

PINUS POLLEN CONES FROM THE MIDDLE EOCENE PRINCETON CHERT (ALLENBY FORMATION) OF BRITISH COLUMBIA, CANADA

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Anatomically preserved pollen cones are described from the Middle Eocene Princeton chert of British Columbia, Canada. Cones are ellipsoidal; range from 2.8 to 6.9 mm in length, 1.6 to 3.5 mm in diameter; and are often subtended by scale leaves. Cone axes contain longitudinally oriented, cortical resin canals and 14–18 vascular bundles. Microsporophylls are helically arranged, each bearing two abaxial pollen sacs, many containing pollen grains. Grains are bisaccate and monosulcate, ranging from 50 to 70 μm in length and 27 to 43 μm in width. Proximally, the corpus is rugulate with a tectate-alveolate infrastructure. Sacci have a well-defined endoreticulum and an external ornamentation that is psilate to scabrate. Variations in cone size, cone anatomy, and pollen morphology indicate that several developmental stages are preserved. The large number of cones present in the chert, especially those representing short-lived ontogenetic stages, and the preservational quality of the cones support depositional interpretations for a rapid burial and preservation. These factors also indicate that the pollen cone-producing plants occupied a marginal position in proximity to the lacustrine environment. Four species of *Pinus*, based on woody twigs, dwarf shoots, leaves, and ovulate cones, are presently known from the Princeton chert. The association of these pollen cones with *Pinus similkameenensis* leaves and *Pinus arnoldii* ovulate cones indicates possible taxonomic affinities among these species. The Princeton chert specimens are the oldest *Pinus* pollen cones to be described and are the first in the genus for which fossil pollen ultrastructure has been described.

Introduction

The Princeton chert locality in southern British Columbia represents one of the most well preserved and most diverse Tertiary assemblages of permineralized plants known and in recent years has provided a wealth of information regarding Middle Eocene angiosperms. To date, 14 dicotyledonous and five monocotyledonous taxa have been described, including several aquatic and semiaquatic plants (for review, see Cevallos-Ferriz et al. 1991; Pigg et al. 1993). In addition to the anatomical information, the depositional data now available indicate that the Princeton chert represents a near-shore lacustrine environment in which many of the plants were preserved in situ (Cevallos-Ferriz et al. 1991). Two polypodiaceous ferns (Basinger 1976; Basinger and Rothwell 1977) and the conifer genera *Metasequoia* and *Pinus* have also been described from the chert. *Metasequoia* is represented by one species, *Metasequoia milleri*, encompassing leaves, wood (Basinger 1981), ovulate cones (Basinger 1984), and pollen cones (Rothwell and Basinger 1979). The genus *Pinus* is circumscribed by four species, including leaves, wood, and ovulate cones.

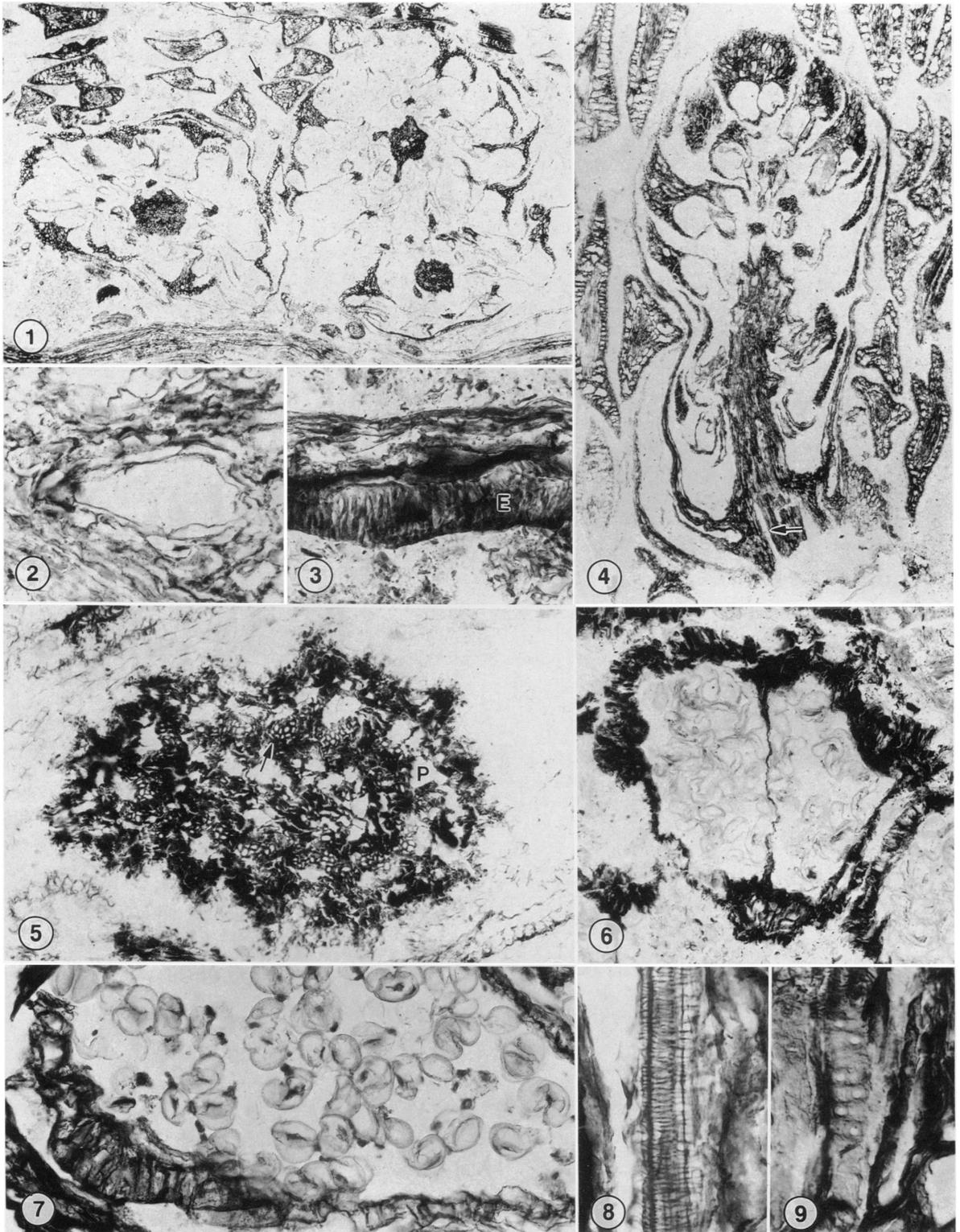
Miller (1973) described *Pinus arnoldii* from ovulate cones and *Pinus similkameenensis* from leaves, woody twigs, and dwarf shoots. In 1984, Stockey described a new species, *Pinus ander-*

sonii, based on leaves. *Pinus andersonii* leaves differed from leaves of *P. similkameenensis* on the basis of the following features, respectively: a three-leaf fascicle versus a five-leaf fascicle, a double vascular strand versus a single vascular strand, and five resin canals versus two resin canals. At the same time, Stockey (1984) emended the *P. arnoldii* description and described a second species based on ovulate cones, *Pinus princetonensis*. The principal morphological differences between these cones concern features of the cone axes. The axis of *P. arnoldii* has one ring of resin canals and a pith consisting of thick-walled parenchyma cells filled with dark contents, whereas the axis of *P. princetonensis* has two rings of resin canals and a pith containing thin-walled parenchyma lacking dark cell contents.

Vegetative remains and ovulate cones have been the organs most frequently examined in the majority of pine fossils. Over 50 megafossil species have been described from pine remains (see Miller 1993 and references therein), but none include pollen cones in the formal description. Two permineralized species, however, have been described with pollen cones in close association (Stockey 1983; Miller 1992). Pollen cones found in association with *Pinus driftwoodensis* ovulate cones, from the Middle Eocene of Smithers, British Columbia, are not well preserved and lack pollen grains (Stockey 1983). The pollen cones recovered with *Pinus foisyi* leaves, dwarf shoots, and ovulate cones, from the Miocene of Washington state, U.S.A., are believed to belong to the same species and are more completely preserved (Miller 1992). These cones also contain pollen grains for which several characters (e.g., corpus

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Figs. 1-9 *Pinus* pollen cones—cone anatomy (LM). Fig. 1, Transverse section of a pollen cone cluster. Three cones are shown. Note also the presence of *Pinus similkameenensis* leaves (arrow) in the surrounding matrix. P1173 B bot (SL 2672). $\times 13$. Fig. 2, Portion of a cone axis showing resin canal in transverse section. Note the epithelial lining. P1302 A #21. $\times 270$. Fig. 3, Longitudinal section of a scale leaf showing abaxial epidermis (*E*) with anticlinal thickenings. P1143 E, top #4. $\times 540$. Fig. 4, Longitudinal section of a cone showing full-length axis with cortical resin canal (arrow), subtending scale leaves, and spirally arranged microsporophylls. P1254 B bot #68b. $\times 14$. Fig. 5, Transverse section of a cone axis showing a slightly degraded pith and a single ring of independent vascular bundles. Note xylem elements (arrow) and the absence of phloem (*P*). P1173 C #9. $\times 135$. Fig. 6, Oblique transverse section of a microsporophyll showing two abaxial pollen sacs with in situ pollen and a single vascular trace. P1254 C bot #4b. $\times 135$. Fig. 7, Detail of a pollen sac wall showing outermost cell layer with

and saccus sizes) were reported on the basis of observations with transmitted light (Miller 1992). Several other studies have addressed fossil pinaceous pollen, also utilizing light microscopy (LM). Most of these have focused on comparisons with the pollen of extant species (see, e.g., Mack 1971) or have examined dispersed grains in a biostratigraphic context (see, e.g., Couper 1957; Hansen and Cushing 1973).

Boneham (1968) identified dispersed pine pollen from the Princeton chert in the first palynological study of the locality. Later, pollen cones with affinities to *Pinus* were noted as components of the Princeton chert in two initial surveys of the flora (Basinger 1976; Basinger and Rothwell 1977). However, no formal description was applied to these cones. In this article, the Princeton chert pollen cones are described and allied with previously described pine species from the locality. In addition to the anatomical/morphological description of the cones, this study provides the first information regarding fossil pollen ultrastructure for the genus *Pinus*.

Material and methods

Specimens were collected from the Princeton chert locality, an outcrop on the east bank of the Similkameen River about 8 km south of Princeton, British Columbia (Princeton map sheet 92 H/7, 1 : 50,000 UTM grid ref. 783-724). The outcrop consists of 49 layers of exposed chert interspersed with coal seams, with infrequent beds of ash replacing chert layers (Stockey 1987). The locality occurs within the Allenby Formation and is considered Middle Eocene in age on the basis of potassium-argon dating (Rouse and Matthews 1961; Hills and Baadsgaard 1967) and the presence of several palynological (Hills 1965; Rouse and Srivastava 1970), mammalian (Russell 1935; Gazin 1953), and ichthyological (Wilson 1977, 1982) index fossils.

The greatest abundance of pinaceous fossils occurs in layers 12–20 of the chert. Over 100 permineralized pollen cones have been identified to date; the 24 most completely preserved of these cones were examined. The surfaces of sectioned chert blocks that contained pollen cones were etched in 48% hydrofluoric acid for 1–3 min and serially peeled with cellulose acetate. For anatomical study, peels were mounted on microscope slides and examined using brightfield and Nomarski illumination. Sectioned blocks, peels, and slides are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

In situ pollen grains were recovered from cones by building wax wells around individual pollen

sacs on the surfaces of the chert blocks. The pollen was then pipette-macerated out with 48% hydrofluoric acid and rinsed several times with distilled water. For scanning electron microscopy, grains were pipetted directly onto aluminum stubs, sputter-coated with gold-palladium, and viewed on a Cambridge Stereoscan 250 SEM at 20 kV. Grains for transmission electron microscopy were pipetted onto cellulose filters, which were then embedded in agar. These were dehydrated in a graded ethanol series and immersed in acetone to dissolve the filters. The agar-coated pollen grains were gradually infiltrated with Spurr low-viscosity resin and embedded in shallow aluminum pans. Blocks were cut from the resulting resin disks to obtain desired grain orientations. Ultrathin sections were cut with a diamond knife, collected on uncoated slot grids, and dried on formvar support films (Rowley and Moran 1975). Grids were stained with 1% potassium permanganate (8–14 min), 1% uranyl acetate (6–10 min), and lead citrate (4–8 min; Venable and Coggeshall 1965). Images were recorded using Philips 400-T and JEOL 100-SX transmission electron microscopes at 60–80 kV.

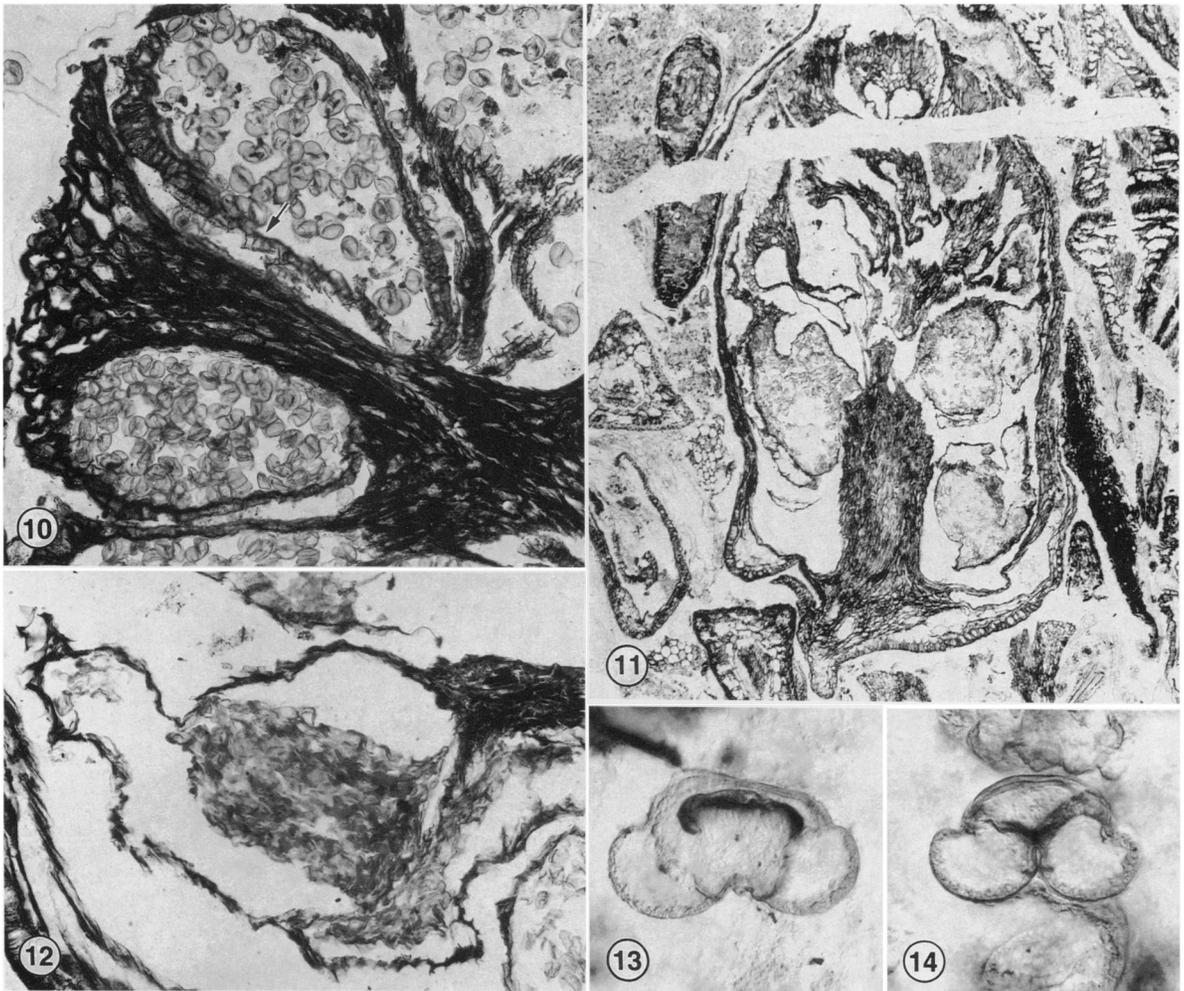
Results

Cones are typically found isolated, although several clusters have been identified (fig. 1). Individual cones are ellipsoidal, consisting of a central axis that supports helically arranged microsporophylls (figs. 1, 4, 11). Many cones have been recovered that are complete in that each bears a full-length axis and is subtended by several sheathing scale leaves (figs. 4, 11). The scale leaves range from 0.6 to 5 mm in length and may completely surround the entire cone (figs. 4, 11). The abaxial epidermis of each scale leaf is characterized by numerous cell wall thickenings (fig. 3).

Cones range from 2.8 to 6.9 mm in length (figs. 4, 11) and 1.6 to 3.5 mm in diameter (fig. 1). Cone axes, ranging from 0.3 to 0.6 mm in diameter, have a parenchymatous pith (figs. 1, 5). The pith is surrounded by a ring of 14–18 distinct vascular bundles (fig. 5). Elements of the xylem appear to be radially aligned (fig. 5) and consist of tracheids with scalariform and pitted secondary wall thickenings (figs. 8, 9). Phloem is not well preserved in these cones. Longitudinally oriented resin canals are present in the cortex (fig. 4), and, in a few instances, an epithelial lining is preserved (fig. 2).

Microsporophylls are parenchymatous (figs. 1, 10) and contain resin canals, and each is vascularized by a single bundle (fig. 6). Each bears two abaxial pollen sacs (fig. 6), which are eusporan-

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endothelial thickenings. P1143 D bot #2. \times 180. Fig. 8, Longitudinal section of cone axis showing several scalariform tracheids. P1143 E₄ top #4. \times 540. Fig. 9, Longitudinal section of cone axis showing a tracheid with circular bordered pits. P1143 E₄ top #32. \times 540.

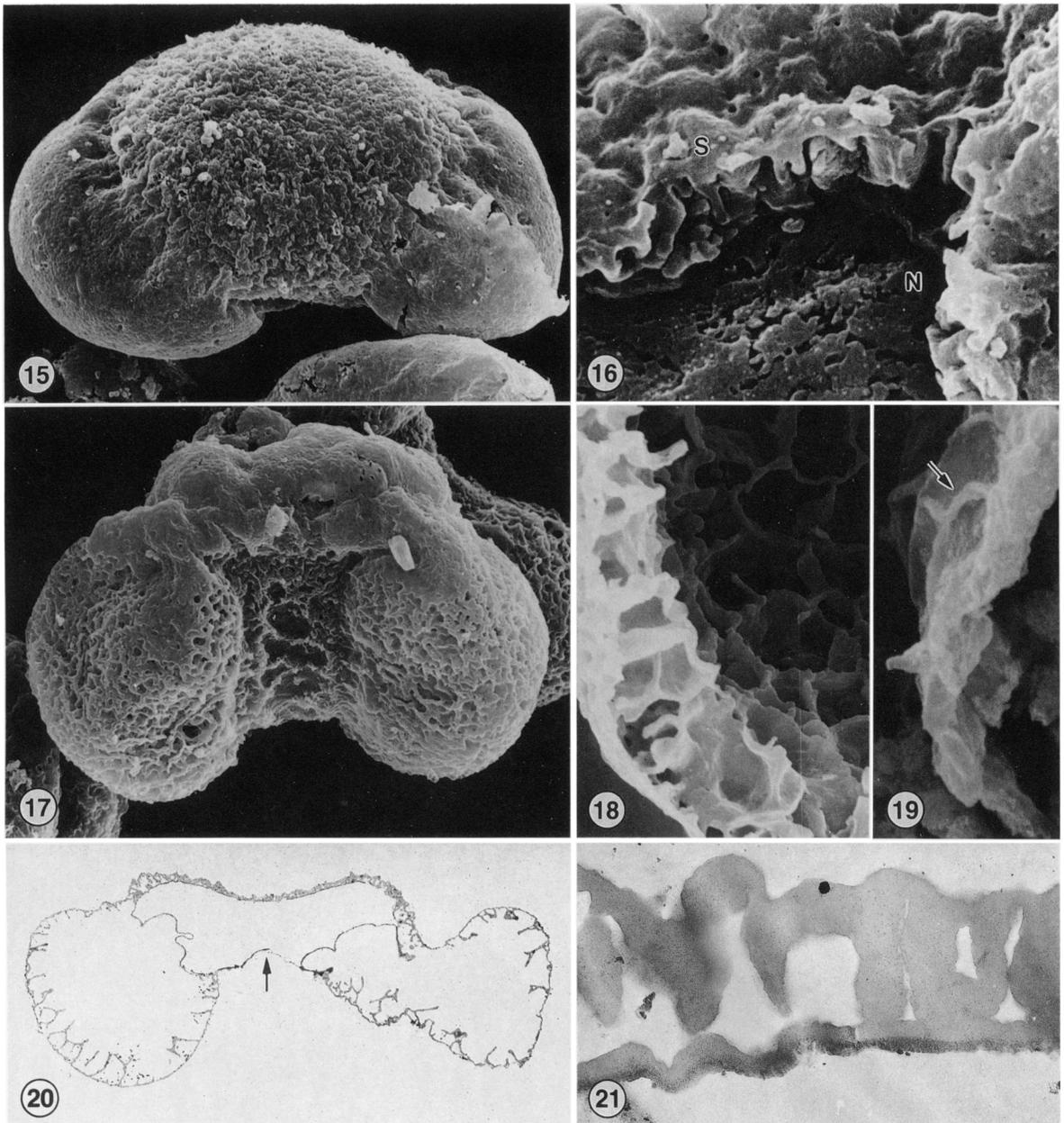


Figs. 10–14 *Pinus* pollen cones—cone anatomy and pollen morphology (LM). Fig. 10, Longitudinal section of microsporophylls showing pollen sacs filled with mature pollen. Note endothelial thickenings in the outermost pollen sac wall layer (arrow). P1143 D bot #2. $\times 87$. Fig. 11, Longitudinal section of an immature cone showing subtending scale leaves enclosing the cone and clumps of pollen within the pollen sacs. P1302 A #24. $\times 31$. Fig. 12, Detail of a pollen sac from an immature cone showing clump of tightly aggregated pollen grains. Note that individual grains with sacchi are not distinguishable (cf. fig. 10). P1302 A #33. $\times 130$. Fig. 13, Equatorial view of a single in situ pollen grain. Note the extended sacchi and the dark contents within the corpus. P1143 D bot #7. $\times 520$. Fig. 14, Equatorial view of a pollen grain showing distally inclined sacchi. P1143 D bot #2. $\times 520$.

giate. In some sacs, the outermost cell layer has distinct wall thickenings (figs. 7, 10). Many pollen sacs contain copious amounts of bisaccate pollen grains (figs. 6, 7, 10–12). In some cones, pollen grains are completely dissociated from one another, having expanded sacchi (figs. 6, 7, 10). In others, the grains are tightly clumped together within the pollen sacs and lack distinct sacchi (figs. 11, 12). Dark material, possibly cell remnants, is present within the corpus lumen of several grains (fig. 13). Grains with laterally attached sacchi (fig. 13) and with distally inclined sacchi (fig. 14) are present. Pollen grains are 50–70 μm ($\bar{X} = 61$) in total length (saccus to saccus). The corpus is 27–43 μm ($\bar{X} = 38$) in width (polar view; fig. 15), 23–50 μm ($\bar{X} = 38$) in length, and 3–33 μm ($\bar{X} = 21$) in height (equatorial view; figs. 13, 14, 20). Sacchi are 27–40 μm ($\bar{X} = 32$) in width (polar view;

fig. 15), 10–23 μm ($\bar{X} = 17$) in length, and 20–30 μm ($\bar{X} = 26$) in height (equatorial view; figs. 13, 14, 20). The corpus exhibits a rugulate ornamentation on the proximal surface and has a relatively broad sulcus on the distal surface (figs. 15–17). The sulcus extends the entire width of the grain, and, although the apertural membrane is not well preserved in many grains, it is psilate when present (fig. 17). Proximally, the exine averages 1.2 μm in height and is two-parted, consisting of a light-staining sexine and a partially dark-staining nexine (figs. 20, 21). The sexine exhibits a tectate-alveolate infrastructure. Alveoli are relatively robust, averaging 0.4 μm in width (figs. 16, 21). Nexine lamellae have not been identified.

Sacchi have an external sculpture that is psilate to slightly scabrate. In many cases, however, the



Figs. 15–21 *Pinus* pollen cones—pollen micromorphology and ultrastructure (SEM and TEM). Fig. 15, Proximal surface of a pollen grain showing rugulate corpus and psilate sacci. P1202 B bot. \times 1,200. Fig. 16, Fractured cappa (proximal wall) showing rugulate corpus surface and exine stratification. Note how the tectate-alveolate sexine (*S*) has pulled away from the nexine (*N*). P1359 C₂ #4. \times 10,680. Fig. 17, Distal surface of a pollen grain. Note the prominent sulcus extending the entire width of the grain and the degraded sacci. P1202 B bot. \times 1,500. Fig. 18, Fractured saccus showing outer wall and endoreticulum. P1202 B bot. \times 4,450. Fig. 19, Detail of saccus floor showing scars (arrow) where endoreticulations were formerly attached before saccus expansion. Saccus cavity is to left. P1359 C₂ #3. \times 1,780. Fig. 20, Median equatorial section through a pollen grain showing thickened, tectate-alveolate cappa, eusacci, and thinned apertural membrane (arrow). P1202 B bot. \times 980. Fig. 21, Detail of cappa showing light-staining, tectate-alveolate sexine and dark-staining nexine layer. The wall is thicker toward the left as its layers are separating to form the saccus. P1359 C₂ #3. \times 24,920.

sacci exhibit preservational degradation, thereby exposing the internal structure (fig. 17). Grains are eusaccate, with intact endoreticulations attached only to the outer walls of the sacci. The platelike endoreticulations project $4.1\ \mu\text{m}$ into the saccus cavity and are spaced $2.6\ \mu\text{m}$ apart, on average (figs. 18, 20). Scars are present on the

saccus floor, indicating the sites of endoreticulum attachment prior to saccus expansion during ontogeny (fig. 19).

Discussion

Despite the fact that the fossil history of *Pinus* is relatively well documented, surprisingly little

is known about the pollen-producing organs of the genus. The Princeton chert specimens are the first well-preserved *Pinus* pollen cones to be formally described and are only the second to be photographically illustrated. The general absence of pollen cones from the fossil record has been suggested by Miller (1992) to be the result of the fragile nature of these organs. Pollen cones typically lack abundant secondary xylem and other sclerotic tissues that enable organs such as leaves, wood, and ovulate cones to be more resistant to damaging preservational influences. Another factor related to the absence of pollen cones in the fossil record may be the brevity of their appearance in the reproductive cycle. Therefore, the discovery of such a large number of cones in the Princeton chert is unusual, and the fact that they are well preserved is even more noteworthy.

Given the wide size range and morphological variation observed in the specimens, we interpret them to be indicative of cones that were preserved in various stages of development. The small cones that are completely surrounded by subtending scale leaves are interpreted as immature. Furthermore, individual pollen grains of these cones lack distinguishable sacci and are tightly aggregated into large clumps within the pollen sacs. Cones considered to be mature are larger in size, with the subtending scale leaves surrounding only a small portion of the basal region of each cone. Pollen grains in these cones are large and dissociated and have well-developed sacci with distinct endoreticulations. Expanded sacci with well-defined endoreticulations present only on the outer walls are characteristic of mature pollen in extant pines (Dickinson and Bell 1970). Endothelial thickenings are present in the outermost wall layer of some pollen sacs in the fossils. The presence of these thickenings provides additional evidence for the mature state of the cones, as such thickenings function to aid in dehiscence in extant cones and do not appear until maturity (Gifford and Foster 1989). Other cones are interpreted as postdehiscent. The pollen sacs of these cones are devoid of pollen grains and appear to be ruptured along the outermost thickened layer.

Taking into account the fragile nature of pollen cones in general, the fact that a large number of well-preserved cones were found in a variety of short-lived developmental stages seems indicative of a rapid preservation. Furthermore, the quality of preservation would imply that little transport occurred. These factors support interpretations of in situ preservation of many of the plants found at the locality. The Princeton chert locality is believed to have been a shallow, near-shore lacustrine environment, with pines occupying a marginal position. This interpretation is based in part on the preservation of rooted plants,

complete flowers, and delicate tissues of aquatic plants, such as aerenchyma, in the chert (Cevallos-Ferriz et al. 1991).

In situ preservation of plants in the area suggests that different organs from the same biological species would likely be found in proximity to one another. Plants that were growing marginally with respect to the aquatic system would also be expected to deposit more organs into the basin than those farther away. The pollen cones are consistently found in association with the leaves of *Pinus similkameenensis*. *Pinus similkameenensis* is the predominant leaf type from the locality, as the only other taxon described from the Princeton chert on the basis of leaves, *Pinus andersonii*, is represented by a single fascicle (Stockey 1984). *Pinus arnoldii* ovulate cones have been correlated with both the leaves and the wood of *P. similkameenensis*, and all three are believed to be organs from the same biological species (Stockey 1984). The fact that *P. similkameenensis* is the only needle type found with the pollen cones described here suggests that the cones and the leaves are related. Definitive whole-plant reconstruction, however, will hinge on recovering specimens in organic attachment.

On the basis of comparisons with other fossil and extant pines, the Princeton chert species have been taxonomically assigned into modern groups (table 1). Despite the fact that *P. similkameenensis* and *P. arnoldii* are believed to be biologically related, they are classified within different subgenera. Although this is taxonomically problematic regarding modern classification schemes, from a geologic perspective it is possible that the extant subgenera *Strobus* and *Pinus* were not yet distinct in the Middle Eocene (Miller 1973). Unfortunately, the pollen cones described here lend no additional information in this regard, because morphological characters of pollen cones are of little taxonomic significance in classifications of extant pines (see, e.g., Mirov 1967; Little and Critchfield 1969). In fact, very few detailed studies (e.g., Konar and Ramchandani 1958) have addressed gross morphology of extant pine pollen cones.

Although little has been published about gross pollen cone morphology, many investigations have focused on various aspects of the development, morphology, and taxonomy of pine pollen grains (e.g., Dickinson and Bell 1970; Rowley and Walles 1987; Kurmann 1989). Historically, grain shape has been used to distinguish pollen of the subgenera *Strobus* and *Pinus*. Pollen grains from the subgenus *Strobus* tend to have an outline in which the sacci are more or less continuous with the corpus, whereas grains of the subgenus *Pinus* have sacci that are distinct from the corpus in outline view. These have been referred to as haploxyton-type and diploxyton-type, respectively,

Table 1
CLASSIFICATION OF PRINCETON CHERT PINES

<i>Pinus</i> L.	Species
Subgenus <i>Strobos</i> :	
Section <i>Strobos</i>	<i>Pinus similkameenensis</i> (leaves, twigs, and wood)
Subgenus <i>Pinus</i> :	
Section <i>Pinus</i> :	
Subsection <i>Sylvestris</i>	<i>Pinus arnoldii</i> (ovulate cones), <i>Pinus princetonensis</i> (ovulate cones)
Subsection <i>Ponderosae</i>	<i>Pinus andersonii</i> (leaves)

Source. Modified from Stockey (1984); classification based on Critchfield and Little (1966).

reflecting subgeneric epithets from the classification system of Shaw (1914). Haploxyton-type grains are further characterized by having a sculptured (verrucate) apertural membrane and a thickened ridge at the saccus-aperture junction, whereas diploxyton-type grains lack both apertural ornamentation and a prominent ridge (Bagnell 1975). Grains from the Princeton chert cones appear to be discontinuous in outline and of the diploxyton type; however, apertural features of these grains are not well preserved and are difficult to assess regarding ornamentation and saccus attachment. In addition, preparation protocols have been shown to create variation observed among these features in extant pollen (Owens and Simpson 1986). Therefore, at this time the Princeton chert grains can only tentatively be regarded as diploxytonoid, and thus with affinities to the subgenus *Pinus*. Definitive characterization of the pollen as the diploxyton type would support Miller's (1973) suggestion that the subgenera *Strobos* and *Pinus* had not yet differentiated by the Middle Eocene. Evidence for this stems from the consistent association of the pollen cones with leaves of *P. similkameenensis* (subgenus *Strobos*; table 1).

Several studies have attempted to taxonomically delineate pine pollen to the species level using palynological characters observed in both extant and *sporae dispersae* taxa. For example, some features examined include overall size, cap-sculpture, and saccus shape/internal composition (Cain 1940; Hansen and Cushing 1973; Sivak and Caratini 1973; Bagnell 1975). The systematic utility of many of these characters, however, especially those relating to size, has been shown by others to be of limited value (Whitehead 1964; Mack 1971). Surface ornamentation of the cappa also appears to be somewhat equivocal regarding species determination (Owens and Simpson 1986). Endoreticulation density is a character that has been applied as being unique at the species level (Sivak and Caratini 1973). In our opinion, however, the reliability of this character is questionable on the basis of the degree of

preservational variability that occurs among grains. Most studies have been based on the examination of a limited number of species within the genus. When additional species are included in such analyses, taxonomic distinctions based on palynological characters become more ambiguous (Mack 1971). In addition, the preparation methods employed as well as preservational effects may greatly influence the observed morphology, such as inducing swelling or shrinking of the grains (Whitehead 1964). Therefore, we do not believe that the Princeton chert pollen cones can conclusively be affiliated with either any extant or *sporae dispersae* species solely on the basis of pollen morphology. Exine infrastructure may have systematic utility; however, this cannot be determined at the present time as comparative data are not available. The Princeton chert specimens represent the only fossil pine for which infrastructural data are known, and, although 94 extant *Pinus* species are recognized (Little and Critchfield 1969), information on exine stratification has been published for only 12 (see Kurmann 1992 and references therein).

The description of these pollen cones provides an important addition to the understanding of the Princeton chert pines and the evolution of the genus as a whole. Despite the crucial role of pollen cones in the reproductive cycle of pines, very little is known about their fossil history. The Princeton chert specimens represent the oldest pollen cones described for *Pinus*, as well as the only fossils of the genus for which pollen ultrastructure has been examined to date. Discovery of additional species that include the description of pollen cones may provide morphological characters that would be useful in a systematic capacity and also serve to develop a more complete evolutionary understanding of the reproductive biology of pines.

Acknowledgments

This study was supported in part by a Council on Undergraduate Research Academic Industrial Undergraduate Research Partnership Fellowship, sponsored by the Burroughs Wellcome Fund,

to Carlie J. Phipps; a Natural Sciences and Engineering Research Council of Canada (NSERC) International Fellowship and a faculty research

grant from Northeast Missouri State University to Jeffrey M. Osborn; and NSERC grant A6908 to Ruth A. Stockey.

Literature cited

- Bagnell RC Jr 1975 Species distinction among pollen grains of *Abies*, *Picea*, and *Pinus* in the Rocky Mountain area (a scanning electron microscope study). *Rev Palaeobot Palynol* 19:203–220.
- Basinger JF 1976 Permineralized plants from the Eocene, Allenby Formation of southern British Columbia. MS thesis. University of Alberta, Edmonton.
- 1981 The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Can J Bot* 59:2379–2410.
- 1984 Seed cones of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Can J Bot* 62:281–289.
- Basinger JF, GW Rothwell 1977 Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Can J Bot* 55:1984–1990.
- Boneham RF 1968 Palynology of three Tertiary coal basins in south central British Columbia. PhD thesis. University of Michigan, Ann Arbor. 105 pp.
- Cain S 1940 The identification of species in fossil pollen of *Pinus* by size-frequency determinations. *Am J Bot* 27:301–308.
- Cevallos-Ferriz SRS, RA Stockey, KB Pigg 1991 The Princeton chert: evidence for *in situ* aquatic plants. *Rev Palaeobot Palynol* 70:173–185.
- Couper RA 1957 British Mesozoic microspores and pollen. *Palaeontogr Abt B Palaeophytol* 103:75–189.
- Critchfield WB, EL Little Jr 1966 Geographic distribution of the pines of the world. *US Dep Agric For Serv Publ* 991: 1–97.
- Dickinson HG, PR Bell 1970 The development of the sacci during pollen formation in *Pinus banksiana*. *Grana* 10:101–108.
- Gazin CL 1953 The Tillodontia: an early Tertiary order of mammals. *Smithson Misc Collect* 1221:1–110.
- Gifford EM, AS Foster 1989 Morphology and evolution of vascular plants. 3d ed. Freeman, New York. 626 pp.
- Hansen BS, EJ Cushing 1973 Identification of pine pollen of Late Quaternary age from the Chuska Mountains, New Mexico. *Geol Soc Am Bull* 84:1181–1200.
- Hills LV 1965 Source of the Allenby Formation, Princeton coalfield, British Columbia. *Can Pet Geol Bull* 13:271–279.
- Hills LV, H Baadsgaard 1967 Potassium-argon dating of some lower Tertiary strata in British Columbia. *Can Pet Geol Bull* 15:138–149.
- Konar RN, S Ramchandani 1958 The morphology and embryology of *Pinus wallichiana* Jack. *Phytomorphology* 8:328–346.
- Kurmann MH 1989 A reinvestigation of the pollen wall in *Pinus balfouriana* Murray. *Pollen Spores* 31:23–28.
- 1992 Exine stratification in extant gymnosperms: a review of published transmission electron micrographs. *Kew Bull* 47:25–39.
- Little EL Jr, WB Critchfield 1969 Subdivisions of the genus *Pinus* (pines). *US Dep Agric For Serv Misc Pub* 1144:1–51.
- Mack RN 1971 Pollen size variation in some western North American pines as related to fossil pollen identification. *Northwest Sci* 45:257–269.
- Millar CI 1993 Impact of the Eocene on the evolution of *Pinus* L. *Ann Mo Bot Gard* 80:471–498.
- Miller CN Jr 1973 Silicified cones and vegetative remains of *Pinus* from the Eocene of British Columbia. *Contrib Mus Paleontol Univ Mich* 24:101–118.
- 1992 Silicified *Pinus* remains from the Miocene of Washington. *Am J Bot* 79:754–760.
- Mirov NT 1967 The genus *Pinus*. Ronald, New York. 602 pp.
- Owens JN, S Simpson 1986 Pollen from conifers native to British Columbia. *Can J For Res* 16:955–967.
- Pigg KB, RA Stockey, SL Maxwell 1993 *Paleomyrtinaea*, a new genus of permineralized myrtaceous fruits and seeds from the Eocene of British Columbia and Paleocene of North Dakota. *Can J Bot* 71:1–9.
- Rothwell GW, JF Basinger 1979 *Metasequoia milleri* nov. sp., anatomically preserved pollen cones from the Middle Eocene (Allenby Formation) of British Columbia. *Can J Bot* 57:958–970.
- Rouse GE, WH Matthews 1961 Radioactive dating of Tertiary plant bearing deposits. *Science* 133:1079–1080.
- Rouse GE, SK Srivastava 1970 Detailed morphology, taxonomy and distribution of *Pistillipollenites macgregori*. *Can J Bot* 48:287–292.
- Rowley JC, DT Moran 1975 A simple procedure for mounting wrinkle-free sections on formvar-coated slot grids. *Ultramicroscopy* 1:151–155.
- Rowley JR, B Walles 1987 Origin and structure of Ubisch bodies in *Pinus sylvestris*. *Acta Soc Bot Pol* 56:215–227.
- Russell LS 1935 A Middle Eocene mammal from British Columbia. *Am J Sci* 29:54–55.
- Shaw GR 1914 The genus *Pinus*. Arnold Arboretum Publication no. 5. Houghton Mifflin, Boston. 96 pp.
- Sivak J, C Caratini 1973 Détermination de pollens de *Pinus* Américains dans le Miocène Inférieur des Landes (France), d'après la structure de l'ectexine de leurs ballonnets. *Grana* 13:1–17.
- Stockey RA 1983 *Pinus driftwoodensis* sp. n. from the Early Tertiary of British Columbia. *Bot Gaz* 144:148–156.
- 1984 Middle Eocene *Pinus* remains from British Columbia. *Bot Gaz* 145:262–274.
- 1987 A permineralized flower from the Middle Eocene of British Columbia. *Am J Bot* 74:1878–1887.
- Venable JH, R Coggeshall 1965 A simplified lead citrate stain for use in electron microscopy. *J Cell Biol* 25:407.
- Whitehead DR 1964 Fossil pine pollen and full-glacial vegetation in southeastern North Carolina. *Ecology* 45:767–777.
- Wilson MVH 1977 Middle Eocene freshwater fishes from British Columbia. *R Ont Mus Life Sci Contrib* 113:1–61.
- 1982 A new species of *Amia* from the Middle Eocene of British Columbia. *Palaeontology* 25:413–424.