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## THE PLATYCARYA PERPLEX AND THE EVOLUTION OF THE JUGLANDACEAE<sup>1</sup>

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### ABSTRACT

We report on the leaves, fruits, inflorescences, and pollen of two fossil species in the genus *Platycarya*. The association of these dispersed organs has been established by their repeated co-occurrence at a large number of localities, and for two of the organs (fruit and pistillate inflorescence, and pollen and staminate inflorescence) by apparent organic attachment of compression fossils. Each of the two species can be distinguished by characteristics of all the known megafossil organs. We also review the fossil record of dispersed platycaryoid fruits and inflorescences, recognizing three additional species of *Platycarya* and two of *Hooleya*. Two of the fossil *Platycarya* species are morphologically very different from the living *Platycarya strobilacea* Sieb. et Zucc., but they show the diagnostic features of the genus. *Hooleya* is a generalized member of the Platycaryeae that is probably close to the ancestry of *Platycarya*.

The two *Platycarya* species known from multiple organs provide a remarkable example of mosaic evolution in which fertile and foliar structures have attained different levels of morphological specialization. The leaves, often considered the most plastic of plant organs, retain several features that are otherwise seen only in the Engelhardieae. These similarities in leaf architecture between the fossil *Platycarya* species and Engelhardieae are advanced features for the Juglandaceae, and thus indicate a sister-group relationship between the two lines. In contrast to the leaves, the fruits, inflorescences, and pollen of the fossil *Platycarya* species are almost as specialized as those of the extant *P. strobilacea* and bear little resemblance to the same structures in other genera of the family.

The morphology, taphonomy, sedimentary setting, and geographic and stratigraphic distribution of three of the fossil platycaryoid species suggest that they were wind-dispersed, early successional plants that grew in thickets. This habit is retained by *Platycarya strobilacea* and is typical of many of the amentiferae (e.g. Myricaceae, Betulaceae). The *r*-selected life-history pattern of the *Platycarya* line may well have contributed to its low diversity through geologic time.

THE RELATIONSHIP of *Platycarya* to the rest of the Juglandaceae has long remained an intractable problem in the systematics of the walnut family. Manning (1938, 1940, 1948) concluded that the inflorescences and flowers of *Platycarya strobilacea*<sup>2</sup> Siebold et Zuccarini retain many features that are primitive for the family as a whole. However, *P. strobilacea* also has advanced features, such as pseudocolpate pollen, condensed pistillate inflorescences and spirally thickened vessel elements, that are

unique in the Juglandaceae. Neither the generalized conditions nor the unique specializations of the genus are of much value in deciphering the relationships between *Platycarya* and the other genera of the family.

For similar reasons the fossil record has also shed little light on intrafamilial relationships. *Platycarya*-like pollen first occurs in the fossil record at or slightly below the Paleocene-Eocene boundary (Frederiksen and Christopher, 1978), but these early Tertiary grains already bear the characteristic pseudocolpi of *Platycarya*, and differ from pollen of *P. strobilacea* chiefly in being larger and in having a more variable shape and arrangement of pseudocolpi. Four published megafossil taxa are attributed to *Platycarya*: two species based on leaves, *P. miocenica* Hu et Chaney (1940) and *P. pseudo-brauni* (Hollick) Wolfe (1979); and two species based on fertile material, *P. richardsonii* (Bowerbank) Chandler (1961) and *P. americana* Hickey (1977). These four species were initially described as being very similar to *Platycarya*

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<sup>2</sup> In this paper we follow Manning (1978) in taking *Platycarya strobilacea* to include *P. longipes* Wu.

*strobilacea*, and so made little contribution to understanding the relationships of the platycaryoid line.

This study differs from previous ones in two ways. First, for two fossil species of *Platycarya* we have studied several organs, including leaves, fruits, inflorescences and pollen. Second, the species of *Platycarya* and *Hooleyia* covered here differ from *Platycarya strobilacea* in ways that provide a key to understanding the relationship of *Platycarya* to the other Juglandaceae.

**TAXONOMIC CONCEPTS—Fossil genera—** Prior to the publication of the 1978 Code of Botanical Nomenclature, paleobotanists recognized two types of genera as "holding categories" for remains whose biological affinities were unclear. The first of these, the form genus, consists of remains unassignable to a family; the second type, the organ genus, constituted remains that could be so assigned (Stafleu et al., 1972). In 1978 the organ generic category was eliminated (Stafleu et al., 1978), nevertheless the feeling has persisted among many paleobotanists that genera based on fossils are in some way artificial because the material is often fragmentary and does not represent the whole plant. In contrast, we do not believe that fossil genera are necessarily artificial; the "naturalness" of a genus depends on characters, not simply on how much of the plant body is known. Failure to make this distinction may lead to the indiscriminate use of form genera, in which are lumped both fossil taxa that are poorly known and those that are well known but morphologically generalized.

In a cladistic sense, each natural genus is defined by a unique character or set of characters that is consistently found in its member species. For convenience in discussion we will consider fossil taxa in two groups: those that possess characters defining a natural genus, and those that lack such characters.

The appropriate "holding category" for a dispersed organ in the first group (i.e., one that has at least one generic autapomorphy, a unique character diagnostic of a natural genus) is a natural genus. The chief argument against placing a dispersed organ in a natural genus is that it creates nomenclatural instability (the eventual discovery of more complete fossil remains may yield characters that would require the species to be transferred to another genus). However, the problem of nomenclatural instability is not as severe as might be thought. Additional organs of a fossil species that are recovered after the initial description can give three kinds of information. One, the newly

found organ(s) may be similar to those of other species in the genus. If so the original generic placement is borne out. Two, the newly discovered organ(s) may be more generalized (plesiomorphic) than are the same organs in other species in the genus. In this case the original generic placement is still correct because the fossil species possesses the diagnostic autapomorphy(-ies) of the genus; the fossil species is simply more primitive than its congeners. (For an example in which a large number of primitive features might influence generic assignment, see discussion of stem groups below.) Three, the newly discovered organ(s) may show new autapomorphies. If these autapomorphies are significant, they may be used as the basis of a new natural generic category. Only this last kind of new information is likely to require a generic transfer. Even if the dispersed organ had originally been placed in a form genus, rather than in a natural genus, the discovery of new generic-level autapomorphies would require a redefinition of the form genus, or the naming of a new natural genus. Thus form genera do not appear to significantly increase nomenclatural stability for fossil taxa that have autapomorphies that should allow them to be placed in a natural genus. The disadvantage of using form genera is that they relegate the fossil material to a category that has no clear place in the hierarchy of botanical nomenclature, a category that does not convey the relationships of the fossil as precisely as does a natural genus.

What about fossil material falling in the second group, those that lack generic autapomorphies? Some fossils lack generic autapomorphies because they are extremely generalized and thus indistinguishable from the hypothetical ancestor of one or more other taxa in the family. For example, the Paleocene juglandaceous fruit *Casholdia* (Crane and Manchester, 1982) has two synapomorphies with *Engelhardia* and *Oreomunnea*, but it differs from them by being more plesiomorphic in four other characters. This fossil lacks any generic-level autapomorphies, yet it is easily distinguished from other juglandaceous genera by its unique combination of plesiomorphies and apomorphies. Such morphological ancestors are best placed in a monotypic stem group (as Crane and Manchester have implicitly indicated for *Casholdia*). This practice expresses phylogenetic history and relationships far better than the use of form genera and also serves to distinguish generalized taxa from those that are just poorly known.

Other fossils may lack generic autapomorphies because they are poorly preserved or be-

cause the organs that bear the significant features have not been recovered. For such fossils, two options are available: the fossil can be left without a formal name, or it can be placed in a form genus. Form genera are most useful when the fossil species is a clearly recognizable entity that has some biostratigraphic or paleoecological importance, even though its botanical affinities are unclear. In our opinion, however, the form-genus category should be used only when affinities are unclear because diagnostic apomorphies are missing or unavailable. It should not be used simply because the species is based on dispersed organs, or in species where the diagnostic characters are present but in the plesiomorphic character state. Although form genera are meant to apply when affinities at the family level cannot be determined, we find this stipulation arbitrary. The essence of the form-genus category is that it allows a formal name to be given to a species that is *incertae sedis* with respect to some more inclusive level in the hierarchy. Whether this more inclusive level is a tribe, family, or a class should make no difference.

In conclusion, we find that fossil genera need not be considered artificial, and that, generally, the use of natural genera is preferable to the use of form genera because it more precisely expresses phylogeny. The use of form genera should be restricted to fossils for which a natural genus cannot be defined or determined because key characters are unavailable as a result of some imperfection of the fossil material. Even under these circumstances it may be better to leave the fossil without a formal name unless it has some biostratigraphic or paleoecological utility.

*Association of dispersed organs*—The study of multiple fossil organs belonging to the same biological species may bring the needs of nomenclatural stability and biological accuracy into conflict. The practice of placing each kind of dispersed fossil organ in its own taxon (at the generic or specific level) preserves nomenclatural stability should the organs later prove to have been spuriously associated and provides separate names for morphological entities that are not usually found connected. However, the use of such organ taxa may hinder the recognition of true biological entities (species), and may thus impede evolutionary or systematic syntheses based on the fossil record. Therefore, we assert that dispersed organs should be included under a single name when there is strong evidence that the dispersed organs belong to a single biological entity.

TABLE 1. Occurrence of the dispersed organs of *Platycarya americana* and *P. castaneopsis* at 26 localities. Symbols: P, present; P?, doubtfully present; A, absent; —, no sample processed for pollen; ψ, localities at which fossils were poorly preserved; \*, localities for which only small samples were available. Detailed locality information is given in Appendix 1

Localities	Leaflets	Fruits	Pistillate inflorescence	Staminate inflorescence	Pollen
<i>PLATYCARYA AMERICANA</i>					
USGS9559*ψ	A	A	P?	A	—
USNM14053*ψ	A	A	P?	A	—
USNM14048	P	P	P	P	P
USGS9394ψ	P	P	P?	P	—
<i>PLATYCARYA CASTANEOPSIS</i>					
UCMP PA114	P	P	P	A	—
UCMP PA104	P	P	P	A	—
USGS8912	P	P	P	A	P
USGS9397	P	P	P	A	—
USGS9051*	P	P	A	A	—
USGS9538*	P	P	P	A	—
USGS9179*	P	P	P	A	—
USGS8894*	P	A	A	A	—
D4309*	P	A	A	A	P
BCT	P	P	P	A	—
CQ	P	A	A	A	P
FL	P	A	P	A	P
WhBgψ	P	A	P	A	P
TAT79ψ	P	A	P	A	P
BCT2ψ	P	A	P	A	—
MBR*	P	A	P	A	—
SLψ	P	A	A	A	—
15MEψ	P	A	A	A	—
Bψ	P	A	A	A	—
15Mψ	P	A	A	A	—
TLψ	P	A	A	A	—
Tψ	P	A	A	A	—
WhBgLψ	P	A	A	A	—
T2ψ	P	A	A	A	—

What evidence is necessary? Petrified material showing anatomical connection between parts is convincing but extremely rare, especially in Tertiary floras. Attachment of structures in compression may provide good evidence, depending on the quality of preservation and the amount of organic matter on the bedding surface. Physical proximity of dispersed organs in the sediment is generally considered weak evidence that the organs were parts of the same plant. However, we argue here that under special circumstances the physical proximity of dispersed plant organs can provide strong evidence that they belonged to the same plant and that placement of such dispersed organs in the same genus and species can be adequately justified.

*The association of dispersed organs in Platycarya americana and Platycarya castaneopsis*—*Platycarya americana* is here emended to

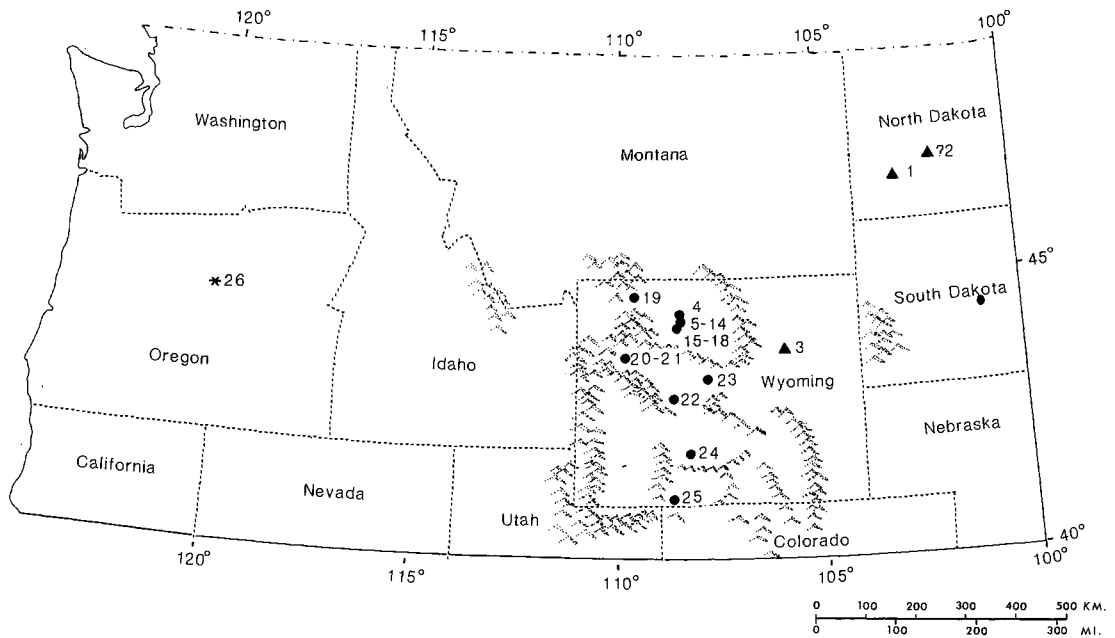


Fig. 1. Index map showing localities for *Platycarya americana* (1-3), *Platycarya castaneopsis* (4-25), and *Hooleyia lata* and *Platycarya manchesterii* (26). See Appendix 1 for precise locality information.

include leaflets, staminate inflorescences and pollen in addition to pistillate inflorescences and fruits. *Platycarya castaneopsis* is a new combination under which we include leaflets, fruits, pistillate inflorescences and pollen. We have used several lines of evidence to establish the association of the dispersed organs placed in each of these species. This evidence includes the repeated physical proximity of dispersed parts, their taxonomic similarity, their congruent stratigraphic distributions, and for some organs their physical connection in compression fossils.

Collections of *P. americana* have been made at quarry sites in Wyoming and North Dakota (Fig. 1). At two quarries, the leaflets, staminate and pistillate inflorescences, fruits, and pollen were all found together in a mass of rock less than 1 m square and 15 cm thick.

Collections of *P. castaneopsis* have been made at 21 quarry sites in three different formations in widely separated areas of western Wyoming (Fig. 1). Five of these small quarry sites produced leaflets, fruits and pistillate inflorescences, five had leaflets and pistillate inflorescences, one yielded leaflets and fruits, and nine more produced only leaflets. Pollen samples were taken at six of the sites, and *Platycarya* pollen was abundant (generally > 15% of the palynoflora) in all of them. Male inflores-

cences of *P. castaneopsis* were not recovered, probably because they were too fragile to be readily fossilized. Quarries that produced fewer than three megafossil organs were localities where preservation was relatively poor and/or collections were small (Table 1).

Three arguments can be advanced to explain the repeated physical association of the same plant parts at different localities: 1) the plant material was sorted by wind or water (i.e., the dispersed organs are hydrodynamically similar); 2) the plants of two or more species that produced the organs all grew in the same habitat; 3) the organs belonged to the same species of plant. For these fossil *Platycarya* species we can effectively eliminate hypotheses one and two.

If the co-occurrence of the organs belonging to *Platycarya* is a result of water sorting processes, then we should expect to find evidence for current flow in the sediment. Field studies of localities where *Platycarya* occurs show that the fossils were all deposited in low-energy fluvial or fluvio-paludal settings (Hickey, 1977; Wing, 1980, 1981, in press, and unpubl. field observ.). The fossiliferous sediment is silt or mixed clay and silt, and current features are generally absent. The plant megafossils are neither torn nor folded. Like other low-energy fluvial settings (Scheibling and Pfefferkorn, 1982), there is extremely low potential here for

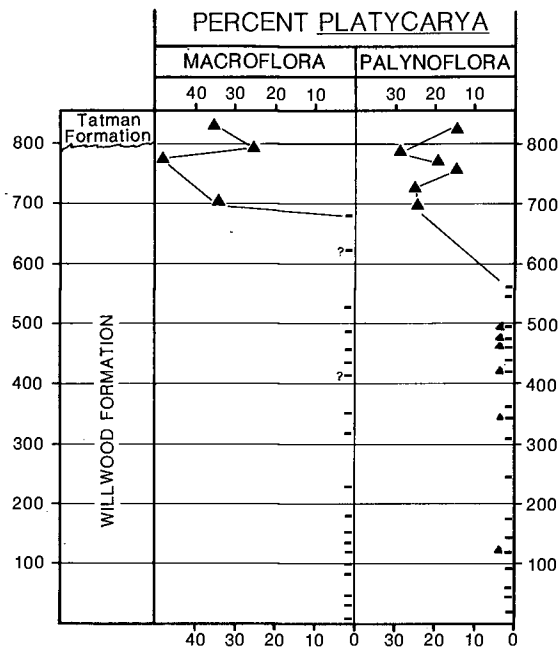


Fig. 2. Stratigraphic occurrence of *Platycarya* micro- and megafossils in the Willwood Formation and Tatman Formation of the Bighorn Basin, Wyoming. Symbols: —, sampled level where no *Platycarya* remains were found; ?, doubtful or uncertain occurrence of *Platycarya*; ▲, present at the plotted percentage of the flora.

the deposition and preservation of allochthonous plant remains. In addition, the dispersed organs of *Platycarya* (small, winged fruits; woody, cone-like pistillate inflorescences; leaflets; pollen) are not hydrodynamically similar to one another.

The hypothesis that the dispersed organs of each *Platycarya* species actually belong to two or more species that are ecological associates is also controverted by the low energy of deposition and the high fidelity of preservation at the *Platycarya* localities. If the organs of each *Platycarya* complex were derived from more than one species, other plant megafossils should occur consistently with *Platycarya* (e.g., the leaves that really belong with the fruits of *P. castaneopsis*). In actuality, no kind of plant megafossil consistently occurs with organs of either *Platycarya* species (Appendix 2), and no other Juglandaceae have been identified at the *Platycarya* localities.

As the two associations of dispersed organs that form *P. americana* and *P. castaneopsis* are unlikely to have been created by sorting or by the mixing of the organs of more than one species, the only remaining hypothesis is that each set of organs belonged to one plant. This hypothesis is further strengthened by the strati-

graphic distribution of *P. castaneopsis* leaflets and pollen.

The stratigraphic evidence is derived from work in the Willwood and Tatman Formations of the Bighorn Basin in northwestern Wyoming (Fig. 1). An 820-m-thick stratigraphic section was measured through these formations, and pollen samples were taken at frequent intervals (Wing, 1981). Pollen of *Platycarya* is sporadic and in low abundance through most of this section (Fig. 2). At 700 m it becomes extremely abundant and constitutes at least 15% of the palynoflora through the rest of the section. This pattern matches the stratigraphic distribution of *P. castaneopsis* leaflets, which have their lowest reliable occurrence at 700 m and dominate the megafloora from this level up (>25% in censused collections). The high abundance of platycaryoid pollen occurs at all six *Platycarya* megafossil localities for which pollen data are available.

Further evidence for considering the dispersed organs as parts of the same species comes from the intrafamilial affinities of each organ type. Within each of the allopatric organ complexes representing *P. americana* and *P. castaneopsis*, the inflorescences, fruits, and pollen show features characteristic of the tribe Platycaryeae, whereas the leaflets have features allying them with both Platycaryeae and Engelhardieae. The consistent affinity of these organs to particular parts of one family further diminishes the probability that they are derived from more than one kind of plant.

The final line of evidence for the association of these organs is organic connection in some compression fossils. Material from the Wind River Formation (University of California Museum of Paleontology [UCMP] locality PA 114) shows the small, winged fruits of *P. castaneopsis* borne in cone-like inflorescences of the type usually found in close proximity to them (Fig. 16, 21, 22). In material from the Golden Valley Formation (U.S. National Museum [USNM] locality 14048; Fig. 10, 12), anthers of the staminate inflorescences of *P. americana* contain the same type of platycaryoid pollen that dominates the dispersed pollen floras of localities that produce *Platycarya* megafossils.

Given the overwhelming evidence from repeated physical association, sedimentary context, stratigraphic distribution, taxonomic affinity, and physical connection, we feel fully justified in treating these two complexes of dispersed fossil organs as biological entities, and in placing the organs of each complex under one name. Because of the strong evidence that each complex of organs represents one kind of

plant, the advantages to systematic and evolutionary discussion of using one name far outweigh the risk of nomenclatural instability.

## SYSTEMATICS SECTION

### Genus *Platycarya* Siebold et Zuccarini 1843

*Emended description:* Description in italics refers to conditions observed in fossil species; leaf architecture terms after Hickey (1979). Leaves odd-pinnately compound with 5–11 leaflets; leaflets with short to long petiolules and rounded, semicordate, *acute or decurrent* bases that may have patches of hair or show some *elaboration and enrollment* of the basilar tissue; margin serrate; teeth Cunonioid (Hickey and Wolfe, 1975), with sharp or *rounded* weakly glandular apices; secondaries leaving the midvein at 65° to 90° and curving gently or *sharply* upward near the margin; intersecondaries weakly to *strongly* developed; tertiary veins percurrent, straight or *retroflexed*, making perpendicular or *obtuse* junctions with the subadjacent secondary; quaternary vein order easily or *not easily* distinguished from higher order veins; areoles 0.15–0.30 mm in diameter, weakly or *strongly* impressed, and with 5%–10%–90% of the areoles having freely ending veinlets; marginal venation with two weak or *strong* veins ascending from each sinus to the superadjacent tooth.

Inflorescence axes usually bisexual (mature pistillate axes bearing lateral scars below the fertile part) with the staminate inflorescences lateral to the pistillate. Pistillate inflorescences 3–8 cm long and 1–2 cm wide, cone-like with woody bracts arranged spirally along the distal part of the axis; bracts 3–11 mm long and 2–5 mm wide, with acute to *rounded* apices; persistent on the axis.

Fruits 2–10 mm wide and 2–5 mm high (proximal-distal direction); bilaterally symmetrical, nutlets winged; lateral wings formed of fused bracteoles and lateral sepals; median sepals reduced, or *persistent and usually extending past the stigmatic region*; styler arms carinal, short (<0.5 mm), stigmatic surface adaxial, or *partly terminal*; nutlet attachment oriented abaxially, *basal/abaxially or basally*.

Staminate inflorescences more slender than pistillate inflorescences, 3–10 cm long and 1 cm wide with no indication of lateral scars on the lower part of the axis, bracts spirally arranged and persistent; more flexible than the bracts of the pistillate inflorescence; bracts ~1 mm long, narrow proximally and slightly expanded distally, apex acute or *rounded*; 4–6–15 bilocular stamens per bract.

Pollen grains triporate, isopolar, with convex sides; diameter 13.5–18.5–23.5 μm, pores not conspicuously elaborated, but atriate; each hemisphere bearing one or two narrow (~1 μm wide), weakly to *strongly arcuate, Y-shaped, or circular* pseudocolpi; surface sculpture finely granulate.

*Diagnosis:* *Platycarya strobilacea* has nine advanced features not seen in other extant genera: 1) condensed pistillate inflorescence; 2) woody primary bracts on the pistillate inflorescences; 3) receptacle of the fruit oriented abaxially; 4) fusion of the lateral sepals and bracteoles; 5) loss or reduction of the median sepals; 6) anteriorly-posteriorly flattened nutlets; 7) spiral thickenings on vessel elements; 8) pseudocolpate pollen; 9) attenuate laminar apices. We consider features 1, 2, 4, and 8 to be characteristic of the whole genus.

***Platycarya americana* Hickey, emend. (Fig. 3–14, 51)**

*Salix heartensis* Hickey 1977 G. S. A. Mem. 150: 117, 118; Pl. 13, fig. 1, 2, 5.

*Platycarya americana* Hickey 1977 G. S. A. Mem. 150: 118, 119; Pl. 14, fig. 4–8; Pl. 15, fig. 2–4, 7.

*Lamanonia borealis* Hickey 1977 G. S. A. Mem. 150: 129–131; Pl. 26, fig. 9; Pl. 27, fig. 2–4, 6; Pl. 28, fig. 1–6; Pl. 29, fig. 1–4; Pl. 30, fig. 1–4.

*Cyperacites* sp. Hickey 1977 G. S. A. Mem. 150: 113; Pl. 8, fig. 4, 5.

*Platycarya* n. sp. "A" Bebout 1977 unpublished doctoral dissertation, Penn. State Univ., pp. 195–197; Pl. 13; fig. 8–10.

*Emended description:* Leaves probably odd pinnately compound with more than 9 leaflets, though no whole leaves preserved; inferred from size variation and proportion of symmetrical to asymmetrical leaflets. Leaflets symmetrical to asymmetrical, especially at the base; straight to falcate, narrow ovate to ovate-lanceolate, sometimes very narrow elliptic to elliptic, or obovate; length 4.5–19.2 cm; width 1.0–5.5 cm; length-width ratio continuously varying from 2.6–10.2; apex attenuate; base acute to decurrent, leaflet substance thickened and margin rounded to truncate at the very base of the blade where it joins the petiolule, in <5% of the leaflets the blade completely decurrent; margin serrate, serrations mostly D4 or A4, sometimes B4 or a previously unrecognized type that has a reverse acuminate basal margin (concave below, convex above) with a convex apical side; leaflet texture chartaceous to subcoriaceous; petiolule long. Venation pinnate; midvein straight or slightly curved and

stout. Secondaries craspedodromous to semi-craspedodromous; 14–44 pairs arising from the midvein at an angle of 50° to 85°; secondary course gently and uniformly curved or abruptly upcurved at the margin, secondaries branching just before reaching the margin and sending one branch to the tooth or sinus and a generally weaker branch along the margin to the superadjacent tooth or secondary; intersecondaries rare to common. Tertiary veins opposite percurrent; course retroflexed, departing from the basal sides of the secondaries at an acute to right angle and meeting the distal side of the secondaries at a right to obtuse angle; tertiaries near the midvein recurved, sometimes forming intersecondaries of variable length. Quaternary vein net not easily distinguished from quinternaries and higher. Areolation closed (no freely ending veinlets); areoles somewhat variable in size and shape, mostly 3–5 sided and less than 0.3 mm in maximum diameter. Teeth glandular Cunonioid; principal vein a secondary or branch that enters the tooth centrally, or eccentrically on either side, and terminates at the apex; principal vein frequently gives off an almost equal branch to the sinus, in some teeth the principal vein travels directly to the sinus; in either case, the vein plexus at the sinus gives off a tertiary vein that passes up the margin of the lamina to the apex of the superadjacent tooth; this marginal branch is usually paralleled on the medial side by the distal part of a secondary, thus forming two veins that follow the leaf margin near the edge (Fig. 25).

Pistillate inflorescences (1.5–4.0 cm long; 0.8–1.3 cm wide; woody bracts arranged spirally on a stout peduncle that is 2–3 mm broad at the base and as much as 3 cm long, and has scars below the base of the fertile portion. Bracts ovate with an acuminate beak as much as 2 mm in length; margin entire; average dimensions 7 mm long by 2.5 mm wide; bracts often slightly curved; venation obscure.

Staminate inflorescences slender, bearing spirally arranged thin-textured bracts; inflorescences 2–4 mm wide and 6–12 mm long, basal part of the axis about 1.5 mm wide and lacking any lateral scars; bracts ~1 mm long, ovate in shape with a rounded apex, possibly constricted near the attachment to the axis; each bract bearing more than 3 but probably fewer than 7 stamens; anthers bilocular and attached to the bract by a filament; anther locules containing numerous pseudocolpate pollen grains (described below).

Fruits dorsiventrally flattened, bilaterally symmetrical, winged nutlets with two laterally arranged locules (Fig. 7, 8); overall shape obovate, length 3.5–4 mm, width approximately equal to or slightly exceeding length, receptacular (basal) end of the fruit containing a rounded socket; distal end of the fruit deeply embayed between the wings, median carinal sepals variable in size but sometimes extending beyond the distal end of the nutlet; surface of the nutlet marked by a longitudinal furrow (the impression of the primary partition of the nutlet) and by a pair of exmedially curved lateral furrows originating at the basal end.

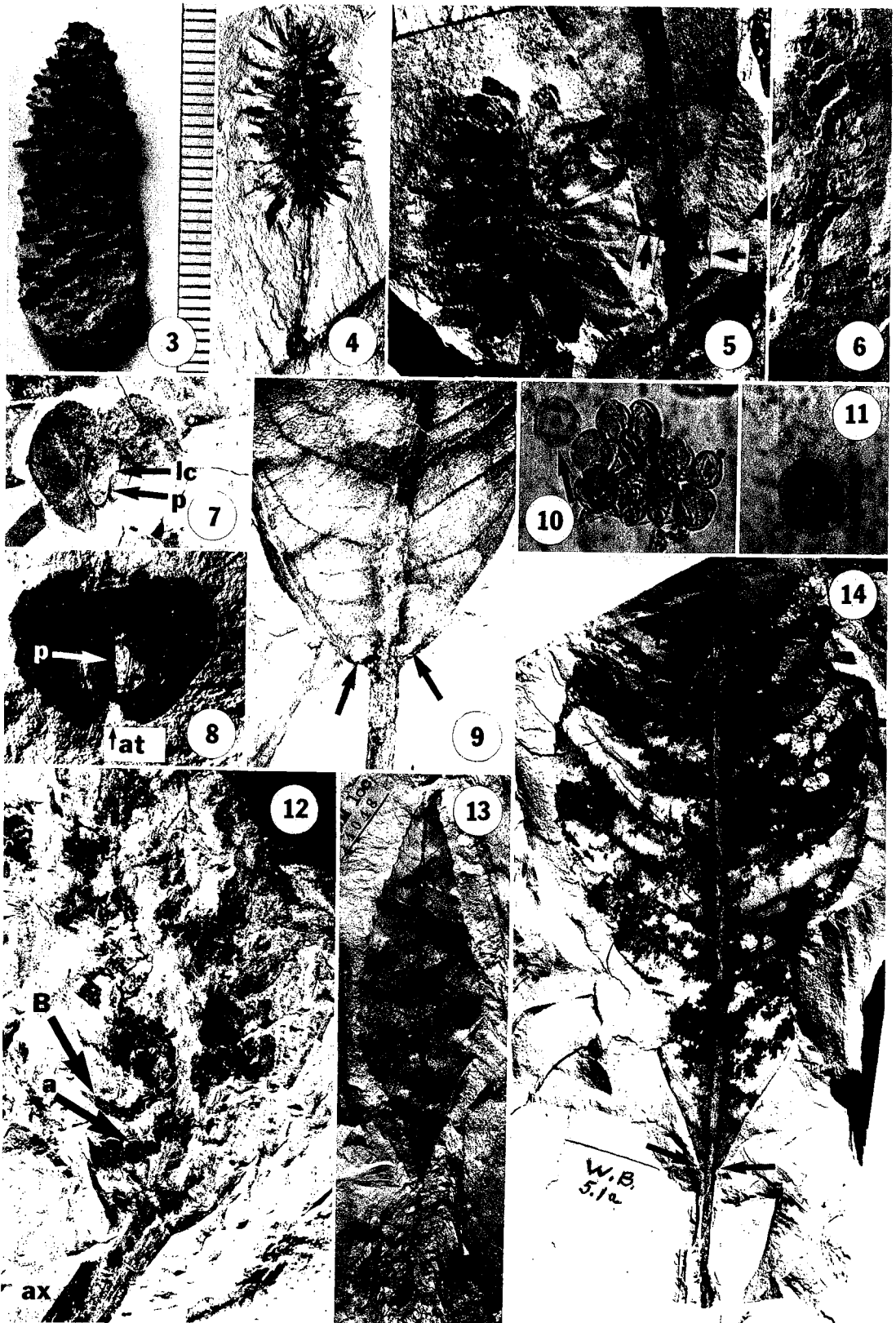
Pollen triporate, isopolar, with convex sides, and unelaborated, atriate pores; diameter 18.5–23.5  $\mu\text{m}$ ; each hemisphere marked by one or two arcuate, circular, or Y-shaped pseudocolpi; sculpture finely granulose.

*Systematic placement:* *Platycarya americana* shares all the floral specializations of *P. strobilacea* except for loss of the median sepals. Minor differences in the shape of the primary bracts and the fruits allow the two species to be distinguished, but the major differences are found in the leaves. Eight leaf features of *P. americana* are absent or very rare in *P. strobilacea*: basilaminar tissue specialization; closed areoles; well-developed intersecondaries; long petiolules; decurrent or acute leaflet bases; rounded tooth apices; two parallel mar-

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Fig. 3–14. *Platycarya americana*. Key to abbreviations at the end of this caption. 3. Limonitized pistillate inflorescence. USNM 356409.  $\times 2.7$ . 4. Compressed pistillate inflorescence showing short axis with slightly expanded base. USNM 356368.  $\times 1.5$ . 5. Left, Paratype, pistillate inflorescence, showing ovate, acute-tipped, closely set bracts. USNM 43167A; Right, base of leaflet showing elaboration of basilaminar tissue (arrows). USNM 356408A.  $\times 3.0$ . 6. Staminate inflorescence. USNM 167478.  $\times 4.0$ . 7. Fruit with a partial locule cast showing the impression of the median septum (arrows). USNM 356406.  $\times 7.0$ . 8. Paratype, limonitized fruit showing median septum and basal attachment scar. USNM 167481B.  $\times 8.0$ . 9. Leaflet base showing paired basilaminar tissue elaboration (arrows). USNM 356371.  $\times 2.9$ . 10. Small mass of pollen macerated from an anther extracted from the staminate inflorescence in Fig. 12. Note one grain with an almost circular pseudocolpus (arrow).  $\times 250$ . 11. Pollen grain from same anther, with a Y-shaped pseudocolpus.  $\times 500$ . 12. Staminate inflorescence showing axis, primary bracts, and anthers. USNM 356367.  $\times 9.0$ . 13. Probable lateral leaflet, with elliptic shape, long petiolule, and rare lack of elaborated basilaminar tissue. USNM 356370.  $\times 1.0$ . 14. Probable terminal leaflet with obovate shape and specialized basilaminar tissue. USNM 356369.  $\times 0.9$ . Abbreviations: a, anthers; at, attachment area of fruit; ax, primary axis of inflorescence; B, primary bract; b, bracteole; lc, locule cast; ls, lateral sepal; ms, median sepal; n, nutlet body; p, median partition; sm, stigmatic surface; st, style arms.





ginal veins; and obtuse junctions of the tertiaries with subadjacent secondaries. All these features are primitive for the Platycaryeae (see section on phylogeny for discussion of character polarities and outgroups) and therefore do not provide a basis for placing the fossil species in a separate genus. Nevertheless, *P. americana* is considerably less specialized than its living congener.

**Occurrence:** See Table 1 for localities. The two formations that have produced *P. americana* also have yielded mammalian faunas. USNM locality 14048 in the upper part of the Camels Butte Member (Hickey, 1977) of the Golden Valley Formation, Stark Co., N.D., is stratigraphically above a mammalian fauna that has been identified as mid-Wasatchian (D. M. Schankler, written commun., 1980). U.S. Geological Survey (USGS) locality 9394 is near the top of the Wasatch Formation on Pumpkin Buttes, Wyoming, and is stratigraphically higher than mammalian faunas determined to be "Lostcabinian" (Delson, 1971). Thus, mammalian biostratigraphic correlation places both localities as later early Eocene or younger. In the areas of the *P. americana* localities, both the Wasatch and the Golden Valley Formations are overlain unconformably by Oligocene White River Formation.

**Collection:** Holotype: pistillate inflorescence—USNM 42992. Paratypes: pistillate inflorescences—Princeton University (PU) 20060, 20061, 20063, and USNM 43165, 43166, 43167A and B, 43171; fruits—USNM 167481A and B, 167482, 167515, 167516. Referred material: staminate inflorescences—USNM 43172A and B, 167478, 167479 (figured specimens of *Cyperacites* sp.), USNM 356366A and B, 356367; fruits—USNM 356365; leaflets—USNM 356363A and B, 356362, 356364, 356408A and B, 356361A and B, 356369, 356370, 356371 and speci-

mens listed under the original description of *Lamanonia borealis*, including the holotype, USNM 43026.

***Platycarya castaneopsis*** (Lesquereux) Wing et Hickey, comb. nov. (Fig. 15–27, 51)

*Quercus castaneopsis* Lesquereux 1883 U.S.G.S. Rept. Terr. 8: 155; Pl. 28, fig. 10. Knowlton 1923 U.S.G.S. Prof. Pap. 131: 161 (synonymy not accepted). Berry 1932 Am. Mus. Nov. 527: 10; text fig. 2. Brown 1934 U.S.G.S. Prof. Pap. 185-C: 55 (synonymy not accepted). Brown 1937 U.S.G.S. Prof. Pap. 186-J: 172; Pl. 50, fig. 9.

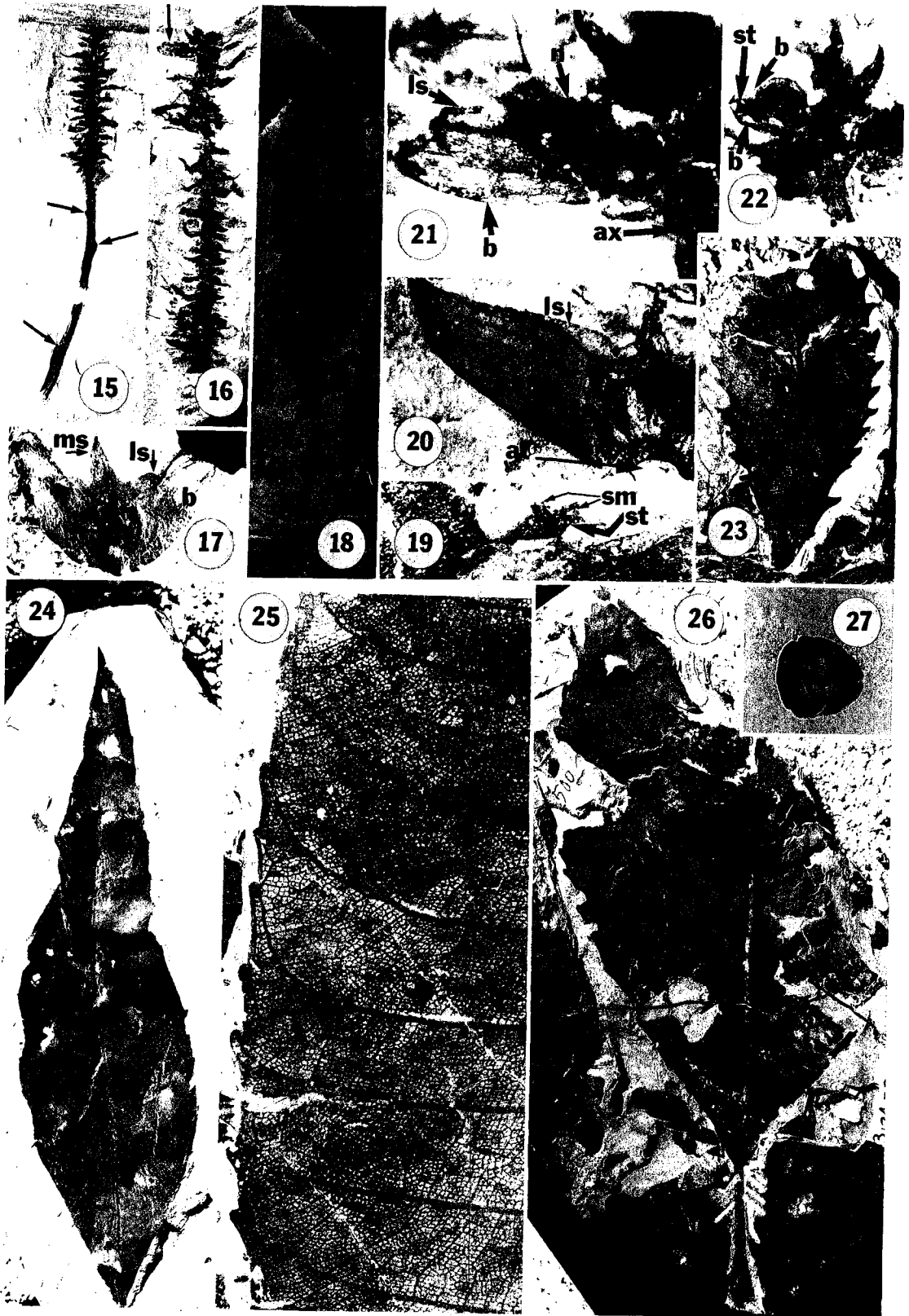
*Platycarya* sp. Leopold and MacGinitie 1972 Development and affinities of Tertiary floras in the Rocky Mountains 177–179; Pl. I, fig. 9.

*Platycarya* sp. Nichols and Ott 1978 Palynology 2:110, Pl. 2, fig. 14.

**Emended description:** Leaves probably odd pinnately compound, though no whole leaves preserved; inferred from degree of asymmetry, size and shape variation of leaflets. Leaflets symmetrical to strongly asymmetrical, wide to very narrow elliptic, ovate to lanceolate, or narrow obovate; obovate leaflets always symmetrical; length 5–20 cm, width 2.2–8.0 cm; apex usually attenuate, very rarely acute or obtuse; base decurrent; margin cut by evenly distributed, small to medium serrations (A3, A4, B3, B4, and the "reverse acuminate" type described above); margin sometimes enrolled, obscuring teeth; texture chartaceous; petiolule long. Venation pinnate; primary vein moderately thick, usually somewhat curved. Secondaries craspedodromous to semicraspedodromous; 9–20 pairs arising from the midvein at about 90°, turning sharply upward near their terminations to follow the margin; intersecondaries usually common. Tertiaries opposite percurrent; course retroflexed, origin on subad-

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Fig. 15–27. *Platycarya castaneopsis*. 15. Compression of pistillate inflorescence showing widely spaced bracts and lateral scars (arrows) at presumed attachment points for lateral staminate inflorescences. UCMP 9004.  $\times 1.1$ . 16. Pistillate inflorescence bearing an unshed winged fruit (arrow). UCMP 9003.  $\times 1.4$ . 17. Dispersed fruit showing long median sepal fused to lateral sepal. USNM 356402.  $\times 4.9$ . 18. Pistillate inflorescence, note squarish bracts with blunt apices. USNM 356407.  $\times 1.7$ . 19. Lateral style arms and terminal stigmatic surfaces. USNM 356401.  $\times 15.0$ . 20. Fruit showing fusion of lateral sepal and bracteole, note shallow attachment scar at fruit base. USNM 356409.  $\times 6.2$ . 21. Close-up of counterpart of specimen in Fig. 16 showing fruit attached to pistillate inflorescence, note lateral sepal, bracteole, and nutlet body. UCMP 9003.  $\times 9.3$ . 22. Less developed fruit than in Fig. 21, note bracteoles, and styles. UCMP 9003.  $\times 5.8$ . 23. Probable basal lateral leaflet, note asymmetry and low length to width ratio. USNM 356404.  $\times 1.4$ . 24. Probable lateral leaflet, note attenuate apex and decurrent base. USNM 356405.  $\times 1.0$ . 25. Venation, note secondaries curving abruptly upward to parallel margin, obtuse junction between retroflexed tertiaries and subadjacent secondaries, double ascending branch in the marginal venation, and closed areolation. USNM 324549.  $\times 4.3$ . 26. Probable terminal leaflet, note long petiolule with expanded base, obovate shape, long acute base, and inter-secondary veins. USNM 324500.  $\times 1.1$ . 27. Dispersed pollen grain from locality WhBg, at which *P. castaneopsis* comprises ~50% of the megafloora and this pollen type makes up over 30% of the palynoflora.  $\times 500$ . Abbreviations as in Fig. 3–14.



adjacent secondary often obtuse, medial tertiaries recurved to midvein, forming intersecondaries. Quaternaries not easily distinguished from higher order veins. Areolation very strongly impressed, but not oriented; areoles 0.15–0.30 mm in maximum diameter, usually 3–5 sided and lacking freely ending veinlets. Tooth venation as in *P. americana*.

Pistillate inflorescences 1.5–4.5 cm long, 0.5–0.9 cm wide; woody bracts arranged spirally on a slender woody axis with lateral scars below. Bracts wide ovate and entire with a rounded or slightly acuminate apex, 2–6 mm long and 2–4 mm wide; bracts more widely spaced than in *P. strobilacea* or *P. americana*, ~2 mm apart; bract venation consisting of ~9 parallel strands, the three central strands thicker than the rest. Staminate inflorescences not recovered.

Fruits dorsiventrally flattened, bilaterally symmetrical winged nutlets with two locules divided by a median partition; 3–9 mm across (lateral direction), 2–4 mm in the proximal-distal direction; style arms <0.5 mm long, transverse and carinal, not united at base, stigmatic surfaces on admedial and terminal surfaces of the stylar arms; ovary inferior, perianth consisting of four persistent sepals and two bracteoles; median sepals roughly triangular in shape, always continuing beyond the stigmatic area, usually 1–2 mm long; abaxial midline of the lateral sepals fused to the bracteoles along  $\frac{1}{2}$  to  $\frac{3}{4}$ ths of their distal edge, thus forming a trough-like structure at the distal end of the fruit (Fig. 50); bracteoles 3–5 mm long and 1 mm across, directed laterally and distally from the wall of the nutlet, each bracteole with several thin vascular strands that are separate to the rounded apex, where they form a plexus; base of the nutlet bearing a small mound of sediment or a shallow embayment apparently representing the sediment-filled area of attachment, or "socket," this socket with an abmedial-basal orientation.

Pollen triporate, isopolar, with convex sides, and unelaborated, atriate pores; diameter 18.5–23.5  $\mu$ m; each hemisphere marked by one or two arcuate pseudocolpi; sculpture finely granulose.

*Systematic placement:* *Platycarya castaneopsis* is less similar to *P. strobilacea* than is *P. americana* because it has more generalized fruits and inflorescences. *P. castaneopsis* has four plesiomorphies not seen in the other two species: well-developed median and lateral sepals, partially terminal stigmatic surfaces, a more basally oriented receptacle, and a less-compressed pistillate inflorescence. The rounded bracts of the pistillate inflorescence

may also be a primitive feature. The leaves of *P. castaneopsis* are almost identical with those of *P. americana* except that they usually lack the expanded basilaminar tissue. We place this fossil species in *Platycarya* because it has six of the diagnostic features of the genus. However, it is clearly more generalized than either *P. strobilacea* or *P. americana*.

*Occurrence:* See Table 1 for localities. Many of the sites that produce *P. castaneopsis* can be correlated with sequences of vertebrate faunas. *P. castaneopsis* from the Niland Tongue of the Wasatch Formation in the Washakie Basin occurs in the part of the section that contains "Lostcabinian" mammal faunas (Roehler, 1969). In the Great Divide Basin *P. castaneopsis* occurs in the Niland Tongue of the Wasatch Formation, which is probably late early Eocene in age (Piperinos, 1961). In the Wind River Basin, megafossils of *P. castaneopsis* are abundant in the upper parts of the Wind River Formation, including near the type area of the Lost Cabin Member (USGS locality 9051), and in volcanoclastic rocks on the western side of the basin. The first occurrence of *P. castaneopsis* megafossils in the Bighorn Basin coincides almost exactly with the appearance of "Lostcabinian" mammal faunas (Schankler, 1980; Wing, 1981). The type specimen of *P. castaneopsis* is from the Green River Formation in Uinta County, Wyoming, probably from the so-called fish-bearing beds on Fossil Butte. These rocks are also of late early Eocene age (Gazin, 1959). Thus the known occurrences of the species are all late early Eocene.

*Platycarya americana* and *P. castaneopsis* are easily distinguished by characters of all megafossil organs, but the recognition of two species is reinforced by their geographic distribution. *P. americana* is known only at localities east of the Front Range of the Rocky Mountains, while *P. castaneopsis* occurs exclusively west of the Front Range (Fig. 1). Within the limits of resolution of mammalian biostratigraphy the two species are contemporaneous. To our knowledge these are the first reported contemporaneous allopatric species in the Tertiary plant record.

*Collection:* Lectotype: leaflet—USNM 1575. Referred material: leaflets—USNM 324500, 324548, 324549, 356404; pistillate inflorescences—USNM 324502A and B, UCMP 9003, 9004; fruits—USNM 356401, 356402, 356409.

*Platycarya richardsonii* (Bowerbank) Chandler (Fig. 33, 34)

*Petrophiloides richardsonii* Bowerbank 1840 Fossil fruits of the London Clay, p. 43–47; Pl.

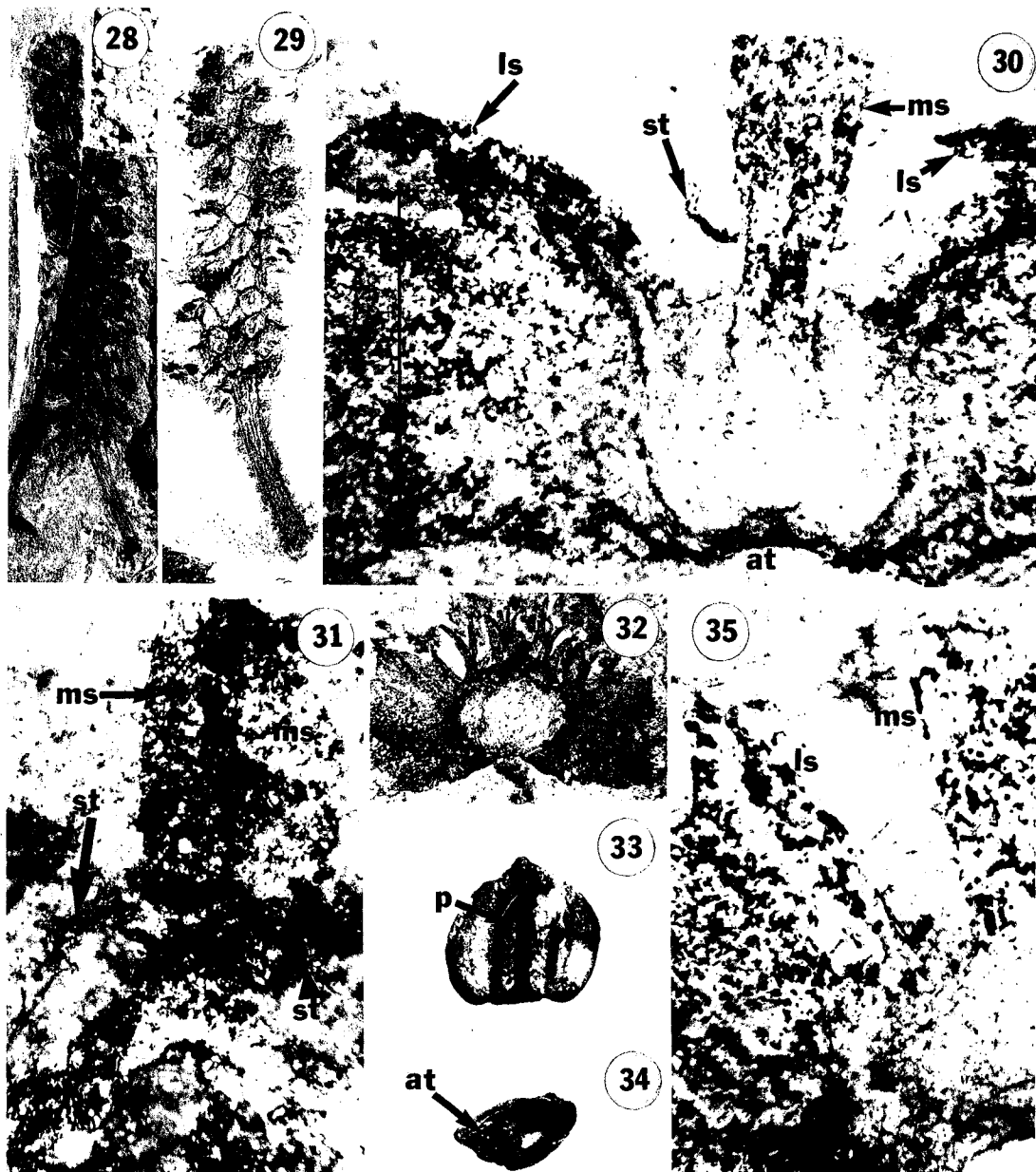


Fig. 28–35. Fossil platycaryoids. 28–29, *Platycarya manchesterii* sp. nov. 28. Holotype. Note short basal portion of axis. USNM 356372A.  $\times 1.4$ . 29. Inflorescence showing rounded bracts. USNM 356373A.  $\times 2.1$ . 30–32, *Hooleyia lata* sp. nov. 30. Holotype. Note elongated, lateral style arms, large median and lateral sepals, partial fusion of the lateral sepals to the large bracteoles, and the shallow embayment at the base of the nutlet. There is no indication that the bracteoles are fused to one another near the nutlet base, as is observed in *Pterocarya* spp. USNM 356376.  $\times 15$ . 31. Distal end of nutlet. Note elongated, lateral arms borne on a common style. Above the style arms are the two, overlapping median sepals. USNM 356383A.  $\times 30$ . 32. Unusual fruit with highly divided perianth. USNM 356381.  $\times 5.4$ . 33–34, *Platycarya richardsonii*. 33. Locule cast showing median partition. USNM 356410.  $\times 10$ . 34. Same specimen showing basal orientation of nutlet attachment. USNM 356410.  $\times 5$ . 35. Central portion of *Hooleyia lata* fruit showing median and lateral sepals.  $\times 15$ . Abbreviations as in Fig. 3–14.

9, fig. 9–15; Pl. 10, fig. 5–8. Reid and Chandler 1933 The London Clay flora, pp. 133–140; text fig. 1a–h; Pl. II, fig. 7–20 (synonymy accepted);

Chandler 1961 The lower Tertiary floras of southern England I, p. 136; Pl. 14, fig. 11–14. *Platycarya richardsonii* (Bowerbank) Chan-

dler 1964 The lower Tertiary floras of southern England IV, p. 110, 111.

*Emended description:* Comparisons of *Platycarya* species are presented in Table 2. Reid and Chandler (1933) noted the persistent perianth in *P. richardsonii*; we add it is much longer than in *P. strobilacea* (see Reid and Chandler, 1933, Pl. II, fig. 12, 13). We also note the tendency for the attachment of the nutlet to be directed more basally (Fig. 46; Reid and Chandler, 1933, Pl. II, fig. 12; text fig. 1i) than is typical in mature inflorescences of *Platycarya strobilacea*. *P. richardsonii* also has shorter, broader bracts than does *P. strobilacea*. In these features *P. richardsonii* more closely resembles *P. americana* and *P. castaneopsis* than it does *P. strobilacea*.

*Systematic placement:* We retain *P. richardsonii* in *Platycarya* because it has four of the diagnostic autapomorphies of the genus: condensed pistillate inflorescences, woody primary bracts, anteriorly-posteriorly flattened nutlets, and spirally thickened vessel elements. Pseudocolpate pollen assigned to *Platycarya* has also been recovered from the London Clay, although no established association exists between pollen and pistillate inflorescences. In spite of the prevalence of mosaic evolution, the unknown organs of *P. richardsonii* probably would not present features that would remove the species from *Platycarya*.

***Platycarya bognorensis*** (Chandler) Wing et Hickey, comb. nov.

*Pterocaryopsis bognorensis* Chandler 1961 The Lower Tertiary floras of southern England I, pp. 142, 143; Pl. 17, fig. 1, 2.

*Pterocaryopsis elliptica* Chandler 1978 Supplement to the lower Tertiary floras of southern England, Pt. 5, pp. 19, 20, Pl. 3, fig. 4, 5.

*Systematic placement:* In her original description of *Pterocaryopsis bognorensis*, Chandler (1961) commented on the deep excavation of the lower surface near the point of attachment and suggested that the fruit must have been borne in a loose spike or cluster. We concur with Chandler's suggestion, and note that the fruit also has wings that are perfectly parallel to its proximal-distal axis. These features are characteristic of *Platycarya* fruits rather than those of the pterocaryoid line, and we therefore transfer *Pterocaryopsis bognorensis* to *Platycarya*. The single specimen of *Pterocaryopsis elliptica* cannot be distinguished from that of *P. bognorensis*.

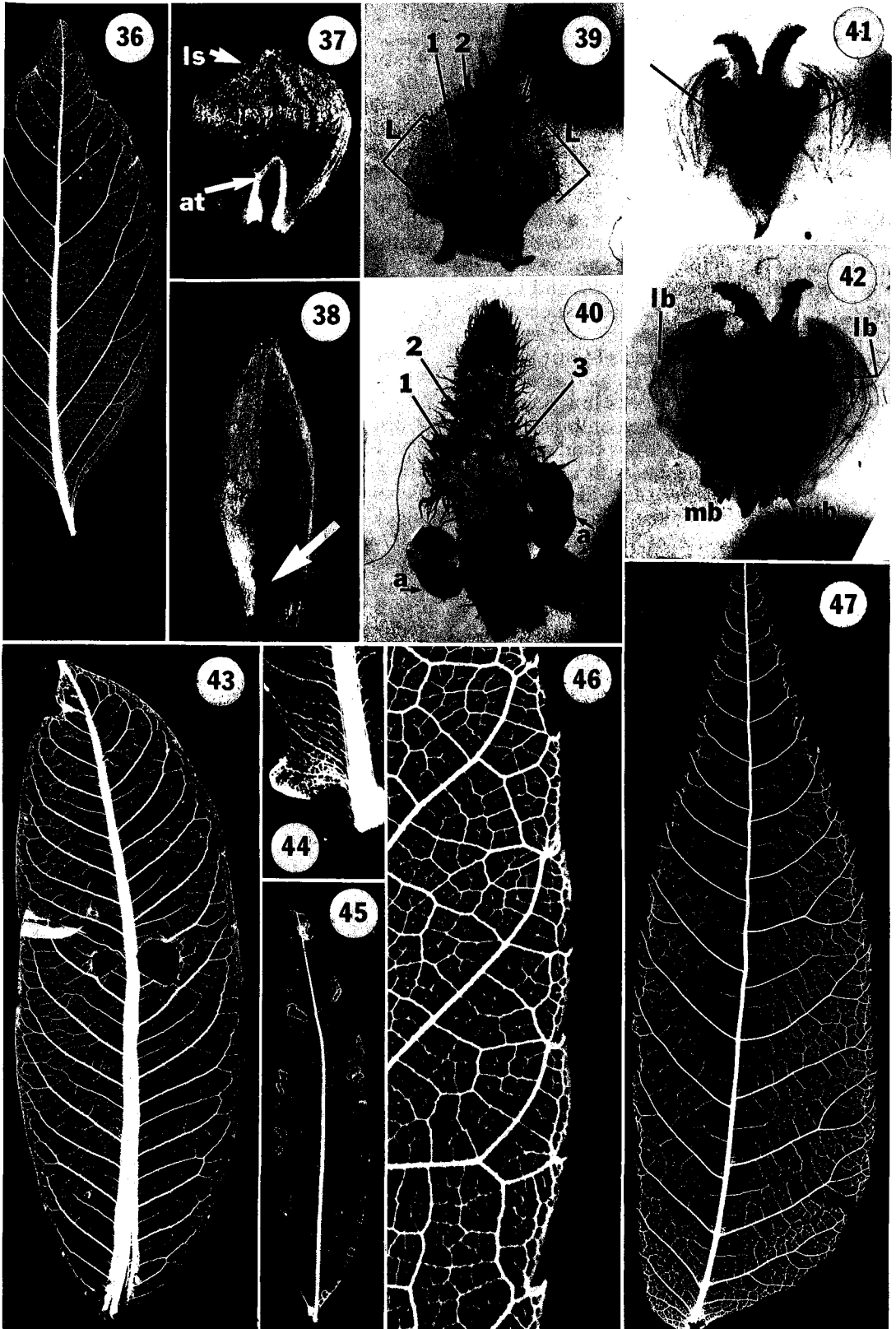
Manchester (1981) suggested that *Pterocaryopsis bognorensis* was the dispersed fruit of *Platycarya richardsonii*, although he retained the two taxa as separate entities. The morphology of these two taxa is consistent with his conclusion, but in the absence of any morphological or statistical association between the two forms we too leave them in separate species.

***Platycarya manchesterii*** Wing et Hickey, sp. nov. (Fig. 28, 29)

*Description:* Known only from pistillate inflorescences. Axes 3–6 cm long and 1–2 mm wide, bearing a spirally arranged series of closely overlapping woody bracts along the distal 1/2 to 2/3 of the axis. Bracts ovate, acute-tipped, 1.5–3.0 mm wide at the base and 2–4 mm long. Base of the axis slightly expanded and terminating in a sharply defined concave surface. One small scar present on the axis just below the fertile part.

*Systematic placement:* We have placed *P. manchesterii* in *Platycarya* because it has two of the diagnostic features of the genus: woody primary bracts and a condensed pistillate in-

Fig. 36–47. Living Juglandaceae. 36. Cleared leaflet of *Engelhardia roxburghiana* Wall., showing decurrent base and obtuse tertiary-secondary junctions. USGS Cleared Leaf Collection 891.  $\times 1.0$ . 37–42, *Platycarya strobilacea* Sieb. et Zucc. 37. Mature fruit with abaxially elongated attachment and reduced lateral sepals. University of California Herbarium (UCH) M286369.  $\times 6.3$ . 38. Primary bract from mature pistillate inflorescence, note elongate shape and short peduncle (arrow) to which the fruit is attached. UCH M286369.  $\times 6.3$ . 39. Cleared bract of immature pistillate inflorescence, note three primary vascular strands in the central portion of the bract (1, 2, 3) and separate vascularization of the small lateral lobes (L).  $\times 30$ . 40. Cleared bract and anthers from staminate inflorescence, note three primary vascular strands in central portion of bract.  $\times 30$ . 41. Cleared immature fruit, note vascular strands passing to the area of the reduced median sepal (arrows).  $\times 35$ . 42. Cleared immature fruit, note that the lateral appendages are vascularized from two sources, the lateral bundles (lb) supplying the bracteoles and the median bundles (mb) supplying the median and lateral sepals.  $\times 35$ . 43. Cleared leaflet of *Alfaroa manningii* Leon showing obtuse secondary-tertiary junctions, frequent intersecondary veins, and closed areolation. USGS Cleared Leaf Collection 889.  $\times 1.0$ . 44–45, *Oreomunnea mexicana* (Standl.) Leroy. 44. Cleared leaflet showing elaboration of basillaminar tissue ("auriculae" of Stone), this region of the leaflet is densely pubescent; also note closed areolation. USGS Cleared Leaf Collection 897A.  $\times 6.4$ . 45. Cleared leaflet showing secondaries almost perpendicular to midvein, and frequent intersecondaries. USGS Cleared Leaf Collection 897A.  $\times 1.0$ . 46, 47, *Platycarya strobilacea*. 46. Aberrant leaflet with closed areolation, small teeth, and a strong double ascending branch in the marginal venation. UCMP Cleared Leaf Collection 541.  $\times 10$ . 47. Normal leaflet with orthogonal secondary-tertiary junctions and areoles with freely ending veinlets, also note slight elaboration of basillaminar tissue. UCMP Cleared Leaf Collection 541.  $\times 2.1$ . Abbreviations as in Fig. 3–14.



florescence. However, this species occurs at the same locality as dispersed platycaryoid fruits (described below) that belong in *Hooleya*. If these dispersed organs prove to belong to the same species, then *P. manchesterii* must be transferred to *Hooleya* because of the apomorphies, such as elongate style arms, seen in *Hooleya*. (See discussion under *H. lata*.)

Living and fossil pistillate inflorescences of *Platycarya* are quite similar in overall appearance and organization, the main distinctions being in the shape of the inflorescences, the shape of the individual bracts, and in the amount of separation between successive bracts. This species resembles *P. castaneopsis* in having short, rounded bracts (4 mm), but it is similar to *P. americana* in having a short basal part of the axis that lacks bracts, and in having closely set bracts. The compressed pistillate inflorescences provide few characters that help to resolve relationships within the Platycaryeae, yet *P. manchesterii* does have a unique combination of overall shape, bract outline and spacing that distinguishes it from other species of *Platycarya*.

The specific epithet is given in honor of Steven Manchester in recognition of his contributions to studies of fossil Juglandaceae, and his valuable assistance with this study.

*Occurrence*: USGS locality 8637 in the lower Clarno Formation near Mitchell, Oregon. The age of these sediments is probably late early to early middle Eocene (J. A. Wolfe, pers. commun., 1982).

*Collection*: Holotype: USNM 356372A and B. Referred material: USNM 356373A and B, 356374A and B, 356375A and B.

#### Genus *Hooleya* Reid et Chandler 1926

*Emended description*: Known only from fruits. Specific name in parentheses denotes conditions observed only in that species. Inferior, posteriorly-anteriorly flattened (*H. Hermis*), winged nutlets with a rounded outline and two probably transverse locules (*H. lata*). Perianth usually four parted (*H. lata*), median sepals free, but lateral sepals partly fused to the distal margin of the wings (*H. lata*), rarely perianth irregularly divided into many narrow lobes. Fruit wings variable in shape, often ovate, obovate, or rounded, with an irregular or erose margin; wing orientation parallel to the fruit axis; venation a loose system of bifurcating strands that rarely anastomose. Apex of the fruit with two elongated (1.0–1.5 mm), transverse style arms bearing two (*H. lata*), or four (*H. Hermis*) stigmas. Base of nutlet slightly concave, with basally oriented attachment area.

Surface of the wings and nut bearing discoid papillae (*H. Hermis*). Overall dimensions 5–19 mm wide by 3–7 mm high; nutlets 2–4 mm wide.

*Emended diagnosis*: *Hooleya* is distinguished from all other juglandaceous genera by a combination of features: nutlet anteriorly-posteriorly flattened, lateral sepals partly fused to bracteoles, style arms elongated, bracteolar wings enlarged, shallowly concave basal attachment.

*Hooleya lata* Wing, sp. nov. (Fig. 30–32, 35, 52)

*Description*: Bilaterally symmetrical, winged nutlets, 5–19 mm wide and 3–7 mm high (proximal-distal direction) at the midline. Nutlet cast with a faint midline depression (transverse locules?); outline rounded, 2.5–4.0 mm wide at the broadest point and shallowly concave at the base; attachment area oriented basally. Distal end of the nutlet bearing two elongate (1.0 mm), transversely oriented stylar arms. Lateral wings of the fruits unusually variable in shape, obovate with rounded tips in the larger specimens, ovate with obtuse tips in small specimens. Lateral wings extending 2–7 mm from the nutlet wall, 3–7 mm across at the greatest basal-distal extent. Wing venation obscure, but appearing to consist of thick strands making a series of low angle dichotomies in passing from the nutlet to the wing margin. Wing margin usually irregular or erose. Perianth of four parts: two lateral and two median sepals. Laterals 0.5–3.0 mm long, free at the tip but fused for part of their length to the medial part of the distal margin of the wing. In some specimens each lateral sepal can be seen to be a double structure with an abaxial and adaxial side that come together at the distal wing margin to form a trough-like structure, the bottom of the trough being at the distal wing margin. Median sepals elliptic and 1–3 mm long, arising from near the middle of the nutlet and extending well beyond the stigmatic area. In some specimens both sepals of the pair can be seen because they do not completely overlap (Fig. 31, 52).

*Systematic placement*: We interpret these fossil fruits as having a floral envelope of two bracteoles that form most of the lateral wing tissue, two lateral sepals that are partly fused to the bracteoles at their own abaxial midline, and two largely free median sepals. Although the overall fruit shape of *H. lata* is similar to that in some *Pterocarya* species, this similarity results from a combination of shared primitive features (four distinct sepals, rounded nutlet



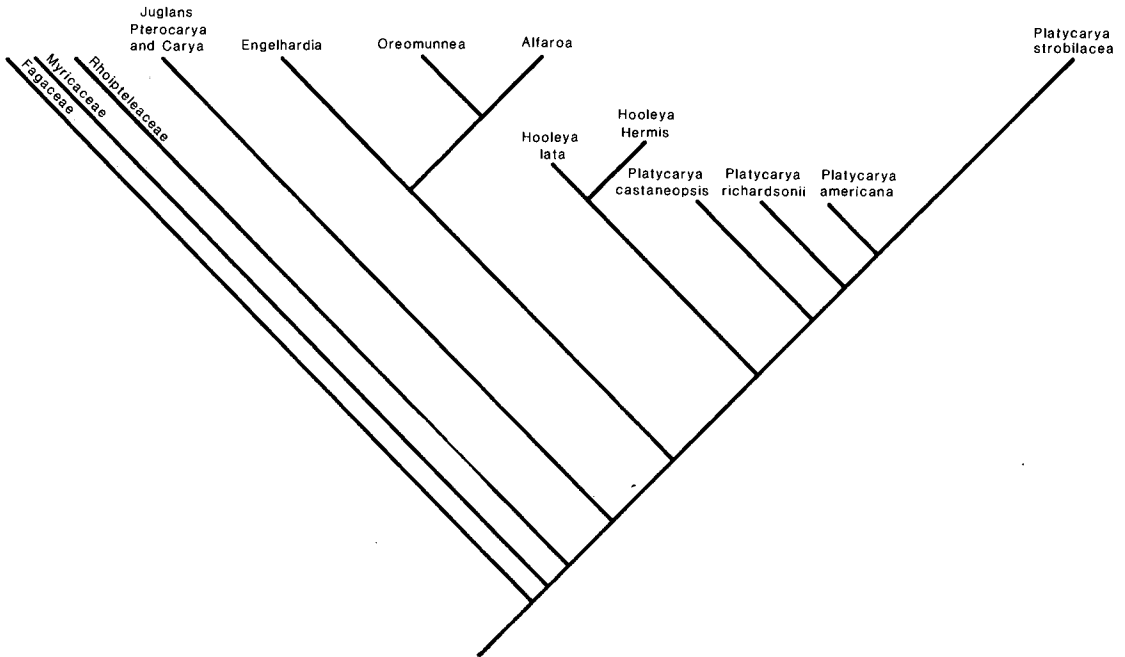


Fig. 48. Relationships in the Juglandaceae. This is one of two equally parsimonious trees based on a cladistic analysis of 30 characters of the leaves, fruits, inflorescences, and pollen (Wing and Hickey, unpublished data). See text for more detailed explanation.

outline, basal attachment), and parallel adaptations for wind dispersal (large bracteolar wings). *H. lata* lacks three apomorphies seen in all *Pterocarya* fruits: median style arms, primary bract borne on the fruit, and fusion of the bracteoles to one another near the fruit base. (This last feature causes the fruit wings to be oriented at an angle to the axis of the nutlet and is readily visible in fossil material, e.g., *Pterocarya protostenoptera* Tanai in Ishida, 1970, Pl. 5, fig. 4, 7.)

*H. lata* has an extremely generalized fruit morphology, but three factors favor its inclusion in the Platycaryeae. One, it has fused lateral sepals and bracteoles, a synapomorphy with *Platycarya*. Two, the features in which *H. lata* differs most from *P. strobilacea* are found in intermediate states in *P. castaneopsis* and *P. americana*. Three, *H. lata* occurs at the same locality as the pistillate inflorescence *P. manchesterii*, and they may belong to the same biological species.

*H. lata* (and *H. Hermis*) have elongate style arms, an advanced feature (Manning, 1940) not seen in any species of *Platycarya*. The great enlargement of the bracteoles and median sepals may also be specialization defining a separate genus. Furthermore, *Hooleyia* lacks all but one of the apomorphies of *Platycarya*. This combination of primitive and derived states is

sufficient to establish *Hooleyia* as a distinct genus in the Platycaryeae.

*Occurrence:* Lower part of the Clarno Formation near Mitchell, Oregon; USGS locality 8637.

*Collection:* Holotype: USNM 356376. Referred material: USNM 356377A and B, 356383A and B, USNM 356388A and B, and USNM 356378–356390.

**DISCUSSION—Phylogeny**—The species reviewed and described above greatly increase the known range of morphologies in the Platycaryeae, and thus offer a broader base both for interpreting the evolution of the tribe and assessing its relationship to the rest of the family. These problems have been approached through a cladistic analysis of the Juglandaceae that uses more than 30 characters and that treats the Rhoipteleaceae, Myricaceae and Fagaceae as outgroups; the character state polarities and branching sequences discussed below are from that work (Wing and Hickey, unpubl. data). A summary diagram is given in Fig. 48.

Recent hypotheses on the relationships of the Platycaryeae have treated the tribe as an early offshoot of the Juglandaceae, implying that it is a sister group to the rest of the family (e.g., Stone and Broome, 1975; Manning, 1978). Our phylogenetic reconstruction differs by

TABLE 2. Summary of character differences between species of *Platycarya*. FEVS = freely ending veinlets

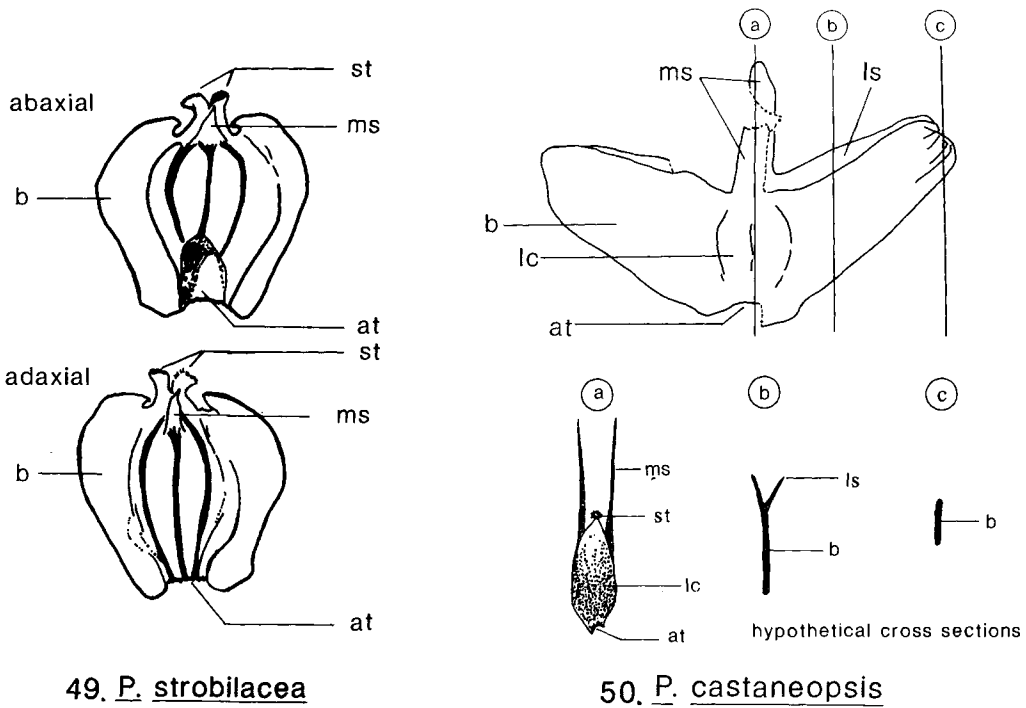
Characters	<i>P. strobilacea</i>	<i>P. castaneopsis</i>	<i>P. americana</i>	<i>P. richardsonii</i>
1° bract of pistillate inflorescence	elongate with acute apex	ovate with rounded apex	elongate to ovate with acute apex	ovate, acuminate apex
Bract spacing	close	lax	close	close
1° bract of staminate inflorescence	strap shaped acuminate apex	?	ovate with rounded apex	?
Bracteoles	very short	very long	moderate	moderate?
Median sepals	reduced or absent	very long	moderate	moderate?
Receptacle orientation	abaxial	basal/abaxial	basal/abaxial	basal/abaxial
Stigmatic surface	adaxial	adaxial/terminal	?	?
Pollen size	13–18 $\mu\text{m}$	17–24 $\mu\text{m}$	17–24 $\mu\text{m}$	?
Basilaminar region	frequently with hairs	unelaborated	elaborated	?
Petiolule	short	long	long	?
Leaflet base	rounded or cordate	decurent	decurent	?
Intersecondary veins	weak and few	strong and many	strong and many	?
Tertiary junction with subadjacent 2°	orthogonal	obtuse	obtuse	?
Tertiary course	straight	retroflexed	retroflexed	?
Areolation	>20% w/FEVS	<10% w/FEVS	<10% w/FEVS	?

placing *Platycaryeae* and *Engelhardieae* as sister tribes that together are the sister group of the rest of the family. Synapomorphies in leaflet architecture between *P. americana*, *P. castaneopsis* and the *Engelhardieae* are the primary data for this relationship.

Seven foliar character states are shared by *Platycarya* and some or all of the *Engelhardieae*: 1) Basilaminar region with dense hair patches (*Alfaroa mexicana* [Stone, 1968] and *P. strobilacea* [Kuang and Lu, 1979; and pers. observ.]) or expanded tissue (*Oreomunnea mexicana* [Fig. 44, 45; Stone, 1972], *P. americana* [Fig. 5, 9, 14], and rarely *P. strobilacea* [Fig. 47]); 2) Fewer than 10% of areoles with freely ending veinlets (*Oreomunnea* [Fig. 44–46; Wolfe, 1959], *Alfaroa* [Fig. 43; Wolfe, 1959], most *Engelhardia* species [Wolfe, 1959; and pers. observ.], *P. castaneopsis* [Fig. 25], *P. americana*, and rarely *P. strobilacea* [Fig. 46]); 3) Well developed intersecondary veins (*Oreomunnea* [Fig. 45], *Alfaroa* [Fig. 43], some *Engelhardia* species, *P. americana*, and *P. castaneopsis*); 4) Distinction between fourth and higher order venation weak or absent (*Oreomunnea*, *Alfaroa*, *Engelhardia*, *P. americana*, and *P. castaneopsis*); 5) Obtuse junctions between tertiary and subadjacent secondaries (*E. roxburghiana* [Fig. 36], *Alfaroa*, *O. pterocarpa*, *P. americana* and *P. castaneopsis*); 6) Moderately long petiolules (juvenile foliage of

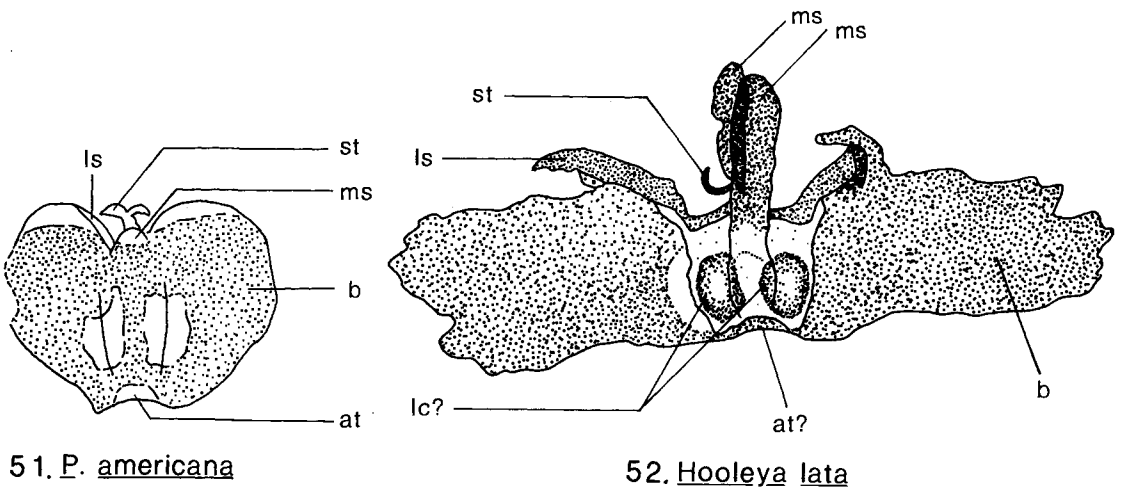
*O. pterocarpa*, *E. roxburghiana*, *P. castaneopsis*, and *P. americana*); 7) Acute to decurrent leaflet bases (*E. roxburghiana*, *O. pterocarpa*, *Alfaroa* spp., *P. americana*, and *P. castaneopsis*). The first four of these character states are synapomorphies; the last three are symplesiomorphies that have been lost in all other Juglandaceae, but are seen in the outgroups.

Our hypothesis that *Platycaryeae* and *Engelhardieae* are sister tribes is also supported by floral morphology. Three-lobed primary bracts are one of the diagnostic features of the *Engelhardieae* (Manning, 1978; Crane and Manchester, 1982). Manning (1978, pp. 1068–1069) observed that primary bracts on pistillate and staminate inflorescences of *P. strobilacea* are occasionally three-lobed. Clearings of the primary bracts of *P. strobilacea* (Fig. 39, 40), display a vascular pattern very similar to that of *Oreomunnea*: the central portion of the bract is supplied by three major strands that pass almost directly to the apex of the lobe, and the lateral lobes are each independently supplied from the base of the bract by three veins. Comparative morphology (Manning, 1940) and the fossil record (Berry, 1916; Dilcher, Potter and Crepet, 1976; Crane and Manchester, 1982) suggest that the *Engelhardieae* evolved from an ancestor that had unlobed primary bracts. If a lobed ancestor evolved before the *Engelhardieae-Platycaryeae* split,



49. *P. strobilacea*

50. *P. castaneopsis*



51. *P. americana*

52. *Hooleyia lata*

Fig. 49–52. Camera lucida drawings of four platycaryoid fruits. 49. *Platycarya strobilacea*, abaxial (above) and adaxial (below) sides of a specimen with small median sepals. UCH 286369. 50. *Platycarya castaneopsis*, showing parts of both median sepals, near sides of both lateral sepals, and fusion of median and lateral sepals. Reconstructed cross sections show the trough-like form of the lateral sepals. USNM 356403A. 51. *Platycarya americana*, limonitized areas indicated by shading. USNM 167481B. 52. *Hooleyia lata*, showing partial fusion of lateral sepals to bracteoles, partly overlapped median sepals, partial locule casts, and irregular margin of bracteolar wing. USNM 356376. All drawings  $\times 5$ . Abbreviations as in Fig. 3–14.

then *Platycarya* has subsequently reverted to an unlobed bract, though it has retained the basic venation. We think it more likely that the common ancestor of both tribes had “in-

cipiently lobed” primary bracts like those of *Platycarya*.

Another feature that may support the alliance of *Platycarya* and the Engelhardieae is the

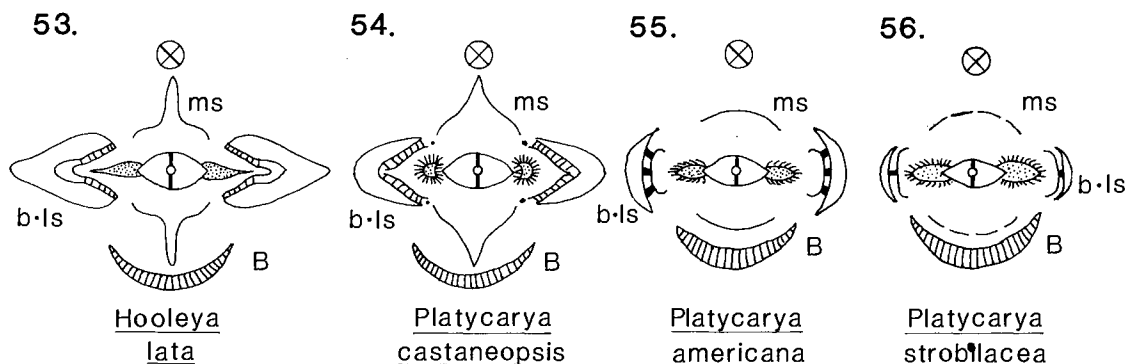


Fig. 53–56. Floral diagrams of pistillate platycaryoid flowers. 53. *Hooleyia lata*. 54. *Platycarya castaneopsis*. 55. *Platycarya americana*. 56. *Platycarya strobilacea*. Note progressive reduction and loss of the perianth. Symbols after Manning (1978): ms, median sepal; ls, lateral sepal; b, bracteole; b·ls, fused bracteole and lateral sepal; ms·ls, fused sepals; B, primary bract. The circle containing an × indicates the position of the primary axis of the inflorescence.

possession of a pedicel on which the fruit is borne. *P. strobilacea* does have a pedicel-like structure (Fig. 38), although it is highly reduced and fused to the primary bract. Finally, a sister-group relationship between Platycaryeae and Engelhardieae is supported by synapomorphies in their steroid and flavonoid chemical characteristics (Niklas and Giannasi, in preparation). If Platycaryeae and Engelhardieae are sister tribes, then the subfamily Platycaryoideae (Manning, 1978) should be expanded to include both.

Nine species of Platycaryeae have now been described from Tertiary megafossils, but in spite of this diversity at the species level there is little evidence for more than one lineage in the tribe. The leaves of *P. americana* and *P. castaneopsis* strongly resemble those of the Engelhardieae because they are less specialized than leaves of *P. strobilacea*. Similarly, the fruits and flowers of all the fossil species are more generalized than those of *P. strobilacea*. Manning (1940, 1978) stated that the basic juglandaceous floral envelope consists of seven parts: primary bract, two bracteoles, and four sepals. *P. strobilacea* usually lacks the median pair of sepals, and has highly fused lateral sepals and bracteoles (Fig. 37, 41, 42, 49, 56). *P. americana* and *P. richardsonii* have median sepals and larger bracteoles. *P. castaneopsis* has fused but distinguishable lateral sepals, and even larger median sepals and bracteoles. *Hooleyia lata* has very large median sepals and bracteoles, and the lateral sepals are only partially fused to the bracteoles.

The fertile and foliar characteristics of all fossil Platycaryeae are more generalized than those of *P. strobilacea* in every respect, with the possible exception of elongated style arms

in *Hooleyia*. Although *H. lata*, *P. castaneopsis*, *P. americana*, and *P. strobilacea* are not an ancestor-descendant sequence (the two fossil *Platycarya* species are contemporaneous, and *H. lata*, the most primitive fruit type, is also the youngest fossil), they show that the early Eocene diversification of the Platycaryeae produced little morphological innovation. The major evolutionary trends in the tribe have been shortening of the petiolules and leaflets, decreasing organization in leaflet venation, greater condensation of the pistillate inflorescences, fusion and loss of floral envelope components, and reduction in overall fruit size (2 cm–4 mm).

*Paleoecology and evolution*—Fossil remains of *Platycarya* are ubiquitous and abundant in early Eocene sediments of the Northern Hemisphere. Platycaryoid pollen first occurs at or just below the Paleocene-Eocene boundary, then becomes abundant in the later early Eocene. It is an important component of palynofloras throughout most of North America, including the Arctic, and Western Europe (Hail and Leopold, 1960; Hopkins, 1967; Rouse, Hopkins and Piel, 1971; Leopold and MacGinitie, 1972; Tschudy, 1973; Nichols, 1973; Elsik, 1974; Elsik and Dilcher, 1974; Kedves and Stanley, 1976; Newman, 1977; Bebout, 1977, 1980; Frederiksen and Christopher, 1978; Nichols and Ott, 1978; Frederiksen, 1979, 1980; Christopher et al., 1980; Gruas-Cavagnetto, Laurain and Meyer, 1980a, 1980b; Nichols, in press; Hickey et al., 1983). Megafossils of *Platycarya* are abundant and numerically dominant at localities we have collected. Of his original discovery of *Platycarya* (*Petrophiloides*) *richardsonii*, Richardson

(quoted in Chandler, 1961) wrote that the specimens were found by the "bushel." There is little doubt that where *Platycarya* grew it was extremely abundant, and that it could form nearly monospecific assemblages.

The small, numerous, winged nutlets of *Platycarya* (living and fossil) are typical of wind-dispersed, weedy plants that reproduce prolifically, mature rapidly, and tend to colonize relatively open areas where low light levels do not limit growth (Harper, Lovell and Moore, 1970; Stebbins, 1971; Stone, 1973). Givnish (1978) has commented that pinnately compound leaves provide early successional species with a metabolically inexpensive ultimate branch equivalent that can be grown quickly and then dropped during periods of physiological stress. The wood of *Platycarya* is considered advanced because it has short, relatively wide, spirally thickened vessel elements, and vessel perforations that are exclusively porous (Heimsch and Wetmore, 1939). Reid and Chandler (1933) observed spiral thickenings in *P. richardsonii*. These features of vascular anatomy may also be adaptations to rapid growth in a stressful environment. Thus, many of the morphological features of the fossil platycaryoids are similar to specializations seen in modern plants that occupy early successional or open habitats.

*Platycarya* does not always occur with the same species in the localities where we collected (Appendix Table 2), however a variety of presumed herbaceous plants are regular associates: *Zingiberopsis isonervosa*, *Equisetum* sp., and several ferns. In the Willwood Formation, a species of *Alnus* is the dicotyledon that most often occurs with *P. castaneopsis*. At USGS 9394, *P. americana* megafossils occur in a monospecific assemblage near the top of a lens inferred to be a filled oxbow pond deposit, suggesting that this species was dominant in the late phases of a hydrosere. These associated species and the distribution of *Platycarya* fossils in the sediment also suggest that early Tertiary *Platycarya* grew in open, early successional habitats.

The ecological requirements of the living *P. strobilacea* provide a final line of evidence about those of the fossil species. *P. strobilacea* is a shrub or small tree (Manning, 1978), and it is a major component of secondary growth in both the Mixed Mesophytic and the Sclerophyllous Evergreen Forests of China (Wang, 1961).

These separate lines of evidence yield similar conclusions on the probable ecology of fossil *Platycarya*. These early Tertiary species are inferred to have been small, probably shrubby

trees that rapidly colonized open or unstable ground, were fast growing and maturing plants that produced large quantities of easily dispersed winged fruits, and may have formed thickets of dense, nearly monospecific growth. This syndrome of weedy features is common to several amentiferous families such as Myricaceae (Elias, 1971) and Betulaceae (Cronquist, 1981), and may well be the primitive condition of the Amentiferae in general (Stone, 1973).

In contrast to the growth form of the plant itself, the phylogenetic tree of *Platycarya* is quite spare. This lack of morphological diversity may seem all the more surprising in a group that was so common and widely distributed, however we believe that the low diversity of the platycaryoid line may result from the ecological characteristics that permitted its "success."

Early successional or weedy species take advantage of ephemeral habitats by being easily dispersed and by growing and maturing rapidly. The chief challenges of these environments are physical: for example, desiccation, low nutrient soils, fire, and flooding. Although the distribution of such habitats may be unpredictable in the short term, the challenges that they create are much the same over long periods of geological time. Thus early successional species tolerate a wide range of physical conditions. Once a lineage becomes adapted to such an environment there is probably little selection for change, unless it is for a more rapid life cycle or greater reduction and simplification of the soma.

A lineage such as the Platycaryeae also may produce few daughter lines because of the difficulty of achieving reproductive or ecological separation between incipient species. Vrba (1980) offered such an "effect hypothesis" as one possible cause of evolutionary trends within higher taxa. She proposed that such trends may be the effect of differential rates of speciation rather than of the selective advantage conferred by a particular trait. A lineage that speciates slowly leaves fewer descendant species than one that speciates rapidly, and thus the characteristics of the rapidly speciating lineage become more common through time, although the "adaptiveness" of those characteristics may not be causally related to the rapid speciation of the lineage. Vrba suggests that lineages with narrow environmental tolerances (stenotopes) have higher speciation rates than those that are eurytopic.

In the present day, the animal-dispersed Juglandaceae (*Juglans*, *Carya*, *Alfaroa*) are more diverse than the wind-dispersed genera (*Pter-*

*ocarya*, *Oreomunnea*, *Engelhardia*, *Platycarya*), but in the early Tertiary the reverse was the case. This change in dominance might well be attributed to the coevolution of angiosperms and mammals through the Cenozoic (Tiffney, in press), but the effect hypothesis offers an alternative explanation.

The *Platycarya* lineage displays reduction and simplification, it is morphologically conservative, and it has produced few if any daughter lineages. Using *Platycarya* as a model, the overall trend in the Juglandaceae toward animal dispersal may result from slow speciation rates in the wind-dispersed lineages (a consequence of their *r*-selected life histories) rather than an adaptive advantage possessed by the animal-dispersed lines.

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APPENDIX: TABLE I.

No. in Fig. 1	Locality no.	Location
1	USNM 14048 USGS 9550	SW ¼ sec. 29, T. 139 N, R. 97 W, Stark Co., ND. Upper Camels Butte Mbr., Golden Valley Fm.
2	USNM	Western pit of the Hebron Brick Company; SW ¼, SW ¼, sec. 4, T. 140 N, R. 90 W, Morton Co., ND. Lower Camels Butte Mbr., Golden Valley Fm.
3	USGS 9394	125 ft. below conglomerate capping the 3rd Pumpkin Butte from the North. On south face. Campbell Co., Wyo. Upper Wasatch Formation.
4	MBR	sec. 10, T. 51 N, R. 97 W, Bighorn Co., Wyo. Upper Willwood Formation.
5	T	NE ¼, SW ¼, sec. 25, T. 49 N, R. 98 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
6	SL	NW ¼, SW ¼, sec. 25, T. 49 N, R. 98 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
7	TL	SW ¼, SW ¼, sec. 25, T. 49 N, R. 98 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
8	FL	NE ¼, NE ¼, sec. 35, T. 49 N, R. 98 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
9	CQ	NE ¼, SW ¼, sec. 31, T. 49 N, R. 97 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
10	15M	NW ¼, SE ¼, sec. 25, T. 49 N, R. 98 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
11	15ME	SW ¼, NW ¼, sec. 32, T. 49 N, R. 97 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
12	WhBg	NE ¼, SE ¼, sec. 1, T. 48 N, R. 98 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
13	WhBgL	SW ¼, sec. 6, T. 48 N, R. 97 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
14	B	NE ¼, SE ¼, sec. 1, T. 48 N, R. 98 W, Bighorn Co., Wyo. Uppermost Willwood Fm.
15	T2	SW ¼, SW ¼, sec. 6, T. 48 N, R. 97 W, Hot Springs Co., Wyo. Lowermost Tatman Fm.
16	TAT79	SE ¼, SE ¼, sec. 1, T. 48 N, R. 98 W, Hot Springs Co., Wyo. Lowermost Tatman Fm.
17	BCT	NE ¼, SW ¼, sec. 35, T. 49 N, R. 97 W, Bighorn Co., Wyo. Lowermost Tatman Fm.
18	BCT2	SW ¼, SE ¼, sec. 35, T. 49 N, R. 97 W, Bighorn Co., Wyo. Lowermost Tatman Fm.
19	USGS 8894	2 miles NW of SE corner T. 54 N, R. 104 W, Park Co., Wyo. Willwood Fm.
20	UCMP PA114, USGS 8912	On north side of highway, 10 miles west of Dubois, Fremont Co., Wyo. Wind River Fm.
21	UCMP PA104	Fremont Co., Wyo. Wind River Fm.
22	USGS 9538	NE corner sec. 28, T. 33 N, R. 95 W, Fremont Co., Wyo. Wind River Fm.
23	USGS 9051	W end of N side of C. B. & Q. railroad cut at milepost 293 about 10 mi W of Lysite, Fremont Co., Wyo. Wind River Fm.
24	USGS 9397, USGS 5286	SE ¼, SW ¼, sec. 24, T. 24 N, R. 96 W, Sweetwater Co., Wyo. Niland Tongue, Wasatch Fm.
25	D4309	Niland Tongue, Wasatch Fm., Carbon Co., Wyo.
26	USGS 8637	1 mi. N of Black Butte, 5 mi. W of Mitchell, Oregon. Lower Clarno Fm.



APPENDIX: TABLE 2. *Floral lists from representative localities yielding Platycarya megafossils*

Locality	Taxa present (other than <i>Platycarya</i> )
MBR	<i>Allantoidiopsis erosa</i> , <i>Amesoneuron</i> sp., <i>Dalbergia</i> ?, <i>Typha</i> -like monocot, <i>Salvinia preauriculata</i> , <i>Zingiberopsis isonervosa</i> .
SL	<i>Amesoneuron</i> sp., <i>Equisetum</i> sp., indet. monocot.
15ME	<i>Allantoidiopsis erosa</i> , <i>Lygodium kaulfussi</i> , <i>Z. isonervosa</i> , indet. magnoliid.
15M	<i>Alnus</i> sp.
TL	<i>A. erosa</i> , <i>Alnus</i> sp., <i>Amesoneuron</i> sp., <i>Averrhoites affinis</i> , <i>Cercidiphyllum genatrix</i> , indet. magnoliid, <i>Dombeya novi-mundi</i> , <i>Equisetum</i> sp., <i>L. kaulfussi</i> , <i>Platanus "nobilis"</i> , <i>Z. isonervosa</i> .
B	<i>Cnemidaria magna</i> , <i>L. kaulfussi</i> , " <i>Sparganium</i> " <i>stygium</i> , <i>Thelypteris iddingsii</i> .
USNM 14048	<i>Acrovena laevis</i> , <i>Betula hesterna</i> , <i>Carpolithes bryangosus</i> , <i>Equisetum magnum</i> , <i>Glyptostrobus europaeus</i> , <i>L. kaulfussi</i> , <i>Palmacites</i> sp., <i>Paraternstroemia hyphovenosa</i> , <i>Peltandra primaeva</i> , <i>Porosia verrucosa</i> , <i>S. preauriculata</i> , " <i>Sparganium</i> " <i>stygium</i> , <i>Stillingia casca</i> , <i>Ternstroemites aureavallis</i> , <i>Z. isonervosa</i> .