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SILICIFIED CONES AND VEGETATIVE REMAINS OF *PINUS* FROM THE EOCENE OF BRITISH COLUMBIA

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SILICIFIED CONES AND VEGETATIVE REMAINS OF *PINUS* FROM THE EOCENE OF BRITISH COLUMBIA[1]

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ABSTRACT—Two new species of *Pinus* are described from silicified cones, needles, dwarf shoots, and stems from the Eocene Allenby Formation of southern British Columbia. Excellent preservation of the fossils permits close comparison with living species. *Pinus arnoldii* includes the cones which are assigned to the subgenus *Pinus* and are most similar to those produced by living species of the subsection *Sylvestres* of the section *Pinus*. The vegetative remains are included in *P. similkameenensis* and belong to the subgenus *Strobus*. They show a mixture of features occurring today in species of the sections *Strobus* and *Parrya*. The possibility that these remains might be conspecific is discussed.

CONTENTS

INTRODUCTION

FOSSIL REMAINS of *Pinus* are not uncommon in Tertiary sediments, but most are of limited value because they are usually preserved as impressions which only allows comparison with present-day species on the basis of gross morphology. Similarly, petrified conifer wood, although abundant, is seldom sufficiently preserved to permit classification with Recent genera, let alone their subdivisions. Described in this report are petrified cones, needles, dwarf shoots, and stems of *Pinus* from the Eocene Allenby Formation of southern British Columbia that are especially important because their well-preserved internal structure makes possible identification not just to subgenera but to their sections and in one case to a subsection. The cones are assigned to *Pinus arnoldii*, a new species named in honor of Dr. C. A. Arnold, Professor Emeritus, The University of Michigan, who collected the petrifactions and made them available for this investigation. These cones belong to the subgenus *Pinus*, section *Pinus*, and compare most favorably with those of living members of the subsection *Sylvestres*. The needles, dwarf shoots, and stems are included in a second new species, *Pinus similkameenensis*, and show a combination of features occurring today in species of the sections *Strobus* and *Parrya* of the subgenus *Strobus*.

Location and Occurrence of the Fossils

The fossils occur in pieces of black chert that come from a single locality within the Allenby Formation of the Princeton coal basin in southern British Columbia. The collecting site is 5¼ miles south-southwest of the main road intersection in Princeton and 2⅓ miles south-southwest of the abandoned town of Allenby on the east bank of the Similkameen River across from the Willis Ranch. Exposed here is an outcrop consisting of 29 feet of interbedded coal, shale, and chert capped by a four-foot thickness of dense black shale. The various layers were numbered, by Boneham (1968) as

[1] This investigation was supported by National Science Foundation Grant GB-19737 to the author.

TABLE 1—SALIENT FEATURES OF STRUCTURALLY PRESERVED *PINUS* CONES.

		P. arnoldii	*P. avonensis*[1]	*P. belgica*[2]
A.	Age	Eocene	Oligocene	Lower Cretaceous
B.	Cone length	5.0–6.0 cm	5.5 cm	4.5 cm
C.	Cone diameter	2.0–2.5 cm	2.5 cm	3.0 cm
D.	Scale length	2.0 cm	1.8 cm	2.0 cm
E.	Scale width	1.5 cm	0.8–1.2 cm	0.9 cm
F.	Apophysis height	5–8 mm	4–6 mm	5–8 mm
G.	Apophysis width	8–12 mm	8–10 mm	7–10 mm
H.	Spine present on umbo	no	yes	no
I.	Thin-walled sclerenchyma forming outer cortex of axis	yes	no	yes
J.	Recurved bract trace	no	no	yes
K.	Thick-walled cells in pith	no	no	yes

[1] Miller, 1969.
[2] Alvin, 1960.

a part of his study of the microflora, and the fossils included in the present treatment came from chert layers nos. 14, 16, 17, and 20 (see table 2).

The Allenby Formation was formerly thought to be Oligocene in age on the basis of 33 species of compressed plant remains which compare favorably with those described by Brown (1935, 1937) from an Oligocene site near Republic, Washington (Arnold, 1955). However, Rouse & Mathews (1961) report a potassium-argon date of 48 million years for an ash bed within the Allenby Formation, so the flora must be regarded as middle Eocene in age. More recently, Axelrod (1966) gave a potassium-argon date of 55 million years for a biotite tuff interbedded within lake beds that provide the Republic flora, so the latter is now considered late Paleocene in age. Thus, the initial comparison of the two floras' remains reasonably accurate.

Nature of the Fossils

In addition to cones described as *Pinus arnoldii*, and stems, dwarf shoots, and needles treated as *P. similkameenensis*, remains of several other types of plants are preserved in the chert. These include conifer roots, rhizomes of an aquatic dicot (Robison & Person, 1971), woody stems of at least two other dicots, poorly preserved rhizomes and petioles of at least two ferns, debris representing one or more mosses, several types of seeds none of which can be attributed to *Pinus*, and hyphae and conidiospores of an ascomycete fungus. Rhizomes of *Dennstaedtiopsis aerenchymata* Arnold & Daugherty (1964) occur in certain layers of the chert (Boneham, 1968) but were not found during the present study.

Most of the organs are well preserved at the anatomical level but were significantly broken up prior to preservation. This is especially true of the *Pinus* remains. None of the stems are longer than 5 cm and most are decorticated. Furthermore, despite the occurrence of literally hundreds of *Pinus* needles in the chert, no complete specimens were found. Even though many were traced in serial peels, none of the fragments was longer than 2.3 cm and none included both the base and apex of the same needle. Thus, there is good reason to conclude that these *Pinus* remains represent trees not growing in the immediate vicinity of the basin of deposition. This conclusion can also be extended to the other remains except the mosses, the aquatic dicot rhizome, and *Dennstaedtiopsis aerenchymata*.

Methods

Study of the fossils is based on ground sections of the chert and on cellulose acetate peels. Attempts to macerate pieces of the chert to obtain complete needles proved unsuccessful. Anatomical details of the stems were compared with those of living species treated by Greguss (1955). Similarly, work on the needle anatomy of living North American pines (Harlow, 1931) supplemented by needle sections of these present-day species in the collection of Dr. C. Gordon, University of Montana, provided a basis for comparing the fossil needles with living forms. Specimens of *Pinus arnoldii* were compared with anatomical sections of cones of the following living species: *P. albicaulis* Engelm., *P. aristata* Engelm., *P. armandii* Franch., *P. attenuata* Lemmon, *P. balfouriana* Grev. & Balf., *P. banksiana* Lambert, *P. contorta* Dougl., *P. coulteri* D. Don, *P. densiflora* Sieb. & Zucc., *P. edulis* Engelm., *P. elliottii* Engelm., *P. flexilis* Jam., *P. lambertiana* Dougl., *P. monophylla* Torrey, *P. monticola* Dougl., *P. mugo* Turra, *P. muricata* D. Don, *P. nigra* Arnold, *P. parviflora* Sieb. & Zucc., *P. radiata* D. Don, *P. resinosa* Ait., *P. rigida* Mill., *P.*

TABLE 2—MEASURED SECTION AT LOCALITY "I."

Cross section of the interbedded coal and chert layers exposed by the erosion of the Similkameen River at Locality "I" as measured by Roger F. Boneham on July 11, 1965. At that time, Black chert layer No. "0" was at water level. The coal and chert layers below Black chert layer No. "0" were under water.

	Thickness	
	Feet	Inches
Dense, black shale (top)	4	0
Black chert layer #29	1	1
Covered interval	1	1
Black chert layer #28	0	6
Coal layer #32	0	1
Black chert layer #27	0	5
Coal layer #31	0	1
Black chert layer #26	0	7
Coal layer #30	0	8
Black chert layer #25	0	5
Coal & shale layer #29	0	4
Black chert layer #24	0	5
Coal layer #28	0	1
Black chert layer #23	0	11
Coal layer #27	0	1
Black chert layer #22	0	4
Coal & shale layer #26	0	7
Black chert layer #21	0	7
Coal layer #25	0	3
Black chert layer #20	0	8
Coal & shale layer #24	0	7
Black chert layer #19	0	4
Coal & shale layer #23	0	2
Black chert layer #18	0	3
Coal & shale layer #22	0	8
Black chert layer #17	0	2
Coal layer #21	0	4
Black chert layer #16	1	4
Coal layer #20	0	6
Black chert layer #15	0	6
Coal layer #19	0	2
Black chert layer #14A	0	3
Coal layer #18	0	1
Black chert layer #14	0	2
Coal layer #17	0	2
Black chert layer #13A	0	2
Coal layer #16	0	1
Black chert layer #13	0	3
Coal layer #15	0	3
Black chert layer #12	0	3
Coal layer #14	0	2
Black chert layer #11	0	9
Coal layer #13	0	9
Black chert layer #10	0	5
Coal layer #12	0	5
Black chert layer #9	0	11
Coal layer #11	0	1
Black chert layer #8	0	2
Coal layer #10	0	4
Black chert layer #7	0	5
Coal layer #9	0	2
Black chert layer #6	0	4
Coal layer #8	0	4
Black chert layer #5	0	9
Coal layer #7	0	2
Black chert layer #4	0	8
Coal layer #6	0	2
Black chert layer #3	1	6
Coal layer #5	0	3
Black chert layer #2	0	1
Coal layer #4	0	1
Black chert layer #1	0	3
Coal layer #3	0	3
Black chert layer #0	0	4
Coal layer #2	0	7
Black chert layer #–1	1	0
Coal layer #1	0	2
Black chert & shale layer #–2	0	5
Coal & shale layer #0	0	11
Black chert layer #–3	0	4

strobus L., *P. sylvestris* L., *P. taeda* L., and *P. thunbergiana* Franco. Critchfield & Little's (1966) classification of *Pinus* is used throughout the text.

CONES

Systematic Description

Order CONIFERALES

Family PINACEAE

Genus PINUS Linnaeus

PINUS ARNOLDII sp. nov.

Pls. 1–3

Diagnosis.—Ovulate cones long-conical, 5–6 cm long by 2.0–2.5 cm at widest diameter; axis 6–10 mm in diameter, surrounded by numerous ovuliferous scales; vascular cylinder of axis about 5 mm in diameter; pith 2 mm in diameter, constructed of large parenchyma cells; primary xylem endarch; secondary xylem 1.5 mm thick, subtle growth ring present, resin canals abundant, rays mostly uniseriate; cortex 1.5–3.0 mm thick, constructed of a thin inner zone of small parenchyma cells, a thick middle layer of large parenchyma cells, and a thick outer layer of thick-walled sclereids; bract-scale-complex trace separating from vascular cylinder as oval unit, dividing in outer part of middle cortex to form a terete bract trace on abaxial side and an abaxially concave scale trace on adaxial side; bract 5 mm long, free from scale;

ovuliferous scale up to 20 mm long by 15 mm wide and about 1 mm thick, making an angle of 5–10° with longitudinal axis of cone, containing up to 15 vascular strands, each strongly rounded on adaxial side; resin canals of scale base abaxial to vascular strand, forming up to 24 canals apically with most abaxial to row of vascular strands but some interfascicular; scale apex about 2 mm thick; apophysis rhomboidal, 5–8 mm high by 8–12 mm wide; umbo abaxially subapical, centrally located on apophysis; spine absent; seed cavities two per scale; seeds absent.

Locality and horizon.—On the east bank of the Similkameen River, 5¼ miles SSW of the main road intersection in Princeton, British Columbia, and 2⅛ miles SSW of the abandoned town of Allenby. Allenby Formation, middle Eocene.

Syntype.—University of Michigan Museum of Paleontology No. 60482.

Anatomical Description

Of the eight cones studied one is complete in longitudinal section and measures 5.3 cm long. The cones are 2.0–2.2 cm at their maximum diameter near the base and taper gradually toward the apex, having a long-conical shape (pl. 2, fig. 1). Numerous scales that are 16–20 mm long surround the axis in spiral arrangement. Each is subtended by but is free from a bract that is 4–5 mm long (pl. 2, figs. 1, 2). Two depressions on the adaxial surface of the scale base represent the original locations of seeds. However, no seeds remain in any of the cones, and the spaces left by them are filled with mineral matter. The scale apex is inflated forming an apophysis that is rhomboidal in face view and bears a raised umbo at its center. "Apophysis" and "umbo" refer respectively to the parts of the ovuliferous scale that are exposed when a mature cone is closed and at fertilization (Mirov, 1967). There is no evidence of a spine.

Axis.—The pith of the cone axis is about 2.0 mm in diameter near the cone base, tapers gradually toward the apex, and eventually disappears. Parenchyma cells make up the tissue. They are 15–75 mμ in diameter and appear circular in transverse outline but are irregularly rectangular in longitudinal view with many cells having oblique end walls and sinuous side walls. These cells are 280–500 mμ long near the cone base and 150–200 mμ near the apex. Cell walls are 5–10 mμ thick and bear numerous simple pits that appear as ellipses or narrow slits in face view. There are no resin canals or sclereids in the pith.

Vascular tissue forms a cylinder in the cone axis that is about 5.0 mm in diameter at the cone base but tapers to about 1.0 mm near the apex, where the remaining tissues branch into the terminal cone scales and bracts. Secondary xylem makes up most of the vascular cylinder (pl. 1, fig. 2), with endarch strands of primary xylem projecting a short distance into the pith and a narrow zone of mineral matter or disorganized cell-wall material at the periphery representing the phloem. Traces to bract-scale complexes diverge from the vascular cylinder in spiral sequence with up to four visible in a given transverse cone section (pl. 1, figs. 1, 2). The trace of each complex is cylindrical at its point of divergence, enclosing a central strand of parenchyma that communicates with the pith through an interruption in the vascular cylinder (pl. 2, figs. 4, 5). These interruptions are not comparable with leaf-gaps since the vascular tissue maintains its continuity around the opening.

Secondary xylem of the axis (pl. 1, fig. 2) forms a cylinder that is about 1.5 mm thick at the cone base and thins gradually to about 0.5 mm near the apex. Tracheids making up the tissue are polygonal in transverse outline except near the periphery where they are more rectangular. They are 15–45 mμ in diameter and have walls that are about 5 mμ thick. Circular bordered pits occur sparsely on the radial walls of the tracheids in a single series. In most cases some decay of the border has occurred and only the outer pit aperture is visible. Resin canals are abundant in the secondary xylem. As many as 34 of them appear in transverse sections near the cone base (pl. 2, fig. 3), but they diminish to about 15 near the apex. These canals are 45–85 mμ in diameter and are lined with 6–12 epithelial cells arranged in a single layer. About half of the resin canals in a given transverse section occur at the inner edge of the secondary xylem within 2–6 cells of the pith or primary xylem. The remainder are scattered in the later-formed secondary xylem. Many, but not all, of the inner canals are directly opposite a primary xylem strand; however, not all of the latter

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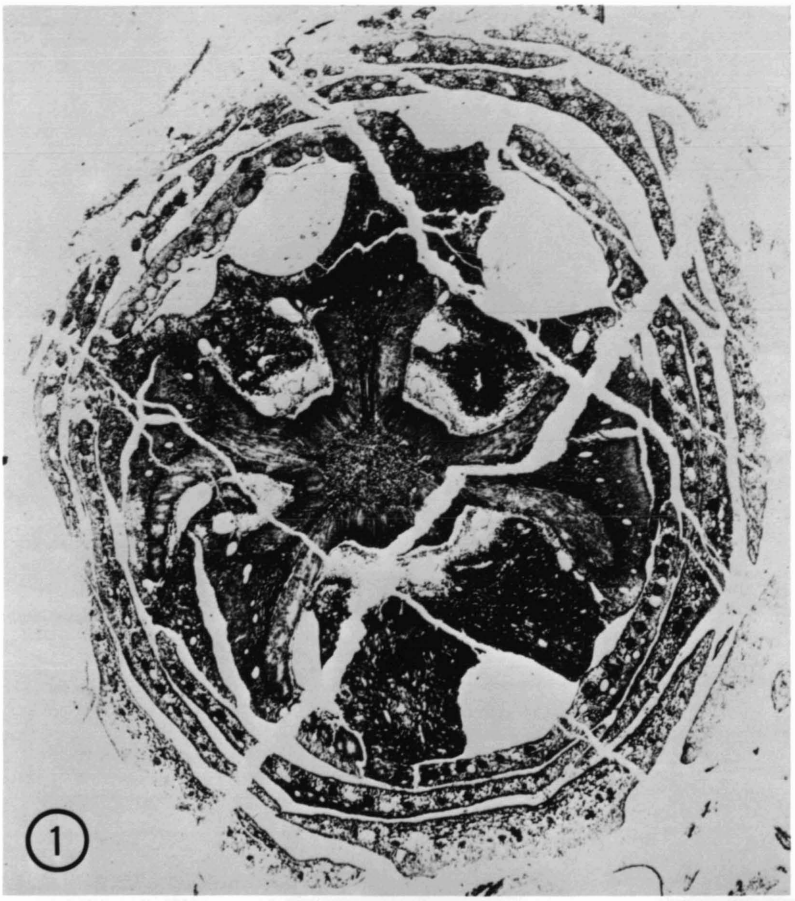
EXPLANATION OF PLATE 1

Pinus arnoldii sp. nov., syntype, UMMP 60482. *1*, transverse section of cone, × 6.2. *2*, transverse section of cone axis near middle of cone, × 18.0. P, original position of phloem; R, resin canal.



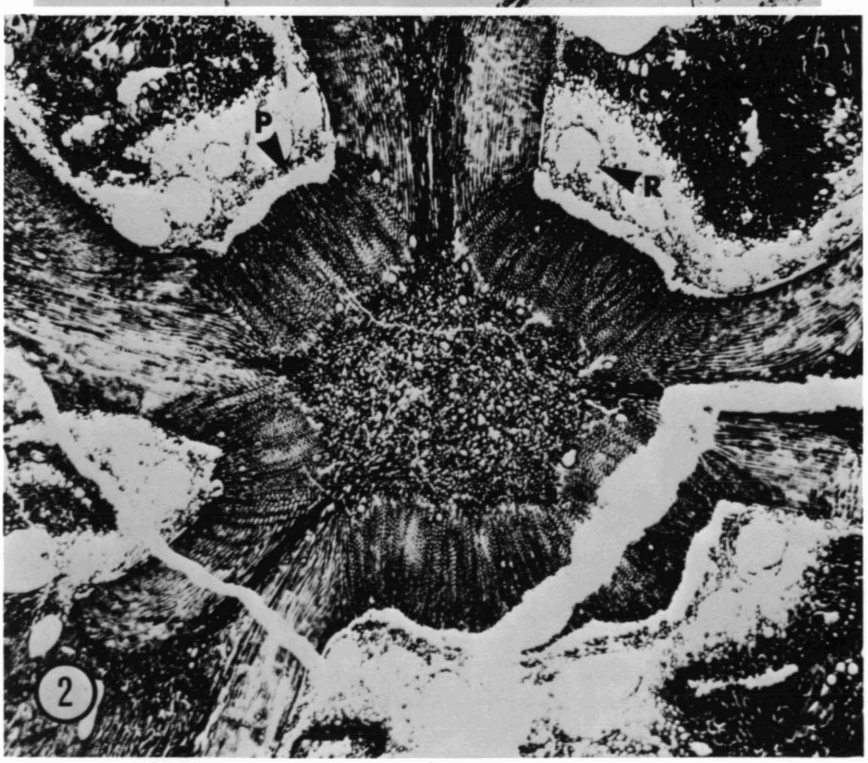


PLATE 1

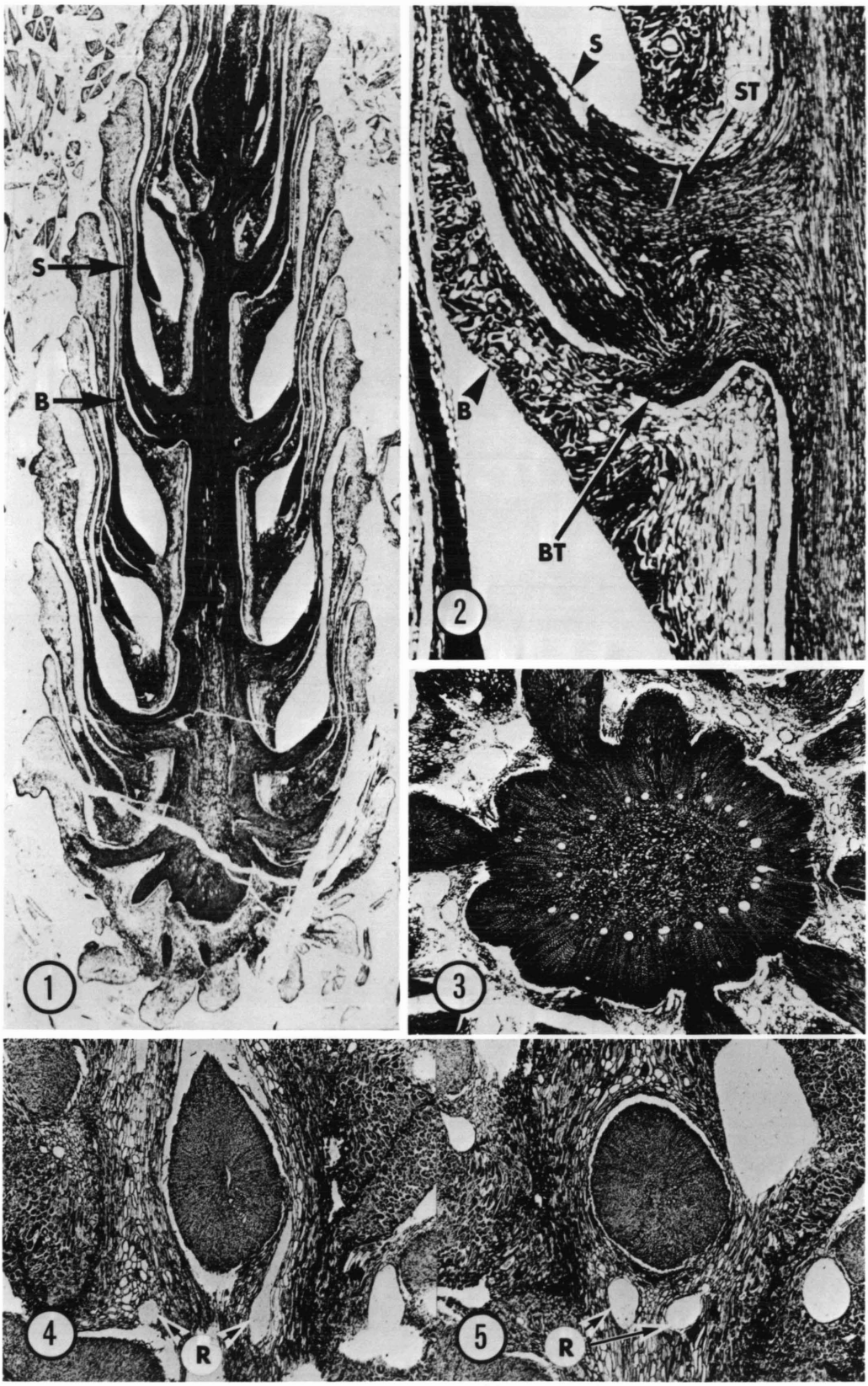


PLATE 2

have an associated resin canal. The xylem rays are uniseriate and lack resin canals. Most are one to seven cells high, but some are as high as 20 cells. Both parenchyma and tracheids make up the rays, with the tracheids usually occupying the upper and lower one or two rows of cells and the parenchyma forming the center.

A conspicuous feature of the secondary xylem is the apparent lack of a growth ring. Tracheid diameter is smallest at the inner edge of the cylinder, increasing gradually outward, reaching a maximum near the middle of the cylinder, and decreasing toward the periphery. Nowhere is there a sufficiently abrupt change in tracheid diameter to mark an annual increment of growth. The absence of a growth ring is inconsistent with the differentiation of the scale apex into an apophysis and an umbo, which denotes two growth seasons (Shaw, 1914), and also with the stems in the chert which show well-developed rings. A similar inconsistency was noted in material of *Pinus avonensis*, from the Montana Oligocene, and was attributed to different thresholds of activity of the stem and cone-axis cambia (Miller, 1969). Further study of Recent cones provides a more accurate explanation. None of the present-day cones studied for comparison with these fossils show apparent growth ring in the axis. However, sections of one-year cones of *Pinus ponderosa*, collected in December in Montana, have a cylinder of secondary xylem that is 20–30 tracheids thick in which there are abundant resin canals. There is no abrupt decrease in cell diameter near the periphery of this cylinder which is surrounded by a broad cambial zone. No doubt this first-year cylinder of secondary xylem is comparable to the inner zone of small diameter tracheids in both mature *P. ponderosa* cones and in the fossils, while the larger diameter cells at the middle of the xylem cylinder represent spring wood with the outer zone of smaller cells being the summer wood of the second growth season. Thus, a growth ring does occur in the vascular cylinder of fossil and living *Pinus* cones, but it is highly inconspicuous.

The original position of the phloem in most places is marked by a narrow band of mineral matter that is about 0.3 mm thick. In a few areas disorganized cell walls are preserved, but the remains are too disrupted for description. Very thin-walled cells having a rectangular transverse outline occur at the periphery of the xylem and probably represent immature tracheids or cambial cells.

The cortex of the axis is 1.8–3.0 mm thick basally, thins to 0.7–1.5 mm near the apex, and consists of three distinct layers. Small diameter parenchyma cells make up the innermost zone. This tissue is 0.1–0.2 mm thick near the cone base but thins apically and eventually disappears. It has a sinuous outline in transverse cone sections with lobes projecting a short distance between the resin canals of the middle cortex. Cells of the inner cortex are 10–25 mμ in diameter and 60–90 mμ long. Walls of most cells are 2 mμ thick but a few cells with walls 8 mμ thick are scattered within the tissue. Simple pits that are circular to elliptical in face view appear on the walls of both types of cells.

The middle cortex is made up of large diameter parenchyma cells and resin canals and shows an abrupt transition with the inner tissue. The middle cortex is 0.5–0.65 mm thick near the cone base and 0.1–0.25 mm near the apex. Its cells are 50–110 mμ in diameter and 100–300 mμ long. Walls of these cells are about 2 mμ thick and bear numerous simple pits that are elliptical or circular in face view. While cells of the middle cortex are oval in transverse outline and rectangular with oblique end walls in longitudinal sections, they are irregularly shaped near departing bract and scales. Up to 22 resin canals are arranged in a ring around the axis at the inner edge of the middle cortex (pl. 1, figs. 1, 2). These canals are most numerous near the cone base and decrease to four in transverse sections near the apex. They are 0.25–1.0 mm in diameter and are lined with a single layer of epithelial cells. These canals are parallel to the longitudinal axis of the cone but branch in the radial direction near each diverging complex trace to connect with canals of each scale and its associated bract.

A sclerotic zone forms the outer layer of the cortex (pl. 1, figs. 1, 2). This tissue is 1.0–2.0 mm thick basally and 0.6–1.0 mm thick apically. It is constructed of cells that are the same size and shape as those of the middle cortex but have walls that are 10–15

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EXPLANATION OF PLATE 2

Pinus arnoldii sp. nov., syntype 60482. *1*, longitudinal section of cone, × 3.3. *2*, longitudinal section of bract and scale base, × 13.3. *3*, transverse section of cone axis near cone base, × 7.2. *4*, transverse section of bract-scale-complex trace in inner cortex of cone axis, × 10.1. *5*, transverse section of bract-scale-complex trace in middle cortex of cone axis, × 10.1. B, bract; S, scale; R, resin canal; BT, bract trace; ST, scale trace.

mμ thick bearing simple pits that appear as narrow slits in face view. The transition between the outer and middle cortical layers is abrupt. Among the Recent cones in the reference collection, an outer cortex of such thick-walled cells occurs only in members of the subsections *Contortae*, *Oocarpae*, and *Sylvestres* of the subgenus *Pinus*.

A trace to each bract-scale complex diverges at right angles from the vascular cylinder of the axis (pl. 2, fig. 2) as an oblate cylinder consisting mostly of secondary xylem (pl. 2, fig. 4). This tissue is surrounded by a thin mineral-filled layer representing the phloem. It also encloses a central strand of parenchyma that is continuous through a gap in the vascular cylinder with the pith. Branching of the complex trace to form a bract trace and a scale trace occurs near the contact of the middle and outer cortical layers. The bract trace diverges from the abaxial side of the cylinder as a terete strand leaving the remaining scale trace deeply indented on the abaxial side (pl. 3, figs. 1, 2). The bract trace maintains its terete shape throughout its passage into the bract. It diverges from the complex trace at an angle of about 30° from the longitudinal axis of the cone (pl. 2, fig. 2) and turns upward only after entry into the bract. The scale trace passes into the scale through the cortex at right angles to the cone axis (pl. 2, fig. 2). In the outer part of the cortex the arms of the abaxially concave scale trace flare outward so that the trace enters the scale base as a more or less flattened strand (pl. 3, figs. 3, 4).

Changes in the secretory system opposite each scale and its associated bract are complex. In the inner part of the middle cortex the cylindrical complex trace passes between two axial resin canals (pl. 2, fig. 4). Both of these branch at right angles in a radial direction just abaxial to the trace, and the resulting canals pass outward parallel to the trace on either side of and slightly abaxial to it (pl. 2, fig. 5). In the outer part of the middle cortex where the bract trace first becomes apparent as a protuberance on the abaxial side of the complex trace, each of the resin canals bifurcates (pl. 2, fig. 5; pl. 3, fig. 1). The adaxial canal on either side of the trace takes a position alongside of the protruding bract trace, while the abaxial canal on either side remains abaxial to the protuberance. The latter canals retain this relative position as the bract trace diverges into the bract. As the bract trace separates, the two adaxial canals move toward the scale trace and branch several times, producing up to ten canals which become aligned near the abaxial surface of the scale trace (pl. 3, figs. 3, 4). All of these canals pass into the scale.

Bract.—The bract is 4–5 mm long (pl. 2, figs. 1, 2). At its point of separation from the axis it has a triangular transverse outline and is about 3–4 mm high and wide (pl. 3, fig. 4) but becomes progressively flatter upward (pl. 3, fig. 5). The sides of the bract are somewhat concave corresponding to the convex shape of the scale on its adaxial side and that of the seed cavities of adjacent scales on the two lateral sides. The bract is free from the scale throughout its length, and its base is decurrent on the axis.

Sclereids that are similar to and continuous with those of the outer cortex of the axis make up the ground tissue of the bract and are bounded by an epidermis of a single layer of small thin-walled cells that are mostly broken or decayed (pl. 2, fig. 2; pl. 3, fig. 5). The vascular strand of the bract occurs slightly adaxial to the center of the structure. It is surrounded by a tissue of thin-walled parenchyma cells about four cell layers thick and is flanked on either lateral side by the two resin canals. Once it enters the bract, the bract trace diminishes in size abruptly from about 0.5 mm in diameter near the bract base to about 0.25 mm, just inside the bract (pl. 3, figs. 3, 4). Toward the bract apex the vascular strand diminishes further and fades out before passing half the length of the bract. Similarly, the resin canals disappear about 0.5 mm beyond the end of the bract trace so that the apical 1.5 mm of the bract consists only of sclerenchyma surrounded by the epidermis.

Scale.—Ovuliferous scales of *Pinus arnoldii* are 16.5–20.0 mm long. They project at right angles from the axis for about 3 mm, bend around the seed cavities, and extend toward the cone apex for 13–16 mm, standing out from the cone axis at angles of 5–10° (pl. 2, fig. 1).

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EXPLANATION OF PLATE 3

Pinus arnoldii sp. nov., syntype, UMMP 60482. *1*, transverse section of bract-scale-complex trace in outer part of middle cortex of cone axis, × 10.1. *2*, transverse section of bract trace and scale trace in outer cortex of axis, × 10.1. *3*, transverse section of bract and scale traces in outermost cortex of cone axis, × 9.8. *4*, transverse section of scale and bract bases at point of attachment to axis, × 7.4. *5*, transverse section of about one-half of cone showing mantle of scales, × 15.0. *6*, longitudinal section of scale apex, × 11.5. B, bract; R, resin canal; S, scale; BP, abaxial parenchyma; BT, bract trace; DP, adaxial parenchyma; SC, sclerenchyma; ST, scale trace.

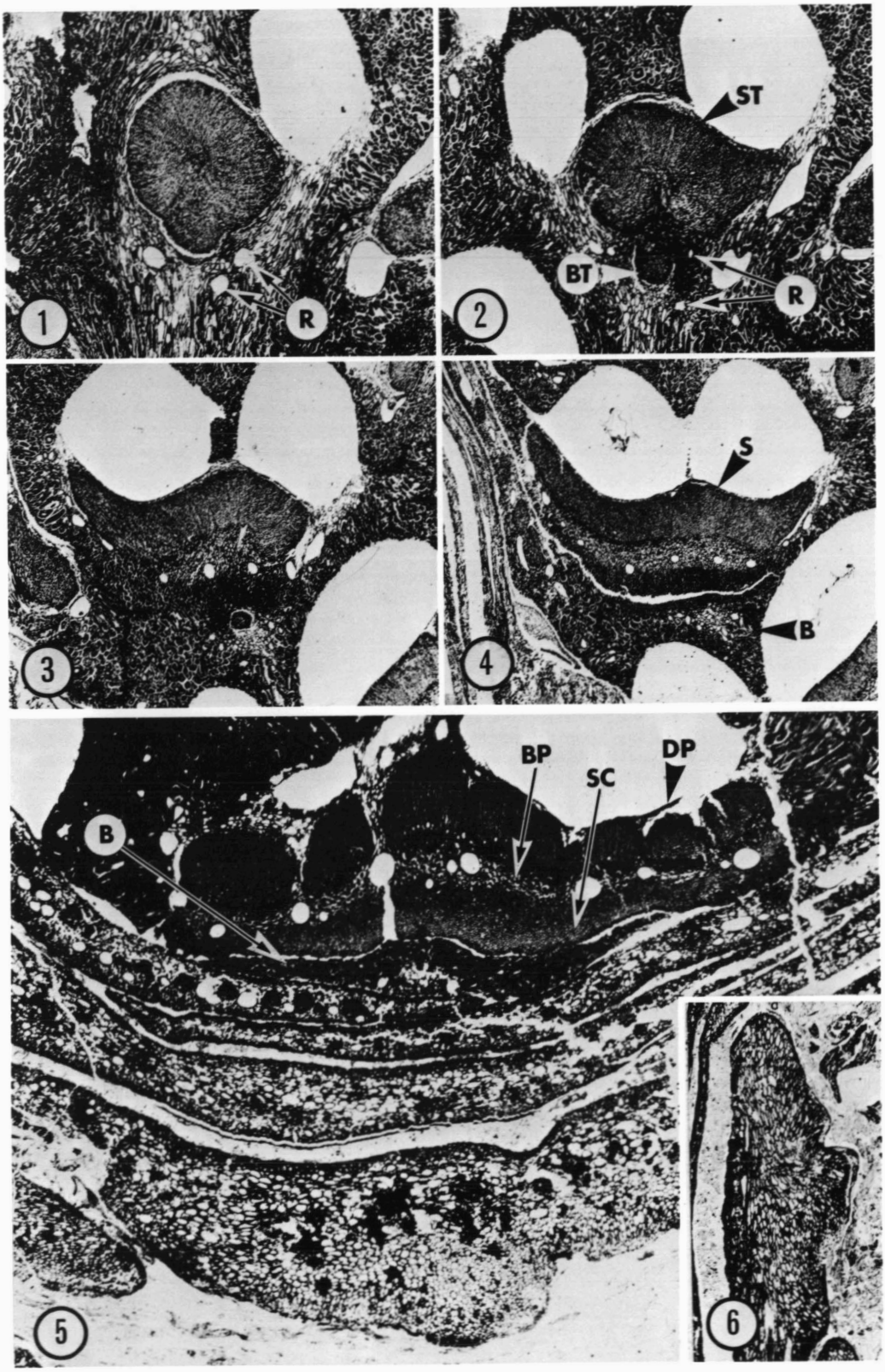

PLATE 3

The scale is 4.5–6.0 mm wide and 1.5–2.2 mm thick. Vascular tissue occupies the adaxial half of the scale base in the form of an unbroken band that has two indentations produced by the overlying seeds (pl. 3, fig. 4). Adaxial to the vascular strand is a thin layer of thin-walled parenchyma (pl. 3, fig. 5) that is continuous with the inner and middle cortex of the axis. This tissue is about four cell layers thick for the most part but thickens medially to form an interseminal ridge that projects for about 0.7 mm between the seed cavities. In all sections of the scale base, cells of this adaxial parenchyma tissue are crushed, probably from the growth of the adjacent seeds during cone development. Immediately abaxial to the vascular strand is another parenchyma tissue that is about 0.5 mm thick (pl. 3, fig. 5). Cells of this layer are continuous through the gap in the vascular cylinder with those of the pith. They are about 40 mμ in diameter at the adaxial and abaxial edges of the tissue and grade inward to cells that are about twice as large. These parenchyma cells have a distinctly circular transverse outline, have walls that are slightly thicker than those of the adaxial parenchyma layer, and have dark contents. Abaxial to this parenchyma tissue is a layer of sclerenchyma of about equal thickness that forms the abaxial portion of the scale base (pl. 3, fig. 5). Sclereids making up the tissue are 20–50 mμ in diameter and have walls that are 8–10 mμ thick. They are thus similar to but slightly smaller than cells of the outer cortex of the axis with which they are continuous. Sclerenchyma extends laterally beyond tissues adaxial to it to form the scale margins. Seven to eleven resin canals occur in the scale base within the abaxial parenchyma layer where they are more or less equally spaced on a line near the abaxial edge of this tissue (pl. 3, fig. 4). Restriction of resin canals of the scale base to tissues abaxial to the vascular strand is a feature that is unique to the genus *Pinus* (Alvin, 1953; Miller, 1969; Radais, 1894).

The scale broadens to a width of about 10 mm where it turns abruptly toward the cone apex. At this location the scale is 1.0 mm thick medially and tapers to about 0.5 mm near each lateral margin. Branching of the vascular tissue results in 10–15 strands that occur on a line midway between the scale surfaces (pl. 3, fig. 5). Concurrently, the adaxial parenchyma layer thickens and both the abaxial sclerenchyma and parenchyma layers thin. About 24 resin canals occur in the latter tissue with most abaxial to the row of vascular strands but with some interfascicular. Further thickening upward of the adaxial parenchyma and thinning of abaxial parenchyma results in the formation of a parenchymatous scale interior. This tissue is continuous with the adaxial parenchyma of the scale base while the abaxial parenchyma is restricted to clusters of 6–10 cells abaxial to each vascular strand.

Midway between its base and apex the scale is 15 mm wide, has a medial thickness of 0.5 mm, and tapers toward each lateral margin. As many as 17 vascular strands occur at regular intervals on a line midway between the scale surfaces. They are 0.1–0.2 mm in diameter with those near the margins generally smaller than those near the middle of the scale. All strands show conspicuous curvature in transverse section on their adaxial or phloem side which is a characteristic of cones of *Pinus* (Alvin, 1953; Miller, 1969; Radais, 1894). The ground tissue of the scale consists of parenchyma of the type restricted to the adaxial side of the scale in more basal sections. Tissue of the abaxial parenchyma is restricted to small clusters of 6–10 cells each that are abaxial to each vascular strand. Over 40 resin canals are scattered throughout the parenchymatous interior of the scale. The adaxial and abaxial scale surfaces are both bounded by sclerenchyma tissue that is 3–7 cell layers thick. The outermost cells of this tissue are about 30 mμ in diameter and grade inward to cells that are about 50 mμ in diameter. Although the lack of seeds in these cones clearly indicates that the scales had opened and closed again prior to preservation, the adaxial sclerenchyma layer of the scale shows no evidence of being compressed and corrugated as was the case in *P. avonensis* (Miller, 1969).

Just basal to the inflated portion of the scale apex, the scale becomes narrower and thicker with a corresponding thickening of the parenchymatous ground tissue. About ten vascular strands extend to this location where they remain on a line midway between the scale surfaces. Clusters of sclereids appear at random within the ground tissue, each composed of 4–10 cells that are 50–70 mμ in diameter (pl. 3, fig. 5). While some clusters occur in contact with both the abaxial and adaxial sclerenchyma, most are scattered in the interior of the scale.

Abrupt thickening of the scale to about 2 mm results in an inflated apex (pl. 2, fig. 1) with an apophysis that is rhomboidal in face view and measures 5–8 mm high and 8–12 mm wide. At its center is an umbo that projects 0.5–1.0 mm (pl. 3, fig. 6). A raised ridge extends from the umbo to each lateral edge of the apophysis. About ten vascular strands pass into the inflated scale apex on a line near the adaxial surface of the scale. They extend to a point opposite the umbo, turn abruptly toward it, and fade out about 0.5 mm from it. While

the parenchymatous ground tissue extends into the scale unchanged adaxial to the line of vascular strands, cells of the tissue abaxial to them become larger and have their longitudinal axes inclined perpendicular to the exposed surface of the scale. These cells are about 150 mμ long and are arranged in rows suggestive of origin from a cambial-like meristem. Both the adaxial and abaxial sclerenchyma tissues fade out and are replaced by a dermal layer of small parenchyma cells. This transition is abrupt on the abaxial side of the scale and occurs at the point of scale apex inflation. On the adaxial side of the scale, however, the sclerenchyma extends to within 1.0 mm of the tip of the scale. Both sclerenchyma tissues are replaced by a tissue of small-diameter parenchyma cells that is about three cell layers thick. Within the transition regions sclerenchyma typically occurs beneath the parenchyma suggesting that the former is subepidermal and that the parenchymatous epidermal tissue was sloughed off in basal sections. Throughout the apex the outermost layer of the parenchymatous epidermis is disrupted and missing in places. At the umbo the dermal layer is about six cells thick. The cells are flattened and are in rows perpendicular to the scale surface giving the impression of cork cells (pl. 3, fig. 5).

Although there is no evidence of a spine on the umbo, one may have been present. In most instances the umbo is irregular with the outer layer of dermal cells showing obvious signs of breakage. Thus, it is possible that *Pinus arnoldii* produced deciduous spines as do a number of living species.

Seed cavities.—Despite the absence of seeds in any of the cones, some idea of their size can be gained from measurements of the mineral-filled cavities. These are typically ellipsoidal and are 5.0–6.5 mm long and 2.0–2.5 mm in diameter. While several different types of seed-like bodies occur in the chert, none can be definitely attributed to these cones.

Discussion.—These Eocene cones clearly belong to *Pinus* as evidenced by such features as the restriction of all resin canals of the scale base to a position abaxial to the vascular tissue, the strong curvature of vascular strands of the scale apex on the adaxial or phloem side, and the inflated scale apices with their dorsal umbos. Among present-day genera of the Pinaceae, each of these features is unique to cones of *Pinus* (Radais, 1894), and their occurrence in combination in the fossil cones leaves no doubt of their affinity.

The relationships of the new species within *Pinus* are more difficult to evaluate. The inflated scale apex and dorsal umbo of *P. arnoldii* suggest affinity with the subgenus *Pinus*, but the long-conical to nearly cylindrical shape of the fossil cones is more typical of the subgenus *Strobus*, a relationship that is further supported by the association of the petrified cones with vegetative remains that clearly belong to this taxon. Certain species of the subgenus *Strobus*, section *Parrya*, satisfy the above criteria in having needles in clusters of five and in bearing elongate cones with inflated scale apices and dorsal umbos. However, all except *Pinus aristata* and *P. balfouriana* produce seeds that are much larger than those indicated by the vacant cavities in *P. arnoldii*. Cones of these two living species differ from *P. arnoldii* in having a cluster of small-diameter parenchyma cells at the center of the pith as compared to large cells at this location in the fossils, a gap in the xylem of the axis opposite the bract-scale-complex trace that is about twice as high as in *P. arnoldii*, and the branching of the complex trace in the inner cortex rather than in the middle-to-outer cortex as in the Eocene cones. In addition, in *P. arnoldii* the outer cortex of the axis consists of very thick-walled sclereids while relatively thin-walled sclereids make up this tissue in *P. aristata* and *P. balfouriana*. In fact, among the Recent cones in the reference collection, which represents about one-third of the genus, only those belonging to species of the subsections *Contortae*, *Oocarpae*, and *Sylvestres* of the section *Pinus*, subgenus *Pinus*, have thick-walled sclerenchyma forming the outer cortex of the axis. While our knowledge of comparative cone anatomy is not sufficient to indicate affinity of the fossil to one of these three taxa on internal structure, two external features suggest a more probable relationship to *Sylvestres*. Most species of *Contortae* and *Oocarpae* produce serotinous cones, many of which are also asymmetrical (Shaw, 1914). The Eocene cones, however, are symmetrical and show no indications of having been serotinous. On this basis it can be concluded that *Pinus arnoldii* belongs to the subgenus *Pinus* and is more similar to cones of the living species of *Sylvestres* than to any other subdivision of the subgenus.

The phylogenetic position of *Pinus arnoldii* is difficult to assess because of the lack of other structurally preserved *Pinus* cones in the fossil record. The only two species described to date are *P. avonensis* Miller (1969) from the Montana Oligocene and *P. belgica* Alvin (1960) from the Lower Cretaceous Wealden Formation of Belgium. All three species belong to the subgenus *Pinus* and are about the same size and shape (table 1), with the Belgian form somewhat more conical. *Pinus avonensis* is the only one of the three in which a spine is preserved on the scale, and it also differs from the

two older forms in having the outer cortex of its axis constructed of relatively thin-walled sclereids (Miller, 1969). *P. belgica* is peculiar in having bract traces that recurve in the cortex from their origin on the complex trace to their entry into the bract, and in having clusters of thick-walled parenchyma cells in the pith of the axis (Alvin, 1960). While the occurrence of these features in geologic time is interesting, any attempt to treat them alone or in combination as representing an evolutionary sequence would amount to mere speculation in view of the small number of structurally preserved cones that are presently known.

VEGETATIVE REMAINS

Systematic Description

Order CONIFERALES

Family PINACEAE

Genus PINUS Linnaeus

PINUS SIMILKAMEENENSIS sp. nov.

Pls. 4, 5

Diagnosis.—Needles, dwarf shoots, and stems. Needles quinate, at least 2.3 cm long, 0.4–0.6 mm wide; vascular strand single; resin canals two, dorsal, external, lacking hypodermal sheath; hypodermis mostly one cell layer thick, two layers in places; fibers smaller than epidermal cells; stomates slightly sunken, in 2–3 rows on each ventral face, lacking on dorsal face; fascicle sheath deciduous. Dwarf shoots 1.0–1.5 mm in diameter, about 2.0 mm long. Stems with well-developed growth rings; pith 1.0 mm in diameter, constructed of large thick-walled parenchyma cells; primary xylem endarch, tracheids with annular and helical thickenings; secondary xylem with vertical tracheids 10–30 mμ in diameter, bearing large circular bordered pits in single series on radial walls; late wood tracheids with small circular bordered pits on tangential walls; resin canals abundant, with a single layer of thin-walled epithelial cells; rays uniseriate, 1–8 cells tall, those with a resin canal biseriate and 10–16 cells tall; ray tracheids rare, marginal, non-dentate, with 1–4 pits per tracheid crossing; ray parenchyma with 1–4 pinoid pits per tracheid crossing; cortex constructed of large thin-walled parenchyma cells, including numerous resin canals; trace to dwarf shoot terete, about 0.5 mm in diameter, surrounded in cortex by several cell layers of small parenchyma cells, separating from stem in axil of cataphyll.

Locality and horizon.—On the east bank of the Similkameen River, 5¼ miles SSW of the main road intersection in Princeton, British Columbia, and 2⅓ miles SSW of the abandoned town of Allenby. Allenby Formation, middle Eocene.

Syntype.—University of Michigan Museum of Paleontology No. 60483.

Anatomical Description

Stems.—All conifer stems in the chert are of the same type and belong to a single species of *Pinus*. They range in size from 3 mm in diameter with three growth rings to 16 mm and up to 24 increments. In addition small pieces of secondary xylem occur in the matrix; they show no perceptible curvature of the growth rings and thus are fragments of large branches and trunks. All of the stems are less than 5 cm long having been broken prior to fossilization.

The pith is about 1 mm in diameter and consists entirely of thick-walled parenchyma cells that are 15–65 mμ in diameter and 50–150 mμ long (pl. 4, fig. 2). They are nearly circular in transverse view with conspicuous intercellular spaces between them. In longitudinal section they are rectangular and have transverse end walls (pl. 4, fig. 6). Cell walls are 4–6 mμ thick and bear numerous simple pits that appear as narrow slits or ellipses oriented transverse to the longitudinal axis of the cell. Although large and small cells are mixed throughout the tissue, larger cells are more abundant near the center.

Around the pith are up to twelve endarch primary xylem strands (pl. 4, fig. 2). Tracheids making up the protoxylem are 10–15 mμ in diameter and have annular or helical wall thickenings (pl. 4, fig. 6). Metaxylem elements are 10–20 mμ in diameter and bear circular bordered pits in one or two series.

The secondary xylem (pl. 4, fig. 1) consists mostly of tracheids that are 10–30 mμ in

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EXPLANATION OF PLATE 4

Pinus similkameenensis sp. nov., syntype, UMMP 60483. *1*, transverse section of secondary xylem, × 28.0. *2*, transverse section of stem showing pith, primary xylem, and inner secondary xylem, × 10.6. *3*, tangential section of secondary xylem, × 14.5. *4*, tangential section of secondary xylem showing circular bordered pits on tangential walls of summer wood tracheids, × 113. *5*, radial section of secondary xylem, × 24.5. *6*, radial section of stem showing pith, primary xylem, and inner secondary xylem, × 286. *7*, radial section of secondary xylem showing cross field pitting, × 300. *8*, radial section of secondary xylem showing circular bordered pits on a ray tracheid, × 1054. P, pith; X, xylem; BP, bordered pit.

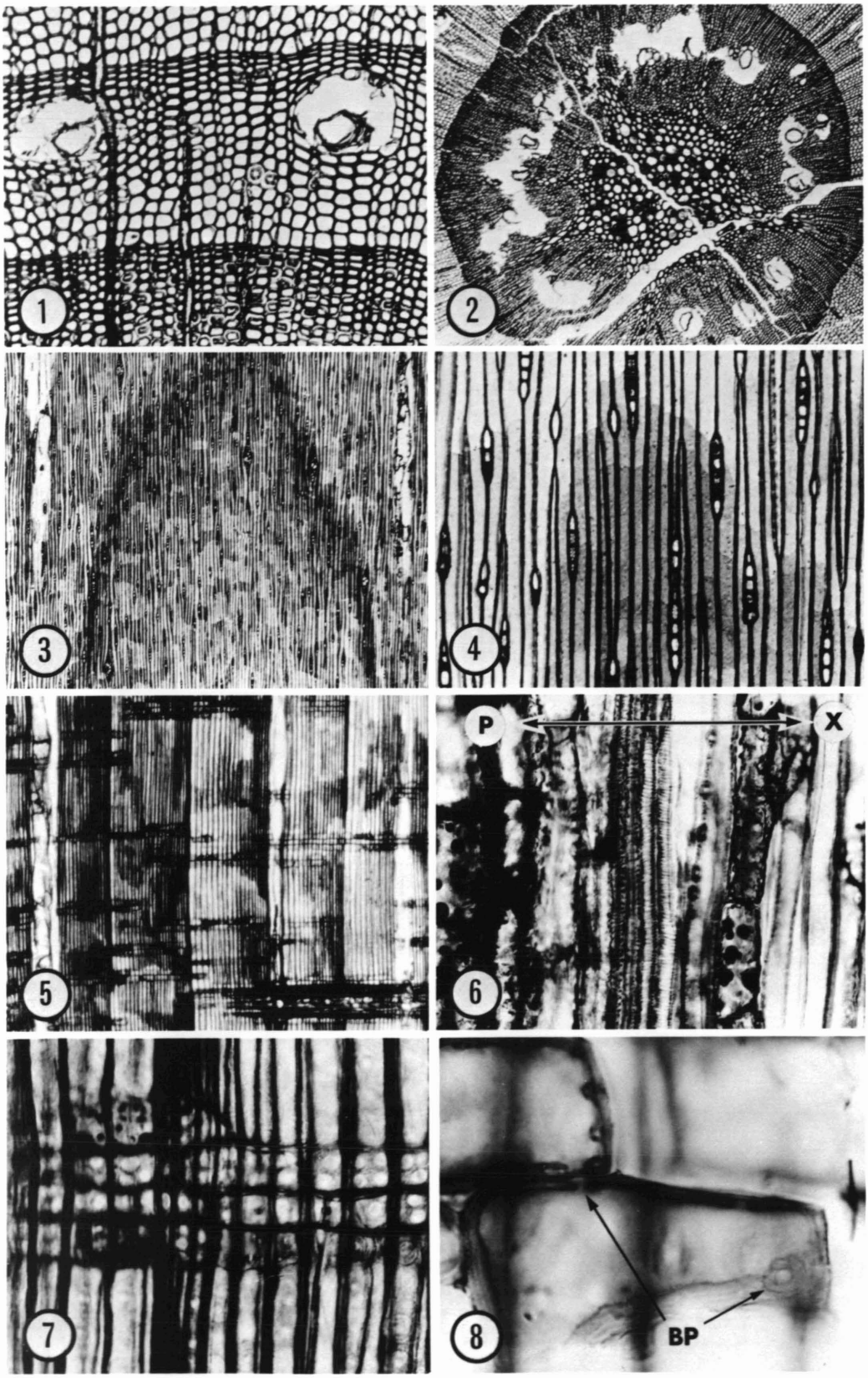

PLATE 4

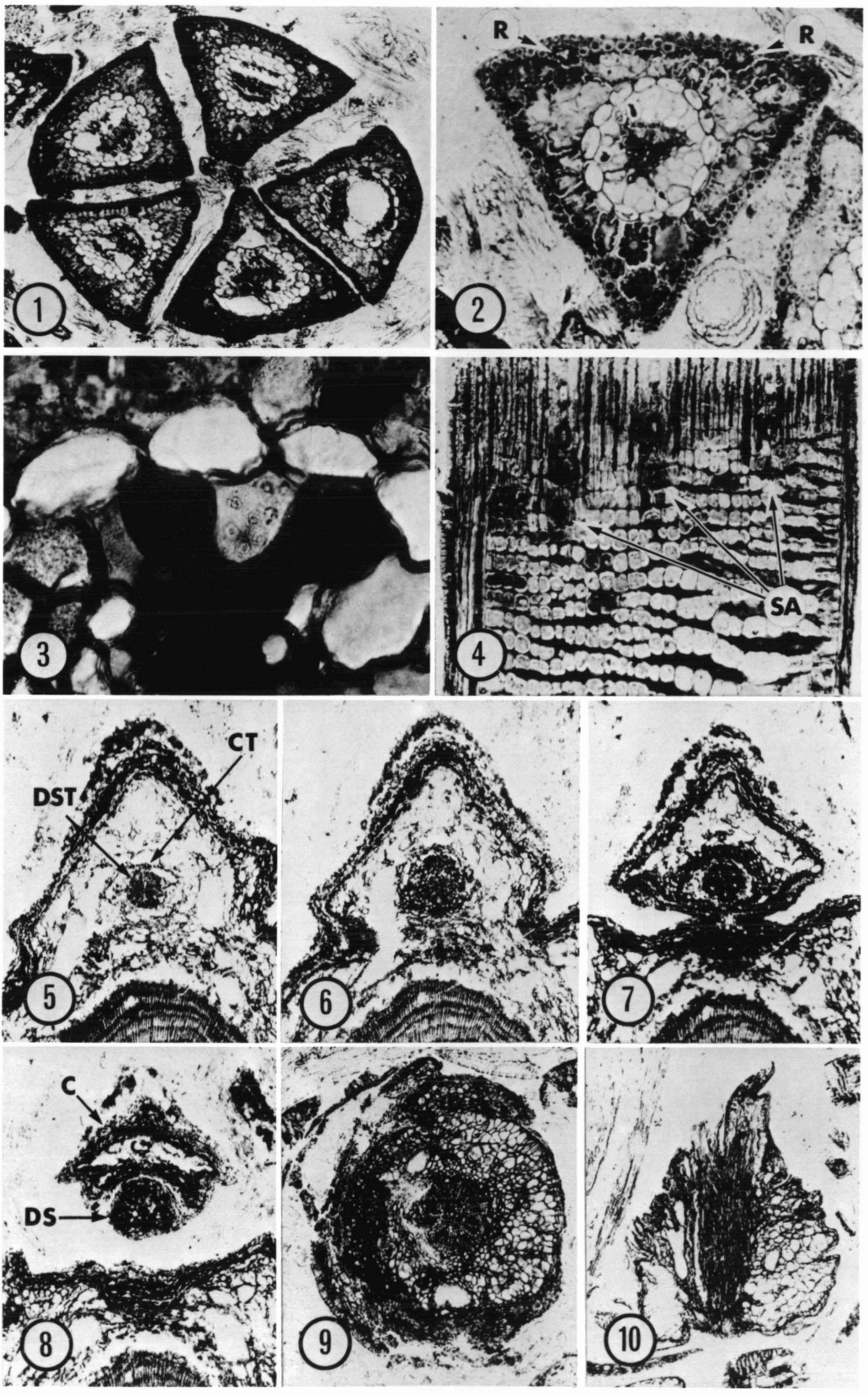

PLATE 5

diameter. Walls of the tracheids are 2–3 mμ thick. Large circular bordered pits occur in a single series on the radial walls of the tracheids (pl. 4, figs. 5, 7), while smaller circular bordered pits appear on tangential walls of summer wood tracheids. These are absent from the tangential walls of the spring wood elements (pl. 4, fig. 4). Tangential pitting is a feature occurring predominantly but not exclusively in the subgenus *Strobus* (Shaw, 1914). Resin canals are abundant in the vertical system of the xylem. They are 50–80 mμ in diameter exclusive of the epithelial layer (pl. 4, fig. 1). The latter is made up of thin-walled parenchyma cells. In most cases only a single layer of these cells remains but the area around them is decayed, suggesting an epithelial layer two or more cells thick in the living condition. Rays are uniseriate and 1–8 cells high if no resin canals are included (pl. 4, figs. 3, 4). Those that contain a resin canal are 10–16 cells tall and are biseriate near the canal (pl. 4, fig. 3). Both types of rays are constructed mostly of parenchyma with ray tracheids present but rare. The latter typically occur in a marginal file of cells but are interspersed with ray parenchyma. Ray tracheids are 35–80 mμ long and 15–26 mμ in diameter. Their cell walls are 1–2 mμ thick and lack projections of the secondary wall into the cell lumen as in dentate tracheids typical of species of the subgenus *Pinaster* (pl. 4, figs. 7, 8). Circular bordered pits occur on the tracheid walls with 1–4 visible in the cross field. Ray parenchyma cells are about the same size and shape as the ray tracheids but bear simple pits that are circular and about 5–7 mμ in diameter in face view. One to four such pits appear in the cross field (pl. 4, fig. 7). Ray parenchyma cells have walls that are 2–3 mμ thick and the lumina of many cells is filled with dark substances or other materials that appear like large oil droplets (pl. 4, fig. 5).

Cortical tissue is preserved in only a few of the smaller stems and in them is disrupted and pulled away from the secondary xylem. Parenchyma cells that are about 50 mμ in diameter and have a circular-to-oval transverse outline make up the bulk of the tissue, with numerous resin canals occurring in the outer part of the cortex. Five to fifteen layers of cork cells surround the cortex, and in places remains of one or two layers of hypodermal and one layer of epidermal cells are present.

Traces to dwarf shoots are visible in all stems with cortices and can be followed by serial sections inward to the vicinity of the primary xylem. In the middle of the cortex they are cylindrical (pl. 5, fig. 5), about 0.3 mm in diameter, and enclose a small pith. As a given trace approaches the periphery of the cortex, the latter tissue enlarges forming a bulge on the stem surface. A small leaf trace consisting of about six tracheids branches from the abaxial side of the dwarf shoot trace and moves with it into the bulge (pl. 5, fig. 6). Apically, the protuberance constricts tangentially to the stem and separates from it (pl. 5, fig. 7). Immediately above the point of separation the protuberance itself divides, with the abaxial portion enclosing the small leaf trace forming a scalelike cataphyll and the adaxial portion forming the cylindrical base of the dwarf shoot (pl. 5, fig. 8).

Needles and dwarf shoots.—All conifer needles in the chert are of the same type, that of a five-needle pine (pl. 5, figs. 1, 2). While most appear as individuals in sections, having either become separated from their fascicle or been cut some distance from it, clusters of five needles are not uncommon. One cluster of only four needles was encountered, but these needles are similar anatomically to those in groups of five and are considered a normal variant of the same species. Such variation is common in living species (Becker, 1964; Mirov, 1967; Shaw, 1914). None of the needle clusters retain their fascicle sheaths which were presumably deciduous as in Recent species of the subgenus *Strobus* (Shaw, 1914).

Structurally, the needles are similar to those of living species of the true white pines, i.e. subgenus *Strobus*, section *Strobus*. In transverse section they approximate an equilateral triangle that is 0.4–0.6 mm on a side. However, some measure as little as 0.1 mm wide and no doubt represent sections of apices or bases. Needles have been traced in the matrix by serial peels for up to 2.3 cm without finding either their apices or bases, and were thus longer in the living condition. Most specimens, in fact,

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EXPLANATION OF PLATE 5

Pinus similkameenensis sp. nov., syntype, UMMP 60483. *1*, transverse section of needle cluster, × 35.0. *2*, transverse section of needle, × 114.0. *3*, transverse section of part of needle showing transfusion cells with circular bordered pits, × 436.0. *4*, paradermal section of needle showing stomates and guard cells, × 68.6. *5–8*, serial transverse sections of stem showing divergence of dwarf shoot and subtending cataphyll, × 22.0. *9*, transverse section of dwarf shoot, × 250. *10*, longitudinal section of dwarf shoot with attached needles, × 17.0. C, cataphyll; R, resin canals; CT, cataphyll trace; DS, dwarf shoot; SA, stomates; DST, dwarf shoot trace.

appear to be broken pieces rather than complete needles. At the center of each needle is a single vascular strand (pl. 5, fig. 2) consisting mostly of secondary xylem in ventral position and secondary phloem dorsally. A few primary xylem elements occur at the ventral periphery of the xylem, and occasional thick-walled cells are located at the dorsal edge of the phloem, probably representing primary phloem fibers. Thin-walled cells that are about 50 mμ in diameter, 80 mμ long, and bear circular bordered pits on their walls form a transfusion tissue one or two cell layers thick around the vascular strand (pl. 5, figs. 2, 3). This tissue is bounded by an endodermis consisting of a single layer of large cells in which the radial and outer tangential walls are thickened. Irregularly shaped parenchyma cells with dentate wall processes projecting into the cell lumen make up a mesophyll that is 2–4 cell layers thick. At the dorsal periphery of this tissue are two resin canals, one to either side of the endodermal cylinder (pl. 5, figs. 1, 2). These canals are in contact with the hypodermis but are not surrounded by a sheath of hypodermal fibers. The hypodermis is 1–2 cell layers thick and is made up of long fibers that are 10–25 mμ in diameter. Their walls are 5–6 mμ thick and bear numerous simple pits. By contrast, the epidermis is constructed of a single layer of cells that are about 15 mμ in diameter and 60–80 mμ long. Stomates are absent on the dorsal face of the needle but occur in 2–3 rows on each ventral face with their longitudinal axes parallel to that of the needle (pl. 5, fig. 4). They are slightly sunken so that the guard cells are aligned with the hypodermis.

Needles of a given cluster constrict basally to a width of about 0.25 mm and converge around a small conical mass of parenchyma that no doubt corresponds to the residual apical meristem of the dwarf shoot in living pines (Mirov, 1967, Sacher, 1955). Just below this point the ventral margins of the needles fuse first with the parenchymatous mass and then with one another, obscuring the former tissue. Fusion continues basally for some distance with the dorsal parts of the needle bases ultimately coalescing to form a solid cylinder. Resin canals of each needle fuse with the adjacent canal of the adjoining needle resulting in a total of five canals in the cortex of the dwarf shoot. Furthermore, the five vascular strands of the needles converge to form a cylinder but remain slightly separated from one another for some distance by five broad rays.

Below this point direct anatomical evidence of the five needles disappears. Inflated bases of cataphylls (Sacher, 1955) protrude from the dwarf shoot enlarging its diameter to 1.5–2.0 mm (pl. 5, figs. 9, 10). Ramification of the resin canals producing branches that go out to the cataphylls results in 3–7 canals in basal sections of the dwarf shoot. Furthermore, small vascular strands diverge from the vascular cylinder with one going to each cataphyll, and gaps produced in the cylinder opposite them obscure the five-parted xylem arrangement apparent in more apical sections. However, even though no dwarf shoots complete with needles have been found attached to the stems, there is little doubt that these organs belong to the same species. All dwarf shoots in the matrix are alike in size, shape, and anatomical construction, and they are fully compatible in these features to the dwarf shoot bases attached to the stems.

Discussion.—The remains included in *Pinus similkameenensis* offer an interesting mixture of features occurring today in different sections of the subgenus *Strobus*. The needles are anatomically inseparable from those of certain living species of the section *Strobus*, namely *Pinus monticola*, *P. parviflora*, *P. puece*, *P. strobiformis*, and *P. strobus*. While features of needle anatomy are sufficiently distinctive to permit identification of most living pines, Harlow (1931) was unable to distinguish between needle sections of these five species. He suggested that their structure represents a generalized tissue arrangement from which other types of quinate needles are derived. The occurrence of the same structure in these Eocene needles supports this hypothesis.

The secondary xylem of stems of *Pinus similkameenensis*, on the other hand, is most similar to that of certain species of the section *Parrya*, such as *Pinus aristata*, *P. cembroides*, and *P. bungeana*. Its affinity with the subgenus *Strobus* is evidenced by the lack of dentations in the ray tracheids and the presence of circular bordered pits on the tangential walls of the summer wood tracheids, both of which are conditions that occur predominantly but not exclusively in Recent woods of this subgenus. The accurate identification of the fossil wood to lesser taxa of the subgenus is hampered by our ignorance of the variation exhibited by each of the many features used in comparative conifer wood anatomy and their relative importance in phylogenetic comparisons. The fossil wood stands out from those species of the subgenus *Strobus* treated by Greguss (1955) in having significantly fewer ray tracheids. Beyond this, however, *Pinus similkameenensis* is most similar to *P. aristata*, *P. bungeana*, and *P. cembroides* even though it compares perfectly with none of these. The fossil wood differs generally from that of members of the section *Strobus*, in lacking the fenestriform pits in the ray parenchyma

typical of the latter. It is best, therefore, to conclude that the wood belongs to the subgenus *Strobus* and compares most favorably, but by no means perfectly, with certain species of the section *Parrya*.

Two types of five-needle pines are known on the basis of foliage impressions from the Allenby Formation, but neither of these is similar to the new species. *Pinus latahensis* Berry (1929) has needles that are 7 cm or more long attached to dwarf shoots that are 5–6 mm long and 2–3 mm in diameter. While lack of complete needles of *P. similkameenensis* prevents comparison of needle length, the dwarf shoots of *P. latahensis* are clearly larger than those of *P. similkameenensis*. The two are thus considered separate species. While *P. tulameenensis* is known from only two reports, it too differs significantly from the new species. Needles of the former are slender, 10–25 mm long, and are attached to dwarf shoots that are 0.5 mm in diameter (Arnold, 1955). The type material shows four needles per cluster (Penhallow, 1908), but Arnold (1955) reports some clusters of five needles in his specimens. On the other hand, only two cases in about a hundred needle clusters of *P. similkameenensis* show departure from the typical quinate arrangement. This, combined with the smaller dwarf shoots of *P. tulameenensis*, indicates that the two-needle types are distinct. All other species of compressed *Pinus* foliage having clusters of five needles from the Tertiary of North America appear larger than the petrified form. Thus, the latter represents a new species.

SUMMARY

Silicified cones, needles, dwarf shoots, and stems of *Pinus* from the Eocene Allenby Formation of southern British Columbia described in this report form the basis for two new species. The cones are assigned to *P. arnoldii* and belong to the subgenus *Pinus*. They are most similar to those of living members of the section *Pinus*, subsection *Sylvestres*, but differ from cones of the subsections *Contortae* and *Oocarpae* only in lacking evidence of the serotinous condition and the asymmetrical shape peculiar to cones of these taxa. In contrast, the vegetative remains are included in *Pinus similkameenensis* which is assigned to the subgenus *Strobus*. The stems are most comparable with those of certain living species of the section *Parrya*, such as *Pinus aristata*, *P. bungeana*, and *P. cembroides*. The secondary xylem differs from that typical of the section *Strobus* mainly in lacking large fenestriform pits in the cross field. The needles, however, are anatomically inseparable from those of certain living species of the section *Strobus*, namely *Pinus monticola*, *P. parviflora*, *P. puece*, *P. strobus*, and *P. strobiformis*. Thus, in this fossil species there is a combination of features of the sections *Parrya* and *Strobus*.

Despite the affinity of the fossil cones to one subgenus and the vegetative remains to another, there is only one type of each organ present in the sample of chert studied during this investigation. This association leads to speculation that all organs may have come from a single species. Such a species would thus have features that are generally regarded as distinctive of the two main subdivisions of the genus, and this mixing of characters would further imply that the subgenera *Pinus* and *Strobus* may not have existed as separate lines of specialization in the Eocene.

The main reason for believing that the cones and vegetative remains may have come from a single species is that despite evidence of transport prior to fossilization there is only one type of each organ present in the chert sample. If there were more than one species of *Pinus* near the basin of deposition, two forms of at least one of the organs should be in evidence. Furthermore, a fossil species exhibiting characters of both subgenera would not be without living counterparts. Such present-day members of the subgenus *Pinus* as *P. lawsoni* Gord., *P. leiophylla* Schl. & Cham., *P. montezumae* Lamb., and *P. ponderosa* Dougl. have cones typical of the subgenus and not uncommonly produce needles in clusters of five as well as other numbers (Shaw, 1909). In *P. pseudostrobus* the quinate needle arrangement is typical, normally occurring to the exclusion of all others. These species now occur in Mexico, and it is not inconceivable that their ancestors may have ranged as far north as southern British Columbia during the Eocene. Thus, there is some basis for considering *P. arnoldii* and *P. similkameenensis* organs of a single species.

The evidence at hand, however, argues against treating these fossils under one binomial. While certain living species show a mixing of features of the two main subgenera they are the exception rather than the rule. Furthermore, an organic connection between the fossil cones and stems is lacking. In addition, even though there was only one type of each organ in the chert studied, this sample was a small one and cannot be considered representative of the deposit. Thus, other types of these organs may well occur in the chert but were just not found during this investigation. These reasons far outweigh those suggesting a single species and, until demonstrated otherwise, the treatment of the fossils in two species

is a more accurate representation of the evidence at hand.

Pinus arnoldii and *P. similkameenensis* are nonetheless important in representing two new types of fossil pines in the Allenby Formation, and these organs indicate the minimal stage of evolution *Pinus* had achieved by Eocene time. More specifically, these organs demonstrate that cones at least as specialized as those presently occurring in the subsection *Oocarpae*, needles at least as advanced as those of the section *Strobus*, and secondary xylem at least as complex as that of the section *Parrya* had all evolved by the Eocene. However, lacking more complete information on the anatomy of Recent *Pinus* cones and in the absence of additional comparable remains in the fossil record, the determination of the role of these two new species in the phylogenetic history of *Pinus* must be left to future work.

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