

## THE FOSSIL FUNGI OF THE PRINCETON CHERT

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The middle Eocene Princeton chert locality in southern British Columbia, Canada, contains one of the best-preserved permineralized Tertiary floral assemblages known in North America. The quality of preservation of the vascular plant and fungal remains is exquisite because anatomical and morphological features have been preserved at the cellular level. Past studies indicate the vascular flora is rich in species diversity and abundance and includes the in situ remains of semiaquatic and aquatic plant communities. Our initial assessment of the fungi in this assemblage indicates a diverse fungal community had developed and that many of the component species are comparable to modern taxa. Fossil fungi include unilocular and multilocular stromatoid fructifications on leaves and fruits. These are comparable to three extant representatives of the Dothideales or eustromatic Coelomycetes of the Fungi Imperfecti. Two of these contain septate conidia but no ascospores. The third lacks spores but resembles the loculoascomycete genus *Mycosphaerella* in size and structure of the uniloculate stromata. Fossil representatives of the Hyphomycetes include a seed-borne sclerotic fungus similar to *Alternaria* and, in the rhizomes of an aquatic plant, *Cercospora*-like conidia along with moniliform cells that resemble those formed by the genus *Rhizoctonia*. The teliospores of an anthericolous smut are present in the anthers of an unidentified flower. This fungus is most similar to *Microbotryum violaceum*, a smut fungus that occurs in the anthers of Caryophyllaceae. The continuing study of the Princeton Chert is allowing us to better understand the role of these, and other, fungal constituents in early Tertiary semiaquatic/aquatic plant communities.

### Introduction

Paleomycology has advanced slowly since the early 1800s from a predominantly descriptive science to one where the significance of fungi in the evolution and diversification of terrestrial ecosystems is being realized. The role of fungi in the establishment and development of terrestrial floras in biomass recycling and nutrient translocation and in coevolution with plants and animals has been emphasized in the last 20 years (Pirozynski and Malloch 1975; Carroll 1988; Clay 1988a, 1988b, 1990, 1991; Stubblefield and Taylor 1988, and references therein; Taylor 1990; Bacon and De Battista 1991; Boddy 1993; Sieber-Canavesi and Sieber 1993). These innovative ideas have created a renewed interest in mycology and paleomycology and are providing new and challenging directions for research.

The middle Eocene Princeton chert locality in southern British Columbia, Canada, contains one of the best-preserved permineralized Tertiary floral assemblages known in North America. Past studies indicate that the vascular and fungal flora is rich in species diversity and abundance (Boneham 1968; Cevallos-Ferriz et al. 1991, and references therein). The quality of preservation of the gymnosperm, angiosperm, pteridophyte, and fungal remains is exquisite because anatomical and morphological features have been preserved at the cellular level.

Boneham (1968) first studied the microflora of the Princeton Basin and reported that 86% of the identified palynomorphs from Locality "I" con-

sisted of fungal spores of *Brachysporium* sp. and algal, fungal, and bryophyte spores assigned to *Inapertisporites* sp. It was not until Currah and Stockey (1991) reported on an anthericolous smut fungus that it was realized many of the floral features previously identified as glands, plant tissues, or floral structures were, in fact, fungal fruiting bodies (Cevallos-Ferriz and Stockey 1988, 1989). In this article we describe and suggest the taxonomic affiliations of seven fossil fungi preserved along with the infected organs of known or characterized vascular plant hosts. Systematic descriptions of these new fossil fungi will be the focus of future studies.

### Material and methods

Abundant well-preserved plant remains are found in the cherts of the Allenby Formation located ca. 8.4 km south of Princeton, British Columbia, Canada (49°13'N, 120°00'W). On the east side of the Similkameen River an interbedded sequence consisting of coal, shale, and plant-bearing chert crops out (Basinger 1981). Up to 49 chert layers, each with a distinct vegetational assemblage, have been recognized by Stockey (1987). This site was initially referred to as Locality I by Boneham (1968), the Ashnola locality by Basinger (1976), and later, the Princeton chert locality by Basinger and Rothwell (1977), Basinger (1981), Stockey (1984, 1987), and subsequent authors (summarized in Cevallos-Ferriz et al. 1991).

Based on palynology (Rouse 1962; Rouse and Srivastava 1970), mammals (Russell 1935; Gazin 1953), fish (Wilson 1977, 1982), and potassium-argon dates (Hills and Baadsgaard 1967), the Princeton chert was determined to be middle Eocene (50 million years ago) in age.

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The fossils are preserved as silica permineralizations. All chert blocks were cut into slabs and studied using the cellulose acetate peel technique as modified for silicifications with hydrofluoric acid (Joy et al. 1956; Basinger and Rothwell 1977; Basinger 1981). The peels were mounted in xylene soluble mounting media (Coverbond and Eukitt) for light microscopy.

Plant specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA), Department of Botany, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

### Environmental setting

Based on the available sedimentological, paleontological, and taphonomic data the paleoenvironments associated with the Princeton chert locality may include riparian, marsh, and shallow fresh-water to near-shore lacustrine environments (Wilson 1988; Cevallos-Ferriz et al. 1991). Articulated remains of a soft-shelled turtle, cf. *Apalone* sp. (Family Trionychidae), a semiarticulated skeleton of *Amia hesperia* Wilson, and disarticulated remains of *Amyzon* sp. (sucker) and *Libotoniuss* sp. (trout perch) occur in the shales associated with the cherty layers (Wilson 1980, 1982). Living representatives of the genus *Apalone* Rafinesque live in large permanent bodies of water (Webb 1962; J. Gardner, personal communication, 1993) and living *Amia calva* L. (bowfin) inhabit swampy to partly vegetated, stagnant, warm, shallow lacustrine to riparian environments (Scott and Crossman 1973). The floral and faunal remains provide unequivocal evidence that the Princeton chert locality was an aquatic to semiaquatic environment during the middle Eocene.

### Results

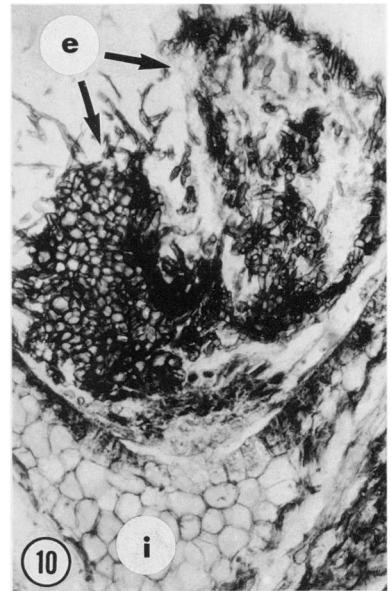
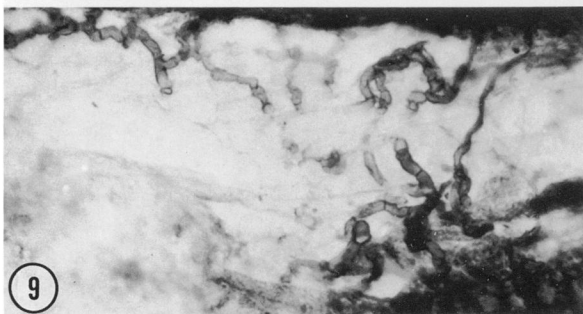
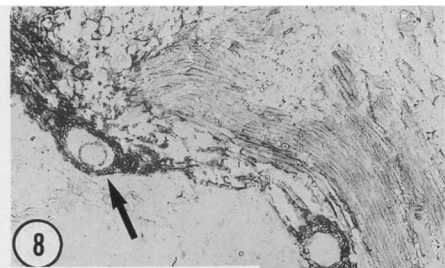
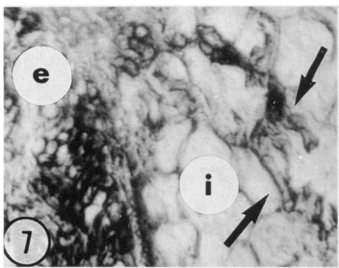
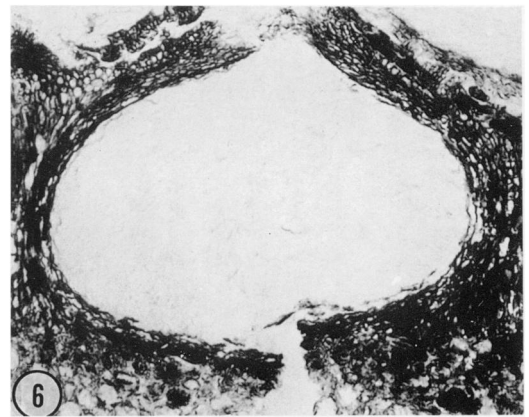
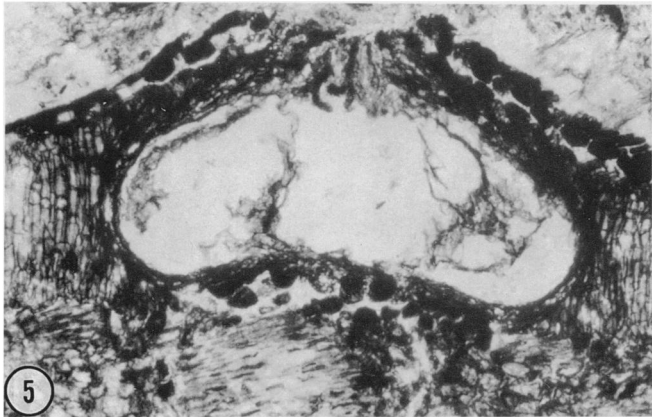
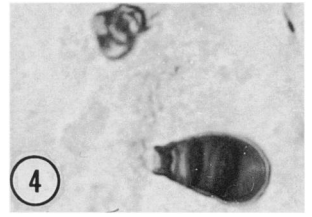
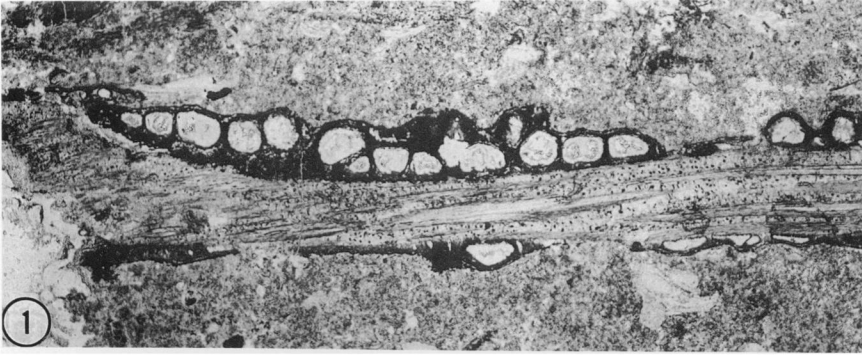
**HOST 1.** Leaves of *Uhlia allenbyensis* Erwin & Stockey (1994) (Arecaceae). On both surfaces of the leaves, erumpment stromata are up to 0.8 mm thick and 12.5 mm broad, with a compact outer rind and a thick pseudoparenchymatous layer of thick-walled, broad columnar cells that are roughly circular in cross section and 6.0–10  $\mu\text{m}$  in diameter (figs. 1, 3). A well-defined external layer of heavily infected epidermal cells overlies some of the stromata on both surfaces (fig. 3). Stromata bear one to many broad ostiolate locules at the same level. Locules are 240–480  $\mu\text{m}$  in diameter and some appear to be lined with prosenchymatous tissue that is composed of thin-walled hyphae two to four layers thick (figs. 5, 6). Clavate phragmoconidia are present in some locules (fig. 2). Conidia are up to 31  $\mu\text{m}$  long and 12.5  $\mu\text{m}$  wide in the broadest part (figs. 2, 4). Although conidiophores are absent, conidiogenesis appears to be acrogenous.

**HOST 2.** Fruits and seeds of *Decodon allenbyensis* Cevallos-Ferriz & Stockey (1988) (Lythraceae). Detailed examination of *D. allenbyensis* shows fungal infection throughout most tissues of the fruits, including the endosperm and integument of the seeds. Hyphae and irregular sclerotium-like aggregates of pseudoparenchymatous tissue up to 125  $\mu\text{m}$  in diameter occur in the tissues of the endosperm (figs. 7, 10) and integument (figs. 7, 9), respectively, and loculate eustromata or pseudothecia occur on the sepals (fig. 8). Eustromata are globose to ovoid and 80–240  $\mu\text{m}$  in diameter, ostiolate, with walls of small closely packed cells, and occur singly or in aggregates of two or three in erumpment, crustose, prosenchymatous stromata. Some pseudothecia contain an empty, spherical, perithecioid structure with a thin (4.0–6.0  $\mu\text{m}$  thick) prosenchymatous wall (fig. 8).

**HOST 3.** Seeds of *Allenbya collinsonae* Cevallos-Ferriz & Stockey (1989) (Nymphaeaceae). Abundant septate hyphae 2.0–3.0  $\mu\text{m}$  in diameter occur throughout the perisperm in a loose mycelial network (fig. 11). In addition, irregular accumulations of sclerotic tissue occur within the perisperm (fig. 11) and dense ovoid to elliptical pseudoparenchymatous sclerotic aggregations that are 335–380  $\mu\text{m}$  long and 190–280  $\mu\text{m}$  wide commonly occur between the integument and perisperm (figs. 11, 12). Discrete stalked or pedicellate spherical sclerotia roughly 50  $\mu\text{m}$  in diameter and composed of 30–40 isodiametric cells that are 5.0–8.0  $\mu\text{m}$  in diameter are present in seed cavities (fig. 13). A solitary, slightly curved, smooth-walled, transversely septate, six-celled conidium, 50  $\mu\text{m}$  long, 12  $\mu\text{m}$  wide is present in one seed cavity (fig. 14). The conidium is clavate and markedly constricted at the septa. The central cells are dark in color and bulge conspicuously, especially through the median portion of the conidium, while the terminal cell is slightly beaklike and less pigmented than the five proximal cells.

**HOST 4.** Rhizomes of *Eorhiza arnoldii* Robison & Person (1973) (family: *Incertae sedis*). In *E. arnoldii* rhizomes two fungal species have been observed. The first consists of short simple-septate chains of swollen, more or less globose cells (monilioid cells), 2.0–4.0  $\mu\text{m}$  in diameter (fig. 17) along with regular (nonmonilioid) hyphae about 2.0–2.5  $\mu\text{m}$  wide (fig. 15). These are present inside many cells of the cortical and aerenchymatous tissues. Chains of monilioid cells branch at wide angles and appear to be proliferating blastically from the terminal cells of the chains (fig. 17).

The second fungus, discussed by Robison and Person (1973), consists of narrow, elongate, smooth, transversely septate phragmoconidia occurring within the intercellular spaces of the



aerenchymatous tissue. The conidia are up to 110  $\mu\text{m}$  long and 7.0  $\mu\text{m}$  wide and have rounded apices (figs. 16, 18). Each conidium is composed commonly of eight to nine cells, but up to 20 cells have been observed. The conidia appear to originate acropleurogenously from a nondescript conidiogenous locus (fig. 18).

**Host 5.** Unidentified flower, Currah & Stockey (1991) (? Aponogetonaceae). Teliospores have been identified in the anthers of a number of small ?aponogetonaceous flowers (fig. 20). The spores are 6.0–8.0  $\mu\text{m}$  in diameter, irregularly ovoid in shape, and minutely pitted (fig. 19). Pollen is absent from the anthers.

**Host 6.** Fruits and seeds of *Princetonia allenbyensis* Stockey & Pigg (1991) (family: *I. sedis*). Septate hyphae, 4.0–6.0  $\mu\text{m}$  in diameter are abundant in many seeds of *P. allenbyensis* (figs. 23, 24). In some seeds the tissues of the endosperm and embryo are reduced to a dense stromatoid mass (fig. 23). Pycnidia 140–190  $\mu\text{m}$  in diameter are embedded in the outer tissues of infected sepals (fig. 21). Pycnidia have walls composed of five to six layers of pseudoparenchymatous thick-walled hyphae and are uniloculate, globose, and separate with a central papillate ostiole. Conidia are cylindrical to slightly allantoid, thin-walled, smooth, medianly one-septate, 13–17  $\mu\text{m}$  long, and 3.0–5.0  $\mu\text{m}$  wide and occur in clusters along the inner surface of the pycnidial wall where some appear to be attached to indistinct conidiogenous cells (fig. 22).

### Discussion

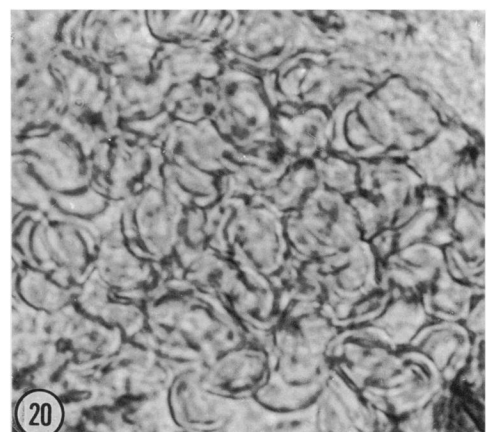
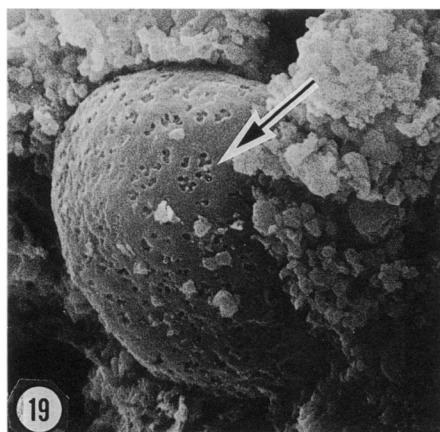
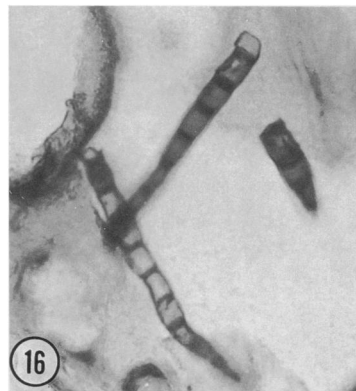
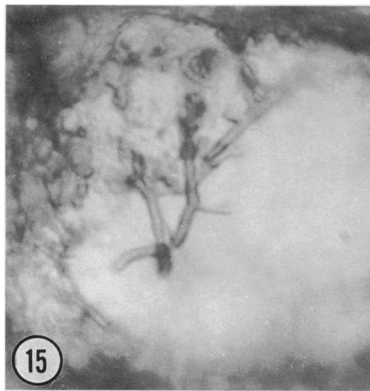
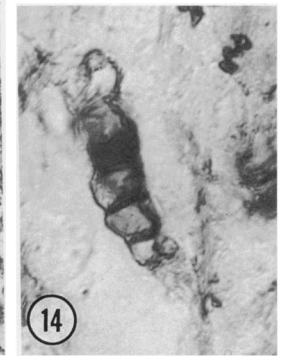
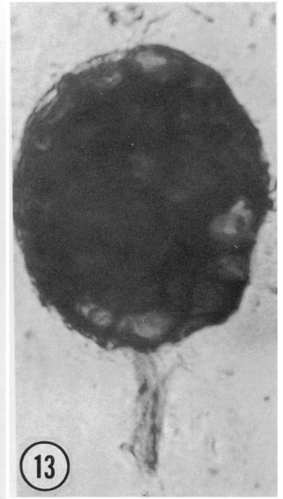
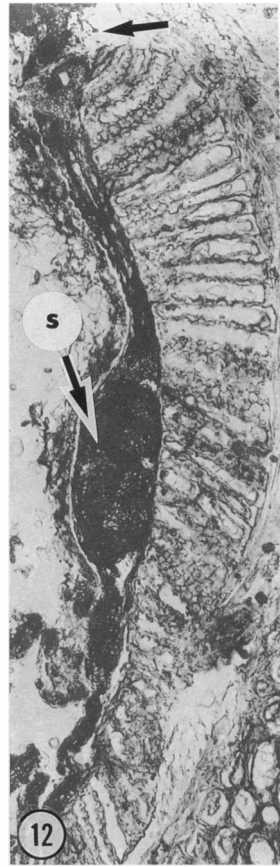
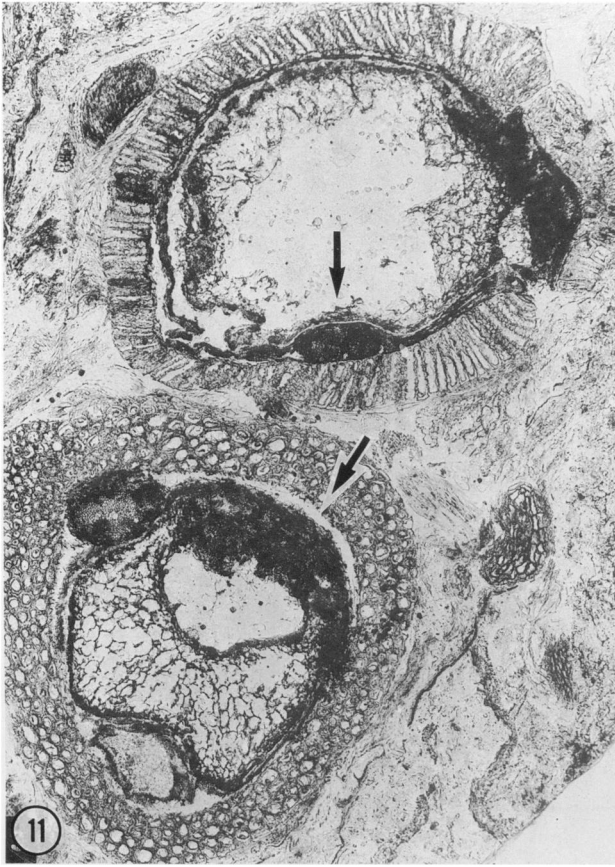
Numerous reports of fossil fungal spores, hyphae, and fruiting bodies exist (Tiffney and Barghoorn 1974, and references therein), but comparison of the fossil forms with living representatives and understanding of their role in ancient environments are difficult challenges. The identification and classification of living fungi is based on the morphology of sporogenous cells, mode of spore formation, the structure, position, and development of associated fructifications, and to some extent, the host plant with which the

fungus is associated. Among living fungal representatives, reports of intact fruiting structures on taxonomically defined hosts are well known (Farr et al. 1989); however, among fossils, such associations are relatively rare or limited to a few well-studied fossil floras (Kidston and Lang 1921; Stubblefield and Taylor 1988, and references therein; Taylor 1990; Taylor et al. 1992a, 1992b; Hass et al. 1994).

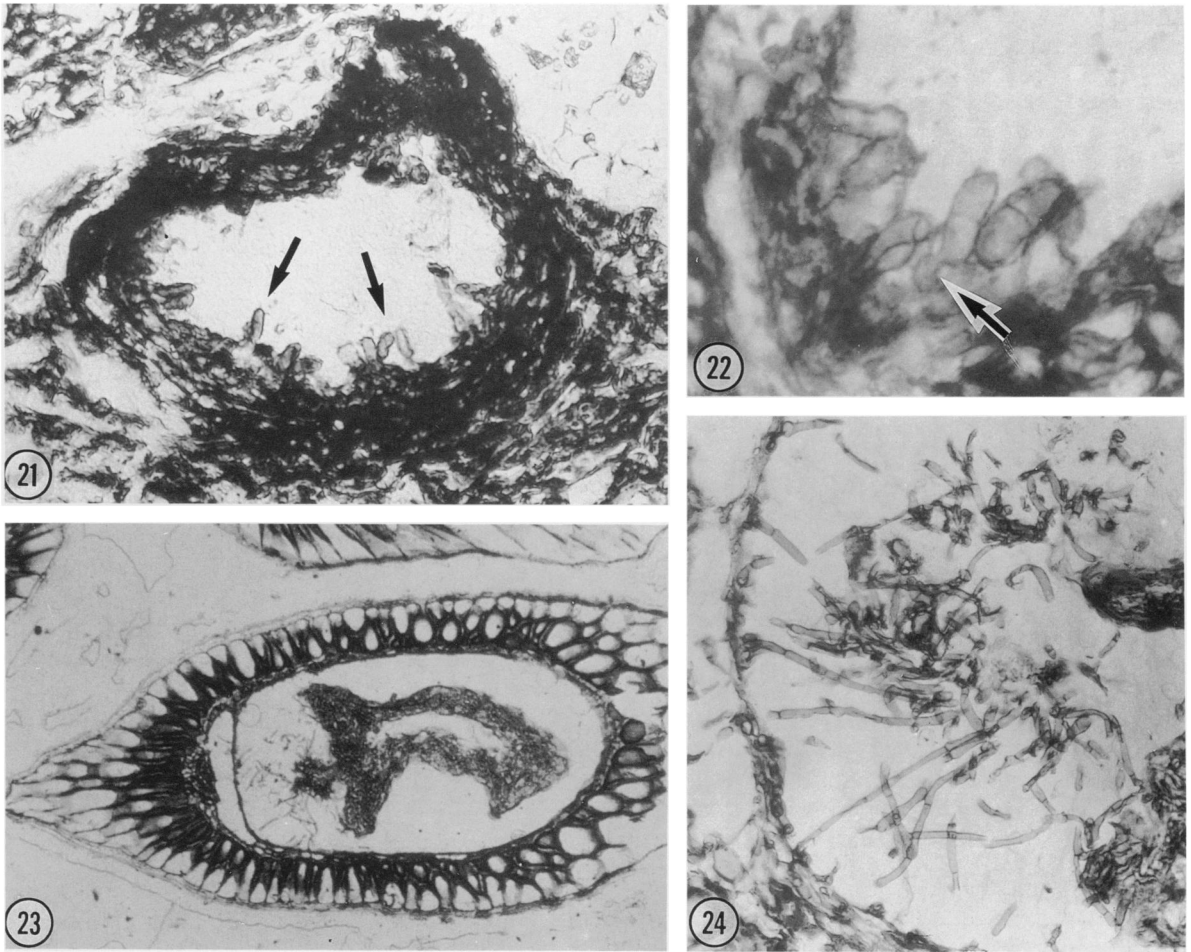
Stubblefield and Taylor (1988) suggest that, without preserved structures such as wall appositions or resinous material in the fossil plant tissues, fungal parasitism may be difficult to distinguish from saprophytism and mutualism. This is certainly true in specimens of Paleozoic and Mesozoic age. However, the relatively young geologic age and preservational quality of the fossils in the Princeton chert permit comparison of the fossil fungi with potential modern analogues. Based on structural features of the fossil hyphae, pseudothecia, and pycnidia, the resemblance of the fossils to modern fungal parasites, and similarity of the fossil host plants to living representatives, we suggest the fungi discussed here were parasitic.

In *Uhlia allenbyensis*, large, erumpent, loculate stromata form conspicuous dark-colored bumps or spots over both surfaces of the leaves (figs. 1, 3). Extant fungi that form similar structures are usually heavily melanized and are referred to as “tar spot” pathogens. There are a diverse number of extant stromatoid fungi that cause large corky or tarry spots on leaves of tropical plants and the majority of these are in the bitunicate ascomycete order Dothideales. Fifty-six families are included in this order (Eriksson and Hawksworth 1993) and are delimited primarily on the basis of developmental and morphological characteristics of the cells and tissues of the centrum. To date, neither ascospores nor paraphyses have been found in the locules associated with *U. allenbyensis* (figs. 5, 6) and definite placement cannot be made. Alternatively, the fossil stromata may have been formed by a eustromatic coelomycete, many of which are anamorphs of the Dothideales. The distinctive phragmoconidia resemble those formed by the

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 Figs. 1–10 Figs. 1–6, *Uhlia allenbyensis* Erwin & Stockey. Fig. 1, Cross section of a leaf showing numerous ostiolate locules embedded in stromatic tissue on both surfaces of the leaf. P1277F Bot No 2.  $\times 12$ . Fig. 2, Clavate phragmoconidia occurring in some locules. P1277F Side 2 No 9.  $\times 720$  (N). Fig. 3, Closeup of a stroma showing the well-defined thick-walled columnar pseudoparenchymatous cells and locules. P1360 Top No 1.  $\times 75$ . Fig. 4, Phragmoconidium. P1277F Side 2 No 16.  $\times 720$  (N). Fig. 5, Ostiolate locule showing remnants of thin-walled prosenchymatous tissue lining the locule. P1277F Bot No 2.  $\times 135$ . Fig. 6, Locule in stromatic tissue. P1277F Side 2 No 12.  $\times 140$ . Figs. 7–10, *Decodon allenbyensis* Cevallos-Ferriz & Stockey. Fig. 7, Closeup of hyphae (arrows) showing infection of the endosperm/embryonic tissue (e) and seed integument (i). P3794C Top No 27.  $\times 430$  (N). Fig. 8, Longitudinal section through a fruiting head showing globose to ovoid pseudothecia on the sepals. Arrow indicates spherical perithecioid inclusion in a locule. P4019D Top No 2.  $\times 70$ . Fig. 9, Septate hyphae on the inner surface of the seed integument. P3794C Top No 33.  $\times 350$ . Fig. 10, Cross section of a seed showing extensive fungal infection of the endosperm/embryonic tissue (e). P3794C Top No 14.  $\times 230$ . N = photos taken using Nomarski optics.







**Figs. 21–24** *Princetononia allenbyensis* Stockey & Figg. Fig. 21, Longitudinal section showing a pycnidium containing conidia (arrows) on the outer surface of a sepal. P3928B Bot No 31.  $\times 350$ . Fig. 22, Close-up of the smooth cylindrical septate conidia. Note that some of the conidia appear to be attached to conidiogenous cells (arrow). P3928B Bot No 32.  $\times 900$  (*N*). Fig. 23, Cross section of a seed showing a dense stromatoid mass in the cavity that probably once contained endosperm and an embryo. P1958B Top No 27.  $\times 170$ . Fig. 24, Close-up of the stromatoid mass showing the septate hyphae. P1958B Top No 27.  $\times 280$ . *N* = photos taken using Nomarski optics.

anamorphs of some representatives of the family Pleomassariaceae (figs. 2, 4) (Barr 1983).

A second extant order to which these fossil fungi might be assigned is the Phyllachorales. The genus *Phyllachora* Nitschke *ex* Fuckel is a group of stromatic perithecial fungi that bear a strong

resemblance to the Dothideales, differing in the morphology of the tissues surrounding the sporogenous locules and in having single-celled ascospores and smaller conidia (Cannon 1991). The Phyllachorales, which are prominent components of the plant parasitic mycoflora in warm

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**Figs. 11–20** Figs. 11–14, *Allenbya collinsonae* Cevallos-Ferriz & Stockey. Fig. 11, Cross section of two seeds showing heavily infected perisperm (lower seed) and dense pseudoparenchymatous sclerotia (arrows). P2674E Bot No 8.  $\times 38$ . Fig. 12, Close-up of the opercular region of the seed (top arrow) and a sclerotium (*s*) located between the seed testa and perisperm. The operculum appears to be the point of entry/exit of the fungus. Note the hyphae extending between the opercular region and the sclerotium. P2674E Bot No 8.  $\times 70$ . Fig. 13, Pedicellate multicellular sclerotium occurring within a seed locule. P3678F Bot No 5.  $\times 900$ . Fig. 14, A slightly curved smooth-walled transversely septate clavate conidium occurring within a seed locule. P3678F Bot No 5.  $\times 900$ . Figs. 15–18, *Eorhiza arnoldii* Robison & Person. Fig. 15, Straight wide-branching hyphae occurring in a cortical cell. P1111D Bot No 21.  $\times 1,120$ . Fig. 16, Long-narrow smooth transversely septate phragmoconidia occurring in the intercellular air spaces of the aerenchyma. P1111D Bot No 35.  $\times 600$ . Fig. 17, Blastically proliferating simple-septate moniloid cells occurring in the cortical and aerenchyma cells. P1111D Bot No 21.  $\times 1,120$  (*N*). Fig. 18, Phragmoconidia. P1111D Bot No 35.  $\times 720$  (*N*). Figs. 19, 20, Unidentified flower. Fig. 19, SEM of a teliospore. Note the minutely pitted surface (arrow). P1631B Top No 37d.  $\times 6,175$ . Fig. 20, Cross section of the anther showing abundant teliospores in the anther of a flower. P1631B Top No 13.  $\times 1,120$ . *N* = photos taken using Nomarski optics.

temperate and tropical regions, and also form "tar spots" on a variety of tropical plants (Canon 1991), including palms (Arecaceae) and Pandanaceae (Farr et al. 1989).

In *Decodon allenbyensis* abundant mycelium-present both as hyphae and sclerotia in the fruits and seeds (figs. 7, 9, 10), along with the loculate fructifications in the sepals (fig. 8)—indicate the fungus was an aggressive and successful colonist on this host plant. The loculate fructifications resemble those produced by the living teleomorph genera, *Didymella* Saccardo ex Saccardo, *Guignardia* Viala & Ravaz, and *Mycosphaerella* Johanson (Dothideales), all of which include species that are common necrotic pathogens causing leaf spots, blights, and fruit rots in a wide range of host plants (Van der Aa 1973; Hawksworth et al. 1983; Farr et al. 1989). Species of the related anamorph taxa, *Phyllosticta* Persoon and *Ascochyta* Libellus have been recorded as leaf-spot fungi on living *Decodon verticillatus* (L.) Elliott (Farr et al. 1989).

The peculiar spherical structures occurring within some of the locules (fig. 8) are difficult to explain. Extant Dothideales can be parasitized by other members of the order that grow among the stomatal tissues and fruit within the locules of the host. A morphologically similar disposition of perithecioid locules within host locules can be seen in the fructification of a fungal parasite similar to *Didymosphaeria* Fuckel (Dothideales), which has been recorded in the pseudothecia of *Leptosphaeria doliolum* (Persoon:Fr) Ces. & de Not. (Leptosphaeriaceae, Dothideales) (Shoemaker and Babcock 1990).

The fungus in the seeds of *Allenbya collinsonae* differs from that found in the seeds of *D. allenbyensis* by its stalked, bulbil-like sclerotia (fig. 13), the production of a unique multiseptate conidium with a hyaline attenuate apex (fig. 14), and the absence of any pycnidial or stromatic fructifications developing from the heavily infected tissues (figs. 11, 12). Based on the stalked sclerotia and multiseptate conidium, the fungus in the seeds of *A. collinsonae* resembles the living genus *Alternaria* Nees, a widespread group of dematiaceous Hyphomycetes that causes blights, leaf spots, and fruit and seed rots in a broad range of plants (Joly 1964; Rossman et al. 1987).

The fossil sample does not permit us to determine if the conidium is indeed a chain-forming porospore typical of the genus *Alternaria* or a terminal conidium typical of the morphologically similar genera, *Ulocladium* Preuss and *Stemphylium* Wallr. However, the single phragmospore with an attenuate apex, extensive development of sclerotic mycelia, and small-stalked sclerotia are features exhibited by some extant species of *Alternaria* (*A. padwickii* [Ganguly] M. B. Ellis) (Ellis 1976; von Arx 1987).

Within the rhizomes of *Eorhiza arnoldii* intracellular hyphae displaying wide-branching chains of inflated cells bear a strong resemblance to the common soil-borne genus *Rhizoctonia* De Candolle. The genus *Rhizoctonia*, in its broadest definition (Parmeter and Whitney 1970), includes sterile root-inhabiting basidiomycetous fungi that produce blastically proliferating swollen cells (moniloid cells) in chains (fig. 17) and hyphae that branch at wide angles with conspicuous constrictions at the branch points (fig. 15) and lacks clamp connections. The segregate genera within *Rhizoctonia* are easily distinguished on the basis of cultural characters (Moore 1987), but specific designations usually require mating tests with known strains (Ogoshi 1987).

Taxa in the *Rhizoctonia* complex vary in the nature of their relationships with host plants from mycorrhizal symbionts in Orchidaceae to virulent root and stem pathogens in a wide range of tracheophytes (Parmeter and Whitney 1970; Tsuneda 1983; Rossman et al. 1987). In both situations moniloid cells can form within the cells of colonized or infected root or rhizome tissues. It is unlikely that the moniloid cells in the rhizome tissues of *Eorhiza* would represent a mycorrhizal association because the tissues are also infected by at least one other fungus. The multiple infections would indicate the tissues were probably moribund at the time of preservation.

Conidia of a second species are present within the intercellular spaces of the rhizomatous tissues. The narrow elongate multicelled conidia originating in clusters from the apex of a conidiogenous cell (figs. 16, 18) are typical of the genus *Cercospora* Fresenius. *Cercospora* is a large and taxonomically difficult collection of molds that are saprophytes or weak parasites on unhealthy plant tissues causing leaf-spot diseases and blights (Ellis 1971, 1976; Rossman et al. 1987). The long multiseptate phragmoconidia, which appear to originate in a pleurogenous manner, and their presence in rhizomatous tissues riddled with fungal hyphae support the suggested affinity to *Cercospora*. A more accurate designation may be impossible because *Cercospora* and similar genera are distinguished on the basis of microscopic morphological and developmental details associated with conidiogenesis.

The compact cluster of pitted fungal spores in the anthers of ?aponogetonaceous flowers (figs. 19, 20) show affinity with anthericolous fungi of the basidiomycetous order Ustilaginales (Currah and Stockey 1991). This order comprises the smut fungi, a group of systemic parasites restricted to angiosperms. In the majority of extant smut taxa, clusters of teliospores form sori in leaves, stems, roots, or ovaries and rarely within anthers. The fossil smut is most similar to the anther smut *Microbotryum violaceum* (Persoon:Persoon) Deml

& Oberwinkler, which occurs among members of the Caryophyllaceae (e.g., *Silene alba* [Miller] E. H. L. Krause) in teliospore morphology and sorus location (Currah and Stockey 1991).

Once infected by *M. violaceum* the female flowers of *S. alba* are induced to produce anthers that become filled with teliospores; infected male flowers also produce teliospores (Webster 1980). However, the mechanism responsible for pollen suppression and production of fungal spores in anthers is not known (Ruddat et al. 1991). The position of the sori and replacement of the pollen by teliospores would seem to indicate some type of anemophilous dissemination of the teliospores, but Jennersten (1983) reports that spores of *M. violaceum* (= *Ustilago violacea* [Persoon: Persoon] Roussel) on caryophyllaceous plants are dispersed by entomophilous vectors. While the anthericolous fruiting habit in the fossil flowers is a good example of biotrophic parasitism it may also be evidence of a coevolutionary dispersal strategy involving insects and fungi.

The fungus in the fruits and seeds of *Princetonia allenbyensis* was an aggressive colonist that converted the embryonic tissues into a dense stromatoid mass (fig. 23). The fungus reproduced by forming pycnidia in the outer layers of the tissues surrounding the seeds (fig. 21). The pycnidia produced two-celled cylindrical conidia (fig. 22).

Extant pycnidial fungi with characteristics similar to those found parasitizing *P. allenbyensis* are similar to either *Ascochyta* Libellus or *Phoma* Saccardo of the Coelomycetes (Fungi Imperfecti). Species of *Phoma*, however, usually have asep-

tate conidia (von Arx 1987). The genus *Ascochyta* includes fungi with single-septate conidia that develop from phialides within thick-walled unilocular pycnidial conidiomata (Sutton 1980). The genus encompasses a widely distributed group of fungi that are often seed borne and cause rots of seeds and fruits (Boerema and Dorenbosch 1973) and necroses of leaves and stems (Rossman et al. 1987). The type of conidiogenous cell in our material is not clear, but the bicelled cylindrical to allantoid spores, the structure of the pycnidium, and parasitic development on flowers are characteristics that indicate *Ascochyta* may be a closely related genus with which to compare these fossil fungi.

By the Late Cretaceous and early Tertiary most major groups of fungi had probably evolved and their roles within the environment determined. In recent studies (Stubblefield and Taylor 1988; Taylor 1990; Taylor et al. 1992a, 1992b; Hass et al. 1994) such aspects as determination of the abundance and diversity of fungi in ancient environments, their role and function within these environments, and their association with the vascular plants have been addressed.

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