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ABSTRACT

Early spermatophytes have been discovered at Red Hill, a Late Devonian (Famennian) fossil locality in north-central Pennsylvania, USA. The Red Hill locality contains an *Archaeopteris*-dominated flora within an outcrop of the Duncannon Member of the Catskill Formation. Palynological analyses of the plant fossil-bearing horizons within the Red Hill outcrop indicate deposition within the VCo palynozone. This is the earliest time horizon known to contain evidence for spermatophytes, and is contemporaneous with well-known spermatophyte-bearing deposits in West Virginia and Belgium. Some of the spermatophyte material from Red Hill compares well with *Aglosperma* sp., previously known as isolated ovules from the latest Devonian of South Wales and England, thus extending its geographic and stratigraphic range. Red Hill specimens of *Aglosperma* sp. occur both as isolated ovules and attached to dichotomously forking axes. Additional spermatophyte cupules discovered at Red Hill are morphologically similar to those of the previously described Late Devonian spermatophytes *Elkinsia* Rothwell, Scheckler, *et* Gillespie, *Moresnetia* Stockmans, and *Xenotheca* Arber *et* Goode. Some of the Red Hill cupule complexes are distinct from the aforementioned taxa in consisting of slender dichotomously forking axes terminating in paired cupules with highly fused and symmetric cupule quadrant lobes. The distinctive nature of these Red Hill specimens warrants the creation of *Duodimidia pfefferkornii* Cressler, Prestianni, *et* LePage *gen. et sp. nov.* Plant fossil remains with sphenopteroid foliage are also present at Red Hill, possibly attributable to the spermatophytes. Previous systematic sampling of the rich plant-fossil bearing layer at Red Hill and analysis of its floristic diversity and abundance as well as the presence and absence of charcoal suggests a pattern of floral turnover from a local-scale *Rhacophyton*-dominated community to spermatophyte colonization following disturbance by wildfires.

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1. Introduction

The earliest known indications of seed plants are based on proto-ovulate structures and date from the Upper Givetian (Gerrienne et al., 2004). It is generally accepted however, that their first major radiation occurred during the Famennian Stage of the Late Devonian Period (Pettitt and Beck, 1968; Gillespie et al., 1981; Rothwell and Scheckler, 1988; Hilton, 1998a; Prestianni, 2005). During the past twenty years, many Upper Devonian ovule-bearing taxa have been described, confirming this assessment. Up to fifteen described species highlight the wide range of morphological variation encompassed by these early ovules.

Based on the morphology of their cupules, integuments, and nucellus, Upper Devonian ovules have been loosely classified into five morphological groups: *Moresnetia*-type; *Aglosperma*-type; *Dorinnotheca*-type;

Condrusia-type; and *Warsteinia*-type (Hilton, 1998a; Prestianni, 2005; Prestianni and Gerrienne, in press). The *Moresnetia*-type is the most common and consists of multi-ovulate cupules. *Dorinnotheca*- and *Aglosperma*-types are both uni-ovulate cupules with the ovules surrounded by four flat integumentary lobes. The *Dorinnotheca*-type has a well developed cupule and the *Aglosperma*-type has an inconspicuous cupule. The *Condrusia*-type is comprised of a bi-segmented uni-ovulate cupule and the *Warsteinia*-type ovules are acupulate and have winged integuments. All types share the same wind pollinating syndrome called "hydrasperman reproduction" (Rothwell, 1986). In this, the distal end of the nucellus had a tube-like structure called a salpinx through which "pre-pollen" was captured and guided to a pollen chamber, which was subsequently sealed by a central column.

Fossil material of most Late Devonian spermatophytes is fragmentary and usually consists of dispersed ovules, cupules, and ovule/cupule complexes. Occasionally these structures are found attached terminally to axes. When foliage is found associated with any of this Late Devonian spermatophyte material, it usually conforms to the form genera *Sphenopteris* (Brongniart) Sternberg or *Sphenopteridium*

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Schimper. To date, *Elkinsia polymorpha* Rothwell, Scheckler, *et* Gillespie is the only whole-plant reconstruction for a Late Devonian spermatophyte (Serbet and Rothwell, 1992).

The Late Devonian spermatophyte assemblage from Red Hill, north-central Pennsylvania, is the same age (VCo miospore zone) as the other oldest known assemblages from the Hampshire Formation of West Virginia and the Evieux Formation of Belgium. Sediments of the Red Hill locality were fluvially deposited and are assigned to the Catskill Formation in Pennsylvania (Woodrow et al., 1995). This locality is known for its diversity of animal fossils, including tetrapods (Daeschler et al., 1994; Daeschler, 2000). Systematic paleoecological sampling of the plant material resulted in the recognition of twelve fossil plant species (Cressler, 2006). Based on observations of the existing fragmentary material, there is at least one spermatophyte form from Red Hill belonging to the *Moresnetia*-type that warrants the creation of a new genus and some material identifiable as the *Aglosperma*-type. This material has been found with a diverse plant assemblage that includes sphenopteroid foliage. All of this material is disassociated and fragmentary and does not lend itself to whole-plant reconstructions.

With at least one *Moresnetia*-type and one *Aglosperma*-type taxon, Red Hill has representatives of the most typical spermatophyte morphologies of this earliest known time horizon for seed plants. The contemporaneous Evieux flora of Belgium is taxonomically more diverse and includes the *Dorinnotheca*- and *Condrusia*-types (Fairon-Demaret, 1996; Prestianni, 2005). Ecological interpretations of the different spermatophyte morphologies are beyond the scope of this paper.

The detailed paleoecological analysis that has been conducted at Red Hill has identified the occurrence of periodic fires in the landscape (Cressler, 2001, 2006). The biotic and abiotic associations at Red Hill provide evidence for a paleoecological interpretation of general aspects of early spermatophyte biology that will be discussed in this paper.

2. Methods and materials

Plant fossil compressions of spermatophytes and sphenopteroid foliage described herein were collected from the Red Hill fossil locality, 2 km (1.2 mi) west of the village of Hyner on PA Route 120, in Clinton County, Pennsylvania, USA (41°20′30″ N, 77°40′30″ W). Fossil specimens are in repository at the Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, 19103.

Specimens were examined under a dissection microscope and some dégagement (Fairon-Demaret et al., 1999) was necessary to remove the matrix to expose more of the plant fossils.

The three-dimensional structure of one of the cupule pairs was further studied by embedding the specimen in resin, and then serially grinding away one end of the specimen at 500 micrometer (μm) increments using 600-grit powder. For a permanent record, black-and-white and color photographs were taken and digital images were recorded with a Quantimet 500 imaging system at each 500 μm increment.

3. Age and stratigraphy

Lithostratigraphically, the Red Hill locality is placed within the Duncannon Member of the Catskill Formation, which is characterized by fluvially derived mudstones, siltstones, and sandstones (Diemer, 1992). Most plant fossils from Red Hill were recovered from a flood-plain pond deposit referred to as the "Plant Layer" (Cressler, 2006), which has been assigned to the poorly calibrated VH palynozone (Traverse, 2003), but is less ambiguously attributed to the VCo palynozone (*sensu* Streel et al., 1987), within the Famennian Stage, Late Devonian Period.

Additional plant material was collected from a loose siltstone block found several hundred meters west of the "Plant Layer". This block is referred to as the "*Barinophyton* slab" in this report due to the presence of a fossil of that taxon in the block (Cressler, 2006). The block had fallen from a layer of gray siltstone approximately 20 m high on the vertical face of the exposure. Due to the slight westward dip of the strata at Red Hill, this block had come from a layer that is stratigraphically higher than the "Plant Layer", but still located within the continuous succession of fluvially derived deposits. An additional palynological investigation was conducted on this loose block. A single sample has been processed. HF 40% has been used for maceration and slides have been fixed using Eukit®.

The palynofloral list is as follows:
Dominant:

> *Aneurospora greggsii* (McGregor) Streel
> *Endoculeospora setacea* (Kedo) Avkhimovitch *et* Higgs
> *Diducites* morph van Veen
> *Rugospora radiata* (Juschko) Byvscheva

Present:

> *Grandispora cornuta* Higgs
> *Vallatisporites hystricosus* (Winslow) Byvscheva

This assemblage is attributed to the VH palynozone (Maziane et al., 1999). As discussed by Streel and Marshall (2007) this palynozone as it is strictly defined, is poorly correlated at long distances such as between Belgium and North America. Following Prestianni and Gerrienne (in press), we will consider this palynozone and the underlying VCo as one unit. In this paper, we accept the prior definition of the VCo palynozone before its split with the controversial VH palynozone (Streel et al., 1987). All plant bearing strata from Red Hill are thus included in the VCo palynozone *sensu* Streel et al. (1987).

4. Results
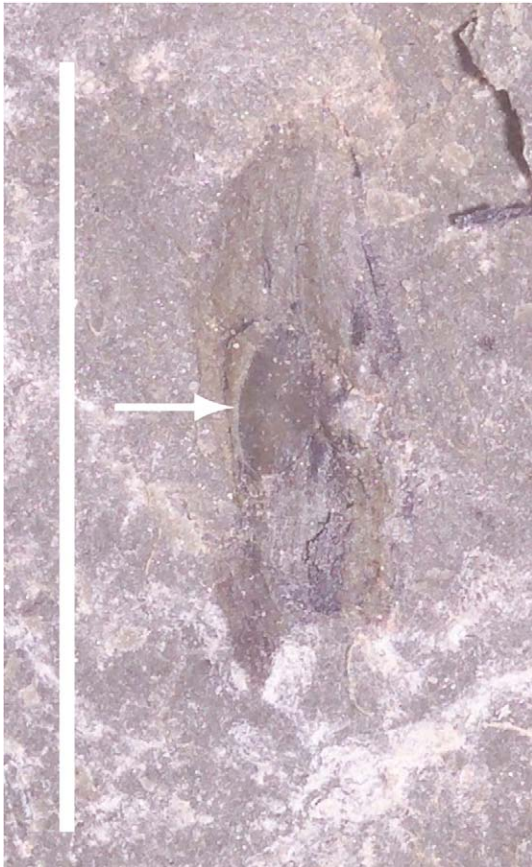
4.1. Aglosperma-type spermatophytes

Evidence for *Aglosperma*-type spermatophytes at Red Hill consists of dichotomously forking branches that terminate in ovules, and dispersed ovules that are attached to pedicels that are at least 1 cm long. In these specimens, the cupule is a tiny structure that inconspicuously covers the base of the integuments. Other ovules occur as isolated organs that are similar to those found attached to the dichotomously forking branches and are found in association with them. These are presumed to be of the same taxon. All of the *Aglosperma*-type spermatophyte material was recovered at Red Hill from a dark-gray siltstone layer representing a floodplain pond deposit designated as the "Plant Layer", in which systematic paleoecological sampling took place (Cressler, 2006). However, most of the *Aglosperma*-type material was discovered during excavations that took place after the systematic sampling study (Figs. 1–6).

4.1.1. Ovules

The *Aglosperma*-type ovules range between 8 and 11 mm in length as measured from the chalaza to the tips of the integument lobes. All are preserved as coaly compressions. ANSP 4525 (Fig. 1) shows details of the integument lobes and the nucellus. The latter has been exposed due to a fortunate split of the specimen between the nucellus and one integument lobe. The base of the nucellus remained covered by the integument lobes, thus prohibiting precise measurements. However, the nucellus seems to be wider towards the middle (~1.5 mm) and progressively narrows to 1 mm towards its distal end. The distal end is characterized by an abrupt reduction in width that is followed by a distal extension respectively identified as a pollen chamber and a salpinx that is 1.5 mm long. One specimen reveals an ovule with an apparent megaspore that is visible in both its part and counterpart

Fig. 1. *Aglosperma* sp. ovule, ANSP 4525. Salpinx emerges from nucellus at arrow. Scale bar = 1 mm.

compressions (Fig. 2). The oval body is 2.14 mm long, parallel to the long axis of the ovule.

The nucellus is surrounded by several integument lobes. In specimen ANSP 4525 two of them are clearly visible and are closely adpressed to the nucellus. A third lobe is partially visible (Fig. 1). The entire length of the ovule is 8 mm, including the integument lobes which protrude beyond the length of salpinx. ANSP 4538 (Fig. 3) consists of two clearly visible integument lobes and another that is partially covered. The nucellus is hidden by the integument lobes. This specimen is 7.4 mm long. Integument lobe number 1 (Fig. 3) is preserved perpendicular to the bedding plane. Splitting of the sediment revealed a side view of that lobe that is flat, with nearly no thickness. Lobe number 3 has been preserved parallel to the bedding plane. It is lanceolate in shape with an acute tip. The first basal third of this lobe is fused to the others.

The Red Hill *Aglosperma*-type ovule specimens show direct evidence for two to four integument lobes (Figs. 1 and 3). However, the dimensions of the integument lobes suggest that four to five integument lobes is the typical condition. In all specimens, the distal two thirds of the integument lobes are free. The level where lobes divide from one another corresponds to the greatest width of the ovules. The integument lobes are lanceolate and taper distally to an acute point. The degree of curvature at the apex can vary, but in most specimens the lobes are straight. Most specimens exhibit distally diverging integument lobes leaving the salpinx free. However, one ovule (Fig. 4) has integument lobes that taper distally. These are indistinguishable from each other as they completely enclose the ovule apex. This ovule is 8.5 mm long. Fig. 5 shows an intermediate condition with a semi-open ovule.

Specimens ANSP 4527 and ANSP 4540 (Figs. 4 and 5) are especially well preserved and attached to a long slender pedicel. The bases of their integuments are characterized by a progressive widening of the pedicel that is interpreted as a cupule. The cupule (Fig. 4 at arrow) is followed by an abrupt reduction that corresponds to its end leaving

Fig. 2. *Aglosperma* sp. ovule with exposed megaspore, at arrow, ANSP 4541. Scale bar = 1 cm.

Fig. 3. *Aglosperma* sp. ovule, ANSP 4538. Attachment point for small cupule at arrow. Integument lobes are labeled 1 through 3. Scale bar = 1 cm.

Fig. 4. *Aglosperma* sp. closed ovule, ANSP 4527. Small cupule at arrow. Scale bar = 1 cm.

the underlying integument visible. Similarly, in specimen ASNP 4538, the basal-most part of the fused integument lobes is covered by an additional structure that is partially buried in the sediment (Fig. 3, at arrow).The general lack of preservation of the cupule prevents any detailed morphological description. It is however interpreted as a collar-shaped organ that inconspicuously covers the base of the ovule.

4.1.2. Dichotomous branches

Many of the *Aglosperma*-type ovules from Red Hill were found singly with an attached pedicel that is up to 1 cm long. The *Aglosperma*-type ovules were also found in association with many dichotomously forked branches. One single specimen (Fig. 6) shows incompletely preserved ovules that conform in morphology to those described above. It consists of a dichotomously forked branch system of two orders of branching with four branches terminating in incompletely preserved ovules. The entire existing branch system is 11.5 cm long. The axis of the most basal preserved portion is 3 mm wide. At the next order of branching, the right fork enters the bedding perpendicularly and is lost in the matrix after several millimeters, but the arrangement as preserved suggests a cruciately forking condition of the branches. This pattern is characteristic of the dichotomous reproductive branches of early spermatophytes (Fairon-Demaret and

Fig. 5. *Aglosperma* sp. semi-open ovules, ANSP 4540. Scale bar = 1 cm.

Fig. 6. Twice-forking axis terminating in *Aglosperma* sp. ovules, ANSP 4528. Scale bar = 1 cm.

Scheckler, 1987). The axes become progressively narrower with each order of branching until the terminal branches have axes that are 1 mm wide or less. The final order of branching of this system is parallel to the previous order of branching, which are both parallel to the bedding plane. This non-cruciate arrangement of the thin terminal branches may reflect either a preservation bias due to their deformation in the sediment or the actual life condition of the plant. It is unclear from the specimen whether the living plant had a strictly cruciate arrangement of branches or exhibited both cruciate and planar growth.

4.1.3. Comparison and discussion

As stated earlier, this material conforms to the *Aglosperma* morphological type (Prestianni and Gerrienne, in press). This type is comprised of the two species from Wales and England, *Aglosperma quadrapartita* Hilton *et* Edwards and *Aglosperma avonensis* Hilton, and the two Belgian species, *Pseudosporogonites hallei* Stockmans and *Xenotheca bertrandii* Stockmans. This group was initially identified as being acupulate (Hilton, 1998a). However, a cupule has been subsequently identified in all species (Prestianni and Gerrienne, in press). All these species are entirely consistent with the generic diagnosis of *Aglosperma* Hilton *et* Edwards (Hilton and Edwards, 1996), aside from the lack of recognition of a cupule in this earlier description. However, they also completely conform to the generic diagnosis of *X. bertrandii* (Stockmans, 1948). Hilton (1999b) revised the generic diagnosis of *Xenotheca* based on Arber and Goode's original (1915) material and concluded that *Xenotheca* (sensu Hilton, 1999b) refers to a *Moresnetia*-type architecture. He further stated that the species *Xenotheca bertrandii* (Stockmans, 1948) conformed to another morphological type and should be excluded from that genus. As the species *Xenotheca bertrandii* (*sensu* Stockmans, 1948) and *Aglosperma* (Hilton and Edwards, 1996) are most probably congeneric, we therefore chose to attribute the specimens from Red Hill to the genus *Aglosperma*. A complete revision of the entire morphotype is however necessary before any further taxonomic discussion.

Aglosperma avonensis (Hilton, 1999a) and *A. quadrapartita* (Hilton and Edwards, 1996) only differ slightly from each other. The specimens from Red Hill conform most closely to *A. quadrapartita*. *A. quadrapartita* have ovules that range from 4.7 to 9.0 mm in length and a salpinx that is at least 0.6 mm long. The Red Hill *Aglosperma*-type ovules fall within this range of variation. They however, show a wider range of variation of
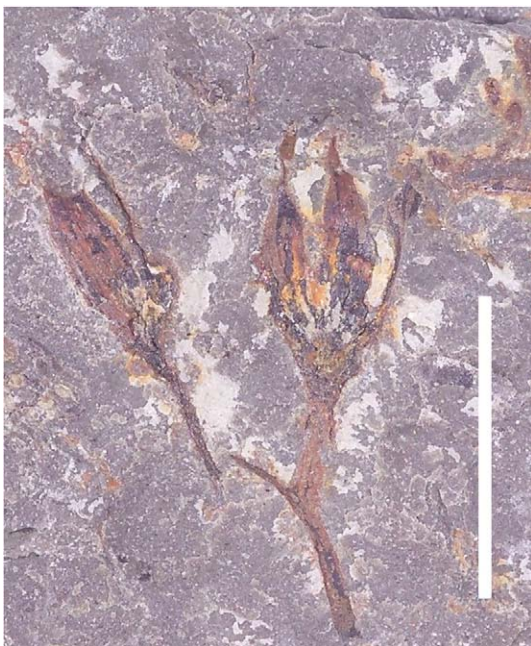
the integument lobe apex, ranging from completely closed to distally diverging lobes. In the specimens of *Aglosperma* sp. from Red Hill, the most common condition observed is the open apex morphology. Most of these ovules are found dispersed and their cupules are poorly preserved. The single specimen with closed apex morphology was found to be well-preserved, with indistinguishable integument lobes and an undamaged cupule. These types of preservation suggest that the closed and open apex morphologies represent immature and mature ovule morphologies occurring prior to pollination. The "closed" apex morphology is interpreted as the immature condition. This contrasts with Rothwell and Scheckler's (1988) hypothesis concerning the terete integumentary lobes of *Moresnetia*-type ovules where open and closed apex states represent pre- and post-pollination morphologies. The "open" apex is there postulated as the non-pollinated (ovule) condition and the "closed" apex the pollinated (seed) condition.

The identification of *Aglosperma*-type ovules from Red Hill extends the geographic and stratigraphic range of this genus. This report marks the first appearance of the genus *Aglosperma* in the Famennian, earlier than the previous record of its initial appearance during the Tournaisian LL palynozone (Hilton and Edwards, 1996). This first North American record of an *Aglosperma*-type spermatophyte is contemporaneous with the Belgian forms of the same morphotype, *X. bertrandii* and *P. hallei* (Stockmans, 1948; Hilton, 1998a). The stratigraphic range of *Aglosperma* extends into the Early Carboniferous (VI miospore zone) with the description of *A. avonensis* from Avon Gorge, Bristol, England (Hilton, 1998b).

4.2. Moresnetia-type spermatophytes (Figs. 7–19)

There is evidence of at least one and possibly two *Moresnetia*-type spermatophyte taxa at Red Hill based on the fragmentary compression fossils recovered there. They conform in morphology to the Late Devonian spermatophytes *Elkinsia*, *Moresnetia*, and *Xenotheca*, but some of the fragmentary material from Red Hill demonstrates a high degree of cupule symmetry that involves a greater degree of fusion of the cupule components than is seen in these other genera.

4.2.1. Cupules from the "plant layer"

One of the *Moresnetia*-type spermatophyte assemblages found at Red Hill was discovered during the systematic paleoecological sampling of the floodplain-pond deposit designated as the "Plant Layer" (Cressler, 2006). This material was not distinguished from the *Aglosperma*-type spermatophytes during the sampling process, so the positional relationship of the two spermatophytes within the "Plant Layer" was not determined. Specimens of the two spermatophyte morphologies were found on bedding surfaces that differ
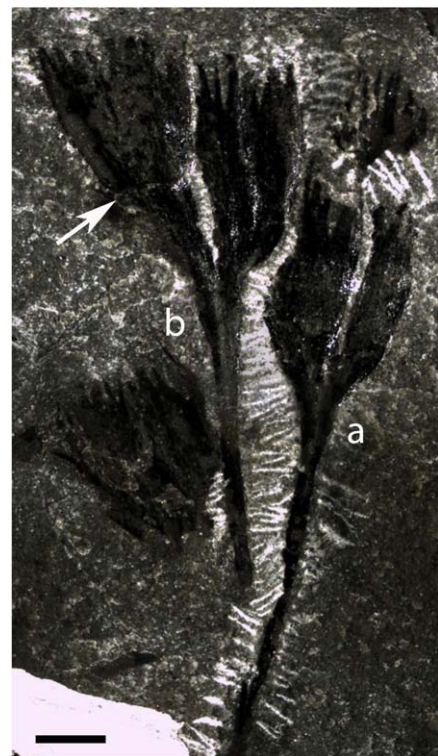

Fig. 8. Two cupule pairs (at "a" and "b") of *Duodimidia pfefferkornii, gen. et sp. nov.,* terminating two forks of a bifurcating axis, ANSP 4532 (holotype). Scale bar = 2 mm.

slightly in color and grain size, so they likely came from different spatial or stratigraphic horizons of the "Plant Layer" and therefore represent slightly different portions of the floodplain landscape. None of the material was transported very far from where the plants grew to

Fig. 7. Partially preserved cupule from "Plant Layer", ANSP 4529. Scale bar = 1 mm.

Fig. 9. Detail of adpressed cupule pair of *D. pfefferkornii*, ANSP 4544. Thin separation of sediment between cupule pairs at arrow. Scale bar = 2 mm.

where they were deposited and buried. All of the plant fossil specimens recovered from the "Plant Layer" during the systematic sampling study were found no more than 11 m from each other on a horizontal dimension and 1 m on a vertical dimension (Cressler, 2006).

Approximately twenty cupules or cupule fragments that all conform to the same general morphology were recovered from the "Plant Layer". ANSP 4529 is typical, and displays the distal ends of what appear to be four cupule quadrants aligned on the same level with four cupule forks on each quadrant (Fig. 7). Sixteen distinct fork tips can be counted on this array. At least two additional indistinct tips can be seen that are possibly integument lobes.

All of the other cupule fragments of this material occur as one to four cupule quadrants. Invariably, the cupule quadrants have four cupule tips each. Most of these cupules and cupule fragments were found associated, but not attached to axes, so their arrangement on the dichotomous reproductive branches is not known.

The poor preservation and the small number of specimens do not allow for precise taxonomic discussion. However, the general morphology of these cupules conforms to the *Moresnetia*-type and more precisely to the *Moresnetia–Xenotheca–Elkinsia* complex. Ovule-bearing plants grouped in these genera are likely to be closely related to one another if not congeneric (Hilton, 1999a). The main diagnostic feature of these plants, besides the branching system, is the manner in which the cupule is constructed. These cupules are deeply segmented, organized in four quadrants, and terminate in many fork tips. The material discussed here compares favorably to this morphology.

4.2.2. Cupules from the "Barinophyton Slab"

Better preserved cupules were found in the "*Barinophyton* slab". Contained in the block were some dichotomously forked branches, as

well as a specimen of *Barinophyton obscurum* (Dun) White bearing five well-preserved strobili (Cressler, 2006) and over forty carbonized compressions of cupule-like structures. No ovules have been identified from this assemblage thus far. However, the morphology of the specimens conforms to a number of spermatophyte remains of coeval age including *Archaeosperma* Pettitt *et* Beck and in particular compressions assignable to *Stamnostoma* Long (Long, 1962; Scott and Meyer-Berthaud, 1985). We consequently consider the material as being derived from early seed plants. The material consists of cupules and cupule fragments that are all morphologically similar to one another.

The proximal portions of the cupuliferous branching system are lacking and only two ultimate dichotomies have been observed (Fig. 8). The cupules appear to be borne in pairs atop terete bifurcating axes (Fig. 8). Specimen ANSP 4532 (Fig. 8) consists of two stalked cupule pairs. Cupule pair labeled (a) is the only specimen showing the entire length of this stalk and measures 16 mm in length. Individual cupules are revealed through the fracture planes that travel along the external surface of the cupules revealing only the external features (Figs. 8 and 9). The cupule pairs are tightly adpressed to one another and separated only by a thin sediment layer (Fig. 9, at arrow). The cupules are quite regular in size and vary from 11 to 12 mm long and 8 to 11 mm wide. Individual cupules are borne on very short (0.5 mm) terete axes and appear to be borne atop the ultimate dichotomy (Fig. 10, at arrow). They are most often asymmetric and slightly overtopped, one cupule being broader than the other and starting at a different level on the branch (e.g. Figs. 8–10).

Figs. 11 and 12 show two stages of dégagement of the specimen ANSP 4539. The individual cupules are labeled (A) and (B). Cupule (A) is incomplete and is borne on the terminal axis approximately 1 mm after the terminal dichotomy; cupule (B) appears to be complete

Fig. 10. *Duodimidia pfefferkornii* cupule, ANSP 4545. Ultimate dichotomy at arrow, showing cupules borne on very short terete axes. Scale bar = 2 mm.
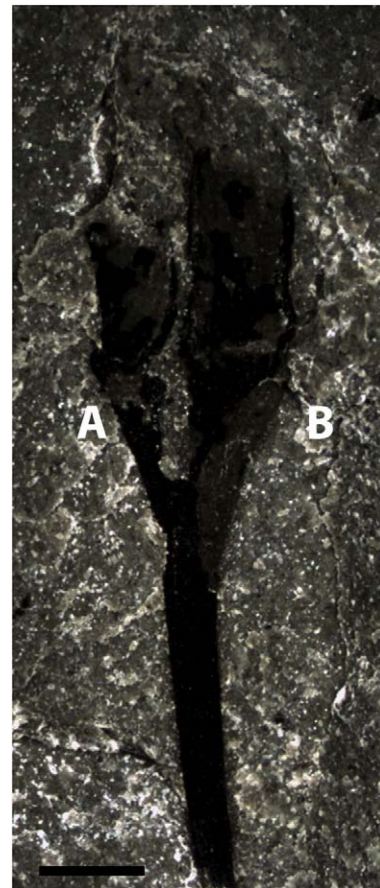

Fig. 11. Early dégagement stage of *D. pfefferkornii* cupule pair, ANSP 4539. Incomplete cupule at (A), complete cupule at (B). Scale bar = 2 mm.

and is borne on the terminal axis at the terminal dichotomy (Fig. 11). Fig. 12 shows cupule (b) completely exposed after dégagement completely removed cupule (a). Cupule (b) appears to consist of two distinct symmetric halves labeled (B1) and (B2). These are formed by an additional dichotomy occurring 1 mm after the previous one dividing the individual cupules. Apparent asymmetry of cupule pairs thus only reflects slight superposition of the individual symmetric cupules rather than actual asymmetry.

Support for this interpretation was obtained by embedding a cupule complex in resin and serially grinding the specimen at 0.5 mm intervals from the base of the structure to its distal end (Fig. 13, nos. 1–13). In this sequence of cross-sections, the compressed pedicel (no. 1), is followed by the emergence of a cupule shown on the right (no. 2), followed by the two cupules diverging over the following 1 mm (nos. 3 and 4). Each cupule has four cupule quadrants that are fused along every margin except medially. The cupules thus each have a medial opening that faces toward one another in the center of the cupule complex. After another 1.5 mm distally, the cupule hemispheres show some separation (nos. 5–7). Fig. 14 illustrates one of these transverse sections performed approximately at the middle of the length of a cupule pair. The cross-section shows two symmetric cupules (a) and (b) and their two symmetric cupule halves (a₁) and (a₂) and (b₁) and (b₂) surrounding a central space that formerly contained the ovules. Cupule pair (b) on Fig. 8 (at arrow) shows the shape of that central space on an unsectioned specimen.

Finally, in nos. 11–13 the cupule forks are distinct. A total of approximately 32 cupule tips can be counted on the entire complex. Their exact number is impossible to know with precision. They all start at approximately the same level. Fig. 15 is a transverse section at the level of the tips and allows confirmation of their regularity. They range from 2 to 2.5 mm in length and are subparallel as shown in the details of the other specimens (Figs. 16 and 17). A reconstruction of the cupule complex is shown in Fig. 18.

4.2.3. Cupule from talus fragment

A single cupule fragment with a different morphology than the other Red Hill *Moresnetia*-type cupules was found on a small piece of siltstone float several tens of meters west of the "Plant Layer". This single cupule fragment has distinct, but short cupule tips that are 1.5 mm long and separate at angles of between 45° and 70° (ANSP 4533, Fig. 19), in contrast to the sub-parallel tip arrangement of the previously described specimens.

4.2.4. Comparison and discussion

Moresnetia-type spermatophytes are characterized by a four to six unit cupule, formed by two successive cruciate dichotomous divisions that define a well-circumscribed space where up to four, and sometimes six ovules are found (Prestianni, 2005). The cupules from the "*Barinophyton* slab" conform to this definition except for the number of dichotomies and thus the number of constituent units. However, we have chosen to treat it as a member of that group. The multi-segmented (at least two) condition of the cupule that circumscribes a central space is indeed the key characteristic of the *Moresnetia*-type morphology. The state of preservation of the "Plant Layer" cupules provides little information beyond their general *Moresnetia*-type morphology, and the material of the talus fragment only preserves the cupule lobes and tips. Additional details of cupule structure are unknown.

More substantial information derived from the "*Barinophyton* slab" cupules indicates that the Red Hill specimens differ from all other members of the *Moresnetia*-type by the degree of fusion of the constituent units. Cupules of the *Moresnetia*-type vary from totally unfused segments in the *Moresnetia–Xenotheca–Elkinsia* complex to the much more fused segments of *Archaeosperma arnoldii* Pettitt *et* Beck (Pettitt and Beck, 1968) and *Glamorgania gayerii* Hilton (Hilton, 2006). *Glamorgania* and *Archaeosperma* cupules thus superficially resemble the "*Barinophyton* slab" cupules, but differ subtly in shape and have much longer ultimate tips. These measure approximately 2 mm among the Red Hill cupules and are more than 6 mm in *Glamorgania* and *Archaeosperma*. These differences in addition to the bisegmented versus four-segmented nature of the Red Hill cupules warrant the designation of a new genus.
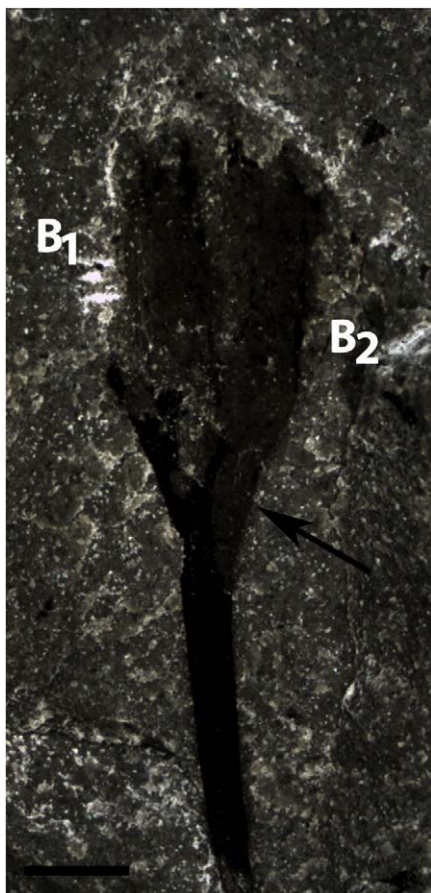
Division: Spermatophyta
Class: Lagenospermopsida
Order: Elkinsiales
Genus: *Duodimidia* Cressler, Prestianni, *et* LePage *gen. nov*.
Generic diagnosis: only cupules and ultimate dichotomies are known. Cupules are borne in pairs on short axes. Symmetric cupules fork dichotomously into two equally sized halves. Each half has a U-shape in cross section.
Etymology: the new genus name is Latin for "two halves".
Type species: *Duodimidia pfefferkornii* Cressler, Prestianni, *et* LePage *sp. nov.* (Fig. 8)
Species diagnosis: cupules pairs are 11 to 12 mm long and 8 to 11 mm wide. Distally, cupule halves fork to form up to 32 short ((~2 mm) pointed tips.
Etymology: the species name recognizes the work in paleobotany by Herman W. Pfefferkorn of the University of Pennsylvania.
Holotype: *Hic designatus*, the Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, 19103, Specimen # ANSP 4532 (Fig. 8).
Type locality: Red Hill, near Hyner, Clinton County, Pennsylvania, USA.
Type stratum: Duncannon Member, Catskill Formation.
Biostratigraphic horizon: VCo *sensu* Streel, et al. (1987).
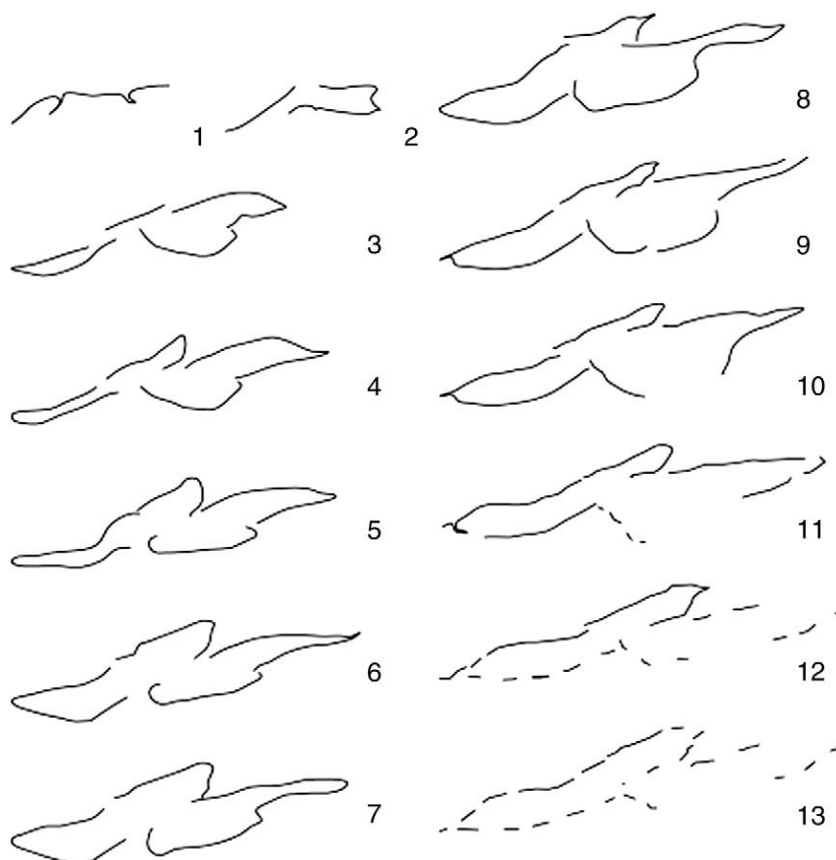Age: Famennian, Late Devonian

Fig. 12. Later dégagement stage of *D. pfefferkornii* cupule pair, ANSP 4539. Cupule (A) from Fig. 11 has been removed; symmetric halves of cupule (B) at (B₁) and (B₂). Scale bar = 2 mm.

Fig. 13. Schematic diagram showing results of serially ground cross-sections through *D. pfefferkornii* cupule pair at 0.5 mm intervals. See text for explanation.

4.3. Stems, roots, and sphenopteroid foliage

Several slabs recovered from the "Plant Layer" at Red Hill exhibit a variety of plant organs that are preserved in close association, but have limited or no organic attachment to one another. Several stems with attached basal roots occur on the same bedding planes with sphenopteroid foliage (Figs. 20 and 21).

Three stems with attached roots occur on one bedding plane (Fig. 21). The stems are all of uniform dimensions and approximately 1.4 cm wide over their entire length. The longest measurable specimen is 18 cm from base of the roots to the edge of the slab where the stem is fractured. There is no surface texture on the stems. The roots consist of a whorl of dichotomously branching structures around the base of the stem and a thicker, 4 cm long non-branching taproot.

The foliage appears to be of two morphologies, one that conforms to the sphenopteroid-type (Fig. 22) and a much more filamentous form (Fig. 23). The sphenopteroid-type foliage consists of frond fragments that are up to 2.5 cm long with pinnae that are 2.5 mm wide. The material is too fragmentary to determine the number of orders of branching that was present. The foliage consists primarily of dichotomously branching narrow-lobed pinnules arranged alternately on pinnate branches. None of these branches have been found attached to larger frond structures. The putative filamentous foliage form also branches dichotomously. The foliage tapers from 1 to 0.3 mm in width and is clustered in a rounded mass on a bedding surface that also includes sphenopteroid foliage, stems, roots, and an amorphous circular compression of indeterminate nature that terminates a twisted axis (Fig. 24).

Sphenopteroid foliage assigned to the genera *Sphenopteris* and *Sphenopteridium* can be of various taxonomic origins, such as zygopterid ferns, progymnosperms, or spermatophytes (Hill et al., 1997). The Red Hill specimens consist of fragmentary compressions that limit detailed description, but they appear to exhibit the forked frond units, lack of aphlebia and adventitious roots, and presence of sclerenchymatous
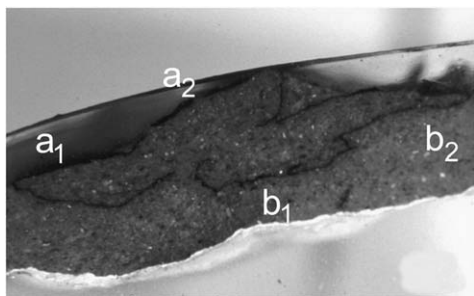

Fig. 14. Cross-section through mid-section of *D. pfefferkornii* cupule pair, showing symmetric cupules (a) and (b) and symmetric cupule halves (a_1) and (a_2); (b_1) and (b_2).

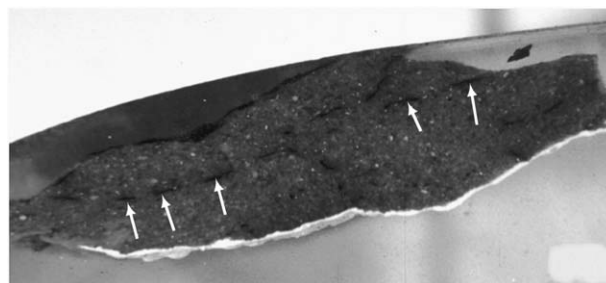**Fig. 15.** Cross-section through cupule tips (some indicated by arrows) of *D. pfefferkornii* cupule pair.
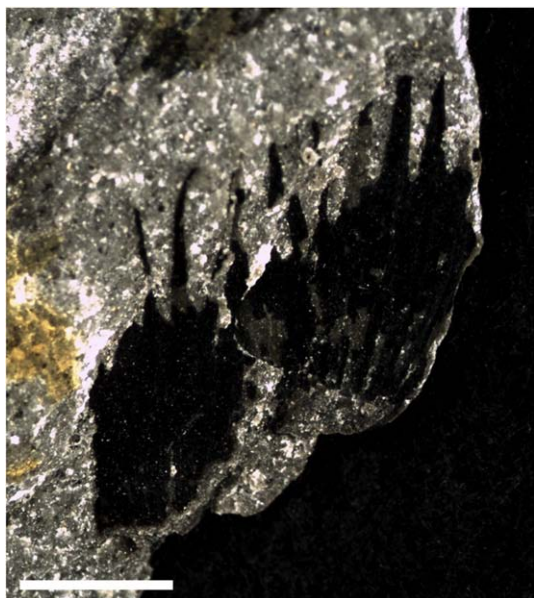
Fig. 16. Detail of cupule tips of *D. pfefferkornii*, ANSP 4546. Scale bar = 2 mm.

lamina with barely discernible dichotomous venation that is characteristic of early spermatophytes (Hill et al., 1997). The stems with roots closely associated on the same bedding planes as the sphenopteroid foliage may also be structures of spermatophytes, but without attachment this inference is tenuous. It is worth noting that the stems preserved with their roots intact in this floodplain pond deposit imply little transport. The plants from which they are derived had a close ecological association with the aquatic environment or its margins.

5. Discussion

5.1. Paleoecological and evolutionary considerations

Previous work on the sedimentological and fossil evidence at Red Hill indicates frequent disturbances in the form of flooding and rapid sediment burial as well as the prevalence of fires (Cressler, 2006). Charcoal has been found interspersed with abundant plant fossils in the "Plant Layer" (Cressler, 2001), a 1-m thick lithologically uniform horizon interpreted as a floodplain-pond deposit. Examination of the charcoal with a scanning electron microscope revealed that most of the burned material was that of the zygopterid fern *Rhacophyton* Crépin (Cressler, 2001). Much of the well-preserved spermatophyte material found in
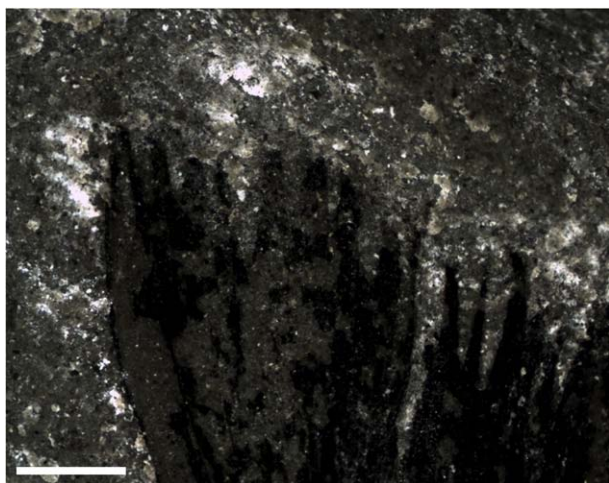

Fig. 17. Detail of cupule tips of *D. pfefferkornii*, ANSP 4532. Scale bar = 2 mm.
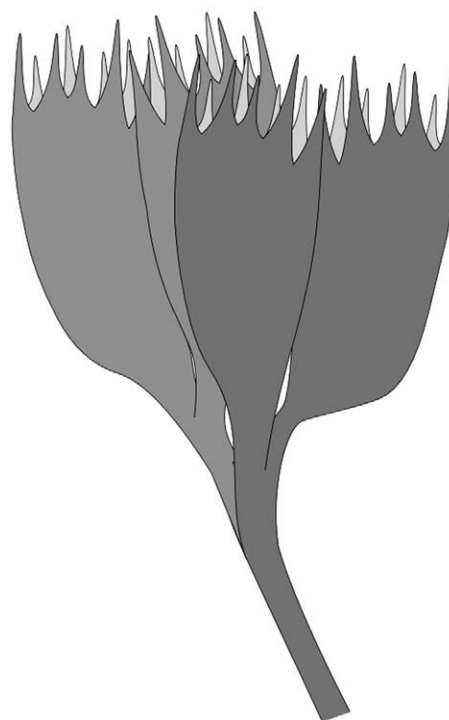

Fig. 18. Reconstruction of *D. pfefferkornii* cupule pair.

this same layer has been found on the same bedding planes as charcoal (Fig. 25) or above it. During the systematic paleoecological sampling of the "Plant Layer" (Cressler, 2006) the appearance of spermatophytes was found to occur above the main charcoal horizons, which coincided with the local disappearance of *Rhacophyton* (Fig. 26) implying a floral turnover following fire. This suggests that the Red Hill spermatophytes were pioneer plants in the recently burned areas, and were subsequently transported and deposited during the same flood events as the charcoal. Similar interpretations have previously been made for spermatophyte paleoecology during the Early Carboniferous (Scott et al., 1994; DiMichele et al., 2006).

The evolution of the seed habit during the Late Devonian was a major innovation in the reproductive strategy employed by vascular plants. While providing considerable protection to the developing embryo, the seed habit allowed plants to occupy and succeed in a diversity of drier habitats that were incompatible to the spore-bearing plants. Present understanding of seed evolution follows a hypothetical transformation series that is based on the stratigraphic distribution of ovules through time in which the earliest ovulate structures with
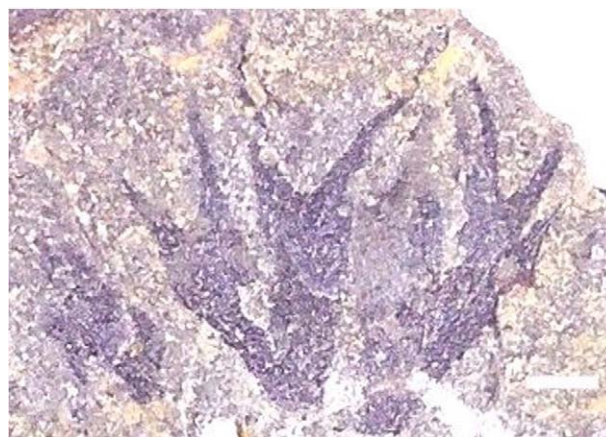

Fig. 19. Cupule tips preserved on "talus fragment", ANSP 4533. Scale bar = 1 mm.

Fig. 20. Sphenopteroid foliage and associated axes, ANSP 4542. Scale bar in cm.

Fig. 22. Sphenopteroid foliage detail, ANSP 4542. Scale bar = 1 cm.

unfused integuments evolved adaptively into more derived ovules possessing fused integuments with an apical micropyle (DiMichele et al., 1989). However, as noted by DiMichele et al. (1989), the transition from basal to more derived morphologies was not stratigraphically linear, for basal and derived forms co-existed during the Early Carboniferous. DiMichele et al. (1989) suggest that the initial diversification of ovular morphologies during the Late Devonian/Early Carboniferous was not due to selective pressures, but rather, diversification that occurred in response to the availability of resources and space with little to no interspecific competition.

Paleogeographic reconstructions place the Red Hill locality in a subtropical climatic belt, and paleosols with vertic features indicate the climate was seasonally wet and dry (Driese and Mora, 1993). The frequency of charcoal in the sediments indicates that fires probably occurred as a regular form of ecosystem disturbance during the dry seasons. Previous research has shown abundant fusain deposits throughout the Early and Late Carboniferous coals and sediments of Eurasia attesting to the prevalence of wildfires in sub-tropical to tropical environments at that time and indicating that fire played an important role in the ecology of those ecosystems (Scott and Jones, 1994). Evidence of wildfires effecting vegetation now extends back to the Late Silurian (Glasspool et al., 2004). Its occurrence during the Late Devonian has been increasingly documented (Rowe and Jones, 2000;
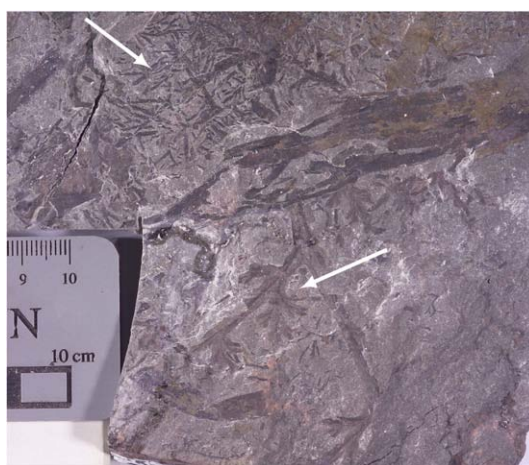

Fig. 23. Foliage detail; typical sphenopteroid form at lower arrow, possible filamentous form at upper arrow, ANSP 4535. Scale in mm.

Cressler, 2001; Fairon-Demaret and Hartkopf-Fröder, 2004). Seed-bearing plants would have probably had some advantage compared to the spore-bearing plants for rapid recovery in fire-disturbed
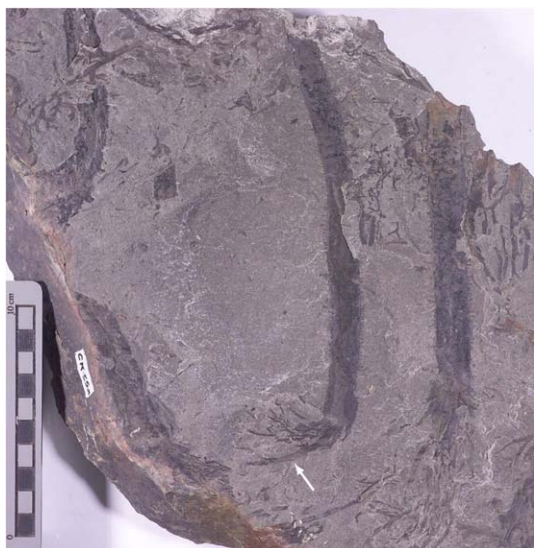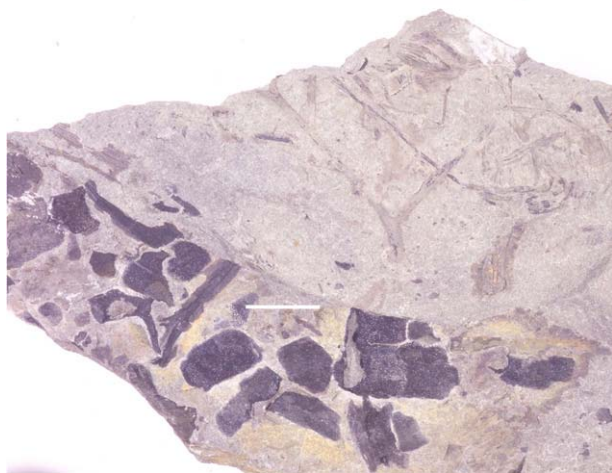

Fig. 21. Sphenopteroid foliage and associated axes with attached roots, ANSP 4534. "Taproot" shown at arrow. Scale bar in cm.

Fig. 24. Axes, roots, sphenopteroid foliage and filamentous "foliage" in association with amorphous circular structure terminating large axis, ANSP 4535. Scale in cm.

Fig. 25. Spermatophyte remains and charcoal from "Plant Layer" in association, ANSP 4543. Scale bar = 1 cm.
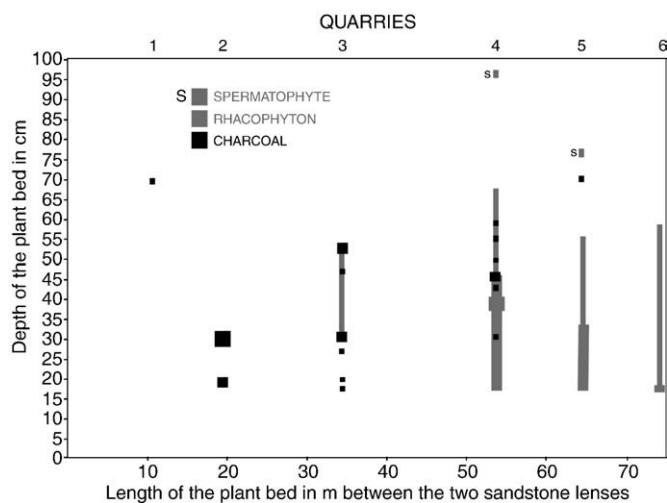
Fig. 26. Schematic diagram with results of systematic sampling of "Plant Layer", a 1-m thick continuous floodplain pond deposit (Cressler, 2006), showing local elimination of *Rhacophyton* Crépin following fires and charcoal deposition and apparent succession by spermatophytes. Only spermatophytes identified during the systematic sampling process are indicated (s) in the diagram. Subsequent specimens in the "Plant Layer" were found in the charcoal layers and above. For each vertical quarry excavation, the width of the vertical line represents the order of magnitude of counts for each taxon (or charcoal) on a 1 cm² grid system. Wide line = thousands; intermediate line = hundreds; narrow line = tens.

ecosystems as a result of the unity of the gametophyte and sporophyte phases of the plant life cycle into one ecological entity. Clearly, the seed habit did not presciently evolve to allow vascular plants to colonize the drier environments that were incompatible with free-sporing reproduction, but rather constituted an exaptation that eventually led to such an adaptive radiation. Furthermore, the key innovation of the seed habit is not the integumented indehiscent megasporangium, but the retention of the megasporangium on the sporophyte until after fertilization (DiMichele et al., 1989). The physiological investment of sporophytic support tissues that aided in the retention of the megasporangium must have been subject to evolutionary selection pressures. The functional result was the ecological unity of the two phases, which is proposed as being advantageous in an ecosystem subject to frequent disturbances such as dry seasons and fire. Limited support for this hypothesis may be sought in an investigation of the evolutionary pressures under which the separate gametophytic and sporophytic phases of living heterosporous plants are subject, as

possible analogues of seed plant ancestors, but obviously their ecological context is vastly different from the earliest spermatophytes and their immediate predecessors.

Acknowledgements

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