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Plant paleoecology of the Late Devonian Red Hill locality, north-central Pennsylvania, an Archaeopteris*-dominated wetland plant community and early tetrapod site*

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ABSTRACT

The Late Devonian Red Hill locality in north-central Pennsylvania contains an *Archaeopteris***-dominated plant fossil assemblage, a diverse fossil fauna, and an extensive sedimentary sequence ideal for investigating the landscapes and biotic associations of the earliest forest ecosystems. Sedimentological analysis of the main plant-fossil bearing layer at Red Hill indicates that it was a flood-plain pond. A seasonal wet-and-dry climate is indicated by well-developed paleovertisols. The presence of charcoal interspersed with plant fossils indicates that fires occurred in this landscape. Fires appear to have primarily affected the fern** *Rhacophyton***. The specificity of the fires, the distribution profile of the plant remains deposited in the pond, and additional taphonomic evidence all support a model of niche partitioning of the Late Devonian landscape by plants at a high taxonomic level. At Red Hill,** *Archaeopteris* **was growing on the well-drained areas;** *Rhacophyton* **was growing in widespread monotypic stands; cormose lycopsids grew along the pond edge; and gymnosperms and** *Gillespiea* **were possibly opportunists following disturbances. Tetrapod fossils have been described from Red Hill—therefore, this paleoecological analysis is the first systematic interpretation of a specific site that reflects the type of wetland environment within which the earliest tetrapods evolved.**

Keywords: *Archaeopteris*; charcoal; cormose lycopsid; *Gillespiea*; gymnosperm; Late Devonian; paleoecology; *Rhacophyton;* tetrapod; wetlands.

INTRODUCTION

By the Late Devonian, plant communities had developed many characteristics that can be observed in modern terrestrial ecosystems (DiMichele et al., 1992). Lowland vegetation had differentiated into forest trees, shrubs, ground cover, vines, and specialized swamp plants. The morphological and ecological complexity of land plants had increased steadily throughout the Devonian. At the beginning of the period, vegetation consisted of small plants with simple architecture occupying low-diversity wetland patches (Edwards and Fanning, 1985). By the end of the Devonian, most of the major vegetative and reproductive features of vascular plants had evolved, and they appear in complex ecosystems (Chaloner and Sheerin, 1979; Algeo and Scheckler, 1998).

The development of plant-animal interactions lagged behind the development of plant community structure (Beerbower, 1985). Terrestrial arthropods throughout the Devonian are all evidently predators and detritivores (Beerbower, 1985; Shear, 1991). Evidence of plant damage repair due to herbivory is negligible and equivocal at best for the period (DiMichele et al., 1992). The earliest tetrapods appeared during the Late Devonian but were all predators that were ecologically linked to aquatic

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ecosystems (Beerbower, 1985). Late Devonian terrestrial ecosystems continued to be detritus based, but the plant biomass from which the detritus was derived increased dramatically during the interval due to the development of forests and the colonization of extrabasinal landscapes by seed plants (Algeo and Scheckler, 1998). Fully integrated terrestrial ecosystems with a complete range of arthropod herbivore guilds and a wide spectrum of low- to high-fiber vertebrate herbivory did not develop until the Late Carboniferous (Labandeira and Sepkoski, 1993; Hotton et al., 1997; Labandeira, 1998).

Although the earliest widespread forests were Late Devonian in age (Meyer-Berthaud, Scheckler, and Wendt, 1999), the first plant lineages to have members that developed secondary growth and the robust architecture of trees appeared during the Middle Devonian. These were aneurophytalean progymnosperms, cladoxylaleans, and lepidosigillarioid lycopsids (DiMichele et al., 1992; Algeo and Scheckler, 1998). Lycopsids formed wetland groves, and aneurophytes and cladoxylaleans grew in drier scrub thickets. The areal extent of these ecosystems was on a much smaller scale than the forests of the Late Devonian (Scheckler, 2001). By the beginning of the Late Devonian, archaeopteridalean progymnosperms became the dominant trees of widespread forests that ranged from tropical to boreal regions of the globe (Beck, 1964; Algeo and Scheckler, 1998). They were moderately sized trees that could reach an estimated height of 20–30 m. They bore the earliest known modern wood but had a free-sporing reproductive biology (Phillips et al., 1972; Meyer-Berthaud, Scheckler, and Wendt, 1999; Meyer-Berthaud, Scheckler, and Bousquet, 2000).

Nearly every Late Devonian plant-bearing terrestrial deposit has yielded fossil material of the progymnosperm tree *Archaeopteris* Dawson (Fairon-Demaret, 1986). The foliage genus *Archaeopteris* Dawson has been synonymous with the wood genus *Callixylon* Zalessky since the two were found in attachment (Beck, 1960). *Archaeopteris/Callixylon* is often found in association with the zygopterid fern *Rhacophyton* Crépin, another Late Devonian biostratigraphic indicator (Banks, 1980). Additional plant taxa that are found in Late Devonian plant fossil assemblages are rhizomorphic lycopsids, the earliest gymnosperms, barinophytaleans, cladoxylaleans, stauropteridalean ferns, and sphenopsids (Scheckler, 1986a). Red Hill, the fossil locality investigated in this study, has most of these floral components (Table 1). Red Hill is unusual for the association of its plant fossils with vertebrates, which include fish as well as early tetrapods (Daeschler et al., 1994; Daeschler, 1998, 2000a, 2000b); for its association with terrestrial invertebrate remains (Shear, 2000); and for the extent of its sedimentological profile (Woodrow et al., 1995). For these reasons, the Red Hill locality is ideal for conducting detailed paleoecological studies and for understanding one set of wetland environments in which the earliest tetrapods evolved.

The paleoecological analysis described here was undertaken at Red Hill with the objective to test the hypothesis of phylogenetic partitioning of the environment by plants in a Late Devonian lowland ecosystem. Observations of plant fossil assemblages in the Pennsylvanian Period have shown that plants partitioned lowland ecosystems at a high taxonomic level during that period (Peppers and Pfefferkorn, 1970; DiMichele and Bateman, 1996). Rhizomorphic lycopsids dominated the wetlands; ferns initially dominated in disturbed environments; sphenopsids dominated aggradational environments; and gymnosperms dominated on well- to poorly drained clastic substrates. This pattern persisted until climatic drying during the middle-to-late Pennsylvanian transition caused extinctions that disrupted the trend of within-clade replacement in each environment. Opportunistic ferns then dominated in many lowland environments during the late Pennsylvanian. They were succeeded by seed plants in the Permian, which have been dominant in nearly every vegetated environment since that time (DiMichele et al., 1992; DiMichele and Bateman, 1996).

The class-level taxa that dominated the various Pennsylvanian lowland environments were well established by the end of the Late Devonian–early Mississippian transition (Scheckler, 1986a). Apparently the ecological patterns of these plant groups were established as part of their evolutionary origin and radiation as basic plant body plans (DiMichele and Phillips, 1996). Observations of Late Devonian plant fossil assemblages have suggested habitat partitioning by plants during that interval also (Scheckler, 1986a, 1986c; Rothwell and Scheckler, 1988; Scheckler et al., 1999). The suggested pattern for the Late Devonian is that cormose lycopsids occupied permanent wetlands, zygopterid ferns occupied ephemeral wetlands, the early gymnosperms were pioneer plants on disturbed habitats, and *Archaeopteris* occupied the better-drained part of the overbanks (Scheckler, 1986a, 1986c; Rothwell and Scheckler, 1988; Scheckler et al., 1999). Niche partitioning among plants in the Shermans Creek Member of the Late Devonian Catskill Formation of Pennsylvania has also been indicated by a study of root traces that vary in different depositional environments (Harvey, 1998). The extinction of *Archaeopteris* after the end of the Devonian and the decline in importance of the zygopteridalean ferns facilitated a transition to the pattern of phylogenetic partitioning seen in the Pennsylvanian. The Late Devonian to middle Pennsylvanian partitioning of lowland environments by plants at a high taxonomic level is an ecological pattern that is not repeated as clearly in subsequent geological periods.

The abundant and relatively diverse plant fossil material at Red Hill and the site's clear sedimentological relationships have provided an opportunity to test the model of habitat partitioning among the components of Late Devonian lowland vegetation. In addition, the flora of the Catskill Formation and related rocks of Pennsylvania has historically been poorly sampled, except by Arnold (1939). He described several species of *Archaeopteris*, "seed-like objects" referred to as *Calathiops* Arnold that were later recognized as seed-bearing cupules called *Archaeosperma arnoldii* by Pettitt and Beck (1968), the lycopsids *Prolepidodendron breviinternodium* Arnold and *Lepidostrobus gallowayi* Arnold, and an enigmatic plant of unknown affinities, *Hostimella crispa* Arnold. In contrast to this situation, the Hampshire Formation flora of equivalent age in Virginia and West Virginia is well known (Kräusel and Weyland, 1941; Andrews and Phillips, 1968; Phillips, Andrews, and Gensel, 1972; Gillespie, Rothwell, and Scheckler, 1981; Scheckler, 1986b; Rothwell, Scheckler, and Gillespie, 1989). The assemblage described here increases our knowledge of the Catskill flora and provides a better basis for comparison with the Hampshire flora and other Late Devonian plant assemblages.

MATERIALS AND METHODS

Geologic Setting—The Catskill Formation

The Red Hill outcrop where this paleoecological study was undertaken is a roadcut exposure of the Duncannon Member of the Catskill Formation (Woodrow et al., 1995), which represents the upper alluvial plain facies of the Late Devonian Catskill Delta Complex (Diemer, 1992). The Catskill Delta Complex was an enormous wedge of sediment that was shed from mountains formed during the collision between ancestral North America, Europe, the Avalon Terrane, and other microcontinents during the Acadian orogeny, as part of the early stages in the closure of the Iapetus Ocean and the formation of Pangaea (Ettensohn, 1985). Sediments were shed from the mountains and prograded toward the west into the foreland basin adjacent to the Acadian fold-thrust belt (Gordon and Bridge, 1987). During the Late Devonian, the subaerial portions of the clastic wedge formed a wide, low-gradient plain traversed by meandering streams that flowed into a shallow epicontinental sea. This fluvial sequence in Pennsylvania constitutes the Catskill Formation (Sevon, 1985).

The Catskill Formation overlies dark marine shales of the Trimmers Rock and Lock Haven Formations, and where they come in contact marks the inception of delta progradation (Glaeser, 1974). In most of north-central Pennsylvania, three members of the Catskill Formation are recognized according to their depositional characteristics with respect to their location on the coastal plain. The Irish Valley Member represents sedimentation along a muddy, low-energy tidal flat (Walker, 1971; Walker and Harms, 1971). The Sherman Creek Member represents deposition on a broad inactive coastal plain, and the Duncannon Member represents deposition higher on the coastal plain where the meandering river facies is most fully expressed (Rahmanian, 1979).

Geologic Setting—The Red Hill Outcrop

Red Hill is the informal local name for a large roadcut in the Duncannon Member of the Catskill Formation on PA highway 120 between the villages of Hyner and North Bend in Chapman Township, Clinton County, Pennsylvania (41°20′30” N latitude, 77°40′30” W longitude; Fig. 1). A clean vertical exposure extends for 1 km along an east-west stretch of the highway, and an additional 170 m of rock to the west is banked and overgrown. The outcrop consists of nearly horizontal layers of fluvial sandstones, siltstones, mudstones, and paleosols (Fig. 2). These lithologies are typical of the Duncannon Member of the Catskill Formation. The layers dip slightly to the west. The Duncannon Member

TABLE 1. RED HILL FLORAL LIST

- Plantae
  - Tracheophyta
    - Zosterophyllopsida
      - Barinophytales
        - ***Barinophyton obscurum*** (Dun) White
        - ***Barinophyton sibericum*** Petrosian
    - Lycopsida
      - Isoetales
        - Isoetalean lycopsid, gen. et sp. nov.
        - cf. ***Lepidodendropsis*** Lutz
    - Filicopsida
      - Zygopteridales
        - ***Rhacophyton ceratangium*** Andrews and Phillips
      - Stauropteridales
        - ***Gillespiea randolphensis*** Erwin and Rothwell
    - Progymnospermopsida
      - Archaeopteridales
        - ***Archaeopteris macilenta*** (Lesq.) Carluccio et al.
        - ***Archaeopteris hibernica*** (Forbes) Dawson
        - ***Archaeopteris obtusa*** Lesquereaux
        - ***Archaeopteris halliana*** (Göppert) Dawson
    - Gymnospermopsida
      - Pteridospermales
        - cf. ***Aglosperma quadripartita*** Hilton and Edwards
        - cupulate gymnosperms, genera et sp. nov.

(Classification scheme based on Stewart and Rothwell, 1993)

Figure 1. Location of the Red Hill site, Clinton County, Pennsylvania, U.S.A. (after Daeschler, Frumes, and Mullison, 2003).

Figure 2. Uncorrected photomosaic of portion of Red Hill outcrop featuring the eastern portion of the plant layer (after Cressler, 2001). © SEPM (Society for Sedimentary Geology).

represents an upper alluvial plain facies that was characteristically far inland from marine deposition, and there is no evidence of marine influence at Red Hill.

A stratigraphic column of a sequence that includes the plant-fossil-bearing layer sampled for this paleoecological study is shown in Figure 3. The sampling of plant fossils took place within a 1 m thick predominantly dark-gray siltstone layer shown in Figure 3 as the "plant layer." The stratigraphic column was measured down through the plant layer at a point 15 m to the west of where it pinches out. The upper and lower margins of the plant layer consist of ~15 cm of unfossiliferous greenish-gray siltstone, not shown in the stratigraphic column. They form uneven zones that grade into the overlying and underlying red beds where the contact area between them is mottled with reduction spots. Above and below the plant layer are alternating sequences of red laminated siltstones and red paleosols. Toward the top of the stratigraphic sequence in the measured section is a gray sandstone lens partially covered by soil and vegetation. The dark-gray and greenish-gray siltstones constitute Lithofacies 3 of Woodrow et al.'s (1995), "Greenish-Gray Mudstone and Very Fine Grained Sandstone." The red laminated siltstones correspond to Lithofacies 1 of Woodrow et al.'s (1995), "Red Hackly-Weathering Mudstone." The red paleosols correspond to Lithofacies 2 of Woodrow et al.'s (1995) "Red Pedogenic Mudstone." Woodrow et al. (1995) refer to the sandstone bodies at Red Hill as Lithofacies 4, "Flat-Laminated Gray Sandstone." Not all of the sandstone bodies are flat-laminated, however.

Geologic Setting—The Dark-Gray Plant-Fossil-Bearing Siltstone Layer (Plant Layer)

As implied by its name, most of Red Hill consists of highly oxidized rocks with hematite coating the sediment grains. Plant fossils are poorly preserved or nonexistent in these red rocks. The reduced horizons are where the well-preserved plant fossils have been found. The only large and easily accessible reduced horizon at Red Hill is the one that was sampled for the paleoecological analysis described in this paper, the "plant layer."

Figures 4 and 5 show the sedimentological relationships of the sampled plant layer at the two ends of where it is exposed in the outcrop. Where it pinches out at its eastern end (Fig. 4) it truncates two layers below it, a red paleosol and a red laminated siltstone. The pinched-out lenticular portion of the plant layer is end-to-end with the apex of a thin sandstone wedge that thickens to the east. The sandstone wedge exhibits small-scale cross-bedded laminations accreting toward the apex of the wedge. Another sandstone body 74 m to the west of the pinched-out eastern end of the plant layer is laterally continuous with the plant layer and marks the western end of the sampled horizon (Fig. 5). The flat lower surface of the western sandstone body is on the same horizon with the lower boundary of the plant layer. The western sandstone body is convex upward for the same thickness as the plant layer. It also exhibits small-scale cross-bedded laminations. Where the western sandstone body crosscuts the plant layer, the reduced horizon is mottled with red at a transition zone and changes to completely red in proximity to the sandstone. On the western side of this sandstone body, the dark-gray siltstone layer continues to the west for another 93 m until it plunges below talus piles and the road, owing to the slight western dip of all the layers at Red Hill.

The total reduced horizon, including the 74-m-long portion of the plant layer where sampling occurred, averages 1 m in thickness over its exposed length of 167 m. The portion of it west of the convex-upward sandstone body has sandstone stringers 1–2 cm thick interspersed regularly throughout the depth of the dark-gray siltstone. The western portion of the plant layer also differs from the eastern portion in that the 15 cm upper margin of greenish-gray siltstone is absent.

Stratigraphic Analyses

To produce the photomosaic of the Red Hill outcrop (Fig. 2), color photographs were taken with a tripod-mounted Pentax K1000 at successive intervals along the face of the outcrop so that there was at least 30% overlap between successive photographs. Photographs were taken from the shoulder of the highway on the opposite side from the exposure. The height of the outcrop necessitated two photographs, one above the other, at each horizontal position. The foreshortening of the images was left uncorrected in the photographs. The outcrop profile of Red Hill was prepared by drawing a diagram of the exposure based on this photomosaic (Figs. 4 and 5).

A stratigraphic section was measured down through the outcrop at a place that included the plant layer at a point 15 m from the eastern end of the layer (Fig. 3). A rope with 1 m, 5 m, and 10 m intervals marked in different colored tape was lowered from the top of the exposure. The widths of the stratigraphic layers were read off the rope by using a pair of binoculars, and the measurements were recorded in a field notebook. Correcting the measurements to account for the angle of the slope was considered unnecessary and impractical due to the relatively short height and uneven nature of the exposure.

Age of Beds

Palynological analyses on several layers including the plant layer at Red Hill place it within the palynomorph biozone Famennian 2c (Fa2c; Traverse, 2003). It is equivalent to the VCo miospore zone, which is distinguished by the palynomorph index species *Grandispora cornuta* Higgs, *Rugispora flexuosa* (Juschko) Streel, and others (Richardson and McGregor, 1986; Streel and Scheckler, 1990).

Paleoecological Sampling

Plant fossils and fossil charcoal were systematically sampled by excavating 12 small quarries (between 0.25 m^3 and 0.5 m^3) along a 64 m transect of the plant layer. The transect followed the exposed face of the layer between the two previously described sandstone bodies, which are 74 m apart.

Within each quarry, bedding surfaces were exposed at successive centimeter-scale intervals throughout the vertical dimension of the plant layer. Plant fossil diversity and abundance and the number of charcoal fragments were counted on these successive bedding surfaces using a line-intercept method. For this method, a grid with recording dimensions of 24 cm x 24 cm was used, consisting of a wooden frame with strings arrayed at right angles to each other. The intersections of the strings were 2 cm apart. The grid was laid over the bedding surfaces and the fossils at the intersections of the strings were identified, counted, and recorded.

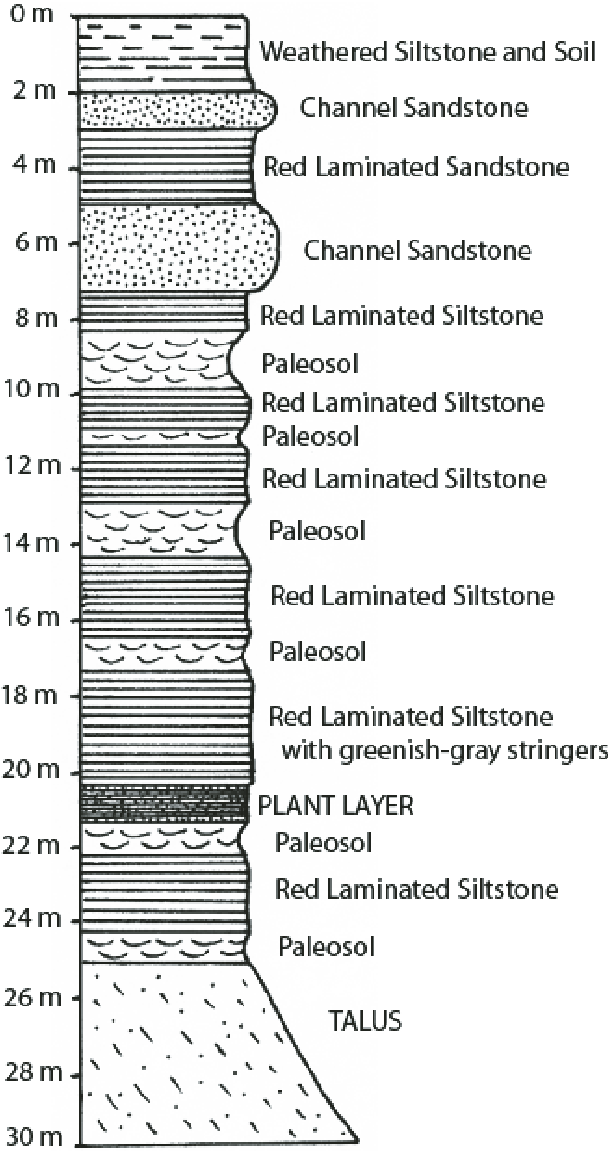

Figure 3. Stratigraphic column of the Red Hill outcrop measured 15 m to the west of the eastern end of the plant layer (after Cressler, 2001). © SEPM (Society for Sedimentary Geology).

The 12 quarries were arranged in pairs in order to determine variation of plant fossil distribution at a smaller spatial scale if that was deemed important upon analysis of the data. Red Hill is a roadcut with a south-facing exposure. The quarries were numbered along the plant layer from west to east. The quarries within each pair were adjacent to each other, with the exception of quarries 2a and 2b, which were 2 m apart. These two quarries could not be made adjacent to each other because of the excessive amount of overburden above the plant layer at this location in the outcrop. The following chart delineates the distances between quarry pairs:

Western Sandstone Body	– 10 m – 1ab – 9 m – 2a – 2 m – 2b – 15 m – 3ab – 19 m – 4ab – 11 m – 5ab – 8 m – 6ab

Quarry 4b was excavated farther into the cut face at the same position as quarry 4a after the rock from quarry 4a had been removed. Excavation lateral to quarry 4a was impractical due to a large amount of overburden. Quarries 6a and 6b were excavated at the extreme eastern end of the plant layer where it pinches out and makes lateral contact with the apex of the wedge-shaped sandstone body. Overall, the unequal distances between pairs of quarries result from the uneven accessibility of the plant layer due to the varying amounts of overburden along its length.

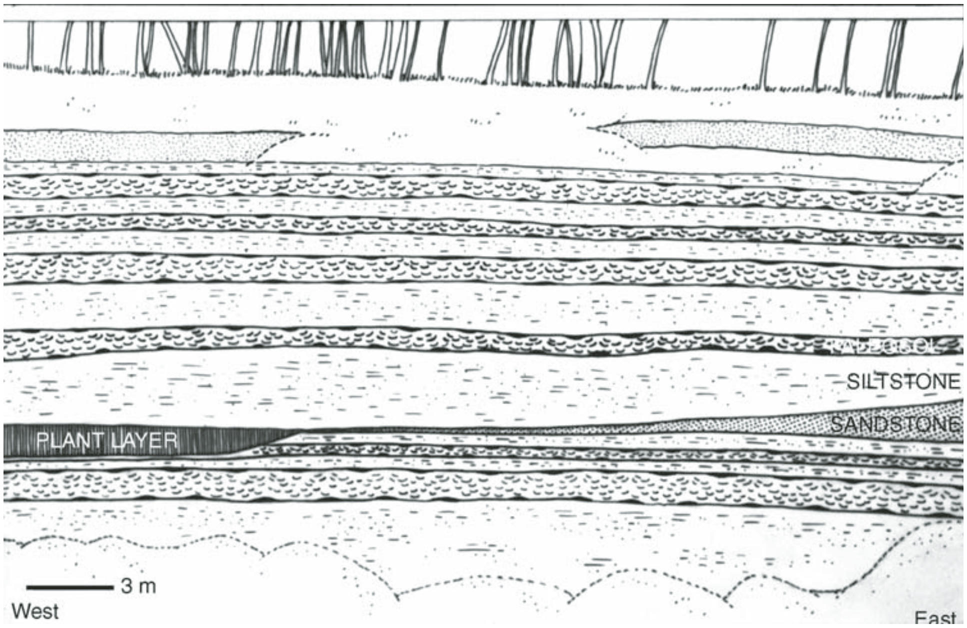

Figure 4. Diagram of the Red Hill outcrop profile that includes 11 m of the eastern portion of the 64 m plant layer where the sampling took place (after Cressler, 2001). © SEPM (Society for Sedimentary Geology). This diagram roughly corresponds to the photomosaic in Figure 2. Dots and dashes = Siltstones/Woodrow's Lithofacies 1 Arcuate stippling = Paleosols/Woodrow's Lithofacies 2 Dark shading = Plant layer/Woodrow's Lithofacies 3 Stippling = Sandstones/Woodrow's Lithofacies 4

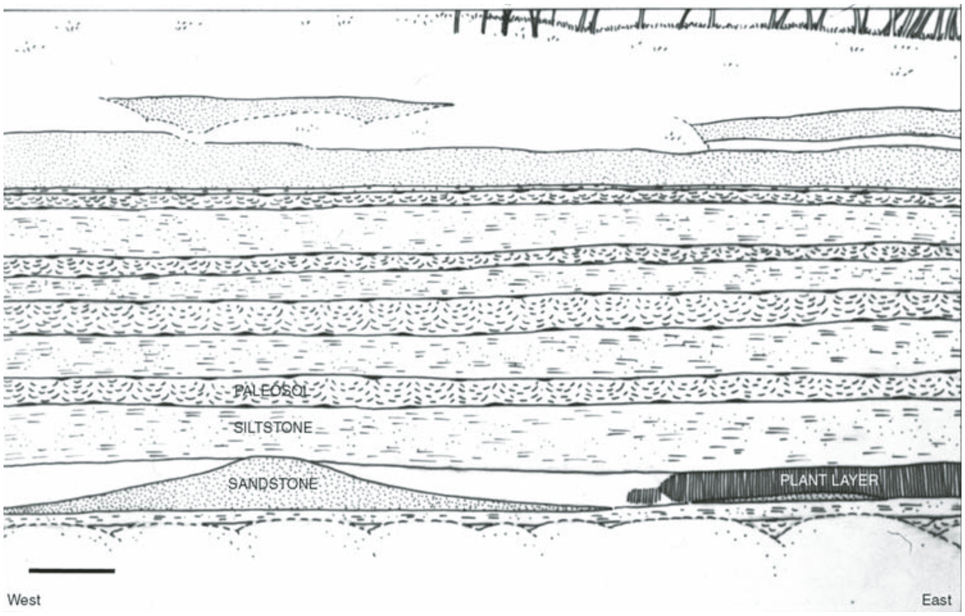

Figure 5. Diagram of the Red Hill outcrop profile that includes 10 m of the western portion of the 64 m plant layer where the sampling took place. Note that ~10 m of highly oxidized siltstone that is laterally equivalent to the sampled plant layer onlaps the sandstone body to the west of it.

Quarries were excavated from between the contact of the gray plant layer with the overlying red laminated siltstone down to the contact between the player layer with either an underlying red paleosol or an underlying sandstone. The depth of the plant layer varied from 33 cm to 106 cm among quarries.

Quarries	Depth of Plant Layer
1a/1b	33 cm
2a/2b	106 cm
3a/3b	83 cm
4a/4b	93 cm
6a/6b	102 cm

The small depth of the sampled portion of the plant layer at quarries 1a and 1b is due to the more highly oxidized nature of the layer where it is in proximity to the western sandstone body. At that location, the presence of the reduced plant-bearing gray siltstone gradually is replaced laterally by red siltstone. Otherwise, the range of thickness throughout the reduced portion of the plant layer only varies between 83 cm and 106 cm. The variation in depth is mostly due to the uneven amount of mottling at the contact between the plant layer and the overlying red laminated siltstone.

The entire depth of the plant layer was sampled in each of the quarries, with the exception of quarries 2b and 6b. The upper 41 cm was missing from quarry 2b and the upper 33 cm was missing from quarry 6b. This material had been removed during previous excavations at these locations in the outcrop. While this activity provided access to the plant layer for the purposes of this study, it also removed some of the data.

An attempt was made to clear bedding surfaces at each quarry that were between 0.25 and 0.5 sq m in area. The exact size and dimension of each set of bedding surfaces were dictated by the accessibility of the surfaces within each quarry. The plant fossil census counts were normalized to 0.5 m^2 for each bedding surface by multiplying each original count times the quantity of 0.5 m^2 divided by the original area where that count was made. The bedding surface areas that were measured for each quarry are as follows:

Quarry	Bedding Surface	Quarry	Bedding Surface
1a	0.28 m^2	4a	0.22 sq m
1b	0.27 m^2	4b	0.13 sq m
2a	0.51 m^2	5a	0.18 sq m
2b	0.26 s m^2	5b	0.20 sq m
3a	0.35 m^2	6a	0.34 sq m
3b	0.29 m^2	6b	0.34 sq m

Quarries were excavated using a 3 lb crack hammer and the chisel edge of a sedimentary rock pick. Sometimes a pry bar was necessary. To remove large amounts of red overburden in order to get down to the plant layer, a gas-powered hammer was used on a number of occasions.

The intervals between counted bedding surfaces varied between 3 cm and 8 cm. The size and sequence of the intervals was established initially by finding the sedimentation breaks in the first quarry excavated, and then varied slightly from quarry to quarry depending on the individual characteristics of the quarry. The sampling intervals were at a smaller scale than the thickness of separate depositional events, so many of the surfaces counted were not smooth bedding planes.

The rock of each successive interval was removed in fragments. The fragments were turned over and laid next to each other on a flat area next to the quarry. The line-intercept counts were made on the undersides of the fragments. These combined surfaces were a close counterpart of the cleared quarry surface, and fossils on them were easier to see because the quarry surface was covered with the dust from the excavation process. For the purposes of comparison, line-intercept counts were initially made on both the cleared in situ surface and on the reassembled counterpart fragments. The counts were virtually identical every time, so for the remainder of the sampling process the line-intercept counts were made only on the more easily discernible reassembled counterpart fragments.

Plant Identification

Most of the plant fossils that were counted during the paleoecological sampling in this study were axis fragments of various sizes. Many of the axis fragments were unidentifiable (52%). They had no diagnostic characteristics that made them assignable to any known taxon. The unidentifiable plant remains were carbonized compressions of plant axes ranging in length from a few millimeters to several centimeters and were smooth and featureless.

Identifiable plant fragments were assigned to five taxa. These five taxa were (1) lycopsid, (2) gymnosperm, (3) *Rhacophyton* Crépin, (4) *Gillespiea* Erwin and Rothwell, and (5) *Archaeopteris* Dawson. The nature of this material is further described in the Results. Figured specimens are on repository at the Academy of Natural Sciences in Philadelphia (ANSP).

In addition, many of the axis fragments found during the paleoecological sampling had the appearance of charred and fragmented pieces of wood. Macroscopic and microscopic analysis of this material, including SEM imaging, has led to its identification as charcoal (Cressler, 2001). The charcoal fragments were counted as a separate category during the plant fossil census.

During removal of the red laminated siltstone to reach the plant layer, some poorly preserved plant material was occasionally encountered. This material consisted mainly of unidentifiable carbonized stems within reduction spots, and limonitized *Archaeopteris* axes. They were not counted during the sampling process because of their poor preservation and lack of stratigraphic control outside the plant layer.

RESULTS

The plant layer and its associated sediments and paleosols at Red Hill are consistent with an interpretation of avulsion processes at work on an aggrading flood plain (Slingerland and Smith, 2004). The lateral migration of a channel belt can leave in its path an anastomosing network of sand deposits and ponded flood-plain scours. The plant layer at Red Hill may represent such ponded water between two sand bodies.

Quarries 1a and 1b have their lower contact with the tapering right extension of the western sandstone body. The sandstone is 25 cm thick beneath quarry 1a and 5 cm thick beneath quarry 1b. The plant layer is highly red-mottled in this region. Another small sandstone body several meters long extends beneath quarry 3a at its eastern end where it is 12 cm thick. The lower contacts of all the other quarries are with the underlying red paleosol. Quarries 6a and 6b are at the pinched-out eastern end of the plant layer, end to end with the wedge-shaped eastern sand body. This location is interpretable as a clear shoreline profile.

The sampling transect goes from the shoreline of the pond to a sand body within the pond some distance from the shore (in reverse order of the numbered quarries). The western end of the 64 m transect may be much less than 64 m away from the nearest shoreline. This cannot be determined with certainty because of the two-dimensional nature of the exposure, which does not permit a map view of the pond. The face of the roadcut may have cut the pond at a tangent, in such a way that none of the plant material found would have been very far away from the shoreline.

The reduction of the plant layer was apparently primary, or syndepositional, and resulted in the preservation of large numbers of plant fossils. Because of their mottled character, the unfossiliferous greenish-gray margins above and below the plant layer are interpreted as possibly being secondarily reduced. The contact of the upper greenish-gray siltstone with the overlying red laminated siltstone is not even throughout its length. There are some dips in its generally horizontal configuration, but the relative thickness of the upper greenish-gray margin stays essentially the same throughout. This irregularity appears to result from uneven geochemical changes, and not disturbances in the flat lamination of sediments.

The thick (3 m) red laminated siltstone layer (Figs. 3, 5, and 6) above the plant layer and its laterally associated sandstones apparently results from a series of overbank floods probably due to a change in proximity of the main active channel. This thick red siltstone layer has abundant articulated and disarticulated fish fossils found in strand-line lenses as well as a series of greenish-gray reduced stringers. Above this layer is a well-developed paleosol, which records an interval during which pedogenic processes exceeded the rate of deposition on the flood plain. Three additional cycles of alternating red laminated siltstones and paleosols continue up the section until they are interrupted by a sandstone layer (Figs. 3–5). Flood-plain strata bounded by paleosols in this fashion are characteristic of avulsion-derived sediment that is subsequently weathered during periods of isolation from flooding (Slingerland and Smith, 2004). The sandstone marks a return to active channel scouring and deposition in this part of the landscape.

Most of the deposition in the pond was through low-energy sedimentation of a suspended load of silt. Individual beds cannot be followed for more than a meter within the plant layer. The plant layer in quarries 5a and 5b was examined closely for subtle changes in lithology throughout its thickness. Slight changes in color and grain size suggest that no more than ten depositional events occurred over the 1 m thickness of the entire reduced horizon.

Occasional higher-energy movement of sediment into the pond is also indicated by observations of sharply curved bedding surfaces such as those that were encountered in quarry 4b and by the presence of some mud pebble conglomerate layers. Thin (1 cm) mud pebble conglomerate layers were found in the lower levels of quarries 4a and 4b and quarries 5a and 5b as well as at

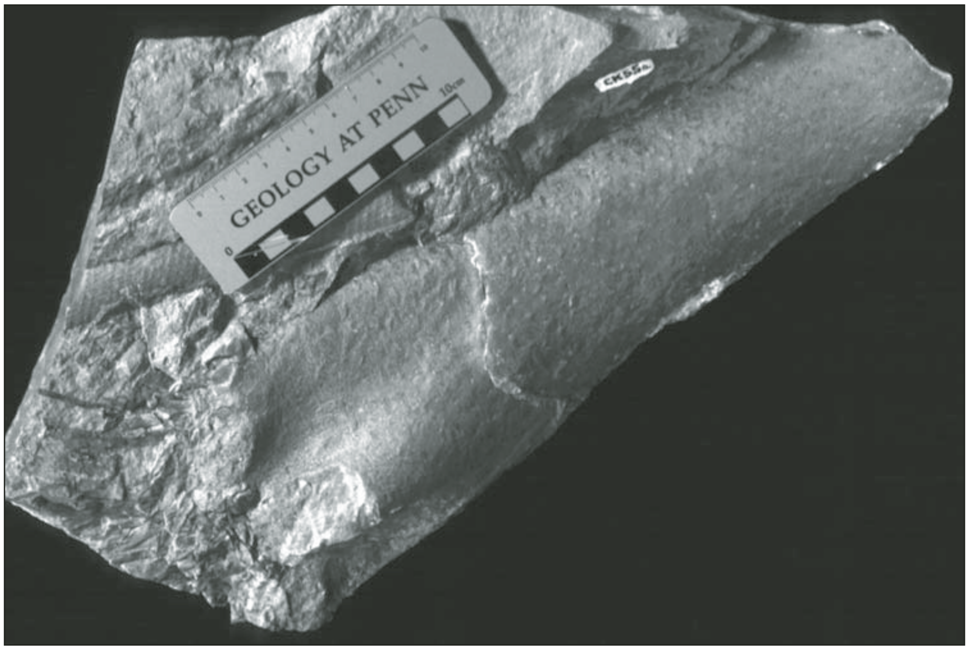

Figure 6. Cormose lycopsid rooting organ and stem (ANSP 4512). Scale in cm.

a spot that was excavated a few meters west of quarries 4a and 4b during preliminary excavations. The rounded mud pebbles are 2–8 mm in diameter and are densely packed on the bedding planes where they occur. Slightly larger pieces of rounded bone and fish scales are scattered among the mud pebbles in some places. The mud pebble conglomerate layers are immediately above the ~15 cm of the lower greenish-gray margin, except in quarry 5a where there is 5 cm of the dark-gray organic-rich siltstone in between. Two layers of mud pebble conglomerate were found 1 cm apart in quarry 5b with unfossiliferous greenish-gray siltstone between them. The mud pebble conglomerate layers represent a higher-energy influx of water into the pond containing a bedload of organic matter and pellets of ripped-up, previously deposited mud. These influxes took place when the pond was occasionally accessible to higher energy flow on the highly dynamic flood plain.

Simultaneous with the plant census, a record was kept of the vertebrate remains found during the sampling effort. Numerous isolated vertebrate fragments were found scattered relatively evenly throughout the lateral and vertical extent of the plant layer. Remains included *Hyneria* teeth and scales, megalichthyid scales, groenlandaspid plates, acanthodian spines, and articulated palaeoniscoid fish.

Determination of Pant Fossil Taxa

Lycopsids

Lycopsid stem fragments constitute 4.5% of the identifiable plant remains in the plant layer at Red Hill. The lycopsid stem fragments vary in size from 1 cm to 10 cm in width and 2 cm to 20 cm in length. They represent various levels of lycopsid stem decortication but are all characterized by the distinctive spiral pattern of lycopsid leaf traces (Stewart and Rothwell, 1993). Two specimens exhibit leaf traces arranged in rows of pseudowhorls and on that basis can be tentatively assigned to the genus *Lepidodendropsis* Lutz pending study of leaf cushion details (Jennings, 1975; Jennings, Karrfalt, and Rothwell, 1983). Most of the other decorticated lycopsid stem specimens resemble *Cyclostigma* in gross appearance or are assignable to form genera that are now only considered to reflect levels of stem decortication. Therefore, all lycopsid fragments have simply been given the designation “lycopsid” for the purpose of the paleoecological analysis.

In addition to stem fragments, several lycopsid rooting organs have been found at Red Hill (Fig. 6). These were found in the plant layer, but not during the paleoecological sampling. They vary in diameter from 2.5 to 10 cm. These extremes in size are represented on one bedding surface (Fig. 6). The rooting organs consist of four-lobed bases of stems with masses of attached rootlets. These four-lobed cormose lycopsid rooting organs represent a new taxon.

Ferns

Remains of *Rhacophyton ceratangium* Andrews and Phillips are abundant at Red Hill (Fig. 7). They constitute 38% of the identifiable plant fossils and consist primarily of foliar axes with a uniform width of ~3 mm that have a distinctive groove down the middle due to the bilobed morphology of the stele (Andrews and Phillips, 1968). Some *Rhacophyton* foliage was found during the paleoecological sampling. The foliage is highly divided and entangled with the distinctive stems in dense mats. There were also several *Rhacophyton* foliar axes found together that were 1 m long and 1 cm in width. These were probably main foliar axes. *Rhacophyton* was a zygopterid fern that has been reconstructed as a 1–2 m high plant and has some wood in its larger foliar axes (Kräusel and Weyland, 1941; Andrews and Phillips, 1968; Dittrich, Matten, and Phillips, 1983).

Gillespiea randolphensis Erwin and Rothwell was discovered at Red Hill during the paleoecological sampling (Fig. 8).

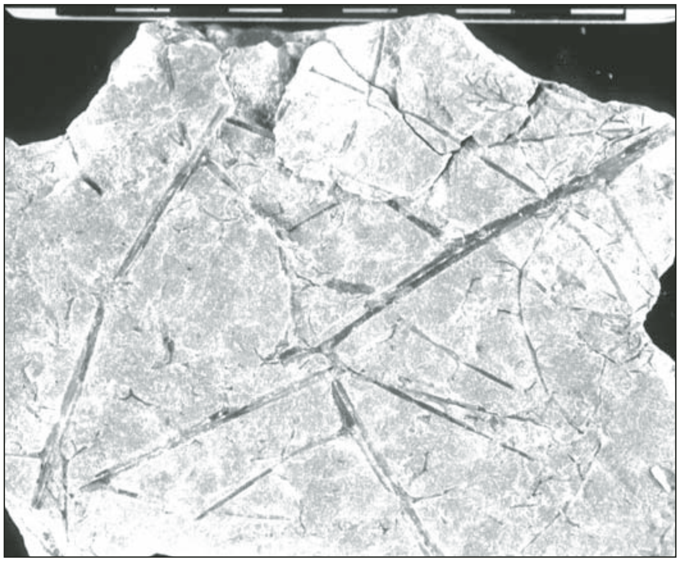

Figure 7. *Rhacophyton ceratangium* Andrews and Philips (ANSP 4500). Scale in cm.

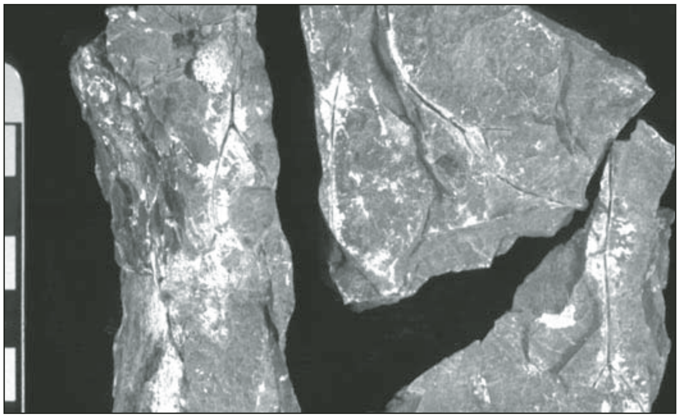

Figure 8. *Gillespiea randolphensis* Erwin and Rothwell (left to right: ANSP 4501, ANSP 4502, ANSP 4503). Scale in cm.

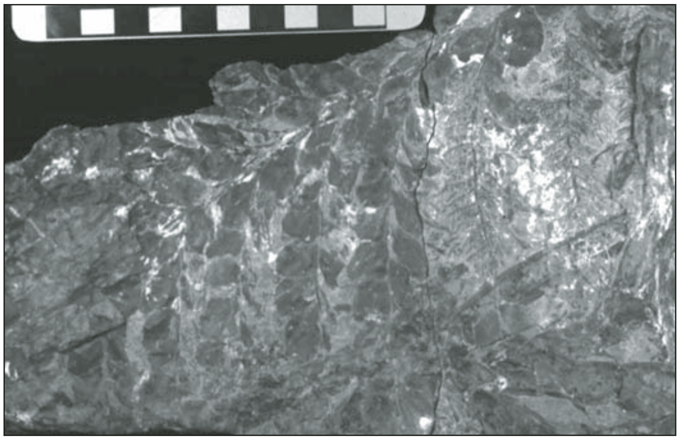

Figure 9. *Archaeopteris hiberni*ca (Forbes) Dawson (ANSP 4506). Scale in cm.

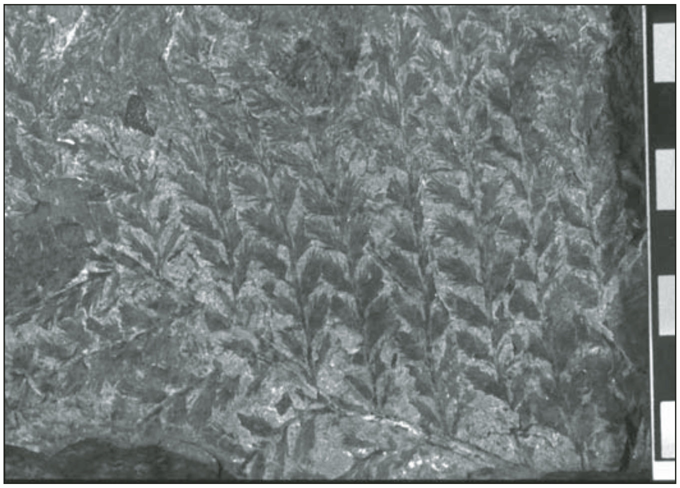

Figure 10. *Archaeopteris macilenta* (Lesquereux) Carluccio et al. (ANSP 4507). Scale in cm.

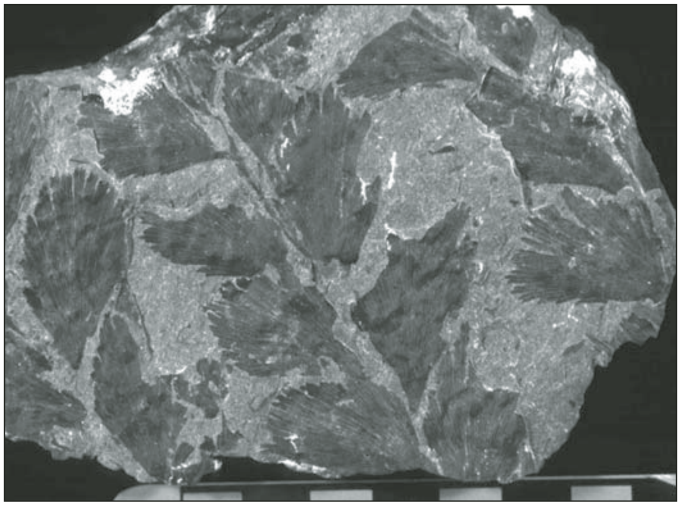

Figure 11. *Archaeopteris obtusa* Lesquereux (ANSP 4508). Incisions in leaves are taphonomic features. Scale in cm.

Gillespiea constitutes 2% of the identifiable plant remains at Red Hill. Axes of *Gillespiea* are 1 mm wide and less, often tapering to a very thin curving distal portion. As is characteristic of *Gillespiea*, small fertile structures emerge from between the dichotomies in some of the axes found at Red Hill. Some specimens of *Gillespiea* have been described elsewhere as having a sclerenchymatous cortex (Erwin and Rothwell, 1989). The stauropteridalean fern *Gillespiea* was a heterosporous plant of slender proportions and wiry, flexible construction (Erwin and Rothwell, 1989).

Progymnosperms

The remains of *Archaeopteris* Dawson (Figs. 9–12) dominate the plant-fossil assemblage at Red Hill, where they constitute 55% of the identifiable plant biomass. *Archaeopteris* remains at Red Hill consist almost entirely of 1-cm-wide penultimate branches, usually with attached biseriate ultimate branches. The penultimate branches have both distinctive longitudinal lineations from the underlying vascular strands and a transverse rugose pattern from clusters of cortical sclereids that help to identify *Archaeopteris* axes even when there is no foliage. The foliage of two *Archaeopteris* species, *A. hibernica* (Forbes) Dawson and *A. macilenta* (Lesquereux) Carluccio et al., and fertile branches with sporangia, were identified during the census study, but by far most of the *Archaeopteris* remains were axes unidentifiable as to species. The designation of *Archaeopteris* species is based on leaf morphologies. Arnold (1939) and Kräusel and Weyland (1941) provided useful keys and synonymy lists that are widely followed. The leaves of *Archaeopteris hibernica* often exceed 2 cm in length and are rounded or obovate (Fig. 9). The leaves of *Archaeopteris macilenta* are less than 1.5 cm in length and are rounded or broadly obovate with deeply cut margins (Fig. 10).

In addition to *A. hibernica* and *A. macilenta*, two other less abundant species of *Archaeopteris* have been collected from Red Hill that are assignable to *A. obtusa* Lesquereux (Fig. 11) and *A. halliana* (Göppert) Dawson (Fig. 12).

Gymnosperms

Gymnosperms at Red Hill consist of both cupulate and acupulate forms of the earliest grade of gymnosperm evolution, constituting 0.5% of the plant fossil assemblage. Their vegetative structures are morphologically similar to those of other Late Devonian gymnosperms such as *Elkinsia polymorpha* Rothwell et al. from West Virginia (Gillespie et al., 1981; Rothwell, 1989; Serbet and Rothwell, 1992) and *Moresnetia* Stockmans (Stockmans, 1948; Fairon-Demaret and Scheckler, 1987) from Belgium. Both are also from the same Famennian 2c time horizon as Red Hill. Their reproductive axes are dichotomously branching and get progressively thinner with each distal dichotomy. They range in width from 1 cm to 1 mm. Cupules, ovules, or both are usually found at the terminations of the dichotomous branches. Because the dichotomous branches of the various gymnosperms are indistinguishable from one another and do not always have fructifications, they have all been designated "gymnosperm" for the purpose of this paleoecological analysis.

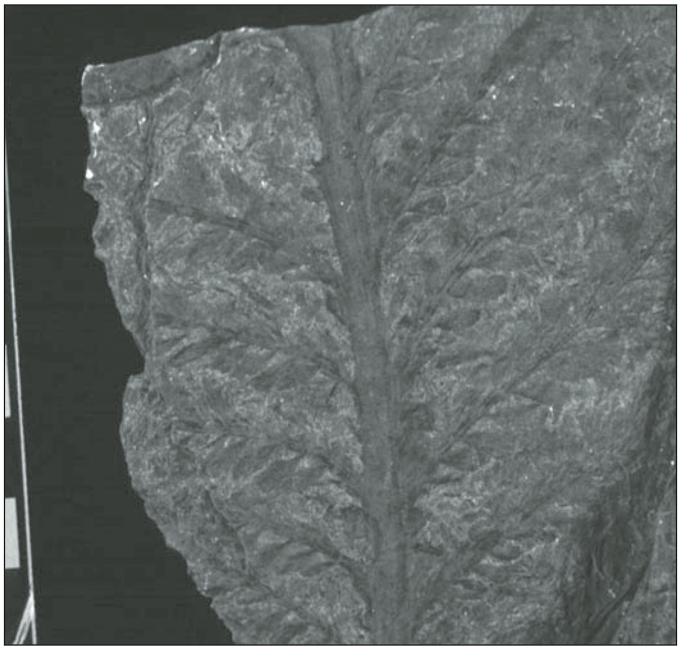

Figure 12. *Archaeopteris halliana* (Göppert) Dawson (ANSP 4509). Scale in cm.

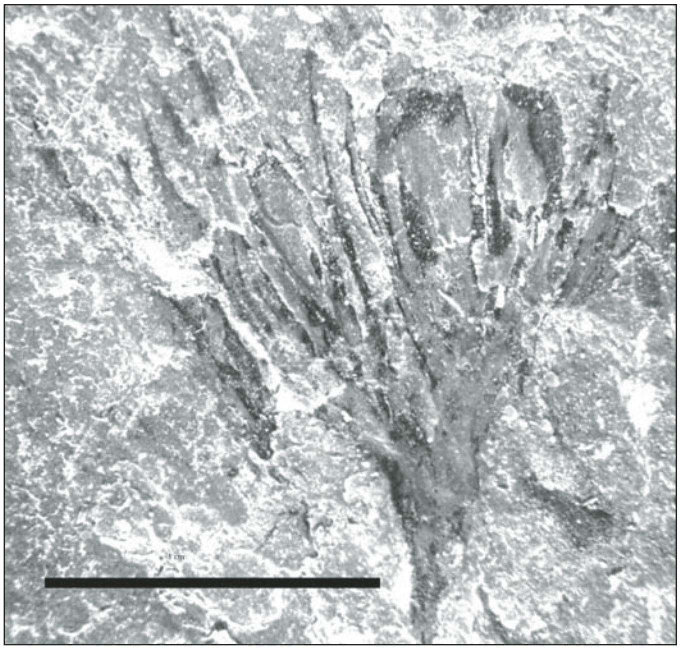

Figure 13. Gymnosperm cupule from plant layer showing three ovules (ANSP 4531).

The cupulate gymnosperms found in the plant layer have associated ovules and look different from *Elkinsia* and *Moresnetia* but may not be preserved well enough to be adequately described as a new taxon (Fig. 13). The acupulate gymnosperms are similar to *Aglosperma quadripartita*, previously described from younger Late Devonian rocks in Wales (Hilton and Edwards, 1996). Cupules found outside the sampling area in a loose block that fell from the far western end of the outcrop in October 1997 are different in morphology from those found in the plant layer. They are more fused than any other Late Devonian gymnosperm cupule besides *Dorinnotheca streelii* Fairon-Demaret (Fairon-Demaret, 1996), but unlike *Dorinnotheca* they are not inverted, and thus far have not been found associated with any ovules.

Barinophytes

Barinophyton White is rare, but isolated specimens of two species have been recovered from Red Hill. They were not recorded during the paleoecological sampling. One specimen of *Barinophyton obscurum* (Dun) White (Fig. 14) was found in a loose block of gray siltstone during a visit to the outcrop in October 1997. It had fallen from a vertical portion of the exposure toward the western end of the outcrop, several hundred meters from the plant layer that was sampled for this study. The loose block was collected because it contained abundant gymnosperm cupules. During further preparation in the lab, a distal branch of *Barinophyton obscurum* was uncovered, which includes five strobili. The sessile morphology of the strobili, with no pedicels at their attachment to the main stem, is diagnostic of *Barinophyton obscurum* (Brauer, 1980). This is in contrast to *Barinophyton citrulliforme* Arnold, first described by Arnold (1939) from New York specimens, but further elaborated by Brauer (1980) on the basis of a large collection from a Catskill Formation site in Potter County, Pennsylvania. *Barinophyton citrulliforme* has pedicels on the strobili where they attach to the main stem. Brauer also found poorly preserved specimens of *Barinophyton* cf. *obscurum* and what he called *Protobarinophyton pennsylvanicum* (Brauer, 1981).

Figure 14. *Barinophyton obscurum* (Dun) White (ANSP 4504). Scale in cm.

Two fragmentary specimens of the long, slender strobili of cf. *Barinophyton sibericum* Petrosian (Fig. 15) were found

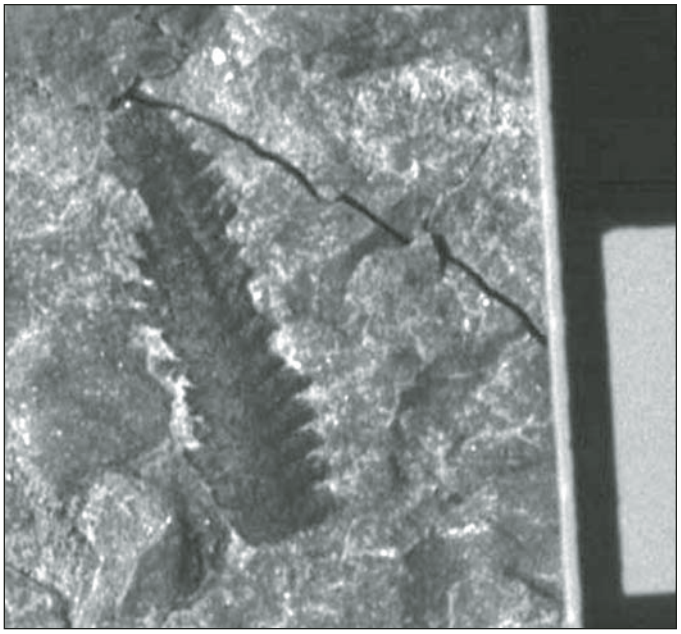

Figure 15. *Barinophyton sibericum* Petrosyan (ANSP 4505). Scale in cm.

by Norm Delaney some years before the systematic paleoecological sampling was conducted. He had found the specimens in the plant layer, but further specimens were not discovered during the extensive sampling there. *Barinophyton sibericum* was also reported by Gillespie et al. (1981) and Scheckler (1986c) for exposures of the Hampshire Formation. This taxon has long pedicels that often bend sharply at the attachments to strobili.

Distribution of Plant Fossils in the Deposit

The distribution of the plant fossils and charcoal in the plant layer at Red Hill as determined by the sampling procedure outlined above is shown in Figures 16–21. The plant fossil designations have been restricted to the following five taxa for the purpose of this analysis: *Archaeopteris*, *Rhacophyton*, *Gillespiea*, lycopsids, and gymnosperms.

Along the vertical axis of each figure are centimeter intervals measured up from the boundary between the plant layer and the underlying red paleosol or sandstone. The average thickness of the reduced horizon is ~1 m, but the plant fossils were found only between 15 cm and 78 cm from the bottom, with an isolated occurrence of gymnosperms at 93 cm from the bottom of quarry 4.

The horizontal axis represents the length in meters of the plant layer between the flat-bottom, convex-upward sandstone lens to the west and the wedge of sandstone to the east. Although the plant layer is shown laterally compressed and vertically exaggerated, the distances between the quarries are shown proportionally in these figures. The pairs of quarries are combined in the figures. The density distributions of the plant fossil taxa are shown as vertical bars beneath the number of the quarries in which they were found. The density distributions, with taxon counts normalized to 0.5 m^2 of bedding surface at each level sampled, are simplified to reflect differences of order of magnitude only. The width of the vertical bars reflects the maximum density of a particular plant fossil taxon within that portion of a particular quarry. Obviously, the distribution densities traverse the vertical dimension of time in the depositional profile. This reflects a particular taxon as having a persistent point source in the landscape through at least several depositional events into the pond.

The right edge of Figures 16–21 corresponds to the shoreline of pond. The left edge of the figures corresponds to the sandstone body at the other end of the transect. As can be seen in Figure 16, the densest concentration of *Archaeopteris* remains is close to the shoreline in the middle levels of quarry 5 and quarry 6. The line-intercept counts of *Archaeopteris* on these bedding planes was consistently in the hundreds. *Archaeopteris* is also best preserved on these bedding planes and has recognizable foliage. Lower concentrations of less well preserved *Archaeopteris* branches are distributed out to quarry 2, farther into the pond.

Rhacophyton was found in its densest and best-preserved concentrations in quarry 4 (Fig. 17), where the line-intercept counts numbered in the thousands on bedding planes between 30 and 40 cm from the bottom of the reduced horizon. These quarries are 19 m along the transect from the shoreline. *Rhacophyton* axes by the hundreds were scattered on bedding planes in the lower portions of quarries 4, 5, and 6. Lighter concentrations of *Rhacophyton* axis fragments were counted in the upper portions of those quarries and in quarry 3.

The distribution of lycopsid stems (Fig. 18) lies in between the densest concentration of *Archaeopteris* and the densest concentration of *Rhacophyton* in the distribution profile. They are concentrated in a diagonal distribution from the bottom of quarry 6 to the top of quarry 4. Some sorting of lycopsid stems by size appears to be in evidence, with the larger stems found toward the shoreline of the pond.

The most significant concentrations of *Gillespiea* were sampled from quarry 2 (Fig. 19) with minor amounts found in quarry 3. The main concentration of *Gillespiea* was centered 53 m along the transect from the shoreline. *Gillespiea* was found in quarry 2 several centimeters above the densest concentrations of charcoal found during the entire sampling process (Fig. 20). Few other recognizable plant remains were found in this quarry.

The gymnosperms that were found during the sampling process were concentrated in two small areas toward the top of quarries 4 and 5 (Fig. 21).

Previous excavations in the plant layer had also yielded significant plant remains. A quarry a few meters west of quarry 4 that E.B. Daeschler designated "9702" yielded numerous *Archaeopteris* branches, cormose lycopsids, and sphenopteroid foliage with associated axes and roots. Seven meters to the east of quarry 4 a trial quarry was excavated just prior to embarking on the systematic sampling. From this quarry were removed cupulate and acupulate gymnosperm material with charcoal on the same bedding planes. The subsequent discovery of gymnosperms in

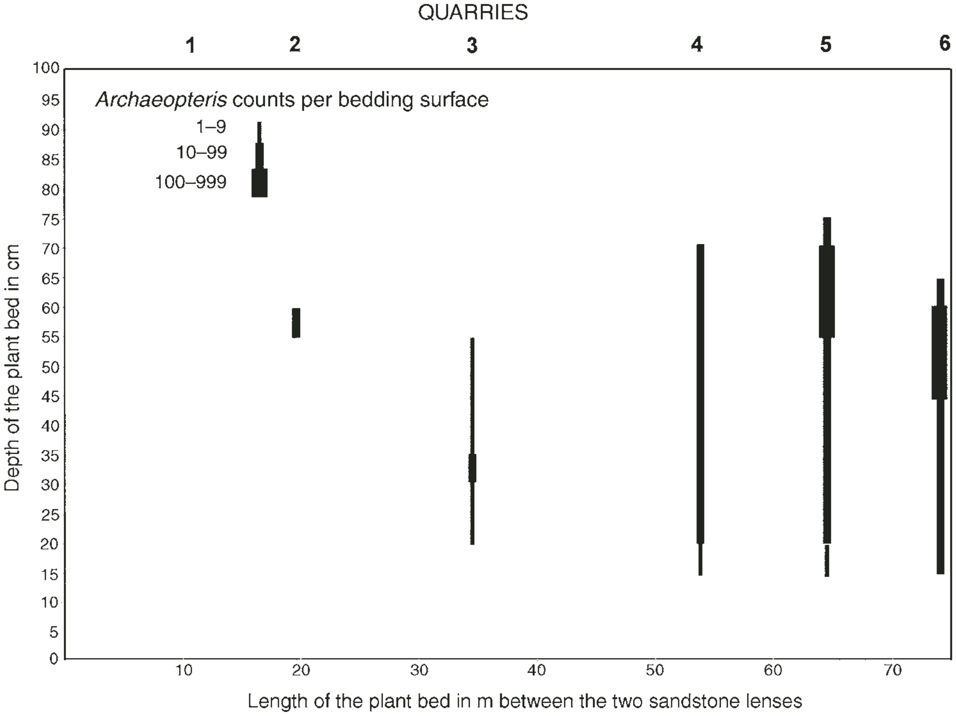

Figure 16. Distribution profile of *Archaeopteris* fossils in plant layer.

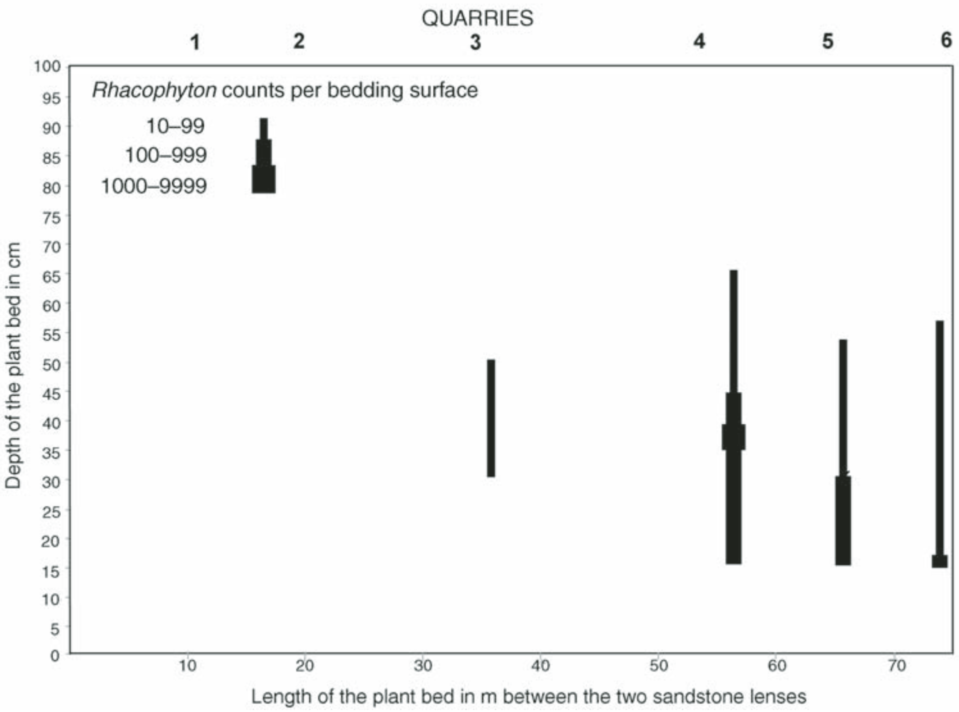

Figure 17. Distribution profile of *Rhacophyton* fossils in plant layer.

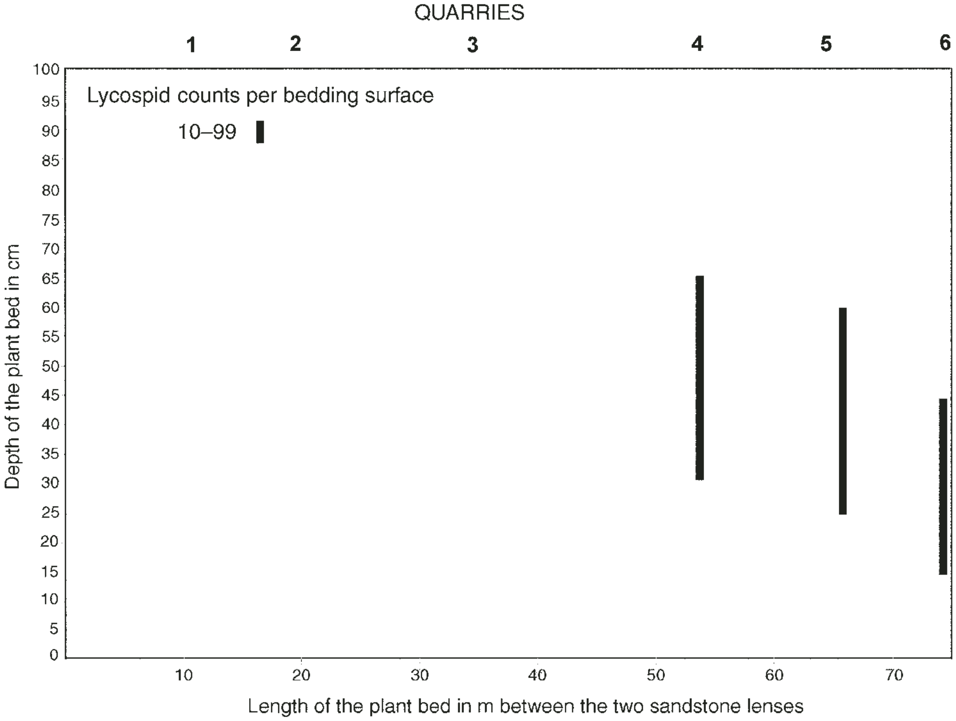

Figure 18. Distribution profile of lycopsid fossils in plant layer.

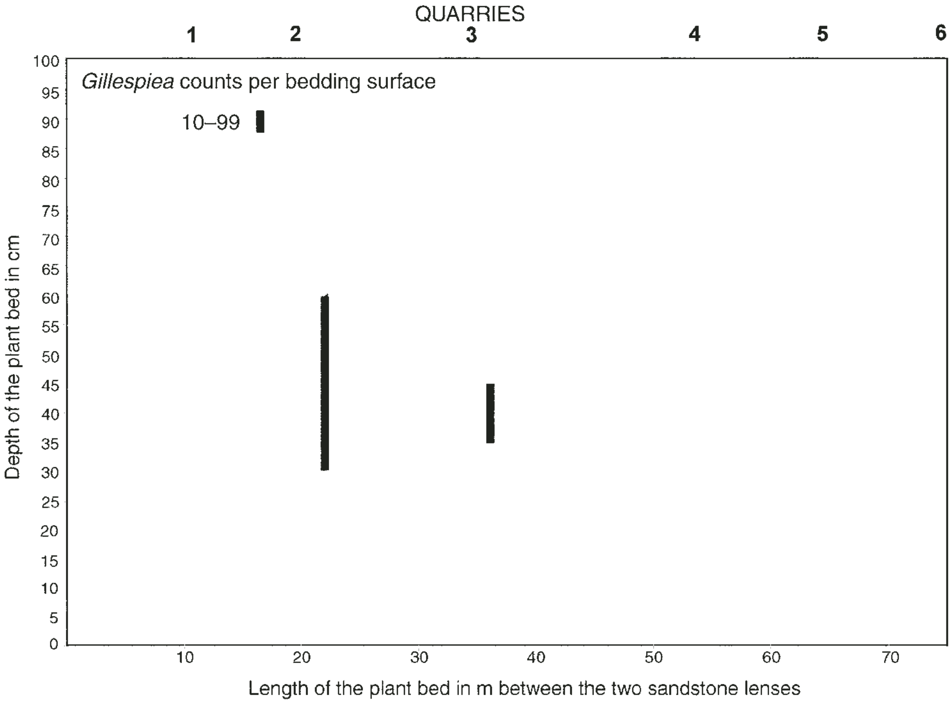

Figure 19. Distribution profile of *Gillespiea* fossils in plant layer.

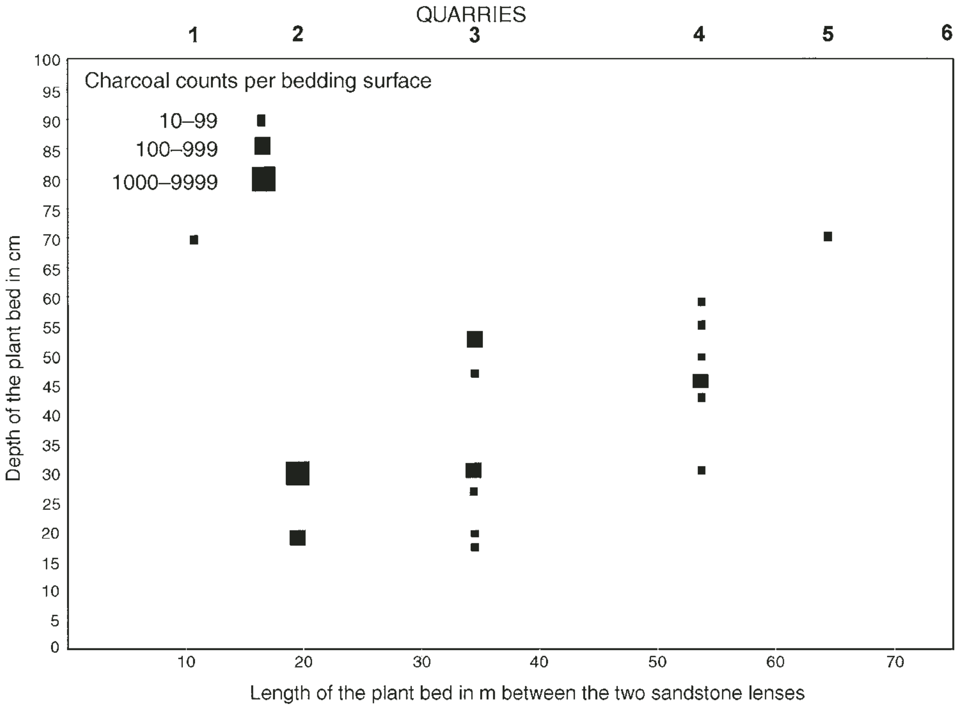

Figure 20. Distribution profile of fossil charcoal fragments in plant layer.

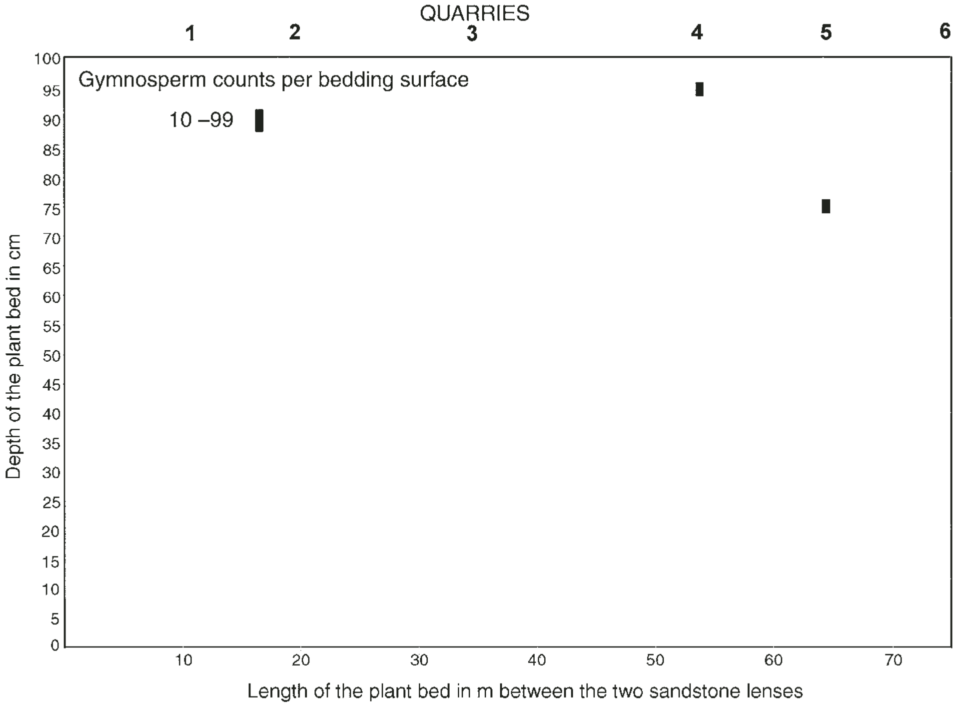

Figure 21. Distribution profile of gymnosperm fossils in plant layer.

quarry 4 and 5 to either side of the initial discovery reinforces the impression that their distribution is concentrated in this portion of the plant layer.

DISCUSSION

The following factors working in combination explain the distribution profile of plant fossils in the deposit:

(1) the limitations of the sampling process;

(2) the differential preservation of the plant fossils for both biological and geochemical reasons;

(3) the different hydrodynamic and aerodynamic properties of the plant parts as they entered the deposit under various flow regimes;

(4) the timing of cyclic and stochastic events before and during deposition, such as wind, fire, floods, and seasonal adaptations of plants, such as the seasonal branch shedding of *Archaeopteris*;

(5) the original distribution of the plants growing in the landscape.

Limitations of the Sampling Process

Several phenomena no doubt contributed to some error in the process of counting the plant fossils. Many of the surfaces on which plant fossils were counted did not cleanly break along bedding surfaces. Frequently, the fragments broke out of a quarry into small uneven pieces. Several of these roughly breaking intervals would regularly occur between two cleanly breaking bedding surfaces. The sampling was simply taking place at a finer scale than the thickness of the depositional packages. Counting the plant fossils on the rough fragmentary surfaces would probably not have contributed any significant error to the plant census. Because the flow regime appears to have remained the same throughout each depositional event, these counts merely add finer resolution to the overall plant count. Even though it is also possible that not every clean sedimentation break was found in every quarry, the sampling was fine enough to have included part of every depositional event.

Another difficulty was that the bedding surface area of the quarries changed slightly as the excavations proceeded. Rock was increasingly difficult to remove from areas immediately adjacent to the back wall of the quarries. Some weathering was required to express bedding planes. This potential decrease in the size of the measured surface area for each interval was always compensated by an increase in surface area along the proximal margin of the quarry due to the sloping hillside. Measuring precisely how well this process maintained uniform area throughout the quarry was impractical, though.

The measured sets of centimeter-scale intervals from quarry to quarry probably do not correspond precisely to each other because the measurements were made for each increment after the previous surface was cleared in each quarry. Distance from the lower contact of the reduced horizon was used as a rough proxy for correlating beds from quarry to quarry. Any imprecision would not have confounded the interpretations made in this paper, since only the coarsest trends in the vertical and lateral distribution of the plant fossils and charcoal are considered in the analysis.

In contrast to the fine-scale vertical sampling within the quarries, the lateral spacing of the quarries left large portions of the plant layer unsampled. Patchiness in the distribution of the plant fossil taxa may have gone undetected as a result. The number and location of the quarries were dictated by practical considerations of the time and effort it would have taken to remove overburden. Differences in spatial scale variation in the distribution of the plant fossils was taken into account by making some quarries adjacent to each other and others some distance apart. A pattern of concentric density gradients of the plant fossils in the distribution profile suggests that significant patchiness does not occur at a smaller scale for the taxa that occur at high densities. At the scale of sampling for this study, the rare taxa do not occur at high enough densities to produce a distribution pattern discernible from statistical noise.

Differential Preservation

Studies of organic detritus in Holocene oxbow lakes and other alluvial settings have determined that the most decay-resistant elements of the local vegetation get preserved in compression-impression assemblages (Scheihing and Pfefferkorn, 1984; Gastaldo et al., 1989). Decay-resistant elements of a Late Devonian tropical lowland flora are all that are represented at Red Hill. The reducing conditions of the pond sediments into which the plant remains were deposited promoted plant preservation. Reduction of sediments was largely maintained by the decay of the less resistant organic detritus. The plant layer underwent this geochemical process. Its reduction state was produced simultaneously with deposition. The mostly unfossiliferous greenish-gray siltstone margins above and below the dark-gray layer were probably secondarily reduced, perhaps by anoxic groundwater migration. The upper greenish-gray siltstone, for example, does not always conform to bedding. There are occasional poorly preserved plant fossils in the immediately overlying red laminated siltstone that are surrounded by greenish-gray reduction spots. These conditions place an upper and lower boundary on the horizon of well-preserved plant fossils.

Laterally, the reducing conditions in the plant layer appear to have been fairly uniform except in quarries 1a and 1b. Excavations in these quarries did not yield any recognizable plant fossils. Conditions there were more highly oxygenated as indicated by extensive red mottling. These conditions are perhaps due to the close proximity of the sandstone body. The high porosity of the sand perhaps promoted groundwater flow at a higher oxygenation state within the accumulating silt in the immediate vicinity.

The waters of the pond itself were probably well oxygenated most of the time as indicated by the numerous articulated specimens of actinopterygian fishes found among the plant remains in the plant layer (Daeschler, 2000a). An occasional anoxic episode in the pond may have killed off schools of these fish, ultimately leading to their incorporation into the fossil record. Supporting evidence for general oxygenating conditions in the pond water itself is the discovery of the green alga *Courvoisiella ctenomorpha* Niklas in a hydrofluoric acid maceration of the plant layer dark-gray siltstone (Niklas, 1976; Pat Gensel, 1998, personal commun.).

Transport into the Deposit

All of the plants fossilized in the plant layer at Red Hill appear to have been transported into the deposit from a range of relatively short distances. Variation in preservational states suggests that some were originally growing along the edge of the pond, and some were growing at somewhat farther distances away on the surrounding flood plain. The pond that the plant layer represents was silting up on the flood plain under predominately low-energy conditions. Silt moved over the landscape suspended in flood waters, which also carried with it plant matter, animal remains, and charcoal. The arrangement of the plant remains and charcoal on all the bedding planes that were examined does not indicate any clear flow direction. Silt-laden waters entered the pond either from a general rise of water level on the flood plain resulting from a nearby active channel overtopping its banks, or from a breach in the pond shoreline that gave access to waters from a more active channel through sporadic crevasse splays. The condition of the plant fossils and the lack of flow-direction indicators imply that a general rise of water level was the more prevalent process. The presence of at least two mud pebble conglomerate layers, however, suggests that shoreline breaches also occasionally occurred during times of higher- energy deposition.

Archaeopteris remains were found scattered throughout the sampling transect, but the densest and best-preserved concentration of *Archaeopteris* remains occurred along the shoreline of the pond. All *Archaeopteris* found consisted entirely of distal branch portions, some of which have attached leaves and sporangia. Their source was probably from the canopies of nearby small to medium-sized trees. The intact condition of many of the branches with attached leaves and sporangia suggests that they were wind carried directly into the deposit. The less well preserved condition of many of the other *Archaeopteris* branches implies that some of the material was dried on the ground before being carried into the deposit by silt-laden floodwaters. Either the wind-blown branches may have either sunk where they landed on the edge of the pond, or they may have accumulated by wind-drift along the shoreline.

Like *Archaeopteris*, the *Rhacophyton* remains were found distributed widely in the plant layer. The condition of these fossils varied widely as well. The densest and best preserved concentration of *Rhacophyton* was found in quarries 4a and 4b, a location more distal from the lakeshore, as indicated by the transect line, than the main concentrations of *Archaeopteris* and lycopsid stems. The condition of these *Rhacophyton* remains indicates that they were transported from close by into the deposit, and in fact were probably growing along the edge of the pond. If the face of the roadcut slices the pond nearly parallel to one of its shorelines, the source of the well-preserved *Rhacophyton* remains may have been from an area of the landscape where they were growing in concentration. If the transect is more perpendicular to the shoreline, *Rhacophyton* may have been more easily transportable into the distal portions of the deposit. Almost all of the *Rhacophyton* material in the rest of the plant layer consists of small, highly transported broken axes.

The decorticated lycopsid stems show evidence for transport not only by their condition, but also by sorting of stem sizes. Smaller stems were found farther out into the deposit away from the shoreline and larger stems were found closer to the shoreline. They may have come in with flood waters from elsewhere in the landscape, but the cormose lycopsid rooting organs with attached rootlets were probably transported from a negligible distance.

The main concentration of *Gillespiea* remains was found farthest from shoreline. They were also found closer to shoreline, but in extremely small concentrations in proportion to the other plant remains. *Gillespiea* was found entirely as small, thin axes. Transport may be the best explanation for its occurrence away from the shoreline compared with the other plant remains, but their low numbers may also indicate that no pattern of distribution is discernible. The highest concentrations of charcoal were also found in the same distal quarries as the highest concentration of *Gillespiea*. Charcoal is light and easily transported, and perhaps *Gillespiea* axes have similar characteristics. On the other hand, *Gillespiea* may have been transported a relatively shorter distance such as from the top of the western sandstone body or a shoreline of the pond that is not discernible from the transect configuration.

Most of the gymnosperms found in the plant layer were associated with fragments of charcoal. They were transported into the deposit together from nearby on the surrounding flood plain.

Aside from the articulated actinopterygian fish, which can be inferred to have died in their original habitat, the isolated vertebrate elements found in the plant layer were most likely transported into the pond from a main river channel. The fish died and became disarticulated at some point between a main channel and the pond, and their isolated elements were part of the bedload of the slowly moving flood waters.

Cyclic and Stochastic Events Influencing Plant Fossil Distribution

Timing of floods and fires due to seasonal influences, as well as any seasonal adaptations of the plants, such as deciduousness, would influence the pattern of plant distribution in the Red Hill pond deposit. For example, *Archaeopteris* penultimate branches are interpreted to be deciduous (Scheckler, 1978), and possibly shed as a dry-season adaptation (DiMichele et al., 1992). When complete they have a swollen abscission region at their base and often occur as dense mats of foliage and penultimate branches only, such as at Red Hill. Within the seasonal parameters, stochastic phenomena such as variation in storm intensities and wind gusts, and the magnitude and directionality of floods also have an influence on plant fossil deposition patterns.

The most direct evidence for seasonality at Red Hill is the abundant paleovertisols. The Red Hill outcrop includes a series of stacked paleovertisols above and below the plant layer where the sampling took place. There are at least two thin paleovertisols below the plant layer, and at least four well-developed paleovertisols above the plant layer (Figs. 3–5).

The shrink-and-swell clays in the paleovertisols of the Catskill Formation have been diagenetically altered to illite (Harvey, 1998). The first paleosol above the plant layer and the intervening red laminated siltstone is 3 m thick. This is a minimum thickness, because the soil horizon could have been partly truncated by erosion or scour without leaving any evidence for it, prior to being buried by the next series of red laminated siltstones. The paleosols have vertical cracks and pedogenic slickensided surfaces arcing away from the cracks in the manner distinctive of mukkara structures (Dudal and Eswaran, 1988). The cracks have been filled, and are distinguished by being reduced to a gray color. The mukkara have angles that range between 20º and 50º with respect to horizontal. They are concentrated between 80 and 180 cm below the apparent surface of the paleovertisol. The paleovertisols have lost all indication of stratification through pedoturbation. They have angular peds ranging in size from 1.0 - 1.5 cm in their upper portions, and from 2 - 4 cm in their lower portions. They also contain numerous carbonate nodules.

The paleovertisols at Red Hill are indicative of a seasonally wet and dry climate when the fossil flora was growing on the landscape (Driese and Mora, 1993). Even though there are no paleovertisols that are laterally continuous with the plant layer, they are found both above and below it. To assume that the plant layer was a free-standing body of water on the flood plain while elsewhere vertisols were being formed in the landscape is not unreasonable. Free-standing bodies of water are found on landscapes where vertisols are being formed today (Dudal and Eswaran, 1988). In this model, deposition of silt into the pond would have also been subject to seasonal changes.

Paleogeographic reconstructions showing the central Appalachian Basin at 20º south of the equator (Scotese and McKerrow, 1990) imply a subtropical region in a latitudinal zone of a single annual wet season and dry season, which possibly resulted from monsoonal circulation patterns in the “Proto-Tethys” sea (Bambach et al., 1999). A seasonally wet and dry climate for the central Appalachian Basin in the Late Devonian is further supported by lithological and paleontological studies in addition to those conducted on the paleosols. Evaporites, calcretes, the structures of stream and flood-plain deposits, and traces of lungfish burrows have led to an estimate of an annual precipitation of 75 cm arriving in the wet season during this Late Devonian climate regime (Woodrow et al., 1973).

The subtle changes in grain size and color observed throughout the entire 1 m thickness of the reduced horizon indicates that only ten depositional events are represented. If deposition in the pond occurred primarily during annual wet-season floods, the lake could have been entirely silted up in as little as ten years.

One outcome of the wet-and-dry seasonality at Red Hill during the Late Devonian was the occurrence of wildfires during the dry season (Cressler, 2001). Small black organic fragments that were subsequently identified as charcoal were discovered in the plant layer when the paleoecological sampling was conducted. Scanning electron microscopy revealed that the anatomically preserved charcoal was *Rhacophyton.*

Distribution of the charcoal in the plant layer is shown in Figure 20. Some bedding planes are densely covered with charcoal fragments along distinct horizons that might connect across sampling quarries. Charcoal is also sparsely scattered throughout many other parts of the deposit. There is no preferred orientation of the charcoal fragments on any of the bedding surfaces. Some bedding planes have varying amounts of charcoal in association with unburned plant material. Dense accumulations of charcoal co-occur with recognizable but poorly preserved penultimate branches of *Archaeopteris*. Dense accumulations of charcoal also occur on the same bedding planes with well-preserved gymnosperms. Most of the gymnosperm material found in the plant layer was found in association with charcoal. Even on the hand specimens where charcoal and unburned plant material occur together, all of the identifiable charcoal fragments are *Rhacophyton*. Well-preserved *Rhacophyton* has not been found on the same bedding planes with charcoal, although occasionally scattered charcoal fragments and small *Rhacophyton* fragments have been found on the same bedding plane. The quarries with the most abundant charcoal (2a and 2b) also had the most abundant *Gillespiea* remains. Abundant *Gillespiea* occurs within 15 cm above a large pulse of charcoal in quarry 2a, and within 30 cm above a large pulse of charcoal in quarry 2b, but *Gillespiea* and charcoal have not been found together on the same bedding plane. Whether the charcoal in quarries 2a and 2b is on the same horizon is ambiguous. Charcoal in quarry 2a is 19 cm above the contact between the greenish-gray siltstone and the underlying red siltstone, while that in quarry 2b is 30 cm above the contact. The two quarries are 2 m apart and beds cannot be followed from one to the other.

Original Growth Position of the Vegetation in the Landscape

Because of the entirely parautochthonous nature of the plant fossils that were sampled, these data provide a less direct test of hypotheses concerning the original growth position of the plants than if they were found in situ. In combination with the available taphonomic information, however, the sampling profile of this parautochthonous assemblage does place many more constraints on plant community models than would an allochthonous assemblage. The model being tested here is whether the Late Devonian tropical lowland plants at Red Hill had phylogenetically partitioned the landscape by environment sensu DiMichele and Phillips (1996).

Plant fossils sampled during this paleoecological analysis all came from the same sedimentological layer. They may have come from different habitats in the landscape, but they ended up buried in the same depositional environment, the silt of a flood-plain pond. The evidence indicates that the plant fragments had been transported from various distances, but the condition of the identifiable plant remains indicates that they were deposited no more than several meters from their growth position. Any discernible habitat partitioning by the plants at Red Hill would therefore have been over a spatial scale on the order of tens or hundreds of square meters rather than square kilometers.

The *Archaeopteris* trees that shed their branches into the deposit were probably growing the farthest away from the shores of the pond of all the plant taxa sampled. There are no remains of *Archaeopteris* trees in the plant layer that are larger than 1-cm-thick penultimate branches. All *Archaeopteris* remains must have arrived in the deposit as wind- or water-borne fragments. The transport distance of the fragments would have been enhanced by their having dropped from the canopies of sizable trees at the edge of a nearby forest. The nearest *Archaeopteris* forest to the pond apparently did not grow up to the edge of the pond, otherwise the trees would have dropped larger branches into the deposit. They probably were growing higher on the flood plain or on a nearby levee where the water table was lower. The *Archaeopteris* forest that supplied the well-preserved, apparently windblown, branches along the pond shoreline may have been growing some distance upslope from the shoreline where their branches accumulated. Alternatively, the concentration of *Archaeopteris* remains along the edge of the pond is due to accumulation by wind transport along the surface of the water. In either case, the *Archaeopteris* forest was not growing very near the pond, but where the water table was consistently high.

Archaeopteris is believed to have been capable of forming closed canopy forests (Retallack, 1985; DiMichele et al., 1992). The flood-plain paleosols at Red Hill have not yielded any clear evidence of *Archaeopteris* root casts or tree stumps. At the extreme western end of the outcrop is a suggestive reduction halo in a paleosol constituting two 85 cm parallel vertical lines ~50 cm apart. The greenish-gray lines flare out from each other at the base, suggestive of a stump with roots. The structure is weathering out from the outcrop in a manner also suggestive of a three-dimensional stump cast. This is the only putative evidence of an in situ plant of *Archaeopteris* proportions in the entire 1-km-long exposure of Red Hill. The scarcity of in situ tree stumps and root casts in the flood-plain paleosols of the Catskill Delta Complex has been addressed by Driese et al. (1997). They list three possible reasons: (1) flood plains may have been unfavorable environments for large trees, (2) preservation is poor due to pedoturbation in fine-grained flood-plain paleosols, or (3) the rates of sediment accumulation were insufficient to bury stumps and root casts. Of these, the second reason seems the most plausible.

The presence of locally concentrated and well-preserved remains of *Rhacophyton* as well as scattered fragmentary remains throughout the deposit indicates that *Rhacophyton* was widespread on the surrounding landscape and grew up to the edge of the pond. *Rhacophyton* probably grew in monotypic clonal patches (Scheckler, 1986a, 1986c) as suggested by the specificity of the wildfires and the evidence for distinct deep-rooted and shallow-rooted areas in the Late Devonian landscape (Harvey, 1998). *Rhacophyton* was shallow rooted (Scheckler, 1986c) and would have dried up even with small reductions of wetland water tables. It was subject to desiccation and ignition during the dry season. In contrast, *Archaeopteris* was a deep-rooted tree that would have been little affected by a temporary, drought-induced drop in the water table (Algeo and Scheckler, 1998; Algeo et al., 2001). Burned-over areas formerly occupied by *Rhacophyton* perhaps provided an opportunity for other plants to colonize, such as the gymnosperms and perhaps *Gillespiea*. At Elkins, West Virginia, study of contemporaneous sediments shows that gymnosperms were pioneers that were quickly overgrown and replaced by *Rhacophyton* (Scheckler, 1986c; Rothwell and Scheckler, 1988), which suggests a complex ecological interaction.

The diagonal profile of lycopsid distribution in the deposit suggests a progradation of lycopsids along the shore of a shallowing pond. This evidence is based on the distribution of decorticated stems, which may have actually come from plants growing in the surrounding flood plain. The discovery of several lycopsid rooting organs with attached rootlets is firmer evidence that cormose lycopsids were growing along the edge of the pond, however. They would have been growing in soft sediment along the edge of the pond, which slumped into the water during floods. For part of the year at least, the cormose lycopsids had their lower portions submerged in the water. Red Hill lacks the coal horizons, similar to those described by Scheckler (1986c) and by Goodarzi et al. (1989, 1994) for other Devonian sites. This suggests that the Red Hill wetlands either periodically dried out or that their waters were too shallow and too well oxygenated to sustain massive carbon burial. The cormose lycopsids show evidence for constituting a multi-aged community, as indicated by specimens of different sizes on one bedding plane (Fig. 6). Other lycopsids, such as *Lepidodendropsis*, may have been growing elsewhere on the flood plain and their decorticated stems washed into the pond during flood events. In the Early Carboniferous, for example, *Lepidodendropsis* inhabited both peat- and non-peat-accumulating wetlands (Scheckler, 1986a).

Gillespiea remains are concentrated at a point along the transect farthest away from the identifiable pond shoreline. This bias could be due to their having been preferentially transported farther because of their lightness and buoyancy. The *Gillespiea* remains are highly fragmented. They could have transported into the deposit from a growth position anywhere in the surrounding landscape, including as close by as the top of the western sandstone body. *Gillespiea* seems to be loosely associated with the presence of charcoal, but that may be due to similar transport characteristics. Nevertheless, the small construction of *Gillespiea* suggests that it might be a quick-growing opportunistic plant of disturbed areas, a lifestyle perhaps aided by its heterosporous reproduction.

Gymnosperms were found on only a few bedding planes during the entire sampling effort. Any pattern of their distribution may be insignificant due to their relative rarity and disarticulation. All gymnosperm remains were found toward the top of the plant layer. Their upper placement in the deposit implies an appearance during the later stages of the pond's existence. Frequent association of gymnosperms on the same bedding planes as charcoal may indicate that they were pioneer plants in the areas of the landscape affected by fires. Gymnosperms at Red Hill show a range of morphologies, from acupulate forms to cupulate forms with differing degrees of fusion of the cupules. This range of reproductive morphologies likely reflects a variety of ecological niches already occupied by gymnosperms as early as their first fossil appearance in the Famennian 2c.

The sum total of taphonomic evidence, the distinct distributions of the plant taxa in the depositional profile, and the specificity of the charcoal modestly support a model of small-scale heterogeneity of the Red Hill landscape with respect to its vegetation. The ecological partitioning of the landscape by the plants at Red Hill does appear to correspond to higher-order taxonomic groups, especially in light of low apparent diversity at the species level. However, since low species diversity necessitated the pre-selection of higher-order categories for the analysis at the outset, some of the higher-order patterning attributed to these results may reflect this conceptual bias. Phylogenetic partitioning of the landscape by major plant groups close to the time of their origin has important implications for understanding macroevolution. The evolutionary appearance of clade-specific, distinct plant architectures appears to be associated with specific ecological modes, which may reflect the divergent biology that underlies these morphotypes (DiMichele and Bateman, 1996; DiMichele and Phillips, 1996).

Comparison of Red Hill with Other Late Devonian Floras

The Late Devonian (Famennian) Hampshire Formation in West Virginia and Virginia includes plant fossil assemblages that represent some of the earliest known coal swamps (Scheckler, 1986c). Older coal beds are now known from the Givetian and Frasnian of Melville Island, Arctic Canada (Goodarzi et al., 1989; Goodarzi and Goodbody, 1990; Goodarzi et al., 1994). Subsequent examination of these deposits reveals that the coal-forming plants were arborescent lycopsids (Stephen Scheckler, 2002, personal commun.). In the Famennian, *Rhacophyton* dominated both deltaic marshes and flood-plain backswamps (Scheckler, 1986c). The Elkins, West Virginia locality in the Hampshire Formation is a deltaic shoreline deposit of Famennian 2c age that has the most diverse Famennian plant assemblage in North America. Five species of *Archaeopteris* are included: *A. macilenta*, *A. halliana*, *A. hibernica*, *A. obtusa*, *A. sphenophyllifolia*, as well as the affiliated progymnosperm wood taxon *Callixylon erianum*. *Rhacophyton ceratangium*, *Gillespiea randolphensis*, and *Barinophyton sibericum* are also present. Seed plant material at Elkins consists of *Sphenopteris* foliage, abundant cupules with ovules, cupuliferous branches, and foliage of *Elkinsia polymorpha*, and cupule fragments of *Condrusia*. Petrified axes of the cladoxylalean *Hierogramma* were also recovered. The Elkins assemblage includes the sphenopsids *Sphenophyllum subtenerrimmum* and cf. *Eviostachya* sp., as well as an arborescent lycopsid (Scheckler, 1986b). Despite the difference in environmental setting, the Red Hill flora is closely comparable to the Elkins flora, except that Red Hill does not have any gymnospermous synangia or any sphenopsids. *Barinophyton* has been found only in the shoreline setting of the Elkins locality in the Hampshire Formation, and has therefore been interpreted as a plant of marine deltaic environments. Two species of *Barinophyton* have now been found at Red Hill, a freshwater fluvial setting high on the alluvial plain. Red Hill is similar in environment to the Rawley Springs, Virginia, locality in the Hampshire Formation, which is at the top of a fluvial fining-upward cycle. The coal-forming *Rhacophyton* swamp at Rawley Springs is interpreted as forming in an oxbow or a backswamp continuous with the adjacent soil. The only other plants found at Rawley Springs are *Callixylon* sp. and an arborescent lycopsid (Scheckler, 1986c).

The flora of the Evieux Formation in Belgium (Stockmans, 1948) is of the same Famennian 2c age as the flora of Red Hill and Elkins, West Virginia. The Evieux flora is dominated by *Rhacophyton* and *Archaeopteris* (Kenrick and Fairon-Demaret, 1991) but also includes the most diverse assemblage of Late Devonian gymnosperm taxa. At least three cupulate taxa (Fairon-Demaret and Scheckler, 1987; Fairon-Demaret, 1996) and two acupulate taxa (Hilton, 1999) are known from the Evieux Formation. Stockmans (1948) described many forms of possible gymnosperm foliage (Rothwell and Scheckler, 1988). The Evieux flora also includes *Eviostachya*, *Barinophyton*, *Condrusia* (Stockmans, 1948), and *Barsostrobus*, a large heterosporous lycopsid cone (Fairon-Demaret, 1977; Fairon-Demaret, 1991). Aside from the possible sphenopsid and several other minor elements, the Red Hill flora is similar to the Belgian Evieux flora.

The Oswayo Formation in northern Pennsylvania has yielded plant fossils of a slightly younger age (Fa2d to Tn1a). *Archaeopteris* has been recovered from the Oswayo Formation (Arnold, 1939), in addition to cupules with ovules of the gymnosperm *Archaeosperma arnoldii* (Pettitt and Beck, 1968).

In Great Britain, the Taffs Well assemblage of South Wales (Tn1a to lower Tn1b; Hilton and Edwards, 1996) includes the acupulate gymnosperm *Aglosperma quadripartita*, similar forms of which are now also known from Red Hill, and the organ genera *Telangiopsis* and *Platyphyllum*. Cupulate gymnosperms are also present at Taffs Well. The highly disarticulated nature of the plant remains there indicates that it is an allochthonous assemblage (Hilton and Edwards, 1996). The Avon Gorge assemblage from near Bristol, England (lower Tn1b) is dominated by *Chlidanophyton dublinensis*, a plant originally identified as *Rhacophyton* (Utting and Neves, 1969) but of unknown affinities (Hilton, 1999). This assemblage also includes the acupulate gymnosperm *Aglosperma*, *Platyphyllum*, the gymnosperm synangium *Telangiopsis*, *Alcicornepteris* sp., and other plant organs of unknown affinities (Hilton, 1999). The environment of deposition for this flora has been interpreted as fluvial. The plant fossils occur either on green, fine-grained sheet-flood-derived sandstones, or on micaceous mudstones within a sedimentological context that suggests flood-plain deposits in a deltaic or estuarine system. Occasional marine incursions are indicated by acritarchs recovered in macerated samples. Elsewhere in Great Britain, the Baggy Beds of North Devon contain the gymnosperm *Xenotheca devonica* (Arber and Goode) emend. Hilton and Edwards (see Figs. 2.3.13 and 2.3.14 *in* Rothwell and Scheckler, 1988), along with gymnospermous foliage *Sphenopteris* sp. and *Sphenopteridium* sp., and gymnospermous synangia *Telangiopsis* sp. (Hilton and Edwards, 1999).

In southwest Ireland, the Kiltorcan flora of County Kilkenny is a diverse assemblage of latest Devonian and earliest Carboniferous age (Tn1a to Tn1b; Fairon-Demaret, 1986; Jarvis, 1990). *Archaeopteris hibernica* is dominant and the lycopsid *Cyclostigma kiltorkense* is common. Other members of the flora are *Ginkgophyllum kiltorkense*, *Sphenopteris hookeri*, *Lepidodendropsis* sp., *Rhacophyton* sp., and *Spermolithus devonicus* (Chaloner et al., 1977). The Kiltorcan flora is similar to the Red Hill flora, but it lacks the diversity of early gymnosperms that Red Hill has. The Hook Head flora from County Wexford (Tn1a to lower Tn1b) is similar to the Kiltorcan flora in having *Archaeopteris hibernica* and cf. *Cyclostigma*, as well as cf. *Pitus*, cf. *Barinophyton*, and the lycopsid *Wexfordia* (Matten, 1995). The Ballyheigue locality in County Kerry (upper Tn1a to lower Tn1b) is less comparable to the Red Hill flora (Klavins and Matten, 1996). This predominantly gymnosperm flora is known from siliceous permineralizations in a deposit interpreted as a crevasse splay (Klavins and Matten, 1996). The gymnosperm domination of the Ballyheigue flora is similar to the younger Cementstone flora of Scotland (Scott et al., 1984; Bateman and Rothwell, 1990) and may mark the transition from progymnosperm dominance to gymnosperm dominance, at least in certain environments (Matten, 1995).

The flora of Bear Island, Norway (Fa2d to Tn1b; Nathorst, 1900; Nathorst, 1902; Scheckler, 1986a; Fairon-Demaret, 1986) is similar to that of the Kiltorcan flora. *Archaeopteris* and *Cyclostigma* are dominant elements, along with the sphenopsid *Pseudobornia ursina* (Kaiser, 1970) and *Cephalopteris mirabilis*, which is similar to *Rhacophyton*. Other plants, including many tree lycopsids, are less common.

Archaeopteris remains are also known from southeastern New York (Carluccio et al., 1966), from the early Frasnian Yahatinda Formation of Alberta (Scheckler, 1978) and many localities of the Frasnian and Famennian of Ellesmere and Melville Islands in Arctic Canada (Nathorst, 1904; Andrews, Phillips, and Radforth, 1965; Hill et al., 1997), South America (Berry and Edwards, 1996), Eastern Europe and Russia (Snigirevskaya, 1982, 1988, 1995a, 1995b), Siberia (Petrosyan, 1968), China (Cai, 1981, 1989; Cai et al., 1987; Cai and Wang, 1995), North Africa (Galtier et al., 1996; Meyer-Berthaud et al., 1997, 1999, 2000), South Africa (Anderson et al., 1995), Australia (White, 1986; Scheckler, 1998, personal commun.), and possibly Antarctica (Retallack, 1997). Investigations at Red Hill add another increment to our understanding of this worldwide flora during the time of the earliest forests.

An Emerging Picture of a Late Devonian Continental Ecosystem

In addition to plants, Red Hill is the source of abundant Late Devonian animal fossils. Red Hill is emerging as the richest known Late Devonian continental fossil site. More components of a Late Devonian terrestrial ecosystem are found at Red Hill than at any other locality. Animal fossils at Red Hill include vertebrates and terrestrial arthropods such as scorpions, myriapods, and a trigonotarbid arachnid (Shear, 2000). Rivers were inhabited by large predatory fish such as tristichopterid, megalichthyid, and rhizodontid lobefins, as well as groenlandaspidid and phyllolepidid placoderms, acanthodians, and ageleodid and ctenacanthid sharks (Daeschler, 1998). The pond deposit yielded numerous palaeoniscoid ray-finned fish. They were found in close association with penultimate branches of *Archaeopteris*, among which they may have been seeking refuge from the larger predators. Red Hill is also the locality for some of the earliest known tetrapods. *Hynerpeton bassetti* (Daeschler et al., 1994) and *Densignathus rowei* (Daeschler, 2000b) were discovered here.

No evidence for herbivory (leaves with chew marks or feeding trails) has been found among the fossils at Red Hill. There is no sign of herbivore damage repair among the plant fossils, and no herbivores have been discovered in the faunal assemblage. It appears that this freshwater-terrestrial ecosystem was largely supported by detritus from the abundant plant biomass growing on the land. The frequent floods across the flood plain transported this organic matter into the aquatic ecosystem. The seasonally rising and falling waters, the migrating channels and ever-changing flood-plain environment, the lush seasonal vegetation growing along the water's edge, and the abundant submerged plant material created a blurred habitat boundary between the aquatic and terrestrial realms. It was in this environment that lobe-finned fish thrived. Members of one lineage of lobe-finned fish, the earliest tetrapods, emerged in this type of environment (Westenberg, 1999).

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