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RAPID COMMUNICATION

INTERCONNECTED REPRODUCTIVE AND VEGETATIVE REMAINS
OF *POPULUS* (SALICACEAE) FROM THE MIDDLE EOCENE
GREEN RIVER FORMATION, NORTHEASTERN UTAH¹

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ABSTRACT

A new specimen from the Middle Eocene Evacuation Creek Member of the Green River Formation in northeastern Utah shows a twig with several leaves of *Populus wilmattae* Cockrell and a fruiting raceme attached. This specimen establishes for the first time the type of fruits borne by *P. wilmattae* and provides additional characters with which to assess its taxonomic and evolutionary status. An associated seed shows attached placental hairs like those of extant species of *Populus*. The Green River fossil differs from extant *Populus* species in having basically palmate leaf venation and in bearing its fruiting axis on a young twig. In other aspects, the fossil species is remarkably similar to the extant species *Populus mexicana*.

FOSSILS SHOWING actual attachment between leaves, stems, and reproductive organs are exceedingly rare but are the only source of unequivocal proof for "whole plant" reconstructions of fossil species. In this paper we describe a specimen of *Populus* showing leaves and fruits attached to the same twig preserved in shale from the Middle Eocene Green River Formation of northeastern Utah. *Populus* is widespread today in temperate Northern Hemisphere floras with 35 species distributed among six sections. The fossil record of *Populus* extends back to the early Tertiary and is known mainly from isolated leaves (LaMotte, 1952) and fruits (Kirchheimer, 1957).

The earliest probable *Populus* occurrence known is that of leaves from the late Paleocene Bear Den Member of the Golden Valley Formation, North Dakota (Hickey, 1977, pl. 22, fig. 2, 5; Wing, 1981, p. 267). During the Eocene, leaves with the architecture of *Populus* were wide-ranging in North America, with occurrences in the Pacific Northwest, the Rocky Mountain, and the Mississippi Embayment regions (Eckenwalder, 1980; Wing, 1981). *Populus* leaves were first identified in the Green

River Formation by Cockrell (1925) and have since been observed at most plant localities of the formation in Utah, Colorado, and Wyoming (MacGinitie, 1969; Grande, 1980). In his monographic treatment of the Green River flora, MacGinitie (1969) recognized two species of poplar coexisting at each locality: *P. wilmattae* Cockrell, with broadly ovate leaves and "two well marked opposite pairs [of secondaries] in the lower third of the leaf"; and *P. cinnamomoides* (Lesquereux) MacGinitie, characterized by slender leaves with a single prominent pair of basal secondaries. Eckenwalder (1977, 1980) called attention to heteromorphism in foliage of extant *Populus* and suggested that the two species recognized by MacGinitie were actually the juvenile (*P. cinnamomoides*) and mature (*P. wilmattae*) forms of a single species, and that the two morphotypes be united under the older name, *P. cinnamomoides*. Our own study supports, but does not conclusively confirm, Eckenwalder's hypothesis. For the purposes of convenience in discussion, we maintain the names *P. cinnamomoides* and *P. wilmattae* as morpho-species for leaves of the narrow and broad architecture, respectively.

An exceptional specimen recently recovered from the Middle Eocene Evacuation Creek Member of the Green River Formation in northwestern Utah provides important new information on the Green River poplar. The specimen (Fig. 1) is preserved on a slab of shale and consists of a twig with leaves of *P. wil-*

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mattae and an attached fruiting raceme bearing several valvate capsules. The same slab of shale also shows a dispersed *Populus* seed and unattached leaves of both *P. wilmattae* and *P. cinnamomoides*. The specimen is important because it demonstrates the degree of foliar heteromorphism present on a single shoot and because it establishes the fruit type borne by this early Tertiary poplar.

MATERIALS AND METHODS—The specimen described here was collected approximately five miles south of Bonanza, UT (I.U. Geol. loc. 15751). The geology and paleontology of this region is reviewed in the context of the entire Green River Formation by MacGinitie (1969) and Grande (1980). The shale was degaged under a dissecting microscope to expose the full length of the axis and to verify connections between the shoot and the fruiting axis and attachments of leaves. The specimen is housed in the paleobotanical collection of Brigham Young University (BYU 3003).

DESCRIPTION—The twig is 3–4 mm in diameter and measures 6.5 cm from the apex to where it is broken at the edge of the slab. The lower 5.5 cm of the twig, although without leaves or branches, bears spirally-arranged circular scars 2 mm in diameter, protruding 1–1.5 mm, and about 5 mm apart. Leaves are attached only along the upper 1 cm and are separated by short (1–2 mm) internodes. Seven leaves are connected to the axis and a few others might be obscured within the sediment. The lowest, and thus earliest, leaves of the spiral are smaller and narrower than the upper leaves. However, the venation of all the leaves is similar.

The petioles are long, 20 to 65 (–75, est.) mm, 1–2 mm wide along most of their length, broadened to 2–3 mm at the base. As preserved in the shale, the petiole frequently appears disrupted or constricted at its union with the lamina, suggesting that it was originally flattened perpendicular to the plane of the leaf blade and twisted upon compression in sediment. The laminae range from 35 to 100 mm in length and from 23 to 75 mm in width. They are ovate to deltoid with a length-to-width ratio of 1.3 (early leaves) to 2.2. The base is obtuse, straight-sided, and symmetrical, while the apex is acuminate (early leaf) to long-attenuate. The margin is crenate except along the basal flanks of the blade. Teeth are regularly spaced, even along the apical tip of the leaf, about 4 to 5 mm apart, and relatively small and rounded. Each tooth has a gland on its upper flank bordering the sinus that is vascularized by a single tertiary

vein. The midvein is slightly irregular in course and medium in thickness, tapering conspicuously toward the apex. A pair of intramarginal veins diverge from the midrib at the base of the lamina and proceed just inside the leaf margin to the first teeth. Two prominent pairs of secondaries (or weak lateral primaries) usually arise in the lower $\frac{1}{6}$ to $\frac{1}{3}$ of the lamina. The lowermost pair arises decurrently from the base of the midvein and then arches smoothly, joining with the superadjacent secondary inside the margin and forming one or two rows of marginal loops. The second pair of secondaries is approximately the same thickness as the first and can be resolved as distinct vascular strands from the base of the lamina but the veins do not actually diverge from the midvein until well above the divergence of the lower pair of secondaries. This pair is also decurrent along the midvein but maintains a lower angle with a more apically oriented course, giving off one or more prominent abmedial branches to the margin and forming larger marginal loops than those of the lower pair of secondaries. The middle one-third of the midvein is without conspicuous secondary veins, although 1 to 3 pairs of intersecondary veins, which extend $\frac{1}{3}$ to $\frac{1}{2}$ of the distance to the margin, are present. The upper one-third of the midvein gives off 4 to 6 pairs of thin secondaries which arise at lower angles than those below. Those within the acuminate tip form obtuse angles with the midvein. The tertiaries are percurrent, opposite, occasionally alternate, and generally oriented perpendicular to the secondaries. Quaternary veins form a reticulum oriented roughly parallel to the tertiaries. Features of higher order venation are not clearly preserved in the attached leaves. However, certain isolated specimens of the species, such as one figured by MacGinitie (1969, pl. 7, fig. 6), are very well preserved, indicating that the areoles are bounded by veins of fifth order and are 0.5 to 1.0 mm in size with freely ending veinlets.

The fruiting axis is a raceme arising from the side of the shoot above the lowest leaf but below the highest leaf. It is 40 mm long, 0.7 mm diameter, and bears eight helically arranged pedicellate fruits, each arising from a swollen area on the axis. The former attachment of additional fruits is indicated by the presence of 7 additional swollen areas on the axis. Pedicels are 4 mm (basal fruits) to 3 mm (apical fruits) and broaden distally, terminating in a conspicuous floral disk scar (1.5 mm diam, 0.25 mm thick) at the base of each fruit. Fruits are capsules with three longitudinal grooves (suggestive of three valves) extending from base to apex. Capsules are ovate-elliptic, 3 to 4.5

mm wide and 5 to 7 mm long, rounded basally, and tapered apically with a persistent style 1–2 mm long and 0.25 mm wide; stigmas are not preserved.

Seeds are not preserved within the capsules. A single well-preserved, dispersed seed on the same slab is elliptical, 1.55 mm long, 0.8 mm wide, and is attached to a tuft of hairs that probably represent the plumose placenta as in modern *Populus*.

DISCUSSION—The occurrence of deltoid leaves with salicoid glandular teeth (Hickey and Wolfe, 1975) and long petioles, together with racemose infructescences bearing valvate capsules with distinct floral disks, confirms the identification of this species with *Populus*. The apparent flattening of the petiole perpendicular to the lamina suggests that these leaves were subject to “quaking,” as in many modern *Populus* species. The associated seed (fig. 6) has an attached hairy placenta and is certainly salicaceous and characteristic of *Populus*. Whether or not the seed represents the same species as the fruiting twig, its presence suggests that adaptation for wind dispersal of seeds occurred early in the evolution of Salicaceae.

Extant species of *Populus* are divided into six sections according to Eckenwalder (1977): *Turanga*, *Abaso*, *Leucoides*, *Populus* (aspens, white poplars), *Tacamahaca* (balsam poplars), and *Aigeros* (cottonwoods and black poplars). Characters important in distinguishing the sections include morphology and persistence of the floral disk, presence or absence of marked foliar heteroblasty, overall leaf shape, distribution and shape of foliar teeth, number of carpels, and flattened vs. round petiole cross-section—as well as some features which are not known for our fossil, such as length of anthers, nature of winter buds, and number of ovules per placenta.

We concur with previous authors (MacGinitie, 1969; Eckenwalder, 1977, 1980) that *P. wilmattae* is most similar to *P. mexicana*, the single living species of section *Abaso*. The leaves of these two species share several features that do not occur in other modern *Pop-*

ulus species, such as percurrent tertiary venation and the continuation of teeth along the flanks of the apical tip of the leaf. The morphological uniformity of the different leaves attached to the fossil twig suggests that foliar heteromorphism along the branch (seasonal heterophylly), a characteristic of some extant sections of *Populus*, was minimal, as in *P. mexicana*. Three isolated, narrow leaves of the *P. cinnamomoides* type occur on the same specimen and might represent conspecific foliage of younger trees growing in the same vicinity. If *P. wilmattae* and *P. cinnamomoides* are correctly interpreted as a single species, then marked maturational heteroblasty is another feature of the Green River poplar in common with *P. mexicana*. The new information from reproductive material also supports affinity with section *Abaso*. The scar subtending each capsule indicates that the floral disks were caducous, as in *P. mexicana*, rather than persistent as in most other sections. However, the capsules of *P. wilmattae* appear to be tri-valvate in contrast to those of *P. mexicana* which are predominantly bi-valvate. The tri-valvate condition of the fossil is common in other extant sections of *Populus* and might be a primitive character.

We conclude that *P. wilmattae* is an extinct species most closely allied to extant *P. mexicana*. By modifying the modern sectional diagnosis to include tri-valvate capsules, the Green River poplar could be placed in the extant section *Abaso*. It differs, however, from all living *Populus* species in two respects. First, the Eocene leaves show a definite tendency toward palmate venation with the lowermost pairs of secondary veins more prominent than those above and visible as separate strands from the midrib that arise independently from the top of the petiole. All of the living species have strictly pinnate venation. Second, the fruiting raceme of the fossil arises from the same young shoot as the leaves, while in modern species the fruiting axes occur on old twigs subtended by leaf scars of a previous season.

Wing (1981) noted that the tendency for palmate venation is typical of Eocene *Populus*

Fig. 1–7. Eocene and modern *Populus*. 1. Twig with leaves of *P. wilmattae* Cockerell and attached fruiting raceme. Rectangle indicates position of dispersed seed shown in Fig. 6, BYU 3003, $\times 0.5$. 2. Same specimen, showing attachment of fruiting axis and petioles to twig. Raceme bears at least eight capsules, $\times 1.5$. 3. Detail of raceme, showing attachment of pedicels to raceme and floral disk scars subtending unopened valvate capsules, $\times 5$. 4. Another capsule on same axis, showing floral disk scar and style, $\times 5$. 5. *P. mexicana* ssp. *dimorpha* (T.S. Brandeg.) Eckenw., from Guasave, Sinaloa, MEX, valvate capsule with floral disk scar and style for comparison with Fig. 5, UC651720 = HS. Gentry 5950, $\times 5$. 6. Detail of dispersed seed shown in Fig. 1, showing attached placental hairs (arrows), $\times 10$. 7. *P. mexicana* ssp. *dimorpha* from El Fuerte, Sinaloa, MEX, seed with attached placental hairs, MO2703736 = M. Medina C. 2162, $\times 10$.

leaves from various localities in North America and suggested that it may reflect a "palmate dilleniid ancestry" of the Salicaceae. Architecturally, the leaves of *P. wilmattae* fall between those of extant *Populus* with true pinnate venation and those of the extant palmate dilleniid genus *Idesia* (Hickey and Wolfe, 1975) which has true palmate venation.

With only one specimen it is difficult to say whether the position of the fruiting axis shown in Fig. 1 was typical for the species. The raceme appears to have arisen from an axillary bud within the young leafy shoot whereas in extant species the inflorescences develop from buds on old growth of the preceeding season. The fossil species apparently flowered and fruited while the shoot had expanded leaves. In extant *Populus* species, flowering occurs on old wood prior to the flush of spring leaves, permitting pollination to take place while the branches are relatively free of leaves. Thus the fossil might not have been as well adapted for wind pollination as the extant species.

The Salicaceae appears to have been essentially modern in most fruit and foliage characters by the Middle Eocene. In addition to *Populus*, the Green River Formation produces abundant foliage of *Salix* (Brown, 1934; MacGinitie, 1969). A particularly important specimen figured by Brown (1929, as *Carpolithus serratifolius*) shows two elongate, slender leaves attached to a twig with a terminal fruiting raceme. Re-examination of the specimen shows that the fruits are valvate capsules and indicates that it is attributable to modern *Salix*. The presence of both extant genera of the Sal-

icaceae in the Eocene contrasts with the abundance of extinct genera known in many other angiosperm families at that time.

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