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GEOLOGY, FLORISTICS AND PALEOECOLOGY OF LATE DEVONIAN COAL SWAMPS FROM APPALACHIAN LAURENTIA (U.S.A.)

by

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(5 figures)

ABSTRACT. - Coal-bearing sediments of the Late Devonian (Famennian) Hampshire Formation of the central Appalachian Mountains of West Virginia and Virginia in the eastern U.S.A. are the first widespread occurrence of true swamp-adapted plant communities in the Paleozoic. Both large deltaic marshes and smaller upland backswamp are dominated by the prefern *Rhacophyton.* Analyses of horizontal and vertical transects reveal that other plants contribute to the swamp peats only as a result of transport during floods and storms or by increased proximity of flood plain communities to swamps as lateral encroachment occurred during ecological succession. The data reveal a near swamp community of tree lycopods whereas the drier floodplain had other trees *(Archaeopteris/Callixylon)* of progymnosperm affinity. The Hampshire coal swamps are remarkable for their lack of diversity and for the near swamp community of tree lycopods. These contrast with Early Carboniferous coal swamps where either tree lycopods dominate or diversity is greater.

RESUME. - Des sédiments contenant du charbon de la Formation Hampshire du Dévonien supérieur (Famennien) de la partie centrale des Monts Appalachiens, dans les Etats de Virginie occidentale et de Virginie, dans l'est des Etats-Unis, représente la première vaste apparition au Paléozoïque de véritables communautés végétales adaptées aux milieux marécageux. De grands marais de delta et de plus petits marais d'arrière-pays sont dominés par la "préfougère" *Rhacophyton.* Des analyses de transects horizontaux et verticaux révèlent que d'autres plantes ont contribué à la formation de la tourbe mais seulement parce qu'elles ont été transportées pendant les inondations et les tempêtes ou bien, à cause de la proximité entre ces marécages et des communautés de plaines inondées, à l'occasion d'empiètements latéraux au cours d'une succession écologique. Les données témoignent de l'existence d'une communauté de lycopodes arborescents, proche du marécage tandis que la plaine moins inondée portait d'autres arbres *(Archaeopteris/Callixylon)* à affinité de progymnospermes. Les marécages tourbeux de la Formation Hampshire sont remarquables par leur manque de diversité et par la communauté de lycopodes arborescents, voisine. Ceci contraste avec les marais tourbeux du début du Carbonifère où soit les lycopodes arborescents dominent, soit la diversité est plus grande.

INTRODUCTION

Coal deposits that predate the Carboniferous are well known. Some are even as old as Algonkian (Stach *et al.,* 1975), but coals do not occur in terrestrial strata until the Devonian when vascular plants became widespread on land. Some of the earliest vascular plants (e.g., some *Zosterophyllum, Rhynia, Horneophyton,* Lele & Walton, 1962; Kidston & Lang, 1917, 1920) seem to have grown in wet, swampy areas, but peat either did not accumulate or the geological circumstances prevented the formation of coal. Coal seams do not become common until the Middle and Late Devonian (Stach *et al.,* 1975). However, these coals are either algal or only questionably of vascular plant origin (Gorsky, 1964; and the extensive literature cited in Meyerhoff 1970 and Heckel & Witzke, 1979). In any case, documentation of peat-forming plant communities in the Devonian from which coal was produced is lacking.

For this reason the extensive coals associated with beds of the upper Hampshire Formation (Famennian) of West Virginia from which the earliest seeds have been found (Gillespie, Rothwell & Scheckler, 1981) were of immediate interest. This curiosity led to an extensive survey of the Hampshire Formation exposed

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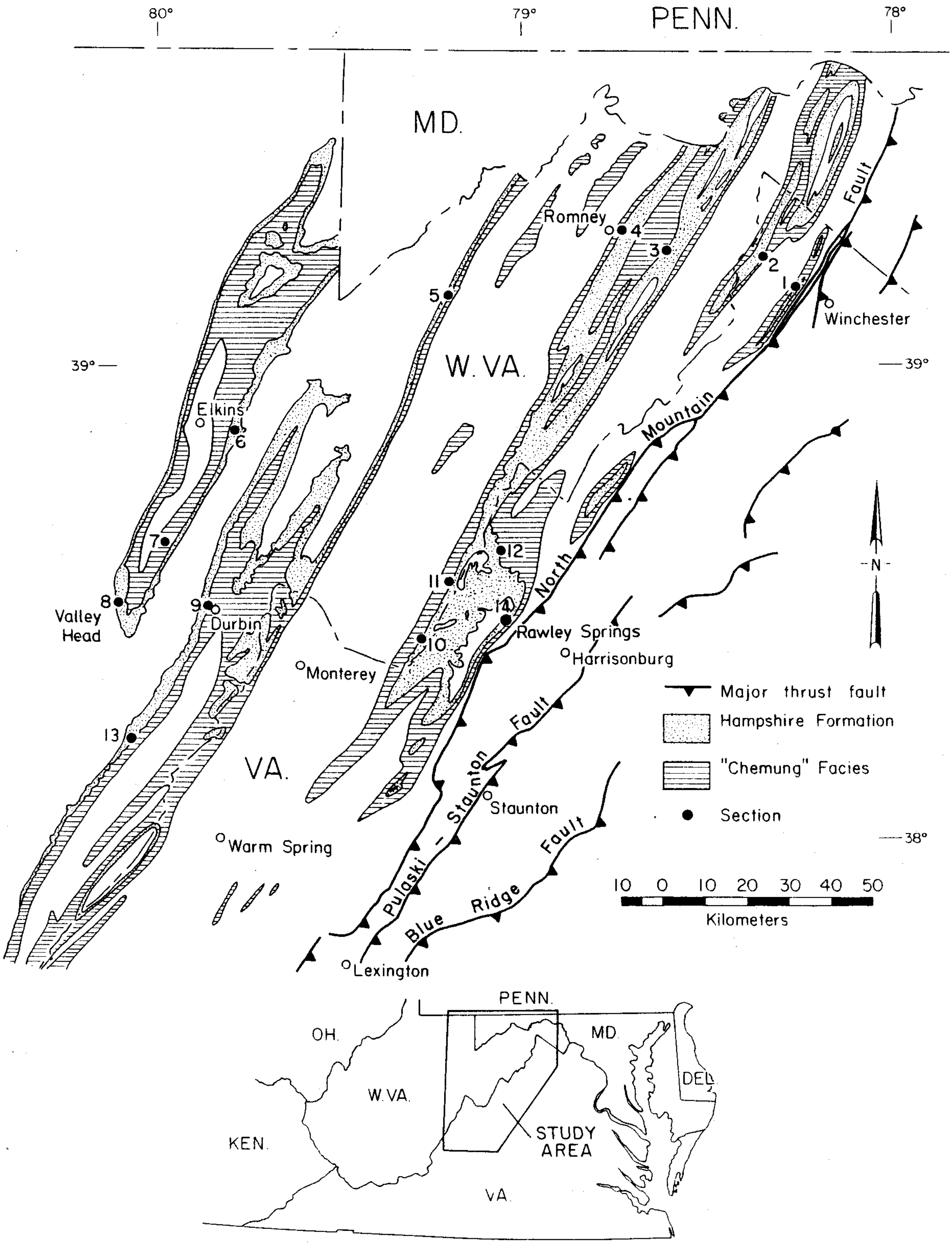


Figure 1. - Study area, distribution of Late Devonian terrestrial (Hampshire Formation) and shore ("Chemung" Facies) beds in the central Appalachians, and some of the localities used.

in roadcuts and private quarries in eastern West Virginia and adjacent Virginia and Maryland for additionnal information on these Late Devonian coals. This initial survey resulted in the selection of over 30 sites that had geological and paleobotanical promise. From these, sites were chosen for this study of coal-bearing strata (fig. 1) and for other studies of non-swamp terrestrial deposits. The criteria for selection were sufficient exposure amenable to excavation to reveal the structure necessary to characterize the depositional history and the presence of identifiable plant fragments.

GEOLOGY OF THE HAMPSHIRE FORMATION

The marine "Chemung" sands and overlying nonmarine red beds of the North American Appalachian Basin are the upper portion of a thick clastic wedge shed to the west from a rapidly uplifted tectonic highland to the east. This wedge thins to the west and the red beds do not extend so far as the underlying marine strata (fig. 1) (Colton, 1970).

The disturbance responsible for this wedge is called the Acadian Orogeny. Acadian events commenced in the Early Devonian in New Brunswick and Maine and gradually progressed southwesterly so that they reached Virginia only by the Late Devonian and Early Carboniferous (Oliver, 1980). This orogeny has been interpreted as the result of the closing of the Iapetus Ocean with subsequent collision between Laurentia, Baltica, Avalonia, and England (Scotese *et al.,* 1979; Bambach, Scotese & Ziegler, 1980). The suturing of Laurentia and Baltica formed the supercontinent Laurussia and resulted in a rapidly uplifted and geologically complex source area, known as the Acadian Mountains (Allen & Friend, 1968). By Late Devonian and Early Carboniferous, however, the Acadian Orogeny had subsided somewhat so that continued erosion of the uplands produced broad, flat coastal plains (Bambach *et al.,* 1980).

Since collision began to the northeast and commenced gradually southwestward, the marine and nonmarine beds are diachronous and are younger to the west. The red bed sequence in West Virginia and Virginia of Late Devonian age is called the Hampshire Formation to distinguish it from the older "Catskill" Formation named from the classic red bed sequence in the Catskill Mountains of New York.

The Hampshire Formation is generally thickest to the northeast and both thins and becomes subsurface to the southwest. Likewise, this formation is older to the northeast.

Hampshire sediments are always regarded as Late Devonian in age, but range from Late Frasnian in adjacent Pennsylvania to Mid to Late Famennian in Randolph County, West Virginia (Oliver *et al.,* 1968; Price *et al.,* 1968). Since correlation of our localities is important to these studies, we have supplemented regional stratigraphy with plant macrofossil floral assemblages (after Banks, 1980) and microfossil spore zonation. Spore zonation at two of our localities (fig. 2A, D) shows that these beds are mid Late Famennian (Fa2C), Cassadaga Stage, Chautauquan Series (Clendening, Eames & Wood, 1980; G. D. Wood, personal communication, 1980; Gillespie, Rothwell & Scheckler, 1981). The other localities have similar macrofossil floral assemblages as these two.

Hampshire beds are mainly deposited under alluvial and fluvial conditions (Meckel, 1970) so that they are not laterally continuous and great areas are presently covered by vegetation and soil. In addition, the docking of Africa with Laurentia in the post-Carboniferous Alleghenian Orogeny (Bambach *et al.,* 1980; Oliver, 1980) compressed and folded these beds so that they are laterally foreshortened (Gwinn, 1970) thus making intra-formational correlation especially difficult.

PROCEDURES

GEOLOGICAL STRUCTURE

The geological interpretations necessary for this study were undertaken primarily by W.S. McClung (1983). Detailed measured sections were prepared for these and many other sites. The data recorded include the vertical sequence relationships, sedimentary structures, gross petrography, flora and fauna, and biogenic structures. Sedimentary structures were related to modern hydraulic regimes and depositional processes. From these were built the paleoenvironmental interpretations upon which the paleoecological conclusions rest. In this we have followed the examples of Oshurkova (1977) and Scott (1977, 1979).

AGE OF BEDS

Age assignment and intra-formational correlation relied upon the analysis of floral assemblages found in our samples and followed the guidelines of Banks (1980) for macrofossils or utilized the kind assistance of J.A. Clendening and G.D. Wood (Amoco Production Company, Houston, Texas) for microfossils.

PLANT IDENTITY

Identification of the plants rests upon prior work done by many paleobotanists to characterize the taxa. Of especial help, however, was the extensive outcrop at Elkins, West Virginia (fig. 2A) which provided thousands of plant fossils preserved in virtually every conceivable way. Study of these helped identify the often less intact plants from the other localities.

Three plants comprise the flora of the coal-bearing rocks and adjacent strata : *Archaeopteris* a progymnosperm tree the wood of which is called *Callixylon* (Beck, 1960, 1964b), the prefern *Rhacophyton,* and a new genus of tree lycopod. Other plants occur in small

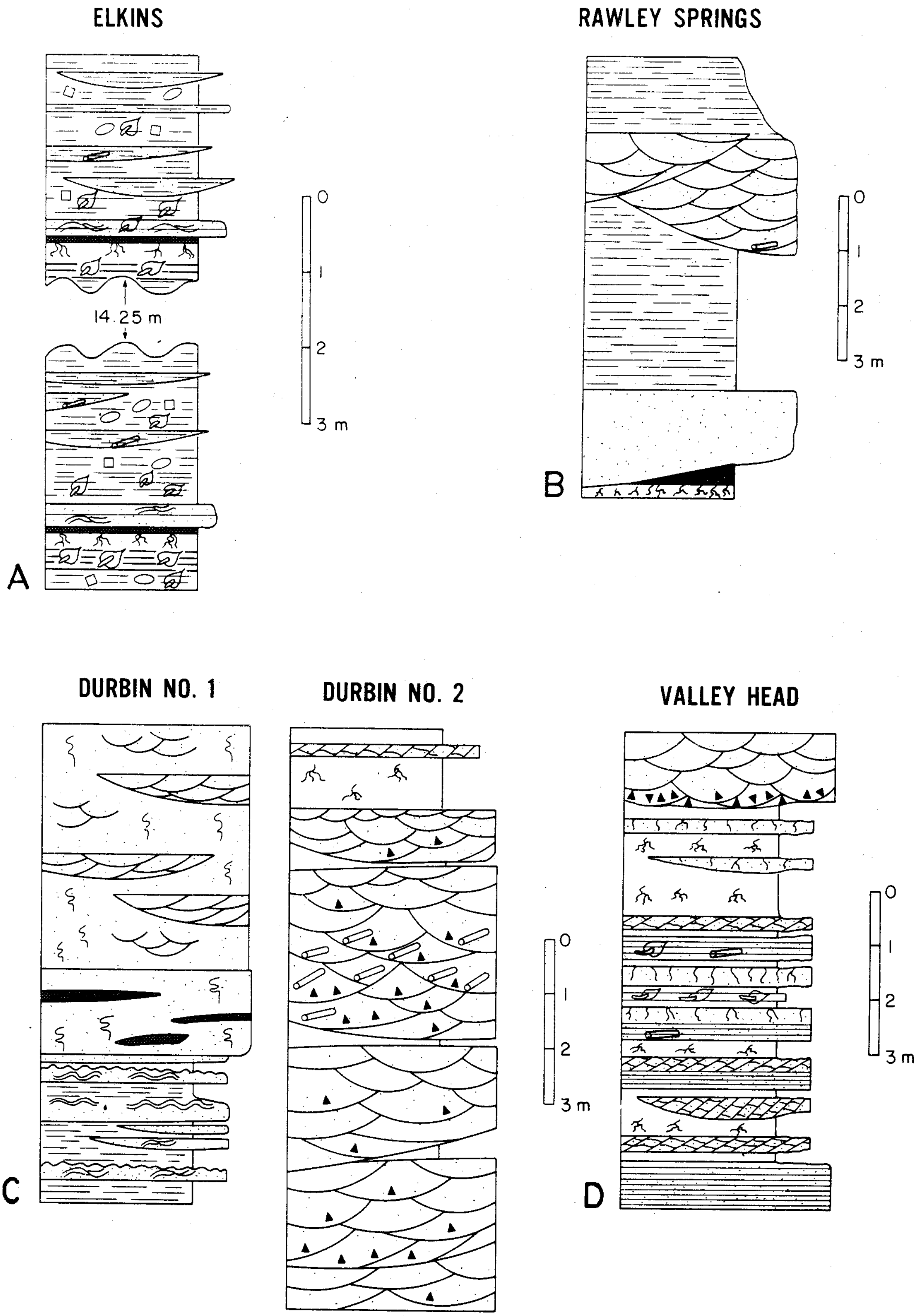


Figure 2. - Generalized geological sections of four study sites that illustrate shore (A, C) and terrestrial (B, D) facies assemblages.

numbers and are listed in the next section on the localities.

Archaeopteris was originally named for leaf-bearing branch systems that resemble compound leaves and was later found to be the terminal twigs of a large tree the trunks and branches of which are called *Callixylon* when they can be shown to have certain features of wood anatomy (Beck, 1960). The tree as a whole has come to be reasonably well understood and is reconstructed by Beck (1962, 1964*a*, 1971, 1981). The identification of species of *Archaeopteris* relies on the leaf morphology for the most part. Many names have been proposed, but we are following the studies of Arnold (1939) and Kräusel & Weyland (1941) who recognize only six species and numerous synonyms. Identification of *Callixylon* species utilizes the anatomy of the wood.

Racophyton is well known from the anatomy and morphology of its sterile and fertile branchlets and frond systems and excellent reconstructions of the plant can be found in Leclercq (1951), Andrews & Phillips (1968), and Cornet, Phillips & Andrews (1976).

The tree lycopod is currently being studied by Beeler and Scheckler (1983) and resembles some of the specimens included by Høeg (1942) and Schweitzer (1965) in *Protolepidodendropsis*. Our specimens include large trunks as well as leafy branches and twigs, some with anatomy.

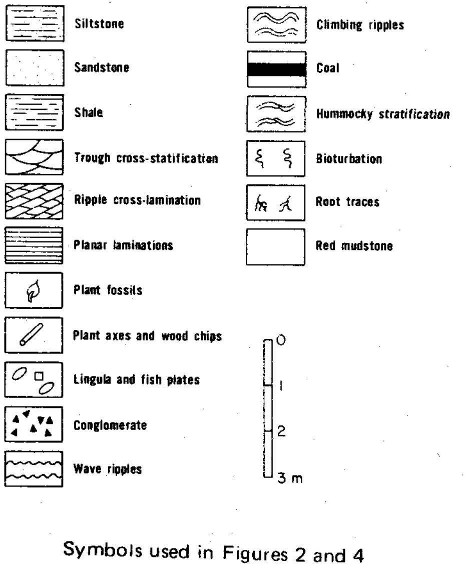
PLANT COVER

Plant cover of the rock matrix or peat residues is an approximation of the biomass contribution of each taxon. Depending upon the kind of preservation, several techniques were employed. For cleared bedding planes, or split blocks where beds could not be extensively excavated, a 0.5 x 1 m quadrat divided into 2.5cm squares was used. This quadrat technique is modified from that of Scott (1977, 1979) by using a larger format and by doing total counts of specimens and surface area covered by each taxon (vs. counts of specimens selected by dropping a needle through a plexiglass sheet [0.5 x 0.5 m] with a random array of 100 holes). Random counts, like Scott's do permit the use of statistical manipulations, but require a much larger sample size to replicate the results than was available in the Hampshire beds. The number of quadrats necessary to replicate the percent cover data was determined for each facies by repeating quadrats and adding the new data to the preceeding until the percentages of each taxon no longer changed.

These techniques are discussed by Scott (1977) who also addresses the topic of data presentation. For the Hampshire beds, the data are expressed as percent cover, normalized to 100 $^{o}/o$, because only a few taxa are involved. For comparison of the samples, however, the total cover of the matrix by plant fragments is also given in Figures 3 and 4.

All of the coal beds have some permineralization of axes by pyrite or hematite, but the two at Elkins, West Virginia (fig. 3) have large pyrite concretions that have permineralized the uncompressed peat matrix before its diagenesis into coal (Gillespie, Rothwell & Scheckler, 1981). These concretions conform to definitions of coal balls (Mamay & Yockelson, 1962) and will be so called herein.

Coal balls were collected from recorded positions within both coal beds at Elkins. Following the procedures developed by Phillips (e.g., Phillips, Kunz & Mickish, 1977) for sampling Carboniferous coal ball peats, hundreds of coal balls from each horizon were slabbed at one cm intervals and the smoothed surfaces examined under a dissecting microscope while covered with a clear acetate film marked in 1 mm squares. Taxa were identified by their anatomical characters and their percent cover of the slab recorded. Over 1500 cm^2 of coal ball slabs were examined for each seam since this quantity was shown by Phillips, Kunz & Mickish (1977) to adequately characterize a peat horizon. For Phillips this quantity was achieved with as few as 10 coal balls per seam. But the small size of the Hampshire coal balls required cutting hundreds in order to reach this number. (Phillips, personal communication, 1981). The data are presented as percentage cover (normalized to 100 $^{o}/o$) histograms, similar to Phillips' treatments.



Symbols used in Figures 2 and 4

LOCALITIES AND THEIR GEOLOGICAL SETTINGS

Four localities were selected as especially pertinent to this study (fig. 2A-D). Two of these (A and C) are shoreline and two (B and D) are flood plain assemblages. These were chosen to facilitate comparisons. The following descriptions are condensed from the more lengthly treatments in McClung (1983) and copies of his measured sections and interpretations are available from Scheckler upon request.

LOCALITY A

Elkins, Randolph County, West Virginia (38° 54'25"N, 79°43'42"W), 10 km east of the intersection of US rt. 33 and WV rt. 219 on the south side of US rt. 33 (fig. 1, 2A, 3). Part of the interval is covered, but the study section consists of two 15 cm thick coal beds separated by 17 m of delta sediments and the surrounding strata. At the bottom of the section are medium bedded mudrocks and sandstones with isolated plant axes and specimens of *Lingula* followed by planar-laminated beds with abundant *Sphenopteris* and seed plant remains. Above this is a thin bioturbated zone with numerous rooted axes of *Rhacophyton* followed by the lower coal bed. Above the coal lies a thick series of mudrocks and sandstones with abundant plant remains and numerous fish scales and bone fragments and isolated *Lingula*. Some sandstones are hummocky cross-stratified. Above this the sequence is repeated as the second coal bed is approached. Both coals are laterally extensive; the upper one has been followed for 30 m, the lower one for over 50 m. Pyrite coal balls are distributed horizontally near the middle of each coal bed.

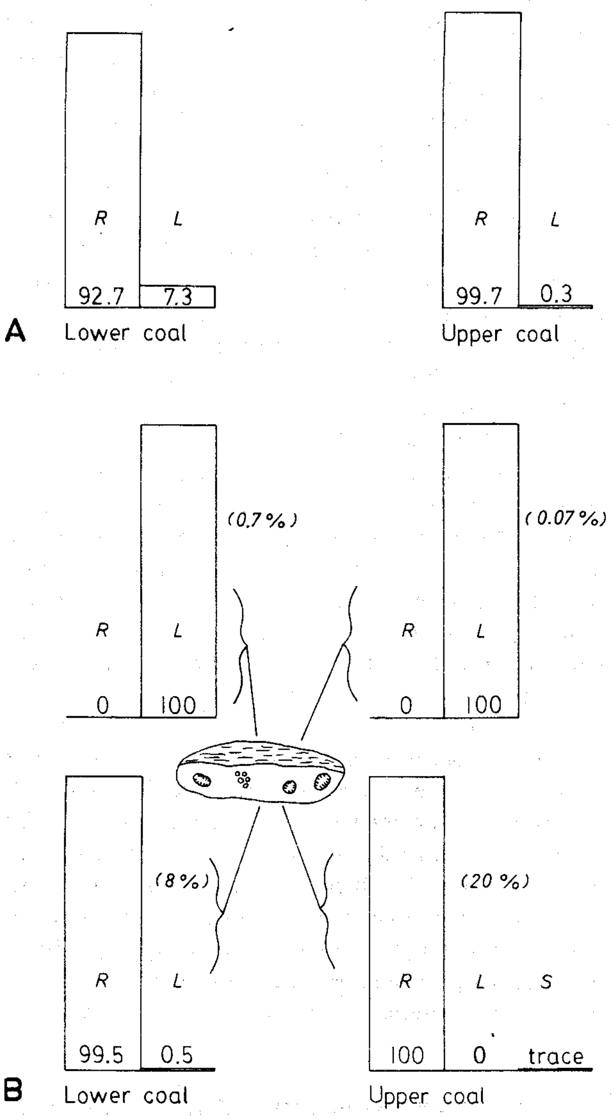


Figure 3. - Histograms showing percent cover of plants (normalized to 100 °/o) determined by analyses of coal balls from two coal beds at Elkins, West Virginia.
Symbols : R. *Rhacophyton;* L. lycopod; S. seed plant. A. Data pooled from upper and lower parts of heterogeneous mixed coal balls. B. Data for the upper allochthonous and lower autochthonous parts shown separately. Actual percent cover (surface area of plants / total surface area X 100) shown in parentheses to the right of each histogram.

The presence of a few hummocky cross-stratified sandstones indicates that the waning stages of storm-wave action were responsible for their deposition. The mixture of beds with plant remains, fish scales, and *Lingula* suggests that this was a shoreline environment where marine and continental conditions interplayed. The bioturbated and rooted zones beneath the two coal beds suggests that these were autochthonous communities that colonized a delta lobe that was temporarily exposed and abandoned. Subsequent de-fluidization returned the delta lobe to active deposition of marine sediments mixed with terrestrial debris. The fine clastic regime of these beds suggests that this was a low energy shoreline with an extended, gently sloping mud beach protected by offshore shoals of the coarser "Chemung" facies found downsection.

Species List

Archaeopteris macilenta, A. halliana, A. hibernica, A. obtusa, A. sphenophyllifolia, Callixylon erianum, Rhacophyton ceratangium, Barinophyton sibiricum, synangia resembling *Aneurophyton olnense, Sphenopteris* sp., seeds and cupules, *Hierogramma* sp., *Xenotheca* sp., *Condrusia* sp., *Sphenophyllum subtenerrimmum,* cf. *Eviostachya* sp., and a new tree lycopod.

LOCALITY B

Rawley Springs, Rockingham County, Virginia (38°31'15"N, 79°03'35"W), 1 km west of Rawley Springs on east side of US rt. 33 (fig. 1, 2B, 4). A coal bed up to 1.5 m thick rests on a bioturbated and partly rooted mudrock with uneven topography (fig. 4A) at the top of a fluvial fining upward cycle. The coal is in turn cut by the high relief erosion surface of the next cycle above. Within both cycles the erosion surface is overlain by trough cross-stratified, hematite cemented sandstones which fine upward into bioturbated and oxidized siltstone and mudstone.

This type of cycle is interpreted to have been deposited by a river or stream wandering or meandering over a low gradient alluvial plain. The trough cross-stratified sandstones comprising the bases of the cycles represent channel deposits while the finer bioturbated siltstones and mudrocks represent overbank or flood plain sediments homogeneized by burrowing organisms or plant roots away from higher energy channels. The presence of a coal bed indicates that a swamp temporarily existed on this flood plain such that peat accu-

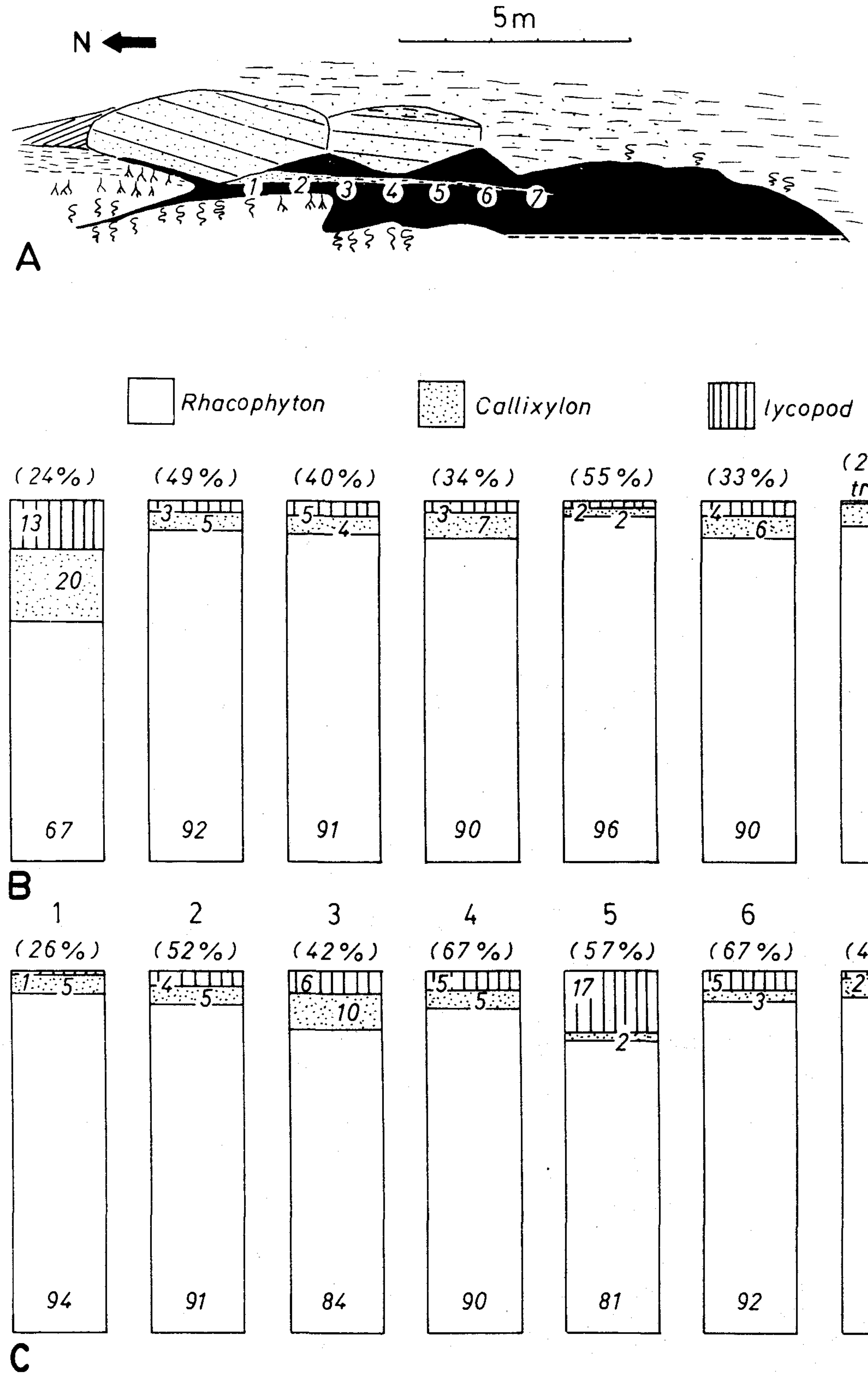


Figure 4. - Coal bed at Rawley Springs, Virginia.

A. Generalized geological cross section showing the depositional topography of the north end (south end buried under the road), adjacent flood plain sediments, positions within the bed (1-7) where samples were taken at 1 m intervals, position of crevasse splay tongue in coal, and erosional contact with the overlying fluvial cycle.

B. Histograms of percent plant cover (normalized to 100 %) from the crevasse splay sampled along the 7 m transect. Actual total percent cover shown in parenthesis at top of each histogram.

C. Histograms of percent plant cover (normalized to 100 %) from the middle of the coal seam the 1, 3, and 5 meter intervals were much siltier than the others. Actual total percent cover shown in parentheses at top of each histogram.

mulated and was preserved. This suggests a very low gradient or low clastic input or both. The topography of the rooted and bioturbated mudrock under the coal suggests that this was an oxbow or backswamp continuous with the adjacent soil. Silty partings in the coal suggest occasional influxes of sediment due to flood events. One parting (fig. 4A) fines laterally and possibly represents a portion of a crevasse splay. Although thick, the coal bed extends only 15 m.

Species List

Racophyton sp., *Callixylon* sp., and a new tree lycopod.

LOCALITY C

Durbin, Pocahontas County, West Virginia (38^{o} 32'55"N, 79^{o}49'11"W), along the north side of US rt. 250 (fig. 1, 2C). The section Durbin No. 1 begins 1 km east of Durbin on US rt. 250 and continues to the eastern edge of town. Durbin No. 2 begins at the western edge of town and continues for 1 km west of Durbin on US rt. 250. Inbetween is a covered interval and possible folding. From the bottom of Durbin No. 1, are medium bedded, plane laminated mudstones and sandstones with hummocky cross-stratification capped by a massive sandstone with trough cross-stratification and with numerous plant axes and coaly lenticels up to 5 cm thick. Fragments of brachiopods and crinoids are common. From the bottom of Durbin No. 2 is found mostly massive sandstones with some tabular but most often trough cross-stratification. Plant axes occur as lags with quartz pebbles. The sandstones become less massive and are capped by red mudstone with root traces and a sandstone with ripple cross-lamination.

This section is dominated by marine channel deposition as is evidenced by fragments of crinoids and brachiopods. Coaly debris suggests the transport of plant material during floods. Portions of the proximal channel system are adjacent to tidal flats colonized by plants.

Species List : *Callixylon* sp.

LOCALITY D

Valley Head, Randolph County, West Virginia (38^{o}32'03"N, 80^{o}03'48"W), 3.5 km west of the intersection of WV rt. 219 and WV rt. 15 on the north side of WV rt. 15 (fig. 1, 2D). The fossiliferous horizons are found within the upper silt to mudrock fraction of a fluvial fining upwards cycle. The lower sandstone fraction of the cycle consists of 1.5 m of plane laminated, hematite cemented sandstone overlying a scoured surface. The plane laminated sandstone indicates upper flow regime conditions and suggests high energy deposition related possibly to a sheet flood or braided stream origin. These two types of environments characteristically have steeper gradients than the meandering stream environment, such as is interpreted for locality B. This cycle is enclosed by numerous other types of fluvial cycles which reinforces the interpretation that it is fluvial (possibly even upper delta plain) rather than lower delta plain in origin.

The main fossiliferous horizon within this cycle was deposited in its upper part where overbank muds and silts accumulated and were bioturbated by burrowing organisms or plant roots. This suggests that this horizon was deposited some distance from the higher energy channel or sheetflood environments suggested earlier.

Species List

Racophyton ceratangium, Archaeopteris macilenta, A. halliana, A. hibernica, Callixylon sp., and a new tree lycopod (very rare).

RESULTS

ELKINS

One of the trenches dug at this locality is shown in Figure 2A where the lower coal bed is exposed. The delta beds just below the plane laminated strata have yielded the only *Barinophyton* yet found in the Hampshire. The plane laminated beds have very high concentrations of *Sphenopteris* and seed plant remains (Gillespie *et al.,* 1981), often forming nearly pure mats. The rooted zone above this contains mostly foliar axes of *Rhacophyton* which suggests that this was a soil colonized by vegetative propogation. We have seen many such specimens. They suggest that *Rhacophyton* was more scrambling than previously thought and that foliar members could reiterate when in contact with a suitable substrate. The delta sediments between the two coal beds contain roughly 40 ^{o}/o *Rhacophyton,* 40 ^{o}/o *Archaeopteris,* 10 ^{o}/o tree lycopod, and 10 ^{o}/o other plants including cupules and seeds. Al together, these storm beds carry the most diverse flora yet seen in the North American Famennian.

The coal beds themselves have been studied both by splitting along shaley partings and by analysis of coal balls, but most of the data comes from the latter (fig. 3). When all the data for the coal balls are pooled (fig. 3A) then the coal flora consists mostly of *Rhacophyton* foliar axes, but has a small component of lycopod fragments. These latter are mostly megaspores and fragments of megasporangiate strobili, but include also some small xylem strands.

A closer look at the coal balls, however, shows that they are all two parted (fig. 3). The lower portion contains uncompressed permineralized peat while the upper part contains mostly compressed peat with a few fish scales, rare brachiopods, and the lycopod spores. The lower portion contains rooted axes in their growth orientation and is obviously autochthonous. Although these coals could possibly be allochthonous beach deposits on previously rooted soil horizons, the nearly perfect correspondance of taxa in the *in situ* rooted communities and the overlying coals suggests that this is not so. This conclusion is also supported by the almost total lack of correspondance between the coal floras and those of the delta storm beds, the plants of which are clearly deposited as allochthonous debris at the shoreline.

When the coal balls are re-examined (fig. 3B) the autochthonous swamp community can be seen to consist of almost pure stands of *Rhacophyton.* The lycopod fragments occur almost exclusively in the allochthonous assemblage and are probably brought to the swamp by the same events that led to the pyrite permineralization. Pyrite forms rapidly in salt marshes (Howarth, 1978; Altschuler *et al.,* 1983) and especially so in sediments covered by marine water (Filipek & Owen, 1980; Maynard, 1980). This suggests that the horizontal distribution of coal balls near the mid seam of both coal beds may indicate inundation by sea water of the swamp during only one or a few nearly synchronous storm events. This inundation was probably only temporary since coal deposition resumed in both beds. Later inundations occurred as the delta lobe subsided and deposition of delta storm beds commenced.

The absence of *Archaeopteris/Callixylon* from the coals, otherwise a major component carried by the delta drainage system, suggests that neither long shore drift nor waves brought much plant debris into the swamp. The rare presence of lycopod debris in the allochthonous portion of the coal balls suggests that a community of tree lycopods existed at the proximal, landward fringes of the marsh and provided the bouyant fragments that were drawn into the swamp as the storm waters retreated from the land.

Although the coal ball data for the two swamps show great uniformity, there are some differences. The coal balls from the upper coal contain more plant material in the autochthonous part (20 vs. 8 $^{o}/o$) and have a high percentage of the total *Rhacophyton* material represented by sporangial clusters (37 $^{o}/o$ of total) whereas no fertile *Rhacophyton* was encountered in the coal balls from the lower coal. The lower coal is also far less pure. In some places it contains so much pyrite as to be a carb-pyrite and in other places it has so much sediment as to be a carb-shale. The upper coal, however is uniformy pure, except for the coal ball horizon in its middle, throughout its observed 30 m span.

RAWLEY SPRINGS

Figure 4A shows the exposed coal bed and the enclos. The floodplain sediments at the north end (fig. 4A) are extensively bioturbated and closer to the swamp are rooted. Some of the roots are permineralized, but their identity has not yet been established. The other beds adjacent to the coal contain no identifiable plant remains. Therefore, the floristic analysis of this locality is confined strictly to the coal. The coal coarsens upward as numerous small partings of silt and shale occur. This suggests the filling in of a topographic low area on the flood plain. Corroborative evidence comes from the topography of the mudrock beneath the coal. In the half that is visible (the other half lies beneath the road) a definite deepening occurs to the south (fig. 4A). Furthermore, this mudrock is rooted beneath the edge of the swamp *but not in its middle,* which is, however, bioturbated. This suggests that the initial colonization of the site occurred at the edges and gradually filled in the depression with peat. Rooted *Rhacophyton* axes are common in the mid and upper coal, however, so that once filled, this plant probably grew throughout the swamp.

Vertical transects through the coal show that the layers in the lower 1/3 are too peatified to show recognizable plant parts; only a few woody fragments are visible. But from the middle upwards plants are well preserved and the floristic content can be studied by splitting the coal for quadrat analysis. This was done along a 7 m horizontal transect (fig. 4A) where coal samples were taken from the middle and from a carb-silt that immediately overlay them. This carb-silt layer extends from the north edge of the coal bed and thins and fines towards the middle. It appears to be continuous with a similar layer extending from the flood plain sheets to the north and is interpreted as a sectional view of a portion of a crevasse splay tongue.

The plants are fragmentary, but show characteristic features of foliar axes and roots of *Rhacophyton,* wood of *Callixylon,* much of which is partly permineralized and was examined anatomically, and axes of the new tree lycopod that show the positions of leaf cushions, leaves, and decortication surfaces.

The results of analyzing the apparent crevasse splay layer are shown in figure 4B. The matrix was quite sandy at the 1 m interval but became silty and shaly and extensively slickensided by the 6 and 7 m intervals. *Rhacophyton* dominates all the samples, but that from the 1 m interval contains an unusually large amount of lycopod and *Callixylon.* The *Callixylon* wood is always fragmentary and none of the terminal twigs *(Archaeopteris)* are present. The lycopod axes are often decorticated although some small twigs still have their leaves.

The mid seam results are shown in figure 4C. These too are dominated by *Rhacophyton,* much of which shows roots. The samples from the 3 and 5 m positions were especially silty and contained more *Callixylon* and lycopod fragments. Here the *Callixylon* is also represented only by fragments and the percentages of each taxon seem to change abruptly from one station to the next within the transect (fig. 4 B, C), replicate (double or triple) analyses of the same stratum demonstrate that this quadrat technique genuinely characterizes the floristic and sediment content of each station. The variation seems not, therefore, to be introduced by the method of data collection, but arises from the positions of the samples with respect to the edges of the swamp or to the presence of internal drainage pathways.

Overall, this evidence suggests that the swamp was colonized almost exclusively by *Rhacophyton.* The other plants are found only when sediment was introduced to the swamp which became more common in the upper layers. In general, the greater the amount or the coarser the sediment (fig. 4), the more other plants occur. The *Callixylon* specimens are obviously transported some distance to the swamp, possibly during floods. The lycopod axes are also probably transported to the swamp, but seem to have suffered much less damage.

DURBIN

All of the coaly plant material seen in the marine channel deposits here consists of rounded logs of *Callixylon.* This contrasts with the deltaic shoreline deposits at Elkins where numerous other plants occurred. Of especial interest is the lack of lycopod remains since these constitute a significant portion of the detritus carried by marine waters at Elkins, especially those penetrating the marshes. Whether these differences result from the differential survival of plant tissues during high energy transport or reflect differences in the distribution of plants along the drainage systems on land or both, remains unknown.

VALLEY HEAD

Rhacophyton and *Archaeopteris/Callixylon* codominate these flood plain deposits with each forming roughly 45-55 °/o of the total. *Rhacophyton* tends to be slightly more abundant in the beds so far sampled, but the distribution of plants is very heterogeneous with large pockets of one or the other. Continued sampling might revise these numbers slightly. Only one specimen of the tree lycopod was seen and it was decorticated. This assemblage contrasts markedly with that from Rawley Springs where the lycopod is not uncommon and often well preserved and where *Archaeopteris/Callixylon* is represented only by fragments of obviously transported wood. At Valley Head the *Archaeopteris* specimens far outnumber the logs of *Callixylon,* but both show some evidence of fragmentation when compared with the material recovered from the Elkins delta storm deposits.

PALEOECOLOGICAL INTERPRETATIONS

The evidence presented here suggests that only one plant, *Rhacophyton,* colonized these Late Devonian swamps. *Rhacophyton,* however, is also abundant on the higher gradient, presumably drier, sites at Valley Head. Little of this material is rooted and most seems to have been transported some distance. But on the whole, the Valley Head *Rhacophyton* was a remarkably tolerant plant or we are unable to detect differences amongst closely related species. There are some differences between the Elkins delta *Rhacophyton* and the Valley Head flood plain specimens. The former have less delicate appearing ultimate foliar segments and have smaller fertile aggregates. However, the anatomy of foliar axes and roots is identical among specimens from the two localities. At present we cannot decide if these apparent differences in morphology are taxonomic and reflect the divergence of species for wet and drier habitats. These *Rhacophyton* collections are currently being studied to resolve this issue. For now, however, they will all be called *R. ceratangium* since there appears to be no simple way to distinguish amongst them.

Where leafy branches of *Archaeopteris* are abundant (Valley Head and Elkins) we note no particular patterns of distribution or species association except that the Elkins site seems to be slightly more diverse. Most of the *Callixylon* material is too compressed to permit tangential views of the wood. Therefore, the species cannot be identified even though the radial grouping of pits does allow one to identify the genus.

Equating the wood genus *Callixylon* with the leafy branch systems of *Archaeopteris* was first suggested by Beck (1960) when he announced his discovery of the connection between the two and has been amplified by him later, (Beck, 1964b). Further study is needed, however, before we will know if all species of *Callixylon* bore branches that we would call *Archaeopteris* and if all *Archaeopteris* had wood like *Callixylon.*

The distribution of *Archaeopteris* and *Callixylon* in shore sediments is interesting. Neither occurs in the storm rafted marine debris found in the Elkins coastal marshes. Yet both occur in the delta storm deposits at Elkins and *Callixylon* is the only plant found in the marine channels at Durbin.

This contrasts with the tree lycopod which seems to constitute the sole plant transported into the Elkins swamps as a result of storms or other unusual events and which is absent from the Durbin sections. The lycopod does, however, occur with *Archaeopteris* and *Callixylon* in the delta storm deposits at Elkins, but is always decorticated.

At Rawley Springs the lycopod occurs with *Callixylon,* but the former is often well preserved and the latter is represented only by transported pieces of wood. These data all suggest that the lycopod tree grew in proximity to *Rhacophyton* swamps and remote from stands of *Archaeopteris. Archaeopteris* seems to have grown on the flood plains where its litter could be easily picked up and transported during floods.

The reconstructions of Late Devonian landscapes in figure 5 combine these data into paleoecological interpretations and add some new information not previously discussed. For example, the seed plant in figure 5A (Rothwell, Scheckler & Gillespie, in manuscript) is interpreted as a pioneer of levees. And the *Barinophyton* in figure 5A (Scheckler, in manuscript) is interpreted as a shore adapted plant.

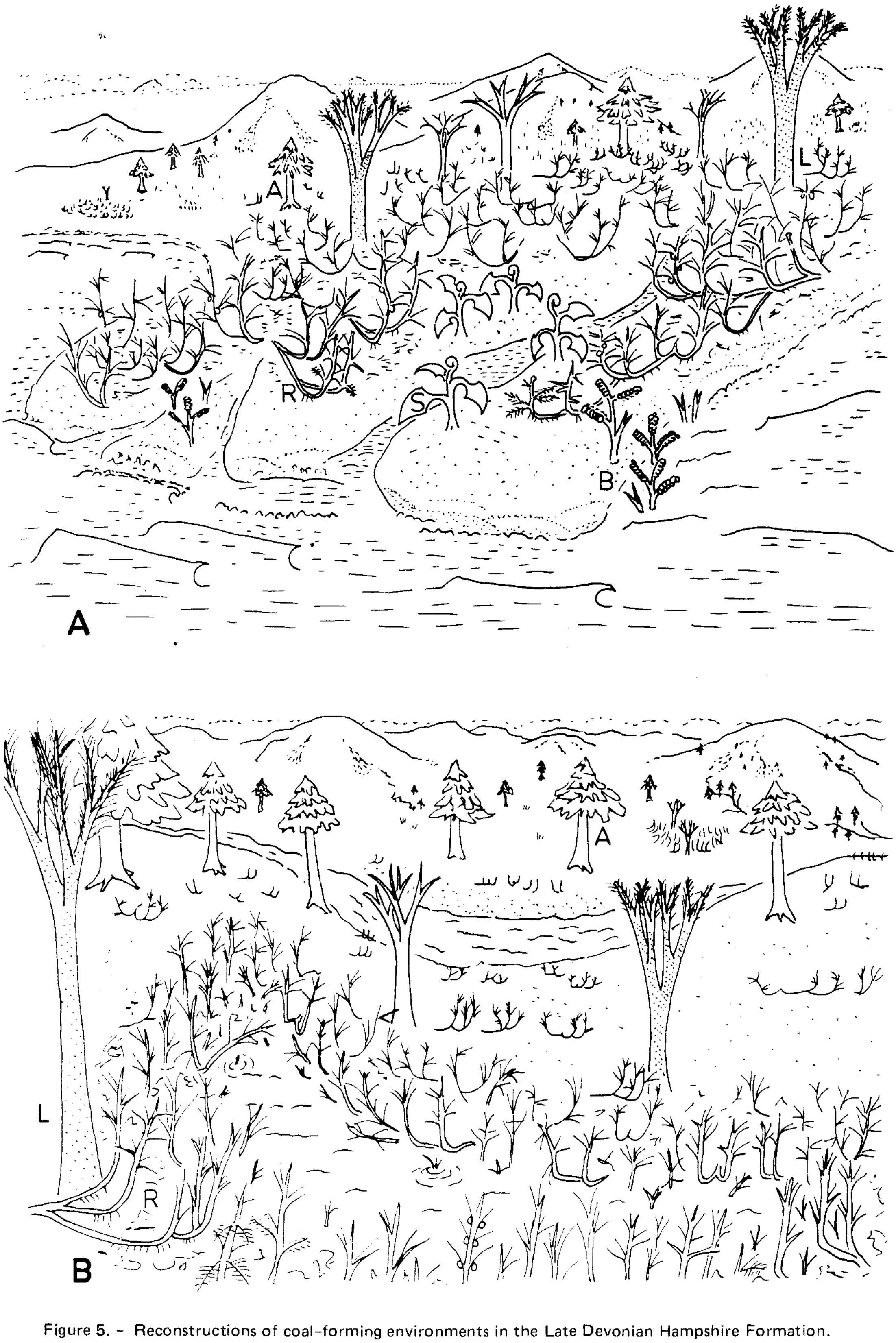


Figure 5. - Reconstructions of coal-forming environments in the Late Devonian Hampshire Formation.
Symbols : R, *Rhacophyton;* B, *Barinophyton;* A. *Archaeopteris (Callixylon);* S, seed plant; L. tree lycopod.
A. Deltaic marsh like those from Elkins, West Virginia.
B. Backswamp on the upland floodplain like that from Rawley Springs, Viriginia.

The large coastal marshes (fig. 5A) consisted mostly of *Rhacophyton* with an inland fringe of tree lycopods in the adjacent near swamp. *Archaeopteris* seems to have preferred drier sites on the coastal plain, but its fragments were still available for fluvial transport to the delta channels.

Upland backswamps (fig. 5B) also consisted mostly of *Rhacophyton.* But their smaller size allowed the near swamp tree lycopods to contribute occasionally to the peat. The drier flood plain was colonized mostly by *Archaeopteris* and *Rhacophyton.* Whether the same species of *Rhacophyton* dominated the swamps and codominated the floodplains will be resolved by further study of collections from all these environments.

In addition to data on plants, these analyses show that different facies carry different portions of the flora. Delta storm beds carry a complex mixture of plants from the deltaic drainage system in which the original associations are now obscure or are lost. Rooted autochthonous communities that lived on portions of the delta may be preserved as subsidence and burial by low energy marine sedimentation occurred. These seem to faithfully reflect the original community structure.

Plants found in floodplain deposits are mainly allochthonous to hypautochthonous, but some, in rooted backswamp beds, may be mostly autochthonous. The percentage of introduced elements into the latter depends upon the frequency with which flood sediments enter the swamp and the size of the swamp. Small swamps, or those being filled in and ecologically succeeded, will show some introduction of adjacent plants as their proximity to the swamp increases.

Proximal channel-dominated marine deposits and the more distal turbidites derived from them will carry a flora restricted either by differential survival during transport, with large woody axes surviving longest, or to those plants growing at the edges of the drainage system or both.

Of all the facies, low energy, delta-dominated shorelines will carry the most extensive and diverse remnants of the flora and high energy, channel-dominated deposits will have the least. Autochthonous communities may also contain some hypautochthonous and allochthonous elements depending on the depositional history.

CONCLUSIONS

As the Acadian Orogeny subsided and swamps became more common, only one plant *(Rhacophyton)* from the Late Devonian (Famennian) flora actually colonized them. This is true regardless of whether the swamps occur at the shoreline or in the uplands and suggests that salinity was unimportant in the floristic zonation of swamps. Since *Rhacophyton* is also an abundant part of non-swamp floras, it was probably not wholly adapted to swamp conditions, but was merely tolerant of them.

rely tolerant of them. No plant was yet adapted solely for swamp life.

A near swamp community of tree lycopods existed, but was only an infrequent contributor to peat accumulation. These Late Devonian swamps are remarkable for both their lack of diversity and their community of near swamp lycopods. Only later in the Early Carboniferous did tree lycopods adapt to swamp life (Scheckler & Beeter, 1984; Scheckler & Jennings, in press). This suggests that new introductions to the swamps came by adaptation of near swamp plants as this ecosystem expanded and became a major habitat in the Carboniferous.

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