The Juglandaceae underwent major evolutionary radiation during the Paleocene and Eocene in the Northern Hemisphere. Probable precursors of the family with bisexual flowers, very small nuts, and triporate pollen are known from the upper Cretaceous of Europe (Friis, 1983) and eastern North America (Crane and Herendeen, 1996), but the first unequivocal Juglandaceae are from the Paleocene of Europe and North America. Four genera are known based upon fruits from the Paleocene: *Cyclocarya* from Wyoming, Montana, and North Dakota (Manchester and Dilcher, 1982; Manchester, 1987, 1989), *Casholdia* from England and France (Crane and Manchester, 1982; Manchester, 1989), *Juglandicarya* (Brown, 1962; Manchester, 1987, 1989), and *Polyptera* (Manchester and Dilcher, 1982; Manchester, 1987, 1989) from Wyoming and Montana.

The genus *Polyptera* was established on the basis of winged fruits from two localities in the Paleocene of southwestern Wyoming (Manchester and Dilcher, 1982). These fossils, together with co-occurring juglandaceous foliage, had formerly been placed in the living genus *Pterocarya* (Brown, 1962). Our study upheld Brown's identification of these fossils to the Juglandaceae, but showed that the fruits could not belong to *Pterocarya*. Based upon fruit morphology, we considered *Polyptera* to be an extinct genus with closest affinities to extant *Cyclocarya*. We did not at that time attempt to evaluate the associated foliage or other organs. In the 15 yr that have elapsed since our earlier study, *Polyptera manningii* fruits have been discovered at eight additional localities in Wyoming and Montana. Repeated association of leaves, leaflets, staminate catkins, and pollen together with the fruits at multiple localities provides a basis for interpreting these organs as elements of a single extinct plant species.

In this paper we describe *Polyptera manningii* more fully, giving characters of the infructescence and fruits as well as those of the associated compound leaves, staminate catkins, and pollen. We present our concept of the whole plant as it may have appeared in life and interpret the phylogenetic position of *Polyptera* relative to extant genera of the Juglandaceae. The geographic and ecological range of the species is discussed. In addition, the age can now be specified more precisely within the Paleocene, indicating that the genus was living in the Torrejonian and Tiffanian stages, about 56–64 million years ago.

**MATERIALS AND METHODS**

In our initial investigation (Manchester and Dilcher, 1982), we studied only fruits from existing collections of the United States National Museum (USNM) and Brigham Young University (BYU). During subsequent years, hundreds of additional *Polyptera* fruits, along with associated foliage and staminate catkins, have been collected at localities of the Fort Union Formation in southwestern Wyoming. These specimens are now housed at the Florida Museum of Natural History, Gainesville (UF). An additional specimen was observed among a collection made by Beth Williams in Montana, now deposited at the Peabody Museum, Yale University, New Haven, Connecticut (YPM).

*Polyptera* was collected from ten localities in southern Wyoming and eastern Montana (Fig. 1, Table 1, Appendix 1). In Wyoming the localities are situated in the southern part of the state on the western and eastern flanks of the Rock Springs Uplift and on the southwest side of...
the Rawlins Uplift; in Montana the only locality currently known is in the southeastern part of the state, on the west side of the Williston Basin. The localities in Wyoming all occur in the Fort Union Formation; in this area the Fort Union has not been formally subdivided into members. The locality in Montana is situated in the Lebo Member of the Fort Union Formation.

Specimens were recovered by prying out blocks of sediment and splitting them with hammer and chisel. Details of individual fossils often required further exposure in the laboratory by removing chips of sediment with fine needles under a dissecting microscope. Pollen was prepared for microscopy by removing carbonaceous pieces of anther from the staminate catkins, cleaning with HCL and HF; and then macerating. Maceration required 10 min in concentrated nitric acid, washing in water, followed by clearing a few minutes in ammonia. The latter step was carried out while viewing with a dissecting microscope in order to stop the clearing process at the correct stage by quickly diluting with water. Resulting pollen masses and individual grains were mounted on glass slides with Canada Balsam, or on aluminum stubs for scanning electron microscopy (SEM). Pollen size measurements were made by light microscopy with the specimens mounted in water on a glass slide, or 32. The fruits were sessile, or on very short pedicels. Additional pollens were embedded and sectioned for transmission electron microscopy (TEM) by Dr. Charles P. Daghlian. The samples for TEM were dehydrated through an ethanol series to absolute ethanol, flat-embedded in L. R. White medium grade acrylic resin, and polymerized for 24 h at 60°C. Sections were stained with uranyl acetate (45 min) and lead citrate (2 min) and imaged with a JEOL 2000FX at 80KV.

**SYSTEMATIC DESCRIPTIONS**

**Family:** Juglandaceae  
**Genus:** Polyptera Manchester et Dilcher 1982.  
**Polyptera manningii** Manchester et Dilcher (Figs. 2–24)  

**Emended diagnosis**—Infructescence with 30 or more sessile, helically arranged fruits. Fruit a nut with a multi-lobed disklike wing. Nut pyramid-shaped, square in cross section, triangular in lateral view, 6–8 mm in diameter. Locule four-parted at base due to intersection of primary and secondary septa. Nut loosely enshathed by a husk with ≈16–20 longitudinal vascular strands that coalesce at the apex. Wing 8- to 12-lobed, forming a flange around the base of the nut, oriented perpendicular to the main axis. Wing lobes rounded, irregular in size, entire-margined, ranging from 2.4 to 4 mm in length and from 1.5 to 4 mm in width; sinuses between wing lobes deep (almost reaching the nut) to relatively shallow; venation subparallel, bifurcating toward the distal margin. Widest diameter of fruit, measured across the wing span, 10–23 mm, average 15 mm.

**Additional specimens**—UF 13133, 13660, 13672, 13703, 13706, 13742, 13752, 13758, 13762, 13763, 13773, 13822, 13858, 17787, YPM 30250.

**Discussion**—Infructescences were unknown at the time of our earlier treatment (Manchester and Dilcher, 1982), but two specimens are now known from Dry Canyon (Figs. 3, 4). The spicate infructescence was at least 10 cm long and bore numerous crowded fruits in helical arrangement. Sixteen fruits are intercepted by the fracture plane through the fossil along the axis of the infructescence, and the full number of fruits present in three dimensions is estimated to have been at least twice this amount, or 32. The fruits were sessile, or on very short (<1 mm) pedicels. The infructescence must have been pendant because its axis (2 mm thick) is not stout enough to have held erect under the mass of numerous fruits.  
**Polyptera** fruits are preserved in various orientations within the sediment (Fig. 2). Transversely compressed specimens (Figs. 5–14) usually split open along the plane of the fruit wing, showing the square outline of the nut and the number and shape of surrounding wing lobes. When a specimen is split along this transverse plane, one of the counterpart halves shows the impression made by the apical end of the nut and typically shows a + shaped mark representing the primary and secondary septa, which intersect at right angles along the axis of symmetry (Figs. 5–7), while the other counterpart reveals the impression made by the basal side of the nut, with a central attachment scar (Fig. 8). The number of wing lobes,

<table>
<thead>
<tr>
<th>Locality name</th>
<th>Infructescence</th>
<th>Fruit</th>
<th>Leaflet</th>
<th>Catkin</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Antelope Butte (UF loc. 18195)</td>
<td>✗</td>
<td></td>
<td>✗</td>
<td>✗</td>
</tr>
<tr>
<td>2. Earnest Butte (UF loc. 18198)</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
</tr>
<tr>
<td>3. Earnest Butte (UF loc. 15747)</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
</tr>
<tr>
<td>4. Dry Canyon (UF loc. 15746A)</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
</tr>
<tr>
<td>5. Big Flat Draw no. 2 (UF loc. 18199)</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
</tr>
<tr>
<td>6. Black Buttes Mine, pit 3 (UF loc. 15886)</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
</tr>
<tr>
<td>7. Black Buttes Mine, pit 10 (UF loc. 18266)</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
</tr>
<tr>
<td>8. Above Bridger Coal Mine (UF loc. 18245)</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
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<tr>
<td>9. Pool Ranch (UF loc. 15758)</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
<td>✗</td>
</tr>
<tr>
<td>10. Mexican Hat (Williams, 1988)</td>
<td>✗</td>
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<td>✗</td>
<td>✗</td>
</tr>
</tbody>
</table>
which we formerly described as 8–10, is now known to range from 8 to 12. The width of individual lobes varies such that one lobe may be twice as wide as another lobe on the same fruit (e.g., Fig. 8). Although in our earlier treatment Polyptera was described as a multiwinged fruit, we now interpret the fruit to possess a single wing divided into many lobes because the sinuses between the lobes are not incised all the way to the nut (Manchester, 1991). In some other taxa of the Juglandaceae, e.g., Cruciptera and Pterocarya, the sinuses are incised completely, so that there are separate wings (Manchester, 1991). Veins of the wing are subparallel, dichotomizing once, twice, to rarely three times before reaching the margin. There is no vein along the wing margin.

Laterally compressed fruits provide a profile view of the nut with the wing attached at its base (Figs. 19–24).
Figs. 9–24. Polyptera manningii fruits from the Paleocene of Wyoming and Montana. 9. Specimen with seven wing lobes and +-shaped mark indicating the intersection of primary and secondary septa, YPM 30250, ×3. 10. Specimen with well-preserved wing venation, UF 13660, ×2. 11. Fruit with eight wing lobes, well-defined septa, UF 17787, ×2. 12. Specimen with locule cast preserved in position of the nut, basal view, UF 13133, ×2. 13. Fruit with loose husk surrounding the nut, UF 13878, ×2. 14. Specimen with loose locule cast of the nut at the center of disk-wing, UF 13706, ×2. 15. Same locule cast removed from the rock, apical view, with horizontal seam indicating the plane of nut dehiscence, ×5. 16. Same locule cast, basal view, showing cleavages representing the primary (vertical), secondary (median horizontal), and tertiary (additional horizontal cleavages) septa, ×5. 17. Detail of wing venation from Fig. 10, ×5. 18. Fruit enlarged to show departure of vascular strands from periphery of the nut, arrows, UF 13758, ×3. 19. Lateral view of a fruit that has broken along plane of septum, showing wings at base of nut, UF 13657, ×2. 20. Lateral view of a nut showing vascular strands of the husk departing from base of nut and arching toward apex, UF 17112, ×2. 21. Lateral view of a fruit with intact husk and apical perianth bulge, UF 13672, ×2. 22. Laterally compressed fruit from specimen in Fig. 2, UF 13858A, ×3. 23. Another fruit in lateral view, showing triangular outline of nut, arched vascular strands of the husk, and three lobes of the basally attached wing, UF 13763, ×3. 24. Laterally compressed fruit from specimen in Fig. 2, showing two divergent style arms at apex, UF 13858B, ×3.

Localities: Fig. 9, Mexican Hat, Custer County, Montana (Williams, 1988); Fig. 10, 13–24, Dry Canyon, Sweetwater County, Wyoming (UF loc. 15746A); Fig. 11, Black Buttes Coal Mine, Sweetwater County, Wyoming (UF loc. 18266); Fig. 12, Pool Ranch, Carbon County, Wyoming (UF loc. 15758).
The nut is rounded-triangular in lateral view, tapering from its broad base to a pointed apex. Surrounding the deeply impressed nut there are usually ensheathing vascular strands that arise from the base of the nut and rejoin at the apex. We were perplexed about the nature of these strands in our first treatment of the fruits (Manchester and Dilcher, 1982) because we had observed only specimens with tattered remains of the strands that were free and spreading from the nut. More completely preserved specimens now show that the strands were borne within a husk-like covering of the nutshell (Figs. 21–24). The vascular bundles evidently were more resistant to decay than the husk, which is only rarely preserved (Fig. 13). Sediment filled in between the hard part of the nut and these strands. Although styles are absent from nearly all of the specimens examined (presumably fallen away as the fruit matured), one laterally compressed specimen shows a pair of stigmatic arms arising from the apex (Fig. 24). In this specimen the style arms diverge in the plane of the dehiscence, indicating that style orientation was carinal. Sepals, which should be visible in laterally compressed specimens if they were present (as in Cruciptera; see figs. 5, 8 in Manchester, 1991), are not well defined. However, an apical bulge of the husk observed in some of the laterally compressed specimens apparently represents a fused perianth (Fig. 24).

Dissection of well-preserved specimens reveals the following sequence of layers (Fig. 25A): (1) Outermost is a smooth surface that is ribbed where the vascular strands are situated. This layer may have been loose and baggy, because it is sometimes filled in with sediment and bulging (Figs. 13, 21, 24). (2) The next surface encountered is the external mold of the nutshell, usually showing the effect of sediment pressing in from the four sides (Figs. 4–7, 11, 20). The nutshell itself is missing, or represented only by carbonaceous fragments within the cast. (3) Some specimens show a locule cast within the cavity left by disappearance of nutshell (Figs. 12, 14–16). The nutshell itself, typically represented only by a space in the sediment between the locule cast and the external mold of the nut, is 0.3–0.5 mm thick. Examination of the nutshell fragments and impression surfaces at high magnification indicates that the nutshell was composed of isodiametric cells, not elongate fibers. The relatively thin nutshell apparently was somewhat flexible because sedimentary molds show the outer surface to be collapsed inward against the septa.

Sedimentary infillings of the nutshell reveal the locule and two large peripheral lacunae. The basal side of the locule cast is formed into four lobes indicating the position of septa. The septa, as in extant Juglandaceae, arise from the base and are incomplete apically. The primary septum arises at the base and extends nearly to the apex of the locule, while the secondary septum extends only about one-quarter of the distance toward the apex. The primary and secondary septa are both thin and intersect at right angles in the central axis of the nut. A longitudinal “seam” in the locule cast marks the plane of dehiscence (where the nutshell had begun to split apart providing the entrance for sediment that filled the locule; Figs. 15, 16). This dehiscence plane is in the same position as the secondary septum (Fig. 25B). A pair of lacunae are situated outside of the locule, oriented approximately parallel to the secondary septum. The surfaces of the lacunae casts are rough, whereas the surface of the locule cast is smooth.

The range of fruit size varies among different localities. Commonly the wing span varies from 12 to 16 mm, but at Dry Canyon the mean size is larger, and the wing span ranges from 15 to 23 mm.

Placement of Polyptera fruits in the Juglandaceae is justified by the morphology of the nut with its incomplete primary and secondary septa intersecting at right angles, two style arms, epigynous perianth, the participation of bracts in the formation of a fruit wing apparently homologous with that of Cyclocarya (Manchester and Dilcher, 1982), and by the spicate infructescence.

Staminate Inflorescences and Pollen (Figs. 26–36)

Description—Staminate inflorescences are slender catkins 35–70 mm long, 4–5 mm wide, consisting of numerous helically arranged florets on a flexible axis (1 mm thick). Each floret consists of a cluster of 10–15 sessile anthers (1.8–2.8 mm diameter). Successive florets on the axis are separated by a space approximately equal to the width of a floret. Anthers are 1.2–1.5 mm long and apparently sessile. Bracts and sepals are not well enough preserved to deduce their morphology within the floret clumps.

Pollen removed from the anthers is tritorporate, oblate, isopolar; shape in polar view is subtriangular with convex interpORIA; equatorial diameter 25–30 μm. Pores are atria, the exopores meridionally elongate. Exine (1.8–2.8 mm diameter) 1 μm thick at the equator, thinned at one pole in a circumpolar ring surrounding a polar island of normal thickness. Foot layer not extending to apertures, but ending at the endopores to form the atria, foot layer thinning slightly toward exopores. Exine surface ornamentation consisting of evenly spaced microspinules. The tectum is 2 times thicker than the granular layer and 5–6 times as thick as the foot layer. There are microchannels through the tectum.
Figs. 26–36. Staminate catkins and in situ pollen associated with *Polyptera manningii*. 26. Catkin showing flexible axis, numerous florets, UF 5223, ×1.5. 27. Shorter catkin showing helically arranged florets, UF 5187, ×2. 28. Same, showing detail of florets, each with six or more sessile stamens and inconspicuous bracts, ×5. 29. Pollen sac removed from the specimen in Fig. 27; abundant pollen grains, ×50. 30. Pollen grains from a stamen of the catkin in Fig. 27, transmitted light microscopy, ×400. 31, 32. Triporate pollen grains from stamen of specimen in Fig. 27, showing the characteristic thin ring in the exine, ×1000. 33. Mass of pollen grains from stamen of specimen in Fig. 27, UF 5187, SEM, ×1000. 34. UF 5223, SEM, ×4800. 35. UF 5187, SEM, ×5250. 36. Section of pollen grain from an anther of the catkin in Fig. 27, showing pollen wall made up of thick tectum, granular interstitium and foot layer about one-third to one-quarter as thick as tectum, UF 5187, TEM ×5000. **Localities**: Figs. 26, 34, Dry Canyon, Sweetwater County, Wyoming (UF loc. 15746A); Figs. 27, 28, 31, 32, Pool Ranch, Carbon County, Wyoming (UF loc. 15758).
**Specimens**—UF 5223, 5187, 22576, 22577.

**Discussion**—The staminate inflorescences occur at two localities in association with abundant *Polyptera* fruits: Dry Canyon (two specimens) and Pool Ranch (three specimens). At both localities, no other juglandaceous fruits: Dry Canyon (two specimens) and Pool Ranch (Nichols et Ott) 1978, Maceopolipollenites amplus (Lefèvre, 1965; Stone and Broome, 1975).

The slender catkins have thin axes and are curved in the sediment indicating that they were flexible and pendulous (Figs. 26, 27) like those of most extant Juglandaceae except *Platycarya*. The in situ pollen has a suite of characters in common with extant Juglandaceae, including porate apertures, tectate-granular wall, and nearly plicate surface with microspinulate ornamentation. These pollen grains, like those of all Juglandaceae, have the microspinules distributed in an even geometric pattern (Figs. 30–32), allowing them to be distinguished from otherwise similar grains of Betulaceae, in which the microspinules are arranged in rows on fine ridges, or of Myricaceae, in which they are arranged irregularly. The fossil pollen may be distinguished as an extinct type by the presence of a distinctive circumpolar ring of thin exine on one hemisphere. The thin ring is best seen in transmitted light microscopy (Figs. 30–32) but can also be seen as a collapsed area on some grains as viewed in SEM (Figs. 33, 34). A similar thin area occurs on the proximal pole in pollen grains of *Carya*, but these genera have heteropolar grains with the pores offset slightly from the equator toward the distal side of the grain (Whitehead, 1965; Stone and Broome, 1975).

The same kind of pollen has been identified previously in the record of dispersed grains in the Paleocene of western North America and was already assigned to the Juglandaceae, although more than one generic name has been applied (Lefèvre, 1965; Nichols and Ott, 1978; Manchester, 1989). Two of the previously described dispersed pollen species appear to be morphologically identical to that from *Polyptera*-associated catkins: *Maceopolipollenites amplus* Lefèvre (1971) from the Powder River Basin of northeastern Wyoming, and *Momipites anellus* Nichols and Ott (1978) from the Wind River Basin of central Wyoming. Although Nichols and Ott placed nearly all isopolar, tritrate, juglandaceous pollen in the fossil genus *Momipites*, we agree with Lefèvre (1971) that those with distinct patterns of exinous thinning should be treated apart from *Momipites*. The pollen genus *Maceopolipollenites* Lefèvre applies to tripolar juglandaceous grains with a pattern of exinous thinning on one hemisphere of the grain. Following the philosophy of Lefèvre (1971), Frederiksen (1979), and Manchester (1989), several of the stratigraphically useful species described as *Momipites* by Nichols and Ott (1978) should be transferred to *Maceopolipollenites*. Accordingly, we present the new combinations *Maceopolipollenites anellus* (Nichols et Ott) Manchester et Dilcher [Basionym *Momipites anellus* Nichols et Ott, 1978, Palynology 2:103, pl. 1, figs. 22–25] and *Maceopolipollenites leffingwellii* (Nichols et Ott) Manchester et Dilcher [Basionym *Momipites leffingwellii* Nichols et Ott, 1978, Palynology 2:103, pl. 1, figs. 27–30], which will be used throughout the remainder of this paper.

The use of pollen grain size as a distinguishing species character is subject to special concern. Whitehead (1965) and others have noted that the size of pollen is affected significantly by the conditions of fossilization and that pollen grains swell in some mounting media such as glycerine jelly. We found pollen grains of two different sizes from catkins from two different localities. Pollen from 5223 is 25–30 μm, pollen from 5187 is 24–25 μm. The full range for the catkin pollen is thus 24–30 μm, which bridges the size gap between *Maceopolipollenites anellus* (18–27 μm) and *M. amplus* (29–38 μm). Whether these populations truly represent distinct species is not clear. If found dispersed, the pollen from the catkins associated with *Polyptera* would probably be placed in *M. anellus*. Pollen grains of *Maceopolipollenites anellus* and *M. amplus*, like those of the *Polyptera*-associated catkins, have convex sides between the pores. Pollen of *Maceopolipollenites leffingwellii* from the Wind River Basin (Nichols and Ott, 1978) has the same pattern of exinous thinning and measures 16–25 μm, but has straight to concave, rather than convex sides, permitting them to be distinguished readily from those described above. Similar pollen grains assigned to *Momipites tenuipollus* Anderson from the lowermost Paleocene of the San Juan basin, New Mexico are 14–20 μm, and have a triangular to subtriangular amb (Anderson, 1960).

Dispersed *Maceopolipollenites anellus* and/or *M. amplus* pollen occur in the sediment at many Paleocene localities, particularly where *Polyptera* is known. The occurrence of this pollen type in the Paleocene of China (Liu, 1983; Zhuang, 1990) invites the prediction that *Polyptera* may also be found in the Paleocene of China. However, juglandaceous megafossils have not yet been observed from the same sediments (Manchester and Guo Shuang-xing, unpublished data). It is not present at Almont, where only *Cyclocarya* fruits have been found (the only juglandaceous pollen there is *Momipites* without exinous thin spots).

Among Paleocene juglandaceous pollen grains with a thin ring in the exine at one pole, Nichols and Ott (1978) observed a gradation from grains that are isopolar and thus easily distinguished from those *Carya*, to those that are subisopolar or heteropolar, with one or more of the pores offset from the equator, and thus indistinguishable from *Carya*. Through a stratigraphic sequence they recorded the replacement of *Maceopolipollenites amplus* (“*Momipites*” in their treatment) and related species by species of *Caryapollenites* (pollen like that of *Carya*) and concluded that *Carya* may have evolved from *Momipites*. This hypothesis is difficult to evaluate on the basis of pollen alone.

Leaves and leaflets (Figs. 37–50)

Genus—*Juglandiphyllites* Boulter and Kvaček
*Juglandiphyllites glabra* (Brown ex Watt) Manchester et Dilcher comb. nov.


**Description**—Leaves compound, imparipinnate, 11–25 cm long when complete, with 5–7 leaflets, rachis 3.8–11
Figs. 37–39. Leaves of *Juglandiphyllites glabra* (Brown ex Watt) comb. nov. from the Paleocene of Wyoming. 37. Leaf showing terminal leaflet and two lateral leaflets, the lower pair of lateral leaflets having been shed. Note short petiolules of the lateral leaflets, UF 13163, ×1. 38. Leaf with three leaflets still attached, showing longer petiolules, UF 13689, ×1. 39. Leaf showing a terminal and two lateral leaflets, indicating that there were at least five leaflets originally, UF 13785, ×0.8. **Localities:** Fig. 37, Pool Ranch, Carbon County, Wyoming (UF loc. 15758); Figs. 38, 39, Dry Canyon, Sweetwater County, Wyoming (UF loc. 15746A).
Figs. 40–42. Leaves and leaflets of *Juglandiphollites glabra* (Brown ex Watt) comb. nov. from Dry Canyon, Sweetwater County, Wyoming (UF 15746A), all ×1. 40. Two leaves that have shed the lateral leaflets and retained the terminal leaflet. Some isolated leaflets may also be seen. Note the acuminate leaflet apex and the expanded base of the rachises, UF 13876. 41. Leaf with three leaflets remaining, with scattered *Polyptera* fruits on the same specimen, UF 13687. 42. Leaf with a terminal, two right lateral, and one left lateral leaflets, UF 17108.
Figs. 43–50. Leaflets of *Juglandiphyllites glabra* (Brown ex Watt) comb. nov. 43. One of the larger leaflets, with an asymmetrical base, UF 13735 ×1. 44. More symmetrical leaflet with elongate petiolule, UF 4689, ×1. 45. Detail of venation and margin showing percurrent tertiaries, closely spaced serrations, UF 13875, ×4. 46. Detail of venation and margin showing percurrent tertiaries and fine serrations, UF 21826, ×4. 47. Leaf showing four leaflets, and a fifth that may be inferred from the symmetry. Note camptodromous secondary veins, UF 13862, ×1. 48. Isolated leaflet showing entire margin. Microscopy revealed a few teeth on the lower left quadrant of the lamina but the rest of the margin is entire, UF 13161, ×1. 49. Same, detail of entire margin, ×4. 50. Detail from leaflet in Fig. 43, showing semicraspedodromous secondary veins, and serrations fed by tertiary veins, ×4. Localities: Figs. 43, 45, 47, 50, Dry Canyon (loc. 15746A); Fig. 44, Earnest Butte (UF loc. 15747); Fig. 46, Big Flat Draw (UF loc. 18199); Fig. 48, Pool Ranch (UF loc. 15758).
cm long. Leaflets elliptical, obovate, length 2.8–15, average 7.9 cm; width 1.2–6.5, average 3.1 cm; length/width ratio 2.2–4.2, average 2.6; nearly symmetrical (terminal leaflets) to markedly asymmetrical (lateral leaflets); base cuneate to rounded, apex acuminate to attenuate; leaflets rarely sessile, usually borne on medium to long (3.5–10 mm) petiolules. Margin toothed, with medium to small teeth, about two teeth per 3 mm, rarely entire-margined over some or all of the leaflet. Teeth 0.25–1 mm wide (from sinus to tooth apex), approximately right-angle, acutes acute to rounded, enervated medially by tertiary veins, occasionally by quaternary veins or by excurrent branches from the secondary veins. Sinuses between the teeth acute to right angle, sometimes enervated by a branch from the supradjacent tertiary. Venation pinnate, midvein straight to slightly curved; secondary veins camptodromous to eucamptodromous to semiscraspedodromous, uniformly curved, uniformly spaced, numerous (10–24, usually = 19 pairs), arising at angles of 40°–45°; intersecondarys uncommon, short; tertiary veins percurrent, opposite, closely spaced, commonly at right angles to the secondary veins; fourth and fifth order veins forming a +/− orthogonal reticulum. Areolation poorly preserved.

Nomenclature—Although this name was at first invalidly published without designating a holotype (Brown, 1962), Watt (1971) subsequently designated the specimen in Brown’s Plate 18, fig. 13 as the type and provided the appropriate institutional specimen number.

Additional specimens—UF 4689, 13122, 13123, 13136, 13143, 13151, 13161, 13163, 13165, 13668, 13670, 13687, 13689, 13735, 13784, 13785, 13790, 13792, 13810, 13819, 13862, 13875, 13876, 13999, 14330, 17108, 17793, 17797, 17860, 17870, 21826.

Discussion—There is a consistent association between Polyptera fruits and the leaves and leaflets that Brown (1962) called Pterocarya glabra (Table 1). This evidence supports Brown’s hypothesis that this foliage was produced by the same plant (he called both the leaves and fruits Pterocarya glabra). By removing the fruits from Brown’s concept of Pterocarya glabra and placing them in Polyptera (Manchester and Dilcher, 1982), we had left the leaves in taxonomic limbo—still assigned to the modern genus in spite of evidence to the contrary. The fossil leaves differ from those of extant Pterocarya by the presence of petiolules on the lateral as well as the terminal leaflets, closely spaced tertiary veins, and usually very fine serrations. We now transfer P. glabra to Juglandiphyllites glabra (Brown ex Watt) Manchester et Dilcher. Juglandiphyllites Boulter and Kvček (1989) is a genus accommodating fossil leaflets with affinity to Juglandaceae. Because of the overlapping leaf architectural characters observed in extant Carya, Cyclocarya, Juglans, and Pterocarya, it is sometimes difficult to determine precise modern generic affinities of some species of fossil juglandaceous foliage.

An argument could be made for the formal transfer of J. glabra to Polyptera, because of the strong circumstantial evidence that this foliage type was borne by the same plants that produced Polyptera fruits. However, the leaves have not been found in physical attachment with the fruiting axes. Although J. glabra has been found at all of the localities from which Polyptera fruits are known, J. glabra foliage occurs at some localities where Polyptera fruits have not been found, leaving open the possibility that more than one fruit type could have been produced by plants with J. glabra foliage.

Distinctive features of Juglandiphyllites glabra include petiolules that commonly are long (Figs. 41, 42, 44), the relatively small number of leaflets (five to seven), and leaves that frequently fall with leaflets still attached to the rachis (Figs. 37–42). Teeth are usually small and regular, but sometimes medium to large. At some localities, the teeth are especially small, grading into entire-margined laminae (Figs. 47–50). Long petiolules occur today in some Engelhardieae, but are rare among extant genera of the Juglandaceae and Hicorieae. In Platycaryaeae, the single living genus has sessile leaves without petiolules, yet Eocene representatives have long petiolules (Wing and Hickey, 1984; Manchester, 1987), suggesting that this may be a primitive character.

Specimens of complete to partially complete leaves with intact lateral leaflets have been recovered from five localities (Table 1). All of them have terminal leaflets, indicating that they are imparipinnate.

DISCUSSION

As indicated in the preceding discussions of individual organs, there is strong circumstantial evidence for the association of fruits, staminate inflorescences, and foliage as part of the same fossil species. First, these organs co-occur in abundance at multiple localities (the foliage and fruits at ten localities; the fruits, foliage, and staminate catkins at two localities; Table 1). Second, each of the organs can be identified to the Juglandaceae on its own merit, independent of the other organs. Third, although other genera of this family occur in the Paleocene Fort Union Formation in Wyoming and Montana (Juglandicarya and Cyclocarya; Manchester, 1987, 1989), they have not been found at the same localities as Polyptera. Reconstructed from infructescences, fruits, staminate inflorescences, pollen, leaves, and leaflets (Fig. 51), Polyptera is now the most completely known extinct juglandaceous genus. Polyptera glabra joins two other extant juglandaceous taxa known from multiple organs: Platycarya americana infructescences and fruits with associated leaflets and staminate catkins, and Paleoplaty- carya wingii infructescences, fruits, and associated leaflets (Wing and Hickey, 1984; Manchester, 1987).

Systematic treatment—The reconstructed Polyptera manningii plant (Fig. 51) provides many characters useful in assessing its systematic position. Polyptera conforms to the Juglandaceae in having spicate infructescences, an incompletely septiculate nut with two longitudinal planes of symmetry, epigynous perianth, two style arms, and inflorescence bracts participating in fruit formation. The foliage corresponds to the Juglandaceae in the once pinnately compound leaves, leaflets with semiscraspedodromous secondary venation, percurrent tertiary venation, and nonglandular teeth. The elongate staminate catkins also
Fig. 51. Diagrammatic reconstruction of *Polyptera manningii*. (A) Twig bearing an elongate infructescence (cf. Fig. 3) and compound leaves (cf. Figs. 37–42). (B) Detail of fruits in lateral (cf. Figs. 5–12) and transverse (cf. Figs. 4, 9–24) view. (C) Staminate catkins (cf. Figs. 26–28). (D) Pollen grain in polar and equatorial view (cf. Figs. 31–35). Diagrams by Meredith Morse.

conform to the Juglandaceae, bearing porate pollen with exine composed of a foot layer, a granular interstitium, a thick tectum, and ornamentation consisting of evenly spaced microspinules.

We adopt Manning’s (1978) placement of extant genera into four tribes: the Engelhardieae (*Engelhardia, Oreomunnea, Alfaroa*), Platycaryeae (*Platycarya*), Hicorieae (*Carya*), and Juglandeae (*Juglans, Pierocarya, Cyclocarya*). Smith and Doyle (1995) conducted a cladistic analysis of extant juglandaceous genera (excluding *Cyclocarya*) based upon cpDNA restriction site variation and morphology. Both morphological and molecular data sets gave most parsimonious trees with the Engelhardieae forming a sister group to the rest of the Juglandaceae (Platycaryeae, Hicorieae, and Juglandeae) and Platycaryeae forming a sister group to Hicorieae plus Juglandeae. Smith and Doyle (1995) did not include *Cyclocarya* in their analysis, but it would also be expected to fall within the Hicorieae–Juglandeae clade. As indicated below, *Polyptera* also has ample characters to place it within the Hicorieae–Juglandeae clade.

Among extant Juglandaceae, characters important for tribal placement include presence or absence of a trilobed inflorescence bract (Engelhardieae), presence or absence of septate pith (Juglandeae), and persistence of inflorescence bract on the axis to form a cone-like structure (Platycaryeae) (Manning, 1978; Manchester, 1987; Stone, 1993). There is no evidence for a trilobed bract in the
staminate catkins or in the fruits of *Polyptera*, indicating that a position within the Engelhardieae is unlikely. Pollen of extant genera of Engelhardieae is triporate and isopolar like that of *Polyptera*, but the polar thin ring in the exine is not found in Engelhardieae. Also, the foliage of Engelhardieae differs in characters of the leaflet margin and by the more common occurrence of intersecondary veins. The nutshell being composed of sclereids, rather than fibers, is another feature that distinguishes *Polyptera* from Engelhardieae. The recovery of *Polyptera* fruits still attached to the infructescence axis shows that the infructescence structure is not cone-like, and that primary bracts did not persist on the axis as in extinct and modern Platycaryaeeae (Wing and Hickey, 1984; Manchester, 1987).

*Polyptera* has more derived characters in common with genera of the Juglandaeae and Hicorieae than with those of the Engelhardieae and Platycaryaeeae. Evidence supporting the placement of *Polyptera* in the Juglandaeae comes from a comparison of the fruits with those of *Cyclocarya* (Manchester and Dilcher, 1982). *Polyptera* and *Cyclocarya* both have a disk-like wing oriented perpendicular to the nut axis. The pyramidal shape of the nut and basal attachment of the wing in *P. manningii* differ from extant *Cyclocarya paliurus*, which has a globose nut and equatorial wing attachment. However, the Paleocene species of *Cyclocarya* also have pyramidal nuts and basal wing attachment (Manchester and Dilcher, 1982), suggesting that these may be primitive characters. The production of a large number of fruits on a spicate infructescence in *Polyptera* is similar to the situation in *Cyclocarya* and *Pterocarya*. In his original treatment of the fossil remains, Brown (1962) recognized the affinity to Juglandaeae by naming the leaves and fruits *Pterocarya glabra*. At that time the extant genera *Pterocarya* and *Cyclocarya* were commonly regarded as a single genus (*Cyclocarya* being sunken within *Pterocarya*; the case for recognizing *Cyclocarya* as a distinct genus was emphasized by Iljinskaya [1953]). *Juglandiphyllites glabra* foliage resembles that of extant Juglandaeae, but is also similar to *Carya*.

Similarities with *Carya* (Hicorieae) include the ring of thin exine at the proximal pole of the pollen grain and the absence of well-defined persistent sepal. In *Carya* the sepal are incorporated into a specialized stigmatic disk (Manning, 1940), but in *Polyptera* the stigmatic arms appear to remain independent of the perianth. The petiolulate leaflets of *Polyptera* differ from the typically sessile leaflets of *Carya* and extant Juglandaeae, and might represent a pleisiomorphic condition shared with some extant Engelhardieae and with extinct Platycaryaeeae (Wing and Hickey, 1984).

In summary, *Polyptera* bears characters that indicate affinities both with *Carya* (Hicorieae) and *Cyclocarya* (Juglandaeae). The disk-like wing oriented perpendicular to the nut axis appears to be an important synapomorphy of *Polyptera*, *Cyclocarya*, and *Cruciptera* (Manchester, 1991; Manchester, Collinson, and Goth, 1994), and readily distinguishes these genera from *Carya*, which has a large wingless nut. The thin ring in the exine at the proximal pole of the pollen grains may be an important synapomorphy uniting *Polyptera* and *Carya*. The precise relationship of *Polyptera* with respect to *Carya* and *Cyclocarya* is difficult to resolve by cladistic means because other characters that might provide a closer link to *Carya* or to *Cyclocarya* have not been identified. It is unfortunate that we do not know the pith condition for *Polyptera* because the three extant genera of Juglandaeae have septate pith, whereas Hicorieae and all other extant Juglandaeae have solid pith.

**Distribution, age, and ecology**—*Polyptera manningii* was distributed from at least southwestern Wyoming to southeastern Montana, based on fossil fruit occurrences (Fig. 1). Pollen morphologically very similar to *Maceopolipollenites anellus* occurs in the Paleocene of New Mexico, Texas, and China, suggesting that *Polyptera* may have been much more widespread, but fruits have not been found at these other locations.

As it is currently understood, *Polyptera* is stratigraphically confined to the Torrejonian and lower portion of the Tiffanian stages of the Paleocene. This corresponds to ~56–64 million years ago following the correlations of Sloan (1987). If pollen may be used as a guide, the occurrence of *Maceopolipollenites*-like pollen in the Puercan to Torrejonian Nacimiento Formation of New Mexico (*Momipites tenuipolus* in Anderson, 1960) may represent an even earlier occurrence of *Polyptera*.

In a survey of numerous sites in the Fort Union Formation of Wyoming, Montana, and North Dakota, many occurrences of juglandaceous fruits and foliage were observed (Manchester, unpublished data). Although *Cyclocarya brownii* Manchester and Dilcher (1982) and *Juglandicarya simplicarpa* Manchester (1987) occur together at some localities and appear to range in their stratigraphic distribution from Tiffanian to Clarkforkian, *Polyptera* does not co-occur with them. The appearance of *Polyptera* seems to predate the occurrence of the other two genera in the Fort Union Formation as well as the extinct juglandaceous genus *Casholdia* from the upper Paleocene of England (Crane and Manchester, 1982). *Polyptera* is thus the oldest genus of Juglandaeae in the fossil record that can be confirmed on the basis of fruits as well as leaflets and pollen. Flowers and fruits referable to the order Juglandaeae are known from the late Cretaceous (Frisi, 1983; Crane and Herendeen, 1996). The Cretaceous flowers are bisexual and their fruits are much smaller than any extant Juglandaeae (Manchester, 1989), but their occurrence in the late Cretaceous, together with the appearance of *Polyptera* and other genera of Juglandaeae in the Paleocene, identify the latest Cretaceous and early Paleocene as an important time in the evolution of the Juglandaeae.

*Polyptera* typically occurs in low-diversity assemblages of 8–15 species (Appendix 1). The abundance of fruits and foliage, together with the occasional preservation of delicate catkins in silty strata, indicates that these plants were growing close to the environment of deposition. It is a dominant or codominant constituent of floodplain assemblages. Commonly associated taxa include *Nordenskioldia*, *Nyssidium*, *Platanus*, *Platanites*, and occasionally *Palaeocarpinus*, all of which are thought to have been r-selected colonizers of stream sides and floodplains based upon their small numerous disseminules and abundant representation in overbank sediments. In addition to sharing a common habitat with these
genera, *Polyptera* conforms to a common pattern of possessing wind-dispersed fruits and pollen. These features indicate that *Polyptera manningii* was probably an early-successional species.

**LITERATURE CITED**


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APPENDIX 1. *Polyptera* locality information (numbers corresponding to points on map, Fig. 1).

1. UF loc. 18195, Antelope Butte, Paleocene Fort Union Formation, SE ¼, NW ¼, sec. 2, T16N, R105W, Kappes Canyon Quadrangle, ≈1.5 mi NW of Antelope Butte, Sweetwater County, Wyoming. Below "Coal A" layer, yellowish gray mudstone containing *Polyptera*, *Trapago*, and *Nordenskiöldia*.

2. UF loc. 18198, Earnest Butte, Paleocene Fort Union Formation. SE ¼, NE ¼, sec. 15, T16N, R105W, Earnest Butte Quadrangle, Sweetwater County, Wyoming. Yellowish gray siltstone, mudstone, and gray shale on south slope of Earnest Butte. Common taxa include *Polyptera*, *Cercidiphyllum arcticum*, *Nyssidium arcticum*, and *Carpites verrucosus*.

3. UF loc. 15747, Earnest Butte No. 4, Paleocene Fort Union Formation. Center of NE ¼, sec. 14, T16N, R105W, Earnest Butte Quadrangle, Sweetwater County, Wyoming. This is the same area as USGS site 8921 from which R. W. Brown described *Pterocarya glabra* fruits and foliage. This site has a yellowish siltstone in which a single well-preserved fruit of *Polyptera manningii* was found and abundant *Juglandiphyllites glabra* leaflets.

4. UF loc. 15746a, Dry Canyon, Paleocene Fort Union Formation. NE ¼, NE ¼, sec. 23, T16N, R105W, Earnest Butte Quadrangle, Sweetwater County, Wyoming. Yellowish buff siltstone layer ≈1 m thick, exposed on both sides of pipeline approximately three-quarters of the way up the hill. This layer yields almost exclusively *Juglandiphyllites glabra* foliage and *Polyptera* fruits.

5. UF loc. 18199, Big Flat Draw, Paleocene Fort Union Formation. NE ¼, NE ¼, sec. 27, T16N, R102W, GPS N41°20.487', W108°51.978', Burley Draw Quadrangle, Sweetwater County, Wyoming. This site is the same as USGS loc. 5259. *Glyptostrobus*, *Juglandiphyllites glabra*, *Polyptera manningii*, "Ficus" artoxarpoides, and *Trochodendroides*.

6. UF loc. 15886, Black Buttes Mine, pit 3, Paleocene Fort Union Formation. S ½, sec. 31, T18N, R100W, Sand Butte Rim Northwest Quadrangle, Sweetwater County, Wyoming. Collected in the spoils of Black Buttes Mine Pit 3, a strip mine in the Little Valley coal seam, in the lower part of the Fort Union Formation. The area was surface mapped by Roehler (1977) prior to coal strip-mining. Locality occurs in an interval ≈30 m stratigraphically above the sites that yielded Torrejonian vertebrates (Winterfeld, 1982, University of Wyoming loc. V77012 and V77009). The age of locality UF 15886 is therefore probably upper Torrejonian or Tiffanian.

7. UF loc. 18266, Black Buttes Mine, pit 10, Paleocene Fort Union Formation. SW ¼, NW ¼ Sec. 13, T19N, R100W, Sweetwater County, Wyoming. Fossils in pink clinker shales from spoils at south end of pit 10, from layer overlying the "C" coal that is being mined. Abundant *Juglandiphyllites glabra* and *Polyptera*. Platanaceae, Cercidiphyllaceae, *Zingiberopsis*, and peltate, lobed menispermaceous leaf.

8. UF loc. 18245, Above Bridger Coal Mine, Paleocene Fort Union Formation. W ½, NE ¼ sec. 36, T21N, R100W Bitter Creek Northwest Quadrangle, Sweetwater County, Wyoming. Leafy shale horizon exposed on SW side of hill near top of ridge. Contains *Juglandiphyllites glabra* in abundance, *Polyptera*, *Potamogeton*, *Cornus* taxaceous needles, ulmaceous leaf fragments, ferns, and *Equisetum*.

9. UF loc. 15758, Pool Ranch, Mexican Flats, Paleocene Fort Union Formation. SE ¼, SE ¼, sec. 16, T16N, R92W, Blue Gap Quadrangle, Carbon County, Wyoming. Master's thesis locality of Roth (1975). *Polyptera* fruits common; *Juglandiphyllites glabra*, juglandaceous catkins, *Platanites*, *Nordenskiöldia*. The locality is at approximately the same stratigraphic level as the adjacent Swain Quarry, which yields a Torrejonian mammalian fauna (Rigby, 1980).

10. Mexican Hat, Paleocene Fort Union Formation. Ca. NE ¼, NE ¼, sec. 29, T8N, R52E, Hogan Creek Quadrangle, Custer County, Montana. Thesis locality of Williams (1988). This is in the Lebo Shale member of the Fort Union Formation of Torrejonian Land Mammal age.