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A PERMINERALIZED FLOWER FROM THE MIDDLE EOCENE OF BRITISH COLUMBIA[1]

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ABSTRACT

A permineralized flower bud, two stamen clusters and one isolated stamen of similar morphology have been found in the black cherts of the Middle Eocene Allenby Formation of Princeton, British Columbia. Specimens were studied using a modified cellulose acetate peel technique and hydrofluoric acid. The single flower specimen, 4.5 mm long and 4.0 mm in diameter, represents half of a relatively mature bud of a bisexual flower with a superior ovary. The two-loculate pistil is 2.5 mm long with a solid style and a lobed stigmatic surface. No ovules have been observed in attachment. Twenty-two to 24 stamens are borne in three whorls or a tight helix. Pollen sacs of the anther are elongate with a thin connective while filaments are laminar. Anther walls contain rectangular cells with dark contents that also can be identified in isolated stamens or stamen clusters. Abundant stephanocolpate (pentacolpate), psilate pollen grains 20 μm in diameter have been isolated and examined using scanning and transmission electron microscopy. Grains are tectate, columellate with a broad foot layer that thins near the apertures, and an endexine of small platelets. The remains of four petals are surrounded by one large sepal, suggesting two in the whole flower. Morphological features of this flower are comparable to taxa of the Flacourtiaceae and Papaveraceae, but show closest similarities to the Eschscholziaeae of the Papaveraceae. Difficulties with reconciling the placement of this flower in the Eschscholziaeae and the known environment of deposition of the Princeton chert are discussed. The fossil material represents a new angiospermous taxon: *Princetonia allenbyensis* Stockey gen. et sp. nov., family *Incertae sedis.*

PERMINERALIZED vascular plants from the Princeton chert locality in British Columbia have been described by various authors since the 1970's (Miller, 1973; Robison and Person, 1973; Basinger, 1976; Basinger and Rothwell, 1977; Rothwell and Basinger, 1979; Basinger, 1981; 1984; Stockey, 1984). Most of these studies have dealt with fossil conifers; however, the angiosperm remains have been just briefly mentioned (Basinger and Rothwell, 1977). Only a dicotyledonous rhizome of unknown affinities, *Eorhiza arnoldii* Robison and Person (1973) and a rosaceous flower, *Paleorosa similkameenensis* Basinger (1976) have been described in any anatomical detail.

Surveys of all 49 layers of the Princeton chert indicate an abundance of flowers, fruits, seeds, wood, and foliage from various angiosperm families. The present report is the first in a series of studies currently underway in our laboratory of the Princeton flowering plant remains and is based on a silicified flower bud and several isolated floral parts of well-preserved specimens with in situ pollen.

MATERIALS AND METHODS—One permineralized flower bud, two stamen clusters and one isolated stamen of similar morphology have been found in chert blocks near Princeton, British Columbia. Specimens come from the east side of the Similkameen River, 8 km south of the town of Princeton. The locality has been referred to as locality "I" (Boneham, 1968) and the "Princeton chert" (Basinger and Rothwell, 1977; Stockey, 1984). Chert deposits are part of the Princeton Group, Allenby Formation and are located 630 m above the Princeton-Black coal seam (Boneham, 1968). The Princeton Group has been dated as Middle Eocene by Wilson (1977, 1982) studying freshwater fish and Hills and Baadsgaard (1967) using K-Ar dates.

All chert blocks were cut into slabs and studied using a modified cellulose acetate peel technique and hydrofluoric acid (Basinger and Rothwell, 1977; Basinger, 1981). Peel sections were mounted in Coverbond xylene soluble mounting medium for microscopic examination. Fifty-one consecutive sections were made

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of the holotype to enable three-dimensional reconstruction (Fig. 24, 25).

Scanning electron microscopy of pollen in the anthers was done using the back side of deeply-etched peels. Peel sections were mounted on stubs with double-sided tape, covered with 150 Å Au on a Nanotek Sputter Coater and viewed at 20 kV with a Cambridge Stereoscan 250.

One small peel section was demineralized in concentrated hydrofluoric acid and washed with several changes of distilled water. The acetate matrix was then dissolved in several changes of acetone. Pollen grains and floral debris were embedded in Spurr's (1969) resin. Sections were cut with a diamond knife and collected on formvar-coated grids and viewed with a Philips EM 200 at 60 kV for transmission electron microscopy.

Comparison of floral morphology with that of extant families was done using the data set of Hansen and Rahn (1969, 1972) with the MEKA 1.1 program provided by T. Duncan and C. A. Meacham, University Herbarium, University of California, Berkeley.

Diagnosis—Princetonia allenbyensis Stockey gen. et sp. nov. Bisexual, bud of an actinomorphic flower, 4.5 mm long by 4.0 mm in diameter, with superior ovary. Pistil 2.5 mm long with two carpels; style solid, 0.7 mm long with expanded, lobed stigmatic surface. Biseriate perianth with free parts; two sepals, four petals. Stamens numerous (at least 24), in three whorls or a tight helix; filaments laminar, 0.7 mm long. Anthers elongate, 2.5 mm long with slender connective and four widely separated pollen sacs; rectangular cells with dark contents in walls of pollen sacs. Pollen 20 μm in diameter, elliptical, pentacolpate, psilate, tectate, columellate exine with thin platelets of endexine, reduced to a thin foot layer at apertures.

Etymology: The generic name is based on the locality, the Princeton chert, the specific epithet on the nearby abandoned mining town of Allenby.

Holotype specimen no. P2152 A and paratypes P1631 B bot, P2604 C bot, P3204 C bot, D top, E, and P3336 B top are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Description—The holotype specimen is one half of a relatively mature flower bud (Fig. 1). Although the initial saw blade cut passed through the center of the bud, pistil and receptacle are still visible in the first few sections (Fig. 1, 3). The bud measuring 4.5 mm long and 4.0 mm wide apparently represents a bisexual actinomorphic flower with a superior ovary (Fig. 1). However, no ovules have been observed in any sections. Although the pistil is not seen in attachment it is clearly in the right position for a hypogynous flower (Fig. 1). The pistil measures 2.5 mm long and was apparently composed of two carpels (Fig. 1, 3). Consecutive sections reveal no further partitioning of the pistil. In further sections (Fig. 3, 4) the style is seen to be solid, 0.7 mm long, and ends in a constricted region and an expanded stigmatic surface that appears to be slightly lobed (Fig. 1, 2).

The perianth is biseriate and parts are free from one another. Remains of one sepal are present (Fig. 1, 3, 6) and enclose one entire side of the flower bud (Fig. 5, 7, 8). The sepal can be distinguished from petal remains by its darker, more compact cells and the presence of scattered swollen areas (Fig. 5, 7, 8). The exact nature of these areas, 0.2 mm in diameter, is unknown; they perhaps represent glands or possible damage by fungi or insects (pre- or postburial). Due to the concave nature of floral parts and based on size and appearance of this sepal, there were probably two sepals in a complete flower. Cells of the sepal are generally crushed and not easily discernible.

Portions of three petals are present in the bud (Fig. 1, 3, 6). One concave petal is observed in a near paradermal section (Fig. 8) and is broken but nearly complete as is seen in consecutive sections (Fig. 5, 7). Sections of two other petals are seen in near median longitudinal sections of the flower. Based on floral symmetry, four petals probably occurred in the complete flower. Vascular tissue is preserved in the petals (Fig. 2, 4, 6) and in longitudinal sections the tracheids exhibit scalariform pitting (Fig. 14). Petals are composed of nearly isodiametric parenchymatous cells 30 μm in diameter and reach 10 cells in thickness in the basal regions (Fig. 4, 8).

Stamens are numerous and, due to the concave nature of the enclosing floral parts, were difficult to count. Color coding of anthers in camera lucida drawings allowed reconstruction of 22 stamens with small portions of two others. Isolated clusters of stamens of identical morphology (Fig. 10, 11) also reveal 24–27 stamens per cluster. Stamens appear to be borne in three whorls or a tight helix (Fig. 6) and probably dehisced longitudinally. Filaments are laminar (Fig. 2) and 0.7 mm long. Anthers are very elongate (Fig. 5, 9), up to 2.5 mm, and anther sacs are adnate to a slender connective. This attachment makes the four anther sacs appear widely separated in transverse sections (Fig. 5, 10, 11, 25). Walls of the pollen sacs are composed of small rectangular cells with dark contents (Fig. 16). These cells are easily distinguished in the chert in the isolated stamens and stamen clusters (Fig. 10, 11).

Numerous well-preserved in situ pollen grains occur within the anthers (Fig. 13, 16). Distinct colpi can be seen at the light microscope level (Fig. 13). Pollen grains average 20 μm in diameter, are elliptical and stephanocolpate (Fig. 17). All grains observed had 5 colpi visible in polar view (Fig. 15). Ornamentation is best described as psilate with small perforations less than 1 μm in diameter.

Transmission electron microscopy of these somewhat flattened grains reveals a tectate, columellate structure over most of the grain surface (Fig. 18–20). The exine is ca. 1.2 μm thick with a foot layer ca. 0.7 μm in thickness (Fig. 19). In regions of the aperture the exine thins to a foot layer 0.35 μm in thickness and columellae are absent (Fig. 21). The endexine of these grains is thin and irregular and appears to be composed of small platelets of material. Remains of possible tapetal material are present on some grains visible with the scanning electron microscope (Fig. 17).

DISCUSSION—Using the MEKA 1.1 program of Hansen and Rahn's (1969, 1972) data set, two families, the Flacourtiaceae and Papaveraceae, match the characters exactly. Characters used were as follows: 50, flowers bisexual; 52, flowers actinomorphic; 54, receptacle small (ovary superior); 59, disc absent; 66, perianth segments 6; 69, perianth of calyx and corolla; 72, sepals 2; 77, sepals all free from one another; 85, petals 4; 93, petals all free from one another; 109, anthers more than 10, fertile; 116, anthers opening by longitudinal slits; 120, stamens free from the corolla; 122, filaments not connate. Ten families (Annonaceae, Cunnoniaceae, Hamamelidaceae, Aquilariaceae (Aquilarioideae of the Thymelaeaceae), Capparidaceae, Euphorbiaceae, Monotropaceae, Clusiaceae, Olacaceae, Sapindaceae) differed in one character; however, since most of the features of this flower are well-known, these other families seem unlikely matches.

The family Flacourtiaceae has great floral diversity and is considered to be basal stock of the Violales (Cronquist, 1981). Usually flowers of this family exhibit numerous stamens, dithecal anthers, modified discs, enlarged receptacles, unilocular ovaries and an undifferentiated perianth (Lawrence, 1951). The variability in sepals and petals from 2–15, possession of hypogyny, perigyny and epigyny, stamens from four to numerous and 2–10 carpels with distinct or united styles (Cronquist, 1981) indicate that this family will arise frequently in the ANGIOFAM program of MEKA. (This is presumably due to the large number of plesiomorphic characters in this family.) However, the combination of characters present in the Princeton flower does not occur in any of the tribes of the Flacourtiaceae (Gilg, 1925). The Oncobeae, for example, contains *Carpotoche* Endl. with 2 (3) sepals, 4 (–12) petals, numerous stamens, long anthers and short filaments (Gilg, 1925). This genus also exhibits unilocular ovaries and four to eight separate styles. *Abatia* Ruiz et Pav., Abatieae, also has numerous stamens, and a 4–5 parted

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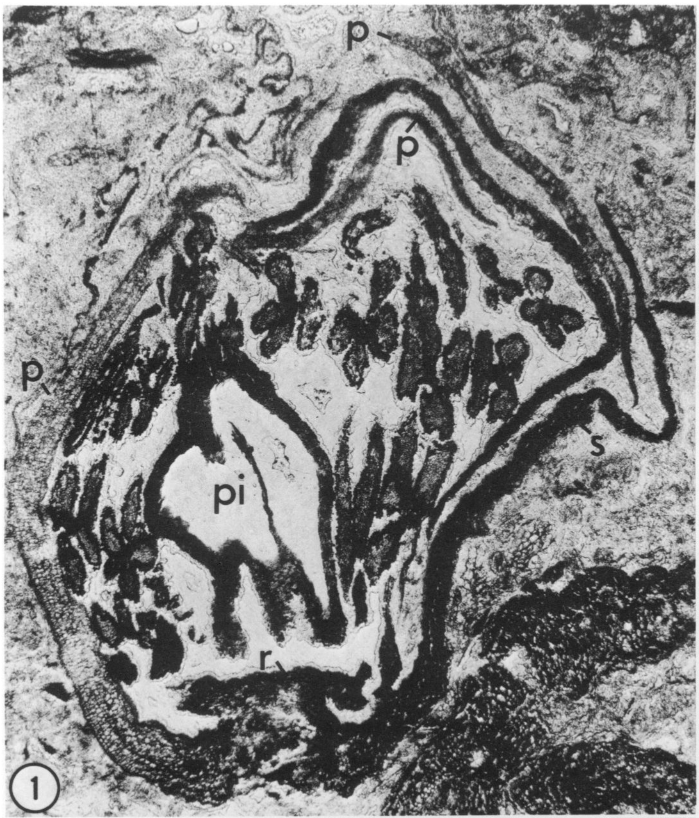
Fig. 1–4. Flower structure of *Princetonia allenbyensis* Stockey gen. et sp. nov. Holotype specimen number P2152 A. **1.** Near median longitudinal section of flower. Slide no. 0. ×23. **2.** Stamens showing broad laminar filaments. Arrows indicate vascular strands in the petal. Slide no. 7. ×49. **3.** Longitudinal section through pistil showing two locules. Slide no. 1. ×23. **4.** Longitudinal section through solid style and petal. Arrow indicates vascular strand. Slide no. 5. ×30. f, filament; p, petal; pi, pistil; r, receptacle; s, sepal; st, style.

Fig. 5–11. *Princetonia allenbyensis* Stockey. **5.** Tangential section of flower bud showing one sepal and one petal enclosing several stamens. Remains of a second petal visible, top right. Arrows indicate swollen areas (fungi?) in sepal. P2152 A Slide no. 31. ×23. **6.** Tangential section of flower bud showing helical arrangement of stamens. P2152 A Slide no. 16. ×23. **7.** Tangential section of one sepal and one petal with remains of two stamens. Arrow indicates swollen area (fungi?). P2152 A Slide no. 47. ×25. **8.** Paradermal section of petal with surrounding sepal. Arrow indicates swollen area (fungi?). P2152 A Slide no. 51. ×25. **9.** Longitudinal section of stamen showing elongated pollen sacs of the anthers. P2152 A Slide no. 10. ×30. **10.** Clump of isolated stamens. P2604 C bot Slide no. 0. ×10. **11.** Isolated anthers. P2604 D top Slide no. 0. ×13. p, petal; s, sepal.

Fig. 12–17. *Princetonia allenbyensis* Stockey. Holotype specimen no. P2152 A. **12.** Longitudinal section of stigma and style. Slide no. 7. ×130. **13.** Anther with numerous colpate pollen grains. Slide no. 7. ×310. **14.** Longitudinal section of vascular bundle in petal showing secondary wall thickenings. Slide no. 51. ×390. **15.** Polar view of pollen grain showing five colpi. ×5,400. **16.** Longitudinal section of anther showing pollen grains and dark contents in cells of the pollen sac wall. Slide no. 7. ×150. **17.** Lateral views of several pollen grains showing colpi and possible remains of tapetal material. ×1,600.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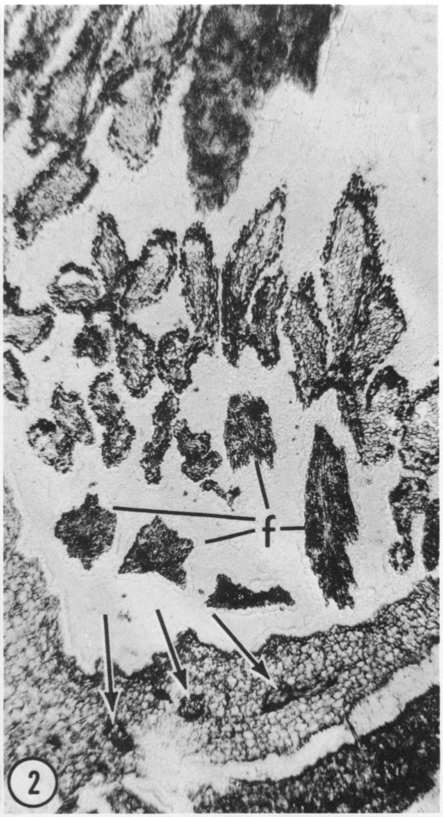
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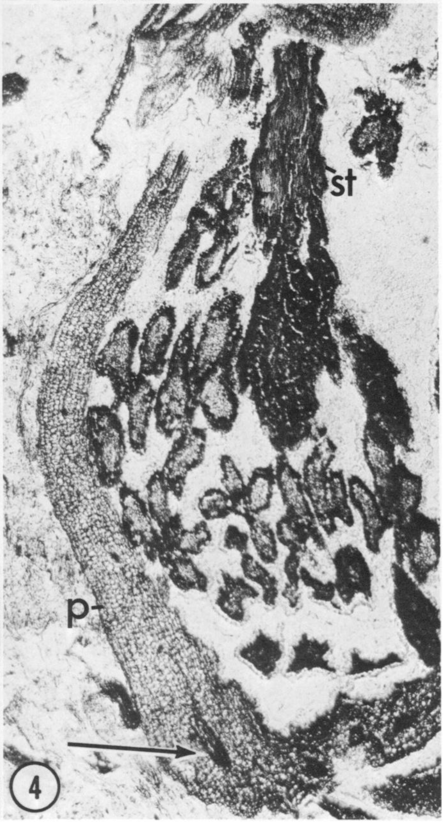
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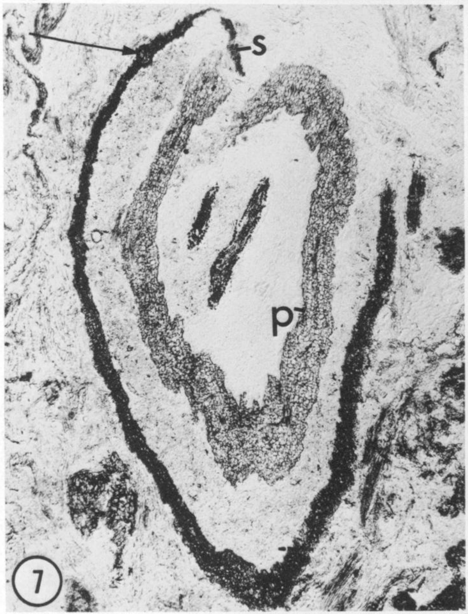
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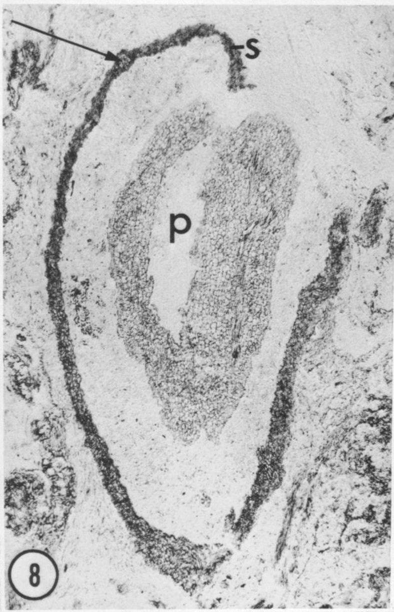
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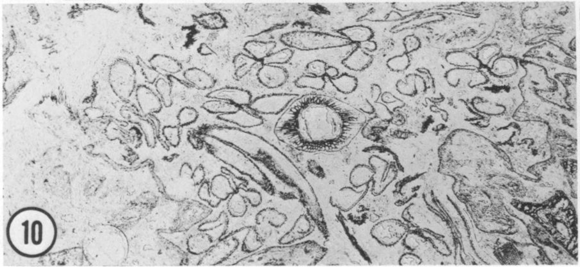
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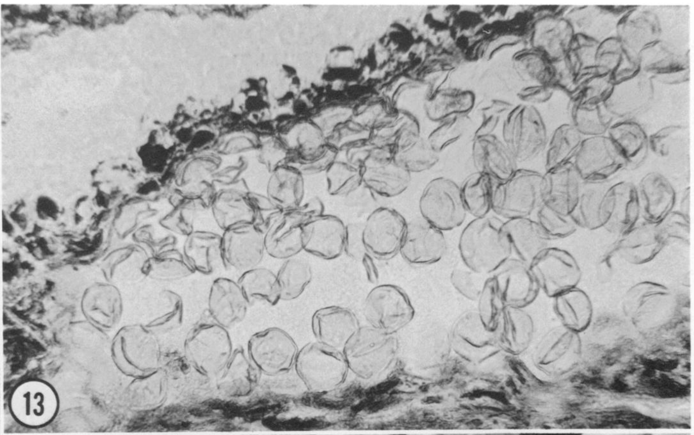
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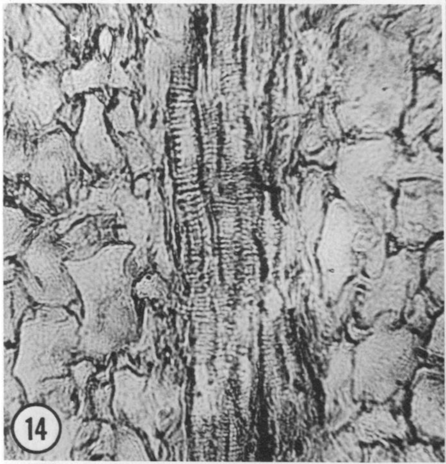
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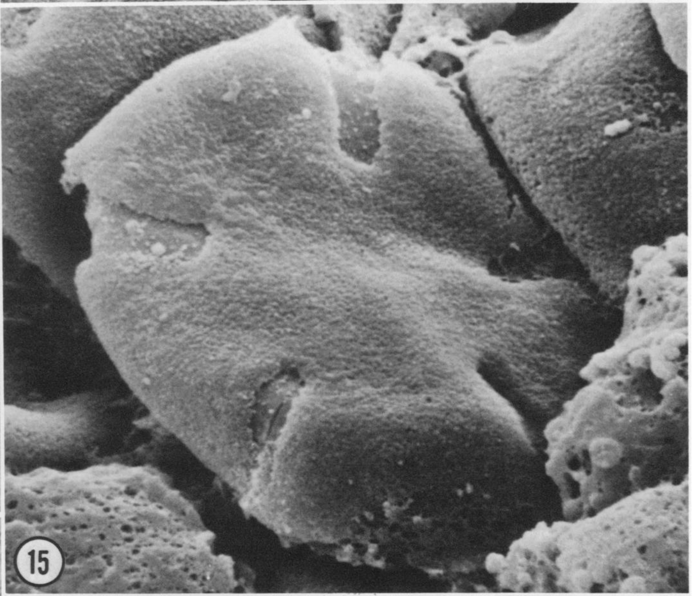
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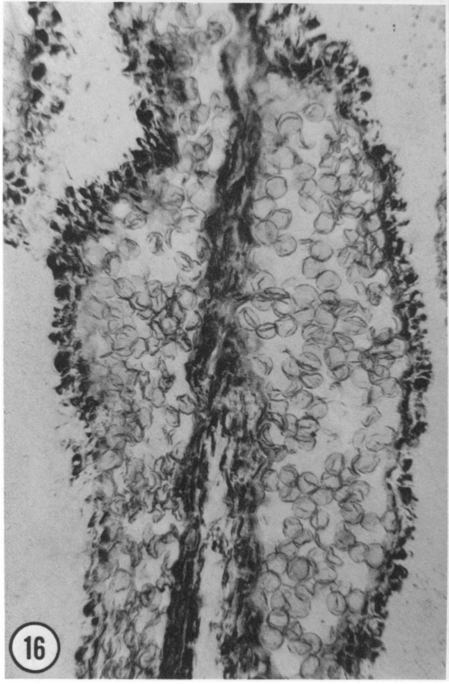
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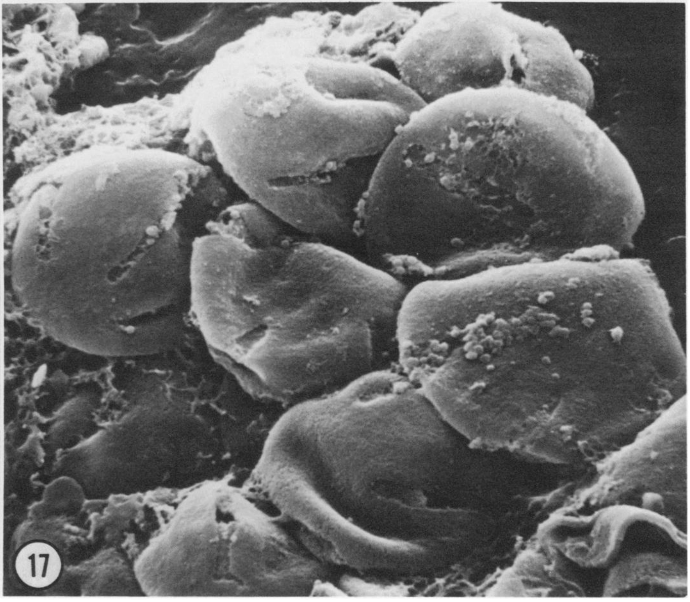
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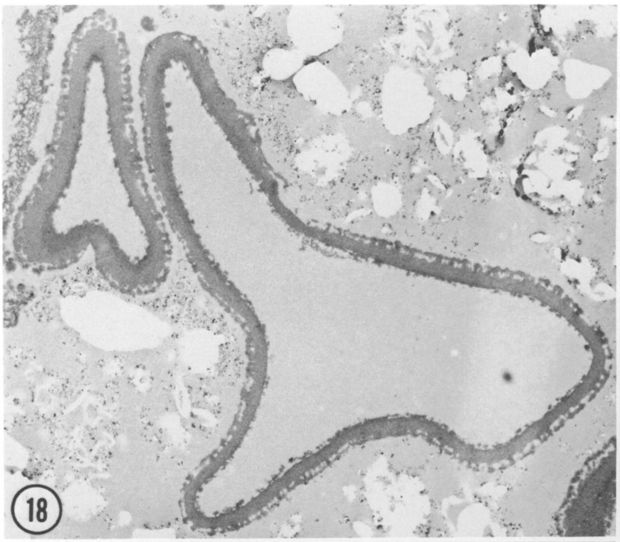
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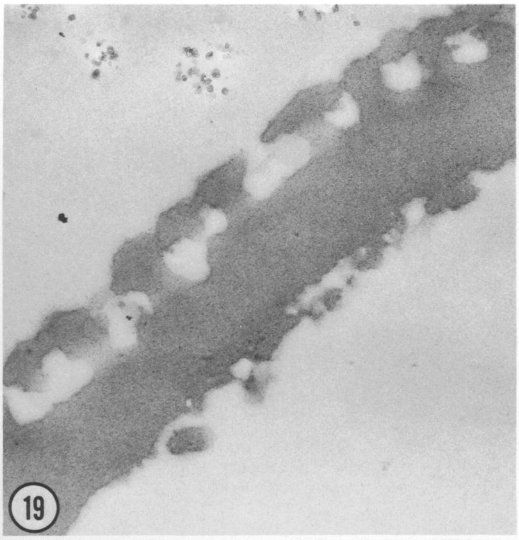
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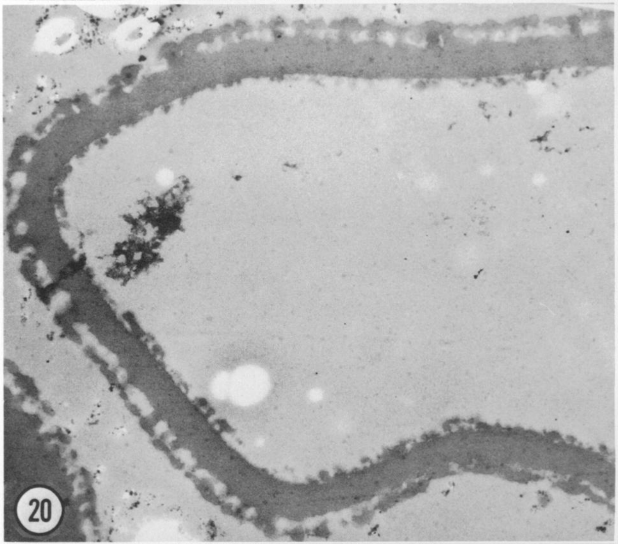
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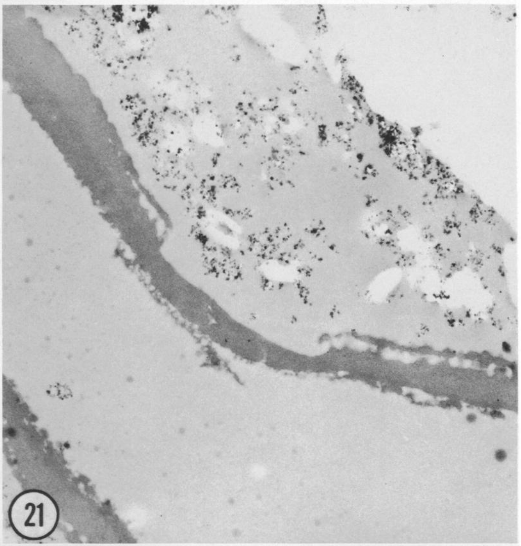
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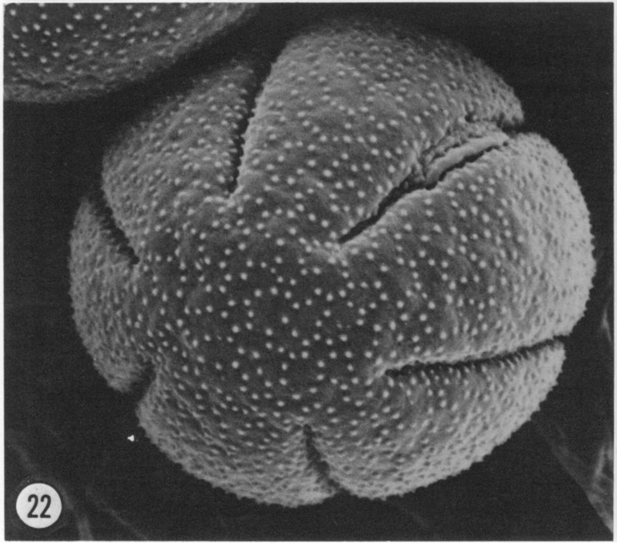
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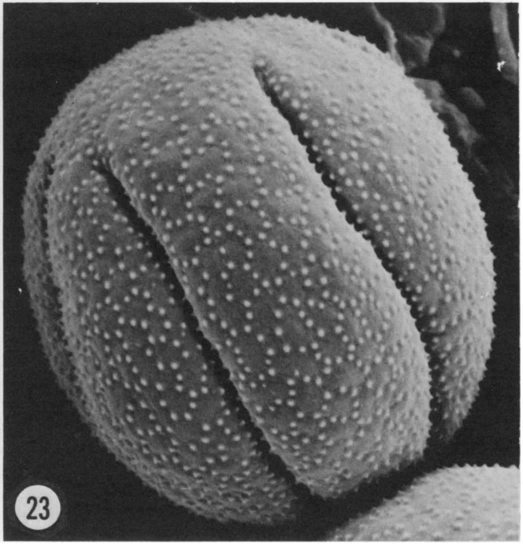
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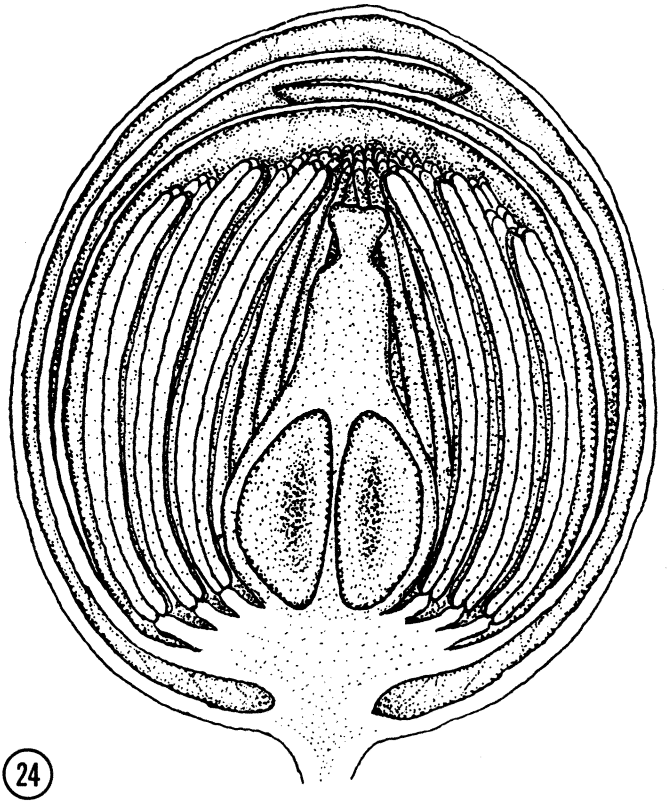

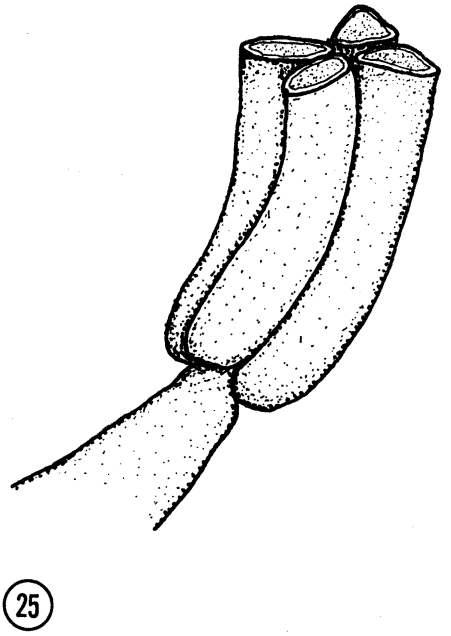

Fig. 24, 25. Reconstructions of *Princetonia allenbyensis* Stockey. **24.** Longitudinal section of flower bud. ×20. **25.** Broad filament and widely separated anther sacs. ×60.

calyx. The corolla, however, in this tribe is absent and ovaries unilocular. In *Flacourtia* (Comm.) L'Hérit. (Flacourtiaeae), the calyx is 4–5 parted and stamens numerous; however, anthers are short with respect to the filaments and pistils show 2–6 short stigmas. Those flacourts with two-loculed ovaries (e.g., Casearieae) have few stamens. Those with many stamens (e.g., *Flacourtia*) usually have short anthers and lack a corolla (Gilg, 1925). Thus, the combination of characters does not match with any living group of flacourts.

With respect to pollen morphology, the Flacourtiaceae is usually triaperturate (Keating, 1973, 1975). However, 4 or 5 apertures have been reported (Cronquist, 1981). Exine ornamentation varies from psilate, verrucate, semitectate, to baculate (Keating, 1973). Comparisons at the level of transmission electron microscopy show that the endexine is prominent in flacourts and thick under the colpus, and that the foot layer, in general, is thinner than in the Princeton pollen (Keating, 1973, 1975, and personal communication).

In the Papaveraceae the tribe Platystemoneae (*Platystemon* Benth.) has stamens with laminar filaments; however, numerous pistils with abundant hairs occur in *Platystemon* unlike those in the fossil flower (Fedde, 1936). The closest similarities in floral structure occur with the tribe Eschscholzieae that show numerous stamens, 2 sepals, 4 petals, superior ovaries and 2 carpels (Fedde, 1936). *Dendromecon* Benth. exhibits elongated anthers and

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Fig. 18–23. Pollen of *Princetonia allenbyensis* Stockey (18–21) and *Eschscholzia caespitosa* Benth. (22, 23). **18.** Section through pollen of *Princetonia allenbyensis* Stockey. ×4,964. **19.** Section through grain wall showing solid foot layer, columellae, and a perforate tectum. ×18,700. **20.** Section of tectate grain wall. ×12,200. **21.** Section through aperture region showing absence of columellae and tectum. ×11,400. **22.** Polar view of pollen of extant *Eschscholzia caespitosa* Benth. ALTA 57606. ×2,700. **23.** Lateral view of pollen of extant *Eschscholzia caespitosa* Benth. ALTA 57606. ×2,800.

short filaments (Fedde, 1936). *Hunnemannia* Sweet, however, unlike the fossils, shows a ribbed pistil. *Petromecon* Greene (*P. palmeris* is usually treated as a species of *Eschscholzia*) shows 80 or more stamens per flower with elongated filaments (Fedde, 1936). The genus *Eschscholzia* Cham. also shows anthers longer than filaments and calyptrate, connate sepals. Thus, within the family Papaveraceae, and within the tribe Eschscholzieae in particular, the actinomorphic flowers with large sepals, numerous stamens in several whorls, and two carpels (Fedde, 1936) show better combinations of similar characters to the fossil than the flacourts.

Pollen morphology in the Papaveraceae is extremely variable. Bicolpate, tricolpate, pericolpate, hexaporate, stephanocolpate, and inaperturate grains, e.g., have all been reported (Layka, 1973, 1976). The Eschscholzieae exhibit 3–10 colpi. Four and five colpi are common in *Dendromecon* species (3–6 occur). Grains of *Petromecon* (6–9) and *Hunnemannia* (9–12) have large numbers of apertures. *Eschscholzia* (3–10) commonly show 4–7 colpi (Fig. 22, 23; Layka, 1976). The endexine in this tribe usually shows small "plaques" of material that are irregular in shape (Layka, 1976). This type of structure is not unlike that seen in the fossil pollen grains. Exine ornamentation in this tribe, however, is usually reticulate (Layka, 1973, 1976). The pollen of *E. caespitosa* Benth. illustrated here (Fig. 22, 23) shows 7 colpi and small supratectal verracae in a reticulate pattern. The 11 species studied by Layka (1976) were reticulate with verrucae or spines on the reticulum.

The fossil record of the Flacourtiaceae is better than that of the Papaveraceae. The pollen record of flacourts extends back only to the Oligocene (Muller, 1981) where *Casearia*-type pollen has been described (Graham and Jarzen, 1969). Previous claims of Middle Eocene papaveraceous pollen, however, have been rejected by Muller (1981). Fossil fruits and seeds of *Oncoba variabilis* (Bowerbank) Reid and Chandler and *O. rugosa* Chandler (Flacourtiaceae) have been described from the lower Tertiary of southern England (Reid and Chandler, 1933; Chandler, 1961, 1962, 1964). These fruits, however, are ovoid to globular and subspherical, lobed, unilocular, large (up to 30 mm) and have a warty external surface.

The Eschscholzieae are plants that usually grow in arid or semiarid regions of North America, e.g., California, Texas, and Mexico. The habitat most likely responsible for the preservation of the Princeton chert, however, is probably that of a small lake or pond. The presence of turtle bones (R. C. Fox, personal communication), fish (M. V. H. Wilson, personal communication) and aquatic or semiaquatic plants (Robison and Person, 1973; Basinger and Rothwell, 1977; Cevallos-Ferriz, 1987) point to this conclusion. Although flowers of the *Princetonia*-type are rare in the chert, compared to the numerous araceous, lythraceous and nymphaceous remains and they may have washed into the basin from higher ground, delicate floral structures with intact stamens could not have travelled far from their actual growth habitat. It is possible that this simple psilate, stephanocolpate grain type was produced by a primitive semiaquatic papaveraceous plant with small flowers that showed close structural similarities to the Eschscholzieae. However, these floral organs may have also been produced by an extinct family of angiosperms.

The scarcity of these remains in the chert has yet to be explained by growth habitat or preservation. At the present time, with only isolated floral organs, these remains are believed to be most closely related to the Eschscholzieae of the Papaveraceae. Until further information is gathered with respect to the other vegetative remains in the chert, however, a family assignment is precluded. As more angiosperm material is being identified from the Princeton chert based on flowers, fruits and seeds, we hope to gain a greater understanding of the angiosperm families present by the Eocene and their evolution.

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