An Eocene tar spot on a fossil palm and its fungal hyperparasite

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Abstract: Two ascomycetes from the middle Eocene (48.7 million yr b.p.) Princeton chert are described. *Palaeoserenomyces allenbyensis* gen. et sp. nov. consists of long, loculate stromata of distinctive columnar cells beneath the epidermis of the extinct fan palm, *Uhlia allenbyensis*. The sporogenous locules are empty but stromatal features and locule shape are similar to extant *Serenomyces*, a genus in the Phyllachorales that forms leaf spots on coryphoid palms. The locules of *P. allenbyensis* contain circular structures that are interpreted as intralocular ascomata of a mycoparasite, *Cryptodidymosphaerites princetonensis* gen. et sp. nov. Two-celled ascospores in uniseriate rows are similar to the genus *Didymosphaeria* of the Melanommatales. These fossils are compared to *Didymosphaeria conoidea*, an extant mycoparasite of stromatic ascomycetes. The large number of exquisitely preserved fungal structures on taxonomically defined hosts in the Princeton chert provides a unique opportunity for studying the diversity of microfungi in Tertiary paleoenvironments.

Key Words: *Cryptodidymosphaerites*, *Didymosphaeria*, leaf spot fungi, Melanommatales, mycoparasite, paleomycology, *Paleoserenomyces*, Phyllachorales, *Serenomyces*

INTRODUCTION

There are few descriptions of fossil microfungi in the literature because their fructifications are rarely found intact. Spores or palynomorphs are encountered frequently (e.g., Kalgutkar and Sigler, 1995) but these are usually detached from sporogenous cells and are difficult to compare to extant taxa. This presents a problem because, while it is generally as-

sumed that microfungi have been important components of ecosystems through geologic time, there is so far relatively little fossil evidence of what these organisms looked like, how they might be related to modern forms and their role in paleoenvironments (Stubblefield and Taylor, 1988).

An interesting but still relatively poorly known phenomenon among extant fungi in natural environments is their role as parasites on other fungi. These hyperparasitic relationships are, and probably were, important in the dynamics of fungal communities (Jeffries and Young, 1994). Evidence of hyperparasitic relationships in the fossil record of the fungi is virtually nonexistent beyond the recent report by Hass et al. (1994) in which chytridiaceous structures are described as parasites of fungal spores.

Recently, we observed some well-preserved stromata on the permineralized leaves of an extinct palm, *Uhlia allenbyensis* Erwin & Stockey (Erwin and Stockey, 1994; LePage et al., 1994). The material is middle Eocene in age and approximately 48 million yr old (Erwin and Stockey, 1994). The stromata, which resemble those formed by genera in the Phyllachoraceae (Cannon, 1991), have been interpreted as representing a type of tar spot disease on the leaves of the host (LePage et al., 1994). The embedded locules (pseudothecia or perithecia) contain spherical structures that appear to be the ascomata of a hyperparasite. A closer examination of the fossils has revealed that some of these intralocular structures contain bicelled ascospores similar in morphology to the extant genus *Didymosphaeria* Fuckel. In this paper we describe in detail the structure of this Eocene tar spot and its fungal hyperparasite, provide names for the fossil taxa, and discuss the relationship of these two fungi to similar extant genera.

MATERIALS AND METHODS

The fossil specimens come from the Princeton chert locality, an outcrop that occurs on the east bank of the Similkameen River, 8.4 km south of Princeton, British Columbia. This locality has been referred to as locality "I" (Boneham, 1968) and most often as the "Princeton chert" (Basinger and Rothwell, 1977; Stockey, 1984, 1987; Cevallos-Ferriz et al., 1991; Pigg and Stockey, 1996). Chert deposits are part of the

Princeton Group, Allenby Formation and are located 630 m above the Princeton-Black coal seam (Boneham, 1968). The outcrop consists of at least 49 interbedded layers of chert and coal with an occasional thin ash bed replacing a chert layer. The Princeton Group has been dated as middle Eocene by Wilson (1977, 1982) studying freshwater fish, and by Hills and Baadsgaard (1967) using K-Ar dates. A recent dating by Baadsgaard (1995, pers. comm.) indicates a best estimate of 48.7 million yr b.p.

The chert blocks were cut into slabs and studied using a modified cellulose acetate peel technique and hydrofluoric acid (Basinger and Rothwell, 1977; Basinger, 1981). Peel sections were mounted in Eukitt (O. Kindler GmbH & Co., Freiburg, Germany) xylene soluble mounting medium for microscopic examination. All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA).

Spores were studied by scanning electron microscopy (SEM) using a Jeol JSM-6301 FXV at 1 and 1.5 kV. The back of a cellulose acetate peel was mounted using double-sided tape and the specimen was coated with 2 nm Cr with a Edwards Xenosput XE 200 chromium coater. All other photographs were taken with a Microlumina slow scan digital camera on a Zeiss Ultraphot and digitally enhanced using Adobe Photoshop 4.0. Herbarium material of *Didymosphaeria conoidea* Niessl was obtained from the National Mycological Herbarium, Ottawa, Ontario, Canada (DAOM).

TAXONOMY

Order: Phyllachorales.

Paleoserenomyces allenbyensis Currah, Stockey et LePage, gen. et sp. nov.   Figs. 1–10

Stromata robust, approximately 1 mm thick, up to 13 cm long, polyloculate, erumpent from both adaxial and abaxial surfaces of leaves of *Uhlia allenbyensis*. Locules in a single layer through stromata, 240–480 μm diam, 180–240 μm deep, lined with prosenchymatous tissue of thin-walled hyphae two to four layers thick, ostiolate, with ostiole borne at apex of short, rounded papilla. Stromatal tissue of columnar cells, circular in cross section with external layer of infected host epidermal tissue. Asci, ascospores, paraphyses and conidiogenous cells absent.

HOLOTYPE. Canada, British Columbia, Princeton, UAPC-ALTA P1360 C top (Figs. 1, 4, 8). PARATYPES. UAPC-ALTA P1277 B bot, F side #2, P1286 G top.

Age. Middle Eocene.

Stratigraphy. Princeton Group, Allenby Formation, British Columbia, Canada, 49° 13′ N, 120° 00′ W (Stockey, 1987).

Etymology. The generic name implies a similarity to the extant genus *Serenomyces* Petrak (1952). The prefix "paleo" refers to the fossil nature of the material. The specific epithet refers to the nearby abandoned mining town of Allenby for which the formation was also named.

Large numbers of infected leaves of *Uhlia allenbyensis* have been found in the chert blocks containing the midribs and laminae (Figs. 1–4). Stromata are robust and have a dark color compared to the underlying leaf tissues (Fig. 1). Stromata are approximately 1 mm thick and up to 13 cm long and are erumpent from both abaxial and abaxial surfaces of the leaves (Fig. 2). Numerous locules are present in each of the tar spot areas on a leaf (Fig. 3). Stromata consist of vertically oriented rows of dark pseudoparenchymatous cells beneath the epidermis of the host (Figs. 4, 8). Cells in this region are elongate and form a distinct palisade (Fig. 8). In transverse section they typically appear circular in outline and parenchymatous (Fig. 9). The epidermis of the host shows a heavy fungal infection, and numerous hyphae are observed in the peeling epidermal cell layer (Fig. 6).
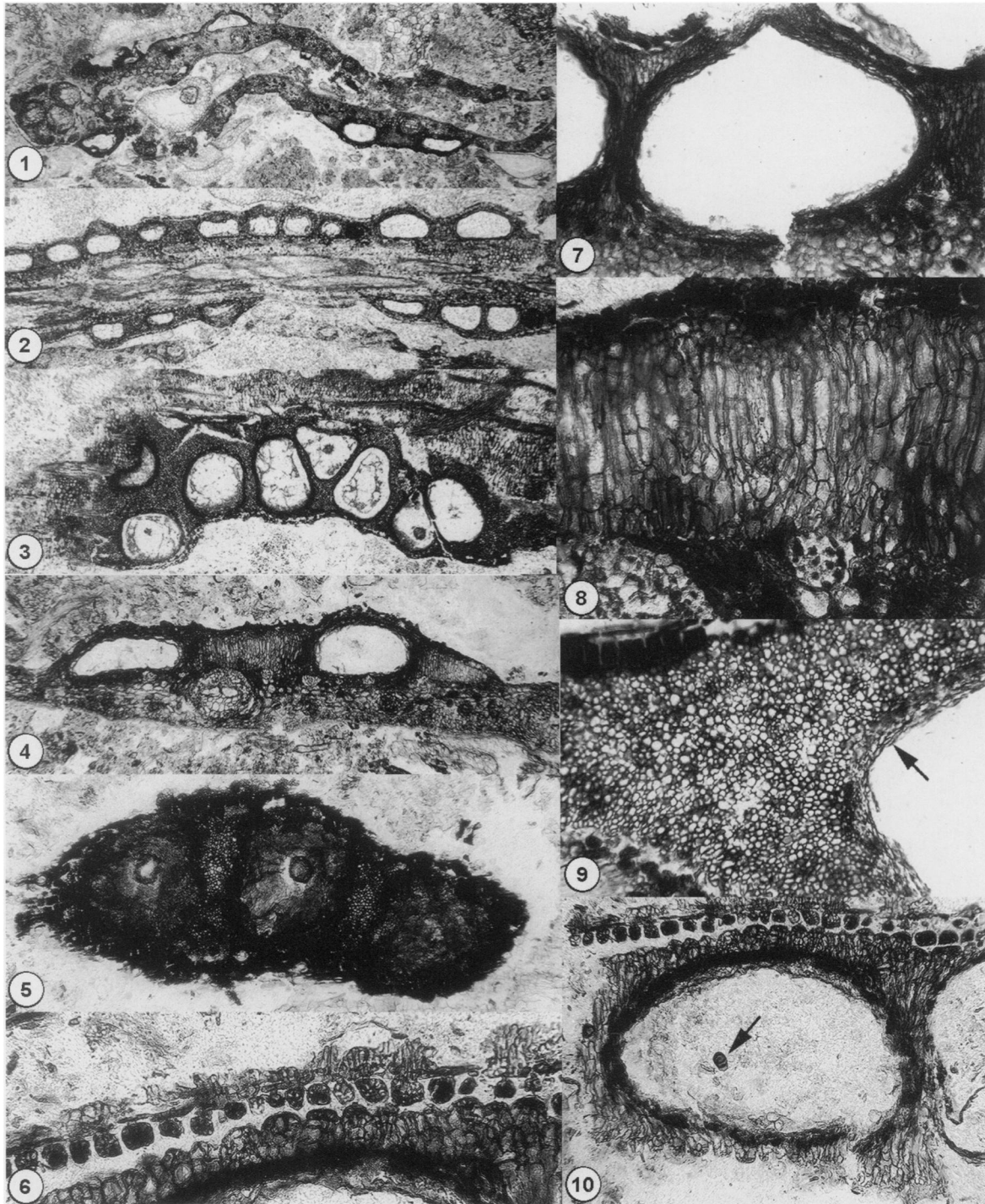
The stroma contains a single layer of what are probably ascogenous locules (Figs. 1–4). These locules are 240–480 μm in diameter and 180–240 μm deep and lined with prosenchymatous tissue two to four hyphae thick (Fig. 9). No asci of *Paleoserenomyces* have thus far been observed. Locules are ostiolate with what appear to be beaked ostioles (Figs. 5, 7). Some locules contain detached conidia that resemble the hyphomycete genus *Brachysporiella* (Fig. 10), but the random position of these spores gives no indication of their origin. Some locules contain amorphous contents (Fig. 3).

Many of the locules of *Paleoserenomyces* contain circular structures that we are interpreting as empty intralocular perithecia of a hyperparasite (Figs. 11, 16). The presence of this mycoparasite (described below) may, in fact, be the cause of the lack of ascogenous cells in the locules of *Paleoserenomyces*.
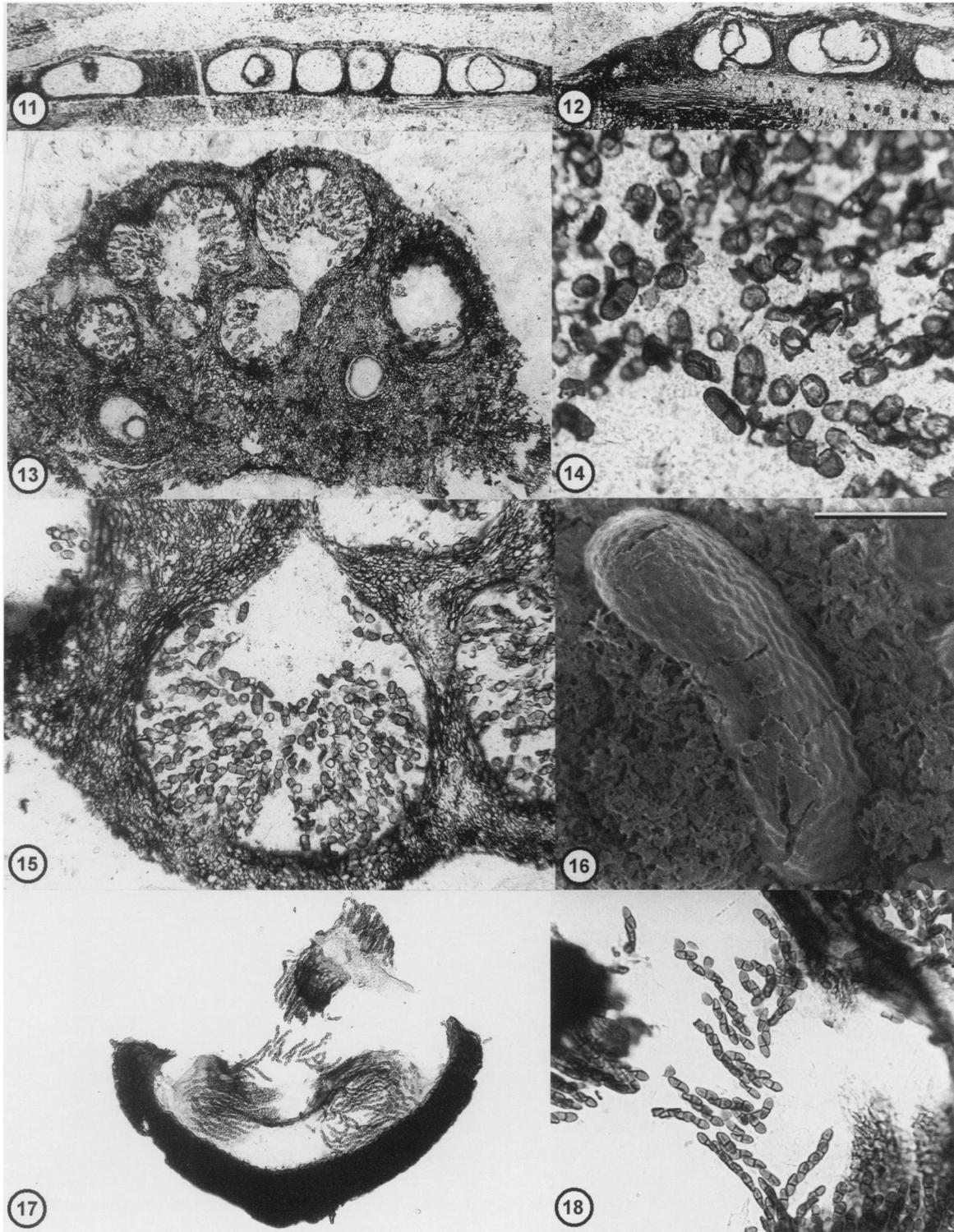
Order: Melanommatales.

Cryptodidymosphaerites princetonensis Currah, Stockey et LePage, gen. et sp. nov.   Figs. 11–16

Ascomata globose, 50–120 μm diam, coalescing, wall 20 μm thick, of several layers of prosenchymatous hyphae, situated within locules of *Paleoserenomyces allenbyensis*. Asci 35–50 μm long and approximately 6 μm wide, containing 8 obliquely uniseriate

FIGS. 1–10. *Paleoserenomyces allenbyensis* on the fossil palm *Uhlia allenbyensis*. 1. Cross section of palm midrib showing three central vascular bundles, attached laminae and stromata. P1360 Dtop #1. (×18). 2. Longitudinal section of palm midrib with both abaxial and adaxial stromata with locules. P1286 G top #4b. (×18). 3. Transverse section of stromatal tissue showing eight locules and oblique section of underlying palm leaf showing venation (upper right). P1277F side 2 #15. (×25) 4. Longitudinal section showing stromatal tissue and locules over a leaf vascular bundle. P1360 D top #1. (×43). 5. Paradermal section of locules showing ostiolar region of two adjacent locules. P1277 F side 2 #11. (×70). 6. Transverse section of leaf showing epidermal cells densely packed with fungal cells. P1277 B bot #4. (×306). 7. Longitudinal section of locule showing general shape and beaked ostiole. P1277 F side 2 #11. (×113). 8. Longitudinal section of columnar cells of the stroma. P1360 D top #1. (×288). 9. Transverse section of the columnar cells of the stroma (locule at right). P1277 F side 2 #8. Arrow indicates prosenchymatous wall of ascoma. (×140). 10. Transverse section of leaf showing infected epidermis, columnar cells of stroma and locule containing a *Brachsporiella*-like conidium (arrow). P1277 B bot #4. (×158).

FIGS. 11–18. Fossil and extant hyperparasites. 11–16. *Cryptodidymosphaerites princetonensis* hyperparasite of *Paleosereno-myces* on palm leaves of *Uhlia*. 11. Longitudinal section of *Uhlia* leaf with stromatal tissue and locules of *Paleoserenomyces* with endoparasite ascomata inside. P1286 D top #1d. (×36). 12. Transverse section of *Paleoserenomyces* with endoparasites in the locules on *Uhlia* leaf. P1277 F side 2 #15. (×43). 13. Transverse section of *Paleoserenomyces* stroma with endoparasite in locules. P1231 B #1. (×67). 14. Bicelled ascospores of *Cryptodidymosphaerites*. P1231 B#1. (×450). 15. *Cryptodidymosphaerites* asci in locule of *Paleoserenomyces*. P1231 B #1. (×167). 16. SEM of ascospore of *Cryptodidymosphaerites* showing shallow reticulum on wall surface. P1231 B #4. Bar = 10 μm. 17, 18. Extant *Didymosphaeria conoidea* on *Leptosphaeria doliolum* var. *conoidea*. DAOM 92169. 17. *D. conoidea* asci in locule of *L. doliolum* var. *conoidia*. (×144). 18. Ascospores of *Didymosphaeria*. (×450).

ascospores. Ascospores clavate, 16–18 μm long and 10–11 μm wide, constricted around a single equatorial septum; wall ornamentation shallowly reticulate.

HOLOTYPE. UAPC-ALTA P1231 B.

Age. Middle Eocene.

Stratigraphy. Princeton Group, Allenby Formation, British Columbia, Canada.

Etymology. A modification of *Cryptodidymosphaeria* (Rehm) von Höhnel, a name assigned to mycoparasite species *Didymosphaeria conoidea* Neissl by von Höhnel. The suffix "-ites" refers to fossil. The specific epithet is based on the collecting locality.

Although the intralocular perithecia of this fungus are very common in the locules of *Paleoserenomyces* (FIGS. 11, 12), the ascospores are rare. We have found one specimen containing several pseudothecia with asci (FIGS. 13, 15). Asci are 35–50 μm long and about 6 μm wide and contain eight obliquely uniseriate ascospores (FIGS. 14, 15). Ascospores are clavate, 16–18 μm long and 10–11 μm wide and constricted around a single equatorial septum (FIG. 14). At the light microscope level, the ascospores within the perithecia show some wall surface irregularities. Using the SEM, this roughness is seen as a pattern of shallow reticulations (FIG. 16).

The mycoparasitic species *D. conoidea* is the only mycoparasite-forming species in the genus and was removed from this genus by von Höhnel (see Aptroot, 1995). Our examination of this taxon on a fungal host *Leptosphaeria doliolum* (Pers.) Ces. & DeNot. var. *conoidea* (De Not.) Sacc. (DAOM 92169) shows a similar appearance to the asci and ascospores (FIGS. 17, 18). Asci appear to form a hymenium lining the periphery of the perithecium (FIG. 17). There are eight obliquely uniseriate ascospores per ascus (FIG. 18). Ascospores are bicelled and about half the size of those found in the Princeton fossil material (FIG. 18).

DISCUSSION

The stromatal morphology, locules with a single papillate ostiole, and a prosenchymatous locule wall indicate affinity to the Phyllachorales. The host plant, a coryphoid palm, lead us to investigate the leaf-spot fungi described from these monocots. The genus *Serenomyces* Petrak (Petrak, 1952; Barr et al., 1989; Hyde et al., 1997) shows many similarities to the Princeton fossil tar spot. This genus occurs exclusively on palms especially on the rachides of palms such as *Serenoa serrulata* (Michaux) G. Nicholson. *Serenomyces californicus* Barr, Ohr & Murphy produces a subepidermal stroma composed of vertically oriented cells beneath and sometimes within the epidermal cells of the host (Barr et al., 1989). The sphaeroid ascomata are of a

similar size range to those seen in our fossil material. They also open to the surface by a short papilla (Barr et al., 1989) as in our fossil material.

One striking characteristic of the fossil is the length of the stromata which can be up to at least 13 cm long. This is comparable to stromata of *S. californicus* (Barr et al., 1989) which are subepidermal, polyloculate, up to 10 cm long on the leaves of *Washingtonia filifera* (Linden) H.S. Wendland in California. The other extant species of *Serenomyces* have much smaller stromata.

Unfortunately, ascospores were not found associated with the fossil stromata. Several explanations are possible. First, the tendency for asci in this group of fungi to deliquesce and for the ascospores to extrude at maturity suggests that mature stromata could have been empty at the time these leaves were preserved. Secondly, the centrum tissues of *Serenomyces* are described as being thin-walled and delicate, and the ascospores as hyaline or lightly colored. These tissues may not have preserved well in the chert matrix. However, it should be noted that other delicate plant tissues have been preserved in the chert including monocot embryos (Cevallos-Ferriz and Stockey, 1988) and pollen within the anthers of sapindaceous flowers (Erwin and Stockey, 1990), for example. Thirdly, the locules may have been sterile due to the effects of the mycoparasite which may have suppressed sporulation or caused spore abortion (Boosalis, 1964). Fourthly, the locules may not have been ascogenous at all but part of an coelomycetous imperfect stage (LePage et al., 1994). Some locules contain detached *Brachysporiella*-like conidia, but the random position of these hyphomycete spores gives no indication of their origin. Dematiaceous phragmoconidia are common on woody and herbaceous tissues (Ellis, 1971, 1976) and their presence among the fossil stromata could be considered incidental.

The taxonomic affinity of the host of the the tar spot, *Uhlia allenbyensis*, also supports a relationship between the fossils and the genus *Serenomyces*. The known species of *Serenomyces* are all parasites on fan palms (Arecaceae, Subfamily Coryphoideae), e.g., *Phoenix* L., *Washingtonia* H.A. Wendland, and *Serenoa* J.D. Hooker. In the original description of *Uhlia* Erwin and Stockey (1994) compared the fossil palm to several taxa of fan palms. The stems, roots, petioles, and leaves showed the closest similarities to the genus *Serenoa* while leaves also show similarities to *Brahea* Martius ex Endlicher and *Rhapidophyllum* Wendland & Drude. Therefore, extant *Serenomyces* and *Paleoserenomyces* are similar in having hosts among the coryphoid palms.

We have chosen to describe the stromata under the new name *Paleoserenomyces* rather than as a fossil spe-

cies within *Serenomyces*. The fossil material is indeed similar to *Serenomyces,* but descriptions of relatively few taxa causing leaf spots on palms are available for comparative purposes (Hyde et al., 1996, 1997). Secondly, ascospore features such as shape, size and wall sculpturing, used to distinguish the extant species, would be essential in making a definitive assignment of the stromata on the fossil palm to the genus *Serenomyces.*

The mycoparasitic ascomycete from the Princeton chert presents sufficient characters such as the presence of a pseudothecium, ascospore morphology, orientation and the mycoparasitic habit to place it close to *Didymosphaeria* of the Melanommatales (Aptroot, 1995). In his recent monograph of *Didymospheria,* Aptroot (1995) lists three taxa of *Didymosphaeria* (or similar fungi) from palms. At least one extant species in this genus, *D. conoidea,* is a mycoparasite of stromatic ascomycetes (Aptroot, 1995; Shoemaker and Babcock, 1990). The species was segregated on the basis of its mycoparasitic habit and placed in the genus *Cryptodidymosphaeria* von Höhnel. As is seen in our examination of this species, *D. conoidea* produces ascospores that are approximately half the size of those in the Princeton chert specimens. Because the morphology of the ascospores indicates a strong relationship with *Didymosphaeria* and because of the mycoparasitic habit of the fossil, we have taken up von Höhnel's name as an indication of this relationship. The added suffix "-ites" indicates that this fossil taxon is only known from the fossil record (Pirozynski and Weresub, 1979).

The presence of bicelled ascospores in a perithecioid ascocarp was used previously to define the middle Eocene fossil taxon *Didymosphaerites pierantonii* Fiore, an organism on the extinct palm *Latanites* (Fiore, 1932). Apparently Fiore was not aware that the genus *Didymosphaerites* (*D. betheli* Cocker) had been proposed previously by Cockerell (1908) for a fossil showing perithecia on the leaves of *Typha* compressions from the Miocene (in Pia, 1927, p. 119; Tiffney and Barghoorn, 1974). In Fiore's material, perithecia were reported to be pyriform, dark brown, 120–150 μm with intact asci that measured 18 × 5 μm. Ascospores are bicelled, constricted at the septa and 6–8 × 3–4 μm. Due to poor preservation and lack of any photographic illustrations, it is not possible to tell if Fiore was looking at the perithecia of a nectriaceous fungus or a pseudothecial ascomycete similar to *Didymosphaeria.* Nectriaceous fungi also have bicelled ascospores but produce them in well-defined perithecia that can be solitary or in clusters on a subiculum (Alexopoulos et al., 1996).

We have proposed a new name for this fossil organism because of problems in the taxonomy of sim-

ilar extant taxa with bicelled ascospores. For example, Aptroot (1995) lists 20 extant genera likely to be confused with *Didymosphaeria.* Critical features for distinguishing among these similar genera include: ascus wall morphology (i.e., unitunicate vs fissitunicate), ascospore color, morphology of sterile elements among the ascospores (i.e., characteristics of the hamathecium), the presence of a gelatinous sheath or appendages on the ascospores, etc. We did not observe these features in the permineralized fossil material. The presence of a shallow reticulum on the ascospores is a feature found in some extant *Didymosphaeria* species but not restricted to this genus (Aptroot, 1995).

Nevertheless, despite the difficulties inherent in the taxonomy of extant members of the Phyllachorales and Melanommatales, we feel that enough characters are present in our fossils to indicate a close relationship respectively, to these two groups of ascomycetous fungi. The Princeton fossils show that the types of complex relationships that exist today among fungi and their vascular plant hosts also occurred in the past. The Phyllachorales were important in the formation of tar spots in fossil as well as extant coryphoid palms. This relationship has been in existence for at least the last 50 million yr.

The Princeton chert is proving to be a rich source of fungi from the early Tertiary (Currah and Stockey, 1991; LePage et al., 1994, 1997; Hill-Rackette et al., 1995). The fine cellular preservation of the organisms in this matrix permits the recognition of microscopic taxa and the reconstruction of relationships of these organisms with larger components of the biota. The majority of the intact and in situ fungi from this locality have been morphologically similar to extant taxa permitting us to assign reasonably accurate names and niche descriptions to these organisms. Continued directed research with the mycota of the Princeton chert should permit the description of many more of the relatively recent common ancestors of modern taxa.

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