American Journal of Botany 96(3): 637–651. 2009.

ANATOMY AND DEVELOPMENT OF FRUITS OF LAURACEAE FROM THE MIDDLE EOCENE PRINCETON CHERT[1]

STEFAN A. LITTLE,[2] RUTH A. STOCKEY,[2,4] AND BONNIE PENNER[3]

[2]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada; and
[3]Department of Botany, University of Manitoba, Winnipeg, Manitoba, R3T 2N2 Canada

Investigations of the Middle Eocene Princeton Chert reveal evidence for the connection of lauraceous flowers to fruits through a developmental series. Youngest fruits are found with attached floral remnants. Later stages show receptacle enlargement, fruit wall thickening, and the development of abundant sclereid clusters. Mature fruits are borne on a shallow receptacle and have an endocarp palisade layer of radially elongate cells with stellate outlines, an inner mesocarp layer of radiately arranged sclereid clusters, and a fleshy outer mesocarp layer containing numerous idioblasts with contents. Each mature fruit bears a single seed retaining the outer integument with an innermost radially elongate transfusion cell layer. Mature seeds contain a cellular embryo bearing idioblasts. Fruits are distinguishable from previously described anatomically preserved fossil taxa. This study represents the only documented developmental reconstruction of fossil fruits of Lauraceae and that self-pruning evolved prior to the Eocene. Anatomical modifications over the developmental sequence indicate that different stages of maturity preserved together, may be erroneously identified as several taxa at a fossil locality. Fossil morphotypes typically underestimate species number, but this study suggests that the number of inferred species based on fruit types may be inflated for Lauraceae, potentially exaggerating the tropical interpretation of the paleoenvironment.

Key words: Eocene; fossil fruit; fruit development; Lauraceae; Princeton Chert.

Lauraceae, a large pantropical family mainly composed of large trees or shrubs, consists of approximately 53 genera and 2500–3000 species, with much of the known diversity described from the neotropics (Meissner, 1864; Pax, 1891; Kostermans, 1957; Hutchinson, 1964, Rohwer, 1993, 1994). Molecular phylogenetic studies clearly show the monophyly of the family (Renner, 1998, 1999), and while intergeneric relationships in Lauraceae are becoming established (Rohwer, 2000; Chanderbali et al., 2001; Rohwer and Rudolph, 2005), generic circumscriptions are plagued by polyphyly (Chanderbali et al., 2001; Li et al., 2004). The family is largely characterized by trimerous flowers, bi- or tetrasporangiate anthers with apical valvate dehiscence, and a unicarpellate gynoecium containing a single anatropous, apically attached ovule (Cronquist, 1981; Heo et al., 1998). Fruits of the family are fleshy, typically black to almost black at maturity (Roth 1977) and usually borne on enlarged receptacles that can form cupulate to fully enclosing structures (Kostermans, 1957; Hyland, 1989; Rohwer, 1993). Roth (1977) acknowledges that fruits of Lauraceae are typically considered drupes, but are better classified as a berry since the "endocarp" is only made up of a thin, single-celled sclerified endodermis. Oil or mucilage idioblasts occur throughout the plant tissues, including the wood (Baas and Gregory, 1985). Anatomy and development are well known in *Persea americana* Mill., the avocado (Roth, 1977), but detailed studies of fruits are few in comparison to the number of species in the family (Corner, 1976; Roth, 1977).

The diverse fossil record of Lauraceae begins in the Cretaceous and includes flowers, fruits, leaves, and wood (Drinnan et al., 1990; Herendeen, 1991; Kvaček, 1992; Herendeen et al., 1999; Crane et al., 1994; Eklund and Kvaček, 1998; Mickle, 1996; Frumin et al., 2004). Fruits and cupulate structures commonly occur throughout the fossil record (Chandler, 1964; Mai, 1971, 1999, 2001; Manchester, 1994; Pingen et al., 1994; Eklund, 2000; Frumin et al. 2004), but few are known anatomically, with some exceptions (Drinnan et al., 1990; Eklund and Kvaček, 1998; Frumin et al., 2004). Numerous lauraceous fruits in the Cenozoic are assigned to extant genera, often based on cupule morphology alone (Chandler, 1964; Mai, 1971), but these assignments are have been questioned because similar cupule morphology occurs in several genera (Kostermans, 1957; Chandler, 1978; Rohwer, 1993; Pingen et al., 1994). Anatomically preserved fruits have been documented, but further systematic surveys are required in the family to test the accuracy of generic identifications (Chandler, 1978; Manchester 1994; Pingen et al., 1994).

This study describes lauraceous fruits first identified by Penner (1996; Little and Stockey, 2003) from the Middle Eocene Princeton Chert. Over 100 specimens were observed at various developmental stages, and this developmental series reveals a sequence from isolated lauraceous flowers, post anthesis, (Sun and Stockey, 1991; Little and Stockey, 2006b) to mature fruits. Thus far, this work is the only known investigation of the development of fossil fruits of Lauraceae, made possible by the parautothochtonously deposited, subcanopy litter of a self-pruning fruit tree.

We show that fossil fruit identification, due to the copreservation of various stages of maturity at a given locality, may overly inflate the number of species of Lauraceae. Fossil morphotypes typically underestimate actual species number, and since high numbers of Lauraceae are indicative of tropical environments (Pole, 2007), inference of a tropical environment may be spurious if based on abundance of Lauraceae fruit types (e.g., Mai, 1971).

---

[1] Manuscript received 19 September 2008; revision accepted 11 November 2008.

The authors thank Dr. M. Summer, University of Manitoba, for the use of paleobotany facilities. This research was supported in part by NSERC grant A6908 to R.A.S., NSERC Canadian Graduate Scholarship to S.A.L., and the Department of Biological Sciences, University of Alberta.

[4] Author for correspondence (e-mail: ruth.stockey@ualberta.ca); phone: 780-492-5518; fax: 780-492-9234

doi:10.3732/ajb.0800318

MATERIALS AND METHODS

Fossil plant remains come from the Princeton Chert locality, part of the Princeton Group, Allenby Formation (Boneham, 1968). The chert crops out on the east bank of the Similkameen River, ca. 8.4 km southwest of the town of Princeton, British Columbia (UTM 10U FK 786725; 49 22′33″N, 120 32′18″W). At least 49 interbedded layers of chert and coal occur, with occasional ash layers (Stockey, 1983; Cevallos-Ferriz et al., 1991). Several of the chert layers split and anastomose, so that ca. 70 separate chert layers are observed in some places along the 10 m high and 30 m long exposure (S. A. Little and R. A. Stockey, personal observation). The locality is dated as Middle Eocene, based on data from pollen (Rouse and Srivastava, 1970), fossil mammals (Russell, 1935; Gazin, 1953), fish (Wilson, 1977, 1982), and potassium-argon dating (Hills and Baadsgaard, 1967). A newer date of 48.7 Ma was more recently obtained for ash layer #22 (H. Baadsgaard, University of Alberta, personal communication).

Chert blocks, containing permineralized plants, were collected in bulk, slabbed on an oil-cooled rock saw, and prepared using the cellulose-acetate peel technique (Joy et al., 1956) modified for hydrofluoric acid (Basinger and Rothwell, 1977; Basinger, 1981). Each specimen was assigned an alphanumeric ID (i.e., P1234 B b). Sequential peels of that specimen were numbered starting with #0, #1, #2, and so forth (i.e., P1234 B b # 25). All fossil specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA). The specimens figured, as well as additional specimens examined for study of the developmental series, are: P1013 B bot a-c, P1013 B side a-c, P1013 B top a-c, P1013 B_2 top a- c, P1013 B_3 top a-f, P1013 C_2 top a, P1013 C side a-b, P1013 D_1 bot a-b, P1013 D_1 top a-c, P1060 D bot a-i, P1060 E bot b-d, P1060 G a-f, P1067 D bot a, P1089 C side a-b, P1089 C_2 top a-b, P1095 D_2 bot a-b, P1105 B bot a-c, P1105 B top a-e, P1105 D bot a-c, P1114 C bot a, P1187 B top a, P1187 C top a-c, P1187 D bot a-b, P1187 D top a-f, P1195 D bot a-b, P1195 D_1 top a-g, P1213 D_2 bot, P1255 B top a, P1255 D_1 a, P1258 G top a, P1269 B_1 top a, P1287 A a, P1287 B a, P1288 B top a-e, P1291 B a, P1312 B bot a-b, P1312 B_2 a-b, P1312 C bot a-b, P1312 C top a-c, P1312 D top, P1312 D bot, P1312 D_3 side, P1326 D_1 bot a, P1326 E_2 bot a, P1326 F_2 top a, P1372 A a, P1372 B a-b, P1377 D bot a, P1377 D top a, P1384 D1 bot a.

At least 111 fruits at various stages of maturity were examined. Sections of consecutive peels were mounted with Eukitt rapid mounting medium (O. Kindler, GmbH, Freiburg, Germany) for light microscope examination. Images were taken with a Microlumina (Leaf Systems) digital scanning camera and a Phase One digital scanning camera (Phase One A/S, Frederiksberg, Denmark) using a Leitz Aristophot and processed using Adobe (San Jose, California, USA) Photoshop. Characters were analyzed, in part, using the Delta Key program (Watson and Dallwitz, 1992).

RESULTS

Overall sequence of development—Flowers (Fig. 1A, 1B) after anthesis (Figs. 1C–E, 2), immature fruits (Figs. 3–5), and mature fruits (Fig. 6) including isolated seeds with adhering pericarp remnants are preserved and represent a sequence of developmental stages that show increasing carpel size and changes in anatomy. Isolated flowers are 0.5–0.8 mm in diameter, including the surrounding perianth. Carpels are 0.6–0.8 mm in diameter in early fruit development, 1.6–1.9 mm in immature fruits, 2.0–3.4 mm in late-immature fruits, and 5–8.0 mm in mature fruits. Although the epidermis is well preserved, stomatal complexes were not observed due to the oblique view of the epidermis in sections of these globose fruits. However, internal tissue differentiation and overall enlargement of fruits is observed well along the continuum of maturation preserved. Several distinct developmental stages are described separately next based on anatomical features.

Flowers and early fruit development—The earliest stages of maturity are represented by flowers with stamens and tepals present (Figs. 1A, 1B; Sun and Stockey, 1991). The trimerous, pedicellate flowers bear a single carpel and have an innermost, extrorse androecial whorl and two outer, introrse androecial whorls (Fig. 1A, 1B). Two whorls of tepals surround the stamens, and trichomes are present on the tepals and hypanthium (Fig. 1A), but are absent from the surface of the gynoecium (Fig. 1B, 1C). The carpel is enlarged (Fig. 1C, 1D), a single apical ovule is visible, and tepals remnants persist (Fig. 1C, 1D, arrowheads). The style is narrow and about the same length as the ovary (Fig. 1D, 1E).

Well-preserved ovules are observed inside carpels of some specimens (Fig. 2). These "late flowers" lack surrounding floral parts, but retain tepal remnants. Unicellular trichomes with simple bases occur on the receptacle and tepal remnants (Fig. 2A, 2B). Carpel/fruit wall (FW) contains idioblasts; inner and outer epidermis are composed of short cells with rectangular outlines in longitudinal section (Fig. 2C). A single elongate embryo sac (ES) within the nucellus (N), and two integuments are present (Fig. 2C). The inner integument (II) is 2–4 cells thick, and the outer integument (OI) is 5–10 cells thick (Fig. 2C).

Immature fruit stage—Later developmental stages bear enlarged ovules and thicker fruit walls compared to previous stages of maturity (Fig. 3). Styles are visible as apical prominences on the enlarged carpels (Fig. 3A). The pericarp shows some cellular differentiation and vascular strands are now visible in the inner fruit wall (IFW; Fig. 3A, 3E). Cells of the inner fruit wall are often filled with dark contents (Fig. 3B). In longitudinal section the innermost cell layer of the fruit wall (Pa) is composed of rectangular cells, similar to those of the outer epidermis (Fig. 3A, 3B, 3D). This innermost layer has cells with somewhat wavy outlines in transverse (Fig. 3D) and oblique section (Fig. 3B, 3D). The mesocarp contains thin-walled cells and idioblasts (Fig. 3A–C, 3E).

The apical ovule is more enlarged at this stage compared to earlier stages and the inner integument, present in earlier developmental stages, has disappeared (Fig. 3B, 3C). The outer integument (I) is uniform, ca. 10 cells thick (but appears thicker in oblique planes of section) (Fig. 3A, 3E). Vascular strands occur throughout the integument, and cellular embryo tissue fills the seed cavity (Fig. 3A, 3E).

Receptacles are thickened, forming a shallow cupule (Fig. 3C). Sclereid clusters are seen at the base of the carpel and in the cupule of some specimens (Fig. 3C). Tepal remnants and trichomes are still present at this stage of development (Fig. 3C, arrowhead).

Late immature fruit stage—Most lauraceous fossil fruits from the Princeton Chert locality are found at a stage of late immaturity (Figs. 4, 5). Fruits are further enlarged compared to fruits at previous stages and are ovate to ellipsoid, with apical stylar protrusions (Figs. 4A, 4B, 5A, 5B). Cupules, when seen attached to fruits, are shallow (Figs. 4A, 4B, 5E). Cupules are composed of thick-walled cells and abundant idioblasts (Figs. 4A, 4B, 5E). Tepal remnants and trichomes are generally absent (Fig. 4A, 4B). However, some tepal remnants occur on a few specimens (Fig. 5E, arrows).

Inner fruit wall cell layers (IFW) contain dark cell contents (Figs. 4A, 4B, 4E), and vascular strands are found below sclereid clusters in the mesocarp. A central idioblast is often present in the center of sclereid clusters (Figs. 4A, 4B, arrows; 4C, 5D). The epicarp/epidermis is more radially elongate compared to that in more immature fruits (Fig. 4C, 4E). The inner fruit epidermis is now radially elongate, forming the endocarp palisade layer (Pa; Figs. 4E, 5F); cell outlines are stellate in transverse section (Fig. 4D). The endocarp palisade is discontinuous in some specimens, but this appears to be mechanical cell damage

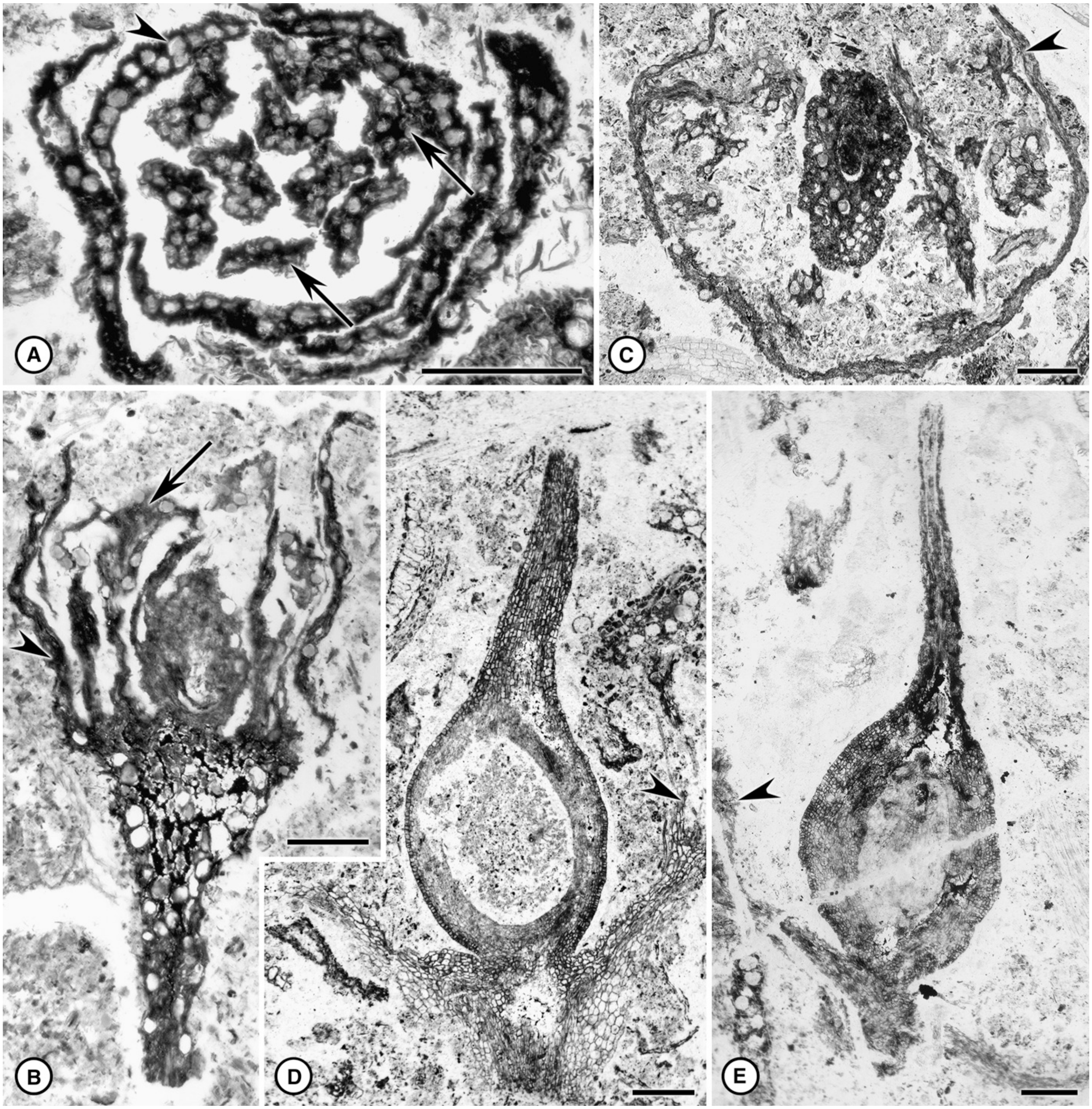

Fig. 1. Princeton Lauraceae, flowers and early fruit development. Scale bars = 0.2 mm. (A) Flower in transverse section showing nine anthers (arrows), two whorls of tepals (arrowhead), and bracts. Trichomes occur on tepals and bracts (at right). Gynoecium out of plane of section. P1060 E bot #1, ×136. (B) Flower in longitudinal section with shallow hypanthium, tepals (arrowhead) and stamens (arrow). Gynoecium at center containing single apical ovule. P1213 D_2 Bot #1, ×69. (C) Oblique section through late flower, with stamens and attached tepals (arrowhead). Ovary swollen, containing single apical ovule. P1326 E_2 bot #5, ×51. (D) Transverse section of late flower/early fruit with attached receptacle, tepals (arrowhead at tepal), and swollen ovary with long style. P1060 D bot #6d, ×53. (E) Transverse section of late flower/early fruit with attached receptacle, tepals (arrowhead at tepal), and swollen ovary with long style. Ovary contains developing seed. P1060 G #50, ×48.

prior to preservation rather than a developmental feature (Figs. 4A, 4E, 5C, 5D [arrow], 5E). Idioblasts are more abundant in the outer fruit wall (FW) at this stage of development compared to previous stages of maturity (Figs. 4A–C, 4E, 5D).

The single remaining seed integument appears proportionately thinner than at earlier stages of maturity due to the enlargement of the fruit and remains ca. 10 cells thick (Fig. 5F) (appearing thicker in oblique sections; Figs. 4E, 5A, 5B). Cells

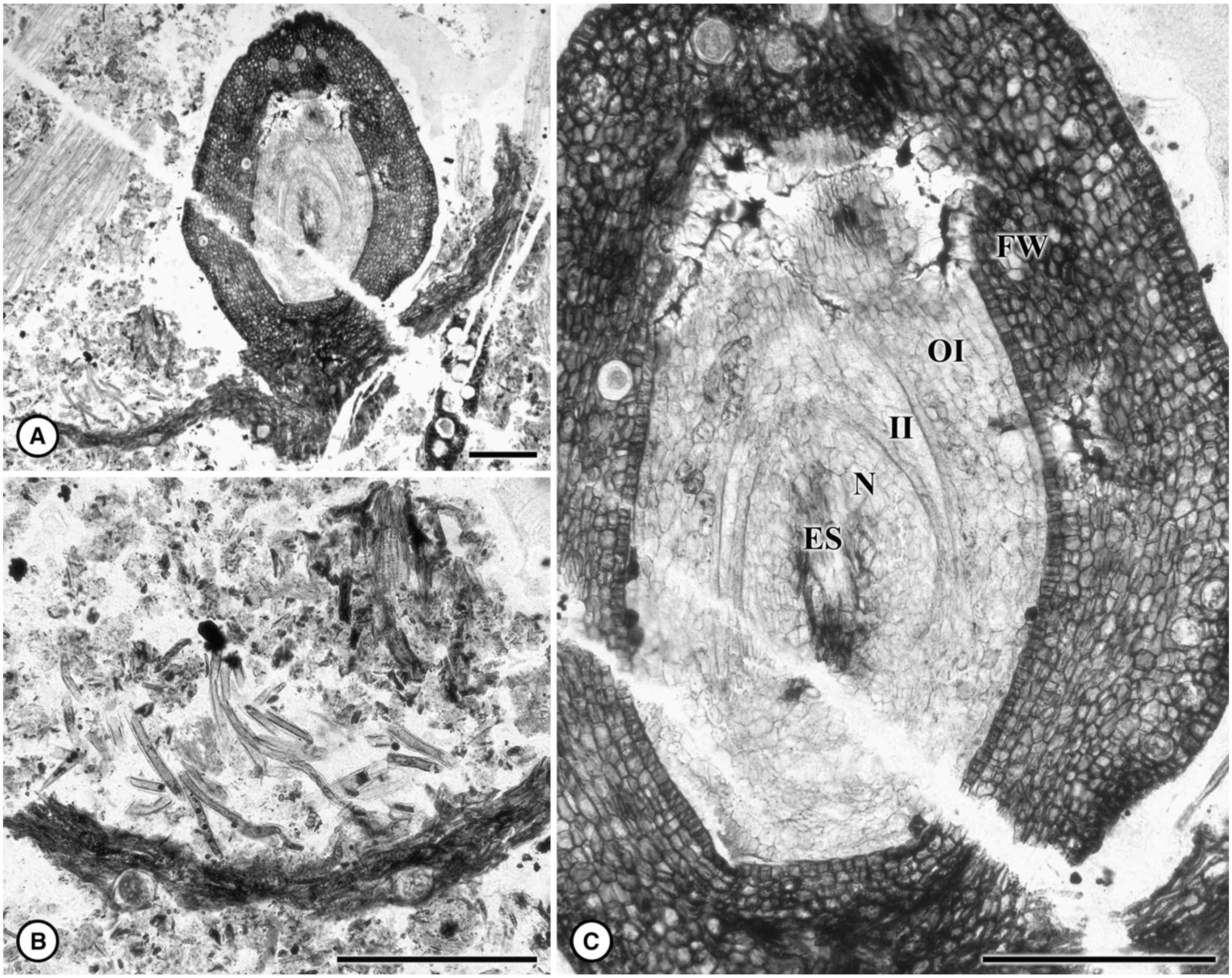

Fig. 2. Princeton Lauraceae, early fruit development. Scale bars, A and C = 0.2 mm, B = 0.1 mm. Longitudinal section through late flower/early fruit, from same peel series as in Fig. 1E. Style is out of plane of section, P1060 G #64. (A) Early fruit in longitudinal section containing developing seed. Receptacle and tepals bear trichomes. ×51. (B) Enlarged view of unicellular trichomes on tepal. ×300. (C) Enlarged view of fruit wall (FW) containing idioblasts. Inner and outer epidermis of pericarp composed of short rectangular cells. Developing seed fills fruit cavity, outer integument (OI) thicker than inner integument (II); nucellus (N) at center containing elongate embryo sac (ES). ×175.

of the integument are filled with dark contents, and the innermost cell layer is radially elongate (Figs. 5A, 5B, 5F), forming the "transfusion layer" (sensu Kasapligil, 1951; Corner, 1976) (not clearly visible in oblique sections, Fig. 4E). Dark contents in cells of the integument obscure the vascular strands that are present throughout. The apical region of the endocarp palisade layer, associated with apical ovule attachment, is narrow and forms what would appear as a ridge if viewed externally (Fig. 5A, 5B). This apical ridge extends toward the epidermis and appears beak-like in longitudinal sections (Fig. 5A, 5B, arrows).

Mature fruit stage—Mature fossil fruits are the rarest in the chert. They are the most enlarged (up to 8 mm in diameter), globose, and may have a slight apical protrusion, a minor remnant of the style (Fig. 6A). Cupules are rarely found attached at this stage of development, but when present, appear shallow as in the previous stage of maturity as described earlier.

Exocarp/epidermis of the fruit is similar to that in the previous stage of development, with a slightly radially elongate cell outline in both longitudinal and transverse section view (Fig. 6C). Fleshy mesocarp forms a relatively thin layer, often incomplete/abraded, and surrounds the inner fruit layers (Fig. 6A, 6C). Tissues of the fruit wall (FW) contain thin-walled cells and idioblasts, similar to those seen in the previous stage of development (Fig. 6A, 6C). The sclereid clusters (Sc), seen in the previous stage of development, are larger in size and now abut one another, forming a more or less contiguous, thick layer (Fig. 6). Cell arrangement in the sclereid clusters is distinctive: radiate/stellate (Fig. 6B, 6C). The innermost zone (IFW) of the mesocarp also appears similar to that seen in the previous stage of development, containing vascular strands and cells with dark contents (Fig. 6). The palisade layer is also similar to that seen in the previous developmental stage.

The seed is also enlarged, but the integument/seed coat is the same thickness as in the previous stage of development

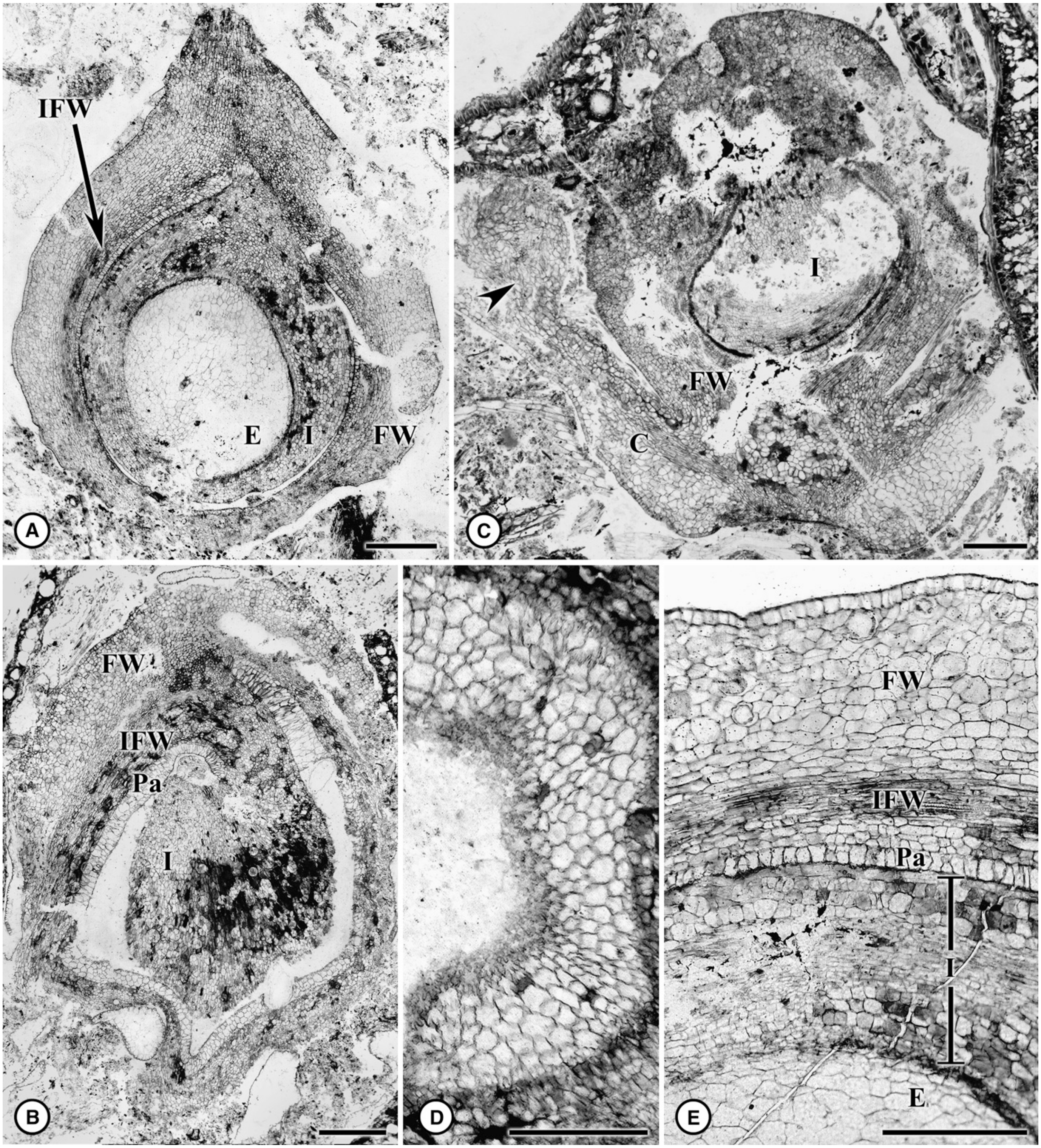

Fig. 3. Princeton Lauraceae, immature fruit stage. Scale bars = 0.3 mm. (A) Longitudinal section, fruit wall (FW), stylar remnant at top, inner fruit wall (IFW) dark, seed with single (outer) integument (I), containing embryo (E). P1095 D_2 bot #0, ×42. (B) Oblique longitudinal section, tangential view of integument (I), oblique view of inner epidermis/future endocarp palisade (Pa). Funiculus at top, dark contents and vascular strands in inner fruit wall (IFW), outer fruit wall (FW) with thin-walled cells. P1288 B_1 top #12, ×40. (C) Longitudinal section with attached cupule (C), tepal remnants (arrowhead), fruit base contains some sclereids. Integument (I) in tangential view. P1187 B top #20, ×38. (D) Inner epidermis/future endocarp palisade layer, same peel series as in (B). Thin-walled cells are polygonal to stellate (at center) P1288 B_1 top #1, ×82. (E) Embryo (E) filling seed cavity, outer integument (I), inner epidermis/future endocarp palisade (Pa) adjacent to seed, inner fruit wall (IFW) contains vascular strands, and outer fruit wall (FW) of thin-walled cells and idioblasts. P1095 D_2 bot #0, ×86.

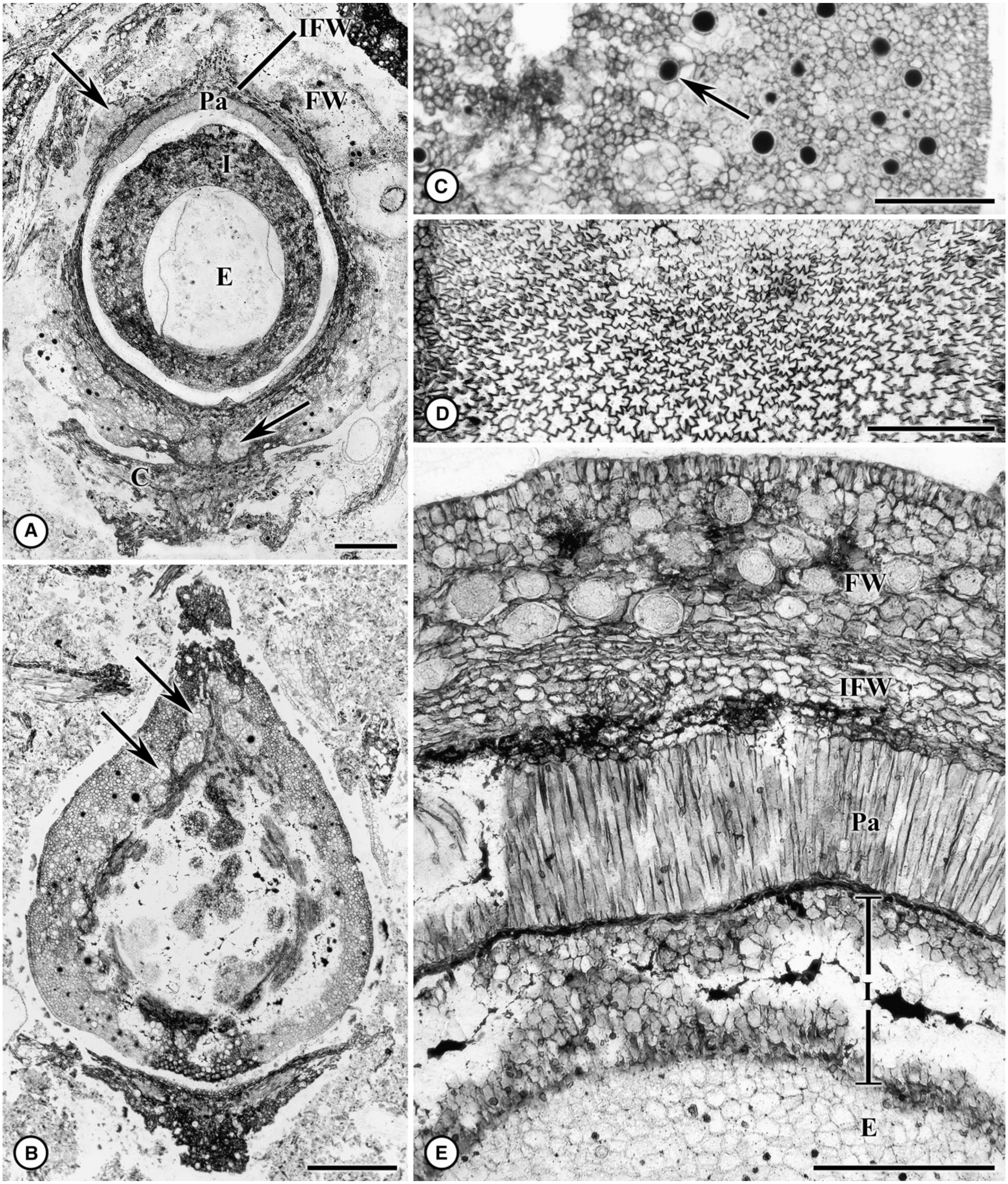

Fig. 4. Princeton Lauraceae, late immature fruit stage. Scale bars, A and B = 0.5 mm, C–E = 0.2 mm. (A) Longitudinal section, stylar remnant at top, shallow sclerotic cupule (C) at bottom, outer fruit wall (FW). Sclereid clusters (arrows), inner fruit with dark contents and vascular strands. Radially elongate endocarp palisade (Pa), seed with embryo (E) and integument (I). P1013 B_3 top #2a, ×23. (B) Oblique longitudinal section, stylar remnant at top, shallow sclerotic cupule at bottom, endocarp palisade and seed at center. Fruit wall with idioblasts, sclereid clusters (arrows). P1013 B bot side3 #0, ×33.

(ca. 5–10 cells thick). Cells of the integument are generally uniform, isodiametric, often with dark contents, and vascular strands occur throughout (Fig. 6A–C, arrows). The innermost layer of the integument is composed of a radially elongate transfusion cell layer (sensu Kasapligil, 1951). Cells of the embryo completely fill the seed, and no endosperm is present (Fig. 6A, 6B). At this final stage of maturity, idioblasts are also observed in the embryo tissue (Figs. 4A, 6A).

DISCUSSION

The Princeton Chert fruits have characters consistent with those of extant Lauraceae (Reid and Chandler, 1933; Kasapligil, 1951; Endress, 1972; Corner, 1976; Rohwer, 1993; Endress and Igersheim, 1997; Heo et al., 1998; Kimoto et al., 2006). The single-seeded, unicarpellate gynoecium, forms a globose drupe (or berry, see Roth, 1977) with a small apical stylar remnant at maturity and has a shallow cupule formed from the receptacle. Fruits have a fleshy outer pericarp, which contains idioblasts, with an inner layer of abutting sclereid clusters, and a single palisade layer composes the endocarp. Endocarp cells are stellate in transverse view, and the endocarp palisade layer forms a protuberance at the apex of the fruit at the point of seed attachment. The mature seed retains an outer integument with an innermost transfusion layer of radially elongate cells, and the embryo, bearing idioblasts, fills the seed cavity.

Isolated, lauraceous floral and fruit remains are observed at various stages of maturity, with fully mature fruits being found least frequently. We interpret these abundantly copreserved, abscised organs as indicative of a parautothochtonously deposited, subcanopy litter of a self-pruning fruit tree. Extant avocado (*Persea americana* Mill.) is known to abscise vegetative and reproductive organs regularly over the growing season, with numerous flowers per inflorescence resulting in few fruits per mature infructescence (Gazit and Degani, 2002; Garner and Lovatt, 2008). Princeton chert plants are typically preserved in situ or parautothochtonously (Cevallos-Ferriz et al., 1991; Pigg and Stockey, 1996; Stockey, 2001; Little and Stockey, 2006a; Smith and Stockey, 2007). The self-pruning, or “fruit drop,” syndrome (Gazit and Degani, 2002) in extant Lauraceae is sufficient to explain the pattern of preservation seen in the chert where abundant, isolated reproductive remains are found in various developmental stages. Thus, we hypothesize that self-pruning evolved early in the evolution of Lauraceae, because the Princeton Chert remains show this process was occurring in the Eocene.

The framework for comparative studies of Lauraceae fruits and seeds was first put forth by the paleobotanists Reid and Chandler (1933) for the purpose of better identification of fossils from the London Clay Flora. They concluded that there is a generally uniform fruit morphology and anatomy across the family. These characters include a typically ellipsoidal fruit shape, with a single seed; fruits have receptacles that may develop into cupules of various depths (Reid and Chandler, 1933). Receptacles may not develop into a cupule at all, producing free fruits on more or less enlarged pedicels; receptacles can develop into flat disks, shallow cupules, or into structures that completely enclose the fruit. Reid and Chandler (1933) observed a suite of anatomical features, including fleshy outer pericarp containing idioblasts, sclerenchyma clusters, and a radially elongate palisade endocarp layer with stellate outlines in transverse view. Each single seed per fruit was observed to have a single integument, lack endosperm, and contain a large embryo with flat cotyledons. Subsequent studies have corroborated these data for fruit morphology and anatomy across the family (Kasapligil, 1951; Vaughan, 1970; Corner, 1976; Roth, 1977; Romanov et al., 2007; Pingen et al., 1994).

Details of fruit development from flowers to mature fruits are known for the fossil fruits from Princeton and include the formation of the shallow cupule, enlargement of the carpel, an increase in number of idioblast cells in the pericarp, formation of sclereids in the inner pericarp, elongation of the endocarp into a palisade layer, enlargement of the embryo, loss of the inner integument, and differentiation of the outer integument transfusion layer. Extant Lauraceae, when studied, also have a similar developmental pattern (Kasapligil, 1951; Kostermans, 1957; Corner, 1976; Roth, 1977). Additional to what is known among extant Lauraceae, fossil fruits show idioblasts appearing in the embryo at the latest stages of maturity. The discontinuity of the endocarp layer, noted in some extant and fossil Lauraceae (Reid and Chandler 1933), is a result of degradation prior to preservation in the Princeton Chert fruits.

Development in lauraceous fruits is known well in the economically important *Persea* (Vaughan, 1970; Roth, 1977), but fruit development has also been studied in a few other taxa (Kasapligil 1951; Corner, 1976). Some species are known from early stages of gynoecial development and embryology only (Endress, 1972; Endress and Igersheim, 1997; Heo et al., 1998; Kimoto et al., 2006). In such investigations of anatomy, the immature gynoecium is similar to that observed in immature Princeton Chert fruits, containing an embryo sac in a nucellus, surrounded by two integuments.

Even in isolation, the fruits described in this study could be confidently assigned to Lauraceae based on anatomy alone. However, it is considered impossible to identify even extant Lauraceae in the absence of floral material (Kostermans, 1957; Rohwer, 1993). Thus, isolated fossil fruits should be cautiously assigned to taxa (Reid and Chandler, 1933; Mai, 1971; Rohwer, 1993; Pingen et al., 1994). The Princeton Chert fruits are distinctive in the fossil record in that they are connected by a developmental series to flowers. Taxonomic assignment of the fossil fruits relies on an upcoming study of flowers and inflorescences, which will provide a suite of characters in addition to the fruit characters described here.

Comparison with fossil taxa—The large number of extant tropical species, the difficulty in identifying these species (Kostermans, 1957; Hyland, 1989; Rohwer, 1993; van der Werff and Richter, 1996; van der Werff, 2001), nonmonophyletic generic circumscriptions (Li and Christophel, 2000; Rohwer,

←

(C) Fruit wall in tangential section. Radially elongate epidermis at right, scattered idioblasts and sclereid clusters, center and left, sclereid clusters with central idioblasts (arrow). P1013C top side2 #31b, ×110. (D) Tangential-transverse section of stellate endocarp palisade cells. P1060 D bot #11c, ×117. (E) Transverse section with embryo (E) filling seed, outer integument (I), radially elongate endocarp palisade (Pa), inner fruit wall (IFW) with dark contents, outer fruit wall (FW) with thin-walled cells, idioblasts, and radially elongate epicarp/epidermis at top. P1326 F_2 top #8, ×166.

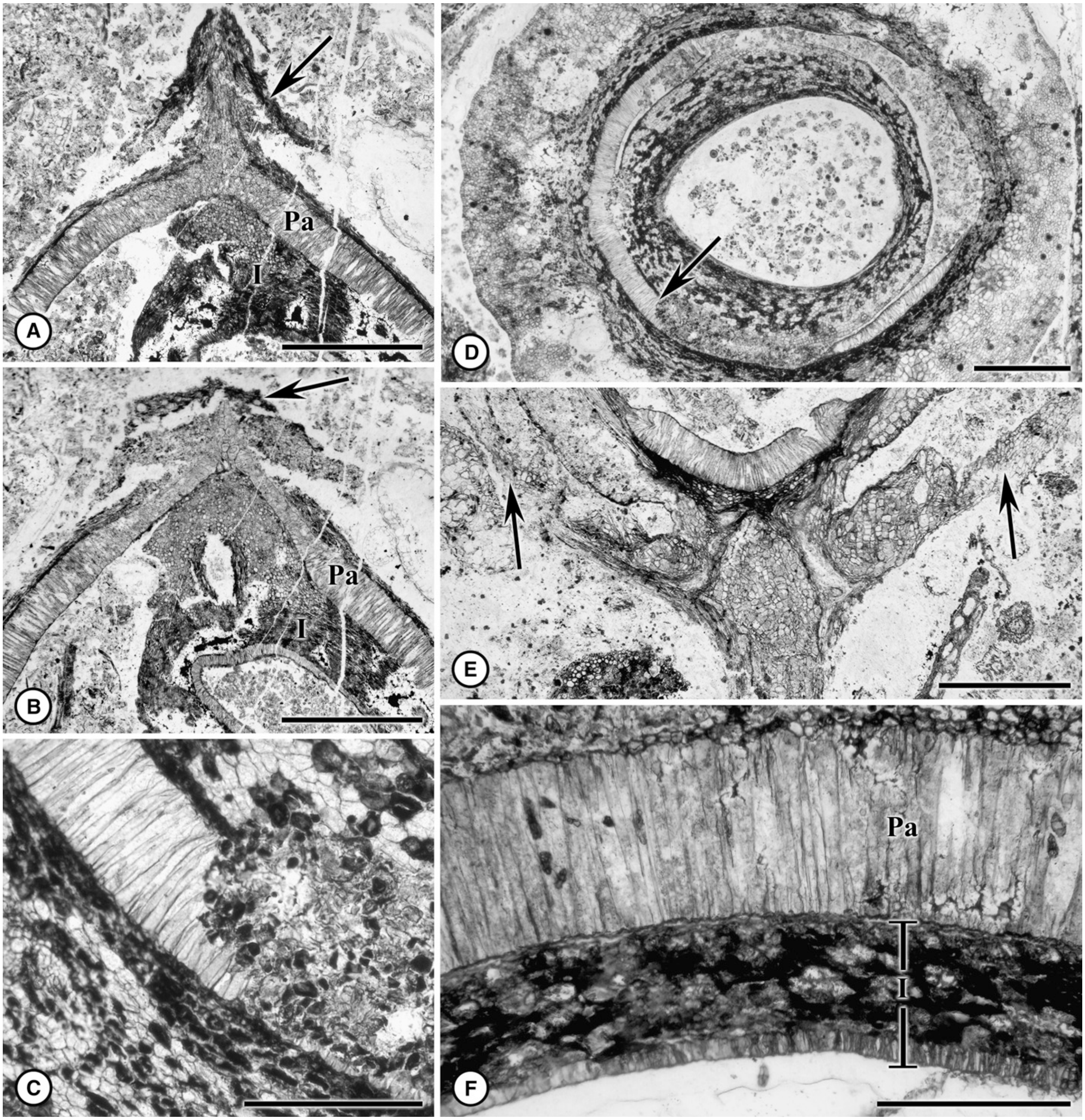

Fig. 5. Princeton Lauraceae, late immature fruit stage. Scale bars A, B, D, and E = 0.5 mm; C and F = 0.2 mm. (A) Longitudinal section, fruit wall largely missing, integument (I) at bottom, area of attachment at center, endocarp palisade (Pa) thinner near apex, forming beak-like protrusion. Epicarp remnant at arrow. P1060 D bot #11b, ×48. (B) Longitudinal section, same peel series as in (A). Integument (I) at bottom, with innermost transfusion layer, funicular area at center, endocarp palisade (Pa) thinner near apex, forming beak-like protrusion. Epicarp remnant at arrow. P1060 D bot #6c, ×48. (C) Transverse section of inner fruit wall. Integument upper right, endocarp palisade diagonal-center, degraded. P1013 C_2 top #12, ×152. (D) Whole fruit shown in C, endocarp palisade discontinuity at arrow. P1013 C_2 top #12, ×33. (E) Longitudinal section of fruit base with cupule containing sclereids, vascular strands, and attached tepal remnants (arrows) P1060 D bot #11c, ×45. (F) Transverse section of endocarp palisade (Pa) and adjacent integument (I). Note thin, few-celled integument with innermost, radially elongate, transfusion layer at bottom. P1326 D_1 top #25, ×165.

2000; Chanderbali et al., 2001; Li et al., 2004; Rohwer and Rudolph, 2005), and the lack of anatomical knowledge across much of the family contributes to the difficulties in identifying any fossil fruits of Lauraceae beyond family level (Kostermans, 1957; Hyland, 1989; Rohwer, 1993). In spite of these difficulties, numerous fruits have been described in the Cretaceous and Paleogene of North America and Europe (Reid and Chandler, 1933; Scott, 1954; Kirchheimer, 1957; Chandler, 1964; Mai, 1971, 1999, 2001; Mai and Walther, 1985; Manchester 1994; Mickle, 1996; Eklund, 2000; Frumin et al., 2004).

The earliest fossil fruits of certain lauraceous affinity occur in the Late Cretaceous of North America. *Mauldinia mirabilis* Drinnan, Crane, Friis, et Pedersen (1990) was described based on whole inflorescences and their subsequent fruits. The young fruits of *Mauldinia* have a cellular endosperm, which is similar to fruits in extant *Cassytha* L. (Drinnan et al., 1990), but differs from the nonendospermic condition in the Princeton Chert fruits at maturity.

The fossil fruit from the Late Cretaceous of North Carolina, *Grexlupus carolinensis* Mickle (1996), has few preserved characters, but does have characters typical of Lauraceae: globose shape, idioblasts, and an innermost palisade layer with undulating cell outlines, (Mickle, 1996). Interestingly, these fruits come from the same locality as three known lauraceous flower types (Eklund, 2000). However, the remains of *Grexlupus* were not ascribed to nor discussed in relation to any floral remains (Eklund, 2000). The characters of *Grexlupus* indicate a probable lauraceous affinity, but preserve too few other characters for further comparison.

Reid and Chandler (1933) described eight lauraceous fruit types from the Paleogene London Clay Flora. Several fossils were assigned to four extant genera, *Endiandra* Brown, *Cinnamomum* Schaeff., *Beilschmiedia* Nees, and *Litsea* Lamarck. Four new genera were erected to accommodate other fossils *Crowella* Reid & Chandler, *Protoravensara* Reid & Chandler, *Laurocarpum* Reid & Chandler, and *Laurocalyx* Reid & Chandler (Reid and Chandler, 1933; Collinson, 1983). Due to the ambiguities within the family with regard to fruit identification, several species from the London Clay were placed in two broadly defined morphogenera: *Laurocalyx* represents lauraceous fruits with cupules/receptacles still attached, while *Laurocarpum* represents isolated fruits lacking cupule or receptacle tissue (Reid and Chandler, 1933). These two morphogenera have since been used to allow paleobotanists to place fossil fruits in Lauraceae when further identification is impossible (Reid and Chandler, 1933; Collinson, 1983).

Although well described, the London Clay Lauraceae, as well as other fossil fruits of the family, need to be reevaluated in light of the rapidly progressing phylogenetic and taxonomic framework for the family (Chandler, 1978; Pingen et al., 1994). For instance, fossil fruits from the London Clay that are placed in *Cinnamomum* Schaeff. are described as lacking cupules, however, species in the genus typically have a well-developed cupule (Kostermans, 1957). Some characters found in London Clay Lauraceae are present in the Princeton Chert fruits. It is not entirely clear, based on the illustrations, if the sclereid clusters in the London Clay fruits are similar to those observed in Princeton fruits. However, based on the descriptions of the material, it is likely that the sclereid cluster layer, seen in the Princeton Chert fruits, is similar to that in the fossil taxa assigned to the extant genera *Endiandra* and *Beilschmiedia* (Reid and Chandler, 1933). Manchester (1994) interprets the "stellate clusters of cells" (Reid and Chandler, 1933) to indicate the arrangement of cells (parenchyma or sclerenchyma) that surround the oil idioblasts. Sclereid clusters in Princeton Chert fruits often have a central idioblast surrounded by the radiately arranged sclereids. Fossil *Endiandra* and *Beilschmiedia* from the London Clay are described as having a discontinuous endocarp layer, and Reid and Chandler (1933) could not determine if this was an artifact of preservation or a feature of the fruit, whereas the endocarp is continuous in the fossil fruits studied here and is only discontinuous in some specimens due to mechanical breakdown of the wall and is not a developmental feature. With the exception of the monotypic fossil genus *Crowella*, none of the London Clay fruits have the shallow cupule observed in the Princeton fruits, but *Crowella* differs in having an enlarged perianth that encloses the fruit, while the Princeton fossils lack tepal remnants at maturity. Thus, the Princeton Chert fruits are distinct from all London Clay Lauraceae.

Anatomically preserved fruits of Lauraceae are also known from the Clarno Nut Beds Flora (Scott, 1954). Manchester (1994) studied several specimens anatomically, allowing comparisons to the Princeton Chert fruits. The fruits from Clarno were assigned to *Lindera* Thunb., *Laurocarpum*, and *Laurocalyx* and are distinguishable from those of the Princeton Chert. *Lindera clarnensis* Manchester, based on a single endocarp with preserved embryo, shares a globose shape and an apical endocarp protuberance with the Princeton Chert fruits (Manchester 1994). However in cross section, the cells of the endocarp are polygonal in contrast to the stellate outlines of endocarp cells in fruits from Princeton. *Laurocalyx wheelerae* Manchester has a shallow cupule like that of the Princeton fruits, but differs in its prolate shape and lack of sclerenchyma throughout the fruit (Manchester, 1994). The remaining species are assigned to the genus *Laurocarpum* and lack the distinctive sclereid cluster layer seen fossil fruits studied here, either having isolated sclereid clusters only or completely lacking sclereids in the fruit wall (Manchester, 1994).

Interestingly, characters seen only in immature fruits from Princeton, such as the presence of isolated sclereid clusters, are similar to anatomically preserved fruits from other localities (Reid and Chandler, 1933; Manchester, 1994; Pingen et al., 1994). Thus, it is possible that without the full developmental sequence as described here, isolated immature fruits from other fossil localities may be erroneously assigned to separate species if various stages of development, preserved together, are mistaken for interspecific variation. In spite of this potential problem, all known anatomically preserved fruits can be differentiated from each preserved developmental stage in the fruits from the Princeton Chert.

Numerous lauraceous fossil fruits are known from Europe (Mai, 1971, 1999, 2001; Czaja, 2003). These fruits are often permineralized or lignified/mummified, and many are placed in extant genera based on cupule characters and gross morphology alone (Mai, 1971; Czaja, 2003). However, identifications based on such characters have been considered questionable due to the large amount of variability in the family and problems inherent with current generic concepts (Kostermans, 1957; Rohwer, 1993; Pingen et al., 1994). As explained above, fruits lacking a cupule are typically placed in the morphogenus *Laurocarpum* (Mai, 1971), as established by Reid and Chandler (1933). When the species studied from Europe have cupules, most fruits have cupules that extend at least over the bottom 1/3 of the fruit, and/or have tepal remnants attached, unlike the

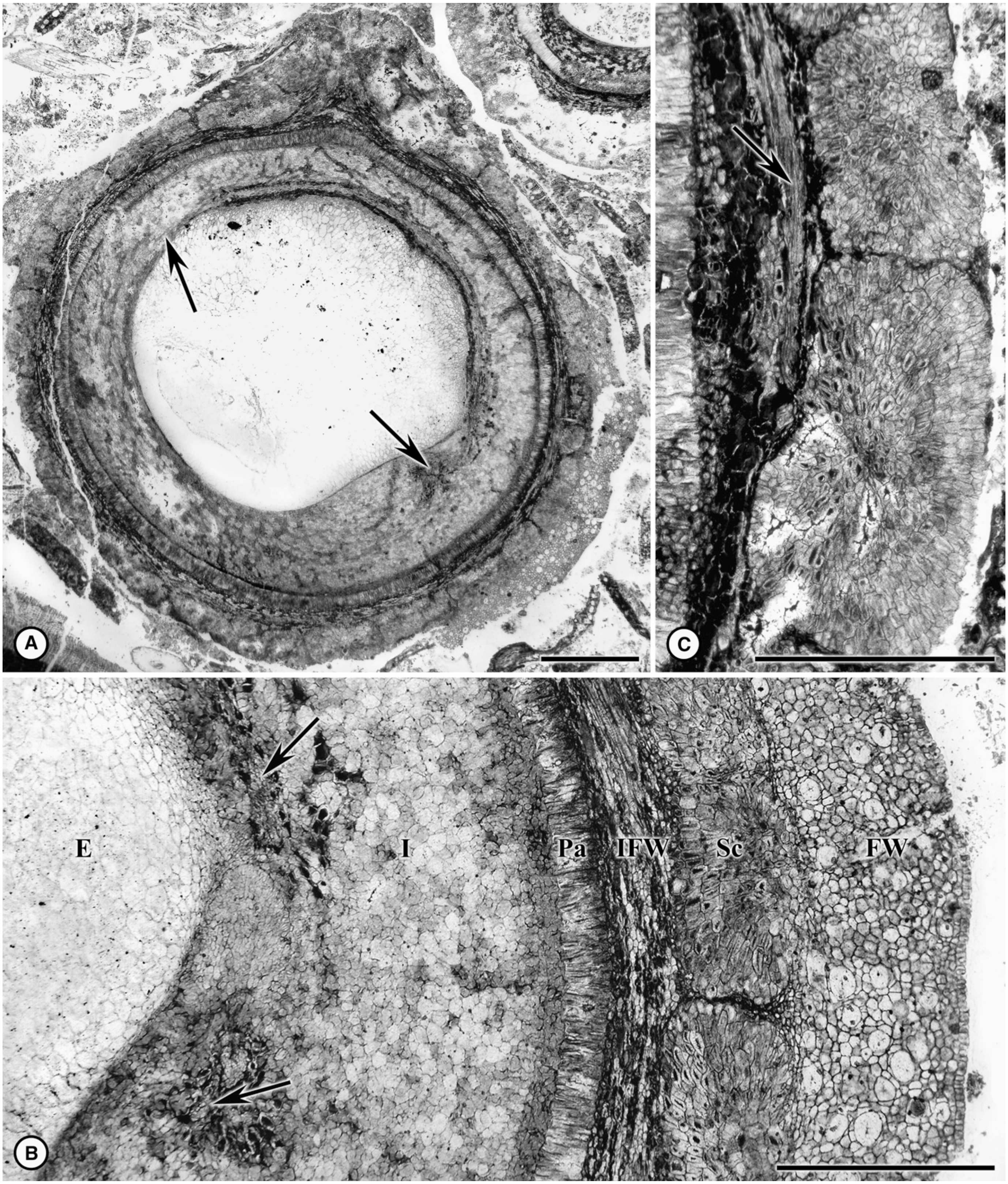

Fig. 6. Princeton Lauraceae, mature fruit stage. Scale bar A = 1.0 mm, B and C = 0.5 mm. (A) Oblique section of mature fruit with seed and embryo. Note inner sclereid layer, patchy fleshy outer fruit wall and vascular tissue in raphe and integument (arrows). P1013 C_2 top #14, ×18. (B) Fruit and seed layers. Embryo (E) at left, filling seed, oblique section of integument (I) containing vascular strands (arrows). *Note:* Integument appears thick due to oblique plane of section, endocarp palisade (Pa) adjacent to seed; inner fruit wall (IFW) with vascular strands and cells with dark contents. Fleshy fruit wall

TABLE 1. Tepal characters of mature fruits of extant genera in Lauraceae.

Tepal character	Genera			Notes on genera and fossil designation
Deciduous	*Aniba* Aubl. *Beilschmiedia* Nees *Brassiodendron* C. K. Allen *Chlorocardium* Rohwer, Richter & van der Werff *Cinnadenia* Kosterm. *Cryptocarya* R. Br. *Dodecadenia* Nees *Endiandra* R. Br. *Endlicheria* Nees	*Eusideroxylon* Teijsm. & Binnend. *Hypodaphnis* Stapf. *Iteadaphne* Blume *Laurus* L. *Licaria* Aubl. *Lindera* Thunb. *Litsea* Lam. *Mezilaurus* Kuntze ex Taubert *Nectandra* Rolander ex Rottb. *Neolitsea* Merr. *Nothaphoebe* Blume	*Parasassafras* Long *Persea* Mill. *Pleurothyrium* Nees ex Lindl. *Potameia* Thouars *Potoxylon* Kosterm. *Povedadaphne* Burger *Rhodostemonodaphne* Rohwer & Kubitzki *Sassafras* Presl. *Umbellularia* (Nees) Nutt. *Williamodendron* Kubitzki & Richter	Princeton Chert Fruits
Subpersistent	*Caryodaphnopsis* Airy-Shaw *Dehaasia* Blume.	*Iteadaphne* Blume *Potameia* Thouars	*Urbanodendron* Mez	Princeton Chert Fruits
Rarely or occasionally persistent	*Actinodaphne* Nees *Aiouea* Aubl.	*Alseodaphne* Nees *Ocotea* Aubl.		Princeton Chert Fruits
Persistent	*Apollonias* Nees *Hexapora* J. D. Hook. *Lindera* Thunb. *Nothaphoebe* Blume	*Parasassafras* Long *Persea* Mill. *Phoebe* Nees *Phyllostemonodaphne* Kosterm.	*Rhodostemonodaphne* Rohwer & Kubitzki *Systemonodaphne* Mez *Umbellularia* (Nees) Nutt. *Urbanodendron* Mez	*Phoebe* and *Apollonias*, base of fruit clasped by indurate tepals
Persistent as minute remnants	*Anaueria* Kosterm. *Aspidostemon* Rohwer & Richter	*Cassytha* L. *Cinnamomum* Schaeff	*Cryptocarya* R. Br. *Dahlgrenodendron* van der Merwe & van Wyk	*Cinnamomum*, only basal parts of tepals persist
Persistent and enlarged	*Dicypellium* Nees & Mart. (*Licaria* Aubl.)	*Neocinnamomum* Liou Ho *Paraia* Rohwer, Richter & van der Werff		*Licaria*, only sometimes persistent or enlarged

Notes: Some genera appear more than once due to variation in genus. Fossil fruits may be interpreted as either deciduous or subpersistent. Data from Rohwer (1993), Kostermans (1957), van der Werff (1997). *Licaria* (= *Gamanthera* van der Werff), *Cryptocarya* (= *Ravensara* Sonn.), *Parasassafras* (=*Sinosassafras* Li)

Princeton chert fruits with a shallow cupule lacking tepal remnants. However, because these fruits were never studied anatomically, further comparisons between these fossil fruits and those from Princeton are essentially impossible until future investigations are undertaken.

Pingen et al. (1994) reinvestigated *Homalanthus costatus* Mai (Euphorbiaceae) and reassigned it to the genus *Cinnamomum* (Lauraceae) based on detailed anatomical comparisons. The authors sampled numerous species of extant *Cinnamomum*, as well as several species in Cinnamomeae (sensu Kostermans, 1957). Pingen et al. (1994) found that in *C. costatum* and in other species of *Cinnamomum* the outlines of endocarp cells are polygonal in transverse view in contrast to the stellate pattern found in the Princeton Chert fruits and other species of extant Lauraceae (Kasapligil, 1951; Corner, 1976; Roth, 1977; Pingen et al., 1994). Although fruit anatomy in Lauraceae is generally considered uniform across the family, the survey of Pingen et al. (1994) suggests that characters of the endocarp, mesocarp, and epicarp may be useful in distinguishing taxa; palisade/endocarp thickness, sclereid patterns in mesocarp, and epicarp/epidermal stomatal arrangements were found to differ among taxa. Thus, further detailed comparative studies may reveal diagnostic, if cryptic, anatomical characters in fruits of Lauraceae. Further, it is obvious from our investigation of the Princeton Chert material that characters seen over fruit development should be taken into account, because we observe features along the developmental sequence that might be confused with taxonomically informative characters if specimens were studied in isolation and considered to be in a mature state.

Comparison with extant genera—Although it is difficult to compare the anatomy of the Princeton Chert fruits to that of living genera, due to the paucity of comparative data (just described), Reid and Chandler (1933) observed that among the extant taxa they sampled, the inner sclereid layer and the beak-like apical endocarp extension, as seen in the Princeton specimens, were only observed in extant *Endiandra* and *Beilschmeidia*. Additionally, numerous extant *Cinnamomeae* bear endocarp cells that are polygonal in transverse view (Pingen et al., 1994), rather than stellate endocarp cells (extant taxa: Kasapligil, 1951; Corner, 1976; Roth, 1977) as observed in the fossil fruits. In regard to mature fruits of extant genera, only cupule morphology and tepal characters have been systematically surveyed for each genus across the entire family. We summarize the distribution of these characters here and compare the fruits of extant genera of Lauraceae to those from the Princeton Chert (Tables 1, 2).

←
(FW) with idioblasts contains inner layer of abutting sclereid clusters (Sc) with radiate cell arrangements. Sclereid clusters abut. P1013 C_2 top #12, ×80. (C) Enlarged view of sclereid clusters with radiate cell arrangements. Note proximity of sclereid clusters. Vascular strand internal to sclereid clusters (arrow). P1013 B bot side #2, ×88.

TABLE 2. Cupule characters of mature fruits of extant genera in Lauraceae.

Fruit/cupule character	Genera		Notes on genera and fossil designation
Fruit free on a ± enlarged pedicel	*Alseodaphne* Nees *Apollonias* Nees *Beilschmiedia* Nees *Caryodaphnopsis* Airy-Shaw *Dehaasia* Blume *Endiandra* R. Br.	*Hexapora* J. D. Hook. *Lindera* Thunb. *Nothaphoebe* Blume *Ocotea* Aubl. *Persea* Mill. *Phoebe* Nees	*Hexapora*, fruit free on accrescent perianth
Small discoid cupule on a ± enlarged pedicel	*Anaueria* Kosterm. *Brassiodendron* C. K. Allen *Mezilaurus* Kuntze ex Taubert *Nectandra* Rolander ex Rottb.	*Neolitsea* Merr. *Potameia* Thouars *Povedadaphne* Burger *Williamodendron* Kubitzki & Richter	*Povedadaphne* with thickened pedicel
Minute cupule	*Cinnadenia* Kosterm. *Iteadaphne* Blume *Laurus* L.	*Lindera* Thunb. *Neocinnamomum* Liou Ho *Parasassafras* Long	*Laurus*, knob-like on thickened pedicel; *Iteadaphne*, knob-like Princeton Chert Fruits
Shallow cupule, some with thickened pedicels	*Aiouea* Aubl. *Aniba* Aubl. *Dodecadenia* Nees *Endlicheria* Nees	*Sassafras* Presl *Umbellularia* (Nees) Nutt. *Chlorocardium* Rohwer, Richter & van der Werff	*Umbellularia,* lobed cupule Princeton Chert Fruits
Shallow to bowl-shaped double-rimmed cup	*Aniba* Aubl. *Dicypellium* Nees & Mart. *Licaria* Aubl. *Ocotea* Aubl.	*Paraia* Rohwer, Richter & van der Werff *Phyllostemonodaphne* Kosterm. *Systemonodaphne* Mez *Urbanodendron* Mez	
Cupule of variable size and/or shape	*Actinodaphne* Nees *Cinnamomum* Schaeff. *Litsea* Lam.	*Neolitsea* Merr. *Ocotea* Aubl.	Princeton Chert Fruits
Well-developed cupule	*Pleurothyrium* Nees *Nectandra* Rolander ex Rottb.	*Rhodostemonodaphne* Rohwer & Kubitzki.	*Pleurothyrium*, usually lenticellate cupule
Deep cupule 1/3 to almost completely enclosed	*Chlorocardium* Rohwer, Richter & van der Werff	*Sextonia* van der Werff	
Completely enclosed in accrescent receptacular tube	*Aspidostemon* Rohwer & Richter *Cassytha* L. *Cryptocarya* R. Br.	*Dahlgrenodendron* van der Merwe & van Wyk *Eusideroxylon* Teijsm. & Binnend. *Potoxylon* Kosterm.	
Completely enclosed in receptacle tissue	*Hypodaphnis* Stapf		

Notes: Some genera appear more than once due to variation in genus. Depending on interpretation of characters, a small, shallow cupule of fossil may be considered "minute"; fossil cupule shape may fall within variation among genera with variable size and/or shape. Data from Rohwer (1993), Kostermans (1957), van der Werff (1997). *Licaria* (= *Gamanthera* van der Werff), *Cryptocarya* (= *Ravensara* Sonn.), *Parasassafras* (=*Sinosassafras* Li)

Tepals remain attached during early development of the Princeton Chert fruits, but are absent at the time of fruit maturation. Deciduous tepals are found in the majority of extant genera in the family (Table 1). However, the tepals of the Princeton fruits could also be classified as subpersistent, because they are present in all but the latest stages of development. The ambiguity of this qualitative character needs refinement in descriptions of extant taxa, and we conservatively indicate all three potential character states for the fossil fruits (Table 1).

Cupule characters were used, in part, for intrafamilial classification in Lauraceae (Kostermans, 1957). Although Kostermans' (1957) subfamilial groupings have largely been rejected by recent molecular phylogenetic studies (Rohwer, 2000; Chanderbali et al., 2001; Rohwer and Rudolph, 2005), we suggest that fruit characters may provide an important character in distinguishing taxa because this character correlates well with some clades resolved from molecular phylogenetic studies (e.g., *Cryptocarya* clade and *Endiandra-Beilschmeidia* clade; Chanderbali et al., 2001). However, morphological characters will probably continue to lack diagnostic utility until the polyphyly in large genera (Chanderbali et al., 2001) is accounted for and is reflected in generic circumscriptions. Among the 53 extant genera in Lauraceae, most bear deep cupules, discoid cupules, or enlarged/swollen pedicels lacking a cupule (Table 2). In contrast, mature fruits from Princeton bear shallow to minute cupules. Among extant taxa with shallow cupules, some genera (e.g., *Paraia* Rohwer, Richter & van der Werff, *Licaria* Aubl., and *Systemonodaphne* Mez) are described as having a double-rimmed cup due to the retention of staminal remnants (Rohwer, 1993). Cupules of variable shape occur in *Actinodaphne* Nees, *Cinnamomum* Schaeff., *Litsea* Lam., *Neolitsea* Merr., and *Ocotea* Aubl., and the variation in these genera may overlap with that seen in the Princeton Chert fruits (some species may have shallow cupules). Taxa regarded as having shallow cupules only, as in the fossil fruits, are observed in six genera: *Aiouea* Aubl., *Dodecadenia* Nees, *Endlicheria* Nees, *Sassafras* Presl., *Umbellularia* (Nees) Nutt., and *Chlorocardium* Rohwer, Richter & van Der Werff. Beyond these features, comparison of isolated fruits to extant taxa is limited by the scant knowledge of anatomy and development across the family.

Conclusions—The Princeton Chert represents an assemblage of plants, the majority of which are preserved in situ or parautothochtonously (Cevallos-Ferriz et al., 1991; Pigg and Stockey, 1996; Stockey, 2001; Little and Stockey, 2006a; Smith and Stockey, 2007), and as such, the site yields numerous well-preserved specimens that have allowed for this developmental study of fossil fruits. Self-pruning of fruits from infructescences along the sequence of maturation is suggested to have occurred for the Princeton Chert plant, indicating that self-pruning or "fruit-drop" (Gazit and Degani, 2002) evolved in Lauraceae prior to the Middle Eocene.

In isolation, fruits are not considered able to provide a suite of characters diagnostic of any extant genus or species (Rohwer, 1993). Difficulties in identifying fossil fruits arise, in part, from insufficient knowledge of extant Lauraceae. However, the Princeton Chert fruits are distinguishable among anatomically studied fossil fruits. The current generic concepts are artificial for most larger genera (Rohwer, 2000; Chanderbali et al., 2001; Li et al., 2004 Rohwer and Rudolph, 2005), and data on anatomy and development is sparse to nonexistent, with rare exceptions in a few taxa (Kasapligil, 1951). Thus, it is challenging, at best, to put the well-understood reproductive anatomy and development of the Princeton Chert fruits into an evolutionary context.

More complete plant concepts in the fossil record are considered essential for useful reconstructions of evolutionary history (Rothwell and Serbet, 1994; Rothwell, 1999; Hilton and Bateman, 2006), and this work represents the only developmental study of fossil fruits in the family known to date. Further, associated inflorescence and vegetative remains will be the subject of upcoming studies and will expand the concept of this fossil lauraceous plant toward a multiorgan/whole-plant reconstruction. No fossil Lauraceae are known as whole plants, and thus the Princeton Chert plant will be key for more confident dating of molecular-based phylogenies and may provide important data on character evolution in the family.

The developmental sequence described here shows immature anatomy that is comparable to some other anatomically studied fossil taxa (Reid and Chandler, 1933; Manchester, 1994). Therefore, previously described fossil fruits (e.g., Mai, 1971) should be reexamined anatomically, where possible, to increase character sets for the purpose of better identification and the discovery of immature stages that may have been erroneously separated into different taxa. A broader sampling of extant Lauraceae, studied anatomically and developmentally, is the only way to make such reassignments possible, but is currently lacking. This situation is atypical because fossil morphotypes are generally considered to underestimate diversity (Pole, 2007). However, fruit morphotypes assignable to Lauraceae (e.g., Mai, 1971) may inflate true numbers of species at a fossil site, prompting researchers to spuriously infer that the high diversity of Lauraceae is indicative of tropical conditions.

LITERATURE CITED

Baas, P., and M. Gregory. 1985. A survey of oil cells in the dicotyledons with comments on their replacement by and joint occurrence with mucilage cells. *Israel Journal of Botany* 34: 167–186.

Basinger, J. F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 59: 2379–2410.

Basinger, J. F., and G. W. Rothwell. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 55: 1984–1990.

Boneham, R. F. 1968. Palynology of three Tertiary coal basins in south central British Columbia. Ph.D. dissertation, University of Michigan, Ann Arbor, Michigan, USA.

Cevallos-Ferriz, S. R. S., R. A. Stockey, and K. B. Pigg. 1991. The Princeton chert: Evidence for in situ aquatic plants. *Review of Palaeobotany and Palynology* 70: 173–185.

Chanderbali, A. S., H. van der Werff, and S. S. Renner. 2001. Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104–134.

Chandler, M. E. J. 1964. The Lower Tertiary floras of southern England, IV. British Museum (Natural History), London, UK.

Chandler, M. E. J. 1978. Supplement to the Lower Tertiary floras of southern England, part 5. Tertiary Research Special Paper no. 4. Tertiary Research Group, London, UK.

Collinson, M. E. 1983. Fossil plants of the London Clay, Palaeontological Association field guides to fossils, no. 1. Oxford University Press, Oxford, UK.

Corner, E. J. H. 1976. The seeds of the dicotyledons, vols. 1, 2. Cambridge University Press, Cambridge, UK.

Crane, P. R., E. M. Friis, and K. R. Pedersen. 1994. Palaeobotanical evidence on the early radiation of magnoliid angiosperms. *Plant Systematics and Evolution, Supplementum* 8: 51–72.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York, New York, USA.

Czaja, A. 2003. Paleocarpological investigations of the taphocoenoses of the Lower- and Middle Miocene from the opencast mine Berzdorf/Upper Lusatica (Saxony). *Palaeontographica B* 265: 1–148.

Drinnan, A. N., P. C. Crane, E. M. Friis, and K. R. Pedersen. 1990. Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America. *Botanical Gazatte* 151: 370–384.

Eklund, H. 2000. Lauraceous flowers from the Late Cretaceous of North Carolina, U.S.A. *Botanical Journal of the Linnean Society* 132: 397–428.

Eklund, H., and J. Kvaček. 1998. Lauraceous inflorescences and flowers from the Cenomanian of Bohemia (Czech Republic, Central Europe). *International Journal of Plant Sciences* 159: 668–686.

Endress, P. K. 1972. Zur vergleichenden Entwicklungsmorphologie, Embryologie and Systematik bei Laurales. *Botanische Jahrbücher für Systematik und Pflanzengeographie* 92: 331–428.

Endress, P. K., and A. Igersheim. 1997. Gynoecium diversity and systematics of the Laurales. *Botanical Journal of the Linnean Society* 125: 93–168.

Frumin, S., H. Eklund, and E. M. Friis. 2004. *Mauldinia hirsuta* sp. nov., a new member of the extinct genus *Mauldinia* (Lauraceae) from the Late Cretaceous (Cenomanian-Turonian) of Kazakhstan. *International Journal of Plant Sciences* 165: 883–895.

Garner, L. C., and C. J. Lovatt. 2008. The relationship between flower and fruit abscission and alternate bearing of 'Hass' avocado. *Journal of the American Society for Horticultural Science* 133: 3–10.

Gazin, C. L. 1953. The Tillodontia: An early Tertiary order of mammals. *Smithsonian Miscellaneous Collections* 121: 1–110.

Gazit, S., and C. Degani. 2002. Reproductive biology. *In* A. W. Whiley, B. Schaffer, and B. N. Wolstenholme [eds.], The avocado: Botany, production and uses, 101–133. CAB International, Wallingford, UK.

Heo, K., H. van der Werff, and H. Tobe. 1998. Embryology and relationships of Lauraceae (Laurales). *Botanical Journal of the Linnean Society* 126: 295–322.

Herendeen, P. S. 1991. Lauraceous wood from the mid-Cretaceous Potomac Group of eastern North America: *Paraphyllanthoxylon marylandense* sp. nov. *Review of Palaeobotany and Palynology* 69: 277–290.

Herendeen, P. S., S. Magallón-Puebla, R. Lupia, P. R. Crane, and J. Kobylinska. 1999. A preliminary conspectus of the Allon flora from the Late Cretaceous (late Santonian) of central Georgia, USA. *Annals of the Missouri Botanical Garden* 86: 407–471.

HILLS, L. V., AND H. BAADSGAARD. 1967. Potassium-argon dating of some Lower Tertiary strata in British Columbia. *Bulletin of Canadian Petroleum Geology* 15: 138–149.

HILTON, H., AND R. M. BATEMAN. 2006. Pteridosperms are the backbone of seed-plant phylogeny. *Journal of the Torrey Botanical Society* 133: 119–168.

HUTCHINSON. J. 1964. The genera of flowering plants, vol. 1. Clarendon Press, Oxford, UK.

HYLAND, B. P. M. 1989. A revision of Lauraceae in Australia (excluding *Cassytha*). *Australian Systematic Botany* 2: 135–367.

JOY, K. W., A. J. WILLIS, AND W. S. LACEY. 1956. A rapid cellulose peel technique in palaeobotany. *Annals of Botany n. s.* 20: 635-637.

KASAPLIGIL, B. 1951. Morphological and ontogenetic studies of *Umbellularia californica* Nutt. and *Laurus nobilis* L. *Publications in Botany, University of California* 25: 115–239.

KIMOTO, Y., N. UTAMI, AND H. TOBE. 2006. Embryology of *Eusideroxylon* (Cryptocaryeae, Lauraceae) and character evolution in the family. *Botanical Journal of the Linnean Society* 150: 187–201.

KIRCHHEIMER, F. 1957. Die Laubgewächse der Braunkohlenzeit. Wilhelm Knapp Verlag, Halle (Saale), Germany.

KOSTERMANS, A. J. G. H. 1957. Lauraceae. *Reinwardtia* 4: 193–256.

KVAČEK, J. 1992. Lauralean angiosperms in the Cretaceous. *Courier Forschungsinstitut Senckenberg* 147: 345–367.

LI, J., AND D. C. CHRISTOPHEL. 2000. Systematic relationships within the *Litsea* complex (Lauraceae): A cladistic analysis based on morphological and leaf cuticle data. *Australian Systematic Botany* 13: 1–13.

LI, J., D. C. CHRISTOPHEL, J. G. CONRAN, AND H.-W. LI. 2004. Phylogenetic relationships within the 'core' Laureae (*Litsea* complex, Lauraceae) inferred from sequences of the chloroplast gene *mat*K and nuclear ribosomal DNA ITS regions. *Plant Systematics and Evolution* 246: 19–34.

LITTLE, S. A., AND R. A. STOCKEY. 2006a. Morphogenesis of the specialized peridermal tissues in *Decodon allenbyensis* from the middle Eocene Princeton chert. *International Association of Wood Anatomists Journal* 27: 73–87.

LITTLE, S. A., AND R. A. STOCKEY. 2006b. Reconstructing fossil Lauraceae: The importance of whole plant concepts. Botany 2006: Annual meeting of the Botanical Society of America, Chico, California, USA (Abstract 765, http://www.2006.botanyconference.org/engine/search/index.php?func=detail$aid=765).

LITTLE, S. A., AND R. A. STOCKEY. 2003. Permineralized fruits of Lauraceae from the Middle Eocene Princeton chert, British Columbia. Proceedings of Botanical Society of America meeting, 2003, Mobile, Alabama, USA, abstract 225. Botanical Society of America, St. Louis, Missouri, USA.

MAI, D. H. 1971. Über fossile Lauraceae und Theaceae in Mitteleuropa. *Feddes Repertorium* 82: 313–341.

MAI, D. H. 1999. Die untermiozänen Floren aus der Spremberger Folge und dem 2. Flözhorizont in der Lausitz, Teil II: Polycarpicae und Apetalae. *Palaeontographica Abt. B* 251: 1–70.

MAI, D. H. 2001. Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz, Teil II: Dicotyledonen. *Palaeontographica Abt. B* 257: 35–174.

MAI, D. H., AND H. WALTHER. 1985. Die obereozänen Floren des Weißelster-Beckens und seiner Randgebiete. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* 33: 1–260.

MANCHESTER, S. R. 1994. Fruits and seeds of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58: 1–205.

MEISSNER, C. F. 1864. Lauraceae. *In* V. A. De Candolle [ed.], Prodromous systematis naturalis regni vegetabilis, vol. 15, 1–260. Masson et Sons, Paris, France.

MICKLE, J. 1996. *Grexlupus carolinensis*, a new probable lauraceous fruit from the Late Cretaceous of North Carolina. *Journal of the Elisha Mitchell Scientific Society* 112: 1–6.

PAX, F. 1891. Lauraceae. *In* A. Engler and K. Prantl [eds.], Die natürlichen Pflanzenfamilien, Band 3, Teil 2, 106–126. Wilhelm Engelmann, Leipzig, Germany.

PENNER, B. M. 1996. Lauraceous fruit from the Middle Eocene, Princeton Chert (Allenby Formation), British Columbia, Canada. Undergraduate thesis, University of Manitoba, Winnipeg, Manitoba, Canada.

PIGG, K. P., AND R. A. STOCKEY. 1996. The significance of the Princeton chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. *Washington Geology* 24: 32–36.

PINGEN, M., D. K. FERGUSON, AND M. E. COLLINSON. 1994. *Homalanthus costatus* Mai: A new Miocene fruit of *Cinnamomum* Schaeffer (Lauraceae). *Palaeontographica Abt. B* 232: 155–174.

POLE, M. 2007. Lauraceae macrofossils and dispersed cuticle from the Miocene of southern New Zealand. *Palaeontologia Electronica* 10(1); 3A:38p, 65MB. Website http:/www.paleo.erdw.ethz.ch/2007_1/zealand/index.html

REID, E. M., AND M. E. J. CHANDLER. 1933. The London Clay flora. British Museum (Natural History), London, UK.

RENNER, S. S. 1998. Phylogenetic affinities of Monimiaceae based on cpDNA gene and spacer sequences. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 61–77.

RENNER, S. S. 1999. Circumscription and phylogeny of the Laurales: Evidence from molecular and morphological data. *American Journal of Botany* 86: 1301–1315.

ROHWER, J. G. 1993. Lauraceae. *In* K. Kubitzki, J. G. Rohwer, and V. Bittrich [eds.], The families and genera of vascular plants, vol. 2, Flowering plants, Dicotyledons: Magnoliid, hamamelid, and caryophyllid families, 366–391. Springer Verlag, Berlin, Germany.

ROHWER, J. G. 1994. A note on the evolution of the stamens in the Laurales with emphasis on the Lauraceae. *Botanica Acta* 107: 103–110.

ROHWER, J. G. 2000. Toward a phylogenetic classification of the Lauraceae: Evidence from *matK* sequences. *Systematic Botany* 25: 60–71.

ROHWER, J. G., AND B. RUDOLPH. 2005. Jumping genera: The phylogenetic positions of *Cassytha, Hypodaphnis*, and *Neocinnamomum* (Lauraceae) based on different analyses of *trnK* intron sequences. *Annals of the Missouri Botanical Garden* 92: 153–178.

ROMANOV, M. S., P. K. ENDRESS, A. V. F. C. BOBROV, A. P. MELIKIAN, AND A. P. BEJERANO. 2007. Fruit structure of Monimiaceae s.str. (Laurales). *Botanical Journal of the Linnean Society* 153: 265–285.

ROTH, I. 1977. Fruits of angiosperms. Gebrüder Borntraeger, Berlin, Germany.

ROTHWELL, G. W. 1999. Fossils and ferns in the resolution of land plant phylogeny. *Botanical Review* 65: 188–218.

ROTHWELL, G. W., AND R. SERBET. 1994. Lignophyte phylogeny and the evolution of spermatophytes: A numerical cladistic analysis. *Systematic Botany* 19: 443–482.

ROUSE, G. E., AND S. K. SRIVASTAVA. 1970. Detailed morphology, taxonomy and distribution of *Pistillipollenites macgregori. Canadian Journal of Botany* 48: 287–292.

RUSSELL, L. S. 1935. A Middle Eocene mammal from British Columbia. *American Journal of Science* 29: 54–55.

SCOTT, R. A. 1954. Fossil fruits and seeds from the Eocene Clarno Formation of Oregon. *Palaeontographica B* 96: 66–97.

SMITH, S. Y., AND R. A. STOCKEY. 2007. Establishing a fossil record for the perianthless Piperales: *Saururus tuckerae* sp. nov. (Saururaceae) from the Middle Eocene Princeton Chert. *American Journal of Botany* 94: 1642–1657.

STOCKEY, R. A. 1983. *Pinus driftwoodensis* sp. nov. from the early Tertiary of British Columbia. *Botanical Gazette (Chicago, Ill.)* 144: 148–156.

STOCKEY, R. A. 2001. The Princeton Chert. *In* D. E. G. Briggs, and P. R. Crowther [eds.], Palaeobiology II, 359–362. Blackwell Science, Maledin, Massachusetts, USA.

SUN, Z., AND R. A. STOCKEY. 1991. Lauraceous inflorescences from the Middle Eocene Princeton Chert (Allenby Formation) of British Columbia, Canada. *American Journal of Botany* (Supplement): 78, abstract 323.

VAUGHAN, J. G. 1970. The structure and utilization of oil seeds. Chapman and Hall, London, UK.

WATSON, L., AND M. J. DALLWITZ. 1992. The families of flowering plants: Descriptions, illustrations, identification, and information retrieval. Website http://delta-intkey.com [accessed 2 June 2007].

VAN DER WERFF, H. 1997. *Sextonia*, a new genus of Lauraceae from South America. *Novon* 7: 436–439.

VAN DER WERFF, H. 2001. An annotated key to the genera of Lauraceae in the Flora Malesiana region. *Blumea* 46: 125–140.

VAN DER WERFF, H., AND H. G. RICHTER. 1996. Toward an improved classification of Lauraceae. *Annals of the Missouri Botanical Garden* 83: 409–418.

WILSON, M. V. H. 1977. Middle Eocene freshwater fishes from British Columbia. *Royal Ontario Museum*, *Life Sciences Contributions* 113: 1–61.

WILSON, M. V. H. 1982. A new species of *Amia* from the Middle Eocene of British Columbia. *Palaeontology* 25: 413–424.