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ON LIGNITIZED CONES FROM THE MIOCENE OF OREGON

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ON LIGNITIZED CONES FROM THE MIOCENE OF OREGON

by

Chester E. Cross

A Thesis Submitted in Partial Fulfillment
of the Requirements
for the Degree of Master of Science,

Massachusetts State College,
Amherst, Massachusetts.

1937

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INTRODUCTION

The central purpose of the present investigation is the determination of a coniferous fossil cone from the Miocene, Empire Formation of Cape Blanco, Oregon.

Simple as the problem, thus stated, may appear, we have discovered that it involved a considerable amount of original investigation, for, although the histology of the vegetative vascular cylinder of the conifers is well-known, the same cannot be said of the reproductive axes. It is, however, obvious that only from a comparison of living types is it possible to determine the affinities of extinct forms, and when, as in the present case, the superficial features of the specimens are inadequate to permit of identification, one is forced back upon the more difficult, but often more satisfactory comparison of microscopic details, with which one must necessarily become familiar.

The problem has, therefore, resolved itself into the following steps:

1. A general introductory taxonomic and geographic study of the Coniferales.
2. A study of the highly debatable subject of the organology and anatomy of the female cone of the Coniferales with the attendant problem of its theoretical phylesis.
3. A histological study of the vegetative and reproductive axes of 38 species of conifers belonging to 13 genera with a view to establishing valid criteria for the definition of generic types.

4. Application of the above differential criteria to the identification of the unknown Miocene cones.

Before one can safely set out on the investigation of a single member of a large group, one must orient that member in relation to its fellows. If that member is, at the outset, unknown in all but its broadest affinities, (in this case it is clearly a specimen of the Coniferales), one must familiarize onesself with the classification of the group, in which it is later to be included. We may, therefore, turn at once to examine the modern classification of the Coniferales.

TAXONOMIC AND GEOGRAPHIC STUDY OF THE CONIFERALES.

The ordinal designation Coniferales, meaning "cone-bearers", stands for the most important group of gymnospermous plants in the contemporary world flora. Though Sequoia and Taxodium represent the greatest and most venerable of plants, and though they are prominent forest makers the world over, still there are only forty genera and three hundred and fifty species of them to be compared with the estimated total of 132,000 species of angiosperms. The ubiquitous distribution of the conifers indicates, as truly as does the extensive and interesting fossil record, that the present few species is but a specialized and lingering remnant of a once larger and more generalized group. This remnant occurs on all the chief continents, and within its ranks are found important lumber trees such as Pinus Strobus L. and Pseudotsuga taxifolia (Lamb.) Britt. in North America, Cryptomeria japonica (L.f.) Don in the East, and the kauri,

Agathis australis (Lamb.) Steud. in the Southern Hemisphere. Yet it is generally conceded that they have reached the end of their evolutionary modification. The long lives of individual conifers is a fact of general knowledge, and the temporal record revealed by the annual rings has been of considerable value as an indicator of climatic shifts since the Glacial Period.

In accordance with a statement by Chamberlain (8) to the effect that a morphologist is not particularly interested in the extreme subdivisions and minute ramifications of a taxonomic system, we shall follow a simple and, as we believe, natural classification, suitable for the purpose of bringing related plants together under appropriate headings and providing a basis for an intelligent investigation. The time has not yet arrived when a system of taxonomy can be constructed, even in the much-studied Coniferales, that will depict the true evolutionary and phyletic arrangement of even the tribes of these plants. This would seem to be true for two reasons: in the first place, evolution, though rightly regarded as a fundamental principle in nature, is still a very puzzling one, and remains inadequately understood by scientists and philosophers alike. Attempted solutions range from highly metaphysical speculations, such as those of Bergson, to theories which force the facts within the rigid canons of mechanism. There is likewise a wide divergence of opinion regarding the actual phyletic affinities of the various groups, and, consequently it is well nigh futile to attempt to express the intimate blood-relationships of the

narrower taxonomic categories such as families, genera, and species.

It is, however, generally agreed that the sequence from Bryophyta through Pteridophyta to Spermatophyta is a valid one and many botanists are prepared to go much farther than this in their affirmations. The morphology, anatomy, and developmental histories of a great number of living conifers has, likewise, been worked out and together with the still incomplete record of Mesozoic and Cenozoic fossils, it provides sufficient knowledge at least for the construction of a workable outline. The worker who has faith in the superior validity of anatomical data over gross morphological resemblance will, however, doubtless produce a far different arrangement than will one whose work has been concerned with external morphology. The following taxonomic classification of the Coniferales is in the nature of a synthesis based in particular upon the system of Seward (37)

Order Coniferales

Family Pinaceae:

Tribe Abietineae - needle leaves, cones with spirally arranged members, bract and ovuliferous scale distinct, the latter bearing two anatropous ovules.
Pinus, Picea, Pseudotsuga, Larix, Abies, Cedrus, Pseudolarix, Tsuga, Keteleeria.

Tribe Sequoiineae - Leaves short and needle-shpaed, cones with spirally arranged members, bract and ovuliferous scale united.
Sequoia.

Tribe Sciadopitineae - leaves needle-like and double on short-shoots, cones with spirally arranged members, bract and ovuliferous scale united, many-seeded ovuliferous scales.
Sciadopitys.

Tribe Taxodineae - cones woody and spherical with spirally arranged members, bract and scale united.
Taxodium, Cunninghamia, Athrotaxis, Glyptostrobus, Cryptomeria, Taiwania.

Tribe Cupressineae - leaves and scales usually cyclic in arrangement, cones usually fleshy, bract and scale united, ovules orthotropous.
Cupressus, Chamaecyparis, Libocedrus, Fokienia, Thuja, Juniperus, Fitzroya, Thujopsis.

Tribe Callitrineae - cones smooth or warty, not fleshy, with spirally arranged members, seeds many per scale.
Callitris, Actinostrobus, Widdringtonia.

Tribe Araucarineae - leaves not needle-like, cones with spirally arranged members, bract and ovuliferous scale completely united, solitary anatropous ovules.
Araucaria, Agathis.

Family Taxaceae:

Tribe Taxineae - leaves short and needle-like arranged spirally, terminal and single fleshy seed.
Taxus, Torreya, Cephalotaxus, Austrotaxus.

Tribe Podocarpineae - leaves linear to lanceolate, rarely needle-like, but always spirally arranged, cones with united bracts and scales, or solitary ovules subtended by a fleshy stalk.
Podocarpus, Dacrydium, Microcachrys, Saxegothaea, Acmopyle, Pherosphaera.

Tribe Phyllocladineae - same as Podocarpineae but has phylloclades which are short-shoots in the axils of scale leaves.
Phyllocladus.

A classification of the conifers perhaps more generally familiar to American botanists is that of Penhallow (32), which appeared some thirty years ago in his "Manual of North American Gymnosperms." At that time relatively little critical work had been done on the xylary histology of the order, and certain relationships were put forward which are now regarded as highly questionable. A correct and workable set of

criteria had not at that time been devised for the true evaluation of facts. It is now generally admitted that the "Canons of Comparative Anatomy" formulated by E.C.Jeffrey (23) are valid phyletic criteria. They should be used consistently and not simply invoked incidentally to substantiate a chain of fallacious reasoning as they seem often to have been. Each of the canons, recapitulation, retension, and reversion, used in this manner, supports its fellow, and the high measure of success attained by the American and English workers on the conifers attests their validity as guiding principles.

Long before the anatomist began to apply his discoveries to the problem of taxonomy, botanists had recognized certain natural groups of coniferous genera. One of these, now called the Abietineae, comprised a group whose fructifications were characterized by a distinct and separated bract and ovuliferous scale. The Taxineae, on the contrary, were those which had fleshy seeds and which could hardly be considered as cone-bearers at all. The Cupressineae bore reduced leaves and decussate, nearly fused bract and ovuliferous scale. The Taxodineae were separated from the preceding by the spiral arrangement and woody nature of the fruiting scales. Sequoia and Sciadopitys were included in the Taxodineae while the Araucarineae, possessing seemingly simple cone scales with no visible bracts, were characteristic plants of the Southern Hemisphere.

Rarely can such a classification based entirely upon superficial characters stand the test of time. But in the present instance further investigation has proved that a natural

close affinity exists between the members of the aforesaid tribes. The resin canals, tracheidal pitting, and ray cytology all seem to substantiate the grouping given by these earlier workers. The lasting success of this taxonomic arrangement, based on superficial features, may be attributed to the fact that the characteristics most used were those of the reproductive organs, which generally represent conservative structures in the plant, which are least liable to change. That a phyletic relationship existed between these groups was practically unrecognized by these earlier and pre-Darwinian botanists. The older taxonomists have but vague ideas concerning this phase of the matter. With the rise of the evolutionary theory it was altogether natural that the Cordaitales of the Paleozoic Era should be compared at once to the woods of the still living araucarian conifers. A similarity in habit and histology led most of the botanists to the immediate conclusion that the two groups were closely allied phylogenetically, and that because of the great antiquity of the Cordaitales they must inevitably be regarded as the ancestors of araucarian conifers. The latter were, therefore, relegated to the base of the phyletic tree of the Coniferales. Since the subject of conifer phylesis is to be taken up in more detail later on, it is sufficient to state here that many botanists now incline to the opinion that this conclusion was premature and that the Paleozoic Cordaitales were not the direct ancestors of the araucarians. Their belief is based chiefly on the Mesozoic coniferous fossils of American deposits, which lend small weight to this view and tend, rather, to show on the contrary,

a close affinity between the Cordaitales and the Abietineae.

The histological features of the conservative regions of the araucarians, on the other hand, suggest the cogent possibility of a derivation from the Abietineae, rather than from the ancient Cordaitales. The tribe Abietineae with its most generalized genus, Pinus, we have, therefore, placed in a position which indicates its probable primitive nature, and not as the older systems of Penhallow and others suggest, in a position at the top of the phylogenetic tree. The Abietineae seem to represent, therefore, the ancient group from which the araucarians and other tribes have developed.

The existing species of Pinus number about 90, and with the exception of one species in the Sunday Islands, all occur north of the Equator. In Mesozoic times the number was at least twice as large, and if one accepts the Paleozoic fossil Walchia as a primitive pine, they will be seen to extend back into the Primary rocks. How close the relationship between Walchia and the Abietineae really is may be revealed soon by Florin's work on the genus. Of the nine other genera of abietineous conifers, Pseudolarix and Keteleeria are montypic. Picea is a northern genus of several species and the same statement applies to Abies. Cedrus has three species scattered respectively on the Atlas, Lebanon, and Himalaya mountains, a condition which can be explained by postulating a far wider distribution in the past and extinction in intermediate regions. Pseudotsuga is native to Western North America but because of its possibilities as a timber tree it is being introduced abun-

dantly into South Africa and Australia. The larch and hemlock are found in the Temperate Zone on all the continents of the Northern Hemisphere.

The bald cypress represents the type genus of the Taxodineae, and its present restriction to the Southern United States and Mexico is but a remnant of its Miocene distribution. In that time it was common on the west coast of North America as far north as Alaska, reaching eastward to Greenland. Glyptostrobus, likewise, was widely scattered through North America during the Miocene, but is now confined to Japan. Sequoia includes two species: S. washingtoniana (L.) Sudw., the "big tree" and S. sempervirens (L.) Sudw., the redwood. The monotypic umbrella pine, Sciadopitys, has been introduced as an ornamental into this country from its native Japan.

The Cupressineae include a bewildering and ubiquitous group of genera bearing small fleshy cones. Various characters, to be discussed later, lead us to suspect that this group of small trees and shrubs, has been recently derived, like the sequoias, from the primitive abietineans.

The araucarians are represented by two genera, Agathis and Araucaria only, and their distribution is confined to the Southern Hemisphere. They have long been a focal point in questions of gymnosperm phylogeny. The matter at issue concerns the relative primitiveness of the Araucarineae and Abietineae and will be treated in another part of this paper.

The Taxineae, Podocarpineae and Phyllocladineae all have fructifications which can scarcely be called cones at

all; in fact, were it not for their foliage and wood structure, it is doubtful if their inclusion in the Coniferales would be so universally accepted. Their anatomy, however, offers an illustration of the immense value of microscopic structures, since details connected with their vascular strands give a clue to their real nature as abietinean derivatives. The taxads, or yews, are native to the temperate regions of the continents of the Northern Hemisphere, while the podocarps, seventy species strong, are to the Southern Hemisphere what Pinus is to the Northern. Phyllocladus, as its name indicates, uses its flattened stems, some of which look like miniature Caryota (palm) leaves, for carrying on its photosynthetic work.

The three tribes, Cupressineae, Taxineae, Taxodineae and Podocarpineae are, on a basis of comparative morphology and embryology, now considered to be specialized offshoots of the old abietineous stock. Transitional types, especially in the Podocarpineae, lend very convincing support to this theory and in so doing provide an interesting parallel to the probable development of the Araucarineae.

ORGANOLOGY AND ANATOMY OF THE FEMALE CONE OF THE CONIFERALES

INTRODUCTION

The true nature and organology of the ovuliferous or seminiferous scale, the most unique and characteristic structure of the female reproductive cones of the Coniferales, is a highly debatable problem. No other single structure in the plant kingdom has received so much attention, such thorough examination, and been assigned to such widely divergement cate-

gories. In fact it has been a subject of debate for more than three hundred years. The major problem revolves about the morphology of the ovuliferous scale itself. It appears to be a simple flattened leaf blade, and, in fact, has been called a megasporophyll or "carpellary leaf." Yet it arises from the axil of a bract - a condition which is not known to obtain for any true leaf. If, therefore, its relation to the bract forbids its relegation to the foliar category, what is it? To this question no less than two dozen answers have been given.

The Ovuliferous Scale as an Historical Problem.

In 1900, W.C.Worsdell (48) summarized the literature on the vexed question of the nature of the ovuliferous or seminiferous scale of the conifers. During the last years of the eighteenth century, when the distinction between Gymnospermae and Angiospermae was ill-defined, and when the difference between them was not recognized as involving the detail of an open carpel, Linnaeus* was able to regard the scale as the calyx of an apetalous flower, each naked seed being regarded as a "pistil" or as we would say, a carpel. Jussieu believed the scale to be a curiously opened bilocular, biovulate ovary whose subtending bract constituted a gynobasic style. Mirbel seemed so utterly at a loss that in the early nineteenth century he coined new phrases for the structures: the scale was a "peduncle", and the integument a "cupule". Only later did he attempt to homologize the structures, when he came close to the conception which, to-day, has widest acceptance; namely that the scale is an open ovary bearing two

*Whenever an authority is quoted without reference to his work, the quotation is taken from Worsdell's article.

"nucelli" or ovules. Thus, he recognized the essential fact of gymnospermy. Richard went astray thinking the seeds were fruits, and called them, as the case warranted, either a caryopsis or a nut. Ray and Robert Brown, however, deserve the credit for being the first to declare the gymnospermous nature of the coniferous seeds, for the former, in 1682, stated that the ovules of conifers were naked, and shortly after, the latter described the cone as a collection of open carpels with ovules at the base. But the problem of the morphology of the scale is more complex than this, for as Schleiden pointed out, a "folium in axilla folii" is unknown. He argued, therefore, that the structures standing in the axil of the bract must be other than foliar by nature. Yet he seems to have erred in regarding the axillary structure as a placenta, thereby being forced to regard the subtending bract as the carpellary leaf. Von Mohl and Alexander Braun, however, took a saner view of the axillary structure, one regarding it as a single leaf on a secondary or lateral shoot, while the latter thought the scale was made of two fused leaves on a secondary axis. Here at least was the recognition of the ramular nature of the coniferous scale. Important with respect to these men, are the close comparisons they made between the vegetative and reproductive organs, thereby paving the way for careful ontogenetic work years later. Caspary accepted Braun's solution.

Throughout the nineteenth century, proliferated cones and other teratological phenomena were recorded, and this study gave rise to still other conceptions of the ovuliferous scales. Parlatore thought the scale a compound secondary axis,

Stenzel and Willkomm interpreted it as two fused leaves on a seoondary axis, while Noll, from a study of proliferated cones of Larix came essentially to the same conclusion, calling the scale "equivalent to an axillary bud bearing two leaves."

Sachs and Eichler, antagonistic to all teratological data, put forward the idea that the scale is a "ventral ligular outgrowth of the bract to be compared with that of Isoetes and Selaginella." The fact that there are no vegetative correlates to these structures does not seem to have appeared as an obstacle to them. To-day we realize that a considerable chasm separates the phyllosiphonic, eligulate gymnosperms from the dendroid, cladosiphonic, ligulate lycopsidan types. It was this unfortunate suggestion of lycopsidan organology for the ovuliferous scale which Seward and Ford later made the starting point in their theory of the lycopod origin of araucarians - a theory which has never gained recruits among botanists.

Celakowsky summarized the previous work, and reasoned out the best and most consistent interpretation we possess. In fact it has stood the test of all the twentieth century ontogenetic studies, which have, indeed, only provided additional evidence in support of the view he so clearly enunciated. To him, the ovuliferous scale is a fertile and highly metamorphosed brachyblast bearing two opposite leaves.

With the generally admitted failure of the lycopod theory to account for the origin of araucarians, botanists are at one in considering the Coniferales a natural and probably monophyletic group. It was this conviction which made it poss-

ible for Chamberlain (8) to say: "The problem of the ovule-bearer is difficult, but if you solve Pinus you solve the whole coniferous problem." We may accept Worsdell's (48) remark that the "true morphology of the cone can only be ascertained by comparison of the many superficially different types found in Coniferae." Yet the pinean condition is so generalized and probably primitive that the elucidation of the condition there would undoubtedly throw a flood of light on the meaning of the more specialized cones of the other tribes.

The evidence that the Abietinean cone scale is a secondary axis bearing two fertile leaves was first taken up from the standpoint of comparative anatomy by Schleiden, whose application of the maxim "non folium in axilla folii" led to the establishment of the "Zapfenschuppe" as a bract (reduced leaf) with a lateral shoot in its axil. This interpretation corresponds with our present notions except in its failure to define what this lateral shoot bears. Alexander Braun maintained it bore two fertile leaves. Van Tieghem, an exponent of the validity of anatomical characters, traced the vascular bundles of both bract and scale, and by it was led to assert that because of the normal orientation of the traces in the bract, and the mode of exit of the bundles from the woody axis, the organ was a leaf. The inverted orientation of the bundles in the scale led him to think that the scale is a single leaf, "or perhaps two fused leaves," on the secondary axis. Von Mohl, seeing the possibility of lending considerable valuable support by a close comparison of the double-needled short-shoots of Sciadopitys

with the ovuliferous scales of the same plant, found that the two structures are so similar as to be in all probability homologous. Arcangeli's weird conclusions, that since the vascular supply starts single in some species of Pinus, Sequoia, Thuja, Cryptomeria, and Cupressus, therefore, the scale is a lateral axis standing in the position of a leaf, and bearing the bract as its first leaf on the dorsal side, hardly deserves attention. It is far more reasonable to think that a slight fusion has occurred at the base of the bract and scale which in other groups has become more and more complete. In concluding the evidence derived from comparative anatomy, Celakowsky makes the statement: "In all Coniferae (cones) the axillary shoot always bears a pair of opposite first leaves and never a single leaf."

Velenowsky has summarized the worth of teratological evidence and is in harmony with what we have said in setting up our criteria for judgment. Parlatore in 1864 described teratological bifoliate short-shoots replacing the ovuliferous scale in Pinus Lemoniana. In the same year, Orsted noticed teratological foliage leaves replacing bracts. Sperks' extensive work on teratology, chiefly concerned the morphology of the coniferous integument. Stenzel and Willkomm observed proliferated cones of Picea Abiea (L.) Karst., and also some androgynous cones of the same plant. Tsuga Brunonia Carr. was observed to produce similar sports. The last two workers have performed a distinct service in explaining very convincingly the inverted bundles of the ovuliferous scale. They say the scale is a fusion product of the two opposite fertile leaves borne on an abbreviated axis.

The leaves were fused by their posterior margins, the two anterior ones swinging out to form the lateral margins of the scale. Also this explanation successfully explains the occurrence of the seeds on the upper ventral (morphologically dorsal) surface. Stenzel and Willkomm have given us a more meaningful and helpful explanation than Chamberlain's (8) which simply says "the bundle of the ovuliferous scale connects above; consequently with this connection, the orientation is not at all peculiar, but only what should be anticipated." Sachs and Eichler have nothing better to offer in explanation of this bundle orientation than that all outgrowths of leaves have inverted vascular supply. The insufficient nature of this statement is a contributory reason for the lack of support given to the "ligule" theory, which attempts to homologize the scale and its ventral appendage with the sporophyll and ligule of Lycopsida.

The numerous and obvious transitions between vegetative leaves and the bracts of the reproductive axes are well-known and generally accepted as evidence, sufficient to establish the true morphology of the bracts as reduced leaves. H.C. Aase (1) has made mention of abnormal bracts which were leaf-like. The fact that the leaves just beneath a strobilus do not bear appendages in their axils, is to be regretted, for it might thereby provide transitions between vegetative axes and the ovuliferous scale. However, if the bract of the cone is nothing but a reduced leaf, the only structure found in coniferous vegetative anatomy which could have been specialized as the ovuliferous scale is a lateral foliage-bearing shoot, in some

cases a brachyblast. The persistent character of the transitional leaves at the very base of the cones of Larix provide a good illustration of the retentive nature of the reproductive axis.

Chamberlain (8) makes the rather questionable assertion that since Worsdell's paper in 1900, "practically nothing has been added" to the solution of the problem. Since that time Hagerup's work, (18) "Zur Organogeny und Phylogenie der Koniferen-Zapfen" (1933) has come out. In it he attempts to prove that the abietinean axis bears first two fertile leaves, each with an ovule, the leaf becoming the integument. Further from the primary axis a single large posterior leaf becomes the conspicuous portion of the scale and by enlargement comes to support the seeds. This explanation would successfully, and perhaps more satisfactorily, account for the inverted orientation of the elements of the vascular supply, which Stenzel and Willkomm explained by a curious fusion of the first two fertile leaves.

Perhaps the most convincing work done since the time of Worsdell's paper(48), has been on the vascular anatomy of the megasporophylls of conifers by H.C.Aase(1). A comparison of the vascular supply of foliage leaf and attendant axillary bud, with the bract and ovuliferous scale in Pinus maritima Lam. and P. Banksiana Lamb. reveals a suggestive similarity. In both cases, the leaf supply comes from the base of the cylinder lacuna while the axis supply has a multiple origin from the sides of the gap. Keteleeria fortunei (Murr.) Carr. has a similar condition, and all three plants are alike in hav-

ing the supply of both scale and bract originating separately except at the crowded base of the cone where the scales are not seminiferous. On this same subject Radais noted that the bundles to "bract and scale are distinct in origin in Abietineae, Sciadopitys, and some of the Taxodineae, as Cryptomeria, Taxodium, and Sequoia, and how this distinction is on its way to obliteration in species of Athrotaxis and more so in Cunninghamia, and is lost in Araucaria Rulei." Practically all modern workers are agreed in considering the scale an axis, though perhaps the appendages and their orientation on the axis may still be disputed. However, Miss Aase (1) makes the statement that if the scale is a metamorphosed fertile shoot, then conifers bear a "suggestive likeness to the Cordaitales." And this is just what Jeffrey has so convincingly shown from his studies in wood anatomy.

In conclusion, the ovuliferous or seminiferous scale of the Coniferales has long been an unsolved enigma to the morphologist, but the minute and painstaking investigations into the histology, teratology, and organogeny of the structure have at last brought the problem to a more or less satisfactory conclusion, verifying many long-held but unproved opinions. The sum total of our present information confirms us in believing that this unit of reproductive anatomy is homologous throughout the Coniferales, since the latter is now convincingly demonstrated to be a natural, monophyletic group. The reproductive strobilus of the Coniferales is an aggregation of fertile shortshoots, each of which is borne primitively in the axil of a

scale leaf. The cone is a compound structure derived from the Cordaitales and specialized and reduced in various ways in the different derivative group.

The Phylogeny of the Abietinean Tribes.

Since the most generalized and, therefore, probably the most primitive condition of these structures is found among the Abietineae, we will briefly summarize the conditions there, and then discuss the probable origin of the taxodinian, cupressinean, araucarian, podocarpinean, and taxinean types by reduction and caenogenetic specialization from the primitive form.

The nine abietinean genera are alike in possessing compact woody cones whose spirally arranged scales stand in the axils of bracts. The latter are always free from the scales with the exception of a little fusion near the point of their attachment to the cone axis. The bract receives its vascular supply as a single strand from the base of the foliar lacuna. The scale normally receives bundles from the sides of the gap. Near the base and apex of the cones, these vascular strands may all fuse at a short distance from their origin, but in the Abietineae they always split apart forming two distinct sets of strands, whose phloem and xylem masses are inversely oriented.

The slight tendency toward fusion in the Abietineae is carried forward in the Taxodineae, where the number of scales is greatly reduced and the bract and scale are united for nearly their whole length. The scales still retain the primitive spiral arrangement, but the cones are, on the whole, smaller

and more globular than those of their probable ancestors. In a certain sense the Sequoiineae and Sciadopitineae are more primitive than the Taxodineae, for their scale number is more nearly the mean of the abietineans, and the double nature of their scales is evident to the naked eye. In all three types, a study of the vascular supply reveals two sets of strands with inverse orientation. Among the Taxodineae, Cryptomeria and Taxodium exhibit the same bundle origin as do the abietineans. Though Cunninghamia, in the feature of its cone scales, is the most primitive genus, it has carried forward the tendency toward fusion of bract and scale bundle-supplies, so that the strands to the nearly fused bract and scale originate in a single vascular member from the cone axis which only later breaks up to give evidence of the double nature of the organs it supplies. Cunninghamia Davidiana exhibits but a few weak strands with inverted orientation, running into the ovuliferous scale, a tendency which appears to have been carried to an extreme condition in the Araucarineae.

The Cupressineae have reduced the sporophyll numbers, and in harmony with this condition they have lost the spiral arrangement of the scales which now are cyclic and decussate in disposition. As is characteristic of all cyclic forms, the leaf gap does not usually close after the departure of the leaf trace. Thuja occidentalis L., Chamaecyparis Lawsoniana (Andr.) Parl., and Juniperus communis L. all have the vascular supply to bract and scale originating separately from the axis. This condition is found in most of the cupressineans,

despite the nearly complete fusion of the bract and scale. In Cupressus lusitanica Mill. var. Benthamii (Endl.) Carr. (Cupressus Benthamii of Miss Aase's paper) the vascular supply arises as a single strand and later splits to form the characteristic opposed sets of bundles. Orsted has pointed out that Actinostrobus is a cupressinean with several abietinean characters, and as a transitional form, gives cogency to the theory that the Cupressineae have been derived from pine-like ancestors. There are many other features which indicate that the Taxodineae and Cupressineae have been derived from the Abietineae: 1. Miss Holden (20) has demonstrated traumatic ray tracheids in them, 2. normal and traumatic resin canals indicate an abietineous origin to "those whose anatomical knowledge of the conifers makes their opinion of weight," [E.C.Jeffrey (23)] and 3. the tracheidal origin of wood parenchyma is evident in some cases, and its diffuse nature in the wood of the stem is a distinct advance over the abietinean condition where it is usually restricted to the end of the annual ring.

The Araucarineae have spherical cones made up of spirally disposed scales. In Araucaria a "ligule" is present on the upper surface of the cone scales. It probably represents the last remnant of the ovuliferous scale of other coniferous tribes. In support of the theory that the araucarian cone scale is of double nature, Aase (1) has described Araucaria Balansi Brongn. et Gris, A. Rulei F. Müll., and A. excelsa (Lamb.) R.Br. in each of which the vascular supply to the scale arises singly from the axis but later breaks up to form two sets of bundles

whose xylems face one another and whose phloems are directed toward the upper and lower surfaces of each. It will be recalled that this is the condition found in cupressinean and taxodinean genera. Cunninghamia Davidiana is particularly notable because it is reducing its scale rather than the bract, a condition parallel to the case in most of the abietinean derivatives. Araucaria Bidwillii Hook. has long been noted for its externally differentiated bract and ovuliferous scale. Its anatomy reveals a double set of bundles arising separately from the cone axis and possessing the usual reversed orientation. Seward's (39) suggestion that large cone scales might require a double set of bundles and develop such a vascular supply de novo is a forced interpretation intended to substantiate a weak phyletic theory. Araucaria Cookii R.Br. has the vascular strands running up to the "ligule" (really the ovuliferous scale) and is regarded by Eames (14) as transitional between the "ligulate" and "non-ligulate" araucarians. The latter are found in the genus Agathis which seems to have carried the tendency toward scale abortion to its final conclusion. But here again we are not without suggestive transitions, for Agathis australis (Lamb.) Steud. has a curious elevation of tissue, resembling the ligule, immediately behind the anatropous ovule. The reduction of the ovuliferous scale is so complete in Agathis that only fragmentary remnants of the double set of bundles are found. Eames has worked out a striking and parallel taxodinean series in which the progressive degradation of the scale can be traced, the species concerned being: Athrotaxis cupressoides Don, A. laxifolia Hook., and A.

selaginoides Don. Cunninghamia sinensis R.Br. shows the same cupressinean and araucarian tendency toward bract enlargement with concomitant obliteration of the ovuliferous scale. Saxegothaea among the Podocarpineae has a strictly parallel reduction of the scale. Eames regards Thomson's terms "aplosporophyllous" and "diplosporophyllous" conifers as misnomers, since the evidence he has accumulated indicates that the strobilar elements of all conifers are homologous.

Numerous anomalous details of reproductive cytology lend weight to the opinion that the araucarians are derivative and are not sufficiently generalized to have been the ancestors of other tribes of conifers. From a study of the ontogenetic development of the cones of araucarians, Hagerup (17) comes to the conclusion that the cone scales are reduced from a primitively double condition. Miss Holden (21), studying the Triassic fossil Voltzia also held that the araucarians are abietinean derivatives. Voltzia has leaves, medullary rays, large pith, and an absence of wood parenchyma, all of which are araucarian features; while its double cone scale with two seeds and the scattered pits on the tracheids link it with the Abietineae. Protodammara of the Cretaceous would seem to be intermediate between the Triassic, abietineous Voltzia and the modern araucarians. Nathorst claims that the Abietineae were abundant in the circumpolar regions in the Triassic. This is a significant statement, when compared with the fact that araucarians are not definitely known before the Jurassic. Seward and Ford (39) say that transitions between normal foliage leaves and cone

scales are very gradual in Araucaria inbricata Pavon, A. Rulei F. Müll., and A. Muelleri Brongn. et Gris, using this illustration as an argument in favor of the simplicity of the araucarian cone scale. Yet the argument is no more cogent than the parallel one which sees the "annulus of the Equisetum cone as a transition between the webbed leaf sheath and the whorled sporangiophores." It is much more probable that the bract has been enlarged and has become the chief structure, while the "ligule" remains as the aborting ovuliferous scale.

The coniferous flora of to-day, likewise, embraces a set of genera which have been brought together in the tribe Podocarpineae. These genera show a rather wide range of features especially with regard to the strobilar structures, a detail which has permitted a complete morphological seriation, and a consequent general acceptance of the view that podocarps have been derived from the Abietineae. It is probably true that if the araucarinean members had persisted to the present as numerously as the podocarps, there would have been far less controversy over the morphology of the reproductive parts. For example, Saxegothaea conspicua Lindl., a monotypic genus from southern Chili, and the species of Microcachrys possess well-formed cones which provide a link between the highly specialized, solitary, often fleshy seeds of the Eupodocarpus group, and the more typical compound fructifications of the Abietineae. Even in the highly modified Podocarpus, Miss Aase (1) has found the typical xylem situation of "opposed sets of bundles with opposite orientation." The epimatium of the Podocarpineae is thought by Sin-

nott (40) to be a remnant of the ovuliferous scale, but such a highly specialized feature presents so few evidences of its ancestry as to make its phylesis very problematical.

The Phyllocladineae with the single genus Phyllocladus have been separated from the Podocarpineae, rather arbitrarily, on the basis of its photosynthetic organs. They but continue the reduction and specialization of the podocarps. In Phyllocladus alpinus Hook. F., however, the female fructification is a cone-like group of fleshy scales in the axil of each of which occurs a sessile ovule. "The vascular supply to the bract springs from the base of the foliar lacuna. Two bundles from the sides of the gap unite to form a semicircle which ends at the base of the ovule." This description by Miss Aase (1) sounds quite like that of the abietinean condition.

The final group, the tribe Taxineae, would likewise, seem to be a recent offshoot from the Abietineae, but its extreme specialization, at least as regards reproductive anatomy, makes the attempt at homologizing its structures a very speculative business. There is a single, terminal ovule in all cases, which in all probability, represents the reduced remnant of a whole strobilus, paralleling the more complete series just summarized for the Podocarpineae. The fleshy aril which develops late in the maturation of the seed, is probably a caenogenetic structure, though of very doubtful homology. Morphologists have little to say with respect to the reproductive anatomy of the Taxineae, and their phylogeny has been more adequately revealed by their wood anatomy.

The Ovuliferous Scale and Paleontology.

The fructifications of the Cordaitales are not very abundantly known, but available evidence indicates that they consisted of a series of short-shoots which combined the vegetative and reproductive functions. Cordaianthus Renault, is the name applied to the male and female fructifications of Cordaites. The ovulate catkin of C. Williamsoni Ren. was composed of spirally arranged bracts in the axils of some of which were ovules, each borne on a short lateral stalk. The relations of bracts and ovules is not well known in C. Grand'Euryi Ren., but the female fructifications of Mesoxylon multirame from the British Coal-measures is now with "good evidence" (Scott (36)) considered the reproductive organs of Cordaiteae. The catkin axis of Mesoxylon and Cordaianthus are identical. In Mesoxylon, a naked axis bears distichously arranged, bud-like branches composed of spirally disposed bracts among which the stamens and ovules have not been found attached. These lateral buds are probably best regarded as short-shoots just as in the very similar Cordaianthus. The differentiation of vegetative and fruiting parts was not nearly so great in the Cordaitales as in the Coniferales. The presence or absence of bracteoles on the ovule stalk of Cordaianthus is considered the telling feature of whether or not the strobilus is compound as in Abietineae, or simple as some botanists have unsuccessfully tried to make out the situation for the Araucarineae. But whether or not the fructification of Cordaianthus is simple or compound, that of Mesoxylon cannot be otherwise interpreted than as a loosely arranged group of mon-

oecious or dioecious short-shoots. Like Cordaianthus and Mesoxylon, which combine the vegetative and reproductive functions in their short-shoots, Samaropsis pitcairniae "shows the brachyblast nature of the ovule-bearing structure." To advance to the abietinean condition from Mesoxylon, the lateral buds would have to be reduced to a single metamorphosed scale in the axil of the long-shoot bract which suntended the bud. The possibility, therefore, of homologizing the fructifications of the Cordaitales and Abietineae, is not by any means unthinkable.

The fossil record of the Coniferales lends a great deal of interesting support to the theory that the Cordaitales are the short-shoot-bearing ancestors of the abietineans. Rudolph Florin (15) in his recent work on Paleozoic conifers, has described the genus Walchia which exhibits short-shoot structures in the female cone. These stand in the axils of bracts, and consist of a secondary axis bearing spirally arranged scales, the uppermost of which are fertile. Such a form as this, looks very much like a transitional type between the loose catkin of the cordaites, and the compact cone of Pinus.

The Abietineae probably existed in very early Mesozoic times, as many fossil seeds and leafy twigs indicate, but the cones are rarely well enough preserved to show either the seeds in place, or the anatomy of the seminiferous scale. The genus Voltzia, because of its lobed scales, which resemble those of the recent genus Cryptomeria, has been referred by Scott (36) to the Taxodineae. The double nature of the scales, however, has not been determined, so there are still efforts being made, as with Walchia, to link up these fossils with the araucarians.

Other abietinean and araucarians fossil cones do not seem to shed much light upon the morphology of that organ.

Before proceding to a consideration of the ovuliferous scale as it appears, and as it probably originated, in the various coniferous tribes, it is well to take up at least briefly a theory which has been recently put forward by Zimmermann. (49) In treating of the most primitive of vascular plants he was faced with the difficult problem of giving an organological designation to the dichotomizing vegetative structures of Devonian Psilophytales which possessed no differentiated roots, stems, or leaves. He adopted the term "telome" to indicate the unit which lies between two adjacent forkings. These undifferentiated vegetative fragments constitute some of the oldest of vascular plant remains. In view of this fact, it is argued that the diversified plant organs of the present Vasculares have had a common origin, and are palingenetically homologous. This conception is thoroughly in accord with Professor Lignier's (27) theory which would derive all of the organs of higher plants from dichotomizing thallophyta. The possession of a protostelic vascular strand separates telomic from thallus plants. The assumption of the subterranean habit by a telome-truss could conceivably have given rise to a root, while the webbing of telomic fragments would have produced fern-like leaves whose venation, like that of modern fern leaves, would be characteristically dichotomous and open. The stem probably differentiated by sympodial development of successive telomes.

It is evident that this telome theory breaks down

the rigid barriers ordinarily thought to separate the various organs of the cormophytes. Both sterile and fertile telomes are regarded as homologous structures, in view of which, Zimmermann would regard the bract and scale of the conifers as fundamentally homologous, except that the scale might possess several fused units, whereas the bract is always a single telome. As might be expected, the telome theory is of far greater use in determining the nature of archaic fossil structures than it is in elucidating the more highly specialized plant organs found to-day. The purposes of comparative anatomy, and the determining of kinship among plant groups requires the designation of plant organs as roots, stems, and leaves, especially in those cases in which, as in seed plants, these organs have been more or less sharply differentiated. It should always be borne in mind, however, that paleobotanical evidence clearly indicates that root, stem, and leaf have sprung from a common source, and the attempt to distinguish between them often results in sterile controversy.

From the preceding discussion involving theoretical organology and paleobotanical testimony, we draw certain conclusions which are essential to the determinative study in which we are engaged. If the fossil cone is an abietinean, its vascular supply should be distributed to two distinct bodies- bract and ovuliferous scale. If, on the contrary, the fossil belongs in one of the derivative tribes - Cupressineae, Taxodineae, etc., the course of the vascular strands to a seeming single body should reveal the fact. The situation which actually

obtains will be discussed on a later page.

HISTOLOGICAL STUDY OF THE VEGETATIVE AND REPROCUTIVE AXES OF ABIETINEAE

Introduction.

In the identification of a fossil coniferous strobilus, two facts render necessary a detailed knowledge of histological structures: 1. the fact that superficial and external structures are commonly lost in the process of fossilization, and 2. the fact that natural relationships cannot be safely determined by a comparison of superficial structures. The termini of the conspicuous bracts of either Abies, Larix, or Pseudotsuga could not be expected to survive as well-preserved structures in a medium of volcanic sand, and though the several fossil cones upon which the following description and identification has been made, possess on the whole, excellently preserved ovuliferous scales and cone axes, the finer characters of the extremities of both these organs, and of the more membranous bracts, have been eroded away during the consolidation processes of the volcanic ash in which they are entombed.

An illustration of the dangers of the identification of a fossil founded upon superficial resemblance is the case of the misnaming of Geinitzia Reichenbachii which was originally referred to that venerable genus or modern trees, Sequoia, because of its foliage resemblances and the similarity of the cone impressions. As soon as the material was investigated anatomically the assignment to the Taxodineae was definitely called in

question. Its affinities with the araucarians were evident in its tracheidal pitting, its sclerotic pith cells, and the absence of resin ducts in its wood. Such anatomical features are far more conservative than the external ones, and reveal more truly and precisely the natural relationship of a plant.

In view of the facts, then, that complete preservation of external structures is uncommon, and that a reliance upon superficial features to indicate natural affinities very often leads into error, the problem of securing constant and reliable criteria for determining true relationships, confronts us. Anatomical details have proved of great assistance in this problem. For example, the Lycopsida have never shown leaf gaps in their stelar structures as Seward has been forced to admit even while arguing the origin of the phyllostiphonic araucarians from them. The ferns and their allies can invariably be distinguished from the lycopsidan cryptogams by the possession of the leaf gap. External features are susceptible to the modifying influences of the environment, while internal histological and cytological features, such as details of pitting, orientation of the primary tissues, etc., are far more stable characters. Because of the value of these anatomical details, and because the internal features of all structurally preserved fossils are open to the investigation of students, the present work is based essentially upon the findings revealed by microscopic sections.

A trivial and seemingly unimportant detail, may be of invaluable assistance in the correct determination of natural

relationships. The "bar of Sanio", (or "crassulae" of modern students) is an instance of this. In 1910, Miss Gerry (16) showed that the "bars" occur in all coniferous genera except Araucaria and Agathis, the only living representatives of the Araucarineae.

HISTOLOGY OF THE ABIETINEAN FEMALE STROBILUS.

Method of Procedure.

The materials for this investigation were collected largely from trees in cultivation upon the Massachusetts State College campus. Wherever technique demanded, the woody axes were treated in hydrofluoric acid to soften them. In all cases the material was imbedded in celloidin preparatory to making thin sections with the Reichert microtome. Transverse sections were made at the base, midway, and apex of the female cone axis, and wherever possible, cross-sections were also made of the peduncle. Longitudinal sections, both tangential and radial, were taken near the base of the axis, since this part seems to possess the significant characters in greater abundance and in more vigorous state of development than does the region at a higher level. Throughout the investigation, safranin and Haidenhain's haematoxylin have been used as the differential stains. Canada balsam was used as the mounting medium.

In the recording of such a mass of detailed information, it has been found advisable to adopt the following method, which will be maintained and applied in the description of each

of the abietinean genera so far investigated. Because of the histological complexity of the xylem, and the stability of its features, it will be taken up first. Its structures will be treated in the following order: 1. annual rings, 2. resin canals, 3. wood rays, 4. tracheidal features, and 5. wood parenchyma. After the xylary elements, the pith will be described; and finally phloem and cortex. The generic description in each case will be followed by a summary of the salient and diagnostic characters. A brief comparison of the histology of reproductive and vegetative axes will serve to relate the findings of the present investigation to the wealth of information which has accumulated concerning the vegetative anatomy of the Abietineae. Since the phyletic relations of the various coniferous tribes have been taken up in considerable detail in previous portions of the paper, they will be mentioned only incidentally here. Also, the suspicion that the fossil cones might belong to the Abietineae, was quickly verified and this fact made unnecessary any extended study of the reproductive histology of other tribes.

The Axis of Pinus.

The generalized and primitive nature of Pinus has made a thorough investigation of the genus advisable, and accordingly the cone axes of ten species were sectioned, stained, and mounted after the manner previously set forth. The well-known fact that it requires two years for the maturation of the cones of Pinus, would lead us to expect two conspicuous annual increments in the cone axis. However, the first year's growth is often trivial and no secondary xylary elements are laid down

until the second season's activity, in which case only a single marked layer of wood is found in the cone axis. Pinus nigra Arnold, P. rigida Mill., and P. virginiana Mill. have shown two well-developed annual rings of wood. Others like P. sylvestris L. and P. Bungeana Zucc. reveal only a small tag of wood near the pith representing the first year's increment. The first formed of the secondary tracheids always have a much larger lumen than the later tracheids, and probably do most of the conduction work.

Resin canals are abundant in the Pinus cone axis especially in the vertical direction, and are linked at intervals by horizontal canals. (See Plate I, Fig. 1.) The number of rows of vertical canals varies from one to six. The lining of the resin ducts is more variable than had been expected. Pinus sylvestris L., (Plate I, Fig. 2.), P. Bungeana Zucc., and P. resinosa Aiton have all shown the resiniparous cells to be sclerenchymatous. Investigation of the peduncle (Plate II, Fig. 3.), and vegetative axes of these three species has revealed a gradual transition between parenchymatous secretory cells, (Plate II, Fig. 4.) and the aforesaid sclerenchymatous elements. Were it not for the existence of other data, this condition would seem to indicate that resin canals whose linings were sclerenchymatous were the primitive type from which those with thinner, cellulose-walled cells were derived. The resiniparous cells give no evidence of retaining resin in themselves, but seem to secrete it into the canal as soon as produced.

The wood rays possess features which are very char-

acteristic of the same structures in the vegetative axis. Large oöpores are present on the parenchymatous cells of the rays of soft pines. However, the thick walled ray cells of the hard pines have tubular simple pits. The ray cells of hard pines possess the so-called "denticulate "walls, the appearance of which is caused by the numerous pits, and irregular nature of the wall thickening. Ray cells with thick walls and irregular contours, resembling those described by Thompson (42) as giving rise to marginal ray tracheids, have been in the cone axis of Pinus palustris Mill. (Plate III, Fig. 5.)

Writing of marginal ray tracheids, R.B.Thomson (44) mentions "their absence from the cone and from the first few years of stem and root wood." Burlingame (7) speaks of "The absence of ray tracheids from the seed cone of Pinus..." W.P. Thompson (42) misrepresents Jeffrey and Chrysler by attributing to them the statement that "True ray tracheids are quite absent from the cone axis." What Jeffrey and Chrysler (24) did say was "We find the marginal tracheary cells entirely absent in most of the rays of the two annual rings of the female cone." Jeffrey mentions the occurrence of the bordered pitted ray cells in Pinus palustris Mill. though they are not found in such abundance as in the vegetative axis. W.P.Thompsom mentions bent over tracheids in the cone axis which seem to assume the functions of the true ray tracheids, but we cannot agree with him on the total absence of the latter from the cone axis of the genus Pinus. The present investigation has revealed abundant marginal ray tracheids, linked together into radial rows by their bordered

pits in Pinus rigida Mill. R.B.Thomson's (44) statement that the marginal tracheids are not found near the pith of the stem should be modified in view of the condition, found in Pinus palustris Mill., where these cells follow the woody rays all the way to the pith. The marginal tracheids in the cone axis are not of general occurrence, however, even among the hardwood pines, a detail which is generally held to indicate their relatively late origin in geological time.

The tendency for the cone axis rays to have a great depth, is thought by R.B.Thomson (44) to indicate and ancestry in rays of this same type. Plate III, Fig. 6. shows such a ray in Pinus Lambertiana Dougl.

Generally speaking, the tracheids of Pinus have no other wall sculpturing than the bordered pits whose typical arrangement is linear and scattered. I.W.Bailey (5), however, writes that tertiary spirals "also occur in Pinus..." The typical disposition of the bordered pits, often gives place to a multiseriate and alternate arrangement on the enlarged and occasionally irregular tracheids found near the primary wood. This feature has been pointed out by R.B.Thomson (44) where he says: "Indeed, in the primitive regions of the latter (Abietineae) there is a considerable amonnt of resemblance to the araucarians. Instead of the opposite pitting, the pitting in the cone axis and early wood of the Abietineae has characteristically biseriate ones which are alternately arranged. Sometimes even these pits are flattened by mutual contact." "Schacht drew attention to this feature as early as 1862, but in late years its significance

seems to have been overlooked." The observations of these alternating pits by earlier workers has been verified by our own findings in the following: Pinus nigra Arnold, P. virginiana Mill., P. Bungeana Zucc., and P. rigida Mill. There seems to be no acceptable reason, however, for considering this pitting condition to be any more araucarian than cordaitalian, and in view of the fact that abietinean opposite pitting preceded the biseriate alternate arrangement in the primitive regions of araucarians, (See Plate IV, Fig. 7. of Agathis cone axis) it would seem more reasonable and logical to suppose that this condition in Pinus reflects its probable cordaitalian ancestry.

The primary wood tracheids are usually densely sculptured with spiral and reticulate thickenings, in the meshes of which incipient bordered pits put in an appearance. Their arrangement may be scattered, paired, and opposite, or crowded and alternate, the first mentioned being more prevalent than the others.

Wood parenchyma was not observed in any of the Pinus species investigated, and since I.W.Bailey (5) says wood parenchyma is found only very rarely in the vegetative organs, and, since we have reason to believe that the pinean ancestors were not characterized by its possession, it would hardly be expected in the conservative cone axis.

Nearly all the species of Pinus investigated revealed a pith whose cells in cross-section were extremely irregular and very variable both in shape and size as well as in wall thickening. Pinus sylvestris L. and P. resinosa Aiton have large, thick-

walled stone cells scattered irregularly through the parenchymatous pith. The cells of the medulla in longisection have rounded extremities, and intercellular spaces are conspicuous. This condition is in sharp contrast to that of Larix and Pseudotsuga where the cells appear as closely-packed rectangles in longisection. The pith cells of Pinus are not resinous.

Pinus densiflora Sieb and Zucc., P. Nigra Arnold, P. Bungeana Zucc., P. resinosa Aiton and occasionally P. sylvestris L. have cones with a well-developed layer of phloem tissue. Pines with moderately large cones like P. Strobus L. and P. rigida Mill. have no phloem at all, a fact which might indicate that the phloem of other pines is but a functionless retention. There are no evident diagnostic features in the phloem layer, and its delicate nature accounts for its rare preservation in fossil remains.

Numerous, and sometimes very large resin canals are found in the cortex of the female cone axis of pines. The canals are usually lined with parenchymatous cells whose walls are so delicate as to remain intact only very seldom. Stone cells are of sporadic occurrence, and may appear singly or grouped into "nests". The characters of the cortex are so generalized and constant throughout the Abietineae that they are of little use in diagnostic work.

Summarizing the characteristics of the Pinus cone axis, it may or may not display two annual rings of wood, its resin canals run both vertically and horizontally and are lined with parenchymatous secretory cells, the wood rays are very var-

iable, all transitions are to be found between thin-walled cells with large oöpores to very thick-walled elements with conspicuous tubular simple pits. Marginal ray tracheids are of sporadic occurrence in the hardwood pines. The secondary tracheids near the primary xylem have a larger lumen than those formed later, and often possess crowded alternate pits. The more mature tracheids have linear and scattered bordered pits. Wood parenchyma is absent in the cones of the pines. The pith has very irregularly-shaped cells and possesses numerous intercellular spaces. Stone cells are found in a few species. The phloem and cortex possess no features of diagnostic value.

The following summary of the xylary characteristics of the vegetative axis of Pinus will serve to indicate certain departures from the conservative features of the cone axis. The resin canals of pine wood run in both directions but are, with the exception of the nut pines and foxtail pines, lined with parenchyma. (See Plate IV, Fig. 8.) In Pinus sylvestris L. there is a gradual change from the parenchymatous lining in the canals of the stem and reproductive peduncle(Plate II, Fig 4., and Plate I Fig. 2.) to the thick-walled type found in the cone axis proper. The wood rays of the stem are far more constant in their make-up than those of the strobilar axis. Hard pines have typically sclerenchymatous ray cells with denticulate walls. The soft pines have marginal ray tracheids. Wherever parenchymatous ray cells are found, their lateral walls possess large and conspicuous oöpores. The soft pines can be distinguished from the hard pines by the presence of tangential pits in the last

tracheids of the annual ring, a feature which has not been observed in the cone axis.

The possession of resin canals running in both directions (See Plate IV, Fig. 9. and Plate V, Fig. 10.) is considered to be a primitive condition from which the other abietinean situations have probably arisen by degeneration, a theory which is supported by both recapitulatory and traumatic phenomena. The parenchymatous epithelium of the resin canals is generally thought to precede the sclerenchymatous condition. The marginal ray tracheids do not occur in other genera except under abnormal conditions, but this very feature, occurring as it does in Abies, Sequoia, and Cunninghamia would indicate that Pinus is probably the primitive genus because of its normal possession of these structures.

The pith, phloem, and cortex have no features of particular interest in either cauline or reproductive axes.

The Axis of Picea.

Three species of Picea have been investigated, and the findings incorporated with the published accounts of other workers. Picea Abies (L.) Karst. and P. mariana (Mill.) BSP. show a very small amount of the first year's wood between the spurs of the pith at the leaf gaps. The tracheids which make up these areas are of larger lumen than those of the following year, and probably are the only ones which carry on the function of conduction. Resin canals are found running in the vertical direction in the axis of Picea Abies, and, curiously enough, they are lined with thin-walled, parenchymatous cells. No resin

canals were found in the other species investigated, nor has the writer seen reference to their occurrence in any other species of the genus.

The ray cells possess smooth thick walls and are simple pitted. They are usually uniseriate and may attain a depth of fifteen cells. There are few significant features in the rays or secondary tracheids. Wood parenchyma is absent from the cone axis.

The cells of the pith appear round in cross-section and are quite regular in shape and size. The thickness of the constituent cell walls seems to be uniform in a given species, as for example, Picea Abies where the cells are entirely sclerotic or in Picea mariana where there is very little wall-thickening. There is a tendency for the diameter of the centrally located cells to be greater than those located in the leaf gaps. Nests of stone cells are to be found in Picea canadansis (Mill.) BSP.

The three species of Picea investigated showed a uniformly well-developed layer of phloem, about 10 - 12 cell-layers in depth. The cortex in every case contained numerous and occasionally very large resin canals always lined with parenchyma.

The stem wood of Picea possesses resin canals with a sclerenchymatous epithelium in opposition to that found in the cone axis. In accordance with the principle of conservatism, this is to be regarded as evidence for the primitiveness of the parenchymatous type. R.B.Thomson and H.B.Sifton (45) assert

that the resin canals of Picea canadensis are all traumatic. They claim to find evidence either of wounding or of abnormal annual rings in association with the resin canals of the main axis. This may apply to the vegetative axis but it can hardly pertain to the canals occurring in the cone axis. The only species, Picea Abies (L.) Karst., in which we have found the canals in the axis, gave no evidence of wounding, now were they characterized by the tangential connections, such as are commonly found in traumatically recalled canals. Tangential pits are found on the terminal tracheids of the summer zone, and, as in the cone axis, wood parenchyma is entirely absent from the vegetative xylary tissues.

The secondary tracheids nearest to the primary wood commonly possess biseriate alternate bordered pitting. It can be seen in Picea Abies in Plate V, Fig. 11.

The most constant histological factor which can be used to distinguish Picea cones from those of Pinus is the presence in the latter of horizontal resin canals. Even vertical canals are not at all abundant in Picea though the Norway spruce has one complete circle of them near the end of the secondary wood layer. If an axis possesses two or more zones of canals it may safely be referred to Pinus. The ray cells of Picea never possess the large obpores characteristic of the large parenchymatous ray cells of Pinus. In no case have we found marginal ray tracheids in the cone axis of Picea, and, though this feature is not of sonstant occurrence in Pinus, when present, it serves to diagnose the material.

The Axis of Pseudotsuga.

The only cones of the Genus Pseudotsuga which we have investigated came from a cultivated specimen of P. taxifolia (Lamb.) Britt. on the Massachusetts State College campus. The slight evidence of annual rings in the cone axis appeared as a differentiation of the few tracheids with large lumina which lie between the radial tongues of pith, and a broader band of very thick-walled tracheids formed the second year.

The resin canals occur in a ring of few canals close to the medulla, and the secretory cells are only partially lignitized. They have a curious way of disintegrating, so that short spurs run into the canal (Plate VI, Fig. 12.). This seemingly trivial character is found also in the fossil Miocene cones described and identified in the concluding portion of this paper, and contributes to the certainty of its final determination. There was no evidence of horizontal canals either in the specimens we investigated or in those described by E.C.Jeffrey. (22).

The wood rays in the cone axis of the Douglas fir vary from one to fifteen cells in depth; they have very thick, denticulate cell walls and are usually uniseriate. Jeffrey makes no mention of the ray condition, probably because it possesses no diagnostic or otherwise significant features.

A study of the tracheids of the secondary wood in the cone axis of Pseudotsuga taxifolia (Lamb.) Britt., however, reveals interesting and taxonomically important fact. First of all, the same cordaitalian pitting (Plate VI, Fig. 13.) which is

found in Pinus, was here found on the tracheids near the primary wood. The bordered pits are often so close to one another as to become hexagonal by crowding. Many of the later-formed tracheids and especially those near the wood rays, are not perfectly perpendicular and smooth sided, but like similar elements occasionally seen in Picea, are irregularly curved and bent and often possess blunt apices where they contact a ray. Elements like these, as well as other more regularly shaped tracheids possess very definite tertiary spirals. (Plate VII, Fig. 4.) Penhallow (31) makes the statement that the spiral sculpturings, so characteristic (and within certain limits, diagnostic) of the vegetative wood of Pseudotsuga, are absent from the cone axis. Jeffrey, (22) accepting the observations of the earlier worker, found it necessary to explain that thick-walled aestival tracheids of the stem wood, likewise, had no tertiary spiral thickenings, and thereby accounted for the supposed absence of this character in the cone axis, whose tracheids as in numerous other genera are particularized by very thick cell walls. However, the presence of these spiral thickenings, which are conspicuous if not particularly abundant in the cone axis, does away with the necessity of such an explanation. Evidences of spiral thickenings have been found in the Oregon fossils, in fact we noted their presence before they were known to be features of the strobilar axis of Pseudotsuga.

There is no wood parenchyma in Pseudotsuga, but the pith shows certain features of diagnostic worth. Its cells are very thick-walled with tubular simple pits penetrating them, and

though intercellular spaces are to be seen in cross-section, none is visible in the longisection. In the latter, the cells appear rectangular, their lower and upper extremities terminated by horizontal walls. All the cells of the pith are filled with resinous contents. The pith cells near the base of the cone axis are nearly isodiametric so that in longitudinal aspect they are square. (See Plate VII, Fig. 15.) Nearer to the apex,however, the constituent cells become greatly elongated until they assume tracheidal dimensions. There is a similar but more abrupt transition from the cells of the center of the pith to those immediately bordering the primary wood. In this respect, the pith of Pseudotsuga bears a strong resemblance to that of Picea. E.C.Jeffrey (23) would correlate the increase in resiniferous cells with the progressive degeneracy of the resin canal system.

There is a definite, if not a large phloem layer, found in Pseudotsuga. The cortex, like the pith, is highly resinous while possessing at the same time a rather extensive system of vertical resin canals, which are lined with parenchyma. Thick-walled, sclerotic cells are common in the cortex of Pseudotsuga.

In summarizing, the annual rings are inconspicuous, resin canals are all vertical forming a single ring near the pith, and disintegrate in a curious fashion. The wood rays are unique in no respect, but the tracheidal walls are sculptured with a regular spiral thickening. Both pith and cortex are entirely resinous, and the latter possesses sclerotic cells and parenchyma-lined resin canals in addition.

The vegetative wood of all Pseudotsugae can be distinguished from other abietineans, except Larix laricina (DuRoi) K.Koch and Pinus Taeda L., by the possession of tertiary spirals on its tracheidal walls. These markings are usually conspicuous and extend through both vernal and aestival regions of the wood, an occurrence which would separate it from Picea, which according to Penhallow possesses no spiral thickenings, but which I.W. Bailey, (5) quoting Gothan, believes to have the sculpturings, restricted, however, to the summer layer of tracheids. Any tertiary spirals in Larix are restricted to the summer zone, likewise. The resin canals of the vegetative axis are lined with thick-walled epithelium, in opposition to the partially parenchymatous nature of the lining in the reproductive axis. Pseudotsuga wood can be particularized from that of other members of the sub-tribe Pineae by the possession of wood parenchyma in the last-formed elements of the xylem. This is evidently a recently acquired feature which has not as yet penetrated the conservative strobilar axis. Mayr has reported spirals thickenings on the ray tracheids of Pseudotsuga macrocarpa Mayr.

E.C.Jeffrey (22) finds two quite constant and reliable characters which separate Larix and Pseudotsuga, namely, the possession by the latter of sclerotic cells in the pith and cortex, and the fact that the single row of resin canals in the latter is found near the medulla, while that of the former occurs, as in Picea, near the end of the annual ring. To these diagnostic features, our investigation has enabled us to add the tracheidal feature of tertiary spirals which when found in both

spring and summer zones of wood is sufficiently diagnostic to identify the material as Pseudotsuga. Another tracheidal feature which seems constant enough to be of determinative assistance is the possession by Pseudotsuga of cordaitalian pitting on the secondary tracheids which borderthe primary wood, a condition which has not been found in either Picea or Larix. The bordered pits of all these genera, Pseudotsuga, Larix and Picea possess slit-like openings. The pith of Pseudotsuga differs from that in Picea in its highly resinous nature, but in this respect it is identical with Larix.

The Axis of Larix.

We have been fortunate in being able to investigate the strobilar histology of three species of the genus Larix, and so we are able to make generalizations with more certainty than would otherwise be possible.

The accumulation of secondary tracheids the first year is not sufficient to make two annual rings conspicuous. The resin canals occur in a single ring in the summer wood, those of Larix Kaempferi (Lamb.) Sargent are found midway between the pith and the cambium, (Plate VIII, Fig. 16.) and those of Larix decidua Mill. in the very last formed tracheids bordering the cambium. (Plate VIII, Fig. 17.) In the former, horizontal canals have been seen connecting the xylary and the cortical ducts. They are invariably lined with parenchymatous cells.

The rays provide many interesting features, foremost among which is the tendency, especially in Larix decidua Mill. to have very irregularly shaped cells similar to those

described by W.P.Thompson (42) which fail to make a solid plate of cells, but have extensive gaps between portions of the cells. In radial sections, the lateral walls of these ray cells are seen to possess numerous, small, half-bordered pits with elliptical pores. Simple pits seem to connect the thick-walled ray cells with one another vertically. The wood rays of Larix are characteristically resinous.

There are no particularizing features on the secondary tracheids of Larix. There seems to be no evidence of the cordaitalian pitting found in the first tracheids of Pseudotsuga and Pinus. Larix laricina (DuRoi) K.Koch possesses evidence of tertiary spirals only in its latest formed wood, and is not to be compared with those of Pseudotsuga which occur throughout the xylary zone.

There is no wood parenchyma in the cone axis of Larix. The pith in the European larch is highly resinous and its cells in cross- and longi-sections gives much the same appearance as was recorded for Pseudotsuga. The Japanese larch does not have the resinous pith, but is otherwise similar to the European species.

Larix decidua Mill. is the only species which has shown a phloem layer and in this case it is grouped into "wedges" very similar to the familiar condition in Tilia twigs. The cortex of Larix Kaempferi (Lamb.) Sargent, like its pith, is not resinous, but possesses numerous parenchyma-like cells lining the resin canals. The European larch, on the other hand, has a considerable proportion of its cells filled with resin. All the

larches possess cortical resin canals.

To conclude: the first annual increment of secondary wood in the cone axis is very scanty, the tracheids like those of all other Pineae, have a larger lumen and thinner walls than those formed later. Resin canals form a single row running vertically in the later formed elements of the xylem. They are always lined with parenchyma. The wood rays tend to be irregular and are composed of cells whose contours are either undulating or very jagged. Small half-bordered pits connect them with the tracheids, and tubular simple pits, found in their horizontal walls, connect the ray cells vertically. The tracheids are without cordaitalian pitting, or any other notably feature. The pith and cortex are sometimes resinous, always possess resin canals, and never bear typical stone cells.

The wood of Larix resembles that of Picea and Pseudotsuga in its sclerenchymatous lining about the resin canals, and its tangential pitting on the last summer tracheids. It is interesting that the retentive cone axis has parenchymatous cells lining its canals, a condition which supports the theory that that type is primitive. Pseudotsuga with its partially sclerenchymatized cells would, in this respect, be more advanced or specialized than either Picea or Larix.

Larix can be differentiated from Pseudotsuga by means of its resin canals which occur either early or late in the summer zone of wood and never in the region bordering the medulla. The latter condition is invariably found in Pseudotsuga.

The presence of resin in either the pith or cortex would help to separate the genus Larix from Picea. There seems to be no constant and reliable histological character which can be used to separate the cones of Larix from Picea. All the features attempted, have broken down, and the only resource left would be to revert to some external feature like the characteristically short bract of the Picea cone, as opposed to the more conspicuous structure in Larix. But such an attempt is of little value to the paleobotanist, for such delicate foliar structures are rarely preserved. The only alternative is to set up a form-genus including Picea-Larix.

The Axis of Abies.

E.C.Jeffrey (22) has done a great deal of work on the strobilar histology of Abies. He records that Abies Appolinis Link. is the only Old World species with normal resin canals in the cone axis. In this country, Abies magnifica Murr. and A. grandis Lindl. are the only ones whose cones possess the normal canals, and the latter has shown them only sporadically. The following have given due evidence of resin ducts in the cone axis: Abies balsamea (L.) Mill., A. Fraseri (Pursh) Poir., A. concolor Lindl. et Gord., A. amabilis Forbes, A. nobilis Lindl., A. bracteata (D.Don) Nuttall, A. Veitchii Lindl., and A. cephalonica Loudon. In the case of A. magnifica it is interesting to note the absence of resin canals from the vegetative axis. In the cones of this species, they are found to be very numerous near the apex of the cone and are so crowded as to form tangential intercommunications. Nearer the base of the cone, they are

less crowded, and they disappear completely in the peduncle. The occurrence of resin canals in the conservative regions of the Abieteae has long been known and provides the best evidence for the theory that this group, whose vegetative wood is normally devoid of ducts, has been derived from the Pineae, the other sub-tribe of the Abietineae. Whenever resin canals do occur in the cone axis of the genus Abies the secreting cells are generally sclerenchymatous. (See Plate VIII, Fig. 18.) This fact gives us the only diagnostic feature of any worth regarding the Abies resin canals.

The rays of Abies are quite irregular, though usually uniseriate. The ray cells have slightly thickened walls of which the lateral ones are covered with small half-bordered pits with elliptical openings. The rays vary in depth from three to eight cells (it will be noted that they do not have the great longitudinal extension that is characteristic of the Pineae) and some of them are highly resinous.

Cordaitalian pitting has been noted on the termini of some of the tracheids, but it is not very commonly found near the primary wood. In the later-formed secondary xylem, wood parenchyma is abundant. (Plate IX, Fig. 19.) The cells are isodiametric in cross-section, but are seen to possess great longitudinal extension in the radial direction.

Abies grandis shows a considerable development of the phloem layer, especially near the base of the cone, but it possesses no features of diagnostic value. The cortex is chiefly parenchymatous with scattered stone cells and several large

resin canals which are lined with thin-walled epithelium.

To sum up; the presence of annual rings is no more reliable a character in Abies than it is in the Pineae. The resin canals are not a sufficiently constant feature to be of value in diagnostic work, though their tendency to possess a sclerenchymatous epithelium would, if found in fossil specimens, be regarded as good evidence of an affinity with Abies. The rays are smaller than those of the pinean genera, but the outstanding diagnostic feature of the genus is the possession of wood parenchyma which is typically restricted to the region of the later-formed xylem. The stone cells should be noted as having significance when comparisons between abietinean genera are to be made.

The Axis of Cedrus.

No original work has been possible on this genus, the difficulty of securing material being so great. Jeffrey describes the parenchyma-lined resin canals of the cortex of Cedrus atlantica Manetti and claims there are none to be found in the woody elements of the cone axis. In spite of the fact that Radais reported resin canals in the cone axis of the deodar, Cedrus deodara (Roxb.) Loudon, Jeffrey has sectioned both this species and the cone of Cedrus libanitica Trew. without finding xylary resin canals.

The Axis of Pseudolarix.

The monotypic genus, Pseudolarix, with its single species, P. Kaempferi (Lindl.) Gord., which is found native on-

ly in China, was not accessible for study, so that our notes on this genus, as in the preceding genus, must simply record what Jeffrey has published on it. The cone axis possessed no resin canals in the xylem, but the corical resin canals in the outermost layers of the axis are known to be continuous with the extra-stelar canals in the ovuliferous scales. Even the bracts of the cone possess resin canals.

The Axis of Tsuga.

The amount of wood in the cone axis of Tsuga canadensis Carr. is not very great, and there is no evidence of two annual accumulations of secondary tracheids. (Plate IX, Fig. 20) Resin canals are absent from the xylary tissues of both Tsuga canadensis and T. mertensiana (Lindl. et Gord.) Carr. The rays are few, with thin-walled, parenchymatous and protoplasmic cells. There are no tracheidal features of note, and wood parenchyma was not to be found in Tsuga canadensis, nor have I seen reference to its occurrence in other species. The pith is composed of irregularly shaped cells whose walls are thin and parenchymatous, but always without resinous contents. There is a well-developed phloem in Tsuga; in fact, the phloem layer equals the xylary layer in radial diameter, but it possesses no outstanding features. The cortex cells are thin-walled and protoplasmic, and among them are many large, parenchymatous resin canals.

Tsuga can, therefore, be differentiated from Abies by the absence of resin canals, wood parenchyma and stone cells, the last two being invariably present, and the first occasionally

present in Abies. There is as yet, insufficient histological knowledge of the strobilar axes of the Abieteae to be able to particularize all of its genera.

The Axis of Keteleeria.

Keteleeria Fortunei (Murr.) Carr. represents another monotypic genus, and its distribution is restricted to China just as Pseudolarix is. Jeffrey (22) has said that it possesses no resin canals in either its reproductive or vegetative axes. To my knowledge, this is the only published work on the cone, and we have no been able to secure material for study. So far as is known, the histology of this strobilus is very similar to that of Tsuga, though the structure as a whole is probably much larger than that in the hemlocks.

CONCLUSION TO THE STUDY OF STROBILAR HISTOLOGY IN THE ABIETINEAE.

Pinus is probably the primitive genus, and its extensive vertical and horizontal resin canal system provides its most outstanding feature. The ducts are usually lined with parenchyma. The pith cells are very irregular both in size and shape, and numerous intercellular spaces are present. There is a complete absence of wood parenchyma, and stone cells are only occasionally seen.

Pseudotsuga has a single ring of vertical resin canals near the pith, and their partially sclerenchymatized secretory cells break down in such manner that short spurs are left extending into the lumen of the duct. Tertiary spirals are present on the tracheids of both spring and summer wood.

Like Pinus the first-formed secondary tracheids commonly possess biseriate alternate pitting. Both the pith and cortex are composed of resin filled cells.

Picea and Larix are very similar in their cone histology and the characters which in some cases distinguish them, break down in others. Both usually possess a single row of vertical resin canals in the summer wood of the cone axis, and are lined with a parenchymatous epithelium. Neither of the genera have been seen to possess biseriate or alternate pitting next the primary wood. Larix usually has a very resinous pith, but this is not true of L. Kaempferi. Picea pith cells are usually free from resin, but again this is not an invariable feature. Both genera are characterized by the absence of wood parenchyma and usually by the absence of stone cells, but the latter have been found in Picea canadensis. Whenever tertiary spirals occur, as in Larix laricina, on the tracheids, they are restricted to the summer wood.

Abies possesses wood parenchyma, and occasionally normal resin canals. Traumatic canals are easily stimulated. Stone cells are common in pith and cortex.

Tsuga has no xylary resin canals, no wood parenchyma, and total absence of stone cells in either pith or cortex.

Cedrus, Pseudolarix, and Keteleeria are insufficiently known to be able to give particularizing features. None possesses normal xylary resin canals, but further than that, the histology of the five species which are the only modern representatives of these genera, is unknown.

However, with the above diagnosis of the pinean genera, and of Abies and Tsuga, we have a key which, though imperfect, is still a serviceable one in determinative work on fossil coniferous strobili. By its means we turn now to the interpretation and identification of the lignitized cones from the Miocene of Oregon.

PERTINENT GEOLOGY AND PALEONTOLOGY OF THE MIOCENE OF WESTERN NORTH AMERICA

Introduction.

The lignitized structures turned over to me by Dr. R.E.Torrey for examination, were collected by him on August 18, 1917, at Cape Blanco, the westernmost extremity of the coast of Oregon. His record of the discovery is as follows: "About two miles south of Blanco [the tip of the peninsula] a black volcanic sand formation uncovered at low tide, containing small fragments of wood with twigs and Picea (?) cones. Collected a half paper bag full. Miocene in age and probably hardly pays for the expense of the journey there." Verbally, Dr. Torrey describes the formation as a friable, soft sandstone in which the cones are imbedded. Weathering has exposed portions of the cones as well as other lignitic fragments. The fact that the entombed plant remains show the effect of water wearing would indicate a marine or brackish origin for the volcanic deposits. Also, because few fossils are ever found in eolian deposits, and since the strata are closely compacted, we are justified in holding to the theory of aquatic origin for the rocks. The sand-

stones and ash form portions of the thirty to fifty foot cliffs along the shore line.

Geology of the Empire Formation of Oregon,

The volcanic sand deposit in which the fossils were imbedded, is described by Arnold and Hannibal (4) under the heading: The Empire Formation, [Middle] Miocene. They say: "In the Empire district about 500 feet of beds, sandstones at the base grading upward into massive shales partially organic in character, but more or less derived from worked over volcanic debris, represent the formation. At Cape Blanco sandstones alternating with compact bedded volcanic ash containing abundant plant remains attain about the same thickness." At other localities the formation attains a thickness of 4000 feet.

Overlying the Empire snadstones at Cape Blanco is a formation of argillaceous sands, 75 feet in thickness, containing calcareous nodules. It is the base of the Elk River Formation and is now referred to the Upper Pliocene.

J.S.Diller (12) speaks of the Coastal Plain as attaining its highest level, 225 feet, at Cape Blanco. Eastward a series of sandy terraces alternates with what used to be sea bluffs like the present promontory at the Cape. "The terraces represent old beaches formerly washed by the waves at the foot of the cliffs."

In early Eocene times a shallow sea laid down the Arago formation on the submerged Coastal Plain, but when the land rose later in the same epoch all evidence of Eocene deposition was eroded away from the Cape Blanco region. This erosion

interval preceded the deposition of the Miocene Empire sediments which consequently were laid down directly on the Cretaceous Myrtle formation. The later Miocene erosion peneplained the coastal area and piled up much land debris along the shore. "The records of this epoch are well exposed in the Empire Formation at Cape Blanco, and contain, besides the ordinary sediment derived from the adjacent land, a bed of volcanic dust which undoubtedly was blown a long distance and may have come from some one of the volcanoes then active along the Cascade Range."

Diller's section of the terrain near Cape Blanco is as follows:

Gravel	25 ft.
Fine whitish sandstone full of minute organisms	100 ft.
Tuff	25 ft.
Yellowish sandstones and near top very shaly sandstones .	475 ft.
	625 ft. Total.

Diller considered this whole section an exposure of the Miocene Empire, but because of a distinct difference between the dip and strike of the upper thinner strata and the lower more massive sandstones and tuffs, a difference which he must have failed to see, more recent accounts relegate the upper strata to the Elk River Pliocene Formation.

The Empire Formation, chiefly sandstones with "a bed of volcanic dust," occupies but a narrow strip along the

coast for a half a mile northeast of Blacklock Point, and a similar strip for about two miles southeast of Cape Blanco to the mouth of Elk River." Dr. W.H.Dall (See 4) correlates the Blanco formation with the Empire of Coos Bay, basing his conclusions on the similarity of the numerous invertebrate fossils. Newbury and Condon (30) also regard the coastal formation as of Miocene age, for they say: "a narrow strip of arenaceous Miocene rocks extends more or less continuously from Cape Blanco to Port Orford." Because of the greater elevation of the Blanco region, the Empire Seas did not extend far inland, but at Coos Bay and near the Columbia River, the deposits indicate a sea of great eastward extension.

Pleistocene deposits overlie what Diller called the Empire Formation but the overlap is réally on Upper Pliocene Elk River strata.

Gold and "platinum-like metals" have long been mined in the Cape Blanco region. In fact "The Klamath Mountains of southwest Oregon and northwest California have probably yielded more platinum than any other portion of the United States."

Numerous lignitic formations, sometimes yielding valuable and even coking coals, indicate "widespread coal-forming conditions at the beginning of the Miocene." Similar conditions must have existed along the coast in Eocene times, for Diller and Pishel (13) report alternating marine and fresh water fossiliferous layers in association with the coal at Coos Bay.

<u>Mammalian Remains from the Miocene.</u>

A side glance at the animal life of the Miocene is in order. It is generally the zoologists who have determined the age and sequence of the fossiliferous beds.

The Miocene Period has been called the "Mammalian Golden Age," (35) and with good reason if one considers the wealth of paleo-zoological material which strata of this horizon have yielded. Parahippus and Meryhippus were no longer using any but the middle toe, and the oldest tailless apes are found as Middle Miocene remains.

Invertebrate Remains from the Miocene.

Not only are the mammalian records abundant and complete in Miocene times but it is from the strata of this period that the most widely known fossil insects are derived. The Florissant Formation, (25) of whose age Andrews (2) says: "the weight of evidence at present, (1935) is in support of the Miocene," has yielded no less than 1000 insect species (33) besides its well-known flora. The Chesapeake Formation of the Eastern United States carries an invertebrate fauna which clearly indicates the breakdown of the Greenland-Norway landbridge in Middle Miocene times, bringing an Arctic fauna to our previously sub-tropical coasts. During the Miocene the Siberia-Alaska land bridge provided the means for the third marked mammalian migration into North America from Asia.

The Empire Formation in the Coos Bay and Cape Blanco regions (4) contains 64 recorded species of marine invertebrates. It was by means of this fauna that Dall was able to work out the age of the strata and correlate it with others

in Washington and California. It was the correlation of the coastal Miocene deposits with others in the Rocky Mountains and at Florissant which definitely established the recency of the Cascadian Revolution. To my knowledge there has been but a single vertebrate fossil recorded from the Empire Formation, a fish described by Arnold and Hannibal.(4)

Pirrson and Schuchert (38) figure that 20-40% of the Miocene species of molluscs are living to-day, and as Diller points out, their remains, from the Miocene to the present, can be found on the successive terraces and cliffs which mount up step-fashion from the Oregon Coast.

Flora of the Miocene of Western North America.

The plant life of the Mesozoic and Cenozoic was long neglected by paleobotanists in favor of the rich remains from the Carboniferous. But slowly the situation is changing as the emphasis shifts to the almost desperate attempt to solve "the abominable mystery" of angiosperm origin. Among the Mesozoic-Tertiary plants, the conifers play a leading role.

Mason (28) only ten years ago, made the statement: "The pines are an old group and were well established prior to the Jurassic," and this sentence takes on more general and deep significance when he says: "fossil records of the genus (Abies) in the western United States, are chiefly from the Jurassic," thereby affirming the general occurrence of the abietineans in western North America during the early Mesozoic. All Mesozoic time, except the uppermost Cretaceous, was dominated phytologically by the gymnosperms, and chiefly by cycads and conifers.

But where the maximum number of coniferous species from any horizon of the Mesozoic is 107, (47) (a condition found in the English Oolites), the Miocene deposits of the Cenozoic Era record not less than 307 species.

Miocene strata throughout the world have yielded more paleobotanical remains than those of any other horizon, even the much investigated and rich Carboniferous deposits. Ward (47) tells us that the figure quoted as indicating the coniferous species of the Miocene, represents 8% of the flora of the times as compared to the present ration which gives gymnosperms one third of one percent of the seed bearing plants. So, whereas the conifers with the cycads were dominant from Carboniferous to Cretaceous, their decline has been rapid and steady throughout Cenozoic time.

The Miocene deposits of remote parts of the world have all yielded abundant coniferous remains. Chamberlain (8) records Pinus, Taxodium, Sequoia, and Glyptostrobus from Greenland; Pinus, Juniperus, and Libocedrus from Spitzbergen; and Pinus, Picea, and Sequoia from Iceland. Seward (38) speaks of Sciadopitys, Glyptostrobus, Sequoia and Taxodium as being common in Europe during Tertiary times, but eliminated, as so many plants were, by the coming of the ice sheet. It was the bald cypress, now native only in southern United States and in Mexico, that formed the Miocene brown coal deposits of Europe. The genus Cryptomeria, now found only in Japan, was a forest maker in Ireland during the Tertiary. Araucarias, cypresses and pines grew, during the middle Tertiary, where southern England now lies, and, speaking of the Miocene Strata at Oeningen

in Switzerland, he says, it is similar but even richer than that at Florissant, Colorado. Thus the European flora of Miocene times was much richer, at least in species, than the coniferous vegetation of the present.

Lesquereux, (26) studying the Miocene flora of Alaska, found well preserved specimens of Taxodium distichum (L.) Richard and Thuites (Chamaecyparis), there besides numerous ferns and equisetums. He makes no mention of finding fructifications of these plants.

Nathorst and Florin think that the Tertiary floras of Japan indicate, as does Lesquereux's discovery of Taxodium in Alaska, a warmer climate than the present, and this condition is exactly matched on the North American side of the Pacific in the Coastal States and British Columbia, where the Miocene flora indicates a distinct "northerly shift of the Tertiary isotherms." (19) The writer is of the opinion that the Siberian-Alaskan land bridge of the Cenozoic Era may well have given to eastern Asia and western North America a warmer bordering sea than the present arctic waters. The central portions of the great land areas like Russia and Siberia, and the Middle-West of North America, would not be climatically affected by this bridge thus lending argument to Kryshtofovich's conclusions that the Tertiary climate of Russia and Siberia was no warmer than at present. The cogency of this hypothesis is perhaps strengthened by the parallel conditions on the Atlantic coast. The influx of an Arctic fauna to the previously temperate and sub-tropical assemblage of organisms on the east coast of the United States

when the Greenland-Norway land bridge broke down in Miocene times, is graphically recorded in the Chesapeake Formation which runs from Massachusetts to Alabama. This interpretation would not irritate Mr. Seward who dislikes "taking liberties with the North Pole."

The remains of Miocene floras are found in many and widely scattered localities in western America. The Florissant volcanic ash beds of Colorado have yielded 250 species; Amethyst Mountain in Wyoming reveals 2000 feet of superimposed Tertiary forests, again preserved in volcanic strata; coal deposits areas in Washington, Oregon and California have yielded numerous plant impressions as well as structurally preserved material; and the Lamar River Flora in the Yellowstone, and the Mascall and Empire Formations of Oregon, have made notable contributions to our knowledge of Tertiary conifers. It was by the correlation of Californian Miocene floras with those of Colorado and others east of the Rockies, that Lesquereux (11) proved "beyond doubt, the recency of Rocky Mountain uplift." The miocenic forest must have been interspersed with numerous grassy plains, a fact which is incontrovertible indicated by the bunodont teeth of Miocene mammals. The marine waters invading the Coastal States carried innumerable diatoms, whose siliceous shells, compacted and crushed, to-day appear as huge, petroleum-yielding* formations in California.

*Dr. Torrey very strongly doubts this assertion made by Schuchert (35) that diatoms are responsible for the occurrence of petroleum. With one questionable exception, diatom shells have never been found in oil, and extensive diatom deposits of Miocene age in Washington have never yielded oil. Spore-filled oil-bearing shale in Russia gives the key to the probable origin of petroleum deposits.

As for the coniferous remains of Miocene strata, Hannibal (19) in 1911 says: "The floras of the Middle and Upper Miocene are as yet largely undescribed." Since that time much has been done to augment our knowledge of this period, which is so important because it is the last to contain plants which have since become extinct. As Schuchert (35) tells us, only "20-40% of Miocene species are living to-day," whereas of Pliocene formations in California, Hannibal says all remains are considered referrable to modern species.

Coniferous Flora of the Miocene of Western United States.

The coniferous remains in the rocks of the Miocene of the Western United States (3), (9), (10), (29), (34), provide an interesting basis for comparison with present floras and their distribution. In general the conifers of Miocene time were more numerous in species and genera than they are in that region to-day, even though it is now the area of densest aggregation in North America. For example, Libocedrus had three well defined species in Miocene time: L. coloradensis from Florissant, L. predecurrens Knowlton from the Latah beds of Spokane, and the still extant species L. decurrens Torr. from the Mascall of eastern Oregon. Taxodium was a western conifer until late Miocene times, when it seems to vanish completely. Read (34) has given a more or less complete summary of Tertiary sequoias and finds that the genus had more species and a wider distribution during Cenozoic time than at present. Berry (6) lends support to this opinion in saying that S. Langsdorfii (Brongn.) Heer. has been "found almost everywhere throughout the northern

hemisphere where plant beds occur." He mentions over a dozen species as far back as the Middle Cretaceous, and "the Miocene witnessed the zenith of Sequoia development." It ranged from "Tasmania to Spitzbergen; Ireland to Japan;" and Alaska to Chili.

Also, from the Lamar River Formations (34) are species of Pinus which find no close resemblance to modern forms. Penhallow (31a) has reported Pseudotsuga miocena Penh. from British Columbia and Torrey (46) has described the wood of Pseudotsuga annulata (Platen) Torrey from the Cape Blanco deposits. In the Mascall (Miocene) strata of southeastern Oregon, Mason (28) records the following genera: Ginkgo, Sequoia, Libocedrus, Pinus, Taxodium, Thuja, Abies, and certain twigs which are tentatively referred to Picea. In the Empire Formation, Pseudotsuga annulata (Platen) Torrey, and Pityoxylon cf. Vateri (Platen) Torrey are the only recorded accounts of the flora I have found.

The task of comparing Tertiary coniferous plants with those of the present day in the western United States has proved interesting to a degree, and many workers have made it their concern. Western North America is the center of the richest coniferous flora of the Northern Hemisphere, and many species are endemic there. Sequoias are confined to the mountains of the Coastal States, and Cupressus macrocarpa Hartweg is restricted to Southern California. Pseudotsuga taxifolia (Lamb.) Britt. is the dominant lumber conifer of North America and flourishes in the western mountains. Besides the endemics

there are large numbers of species of mostly abietinean or cupressinean genera scattered widely and occurring abundantly.

Yet, even with this formidable array, The Miocene flora seems to have excelled it, and provides evidence that the conifers, and trees in general are giving place to the more typically herbaceous angiosperms. The geographically and numerically restricted Sequoias of our times, were numerous in species and individuals; and the Miocene formations, replete with their remains, indicate an ubiquitous distribution, for Greenland, Iceland, England, continental Europe, eastern America, Chili, and Asia have all yielded valuable specimens, and the European fossils were known to botanical science long before the living giants were discovered in America. The bald cypress, now restricted to southeastern United States and Mexico, has been identified from the Miocene formations of Virginia and Oregon, Japan, Austris, Italy, and Switzerland; and it was Taxodium which yielded most of the Miocene brown coal beds of Germany. Glyptostrobus was present in both eastern and western United States in Miocene times and is now native only in Japan.

In the very nature of things, our comparison of the living with the fossil genera, cannot be supplemented by facts concerning the relative abundance of individuals belonging to these genera, but we may safely infer, in view of the generally accepted law of uniformitarianism, that Miocene times may have witnessed the same verdant growths as to-day make it possible for H.S.Conard (9) to write "by hard work one can travel a quarter of a mile an hour off the trails," through the

highly coniferous vegetation of the Olympic Peninsula. This flora in Washington, consisting chiefly of Pseudotsuga taxifolia (Lamb.) Britt., Abies amabilis (Dougl.) Forbes, A. lasiocarpa (Hook.) Mill., Thuja plicata Don, Chamaecyparis nootkatensis (Lamb.) Spach., Picea sitchensis (Bongd.) Carr., and Tsuga mertensiana (LIndl.et Gord.) Carr., finds a close parallel along the coastal ranges in Oregon; and in view of the fact that every modern genus has some Miocene fossil representative, and also that these remains are abundant and widespread, we feel justified in reconstructing a Miocene landscape replete with conifers.

Mason (28) has given us a useful list of conifers growing in the Klamath Mountain area of Oregon, which is a section just east of Cape Blanco. The following conifers are itemized:

Pinus Lambertiana Dougl.
P. ponderosa Dougl.
P. Jeffreyi Balfour
P. attenuata Lemmon

Abies grandis Lindl.
A. magnifica Murray

Picea Breweriana Wats.
P. sitchensis (Bongd.) Carr.

Tsuga heterophylla (Raf.) Sargent
T. mertensiana (Lindl.et Gord.) Carr.

Sequoia sempervirens (Lamb.)Endl.

Libocedrus decurrens Torr.

Thuja plicata Don

Chamaecyparis Lawsoniana (Andr.) Parl.

Taxus brevifolia Nutt.

Diller (12) writes of the Port Orford quadrangle as

having "coniferous forests of great extent," much of which is good lumbering wood, "but a large portion of the wooded tracts is of little importance."

A HISTOLOGICAL AND TAXONOMIC STUDY OF CERTAIN MIOCENE CONES

Description of Gross Material.

More than a dozen cones, some of them fragmentary, provide the material of this investigation. They are jet black except in places where the gray sandy material has lodged between the cone scales. The longest cones in the group measure four centimeters, but in life they must have been somewhat longer, since the terminal scales of the specimens are either partially broken and eroded or entirely missing. The greatest diameter is 17 millimeters, and again, the living cone must have been larger as the terminal portions of all the scales and bracts are missing.

The fossils have about thirty-five cone scales each, a number which is slightly less than that of the living Douglas fir. Their arrangement corresponds closely to the low spiral of *Picea* or *Pseudotsuga* cones. As previously mentioned, the upper and thinner portions of the cone scales have been lost, probably by the settling and compacting movements of the volcanic sand in which they are found imbedded. The broader, thicker, and more woody bases persist with several terminal spurs, which represent the more resistant vascular strands. These carbonized scales are brittle and fragile and separate easily from the better preserved cone axis. The thickness and

unusual breadth of the cone scales, coupled with the characteristically erose extremities, reminds us immediately of the short and very broad ovuliferous scales of Douglas fir cones.

Working on the cones in a shallow dish of water, it is possible to remove the sandy material from between the cone scales and observe the fragmentary remains of the bract, which even in gross aspect appears as a structure separate from the seminiferous scale. Mostly it is preserved as a needle-like projection lying close under the scale which it axillates. In no case have I seen one extending beyond the scale, but this may be an effect of its fragile character and consequent poor preservation. Nearer the axis one finds brittle flakes of carbon in the position the bract should occupy. Yet it would going beyond what the facts warrant to aver that they are the wing-like expansions of the fairly well preserved midribs of the bracts.

The cone axis is the most resistant part of the cones and is commonly found with the scales completely eroded away from it. In such cases the point of attachment is represented by a prominent saliency from the axis. Better preserved cones have only the basal and apical scales removed, with the axis still indicating the length of the original strobilus. In no case has a curved axis been found which might indicate a curved peduncle at the base of the cone axis similar to the condition of Pseudotsuga taxifolia. The cone axis in all cases is straight.

From this superficial glance at the cones we are led first of all to consider the fossils as representatives of

the Abietineae, and more specifically as belonging to Pseudotsuga or, as the discoverer's notes suggest, "Picea (?) cones."

Treatment for Study.

After the fossils were found they were wrapped in moist paper and sent to the Harvard University laboratories, where they were kept from drying out until the collector returned. They were then placed in a solution of glycerine and alcohol. In this condition they were presented to me for anatomical study, with the object in view of correct identification based on histological and morphological details. To prepare them for further study they were washed in water and placed in hydrofluoric acid for two weeks to remove the abundant grains of silica from the material packed between the cone scales, and to soften the harder woody tissues. Thus prepared, the cones, scales, and cone axes were cut into convenient lengths and imbedded in celloidin. The imbedded material was allowed to remain for some time in glycerine-alcohol before attempts were made to cut sections. Using the Reichert microtome and a sharp knife,(microtome) cross-sections, and radial and tangential longitudinal sections were made at thicknesses varying from eight to twelve microns. Staining being unneccessary, the sections were dehydrated, cleared, and mounted immediately in balsam. Weighting the cover glasses so flattened the sections that microscopical examination was facilitated.

Histology of the Fossil Cone.

Examining a cross-section of the cone axis taken

near the base (Plate X, Fig. 21. and Plate XII, Fig. 26.) one discovers that a single row of resin canals lies in the secondary xylem near the primary wood. Though the secreting layer in most cases is incompletely preserved, the cell wall fragments indicate that it was parenchymatous. (See Plate XII, Fig. 25.)

The secondary wood is best preserved where it lies between the numerous and large tongues of pith. The reason for this is ovious after one sees the heavily protective and entirely sclerenchymatized condition of the pith cells whose cell cavities are without exception, filled with resin. Further from the pith, the secondary xylem shows all stages of fracture and collapse, though accasionally areas of tracheids have preserved their form and radial arrangement. There is no evidence of annual rings, though it is probable that two years was required for cone maturation.

Some of the sections show the phloem well preserved. These cases indicate again the preservative nature of conifer resin, for only those portions can be investigated which have the typical dark brown coloring which the resin imparts.

A discontinuous but well preserved cortex surrounds the secondary wood of the axis. Its cells are completely filled with resin as are those of the pith, but differ in their thin walls. Very large cortical resin canals are conspicuous everywhere.

Wood rays are generally uniseriate except near the pith where they are commonly multiple. Sometimes they remain two

cells in thickness all the way from pith to cortex.

Turning to a cross-section midway up the cone axis, the resin canals are found to be somewhat further from the primary wood region. The pith diameter has decreased, but its cells have thicker walls and it still retains its entirely resinous character. The secondary wood is far more abundant at this point than below, and is star shaped from the numerous leaf gaps which accompany the vascular strands in their exit to the scales.

In the cross-section near the apex of the cone, the pith shows its sclerotic and resinous nature maintained to the very tip of the axis. Shortly above the mid-region, the resin canals die out.

Tangential sections reveal the depth of the rays as varying from 2 to 40 cells, with most of them averaging 6 to 8 cells. Occasionally horizontal resin canals are seen in widened or "fusiform rays".

Some sections follow the layer of primary wood just tangent to the pith. In these cases, the elongated tracheids with spiral thickenings are strikingly evident.

The tangential walls of the secondary tracheids bear no pitting.

Certain tangential sections of a cone fragment with scales still attached to the axis, show good cross-sections of the ovuliferous scale with its subtending bract. The bract and scale are fused for a short distance outward from the axis. (See Plate XI, Fig. 24.)

In median longitudinal sections, the pith is found

to consist of angular and closely packed cells. (Plate X, Fig.22.) Most of them appear square in section at the base of the axis, but they are gradually more and more elongated as the apex is approached where they take on dimensions characteristic of tracheids. The conspicuous tubular pits are everywhere in evidence. All pith cells have heavily thickened walls.

Just outside the pith are 4 to 5 vertical rows of primary tracheids with their identificatory spirals. Their diameter is only slightly less than the cells of the secondary wood. The outermost layer of primary tracheids bears scattered bordered pits, partially obscured by the primary wall thickenings.

The region immediately exterior to the primary xylem is often confusing owing to the presence of resin canals, and also by irregular sclerenchymatous ray cells, whose similarity to the elements of the medulla is very marked. However, the first tracheids of the secondary wood are often larger and more irregular than those exterior to them, and like corresponding elements in living abietinean cones, the bordered pits are occasionally observed in the staggared "cordaitean condition." Exterior to this the pits are less numerous and are invariably in linear alignment.

Some of the secondary tracheids give evidence, despite their poor preservation, of tertiary spiral thickneings. (Plate XI,Fig. 23.) These wall sculpturings are not to be confused with the spiral splittings of tracheidal walls which are undergoing disintegration. Both of these features have been

observed on the same tracheiddin our Miocene cones.

Final Summary.

To summarize, the cones are about the size of those of the red fir or of modern spruces, and the number and arrangement of the scales is also similar. The cone axis is about 6mm. in diameter, and running up its center is an entirely sclerotic pith whose greatest breadth is at the base and gradually tapers to a very few cells at the apex. This general decrease in size is accompanied by steady increase in the length of the pith cells, which are nearly isodiametric at the base. Surrounding the pith is a substantial layer of primary wood whose elements are strongly sculptured with spiral and reticulate thickenings besides occasional bordered pits which seem to have found their way from their secondary wood origin back into the younger wood. The first-formed tracheids commonly bear alternating, cordaitean pits, especially near their termini. There are no bars of Sanio (crassulae) to be found between such pits. The later-formed secondary tracheids have fewer bordered pits always scattered and linear in arrangement. In the middle and latest formed secondary wood, evidence of spiral thickenings were observed on the tracheids. These were most evident just beneath the rays. The cambium was in all cases destroyed, but the presence ofthe pith was rendered possible by the preservative action of the resin. The phloem and cortex, likewise, seem to owe their fossil preservation to the abundant resin. The cortex contains conspicuous and large resin canals.

The sclerotic nature of the bases of the cone scales

and bracts, preserved them intact. The vascular supply from the axis originates as two separate strands, the smaller from the base of the gap, and the larger from above the gap. They quickly unite and shortly after, a substantial strand breaks off from the lower side and becomes the midrib of the bract. (Plate XI, Fig. 24.) The chief strand continues until it finally breaks up into a horizontal series of strands whose termini were visible as carbonized spurs on all the cone scales investigated. Resin canals were absent from the wood of the cone scale, but appeared in the outer sclerenchymatous zones of the scale.

Conclusion.

Using the morphological and histological information above recorded we conclude that the Miocene cones, here described, belong to the genus Pseudotsuga. The presence of tertiary spirals on the tracheids coupled with the entirely sclerenchymatous pith with resiniferous cells, assures us that we are dealing with this genus. The pith closely resembles that sometimes found in Larix, but differs in its highly resinous nature and the invariable absence of parenchymatous cells. In view of the fact that the cone dimensions and the scale numbers do not coincide with those of the living Pseudotsuga taxifolia (Lamb.) Britt. we must look elsewhere for the specific name of the plant which bore these cones. From the same rocks, Torrey (46) has described Pseudotsuga annulata wood, and it is highly probable that these cones represent the fructifications of the plants whose vegetative remains are so designated. The stem wood of Pseudotsuga annulata is characterized by tertiary spirals on the

tracheidal walls, as may be seen in Plate XIII, Fig. 27.

MacGinitie (29) has done a deplorable job in describing what he considers a Pseudotsuga seed from the Trout Creek district of southeastern Oregon. We are bound to object when in the original description of Pseudotsuga masoni, he calls the seed a fruit because it possesses a wing! The seed is too large to belong to Pseudotsuga annulata, but, for that matter we are compelled to question the attribution of a seed to the genus Pseudotsuga when one has only superficial features to go on!

Penhallow (31a) gives us a description of Pseudotsuga miocena from British Columbia and Saskatchewan, and remarks on its similarity with the modern P. taxifolia (Lamb.) Britt. He also mentions the occurrence of wood of this species in the Miocene strata of Oregon, where the tracheidal walls have been found degenerating in spiral fashion coinciding with the tertiary wall thickenings.

Phyletic Considerations.

The material providing the object of this investigation, is from a retentive structure of the trees which bore it, and might logically be expected to throw some light on either the phyletic position of the genus, or that of organs or features in the plant. The tertiary spirals, so characteristic and (within certain limits) diagnostic of the genus Pseudotsuga, are not found in the first layers of secondary tracheids in the cone axis, but occur abundantly in the later wood. This feature is observable in both the modern and Miocene cones. It would

seem to indicate that the tertiary spiral is a cenogenetic feature which, in accordance with the canons of comparative anatomy, is being introduced into the most impressionable part (the last formed wood) of the typically conservative and retentive cone axis; and, just as the bordered pits have finally progressed inward into the primary xylem, the tertiary spirals are appearing progressively earlier and earlier in the development of the woody cone axis. It is unfortunate that the preservation of the secondary wood of the cone axis of Pseudotsuga annulata (Platen) Torrey is not sufficiently perfect to permit a detailed comparison of the relative position in the cone axis at which the tertiary spirals appear in the modern and fossil cones.

The presence of vertical and horizontal resin canals in the cone axis was to be expected, as those structures are characteristic of the most primitive conifers, and only die out in the reproductive axes of groups which have long since ceased to possess them in their vegetative parts.

Final Conclusion.

The trees, Pseudotsuga annulata (Platen) Torrey, which bore the cones we have investigated, formed a part of the outstanding gymnospermous flora of Miocene times. Pseudotsguae of several species must have found the climate of the west coast of North America very suitable to their growth and development, a fact indicated by their widespread distribution. It is highly probable that the orogenic movements initiated in the late Miocene and consummated later by the Cascadian Revolution, produced

such changes as obliterated all but the mountain-loving modern species, Pseudotsuga taxifolia (Lamb.) Britt.

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PLATE I

Figure 1. - *Pinus nigra*: cross-section near the base of the female cone axis, showing the two annual increments of secondary wood, and two vertical resin canals sonnected by a horizontal one.

Figure 2. - *Pinus sylvestris*: cross-section near the base of the female cone axis showing a single vertical resin canal lined with thick-walled epithelial cells.

Plate I

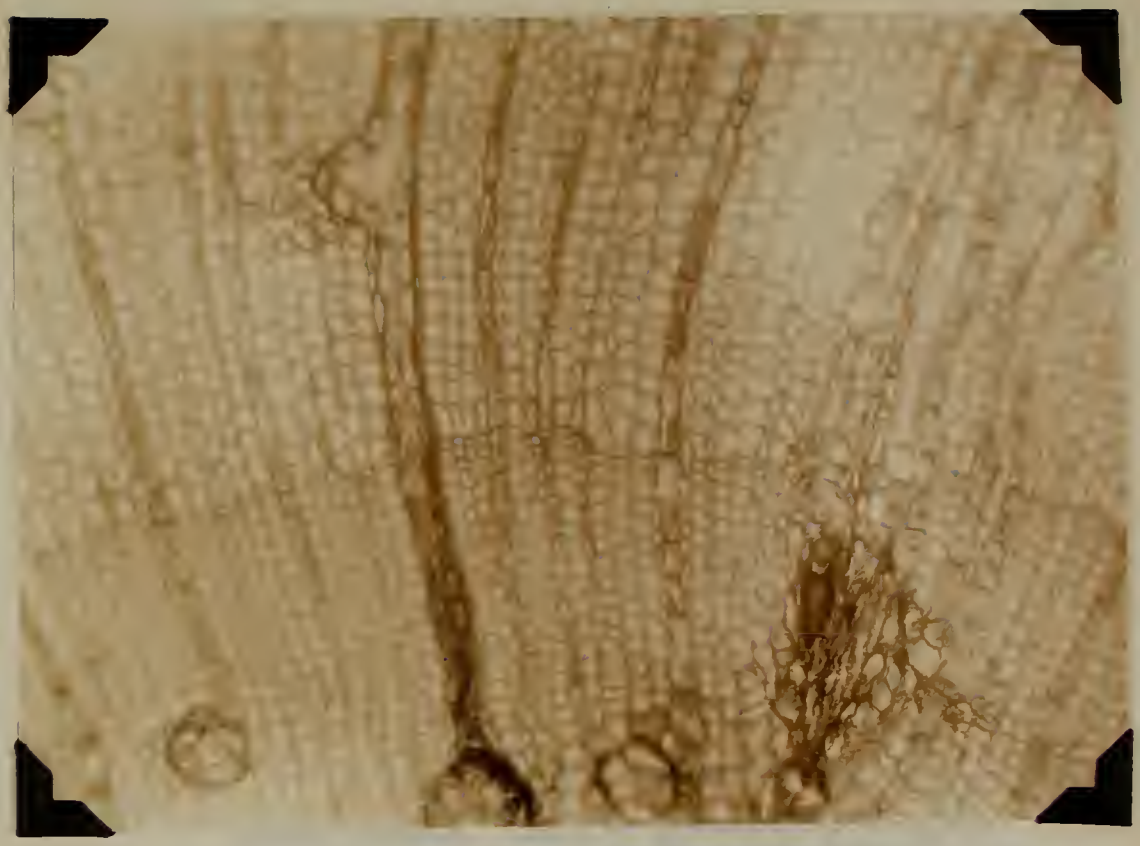

Fig. 1.

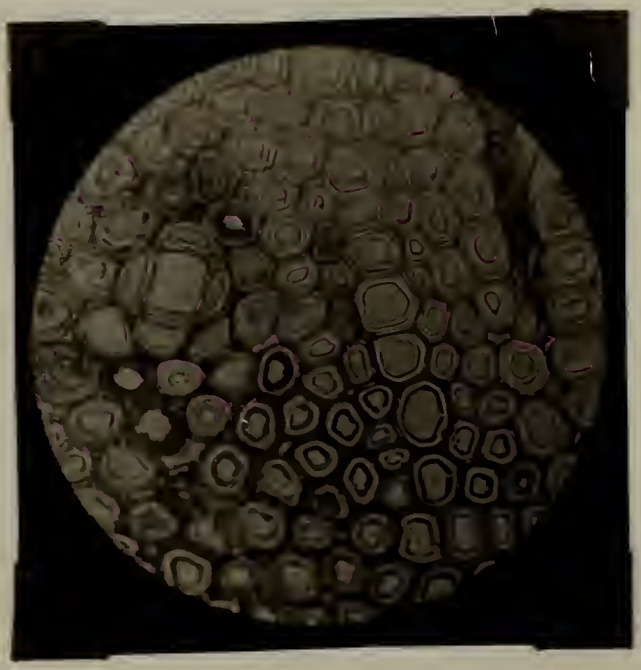

Fig. 2.

PLATE II

Figure 3. - *Pinus sylvestris*: cross-section of the peduncle of the female cone.

Figure 4. - *Pinus sylvestris*: cross-section of the stem wood to show the parenchyma-lined resin canals. In the peduncle illustrated above, the ducts have the same type of lining, but the secretory cells become sclerenchymatized in the cone axis.

Plate II

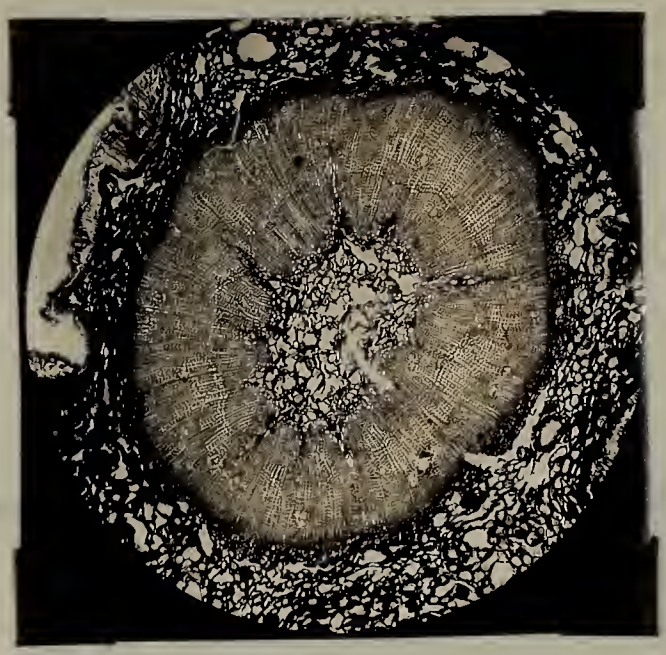

Fig. 3.

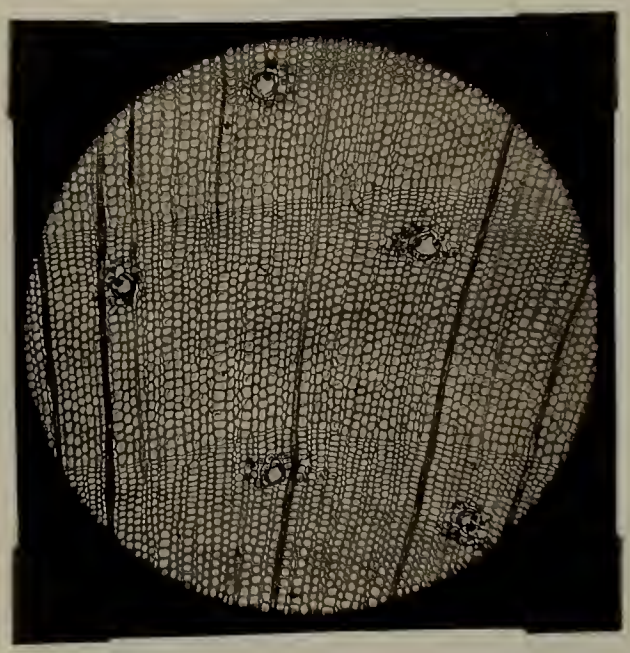

Fig. 4.

PLATE III

Figure 5. - Pinus palustris: median longitudinal section of the female cone axis illustrating the irregularly-shpaed cells which are thought to be transitional between tracheids and the radially directed elements of the xylem.

Figure 6. - Pinus Lambertiana: radial section of female cone axis showing a typically large ray.

Plate III

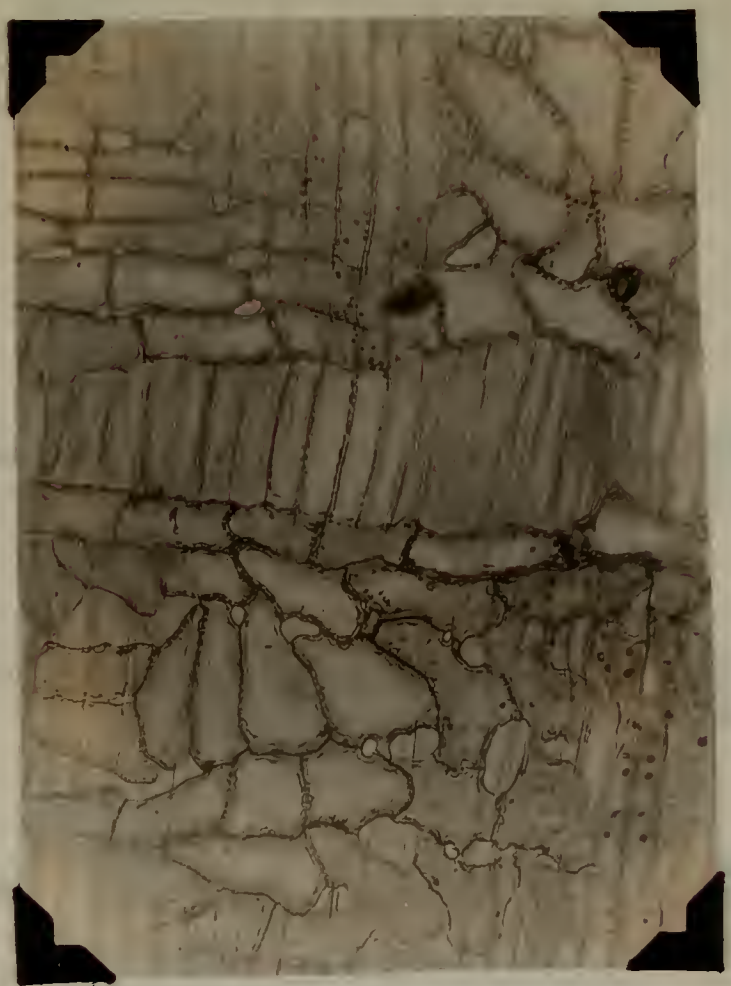

Fig. 5.

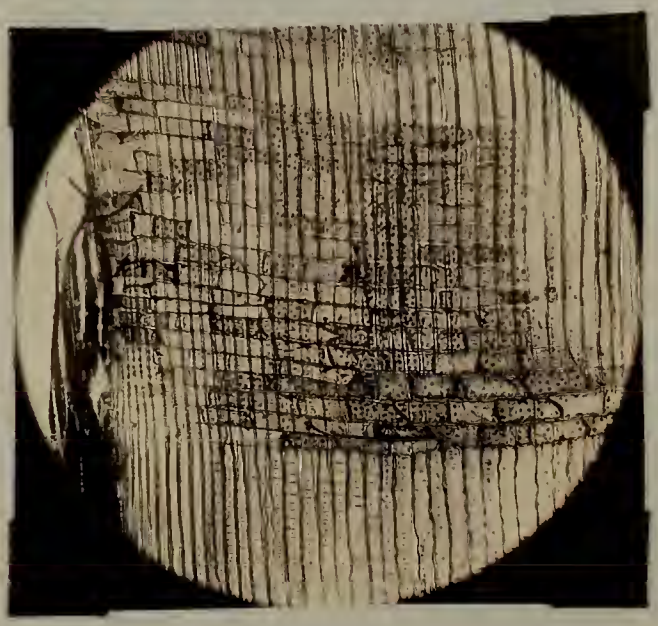

Fig. 6.

PLATE IV

Figure 7. - Agathis: longisection of the female cone axis revealing the pitting conditions of the primary tracheids and of the first formed secondary elements.

Figure 8. - Pinus densiflora: cross-section near the base of the female cone axis. The resin canal is lined with thin-walled secretory parenchyma.

Figure 9. - Pinus rigida: longisection of the stem showing the vertical and horizontal resin canal system linked together.

Plate IV

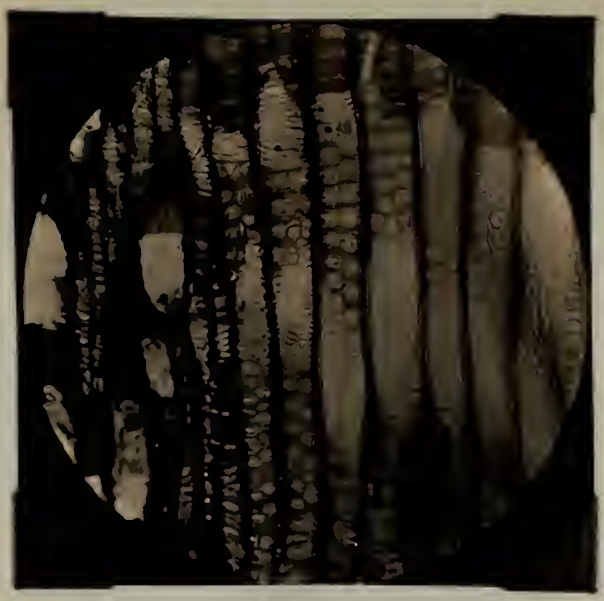

Fig. 7.

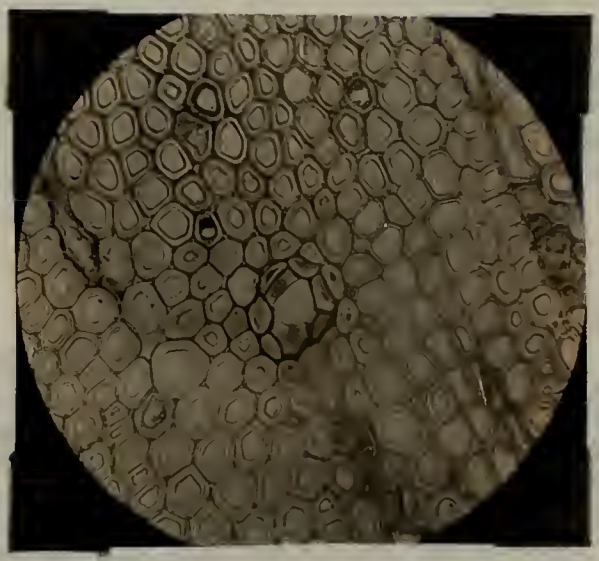

Fig. 8.

PLATE V

Figure 10. - *Pinus rigida*: cross-section of a first year shoot revealing the numerous vertical resin canals, and in the upper part of the figure, a horizontal canal connecting a vertical xylary canal with one in the cortex.

Figure 11. - *Picea Abies*: radial section of the female cone axis. Two of the reticulated elements of the primary wood are visible on the left. On the right, one of the first formed tracheids of the secondary wood may be seen bearing bordered pits in a staggered formation resembling the cordaitalian condition.

Plate V.

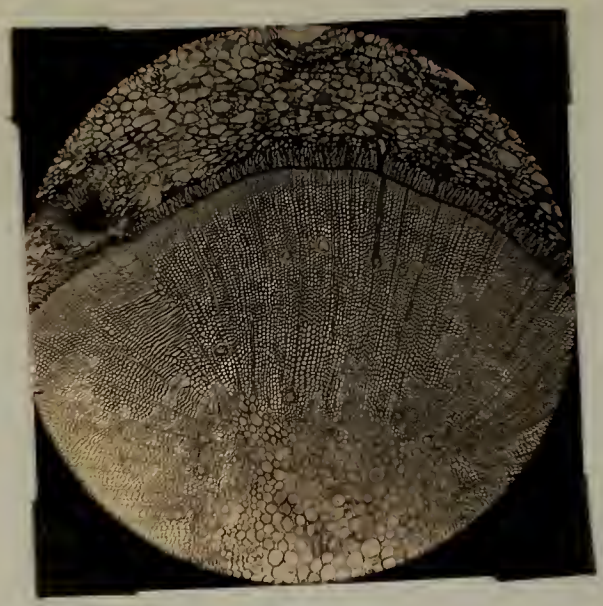

Fig. 10.

Fig. 11.

PLATE VI

Figure 12. - Pseudotsuga taxifolia: cross section near the apex of the female cone axis. A small parenchyma-lined resin canal showing the disintegrated secretory cell walls projecting as short spurs into the lumen of the duct is visible.

Figure 13. - Pseudotsuga taxifolia: longisection of the female cone axis showing cordaitalian pitting on the first-formed tracheids of the secondary wood.

Plate VI

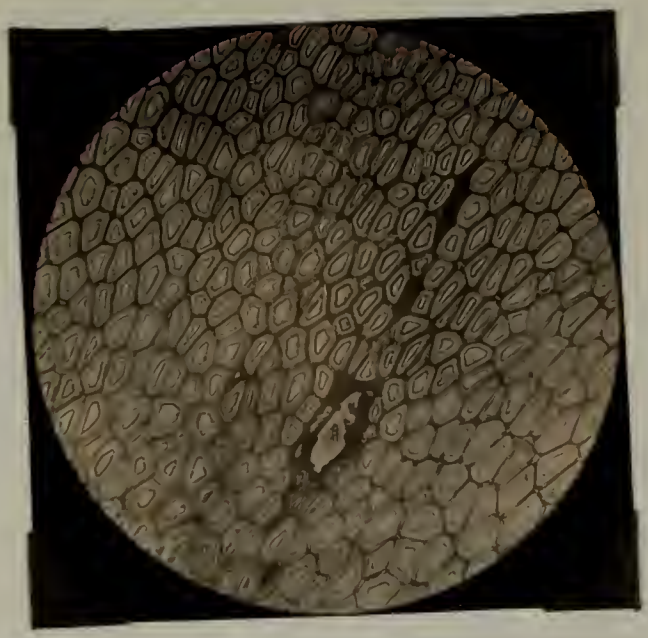

Fig. 12.

Fig. 13.

PLATE VII

Figure 14. - Pseudotsuga taxifolia: median longisection of the female cone axis showing tertiary spiral thickenings on the secondary tracheidal elements.

Figure 15. - Pseudotsuga taxifolia: median longisection of the female cone axis, illustrating the resin-filled, rectangular pith cells.

Plate VII

Fig. 14.

Fig. 15.

PLATE VIII

Figure 16. - Larix Kaempferi: cross section near the apex of the female cone axis, showing position of the xylary resin canals.

Figure 17. - Larix decidua: cross section near the base of the female cone axis, showing the resin canals restricted to the terminal rows of secondary tracheids.

Figure 18. - Abies grandis: cross-section near the base of the female cone axis showing absence of resin canals from the xylary tissues, but present in abundance in the cortical region.

Plate VIII

Fig. 16.

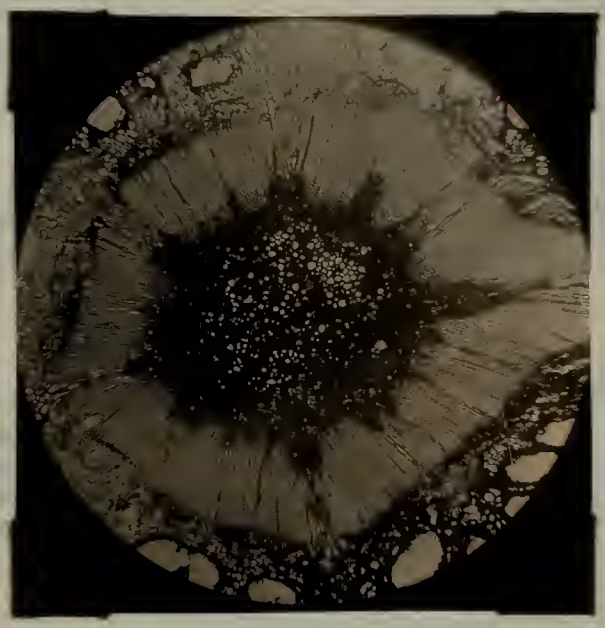

Fig. 17.

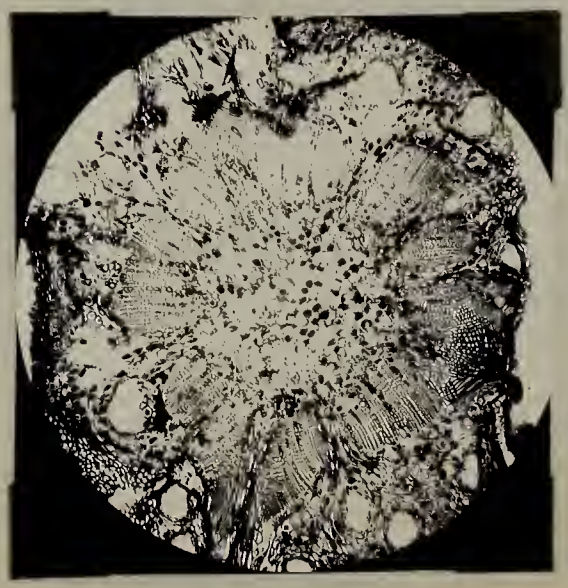

Fig. 18.

PLATE IX

Figure 19. - *Abies grandis*: cross section of the female cone axis showing abundant wood parenchyma near the outer margin of the xylem.

Figure 20. - *Tsuga canadensis*: cross section taken near the base of the female cone axis, revealing the fact that the xylem has neither resin canals nor wood parenchyma.

Plate IX

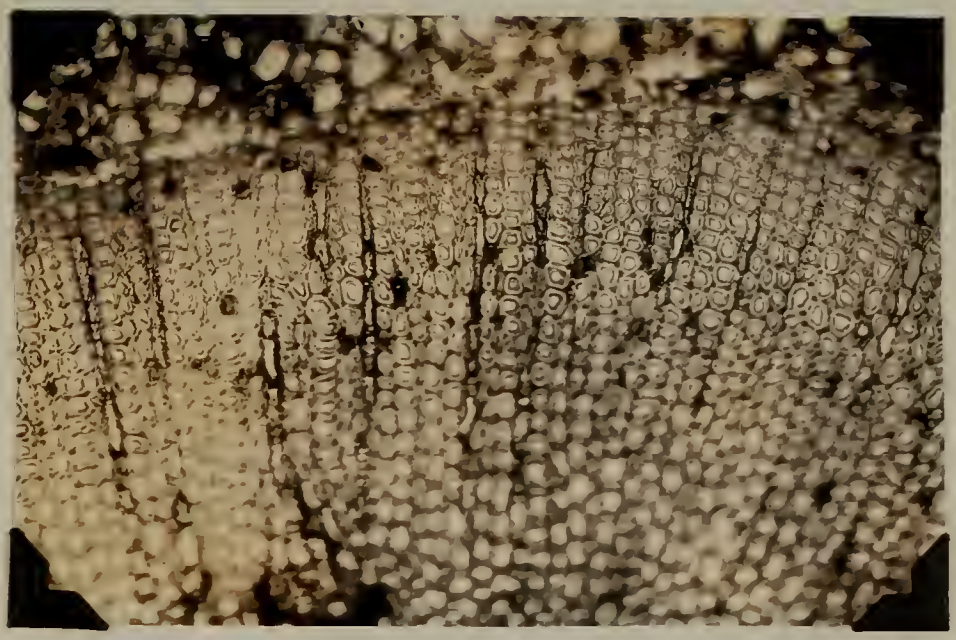

Fig. 19.

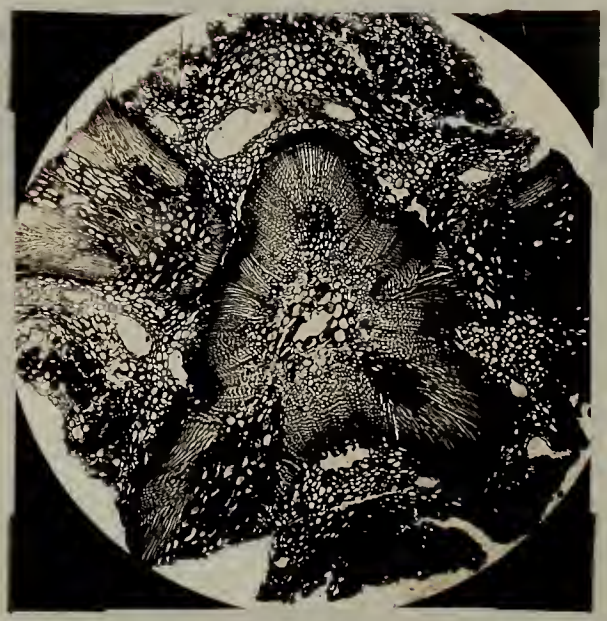

Fig. 20.

PLATE X

Figure 21. - Pseudotsuga annulata: cross section of the fossil cone axis showing occasional resin canals in the secondary xylem.

Figure 22. - Pseudotsuga annulata: median longitudinal section of the cone axis showing the sclerotic, resin-filled pith cells. On either side of the pith, may be seen the spirally thickened elements of the primary wood.

Plate X.

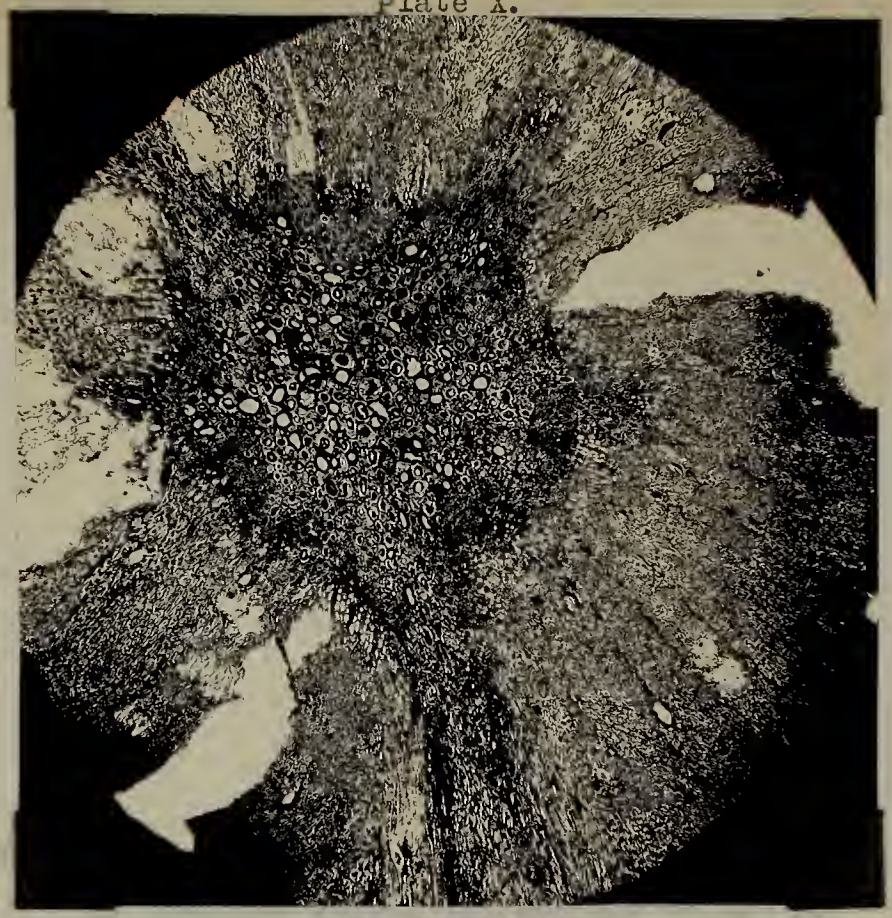

Fig. 21.

Fig. 22

PLATE XI

Figure 23. - Pseudotsuga annulata: longisection of the female cone axis, revealing evidence of tertiary spiral thickenings on the secondary tracheids.

Figure 24. - Pseudotsuga annulata: longisection of the bract and ovuliferous scale showing that they become separate structures a short distance from the axis.

Plate XI

Fig. 23.

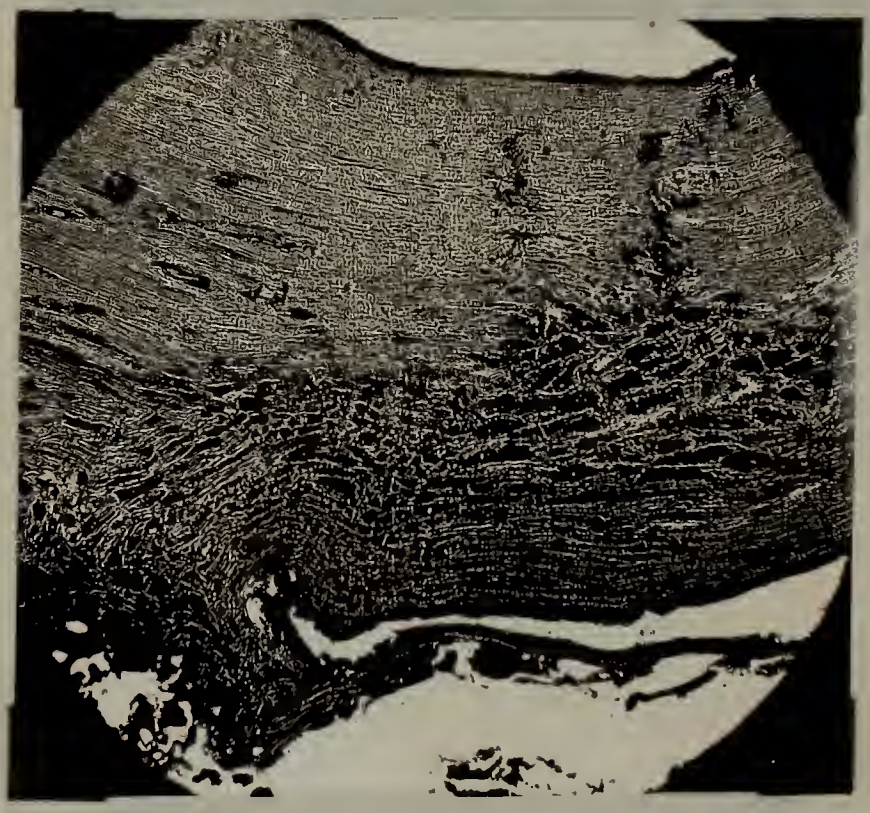

Fig. 24.

PLATE XII

Figure 25. - Pseudotsuga annulata: cross section near the base of the female cone axis showing a typical resin canal. The short spurs which run into the lumen of the canal are remnants of the secretory cells.

Figure 26. - Pseudotsuga annulata: cross section of the female cone axis showing pith, leaf gaps, and xylary resin canals in the medullary region of the secondary wood.

Plate XII

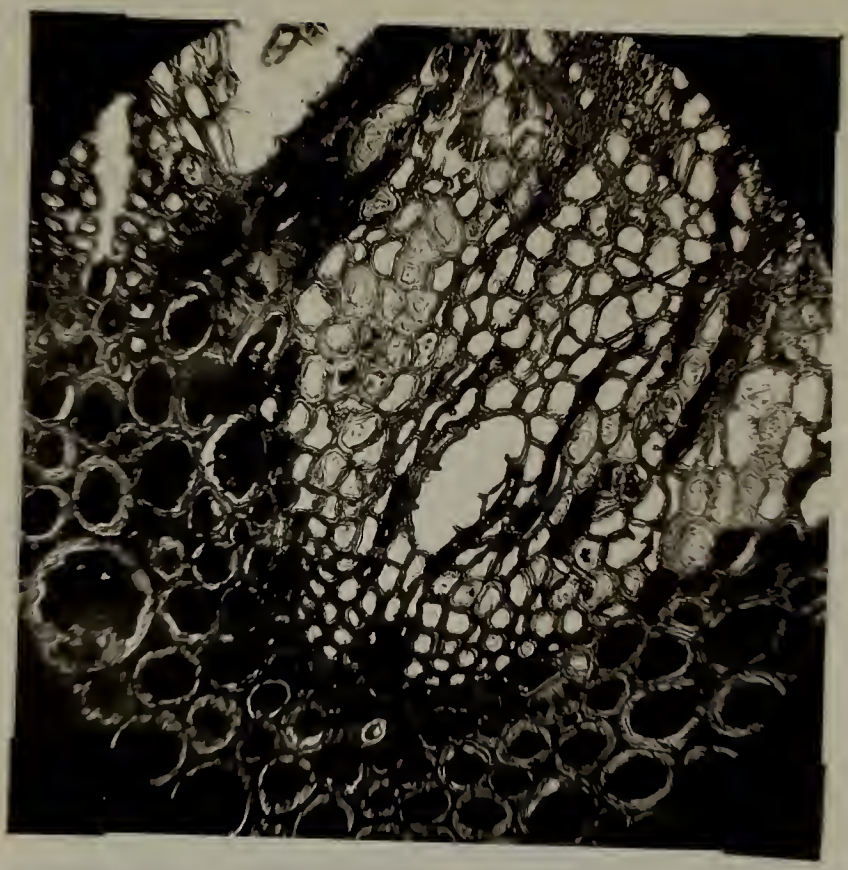

Fig. 25.

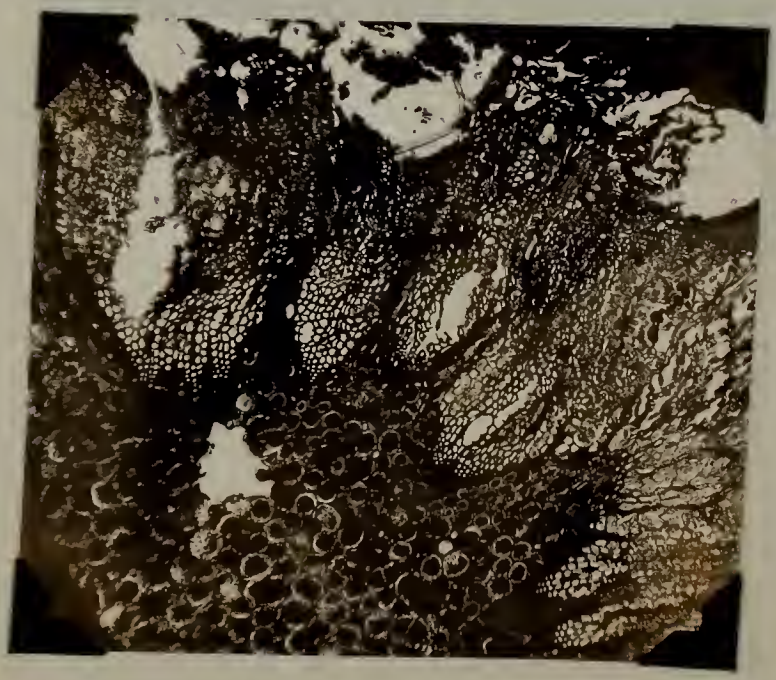

Fig. 26.

PLATE XIII

Figure 27. - *Pseudotsuga annulata*: radial section of the stem wood clearly showing the tertiary spiral markings on the secondary tracheids, a feature which identifies the wood as *Pseudotsuga*.

Plate XIII

Fig. 27.

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Graduate Committee

Date May 28, 1937.