Pinus buchananii a new species of petrified seed cone from the Oligocene of the Olympic Peninsula Washington

James Craig Underwood
*The University of Montana*

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PINUS BUCHANANII, A NEW SPECIES OF PETRIFIED SEED CONE FROM
THE OLIGOCENE OF THE OLYMPIC PENINSULA, WASHINGTON

By
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B.A., University of California, Los Angeles, 1975

Presented in partial fulfillment of the requirements for the degree of
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ABSTRACT

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Pinus buchananii, A New Species of Petrified Seed Cone from the Oligocene of the Olympic Peninsula, Washington

Director Charles N. Miller Jr.

Pinus buchananii is a new species of ovulate cone from the Oligocene of the Olympic Peninsula, Washington. Excellent preservation allowed close comparison of the fossil with modern cones. The new cone is assigned to the section Pinus, subgenus Pinus, and shows the closest affinities with the living species of the subsection Ponderosa. A combination of anatomical and morphological features not found in the other fossil species of Pinus warrants the designation of this fossil as a new species. This Oligocene cone is the fifth structurally preserved Pinus cone on record.
ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. C. N. Miller Jr. for advice and guidance above and beyond that required as chairman of my Master's thesis committee. Further, I thank Dr. C. R. Robinson for his assistance in teaching me various laboratory techniques used in the research of this thesis.

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Chapter 1

INTRODUCTION

Current research is involved with elucidating the evolution of modern genera within the Pinaceae. Ovulate cones were selected as the basis of this work as they circumvent many of the problems found in traditional fossil types (i.e. pollen, wood, etc.) (Miller, 1976). Numerous anatomical and structural features which are unique and distinct to each genus and are repeatable many times within the cone may be used to determine affinities. Of diagnostic value in determining generic affinities are the branching patterns of the vascular and secretory systems to each bract-scale complex (Miller, 1976).

On record are 20 structurally preserved pinaceous cones from the Cretaceous and representatives of the modern genera Pinus and Picea\(^1\) from the early Tertiary.

Research is underway to establish the occurrence of extant genera in the fossil record. Numerous cones have been collected and studied from the Oligocene of the Olympic Peninsula, Washington. Pinus buchananii is the first species to be described from this collection.

\(^1\)Recent examination of the holotype of Picea cliffwoodensis Berry (1905), from the Late Cretaceous of New Jersey, by Dr. C. N. Miller indicates that the specimen has been placed incorrectly in this modern genus.
Chapter 11

MATERIALS AND METHODS

The material studied consisted of one of 25 structurally preserved ovulate cones collected from the northern coastal area of the Olympic Peninsula, Washington. These cones were generally silicified and preserved in silt-sandstone concretions which were found free on the beach or in situ in outcrops of the Oligocene Twin River Formation (Arnold and Hannibal, 1913). The cone that formed the basis for this work was found by Mr William Buchanan of Clallum Bay, Washington, one quarter mile west of the mouth of Jansen Creek, and was given to the University of Montana for study.

The geological history of the northern Olympic Peninsula is one of mostly submarine volcanic or marine sedimentary deposition until sometime in the Miocene or Pliocene (Mallory and Tompkins, 1964). Sediments of the Peninsula are no older than early Tertiary except for exposed areas of igneous and sedimentary rocks south of the Point of Arches which may represent a submerged piece of the North American continent of seventy million years ago (Mallory and Tompkins, 1964).

The Twin River Formation consists primarily of siltstone, sandstone, and abundant silt-sandstone concretions. Deposition occurred until Late Oligocene or Early Miocene when deposition was interrupted by uplifting. Subsequent submergence resulted in the deposition of the Clallum Formation over the Twin River Formation in the Early Miocene. In post Clallum times the Olympic Mountain uplift took place
and has continued intermittently through the Pleistocene to the present. Sediments of the northern peninsula area have been dated by the use of marine foraminifera (Rau, 1964).

Internal cone structure of the new species was studied by means of thin sections and was compared with that of modern cones in a reference collection consisting of about one half the known species of the Pinaceae (Appendix 1). In addition, comparison of morphological and anatomical features of the Oligocene cone was made with the four fossil Pinus cones on record. Type material was used in the examination of Pinus arnoldii Miller (1973) and P. avonensis Miller (1973). Comparison with P. wolfei Miller (1974) and P. belgica (Alvin, 1960) was made on the basis of published reports.

All sectioned material is now on deposit with the Dept. of Botany, University of Montana.
Chapter 111

SYSTEMATIC DESCRIPTION

Division Coniferophyta
Class Coniferopsida
Order Coniferales
Family Pinaceae
Genus Pinus Linnaeus

Pinus buchananii sp. nov.

DIAGNOSIS

Ovulate cone long-conical, 7-8 cm long by 3.0 cm at widest diameter; axis 11-11.5 mm in length, surrounded by numerous ovuliferous scales and their subtending bracts; pith 4.0 mm in diameter, constructed mostly of parenchyma cells with a thin outer zone of sclereids; primary xylem endarch; secondary xylem 1.3 mm thick; growth ring evident but subtle; resin canals in xylem arranged in single ring; rays uniserate; cortex 4.0-4.5 mm thick, composed of a thin inner zone of small diameter parenchyma cells, a thick middle layer of large parenchyma cells, an outer layer of sclereids two or three cells thick; bract-scale complex trace separating from the vascular cylinder of axis as an oval unit, dividing in outer part of middle cortex to form an adaxially concave bract trace on the abaxial side and an abaxially concave scale trace on the adaxial side; bract 3-5 mm long,
free from scale; ovuliferous scale up to 30 mm long by 14 mm wide and about 2 mm thick, making an angle of 15-20 degrees with longitudinal axis of cone, containing up to 15 vascular strands, each strongly rounded on abaxial side; resin canals of scale base abaxial to vascular strand, forming up to 26 canals apically with most abaxial to row of vascular strands but some interfascicular; scale apex 3-4 mm thick; apophysis rhombodial, 5-6 mm high, 10-12 mm wide; umbo abaxially subapical, centrally located on apophysis; spine absent; seeds two per scale, ovoid in shape, 5 mm in length, tangential diameter 2-2.5 mm, radial diameter 1-1.5 mm, lateral margins ridged; seeds mostly absent.

**HOLOTYPE**

Preparations of the holotype are on deposit in the University of Montana Paleobotanical Collection.

**LOCATION AND HORIZON**

Twin River Formation, Oligocene; one quarter mile west of the mouth of Jansen Creek; specific geographic coordinates are T. 33 N., R. 14 W., S.E. corner; Clallam Bay, Washington.
Chapter IV

ANATOMICAL DESCRIPTION

The cone is incomplete with lateral and apical portions missing (Plate 1). When intact the cone was probably 7-8 cm long with its largest diameter near the base at 3.2 cm and tapering to roughly 2.0 cm at its apex. The cone is generally long conical in shape.

The axis is surrounded by numerous ovuliferous scales 2-3 cm in length. These are 12-14 mm wide and about 2 mm thick. Each scale is subtended abaxially by a bract that is 3-5 mm long (Plate III). Two seed cavities are present on the adaxial side of each scale. Seeds are generally absent and cavities left by them are filled with mineral matter. The scale apex is inflated and bears a dorsal umbo. There is no evidence of a spine.

CONE AXIS

The cone axis is 1.6-1.8 cm in diameter basally with the pith 4-5 mm in diameter. The pith is composed mainly of thin-walled parenchyma cells with an outer zone of thick-walled cells (Plate V). In transverse section the thin-walled cells appear circular to oval and are 50-200 µm in diameter. These cells are generally irregularly rectangular in longitudinal section with lengths up to about 260 µm. Cell end walls are oblique. The interior of the pith composed of thin-walled parenchyma cells gradually grades into an outer zone of
thicker walled cells. These are 40-85 μm in diameter and are oval to circular in shape. Their cell walls are 10-20 μm thick. No resin canals are present within the pith.

The vascular cylinder of the axis is approximately 7 mm at its widest diameter and tapers towards the cone apex. The cylinder is about 1.4 mm thick and is composed mainly of secondary xylem (Plate VI). Interior wedges of primary xylem are present with annular and helical thickenings being evident on tracheid walls. Primary xylem maturation is endarch. A cambial zone is represented by a layer of two or three distinctly rectangular thin-walled cells outside the cylinder of secondary xylem. Peripherally a layer of crushed cells two or three cells thick probably represents the phloem.

Tracheids within the secondary xylem are about 30 μm in tangential diameter narrowing to 20 μm towards the interior of the cylinder. A subtle growth is observable on the basis of tracheid diameter, but the first year's growth can be distinguished from the second year's growth best by a single ring of small diameter resin canals. Vascular rays are regularly five to twenty-five cells high and are uniserate. Pitting of ray cells seen in longitudinal cone section is simple. Pit pairs in the cross field pitting are not visible.

The cortex of the axis is approximately 4 mm thick and consists mainly of thin-walled parenchyma cells arranged in two zones (Plate VII). A preponderance of small cells occupies an inner zone of the cortex that is 1.05-1.18 mm thick. The diameters of these cells range from 10-50 μm, and their cell walls are about 5 μm thick. Large
thin-walled parenchyma cells predominate within the outer two thirds of the cortex. These cells are 30-306 \( \mu m \) in diameter and reach lengths of up to 524 \( \mu m \). Their cell walls are 8-12 \( \mu m \) thick and cell wall pitting is simple. Peripheral to these large cells is a thin layer of thick walled cells. The shape of the cells is polygonal. In transverse cone section cell diameters are 82-164 \( \mu m \).

Parallel to the vascular cylinder is a system of resin canals. In transverse cone section the canals form a single ring within the inner portion of the cortex surrounding the vascular tissues (Plate V). Near the points of divergence of vascular traces the resin canals dilate and branch to meet canals converging from the bracts and scales. There are 8 such canals comprising the ring in preserved part of the transverse cone section; and based on their spacing, 12 canals were probably present in the intact cone. The canals are 260 \( \mu m \) in diameter expanding to as much as twice this size when branching. The canals are lined by a single layer of thin-walled epithelial cells.

Vascular traces to each scale and its subtending bract branch as a cylindrical unit from the vascular cylinder of the cone axis. Divergence of the bract and scale traces from one another occurs within the middle of the cortex forming an abaxially concave scale trace and a smaller adaxially concave bract trace (Fig. 1, A). The bract trace remains intact until its disappearance within the bract while the scale trace branches to give rise to numerous vascular strands within the scale.

Two axial resin canals branch somewhat basal to the point of divergence of the vascular traces. Each branch resin canal bifurcates
Fig. 1. A. Divergence of vascular traces to bract-scale complex. Adaxial concavity of the bract trace is not shown. B. Secretory system of the bract-scale complex and its connection with the axial system. For clarity only canals on one side of the diverging traces are diagrammed. (Redrawn from Miller, 1976)
to give rise to an abaxial bract and an adaxial scale canal (Fig 1, B). The two canals leading to the bract are located abaxial to and to either side of the bract trace. Canals in the scale remain abaxial to the vascular tissue initially branching within the cortex and with each branch subsequently giving rise to the numerous canals within the scale.

**BRACT**

Subtending each ovuliferous scale is a tongue-shaped bract that is triangular in cross section and 7-8 mm wide (Plate XI). The bract is composed mainly of thin-walled parenchyma cells with an abaxial and adaxial zone of thick-walled cells similar to those found in the outer cortex of the cone axis. The vascular strand is adaxially concave and occurs medially in the bract but is closer to the adaxial side of the bract than the abaxial side (Plate XII). Two small resin canals are abaxial to and to either side of the vascular strand. The vascular strand extends substantially into the bract though the exact distance could not be ascertained. Initial separation of the bract and scale was not visible in the sectioned material.

**OVULIFEROUS SCALE**

Each ovuliferous scale is approximately 25-30 mm long, 12-15 mm wide, and is about 2 mm thick (Plate III, IV). The scale is roughly tongue-shaped decreasing in width and becoming thicker near the scale tip. An inflated apex and a dorsally located umbo can be distinguished in both transverse and longitudinal cone sections. Initial divergence of the scale from the cone axis is at an angle of about 25-30 degrees.
Within two or three mm of the scale base the scale bends around the seed cavity forming a new angle with the central axis of 1-5 degrees.

At its base the scale is about 7 mm wide (Plate XI). Medially the scale is 2.0-2.5 mm thick, and it tapers to either lateral margin. Two large vascular traces occupy the adaxial portion of the scale. These traces will branch and form up to 15 vascular strands within the scale midway between the scale base and its apex (Plate IV). Immediately abaxial to the vascular traces is a row of about 7 resin canals. These canals are continuous with those of the inner cortex and branch to form as many as 25 separate canals within each scale. Enveloping the vascular traces and the resin canals is a zone of thick-walled parenchyma cells approximately 200 mm thick. These cells are 28-50 μm in diameter and have a wall thickness of about 4 μm. This zone cannot be observed soon after the scale diverges from the cortex. Adaxial to the vascular traces is a layer of thin-walled parenchyma six to eight cells thick. This zone projects towards the cone axis medially forming an intraseminal ridge about 0.4 μm high. At the expense of the other tissue layers this zone increases in thickness towards the scale tip and eventually occupies the entire scale interior near the scale apex. The abaxial one third of the scale is taken up by a zone of thick-walled sclereids that are continuous with those of the outer cortex. These cells are 20-70 μm in diameter and have a wall thickness of about 8 μm. The zone initially is 0.8-0.9 mm thick and thins towards the scale tip.

The scale width gradually increases and reaches a maximum of 14 mm about 5 mm from the base of the scale. The scale thickness
decreases to about 2 mm. There are about 15 vascular strands medially and they are abaxially rounded as is typical of the genus *Pinus* (Radais, 1894). About 16 resin canals occur at this location within the scale with the central ones being largest. Abaxially the zone of thick-walled cells is 0.5 mm thick while the adaxial parenchyma zone occupies almost two thirds of the scale.

Midway between the base of the scale and the scale apex the scale width is approximately 13 mm. There are 11 vascular strands, and they are aligned medially within the scale. Abaxial to the vascular strands there are 18 resin canals and they have started to diverge from any adherence to a medial line. The adaxial parenchyma layer occupies almost three quarters of the scale while the thick-walled abaxial layer has decreased to less than a quarter of the scale thickness.

About 5 mm from the scale tip a pronounced umbo projects from the abaxial surface of the scale (Plate Xlll). The scale width is 10 mm, and the thickness is 3.0 mm including the raised umbo. There are 11 vascular strands while the number of resin canals have increased and are now somewhat randomly distributed throughout the parenchyma tissue. The abaxial zone of thick-walled cells is essentially gone, and the interior of the scale is composed mainly of parenchymatous tissue.

Near the inflated scale tip, there is a decrease in scale width and an increase in lateral margin thickness. The scale is about 2 mm thick with what is now a slight taper to either margin. Vascular strands are absent and the numerous resin canals are randomly
distributed throughout the parenchymatous matrix.

SEEDS

The seeds are oval in transverse section with tangential diameters 2-2.5 mm (Plate X1V). Seed length is about 5 mm longitudinally, and radially seed diameters are approximately 1.4 mm. Many of the seeds were absent indicating normal dispersal before fossilization. Two seeds were produced adaxial to each scale as indicated by mineral filled cavities. The seed coat is 170-255 μm thick and consists of an inner endotesta, a middle sclerotesta, an outer sarcotesta. The endotesta is 50-75 μm thick and is represented by a layer of organic material that is not sufficiently preserved to distinguish cellular characteristics. The sclerotesta is 60-85 μm thick and is composed of thick-walled cells whose lumens are almost occluded by cell wall material. This layer forms a ridge which projects approximately 100 μm from either lateral side of the seed. An outer sarcotesta is represented by a layer of pyrite that is 40-50 μm thick. The seed wing extends at least 8 mm along the adaxial surface of the scale and is continuous with the scale epidermis. No embryonic tissue is preserved and the seed cavities are generally filled with mineral matter.
Chapter V

DISCUSSION

This Oligocene cone clearly belongs to the genus *Pinus* as indicated by its having such features as the restriction of resin canals to a position abaxial to the vascular strands in the scale base, strong adaxial curvature of the scale vascular strands, and inflated scale apices each with a subapical dorsal umbo. These features are individually unique to the modern genus *Pinus* (Alvin 1960; Miller, 1969, 1976; Radaia, 1894) and in combination leave no doubt as to the affinity of the fossil.

Affinities below the generic level are more difficult to determine. Among modern groups only the genus *Pinus*, subgenus *Pinus* have inflated scale apices with dorsal umbos (Shaw, 1909, 1914). However the long conical shape and symmetry suggest an affinity with the subgenus *Strobus*. Within the subgenus *Strobus*, section *Parrya* (Classification of Critchfield and Little, 1966) there are species which meet the above criteria in having inflated scales and dorsal umbos. Except for *P. balfouriana* and *P. aristata* the seeds of the cones within this subsection are too large to show affinity with *P. buchananii*. *Pinus balfouriana* and *P. aristata* differ from *P. buchananii* in having groups of small diameter parenchyma cells in the center of the pith compared to large cells in this location in the fossil, a gap in the xylem opposite the bract-scale complex almost twice as high as that of the
fossil, and the branching of the bract-scale complex in the inner
cortex as compared to a middle to outer cortex branching in the fossil
specimen.

Of the Recent cones studied anatomically (Appendix 1, 11) those
in the subsection Ponderosa, section Pinus, subgenus Pinus show the
closest similarity to the new Oligocene cone in their internal con-
struction. The cones within the subsections Ponderosa, Australes, and
Sabinianae are similar to P. buchananii in possessing a central pith
constructed mainly of thin-walled parenchyma cells surrounded by a
vascular cylinder composed of tracheids and uniserate or biserate rays.
The cortex is made up of an inner zone of predominately small
diameter cells and an outer zone of large diameter cells. In this
respect the new species differs significantly from those of subsections
Sylvestres, Oocarpae, and Contortae. In these groups the outer one
third to one half of the cortex is composed of a layer of thick-walled
cells. This is in contrast to P. buchananii where the outer portion
of the cortex is predominately large thin-walled parenchyma cells with
only a thin layer of thick-walled cells distally. The new cone differs
from the cones of the subsections Australes and Sabinianae in the posi-
tion of resin canals within the vascular cylinder. In P. taeda, P.
elliotii, and P. coulteri the resin canals are diffusely scattered
throughout the inner portion of the cylinder while in the fossil a dis-
tinct ring of canals is apparent. Further P. coulteri differs from
the new petrified seed cone in having cortical resin canals located in
middle to outer portion of the cortex. In the fossil the ring of canals
is near the inner edge of the cortex.
While our knowledge of comparative cone anatomy is not sufficient to determine affinity of the fossil more precisely the above accumulated evidence permits the conclusion that *P. buchananii* belongs to the section *Pinus*, subgenus *Pinus*, and shows greatest similarity to cones of the living species of the subsection *Ponderosa*.

The phylogenic importance of *P. buchananii* is difficult to determine because of the small number of structurally preserved *Pinus* cones reported in the fossil record. Only four species have been described to date: *P. belgica* Alvin (1960), from the Early Cretaceous Wealden Formation of Belgium; *P. arnoldii* Miller (1973), from the Allenby Formation, Middle Eocene, British Columbia; *P. avonensis* Miller (1969), from the Middle Oligocene; and *P. wolfei* Miller (1974), from the Late Eocene Cowlitz Formation of Washington (Appendix 111).

*Pinus buchananii* shows greatest similarity to *P. arnoldii* in its external construction (Appendix 111), but differs significantly from the Eocene species in its internal construction in lacking a thick outer cortical layer of sclereids and in having an adaxially concave vascular strand in the bract base. Further the new species differs from *P. avonensis* and *P. belgica* in the occurrence of an adaxially concave bract trace verses one circular in outline and in the presence of a distinct ring of resin canals in the inner zone of vascular tissue as compared to few or no canals in this position in the two latter species. *Pinus wolfei* differs in having three concentric rings of resin canals in the xylem as opposed a single one in *P. buchananii*. On these bases and a combination of unique anatomical and morphological features found in the new Oligocene cone the fossil specimen warrants treatment as a new species of *Pinus*. 
**Summary**

*Pinus buchananii* is a new species of ovulate cone from the Oligocene of the Olympic Peninsula, Washington. Excellent preservation allowed close comparison of the fossil with modern cones. The occurrence of such features as the restriction of resin canals to a position abaxial to the vascular strands in the scale base, strong adaxial curvature of the scale vascular strands, and inflated scales apices each with a subapical dorsal umbo clearly indicate that the Oligocene cone belongs to the genus *Pinus* (Alvin 1960; Miller, 1969 1976). Within the genus *Pinus* the new cone is assigned to the section *Pinus*, subgenus *Pinus* and shows greatest similarity to the cones of the living species of the subsection *Ponderosa*.

A combination of anatomical and morphological features not found in the other fossil species of *Pinus* warrants the designation of this fossil as a new species.


APPENDIX 1. List of modern pinaceous cones in reference collection.

Abies balsamea (Linnaeus) Miller
A. concolor (Gordon) Hildebrand
A. grandis Lindley
A. lasiocarpa (Hooker) Nuttall

Cedrus atlantica (Endlicher) Carriere
C. deodara (Roxburgh) G. Don in Loudon
C. libani A. Richard

Keteleeria davidiana (Bertrand) Beissner

Larix decidua Miller
L. eurolepis A. Henry
L. gmelinii (Ruprecht) Kuzeneva
L. kaempferi (Lambert) Carriere
L. laricina (Du Roi) K. Koch
L. occidentalis Nuttall
L. russica (Endlicher) Sabine et Trantvetter

Picea abies (Linnaeus) Karsten
P. asperata Masters
P. breweriana S. Watson
P. engelmannii (Parry) Engelmann
P. glauca (Moench) Voss
P. mariana (Miller) Britton, Sterns et Poggenberg
P. montigena Masters
P. omorika (Pancic) Purkyne
P. polita (Siebold and Zuccarini) Carriere
P. pungens Engelmann
P. rubens Sargent
P. sitchensis (Bongard) Carriere
P. wilsonii Masters

Pinus albicaulis Engelmann
P. aristata Engelmann
P. armandii Franchet
P. attenuata Lemmon
P. balfouriana Jeffrey ex A. Murry
P. banksiana Lambert

P. bungeana Zuccarini
P. contorta Douglas
P. coulteri B. Don
P. densiflora Siebold et Zuccarini
P. edulis (Engelmann) Voss
P. elliottii Engelmann
P. flexilis James
P. kesiaya Royle ex Gordon
P. lambertiana Douglas
P. leiophylla Schiede et Deppe
P. longeava Bailey
P. monophylla Torrey et Fremont
P. montezumae Lambert
P. muricata D. Don
P. nigra Arnold
P. parviflora Siebold et Zuccarini
P. pringlei Shaw
P. ponderosa Lawson
P. radiata D. Don
P. resinosa Aiton
P. strobus Linnaeus
P. sylvestris Linnaeus
P. tabulaeformis Carriere
P. taeda Linnaeus
P. teocote Schiede et Deppe
P. thunbergiana Franco
P. virginiana Miller

Pseudolarix amabilis (Nelson) Rehder
Pseudotsuga macrocarpa Mayr
P. menziesii (Mirbel) Franco

Tsuga canadensis (Linnaeus) Carriere
T. caroliniana Engelmann
T. heterophylla (Rafinesque) Sargent
T. mertensiana (Bongard) Carriere
T. sieboldii Carriere
APPENDIX II. Classification system of the modern genus Pinus of Critchfield and Little, (1966).

Genus Pinus
Subgen. Ducampopinus
  Subsect. Krempfii
    Pinus krempfii

Subgen. Strobus
  Subsect. Strobi
    *P. strobis
    *P. monticola
    *P. lambertiana
    *P. flexilis
    P. strobiformis
    P. ayacahuite
    P. peuce
    *P. armandii
    P. griffithii
    P. dalatensis
  Subsect. Strobiae
    P. koraiensis
    P. pumila
    P. sibirica
    P. cembra
    *P. albicaulis

Subsect. Strobii
  *P. strobis
  *P. monticola
  *P. lambertiana
  *P. flexilis
  P. strobiformis
  P. ayacahuite
  P. peuce
  *P. armandii
  P. griffithii
  P. dalatensis
  *P. parviflora
  P. morrisonicola
  P. fenzeliana
  P. wangii

Subgen. Ducampopinus
  Subsect. Ducampopinus
    Pinus krempfii

Subgen. Strobus
  Subsect. Cembrae
    P. koraiensis
    P. pumila
    P. sibirica
    P. cembra
    *P. albicaulis
  Subsect. Cerabrae
    P. koraiensis
    P. pumila
    P. sibirica
    *P. cembra

Subgen. Pinus
  Subsect. Balfourianae
    *P. balfouriana
    *P. aristata

  Subsect. Leiophyllae
    *P. leiophylla
    P. lumholtzii
  Subsect. Canarienses
    P. canariensis
    P. roxburghii
  Subsect. Pineae
    P. pinea

  Subsect. Sylvestres
    *P. resinosa
    P. tropicalis
    *P. nigra
    P. heidreichii
    P. mugo
    P. pinaster
    P. halepensis
    P. brutia
    *P. sylvestris
    *P. densiflora
    *P. thunbergiana
    P. massoniana
    P. taiwanensis
    P. luchuensis
    P. hwangshansensis
    *P. tabulaeformis
    P. yunnanensis
    *P. insularis
    P. merkusii
  Subsect. Australes
    P. palustris
    *P. taeda
    P. echinata
    P. glabra
    P. rigida

Subsect. Gerardianae
  P. gerardiana
  *P. bungeana
Subsect. Australes (cont.)
P. serotina
P. pungens
*P. elliotii
P. caribaea
P. occidentalis
P. cubensis
Subsect. Ponderosa
*P. ponderosa
P. washoensis
P. jeffreyi
P. englemanii
P. durangensis
P. cooperi
*P. montezumae
P. hartwegii
P. michoacana
P. pseudostrobus
P. douglasiana
*P. teocote
P. lawsonii
Subsect. Sabinianae
P. sabiniana
*P. coulteri
P. torreyana
Subsect. Contortae
*P. banksiana
*P. contorta
*P. virginiana
P. clausa
Subsect. Oocarpae
*P. radiata
*P. attenuata
*P. muricata
P. patula
P. greggii
P. oocarpe
*P. pringlei

*Indication that species is found in the reference collection.
APPENDIX III. Salient features of structurally preserved *Pinus* cones.

<table>
<thead>
<tr>
<th>Features</th>
<th><em>P. buchananii</em></th>
<th><em>P. wolfei</em></th>
<th><em>P. arnoldii</em></th>
<th><em>P. avonensis</em></th>
<th><em>P. belgica</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>Oligocene</td>
<td>L. Eocene</td>
<td>M. Eocene</td>
<td>Oligocene</td>
<td>E. Cretaceous</td>
</tr>
<tr>
<td>Location</td>
<td>Olympic Peninsula Washington</td>
<td>Washington</td>
<td>British Columbia</td>
<td>Montana</td>
<td>Belgium</td>
</tr>
<tr>
<td>Length (cm)</td>
<td>7-8</td>
<td>9-10</td>
<td>5-6</td>
<td>5.5</td>
<td>4.5</td>
</tr>
<tr>
<td>Diameter (cm)</td>
<td>3.0</td>
<td>3-4</td>
<td>2.25</td>
<td>2.5</td>
<td>3.0</td>
</tr>
<tr>
<td>Scale length (cm)</td>
<td>3.0</td>
<td>2.2</td>
<td>2.0</td>
<td>1.8</td>
<td>2.0</td>
</tr>
<tr>
<td>Apophysis height (mm)</td>
<td>5-8</td>
<td>Not preserved</td>
<td>5-8</td>
<td>4-6</td>
<td>5-8</td>
</tr>
<tr>
<td>Apophysis width (mm)</td>
<td>10-12</td>
<td>Not preserved</td>
<td>8-12</td>
<td>8-10</td>
<td>7-10</td>
</tr>
<tr>
<td>Spine on umbo</td>
<td>No</td>
<td>Not preserved</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Thick layer of sclerids outer cortex</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Vas. strand of bract</td>
<td>Adaxially concave</td>
<td>Adaxially concave</td>
<td>Terete</td>
<td>Terete</td>
<td>Terete</td>
</tr>
<tr>
<td>Resin canals in xylem</td>
<td>Abundant</td>
<td>Abundant</td>
<td>Abundant</td>
<td>Present but rare</td>
<td>Present but rare</td>
</tr>
<tr>
<td>Resin canals of bract dist. unequal in dia.</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
</tbody>
</table>

PLATES

PLATE 11. *Pinus buchananii*. Transverse section of cone scale showing adaxial curvature of vascular strands, X 35.
PLATE III. *Pinus buchananii*. Longitudinal section of the cone axis showing the vascular cylinder within the axis, X 3.5.

PLATE IV. *Pinus buchananii*. Transverse section of cone axis, X 4.
PLATE V. *Pinus buchananii*. Transverse section of cone axis showing central pith and vascular cylinder, X 15.

PLATE VI. *Pinus buchananii*. Transverse section of cone axis showing portion of vascular cylinder, X 21.
PLATE VII. *Pinus buchananii*. Transverse section of cone axis showing portion of cortex. Note two zones of thin-walled parenchyma cells, X 18.5.

PLATE VIII. *Pinus buchananii*. Longitudinal cone section showing vascular trace diverging from the vascular cylinder as a cylindrical unit, X 30.
PLATE IX. *Pinus buchananii*. Longitudinal cone section showing division of vascular trace to form an adaxial scale trace and an abaxial bract trace, X 14.5.

PLATE X. *Pinus buchananii*. Transverse section of cone axis showing scale trace diverging from the vascular cylinder and adaxially concave bract trace, X 11.
PLATE XI. *Pinus buchananii*. Transverse section of scale base and subtending bract, X 13.

PLATE XII. *Pinus buchananii*. Transverse section of bract showing the adaxially concave vascular trace, X 35.
PLATE XIII. *Pinus buchananii*. Transverse section of scale apex showing dorsially located umbo, X 13.5.

PLATE XIV. *Pinus buchananii*. Transverse section of cone axis showing laterally ridged seed, X 16.5.