Plant Taphonomy and Paleoeocology of Late Pennsylvanian Intramontane Wetlands in the Graissessac–Lodeve...

Article in Palaios - June 2005
DOI: 10.2110/palo.2003.p03-119

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INTRODUCTION

Pennsylvanian coal swamps are among the best-known plant communities of the fossil record. During the second half of the 20th century, developments in sedimentology and taphonomy led to a revision of previous concepts, and new models were proposed that take into account depositional environments, biostratinomic constraints, and plant ecological interpretations, such as population density, community structure, or forest succession (see DiMichele et al., 1992 for a summary).

Pennsylvanian peat mires were diverse taxonomically, ecologically, and paleogeographically. Most models of Carboniferous woodland vegetation arose from North European and North American paralic peat mires. The pioneering works of Phillips et al. (1974) and Scott (1977, 1978) established the methodological basis for the paleoecological study of these environments. Later, the research progressed to cover different environments and the entire Pennsylvanian fossil record. This led to the characterization of a number of diverse Westphalian and Stephanian peat mires (e.g., DiMichele and Phillips, 1994), clastic swamps (Gastaldo, 1987; Demko and Gastaldo, 1992), drylands (Falcon-Lang, 2003), and faunal-floral interactions in these environments (Scott, 1980; DiMichele et al., 1992). Global climatic change, which controlled the evolution of woodland vegetation in the Late Carboniferous, was another important research focus (DiMichele and Phillips, 1996; DiMichele et al., 2001, 2002).

Aims of the Present Study

In contrast to the large quantity of data gathered from paralic (i.e., coastal, freshwater to brackish) environments, only a few paleoecological studies dealt with limnic (i.e., inland, freshwater) coal swamps. Elevated intramontane basins not connected with the ocean were especially abundant during the Stephanian within the South European sector of the Hercynian Range. Up to now, only particular paleoecological aspects were studied either from quantitative (Iwaniw, 1985; Galtier and Phillips, 1985) or qualitative (Wagner, 1989) points of view. The Graissessac Basin is one of the best-preserved examples of limnic Stephanian wetlands in southern Europe. The outcrops are excellent and the effect of Alpine tectonics in the area was limited. These conditions allow for sedimentologic and taphonomic analyses in different depositional settings, including peat mires, floodplains, fluvial channels, and alluvial fans, which provides more insight into the paleoecology of Late Pennsylvania limnic swamps.

Methods

Two main areas were studied: Col-du-Rulladou (Découverte Rive Droite) and Mont Sénégra (Découverte de l’Orb). Other outcrops either were inaccessible for sampling (Padenes-Découverte Rive Gauche) or already buried (Cap Nègre-Alzou area) during landscape reclamation. The outcrops studied provide a good representation of the...
vertical depositional evolution of the eastern Graissessac Basin because they record most of the lower and upper part of the coal-bearing deposits, according to the correlation of Saint-Martin (1993). Detail stratigraphic logs were constructed and lithostratigraphically correlated. Layer-by-layer sampling was carried out in parallel with taphonomic and sedimentologic analyses. Quantitative evaluation of plant remains was conducted in Mont Sénégra using the point-quadrat technique developed by Scott (1977, 1985). The percentage cover data provided by the point-quadrat technique are considered an indicator of the standing biomass (Scott, 1977). In Col-du-Rulladou, the outcrop conditions did not allow this approach; the results for this locality are qualitative. With the exception of rare permineralized wood samples, the material in Graissessac is comprised of compressions. More than 500 macroscopic specimens of these plants (some of them of large size) are housed in the collections of the Laboratoire de Paléobotanique (Université de Montpellier II), where identification of the material was done.

GEOLOGICAL AND PALEOBOTANICAL SETTINGS

The Graissessac-Lodève basin is one of the southernmost intramontane rift-basins that developed during the Stephanian and early Permian in the French Massif Central due to the post-thickening collapse of the Hercynian Orogen (Echtler and Malavieille, 1990). The Basin has an elongated-triangular shape with a main east-to-west axis, and shows significant widening towards the east (Fig. 1). One major listric fault bounds the basin to the south that, according to Echtler and Malavieille (1990), separates it from the granites, gneisses, and associated metamorphic rocks of L’Espinouse Massif (northern Hercynian axial zone at the Montagne Noire). To the north, the basin limit is defined by minor faults in contact with the Hercynian thrust sheets of Mégues and Avène-Mendic (Bogdanoff et al., 1984). The basin infilling was almost continuous during the Late Stephanian and Permian (Becq-Giraudon and Van den Driessche, 1993). There are two main sedimentary units in the basin, which are stratigraphically conformable in the southeast, but become bounded by a progressive angular unconformity towards the north and northwest. The lower unit is Late Stephanian in age, and is the object of the present study. The outcrops of this unit occur in the western, narrower part of the basin, or Graissessac Subbasin. In contrast, the upper unit is Permian in age, and crops out in the widest, eastern part of the basin or Lodève Subbasin (Bogdanoff et al., 1984).

The Graissessac Subbasin forms a narrow asymmetrical synclinorium, 30 km in length and 2.5 km in maximum width. The east-to-west axis is closer to the southern border of the basin (Becq-Giraudon, 1973). This subbasin was divided into two main sectors, possibly by a paleogeographic high (Becq-Giraudon, 1984; Saint-Martin, 1993). In the western part of the subbasin, up to 600 m of silici-
clastics developed unconformably upon the Proterozoic and Cambrian basement. This succession consists of the alluvial fan red conglomerates of Croix-de-Mounis, which grade laterally and vertically to the east (Pabau area) to fluvial sandstones and shales with intercalated anthracite layers (Becc-Giraudon, 1973; Saint-Martin, 1993).

The eastern sector of the Graissessac Subbasin crops out from Saint-Geniès-de-Varensal to Le-Bousquet-d’Orb, and includes most of the coal-mining district (Fig. 1). This sector consists of fluvio-palustrine deposits up to 500 m thick (Becc-Giraudon, 1984; Bogdanoff et al., 1984). Arkosic sandstones deposited in braided fluvial systems dominate in the southern part, near Camplong. In contrast, the northern half of the sector, near Graissessac, records a heterolithic series formed by alluvial-fan and fluvial sandstones with associated overbank shales and coals (Bogdanoff et al., 1984; Saint-Martin, 1993). Towards the top of the stratigraphic sequence, near Mont Sénégé, shales and coals were covered first by arkosic sandstones, and then by the Permian basal conglomerate, which are progressively unconformable as shown by Becc-Giraudon and Van den Driessche, 1993.

The Pennsylvanian flora of Graissessac has been known since the 19th century when Grand’Eury (1877) published a list of 40 morphotaxa from the mining district. The same diversity was reported by Becc-Giraudon (1973) in his study about the geology and biostratigraphy of the basin, for which the plant assemblages were interpreted as Stephanian B in age. However, they are now considered as typical of the Upper Stephanian according to the revision of the Saint-Etienne flora by Doubinger et al. (1995). A revised list of the Graissessac flora was provided by Doubinger et al. (1983), who recognized about 70 different morphotaxa that may correspond to about 30 whole-plant species. This flora never has been the object of a taxonomic monograph, but a number of taxa have been characterized by Galtier et al. (1985, 1997), Galtier and Daviero (1999), and Galtier (2004). Table 1 is a revised list of selected macrofossil taxa.

<table>
<thead>
<tr>
<th>Taxonomic List</th>
<th>Col-du-Rulladou</th>
<th>Mont Sénégé</th>
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</thead>
<tbody>
<tr>
<td>Lycopods</td>
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<td>Stigmaria sp.</td>
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<td>Cardiocarpus expansus</td>
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</table>

Sedimentology

Depositional environments were interpreted from stratigraphic sections in the opencast mines of Col-du-Rulladou and Mont Sénégé (Fig. 1). The mine at Col-du-Rulladou exposes a basal, thick alluvial-fan sandstone overlain by a coal seam that in turn is overlain by floodplain and fluvial deposits in which there are a number of intercalated coals (Fig. 2). In Mont Sénégé, the stratigraphic log begins with alluvial-fan sandstones, and continues into a thick succession of fluvial, floodplain, and alluvial-fan siltstones in which there are as many as five intercalated coals (Fig. 3). The section at Mont Sénégé is stratigraphically above the sections studied at Col-du-Rulladou and, in comparison, represents a more proximal sedimentary setting.

Alluvial Fans

Large, tabular sandstone bodies of up to 1 km in lateral continuity and 25 m in thickness are found at the base of the Col-du-Rulladou outcrop (Fig. 2) and throughout the
section of Mont Sénéra (Fig 3). They are formed by white to yellow coarse-grained arkosic sand and conglomerate. Stratification is poor, and results in 1.5-m- to 5-m-thick, massive beds, arranged in thickening-upwards sequences. Quartz pebbles up to 10 cm in diameter, and highly fragmented phytoclasts, as well as some seeds (*Trigonocarpus*, *Cardiocarpus*), are suspended in the matrix. The sandstone is poorly sorted. Small trunks and rounded, parallel-oriented woody fragments form pavements at the base of some strata. The top may show a rippled sandstone layer and may be covered by a coal bed.

These sandstone bodies are interpreted as an accumulation of debris-flow deposits. Massive bedding, matrix-supported pebbles, and absence of sorting are features characteristic of these facies, which are abundant in proximal areas of alluvial fans (Collinson, 1996). The top, rippled layer indicates that the final stages of deposition occurred under more tractive-flow conditions, which may correspond to more distal areas of the alluvial fan or to interfan areas (Collinson, 1996), where the peat of overlying coal beds was deposited.

Fluvial Channels and Crevasse-Splay Deposits

Tabular sandstone bodies, normally about 3–5m thick (but as much as 25 m thick in one case) and 1 km wide, occur mainly in the Col-du-Rulladou outcrop and wedge out into dark, laminated mudrocks (Fig. 2). They consist of a number of 1–2-m-thick coarse-grained, arkosic, sandstone layers. The conglomeratic bases of layers grade upwards into a sequence of coarse- to medium-grained arkosic sandstone and finally to a centimeter-scale drape of shales. These layers normally are massive and sometimes cross-bedded. The bases of sandstone bodies are flat and erosive. Lag-deposits are formed by quartz pebbles, compressed trunks up to 1–2 m long, and other decimeter-scale, woody plant fragments (Fig. 2).

Underlying one of these tabular bodies at Pradinas is a lenticular, 20-m-long, 5-m-thick sandstone body that shows a thickening-upward sequence of well-stratified, cross-laminated, fine-grained sandstone. Progradation of this sequence onto laminated shales and siltstones has been observed in the outcrop (Fig. 2).

The tabular, sandstone bodies of Col-du-Rulladou are interpreted as the result of multiepisodic infilling of fluvial channels. The top fluvial channel at Layrac shows a succession of stacked channels, which could be termed a paleovalley in the sense of Gibling and Bird (1994). However, most of the fluvial channels in the basin are individual channels showing facies characteristic of braided rivers. They were infilled in multiple events after periods of
FIGURE 3—Stratigraphic column at Mont Sénégara opencast mine with interpretation of depositional environments.
turbulent-flow regime, as indicated by massive or graded bedding (Collinson, 1996). The thickening-upwards sequence observed at the base of the fluvial channel between the Brochin and St. Étienne coal beds at Pradinas is interpreted as a prograding crevasse-splay lobe within the floodplain deposits. These features have been observed in a number of extant crevasse-splay models (Collinson, 1996).

**Floodplains**

Black, evenly laminated siltstones and shales form successions up to 50 m thick between fluvial channels at Col-du-Rulladou (Fig. 2) and intercalated with coal beds in Mont Sénégra (Fig. 3). Two types of deposits were distinguished on the basis of lithology and plant preservation. Black, laminated siltstones with siderite nodules contain few plant remains, whereas alternating black shales and siltstones include much richer and well-preserved plant assemblages. These two lithologies are easy to identify in the first 20 m and last 10 m of the Layrac-Center outcrop, respectively (Fig. 2), but occur elsewhere. At Layrac-W, these sediments grade laterally to a 24-m-thick lenticular body of fine-grained rippled sandstone and siltstone with a lateral continuity of about 150 m (Fig. 2).

These rocks are interpreted as fine-grained overbank deposits formed by suspension-load deposition after flooding events (Collinson, 1996). The high content of organic matter (black color of shales and siltstones) is attributed to permanent inundation of the floodplain, while the origin of siderite nodules relates to organic decay and Eh/pH conditions (Martin, 1999). The difference between both lithologies observed in floodplain deposits at Col-du-Rulladou is interpreted as relative distance to the source area of sediment. Sediments close (proximal) to the supplying fluvial channel were coarser than sediments deposited far (distal) from this point. As a consequence, only silts were deposited in the proximal floodplain, whereas an alternation of silts and muds characterized the distal floodplain. This difference is important in the interpretation of plant biostatigraphic features observed in floodplain deposits.

The large, lenticular body observed at Layrac-W is interpreted as an infilling of a sluggish, shallowly incised channel within the floodplain. The shape of the body and the presence of tractive fine-grained sand support this interpretation. The presence of small channels with tractive structures also is evident in floodplain sediments between “Couche 3” and “Couche 4” at Mont Sénégra.

**Peat Mires**

Coals of the Graissessac Basin range from medium–low-volatile bituminous coal to anthracite (Copard et al., 2000). The coal beds are formed by a succession of bright and dull centimeter-scale horizons, which may result in as much as 7 m of total accumulated coal thickness. These coals were the object of organic geochemical studies that determined that they matured under geothermal flows ranging from 125–155°C during the later stages of the Hercynian Orogeny (Copard et al., 2000). At these temperatures, palynomorphs are dark brown to black, and their taxonomic determination is difficult or impossible, which accounts for the scarcity of palynological data in the basin and the need to extrapolate paleoecological data from plant macroremains found at the base and roof-shales of the coal beds.

Most coal seams preserve compressed rooting structures on bedding planes at the base of the coal bed, indicating that they were initiated by in situ accumulation of organic remains within peat-mires, rather than being formed by allochthonous accumulation of organic debris. They are found overlying three different deposits: (1) alluvial-fan sandstones, (2) fluvial sandstones, and (3) floodplain shales and siltstones (Figs. 2–3). Coals overlying alluvial-fan sandstones have an important lateral continuity (e.g., >1 km for Grand Pas). Sharp boundaries between both deposits probably indicate that coals are superimposed on inactive alluvial-fan deposits, and represent a different event in time. This does not exclude that the high water table of the mire was fed with ground water from the underlying sandy alluvial fan deposits, as was the case in some Pennsylvanian rheotrophic mires (Calder, 1994). Coals on top of fluvial channels have continuity on the order of 100–300 m, and they are either cut by fluvial deposits (Burelle coal), or grade vertically into floodplain deposits (Brochin coal, Fig. 2). The peats forming these coals are interpreted as deposited within the abandoned channels, though they were not exactly equivalent to oxbow lakes because most of the channels were of low sinuosity. Such peat-mires were elongated and narrow in shape. Coals overlying floodplain deposits include most of the seams at Mont Sénégra. In “Couche 4” and “Couche 5,” these coal seams are split by clastic horizons that are a few centimeters in thickness, similar to those of the neighboring floodplain deposits, indicating similar conditions of deposition (Fig. 3).

The tops of a number of coal seams contain cm- to dm-thick mudstone horizons that become progressively thicker upwards until the coal completely disappears. Gradual development of roof-shales from the underlying coal indicates that they constituted a natural extension of peat-mires during their latter infilling stages (Type B roof-shales of Gastaldo et al., 1995: Fig. 3). In some cases, however, sedimentary interruptions occur between coals and the overlying roof-shales. Siderite nodules present in roof-shales of the Grand Pas and “Couche 7” coals may indicate pore-water reactions during prolonged water inundation (Type C roof-shales of Gastaldo et al., 1995; Fig. 3). This situation may kill all of the mire vegetation and result in significant sedimentary gaps between coals and their roof-shales (Gastaldo et al., 1995).

**PLANT TAPHONOMY**

Features from the base and top of coal seams supplied most of the plant-taphonomic data used for paleoecological interpretations. Other data were obtained from floodplain and fluvial assemblages.

**Peat Mires**

Assemblages of macroscopic remains were studied at the base and especially in roof-shales of coal seams. Palynological data are limited to one productive sample of the Brochin coal (Doubinger et al., 1983).

Grand Pas coal (Layrac, Col-du-Rulladou): Stigmaria
mudcasts, some of them with rootlets preserved in three dimensions, were observed at the top of alluvial-fan deposits underlying the Grand Pas coal (Fig. 4A). This type of preservation corresponds to the siliciclastic infilling of rooting structures during long periods without organic deposition, and indicates a time-hiatus between the alluvial fan deposit and the overlying coal (Gastaldo, pers. comm., 2004). Locally, the base of the Grand Pas coal is split from the underlying alluvial-fan deposit by a succession of laminated coalyl siltstones that grade into the coal, and contain an accumulation of compressed Sigillaria logs of several meters in length mixed with lycopsid foliage (Cyperites, Fig. 4B). The association of different organs of the same taxon and the absence of any preferential alignment of the organs were shown by Gastaldo et al. (1996) to indicate parautochthony, and suggest that the remains correspond to the floor litter of a Sigillaria forest growing in the early stages of peat-mire formation. Most of the roof-shales of this coal seam were removed during mining. In the only locality where they occur (Layrac-Center), they display features indicating interruption in the sedimentary succession from coal to the overlying floodplain deposits (see Sedimentology section).

**Brochin Coal (Pradinas, Col-du-Rulladou):** The thick Brochin coal seam of Pradinas was well exposed during fieldwork, which allowed study of the base and roof-shales (Fig. 2). It is significant that Sigillaria bark was identified within the coal itself. The top of the underlying fluvial sandstone showed a number of well preserved, compressed Stigmaria rooting systems radiating from in situ stumps. Only rounded marks of these stumps were preserved on the bedding plane, which indicates that the stumps themselves were in the overlying coal (Fig. 4C, D). Eight stumps were present on a bedding surface of 30 m², suggesting a density of about 25 stumps per hectare. This low density could be even less if it is assumed that the stumps were not growing during the same colonization event. The only rooting structures observed at the base of the coal were Stigmaria.

Roof shales of the Brochin coal were studied in two different localities 350 m apart. One locality yielded erect, three-dimensional mudrock casts of Sigillaria stumps (~60 cm in diameter, Fig. 5B). The rootstock of these stumps were not preserved, indicating that they were in the underlying coal as is typical for type A roof-shale floras of Gastaldo et al. (1995). The mudrock casts did not show obvious lamination, but they did contain some coaly horizons inside, suggestive of a long-lasting infilling sequence (Gastaldo et al., 1989). In the other locality, a well-developed roof system of Psaronius was encountered, indicating autochthony in clastic beds of the roof-shales (Fig. 5D). In a roof-shale bed overlying this rootstock, a fallen, Psaronius/Caulopteris trunk and well-articulated Pecopteris-type foliage occurred (Fig. 5C). The excellent preservation as compressions and the assemblage of different organs of the same taxon indicate rapid burial of a forest-floor litter horizon. These observations are used to interpret the Brochin coal seam as an autochthonous peat deposit that formed by the accumulation of a Sigillaria brardii-dominated forest, at least in the first and last mire stages. The presence of rooting structures of Psaronius in the roof-shales, but not at the base of the coal seam, provides evidence that tree ferns did not grow in the initial stages of the peat accumulation.

Additional information on the plants that accumulated in the peat of the Brochin coal is provided by the palynological analysis of Doubinger et al. (1983), which showed that monolete spores were dominant, with 40% Laevigatosporites, 14% Punctatosporites, and 10% Punctatisporites, in contrast to 16% of the trilete spore Lycospora. These results are similar to miospore distributions from some Upper Pennsylvanian coal beds of the Appalachian Basin (Ehle, 1996). Assuming that the spores were autochthonous in the peat, the contribution of tree ferns and calamites to peat accumulation appears to be significant, while the contribution of sigillarians (Crassispora) and other lycopsids (Lycospora) was relatively low. The occurrence of Lycospora is difficult to explain in the absence of macroscopic remains of lycopsids other than Sigillaria. The contradiction between the miospore content and the constant occurrence of Sigillaria in the coal may indicate, according to DiMichele and Phillips (1994), that Sigillaria was a gross under-producer of spores, making it difficult to extrapolate its biomass from the total content in dispersed spores of Crassispora.

**“Couche 3” Coal (Mont Sénégro):** Well preserved, compressed Sigillaria rooting systems and, locally, compressed logs of Sigillaria brardii are found directly beneath the coal, and indicate that Sigillaria was growing, as in previous coals, at the beginning of peat formation. The roof-shales (Type B roof-shales of Gastaldo et al., 1995) were well exposed allowing for acquisition of a data set (Fig. 6A). The succession begins with a Sigillaria-dominated horizon, including compressed Sigillaria trunks, Cyperites foliage, and dispersed Laevigatosporites megaspores. This assemblage passes upwards to a Psaroniuseominated horizon, and, subsequently, to a set of beds preserving large fronds of Pecopteris with less-common Odontopteris (Figs. 5A, 6A). Criteria supporting the parautochthony of these remains include excellent preservation of different organs of the same whole-plant taxon in compressions, abundance of highly articulated Pecopteris-foliage, and absence of aligned axes. The presence of marattialean remains in roof-shales above the sigillarian-dominated beds indicates that these tree ferns grew during the final stages of the peat accumulation. Also, the occurrence of lycopsid and tree-fern remains at different horizons appears to indicate that the plants did not occur together in the same community, but were separated in slightly different stages of the succession or in different laterally related areas.

**“Couche 4” and “Couche 5” Coals (Mont Sénégro):** Well-preserved, compressed rooting systems of Sigillaria occur at the base of these coal seams. Roof-shales of both coals show erect mudstone casts of Sigillaria stumps without rooting structures, indicating that the roof-shales were in continuity with the underlying peat accumulation where the stigmatic axes were buried (Type B roof-shales of Gastaldo et al., 1995). Point-quadrat data from roof-shales and clastic deposits overlying “Couche 5” of Mont Sénégro (Fig. 6C) show a succession of sigillarian remains followed by marattialean tree-fern remains similar to those described for “Couche 3.” In contrast, roof-shales of coal seam “Couche 4” preserve distinctive features (Fig. 6B). The first clastic bed, formed by a massive gray mudstone, has
FIGURE 4—Plant taphonomic features at the base of coal seams. (A) Stigmaria with attached rootlets found at the top of the alluvial sandstones basal to the Layrac outcrop; camera cap (6 cm in diameter) for scale. (B) Assemblage of compressed Sigillaria brandii logs associated with Stigmaria and Cyperites at the base of coal seam “Grand Pas” at Layrac; hammer (28 cm) for scale. (C) Compression of Stigmaria rooting system (arrows) at the base of coal seam “Brochin.” (D) Soil containing Stigmaria shown in (C); position of stumps marked with arrows.
FIGURE 5—Plant taphonomic character of roof-shales. (A) Assemblage of Pecopteris impressions found in the roof-shales of coal seam "Couche 3" showing multiple orders of frond organization. (B) Erect cast of Sigillaria stump in shales overlying "Brochin" coal seam; hammer (28 cm) for scale. (C) Trunk of the tree fern Psaronius with characteristic oval leaf scars (arrows), found in roof-shales of coal seam "Brochin"; camera cap (6 cm in diameter) for scale. (D) Autochthonous rooting system in the roof-shales of coal seam "Brochin" associated with (C); the brush-like morphology of dense roots attached to an axis—too broad to be a stigmarian axis—suggests a Psaronius root mantle. (E) Alliopteris erosa plant growing across the shales on top of "Couche 4" coal seam; arrow indicates the section of main rachis with articulated fronds evident on the bedding surface. (F) Assemblage of Cyperites-type sigillarian foliage found in roof-shales of "Couche 4."
FIGURE 6—Percentage composition of plant taxa recorded in roof-shales and floodplain sediments above the Mont Sénègra coal seams studied using the point-quadrat technique of Scott (1977, 1985). (A) Results above coal seam “Couche 3.” Dashed line separates a lower interval showing trunk remains of a sigillarian-marattialean succession from an upper interval dominated by sphenopsid remains and Pecopteris foliage. (B) Results above coal seam “Couche 4.” The three intervals described in the text are separated by dashed lines. (C) Results above coal seam “Couche 5.” The two lower intervals show a succession of sigillarian and marattialean remains. The upper sandstone contains
an association of rhizomes and autochthonous erect fronds of the herbaceous fern Alloiopteris erosa (Galatier, 2004; Fig. 5E), with subordinate Sigillaria and Sphenopteris remains (Fig. 6B). The second interval is 60 cm thick and yields abundant autochthonous sigillarian remains, such as erect mudstone stumps and fallen compressed logs of Sigillaria brardii, Cypreites foliage, and occasional compressed Stigmaria (Figs. 5F, 6B). This is overlain by a third, 20-cm-thick interval preserving large and well-articulated fronds of Pecopteris and Odontopteris (Fig. 6B). Overlying beds (170 cm thick) generally were sphenopsid dominated.

The succession above “Couche 4” differs from other such successions by the presence of autochthonous Alloiopteris in the first bed overlying the coal. Above this bed, the more general association of sigillarian remains followed by tree ferns persists. The growth of these herbaceous ferns may be related to edaphic factors of the floodplain soil, which are difficult to determine based on compression floras. The occurrence of parautochthonous Odontopteris associated with the marattialean remains in “Couche 4” suggests that it coexisted with the tree ferns in clastic horizons overlying the mires.

Floodplains

Plant remains are very abundant in floodplain sediments. They consist of a large diversity of frond organ taxa, including ferns (Pecopteris, mainly P. polymorpha, and Sphenopteris) and pteridosperms (Dicksonites plucinetii, Odontopteris reichiana, and Calipteris cordaites, Figs. 7A–C). Sphenopsid remains also are abundant, and include large fragments of Calamites (C. cistii and C. suckowi), Annularia sp., and Sphenophyllum oblongifolium. Large, isolated cordaitalean leaves (Pachycordaites sp.) also occur but, in one case, a fan-shaped cluster of 15 of these leaves was found. Some of the fronds are complete (Dicksonites, Galtier and Béthoux, 2002) or nearly complete, indicating parautochthon, but no rooting structures or edaphic features were found. In floodplain successions with abundant shales, interpreted as the result of more distal to fluvial clastic supply, the abundance of these remains increased. This suggests that the parent plants grew close to the floodplain margins, but not in the floodplain itself.

Bed-by-bed data were acquired in floodplain mudstones overlying the roof-shales at Mont Sénégura (Fig. 6A–C). The floodplain succession above “Couche 3” shows that plant taphofacies were dominated by sphenopsids with subsidiary fern (Pecopteris) and pteridosperm (Dicksonites, Odontopteris) foliage (Fig. 6A). The sphenopsid remains are well-preserved logs of Calamites cistii and Calamites suckowi, along with Annularia and Calamostachys. Autochthon of Calamites is supported by erect mudstone pith-casts of stumps in place within the floodplain siltstones. Similar pith-casts were found at Layrac-Center across drained floodplain deposits (Fig. 7D), associated with abundant and highly connected remains of sphenopsid foliage (Asteroxylites, Annularia, Sphenophyllum). Some erect Calamites pith-casts may show development of rootlets from nodes, vertical increase in pith-cast diameter, or lateral-branch bud development, which indicate regenerative growth after burial (Gastaldo, 1992).

Three meters above “Couche 3,” the frond and sphenopsid assemblage is enriched with twigs with attached small leaves of Poacordaites (Fig. 7E). The high degree of articulation of these remains, which probably indicates removal from the parent plant during windstorms, suggests that this plant was parautochthonous on the floodplain. In the upper part of the succession, close to “Couche 4,” the sphenopsid assemblage becomes enriched with well-preserved, highly articulated, Odontopteris fronds. Similar features are observed in floodplain deposits between coal seams “Couche 4” and “Couche 5,” where locally parautochthonous fern (Sphenopteris) and pteridosperm foliage remains (Dicksonites) also occur.

Fluvial Channels and Crevasse-Splay Deposits

The few identifiable remains in fluvial channels at Col-du-Rulladou are long, compressed coaly logs attributed to Cordaites and Calamites. Compressed logs and pith-casts, found at the base of fluvial bodies. One cordaitalean log, with preserved anatomy (Dadoxylon cf. bradlingii) and similar morphology to compressed logs, was reported in the basin by Galtier et al. (1997). Underlying one of these large fluvial channels at Pradinas is a crevasse-splay deposit that preserves a monotypic assemblage of compressed Cordaites (Pachycordaites-type) leaves (Fig. 7F). They are well preserved, show no signs of tearing or other indicators of transport by bed-load traction, and most are in the same size range (~40 cm in length). Their homogeneous nature and size suggest some type of sorting, which may have been produced by fluvial flotation and/or an exclusive supply of Cordaites leaves to the fluvial channel. The fluvial channel immediately above the crevasse-splay sequence contains large wood fragments and logs attributable to Cordaites. Hence, a plausible hypothesis to explain the monotypic Pachycordaites assemblage is that leaves in the river channel were derived from the riverbank upstream. Falcon-Lang and Scott (2000) report in situ Cordaites in such an environmental context. The results of Gastaldo et al. (1987) from a recent crevasse splay in the Mobile Delta, Alabama also suggest that these large and complete Cordaites leaves could be supplied from the levee plant community.

Alluvial Fans

In the basal alluvial-fan sequence of Col-du-Rulladou, plant remains are extremely fragmented, and consist of several-centimeters-long woody debris suspended in the...
FIGURE 7—Plant taphonomic character of fluvial plains and crevasse-splay deposits. All from Col-du-Rulladou Opencast mine except E, from Mont Sénégra. (A) Assemblage of parautochthonous Pecopteris fronds and a Pachycordaites leaf found in siltstones of the Layrac outcrop. (B) Paraautochthonous bipinnate frond of Dicksonites plucknetii in floodplain shale (graphic scale equals 20 cm). (C) Paraautochthonous medullosan branches, showing characteristic orthogonal branching, in floodplain shale. (D) Erect pith-cast of Calamites stump in floodplain silts of the Layrac outcrop; camera cap (6 cm across) for scale. (E) Twig-bearing articulated Poacordaites leaves found in floodplain silts above coal seam “Couche 3”; scale in millimeters. (F) Monotypic assemblage of large Pachycordaites leaves in crevasse splay deposits at Pradinas; hammer head (17.5 cm) for scale.
TABLE 2—Comparative list of settings and floras.

<table>
<thead>
<tr>
<th>Lithofacies</th>
<th>Sedimentary features</th>
<th>Interpretation of depositional setting</th>
<th>Plant assemblages</th>
<th>Plant taphonomy</th>
<th>Paleoenological interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Massive, tabular coarse-to-medium-grained sandstone bodies, 20 m thick and 1 km large</td>
<td>Matrix-supported quartz pebbles and phytozoa; absence of grain-size sorting</td>
<td>Debris flows in alluvial fans</td>
<td>Indeterminate, except for Cardiocarpus and Trigonocarpus</td>
<td>Centimeter-large angular woody fragments; seeds</td>
<td>Allochthonous</td>
</tr>
<tr>
<td>Medium-grained sandstone bodies, 300–500 m large</td>
<td>Normal graded to cross-bedded, grain-size sorting, conglomeratic lag-deposits</td>
<td>Multi episodic infilling of fluvial channels; rare paleovalleys</td>
<td>Rare Dadoxylon, mostly indeterminate cordaitalean and calamitean logs</td>
<td>3–4 m large compressed logs and rounded woody fragments</td>
<td>Allochthonous</td>
</tr>
<tr>
<td>Fine-grained sandstone lenticular body</td>
<td>Ripple-marks; thickening upward sequence</td>
<td>Crevasse-splay lobe</td>
<td>Pachy cordaites monospecific assemblage</td>
<td>Well-preserved, size-sorted leaves</td>
<td>Para autochthonous to allochthonous</td>
</tr>
<tr>
<td>Gray to black siltstones</td>
<td>Lamination, with sierite nodules</td>
<td>Inundated floodplain closer to fluvial supply</td>
<td>Diverse pteridophytes, fern, and sphenopsid axes and foliage; Cordaites</td>
<td>Not abundant; medium articulation of foliage and axes</td>
<td>Para autochthonous to allochthonous</td>
</tr>
<tr>
<td>Black shales alternating with gray siltstones</td>
<td>Lamination; high content in organic matter</td>
<td>Inundated floodplain far from fluvial supply</td>
<td>Diverse pteridophytes, fern, and sphenopsid axes and foliage; Cordaites</td>
<td>Very abundant; high articulation of foliage and axes</td>
<td>Para autochthonous</td>
</tr>
<tr>
<td>Gray fine-grained sandstone in lenticular bodies adjacent to 2 previous lithologies</td>
<td>Well-stratified and rippled</td>
<td>Well-drained areas of floodplain</td>
<td>Calamites, Annu laria, Spheno phyllum</td>
<td>Erect pith casts of Calamites associated with sphenopsid foliage beds</td>
<td>Autochthonous sphenopsid thicketts</td>
</tr>
<tr>
<td>Roof-shales of coal</td>
<td>Alternation of coaly and shaly horizons overlying coal seam</td>
<td>Late stages of mire accretion</td>
<td>Stig maria, Sigi l laria, Cy per ites, Psaron ius and Pecop teris</td>
<td>Stigmarian soils; erect mud casts of stumps and prostrate logs</td>
<td>Autochthonous late forest mire of Sigillaria and Psaronius</td>
</tr>
<tr>
<td>Bituminous coal to anthracite</td>
<td>Alternation of bright and dull laminae</td>
<td>Peat mire</td>
<td>Sigillaria; pollen and monolete spores</td>
<td>Diagenetic darkening of palynomorphs</td>
<td>Autochthonous forest mire of Sigillaria</td>
</tr>
<tr>
<td>Base of coal</td>
<td>Above fluvial, alluvial-fan, or floodplain deposits</td>
<td>Initial stages of mire accretion</td>
<td>Stig maria</td>
<td>Stigmarian soil</td>
<td>Autochthonous pioneer forest mire of Sigillaria</td>
</tr>
</tbody>
</table>

sandstone matrix. Three-dimensional *Trigonocarpus* and *Cardiocarpus* seeds were identified.

The base of the Mont Sénégara succession consists of alluvial-fan deposits. The most abundant remains are woody fragments, 10–20 cm in main diameter, mainly located in lag deposits. Most plant remains were impossible to identify taxonomically. In only a few cases were *Calami tites* and *Calamostachys* recognized (Fig. 3). The middle part of the stratigraphic succession is a white sandstone that is up to 26 m thick, and splits the uppermost “Couche 5” and “Couche 6.” Some beds contained an assemblage of highly articulated fronds and sphenopsid remains analogous to other assemblages of the floodplain facies described in the basin. The top of the channelized facies may contain autochthonous erect pith-casts of *Calamites* stumps with regenerative growing structures.

**PALEOECOLOGY**

The sedimentologic and taphonomic settings discussed in previous sections are summarized in Table 2 and allow for a paleoecological interpretation. The taphonomic observations are explicit about the habitat of autochthonous plants, especially lycopsids, some ferns, and some sphenopsids. However, the habitats of other plants are subject to a certain degree of interpretation. A reconstruction is proposed for the peat swamps of Graissessac, as well as a comparison to other paleoecological models supplied by previous authors (Fig. 8).

**Paleoecological Reconstruction of the Graissessac Plant Community**

*Sigillaria*: The only lycopsid found in the basin, and probably the main peat-producer, was *Sigillaria brardii*. However, limited palynological data appear to indicate that other lycopsids, tree ferns, and sphenopsids also were contributing to peat accumulation. The continuity of *Sigillaria* throughout the whole of peat deposition is suggested by: (1) presence of *Sigillaria* bark within the coal, (2) abundant compressions of *Stigmaria* and associated *Sigillaria brardii* logs found at the base of most coal seams (Fig. 4C, D), and (3) compressed and erect stumps with associated *Cyperites* litter found in roof-shales (Fig. 5B, F).
Sigillaria brardii appears to have tolerated a broad range of environmental conditions given that it is found in coal mires deposited in a number of contexts (in abandoned fluvial channels, in the floodplain, or on abandoned alluvial-fan lobes). Pioneer peat-forming mire-forests of *Sigillaria brardii* were monotonous and open, as deduced from the calculated density of stumps on the bedding surface at the base of the Brochin coal seam (Fig. 4D).

*Psaronius*: The association of autochthonous *Sigillaria brardii* and the marattialean tree-fern *Psaronius* occurs in a number of roof-shales and indicates that the coal mires became slightly more diverse in late successional stages. However, the occurrence of these two taxa in different horizons of roof-shales at Mont Sénégra indicates that the plants did not share the same habitat, but grew in neighboring areas (Fig. 8A). Three hundred and fifty meters separate the two laterally equivalent sites at the top of the Brochin coal seam where sigillarian and marattialean stumps occur. The abundance of paraautochthonous *Pecopteris* foliage in the floodplain siltstones immediately above roof-shales suggests that *Psaronius* grew in the floodplain immediately around the mire and eventually colonized the last mire horizons. In some of the coal seams, highly articulated odontopterid foliage suggests that this pteridosperm may have colonized the late mire horizons together with *Psaronius*.

*Sphenopsids*: *Calamites cistii* and the less-abundant *Calamites suckowii* appear to be autochthonous at a number of different sites. Erect mudstone pith-casts of stumps were localized in the floodplain silts (Col-du-Rulladou, Mont Sénégra) or in distal alluvial fans (Mont Sénégra). In these locations, paraautochthonous *Sphenophyllum oblongifolium* may be associated with *Calamites*, but without evidence of rooting, which may indicate a preservational bias. From about a dozen points where these associations occur, it is concluded that thickets of *Calamites cistii*, *Calamites suckowii*, and associated *Sphenophyllum oblongifolium* were the only vegetation growing in floodplains (Fig. 8).

*Seed Ferns and Small Ferns*: *Odontopteris* and *Alloiopteris* have been found in roof-shales at Mont Sénégra and probably were autochthonous in the last infilling stages of mires. Medullosan pteridosperms and a large number of smaller pteridosperms and ferns were always paraautochthonous in the floodplain and especially abundant in shales deposited in distal floodplains. Some plants were large enough to have left evidence of rooting structures if they were growing in the floodplain, but this appears not to be the case. Hence, a habitat in an exposed area close to this part of the floodplain appears to be the best hypothetical location for these plants in the paleoenvironment (Fig. 8A). There, they constituted the most diverse plant association of the Late Stephanian swamps of Graissessac. A variety of growing strategies have been documented for
them, including the tree habit of some medullosans, and the creeping habit of Dicksonites (Galtier and Béthoux, 2002). This higher diversity is compatible with a less-stressed habitat, away from the waterlogged soils.

Cordaitaleans: Large cordaitalean leaves (Pachycordai-

tes) are the most allochthonous plant remains in the Graissessac wetland. A source of the leaves outside the swamp is evident; however the abundance and preservation of the leaves found in the crevasse-splay deposit at Pradinas suggest that the trees were growing upstream, close to the river channel, probably in the levee. Clusters of articulated leaves in floodplain siltstones and shale at Layrac also indicate that these plants were not growing far away from the area. Finally, the presence of coalified and permineralized cordaitalean logs found in the lag deposits of fluvial channels suggests that the trees were growing in the riparian community (Fig. 8A). In contrast, cordaitalean twigs of a distinct species with attached small leaves (Poacordaites-type) are parautochthonous in the floodplain sediments of Mont Sénégra.

Comparison with Other Late Pennsylvaniaan Coal Swamp Reconstructions

North America: Numerous paleoecological studies from Pennsylvaniaan coal swamps have been carried out in the North American Illinois Basin, and have been summarized by DiMichele and Phillips (1994, 1996). The Bristol Hill, Friendsville, Duquesne, and Calhoun coals from this basin provide significant information for comparison with the present results. Many of these studies were drawn from coal balls, which are considered to be a more accurate representation of the peat mire than compression roof-shale floras. Palynology also provided significant data, especially where coal balls were not available (Willard and Phillips, 1993; Willard et al., 1995).

Coal balls from most of the Late Pennsylvaniaan (Ste-

phanian equivalent) coal swamps of the Illinois Basin are dominated by remains of Psaronius, which represent 75% to 90% of the so-called biovolume (the volume of the fossil tissue in a coal ball). The Calhoun coal is somewhat different because it has a larger content of sigillarian lycopsids, which represent up to a 30% of the biovolume in comparison to nearly 60% Psaronius (DiMichele and Phillips, 1994). These high percentages of tree fern contrast with the composition of the underlying Middle Pennsylvaniaan (Westphalian equivalent) seams, which were dominated by highly diverse assemblages of tree-lycopsids, mostly Lepidophloios and Diaphorodendron species. This difference has been attributed to major regional extirpations within the lycopsid lineage at the Westphalian–Stephanian boundary. According to DiMichele and Phillips (1996), approximately 68% of the peat-forming species and about 50% of the species growing in clastic wetlands became extinct regionally at the end of the Westphalian. Global climatic change leading to moisture deficiency or exaggeration of seasonal dryness in the paleotropics is considered to have been responsible for the ecological turnover of mire biotopes (Phillips and Peppers, 1984; DiMichele and Phillips, 1996). The effects were especially significant in the North American Stephanian peat mires that became opportunistically occupied by cheaply constructed plants, especially Psaronius, after the extinction of most Westphalian tree-lycopsids (DiMichele and Phillips, 1996; DiMichele et al., 2001). Sigillaria was the main lycopsid survivor of this crisis in North America, probably because of a pre-adaptation to periodic moisture limitation. In the Westphalian of the Illinois Basin, it already opportunistically occupied disturbed stream margins (Phillips and DiMichele, 1992).

The study of coal balls and palynology in coal profiles sheds light on the detailed vertical evolution of the preserved plant cover within a mire. A typical Late Pennsylvanian coal seam of the Illinois Basin shows early colonization by the lycopsid Sigillaria brardii or Chaloneria, which then are replaced vertically by up to three different marattialean fern assemblages with a subordinate dominance of medullosans and Calamites (DiMichele and Phillips, 1996). Pryor (1996) reported such a successional trend from the Duquesne coal seam in Ohio. In this case, an initial Chaloneria-dominated mire was succeeded first by a pteridosperm-Neuropteris and tree fern-Psaronius dominated community with abundant epiphytes, lianas, and herbaceous ground cover (Fig. 8B). The last successional stage consisted of a canopy of Psaronius tree ferns. Compression floras, such as those available in the Graissessac basin, do not allow for such a detailed profile, but do provide general trends of the mire’s evolution. In the coal seams studied, Sigillaria brardii is present in the very early stages of peat accumulation, like in North American mire profiles, but, in contrast to them, it does not disappear in the late successional stages. Psaronius, pteridosperms (Odontopteris), and small ferns (Allopteris) were present in these later stages, but were rarely dominant in roof-shales as the representatives of these groups were in North American Upper Pennsylvaniaan mires (Fig. 8).

Europe: Floras from Stephanian basins of the Massif Central (France) have been studied taxonomically since the very beginnings of paleobotany. A modern taxonomic synthesis from the Saint-Etienne basin is provided by Doubinger et al. (1995), but paleoecological reconstructions based on modern criteria are not yet available. Phillips and Galtier (1984) proposed a preliminary comparison among the Stephanian permineralized floras of Grand’Croix, Saint Etienne basin, and coal-ball peats of the Illinoi Basin. The floras from Grand’Croix were similar in the abundance of tree ferns and pteridosperms, but differed in their greater quantity of cordaitalean remains. Unfortunately, the Grand’Croix permineralizations were allochthonous in conglomerates and did not enable the authors to propose a more detailed paleoecological reconstruction. In Spain, Iwaniw (1985) and Wagner (1989) described a few Stephanian coal-swamp plant assemblages related to distal alluvial fans and peat mires. In the base of the Stephanian (Early Cantabrian), at least two arborescent lycopsids (Lepidodendron and Sigillaria) persisted in a peat mire of León (Northwest Spain), whereas Sigillaria was the only tree lycopsid of another Early Stephanian (Cantabrian) peat-mire horizon in Palencia (north-central Spain). The genus Omphaloploios was the only arborescent lycopsid in a Late Stephanian peat mire of Puertolano (Southern Spain), where it grew in association with marattialean tree ferns. This situation is somewhat comparable to the later stages of development of the Graissessac mires.
**DISCUSSION AND CONCLUSIONS**

Pennsylvanian limnic mires are poorly studied paleoe
cosystems in comparison with contemporaneous paralic
mires. Limnic mires were well developed in Late Hercyni-
an intramontane basins of southern Europe, such as the
fluvio-palustrine basin of Graissessac (France), which
occurred in the Massif Central axial zone of the Hercynian
Range. In this basin, peat developed in a number of sedi-
mentary contexts, including fluvial abandoned channels,
floodplains, and above distal alluvial fans. From compres-
sion floras studied at the base and top of the coal seams, it
appears that they were colonized by a monotonous, open
forest of *Sigillaria brardii* in the early stages of mire de-
velopment, and that only in later stages were monospecific
lycopsid associations enriched with the marattialean tree-
development, and that only in later stages were monospecific
Dadoxylon and, occasionally, by pteridosperms (*Odon-
topteris*) and small ferns (*Alloiopteris*). This situation is in
contrast with coal mires from the North American Illi-
nois Basin that were dominated by tree ferns and pteri-
dosperms from the very beginning of the peat-mire profile
or preserved subsidiary sigillarian tree-lycopsids only in the
early stages. However, in the absence of complete pal-
ynological analyses from the Graissessac coals, the results
presented do not allow for a more detailed interpretation of
the flora that produced the main mire development.

Floodplain environments were extensively developed in
the Graissessac Basin and contain a well-preserved flora
dominated by ferns, pteridosperms, and sphenopsids.

ACKNOWLEDGEMENTS

The manuscript was greatly improved during the peer-
review process by W.A. DiMichele, H. Falcon-Lang, R.A.
Gastaldo, and A.C. Scott. Criticisms by T.L. Phillips also
improved an early version of the manuscript. C. Martín-
Closas’s research in taphonomy is financed by the Spanish
Government under Projects BTE 2002-02650 and BTE
2002-04453-C02-01, and by the Catalan Autonomous
Government under Project 2001 SGR-00075.

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ACCEPTED NOVEMBER 16, 2004