

AN EXTINCT GENUS OF SALICACEAE BASED ON TWIGS WITH ATTACHED FLOWERS, FRUITS, AND FOLIAGE FROM THE EOCENE GREEN RIVER FORMATION OF UTAH AND COLORADO, USA¹

LISA D. BOUCHER,^{2,5} STEVEN R. MANCHESTER,³ AND WALTER S. JUDD⁴

²Department of Biology, University of Nebraska-Omaha, Omaha, Nebraska 68182 USA;

³Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611 USA; and

⁴Department of Botany, University of Florida, Gainesville, Florida 32611 USA

A newly recovered twig with attached leaves and flowers from the Eocene Green River Formation of Utah provides the basis for recognizing a new, extinct genus of Salicaceae sensu lato (s.l.). *Pseudosalix handleyi* gen. et sp. nov. has alternate lanceolate leaves with pinnate, semicraspedodromous venation and a serrate margin with glandular teeth. The inflorescence is terminal on the twig and is unisexual, composed of flowers organized in a paniculoid cyme, with lateral paraclades of pedicellate flowers. The attached pistillate flowers have four prominent sepals that are valvate in bud, spreading but basally fused at anthesis; the single pistil of each flower is ovoid with three or four longitudinal sutures, indicating development to a capsular fruit. Three or four recurved styles radiate from the apex of the pistil, each with a distal globose stigma. The infructescence, verified by attachment to twigs with the same kind of leaves, bore capsular fruits of three and four valves. Associated but unattached, staminate flowers also have four well-developed, basally connate sepals. They are pedicellate and bear several stamens, each with a short filament and globose anther. The available morphological characters place the fossil species within the Salicaceae s.l. as an immediate sister to the clade containing *Populus* and *Salix*. Although the likely outgroup genera (including *Itoa*, *Poliothyrsis*, *Carrierea*, and *Idesia*) to tribe Saliceae all occur in Asia today and not North America, the occurrence of both *Pseudosalix* and *Populus* in the Eocene of Utah raises the possibility of a North American origin for the Saliceae.

Key words: Eocene; flower; Green River Formation; inflorescence; infructescence; *Pseudosalix handleyi*; Salicaceae; Utah.

Fossil plant specimens showing physical attachment between foliage and reproductive structures are extremely rare but are exceedingly important to prove the conspecificity of organs that are usually found isolated. Sometimes the recovery of fossil twigs with mutually attached leaves and fruits or flowers provides sufficient morphological characters to facilitate critical evaluation of systematic position relative to extant taxa. Here we introduce a new extinct genus of Salicaceae based on twigs with attached leaves, inflorescences, and infructescences from the Middle Eocene Green River Formation of eastern Utah and western Colorado, USA. These specimens allow us to link vegetative and reproductive organs that are usually found isolated in the lacustrine shales.

The family Salicaceae, formerly circumscribed narrowly to include only *Populus* and *Salix*, was recently emended to include most of the noncyanogenic genera formerly placed in Flacourtiaceae (Chase et al., 2002). The revised classification is necessary because *rbcL* and morphological characters indicate that traditional Flacourtiaceae are rendered paraphyletic if *Salix* and *Populus* are treated as a distinct family (Judd, 1997;

Chase et al., 2002; Judd et al., 2002). Many earlier systematists also noted the similarity between *Populus* and *Salix* and various genera formerly attributed to Flacourtiaceae, especially the genera *Itoa*, *Poliothyrsis*, *Carrierea*, *Idesia*, *Bennettiodendron*, and other members of the tribe Flacourtiaceae (Holm, 1969; Dahl, 1972; Hegnauer, 1973; Keating, 1973; Meeuse, 1975; Miller, 1975; see also discussion in Judd [1997]). In this article, we introduce the new genus *Pseudosalix* and interpret its phylogenetic position to be within the paraphyletic tribe Flacourtiaceae, as the immediate sister group to the clade containing extant *Salix* and *Populus* (tribe Saliceae of Chase et al. [2002]).

MATERIALS AND METHODS

The holotype, which consists of attached leaves and pistillate flowers, is housed in the paleontological collection at the Utah Museum of Natural History, Salt Lake City, USA (UMNH). The paratypes, one a twig with attached leaves and fruits, is housed in the Bruce Handley collection at the Museum of Paleontology, University of California, Berkeley, USA (UCMP). Additional specimens of isolated leaves, staminate flowers, and fruits were examined at UCMP, the Florida Museum of Natural History at University of Florida, Gainesville, USA (UF), the Denver Museum of Nature and Science, Denver, USA (DMNH), and the Smithsonian Institution, Washington, D.C., USA (USNM).

The fossils were collected from lacustrine shales of the Parachute Creek Member of the Green River Formation in the vicinity of Bonanza, Utah, USA. The very fossiliferous horizon, from which these specimens were collected, has been traced laterally over several kilometers and is situated about 129 m above the Mahogany marker bed (Bruce Handley, personal communication) and includes UCMP site PB02016 and UF sites 15753, 15884. The fossiliferous layers correspond approximately to the level of the Wavy tuff, recently dated by ⁴⁰Ar/³⁹Ar laser fusion of biotite and hornblende crystals at 48.13 ±

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⁵ E-mail: boucher@unomaha.edu.

0.71 and 48.22 ± 0.71 million years (Machlus et al., 2002), and are considered early Middle Eocene.

The flora of the Green River Formation in eastern Utah and adjacent western Colorado was monographed by Knowlton (1923), Brown (1929, 1934), and MacGinitie (1969), but new discoveries and continuing comparative work have led to improved understanding of the floristic composition. Also common at this horizon of the Parachute Creek Member are leaves of *Macginitiea* (Platanaceae; Manchester, 1986), leaves and fruits of *Cedrelospermum* (Ulmaceae; Manchester, 1989), leaves and fruits of *Populus* (Salicaceae; Manchester et al., 1986), and foliage of *Parvileguminophyllum* (Leguminosae; Call and Dilcher, 1994).

Fine details of leaf margins, styles, and sepals were exposed by removal of thin layers of sediment with a needle under the dissecting microscope. Exposure of the stipule scars required the brushing away of carbonaceous matter from the impression surface. Cellular and structural details were further examined by preparing silicone casts of the flowers, which were subsequently observed with a Philips Model 515 (Philips Electron Optics, Hillsboro, Oregon, USA) scanning electron microscope (SEM).

The initial keying to family was performed using computerized software including MEKA version 3.0 for Windows using the "angiofam" database (Duncan and Meacham, 1996) and INTKEY version 5.0 (Watson and Dallwitz, 2000). The terminology used in description of the fossils follows that of the Leaf Architecture Working Group (1999) for leaf architecture and Judd et al. (2002) for morphology of inflorescences, flowers, and fruits. Herbarium specimens from Harvard University (Gray Herbarium and Arnold Arboretum) and University of Florida (FLAS) were consulted in the comparative analyses.

SYSTEMATICS

Genus—*Pseudosalix* gen. nov. Figs. 1–33.

Generic diagnosis—Plant with unisexual tetrasepalous flowers borne in a compound cymose inflorescence. Stigmas three or possibly four, prominently expanded. Fruit a capsule of 3–4 valves. Leaves slender, serrate with glandular teeth and pinnate venation with frequent intersecondary veins.

Type species—*Pseudosalix handleyi* gen. et sp. nov.

Specific diagnosis—As for genus.

Holotype—UMNH PB-1 (Figs. 1–8, 16, 18–20).

Paratypes—UCMP 390080 (locality UCMP PB02016; specimen with attached leaves and infructescence), 390082 (locality UCMP PB02016; detached infructescence).

Other specimens—UCMP 390084, 390085, UF 15753-22965 (leaves); DMNH 24354 (locality DMNH 323) (detached pistillate flower); UF15753-22931, UF 15753-34806, UF 15753-34807, UF 15884-8925, USNM 38625, USNM 38628, UCMP 390081 (locality UCMP PB02016), DMNH 23391 (locality DMNH 2347), DMNH 23392 (locality DMNH 316), DMNH 24355, 24454 (locality DMNH 323) (staminate flowers).

Etymology—*Pseudo*, meaning "false," and *Salix*, emphasizing that it is not the genus *Salix*, although the leaves are similar. The specific epithet recognizes the contributions of Bruce Handley, whose magnificent collection of Green River fossil plants, now housed at UCMP, facilitated the completion of this study.

Description—Inflorescence terminal, 7.9–8.2 cm long and 2.0–2.7 cm wide, compound, panicle-like, with an apparently

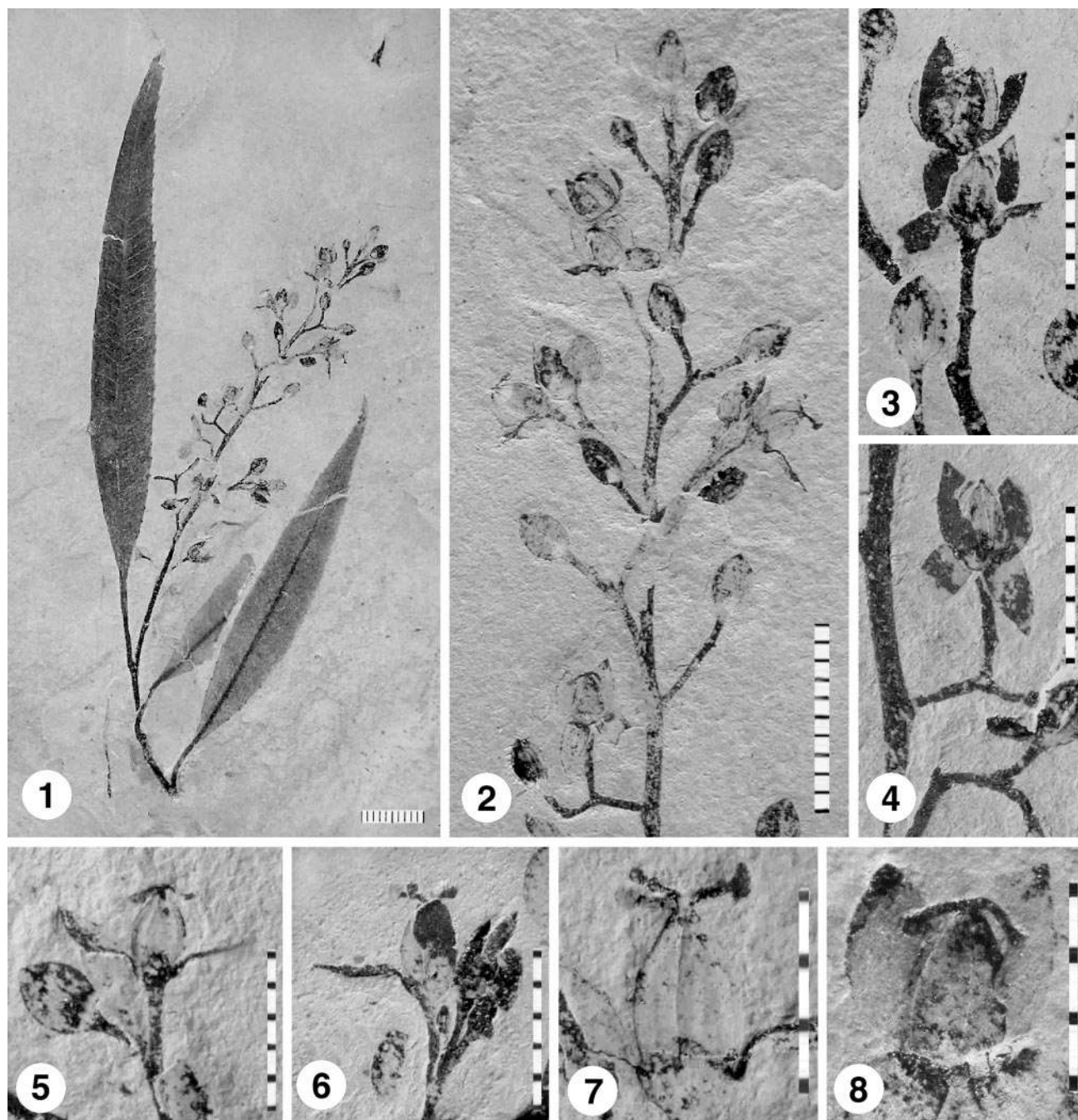
determinate main axis and cymose side branches (Figs. 1–2). Buds and flowers pedicellate, pedicels 2.5–4 mm long with bract scars at their junction with peduncle (Fig. 3). Flower buds ovoid, smooth, about 3 mm long and 2 mm wide with valvate sepals. Flowers unisexual, apetalous. Pistillate flowers actinomorphic with hypogynous calyx of four prominent, basally connate sepals; staminodes lacking (Figs. 3–4 and 24). The single pistil of each flower consisting of a smooth, ovoid ovary about 3 mm long and 2 mm wide, rounded basally and apically, with at least three (perhaps four in some specimens) recurved style arms, 0.9 mm long, radiating from the apex and terminated by globose stigmas (Figs. 5–8). Three to four longitudinal grooves on the ovary wall (Figs. 7–8). Attached opened flowers 7 mm in diameter, detached flowers up to 11 mm in diameter (Fig. 28). Fruits ovoid capsules 5.5–7.5 mm long and 3.0–4.5 mm wide with 3–4 valves, splitting longitudinally (Figs. 12–15).

Associated staminate flowers, pedicellate, actinomorphic, apetalous, four- and rarely five-sepalled, 7.0–9.5 mm in diameter, with approximately 30 stamens, consisting of 1.5–2 mm long filaments, and globose anthers 0.4–0.5 mm in diameter (Figs. 29–33).

Leaves simple, attached alternately along the axis with an internode width of 1.0 cm (Figs. 1 and 9). Laminae generally symmetrical and slender, ovate to oblong, up to 8.3 cm long and 1.0 cm wide; length to width ratio is 6 : 1 to 15 : 1. Petioles up to 1.4 cm long and about 1 mm wide with marginal attachment and not significantly swollen at the base. Stipule scars present on the twig immediately lateral to the attachment of the petiole (Fig. 19). Lamina base and apex both acute; base decurrent to cuneate; apex shape acuminate to straight. Margin serrate with circular glands on the teeth (Figs. 16–18). Venation is pinnate with a moderately thick midvein. Secondary venation semicraspedodromous with irregular spacing, uniform angles of 50–60 degrees from the midvein, and with frequent weak intersecondary veins (Figs. 16, 21). Position of intersecondaries somewhat variable, but often central between adjacent secondary veins. Secondary veins usually branch before reaching the margin, sending one branch to the tooth and the other to loop with the supra-adjacent secondary (Figs. 21–23). Each tooth usually enervated by three veins: the principal vein of the tooth, often extending directly from the secondary vein and entering the tooth medially and a pair of adjacent, slightly thinner accessory veins on each side that originate from veins above and below (Fig. 20). Teeth somewhat irregularly spaced, typically six per centimeter. Space between secondary veins approximately equivalent to the distance between successive teeth along the margin. Teeth simple; each one less than 1 mm from base to apex; however, there appear to be two orders of teeth near the middle of the lamina, arranged by alternating size along the margin (Fig. 16). Tooth shape concave on the apical side of the tooth and convex to straight on the basal side, with a rounded sinus. The tooth apex ends in a circular gland (Figs. 18, 20–23). Tertiary venation random reticulate to possibly alternate percurrent, with the vein angle variably obtuse to the primary vein. Highest order of veins appears to be dichotomizing quaternary veins, but not readily apparent. Areoles not preserved.

DISCUSSION

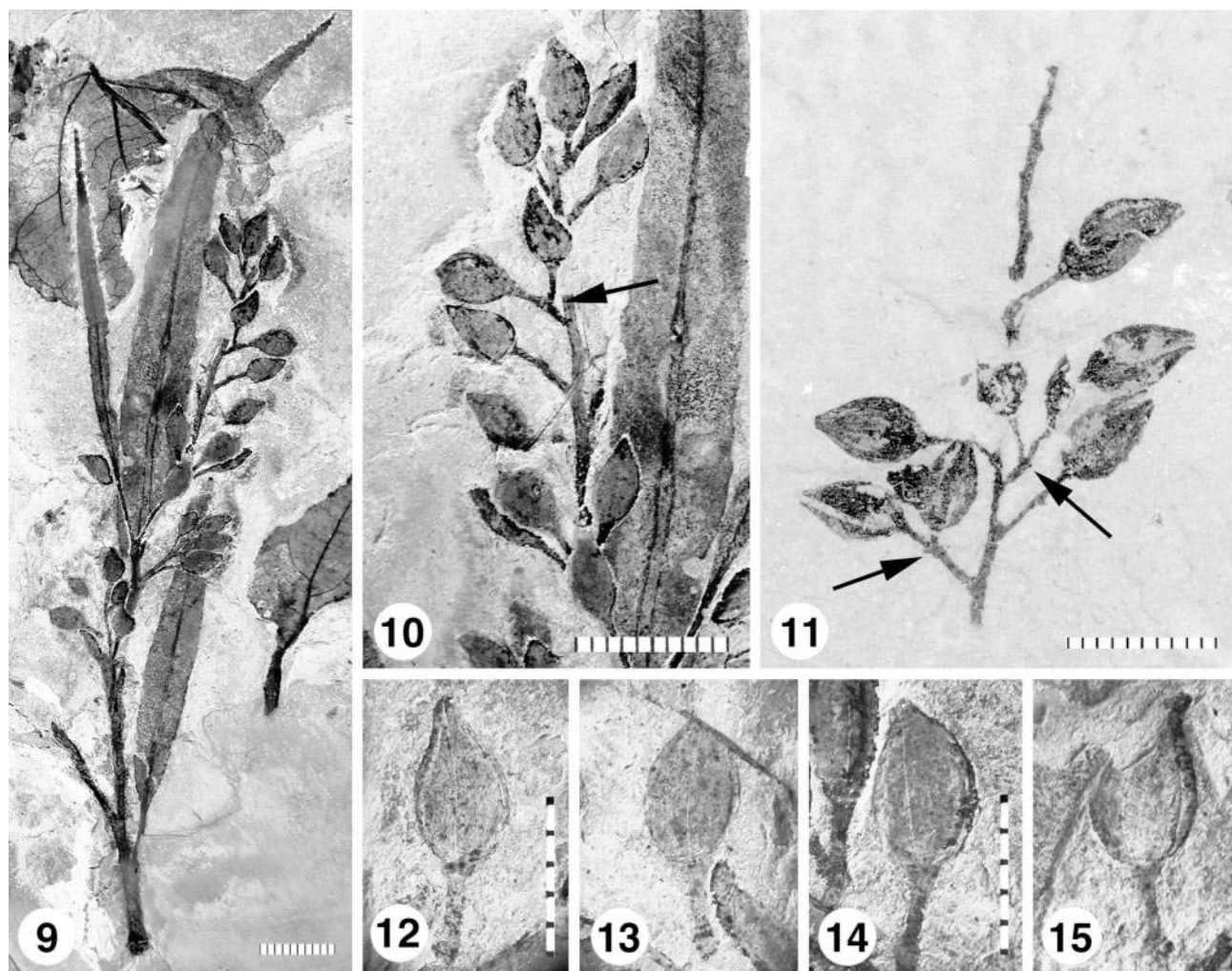
The leaves of *Pseudosalix handleyi*, when found isolated, would likely have been confused with those of *Salix* because



Figs. 1–8. *Pseudosalix handleyi* gen. et sp. nov., twig with attached leaves and pistillate inflorescence. Holotype, UMNH PB-1 a, b. **1.** Complete twig showing attached inflorescence and alternate phyllotaxy. Scale bar = 1 cm. **2.** Detail of inflorescence from Fig. 1. Note compound, rather than racemose, structure. Scale bar = 1 cm. **3.** Pistillate flowers, with prominent opening sepals, counterpart to the specimen in Figs. 1 and 2. Scale bar = 0.5 cm. **4.** Detail of branched inflorescence from Fig. 2, showing flower with four sepals. Scale bar = 0.5 cm. **5.** An unopened flower attached below an opened flower that has two sepals in sectional view and an ovary with two suture lines that demarcate three longitudinal valves of the developing capsular fruit. Scale bar = 0.5 cm. **6.** Cyme with one opened flower with apical style arms protruding. Scale bar = 0.5 cm. **7.** Counterpart of the flower in Fig. 6, showing one of the longitudinal grooves that divides the ovary into three valves and three style arms with enlarged distal stigmas. Scale bar = 0.3 cm. **8.** Opened flower showing two of the style arms and stigmas. The ovary shows two longitudinal ridges that define the margins of three valves of the developing capsular fruit. These two ridges, together with the additional pair observed on the counterpart half of the same flower (Fig. 4), indicate that the ovary would have developed into a four-valved capsule. Middle Eocene of Bonanza, Utah. Scale bar = 0.3 cm.

of the shared characters of elongate lamina, semicraspedodromous venation, and salicoid teeth. However, the fortuitous discovery of twigs with attached inflorescences and infructescences proves that this species was distinct

from all modern *Salix*, *Populus*, and other Salicaceae sensu lato (s.l.). Because the organs are commonly found detached, we discuss the leaves and reproductive organs separately below.

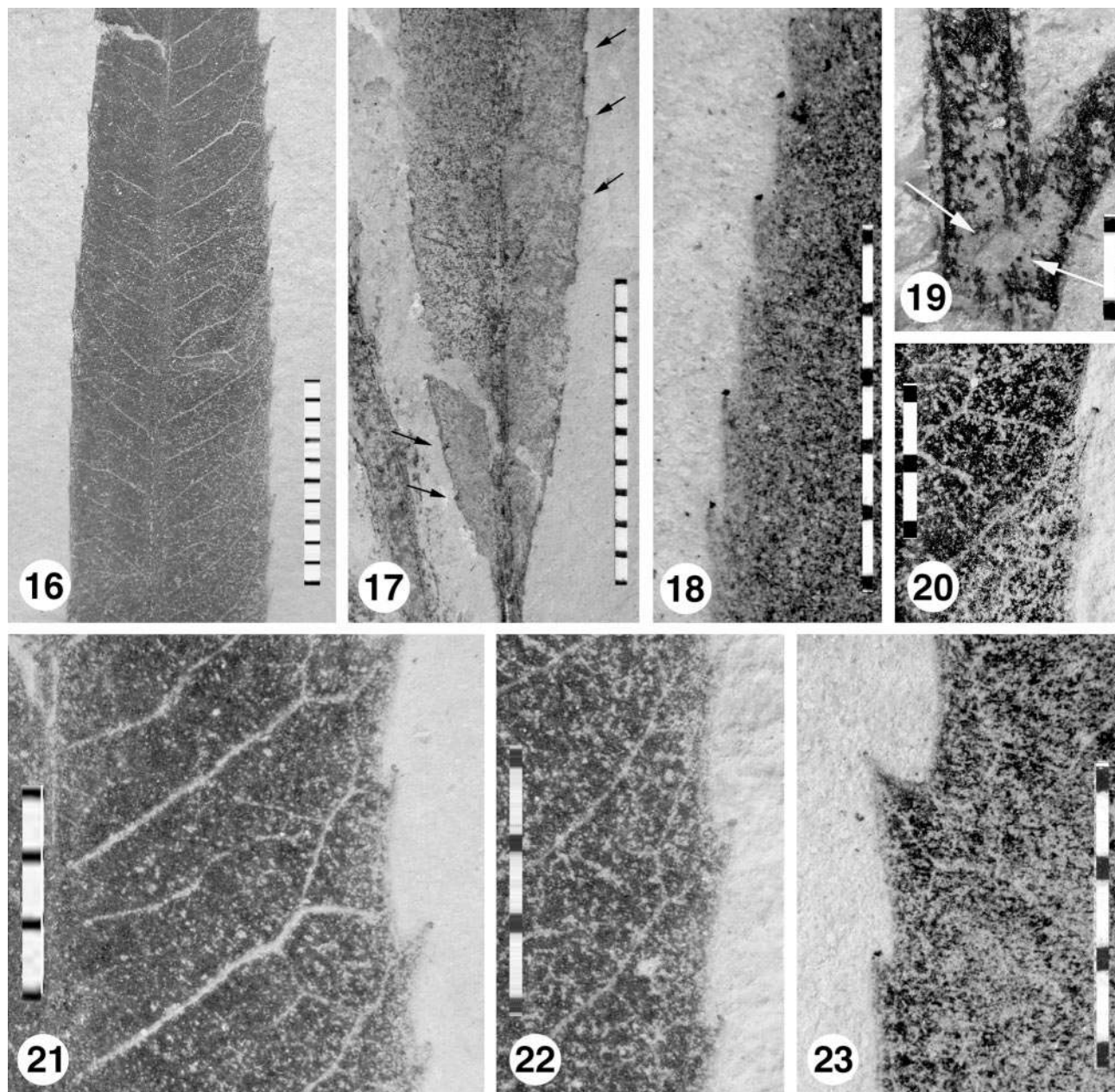


Figs. 9–15. *Pseudosalix handleyi* gen. et sp. nov., leaves, infructescences, and fruits. **9.** Twig with attached alternate leaves and infructescence, UCMP 390080. Scale bar = 1 cm. **10.** Counterpart from the specimen in Fig. 9, showing branched inflorescence. Arrow indicates one of the cymules. Scale bar = 1 cm. **11.** Detached compound infructescence with several intact capsules. Arrows indicate secondary branching that is not known in *Populus* and *Salix*. UCMP 390082. Scale bar = 1 cm. **12–13.** Matching counterparts of a capsule from the specimen in Figs. 9 and 10, showing collectively four distinct longitudinal ribs, indicating a four-valved fruit. Swelling of pedicel at base of the fruit represents the scar from the detached calyx. Scale bar = 0.5 cm. **14–15.** Matching counterparts of a capsule from the specimen in Figs. 9 and 10, documenting a fruit with three valves. Middle Eocene of Bonanza, Utah (UCMP locality PB02016). Scale bar = 0.5 cm.

Leaves—The spherulate gland at the tooth apex is most similar to what has been termed a salicoid tooth (Hickey and Wolfe, 1975; Judd et al., 2002). There is no indication that it was deciduous, as the setae of theoid teeth. The tooth apex with its gland is enervated by a medial principal vein (secondary or intersecondary) and usually a pair of thinner accessory veins, one along the apical margin of the tooth, the other along the basal flank (Fig. 20). Fine venation in the leaf appears to be poorly developed, but this may be due to poor preservation of the higher orders of veins. Based on tertiary venation and the relatively poor petiole-blade separation, the leaf is considered low ranking, i.e., is not highly organized (Leaf Architecture Working Group, 1999). Although stipules are not directly observed on the fossil twigs, a pair of scars immediately below the petiole attachment (Fig. 19) are positioned precisely where the stipules would be expected, indicating that stipules were likely present, but deciduous.

Among leaves previously described from the Green River

flora, the leaf of *Pseudosalix handleyi* is most similar to *Salix cockerelli* Brown and *S. longiacuminata* Brown (Brown, 1934; USNM 38594–38596, 168963, 38587, 38588). However, in those syntypes of *S. cockerelli* with the base preserved, the base is obtuse and more rounded than in *Pseudosalix handleyi*. In addition, there are notable differences in the venation of *S. cockerelli*. The secondary veins and intersecondaries are both more prominent and organized in *S. cockerelli* than in *P. handleyi* leaves. Further, the spacing and looping of the secondaries are better defined in *S. cockerelli* and the tertiary venation is mixed alternate-opposite percurrent. In *S. longiacuminata*, the secondary veins are more prominently looped than in *P. handleyi*, and the angle of the secondary veins increases significantly towards the base. However, it is possible the mature vegetative leaves of *Pseudosalix* were larger and perhaps varied in their leaf architecture. Other leaves comparable to *Pseudosalix*, but not previously described from the Green River, are listed above under “Other specimens.”

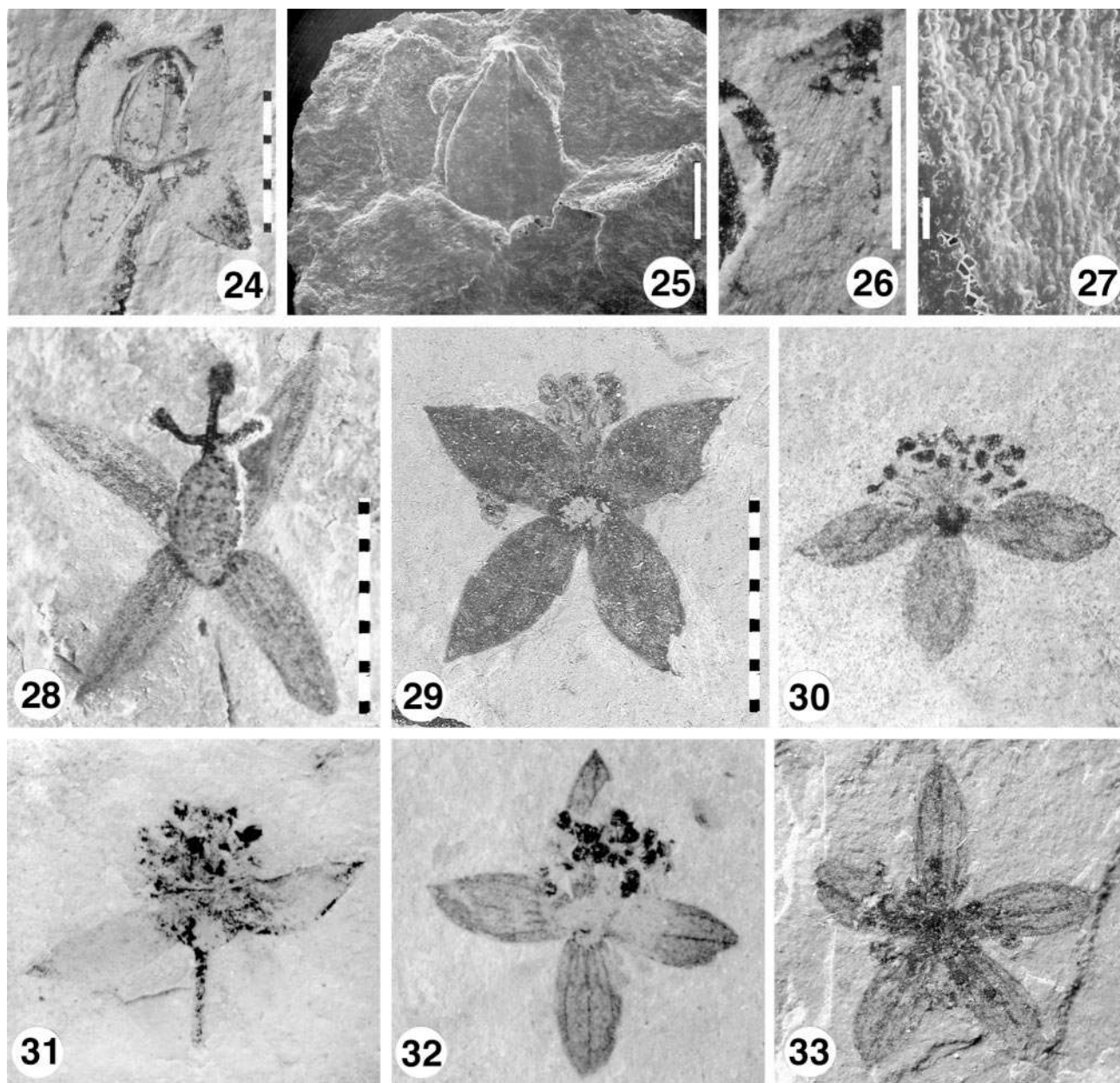


Figs. 16–23. *Pseudosalix handleyi* gen. et sp. nov., leaves. **16.** Detail of leaf from the holotype, showing teeth of variable prominence, looping secondary veins, and frequent intersecondary veins, UMNH PB-1 a, b. Scale bar = 1 cm. **17.** Detail of leaf from twig with attached fruits in Fig. 9, showing acute base, subtle teeth (upper right arrows) and circular dark glands on the margin (lower left arrows). Scale bar = 1 cm. **18.** Detail from lower leaf of the holotype twig, showing dark circular glands at each tooth. Scale bar = 0.5 cm. **19.** Enlargement of the twig from Fig. 1, showing elliptical scar (arrows) on the twig adjacent to the junction of the leaf petiole. Scale bar = 0.1 cm. **20.** Detail of margin, showing a glandular tooth enervated by a thick central vein and a pair of thin outer veins. Scale bar = 0.2 cm. **21–23.** Additional detailed views of venation and margin from the leaf in Fig. 16. Middle Eocene of Bonanza, Utah. Scale bar = 0.3 cm.

Flowers and fruits—The inflorescence of *Pseudosalix* differs from that of *Salix* in its broader ovaries, well-developed calyx, and wider spacing of the flowers. It differs from both *Salix* and *Populus* in having a paniculoid cyme with lateral paraclades of pedicellate flowers, as in *Idesia*, *Bennettiodendron*, and *Poliothyrsis*, rather than the racemose inflorescence of *Salix* and *Populus*. In addition, the branch bearing the terminal inflorescence is fully developed, bearing large leaves, and not reduced as in *Salix* and *Populus*.

By studying the surface impression of the same flowers

from both counterparts, it was possible to count the number of valves in ovaries of pistillate flowers and in the capsules of mature fruits. This ranged from three to four (Figs. 7–8 and 12–15). The number of styles per ovary was not immediately apparent in the natural fracture of the shale, although two styles could easily be seen in some of the flowers (Figs. 5 and 8). However, it was possible to expose additional styles that had been protruding into the shale (Figs. 6–7), indicating that there were at least three per ovary. The styles appear to be aligned with the center of each valve of the developing fruit,



Figs. 24–33. *Pseudosalix handleyi* gen. et sp. nov., attached flowers and associated detached flowers. **24.** Pistillate flower on the holotype twig showing pedicel, four sepals, and ovary and two of the style arms; same specimen as Figs. 1 and 8. Scale bar = 3 mm. **25.** Scanning electron microscopy (SEM) of silicone cast of the counterpart to the middle flower in Fig. 3, showing four sepals arising from the base of the developing capsule. Scale bar = 1 mm. **26.** Detail of upper right sepal from the flower in Fig. 24, showing striated surface. Scale bar = 1 mm. **27.** Scanning electron microscopy of silicone cast of the sepal surface, showing aligned epidermal cells. Scale bar = 0.1 mm. **28.** Detached pistillate flower from Bonanza, Utah, showing four sepals with prominent venation, elliptical ovary with longitudinal sutures, and three prominent style arms. Composite image prepared from both counterparts, DMNH 24354 (loc. 323). Scale bar = 5 mm. **29–33.** Detached staminate flowers with globose anthers. Scale bar for each = 5 mm. **29.** Flower with four sepals and several protruding stamens, Roan Plateau, Colorado (originally figured as “Species of *Antholithes*,” Brown, 1934, pl. 15, fig. 6), USNM 38628. **30.** Flower showing three sepals, the fourth apparently hidden in sediment behind the stamens, Bonanza, Utah, UF 15884-8925. **31.** Laterally compressed flower showing pedicel, tuft of stamens, and two of the sepals, UF 15753-34806, Bonanza, Utah. **32.** Flower with four sepals with well-preserved venation, UF 15753-34807, Bonanza, Utah. **33.** Flower with five sepals with venation similar to that seen in Fig. 32, and typical tuft of stamens, DMNH 24454 (loc. 323), Bonanza, Utah.

so it is likely that the number of styles varied from three to four as did the number of fruit valves.

The holotype specimen shows the pistillate inflorescence with both closed buds and opened flowers nearing anthesis (Figs. 2–8). The buds, which are protected by the fully closed valvate sepals, are easily distinguished from mature fruits because there is no scar of shed calyx on the pedicel and by their

relatively small size. Isolated pistillate flowers show the same arrangement of sepals and a three or four valved gynoecium, but differ from the attached flowers by somewhat larger size, the presence of more obvious longitudinal venation within the sepals, and by the orientation of the style arms. Whereas the style arms in the attached flowers are distally recurved, those in the detached specimen are erect. It is likely that these de-

tached flowers represent a more mature stage of development. This kind of isolated flower was described by Brown (1929) as *Antholithes polemonioides*.

Associated, but unattached, isolated staminate flowers occur in the same horizon as the twigs described above. Previously illustrated as *Potentilla* (?) *byrami* Cockerell (1925, Pl. 2, Fig. 9) and “species of *Antholithes*” Brown (1934, Pl. 15, Figs. 3 and 6), they are similar to the pistillate flowers in being pedicellate and typically four-sepalled, with longitudinally aligned isodiametric epidermal cells. They show 3–5 longitudinal veins in each sepal, as is also observed in the detached pistillate flowers mentioned above. They bear up to about 30 stamens, each with a short (1.5–2 mm) filament, and globose anther. Attempts to process pollen from stamens of these flowers were unsuccessful. Globose anthers and short filaments also characterize *Populus* and *Salix*, but their flowers do not have such a well-developed calyx (*Populus*) or entirely lack a calyx (*Salix*). However, laboratory-generated anther-derived plants of *Populus maximowiczii* bore unusual single terminal flowers that possessed a “cup-shaped, calyx-like structure with 3–4 lobes from which the stamens emerged” (Stoehr et al., 1988). These male flowers had 14–18 stamens per flower with globose anthers on short filaments. These abnormal *Populus* flowers, although smaller (about 3 mm diameter) than those associated with *Pseudosalix*, closely resemble the fossil flowers in venation and shape of the calyx lobes as well as androecial morphology.

Familial assignment—Salient features of the fossil, which we used in our search of extant families via the MEKA 3.0 angiofam key (Duncan and Meacham, 1996), included: leaves alternate, simple, pinnately veined, serrate margined, stipules present, flowers unisexual and actinomorphic with four sepals, 3–4 carpels, capsular fruits, inflorescence compound, superior ovary (receptacle small), nectariferous disk absent, and multiple styles. The MEKA search indicated that the following eight families share the above set of characters: Dilleniaceae, Cunoniaceae, Flacourtiaceae, Malvaceae (cited as both Sterculiaceae and Malvaceae), Euphorbiaceae, Sapindaceae, Rubiaceae, and Caryophyllaceae. We note that Salicaceae was not included in the results because the database uses the older concept of this family, and only *Salix* and *Populus* characters were included. This family was excluded by the database based on the scoring of four sepals. However, Flacourtiaceae, a large number of which are now included in Salicaceae (Chase et al., 2002; Judd et al., 2002), are among the results. A review of each of the other conforming families indicates discrepancies in other characters that are inconsistent with the fossil, such as the lack of salicoid teeth in all but the Flacourtiaceae.

We also compared the fossil with the angiosperm family database of INTKEY 5.0 (Watson and Dallwitz, 2000), using a different but somewhat overlapping set of characters from those used in MEKA: fertile gynoeceum present, syncarpous, superior, fruit a capsule, calyx four-parted, flowers unisexual, small, actinomorphic, aggregated into inflorescences, leaves stipulate, well-developed, simple, alternate, spiral, petiolate, serrate, pinnately veined, medium-sized, lanceolate, non-sheathing, and nonsucculent. Fifteen families conformed to this set of search criteria: Actinidiaceae, Buddlejaceae, Caparpaceae, Caryophyllaceae, Celastraceae, Cunoniaceae, Elaeocarpaceae, Flacourtiaceae, Gyrostemaceae, Hamamelidaceae, Molluginaceae, Salicaceae, Sapindaceae, Sterculiaceae, and

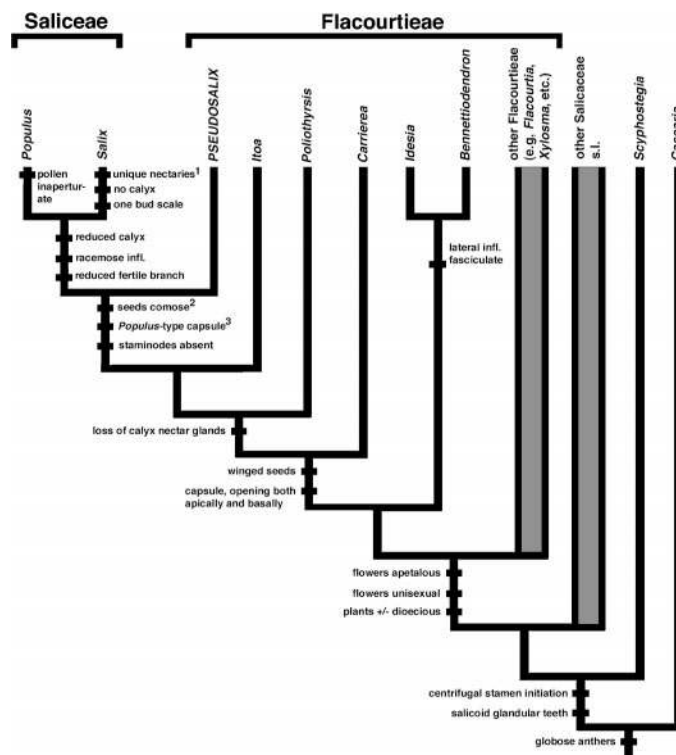


Fig. 34. Phylogenetic relationships within Salicaceae s.l. modified from Chase et al. (2002), showing inferred position of *Pseudosalix* and key morphological synapomorphies. ¹“Unique nectaries” refers to the stipular nectaries that occur below the flowers of *Salix*. ²Comose seeds are inferred for *Pseudosalix* based on the observed capsular fruits and the absence of winged fruits of the kind characteristic of Flacourtiaceae. Comose seeds co-occur with *Pseudosalix*, but could alternatively belong to the sympatric species, *Populus wilmattae*. ³By “*Populus*-type capsule,” we refer to capsules that open only apically, without fracturing basally, and that maintain the integrity of the surface layer, in contrast to capsules of *Itoa*, *Poliothyrsis*, and *Carrierea*, in which the epicarp layer of the capsule flakes away at maturity.

Zygophyllaceae. Again, most of these families can be dismissed as being related to our fossil by various characters not included in the available database. Significantly, both Salicaceae sensu stricto (s.s.) and Flacourtiaceae are among the candidates from this search. Those families selected in both MEKA and INTKEY searches include the Cunoniaceae, Flacourtiaceae (i.e., Salicaceae s.l. and Achariaceae; Chase et al., 2002; Judd et al., 2002), Sterculiaceae, Sapindaceae, and Caryophyllaceae. The presence of circular glands on teeth of the leaf margin, i.e., salicoid teeth, distinguishes Salicaceae s.l. (and our fossil) from the other candidate families. These distinctive teeth are likely a synapomorphy of all members of Salicaceae s.l. except for the basal genus *Casearia* (Chase et al., 2002; Judd et al., 2002; see also Fig. 34), and their presence in *Pseudosalix* provides strong support for its placement in Salicaceae s.l. The presence of alternate, stipulate leaves is also consistent with a placement in this family.

Reproductive features consistent with placing the fossil in the Salicaceae s.l. include the presumably dioecious condition, unisexual, actinomorphic and apetalous flowers, with a superior ovary of 3–4 carpels, each with a distinct style and globose stigma. In addition, the globose anthers of the associated staminate flowers are also consistent with a placement in Salicaceae s.l., and this apomorphic character may support the

Feature	<i>Pseudosaxif</i>	<i>Populus</i>	<i>Salix</i>	<i>Itea</i>	<i>Poliothyrsis</i>	<i>Carrierea</i>	<i>Bennettiodendron</i>	<i>Ilexia</i>
Geography	western USA (Eocene)	North temperate	North temperate & Arctic	South China, East Malaysia	central & South China	South & West China, Indochina	China, Indomalaysia	China, Japan
Inflorescence								
Fruit type	paniculoid cyme 3-4-valved capsule	racemose 3-2-valved capsule	racemose 2-valved capsule	racemoid cyme 6-valved capsule	paniculoid cyme 3-valved capsule	paniculoid cyme 3-valved capsule	paniculoid cyme berry	paniculoid cyme berry
Capsule								
dehiscence	apically ?comose	apically comose	apically comose	apically + basally wraparound wing	apically + basally wraparound wing	apically + basally laterally extended wing	n/a	n/a
Seeds							noncomose, nonalate	noncomose, nonalate
Calyx	4-5 valved	reduced	absent	3-4 valved	4-5 valved	5 valved	3-4 valved	3-6 valved
Staminodia in pistillate flowers	absent	absent	absent	present	present	present	present	present
Calyx nectar								
glands	absent	absent	absent	absent	absent	present	present	present
Pollen	?	inaperturate	tricolporate	tricolporate	tricolporate	tricolporate	tricolporate	tricolporate
leaf venation	pinnate	palmate, pinnate	pinnate	pinnate	palmate	pinnipalmate	pinnate	palmate

oles; yet some living species of *Populus*, such as *P. angustifolia* James, have more slender leaves with pinnate venation and short petioles similar to those of *Pseudosalix*. There is also some indication from ontogeny that slender leaves may be plesiomorphic in *Populus* (Eckenwalder, 1980, p. 367). The morphology of the capsules in *Pseudosalix* compares favorably with those of *Populus*. However, as discussed above, the fossil is distinguished from all modern species of *Populus* by the compound inflorescence terminating a well-developed leafy twig and a well-developed calyx in both pistillate and staminate flowers. The corresponding synapomorphies for the taxa of Saliceae are absent in *Pseudosalix*, indicating clearly that the fossil must be placed outside of the *Populus* + *Salix* clade. We consider that the fossil is best placed immediately adjacent to the Saliceae clade, forming a larger clade, defined by terminally opening capsules, comose seeds, and absence of staminodes in pistillate flowers (Fig. 34).

In summary, *Pseudosalix* has stipulate, alternate leaves with salicoid teeth, flowers with globose anthers, and gynoeceia with parietal placentation (inferred by the close similarity of the capsule morphology of *Pseudosalix* to that of *Salix* and *Populus*), indicating with some confidence a taxonomic placement within the Salicaceae s.l. (Fig. 34). It would be useful to determine whether the fossil had centrifugal initiation of its stamens, as this is likely an additional synapomorphy of Salicaceae s.l. (Bernhard and Endress, 1999). The likely dioecious condition, unisexual, and apetalous flowers of *Pseudosalix*, point to a placement within the tribe Flacourtieae. The capsular fruits of *Pseudosalix* indicate that this fossil belongs in a monophyletic group consisting of *Poliothyrsis*, *Carrierea*, *Itoa*, *Populus*, and *Salix*, all of which have capsules. *Idesia* and *Bennettiodendron* are morphologically similar, although with fleshy fruits, and are likely also related (Fig. 34). *Pseudosalix* may be phylogenetically adjacent to *Itoa*, *Poliothyrsis*, and *Carrierea* on one hand and *Populus* and *Salix* on the other. The fossil is most likely sister to *Populus* and *Salix* (i.e., the Saliceae, a tribe nested within the Flacourtieae; see Fig. 34) based on similarities in the structure of its capsules and lack of staminodes in the carpellate flowers, but cannot be placed within either *Salix* or *Populus* because it possesses a well-developed calyx and branched inflorescences. Both of these are plesiomorphic features, also seen, for example, in *Poliothyrsis*, *Idesia*, and *Bennettiodendron*. Taken together, the synapomorphic features evident in the fossil clearly support a placement, well nested within Salicaceae s.l.

Other fossil Salicaceae s.l.—The fossil record of Salicaceae s.l. extends back to the late Paleocene based on reports of *Populus* foliage from sites in western North America (Wing, 1981; Collinson, 1992), but the first unequivocal records supported by both fruits and foliage are from the early Middle Eocene Green River Formation of Utah and Colorado. *Populus wilmattae*, typically with wide-ovate leaves, is one of the dominant elements of the Green River leaf flora and is also known from a twig with attached infructescence and leaves (Manchester et al., 1986). A second morphotype, with linear leaves having strongly ascending basal secondary veins, *Populus cinnamomoides*, is also common in the Green River leaf flora and is thought to represent the foliage of young trees of *Populus wilmattae* (Eckenwalder, 1980). Based on comparison with the heteromorphism observed in a similar modern relative *Populus mexicana*, Eckenwalder concluded that *Populus wilmattae* and

P. cinnamomoides must be merged as one species and that the older name, *P. cinnamomoides*, would take priority.

Despite the reports of leaves identified to *Salix* from the Green River Formation (Brown, 1934; MacGinitie, 1969), it remains unknown whether the extant genus was really present by the Eocene. Neither the diagnostic racemose infructescences nor the bivalvate capsules characteristic of *Salix* have been recovered. It is likely that some of the *Salix*-like leaves represent *Pseudosalix* or other genera. For example, another specimen recovered from the Green River Formation of Colorado (*Carpolithes serratifolius* Brown, 1929, p. 292, Pl. 76, Fig. 5) shows a fossil twig with elongate, *Salix*-like leaves and a terminal infructescence that is morphologically more similar to *Populus* (Collinson, 1992, p. 164, Pl. 1 Fig. b).

MacGinitie (1937) recognized *Idesia* based on leaves with well-preserved venation from the northern California Weaver-ville flora of probable early Miocene age (Barnett, 1989). According to MacGinitie, every character of the fossil leaves of *Idesia cordata* MacGinitie is matched in the leaves of extant *I. polycarpa* Maxim. If correctly determined, the occurrence of *Idesia* in western North America indicates that this genus, now endemic to China, crossed between Asia and North America sometime during the Tertiary.

Iljinskaya and Chelebaeva (2002) described a new genus, *Utkholokia*, based on leaf imprints from the Paleocene of western Kamchatka, which they think combine leaf characters of *Populus* with those of *Idesia* and *Poliothyrsis*. The leaves of *Utkholokia ulevenensis* (Cheleb.) Iljinskaja et Chelb. are ovate to wide-ovate and asymmetric. Several veins arise palmately from the base of the lamina, as in *Idesia*. The tertiary veins are mainly straight and perpendicular to the primary vein. Marginal teeth are small, often having attenuate tooth apices with the apical side of each tooth parallel to the basal side of the neighboring adjacent tooth, a feature these authors have observed in extant *Idesia* but not in *Populus* or *Poliothyrsis*. Iljinskaya and Chelebaeva (2002) note that the fossils compared very favorably with leaves of extant *Populus ciliata* Wall ex Royle and the monotypic genera *Idesia* and *Poliothyrsis*. However, the leaves differ from those of all three modern genera in their prominent asymmetry. The reproductive structures of *Utkholokia* remain unknown.

Mai (1980) recognized five species of *Poliothyrsis* based on lignitized seeds from the Tertiary of Europe and western Siberia. *Poliothyrsis eurorimosa* Mai, from the late Oligocene to middle Miocene of northwestern Saxony, Germany, was described both from fruits and seeds. The seeds are oval to oblong-oval, 0.7–1.5 mm long, 0.5–1.2 mm wide, and have a testa composed of a layer of thickened, radially arranged sclereids. The capsules are ovoid to oblong heart-shaped, 6–9 mm, and composed of three thin, woody-leathery valves with dehiscence slits that reach the lower one-third of the capsule and parietal placentae along the midline of each valve. The seeds are preserved without the encircling wing diagnostic of *Poliothyrsis* and are about half the size of seeds of the extant species. The younger species, *P. lutetianoides* (Szafer) Mai from the Pliocene of Kroszno, Poland, and *P. hercynica* Mai from the Pliocene of Reuver, Netherlands, Berga, Germany, and Villafranca, d'Asti, Italy, are larger (1.9–2.5 mm long) and more similar in size to those of the extant species, *P. sinensis*.

The genus *Saxifragispermum* Reid and Chandler, based on permineralized, anatomically preserved fruits from the Eocene of England (Reid and Chandler, 1933; Chandler, 1961) and

Oregon (Manchester, 1994), has 3–4 carpellate capsules with parietal placentation that led to their assignment to Flacourtiaceae (Chandler, 1961; Manchester, 1994). As the Flacourtiaceae has been abandoned (Chase et al., 2002), these characters now indicate that *Saxifragispermum* probably belongs in the Salicaceae s.l.

It is interesting that *Pseudosalix* appears at about the same time as the first unequivocal records of *Populus*. The extinct genus was sympatric with *Populus wilmattae* and *P. cinnamomoides*. Leaves have been identified to extant *Salix* from the Eocene of the Green River Formation (Brown, 1934; MacGinitie, 1969). We regard the assignment as possible, but uncertain, in view of the lack of *Salix* infructescences. Informed evaluation of whether these leaves represent an extinct taxon such as *Pseudosalix* or the extant genus requires more complete material. The main floral feature distinguishing *Pseudosalix* from *Populus* and *Salix* is the occurrence of well-developed sepals. Morphologically similar flowers of *Idesia* attract insects as pollinators. *Pseudosalix* may have been well suited for insect pollination and less adapted for wind pollination than extant *Populus* and *Salix*. Eckenwalder (1996) noted that (except in some subtropical species) poplar species flower before leaf emergence in spring, as is common in wind-pollinated trees. Judging from the occurrence of mature flowers on a twig with expanded leaves, we infer that the timing of pollination in *Pseudosalix* was after the flush of new foliage.

Table 1 shows the geographic distribution and selected morphological characters of *Pseudosalix* and selected extant salicaceous genera with which it has been compared. Geographically, it is interesting that the successive outgroup genera to the Saliceae, including *Itoa*, *Poliothyrsis*, *Carrieria*, *Idesia*, and *Bennettiodendron* all are distributed in Asia today but not in North America. This distribution pattern, together with the cladistically nested position of the tribe Saliceae relative to these genera in the tribe Flacourtiaceae would lead to the suggestion that Saliceae originated in eastern Asia prior to dispersing across North America and Europe. However, the early fossil occurrence of both *Populus* and *Pseudosalix* in the Eocene of North America introduces the possibility of a North American diversification of the Saliceae. If this were the case, we would expect to find other fossil representatives of the Flacourtiaceae in North America. If the group actually evolved in Asia and subsequently dispersed to North America, then we may expect to find fossils of *Pseudosalix* and/or other extinct Flacourtiaceae, such as *Utkholokia* Iljinskaya & Chelebaeva, in the early Tertiary of Asia.

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