PALEOECOLOGY OF THE CHINLE FORMATION IN THE PETRIFIED FOREST NATIONAL PARK, ARIZONA

by

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ABSTRACT

The Blue Forest area of the Petrified Forest National Park is an excellent area to attempt community reconstructions for the Upper Triassic landscape. Examination of the fossil plants, vertebrates, invertebrates, sedimentation, and dispersed spores and pollen has allowed the reconstruction of three Triassic biotic communities. A flood-plain swamp of cycadophytes and ferns was inhabited by metoposaurs, phytosaurs, dicynodonts, lungfish, and semionotids. A nearby lowland closed canopy forest was composed almost entirely of *Araucarioxylon arizonicum* with an understory of ferns and bennettitites. An upland community composed of diverse gymnosperms is inferred from the pollen record. The pollen contribution from the Chinle upland community seems to require a source area within ten miles of the lowland communities. The effect of sorting of pollen in the Chinle fluvial deposits is estimated by comparison with unsorted samples from soil horizons.

The climate of Chinle time is believed to have been warm with prevailing or seasonal aridity. Through-flowing streams from the south explain the occurrence of locally wet habitats.

CHAPTER 1

INTRODUCTION

Studies of the Upper Triassic Chinle formation in Arizona have brought us to the point where enough information is available so that work on the paleoecology of this period is feasible. In order for one to study the ecology of ancient times it is imperative to know all that one can about the area, especially the flora and fauna of the period and the physical environment. Knowledge of the flora and fauna can be obtained through studying fossils. Inference regarding the ancient environment is based on all fossil and geological information at hand, plus whatever analogies can be drawn from other fossil assemblages and the present day ecosystems. Foremost among the latter is the idea that plants do group themselves into distinct associations as they do now. It is to be expected that hygric communities have never contained the same species as upland communities and that the vegetation of a deeply shaded forest floor will not contain the same species as that of open areas.

A paleoecologic study of the Chinle formation in the Petrified Forest National Park is especially desirable because of the large number of visitors who come to the Park. Here they are faced with a spectacular, almost unbelievable display of petrified wood and naturally become curious as to how the petrified logs formed and as to what the conditions were when they grew. This presents a great opportunity for educating the public in the principles of geology and paleontology. In 1964 and 1965 nearly 900,000 visitors came to the Petrified Forest each year (Anonymous 1966). In 1968 the figure was undoubtedly higher, perhaps near 1,000,000.

The paleontology of the Chinle formation is well-known. The plant macrofossils have been excellently described by Daugherty (1941) and recently this work was updated by Ash (1966). The plant microfossils are less well-known, but information is available from Peabody and Kremp (1964). Additional work on the palynology of the Chinle formation was done by the author in connection with this thesis project. The Chinle formation has been well-known for its vertebrate fossils for over 70 years. Reviews of the important vertebrate fossils of the Chinle formation are available. The metoposaurs are reviewed by Colbert and Imbrie (1956), the phytosaurs by Camp (1930) and Colbert (1947), the desmatosuchids by Camp (1956), and Camp and Welles (1956), and the fishes by Schaeffer and Dunkle (1950). While the invertebrates of the Chinle formation are less well-known and the literature is scattered, it appears that all of the important Chinle species have been described.

The stratigraphy of the Chinle formation is also well-known. Several studies have been made of the Chinle stratigraphy since the pioneering work of H. E. Gregory in 1917. The Petrified Forest region has been studied by a series of students and former students from The University of Arizona including M. E. Cooley (1957, 1958), J. Roadifer (1966), and P. Seff (1965).

Despite all this available information on the Chinle formation, there are still major stumbling blocks toward an understanding of its paleoecology. Inferences from the stratigraphy and sedimentology must be based on much finer scale work than that which has been done previously. A reconstruction of the physical environment requires detailed observation of sedimentary structures, limits of river channels, of local ponds, and of surface relief. There are things which the ordinary stratigrapher may notice and even enter in his field book, but which usually remain there.

Paleontologic information also has its difficulties of interpretation. Organisms are not equally likely to be preserved. Consequently one can rarely say that because a fossil is abundant, it was an important organism in the community in which it existed. Large carnivores are by far the most abundant vertebrate fossils in the Chinle formation, but this could hardly have been the case when they were alive. They were certainly outnumbered by their prey which were herbivores or smaller carnivores. Plant and animal species from upland communities rarely find their way into the fossil record. At best one can hope to find occasional battered plant remains which have been washed down from the uplands, and the remains of upland animals which came to lowland sites in search of water or food, died, and were subsequently preserved. These objections can in part be overcome through a study of localities where preservation is exceptional in that the constraints enumerated above are not so limiting. Indeed, it appears that a few species of upland plants and animals are known, that a few of the smaller animals (fishes) have been found, and that there are a few areas in which the natural proportions of the organisms (in this case, plants) are ascertainable.

Palynology has proved itself to be of great value in studies of Quaternary and Tertiary ecology, and is potentially so in studies of the ecology of older periods. Because of the great production of spores and pollen by plants, and the highly resistant nature of the spore wall, palynomorphs are likely to be preserved in many sediments. In the Mesozoic most plants are assumed to have been wind pollinated, presumably shedding pollen and spores in abundance. Consequently a study of the palynomorphs contained in the sediment is likely to provide a much better indication of the number of species in a flora than a study of the macrofossils. This is true for the Chinle formation in which there are about three times the number of pollen and spore species than plant macrofossil species. In addition the abundance of pollen in many sediment samples makes the collection of adequate numbers of specimens for study relatively easy. Finally, since pollen and spores are easily dispersed, upland communities, if present, are likely to be represented in the palynomorph assemblage. Consequently, the composition and distance of upland communities from the depositional site can be inferred.

The Blue Forest area is an excellent area for attempting a paleoecologic reconstruction. In about one square mile and a stratigraphic interval of about 100 feet a tremendous amount of fossil material is available. Included in this area is Daugherty's principal plant locality, which is probably the best Triassic locality in North America. In the vicinity of the Blue Forest are many of Camp's phytosaur localities including the type localities of three of his species. Seff's (1965) detailed stratigraphic work included this area. In addition there is evidence of more than one plant community, evidence of variable sedimentation and river channels, excellent geologic exposures and ready accessibility.

The emphasis of this paleoecologic study is on the plants and plant communities. This emphasis is proper since the plants are in large measure the dominant factor in the environment of the coexisting animals. The vegetation is also what gives an environment its overall aspect, and to some large extent controls or influences the sedimentary processes that occur.

In summary, the problem dealt with in this thesis is: given an excellent leaf flora, a vast amount of petrified wood, abundant, if unvaried vertebrates and invertebrates, and detailed stratigraphic information, all this representing local depositional environments -- and with a pollen and spore flora representing an integration of the pollen and spore production of the varied plant communities, can the Chinle biotic communities be reconstructed? This problem will be attacked by first examining the stratigraphic information, then the various groups of fossil organisms, and finally tying all this information together and reconstructing the Chinle communities. The discussions of the stratigraphy and macropaleontology are based in large part on an extensive literature review.

CHAPTER 2

STRATIGRAPHY

The Triassic rocks of Northern Arizona are the Moenkopi formation, Chinle formation, Wingate sandstone, and the Moenave formation. The Moenkopi formation of Early and Middle (?) Triassic age consists of nonmarine locally gypsiferous sandy and silty redbeds interfingering to the north with a few marine limestone beds. Its thickness ranges from a maximum of about 1600 feet in northwestern Mohave County (Moore 1958), to about 300 feet in the Cameron area west of the Petrified Forest National Park, to from 150-250 feet in the area of the Park itself (Akers, Cooley, and Repenning 1958).

Overlying the Moenkopi formation is the Shinarump conglomerate, the basal member of the Chinle formation. The Chinle formation of Upper Triassic age is made up of mudstone and fine to coarse grained clastic continental deposits. Minor amounts of freshwater limestone are found in the upper member. The Chinle formation is predominantly of red color except for the variegated Petrified Forest member. The outstanding characteristic of the Chinle formation is the presence of vast quantities of petrified wood. The Chinle formation ranges from about 900 feet thick near the Utah border to over 1500 feet in the Petrified Forest area. This formation and its members are discussed in greater detail in the following pages.

Overlying the Chinle formation is the Glen Canyon group of Late Triassic and Early Jurassic age. The oldest formation of this group is the Wingate sandstone. It consists of a lower Rock Point member of reddish silty sandstone, similar to the underlying Chinle formation, and an upper unit of massive crossbedded sandstone much of which is of aeolian origin. It reaches a maximum thickness of over 900 feet. Overlying the Wingate sandstone is the Moenave formation (Harshbarger, Repenning, and Irwin 1957, 1959) of probable Triassic age. This formation consists of red siltstone and sandstone of fluvial and aeolian origin. In the area of the Hopi Indian reservation it intertongues with the top of the Wingate sandstone. "The Chinle formation and Glen Canyon group represent an essentially continuous sequence of deposits" (Harshbarger, Repenning, and Irwin 1957, p. 31). They were deposited in a lowland environment with streams flowing north-northwest toward a marine basin connected to an extension of the Pacific Ocean running from central Nevada to western Sonora. In the Petrified Forest area strata younger than the Chinle formation and the upper part of the Chinle itself have been removed by erosion. The total thickness of Triassic rocks remaining in the Petrified Forest area exceeds 1800 feet.

Chinle Stratigraphy

The Chinle formation is of early to middle Upper Triassic age, equivalent to the Keuper of Germany and the Karnian and part of the Norian of the Alps (McKee, et al. 1959). Radiometric determinations of the age of pitchblend in the Petrified Forest member of the Chinle formation in the Cameron uranium district give an age of 218±5 m. y. (Miller 1960). But the relationship of this to Triassic tectonics and sedimentologic events as well as to local Cenozoic intrusions remains problematic. An age of about 200 m. y. seems to me more likely for the Chinle formation.

In the Navajo country, H. E. Gregory (1917) recognized four divisions of the Chinle formation, informally called units A, B, C, and D. Division A, the youngest unit, has been removed from the Chinle formation and is now known as the Rock Point member of the Wingate sandstone (Harshbarger, Repenning, and Irwin 1957). This lowermost member of the Glen Canyon group is separated from the underlying Chinle formation in many areas by an erosional surface of little relief. In the Central Black Mesa Basin, which includes the type area of the Rock Point member, the Chinle-Wingate boundary appears to lie in a continuous sequence of deposits and the placement of the Chinle-Wingate boundary is somewhat arbitrary.

Divisions B, C, and D of H. E. Gregory are now known in descending order as the Owl Rock member, the Petrified Forest member, and as the "lower red member." The Shinarump conglomerate, considered a separate formation by Gregory is now almost universally included in the Chinle formation as the basal Shinarump member. The Shinarump member is generally uniform in thickness, although it is locally absent in some areas, such as south of the Petrified Forest National Park. It reaches a maximum thickness of 350 feet in the Monument Valley area (Eversen 1958). It is composed of coarse sandstone and conglomerate with few minor siltstone beds. Notable is the presence of numerous pieces of petrified wood and chert pebbles containing Permian invertebrate fossils. A similar occurrence of fossiliferous chert pebbles of Permian age is found in the Sonsela sandstone bed of the Petrified Forest member. The basal contact of the Shinarump is a surface of considerable relief. In many places the relief is measured in hundreds of feet. These deep channels have been intensively explored, due to the uranium ores concentrated in them. In places near the Petrified Forest, hills of the Moenkopi formation extend up through the Shinarump conglomerate. The top of the Shinarump grades up into and interfingers with the "Lower Red" and Mesa Redondo members of the Chinle.

The "Lower Red" member consists of interbedded mudstone, sandstone and conglomerate. It is present only in the eastern part of the Navajo country where it is 200 to 300 feet thick, thinning to the westward. To the south it intergrades with the Mesa Redondo member and in the Monument Valley area with the Monitor Butte member. The Mesa Redondo member is present in the Petrified Forest National Park. It unconformably underlies the Petrified Forest member in the Blue Forest area (see Figure 2).

The Petrified Forest member is divided into lower and upper parts by the Sonsela sandstone bed. Both the lower and upper parts of the member are characterized by the presence of large quantities of bentonite which swells when wet, forming a puffy crust. The badlands formed in the areas of exposure of these beds are usually barren of plant life and form the painted desert scenery of the south and west edges of the Black Mesa Basin. The units of the Petrified Forest member are characteristically gray, green or blue interbedded with bright red layers.

Petrified logs are concentrated, often in tremendous quantities in the few thin sandstone beds and the Sonsela sandstone bed of the Petrified Forest member. The concentrations of silicified logs in the Blue Mesa area, Jasper Forest, Agate Bridge, and Rainbow Forest are derived from beds of the Sonsela sandstone (Bryant and Roadifer 1965). The logs of the Black Forest area are derived from sandstone beds in the upper part of the Petrified Forest member. In many localities, as in the Petrified Forest, a dark-blue siltstone zone is found immediately below the Sonsela sandstone. Blue Mesa is named after exposures of this unit which can be seen from the top of the mesa which is formed by the Sonsela sandstone. The predominantly gray to blue-gray beds beneath the Sonsela sandstone are believed to be continuous with those exposed north of Cameron (Akers, Cooley, and Repenning 1958). In this unit numerous Araucarioxylon stumps occur in place in at least two localities near Cameron in a stratigraphic position which is close to, if not identical to that of the stumps of the Blue Forest area described in a later section. Vertebrate localities near the "Ward Bone Bed" east of Cameron also correspond in stratigraphic position to those of the Blue Forest area. In the Petrified Forest area the upper member of the Chinle is present in the Painted Desert section and is unconformably overlain by the Tertiary Bidahochi formation which includes several prominent basalt flows, one of which underlies the area of the headquarters and museum in the Petrified Forest National Park.

The upper member of the Chinle is called the Owl Rock member and consists of 100-300 feet of interbedded red calcareous siltstone and freshwater limestone beds. The limestone contains abundant chert nodules and mud pellets. Several of these beds contain a fauna of five species of fresh-water prosobrach gastropods (Yen 1951). A map of the Petrified Forest showing significant fossil localities is given in Figure 1. Typical stratigraphic sections for the Chinle in northern Arizona are given by Akers et al. (1958).

Stratigraphy of the Blue Forest Area

The stratigraphy of the Petrified Forest is rather well-known. Jack Roadifer studied the stratigraphy of the Petrified Forest in 1963 to 1966. The results of this study were submitted as a doctoral dissertation (1966) in the Department of Geology at The University of Arizona. Almost all of his study was concentrated on the sandstone beds, which he attempted to use for correlation within the Petrified Forest. This is unfortunate since almost all of the fossils in the Petrified Forest occur in the finer-grained sediments between the sandstones. In 1962 Seff made an extensive study of the stratigraphy of the Blue Forest area. The report of his study (Seff 1965) is available in the files of the Petrified Forest National Park museum. A composite stratigraphic diagram, derived from Seff's work, is given in Figure 2. Stratigraphic occurrences of significant fossils are shown to the right of the diagrammatic section.

At the southern end of the exposure of the Newspaper Rock sandstone unit the principal sandstone bed consists of a single broad

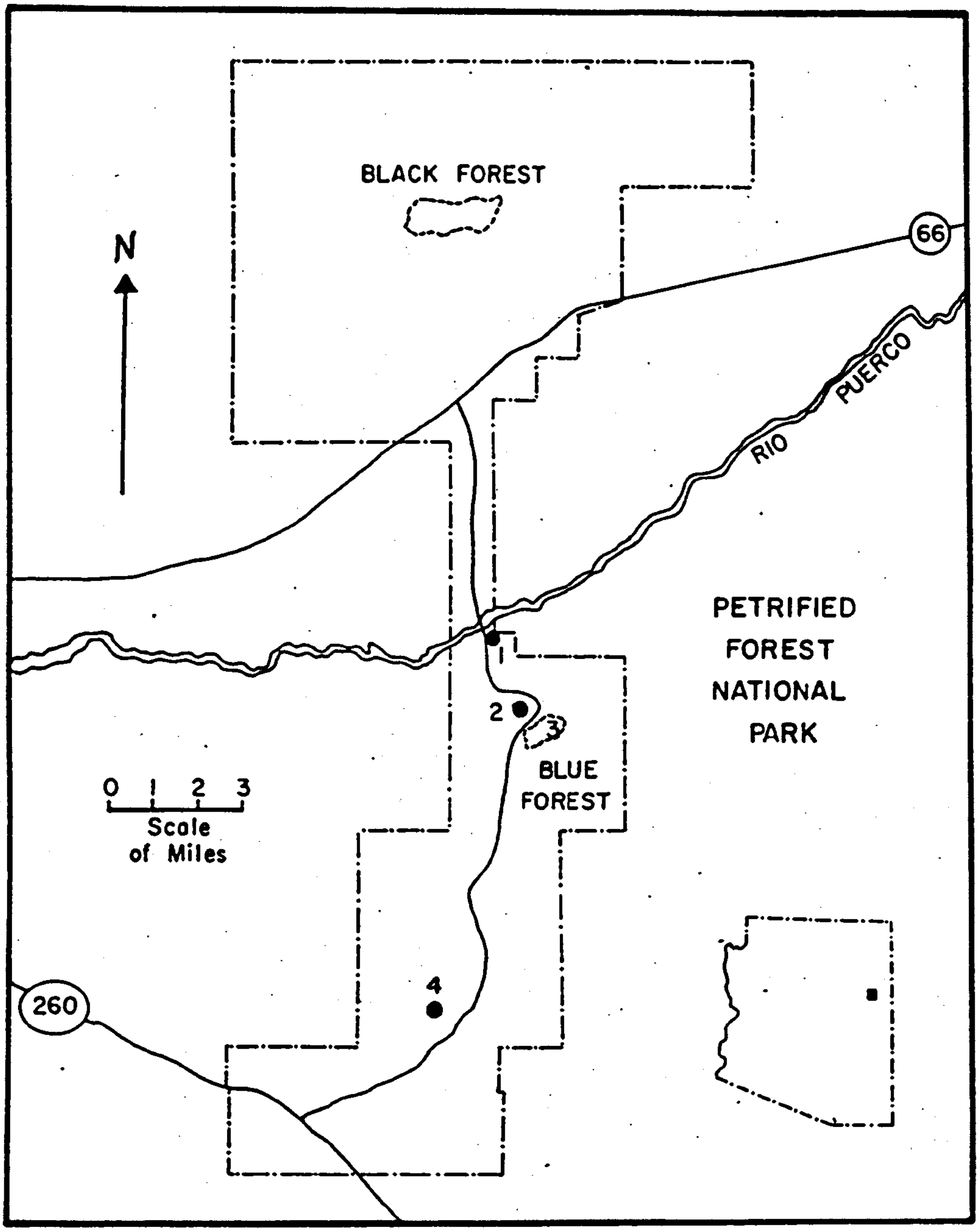

Figure 1. Index map of principal fossil localities.

1 = Puerco River ruins
2 = Tepees
3 = Blue Forest stump field
4 = Walker's standing stump.

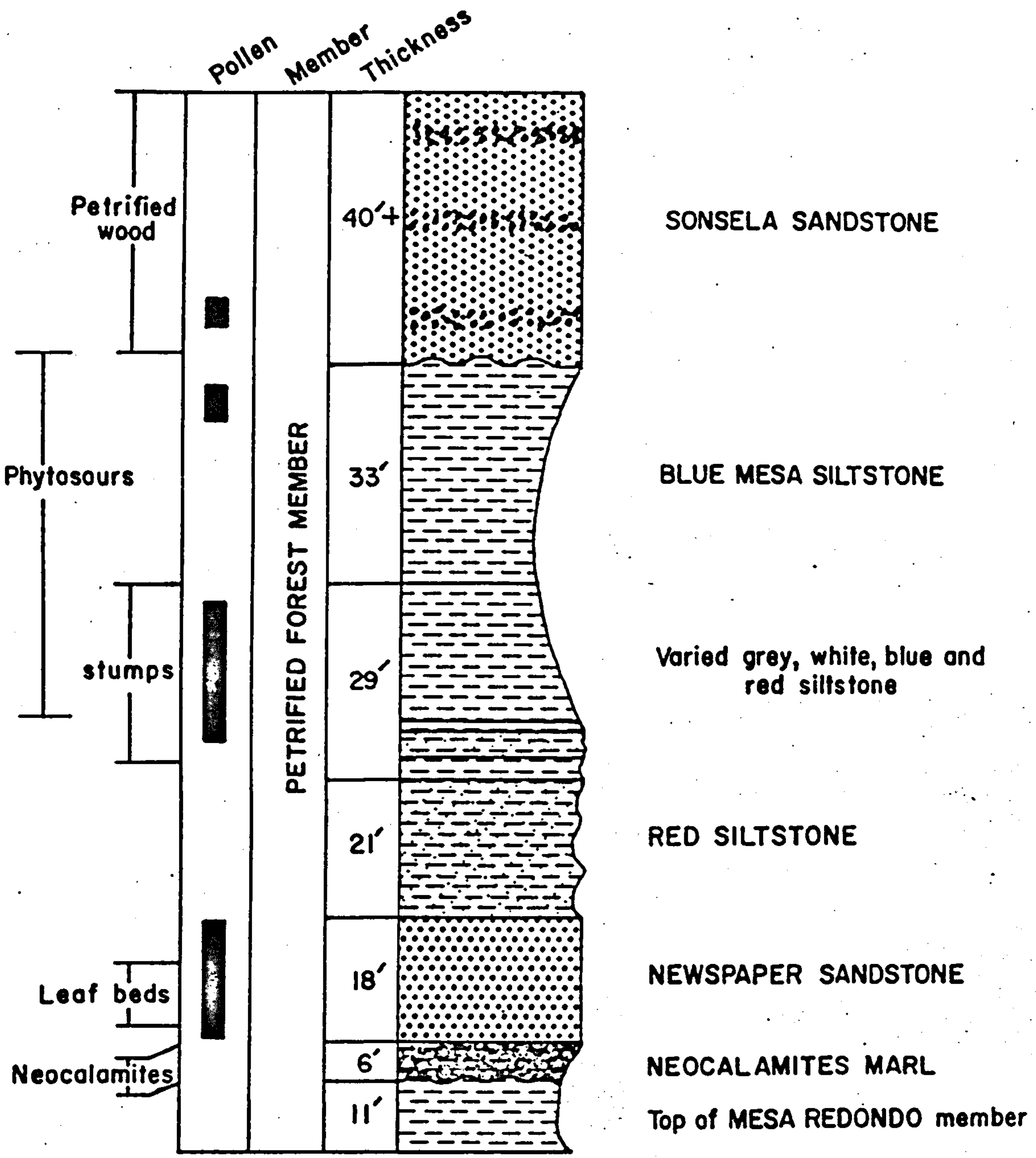

Figure 2. Composite stratigraphic section of the Chinle formation, Blue Mesa area.

The solid bars represent stratigraphic intervals in which pollen is preserved.
Macrofossil occurrences are shown on the left.

Modified from Seff 1965.

channel of finely cross-laminated sandstone which weathers dark brown. On the edges of this channel sandstone a series of silts were deposited. In these deposits extremely well-preserved leaf macrofossils and pollen and spores may be found. The adjacent channel deposits are barren of organic material, presumably because the higher permiability of the sandstones has permitted the organic material to be oxidized by vadose groundwater. The second Tepees profile, taken through 9.70 meters (31 feet) of siltstones extends through most of this lateral equivalent of the Newspaper sandstone and about three meters into the overlying red siltstone unit. The lower 3.84 meters (12 feet) contain plant macrofossils. Pollen preservation extends 2.04 meters (6.7 feet) further up the profile. The first Tepees profile was taken near the edge of the channel. The second Tepees profile was taken about 100 meters from the channel and the first Tepees profile. Correlation of the two profiles by pollen analysis seem to indicate that while 241 centimeters of the lower part of the first Tepees profile was deposited, only 98 centimeters were deposited at the second Tepees locality. The remaining 222 centimeters of the first Tepees profile is equivalent to 163 centimeters at the second Tepees locality. These profiles and their correlation are discussed more fully in the palynology chapter (p. 73).

Sediment size analysis data for the first Tepees profile are summarized in Table 1. In the range of 4-10 ϕ, the mean silt and clay size of the sediments at the first Tepees locality ranges from 5.96 ϕ to 6.72 ϕ with a mean of 6.22 ϕ. Sand is absent in the lower part of the profile, but increases to about 10% near the top of the profile.

Table 1. Sediment size variation (dry weight) in the first Tepees profile.

	Mean of total silt and clay	sand	%silt 4-7Ø	mean size 4-7Ø
1T1	5.96		50.7	5.06
1T2	6.53		43.0	5.36
1T3	6.72		38.8	5.33
1T4	6.54		38.6	5.26
1T6	5.96		57.9	5.24
1T7	6.04	+	56.1	5.27
1T8	5.96	+	58.2	5.21
1T9	6.02	++	56.7	5.27
1T10	6.46	+++	55.7	5.50
1T11	6.21	+++	58.0	5.26
1T12	5.97	+	68.9	5.32

+ = sand present 1%

++ = sand present 1-5%

+++ = sand present 5-10%

Silt particles from 4 ∅ to 7 ∅, have the same settling volocity as most of the pollen and spores found at the Tepees (see discussion in paleoecology chapter p. 74). The proportion of silt in this size range varies from 38.6 to 68.9% of the total silt and clay sized particles at the first Tepees profile. The mean size of the sedimentary particles in the samples range from 5.06 ∅ to 5.50 ∅. The phi (∅) size of a sediment particle is the negative logarithm to the base 2 of the size in millimeters (Krumbein and Pettijohn 1938).

CHAPTER 3

PALEOBOTANY OF THE CHINLE FORMATION

The area of the Petrified Forest National Park has had a long history of paleobotanical research. The magnificent display of agatized wood in the highly colored Chinle badlands, early attracted attention; however, it was not until the 1930's that serious paleontologic work was begun by L. H. Daugherty on the plant fossils of the Petrified Forest region. With the discovery of the rich leaf-fossil beds at the Tepees in 1932 by M. V. Walker, paleobotany began its modern phase.

History of Paleobotany of the Southwestern Triassic

With the acquisition of Arizona from Mexico in 1848, expeditions were sent out to explore the newly acquired territory. In 1851 Captain Sitgreaves (Sitgreaves 1854) first recorded the vast exposures of fossil wood in northern Arizona.

In 1853 L. T. Whipple led an expedition to map a railroad route to the Pacific coast. Möllhausen, a German traveler and naturalist went along with the party and collected specimens of the fossil logs of what is now the Petrified Forest area. His report (Möllhausen 1858) included a description of this new species by the paleobotanist H. R. Göppert who named the wood _Araucarites mollhausianus_. However, according to Ward (1900, p.317) this name is a _nomen_ nudum since Göppert did not describe any specific characters of this species which distinguish it from other species of Araucarites.

In 1859 Newberry made a small collection of plant fossils from the Poleo sandstone member of the Chinle formation at Abiquiu, New Mexico. In 1876 he described five species from this collection. They are Otozamites macombi, Zamites occidentalis, Brachyphyllum (?) (a confierous branch), Pachyphyllum (?) (a coniferous branch), and Pachyphyllum (?) (a coniferous cone).

In 1879 Lt. J. T. C. Hegewald collected three logs in the Petrified Forest area to send to the U. S. National Museum. These logs were described by Knowlton (1888) as Araucarioxylon arizonicum. Presumably this is the same species described in 1858 as Araucarites mollhausianus by Göppert.

In 1886 Major J. W. Powell made a small collection of fossil plants at Newberry's locality near Abiquiu, New Mexico. Three years later this locality was visited by Knowlton. The specimens collected in these trips were described by Fontaine and Knowlton in 1890 and included the bennettitalean fron Zamites powelli and the sphenopsid stem Equisetum abiquense = pith cast of Neocalamites virginiensis. Equisetum knowltoni and Araucarioxylon arizonicum were also reported from this locality. In 1899 Ward briefly examined the region in the vicinity of Holbrook, Arizona. He found a small cone resembling the extant Araucaria and named it Araucarites chiquito (Ward 1900, p. 322). This unique specimen was inadequately described and subsequently lost.

In 1901 Barnum Brown and L. F. Ward spent a summer studying the Triassic of northern Arizona, especially the area around the

Little Colorado River. Ward discovered some coniferous twigs in the Shinarump conglomerate which he illustrated (Ward 1905) and named Araucarites shinarumpensis, but did not adequately describe. Within a quarter mile of Brown's vertebrate locality near Tanner's crossing of the Little Colorado, he found over twenty stumps in place. These stumps had nut-like objects included in the wood, the basis of the name Araucarites monilifer. Daugherty (1941) has shown these bodies to be those of a fungus similar to the pecky heart rot of Libocedrus. Since the wood structure is the same as Araucarioxylon arizonicum, A. monilifer is reduced to a synonym of A. arizonicum. These fungal bodies have been named Polyporites wardii by Daugherty (1941).

In 1910 Jeffrey described a new coniferous tree from the Petrified Forest, which had been collected by J. B. Lewis, Jr. in 1906. Jeffrey named it Woodworthia arizonica. In 1921 R. C. Moore made a small collection of plants from a brown sandstone in the Shinarump conglomerate of Garfield County, Utah. These specimens were described by Berry (1927, pp. 303-307) as Otozamites powelli (= Zamites powelli of Fontaine).

In 1932 J. A. Schilder gave Daugherty a specimen of fossil wood with prominent multiseriate rays. This was described by Daugherty (1934) as Schilderia adamanica. Daugherty began work at this time on the Triassic flora of Arizona. In 1941 he published an excellent monograph on the Upper Triassic flora of Arizona. In this work 35 species of plant macrofossils placed in thirty genera, were recognized. Most of his species were based on leaf material. In addition to the macrofossils Daugherty named four new species of pollen and a single fungal microfossil. In this monograph Daugherty described seventeen new species and seven new genera.

Daugherty believed the Chinle flora to be closely related to the floras from the Newark Series of the East Coast. He considered six species of the Chinle and Newark floras to be identical and nine others closely related. Ash (1966, 1967a, 1967b) believes that these two floras are not closely related. He states (1967b, p. 20) "five of the six species used for correlation are misidentified in the Chinle flora. The sixth is poorly characterized and is at present of no index value. At least 37 of the species and 16 of the genera in the flora are peculiar to the Chinle, and the Chinle flora appears to be unique." This finding is in conflict with the evidence from the microflora. 50-60% of the species of pollen and spores of the Chinle formation are the same as or closely related to those of the Newark group in North Carolina. At least 14 of the 16 common genera of pollen and spores from the Petrified Forest are found in the North Carolina microflora as well.

In 1960 Daugherty described a new genus of petrified osmundaceous ferns (Itopsidema) from the Petrified Forest. In 1963 he described a new genus and species of araucarian root. This species Araucariorhiza joae is presumably the root of Araucarioxylon arizonicum. In this paper Daugherty also reports the occurrence of stems of the bennettitaleans Cycadeoidea and Williamsonia in the Petrified National Park. In 1947 Arnold in his textbook of paleobotany transferred Laccopteris smithii to Phlebopteris. In 1965 Arnold reported the occurrence of Cordaites-type foliage from the Upper Triassic

Dolores formation of southwest Colorado in the same beds as those containing Sanmiguelia lewisi. These cordait-type leaves are the same which Daugherty described as Yuccites poloensis. Arnold reports this name as being preoccupied and reassigns the species to Pelourdea.

Brown (1956) described Sanmiguelia lewisi from the Dolores formation of southwest Colorado. This large leaf looks like a palm frond. Brown concludes that if this leaf were found in younger rocks it would unhesitantly be considered a palm. This occurrence is the most believable of the proposed records of a pre-Cretaceous angiosperm. Occurring with this leaf are abundant stems of the coniferous form genus Brachyphyllum. In 1958 Brown reported the occurrence of a strobilus of a fossil quillwort Isoetites circularis in the same beds. This form is also known from the Petrified Forest. Daugherty (1941) considered this fossil to be the basal portion of a Williamsonia flower.

Recently S. Ash (1967a, 1967b) has published two papers on the flora of the Chinle formation. These are based on his doctoral dissertation at The University of Reading, England which is a review of the Chinle plant megafossils. The list of species and their occurrence in Ash's dissertation show that in the Petrified Forest National Park the flora includes fifteen species of ferns (two as petrified stems), seven conifers (two as petrified stems, one as a petrified root), four bennettitites (one as a petrified trunk), four sphenopsid stems and pith casts, two cordaitaleans (one as a petrified stem), and a single species each of ginko, isoetalean and gnetalean. In addition there are two species of seeds, and two species of uncertain affinities (Sanmiguelia lewisi and "Ctenis" neuropteroides). In his dissertation Ash describes three new genera and six new species. Three of the new species (in two new genera) are ferns from the Chinle of New Mexico, not yet found in Arizona. Cladophlebis microphylla of Daugherty is redescribed as C. daughertyi n. sp., Lonchopteris virginiensis of Daugherty is described as Cynepteris lasiophora, and Macrotaeniopteris magnifolia of Daugherty is transferred to Nilssoniopteris sp. Ash concludes that the Chinle flora is unrelated to other known Triassic floras, and that the climate of the Chinle was warm and humid, since the leaf cuticles studied do not show marked xeromorphic adaptations.

Discussion of the Important Chinle Plants

Ferns are the most important element of the Chinle flora in the environments represented by well-preserved macrofossils. Of the fifteen species known, only three are common and presumed to be important species in the Chinle flora. These are Phlebopteris smithii, Clathropteris walkeri, and Cynepteris lasiophora. The following discussion of these three species is taken in part from Ash (1966).

Ferns of the Chinle Formation

Phlebopteris smithii (Figure 3, numbers 1, 2), a member of the Matoniaceae, is a rather large [up to 20 centimeters in the largest fragment (Ash 1966)] palmate frond. The main rachis divides at the top into two short basal arms each of which bear 4-7 pinnae. The pinna rachis is up to ten centimeters long and bears numerous

Figure 3. Plant macrofossils of the Chinle formation.

Number 1. *Phlebopteris smithii.* The pinnae may be seen extending upward into the enclosing siltsone.
Scale = 1 inch

Number 2. *Phlebopteris smithii.* Fertile pinna.
Scale = 1 inch

Number 3. *Otozamites powelli.*
Scale = 1 inch

Number 4. *Neocalamites virginiensis.* Pith cast.
Scale (on right) = 1 inch

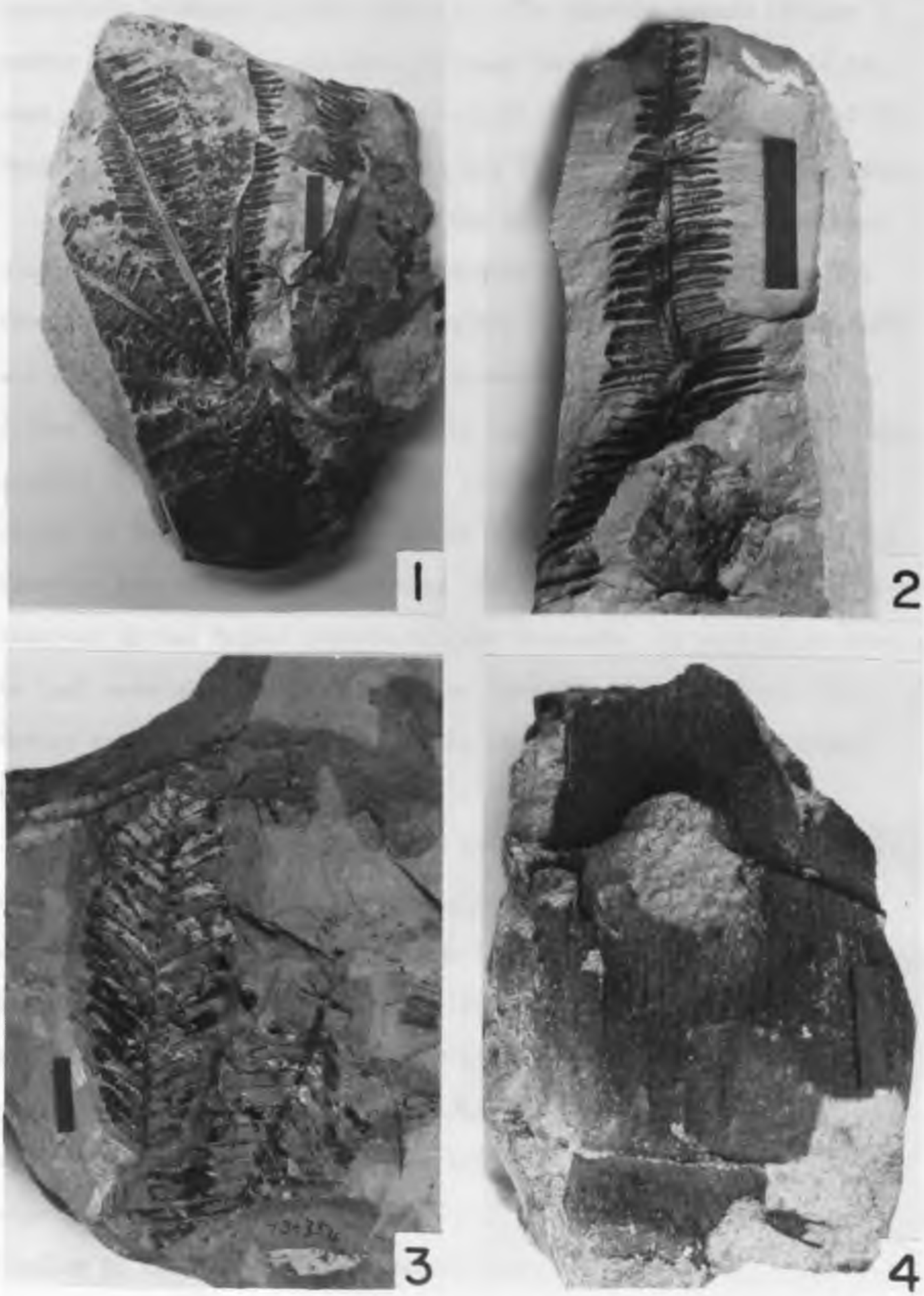

fig. 3. Plant macrofossils of the Chinle formation

oppositely arranged lateral pinnules. The fertile fronds (Figure 3, number 2) are similar and bear circular sori with 7-14 sprangia in each sorus. This species is abundant in the Fort Wingate area of New Mexico and in the Petrified Forest and Dinnebito Wash areas of Arizona.

Clathropteris walkeri, in the Dipteridaceae, is of moderate size (sixteen centimeters in the largest specimen, Ash 1966). The fertile and sterile leaves are similar, palmate, orbicular as a whole and divided into 6-9 pinnae. The pinnae are linear to lanceolate, united at the base and with strongly toothed margins. The spores are rounded triangular, 32-42μ in size with a trilete mark extending nearly to the edge of the spore (Ash 1966). The surface of slightly immature spores is microverrucate. Spores similar to these have been observed in the Tepees deposit but are uncommon. C. walkeri is common in leaf assemblages of the Petrified Forest and Fort Wingate, New Mexico areas. Clathropteris is also known from the Newark series (Daugherty 1941).

Cynepteris lasiophora (Ash 1966) of the Schizeaceae, is the fern called Lonchopteris virginiensis by Daugherty (1941). It is a minor but persistent element of the Chinle flora. The leaf as a whole is up to twenty centimeters wide. Its length is unknown but is possibly up to one meter. The spores are borne is sporangia scattered over the lower surface of the pinnules, are rounded to rounded-triangular, 38-49μ, with a simple trilete mark reaching nearly to the edge (Ash 1966). The spore wall is microverrucate. Occasional spores similar to these have been observed in dispersed form in the Tepees sediments.

Two species of osmundaceous ferns, _Itopsidema vancleavei_, and _Osmundites walkeri_, are known from the Petrified Forest from petrified stems. These are two of the oldest records of the Osmundaceae (Daugherty 1941, 1960).

Conifers of the Chinle Formation

At least six species of conifer macrofossils are known in the Petrified Forest region. Needles and scale leaves of at least three undescribed species of conifers have been found at Walker's Standing Stump and in the area of the Puerco River ruins. _Podozamites arizonensis_, known from only a few specimens in the Petrified Forest, was a conifer with linear leaves 8 to 10 centimeters in length and resembling those of _Agathis_ (Seward 1919, 1931; Harris 1926). The coniferous wood _Araucarioxylon arizonicum_ (Figure 4, numbers 1, 2) is the best-known and most abundant of the Chinle macrofossils. It can be collected almost everywhere where the Chinle formation outcrops in Arizona, New Mexico, and Utah. The growth rings of this wood are usually poorly defined. "The tracheids have moderately thick walls, which are provided on the radial slides with a single row of large contiguous pores or rarely with two rows of alternating pores, and on the tangential sides with numerous, separated, perfectly round small pores; medullary rays numerous, composed of a single series of 1-22 short, superimposed cells; resin ducts none"(taken from the original description of Knowlton 1913).

The wood of _Woodworthia arizonica_ differs from that of _Araucarioxylon_ in the presence of numerous small persistent branches.

Figure 4. *Araucarioxylon* and *Unio*.

Number 1. *Araucarioxylon arizonicum* with irregular growth bands.
Scale = 1 inch

Number 2. *Araucarioxylon arizonicum* with three types of beetle burrows.
Scale = 1 inch

Number 3. *Unio arizonensis*.
Scale = 1 inch

Number 4. *Unio thomasi*.
Scale = 1 inch.

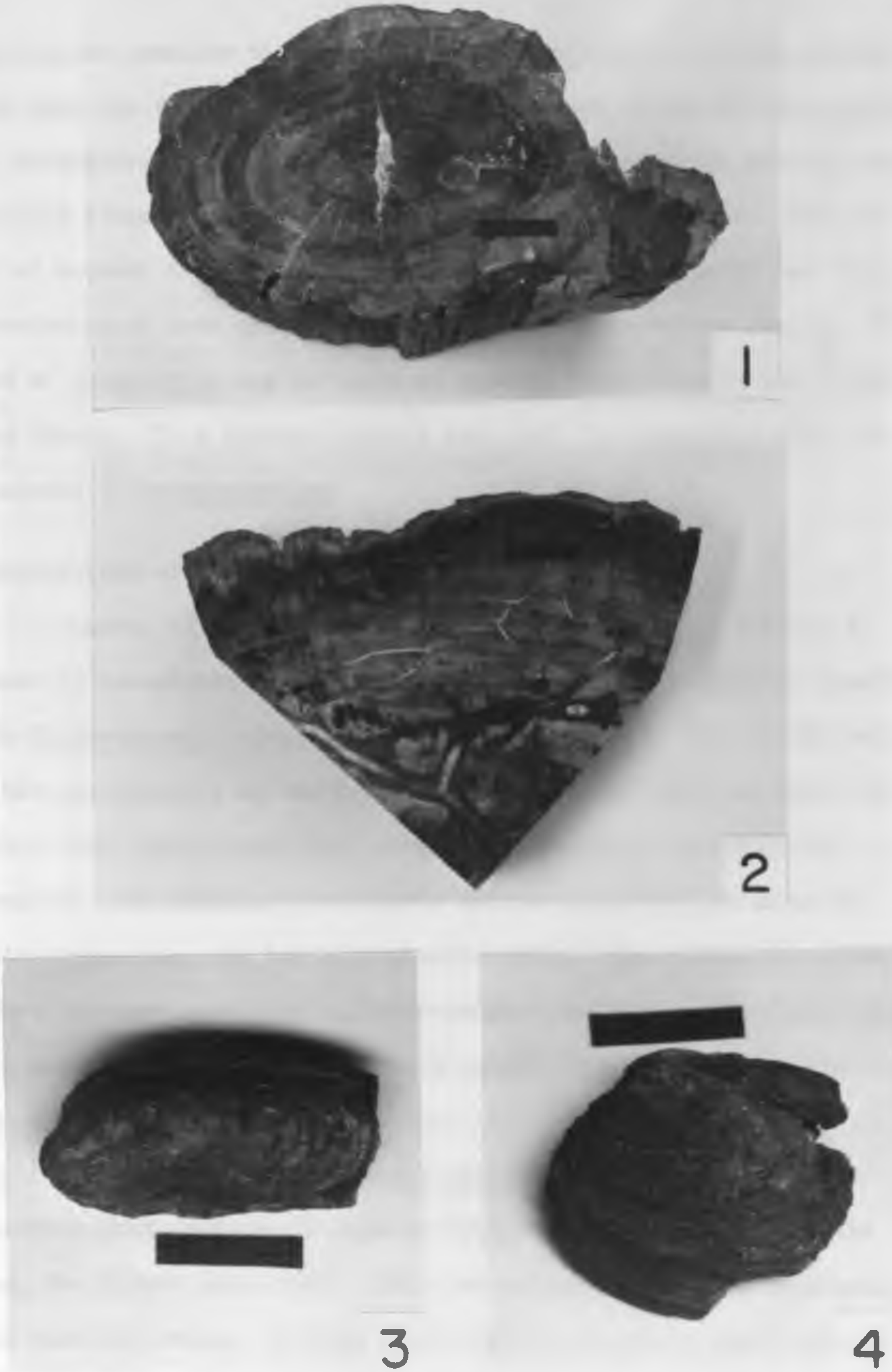

fig. 4. Araucarioxylon and Unio spp.

The logs are smaller than those of the A. arizonicum and are usually less than two feet in diameter. The persistent shoots of Woodworthia are interpreted as an abietinian feature (Jeffrey 1910); however, the tracheid structure bears resemblance to the Araucariaceae. This is one of several Permian and Triassic coniferous woods which has characteristics of both groups and can't be placed in either family. The wood of Woodworthia may be found at several localities in the Petrified Forest. This species appears rare only in comparison with the abundance of Araucarioxylon.

Bennettitites of the Chinle Formation

Leaves of the bennettitalean Otozamites powelli (Figure 3, number 3) are abundant in the Petrified Forest. This species together with Clathropteris walkeri and Phlebopteris smithii make up the bulk of the macrofossils at the Tepees locality. This leaf has been collected from nearly every leaf macrofossil locality in the Chinle formation (Ash 1967a). The pinnate oblanceolate leaf is up to 15 centimeters long, and has a prominent rachis. The pinnae are linear with a truncate apex, 1-7 millimeters wide and 8-60 millimeters long. This species is similar to the much smaller Pterophyllum fragile from Sonora (Silva Pineda 1961).

The bennettitite Nilssoniopteris magnifolia is known from Dinnebito Wash, Arizona (Daugherty 1941) and from the Fort Wingate area, New Mexico (Ash 1966). It's leaves are long and strap-shaped with parallel veins. At both localities it occurs in local beds of dark brown shale. Nilssonipteris apparently lived in or at the edge of small swamps or ponds (Ash 1966). At least two additional species of bennettitaleans are known from the Petrified Forest area in the form of silicified trunks. These are Lyssoxylon grigsbyi and Cycadeoidea sp. (Daugherty 1941, 1963).

Other Chinle Plant Fossils

The Chinle flora also contains sphenosids, cordaits, and a single species of ginkgo. A group of pith casts of a large species of Neocalamites (Figure 3, number 4) occurs about one-half mile west of the Tepees locality. These casts, up to twenty centimeters in diameter, are found in an upright position having grown along the edge of sandbars of a northward-flowing stream.

The predominantly Paleozoic cordaitaleans are represented by two species in the Chinle flora. Dadoxylon chaneyi is a rare species of petrified wood with a large central pith. The strap-shaped leaf, of cordaitalean appearance Pelourdia poloensis, is known from several localities in the Southwest but occurs rarely and in poor condition at the Tepees. Pelourdia and Baiera arizonica, a primitive ginkgo, were probably upland species in the Chinle flora, as suggested by the weatherbeaten appearance of the few specimens found at the Tepees. These two species and an occasional detached conifer needle suggest the existence of an upland community otherwise unrepresented by macrofossils in the Petrified Forest area.

CHAPTER 4

PALYNOLOGY OF THE CHINLE FORMATION

Little is known of the palynology of the Triassic of North America despite the importance of this period in the evolution of the gymnosperms. The pioneering contribution to American Triassic palynology was made by Daugherty (1941) when he described four species from the Chinle of the Petrified Forest National Park and compared them with pollen from the Keuper of Europe. His genus *Alisporites* has become an important and widely used genus in late Paleozoic and Mesozoic palynology. R. A. Scott (1960) demonstrated that Daugherty's *Equisetosporites chinleana* was actually a pollen grain similar to modern *Ephedra* and placed it in that genus. It is likely that in the Permian and Triassic there were many gymnosperms with pollen similar to the modern *Ephedra* and *Welwitschia*. The presence of ephedroid pollen alone does not prove that the genus *Ephedra* existed in the Triassic, consequently referring this pollen grain to *Ephedra* is premature. The proper generic name for fossil ephedroid pollen of this type is *Gnetaceapollenites* (Thiergaart 1938). *Gnetaceapollenites chinleana* may be the pollen of *Schilderia adamanica* which has secondary wood similar to *Ephedra* (Daugherty 1941).

In 1963 members of the Geochronology Department of The University of Arizona began a detailed study, which is still in progress, of the Chinle formation. In 1964 an interim research report was issued by the Geochronology Laboratories which included a report on the pollen and spores (Peabody and Kremp 1964). Since then two abstracts have been published which include information on the palynology of the Petrified Forest (Gottesfeld and Kremp 1966; Gottesfeld 1967).

Preliminary study of the palynology of the Chinle formation and its equivalents in the Southwest has disclosed a varied and abundant flora of over one hundred species. Most of my work has been concentrated in the Petrified Forest National Park, although pollen-bearing samples have been examined from near Fort Wingate, Santa Rosa, and Logan, New Mexico, and from south of Moab, Utah. These localities extend over an area of 350 miles east-west and 230 miles north-south. All these pollen-bearing sediments are from the lower half of the Chinle formation and its equivalents in central and eastern New Mexico. In the Petrified Forest National Park over one hundred pollen-bearing samples have been collected in the lower half of the Petrified Forest member and in the lower part of the Sonsela sandstone bed.

Most of the Chinle deposits are highly oxidized and barren of pollen. However, I have had moderate success in collecting by concentrating on gray beds, especially where associated with rapid channel fill deposits, and on carbonaceous seams and buried soil remnants.

Of the more than one hundred species of pollen and spores found, about 36% are disaccate, 10% monosaccate, 24% trilete, 12% monosulcate, 8% inaperturate, and 10% of other types. Of a sample count of 1200 grains taken from eleven samples, 52% are disaccate, 14% monosaccate, 15% trilete, 10% monosulcate, 7% inaperturate, and 2% of other types. About 50% of the species are likely derived from conifers, 25% from ferns, 12% from bennettitaleans and cycads, with the rest attributable to several species of cordaitaleans, gnetaceans, caytonialeans and other gymnospermous groups.

The Chinle microflora contrasts strongly with the macroflora which is dominated by ferns and bennettitites. In the microflora, coniferous saccate species are the most abundant and varied element. Only one species of fern spore /Dictyophyllidites mortoni (de Jersey) Playford and Dettman 1964/ is commonly present in frequencies of over 5%. This spore was incorrectly identified as Gleicheniidites in Gottesfeld and Kremp (1966) and Gottesfeld (1967). Gleicheniidites is present in the Chinle assemblage but is rare. Dictyophyllidites mortoni is probably the spore of some species of Phlebopteris.

Many species of Triassic plants whose existence can be inferred from the pollen record are unrepresented as macrofossils. Of the species found as leaf macrofossils it is likely that nearly all grew in moist environments near the site of deposition. Consequently a large part of the macroflora is still unknown. Not represented in the macroflora is Vitreisporites pallidus (Reissinger) (Nilsson 1958), which occurs in frequencies up to 17%. This pollen grain is derived from Caytonia (= Sagenopteris) an aberrant but important Mesozoic gymnospermous group. Sagenopteris is known from the Newark group of North Carolina and Pennsylvania, as well as from several localities in Mexico.

Abundant genera of the Chinle flora include the disaccate genera Klausipollenites, Vitreisporites, Alisporites, and Pityosporites;

the monosaccate genera Zonalasporites, Patinasporites, and Callialasporites (?); the trilete genera Dictyophyllidites and Verrucosisporites; the monosulcate genera Cycadopitys and Monosulcites; and the inaperturate genus Camerosporites. These genera are illustrated in Figures 5 and 6. All specimens are from the Petrified Forest National Park. The pre-colpate gymnospermous genus Eucomiidites (Figure 6, numbers 25 and 26) has one of its earliest known occurrences in this assemblage.

In Table 2, Triassic pollen assemblages from the Southwest and North Carolina are compared. The pollen assemblage from Fort Wingate, New Mexico is very similar to that of the Petrified Forest. Klausipollenites seems less abundant than in most of the Arizona samples and several minor types are more abundant. Further study of this locality will probably show the existence of additional genera which are found in Arizona. The Moab, Utah sample is dominated by a single species of fused spore tetrad which is tetrahedrally arranged, laevigate and about 80μ in size. The rest of the Moab assemblage is poorly preserved but contains most of the genera of the Petrified Forest in similar proportions. The Santa Rosa and Logan, New Mexico samples are extremely poorly preserved but insofar as can be judged, are similar to that of the Petrified Forest.

The pollen flora from the Cumnock formation of North Carolina, now being studied by John Koob at The University of Illinois, is remarkably similar to that of the Chinle formation. It contains at least fourteen of the sixteen genera mentioned earlier in this paper, and has many species in common with the Chinle formation. Although

Figure 5. Disaccate pollen of the Chinle formation.

All specimens from the Petrified Forest National Park, X 875 unless otherwise noted; all unretouched photos.

Klausipollenites sp.	1, 2, 3	
Vitreisporites sp.	4	
Vitreisporites pallidus	5	
Alisporites spp.	6, 7	#7 X 700
Alisporites opii	8, 9	#8 X 580
Pityosporites chinleana	10	

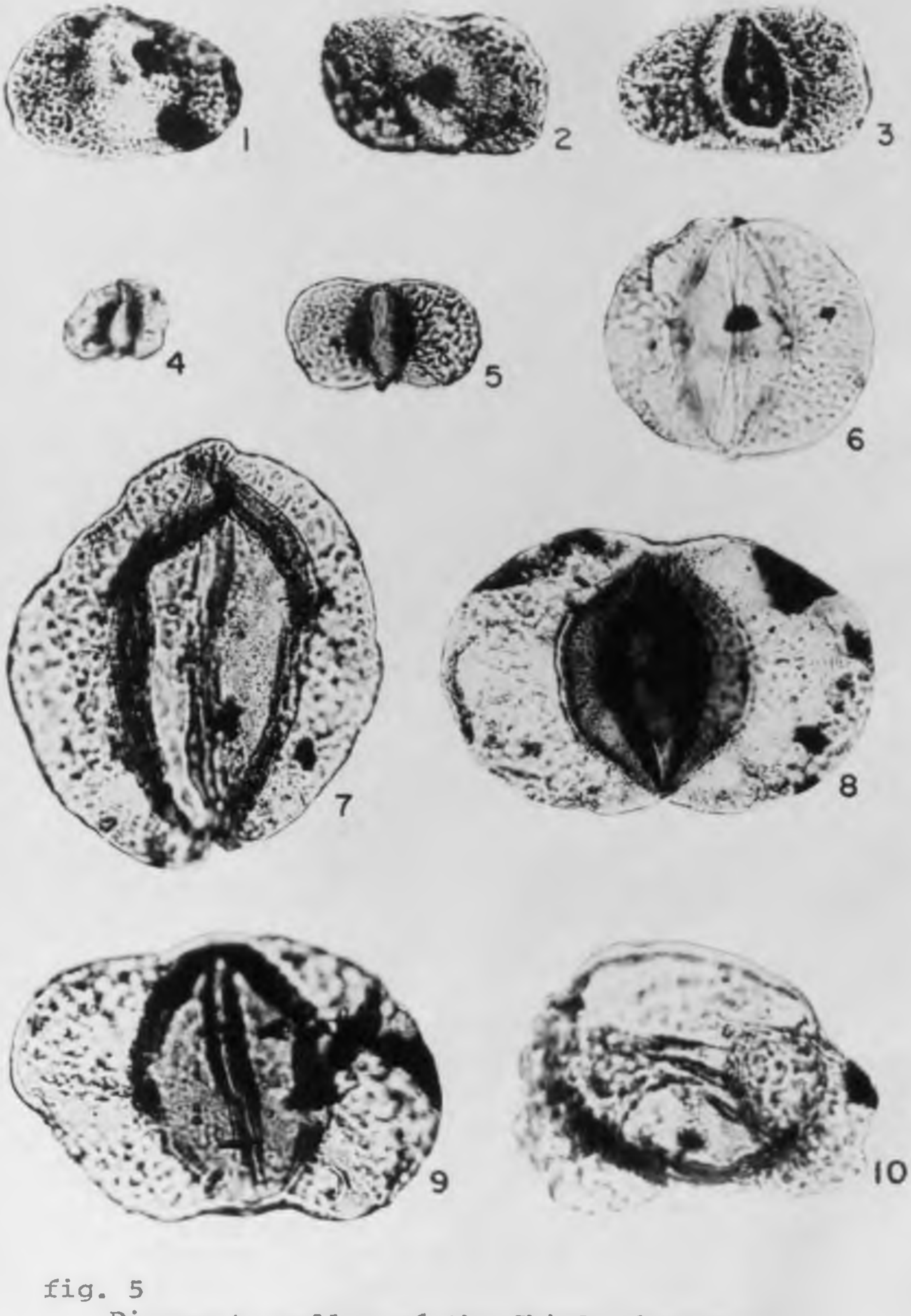

fig. 5
Disaccate pollen of the Chinle formation

Figure 6. Pollen and spores of the Chinle formation.

All specimens from the Petrified Forest National Park, X 875 unless otherwise noted; all unretouched photos.

Zonalasporites spp.	11, 12
Patinasporites spp.	13, 14, 15
Callialasporites (?) sp.	16
Callialasporites (?) *chinleana*	17
Dictyophyllidites mortoni	18, 19
Verrucosisporites sp.	20
Monosulcites sp.	21
Cycadopitys sp.	22
Camerosporites sp.	23, 24 (#23- four spores arranged in a tetrad)
Eucommiidites sp.	25, 26
Gnetaceapollenites chinleana	27- one-half of broken pollen grain.

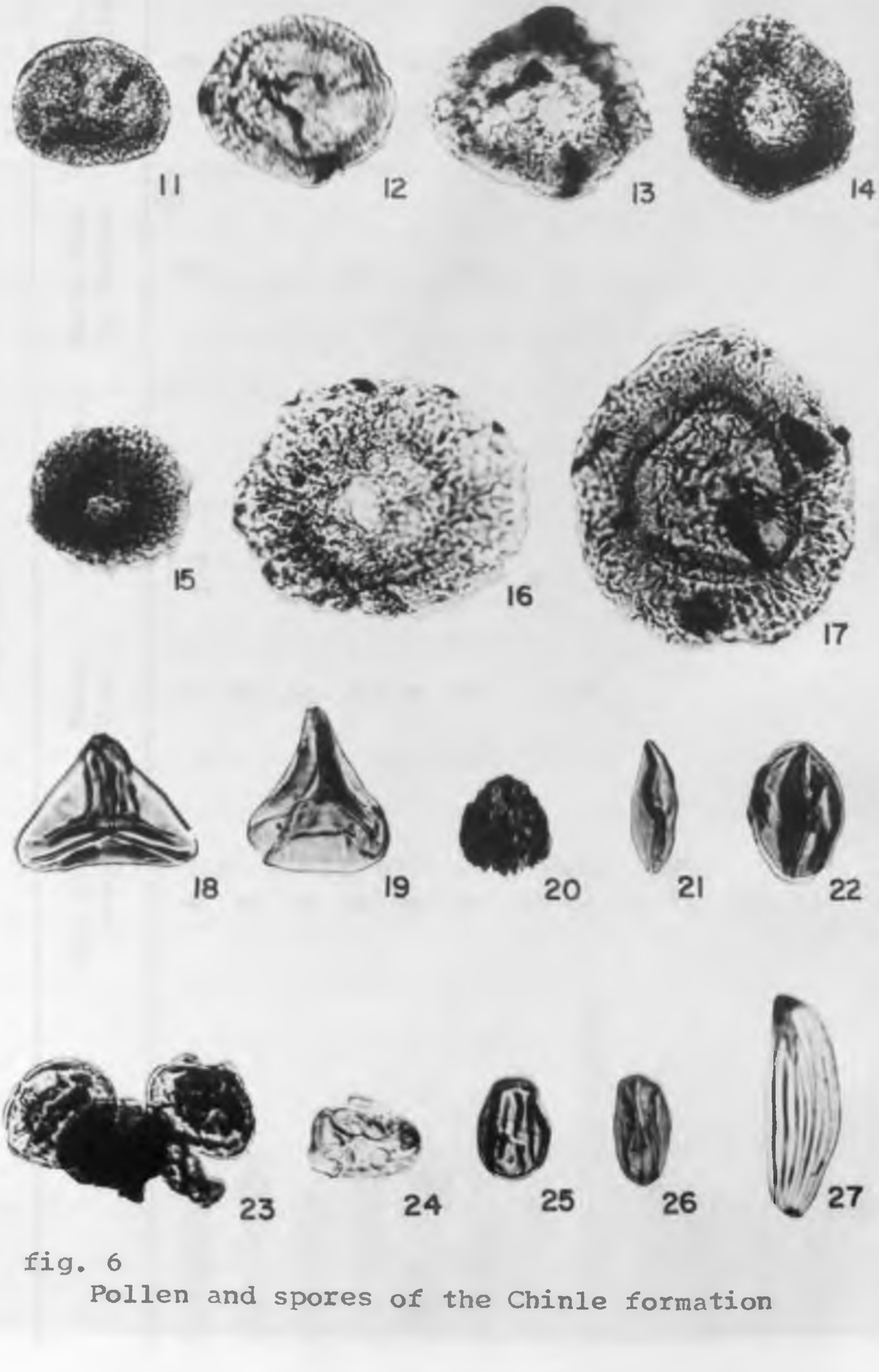

fig. 6
Pollen and spores of the Chinle formation

Table 2. Distribution of common Upper Triassic spores and pollen in the Southwest and North Carolina.

	Petrified Forest	Moab, Utah	Ft. Wingate, N. Mexico	Santa Rosa N. Mexico	Cumnock fm., N. Carolina
Klausipollenites	X	X	X	X	X
Vitreisporites	X	X			
Alisporites	X	X	X		X
Pityosporites	X	X	X	X	X
Zonalasporites	X	X	X		X
Patinasporites	X	X	X	X	X
Callialasporites (?)	X		X		X
Dictyophyllidites mortoni	X	X	X		X (?)
Verrucosisporites	X				X
Cycadopitys	X				X
Monosulcates	X				X
Camerosporites	X				

each of these floras contain species not found in the other, a conservative estimate is that at least 50% of the species of these two floras are the same or closely related.

The Chinle and Cumnock microfloras differ greatly from those of equivalent age in Europe, India, Australia, and South America. They are distinctive in the complete absence of striate disaccate pollen, the abundance and diversity of coniferous saccate forms and the relative scarcity of fern spores. These differences may be due to the differences in paleolatitude and climate. The composition of the Chinle microflora is consistent with a middle Keuper age for the lower Chinle as suggested by J. T. Gregory (1957).

Tepees Pollen Profiles

Two profiles have been collected and analyzed for pollen content. The Tepees I profile (Figure 7), 4.62 meters in length, was collected at the north end of the Tepees (Figure 10, number 1) (see Chapter 7) at 45 centimeter intervals. It is located at the edge of a former wide river channel the sediments of which can be seen in the foreground of Figure 10, number 1. The second Tepees profile (Figure 8) collected at 15 centimeters intervals about 100 yards south of the first profile at a corresponding distance from the river margin, is 9.3 meters in length. Correlation of the two pollen profiles show that 2.41 meters of sediment making up the middle part of the first Tepees profile, 1T2-1T9, are represented by .98 meters of sediment at the second Tepees profile, 2T5-2T3. Presumably this reflects a variable rate of sedimentation along the stream. The upper and lower

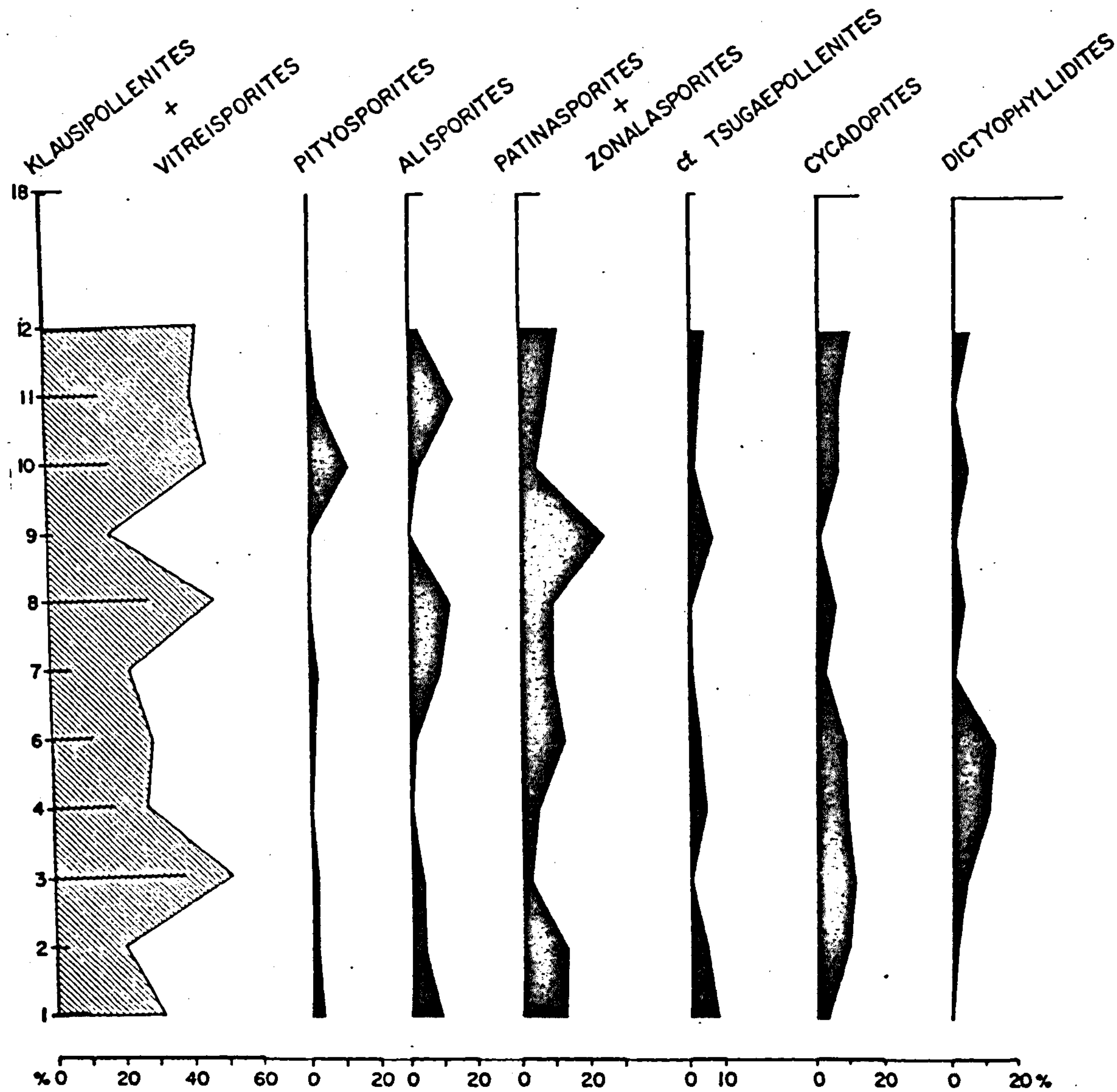

Figure 7. Tepees I profile, pollen and spore frequencies.

Samples 1-11 are separated by 45 cm., sample 12 is 90 cm. above sample 11.
Sample 18 is a typical stump soil pollen count from the Blue Forest stump field.

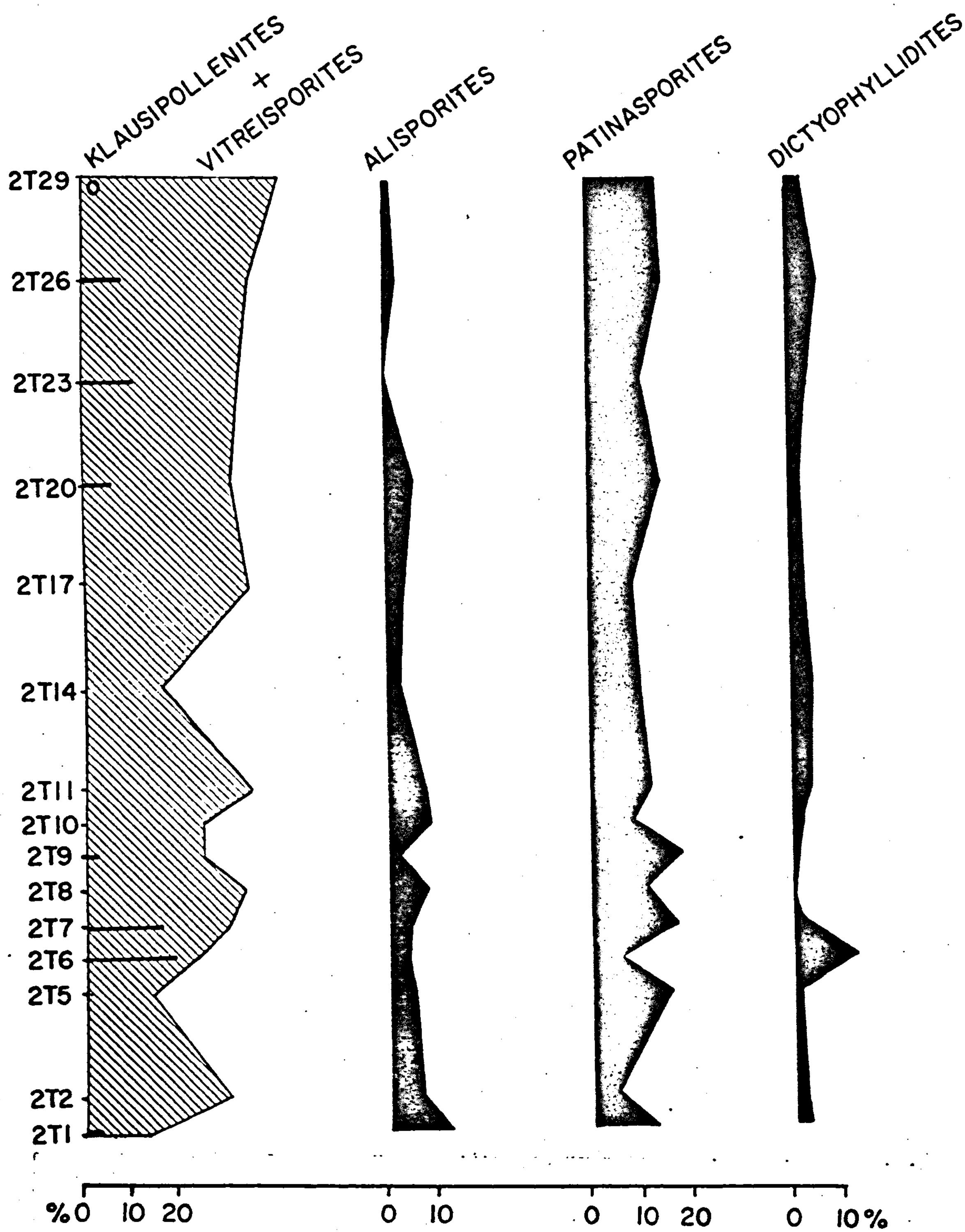

Figure 8. Tepees II profile.

Samples are separated by 15 or 45 cm., shown to scale. Horizontal lines are Vitreisporites subsum.

parts of the two profiles show approximately the same rate of sedimentation in both profiles. The sum of Klausipollenites and Vitreisporites pollen is shown in both profiles. The bars within this curve represent the Vitreisporites component. The proportion of Vitreisporites in some levels of the second Tepees profile was not recorded and consequently is not shown in Figure 8; Vitreisporites is not present in sample 2T29 or is present in low abundance. Each level represents a count of 100 grains. The significance of the fluctuations in pollen and spore frequency is discussed in the paleoecology section.

Palynological Notes

Several interesting pollen grains were found during the examination of the Chinle sediments. Figure 9, number 2, is a pollen grain of Pityosporites chinleana which contains within its central body ten cells with cell walls and indications of one or two additional cells. Seven of these ten cells are visible in plane of focus of Figure 9, number 2. Figure 9, number 1 is another pollen grain of the same species which has on the broken wall of the central body impressions of cells similar to those visible in the other specimen. These specimens are interpreted as fossilized microgametophytes. Extant conifers usually have from two to five cells in the microgametophyte, although Podocarpus, Dacrydium, and Phyllocladus have several additional prothallial cells and Araucaria has up to forty cells in the microgametophyte (Chamberlain 1935). None of the modern conifer microgametophytes have cell walls, such as those seen in these specimens of Pityosporites chinleana. Of about 100 grains of

Figure 9. <u>Pityosporites</u> microgametophyte and <u>Taeniaesporites</u>.

Number 1. <u>Pityosporites</u> <u>chinleana</u> with imprint of microgametophyte cells on ruptured central body.

Number 2. <u>Pityosporites</u> <u>chinleana</u> microgametophyte containing 10 cells with discrete cell walls. Seven of the 10 cells are visible at this focal plane.

Number 3. <u>Taeniaesporites</u> sp., a redeposited Upper Permian pollen grain.

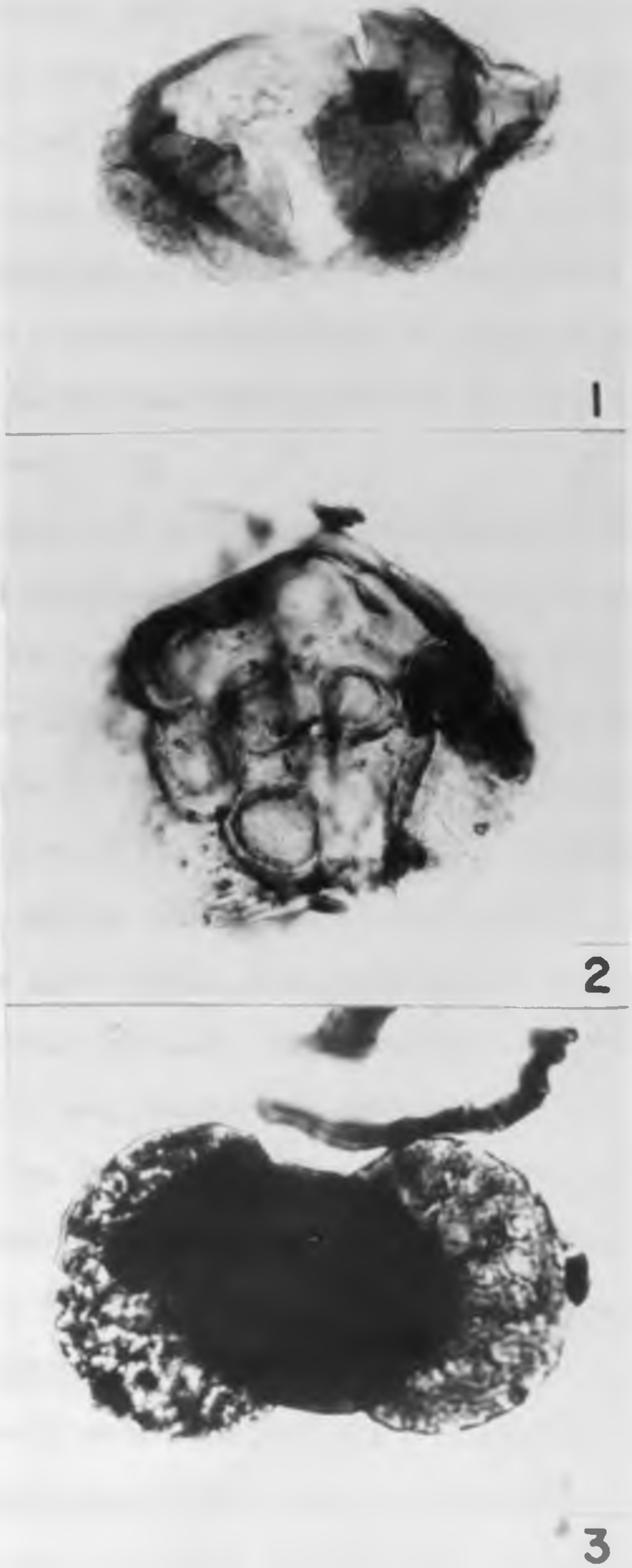

fig. 9. Pityosporites microgametophyte and Taeniaesporites

P. chinleana examined, only these two show traces of the microgametophyte. Figure 5, number 10, is a specimen of *P. chinleana* without any trace of internal cells. This is probably due to destruction of these cells before or soon after burial. About three per cent of the pollen grains of *Klausipollenites* also have preserved internal structures. Figure 5, number 3 is an example of one of these pollen grains. Figure 5, number 2 is the same species without the additional internal membrane preserved.

The existence of redeposited pollen in the Chinle formation is indicated by the occurrence of a single specimen of what is probably *Taeniaesporites* (Figure 9, number 3). The carbonized condition of this pollen grain makes certain identification impossible. This pollen grain is probably of Late Permian age, and indicates a Permian source area for some of the Chinle sediments. Invertebrate fossils of Late Permian age may be found in chert pebbles throughout the Chinle formation (McKee 1936; Bryant 1965), confirming the likelihood of a Permian age for this specimen. The carbonized condition of this pollen grain makes it very conspicuous when compared with the excellent preservation of the Chinle pollen and spores. I think it is unlikely that other redeposited Permian pollen grains were overlooked.

Figure 6, number 17, is a specimen of *Spencerites chinleana* of Daugherty. *Spencerites* (D. K. Scott 1897, 1898) is a genus of Paleozoic lycopodiaceous cones (Andrews 1952). Daugherty placed this pollen grain in *Spencerites* on the supposed resemblance to modern lycopod spores. It is most likely that this species is a coniferous pollen grain, of an undescribed genus. Among the described monosaccate pollen grains "*Spencerites*" *chinleana* is closest to *Callialasporites*. The two other pollen grains named by Daugherty, *Gnetaceapollenites chinleana* and *Alisporites opii*, have been discussed in the preceding pages.

CHAPTER 5

INVERTEBRATES OF THE CHINLE FORMATION

Invertebrate remains are surprisingly scarce in the Chinle formation. At the localities where mollusks are found they are usually poorly preserved, occurring as coarsely crystalline calcite casts or as incomplete silicified casts.

Pelecypods of the Chinle Formation

Three species of unionid fresh-water pelecypods have been described from Arizona. Reeside (1927) described *Diplodon gregoryi*, a small (13 mm. X 11 mm.) ribbed pelecypod from Beautiful Valley near Chinle, Arizona. This species is apparently not found in the Petrified Forest. In 1934 Henderson described *Unio thomasi* (Figure 4, number 4) and *U. arizonensis* (Figure 4, number 3) from material collected near Seven Springs in Apache County. *U. thomasi* is a rounded heavy-shelled form while *U. arizonensis*, also heavy-shelled, is elongate in outline, somewhat like the extant *Margaritifera*. These two species are found in great abundance above the Sonsela sandstone bed just east of Blue Mesa. Unios similar to *U. thomasi* are abundant in many outcrops in the Petrified Forest area of the Camp Wash zone of Roadifer (1966). The Camp Wash zone occurs about 90 feet above the Sonsela sandstone bed.

Gastropods of the Chinle Formation

Yen (1951) has described five species of fresh-water gastropods from chert casts which occur in the thin limestone beds of the Owl Rock member of the Chinle of northern Arizona. These include a species of "*Valvata*," three species of *Triasamnicola* and a species of *Lioplacodes*. Bryant (1965) and Roadifer (1966) report small gastropods weathering out of clay hills in Lithodendron Wash south of where it leaves the Painted Desert section of the Park.

Arthropods of the Chinle Formation

M. V. Walker, a former park naturalist at what was then the Petrified Forest National Monument discussed the occurrence of numerous fossil beetle galleries within the petrified wood of *Araucarioxylon arizonicum* (M. V. Walker 1938). He describes five species of larval beetle tunnels in three new genera. Walker divides these tunnels into two groups. Tunnels of group 1 were made by bark beetles boring just below the bark. For these galleries he erected *Paleobuprestis* and *Paleoscolytus*; these genera are named after their resemblance to galleries made by extant beetles of the families Buprestidae and Scolytidae respectively. Evidence of bark beetle activity is very abundant in logs found in the Black Forest area. Walker estimates that at one level in the Park 50% of the petrified logs show evidence of bark beetle activity. Borings of group 2 penetrate the heart wood of the attacked trees. Beetle tunnels of this group are place in *Paleoipidus* by Walker. These tunnels are less common than those of group 1. Two types of beetle tunnels from this group may be seen in

Figure 4, number 2, in a polished slab of _Araucarioxylon arizonicum_. The larger tunnels are probably _Paleoipidus perforatus_. The smaller tunnels are undescribed.

In 1944 K. E. Caster described a very interesting invertebrate track from the Newspaper sandstone bed near the Tepees in the Petrified Forest National Park. This track was made by an early horseshoe crab and was described as _Koupichnium arizonae_. The track is particularly valuable since the left side bears the flabellar imprint while the right side does not. This enabled Caster to show that what were previously thought to be two different types of vertebrate tracks were made by a single species of limuloid. The occurrence of this track suggests that during this interval of Chinle time the Petrified Forest area was not very distant from the sea, since _Koupichnium_ probably was a habitual inhabitant of salt or brackish water with only occasional individuals traveling upstream into fresh-water areas.

CHAPTER 6

VERTEBRATES OF THE CHINLE FORMATION

The vertebrate deposits of the Chinle formation in Arizona are among the best in the Triassic of North America. The study of these vertebrates has allowed the correlation of the lower Chinle formation with the Bunte Mergel, the middle part of the Keuper of Germany (J. T. Gregory 1957). Evidence from other groups of fossils in the Chinle agree with this age assignment.

Fishes of the Chinle Formation

Well-preserved fish fossils are scarce in the Chinle formation. However, teeth of the lungfish *Ceratodus* have been found at many localities in the Chinle including several in the Petrified Forest area (Schaeffer and Dunkle 1950). These teeth are apparently all from one species of *Ceratodus* (Branson and Mehl 1931).

Several species of semionotid holostean fishes have been described from the Chinle of southern Utah. These are *Lepidotes walcotti*, *Semionotus* cf. *gigas* and *Semionotus kanabensis*. These species of semionotids probably also occurred in the Chinle of Arizona. Colbert (1952) reports the presence of semionotid scales at the quarry of the "Ward Bone Bed" near Cameron at a level probably correlative with the Petrified Forest deposits.

Amphibians of the Chinle Formation

The predominantly Paleozoic labyrinthodont amphibians make their last appearance in North America in the Upper Triassic. Eight genera and fourteen species of metoposaurid stereospondylls have been described from North America. Colbert and Imbrie (1956) have re-examined the North American Upper Triassic metoposaurs and placed them all within two species of *Eupelor*. The Eastern Triassic forms are placed in *E. duras* while the Western Triassic forms are placed in *E. fraasi*. *Eupelor* was adapted to an aquatic existence. It had a weak vertebral column and had comparatively small feeble limbs. The skull roof was massive, heavily sculptured, and pierced only by the orbits, nostrils, and the pineal opening. The clavicle and interclavicle were similarly massive and ornamented by coalescing ridges. The resistant nature of the skull, clavicle and interclavicle are probably responsible for the abundant representation of *E. fraasi* in the vertebrate faunas of the Chinle.

Reptiles of the Chinle Formation

The reptiles are the most varied and often the most abundant element of the Chinle vertebrate fauna. The reptile fauna includes phytosaurs, desmatosuchids, ornithosuchids, saurichian dinosaurs and dicynodont therapsids. These are discussed below.

Phytosaurs

Seven species of phytosaurs, all in the genus *Machaeroprosupus*, have been described from the lower Chinle of Arizona (Case 1920; Mehl

1928; Camp 1930). Of these seven species, five were described by Camp (1930). Camp proposed these species in a study to demonstrate the stratigraphic usefulness of phytosaurs, although he recognized that these groups of specimens were probably not distinct enough to be called species. Three of the species were based on material collected in the Petrified Forest area. The five species of Camp, and _Machaeroprosopus validus_ of Mehl, are all found within the lower 400 feet of the Chinle formation. In a review of the phytosaurs of Arizona, Colbert (1947) concluded that these species "represent at least to a fairly large degree, a growth series within a chronocline that probably may best be considered as a single species." He also states that five of the species of _Machaeroprosopus_ together show more uniformity in skull pattern than is seen in an ontogenetic series of a single species of _Alligator_. According to Colbert, the only valid taxonomic difference between these species is the shape of the squamosal. Although Colbert stops short of assigning the seven species of Arizona phytosaurs to a single species, it seems that these species should be considered at most as subspecies with characters varying in a chronocline. I believe all the Arizona specimens can safely be place in _M. validus_ (Mehl, Taepelmann, and Schwartz 1916).

Desmatosuchids

A second group of alligator-like reptiles in the Chinle fauna were the pseudosuchian desmatosuchids (Camp 1934; Brady 1954, 1958). These are represented in Arizona by _Desmatosuchus_ and _Typothorax_.

These amphibious reptiles had a highly developed armor of large spines and heavy dermal plates. Desmatosuchus appears more advanced than Typothorax in that it has much more highly developed and larger spines (Sawin 1947). Desmatosuchus and Typothorax were probably swamp-dwellers. Their short jaws, and straight teeth suggest carrion feeding. Complete specimens of these genera (from the Dockum of Texas) are found among scattered remains of phytosaurs and metoposaurs, suggesting that they fed upon and scattered the bodies of the other vertebrates (Sawin 1947). Their heavy armor suggests a rather sedentary life. Desmatosuchian remains are rather scarce in Arizona. Usually only isolated horns are found (Brady 1954, 1958).

Other Reptiles

Another probable Triassic swamp-dweller was the dicynodont therapsid Placerias. Camp and Welles (1938) report the discovery of at least 34 individuals of Placerias in the lower Chinle near St. Johns, Arizona in what was probably a temporary pond. Placerias was a short-limbed heavy-bodied, rhinocerous sized reptile with greatly reduced dentition. Horny beaks apparently took the place of teeth. Camp and Welles (1956) suggest that Placerias fed on coarse fibrous plant tissues, most likely roots, rhizomes and tubers which it dug up with its recurved beak.

Two probable upland dwellers have been reported among the Chinle vertebrate fauna. These are the ornithosuchid pseudosuchian Hesperosuchus agilis, and the small saurichian dinosaur Coelophysis. Hesperosuchus is known from the "Ward Bone Bed" near Cameron. It was a 4-5 foot long, lightly built, predominantly bipedal reptile (Colbert 1952). The large mouth and sharp teeth suggest it was an active predator. Its adaptations toward bipedalism suggest it was an upland animal most at home on firm surfaces (Colbert 1952). Coelophysis, known from the vicinity of St. Johns (Camp 1934; Camp and Welles 1938), as well as from the upper Chinle of New Mexico (J. T. Gregory 1957), was six or eight feet long and similarly adapted for an active predatory life.

Concluding Remarks on the Arizona Vertebrate Fossils

In the Petrified Forest area abundant vertebrates are known from the Black Forest area and from a band of country stretching for several miles east and west of Blue Mesa. Reptile tracks have been found in the channel sandstones interbedded with the Tepees sediments (Caster 1944; Seff 1965). Although it is not known which of the previously mentioned species, if any, made these tracks, it is likely that they were made by species as yet unknown from skeletal remains. Although many small vertebrates must have existed during Chinle time, preservation of skeletal remains in the Chinle is exclusively limited to large vertebrates. The smallest vertebrate known is Hesperosuchus (Colbert 1952).

CHAPTER 7

PALEOECOLOGY OF THE CHINLE FORMATION

Upper Triassic redbeds of the Chinle formation cover a large area in Arizona, New Mexico, and Utah. Despite excellent exposures and an abundance of work on the paleontology little has been done to recreate the Triassic paleoecology of this area.

Most workers in the Chinle of Arizona have envisioned the Chinle formation as being deposited in a broad lowland, near sea level, interspersed with numerous streams and ponds. Daugherty (1941) characterized the Chinle vegetation as occurring in dense forests along the streams with open stands in the uplands. The cover of McKee et al. (1959) bears a reconstruction of the Chinle landscape of the Petrified Forest area. It features a low broad swamp of cycadophytes and ferns interspersed with scattered *Araucarioxylon*.

The climate of Chinle time has been assumed by most authors to have been semitropical or tropical. There is considerable diversity of opinion concerning the extent of aridity during this interval. Hinds (1937) and Daugherty (1941) believed there was evidence for a distinct dry season, but with sufficient rainfall for permanent streams in the lowlands. Earlier, Knowlton (1913) proposed that the Chinle climate was moist and warm. This idea has been recently supported by Ash (1967a, 1967b), mostly on the basis of leaf cuticular structure of the Chinle plants. He points out that the living relatives of the Chinle ferns now mostly inhabit humid tropical areas.

Daugherty (1941) and McKee et al. (1959), have pointed out that there is evidence for increasing aridity during the deposition of the Late Triassic sediments.

Work was begun by the writer in 1966 to attempt a paleoecologic reconstruction with the help of palynology, as part of the continuing program of study at The University of Arizona, on the history of the Chinle formation. The Blue Forest area, of the Petrified Forest National Park, just south of the Puerco River, is an exceptional area for paleoecologic studies. Within an area of a few square miles and in less than 100 feet of stratigraphic section a tremendous amount of fossil material may be found. Within this area numerous vertebrates, plant leaf fossils, <u>Araucarioxylon</u> stumps and other stem macrofossils, and excellently preserved pollen may be found. In addition the stratigraphy of these beds has been intensively studies by Seff (1965) and Roadifer (1966). Figure 1 is a map of the Petrified Forest National Park showing the principal fossil localities mentioned in this chapter.

Stratigraphic Evidence

Sediments of the Blue Forest area of the Petrified Forest consist almost entirely of the lower half of the Petrified Forest member of the Chinle formation. A composite stratigraphic section of the Blue Forest area, modified from Seff (1965) is given in Figure 2. These sediments are separated by erosional disconformities from the underlying Mesa Redondo member and the overlying Sonsela sandstone which marks the middle of the Petrified Forest member.

Six feet of calcareous siltstone (Neocalamites marl) underlies the massive Newspaper sandstone bed which forms a prominent scarp on the northern and western limits of the Blue Forest area. Overlying the Newspaper sandstone is a prominent bright red siltstone unit which in turn underlies a varicolored unit which contains numerous stumps and phytosaur fragments. The bright blue Blue Mesa siltstone unit of Seff (1965) is found at the top of the section underlying the coarsely crossbedded Sonsela sandstone unit.

Pith casts of Neocalamites (Figure 3, number 4), a large Triassic horsetail as much as 25 centimeters in diameter, occur in the coarser parts of the lower marly unit. These tree-size sphenopsids apparently grew in a swamp environment along the edge of a northward-flowing stream (Seff 1965).

The Newspaper sandstone bed was deposited by a wide stream meandering in a general northward direction. Meanders of this channel can be traced northward from the Tepees, a series of low conical hills (Figure 1). Along the edge of the Newspaper sandstone channel fine-grained bentonitic siltstone was deposited. In the foreground of Figure 10, number 1, blocks of the channel sandstone can be seen. The leaf containing sediments along the edge of the channel appear at the base of the hill in the midground. In these beds abundant well-preserved leaf fossils may be found. These plant fossils may be found in fine-grained sediments associated with the Newspaper sandstone for three and one-half miles along its course from Haystack Butte at the

Figure 10. The Tepees and the Blue Forest stump field.

Number 1. The Tepees locality from the north. In the foreground blocks of the channel sandstone may be seen, these grade into leaf bearing silts at the base of the hill.

Number 2. The Blue Forest stump field. In the midground a stump surrounded by soil remnants appears. Several other (less obvious) stumps each surrounded by a dark carbonaceous zone may be seen along the ridge behind the prominent stump. The Sonsela sandstone caps the ridge on the right skyline.

Number 3. A close up of one of the stumps at the east end of the stump field. Appearing in the photo are (left to right) the author, Park Naturalist Keith Trexler, and Assistant Park Naturalist Larry Henderson.

Photos by Terah L. Smiley

fig. 10
The Tepees and the Blue Forest Stump Field.

western edge of the Petrified Forest National Park to the Puerco River ruins just east of the present-day highway. These plants were apparently buried in place during floods which overtopped the channel in which the Newspaper sandstone was deposited, and probably provide an accurate sample of the vegetation growing along the margins of the lower Chinle streams. Sedimentation was apparently rapid in this streamside environment. Most of the plants at the Tepees locality are buried in growth position. Stems of Phlebopteris, the most common fern fossil at the Tepees locality, may be traced down 10-20 centimeters or more into the deposits enclosing them. Any bedding which may have been present in these floodplain deposits has been destroyed by the formation of bentonites from the original volcanic ash constituents of the sediment. Leaf macrofossils found in association with channel deposits and apparently representing a similar plant community are found in the Santa Rosa sandstone near Santa Rosa, New Mexico and in the Chinle formation near Thoreau and Fort Wingate, New Mexico (Ash 1966).

A large area of Araucarioxylon stumps in situ occupies most of the northwest quarter of section 23, T 18 N, R 24 E (outlined area in Blue Forest Figure 1). In this area hundreds of stumps are exposed in various states of preservation occurring as small groups scattered through about 20 feet of strata in the variegated siltstone below the Blue Mesa siltstone of Seff (1965). Stump fields of Araucarioxylon, in situ, occur in approximately the same stratigraphic position about ten miles north of Cameron and near the "Ward Bone Bed" along the Little Colorado River (Ward 1900). In 1936, M. V. Walker excavated one of the stumps in the Blue Forest and was able to confirm by tracing the roots that the tree was buried on the site where it is now found. Additional excavation of two other stumps by the author and T. L. Smiley in 1966 with the help of Park Service personnel confirmed this observation. Preserved around many of the stumps are patches of carbonaceous material representing the forest floor, above which the *Araucarioxylon* trees spread (Figure 10, numbers 1, 2).

Vertebrate fossils are found scattered through the section above the Newspaper sandstone bed usually associated with stratigraphic evidence of local ponding. These are composed almost entirely of phytosaurs and are concentrated in the Blue Mesa siltstone unit, in which many well-preserved skulls have been collected (Colbert 1947).

Abundant well-preserved pollen is found through much of the section in the Blue Forest (Figure 2, solid bars). The pollen and spores are present in deposits where they have been protected from intensive postdepositional oxidation. Pollen and spores occur continuously throughout 22 feet of deposit at the Tepees, where rapid deposition has apparently protected them from oxidation. Pollen and spores also occur in the soil remnants surrounding the *Araucarioxylon* stumps, and in the carbonaceous trash found in the base of stream fills in the Sonsela sandstone bed and at several horizons in the Black Forest area.

The pollen profiles taken at the Tepees at 45 and 15 centimeter intervals show considerable short term changes in pollen and spore frequencies. One of these profiles is shown in simplified form in Figure 7. It is likely that these changes in pollen and spore frequency are primarily due to sorting in the fine-grained sediments at the Tepees. To quantify this relationship, silt size analyses were performed on the sediments of the Tepees 1 profile. In order to compare the settling velocity of pollen and spores with that of silt particles we must know the size of the pollen and spores and their specific gravity. If a spherical shape is assumed for these palynomorphs, Stokes law may be used to predict the settling velocities.

Densities derived from data from Dyakowska (1937) and Dyakowska and Zurzycki (1959) give pollen densities for fresh dry pollen of from about 0.5 to 1.0; fresh pollen in equilibrium with water has a density considerably higher. Harrington and Metzger (1963) report a density of 1.28 for Ambrosia pollen in equilibrium with water. Common pollen and spore species in the Chinle assemblage range in size from about 20u to 170u. Funkhouser and Evitt (1959) report specific gravity for organic particles as ranging from 1.3 to 1.7. A value of 1.3 for fresh pollen in equilibrium with water seems most probable and this value has been used to compare pollen sorting with sediment particle sorting in the Chinle sediments. Using this value and assuming a sediment particle density of 2.65, pollen from 18µ to 37µ is equivalent in settling velocity to silt particles from 8µ to 16µ (7 ø to 6 ø); pollen from 37µ to 73µ equivalent to silt from 16µ to 31µ (6 ø to 5 ø); and pollen and spores from 73µ to 146µ is equivalent to silt from 31µ to 63µ (5 ø to 4 ø).

The species of pollen and spores from the Tepees I profile have been assigned to these three size classes. Changes in frequency of these pollen and spore size classes have been compared with changes in frequency of silt size particles of equivalent settling velocity. Correlation values for these comparisons are r=.42 for the large pollen vs. silt of 4 ∅ to 5 ∅, r=.73 for medium pollen and spores vs. silt of 5 ∅ to 6 ∅, and r=.61 for small pollen and spores vs. silt of 6 ∅ to 7 ∅.

Correlation values as high as .73 are surprising since the pollen grains are not all spherical, presumably had varying densities, the size classes used for the comparison are so large, and some pollen and spores were likely clumped at the time of deposition. Furthermore, some of the sediment now represented by bentonite was probably volcanic ash of silt size at the time of deposition (Allen 1930).

These high correlation values indicate that as much as 50% of the variation observed in these pollen profiles may be due to sorting alone. Other factors which probably contribute to the variation observed are climatic and edaphic changes and successional changes due to flooding and channel shifting of the Chinle streams.

The Flood-plain Swamp Community

The first vegetation community to be discussed here was composed predominantly of low-growing ferns and bennettitaleans growing along the streams, which probably formed extensive swamps that crossed the great Chinle lowlands. An excellent sample of the community is preserved in the deposits at the Tepees along the road which traverses the National Park from north to south. The extensive leaf deposits at this locality show every evidence of being preserved at or very close to the point where the plants grew (Ash 1966). The leaves are excellently preserved and can usually be removed from the rock that encloses them, allowing a microscopic study of the leaf cuticles. The fronds and leaves are usually complete and show no damage suggestive of transport. They are usually found extending up through the sediment surrounding them. Figure 3, number 1, is a prepared leaf of the fern Plebopteris smithii. Here the pinnae can be seen spreading from the ventral stalk and extending upward through the surrounding siltstone in what is probably the natural growing position. Similar evidence of rapid burial of plants in their normal position of growth may be seen at Walker's Standing Stump in the Flattops area of the Park.

The flood-plain swamp community was apparently dominated by a single species of bennettitalean, Otozamites powelli (Figure 3, number 3) and by the ferns Phlebopteris smithii, Clathopteris walkeri, and Todites fragilis. Of the specimens examined from this locality it appears that Phlebopteris smithii (Figure 3, numbers 1, 2) was the most common species, followed by Otozamites powelli. At other localities in the Upper Triassic of the Southwest where leaf macrofossils have been found along with sedimentary structures indicative of stream or streamside deposition Otozamites powelli or a similar species is almost always the most common element.

Occasional conifer needles may be found at the Tepees locality, especially in beds overlying the principal fossil horizon. These usually occur as isolated needles, suggesting transport from another community. The occurrence of excellently preserved ferns and bennettitalean leaf fossils at localities such as the Tepees stand in marked contrast to the occurrences of abundant, but poorly preserved, coniferous needles at other localities. Abundant coniferous needles associated with cone scales and seeds may be found at the base of the *Araucarioxylon* tree preserved at Walker's Standing Stump, in the soil zone surrounding the stumps in the Blue Forest, and in association with numerous small twigs in the Black Forest area of the Park. At these three localities the coniferous needles are associated with *Araucarioxylon* trunks or branches and are representative of the surface litter from the *Araucarioxylon* forest to be discussed later. This community and perhaps the upland community provide a likely source for the occasional coniferous fossils found at the Tepees.

Assuming that the vegetation represented by the Tepees macrofossils is in place or buried near its site of growth and that most of the plant species have survived as fossils, it is surprising to find that a high proportion of the pollen and spores enclosed in the sediment cannot be derived from plants known from macrofossils. Most of the extra pollen types are monosaccate or disaccate and derived from gymnospermous plants, mostly conifers. These "foreign" pollen and spores amount to 60% to 70% of the pollen assemblage. Examination of the unsorted sediments in the soil zones of the Blue Forest stump field allow a more accurate estimation of the source of these "foreign" pollen types.

Some of the pollen and spores in the Tepees sediments may have come from a considerable distance along with the sediment load of the Chinle streams. Cross, Thompson and Zaitzeff's (1966) study of pollen deposition in the Gulf of California show concentrations of montane pollen types on the submarine deltas of rivers in the east side of the Gulf which have clearly been brought up to 400 kilometers downstream from their source areas. However, this was probably not the case in the Petrified Forest area in Chinle time. The pollen spectra of the Tepees sediments and of the unsorted stump soils is similar, and both contain the same species. This suggests that if some of the pollen and spores originated in distant sites, the vegetation in the source areas was similar to that of the Petrified Forest area.

A reconstruction of the flood-plain swamp community is shown in Figure 11. Two large Neocalamites virginiensis may be seen growing along the edge of a large stream and on sand bars in the stream in a position similar to that in which they are found preserved about one-half mile west of the Tepees locality. In the right background are two Schilderia trees growing at the edge of the stream. These interesting trees, which have a microscopic wood structure indicative of a relationship to the Gnetales (Daugherty 1941) had swollen fluted bases similar to that of the modern bald cypress, Taxodium distichum. By analogy to the living Taxodium these swollen bases probably were an adaptation for growth in soft-bottomed swamps. The broad swamp itself is composed of Otozamites and several species of ferns. In the left background may be seen the edge of the Araucarioxylon forest which comprises the second community, to be discussed below (page 63). Large fish-eating Phytosaurs (Machaeroprosopus sp.) were abundant in the swamp community. Metoposaurs, large amphibians with weak legs, also occupied this community as did several species of semionotid fishes.

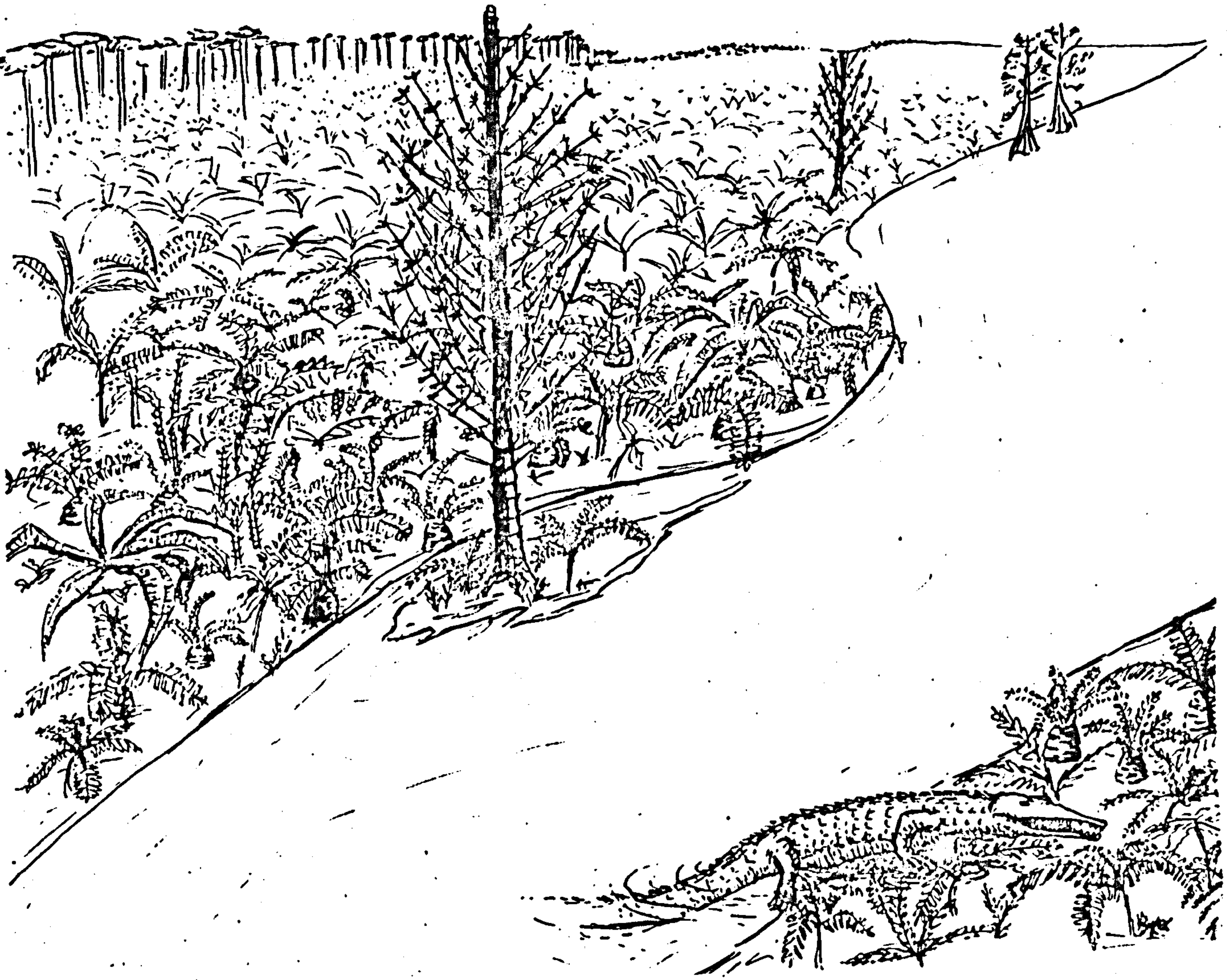

Figure 11. Reconstruction of the flood-plain community.

The rhinoceros sized dicynodont reptile, _Placerias gigas_, was a conspicuous herbivore of the community and lived by digging up roots and rhizones with its enlarged curved beak (Camp and Welles 1956). At least two species of the pelecypod _Unio_ probably lived in the bed of streams crossing this community. Occasional horseshoe crabs (_Paleolimulus_) found their way this far upstream from their usual estuarine habitat. Upland reptiles such as the small dinosaur _Coelophysis_ made their way down to the waters edge to drink, occasionally leaving their tracks to be preserved on the banks of the stream.

Organisms living in the flood-plain swamp community were the most likely to be preserved as fossils owing to the extremely favorable paleogeographic setting. Floods were probably common, as evidenced by the numerous log jams of the petrified trees preserved throughout the area of Chinle deposition. Ash falls from volcanoes far distant to the south contributed to the severity of the floods forming slurries even more conducive to fossilization.

If the climate of Chinle time was prevailingly or seasonally dry the organisms in this community need not show xeromorphic adaptations since they were living in an unusually wet microenvironment.

The _Araucarioxylon_ Forest

This community was composed of a dense forest of _Araucarioxylon arizonicum_, the common petrified wood throughout the area of exposure of the Chinle formation. Well-preserved trunks of _Araucarioxylon_ show that branches were usually restricted to the tops of the trees which were often 150 to 200 feet high. This suggests that these trees usually grew in dense stands in which shading by neighboring trees caused a suppression of branch growth further down on the trunk. This supposition is supported by the occurrence of groups of stumps in place at the same horizon in the Blue Forest area. Here, stumps four and five feet in diameter may be found which grew only ten to fifteen feet apart. This would seem to assure a dense closed canopy, composed of small-crowned forest with the forest floor in dense shade. The overall effect was probably much like that of the modern forests of Coast Redwood (*Sequoia sempervirens*) along the Pacific Coast. The *Araucarioxylon* forest reconstruction differs from that of McKee et al. (1959) in which the *Araucarioxylon* trees are pictured as being widely spaced but self-pruning nevertheless.

The forest community appears to have been almost a pure stand of *Araucarioxylon*. Of the several hundred stumps preserved in the Blue Forest area only three have been found that appear to belong to another species. These occur at the northwest edge of the stump field. Unfortunately the preservation of these stumps is too poor to permit the wood to be identified.

Six soil samples from soil remnants surrounding the stumps in the Blue Forest stump field have been examined for pollen and spore content. These samples are from four stumps. Three of the samples are from different levels in the soil zone around a single stump (4-22, 4-27, 4-30). A typical stump soil pollen count is given as sample 18 at the top of Figure 7. The six pollen and spore counts are given in Table 3.

Table 3. Abundance in per cent of the principal pollen and spore genera in six samples from the Blue Forest stump field.

Each sample is 100 grains.

	Stump 3 (# 18)	1-6	4-30	4-27	4-22	Stump 2
Klausipollenites	7	22	7	7	13	-
Vitreisporites	2	13	3	2	4	-
Pityosporites	3	14	10	6	8	-
Alisporites	5	2	4	5	8	-
Patinasporites	7	8	19	6	8	1
Zonalasporites	0	1	0	0	2	-
Cycadopitys	13	4	10	17	12	99
Dictyophyllidites	33	15	17	27	21	-
Minutosaccus	?	7	5	18	10	-

The stump soil samples are presumably unsorted, unlike those of the Tepees profiles. They occur in organic rich soils which originated subaerially. It is to be expected that in this closed canopy forest local pollen producers (understory vegetation and trees) be overrepresented because of the decreased wind velocity in the forest. Furthermore, outside pollen tends to bypass the forest area. If a pollen type is much more abundant in the forest soils than in the open area sediments, as represented by the Tepees deposits, we may presume that it is a member of the forest community.

The determination of which pollen and spore types belong to the forest community is complicated by the sorting that has occurred at the Tepees deposit. However, the Tepees sediments are not very well sorted with respect to pollen and spores and consequently the greatest effect should be on the frequencies of pollen and spore types rather than the elimination of some types altogether. Sorting at the Tepees has apparently been acting against large size pollen. *Alisporites opii*, the most common species of large pollen grain in the Chinle assemblage, comprises 5.2% of the assemblage at the Tepees (26 samples) and 5.4% in the stump soils (5 samples). *Alisporites* is probably derived from outside both of these communities. The effect of the closed canopy reduces the abundance of *Alisporites* at the stumps. At the Tepees sorting against large pollen grains also decreases *Alisporites* abundance. The net effect in these two communities is apparently approximately equal.

Comparison of the stump soil samples with the Tepees deposit show several significant differences in pollen abundance. Among the small pollen types, Vitreisporites and Klausipollenites are about three times as abundant in the Tepees sediments as in the Araucarioxylon forest deposits (29.8%, 26 samples at the Tepees, 11.2%, 5 samples from the stump soils). Sorting seems to have enriched this class of pollen and spores, while the closed canopy decreased the abundance of these forms in the soils. A relative enrichment of times three of Vitreisporites and Klausipollenites in the open area is the result. However, Patinasporites and Zonalasporites of similar size to Klausipollenites occur in a joint frequency of 10.9% in 26 samples at the Tepees and 10.2% in 5 samples from the soil zones.

The fern spore Dictyophyllidites mortoni is six times as abundant in the soils as in the Tepees deposits (22.7% in 5 soil samples, 3.8% in 26 Tepees samples), despite the apparent sorting of the Tepees sediments for spores of this size. Therefore I conclude, that the fern producing this spore was present as an understory element in the forest community. Spores of D. mortoni have been found in sporangia of the European Triassic fern Phlebopteris polypodioides (Lundblad 1950; Potonie 1962). A species of Phlebopteris similar to P. polypodioides has been reported from New Mexico as P. sp. (Ash 1966), and this is a possible source for the Dictyophyllidites mortoni spores. A similar but smaller species of Dictyophyllidites occurs with greater frequency at the Tepees and is probably the spore of P. smithii. The fern Thaumatopteris has spores similar to those of Phlebopteris and is a possible source for the D. mortoni spores. Thaumatopteris is known from the Upper Triassic of Mexico, both in Sonora and in Hidalgo (Silva Pineda 1961, 1963).

Several other pollen and spore types, because of their greater abundance in the stump soils, may be considered components of the Araucarioxylon forest community. These include a fern with a simple small psilate monolete spore (Laevigatosporites sp.) which occurs in a frequency of less than ½% in 11 samples at the Tepees but occurs in a frequency of 5% in one of the soil samples. This might have been one of the minor understory species in the Araucarioxylon forest.

The small disaccate pollen grain Minutosaccus sp. is rare in the Tepees samples occurring in frequencies of less than 1%. In the soils it occurs in a frequency of 9.8%, indicating that this is another candidate for inclusion in the forest community. This is the only coniferous pollen type which is noticeably more abundant in the soils, raising the question as to whether it is the pollen of Araucarioxylon arizonicum. A decision cannot be made on the basis of this evidence alone.

The living Populus (poplar and aspen) produces extremely abundant pollen, but it is soon destroyed on burial. In atmospheric samples from Manitoba deciduous upland forests Populus pollen accounts for 28% to 57% of the total, in sediment samples from the same region Populus pollen ranges in abundance from 0.8% to 1.6% (Lichti-Federovich and Ritchie 1965). Among the conifers Chamaecyparis thyoides pollen also appears not to be preserved. Larix decidua has pollen that is preserved in sedimentary deposits but produces very little pollen so that in Larix swamps low frequencies of Larix pollen are found. By analogy, pollen of A. arizonicum might not be readily preserved or might be produced in low abundance thus accounting for its absence in the soils.

No pollen similar to that of the living Araucaria has been found in the Chinle formation, even though Araucaria type pollen is generally preserved in fossil deposits. Araucaria type pollen is known from the Cretaceous and Tertiary of North America.

Small simple Cycadopitys pollen grains, likely derived from several species of bennettitites, occur in a frequency of 4.6% in 11 samples of the Tepees sediments, and in a frequency of 11.2% in 5 samples from the Araucarioxylon forest, despite the sorting for small size pollen at the Tepees. Furthermore one of the soil samples contains thousands of pollen grains of one species of Cycadopitys. The most likely explanation for this occurrence is that the pollen sample extracted contained a bennettitite microsporophyll, thus establishing that at least one bennettitite was a member of the Araucarioxylon community.

A reconstruction of the Araucarioxylon forest is shown in Figure 12. The ferns growing as an understory are not drawn to scale and are meant to be diagrammatic only.

Sedimentation in the Blue Forest stump field was apparently slow enough to allow the continuous existence of the forest while about 20 feet of sediment was deposited, but rapid enough to allow burial of the bases of some trees and their mineralization before they had completely rotted. As would be expected only the largest roots escaped decay, and were mineralized. Most of the roots are now represented only by carbonized wood and limonite accumulations.

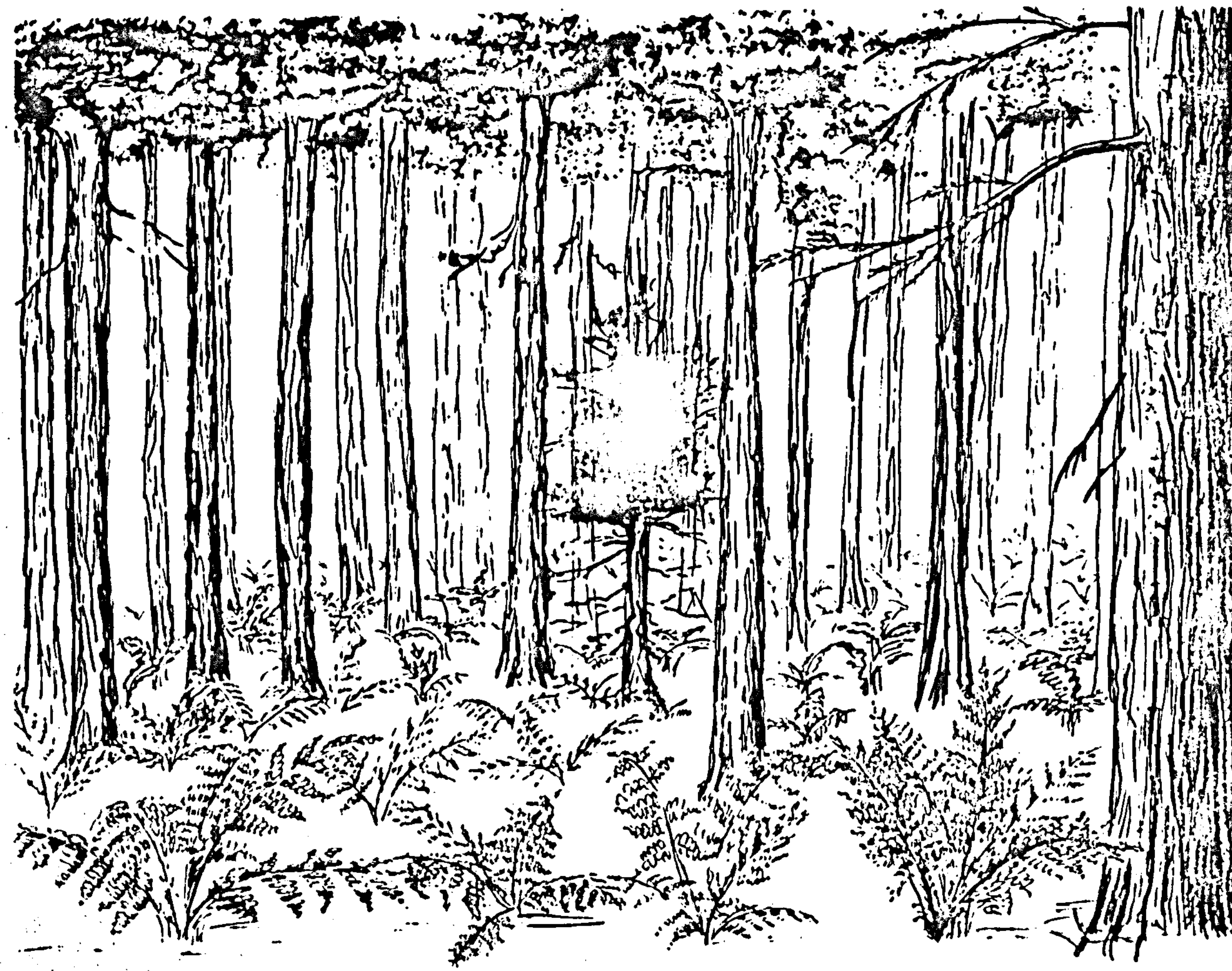

Figure 12. Reconstruction of the *Araucarioxylon* community.

The *Araucarioxylon* forest community is believed to have occurred on the flood plain but in more stable locations than the previous community. Stability is indicated by the size which the trees reached which on the basis of poorly preserved tree rings must have been several hundred years old. The sediments surrounding stumps at several other localities also indicate a lowland habitat. A location on the flood plain is also indicated by the great abundance of petrified wood. Occasionally the rivers of Chinle time changed course and cut through the forests undercutting large numbers of trees which were carried downstream to form the spectacular log jams which are found in some of the sandstones in the Petrified Forest. If the climate of Chinle time was arid or semi-arid the occurrence of dense forests would be limited to lowlands, especially flood plains where a permanent supply of water can be reached by the roots of the trees.

It is likely that few large vertebrates inhabited the interior of the *Araucarioxylon* forest because the densely shaded ground level provided little food. They may have used the forests when seeking shade or shelter. The trees may have been inhabited by small reptiles feeding on the insects that themselves used the trees for food. M. V. Walker (1938) has described five species of bark beetles whose burrows are distinctive, and strikingly like modern beetle tunnels. In addition I have seen representatives of at least two undescribed forms of insect tunnels. John Matthews, at The University of Alberta, has attempted unsuccessfully to find insect remains in the soils surrounding the *Araucarioxylon* stumps.

Araucarioxylon was parasitized by at least one species of fungus. Daugherty (1941) has described a pecky heart rot of Araucarioxylon as Polyporites wardii. The other species of fungus Daugherty describes is Rhizophidites triassicus, which he thought was parasitic on a pollen grain of Alisporites. Its true nature is problematic.

The Upland Gymnospermous Community

"Only rarely can insight be gained from (plant) macrofossils regarding the forests that lived in the uplands" (Chaney 1964). Because of their small size and great dispersal ability pollen and spores may be brought to the sites of deposition from a wide range of habitats and elevations. Consequently speculation on the existence and character of upland communities (if any) must be based in large part on the micropaleobotanical record.

Sediments deposited around vegetation of the two lowland communities contain a great diversity of pollen and spore types numbering over 100 species. A reasonably complete inventory of the species of these two communities can be expected because of the exceptionally favorable chances of fossilization. But even a generous count of the number of higher plant macrofossil species in the Petrified Forest is less than 40 (Daugherty 1941, 27 sp.; Ash 1966, 35 sp.). The absence in lowland sediments of macroscopic plant remains of species whose existence can be inferred from the pollen record, suggests their occurrence on adjacent upland sites. The abundant pollen types with no macrofossil equivalents are predominantly monosaccate and disaccate, and are likely derived from conifers, cordaitaleans and caytonialeans. To account for these species a diverse upland gymnosperm community is hypothesized.

The samples from the stump soils have been analyzed for the derivation of the various species of pollen and spores which occur within them in an attempt to quantify the importance of these three communities as pollen and spore sources in Chinle time. The assumption is made that all of the spores from ferns and pollen grains from cycadalean and bennettitalean plants are from the flood-plain swamp community except for Dictyophyllidites mortoni, Laevigatosporites sp. and 1/3 of the small Cycadopitys pollen grains, these three types being assigned to the Araucarioxylon forest. These assignments are predicated on the assumption that we have a realistic appraisal of the composition of the flood-plain swamp community. Those pollen types assigned to the Araucarioxylon forest in the previous section are included in the Araucarioxylon forest total.

This analysis gives a contribution to the forest pollen rain of from 3% to 16% (5 samples, $\bar{X}$=10.4%) from the flood-plain swamp community. The contribution of pollen and spores from plants assumed to be living within the forest community is from 26% to 56% (5 samples, $\bar{X}$=41.6%). Pollen presumably from neither of these two communities are principally gymnospermous pollen types, the largest contributors being Klausipollenites, Vitreisporites, Alisporites, Patinasporites, Zonalasporites, and Pityosporites. These make up from 26% to 68% (5 samples, $\bar{X}$=46.2%) of the forest pollen rain.

Thus on the average in the soils, which are presumably unsorted, about half the pollen may be coming from upland communities. At the Tepees where the pollen and spores have been sorted, and no closed canopy affects pollen fallout, gymnospermous pollen types are present in higher percentages ranging up nearly to 70%.

A contribution of foreign pollen of nearly 50% would seem to require a nearby source. The surface sediments of Willcox Playa of southeastern Arizona which is barren of vegetation, and hence has no local pollen contribution contain 5% to 20% Pinus pollen which has its nearest source area 10 to 15 miles away (Martin 1963). From this I conclude that if even half the pollen assigned to the upland community in the Blue Forest area is correctly assigned to it, communities of this upland aspect were probably within 10 miles of the site of deposition. These "upland" sites need not be much above base level, just as long as the plants growing there are out of reach of the water table. Perhaps a relief of 20 to 20 feet is required, a condition which seems possible considering the extremely variable sedimentation and erosion of the Petrified Forest member.

A reconstruction of this upland community is given in Figure 13. Included in this community are one or more species of ginkophytes which are shown at the left border and in the middle of the reconstruction, several species of conifers with varying growth forms, a cordaitalean such as Dadoxylon known from two specimens in the Petrified Forest, and Sagenopteris whose pollen Vitreisporites pallidus is common but which is not known from macrofossils in the Chinle although it has been found in the Triassic of Mexico and in the Newark

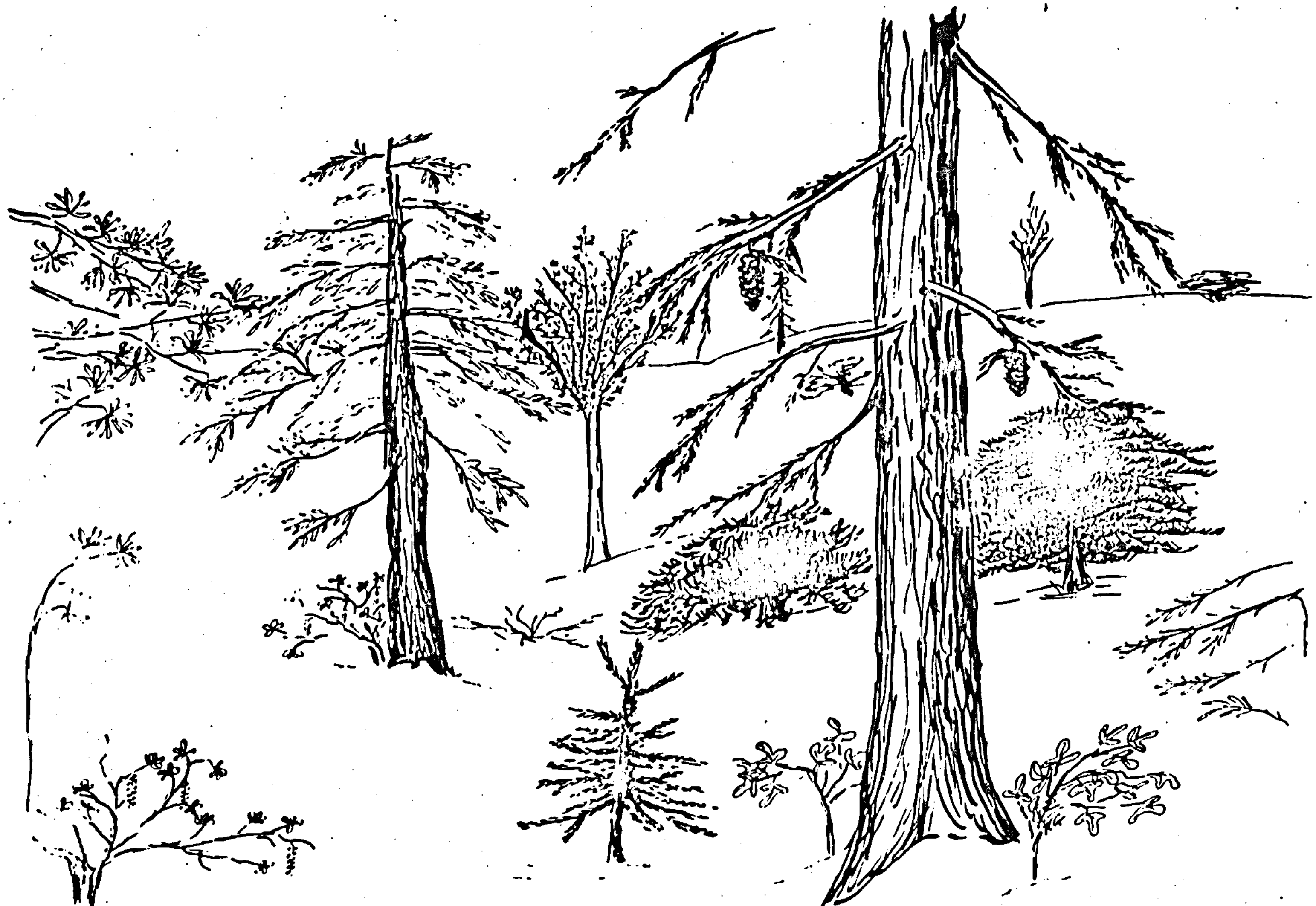

Figure 13. Reconstruction of the upland community.

series of the east. This community is assumed to be open, perhaps with many shrubby species because of the assumed aridity of Chinle times. Evidence for this aridity is discussed in the next section of this paper. This community was probably inhabited by a variety of small and medium sized reptiles. Hesperosuchus is a good candidate for a habitual inhabitant of this community. Colbert (1952,p566) says "the adaptations of this pseudosuchian indicate that it was primarily an 'upland' animal, living on firm, dry ground." The primitive dinosaur Coelophysis which is found in slightly younger beds of the Petrified Forest member is another possible inhabitant of this community, as are other Upper Triassic reptiles the remains of which may be expected but have not yet been discovered.

A diagram of the relationships of the three Chinle communities is given in Figure 14. To the left is the flood-plain swamp community, along the stream. An Araucarioxylon forest occupies a moist but better drained and more stable site. The hypothesized upland community is shown on the right. These communities did not necessarily occur in as neatly a spatial arrangement as illustrated in the diagram. They probably occurred in a shifting mosaic with the first two communities being especially intimately related. At the Walker's Standing Stump locality Otozamites apparently grew after the base of an Araucarioxylon was buried and the tree presumably dead (M. V. Walker 1938).

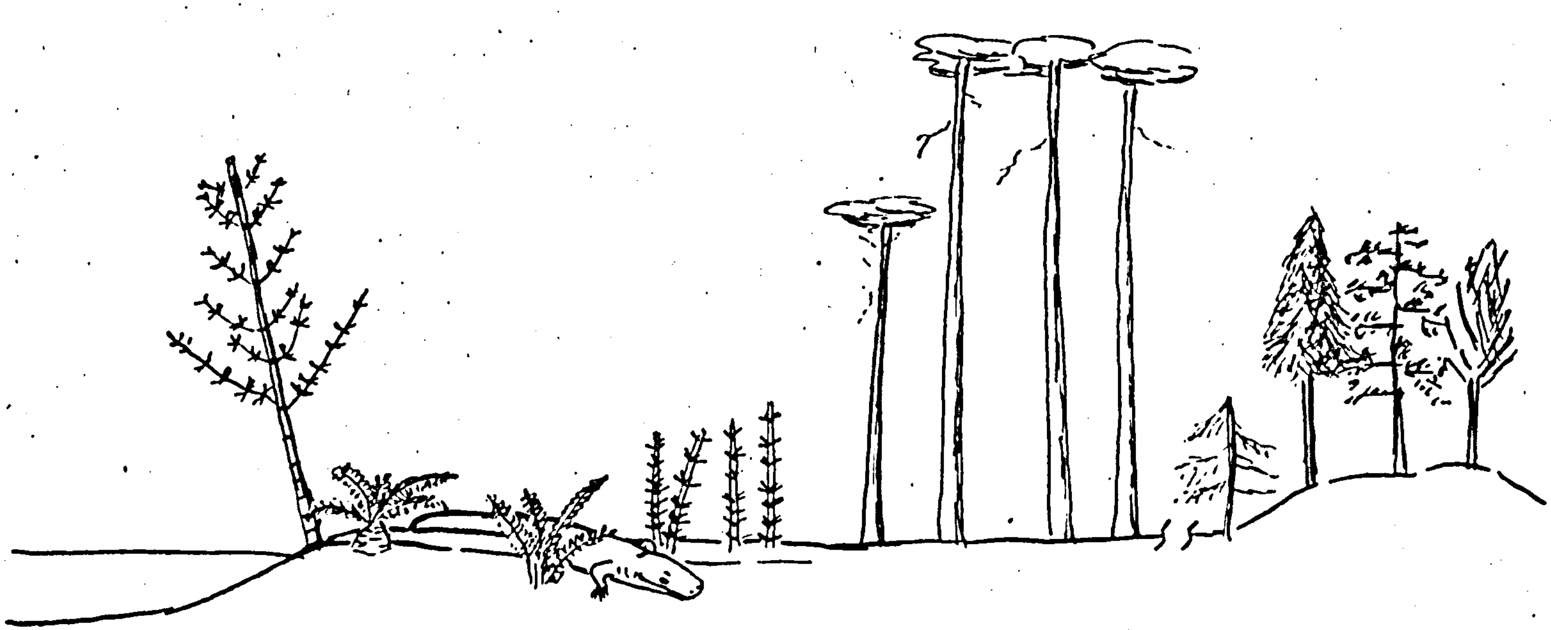

Figure 14. Diagram of the relationship of the three Chinle plant communities.

The Climate of Chinle Time

Evidence from paleomagnetism indicates a latitude of about $16^{\underline{o}}$ 18^{o} North for the Petrified Forest in the Triassic (Dubois 1964, Figure 5; Irving 1964). If this is assumed, the Chinle lowland climate can hardly have been anything else than hot. The large number of species in the pollen flora is another indication of a tropical climate, since the number of species of many groups increase as one goes toward the equator (Wimpenny 1941; Fischer 1960). The large reptiles and amphibians of the Chinle fauna are evidence of a mild climate at least.

The remaining question of whether the climate was moist or arid is more difficult to decide. The abundance of water-inhabiting vertebrates and of lush swamp vegetation is not necessarily an indication of a moist climate. Through-flowing streams from the mountainous area to the south could supply the water to an arid or semi-arid lowland.

There is abundant evidence of volcanism in the Upper Triassic of southeastern Arizona. In the Santa Rita Mountains there are over 10,000 feet of Triassic extrusives (Hayes and Drewes 1968) which indicate the likelihood of high mountains and give a possible source area for the bentonites of the Chinle formation.

In many parts of the central part of the Black Mesa Basin the Chinle formation grades upward into the Wingate formation, also of Upper Triassic age without an apparent depositional hiatus (Akers, Cooley, and Repenning 1958). The Wingate formation contains great quantities of coarsely cross-bedded sandstone of aeolean (dune) origin.

Underlying the Chinle formation is the Moencopi formation of Early Triassic age which contains an abundance of evaporite beds. With this geologic framework it would be surprising if the climate of the Chinle formation were anything but dry.

The *Placerias* quarry near St. Johns, Arizona located in the lower Chinle contains a Triassic pond filled with sedimentary gypsum (Camp and Welles 1956), a strong indication of at least a seasonally arid climate. The abundance of redbeds in the Chinle formation is also indicative of an arid climate. The red color of the Chinle sediments probably originated *in situ*, in a manner similar to that proposed by T. R. Walker (1967). The presence of abundant silification, to which we owe the magnificent Petrified Forest, is usually an indication of a dry climate (Schwartzbach 1963, p. 65). Perhaps the climate of the Chinle time was seasonal with an extended dry season.

The abundance of thick walled pollen in the Chinle formation may be an indication of low atmospheric moisture. Growth rings in *Araucarioxylon* are poorly defined, a character which immediately separates this wood from the younger petrified woods of Arizona. The lack of pronounced growth rings in *Araucarioxylon arizonicum* is not necessarily due to the lack of variability of climate. Many modern tropical angiosperms do not have a visible growth response to the alternation of dry and wet seasons. Modern *Araucarias* from temperate areas with marked seasonality do not show growth rings in any environment (Antevs 1954). Similarly, *Araucarioxylon* may not have had a clear growth response to seasonal changes. *Araucarioxylon* grew in lowland areas where it was probably in reach of the water table, which would tend to minimize water stress in the dry season.

It appears that the increase in red beds as one goes up in the Chinle section, and the rapid decrease in occurrence of vertebrate and plant fossils resulted from an increasing aridity culminating in the aeolean regime of the Wingate landscape.

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