Chapter 7. Paleozoic Paleobotany of Grand Canyon National Park

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Introduction

Grand Canyon National Park (GRCA) is certainly one of the most awe-inspiring natural sculptures on Earth. From the rich black Vishnu Schist lining the depths of the canyon, to the shining white cliffs of the Kaibab Formation perched on the canyon rim, the exposed rocks display approximately one-third of all of Earth's history in a well-exposed geologic section. Each of the rock layers that form the intricacies of Grand Canyon's walls represents a different environment that existed in this place as the Colorado Plateau changed over hundreds of millions of years. Many of the sediments deposited in these different environments preserve fossils that provide an immense wealth of information about the evolution of life on earth.

Grand Canyon exposes rocks that were formed starting in the Precambrian through the middle Permian in the Paleozoic and are ~1800–270 million years (Ma) old. The most visible rocks in the canyon—the flat lying layers that dominate many vistas from the rim—are the Paleozoic portion of Grand Canyon's stratigraphy. During the early and middle Paleozoic, the Colorado Plateau was largely inundated by shallow seas and the marine sediments deposited during this time (~545–335 Ma) reflect these conditions. Local sea level started falling during the Mississippian, and the resulting deposits of the Surprise Canyon Formation, Supai Group, Hermit Formation, and Coconino Sandstone represent a range from nearshore to estuarine to terrestrial environments. The fossil plants reported from Grand Canyon National Park are found in the Surprise Canyon Formation, members of the Supai Group, and the Hermit Formation.

The Hermit Formation preserves the most diverse and well-preserved flora from Grand Canyon, with 42 different species reported, and 25 type specimens known from the associated collections (Appendix 7-A). There are seven identified plant taxa reported from the Supai Group and 12 from the Surprise Canyon Formation, many of which are fragmentary and more poorly preserved. Whereas plant fossils are not overly abundant in Grand Canyon, they are certainly significant because they add to the limited record of Mississippian, Pennsylvanian, and Permian age paleofloras from the western margin of the Pangean supercontinent, a region subject to considerably different climatic conditions than contemporaneous areas in the more central Euramerican regions.

History of Research

The first paleobotanical remains from the Grand Canyon were discovered by Charles Schuchert in 1915 in the Hermit Formation along the Hermit Trail in the Waldron Basin at a locality called Red Top. Schuchert sent a small collection of these specimens to U.S. Geological Survey (USGS) paleobotanist David White for identification. White noted *Walchia*, "*Gigantopteris"* (likely *Supaia*), *Sphenophyllum*, and *Callipteris* in this initial sampling, and these findings were published in 1918 (Schuchert 1918; White 1929b). A few more plant fossils were found and reported to White by Levi F. Noble and Charles Gilmore between White's 1918 publication and his Carnegie Institution funded collecting trips during the summers of 1926–1928. White's systematic collecting during these field trips yielded the specimens that he would publish in his 1929 monograph on the Hermit Formation paleoflora. Most of his plant collection came from a quarry he made along the Yaki Trail (now called the South Kaibab Trail) and is marked today by the "fossil fern exhibit" constructed by the Civilian Conservation Corps (CCC) in 1937 just to the west of the trail on Cedar Ridge (Figure 7-1).

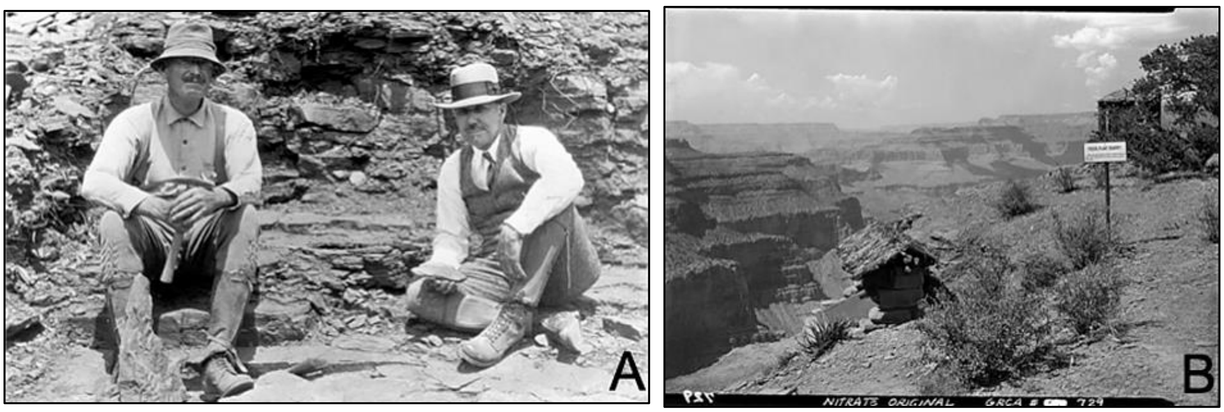

Figure 7-1. A. Paleobotanist David White (left) and John C. Merriam working in the Cedar Ridge fossil quarry during field work in the summer of 1927 (NPS). **B.** Fossil Fern Exhibit constructed by the Civilian Conservation Corps (CCC) at the site of White's quarry on Cedar Ridge, South Kaibab Trail (NPS).

David White also spent time searching the Supai Group for plant fossils, particularly during the summer of 1928, and published a mention of his findings in his 1929 Hermit Formation monograph (White 1929a). White reported the conifer *Walchia* and algal trace fossil *Rivularites* from multiple horizons in the lower and middle Supai, and an assemblage of *Walchia*, *Taeniopteris, Neuropteris*, (*incertae sedis*), *Cordaites* (conifer), and *Calamites* (horsetails) from 7.6 m (25 ft) above the base of the Watahomigi Formation near the South Kaibab Trail (McKee 1982). Plant fossils were next reported from the Supai Group by Edwin D. McKee in a large USGS report, having been found during field work supporting this publication. From many measured sections throughout the Supai, occurrences of *Walchia*, stems, ferns, *Rivularites*, stromatolites, miscellaneous algae, and bioclasts are noted (McKee 1982).

The Surprise Canyon Formation is the most recently recognized sediment package in GRCA. USGS geologist George Billingsley first noticed the large dark red-brown channel fills sitting on top of the Redwall Limestone during mapping reconnaissance flights in the 1970s (Beus 1986). Between 1975 and 1983, Billingsley and Beus measured sections for many of the larger Surprise Canyon outcrops and observed a fairly consistent assemblage of plant fossils in the terrestrial deposits at the base of these channels. They repeatedly reported tree impressions, wood fragments, and leaves, and spores attributable to ferns and lycopods like *Lepidodendron* (Beus 1986). A brief description of this flora was published in Billingsley and McKee (1982), with USGS paleobotanist Serge Mamay identifying two ferns and five sphenophytes. Other unidentified plant fragments and 22 spore and pollen taxa were described in this report as well, but none of the plant or palynological specimens were figured (Tidwell et al. 1992). Beus later collected 40 additional plant specimens, and these contributed to a closer review of the Surprise Canyon flora by Tidwell et al. (1992) who identified a total of 12 plant taxa.

Stratigraphic Distribution of Fossils

The Paleozoic rocks of Grand Canyon include, from oldest to youngest, the Tapeats Sandstone, Bright Angel Shale, Muav Limestone, Temple Butte Formation, Redwall Limestone, Surprise Canyon Formation, the Supai Group, Hermit Formation, Coconino Sandstone, Toroweap Formation, and Kaibab Formation (McKee 1982). Some portions of the Surprise Canyon Formation, the Supai Group, and all of the Hermit Formation were deposited under terrestrial and/or estuarine conditions and account for the Paleozoic floras reported from GRCA. The Surprise Canyon Formation represents ancient coastal plain and estuarine environments and records a sparse assemblage of fossil plants. The Supai Group preserves sporadic plants in some of its members, in the sandy and silty terrestrial deposits left by intervals of low sea level. The Hermit Formation was deposited in a seasonally dry (Cecil 2003; Gastaldo and Demko 2011) lowland environment, an interpretation based on the composition of the paleoflora, and preserves the most robust fossil plant assemblage in the canyon.

Plant fossils from the Hermit Formation and the Supai Group are mostly known from eastern portions of GRCA, especially from outcrops near the South Kaibab, Bright Angel, and Hermit Trails. This is somewhat unsurprising, given the difficulty and exposure of the general terrain—prospecting for new fossil sites can be rather challenging. Conversely, the Surprise Canyon flora is mostly reported from sites in western GRCA, where the isolated channels of this formation are largest. Most of the access to these sections was helicopter supported through a USGS project, so the fossil sites reflect a larger spatial distribution and are largely inaccessible by foot.

Surprise Canyon Formation

The Surprise Canyon Formation is latest Mississippian in age (~325 Ma) and is exposed throughout Grand Canyon as isolated lenses filling old erosional valleys, caves, and karst collapse structures in the top of the Redwall Limestone (Billingsley and Beus 1985; Beus 1986). The conglomerate and mudstone beds that make up the channel fills were originally considered to be part of the Watahomigi Formation, the basal unit of the Supai Group. The rocks that form the Surprise Canyon Formation were only identified as a unique sediment package in 1979 by George Billingsley (Billingsley 1979), and formally described by Billingsley and Beus (1985). The Surprise Canyon Formation occurs throughout Grand Canyon and in parts of Marble Canyon, and is rather difficult to identify because of its discontinuous nature and because its larger, more visible outcrops occur in remote areas of western Grand Canyon (Tidwell et al. 1992).

In the western Grand Canyon, the Surprise Canyon Formation occurs as thicker sections in western Grand Canyon with channels typically 45 to 60 m (150 to 200 ft) wide, and as thick as 120 m (400 ft) (Tidwell 1992). It is divided into three major units: 1) terrestrial conglomerate and sandstone; 2) marine skeletal limestone; and 3) marine siltstone and silty to sandy limestone (Tidwell 1992). Most channels, however, only contain the basal terrestrial and the upper fine-grained clastic and carbonate rocks. Plant fossils are found only in the sandstone, siltstone, and shale beds of the lower unit, particularly in western GRCA, and include tree impressions, wood fragments, and plant compressions (Billingsley and Beus 1985).

Identified taxa include the horsetails *Calamites cistiiformis*, *Calamites* sp., the lycopods *Lepidodendron aculeatum*, *L. mannabachanese*, *L. volkmannianum*, *Lepidostrobus* sp. cf. *L. ornatus*, *Lepidostrobophyllum* sp., *Stigmaria ficoides*, the ferns *Pecopteris* cf. *P. aspera*, the pteridosperm seed *Wardia* sp., and *Cyperites* sp. and *Knorria* sp. (*incertae sedis*) (Beus 1990, 1995; Tidwell et al. 1992; Hodnett and Elliot 2018). There are also poorly preserved plants that Billingsley and McKee (1982) reported, based on personal communication with Mamay, as two ferns (one described as "a very delicate, small-pinnuled sphenopterid or pecopterid"), five sphenopsids ("the sphenopsid fragments are parts of the fruiting organs of a phyllothecoid plant"), and other unidentifiable plant fragments. A brief mention of stromatolites at the top of the Surprise Canyon sequence at the Quartermaster Canyon section was made by Beus (1990). While this flora is neither well-preserved, abundant, or diverse, it is significant because Mississippian and early Permian age floras are rare in the western US, and this is the first flora of this age reported from Arizona (Tidwell et al. 1992).

In addition to the megaflora, an assemblage of 22 pollen and spore taxa was recovered from the Surprise Canyon Formation (see list below) and suggests that this plant community was more diverse than its megafossil record implies (Billingsley and McKee 1982; Tidwell et al. 1992). The palynological samples were collected from the basal terrestrial sand and conglomerate unit at the Granite Park section locality (Billingsley and McKee 1982).

Per Billingsley and McKee (1982), pollen and spore taxa known from the Surprise Canyon Formation include the following:

- *Anapiculatisporites concinnus*
- *Anaplanisporites globulus*
- *Auroraspora solisortus*
- *Calamospora* sp.
- *Convolutispora florida*
- *Convolutispora* sp.
- Dictyotriletes cf. *D. clatriformis*
- *Granulatisporites granulatus*
- *Granulatisporites* sp.
- *Hadrohercos stereo*
- *Knoxisporites triradiatus*
- *Lycospora* spp.
- *Punctatisporites* cf. *P. heterofiliferous*

- *Punctatisporites* cf. *P. nitidus*
- *Punctatisporites pseudolevatus*
- *Punctatisporites solidus*
- *Punctatisporites validus*
- *Punctatisporites* spp.
- *Reticulatisporites* sp.
- *Schulzospora rara*
- *Triquitrites* sp.
- Monosaccates indet.
- Unassigned (? Algal)

Lepidodendrales

Several fossils from the Surprise Canyon flora represent different organ or tissue types of arborescent lycopsid, an extinct plant group commonly known as scale trees or giant clubmosses. The trunk impressions that preserve different leaf cushion patterns belong to three species of the genus *Lepidodendron*, the spore producing lycopsid cones are assigned to *Lepidostrobus* sp. *cf. L. ornatus*, isolated sporophyll impressions to *Lepidostrobophyllum* sp., and the root structures to *Stigmaria ficoides* (Tidwell et al. 1992). Based on the leaf cushion patterns on the trunks' exterior, three different types of lycopsid bark were identified: *Lepidodendron aculeatum*, *L. mannabachanese*, and *L. volkmannianum* (Tidwell et al. 1992).

Filicales and Pteridosperms

Fragmentary remains of the marattialean tree fern frond *Pecopteris* sp. were reported by Tidwell et al. (1992), who mentioned it closely resembles *P. aspera*, but there is not sufficient evidence to conclusively make this identification. Seeds that have been recovered from limestone beds were reported as *Wardia* sp.—platyspermic winged seeds: bilaterally flattened, spherical bodies with small wing-like projections along their lateral flanks. Based on other floras from North America, *Wardia* sp. is associated with the compound, pinnate (fern-like) foliage of the pteridosperm *Aneimites* (Tidwell et al. 1992).

Incertae Sedis

Several impressions of what appear to be the subsurface bark layer of lycopsid trunks are tentatively reported from the Surprise Canyon flora, and have been listed as *Knorria* sp. (Tidwell et al. 1992). These fossils show the pattern of leaf vasculature where it connects from the lycopsid trunk to its leaves, and the best preserved specimen shows helically arranged leaf bases, but lacking features allowing more detailed classification. Arborescent lycopsids belong to the still-extant order Isoetales, commonly known as the quillworts, one of three extant orders in the class Lycopsida, the earliest still extant group of vascular plants (Taylor et al. 2009). Additionally, isolated, fragmentary leaves of *Cyperites* sp. are poorly preserved in the Surprise Canyon Formation and their taxonomic relationships to particular lycopsid stem taxa is indeterminate (most of the stem forms produced very similar, grass-like leaves that are difficult to differentiate in compression preservation).

Supai Group

The Supai Group spans the Early Pennsylvanian to the middle early Permian (315–285 Ma), and crops out prominently as a red, stair-stepped slope throughout the Grand Canyon (McKee 1982). The erosion resistant Esplanade Sandstone at its top creates the iconic Esplanade Platform in the western reaches of GRCA. Sediments of the Supai Group were deposited during the late Paleozoic Ice Age. The sediment packages range from terrestrial to fully marine deposits (with intermediate environments also represented), reflecting a time of great sea-level fluctuation caused by global glacial-interglacial cycles (Fielding et al. 2008; Montañez and Poulsen 2013). The Supai Group records four separate marine transgressions, and each distinct event corresponds to one of the four formations in the Supai Group: the Watahomigi Formation, Manakacha Formation, Wescogame Formation, and the Esplanade Sandstone (McKee 1982). With each transgression, the sea level rose progressively higher and flooded increasingly large portions of Arizona and the San Juan Basin (New Mexico, Utah, and Colorado) (McKee 1982).

Each of the four members of the Supai Group have some portion of terrestrial deposits that contain plant fossils belonging to the horsetails, seed ferns, conifers, and plant remains of undetermined affiliation (White 1929a; McKee 1982). These terrestrial sediments largely consist of siltstones and mudstones, and somewhat commonly preserve mud crack and raindrop surfaces (White 1929a; McKee 1982). From the marine limestones of the Supai, fossils identified as algae or algal structures, and several types of bioclasts have also been reported (McKee 1982).

<u>Watahomigi Formation</u>

This marine deposit is composed mostly of limestone that grades into sandstone and siltstone beds that are thicker in the eastern part of the Grand Canyon. The environment of deposition is interpreted to be a relatively shallow, low energy embayment. Plants reported from the Watahomigi Formation include the horsetail relative *Calamites* sp., the seed ferns *Neuropteris* sp., the conifer relative *Cordaites* sp., the conifer *Walchia* sp., *Taeniopteris* sp. (*incertae sedis*), and other unidentified plant fragments. These are found in the siltstone and sandstone beds in the eastern Grand Canyon near the base of the Watahomigi. These beds also preserve mud crack and rain drop surfaces, and their equivalent facies to the west are limestone (White 1929a; McKee 1982). Miscellaneous algal structures are also reported from the Watahomigi Formation, but without much accompanying information (White 1929a; McKee 1982).

<u>Manakacha Formation</u>

The Manakacha Formation was deposited during a second, larger transgression that flooded further inland to the northeast. Hence, it is mostly marine sandstone with some carbonate rock. The only identifiable plant foliage reported from the Manakacha Formation are ultimate branches of the conifer *Walchia* sp., and an undetermined fern (Filicopsida), which are found in shaly mudstone beds. Other reported plant fossils include algal limestone nodules, *Girvanella* bioclasts and calcisphere bioclasts (White 1929a; McKee 1982). The *Girvanella* and calcisphere bioclasts occur as bioclastic debris in carbonate facies in central and eastern Grand Canyon.

Wescogame Formation

The base of the Wescogame Formation lies on an unconformable surface marked by large (up to 24 m/80 ft deep) channel cuts (McKee 1982). The channel cuts are filled with conglomerate, and the overlying Wescogame Formation above consists largely of sand and mud in eastern Grand Canyon, that grades into limestone to the west. The Wescogame Formation, having been deposited in a higher energy marine environment, does not include well-preserved plant remains. Plants found in this formation are miscellaneous algae, including *Rivularites* (Spamer 1992), and possible algal and organic features (White 1927; McKee 1982). Additionally, some occurrences of *Walchia* sp. have been noted in the Grand Canyon area by Spamer (1992). "Fern or cycadofilice" fragments are reported from shaly beds with many mud crack and rain pit surfaces, but these may be from the overlying Esplanade Sandstone (Schuchert 1918; McKee 1982).

Esplanade Sandstone

The Esplanade is the thickest and most extensive member of the Supai Group. Its base is mostly mudstone and siltstone, coarsening upwards to cross bedded sandstone, which is especially prominent in central and eastern Grand Canyon (McKee 1982). The Esplanade Sandstone preserves rare shoots of *Walchia* sp., some undetermined plants, and plant fragments (White 1929a; McKee 1982).

Hermit Formation

The Hermit Formation, often referred to as the Hermit Shale, is early Permian in age (~280 Ma), and forms a soft, deep red slope near the top of Grand Canyon. It is composed of interbedded mudstones, shale, and fine sandstones, and represents sediments accumulating on a broad coastal plain in an environment that experienced strong seasonal drought (White 1929a). The Hermit Formation is one of very few fully terrestrial deposits in Grand Canyon and preserves by far the most detailed and diverse paleoflora from the park. The Permian represents a time of dramatic fluctuation in climate, in response to global cyclic glaciation (Fielding et al. 2008; Montañez and Poulsen 2013). In addition to these overall global-scale cycles, a more seasonal drought regime is interpreted for equatorial Pangea, in which dry periods became increasingly drier (Fielding et al. 2008; Montañez and Poulsen 2013). The Hermit Formation provides unique insight into less-often preserved plant communities that inhabited the continental basins during drier times.

The Hermit Formation flora is significant in that it is distinct from all other North American Permian floras, being a mix of cosmopolitan Permian species, and species with greater affinities to Gondwanan taxa than to North American taxa. Additionally, there are 24 type specimens from the David White collection (see Appendix 7-A).

The Hermit Formation lies directly above the Supai Group, filling erosional channels cut into the top of the Esplanade Sandstone, and forming an extensive deep red slope throughout the canyon. It was at one time included as part of the Supai Group, and was officially named a separate unit in 1922 by L. F. Noble, who removed the upper red shaley beds from the Supai Formation and named them the Hermit Formation (Noble 1922). The Supai Formation was later subdivided into the four current members of the Supai Group by McKee (1982). The Hermit Formation is composed mostly of thinly bedded silts and sandy silts, with thin discontinuous sandstone beds occurring in the basal and top portions of the formation, and represents deposition in a broad fluvial environment. The Hermit Formation thickens to the west, measured as ~68.6 m (225 ft) thick at the South Kaibab trail and ~83.8 m (275 ft) thick in the Hermit Basin (near the Hermit Trail) (White 1929a).

This fossil flora is described only in a 1929 monograph by David White, but the record of known Permian floras extends to other localities in Arizona, Utah, Colorado, New Mexico, and Texas in the western United States, and also from China, France, Spain, and the Czech Republic (White 1929a; Gand et al. 1997; Wang 1997; DiMichele et al. 2005, 2006, 2007, 2012, 2013; Galtier and Broutin 2008; Opluštil et al. 2017). Of the 32 fully named plant fossil species listed by White (1929a) (with 10 additional species only identified to genus level, or of uncertain identification), about half of them were newly described species at the time he published them (see Appendix 7-A). However, it is likely that there are truly about half that many species in the Hermit Flora because many were poorly preserved and doubtfully described (Read and Mamay 1964). The major groups represented include Spermatopsida (seed plants, including seed ferns), conifers, horsetails, Ginkgoopsida, and algae (White 1929a).

Spermatopsida

The seed ferns (Spermatopsida) are a group of plants that were abundant in the Paleozoic and Mesozoic (Taylor et al. 2009), and they are an informal grouping of seed plants that otherwise cannot be firmly attributed to the seed plant lineages, conifers, cycadophytes, gnetaleans, or ginkgoes (Hilton and Bateman 2006). Their foliage superficially resembles that of ferns, but they produced seeds instead of spores as true ferns do. White listed 18 different species of seed fern (and five additional unidentified species) belonging to six different genera. The genera include *Autunia* or *Rhachiphyllum* (formerly *Callipteris* [Kerp and Haubold 1988]); *Supaia*, *Brongniartites*, *Yakia*, and *Neuropteridium* (Supaiaceae); and *Taeniopteris* (*incertae sedis*; *Taeniopteris* is included under seed ferns in White (1929a) but is truly a vast form genus that includes species of seed ferns and ferns) (Table 7-1).

The genus *Supaia* was established by White (1929a) to describe fern-like foliage dominant in the Hermit Formation flora (Figure 7-2). A key character of this genus is a single bifurcation in the lower frond that splits into two simply pinnate sections. The angle of the split is acute. White interpreted *Supaia* to be closely related to *Autunia* or *Rhachiphyllum* (what White referred to as *Callipteris*) (Kerp and Haubold 1988). DiMichele et al. (2018) commented specifically on *Supaia anomala*, and moved it into the genus *Auritifolia* Chaney, as *Auritifolia anomala*. The authors Kerp and Haubold (1988) commented specifically on the species *Callipteris conferta*, designating it *Autunia conferta*, and on the species *Callipteris raymondii*, designating it to the morphogenus *Sphenocallipteris raymondii*, as they argued that the name *Callipteris* should be abandoned. Kerp et al. (1991) then renamed *Sphenocallipteris* as *Gracilopteris*, meaning the most current name for *Callipteris raymondii* is *Gracilopteris raymondii*. The other species of *Callipteris* mentioned by White (1929) likely belong to the morphogenus *Rhachiphyllum* (Kerp and Haubold 1988), but no formal evaluation is presented here.

Table 7-1. List of all pteridosperm species reported in White (1929a), including locality information. Taxa marked with an asterisk are new species described by White (1929a). (Note: *Callipteris* is no longer a valid name, and these species likely belong to *Autunia* or *Rhachiphyllum* [Kerp and Haubold 1988]).

Fossil Plant Species	**Family**	**Localities**
Autunia conferta (*Callipteris conferta*)	*Incertae sedis*	Bright Angel Trail and South Kaibab Trail
*Callipteris arizonae**	*Incertae sedis*	Hermit Basin
Gracilopteris raymondii (*Callipteris raymondii*)	*Incertae sedis*	Bright Angel Trail and Hermit Trail
Callipteris ? sp.	*Incertae sedis*	Hermit Basin
*Supaia thinnfeldioides**	Supaiaceae	Hermit Basin
*Supaia rigida**	Supaiaceae	Hermit Basin
*Supai sturdevantii**	Supaiaceae	Bright Angel Trail
*Supaia merriami**	Supaiaceae	Hermit Trail
Supai compacta	Supaiaceae	Hermit Trail
Auritifolia anomala (*Supaia anomala**)	Supaiaceae	Hermit Basin and Bright Angel Trail
*Supaia linearifolia**	Supaiaceae	Bright Angel Trail
*Supaia breviloba**	Supaiaceae	Bright Angel Trail
*Supaia subgoepperti**	Supaiaceae	South Kaibab Trail
Supaia sp.	Supaiaceae	Hermit Basin
Supaia sp. indet	Supaiaceae	Hermit Basin
Supaia ? sp.	Supaiaceae	South Kaibab Trail
Brogniartites ? *yakiensis**	Supaiaceae	South Kaibab Trail and Hermit Trail
Brogniartites ? *aliena**	Supaiaceae	South Kaibab Trail
*Yakia heterophylla**	Supaiaceae	Hermit Basin and Bright Angel Trail
Neuropteridium sp.	Supaiaceae	Bright Angel Trail
Taeniopteris cf. *eckhardti*	*Incertae sedis*	Bright Angel Trail and Hermit Trail
*Taeniopteris angelica**	*Incertae sedis*	Bright Angel Trail
Taeniopteris coriacea	*Incertae sedis*	Bright Angel Trail, Hermit Basin

White reported several seeds potentially attached to different specimens of *Supaia* in both his 1929 monograph and in another article published in 1934 (which did not include any figures or references to specimens). Evidence for physical attachment of these seeds to foliage was unclear at best, was reviewed by Mamay and Watt (1971), and is currently interpreted to be some type of insect damage (William DiMichele and colleagues, pers. comm.).

Yakia was another genus newly established by White (1929a) and is defined by "closely spaced, relatively even and parallel ultimate divisions, and by the rather distant, narrow, crooked leaves, which have the appearance of being irregularly lobed…" (Figure 7-3). White also tentatively assigned a fructification that appears as five oblong bodies packed together in what White called "clusters of sporangia or (possibly seeds)", located at the bases of the pinnules (White 1929a: Plate 40, Figures 1 and 2). The distinction between *Supaia* and the other genera included by White in Supaiaceae (*Brogniartites* and *Yakia*) is the size and overall shape (proportion) of the foliage—the bifurcated fronds, pinnules, and venation are all otherwise very similar (it may be that they represent different leaf sizes produced by the same parent taxon).

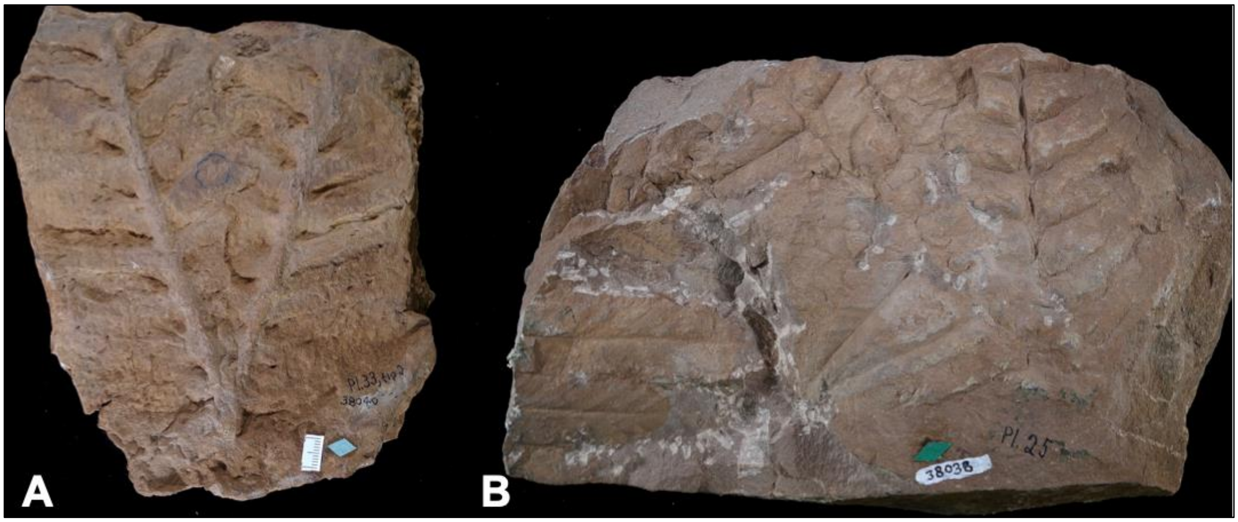

Figure 7-2. *Supaia* specimens (CASSI KNIGHT). **A.** *Supaia* sp. specimen USNM 38040; **B.** *Supaia subgoepperti* specimen USNM 38038.

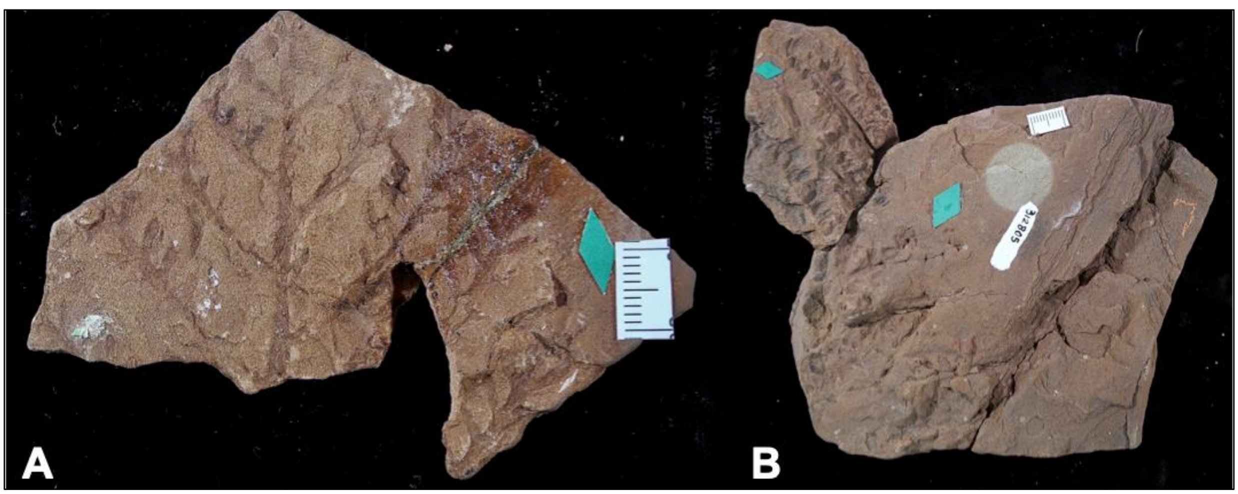

Figure 7-3. *Yakia heterophylla* (CASSI KNIGHT). **A.** USNM 312802 **B.** USNM 312805. The "clusters of sporangia or possibly seeds" mentioned by White (1929a) can be seen in the upper left corner of the specimen.

<u>Coniferophyta</u>

The conifers found in the Hermit Formation number ten different species (and two undetermined species) belonging to seven different families (Table 7-2). These include *Walchia*, *Ullmannia*, and *Voltzia* (Araucariaceae); *Paleotaxites* and *Taxites* (Paleotaxaceae); and *Brachyphyllum* and *Pagiophyllum* (Pinales?).

Table 7-2. List of all conifer species reported in White (1929a), including locality information. Taxa marked with an asterisk are new species described by White (1929a).

Fossil Plant Species	Family	Locality
Brachyphyllum arizonicum	?	Hermit Basin
Brachyphyllum tenue	?	Hermit Basin and Bright Angel Trail
Feysia sp. ? (*Ullmannia frumentaria*)	?	Hermit Basin and Bright Angel Trail
Hermitia dawsoni (*Walchia dawsoni**)	?	Hermit Basin
Hermitia sp. ? (*Walchia gracillima**)	?	South Kaibab Trail
Otovicia hypnoides ? (*Walchia hypnoides*)	?	South Kaibab Trail
Pagiophyllum dubium	?	Hermit Basin
Paleotaxites precursor	Paleotaxaceae	Hermit Basin and South Kaibab Trail
Taxites ? sp.	Paleotaxaceae	Hermit Basin
Voltzia dentiloba	?	Hermit Basin
Voltzia sp.	?	No locality given
Walchia piniformis	?	Hermit Basin, South Kaibab Trail, and Bright Angel Trails

Walchia is a morphogenus that describes leafy coniferous foliage, ultimate shoots and penultimate branch systems, that are all visually similar and typically too poorly preserved to allow certain identification (and with no preserved epidermal structure) (Visscher et al. 1986). There are several species of *Walchia* reported in White (1929a), and the author recognized the fact that there are multiple different species of conifer included under each name, noting that sometimes different cones are attached to branches of the same morphological form. *Walchia* is restricted to Euramerica during the Permian, and the species reported in the 1929 monograph were described based on their similarities to species of *Walchia* described from Europe by European authors. Visscher et al. (1986) established a new morphogenus (*Hermitia* Kerp and Clement-Westerhof) "to accommodate coniferous foliage without preserved epidermal structure; uncertain affinity at the family level" and commented on its relevance to some of the *Walchia* specimens described by White (1929a). Visscher et al. (1986) considered *Walchia piniformis* Sternberg sufficiently well known for the name to stand, placed *Walchia dawsoni* in *Hermitia* as *H. dawsoni* (White 1929a) Kerp and Clement-Westerhof. Kerp et al. (1990) transferred *Walchia hypnoides* to a new genus *Otovicia hypnoides*. *Walchia gracillima* fits the description of *Hermitia* (leafy shoots with needle-like leaves that lack preserved epidermal structures) and likely belongs to this morphogenus (Visscher et al. 1986; Broutin and Kerp 1994), but without preserved epidermal features or reproductive structures, no formal analysis will be presented here.

White reported some specimens of *Ullmannia frumentaria* with small, oval seeds or cones associated with foliage, and compared *U. frumentaria* to *Buriadica*, a genus found in India. His comparison is based on leaves that fork near their apex, but the description for *Ullmannia* does not include bifurcated leaves; this is common for penultimate leaves and cone bracts of Walchian conifers

(Schweitzer 1986). Furthermore, Broutin and Kerp (1994) designated a new morphogenus *Feysia* (which accommodates broad-leaved conifers), and strongly suggested that many specimens of *Ullmannia* likely could be referred to a species of *Feysia* (Broutin and Kerp 1994).

There are several conifer taxa that are only known from very few specimens or are particularly rare in the Hermit Formation flora. *Voltzia dentiloba* is known from the Hermit only by two moderately well-preserved cone bracts, and *Voltzia* sp. is known only from a single cone bract. *Paleotaxites* is a new morphogenus established by White (1929) of conifer with short, compact needles that are densely packed and spirally arranged. Some branches have cones closely associated, which are leathery in texture and have small scales at their base. The single species of *Paleotaxites* reported from the Hermit Formation, *P. precursor*, is rather rare.

White (1929a) also created a new species, *Pagiophyllum dubium*, to include fragmentary twigs and leaves that are not detailed enough to allow certain description, but all distinctly belong to a single species. These plants are loosely assigned to the genus *Pagiophyllum*, but more evidence is needed to confirm this assignment (White 1929a).

<u>Equisetopsida</u>

A single species of horsetail, *Sphenophyllum gilmorei* (Figure 7-4A), is reported from the Hermit Formation paleoflora, and is yet another new species established by White (1929a). The genus *Sphenophyllum* was originally assigned to Arthrophyta by White, but this division is an old name that is no longer used, and the genus *Sphenophyllum* is now attributed to Equisetopsida, which is the class commonly known as horsetails. *S. gilmorei* is similar to only one other species from this genus, *S. stoukenbergi* from the Ural Mountains, but has much larger, more elongate leaves.

Figure 7-4. Various taxa (CASSI KNIGHT). **A.** *Sphenophyllum gilmorei* specimen USNM 38025. **B.** *Psygmophyllum* sp. specimen USNM 38050. **C.** *Rivularites permiensis* specimen USNM 38024.

Sphenophyllum gilmorei is most commonly found in thin sandstone beds deposited within the channel cuts in the Esplanade Sandstone. It reportedly becomes much rarer outside the Hermit Basin, and a few specimens have been found near the Bright Angel and South Kaibab Trails. It can be found preserved in association with small vertebrate tracks on “slime mud” surfaces. Some specimens are preserved perpendicular to bedding, suggesting that *S. gilmorei* grew in shallow pools of water and were buried in situ. White interpreted the ecology of the plant to be one that grew in dense stands in sandy bottomed, intermittent pools, reaching a height of up to 1 m (3 ft) (White 1929a).

Ginkgoopsida

White reported one species of ginkgo in his 1929 monograph, and a second species of ginkgo is known from specimens in the Grand Canyon Museum collections. These plants are *Psygmophyllum* ? sp. and *Rhipidopsis* sp.?, respectively. *Psygmophyllum* ? sp. is known only from a single, poorly preserved leaf fragment found in the lower part of the Hermit Formation in the Hermit Basin (Figure 7-4B). The leaf fragment appears to be covered in a veil of silt and "slime", obscuring many of the detailed features. White also compared this specimen to the ginkgo *Rhipidopsis ginkgoides*. Both ginkgoes are known from the Asian portion of Gondwana (White 1929a).

Algae

One species of algae, *Rivularites permiensis* (Figure 7-4C), is found in the Hermit Formation. White described this as a new species in his 1929 monograph, and attributed *R. permiensis* to Thallophyta, which as a now abandoned term for algae. *R. permiensis* was identified based on its similarity to fossil *Rivularites* from France and living *Rivularites* from the French coast, but described as a new species because of some notable round protuberances that occurred in the Arizona specimens, but not those from Europe. There is, however, no firm evidence to suggest a direct relation between the fossil and modern blue-green algae.

Rivularites is common in the lower portion of the Hermit Formation, but has only been found in the channels that are cut into the underlying Esplanade Sandstone in the Hermit Basin. Colonies of the algae are found often on large ripple surfaces and may reach 0.5 m (nearly 2 ft) in diameter, but most tend to be smaller in size. White proposed that the algae grew in mats in moving water, based on the presence of associated ripple marks and the observation that all the protuberances were consistently pointed or pulled in a single direction (White 1929a).

Other Plants

A category for "fruits of uncertain affinities" includes three genera of different seed types, *Cyclocarpon*, *Carpolithus*, and *Eltovaria*, and gymnospermous ament. (Table 7-3). The different seed types are reportedly very rare in the Hermit Formation, and not many specimens have been found. The seeds *Cyclocarpon angelicum*, *C*. sp., and *Carpolithus* sp. both are small, round forms that are associated with pteridosperms, meaning they came from plants belonging to *Autunia*, *Rhachiphyllum*, or *Supaia*. There is only one known specimen of *Carpolithus* sp., and it is not particularly well-preserved.

Table 7-3. Fruits of uncertain affinities reported by David White (1929a) with locality information. Taxa marked with an asterisk are new species described by White (1929a).

Fossil Species	**Locality**
*Cyclocarpon angelicum**	Bright Angel Trail
Cyclocarpon sp.	No locality given
Carpolithus sp.	Hermit Basin
Eltovaria bursiformis	Bright Angel Trail and Hermit Basin

What is likely some type of fruitification formed by a modified leaf that is apparently folded longitudinally to create a type of pod is identified as *Eltovaria bursiformis*, *Eltovaria* being a new genus established by White for this form (White 1929a). The modified leaf most closely resembles *Taeniopteris* or *Supaia*, and White interpreted this structure as belonging to *Taeniopteris*. A small, single fragment of poorly preserved material is tentatively described as an ament (catkin-like structure) from a gymnosperm and, in this case, is likely some type of female pollen cone.

Acknowledgments

A sincere thank you to all who contributed to this report. I appreciate Klara Widrig and Diana Boudreau for spending their time to help track down needed references. I also greatly appreciate Klara, Diana, Anne Miller, Justin Tweet, and Vincent Santucci for their helpful comments and editorial eyes. Thank you to William DiMichele and Cindy Looy for reviewing this report and for their absolutely invaluable feedback. Finally, thank you to the Grand Canyon Association and Grand Canyon National Park for their support of this work, and many kind thanks to Vincent Santucci for giving me the opportunity to be involved in this project. You all made this possible. "Still the Grand Canyon is the sublimest thing on earth. It is so not alone by virtue of its magnitudes, but by virtue of the whole—its *tout ensemble*."—Clarence Dutton

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Appendix 7-A. Paleobotanical Type Specimens

Appendix Table 7-A-1. Table of all known paleobotanical type specimens from GRCA, including name and specimen numbers. All of the newly created plant species were described by David White in his 1929 monograph (White 1929a),and were originally discovered in the Hermit Formation flora.

Species	Age	Lithology	Reference	Plant Group	Syntype Specimens
Brachyphyllum arizonicum	Permian	Hermit	White 1929a	Conifer	USNM 38060
Brachyphyllum tenue	Permian	Hermit	White 1929a	Conifer	USNM 38061, 312783, 312784
Brongniartites? yakiensis	Permian	Hermit	White 1929a	Pteridophyte	USNM 38042, 312807–312812, 324554–324559
Brongniartites? aliena	Permian	Hermit	White 1929a	Pteridophyte	USNM 38043, 312785–312789
Rhachiphyllum sp. (*Callipteris arizonae*)	Permian	Hermit	White 1929a	Pteridophyte?	USNM 38027
Cyclocarpon angelicum	Permian	Hermit	White 1929a	Seed/Fruit	USNM 38063
Eltovaria bursiformis	Permian	Hermit	White 1929a	Seed/Fruit	USNM 38066
Pagiophyllum dubium	Permian	Hermit	White 1929a	Conifer	USNM 38062, 312790–312792
Palaeotaxites praecursor	Permian	Hermit	White 1929a	Conifer	USNM 38058, 38060, 324560–324564
Sphenophyllum gilmorei	Permian	Hermit	White 1929a	Pteridophyte	USNM 38025, 324567–324575
Supaia anomala	Permian	Hermit	White 1929a	Pteridophyte	USNM 38035, 324581–324588
Supaia breviloba	Permian	Hermit	White 1929a	Pteridophyte	USNM 38037
Supaia compacta	Permian	Hermit	White 1929a	Pteridophyte	USNM 38034, 324590–324593
Supaia linearifolia	Permian	Hermit	White 1929a	Pteridophyte	USNM 38036 and 324594
Supaia merriami	Permian	Hermit	White 1929a	Pteridophyte	USNM 38033
Supaia rigida	Permian	Hermit	White 1929a	Pteridophyte	USNM 38031, 324595, 324596
Supaia sturdevantii	Permian	Hermit	White 1929a	Pteridophyte	USNM 38032, 38038, 324597
Supaia subgoepperti	Permian	Hermit	White 1929a	Pteridophyte	USNM 38038
Supaia thinnfeldioides	Permian	Hermit	White 1929a	Pteridophyte	USNM 38030, 324598–324603
Taeniopteris angelica	Permian	Hermit	White 1929a	Pteridophyte or Gingko	USNM 38048, 324565, 324566, 342587
Voltzia dentiloba	Permian	Hermit	White 1929a	Conifer	USNM 38056
Hermitia dawsoni (*Walchia dawsonil*)	Permian	Hermit	White 1929a	Conifer	USNM 38052, 312796–312798

Appendix Table 7-A-1 (continued). Table of all known paleobotanical type specimens from GRCA, including name and specimen numbers. All of the newly created plant species were described by David White in his 1929 monograph (White 1929a),and were originally discovered in the Hermit Formation flora.

Species	Age	Lithology	Reference	Plant Group	Syntype Specimens
Hermitia sp. (*Walchia gracillima*)	Permian	Hermit	White 1929a	Conifer	USNM 38053, 312793–312795
Yakia heterophylla	Permian	Hermit	White 1929a	Pteridophyte	USNM 38044, 312799–312804
Rivularites permiensis	Permian	Hermit	White 1929a	Cyanobacteria colonies	USNM 38024