Anatomically preserved *Liquidambar* (Altingiaceae) from the middle Miocene of Yakima Canyon, Washington state, USA, and its biogeographic implications[1]

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Liquidambar changii Pigg, Ickert-Bond & Wen sp. nov. (Altingiaceae) is established for anatomically preserved, middle Miocene infructescences from Yakima Canyon, Washington, USA. Specimens are spherical, ~2.5 cm in diameter, and have ~25–30 tightly packed, bilocular fruits per head. Fruits are 3.4–4.7 mm wide × 2.6–3.5 mm long and wedge shaped, fused at the base, and free distally. Each locule contains 1–2 mature, elongate seeds proximally and 5–9 aborted seeds of more irregular shape distally. Mature seeds are 1.5 mm long × 1.2 mm wide, elongate, and triangular transversely, with a slight flange. Seeds have a seed coat for which three zones can be well defined, a uniseriate outer palisade layer, a middle region of isodiametric cells comprising most of the integument, and a uniseriate inner layer of tangentially elongate cells lining the embryo cavity. *Liquidambar changii* is most similar to the eastern Asian *L. acalycina* H.-T. Chang on features of infructescence, fruit, and seed morphology and quite unlike the North American *L. styraciflua* L. and other species. Such a close relationship between these two species supports a Beringian biogeographic track between eastern Asia and western North America during the Miocene. Previous phylogenetic and allozyme analysis of modern *Liquidambar* demonstrates a close relationship between North American-western Asian taxa and suggests a North Atlantic biogeographic track in the middle Miocene. Together, these biogeographic tracks underscore the complexity of the biogeographic history of the Altingiaceae in the Northern Hemisphere throughout the Neogene.

Key words: *Altingia*; Altingiaceae; biogeography; fossil fruit; infructescence; *Liquidambar*; Miocene; silicification.

The Altingiaceae Lindl. consist of three genera (*Liquidambar* L., *Altingia* Noronha, and *Semiliquidambar* H.-T. Chang) and ~15 species that have an intercontinental disjunct distribution in eastern and western Asia and North and Central America (Ferguson, 1989; Wen, 1999). Today, *Liquidambar* (the sweet gum) is comprised of around five species with two occurring in eastern Asia (*L. acalycina* H.-T. Chang and *L. formosana* Hance), one in western Asia (*L. orientalis* Mill.), and one in eastern North America extending into central Mexico and further into Central America (*L. styraciflua* L.). Morphological variants similar to *L. styraciflua* occurring in Mex-

ico to Honduras are sometimes recognized as *L. styraciflua* var. *mexicana* Oerst. and *L. macrophylla* Oerst. (Ernst, 1963; Ferguson, 1989; Zhang et al., 2003). *Altingia* and *Semiliquidambar*, exclusively eastern Asian in distribution, have approximately eight and three species, respectively (Ferguson, 1989; Zhang et al., 2003), although revisions of these genera are needed (Endress, 1993). *Liquidambar* has been distinguished from *Altingia* based on a combination of vegetative, particularly leaf features, as well as reproductive characters. Whereas *Liquidambar* leaves are typically deciduous and palmately 3–7 lobed with actinodromous venation, those of *Altingia* are evergreen, commonly obovate and entire with pinnate venation. *Semiliquidambar* shows an intermediate morphology between the two other genera and has been suggested to possibly represent an intergeneric hybrid (Bogle, 1986). With respect to infructescence characters, those of *Liquidambar* tend to have been interpreted to have fruits with septicidal dehiscence and persistent styles while in *Altingia* both septicidal and loculicidal dehiscence are reported, and styles are typically deciduous. Features of *Semiliquidambar* are intermediate.

Historically, these genera have comprised a subfamily of the Hamamelidaceae, recognized as either the Liquidambaroideae or the Altingioideae on the basis of traditional taxonomic characters including morphology and biochemistry (Harms, 1930; Chang, 1979; Bogle, 1986; Endress, 1989a, b; Ferguson, 1989; Qui et al., 1998; Zhang et al., 2003). The most recent phylogenies based on combined morphological and molecular data place this group within the order Saxifragales of the rosid clade of core eudicots (Magallón et al., 1999; Judd et al., 2002).

Within the genus *Liquidambar*, two sections have been traditionally delimited on the basis of fruiting head ornamentation (Harms, 1930; Chang, 1979). Sect. *Cathayambar* Harms (one species, *L. formosana*) is characterized by the presence of elongate structures (''Borsten'' or ''setae'' of Harms, 1930) positioned between fruits while in sect. *Liquidambar* (4–5 species) comparable structures are either lacking or inconspicuous. Species of sect. *Liquidambar* are distinguished from one another by additional features of infructescence morphology including thickness and ornamentation of the outer hypanthial tissues that comprise the areas between adjacent fruits, resulting in a honeycomb-like appearance, which is sometimes called the ''peripheral rim'' (Gregor, 1978 p. 34–35; Ferguson, 1989). Recent phylogenetic analyses (Li et al., 1997, 1999), however, do not support this traditional classification. The main distinguishing character of the two sections, the presence of elongate structures, is thus an autapomorphy for *L. formosana*. *Liquidambar formosana* of sect. *Cathayambar* is most closely related to *L. acalycina* of sect. *Liquidambar*. Isozyme studies of *Liquidambar* (Hoey and Parks, 1991, 1994) showed that the genetic similarity of extant forms is greater between eastern North American *L. styraciflua* and western Asian *L. orientalis* than it is between eastern North American and eastern Asian forms. More recently, DNA molecular phylogenetic studies have confirmed this same pattern (Li et al., 1997, 1999; Shi et al., 1998, 2001; Li and Donoghue, 1999). Today the center of diversity of the Altingiaceae is eastern Asia, with *Liquidambar* primarily inhabiting temperate regions and *Altingia* and *Semiliquidambar* with a tropical and subtropical distribution (Wen, 1998). In general *Liquidambar* has a more northerly distribution, and the ranges of *Liquidambar* and *Altingia* overlap in South China, where *Semiliquidambar* occurs (Chang, 1979).

A better understanding of the diversification of the Altingiaceae requires detailed analysis of related fossil taxa. However, several factors have prevented a comprehensive analysis of the group, including preservational limitations and lack of well-delineated taxonomic characters. In compression/impression floras and fruit and seed assemblages, the spherical infructescences of this family provide few defining features. Two of the most important taxonomic characters that have been used to separate *Liquidambar* and *Altingia* are the presence or absence of persistent styles and the type of dehiscence. Both of these characters can be easily lost or obscured by abrasion or degradation prior to fossilization. Additionally, comparison with extant species has often been limited to only the species locally available for study. This problem can be particularly confusing in a genus with an extant disjunct distribution such as *Liquidambar*.

The spherical infructescences of the Altingiaceae have sometimes been confused with those of Platanaceae Dum. (e.g., *Platanus L.*, *Macginicarpa* Wolfe & Wehr), and, to a lesser extent, with the aquatic plant *Sparganium* L. (Sparganiaceae), resulting in misidentifications that lead to erroneous ideas about their distribution. Since the fossil record of the Platanaceae has become better understood, this similarity has become less problematic (Manchester, 1986; Maslova and Krassilov, 1997). Fruits of Altingiaceae are consistently bicarpellate and typically lack a perianth, while platanaceous florets vary from four- to five-loculate Cretaceous forms with conspicuous tepals (e.g., Friis et al., 1988; Magallón-Puebla et al., 1997) to younger forms with more plastic merosity, reduced perianth, and the presence of dispersal hairs (Pigg and Stock-

ey, 1991). Altingiaceae fruits dehisce to release seeds, while platanaceous carpels develop into single-seeded achenes that are dispersed. *Sparganium* infructesences bear single-seeded drupaceous fruits (Manchester, 1986).

Although *Liquidambar* compressed leaf and infructescence remains are widespread in the Northern Hemisphere during the Neogene, until recently there has been little pre-Tertiary record of this group. The earliest fossil reproductive structures assigned to the family are inflorescences from the Late Turonian (Late Cretaceous) Lower Magothy Formation of New Jersey (Zhou et al., 2001) and the Late Santonian (Late Cretaceous) Allon flora of central Georgia (Herendeen et al., 1999). These tiny spherical heads are 1.6–7.0 mm in diameter, each with ~20 apetalous florets. Each floret is bilocular, with carpels that are fused basally and free distally. There are numerous ovules per carpel and phyllophores surrounding the gynoecia. Zhou et al. (2001) interpret the stratigraphically older of these, *Microaltingia* Zhou, Crepet & Nixon, as most similar to the Altingiaceae; however, these fossils have a mosaic of characters including tricolpate rather than polyporate pollen typical of Altingiaceae.

A Paleocene fruit with possible altingioid affinities, *Evacarpa polysperma* Maslova & Krassilov was described from a compression flora from western Kamchatka (Maslova and Krassilov, 1997). This taxon is based on a single reproductive axis bearing a cluster of pedunculate spherical fruiting heads, 4–5 mm in diameter that are composed of approximately 16 florets with apparently bilocular ovaries. Beyond the basic organization, details of *Evacarpa* are difficult to interpret, but suggest that plants with the general morphology of Altingiaceae were present in the Paleocene.

By the Eocene and extending into the Oligocene, *Liquidambar* leaves are known from several compression floras in western North America, Europe, and Asia (MacGinitie, 1941; Maslova, 1995; Meyer and Manchester, 1997). Also in the Eocene (and perhaps the Late Cretaceous of Amur; Krassilov, 1976), infructescences of the widespread but poorly understood taxon *Steinhauera subglobosa* Presl (1838) are known from numerous localities in Europe including the Czech Republic, Germany, and France (Kirchheimer, 1943, 1957; Mai, 1968). *Steinhauera* is a relatively large, ovoid infructescence approximately 1.8–3.0 cm in diameter with bilocular fruits like those characteristic of extant Altingiaceae. Its relationship to extant genera has been debated and still remains unclear. Kirchheimer (1943) suggested that *Steinhauera* Presl was closely related to *Liquidambar*. In contrast, Mai (1968) emphasized its resemblance to *Altingia*, including the septicidal and loculicidal dehiscence and the apparent lack of persistent styles. Seeds assigned to *Liquidambar* have also been reported from the Paleocene and Eocene of western North America, but the identity of these specimens as altingioid is questionable (Brown, 1962; Wehr, 1995).

Infructescences very similar to modern forms are associated fairly often with *Liquidambar* leaves in Tertiary compression floras, particularly in the Miocene of Asia (Endo and Morita, 1932; Suzuki, 1961; Huzioka and Uemura, 1979; Uemura, 1983), Europe (Czeczott and Skirgiello, 1959; Ferguson, 1971, 1989; Koch et al., 1973), and western North America (MacGinitie, 1941; Smiley and Rember, 1985; Rember, 1991). Lignitic fruit and seed assemblages of Miocene and Pliocene age from Europe also commonly contain altingioid reproductive remains (Hantke, 1954; Lancucka-Srodoniowa, 1966; Koch et al., 1973; Gregor, 1978; Friis, 1985; Martinetto,

1998). However, the precise relationships of these fossils to extant species remain unclear.

In addition to leaves and reproductive remains, wood assignable to *Liquidambar* and the fossil genera *Ambaroxylon* Houlbert and *Liquidambaroxylon* Felix has been described from western and central Europe, North America (including the Miocene Vantage and Yakima Canyon woods of Washington State), India, and Japan (Beck, 1945; Prakash and Barghoorn, 1961a, b; Van der Burgh, 1964; Prakash, 1968; Ferguson, 1989; Agarwal, 1991). In some instances, wood anatomy of Altingiaceae may provide a useful set of characters for delimitation of infrafamial groups (E. A. Wheeler, North Carolina State University, personal communication).

Fossil pollen of the *Liquidambar*-type is known from as early as the Paleocene of southern Europe (Kuprianova, 1960; Muller, 1981), the Rocky Mountains (Graham, 1965, 1999; Wolfe, 1973), and the Eocene of Japan (Takahashi, 1964). Recognition of pollen of Altingiaceae in the fossil record is of particular taxonomic value because it is distinct in being polyporate rather than tricolpate, which is more typical of hamamelid genera (Zavada and Dilcher, 1989).

In the present study we describe a new species, *Liquidambar changii* Pigg, Ickert-Bond & Wen, based on anatomically preserved infructescences from the middle Miocene of central Washington State, USA. *Liquidambar changii* provides the first anatomical information for reproductive remains of fossil *Liquidambar*. This material demonstrates that plants possessing a number of modern features are present in northwestern North America by the middle Miocene. *Liquidambar changii* is most similar to the extant *L. acalycina* of central and south China, documenting a Beringian biogeographic connection among sweet gums during the Neogene.

MATERIALS AND METHODS

Silicified plants occur in chert deposits in the Yakima Canyon area of central Washington State, USA, in Yakima County, between the cities of Ellensburg and Yakima. Fossils were recovered from the locality referred to locally as the "County Line Holes," primarily from the area within the site designated "Hi Hole" by the original collectors, T. H. Tuggle and Raymond D. Foisy. Previously we stated that they were found within interbeds of the Sentinel Bluffs Unit of the Grand Ronde Basalt within the Museum Flow Package of N_2 Grand Ronde Basalt and dated 15.6 million years old by Ar/Ar dating (Borgardt and Pigg, 1999). Reevaluation of the deposit demonstrates that fossils occur directly within the basalt flow and not within an interbed (W. C. Rember, University of Idaho, personal communication), and additional study suggests that the stratigraphic position may be within the Wapanum Basalt and somewhat younger than previously thought (S. Reidel, Pacific Northwest National Laboratory, Richland, Washington, personal communication).

The Yakima Canyon fossils were wafered in serial section with either a Buehler Isomet Low-Speed saw, Buehler Isomet 1000, or an intermediate-sized diamond-blade saw. Sections were mounted onto microscope slides with UV-cured adhesive (UV-154, T.H.E. Company, Lakewood, Colorado, USA), ground, covered with a cover slip mounted in xylene-soluble Permount adhesive (Fisher Scientific), and studied with Darklite (Micro Video Instruments, Avon, Massachusetts, USA) optics and/or reflected and transmitted light.

Comparative material of extant inflorescences and infructescences was initially soaked in 10% ethylene diamine (Carlquist, 1982), rinsed and dehydrated, and then embedded and sectioned by standard techniques. Additional specimens were mounted on stubs for study with scanning electron microscopy (SEM). Specimens are housed as part of the Tuggle/Foisy Collection at the Burke Museum of Natural History and Culture, University of Washington, Seattle (UWBM), and in the Fossil Plant Collections, Arizona State University (ASU).

Four areas of endemism were defined for *Liquidambar* and Altingiaceae

for discussions on the biogeographic diversification, based on the distributions of extant and fossil taxa and previous biogeographic studies of the Northern Hemisphere (e.g., Wood, 1970; Patterson, 1981; Hoey and Parks, 1991; Li and Donoghue, 1999; Wen, 1999). These areas are western North America, eastern North America, Europe/western Asia, and eastern Asia.

RESULTS

Systematics

Family—Altingiaceae Lindl.

Genus—*Liquidambar* L.

Type species—*L. styraciflua* L.

Liquidambar changii—*Pigg, Ickert-Bond et Wen*, sp. nov. (Figs. 1–5, 7–9, 11–18, 20–24, 26–27, 29).

Specific diagnosis—Infructescence spherical, pedunculate, 2.5 cm in diameter; comprised of up to ~25–30 helically arranged, bilocular capsules; capsules elongate, fused at base and free distally; 2.6–3.5 mm long × 3.5–4.7 mm wide, 1–2 mature and 5–9 aborted seeds present per locule; seeds attached broadly to ventral carpel margin, maturing seeds occurring proximally, aborted seeds proximally and distally; mature seeds 1.5 mm long × 1.2 mm wide, elongate, triangular in cross section, with a slight encircling flange and lacking distal wing; integument three-zoned, prominent outer uniseriate palisade layer 125–150 μm high × 75–100 μm wide, middle region of isodiametric cells ~50–75 μm in diameter comprising most of the seed coat, inner uniseriate layer of tangentially elongate, flattened cells lining embryo cavity, aborted seeds with similar palisade integumentary layer, other integumentary layers undeveloped; infructescence margin irregular, remnants of styles persistent.

Derivation of specific epithet—The specific name, *changii*, honors Professor H. T. Chang from Sun Yat-Sen University, China, for his significant contributions to the study of the family Altingiaceae and close relatives. Professor Chang also described *Liquidambar acalycina* from central China, the closest extant relative of our new fossil species.

Holotype—UWBM 94723 (Figs. 13, 24).

Paratypes—UWBM 97418 (Figs. 1, 12), UWBM 97419 (Fig. 2), UWBM 97420 (Fig. 3), UWBM 55136 (Fig. 4), UWBM 55145 (Fig. 5), UWBM 55143 (Fig. 7), UWBM 97421 (Fig. 8), UWBM 55111 (Fig. 9), UWBM 97422 (Fig. 11), UWBM 94724 (Figs. 14, 16, 18), UWBM 55104 (Fig. 15), UWBM 55131 #9 bot (Fig. 17), ASU-YCT 11 (Figs. 20, 23, 29), UWBM 97425 (Figs. 21, 26), ASU-YC 97 (Fig. 22), ASU-2 top (Fig. 25), UWBM 55133 (Fig. 27). Not figured: UWBM 55078, UWBM 55084, UWBM 55104, UWBM 55107, UWBM 55111, UWBM 55129, UWBM 55131, UWBM 55136, UWBM 97417–97441, UWBM 97417, UWBM 97426–97441, ASU-YC-np8, ASU-YC-np26, ASU-YCT6–9, ASU-YC13.

Type locality—The "Hi Hole," one of the "County Line Holes" approximately 11.2 km north off Interstate 82, Firing Center Exit, Yakima County, on Yakima Canyon Road (T14N, R19E, NE 1/4 of NW 1/4 of Sec. 3).

Age and stratigraphy—Middle Miocene, Columbia River Basalt group.

Description—Forty-two of a total of 71 silicified infructescences of *Liquidambar changii* were studied in detail (Figs. 1–5, 7–9, 11–18, 20–24, 26–27, 29) and compared with extant *Liquidambar* (Figs. 6, 10, 19, 25, 28). Many of the specimens were found on weathered surfaces (Figs. 1, 2, 5, 12) or encased within the chert (Figs. 8, 9, 13–18, 20–24, 26, 27, 29). Others were found secondarily weathered out from the matrix, revealing their three-dimensional organization (Figs. 3, 4, 7). Still other specimens represent casts of individual fruits (Fig. 11). Although most specimens are somewhat flattened as a result of preservation, they were apparently spherical in life, like those of extant *Liquidambar* (Figs. 6, 10).

Infructesences are generally spherical and up to 2.5 cm across. All of the specimens examined contain seeds with well-developed integuments, suggesting that all are mature or nearly mature infructescences rather than inflorescences or young infructescences. Some specimens that are less well preserved are probably the remains of senescent fruits, possibly from an earlier growing season, that have partly degraded and have become part of the accumulated forest litter some time before fossilization. Some of these fragments have the roots of a later season of plants growing through their tissues (Fig. 22). The infructesences are pedunculate with the most complete peduncles 16 mm long and 2–3 mm in diameter (Figs. 1, 5, 13). Several peduncles have a woody axis up to 2 mm in diameter with a small amount of secondary xylem around 160 µm thick, surrounding the stele (Figs. 8, 9). The wood persists up into the basal area of the infructescence in these and other specimens, with the infructescence axis containing less secondary xylem at higher levels. Gum or resin ducts occur throughout the axial and fruit tissues, as is characteristic of plant tissues in *Liquidambar* (Figs. 17, 26).

Infructescences consist of dense clusters of ~25–30 bilocular fruits per head. Each fruit within the head is a bilocular capsule, with 1–2 mature seeds and up to 5–9 aborted seeds present per carpel (Figs. 3, 7, 13, 24, 26, 29). Capsules are elongate, wedge shaped, 2.6–3.5 mm long, up to 3.5 mm wide at the point of attachment to the axis and flare outward to become up to 4.7 mm across at the infructesence margin (Figs. 1, 12, 13, 24). They are formed by the fusion of ventral margins of two facing carpels (Fig. 20). Carpels are fused basally and free distally, at about one-half of their length (Fig. 24). The carpel wall is two-zoned. The inner zone is composed of short, tangentially elongate cells that extend around halfway across the carpel, interdigitating with one another from either side, resulting in a zig-zag appearance (Fig. 16). The outer zone is approximately 4–5 cells thick and commonly contains resin ducts, usually in association with the very small vascular strands (Fig. 17). Adjacent fruits abut against one another tightly and appear to be helically arranged around the central infructescence axis when followed in serial section (Figs. 7, 13).

Seeds are broadly attached to the ventral carpel margin (Fig. 14). As in extant *Liquidambar*, a larger number of ovules are initiated (Fig. 25), only some of which mature. Typically, there are a larger number of smaller, presumably aborted seeds present and only 1–2 large, maturing seeds per capsule (Figs. 24, 26, 29). As a general rule, the large maturing seeds are present proximally, toward the inner part of each fruit near its attachment to the infructesence axis, while aborted seeds typically occur both proximally, to the inside along with viable seeds, and distally, near the periphery (Figs. 13, 24, 26, 29). Mature seeds are 1.5 mm long × 1.2 mm wide, elongate, and triangular in cross section with a slight encircling flange. Seeds lack a distal wing (Fig. 27).

Seeds have a seed coat for which three zones can be well defined: a prominent outer uniseriate layer of palisade cells 125–150 µm long × 75–100 µm wide, a broad middle region of isodiametric cells 50–75 µm in diameter comprising most of the seed coat, and an inner uniseriate lining of tangentially elongate, flattened cells surrounding the embryo cavity (Figs. 14, 15, 17, 24, 26, 27). A simple raphe is present on the ventral side of the seed, closest to the placenta (Figs. 15, 27). Externally, cells of the outer palisade layer appear four-sided and relatively isodiametric in paradermal view (Figs. 16, 18). Aborted seeds have a palisade outer layer similar to that of mature seeds, but other integumentary layers are not developed (Figs. 24, 26, 29).

The most complete specimens have an irregular outer surface containing several types of protruding structures, including the outer tips of fruits, areas between adjacent fruits, and smaller bump-like protrusions (Figs. 21–23). Although no stigmatic surfaces have been discovered, and the overall length of styles is unknown, the bases of abraded outer margins of fruits and styles are present on some specimens (Figs. 21–23).

DISCUSSION

Taxonomic and phylogenetic position of Liquidambar changii—*Liquidambar changii* is assignable to the family Altingiaceae on the basis of the following morphological characters: woody, spherical infructescences composed of helically arranged, half inferior, bilocular fruits with fused bases and free distal regions, abundant resin ducts throughout the tissues, and seeds with either a distal wing or lateral flange. These

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Figs. 1–12.   Figs. 1–5, 7–9, 11–12. *Liquidambar changii* fossil infructescences. Figs. 6, 10. Extant *L. styraciflua* for comparison. **1.** Surface view of weathered specimen in longitudinal view. Note fruits and peduncle. UWBM 97418 top ×2.5. **2.** Surface view of weathered specimen in oblique transverse view. UWBM 97419 ×2. **3.** Three-dimensionally preserved specimen in oblique view showing casts of some locules (left) and remnants of carpel walls (right). UWBM 97420 ×2.7. **4.** Three-dimensionally preserved specimen showing honeycomb-like shape of peripheral rim (sclerified hypanthial tissues; at arrow). UWBM 55136 ×2.5. **5.** Longitudinally compressed specimen showing peduncle continuing into infructescence as central axis. UWBM 55145 ×3.3. **6.** Extant *L. styraciflua* infructesence that has been flattened and partially weathered, but retains persistent styles. ×1.3. **7.** Three-dimensionally preserved infructesence showing well-preserved detail of bilocular fruits. UWBM 55143 ×1.6. **8.** Transverse section through infructescence peduncle showing vascular tissues (small arrow heads at left) and gum duct (large arrow). UWBM 97421 #6 top ×11. **9.** Transverse section through infructesence peduncle showing secondary xylem development. UWBM 55111 #1 top ×20. **10.** Extant *L. styraciflua* infructesence that has been weathered sufficiently to abrade persistent styles and external edges of fruits, leaving honeycomb-like appearance of peripheral rims (sclerified hypanthial tissues) typical of fossils (compare with Figs. 3, 4, 22) ×2. **11.** Internal cast of bilocular fruit of *L. changii* with proximal area toward top. UWBM 97422, ×6.4. **12.** Infructescence on weathered surface, partly fractured to reveal carpel layers. UWBM 97418 side ×2.6.
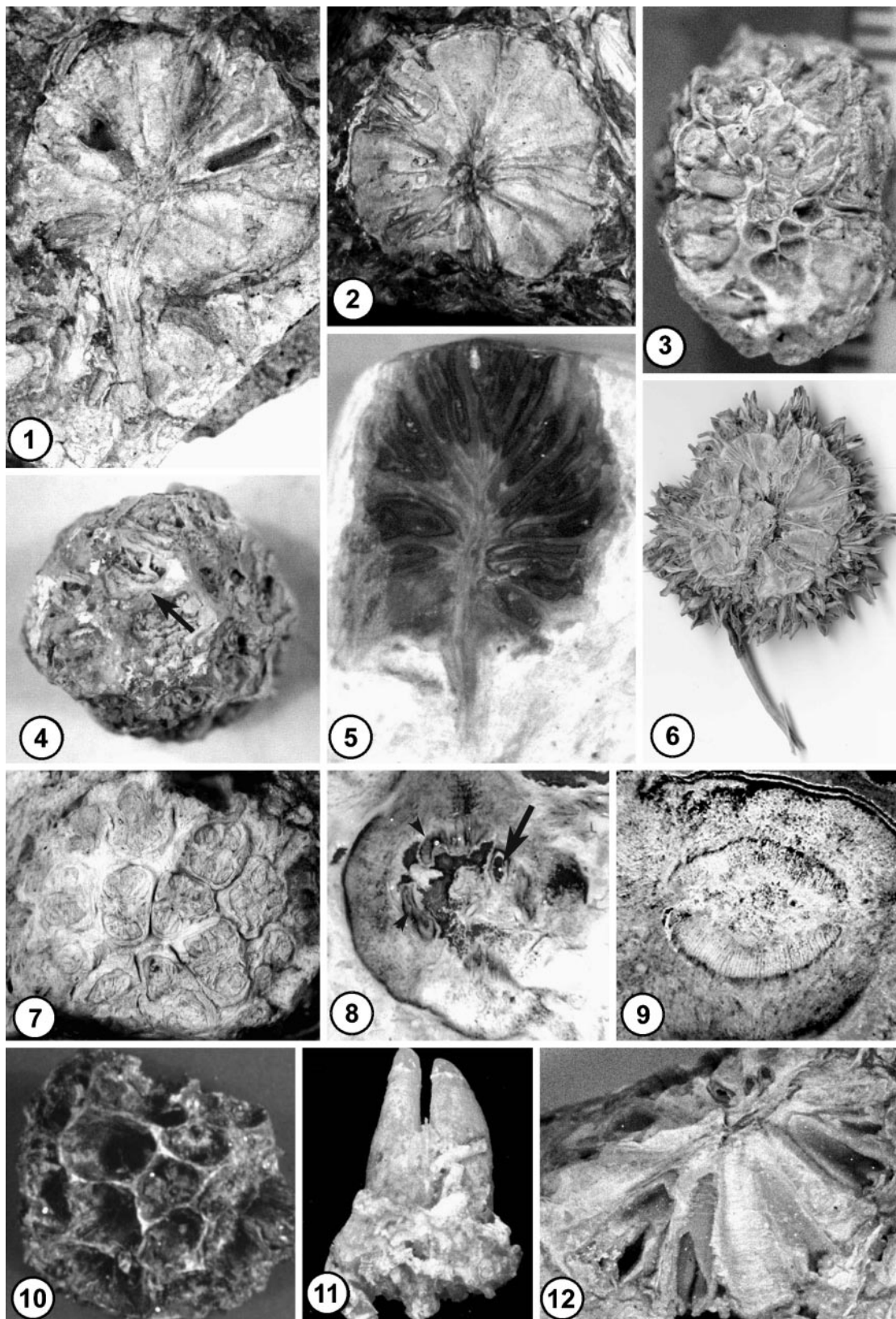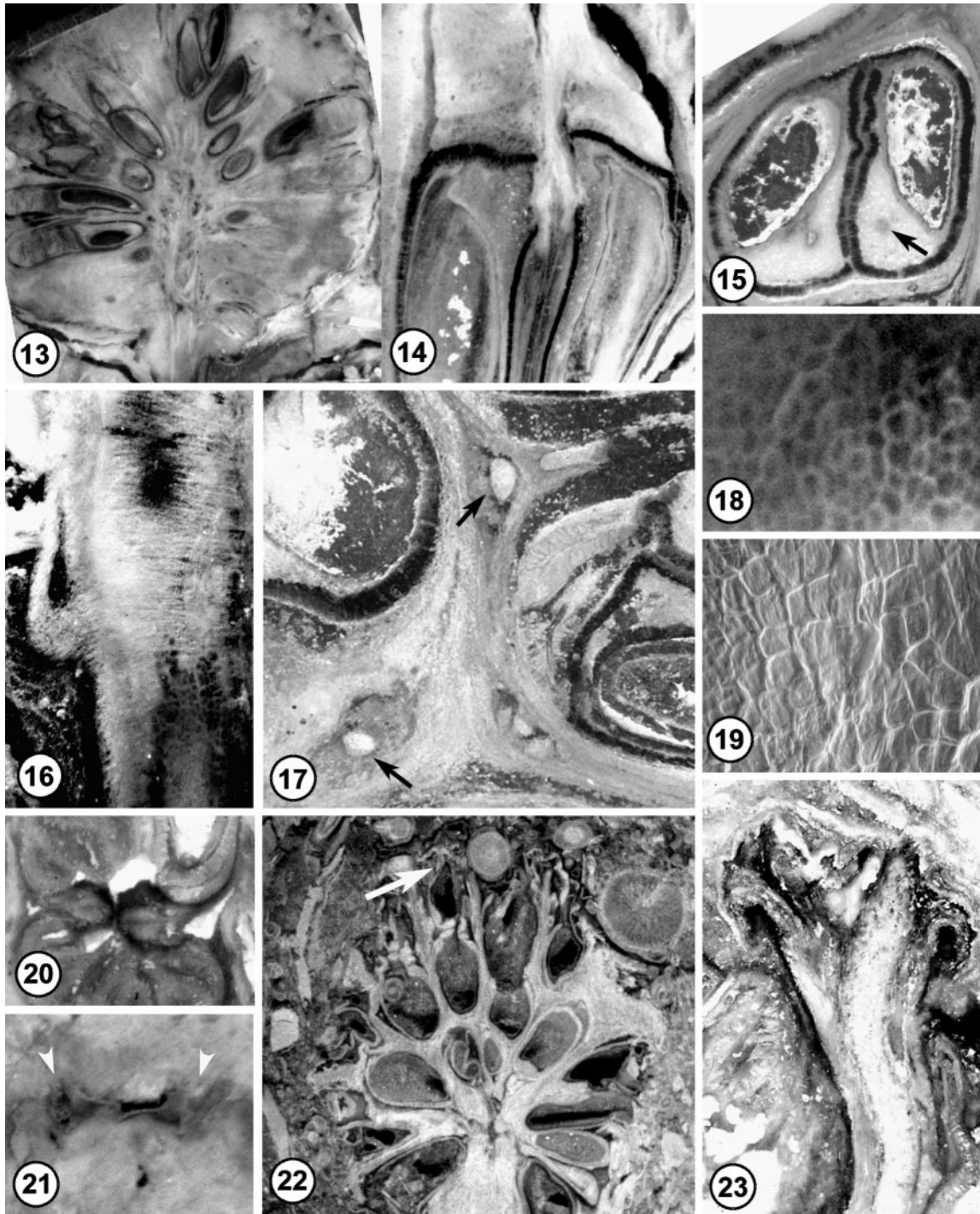
Figs. 13–23. Figs. 13–18, 20–23. *Liquidambar changii* fossil infructescences, fruits and seeds. Fig. 19. *Liquidambar acalycina* seed integument. **13.** Holotype specimen. Longitudinal section through infructesence showing peduncle, central axis, and bilocular fruits containing mature and abortive seeds. UWBM 94723 #5 top ×3.8. **14.** Longitudinal section through fruit showing broad attachment of mature seeds. UWBM 94724 #2 bottom ×15. **15.** Transverse section through carpel showing two mature seeds, each with three-zoned integument and raphe (arrow). UWBM 55104 #2 top ×20. **16.** Paradermal section of carpel showing transversely aligned cells of inner carpel layer (top), and paradermal section through outer layer of seed integument (bottom). UWBM 94724 #4 top ×20. **17.** Transverse section through several fruits showing adjacent carpels containing mature seeds and prominent gum ducts (arrows) in carpel wall. UWBM 55131 #9 bottom ×22. **18.** Paradermal section through outer cells of seed integument, showing integument surface pattern. UWBM 94724 #4 top ×25. **19.** Scanning electron microscopy of *L. acalycina* seed integument (compare with Fig. 18). ×36. **20.** Detail of Fig. 29 showing central area of bilocular fruit at level of fusion. ASU-YCT 11 #1 bottom ×15. **21.** Detail of infructescence margin showing small persistent styles (arrows). UWBM 97425 #1 top ×3. **22.** Oblique longitudinal section of infructescence showing several fruits with persistent styles (arrow) and other ornamentation. ASU-YCT 97 B top ×3. **23.** Detail of persistent style. ASU-YCT 11 #2 bottom ×27.
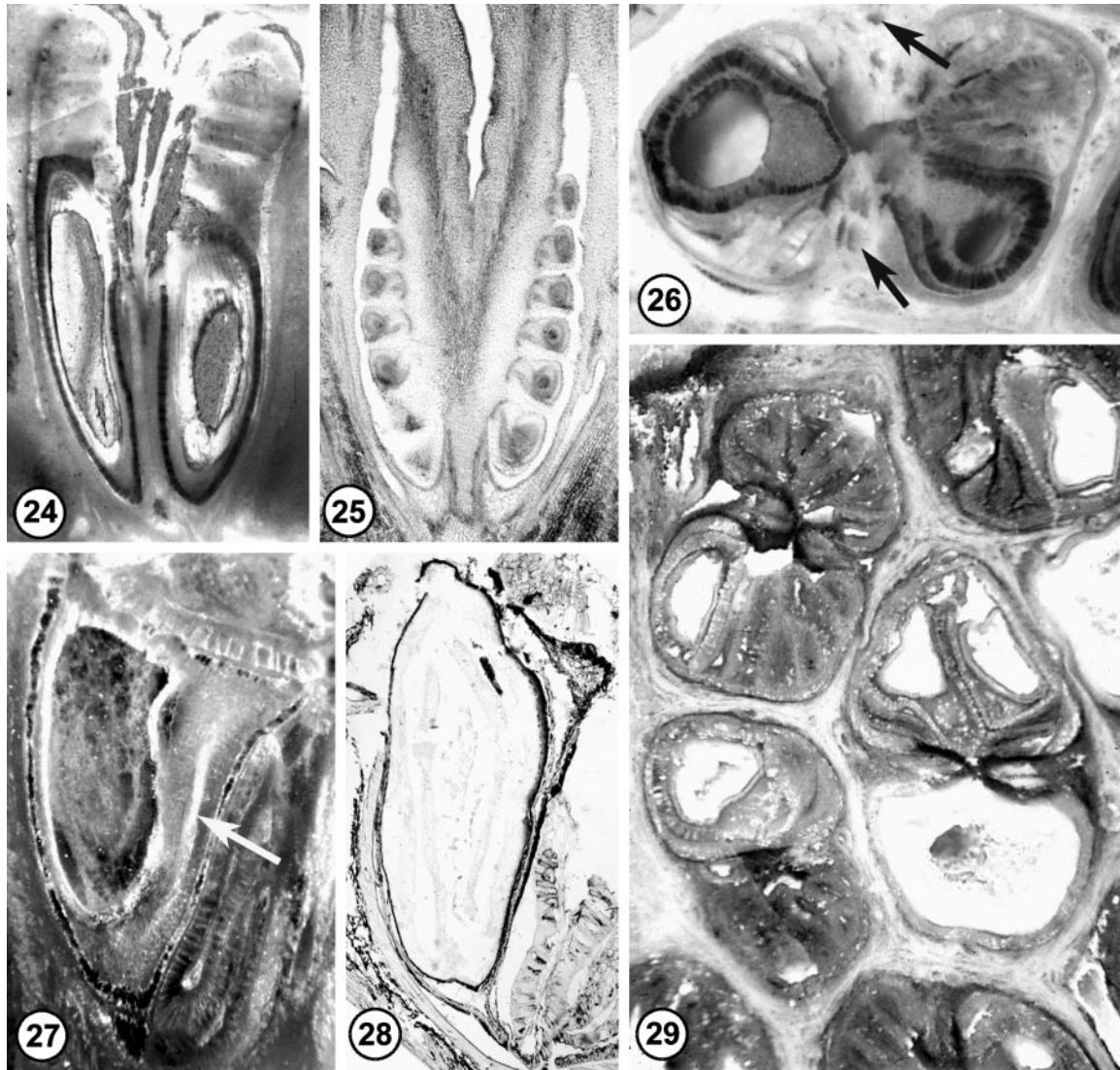
Figs. 24–29.   Figs. 24, 26–27, 29. *Liquidambar changii* fruits and seeds. Fig. 25. *L. styraciflua* young fruit. Fig. 28. *L. acalycina* seed. **24.** Holotype specimen. Longitudinal section through a bilocular fruit showing mature seeds proximally and aborted seeds distally. Carpels are fused proximally and free distally. UWBM 94723 #5 top ×12. **25.** Longitudinal section of young *L. styraciflua* fruit with developing ovules or seeds. ASU 2 top ×17. **26.** Transverse section of fruit showing two large, mature seeds and several abortive seeds. Note integumentary layers of mature seeds and gum ducts (arrows) in ventral carpel walls. UWBM 97425 #1 bottom ×18. **27.** Longitudinal section through mature seed showing integumentary layers including prominent outer palisade layer, central layer with isodiametric cells and raphe (arrow), and inner layer surrounding the embryo cavity (compare with Fig. 28). UWBM 55133, #7 bottom ×20. **28.** Longitudinal section through extant *L. acalycina* seed showing triangular shape of seed (compare with Fig. 27) ×25. **29.** Transverse section through infructescence showing several bilocular fruits in cross section. ASU-YCT 11 #1 bottom ×10.

characters delimit the family Altingiaceae in comparison to other hamamelids with which it has been previously allied (Bogle, 1986; Endress, 1989a, b; Ferguson, 1989; Hufford, 1992). Reproductive features that have usually been cited as differing between *Liquidambar* and *Altingia* include size and shape of inflorescence, number of florets (and fruits) per head, degree of persistence of styles on the infructescence, and mode of fruit dehiscence. *Semiliquidambar* has intermediate features.

Characters that place the fossil in the genus *Liquidambar* include size and shape of bilocular fruits, details of the carpel wall and broad, persistent styles. In comparison with extant species, *L. changii* is most similar to the eastern Asian species *L. acalycina*. The wedge-shaped carpels in the biloculate fruits of *L. changii* are most similar to those of *L. acalycina*, in contrast to the longer and more slender carpels of other *Liquidambar* species. Like this extant species, *L. changii* has triangular-shaped seeds with a centrally thickened flange, rather than a prominent distal wing (Figs. 27, 28). These two species also possess seed coats with a surface pattern of mostly four-sided, short, more or less barrel-shaped cells and a carpel lined with tangentially oriented, laterally alternate cells that each span about half the width of the carpel and interdigitate toward the center of the carpel (Figs. 18, 19). *Liquidambar orientalis*, *L. formosana*, *L. styraciflua*, and *L. macrocarpa* all have narrow seeds with elongate distal wings rather than relatively shorter, broader seeds with encircling flanges. The infructescence of *L. formosana* is further distinguished by the presence of elongate structures that are lacking or inconspicuous in oth-

er species. Harms (1930) referred to these structures as "Borsten" (setae) and interpreted them as being inserted between the fruits. Others have suggested alternative homologies (Bogle, 1986; Ferguson, 1989), including phyllomes (Bogle, 1986), staminodes (Tong, 1930), or perianth parts (Oliver, 1867; Chang, 1962, 1973). Some authors have suggested that they are equivalent to the more reduced ornamentation of other *Liquidambar* species or those seen in some *Altingia* species (Chang, 1962, 1973); however, the relationships of these structures remain unresolved. *Liquidambar styraciflua* and *L. macrocarpa* (which may be conspecific), previously have been distinguished from *L. orientalis* by rather ambiguous characters of the relative thickness of the sclerified hypanthial tissues (peripheral rim) and the degree and type of external ornamentation, with *L. orientalis* tending to have thicker and smoother peripheral rims than the North American forms. Some authors have even suggested synonymy of these two disjunct species because of the relatively subtle morphological differences between their infructescences and the continuous, clinal variation among their leaves (see Ferguson, 1989).

Liquidambar changii and *L. acalycina* share some features with *Altingia* including shorter, broader fruits, and seeds with a central flange rather than a distal wing; however, *Altingia* differs in several features from these two species, including details of carpel anatomy, resin duct distribution, and micromorphology of carpel wall surface. In contrast to the shorter, interdigitating cells lining the inner carpel wall in *L. changii* and *L. acalycina*, carpel walls of *Altingia* have tangentially elongated cells that are parallel to one another and appear to extend the breadth of the carpel.

This investigation has demonstrated to us the need for more detailed understanding of the morphological and anatomical variation among fruits of the Altingiaceae. Previous studies of this group have been focused on floral anatomy and development (Wisniewski and Bogle, 1982; Bogle, 1986; Igersheim and Endress, 1998), pollen (Chang, 1958, 1959, 1964; Kuprianova, 1960; Bogle and Philbrick, 1980; Zavada and Dilcher, 1989); leaves (Chang, 1962, 1979; Li and Hickey, 1988; Pan et al., 1990); and wood anatomy (Metcalfe and Chalk, 1950; Greggus, 1959; Rao and Purkayastha, 1972; Huang, 1986). Several authors have surveyed seed coat anatomy and micromorphology of a few species in relationship to other hamamelids (e.g., Melikian, 1973; Mohana Rao, 1974; Zhang and Wen, 1996), however, fruit and seed characters which may be of value in better delimiting species are not known for all taxa. In connection with ongoing investigation of the phylogeny within the Altingiaceae, we are currently surveying this interfamilial variation (Ickert-Bond, Pigg, and Wen, unpublished manuscript).

Our taxonomic delimitation of *Liquidambar changii* as a distinctive new species is based on seed and fruit morphological and anatomical characters. The decision to name a new species rather than placing this material in the extant species *L. acalycina* is based on the recognition that not all of the diagnostic characters of *L. acalycina* can be determined from the fossil material. *Liquidambar changii* is, however, thought to be close to this modern species.

The Tertiary fossil record, particularly the Neogene, contains *Liquidambar* infructescences fairly commonly that are preserved as compression/impression remains. Whereas *Liquidambar changii* shows a suite of distinctive anatomical features that can, for the first time in the fossil record, be compared with extant species in detail, compression–impression remains provide an external view of crushed infructescences. Since it is not possible to deduce the features of internal anatomical structure as seen in *L. changii* from this preservational type, they cannot be compared in detail. Several geographically close floras of similar age contain *Liquidambar* infructescences that are preserved as compression/impression remains. Although these fossils lack the preservation that shows anatomical details we see in *L. changii*, they are of generally similar size and shape and may be closely related to *L. changii*, but fossilized in a different preservational mode. Although it is difficult to resolve these relationships, it is of value to point out the floristic similarities. Among the other Miocene localities of western North America that include *Liquidambar* leaves and infructescences are the Latah Formaton of eastern Washington, the Clarkia and Emerald Creek floras of adjacent Idaho, and the Ellensburg, Washington, and Succor Creek floras, among others (Smiley, 1963; Graham, 1965, 1999; Smiley and Rember, 1985; Rember, 1991). They are associated with three- and five-lobed leaves called *Liquidambar pachyphyllum* Knowlton (Chaney and Axelrod, 1959 and synonymy therein). Further analysis of the compression—impression species of *Liquidambar* in light of the anatomy seen in *L. changii* may allow for better interpretation of these less-informative fossils. The analysis will also enhance our understanding of the patterns of morphological differentiation for disjunct plants of the Northern Hemisphere, in which the hypothesis of morphological stasis has sometimes been applied (Wen, 1999).

Biogeographic implications—*Liquidambar* has been employed to construct the relationships of major biogeographic areas (eastern North America, western Asia, and eastern Asia) of the Northern Hemisphere (Hoey and Parks, 1991, 1994; Li et al., 1997, 1999). Molecular evidence so far has suggested that *L. styraciflua* from eastern North America and *L. orientalis* from western Asia form an intercontinental sister-species pair among the four extant species sampled. The most likely explanation for the pattern in *Liquidambar* is the migration of species along the Tethys seaway in the Tertiary and across the North Atlantic land bridge (Tiffney, 1985a, b). Our fossil evidence presented here suggests that *Liquidambar changii* is most closely related to the eastern Asian *L. acalycina*. Such a close relationship between the two species may be explained by migration across the Bering land bridge (Hopkins, 1967) and thus suggests a Beringian biogeographic track (Wen, 1999; Donoghue et al., 2001) between eastern Asia and western North America during the Miocene. The Beringian connection has been reported in several recent studies on modern Asian-North American disjunct plants, such as *Aralia* L. sect. *Aralia* (Wen et al., 1998), *Hamamelis* L. (Wen and Shi, 1999; Li et al., 2000), *Osmorhiza* Raf. (Wen et al., 2002), *Panax* L. (Wen and Zimmer, 1996); and *Torreya* Arn. (Li et al., 2001). The Beringian connection was emphasized by Li (1952) and Graham (1972) in explaining the evolution of the Asian and North American disjunctions. Our study provides anatomical fossil evidence that would help support a Beringian biogeographic track in the middle Miocene.

Modern and fossil evidence documents at least these two biogeographic tracks for the Altingiaceae within the Northern Hemisphere and thus underscores the complexity of the biogeographic history of the family throughout the Neogene. Such complexity has been reported in studies of other plant groups such as *Acer* L. (Wolfe, 1981), Juglandaceae (Man-

chester, 1987), and *Prunus* L. (Lee and Wen, 2001), as well as comparisons of many fossil (Manchester, 1999) and modern groups (Wen et al., 1996; Donoghue et al., 2001).

Our results strongly support the theory that the classic eastern Asian and eastern North American disjunction as it is seen today largely represents the relicts of temperate forests that achieved their maximum development and distribution during the Tertiary, especially the middle Miocene (Wen, 1999). In *Liquidambar*, at least two biogeographic tracks are supported, suggesting that development of the temperate forests involved complex migrations of plants. It is thus vitally important to incorporate phylogenetic evidence from both modern and fossil taxa to construct the biogeographic history of the Northern Hemisphere.

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