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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.

1. 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 and 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 (10^5 years) climate rhythms linked to orbital cycles (Falcon-Lang, 2004; 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 and Phillips, 1996; DiMichele et al., 2001). Current debate is centered on whether this changeover was broadly coincident with a major climate shift (Phillips and Peppers, 1984; DiMichele et al., 2009), or if reorganization was diachronous and related to regional tectonism and increased sediment production (Cleal and Thomas, 2005).

This paper presents a paleoecological study of the Late Pennsylvanian (middle to late Kasimovian, ≈305 Ma) La Magdalena Coalfield

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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., 2009; Opluštil et al., 2009). Thus, the method offers a new way to reconstruct the structure of ancient vegetation using quantitative studies of plant assemblages in vertical succession.

2. 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. 1A; 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 may be tectonic and erosional remnants of a large, 'post-Asturian' foreland basin that drained northwards and eastwards toward the western end of the Paleo-Tethys Ocean (R.H. Wagner, unpublished data), with diachronous onlapping of basement rocks explained by progressive basin expansion (Evers, 1967; Wagner, 1970; Wagner and Winkler Prins, 1985). This scenario is supported by the occurrence of rare horizons with brackish faunas in the Sabero, Ciñera-Matallana, and La Magdalena coalfields (Fig. 1A), implying periodic marine connections (Eagar and Weir, 1971; Knight, 1971; Iwaniw and 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 and Artieda, 1970; Knight in Wagner, 1971b; Knight, 1974, 1983), 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. 1B, 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 and 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).
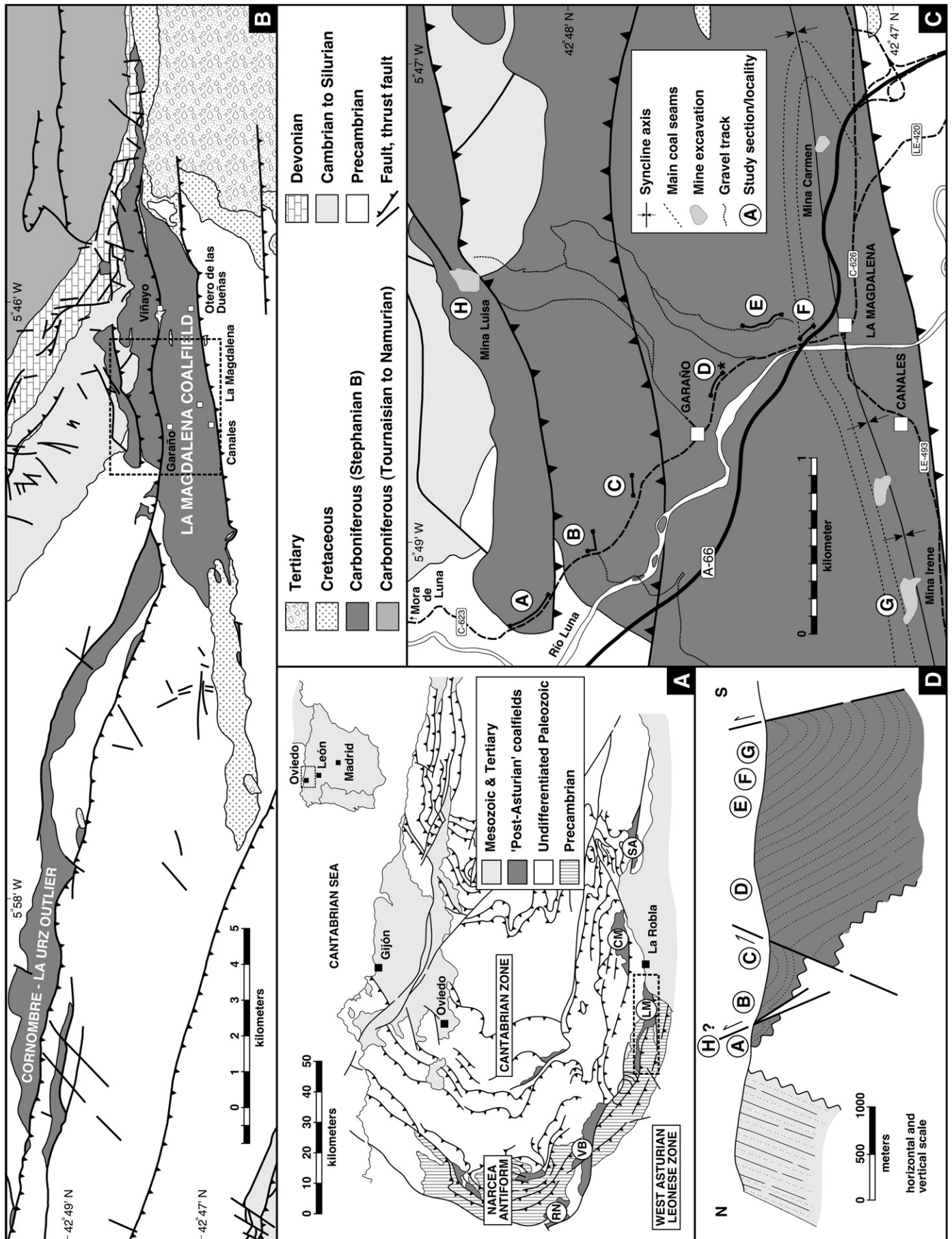
The coalfield is subdivided into an eastern part, the focus of this study (La Robla 129/13-8 map sheet; Leyva et al., 1984), and a western part comprising the Cornombre–La Urz outlier (Riello 128/12-8 map sheet; Martín Parra et al., 1989; Fig. 1B). In La Magdalena Coalfield, basin-fill rests with angular unconformity atop lower Paleozoic strata of the Cantabrian Zone in the east and Precambrian strata of the Narcea Antiform in the west (Fig. 1A, B; Colmenero et al., 2002). It is bound by a steeply dipping thrust fault to the south (Fig. 1D; Leyva et al., 1984), and strata are folded into an E–W-oriented syncline whose axis lies close to the southern faulted margin (Fig. 1C, 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. Biostratigraphy and age

Determining the age of La Magdalena Coalfield and its correlation with the ratified IUGS timescale (Davydov et al., 2004; Heckel and Clayton, 2006) is challenging because stratigraphic subdivision of the middle and late Stephanian is in a state of flux. The reader is referred to Wagner (1998) and Wagner and Martínez-García (1998, p. 103) for summaries of the problems. To précis, the Stephanian B Substage, as defined by the IUGS, can be divided into two units (Fig. 2). The older unit correlates with strata in the Carmaux Basin of the French Massif Central, and has been assigned to a proposed 'Saberian substage' equivalent to the *Alethopteris zeilleri* Biozone of Wagner (1984; unpublished data). The younger unit represents the Stephanian B Substage (*sensu stricto*) as conceptualized in the St. Étienne Basin of the Massif Central, and is equivalent to the *Sphenophyllum angustifolium* Biozone.

Within this stratigraphic context, Castro (2005a) 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. 2). 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, 2008). 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. 2). Both biostratigraphic and radiometric data allow <1 Ma for the interval encompassing the middle *A. zeilleri* to lower *S. angustifolium* biozones (Cleal, 2008), inferring very rapid accrual 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, 2005a), with little evidence for evolutionary change in the flora.

Series	Global Stages	North America	Western Europe	Saint-Étienne Basin	Carmaux Basin	La Magdalena Coalfield	Biozones
Upper Pennsylvanian	Gzhelian	Virgilian	Stephanian C (= lower Autunian)	Assise d' Avaize			*Autunia conferta*
	—303.9 ± 0.9 Ma—	—303.0 Ma—	Stephanian B (*sensu stricto, sensu* St.-Étienne)	Assise de St.-Étienne		?	*Sphenophyllum angustifolium*
	Kasimovian	Missourian	? 'Saberian' (= Stephanian B *sensu* Carmaux)		Zone de Tronquié	STUDY SITE	*Alethopteris zeillerii*
			Barruelian	Assise de Rive de Gier	Zone de Lentin	?	*Lobatopteris lamuriana*
	—306.5 ± 1.0 Ma—	—305.4 Ma—	Cantabrian				*Odontopteris cantabrica*
Middle Pennsylvanian	Moscovian	Desmoinesian					

Fig. 2. 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 (2005a). Vertical dimension not uniform as to time scale.

4. Depositional facies

Sedimentary facies were analyzed to provide depositional context to the megafloral assemblages studied. An oblique transverse section through the coalfield, exposed along Highway C-623 (Fig. 1C), was focused on. 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 a cm-scale and tied to the reference section of Heward (1978a, fig. 13; Fig. 3). In addition, a m-scale reconnaissance section was measured between Sections D and E, and an inaccessible 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 1). Characteristics of the dominant facies associations (FA 2 and FA 3) are illustrated in Fig. 4, but the complete set of logs are available online [Fig. S1A to E].

4.1. Facies Association 1 (FA 1): Debris flow deposits

4.1.1. 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. 1C, 3; Table 1). It comprises red, stacked breccia units (DFB facies) that rest with angular unconformity atop reddened Precambrian metasediments, the source of virtually all clasts. Strata 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.

4.1.2. 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 and 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 and 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. 1B), implying that a long interval of weathering predated emplacement of debris flow deposits.

4.2. Facies Association 2 (FA 2): Braided channel belt

4.2.1. Observations

This association is restricted to the lower half of the succession (Sections A, C, D; Figs. 1C, 3), and makes up ≈12% of the basin-fill (≈173 m aggregate thickness; Table 1). It comprises stacked, composite units of conglomerate and sandstone, intercalated with thin, fine-grained intervals (Fig. 4). 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 (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 (either 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).
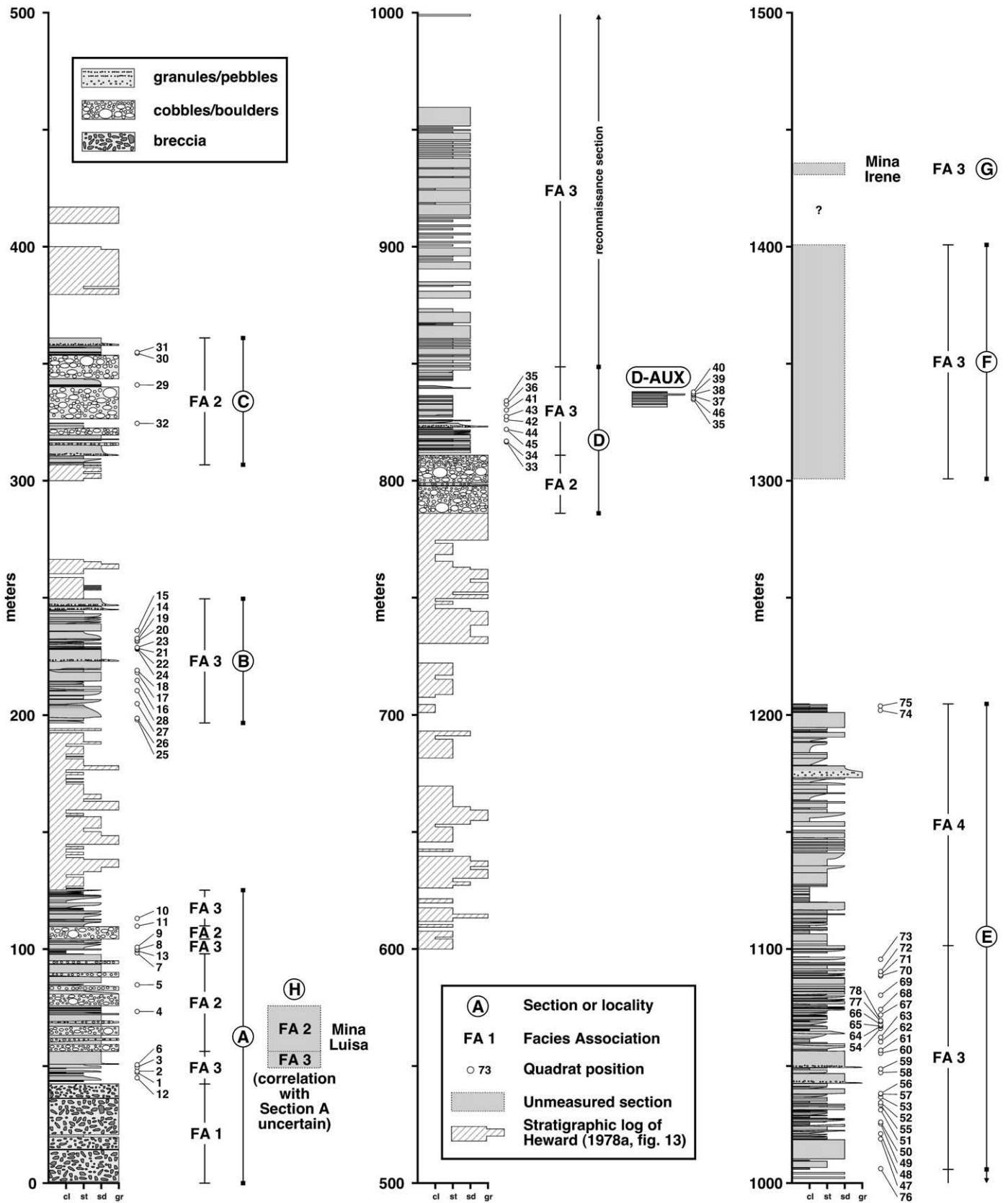
Fig. 3. Stratigraphic log through La Magdalena Coalfield, showing the vertical distribution of Sections A to E (measured at cm-scale), unmeasured localities (F to H), Facies Associations (FA 1 to 4), and quadrats (MG-1 to 78). Gaps in log partially filled by log of Heward (1978a, fig. 13), after correlation 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 Fig. 1 for position of study sections and localities.

Table 1

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.

Depositional facies	Description	Interpretation	Megafloral assemblages	Dominant taphonomic mode	Quadrats; total quadrats [n]	Total bedding plane area sampled (m²)
Facies Association 1 (FA 1): Debris flow deposits — 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 flow deposits 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][a, b]	32.00[c]
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[d]
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	

Table 1 (continued)

Depositional facies	Description	Interpretation	Megafloral assemblages	Dominant taphonomic mode	Quadrats; total quadrats [n]	Total bedding plane area sampled (m^2)
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]	34.50[e]

[a] Quadrats of marginal wetlands (FA 3): MG-1, 2, 3.1 to 3.3, 6, 12 (n = 7).
[b] Quadrats of interfluve wetlands (FA 3) adjacent to braided channel belt: MG-7 to 9, 11, 13 (n = 5).
[c] 19.5 m^2 without DSC facies.
[d] Each quadrat ≈ 2.5 m^2.
[e] 22.00 m^2 without DSC 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. 1C, 3), 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). Mega-floral assemblages abound in the LCU and UCU facies, which typify and are better developed in FA 3 (Section 4.3).

4.2.2. 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. 1C, 3), 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.

4.3. Facies Association 3 (FA 3): Marginal and interfluve wetlands

4.3.1. Observations

This association (Sections A, B, D, D-AUX, E; Figs. 1C, 3) makes up ≈78% of the basin-fill (≈1170 m aggregate thickness; Table 1).

The dominant motif is lensoid, coarsening-upward units, 0.2 to 4.9 m thick (mean = 0.9 m, n = 128) and up to 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. 4). 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 in-dividual 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. 1C, 3) 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
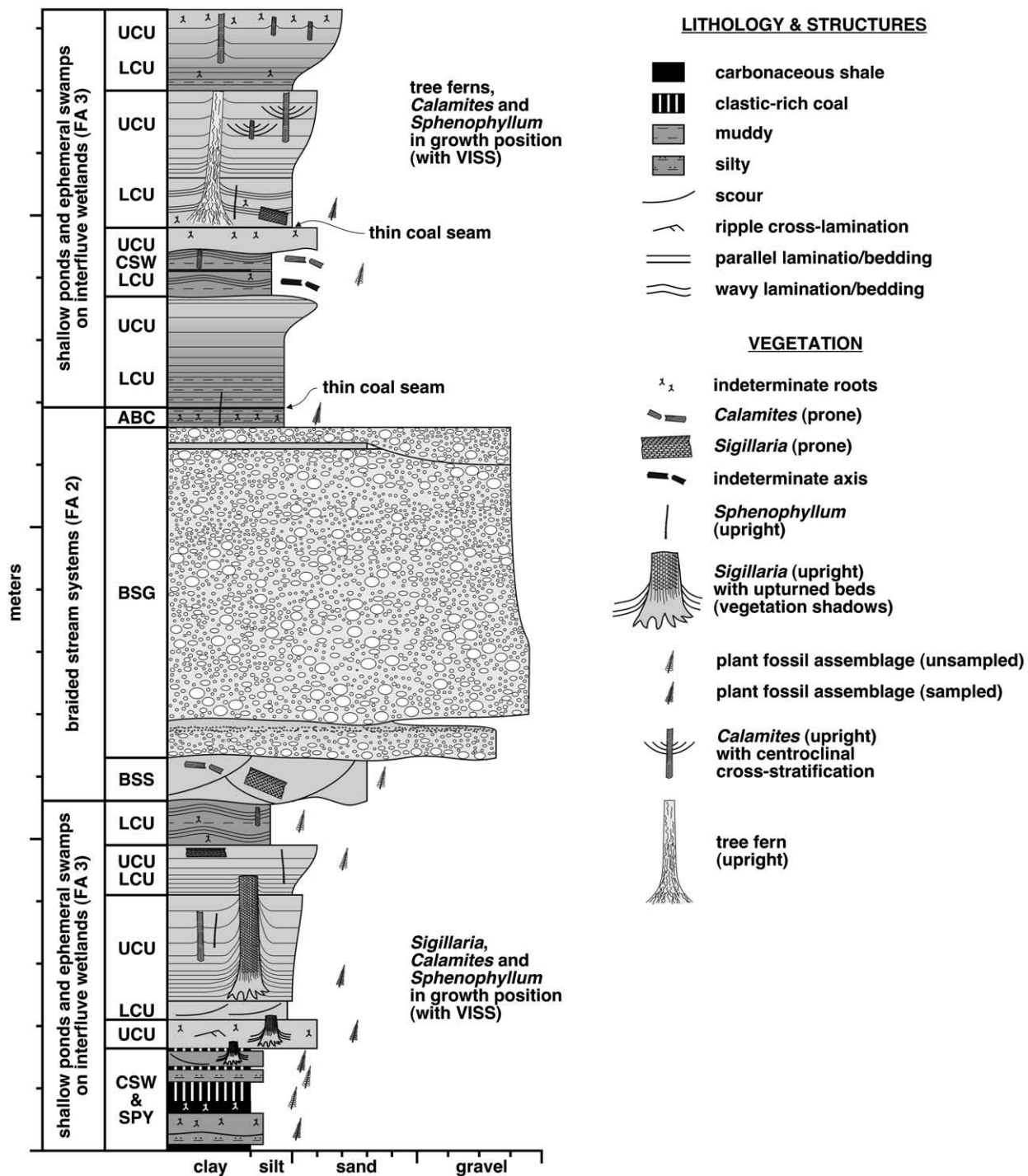
Fig. 4. Representative stratigraphic section through braided channel belt (FA 2) and interfluve wetland (FA 3) deposits (98.0 to 116.3 m above base of section). These two facies associations comprise ≈ 90% of the basin-fill. Upright axes, although abundant in this section, are rare in the succession. See Table 1 for abbreviations of depositional facies.

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. 3).

4.3.2. Interpretation

The profusion 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 and 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. 1C, 3), 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 and Dulong, 2003), although increased accommodation due to subsidence (Pashin, 1998) or inland ponding of freshwater during marine transgression (Kosters and 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 and Gibling, 1999).

4.4. Facies Association 4 (FA 4): Large lakes

4.4.1. Observations

This association is only found in the upper half of the succession (Section E; Figs. 1C, 3), and makes up $\approx$ 7% of the basin-fill ($\approx$ 103 m aggregate thickness; Table 1). 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.

4.4.2. 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.

4.5. Climate

In the modern tropics, peat accumulation and sediment supply are closely linked to the amount and seasonality of rainfall (Cecil, 1990; Cecil and 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 and Ober, 2005) in a uniformly poorly drained environment, promoting the preservation of buried plant remains (DiMichele and Gastaldo, 2008; Gastaldo and Demko, in press). Vertisols, which develop under seasonally variable conditions (Wilding and Tessier, 1988; Driese and Ober, 2005), are conspicuously absent. The degree of seasonality and general climate of La Magdalena Coalfield remains an open question.

4.6. 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
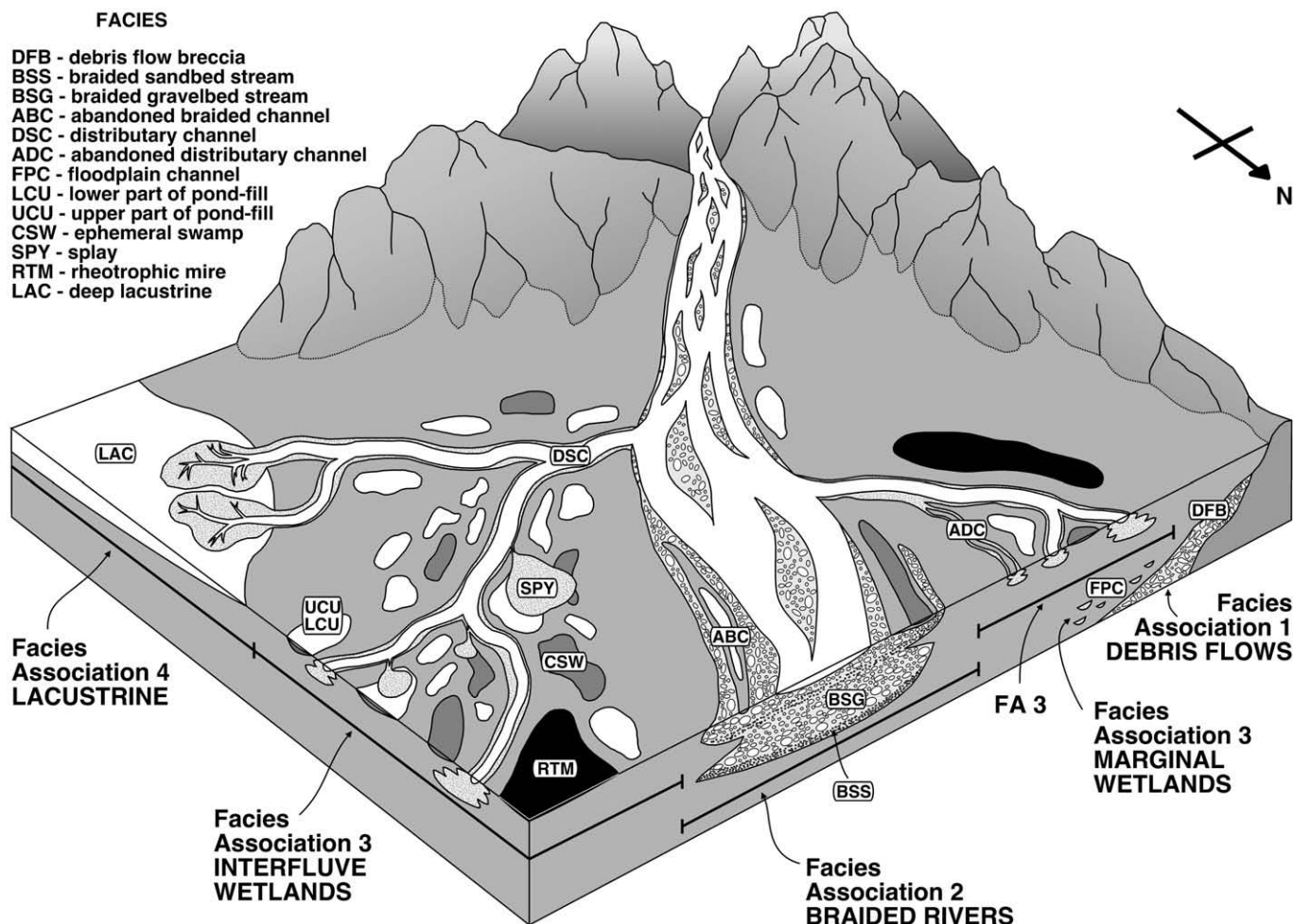
FACIES

DFB - debris flow breccia
BSS - braided sandbed stream
BSG - braided gravelbed stream
ABC - abandoned braided channel
DSC - distributary channel
ADC - abandoned distributary channel
FPC - floodplain channel
LCU - lower part of pond-fill
UCU - upper part of pond-fill
CSW - ephemeral swamp
SPY - splay
RTM - rheotrophic mire
LAC - deep lacustrine

Fig. 5. Paleoenvironmental reconstruction illustrating the 13 depositional facies and 4 facies associations in La Magdalena Coalfield. See Table 1 for depositional facies. No spatial scale implied.

ongoing subsidence, which captured major north-flowing rivers in a broad basin or paleovalley 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. 5) 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 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.

5. 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.

5.1. 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 50×50 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 1). 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. 3) were analyzed, with 93 quadrats sampled due to replicates made along-strike at nine horizons (Table 1). The meterage of each quadrat was recorded on the cm-scale stratigraphic log, and nine depositional facies were sampled (Table 1). In each quadrat, every plant fragment was identified using Castro (2005a,b) and counted as a single individual. Most remains could be identified to species level, although poorly preserved examples or those lacking diagnostic features were recorded at the genus rank. A small representative collection was made to verify field identifications. A total of 12,553 plant fragments were counted, with quadrats containing 11 to 406 specimens (mean = 135). Fig. 6 shows the composition of all quadrats arranged in stratigraphic order, with plants segregated into the five major clades (lycopsids, sphenopsids, ferns, pteridosperms, cordaitaleans).

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.

5.2. Data matrices and general dominance-diversity characteristics

Of the 84 morphotaxa recorded (Table 2), 80 could either be assigned to the morphospecific ($n = 55$) or morphogeneric ($n = 25$) 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
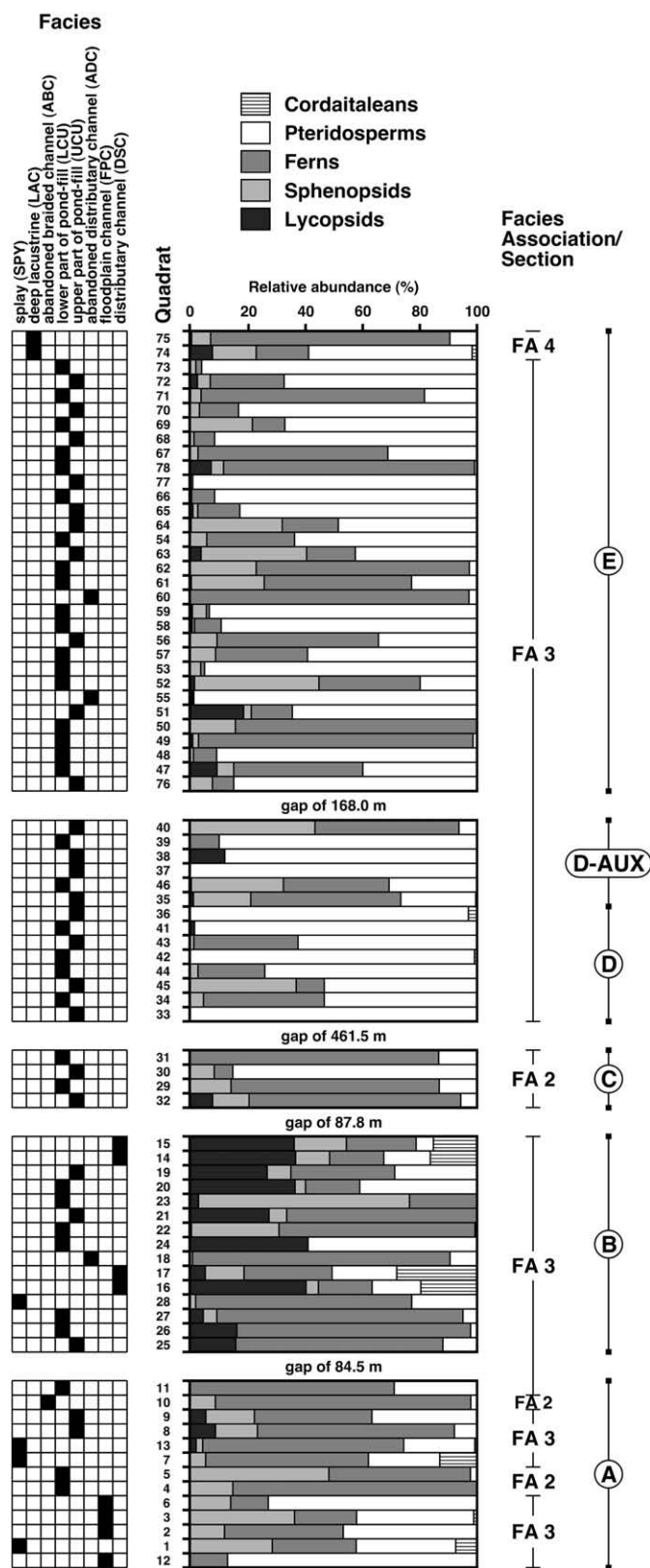
Fig. 6. Vertical changes in proportional distribution of five main plant clades (lycopsids, sphenopsids, ferns, pteridosperms, cordaitaleans) through La Magdalena Coalfield. Depositional facies (see Table 1) denoted for each quadrat.

formed almost all of the remaining three morphotaxa (2932 or 23.4%, and 219 or 1.7%, respectively), with two seeds of unknown affinity comprising the third morphotaxon. Prior to analyses, all morphotaxa

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 S1], 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 morphotaxon 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 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; Table S2], from which all subsequent analyses were performed, and raw abundance matrix [Table S3] are available online.

When the 27 biological genera are ranked by relative abundance (Table 3), *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%) are rare (Table 4). However, when species diversity is analyzed, ferns are richest (25 of 52 species or 48.1%), pteridosperms (28.8%) and sphenopsids (17.3%) are less rich, and lycopsids (5.8%) are 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.

5.3. Comparison with analyses of Castro (2005a)

Castro (2005a, table 2) recorded 140 morphotaxa based on a collection of 10,530 plant fragments. When proportionately redistributed, the population contains 40 biological genera and 90 biological species (Tables 3, 4). 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 3). 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 3). *Pecopteris* and *Callipteridium* are the dominant biological genera in both samples, 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 dissimilarity exists. *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 S1], whereas Castro did not. Castro also noted a much higher proportion of *Sphenophyllum* (8.4%, third rank) than this study 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. 7). The difference is likely related to collection protocols. As Castro's was a taxonomic study, rare taxa probably 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 her 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.

6. 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.

6.1. 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 and DiMichele, 1995; DiMichele and 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 and Staub, 1999). This removes the potential bias of taphonomic time-averaging (Wing and 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., 1989). 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., 1989). Preservation only occurs 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 and Demko, in press).

6.2. 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 1, 5). 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 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 prograded and filled the ponds. Rapid burial promoted preservation, and megafloral assemblages are interpreted as near-autochthonous, recording vegetation growing on exposed

Table 2
List of 84 morphotaxa recorded in La Magdalena Coalfield, segregated by clade.

Plant group	Number of specimens (*n*)
Lycopsids	*558*
Morphospecies	
Asolanus camptotaenia	4
"*Lepidodendron*" *dissitum*	12
Lepidostrobophyllum majus	2
Sigillaria rugosa	30
Stigmaria ficoides	4
Morphogenera	
Cyperites sp.	400
Lepidostrobus sp.	1
Sigillaria sp.	62
Sigillariostrobus sp.	15
Syringodendron sp.	9
Assignable to group	
Decorticated lycopsid axes	19
Sphenopsids	*1341*
Morphospecies	
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
Morphogenera	
Annularia sp.	25
Calamites sp.	182
Macrostachys sp.	4
Sphenophyllum sp.	131
Sphenophyllum axes	95
Ferns	*3031*
Morphospecies	
Danaeites emersonii	1
Diplazites longifolius	99
Lobatopteris corsinii	4
Lobatopteris viannae	14
Nemejcopteris feminaeformis	380
Oligocarpia gutbieri	73
Oligocarpia leptophylla	58
Pecopteris a[meromii	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 gruneri	11
Sphenopteris fayolii	2
Sphenopteris magdalenae	9
Sphenopteris mathetii	1
Sphenopteris rossica	9
Morphogenera	
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*
Morphospecies	
Alethopteris bohemica	60

Table 2 (*continued*)

Plant group	Number of specimens (*n*)
Pteridosperms	*4434*
Morphospecies	
Alethopteris zeilleri	84
Callipteridium pteridium	1668
Dicksonites plueckenetii	77
Eusphenopteris rotundiloba	9
Eusphenopteris talensii	1
Lescuropteris genuina	1
Linopteris gangamopteroides	1
Linopteris neuropteroides	382
Mixoneura wagneri	57
Neuropteris obtusa	108
Neuropteris ovata	1396
Odontopteris brardii	190
Pseudomariopteris busquetii	24
Pseudomariopteris cordato-ovata	284
Morphogenera	
Cyclopteris sp.	43
Hexagonocarpus sp.	37
Trigonocarpus sp.	9
Petioles of *Callipteridium*	3
Cordaitaleans	*36*
Morphogenera	
Artisia sp.	6
Cordaicladus sp.	1
Cordaites sp.	29
Uncertain affinity	*3153*
Punctate axes	219
Striate axes	2932
Small seeds	2
Total	12,553

substrates around ponds that were essentially filled (meters to tens of meters transport distance). Although not common, 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 as 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.

6.3. 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 5) to measure the distribution of biological species in each patch. The indices, combined with qualitative and quantitative inspection of taxonomic data, reveal important

Table 3

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 ($N = 12,553$) and Castro (2005a, Table 2, $N = 10,530$).

This study		Castro (2005a)	
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	7.30
Sigillaria	4.18	Polymorphopteris	5.46
Nemejcopteris	3.89	Odontopteris	5.11
Linopteris	3.81	Alethopteris	4.69
Pseudomariopteris	3.60	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	1.40	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	0.40
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
		Lescuropteris	0.07
Non-biological genera		Dicranophyllum[a]	0.07
Woody axes in DSC facies	0.96	Ulvopteris[a]	0.07
Calamites	0.38	Remia[a]	0.05
Caulopteris[a]	0.06	Omphalophloios(?)[a]	0.05
Megaphyton[a]	0.01	Renaultia[a]	0.03
Total	99.98	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

[a] Unique to sample population.

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. 8). 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. 8), 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 6. Pteridosperms are also the primary component of some medium- and high-diversity quadrats, but these assemblages may record taphonomic mixing of several communities.

In fern-dominated assemblages (Fig. 8), 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. 8), 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

Table 4

Relative abundances of five plant groups in La Magdalena Coalfield, comparing sample populations from this study and Castro (2005a, Table 2).

Plant group	This study				Castro (2005a)[a]			
	Relative abundance (%)	Relative generic diversity (%)[b]	Relative specific diversity (%)	Biological genera (species)	Relative abundance (%)	Relative generic diversity (%)	Relative specific diversity (%)	Biological genera (species)
Lycopsids	4.44	11.11	5.77	3 (3)	0.60	13.89	5.81	5 (5)
Sphenopsids	10.68	14.81	17.31	4[c] (9)	20.63	11.11	10.46	4 (9)
Ferns	35.23[d]	33.33	48.08	9[e] (25)	38.98	36.11	60.46	13 (52)
Pteridosperms	49.03[d]	37.04	28.85	10 (15)	39.65	36.11	23.26	13 (20)
Cordaitaleans	0.60[d]	3.70	–	1 (–)	0.14	2.78	–	1 (–)
Total	99.98	99.99	100.01	27 (52)	100.00	100.00	99.99	36 (86)

[a] To remain consistent with Castro (2005a), Taeniopteris, Dicranophyllum, Ulvopteris, and Desmopteris removed from data set (combining for only 0.34% of sample population) because group affinity uncertain.
[b] Values ignore woody axes from DSC facies.
[c] Does not include Calamites.
[d] Values include 1/3 of woody axes from DSC facies (i.e., 0.32% each; see Table 3).
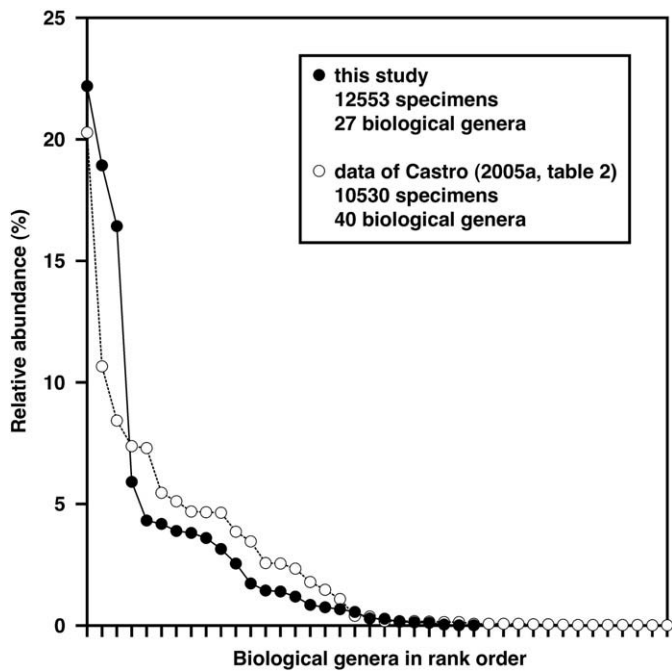[e] Does not include Caulopteris or Megaphyton.

Fig. 7. Relative abundance distribution curves, with biological genera arranged in rank order, comparing sample populations in this study and Castro (2005a, Table 2). The latter overestimates the abundance of rare taxa and underestimates the abundance of common taxa.

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.

6.4. 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 lycop-

sids. To provide more conclusive evidence for patchiness, particularly among the pteridosperms, some key, very low-diversity assemblages (Table 6) 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 m²) was obtained from Section D along Highway C-623 (Figs. 1C, 3), and a large (2.5 m high × 11.0 m wide; 27.5 m²) 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 (Table 6), 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 and Broushmiche, 1985; Zodrow and 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 in Table 6, 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 m²) were obtained from Section D, and two replicates (MG-35.4, 35.5; 0.50 m²) from Section D-AUX ≈14 m along-strike (Figs. 1C, 3, 9). 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 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

Table 5
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. S = number of biological species in quadrat; $H = -\sum p_i \ln p_i$, where $p_i = n_i/N$ (proportion of ith species), n_i (number of observations of ith 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	12,553
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 (m²)	0.25	≈12.50[a]	0.75	1.50	9.00	8.75	1.25	0.50	34.50[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

[a] Each quadrat ≈2.5 m².
[b] 22.00 m² without DSC facies.
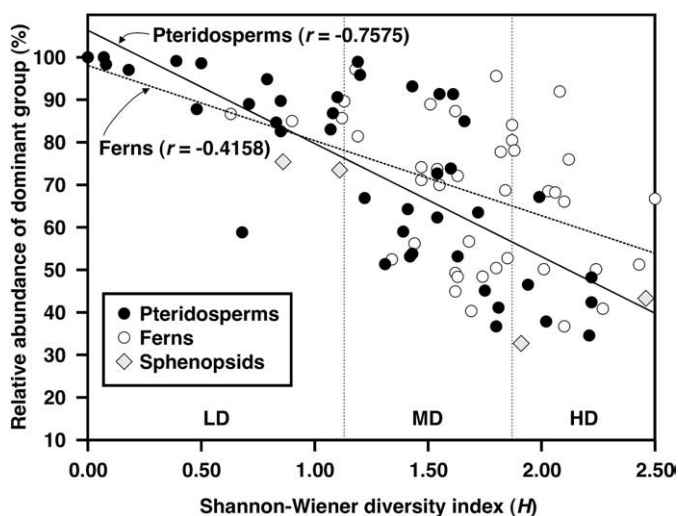
Fig. 8. Scatterplot showing relative abundance of dominant plant group in 86 (par)autochthonous quadrats versus Shannon–Wiener diversity index (H). Linear correlation coefficients (r) given for pteridosperms and ferns. Low diversity (LD): 0.00 to 1.13 (<25th percentile); medium diversity (MD): 1.13 to 1.87; high diversity (HD): 1.87 to 2.50 (>75th percentile).

in all five replicates, the radius of the pteridosperm-dominated patch would have been >15 m.

7. 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.

7.1. 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 morphogenera (*Calamites*, *Caulopteris*, *Megaphyton*) were removed from the redistributed abundance matrix [Table S2]. Quadrats were divided into four groups (Table 1), 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 and 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 and Harper, 2006). The ordination was run in two dimensions using PAST (v. 1.86b; Hammer et al., 2001).

The NMDS ordination plot (Fig. 10A) 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 PERMANOVAs between all pairs of groups in a post-hoc test indicate that the two groups cannot 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. 10B; ferns: Fig. 10C; pteridosperms: Fig. 10D).

7.1.1. 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. 10D). Quadrats co-dominated by sphenopsids (particularly *Annularia*; Fig. 10B) and ferns (*Pecopteris*; Fig. 10C) plot closer to the center of the point cloud. Based on these

Table 6
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. 3, 6 for position). N is number of counts in quadrat; H is Shannon–Wiener diversity index.

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 plueckenetii* (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%)

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.

7.1.2. 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. 10C). 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. 10B). MG-30 deviates from this pattern, being dominated by *Callipteridium* (Fig. 10D), indicating that pteridosperms were not entirely excluded from disturbed channel belts.

7.1.3. 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. 10A). 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. 10C), together with significant *Nemejcopteris* (Fig. 10C) and *Pseudomariopteris* (Fig. 10D) 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. 10D).

7.1.4. 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. 10D). 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. 10D); 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. 10C), *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. 10B), although the latter is much more common here than elsewhere.

7.2. Summary of ecological gradients

The NMDS analysis reveals clear ecological gradients in La Magdalena Coalfield. On the whole, marginal wetlands were
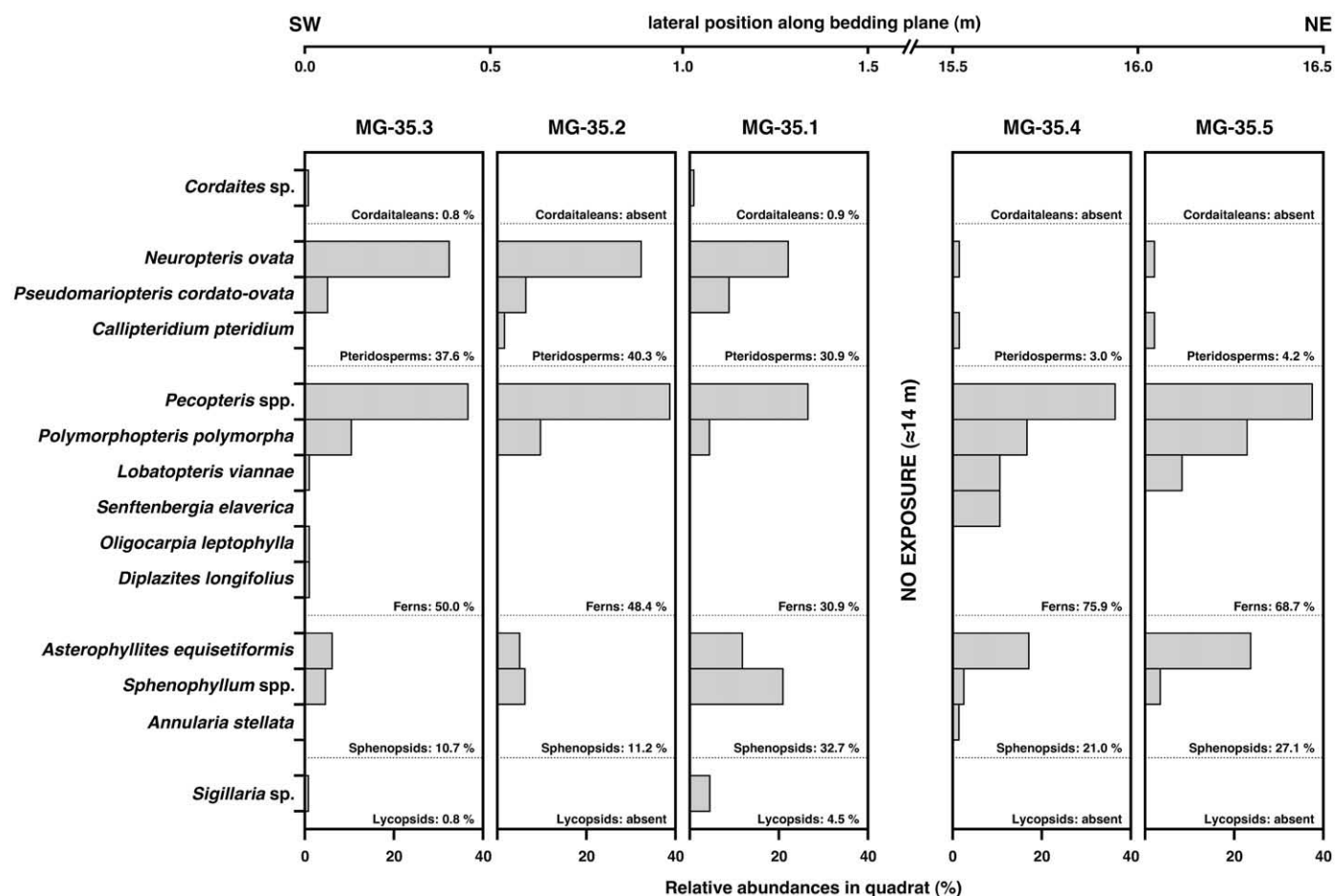

Fig. 9. Schematic diagram showing relative abundances of biological taxa in five replicates taken along single bedding plane (MG-35) in Section D and laterally correlative Section D-AUX (at 834.0 m above base of succession).

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 of 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.

8. Paleoecological synthesis

Drawing together results from Sections 4 to 7, 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.

8.1. Communities on marginal wetlands (FA 3)

The vegetation of marginal wetlands, which developed alongside the basin margin, differed from that of interfluve wetlands higher in the succession. In particular, they 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
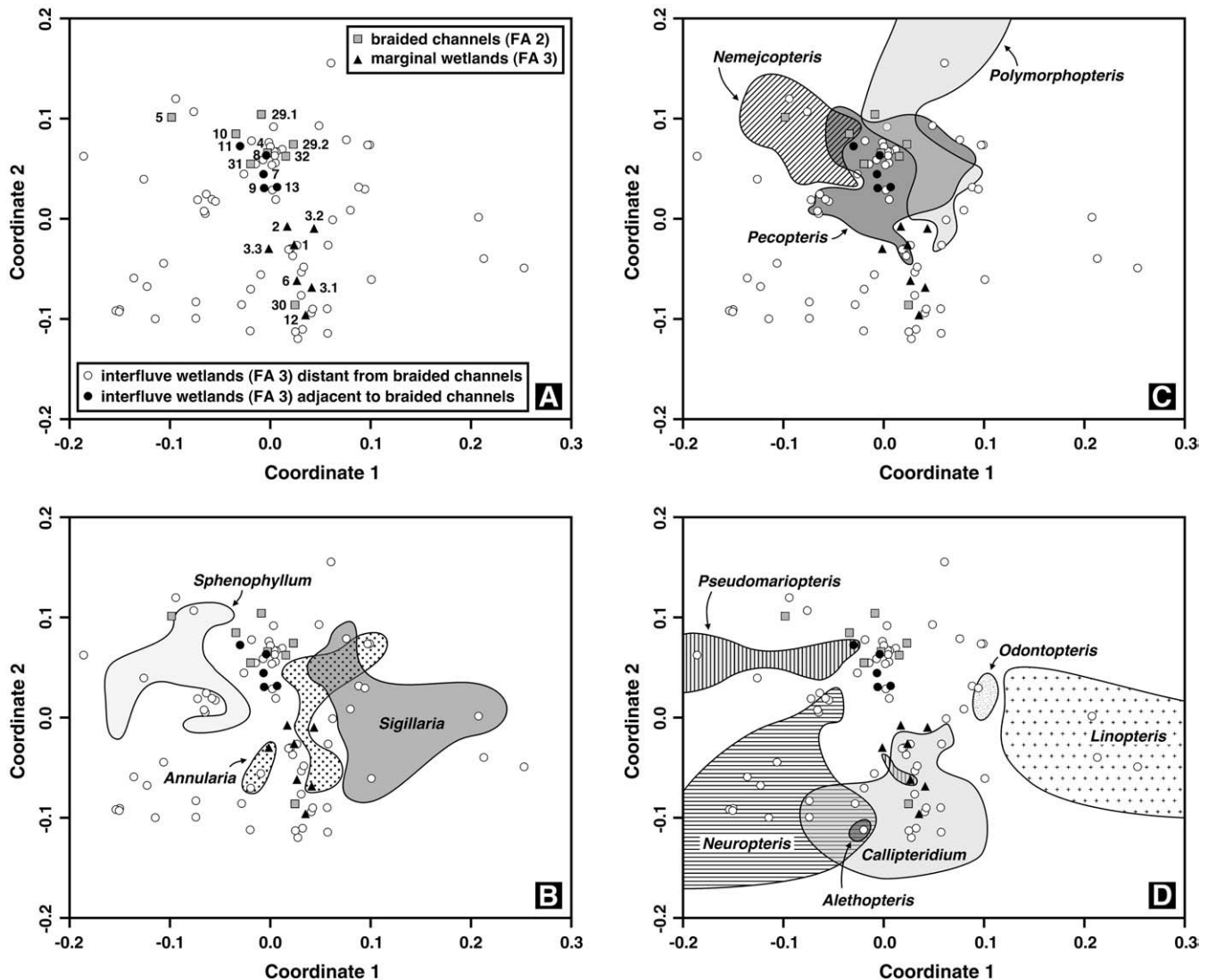
Fig. 10. A. Two-dimensional ordination plot after non-metric multi-dimensional scaling (NMDS) of 86 (par)autochthonous quadrats separated into four groups: (i) marginal wetland deposits (FA 3, n = 7) overlying debris flow breccias (FA 1); (ii) braided channel belt deposits (FA 2, n = 8); (iii) interfluve 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 S2] 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*).

the marattialean tree fern *Pecopteris* (Morgan, 1959; Willard and Phillips, 1993; DiMichele and Phillips, 2002). The understory consisted of sub-arborescent *Calamites* bearing *Annularia* foliage, and the callistophytalean pteridosperm *Pseudomariopteris* was either groundcover or a liana (Krings and Kerp, 2000).

Conchoidally weathered siltstones in the breccia pile (FA 1) may record weak rooting, but the source vegetation is equivocal. Nonetheless, the lowest quadrat (MG-12) lies just 1.6 m above the breccia pile (Fig. 3), 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. 1C, 3), 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 and Noll, 1999). Castro (2005a,b) also recorded this species, but only from Mina Luisa (Section H; Figs. 1C, 3) 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.

8.2. Communities in braided channel belts (FA 2)

The NMDS analysis (Fig. 10) indicates that ferns dominated braided channel belts (Fig. 11A), 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 and Galtier, 2005). Sphenopsids were locally abundant, especially sub-arborescent calamiteans bearing *Annularia* foliage and thicket-forming sphenophylls (Batenburg, 1977, 1981; Galtier and Daviero, 1999; Bashforth and 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 and Phillips 1994, 2002; Baker and 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 reproduced infrequently or over extended intervals (DiMichele et al., 2006). 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 pterido-

sperm 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 and Pfefferkorn, 1984; Latterell and 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 and Degges, 2007; Gibling et al., 2010).

8.3. 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. 11B). 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.

8.3.1. 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 directly overlie swamp deposits ($n = 17$) record the drowning of swamp vegetation (Fig. 11B), 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, the (par) autochthonous megafloral assemblages from these 17 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, 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) that 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 5), 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 5).

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 and DiMichele, 1992), were surprisingly rare, although they likely were more common in swamps than in non-peat-forming habitats on interfluve wetlands.

8.3.2. 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
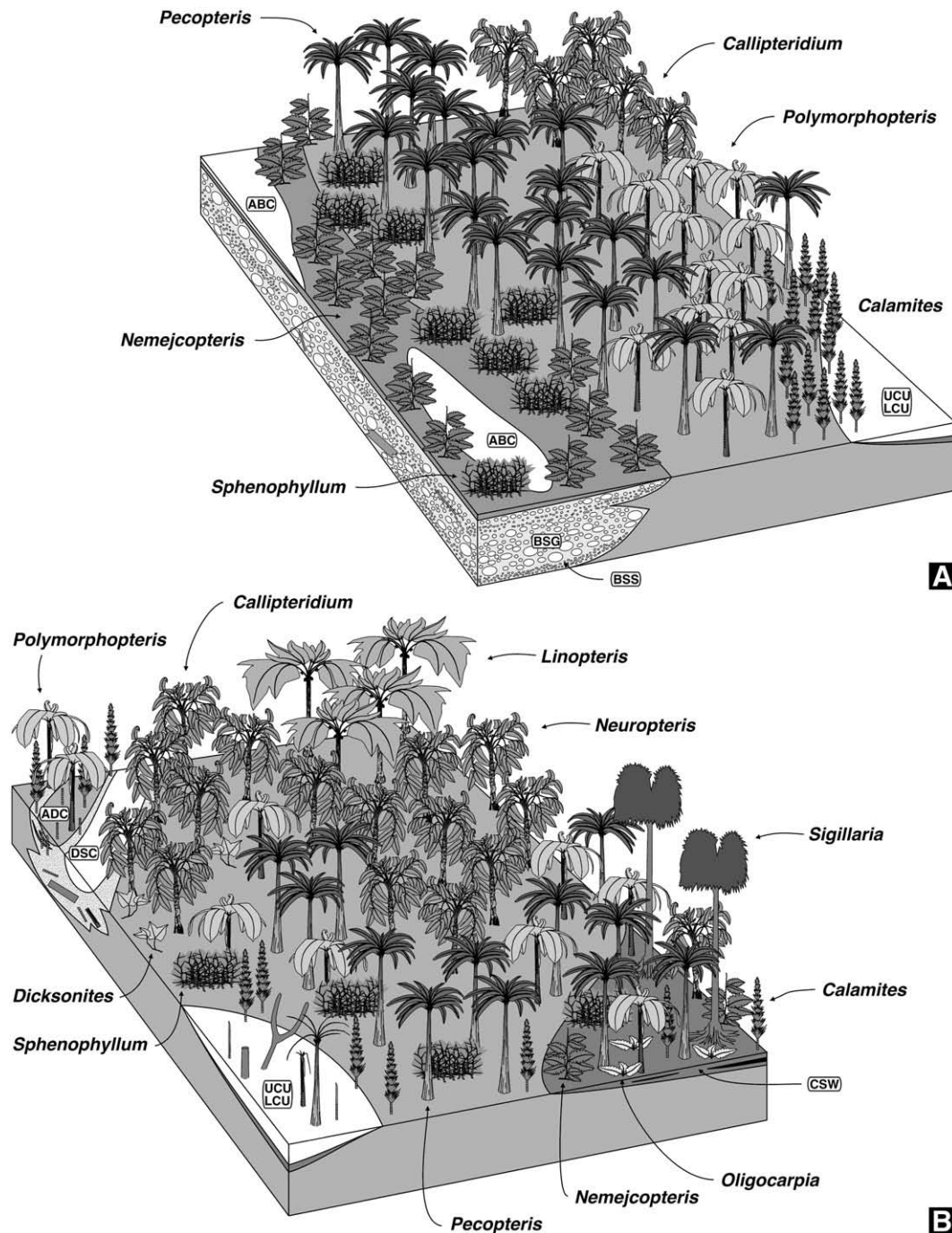
Fig. 11. Reconstruction of plant communities on braided-river plain of La Magdalena Coalfield. A. Vegetation adjacent to braided channel belt (FA 2). Low-stature *Nemejcopteris* and *Sphenophyllum* occupy newly exposed substrates of an abandoned braided channel (ABC facies), and form the groundcover 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.

reclamation precluded quantitative sampling of this facies, although an exposed 'seat earth' at Mina Irene (Section G; Fig. 1C) 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 and 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.

8.3.3. 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. 10) 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. 8), together with along-strike compositional changes on bedding planes (Fig. 9), 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 6).

In fern-dominated communities (Fig. 11B), *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 and Hilton, 2009). Ground-cover presumably formed in canopy gaps, possibly sustained by recurring disturbance. Monospecific or low-diversity patches of medullosalean pteridosperms (Fig. 11B), comprising *Callipteridium*, *Alethopteris*, *Neuropteris* (Laveine and Brousmiche, 1985; Zodrow and 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 and Béthoux, 2002; DiMichele et al., 2006) and the medullosalean pteridosperm *Odontopteris* (Šimůnek and Cleal, 2004; Krings et al., 2006). Again, groundcover and lianescent taxa probably thrived in canopy gaps. The arborescent lycopsid *Sigillaria* and tall cordaitalean trees (Falcon-Lang and 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. 11B; DiMichele et al., 2005, 2006).

8.4. 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 la-

custrine environments, plant litter tends to be blown into lakes from surrounding vegetation (Spicer, 1981; Ferguson, 1985; Spicer, 1989), 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 5). 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.

9. 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, but 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. (2009) and Opluštil et al. (2009) 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.

10. Conclusions

La Magdalena Coalfield was situated in the proximal reaches of a large foreland basin on the western end of the Paleo-Tethys 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, whereas 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.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2010.03.037.

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