

SYNOPSIS OF THE UPPER TRIASSIC FLORA OF PETRIFIED FOREST NATIONAL PARK AND VICINITY

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INTRODUCTION

Although Petrified Forest National Park was originally established for the protection and study of the brightly colored petrified logs found there in the Chinle Formation of Late Triassic age, the area also contains significant deposits of compressed leaves, seeds and cones, as well as abundant palynomorphs. As striking and impressive as the petrified logs maybe, the compressions in the flora are the most valuable for stratigraphic correlations, environmental interpretations and for investigating the evolutionary history of plants. Here, the plant megafossil portion of the ecosystem preserved in the park is briefly reviewed. Also, a few brief words concerning the evidence of the interaction between insects and plants in this area 225 million years ago are included in the following pages. The Late Triassic palynoflora of the park which was studied several years ago (Litwin, et al., 1992) and is now being reevaluated by Alfred Traverse of Pennsylvania State University, and is not considered here. Readers can find more in depth data on the Chinle flora as well as the palynoflora in the references listed at the end of the paper.

Estimates of the age of the Chinle Formation have been refined since Marcou (1855) correlated the unit with the Late Triassic Keuper Stage of Germany. A century later it was suggested on the Triassic correlation chart for North America (Reeside, et al, 1957) that the boundary between the Carnian and Norian stages lay at the base of the Petrified Forest Member of the Chinle Formation. About 35 years later Litwin, et al. (1992) determined, by using palynomorphs, that the Petrified Forest Member straddles the boundary between the Carnian and Norian stages of the Late Triassic and suggested that it was in or just above the Sonsela Sandstone Bed. Ongoing palynological studies by Alfred Traverse of Pennsylvania State University seem to indicate that the boundary probably lies just below what has traditionally been called the Sonsela Sandstone Bed, and close to the top of the underlying Rainbow Forest Bed. Radiometric dating indicates (Riggs et al., 2003) that the

Black Forest Bed in the upper part of the Petrified Forest Member of the Chinle is about 209-213 Ma.

THE PETRIFIED FORESTS

Petrified wood occurs at several horizons in the Chinle Formation in the park and the largest concentrations exposed in the park are termed forests which have been given names reflecting some particular aspect of the wood (Ash, 1987). The wood in these forests consists dominantly of long prostrate logs and short broken sections derived from prostrate logs. Typically, the ground surface in each forest is covered with a pavement of fragments of petrified wood derived from the logs. The stratigraphic position of the forests is shown in Fig. 1. In the southern part of the park they include Rainbow Forest which occurs in the Rainbow Forest Bed, Crystal Forest in the interval between the Rainbow Forest Bed and the overlying Sonsela Sandstone Bed, and Jasper Forest in the Sonsela Sandstone Bed. Another important concentration of logs occurs in the northern part of the park and is called the Black Forest for its dark colored wood. The Black Forest occurs in the Black Forest Bed (Ash, 1992), a reworked volcanic tuff. Some stumps that are in the position of growth also occur at a few localities in the park. Most of them occur in the Black Forest Bed in the northern part of the park as well as a stump field in the southern part of the park, north of Blue Mesa slightly above the Newspaper Sandstone Bed (Ash and Creber, 1992). Appropriately, this stump field is called the Blue Mesa Stump Field.

Although nine species of plants based on petrifications occur in the Petrified Forest, most of the petrified wood in the park is thought to belong to *Araucarioxylon arizonicum*, although there are indications that some of this wood may represent at least one other species (Savidge, personal commun.). *Araucarioxylon arizonicum* is the only species found in Rainbow, Crystal, and Jasper Forests, and is common in the Black Forest where it is associated with the next most common wood species,

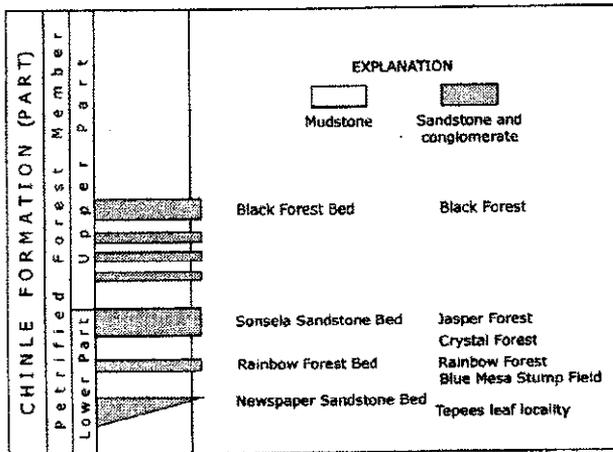


FIGURE 1. Stratigraphic section of the lower part of the Chinle Formation in Petrified Forest National Park showing the relative positions of the petrified forests, the Blue Mesa Stump Field, and the Tepees leaf locality. Adapted from Ash, 1987.

Woodworthia arizonica and *Schilderia adamanica*, which were smaller trees. The other petrified stem material found in the park represents small shrubby plants, not trees, and are discussed elsewhere in this paper.

THE *ARAUCARIOXYLON ARIZONICUM* TREE

Since the most obvious and dominant fossils in the park are pieces of petrified wood attributed to *Araucarioxylon arizonicum*, this summary will begin with a discussion of that species. When the internal structure of this wood was examined microscopically by some of the 19th century paleobotanists, they recognized that it was similar to the wood of the living *Araucaria* trees of the southern hemisphere (e.g., Goepfert, 1858). Therefore, it was felt by those scientists that the Arizona fossil wood came from trees that were closely related to living araucarians. Consequently, the American paleobotanist Frank Knowlton (1888) felt justified in assigning it to the genus *Araucarioxylon* a name which means "araucaria-like wood." When reconstructions of the Chinle environment were made, they usually included at least a few araucaria-like trees with the branches grouped together at the top of the tall trees. However, in the years that followed Knowlton's determination, much living and fossil wood from around the world was studied and it soon became apparent that similar wood also occurred in other families of living and fossil conifers besides the Araucariaceae. For example, the trunk of the *Glossopteris* tree from the Permian of the southern hemisphere had identical structure (Gould and Delevoryas, 1977). Regrettably, the name cannot be changed to correct this misnomer because of the principal of priority.

Recent studies of the trunks assigned to *Araucarioxylon arizonicum* indicate that the living tree

did not closely resemble any of the present day *Araucaria* trees as often shown in reconstructions (Creber and Ash, 2000). These studies show that the living *Araucarioxylon arizonicum* tree had a monopodial trunk ranging in height up to nearly 60 m and a maximum diameter near the base of as much as 3 m. In general, the lateral branches were small and were haphazardly arranged on the trunk from the base to the crown unlike those of living araucarians and most conifers, which are usually in whorls (Fig. 2). The bark was not very distinctive, and like many living trees, had an irregular surface broken into narrow (5-15 mm), short usually undulating strips by shallow (1-3 mm) irregular fissures 1 - 8 mm wide (Ash and Savidge, 2004). The root system consisted of a ring of four to six steeply inclined lateral roots surrounding a large tap root. Although the structure of the wood in the trunk was similar to that of many conifers, it generally lacked growth rings, as is typical of most trees that inhabit humid tropical parts of the world (Ash and Creber, 1992).

Most of the petrified wood in the park has been either permineralized or replaced by the mineral quartz. The so-called rainbow wood which is so prized by collectors is an example of replacement whereas the more somber colored wood has been permineralized. Because much of the cell structure is visible in this less-brightly colored wood, it is more valuable to paleobotanists than the rainbow wood. A small amount of carbonized wood is also present at a few localities in the park.

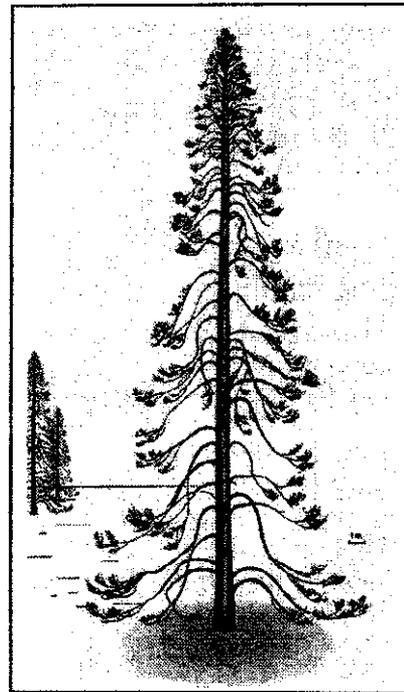


FIGURE 2. Modern reconstruction of the *Araucarioxylon arizonicum* tree based on the logs preserved in Petrified Forest National Park. The living tree ranged up to about 60 m in height. Adapted from Ash and Creber, 2000.

OTHER PLANT FOSSILS

In contrast to the petrified wood and logs, deposits of compressed plant remains are much less common and are smaller in extent than the forests with none of the deposits covering more than a few hundred square meters. The most productive of the compressed plant deposits are found in the strata laterally equivalent to the Newspaper Sandstone Bed in the area near the Tepees in the central part of the park. Smaller deposits occur also elsewhere in the park at other horizons. In many, if not all cases, the compressed plant remains occur either in overbank deposits or in local swamp deposits.

Plant compressions were not discovered in the Petrified Forest until about 80 years after petrified wood was discovered there in 1853 (Ash, 1972b). They were first observed during the early 1930s by the CCC crew that was building an all-weather road through Petrified Forest National Park (Daugherty, 1941, Ash, 1972b). The fossils occurred in grayish mudstones adjacent to the Newspaper Sandstone Bed in a cut that the crew was excavating for the roadbed in the central part of the park near the Tepees. At this locality the workers found compressions of fern fronds, some of which were complete, as well as compressed leaves, cones and seeds of cycadophytes, conifers, and other plants in addition to horsetail stems. Fortunately for science, Myrl Walker, the first naturalist hired by the park, recognized the importance of the discovery and saw to it that many of the fossils were collected and preserved for exhibit and research. Later he arranged for their study by Lyman Daugherty, a botanist at San Jose State University in California who published the results of his investigation a few years later (Daugherty, 1941). Since that time, compressed plant fossils have been discovered at many other localities in the park and in equivalent strata elsewhere in the southwestern United States and studied by several authors in addition to myself (e.g., Arnold, 1964, Bock, 1969, Tidwell, et al., 1977, Cornet, 1986, 1989). The Chinle flora of Petrified Forest National Park is now known to include 42 well-characterized species (in 41 genera) based mostly on compressions and petrifications. Many additional species are found in the Chinle Formation beyond the boundaries of the park, pushing the size of the known Chinle flora to some 83 well-characterized species (in 58 genera). The flora also includes pith casts and small petrified stems in addition to compressions. Selections of the more significant members of the flora are systematically reviewed in the sections that follow.

Lycopsids

During the late Paleozoic, this group of plants was abundant and represented principally by many large treelike forms as much as 50 m tall that inhabited the famous coal-forming swamps of the time. However, when the climate became more arid during the Permian, they became extinct

except for the small forms which had also been present during the late Paleozoic survived. A few of these survivors are present in the Chinle Formation in the park. They include small (10 mm in diameter) petrified stems called *Chinlea campii* and some narrow isolated leaves about 20 mm long that are tentatively referred to *Lycopodites*.

Sphenopsids

The members of this group which are commonly called horsetails are characterized by having hollow stems. Sometimes, under the right sort of circumstances, the hollow stems filled with sediment after the plants died and the thin wall of the stem disappeared leaving pith casts. Like the Lycopsids, many of these plants were also treelike during the Late Paleozoic but others were small and closely resembled the living horsetails called *Equisetum*. However, the large forms did not become extinct in the Permian like the large Lycopsids, but they did begin to become somewhat smaller and eventually disappeared in the Jurassic. Specimens that have stems as much as 30-40 cm in diameter and 10 m or more tall are known in the Late Triassic of Petrified Forest and nearby areas. Remains of the large forms are assigned to *Neocalamites virginensis* (Fig. 3.1) and the small forms are referred to *Equisetites bradyi* (Fig. 3.2). Recently, a sphenopsid cone which is more than 10 cm long and 2 cm was described from the Chinle and may have been the link between the giant Paleozoic sphenopsids and the modern horsetails. It was called *Equicalastrobus chinleana*. Living horsetails rarely have stems more than 6-10 mm in diameter and 2 m tall, and they always live near a permanent source of water such as rivers and streams and lakes.

Ferns and fern-like foliage

As in many ancient floras, the Chinle flora contains several small delicate leaves that look like those of ferns but do not bear sporangia. It is possible that some of these fossils are in fact the leaves of seed ferns, a group of extinct plants that had fern-like leaves but reproduced by means of seeds, not spores. Because fern-like leaf bearing seeds has been found in the Chinle Formation near Cameron, Arizona (Ash, 2005) it is not beyond the realms of possibility that one or more of the fern-like leaves in the park will ultimately be found to bear seeds. In the meantime, since by convention fern-like leaves are usually treated as ferns, they will be discussed in the following paragraphs.

With ten species, the ferns (and fern-like foliage) constitute the largest group of plants in the Petrified Forest. Most of them are the remains of plants that had underground stems, but one is the remains of a plant that had an aerial stem with a crown of leaves at the top and is classified as a "tree fern." Since most Paleozoic ferns became extinct at the end of the Permian it is not surprising that the Chinle ferns generally have a modern look about them and that four of them are assigned to living families, two are assigned to extinct Mesozoic families, and the others are unassigned;

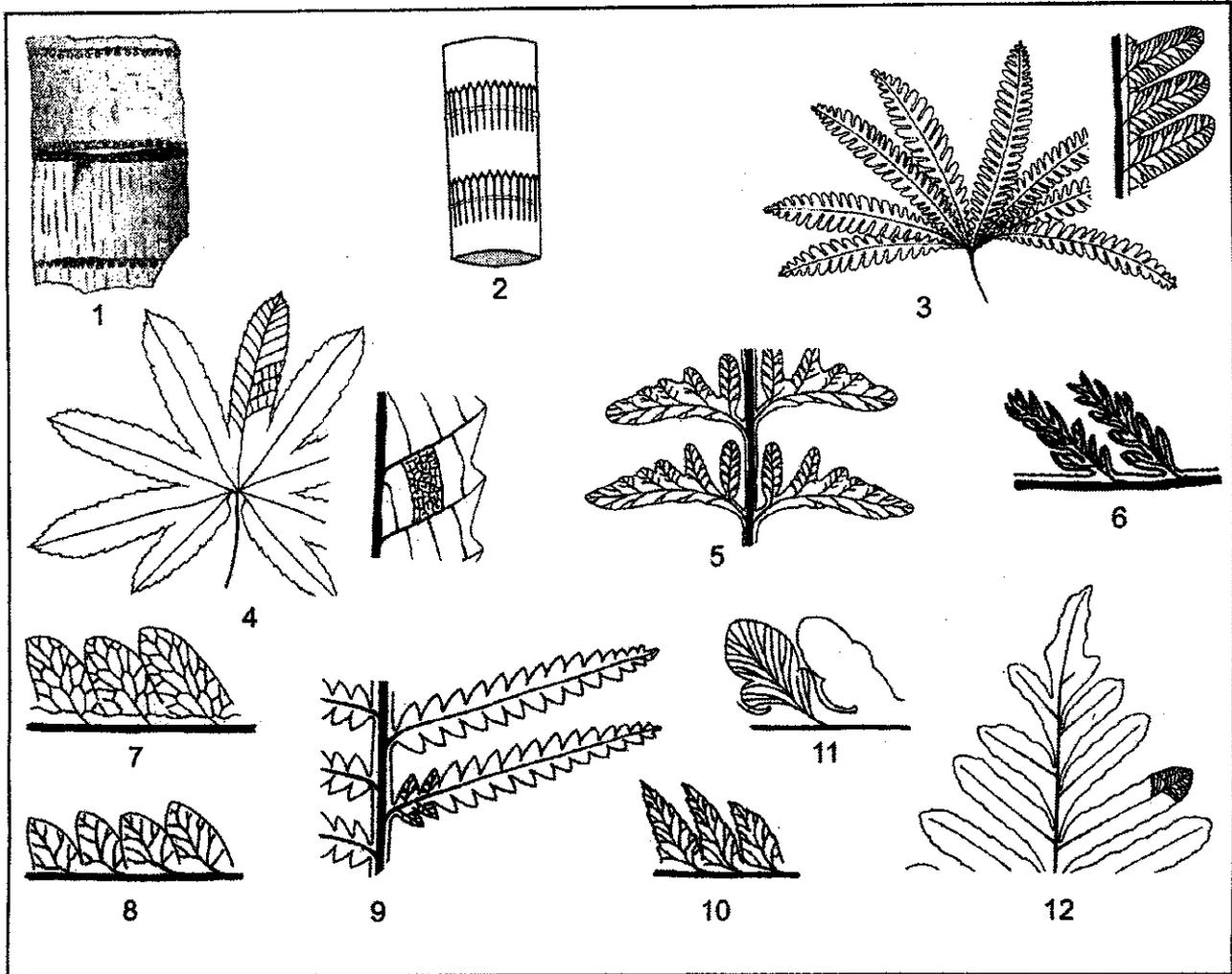


FIGURE 3. Sketches of some of the Sphenopsid fossils (1, 2) and fern and fern like leaves (3-12) found in the Chinle Formation. 1, Pith cast of *Neocalamites virginiensis*, $\times\frac{1}{2}$; 2, Compressed stem of *Equisetites bradyi*, $\times 1$; 3, Entire leaf of *Phlebopteris smithii*, $\times\frac{1}{2}$; 4, Entire leaf of *Clathropteris walkerii*, $\times\frac{1}{2}$; 5, *Todites fragilis*, $\times 1$; 6, *Wingatea plumosa*, $\times 2$; 7, *Cynepteris lasiophora*, $\times 2$; 8, 9, *Cladophlebis daughertyi*, 8, $\times 2$, 9, $\times 1$; 10, *Cladophlebis yazzia*, $\times 2$; 11, *Sphenopteris arizonica*, $\times 2$; 12, *Marcouia neuropteroides*, $\times 1$. Adapted from several sources including Ash, 1970, 1972a, d, 1973, 1980, 1999; Bock, 1969.

one of them resembles a Paleozoic fern. The four species assigned to living families are some of the earliest representatives of their respective groups. Two of them are *Phlebopteris smithii* (Fig. 3.3) and *Clathropteris walkerii* (Fig. 3.4), both of which have distinctive palmate leaves and have descendants now living naturally in humid tropical parts of southeast Asia. Another species assigned to a living family is *Todites fragilis* (Fig. 3.5). It has a small, delicate bipinnate leaf and has been assigned to a family which now naturally inhabits humid subtropical to tropical parts of the world such as southeast Asia. *Wingatea plumosa* (Fig. 3.6) has a large, highly dissected tripinnate leaf with very small ultimate segments that vary in outline from oblanceolate to narrowly lobed. This fern is tentatively assigned to

the Glecheniaceae. Another distinctive fern found in the park is *Cynepteris lasiophora* (Fig. 3.7) which has been confused with the Paleozoic fern-like leaf *Lonchopteris*. However, the open reticulate venation and solitary surficial sporangia distinguish it from the older form. It is widely distributed in the Late Triassic strata in the Southwest (Ash, 1970). This fern has been assigned to the extinct family Cynepteridaceae.

One of the most common of the fern-like leaves in Petrified Forest National Park is assigned to *Cladophlebis daughertyi* (Figs. 3.8, 3.9). It is a fairly large bipinnate leaf with small delicate pinnules that are falcate in outline with smooth margins. *Cladophlebis yazzia* (Fig. 3.10) is another fern-like leaf described from the Petrified Forest

where it is represented by just a few small fragments. The species is somewhat similar to *C. daughertyi* but smaller and the pinnules have dentate margins. Of all the fern-like leaves in the park the one known as *Sphenopteris arizonica* (Fig. 3.11) has the possibility of actually being a seed fern, because other species assigned to the genus have been assigned to this group. The leaves of this fossil are fairly large and tripinnate below becoming bipinnate in the upper part. *Marcouia neuropteroides* is another example of a fern-like frond found in the Chinle Formation in Petrified Forest National Park and elsewhere in the Colorado Plateau region. This leaf is palmately compound and perhaps was as large as one meter in diameter. The pinnae are linear-lanceolate and are divided into oval to linear pinnules which have wavy to lobed margins (Fig. 3.12). Numerous lateral veins arise from the pinnule midrib at a high angle and divide and anastomose one or more times with adjacent veins. Usually the anastomosing takes place near the margins and the lateral veins are rarely free at the margins. Originally Daugherty (1941) attributed this species to the genus *Ctenis* but that assignment was found unacceptable by Ash (1972d) and the fossil was reassigned to the new genus *Marcouia*.

The fossil that represents a tree fern is a small petrified stem about 1 m tall and 100 mm in diameter. During life the sides of the stem covered with diamond-shaped scars where leaves had been attached before dying and falling off as the plant grew taller. The apex of the stem bore a crown of leaves of unknown type. The plant, *Itopsidema vanclievei* probably superficially at least, resembled tree ferns in the Osmundaceae in general morphology, a family of tree ferns that live naturally in moist tropical habitats. In fact all modern tree ferns live in humid tropical and subtropical parts of the world.

Cycadophytes

Like most Triassic and Jurassic floras, the Chinle flora of Petrified Forest National Park and vicinity contains abundant cycadophyte fossils. However, they represent both the true or living cycads (Cycadales) and the extinct Bennettitales (Cycadeoidales). The fossils include leaves, reproductive organs, and stems, with the most abundant being the distinctive Bennettitalean leaf *Zamites powellii*. This leaf is usual present wherever foliar remains are found in the Chinle formation. It is pinnate with stiff rectangular pinnae up to 5 cm long and 1 cm wide that have abruptly truncate apices and are broadly attached at a high angle to the sides of a robust rachis. The pinnae contain many parallel veins. Whole leaves range up to about 35 cm in length and possibly 10 cm broad (Fig. 4.1). The only other bennettitalean fossil found in the park is a single specimen of the flower-like female reproductive structure *Williamsonia* n. sp. (Fig. 4.2). This specimen has been compressed laterally. As a result the fossil shows what the structure would have looked like if it had been bisected longitudinally.

Oddly, the true cycads are represented by a slightly larger variety of fossils, although they are not as

common as the bennettitaleans. They include the pinnate leaf *Aricycas paulae*, the stems *Charmorgia dijolli* and *Lyssoxylon grigsbyi*, and the cone scale *Cycadospadix* n. sp. Leaves attributed to *Aricycas paulae* (Fig. 4.3) can be easily distinguished from the leaves called *Zamites powellii* by their pinnules which are narrowly linear with pointed apices and narrow contracted bases and contain a single midvein. These leaves range up to 40 cm or more in length and up to 14 cm in width and the pinnae are 3-5 mm in width and 7 cm long. Most living cycads have either a short squat trunk reminiscent of an old-fashioned bee hive or a columnar stem that may reach several meters in height. Both types of stems have been found in the park. *Charmorgia dijolli* had a short squat trunk about 30 cm in diameter and had a mass of leaves on the top. The sides of the stem were covered with low diamond-shaped leaf bases and a mantle of hair growing out between them. The fossil *Lyssoxylon grigsbyi* had a columnar stem about 1 meter tall and 15 cm in diameter. Its sides were also cover by leaf bases. When living, there was a crown of leaves on the top of the stem. The leaf *Aricycas paulae* could have been borne by either of these stems but there is no way of knowing at this time.

These fossils are important because they are among the earliest known representatives of the Cycadales and show that many of the characteristic features of the order had developed by Late Triassic time. Although they once were distributed throughout the world during the Mesozoic, the Cycadales now live naturally in southern Florida, southern Mexico, Australia, southern Africa, South America, etc.

Ginkgophytes

The history of this strange group of plants goes back to the Permian. They were present in the Triassic in small numbers and became common in many younger floras throughout the world. For some unknown reason they almost became extinct during the last few million years, and specimens of the only living species, *Ginkgo biloba*, was found living in temple gardens in the Far East a few hundred years ago by western Europeans. Because then they have been planted throughout the western world wherever the climate is not too severe. Although Daugherty identified a poorly preserved fossil as a ginkgo leaf in the Chinle flora that discovery has not been verified. Recently, the remains of two specimens of another leaf that clearly is ginkgoalean has been found in the park. It is a wedge-shaped leaf (Fig. 4.4) about 3 cm wide which is composed of narrow (.1 mm wide) dichotomously divided segments and is referred to *Czekanowskia* n. sp.

Conifers

Although conifers are often major components of Mesozoic floras, they are comparatively rare in the Petrified Forest except for the petrified logs of *Araucarioxylon arizonicum* and *Woodworthia arizonica* as discussed above. For some unknown reason, coniferous foliage is limited



FIGURE 4. Sketches of some of the gymnosperm leaves (1, 3 - 6, 8) and reproductive structures (2, 7) and leaves that have been attacked by phytophagous insects (Figs. 9-11) found in the Chinle Formation. 1, The Bennettitalean leaf *Zamites powellii*, one of the most common leaves in the Chinle Formation and equivalent strata in the southwestern United States, x1; 2., The laterally compressed Bennettitalean seed-bearing structure *Williamsonia* n. sp. st = stalk, b = bracts (similar to petals in many living flowers), s = seeds, x1; 3, Portion of the Cycad leaf *Aricycas* showing some of its narrow linear pinnae, x1; 4, The filiform ginkgophyte leaf *Czekanowskia*, x1; 5, A leafy shoot of the conifer *Pagiophyllum simpsonii*, x5; 6, A leafy shoot of the conifer *Brachyphyllum hegewaldia*, x5; 7, Leafy shoot (on left) and seed-bearing samara (on right) of *Dinophyton spinosus* some of the most common plant megafossils found in the Chinle and equivalent strata in the southwestern United States, x1; 8, The pollen bearing organ *Pramelreuthia yazzi*. Each of the purse-like structures on the side of the central stalk contain bisaccate pollen grains similar to the dispersed grains called *Pityosporites chinleana*, x1½; 9, 10, Marginal feeding traces on pinnules of the fern *Sphenopteris arizonica* (Fig. 9) and *Cynepteris lasiophora* (Fig. 10), x5; 11, Marginal window feeding trace extending across several veins (lower left) and a slot window feeding trace (upper right) on a pinnule of the Bennettitalean leaf *Zamites tidwellii*, x5. Sketches adapted from several sources including Ash, 1970a, b, c, 1973, 1975, 1991, 1996, 1999, 2001, Ash and Litwin, 1996.

to a few specimens of the leafy shoots of *Brachyphyllum hegewaldia* (Fig. 4.5) and *Pagiophyllum simpsonii* (Fig. 4.6), and possibly a species of the large pinnate leaf *Podozamites*. Two possible coniferous cones recently collected in the park are under study but their relationships are not entirely clear at this time. The low numbers of coniferous leaves and cones in the Petrified Forest is all the more strange because they are so common at some localities in the Chinle Formation in southern Utah.

Classification Uncertain

The Chinle flora includes a number of species that are difficult to classify. One of the most curious is *Dinophyton spinosus* (Fig. 4.7). It is represented by leafy shoots bearing narrow linear leaflets that look very much like those of some conifers. However, the reproductive structures of this fossil are very unusual and unlike those of any other known plant. They are four winged cross-like samaras that bear a sac contained a seed where the arms crossed. These samaras apparently were attached individually to the main axes of the leafy shoots by a long stalk. The surfaces of both the leafy shoots and the samaras are covered with many distinctive small spine-like trichomes. Some authors have suggested that *Dinophyton* is related to the living Gnetales but not all workers agree.

Another fossil that is difficult to classify at this time is the pollen bearing organ *Pramelreuthia yazzi* (Fig. 4.8). It is a pinnate organ with a stalk that is about 4 cm long that bears small rectangular pollen-bearing structures in two ranks. The rectangular structures are purse-like and are about 2-3 wide and 1-2 mm high. They contain a single row of tubular sporangia that contain bisaccate pollen grains resembling the dispersed grain *Pityosporites*. It is possible this fossil should be classified as a seed fern.

INSECTS VS. PLANTS IN THE PETRIFIED FOREST

Not surprisingly, just like their modern counterparts, the plants that once lived in the Petrified Forest and vicinity during the Late Triassic, were besieged by insects and other small arthropods such as mites. Although they probably were common, insects are some of the least known elements of the 225 million year old Late Triassic ecosystem preserved in the Chinle Formation in Petrified Forest National Park, Arizona and adjacent areas. Actual body fossils of insects are quite rare in the Chinle and the few that have been found have never been described. All of them are the remains of relatively small insects and in spite of statements to the contrary in several popular publications, there is no record of "dragonflies as large as swallows" in the Chinle Formation in the park or elsewhere. Sadly, no insect remains have yet been found in the amber that occurs at several localities in the Chinle Formation in the park and adjacent areas.

The most common of the insect body fossils found in the park and adjacent areas are the isolated elytra of

beetles (Order Coleoptera). These structures are the thick leathery fore wings, used as a covering for the hind wings when they are at rest. The elytra found in the park are narrowly elliptical and are about 6 mm long and about 2 mm wide. Because of their tough composition, elytra are commonly found as fossils. It is not surprising that elytra are the commonest of the insect body fossils found in the park because many of the trace fossils (tunnels) on fossil tree trunks in the park and on some of the leaves probably were caused by these insects, because similar damage recorded on living plants is directly attributable to beetles. Other body fossils found in the Chinle Formation include representatives of three living orders: the Diptera (true flies, gnats, etc.), the Neuroptera (Dobsonflies, lacewings, etc.), and the Orthoptera (grasshoppers, locusts, etc.).

Most of our knowledge of insects and their activities in the park is based on trace fossils, primarily various types of channels and burrows reported in petrified wood by Walker (1937), Ash (2000) and Ash and Savidge (2004) and feeding traces on fossil leaves described by Ash (1997, 1999). The first report of insect trace fossils in the park was published by Walker (1937). In this often referenced article, Walker identified and named five new species assigned to three new genera of trace fossils consisting of channels that formed just under the bark of the trees preserved in the park and tunnels and burrows excavated into the wood of the trunks. Walker reported (1937) that he had observed them only in the wood of the dominant tree in the park, *A. arizonicum*. However, I have recently noted at least one type of the burrows he recognized in the wood of *Schilderia adamanica* at several localities in the park. Also, I have described (Ash and Savidge, 2004) at least one type of tunnel that Walker did not recognize under and in the bark of the *A. arizonicum*. All of the types of burrows and channels reported in the wood in the Petrified Forest match similar structures produced by living beetles and it is probably appropriate to attribute the trace fossils to the activities of beetles.

Some of the most interesting insect trace fossils are the feeding traces found on several types of fossil leaves in the park. For example the tips of pinnules in *Sphenopteris arizonica* (Fig. 4.9) *Cynepteris lasiophora* (Fig. 4.10) commonly show crescent-shaped marginal excisions. Non-marginal types of traces include window feeding and slot and oval traces which are present on the pinnules of the bennettitalean leaf *Zamites* sp. (Fig. 4.11). All of these excisions are bordered by dark rims of reaction tissue indicating that the leaves were alive when attacked and that they lived for sometime afterwards. Several types of living beetles produce similar excisions on ferns and the leaves of other plants Ash, 1997, 1999.

Small coprolite-bearing cavities reported by Ash (2000) in the tree fern stem *Itopsidema vancleaveii* indicate that the living plant provided shelter and food for a small arthropod. The cavities occur in and near the leaf petioles and in the root mantle, are round to irregularly shaped and range up to a few millimeters in diameter. Although the cavities are not lined with reaction tissue, a few masses of

it are present in some of the cavities, showing that the plant was alive when attacked. The coprolites are oval to weakly hexagonal in shape and the largest are slightly less than 0.1 mm in length. The mite responsible for the damage is unknown.

PALEOCLIMATOLOGICAL IMPLICATIONS

It is generally accepted that plants are very sensitive to the climate that they live under. Thus, by using the nearest living relative factor and the morphological features of the fossil plants found in the park it is possible to determine the type of climate they lived under. An analysis of this evidence that the flora in the lower part of the Chinle Formation lived under a humid tropical to subtropical climate, which could have been monsoonal. The ferns, which are comparatively abundant in the flora found in the lower part of the Chinle Formation, are especially useful for reconstructing the climate under which it was deposited. Such reconstruction using fossil ferns and/or other plants such as the Sphenophytes and cycads is based on two assumptions: first, that the climatic preferences of fossil plants were similar to that of their nearest living relatives, and second, that the morphological features of fossil species are similar to those of extant plants inhabiting a particular existing climate.

Before discussing the paleoecological implications of the Chinle ferns it should be noted that most (about 80%) living ferns are restricted to the tropics and subtropics where the regional climate ranges from consistently wet to monsoonal (Lellinger, 1985). In those regions, the climate is humid throughout the year, although it may be slightly less so during the dry part of the monsoonal cycle. Also, it should be noted that the uplands in those regions are as humid as the river valleys, if not more so (Tryon, 1986). The relatively specialized, so called desert ferns live in more arid areas, but they are easily distinguished from the more common ferns that inhabit the humid tropics and subtropics.

The nearest living relatives of all the Chinle ferns live in the humid tropics and subtropics. Two of them, *Clathropteris walkerii* and *Phlebopteris smithii*, belong to families that formerly had a worldwide distribution (Tidwell and Ash, 1995) but now only occur in areas of southeast Asia that have a monsoonal climate (Bower, 1928). The other Chinle ferns are not as closely related to any living ferns but nevertheless their relatives always inhabit the humid tropics and subtropics where some may even live under a monsoon climate. None of the Chinle ferns are at all closely related to the desert ferns.

The morphological features of the Chinle ferns are comparable to those of ferns that now live in consistently wet to monsoonal tropical to subtropical climates. Just like their living counterparts from those climatic regimes, the Chinle ferns have superficial, unprotected stomata on both sides of the leaves. The leaves of most, including *Todites fragilis*, *Cynepteris lasiophora*, and *Wingatea plumosa* as well as the two species of *Cladophlebis* were originally

thin and delicate. These ferns, like their living counterparts, probably inhabited shady areas under larger plants such as cycadophytes and conifers and perhaps other ferns such as *Phlebopteris smithii* and *Clathropteris walkerii*, which had somewhat more robust leaves. These latter two ferns, just like their nearest living relatives, probably lived in an open environment and provided shelter for the more delicate ferns and other plants, as is characteristic of their descendants in the monsoonal tropics (Bower, 1928).

The Chinle ferns have none of the special morphological adaptations that permit ferns to survive in areas where the water supply is severely limited. For example, the leaves in the Chinle ferns are generally broad (always narrow in desert ferns) and remain flat (curl up when the weather gets extremely dry in desert ferns), and the stomata in the Chinle ferns occur on both sides of the leaves (restricted to the lower side in desert ferns) and are virtually unprotected (protected by hairs and scales in desert ferns). A desert fern that shares these later characters is *Notholaena parryi*. It inhabits the Colorado Desert and has small leaves that curl up when the weather becomes extremely dry. Nearly all of the stomata occur on the lower surface of the leaves in this species and they are protected by hairs and scales (Helvy, 1963). Similar characters also are present in the several species of the desert fern *Cheilanthes* which inhabit the arid parts of India (Nayar (1962) and elsewhere (Marsh, 1914).

The morphology and nearest living relatives of many of the fern and non-fern species found in the Chinle Formation indicate that they lived under a regional humid tropical to subtropical climate. Although most of them obviously lived along streams and around lakes, a few were transported some distance from uplands to where they were deposited, and provide data on the paleoclimate of those areas. Particularly useful in this respect are the leafy shoots and isolated leaves of the conifers in the flora. They are generally rare and fragmentary, indicating that they were transported some distance before burial. None of these fossils have the epidermal features that are said (Parrish, 1998) to be indicative of a strongly arid climate, such as deeply sunken, strongly protected stomata, stomata in grooves, exceedingly thick cuticles, or stomatal plugs. Rather, their epidermal features are close to those of the plants, including the ferns, of the contemporary riparian communities, indicating that they too inhabited a similar climate. Thus, when all of the evidence provided by the plants is considered it is apparent that both the riparian and upland communities lived under a humid subtropical to tropical climate that could have been monsoonal or consistently wet.

Thus, it is apparent that the theory of Demko, et al. (1998) that the compressed plant fossils in the lower part of the Chinle Formation reflect only the humid climate along streams and around lakes and not the climate of the surrounding region ignores important facts. First, the climate along modern rivers is little different than that of the region they pass through, and this was most probably true in the past. Second, humid climates simply could not and do

not exist in narrow corridors along water courses or around lakes under an otherwise arid or strongly seasonal climate as visualized by Demko et al. (1998). Although large trees may grow along the banks of some rivers in arid regions such as the Sonoran Desert, the climate (humidity) along such corridors is very similar to that of the surrounding region and the trees obtain water from the water table. Furthermore, ferns can not and do not survive along the Rio Grande, the Colorado, the Nile, the Darling, and other rivers passing through arid lands. Not even desert ferns live along the water courses. Instead they inhabit certain specialized microhabitats. For example, the desert fern *Notholaena parryi* typically grows in crevices and under rocks in the Colorado desert (Nobel, 1978) and *Cheilanthes mysurensis* and related species grow on gravelly or rocky substrata in the deserts of India (Nayar, 1962).

CONCLUSION

In conclusion, using both their morphology and the climatic preferences of their nearest living relatives of the fossil plants in the Chinle flora, it is evident that the majority of them at least lived under a humid subtropical to tropical climate. The climate could very well have been monsoonal since the nearest living relatives of two of the ferns now inhabit monsoonal southeast Asia and more distant relatives of the other ferns and other plants such as the cycads also live there, in addition to other parts of the tropics..

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