

APPENDIX 1: COLLECTION DATA FOR THE ADDITIONAL SAMPLES OF JUGLANDACEAE,  
INCLUDING GENBANK ACCESSION NUMBERS FOR THE THREE NUCLEOTIDE REGIONS USED  
IN THE ANALYSIS.

*Alfaropsis roxburghiana B* (PS Manos 1594/DUKE: China; Guangxi Prov., Shen Tan Shan; 23° 56.5' N 110° 06.8' E; *rbcL/atpB* EF140989; *trnL/F* EF140998; ITS EF141007);  
*Alfaropsis roxburghiana C* (DE Stone 4101/DUKE: Vietnam; Hou Binh Prov.; 20° 38.16' N, 105° 12.32' E; EF140990; EF140999; EF141008); *Alfaropsis roxburghiana D* (DE Stone 4111/DUKE: Vietnam; Yen Bai Prov.; 22° 02.43' N, 103° 58.19' E; EF140991; EF141000; EF141009); *Engelhardia serrata* (DE Stone 4103/DUKE: Vietnam; Son La Prov.; 21°16.90' N, 103° 58.78'; EF140992; EF141001; EF141010); *Juglans regia uc151* (ARS-Germplasm Repository, Univ. of California, Davis DJUG0151: EF140993; EF141002; EF141011); *Oreomunnea mexicana B* (DE Stone 4174/DUKE: Costa Rica; Cartago Prov.; on road to La Estrella, just south of Cartago; EF140994; EF141003; EF141012); *Oreomunnea mexicana C* (DE Stone 4178/DUKE: Costa Rica; Cartago Prov.; on road to La Estrella, just south of Cartago; EF140995; EF141004; EF141013); *Oreomunnea pterocarpa A* (DE Stone 4120/DUKE: Costa Rica; Alajuela Prov.; Monteverde, Refugio Eladio; EF140996; EF141005; EF141014); *Oreomunnea pterocarpa B* (DE Stone 4121/DUKE: Costa Rica; Alajuela Prov.; Monteverde, Refugio Eladio; EF140997; EF141006; EF141015).

APPENDIX 2: DETAILS ON THE PROCESS OF COMBINING FOSSIL ORGAN GENERA INTO COMPOSITE, TERMINAL TAXA AND JUSTIFICATION OF CHARACTERS AND CHARACTER STATES.

*Criteria for Reconstructing Fossil Species*

The only unequivocal proof that an extinct fossil leaf type belongs to the same species as a particular fruit or pollen type is to find the organs in physical connection; however, fossil representatives of Juglandaceae are known only from detached organs. We used proximity of association and taxonomic evidence to support conspecificity of isolated organs in order to reconstruct the plants thereby increasing the number of characters for inclusion in phylogenetic analyses. The following lines of evidence were used to support the reassembly of disarticulated elements as representatives of the same species. (1) *Shared relationship to extant taxa*. If a fossil locality has a single fruit type that has features diagnostic of a particular extant tribe, and also contains a single kind of juglandaceous foliage that bears characters diagnostic of the same extant tribe, then we may infer that these two fossil organs were produced by the same taxon. (2) *Repeated co-occurrence*. Co-occurrence of leaves, fruits, catkins, and pollen at multiple localities strengthens support for hypotheses of conspecificity of the detached organs. (3) *Depositional environments, distance of transport*. If the sediment in which the fossils are preserved shows features that indicate low energy and minimal transport, then the plant organs found together at a given site are more likely to be from a limited source area. In such instances it is likely that associated leaves and reproductive structures may be derived from the same individual plants. However in other settings, the plants may have

been carried long distances from the source, and then the likelihood of correctly matching fruits and foliage from the same population of individuals is decreased. *Polyptera*, *Paleoplatycarya*, and *Platycarya* fossils are found in localized paraautochthonous concentrations within floodplain overbank deposits in small ponds so the association of their vegetative and reproductive organs is well supported. However, *Cruciptera* is found in larger lake deposits, indicating the potential for greater distance of transport and more mixing with other elements of the lakeside vegetation. The association of foliage and pollen of *Cruciptera* thus remains conjectural, and we were unable to code many of the non-fruit characters for this genus.

#### *Summary of the Five Fossil Taxa Selected and Inferred Multiple Organ Data*

*Polyptera* is an extinct genus based upon nuts with a multilobed wing from the mid-Paleocene of Wyoming and Montana (Fig. 2A,B; Manchester and Dilcher, 1982). At the eleven sites from which these fruits are known, only one type of foliage diagnostic of Juglandaceae has been found (Manchester and Dilcher, 1997). At three of these sites, staminate catkins are found, containing triporate pollen with well organized microspinulate ornamentation characteristic of Juglandaceae. The pollen is a distinctive type, with a proximal thinning of the exine similar to that of *Carya*, but with the pores situated equatorially rather than subequatorially (Fig. 2B). The delicacy of the catkins, and the fact that they were found unbroken, suggest relatively little transport from the source plants, which probably also provided leaves and fruits to the sediment. We have therefore pooled the characters of the associated fruits, catkins, pollen and foliage to evaluate the phylogenetic position of *Polyptera manningii* Manchester and Dilcher.

The extinct genus *Cruciptera* is known by its 4-winged propeller-like fruits from the Middle Eocene of Oregon and Washington (Manchester, 1991), Germany, and England (Manchester et al., 1994). For this analysis, we used the species from Oregon, *C. simsonii* (Brown) Manchester, which is known from specimens showing the internal nutlet morphology and anatomy (Fig. 2D-E). The pollen morphology of *Cruciptera* remains a mystery, and the foliage characters are known only to a limited degree. Both in Oregon and Germany, *Cruciptera* fruits occur in lakebed deposits where foliage of Juglandaceae is also common. However, at both locations, there is a diversity of juglandaceous fruit genera and foliage types so that it is difficult to be certain which of the three or four foliage types (summarized by Wilde, 1989 and Manchester et al., 1994) corresponds to *Cruciptera*, rather than the other associated fruit taxa (*Hooleya*, *Palaeocarya*). Nevertheless, by assuming that one of the four co-occurring foliage types is indeed that of *Cruciptera*, we can deduce some foliage characters for this extinct genus. All of the four foliage types are serrate and have peltate scales, for example, so these characters can be inferred without having to know which of the candidates is truly *Cruciptera*.

*Platycarya americana* (Hickey) Wing & Hickey is based on a suite of associated leaves, infructescences, and staminate catkins containing exquisitely preserved pollen from the Early Eocene of Wyoming and North Dakota (Wing and Hickey, 1984; Manchester, 1987). Assignment to the modern genus is supported by the morphology of the cone-like infructescences and their small biwinged fruits (Fig. 2H). The original treatments emphasized the co-occurring infructescences, fruits, staminate catkins, pollen (Fig. 2I), and leaves of *P. americana* from a single site at White Butte, North Dakota

(Wing and Hickey, 1984; Manchester, 1987). Subsequent field work has revealed the same association of infructescence, fruit, and foliage remains from another locality of equivalent age about 700 km to the southwest, in the Great Divide Basin of Wyoming (Dennison Cap; UF loc. 18120). At both sites, the infructescences are virtually identical to those of extant species, *P. strobilacea*, yet the foliage is very distinct. The *P. americana* laminae are symmetrical, cuneate-based, have numerous intersecondary veins, and have paired auriculate tissue flaps at their bases. Extant *P. strobilacea* leaflets are sessile, asymmetrical, have few intersecondary veins, and lack basal domatia. The *P. americana* laminae are borne on long petiolules that are flared at the base and apparently deciduous. Although these fossils are based on impression specimens lacking internal anatomical preservation, they are of about the same age as the anatomically preserved infructescences of *Platycarya richardsoni* from southern England. *Platycarya richardsoni* infructescences show internal morphology and anatomy identical to that of extant *Platycarya* (see Fig. 10 in Manchester, 1987).

*Paleoplatycarya wingii* Manchester is known from infructescences and dispersed fruits and associated foliage from the Early Eocene of Wyoming. The infructescences are cone-like as in extant *Platycarya*, but the fruits have persistent tepals and prominent wings with well-developed venation (Fig. 2G). Whereas Manchester (1987, 1989) treated this as an extinct genus of platycaryoid affinity, Wing and Hickey (1984) actually emended the diagnosis of extant *Platycarya* to include features of the fossil that do not occur in the living representatives, and then assigned the fossil to *Platycarya*. Thus, the plant which Wing and Hickey called *Platycarya castaneopsis* is the same concept as the plant *Paleoplatycarya wingii* of Manchester. We accept the hypothesis of Wing and

Hickey that the foliage, fruits, and infructescences are conspecific. The foliage resembles that of *Platycarya americana* in the symmetrical laminae, numerous intersecondary veins, and long petiolules, but differs by the lack of prominent basal auriculate tissue flaps.

*Paleooreomunnea stoneana* Dilcher, Potter and Crepet is an extinct fruit type from the middle Eocene Clay of western Tennessee and adjacent Kentucky. The fruit has a three-lobed bract, like that of extant engelhardioids, except that the sinuses between the lobes are shallow (Fig. 2C). It also has a rounded prophyllum corresponding to the structure seen in extant *Engelhardia* and *Oreomunnea* fruits. However, the nutlet is larger in proportion to the wing than is the case in extant genera. *Paleooreomunnea stoneana* fruits co-occur with foliage of the fossil genus *Oreoroa* Manchester and Dilcher (1986), although the story is complicated by the fact that another genus of engelhardioid fruit is also present at many of the same clay pits: *Palaeocarya claibornensis* which combines characters found today in *Engelhardia* and *Oreomunnea*. In the absence of another clearly distinct type of juglandaceous foliage in the localities where these fruits occur, we infer that foliage of the *Oreoroa* type was produced by *Paleooreomunnea* as well as *Palaeocarya*, and we have coded the foliar characters of *Paleooreomunnea* in our matrix based on this assumption.

Morphological analysis was based on the 64 characters, including 50 used in the previous analysis of Manos and Stone (2001). Below, we summarize all of the characters used in this analysis and provide justification as to how the fossils were coded.

Definitions of individual character states and explanation/justification of scoring decisions for extant taxa, are provided here for those characters that are supplemental to,

or altered from, Manos and Stone (2001). Characters 1-17, 20-35, 46-50 follow Manos and Stone (2001) and, unless indicated below, their state definitions are unchanged.

1. *Phenology*. There is some vagueness in the literature as to whether *Engelhardia spicata* is evergreen or deciduous. For the fossil *Platycarya*, *Paleoplatycarya* and *Polyptera*, the associated foliage is found in great abundance and inferred to be deciduous (Manchester 1987, Figs. 8, 9; Manchester and Dilcher 1997, Figs. 37-42).
2. *Terminal buds naked or with scales*. This character is polymorphic within *Carya*, and was coded as appropriate to the individual species in this matrix.
3. *Pith solid vs. chambered*. Unfortunately this character remains unknown for the fossil taxa. An extinct genus of juglandaceous wood, *Clarnoxylon*, has solid pith, but it co-occurs with the genera *Paleoplatycarya*, *Hooleya*, *Cruciptera* and *Juglans*. We cannot be certain to which of the co occurring fruits it belongs, but the occurrence of crystals in idioblasts of the rays suggest platycaryoid affinity (Manchester and Wheeler, 1993).
4. *Stipules*. Presumed to be absent in the fossil taxa as in all extant Juglandaceae, but as it was not actually observed in the fossils, we left question marks in the matrix.
5. *Phyllotaxy*. Among the four fossil taxa, phyllotaxy has been inferred only for *Polyptera*. At localities where fruits and foliage of *Polyptera* predominate, twigs also have been recovered (e.g., Dry Canyon, Wyoming, UF15746A-13855). These twig impressions do not retain the leaves or fruits, but bear leaf scars in an alternate (not opposite) arrangement, and have been coded accordingly in the

matrix for *Polyptera*. Opposite phyllotaxy is a synapomorphy of the extant American members of Engelhardioideae (*Oreomunnea* and *Alfaroa*), but we have been unable to determine the phyllotaxy for *Paleooreomunnea*. Likewise, we lack information on the phyllotaxy of *Cruciptera*, *Platycarya americana* and *Paleoplatycarya wingii*; these are coded as question marks.

6. *Leaflet arrangement*. Even-pinnate leaves are a synapomorphy of the engelhardioid clade. In contrast to most literature, and the matrix of Manos and Stone (2001), which treats *Pterocarya* as uniformly odd-pinnate, we coded *Pterocarya stenoptera* as polymorphic for this trait, as trees commonly show both paripinnate and imparipinnate leaves (Schaarschmidt, 1988; S. R. Manchester, pers. obs.). The fossil leaves consistently associated with *Polyptera* are uniformly odd pinnate, often retaining the terminal leaflet when the laterals are shed (Manchester and Dilcher, 1997, Fig. 39). *Paleooreomunnea* has been treated as paripinnate based on a few specimens of the co-occurring juglandaceous foliage (*Oreoroa*) which in the few specimens observed so far (Manchester, 1987, Fig. 21G; Dilcher and Manchester, 1986, Fig. 21) have terminal leaflets.

7. *Leaflet margins*. Whereas Manos and Stone treated each species as being either serrate (0) or entire (1), we coded some species as polymorphic, which commonly have both conditions: *Engelhardia spicata*, *Oreomunnea mexicana*, and *Alfaroa costaricensis* (see photos in Manchester and Dilcher, 1986, Figs. 8, 9, 11, 12). The foliage of *Polyptera* clearly is serrate, as are the leaflets associated with *Platycarya americana* and *Paleoplatycarya wingii*. We treat *Paleooreomunnea* polymorphic for this trait because the associated leaflets (*Oreoroa*) range from

- entire margined to serrate (Manchester and Dilcher, 1986). We also infer that the leaflets of *Cruciptera* are serrate because all of the juglandaceous leaflet types found at sites where *Cruciptera* fruits are present, are serrate.
8. *Leaflet abaxial surface*. The leaflets of extant North American representatives of the engelhardioid clade (*Oreomunnea* and *Alfaroa*) are conspicuously papillate on the lower epidermis, whereas those of all other extant genera are smooth beneath the trichomes. We code *Paleooreomunnea* as papillate, based on the well documented condition in associated leaves, *Oreoroa* (Manchester and Dilcher, 1986, Figs. 25, 26, 32, 34). On the other hand, we treat *Cruciptera* as smooth because all of the juglandaceous leaf types found in association with *C. schaarschmidii* lack papillae. The foliage of *Platycarya americana* has smooth lower epidermis as verified by specimens from Dennison Cap, Wyoming (UF locality 18120).
- 9-14. Characters for which the state remains unknown for the fossils. Explanation and coding for these characters as in Manos and Stone (2001): *Druse crystals, rhomboidal crystals, wood porosity, vessel perforations, vessel element length, and pore shape*.
15. *Inflorescences androgynous vs. unisexual*. We treat *Paleoplatycarya wingii* and *Platycarya americana* as having an androgynous inflorescence, like the extant species of *Platycarya* (Manning 1938) because the fossil infructescences are borne on long peduncles which bear lateral scars positioned in the pattern of staminate catkin scars as they occur in extant *Platycarya strobilacea* (Manchester et al., 1994, Fig. 11b, pers. obs.).

16. *Number of staminate catkins per inflorescence*. This character has been modified from two states (Manos and Stone, 2001) to four unordered states: variable 1-10 (0), 5-8 (1), clusters of 3-5 (2), and exclusively single (3). State 0 was used to accommodate the staminate clusters of *Engelhardia*, *Oreomunnea*, *Alfaroa* and *Platycarya*. *Polyptera* is indicated as state 2, based on specimen UF 5223.
17. *Pistillate catkin stance*. We coded *Rhoiptelea* as “pistillate catkin pendant,” despite the fact that it is really bisexual, because we interpret this to be a homologous feature of inflorescence structure. *Polyptera* is considered pendant, because the infructescence is very long on a relatively thin axis (Manchester and Dicher, 1997, Fig. 3). *Platycarya americana* and *Paleoplatycarya americana* are erect, matching the modern species (based on their similarly thick infructescence axis). The erect pistillate catkin of *Paleooreomunnea* was illustrated by Manchester (1987, Fig. 28L).
18. *Flower sexuality* (character 19 in Manos and Stone, 2001). This differs from character 18 of Manos and Stone (2001) (primary bract woody, retained on infructescence, an autapomorphy of *Platycarya*), which was deleted in the present analysis because of overlap with characters 17 and 38.
19. *Staminate flower sessile vs. pedicellate*. This character was not included in the Manos and Stone (2001) matrix. The flowers are sessile in the fossil *Platycarya americana*.
20. *Staminate bract lobation*. Coded as unlobed for *Platycarya americana* (Manchester, 1987, Fig. 6), and as 3-lobed for *Paleooreomunnea* based on associated *Eokachyra* catkins (Crepet et al., 1975).

21. *Staminate bract vasculature* (character 19 in Manos and Stone, 2001). This condition unknown for the fossils.
22. *Staminate flower bracteoles present or absent*. Bracteoles are observed to be absent in the catkins of *Platycarya americana*; condition unknown for the other fossil taxa.
23. *Staminate flower sepals*. Absent in *Platycarya americana*, and not determined for the other fossil taxa.
- 24-30. *Pollen characters*. These features were reviewed for the fossils *Platycarya*, *Paleoplatycarya*, and *Polyptera* by Manchester (1989). Pollen characters for *Paleooreomunnea* were coded based on *Eokachyra* (Crepet et al., 1975). Although staminate catkins of *Cruciptera* remain unknown, we coded the pollen as having equatorial pores, because none of the dispersed juglandaceous pollen types found in association with the fruits in Oregon and Germany have heteropolar or subequatorial apertures.
- 31-32. *Ovary position and number of locules per ovary*. These characters of Juglandaceae are observed in all of the fossil and living representatives.
33. *Carpel fusion median vs. transverse*. Based on position of the primary septum relative to the bract; carpels are observed to be transverse in *Paleoplatycarya*, *Platycarya* and *Paleooreomunnea*.
34. *Stigmatic disk*. This novel structure, representing a modification of the sepals (Manning 1940), is present all *Carya* species, but is not present in any of the other genera including the fossils.

35. *Stigma orientation*. The orientation of stigmatic arms in relation to the primary septum indicates a carinal orientation for *Polyptera* (Manchester and Dilcher, 1997, Fig. 24), *Paleoplatycarya* (Manchester, 1987, Fig 11j) and *Platycarya* (Manchester, 1987, Fig. 10r).
36. *Stylar morphology*. Two long style arms (0); two short style arms (1), four lobed (2), no style arms (3, only disk). *Polyptera*, *Paleoplatycara* and *Platycarya* are coded as 1, and *Cruciptera* as 0 (Manchester, 1987, fig. 10). [Character 36 of Manos and Stone (2001) combined characters of style length and position of indumentation, which we now treat separately as characters 36 and 51]
37. *Ovule type*. The fossils are orthotropous as all other Juglandaceae, as distinguished from *Rhoiptelea*.
38. *Ovule layers*. Based on the permineralized seed coat preserved in *Cruciptera*, that genus is coded as unitegmic, like extant Juglandaceae. The condition for the other fossils remains unobserved and was left as question marks.
39. *Pistillate bract in fruit*. Attached (0); free (1). *Platycarya* and *Paleoplatycarya* are coded as 1, because the bract remains attached to the inflorescence axis and does not become attached to the fruit (Wing and Hickey, 1984; Manchester, 1987).
40. *Bract in fruit*. Enlarged (0); small or fused to other parts (1). The bract is visibly enlarged in the fossil fruits of *Paleoplatycarya*, *Platycarya*, and *Paleooreomunnea* (Fig. 2 C, G, H). However in *Polyptera* and *Cruciptera*, it is not clear whether the bract, or only the bracteoles, participate in formation of the prominent fruit wings and these are left as question marks.

41. *Pistillate bract lobing*. The bract is coded as trilobed in *Paleooreomunnea* and unlobed in the other fossil taxa.
42. *Pistillate bracteole configuration*. Bracteoles rudimentary or absent, the ovary and stigmas exposed (0); bracteoles 2, posterior, forming a moderately high lobe obscuring the ovary but leaving the stigmas exposed, loosely to tightly adhering to the ovary (1); bracteoles 2, posterior, forming a high lobe obscuring the ovary and stigmas, fused to the ovary about halfway up (2); bracteoles 2, lateral, fused to ovary about half way up (3); bracteoles 2, lateral, fused to top of ovary (4); and bracteoles 3 to 5, lateral and posterior, fused to the top of the ovary (5).
43. *Fruit types*, following Manos and Stone (2001, character 43).
44. *Fruit chambers at base*. In contrast to Manos and Stone (2001), we coded *Cyclocarya* as polymorphic, because the modern species can be either four chambered (Manchester and Dilcher, 1982, Fig. 8) or two-chambered (Manos and Stone, 2001, Fig. 6C). Both *Polyptera* and *Cruciptera* have four chambers at the base (Fig. 2A, F) whereas *Paleoplatycarya* and *Platycarya* each have two.
45. *Nutshell schlerenchyma*. The nutshell is composed of isodiametric sclerieds in *Platycarya americana* (based on *P. richardsoni* permineralized specimens from England) and *Cruciptera simsonii* (Fig. 2F), and *Paleooreomunnea* has fibers (Fig. 2C).
- 46-50. *Cotyledon germination, cotyledonary node, seed oils, and base chromosome number*. These characters remain unknown for the fossils.
- 51-64. Additional characters that were not included by Manos and Stone (2001).

51. *Stigmatic area*. This refers to the position of the trichomes or papillae indicative of stigmatic surfaces. Outer-facing part of the style arms (0); inner-facing part of the style arms (1); all surfaces of the stylar arms (2). In *Carya*, there are no obvious style arms, but a stigmatic disk. This character was modified from character 36 of Manos and Stone (2001). *Cruciptera* is observed to be papillate on the inner arms (Manchester 1991, Fig. 10).
52. *Wood idioblasts*. Rhomboidal crystals absent (0), present in unchambered axial parenchyma (1); present in chambered axial parenchyma (2); present in ray parenchyma (3).
53. *Lateral buds*. Compact (0); elongate (1).
54. *Lateral leaflets*. Sessile or subsessile (0); petiolulate (1).
55. *Mean leaflet number*. 12 or more (0); fewer than 12 (1). Ranges and means of leaflet number are among the characters useful in keying out genera, sections, and species of Juglandaceae (Schaarschmidt, 1998). This scoring recognizes a gap between taxa with high numbers of leaflets (as occurs in *Pterocarya*, *Juglans* sect. *Cardiocaryon*, and *Carya illinoensis*), and most other Juglandaceae. This character contributes to the placement of fossil *Polyptera* which has 5 to 7-leaflets (Manchester and Dilcher, 1997).
56. *Serration spacing*. Teeth on serrate leaflet margins distributed one or fewer per secondary vein (0); two or more more per secondary vein (1).
57. *Intersecondary veins in the leaflets*. Rare (0); common (1).
58. *Freely ending veinlets of the higher order venation on leaves*. Less than 10 percent (0); 10 percent or more (1). This character expresses the distinction between the

- closed areolation of *Alfaroa* and *Oreomunnea*, with almost no freely ending veinlets, and the open areolation with many freely ending veinlets found in other members of the Juglandaceae (Manchester 1987, pp. 40-41).
59. *Peltate scales on the leaflet*. Less than 100  $\mu\text{m}$  diam. (0); greater than 120  $\mu\text{m}$  diam. (1). This is a character from Nagel (1914) augmented by observations of leaves by light microscopy.
60. *Nutshell lacunae*. Absent (0); present (1). Presence of lacunae is known for *Cruciptera* (Manchester, 1991, Figs. 14, 15) and *Polyptera* (Manchester and Dilcher, 1997, Figs. 16, 25). *Platycarya americana* is coded for absence of lacunae because they are missing both in extant species and in *P. richardsoni* from the early Eocene of England (Manchester, 1987, Fig 10h).
61. *The primary septum of the fruit*. Thick (0); thin (1). Primary septum was measured at its thickest portion in an equatorial transverse section, and expressed as a ratio in relation to complete fruit width measured along the same line. This ratio is 0.1 and higher (to 0.5) in most taxa, but only 0.03 to 0.05 in *Alfaroa*, *Oreomunnea* and *Anamocarya*. The gap between "thin" and "thick" did not appear to be arbitrary, but additional states (within the "thick" category) may be recognized by analyzing a larger number of measurements.
62. *Position of vascular bundles relative to ribs on nuts*. The vascular bundles may lie: on a smooth, unribbed surface (0); along ridges (1); follow grooves (2). This was a character used by Iljinskaya (1953) to distinguish *Cyclocarya* from *Pterocarya*. It seems also to have application in distinguishing between *Carya* and *Juglans*.

63. *Fruit wing orientation relative to the long axis of the nutlet.* Parallel (0); oblique (1); perpendicular (2).

64. *Fruit wing venation.* Absent (0); subparallel (1); pinnate (2). Although inapplicable to nonsamaroid fruits, this character distinguishes the fruit wings of the engelhardioid clade (with a midvein and pinnate reticulate venation), from all others that have sub-parallel, dichotomizing and anastomosing venation of a single order, and emphasizes a difference from the outgroup genus *Rhoiptelea*, whose wings lack venation. This character is useful for fossils, as well as extant genera.