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THE UNIVERSITY OF ALBERTA

STRUCTURALLY PRESERVED *METASEQUOIA* FROM THE MIDDLE EOCENE OF SOUTHERN BRITISH COLUMBIA, CANADA

by

JAMES FREDERICK BASINGER

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Structurally Preserved Metasequoia from the Middle Eocene of Southern British Columbia, Canada", submitted by James Frederick Basinger in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Date Sept. 6, 1979

ABSTRACT

Permineralized remains of Metasequoia milleri Rothwell and Basinger are described from Late Middle Eocene sediments of the Allenby Formation of south-central British Columbia. Stratigraphic relationships of deposits within the Princeton Basin are reviewed, and the stratigraphic position, age, and formation of the Princeton chert are discussed.

Anatomical features of stems, wood, roots, leaves, pollen cones, and seed cones are well preserved. Mature wood of the fossil resembles that of Metasequoia glyptostroboides in having: traumatic resin cysts; opposite pitting on radial walls of tracheids; taxodioid cross-field pitting; tall, uniseriate rays; smooth-walled ray parenchyma; and diffuse, resinous, smooth-walled wood parenchyma. Leaves are linear, hypostomatic, and borne decussately, and have one or three resin ducts and slightly undulate to smooth epidermal cell walls. Leaves of living M. glyptostroboides differ in consistently have three resin ducts and in having much more pronounced undulations of epidermal cell walls.

Pollen cones of M. milleri are up to 3.0 mm long and are subtended by a vegetative zone of decussately arranged scale-like leaves. About 30 microsporophylls are helically arranged on the axis, and each bears three pollen sacs. Sporophylls have a single resin duct in the stalk and three resin ducts in the distal laminae. The fertile region is

enclosed by the distal-most subtending leaves. Pollen grains are 19-27 µm in diameter, subspheroidal, and papillate. Pollen cones of M. glyptostroboides differ from those of the fossil in having one resin duct throughout the sporophyll and reportedly bearing sporophylls decussately. The fertile region of pollen cones of M. glyptostroboides elongates during development to facilitate pollen release, but no evidence of similar elongation has been found in cones of M. milleri.

Seed cones of M. milleri are about 17 mm wide and 25 mm long, borne terminally on sparsely-leaved stalks, and bear about 30 decussately arranged cone scales. Seeds are about 5 mm long and 3-4 mm wide, with two lateral wings roughly equal in size to the seed body, and are attached distally on the stalk, with the micropyle directed toward the cone axis.

The differences between M. milleri and M. glyptostoboides are not discernible from compression fossils of M. occidentalis. M. milleri contributes to a clearer interpretation of the structure and evolution of Metasequoia during the Tertiary than has been possible on the basis of compression remains.

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I wish to express my gratitude to the following individuals for support and assistance that they have freely given to me in the course of this study and in the preparation of this thesis: Dr. Gar W. Rothwell, who conducted the first mass collection of material from the locality, and who initiated study of the pollen cones of Metasequoia; Mr. A. Randall Olson, who assisted in the preparation of material of M. glyptostroboides for comparative study, and who has, through friendship, given support; and to my sister, Mrs. Joyce White, who has typed the drafts of this thesis and has shown inexhaustible patience in doing so. Sincere thanks are due especially to Dr. Wilson N. Stewart, whose enthusiasm and ability as a lecturer secured my interest in paleobotany, and with whom it has truly been a priviledge and a pleasure to work. His inspiration and guidance has been felt throughout my many years with him, and his generous allocation of N.S.E.R.C. funds (grant #A-4259) has made this work possible. Finally, my deepest thanks to my wife, Marilyn, who has shown interest and understanding throughout this study and who has given me the encouragement I required to see this work to completion.

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CHAPTER 1

INTRODUCTION

Large quantities of fossiliferous chert have been collected from the Princeton locality during the summers of 1974 to 1978. The locality is on the Similkameen River, about 8 km SSW of the town of Princeton, southern British Columbia. The fossil plants are in layers of silicified peat interbedded with thin seams of lignite. The Princeton locality occurs in the Middle Eocene, Allenby Formation, one of several small, Early Tertiary deposits in south-central British Columbia.

Only recently has the significance of the Princeton chert locality been recognized. Plant parts are not readily apparent on the surface of the blocks of chert. As a result the locality had escaped collection by amateurs and many blocks of fine quality were easily available. A small collection of chert was taken by Chester A. Arnold and Roger F. Boneham in the early 1960's, primarily for the purpose of palynological sutdies of the Princeton basin (Boneham, 1968). This collection was given to Charles N. Miller (University of Montana, Missoula) and formed the basis for the description of <u>Pinus arnoldii</u> Miller, <u>P. similkameenensis</u> Miller, and <u>Eorhiza arnoldii</u> Robison and Person (Miller, 1973; Robison and Person, 1973). Boneham (1968), Miller (1973), and Robison and Person (1973) also reported the presence of two or three ferns, including <u>Dennstaedtiopsis</u>

aerenchymata Arnold and Daugherty, dicot stems, an ascomycete fungus, fragments of one or more moss gametophytes, and a few seeds of unknown affinity.

I presented a broad overview of the flora of the Princeton locality based on the first collections made in this continuing study (Basinger, 1976a). In addition to Dennstaedtiopsis aerenchymata, two other types of ferns were figured. Also reported were remains of Metasequoia, numerous types of seeds, two types of fruits, many types of woody dicot stems, and remains of a sabaloid palm. Also described were flowers of Paleorosa similkameenensis (Basinger, 1976b). A brief description of part of the flora and of the potential of the Princeton chert was presented by Basinger and Rothwell (1977).

The present study is an extension of the work begun by Basinger (1976a, b) and Basinger and Rothwell (1977). Reproductive and vegetative structures of Metasequoia have been discovered and are described. These include pollen and seed cones, seeds, pollen, leaves, leafy shoots, wood, and roots. An opportunity is available for the comparison of whole fossil and living plants. The Princeton Metasequoia is closely comparable with the living M. glyptostroboides, but certain features of anatomy reveal a number of differences that are not recognizable in compression material of M. occidentalis.

The Eocene is an epoch well represented by fossil plants, but in nearly all instances only compressed remains or palynomorphs are present. These types of fossils provide valuable information of external morphology, paleofloristics and paleoclimatology, but in most cases only permineralized plants reveal features of internal anatomy, organ development, and reproductive mechanisms. The structurally preserved plants of the Princeton chert present a rare opportunity for studies of this kind.

Structurally Preserved Plants of the Tertiary

Occurrences of anatomically preserved Tertiary plants, as noted above, are not common. With the exception of woods, which occur frequently as isolated fragments <u>in situ</u> or in Pleistocene glacial till, seldom more than a few specimens are found at any one locality. Isolated permineralized organs such as coniferous seed cones and leaf-bearing twigs, palm stems and roots, and fern rhizomes have been reported by Arnold (1945, 1952), Miller (1967, 1969, 1970, 1971, 1974, 1977a, 1978), Tidwell, et al. (1972), and others. The larger assemblages of structurally preserved Tertiary plants can be broadly grouped into unaltered remains, often called subfossils, and permineralized remains.

Unaltered peats, with plant parts that may be handled as fresh material, are common in Holocene to Pliocene sediments. However, these deposits are rare in the Miocene (eg. Hills and Ogilvie, 1970; Hills, et al., 1974), and are almost unknown from the Paleogene. Lignitic deposits such as the Miocene Braunkohle of Germany and the Oligocene Brandon Lignite of Vermont (Barghoorn and Spackman, 1949; Tiffney and Barghoorn, 1976, 1979) are regarded as unaltered remains.

Another type of fossil that may be termed "unaltered" is that preserved in amber. Fossiliferous ambers, including the well-known Baltic and Chiapas ambers, are described by Goeppert and Menge (1883), Conwentz (1886), Czeczott (1960), Hurd, et al. (1962), Miranda (1963), Langenheim (1964), McAlpine and Martin (1969), and others.

Other localities containing structurally preserved plants that really are not permineralized or preserved in a way comparable to the Princeton fossils are the nut beds of the London Clay and of the Clarno Formation (Ried and Chandler, 1933; Scott, 1954).

An assemblage of woody roots preserved in a permineralized soil was described by Wheeler (1972) as part of the Miocene taper Hill Flora of Colorado. Apparently little else was preserved in the nodules.

Limited occurrences of permineralized peats, such as those described by Ting (1972), Ting and Harr (1976), and Harr and Ting (1976) from the Paleocene of North Dakota, are occasionally found, but preservation is usually poor due to advanced decay and degradation of the peat prior to permineralization. Ting's (1972, p. 165) reference to preservation in his material as "comparable to that of carboniferous coal balls" is not supported by published photographs of the material. Ting also stated (p. 165) that this was "the first reported finding of such material in North America". Arnold and Daugherty (1963, 1964) had earlier described two ferns from permineralized peats of the Clarno

Formation of Oregon, and Boneham (1968), in his unpublished dissertation, had reported on the Princeton chert and some of the plant parts contained. The bed of silicified peat reported by Ting (1972) was, unfortunately, not extensive, but Harr and Ting (1976) have recovered cherts from numerous localities in North Dakota. Preservation is sufficient for the recognition of roots, wood fragments, leaves, seeds, and fragments of fern sporangia, but an accurate picture of the quality of preservation and the potential significance of this material has yet to be revealed.

Only three occurrences showing a diversity of well-preserved, permineralized plants in the Early Tertiary are known to date: the Deccan Intertrappean cherts; the Clarno cherts; and the Princeton cherts.

The Deccan Intertrappean Series of India contains the best known and most diverse assemblage of Tertiary permineralized plants. A review of the area, its fossils and an extensive bibliography have been presented by Basinger (1976a) and Basinger and Rothwell (1977). Only a synopsis is required here. Extensive lava flows (Traps), and occasional beds of siliceous and frequently fossiliferous sediments that are sandwiched between them (Intertrappeans), cover an area of over 200,000 square miles in central India (Rao, 1936). The lowermost Traps are Eocene (Sahni, 1934, 1941; Sahni and Rode, 1937; Rao, 1935; Crookshank et al. 1937; Rao and Rao, 1939; Prakash, 1960; Lakhanpal, 1970a, b) or possibly Paleocene (McElhinny and Wellman, 1969), while the uppermost layers may be as young as Miocene (Rao, 1936).

The flora of the Intertrappean cherts is extremely rich, with about 200 species reported to date. However, the numerous chert localities are scattered over a very broad area and may represent a great span of time. Only three of these localities are of much significance: Rajahmundry; Sausar; and Mohgaon Kalan. The Rajahmundry locality contains basically an estuarine aquatic assemblage, with _Chara_ and numerous algal forms (Pia, Rao, and Rao, 1937a, b; Rao and Rao, 1939; Rao and Rao, 1940). At Sausar are deposits of a fresh water lake or marsh, with charophytes, algal forms, _Azolla_, and other pteridophytes (Sahni, 1941; Sahni and Rao, 1943; Lakhanpal, 1970). The most diverse assemblage is found at Mohgaon Kalan where, like the Princeton locality, the peaty soil of a shallow marsh has been permineralized. Found at this locality are algae, bryophytes, water ferns, conifers, dicots, and monocots. Lists of species present at Mohgaon Kalan have been compiled by Sahni (1931), Prakash (1960), Lakhanpal (1970a, b), and Rao and Achuthan (1971).

The Princeton locality very closely resembles the Mohgaon Kalan locality not in the types of plants present, but in the nature of preservation and the types of plant organs that are found. The greater diversity of the Mohgaon Kalan locality is probably a result of the greater area of available outcrop at the former locality, the intensity with which it has been studied, and the much greater diversity of the tropical forest that once grew in India during the Early Tertiary. The nature of preservation at the Mohgaon Kalan locality is often excellent, but the material generally can be studied only from thin-section or polished surfaces. Not enough of the original carbon has remained to allow study by the peel technique.

The Clarno chert from the Eocene Clarno Formation of Oregon is the preserved peaty soil of a marsh, as is the Princeton chert. Dennstaedtiopsis aerenchymata occurs at both localities, and it is possible that other floristic similarities may be discovered when both floras are better known. The flora of the Clarno chert appears to be fairly diverse. Arnold and Daugherty (1963, 1964) described D. aerenchymata and Acrostichum preaureum and reported the presence of wood of Ginkgo, twigs of herbaceous and woody dicotyledons, a rich pollen flora, and a species of Equisetum recently described by Brown (1975).

Tertiary permineralized plants, because they are uncommon, offer little to our understanding of Tertiary vegetation. This is unlike the Carboniferous, where much of our knowledge of Upper Paleozoic vegetative and reproductive plant structure is based on the coal-ball floras. It is expected that the discovery and investigation of permineralized plants from the Tertiary could contribute a wealth of knowledge of Cenozoic plant structure and reproductive mechanisms. The discovery of the Clarno cherts provided the first opportunity to study a large assemblage of structurally preserved plants in the Lower Tertiary of North America. The Princeton chert provides the second.

CHAPTER 2

GEOLOGY

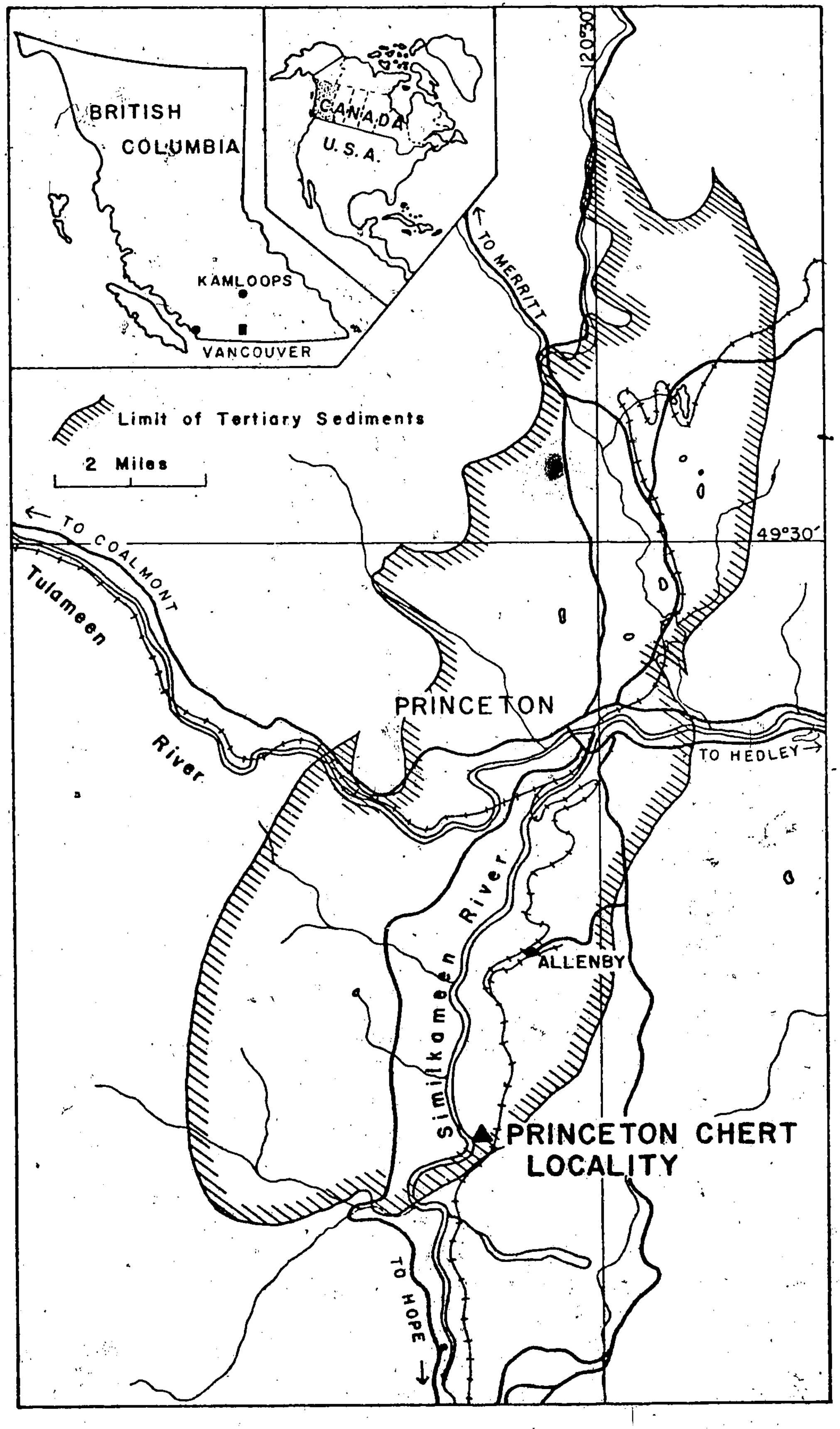
Locality Data and Geography

The Princeton locality outcrops are on the east bank of the Similkameen River, about 8 km SSW of the town of Princeton, British Columbia. The locality is slightly more than 3 km SSW of the abandoned town of Allenby and almost directly across the river from the site of the abandoned mining camp of Ashnola (Princeton Map Sheet 92 H/7 1:50,000, U.T.M. Grid Ref. 783 724; 49° 22.7' N 120° 32.7' W) (see Text Fig. 1).

Boneham (1968) referred to this as Locality "I" of his palynological studies of the Princeton basin. Basinger (1976a) subsequently referred to it as the Ashnola locality, after the abandoned mining camp of Ashnola. However, Ashnola no longer exists, and its former location is seldom found even on older maps of the area. In addition, the locality is found within the Princeton basin and has been referred to as the "Princeton locality" by Basinger and Rothwell (1975, 1977), and the material has been referred to as the "Princeton chert" by the same authors. In order to avoid confusion, the locality is referred to as the Princeton chert locality or the Princeton locality throughout this thesis.

The town of Princeton lies at the approximate center of

Text - Fig. 1. Map of the Princeton area showing the Princeton chert locality. (After Shaw, 1952).


BRITISH COLUMBIA
CANADA
U.S.A.
KAMLOOPS
VANCOUVER
Limit of Tertiary Sediments
2 Miles
120°30′
49°30′
TO MERRITT
TO COALMONT
Tulameen River
PRINCETON
TO HEDLEY
Similkameen River
ALLENBY
PRINCETON CHERT LOCALITY
TO HOPE

a small basin which contains a great thickness of Eocene sediments. The Princeton chert locality is found near the southern limit of these sedimentary rocks. Weathering of these relatively soft rocks lends a rolling appearance to much of the basin floor. Rugged terrain of highly resistant Triassic and Tertiary volcanics surround the Eocene sediments and form a rather well-defined perimeter for the basin. A thick blanket of glacial drift over much of the basin adds to the rounded appearance of hills and solid rock is usually exposed only along stream cuts (Camsell, 1907).

In the vicinity of the Princeton locality the Similkameen River flows at the foot of a steep embankment on the eastern side of a broad, deep valley. The water has carved softer rocks from the east bank, but the Princeton chert and more resistant layers of sandstone form partial dikes across the river. These resistant layers disappear beneath a broad flood plain on the west side of the valley.

The Princeton basin lies between two forks of the Cascade Mountain Range; contained to the west and south by the true Cascades (including the Hozameen and Hope Mountains), and to the east by the Eastern Cascades (Okanagan Range). To the north the country opens out into the Great Interior Plateau of British Columbia (Camsell, 1907).

The elevation of the Princeton locality is slightly more than 700 m above sea level and about 100 m above the townsite of Princeton. Nearby hills approach 1300 m, and altitude gradually increases to the south, east, and west.

Regional Geology

Geological studies of south-central British Columbia in general, and the Princeton basin specifically, have been presented by Dawson (1879), Bauerman (1884), Camsell (1907, 1915), Rice (1947), Shaw (1952), Hills (1962, 1965a, b), and Boneham (1968). The Tertiary deposits of the Princeton basin lie unconformably on the Triassic volcanics of the Nicola Group (Dawson, 1879; Boneham, 1968). Uplift during the Late Cretaceous resulted in distortion and severe erosion of the Triassic basement rocks. There appears to have been no deposition in the area during the Upper Cretaceous (Camsell, 1907; Shaw, 1952). Localized subsidence in western Washington and south-central British Columbia during the Early and Middle Eocene created numerous small depositional basins (Shaw, 1952). Six of these areas of deposition are recognized in British Columbia: Princeton, Tualameen, Quilchena, Kamloops, Horsefly, and Driftwood Creek. Subsidence resulted in accumulation of great thicknesses of volcanics and sediments (about 3000m in the Princeton area). It is believed that deposition in all six of these areas as well as in western Washington (Klondike Mountain Formation) was synchronous (Mathews, 1964; Hills, 1965a; Hills and Baadsgaard, 1967; Wilson, 1977; Rouse, 1978).

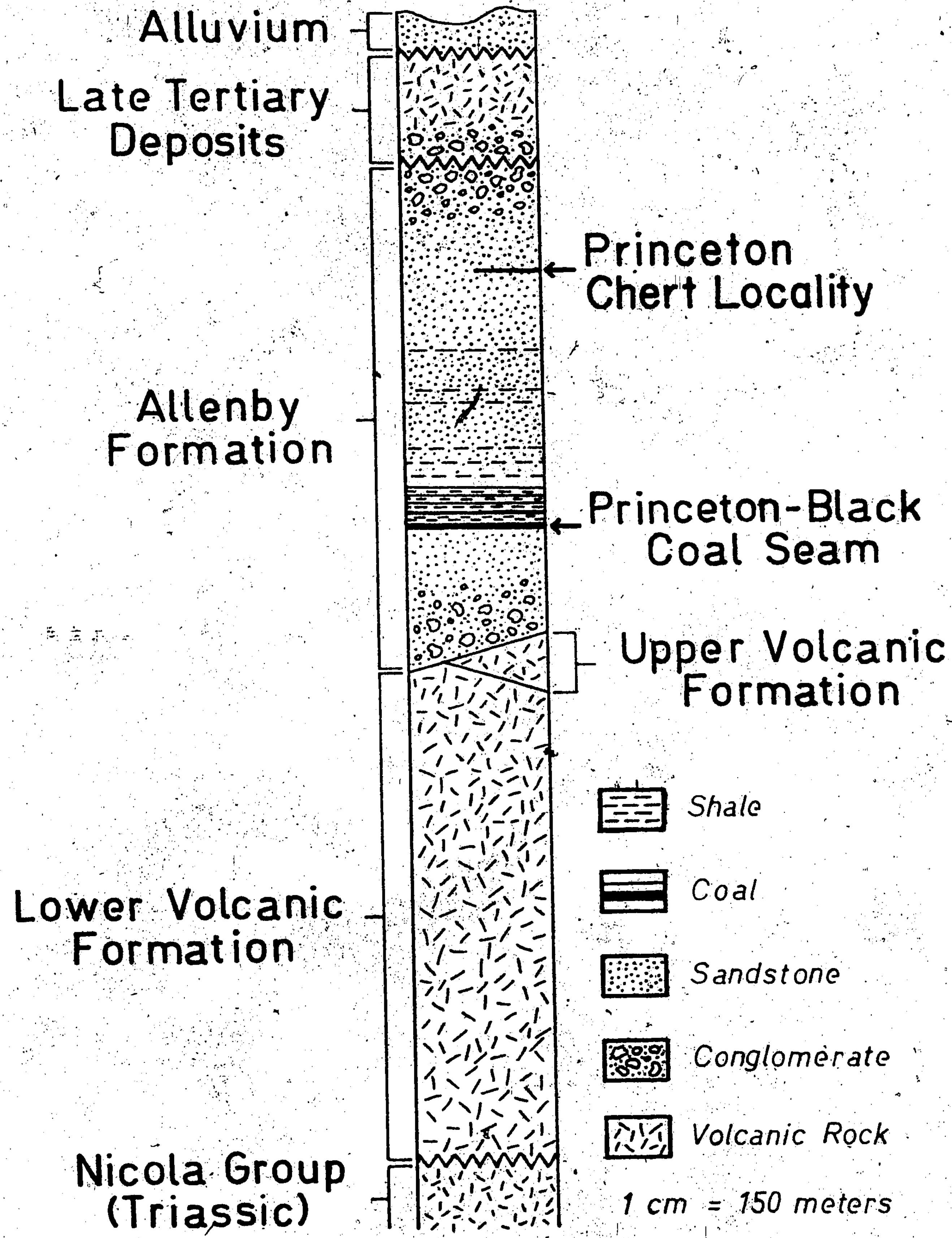
Uplift of the region at the close of the Eocene resulted in termination of deposition and severe distortion of the Middle Eocene rocks (Russell, 1954; Mathews, 1964; Piel, 1971; Hopkins et al., 1972). The next major interval of deposition occurred in the Late Miocene (Mathews and Rouse, 1963; Mathews, 1964).

The Princeton Basin

Both volcanic and sedimentary rocks were recognized as part of the Tertiary depositional sequence of the Princeton basin by Dawson (1879), Camsell (1907), and Rice (1947). Shaw (1952) first gave a detailed description of these deposits and recognized three formations collectively called the Princeton Group. They were, in ascending order, the Lower Volcanic Formation (1500 m thick), the Allenby Formation (1200m thick), and the Upper Volcanic Formation (200 m thick) (see Text Fig. 2).

The Lower Volcanic Formation outcrops and is at its greatest thickness at the southern and western margins of the basin. The Lower Volcanics wedge out toward the northeast and are not found at the northern and eastern limits of the Tertiary deposits. This formation lies unconformably on Nicola volcanics, and is overlain by the Allenby Formation in the central to northern and eastern parts of the basin. The Upper Volcanic Formation outcrops at the northern and eastern parts of the basin, is greatest in thickness in the east, and wedges out toward the center of the basin. Hills (1962) reinvestigated the Princeton volcanics and found that both Rice (1947) and Shaw (1952) were in error in their placement of the Upper Volcanic Formation above the Allenby Formation, and suggested that the Upper Volcanics of

Text - Fig. 2. Stratigraphic relationships of Tertiary deposits of the Princeton basin.


Alluvium
Late Tertiary Deposits
Princeton Chert Locality
Allenby Formation
Princeton-Black Coal Seam
Upper Volcanic Formation
Lower Volcanic Formation
Nicola Group (Triassic)
Shale
Coal
Sandstone
Conglomerate
Volcanic Rock
1 cm = 150 meters

Shaw may actually be a part of the Lower Volcanic Formation. Hills (1962) noted the presence of some small volcanic outcrops of a Late Tertiary age and believed that these may have been confused with the Early Tertiary volcanics by the earlier workers.

The lowermost strata of the Allenby Formation are composed primarily of conglomerates with a high percentage of volcanic detritus of a local origin (Hills, 1965b). Hills also noted some volcanic flows in this zone and inferred that the Allenby Formation and the Lower Volcanic Formation are conformable.

The Allenby Formation

The Allenby Formation covers an area of approximately 100 sq. km., extending about 25 km north to south and about 6 to 9 km east to west (see Text Fig. 1). Sediments of the Allenby Formation were described by Shaw (1952, p. 8) who states:

> "The Allenby Formation consists predominantly of massive, crossbedded granule- and pebble-conglomerate, sandstone, and massive and thinly bedded shale, with intercalated beds of coal, carbonaceous siltstone and shale, and bentonite. All size gradations between conglomerate and siltstone are represented, but granule-conglomerate and coarse sandstone seem to predominate."

Shaw (1952) noted that the coarser conglomerates were confined to the lowermost strata, below the major coal zones, although less coarse conglomerates can be found throughout the Allenby Formation.

The composition of the sediments was recognized as being primarily granitic by Rice (1947) and Shaw (1952). From a more detailed study of the mineral composition of the Allenby Formation as well as of the surrounding volcanics, Hills (1965b) determined the provenance of the Allenby sediments to be the Osprey Lake Intrusion which lies to the north of the Princeton deposits and actually contacts the Allenby Formation on the northern margin. Hills (1965b) also found evidence for a paleocurrent flow from the north or northwest.

The existence of unconformities within the sediments of the Princeton basin has been considered unlikely by Rice (1947), Shaw (1952), Russell (1958), and Hills (1962, 1965a, b).

Coal has been mined from exposures near the Princeton townsite since the early part of this century. The Princeton-Black Seam is the thickest and most extensive seam as well as the lowest occurrence of mineable coal in the stratigraphic sequence (Rice, 1947; Shaw, 1952) and has been well mapped with the use of outcrops and boreholes. The Princeton-Black coal is part of a zone of coal-bearing strata less than 100 m thick called the Princeton-Black Coal Zone. This zone has been used by Hills (1962, 1965b) to divide the Allenby Formation into an upper and a lower unit. The sediments below the Princeton-Black Coal Zone are over 300 m thick and consist basically of coarser conglomerates and sandstones. Above the coal zone are over 600 m of shaley to sandy strata.

Hills (1965a) notes that sandstone lenses increase in frequency and thickness upward in this upper unit. Since the Princeton-Black Seam is easily recognized and its extent fairly well known, localities within the Allenby Formation are often assigned a stratigraphic position relative to it.

Stratigraphic zonation has also been recognized within the Allenby Formation by Hills (1965a) and Boneham (1968) on the basis of microfloral changes. Although species vary in abundance, there are no abrupt changes in floral composition that would indicate an unconformity. Hills (1965a) lists a lower Bisaccate Zone (60 m thick), an Azolla primaeva Zone (250 m thick), the Princeton-Black Coal Zone (40 m thick), and a Pistillipollenites macgregorii Zone which can be subdivided into an upper, bisaccate (600± m thick), and a lower, Taxodium (60 m thick) dominance subzone. Boneham (1968) in part disagrees with Hills' interpretation, but supports the idea of zonation within the Allenby Formation. It should be noted that Hills based his work on collections made primarily within 60 m above and 300 m below the Princeton-Black Seam. Boneham, on the other hand, primarily studied samples taken above the Princeton-Black Seam. The only zone in which both Hills' and Boneham's studies have overlapped is in the Taxodium dominance subzone. Of this subzone Boneham (1968, p. 33) states:

> "Apparently the only stratigraphic zone Hills and I agree upon is his Taxodium dominance subzone."

Boneham goes on to say that he could not substantiate the presence of Hills' lower zones due to the lack of representative sampling. It appears that Hills may have overinterpreted results from his single sample in the upper zone of the Princeton basin and from his determination of zonation in the nearby Tulameen (Coalmont) basin. However, consideration of the findings of both Hills and Boneham should give a reasonably accurate appraisal of zonation in the Princeton basin.

In addition to studies of the Princeton chert by Boneham (1968), Miller (1973), Robison and Person (1973), Basinger (1976a, b), Basinger and Rothwell (1977) and Rothwell and Basinger (1979), compression fossils of the Allenby Formation have been described by J.W. Dawson (1879, 1890), Penhallow (1908) and Arnold (1955a, b).

The Princeton Chert Locality

Boneham (1968) determined that the Princeton locality was about 550 m stratigraphically above the Princeton-Black Seam and about 850 m above the base of the Allenby Formation. A dense, black shale lies above the chert beds and a sandy shale is found beneath. Most associated strata are covered, but those that are exposed are of massive and resistant sandstones.

There is a lack of mineable coal near the Princeton locality as well as in the northern and eastern parts of the basin, where the uppermost strata of the Allenby Formation outcrop. The fact that a thick coal deposit exists at the

Princeton locality in a stratigraphic zone generally devoid of sizable coal seams would indicate that the Princeton locality represents a local phenomenon and that such deposition was not widespread.

The Princeton locality is well into Hills' (1965a) Pistillipollenites macgregorii, bisaccate dominance subzone. Although Boneham (1968) rejected the existence of this subzone on the basis of a general lack of P. macgregorii and bisaccate grains, both types are abundant at the Princeton locality (Boneham, 1968), and remains of Pinus form a significant component of the megafossil flora. Microecological factors may have resulted in variability within the basin which makes Hills' findings and the microflora of the Princeton locality apparently incompatable with Boneham's results. Differences in microfloral composition are not sufficient to suggest an unconformity between the Princeton locality and other localities within the basin (Boneham, 1968).

Structure -

As noted previously, the Princeton locality is a 10 m thick outcrop of interbedded chert and coal (see Figs. 1, 2). Boneham (1968) has determined a strike of 27° E and a dip of 34° N for the beds. The chert layers are sharply folded 10 to 15 m up the bank, but this is probably the result of slumping.

Boneham (1968) numbered and sampled each of the 30 or more layers of chert and the corresponding number of coal layers, but found no evidence of floristic change during deposition of the beds. Basinger (1976a) noted that the layers were often found to anastamose or terminate and that Boneham's system of numbered layers was inconsistent at various places on the outcrop. Basinger (1976a) sampled chert from 9 broad units, each separated by a thick and continuous layer of coal, and found as much variability laterally as vertically. This variability is basically one of abundance (dominance) and less of actual presence or absence of a species.

The plant fragments are preserved in an organic matrix composed of small bits of wood, leaves, pollen grains, and other organic debris. Silt and other inorganic material is not a prominant component of the coal layers and is apparently absent in many. This indicates an absence of stream flow into the marsh. Thus, plant organs found in the chert represent parts of a plant community that grew adjacent to the depositional area. Preserved plant organs probably fell directly into the organic debris shortly before silicification. Some of the rhizomes and roots possess rootlets that ramify through the matrix and have been preserved <u>in situ</u>; therefore, water levels were low and the marsh may have experienced seasonal flooding and drying.

The silicates penetrated only the top several inches of debris on the bottom of the marsh. A layer of chert formed on a thickness of peat that would later be compresssed

22a

Fig. 1. View of the Princeton chert locality looking northwest from the east bank of the Similkameen River.

Fig. 2. Closeup of outcrop showing interbedded layers of chert and coal.

to coal. There appears to have been little or no compaction of the infiltrated layer, for plant parts show almost no evidence of crushing or distortion, and the particles of the organic matrix are quite loosely arranged.

Deposition of the Chert -

The chert beds disappear beneath the broad flood plain on the west bank of the Similkameen River. The beds apparently do not extend far beneath the west bank, for Boneham (1968) noted that there is no trace of chert in the well log of Blakemore Borehold #1, which was sunk almost directly across the river from the outcrop. Boneham concluded that the beds and the ancient marsh that they represent were very restricted in lateral extent. Boneham (1968) has discussed the formation of chert as it applies to the Princeton locality. Deposition of fossiliferous chert depends on certain requirements: 1) a relatively quiet body of water; 2) a source of soluble silicates; and 3) precipitation of the minerals.

The Princeton locality was undoubtedly a quiet, marsh-like area during deposition of the considerable thicknesses of peat. Flooding and precipitation of mineral-rich water occurred repeatedly, resulting in many layers of chert, with each episode being separated by considerable time. In relatively productive peat-forming environments, such as may be found in the warm temperate zones of eastern North America, it is estimated that 2,000 to 10,000 years are required for the deposition of the equivalent of one meter of coal (Giles, 1930; Cameron, 1970). This is roughly 20 to 100 years per centimeter. Most coal layers at the Princeton locality are several centimeters thick, indicating uninterupted accumulation for over a century, possibly several centures, at a time.

The source of silicates in chert formation is generally believed to be hot mineral springs or geysers (Boneham, 1968). Volcanic ash may contain highly soluble silicates, but there is no indication of ash in any of the layers of chert or coal. An influx of water, hot or cool, that contained the mineral load to permineralize several centimeters of peat must have killed the plants of the marsh. Precipitation of silicate from the water must have been rapid, for some very delicate plant tissues have been beautifully preserved. In addition, the microcrystalline nature of the chert itself indicates rapid permineralization. The time required for permineralization may be estimated at no more than a few days. Greater lengths of time would probably have resulted in degradation and collapse of some of the more delicate tissues even though microbial action may have been arrested.

Permineralization is a poorly understood process. Precipitation requires conditions of supersaturation which may have been accomplished by excessive evaporation (Arnold and Daugherty, 1963), a drop in temperature, or a change in pH. Correns (1950) has shown that a change in pH from 9 to

5 results in the precipitation of 2/3 of dissolved silicates from a concentrated solution. Boneham (1968) believes that the waters of the marsh were acidic and that both rapid evaporation of mineral water and a mixing with acidic water caused precipitation. Arnold and Daugherty (1963) interpreted the formation of the Clarno chert beds by the formation of a silica gel upon precipitation of dissolved silicic acid and accumulation of the gel in the soil. Expulsion of water by the weight of a sheet of lava resulted in solidification. However, some degree of compaction and probably a great deal of distortion of contained plant parts would be expected during compression of an unstable layer of silica gel. That a gel phase always occurs during permineralization has not been established (J.M. Schopf, pers. comm.). Dissolved silicates may have entered the crystalline phase directly. The Princeton chert may have formed by bypassing a gel phase, for there is little distortion of plant parts.

The Clarno chert shows some similarity in appearance and vegetational composition to the Princeton chert. It is probable that both deposits were formed in much the same way, that is, by periodic influx of minerals rather than slow accumulation of silica in the soil. Gradual accumulation of silica certainly did not occur at the Princeton locality, for the chert layers are quite discrete and the coal layers are relatively free of silicate. The Clarno chert does not show cyclic deposition in the same way as the Princeton chert and is closely associated with beds of volcanic ash and lava (Arnold and Daugherty, 1963), indicating a brief development of a flora during a fairly unstable period of volcanism. In this way the Clarno chert resembles the cherts of the Deccan Intertrappean Series of India, where chert beds are contained in thin sedimentary layers trapped between lava sheets. The mineral sources for the Clarno Intertrappean cherts may have been either hot springs or volcanic ash.

The Permian cherts reported by Schopf (1970, 1971) from Antarctica also represent silicified peats. From Schopf's description it is apparent that these cherts, like the Clarno and Intertrappean cherts, were formed by a single episode of flooding.

The Devonian Rhynie chert locality of Scotland is the only extensive deposit other than the Princeton locality known to the author showing cyclic accumulation of fossiliferous chert. Kidston and Lang (1917, p. 764) note layering of the Rhynie cherts and interpret chert formation as follows:

> "... this process of the formation of beds of peat, with the deposition of thin layers of sand, went on till a total thickness of 8 feet had accumulated.
>
> After the formation of 8 feet of alternating peat and sand local physical conditions must have altered, for water with silica in solution, possibly discharged from fumaroles and geysers, poured over the peat bed and sealed it up."

However, fine quality of preservation in the various layers of the chert indicates periodic permineralization by inundation with silica-rich water rather than a single flooding. It is likely that the Rhynie and Princeton cherts were deposited under similar circumstances.

The deposition of numerous layers of chert contributes to a diversity unmatched at the Clarno and most of the Deccan Intertrappean localities, where only a single layer is generally found at any one locality. The Princeton cherts record changes in dominance and to some degree in community composition. These changes are not a result of seasonal variation in floral composition, for estimates of diversity are based primarily upon woody axes and underground rhizomes. Of significance is the preservation of different developmental stages of reproductive organs in the different layers of chert. This is probably due to the time of year that the various layers of peat were permineralized.

The Princeton locality has proven to be unique among Tertiary permineralization localities in abundance of material, diversity of the flora, and quality of preservation. In these respects the Princeton chert is comparable to the best coal ball localities of the Pennsylvanian.

Other Chert Beds in Southern British Columbia

Basinger (1976a) referred to a report of extensive chert deposits at Vermillion Bluffs, about 5 km west of Princeton on the Tulameen River, by Dawson (1879, p. 131B). Dawson noted the presence of "silicified grass stems" and other "vegetable fragments" in the chert. This locality had not been examined by the author at that time, but a small amount of material has since been collected from what will be referred to as the Vermillion Bluffs locality. I have not recognized grass stems, but have been able to identify rhizomes of Eorhiza arnoldii and seed cones of Metasequoia. The chert is highly oxidized by the smouldering of associated coal seams, so that most layers lack organic residues. Chert layers, shales and coal ash are all colored from red to orange by baking and form steep cliffs of up to 50 m high (hence the name Vermillion Bluffs). Some darker layers do occur, however. Most chert layers contain fresh-water invertebrates such as snails and probably represent silicified lake mud. Other layers contain plant material and may prove to be very similar to the cherts of the Princeton locality. The Vermillion Bluffs locality is quite near stratigraphically to the Princeton-Black Coal Zone and is, therefore, about 500 m below the Princeton chert locality.

I have also found small pieces of fossiliferous chert of an unknown, but certainly local, origin in a coal dump on the west side of the town of Princeton (the Princeton Schoolyard locality). Thus, conditions for cyclic deposition of shales or coal and fossiliferous chert may have been widespread in the Princeton area throughout deposition of the Allenby Formation, and it is possible that other localities may be discovered in the basin or perhaps in similar Tertiary basins in other parts of southern British Columbia.

Age of the Princeton Chert

The Princeton locality has been shown to be a part of the Allenby Formation, and there appear to be no unconformities within the Allenby, or between it and the underlying Lower and Upper Volcanic Formations (see pp. 17 - 21). Therefore, dates determined for any of the rocks of these formations are applicable to the Princeton locality.

Early workers believed, with some reservation, that sediments of the Princeton basin as well as of other Tertiary basins in the area were of a Late Tertiary age (G.M. Dawson, 1879; J.W. Dawson, 1879, 1890; Scudder, 1879, 1895; Camsell, 1907; Rice, 1947; Shaw, 1952).

Russell (1935) and Gazin (1953) reported remains of Tillodont mammals from the Allenby Formation and concluded that the sediments were of Eocene age. Palynological investigations by Rouse and Mathews (1961), Rouse (1962), and Hills (1965a) reveal some comparability of microfloras from the Allenby Formation to those of the Burrard, Kitsilano, McIntosh, and Green River Formations, all of which have been considered Middle to Upper Eocene in age. <u>Pistillipollenites macgregorii</u> Rouse (1962), which appears to be a palynomorph characteristic of the Middle Eocene (Rouse and Srivastava, 1970), has been reported from the Allenby Formation by Rouse (1962), Mathews and Rouse (1963), Hills (1962, 1965a), Hills and Baadsgaard (1967), and Boneham (1968), and is found in abundance at the Princeton locality (Boneham, 1968).

The age of the Allenby Formation remained in some doubt until potassium-argon (K-Ar) dates were recorded by Rouse and Mathews (1961), Mathews (1964), Hills (1965a), and Hills and Baadsgaard (1967). The results of these studies are presented in Table 1. Those determinations from the Princeton basin are noted; other localities are in other basins of south-central British Columbia. Discrepant dates are explained by contamination or argon loss. Dates from the Princeton Group range from 47 to 52 million years (m.y.), with a mean of 49 m.y., most of which are from the upper parts of the Lower Volcanic Formation. However, one date from the Princeton ash, near the Princeton-Black coal zone, of 48 m.y. (note that Mathews (1964) included dates from Rouse and Mathews (1961) in his report), and one date of 47 m.y. from Collins Gulch, near the coal-bearing strata of the Tulameen area, reveal little difference in age between the sediments and the volcanics. The coal zones of both the Princeton and Tulameen basins have been correlated on geological and palynological evidence by Hills (1965a) and Hills and Baadsgaard (1967).

The Princeton chert locality is roughly the same distance stratigraphically above the Princeton ash as the latter is above the dated volcanics. If the radiometric dates were without error, it may be expected that the Princeton locality would be roughly 2 m.y. younger than the Princeton ash, or about 46 m.y. old. The close correlation of the dates from the volcanics indicate relative accuracy,

Table 1. Potassium-argon dates of Lower Tertiary sediments in southern British Columbia. Those dates from the Princeton Group are noted (*).

Author	Locality		Age (x10^6 yrs.)
Rouse and Mathews (1961)	Princeton	(Allenby Fm., Princeton Gp.)	48*
	Tranquille	(Kamloops Group)	49
	Savona Mountain	(Kamloops Group)	45
	Rock Creek	(Midway Group)	49
Mathews (1964)	Princeton	(Allenby Fm., Princeton Gp.)	48*
	Rock Creek	(Midway Group)	49
	Kettle River	(Midway Group)	48
	Joe Rich	(Kettle River Fm.)	46
	Savona	(Kamloops Group)	45
	Tranquille	(Kamloops Group)	49
	Shorts Creek	(Kamloops Group)	47
	T. Allin	(near Driftwood Creek)	53
	Hicks' Hill lava	(near Driftwood Creek)	48
Hills and Baadsgaard (1967)	Sunday Summit	(Princeton Group)	50*
	"	"	48*
	"	"	52*
	Allenby	(Princeton Group)	50*
	"	"	49*
	Sunday Creek	(Princeton Group)	47*
	"	"	50*
	McAbee	(Kamloops Group)	50
	"	"	48
	"	"	51
	"	"	57,56
	"	"	67,56
	Battle Bluff	(Kamloops Group)	51
	"	"	50
	"	"	50
	"	"	48
	Quilchena		79
	"		22
	Collins Gulch	(Tulameen, Princeton Gp.)	47*
	Driftwood Creek		126

but the date from the Princeton ash may be expected to be accurate within ±2 m.y. (Mathews, 1964). However, the agreement of the ages of the Collins Gulch and Princeton ashes gives more credence to the age of the latter. In addition, a span of 2 m.y. is acceptable for the deposition of 500 m of sediments, and there are no sizable hiatuses recognizable in the Allenby Formation above the Princeton-Black coal zone.

The date in Table 1 indicates that numerous other deposits as far north as Driftwood Creek are of roughly the same age as the Allenby Formation. This depositional phase was terminated in all of these areas about 45 m.y. ago (Mathews, 1964). The nearness of the Princeton locality to the top of the Allenby Formation and, therefore, to the end of the depositional phase also suggests that the chert is no younger than 45 m.y., and probably not much older.

The deposition of the Allenby Formation, therefore, was begun about 49 m.y. ago and continued until about 45 m.y. ago. Using the time scales of Kulp (1961) and Harland et al (1964) this interval corresponds to the Early Middle to Late Middle Eocene, or to the Clairbornian or Bridgerian Stages of the Eocene. The Allenby Assemblages are roughly equivalent in age to the Claiborne (southeastern United States), Kissinger Lakes (Wyoming), early Green River (Wyoming, Utah, and Colorado), and Burrard (coastal British Columbia) assemblages, are older than those of the Susanville

(California), Clarno (Oregon), Kitisilano (coastal British Columbia), and Ravennian (Alaska) beds, and younger than the Wilcox (southeastern United States), Wind River (Wyoming), and Chalk Bluffs (California) assemblages (Dilcher, 1973; Leopold and Macginitie, 1972; Macginitie, 1974; Rouse, 1977; Rouse et al., 1971; Wolfe, 1971, 1972, 1977).

Since the Princeton chert locality was deposited in late Allenby time, about 46 m.y. ago, it is of middle or late Middle Eocene age.

CHAPTER 3

MATERIALS AND METHODS

Collections

Blocks of chert varying in size from a few centimeters to more than half a meter in diameter were mass collected from the Princeton locality on several occasions between 1974 and 1976 (see Basinger, 1976a). Small amounts of chert were recovered by C.A. Arnold and R.F. Boneham in the early 1960's. Material was selectively collected during the summers of 1976, 1977, and 1978 by W.N. Stewart, M.R. Basinger, W.J. Basinger, M.V.H. Wilson, A. Lindoe, and the author. All material is deposited in the University of Alberta Paleobotanical Collection, Department of Botany, University of Alberta, Edmonton, Alberta (UAPC), with the exception of chert collected by G.W. Rothwell, W.N. Stewart, R.L. Dennis, and M.S. Brosier in 1975 which has been deposited in Department of Botany, Ohio University, Athens, Ohio. All material figured in this thesis is deposited in the UAPC.

Materials

Over 30 layers of chert were recognized by Boneham (1968); however, chert layers frequently anastomose or are discontinuous horizontally, and thickness of individual layers is highly variable. Basinger (1976a) broadly grouped the layers into 9 units and found changes in dominance, but no floristic differences, between units. Changes in dominance have also been found with horizontal sampling. For these reasons no further attempt has been made to number or correlate the layers of chert. Numbering of the layers has also been impractical due to the large amount of material collected from rubble at the base of the outcrop and for a short distance downstream. Blocks of chert are very difficult to remove from the outcrop, and attempts to break the chert frequently result in shattering. Over four tonnes of material have been removed from the outcrop and the locality is now stripped of most of the easily accessible, productive chert.

Chert blocks vary from black to light grey in color, with colorless to blue, white, or red fracture infillings. Weathered faces are white to buff in color, with plant parts clearly visible on the surface. Surfaces of freshly broken pieces may or may not reveal the presence of preserved plants. The quality of preservation and degree of degradation prior to preservation varies greatly among blocks. Often the general appearance of a block gives some indication of the nature of preservation of the plants inside. For example, black, opaque chert, fracturing conchoidally, and with a smooth and shiny appearance to a fresh surface, usually contains well-preserved material that is easily studied from peels. A continuum of shades exists between the extremes of black and light grey cherts, and, in general, preservation is better in darker blocks.

If the above descriptions are considered when collecting, a minimum of waste rock is taken. Well-preserved plants can be found, however, in all types of chert. The first mass collection of the present study tended to be indiscriminate in an effort to reduce bias of sampling. However, upper layers of chert tend to be lighter in color and contain less well-preserved plants than the black chert of the lower layers. As a result, most material has been taken from the lowest levels of the outcrop. In addition, no plants have yet been found in these light colored blocks that cannot be found, better preserved, in the darker blocks.

Methods

Preparation of the material for study requires slabbing of the chert blocks with an oil-cooled rock saw, followed by thin-sectioning or peeling of the surface. If plant organs are visible on the surface, the block is cut so as to provide the most useful orientation of the section. If no plant parts are visible, or there is no indication of their orientation, blocks are cut so that the saw kerf is perpendicular to the bedding plane. In this way cross-sections of axes, which have fallen into the peat and thus are horizontal, are most frequently obtained. Thickness of slabs varies from 1 to 2 cm depending upon the type of plant parts preserved.

Thorough removal of saw oil with detergent extends the life of the acid bath used in etching. However, residual oil that has penetrated the rock surface and seeped into cracks will not affect the etching process or the quality of the peel, even if it oozes to the surface during the procedure.

As noted under "Materials", there is considerable variation in the color of the chert. Color is a result of the amount of carbonaceous residue remaining in the rock. It is not known whether organic residues of the pale blocks escaped during or after fossilization. As a result, many blocks cannot be peeled, but must be thin-sectioned for study. Thin-sections were necessary for the study of wood structure as well. These were made by standard thin-sectioning techniques.

Peels of black, carbonaceous blocks were made by a modification of the cellulose-acetate peel technique of Joy, Willis, and Lacey (1956). Modifications include etching in full-strength (about 50%) hydrofluoric acid (HF) for about 1 minute and neutralizing in a saturated solution of sodium bicarbonate ($NaHCO_3$). Since the time required for a proper etch varies with the type of chert and the strength of the acid, methods depending on factors other than timing were developed. The best indicator of the depth of etch is color. A very dark slab will change color from black to bluish to pale brown to darker brown. The change from bluish to brownish is relatively abrupt and this is the point at which the slab must be retrieved from the acid and neutralized. Gray or brown blocks may show other color changes while being etched, and experience is required to determine the appropriate etching times.

I previously recommended neutralization in a saturated $NaHCO_3$ solution for at least 15 minutes (Basinger, 1976a). Since then I have found that a crystalline deposit forms on the surface of slabs left in the $NaHCO_3$ solution. This deposit is transferred to the peels. To avoid this deposit it is important that the slabs are removed from the base and flooded with water soon after vigorous bubbling stops. No technical problems have been encountered as a result of residual HF on the slabs.

Cellulose-acetate film of 0.003 inches (3 mil) thickness (about 0.08 mm) was found most suitable, for it resists tearing more so than thinner sheets, but is thin enough for even critical microscopic examination under oil. Demineralization is another questionable procedure. Basinger (1976a) and Basinger and Rothwell (1977) recommended demineralization in full strength HF for 1 minute. Not all acetate films can withstand treatment with concentrated HF; therefore, it is advised that this procedure be dropped or used with extreme caution. In most cases demineralization is unnecessary, but, if attempted, a concentration of no more than about 25% should be used and a piece of clear acetate film should be placed in with the peel to give an indication of the damage or cloudiness being caused by the acid.

Peels are rendered transparent by many types of clearing agents, but Burgamot Oil is preferred for its low volatility. Cleared peels were mounted in Harleco Synthetic Resin or Permount.

Bulk maceration of chert was attempted by Miller (1973) for the retrieval of pine needles from the matrix, but was unsucessful. I have had success freeing thick-walled seeds from the matrix by bulk maceration with full strength HF. Even these seeds are extremely fragile and are little more than loosely assembled organic dust. The silicate matrix appears to be all that holds the carbonaceous residues together, and loss of the matrix results in disintegration. This procedure may be useful for studying small, resistant structures such as seeds, for microscopic features such as tracheid pitting or stomatal structure, or for palynomorphs (Boneham, 1968). Larger, complex, or more delicate organs cannot be retrieved by maceration and must be studied by sectioning.

Any attempts at fracturing blocks along surfaces of leaves or other organs have been unsuccessful. Blocks fracture along infilled cracks or fracture conchoidally without any notable effect by the plant parts contained.

CHAPTER 4

DESCRIPTION

Vegetative and reproductive organs of Metasequoia are abundant in the Princeton chert. Organic connection of roots, stems, leaves, and cones has not been found, but their former connection may be inferred by association and morphological and anatomical comparson. The various plant parts are individually described and discussed before being collectively interpreted.

Wood

Coniferous wood and twigs are common in the chert. On first appearance these remains can be grouped into two types: those with and those without true resin ducts. All remains with true resin ducts are presumed to belong to Pinus similkameenensis Miller (1973), for all specimens critically examined do conform to this species. The second type lacks true resin canals, although traumatic resin cysts may be present. Remains of the latter type include leafy shoots, small and large twigs, some large branches of several centimeters diameter, and numerous small fragments of large axes.

In most instances, single definitive features of secondary wood that can be called "characteristic" of a particular species, genus, or even family of conifers, do not exist. Rather, a suite of features, none of which is truly characteristic for the species of wood examined, must be relied on.

Care must be exercised with all characteristics used, for variability within a species may complicate identification. This variation may be caused by a number of environmental factors such as moisture, temperature, seasonal temperature fluctuations, and soil type. For these reasons, as many features of wood anatomy as possible, particularly those showing most consistency, must be used for identification. Similarly, the origin of the wood must be considered, since growth rates and therefore the sppearance of the wood may vary greatly in different parts of a single tree. Wood to be identified should be of a similar origin to that indicated for the descriptions of species used for comparison. Such descriptions are generally based on the mature wood of the trunk. Wood of the branches and twigs of the fossil is discussed following description and discussion of the mature wood.

One of the greatest handicaps to the study and identification of fossil wood is the often limited quantity and quality of material available for study. This results in a failure to see numerous features and limits interpretation of the range of variability in the fossil species. The abundance of material available for the present study contributes to a relatively good understanding of the wood anatomy of the Princeton fossils.

Wood Description -

Transverse Section:

Tracheids are 25 - 95 µm in radial diameter and 25 - 65 µm in tangential diameter. Fiber tracheids are of a similar tangential diameter, but are usually only 8 - 15 µm in radial diameter. Larger tracheids and fiber tracheids are distinctly angular in cross-section; smaller ones, oval to circular (Figs. 5 - 8).

The distinction between early and late wood may be sharp (Fig. 6) to vague (Fig. 5). Wood of larger axes most often exhibits an abrupt change, although some branches of moderate size show either or both patterns (Fig. 3). Growth rings are 0.3 - 1.3 mm wide; those with a gradual change from early to late wood typically are thicker and have a smaller ratio of early to late wood thicknesses (1:1 - 1:4) than those with a very abrupt change (3:1 - 10:1). Such unequal development on different sides of a limb is typical of the exaggeration of growth and fiber production in the development of compression wood. Wood of the first few growth increments (juvenile wood) has a similar appearance, but is due to rapid increase in girth of young shoots.

Cell walls of most specimens have undergone significant degradation prior to or during permineralization, or may have been disrupted by crystal growth of the silicate matrix. As a result, the walls may have a reticulate appearance or may be somewhat indistinct and appear "fuzzy". In well preserved material, cell wall thicknesses of early wood

(1.5 - 2.5 µm) and late wood (4.0 - 5.0 µm) can be measured (Fig. 7).

Horizontal walls of ray and wood parenchyma cells show no evidence of pitting.

Tangential Section:

Some early wood tracheids are pitted on their tangential walls. Pits are circular bordered, 15 - 20 µm in diameter, and scattered (Fig. 13). Apertures are circular and 5 - 7 µm wide. Pits have not been found on tangential walls of fiber tracheids of the late wood.

Rays are uniseriate (Figs. 12, 13), occasionally showing pairing of cells in the body of the ray (Fig. 30), and are highly variable in height. Rays may be a single cell to as many as 80 cells (1.5 mm) high (Fig. 12). Rays of such great heights are not isolated occurrences. Many rays exceed 50 cells in height, and rays of over 35 cells are very common.

Ray cells are 16 - 19 µm high and 13 - 16 µm in tangential diameter. No evidence of pitting has been found on the tangential walls of ray cells.

Radial Section:

Tracheids have been measured to 6 mm in height and lack tertiary or spiral thickenings. Fiber tracheids often show spiral striations or spiral checks (Fig. 33) that are a result of preservation and "due to mechanical changes in the tracheids and are in fact cracks or fibrils bearing upon the micellar structure of tracheidal walls" (Greguss, 1955, p. 31) (see Fig. 35). These striations are not of taxonomic significance and are not to be confused with spiral thickenings.

Circular bordered pits on radial walls of tracheids are in uni- to quadraseriate rows, opposite, and close but not crowded (Figs. 17, 22, 23). Pits 17 - 23 µm in width with apertures 5 - 7.5 µm wide occur in a uniseriate row on fiber tracheids of the late wood. Crassulae (Bars of Sanio) are consistently observed in bi-to quadraseriate rows of pits and are less frequently found between pits of a uniseriate row (Fig. 23).

Rays appear to be homogeneous; ray tracheids have not been recognized. Ray cells are 50-250 µm in length (radial dimension) with tangential walls usually nearly vertical but occasionally inclined to as much as 45°. Tangential and horizontal walls are about 2.5 µm thick and smooth. Indentures are present but not conspicuous (Fig. 26). Resinous material occurs rarely within ray cells.

One to five taxodioid, half-bordered pits are found in the cross-field. Pits are 9 - 14 µm in diameter and occur in one or two horizontal rows on broad tracheids of the early wood, and singly, diagonally, or in one or two vertical rows on narrower tracheids and fiber tracheids (Figs. 17, 19, 20). Pit borders are broad-elliptical to round; apertures are oval to slit-like and commonly inclined at about 45° (Fig. 24).

Wood Parenchyma:

Wood parenchyma is diffuse (metatracheal) and common but not abundant. Cells are filled with globules of resin (Fig. 30). Individual cells are 25-50 µm in tangential diameter, somewhat thinner in radial diameter, and 70 - 160 µm in height. They are usually somewhat smaller in diameter than surrounding tracheids. Hroizontal (end) walls are smooth to slightly bead-like. Half bordered pits, 6 - 12 µm in diameter with oblique, eye-shaped apertures (similar to pits of the cross-field), normally occur in a single row on vertical walls (Fig. 32). Not all wood parenchyma exhibits pitting.

Traumatic Resin Cysts:

Schizogenous traumatic resin cysts or resin bladders, about 50 µm in diameter, are formed in tangential rows that often extend over much of the circumference of the stem (Figs. 5, 27); horizontal resin cysts have not been found. Resin cysts usually occur within the first few rows of early wood tracheids (Figs. 5, 27), but may be formed at other times of the season as well. The term cyst is used in preference to canal since the cavities are not continuous either vertically or tangentially (Penhallow, 1907). Resin cysts are not tylosed.

Resin cysts are surrounded by an epithelium and parenchyma cells typical of those found in association with resin cysts in other types of conifers (Penhallow, 1907; Greguss, 1955) (Figs. 27 - 29). Epithelial cells are short and irregularly shaped with bead-like to nodose walls (Fig. 28). A second layer of similar cells may be present. Outermost is a layer of cells similar to wood parenchyma, but with or without resin and frequently heavily pitted with up to 3 parallel, vertical rows of pits (Figs. 30, 31).

Cysts and surrounding parenchyma cells are generally devoid of resinous contents, although wood parenchyma cells elsewhere in the same specimen have resin globules. This brings to question their description as "resin" cysts. The type of material contained in the cysts was certainly different from that of the wood parenchyma cells.

Other Structures:

Large, amber-colored bodies are occasionally found in association with ray cells and may represent resin deposits within so-called resin tracheids of Penhallow (1907) (Fig. 39). These globules are abundant to scarce or absent in various samples of the fossil wood. The proximity to ray parenchyma would suggest that these structures may be tyloses, but resinous material is rarely found within ray cells. In addition, a cellular nature has not been established for these bodies.

Basinger (1976a) noted the occurrence of spherical bodies that occluded some tracheids. Their occlusive nature is the only resemblance to tyloses and it is now certain that the use of the term "tylosis" in reference to these structures (Figs. 37, 38) is inappropriate. What they are is still uncertain.

Wood Discussion -

In the following comparisons with other woods, all descriptions are based on the mature wood of larger axes except where noted.

Identification of the fossil wood as taxodioid is supported by the following features:

1. absence of true resin ducts, although traumatic resin cysts may be common.
2. very tall, uniseriate rays.
3. taxodioid pitting in the cross-field.
4. smooth tangential walls of the ray cells.
5. up to 3 or 4 rows of opposite pits on the radial walls of tracheids; crassulae conspicuous.
6. wood parenchyma present, diffuse, resinous.
7. absence of spiral thickenings on tracheid walls.
8. distinctness of growth rings and growth ring delimitations.

Distinctness of growth rings and ring delimitations was used by Greguss (1955) for recognition of members of Taxodiaceae. However, the primary value of this characteristic is as an indicator of physical conditions under which growth occurred.

Tracheid size is highly dependent on growth rates and height on a tree, so is of questionable taxonomic importance. Brown and Panshin (1940) note that this character may be of some use particularly when size extremes are reached. For instance, maximum tangential diameters of 70 - 80 µm recorded for Taxodium distichum and Sequoia sempervirens tracheids are greater than those of other conifers. The fossil wood similarly has very wide tracheids (65 µm maximum). As may be expected, tracheid length is directly proportional to width. Tracheids of S. sempervirens measured by Brown and Panshin (1940) and Hida (1953) are generally between 4 and 8½ mm in length, and those of Sequoiadendron giganteum and Metasequoia glyptostroboides are also significantly greater than those of other conifers (Hida, 1953). Tracheids of the Princeton fossil are up to 6 mm in length.

Ray height is highly variable within a species or within a single tree. However, maximum ray height may be useful in identification, particularly if extremes are reached (Brown and Panshin, 1940; Peirce, 1936). Ray heights approaching those of the Princeton fossil (80 cells) have been recorded only for S. sempervirens (40+) and T. distichum (60+) (Brown and Panshin, 1940; Greguss, 1955).

Although various combinations of these features appear in other coniferous families, and in some cases show some inconsistency within a single species, all together they are a rather good indication of affinity to the Taxodiaceae.

Woods of the Cupressaceae could be most easily confused with those of the Taxodiaceae. Although Greguss (1955) maintains that they are easily distinguishable by characters such as bead-like thickenings on the tangential walls of ray cells in the former, inconsistency of such features throughout the family have resulted in confusion of fossil woods of these families (Torrey, 1923). The presence of traumatic resin cysts in the Princeton material, however, indicates a relationship to the Taxodiaceae.

The Taxodiaceae may be divided into two groups on the basis of dentate (Glyptostrobus and Taxodium) or smooth (Sequoia, Sequoiadendron, Metasequoia, Cryptomeria, Athrotaxus, Taiwania, and Cunninghamia) horizontal walls of wood parenchyma cells (Greguss, 1955). The smooth to slightly bead-like horizontal walls of wood parenchyma in the fossil clearly indicates affinity to the latter group. Sequoia, Sequoiadendron, and Metasequoia tend to have higher rays and thicker horizontal walls of ray cells than the other four genera of the second group (Greguss, 1955). Traumatic resin cysts have been reported for Sequoia, Metasequoia, Athrotaxus and Sequoiadendron (Torrey, 1923; Greguss, 1955). On these features the fossil wood can be aligned with the three living redwoods, Sequoia, Metasequoia and Sequoiadendron. Wood of Sequoia sempervirens, Sequoiadendron giganteum, and Metasequoia glyptostroboides is probably indistinguishable, although some general trends may be evident (Greguss, 1955; Schwarz and Weide, 1962). For example, Greguss (1955) notes that bordered pits on the radial walls of tracheids are larger in diameter in M. glyptostroboides (20 - 22 um) than in either S. sempervirens (14 - 16 um) or S. giganteum (14 - 17 um). Pits of the Princeton fossil are 17 - 23 um in diameter.

In the absence of other evidence for identifying the fossil wood, assignment to a form-genus for taxodioid wood would be necessary. Woods of many redwood-like species of Tertiary and Late Cretaceous age have been assigned to Sequoioxylon, Taxodioxylon, Cupressinoxylon, and recently to Metasequoioxylon. Confusion exists due to the overlap of diagnostic generic characters, limited knowledge of a fossil as a result of inadequate quantity or quality of material, and the considerable natural variability within a species. The use of the form-genus Metasequoioxylon (eg. Greguss, 1967) should be questioned, since assignment to this genus infers relationship to just one of three living species when a fossil most likely is less similar to the extant species than the three extant species are to each other. Schönfeld (1955) preferred to retain the generic name Taxodioxylon for material he believed represented Metasequoia. Although Krausel (1949) preferred to refer all species of Sequoioxylon to Taxodioxylon, the former genus may be useful for referral of some more assured redwoods, such as the Princeton fossil.

Identification of the fossil wood and branches from the Princeton chert as Metasequoia, not Sequoioxylon or Taxodioxylon, is based upon the following evidence:

1. decussate branching found in smaller branches (Fig. 4).
2. consistent association with leafy twigs, pollen cones and seed cones of Metasequoia.
3. apparent absence of more than one taxodioid species

at this locality represented by vegetative or reproductive remains.

4. the range of wood features of fragments of the largest axes to leafy twigs forms a continuum.

There is a possibility that more than one species is represented among the woody remains, but evidence overwhelmingly supports the recognition of a single species. Two twigs and a few leaves of taxodiaceous affinity do differ from the bulk of the material (Fig. 55), but the possibility that they are aberrant Metasequoia remains is as great as their belonging to a different taxon.

The wood remains could have been assigned to Metasequoia for the four reasons noted above. However, it was important to establish taxonomic relationships for the woody remains independently to ensure that there could be no contradiction between identifications based on various organs, and that circular reasoning in the determination of various organs could be avoided.

A comparison of the Princeton fossils to other fossil taxodioid woods of the Tertiary and Late Cretaceous would be a monumental task and possibly of limited significance. More important is a comparison of this relatively well-known species of fossil Metasequoia with the only extant member of the genus. Other fossil species of Metasequoia have only been recognized from compression fossils of leafy twigs and reproductive structures, and anatomical comparisons have not been possible between these and M. glyptostroboides.

This fossil material provides the first opportunity for detailed comparison of wood features of an early Tertiary *Metasequoia* with those of the only living member of the genus.

Comparison with *M. glyptostroboides*:

Information on *M. glyptostroboides* has been gathered from descriptions presented by Li (1948), Florin (1952). Greguss (1955), Maácz (1955), Schönfeld (1955), Schwarz and Weide (1962), and Böcher (1964).

As noted above, tracheid dimensions may be of some significance as a comparative feature if size extremes are reached. *M. glyptostroboides*, *Sequoia*, and *Taxodium* have very large tracheids (to 80 µm in tangential diameter and 8 mm long) and the Princeton fossil also tends to gigantism with tracheids being in excess of 65 µm in tangential diameter and at least 6 mm long. Related to tracheid size is the distinctness of growth rings and late wood delimitation. In the Princeton fossil and *M. glyptostroboides* are found distinct growth rings with both abrupt and gradual transition from early to late wood (Figs. 8, 9). Both types may appear in a single-cross section, although trunk wood tends to be of the former type, while branch wood, the latter.

Distribution of pits on radial walls of tracheids is uni- to quadraseriate opposite in both fossil and living species (Figs. 17, 18, 22, 23). Pit diameter is also comparable; 17 - 23 µm in the Princeton fossil, 20 - 22 µm in M. glyptostroboides (Greguss, 1955). Crassulae are present in both species (Figs. 18, 23). Tangential pitting is also similar (Figs. 13, 16). Greguss (1955) reports diameters of tangential pits of 9 - 10 (13) µm for M. glyptostoboides. However, living material that I have examined exhibits tangential pits of about 17 µm in diameter, compared to 15 - 20 µm for the fossil.

Great ray height is a striking feature of the Princeton fossil wood. As noted previously, ray height is an unreliable comparative feature except where there is a tendency to form very short or very tall rays (Torrey, 1923; Peirce, 1936). The tallest uniseriate rays recorded for living conifers are found in the Taxodiaceae, where heights may be in excess of 60 cells (Taxodium distichum). Uniseriate rays of the fossil frequently exceed 50 cells in height and reach a maximum of over 80 cells, and are among the tallest known for extant or extinct conifers. Maximum ray height in M. glyptostroboides is about 30 cells (Greguss, 1955).

Ray cell sizes are similar in both the Princeton fossil and M. glyptostroboides and show relatively little size variation from large to small axes. Tangential and horizontal walls in both species are smooth, of similar thickness, and apparently not pitted. Indentures are present in the Princeton fossil and in M. glyptostroboides (Schönfeld, 1955), although they were not found by Greguss (1955). This feature appears to be extremely variable and not a reliable identifying character. Although ray cells of M. glyptostroboides may contain resin (Li, 1948), they typically do not. Ray cells of the fossil rarely contain resin.

Ray tracheids are infrequent in the Taxodiaceae, having been reported in _Sequoia_, _Sequoiadendron_, and _Metasequoia_ (Greguss, 1955). They have not been recognized in the Princeton fossil. However, half-bordered pits on ray parenchyma walls of the type found in _Metasequoia_ (taxodioid), scarcely differ in appearance from the bordered pits on ray tracheids. In addition, cell walls of both types are not significantly different and cell contents are no longer available as an indicator or parenchyma. Reliable identification of ray tracheids can be made only by demonstration of a border on each side of the pit in section view. Ray tracheids are not common in living _Metasequoia_. The absence of these cells in the fossil could be the result of an inability to find or identify them.

Cross-field pitting has been shown by Schwarz and Weide (1962) to be quite variable in _M. glyptostroboides_. Poor preservation of wall details in most of the fossil specimens makes it difficult to determine variability of aperture size, shape, and inclination. Those pits measured reveal no differences from living material (Figs. 24, 25). Numbers and distribution of pits in the cross-field are similar in both species (Figs. 17 - 21).

Traumatic resin cysts are similar in appearance and distribution in the Princeton fossil, _Metasequoia_, and _Sequoia_, although the frequency with which they are formed in the fossil seems to be greater than in M. glyptostroboides.

Wood parenchyma of the Princeton fossil and M. glyptostroboides is also similar. Wood parenchyma is diffuse and common but not abundant. Horizontal walls are smooth to bead-like, vertical walls bear half-bordered pits (Figs. 32, 35), and cells typically contain deposits of resin (Figs. 30, 36). Penhallow (1907) considered this latter feature to be diagnostic of woods of Sequoia.

The significance of what appear to be resin tracheids in the fossil is unclear. Resin tracheids are common in the Araucariaceae and Abies and are sporadically distributed among other groups of conifers (Penhallow, 1907; Brown and Panshin, 1940; Greguss, 1955). They have not been reported for M. glyptostroboides.

The only apparent difference between wood of the Princeton fossil and of M. glyptostroboides is the height of the rays. Whether this disparity could be the result of physical conditions during growth is unknown. The magnitude of the difference must at this time be considered significant.

Younger Branches and Twigs -

Brown and Panshin (1940) have noted various trends in wood development relative to position within a tree. Growing conditions change rapidly during the first few years of growth of a stem. Wood of the first few growth increments of a stem, the "juvenile" wood, differs greatly from mature wood at the same height as a result of rapid growth under moisture and nutrient conditions that differ greatly from that experienced at later stages of development. As may be expected, juvenile wood and branch wood are quite similar in appearance. The following are some of the differences that occur:

1. tracheids are smaller in diameter and shorter in juvenile and branch wood than in mature wood.
2. the proportion of early to late wood is lower in juvenile and branch wood than in mature wood.
3. wood rays are most numerous in branch wood, although ray volume in conifers varies little from roots, trunks, and branches (i.e. rays are lower in branches). Similarly, rays are lower in juvenile wood since ray height increases outward to a maximum.

In consideration of these structural variations, Brown and Panshin (1940, p. 225) state that:

> "in general, in wood identification, it is best to avoid samples taken from near the center of a tree since they would not be typical; the same holds, often to an even greater degree for branch wood."

For these reasons, it was necessary to separate discussion of features of branches and twigs from the foregoing description of wood of the Princeton fossil. The following description of branch wood serves to illustrate the range of variability encountered within the fossil species of the Princeton chert and to establish that twigs, branches, and stems are attributable to a single species. Branches from which the following data were obtained are less than 2 cm in diameter.

Branches:

Early wood tracheids are 9 - 19 µm in tangential diameter and 13 - 25 µm in radial diameter; late wood to 15 µm in radial diameter. Growth rings are distinct; demarcation between early and late wood of the same ring is indistinct. Early and late wood is roughly equal in thickness (Fig. 10).

Rays are 1 to 15 cells high (Fig. 14). Ray cells are 12 - 15 µm in tangential diameter, 12 - 18 µm high.

Tracheids generally have a single row of pits on their radial walls due to restrictions in diameter of the cells. Pitting is occasionally biseriate and opposite. Pits are 9 - 12 µm in diameter.

Ray cells are 45 - 65 µm in radial length. One to 5 taxodioid pits, 6 - 8 µm in diameter, occur in one, occasionally two or three vertical rows in the cross-field (Fig. 19).

Traumatic resin cysts, similar in structure but smaller than those of mature wood, frequently occur in smaller branches.

Wood parenchyma cells are resinous and have smooth, to bead-like horizontal walls.

Leafy Twigs:

Tracheids are 8 - 15 µm in diameter. Pits on radial walls are uniseriate and 7 - 12 µm in diameter. Rays are uniseriate and 1 - 10 cells high (Fig. 15); ray cells are 11 - 19 µm in tangential diameter, 15 - 35 µm in height, and

30 - 60 µm in radial length. Two to five pits, about 5 µm in diameter, are arranged in one or two vertical rows in the cross-field. Resin cysts have not been found in the wood of small twigs.

Discussion:

Differences between branch and trunk wood are those predicted. Tracheids are considerably smaller in branches and the proportion of early to late wood is low. Pits on radial walls are restricted in size and seriation by tracheid diameter. Cross-field pitting is similarly restricted. Rays are considerably shorter in the branches, although ray cells show little difference in size from the smallest to largest axes. Consistency in the size of ray cells was noted for M. glyptostroboides by Schwarz and Weide (1962). There is no indication that more than one species could have contributed to the assemblage of taxodiaceous wood, branches and twigs at the Princeton locality.

Pith, Phloem, and Cortex

Pith and Primary Xylem -

The pith of smaller branches is generally about 0.5 mm wide, rhomboid to square in cross-section, with xylem in four wedge-shaped bundles (Figs. 53, 54). The pith elongates in the direction of departure of opposite pairs of traces. The primary body of larger branches may not be clearly four-angled, but may approach a five-sided condition (Fig. 42).

Pith cells are circular in cross-section and are largest in diameter (to 50 μm) at the center, decreasing in size toward the periphery. Wide cells are usually short in longitudinal section, while narrower cells tend to be more elongate. Walls are heavily thickened and often appear nodular in section view as a result of simple pitting of all surfaces (Fig. 44). Many pith cells have dark, possibly tanniniferous or resinous, contents.

Primary tracheids may have annular, helical, or scalariform thickenings. Some tracheids of the late metaxylem show a combination of scalariform thickening and circular-bordered pitting.

Phloem -

Poorly preserved secondary phloem has been found on many branches of less than 1 cm in diameter. Larger axes are fragmented or decorticated.

Phloem consists of tangential bands of fibers, parenchyma, and sieve cells. These bands may be arranged in a regular sequence of fibers, sieve cells, parenchyma, sieve cells, fibers, etc. (Figs. 45, 49). However, irregularity in this pattern is common and normally is a result of deletion of fiber layers (Fig. 47).

Fibers are the most prominent part of the phloem and are 20 - 30 μm in diameter, square to slightly elongate in cross-section, and have heavily thickened walls. In many cases the lumen has nearly been obliterated. Fiber length is at least 1 mm; actual length could not be determined due to distortion of tissues.

Sieve cells are about 10 µm in radial diameter. Bands of parenchyma are similar in diameter to the sieve cells and frequently have dark contents (albuminous cells)(Figs. 46, 49). Sieve cells and parenchyma are frequently very poorly preserved and are not distinguishable unless albuminous cells are conspicuous.

Details of wall structure have not been preserved well enough for the recognition of sieve areas. Fiber walls often appear fibrous or granular, and distinction between very thick cell walls and opaque cell contents may be difficult. Pits have not been found on fibers.

Rays are uniseriate near the cambial zone, but frequently are greatly dilated peripherally to accommodate stem enlargement (Fig. 43). Ray parenchyma cells in such cases balloon to over 50 µm in diameter and may be irregular in shape and disorganized.

Secondary phloem resembles that found in other members of the Taxodiaceae. Tangential, uniseriate bands of phloem fibers are consistently present in members of the Taxaceae, Taxodiaceae, and Cupressaceae, although cupressoid bark possesses resin canals and thus does not resemble the Princeton fossil (Chang, 1954; Ramanujam and Stewart, 1969; Esau, 1977). Phloem of M. glyptostroboides has been described by Böcher (1964) and Kollman and Schumaker (1961). Böcher (1964) reported that bands of fibers, parenchyma, and sieve cells are all uniseriate and are produced in a repetitive sequence of fibers, sieve cells, parenchyma, sieve cells (Fig. 50). However, thickness, sequence, and tangential continuity of these bands may be somewhat variable in both M. glyptostroboides and the Princeton fossil (Fig. 47, 48). Phloem fibers of the fossil are typically square in cross section, while those of M. glyptostroboides are more commonly narrow in radial dimension.

Permineralized bark is rare in Mesozoic and Tertiary sediments and only in few instances can its origin be determined (Ramanujam and Stewart, 1969). The only other report of taxodiaceous bark is that of Taxodioxylon gypsaceum from the Upper Cretaceous of Alberta by Ramanujam and Stewart (1969). The lack of important characters of the Princeton fossil due to poor preservation, the variability of features within M. glyptostroboides, and the general similarity of bark of many of the Taxodiaceae precludes consideration of evolutionary trends at this time.

Cortex and Cork -

Cells of the primary cortex are parenchymatous and irregular in size and shape. Some cortical cells are filled with dark, possibly tanniniferous, substances. Preservation of these cells may not be adequate to distinguish heavily thickened sclereids from occluded parenchyma, as noted previously for phloem fibers and parenchyma. The interpretation of these cells as parenchymatous is supported by the general absence of sclerenchyma from the primary cortex of conifers (Esau, 1977).

Cork of branches about 4 years old forms a continuous layer about 0.1 mm thick (Fig. 43). Phellogen and phelloderm are not recognizable. Phellem is composed of radial files of thin cells that are about 20 µm wide, less than 5 um thick, and square in tangential view. Additional layers of cork within the secondary phloem had not yet been produced by these young branches, and bark of older stems has not been found.

Leaves and Leaf-bearing Shoots

Description -

Leaves have been found attached only to small twigs. These twigs are consistent in structure and size. Leaves or leafy shoots have not been found attached to the associated woody branches. Shoots vary from just over 1 mm in diameter at the base to less than 0.8 mm in distal regions. The base of the shoot is slightly swollen and is surrounded by persistent, decussate scale leaves (Figs. 52, 53). Scale leaves are up to 3 mm long and are broadly ovate. A single resin duct occurs centrally and a small vascular trace is found adaxial to it. One or two layers of elongate fibers, about 15 µm in diameter, occur on the abaxial surface. On the adaxial side is a zone of generally larger, thin-walled cells that often contain a dark substance. This adaxial layer is very thin in lateral and distal regions. Stomata are not present on the scale leaves. Foliage leaves arise decussately at intervals of about 1.4 mm (Fig. 51).

Vascular tissue in leaf-bearing shoots forms 4 wedge-shaped bundles that surround a pith of 0.1 - 0.2 mm in diameter (Figs. 53, 54). A small amount of secondary xylem and secondary phloem is present. Leaf traces pass into decurrent leaf bases a short distance before the leaf abruptly departs. These decurrent leaf bases form the bulk of tissues external to the vascular cylinder. A single resin duct originates in the cortex soon after departure of the preceding leaf and before the formation of the expanded leaf base. If marginal resin ducts are present in the leaf, they are formed at or near the point of departure of the blade. Large, intercellular spaces are lacking in the mesophyll of the leaf bases.

Leaves expand abruptly to maximum diameter almost immediately after departure. Leaves are 0.7 - 1.5 mm wide and 0.3 - 0.4 mm thick, varying from broadly flattened to oval in cross-section (Figs. 58 - 60). Length has not been determined.

The vascular bundle is 1/3 to 1/2 the leaf thickness in diameter. Some activity of a vascular cambium is evident. The vascular tissue is surrounded by a poorly organized parenchymatous sheath and lacks an endodermis (Figs. 65, 68). Transfusion cells are present to the left and right of the vascular bundle (Fig. 65).

Photosynthetic cells form a regular network of transverse plates of cells and large intercellular spaces (Fig. 69).

No organization of mesophyll into a palisade layer is evident.

The conspicuous hypodermis is continuous except in stomatal areas (Fig. 58). Cells of the hypodermis are circular in cross-section, elongate longitudinally, and filled with dark substances (Figs. 58, 65). Walls of these cells are not heavily thickened. Cells similar to those of the hypodermis are present in clusters above and below the vascular bundle (Figs. 65, 68).

The cells of the epidermis are also filled with dark substances (Fig. 65). Epidermal cells are longitudinally elongate, about 20 µm wide and 100 µm long. They may be irregular in shape when associated with stomata. Cell walls are straight to slightly wavy (Fig. 71).

Stomata are restricted to two broad bands on the abaxial surface and are irregularly distributed. Guard cells are usually parallel with the long axis of the leaf, although some may be at an oblique angle (Fig. 70). Stomata are paracytic and monocylic, with usually 2 polar subsidiaries and 2 - 4 lateral subsidiaries (Fig. 72). Guard cells are about 40 µm long and 15 µm wide and are slightly sunken.

Smaller leaves normally have a single resin duct between the vascular bundle and the abaxial epidermis (Fig. 58). Many of the larger leaves and a few of the smaller ones have three resin ducts: one beneath the vascular bundle and one at each margin (Fig. 60). All resin ducts are in contact with the hypodermis (Figs. 65, 68, 73). Thin-walled epithelial cells line the ducts. The median resin duct is slightly larger (about 40 μm wide) than the marginal ducts (about 25 μm wide).

Discussion -

The occurrence of many shoots that have an intact base and attached leaves indicates an abscission of branch units as in other species of *Metasequoia*. The interpretation of these as "short shoots" is also supported by very short internodal distances. Decussate leaf arrangement is typical of *Metasequoia*, but as noted by Christophel (1976) this arrangement may occur infrequently on shoots of other Taxodiaceae, and a decussate arrangement may not always be apparent on shoots of *Metasequoia*. However, examination of a large number of specimens from the Princeton chert reveals consistency in leaf arrangement. Decussate leaf arrangement in *Metasequoia* is clearly distinguishable from the spiral arrangement of other genera of the Taxodiaceae when shoots are examined in cross-section (Figs. 54, 56, 57).

Single-veined, flattened, needle-like leaves are common to many groups of conifers. The absence of an endodermis and the presence of a resin duct between the vein and the abaxial epidermis are features restricted to the Cupressaceae, Taxodiaceae, Podocarpaceae, Taxaceae, and Cephalotaxaceae. Members of the last three families tend to develop distinct palisade layers and bundle sheaths and do not compare well with the Princeton fossils. Nor is there evidence of other remains of these families in the chert; wood and reproductive structures would be clearly distinguishable from those present. The Cupressaceae has predominantly scale-leaves; some species of Juniperus are exceptions.

The fossil leaves most closely resemble those of some Taxodiaceae. Within this family, Taxodium (Fig. 64) and Glyptostrobus bear superficial similarity to the fossil leaves with only one resin duct. However, the leaves of Taxodium have a bundle of heavily thickened sclerenchyma between the vein and the adaxial epidermis (Fig. 67). These sclereids have not been found in the fossils. Hypodermis-like cells with dark contents that extend into this region in the fossil leaves should not be interpreted as heavily lignified cells (Fig. 65). In addition, stomata are irregularly transverse in Taxodium, but are longitudinally oriented in Metasequoia, Sequoia, Glyptostrobus, and the Princeton fossil leaves (Stebbins, 1948; Chaney, 1951). Glyptostrobus leaves are similar to the single duct leaves of the fossil, but other genera of this family bear less resemblance.

Within the Taxodiaceae, three resin ducts may be found in leaves of Sequoia (Fig. 63), Metasequoia (Fig. 62), and Cunninghamia. The resin ducts of Cunninghamia tend to be internal, that is, they are surrounded by cells of the mesophyll. In Sequoia, Metasequoia, and the Princeton fossils resin ducts are external, contacting the hypodermis (Figs. 65, 66).

Leaves of Sequoia sempervirens tend to develop a strong palisade of tanniniferous cells that appear to have no counterpart in the fossil leaves. Leaves of M. glyptostroboides bear both similarities and dissimilarities to the fossil leaves. However, for reasons such as decussate leaf arrangement and attachment or association with twigs, wood, pollen cones, and seed cones of Metasequoia, the fossil leaves are assigned to Metasequoia.

It has been noted by Sterling (1949) and Harr and Ting (1976) that M. glyptostroboides does not have a hypodermis, but some smaller leaves that I have examined do show development of this layer (Figs. 62, 66). Both the epidermis and this hypodermis-like layer are highly tanniniferous and bear resemblance to surface layers of the fossil. In larger leaves of M. glyptostroboides, arm palisade mesophyll lies directly beneath the adaxial epidermis (Sterling, 1949). This type of mesophyll was not found in the Princeton fossil, but the organization of the spongy mesophyll of living M. glyptostroboides leaves into transverse plates is similar to the fossil (Fig. 69, 75).

Although the structure of mesophyll and hypodermal layers of some leaves of M., glyptostroboides may resemble that of the Princeton fossil, the typical structure of living Metasequoia leaves as described by Sterling (1949), Florin (1952), Böcher (1962), and others represents a major disparity with the fossil material. The variability exhibited in living material indicates that this feature may have limited significance. However, variability within the fossil leaves of the

Princeton chert does not include the structure typical of *M. glyptostroboides*.

The walls of epidermal cells of *M. glyptostroboides* are highly undulate (Fig. 74), an unusual feature within the Taxodiaceae. Walls of some epidermal cells of the fossil leaves are also undulate, but only slightly so (Fig. 71). Other species of fossil *Metasequoia* show varying degrees of epidermal wall undulations (Miki, 1941; Sveshnikova, 1975).

Leaves of both *M. glyptostroboides* and the Princeton fossil are hypostomatic and have indistinct rows of longitudinally oriented, monocyclic stomata arranged in two broad bands (Figs. 70, 75). Miki and Hikita (1951) examined fossil and living leaves of *Metasequoia* and *Sequoia* in an attempt to determine possible chromosome numbers of fossil species. In closely related species of plants, differences in chromosome number are reflected in epidermal cell and guard cell stomatal size. *M. glyptostroboides*, with a chromosome number of 2N = 22, has epidermal cells with a mean width of about 16 µm and length of about 50 µm and guard cells stomata of about 42 µm in length. *S. sempervirens*, with a chromosome number of 2N = 66, has epidermal cells of about the same width as *Metasequoia*, but of over twice the length, and has guard cells stomata about 58 µm long (Miki and Hikita, 1951). Standard deviation of these guard cell stomatal lengths is less than 5 µm. Fossil species of *Sequoia* and *Metasequoia* measured by Miki and Hikita were consistent with living species and they concluded that chromosome numbers of the fossils were the same as those of living representatives. Leaves of the Princeton material have epidermal cells of about 50 μm in length and 20 μm in width and have guard cells stomata about 40 μm long. This would indicate that the chromosome number for the Eocene Princeton species may have been similar to that of the living M. glyptostroboides.

The presence of one or three resin ducts in the Princeton fossil leaves is another contrast to M. glyptostroboides. Both leaf types are borne decussately on similar twigs of the fossil material. Marginal ducts tend to occur on larger leaves, although large leaves may have a single duct and some smaller leaves have three. The possibility of there being two species represented is not supported by any other features.

All sizes of leaves of M. glyptostroboides consistently have three resin ducts. Marginal resin ducts appear at or near the point of departure of the leaf blade and extend to very near the leaf tip, so that virtually the entire length of the leaf is furnished with three resin ducts. The median duct originates in the cortex of the stem below the decurrent base of the leaf and extends slightly beyond the marginal ducts in the leaf tip. It is not possible, therefore, that the single duct leaves in the Princeton fossil could be the proximal or distal ends of a leaf typical of M. glyptostroboides.

Principal differences between leaves of M.

glyptostroboides and the Princeton fossils are in anatomical structure. These features are not recognizable from compression remains. Permineralized leaves and shoots of Metasequoia have been described from the Paleocene Fort Union Formation of North Dakota by Harr and Ting (1976). Harr and Ting have grouped their Metasequoia remains into four "types" that apparently represent varying degrees of distortion and degradation. All four types probably are of the same species, but this is not clearly stated by the authors. These leaves apparently have three resin ducts, but the lateral ducts are adjacent to the abaxial surface and somewhat removed from the margin of the leaf. This is a feature more typical of Sequoia than Metasequoia, although leaves are borne decussately. A distinct hypodermis is present, as in the Princeton fossils. Until the Fort Union leaves are more clearly described and circumscribed, it is difficult to speculate on their relationship to M. glyptostroboides or the Princeton fossils.

Two shoots and a few leaves have been found in the Princeton chert that differ in appearance from other remains. The shoot in Fig. 55 produces spirally arranged leaves with three resin ducts. Leaves such as in Fig. 61 generally have a distinct palisade of elongate cells resembling that found in Sequoia (Fig. 63). These remains may represent the rare occurrence of a second taxodiaceous genus, such as Sequoia, within the fossil flora. They may also be aberrant forms of the same species of Metasequoia to which all other remains belong. Their presence is recorded, but no conclusions may be drawn from them due to the limited number of specimens available.

Roots

Roots are heteromorphic. Vigorous long roots (Figs. 76, 78) have 5 to 6 protoxylem ridges and are rarely found without considerable secondary growth. Short roots (rootlets) (Fig. 90) have 2 or 3, sometimes 4, protoxylem ridges and are found with little or no secondary development. Both types are found in attachment (Fig. 89). These two types of roots are described separately.

Long Roots, Description -

The primary xylem of long roots may be somewhat compact (as in Fig. 88) to highly parenchymatous. Surrounding the primary vascular tissue is both a pericycle and endodermis (Fig. 92). The stele occupies roughly 1/3 the diameter of the root.

Inner cortex is thin-walled and rarely preserved. Outer cortex and epidermis are somewhat more resistant. Cortical cells are cylindrical to somewhat broader tangentially, about 40 µm in diameter and 80 µm long. The cortical cells adjacent to the endodermis develop phi-shaped wall thickenings on radial and horizontal walls (Fig. 92). These thickenings may be present on other cortical cells in older roots. The phi-shaped thickenings may remain even if inner cortical cells have not been preserved) and form a ring or rings of small dots about the stele. Cells of the epidermis are not distinct from cortical cells and do not have root hairs. Intracellular fungal hyphae occur throughout the root cortex, although they are most abundant in cells of the inner cortex (Fig. 91). These hyphae are highly branched within the host cells and are very irregular in shape.

Secondary vascular tissue and cork are initiated at about the same time (Fig. 93). The vascular cambium is first formed in the innermost layer of primary phloem. Growth may proceed until these isolated cambial zones have formed wedges of secondary tissue well beyond protoxylem poles before fusion to form a cylinder. The first cork cambium is formed within the pericycle (Fig. 93). Primary cortex is sloughed soon after secondary development begins (Fig. 88).

Wood -

Transverse Section:

Growth rings are indistinct, usually delineated by only one or two rows of fiber tracheids (Fig. 76, 80). Tracheids are 30 - 60 µm in tangential diameter, square to slightly elongate radially. Wood parenchyma is diffuse, common to abundant, and similar in diameter to the tracheids. Resin ducts are present in larger roots and are similar in structure to those of the stems.

Tangential Section:

Tracheids are over 6 mm in length. Tangential pits are uncommon. Rays are uniseriate, occasionally with paired cells in the body of the ray, and are 1 to 15 cells tall (Fig. 79). Ray cells are about 20 µm in tangential diameter and 20 - 25 µm high.

Radial Section:

Tracheids have uni- to triseriate, opposite pitting on radial walls. Pits are about 15 µm in diameter. Crassulae are distinct when pits are bi- or triseriate (Fig. 81). Two to six taxodioid pits occur in the crossfield (Fig. 82). Ray cells have smooth horizontal and tangential walls.

Wood parenchyma cells are about 100 - 200 µm high and usually filled with resin (Fig. 79). Horizontal walls are smooth to bead-like.

Secondary Phloem -

Preservation of root phloem is superior to that of stem phloem. The basic pattern of alternation of uniseriate tangential rows of sieve cells, parenchyma, and fibers, as noted for stems, is present in the roots (Fig. 84). Variability of this pattern is basically a result of a tendency to reduce the number of fiber layers (Fig. 86).

Sieve cells are 20 - 40 µm in tangential diameter, and tangentially flattened; length has not been determined. Sieve areas occur on radial walls and are evenly distributed (Fig. 87).

Fibers may be squarish in cross section but are more commonly tangentially flattened (Fig. 84). No pitting has been found on fiber walls.

Parenchyma may or may not be albuminous (Fig. 86). Both types of cells are about 100 µm long. They tend to be tangentially flattened in younger phloem, but in mature phloem are expanded to the extent that sieve cells are generally constricted (Fig. 86). Radial walls of parenchyma cells have large, circular, simple pits.

Ray cells are generally more rotund than those of the wood. Ray parenchyma is rarely albuminous. Some rays are dilated peripherally for root expansion (Fig. 84).

Cork -

Additional cork cambia within the secondary phloem form an overlapping network of convex layers (Fig. 83). Cork cambium occasionally approaches the vascular cambium (Fig. 85) and may at these places be produced directly by the vascular cambium, rather than the more common derivation of phellogen by transformation of parenchyma cells within the secondary phloem. Both phellem and phelloderm are produced by the phellogen (Figs. 84, 86). Cells of the phellem are about 10 µm thick, from 10 to more than 60 µm wide, and are square in tangential view. Phelloderm is not more than two or three cells thick.

Short Roots -

Short roots are frequently but not profusely branched. Di- or triarch rootlets seldom produce secondary tissues. Tetrarch roots usually undergo limited secondary development, and may develop as long roots. Vascular tissue of smaller rootlets is limited in extent (Fig. 90). Phloem and inner cortex is rarely preserved. The cortex is similar to that of the long roots; a layer of cells with phi-shaped thickenings lies external to the endodermis and cortical cells are host to highly-branched fungal hyphae. Epidermal cells lack root hairs in all sections studied (Fig. 90).

Discussion -

Roots, stems, and branches experience quite different environmental conditions and growth varies accordingly. Brown and Panshin (1940) have noted the following differences between mature wood of roots and of stems:

1. root wood has indistinct annual rings, uniformity of growth;
2. tracheids are largest in the roots, smallest in twigs;
3. Ray volume varies little in different parts of a coniferous tree, but rays are shorter and more numerous in the roots.

These differences result in a considerably different appearance of stem and root wood, but important features of pitting, wall thickening, wood parenchyma, resin canals, etc. are the same. The root wood described here does have indistinct growth rings and shorter, more numerous rays. Tracheids are roughly equal in diameter to the larger tracheids of trunk wood, although root tracheids are more uniform in size and do not achieve as great a maximum diameter. Tracheid length in both stems and roots may exceed 6 mm. In other characters there is good agreement between root and trunk wood.

Resin cysts like those of the stems occur in the wood of larger roots. Böcher (1964) did not find resin cysts in the roots of M. glyptostroboides. However, Brown and Panshin (1940, p. 227) state that "resin canals in the conifers, if normal in the trunk wood, were also present in the root and branch wood". The "normal", rather than solely "traumatic", occurrence of resin cysts in Sequoia, Abies, and other conifers was suggested by Penhallow (1907), and the regularity of cyst production in Metasequoia would suggest their presence is normal in this genus as well.

The secondary phloem of some roots has been exquisitely preserved. This could be attributable to in situ preservation of roots and to initiation of permineralization while the roots were still alive. Although secondary phloem of stems is not well preserved, features available are common to the phloem of the roots. Böcher (1964, p. 45) noted that the secondary phloem of roots of M. glyptostroboides "corresponds entirely to that found in stems". It was noted during discussion of secondary phloem of stems that there was a strong similarity between the Princeton fossil and M. glyptostroboides. My observations support this contention.

Although fibers tend to be squarish in section view and very heavily thickened in phloem of the stems, fibers of root phloem are more commonly tangentially flattened.' The variability of this feature in both living and fossil material diminishes its significance as a comparative feature. Similarly, variability in the sequence of deposition of cell types, as noted previously for stem phloem, is present in both the Princeton fossil and M. glyptostroboides. The structure of the fossil phloem is typical of many Taxodiaceae, as noted previously, and is essentially the same as that of M. glyptostroboides.

Phelloderm and phellem of cork zones of roots are similar in structure and thickness to those of M. glyptostroboides (see Böcher, 1964). Initiation of cork cambium in conifers generally occurs within secondary phloem by conversion of parenchymatous cells to meristematic cells (Esau, 1977). An unusual mode of phellogen initiation was noted in the fossil material; in cross section, a cork layer arches through the phloem and at one end approaches the vascular cambium (see Fig. 85). At that point meristematic cells of the phellogen may have been derived directly from the vascular cambium. The layer of cork would presumably have been enlarged tangentially, had growth continued, and more secondary phloem been built up between the two cambial zones. The extent to which this form of development occurred in the fossil Metasequoia is unknown.

The appearance of the mature "polyderm", with overlapping, arching bands of cork separated by mature phloem, is similar in both the Princeton fossil and M. glyptostroboides.

Hida (1952) found that the numbers of protoxylem poles in long and short roots was a fairly consistent feature within species of the Taxodiaceae. Hida distinguished Metasequoia, Sequoia, Sequoiadendron, Taxodium, and Glyptostrobus as having tri- to polyarch long roots and di- to triarch short roots, noting that organization in these genera was essentially the same.

Short roots and young long roots show the following features indicative of association with endotrophic mycorrhizae:

1. lack of root hairs (Fig. 90);
2. presence of a layer of phi-cells, cells with phi-shaped wall thickenings, external to the endodermis (Fig. 92).

Phi-cells are believed to limit the inward development of fungal hyphae and prevent infection of the stelar region (Böcher, 1964). It is likely, then that the highly-branched fungal hyphae within cortical cells of the roots (Fig. 91) were mycorrhizal and not simply a sign of decay. Similar rootlet structure is found in M. glyptostroboides and other Taxodiaceae (Böcher, 1964).

Fungi

Several different types of fungi were found within all organs of the fossil Metasequoia (Figs. 40, 41). The mycorrhizal fungi of root cortex are morphologically distinct from these other forms. The abundance and diversity of fungi indicate rapid decay within the soil of the ancient marsh. This activity also suggests that the marsh may have been nutrient rich and that the water was probably neither deep nor strongly acidic, although many fungi are highly tolerant of low pH.

Seed Cones and Seeds

Description -

Seed cones are uncommon relative to the vegetative material in the chert; 30 cones have been recognized during this study. Cones are about 17 mm wide, 25 mm long (Figs. 94, 95).

Seed cones are borne terminally on a sparsely-leaved stalk or peduncle about 2 mm wide and of undetermined length (Fig. 96). The leaves are borne decussately, are about 1 mm wide and less than 2 mm long, and have a single resin duct abaxial to the vascular bundle. These reduced leaves do not resemble the broad, thin scale leaves found at the bases of vegetative shoots. Stalks are roughtly four-sided externally and resemble small, vegetative branches in anatomy.

The cone axis is about 4 mm in diameter, considerably wider than the stalk. The pith is about 0.6 mm in diameter.

Cells of the pith are about 30 - 50 µm wide, 70 µm long, thick-walled, and bear simple pits (Fig. 99).

Secondary xylem is abundant and composed mostly of small, thick-walled tracheids less than 20 µm in diameter. No growth rings are apparent within the wood, although a thin zone of larger tracheids is present at the inner margin. Tracheids have a uniseriate row of circular bordered pits on radial walls. Rays are uniseriate, and 1 to 12 cells high (Fig. 97). Resin cysts usually occur in a nearly continuous tangential band in the later-formed wood and may be present elsewhere in the wood as well (Fig. 98, 100). Resin cysts as well as other features of the wood resemble those of small vegetative branches.

Secondary phloem is thin (Fig. 100), but shows regular deposition of tangential bands of sieve cells, fibers, and parenchyma, as is found in phloem of stems and roots.

Primary cortex is composed mostly of large, thin-walled parenchyma cells and cells with dark contents. Sclereids as large as 150 µm in diameter with heavily thickened walls are present in the cortex. Secondary cortex is thin to apparently absent (Fig. 100). Where cork is absent, cells of the surface layers are heavily thickened.

About 30 cone scales are borne in a decussate arrangement. The [illegible]st proximal and distal pairs of scales are smaller than the rest (Fig. 94), are nearly parallel with the cone axis, and have not been found to bear seeds. Lower cone scales become reflexed during development (Fig. 102).

The downward direction of these lower scales may complicate interpretation of structure. For example, the cone shown in Fig. 95 has been sectioned near the base; the scales directed toward the top of the photograph are actually indicating the direction of the cone base. In addition, the scale numbered "7" is sectioned so that its abaxial surface is closest to the cone axis, that is, upward on the photograph.

Cone scales have a slender stalk, 2 - 3 mm wide and about 3 mm long, and are expanded distally to form a shield-shaped apex or escutcheon (Figs. 95, 101, 103 - 106). The external surface of the cone scale is irregularly hexagonal (Figs. 95, 106), and up to 15 mm wide and 6 mm high. A horizontal groove cleaves the outer surface of the scale into upper and lower "lips" which are about equal in size (Fig. 101). There is no evidence of a mucro or boss on the external surface.

A cylinder of secondary xylem, similar in appearance to that of a vegetative branch, enters the base of each cone scale (Fig. 103). However, primary xylem occurs in two horizontal bands separated by a thin band of parenchyma. This parenchyma resembles that of the cortex rather than the pith and frequently contains resin canals. Resin cysts often form a nearly complete tangential band within the peripheral secondary xylem. The vascular cylinder is deeply cleft on the adaxial side immediately after departing from the cortex of the axis (Fig. 104). The vascular tissue rapidly divides into many bundles before entering the expanded distal region of the cone scale (Fig. 105), and the bundles continue to divide until the scale margin is reached. Vascular bundles occur in an adaxial and an abaxial row within the expanded apex (Fig. 106). Bundles of the adaxial row have phloem on the adaxial side (inverted); those of the abaxial row, the abaxial side. The median bundle of the abaxial row is further from the abaxial surface than the other bundles (Fig. 106). The vascular bundles extend to near the external surface and terminate in masses of transfusion cells (Fig. 108).

Heavily thickened, elongate fibers or idioblasts that occur throughout the expanded region of the cone scales are parallel with the vascular bundles (Fig. 109). Radial files of parenchyma cells and cells with dark contents make up the bulk of the tissue in the distal regions. Resin canals are present peripheral to the vascular bundles in scale apices (Fig. 106). Surface layers of the cone scales are composed of small, heavily thickened cells and small cells with dark contents.

Seeds are inverted, with the micropyle directed toward the cone axis and are borne in a single row on the adaxial surface at the point where the scale flares. Up to four seeds have been found attached to a cone scale (Fig. 113), but most seeds have been shed prior to preservation. The maximum number of seeds per scale was presumably greater.

Seeds are flat 3 - 4 mm wide, 0.5 - 0.8 mm thick, about

5 mm long, and are comprised of two lateral wings that are hollow and a central seed body that is roughly equal in size to each of the wings (Figs. 110, 112). The seed coat is composed of: 1) an outer layer, 1 - 2 cells thick, of very thick-walled isodiametric cells less than 20 µm in diameter; and 2) an inner layer of larger, elongate cells about 40 µm wide and over 100 µm long (Figs. 111, 114). The inner layer is variable in thickness and may be weakly developed between the cavities of the seed body and wings. The margin of the seed is thin and wedge-shaped (Fig. 110). The seed base is slightly asymmetric, with the wings extending below the level of the seed body (Fig. 112). Wings narrow toward the micropylar end (Fig. 112). The nucellus is fused only at the base of the seed (Fig. 112). Embryos have not been preserved within the seeds.

Discussion -

The fossil seed cones resemble those of *Metasequoia glyptostroboides* in all features examined (see Hu and Cheng, 1948; Stebbins, 1948; Sterling, 1949; Chaney, 1951; Florin, 1952; Hida, 1957, 1961; Schwarz and Weide, 1962; and others). Within the Taxodiaceae, *Metasequoia* is the only genus with decussate cone scales and sparsely leaved stalks or peduncles (Stebbins, 1948; Chaney, 1948, 1951; Li, 1964; Christophel, 1976).

Hida (1957, 1961) recognized five groups within the Taxodiaceae on the basis of cone scale development, morphology, and vascularization. <u>Sequoia</u>, <u>Sequoiadendron</u>, and <u>Metasequoia</u> form Hida's "Group IV" and share the following characteristics:

1. bract and ovuliferous scale are indistinguishable throughout development;
2. mature scales are peltate and have a labial external appearance; and
3. the bract tip is barely noticeable (Hida, 1957 p. 51).

Sterling (1949 p. 467) believes that the horizontal groove is "apparently marking the phylogenetic boundary of the bract and seed scale complex". Hida (1961), however, believes that the groove is not coincident to this boundary. This argument is based upon developmental studies; anatomical studies of mature scales do not distinguish bract from scale in the fossil cones. Vascularization of cone scales is similar in both <u>M</u>. <u>glyptostroboides</u> and the Princeton fossil (compare Figs. 103 - 106 with Sterling, 1949 Fig. 38).

Seeds of <u>Metasequoia</u>, <u>Sequoia</u>, <u>Sequoiadendron</u>, <u>Athrotaxis</u>, <u>Taiwania</u>, <u>Cunninghamia</u>, and the Princeton cones are inverted during development of the cone scale so that the micropylar end is directed toward the cone axis. Cones of <u>Glyptostrobus</u> and <u>Taxodium</u> bear erect seeds (Stebbins, 1948). As many as four seeds have been found attached to a single cone scale of the fossil species. <u>M</u>. <u>glyptostroboides</u> usually bears 5 - 8 seeds per cone scale (Dallimore and Jackson, 1966), but a comparison with the fossil is limited by the uncertainty of the numbers of seeds originally borne by the fossil cones.

Seeds of Sequoia, Sequoiadendron, and Metasequoia are all similar in appearance. Stebbins (1948) Gaussen (1955), and Chandler (1964) note that Sequoia seeds tend to have narrower wings than the other two genera, but in all three genera the wings are roughly equal in width to the seed body. Chandler (1922, 1964), in her comparison of Sequoia couttsiae with other Taxodiaceae, notes such differences as size, texture and surface striation, and shape of hilar scar among Sequoia, Sequoiadendron, and Metasequoia. Texture of the Princeton seeds has not been determined. In addition, the great variability in size and shape of seeds of the living redwoods makes further comparisons with the fossil seeds difficult, particularly when the limited number of fossil specimens for which this information is available is considered.

The absence of a growth ring within the wood of the cone axis is evidence that the cones matured in a single year, as cones do in Metasequoia and Sequoia.

Cones with peltate scales, winged seeds, and decussate arrangement of scales are also found in Chamaecyparis, Cupressus, and Fokienia of the Cupressaceae. However, cones of these three genera differ from the Princeton fossil specimens in the following ways:

1. scales are fewer per cone;
2. the scale apex or escutcheon tends to be ovoid to circular in tangential view;
3. scales have a mucro or boss on the external surface; and

4. seeds are erect and borne at the base of the scale stalk (Dallimore and Jackson, 1966).

Pollen Cones

Description -

Pollen cones are 1.0 - 3.0 mm long and 1.2 - 2.9 mm in maximum diameter, each consisting of a central axis that bears sporophylls in the terminal region and sterile scale-like leaves below (Figs. 115, 116, 136). One cone (Fig. 117) is attached to a decussately branched stem fragment. This is the only specimen found showing cone attachment. Proximal to this cone is attached a branch that lacks sporophylls, but in vegetative respects resembles the base of a pollen cone more closely than it does vegetative buds and leafy shoots of <u>Metasequoia</u> which are found in association. Between the cone and the proximal end of the axis there are four pairs of decussately arranged branches, as evidenced by branch traces, scars, and subtending leaves. Whether these branches are fertile or vegetative cannot be determined, but it appears likely that pollen cones were borne on decussately-branches axes, as they are in <u>M</u>. <u>glyptostroboides</u> (Merrill, 1948; Field Museum Herbarium specimen #1289779) and <u>M</u>. <u>occidentalis</u> (Chandrasekharam, 1974). Also, it has not been possible to determine whether the attached pollen cone was borne as one of a pair of cones with the distal portion of the axis missing, or in a terminal position on the axis. A pollen cone may terminate the specialized cone-bearing shoots of M. glyptostroboides and M. occidentalis; therefore, either interpretation of the fossil is compatable with other species of Metasequoia.

About 30 sporophylls, each bearing three adaxially attached pollen sacs, diverge from the cone axis (Fig. 132). Sporophylls are helically arranged on immature cones (Fig. 122) but irregularly disposed on mature specimens, where the helical arrangement is shown only by the resin ducts of the axis (Figs. 123, 124). Immature cones are represented by several stages of development (Fig. 119 - 122). Some are very immature and clearly show the spiral arrangement of sporophylls (Fig. 122). In longitudinal view specimens of this type exhibit a very short fertile axis (Fig. 120). Somewhat more mature cones show considerable elongation of the axis (Fig. 119). There is very little change in axis length from this stage of development to cones that are apparently near or at sporangial dehiscence and pollen release (Fig. 116). This is unlike cones of M. glyptostroboides, where a dramatic elongation of the axis prior to pollen release carries the sporophylls beyond the tips of the subtending leaves.

The sterile zone of isolated specimens is 0.9 - 2.5 mm long, and leaf arrangement is decussate. Leaves are scale-like near the base of the axes, but increase in size distally (Figs. 116, 119). Distal leaves imbricate and completely enclose the fertile region (Figs. 115, 116, 119, 120). Microsporangia of larger cones are typically filled with well-developed pollen grains (Figs. 115, 116).

Axis:

In the vegetative region the axis measures approximately 0.6 mm in diameter and exhibits a prominent parenchymatous pith. Longitudinal sections of the pith reveal isodiametric cells with amber-colored contents (Figs. 120, 125). The vascular tissue is arranged as four wedged-shaped bundles that are composed mainly of radially aligned secondary tracheids (Fig. 126). Vascular cambium and secondary phloem are poorly preserved. The cortex is 30 - 120 µm thick and consists of irregularly shaped parenchyma cells (Fig. 125) and small, inconspicuous resin canals which are often difficult to distinguish from areas of broken tissue.

The fertile portion of the axis is smaller and often poorly preserved (Figs. 115, 116, 118). In cones of M. glyptostroboides secondary vascular tissues are absent from this zone and primary tracheids are poorly developed (Sterling, 1949). In the fossils, vascular tissues are not present in even well preserved cones (Fig. 118). Resin canals are typically a prominent feature of the axis at this level (Fig. 130). Individual canals either continue from the sterile zone or originate near the center of the axis. They increase in size distally, and then bend outward to enter the sporophylls (Figs. 130, 131). Resin canals occupy a relatively larger proportion of the axis near its apex (Fig. 123).

Vegetative Leaves:

Seven to eight pairs of decussately arranged vegetative leaves subtend the fertile region of each cone (Figs. 116, 118). Leaves increase in size distally, with the distalmost three or four pairs overarching and enclosing the fertile region (Figs. 116, 119). Similar subtending leaves are present in the pollen cones of M. glyptostroboides. The leaves of the fossil are relatively thick at the base, with tapering margins. Distally they are laterally expanded and reduced in thickness (Figs. 115, 116, 117, 128). The overall leaf shape is ovoid with a bluntly pointed apex.

Internally, each leaf exhibits a prominent resin canal with amber-colored contents and two or three layers of somewhat flattened epithelial cells (Fig. 127). A zone of longitudinally elongated fibers occurs on the abaxial side of the resin canal. Adaxially, the cells are larger and thin-walled (Fig. 127). The latter zone of thin-walled cells is reduced in thickness both distally and laterally and is absent from the leaf margin (Fig. 128). Individual leaves are vascularized by a terete strand of six to eight tracheids near the adaxial margin of the resin canal (Fig. 127). A single layer of relatively thin-walled cells forms an indistinct bundle sheath. The epidermis is composed of longitudinally elongated cells that may be slightly laterally expanded in transverse section. Dark contents are frequently present within cells of the abaxial epidermis.

Sporophylls:

The sporophylls are roughly cylindrical at the point of attachment (Fig. 134). Individual sporophylls extend toward the periphery of the cone, bend distally and terminate in a radially flattened, spatulate lamina (Figs. 130, 131). The change in shape from cylindrical to flattened is abrupt. Three sporangia are attached to the abaxial surface of the sporophyll at the junction of the stalk and distal lamina (Figs. 131, 132). Sporangial attachment extends for a short distance along the abaxial surface of an extremely abbreviated hypopeltate keel (Fig. 131). Transverse sections of the stalk reveal a prominent resin canal (Figs. 132, 134) surrounded by a few layers of cortical cells. In the region of sporangial attachment a smaller resin canal appears on each side of the large canal (Figs. 115, 130). These lateral canals are short and terminate before the central canal. Although the central canal seems to have divided, the three canals are not contiguous. Similar levels of M. glyptostroboides microsporophylls reveal only one resin canal in this region. Vascular tissue can not be identified in even the best preserved sporophylls of the fossil material, a feature that agrees with the vascularization of the extant species (Sterling, 1949).

Sporangia:

The sporangia are oblong, with the long axis extending inward and downward from the point of attachment (Figs. 115, 116). Individual sporangia measure up to 0.8 mm long and

0.3 - 0.35 mm in diameter. As in the mature sporangia of M. glyptostroboides, sporangial walls are one cell thick, with remnants of tapetal cells sometimes adhering to the inner surface of the wall (Fig. 133). However, unlike the extant species, sporangia of the Princeton fossil exhibit no evidence of an adaxial, longitudinal line of dehiscence; the sporangial wall cells have uniformly thin walls (Fig. 133). Thickenings of the external cell walls, as are found in M. glyptostroboides (Sterling, 1949), have not been observed.

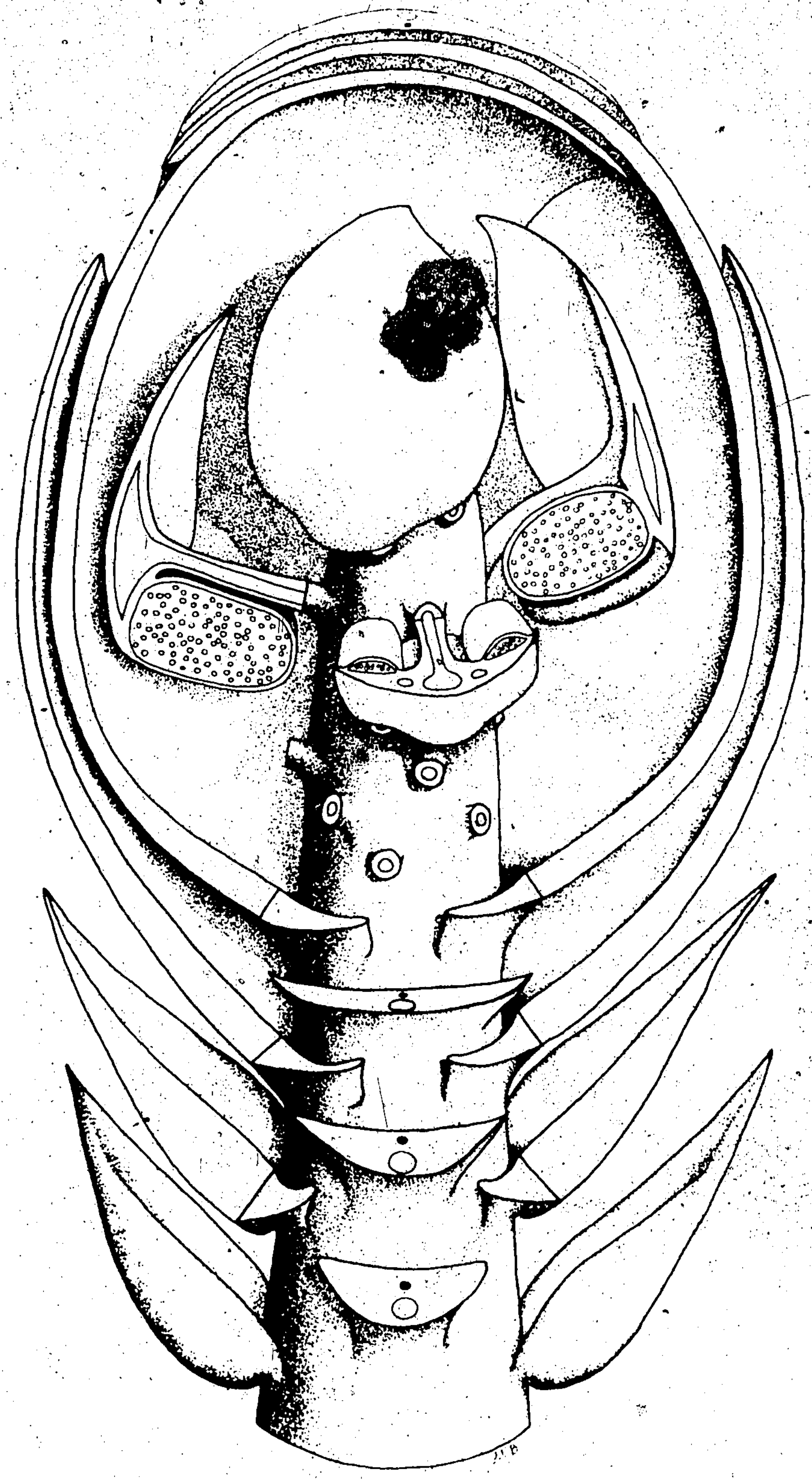
Pollen:

Sporangia of relatively mature cones contain a large number of subspheroidal, papillate pollen grains. Equatorial measurements of 100 grains are 19 - 27 µm, with a mean diameter of 22.5 µm.

Discussion -

The fossil pollen cones are similar to cones of M. glyptostroboides in size, shape, mode of sporangial attachment and number of sporangia per microsporophyll. The arrangement of the cones on the plant is probably similar for the two species as well. Other features of the fossil that agree with M. glyptostroboides are decussate phyllotaxis of the subtending leaves and an irregular arrangement of sporophylls on relatively mature specimens. General features of the pollen and many histological details described above are also comparable for the two species.

Text - Fig. 3. Reconstruction of pollen cone of _Metasequoia milleri_. Many leaves and sporophylls have been removed or cut away for clarity. For further explanation of details see text.


J.B.

Features that distinguish the fossil cones from specimens of M. glyptostroboides include the number of resin canals in the distal region of the microsporophylls and histology of the sporangia. The fossil cones may also exhibit several distinct developmental features. The Eocene specimens have two small resin canals that flank the larger, centrally located canal in the distal zone of the microsporophylls. The former have not been observed in cones of M. glyptostroboides. The sporangial walls of the fossil may also be distinguished from those of the extant species by an absence of the adaxial, longitudinally oriented line of dehiscence and by the absence of thickenings on the external cell walls.

Developmental aspects of the fossil cones have been interpreted by comparing specimens preserved at different developmental stages and provide the basis for suspecting that a unique and unexpected set of ontogenetic events occurred in these cones. The axis of the fertile zone underwent considerable elongation during the early stages of sporophyll differentiation (compare Figs. 116, 119, 120), but there is no evidence to suggest that additional elongation of the axis facilitated pollen dispersal as it does in pollen cones of M. glyptostroboides. The most mature cones of the fossil have little or no pollen remaining within the pollen sacs but show no evidence of axis elongation. Rather, the overarching bracts of these specimens are reflexed away from the sporophylls as if to allow for pollen excape via alternate means. If correctly interpreted, this represents a significant dissimilarity in the developmental and dispersal mechanisms of the Princeton species and M. glyptostroboides.

Equally intriguing and unexpected is the discovery that sporophylls of immature fossil cones are borne in a helical arrangement. In both fossil and extant species the sporophylls of relatively mature specimens show no regular phyllotaxis. For the extant species it has been assumed that the irregular arrangement was the result of developmental torsion acting upon sporophylls that were initiated in an opposite and decussate fashion (Sterling, 1949). The assumption was supported by the opposite arrangement of leaves, branches and other appendages of M. glyptostroboides shoots, and by the decussate phyllotaxis of the leaves that subtend the pollen cones of both M. glyptostroboides and the fossil. However, the helical arrangement of sporophylls on the fossil specimens calls to question the manner in which microsporophylls of M. glyptostroboides are initiated, and amplifies the continued need for detailed developmental studies in many extant gymnosperm taxa. If opposite or whorled phyllotaxis is a derived condition within the Taxodiaceae, as it may be in conifers in general (Namboodiri and Beck, 1968), then the helical initiation of microsporophylls in M. milleri may reflect the ancestral appendage arrangement for the genus as a whole.

SYSTEMATIC DESCRIPTION

Order Coniferales

Family Taxodiaceae

Genus Metasequoia Miki, 1941

Metasequoia milleri Rothwell and Basinger, 1979

ORIGINAL DESCRIPTION: (Rothwell and Basinger, 1979). Anatomically preserved pollen cones 1.0 - 3.0 mm long, 1.2 - 2.9 mm in diameter, subtended by vegetative zone 0.9 - 2.5 mm long. Subtending leaves overarch and enclose a fertile zone consisting of approximately 30 sporophylls. Sporophyll arrangement helical, becoming irregular in mature cones. Sporophyll unvascularized, with one resin canal in the stalk and three resin canals distal to the zone of sporangial attachment; each sporophyll bearing three sporangia. Sporangial wall of one cell layer of uniformly thin-walled cells with no specialized zone of dehiscence. Pollen subspheroidal, 19 - 27 um in diameter, verrucate and orbiculate, with erect protruding leptoma.

EMENDED DIAGNOSIS: Trees with long shoots bearing leaves at widely spaced intervals, and short, deciduous shoots with internodes of about 1.5 mm and bulbous clusters of several pairs of scale leaves at base of shoot. Scale leaves decussate, ovate, persistent. Foliage leaves decussate, usually rotated into a distichous position, linear, 0.7 - 1.5 mm wide, flattened, uninerved, very short petiolate, with a decurrent base; lamina containing one median resin duct below the vascular bundle, or one median resin duct and two marginal ducts, all resin ducts in contact with the hypodermis; bundle sheath indistinct, parenchymatous; palisade mesophyll poorly differentiated or absent; hypodermis distinct; hypostomatic, stomata in two broad bands, guard cells parallel to long axis of leaf; epidermal cells with straight to slightly wavy walls. Mature wood with distinct growth rings; tracheids to 95 um in diameter and 6 mm long, with uniseriate to quadraseriate, opposite pitting on radial walls, pits 17 - 23 um in diameter, crassulae distinct, tangential pitting occasional in early wood; rays uniseriate, one to over 80 cells high, paired cells infrequent in body of ray, ray cells with smooth horizontal and tangential walls; cross-fields with 1 - 5 taxodioid pits; wood parenchyma diffuse, resinous, with smooth to slightly beadlike horizontal walls and taxodioid pits on vertical walls; vertical traumatic resin cysts in tangential bands, usually at the beginning of a growth increment, cysts with up to three layers of surrounding parenchyma and epithelial cells. Seed cones globose to cylindrical, up to 25 mm long, terminal on sparsely-leaved branches bearing decussate, reduced leaves; cone scales to 30, decussate, stalked, peltate or shield-shaped, outer surface transversely elliptic with a median horizontal groove, upper and lower 2 - 3 pairs of scales smaller than the rest. Seeds several per scale, attached at junction of stalk and escutcheon, inverted; seeds flattened, slightly asymmetric with 2 lateral wings equal in width to the seed body, broadly ovate, notched at base, tapering distally, about 5 mm long and 4 mm wide overall; seed coat continuous over body and wings, with an outer layer of small, thick-walled isodiametric cells and an inner layer of larger, elongate, thin-walled cells; nucellus fused to seed coat only a base. Pollen cones 1.0 - 3.0 mm long, 1.2 - 2.9 mm in diameter, subtended by vegetative zone 0.9 - 2.5 mm long. Subtending leaves overarch and enclose a fertile zone consisting of approximately 30 sporophylls. Sporophyll arrangement helical, becoming irregular in mature cones; sporophyll unvascularized, with one resin canal in the stalk and three resin canals distal to the zone of sporangial attachment; each sporophyll bearing three sporangia; sporangial wall of one cell layer of uniformly thin-walled cells with no specialized zone of dehiscence. Pollen subspheroidal, 19 - 27 um in diameter, verrucate and orbiculate, with erect protruding leptoma.

Figs. 3 - 8. Metasequoia milleri. Woody axes.

Fig. 3. Cross section of large axis showing narrow growth rings with a high proportion of early wood (right) and wide rings of principally fiber tracheids (left). P1209 A 1, SL5438, x 2.

Fig. 4. Cross section of an axis bearing an opposite pair of branches (br). P1289 B 1, SL5439, x 12.

Fig. 5. Broad growth rings (possibly compression wood) of the axis shown in Fig. 3. The transition from early to late wood is not distinct. Note traumatic resin cysts (r). P1209 A 1, SL5438, x 34.

Fig. 6. Cross section of wood showing a high proportion of early to late wood and a sharp distinction between early and late wood of a growth increment. P1102 G 1, SL5440, x 34.

Fig. 7. Cross section of early and late wood tracheids. Note considerable wall thickening in the latter. Bar equals 10 um. P1102 E, SL2640, x 580.

Fig. 8. Cross section showing early and late wood transition. P1102 E, SL2640, x 150.

Fig. 9. Metasequoia glyptostroboides. Cross section of part of growth increment for comparison with Fig. 8. x 110.

ing in the latter. Bar equals 10 um.
P1102 E, SL2640, x 580.

Fig. 8. Cross section showing early and late wood transition. P1102 E, SL2640, x 150.

g. 9. <u>Metasequoia glyptostroboides.</u> Cross section of part of growth increment for comparison with Fig. 8. x 110.

Fig. 10. <u>Metasequoia milleri</u>. Cross section of a small branch. P1249 C top 6, SL5441, x 16.

Fig. 11. <u>M</u>. <u>glyptostroboides</u>. Cross section of a small branch for comparison with Fig. 10. x 15.

Figs. 12 - 15. <u>M</u>. <u>Milleri</u>. Wood.

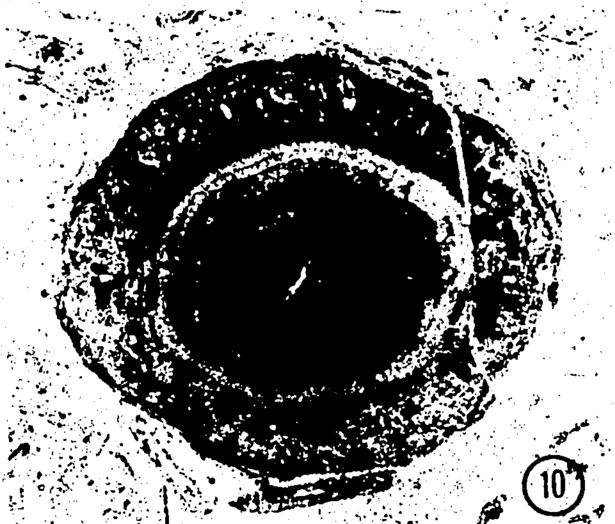
Fig. 12. Tangential section of a wood fragment from a large axis. Note tall, uniseriate rays. The ray to the left of center (at arrow) is 80 cells high. P1102 E, SL2641, x 60.

Fig. 13. Tangential pitting of tracheids. P1102 E, SL2641, x 70.

Fig. 14. Tangential section of a small branch showing uniseriate rays of moderate height. P1228 A, SL5040, x 150.

Fig. 15. Tangential section of small twig showing uniseriate rays. P1095 D d5, SL5442, x 150.

Fig. 16. <u>M</u>. <u>glyptostroboides</u>. Tangential section showing uniseriate rays and tangential pitting on tracheids. x 70.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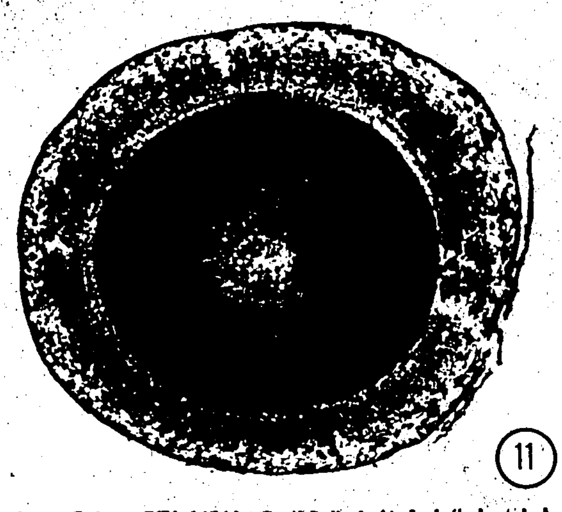
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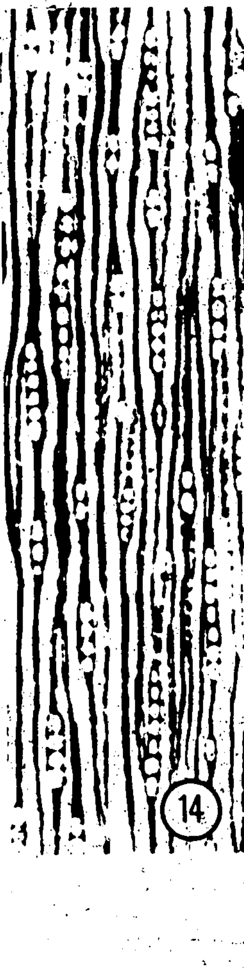
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Fig. 17. *Metasequoia milleri*. Radial section of mature wood. P1102 E, SL2642, x 130.

Fig. 18. *M. glyptostroboides*. Radial section of mature wood showing opposite pitting and crassulae. Note the single horizontal row of taxodioid pits in the cross-field. x 110.

Fig. 19. *M. milleri*. Cross-fields in branch wood. Note arrangement of pits in one to three rows. Pits appear circular and simple due to inadequate preservation of borders. P1089 C 1, SL5443, x 310.

Fig. 20. *M. milleri*. Cross-fields in mature wood with pits arranged in a single horizontal row. Compare with Fig. 18. P1099 C 3, SL5444, x 200.

Fig. 21. *M. glyptostroboides*. Cross-field pitting of branch wood. Compare with Fig. 19. x 360.

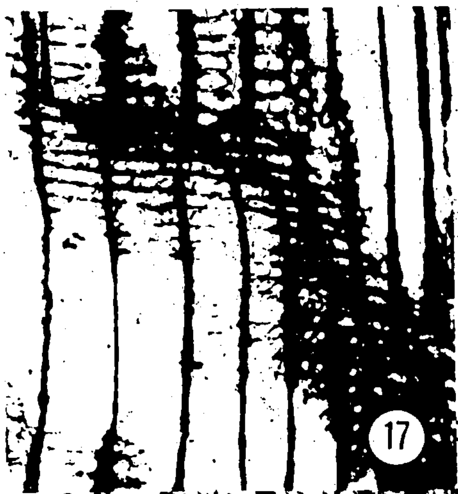
Fig. 22. *M. milleri*. Circular bordered pits on radial walls of tracheids. Note opposite arrangement. P1102 E, SL5445, x 450.

Fig. 23. *M. milleri*. Radial walls of tracheids showing opposite pitting and crassulae. P1102 E, SL5445, x 450.

Fig. 24. *M. milleri*. Radial section showing taxodioid pitting in the cross-field. P1088 B, SL5446, x 1300.

Fig. 25. *M. glyptostroboides.* Cross-field pitting for comparison with Fig. 24. x 1400.

Fig. 26. *M. milleri*. Radial section of ray parenchyma showing slight indentures (i) associated with tangential walls. P1102 E, SL5445, x 1000.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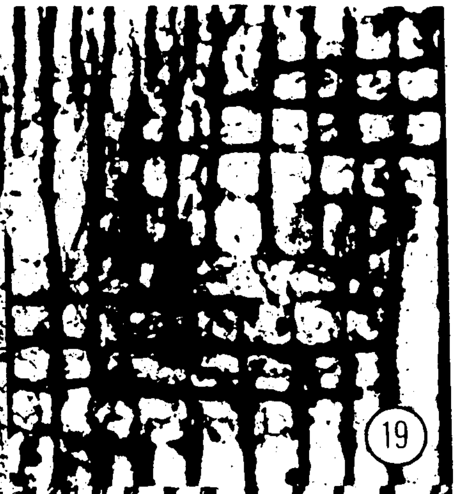
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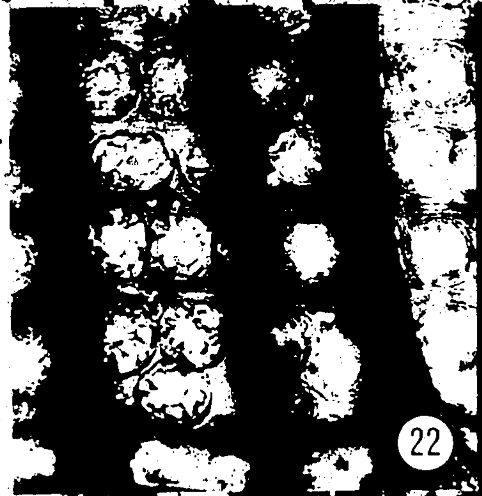
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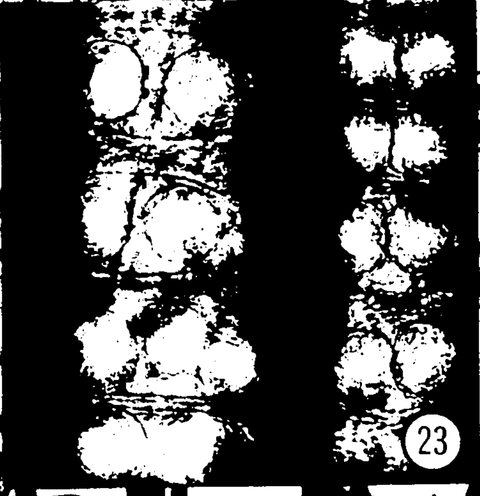
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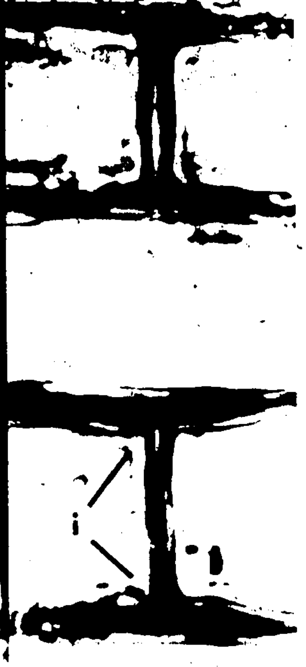

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Figs. 27 - 33. Metasequoia milleri. Wood.

Fig. 27. Cross section of traumatic resin cysts (r). Note location at the beginning of the growth ring. P1102 E, SL2640, x 190.

Fig. 28. Tangential section of one resin cyst showing the irregular shapes of the epithelial cells. P1102 E, SL2641, x 180.

Fig. 29. Radial section of several resin cysts. Note that up to 3 layers of parenchyma (at arrows) may surround resin cavities. P1102 E, SL2643, x 130.

Fig. 30. Tangential section showing wood parenchyma. Note smooth to slightly bead-like horizontal walls and large resin droplets. Note also paired cells in body of ray at lower left. P1102 E, SL2641, x 220.

Fig. 31. Bordered pits on walls of cells of the outermost parenchymatous sheath of traumatic resin cysts. Note the large number of pits and their tendency to form opposite rows. P1099 C 1, SL3559, x 220.

Fig. 32. Pitting on walls of wood parenchyma. P1088 B 2, SL5447, x 500.

Fig. 33. Spiral checks on walls of late wood. P1102 G 1, SL5448, x 110.

Figs. 34 - 36. M. glyptostroboides. Wood.

Fig. 34. Spiral checks on walls of late wood for comparison with Fig. 33. x 280.

Fig. 35. Pitting on wood parenchyma for comparison with Fig. 32. Note similarity of pits to those of the cross-field in Fig. 25. x 500.

Fig. 36. Wood parenchyma with smooth to slightly bead-like horizontal walls and dark, resinous contents. x 200.

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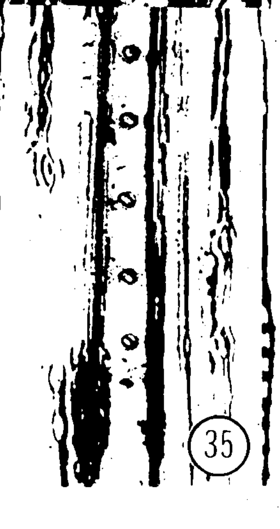

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Figs. 37 - 45. Metasequoia milleri. Woody axes.

Fig. 37. Radial section through several thracheids occluded by unidentified spherical bodies. P1102 E, SL2642, x 120.

Fig. 38. Closeup of these bodies reveals a cellular nature. P1102 E, SL5445, x 360.

Fig. 39. Tangential section of wood with "resin tracheids". Resin droplets are consistently associated with ray parenchyma. P1386 C, SL5449, x 120.

Fig. 40. Radial section of wood ray with fungal hyphae. P1088 B 2, SL3551, x 525.

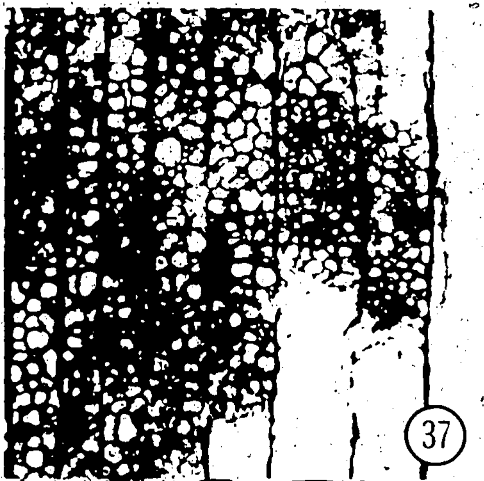
Fig. 41. Flask-shaped fungal cells within tracheid. P1089 C, SL3542, x 525.

Fig. 42. Cross section of stem showing pith, primary xylem, and first growth ring. Note that some cells of the pith are filled with dark contents. P1249 C top 5, SL5450, x 55.

Fig. 43. Cross section of bark showing vascular cambial zone (c), secondary phloem (p), and cork (ck). Cortex has been crushed. P1249 C top 1, SL5451, x 55.

Fig. 44. Longitudinal section of pith. Note simple pitting and sometimes nodular appearance of cell walls. P1249 B 3, SL5452, x 250.

Fig. 45. Radial section of 4-year-old stem. Note position of vascular cambium (c). P1249 B 1, SL5453, x 60.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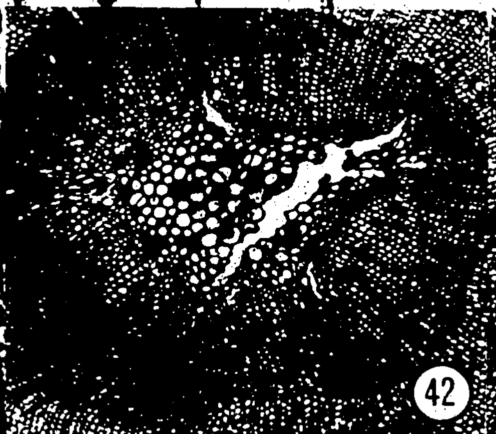
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Fig. 46. Metasequoia milleri. Cross section of secondary phloem. Note regular arrangement of tangential rows of fibers (f) and parenchyma (pa). Tangential rows of sieve cells between fibers and parenchyma have not been preserved. P1195 D bot 1, SL5036, x 150.

Fig. 47. M. milleri. Cross section of phloem showing less regular arrangement of rows of fibers (f), parenchyma, and sieve cells. Parenchyma and sieve cells are not easily distinguished. P1249 A, 1, SL5454, x 150.

Fig. 48. M. glyptostroboides. Cross section of phloem showing somewhat irregular arrangement of cell types in younger phloem. Large, dark cells are albuminous cells. Compare with Fig. 47. x 120.

Fig. 49. M. milleri. Radial section of secondary phloem. Note regular alternation between fibers (f) and parenchyma (pa). Empty areas between fibers and parenchyma represent sieve cells. P1195 D 15, SL5455, x 160.

Fig. 50. M. glyptostroboides. Cross section of secondary phloem showing regular alternation of sieve cells (sc), fibers, and parenchyma. x 170.

Figs. 51 - 54. M. milleri. Twigs.

Fig. 51. Longitudinal section of shoot bearing opposite pairs of leaves (at arrows). P1261 B top 2a, SL5456, x 15.

Fig. 52. Longitudinal section of base of shoot. Note persistant scales. P1181 C bot 2, SL5457, x 14.

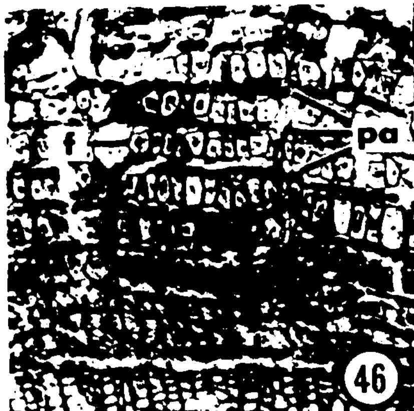
Fig. 53. Cross section of shoot near base showing decussate arrangement of scales. Note four-angled pith at center surrounded by four wedges of xylem. P1261 C 1, SL5458, x 18.

Fig. 54. Cross section of leaf-bearing shoot showing an opposite pair of leaf traces (lt) entering decurrent leaf bases. Note resin ducts abaxial to leaf traces. P1095 B bot 1, SL5012, x 55.

Fig. 55. Unidentified taxodioid shoot and leaf. Note helical leaf arrangement. P1315 D 1, SL5459, x 20.

Fig. 56. *Taxodium distichum*. Cross section of leafy twig showing helical leaf arrangement. x 60.

Fig. 57. *Metasequoia glyptostroboides*. Cross section of leafy shoot showing decussate leaf arrangement. Compare with Fig. 54. x 40.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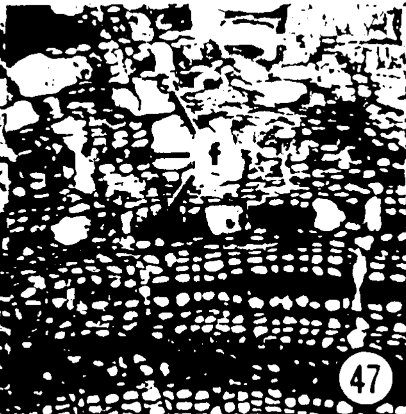
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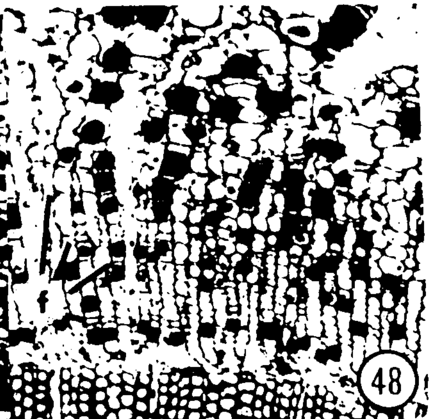
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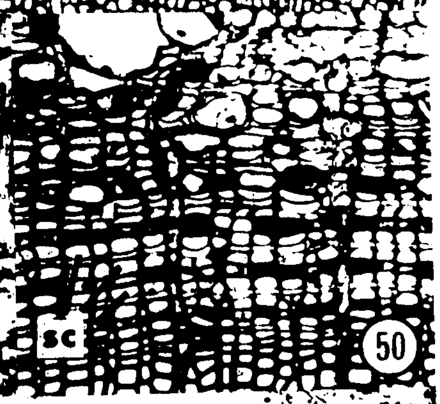
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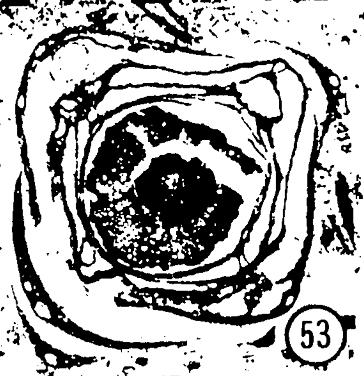
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Fig. 58. Metasequoia milleri. Cross section of leaf of moderate size. Note single resin duct (r) abaxial to vascular bundle. P1095 D top 1b, SL2632, x 85.

Fig. 59. M. milleri. Cross section of large leaf with a single resin duct (r). P1095 E al, SL2626, x 65.

Fig. 60. M. milleri. Cross section of large leaf with two marginal resin ducts (r) in addition to the median, abaxial duct. P1181G bot 1, SL5041, x 70.

Fig. 61. Unidentified taxodioid leaf. Note on the adaxial side elongate cells with dark contents. P1095 E 1b, SL2626, x 50.

Fig. 62. M. glyptostroboides. Cross section of leaf. Note abaxial and marginal resin ducts. x 145.

Fig. 63. Sequoia sempervirens. Cross section of leaf. Note three resin ducts (r) and elongate cells with dark contents found beneath adaxial epidermis. x 75.

Fig. 64. Taxodium distichum. Cross section of leaf. Note single, abaxial resin duct. x 105.

Fig. 65. M. milleri. Cross section of leaf showing vascular bundle (x - xylem), abaxial resin duct (r) and transfusion cells (tc). Note that cells of both epidermis (e) and hypodermis (h) have dark contents. Cells similar to those of the hypodermis are found adaxial and abaxial to the vascular bundle. P1095 D top 1b, SL2632, x 165.

Fig. 66. M. glyptostroboides. Cross section of leaf for comparison with Fig. 65. x 350.

Fig. 67. Taxodium distichum. Cross section of leaf. Note bundle of sclereids (sl) adaxial to the vascular bundle. x 235.

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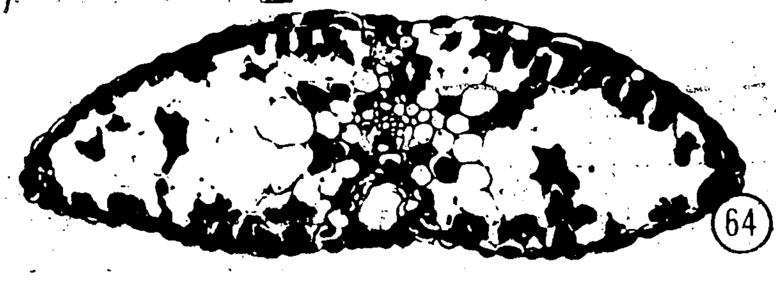

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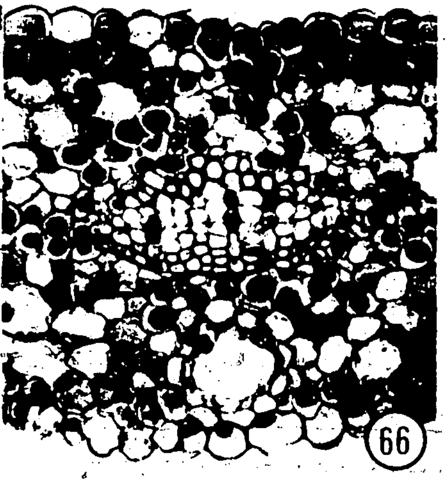

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Figs. 68 - 73. Metasequoia milleri. Leaves.

Fig. 68. Cross section near base of leaf. Note the presence of a poorly organized parenchymatous bundle sheath (bs). P1095 B bot 1, SL5012, x 180.

Fig. 69. Oblique longitudinal section of leaf showing organization of mesophyll. Note large intercellular spaces. P1181 G top 1c, SL5460, x 48.

Fig. 70. Paradermal section (abaxial) showing stomata. Note basically longitudinal orientation of guard cells. P1181 G top fl, SL5461, x 130.

Fig. 71. Paradermal section (abaxial) showing slightly undulate walls of epidermal cells (at arrows). P1261 B top la, SL5462, x 150.

Fig. 72. Paradermal section (abaxial) showing stomata surrounded by guard cells with dark contents. P1181 G top gl, SL5463, x 230.

Fig. 73. Cross section of leaf margin showing marginal resin duct (r). Note thin-walled epithelial cells lining duct. Note also direct contact of resin duct and hypodermis (h). P1181 G bot 1, SL5041, x 270.

Fig. 74. M. glyptostroboides. Paradermal section (abaxial) of leaf showing undulate walls of epidermal cells. Compare with Fig. 71. x 180.

Fig. 75. M. glyptostroboides. Paradermal section (abaxial) of leaf showing distribution of stomata (at arrows) and longitudinal orientation of guard cells. Note also structure of mesophyll and compare with Fig. 69. x 90.

Fig. 76. M. milleri. Cross section of root. Note indistinct growth rings and eccentric growth. P1181 H bot 1, SL5043, x 4.

Fig. 77. M. glyptostroboides. Cross section of young pentarch root. x 12.

Fig. 78 - 82. <u>M</u>. <u>milleri</u>. Roots.

Fig. 78. Cross section of hexarch stele of root in Fig. 76. P1181 H bot 1, SL5043, x 58.

Fig. 79. Tangential section of root wood. Note resinous wood parenchyma. P1108 D top 1a, SL5464, x 40.

Fig. 80. Cross section of root wood showing two uniseriate bands of late wood (at arrows). P1181 H bot 1, SL5043, x 45.

Fig. 81. Radial wall of tracheid with biseriate, opposite pitting. Note crassulae. P1181 H 3, SL5047, x 480.

Fig. 82. Radial section of root wood showing taxodioid cross-field pitting. P1181 H 3, SL5047, x 500.

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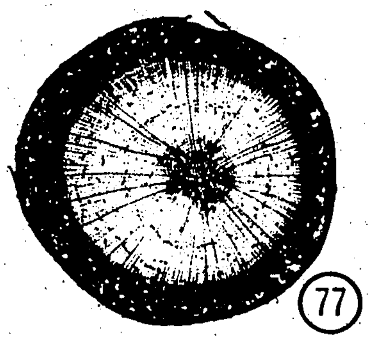

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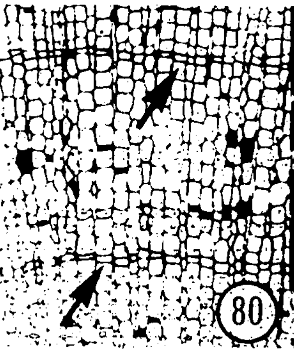

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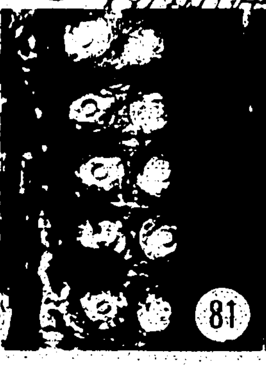

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Figs. 83 - 93. Metasequoia milleri. Roots.

Fig. 83. Cross section of bark of root shown in Fig. 76. Note multiple layers of cork (ck) which interupt the secondary phloem. Note also position of the vascular cambium (vc). P1181 H bot 1, SL5043, x 30.

Fig. 84. Cross section of mature phloem. Note tangential bands of fibers and parenchyma. Sieve cells are usually crushed. Note also layers of cork with phelloderm, phellogen or cork cambium (cc), and phellem preserved. P1181 H bot 1, SL5043, x 100.

Fig. 85. Cross section of vascular cambium (vc) and young cork cambium (cc). P1181 H bot 1, SL5043, x 160.

Fig. 86. Radial section of bark. Note alternating rows of fibers (f), parenchyma (pa), and sieve cells (sc). Note also cork cambium (cc) and derivatives at right. P1181 F 4a, SL5465, x 96.

Fig. 87. Sieve areas on radial walls of sieve cells. P1181 F 4a, SL5461, x 900.

Fig. 88. Cross section of small root. Note pentarch stele and remnants of cortex. P1413 E top 1, SL5466, x 28.

Fig. 89. Attachment of rootlets to a small root, and of the small root to the large root at left. P1266 A, SL5467, x 10.

Fig. 90. Cross section of small, diarch rootlet. Note absence of root hairs. P1413 F top 1a, SL5468, x 135.

Fig. 91. Longitudinal section of rootlet showing proliferation of probable mycorrhizal fungal hyphae within cortical cells. P1413 G top 1, SL5469, x 140.

Fig. 92. Cross section of stelar region of young root showing protoxylem poles (px), pericycle (pc), endodermis (e), and a layer of cells with phi-shaped wall thickenings (ph). P1181 G top 2f, SL5470, x 240.

Fig. 93. Cross section of stele of young triarch root showing initiation of cork in the region of the pericycle indicated by radially aligned cells. Note also indication of activity of a vascular cambium. P1413 F bot 1, SL5471, x 160.


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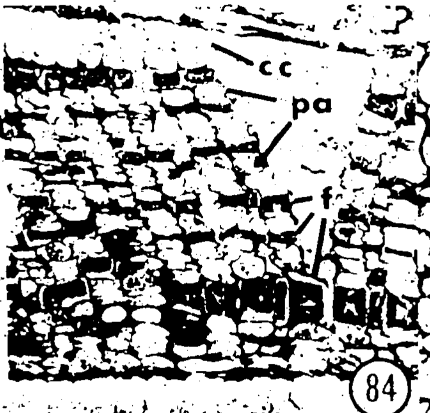
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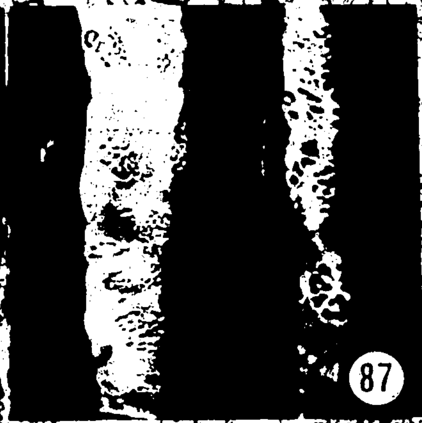
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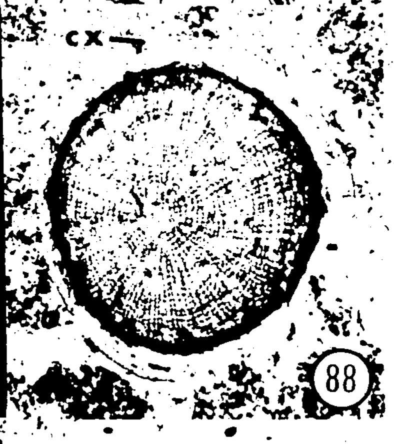
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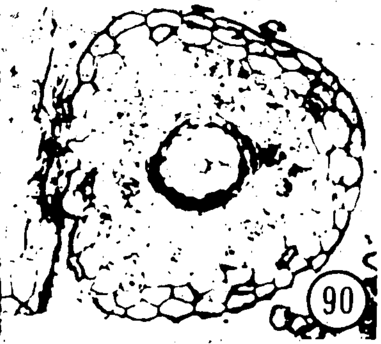
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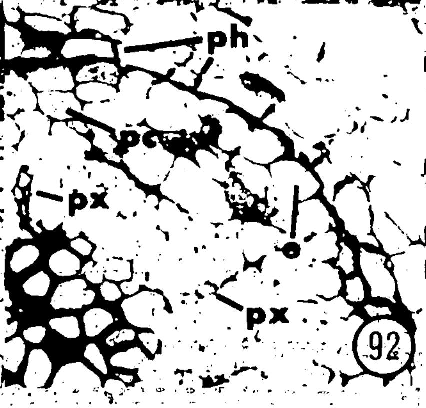
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Figs. 94 - 102. *Metasequoia milleri*. Seed cones.

Fig. 94. Longitudinal section of cone showing decussate arrangement of scales. Opposite pairs of scales are numbered consecutively from the base of the cone. Note that the first three pairs of scales are relatively small. P1258 J top 6, SL5472, x 4.

Fig. 95. Oblique transverse section near base of cone. Opposite pairs of scales are numbered from the base of the cone. Upper scales are reflexed toward the base of the cone; the cone apex is downward and beneath the plane of section. P1258 F2 top 2, SL5020, x 5.

Fig. 96. Cross section of cone stalk or peduncle. Note the presence of the small leaf (l). P1258 G bot 11, SL5473, x 14.

Fig. 97. Tangential section of wood of cone axis. Note uniseriate rays. P1258 J top 14, SL5033, x 50.

Fig. 98. Longitudinal section of wood of cone axis showing resin cysts. P1258 F2 top 16, SL5027, x 60.

Fig. 99. Longitudinal section of pith of cone axis. Note simple pitting. P1258 J top 12, SL5031, x 150.

Fig. 100. Cross section of cone axis showing outermost secondary xylem, secondary phloem, and crushed cortex. Note resin cysts (r) at right and position of vascular cambium (c). P1258 F2 top 16, SL5027, x 60.

Fig. 101. Radial section of cone scale showing expanded distal region and horizontal groove (at arrow) on external surface. P1258 F2 top 14, SL5025, x 10.

Fig. 102. Radial section of area of attachment of a reflexed scale in the basal region of a cone. The large vascular trace is attached to the vascular cylinder of the axis at the right and extends downward to the left. P1258 J top 15, SL5474, x 20.

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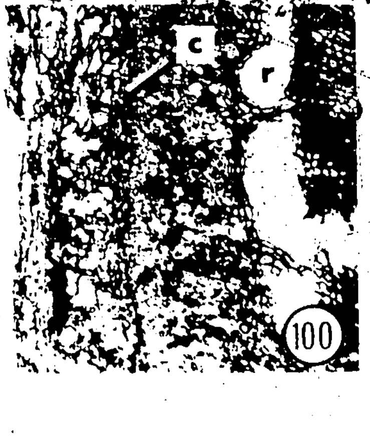

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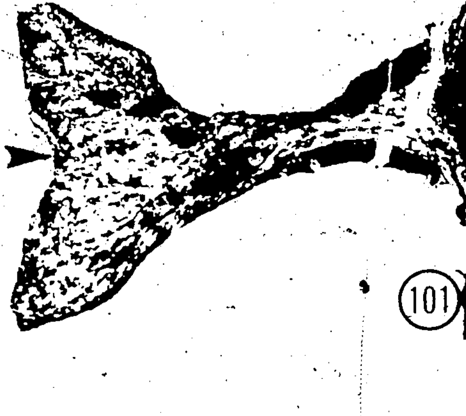

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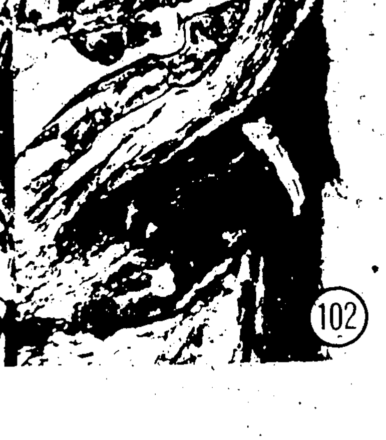

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Figs. 103 - 111. Metasequoia milleri. Seed cones.

Figs. 103 - 106. Sections through cone scales.

Fig. 103. Base of scale near attachment to cone axis. P1258 J top 5, SL5475, x 20.

Fig. 104. Section of scale stalk showing first splitting of the vascular cylinder. P1258 J top 5, SL5475, x 20.

Fig. 105. Section in region of expansion of scale. P1258 F2 top 9, SL5022, x 8.

Fig. 106. Large, distal region of scale. Note arrangement of vascular bundles into two roughly equal horizontal rows. Note also resin ducts (r). P1258 F2 top 2, SL5020, x 8.

Fig. 107. Abaxial vascular bundles of the cone scale shown in Fig. 106. Note also numerous isolated sclereids. P1258 F2 top 2, SL5020, x 70.

Fig. 108. Distal margin of cone scale showing termination of vascular bundles in masses of transfusion cells (tc). P1258 F2 top 16, SL5027, x 80.

Fig. 109. Radial section through cone scale showing elongate sclereids (sl) aligned parallel to the vascular bundles (vb). P1258 J top 10, SL5029, x 35.

Fig. 110. Cross section of seed showing the central seed body and two lateral wings. P1233 D1, SL5476, x 30.

Fig. 111. Longitudinal section of seed coat. Note inner layer of large, elongate cells (left) and outer layer of small, spherical, heavily-thickened cells (right). P1258 K top 4, SL5477, x 130.

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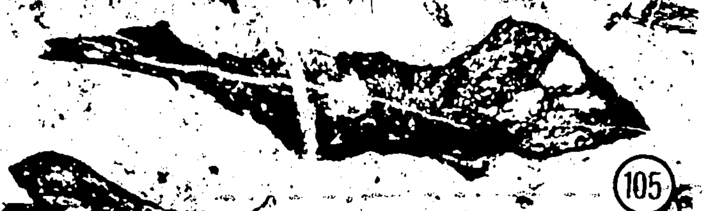

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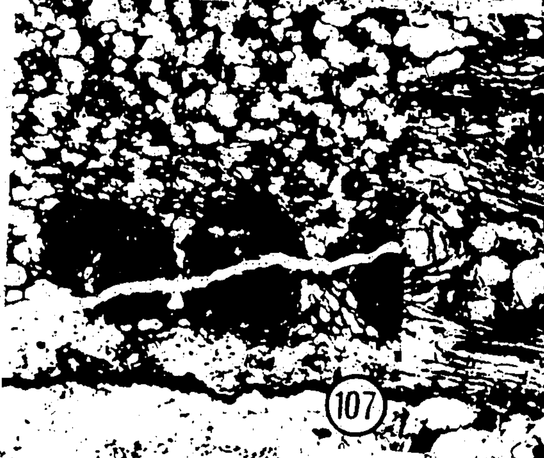

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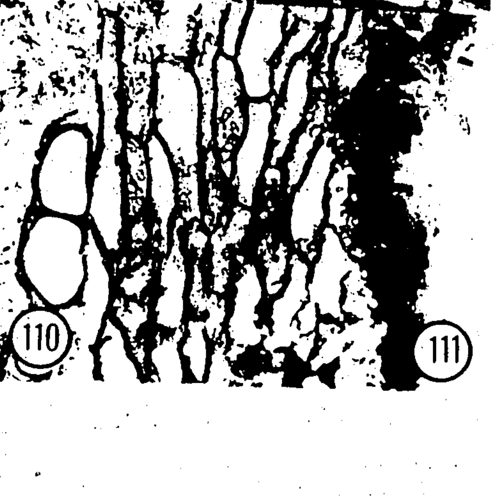

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Figs. 112 - 114. *Metasequoia milleri*. Seed cones.

Fig. 112. Longitudinal section of seed showing central body and lateral wings. Note slight assymmetry of base. Note also fusion of nucellus (n) only at base of seed. P1258 K top 6, SL5478, x 20.

Fig. 113. Oblique section of cone showing attachment of four seeds to the upper scale and two to the lower scale. Note distal attachment of seeds to scale. P1258 G2 bot 8, SL5019, x 8.

Fig. 114. Cross section of seed coat showing large, thin-walled inner cells and small, thick-walled outer cells. A dark layer of crushed cells lines the body (b) and wing (w) cavities. P1342 B bot 1, SL5479, x 90.

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Figs. 115 - 118. Metasequoia milleri. Pollen cones.

Fig. 115. Oblique longitudinal-section of Holotype showing general features. Note sporophylls with large resin ducts (r) and, in the sporophyll at the top (arrow), smaller lateral resin ducts. Note also attached sporangia and imbricating leaves (lf). P1195 D top 1a, SL5271, x 24.

Fig. 116. Longitudinal-section of cone showing scale-like proximal leaves and imbricating distal leaves (lf). Most of the axis in the sterile region has not been preserved. P1013 B2 bot 10a, SL5116, x 25.

Fig. 117. Attachment of cone to cone-bearing shoot. The cortex of both the cone and shoot are continuous. Note the opposite arrangement of lateral branches (l). P1013 B2 bot 18b, SL5099, x 15.

Fig. 118. Cross-section of cone surrounded by imbricating, subtending leaves. Note that the leaves are decussately arranged (arrows). Note also that the fertile axis is parenchymatous and lacks vascular tissue. P1269 A 1, SL5329, x 35.

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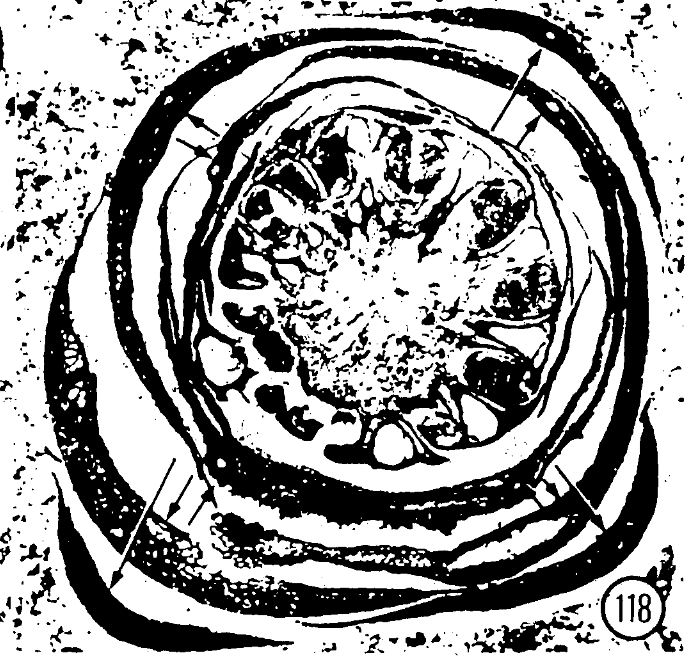

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Figs. 119 - 122. Metasequoia milleri. Pollen cones.

Fig. 119. Longitudinal-section of immature cone with poorly developed sporangia (sp). Note the thick, scale-like proximal leaves and the imbricating distal leaves. P1311 C top 6, SL5378, x 30.

Fig. 120. Longitudinal-section of very immature cone. Sporangia are represented only by small protuberances on the abaxial side of the sporophylls (sl). Note imbricating distal leaves. Note also pith cells (p) with dark contents found in the sterile region of the axis. P1343 C bot 11, SL5427, x 30.

Fig. 121. Cross-section of immature cone showing sporophylls (sl) with undeveloped sporangia. Compare general appearance of cone and sporophylls with Fig. 9. P1255 D 3b, SL5323, x 40.

Fig. 122. Cross-section of very immature cone showing spiral arrangement of sporophylls (sl). Sporangia are not present. Note that the decussate arrangement of the leaves is apparent (arrows) although some leaves are poorly preserved. P1366 B 1, SL5080, x 51.

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Figs. 123 - 129. *Metasequoia milleri*. Pollen cones.

Fig. 123. Cross-section through upper part of axis showing numerous spirally arranged resin ducts. P1332 C bot 9, SL5402, x 21.

Fig. 124. Tangential section through fertile axis of immature cone showing spiral arrangement of resin ducts passing into sporophylls (sl). P1195 D top 4b, SL5293, x 30.

Fig. 125. Close up of axis in sterile region showing pith cells (p) frequently filled with dark contents and the empty cells of the cortex (c). P1311 C top 6, SL5378, x 50.

Fig. 126. Cross-section of axis in sterile region showing four wedge-shaped vascular bundles. P1105 D bot 44, SL5164, x 80.

Fig. 127. Cross-sections of bases of subtending leaves showing resin ducts (r) and vascular bundles (vb). A single layer of small, thin-walled cells forms an indistinct bundle sheath. Note the abaxial layers of small cells filled with dark contents. Adaxial cells are larger and usually empty. P1013 B2 bot 33a, SL5132, x 39.

Fig. 128. Cross section through distal portions of imbricating leaves (lf). Note the conspicuous abaxial layers of small cells with dark contents and the thin zone of larger, adaxial parenchyma cells. Adaxial parenchyma is much thinner in the distal portions than the proximal (compare with Fig. 14). P1269 A 16, SL5339, x 50.

Fig. 129. Tracheids found in the axis of the sterile region showing uniseriate to biseriate circular-bordered pits. P1187 D bot 8, SL5270, x 800.


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Figs. 130 - 135. <u>Metasequoia</u> <u>milleri</u>. Pollen cones.

Fig. 130. Cross-section of cone showing attachment of sporophylls to the axis. Note large resin duct (r) of sporophyll and smaller resin ducts present in laminar part of sporophyll. P1060 E top 17, SL5086, x 25.

Fig. 131. Oblique longitudinal-section of cone showing sporangial attachment to a sporophyll (sl). P1195 D top 14c, SL5313, x 23.

Fig. 132. Tangential-section of cone showing attachment of three sporangia per sporophyll (at arrows). Note that resin duct nearly completely occupies sporophyll stalk. P1060 C top 5, SL5206, x 36.

Fig. 133. Cross-section of two sporangia showing structure of sporangial wall. No zone of dehiscence is recognizable. P1013 C1 top 11, SL5173, x 130.

Fig. 134. Cross-section through base of sporophyll stalk. Distally the diameter of the resin duct relative to the stalk increases so that the resin duct occupies almost the entire volume. (see Fig. 132). P1195 D top 14a, SL5283, x 180.

Fig. 135. Cross-section through fertile region showing broad, thin (often only one cell thick) distal laminae (dl) of the sporophylls. P1013 B2 bot 21a, SL5126, x 112.

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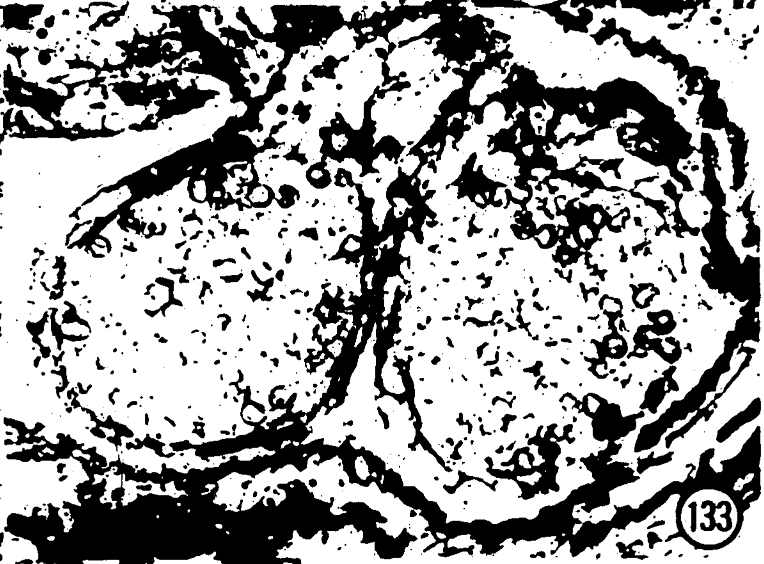

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CHAPTER 5

DISCUSSION

Organic connection between pollen cones and twigs and between seed cones and seeds has been found in the Princeton material. However, connection of the other organs must be established on the basis of other evidence in order to assemble all remains in a single species. Indirect evidence is as follows:

1. consistent association of organs;
2. independent identification of all organs as belonging to the genus <u>Metasequoia</u> or at least as showing affinity to the redwoods (<u>Sequoia</u>, <u>Sequoiadendron</u>, or <u>Metasequoia</u>);
3. apparent existence of only one type of each organ in the Princeton chert;
4. anatomical similarity between organs (for instance, wood structure of vegetative and fertile axes of similar size); and
5. all appendages, except the microsporophylls, are borne decussately (within the Taxodiaceae, this arrangement is unique to <u>Metasequoia</u>).

Woody stems of all sizes are believed to have been borne by trees of a single species. Features of wood anatomy form a continuum from twigs to the largest axes. Although roots and stems are not attached, anatomical similarities and differences between stem and root wood are those predicted by workers such as Brown and Panshin (1940). Roots of various sizes have been found in organic connection.

Seed cones are borne on a sparsely-leaved stalk. Pith and wood of both the stalk and the cone axis are similar to those of small branches.

Although there are apparently two types of taxodiaceous leaves in the chert, those with one resin duct and those with three, both types are borne decussately on similar twigs. Anatomical differences seem to be related to leaf size.

The similarity of organs of both fossil and living *Metasequoia* indicate that all organs from the chert could certainly be borne by a single species. Therefore, if closely related species of *Metasequoia* existed within the Princeton chert, they would be recognized only by distinction of more than one type of a single organ. Since it is the author's belief that only one species is represented by each type of organ, identification of more than one species is not possible.

The evidence overwhelmingly supports the recognition of one species of *Metasequoia*, *M. milleri*, from the Princeton chert.

A detailed comparison of *M. milleri* and *M. glyptostroboides* reveals the following differences:

1. wood rays of larger axes attain much greater heights in *M. milleri*;

2. leaves of <u>M</u>. <u>milleri</u> have one or three resin ducts; leaves of <u>M</u>. <u>glyptostroboides</u> are found only with three resin ducts;
3. the mesophyll of leaves of <u>M</u>. <u>milleri</u> is not well differentiated into palisade and spongy layers; leaves of <u>M</u>. <u>glyptostroboides</u> usually have a characteristic layer of arm palisade cells;
4. the epidermis of <u>M</u>. <u>milleri</u> leaves has straight to slightly wavy walls, and a hypodermis is generally distinct; leaves of <u>M</u>. <u>glyptostroboides</u> have highly undulate epidermal walls and generally lack a hypodermis;
5. microsporophylls of <u>M</u>. <u>milleri</u> are initiated helically; those of <u>M</u>. <u>glyptostroboides</u>, reportedly decussately;
6. microsporophylls of <u>M</u>. <u>milleri</u> have three resin ducts in the distal lamina; <u>M</u>. <u>glyptostroboides</u>, one resin duct.

All apparent differences between <u>M</u>. <u>milleri</u> and <u>M</u>. <u>glyptostroboides</u> are anatomical, and are not recognizable on external examination.

Remains of <u>Metasequoia</u> constitute one of the most common of Late Cretaceous and Early Tertiary megafossils. Most of these remains are leaf compressions; no internal anatomy has been previously reported for fossil <u>Metasequoia</u>. A single species of fossil <u>Metasequoia</u>, <u>M</u>. <u>occidentalis</u> (Newberry) Chaney, has been recognized by Chandrasekharam

(1974) and Christophel (1976), although a second, older (Upper Cretaceous) species, M. cuneata (Newberry) Chaney, has been recognized by Chaney (1951) and Bell (1957). Other species have been described recently (eg. Sveshnikova, 1975), but are not well understood, and may prove to be conspecific with M. occidentalis.

Since essentially all known Early Tertiary remains of Metasequoia appear to belong to M. occidentalis, and these remains are exceedingly abundant, it may be suggested that the Princeton specimens should also be placed in this species. In addition, on the structural evidence available it is quite possible that M. milleri and M. occidentalis are conspecific. However, difficulties arise when attempts are made at placing permineralized specimens in a species that has been based upon compressed specimens. Anatomical details of M. occidentalis are unknown; similarly, detailed knowledge of morphological features, such as leaf arrangement, angle of divergence, and leaf length are not readily available for M. milleri. Distinction at the species level must be made.

Metasequoia-like conifers first appeared during the Upper Cretaceous (Arnold and Lowther, 1955; Miller, 1977b), and by Late Cretaceous time Metasequoia was abundant. The similarity among M. cuneata, M. occidentalis, and M. glyptostroboides has led to the conclusion that Metasequoia has changed little since the Late Cretaceous and that all three species may represent the same lineage or are possibly conspecific (Chaney, 1951; Schwarz and Weide, 1962; Christophel, 1976; Miller, 1977b; etc.). The morphology of *M. milleri* supports the concept that *Metasequoia* has changed very little since the close of the Cretaceous. However, *M. milleri*, and probably other Early Tertiary *Metasequoias*, were certainly not identical to *M. glyptostroboides*.

The taxonomic significance of the differences between *M. milleri* and *M. glyptostroboides* may be questioned, especially if examination of the pollen cones of the latter reveals a helical disposition. Although *M. milleri* is a relatively well known species, and comparisons with *M. glyptostroboides* are close, the present lack of numerous anatomical, morphological, developmental, ecological, and physiological characteristics of the fossil species precludes synonymy. The practical solution in the description of fossil material is to distinguish between fossil and extant organisms by placing them in separate species.

While *M. milleri* is clearly a member of the genus, it is significant to note that not all organs are clearly identifiable as such. For instance, those leaves with a single resin duct resemble leaves of the genus *Glyptostrobus*. Although *Sequoia*, *Metasequoia*, *Taxodium*, and *Glyptostrobus* were differentiated at the generic level by the end of the Mesozoic, the fragmentary nature of most plant fossils leaves open the possibility that extinct members of genera may have had some organs characteristic of one extant genus and other organs that would be expected to belong to another genus. In this regard, it is perhaps wise to proceed with caution when attempting to assemble fossil organs by comparison with extant forms.

The large quantity of well preserved material from the Princeton chert locality has made it possible to assemble all organs into a single species, *Metasequoia milleri*, and has contributed to a detailed understanding of its anatomy and morphology. As a result, comparisons with extant members of the Taxodiaceae (see Table 2) and an interpretation of the evolution of *Metasequoia* during the Tertiary have been made with some confidence. Further investigation of the many undescribed plants in the Princeton chert will continue to contribute to the understanding of the anatomy of some Early Tertiary plants. Continuing study will also result in a better understanding of the composition of the community that lived in an around the ancient marsh.

Table 2. Comparison of _Metasequoia milleri_ with some other members of the Taxodiaceae. Data have been obtained in part from Brown and Panshin (1940), Christophel (1976), Dallimore and Jackson (1966), Erdtman (1965), Gaussen (1955), Greguss (1955), Rothwell and Basinger (1979), Stebbins (1948), and Wodehouse (1935).

* _Metasequoia_, as well as other taxa, has clusters of scale-like leaves at the base of the shoot.

** This is the greatest number of seeds found attached to a scale. Determination of numbers of seeds originally borne on scales is difficult due to inadequate preservation and the probability of seed loss prior to permineralization.

*** The diameters of pollen grains and the form of the exit papillae may be highly variable. Data presented here indicate trends within the Taxodiaceae and may not be in agreement with all sources.

Features / Taxon	Taxodium ascendens T. distichum T. mucronatum	Glyptostrobus pensilis	Sequoia sempervirens	Sequoiadendron giganteum	Metasequoia glyptostroboides	Metasequoia milleri
WOOD						
Resin cysts	absent	absent	present	present	present	present
Ray height (numbers of cells)	1 - 60+	1 - 20+	1 - 40+	1 - 20+	1 - 20+	1 - 70+
Wood parenchyma, horizontal walls	nodular	nodular	smooth	smooth	smooth	smooth
LEAVES						
Phyllotaxy	helical	helical	helical	helical	decussate	decussate
Leaf shape *	linear to scale-like	linear to acicular to scale-like	linear to scale-like	scale-like	linear	linear
Number of resin ducts	1	1	3	1	3	1 or 3
Sclereids adaxial to vascular bundle	present	absent	absent	absent	absent	absent
Stomatal orientation	irregularly transverse	parallel to long axis of leaf	parallel	parallel	parallel	parallel
Epidermal cell walls	straight	straight	straight	straight	wavy	straight to slightly wavy
SEED CONES						
Stalk	scaley	scaley	scaley	scaley	naked	naked
Scale shape	peltate	non-peltate, imbricate	peltate	peltate	peltate	peltate
Scale arrangement	helical	helical	helical	helical	decussate	decussate
Orientation of seeds	erect	erect	inverted	inverted	inverted	inverted
Number of seeds per scale	2	2	3 - 9	3 - numerous	3 - 9	4 **
Number of wings per seed	3	1	2	2	2	2
POLLEN CONES						
Attachment	terminally and laterally on specialized shoots	terminally on unspecialized shoots	terminally on unspecialized shoots	terminally on unspecialized shoots	terminally and laterally on specialized shoots	terminally and laterally on specialized shoots
Arrangement of subtending scale-leaves	helical	helical	helical	helical	decussate	decussate
Arrangement of microsporophylls	helical	helical	helical	helical	decussate?	helical
Number of pollen sacs per microsporophyll	6 - 9	3 - 4	2 - 5, usually 3	2 - 5, usually 3	3	3
Attachment of cones at time of pollination	short-stiped	short-stiped	short-stiped	sessile	short-stiped	sessile
POLLEN						
Exit papilla	low protuberance	short, bent sharply	long, bent sharply	very long, bent sharply	moderate length, bent sharply	moderate length, erect
Average equatorial diameter (μm) ***	25	33	35	25	28	23

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