. A four-stage model for channel evolution is proposed (Fig. 43). Under the strongly seasonal climate of the South Bar Formation, aggradation of as much as 6 m of flood sediment would have substantially filled many channels (Stage 1). Preservation of HFS sediments implies deposition sufficiently rapid to prevent bedform reworking under lower flow conditions. Overlying log accumulations commonly have a matrix of sandstone that is one to two grades finer than the HFS deposits below, and are inferred to have been deposited high in the channel, probably under conditions of less active sediment transport. Building up on top of the sands, the logs would have contributed

Figure 43. Four stages in the filling, abandonment, and reoccupation of channels in the South Bar Formation. Vegetation types in order of decreasing size are *Sigillaria, Lepidodendron,* and *Calamites*.


1: Flood-sediment buildup in channel
2: Log jam buildup, channel widening & bank erosion
3: Avulsion & channel abandonment
4: Channel reoccupation

further to reduced channel capacity after aggradation had decreased the cross-sectional area. Mudstone and coal clasts are uncommon in the channel-sandstone deposits, and their prevalence with the log accumulations suggests that bank erosion and channel widening took place at a late stage of filling (Stage 2). Similarly, the abundance of pebbles with the logs may reflect reworking of unconsolidated, pebbly sands in the adjacent channel banks. The introduction of toppled bank materials, including peat and riparian vegetation, may further have impeded the channel, leading to abandonment (Stage 3), followed sometime later by reoccupation (Stage 4).

4.7.2. Log Jams in Modern Rivers

The evidence for avulsion following log accumulation suggests that many South Bar organic accumulations acted as log jams, which may act as avulsion triggers in modern channels. We briefly summarize some of the abundant literature on log jams in modern rivers, which has rarely been applied to the ancient record. Due to agriculture, deforestation, and removal of in-channel woody debris, few modern rivers are pristine, and plant material would have been much more effective in fluvial systems prior to anthropogenic landscape modification (Naiman et al., 2000; Brooks et al., 2003).

Log jams are accumulations of woody and other plant material in channels and on adjacent floodplains. Although the term is widely used for any notable accumulation of organic material, without implying channel blockage, most log jams affect channel dynamics. Although prominent in small upland channels, log jams are also common in larger braided rivers (Montgomery & Piégay, 2003; Abbe & Montgomery, 2003; Gurnell et al., 2000). Organic accumulations may be meters thick and may extend for tens of meters down channel. A blockage ratio is given by A'/A, where A' is the projected area of large woody debris and A is the channel cross-sectional area in m^2. A 10% blockage ratio is typically associated with significant blockage (Webb & Erskine, 2003).

Log jams comprise key, racked, and loose members (Table 22; Abbe & Montgomery, 2003). Many jams have one to four key members and ten to one hundred times as many racked pieces. In some Australian log accumulations, most fragments are <300 mm in diameter and <5 m long, although the bulk of the volume comes from pieces 300 to 700 mm in diameter (Webb & Erskine, 2003). Organic debris is recruited by undercutting of banks, especially during floods (Robison & Beschta, 1990; Alexander et al., 1999), with contributions from tree senescence and windthrow (Keller & Swanson, 1979; Webb & Erskine, 2003).

Abbe & Montgomery (2003) classified log jams into three groups based on whether debris is *in situ* or transported (Table 22). *Autochthonous jams* comprise debris that has not moved from the point of entry, for example toppled trees that span or lie within the adjacent channel. *Combination jams* have stable debris that obstructs and traps driftwood transported during high flows. *Transport jams* comprise woody debris, all of which has moved some distance downstream. Sub-groups are recognized based on the extent of the accumulations for combination jams and on the location of the accumulation within the channel for transport jams (Table 22). Jam types may be difficult to distinguish in the field because some wood may be buried by sediment and because racked debris is the most visible component.

By increasing roughness, log jams cause large energy losses and promote sediment buildup, reducing channel capacity (Curran & Wohl, 2003). Webb & Erskine (2003)

Table 22. Plant debris types within river accumulations, and classification of log jams. From Abbe & Montgomery (2003).

Plant Debris Types		
Key members	Trees and large plant fragments that anchor other debris; have sufficient size and mass to resist transport during high flows	
Racked members	Fragments lodged against a channel obstruction (key member, boulder)	
Loose members	Fragments that fill interstitial space but add little physical integrity to the jam	
Log Jam Group	**Subgroup**	**Features**
1) Autochthonous		Key member has not moved from point where it entered channel; affects flow conditions
	Bank input	Tree fell directly into channel from growth position, commonly lying partially on the bank
	Log steps	Tree lies within channel, completely or partially blocking it and usually normal to flow, creating a step in the channel bed
2) Combination		Key member obstructs channel and traps waterborne materials (racked and loose members)
	Valley	Jam width exceeds channel width and influences valley bottom
	Flow-deflection	Jam width less than channel width, but deflects channel course
3) Transport		All members moved some distance downstream
Stable		Jam persists for prolonged period
	Debris flow/flood	Chaotic accumulation laid down by debris flows or major floods; key members uncommon or absent
	Bench	Key members become wedged along channel margin, forming bench-like surfaces and stabilizing banks
	Bar apex	Debris accumulates at upstream apex of mid-channel bars and vegetated islands
	Meander	Debris accumulates along outside of meander bends, limiting channel migration
	Raft	Large floating accumulations capable of plugging large channels and causing backwater areas
Unstable		Debris deposited as flood peak recedes and likely to be transported during the next flood; on bar tops and banks

estimated that about 50% of sediment storage is associated with large woody debris in some Australian channels. Makaske et al. (2002) noted that log jams reduce discharge and promote sediment buildup, decreasing depth and thus increasing the width/depth ratio of the channel. By impeding flow, log jams can cause overflows onto the adjacent floodplain (Assani & Petit, 1995; Brooks & Brierley, 2002; Jeffries et al., 2003), which may assist in floodplain aggradation and promote meander cutoff. For the Columbia River, log accumulations cause an elevated water table upstream, resulting in more frequent levee overtopping and possibly assisting the formation of crevasses that promote avulsion (Makaske et al., 2002). In this multichannel system, impeded channels may lose flow to other channels, resulting in channel abandonment. Logs also build up at the entrance to secondary channels (Nakamura & Swanson, 1994).

Of particular importance is the promotion of scour near log accumulations, locally generating pools and causing bank erosion and channel expansion. Makaske et al. (2002) documented a log jam that extended across the entire channel width and for 50 m downstream, with logs packed in all orientations; at this site, channel width had nearly doubled due to increased bank scour.

Woody debris accumulates in the larger lowland reaches of many rivers (Desloges & Church, 1987). The Tagliamento River of Italy (Gurnell et al., 2000) is a braided, gravelbed river with multiple channels, bars, and vegetated islands. Floating wood is stranded at bar crests, where it may assist in producing “pioneer islands”, and along the upstream sections, margins, and surfaces of vegetated islands. In multi-channel reaches of the coastal plain, erosion of floodplain woodlands increases the abundance of in-channel debris. In strongly seasonal rivers, such as the sandbed Burdekin of Australia, peak flows are short, resulting in large volumes of stranded material during the falling stage (Alexander et al., 1999). Logs stranded on emergent bars may be partially filled by sand and gravel.

Although log accumulations are prominent in modern rivers, it is not always clear to what degree they promoted channel abandonment and avulsion. However, in some instances, field observations confirm a direct relationship between log jams and flow diversion. On the Athabasca Delta in northern Canada, a log jam on the Embarras distributary channel in the early 1980s led to the formation of a crevasse channel and caused an avulsion that is still enlarging, rerouting flow into an adjacent lake (D.G. Smith, written communication, 2009). Within the anastomosing channel belt of the Columbia River, Makaske et al. (2002) documented a completely filled channel (Channel 4) similar in size to the present main channel (Channel 3). At the upstream entrance of the filled channel, a fallen tree hinders flow from entering the channel, which is partially blocked by a largely buried log jam. The formation of Channel 3 was dated at about 1000 years B.P., and a stable bifurcation probably existed at the avulsion point until the log jam initiated abandonment of Channel 4 more recently (B. Makaske, written communication, 2009).

The orientation of large woody debris in modern channels is highly variable. Individual logs in channels may lie parallel to flow, but many log jams show little preferred orientation, although some logs show a sub-perpendicular orientation (Gastaldo & Degges, 2007). Gastaldo (2004) noted that large data sets are needed to confirm a preferred orientation.

4.7.3. Interpretation of the Organic Accumulations as Log Jams

Based on the preceding summary, we now interpret log accumulations in the South Bar Formation, recognizing that not all the accumulations are sufficiently well exposed to be interpreted with certainty. The accumulations closely resemble modern log jams in their thickness and the size of the debris. Log accumulation SB 5.1 is 1.2 m thick but, applying a compaction ratio of 4.2 (Table 21), was originally 5 m thick. It is exposed as a sheet for 5 m along depositional strike between beach and cliff top, with a cross-sectional area of 25 m^2. Assuming a host channel 8 m deep and 160 m wide (see discussion of South Bar channel dimensions, above) with a cross-sectional area of 1280 m^2, the blockage ratio would have been 2%. However, the exposure width is a minimum as neither margin is exposed. Assuming an extent of 20 m (the exposed width of the log accumulation in Fig. 37), the cross-sectional area would have been 100 m^2, yielding a blockage ratio of 7.8%. Additionally, SB 5.1 caps HFS deposits, the accumulation of which would have reduced channel depth considerably prior to log buildup, further increasing the blockage ratio. Although our blockage ratio estimate involves many uncertainties, it approaches the 10% value recognized to cause significant blockage in modern rivers, and we infer that log accumulations in the South Bar Formation had the ability to affect channel dynamics.

Few fragments might seem to qualify as key members. However, most logs are only partially exposed, and key members form a small proportion of many modern jams and might not have been observed in the South Bar accumulations. Additionally, larger fragments correspond to substantial trees, although some trunks may have broken up. Based on growth form, cordaitaleans in particular could have formed key members, with their large canopy of branches able to snag racked and loose members (see the reconstruction in Falcon-Lang & Bashforth, 2005). Less likely candidates for key members are the lycopsids, most of which lacked branches until the final phases of life, and tree ferns, *Calamites*, and medullosalean pteridosperms, all of which were less than 10 m high. We conclude that all the South Bar Formation accumulations include possible key members. The coal intraclasts, which would have been thicker prior to coalification, may have formed key members in places.

Although autochthonous jams and combination jams (flow-deflection jams) may be present, most accumulations are probably transport jams of the stable, flood-jam sub-group, or unstable bartop accumulations (Table 22). The former are commonly associated with channel alteration in modern settings (Abbe & Montgomery, 2003, fig. 14). Most plant groups represented, especially the cordaitaleans, had true wood in their structure, but many had rather soft inner tissues. Thus, the logs would probably have floated well, and some accumulations may represent unstable transport jams formed by stranding of logs during waning of seasonal flows with short peak discharges. Most fragments are highly compressed, suggesting that rapid burial precluded decay and sediment infilling at the surface. However, a few sandstone-cast logs (or filled pith cavities in *Calamites* and the cordaitaleans) may have partially decayed while lying on bar tops or submerged on channel bottoms, to be filled with sediment (Rex, 1985; Gastaldo et al., 1989b) and buried or reworked during the next flood. Some axes may have partially decayed prior to toppling into the channels, and their hollow interiors may have filled rapidly with sediment.

Based in part on their common association with mudstone intraclasts, the log accumulations were inferred above to have been associated with bank erosion and channel expansion, which would have increased channel width/depth ratio (Stage 3, Fig. 42) and might have resulted in catastrophic stripping of the adjacent floodplain (Nanson, 1986). Where sheets and mounds of logs are present lower in the channel fills (Fig. 39A, D), they may have increased roughness and promoted sediment buildup. The mud-filled hollow bordering the log jam of Figure 37 may reflect scour and pool formation in such an area of channel roughness. Finally, the log accumulations may have assisted in stabilizing bars high in the channel, contributing to the formation of vegetated islands.

Floral analysis suggests that most logs were derived from riparian vegetation and vegetated islands within the alluvial tract, where rapid lycopsid growth rates and the development of plant cohorts (Phillips & DiMichele, 1992) would have ensured a plentiful supply of woody debris. Charcoal was not noted in the log jams, and there is no evidence that wildfires aided recruitment. Extrabasinal factors may have destabilized some forests or caused biome replacement, contributing to log availability. For example, sea-level fall associated with Gondwanan glaciation could have caused regional incision, peat destruction, and modification of interfluve landscapes (Falcon-Lang, 2004a), and frequent changes in climate, as documented for the overlying Sydney Mines Formation (Tandon & Gibling, 1997), could have caused rapid forest turnover (cf. Hilbert et al., 2007).

4.7.4. Explanation of Sparse Plant Remains in Abandoned-channel Mudstone

Although there is compelling evidence that vegetation was frequently added to the South Bar braided rivers, abandoned-channel mudstone beds are virtually bereft of plant fossils. Despite targeted searches, only rare comminuted plant debris and exceedingly rare foliage fragments were found, and this circumstance requires explanation.

It is intuitive that high-energy flow will mechanically degrade plant remains, particularly delicate foliage, and some studies in modern rivers have suggested this (Alexander et al., 1999). However, experiments using tumbling barrels have demonstrated that freshly abscised leaves are surprisingly robust (Spicer, 1981; Ferguson, 1985). Upon entering the water column, fresh foliage absorbs water until sinking when specific gravity exceeds unity (Spicer, 1981, 1989; Ferguson, 1985; Spicer & Greer, 1986). However, if a leaf is transported in suspension, it can potentially be transported intact for considerable distances (Gastaldo, 1994). Based on these observations and flow conditions inferred for the South Bar channels, foliage may have been quickly stripped from toppled plants, flushed through the fluvial system, and deposited in an ocean to the northeast. In comparison, the trunks and defoliated petioles remained in the system due to their higher specific gravity.

Following channel abandonment, riparian vegetation would have contributed detritus to the standing water by senescence and windfall. Experiments on the dispersal of leaves from plants growing around lakes indicate that the horizontal distance of transport is limited (Rau, 1976; Spicer, 1981), rarely exceeding the height of the source tree (Ferguson, 1985). With abandoned channels in the order of 140 to 200 m wide (see above), little identifiable foliage may have reached parts of the water body.

In comparison with robust, freshly abscissed leaves, foliage that has experienced even slight microbial decay is substantially more susceptible to mechanical degradation (Spicer, 1981). Leaves typically become partly saturated and flexible shortly after falling onto a forest floor, predisposing them to fungal and bacterial degradation that is pronounced in humid tropical climates (Ferguson, 1985; Gastaldo, 1994; Alexander et al., 1999; Gastaldo & Staub, 1999). Considerable quantities of partially saturated and decayed forest-floor litter would have entered South Bar channels along with collapsed peat. This material would have suffered rapid mechanical degradation, and may constitute much of the finely comminuted plant debris in the sandstone beds. Additional phytoclasts might have broken from pieces of bark, wood, and peat fragments during flow.

4.8. DISCUSSION

We have identified log jams and flood sediment buildup as major factors in channel abandonment and avulsion of Middle Pennsylvanian braided channels. As far as we are aware, log jams have not previously been implicated in the evolution of pre-Quaternary fluvial systems. In the following discussion we review relevant information about plant evolution, terrestrial ecosystems, and paleoclimate in order to predict when log jams first began to influence fluvial systems (Fig. 44). We then review known examples of ancient log jams to critically test that hypothesis.

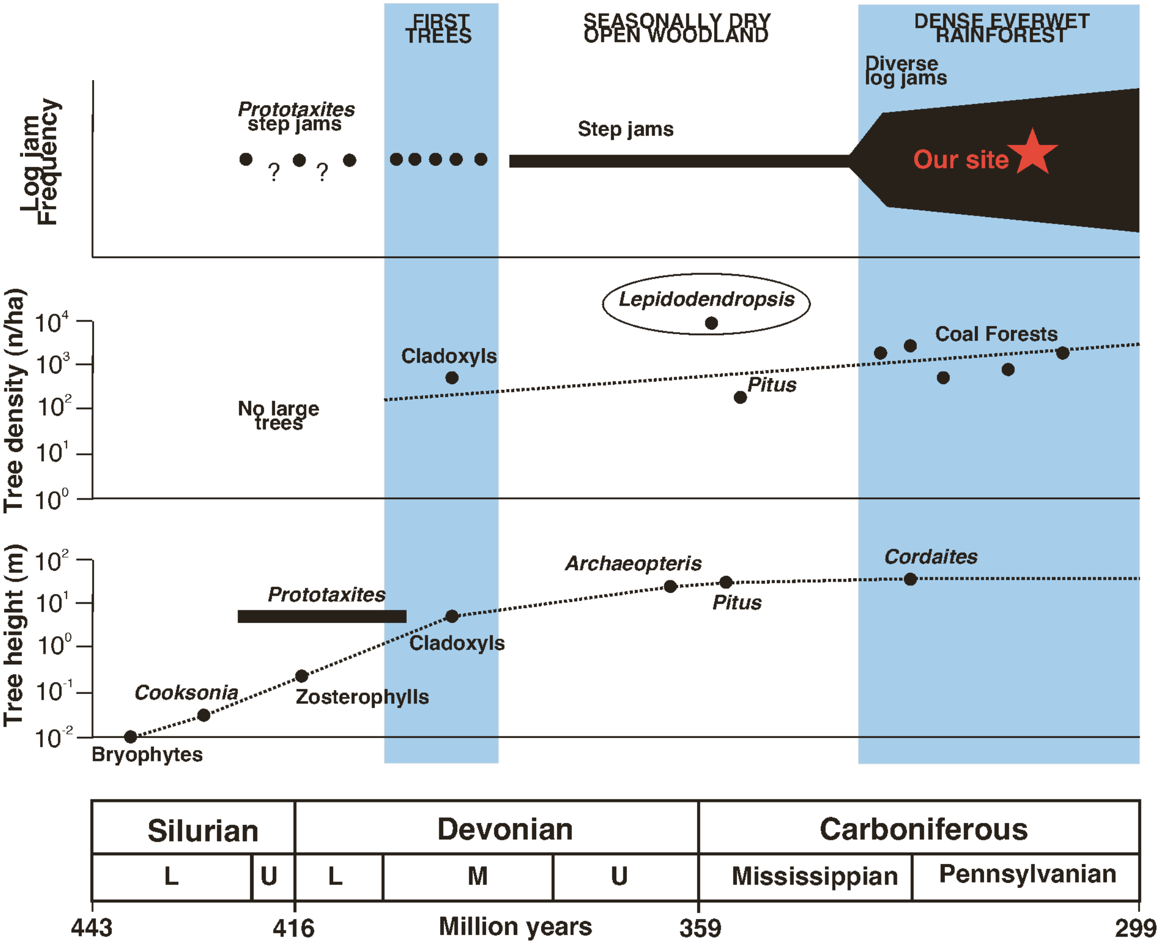


Figure 44. Diagram showing the increase in stem density and canopy height through the Silurian to Carboniferous (443 to 299 Ma) and summarizing evidence for log jams. The increase in the frequency of log jams in late Mississippian fluvial systems probably reflects the onset of humid tropical conditions and the rise of dense forests. See text for a summary of sources.

4.8.1. Evolution of Trees and the Earliest Log Jams

The formation of log jams requires the existence of large trees and their occurrence in high abundance adjacent to fluvial systems. The first ‘trees’ encountered in the fossil record (Fig. 44) are those of *Prototaxites* (Dawson, 1859), an arborescent fungus that produced trunks up to 8.8 m long and >1 m in diameter (Hueber, 2001). Although locally found anchored in growth position (Dawson, 1871), little is known of the density of these enigmatic structures on Late Silurian to Middle Devonian (421 to 385 Ma) landscapes (Hillier et al., 2008). Given their nutritional status as saprophytic heterotrophs (Boyce et al., 2007), it seems improbable that soils could have sustained dense populations. We have observed *Prototaxites* logs and fragments in Early Devonian (Emsian) braided channel deposits of the Battery Point Formation of Québec and in braided-channel and distal alluvial-fan deposits of the Emsian to Eifelian Trout Valley Formation of Maine. However, such single large trunks are likely to have generated only bank-input and log-step jams (Table 22).

In Middle Devonian times, the first true trees evolved. These cladoxylopsids constructed trunks using an architecture supported by adventitious roots similar to those of some extant tree ferns (Soria & Meyer-Berthaud, 2004). Fossil forests of cladoxylopsids occur in late Middle Devonian strata at Gilboa, New York (≈385 Ma). The stumps show a cormose base, up to 1 m diameter, which rapidly tapers upwards, implying a maximum height of 15 to 17 m based on biomechanical considerations (Mossbrugger, 1990). However, such calculations may overestimate true height because, where preserved in entirety, the trees are up to 8 m high only (Stein et al., 2007). Although many tens of stumps have been found in growth position at three horizons over the past 150 years, stump density has rarely been recorded in detail. Two exceptional studies report small patches of autochthonous vegetation, which scale up to densities of ≈775 trees per hectare (Goldring, 1924, 1927) and ≈615 trees per hectare (Driese et al., 1997), suggestive of medium-density forest. However, other reports imply that these were rather dense clumps within generally more open vegetation (Moore, 1933). Although locally incorporated into fluvial systems, observed concentrations of cladoxylopsid trunks do not approach levels that could be interpreted as large log jams.

In Late Devonian and Mississippian times a diverse range of large trees emerged, with trunks constructed of pycnoxylic wood similar to that of extant conifers. Famennian stumps of *Callixylon* (375 to 359 Ma) attributed to archaeopterid progymnosperms (Beck, 1960) have basal diameters >1.5 m where found in growth position in Oklahoma (Arnold, 1947). Mississippian stumps of the pteridosperm *Pitus primaeva* (359 to 345 Ma) are even larger, attaining a maximum diameter of 2.5 m at King Water, Cumbria, UK (Long, 1979). Based on biomechanical considerations these trees would have had trunks up to 30 m and 43 m high, respectively (Mossbrugger, 1990). These estimates are, in part, confirmed by discoveries of incomplete trunks of *Pitus withami* up to 22 m long near Edinburgh, UK (Witham, 1833; Balfour, 1872). Tree densities are not known in detail for archaeopterid or *Pitus* communities, although the distribution of 10 stumps of *Pitus primaeva* at the King Water site are suggestive of a scattering of trees across an open landscape (Day, 1970) with a density of <200 trees per hectare (Falcon-Lang et al., 2010). Where found in braided channels, logs are generally isolated, the famous Craigleith Quarry site in Edinburgh yielding only seven large trunks during nearly fifty years of intensive quarrying (Long, 1979).

Thus, although very large trees had evolved by Late Devonian and Mississippian times, it is uncertain whether vegetation was sufficiently dense to cause significant obstructions when introduced to fluvial systems, apart from effects associated with individual logs. Tree density is controlled in part by water availability. In modern tropical ecosystems, the ecotone between closed rainforest and open savanna corresponds to a mean annual rainfall of 1200 to 1500 mm and moderate seasonality (Mauseth, 2008). Our knowledge of Late Devonian and Mississippian plants is based primarily on the paleoequatorial regions of North America and Europe, which were subject to the combined effects of monsoonal seasonality (Falcon-Lang, 1999a, b) and a greenhouse climate mode (Wright & Vanstone, 2001). This may explain why dense continuous forest appears to have been absent from these regions at this time, despite the scattered occurrence of large trees. Dense forest appears to have existed only in wetlands of rather limited extent during this interval (Falcon-Lang, 2004c).

During late Mississippian times (≈326 Ma), a pronounced shift in tropical climate accompanied the increased intensity of high-latitude glaciation in early Namurian (Serpukhovian) times (Fielding et al., 2008a). Associated changes in thermal gradient would have enhanced convective precipitation in tropical regions (Peyser & Poulsen, 2008) and would have amplified cyclic fluctuations between cool/dry and warm/wet states (Falcon-Lang, 2004a). Everwet tropical rainforest covered large areas of the equatorial belt (Greb et al., 2003), at least during interglacial phases when precipitation was greatest (Falcon-Lang et al., 2009). Interglacial rainforest was dense and diverse (DiMichele & Phillips, 1994), with trees up to 50 m high (Falcon-Lang & Bashforth, 2004) and forest densities up to 1800 trees per hectare (DiMichele et al., 1996b, 2001).

We infer that, in the late Mississippian (Serpukhovian), the tropical landsurface crossed a threshold, which thereafter permitted the frequent occurrence of large log jams.

4.8.2. Ancient Records of Log Jams

Consistent with our knowledge of evolving terrestrial ecosystems summarized above, we find no evidence of major log jams in pre-Serpukhovian fluvial systems. Although logs are present in channel fills from the Early Devonian onwards, they do not appear to have been sufficiently abundant to form log jams other than bank-input and log-step jams. Currently, the oldest known accumulations of numerous logs within channels—although poorly documented—are in the late Mississippian and earliest Pennsylvanian 'Millstone Grit' facies of northern Britain. The earliest log jam that we have observed firsthand occurs in the lowermost Pennsylvanian (late Namurian) Boss Point Formation of Atlantic Canada. Here, large cordaitalean logs, locally calcite-permineralized, are abundant within braided channels, together with less common trunks of lycopsids, sphenopsids and tree ferns. The largest cordaitalean logs are 8 m long and 1 m in diameter, and some show rootstocks indicating that trees were undercut on eroding channel margins (Falcon-Lang, 2006a). Log accumulations are present in the upper parts of channel fills at several levels, reminiscent of the South Bar occurrences. Although not yet documented in detail, these log accumulations are briefly described in Calder (1998) and Falcon-Lang & Scott (2000).

Slightly younger is a Lower Pennsylvanian (Langsettian) log jam in Alabama (Liu & Gastaldo, 1992; Gastaldo & Degges, 2007). In this occurrence, most logs occupy a bed 0.35 m thick at the top of a channel fill nearly 3 m thick. The logs are up to 7 m long and 500 mm wide, but most are less than 2 m long and 300 mm wide—comparable with the size of most South Bar logs. Most lack crown and root structures. Although not explicitly inferred by Gastaldo & Degges (2007), the concentration of logs high in the channel fill suggests that the accumulation contributed to channel abandonment. The logs are mainly oriented sub-perpendicular to paleoflow, inviting comparison with some modern log jams. Erect trees that project up into the channel base could have impeded floating logs, suggesting an origin as a log raft similar to the Great Raft of Louisiana (cf. Gastaldo & Degges, 2007). In contrast with the South Bar occurrences, many logs are completely or partially filled with sand and gravel, implying decay of soft tissues and filling during periods of exposure. The scarcity of gravel elsewhere in the Alabama succession suggests that many logs were derived from gravelly locations upstream in the Appalachian Orogen (Liu & Gastaldo, 1992), in contrast to most of the South Bar Formation accumulations.

Another Lower Pennsylvanian (Duckmantian) log jam has been documented from the Czerwionka quarry in Poland. Here, a 4 m thick sandstone body, interpreted as a meandering fluvial channel, contains in its uppermost part abundant coalified trunks, branches and roots of cordaitaleans, *Calamites*, lepidodendroids, and other plant debris in a concentrated accumulation. Logs are typically 2 to 3 m long with some attaining 4.5 m and up to 300 mm diameter. Most logs are sandstone-cast and oriented sub-perpendicular to the channel axis (Gradziński et al., 1982). Of similar age is an accumulation of large logs in a 25 m thick braided-fluvial sandstone above the Lower Pennsylvanian (Duckmantian) High Main Coal at Priory North, Durham (Johnson, 1999). Here, during just a few weeks of strip mining, about 30 large cordaitalean trees, more than 2 to 3 m long, were observed in a concentrated deposit (Falcon-Lang & Scott, 2000).

Another accumulation of enormous cordaitalean trees in Middle Pennsylvanian (Bolsovian) fluvial deposits in Newfoundland probably represent log jams (Bashforth, 2005; Falcon-Lang & Bashforth, 2004, 2005). The logs are permineralized with carbonate and are up to 7.6 m long and 1.9 m in diameter, but most are between 200 and 800 mm in diameter. It is notable that almost half the specimens are stumps with attached roots. They are preserved in fining-upward channel lag and point-bar deposits up to 4 m thick, laid down in shallow, coarse-grained meandering streams. Log orientations are widely variable, with many preferentially dipping upstream or perpendicular to the regional paleoflow. Most logs are solitary, but accumulations in some channel lags are randomly oriented and occasionally in contact. Pebbles are commonly concentrated around the logs, indicating increased turbulence and winnowing of finer particles. Individual trunks of this size (especially those with attached root wads) could have formed key members for autochthonous log-step jams and combination jams (Table 22). The logs lie at channel bases rather than channel tops, suggesting that they contributed little to channel abandonment beyond increasing roughness, promoting sediment buildup, and perhaps promoting overbank flow.

Examples of Upper Pennsylvanian log jams are numerous. One of the earliest to be described was documented by King (1854) within a 4 m thick sandstone body above the Pittsburgh Coal, which was exposed over a wide area in strip mines in Pennsylvania. King (1854) noted hundreds of fossil logs, 2 to 3 m long and up to 1 m diameter, typically piled up in an irregular manner. The largest log was nearly 9 m long and probably acted as a key member in this accumulation.

In summary (Fig. 44), our literature review suggests that logs influenced fluvial systems from the Early Devonian onwards. However, landscapes may have crossed a threshold in the late Mississippian (326 Ma), after which high-density stands of large trees exerted a major influence on fluvial dynamics and morphology through the construction of frequent, diverse log jams. We note that, along with the ability of vegetation to stabilize banks and promote single-channel systems (Tal & Paola, 2007), the capability of logs to influence channels (as they do so effectively in landscapes unmodified by humans) represents an important change in fluvial dynamics. This capability would have promoted complex feedback chains between vegetation and sedimentation (Murray et al., 2008).

4.9. CONCLUSIONS

1. We present evidence for the buildup of thick flood-sediment and log accumulations in the South Bar Formation of Atlantic Canada, a Pennsylvanian braided-river deposit. The presence of thick units of plane beds, sigmoidal cross-beds, and antidune bedforms indicates that large volumes of sand were mobilized and deposited by floods with high peak discharges that declined rapidly, and these beds are commonly capped by log accumulations. Mudstones that overlie the log accumulations indicate that the local channel reach was abandoned. Some overlying channel sandstones exhibit radical changes in paleoflow when compared with underlying sandstones, suggesting that some abandonment events record

avulsion to distant parts of the alluvial plain. Although a direct cause-and-effect relationship cannot be established, it is probable that the rapid accumulations of flood sediment and logs were key factors in promoting channel relocation. Such intrinsic effects are normally difficult to document for ancient fluvial systems.

2. Log accumulations comprise a wide range of Pennsylvanian floral groups, and mainly represent vegetation toppled by bank undercutting from riparian habitats and forested mires on inactive braided tracts. Permineralized cordaitalean logs in basin-margin locations were probably transported from nearby uplands. The log accumulations are interpreted as stable transport log jams laid down during floods, along with unstable accumulations of logs stranded as floods receded. Many logs were parts of large, canopied trees, particularly the cordaitaleans, which could have acted as key members in log jams, trapping other debris.
3. Compaction estimates for log accumulations are based on log/sediment proportions and the size distribution of the logs. Results indicate that some beds may originally have been more than four times their present thickness. Although the outcrops do not expose the full width of the log accumulations, estimates of cross sectional-area of the log accumulations, in comparison with estimated South Bar channel dimensions, suggest that some accumulations would have been large enough to influence channel dynamics.
4. Large log accumulations are known from several Pennsylvanian formations, but none are apparent earlier in the geological record. Although large trees had evolved by the Early Devonian, forests may not have been sufficiently dense to promote frequent, large log jams, apart from effects associated with individual logs.

Landscapes may have crossed a density threshold early in the latest Mississippian, after which vegetation would greatly have affected river dynamics.

5. We suggest that the impact of woody material and plant evolution on ancient fluvial systems has been accorded insufficient emphasis. Few modern rivers are pristine, and plant material would have been an effective agent prior to anthropogenic landscape modification.

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CHAPTER 5: DISCUSSION

5.1. INTRODUCTORY STATEMENT

Because most fossilized plant remains were transported from their site of growth prior to burial, a primary goal of paleoenvironmental reconstructions is to determine the original distribution of vegetation over the landscape—what was growing where, with what, and why? These fundamental questions are the 'raison d'être' for paleobotanists who study the paleoecology of Pennsylvanian plant communities.

This thesis provides insight into the paleoecology of vegetation that occupied basin-margin or inland settings during the Pennsylvanian, which are poorly constrained in comparison with contemporaneous floras in basinal lowland environments. Marginal settings were characterized by steep gradients and high-energy flow due to their proximity to elevated uplands, and the prevalence of coarse-grained sediment enhanced the drainage of surface water into the groundwater column, thus reducing the availability of near-surface water to plants and the substrates that might preserve them. At all localities studied, clastic substrates were the primary habitat available for colonization by plants. Although mires developed locally, either due to allocyclic and/or autocyclic processes, most peat accumulation was restricted in time and space.

In general, basin-margin settings contrasted with those in coeval basinal lowlands, where low gradients, low-energy flow, greater accommodation space, proximity to oceans and lakes with high base levels, and a higher fraction of fine-grained sediment resulted in the retention of surface water and the prevalence of poorly drained soils. Such conditions promoted the preservation of plant remains. With these geologic and edaphic requisites in place, thick and widespread mires and associated clastic wetlands developed, particularly during humid climatic excursions.

Regardless of substrate conditions and habitat preferences, heterogeneity was the primary motif of plant communities in both basin-margin and basinal lowland settings, with patchiness occurring at all spatial and temporal scales.

5.2. HABITAT PREFERENCES OF VEGETATION ON PENNSYLVANIAN BASIN MARGINS

Following the theme of the thesis, the body of this discussion presents a synthesis of what is known about vegetation that occupied largely non-peat-forming habitats during the Pennsylvanian, with a focus on communities that occupied relatively high-energy environments in inland settings or along the periphery of basins. Based on new findings described in the preceding chapters, and drawing on previous paleoenvironmental reconstructions from both limnic and paralic basins, the composition and distribution of plant communities in a variety of depositional environments throughout Euramerica can now be evaluated systematically for the first time. The study sites selected for this thesis deliberately included examples that spanned much of the Pennsylvanian, thereby facilitating an analysis of long-term evolutionary trends in vegetation and ecosystems. The synthesis is arranged below by plant clade (lycopsids, calamiteans, sphenophylls, tree ferns, herbaceous ferns, medullosalean pteridosperms, non-medullosalean pteridosperms, cordaitaleans), and where relevant, paleoecological interpretations for certain groups are thereafter discussed geochronologically (Early, Middle, and Late Pennsylvanian epochs). This organization scheme allows broad floristic patterns to emerge from the evaluation, with temporal comparisons indicating whether or not the habitat preferences of plant clades shifted through the Pennsylvanian. The material presented in this discussion is intended to form the basis of one or more subsequent publications.

5.2.1. Landscape Reconstructions Included in the Survey

A summary of the dominant paleoenvironmental setting for each basin/coalfield in the survey, along with the interpreted habitat or landform preference(s) of each plant group, is given in Table 23. Previous landscape reconstructions included are based on megafloral data collected in different ways from successions constrained by varying approaches of sedimentologic and taphonomic analysis, the result being that depositional environments and interpreted habitat preferences of plant groups are presented at varying degrees of resolution.

5.2.1.1. Early Pennsylvanian

Falcon-Lang (2006a) provided the only known paleoenvironmental reconstruction for Early Pennsylvanian plant communities that occupied non-peat-forming, basin-margin habitats. In his study, the Boss Point and Tynemouth Creek formations of the Cumberland Basin, New Brunswick were interpreted as alluvial fan and piedmont deposits after Plint & van de Poll (1982), but Falcon-Lang et al. (2010; Section 1.3.6.6) attributed these strata to a fluvial megafan that accumulated under strongly seasonal conditions. Together with the interpretations of Falcon-Lang (2006a), preliminary quantitative data from the Tynemouth Creek Formation (Section 1.3.5.1), viewed in a fluvial megafan facies context, are used to infer habitat preferences.

5.2.1.2. Middle Pennsylvanian

Three vegetative reconstructions for Middle Pennsylvanian marginal landscapes facilitate comparison with the paleoenvironmental model proposed for latest Middle Pennsylvanian braided-river plain deposits of the Nýřany Member in the Central and Western Bohemian Basin, Czech Republic (Bashforth et al., in prep; Chapter 2). Libertín et al. (2009b) analyzed lower Duckmantian (lowermost Middle Pennsylvanian) strata that accumulated in a paleovalley traversed by braided to low-sinuosity meandering rivers in the intramontane Intrasudetic Basin of the Czech Republic. Bashforth (2005) studied late Bolsovian (middle Middle Pennsylvanian) coarse-grained meandering stream deposits in a narrow, elevated paleovalley on the northern edge of the Maritimes Basin of southwestern Newfoundland. Iwaniw (1985) examined early Cantabrian (latest Middle Pennsylvanian) paleovalley fills and alluvial fans on the elevated fringes of the paralic ‘post-Leonian’ Basin (*sensu* Wagner et al., 1983) of northwestern Spain.

5.2.1.3. Late Pennsylvanian

Three vegetative reconstructions for Late Pennsylvanian marginal landscapes facilitate comparison with the paleoenvironmental model proposed for middle Late Pennsylvanian braided-river plain deposits in La Magdalena Coalfield (Bashforth et al., 2010; Chapter 3). Martín-Closas & Galtier (2005) studied Stephanian B (middle Late Pennsylvanian) braided-river plain strata in the intramontane Graissessac-Lodève Basin of southern France. Charbonnier et al. (2008) analyzed plant remains in siderite concretions from Stephanian B (middle Late Pennsylvanian) braided-river plain and lacustrine delta deposits in the intramontane Blanzy-Montceau Basin of central France.

In the intramontane Surroca-Ogassa Coalfield of northeastern Spain (Stephanian C, late Late Pennsylvanian), Martín-Closas & Martínez-Roig (2007) studied a distal alluvial fan and braided-river plain succession.

5.2.2. Lycopsids

In all paleoenvironmental reconstructions surveyed, lycopsids were centered in the wettest parts of landscapes, consistent with their paleoecological preference for wet or waterlogged soils (DiMichele & Phillips, 1985, 1994; Phillips & DiMichele, 1992). Deposition under strongly seasonal conditions precluded prolonged or perennial development of such habitats in the Lower Pennsylvanian Tynemouth Creek Formation (Falcon-Lang et al., 2010), accounting for the paucity of lycopsids in the fluvial megafan succession (Falcon-Lang, 2006a). Where present, they are confined to grey fine-grained strata that locally punctuate redbed-dominated successions, interpreted to be poorly drained depressions or 'waterholes' (cf. Hebert & Calder, 2004; Falcon-Lang et al., 2004; Calder et al., 2005) on otherwise well-drained floodplains. Scattered lycopsids probably grew where drainage was poorest, particularly where co-seismic events resulted in rapid subsidence that created shallow, water-filled depressions (Plint, 1985).

In the Middle and Late Pennsylvanian, lycopsids were an important component of swamps and dominated most mires, particularly on poorly drained distal parts of floodplains well away from the influence of fluvial channels. They also dominated swampy substrates along lake margins in the 'post-Leonian' Basin (Iwaniw, 1985), and some occupied levees flanking meandering rivers in the Bay St. George Basin (Bashforth, 2005).

Proportional abundances of the various arborescent lycopsid genera present in basin-margin habitats show distinct changes in dominance patterns through the Pennsylvanian. Although lycopsid remains are very rare in the Lower Pennsylvanian Tynemouth Creek Formation (Falcon-Lang, 2006a), *Sigillaria* has a much higher relative abundance than the lepidodendroids (e.g., *Lepidodendron*, *Diaphorodendron*, *Lepidophloios*). In contrast, Middle Pennsylvanian mires and swamps were dominated by lepidodendroids, whereas sigillarians were less common to absent. In the Late Pennsylvanian, *Sigillaria* once again reestablished as a dominant or co-dominant element in mires, together with *Omphalophloios*.

This floristic pattern is consistent with coal-ball and palynological data from basinal lowland wetland successions in North America, where sigillarians were most common in Early and Late Pennsylvanian mires. *Sigillaria* was the most drought-tolerant lycopsid (Phillips & DiMichele, 1992) and was capable of tolerating minor flooding and sediment influx (Calder et al., 2006), and DiMichele & Phillips (1994) correlated changes in the temporal distribution of this genus with a broad increase in seasonality and reduction in rainfall across Euramerica in the Early and Late Pennsylvanian (Phillips & Peppers, 1984; Cecil, 1990). The resurgence of sigillarians in the basinal lowlands at the Middle to Late Pennsylvanian boundary was related to a major reorganization event among wetland vegetation, during which tree ferns replaced lycopsids as the dominant peat-forming clade over parts of tropical Pangea, particularly in North America (Phillips et al., 1974, 1985; DiMichele & Phillips, 1996a, b; DiMichele et al., 2001, 2009a). Coincident with this changeover, most lepidodendroid genera that flourished in Early and

Middle Pennsylvanian mires went extinct, whereas *Sigillaria* and *Omphalophloios* persisted into the Late Pennsylvanian.

Cleal et al. (2009) have emphasized that the aforementioned floristic patterns are largely based on data from coal seams in basinal lowland successions of North America, and that the patterns do not always hold in European successions. Instead, Cleal et al. (2009) have suggested that the reorganization event recognized at the Middle to Late Pennsylvanian boundary in North America merely represents the culmination of a more gradual vegetational change that occurred over ≈3 to 4 Ma. Nonetheless, on the whole, arborescent lycopsids in basin-margin settings clearly experienced shifts in dominance through the Pennsylvanian similar to those recognized in the basinal lowlands of North America. However, lycopsids, rather than tree ferns, remained the dominant contributor to biomass in Late Pennsylvanian mires on basin-margins. *Sigillaria* and *Omphalophloios* may have been able to persist in basin-margin mires because they had adapted to relatively drier peat substrates (Wagner, 1989; Phillips & DiMichele, 1992).

5.2.3. Calamiteans

The calamiteans were woody, subarborescent plants that formed clonal, regenerative groves, typically on frequently disturbed, rapidly aggrading landforms (Scott, 1978, 1979; Gastaldo, 1992; Pfefferkorn et al., 2001; Calder et al., 2006) but also in mires (DiMichele & Phillips, 1994; DiMichele et al., 2009b). They were opportunists that occupied a variety of habitats on Pennsylvanian basin margins, but were especially prominent within or adjacent to fluvial channels, on exposed floodplains, and on the fringes of wetland ponds or large lakes. The unique growth strategy of *Calamites* enabled it to occupy settings uninhabitable to other plants, exemplified by the fact that it frequently comprised essentially monotaxic thickets. Despite being preserved in a range of depositional facies in basin margin successions, the calamiteans were always centered on the most disturbance-prone habitats throughout the Pennsylvanian.

5.2.4. Sphenophylls

The opportunistic sphenophylls were herbaceous plants that formed dense, scrambling thickets (Batenburg, 1977, 1981; Galtier & Daviero, 1999; Bashforth & Zodrow, 2007), and were part of low-stature pioneering communities that colonized newly exposed substrates. On Pennsylvanian basin margins, they were most common in wet, frequently disturbed habitats, such as abandoned channels, low-lying floodplains, and poorly developed levees. *Sphenophyllum* also formed groundcover beneath arborescent vegetation in mires in the Intrasudetic and 'post-Leonian' basins (Iwaniw, 1985; Libertín et al., 2009b) and swamps in La Magdalena Coalfield (Bashforth et al., 2010; Chapter 3), and dominated marshes in the Central and Western Bohemian Basin (Bashforth et al., in prep.; Chapter 2). Sphenophyll thickets also formed along lake margins in the 'post-Leonian' Basin and in La Magdalena Coalfield. *Sphenophyllum* occupied such a wide array of depositional environments in basin margin regimes that it is difficult to discern any shifts in paleoecological preference through the Pennsylvanian.

5.2.5. Tree Ferns

The arborescent ferns produced abundant spores, grew rapidly, and were capable of regeneration after burial, all indicators of an opportunistic life history strategy with rapid dispersal and colonization of disturbed habitats (Willard, 1993; DiMichele & Phillips, 1994, 2002; Baker & DiMichele, 1997; Falcon-Lang, 2006b). They had an indeterminate growth strategy and were free-sporing, and thus required damp but exposed substrates to complete their sexual cycle. In basin-margin habitats, tree ferns were commonly associated with the equally opportunistic sphenophylls, herbaceous ferns, and non-medullosalean pteridosperms.

In the Lower Pennsylvanian Tynemouth Creek Formation, arborescent ferns, together with pteridosperms and rare lycopsids, probably persisted in poorly drained depressions or ‘waterholes’ scattered over largely dry, mud- and silt-dominated floodplains. Tree ferns also grew on poorly drained, muddy to sandy substrates on Middle Pennsylvanian basin-margins, particularly in abandoned channels, low-lying floodplains, and swamps, but also occupied raised channel banks that comprised unconsolidated sands and gravels in the Bay St. George and Intrasudetic basins (Bashforth, 2005; Libertín et al., 2009b). In the Late Pennsylvanian, arborescent ferns continued to thrive on poorly drained, fine-grained substrates, but they also were the dominant plant group within and adjacent to disturbance-prone braided channel belts, where sandy and gravelly sediment was prevalent (Martín-Closas & Martínez-Roig; 2007; Charbonnier et al., 2008; Bashforth et al., 2010; Chapter 3).

Taken together, these data provide evidence that arborescent ferns on basin peripheries were able to tolerate growth on an increasingly broad array of substrates through the Pennsylvanian. In the Early and Middle Pennsylvanian, they tended to occupy poorly drained, muddy to sandy soils situated some distance from the direct influence of fluvial channels, although they were present on better-drained channel margins at scattered localities. By the Late Pennsylvanian, however, they were the dominant clade in most disturbance-dominated braided channel belts, indicating that they were fully capable of growing on unconsolidated and relatively well-drained sands and gravels alongside high-energy channels.

This secular change was probably evolutionary and recorded the appearance of a new group of tree ferns, some of which had adapted to life on coarser grained, shifting substrates. Leading up the Middle to Late Pennsylvanian boundary, changes were indeed afoot among the arborescent ferns in basinal lowlands. Tree ferns became an increasingly abundant component of plant communities in both clastic and peat-forming habitats (Gillespie & Pfefferkorn, 1979; Pfefferkorn & Thomson, 1982; Phillips et al., 1985; DiMichele & Phillips, 1996b). Concurrent with this proliferation was an increase in stature, with small and 'weedy' species typical of the Westphalian being replaced by taller, stand-forming species in the latest Westphalian (Lesnikowska, 1989), forms that dominated in the Stephanian after reorganization of wetland vegetation at the Middle to Late Pennsylvanian boundary (DiMichele & Phillips, 1996b; DiMichele et al., 2001). In the basinal lowlands, the timing of the transition from small to large growth habits coincided with a trend towards greater ecological tolerance among marattialean tree ferns, which began to dominate most wetland habitats. The proliferation of tree ferns evidently occurred in basin-margin settings as well. With an increase in stature, the new stock of arborescent ferns that appeared during the later part of the Middle Pennsylvanian would have had larger fronds, as well as larger, more laterally extensive, and more deeply penetrating rooting organs. These features would have enhanced the potential for water uptake and transpiration, a requisite for living on better-drained sands and gravels typical of high-energy fluvial systems along basin margins.

Tree ferns also were an important component of most basin-margin mires in the Middle and Late Pennsylvanian, particularly in late stages of development when floods introduced clastic sediment and increased the nutrient content of the peat (Martín-Closas & Galtier, 2005; Bashforth et al., in prep; Chapter 2). However, although arborescent ferns dominated Late Pennsylvanian mires in basinal lowlands, palynological and megafloral evidence indicates that arborescent lycopsids remained the dominant peat-forming clade in almost all mires in basin-margin settings. It is plausible that aspects of the reorganization of wetland vegetation that occurred at the Middle to Late Pennsylvanian boundary in basinal lowlands occurred later in basin-margin settings, and that mires in more marginal positions acted as refugia for some lycopsids (DiMichele et al, 2006a; Falcon-Lang & DiMichele, 2010).

5.2.6. Herbaceous Ferns

Herbaceous ferns, together with sphenophylls and non-medullosalean pteridosperms, were opportunists that formed low-stature, pioneering communities on newly exposed substrates shortly after a disturbance (DiMichele & Phillips, 2002; Phillips & Galtier, 2005; Libertín et al., 2009a). As part of the groundcover, they generally are underrepresented in megafloral assemblages (Scheihing, 1980), making it difficult to ascertain which depositional environments they inhabited. However, they apparently were most common on wetter, fine-grained sediment, such as in abandoned fluvial channels and on poorly drained floodplains, particularly within or adjacent to swamps and mires. Herbaceous ferns also comprised part of the groundcover in communities that inhabited channel flanks in the Intrasudetic Basin (Libertín et al., 2009b), and that grew atop abandoned sheetflood surfaces in the 'post-Leonian' Basin (Iwaniw, 1985).

5.2.7. Medullosalean Pteridosperms

The medullosalean pteridosperms, which comprised both arborescent and lianescent growth forms, were architecturally complex, bore large seeds, and had a low reproductive output, all characters of slow-growing colonizers or site-occupiers that reproduced infrequently or over extended intervals (DiMichele & Phillips, 1994; Dimitrova et al., 2005; DiMichele et al., 2006b). Although medullosalean pteridosperms were an important component of plant communities on peat and wet, clastic substrates, having seeds allowed them to live in moisture deficient regimes that were inaccessible to free-sporing clades (DiMichele & Aronson, 1992). It is thus not surprising that they formed a conspicuous element of the vegetation on Pennsylvanian basin margins.

In the Lower Pennsylvanian Tynemouth Creek Formation, medullosalean pteridosperms probably occupied poorly drained depressions scattered over otherwise dry floodplains of the fluvial megafan, although they also may have persisted on channel flanks. On Middle Pennsylvanian basin margins, they dominated habitats characterized by relatively better-drained soils, such as raised channel banks that comprised sand and gravel, and fine-grained sediment on well-drained floodplains. They also apparently occupied more elevated and drier paleovalley margins and slopes in the Intrasudetic and 'post-Leonian' basins (Iwaniw, 1985; Libertín et al., 2009b). In the Late Pennsylvanian, medullosalean pteridosperms were centered in relatively poorly drained wetland habitats, particularly on distal floodplains where they were less prone to flood-induced disturbances. They grew alongside floodplain channels and the periphery of shallow ponds in La Magdalena Coalfield (Bashforth et al., 2010; Chapter 3), and formed a significant component of diverse communities directly adjacent to mires in the Graissessac-Lodève Basin (Martín-Closas & Galtier, 2005) and Surroca-Ogassa Coalfield (Martín-Closas & Martínez-Roig, 2007). Compelling evidence for habitat partitioning along generic and even specific lines is present in the Bay St. George Basin (Bashforth, 2005) and in La Magdalena Coalfield (Bashforth et al., 2010; Chapter 3).

These observations provide evidence for secular changes in the habitat preferences of medullosalean pteridosperms in basin-margin settings through the Pennsylvanian. Specifically, Middle Pennsylvanian members of the clade were centered on relatively better-drained substrates adjacent to fluvial channels, whereas Late Pennsylvanian examples were most common on poorly drained soils away from channel influence. There was, therefore, a transition towards the wetter end of the wet-dry gradient through time. As discussed in Section 5.2.5, a coincident shift occurred among the arborescent ferns, albeit from the wet towards the dry end of the spectrum (i.e., in the opposite direction). It is thus tempting to hypothesize that, at or near the Middle to Late Pennsylvanian boundary, the clades ‘exchanged places’ along the wet-dry gradient in basin-margin habitats. Medullosalean pteridosperms that appeared near the boundary may have been better adapted to wetter substrates in less disturbed wetlands, whereas the new stock of arborescent ferns could tolerate living on drier and more disturbance-prone habitats nearer channels.

According to DiMichele & Phillips (1996a), however, species replacement in Pennsylvanian wetlands generally occurred from *within* a clade, members of which had similar ecologies, as opposed to replacement from *across* clades, between which ecological preferences were different. Thus, it is unlikely that the ecological centroids of the medullosalean pteridosperms and marattialean tree ferns ‘switched places’ in basin margins. Instead, it is more probable that the decrease in abundance of the medullosaleans on relatively better-drained substrates (e.g., channel margins) records the expansion of the more opportunistic tree ferns into those habitats following the marked extinction of Middle Pennsylvanian arborescent vegetation near the Middle to Late Pennsylvanian boundary (DiMichele & Phillips, 1996b). The change in ecosystem dynamics was also expressed in basin-margin settings. The new and larger tree ferns that appeared after the extinction event proliferated to dominate most available landforms, whereas the new stock of medullosalean pteridosperms largely comprised species that preferred poorly drained habitats.

5.2.8. Non-medullosalean Pteridosperms

In contrast to the medullosalean pteridosperms, low-stature, scrambling or lianescent forms dominated other seed-fern lineages. (The systematics of the non-medullosalean pteridosperms is unresolved. They could be separated into the Order Lyginopteridales and Order Callistophytales, although the term ‘other’ pteridosperms is used in Chapter 2). They had relatively small seeds that were produced in abundance and probably shed en masse, features typical of fast-growing, opportunistic or ‘weedy’ taxa that formed pioneering communities (DiMichele et al., 2006b; Cleal, 2008c).

The non-medullosalean pteridosperms occupied a wide variety of landforms on basin margins, but they most commonly occurred on freshly disturbed substrates in association with the equally ‘weedy’ sphenophylls and herbaceous ferns. Where present, they probably formed only a minor component of communities, either as groundcover or lianas. Inferred habitats include abandoned channels, wetter parts of floodplains, channel flanks, and mires. As in basinal lowland habitats, the lyginopteridaleans were the most common non-medullosalean pteridosperm in basin-margin settings until the late Middle Pennsylvanian, after which they were progressively replaced by the callistophytaleans (Cleal, 2008c; Uhl & Cleal, 2010).

5.2.9. Cordaitaleans

The seed-bearing cordaitaleans had dense, conifer-like wood, a feature that implies slow growth and longevity (DiMichele & Phillips, 1994). The clade comprised a variety of growth forms and had a broad ecological range. In the basinal lowlands, scrambling and shrubby habits were most prevalent in mires, swamps, and low-lying coastal plains (Raymond, 1988; Raymond et al., 2010; Falcon-Lang, 2005), whereas arborescent forms were most common on relatively better-drained to dry clastic substrates (DiMichele & Phillips, 1994; Falcon-Lang & Bashforth, 2004, 2005).

Large cordaitalean logs are frequently found in fluvial strata deposited adjacent to Pennsylvanian uplands, an observation that has propelled the hypothesis that forests of gigantic cordaitalean trees blanketed elevated basin slopes throughout much of Euramerica (Falcon-Lang & Scott, 2000; Bashforth, 2005; Falcon-Lang & Bashforth, 2004, 2005; Falcon-Lang, 2006a; Gibling et al., 2010; Chapter 4). Based on the abundance of cordaitalean remains in basin-margin successions studied in this thesis, as well as those surveyed in this section, this interpretation remains tenable.

In the Lower Pennsylvanian Tynemouth Creek Formation, cordaitalean remains are dominant to exclusive in all megafloral assemblages quantified (Section 1.3.5.1) from the fluvial megafan succession, indicating that they often comprised monotaxic stands. They are interpreted to have lived on basin slopes (Falcon-Lang, 2006a), along the margins of channels that contained ephemeral flow, and on well-drained, degraded floodplains, consistent with their tolerance for seasonally dry edaphic conditions (Falcon-Lang, 2003a, b; Falcon-Lang, 2004a; Falcon-Lang et al., 2009). Based primarily on allochthonous leaves and trunks in fluvial channels, giant cordaitaleans on Middle and Late Pennsylvanian basin margins were inferred to have lived on paleovalley or basin slopes, the flanks of fluvial and alluvial fan channels, and well-drained floodplains. Large cordaitalean trunks are preserved in distributary channels that transected wetlands in La Magdalena Coalfield, but leaves (*Cordaites*) are exceedingly rare in associated fine-grained strata (Bashforth et al., 2010; Chapter 3), suggesting that this clade was not prevalent on all basin margins. In addition, scrambling or shrubby species formed monodominant stands on the periphery of shallow ponds that formed above drowned swamps in the Bay St. George Basin (Bashforth, 2005).

5.2.10. Summary

This survey of habitat preferences of vegetation on basin margins indicates that the landscape-scale distribution of major plant clades was remarkably similar through the Early to Middle Pennsylvanian. Lycopsids occupied the wettest available habitats, calamiteans inhabited aggrading sediment, and most gymnosperms (i.e., medullosalean pteridosperms and cordaitaleans) preferred relatively better-drained conditions. Arborescent and herbaceous ferns, together with sphenophylls and non-medullosalean pteridosperms, favored damp and frequently disturbed areas.

As in the basinal lowlands, such ecosystem stability reflected the reproductive strategies and physiological requirements intrinsic to each plant group. Although a unique suite of habitable landforms existed on each basin margin, the persistence of clades or ecomorphic groups in habitats characterized by discrete edaphic parameters through the Early to Middle Pennsylvanian was probably related to prior phylogenetic partitioning of ecological resource space (DiMichele & Phillips, 1996a, b; DiMichele et al., 1996a, 2002, 2009a). Although taxonomic turnover through this interval resulted in different species pools at each locality, species extinction generally saw replacement by a close relative with similar ecological preferences (an ecomorph) drawn from the same family or genus (a congener).

Basinal lowland ecosystems began to destabilize in the latest Middle Pennsylvanian, possibly due to changing climatic conditions that saw protracted moisture deficits and increased seasonality (Phillips & Peppers, 1984; Cecil, 1990), or due to changing drainage patterns and an influx of clastic sedimentation resulting from renewed uplift in the Variscan Orogen (Cleal & Thomas, 2005; Cleal et al., 2009). In North America, a major extinction event among arborescent vegetation culminated in an abrupt floristic change at the Middle to Late Pennsylvanian boundary, expressed as a collapse of the lycopsid-mire framework (DiMichele & Phillips, 1996a, b; DiMichele et al., 1996a, 2001, 2009a). Changes in dominance-diversity patterns among plant clades also are recognized in basin-margin vegetation around this time, although adjustments within the largely non-peat-forming biome were manifested somewhat differently.

As in the basinal lowlands, the opportunistic tree ferns became more abundant, both in absolute numbers and in species, and a broadening of their ecological tolerances allowed them to dominate a wider array of habitats. On basin margins, this was expressed by an expansion to better-drained substrates within and adjacent to high-energy fluvial channel belts, where the increased height and girth of Late Pennsylvanian forms may have facilitated their growth on sandy or gravelly sediment. Although medullosalean pteridosperms had previously characterized such habitats, Late Pennsylvanian taxa preferred undisturbed settings distant from channel influence, indicating a shift in their ecological centroid towards the wetter end of the wet-dry gradient. In the basinal lowlands, the proliferation of tree ferns across the landscape included a rise to dominance in mires. This did not happen on basin margins, where arborescent lycopsids, particularly *Sigillaria* and *Omphalophloios*, persisted as the primary contributor to biomass in peat-forming habitats. The reason(s) for the disparity in mire composition in basinal lowlands versus basin margins is unclear. Mires in marginal settings may have acted as refugia where some lycopsids persisted, particularly those with a prior adaptation to relatively drier peat substrates.

5.3. COVERAGE OF PENNSYLVANIAN AND EARLIER LANDSCAPES BY VEGETATION

Observations and interpretations presented in this thesis provide the grounds for making broader statements about the crucial role plants played in the evolution of early landscapes.

As documented in this thesis, megafloral assemblages abound in Pennsylvanian basin-margin successions, and paleoenvironmental reconstructions indicate that plants had adapted to inhabit a wide array of landforms that existed under various edaphic and climatic conditions. This section briefly explores the timing of plant dispersal from basinal lowland or coastal settings to more inland and elevated habitats, and the effect that vegetation had on landscape evolution during the process. Direct paleobotanical evidence for this transition is limited due to poor preservation in strata that accumulated under well-drained conditions typical of inland settings, and because the fossil record from upland successions has largely been removed by erosion.

All but the most inhospitable landscapes probably were covered by vegetation by the Pennsylvanian. Lycopsid-dominated mires certainly existed in paralic lowlands by the latest Mississippian (Serpukhovian; Phillips, 1980; Wagner et al., 1996), and vast tracts of low-lying paleotropical wetlands were blanketed by peat-forming habitats by the Early Pennsylvanian (Bashkirian; Cleal & Thomas, 2005). However, the Lower Pennsylvanian Tynemouth Creek Formation in New Brunswick provides clear evidence that vegetation also existed well inland and well above sea level by this time (Section 1.3.5.1). The unit records deposition on a fluvial megafan characterized by narrow fixed-channels containing ephemeral flow and red-bed dominated floodplains that show clear evidence of landscape degradation, indicators of accumulation under strongly seasonal climatic conditions (Falcon-Lang et al., 2010). In essence, the landscape could be compared with that of modern ‘badlands’, which are typified by prolonged drought, intense erosion during the rainy season, and widely scattered pockets of standing or near-surface water. Yet, fossilized plant remains are common throughout the megafan succession, indicating that all major plant clades had adapted to living in rather harsh, moisture-deficient environments by the Early Pennsylvanian.

The record of terrestrial vegetation in inland settings, and by inference on elevated terrains, can be pushed back much further in time. Tomescu & Rothwell (2006) described primitive, thalloid-like communities that existed on Early Silurian (Llandoverian) floodplains alongside braided rivers, which represented the wettest available terrestrial environments at the time. Hillier et al. (2008) described roots of uncertain affinity (giant fungi?) from Early Devonian (Lochkovian to Pragian) fluvial deposits in the Anglo-Welsh Basin, some of which were preserved in vertisols that record highly seasonal conditions. Hotton et al. (2001) interpreted the paleoecological distribution of early land plant communities from the upper Lower Devonian (Emsian) Battery Point Formation on Gaspé Peninsula, Québec, and recognized two distinct plant associations that colonized different landforms on a low-lying fluvial plain subjected to tidal influence (Griffing et al., 2000). However, a third community association, containing the remains of bizarre fungi with arborescent stature, was inferred to have lived in riparian habitats further upstream, based on their preservation as allochthonous fragments in fully terrestrial braided channel deposits. Furthermore, various kinds of *in situ* roots and permineralized plant remains were recorded from higher in the Battery Point Formation (upper Emsian) in high-energy, braided fluvial deposits that contain indications of accumulation under seasonal conditions (Elick et al., 1998; Hotton et al., 2001). These observations imply that plant communities were fully capable of growing in moisture-deficient environments by the Early Devonian.

Although it seems logical that the earliest land plants evolved in coastal settings, morphological adaptations to salinity stress are lacking, suggesting that the first terrestrial vegetation grew under freshwater conditions (Greb et al., 2006). How far inland this occurred remains an open question. Nonetheless, the landward movement of vegetation to increasingly inland and elevated habitats may have occurred quite soon after early land plants became established, and the most logical pathway for terrestrialization would have been along riparian corridors. Riparian zones are recognized as important conduits for plant (and animal) dispersal in modern drainage systems (Gregory et al., 1991), and provide the means for new or exotic species to spread through landscapes (Naiman et al., 2000).

In tandem with vegetation reaching further upstream and upslope, evolutionary processes gave rise to an increasingly diverse and complex array of plant taxa. Chief among the ecological and evolutionary innovations was the development of seeds, which released plants from dependence on wet substrates, and the attainment of arborescence, which resulted in more robust root systems that played a fundamental role in altering weathering, erosional, and depositional cycles (Algeo & Scheckler, 1998). In a comprehensive review of Cambrian to Devonian alluvial successions, Davies & Gibling (2010b) recognized a series of changes in alluvial regimes through this interval that they correlated with specific evolutionary advances in land plants. For example, pedogenic calcite and bioturbated floodplain strata appear in alluvial systems near the time that vascular plant macrofossils become abundant in the late Silurian. In addition, the appearance of underground rooting systems near the Silurian-Devonian boundary broadly corresponds with an increase in lateral accretion sets in channel deposits (Davies &

Gibling, 2010a), indicating that plant roots helped to stabilize river banks, thereby promoting the development of meandering rivers. Finally, Davies & Gibling (2010b) noted that coal and charcoal, evidence for peat accumulation and wildfires, become common in alluvial systems in the Late Devonian, shortly after true trees appear in the rock record. These first-order correlations indicate that the evolution and diversification of early land plants had a profound influence on fluvial processes and deposits in particular, and on landscape evolution in general.

The attainment of arborescence and the influence that large woody debris had on fluvial dynamics is discussed more fully in Section 4.8.1 (Chapter 4). Although the first true trees had evolved by the latest Middle Devonian, and although very large trees existed during the Late Devonian to late Mississippian (Serpukhovian), we concluded that forests were not sufficiently dense to cause significant obstructions when introduced to fluvial systems. With a prominent increase in forest density in the late Mississippian, however, log jams became commonplace and began to play a significant role in fluvial regimes by promoting channel abandonment and avulsion. Although meandering rivers developed near the Silurian-Devonian boundary because roots began to stabilize channel flanks (Davies & Gibling, 2010b), fluvial dynamics became decidedly modern in aspect once dense forests of large trees appeared in the late Mississippian. Furthermore, evidence from the Middle Pennsylvanian South Bar Formation (Gibling et al., 2010; Chapter 4) suggests that braided rivers became deeper and channels more confined once banks were colonized by vegetation.

5.4. PATCHINESS OF VEGETATION

Although a myriad of plant communities existed on a Pennsylvanian landscape at any given slice of time, fossilized (par)autochthonous megafloral assemblages do not record the entire spectrum (beta diversity) of vegetation in the area. Rather, individual collecting sites are characterized by a small number of species (alpha diversity), representing a tiny fraction of plants that coexisted in the area. One can return time and time again to a particular site, knowing that the fossiliferous bed will yield the same species and that the assemblage will have similar dominance-diversity patterns. Furthermore, a single fossiliferous bed can bear a series of low-diversity and peculiar megafloral assemblages when traced laterally over even short distances. Likewise, careful extraction of fossils at a single site will show that unique species assemblages are present in adjacent beds, even over very short vertical distances. Although rarely stated explicitly in the paleobotanical literature, these features are an expression of the original patchiness of Pennsylvanian vegetation. In fact, given that most megafloral assemblages are parautochthonous and derived from a local patch of vegetation (Burnham, 1989, 1993; Wing & DiMichele, 1995; DiMichele & Gastaldo, 2008), I have argued (Bashforth et al., in prep.: Chapter 2) that Pennsylvanian plant communities in riparian habitats comprised a closely spaced collage of low diversity to even monospecific clusters.

That Pennsylvanian vegetation was heterogeneous is becoming increasingly apparent, but almost all publications deal with patchiness among peat-forming communities (e.g., DiMichele & Nelson, 1989; Gastaldo et al., 2004a; DiMichele et al., 2007, 2009b; Opluštil et al., 2007). In some of the most informative deposits, in which mire vegetation was buried *in situ* in a geological instant by volcanic ash (T^0

assemblages), it is clear that peat-forming environments were very patchy at local scales [Libertín et al., 2009a; Opluštil et al., 2009a (Section 1.3.6.2), b]. Heterogeneity also characterized plant communities that occupied clastic substrates associated with Pennsylvanian mires in basinal lowlands (e.g., Scott, 1977, 1978, 1979; Gastaldo, 1987; Gastaldo et al., 2004b; Calder et al., 2006), but the extent of patchiness is not as well constrained for such habitats.

One of the key components to emerge from this thesis is a quantification of the size, composition, and distribution of vegetation patches within riparian habitats on Pennsylvanian basin-margins, namely from braided river systems. In modern lotic ecosystems, the configuration of riparian vegetation is largely a function of the frequency, magnitude, and duration of flooding (Osterkamp & Hupp, 1984; Harris, 1987; Pollock et al., 1998; Rot et al., 2000), the result being that riparian habitats are patchy at all temporal and spatial scales and are among the most complex ecosystems on Earth (White, 1979; Gregory et al., 1991; Naiman & Décamps, 1997; Naiman et al., 2000). The recognition that Pennsylvanian riparian vegetation was also patchy on disturbance-prone braided river-plains does not come as a surprise, but what is remarkable is just how similarly plant communities were organized in modern and ancient fluvial systems.

In the Nýřany Member, which records deposition on a latest Middle Pennsylvanian braided river-plain (Chapter 2), megafloral assemblages from each locality/site are characterized by a unique suite of species, either typified by a single taxon or the consistent association of two to five dominant taxa (Section 2.6). As in modern lotic ecosystems, habitats were strongly partitioned among different clades, with plants organized along ecological gradients controlled by the drainage and stability of habitable landforms. Better-drained and more stable sites, such as raised channel margins, were occupied by long-lived and slow-growing gymnosperms (medullosalean pteridosperms and cordaitaleans) that formed very low-diversity or even monospecific stands. These are comparable to 'dominance-controlled' or 'climax' communities in modern riparian biomes, in which one or more K-selected species are competitively superior to all others (Townsend, 1989). In contrast, poorly drained and frequently disturbed sites, such as the shifting substrates of abandoned channels and low-lying floodplains, were inhabited by clumps of fast-growing and opportunistic spore-producing plants, especially sphenopsids and ferns. These associations had somewhat higher (but still low) diversity, and are comparable to 'founder-controlled' or 'pioneering' communities in modern riparian systems, in which several r-selected species have similar competitive abilities (Townsend, 1989).

In La Magdalena Coalfield, where the basin-fill comprises middle Late Pennsylvanian braided river-plain deposits (Chapter 3), dominance-diversity trends among megafloral assemblages indicate similar patterns between seed-bearing and spore-producing plants (Section 3.7). On interfluve wetlands, medullosalean pteridosperms most commonly comprised low-diversity to monospecific stands that were interspersed within a more diverse matrix of ferns. The distribution of megafloral remains on large, exposed bedding planes indicates that pteridosperm-dominated clumps were at least 20 to 30 m in diameter ($\geq$400 to 900 m^2). This result alone is important because it provides one of the first size constraints for a patch of Pennsylvanian vegetation on a non-peat-forming substrate. The only other example I know of is from late Middle Pennsylvanian swamp deposits in the USA, where pteridosperms dominate a ≥600 m^2 patch (Wnuk & Pfefferkorn, 1984).

The fossil record indicates that heterogeneity was probably intrinsic to early terrestrial plant communities, and that monospecific to low-diversity patches were the norm rather than the exception. For example, some late Visean (late Middle Mississippian) lyginopterid pteridosperms were weedy and probably formed dense, monospecific thickets of groundcover on floodplains (LePage & Pfefferkorn, 2000; DiMichele et al., 2006b). Further back in time, plant assemblages found in the upper Lower Devonian (Emsian) Battery Point Formation (Gaspé Peninsula, Québec) point to clade-dependent partitioning of riparian habitats and the presence of monotypic stands in even early land plants (Elick et al., 1998; Griffing et al., 2000; Hotton et al., 2001).

If the terrestrialization of inland settings occurred along riparian corridors (Section 5.3), and if habitat distribution was controlled by flood-induced disturbances as it is today, then it should come as no surprise that the earliest riparian vegetation had a patchy distribution. Hence, it is clear that vegetational heterogeneity is not unique to modern lotic ecosystems, but instead records a pattern that has persisted since the very first plants began to colonize terrestrial landscapes.

5.5. 'UPLAND' VERSUS 'LOWLAND' FLORAS: SPATIALLY OR ENVIRONMENTALLY DISTINCT BIOMES?

The vast majority of our knowledge of Pennsylvanian vegetation is derived from fossil assemblages preserved in, or associated with, peat-forming ecosystems, inferred to be communities that inhabited damp to waterlogged substrates, particularly in basinal lowlands. However, paleobotanists have long recognized compositionally distinct assemblages, either in strata between coal-bearing intervals or in regions where peat accumulation was minimal to absent, that show signs of having grown on slightly or markedly more moisture-deficient habitats.

5.5.1. Spatially Distinct Biomes (Early Interpretations)

In most early studies (e.g., Gothan & Gimm, 1930; Moore et al., 1936; Chaloner, 1958; Cridland & Morris, 1963; Havlena, 1961, 1971), the ‘wet’ versus ‘dry’ biomes were assumed to have coexisted on different parts of Pennsylvanian landscapes, with wetland floras preserved essentially in place in basinal lowlands [e.g., ‘lowland’ or the ‘Flöznah’ (= ‘near coal’) floras of Havlena (1961, 1971)], and dryland (xeromorphic) floras transported down from extrabasinal habitats to be preserved in lowland deposits [e.g., ‘upland’ or the ‘Flözfern’ (= ‘far from coal’) floras]. In other words, the biomes were contemporaneous but *spatially distinct*, and differences in edaphic conditions under which they grew were controlled by elevation rather than climate.

5.5.2. Environmentally Distinct Biomes (New Interpretations)

In the past 25 or so years, there have been tremendous advances in our knowledge of the role that climate and taphonomy played in the distribution, composition, and preservation of Carboniferous plant fossil assemblages. It now appears that climate (particularly temperature and seasonality of rainfall) is the primary control on the composition and biogeographic distribution of modern vegetative biomes, and it is increasingly clear that late Paleozoic plants also tracked climate (e.g., Phillips & Peppers, 1984; DiMichele & Aronson, 1992; Gastaldo et al., 1996; Rees et al., 2002; Falcon-Lang, 2004a; DiMichele et al., 2006a, 2008, 2009a, 2010; Montañez et al., 2007). In addition, the distribution of coal-bearing versus non-coal-bearing strata, and the paleosols and plant fossil assemblages they contain, is in large part a function of the climatic conditions under which they accumulated, especially seasonality of rainfall (e.g., Cecil et al., 1985; Cecil, 1990; Calder et al., 1991; Calder, 1993, 1994; Cecil & Dulong, 2003). Most fossilized megafloral assemblages are inferred to be parautochthonous and a record of local plant communities (Burnham, 1989, 1993; Wing & DiMichele, 1995; DiMichele & Gastaldo, 2008), based on observations in modern ecosystems that most abscised leaves and other non-woody canopy organs remain close to their source, can not withstand reworking after burial, and decay very rapidly in tropical environments (Ferguson, 1985; Gastaldo, 1994; Gastaldo & Staub, 1999). Furthermore, the plant fossil record is strongly biased towards vegetative biomes that grew in or around wet habitats, where burial and long-term preservation was greatly enhanced (Gastaldo, 1989; Gastaldo et al., 1989a; Behrensmeyer et al., 2000; DiMichele & Gastaldo, 2008; Gastaldo & Demko, in press). Finally, the so-called late Paleozoic 'upland floras' are exclusively known from *within* basinal lowland successions, whereas erosion has obliterated evidence of deposition in elevated extrabasinal or hinterland habitats (DiMichele et al., 2008, 2010).

Armed with these empirical observations, DiMichele et al. (2006a, 2008, 2010) developed a more integrated, heuristic model to explain the spatial and temporal distribution of 'lowland' versus 'upland' biomes on late Paleozoic landscapes. The essence of this model maintains that peat-forming and other wetland vegetation thrived under humid to perhumid conditions, primarily in basinal lowlands but perhaps even blanketing elevated landscapes well above base-level, whereas plant communities that occupied better-drained soils occurred everywhere, including basinal lowlands, during times of increased seasonality and climatic drying. Accordingly, these authors concluded that the 'lowland' and 'upland' floras were *environmentally distinct* biomes, the distribution of which was largely controlled by oscillations in climate and attendant edaphic conditions and preservation potential. In accord with this hypothesis, DiMichele et al. (2010) suggested replacement of the term 'upland' floras with 'seasonally-dry' floras.

5.5.3. Comments on Models Based on Present Research

Analyses of depositional environments and megafloral assemblages in basin-margin settings permit assessment of whether 'lowland' and 'upland' plant complexes represent spatially or environmentally distinct biomes. This section provides comments on the aforementioned models, in the context of studies contained in this thesis.

5.5.3.1. Transport of 'Upland' Elements to Basin Margins and Basinal Lowlands

Experimental and empirical evidence indicates that, contrary to intuition, freshly abscised leaves are remarkably robust and can be transported considerable distances while suspended in high-energy, turbulent, and even sediment-rich waters in fluvial channels, so long as they do not come in contact with the bedload (e.g., Spicer, 1981, 1989; Ferguson, 1985, 2005; Gastaldo et al., 1987; Gastaldo, 1994). Accordingly, if 'upland' plants occupied elevated, extrabasinal habitats, adjacent to and upstream of basin margins and basinal lowlands that supported different communities (i.e., coexisting but spatially distinct biomes), remnants of the ‘upland’ floras should regularly form a component (albeit minor) of megafloral assemblages preserved in basin-margin and basinal lowland successions.

As noted in the Introduction (Section 1.2.1), however, this is not the case. Virtually all megafloral remains recovered from basin-margin successions comprise a subset of the taxa that typify clastic wetland deposits laid down in basinal lowlands. Of the ≈35000 foliar fragments identified in the study areas, only a handful could be attributed to what is traditionally known as an ‘upland’ floral element [e.g., *Megalopteris* in the Tynemouth Creek Formation (Falcon-Lang, 2006a; Section 1.3.5.1) and *Dicranophyllum* in La Magdalena Coalfield (Castro, 2005a, b; Chapter 3)]. Furthermore, permineralized cordaitalean trunks attributed to more elevated habitats were found in the South Bar Formation (Chapter 4), particularly near the margin of the Sydney Basin at Bateston, Kempt Head, and Cape Dauphin, but these are rare in the succession and may not be taxonomically distinct from the more common adpressed cordaitalean axes inferred to have occupied more distal braided channel margins. These observations suggest that whatever biome was growing on basin-margin habitats also was present on contemporaneous hinterland environs, providing indirect support for the model that different vegetational complexes were environmentally rather than spatially distinct.

5.5.3.2. Did Mires Blanket Pennsylvanian Uplands?

DiMichele et al. (2010) proposed that peat-forming vegetation may have enveloped elevated, extrabasinal landscapes during times when humid to perhumid (everwet) climates prevailed. Although a provocative idea, it is certainly not unprecedented, as ombrogenous (domed, rainwater-fed) mires ('blanket bogs') cover vast upland areas in Ireland and Scotland today under similar (albeit temperate) conditions.

Perhaps the most promising evidence for the occurrence of this phenomenon in the Pennsylvanian comes from the St. Étienne Basin (Grand'Croix) in France, where large, angular clasts of silicified peat dominated by cordaitaleans occur in an alluvial fan conglomerate (Grand'Eury, 1877; Galtier & Phillips, 1985). Although the provenance of the original peat is uncertain, Falcon-Lang (2004b) suggested that the vegetation may have been growing atop extrabasinal fault blocks.

In contrast, Opluštil (2005b) mapped the paleogeographic distribution of coal seams (Radnice Member; Fig. 6) within paleovalley systems in the Central and Western Bohemian Basin in the Czech Republic, and noted that coal seams wedge out directly against, rather than cover, the slopes of adjacent, elevated ridges. However, these were groundwater-fed, rheotrophic mires (Opluštil et al., 1999), which presumably precluded their development on paleovalley slopes. Likewise, Calder (1994) showed that coal seams in the Springhill Coalfield of Nova Scotia abutted coalesced alluvial fans shed from adjacent uplands, but did not onlap the fans or bedrock slopes.

None of the basin-margin successions studied in this thesis provide direct evidence that mires blanketed elevated habitats. However, in La Magdalena Coalfield (Chapter 3), one of the thickest coals in the basin-fill is situated just above the base of the section, in Mina Luisa (Section H; Figs. 24C, 26). The ≈2 m thick and laterally extensive coal seam may lie only a few metres above lower Paleozoic basement, which formed a steeply sloping basin margin. (Note that this observation is based on aerial photographs, which indicate that lower parts of the basin-fill need to be remapped—Figure 24C is based on currently published maps). Although we interpreted the coal seam at Mina Luisa to represent a rheotrophic mire that preferentially developed above a stable, less compactable breccia pile (Section 3.5.3.2), given its proximity to basement rocks, it also is plausible that it was an ombrotrophic mire that spread laterally to cover parts of adjacent uplands.

5.5.3.3. Did 'Upland' Floras Occupy Basinal Lowlands?

DiMichele et al. (2010) reviewed the temporal and spatial distribution of so-called 'upland' or 'seasonally-dry' floras that existed during the Pennsylvanian, which they segregated into three biomes: one dominated by cordaitaleans, one typified by the putative seed plants *Megalopteris* and *Lesleya*, and one containing primitive conifers. Although all three biomes were inferred to have existed on basin-margin and elevated, extrabasinal habitats through the Pennsylvanian, DiMichele et al. (2010) noted that they appear with increasing frequency in later Pennsylvanian and Permian non-coal-bearing, basinal lowland deposits that accrued during episodes of climatic drying and consequent moisture deficiency.

Of these 'seasonally-dry floras', the cordaitalean-rich biome is the most commonly encountered. Excellent examples of this floral complex have been documented from Early Pennsylvanian strata at Joggins, Nova Scotia (e.g., Falcon-Lang, 2003a, b; 2004a; Falcon-Lang et al., 2004) and Middle Pennsylvanian deposits in Newfoundland (Falcon-Lang & Bashforth, 2004, 2005; Bashforth, 2005), and DiMichele et al. (2010) suggested that the biome represents a transitional state between typical wetland and dryland vegetation. Early Pennsylvanian assemblages containing *Megalopteris* and *Lesleya* are generally found on peripheral parts of basins, such as in paleovalleys within limestone bedrock along the margin of the Illinois Basin (Leary & Pfefferkorn, 1977; Leary, 1981). *Megalopteris* also is present in Lower Pennsylvanian basinal lowland deposits at the 'Fern Ledges' locality in New Brunswick (Stopes, 1914; Falcon-Lang & Miller, 2007), whereas a single fragment of *Lesleya* was recorded in the Culm Measures in northwest Devon, UK (Leary, 1980); these rare occurrences presumably were transported to basinal lowlands from more elevated habitats. By the Middle Pennsylvanian, however, *Megalopteris* and *Lesleya* become more common in basinal lowlands in paralic basins in the U.S.A. (e.g., Arnold, 1949; Canright, 1959) and limnic basins in Europe (e.g., Remy & Remy, 1975; Šimůnek, 1996). Similarly, most Early to Middle Pennsylvanian conifer remains are allochthonous and only found adjacent to known uplands (Lyons & Darrah, 1989), whereas parautochthonous conifer remains become increasingly common in non-coal-bearing strata in Middle and Late Pennsylvanian basinal lowlands of U.S.A. and Europe (e.g., Galtier et al., 1992; Falcon-Lang et al., 2009; Plotnick et al., 2009). Thus, in general, early evidence of the 'seasonally-dry' floras tends to be fragmentary or preserved under exceptional circumstances, only to be followed somewhat later by more fully developed assemblages in distal, low-lying parts of basins (DiMichele et al., 2010).

Of the three 'seasonally-dry' biomes distinguished by DiMichele et al. (2010), only the cordaitalean-rich complex is present with certainty in the basin-margin successions studied in this thesis, specifically in the Lower Pennsylvanian Tynemouth Creek Formation of New Brunswick (Section 1.3.5.1; Falcon-Lang, 2006a), and possibly in the Middle Pennsylvanian South Bar and Waddens Cove formations of Nova Scotia (Section 1.3.5.2). In contrast, evidence of the *Megalopteris* and *Lesleya* biome is restricted to a few fragments of *Megalopteris* in the Tynemouth Creek Formation (Falcon-Lang, 2006a), and megafloral conifer remains are strikingly absent in all study sections. These observations suggest that, in accordance with the suggestions of DiMichele et al. (2010), the cordaitalean-rich biome represented a transition between dryland and wetland floral associations. Accordingly, although it undoubtedly existed in some elevated habitats, it is not considered an 'upland flora' in the same sense as the *Megalopteris*/*Lesleya* and conifer-rich biomes.

The virtual absence of the *Megalopteris*/*Lesleya* and conifer-rich biomes in the study areas is truly perplexing. The basin-margin successions analyzed accumulated about as far inland as one would expect terrestrial deposits to be preserved. In fact, bedrock that formed the original basin slopes is exposed at Cape Dauphin, Nova Scotia (South Bar Formation, Chapter 4, Fig. 35B) and along the margin of La Magdalena Coalfield (Chapter 3, Fig. 24C), and localities in the Tynemouth Creek Formation, New Brunswick (Section 1.3.5.1) and Nýřany Member, Czech Republic (Chapter 2) were probably laid down within hundreds of metres to a few kilometres from elevated source rocks. Furthermore, there is evidence for strongly seasonal conditions in the Tynemouth Creek (redbeds, ephemeral flow, degraded floodplains) and Waddens Cove formations (redbeds, siliceous duricrusts). And using the criteria of some authors (e.g., Cecil et al., 1985; Cecil, 1990, 2003; Cecil & Dulong, 2003), the thick siliciclastic successions containing sporadic, thin and ash-rich coal seams at all other study localities indicate periodic seasonality of rainfall.

If all study areas were proximal to elevated uplands, and if edaphic conditions were those typical of mildly to strongly seasonal conditions, where on Earth were the 'upland floras' (pun intended)? These are just the types of setting in which one might reasonably expect to find the remnants of such plants. Based on the evidence at hand, along with that summarized by DiMichele et al. (2010), I suggest the following explanation for the virtual absence of typical 'upland floras' (i.e., *Megalopteris*/*Lesleya* and conifer biomes) in the study areas. These plants did indeed occupy elevated landscapes throughout the Pennsylvanian. However, they existed far inland during early parts of the epoch, with only scattered pockets reaching basin margins during intervals of extreme or prolonged climatic drying. Hence, although the Tynemouth Creek Formation accrued under strong seasonality, the fluvial megafan was still far enough away from hinterland habitats that the remains of 'upland floras' almost never reached the basin margin. As the Pennsylvanian progressed and the frequency and amplitude of wet-dry climatic oscillations tended towards increasingly drier conditions, the 'upland' floras appeared more regularly in distal settings, albeit only during the driest intervals. Hence, although the South Bar and Waddens Cove formations, Nýřany Member, and the succession in La Magdalena Coalfield may have accumulated under mildly to moderately seasonal rainfall, these braided-river plains were simply not dry enough to support conifers and associated 'upland' plant complexes containing *Megalopteris* and *Lesleya*.

5.5.3.4. Was Climate the Primary Control on Peat Accumulation and Sedimentation?

The models of DiMichele et al. (2006a, 2008, 2010), which hypothesize that floral dynamics reflect cyclic changes in climate (i.e., environmental tracking), are bound by the assumption that climate is the *primary* control on peat accumulation and sediment supply. According to C.B. Cecil and collaborators (e.g., Cecil et al., 1985, 1993, 2003;

Cecil, 1990; Cecil & Dulong, 2003; hereafter termed the 'Cecil model'), highly seasonal precipitation corresponds to a high sediment yield, and the widespread accumulation of low-ash peat (the precursor to economic coal) only occurs in humid to perhumid climates where a dense vegetation cover minimizes erosion and sediment yield. In the transition between these end-member climatic states, rheotrophic mires develop under minimally to moderately seasonal conditions (cf. Calder, 1993, 1994). Reading between the lines in these papers, it is clear that climate alone is regarded as the driving force behind the distribution and composition of sedimentary rocks in Pennsylvanian successions. In essence, in the 'Cecil model', the presence of a thick, low-ash coal seam is *de facto* evidence that, at that locale in time and space, humid to perhumid conditions must have prevailed, whereas the presence of siliciclastic strata implies accumulation under more seasonal precipitation. Other allocyclic (tectonics, eustasy) or autocyclic mechanisms are either ignored or acknowledged to play a minor role in the spatial and temporal distribution of chemical versus siliciclastic rocks.

There is no question that prevailing climatic conditions were fundamental to the distribution of peat-forming versus clastic substrates during the Pennsylvanian, but the 'Cecil model' should be considered an end-member scenario. Tectonics and eustasy played an equally vital role in the development, sustenance, and preservation of peat-forming environments, and local autocyclic processes also controlled the distribution, thickness, and quality of resulting coal seams. It is outside the scope of this thesis to examine such processes in detail (cf. Calder, 1994), but some examples are given to show that the accumulation and distribution of economic Pennsylvanian coal seams (and siliciclastic sediment) depended on a wide variety of controls.

In paralic settings, widespread and long-lived mires will only form when and where accommodation space equals or slightly exceeds the production rate of peat (Bohacs & Suter, 1997) – the 'coal window' of Calder & Gibling (1994). Accommodation is a function of subsidence and base level, and there is a clear link between peat accumulation and potential accommodation created during the transgressive to highstand part of base level transit cycles (Gastaldo et al., 1993; Hartley, 1993; Shanley & McCabe, 1993; Gibling & Bird, 1994). For example, in the paralic Sydney Basin of Nova Scotia, Gibling et al. (2004) noted a positive correlation between the thickness of coal seams and the thickness of sequences within which they occur, indicating that high-accommodation events promoted prolonged peat accumulation. Most economic (i.e., thick, low-ash) coal seams, particularly in the Sydney Mines Formation, record blanket coastal peats that accumulated just prior to maximum transgression (Gibling et al., 2004), highlighting the fact that their initiation was largely controlled by eustasy.

A rise in sea level also can cause ponding of groundwater well inland of the coast, thereby promoting the development of extensive freshwater mires (Kosters & Suter, 1993; Bohacs & Suter, 1997). For example, in the Sydney Basin of Nova Scotia, the Mullins Seam (≈15 km wide, ≤2 m thick) occurs in the midst of the South Bar Formation, a thick package of braided fluvial strata (Section 1.3.5.2; Chapter 4). There are no signs of major climatic changes above or below the coal seam. Instead, the Mullins Seam is attributed to prolonged peat accumulation after marine transgression and consequent landward inundation of a stable platform of sandy fluvial sediments (Tibert & Gibling, 1999). This indicates that economic coals can form in high-energy fluvial systems that are characterized by active sediment transport, with eustasy, rather than climate, the dominant allocyclic control on their stratigraphic distribution.

In tectonically active regions, in both paralic and limnic basins, peat accumulation also has been linked to increased accommodation space due to differential subsidence associated with synsedimentary faulting and inherited basement topography (Fielding, 1987; Titheridge, 1993; Hartley, 1993). Furthermore, tectonic activity may divert drainage systems, and extensive mires may form where sediment supply is reduced (Wise et al., 1991).

In inland settings, particularly in limnic basins where eustatic influences are absent, a variety of mechanisms have been invoked to explain widespread mire development. Peat accumulation may reflect lake level (Courel et al., 1986; Lojka et al., 2009) or differential compaction, sediment supply, and groundwater levels within river valleys (Rust & Gibling, 1990a; Opluštil et al., 1999; Opluštil, 2005b). Furthermore, Calder (1993, 1994) summarized evidence for rheotrophic mire development in recharge zones along the distal margin of coalesced alluvial fans. Due to the high transmissibility of meteoric waters through coarse-grained alluvial fans, shallow or emergent water tables can develop along alluvial aprons where topographic and hydraulic gradients decrease rapidly. Importantly, the ponding of groundwater can sustain wetland vegetation and even rheotrophic mires in regions characterized by low precipitation, thereby pushing the window of peat formation into moderately seasonal climates (Calder, 1993, 1994).

A problem inherent to the 'Cecil model' is the assumption that the same type of strata (i.e., peat versus red or grey siliciclastic sediment) will accumulate over the entire area characterized by a particular climatic regime. On the updated world map showing the Köppen-Geiger climate classification system (Kottek et al., 2006), in which climate zone boundaries are delineated by the distribution of native vegetation, distinct plant biomes in the modern tropical realm can reach hundreds to thousands of kilometres across. For example, at the upper size limit, the 'equatorial fully humid' climate zone in South America is roughly 3250 km wide (E-W) and 1200 km long (N-S), a staggeringly immense area of 3.9×10^6 km^2 within the Amazon Basin. If climate zones were similar in size in the Pangean tropics during the Pennsylvanian, strict adherence to the 'Cecil model' would imply that a uniform layer of peat blanketed all landscapes over such an area when humid to perhumid climatic conditions prevailed, a notion promoted by DiMichele et al. (2010). Indeed, in the paralic Interior basins of the U.S.A., the coincidence of prime climatic, eustatic, tectonic, and edaphic conditions during the Middle Pennsylvanian resulted in single rheotrophic mires reaching areas of 2.0×10^5 km^2 (Greb et al., 2003). However, this is almost certainly at the upper size limit for Pennsylvanian mires, and most were probably smaller by 1 to 2 orders of magnitude. Thus the size and distribution of Pennsylvanian mires must have been controlled by a complex interplay of allocyclic and autocyclic controls, although climate was the key factor (Calder, 2003, 2004).

The lateral margins of many coal seams split into thinner benches separately by clastic strata, and/or pass laterally into carbonaceous shales or even coarse-grained deposits (Fielding, 1987; Calder, 1993, 1994). According to the 'Cecil model', these strata have very different climatic signatures, yet the transitions occur over only hundreds of metres to a few kilometres. For example, Tibert & Gibling (1999) noted that the Mullins Seam in the South Bar Formation is thickest and of highest quality above an uplifted fault block that comprises less compactable sandstones, whereas it thins and splits into low-quality benches and carbonaceous shales above topographically lower areas that contain more compactable mudstones. Thus, differential subsidence and/or compaction were the primary control on peat versus clastic accumulation (Tibert & Gibling, 1999).

Furthermore, braided river deposits of the South Bar Formation are laterally and vertically transitional into anastomosing river deposits of the Waddens Cove Formation (Rust et al., 1987; Rust & Gibling, 1990a). Coal seams are generally thin, ash-rich, and laterally restricted in both units, but mudrocks in the South Bar Formation are grey, whereas those of the Waddens Cove Formation are generally red and associated with siliceous and calcareous duricrusts (Gibling & Rust, 1990). If viewed in isolation, these units would be ascribed to quite different climatic regimes, with redbeds and duricrusts in the Waddens Cove Formation pointing to strongly seasonal rainfall. However, both units were laid down in the same basin, comprise similar bed material (Rust & Gibling, 1990a), and both may have developed under strongly seasonal tropical conditions (Gibling & Rust, 1990; Fielding, 2006; Fielding et al., 2009). In fact, the Waddens Cove Formation is attributed to deposition on a relatively elevated part of an alluvial plain with a persistently low groundwater level (Gibling & Rust, 1990). Thus, clastic strata containing rather different 'climatic' indicators can coexist in proximity, serving as a reminder that controls such as fluvial style and sedimentary regime are important to consider when interpreting climate from the rock record.

Finally, even if climatic conditions are conducive to mire development, the composition and porosity of subjacent substrates dictate whether or not peat will accumulate. For example, although climatic conditions, plant biomes, and sedimentary regimes are similar on either side of the equatorial island of Borneo, Southeast Asia, mires do not occur on the eastern side (Gastaldo, 2010). Thick and extensive ombrotrophic mires on the Rajang River delta and coastal plain (western side) occur because clay minerals within fine-grained sediment restrict pore water flow and create an aquiclude above which organic matter can accumulate. In contrast, stilting of the water table is precluded on the Mahakam River delta and coastal plain (eastern side) where fine-grained substrates are more porous, thereby negating the accumulation of organic matter because paludal conditions cannot be maintained (Gastaldo, 2010).

In conclusion, it is clear that the composition, quality, and spatial and temporal distribution of coal are the manifestation of numerous allocyclic and autocyclic processes. Although climate may have been the overriding control (Calder & Gibling, 1994), climate alone cannot explain the presence or absence of coal seams in Pennsylvanian strata. Despite this, the foundation of the 'Cecil model' remains intact, namely that humid to perhumid (everwet) climatic conditions were required for ombrotrophic mires (precursors of many economic, low-ash coal seams) to develop. However, such mires did not occur everywhere within the everwet climate zone, but only where other tectonic and edaphic conditions were conducive to peat accumulation. Likewise, I wholeheartedly agree with the conclusions of Calder (1993, 1994), who argued that rheotrophic mires, many of which also resulted in economic coal seams, could have persisted where mildly to even moderately seasonal conditions prevailed, so long as the necessary tectonic (subsidence), eustatic (transgression), and/or edaphic (aquicludes) controls were in place.

Although I wholeheartedly agree that climate played a fundamental role in determining substrate conditions, and that the distribution of Pennsylvanian plant biomes reflected the distribution of habitat types, I would argue that plant biomes with somewhat different edaphic preferences could coexist in proximity. I am not implying that biomes from opposite ends of the wet-dry spectrum could cohabit (e.g., an ombrotrophic mire would not have been situated directly adjacent to well-drained clastic substrates that supported primitive conifers). Instead, biomes that shared similar edaphic preferences, collectively occupying a short range along the wet-dry gradient, may have coexisted, with mainly autocylic factors responsible for habitat partitioning and the position of each biome on the landscape. In paralic settings, especially where vast mires blanketed low-gradient platforms dissected by a few low-energy channels, individual biomes probably had great aerial extent, and ecotone boundaries between biomes may have been relatively gradational. In contrast, in basin-margin settings or in small limnic basins, where the abundance of high-energy channels resulted in habitable landforms that were irregularly distributed and aerially restricted, individual biomes may have been organized into smaller patches that had sharper ecotone boundaries. For example, a rheotrophic mire, characterized by a distinct biome, may have occurred on distal, low-lying parts of a floodplain, whereas another distinct biome inhabited relatively well-drained sand and gravel alongside a contemporaneous, high-energy fluvial channel. Thus, the types of vegetation present at any given time and place were a reflection of regional climatic conditions (*environmentally distinct* biomes), but their local-scale distribution was more heterogeneous and recorded subtle differences in available habitat (*spatially distinct* biomes).

5.6. PRELIMINARY CLASSIFICATION OF PENNSYLVANIAN VEGETATIONAL BIOMES

Pennsylvanian landscapes were complex, and the wide array of available habitats was occupied by an equally wide array of compositionally distinct plant associations. In other words, although the 'lowland' or 'wet' and 'upland' or 'seasonally-dry' biomes represented opposite ends of the wet-dry spectrum, other discrete floral complexes existed between those end-member states. As noted above (Section 5.5.3.3), DiMichele et al. (2010) provided descriptions of several vegetational biomes, but focused on those that persisted on moisture-deficient soils ('seasonally-dry floras'). Expanding on their classification, together with arguments presented in Section 5.5.3.4, I offer a preliminary subdivision of Pennsylvanian plant associations, and the climatic and edaphic conditions under which they were most likely to have existed. Six different vegetational biomes are recognized, with varying degrees of compositional overlap, in part segregated based on the precipitation regimes proposed by Cecil (2003) and Cecil & Dulong (2003). This categorization provides a foundation for additional studies, and of relevance to this thesis, provides a more robust environmental context for Pennsylvanian plant communities in basin-margin settings.

5.6.1. Ombrotrophic Mires [Biome 1a]

This biome comprised peat-forming vegetation that grew in ombrotrophic (domed) mires, and as all water and nutrients were derived from precipitation, humid to perhumid climatic conditions are implied (i.e., rainfall exceeding evapotranspiration for 11 to 12 'wet months' per year). The mires were the precursor to thick and laterally extensive, low-ash (i.e., economic) coal seams. The vegetation was characterized by low diversity and comprised specialists that could tolerate low-nutrient and acidic conditions, particularly lycopsids (Early to Middle Pennsylvanian) and arborescent ferns (Middle to Late Pennsylvanian). Plants in this biome are typically referred to as ‘lowland’ floras, although they may have blanketed elevated habitats during the wettest climatic intervals.

5.6.2. Rheotrophic Mires [Biome 1b]

This biome comprised peat-forming vegetation that grew in rheotrophic (planar) mires, with water and nutrients derived from a combination of groundwater, surface water, and precipitation. Most mires accumulated under humid climates (9 to 11 ‘wet months’), although some may have developed under dry subhumid to moist subhumid conditions (3 to 8 ‘wet months’) where edaphic, tectonic, and/or eustatic conditions were favorable. These mires could be widespread and thick, although some were relatively thin and less extensive, and resulting coal seams are generally high in ash. The vegetation was more diverse than that of ombrotrophic mires (Biome 1a), but still had to tolerate low-nutrient and acidic conditions. Lycopsids (Early to Middle Pennsylvanian) and arborescent ferns (Middle to Late Pennsylvanian) were the dominant clades, but sphenopsids, pteridosperms, and some cordaitaleans also were present. Plants in this biome would typically be referred to as ‘lowland’ floras.

5.6.3. ‘Wet’ Clastic Wetlands [Biome 2]

This biome comprised non-peat-forming, wetland vegetation that grew under moist subhumid to humid climates (6 to 11 ‘wet months’) on siliciclastic soils, generally in lateral or temporal association with rheotrophic (Biome 1b) mires. The clastic soils ranged from waterlogged to moist to seasonally dry, but paleosols generally are gleyed. This biome was typical of swamps and marshes, and includes the ‘clastic swamps’ of Gastaldo (1987). The descriptor ‘wet’ is used to connote climatic conditions, as well as increased potential for paludification due to the prevalence of fine-grained sediment. The vegetation comprised the same families and genera as those in associated mires, but featured different species in different proportions. The biome was very diverse and included all major Carboniferous plant clades (lycopsids, sphenopsids, ferns, pteridosperms, cordaitaleans), reflecting the availability of nutrients, water, and habitable landforms. The overwhelming majority of adpressed megafloral assemblages documented in the Carboniferous paleobotanical literature fit into this category, particularly those collected from ‘roof shales’ or subjacent mudstones in gradational contact with coal seams. These would typically be referred to as ‘lowland’ floras.

5.6.4. ‘Dry’ Clastic Wetlands [Biome 3]

This biome comprised non-peat-forming vegetation that grew under dry subhumid to moist subhumid climates (3 to 8 ‘wet months’) on siliciclastic soils that experienced alternations between moist and dry conditions for extended periods. Strata are sometimes associated with thin, laterally restricted, and very high-ash coal seams, which record poorly developed, ephemeral rheotrophic mires (Biome 1b), or carbonaceous shales, which represent swamps and marshes (Biome 2). The descriptor ‘dry’ is used to connote more seasonal climatic conditions, as well as decreased potential for paludification due to the prevalence of coarse-grained sediment. The flora consisted of a subset of the same taxa that dominated rheotrophic mires (Biome 1b) and ‘wet’ clastic wetlands (Biome 2), but the proportional abundances of plant clades were different. Cordaitaleans and pteridosperms were dominant, although arborescent ferns became increasingly prominent beginning in the late Middle Pennsylvanian. The biome was transitional between those of 'wet' clastic wetlands (Biome 2) and the dryland flora with *Megalopteris* and *Lesleya* (Biome 4a).

5.6.5. Dryland Flora with *Megalopteris* and *Lesleya* [Biome 4a]

This biome comprised non-peat-forming vegetation that grew under semiarid to dry subhumid climates (1 to 5 'wet months') on siliciclastic soils that were alkaline, low in nutrients, and moisture-deficient for most of the year. *Megalopteris*, *Lesleya*, cordaitaleans, and other xeromorphic plants characterized this association, which forms part of what has been termed the classic 'upland' or 'seasonally-dry' flora. It existed on elevated habitats throughout the Pennsylvanian, but appeared increasingly regularly in basinal settings during the driest climatic intervals.

5.6.6. Dryland Flora with Conifers [Biome 4b]

This biome comprised non-peat-forming vegetation that grew under semiarid to dry subhumid climates (1 to 5 'wet' months) on siliciclastic soils that were moisture-deficient for most of the year. Walchian conifers, callipterid peltasperms, and other xeromorphic plants characterized this association, which forms part of what has been termed the classic 'upland' or 'seasonally-dry' flora. It existed on elevated habitats throughout the Pennsylvanian, but appeared increasingly regularly in basinal settings during the driest climatic intervals.

5.6.7. Biomes in Basin-margin Successions

Based on the preliminary subdivision of Pennsylvanian biomes offered above, the final exercise in this section is to determine which floral complex(es) existed in basin-margin successions examined in this thesis. In each of the study areas, a range of habitable landforms existed at any particular time interval, as all were characterized by relatively steep gradients and high-energy fluvial systems due to proximity to elevated uplands. As a result, vegetation on basin margins was strongly compartmentalized, resulting in the presence of one or more biomes in any given interval. Nonetheless, as a general rule, Pennsylvanian basin-margins were dominated by what I have termed ‘dry’ clastic wetland vegetation (Biome 3).

In all study areas, clastic sediments are far more abundant than peat substrates, and as a consequence, non-peat-forming vegetation dominated basin margins. Megafloral assemblages comprise a subset of the same taxa that occupied rheotrophic mires (Biome 1b) and ‘wet’ clastic substrates (Biome 2). Cordaitaleans dominated in the Early Pennsylvanian Tynemouth Creek Formation (Section 1.3.5.1), whereas cordaitaleans and pteridosperms co-dominated in the middle Middle Pennsylvanian South Bar Formation (Section 1.3.5.2). Tree ferns became increasingly common in the late Middle Pennsylvanian (Nýřany Member; Chapter 2), and by the Late Pennsylvanian (La Magdalena Coalfield; Chapter 3), they formed a major component of vegetation on clastic substrates. All of these observations are consistent with inclusion in the ‘dry’ clastic wetland biome (Biome 3). Dryland floras containing *Megalopteris* and *Lesleya* (Biome 4a) or conifers (Biome 4b) did not inhabit the basin margins studied, but may have been contemporaneous on distant, elevated hinterland habitats.

The thick siliciclastic successions present in basin-margin settings suggest moderately to strongly seasonal conditions, with alternations between moist and dry conditions for extended intervals. The strongest evidence for seasonality is in the Tynemouth Creek Formation, where redbeds and vertisols abound. However, the Nýřany Member also contains a few vertisols and redbeds that point to moderate seasonality of rainfall, and high-flow-stage bedforms and abundant log jams in the South Bar Formation (Gibling et al., 2010; Chapter 4) likely resulted from flooding due to torrential rainfall during the wet season. In La Magdalena Coalfield, there is less evidence for seasonal precipitation, although the prevalence of clastic sediment in general, and the presence of coarse-grained conglomerates deposited in high-energy braided streams in particular, imply some seasonality of flow. In general, these strata may have accumulated under dry subhumid to moist subhumid climates, with rainfall exceeding evapotranspiration for 3 to 8 'wet months' per year.

Lenses of carbonaceous shale are present in all basin-margin successions studied, and record the development of ephemeral and localized swamps (vegetated by trees) and/or marshes (vegetated by shrubs and groundcover) typical of 'wet' clastic wetlands (Biome 2). In addition, in all but the Tynemouth Creek Formation, thin, laterally restricted, and high-ash coal seams are present, reflecting poorly developed and ephemeral rheotrophic mires (Biome 1b). A shift to less seasonal precipitation was not a prerequisite for the presence of these vegetative complexes, which typified the wetter end of the wet-dry gradient. Instead, they existed in low-lying, poorly drained parts of the landscape, and were contemporaneous with the dominant 'dry' clastic wetland biome. These biomes had a heterogeneous distribution, and ecotone boundaries were probably sharp. However, widespread and prolonged rheotrophic mires did occasionally develop in basin-margin settings, either due to marine transgression (Mullins Seam, South Bar Formation), or when rainfall became less seasonal (upper part of La Magdalena Coalfield).

5.7. CONCLUSIONS

The majority of paleobotanical studies involving Pennsylvanian vegetation have focused on basinal lowland settings in paleoequatorial Euramerica, where prolonged peat accumulation occurred in vast coastal mires that were transformed into economic coals after burial. Far less attention has been paid to contemporaneous plant communities situated on inland alluvial plains, on the periphery of basins, or on upland tracts, despite the fact that these systems covered most terrestrial surfaces during the Pennsylvanian. Due to the relatively poorer preservation potential of plant remains in erosional and moisture-deficient settings, our understanding of the vegetation that inhabited such regimes is poorly constrained. Without knowledge of the composition and distribution of floral communities on inland and elevated landscapes, our understanding of the environmental tolerances and global evolution of Pennsylvanian plant clades is greatly reduced, as is our understanding of the contribution vegetation made to the carbon cycle in the late Paleozoic icehouse world.

To address the inadequacies in our knowledge of total vegetation cover in tropical regions of Euramerica, this thesis documents floral assemblages from Early, Middle, and Late Pennsylvanian strata in the Czech Republic, Spain, and eastern Canada. The selected study sites represent inland or elevated alluvial tracts within basins that formed in or adjacent to mountain belts during the final assembly of Pangea, and the plant remains found can be compared with coeval lowland plant assemblages from these and other basins. All localities are situated close to former basin margins, where it was expected that poorly resolved 'upland floras' might have lived and ultimately fossilized. Through the course of investigation, 43779 plant fragments were collected in facies context from thin fossiliferous units in measured sections and from historical collections stored at various institutions. A standardized census-sampling technique, in which fossil-bearing slabs were randomly assembled into 50 x 50 cm quadrats prior to counting, was used at all study localities. This coordinated approach allowed for a statistically robust comparison of differences in floral abundances in various sub-environments, and permitted assessment of changes in paleoecological preferences of plant groups that inhabited selected basin-margin settings through the Pennsylvanian. Together with taphonomic observations, the results provide the first comprehensive assessment of the composition, distribution, and ecology of Pennsylvanian plant communities on inland and basin-margin environs.

The complexity of basin-margin settings is a crucial factor in characterizing Pennsylvanian plant communities. Basin margins occupy a transitional position between elevated hinterland terrains, where the processes of denudation dominate, and topographically low-lying basinal lowlands, where depositional processes dominate. In mountainous regions of equatorial Pangea, Pennsylvanian basin margins were characterized by steep gradients and high-energy depositional systems (e.g., alluvial fans, braided rivers) due to their proximity to upland environs. The temporal and spatial distribution of landforms was constantly in a state of flux in such disturbance-dominated regimes, and the prevalence of coarse-grained soils enhanced the drainage of surface water into the groundwater column. As a consequence, prolonged and widespread mire development was hindered, and clastic substrates were dominant. However, due to autocyclic processes, ephemeral rheotrophic mires and swamps developed locally in topographically low-lying areas or in groundwater recharge zones where edaphic conditions were conducive to stilting of the water table. More extensive and long-lived ombrotrophic and/or rheotrophic (rain- and groundwater-fed, respectively) mires generally resulted from allocyclic processes, such as a shift to humid to perhumid climatic conditions, or inland ponding of freshwater during marine transgressions.

The following major conclusions about Pennsylvanian vegetation in basin-margin settings emerge from the suite of localities studied:

1. The distribution of major plant clades on basin margins reflected the life history strategies and physiological requirements intrinsic to each group, and partitioning of ecological resource space was dependent on the edaphic parameters proffered by habitable landforms. In the Early to Middle Pennsylvanian, lycopsids occupied the wettest available habitats, calamiteans inhabited aggrading sediment in the most disturbed locales, and medullosalean pteridosperms and cordaitaleans preferred better-drained conditions. Arborescent and herbaceous ferns, together with sphenophylls and non-medullosalean pteridosperms, favored damp and frequently disturbed areas.

The late Middle Pennsylvanian witnessed a proliferation of tree ferns over basin-margin landscapes, coincident with the expansion of this group in basinal lowlands. On Late Pennsylvanian basin margins, arborescent ferns rose to prominence along disturbance-prone fluvial channel belts. Although medullosalean pteridosperms had previously characterized such habitats, Late Pennsylvanian members of this clade preferred undisturbed settings distant from channel influence. In the basinal lowlands, the tree ferns also expanded to replace arborescent lycopsids in most Late Pennsylvanian mires. On basin margins, however, lycopsids persisted as the primary contributor to biomass in peat-forming habitats.

2. A preliminary subdivision of Pennsylvanian biomes indicates that six different plant associations existed in tropical Euramerica. Impoverished communities that comprised specialists adapted to acidic and nutrient-poor peat substrates inhabited *ombrotrophic mires* (Biome 1a), particularly lycopsids (Early to Middle Pennsylvanian) and tree ferns (Middle to Late Pennsylvanian). These two plant groups also dominated *rheotrophic mires* (Biome 1b), although increased nutrient availability resulted in more diverse communities that contained sphenopsids, pteridosperms, and cordaitaleans. *'Wet' clastic wetland floras* (Biome 2) consisted of non-peat-forming communities on siliciclastic substrates that were wet for most of the year, such as swamps and marshes. The vegetation comprised the same families and genera as those in associated mires, but featured different species in different proportions. The biome was very diverse and included all major plant clades, reflecting the availability of nutrients, water, and habitable landforms. *'Dry' clastic wetland floras* (Biome 3) comprised non-peat-forming vegetation on siliciclastic soils that experienced alternations between moist and dry conditions for extended periods. The biome consisted of a subset of the taxa in rheotrophic mires and 'wet' clastic wetlands, but the proportional abundances of plant clades were different. Cordaitaleans and pteridosperms were dominant, although arborescent ferns became prominent in the late Middle Pennsylvanian. Two types of non-peat-forming vegetation occurred on soils that were moisture-deficient for most of the year. The *dryland flora with* Megalopteris *and* Lesleya (Biome 4a), usually associated with cordaitaleans and other xeromorphic plants, was most common on alkaline substrates that were low in nutrients. Walchian conifers, callipterid peltasperms, and other xeromorphic taxa characterized the *dryland flora with conifers* (Biome 4b).

3. Because disturbance played a fundamental role in depositional environments at basin margins, habitable landforms were restricted in size and irregularly distributed in time and space. A consequence of such strong compartmentalization was the coexistence of several biomes that shared similar edaphic preferences, collectively occupying a short range along the wet-dry gradient. Primarily autocyclic processes were responsible for habitat partitioning and the position of each floral association on the landscape, and individual biomes may have been organized into small patches separated by sharp ecotone boundaries. The range of plant complexes present in any given interval reflected prevailing or regional climatic conditions.

The *'dry' clastic wetland flora* (Biome 3) dominated basin-margin settings at all localities studied in this thesis. This biome comprised non-peat-forming vegetation that grew on siliciclastic soils typical of dry subhumid to moist subhumid climates. The descriptor 'dry' refers to alternations between moist and dry soil conditions resulting from rainfall seasonality, as well as to the decreased potential for stilting of the water table due to the prevalence of coarse-grained sediment. Cordaitaleans and medullosalean pteridosperms dominated plant communities during the Early to Middle Pennsylvanian, and beginning in the late Middle Pennsylvanian, arborescent ferns proliferated over basin-margin landscapes. Biomes more typical of poorly-drained basinal lowlands coexisted with the principal 'dry' clastic wetland flora, but were confined to topographically low-lying, wet to waterlogged areas where ephemeral rheotrophic mires (the precursor of thin, laterally restricted, very high-ash coal seams) or swamps and marshes (the precursor of carbonaceous shales) developed.

Widespread and prolonged peat accumulation in ombrotrophic or rheotrophic mires, each of which was characterized by biomes tolerant of nutrient deficiency and acidic conditions, only occurred in basin margins under exceptional circumstances. In particular, rheotrophic mires required supplementary groundwater sources during dry seasons. In the basins studied, such mires developed as a result of prominent climatic oscillations to more humid conditions, inland ponding of freshwater during marine transgressions, and increased accommodation due to rapid subsidence.

Likewise, during times of extreme or prolonged climatic drying, particularly in the Middle to Late Pennsylvanian, xeromorphic plant associations (e.g., *Megalopteris*, *Lesleya*, conifers) that were adapted to semiarid to dry subhumid climates inhabited basin margins. These biomes, often referred to as 'upland' or 'seasonally-dry' floras, were otherwise confined to elevated, extrabasinal habitats throughout the Pennsylvanian. Two possible mechanisms can be invoked to account for the scarcity of these 'upland' or 'seasonally-dry' floras in the study areas: (i) plant remains were rarely transported from hinterland environs to basin margins or basinal lowlands; and/or (ii) under equable climatic conditions, the 'dry' clastic wetland flora that existed on basin margins also covered extrabasinal landscapes.

4. Riparian ecosystems are disturbance-dominated regimes, and as a result, modern riparian vegetation is patchy at all spatial and temporal scales. At the study sites, the high degree of variability of megafloral assemblages in vertically adjacent beds and, in some cases, even along single bedding planes shows that most Pennsylvanian plant communities were very heterogeneous. Patchiness was especially prominent in high-energy depositional environments where riparian habitats were perpetually being destroyed or disrupted by flooding. The distribution and composition of Pennsylvanian megafloral assemblages from braided-river plain deposits indicate that riparian vegetation in basin-margin settings comprised a closely spaced collage of low diversity to even monospecific clusters. The fossil record indicates that vegetational heterogeneity and clade-dependent partitioning of habitats (key features in modern analogues) was intrinsic to even the earliest riparian plant communities. It is clear that patchiness in modern riparian ecosystems records a pattern that has persisted since the very first plants colonized terrestrial landscapes.

5. Vegetation played a fundamental role in the evolution of early landscapes. In particular, fluvial systems became increasingly contemporary near the Silurian-Devonian boundary, when plants evolved extensive rooting systems that helped to stabilize channel banks, thereby promoting the development of meandering rivers. Through the Devonian and Mississippian, when plants attained arborescence and seed-bearing groups diversified and spread over a wider array of habitats, fluvial regimes became progressively more modern in appearance. Nonetheless, large woody debris introduced to river channels did not cause major obstructions to flow because forests were not yet sufficiently dense. Fluvial regimes became decidedly modern in aspect in the late Mississippian, however, when a prominent increase in forest density promoted the development of log jams that caused channel abandonment and facilitated avulsion.

The abundance of plant remains in all Pennsylvanian basin-margin successions studied clearly shows that vegetation occupied a full range of habitats by this time. Accumulations of large woody debris are present in fluvial deposits at most sites, and especially superb examples of early log jams are found in Middle Pennsylvanian strata in the Sydney Coalfield.

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APPENDIX 1: STUDENT CONTRIBUTION TO MANUSCRIPTS IN THESIS FORMS

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Student Contribution to Manuscripts in Thesis

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Name:	Arden Roy Bashforth	**Student ID #:**	B00453596
Department:	Earth Sciences	**Programme:**	Ph.D.
Phone:	+45 33 31 52 50	**E-Mail:**	arden.bashforth@dal.ca

Manuscript Authors:	Arden R. Bashforth, Jana Drábková, Stanislav Opluštil, Martin R. Gibling, and Howard J. Falcon-Lang
Manuscript Title:	Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nýřany Member, Central and Western Bohemian Basin, Czech Republic)
Journal:	Review of Palaeobotany and Palynology (submitted 5 March 2010)
Student Contribution:	I conducted all of the background research, collected almost all data, drafted all of the figures and plates and most tables, did all statistical analyses, and wrote almost all of the text in this manuscript. Jana Drábková processed palynological samples, contributed information on processing techniques, and created Tables 7 and 8. Stanislav Opluštil provided logistical and historical details about the Nýřany Member, allowed me access to his own paleobotanical collection from the Rozdělov locality, and helped collect data at some sites. Martin Gibling contributed to all sedimentological aspects of the paper, and his insight was instrumental to subdivision of the fine-grained, fossiliferous strata, resulting in Table 1. Howard Falcon-Lang provided editorial comments that helped to add more structure to the paper.
Supervisor Signature:	

Manuscript Authors:	Arden R. Bashforth, Howard J. Falcon-Lang, and Martin R. Gibling
Manuscript Title:	Vegetation heterogeneity on a Late Pennsylvanian braided-river plain draining the Variscan Mountains, La Magdalena Coalfield, northwestern Spain
Journal:	Palaeogeography, Palaeoclimatology, Palaeoecology (accepted 15 March 2010)
Student Contribution:	Collection of megafloral data was undertaken jointly by Howard Falcon-lang and myself. Simultaneously, Martin Gibling logged the stratigraphic section. I performed all subsequent statistical analyses, based in part on suggestions from Howard Falcon-Lang. Martin Gibling summarized current interpretations of the basin history and geological setting, and provided an exhaustive account of depositional environments, all of which was condensed in successive versions of the text written by myself. I created all figures and tables, although Martin Gibling provided measurements and stratigraphic interpretations for Figures 26, 27, and 28. I redrew the suite of logs (Appendix 3) originally measured by Martin Gibling. Howard Falcon-Lang made extensive editorial comments and written sections that helped to give the paper more structure.
Supervisor Signature:	

Manuscript Authors:	Martin R. Gibling, Arden R. Bashforth, Howard J. Falcon-Lang, Jonathan P. Allen, and Christopher R. Fielding
Manuscript Title:	Log jams and flood sediment buildup caused channel abandonment and avulsion in the Pennsylvanian of Atlantic Canada
Journal:	Journal of Sedimentary Research 80(3): 268–287

STUDENT CONTRIBUTION TO MANUSCRIPTS IN THESIS

STUDENT CONTRIBUTION:	THIS PAPER RESULTED FROM FIELD DISCUSSIONS BETWEEN MARTIN GIBLING AND MYSELF. MARTIN GIBLING MEASURED ALL STRATIGRAPHIC SECTIONS, AND THEREAFTER, I DID QUANTITATIVE AND STATISTICAL ANALYSES OF LOG ACCUMULATIONS. MARTIN GIBLING WROTE MOST SECTIONS IN THE PAPER, ALTHOUGH I WROTE OR CONTRIBUTED TO STAND-ALONE SECTIONS (SECTIONS 4.5.1, 4.5.2, 4.5.3, 4.7.4, 4.8.2). I ALSO CREATED FIGURE 41. HOWARD FALCON-LANG WROTE OR CONTRIBUTED TO SECTIONS 4.8.1 AND 4.8.2, AND CREATED FIGURE 44. JONATHAN ALLEN AND CHRISTOPHER FIELDING WERE CONCURRENTLY INVESTIGATING THE SOUTH BAR FORMATION, AND SOME OF THEIR RESULTS WERE INCORPORATED INTO THE MANUSCRIPT.
SUPERVISOR SIGNATURE:	

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Article: BASHFORTH’ A.R., DRÁBKOVÁ’ J., OPLUŠTIL’ S., GIBLING’ M.R., FALCON-LANG’ H.J., in prep., Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nýřany Member, Central and Western Bohemian Basin, Czech Republic). Review of Palaeobotany and Palynology.

This article comprises Chapter 2 of the thesis.

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Article: BASHFORTH, A.R., FALCON-LANG, H.J., GIBLING, M.R., 2010. Vegetation heterogeneity on a Late Pennsylvanian braided-river plain draining the Variscan Mountains. Palaeoecology, Palaeoclimatology, Palaeoecology 292(3–4): 367–390. doi:10.1016/j.palaeo.2010.03.037

This article comprises Chapter 3 of the thesis.

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Arden Bashforth
PhD Candidate
Department of Earth Sciences
Dalhousie University
Arden.Bashforth@dal.ca

Dr. Bashforth:

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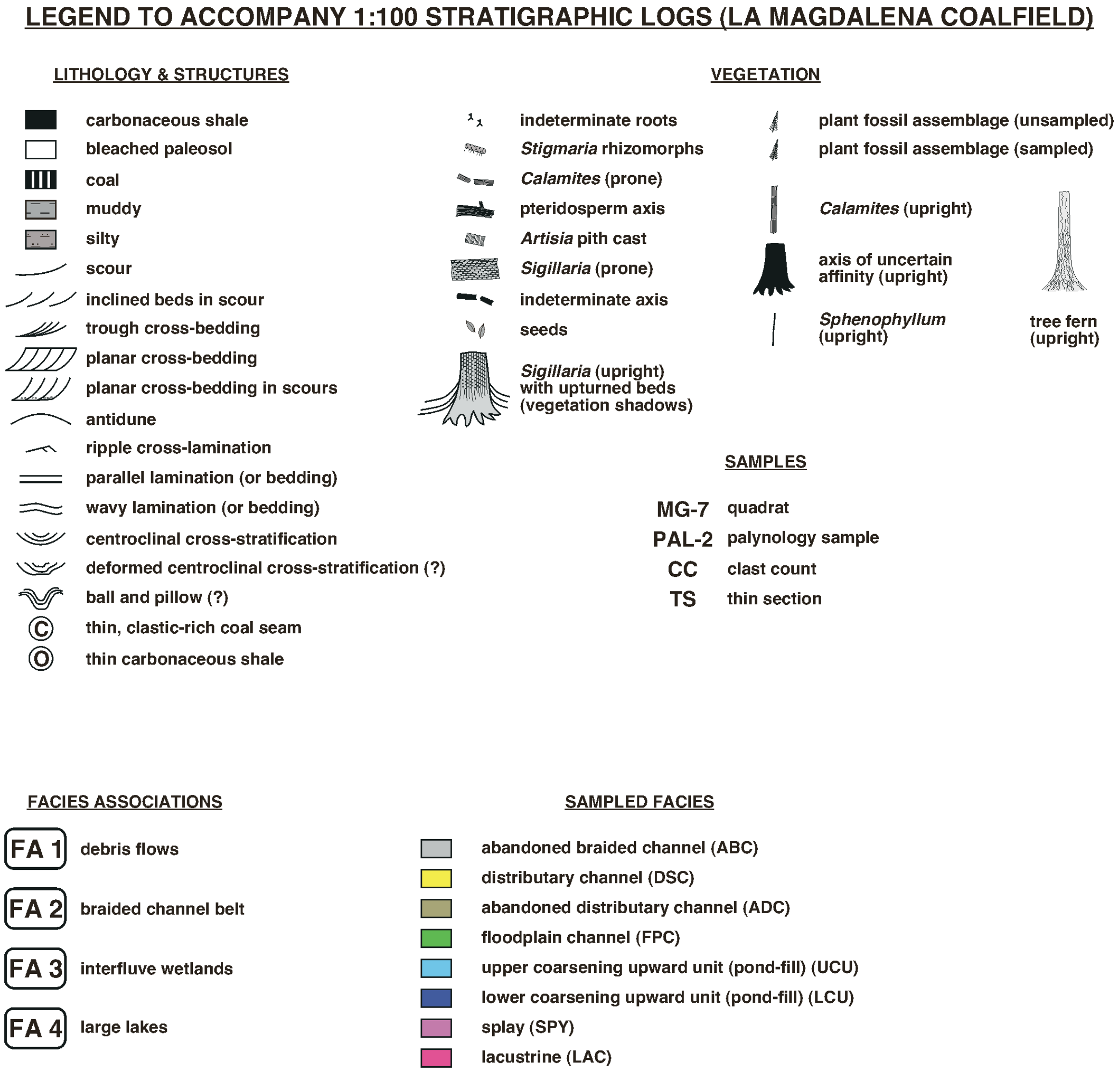
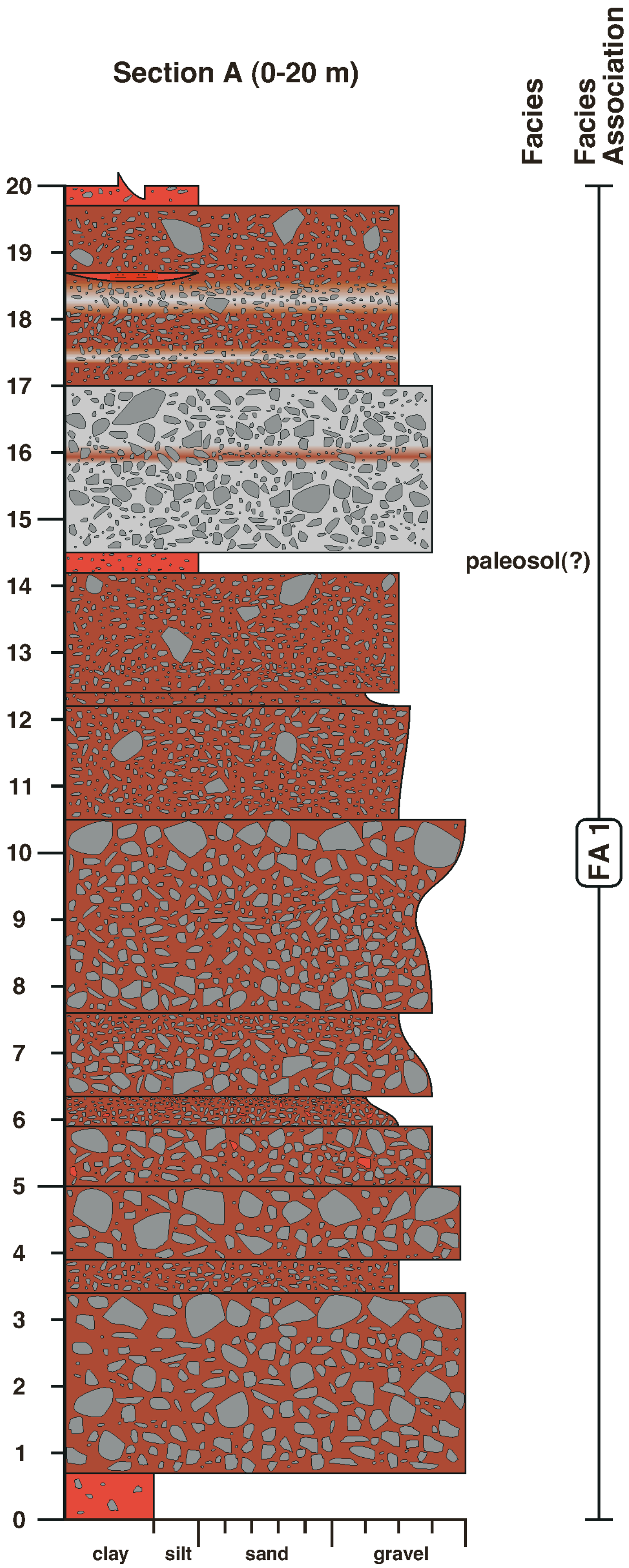
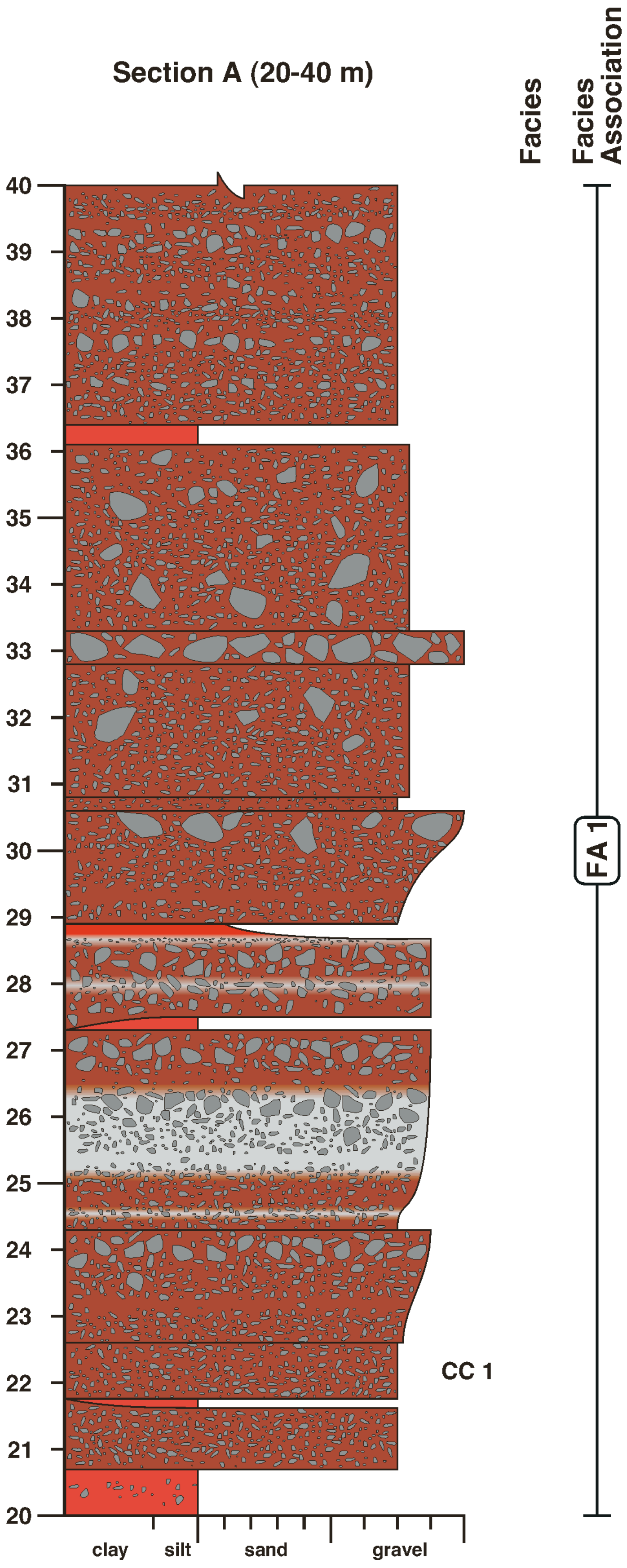
APPENDIX 3: STRATIGRAPHIC LOGS FOR LA MAGDALENA COALFIELD

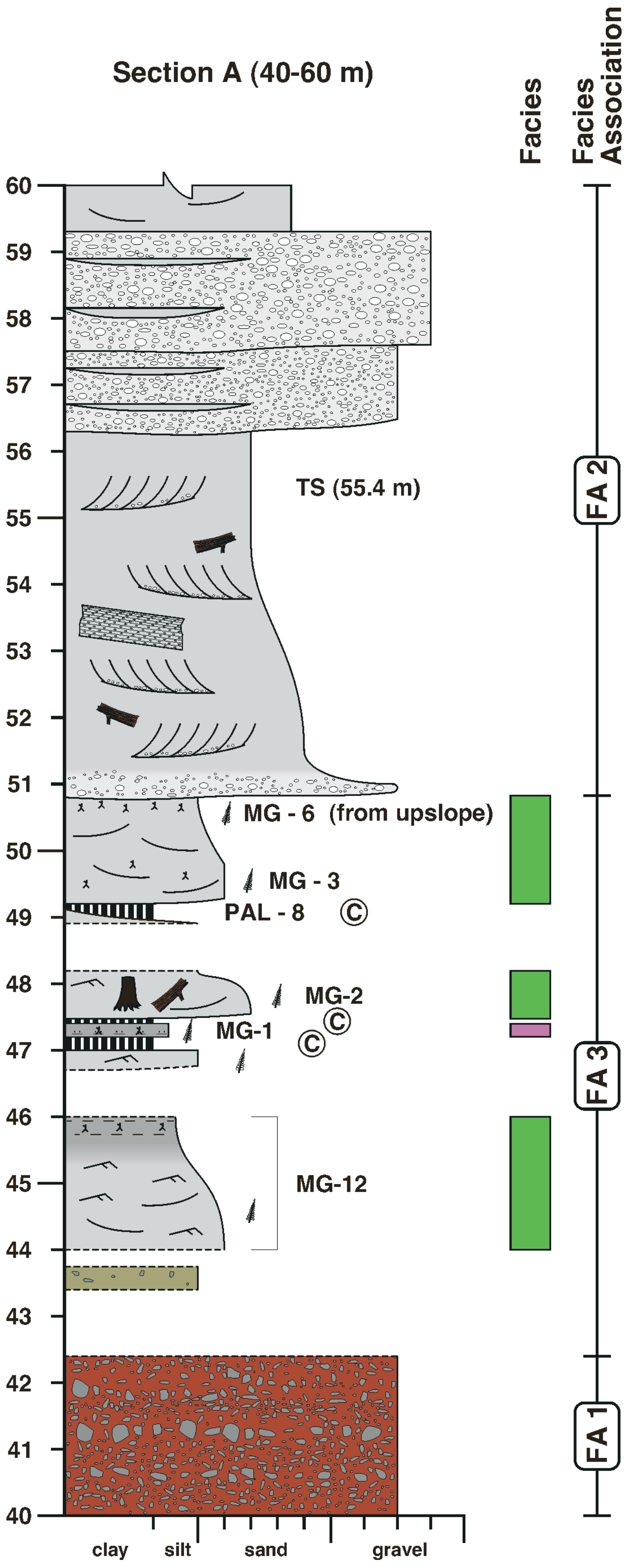
Stratigraphic logs (≈1:100 scale), measured at cm-scale, through 493.7 m (≈33%) of the ≈1500 m thick basin-fill in La Magdalena Coalfield. See Figure 26 for stratigraphic position of sections. A. Legend and Section A (0.0 to 125.2 m of basin-fill). B. Section B (196.7 to 249.6 m). C. Section C (306.8 to 361.0 m). D. Sections D (786.1 to 848.6 m) and D-AUX (831.4 to 837.9 m). E. Section E (1005.9 to 1204.8 m).

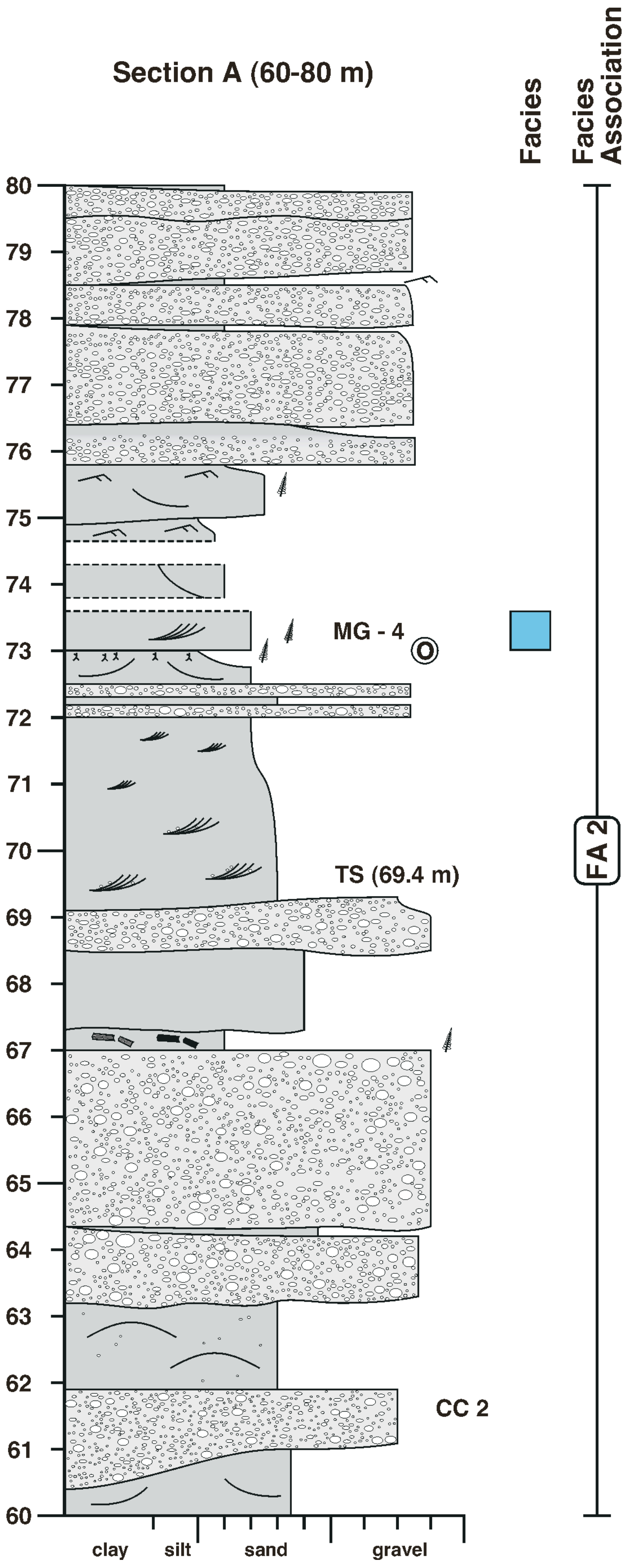


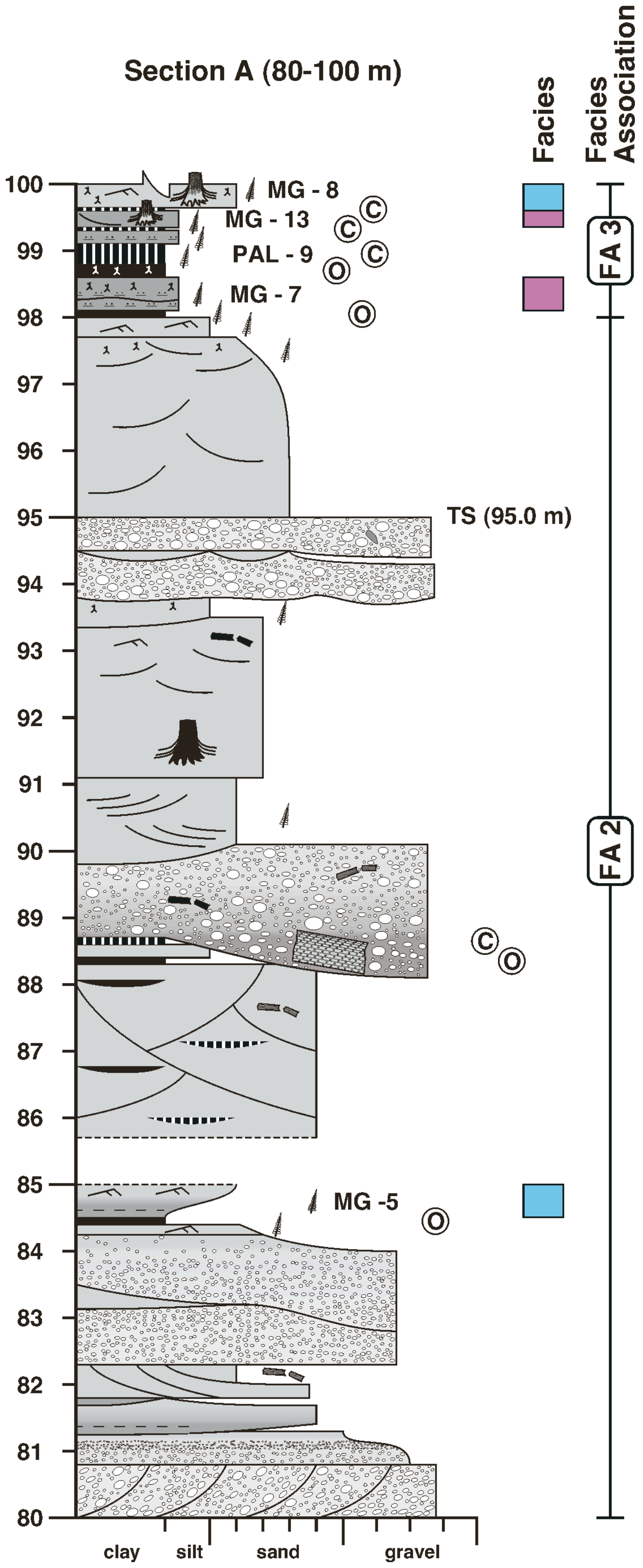


Section A (0-20 m)


Section A (20-40 m)
Facies
Facies Association
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
FA 1
CC 1
clay
silt
sand
gravel


Section A (40-60 m)
Facies
Facies Association
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
45
44
43
42
41
40
TS (55.4 m)
MG - 6 (from upslope)
MG - 3
PAL - 8
Ⓒ
MG-2
Ⓒ
MG-1
Ⓒ
MG-12
FA 2
FA 3
FA 1
clay
silt
sand
gravel

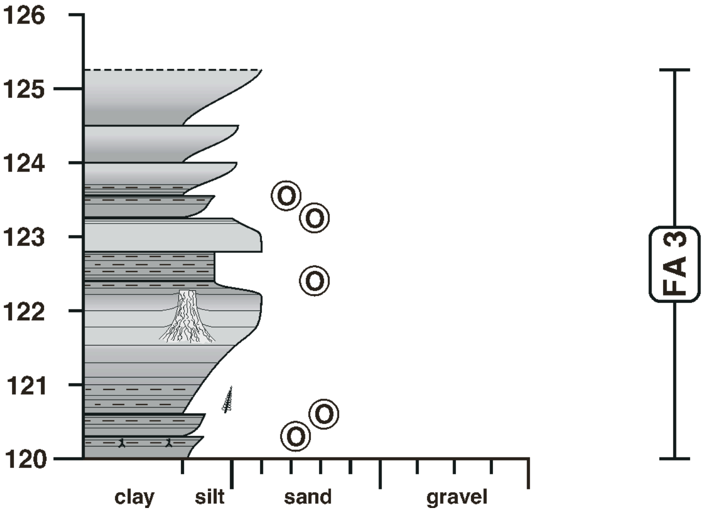

Section A (60-80 m)
Facies
Facies Association
80
79
78
77
76
75
74
73
72
71
70
69
68
67
66
65
64
63
62
61
60
MG - 4
TS (69.4 m)
CC 2
FA 2
clay
silt
sand
gravel

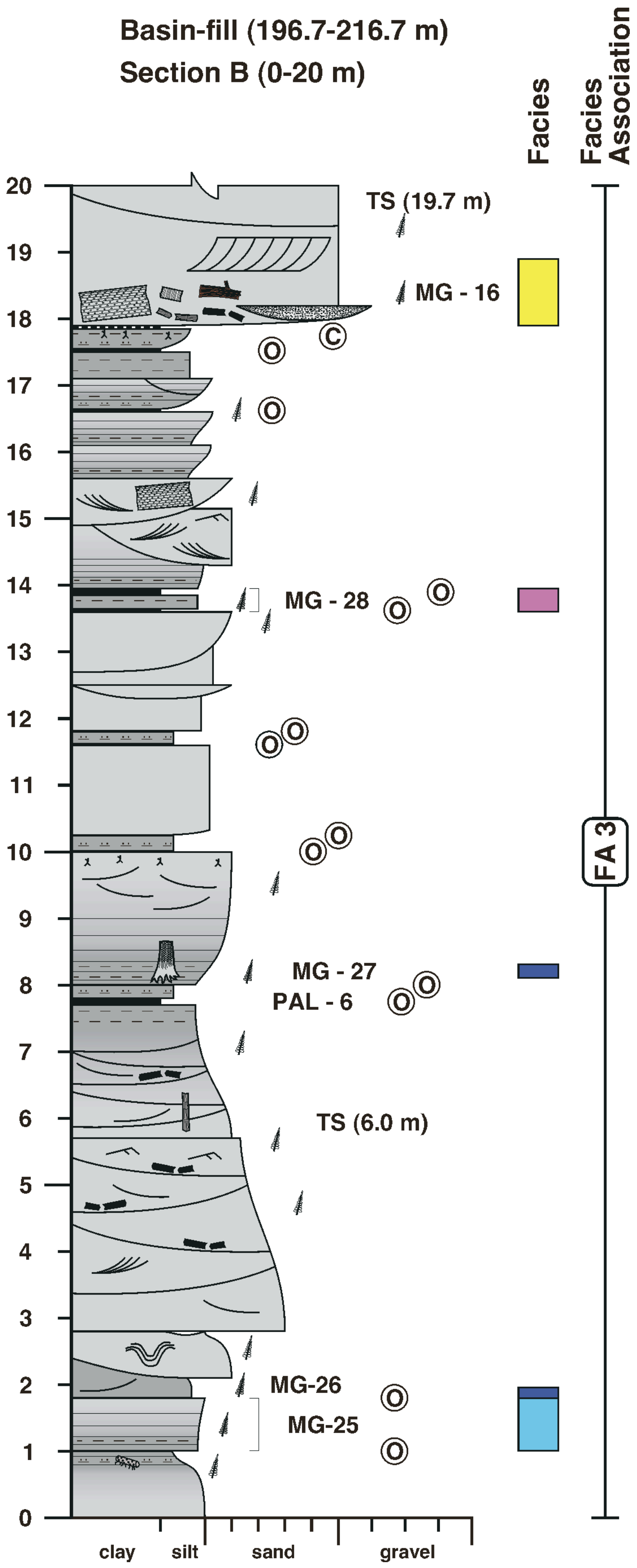

Section A (80-100 m)
Facies
Facies Association
100
99
98
97
96
95
94
93
92
91
90
89
88
87
86
85
84
83
82
81
80
MG - 8
MG - 13
PAL - 9
MG - 7
TS (95.0 m)
MG -5
C
O
FA 3
FA 2
clay
silt
sand
gravel

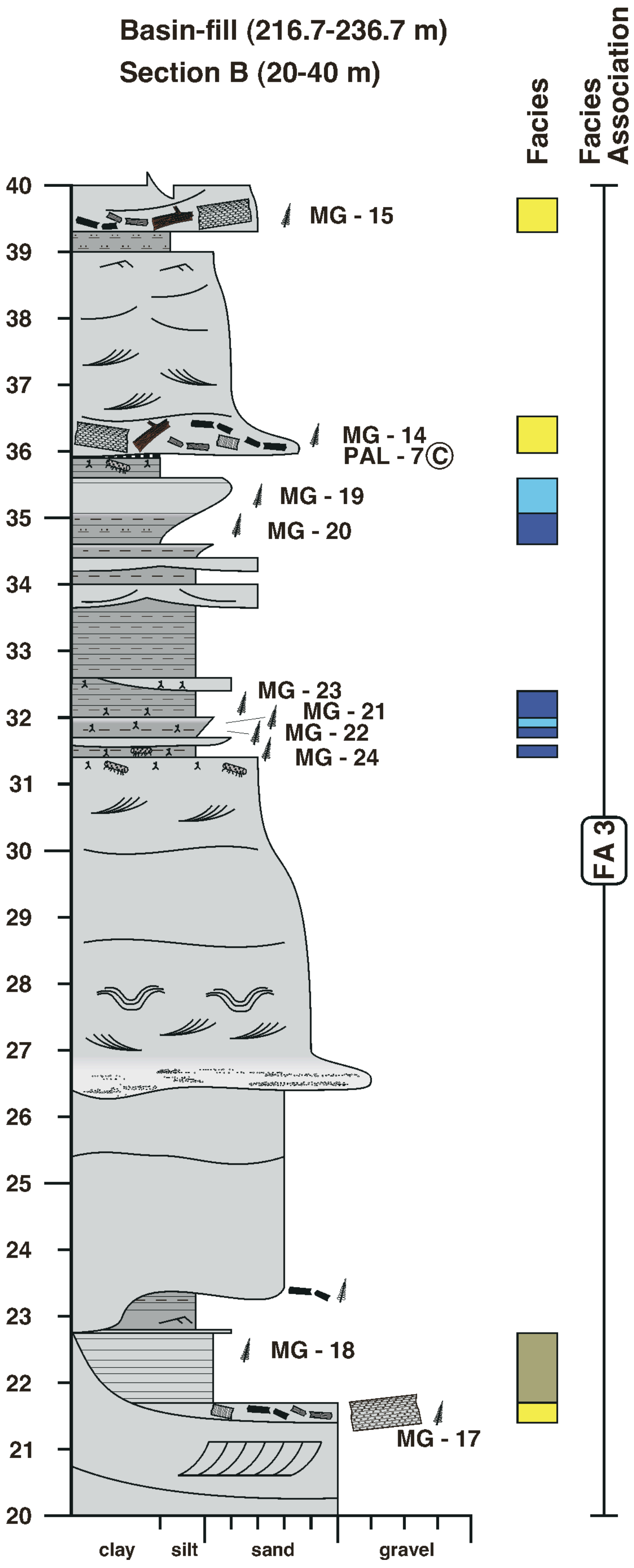
Section A (120-125.2 m)

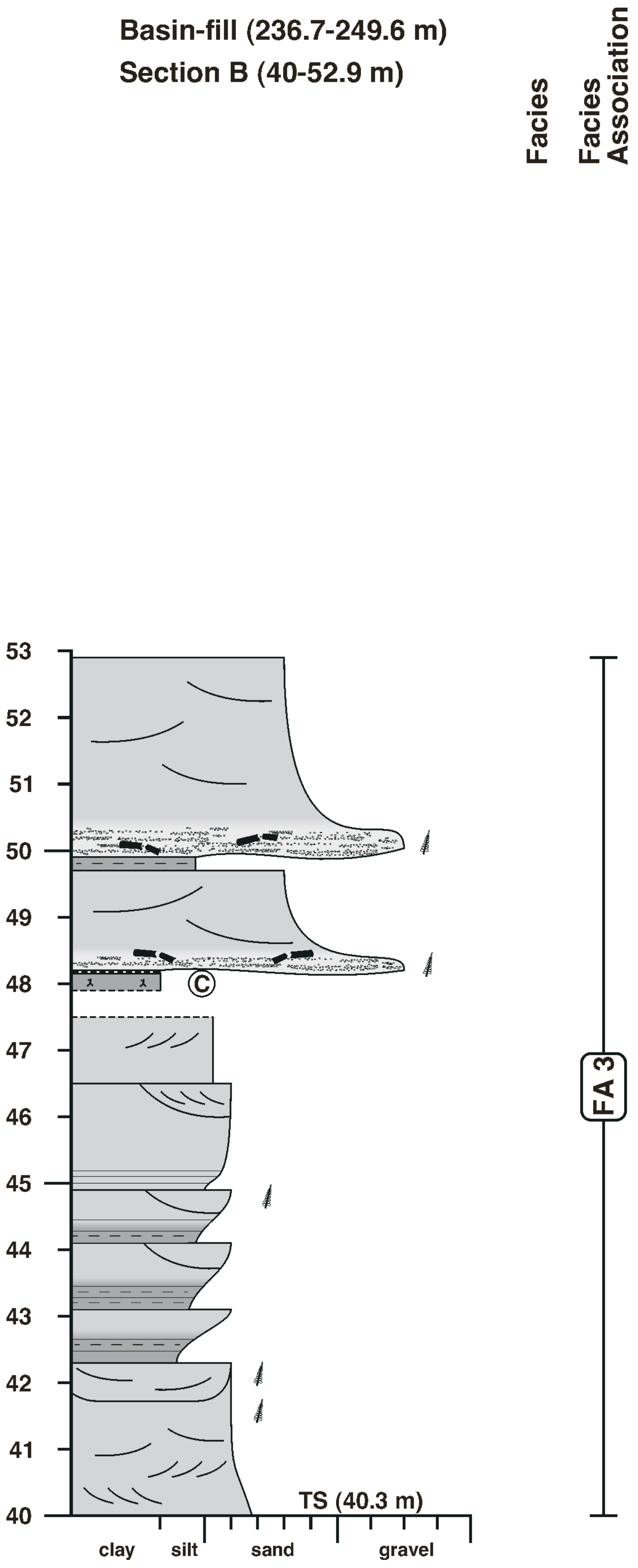
Facies

Facies Association

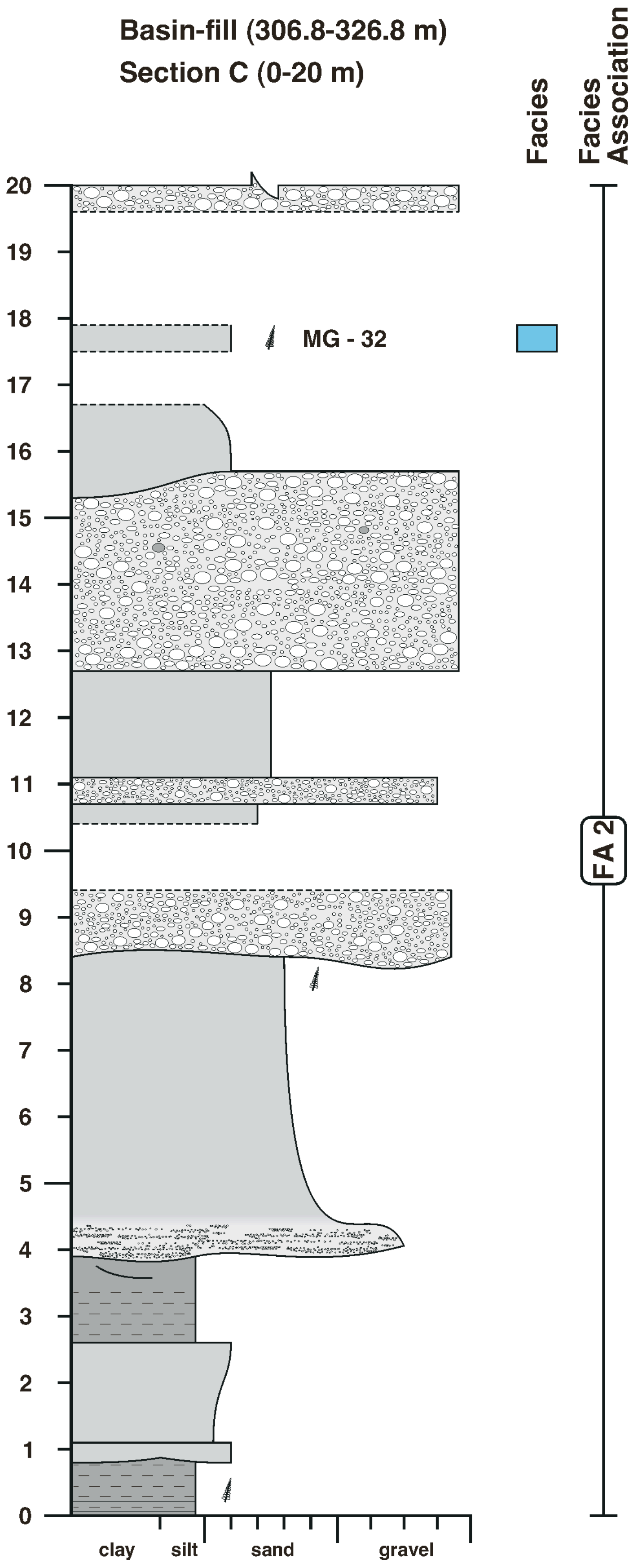


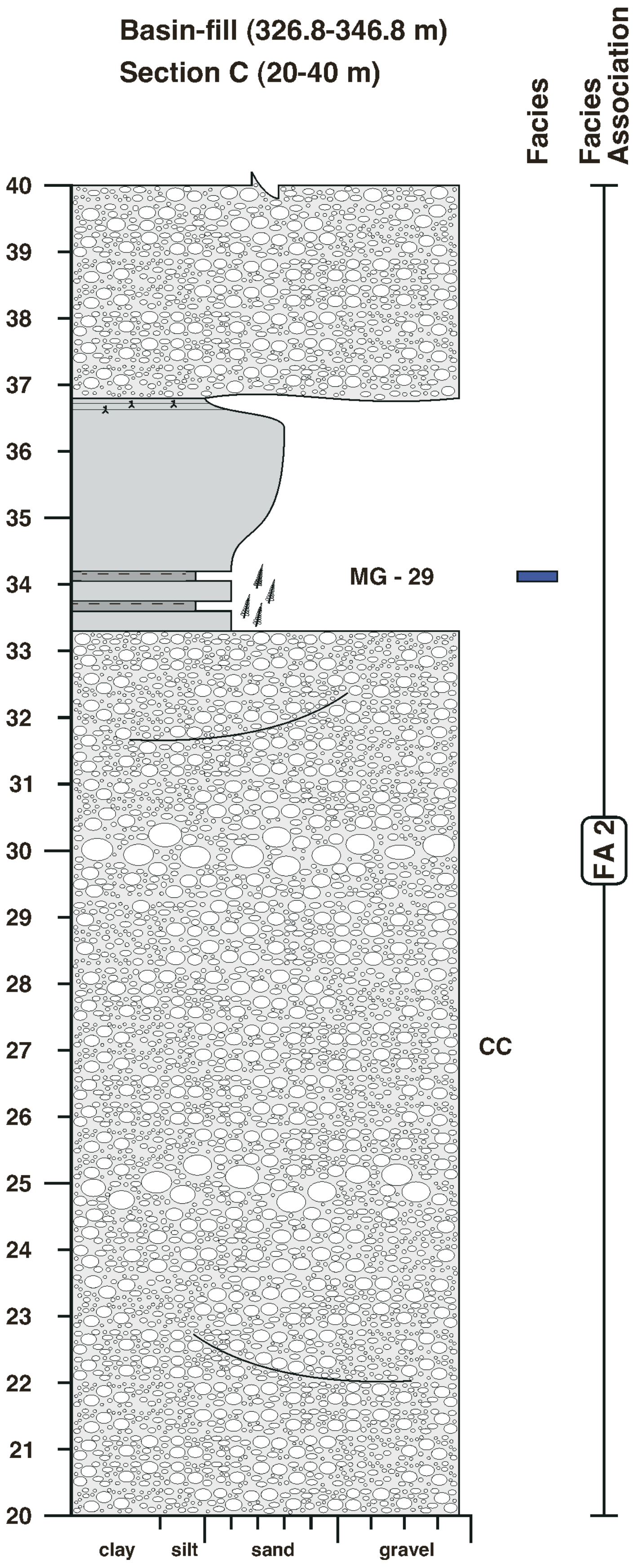

Basin-fill (196.7-216.7 m)
Section B (0-20 m)
Facies
Facies Association
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
TS (19.7 m)
MG - 16
C
O
MG - 28
MG - 27
PAL - 6
TS (6.0 m)
MG-26
MG-25
FA 3
clay
silt
sand
gravel


Basin-fill (216.7-236.7 m)
Section B (20-40 m)
Facies
Facies Association
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
MG - 15
MG - 14
PAL - 7Ⓒ
MG - 19
MG - 20
MG - 23
MG - 21
MG - 22
MG - 24
FA 3
MG - 18
MG - 17
clay
silt
sand
gravel


Basin-fill (236.7-249.6 m)
Section B (40-52.9 m)

Basin-fill (306.8-326.8 m)
Section C (0-20 m)

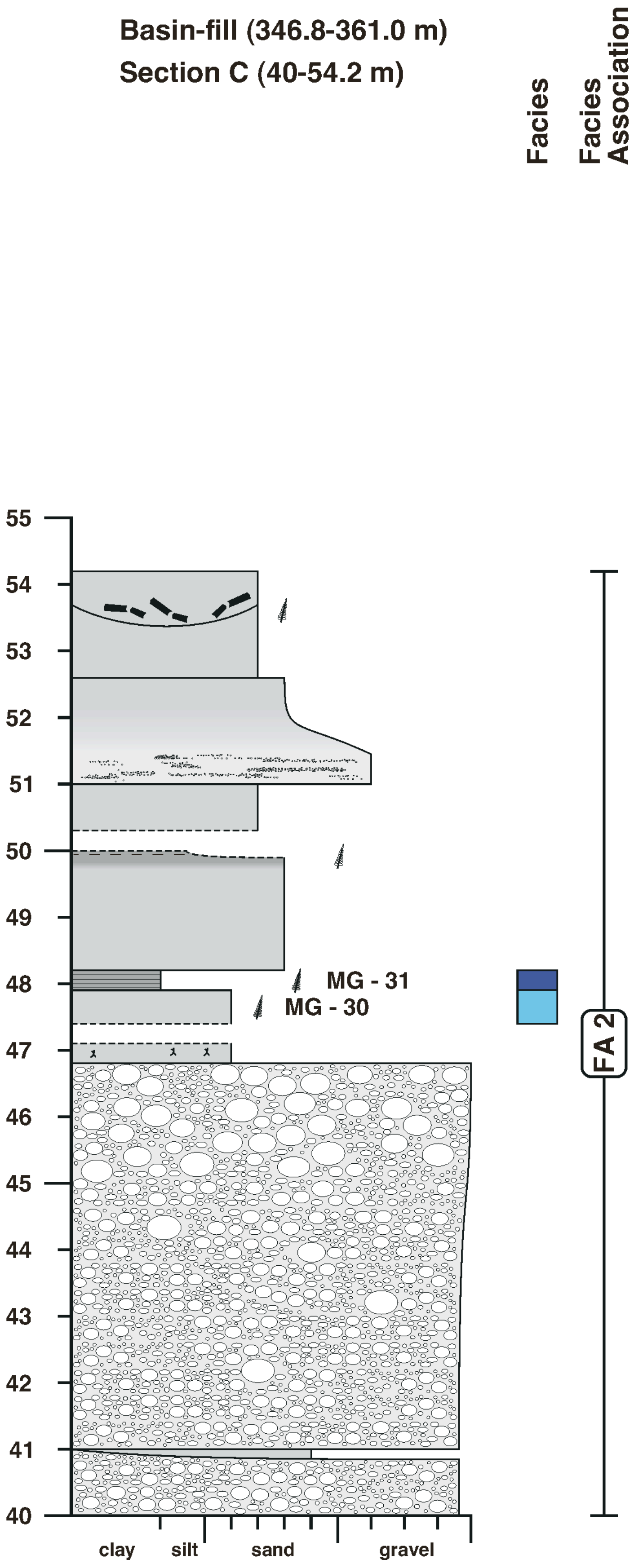


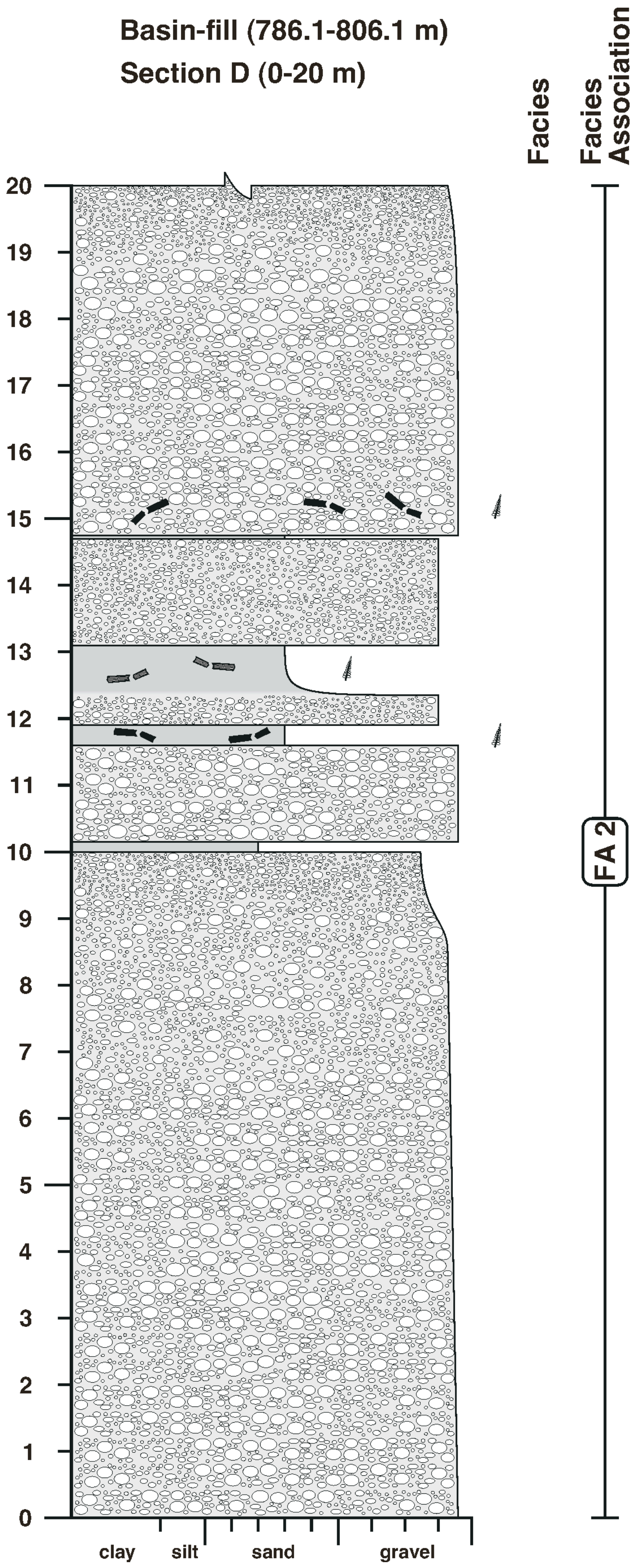


Basin-fill (326.8-346.8 m)

Section C (20-40 m)

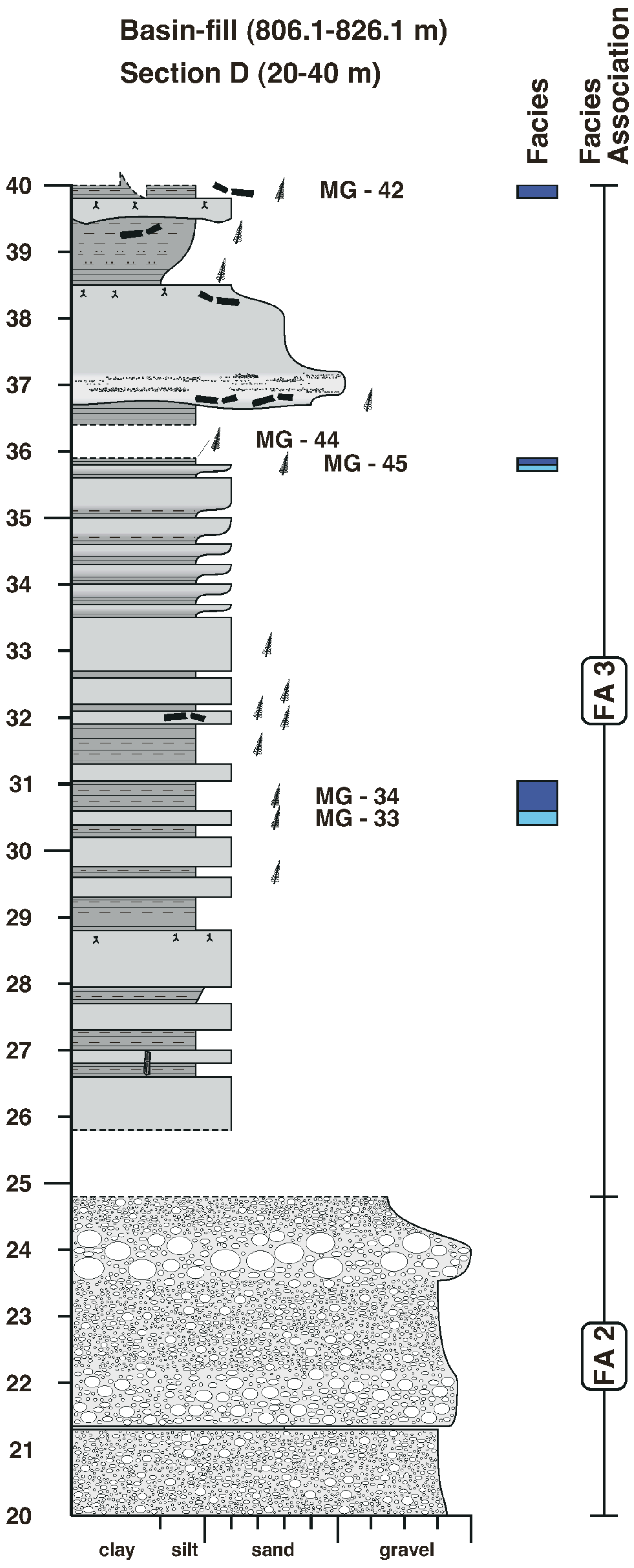
Basin-fill (346.8-361.0 m)
Section C (40-54.2 m)



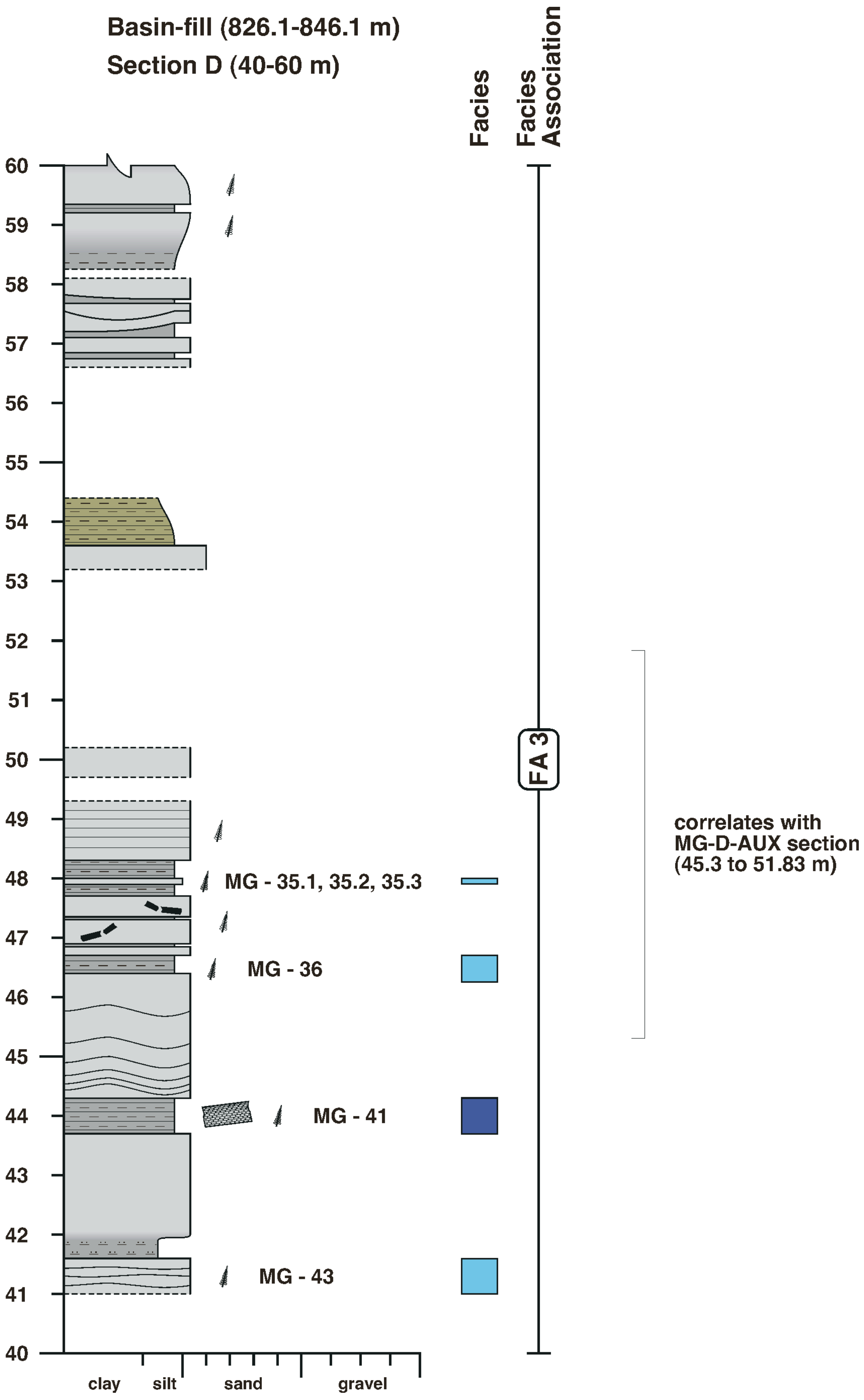


Basin-fill (786.1-806.1 m)

Section D (0-20 m)


Basin-fill (806.1-826.1 m)
Section D (20-40 m)

Basin-fill (826.1-846.1 m)
Section D (40-60 m)

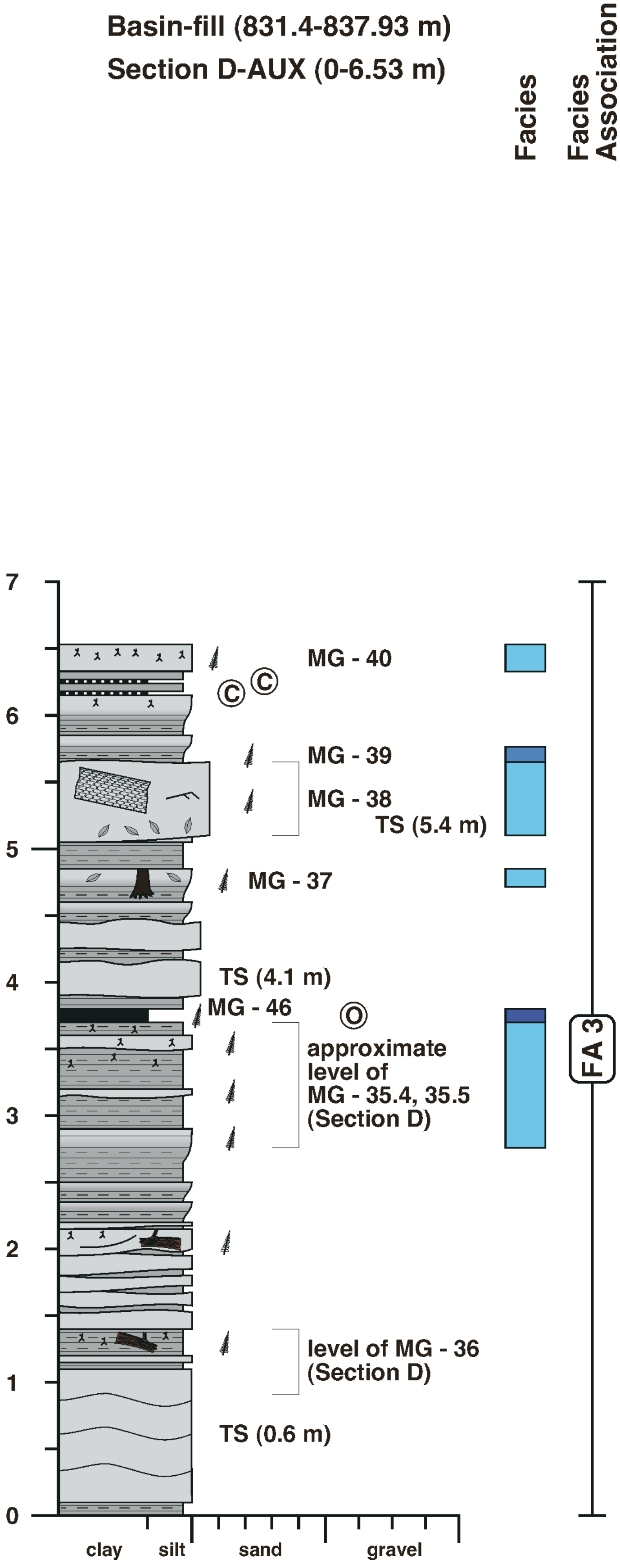


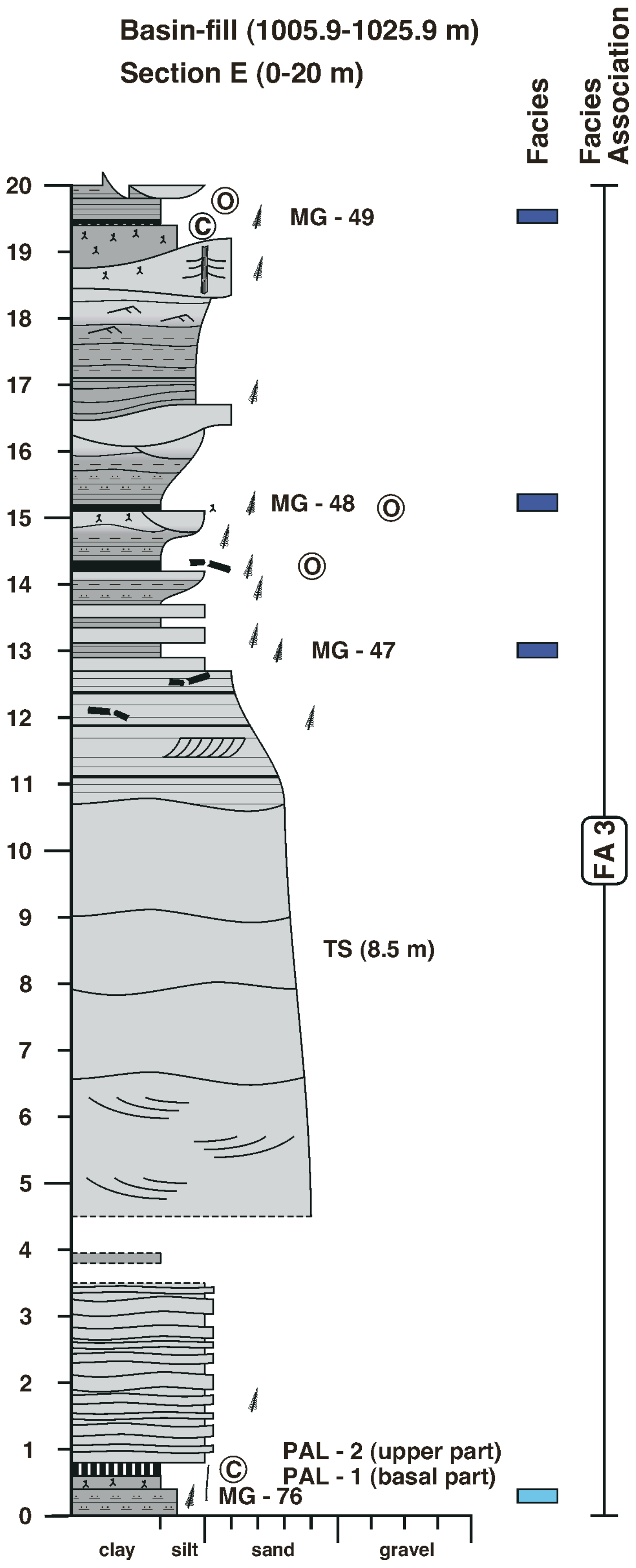
Basin-fill (846.1-848.6 m)

Section D (60-62.5 m)

Basin-fill (831.4-837.93 m)

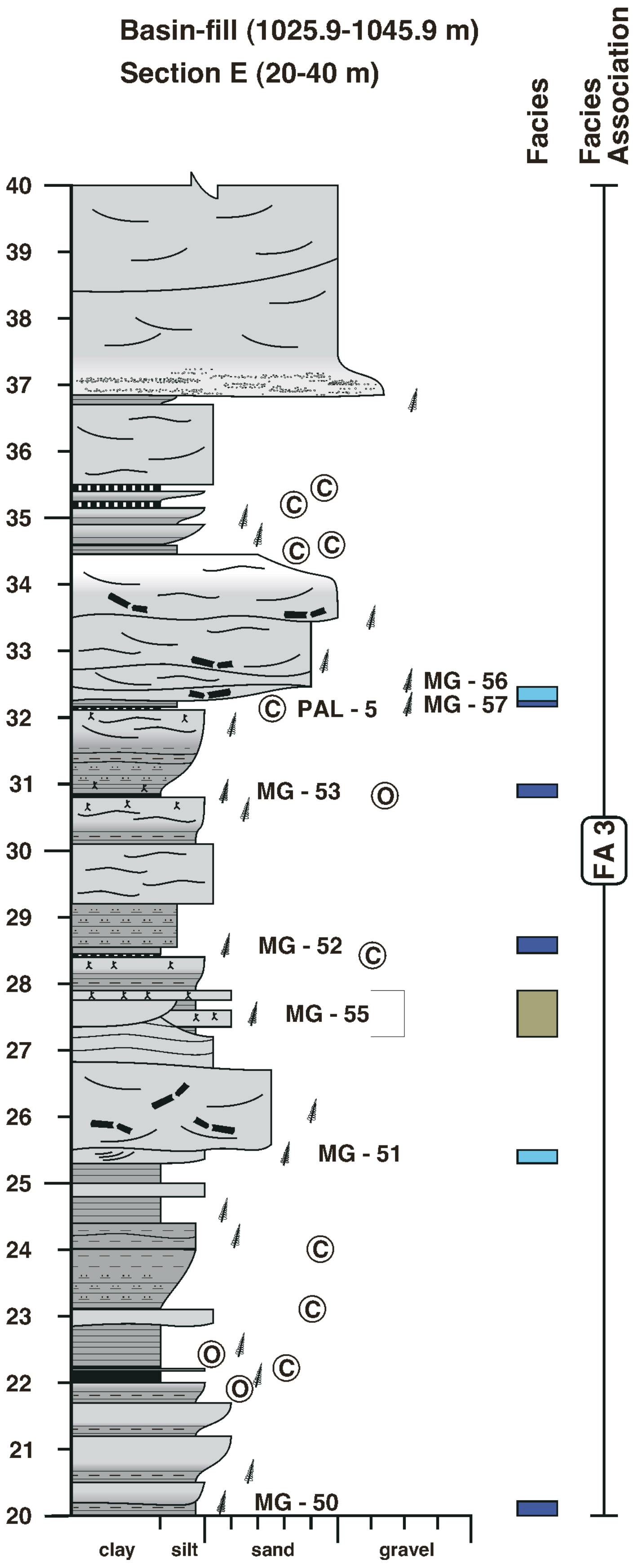
Section D-AUX (0-6.53 m)



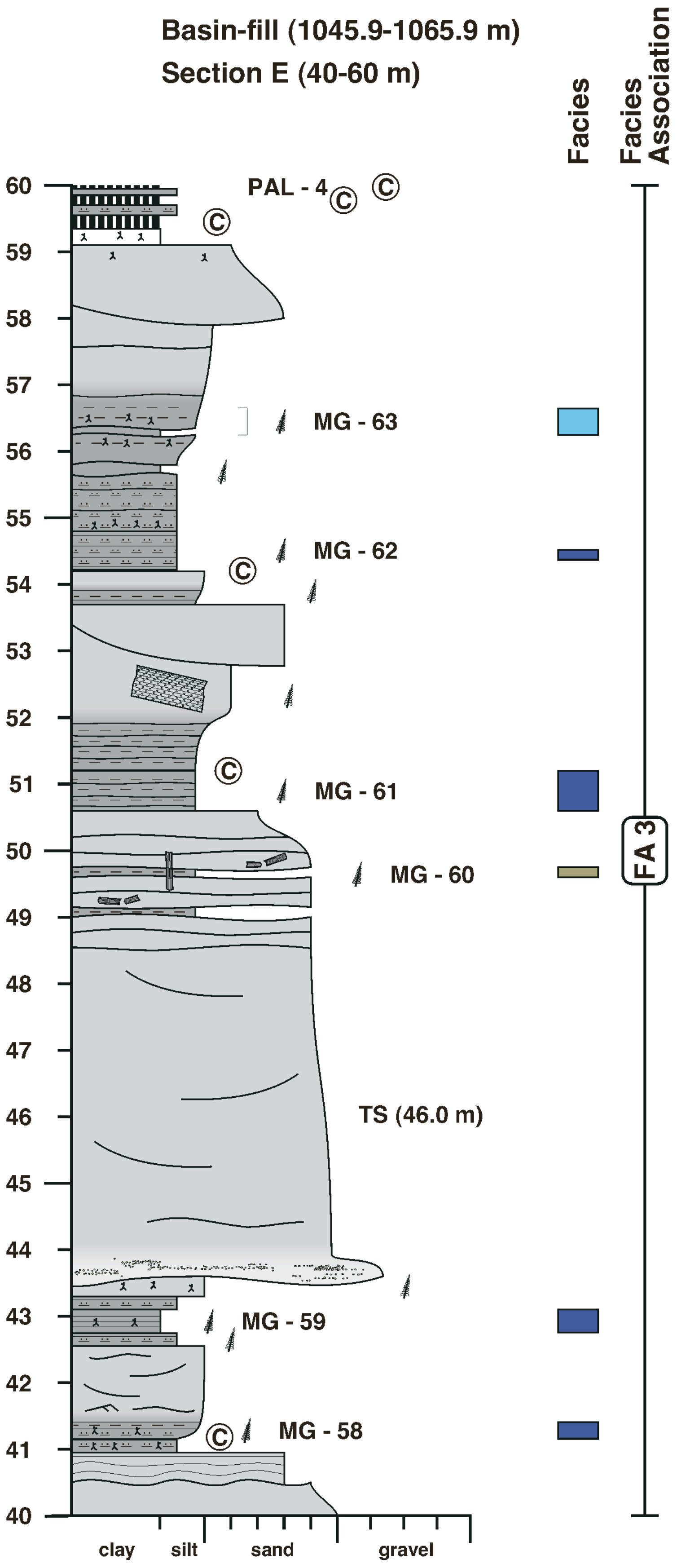


Basin-fill (1005.9-1025.9 m)

Section E (0-20 m)



Basin-fill (1025.9-1045.9 m)
Section E (20-40 m)

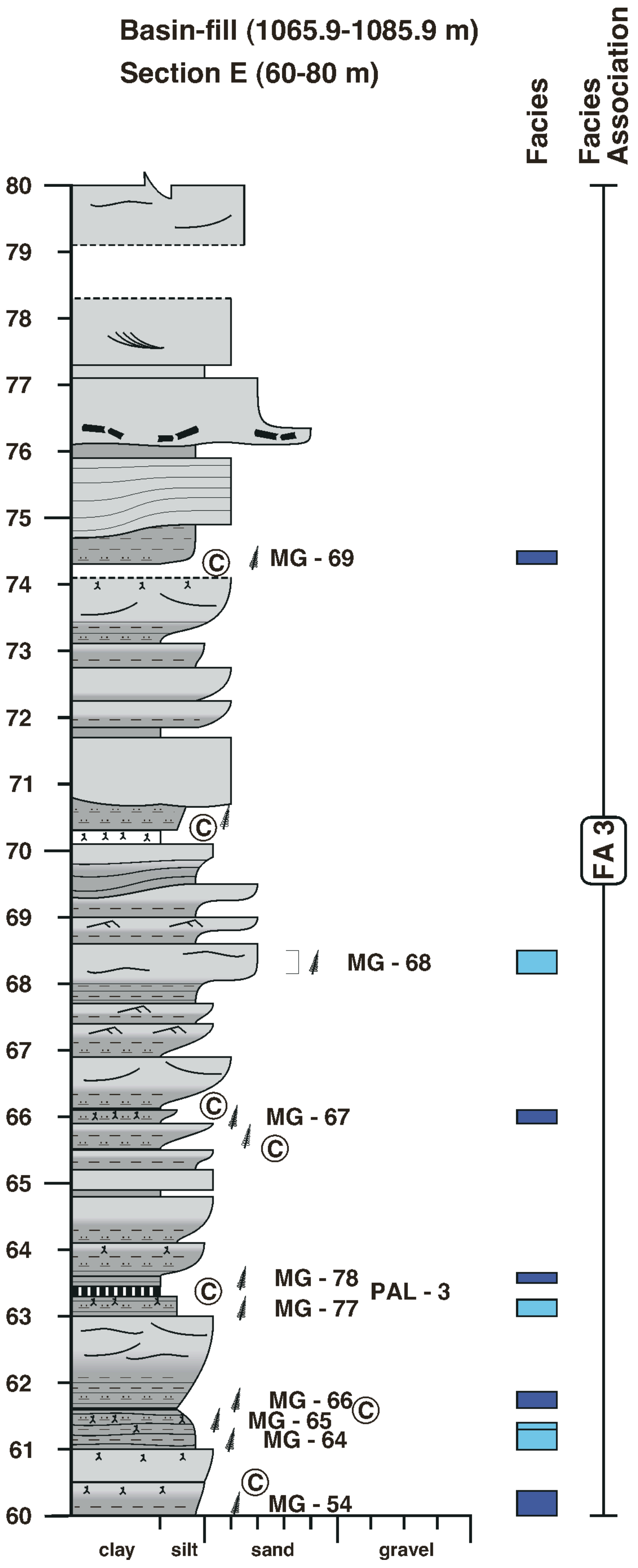


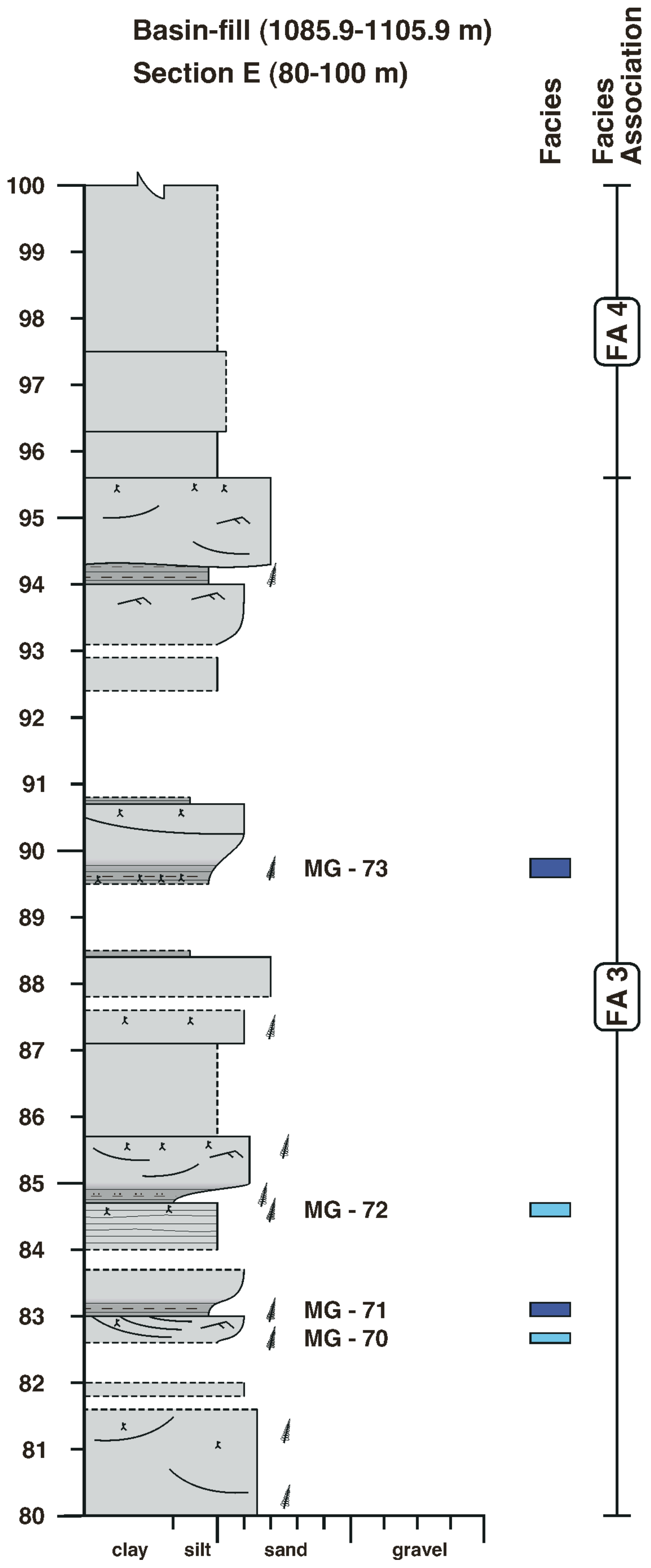
Basin-fill (1045.9-1065.9 m)

Section E (40-60 m)

Basin-fill (1065.9-1085.9 m)

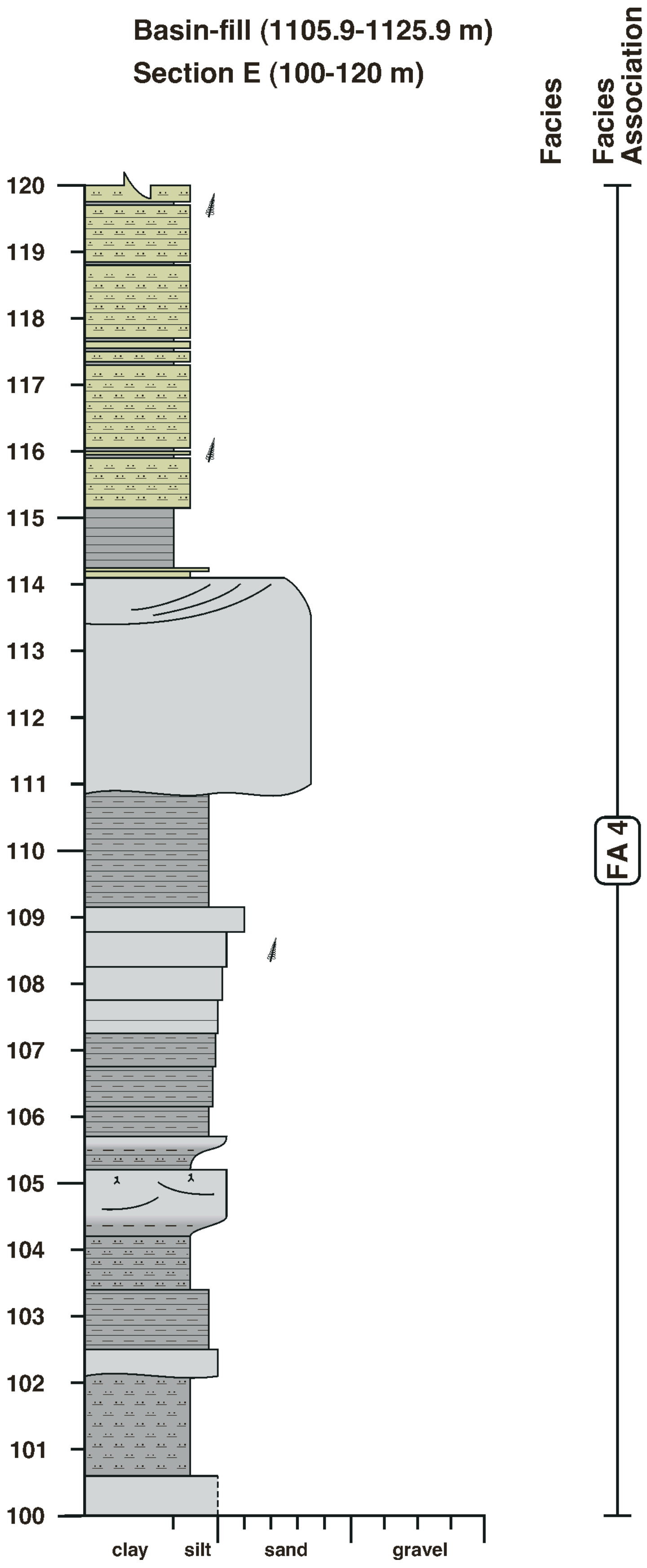
Section E (60-80 m)

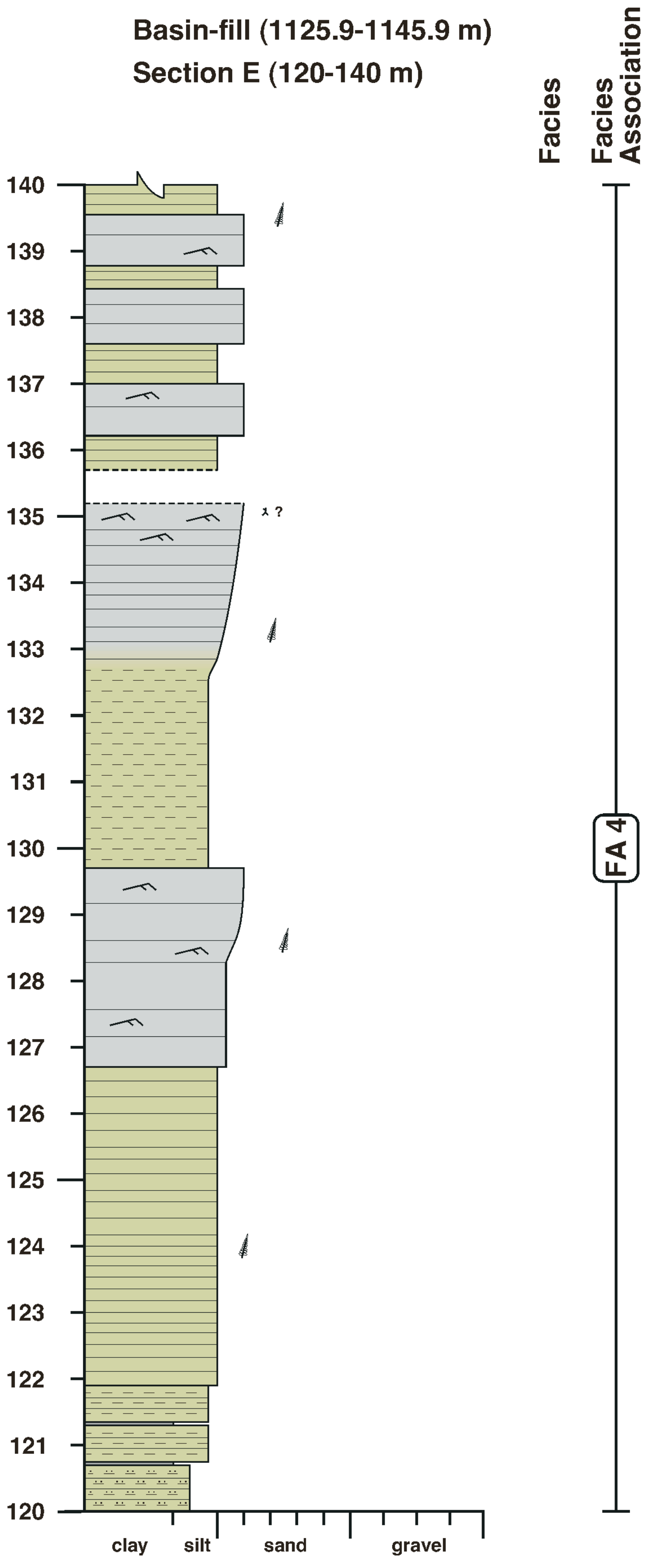




Basin-fill (1085.9-1105.9 m)
Section E (80-100 m)

Basin-fill (1105.9-1125.9 m)
Section E (100-120 m)





Basin-fill (1125.9-1145.9 m)
Section E (120-140 m)
Facies
Facies Association
140
139
138
137
136
135
134
133
132
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130
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128
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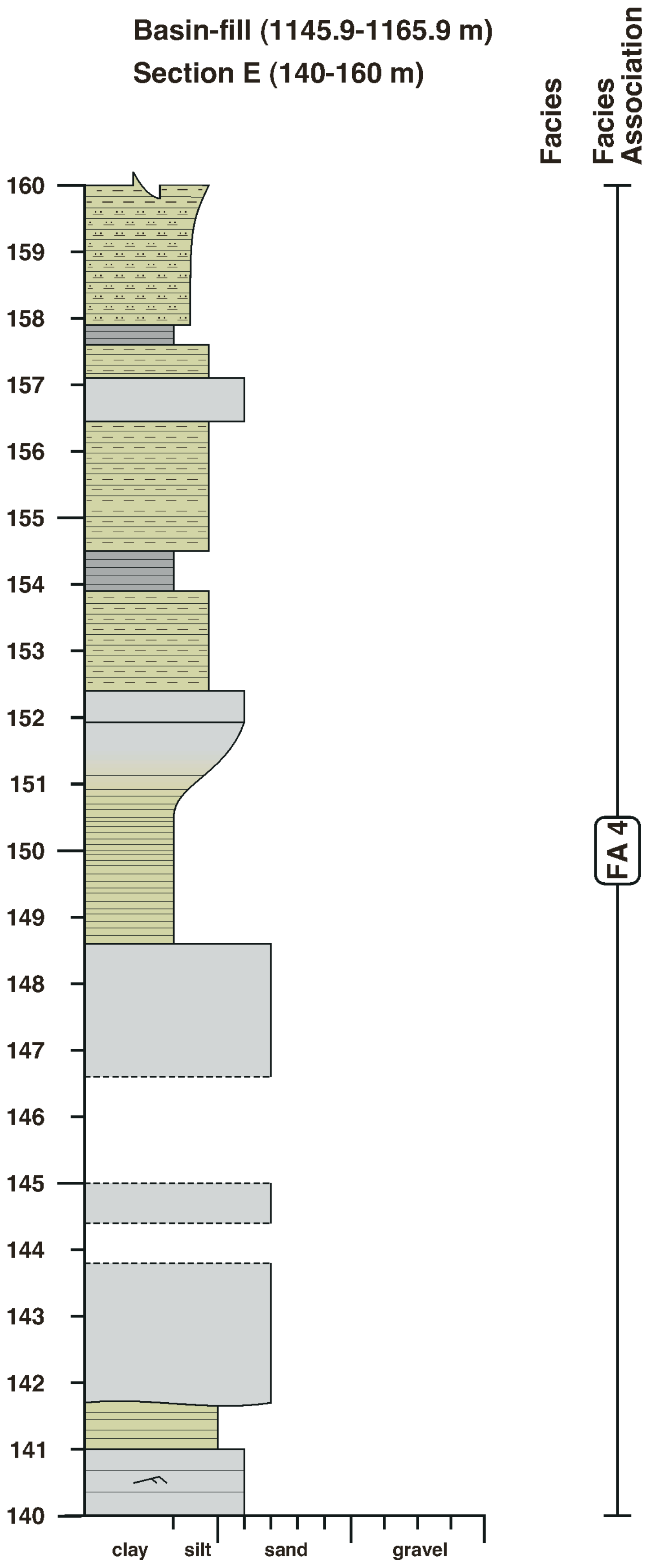
126
125
124
123
122
121
120
?
FA 4
clay
silt
sand
gravel

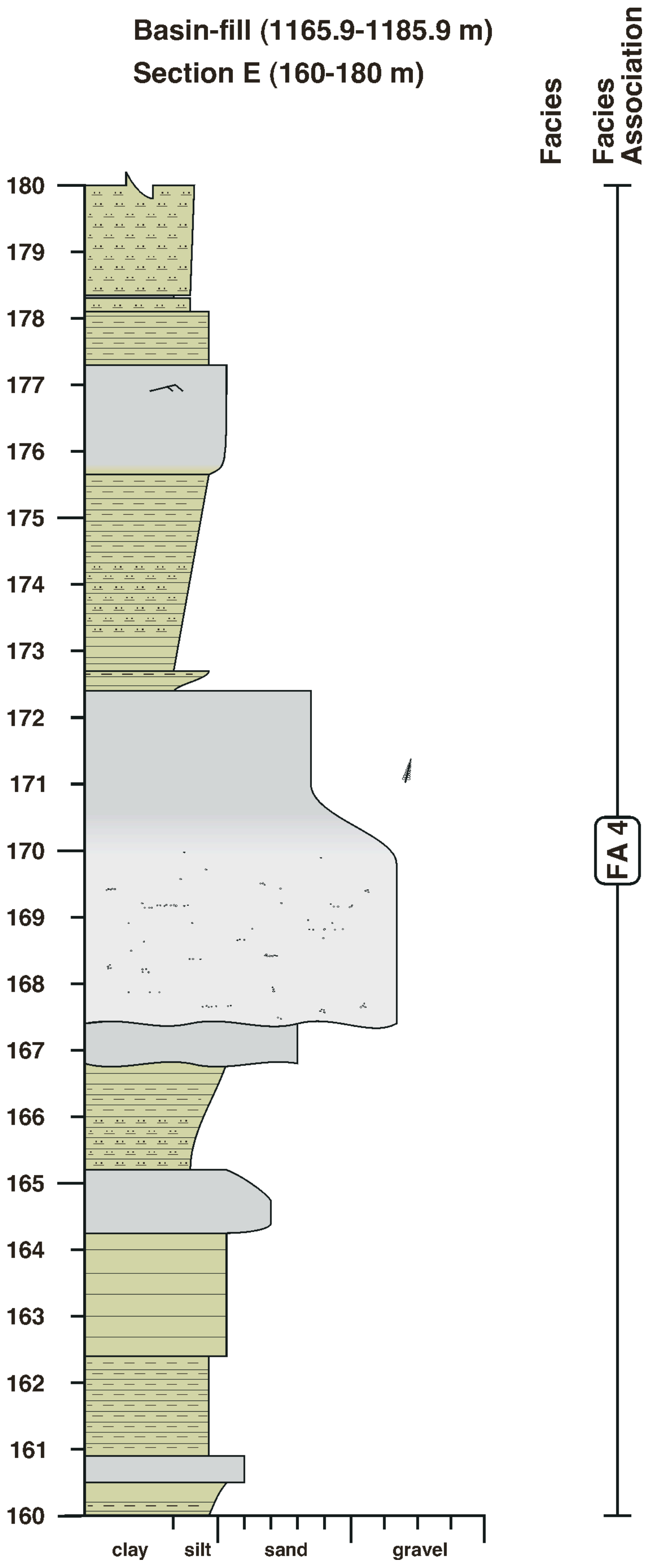


Basin-fill (1145.9-1165.9 m)

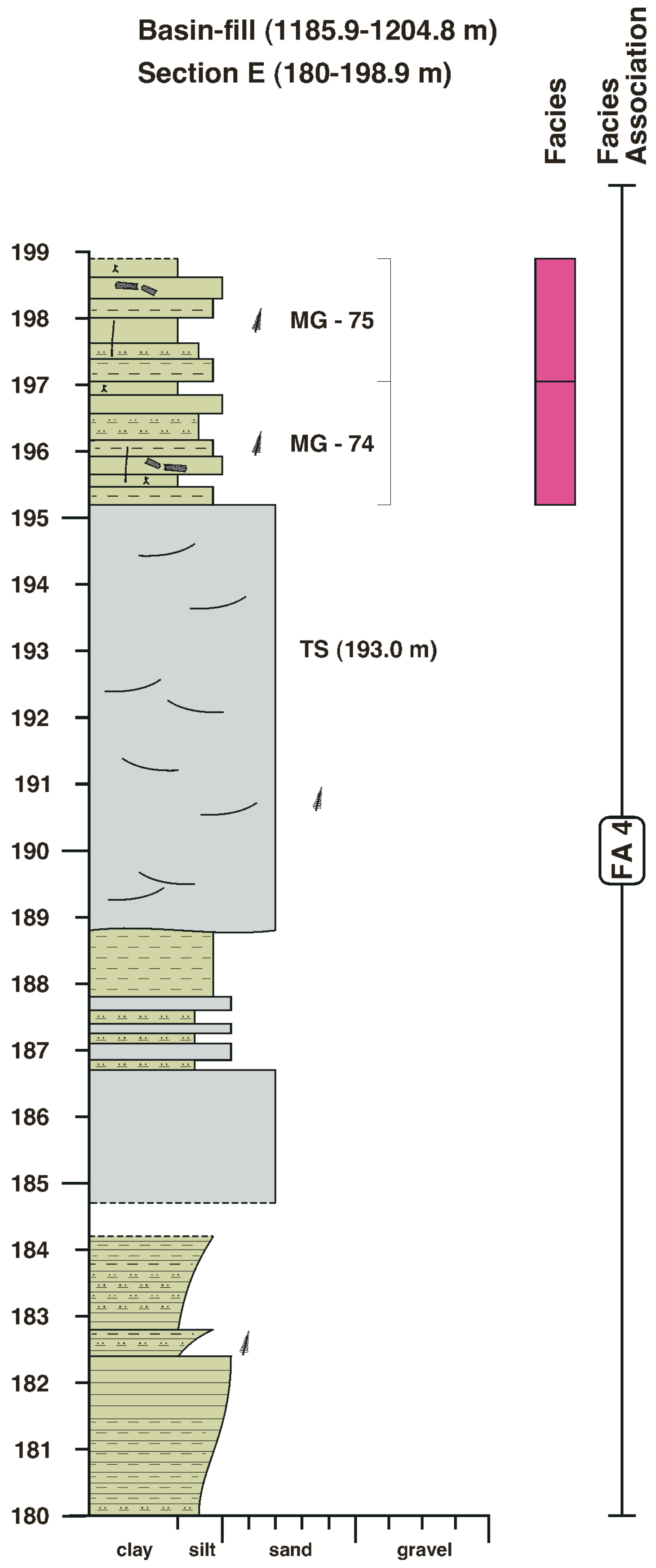
Section E (140-160 m)

Basin-fill (1165.9-1185.9 m)

Section E (160-180 m)



Basin-fill (1185.9-1204.8 m)
Section E (180-198.9 m)



Taxon	**Reference(s) containing illustrations of conspecific taxa**	**Comments**	**Localities/sites**	**Number of specimens**
"*Lepidodendron*" *subdichotomum* Sterzel[b]	Němejc (1947a); Thomas (1970); Šetlík (1977); Šimůnek (2008)	Lacks infrafoliar parichnos - not true *Lepidodendron*	LB-2	1423
***Annularia asteris* Bell**	Bell (1944); Abbott (1958)	First record from Nýřany Member	JV, RZ	2
***Annularia carinata* von Gutbier**[a]	Barthel (2004); Abbott (1958) under *Annularia mucronata* Schenk	Some specimens similar to *Annularia spinulosa* Sternberg [= *Annularia stellata* (Schlotheim) Wood]	JV, VR, LB-2, LB-1, RK, RZ	446
Annularia "spicata"	Šetlík (1968a)	Included under *Annularia spicata* (von Gutbier) Schimper in Pešek (2004), but not conspecific with that species	LB-2, LB-1, NZ	358
***Annularia sphenophylloides* (Zenker) von Gutbier**	Abbott (1958)		JV, LB-1, RZ	17
***Annularia vernensis* (Arnold) Abbott**	Arnold (1949); Abbott (1958)	First record from Nýřany Member. Similar to *Annularia galioides* (Lindley et Hutton) Kidston	TU	13
***Asterophyllites equisetiformis* (Schlotheim) Brongniart**	Abbott (1958)		LB-2, LB-1, OV	20
***Asterophyllites longifolius* (Sternberg) Brongniart**	Abbott (1958)		VR, RZ	6
***Sphenophyllum emarginatum* (Brongniart) Brongniart**[a]	Storch (1966); Batenburg (1977); Šimůnek (2008)		VR, LB-2, LB-1, RK, OV, NZ, RZ	712
***Sphenophyllum mirosoviense* Daňková-Pokorná**[b]	Daňková-Pokorná (1951)	Supposedly endemic to 'Mirošov Horizon'	JV	269
***Sphenophyllum oblongifolium* (Germar et Kaulfuss) Unger**	Bell (1938); Abbott (1958); Šetlík (1977) Galtier & Daveiro (1999)		TU, OV, NZ, RZ	828
***Acitheca polymorpha* (Brongniart) Schimper**[b]	Zodrow et al. (2006)	Range extended down to Nýřany coal seam group	VR	74
***Acitheca* sp. A**[b]	Bek & Opluštil (1998) under *Acitheca ambigua* (Sternberg) Němejc	Compares closely with *A. ambigua* (see Zodrow et al., 2006), but isolated spores distinct (J. Bek, pers. comm.)	RZ	91
***Acitheca* sp. B**		Sparse *Polymorphopteris*-type venation (Wagner, 1958a; Zodrow et al., 2006)	TU	1
***Cyathocarpus* sp. A**	Identity(?) with *Pecopteris ocejensis* Wagner (see Wagner, 1966); similar to *Pecopteris nyranensis* Němejc	Possibly recorded under *P. nyranensis* Němejc in Pešek (2004)	RK, OV	145
***Lobatopteris* sp. A**	Compares best with *Pecopteris polypodioides* (Presl *in* Sternberg) Němejc (see Němejc, 1948; Šimůnek 1994, 2008)	*Lobatopteris*-type venation and frond habit (Wagner, 1958b)	VR, RK, OV, NZ	770
***Lobatopteris* sp. B**[a]		*Lobatopteris*-type venation (Wagner, 1958b) in distal parts, but with subtriangular pinnules atypical of genus in proximal parts	JV, VR, LB-2, LB-1, RK, RZ	1078
***Pecopteris nyranensis* Němejc**	Němejc (1948); Šimůnek (1994)		JV	15
***Pecopteris raconensis* Němejc**	Šetlík (1977); Wagner (1966, 1983); Wagner & Lemos de Sousa (1983, pl. 2, figs 4, 5, *non* fig. 3); Šimůnek (1994)	Some specimens resemble possible synonyms *Pecopteris folchwillerensis* Corsin and *Pecopteris tenuinervosa* Corsin (see Corsin, 1951)	JV, VR, OV, RZ	66
***Pecopteris* sp. F**		Pinnules markedly confluent, subtriangular, and oblique to rachis; lateral veins divide near midvein, upper branches again in large pinnules, ending oblique to lateral margin	RZ	29
***Pecopteris* sp. G**	Conspecific(?) with *Pecopteris raconensis* Němejc *sensu* Wagner & Lemos de Sousa (1983, pl. 2, fig. 3, *non* figs 4, 5); similar to *Pecopteris victoriae* Corsin (see Corsin, 1951)	Midveins strictly non-decurrent; lateral veins once-divided at midvein, ending nearly normal to lateral margin	TU, RZ	213
***Ptychocarpus unitus* (Brongniart)**	Corsin (1951); Wagner (1983); Šimůnek (1994)		LB-2, LB-1, RK, RZ	168
***Alloiopteris erosa* (von Gutbier)**[b]	Danzé (1956); Brousmiche (1983)	Probably recorded under *Alloiopteris winslovii* White in Pešek (2004); Brousmiche (1983) proposed synonymy	TU	208
***Myriotheca* sp. A**	Danzé (1956, 1960)		RZ	1
***Oligocarpia* sp. cf. *O. bellii* Zodrow et McCandlish**	Zodrow & McCandlish (1982); Zodrow et al. (2005)	Small sori irregularly scattered over pinnule	RZ	4
***Oligocarpia gutbieri* Göppert**[b]	Šetlík (1977); Brousmiche (1983); Stockmans & Willière (1965) and Wagner (1966) under *Pecopteris bredovi* Germar	Large sori astride pinnule midvein	TU	163
***Renaultia schatzlarensis* (Štur)**	Danzé (1956); Brousmiche (1983)		VR	6
***Senftenbergia plumosa* var. *delicatula* (Brongniart)**	Dalinval (1960)	Probably included under *Pecopteris plumosa* (Artis) Brongniart in Pešek (2004)	JV, RZ	3
***Sphenopteris ovalis* von Gutbier**	Daber (1955)	Pinnules pecopteroid, midveins strongly decurrent and S-shaped	RZ	2
***Zeilleria* sp. cf. *Z. frenzlii* (Štur)**	Brousmiche (1983)	Typically confined to Bolsovian Radnice Member (Pešek, 2004)	RZ	12
"*Alethopteris*" *kettneri* Havlena	Havlena (1951); Šimůnek (1988) under *Alethopteris grandinioides* var. *kettnerii* (Havlena) Šimůnek	Belongs to *Callipteridium*	RZ	8
cf. *Blanzyopteris* sp. Krings et Kerp	Knight (1983a) under *Neuropteris* sp. nov., cf. *praedentata* Gothan; Wagner (1983) under *Neuropteris praedentata* Gothan; Castro (2005a) under *Mixoneura wagnerii* Lorenzo	Pinnule poorly preserved; labeled as *Neuropteris crenulata* Zeiller (see Krings & Kerp, 1999)	RK	1
***Callipteridium rubescens* (Presl *in* Sternberg) Wagner**	Němejc (1936a)		VR, LB-1, RK, RZ	51
***Linopteris neuropteroides* (von Gutbier) Potonié**[a]	Laveine (1967); Laveine et al. (1993)	All belong to var. *minor* Potonié	JV, VR, LB-2, LB-1, RK, RZ	1626
***Linopteris obliqua* (Bunbury) Zeiller**[b]	Laveine (1967); Zodrow & McCandlish (1978); Laveine et al. (1993); Zodrow et al. (2007)		JV	61
***Linopteris palentina* Wagner**	Wagner (1983); Wagner (1964) under *Linopteris linearis* Wagner; Wagner (1966) under *Linopteris neuropteroides* var. *linearis* Wagner	First record from Nýřany Member; according to Wagner (1983), venation intermediate between *Linopteris neuropteroides* (von Gutbier) Potonié and *Linopteris obliqua* (Bunbury) Zeiller	LB-1	9
***Neuropteris plicata* Sternberg**	Němejc (1949) under *Mixoneura plicata* (Sternberg); Laveine (1967) under *Neuropteris ovata* Hoffmann	Probably earlier synomyn of *N. ovata*	LB-1, RK, RZ	73
***Neurocallipteris planchardii* (Zeiller) Cleal, Shute et Zodrow**	Havlena (1953); Doubinger et al. (1995)	First record from Nýřany Member	LB-1, RZ	32
***Odontopteris reichiana* von Gutbier**	Němejc (1949); Daber (1955); Laveine (1989); Šimůnek & Cleal (2004)		RK, RZ	10
***Dicksonites plukenetii* (Schlotheim ex Sternberg) Sterzel**	Danzé-Corsin (1953); Laveine (1989, pl. 54, figs 2, 3; pl. 55, fig. 1); Doubinger et al. (1995); Galtier & Béthoux (2002); Castro (2005a)		JV, LB-2, RK, RZ	39
***Dicksonites sterzelii* (Zeiller) Danzé-Corsin**[b]	Stockmans & Willière (1965); Doubinger et al. (1995); possibly Šimůnek (2008) under *Dicksonites plukenetii* (Schlotheim)	First record from Nýřany Member; previously recorded under *Dicksonites plueckenetii* (Schlotheim) Sterzel in Pešek (2004)	TU	192
***Eusphenopteris nummularia* (von Gutbier) Novik**	van Amerom (1975)		JV, LB-2, LB-1, RK	97
***Eusphenopteris scribanii* van Amerom**	van Amerom (1975); Laveine (1993)	First record from Nýřany Member	RZ	1
cf. *Eusphenopteris* sp.		Tiny specimen of uncertain affinity	NZ	1
***Pseudomariopteris cordato-ovata* (Weiss) Gillespie, Clendening et Pfefferkorn ex Krings et Kerp**	Knight (1983a); Krings & Kerp (2000); Castro (2005a)	Recorded under *Pseudomariopteris ribeyronii* (Zeiller) Danzé-Corsin in Pešek (2004)	VR, RK	5
***Cordaites* sp.**[a]		Cuticles needed for differentiation of species (Zodrow et al., 2000)	JV, VR, LB-2, LB-1, RK, OV, NZ, RZ	3055
TOTAL				**12404**

Table 5. Taxa identified, their distribution in localities/sites, abundance in sample population, and useful references for comparison.
(a) Occur at ≥6 localities/sites. (b) Abundant at one locality/site but rare or absent elsewhere.

	JV-1.1	JV-1.2	JV-1.3	JV-2	JV-3.1	JV-3.2	JV-4	VR-1.1	VR-1.2	VR-2	VR-3	LB-1.1D	LB-1.2D	LB-1.3D	LB-1.4D	LB-1.5D	LB-1.6D	LB-1.7D	LB-1.8D	LB-1.9D	LB-1.10D	LB-1.11D	LB-1.1L	LB-1.2L	LB-1.3L	LB-2.1	LB-2.2	LB-2.3	LB-2.4	LB-2.5	TU-1.1	TU-1.2	TU-1.3	TU-1.4	TU-1.5	RK-1.1	RK-1.2	OV-1	NZ-1	RZ-1F	RZ-1C	Totals
"_Lepidodendron_" _subdichotomum_	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	223	299	391	45	465	0	0	0	0	0	0	0	0	0	0	0	**1423**
Annularia asteris	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**2**
Annularia carinata	4	6	2	218	4	16	0	14	5	0	0	0	0	2	13	5	7	3	9	8	7	2	0	3	0	2	0	3	12	23	0	0	0	0	0	5	3	0	0	53	17	**446**
Annularia sphenophylloides	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	6	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**17**
Annularia "spicata"	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4	2	0	0	0	0	0	0	0	0	350	0	0	**358**
Annularia vernensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	2	3	1	0	0	0	0	0	0	**13**
Asterophyllites equisetiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	1	0	0	9	0	0	0	0	0	0	0	0	4	0	0	0	**20**
Asterophyllites longifolius	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	**6**
Sphenophyllum emarginatum	0	0	0	0	0	0	0	1	2	0	11	0	1	0	2	0	8	15	10	31	10	23	2	2	7	27	14	21	123	157	0	0	0	0	0	11	0	159	14	57	4	**712**
Sphenophyllum mirosoviense	2	1	7	47	59	56	97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**269**
Sphenophyllum oblongifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	216	133	84	245	117	0	0	5	5	21	2	**828**
Acitheca polymorpha	0	0	0	0	0	0	0	7	7	56	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**74**
Acitheca sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65	26	**91**
Acitheca sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**1**
Cyathocarpus sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	16	122	0	0	0	**145**
Lobatopteris sp. A	0	0	0	0	0	0	0	9	12	1	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	380	124	178	27	0	0	**770**
Lobatopteris sp. B	0	0	0	0	19	7	1	0	1	0	0	18	36	13	15	2	107	127	137	128	199	190	17	11	26	0	0	0	0	17	0	0	0	0	0	5	0	0	0	2	0	**1078**
Pecopteris nyranensis	0	0	0	0	9	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**15**
Pecopteris raconensis	0	0	0	0	8	10	12	17	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	3	0	**66**
Pecopteris sp. F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	3	**29**
Pecopteris sp. G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31	71	20	11	44	0	0	0	0	31	5	**213**
Ptychocarpus unitus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	0	1	0	0	0	0	3	2	6	149	0	0	0	0	0	0	1	0	0	1	0	**168**
Alloiopteris erosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48	31	21	46	62	0	0	0	0	0	0	**208**
Myriotheca sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**
Oligocarpia sp. cf. _O. bellii_	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	**4**
Oligocarpia gutbierii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60	36	27	20	20	0	0	0	0	0	0	**163**
Renaultia schatzlarensis	0	0	0	0	0	0	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**6**
Senftenbergia plumosa var. _delicatula_	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	**3**
Sphenopteris ovalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	**2**
Zeilleria sp. cf. _Z. frenzlii_	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	**12**
"Alethopteris" kettnerii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4	**8**
cf. _Blanzyopteris_ sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	**1**
Callipteridium rubescens	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	23	22	**51**
Linopteris neuropteroides	281	318	345	6	281	179	13	0	0	1	0	0	0	0	1	2	14	0	1	0	1	0	0	0	86	0	0	0	0	1	0	0	0	0	0	17	24	0	0	47	8	**1626**
Linopteris obliqua	0	0	0	0	1	19	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**61**
Linopteris palentina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**9**
Neuropteris plicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	3	3	7	4	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	12	33	**73**
Neurocallipteris planchardii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	5	**32**
Odontopteris reichiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	7	0	**10**
Dicksonites plukenetii	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	19	0	0	0	0	0	0	3	0	0	2	4	**39**
Dicksonites sterzelii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	90	25	15	25	0	0	0	0	0	0	**192**
Eusphenopteris nummularia	0	0	0	0	0	0	2	0	0	0	0	1	8	12	4	0	1	1	2	8	15	33	5	0	0	0	0	0	0	4	0	0	0	0	0	0	1	0	0	0	0	**97**
Eusphenopteris scribanii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**
cf. _Eusphenopteris_ sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Pseudomariopteris cordato-ovata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	**5**
Cordaites sp.	8	11	11	13	15	38	93	0	1	1	6	190	269	334	219	276	118	206	182	174	115	167	135	135	76	26	21	29	0	8	0	0	0	0	0	122	52	1	1	2	0	**3055**
TOTALS	**295**	**337**	**365**	**287**	**396**	**328**	**274**	**52**	**43**	**61**	**62**	**209**	**315**	**361**	**254**	**285**	**266**	**353**	**353**	**353**	**358**	**429**	**164**	**152**	**202**	**279**	**337**	**447**	**199**	**845**	**394**	**366**	**180**	**340**	**269**	**548**	**237**	**474**	**398**	**404**	**133**	**12404**

Table 6. Redistributed abundance matrix comprising 46 biological species in 41 quadrats collected in Nýřany Member.

PLANT GROUP	PLANT FAMILY	MIOSPORE FOSSIL TAXON	PAL-10 LB-2	PAL-11 LB-2	PAL-12 LB-2	PAL-15 LB-2	PAL-13B LB-3	PAL-7 JV-3	PAL-17 VR-1	PAL-18 VR-2	PAL-19 RZ-1F
Lycopsids	Lepidocarpaceae	*Lycospora (non L. orbicula)*	8.0	13.2	3.0	10.5	50.3	4.8	7.0	1.0	1.0
	Diaphorodendraceae	*Cappasporites*	1.0	14.2	0	1.5	0	2.0	0	1.0	0
	Sigillariostrobaceae (?)	*Cadiospora magna*	0	0	0	0.5	0	0.4	0	0.5	1.0
	Sigillariostrobaceae	*Crassispora*	0	0	0	0	0	1.2	0	0	0
	Sporangiostrobaceae	*Densosporites*	0	0	0	0	0	0	0	0	0
	Chaloneriaceae	*Endosporites*	0.5	0.3	1.5	0	0.3	0.8	0.5	0	0
	Selaginellaceae	*Cirratriradites*	0	0	0	0	0	0.8	0	0	0
	Selaginellaceae	*Lundbladispora*	0	1.0	2.0	0	0.3	0	0.5	1.0	3.5
SPORES OF LYCOPSIDS			**9.5**	**28.7**	**6.5**	**12.5**	**50.9**	**10.0**	**8.0**	**3.5**	**5.5**
SPORES OF CALAMITEANS		*Calamospora*	**8.5**	**11.5**	**8.5**	**10.0**	**3.8**	**10.4**	**11.5**	**13.0**	**11.0**
Sphenophylls		*Laevigatosporites* and *Latosporites* (>35um)	39.5	7.4	26.5	10.0	1.6	21.6	18.0	17.9	1.5
		Vestispora	1.9	2.3	14.0	1.0	4.5	0	0	0	0.5
		Reticulatisporites muricatus	0	0	0	0	0	0	1.0	0.5	0
SPORES OF SPHENOPHYLLS			**41.4**	**9.7**	**40.5**	**11.0**	**6.1**	**21.6**	**19.0**	**18.4**	**2.0**
Ferns	Marattiales	*Laevigatosporites* and *Latosporites* (<35um)	0.5	0	2.0	0.5	2.9	3.2	15.0	11.9	6.0
		Torispora	0	0	0	0	0	4.0	0	0	1.5
		Punctatosporites	1.9	39.9	3.0	9.0	14.4	12.8	0	1.0	8.0
		Speciososporites	0	0	0	1.5	1.6	2.4	0	0	0.5
		Thymospora	0	0	0	0	0	0	0	0	1.0
		Cyclogranisporites	1.4	0.3	0.5	0.5	0.3	0.8	1.5	1.0	4.5
		Spinosporites	0	0	0	1.0	0	0.8	0.5	0.5	0
	Tedelaceae	*Raistrickia*	1.4	0	1.0	0	0.3	1.2	0	1.5	1.5
		Savitrisporites	0	0	0.5	0	0	1.6	0	0.5	1.0
	Gleicheniaceae	*Triquitrites*	12.8	2.3	3.0	10.5	6.1	8.4	3.0	7.0	1.0
		Microreticulatisporites	0	0	0.5	3.5	0.3	0.4	13.5	19.9	0
	Sphenopteroid' ferns	*Granulatisporites*	0	0	1.0	0	0.6	0.8	2.5	0	0.5
		Leiotriletes	1.4	0	1.5	7.5	8.0	3.6	6.5	7.0	6.0
		Lophotriletes	0	0	0	0.5	0	0.8	1.0	0	0.5
		Convolutispora	1.0	0	0.5	0.5	0	0.4	0.5	0	0.5
	Diverse ferns	*Verrucosisporites*	0	0	0	0	0	0	3.5	3.0	0.5
		Apiculatisporites	1.0	1.0	0.5	1.5	0.3	0.8	0	1.0	4.0
		Knoxisporites	0	0.3	0	1.0	0	0	0	0.5	2.0
	Uncertain affinity	*Converrucosisorites*	0	0	0.5	1.5	0	0	0	0	0
		Gillespieisporites	0	3.5	0.5	0	0	0	0	1.0	1.0
SPORES OF FERNS			**21.4**	**47.3**	**15.0**	**39.0**	**34.8**	**42.0**	**47.5**	**55.8**	**40.0**
Pteridosperms	Medullosales	*Schopfipollenites*	0	0	0	0.5	0	0.4	0.5	1.0	6.0
	Callistophytales	*Vesicaspora*	0	0	0	0.5	0	0	0	0	0
	Peltaspermales	*Wilsonites*	2.9	0.3	4.5	3.5	0	2.0	0	0.5	6.5
		Protohaploxipinus	0	0	0	0	0	0	0	0	1.0
		Alisporites	0	0	0	0.5	0	0	0	0	0
POLLEN OF PTERIDOSPERMS			**2.9**	**0.3**	**4.5**	**5.0**	**0.0**	**2.4**	**0.5**	**1.5**	**13.5**
POLLEN OF CORDAITALEANS		*Florinites*	**11.4**	**1.6**	**20.5**	**15.0**	**3.2**	**7.2**	**6.0**	**6.0**	**20.0**
POLLEN OF CONIFERS		*Potonieisporites*	**0.5**	**0.0**	**0.0**	**0.5**	**0.3**	**0.8**	**1.0**	**0.0**	**1.0**
Conifers or Pteridosperms		*Candidispora*	1.0	0.3	0	1.5	0	0.4	0	0	0
		Latensina	1.0	0	2.0	1.0	0.3	2.4	1.5	0	1.0
		Other trilete monosaccate pollen	0	0	0	0	0	0	0	0	2.0
		Limitisporites	0	0	0	0.5	0	0	0	0	1.0
		Illinites	0	0	0	1.0	0	0.8	0	0	0
		Nonstriate bisaccate pollen	1.4	0	0	0	0	0	0	0	1.0
		Striate bisaccate pollen	0	0	0	0	0	0	0	0.5	0.5
POLLEN OF CONIFERS OR PTERIDOSPERMS			**3.4**	**0.3**	**2.0**	**4.0**	**0.3**	**3.6**	**1.5**	**0.5**	**5.5**
Others		*Westphalensisporites*	0	0	0	0	0	0	3.0	1.0	0
		Punctatisporites	1.0	0.6	1.5	3.0	0.3	2.0	1.0	0.5	1.0
		Cadiospora butterworthii	0	0	1.0	0	0	0	0.5	0	0
		Punctatisporites minutus	1.0	0	0	0	0	0	0	0	0
		Dictyotriletes sp.	0	0	0	0	0	0	0	0	0.5
		Punctatisporites bifurcatus	0	0	0	0	0	0	0	0	0.5
OTHER MIOSPORES			**1.0**	**0.6**	**2.5**	**3.0**	**0.3**	**2.0**	**4.5**	**1.5**	**2.0**

Table 7. Relative abundances of miospore morphotaxa, segregated by plant group (and family, where possible).

Depositional facies	**Description**	**Interpretation**	**Megafloral assemblages**	**Dominant taphonomic mode**	**Quadrats; total quadrats [*n*]**	**Total bedding plane area sampled (m^2)**
Facies Association 1 (FA 1): Debris flows - aggregate thickness 42.4 m (3% of 1500 m basin fill)						
Debris flow breccia (DFB)	Red, clast-supported phyllite breccia, with minor red siltstone	Debris flows shed from basin margin	Unfossiliferous			
Facies Association 2 (FA 2): Braided channel belt - aggregate thickness 173 m (12% of 1500 m basin fill)					**[8]**	**2.00**
Braided sandbed stream (BSS)	Sandstones at base of composite sandstone/conglomerate units	Braided rivers	*Sigillaria, Calamites,* pteridosperm axes	Allochthonous	not quantified	
Braided gravelbed stream (BGS)	Clast-supported quartzite conglomerates at top of composite sandstone/conglomerate units	Braided rivers; some deposition by hyperconcentrated or debris flows	*Sigillaria, Calamites* axes	Allochthonous	not quantified	
Abandoned braided channel (ABC)	Thin, fine-grained intervals abruptly overlying composite sandstone/conglomerate units	Abandonment of braided streams due to rapid waning of flow	Rich megaflora	Parautochthonous	MG-10 [1]	0.25
Lower coarsening upward unit (LCU)	Mudstone or siltstone at base of coarsening upward units	Deeper water component of small, shallow ponds near braided channels	Rich megaflora	Parautochthonous	MG-29.1, 29.2, 31 [3]	0.75
Upper coarsening upward unit (UCU)	Siltstone or sandstone at top of coarsening upward units	Infilling of ponds near braided channels by sediment progradation	Rich megaflora	Near-autochthonous	MG-4, 5, 30, 32 [4]	1.00
Swamp (CSW)	Thin, clastic-rich coal seams and carbonaceous shales	Ephemeral swamps near braided channels subjected to frequent clastic incursions	No fossils observed		not quantified	
Facies Association 3 (FA 3): Interfluve wetlands - aggregate thickness 1170 m (78% of 1500 m basin fill)					**[83]$^{d, e}$**	**32.00^{b}**
Distributary channel (DSC)	Large, fining-upward sandstone bodies	Narrow, relatively deep distributary channels traversing wetlands	Large log accumulations at channel bases	Allochthonous	MG-14, 15, 16.1, 16.2, 17 [5]	≈12.50^{a}
Abandoned distributary channel (ADC)	Interbeds of siltstone and sandstone at top of large, fining-upward sandstone bodies	Abandonment of distributary channels traversing wetlands	Rich megaflora	Parautochthonous	MG-18, 55, 60 [3]	0.75
Lower coarsening upward unit (LCU)	Mudstone or siltstone at base of coarsening upward units	Deeper water component of small, shallow ponds in wetlands	Rich megaflora	Parautochthonous	MG-**11**, 20.1, 20.2, 22, 23.1, 23.2, 24, 26, 27, 34, 39, 41, 42, 44, 46 to 50, 52 to 54, 57 to 59, 61, 62, 66, 67, 69, 71, 73, 78 [33]	8.25
Upper coarsening upward unit (UCU)	Siltstone or sandstone at top of coarsening upward units	Infilling of wetland ponds by sediment progradation	Rich megaflora	Near-autochthonous	MG-**8**, **9**, 19.1 to 19.4, 21.1, 21.2, 25, 33, 35.1 to 35.5, 36 to 38, 40, 43, 45, 51, 56, 63 to 65, 68, 70, 72, 76, 77 [31]	7.75
Floodplain channel (FPC)	Small, fining-upward sandstone bodies	Narrow, shallow floodplain channels draining precursory wetlands	Rich megaflora	Parautochthonous	MG-2, 3.1 to 3.3, 6, 12 [6]	1.50
Ephemeral swamp (CSW)	Thin, clastic-rich coal seams and carbonaceous shales	Ephemeral wetland swamps subjected to frequent clastic incursions	Upright axes of *Sigillaria,* marattialean tree ferns, sphenophylls	Autochthonous	not quantified	
Splay (SPY)	Mudstone and siltstone horizons splitting thin, clastic-rich coal seams and carbonaceous shales	Blanketing of swamps with splay sediment during major floods	Rich megaflora	Parautochthonous	MG-1, **7**, **13**, 28.1, 28.2 [5]	1.25
Rheotrophic mire (RTM)	Thick coal seams (dm- to m-scale)	Rheotrophic (planar) mires	Rooting structures of *Omphalophloios* and *Sigillaria*(?); prone *Sigillaria, Asolanus, Calamites,* frond petioles	Autochthonous	not quantified	
Facies Association 4 (FA 4): Deep lakes - aggregate thickness 103 m (7% of 1500 m basin fill)					**[2]**	**0.50**
Lacustrine (LAC)	Thick coarsening-upward cycles	Infilling of extensive, deep lakes by shoreline progradation	Rare megaflora	Allochthonous	MG-74, 75 [2]	0.50
Distributary channel (DSC)	Large, fining-upward sandstone bodies	Narrow, relatively deep distributary channels feeding into lakes	Unfossiliferous			
Totals					**[93]**	**34.5^{c}**

Table 10. Summary of 13 depositional facies comprising four facies associations in La Magdalena Coalfield, indicating dominant taphonomic mode of plant fossils, quadrats sampled, and total bedding plane area represented.

(^{a}) Each quadrat ≈2.5 m^2. (^{b}) 19.5 m^2 without DSC facies. (^{c}) 22.0 m^2 without DSC facies. (^{d}) Quadrats of marginal wetlands (FA 3) underlined [MG-1, 2, 3.1 to 3.3, 6, 12 (n = 7)].

(^{e}) Quadrats of interfluve wetlands (FA 3) adjacent to braided channel belt in **bold** [MG-7 to 9, 11, 13 (n = 5)].

Quadrat	Meterage (m)	Facies	N	*Asolanus*	*Lepidodendron*	*Sigillaria*	*Annularia*	*Asterophyllites*	*Calamites*[a]	*Parasphenophyllum*	*Sphenophyllum*	*Caulopteris*[a]	*Danaeites*	*Diplazites*	*Lobatopteris*	*Megaphyton*[a]	*Nemejcopteris*	*Oligocarpia*	*Pecopteris*
MG-75[b]	1203.9	LAC	290	0	0	2	0	0	6	0	13	0	0	34.19	0	0	25.08	0	141.34
MG-74[b]	1202.0	LAC	177	0	0	14	0	0	7	0	20	0	0	12.60	0	0	1.40	0	15.40
MG-73	1095.7	LCU	375	0	0	1	5	0	0	0	2	0	0	1.90	0	0	0	0	5.69
MG-72	1090.5	UCU	224	0	0	6	9	0	0	0	1	0	0	1.60	0	0	12.80	0	43.20
MG-71	1089.0	LCU	355	0	0	1	11	0	0	0	2	0	0	24.36	4.06	0	2.03	2.03	243.57
MG-70	1088.6	UCU	206	0	0	0	7	0	0	0	0	0	0	0	0	0	24.67	3.29	0
MG-69	1080.2	LCU	289	0	0	0	63	0	0	0	0	0	0	0	0	0	0	0	31.31
MG-68	1074.2	UCU	406	0	0	0	0	0	1	0	5	0	0	1.27	0	0	0	1.27	24.13
MG-67	1071.9	LCU	315	0	0	0	8	0	0	0	1	0	0	0	0	0	0	3.06	168.30
MG-78	1069.4	LCU	187	0	0	14	8	0	0	0	0	0	1.68	1.68	3.37	0	0	0	114.49
MG-77	1069.0	UCU	258	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1.76
MG-66	1067.7	LCU	288	0	0	0	1	0	0	0	1	0	0	1.43	0	0	0	0	18.62
MG-65	1067.2	UCU	179	0	0	2	3	0	0	0	0	0	0	5.23	0	0	0	1.31	19.62
MG-64	1067.1	UCU	205	0	0	1	59	0	0	0	6	0	0	10.69	0	0	5.35	0	10.69
MG-54	1066.1	LCU	168	0	0	0	8	0	0	0	2	0	0	0	0	0	5.40	2.70	31.06
MG-63	1062.3	UCU	150	0	0	6	48	0	0	0	7	0	0	0	0	0	1.82	12.71	10.90
MG-62	1060.4	LCU	177	0	0	0	39	0	0	0	2	0	0	0	0	0	1.19	1.19	124.07
MG-61	1056.8	LCU	181	0	0	1	35	0	0	3.67	7.33	0	0	25.77	0	0	10.31	0	20.62
MG-60	1055.6	ADC	97	0	0	0	0	0	0	0	0	0	0	0	0	0	2.73	0	10.93
MG-59	1048.9	LCU	223	0	0	2	5	1	0	0	5	0	0	0	0	0	1.12	0	1.12
MG-58	1047.1	LCU	117	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	10.86
MG-56	1038.2	UCU	158	0	0	0	7	2	0	0	6	0	0	0	0	0	0	0	84.29
MG-57	1038.0	LCU	156	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	42.07
MG-53	1036.8	LCU	157	0	0	0	2	0	0	2	2	0	0	0	0	0	0	0	2.11
MG-52	1034.6	LCU	120	0	0	2	21.91	2.09	0	0	28	0	0	0	3.96	0	5.28	0	30.36
MG-55	1033.5	ADC	213	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0
MG-51	1031.2	UCU	112	0	0	21	0	0	1	0	2	0	0	0	0	0	0	0	4.57
MG-50	1026.0	LCU	113	0	0	0	4	4	0	0	10	0	0	0	0	0	12.26	0	36.77
MG-49	1025.4	LCU	98	0	0	1	2	0	0	0	0	0	0	1.34	0	0	4.01	0	70.92
MG-48	1021.0	LCU	229	0	0	0	1	2	0	0	0	0	0	0	0	0	2.46	1.23	14.78
MG-47	1018.9	LCU	137	0	0	13	0	0	8	0	0	0	0	0	0	0	3.55	0	46.16
MG-76	1006.1	UCU	228	0	0	0	0	0	0	0	18	0	0	2.12	0	0	0	0	14.85
MG-40	837.8	UCU	39	0	0	0	1.38	9.63	0	0	6	0	0	0	1.22	0	0	1.22	13.44
MG-39	837.0	LCU	84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-38	836.8	UCU	41	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-37	836.1	UCU	287	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-46	835.1	LCU	193	0	0	1	2.20	19.80	0	0	40	0	0	0	1.87	0	0	9.33	44.78
MG-35.1	834.0	UCU	110	0	0	5	0	13	0	0	23	0	0	0	0	0	0	0	29.14
MG-35.2	834.0	UCU	80	0	0	0	0	4	0	0	5	0	0	0	0	0	0	0	30.98
MG-35.3	834.0	UCU	131	0	0	1	0	8	0	0	6	0	0	1.37	1.37	0	0	1.37	47.92
MG-35.4	834.0	UCU	81	0	0	0	1.15	13.85	0	0	2	0	0	0	8.62	0	0	1.23	29.54
MG-35.5	834.0	UCU	59	0	0	0	0	14	0	0	2	0	0	0	4.91	0	0	0	22.11
MG-36	832.7	UCU	168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-41	830.1	LCU	299	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-43	827.4	UCU	70	0	0	0	1	0	0	0	0	0	0	0	0	0	4.06	0	20.30
MG-42	826.0	LCU	114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-44	822.0	LCU	105	0	0	0	2	0	0	0	1	0	0	2.33	0	0	0	1.16	11.65
MG-45	821.9	UCU	81	0	0	0	0	0	1	0	29	0	0	0	0	0	1.13	0	6.80
MG-34	816.9	LCU	104	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	34.71
MG-33	816.5	UCU	101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-31	354.8	LCU	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15.60
MG-30	354.5	UCU	47	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	3.07
MG-29.1	340.9	LCU	76	0	0	0	0	3	0	0	9	0	0	0	0	0	7.25	2.42	13.28
MG-29.2	340.9	LCU	77	0	0	0	6	2	0	0	2	0	0	1.72	0	0	0	0	32.64
MG-32	324.5	UCU	63	0	0	5	8	0	0	0	0	0	0	0	0	0	0	0	32.14
MG-15[b]	236.0	DSC	11	1.33	0	2.67	0	0	2	0	0	2	0	0	0	0	0	0	0
MG-14[b]	232.7	DSC	76	1.56	1.56	24.89	0	0	9	0	0	0	0	0	0	1	0	0	2
MG-19.1	232.0	UCU	54	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	9.07
MG-19.2	232.0	UCU	64	0	0	11	5	1	0	0	1	0	0	0	0	0	0	0	7.85
MG-19.3	232.0	UCU	46	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	8.90
MG-19.4	232.0	UCU	103	0	0	30	14	0	0	0	1	0	0	0	0	0	0	0	16.63
MG-20.1	231.5	LCU	169	10.43	0	63.57	7.88	1.13	0	0	1	0	0	0	0	0	0	2.18	3.28
MG-20.2	231.5	LCU	248	0	0	79	5	0	0	0	0	0	0	0	0	0	0	7.67	41.62
MG-23.1	228.9	LCU	98	0	0	3	70	0	0	0	2	0	0	0	0	0	1.21	1.21	20.58
MG-23.2	228.9	LCU	118	0	0	3	89	0	0	0	0	0	0	0	0	0	0	0	26
MG-21.1	228.6	UCU	128	0	0	16	8	0	0	0	1	0	0	0	0	0	0	52.82	36.97
MG-21.2	228.6	UCU	115	0	0	51	3	0	0	0	3	0	0	0	0	0	1.16	23.20	27.84
MG-22	228.5	LCU	164	0	0	1	8	0	0	0	42	0	0	7.99	0	0	58.21	20.55	21.69
MG-24	228.1	LCU	17	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-18	219.2	ADC	103	0	0	0	0	0	0	0	1	0	0	0	0	0	1.07	0	91.26
MG-17[b]	218.2	DSC	37	0	0	2	0	0	5	0	0	3	0	0	0	0	0	0	0
MG-16.1[b]	214.7	DSC	85	1.03	0	36.97	0	0	2	0	0	2	0	0	0	0	0	0	0
MG-16.2[b]	214.7	DSC	31	0	0	9	0	0	3	0	0	0	0	0	0	0	0	0	0
MG-28.1	210.5	SPY	147	0	0	0	5	0	0	0	0	0	0	23.21	2.73	0	1.37	12.29	79.19
MG-28.2	210.5	SPY	93	0	0	0	0	0	0	0	0	0	0	12.57	0	0	0	0	21.36
MG-27	204.9	LCU	127	0	0	6	0	0	0	0	6	0	0	0	0	0	90.36	3.08	13.35
MG-26	198.7	LCU	122	0	0	20	0	0	0	0	0	0	0	0	0	0	12.08	0	87.24
MG-25	198.1	UCU	106	0	17	0	0	0	0	0	0	0	0	0	0	0	4.63	0	70.63
MG-11	113.1	LCU	52	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1	24
MG-10	109.7	ABC	146	0	0	0	0	0	0	0	13	0	0	0	0	0	60.74	0	68.07
MG-9	100.8	UCU	71	0	0	4	0	2	0	0	10	0	0	1.53	0	0	6.11	0	21.39
MG-8	99.8	UCU	89	0	0	8	5	0	0	0	8	0	0	0	0	0	9.38	2.34	44.55
MG-13	99.5	SPY	133	0	0	3	1	0	0	0	2	0	0	0	0	0	5.73	0	87.34
MG-7	98.3	SPY	54	0	0	0	0	0	2	0	1	0	0	0	0	0	7.65	0	22.96
MG-5	84.7	UCU	128	0	0	0	14.64	31.36	0	0	16	0	0	0	0	0	52.80	0	10.27
MG-4	73.3	UCU	100	0	0	0	11	0	0	0	4	0	0	0	0	0	6.30	1.05	77.65
MG-6	50.5	FPC	70	0	0	0	2.50	7.50	0	0	0	0	0	0	0	0	0	0	9.13
MG-3.1	49.5	FPC	94	0	0	0	30.60	5.40	0	0	0	0	0	0	0	0	0	0	7.40
MG-3.2	49.5	FPC	52	0	0	0	12	0	0	0	3	0	0	3.43	0	0	0	1.71	8.57
MG-3.3	49.5	FPC	117	0	0	0	41	0	0	0	4	0	0	2.92	0	0	5.83	0	13.13
MG-2	47.8	FPC	33	0	0	0	2	0	0	0	2	0	0	0	0	0	6.82	0	6.82
MG-1	47.3	SPY	94	0	0	0	19	3	0	0	5	0	0	0	1.25	0	12.50	1.25	12.50
MG-12	44.5	FPC	42	0	0	0	0	0	0	0	0	0	0	0	2.21	0	0	0	3.32
		TOTAL	**12553**	**14.35**	**18.56**	**525.10**	**742.25**	**149.75**	**48.00**	**5.67**	**395.33**	**7.00**	**1.68**	**181.25**	**35.56**	**1.00**	**487.85**	**175.88**	**2785.25**

Table 13 (Part A). Redistributed abundance matrix comprising 27 biological genera in 93 quadrats collected in La Magdalena Coalfield.
([a]) Non-biological morphotaxa that could not be reallocated; ([b]) Quadrats comprise allochthonous assemblages.

Quadrat	Meterage (m)	Facies	N	*Polymorphopteris*	*Senftenbergia*	*Sphenopteris*	*Alethopteris*	*Callipteridium*	*Dicksonites*	*Eusphenopteris*	*Lescuropteris*	*Linopteris*	*Mixoneura*	*Neuropteris*	*Odontopteris*	*Pseudomariopteris*	*Cordaites*	Woody axes in DSC facies[a]
MG-75[b]	1203.9	LAC	290	38.75	2.28	0	0	9.12	0	2.28	0	4.56	0	9.12	0	2.28	0	0
MG-74[b]	1202.0	LAC	177	0	0	2.80	0	26.60	0	0	0	47.60	0	4.20	0	22.40	3	0
MG-73	1095.7	LCU	375	0	0	0	3.80	235.81	0	5.71	0	0	0	20.92	85.57	7.61	0	0
MG-72	1090.5	UCU	224	0	0	0	0	62.40	0	0	0	0	54.40	0	0	33.60	0	0
MG-71	1089.0	LCU	355	0	0	0	0	2.03	0	0	0	0	0	24.36	16.24	22.33	0	0
MG-70	1088.6	UCU	206	0	0	0	0	1.64	37.83	0	0	0	0	0	0	131.57	0	0
MG-69	1080.2	LCU	289	0	0	1.36	0	181.07	0	0	0	0	0	12.25	0	0	0	0
MG-68	1074.2	UCU	406	0	0	2.54	0	172.70	25.40	0	1.27	0	0	118.10	11.43	41.90	0	0
MG-67	1071.9	LCU	315	18.36	3.06	15.30	3.06	45.90	0	0	0	0	0	12.24	33.66	3.06	0	0
MG-78	1069.4	LCU	187	40.41	1.68	0	0	0	0	0	0	0	1.68	0	0	0	0	0
MG-77	1069.0	UCU	258	0	0	0	70.41	112.66	0	1.76	0	0	0	68.65	0	1.76	0	0
MG-66	1067.7	LCU	288	2.86	0	0	31.51	10.07	2.86	1.43	0	0	0	207.18	0	10.03	0	0
MG-65	1067.2	UCU	179	0	0	0	0	143.91	0	0	0	0	0	0	3.92	0	0	0
MG-64	1067.1	UCU	205	0	13.37	0	0	56.13	0	0	0	0	0	37.42	5.35	0	0	0
MG-54	1066.1	LCU	168	10.80	0	1.35	0	91.83	0	0	0	0	0	1.35	13.50	0	0	0
MG-63	1062.3	UCU	150	0	0	0	0	23.61	0	0	0	0	0	9.08	30.88	0	0	0
MG-62	1060.4	LCU	177	4.77	0	0	0	0	0	2.39	0	0	0	0	0	2.39	0	0
MG-61	1056.8	LCU	181	25.77	0	10.31	0	0	0	0	0	0	0	20.62	20.62	0	0	0
MG-60	1055.6	ADC	97	80.61	0	0	0	0	0	0	0	1.37	0	0	1.37	0	0	0
MG-59	1048.9	LCU	223	0	0	0	0	61.76	0	0	0	0	1.12	138.13	0	6.74	0	0
MG-58	1047.1	LCU	117	0	0	0	0	94.55	0	0	0	0	0	0	1.37	8.22	0	0
MG-56	1038.2	UCU	158	4.52	0	0	16.56	33.12	0	0	0	0	0	3.01	0	1.51	0	0
MG-57	1038.0	LCU	156	6.57	1.31	0	9.20	77.57	0	0	0	0	0	3.94	0	1.31	0	0
MG-53	1036.8	LCU	157	0	0	0	0	127.62	0	0	0	0	0	17.02	4.25	0	0	0
MG-52	1034.6	LCU	120	0	1.32	1.32	0	3.96	2.64	1.32	0	0	10.56	0	0	5.28	0	0
MG-55	1033.5	ADC	213	0	0	0	0	27.13	0	0	0	1.18	0	181.69	0	0	0	0
MG-51	1031.2	UCU	112	0	11.43	0	0	60.57	0	0	0	0	0	0	10.29	1.14	0	0
MG-50	1026.0	LCU	113	41.37	3.06	1.53	0	0	0	0	0	0	0	0	0	0	0	0
MG-49	1025.4	LCU	98	17.39	0	0	0	1.34	0	0	0	0	0	0	0	0	0	0
MG-48	1021.0	LCU	229	0	0	0	0	58.97	0	0	0	0	0	141.01	3.85	3.69	0	0
MG-47	1018.9	LCU	137	9.47	2.37	0	0	0	0	0	0	0	0	54.45	0	0	0	0
MG-76	1006.1	UCU	228	0	0	0	0	0	0	0	0	0	0	178.18	0	14.85	0	0
MG-40	837.8	UCU	39	0	1.22	2.44	0	0	0	0	0	0	1.22	0	1.22	0	0	0
MG-39	837.0	LCU	84	0	0	8.62	0	61.31	0	0	0	10.78	0	0	3.28	0	0	0
MG-38	836.8	UCU	41	0	0	0	0	1.03	0	0	0	34.97	0	0	0	0	0	0
MG-37	836.1	UCU	287	0	0	0	0	0	0	0	0	287	0	0	0	0	0	0
MG-46	835.1	LCU	193	9.33	0	5.60	0	6.13	0	0	0	1.87	0	51.11	0	0	0	0
MG-35.1	834.0	UCU	110	4.86	0	0	0	0	0	0	0	0	0	24.29	0	9.71	1	0
MG-35.2	834.0	UCU	80	7.75	0	0	0	1.29	0	0	0	0	0	25.82	0	5.16	0	0
MG-35.3	834.0	UCU	131	13.69	0	0	0	0	0	0	0	0	0	42.44	0	6.85	1	0
MG-35.4	834.0	UCU	81	13.54	8.62	0	0	1.23	0	0	0	0	0	1.23	0	0	0	0
MG-35.5	834.0	UCU	59	13.51	0	0	0	1.23	0	0	0	0	0	1.23	0	0	0	0
MG-36	832.7	UCU	168	0	0	0	0	0	0	0	0	1.27	0	161.73	0	0	5	0
MG-41	830.1	LCU	299	0	0	0	0	0	0	0	0	0	0	294	0	0	0	0
MG-43	827.4	UCU	70	1.02	0	0	3.21	31.05	0	0	0	5.08	1.07	3.21	0	0	0	0
MG-42	826.0	LCU	114	0	0	0	0	100.96	0	0	0	0	0	12.04	0	0	1	0
MG-44	822.0	LCU	105	5.82	0	3.49	0	2.45	0	0	0	5.82	0	59.95	0	9.32	0	0
MG-45	821.9	UCU	81	0	0	0	0	2.27	23.80	0	0	1.13	0	3.40	0	12.47	0	0
MG-34	816.9	LCU	104	9	0	0	0	52.71	2.57	0	0	0	0	0	0	0	0	0
MG-33	816.5	UCU	101	0	0	0	0	0	1.42	0	0	0	0	99.58	0	0	0	0
MG-31	354.8	LCU	18	0	0	0	0	0	0	0	0	0	0	2.40	0	0	0	0
MG-30	354.5	UCU	47	0	0	0	10.75	21.50	0	0	0	3.07	0	3.07	1.54	0	0	0
MG-29.1	340.9	LCU	76	26.57	0	1.21	0	0	0	0	0	3.62	0	2.42	4.83	2.42	0	0
MG-29.2	340.9	LCU	77	25.77	0	0	0	0	0	0	0	6.87	0	0	0	0	0	0
MG-32	324.5	UCU	63	7.14	0	7.14	0	0	0	0	0	0	0	0	3.57	0	0	0
MG-15[b]	236.0	DSC	11	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
MG-14[b]	232.7	DSC	76	0	0	0	0	1	0	0	0	0	0	0	0	0	1	34
MG-19.1	232.0	UCU	54	19.27	0	0	0	5.67	0	0	0	0	0	0	0	0	0	0
MG-19.2	232.0	UCU	64	17.95	0	0	0	20.20	0	0	0	0	0	0	0	0	0	0
MG-19.3	232.0	UCU	46	13.35	0	0	0	10.63	0	0	0	2.13	0	0	0	0	0	0
MG-19.4	232.0	UCU	103	3.56	0	0	0	4.88	0	0	0	1.19	0	0	31.74	0	0	0
MG-20.1	231.5	LCU	169	3.28	0	0	18.57	37.82	0	0	0	15.29	1.15	3.44	0	0	0	0
MG-20.2	231.5	LCU	248	18.62	0	2.19	2.23	29.88	0	0	0	28.48	0	1.15	32.18	0	0	0
MG-23.1	228.9	LCU	98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-23.2	228.9	LCU	118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-21.1	228.6	UCU	128	13.21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-21.2	228.6	UCU	115	5.80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-22	228.5	LCU	164	0	0	3.42	0	0	0	0	0	0	0	0	0	1.14	0	0
MG-24	228.1	LCU	17	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0
MG-18	219.2	ADC	103	0	0	0	0	3.22	0	0	0	0	0	3.22	0	3.22	0	0
MG-17[b]	218.2	DSC	37	0	0	0	0	0	0	0	0	0	0	0	0	0	2	25
MG-16.1[b]	214.7	DSC	85	0	0	0	0	0	0	0	0	0	0	0	0	0	2	41
MG-16.2[b]	214.7	DSC	31	0	0	0	0	0	0	0	0	0	0	0	0	0	1	18
MG-28.1	210.5	SPY	147	4.10	10.92	1.37	0	6.83	0	0	0	0	0	0	0	0	0	0
MG-28.2	210.5	SPY	93	1.26	10.05	0	0	46.50	0	0	0	1.26	0	0	0	0	0	0
MG-27	204.9	LCU	127	0	0	2.05	0	6.16	0	0	0	0	0	0	0	0	0	0
MG-26	198.7	LCU	122	0	0	0	0	0	0	0	0	0	0	0	0	2.68	0	0
MG-25	198.1	UCU	106	1.16	0	0	1.16	7.61	0	0	0	0	3.81	0	0	0	0	0
MG-11	113.1	LCU	52	1	0	1	0	0	0	0	0	0	0	0	0	15	0	0
MG-10	109.7	ABC	146	0	0	1.05	0	0	0	0	0	0	0	0	0	3.14	0	0
MG-9	100.8	UCU	71	0	0	0	15.28	6.11	3.06	0	0	0	0	0	0	1.53	0	0
MG-8	99.8	UCU	89	0	0	4.69	0	0	4.69	0	0	0	0	0	0	2.34	0	0
MG-13	99.5	SPY	133	0	0	0	2.86	25.77	1.43	0	0	0	0	0	0	2.86	1	0
MG-7	98.3	SPY	54	0	0	0	7.65	3.83	0	0	0	0	0	0	0	1.91	7	0
MG-5	84.7	UCU	128	0	0	0	0	0	0	0	0	0	0	2.93	0	0	0	0
MG-4	73.3	UCU	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MG-6	50.5	FPC	70	0	0	0	0	27.39	0	0	0	1.30	2.61	0	0	19.57	0	0
MG-3.1	49.5	FPC	94	0	0	0	4.94	40.72	0	0	0	0	0	0	0	4.94	0	0
MG-3.2	49.5	FPC	52	0	0	13.71	0	8.57	0	0	0	0	0	0	0	0	1	0
MG-3.3	49.5	FPC	117	0	0	0	1.46	18.96	0	0	0	0	2.92	0	0	24.79	2	0
MG-2	47.8	FPC	33	0	0	0	6.82	6.82	0	0	0	1.71	0	0	0	0	0	0
MG-1	47.3	SPY	94	0	0	0	7.50	22.50	1.25	0	0	1.25	0	0	0	0	7	0
MG-12	44.5	FPC	42	0	0	0	0	29.84	0	1.11	0	0	3.32	1.11	0	1.11	0	0
		TOTAL	**12553**	**542.19**	**70.70**	**94.51**	**216.97**	**2376.16**	**106.95**	**15.99**	**1.27**	**478.79**	**83.85**	**2062.67**	**320.65**	**451.82**	**36.00**	**120.00**

Table 13 (Part B). Redistributed abundance matrix comprising 27 biological genera in 93 quadrats collected in La Magdalena Coalfield.
(a) Non-biological morphotaxa that could not be reallocated; (b) Quadrats comprise allochthonous assemblages.

Asolanus camptotaenia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
"Lepidodendron" dissitum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lepidostrobophyllum majus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigillaria rugosa	0	0	0	0	0	0	0	0	0	0	3	8	4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0
Stigmaria ficoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyperites sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	11	6	0	0	0	0	0	0	0	0	12	45	3	3	66	78	20	11	11	30	0	0	5	0	0	0	0	0	0	0	0
Lepidostrobus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigillaria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	30	6	2	0	3	0	0	0	0	0	6	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Sigillariostrobus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	6	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syringodendron sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
decorticated lycopsid trunk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1	0	0	0	0	0	0	0	0	0
Annularia mucronata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	8	3	5	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Annularia sphenophylloides	0	19	2	17	6	24	2	11	0	0	1	5	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
Annularia stellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	0	0	61	86	7	2	0	5	0	10	0	0	0	0	0	0	0	0	3	0	2
Asterophyllites equisetiformis	0	3	0	3	0	0	6	0	30	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	3	2	0	0	0	0	0	0
Calamites sp. cf. *C. brongniartii*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parasphenophyllum crenulatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum alatifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum incisum	0	5	2	0	2	0	0	0	0	0	0	0	0	1	0	0	0	4	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Sphenophyllum longifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum oblongifolium	0	0	0	0	1	1	0	4	6	0	0	1	6	3	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	2	0	0	1	27	1
Annularia sp.	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	6	2	0	0	0	0	0
Calamites sp.	0	0	0	16	6	17	2	0	2	2	0	0	0	0	0	0	0	0	0	0	2	3	5	0	0	0	0	0	3	3	1	2	0	0	0	1	9	2	0	0	0	0	0	0	1	1	0
Macrostachys sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum sp.	0	0	0	0	0	0	0	0	4	1	1	7	0	5	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum axes	0	0	0	0	0	3	0	0	6	0	1	0	4	4	0	0	0	2	0	0	0	0	0	1	0	1	1	2	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0
Danaeites emersonii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplazites longifolius	0	0	0	0	2	2	0	0	0	0	0	0	1	0	0	0	0	0	17	10	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Lobatopteris corsinii	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobatopteris viannae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemejcopteris feminaeformis	0	10	4	0	0	4	0	6	36	4	4	4	4	58	10	4	9	88	1	0	0	0	0	1	0	51	0	1	1	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	1	0
Oligocarpia gutbierii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	12	33	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oligocarpia leptophylla	0	1	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	9	0	0	0	0	0	0	6	7	11	1	0	2	7	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1
Pecopteris ameromii	0	0	0	0	0	0	0	0	0	0	4	1	3	2	0	15	0	0	5	0	0	0	0	2	0	2	2	3	0	4	1	8	1	3	3	3	0	0	0	0	1	0	0	0	0	0	0
Pecopteris apicalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris arborescens	0	1	0	0	0	0	0	0	1	0	7	3	5	26	4	4	12	2	1	0	0	0	0	60	0	0	4	6	0	4	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0
Pecopteris candolleana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0
Pecopteris sp. cf. *P. longiphylla*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris daubreei	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris densifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris jongmansii	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Pecopteris melendezii	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris monyi	0	8	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polymorphopteris magdalenae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	2	6	3	0	0	0	0	0	0
Polymorphopteris polymorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	17	16	12	3	0	0	2	9	10	0	0	0	6	0	5
Senftenbergia elaverica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Senftenbergia grunerii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenopteris fayolii	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenopteris magdalenae	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sphenopteris mathetii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenopteris rossica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobatopteris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oligocarpia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris sp.	3	0	2	6	5	9	7	72	6	12	50	15	6	37	20	42	53	11	34	17	0	0	0	23	0	16	22	15	17	9	2	30	7	4	5	11	2	0	18	10	17	2	1	0	19	6	10
Polymorphopteris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	3	0	0	0	0	0	0	0	7	3	0	0	0	17	0	0	0	0	0	0	0	7	2	0	0	0	1	0	0
Senftenbergia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenopteris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	1	0	0	0	0	0	0	3	0	0	0	0	0	2	0	0	0	0	0	0	4	0	0	0	0	0	0	0	3
Caulopteris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0
Megaphyton sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Alethopteris bohemica	0	5	4	4	0	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alethopteris zeillerii	0	1	0	0	0	0	0	0	0	0	2	0	10	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0
Callipteridium pteridium	27	18	4	32	5	13	21	0	0	2	18	0	4	0	0	6	0	6	5	37	0	0	0	3	0	0	0	0	0	0	33	26	5	18	10	4	0	0	0	0	0	14	0	0	41	2	2
Dicksonites plukenetii	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	21	0
Eusphenopteris rotundiloba	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eusphenopteris talensii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lescuropteris genuina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linopteris gangamopteroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Linopteris neuropteroides	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	10	0	0	0	0	0	14	26	0	0	2	1	0	0	0	3	4	1	0	0	0	1	5
Mixoneura wagnerii	3	0	0	0	0	2	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neuropteris obtusa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neuropteris ovata	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	2	0	2	2	67	0	3	49
Odontopteris brardi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	26	0	0	2	4	0	1	0	0	0	0	0
Pseudomariopteris busquetii	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	11	2
Pseudomariopteris cordato-ovata	1	0	0	3	0	17	15	0	0	1	2	1	1	3	15	0	2	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Cyclopteris sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	1	0	0	0	0	0	0	0	3	0	0	3
Hexagonocarpus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonocarpus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petioles of *Callipteridium*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Artisia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cordaicladus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cordaites sp.	0	7	0	0	1	2	0	0	0	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Punctate axes	0	0	0	0	0	0	0	0	5	1	1	13	6	2	0	0	8	1	18	8	1	0	0	0	0	2	2	1	0	0	0	0	4	4	1	2	0	0	0	3	2	0	1	0	0	3	1
Striate axes	4	12	12	11	15	22	14	4	16	20	37	26	13	4	0	12	18	2	20	11	41	18	25	7	0	12	23	7	4	9	7	14	0	1	1	7	34	2	22	8	26	15	2	30	22	3	13
Small seeds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
QUADRAT	MG-12	MG-1	MG-2	MG-3.1	MG-3.2	MG-3.3	MG-6	MG-4	MG-5	MG-7	MG-13	MG-8	MG-9	MG-10	MG-11	MG-25	MG-26	MG-27	MG-28.1	MG-28.2	MG-16.1	MG-16.2	MG-17	MG-18	MG-24	MG-22	MG-21.1	MG-21.2	MG-23.1	MG-23.2	MG-20.1	MG-20.2	MG-19.1	MG-19.2	MG-19.3	MG-19.4	MG-14	MG-15	MG-32	MG-29.1	MG-29.2	MG-30	MG-31	MG-33	MG-34	MG-45	MG-44
TOTAL SPECIMENS (N)	42	94	33	94	52	117	70	100	128	54	133	89	71	146	52	106	122	127	147	93	85	31	37	103	17	164	128	115	98	118	169	248	54	64	46	103	76	11	63	76	77	47	18	101	104	81	105
FACIES	FPC	SPY	FPC	FPC	FPC	FPC	FPC	UCU	UCU	SPY	SPY	UCU	UCU	ABC	LCU	UCU	LCU	LCU	SPY	SPY	DSC	DSC	DSC	ADC	LCU	LCU	UCU	UCU	LCU	LCU	LCU	LCU	UCU	UCU	UCU	UCU	DSC	DSC	UCU	LCU	LCU	UCU	LCU	UCU	LCU	UCU	LCU
METERAGE (m)	44.5	47.3	47.8	49.5	49.5	49.5	50.5	73.3	84.7	98.3	99.5	99.8	100.8	109.7	113.1	198.1	198.7	204.9	210.5	210.5	214.7	214.7	218.2	219.2	228.1	228.5	228.6	228.6	228.9	228.9	231.5	231.5	232.0	232.0	232.0	232.0	232.7	236.0	324.5	340.9	340.9	354.5	354.8	816.5	816.9	821.9	822.0

Table 14 (Part A). Raw abundance matrix comprising 84 morphotaxa in 93 quadrats collected in La Magdalena Coalfield.

Asolanus camptotaenia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
"Lepidodendron" dissitum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidostrobophyllum majus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigillaria rugosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stigmaria ficoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyperites sp.	0	0	3	0	5	0	1	0	0	0	0	0	0	0	0	13	0	1	0	20	0	2	0	0	0	1	2	0	1	0	6	0	1	2	0	1	14	0	0	0	0	1	5	1	14	2
Lepidostrobus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigillaria sp.	0	0	2	0	0	0	0	0	0	1	0	4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Sigillariostrobus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syringodendron sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
decorticated lycopsid trunk	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Annularia mucronata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	28	1	0	0	0	0	0	0	0	0	0	0	0	0
Annularia sphenophylloides	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	7	0	5	0	5	38	11	4	11	1	1	0	4	6	0	41	0	10	8	3	0	0
Annularia stellata	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	1	2	3	0	0	20	2	0	0	0	0	0	23	0	4	4	14	0	0	0	0	0	0	11	2	0	0	0	0	0
Asterophyllites equisetiformis	0	0	0	0	11	4	7	12	14	18	0	0	0	7	0	0	2	0	3	0	0	2	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calamites sp. cf. *C. brongniartii*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parasphenophyllum crenulatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum alatifolium	0	0	0	0	0	0	0	0	0	30	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum incisum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	3	7
Sphenophyllum longifolium	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum oblongifolium	0	0	0	0	15	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
Annularia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calamites sp.	0	0	0	0	2	0	1	2	0	1	0	0	0	0	0	8	0	0	1	1	1	1	0	2	0	0	0	0	4	0	33	0	6	1	0	0	4	2	1	11	5	1	1	2	7	6
Macrostachys sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenophyllum sp.	0	0	0	0	0	0	1	0	1	2	0	0	0	2	16	0	0	0	6	2	0	12	0	0	3	1	0	0	4	0	2	1	1	0	1	0	0	1	1	0	0	2	1	2	16	5
Sphenophyllum axes	0	0	0	0	7	5	4	2	1	5	0	0	0	1	2	0	0	0	4	0	0	9	2	0	3	0	5	0	5	2	1	1	4	0	0	0	0	0	0	0	0	0	0	0	1	1
Danaeites emersonii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Diplazites longifolius	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	5	0	0	0	4	4	1	0	1	0	1	0	0	12	1	1	9	15
Lobatopteris corsinii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Lobatopteris viannae	0	0	0	0	0	0	1	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemejcopteris feminaeformis	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	3	8	0	0	4	0	0	0	0	1	2	2	1	1	4	2	0	0	0	0	0	0	0	15	1	8	0	1	11
Oligocarpia gutbierii	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0
Oligocarpia leptophylla	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pecopteris ameromii	0	0	0	0	0	2	0	3	1	0	0	0	0	3	2	1	0	9	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	2	7	0	39	24	4	0	0	5	1	0	9	18
Pecopteris apicalis	0	0	0	0	1	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	0	0	1	0	0	0
Pecopteris arborescens	0	0	0	0	0	0	2	4	1	0	0	0	0	0	0	0	0	15	2	3	0	1	0	0	0	0	0	0	0	29	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pecopteris candolleana	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	71	7	0	0	23
Pecopteris sp. cf. *P. longiphylla*	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris daubreei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Pecopteris densifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0
Pecopteris jongmansii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris melendezii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pecopteris monyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polymorphopteris magdalenae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polymorphopteris polymorpha	0	0	0	0	3	6	10	11	11	3	0	0	0	0	0	8	0	4	21	0	0	0	0	5	0	0	0	17	3	2	0	7	0	0	2	0	24	6	0	0	0	0	0	0	0	17
Senftenbergia elaverica	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	2	0	0	0	10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Senftenbergia grunerii	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	1	0	0	0	0	0	0	0	1
Sphenopteris fayolii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenopteris magdalenae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenopteris mathetii	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenopteris rossica	0	0	0	0	0	0	0	0	0	0	0	0	8	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobatopteris sp.	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Oligocarpia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Pecopteris sp.	0	20	0	0	17	20	25	17	14	23	0	0	0	8	5	35	12	28	22	1	0	0	1	32	56	8	1	6	4	72	3	15	4	11	6	1	29	25	13	17	0	44	5	3	2	21
Polymorphopteris sp.	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	9	6	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Senftenbergia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenopteris sp.	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	5	2	1	0	0	0	0	2	0
Caulopteris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megaphyton sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alethopteris bohemica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	2	0	0
Alethopteris zeillerii	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	11	0	0	0	0	0	0	0	0	0	0	40	0	1	0	0	0	0	0	0	0	0
Callipteridium pteridium	74	29	0	0	0	1	0	1	1	3	0	1	56	0	0	0	46	1	0	53	23	3	60	59	22	69	55	0	0	0	13	68	21	110	7	64	0	15	136	133	1	1	39	124	19	4
Dicksonites plukenetii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	20	0	23	0	0	0	0	0
Eusphenopteris rotundiloba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	3	0	1
Eusphenopteris talensii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lescuropteris genuina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Linopteris gangamopteroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linopteris neuropteroides	0	5	0	1	0	0	0	0	0	1	254	2	10	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	2
Mixoneura wagnerii	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	8	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	34	0	0	0
Neuropteris obtusa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	2	0	28	0	0	0	2	0	2	0	41	0	0	0	0	7	0	12	0	8	0	0
Neuropteris ovata	9	3	278	113	15	20	31	1	1	25	0	0	0	0	84	46	110	0	0	0	154	0	2	3	0	0	95	0	4	0	3	1	12	0	103	39	0	4	93	2	0	0	0	3	3	4
Odontopteris brardi	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	3	0	0	9	0	0	2	0	0	1	0	1	4	0	17	10	2	3	0	0	0	11	9	0	0	8	0	45	0	0
Pseudomariopteris busquetii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Pseudomariopteris cordato-ovata	0	0	0	0	6	4	5	0	0	0	0	0	0	0	7	0	3	0	0	1	0	3	0	1	1	6	2	0	0	1	0	0	0	0	7	1	0	1	33	0	80	9	21	4	16	1
Cyclopteris sp.	6	0	0	14	0	0	0	0	0	1	0	0	1	0	0	0	6	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hexagonocarpus sp.	0	0	0	0	0	0	0	0	0	0	5	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonocarpus sp.	0	2	0	0	0	0	0	0	0	4	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petioles of *Callipteridium*	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artisia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordaicladus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordaites sp.	1	0	0	5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Punctate axes	0	1	0	0	4	1	2	8	5	25	17	1	2	4	0	5	0	8	4	2	0	5	0	0	0	0	0	0	0	0	0	7	5	0	1	1	4	0	3	0	5	0	2	2	1	4
Striate axes	22	0	16	35	22	15	29	4	3	33	11	0	4	0	111	13	41	16	29	9	32	11	79	34	48	30	23	26	108	22	40	34	82	41	85	110	63	206	82	60	73	173	76	171	37	147
Small seeds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
QUADRAT	MG-42	MG-43	MG-41	MG-36	MG-35.1	MG-35.2	MG-35.3	MG-35.4	MG-35.5	MG-46	MG-37	MG-38	MG-39	MG-40	MG-76	MG-47	MG-48	MG-49	MG-50	MG-51	MG-55	MG-52	MG-53	MG-57	MG-56	MG-58	MG-59	MG-60	MG-61	MG-62	MG-63	MG-54	MG-64	MG-65	MG-66	MG-77	MG-78	MG-67	MG-68	MG-69	MG-70	MG-71	MG-72	MG-73	MG-74	MG-75
TOTAL SPECIMENS (N)	114	70	299	168	110	80	131	81	59	193	287	41	84	39	228	137	229	98	113	112	213	120	157	156	158	117	223	97	181	177	150	168	205	179	288	258	187	315	406	289	206	355	224	375	177	290
FACIES	LCU	UCU	LCU	UCU	UCU	UCU	UCU	UCU	UCU	LCU	UCU	UCU	LCU	UCU	UCU	LCU	LCU	LCU	LCU	UCU	ADC	LCU	LCU	LCU	UCU	LCU	LCU	ADC	LCU	LCU	UCU	LCU	UCU	UCU	LCU	UCU	LCU	LCU	UCU	LCU	UCU	LCU	UCU	LCU	LAC	LAC
METERAGE (m)	826.0	827.4	830.1	832.7	834.0	834.0	834.0	834.0	834.0	835.1	836.1	836.8	837.0	837.8	1006.1	1018.9	1021.0	1025.4	1026.0	1031.2	1033.5	1034.6	1036.8	1038.0	1038.2	1047.1	1048.9	1055.6	1056.8	1060.4	1062.3	1066.1	1067.1	1067.2	1067.7	1069.0	1069.4	1071.9	1074.2	1080.2	1088.6	1089.0	1090.5	1095.7	1202.0	1203.9

Table 14 (Part B). Raw abundance matrix comprising 84 morphotaxa in 93 quadrats collected in La Magdalena Coalfield.

Basin	**Lithostratigraphic unit(s)**	**Age**	**Dominant depositional setting**	**Lycopsids**	**Calamiteans**	**Sphenophylls**	**Tree ferns**	**Herbaceous ferns**	**Medullosalean pteridosperms**	**Non-medullosalean pteridosperms**	**Cordaitaleans**	**Reference(s)**
LATE PENNSYLVANIAN (Kasimovian and Gzhelian: 299.0 to 306.5 Ma)												
Surroca-Ogassa Coalfield, Spain	Unitat de Trànsit (Boundary Unit)	Stephanian C (late Late Pennsylvanian)	distal alluvial fan and braided river-plain	mires	well-drained floodplains; within and on flanks of braided channels	braided channel flanks	sluggish or abandoned braided channels	distal floodplains near mires	distal floodplains near mires	uncertain	distal alluvial fans	Martín-Closas & Martínez-Roig (2007)
Blanzy-Montceau Basin, France	Assise de Montceau (Great Seams Formation	Stephanian B (middle Late Pennsylvanian)	braided river plain and lacustrine deltas	mires	lacustrine deltas and shorelines	uncertain	well-drained channel belts	uncertain	poorly drained wetlands	uncertain	well-drained channel belts; basin margins	Charbonnier et al. (2008)
Graissessac-Lodève Basin, France	Graissessac shale and coal *(sensu* Martín-Closas & Galtier, 2005, fig. 1)	Stephanian B (middle Late Pennsylvanian)	braided river-plain	mires	exposed floodplains	exposed floodplains	distal floodplains near mires; late stages of mires	distal floodplains near mires; late stages of mires	distal floodplains near mires	distal floodplains near mires	channel flanks	Martín-Closas & Galtier (2005)
La Magdalena Coalfield, Spain	undivided	middle 'Saberian' to earliest Stephanian B (middle Late Pennsylvanian)	braided river-plain	mires; swamps	floodplain channel flanks; periphery of deeper ponds; swamps; distributary channel flanks	abandoned braided channels; ponds; swamps; lake margins	braided channel belt; disturbance-prone wetlands; periphery of deeper ponds; swamps; mires)	abandoned braided channels; swamps	floodplain channel flanks; less disturbed wetlands; periphery of shallower ponds	floodplain channel flanks; periphery of shallower ponds	uncertain	Bashforth et al. (in press); Chapter 3
MIDDLE PENNSYLVANIAN (Moscovian: 306.5 to 311.7 Ma)												
'post-Leonian' Basin, Spain	Ocejo Group and Tejerina Formation	early Cantabrian (latest Middle Pennsylvanian)	paleovalley and alluvial fans	mires; swampy lake margins; poorly drained floodplains	active sheetflood surfaces	poorly drained floodplains; mires; abandoned sheetflood surfaces; lake margins	poorly drained floodplains; abandoned sheetflood deposits	abandoned sheetflood surfaces	paleovalley margins; channel flanks; well-drained floodplains	poorly drained floodplains; mires	well-drained floodplains	Iwaniw (1985)
Central and Western Bohemian Basin, Czech Republic	Nýřany Member, Kladno Formation	late Asturian to middle(?) Cantabrian (latest Middle Pennsylvanian)	braided river-plain	mires; swamps	lake margins; abandoned braided channels	abandoned braided channels; floodplains; marshes	abandoned braided channels; floodplains; mires	abandoned braided channels	braided channel flanks; floodplain channel flanks	abandoned braided channels	braided channel flanks	Bashforth et al. (in prep.); Chapter 2
Bay St. George Basin, Newfoundland, Canada	Blanche Brook formation *(sensu* Bashforth, 2005)	late Bolsovian (middle Middle Pennsylvanian)	paleovalley traversed by coarse-grained meandering rivers	swamps; poorly drained floodplains; levees	point bars; levees; floodplains	levees; poorly drained floodplains	levees; swamps	uncertain	levees; floodplains	uncertain	paleovalley margins; levees; ponds above drowned swamps	Bashforth (2005)
Intrasudetic Basin, Czech Republic	Lampertice Member, Žacléř Formation	early Duckmantian (lowermost Middle Pennsylvanian)	paleovalley traversed by braided to low-sinuosity meandering rivers	mires; poorly drained floodplains	well-drained floodplains; channel flanks	mires; poorly drained floodplains	poorly drained floodplains; mires	well-drained floodplains; channel flanks; mires	channel flanks; paleovalley margins and slopes; well-drained floodplains	channel flanks; poorly drained floodplains	paleovalley margins and slopes	Libertín et al. (2009b)
EARLY PENNSYLVANIAN (Bashkirian: 311.7 to 318.1 Ma)												
Cumberland Basin, New Brunswick, Canada	Boss Point and Tynemouth Creek formations	Yeodonian(?) to Duckmantian(?) (middle Early Pennsylvanian)	seasonally dry fluvial megafan	poorly drained floodplain depressions	levees; floodplains	uncertain	poorly drained floodplain depressions	poorly drained floodplain depressions	poorly drained floodplain depressions	uncertain	basin margins and slopes; channel flanks; well-drained floodplains	Falcon-Lang (2006a); unpublished data herein

Table 23. Summary of basins/coalfields dominated by coarse-grained, siliciclastic strata laid down in high-energy environments on basin margins. Interpreted habitat or landform preferences(s) given for each major plant group based on landscape reconstructions provided in references.